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Ecology, Behavior, and Adult Anatomy of the Albida Group of the Genus *Epicauta* (Coleoptera, Meloidae)

RICHARD B. SELANDER and JUAN M. MATHIEU

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INTRODUCTION

This work is a systematic study of eight North American species of blister beetles (Meloidae) of the genus *Epicauta* which form a previously unrecognized but distinct group definable on the basis of both anatomical and behavioral characters. The main objectives of the study were to characterize the group ecologically, behaviorally, and anatomically; to describe the species in the same terms; to arrange the species taxonomically in a manner clearly expressing their phenetic relationships; and to determine, insofar as possible, how the species are related phylogenetically.

In the pages that follow an attempt is made initially to establish the taxonomic limits of the group and to indicate its general position within the genus *Epicauta.* Available information is then summarized and discussed regarding geographic distribution, seasonal distribution, food plant relationships, nonsexual behavior of adults, patterns of sexual behavior and the relation of this behavior to other activities throughout adult life, and, finally, characters of adult anatomy. Following this, analyses of phenetic and phylogenetic relationships of the species are made.

In the course of this study each of the species of the group was reared in the laboratory from the egg to the adult stage. These rearings provide useful comparative data which will eventually be incorporated in taxonomic and phylogenetic analyses. It is, however, beyond the scope of the present work to treat information from this source.

The study is, we believe, of significance from several viewpoints. First, as a result of the study the Albida Group is probably better understood biologically than any other single supraspecific taxon of blister beetles. Second, the body of information assembled during the study will serve as a sound foundation for systematic investigation of the entire subgenus *Macrobasis*. Third, knowledge gained concerning the patterning of sexual behavior during adult life provides, for the first time, criteria for judging the validity of interspecific behavioral comparisons of species of blister beetles based on studies, such as those of Selander (1964), of adults collected in the field and consequently of unknown age and experience.

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MATERIALS AND METHODS

Source of Material

The analysis of anatomical and distributional characters of the species of the Albida Group presented herein is based on a study of nearly 7,000 adult specimens. Most of these were drawn from 30 institutional and private collections, as specified in the acknowledgments. A small but significant fraction was obtained in the field during the present investigation, either expressly as museum material or as individuals destined for prior use in behavioral and ontogenetic studies.

Collections of live adults used in the study of behavior and as sources of eggs for laboratory rearings were made in the years 1959 to 1966, mainly in Illinois, Texas, and northern Mexico (Table 1). Over this period adults of all species of the group were obtained. Sample size varied among species and localities. As a general rule 30 to 50 adults of a species were taken at a single locality, but in some instances 100 or more individuals constituted a sample. The only species in which availability of adults in the field actually limited the number studied was *E. longicollis,* of which only 21 adults (many of them apparently old) were obtained.

For *E. albida, E. sublineata,* and *E. immaculata,* laboratory rearings from the egg stage provided an additional source of live adults for behavioral studies. The rearing methods employed were, in general, similar to those described by Selander and Weddle (1969) for their rearings of species of the meloid genus *Epicauta*. Relative humidity was maintained at 100 per cent and temperature at 27°C or 32-35°C except that coarctate larvae were stored at 4-5°C for a month or more in an attempt to break diapause. Larvae of *E. albida* and *E. sublineata* reared at 27°C occasionally developed from the last feeding instar (first grub phase) directly to the pupal stage without intervention of the coarctate phase or diapause, while in one rearing of *E. sublineata*

TABLE 1

SOURCE OF LIVE FIELD-CAUGHT ADULTS AND THEIR USE IN BEHAVIOR STUDIES

SPECIES	LOCALITY AND DATE OF COLLECTION[a]	FORM OF DATA ON SEXUAL BEHAVIOR[b]	NOTE NUMBER
E. atrivittata	Sanderson, Texas August 7, 1959	B	None
	12 mi. W La Rosa, Coahuila July 23, 1960	B,D	None
	3 mi. S Toyahvale, Texas July 8, 1963	C,D,E	19–63
E. longicollis	Fort Davis, Texas July 6, 1963	B,C,D,E	13–63
E. texana	Fort Davis, Texas July 10, 1963	B,C,D,E	26–63
E. albida	Apodaca, Nuevo León July-August, 1960	A,B,C	None
	Quemado, Texas September 1, 1961	B	None
	Woodsboro and Sinton, Texas August 4, 1962	B,D	5–62
	Quemado, Texas September 1, 1962	B,D	20–62
	1.5 mi. N Munday, and Sweetwater, Texas July 4, 1963	B,C	12–63
E. sublineata	Apodaca, Nuevo León July-August, 1960	B,D	None
	Quemado, Texas August 27, 1961	B	None
	Apodaca, Nuevo León July-August, 1962	B	16–62
	Quemado, Texas September 1, 1962	B,D	25–62

TABLE 1 — Continued

SPECIES	LOCALITY AND DATE OF COLLECTION[a]	FORM OF DATA ON SEXUAL BEHAVIOR[b]	NOTE NUMBER
E. immaculata	2 mi. N Etherton, Illinois July 6, 1961	B,D	7–61
	Mason, Illinois July 28, 1962	B	None
	Quemado, Texas September 1, 1962	B	26–62
	5 mi. W Springfield, Missouri July 2, 1963	C	10–63
	3 mi. N Shawnee, Oklahoma July 3, 1963	A	9–63
	1.5 mi. N Munday, Texas July 4, 1963	C,D,E	None
	Edgewood, Illinois July, 1963	C	None
	3 mi. S Toyahvale, Texas July 8, 1963	A	8–63
E. segmenta	Fort Davis, Texas July 28, 1966	B,D	16–66
E. valida	Fort Davis, Texas July 7, 1963	B,C,D,E	16–63

[a] In several cases a specific date given for a locality is the first of several on which live adults were collected there.

[b] A, descriptions, entirely qualitative, of field observations. B, descriptions, largely qualitative, of laboratory observations. C, quantitative records in the laboratory (see Table 2). D, motion pictures. E, still photography.

at 32°C, 31 of 35 larvae followed this abbreviated ontogenetic pattern. As far as could be determined, adults produced by diapausing and nondiapausing larvae did not differ significantly in either anatomical or behavioral characters.

Methods

FIELD OBSERVATIONS

While the primary objective of field work was to obtain live adult material for laboratory use, ecological and behavorial information was recorded at each of the collection sites listed in Table 1. Field data pertain largely to habitat relationships, food plants and feeding behavior, and qualitative aspects of sexual behavior. A field station maintained near Apodaca, Nuevo León, Mexico, in 1960 and another at Fort Davis, Texas, in 1963 provided the opportunity of making nearly daily observations on populations of beetles in these areas over extended periods of time. In addition, because of its proximity to the Urbana campus of the University of Illinois, the locality at Mason, Illinois, was visited frequently during this investigation. A few of the localities listed in Table 1 were visited only once or twice.

LABORATORY STUDIES OF SEXUAL BEHAVIOR

All of the quantitative data and many of the qualitative data on sexual behavior were obtained from caged beetles at one of the field stations already mentioned or in a laboratory at Urbana, Illinois. At Apodaca a screened insectary on the experimental farm of the Instituto Tecnológico y de Estudios Superiores de Monterrey served as a laboratory from July 5 to 30, 1960. The station at Fort Davis was a house rented for the purpose. Here a laboratory was set up on a covered porch screened on two sides and was maintained from July 7 to August 2, 1963. At both field stations temperature and humidity were variable. In the Urbana laboratory temperature was held at 25 ± 1°C and relative humidity within a range of 40-60 per cent, except during some of the early observations of *E. immaculata* and *E. sublineata*. Indirect sunlight was the primary source of illumination at Apodaca. Fluorescent light fixtures, each with two 40-watt tubes, were the main source of illumination at the Fort Davis station and the sole source in the Urbana laboratory, where a 12-hour daily photoperiod was used routinely. For both maintenance and observation of beetles the fluorescent lights, when employed, were suspended 32 cm above the floor of the cage or cages in which the beetles were confined.

The ages of field-caught adults were unknown but could generally be estimated roughly from the condition of the beetles and their mortality rate in the laboratory. For reared material individual records of sexual and other activities (including patterns of feeding and oviposition) throughout adult life were obtained under the individual pairs and related systems of observation (see below).

Care of caged beetles consisted largely of supplying fresh food plant material every day and cleaning the cages periodically (usually daily). At the field stations, under dry conditions, the plants in each cage were sprinkled with water every afternoon. Whenever possible plants known to be acceptable in nature were provided as food, but in some instances it was necessary to make substitutions, at least temporarily. Species of the genus *Solanum* proved to be acceptable to all species of beetles in the laboratory. For further discussion, see the section on bionomics.

Two observational situations (mixed group and individual pairs) were employed in the study of sexual behavior and other aspects of reproduction. In the mixed group situation a variable number of beetles (usually 5 to 30), representing both sexes, were confined together in a glass and lucite cage (hereafter referred to as a "large cage"), measuring internally 21 cm in width, length, and height and provided with screened ports on three sides 10 cm in diameter and a floor covering of gray blotting paper (Fig. 2). Beetles in these cages were free to interact with one another except during irregular intervals of one to several days when the sexes were isolated. This observational situation was used for much of the general description of the behavior and for most of the motion picture photography. No record was kept of the total time spent observing mixed groups of beetles, but it amounted to several hours for each species.

Quantitative studies of sexual behavior and oviposition involved systematic, daily observation of individual pairs of adults. Under this system beetles were isolated individually except for a period of 30 minutes daily when each was placed with a pre-assigned member of the opposite sex. Courtship behavior was observed and recorded in some cases for the first 15 minutes and in others for the entire 30 minutes of each period. Copulation was always recorded if it occurred during the 30-minute period. Systematic observation of individual pairs of field-caught beetles was generally carried on for a maximum of 20 days, although in one case involving five pairs of *E. immaculata*, it was continued for 35. Pairings involving reared individuals were established early in adult life and daily observations were continued until the death of one of the members. In a few cases in which the male member of the pair died prematurely (within a month or so of the establishment of the pair), he was replaced by another male of comparable age and experience. When the male preceded the female in death later in life, however, permanent replacement was not made, although a female that survived a male and continued to oviposit was occasionally given the opportunity of copulating with a male. In any event the record of oviposition was continued until the death of each female.

The cage used both for housing and observation of beetles under the individual pairs system was a transparent plastic container (Tri-State Plastic Molding Company), measuring 8 and 12 cm in width and length, respectively, and 6 cm in height, with a nested lid of the same material (Fig. 1). A screened hole 3.5 cm in diameter in the center of the lid provided ventilation; the floor of the cage was covered with a paper towel. Members of a pair were transferred from their own cages to a fresh cage before each observation. All observations of individual pairs were made under standard fluorescent lighting; temperature and humidity were controlled or not, depending on the nature of the laboratory used. Information regarding the source, number of pairs, nature of the records taken, and temperature is given for each species in Table 2. Records of courtship may be categorized as either timed or untimed. Timed records included measures of both the frequency and duration of behavioral acts and their temporal relationship. They were generally made with the aid of a 20-pen event recorder (Esterline Angus Instrument Company, Inc.). Untimed records were simply counts of the frequency of occurrence of various acts.

Descriptions of acts and general accounts of behavior were dictated into a tape recorder during observation periods or were written immediately after the observations were completed. These descriptions and accounts were supplemented by 350 still photographs and 4,000 feet of motion picture film. From 250 to 800 feet of motion pictures were taken of each species of the group except *E. segmenta,* which was not photographed. The technique used in the motion picture photography of behavior was described by Selander (1964).

TABLE 2

OBSERVATIONS OF INDIVIDUAL PAIRS OF BEETLES

SPECIES	NUMBER OF PAIRS	NATURE OF RECORD	LENGTH OF DAILY RECORDING PERIOD (min.)	TEMPERATURE (°C)		SOURCE OF ADULTS	NOTE NUMBER[a]
				MEAN	RANGE		
E. atrivittata	3	Timed	15	30	26–35	Field	19–63
	6	Untimed	30	30	26–35	Field	19–63
E. longicollis	3	Timed	15	30	26–35	Field	13–63
E. texana	3	Timed	15	30	26–35	Field	26–63
	6	Untimed	30	30	26–35	Field	26–63
E. albida	7	Untimed	30	25	. . . .	Reared	5–62(II), 20–62(II)
E. sublineata	3	Timed	30	27	25–30	Reared	16–62(II)
	5	Untimed	30	27	25–30	Reared	16–62(II)
E. immaculata	2	Timed	15	25	. . . .	Reared	7–61(III)
	3	Timed	15	25	. . . .	Reared	None[b]
	7	Untimed	30	30	26–35	Field	8–63
	5	Untimed	30	25	. . . .	Field	8–63
E. valida	3	Timed	15	30	26–35	Field	16–63
	6	Untimed	30	30	26–35	Field	16–63

[a] See Table 1, where note numbers are matched with localities from which pairs or their parental stocks were obtained. Roman numerals distinguish first and second reared generations.

[b] Progeny of a male from western Texas (notes 8-63) and a female from Illinois.

COMPOSITION AND SYSTEMATIC POSITION OF THE ALBIDA GROUP

This section serves to introduce the concept of the Albida Group and to orient this group in relation to other groups of the genus *Epicauta*. The group and its subdivisions will be defined in later sections on the basis of both anatomical and behavioral characters. Classification of the species will be considered in detail in a second taxonomic section, following the analysis of specific characteristics.

The Albida Group is proposed for eight species of *Epicauta* arranged in three subgroups, as shown in Table 3. The Albida Subgroup is equivalent to group F of Werner (1945) and nearly equivalent to Group 3 of Werner, Enns, and Parker (1966). The species of the Immaculata Subgroup fall into group FF of Werner (1945) and Group 2 of Werner, Enns, and Parker (1966). The synonymy of these species is given in a later section. Newly proposed taxonomic changes at the specific level are as follows: (1) *Epicauta valida,* long regarded as a junior synonym of *E. segmenta* (e.g., Horn, 1873; Werner, 1945), is accorded full specific rank. (2) *Epicauta megacephala,* previously treated as a junior synonym of *E. sublineata* by Werner (1945) but resurrected by Dillon (1952), is returned to the synonymy of that species. (3) Dillon's (1952) *E. reinhardi* is added to the synonymy of *E. sublineata.*

Table 3

CONSPECTUS OF CLASSIFICATION OF THE ALBIDA GROUP

- Atrivittata Subgroup
  - *Epicauta atrivittata* (LeConte)
- Albida Subgroup
  - *Epicauta longicollis* (LeConte)
  - *Epicauta texana* Werner
  - *Epicauta albida* (Say)
- Immaculata Subgroup
  - *Epicauta sublineata* (LeConte)
  - *Epicauta immaculata* (Say)
  - *Epicauta segmenta* (Say)
  - *Epicauta valida* (LeConte)

The species of the Albida Group have been more or less closely associated with one another in previous classifications, although it has not been suggested before that they form, by themselves, a discrete taxon. All except *E. texana,* which was not described until 1944, were for many years placed with a number of additional species in LeConte's (1862) genus *Macrobasis.* In Werner's (1945) classification of the species of *Epicauta* in North America north of Mexico, wherein *Macrobasis* was regarded as a strict junior synonym of *Epicauta,* all species of the group except *E. atrivittata* (which was misplaced because of an error in recording its characters) were assigned to the first (A) of two sections of the genus and within this section to a common division (EE).

As the classification of *Epicauta* now stands (Werner, 1954, 1962; Werner, Enns, and Parker, 1966), the species of the Albida Group are assigned to the nominate subgenus, while most of the species with which they were formerly associated in *Macrobasis* are placed in the subgenus *Gnathospasta* Horn, an equivalent of section AA of Werner's earlier classification. *Gnathospasta* was defined by Werner (1954) as including all species of *Epicauta* in which the male has a comblike row of teeth (presumably modified setae) on the inner side of the posterior tibia (see Fig. 17). In most species in which the comb occurs it is a distinct and constant characteristic. But as already indicated by Werner (1958, 1962), it is in some species (e.g., *E. terminata* (Dugès) and *E. fabricii* (LeConte)) poorly formed at best and frequently absent. Werner (1962) has, in fact, recognized that presence or absence of the comb is not a sufficient criterion for defining *Gnathospasta,* since he has permitted the inclusion in that subgenus of one species (*E.*

murina (LeConte), a close relative of *E. fabricii*) in which the comb is apparently entirely lacking.

Additional reason for a reappraisal of Werner's classification of *Epicauta* is to be found in the previously overlooked fact that in the Albida Group the comb is consistently present in well-developed form in *E. longicollis* and *E. texana.* Strict application of Werner's original criterion for membership in *Gnathospasta* would thus result in these species being isolated at the subgeneric level from *E. atrivittata* and *E. albida,* an arrangement hardly more acceptable than isolating, in the same manner, *E. fabricii* from *E. murina.*

As an alternative to the present unsatisfactory arrangement, we now propose to add all species currently remaining in Werner's (1945) section EE of the nominate subgenus of *Epicauta* to those which he has assigned to *Gnathospasta* and to redefine this subgeneric taxon by the incorporation of antennal characters similar to those employed by LeConte (1862) in his definition of *Macrobasis.* With these changes there are two available genus-group names having priority over *Gnathospasta.* These are *Macrobasis* LeConte and *Apterospasta* LeConte. Both date from 1862 and both were published on the same page, but there is no difficulty in choosing between them. Thus while *Macrobasis* was widely used for a sizeable group of species until 1945, *Apterospasta* was never applied to more than two species and has not been used at all since it was synonymized with *Macrobasis* in 1873 by Horn. The proposed synonymy may be summarized as follows:

Subgenus *Macrobasis* LeConte, new status

Macrobasis LeConte, 1862:272 [Type-species: *Lytta albida* Say; fixed by subsequent designation (Wellman, 1910:396)].

Apterospasta LeConte, 1862:272 [Type-species: *Lytta segmenta* Say; fixed by subsequent designation (Wellman, 1910:393)].

Gnathospasta Horn, 1875:154 [Type-species: *Gnathospasta mimetica* Horn; fixed by monotypy]. *New synonymy.*

In addition to the Albida Group and the 13 species groups recognized in *Gnathospasta* by Werner (1954, 1962), *Macrobasis* includes *E. tenuis* (LeConte), *E. excors* (Fall), *E. tenuilineata* (Horn), and *E. languida* (Horn), which may be referred to collectively as the Tenuis Group. This group may be recognized by the following combination of characteristics: body size moderate to small for the subgenus; male antennal segments I and II flattened and denuded, I elongated, II as long as I or longer; fore tibiae each with one or two spurs; fore tarsus not modified; hind tibial comb absent; female with antennal segment II longer than III.

Within the subgenus *Macrobasis* the Albida and Tenuis groups most closely resemble and are presumably most closely related to the Fabricii Group. In all three groups sexual dimorphism of the antennae is strongly developed in at least a part of the species, the male fore tarsus is not modified, and, except in two species of the Albida Group, the male hind tibial comb is vestigial or absent. In addition, there is good evidence from studies of sexual behavior, to be discussed in another section, for associating at least the Albida Group with the Fabricii Group. The relationships of the three groups with other groups of *Macrobasis* are uncertain at present. A thorough revision of the classification of the species of *Macrobasis* would seem to be in order, but such an undertaking is decidedly outside the scope of the present study.

An anatomical diagnosis of the subgenus *Macrobasis* may be framed as follows: male hind tibial comb consistently present in most species, poorly developed and not consistently present in a few, and entirely lacking in still a few others. In all species in which the presence of the comb is not a constant characteristic (and in many of those in which it is), antennal segment II is elongated, being at least as long as III in males and at least two-thirds as long as III in females.

Recognition of *Macrobasis* as a taxon is not, of course, dependent on the utility of the above diagnosis. Anatomically, there are several characteristics or tendencies which serve to unite the species of the subgenus, and, in addition, sufficient evidence is now available to suggest that the species share a basic pattern of courtship behavior.

In all species of *Macrobasis* there is definite sexual dimorphism of the antennae, although its degree of expression varies considerably. At one extreme the dimorphism involves simply a thickening of male antennal segment I, as in *E. alastor* Skinner. In a somewhat intermediate state, as represented by the Uniforma and Funesta groups and the Immaculata Subgroup (Fig. 54), there is a lengthening of this segment, accompanied by a tendency for increased curvature. At the other extreme there are dramatic modifications of size, form, and texture of two or more of the basal segments of the male antennae, as in the Diversicornis Group and Albida Subgroup (Fig. 54). Studies of behavior in a number of species of the subgenus, discussed in detail later, provide insight into the functional significance of these (and other) modifications of the males, although by no means has a complete understanding of this subject been achieved. In general, males of the subgenus make extensive use of the antennae as probing and testing devices in addition to using them in a variety of ways to provide tactile stimulation of the female. As will be shown, there is a general correlation between the elaborateness of the modifications of the male antennae and the extent and complexity of their role in courtship behavior.

In addition to the sexual dimorphism in *Macrobasis* involving the development of the hind tibial comb of the males, there is in most species some modification of the male fore legs. The more highly developed dimorphic states are characteristic of the Alastor, Diversicornis, Ochrea, and Disparilis groups. In males of these one of the usual pair of fore tibial spurs has been lost (in *E. alastor* both pairs are missing), and the first fore tarsal segment is shortened, compressed, distorted, and partially denuded. One of the fore tibial spurs is absent also in males of the Torsa and Virgulata groups, but in these the condition is associated with less drastic modification of the fore tarsus. Still less modification of the male fore legs is seen in the Uniforma and Tenella groups, where both fore tibial spurs are present and the first fore tarsal segment, while at least slightly thicker and often shorter than that of the female, is otherwise normal. Finally, a few species, such as those of the Fabricii Group and the Immaculata Subgroup, have no appreciable dimorphism of the fore legs.

The modifications of the male legs just described represent adaptations for grasping the female during courtship, and it is therefore not surprising that the degree of dimorphism of the fore legs is correlated fairly strongly with the strength and consistency of development of the male hind tibial comb. In all species of the subgenus whose sexual behavior has been studied, there is a phase in which the male is mounted directly on the female and facing in the same direction (Fig. 11). During this riding phase the male supports himself and maintains his hold on the female with his fore and hind legs, the middle legs being extended laterad. Except in a few species having very short mounted phases, the position of the male legs during this mounted phase is rigidly fixed. Fore leg contact with the female is made primarily or entirely with the end of the tibia and the ventral surface of the first tarsal segment, which grasp the female just behind the pronotum or, as in *E. polingi* Werner and presumably in other species with highly modified fore legs, actually beneath the hind margin of the pronotum (Fig. 11). The absence of one of the spurs presumably permits more intimate contact of the tibial apex with the thorax of the female than would be possible otherwise. The various modifications of the first fore tarsal segment facilitate the grasping function both by increasing the effective size of the segment and by conforming the segment to the contact surface on the female.

The hind leg grasp of the male is made entirely with the inner side of the tibial apex, which is pressed against the lateral edge of the female's elytron or against the side of her abdomen just ventrad of the elytral margin. With the legs so placed, the tibial comb acts as a spur or friction plate, possibly aided in this function by a tendency for the female's clothing setae to catch between its teeth. In some species, such as *E. lauta* (Horn), there is a periodic rubbing of the ends of the hind tibiae against the female during the mounted phase, and here the comb may have the additional function of a scraper.

In general, it would appear that the length of the mounted or riding phase, which varies greatly among species and groups of species, is correlated with the degree of sexual dimorphism of the fore and hind legs. In most members of the Albida Group, for example, the male normally mounts the female only when she is ready to copulate and seldom remains mounted on her for more than a few seconds. In these species the grasp of the female by the male is less stereotyped and the fore and middle legs are not at all, or at least not strongly, modified. Most species of the subgenus studied mount frequently and for longer periods. The most lengthy mounted phase recorded occurs in *E. polingi*, males of which often ride females for an hour or more; during this time the latter often move about and perform various nonsexual activities. In such species the grasp of the female by the male is extremely secure, with the result that even the most violent exertions of the female are seldom successful in dislodging him. At the same time, because of the positioning of his legs, and particularly the elevation of the middle pair, there is minimal interference with the movements of the female's legs. Here, apparently, there has been a remarkable balance struck between selective forces. Thus, while the male forceably maintains his position on the female, he does so in such a manner that her ability to stand, walk, or groom is not seriously impaired.

Aside from male adaptations for courtship behavior there are apparently no anatomical characters of any practical value in defining *Macrobasis*. Consequently, the present basis for taxonomic recognition of the subgenus is, in a real sense, entirely behavioral, as indeed it very probably is in the case of a great many animal taxa. Sexual behavior in the Albida Group of *Macrobasis* will be described in detail in later sections of this work; here it is appropriate to anticipate this treatment by giving a brief outline of the general pattern of courtship behavior in the subgenus. So far as is known, this pattern is completely diagnostic of the taxon.

On approaching and recognizing a female, the male typically enters an extended period of orientation during which he stimulates her in one or more ways by means of his antennae while at the same time apparently testing her responsiveness. During this phase the male maintains a characteristic stance, with the antennae lowered and directed toward the female (Figs. 10, 15). Periodically he touches or presses his antennae on her body, whips them in her direction, or attempts to wrap them around her antennae (Figs. 12, 16). Following orientation, the male mounts the female and rides in the manner already described. In some species the mounted or riding phase alternates with additional periods of orientation; in others, as previously indicated, it occurs normally only as an immediate prelude to copulation. If the female is not in a receptive state, she is likely to attack a courting male. When ready to copulate, she tips her body sharply forward and remains immobile. In response, the male mounts, if he has not already done so, and establishes genital contact. Before turning off to assume the linear copulatory position characteristic of all meloine Meloidae the male typically raises the middle and hind legs from the female and extends them laterad and posteriad, respectively (see Fig. 14).

BIONOMICS

This section is a summary of available information on the distributional (geographic and seasonal) and ecological relationships of the species of the Albida Group. Some information on adult nonsexual behavior is included also. Sexual behavior, which received special attention in this study, will be treated in a separate section.

Geographic Distribution

The geographic range of the Albida Group is confined to temperate North America, where it is centered in an area encompassing the southern Great Plains of the United States and an adjacent southeastern portion of the Intermontane Plateau region of Texas and New Mexico. Southward it extends to about the latitude of the Tropic of Cancer in Mexico. Northward its limits are roughly the southern borders of Utah and Colorado in the western United States, South Dakota in the central region, and southern Ohio in the east. The westernmost record of the group is in southeastern California, near the Arizona border. The eastern limits of the range are reached in Ohio and Tennessee. The area of greatest density of species of the group is western Texas. Here all eight species are represented, and in certain localities as many as six of them may occur together. On the other hand, only one species (*E. immaculata*) is represented in the range of the group east of the plains states.

The ranges of the individual species, shown in Figs. 3-9, are discussed below. Locality records are given in a later section.

In the Albida Subgroup *E. albida* (Fig. 4) has the most extensive range and is the only species that makes a significant penetration of the Great Plains and the Gulf Coastal Plain. Although extensively sympatric with *E. longicollis* (Fig. 3) and *E. atrivittata* (of the Atrivittata Subgroup) (Fig. 5) in western Texas and New Mexico, it has actually been collected with those species at relatively few localities. Whether this is a result of low population density of *E. albida* in these areas or a reflection of subtle habitat differences remains to be seen. The ranges of *E. longicollis* and *E. atrivittata* are similar to each other except for the westward extension of the range of *E. longicollis* into central and northern Arizona. These species occur together commonly in their area of sympatry. *Epicauta texana* (Fig. 4) apparently has the most restricted established range of any of the species of its subgroup. It has been taken at several localities in and near the Chiricahua Mountains of southeastern Arizona, at several others in the Davis Mountains–Big Bend region of Texas, and at a single locality in northeastern Durango. This discontinuity of range is presumably the result of habitat restriction; on the basis of our records the species is limited largely to elevations above 5,000 feet. In the northern part of its range *E. texana* occurs with both *E. longicollis* and *E. atrivittata*. As indicated in Fig. 4, however, it is apparently strictly allopatric (or, better, parapatric) with *E. albida*.

The range of the Albida Subgroup is almost entirely overlapped by that of the Immaculata Subgroup. In the latter taxon *E. immaculata* (Fig. 7) is noteworthy in having the largest range of any species of the entire group. The range of *E. immaculata* extends from the western edge of the Appalachian Mountains westward to South Dakota and the Rio Grande River. It very probably continues southward into all the Mexican states bordering this river, although at present the species is known in Mexico only from a single locality in Coahuila.

Along the valley of the Rio Grande *E. immaculata* occurs with *E. sublineata,* the most restricted and distinctive, geographically speaking, of all the members of the Albida Group. This species (Fig. 6) is limited largely to the Gulf Coastal Plain from central Tamaulipas and Nuevo León northward to the Rio Grande Valley; in Coahuila and along the river to the north it reaches the eastern edge of the Mexican Plateau country. It is apparently strictly allopatric with both *E. segmenta* and

E. valida in the Immaculata Subgroup, as well as with *E. longicollis* and *E. texana* in the Albida Subgroup.

Available records indicate that *E. segmenta* (Fig. 8) and *E. valida* (Fig. 9) range broadly together through the Great Plains of the United States, or at least that they once did so (see below). South of Kansas, however, their ranges would appear to be nearly mutually exclusive. Thus *E. segmenta* is conspicuously absent from an extensive area in eastern Oklahoma and eastern Texas occupied by *E. valida,* while *E. valida* does not occur with *E. segmenta* over most of its range in western Texas and fails to accompany that species as it extends westward to Arizona and southward into Mexico, where it reaches southern Sinaloa to the west of the Sierra Madre Occidental and northern Durango to the east. As a matter of fact, the only southern area where large populations of *E. segmenta* and *E. valida* are known definitely to occur together is the Davis Mountains region of extreme western Texas. This is at the southwestern limit of the range of *E. valida,* where the population of that species is presumably isolated from the main species population and may be relict. Elsewhere sympatry of the two species is indicated by a mixed series of three specimens labeled as collected at Fedor, Texas, and another of four specimens labeled as from Brownwood, Texas.

In the process of listing dates of collection of museum specimens of *E. segmenta* and *E. valida* for the summary of adult seasonal distribution given in a later section, a scarcity of recent records of these species in the northern portion of their ranges was noted. An analysis of the collection records by year was therefore undertaken, with the following results.

In the area south of Oklahoma during the period 1875-1930, *E. segmenta* is represented by 46 records (series) and *E. valida* by 12, while from 1930 to 1965 there are, respectively, 93 and 24 records of these species. In the area north of Oklahoma the situation is different. Here there are 25 records of *E. segmenta* and 28 of *E. valida* from 1875 to 1930. But from 1930 to 1965 these species are represented, respectively, by only 10 and 17 records. Furthermore, there are, among the records available to us, none for *E. segmenta* since 1942 and only two (four specimens) for *E. valida* since 1946.

In the southern area the greater number of records of *E. segmenta* and *E. valida* in the more recent period can be accounted for by increased collecting activity, particularly in the past two decades. In the midwestern United States, however, it is difficult to attribute the apparent decline in the population levels of these species solely to variation in sampling intensity. As late as the early 1940's, when potato-growing was still an important activity in the Midwest, both species were familiar to entomologists (although it was not recognized then that more than one species was involved) as pests of gardens and particularly of potatoes (see, for example, Gilbertson and Horsfall, 1940). Since World War II potatoes have ceased to be a major crop in the area, and the lack or scarcity of recent records could be at least partially attributable to lessened interest in the species. However, it is not unlikely that the reduction in potato acreage has actually affected population size, while progressive destruction of natural habitats and more intensive and widespread use of insecticides have undoubtedly had their effect, either directly or by modifying populations of grasshoppers, which the species utilize as larval hosts. Thus while the available information is insufficient to demonstrate a change in the population density of *E. segmenta* or *E. valida* in the present century, it seems likely that a rather profound one has occurred.

Further evidence on this question is provided by the result of a field trip to central and southwestern Kansas made in July, 1964, specifically for the purpose of collecting adults of *E. segmenta* and *E. valida.* On that trip four entomologists spent four days at the presumed time of maximum abundance of adults searching in a variety of habitats, including potato fields, without finding a single individual of either species. Considering the brevity of the trip, this certainly does not mean that the species were not present. It does suggest, however, that they were much less abundant than they have been for at least the past several years in the southern part of their ranges. By way of contrast, in the Davis Mountains region of Texas in July, 1963, and again in July, 1966, it would have been possible, with a comparable expenditure of time and effort by four collectors, to secure hundreds if not thousands of adults of both species. Moreover, it is our impression, based on experience with other members of the Albida Group and many additional species of Meloidae, that had the population levels of *E. segmenta* and *E. valida* in Kansas been at the level suggested by the large number of records and museum specimens available from the Midwest, we should have been able to find both species without difficulty.

THE INDEX OF SYMPATRY

It is desirable at this point to develop a means of expressing degree of sympatry in the individual species, since a measure of this sort will be useful in future work attempting to relate levels of potential or actual interspecific contact and interaction to levels of phenetic divergence in various characters. In addition, it may be of value to have a measure of sympatry for the species as a whole, in order to compare eventually the Albida Group with other supraspecific taxa of Meloidae. It is to be recognized, of course, that level of sympatry itself may be of little significance in terms of interactions between species. One would expect, however, at least a fair correlation between extent of sympatry and opportunity for interaction in groups such as the present one where the species generally have broadly overlapping seasonal ranges of adults and utilize several food plants in common.

In assessing the potential for interaction of one species with others, both the number of species involved and the extent of overlap of their ranges on that of the species in question are pertinent. Obviously, population density should be taken into consideration also, but in the present case no reliable measure of this factor is available. The index of sympatry that will be used is formed by scoring, on a scale of 0 to 3, the degree to which the range of a species is overlapped individually by the range of every other species of the group and then taking the sum of the scores as a percentage of 21, the maximum sum possible in a group of eight species.

The scale used is as follows: a value of 0 indicates allopatry (no overlap of ranges); 1, limited sympatry, with one-third or less of the range of a species overlapped by that of another; 2, moderate sympatry, with more than one-third but less than two-thirds of the range of a species overlapped; and 3, extensive sympatry, with two-thirds or more of the range of a species overlapped. The individual scores and the resulting index values are shown in Table 4. The mean number of sympatric relationships for the group is 6.0, with a range of 4 for *E. sublineata,* to 7 for both *E. longicollis* and *E. atrivittata.* The mean of the several index values is 51.25, with a range of 33.3 for *E. sublineata,* to 66.7 for *E. atrivittata.* It is immediately apparent that the correlation between the number of sympatric relationships and the index of sympatry is not perfect. The most striking divergence in these two values occurs in the case of *E. immaculata.* This species is sympatric with all others in the group but in no case to more than a moderate extent, relative to the size of its range. Thus its index value is actually the third lowest in the group.

It would be of some interest to compare, in the species of the Albida Group, the index of sympatry with a quantitative measure of degree of ecological correspondence. Unfortunately, we do not have nearly enough information to formulate a useful index of ecological similarity of species directly. We may infer, however, that there is likely to be a positive relationship between such an index and the general level of phenetic divergence of species. In a later section of this work we com-

TABLE 4

LEVELS OF SYMPATRY IN THE ALBIDA GROUP

Epicauta SPECIES	EXTENT OF RANGE OVERLAP BY OTHER SPECIES (SCORES DEFINED IN TEXT)								NUMBER OF SYMPATRIC RELATIONSHIPS	INDEX OF SYMPATRY[a]
	longicollis	*texana*	*albida*	*atrivittata*	*sublineata*	*immaculata*	*segmenta*	*valida*		
longicollis	. .	1	2	3	1	1	3	1	7	57.1
texana	3	. .	0	3	0	1	3	1	5	52.4
albida	1	0	. .	1	1	3	2	3	6	52.4
atrivittata	3	2	2	. .	1	2	3	1	7	66.7
sublineata	1	0	3	1	. .	2	0	0	4	33.3
immaculata	1	1	2	1	1	. .	2	2	7	47.6
segmenta	2	1	1	1	0	2	. .	2	6	42.9
valida	1	1	3	1	0	3	3	. .	6	57.1
								Mean	6.0	51.2

[a] Sum of scores × 100, divided by maximum possible sum of scores (21). For further explanation see text.

pute average distance coefficients for all pairings of species of the group, based on 39 characters of adult anatomy and sexual behavior (see Table 27). By summing the values of the coefficients for each species, we obtain for each a single value reflecting average degree of phenetic distinctiveness in the characters considered. When these values are then compared with those of the index of sympatry in the various species, a degree of dependence is evident. Thus phenetic distinctiveness in the adult stage is positively correlated with intensity of sympatry ($r = .67$, df = 6, P slightly greater than .05). This finding is, of course, not unexpected, since it is consistent with current evolutionary theory regarding competitive relationships and the coexistence of related species (DeBach, 1966). Further evidence that the species of the Albida Group are not ecologically independent of one another is given in the following sections on the seasonal distribution of the adult stage, food plant relationships, and sexual behavior.

Habitats

The Albida Group is confined largely to arid and semi-arid temperate areas supporting desert scrub or prairie vegetation. One of the species, *E. immaculata,* ranges well into the realm of the eastern deciduous forest in the United States but occurs there largely in pastures and prairie remnants rather than in the woodland itself. Adults of all species of the group are found most frequently and in greatest abundance along roadsides, near ditches, in swales, and in other situations where the amount of soil moisture is sufficient to support the growth of herbaceous plants through the summer season. Many of the food plants of the adults are not palatable to range animals, and adults may occur in great numbers even in heavily grazed pastures and ranges. Indeed, because of the variety of weedy plants utilized by the adults, it seems likely that the group has benefited from both grazing of livestock and cultivation of the land.

At present there is no evidence of differential habitat selection by adults of species of the Albida Group occurring in a given area, apart from that associated with interspecific differences in food plant preferences. As we have indicated, however, no species of the group is isolated completely from any other by differences in adult feeding behavior.

Observation of the distribution of the species of the Albida Group in the trans-Pecos region of western Texas suggests that in several cases species are at least partially isolated from each other by the differences in altitudinal range. Seven of the eight species of the group occur in the trans-Pecos region (only *E. sublineata* is lacking). *Epicauta longi-*

collis, E. immaculata, and *E. segmenta* are common throughout the region at elevations from 2,500 to nearly 6,000 feet. *Epicauta albida* seems to be confined to lowlands. It has been reported from the Davis Mountains, but we have been unable to find it either in the mountains themselves or in the lowlands surrounding them. *Epicauta atrivittata* is more generally distributed and apparently more abundant than *E. albida*; it ranges into the Davis Mountains to an elevation of about 4,000 feet. *Epicauta texana,* on the other hand, although fairly widely distributed altitudinally in the trans-Pecos region, seems to be rare in lowlands. Finally, *E. valida* is apparently limited, within the region, to elevations between 5,000 and 6,000 feet in the Davis Mountains. So far as we can determine, interspecific differences in altitudinal range in the Albida Group are not determined by the distributional relationships of food plants of the adults. Presumably they reflect competitive interactions of species of the group with each other as well as with other species of Meloidae. Unfortunately, lack of information presently rules out meaningful assessment of these interactions.

Food Plants of the Adult Beetles

The food plant relationships of adults of species of the Albida Group are summarized in Table 5. This table contains information from field observations and laboratory tests during the present study, from labels of museum specimens of beetles, and from the published literature. For reasons discussed below it is limited to plant associations known to have been recorded on more than one occasion.

In the field the species of the group have been found to feed on 23 species of plants, representing 15 genera and 9 families. The frequency distribution of records (series of beetles) by family of plants is: Solanaceae, 67; Compositae, 14; Leguminosae, 13; Zygophyllaceae, 13; Chenopodiaceae, 8; Asclepiadaceae, 7; Ranunculaceae, 5; Amaranthaceae, 4; and Cruciferae, 2.

From the standpoint of both number of field records and number of plant species involved, the most important family is Solanaceae and the most important genus *Solanum.* The apparent pre-eminence of *Solanum* as a food source for adults of the Albida Group rests largely on the contribution of *S. elaeagnifolium* and *S. tuberosum. Solanum elaeagnifolium* is the only plant known to be utilized by all species of the Albida Group. In the laboratory it is readily acceptable to all and apparently nutritionally adequate. Thus caged populations of the various species maintained on it to the exclusion of other food for periods of two weeks or more invariably remained in good condition and continued

TABLE 5

FEEDING RECORDS OF ADULTS OF SPECIES OF THE ALBIDA GROUP IN THE FIELD AND LABORATORY

PLANTS	*Epicauta* SPECIES[a]							
	atrivittata	*longicollis*	*texana*	*albida*	*sublineata*	*immaculata*	*segmenta*	*valida*
Amaranthaceae								
Amaranthus palmeri							FL	FL
Asclepiadaceae								
Asclepias incarnata						F		
A. syriaca						FL		
A. latifolia						—		
Chenopodiaceae								
Atriplex canescens								F
Beta vulgaris				F		F		F
Salsola kali							F	
Compositae								
Hymenotrix wislizeni							F	
Lactuca sativa						L		
Verbesina encelioides						F		
Vernonia baldwini						F		
V. crinita						FL		
V. missurica						FL		
Cruciferae								
Brassica oleracea						F		

TABLE 5 — Continued

PLANTS	*Epicauta* SPECIES[a]							
	atrivittata	*longicollis*	*texana*	*albida*	*sublineata*	*immaculata*	*segmenta*	*valida*
Leguminosae								
Amorpha canescens						F		
Medicago sativa				F		F	F	
Prosopis glandulosa	F	F						
Ranunculaceae								
Clematis drummondii							—	FL
Solanaceae								
Physalis viscosa							—	FL
Solanum carolinense				L	L	L		
S. dulcamara				L	L	L		
S. elaeagnifolium	FL	FL	FL	FL	FL	FL	FL	FL
S. heterodoxum	F							
S. lycopersicum					—	FL	F	F
S. melongena				F				
S. tuberosum		F		FL	L	FL	FL	FL
Zygophyllaceae								
Tribulus terrestris	F	F	FL	F		FL	FL	L

[a] F indicates feeding recorded in the field, L feeding recorded in the laboratory, and the negative sign (—) a negative feeding response in the laboratory.

to produce viable eggs. The potato (*S. tuberosum*), recorded as a food plant in the field for five species of the Albida Group, was used with success in maintaining populations of four of them in the laboratory. In addition, it was eaten by reared adults of *E. sublineata*, although in this case the results were poor in terms of beetle longevity and fecundity (see discussion of longevity below).

From the data available (Table 5) it appears that the genus *Solanum* is a generally acceptable source of food for the Albida Group. Thus all but one of the species of the group are known to accept two or more species of the genus, while both *E. albida* and *E. immaculata* are capable of feeding on at least five species. The only negative feeding response of beetles to *Solanum* recorded in the laboratory involved *E. sublineata* and tomato (*S. lycopersicum*). The rejection of this plant occurred in a single trial in which several beetles were offered leaves from greenhouse plants. The variety of tomato used had unusually tomentose leaves that wilted rapidly after being removed from the plant, and it is possible that the negative response of the beetles was to these particular characteristics rather than to a more general attribute of the plant species. On the other hand, adults of *E. immaculata* did not find tomato particularly attractive, even when offered leaves of a relatively glabrous and succulent variety. Moreover, there are several species of *Epicauta* outside the Albida Group that will not eat tomato although they readily accept both *S. elaeagnifolium* and *S. tuberosum* (Selander, in preparation).

Ranking second to *Solanum* in terms of the number of species of the Albida Group utilizing it is the genus *Tribulus*, represented in North America by the introduced puncture-vine, *T. terrestris*. This species has been recorded in nature as a food plant of five species of the group and has proved in the laboratory to be highly acceptable to another (*E. valida*, see below). In view of its apparent general attractiveness, it is interesting that there are no records of adults of the Albida Group from our native *Larrea* (creosote-bush), although plants of this genus of Zygophyllaceae constitute a dominant floristic element through much of the range of the group.

For the first five species of beetles listed in Table 5, there is little basis for determining the order of preference of the recorded food plants. *Epicauta longicollis*, *E. albida*, and *E. atrivittata* have been taken most commonly on *Solanum elaeagnifolium*; *E. texana* has been found about equally often on *Tribulus* and *Solanum elaeagnifolium* (there are only a few records in all); and *E. sublineata* is known in the field only from the last mentioned species of plant (again on the basis of few records).

For *E. immaculata* there are verified field records of 13 species of plants, including representatives of one family (Asclepiadaceae) apparently not utilized by other species of the Albida Group and another (Compositae) that is known to be utilized by only one other species of the group (*E. segmenta*). In their descending order of importance, based on the frequency of records, the more commonly recorded food plants of *E. immaculata* are *Solanum tuberosum, Vernonia missurica, Asclepias syriaca, Solanum elaeagnifolium,* and *Medicago sativa.* In laboratory choice-tests with leaves, however, a large group of beetles from Illinois preferred *Asclepias syriaca* to *Solanum tuberosum,* while a group of 15 individuals of *E. immaculata* from the Davis Mountains, Texas, tested in July, 1966, preferred leaves of *Tribulus terrestris* to those of *Solanum elaeagnifolium.*

Interspecific differences in the genus *Asclepias* having a marked effect on the feeding responses of adults of *E. immaculata* were demonstrated in tests with beetles of this species from the Davis Mountains in 1963 and 1966. In the former year leaves of a broad-leafed *Asclepias* from the region were rejected when offered alone to several beetles, although they and others from the region later accepted leaves of *A. syriaca* and were maintained on them for several weeks. In 1966 about 20 adults of *E. immaculata* were found on a single *Asclepias* plant in the Davis Mountains, near Fort Davis. Although there was no evidence that the beetles had fed on this plant, their association with it was sufficiently interesting to prompt further investigation. In the first test in that year leaves of the *Asclepias* plant were offered along with those of *Solanum elaeagnifolium* to a group of 15 beetles. After a period of 12 hours the *Solanum* was completely defoliated, but the *Asclepias* leaves remained intact except for evidence of minor sampling along the edges of a few of them. A few days later the beetles used in this test were taken to the laboratory in Urbana, Illinois, where, paralleling the results of 1963, they accepted *Asclepias syriaca* immediately.

Gilbertson and Horsfall (1940) indicated that in certain areas of South Dakota in the years 1934 to 1938 *E. immaculata* was of some importance as a pest of potato. This was apparently the preferred food source of the species, but the authors listed a wide variety of additional cultivated and naturally occurring species of plants as also being attacked. Some of these (tomato, sugar beet, garden beet, Russian thistle, cabbage, and alfalfa) have been recorded by other workers as food plants of *E. immaculata* on one or more occasions, but verification is lacking for most of the food plant associations reported by Gilbertson and Horsfall. The unverified records involve the following plants, as listed by these authors: sweet clover, bean, pea, onion, radish, matrimony bush, caragana, squash, pumpkin, hollyhock, moss rose, gaillardia, marigold, sunflower, cactus (blossoms), wild lettuce (young), "various wild legumes," mullen, and dwarf lima bean. The last species was reportedly found to be toxic to the beetles before blossoming but not after.

Because *E. immaculata* is known to utilize food plants of several families and genera more or less regularly, exclusion of the plants just listed from Table 5 would seem to be highly arbitrary. There are, however, several good reasons for wishing to exercise selection in the acceptance of food plant records, especially when there is no accompanying information regarding the circumstances under which records were obtained. In preparing Table 5 an attempt was made to distinguish between records of feeding associations of more or less regular and frequent occurrence and records that are spurious, based on accidents, or, if valid, so infrequent as to be of little or no consequence in the ecology of the species of beetles concerned. Spurious and accidental records need little comment; at least part of them are likely to be eliminated if a criterion of verification is invoked.

Two other potential sources of error in the reporting or evaluation of observed associations of blister beetles with plants arise from specific patterns of behavior of the beetles themselves. First, in many Meloidae adults may, under threat of starvation or in the absence of an adequate supply of moisture, attack plants that are normally ignored. When these attacks involve large aggregations and particularly when they are on crops or other cultivated plants, they are likely to be noticed, even though they may be sporadic and temporary. The danger is, of course, that such an association will be recorded without proper evaluation of its significance in terms of duration and the proportion of the population of the species of beetles involved. Such associations are real and deserve to be recorded, but it seems important to distinguish them from those that occur under more normal conditions.

Second, some species of blister beetles, including *E. immaculata* and *E. segmenta,* are known to form nonfeeding aggregations on plants, including species that are apparently never utilized as food sources. The functional significance of this behavior has not been determined, but it seems likely that temperature regulation is involved. That is, at a certain threshold of temperature during the day the beetles leave their food plants, if the latter are of insufficient height or density, to seek lower temperatures. A striking example of this nonfeeding gregarious behavior was observed at a locality 3 mi. south of Toyahvale, Texas, in the early afternoon of August 1, 1966. Air temperature at about 5 feet above ground level was 37°C. Large numbers of adult *E. immaculata* were feeding on *Verbesina encelioides* plants, most of which were nearly completely defoliated. Few of the feeding beetles, however, were attacking plants less than 6 inches in height, although plants of this size were common enough and showed evidence of having been eaten heavily. Near one of the areas of extensive damage to *Verbesina* two plants of a species of *Croton* were found, each growing to a height of about 2½ feet. On each of them was a dense aggregation of about 100 adults of *E. immaculata*, nearly all situated at the crown level and in some parts of the plant crowded together as closely as possible without touching one another. Some courtship was in progress, and from time to time a beetle flew to or from the plants. Otherwise the beetles were standing still, inactive. Inspection of the plants indicated that the beetles had not been feeding on them. Presumably the aggregations were formed largely of individuals that had been feeding earlier on the smaller of the *Verbesina* plants. Additional observation in the area revealed that individuals of *E. immaculata* were resting, usually in small groups, on squash, an unidentified composite, *Sphaeralcea* sp., *Salsola kali, Solanum elaeagnifolium,* and several tall grasses. There were, however, none on *Tribulus terrestris* or other prostrate plants.

Although *E. segmenta* and *E. valida* share several species of food plants, there are some striking differences in the food plant relationships of these beetles. These were detected in the course of laboratory tests and field observations of beetles in the Davis Mountains region in 1963 and 1966, the results of which are reported below.

Experimental investigation of the feeding behavior of *E. segmenta* and *E. valida* involved a series of choice-tests conducted on caged adults from Fort Davis, Texas (Table 6). Plant material used in these tests was offered the beetles as bouquets standing in water-filled 2-oz. jars placed in the center of a large cage. Each bouquet consisted of fresh cuttings of two species of plants arranged on opposite sides. Access to the plants from the floor of the cage was provided by a paper napkin folded tentlike and arranged symmetrically with respect to the two plant components of the bouquet. Tests were conducted on July 30, 1966, and the following two days in a motel room in Fort Davis. The length of each test period was 12 hours. Temperature and humidity were not controlled; the estimated mean temperature was 30°C. All plant pairings were tested separately on males and females of each species of beetles. Pairings 1 and 2 (Table 6) were tested the first day, 3 and 4 the second, and 5 the third. Within species and sex beetles were divided randomly each day between pairings of plants, except that all available *E. segmenta* adults were used in the test of

Table 6

RESULTS OF FEEDING CHOICE-TESTS PERFORMED ON ADULTS OF *E. SEGMENTA* AND *E. VALIDA*

Order of Feeding Preference in Plant Pairings[a]	*E. segmenta* Amount of Feeding on Nonpreferred Plant	*E. segmenta* N Beetles	*E. valida* Amount of Feeding on Nonpreferred Plant	*E. valida* N Beetles
Solanum over *Physalis*	none	41	moderate	20
Solanum over *Clematis*	none	41	light	19
Solanum over *Amaranthus*	light	38	light	18
Clematis over *Amaranthus*	. . . .	. .	light	19
Tribulus over *Solanum*	light	38	light	35

[a] The species of plants utilized were *Tribulus terrestris, Solanum elaeagnifolium, Physalis viscosa, Clematis drummondii,* and *Amaranthus palmeri.*

the *Tribulus-Solanum* pairing. For several days before the first test day and in periods between tests all beetles were maintained on leaves of *Solanum elaeagnifolium.*

In reporting the results (Table 6), light feeding on the nonpreferred plant means that a few leaves were chewed along their edges. Moderate feeding means that nearly all leaves showed some feeding damage.

In tests with both species of beetles *Tribulus* was greatly preferred to *Solanum* and the latter to *Amaranthus.* From the data obtained for *E. valida,* it can be inferred that *Physalis* is preferred to *Clematis,* although the appropriate pairing was not tested. If this inference is correct, the complete order of preference for *E. valida* is *Tribulus, Solanum, Physalis, Clematis,* and *Amaranthus.*

In the course of field work in the Davis Mountains *E. segmenta* was found feeding on all three of the plants that it accepted in the tests described above, although the field records give no clearcut evidence of an order of preference among these. In concordance with the negative test results with *Physalis* and *Clematis,* there were no observations of *E. segmenta* on these plants in the field.

In the case of *E. valida* there are major discrepancies between the results of the laboratory tests and field observations. In the field, at least in the Davis Mountains, this species seemed to show a definite preference for *Clematis* over either *Physalis* or *Amaranthus.* Moreover, although there are records of its having been taken on *Solanum elaeagnifolium* several times elsewhere, *E. valida* was not observed on this plant in the Davis Mountains. Even more surprisingly, it apparently has never been recorded in any part of its range from *Tribulus terrestris.*

There is little doubt that differences in abundance and conspicuousness of species of plants in the field introduce bias into estimates of feeding preference levels derived from observational data. Nevertheless, for *E. valida* at least there seem to be real differences between the order of preference for food plants shown by the beetles in the laboratory and that expressed by their distribution in nature. Unfortunately, these differences are difficult to evaluate in the absence of detailed knowledge of the factors affecting food plant selection in blister beetles in general and these species in particular. Although it is very probable that food plant selection by the species of the Albida Group involves, as it does in most phytophagous insects that have been studied, responses to specific chemical and physical properties of the plant tissue, it is evident that these responses may be strongly modified or overridden by other factors. It is likely that one such factor, already mentioned in the discussion of nonfeeding aggregations of adults of *E. immaculata,* is temperature. In particular, the absence of records of *E. valida* from *Tribulus* may have a basis in the fact that this plant is prostrate, for as a result of this growth form the temperatures to which beetles feeding on it would be subjected during much of a normal, sunny day would be considerably higher than those encountered in higher vegetation. In this connection the flightlessness of *E. valida* adults may be of special pertinence. Thus, unlike their relatives, beetles of this species feeding in relatively barren areas commonly inhabited by *Tribulus* could not escape readily when the temperature on and near the ground reached a dangerously high level. Obviously further investigation of this subject is needed. As a beginning it would be interesting to compare the optimal, preferred, and lethal temperatures of *E. valida* with those of the other species of the Albida Group.

Despite the large amount of information available regarding the food plant relationships of the species of the Albida Group, it would be premature to attempt a critical evaluation of the role of food plant selection in interspecific isolation in this group. Some interspecific differences have been demonstrated or are deemed highly likely on circumstantial grounds, but in the absence of statistically adequate quantification of the degree to which sympatric populations do or do not utilize plant species in common, it is impossible to evaluate properly the ecological or evolutionary significance of these differences or others like them. The most that can be said, probably, is that *E. immaculata* enjoys partial isolation from its relatives by its apparently common utilization of Compositae and Asclepiadaceae, and that *E.*

valida, as a result of its utilization of *Clematis* and *Physalis,* is partially isolated from its closest relative, *E. segmenta,* and presumably from the other species of the group as well.

Seasonal Distribution

ADULT STAGE

For most of the species of the Albida Group dates of collection of specimens constitute the only significant source of information regarding the seasonal distribution of the adult stage. Table 7 presents a summary of this information in the form of relative frequency distributions of records by month. For species of extensive latitudinal distribution the seasonal data for northern and southern portions of the range are shown separately. In each case the division of range was along parallel 37°N, the latitude of the southern boundary of Kansas. Relative frequency of records (series) rather than of specimens is given because the former measure is presumably less apt to be biased by extraneous factors such as differences in the interests and techniques of collectors.

From the data in Table 7 it appears that the seasonal ranges of most of the species are quite similar. For most of the populations shown the earliest records are in May. Exceptions occur in southern *E. albida* and in *E. atrivittata,* where there are a few records as early as March or April, and in *E. texana,* where adults have not been recorded before June. Generally there is a two-month period of high frequency of records, followed by an abrupt decline, with the latest records falling in September or October.

A north-south trend for later emergence of adults of *E. segmenta* is indicated by the comparison of absolute frequency distributions of records in northern and southern portions of the range ($\chi^2 = 88.412$, df $= 1$, $P < .001$). For *E. immaculata, E. valida,* and *E. albida* the geographic differences in the seasonal data are not significant ($P > .05$) on the basis of the Chi-square test.

Because of special interest attached to the possibility of seasonal differences between *E. segmenta* and *E. valida* (see discussion given later), their distributions of records were also compared by means of the Chi-square test. Separate comparisons were made for the northern and southern ranges. In the north the seasonal distributions of adult records in the two species do not differ significantly ($\chi^2 = .006$, df $= 1$, $P > .9$). In the south *E. valida* tends to emerge in numbers earlier than *E. segmenta* ($\chi^2 = 10.392$, df $= 1$, $P < .005$).

Table 7

SEASONAL DISTRIBUTION OF ADULTS, EXPRESSED AS A PERCENTAGE DISTRIBUTION OF RECORDS BY MONTH

Species	Month								N Records
	March	April	May	June	July	Aug.	Sept.	Oct.	
E. atrivittata	0.9	3.8	11.3	17.9	42.4	22.6	0.9		106
E. longicollis			10.8	41.2	36.3	9.8	2.0		102
E. texana				2.4	50.0	31.0	16.7		42
E. albida									
northern range			2.0	7.8	41.2	41.2	7.8		51
southern range		1.1	3.2	7.0	27.0	46.0	13.0	2.7	185
E. immaculata									
northern range			0.9	25.0	58.2	14.1	0.9	0.9	220
southern range			6.1	38.9	38.2	14.9	1.9		262
E. sublineata			11.8	14.7	32.4	35.3	2.9	2.9	34
E. segmenta									
northern range			3.7	63.0	29.6	3.7			54
southern range			1.3	7.9	38.2	36.4	15.4	0.9	228
E. valida									
northern range			8.1	58.1	25.8	8.1			62
southern range			14.3	30.4	48.2	3.6	3.6		56

While the data in Table 7 are valuable for some purposes, they have serious limitations. First, they are biased by the fact that collectors, for various reasons, tend to concentrate their activities in June, July, and August. Presumptive evidence of heavy bias from this source is to be found in the comparison of data for this species in Table 7 with the results of light trap sampling in the summer of 1959 near Apodaca, Nuevo León, Mexico, as reported by Hernández (1960). The trap, utilizing a 200-watt incandescent bulb, was operated nightly from the beginning of May to the end of November at a fixed position bordering cultivated fields. The relative frequency of monthly captures of *E. sublineata* adults was as follows (in percentages of a total of 2052): May, 0.5; June, 3.0; July, 12.7; August, 29.0; September, 43.7; October, 9.5; November, 1.5. Thus while only 6 per cent of the series of specimens examined in the present study were collected in September and October (Table 7), more than half the adults in the Apodaca light trap were taken after August.

A second limitation of the data in Table 7 results from the fact that they incorporate variance associated with differences between localities and between years. Strikingly different frequency distributions of records probably do indicate that populations are isolated seasonally to some extent, but it would be hazardous to infer the degree of seasonal isolation occurring in nature between populations without additional information.

As suggested by Table 7 and confirmed in the course of field work during the present study, no species of the Albida Group is totally isolated seasonally in the adult stage from any other with which it is sympatric. There is, however, evidence in the case of *E. longicollis* and *E. texana* of much more marked seasonal succession of sympatric adult populations than the data in the table might suggest.

This evidence was obtained in the Fort Davis, Texas, area in 1963 and 1966. In the former year habitats supporting adults of both species were visited at frequent intervals from July 6 to July 28. Twenty-one individuals of *E. longicollis* were found, all on or before July 10. Without exception these were of considerable age. All were badly rubbed and most had suffered injury to the antennae, legs, or both. As a group they exhibited a generally low level of sexual activity in the laboratory. Moreover, mortality was high, with no beetle surviving more than 15 days in confinement. A few females did, however, produce viable egg masses.

The population of adults of *E. texana* was apparently quite young. When first observed on July 6 it was considerably larger than that of *E. longicollis*; through the observation period it maintained roughly its original level. The adults themselves, in contrast to those of *E. longicollis,* were so fresh in appearance when first observed as to suggest that they had only recently emerged. In the laboratory a large sample of them maintained a high level of sexual activity and suffered practically no mortality over a period of nearly one month. Additional indication that there is little interaction between adult populations of the two species in the area from July on was obtained in 1966, when intensive searching from July 29 to August 5 yielded several records of *E. texana* but none of *E. longicollis.*

IMMATURE STAGES

Published information regarding the seasonal distribution of the larval and pupal stages of the Albida Group is limited to Gilbertson and Horsfall's (1940) brief outline of the life cycle of *E. immaculata* in South Dakota. According to their account, which is perhaps largely inferential, eggs of this species are normally found from early July to mid-August, with a peak hatching period occurring in early August. Young larvae, which are capable, if necessary, of living for three weeks or more without food, search out egg pods of grasshoppers, feed on the eggs through five instars, and then usually enter the inactive coarctate instar, in which they pass the winter. The following spring there is a return to an active larval phase, followed shortly by pupation and emergence of the adult.

Evidence from rearings carried out in connection with the present study suggests that other species of the Albida Group usually have much the same seasonal pattern of development as described for *E. immaculata.* That is, feeding is completed in a matter of a few weeks during the summer in which the larva is produced, and development is then interrupted by prolonged diapause of the coarctate larva, which presumably overwinters.

In our rearings of *E. albida* and *E. sublineata* part of the larvae circumvented the diapause period by molting directly from the last feeding instar to the pupal stage, in which case complete development required a total of about 30 days. A partial second generation was also noted by Gilbertson and Horsfall (1940) in their rearings of *E. immaculata.* As yet there is no evidence from the field for the occurrence of more than a single generation per year. In particular, frequency distributions of records for every species are unimodal. Yet with such data as these even a large partial second generation might easily escape detection if the emergence of its adults occurred within the period of maximum emergence of the first-generation adults.

TABLE 8

LONGEVITY (IN DAYS) OF REARED ADULTS

SPECIES	MEAN[a]	RANGE	N	FOOD PLANTS	TEMPERATURE (°C)
E. albida					
Males	87.1 ± 20.0	35–175	13	*Solanum* spp.	25
Females	76.9 ± 16.6	8–120	16		
E. sublineata					
Males	104.7 ± 29.0	40–181	12	*Solanum* spp.	27
Females	88.2 ± 23.0	32–147	15		
E. immaculata					
Males	72.0 ± 22.2	9–135	16	*Asclepias syriaca*	25
Females	66.4 ± 16.0	15–139	18		

[a] Here and elsewhere in this work an interval associated with a mean is its 95 per cent confidence interval.

Longevity of Adults

Longevity data for adults of three species of the Albida Group summarized in Table 8 fail to demonstrate significant sexual or interspecific differences. Combining the data for species and sexes (N = 90), the mean length of adult life is 81.0 days, with a range of 8-181 days. Comparison of these data with those tabulated by Clark and Rockstein (1964:232-233) for representatives of five orders of insects indicates that while adults of species of the Albida Group are moderately long-lived for insects as a whole, they have relatively short lives for Coleoptera. Strictly speaking, of course, the values recorded by us can be regarded as representative of the species only within the limits of the conditions under which they were obtained. In particular, it is likely that adult longevity in natural situations is quite different from that recorded here.

In preparing Table 8, we excluded data for a few individuals in which very short adult life was associated with gross anatomical defects, such as distortion of appendages or failure to inflate the elytra. Also excluded are data for adults obtained from two rearings of *E. immaculata* started in summer 1962. Larvae in each of these rearings were obtained from a single egg mass. In one of the rearings (started in July) the individuals constituted a second laboratory generation of an Illinois stock, in the other (started in September) a first laboratory generation of a different Illinois stock. The rearings were carried out at 27°C. Adults were kept at a mean temperature of 27°C and were fed leaves of *Solanum tuberosum* from plants grown in a greenhouse. In both cases adult longevity was short, with a mean of 30.2 ± 5.4 (range, 6-80) days for 17 males and 18 females in the second laboratory generation and a mean of 21.4 ± 7.3 (range, 5-32) days for five males and four females in the first generation. Associated with short adult life in both rearings was a marked reduction in fecundity. Thus, only nine egg masses were obtained (four of them from moribund females), and in only two of them was there detectable embryonic development.

At present we are unable to account for the abnormal physiology of these beetles. Since there were two separate stocks, we assume that a genetic defect was not involved. Possibly the data show that *Solanum tuberosum* is nutritionally inadequate or even toxic to *E. immaculata.*

Nonsexual Behavior of Adults

BEHAVIOR OF NEWLY EMERGED ADULTS

Adults reared in the laboratory emerged from pupae lying in cells excavated by last-instar larvae in moist sand (or a mixture of sand and soil) packed in individual 3-dram glass vials. When a cell was formed along the side of a vial, as was frequently the case, it was possible to observe the behavior of the individual from the beginning of adult life. Early adult behavior in *E. immaculata* was followed closely on many occasions, and the following notes refer to this species unless otherwise indicated. However, limited observations of adults of *E. sublineata, E. albida,* and *E. segmenta* suggest that their patterns of early behavior are much the same as that of *E. immaculata.*

On shedding the pupal skin the first act of the adult is to inflate the elytra and wings, which are then folded in proper position. During the next six to eight hours nearly full coloration is attained. For the first day or two of adult life, however, the clothing setae have a peculiar silky sheen, producing a general quality of sleekness not apparent in older beetles.

If left undisturbed, newly emerged adults remained immobile in the pupal cells for two or three days before burrowing out by means of the mandibles and legs, but as a general procedure, premature exit from the cell was induced by scraping the substrate away to expose the head of the adult and then placing the vial containing the adult in a horizontal (rather than the original vertical) position. With this treatment adults often left their cells as early as the day after emergence from the pupal stage. Adults that left cells prematurely were capable of feeble walking movements, but if left undisturbed they soon assumed a relaxed "sleeping" position in which they remained until the age of three or four days. This "sleeping" behavior was also noted rarely in beetles still a few days older.

Normal patterns of walking and searching as well as of defensive and cleaning behavior generally appeared in adults at the age of three or four days. Feeding was initiated one or two days later, following discharge of a small yellow meconium. Sexual behavior developed still later; its ontogeny is discussed in another section.

FEEDING BEHAVIOR

In discussing the life history of *E. immaculata* Gilbertson and Horsfall (1940) indicated that "as soon as adult beetles appear, they feed voraciously for a week or 10 days before mating, and then [enter] a period [of 15 to 21 days] of minimum feeding during which mating and development of eggs take place." Whether subsequent periods of mating and egg development were associated in their material with a decline in feeding activity was not indicated.

In our study of *E. immaculata* quite a different pattern of feeding activity was found. From the time that adults first fed until they were about 10 days old, the total amount of food taken was small and the daily amount varied erratically. Subsequently large amounts of food were eaten daily with considerable consistency. In males the fully adult pattern of feeding, once established, persisted throughout life. Females, however, invariably stopped feeding one or sometimes two days before ovipositing, following which they generally ate more than usual for a day or two. In addition, very old females which had become egg-bound (i.e., engorged with eggs but unable to oviposit) fed irregularly, often going an entire day without taking food.

A general consistency in daily amount of food intake was also observed in field-caught adults of most other species of the group (*E. texana, E. albida, E. atrivittata, E. sublineata, E. segmenta,* and *E. valida*) held in the laboratory over periods of three weeks or more.

Adults of *E. immaculata* feeding on composites show a preference for leaves over flowers. Otherwise the adults of the group eat flowers, peduncles, buds, and leaves of their food plants rather indiscriminately. If pressed for food, they will chew on stems and heavy leaf ribs, but these hard tissues are generally ignored when softer food material is available. Utilization of both reproductive and vegetative parts of plants as food seems to be generally characteristic of members of the genus *Epicauta* and allied genera. In contrast, flowers or parts of them are the sole or preferred adult food of most non-epicautine meloids.

In accord with the general pattern in Meloidae, females of all species of the Albida Group eat much more than do males. For females, at least, feeding is the principal daily activity and is often performed in uninterrupted bouts of several hours' duration. Males, even in isolation, spend considerably more time than females in walking and searching activities. Moreover, when sexual motivation is high and females are present, feeding by males may be inhibited for hours at a time by courtship behavior.

CLEANING

Cleaning or preening behavior involves many of the same activities or motor patterns in all Meloidae that have been observed, although there are notable differences in certain features among some taxa. The pattern of cleaning behavior in the Albida Group is typical of that of species of the genus *Epicauta* in general. It differs strikingly from that of most Meloidae in the manner in which the antennae are manipulated (Selander and Pinto, 1967).

Antennal cleaning in *Epicauta* is the most common form of cleaning behavior. In most meloids the antennae are cleaned with the mouthparts, but in *Epicauta* the action is performed by the fore legs. In adults of this genus there is on the ventral surface of the fore femur, near its base, a shallow excavation lined with silky appressed setae; in addition, the ventral surface of the fore tibia is similarly but less strongly modified. When the fore leg is flexed, the modified areas of the two segments oppose each other to form a channel through which the antenna passes during the cleaning action. The cleaning action, which may be performed rapidly or leisurely, begins as the adult lowers the antenna by cocking the head while at the same time flexing the appropriate fore leg and raising it to catch the antenna near its base in the cleaning channel. Then, by simultaneously straightening the head and lowering the fore leg, the antenna is pulled through the cleaning channel. Almost invariably after one antenna has been cleaned the other one will be cleaned immediately, and more often than not an adult will clean each of the antennae several times during a single bout.

Other cleaning acts, which may be combined with antennal cleaning and with one another in extended and complex patterns of behavior, include brushing the head (especially sides) with the fore legs, rubbing the middle and hind legs along the sides of the body and over the elytra, entwining and rubbing the middle and hind legs together, and passing the fore and middle legs through the mouthparts. In addition, the elytra may be elevated and the middle or hind legs, or both, brushed over the hind wings and the dorsum of the abdomen beneath them.

Simple antennal cleaning, with or without subsequent fore leg cleaning, occurs many times a day in a variety of situations. More thorough cleaning occurs much less frequently, and the complete repertoire of cleaning activity is rarely observed in a single bout.

Bouts of cleaning involving more than the act of brushing the antennae with the fore legs tend to be associated with the termination of extended periods of other behavior such as sexual activity, feeding, and response to disturbance. This association, which has been noted in other animals, is generally explained on the basis of selective inhibition of responses. Presumably cleaning responses have low priority in many situations, so that they tend to be postponed until other drives are satisfied or specific stimulation for other behavior is absent or at a low level. In addition, it appears that cleaning in blister beetles, as in many other animals, is associated with thwarting, as a displacement activity.

DIEL PERIODICITY

Although the influence of light on the behavior of adults of the Albida Group has not been investigated formally, it would appear on the basis of casual observations and records that none of the species is either strongly diurnal or strongly nocturnal. In the field adults of all species are active in the daytime. In addition, however, they are also commonly attracted to lights at night, which is fairly good evidence that they are normally active nocturnally. In the laboratory the usual practice was to provide fresh food material early in the light period of the day, and under this regime most of the feeding occurred during that period. But beetles were often observed feeding at very low light levels in the evening or morning, and on several occasions it was established that feeding occurred in *E. immaculata* and *E. segmenta* even in complete darkness. Courtship behavior by the male was also observed under a wide range of light levels. This behavior, since it involves an important visual component, presumably cannot be performed very effectively at very low light levels or in darkness. At the same time, there is no indication that light level itself affects the sexual motivation of the male.

DEFENSIVE BEHAVIOR

There are several behavioral patterns exhibited by adults of all species of the Albida Group that are presumably functional in protecting the individual from injury in interactions with other organisms. For the most part these patterns occur in the behavioral repertoires of most Meloidae that have been studied. Most, if not all, of them would seem to be adaptive primarily as mechanisms for escaping predation. In addition, some are probably of value in reducing the likelihood of accidental injury or mortality produced by intruders such as animals grazing on or near food plants occupied by the beetles. Finally, one pattern, decamping or withdrawing, is the common response to attacks by conspecific individuals.

Although it is reasonable to assume that adults of the group are subject to predation by a number of animals, there is at present little specific information regarding either its nature or extent. As a group Meloidae are known to be attacked by several types of predators, including birds, toads, lizards, and, among the insects, asilids, mirids, phymatids, and reduviids. However, of the published accounts of predation on Meloidae, only one is known to pertain specifically to a member of the Albida Group. This is Larson's (1943) report of finding the remains of 94 individuals of *E. immaculata* in the course of examining the stomach contents of 100 individuals of the toad *Bufo americanus* Holbrook, taken in potato fields at Fort Thompson, South Dakota. Larson also recorded 63 individuals of *E. maculata* (Say) in these stomachs, and he unfortunately did not distinguish between the two species in reporting the frequency distribution of the prey. According to his report, 65 of the 100 stomachs contained one or more of these meloids. Twenty-seven stomachs contained one beetle each; one contained nine beetles; and the rest contained from two to seven beetles each.

The only other known predator of Albida Group adults is an unidentified species of asilid fly of the genus *Stenopogon*. On August 1, 1966, at a site 3 mi. south of Toyahvale, Texas, we captured one of these flies carrying an adult of *E. immaculata*. This species of fly is presumably a rather general predator of meloids. Several days before the above record was obtained, another individual of the species had been found carrying an adult of the meloid *Pyrota plagiata* (Haag-Rutenberg) near Fort Davis, Texas.

Ecological considerations and the results of an extensive series of feeding tests by Miller (1965) suggest that lizards may be of special importance as predators of Meloidae. Many groups of meloids, including the Albida Group, are either limited to or centered geographically in areas where lizards reach their maximum abundance and diversity. In addition, although meloids utilizing tall food plants would be more or less inaccessible to many lizards, a good proportion of the species of Meloidae, and again the members of the Albida Group are included, commonly feed on low or prostrate vegetation. Moreover, there are occasions in the lives of adults of most Meloidae when they are forced to stand or walk on the ground itself. In members of the Albida Group (and other Meloinae) these occasions would include emergence of the adults from their pupal chambers in the soil and oviposition by females. In Miller's study adults of *E. albida, E. immaculata, E. sublineata,* and several other species of Meloidae proved to be highly acceptable as food items for caged adults of the horned lizard, *Phrynosoma cornutum* Harlan. It was also shown that whiptailed lizards, *Cnemidophorus sackii gularis* Baird and Girard, would pursue and investigate adult meloids, although they were consistently refused as food, apparently because of chemotactic repellency.

In general, adults of species of the Albida Group are among the most wary of all blister beetles, and those of *E. atrivittata* and *E. sublineata* seem to be particularly sensitive to novel stimuli. Newly emerged adults and those fresh from the field were, in fact, so easily disturbed that it was difficult to make observations of their sexual behavior or to carry out maintenance activities in the laboratory. Thus, for example, after placing a pair of beetles in an observation cage, it was commonly necessary to wait for an hour or more before the first movement occurred, and thereafter the observer, even when seated 3 or 4 feet from the cage, was required to remain essentially motionless in order to avoid further disturbance of the beetles. After a few days in captivity, however, adults of all species became habituated to common disturbing stimuli of the laboratory environment, and those held for a month or more often became so tame that even handling of them failed to evoke defensive responses.

Defensive behavior may be elicited by the movement of an object, a rapid change of light level, a sudden movement of the air or the substrate, and by tactile stimulation. In response to an initial stimulus, particularly one of a mild nature, the common behavior of the adult is to become immobile. Immobility undoubtedly reduces the chance of detection of the beetle by an enemy and may be further adaptive in minimizing the stimulus received by a predator which has already fixated visually on a beetle. Thus, for example, Miller (1965) found that even when oriented on an insect, *Phrynosoma* lizards were unlikely to make a capture unless the prey moved. An additional adaptive aspect of immobility may be facilitation of perception of movement by the beetle.

Higher levels of initial stimulation or lower levels of stimulation following an initial disturbance of an adult beetle generally lead to withdrawal or dropping from the vegetation. After dropping to a lower position on a plant or to the ground a beetle may become immobile at once or may seek cover before doing so, may walk or run away from the disturbing stimulus, or may begin climbing up the vegetation again. Adults capable of flying (those of *E. valida* are not) may do so either from vegetation or from the ground. This response, however, is less commonly evoked than the others mentioned.

Responses to seizure include struggling, biting, regurgitation, defecation, reflexive bleeding, and death feigning. The last two responses may also be elicited by touch or, in rare instances, by strong stimulation short of actual physical contact. Reflexive bleeding may occur with or without death feigning. The fluid exuded commonly appears at the femoro-tibial joints of the legs. Rarely droplets form on the antennae, and in one case an old female of *E. immaculata* produced a very large drop of fluid on the anterior dorsal surface of the abdomen. In most, if not all, Meloidae this fluid, which is at least in large part hemolymph, has a high content of cantharidin, and it is generally supposed that this compound, since it is highly toxic to man and certain other mammals, acts as a chemotactic repellent. In addition, the fluid contains a volatile, odiferous substance which, as first suggested by Fumouze (1867), may act as an olfactory repellent. In adults of the Albida Group the odor of the fluid is similar to that of crushed leaves of *Solanum*. The substance producing it is not, however, a plant product, as shown by the fact that adults of several species of the group reared in the laboratory were capable of giving off the odor even before they had begun to feed.

Death feigning involves drawing the head and antennae downward, folding the legs against the body, and remaining immobile. The length of time that a beetle remains in this position varies greatly with the strength of the stimulus received. In our observatons it was commonly on the order of five minutes or less.

INTERACTIONS OF INDIVIDUALS

Adult Meloidae are characteristically gregarious, and this behavior is well marked in all species of the Albida Group. Within aggregations or groups adults commonly rest, feed, clean, and perform other activities in close proximity to other individuals, as though oblivious to them. However, very little observation is required to demonstrate that adults of the group, except for those of *E. atrivittata*, under normal circumstances maintain a minimum distance within which approach of a conspecific is discouraged, and that they do not permit sustained bodily contact with another individual. Both males and females use the legs to fend off other individuals when they approach too closely, and both sexes frequently attack intruders. Attacks consist of butting the intruder with the head or attempting to bite, or both. Generally an attack consists of a single lunge or biting attempt. But persistent intrusion may lead to a more sustained attack, especially by females, in which the transgressor is usually chased from the area. As mentioned previously, the common response to attack is withdrawal; however, attacked individuals sometimes respond by butting or attempting to bite their attacker. Adults are capable of causing serious damage to one another with their mandibles, but it appears that even the most vigorous and prolonged attacks seldom result in injury.

Disturbance from an outside source inhibits fending and attacking behavior among adults. This was particularly apparent in instances where captive adults, in attempting to avoid being picked up, gathered in dense clusters in the corners of their cage and often remained there with extensive body contact for long periods of time. However, once the disturbing stimulus was removed and the beetles began to move, they quickly re-established their original pattern of individual spacing.

Epicauta atrivittata differs strikingly from the other species of the Albida Group in that adults more often than not seem relatively oblivious to casual physical contact with conspecifics. Both in the field and laboratory adults were commonly observed resting or feeding in tight groups in which some individuals were standing partially or entirely on others. Moreover, in the series of observations of individual pairs made as part of the study of sexual behavior in the species, females generally showed little inclination to fend off or attack courting males, even when the latter walked or stood on them.

SEXUAL BEHAVIOR

In describing the sexual behavior of most species of Meloidae that have been studied, a convenient distinction can be drawn between courtship, consisting of activities of both sexes that occur before genital coupling is achieved, and copulation, or behavior during the period that the sexes are coupled. Under these definitions, an unsuccessful attempt of a male to establish genital coupling is a courtship activity. This seems reasonable, since in many species presentation of the genitalia by the male to the female is an integral and regularly repeated part of the courtship or precopulatory display. In the Albida Group, however, presentation of the male genitalia is made as part of a discrete sequence of acts which normally occurs only when the female is ready to copulate. Moreover, since receptiveness develops in the female only infrequently during her adult life, the acts and interactions of the pair of beetles immediately preceding copulation are, in a real sense, external to the flow of most courtship behavior that one observes from day to day. Rather than attempt to classify this precopulatory sequence either as a part of courtship or as the initial stage of copulation, we will recognize three stages of sexual behavior in the Albida Group: courtship, the precopulatory sequence, and copulation.

General Description of the Behavior and Its Component Acts and Positions

In most species of Meloidae there is an initial, preliminary phase of courtship during which the male, having recognized the female, advances and prepares to begin his display. In many species this phase is of momentary duration. But in others, and particularly in those in which the male is likely to be attacked by an unreceptive female, there may be an extended period before the male contacts the female and initiates overt courtship activity. In the simpler forms of extended preliminary phase the male may repeatedly reposition himself in relation to the female or may approach and withdraw several times, as though seeking the optimal opportunity for contacting the female. In more elaborate forms of the phase the male, in addition to maneuvering in the manner described, appears to test the responsiveness of the female in one or more ways. Finally, in the most complex pattern of this type the preliminary phase incorporates elements of display, such that one or more acts of the male appear to have a visual or tactile signal function, promoting recognition by the female or serving to stimulate her to receptiveness, or both.

Within the subgenus *Macrobasis* it is possible to recognize several stages of progressive increase in the complexity of the preliminary phase of male courtship. Minimal development of the phase occurs in the Uniforma Group. A somewhat more extended phase is characteristic of the Diversicornis Group (Figs. 10-11), but there seems to be little testing of responsiveness or stimulation of the female by the male prior to mounting. In the Fabricii Group there is a rather highly developed preliminary phase in which there may be extended testing by the male and in which, in all probability, there is an important component of visual stimulation of the female. At the same time, in the last group the mounted or dorsal phase, which in the other groups is the principal component of courtship, is normally of short duration and occurs only sporadically. Finally, in members of the Albida Group the activities of the preliminary phase have come to constitute the normal complement of courtship behavior, while the dorsal phase has been reduced to the precopulatory sequence of short duration, which occurs normally only after the female has indicated a readiness to copulate.

Male Courtship Behavior

ORIENTATION

For the entire period of courtship activity of the male, from the time he orients on the female until he abandons her, loses contact with her, or begins the precopulatory sequence of acts, we will use the term *orientation.* In addition, we will refer to the overall activity of the male during this period as *orienting.*

Orientation begins as a sexually motivated male, having encountered a female (or in some situations another male, see below), turns to face directly toward her and adopts a distinctive posture and demeanor (Figs. 15, 19, 23, 27-30, 32-33, 35-36, 39-40, 43-44, 47). Commonly the male is within touching distance of the female before orientation occurs; in no case is he capable of orienting at a distance of more than a few centimeters.

During orientation the male stands with the legs well spread and the body slightly lower than usual, giving the impression of crouching. When standing on a flat surface, the body is nearly parallel to it. The head is elevated to a prognathous position. The antennae are directed forward in a plane roughly paralleling that of the head. In males of the Immaculata Subgroup they are straight and diverge appreciably. In those of the Albida and Atrivittata subgroups the first antennal segment, which is greatly enlarged, is directed laterad, and the remainder of the antennae extends diagonally forward or, as is frequently the case in *E. atrivittata,* directly forward. The palpi are generally withdrawn during orientation, although one or both pairs may be extended periodically. In *E. albida* (Figs. 15, 27-30) the male genitalia are partially extruded much of the time that the male is orienting. Typically the distal part of the genitalia is exposed and extends straight posteriad. But movements of the female, which seem to heighten the motivation of the male, tend to increase the degree of extrusion of the genitalia and, in addition, result in their being directed somewhat ventrad. On the other hand, an attack or a feint by the female results in withdrawal of the genitalia to the normal position within the abdomen of the male. Other species of the group do not extrude the genitalia during orientation.

The demeanor of the orienting male suggests tenseness and wariness, as though he anticipates an attack. These attributes are best developed in *E. sublineata, E. immaculata, E. albida,* and *E. longicollis* and least so in *E. atrivittata,* with *E. segmenta* and *E. valida* occupying a somewhat intermediate position in this regard.

An orienting male attempts to remain constantly in close proximity to the female but avoids contact other than that involved in the specific stimulatory acts to be described below. In *E. segmenta* and *E. valida* he generally orients toward the posterior half of the female's body, and males of these species frequently court from directly or diagonally behind the female. In the other species, and particularly in the members of Albida and Atrivittata subgroups, there is a definite tendency to orient on the head of the female, and males are likely to take positions directly or diagonally in front of the female when this is possible (Fig. 15). Regardless of the species involved, however, the relative position of the male and female seldom remains fixed for more than a few seconds at a time. Thus, fending behavior, turning movements, real or feigned attacks, and locomotion by the female tend to result in almost constant and often elaborate maneuvering and repositioning by the male. But even when the female is stationary and not responding negatively, the male characteristically adjusts his point of orientation and degree of proximity to her at short intervals. A common pattern of behavior observed in *E. albida,* for example, involved the male's orienting originally on the female from behind, working gradually around until he faced her, and then moving posteriad again, from either the same or opposite side, with subsequent repetitions of this cycle.

A male courting an antagonistic female tends to remain farther away than a male courting a passive female. But in either case there is an attempt to remain close enough to allow contact of the male's antennae with the female's body.

In the course of orientation the male commonly responds to fending movements of the legs of the female or minor movements of her body by leaning back without moving the legs. In other cases he may step backward or to the side. In general the nature and amount of response of the male are appropriate to the stimulus received from the female, and there is little stereotypy in this aspect of male behavior. There is, however, a rather strongly stereotyped act performed in such situations which has the appearance of a startle reaction (Figs. 13, 45). This act is performed in much the same way in all species. It involves a sudden and marked leaning back by the male, accompanied by rapid withdrawal of the antennae. It is performed in response to movements of the female which are more energetic or of greater amplitude than the ordinary and is particularly likely to occur when the female turns toward the male or moves toward him suddenly.

Although not a regular component of orientation, lifting of the male fore legs has been observed commonly in *E. albida* and occasionally in *E. texana* and all species of the Immaculata Subgroup. This act occurs with considerable regularity in males of all species of the Albida Group as the first element of the precopulatory sequence, just before the male mounts the female. Hence its occurrence during courtship presumably indicates that a male is on the threshold of mounting. This is borne out by the fact that it generally occurs as an isolated event when the male is very close to the female and is displaying intensively.

SPECIFIC STIMULATORY ACTS DURING ORIENTATION

These are rather highly stereotyped male acts of short duration which are typically performed repeatedly in the course of courtship. Four of them involve the antennae, one the palpi. Their presumed functions are discussed below.

Touching. In performing this act the male lowers one of the antennae and lightly touches the head, pronotum, or elytron of the female with the last segment or the last two or three segments (Figs. 12, 41). In making the touch the male usually leans forward. If the female responds negatively, as is usually the case, the antenna is withdrawn immediately. If the female is receptive, touching may develop into pressing.

Pressing (Figs. 48-49). The male lays both antennae on the dorsum of the female and moves them rapidly from side to side. This act is more forceful than touching and of longer duration, although even a very lengthy press seldom lasts longer than two seconds. It is invariably accompanied by a leaning forward or lowering of the body of the male. Although not confined to situations where mounting by the male is imminent, pressing is often followed by an attempt to mount, and in all species where it occurs, it is almost invariably a component of a successful precopulatory sequence.

Antennal whipping. Whipping of the antennae occurs only in males of the Albida and Atrivittata subgroups, all of which have the first antennal segment greatly enlarged and distorted and the second or third segments modified in form to a greater or lesser extent (Fig. 54). The act consists basically of rapidly curling and uncurling the second to eleventh segments of the antenna, accompanied in many instances by movement of the first segment (Figs. 20, 34, 37). The degree of curling and the extent of movement of the first segment vary considerably depending on the motivational level of the male. Generally, both antennae are whipped at the same time, but unilateral whipping is occasionally observed.

In low intensity whipping the first segment remains stationary (usually nearly horizontal and directed diagonally forward) while the apical segments are curled slightly mesad and then released. At high intensity the first segment is swept rapidly posteriad and elevated while at the same time the flagellum is brought into a full circle so that the antenna loops over itself. The loop is formed of segments 2-5; the rest of the flagellum is more loosely curled. Frame counting of motion picture sequences of whipping indicates that a full whip requires about one-fourth second in all species. Most of this interval is used in bringing the antennae into a loop and only a small fraction in straightening them again. *Epicauta atrivittata* curls the antennae more rapidly than the other species but compensates for this by holding the loop for a longer period of time.

Whipping tends to occur as a series of several rapidly repeated individual acts. Males may whip the antennae while oriented on the female from any direction and at any distance from which orientation is still maintained. High intensity whipping tends to be associated with close proximity of the male to the female's antennae, in which case it is frequently evident that the male is motivated to wrap his antennae around those of the female.

Antennal wrapping. Successful enclosure of the antenna of the female in the loop of the male antenna formed by the whipping action is termed antennal wrapping. Usually the loop of the male's antenna is thrown around the female's antenna near its middle, but wrapping may occur on any portion (Figs. 16, 18, 21, 38). In addition, accidental contact of the male's antenna with the leg of the female may lead to repeated wrapping of that appendage (Fig. 25). A bout of wrapping usually occurs after one or more bouts of whipping, although males sometimes wrap without this preliminary behavior. As in the case of whipping, a wrapping bout generally consists of several rapidly repeated individual acts.

The degree of curvature attained by the male's antennae and the forcefulness with which they are applied to those of the female vary considerably within species, depending on (or so it would appear) the motivational level of the male. Low intensity wrapping, which is observed rather infrequently, entails nothing more than a loose winding of the male's flagellum about that of the female. High intensity wrapping involves full, tight curling of the male's antennae and gives the impression that the male is exerting considerable pressure on the antennae of the female (Fig. 18). In addition, at the height of the act the second or second and third segments of the male's antenna may be directed backward in such a manner as to force the female's antenna against the first antennal segment. In *E. atrivittata* (Fig. 16) the female's antenna is received in a large groove on the dorsal surface of the male's first antennal segment. In the species of the Albida Subgroup the point of contact is an excavated area of the apicolateral margin of that segment (Fig. 18). Although the details of high intensity wrapping are difficult to observe, sufficient observations were made to establish beyond question that trapping of the female's antenna against the male's first antennal segment does not occur consistently in even the most intense bouts of wrapping.

Palpating. When especially close to a female, a male of the Immaculata Subgroup may occasionally extend the maxillary palpi and touch her with one or both of them (Fig. 24). Palpation of this nature is particularly likely to occur in conjunction with antennal touching or pressing. Its occurrence under any circumstances, however, is sporadic.

ABORTIVE MOUNTING

In the normal precopulatory sequence, as described below, the male mounts the female in response to a signal from her indicating receptiveness, and under such circumstances the female cooperates with the male in establishing the genital coupling. A male sometimes attempts to initate this sequence prematurely, however, in which case the unreceptive female, unless extremely feeble due to age or disease, reacts in a strongly negative manner and is invariably able to dislodge the male rapidly or at least prevent him from copulating. These abortive mounts (Figs. 18, 46), as we will call them, occur infrequently except when a male is sexually deprived for several days. Some of them probably represent mistakes in the sense that a movement by a female is erroneously interpreted by a male as a sign of receptiveness. For the most part, however, they would seem to be attributable primarily to extraordinarily intense motivation on the male's part, resulting in attempted performance of the precopulatory behavior in the absence of appropriate stimulation. In general we have recorded as an abortive mount any mounting of a female by a male that did not result in copulation, except in a few instances in which copulation was not achieved despite the evident cooperation of the female. In *E. atrivittata* a somewhat different definition is required, since in this species females, even when unreceptive, frequently allow males to stand on or above them during orientation. In *E. atrivittata* the equivalent of abortive mounting in other species was taken as behavior involving clasping of the female with the legs and an attempt to make genital insertion.

Abortive mounting is generally terminated within a few seconds. In some cases the male, having presumably detected that the female is not receptive, abandons his position or, in the case of *E. atrivittata*, discontinues the attempted genital insertion. Except in *E. atrivittata*, however, abortive mounting usually terminates as a result of the male's having been forcibly dislodged by the female. Following an abortive mount, the male may abandon the female entirely or may resume orientation behavior.

Female Response to Male Courtship

Behavior of the female during courtship varies greatly, depending in large measure on her level of sexual receptiveness and the motivational level of the male, as judged by the intensity of his courtship. The behavior of females when ready to copulate is described in the next section. Here we will be concerned with the response of unreceptive females.

Studies to be described below indicate that while females can be stimulated to copulate only at intervals of several days, they maintain a more or less continuous level of attractiveness to males from shortly after emergence until essentially the end of adult life. Consequently, all but a very small fraction of the bouts of courtship that occur in laboratory populations, and apparently in natural ones as well, involve unreceptive females and therefore fail to terminate in copulation. In general the response of an unreceptive female to an orienting male is much the same as her response to an individual of either sex in a nonsexual encounter. If the courting male does not approach too closely and if he refrains from contacting her, the female usually ignores him. Except in *E. atrivittata,* however, physical contact leads to withdrawal, fending behavior, or attack by the female (Fig. 22). Sustained close proximity of the male may elicit these negative responses even in the absence of actual contact. In *E. atrivittata* negative responses, including attacks, occur in some encounters, but females are generally much more tolerant of courtship activities of the male than are those of the other species of the group (Fig. 31). The more passive nature of females of *E. atrivittata* is especially evident when one considers the response to attempted mounting by the male. In the other species of the group unreceptive females react immediately and violently by attempting to brush the male from them and usually by attacking. In *E. atrivittata,* on the other hand, females commonly respond to antennal wrapping and attempted genital coupling (the equivalent in this species of abortive mounting in the others) by lowering the head and antennae and remaining still (Figs. 35-38).

Withdrawal by the female may consist of moving a step or two away from the male or, at the other extreme, walking completely out of the male's range of activity and thus breaking the encounter.

Fending behavior involves raising one or more of the legs and either brushing them over the body, extending them in the direction of the male, or (except in *E. atrivittata*) pushing or kicking them at the male. These acts often involve only one leg, but in some cases both hind legs or a pair of adjacent legs on one side of the body may perform a fending act stimultaneously. Fending is usually performed as an immediate response to physical contact (touching and pressing, antennal wrapping, or attempted mounting) by the male. Yet in some cases the visual stimulus of an orienting male is sufficient to elicit them. In addition, fending behavior of an apparently spontaneous nature has been observed. Thus a female which has been subjected to extended courtship may continue to perform fending acts after the termination of the bout and departure of the male.

While a female may, on occasion, attack a male at the onset of a bout of courtship, the likelihood of attack is much greater after the bout has progressed to a point where the female has already attempted to withdraw from the male or has at least performed fending behavior in response to physical contact. In addition, we have noted that feeding females are more likely to attack courting males than are females not engaged in this activity. Presumably this is explained on the basis that hunger has an inhibitory effect on withdrawal.

Following an attack, the female may withdraw rapidly, may continue her previous activity, or, in situations where she is unusually agitated, may approach and attack nearby individuals of either sex. Males usually respond to attack by attempting to escape, and in most cases courtship behavior is terminated, at least temporarily. Although it is difficult to detect signs that a female is approaching the threshold of sexual receptiveness until shortly before copulation occurs, there is an obvious change in behavior at that time. Specifically, she becomes immobile, refrains from fending activity, and usually lowers the head and antennae at least slightly. Males respond by intensifying their courtship activity and, in many cases, by repositioning themselves so as to orient from the front.

The Precopulatory Sequence

When a female has reached a proper state of sexual receptiveness, the precopulatory sequence is performed and a lengthy period of copulation ensues. In the mixed group situation it was not unusual for the precopulatory sequence to be preceded immediately by one or more hours of courtship. But commonly in this situation, as well as in the individual pairs situation, where females were usually exposed to males for a period of 30 minutes each day, only a few minutes of courtship were required to bring the female to the receptive state, and occasionally the precopulatory sequence was performed successfully without preliminary courtship (Table 9).

The precopulatory sequence in all species of the group is composed

Table 9

MALE COURTSHIP IMMEDIATELY PRECEDING COPULATION IN THE INDIVIDUAL PAIRS SITUATION[a]

Behavioral Parameters	Mean	Range
Epicauta immaculata (9 periods, at 25°C)		
Courtship time (sec.)	183.7 ± 73.9	3–302
Touches	2.6 ± 1.5	0–7
Presses	1.7 ± 1.3	0–5
Abortive mounts	0.0	....
Epicauta sublineata (12 periods, at 27°C)		
Courtship time (sec.)	171.4 ± 10.5	0–540
Touches and presses	6.5 ± 1.3	0–22
Palpation (bouts)	0.2 ± 0.1	0–2
Abortive mounts	0.3 ± 0.1	0–2

[a] The data for each species were obtained from three pairs of reared adults. Members of each pair were allowed to interact with each other for a period of 30 minutes daily. Records of all courtship during periods in which copulation occurred are summarized.

of several distinct and for the most part highly stereotyped acts, as follows.

TIPPING

In this act the female elevates the hind portion of the body and lowers the head to or near the substrate by extending the hind legs beneath her (Fig. 25). The angle of tipping thus achieved varies somewhat but is generally about 45° from the horizontal. The antennae are lowered in relation to the head and directed posteriad as tipping occurs and usually lie on the substrate. The apex of the abdomen is opened, exposing the gonopore. In addition, the end of the abdomen may be bent dorsad.

In the vast majority of perhaps 50 copulatory sequences that we observed in species of the Albida Group, tipping was the initial element or act. In some, however, the male mounted the female before tipping was discernible to us, and in a few sequences tipping was not recorded. The response of the male suggests that tipping is either a visual signal of receptiveness or that it occurs simultaneously with the release of an odor having such signal value, or both. In this connection it should be emphasized that the apparent absence of tipping by a female before she is mounted does not rule out the possibility of a subtle visual signal from the female before mounting occurs. In motion pictures of a precopulatory sequence of *E. albida,* for example, it appeared, when the film was run at normal speed, that tipping occurred after the male had begun to mount. But examination of single frames showed that a slight elevation of the female's abdomen occurred just before the male began to move forward.

Often the angle of tipping of the female is increased as the male climbs onto her dorsum. Once the maximum angle is attained, the female remains still until the male inserts the genitalia, at which time she lowers her body to its normal, horizontal position.

MOUNTING

When the male detects that a female is ready to copulate, he immediately brings the antennae more or less parallel to each other, advances, and mounts to her dorsum (Fig. 25). In most sequences observed the male mounted from the front, but mounting from any direction is apparently possible in all species of the group. Males of the Immaculata Subgroup invariably perform a strong antennal press as they mount (Fig. 49) and subsequently lash the head and pronotum of the female rapidly with the antennae until genital insertion is accomplished. Those of the Albida and Atrivittata subgroups frequently bring the antennae onto the female while mounting and lash them about rather irregularly, but the characteristic press of the Immaculata Subgroup is lacking. Males of the former subgroups also commonly whip the antennae a few times just before or during the mount. Actual wrapping of the antennae of a receptive female by a mounted male is uncommon.

In all species of the group the maxillary and labial palpi are extended and applied to the female as the male mounts. Having attained the mounted position, the male then brushes the palpi on the head of the pronotum of the female. This palpation, which is quite different from that performed during orientation, is accompanied by a rapid nodding of the head. It continues until the genitalia are inserted, at which time the palpi may either be withdrawn or allowed to remain motionless on the female.

THE MOUNTED POSITION

Once on the dorsum of the female the male orients so as to face in the same direction as his partner and immediately clasps her with his legs (Figs. 14, 42, 50). The fore legs are invariably placed so that the end of each tibia contacts the female's thorax ventrolaterally just behind her fore coxae (Fig. 14). Positioning of the middle and hind legs of the male is variable. Typically the middle legs partially encircle the female at about the level of the anterior third of her elytra, while the hind legs clasp her lightly around the abdomen. As in the case of the fore legs, the principal point of contact of the male's middle and hind legs with the female is the tibial apex, although very commonly the tarsi assist in the clasp by wrapping under her body. When the female lowers her body from the tipped position, it is not unusual for the male to place one or both of the hind legs on the substrate and, less commonly, one or both of the middle legs may be brought to this position also. Occasionally we have observed males clasping females with the hind legs in the manner described earlier for other members of the subgenus *Macrobasis*, i.e., pressing the inner surface of the tibial apex against the lateral margin of the elytron or against the side of the abdomen. In no case, however, did a male maintain such a clasp for more than a few seconds at a time, and there was no indication from the male's behavior of a preference for this particular positioning of the hind legs.

GENITAL INSERTION

Once the mounted position is attained, the male extrudes the genitalia, directs them downward and anteriad, probes with the apices of the lateral lobes (gonostyli) until he finds the gonopore of the female, and then inserts the aedeagus. As the insertion is made, the antennae are lifted and extended anterolaterad and palpation terminates. After entering the vagina, the aedeagus expands and is firmly secured by means of an apical hook on its ventral side and a dorsal hook formed from a sclerotized portion of the ejaculatory duct.

LEG RAISING

Following genital insertion the male remains still for a period during which, presumably, definitive coupling of the genitalia is accomplished. Then, typically, the middle and hind legs are extended and raised so that the male now holds the female only by means of a fore leg clasp and appears to be using the other legs as aids in balancing above her body. The middle legs are usually extended and raised shortly before the hind legs (Figs. 14, 50). In well-developed behavior of this sort, the legs are held nearly straight and are elevated to at least a horizontal plane. However, there may be a mere loosening of the clasp of the legs without appreciable extension or elevation.

TURNING OFF

Once the clasp of the middle and hind legs is loosened, the male is prepared to assume a linear copulatory position. This may be accomplished by his walking off the female and turning to face in the opposite direction. More commonly he falls over backward and then rights himself (Fig. 26). In any case, assumption of the linear position involves a 180° rotation of the male's body with respect to his genitalia, as in other Meloinae (Selander, 1964). In most cases observed the male's turning-off behavior seems to have been stimulated by the resumption of movement of the previously immobile female. In others the male's behavior was apparently spontaneous. Finally, in a few instances the male was pushed off by the female or was stimulated to release her as a result of disturbance from an intruding adult.

Although courtship preceding copulation is often an extremely prolonged affair, the precopulatory sequence, once initiated, proceeds at a rapid pace. Thus, for example, in 12 timed sequences of *E. immaculata* (Table 10), males mounted females, inserted the genitalia, and turned off in a mean of slightly less than one minute. These data are quite representative of the species group as a whole.

Copulation

The behavior of copulating adults of species of the Albida Group is similar to that described for species of *Pyrota* by Selander (1964), except that the pronounced pumping movement of the male's abdomen early in the copulatory period is absent. Immediately following the initiation of copulation, individuals often groom themselves. Sub-

TABLE 10

ELAPSED TIME (SEC.) BETWEEN EVENTS IN 12 PRECOPULATORY SEQUENCES OF *E. IMMACULATA* AT 25°C

TIME PERIODS	MEAN	RANGE	N SEQUENCES[a]
Female tipping to male mount	3.9 ± 2.1	1–10	9
Male mount to genital insertion	6.2 ± 2.6	2–14	12
Genital insertion to leg raising	23.6 ± 14.4	12–58	7
Leg raising to turn off	30.3 ± 14.7	2–46	7
Genital insertion to turn off (without leg raising)	48.6 ± 7.5	38–55	5
Male mount to turn off	57.9 ± 4.6	43–66	12
Female tipping to turn off	60.0 ± 6.0	44–70	9
Turn off to righting of male	15.0 ± 7.3	2–34	12

[a] Female tipped after male mounted in two sequences and did not tip at all in one. Leg raising did not occur in five sequences.

sequently they often feed or, if not disturbed by other adults, remain still. In locomoting, the female invariably leads, forcing the male to walk backward. Copulating males do not under any circumstance exhibit courtship behavior. Females, on the other hand, are attractive to other males.

DURATION OF COPULATORY PERIOD

In contrast to Nemognathinae, Meloinae characteristically have a long copulatory period (Selander, 1964). Based on relatively few observations, the duration of the period varies from one to five and a half hours in *Pyrota* (Selander, 1964) and from slightly less than one and a half to more than 24 hours in *Lytta* (Selander, in preparation). Data for 50 copulatory periods in six of the species of the Albida Group of *Epicauta* are summarized in Table 11. The total recorded range for the group is one and a half to four hours with sample means ranging from about two hours for *E. texana* to nearly three and a half hours for *E. albida* and for *E. immaculata* at 25°C.

The mean temperatures indicated in Table 11 are for all periods of study of the samples of the respective species, not merely for the copulatory periods. The means of 25°C are accurate for copulatory periods within a range of 1°. The other values are, in general, only fair approximations of the actual means for the copulatory periods. Assuming that all means are reasonably accurate, the data indicate an inverse relationship between temperature and the length of the copulatory period amounting to something on the order of a 10-15 minute decrease in length of the period for every 1°C increase in temperature. Restricting the comparison of species to data obtained at the same estimated mean temperature, the only statistically significant differences are between *E. sublineata* and *E. immaculata* at 27°C ($t = 3.236$, $P < .01$) and between *E. texana* and *E. valida* ($t = 10.428$, $P < .001$).

On the basis of a few cases in which more than one copulatory period was timed for a pair of beetles, it does not appear that the duration of copulation is affected by the age of the beetles.

Sensory Modalities and the Organization of Sexual Behavior

Little formal investigation of the sensory modalities operating in the sexual behavior of the Albida Group has been attempted as yet, but repeated observation of the behavior under a wide variety of

Table 11

DURATION (MIN.) OF COPULATION

Species	Mean	Range	N Bouts	N Pairs	Mean Temperature[a] (°C)
E. texana	113.7±7.6	111–117	3	3	30
E. albida	200.0±21.6	190–206	3	3	25
E. atrivittata	146.5	143–150	2	2	30
E. sublineata	130.8±20.1	90–165	8	3	27
E. immaculata	198.6±23.1	159–240	14	12	25
	171.4±22.5	135–205	7	4	27
	161.3±102.6	114–190	3	3	30
E. valida	142.9±17.4	91–180	10	8	30

[a] Mean over all observation periods for samples of each species (see text).

conditions, coupled with some experimental studies of *E. immaculata* and several other species of *Epicauta*, provide preliminary insight into the subject. At the very least, one can say with considerable confidence that sexual interactions normally depend on a complex exchange of information involving visual, tactile, and olfactory stimuli, if not also chemotactic ones. Moreover, it is apparent that the internal organization of courtship behavior is such that few, if indeed any, of the stimuli normally received by either sex are individually prerequisite to copulation.

Experimental studies of several species of *Epicauta* performed by Richard Weddle (in preparation) suggest that females produce a volatile substance which stimulates both locomotor and homosexual behavior in sexually isolated males. In those species in which male courtship display involves sustained antennation or palpation of the female, the presumptive female pheromone may cause males to direct their displays to the substrate or other parts of the inanimate environment. In *E. immaculata,* however, males, unless severely deprived sexually, do not perform any elements of orientation in the presence of the pheromone unless there are females or other males present toward which the behavior can be directed.

While odor of the female seems to have the effect of increasing the level of sexual motivation in males of *E. immaculata,* the possibility of other effects remains to be investigated. In the laboratory there was no evidence that males were capable of locating females by olfaction. But the cages, and indeed the laboratory itself, may have been so thoroughly permeated with the female pheromone as to prevent the male's orienting on a source of the substance.

Vision is an extremely important sensory modality in male courtship, for the male not only maintains his position with respect to the female by visual means but is constantly adapting the pattern and flow of his behavior to the visual perception of the female's responses to his activities. Moreover, the signal of the female's readiness to copulate is, as we have indicated, partially, if not entirely, visual in nature. Conversely, it seems likely that visual stimulation provided by the male's presence and display activities plays a role in bringing the female to a state of sexual receptiveness. Particularly in species of the Albida and Atrivittata subgroups the tendency of the male to orient on the head of the female suggests that the posturing and antennal whipping stimulate the female visually. In this connection, attention should be drawn to the possibility that the yellow color of the basal antennal segments and maxillary palpi of males of *E. albida* and *E. texana* may be adaptive in increasing the conspicuousness of these structures.

While olfactory stimulus in the absence of a suitable object toward which courtship can be directed does not result in the performance of that behavior in *E. immaculata,* visual perception of a small, moving object such as the end of a pencil or a finger can release orientation behavior in males of this and other species of the Albida Group, provided that their level of sexual motivation is relatively high.

Tactile stimulation is a normal component of courtship behavior and probably constitutes the primary, if not sole, means of communication between individuals in the precopulatory sequence. During courtship the male repeatedly contacts the female by touching or pressing his antennae on her, palpating her, or wrapping the antennae about hers. The possibility of chemotactic stimulation during one or more of these acts cannot be ruled out at present, but the very nature of the acts and in particular the vigor with which most of them are performed argues strongly that they are primarily tactile in nature. The female's immediate response to the acts is usually negative. Repeated stimulation is necessary before copulation occurs. Yet, following sexual deprivation of several days, receptive females may perform tipping and permit the male to mount before receiving any tactile stimulation from him. In this case it would appear that the mere sight of a male in orientation posture is sufficient to release copulatory behavior in the female.

The various courtship acts may be arranged in a linear series reflecting their typical order of performance in a complete bout of courtship leading directly to the precopulatory sequence and copulation. In *E. immaculata* and *E. sublineata* the series is, for example, initial orientation, approach, touching, and pressing (with or without palpation), while for members of the Albida and Atrivittata subgroups, the series is initial orientation, approach, antennal whipping, and wrapping. In practice, however, a bout of courtship rarely consists of a single series of events, for if the female is ready to copulate when the male encounters her, one or more of the specific stimulatory acts are usually omitted, while the response of unreceptive females invariably leads to a complicated pattern of repetition of acts, coupled with maneuvering of the male about the female.

In contrast to the extreme flexibility of organization characterizing courtship behavior of the male, the precopulatory sequence is, as we have indicated, relatively rigid. That these two behaviors should differ so much in their organizational aspect is, in our opinion, ultimately explained by functional differences between them. In courtship behavior the male's objectives, so to speak, are to identify himself to the female and to stimulate her to the point of soliciting mounting and copulation. Once this point has been reached, the male must be able to respond rapidly by mounting. But males are apparently unable to distinguish effectively between females that have recently mated (and are therefore unlikely to mate again for some time) and those which have reached or are about to reach a proper physiological state for insemination to occur. As a result of this, much of the male's time is spent in fruitless courtship of females which not only thwart his behavior by various negative responses but which may at any time turn on him and attack. Under these circumstances, then, there is evidently great utility in flexibility of response on the part of the male.

Once the female has been stimulated to the point of tipping, however, the situation is markedly changed, since the behavior of both male and female is now directed toward a common and immediate objective, i.e., copulation. At this point it is advantageous to both individuals to cooperate in performing the precopulatory sequence as rapidly and efficiently as possible. Thus a high degree of stereotypy is not only permissible in this situation but undoubtedly is conducive to effective interaction of the sexes and attainment of the common objective.

The distinction drawn between courtship behavior and the precopulatory sequence is, of course, only a special case of the more general distinction commonly made between appetitive and consummatory behavior. The former behavior is commonly flexible and complex, while the latter characteristically involves a high degree of stereotypy. Ultimately, this difference may be traced, as in the case of the behavior discussed above, to differences in the complexity and particularly the variability of the stimulus situation under which they are normally performed.

Patterning of Sexual Behavior During Adult Life

Up to this point sexual behavior in the Albida Group has been described largely in terms of sequences of acts comprising individual bouts of behavior. Attention will now be turned to the patterning of behavior on a larger scale. Specific topics to be considered are: the timing of initial development of sexual behavior; the relationship of oviposition and sexual responsiveness of the female; the effects of changes in female responsiveness and of copulation on male behavior; and, finally, the question of trends in courtship behavior associated with age. These and other aspects of the general phenology of sexual behavior are, of course, of interest and importance in their own right. In addition, they have an immediate practical importance. In the present study, all of the behavioral information for five of the species was obtained from samples of adults of unknown age and history collected in the field. If this information is to be used in a meaningful way in interspecific comparisons, the effects on sexual behavior of factors of age, experience, and physiological condition of the adults must be taken into consideration.

Daily records of courtship, copulation, and oviposition in individual pairs of beetles reared in the laboratory and maintained in the individual pairs situation (see Introduction) until death provide the main source of information discussed in this section. Records of this nature were obtained for eight pairs of *E. sublineata*, seven of *E. albida*, and five of *E. immaculata*. Courtship records for all pairs of *E. immaculata* and three pairs of *E. sublineata* include both the duration and frequency of occurrence of events. In records of courtship of other pairs only the frequency counts are available.

In addition to the data for individual pairs of beetles, complete records of copulation and oviposition throughout life were obtained for two females of *E. immaculata* that were allowed to interact for a 60-minute period daily with four males of their species and for one female of *E. immaculata* exposed daily for the same period to two conspecific males.

In the discussion that follows, no consideration is given to the form of individual acts and positions comprising courtship, the precopulatory sequence, and copulation. This omission reflects the fact that in the course of the extensive series of observations carried out during the present study, we have failed to detect any variation in the nature of these acts that can be associated with age or experience of adults, factors of the physical environment, or, within normal limits, the physiological condition of either sex. Old adults that had lost parts of their legs (commonly the tarsi) showed behavioral anomalies resulting from impairment of their ability to walk or, in the case of males, to grasp the female. But in intact individuals sexual behavior was, so far as we could determine, qualitatively invariable during the life of the individual.

The Ontogeny of Sexual Behavior

In a sample of seven males of *E. immaculata* exposed from an age of one week or less to one or two females of the same or nearly the same age for periods of 30 or 60 minutes daily, the mean age at which courtship first appeared was 9.8 days (range, 8-13). Comparable figures for three males each of *E. sublineata* and *E. albida* in the individual pairs situation were 10.0 (9-11) and 12.3 (11-14) days, respectively. Copulation generally occurred on the first day of courtship or on the following day, but in one pair of *E. immaculata* three days of courtship preceded copulation and in another pair five days. When copulation was delayed one or more days beyond the first day of courtship, the display of the male on that day was invariably of low intensity and short duration.

On several occasions newly emerged females were exposed to older, sexually active males, and in every case males were stimulated to lengthy courtship activity at a normal level of intensity. On this basis, it seems unlikely that the latency period for development of courtship behavior in young males is affected by the age of the females with which they are paired. Further evidence of this is found in the results of three pairings of newly emerged males with older females. Thus, two young males of *E. immaculata* paired with females one week older than themselves first courted at the ages of 8 and 11 days, respectively, and a young male of *E. albida* paired with a female 25 days older than himself began to court at an age of 10 days. Unfortunately, none of the pairings of a young female with an older male was continued until the development of sexual receptiveness in the female. Consequently, there is no information bearing on the question of whether courtship by a male has an effect on the rate at which sexual receptiveness develops in the female.

The Relationship Between Sexual Behavior and Reproduction in the Female

During their adult lives females undergo a series of reproductive cycles, in each of which 100-200 eggs are matured and then deposited in a single bout of oviposition. In our data the length of the interval from first copulation to first oviposition was not significantly correlated with the age of females at the time of first copulation. Thus there is no indication that at the time of first copulation older females were any further advanced reproductively than were younger ones. Additional evidence of the role of initial copulation in stimulating reproductive development is found in the fact that virgin females rarely lay eggs and then only in very small batches late in life.

OVIPOSITION

Three of the reared females of *E. albida* and one of those of *E. immaculata* failed to oviposit. Two of these individuals died prematurely (14 and 17 days, respectively) after copulation. But two of the females of *E. albida* lived 52 and 61 days, respectively, beyond this point. Data for females that oviposited at least once are summarized in Table 12.

All females that lived more than three weeks after initial copulation oviposited at least twice. The maximum number of ovipositions was eight, recorded for two females of *E. sublineata*, each of which lived 100 days after first copulation. On the average, oviposition occurred 12.0 days after first copulation. Except for one female that laid eggs the day following first copulation, the minimum length of the pre-oviposition period was 5 days; the maximum length recorded was 22 days. Length of periods between ovipositions varied from 3 to 23 days, with an overall mean for the three species of 10.8 days. There is no significant correlation between the length of these periods and their order of occurrence.

Although a few of the females seemed to lose the ability to produce eggs in old age, most of them, and particularly those that had extended periods between last oviposition and death, died in an egg-bound condition, with the abdomen literally bulging with fully developed eggs. In a later study of *E. segmenta* females became egg-bound early in life, in some cases before first oviposition. In that study the condition was corrected by transferring females to a substrate of moist soil as soon as it became apparent that oviposition was inhibited. In every case in which this was done the female within a few days of

SUMMARY OF RECORDS OF COPULATION AND OVIPOSITION IN REARED FEMALES OF THREE SPECIES OF THE ALBIDA GROUP[a]

(ages and intervals in days)

Females	Age at First Copulation	Length of Interval from First Copulation to:			Sequence of Copulations (M) and Ovipositions (O)	Length of Successive Intervals from:	
		First Oviposition	Last Oviposition	Death		Copulation to Copulation	Oviposition to Oviposition
E. albida							
1	34	11	34	39	MOMOO	12	9,14
2	11	19	37	63	MOMO	23	18
3	41	9	42	72	MOOMO	26	14,18
4	20	11	31	92	MOMOOM	18,38	10,10
E. sublineata							
5	21	9	19	21	MMOOMO	2,14	7,3
6	32	9	60	62	MOOOMOOOMMO	25,24,4	8,6,10,7,7,13
7	22	7	56	73	MOMOOMOOMO	9,12,23	7,5,6,8,23
8	10	5	72	76	MOMOOMOOOMO	5,18,33	9,5,11,11,14,17
9	14	16	52	86	MMOMOOOMM	9,15,28,4	12,7,17
10	21	22	72	96	MMOOMOO	12,33	20,17,13
11	21	9	80	103	MOMOMOMOOMOOMOM	11,13,5,18,24,16	11,8,11,5,8,11,16
12	21	9	67	104	MOOMOMOOOMOO	17,13,26	6,13,7,10,8,8,6
E. immaculata							
13	16	20	16	36	MMMO	5,4	. .
14	17	12	42	43	MOOOMO	31	11,8,11
15	16	18	53	53	MMOOOOMMO	13,32,6	19,4,4,8
16	12	17	64	64	MOOMOO	40	22,18,7
17	19	6	51	54	MOOMOOOMO	20,25	10,9,14,6,6
18	10	17	70	75	MOOMOOO	31	12,17,12,12
19	9	1	53	81	MOOMOOOM	19,34	10,17,22,3
Mean	19.3	12.0	51.1	68.0		18.4	10.8

[a] Females 1 through 16 were exposed daily to a male partner for a period of 30 minutes. Females 17 and 18 were exposed daily to four males, and female 19 to two males, for a period of 60 minutes. See Table 2 for additional information.

transfer performed the excavating behavior that is the normal prelude to oviposition in species of Meloinae and then oviposited.

COPULATION

The total number of copulations permitted by a female during her adult life varied from two to seven (Table 12). The maximum number was recorded over a period of 88 days for a female of *E. sublineata*. The mean length of intercopulatory periods was 18.4 days, the range 2 to 40 days. As in the case of oviposition, the data are not adequate to demonstrate significant interspecific differences in the length of the periods. Because several females copulated twice in relatively rapid succession before first oviposition, the mean length of the first intercopulatory period was significantly shorter than those of succeeding periods. Otherwise there is no substantial evidence of systematic variation in the length of intercopulatory periods with time.

The pattern of repetitive cycles of egg production in the female is clearly reflected in the periodicity of her sexual responsiveness. However, because females commonly accomplished two, and exceptionally three or four, ovipositions between successive copulations (Table 12), it is evident that development of a responsive state in the female does not depend directly on her physiological state with respect to egg production. (Disregarding instances of consecutive copulations, the mean number of ovipositions between copulations or between copulation and death was 1.8.) Moreover, it is apparent that the act of copulation itself exerts at most only a brief inhibitory effect on female responsiveness.

An hypothesis to the effect that sexual responsiveness of the female is normally inhibited by the possession of sperm sufficient to fertilize at least one batch of eggs and is released when this supply is depleted is supported by evidence from two sources. The first is the restriction of consecutive copulations, without intervening oviposition, to periods of adult life in which inadequate reproductive states would be expected to occur most frequently in either females or males. As shown in Table 12, five cases of consecutive copulations occurred at the beginning of reproductive life of the female. In these cases the temporal relationship between initial copulation and first oviposition permits the interpretation that the first reproductive cycle of the female was not initiated by the first copulation, and in three of the cases such an interpretation is very strongly suggested by the data. Three cases of consecutive copulations were recorded in older females. Two of these occurred shortly before the death of the female, while in the third case the female subsequently failed to oviposit despite a longevity of nearly a month beyond the last copulation.

A second source of evidence supporting the hypothesis stated above is provided by data relating to the temporal relationship of successive acts of copulation and oviposition. During the lives of the 19 females studied, there were 33 periods between copulation and a preceding oviposition. These periods ranged in length from zero to 12 days, with a median of only 2 days and a mean of 2.5 ± 1.1 days. In contrast, records of 47 intervals from copulation to succeeding oviposition yield a range of 1 to 17 days, with a median of 8 days and a mean of 8.6 ± 1.2 days.

Temporal Variation in Male Behavior

The results of studies in which the behavior of beetles (both reared and field-caught) was recorded systematically from day to day indicate that the pattern of sexual activity during the life of the male is basically similar in all species of the Albida Group. The major features of this pattern are discussed below with particular reference to data shown graphically in Figs. 51-53 for three pairs of *E. immaculata* (see also Table 13). The adults forming these pairs were selected from progeny of an Illinois female and a Texas male (females of pairs 1, 2, and 3 are labeled 14, 15, and 16, respectively, in Table 12). The behavorial record of each pair was terminated by the death of the female.

COURTSHIP BEHAVIOR

Although the general level of courtship of a mature male apparently varies relatively little during life, there was in all of the studies marked daily variation in courtship, as measured by time spent in this activity, the number of courtship bouts, and rates of performance of specific stimulatory acts (touching and pressing in the case of *E. immaculata*). Variability in courtship time and number of bouts per period was obviously produced in part by day-to-day differences in the observational situation itself. Although considerable care was taken to handle beetles as uniformly as possible in transferring them to observation cages, it was inevitable that the degree of disturbance caused by this procedure varied a great deal. In addition, these specific parameters of behavior were greatly influenced by apparently random fluctuations in the length of time that elapsed at the beginning of a period before the male encountered the female at a range close enough to permit orientation to occur.

In the case of rates of performance of specific stimulatory acts, there are complex interrelationships which are not fully understood. All other things being equal, the frequency of these acts is likely to be low when the female's response, as measured by rates of kicking and attacking, is more negative than usual. These acts also tend to break the courtship into short bouts. On the other hand, some of the most intense and sustained male courtship occurred in situations where the female's response was highly negative, as for example during several of the last recording periods for pair 3 (Figs. 51, 53).

Although it is not apparent in the graphed data for *E. immaculata,* there was a decided increase in the rate of performance of pressing in periods in which copulation occurred. In nine such "mating periods" in this species the mean rate of pressing was 45.4 ± 35.6 acts per 1,000 seconds of courtship (range, 0-333), which is significantly different ($t = 12.032$, $P < .001$) from a mean rate of 6.3 ± 0.8 (range, 0-83) recorded during 130 periods in which copulation did not occur. Similarly, in *E. sublineata* (where the distinction between touches and presses was not made in recording behavior) the mean rate of the combined acts in 12 periods in which three pairs copulated was higher (37.4) than that in all other periods (18.2). In the course of numerous casual observations of species of the Albida Subgroup we gained the impression that high rates of antennal wrapping were associated with impending copulation. However, actual records of behavior in this situation are inadequate to demonstrate that this is indeed the case.

In contrast to the rate of pressing, that of touching in *E. immaculata* was not appreciably increased during "mating periods." Nor is there evidence that abortive mounting in any of the species was more frequent before copulation than at other times.

A striking and immediate postcopulatory effect constitutes a third source of variation in the overall pattern of male courtship behavior. This effect, recorded in all species of the Albida Group and several other species of the genus *Epicauta,* is a partial or complete suppression of courtship behavior for a period of one or two days following copulation.

Behavioral experiments with other species of the genus in which sexual partners were changed each day indicate that the postcopulatory effect on courtship observed in the individual pairs situation does indeed result from inhibition of the male's behavior and not from a decrease in the intrinsic attractiveness of the female. This has been confirmed several times in the course of casual observations of most of the species of the Albida Group in the mixed group and other situations.

Since sexual motivation in males generally returns to its normal level on the second or third day following copulation, the effect of copulation on male courtship behavior may be largely removed from the data obtained for individual pairs of beetles by disregarding records for the first two days after each copulation. This procedure was followed consistently in computing the mean levels of activity for pairs 1-3 in Figs. 51-53 and in preparing summaries of quantitative data for interspecific comparison (Table 13). In addition, for the reason indicated above, courtship data for periods in which copulation occurred were excluded.

Assuming that a male of the Albida Group seriously depletes or exhausts his supply of sperm during copulation, suppression of sexual motivation in the period immediately following would have significant selective value. Courtship undoubtedly entails a considerable increase in the probability of a male's being captured by a predator. He is more conspicuous during courtship than at other times and is apparently insensitive to environmental stimuli, other than those provided by the female to which the courtship is directed. Following this line of reasoning, it would be most interesting to determine if the latency period of restoration of the supply of sperm coincides with the postcopulatory period of suppression of courtship behavior in the male.

Since courtship by a male presumably also increases the chance of attack by a predator on the female, one might expect the female to be least attractive sexually during periods of minimal probability of copulation. However, since visual stimulation appears to play a major role in initiating and sustaining courtship behavior in the male, no effective means by which the female can temporarily discourage the attention of the male may be available to natural selection.

Aside from the immediate effects of female receptiveness and the act of copulation mentioned above, there appears to be little or no systematic variation in the courtship behavior of the male. As females of *E. immaculata* aged in the individual pairs situation, they tended to become more negative in their responses to courtship, as shown by the curves for rates of kicking and attacking in Fig. 53. Similar trends were observed in reared females of *E. albida* and *E. sublineata*. There is, however, no compelling evidence in any of the species studied of trends in quantitative parameters of male courtship behavior through adult life. Moreover, the periodic occurrence of oviposition in itself did not seem to affect the ability of the female to elicit courtship behavior in the male. Finally, and rather surprisingly, there is no indication whatsoever of trends in either the duration or intensity of male courtship in intercopulatory intervals, if one excludes the first two days.

THE PRECOPULATORY SEQUENCE AND COPULATION

Studies of reared adults of *E. albida, E. sublineata,* and *E. immaculata* in the individual pairs situation demonstrate that males are capable of copulating repeatedly during their adult lives, but the pattern of occurrence of the behavior in this situation is completely determined by the periodicity of female sexual responsiveness. In the mixed group situation and in the course of experimental studies, males of these and other species of the group have copulated with two different females within an interval of three or four days. In addition, it will be recalled that several instances of comparably rapid successive copulation were recorded in individual pairs of beetles (Table 12). The nature of long-range patterning of copulatory behavior in the male under conditions of regular or constant exposure to a receptive female remains to be investigated.

Summary of Records of Sexual Behavior in Individual Pairs of Beetles

Table 13 contains a summary of the scores of three individual pairs each of five species of the Albida Group in several behavioral parameters. The information is intended to serve primarily as a supplement to the description of sexual behavior presented above in largely qualitative terms. Its main function is to provide insight into the tempo of the behavior under the particular conditions of the individual pairs situation. In addition, despite the small size of the samples from which they were obtained, the data are useful, when interpreted in the light of additional information, in the investigation of interspecific behavioral differences.

For the first four species listed in Table 13, duration of courtship behavior and the frequency of occurrence of component activities were measured daily for a period of 15 minutes over a span of two weeks or more. Data of the same type, i.e., timed records, were obtained also for three pairs of *E. sublineata,* but the length of the daily recording period for this species was 30 minutes. Although comparison of absolute measures of behavior in *E. sublineata* and the other species is ruled out, useful comparison of rates of performance of acts may be made. Data for *E. albida* are omitted since time in courtship was not measured for this species. In the case of *E. longicollis* the information obtained is too meager for meaningful comparison; moreover, it was recorded from badly worn, apparently old adults. Finally, *E. segmenta* was not studied in the individual pairs situation.

TABLE 13

SUMMARY OF RECORDS OF COURTSHIP BEHAVIOR IN THREE PAIRS EACH OF FIVE SPECIES OF THE ALBIDA GROUP IN THE INDIVIDUAL PAIRS SITUATION

PARAMETERS	*E. atrivittata*		*E. texana*		*E. immaculata*		*E. valida*		*E. sublineata*	
	MEAN	RANGE	MEAN	RANGE	MEAN	RANGE	MEAN	RANGE	MEAN	RANGE
Mean courtship time (sec.) per period	26.4	1–49	172.1	135–228	400.4	350–446	253.6	228–277	277.1	203–336
Mean courtship time (sec.) per period in which courtship occurred	209.0	4–524	239.6	180–352	404.5	350–458	284.8	241–328	401.2	271–491
Mean number of bouts of courtship per period	0.8	0.2–1.8	4.1	4–5	6.9	6–9	9.9	9–12	5.2	4–7
Rates (acts per 100 sec. of courtship) of:										
Whipping	59.70	15.4–97.0	24.82	22.1–29.1	0.0	....	0.0	....	0.0	....
Wrapping	3.98	0.8–7.7	0.50	0.1–1.0	0.0	....	0.0	....	0.0	....
Touching	0.0	....	0.0	....	1.25	1.2–1.3	0.0	....	1.82	1.8–2.0[c]
Pressing	0.0	....	0.04	0.0–0.1	0.51	0.5–0.6	2.44	1.9–2.9		
Abortive mounting	0.38	0.0–1.1	0.30	0.26–0.32	0.004	0.00–0.01	0.12	0.05–0.21	0.01	0.0–0.2
Female kicking	0.0	....	0.12	0.0–0.4	7.60	7.3–7.8	0.49	0.4–0.6	Acts not recorded separately	
Female attacking	0.33	0.0–0.8	0.11	0.0–0.2	0.31	0.2–0.4	0.69	0.4–0.9	0.18	0.4–2.6

TABLE 13 — Continued

NATURE OF RECORDS	*E. atrivittata*	*E. texana*	*E. immaculata*	*E. valida*	*E. sublineata*
Length of daily recording periods (min.)[a]	15	15	15	15	30
Number of recording periods included per pair (mean and range)[b]	17.3 (16–18)	16.7 (16–17)	43.3 (36–57)	19.0 (18–20)	33.3 (12–46)
Percentage of recording periods in which courtship occurred (mean and range)	24.4 (6–50)	74.0 (65–82)	99.1 (97–100)	89.5 (84–94)	74.1 (69–78)
Mean temperature (°C) during recording periods	30	30	25	30	27
Source of adults	Field (notes 19–63)	Field (notes 26–63)	Reared (Texas × Illinois progeny)	Field (notes 16–63)	Reared (notes 16–62 (II))

[a] Pair members were exposed to each other 30 minutes daily, with recording of courtship behavior during first 15 minutes of period or (for *E. sublineata*) during entire period.

[b] Periods in which copulation occurred and the two following periods are excluded. In addition, for *E. sublineata* all periods beyond day 60 were excluded.

[c] Combined rate of touching and pressing.

In preparing the table a single score (total, mean, or rate) was computed for each pair of beetles, and these scores were then averaged to obtain the means for species (i.e., the score of each pair constituted a datum). Number of periods of recording and other information about the individual pairs utilized are given at the bottom of Table 13 (see also Table 2).

Attention is called to the fact that the mean temperature at which records were taken was not the same for all species. Moreover, there was appreciable variation in temperature between recording periods for *E. texana*, *E. atrivittata*, and *E. valida*. For *E. texana* and *E. valida* the relationship between several behavioral measures (courtship time, number of bouts, rates of pressing and whipping) and temperature was tested by means of partial correlation, holding chronological order of periods constant. In no case did a correlation coefficient differ significantly from zero at the 5 per cent level. Thus it is probably safe to conclude that temperature effects in the present data are relatively minor.

In view of the lack of control of several independent variables, rigorous or elaborate statistical analysis of the data on interspecific differences summarized in Table 13 is not justified. The procedure adopted is to regard as probably significantly different those means whose 95 per cent confidence intervals do not overlap.

TIME IN COURTSHIP

As shown in Table 13, there were marked differences between species in the relative amount of time that males spent in courtship. Minimal sexual activity was recorded in *E. atrivittata,* males of which averaged less than 30 seconds of courtship per period of exposure to females. In contrast, *E. immaculata* males courted an average of more than 6 minutes per period. *Epicauta valida* and *E. texana* had scores which are intermediate and not significantly different from each other. *Epicauta sublineata* belongs in an intermediate category also, since its mean courtship time per 30 minutes was not much more than that of *E. valida* per 15 minutes.

Intensity of courtship may also be analyzed in terms of the proportion of periods in which courtship occurred and the mean courtship time in those periods. When this is done, it is evident that interspecific differences in mean courtship time over all recording periods are accounted for in large part by differences in the relative number of periods in which males were stimulated to courtship. There is, however, a positive correlation between the proportion of periods with courtship and the mean level of performance of the male in periods in which courtship occurred.

Additional data, obtained from 30-minute records of five to 10 pairs each of the species listed in Table 13, indicate that the values for the proportion of the periods in which courtship occurred as shown in Table 13 are quite representative of the species.

While it is tempting to infer from the measures of time in courtship in the individual pairs situation that there are intrinsic differences between species in the general level of male sexual motivation, it would be a serious mistake to overlook the possibility that the recorded differences reflect nothing more than degrees of adaptability of individuals of the various species to the laboratory environment. In this connection it should be pointed out that marked differences in "wariness" were noted among several of the species and that, further, *E. atrivittata* and *E. sublineata,* both of which courted irregularly and then for relatively short intervals, were judged to be especially sensitive to disturbance.

RATES OF ACTIVITY

As indicated earlier, the acts of antennal whipping and wrapping are performed only by males of species of the Albida and Atrivittata subgroups. Rates of performance of these acts vary greatly among individuals in both *E. texana* and *E. atrivittata,* and the interspecific difference indicated in Table 13 is not statistically significant. Nevertheless, it would appear, on the basis of extensive casual observation, that *E. atrivittata* does in fact tend to perform these acts more frequently during courtship than does *E. texana.*

Antennal pressing occurs as a regular component of courtship in all species of the Immaculata Subgroup. Otherwise it occurs during courtship only in *E. texana* and then infrequently and irregularly. Returning to the Immaculata Subgroup, it is seen in Table 13 that *E. valida,* in effect, compensates for a lack of the act of touching by pressing much more frequently than does *E. immaculata.* Although separate measures of touching and pressing rates were not obtained for *E. sublineata,* it is our impression that the relative frequency of the two acts is about the same in that species as in *E. immaculata.* Further, the rates of performance of the respective acts are of roughly the same order in the two species, as suggested by the fact that the rate of combined touching and pressing acts recorded in Table 13 for *E. sublineata* is very close to the sum of the rate of touching and rate of pressing recorded for *E. immaculata.* On the other hand, *E. segmenta* appears to press at a rate nearly equivalent to that of *E. valida.*

In the case of abortive mounting the data suggest higher rates of performance for *E. texana* and *E. atrivittata* than for the species of the Immaculata Subgroup. In the course of our observations of sexual behavior it seemed that males of the Albida and Atrivittata subgroups not only performed this act more frequently than those of the Immaculata Subgroup, but did so much more vigorously.

Females of *E. atrivittata* do not perform kicking in response to male courtship, although they appear to be as likely to attack a courting male as are females of other species of the group. Rates of kicking recorded in Table 13 for *E. texana, E. immaculata,* and *E. valida* are all significantly different. But inasmuch as rate of kicking has been shown to vary with the age of the female, direct comparison of the means is not particularly meaningful.

Summary of Interspecific Differences in Sexual Behavior

Table 14 contains a summary of interspecific differences that seem sufficiently well established to merit incorporation in the systematic analysis of the group presented later in this work. This table should be self-explanatory since all of the characters that it presents have been discussed in detail.

Heterospecific Sexual Behavior

In previous sections of this work we demonstrated extensive sympatry among the various species of the Albida Group and considerable overlap in the seasonal periods of adult activity of most of them. In addition, we presented evidence that in a single area differential food plant preference or selectivity does not provide the basis for rigorous isolation of species in the adult stage. These relationships indicate that in nature there is ample opportunity for heterospecific interaction of adults. In the present section we record the results of an investigation of heterospecific sexual interaction among adults in confinement.

In a series of observations performed at Fort Davis, Texas, freshly collected males and females of several species of the group were exposed to each other in heterospecific combinations over a period of several days. The combinations tested in this manner were determined largely by the availability of adult material. Females were isolated sexually and specifically in cages of the larger type, from which they were drawn indiscriminately just before the observations of the day. Males were isolated individually except during a 30-minute period daily

TABLE 14

SUMMARY OF INTERSPECIFIC DIFFERENCES IN SEXUAL BEHAVIOR IN THE ALBIDA GROUP[a]

CHARACTERS AND CHARACTERISTICS	ATRIVITTATA SUBGROUP	ALBIDA SUBGROUP			IMMACULATA SUBGROUP			
	atrivittata	*longicollis*	*texana*	*albida*	*sublineata*	*immaculata*	*segmenta*	*valida*
Specific stimulatory acts of the male:								
Whipping and wrapping	+	+	+	+	–	–	–	–
Touching	–	–	–	–	+	+	–	–
Pressing	–	?	+[b]	–	++	++	+++	+++
Relative speed of flagellar curling during whipping	++	+	+	+	NC	NC	NC	NC
Female antenna contacts dorsal (rather than lateral) surface of male antennal segment I during wrapping	+	–	–	–	NC	NC	NC	NC
Tendency of male to orient on head of female	++	++	++	++	+	+	–	–
Fore leg lifting by male during orientation	–	?	+	++[c]	+	+	+	+
Abortive mounting	++	?	++	++	+	+	+	+
Genitalia extruded by orienting male	–	–	–	+	–	–	–	–
Female often permissive of mounting by male[d]	+	–	–	–	–	–	–	–
Antennal lashing by male during precopulatory sequence[d]	–	?	+	+	–	–	–	–

[a] Plus signs (+) are used to indicate positive character states and (within individual characters) relative frequency of acts or strength of development of characteristics. Negative signs (–) denote absence of acts or specified conditions. The symbol NC is used where comparison is inappropriate.

[b] Occurs only rarely.

[c] Commonly observed in *E. albida*, infrequently in other species in which it occurs.

[d] Female does not kick at male when approached or contacted. Male often courts while partially or fully mounted on female.

when each was paired with a female of a species other than its own. The number of pairings of a male with females of a given species varied somewhat, although in no case was the nature of the heterospecific pairing the same for a male on successive days. Pairings were made in cages of the smaller type used regularly in observations of individual pairs of beetles.

The proportion of observation periods in which courtship occurred is given for each combination in Table 15. The courtship behavior of the males was qualitatively normal and for the most part comparable in intensity and persistence to that observed in homospecific pairings under similar circumstances. As indicated in the table, courtship was recorded in nearly all heterospecific combinations tested. The data for males of *E. texana* suggest that some heterospecific combinations are more conducive to courtship behavior than are others, but we would hesitate to draw a definite conclusion regarding this point without making a properly controlled experiment.

As the series of observations of heterospecific pairs progressed, courtship became generally more intense and prolonged, and the frequency of negative response of females to males decreased markedly. On several occasions a female seemed to solicit mounting by a male by standing directly in front of him and touching him repeatedly with the antennae and maxillary palpi. The male usually responded to this behavior with especially intense courtship display and one or more attempts to mount the female. Rarely, however, was the male able to induce the female to perform the initial act of the precopulatory sequence (tipping), and mounting by the male was consequently almost invariably abortive.

Striking evidence that females that approached males in the manner described above were ready to copulate but were not receiving the proper stimulus from their heterospecific partners was obtained in one case in which a female of *E. texana* was paired with a homospecific male immediately after a 30-minute period of exposure to a male of *E. immaculata*. During that period the female performed what we have interpreted as copulatory solicitation several times, and the male responded by performing almost continuous courtship, in the course of which he made one antennal touch, 20 antennal presses, and six abortive mounts, all of which were prolonged. At the end of the observation period the male of *E. immaculata* was carefully removed and replaced with the homospecific male. The latter oriented on the female and whipped his antennae within a few seconds of being placed in the cage. Whether stimulated by the sight of the homospecific male or an odor emanating from it, the female apparently found the stimulus

TABLE 15

PERCENTAGE OF 30-MINUTE OBSERVATION PERIODS IN WHICH HETEROSPECIFIC COURTSHIP BEHAVIOR OCCURRED[a]

MALES	FEMALES				
	E. longicollis	*E. texana*	*E. atrivittata*	*E. immaculata*	*E. valida*
E. longicollis	X	50 (2)[b]	33 (3)[c]	..	..
E. texana[d]	0 (12)	X	47 (15)	0 (15)	47 (15)
E. albida[e]	80 (15)	90 (10)	67 (18)	..	..
E. atrivittata	..	44 (18)	X	..	..
E. immaculata	..	89 (18)	..	X	67 (15)
E. valida	..	17 (12)	..	6 (18)	X

[a] Number of recording periods employed is indicated in parentheses following percentage value. Except as noted, three males of each species were used an equal number of times (4 to 6) to establish the number of periods indicated. Females were drawn indiscriminately from sexually and specifically isolated stocks before each period.

[b] Two males, each used for one period.

[c] Three males, each used for one period.

[d] One set of three males was tested with females of *E. valida* and *E. immaculata*, another with females of *E. longicollis* and *E. atrivittata*.

[e] One set of three males was tested with females of *E. longicollis* and *E. atrivittata*, and another set of two males was tested with females of *E. texana*.

to be appropriate since she immediately performed the act of tipping, whereupon the male mounted and initiated copulation. The elapsed time from introduction of the homospecific male to his turn off to the linear copulatory position was 60 seconds.

Further evidence of the superiority of homospecific courtship (or sexual exposure) in promoting copulatory behavior in females of species of the Albida Group was obtained on the last day of the series of heterospecific observations, when, following the observations of the day, males and females were paired homospecifically. The heterospecific combinations tested that day paired females of *E. atrivittata*, *E. immaculata*, and *E. valida* with males of *E. albida*, *E. atrivittata*, and *E. texana*, respectively. (Females of *E. albida* were not available; females of *E. valida* were paired with homospecific males not tested heterospecifically on the last day.) In the homospecific situation two of three pairs of *E. atrivittata*, one of three pairs of *E. immaculata*, and one of three pairs of *E. valida* copulated. All copulations were initiated within 30 minutes of exposure of the partners.

Four copulations were recorded in the course of observations of heterospecific pairs. These occurred from 16 to 24 days after the series was initiated. One involved a male of *E. albida* and a female of *E. atrivittata*; the others involved males of *E. immaculata* and females of *E. texana*. All lasted about three hours. In addition, in Nuevo León, Mexico, in 1960 we observed copulation between a male of *E. albida* and a female of *E. sublineata*. This copulation, which lasted at least an hour, took place in a cage containing several males and females of each species. In all heterospecific copulations that we have seen, the behavior of the adults during the precopulatory sequence and the extended period of coupling in the linear position seemed quite normal, except that in one of the bouts involving a male of *E. immaculata* the spermatophore was not inserted fully in the female.

Following heterospecific copulation, males and females were isolated individually and observed closely for two or three weeks. Males showed no ill effects. Two of the females of *E. texana*, however, were lethargic and would not eat for several days after copulation. Moreover, in both individuals the apex of the abdomen was noticeably swollen on the third day after copulation and remained so for a day or two. Two of the females of this species failed to lay eggs; the third female oviposited while in a moribund state 12 days after copulation. The female of *E. atrivittata* oviposited 21 days after copulation. The female of *E. sublineata* died a few days after copulation without ovipositing. None of the eggs obtained from females that had copulated heterospecifically developed embryos.

In addition to establishing that fully developed male courtship behavior may occur in at least many heterospecific combinations, the observations described above are of interest for their suggestion that the sexual stimulation presented by heterospecific males is relatively ineffective in inducing female copulatory behavior. These observations do not indicate whether males court homospecific females preferentially. This important question was investigated in the following experiment.

The experiment was performed in the laboratory in Urbana with adults of *E. segmenta* and *E. valida* collected at Fort Davis, Texas. The adults were isolated specifically and sexually for a week before tests were initiated. From the day before the experiment began until it ended, they were isolated individually. Tests were performed under the individual pairs system of observation.

The experiment entailed individual exposure of 10 males of each species to an equal number of homospecific and heterospecific females on alternate days for eight days. The order of presentation of females was balanced. Females were rotated among males in a Latin Square design. During the first four days of the experiment each female was paired, at random, with two homospecific and two heterospecific males. During the last four days the original pattern of pairings was repeated, insofar as possible. The period of daily exposure of the sexes to each other was 60 minutes. Courtship behavior was recorded for the first half of this period. Copulation was recorded if initiated during the 60-minute period.

When copulation occurred, the courtship data obtained during the period were discarded and both adults were removed from the experiment. In this case, and in cases of death, the places of the missing individuals were taken in subsequent periods by previously isolated adults held in reserve. However, scores for pairings involving replacements were not included in the analysis of the experiment. Excluding periods in which copulation occurred and those involving replacements, the experiment yielded 30 homospecific and 32 heterospecific scores for males of *E. segmenta* and 27 homospecific and 25 heterospecific scores for males of *E. valida.* Three males of *E. segmenta* had four scored pairings, three males had six, and four males had eight. Four males of *E. valida* had four scored pairings, one male had five, one male had seven, and three had eight.

The experiment involved eight main factors, each at two levels. These were (1) male species; (2) female species; (3) order of pairing (homospecific or heterospecific) for males, within species; (4) order of pairing for females, within species; (5) replication (four-day periods); (6) two-day periods within replicates; (7) days within two-day periods; and (8) nature of the pairing, whether homospecific or heterospecific, which was the factor of primary interest. Because of the nature of the design, each of these factors except that of replication is confounded with a two-factor interaction. Of particular importance in interpreting the results is the fact that male species is confounded with the interaction of two-day periods and order of pairing for females, and the nature of the pairing factor is confounded with the interaction of days and male species. It is, however, reasonable to assume that both interactions have a value of zero, and we will proceed with the analysis on that basis.

It should also be noted that the factors male species, nature of the pairing, and female species are related in such a way that each is confounded with the interaction of the other two. In the analysis male species and nature of the pairing are interpreted as main factors and female species as their interaction.

The results of the experiment were analyzed by multiple regression, which yielded, with suitable coding of factor levels, the equivalent of an analysis of covariance. Two dependent variables were analyzed: time in courtship (measured in units of one-half minute) and number of bouts of courtship. In the multiple regression analysis constants were fitted for all eight main factors mentioned and for all mutually

Table 16

HOMOSPECIFIC AND HETEROSPECIFIC COURTSHIP IN *E. SEGMENTA* AND *E. VALIDA*

Effects of the factors male species and nature of the pairing and their interaction on courtship time (in units of one-half minute) and number of courtship bouts, are expressed as partial regression coefficients obtained in multiple regression analysis in which these and several other variables (see text) were entered.

Variables	Partial Regression Coefficients (and *t*-values)[a]	
	Courtship Time	Bouts
Male species (*E. segmenta* = −1, *E. valida* = 1)	3.78 (2.912**)	1.87 (5.465**)
Nature of the pairing (heterospecific = −1, homospecific = 1)	7.86 (6.782**)	1.27 (4.150**)
Interaction (= female species, scored as for male species)	−1.66 (−1.381)	0.18 (0.570)
R^2	0.78	0.78
Error variance	125.92	8.78

[a] Degrees of freedom = 54.

orthogonal two-factor interactions not confounded with main factors. Additional constants were fitted for males and females of each species, for order of presentation of homospecifics and heterospecifics, and for a variable indicating whether females copulated during the experiment.

Constants (partial regression coefficients) for the factors male species, nature of the pairing, and their interaction are given in Table 16. Adjusted means for time in courtship and number of bouts of courtship are given in Table 17. Both the main and simple effects of nature of the pairing were significant. Males of both species courted homospecific females preferentially to a significant degree, as measured both by time in courtship and number of bouts. Males of *E. valida* courted longer and had more bouts than did those of *E. segmenta,* but in homospecific pairings the difference between males in courtship time was not significant. Lack of a significant interaction between male species and nature of the pairing may indicate that males of the two species do not differ appreciably in their levels of preference for homospecific females, but because of the confounding of the interaction with the factor of female species, other interpretations are possible.

We conclude from the experiment that the stimulus received by males from heterospecific females is inferior, either qualitatively or quantitatively or both, to that received from homospecific females. Never-

TABLE 17

COURTSHIP TIME AND NUMBER OF BOUTS

Time (in units of one-half minute) and number of bouts during 30-minute periods of homospecific and heterospecific pairing of adults of *E. segmenta*[a] and *E. valida*,[b] expressed as adjusted means per period.

MALE SPECIES	NATURE OF THE PAIRING: HOMOSPECIFIC	NATURE OF THE PAIRING: HETEROSPECIFIC	*t*
	COURTSHIP TIME		
E. segmenta	23.0	4.0	5.348**
E. valida	27.3	14.8	3.485**
t	1.241		
	BOUTS		
E. segmenta	4.8	2.6	2.682**
E. valida	8.9	6.0	3.086**
t	4.542**		

[a] Ten males, 62 periods.
[b] Nine males, 52 periods.

theless, the heterospecific stimulation is sufficient to release courtship behavior in the male and to sustain it for considerable periods of time.

In the course of the experiment and two others of a similar nature eight copulations occurred. Four were homospecific *E. segmenta* unions, two were homospecific *E. valida* unions, and two were heterospecific unions involving males of *E. segmenta* and females of *E. valida*. Since females were exposed regularly to homospecific males on alternate days, heterospecific copulation was quite unexpected. Presumably it indicates that sexual receptiveness in the female develops to a threshold level abruptly and more or less spontaneously.

ADULT ANATOMY

The present treatment is confined to characters of the external anatomy of the adult stage. Internal anatomical characters have not been investigated in any of the species of the group, either by us or others. Comparative studies of the anatomy of the larval stage are in progress, but the description and analysis of larval characters must be reserved for a separate work.

Although there is little doubt that the species constituting the Albida Group are closely related, it is presently impossible to frame a concise diagnosis of the group on the basis of adult anatomy. One of the more distinctive features of the group in the adult stage is the large size and rather robust appearance of the body. Body length, analyzed in Fig. 57 on the basis of 40 specimens of each species sampled randomly from available museum material, ranges in the group from 9 to 30 mm. Except in *E. sublineata,* however, few adults are less than 12 mm long.

The cuticle of the adult is black in all species of the group, but several strikingly different color patterns are produced by variation in the color of the clothing setae that densely cover almost the entire body. The antennae, labial palpi, legs, and last visible (eighth) abdominal sternum are sexually dimorphic to various degrees. The male genitalia are of the same type in all species; there are, in fact, no consistent differences between the species with regard to the form of the aedeagus.

The Albida and Atrivittata subgroups are characterized by very strong sexual dimorphism of the antennae (Fig. 54). In the male, segment I is denuded, greatly elongated, and expanded; in addition, it is strongly distorted by the presence of a large apical excavate area either dorsally (*E. atrivittata*) or laterally. Segment II is also denuded and distorted; in particular, it exhibits marked asymmetry in that its lateral surface is drawn out apically to form a distinct process. Except in *E. longicollis,* segments III and IV are noticeably modified in form, while in *E. texana* and *E. albida* segment III is also denuded.

Several of the antennal modifications of the male in these two subgroups are adaptive in the courtship act of antennal wrapping. In this act the antenna of the female is pressed into the excavation of antennal segment I of the male. The pressure is exerted by antennal segment II or II and III together; the lateral process of segment II is apparently a specific adaptation for this action. The functional significance of the great elongation of segment I is questionable. Elongation of this segment itself is not a specific adaptation for the act of wrapping since there are a number of species of *Macrobasis* in which this act does not occur but in which the male antennal segment I is at least as long as in the species of the Albida Subgroup. Certainly the elongation of segment I is useful to the performance of antennal wrapping inasmuch as it permits the male to manipulate the antennae of the female from a distance and also facilitates wrapping when the male is in the mounted position attempting genital insertion. As suggested previously, it is also possible that the great size of antennal segment I is of significance in visual display.

The Immaculata Subgroup is characterized by weak sexual dimorphism of the antennae. In the male, segments I and II are slightly elongated, the setae of the basal three or four antennal segments are sparser and shorter than in the female, and there is a tendency for the lateral surface of segment I to be flattened apically.

Interspecific Variation

Interspecific variation is summarized in Table 19 by means of a list of character state values for each species in 28 characters of adult anatomy which are defined and coded numerically in Table 18. In the selection of these characters two considerations were paramount. First, only those characters exhibiting intuitively obvious interspecific differences were considered. Second, care was exercised to avoid undue

TABLE 18

DEFINITION AND NUMERICAL CODING OF ADULT ANATOMICAL CHARACTERS

CHARACTER NUMBER	CHARACTERS AND CHARACTER STATES
1	Color of pronotum: pronotum consistently gray or tan (0); marked with black in about half of the individuals (1); nearly always well marked with black (2); consistently black except, commonly, for extreme margin (3).
2	Color of elytra: elytra consistently gray or tan (0); inconsistently marked with black, which, when present, varies considerably in extent (1); consistently well marked with black (2); consistently black (3).
3	Color of abdominal sterna: abdominal sterna consistently gray or tan (0); rarely marked with black (1); commonly marked with black (2); consistently black except for white posterior fringe (3).
4	Color of wing veins: light brown (0); medium to dark brown (1); black (2).
5	Color pattern of hind wing: unicolored (0); bicolored (1).
6	Color of discal cell of hind wing: colorless (0); light yellow (1); light tan (2); tan (3).
7	Body length measured from front of head to apices of elytra, in mm (Fig. 57).
8	Size (volume) of head relative to that of rest of body: normal (about average for the genus) (0); slightly larger than normal (1); decidedly enlarged (2).
9	Head shape: quadrate (0); subquadrate (1); subtriangular (2).
10	Shape of eye: narrow (0); intermediate (as in *E. albida*) (1); wide (2).
11	Convexity of eye: slight (0); moderate (as in *E. albida*) (1); strong (2).
12	Length of male antennal segment I as a percentage of total antennal length.
13–15	Same relationship as above for segments II, III, and IV, respectively.
16	Male antennal segments I and II denuded and distorted: no (0); yes (1).
17	Degree of expansion of male antennal segment I in the Atrivittata and Albida subgroups (Fig. 54): four classes are recognized, from least (0) to greatest (3).
18	Development of apicolateral process of male antennal segment II in the Albida Group: weak (0); moderate (1); strong (2).
19	Width of male antennal segment X as a percentage of length of that segment.
20	Color of cuticle of basal antennal segments: orange-yellow (0); black (1).
21	Color of cuticle of maxillary and labial palpi: yellow (0); brown (1); black (2).

TABLE 18 — Continued

CHARACTER NUMBER	CHARACTERS AND CHARACTER STATES
22	Degree of enlargement of male labial palpi (Fig. 55): slight (0); moderate (1); great (2).
23	Elytra: normal elongate form for species of *Macrobasis* (0); noticeably shortened (1).
24	Wings: reduced in size and not functional in flight (0); fully developed (1).
25	Male fore tibiae: lacking one spur (0); with both spurs present (1).
26	Hind tibial row of teeth (comb): absent (0); present (1).
27	Basal piece of male gonoforceps: as wide as long (0); wider than long (1).
28	Male gonostyli (Fig. 56): slender, distinctly tapered (0); intermediate (1); heavy, not much tapered (2).

emphasis on any single type or functional complex of characters. In particular, several distinctive features of body proportions in *E. valida* were not considered because of their obvious functional association with loss of flight. With respect to the nature and number of characters and the precision of specification of character states (mainly on an ordinal scale), the present description meets contemporary standards employed in taxonomic revisionary studies of Meloidae. For the most part these characters require no explanation. The values entered in Table 19 for character 7 are the means of the samples analyzed in Fig. 57. Values for the relative length of antennal segments (characters 12-15, 19) are means of samples of 10 specimens of each species. *Epicauta valida* was not scored for character 23 (length of elytra) since in this species, as opposed to *E. texana*, shortening of the elytra is clearly related functionally to atrophy of the hind wings, as it is in many other flightless Meloidae.

The phenetic relationships of the species in the characters scored in Table 19 are analyzed in a later section of this work.

Intraspecific Variation

There is marked intraspecific variation in body size of the adult in all species of the group and in the color of the clothing setae of the body in all species except *E. longicollis* and *E. texana*. In addition, there is great instability in the degree of development of the hind wings

Table 19

ANALYSIS OF INTERSPECIFIC VARIATION IN ADULT ANATOMICAL CHARACTERS DEFINED AND CODED IN TABLE 18

Character Number	Species							
	atrivittata	*longicollis*	*texana*	*albida*	*sublineata*	*immaculata*	*segmenta*	*valida*
1	2	0	0	2	1	0	3	3
2	2	0	0	1	1	0	3	3
3	2	0	0	2	2	1	3	3
4	2	1	0	0	0	1	1	1
5	0	1	0	0	0	0	0	0
6	0	3	0	1	2	3	3	2
7	24.0	20.1	17.4	20.9	15.3	17.2	18.6	19.2
8	0	0	0	0	2	0	0	1
9	0	2	2	2	1	1	1	2
10	2	0	0	1	1	1	1	1
11	2	1	1	1	1	1	1	0
12	38.4	27.8	31.0	27.9	16.2	15.7	18.3	17.6
13	6.1	6.2	8.5	7.8	8.1	10.1	8.1	7.3
14	3.0	6.7	4.1	4.1	8.6	9.1	9.1	8.3
15	4.6	6.7	7.8	5.7	8.1	8.6	8.6	8.3
16	1	1	1	1	0	0	0	0
17	3	0	1	2	NC[a]	NC	NC	NC
18	2	0	1	1	NC	NC	NC	NC
19	43.4	38.7	34.4	35.7	21.7	27.7	30.3	31.2
20	1	1	0	0	1	1	1	1
21	2	1	0	0	0	1	2	2
22	2	1	1	1	0	0	1	0
23	0	0	1	0	0	0	0	NC
24	1	1	1	1	1	1	1	0
25	0	0	1	1	1	1	1	1
26	0	1	1	0	0	0	0	0
27	1	1	1	1	0	1	1	1
28	2	1	1	0	0	1	1	1

[a] NC indicates that comparison is either not possible or not appropriate.

of *E. valida.* Variation in these characters is described in the present section.

SIZE

Ranges and coefficients of variability of body length in samples of 40 specimens for each of the species of the group are given in Fig. 57. There is no significant pattern of geographic variation in this character in any of the species.

The tendency, shown in Fig. 57, of the coefficient of variability to vary inversely with the mean of body length may be of interest from an ecological viewpoint and deserves further investigation. Results of rearings of all species of the group indicate that variation in the amount of food available to individual larvae is the dominant factor influencing intraspecific variation in body size of the adult insect. Further, they establish that for optimal expression of the genetic potential of size, larvae must in nature have available a food supply comparable in quantity to that provided by the large egg pods of the acridid *Melanoplus differentialis* (Thomas). Within limits, of course, larvae are capable of completing development in egg pods of smaller size, but the probability of success undoubtedly decreases with egg pod size to the minimum point at which development is no longer possible. It is reasonable to assume that within any geographic area, species of the Albida Group in general utilize egg pods of the larger species of grasshoppers and that, further, egg pods suitable for development of larvae occur in relatively low population density as compared with the pods of smaller grasshoppers. If this is the case, then the observed relationship between mean body size and variance might be explained on the basis that an increase in the body size of a species, as determined by genetic factors, tends to restrict the lower limit of size of the food supply that can be utilized successfully by the species. It is interesting to note that the hypothesis would predict that distributions of body size would be skewed to the left in the larger species of the group, which may be observed in Fig. 57 for the largest three species. It does not, however, explain the skewing to the right of the distribution of *E. sublineata*, nor does it account for the extreme variability of that species, unless, of course, one wishes to invoke a threshold effect at the minimum of the size range of the group. The latter alternative is not particularly attractive, however, since several other species of *Epicauta* comparable in mean body length to *E. sublineata* occur within the geographic range of that species without exhibiting unusual variability.

DEVELOPMENT OF THE HIND WINGS IN *EPICAUTA VALIDA*

Normal, functional hind wings, as illustrated for *E. longicollis* and *E. segmenta* in Fig. 58, are consistently present in all species of the Albida Group except *E. valida*. In repose fully developed wings are folded both laterally and transversely (at the apex) in order to be accommodated beneath the elytra. When unfolded and directed posteriad, they attain or exceed the last visible (eighth) abdominal tergum.

In *E. valida* the hind wings are apparently always present but are

TABLE 20

VARIATION IN THE DEGREE OF ATROPHY OF THE HIND WINGS OF *E. VALIDA*

GEOGRAPHIC REGION	NUMBER OF ABDOMINAL TERGA COVERED BY WINGS[a]						TOTAL NUMBER OF SPECIMENS
	1–2	2½	3	3½	4	4½–5	
Northern (South Dakota to Oklahoma)	12	46	29	38	45	6	176
Southern (Texas and New Mexico)	16	176	30	3	5	1	231

[a] $\chi^2 = 17.08$, df $= 5$, P $< .005$.

atrophied to the extent that they no longer serve as functional organs of flight. Like many vestigial structures, they vary greatly in size and shape. Even when best developed they extend only to the fourth or fifth abdominal tergum and can easily be covered by the elytra without folding; in addition, they are highly distorted in form and lack much of the venation. In their least developed form they are reduced to tiny membranous tabs no longer than the first abdominal tergum. (Wings of near minimal, intermediate, and near maximal degrees of development are shown in Fig. 58.) Table 20 demonstrates a significant difference between northern and southern populations of *E. valida* in the mean extent of atrophy of the wings.

With very few exceptions (*Meloetyphlus fuscatus* Waterhouse and species of *Gynapteryx*) flightless Meloidae lack the wings entirely, and on this basis it is probably safe to conclude that the hind wings of *E. valida* are not now subjected to positive natural selection. Consequently, one can conjecture that flightlessness evolved initially in the southern part of the range of *E. valida* and subsequently spread northward. This is an interesting possibility, since within the area of sympatry of *E. valida* and its close relative *E. segmenta* the latter species is apparently the more successful in the south. Thus one is inclined to wonder whether the evolutionary loss of flight in *E. valida* was in some manner influenced by competitive interaction with *E. segmenta*. Unfortunately, we have no understanding at present of the ecological conditions under which flight ceases to have positive selective value in Meloidae.

The wing of a presumed hybrid between *E. valida* and *E. segmenta* from New Mexico is illustrated in Fig. 58. This wing, which lacks folding, has a value of 6½ on the scale used in Table 20. The discovery of this presumptive hybrid raises the question of whether the maintenance of vestigial wings in *E. valida* reflects introgression from *E. segmenta*. It should be noted, however, that there is no evidence of introgression of *E. valida* in *E. segmenta*.

VARIATION IN COLOR

This variation has been analyzed largely in terms of frequency distributions of adult specimens in arbitrarily defined classes or categories, expressing either degree of intensity of shading of a general or basic color or, in some cases, progressive states of development of black markings. In using the term "black markings" with reference to the elytra, we exclude specifically the immediate base of the elytra, which is partially or entirely black in all species of the group.

Epicauta atrivittata. This species shows a very striking and handsome pattern of alternate black and light gray areas. The extent of black areas on the pronotum and abdominal sterna varies noticeably. At one extreme the pronotum is gray except for a pair of heavy longitudinal black lines on the disk, and each of the abdominal sterna is marked with a pair of obliquely transverse black bands. At the other extreme the pronotum and individual abdominal sterna are solid black except for a narrow fringe of light gray setae. The elytra in this species are each marked with a pair of heavy black vittae which fuse near the elytral apex. In specimens marked with black on the pronotum and abdomen, the elytral vittae tend to be wider than usual. There is no appreciable geographic component in any of the variation.

Epicauta albida. The basic color in this species varies from olive to yellow. The vast majority of specimens examined can be described as tan or olive-tan. The variation does not seem to be at all geographic, although we have not analyzed it in detail.

Conspicuous black markings occur on the pronotum of about 95 per cent of the specimens examined and on the abdomen of about 98 per cent. In addition, about 13 per cent of the specimens have one or two fine black vittae on each of the elytra. In order to analyze variation in the development of the markings, we scored each of the available specimens on each of the following three scales:

Pronotal markings: absent or barely discernible under magnification (0); represented by a pair of fine longitudinal lines easily visible to the naked eye (1); represented by a pair of heavy longitudinal dashes (2).

Elytral markings: absent (0); represented on each elytron by a fine black vitta which is aligned with and sometimes joins the sutural spot at the immediate elytral base (1); each elytron with an additional fine vitta which is aligned with and sometimes joins the humeral basal spot (2).

Table 21

PERCENTAGE DISTRIBUTION OF SPECIMENS OF *E. ALBIDA* IN COLOR CLASSES

(classes defined in text)[a]

Body Region	Classes		
	0	1	2
Pronotum	5.3	22.4	72.3
Elytra	87.1	9.7	3.2
Abdomen	2.0	20.5	77.5

[a] N = 1172.

Abdominal markings: absent or at most represented by faint transverse streaks on the fourth or fifth sternum (0); represented on the second to fifth sterna by a narrow transverse band, which is divided on the midline (1); represented on these sterna by wide bands which nearly or actually fuse with each other on the midline (2).

The color variation is summarized in Table 21.

Segregation of specimens by major political division (states) failed to reveal significant geographic variation in the strength of development of any of the markings. Further, there is apparently little, if any, correlation between degrees of development of markings on the three areas of the body. Among all specimens scored, 51.6 per cent exhibited the combination 3-1-3 (pronotal, elytral, and abdominal values, respectively), 7.8 per cent were scored 3-2-3, 8.2 per cent 3-1-2, 12.1 per cent 2-1-3, 8.4 per cent 2-1-2, and the remaining 11.9 per cent were distributed among 14 additional score combinations.

Epicauta sublineata. The pronotum and abdomen have black markings similar in form to those of *E. albida* and comparable in their range of variation. The elytra vary from uniform tannish gray to uniform black. Intermediates exhibit a variety of complex patterns of gray and black setae. Color classes which we have recognized within the spectrum of elytral variation are defined below. The distribution of specimens in these color classes is given in Table 22. The development of black coloration on the elytra seems to be independent of that on other areas of the body. As in the species already discussed, none of the characters of color seems to vary geographically in a systematic way.

The elytral color classes are:

Uniform tannish gray (0); each elytron faintly marked with two fine vittae in medial half, these fusing near apex at a point marked by a diffuse black spot

TABLE 22
PERCENTAGE DISTRIBUTION OF SPECIMENS OF *E. SUBLINEATA* IN COLOR CLASSES
(classes defined in text)[a]

Classes							
0	1	2	3	4	5	6	7
2.4	11.5	17.7	19.8	16.0	14.9	8.3	9.4

[a] N = 288.

(1); each elytron with two additional fine black vittae in lateral half (these fusing with the others near the apex), black spot at point of fusion somewhat enlarged (2); elytral vittae more distinct, black subapical area enlarged, extending anteriad to near middle of elytron in lateral half, gray area of disk darkened by an admixture of black setae (3); diffuse black marking of each elytron extending to base in lateral half, gray area much darkened, fine vittae still clearly discernible (4); elytra black except for light gray apex and a dark gray longitudinal discal area, fine vittae largely obscured (5); elytra black except for apical margin (6); elytra uniformly jet black (7).

Epicauta immaculata. Through most of the range of this species the body lacks black markings except for those at the immediate base of the elytra. In the northeastern part of the range (Iowa to Ohio and West Virginia) the individual clothing setae are white, translucent, and relatively short. Against the black of the body surface they produce a uniform gray coloration. To the west the setae have a yellow cast and are more opaque. Moving southward to New Mexico and Texas, the yellow color tends to be intensified and darkened; in addition, the setae become longer, with the result that they more effectively mask the color of the body surface. At an extreme the general body color is deep brownish yellow or orange.

In the southeastern United States, on the other hand, the clothing setae remain translucent and relatively short, but there is a strong tendency for them to become piceous on large areas of the head, pronotum, and elytra, and the general color of these areas consequently varies to a nearly pure black. Moreover, in extreme cases the abdominal sterna develop transverse black markings suggestive of those in *E. albida* and many specimens of *E. sublineata*.

In Table 23 we have analyzed variation in the general color of the discal portion of the elytra, as seen without magnification. Nine classes are employed, and the linear ordering of classes is in part arbitrary. In classes 0 to 2 the general color is influenced to a considerable extent by the underlying black cuticle. In classes 3 to 8 the setae are

TABLE 23

PERCENTAGE DISTRIBUTION OF SPECIMENS OF *E. IMMACULATA* IN COLOR CLASSES

(classes defined in text)

GEOGRAPHIC REGION	CLASSES									N
	0	1	2	3	4	5	6	7	8	SPECIMENS
Mississippi, Alabama	5.9	94.1								17
Georgia, Tennessee	68.4	31.6								38
West Virginia, Kentucky, Ohio		100.0								28
Indiana, Illinois, Iowa		100.0								151
Missouri, Arkansas		64.1	30.8	5.1						39
South Dakota, Nebraska, Colorado, Kansas		2.8		22.2	21.3	37.0	5.2	11.1	0.4	478
Oklahoma, Texas, Louisiana		5.7		27.0	14.3	33.7	4.2	13.0	2.1	700
New Mexico, Arizona				5.0	1.3	69.4	15.3	7.4	1.6	379
Coahuila						16.7		50.0	33.3	6
Laboratory hybrids										
F_1 generation						100.0				25
F_2 generation		27.5		38.0	13.8	10.3	6.9	3.4		29

sufficiently long and opaque that the cuticle has little or no effect on the general color.

The definitions of classes of color are:

Black (setae piceous, translucent) (0); gray (setae white, translucent) (1); yellowish gray (setae light yellow, moderately translucent) (2); light yellow (3); yellow (4); olive-yellow to brownish yellow (5); dark golden yellow (6); dark brownish yellow (7); orange (8).

Evidence that color variation in *E. immaculata* involves genetic differences between populations is provided by the results, summarized at the bottom of Table 23, of a laboratory cross between a Texas male of class 8 and an Illinois female of class 1 and a subsequent cross between two of their progeny. All F_1 individuals fall into class 5. In the F_2 generation phenotypes ranged from class 1 to class 7, indicating multifactorial inheritance.

Epicauta segmenta and *E. valida*. It will be convenient to treat these species jointly. They have essentially the same color pattern: adults of both are black except, commonly, for fringes of white setae on the thoracic sclerites, coxae, and the abdominal sterna. Excluding the pronotal fringe of *E. segmenta*, the amount of white on one part of the body is rather closely correlated with that on another. We will limit analysis to the pronotum, mesepimera, and abdominal sterna. The classes recognized are as follows:

Pronotal fringe: entirely white or with only a few, very sparsely distributed black setae (0); darkened, consisting of a good mixture of white and black setae (1); lacking, or represented by a few, very sparsely distributed white setae (2).

Mesepimeral fringe: same classes as above.

Abdominal fringes: In this character specimens were scored by counting the number of sterna having a fringe of setae at least 2 mm wide on the midline of the abdomen.

The data for pronotal and mesepimeral fringing are summarized in Table 24. The development of the pronotal fringe is nearly constant in *E. segmenta*, while in *E. valida* the means of class scores ranged from 1.1 in the north (Nebraska and South Dakota) to 0.5 or 0.6 in the south (parts of Texas and in New Mexico). Mesepimeral fringing in *E. segmenta* exhibits an irregular trend for decreased development from north to south. In *E. valida* the trend is in the opposite direction, paralleling that of pronotal fringing.

Opposite trends in the two species are seen also in the character of abdominal fringing, analyzed in Fig. 59. Although the functional significance of fringing of the sclerites in the two species is unknown, it is probable that we are dealing here with a case of sympatric character divergence, which in some way relates to interaction between

TABLE 24

VARIATION IN THE DEVELOPMENT OF WHITE FRINGING

Fringing of the pronotum and mesepimera in *E. segmenta* and *E. valida*; variation expressed as means of samples of adults scored in classes defined in the text.

GEOGRAPHIC REGION	*E. segmenta*			*E. valida*		
	PRONOTAL FRINGE	MESEPIMERAL FRINGE	N SPECIMENS	PRONOTAL FRINGE	MESEPIMERAL FRINGE	N SPECIMENS
South Dakota	0.02	0.00	44	1.10	1.60	17
Nebraska	0.00	0.00	10	1.10	1.30	30
Kansas, Oklahoma	0.04	0.02	81	0.50	0.60	137
Northern Texas	0.00	1.40	33	0.30	0.30	3
Central Texas	..	..	..	1.50	1.20	26
Southwest Texas	0.00	1.90	217	0.50	0.90	221
New Mexico	0.00	1.90	19	0.60	0.80	38
Arizona	0.00	1.90	646	..	..	..
Sonora, Sinaloa	0.00	2.00	20	..	..	..
Chihuahua	0.00	1.70	10	..	..	..
Durango, Coahuila	0.00	0.80	9	..	..	..

populations of the two species. Particularly instructive in this regard, we believe, is the phenotype of the population of *E. valida* in central Texas. This population, which is geographically isolated, deviates from the general trend of variation in pronotal, mesepimeral, and abdominal fringing in resembling more closely than one would anticipate northern *E. valida* and southern *E. segmenta*. Since central Texas is the only area where *E. valida* is not accompanied by *E. segmenta*, the implication is that the absence of the latter species permits *E. valida* to approach it phenetically.

ANALYSIS OF INTERSPECIFIC RELATIONSHIPS

Phenetic Relationships

METHOD OF ANALYSIS

The phenetic relationships of the species of the Albida Group in the adult stage were analyzed on the basis of characters of both external anatomy and sexual behavior. The general method of the analysis is described by Sokal and Sneath (1963). These authors recommended a z-score transformation as a means of standardizing characters before the computation of measures of resemblance. This transformation, which expresses character state values in units of standard deviation, permits the variance of the character to influence directly the contribution of that character to the estimate of overall similarity. However, it is intuitively more attractive and, we believe, more in keeping with traditional taxonomic practice to interpret similarity between taxa in a character simply as a function of the distance relative to the range, rather than the variance, of the character.

The average distance coefficient (d) was used as a measure of resemblance. Each character was rescaled so as to range from 0 to 1; the maximum value of d is therefore 1. The unweighted pair-group method with simple arithmetic averages was used for cluster analysis of matrices of distance coefficients.

Separate analyses were performed on the anatomical and behavioral data before they were combined for the final analysis. The anatomical data are the scores of the species in 28 characters recorded in Table 19. The behavioral data consist of character state scores (coded numerically) of the species in 11 of the 12 characters listed in Table 14. Rate of antennal pressing was omitted because of the previously mentioned relationship, in species of the Immaculata Subgroup, between this character and the presence or absence of antennal touching.

RESULTS

Matrices of distance coefficients obtained in the analyses are given in Tables 25-27. Phenograms (diagrams of phenetic relationships) resulting from the cluster analysis of coefficients based on anatomical characters alone and combined anatomical and behavioral characters were identical in pattern (see Fig. 60). The phenogram based on behavioral characters differed in that *E. texana* joined *E. longicollis* before connecting with *E. albida,* and *E. atrivittata* clustered with the species assigned to the Albida Subgroup before the cluster formed by those species was united with the Immaculata Subgroup.

In all three analyses the Immaculata Subgroup emerged as a clearly differentiated and relatively homogeneous taxon. Within the subgroup a consistent division is indicated between *E. segmenta* and *E. valida,* which are more closely related phenetically than any other pair of species of the entire group, and *E. sublineata* and *E. immaculata,* whose mutual relationship is considerably closer than the average relationship of either species to *E. segmenta* and *E. valida.*

When behavioral or combined characters are considered, *E. longicollis, E. texana,* and *E. albida* form a cluster which is maximally cohesive in the sense that all relationships within it are closer than the closest relationship of an included species to an outsider. However, unlike the Immaculata Subgroup, which possesses this property in all three analyses, the cluster loses much of its cohesiveness when only anatomical characters are considered, since on this basis *E. longicollis* is more similar to *E. immaculata* than to *E. albida,* and *E. albida* in turn is more similar to three of the four species of the Immaculata Subgroup than to *E. longicollis.*

While *E. atrivittata* is obviously more similar to *E. texana, E. longicollis,* and *E. albida* than are the species of the Immaculata Subgroup in behavioral characters, the similarity is not strong enough to offset the greater similarities of *E. texana, E. longicollis,* and *E. albida* to species of the Immaculata Subgroup in anatomical characters. On the

TABLE 25

MATRIX OF AVERAGE DISTANCE COEFFICIENTS, BASED ON 11 CHARACTERS OF SEXUAL BEHAVIOR

	longicollis	*texana*	*albida*	*atrivittata*	*sublineata*	*immaculata*	*segmenta*	*valida*
longicollis	.000							
texana	.000	.000						
albida	.378	.522	.000					
atrivittata	.655	.707	.707	.000				
sublineata	.671	.687	.898	.810	.000			
immaculata	.671	.687	.898	.810	.000	.000		
segmenta	.632	.666	.882	.791	.373	.373	.000	
valida	.632	.666	.882	.791	.373	.373	.000	.000

TABLE 26

MATRIX OF AVERAGE DISTANCE COEFFICIENTS, BASED ON 28 CHARACTERS OF ADULT ANATOMY

	longicollis	*texana*	*albida*	*atrivittata*	*sublineata*	*immaculata*	*segmenta*	*valida*
longicollis	.000							
texana	.486	.000						
albida	.520	.388	.000					
atrivittata	.618	.673	.537	.000				
sublineata	.617	.604	.509	.740	.000			
immaculata	.513	.547	.500	.669	.372	.000		
segmenta	.579	.646	.495	.576	.447	.353	.000	
valida	.632	.654	.538	.661	.477	.454	.295	.000

Table 27

MATRIX OF AVERAGE DISTANCE COEFFICIENTS, BASED ON 39 CHARACTERS OF ADULT ANATOMY AND SEXUAL BEHAVIOR

	longicollis	*texana*	*albida*	*atrivittata*	*sublineata*	*immaculata*	*segmenta*	*valida*
longicollis	.000							
texana	.434	.000						
albida	.495	.430	.000					
atrivittata	.625	.682	.587	.000				
sublineata	.626	.627	.632	.757	.000			
immaculata	.542	.586	.627	.705	.320	.000		
segmenta	.588	.651	.618	.633	.429	.358	.000	
valida	.632	.657	.647	.695	.452	.434	.253	.000

contrary, the effect of adding behavioral characters to the anatomical ones is to increase the average distance between *E. atrivittata* and the rest of the species of the group.

The relationships of the species of the group in the matrix of distance coefficients based on combined anatomical and behavioral characters are quite straightforward and therefore suffer little distortion as a result of clustering to form the phenogram. The correlation of original d values with cophenetic values obtained from the phenogram is .97.

Phylogenetic Relationships

The phenetic relationships of the species of the Albida Group shown in Fig. 60 are fully congruent with inferences we have made concerning the cladistic relationships. At the present time the available information does not justify a detailed exposition of the phylogeny of the group, but there is no inconsistency between the phenetic relationships expressed in Fig. 60 and those inferences that do seem justified by the data.

In order to trace the phylogeny of the species of a group, one has to specify for one or more characters those states that are primitive, i.e., were present in the presumed common ancestor of the group. In the absence of critical paleontological and ontogenetic evidence it is necessary to infer ancestral characteristics on the basis of comparative studies. In the present case it is reasonable to assume that character states shared by the Fabricii and Albida groups are probably primitive for the species of both groups. Anatomically and behaviorally the Albida Group is most similar (among the groups of *Macrobasis* studied behaviorally) to the Fabricii Group. Further, the two groups are alike in occupying the northern part of the range of the subgenus and are the only groups that have entered the Great Plains area. Assuming that they are closely related phylogenetically, continuation of the present argument requires only that we establish a reasonable basis for concluding that (1) the groups represent a separate line of *Macrobasis,* and (2) the Fabricii Group was not derived from the Albida Group itself.

Evidence for these conclusions is found in the relationship between the pattern of male courtship behavior and the consistency and strength of development of the hind tibial comb of the male in the subgenus *Macrobasis*. In all species of the Diversicornis, Uniforma, and Funesta groups studied behaviorally, the comb is consistently present in well-developed form, as it is in the vast majority of species of the subgenus.

In the three groups named, the orientation phase of courtship is short, serving merely as a preliminary to an extended mounted phase in which the male rides atop the female in the manner described in the introductory account of systematics. During the mounted phase the comb seems to serve an important function in assisting the male in maintaining the riding position. In addition, in at least one species it apparently facilitates tactile stimulation of the female.

Courtship behavior in the Fabricii Group is deviant in that the orientation phase is prolonged, being often comparable in length to that of the Albida Group. The male mounts the female and rides periodically but only for brief periods (at most a minute or two). Furthermore, in contrast to the condition in the Diversicornis, Uniforma, and Funesta groups, riding in the Fabricii Group entails continuous effort by the male to establish genital contact with the female. Thus the mounted phase has many of the qualities of the act of abortive mounting in the Albida Group.

As previously described, the hind tibial comb is frequently absent in males of the Fabricii Group and at best is poorly developed. One may infer that the comb has lost its selective value in the group as a result of an evolutionary reduction in the length and importance of the mounted phase of courtship. Similarly, lack of the comb in most of the species of the Albida Group is presumably explicable on the basis that males do not perform the act of riding as such. As a matter of fact, since there is no fixed riding position during courtship in any of the species of the group, it is difficult to account for the retention of the comb by males of two of the species (*E. longicollis* and *E. texana*), except possibly on the basis that the comb has functional value during the precopulatory sequence. We have not, however, noted any difference between males which have and those which lack the comb with regard to the positioning of the hind legs during that sequence.

We are now in a position to characterize the common ancestor of the Fabricii and Albida groups and then to conjecture on the pattern of phylogeny within the latter group. We may infer with some confidence that the ancestor exhibited strong structural sexual dimorphism of the antennae, with enlargement of segments I and II; that the male had only a single fore tibial spur; that the hind tibial comb was present in the male; that the antennae and palpi were black or brown in color, or at least no different in color than the female counterparts; and, obviously, that adults possessed fully developed hind wings. With regard to characters of sexual behavior, we postulate that the ancestor closely resembled the Fabricii Group. During the extended orientation phase the male showed a strong tendency to orient on the head of the female and from this position periodically reached forward with the antennae to manipulate those of the female and perhaps (as in the modern *E. fabricii*) to press the antennae on the body of the female. The antennal manipulation had possibly something of the quality of low intensity wrapping in the Albida Group. Ancestral males presumably rode in a stereotyped manner, as do modern males of groups other than the Albida Group, holding the female with the fore and hind legs and extending the middle legs laterad.

In the evolution of the Albida Group from the common ancestor with the Fabricii Group, antennal manipulation was elaborated into full whipping and wrapping, and the male antennae developed concomitant specializations. In addition, the mounted phase of courtship was finally reduced to a sporadic, very brief, and relatively unstereotyped attempt of the male to initiate copulation forceably.

Under the present interpretation of phylogeny the Immaculata Subgroup is to be regarded as a monophyletic taxon derived from a line in which antennal whipping and wrapping declined in importance as elements of courtship display and were eventually supplanted by the act of antennal pressing. Whether this act may be traced back to the common ancestor of the Fabricii and Albida groups or arose independently in the Immaculata Subgroup by emancipation from the precopulatory sequence is highly problematical. Within the subgroup the act of touching was presumably a specialization of the ancestor of *E. sublineata* and *E. immaculata*. We have already implied that this act may have developed at the expense of pressing.

At the present time it is not possible to ascertain, by phylogenetic reasoning, the point of derivation of the Immaculata Subgroup. Consequently, the relationships of the subgroup indicated in the phenogram (Fig. 60) must be taken as the best approximation.

Among the species of the Albida Subgroup, *E. texana* and *E. albida* are specialized with respect to the color of the antennae and palpi and the possession of two spurs on each of the fore tibiae.

Strict phylogenetic interpretation of the phenogram implies either that the ancestor of the Albida Group had a striped pattern which was subsequently lost on several occasions, or that *E. atrivittata, E. albida,* and *E. sublineata* converged in characters of color patterning. In the absence of any knowledge of either the physiology or functional significance of striped coloration in this group, it is quite impossible to choose between these alternatives.

Classification of the Group

Early in the present study, on intuitive grounds, we divided the species of the Albida Group into two subgroups. The Immaculata Subgroup of that classification had the same composition as it does in the present work except that we initially were not aware of the specific distinctness of *E. segmenta* and *E. valida*. The Albida Subgroup, as defined then, included its present constituents as well as *E. atrivittata*. As a result of our study, however, it would appear that *E. atrivittata* should be placed in a subgroup by itself. In the first place, if the pattern of branching of lines in Fig. 60 does indeed represent the phylogeny of the species of the Albida Group, incorporation of *E. atrivittata* in either the Albida or Immaculata subgroups yields a polyphyletic taxon. In addition, we note that while males of *E. atrivittata* and those of the Albida Subgroup perform antennal whipping and wrapping in courtship and have similar antennal modifications, they otherwise have little in common that is not shared by one or more species of the Immaculata Subgroup.

For the present we propose to maintain the division of the Albida Group into three subgroups, as outlined in Table 3. At the same time, we recognize that with the integration of characters of larval anatomy and bionomics with those described and analyzed in this work, it is not unlikely that some modification of the classification will be required.

SPECIFIC IDENTIFICATION, SYNONYMY, AND LOCALITY RECORDS

Identification

The following key, based in part on characters utilized by Werner (1945), is provided as a convenience in the specific identification of adults of the Albida Group. Reference to Tables 18 and 19, the photographs constituting Figs. 19 to 50, and the line drawings in Figs. 54, 55, 56, and 58 will facilitate this process. Except for the fact that *E. segmenta* and *E. valida* are not differentiated in it, Werner's (1945) key is adequate for the identification of most specimens of species assigned to the group.

Specific Key to Adults

1. Body (including elytra) entirely black except, usually, for white fringing on pronotum, metathorax, coxae, and abdominal sterna 2
   If elytra entirely black, rest of body largely gray or tan 3
2. Hind wings fully developed, folded in repose, extending beyond apex of abdomen when unfolded; middle coxae well separated from hind coxae .... *E. segmenta*

Hind wings partially atrophied, not folded in repose, at most covering first five abdominal terga; middle and hind coxae approximate; body surface less sleek than in above species. . . . *E. valida*

3. Cuticle of maxillary and labial palpi yellow; basal antennal segments yellow or orange, paler than distal ones. 4

Cuticle of maxillary palpi black, of labial palpi black or yellow; basal antennal segments piceous or black, not paler than distal ones. 5

4. Pronotum and abdominal sterna immaculate gray or tan; discal cell of hind wing colorless; male antennal segment I relatively slender; male hind tibiae with an apical comb (row of teeth). Arizona to western Texas and Durango. . . . . *E. texana*

Almost invariably with some black marking on pronotum or abdominal sterna, or both; male antennal segment I more strongly expanded; male hind tibiae lacking an apical comb. Wyoming and Nebraska to New Mexico and Tamaulipas. . . . . *E. albida*

5. Elytra each with two wide, well-defined, black vittae which meet subapically; head, pronotum, and under surface of thorax with extensive, well-defined, black markings; male antennal segment I strongly modified; female antennal segment I as long as following three segments combined. . . . . *E. atrivittata*

If elytra marked with black (apart from extreme base), under surface of thorax gray, without contrasting pattern; abdominal sterna rarely as above; male antennal segment I not, or not so strongly, modified as above; female antennal segment I shorter than following three segments combined. 6

6. Cuticle of labial palpi yellow; head, pronotum, elytra, under surface of thorax, or abdomen, or a combination of these regions, generally marked with black; antennae slender; head noticeably enlarged. Southcentral Texas to Tamaulipas. . . . . *E. sublineata*

Cuticle of labial palpi black; body, apart from extreme base of elytra, immaculate gray or tan (exceptions in *E. immaculata* in the southeastern United States, well outside the geographic range of *E. sublineata*). 7

7. Base of tarsal segments of fore and middle legs clothed dorsally with gray or tan setae; each elytron with a well-defined black spot adjacent to scutellum; male basal antennal segments modified; female antennae heavy. . . . . *E. longicollis*

Tarsal segments entirely black-setate; male antennae not modified; elytra lacking scutellar spots; female antennae relatively slender, especially distally. . . . . *E. immaculata*

Synonymy and Locality Records

Epicauta atrivittata (LeConte)

Lytta atrivittata LeConte, 1854:224. [Type locality: "San Diego trip"; holotype, male, in the Museum of Comparative Zoology, Harvard University.] LeConte, 1853:39.

Macrobasis atrivittis [*sic*], LeConte, 1863-66:68 (*lapsus calami*).

Macrobasis atrivittata, Horn, 1873:90. Snow, 1907:186. Fall and Cockerell, 1907:209.

Epicauta atrivittata, Werner, 1945:509, fig. 24. Vaurie, 1950:35. Dillon, 1952:402. Selander, 1954:85. Werner, 1954:25. Werner, Enns, and Parker, 1966:36, fig. 73.

LOCALITY RECORDS AND SPECIMENS EXAMINED

MEXICO *Chihuahua:* 20 mi. SW Camargo, 1; 11 mi. S Camargo, 1; 3 mi. N Camargo, 25; 70 mi. NNW Casas Grandes, 1; 10 mi. S Delicias, 16; 10 mi. N Jiménez, 1; Villa Ahumada, 1. *Coahuila:* 12 mi. W La Rosa, 36. *Durango:* Tlahualilo [de Zaragoza] (Werner, 1945).

UNITED STATES *Arizona:* Douglas, 42; Gambles, 4 (not found); McNeal, 1; Sulphur Spring Valley, 2; Willcox, 1; 3 mi. S Willcox, 1; 6 mi. SE Willcox, 105. *New Mexico:* Alamogordo, 1; Albuquerque, 26; Artesia, 1; 5 mi. W Carlsbad, 3; Eddy County, 2; Las Cruces, 13; Las Vegas, 3; Lordsburg, 1; Lumberton, 3; Malpais Lava Beds, 6 mi. NW Carrizozo, 1; Organ, 1; Roswell, 2; San Marcial, 1; Santa Fe, 1; Socorro, 6; Whites City, 4. *Texas:* Alpine, 6; Big Bend National Park, 37; Big Springs, 1; Brewster County, 1; Burnet County (Dillon, 1952); Chisos Mountains, 12; Culberson County, 1; Davis Mountains, 4; 9 mi. SW Dell City, 1; Del Rio, 7; 14 mi. SE Dryden, 3; El Paso, 5; Fort Stockton, 5; Hueco Mountains, 1; 8 mi. E Hueco, 3; Jeff Davis County, 1; Kingsville, 1; 15 mi. NW Langtry, 2; Lozier Canyon, Terrell County, 3; Marathon, 10; 12 mi. S Marathon, 35; Marfa, 12; Pecos, 1; between Pecos River and Guadalupe Mountains, 1; Presidio County, 2; Presidio, 18; Rio Grande, Brewster County, 14; Sanderson, 2; 10 mi. W Sanderson, 1; 14 mi. N Sanderson, 73; Sheffield [as "Sheffield County" (Dillon, 1952)]; Shovel Mountain, 1; Sierra Blanca, 18; 3 mi. S Toyahvale, 58; Valentine, 20; Val Verde County, 5; Van Horn, 20.

REMARKS

LeConte in his original description of this species stated that he had only a single specimen (a male). Werner's (1945) designation of a lectotype was therefore unnecessary.

Epicauta longicollis (LeConte)

Lytta longicollis LeConte, 1853:343. [Type locality: "Missouri Territory and Santa Fe"; lectotype, male, from Santa Fe, New Mexico, in the Museum of Comparative Zoology, Harvard University, no. 4978, designated by Werner (1945:509).] LeConte, 1858:39.

Macrobasis longicollis, LeConte, 1863-66:68. Horn, 1873:90. Champion, 1891-93:397. Snow, 1906:174; 1907:186. Fall and Cockerell, 1907:209. Cockerell and Harris, 1925:31.

Epicauta longicollis, Werner, 1945:508, figs. 28-29. Vaurie, 1950:35. Dillon, 1952:406. MacSwain, 1956:56, pl. 9. Werner, Enns, and Parker, 1966:36, fig. 72.

LOCALITY RECORDS AND SPECIMENS EXAMINED

MEXICO *Chihuahua:* 182 km. N Chihuahua, 24; 10 mi. S Delicias, 1; Ojo de Laguna, 5. *Coahuila:* Serranías [=Sierra] de los Burros, 1.

UNITED STATES *Arizona:* Baboquivari Mountains, 1; Benson, 1; Bonita, 1; 5 mi. S Bonita, 8; Chino Valley, 18; Chiricahua Mountains, 13; Dos Cabezas, 1; Douglas, 5; 5 mi. N Elfrida, 1; Elgin, 1; Empire Mountains, 2; Fort Grant (Werner, 1945); Gray Mountain, 1; 10 mi. W Gray Mountain, 28; Kaibab National Forest, 3; Pearce, 15; 3 mi. N Pearce, 6; Phoenix, 2; Pinery Canyon, Chiricahua Mountains, 1; Portal, 1; Prescott (Werner, 1945); San Bernardino Ranch (Snow, 1906); Santa Rita Mountains, 10; Seligman, 5; Sulphur Springs (Werner, 1945); Tempe (Werner, 1945); Tombstone, 1; Verde River, 15; Willcox, 22; 6 mi. SE Willcox, 37; 8 mi. SW Willcox, 1; Williams, 1. *Colorado:* La Junta, 3. *New Mexico:* Aden, 1; Albuquerque, 60; Bernalillo County, 9; 5 mi. E Carlsbad, 1; Carrizozo, 4; Columbus, 1; Deming, 3; Eddy County, 5; Faywood, 16; Grant County, 2; Las Cruces, 60; Las Vegas, 1; Lava (Cockerell and Harris, 1925); Lordsburg, 18; Loving, 13; Malaga, 1; Mesilla Valley (Fall and Cockerell, 1907); 2 mi. N Rodeo, 1; Roswell, 1; 10 mi. W Roswell, 1; Socorro, 1; Tucumcari, 1; Walnut Creek, about 12 mi. N Silver City (Snow, 1907); Whites City, 4. *Texas:* Allamoore, 1; Alpine, 14; Big Bend National Park, 1; Brewster County, 2; Castolon, 1; Clarendon, 1; Davis Mountains, 19; Del Rio, 1; Fort Davis, 93; Fort Stockton, 6; Macdona, 1; Marathon, 2; Marfa, 37; Midland, 6; Red Bluff, 13; Sierra Blanca, 1; Valentine, 14; Van Horn, 56.

REMARKS

This species was recorded from Oklahoma (Murray County) by Hatch and Ortenburger (1930), but the record is questionable on geographic grounds. Champion's (1891-93:397) record from "Northern Sonora," based on material collected by Morrison, has not been accepted because of evidence (Selander and Vaurie, 1962) that Morrison labeled as Sonoran material actually collected in Arizona.

Epicauta texana Werner

Epicauta texana Werner, 1944:73. [Type locality: Davis Mountains, Texas; holotype, male, in the collection of The Ohio State University.] Werner, 1945:512, fig. 26. Werner, Enns, and Parker, 1966:36, fig. 71.

LOCALITY RECORDS AND SPECIMENS EXAMINED

MEXICO *Durango:* Bermejillo, 1.

UNITED STATES *Arizona:* 14 mi. SW Apache, 1; Benson (Werner, Enns, and Parker, 1966); Canelo, 1; Cochise County, 1; Douglas, 8; Dragoon Mountains, 1; 5 mi. N Elfrida, 18; Huachuca Mountains, 1; Lochiel, 1; 4 mi. S McNeal, 4; Pearce, 18; Phoenix, 2; Safford, 1; San Bernardino Ranch, Cochise County, 1; San Rafael, 1; Santa Rita Mountains, 2; Sonoita, 1; 10 mi. E Sonoita, 39; 5 mi. SE Willcox, 129. *New Mexico:* Rodeo, 1. *Texas:* Alpine, 1; Chisos Mountains, 1; Davis Mountains, 1; Fort Davis, 60; 9 mi. W Fort Davis, 22; Jeff Davis County, 3; Marfa, 4; 3 mi. S Toyahvale, 1.

Epicauta albida (Say)

Lytta albida Say, 1823-24:305. [Type locality: "Arkansas . . . near the Rocky Mountains" (type lost); neotype, male, from La Junta, Bent County, Colorado, in the Museum of Comparative Zoology, Harvard University, designated by Werner (1945:512), examined.] LeConte, 1858:39.

Lytta luteicornis LeConte, 1854:84. [Type locality: "Laredo to Ringgold Barracks," Texas; lectotype, male, in the Museum of Comparative Zoology, Harvard University, no. 4977, designated by Werner (1945:512).]

Macrobasis albida, LeConte, 1863-66:68. Horn, 1873:89. Snow, 1879:69. Dugès, 1889:57. Champion, 1891-93:397. Chittenden, 1903: 26. Fall and Cockerell, 1907:209.

Epicauta albida, Werner, 1945:511, figs. 25, 27. Dillon, 1952:403, fig. 2. MacSwain, 1956:55, pl. 9. Parker and Wakeland, 1957:26, tbl. 12.

Epicauta texana, Dillon, 1952:404 (misidentification).

LOCALITY RECORDS AND SPECIMENS EXAMINED

Mexico *Coahuila:* 12 mi. N Hermanas, 141. *Nuevo León:* Apodaca, 18; Monterrey, 4; Pesquería, 2; Sabinas Hidalgo, 2; Villa de Santiago, 1. *Tamaulipas:* Ciudad Victoria, 1; Nuevo Laredo, 1.

United States *Colorado:* Denver, 1; Durango, 8; Fort Collins, 1; Fort Morgan, 1; Holyoke, 2; Hugo, 2; Julesburg, 2; La Junta, 10; Lolita, 3; Pueblo, 6; Rocky Ford, 10; Weld County, 1; Wild Horse, 1. *Kansas:* Dodge City, 4; Ellis, 1; Ellsworth, 6; Garden City, 7; Goodland, 14; Gove County, 1; Greeley, 2; Hays City, 2; Hodgeman County, 3; Liberal, 7; Logan County (Werner, 1945); Manhattan, 2; 13 mi. S Meade, 1; 5 mi. N Minneola, 22; Oakley, 4; Oxford, 1; Pawnee County, 2; Pratt County, 2; Reno County, 1; Wallace, 4; Wellington, 2. *Nebraska:* Alliance, 1; Lincoln, 1; Ogallala, 1. *New Mexico:* Albuquerque, 4; 16 mi. W Caprock, 1; 5 mi. E Carlsbad, 37; Clovis, 1; Georgetown (Fall and Cockerell, 1907); Hot Springs, 2; Las Truchas (Fall and Cockerell, 1907) (not found); Las Vegas, 1; Lovington, 13; Malaga, 13; Mesilla Park, 2; Roosevelt County, 3; Roswell, 6; San Jon, 2; Santa Rosa, 4; Tucumcari, 17; Vaughan, 4. *Oklahoma:* Alfalfa County, 1; Beaver, 1; Boise City, 13; Carnegie, 1; Cotton County, 2; Fort Sill, 1; Kenton, 1; Laverne, 1; Lawton, 7; Mangum, 1; Marshall County, 3; Murray County, 1; Noble County, 1; Shattuck, 4; Springfield, 1 (not found); Stillwater, 6; Woodward, 31. *Texas:* Abilene, 2; Abilene State Park, 1; Albany, 1; Alice, 2; Alpine, 1; Amarillo, 13; Arlingen (Werner, 1945); Austin, 5; Bastrop, 49; Beeville, 2; Boerne, 1; Bowie County, 9; Breckenridge, 15; Brownsville, 47; Brownwood, 3; Canadian, 7; Canyon, 1; Carrizo Springs, 4; Catarina, 4; Childress, 5; Cisco, 4; College Station, 14; Colorado, 2; Comal County, 4; Comfort, 1; Corpus Christi, 1; 3 mi. N Cotulla, 53; 14 mi. S Cotulla, 2; Coyote Lake, 16; Cuero, 31; Cypress Mill, 9; Dalhart, 11; Dallas, 5; Dallas County, 1; Davis Mountains, 1; Del Rio, 1; Dilley, 1; Eagle Pass, 22; 10 mi. NW Eagle Pass, 5; El Indio, 8; El Paso, 1; Encinal, 3; Falfurrias, 1; Fedor, 7; Fort Sam Houston, 29; Fort Worth (Dillon, 1952); Friona, 1; Gainsville, 2; Georgetown, 4; Goldthwaite, 3; Gregory, 2; Harlingen, 1; Harris County, 1; Hearne, 7; Helotes, 1; Hidalgo County, 4; Junction, 19; Karnes City, 2; Karnes County, 10; Kerrville, 24; Kingsville, 29; Kyle, 2; Laredo, 2;

19 mi. E Laredo, 12; Leon County, 2; Littlefield, 1; Llano, 1; McAllen, 1; McLennan County, 7; Madison County, 1; Madisonville, 4; 10 mi. NE Marquez, 1; Mason, 3; Mathis, 1; Mercedes, 1; Mexia, 1; Nocona, 1; Odessa, 5; Palestine, 1; Palo Duro State Park, 1; Palo Pinto County, 1; Pecos, 2; Premont, 3; 10 mi. N Premont, 4; N Pyote, 3; Quemado, 21; Rock Island, 1; Round Mountain, 2; Sabinal, 1; San Antonio, 5; San Patricio County, 19; near Sinton, 21; Skellytown (Dillon, 1952); Sonora, 4; Stamford, 4; Sterling City, 16; Temple, 1; Terrell, 1; Texline, 1; Thurber, 6; Uvalde, 64; 8 mi. S Uvalde, 3; Victoria, 8; Waco, 1; Woodsboro, 6. *Wyoming:* state label only, 6; Cheyenne, 1.

REMARKS

Two records of this species from Utah published by Knowlton (1930, 1939) have been rejected. They are based on two specimens in the collection of the Utah State University, one purportedly from Salt Lake City and the other from Myton, Duchesne County. Both specimens are very probably mislabeled.

The southernmost specific locality recorded for *E. albida* is Ciudad Victoria, Tamaulipas. However, the species presumably ranges even farther southward, since Dugès (1889) recorded it from the Huasteca Potosina, an ill-defined geographic area centered on the state of San Luis Potosí and with its northern limit near Ciudad Valles, San Luis Potosí.

Epicauta sublineata **(LeConte)**

Lytta sublineata LeConte, 1853:477. [Type locality: "Vicinity of Eagle Pass," Texas; holotype, female, in the Museum of Comparative Zoology, Harvard University, no. 4979.] LeConte, 1858:39.

Macrobasis sublineata, LeConte, 1863-66:68. Horn, 1873:94.

Macrobasis megacephala Champion, 1891-93:402, pl. 18, fig. 24. [Type locality: Monclova, Coahuila; syntypes (two), presumably in the British Museum (Natural History).] Dillon, 1952:405. *New synonymy.*

Epicauta sublineata, Werner, 1945:491. Vaurie, 1950:32. Dillon, 1952:405.

Epicauta reinhardi Dillon, 1952:413. [Type locality: Dimmit County, Texas; holotype, male, in the collection of the Texas Agricultural and Mechanical University, examined.] *New synonymy.*

LOCALITY RECORDS AND SPECIMENS EXAMINED

MEXICO *Coahuila:* 12 mi. N Hermanas, 2; 12 mi. NW Jiménez, 1; Monclova (Champion, 1891-93). *Nuevo León:* Apodaca, 30; El Cercado, 1; 7 mi. NE Monterrey, 1; Pesquería, 1; Sabinas Hidalgo, 34; 17 km. N Sabinas Hidalgo, 2. *Tamaulipas:* Ciudad Victoria, 17; 2 mi. N Ciudad Victoria, 2; Güemes, 1; 10 km. N Padilla, 1; Sierra San Carlos [= San Carlos Mountains], 1.

UNITED STATES *Texas:* Del Rio, 11; Devils River, 1; Dimmit County, 2; Eagle Pass, 9; 10 mi. NW Eagle Pass, 89; El Indio, 11; Goldthwaite, 1; Hidalgo County (Dillon, 1952); Lozier Canyon, Terrell County, 2; Mathis (Dillon, 1952); Quemado, 130; San Diego, 1; Uvalde, 3; Val Verde County, 6; Winter Haven (Dillon, 1952).

Epicauta immaculata (Say)

Lytta immaculata Say, 1823-24:304. [Type locality: "Arkansa" (type lost); neotype, male, from Cambridge, Nebraska, in the Museum of Comparative Zoology, Harvard University, designated by Werner (1945:489).] LeConte, 1853:342.

Lytta articularis Say, 1823-24:304. [Type locality: "Arkansa . . . near the Rocky Mountains" (type lost).]

Lytta fulvescens LeConte, 1853:477. [Type locality: Texas; lectotype, male, in the Museum of Comparative Zoology, Harvard University, no. 4989, designated by Werner (1945:489).] LeConte, 1858:39.

Macrobasis fulvescens, LeConte, 1863-66:68. Snow, 1879:69.

Macrobasis immaculata, LeConte, 1863-66:68. Horn, 1873:93. Ulke, 1875:826. Chittenden, 1903:26. Blatchley, 1910:1359. Milliken, 1921: 7, figs. 7-8, 10-11. Hatch and Ortenburger, 1930:13. Böving and Craighead, 1931: pl. 96, figs. a, c-d. Carruth, 1931:53. Gilbertson and Horsfall, 1940:5. Montgomery and Amos, 1941:254. Schwitzgebel and Wilbur, 1942:42.

Epicauta immaculata, Werner, 1945:489, figs. 32-33. Dillon, 1952: 407. MacSwain, 1956:52, pl. 9.

LOCALITY RECORDS AND SPECIMENS EXAMINED

MEXICO *Coahuila:* 12 mi. N Hermanas, 6.

UNITED STATES *Alabama:* Huntsville, 1. *Arkansas:* Hot Springs National Park, 1; Imboden, 1; Lawrence County, 1. *Colorado:* Bent County, 1; Fort Collins (Werner, 1945); Granada, 1; La Junta, 6; W Las Animas, 2; Prowers, 2; Rocky Ford, 3. *Georgia:* Chickamauga, 1. *Illinois:* Alexander County, 1; Brownstown, 8; Cache, 1; Carbondale, 1; Carterville, 1; Clay City, 1; Dubois, 2; SE Eddyville, 1; Edgewood, 21; 2 mi. N Etherton, 18; Farina, 1; Flora, 4; Goreville, 1; Grand Tower, 1; Jerseyville, 1; Jonesboro, 2; 1 mi. S Louisville, 1; 8 mi. W McLeansboro, 3; Mahomet, 1; Mason, Effingham County, 130; 2 mi. E Norris City, 6; Peoria, 18; Raymond, 1; Urbana, 1; West Vienna, 7; Zeigler, 1. *Indiana:* Clark County, 3; Clinton County, 1; Crawford County, 1; Harrison County, 5; Jackson County, 8; Knox County, 1; Lawrence County, 4; Posey County, 3; Putnam County, 1; Vermillion County, 2; Warrick County, 1. *Iowa:* Ames, 2; Davis County, 1; Floris, 1; Fairfield, 1; Lewis (Werner, 1945). *Kansas:* Allen County, 1; Barber County, 14; Beeler (Werner, 1945); Belleville, 1; Beloit, 2; Belvidere, 1; Bourbon County, 2; Caldwell, 1; Chase County, 1; Cloud County, 1; Comanche County, 2; Coolidge, 2; Decatur County, 1; Dickinson County, 1; Dodge City, 1; Douglas County, 5; Edwards County, 1; Ellis, 4; Ellis County, 12; Ellsworth County, 2; Finney County, 1; Fort Hayes (Werner, 1945); Garden City, 28; Goodland, 63; Gove County, 4; Gray County, 4; Grinnell, 1; Hamilton County, 22; Harper County, 5; Hays, 1; Kensington, 1; Kiowa County, 2; Lawrence, 1; Leavenworth, 1; Linn County, 1; Logan County, 15; McAllaster, 5; Manhattan, 15; Meade County, 3; Medora, 2; 5 mi. N Minneola, 3; Morton County, 14; Ness County, 5; Onaga, 1; Osborne County, 1; Partridge, 2; Pawnee County, 10; Riley County, 25; Rossville, 36; Rush County, 1; Russell County, 3; Saint George, 1; Saint John, 1; 4 mi. E Salina, 1; Saline County, 2; 3 mi. S Sawyer, 1; Scott City, 1; Scott County, 3; Sharon Springs, 1; Sheridan County, 1; Sitka, 1; Stanton County, 1; Stockton, 3; Thomas County, 1; Topeka, 1; Trego County, 1; Wabaunsee County, 3; Wallace County, 17; Wellington, 2; "West Kansas," 28; Wichita, 2; Wilson County, 2. *Kentucky:* state label only, 13; Berheim Forest, 1 (not found); Henderson, 3; Taylorsville, 2. *Louisiana:* Shreveport, 1. *Mississippi:* Agricultural and Mechanical College (near Starkville), 3; West Point, 12. *Missouri:* Branson, 7; Cameron, 2; Columbia, 6; Cuba, 1; Lathrop, 2; Loggers Lake, 6 mi. SW Bunker, 3; Montier, 1; Ranken, 1; Saint Marys, 1; 5 mi. W Springfield, 2; Williamsville, 15. *Nebraska:* Bartley, 2; Bloomington, 3; Cambridge, 11; Culbertson, 2; Curtis, 2; Deshler, 1; Haigler, 1; Harvard, 2; Indianola, 13; Lincoln, 7; Lynch, 2; McCook, 2; North Platte, 1; 20 mi. SE North Platte, 2; O'Neill, 1; Spalding, 1; Stockham, 4; Stratton (Werner, 1945); Verdigre, 1. *New Mexico:* Artesia, 2; Carlsbad, 3; Eddy County, 2; Hope, 157; Las Cruces, 2; Loving, 19; Malaga, 166; Roswell, 29; San Jon, 3. *Ohio:* Cincinnati, 6; Hamilton County, 1; Marietta, 1. *Oklahoma:* Alfalfa County, 1; Alva, 1; Bartlesville, 1; Beaver, 2; Beckham County, 2; Boise City, 2; Carter

County, 1; Centralia, 4; Cherokee County, 1; Cherokee Salt Plains, 1; Cheyenne, 1; Clinton, 8; Cushing, 1; Dunlap, 1; El Reno, 4; Erick, 1; Fort Sill, 3; Grandfield, 1; Harmon County, 1; Harper County, 1; Kenton County, 1; Lawton, 3; Marshall County, 13; Murray County (Hatch and Ortenburger, 1930); Oklahoma City, 1; Oklahoma County, 2; Pawnee County, 2; Payne County, 3; Quartz Mountain, 1; Shattuck, 1; 3 mi. N Shawnee, 9; Stillwater, 3; Vinson, 1; Washington County, 1; Wichita National Forest, 2; Woods County, 19; Woodward, 4. *South Dakota:* Belle Fourche, 1; 3 mi. W Belle Fourche, 1; Beresford, 1; Chamberlain, 4; Fruitdale, 3; Lake Andes, 1; Oacoma, 1; 5 mi. NW Oglala, 1; Onida, 5; Saint Onge, 1; Spearfish, 2; Wessington, 1; Wheeler Bridge, 1 (not found); White River, 2; White Wood, 1. *Tennessee:* Clarksville, 1; Concord, 1; Gatlinburg, 3; Knox County, 1; Lawrenceburg, 5; Lewisburg, 1; Oak Ridge, 4; 10 mi. W Oak Ridge, 18; 9 mi. W Pulaski, 1; Spencer, 1; Van Buren, 1. *Texas:* Abilene, 1; Adrian, 1; Albany, 12; Alpine, 8; Amarillo, 6; Austin, 12; 17 mi. E Balmorhea, 4; Bexar County, 3; Big Bend region, 5; Big Springs, 5; Boquillas Canyon, Big Bend region, 3; Brazoria County, 2; Brazos, 2; Breckenridge, 1; Brownsville, 4; Brownwood, 4; Burkburnett, 3; Camp Berkeley, 1; Canadian, 1; Carrizo Springs, 5; Catarina, 13; 3 mi. E Childress, 3; Chisos Mountains, 1; Cisco, 3; Clarendon, 2; Clarksville, 5; Clear Creek, Sanger, 2; Coahoma, Howard County (Dillon, 1952); College Station, 3; Comal County, 3; Corpus Christi, 5; 3 mi. N Cotulla, 2; 2 mi. S Cuero, 1; Dalhart, 2; Dallant, 1; Dallas, 5; Dallas County, 3; Davis Mountains, 6; Del Rio, 3; Dimmit County, 1; Eagle Pass, 3; 10 mi. NW Eagle Pass, 1; El Paso, 8; 2 mi. W Estelline, 10; Fedor, 13; Florence, 1; Floresville, 14; Forestburgh (Dillon, 1952); Fort Davis, 47; 14 mi. N Fort Davis, 2; Fort Griffen State Park, 6; Fort Hood, 4; Fort Stockton, 2; 25 mi. W Fort Stockton, 1; Fort Worth, 2; 10 mi. N Friona, 6; Frio State Park, 1; Georgetown, 1; Gillespie County, 1; Gordon (Dillon, 1952); Harris County, 6; Hearne, 21; Henrietta, 25; 5 mi. NE Hillsboro, 3; Howard County, 1; Italy, 1; Jeff Davis County, 2; Kingsville, 8; Kinney County, 2; Laredo, 14; 19 mi. E Laredo, 3; La Vaca County, 1; Lee County, 3; Lexington, 15; McAllen, 2; McLennan County, 1; Marathon, 4; 9 mi. S Marathon, 2; 16 mi. S Marathon, 1; 23 mi. S Marathon, 3; Marble Falls (Dillon, 1952); Mathis, 1; Memphis, 6; Menard County, 1; Mercedes, 1; Midland, 1; Mineral Wells, 6; Moore, 1; 1.5 mi. N Munday, 20; Navarro County, 1; New Braunfels, 8; Odessa, 2; Oklaunion, 1; Old Dime Box, 1; Orla, 1; 2 mi. S Orla River, 1; near Ottine, 5; Palmetto State Park, 1; Palo Duro State Park, 13; Palo Pinto, 10; Pearsall, 2; Pecos, 5; Perryton, 1; Presidio, 12; N Pyote, 9; Red Bluff, 2; Reeves County, 3; Rio Grande, Brewster County, 3; Rio Grande City (Werner, 1945); Rosillo Mountains, 2; Sabinal, 1; San Antonio, 2; Shamrock, 2; Sheffield, 3; Sherman, 1; Sinton, 2; Sonora, 1; Stamford, 8; Sutton, 1; Sweetwater, 2; Tarrant County, 1; Taylor County, 2; Temple, 1; Terrell, 6; Tornillo, 7; 3 mi. S Toyahvale, 66; Uvalde, 3; Valley Mills, 1; Val Verde County, 3; Van Horn, 4; 14 mi. S Vernon, 1; Victoria, 1; Waxahachie, 1; 4 mi. NE Weatherford, 7; White Rose, Jeff Davis County, 2. *West Virginia:* Wayne, 1.

REMARKS

Three specimens examined, purportedly from Tampico, Tamaulipas, are probably mislabeled. On the basis of several geographically variable characters they appear to have been drawn from a population in the northeastern United States.

Epicauta segmenta (Say)

Lytta segmenta Say, 1823-24:303. [Type locality: "near Purgatory river of the Arkansa" (type lost); neotype, male, from Fort Hayes, Kansas, designated by Werner (1945:491) (this type lost also); replacement neotype, male, from Fort Hayes [= Hays], Kansas, June, in the Museum of Comparative Zoology, Harvard University, no. 31172 (present designation).]

Lytta segmentata, LeConte, 1853:342 (emendation) (in part).

Apterospasta segmentata, LeConte, 1862:272; 1863-66:68.

Macrobasis segmentata, Horn, 1873:93 (in part). Champion, 1891-93:401, pl. 18, fig. 22. Chittenden, 1903:26. Snow, 1906:174; 1907:150. Carruth, 1931:54 (in part). Whelan, 1939:118.

Macrobasis cinctothorax Dugès, 1889:56. [Type locality: "Chihuahua?"; disposition of syntypes (two females) unknown.]

Epicauta segmenta, Werner, 1945:490 (in part). Vaurie, 1950:31, fig. 9. Dillon, 1952:403. Werner, Enns, and Parker, 1966:35, fig. 69. Selander and Weddle, 1969:27.

LOCALITY RECORDS AND SPECIMENS EXAMINED

MEXICO *Chihuahua:* Cañon de Bachimba, 27 mi. S Chihuahua, 8; 60 mi. NW Casas Grandes, 1; Catarinas, 1; Delicias, 1; 10 mi. S Delicias (Vaurie, 1950); 12 mi. NW Gran Morelos, 3; 10 mi. S Hidalgo del Parral, 1; Santa Clara, 1; Valle de Olivos (Vaurie, 1950); 1 mi. N Villa Matamoros, 1. *Coahuila:* Ojo de Agua, Sierra de Tlahualilo, 1. *Durango:* Ciudad [= Villa] Lerdo, 5; near Mimbrera, Route 45, 1; Tlahualilo, 1. *Sinaloa:* Escuinapa de Hidalgo, 3. *Sonora:* 4 mi. W

Guasabas, 2; Guaymas, 1; 40 mi. N Guaymas, 13; Hermosillo, 1; Naco (Vaurie, 1950).

United States *Arizona:* Apache Pass, Cochise County, 1; Atascosa Mountains, 2; Baboquivari Mountains, 27; Bagdad, 2; Benson, 10; 8.5 mi. W Benson, 2; Bernardino, 1; Bisbee, 5; Brown Canyon, Baboquivari Mountains, 1; Camp Verde, Yavapai County, 1; Capitan Mountains, 13; Carr Canyon, 5 (not found); Cat Pass, Tucson Mountains, 2; Chihuahua Mountains (Werner, 1945); Chiricahua Mountains, 51; Cleator, 4; Congress Junction, 1; Continental, 2; Desert Grass Lands Station, 35 mi. S Tucson, 4; Dos Cabezas, 83; 4 mi. S Dos Cabezas, 4; Douglas, 9; 6 mi. E Douglas, 1; 17 and 18 mi. E Douglas, 2; Elfrida, 3; Elgin, 1; Far Away Ranch, 4; Far Away River, 7 (not found); Fish Creek (Werner, 1945); Fort Grant, 3; 1 mi. W Gleeson, 9; Globe, 27; Grand Canyon, 38; Hayden, 1; Hereford, 1; Huachuca Mountains, 33; Lochiel, 3; Madera Canyon, Santa Rita Mountains, 3; Maricopa County, 1; Nogales, 10; 5 mi. NE Nogales, 27; 10 mi. E Nogales, 6; Noon Creek, Graham Mountains, 6; Pajarito Mountains, near Nogales, 6; Palmerlee, 21; Palo Alto, 1; Patagonia, 5; Payson, 7; 7 mi. N Payson, 1; Pearce, 2; Peeples Valley (Werner, Enns, and Parker, 1966); Phantom Ranch, Grand Canyon, 19; Pinery Canyon, west slope, 3; 5 mi. W Portal, 1; Prescott, 7; Ramsay Canyon, Huachuca Mountains, 1; Ray, 1; Redington, 1; Sabino Canyon, Santa Catalina Mountains, 2; San Carlos (Werner, Enns, and Parker, 1966); San Bernardino Ranch, Cochise County, 6; Sand Tank Canyon, Sierra Ancha Mountains, 1; San Rafael, 3; Santa Catalina Mountains, 1; Santa Cruz Village, Cobabi Mountains, 1; Santa Rita Mountains, 5; Six Shooter Canyon, Gila County, 4; Snow Line Ranch, Mount Graham, 20; Sonoita, 1; 8 mi. N, 2-9 mi. W, and 6-25 mi. E Sonoita, 20; Stockton Pass, Pinaleño Mountains, 2; Tombstone, 30; 10-12 mi. S Tombstone, 4; Tucson, 4; Tucson Mountains, 7; Turkey Creek, Yavapai County (Werner, Enns, and Parker, 1966) (not found); 8 mi. N Vail, 1; Verde Hot Springs, 9; White Mountains, 4; Whiteriver, Navajo County (Werner, Enns, and Parker, 1966); 5 mi. NE Willcox, 1; Yarnell, 4. *California:* Ivanpah, San Bernardino County, 1. *Kansas:* Belvidere, 1; Coats, 1; Dodge City, 1; Ellis, 1; Fort Hayes, 2; Garden City, 3; Gove County, 10; Gray County, 1; Hamilton County, 5; Hodgeman County, 4; Kenneth, 1; Kingsley, 1; Lakin, 6; Manhattan, 1; Meade County, 6; Morton County, 5; Oakley, 4; Reno County, 4; Russell County, 1; Seward County, 1; Sharon Springs, Wallace County, 1; Wallace County, 2. *Nebraska:* Archer, 1; Concord, Dixon County, 1; Cozad, 1; Curtis, 1; Lincoln, 2; O'Neal, 1; Scotia, 2; Seward County, 4; Sioux City, 1. *New Mexico:* Alamogordo, 3; Artesia, 8; 5 mi. N

Carlsbad, 1; Eddy County, 1; Grants, 2; Hope, 1; Montoya, Quay County, 1; Pinto, 1 (not found); Roswell, 2; Silver City, 2; Sitting Bull Falls, 42 mi. SW Carlsbad, 2; Whites City, 1. *Oklahoma:* Boise City, 1. *South Dakota:* 12 mi. N Batesland, 1; Beresford, 1; Brookings, 5; Chamberlain, 1; Gaan Valley, 1; Grass Rope, 1 (not found); Hisle, 1; Interior, 2; Kennebec, 2; 8 mi. NW Kyle, 1; 5 mi. NW Oglala, 1; Onida, 2; Pierre, 2; Rosebud, 1; Slim Butte, 2; Wanblee, 1; 22 mi. E Wanblee, 1; Wessington, 5; White River, 2; Whitewood, 1; Wounded Knee, 1. *Texas:* Abilene State Park, 1; Alpine, 49; 15 mi. SE Alpine, 1; Big Bend National Park, 5; Blackwell, 1; Brazos County, 1; Brownwood, 3; Buster County, 1; Cherry Canyon, Fort Davis Quadrangle, 2; Childress, 20; Chisos Mountains, 13; Davis Mountains, 26; Davis Mountains State Park, 1; El Paso, 1; Fedor, 1; Fort Davis, 12; 6-10 mi. W Fort Davis, 1; 9 mi. N Fort Davis, 7; Glenn Spring, Brewster County (Dillon, 1952); Goldthwaite, 3; Hueco Mountains, El Paso County, 1; Jeff Davis County, 17; Juniper Canyon, Chisos Mountains, 1; Kingsville, 3; Marathon, 3; 6-9 mi. S Marathon, 4; 12 mi. NE Marathon, 1; Marfa, 14; 8 mi. N Marfa, 1; 20 mi. S Marfa, 3; 1.5 mi. N Munday, 1; Oak Spring, Big Bend National Park, 1; Palo Duro State Park, 1; 20 mi. N Sanderson, 31; Sheffield, 1; Sterling City, 2; Sweetwater, 2; Toyahvale, 2; 3 mi. S Toyahvale, 15; Valentine, 3; ½ mi. S Valentine, 5. *Wyoming:* Hulett, 1.

REMARKS

For the following citations there is at present no basis for deciding whether the species referred to is *E. segmenta* or *E. valida:* Ulke (1875:826, as *Macrobasis segmentata*), Fall and Cockerell (1907:210, as *Macrobasis segmentata*), Gilbertson and Horsfall (1940:20, as *Macrobasis segmentata*), and MacSwain (1956:53, pl. 9, as *Epicauta segmenta*).

Epicauta valida (LeConte), new status

Lytta segmentata, LeConte, 1853:342 (in part).

Lytta valida LeConte, 1858:39. [Type locality: Texas; lectotype, male, in the Museum of Comparative Zoology, Harvard University, no. 4990, designated by Werner (1945:491).]

Apterospasta valida, LeConte, 1862:272; 1863-66:68.

Macrobasis segmentata, Horn, 1873:93 (in part). Carruth, 1931:54 (in part).

Epicauta segmenta, Werner, 1945:490 (in part).

LOCALITY RECORDS AND SPECIMENS EXAMINED

United States *Colorado:* Trinidad [= Trinity], 2. *Kansas:* Belvidere, 7; Clark County, 1; Coats, 1; Dickenson County, 2; Edwards County, 2; Finney County, 1; Fort Hayes, 1; Garden City, 1; Gove County, 6; Gray County, 3; Greenwood County, 1; Hamilton County, 26; Lakin, 5; Logan County, 2; Manhattan, 3; Meade County, 5; Morton County, 14; Ness County, 1; Onaga, 5; Reno County, 7; Riley County, 5; Russell County, 2; Saint Francis, 1; Saint John, 2; Saline County, 1; Scranton, 1; Topeka, 2; Trego County, 1; Wallace County, 2. *Louisiana:* Vowell Mill, 1. *Nebraska:* Archer, 4; Bartley, 1; Cambridge, 1; Concord, 5; Curtis, 1; David City, 4; Fullerton, 4; Indianola, 1; Lincoln, 2; O'Neal, 1; Seward County, 9; Sioux City, 1; Sioux County, 1; Taylor, 1. *New Mexico:* Albuquerque, 7; Carlsbad Cave, 1; Roosevelt County, 14; Sandon, 1; San Jon, 5; Santa Rosa, 2; Tucumcari, 11. *Oklahoma:* Boise City, 11; Cimarron County, 1; Delaware County, 1; Jackson County, 1; Kenton, 5; Murray County, 1; Optima, 1; Quartz Mountain State Park, 1 (not found); Wichita National Forest, 1; Wilkins, 1 (not found); Woods County, 2. *South Dakota:* Brookings, 1; Chamberlain, 1; Grass Rope, 3 (not found); Kennebec, 1; Oglala (Bad Lands), 1; Pine Ridge, 1; Wessington, 3; Wounded Knee, 2; Yankton County, 1. *Texas:* Alpine, 54; Amarillo, 3; Austin, 1; Brownwood, 1; Cypress Mills, 3; Dallas, 3; Dallas County, 1; Davis Mountains, 18; Fedor, 2; Fort Davis, 78; 10 mi. W Fort Davis, 30; Fredericksburg, 1; Gillespie County, 4; Llano County, 1; Marfa, 38; Round Mountain, 6; Twin Sisters, 3. *Utah:* Arch Canyon, San Juan County, 1.

REMARKS

See remarks for *E. segmenta.*

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PLATES

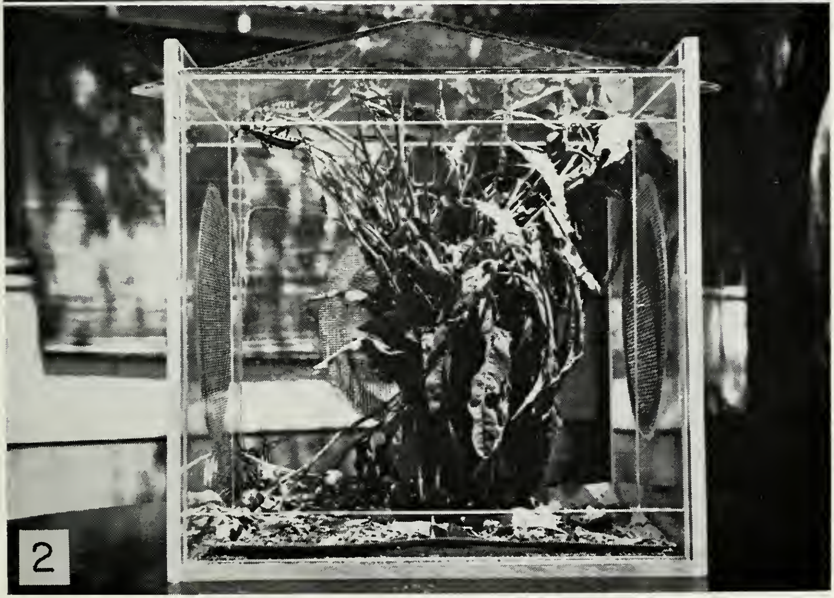


Fig. 1. Small cage of the type used in maintaining isolated individuals and in recording behavior under the individual pairs system.

Fig. 2. Large cage used in the mixed group situation.

FIG. 3. Geographic distribution of *E. longicollis*.

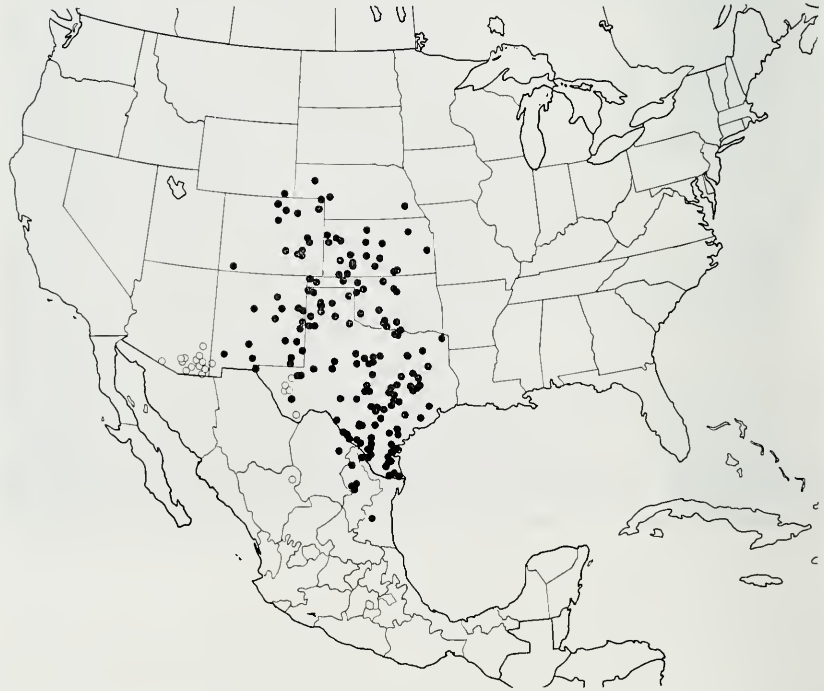


FIG. 4. Geographic distribution of *E. albida* (solid circles) and *E. texana* (open circles).

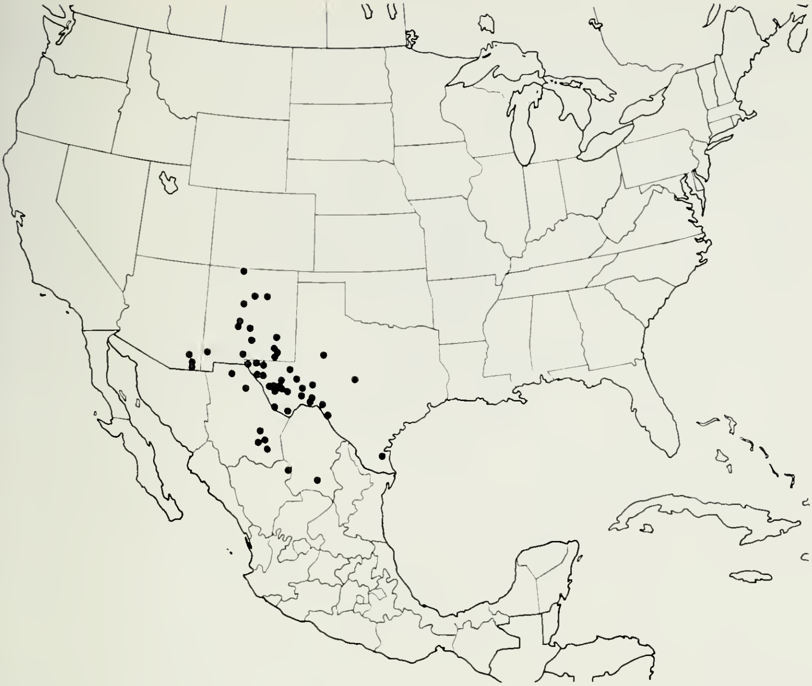


FIG. 5. Geographic distribution of *E. atrivittata*.

FIG. 6. Geographic distribution of *E. sublineata*.

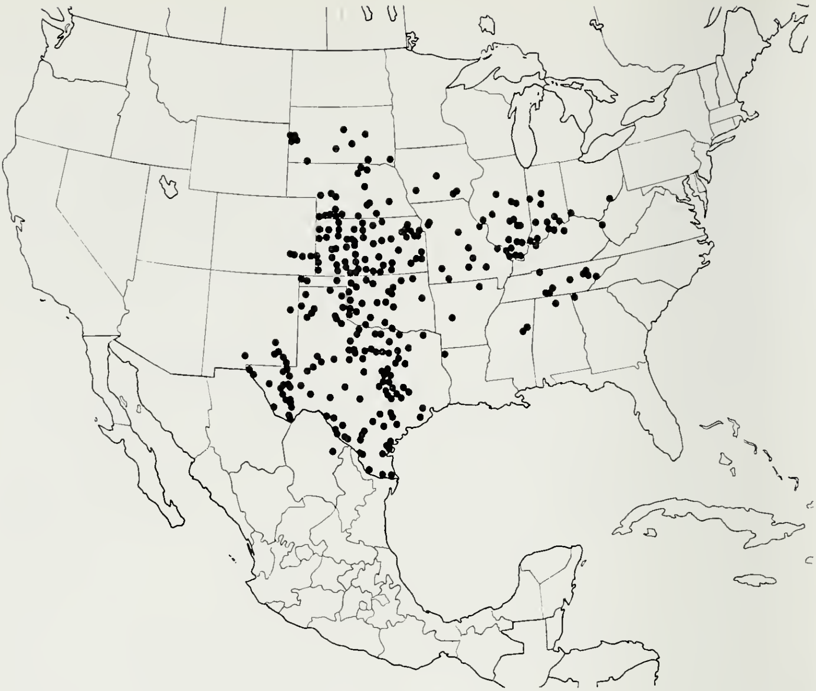


FIG. 7. Geographic distribution of *E. immaculata*.

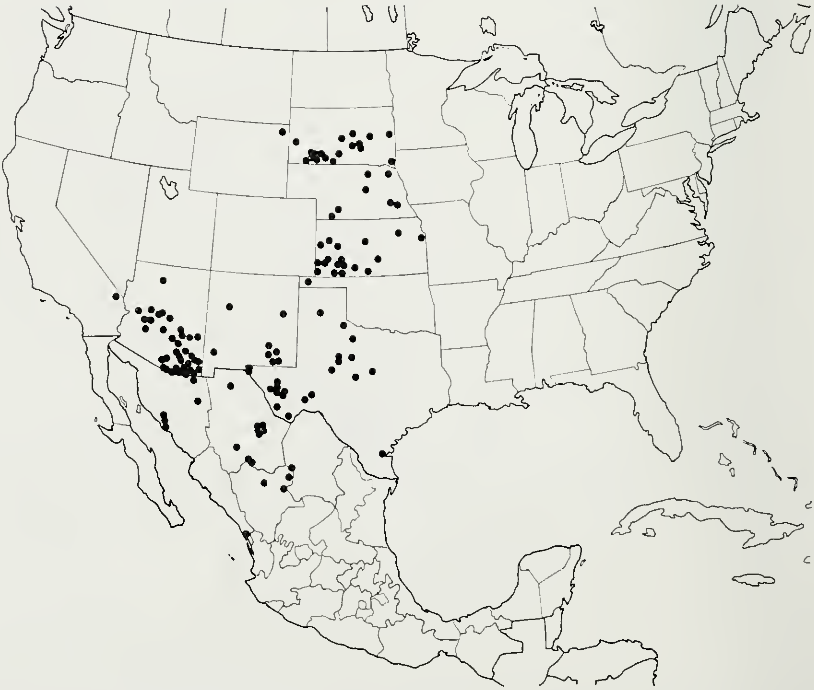


FIG. 8. Geographic distribution of *E. segmenta*.

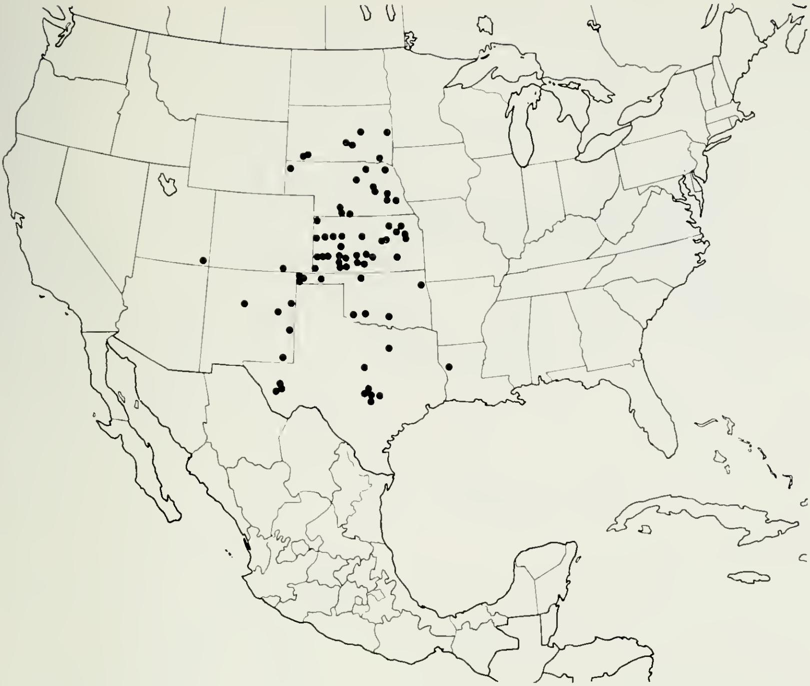
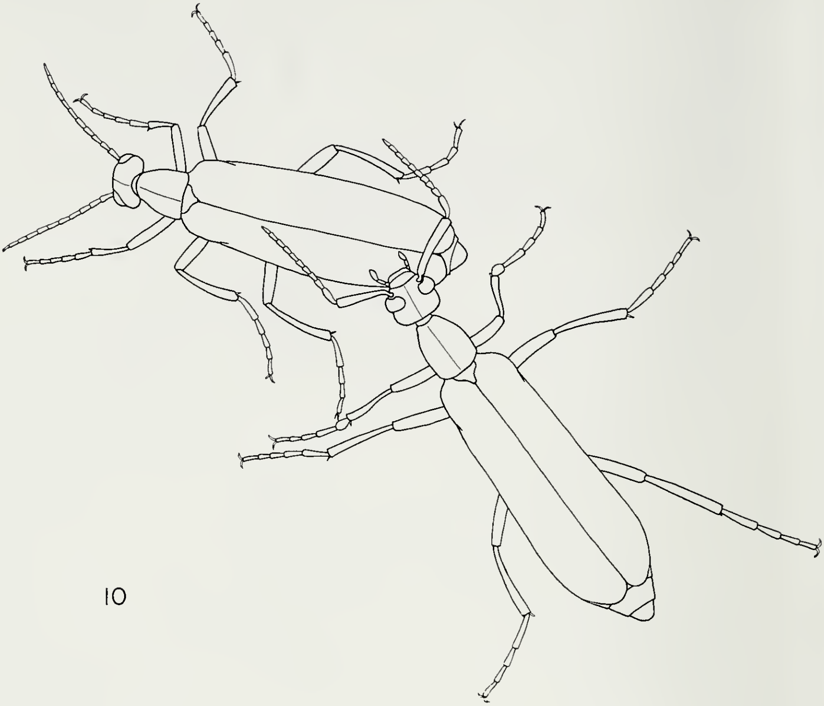


FIG. 9. Geographic distribution of *E. valida*.



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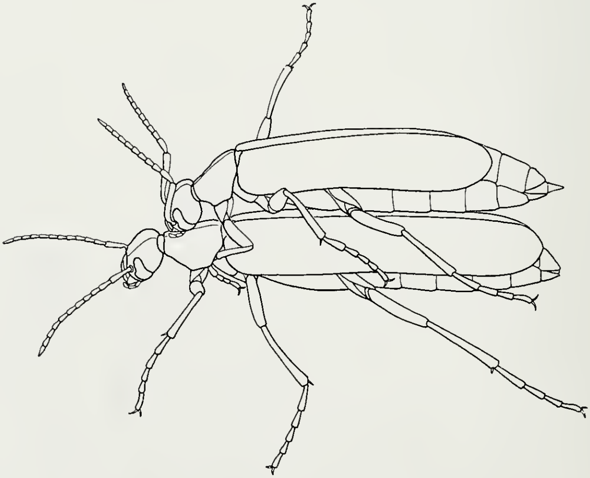

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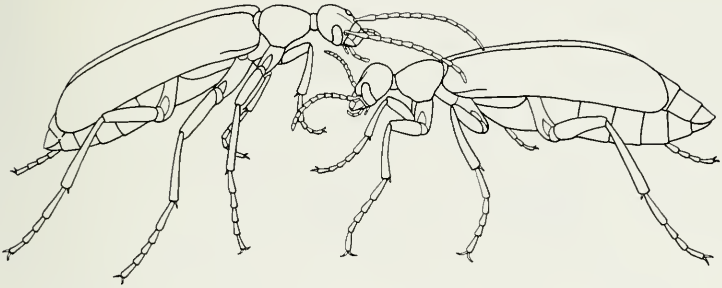
Figs. 10-11. Courtship in *E. polingi*, a member of the Diversicornis Group of *Macrobasis*. Fig. 10. Male at right in characteristic orienting position behind female. Fig. 11. Male riding female in dorsal phase.



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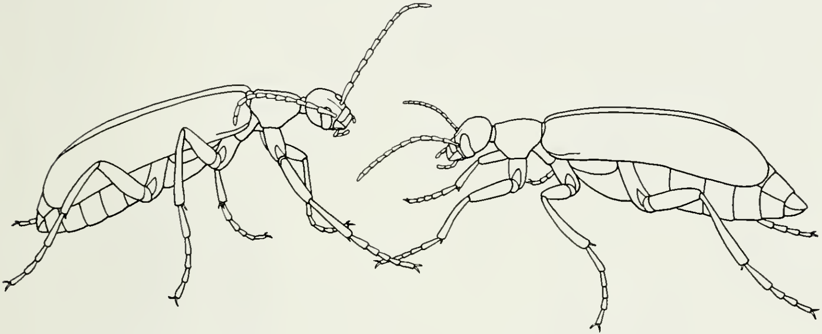

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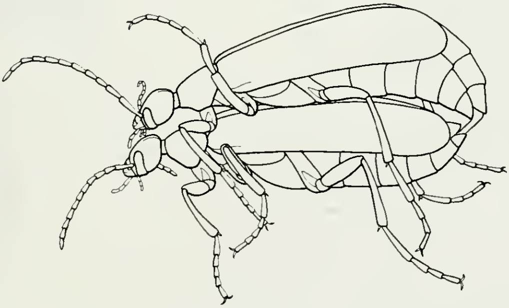

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Figs. 12-14. Courtship and precopulatory sequence in *E. immaculata*. Fig. 12. Male at left, reaching over head of female to perform the touching act. Fig. 13. Male at left, showing startle reaction in response to movement by female. Fig. 14. Male, mounted on female, lifting middle legs near the end of the precopulatory sequence.

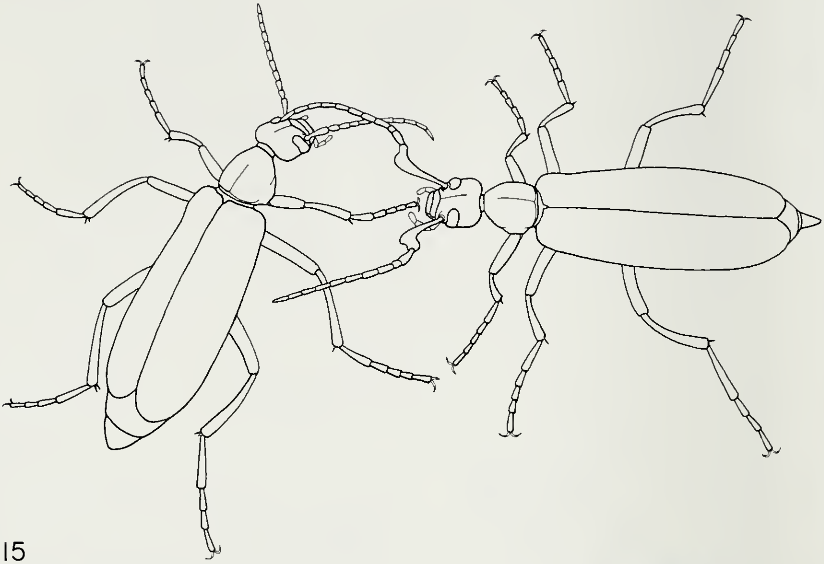

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FIG. 15. Courtship in *E. albida.* Male at right, orienting on female. Note extrusion of male genitalia.

FIG. 16. Antennal wrapping during courtship by male of *E. atrivittata.*

FIG. 17. Inner side of apex of hind tibia of male of *E. polingi,* showing tibial comb characteristic of many species of the subgenus *Macrobasis.*

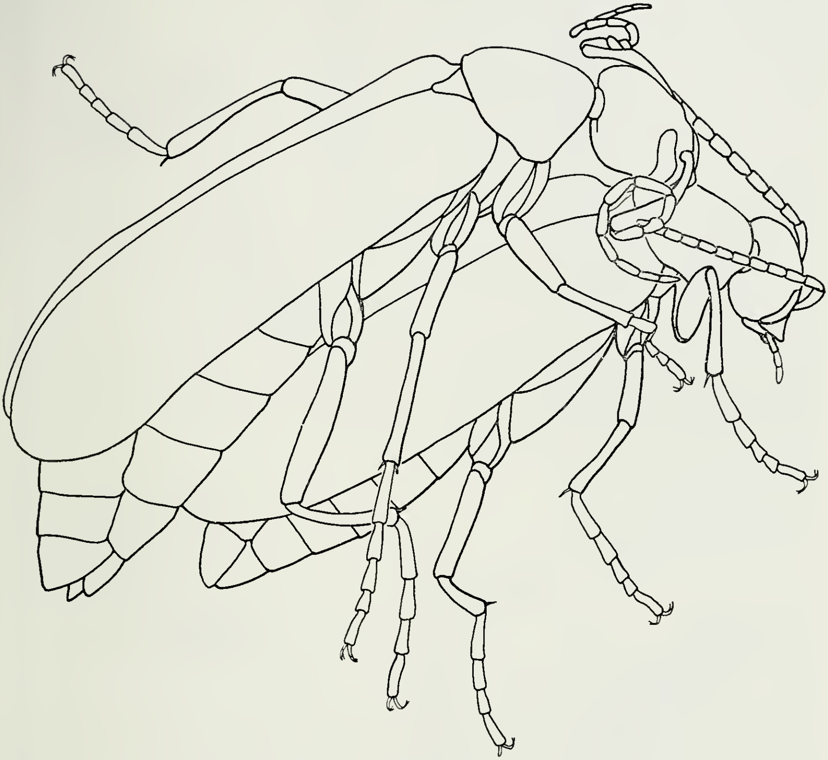

Fig. 18. *Epicauta texana* male wrapping antennae of female in abortive mount during courtship.

Figs. 19-22. Courtship in *E. longicollis.* Fig. 19. Male at left, orienting. Fig. 20. Male performing antennal whipping. Fig. 21. Male attempting to wrap female antennae. Fig. 22. Female at right, beginning attack on male.

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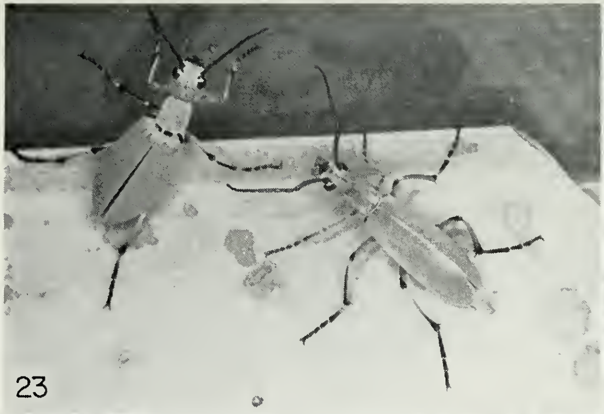
Figs. 23-26. Sexual behavior in *E. texana*. Fig. 23. Male at right, orienting. Fig. 24. Male palpating female during orientation phase of courtship. Fig. 25. Male mounting receptive, tipped female. Note that male's right antenna is wrapping, by mistake, around legs of female. Fig. 26. Copulating pair immediately after release of female by male. The male will now right himself.



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Figs. 27-30. Courtship in *E. albida*. Fig. 27. Male orienting. Fig. 28. Same. Fig. 29. Same. Note in this and other figures that the male genitalia are partially extruded. Fig. 30. Male orienting on female of *E. atrivittata*.


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Figs. 31-34. Resting and courtship behavior in *E. atrivittata*. Fig. 31. Male at right, resting with left front tarsus on elytra of female. Individuals of this species, unlike those of other species of the Albida Group, are relatively tolerant of physical contact by conspecifics. Fig. 32. Male orienting on female during courtship. Fig. 33. Same. Fig. 34. Whipping of right antenna by an orienting male.

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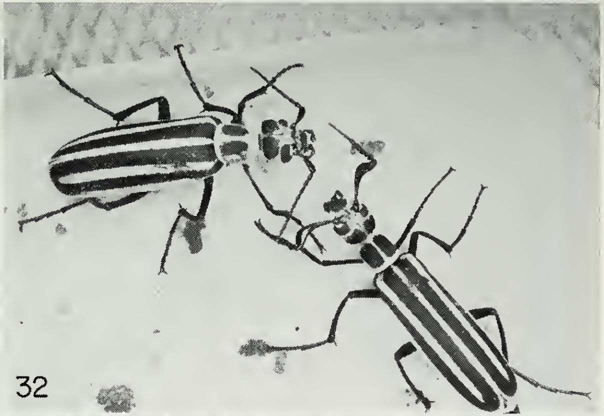

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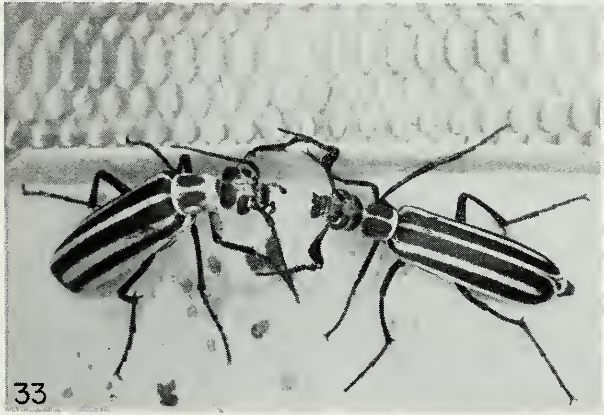

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Figs. 35-38. Courtship in *E. atrivittata*. Fig. 35. Male orienting on unreceptive, passive female which has lowered the head. Fig. 36. Same, but male is closer to female, preparatory to wrapping the antennae. Fig. 37. Male whipping antennae before unreceptive female. Fig. 38. Male attempting to wrap antennae of an unreceptive female from a mounted position.


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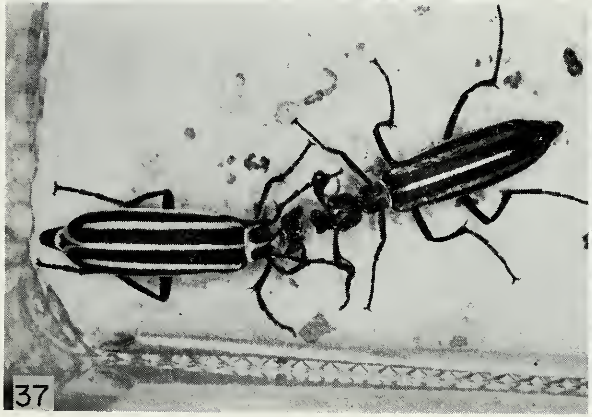
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Figs. 39-42. Courtship and precopulatory sequence in *E. sublineata*. Fig. 39. Male at right, orienting. Fig. 40. Same. Fig. 41. Male touching female with left antenna. Fig. 42. Male in mounted position on female.


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Figs. 43-46. Courtship in *E. immaculata.* Fig. 43. Male at bottom, orienting. Fig. 44. Same. Fig. 45. Male at right with antennae withdrawn after kick or sudden movement by female. Fig. 46. Male in abortive mount of unreceptive female.

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Figs. 47-50. Courtship and precopulatory sequence in *E. valida*. Fig. 47. Male at left, orienting. Fig. 48. Male about to execute antennal press. Fig. 49. Male mounting female from rear while pressing antennae on her elytra. Fig. 50. Male with middle legs lifted preparatory to turning off.


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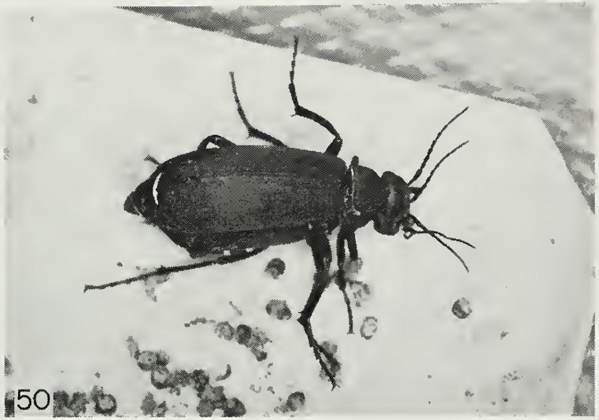
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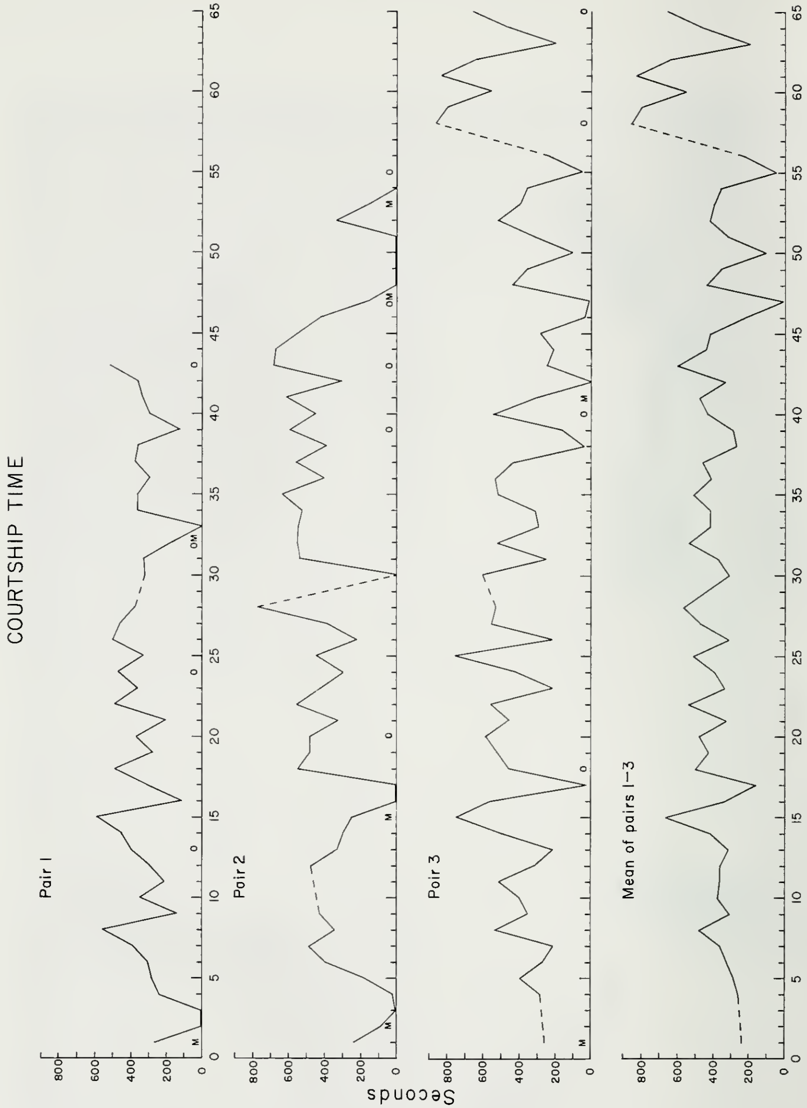


Fig. 51. Time spent in courtship by three pairs of *E. immaculata.* Data were obtained during the first 15 minutes of a daily 30-minute period of exposure of pair members to each other from shortly after emergence of adults until death of the female. The top three graphs are records for the pairs separately; the bottom graph presents daily means. In computing means, records for a period in which copulation occurred and those for the following two periods were omitted. Days on which oviposition and copulation occurred are marked with the symbols O and M respectively.

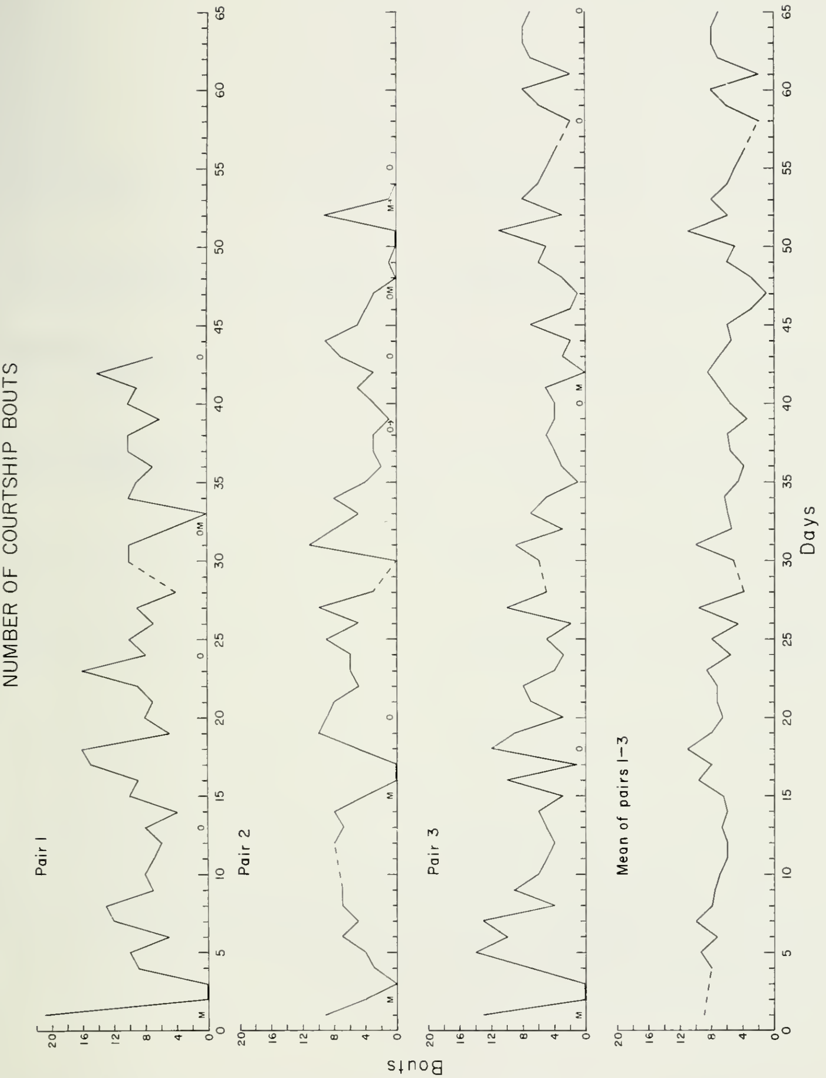


Fig. 52. Number of courtship bouts in three pairs of *E. immaculata*. For further explanation, see legend for Fig. 51.

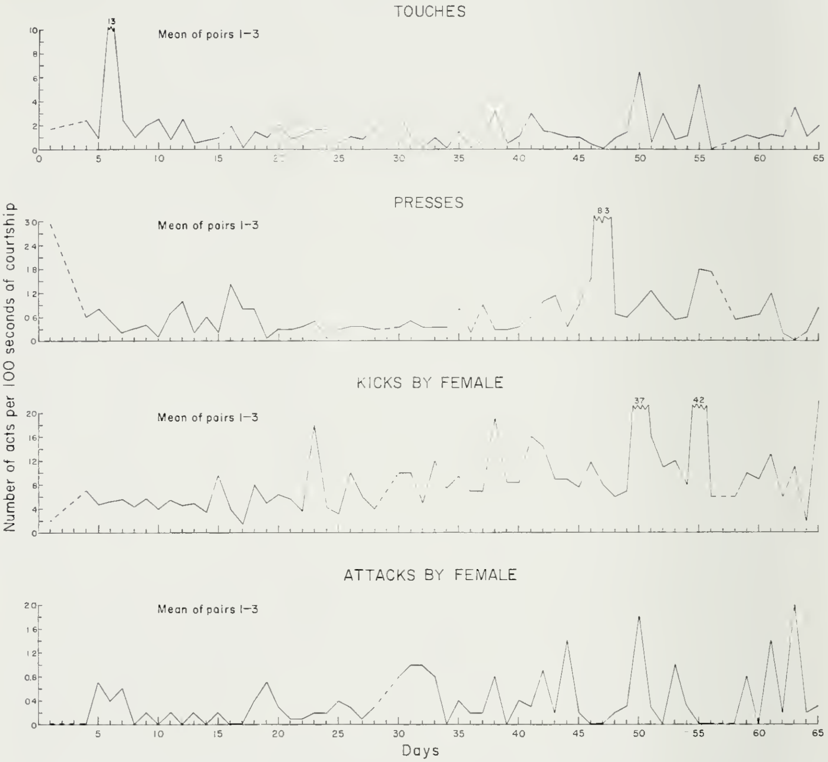


Fig. 53. Rates of occurrence of four acts performed during courtship in *E. immaculata*. Each graph is based on daily means for three pairs of beetles. Further explanation is given in the legend for Fig. 51.

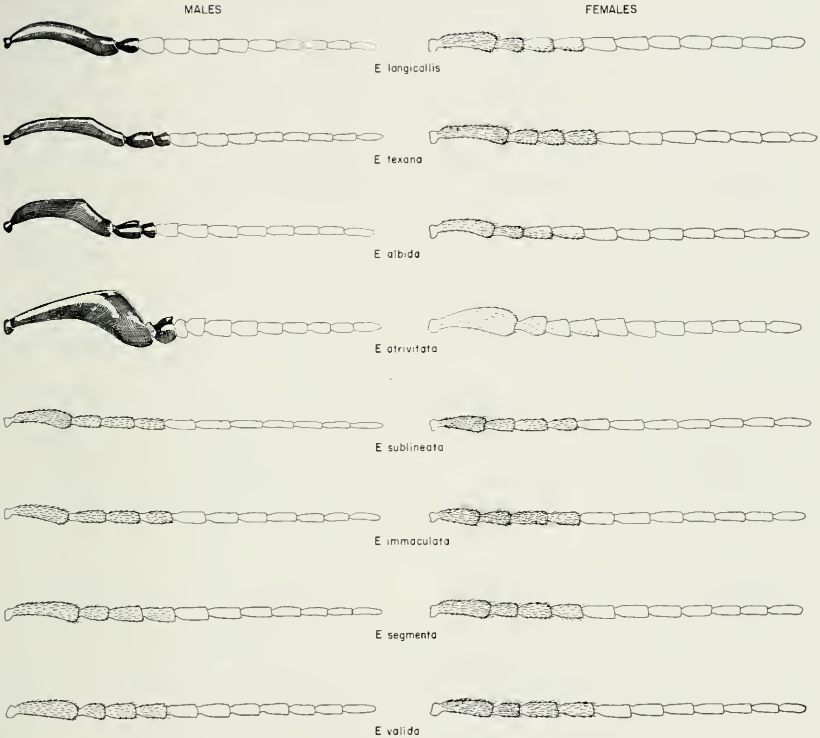


FIG. 54. Antennae of the species of the Albida Group, as labeled.

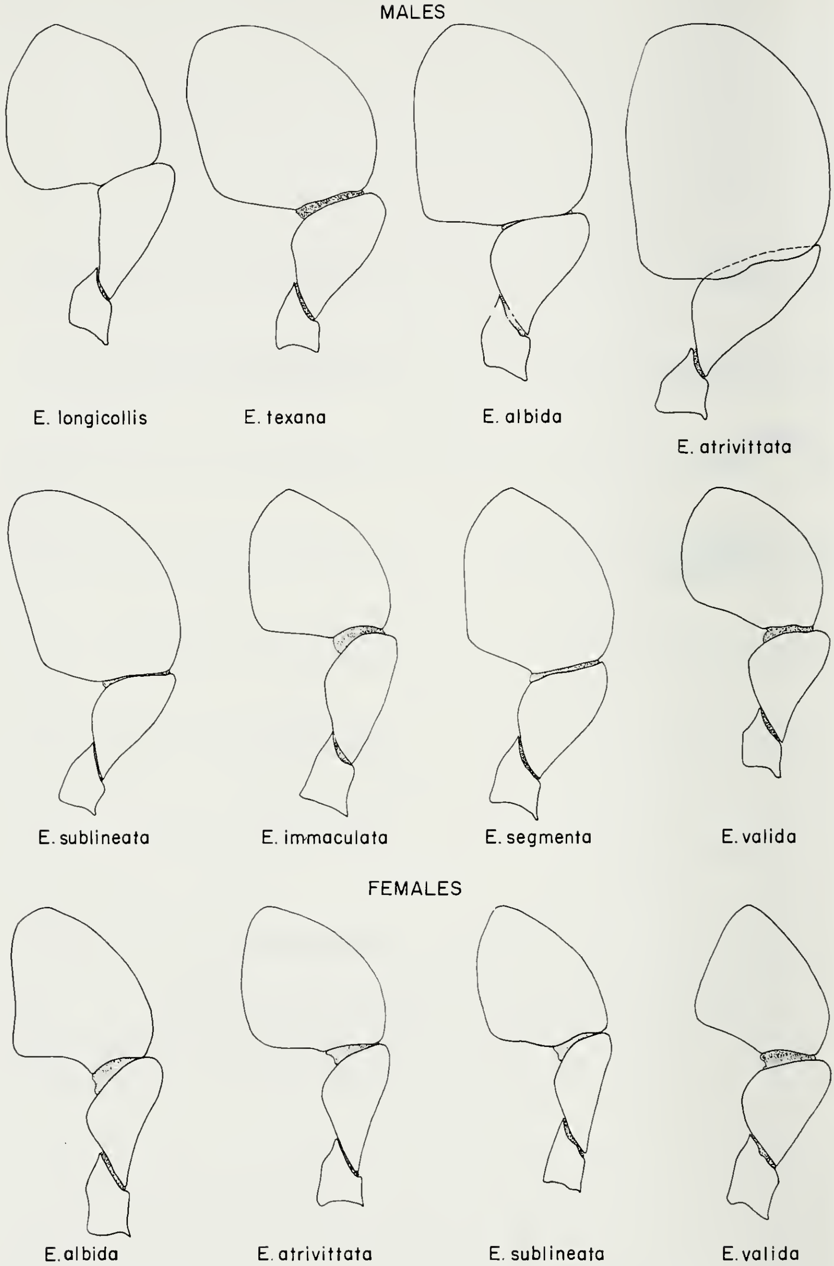
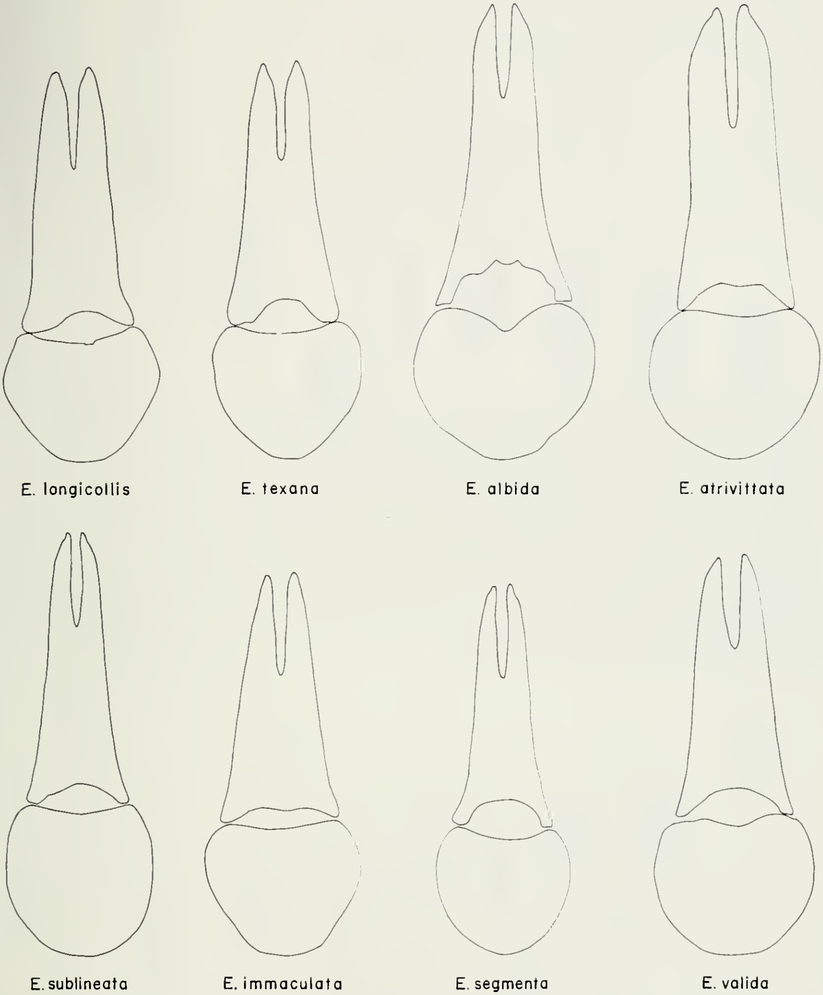


Fig. 55. Labial palpi of the species of the Albida Group, as labeled. Palpi are from adults of approximately equal body length and are drawn to the same scale. Female palpi of *E. longicollis* and *E. texana* are similar to those of *E. albida;* female palpi of *E. immaculata* and *E. segmenta* are like those of *E. valida.*

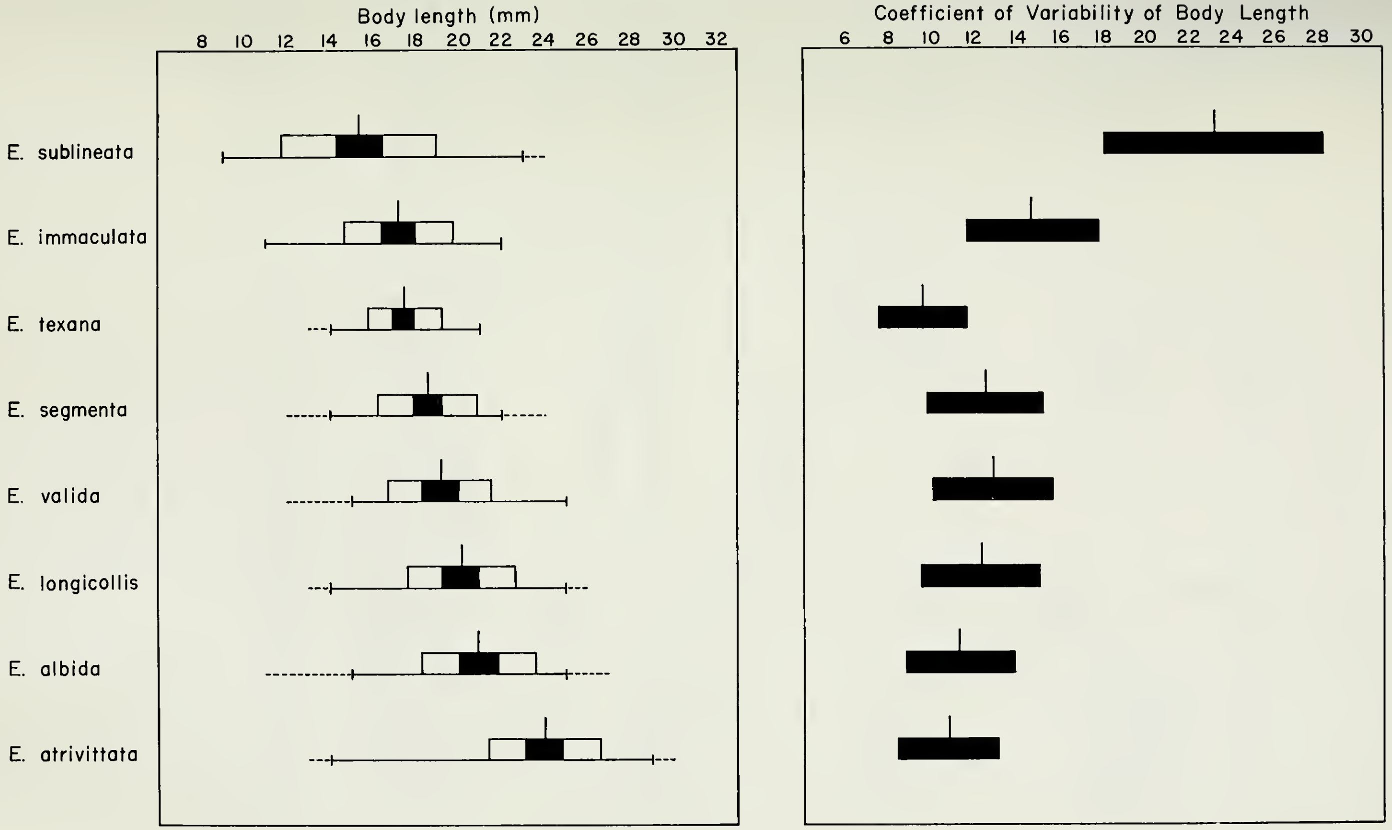


E. longicollis E. texana E. albida E. atrivittata

E. sublineata E. immaculata E. segmenta E. valida

Fig. 56. Dorsal view of male gonoforceps of the species of the Albida Group.

Fig. 57. Variation in adult body length (distance from front of head to apices of elytra) in the species of the Albida Group. N = 40 for each species. In the left graph a dashed horizontal line indicates the range among all specimens available for study, a solid horizontal line the range within the sample of 40 specimens, a vertical line the mean of the sample, a horizontal bar one standard deviation on each side of the mean, and the black portion of that bar the 95 per cent confidence interval of the mean. In the right graph a vertical line indicates the value of the coefficient of variability and a horizontal bar the approximate 95 per cent confidence interval of the coefficient (see Simpson, Roe, and Lewontin, 1960).


Body length (mm)
8
10
12
14
16
18
20
22
24
26
28
30
32
Coefficient of Variability of Body Length
6
8
10
12
14
16
18
20
22
24
26
28
30
E. sublineata
E. immaculata
E. texana
E. segmenta
E. valida
E. longicollis
E. albida
E. atrivittata

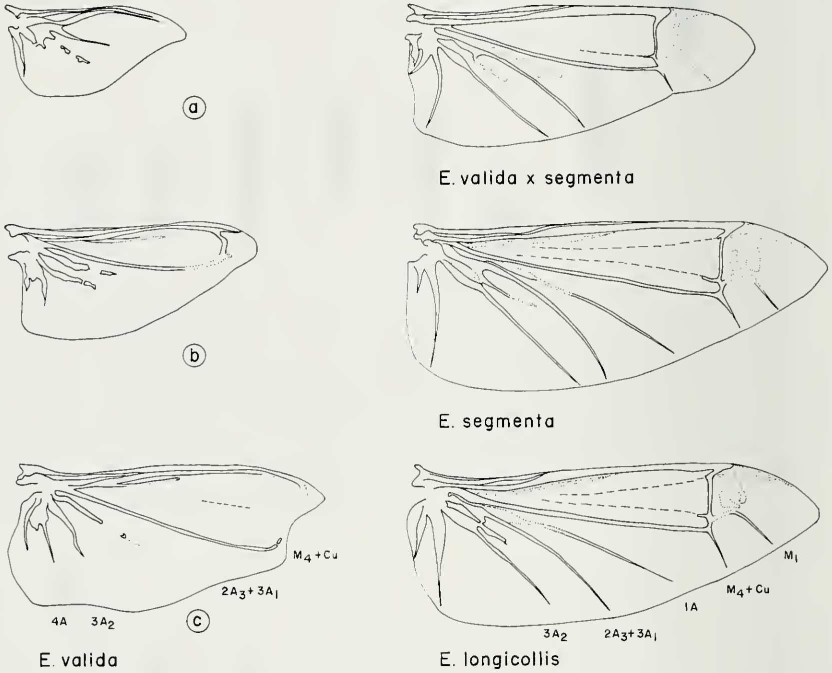


Fig. 58. Hind wings of the Albida Group, as labeled. All drawings are to the same scale. For *E. valida* the figures labeled a, b, and c show respectively wings covering 2½, 3½, and 4½ abdominal terga. The wing labeled *E. valida* × *segmenta* is that of a presumed hybrid of those species.

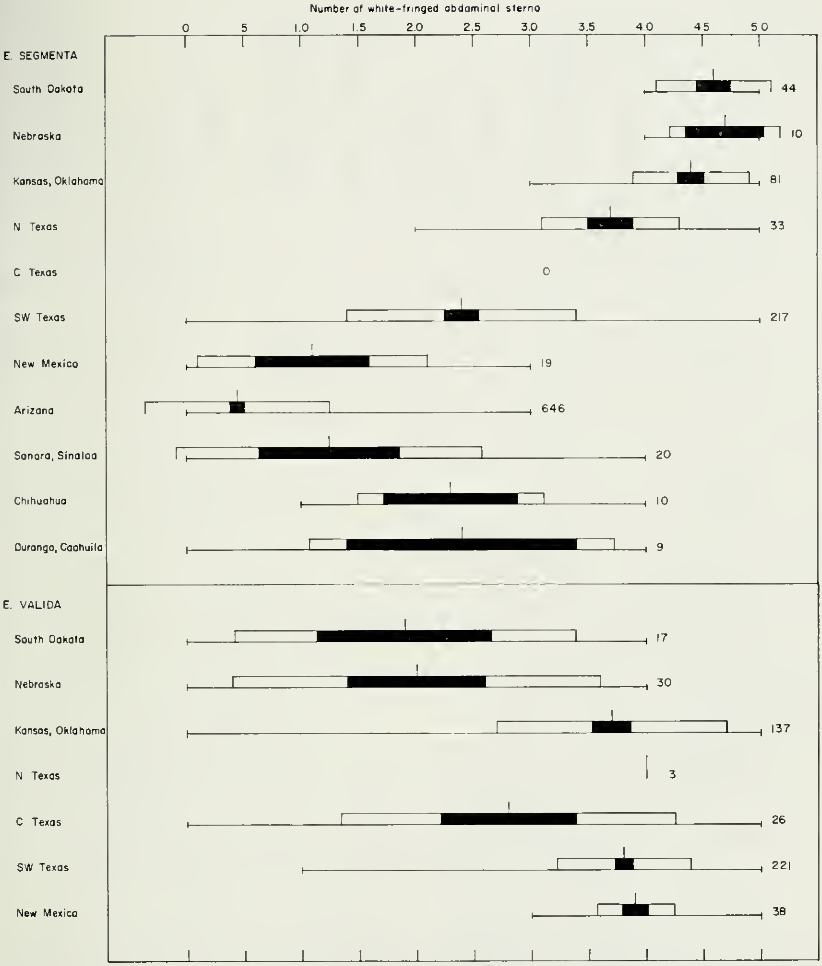


FIG. 59. Variation in the color of the clothing setae fringing the abdominal sterna in *E. segmenta* and *E. valida*. For explanation of symbols, see legend for Fig. 57 (left graph).

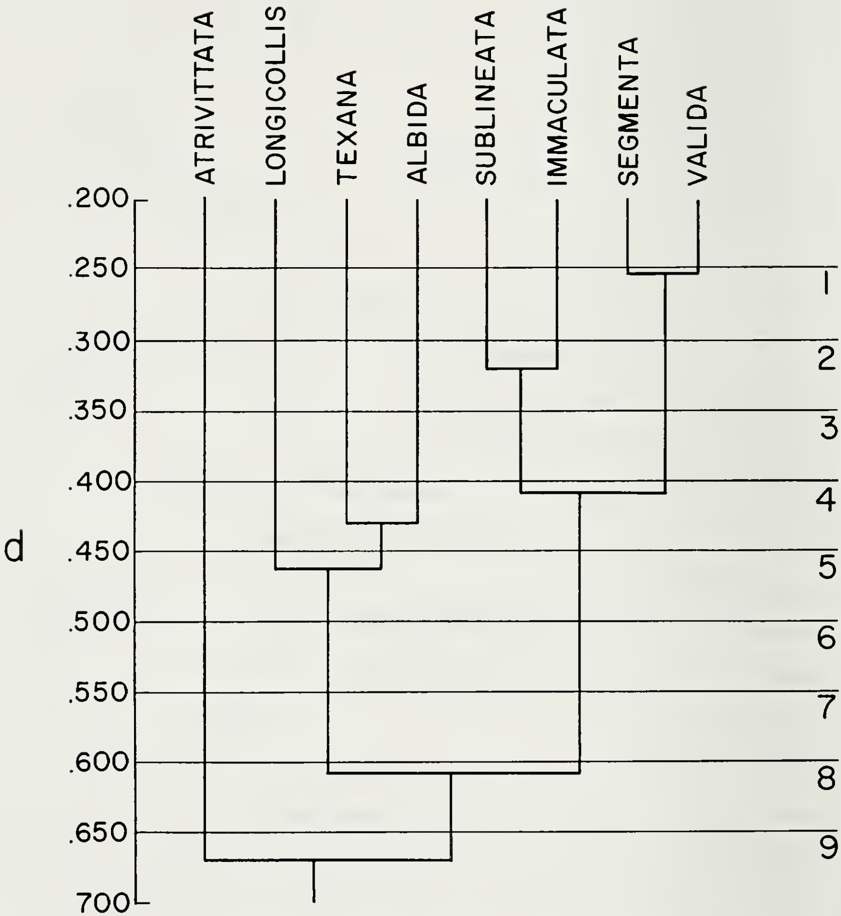


Fig. 60. Phenogram of the species of the Albida Group, based on an analysis of 39 characters of adult anatomy and sexual behavior. Average distance coefficients are scaled at the left and cophenetic values at the right. For further details, see text.

INDEX

Scientific names of species are arranged by genera except in the case of species of the Albida Group. Invalid names are italicized.

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