ENTOMOLOGICA AMERICANA

A JOURNAL OF ENTOMOLOGY.

Volume XLI (New Series)
for 1961

PUBLISHED BY THE
BROOKLYN ENTOMOLOGICAL SOCIETY
1961

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Vol. XLI (N.S.), for 1961

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Published for the Society by the
Business Press Inc.
N. Queen St. and McGovern Ave., Lancaster, Pa.
Subscription $6.00 Per Year
Date of Issue April 9, 1962

ENTOMOLOGICA AMERICANA

VOLUME XLI

A REVISION OF THE GENUS COPRIS MÜLLER OF THE WESTERN HEMISPHERE (COLEOPTERA, SCARABAEIDAE)

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INTRODUCTION

Copris Müller is a genus of principally Old World coprophagous scarabs represented in the New World primarily in North and Central America. The present work deals only with the adults of the Western Hemisphere species.

The name *Copris* is fairly old; it was coined by Geoffroy (1764) to include all those species in the Linnaean genus *Scarabaeus* characterized by the absence of a visible scutellum. However, since Geoffroy's work has been discarded for nomenclatorial purposes*, the first valid user of the name was Müller (1764), who included an indication but no species. The first valid inclusion of species was by Fourcroy (1785), who included ten species, the first of which was *lunaris* L. Fabricius did not adopt the name *Copris* until 1798 in the Supplementum Entomologiae Systematicae. Thereafter the name was in wide use but the first valid type designation appears to be that of Curtis (1832), who designated *Scarabaeus lunaris* Linnaeus as the type of the genus.

Following Olivier's (1790) very broad concept of the genus (including even many scutellate dung beetles) numerous groups were separated off as independent genera and by the end of the first third of the 19th century the name *Copris* had become restricted to a fairly homogeneous assemblage. In 1837 Hope proposed the first of several further subdivisions, in which he was followed by Burmeister (1846) and Erichson (1847). These subdivisions Lacordaire (1856) did not accept, preferring to go back to the broader concept. Nevertheless, the genera and subgenera proposed by Hope, Burmeister, and Erichson subsequently became largely accepted and it was the latter author who formulated the restricted concept of *Copris* which exists, in largely unmodified form, today, although several additional small genera have been separated off since. Recently Balthasar (1958) divided the genus into four subgenera (one of which is *Litocopris* Waterhouse, 1891).

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* Opinions and declarations rendered by the International Commission on Zoological Nomenclature, Vol. 4, Opinion 228, 1954.

All the American species belong to the subgenus *Copris* as understood by Balthasar.

There have been very few attempts at any revisional study of the large genus *Copris* and these have been restricted to relatively small geographical areas. The American species of the genus have been investigated very perfunctorily from two geographical vantage points—the United States and Central Mexico—with no attempt, until now, at coordinating the results. Fortunately, the two areas are sufficiently distinct zoogeographically that a minimum of synonymization has resulted. All the literature consists of scattered new species descriptions with four exceptions: Harold (1869), while describing most of the Mexican species, presented a key to them with short discussions of means of distinguishing them; Horn (1873) presented a key and descriptions of the four United States species known at the time; Bates (1887–1889), in the Biologia Centrali Americana, reviewed the Mexican and Central American species known to him; and Schaeffer (1906) presented a short but quite usable key to the United States species known at that time. In his review, Bates used only Harold's names, even though he was looking at several undescribed species which he attempted to fit into Harold's descriptions. As a result, the range extensions given by Bates for Harold's species, repeated in all subsequent catalogues and lists, are largely erroneous. There followed some individual species descriptions and Gillet (1911), in the Coleopterorum Catalogus, lists 16 species and two ''varieties'' for the Western Hemisphere. Thereafter there were several more species descriptions. The Leng Catalogue and Supplement (1920–1948) list eight species for the United States and Canada, while Blackwelder (1944) lists 12 species and two varieties for America exclusive of these two countries, of which one species and one variety are listed as common to both areas. Subsequently Pereira and d'Andretta (1955) synonymized one name, Matthews and Halffter (1959) described five new species and synonymized one name, and Matthews (1959) described one additional species and elevated one variety to species rank, presenting a key to the males of the Mexican species.

There were until now, therefore, 24 species and one variety known from the Western Hemisphere. The present work describes one new species and three new subspecies, elevates the one remaining variety to species rank, lowers two species to subspecies level, synonymizes two names and resurrects one, bringing the total to 23 species and five subspecies known for this hemisphere at present.

In the world as a whole the genus at present contains approximately 160 described species which are distributed about as follows among the zoogeographical regions (with some species counted twice): Ethiopian—77, Oriental—46, Palaearctic—27, Neartic—16, Neotropical—8. It does not occur in Madagascar or in Australia. The northern limits of the genus in the Eastern Hemisphere appear to coincide approximately with the 50th parallel (Kolbe, 1905), except that one species occurs very locally in southern England. Of the Coprini, this is by far the most boreal of the genera, all the others being rather strictly tropical (except *Synapsis*).

In the Western Hemisphere (map, fig. 1) *Copris* is represented in the United States east of the 100th meridian, in all of Mexico and U. S. territory immediately bordering on Mexico (except California), and in all of Central America to Panama. In South America it is represented by a single species from North and Central America occurring in the mountains of Colombia and Ecuador. It is absent from the Antilles and the Galapagos Islands. One species has been introduced by man into Hawaii.

The American forms are distributed by countries as follows:

CANADA: *f. fricator* (F.).

UNITED STATES: *arizonensis* Sch., *f. fricator* (F.), *f. cartwrighti* Rob., *gopheri* Hubb., *howdeni* M. and H., *incertus* Say, *inemarginatus* Blatch., *l. lecontei* n. sp., *minutus* Dru., *r. remotus* Lec.

MEXICO: *arizonensis* Sch., *armatus* Har., *boucardi* Har., *costaricensis dolichocerus* n. subsp., *halffteri* Matt., *incertus* Say, *k. klugi* Har., *k. sierrensis* n. subsp., *laeviceps* Har., *l. lecontei* n. sp., *l. isthmiensis* n. subsp., *lugubris* Boh., *megasoma* M. and H., *mexicanus* M. and H., *moechus* Lec., *rebouchei* Har., *r. remotus* Lec. *r. dicyrtus* M. and H., *sallei* Har.

GUATEMALA: *aspericollis* Gill., *boucardi* Har., *costaricensis dolichocerus* n. subsp., *laeviceps* Har., *lugubris* Boh.

BELIZE: *laeviceps* Har., *lugubris* Boh.

EL SALVADOR: *boucardi* Har., *lugubris* Boh.

HONDURAS: *laeviceps* Har., *lugubris* Boh.

NICARAGUA: *lugubris* Boh.

COSTA RICA: *c. costaricensis* Gahan, *incertus* Say, *laeviceps* Har., *lugubris* Boh., *subpunctatus* Gill.

PANAMA: *c. costaricensis* Gahan, *lugubris* Boh., *subpunctatus* Gill.

COLOMBIA: *incertus* Say.

ECUADOR: *incertus* Say.

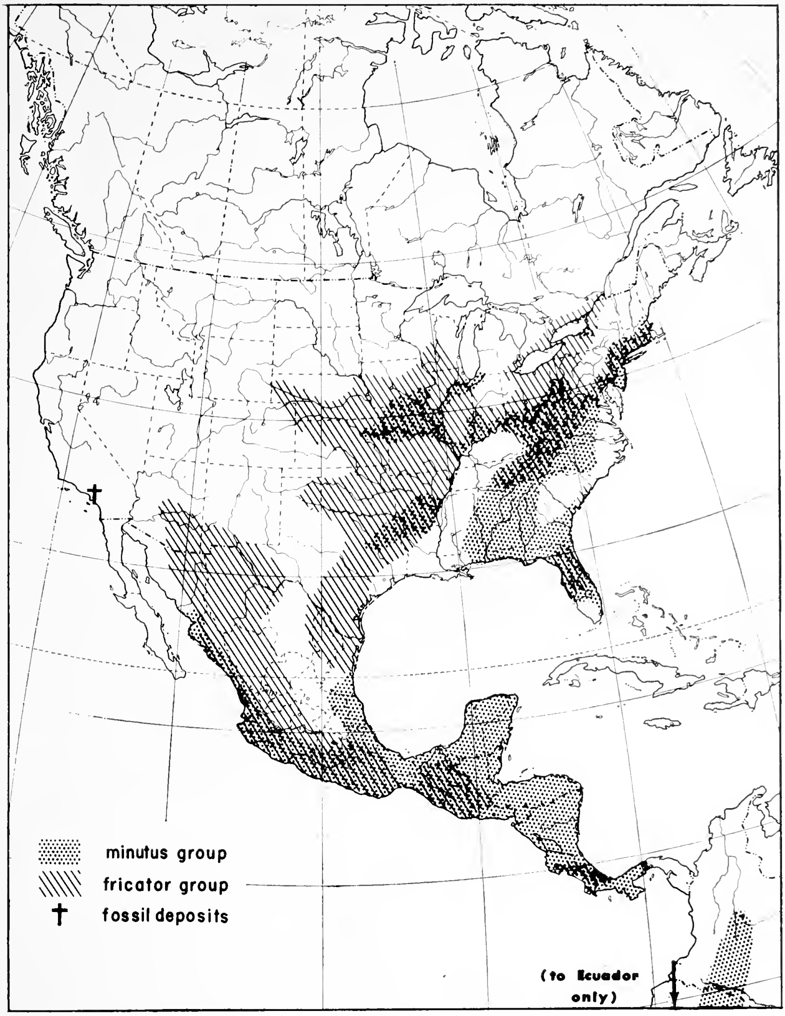

Fig. 1. The apparent distribution, based on material in collections, of the genus *Copris* in the Western Hemisphere.

MATERIALS AND METHODS

The present study was based on the collections of several institutions and individuals and was supplemented by field excursions into certain critical areas from which adequate material was found to be lacking.

The methods used were those standard to taxonomic procedure. An attempt was made to investigate cryptic characters for use in classification by examining one specimen of both sexes of each species in minute detail, dissecting it to its minimum component parts and examining all interior as well as exterior surfaces. In this manner the possible taxonomic significance of the mouthparts, antennae, wing venation, dorsal abdominal surface, metendosternite, male genitalia and female spermathecum was investigated. The results were disappointingly negative; although some characters, such as the male genital capsule, reflected species differences to a slight extent, these could be much more easily seen using external features. Consequently, the use of cryptic characters was abandoned and the study was confined to those external ''classical'' characters familiar to investigators for centuries.

In the descriptions, characters cited in the group and complex descriptions are not repeated under the species.

In the present classification the use of the male armament has been avoided completely in arriving at a natural system. However, the male armament, when developed, provides one of the easiest ways of identifying a species quickly; for this purpose facies illustrations have been provided on plates IV–VII and the first key to the species is based largely on male secondary sexual ornamentation. It is recommended that, if a series includes some major males, the first key be used for determination. However, all forms of both sexes should key through the second key.

With regard to the geographical localities cited on labels, some judicious elimination has proved necessary. If a locality written on a label appeared to be unreliable for any reason, it was disregarded. A certain amount of difficulty was experienced in locating many Mexican and Central American localities on a map. It would greatly faciliate the work of future investigators if collectors in these areas would confine themselves to citing localities which are listed in the Index to the Map of Hispanic America, 1:1,000,000 (1943, 1944). In Central America, the Department in which a town is located is essential information. In the ''material examined'' section, localities for which the department or state was given but which could not be found on any map are preceded by a question mark. Additional pertinent information not provided on the label, such as the altitude, was added to the citation in brackets. Information added to the Champion localities was obtained from Champion (1907).

In the case of certain groups of insects, such as the present one, much useful biological information can be gleaned from the data on labels if the collector includes a word about how the insect was collected. The only collector in this group who has consistently done this is the late F. Nevermann of Costa Rica.

All illustrations are by the author. The facies illustrations (plates IV–VII) showing the male armament were drawn by eye with the aid of proportional dividers. These illustrations are meant to show only the overall aspect of the forebody of a major male of each species and a general indication of the distribution of simple and complex punctures. Such details as the distribution of setae and the proportions of the mouthparts are only roughly indicated and not meant to be exact. The mouthparts and genitalia illustrated were mounted on slides and projected on paper with a standard projector. All other illustrations except the nest diagrams were done with the aid of an ocular grid and cross-lined paper. The nest diagrams were redrawn from field sketches and measurements.

A total of 3,400 specimens was examined, including the holotypes of 14 names. Many of the Mexican species were described by the Baron de Harold. Harold's types are presumed to be in the Paris Museum, but I was unable to obtain verification from that institution. Fortunately, Harold's descriptions, although short, are excellent and little doubt remains in my mind as to which of his names belongs to which species.

ACKNOWLEDGEMENTS

I wish to thank the curators of the collections at the following institutions for the loan or examination of material: American Museum of Natural History (AMNH), British Museum (Natural History) (BM), California Academy of Sciences (CAS), Carnegie Museum (CM), Cornell University (CU), Defensa Agrícola (Mexico) (DA), Department of Agriculture (Canada) (CNC), Musée Royal d'Histoire Naturelle (Brussels) (MRHN), Museum of Comparative Zoology (MCZ), Naturhistoriska Ricksmuseum (Stockholm) (NR), Instituto Rockefeller (Mexico) (IR), Philadelphia Academy of Sciences (PAS), United States National Museum (USNM), University of Kansas (UKs), University of Michigan (UMich).

In addition, the following individuals generously made available material from their private collections: O. L. Cartwright (Washington) (OLC), G. Halffter (Mexico) (GH), H. F. Howden (Ottawa) (HH).

I am particularly indebted to the following scarab specialists for invaluable advice and encouragement: V. Balthasar (Prague), O. L. Cartwright (Washington), G. Halffter (Mexico), H. F. Howden (Ottawa), A. Martínez (Buenos Aires), F. S. Pereira (São Paulo).

Mr. R. A. Crowson of Glasgow kindly made comparisons of specimens with a Fabrician type in the Hunterian Collection.

Drs. S. E. Neff and O. S. Flint, formerly at Cornell University, provided much help in the field work in Central America and North Carolina respectively.

MORPHOLOGY

The morphology of the adult Scarabaeinae has been the subject of some investigations. Hardenberg (1907) presented an excellent discussion of the mouthparts of *Pinotus carolinus* (L.), *Copris fricator* (F.), *Canthon pilularius* (L.), and several other Coprini, plus many other scarabs. Mohr (1930) compared the external morphology of *Canthon pilularius* (L.) with that of an aphodiine and a geotrupine. Halffter (1952) discussed aspects of the external morphology of *Phanaeus quadridens* Say. Pereira and Martínez (1956) presented illustrations of the mouthparts and genitalia of many Canthonini and Matthews and Halffter (1959) discussed the external morphology of a species of *Copris*. For purposes of comparison, frequent mention is made below of some of these papers and of one on a melolonthine (*Amphimallon majalis* Razoumowski) by Butt (1944) because of the detail in which the morphology of this species is there treated.

The following discussion is confined to those features of the external morphology of adult *Copris* which are of taxonomic significance, i.e. which may serve to distinguish the genus from others closely related or which vary among the species.

MICROSCULPTURE

The interpunctural surfaces are generally quite smooth in the American species except in *fricator* and *howdeni*, where the surfaces show a very fine shagreening.

The punctures are of two basic types which in turn vary importantly among the species groups and complexes:

1. Simple punctures. This term refers to simple surface depressions which have no raised areas within them and which usually have indistinct edges. They are found on the dorsal head surface and on the convex portions of the pronotum and elytra in all species.

2. Complex punctures. These are of varying type but always show a raised area within them and sharp edges. The raised area may or may not bear a seta; in the former case the puncture is said to be setigerous or umbilical and setigerous; in the latter it is said to be simply umbilical or, if very large, annular.

The following areas show round setigerous punctures with the seta more or less erect (fig. 23): along the posterior margin of the inner, smooth area of the proepimeron, on the sternellum, the mesosternum, the mesepimeron, occasionally the median lobe of the metasternum and the median coxae, and the abdominal sterna.

All other areas with setigerous punctures show a reniform type (fig. 21), which is a setigerous puncture one side of which has been pushed in with the result that the seta appears to issue from the side of the puncture and is recumbent, being directed away from the pushed-in edge.

The following areas normally show round or oval umbilical punctures which are not setigerous (figs. 20, 22): the dorsal surface of the genae, the frontal area behind the horn, all depressions on the pronotum and the pygidial surface.

Finally, some species complexes show a remarkable modification of the inside surface of the punctures, which is distinctly granulate (when seen at above 90 × magnification) (figs. 20, 21). This type of surface is seen inside all complex punctures, of whatever type, which are large enough to show the inner surface, on both the dorsal and ventral body surfaces. Punctures of this type are said to be granular and occur throughout the *minutus* species group, recurring in the *fricator* group only to a lesser extent in the *rebouchei* complex.

HEAD

The cephalic taxonomic characters which are not self-explanatory are the following:

Posterior oblique carina.—This is a carina on the dorsal surface which runs from just behind the eye obliquely inward towards the base of the horn. When present, it is usually very sharp immediately near the eye and then stops abruptly, being continued inward and forward by a raised ridge of varying sharpness (fig. 25, poc).

Transverse occipital groove.—Running very near the edge of the dorsal portion of the occipital margin is a groove bearing short, closely set setae (figs. 24, 25, tog). This groove may be complete across the entire occipital margin, or it may be divided into three approximately equal parts with the lateral ones displaced slightly forward (fig. 25). Occasionally the median section is missing.

Transverse occipital carina.—This is a carina of varying sharpness which runs in front of and closely parallels the transverse occipital groove (fig. 24, toc). It is found only in the *incertus* complex.

Immediately behind the front margin of the head dorsally is a row of seta tufts which are most conspicuous medially but which extend for varying distances laterally and posteriorly, sometimes extending onto the genae. The extent of this row of tufts apparently varies significantly among the species, but this character was not used in the classification because of the difficulty of seeing the setae in worn specimens.

The mouth cavity is rectangular in shape and is margined with a very broad, smooth margin which is anteriorly drawn out into a point. The shape of the mouth cavity differs somewhat in different coprine genera.

MOUTHPARTS

The mouthparts of *Copris* and all other Scarabaeinae are quite remarkable for their modification of a basically primitive type towards very highly sensory and membranous appendages (plate II). A good description of the mouthparts of *Copris fricator* (F.) (= *C. anaglypticus* Say) is given by Hardenberg (1907). Since the mouthparts do not appear to provide useful taxonomic characters at the species level in this genus, they will not be further discussed here.

PROTHORAX

The prothoracic taxonomic characters which are not self-explanatory are the following:

Lateral pronotal carina.—This is a carina which runs from an anterior point on the pronotal lateral margin upwards and backwards to pass just under the lateral fossa, after which it disappears. It is absent in the *minutus* group.

Prosternal-proepisternal suture (fig. 26. pp).—This is the suture between the anterior portion of the prosternum and the pleuron. In the *incertus* complex it appears carinate because of a deep depression of the pleural surface immediately next to it.

Pleural elements.—The interpretation of the lower surface of the prothorax adopted here differs radically from that of many coleopterists (who call the entire lower surface the sternum) and that of Butt for *Amphimallon,* but agrees with that of Mohr and Halffter. Butt considers the lateral portions of the lower surface as parts of the pronotum, which is therefore believed to join directly with the sternum with a resultant complete inflection of the pleural elements, which Butt considers to be represented only by a tiny sclerite fused to the dorsolateral wall of the pronotum on the inside.

In my opinion, it is more logical to assume merely that the sutures delimiting the pleural sclerites, seen in the primitive Coleoptera, have become completely fused and effaced in order to reinforce the prothorax. This would mean that most of the under surface lateral to the sternum in scarabs is made up of pleural elements fused together.

On this pleural area in *Copris* there is seen a distinct oblique carina running from the coxal cavity outward (fig. 26, pc). This carina is absent in many coprines and other scarabs and may be assumed to be a secondary modification evolved to further reinforce the prothorax. For the purposes of convenience, the area anterior to this carina is called the proepisternum, and that posterior to it is called the proepimeron. However, it should be understood that these areas do not in all probability correspond to the true morphological sclerites called by these names.

The longitudinal proepimeral carina.—The proepimeron in *Copris* and a few closely allied genera bears another characteristic carina which arises perpendicularly from the posterior proepimeral margin and quickly fades out (fig. 26, lpc). This carina serves to partly delimit a densely, setigerously punctate outer area of the proepimeron from an almost smooth inner one (except in *C. minutus*).

PTEROTHORAX

Very few taxonomic characters have been found in the pterothorax and all are self-explanatory. The proportions and shapes of the sclerites do not differ among the American species of *Copris.*

ELYTRA

There are ten distinct elytral striae in the genus *Copris*, of which the ninth is practically always present only for its posterior half and lies very close to the tenth. The eighth stria is of great taxonomic importance and may be present merely as a short segment near the middle of the sides, in which case it is said to be obsolescent, as a line more or less interrupted posteriorly at the hind angles, in which case it is said to be incomplete, or as a complete, uninterrupted line.

LEGS

The general shape and proportion of the legs in *Copris* may be seen in fig. 26. There is one strong spur terminally on the anterior tibia, called the forespur, the shape of which is of great taxonomic significance.

The fore coxae are elongated cylinders very deeply sunk into the prothorax (fig. 27). They are rigidly pivoted at the two opposite ends of this cylinder such that the only possible movement is a rotation. The outer pivot consists of a knob formed by an invagination of the pronotal surface, called the lateral fossa of the pronotum.

The median coxae are oriented parallel to the body axis and widely separated. Their ventral (visible) surfaces are longitudinally obtusely carinate. The area exterior to this carina is called the outer face of the median coxa.

The arrangement of setae on the middle and hind tibiae was found to be of taxonomic significance with regard to two sets of setae, as follows:

Ventral seta tufts, also called distal seta tufts (fig. 49, st).—These terms refer to a row of tufts on the lower surface of the tibiae. The tibia is seen to be quadrate in cross section with a row of teeth and setae running down each ridge forming the corners. The ventral seta tufts are situated along the middle of the ventral face between the usual ridge setae and are usually confined to the distal end.

Supplementary setae (fig. 50, ss).—These are confined to the *incertus* complex and consist of an oblique row of very few, indistinct setae near the distal end of the dorsal tibial surface.

The tarsi are unmodified and always present. Each segment is somewhat expanded distally and gradually diminishes in size apically. There is some variation in the comparative width of the tarsal segments in different species, but this character was not used in the taxonomy. The tarsal claws are small, parallel, and equally developed, with a small plate-like empodium at their base.

Abdomen

The only taxonomic characters on the abdomen involve the pygidium, which may be incompletely margined ventrally. The visible sternites are six in number and do not merge together along the ventral mid-line.

The tergites of segments VII and VIII are of particular interest because they make up the ventral portion of the stridulatory apparatus. The dorsal portion of tergite VIII (the propygidium) is heavily sclerotized and bears a deep longitudinal groove medially. This groove firmly holds the down-turned median edges of the elytra in repose. The actual stridulatory surface is not on this segment, however, but on the preceding one, where it consists of a finely sclerotized median area bearing some extremely fine transverse ridges. These ridges rub against some similar ridges or teeth on the elytral ribs when the abdomen is moved against the inside elytral surface, the groove on tergite VIII serving to keep the two parts in line.

Both sexes of every species of *Copris* I have examined show this apparatus and all those which I have collected in the field could be induced to squeak. For a discussion of stridulation in the lamellicornia the reader is referred to Arrow (1904).

Genitalia

On the whole, the male genitalia in this genus are not of any use in determining the species, at least as far as their gross aspect is concerned. The possibility that the internal sac may bear taxonomic characters was not examined.

SEXUAL DIMORPHISM

The phenomenon of sexual dimorphism in the lamellicorn beetles has been the subject of much speculation but, unfortunately, little organized investigation. Darwin (1871) used the scarabs as examples for his celebrated theory of sexual selection. Since then the diversity and possible uses of the horns or enlarged mandibles in the lamellicorns have been discussed in numerous works. It is not the purpose of this discussion to review this voluminous literature; for a recent survey the reader is referred to Arrow (1951). For some of the theoretical implications of horn allometry in the scarabs see Huxley (1932) and Paulian (1935). An excellent recent quantitative survey of horn allometry in a single dynastine species is presented by Bowden (1959).

However, no one has examined the nature of the variation in horn size among related species of a single genus. It is the purpose of this survey to examine intra- and interspecific variation in horn size and general qualitative differences in armament among all the American species of *Copris*.

The Sexual Armament in *Copris*

Nearly all the males of the American species display armament of a single type: there is one horn arising from the middle of the frontoclypeal suture on the head and the pronotum bears four forwardly directed prominences in a transverse row (plates IV–VII). The median two of these prominences are variable in shape (blunt, acute, or truncated) and sometimes merge into a single process. The lateral pronotal prominences are always strongly compressed and acute when developed.

The females typically bear a transverse crest on the frontoclypeal suture of the head. This crest is low and truncate apically, transversely oval and slightly excavate in dorsal view, and its sides converge apically, are parallel, or diverge, depending on the species or degree of development. The pronotum of the female does not bear any corniform prominences but does bear a median transverse carina (sometimes interrupted medially) and a small tumosity to either side of this carina. In the species descriptions female armament of this type is simply described as ''normal for the genus.''

Following the established custom among scarabaeidists I have called specimens (male or female) showing very little or no development in sexual armament ''minor'' individuals, and those showing strong development ''major''. It should on no account be inferred that these are clear-cut categories, but rather that they represent the two extremes of a spectrum of variation. Alternately I have called these specimens poorly developed and well developed, respectively.

The following exceptions to the above descriptions of armament are seen in the American species:

In the *minutus* group, the female head horn (or crest) is narrow, high, and rather corniform but still apically truncate in the *incertus* complex, completely corniform (apically acute) in the *minutus* complex. In the latter complex, in fact, it is very difficult to distinguish between the sexes, since the pronotal armament is often scarcely developed. The *incertus* complex is further distinguished by the presence of a corniform tubercle on the frons of the male behind the head horn.

In the species *halffteri* Matthews an extraordinary reversal has taken place: the male has acquired female armament. This phenomenon must not be confused with the similarity to females shown by very minor males of many species. In *halffteri* the males I have seen are well developed and show strong armament, but this is always of an exaggerated female type (fig. 77) which few females of any species ever achieve, because they are seldom so developed. This species is apparently very localized and shows strong affinities with a common and widespread species (*C. rebouchei* Harold), from which it evidently evolved. It is interesting that this form, which is most certainly a separate species, is completely sympatric with its parent species, both having been found in the same pile of cow dung.

Intraspecific Variation in Horn Height

The measurements used in the following analysis represent the height of the male head horn from the edge of the clypeus to the tip of the horn in direct front view. This is compared with the maximum length of the hind femur in ventral view. The measurements were carried out with an ocular micrometer at 9 × magnification, the units used being one micrometer unit or .097 mm in this case. Since only ratios are dealt with, the measurements were not converted to millimeters. For calculating curvilinear regression lines, a constant factor was subtracted from each measurement of horn height to insure that the horn itself, and not also the height of the frons, was being taken into consideration. This factor was taken as the height from the clypeal edge to the tip of the frontal protuberance in the least developed specimens (those with no horn as such) of the species involved.

The mathematical interpretations of the curves obtained were taken to be either the "simple heterogony" formula of Huxley (1932) ($y = bx^k$, where y represents the magnitude of the differentially growing organ—in this case, the horn, x represents the magnitude of the animal or some reference structure—the femur, and b

Table I. Regression of Male Cephalic Horn Height (y) on Length of Hind Femur (x) in 14 Species of *Copris*.
1 unit = .097 mm

No.	Species from smallest to largest	Regression $y = ax + b'$ *or* $\log y = k \log x + \log b$	Origins of deviations $(\bar{x}, \bar{y})$	Mean horn to femur ratio $(\bar{y}/\bar{x})$	Number of individuals measured (N)
1	*minutus*	$\log y = 9.40 \log x - 12.967$	30.41, 15.42	.507	203
2	*incertus*	$\log y = 10.57 \log x - 16.192$	41.50, 17.13	.413	35
3	*costaricensis*	$y = 4.36x - 150.21$	42.67, 35.83	.840	6
	"	$(y = 9.99x - 345.65)$	37.67, 30.67	.814	3
4	*rebouchei*	$y = 4.93x - 166.59$	42.42, 42.54	1.003	24
5	*remotus*	$y = 3.95x - 278.35$	42.83, 42.42	.990	12
6	*lecontei*	$y = 3.99x - 147.38$	44.65, 30.77	.689	48
	"	$(y = 3.08x - 89.94)$	43.00, 42.50	.988	4
7	*lugubris*	$y = 5.33x - 207.34$	46.77, 41.94	.897	95
8	*klugi*	$y = 4.14x - 150.59$	48.17, 48.83	1.104	24
	"	$y = 5.86x - 251.28$	48.50, 32.93	.679	16
9	*fricator*	$\log y = 15.9 \log x - 24.294$	49.10, 21,83	.445	68
10	*moechus*	$\log y = 20.13 \log x - 32.982$	50.12, 30.34		
	"	$(y = 2.63x - 88.02)$	54.29, 54.76		
	"	combined:	52.90, 48.70	.921	60
11	*arizonensis*	$y = 3.88x - 151.59$	54.35, 59.29	1.091	17
12	*boucardi*	$y = 5.20x - 251.94$	59.22, 56.00	.946	9
13	*armatus*	$y = 6.29x - 325.59$	60.11, 52.50	.873	18
14	*subpunctatus*	$y = 4.40x - 471.39$	62.86, 57.14	.909	14
		Average of *a* except those in parentheses: 4.76		Average: .825	Total 656

and *k* are constants) or a simple linear relationship ($y = ax + b'$) such as that found by Bowden (1959), whichever seemed to fit best. These different interpretations are of no real significance, in my opinion, the linear curve probably being merely the top part of a power function curve. In the case of *C. moechus,* it seems that both a power function and a linear curve fit the data (fig. 4 and table I), with the break occurring near the middle.

It may be objected that the material measured here was taken from museum collections and therefore not collected under proper statistical sampling procedure. To this it should be pointed out that we are concerned here with the positions of curves only, not with their slope or the positions of their origins of deviation (the common mean of the two variables). It should, theoretically, make no difference *where* along a common curve a sample is taken; the subsequent plotting of these samples should reveal the position of the curve.

One of the main purposes of this study is to determine whether significant differences can be found in horn development patterns within a single species and to analyze the nature of these differences if they occur. When plotted on a graph, the data points representing horn height to femoral length ratios for an intraspecific grouping, such as a population or geographical race, could differ from those representing another grouping, or the rest of the species, in two quite different respects: 1) they could fall along only a section of a common species curve, that is to say, a race may fall near the bottom of the curve, another near the top, etc. or 2) much more significantly, one or more populations may fall along a recognizably different curve, thus showing a different allometric relationship with at least a different value of *b*.

Individual populations could not be examined in this respect since they were almost never represented in sufficient numbers. With regard to geographical groupings, however, significant differences were found within five of the 14 species examined. In *minutus* (Drury) (fig. 2) specimens from a relatively small area of the range, represented by Mobile and Montgomery, Ala. and Clarksville, Fla. (in the Florida panhandle), are seen to fall almost entirely along the extreme upper portion of the curve (open circles) with little overlap with the rest of the species (dots). Mysteriously, two specimens from this area fall near the bottom of the species curve. It will be noted, however, that all specimens from this area give every appearance of falling along the common species curve. Visually these specimens are conspicuous for their great size and horn development.

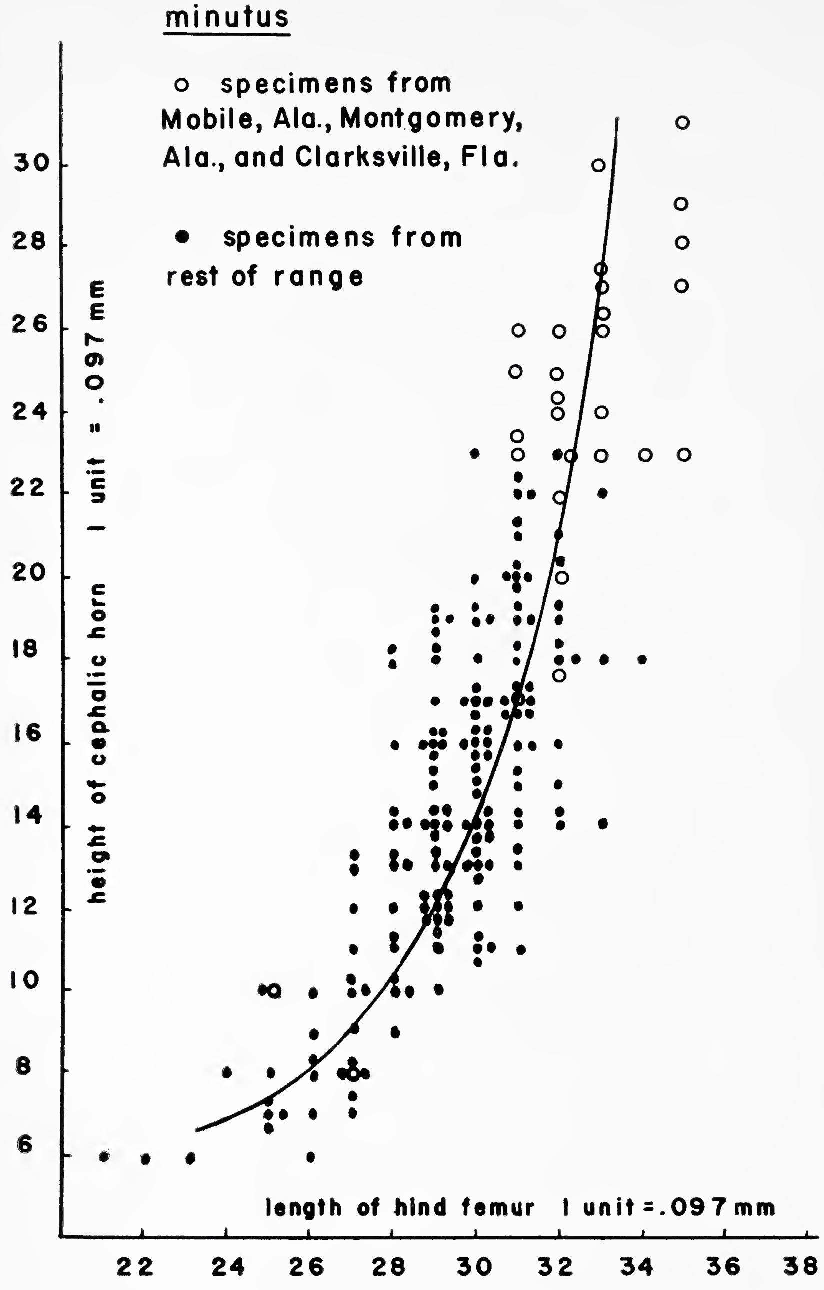

Fig. 2. *C. minutus* (Drury). Plot of horn height (y) against femoral length (x); k = 9.40 for random 25% sample (N = 53). For this and the following figures refer to text and table I for explanations of the symbols used.

In *fricator* (F.), on the other hand (fig. 3), specimens from a wide geographical area in the southwestern portion of the range (open circles) are all grouped in the lower part of the common curve. Visually these specimens also stand out, but in this case for their hornless condition and small size. Here, however, there is a suggestion that these specimens fall along a slightly different curve situated higher than the common species curve.

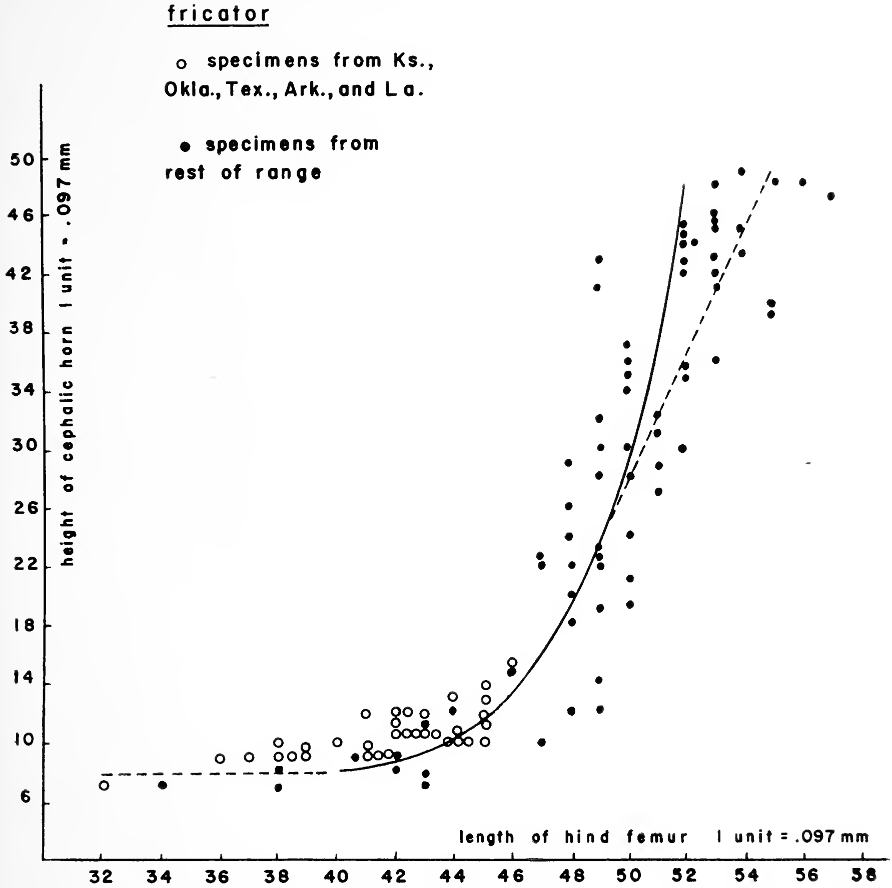

Fig. 3. *C. fricator* (F.), $k = 15.09$ for $x = 42$ to 50. Interrupted lines estimated.

The previous two examples of geographical variation come under category (1) above. The geographical race falls along a special part of the common species curve, with little or no evidence for any different allometric relationship.

The most interesting and significant type of variation is the one in which a geographical grouping falls along a totally diferent curve from the one which characterizes the rest of the species. This is unmistakably seen in three species of the genus (figs. 6–8). In the first (*klugi* Harold), when the data from specimens originating in the Sierra Madre Occidental are plotted, they are seen to fall along a line which is significantly to the right of those from the rest of the species, orignating in the Transverse Volcanic Range. The degree of significant separation may be judged by noting the extent of overlap of the 95% confidence intervals shown. Visually this difference is expressed by the northern specimens possessing consistently shorter horns for their size, in comparison with the southern form, but this difference is so slight as to be all but undetectable to the eye. This is in sharp contrast to the visually conspicuous but much less important difference in category (1) above.

This shift in the position of the relationship curve in different geographical groupings is much more strongly accentuated in two additional species: in *costaricensis* Gahan, comparing specimens from Chiapas with those from Costa Rica (fig. 7), and in *lecontei* n. sp., comparing specimens from north and south of Cabo Corrientes on the west coast of Mexico (fig. 8). For each of these three species there are therefore two separate relationship curves (table I).

In the last three examples the differences in allometric relationship are reflected in morphological differences only in the first species (*klugi*). Here the northern specimens consistently show a faint sclerotized diagonal band on the male parameres; this band is absent in the southern form. In the other two species I could detect practically no morphogical differences between the geographical groupings thus separated by their horn relationships. Hence, this procedure gives us a taxonomic tool of some sensitivity in the horned scarabs. It should further be noted that even if different geographical groups or different species fall along different curves the slopes of these curves are approximately the same, allowing for sampling error and bearing in mind the very small samples in some cases.

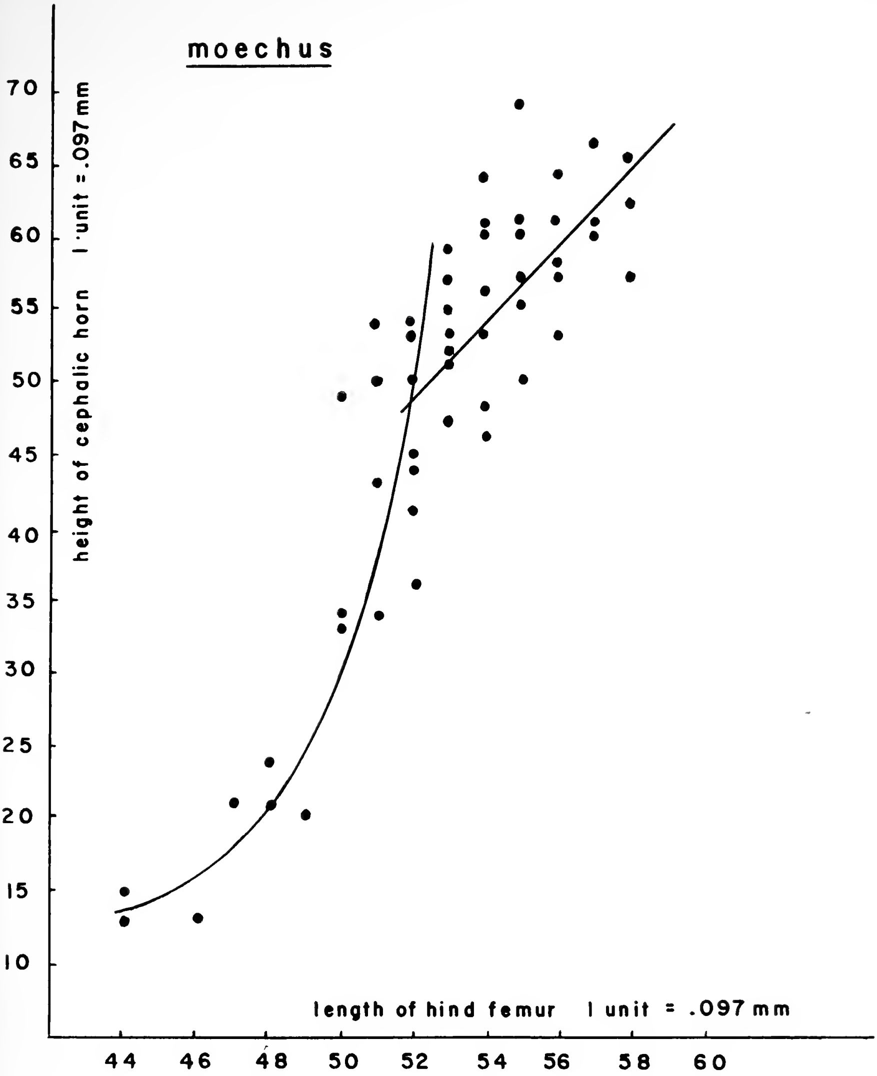

Fig. 4. *C. moechus* Lec., $k = 20.13$ for $x = 44$ to 52; $a = 2.63$ for $x = 52$ to 58.

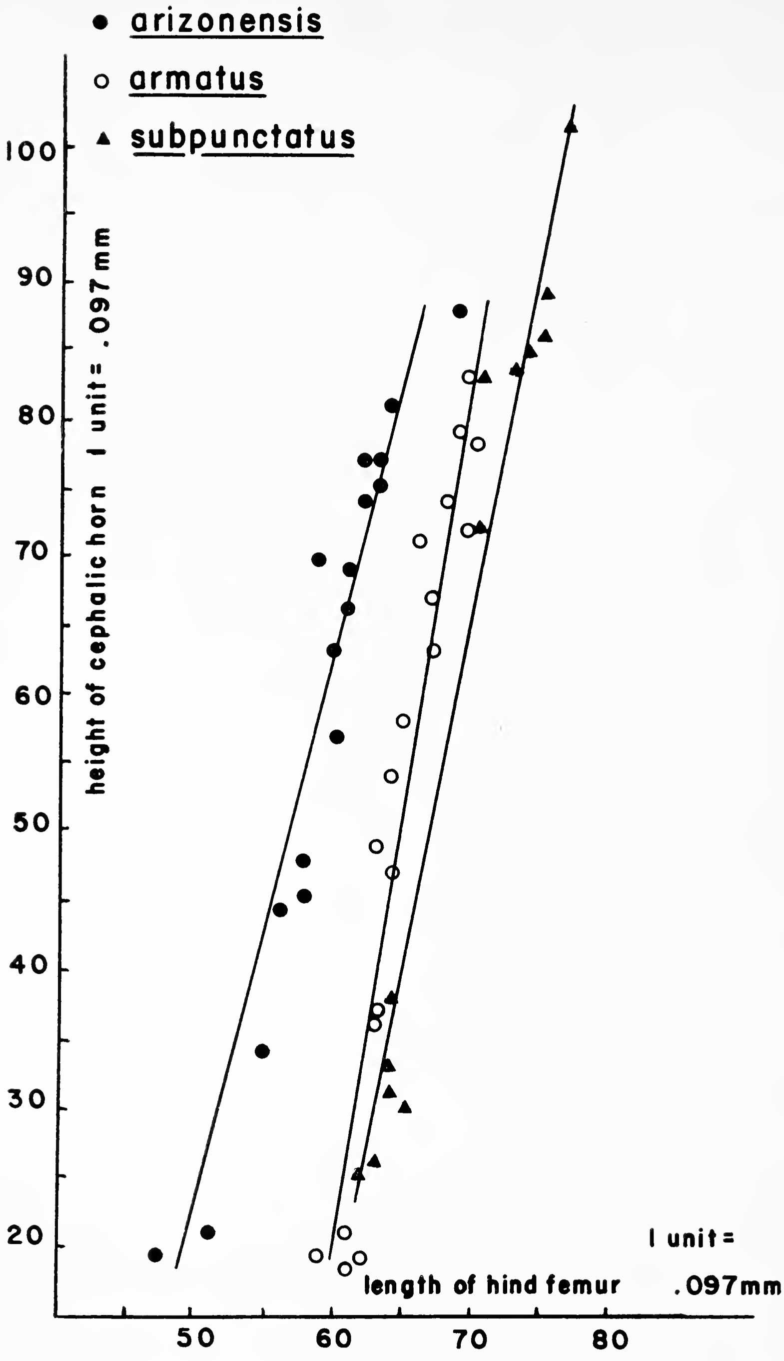

Fig. 5. *C. arizonensis* Schaeff, *C. armatus* Har., and *C. subpunctatus* Gillet, $a = 3.88$, 6.29, and 4.40 respectively.

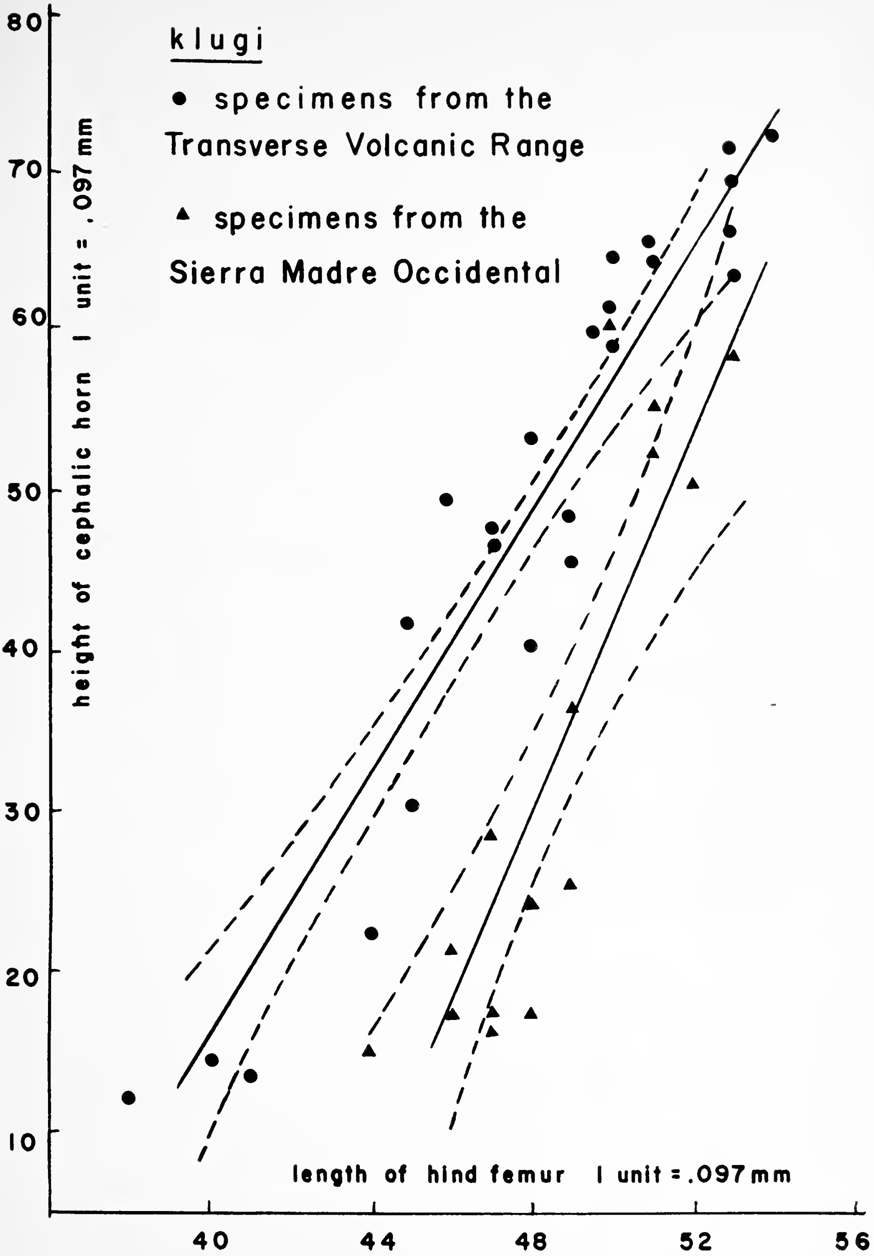

Fig. 6. *C. klugi* Har., $a = 4.14$ for Transverse Volcanic Range, 5.86 for Sierra Madre Occidental. Interrupted lines indicate 95% confidence intervals for regression lines.

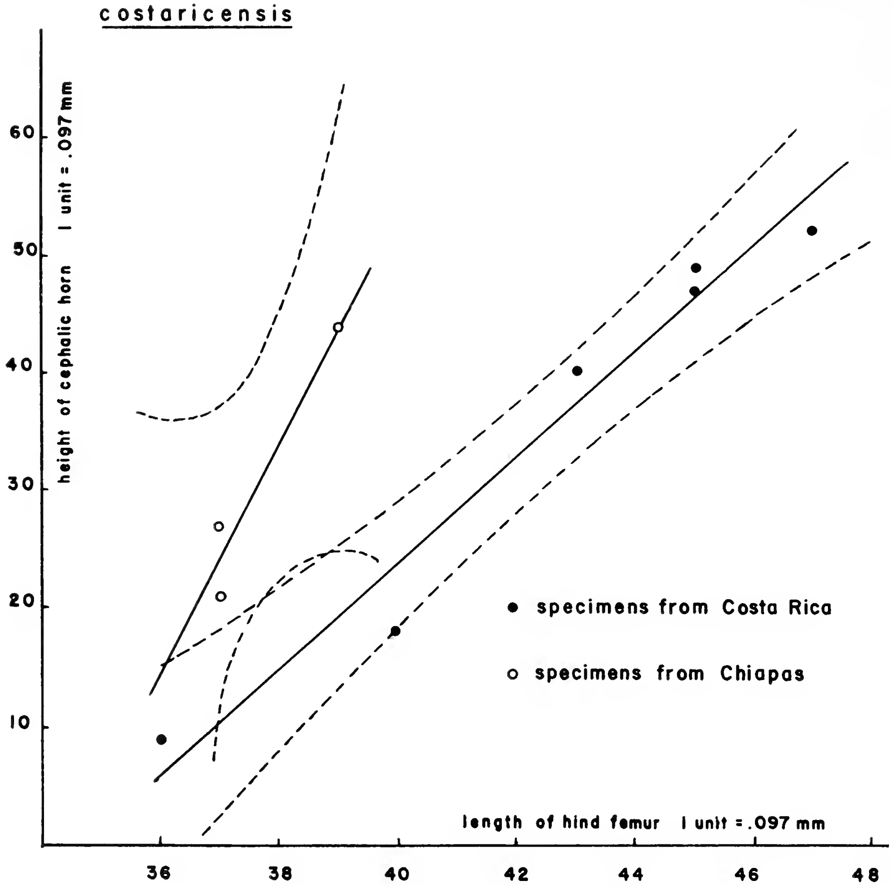

Fig. 7. *C. costaricensis* Gahan, $a = 4.36$ for Costa Rica, 9.99 for Chiapas. Interrupted lines indicate 95% confidence intervals for regression lines.

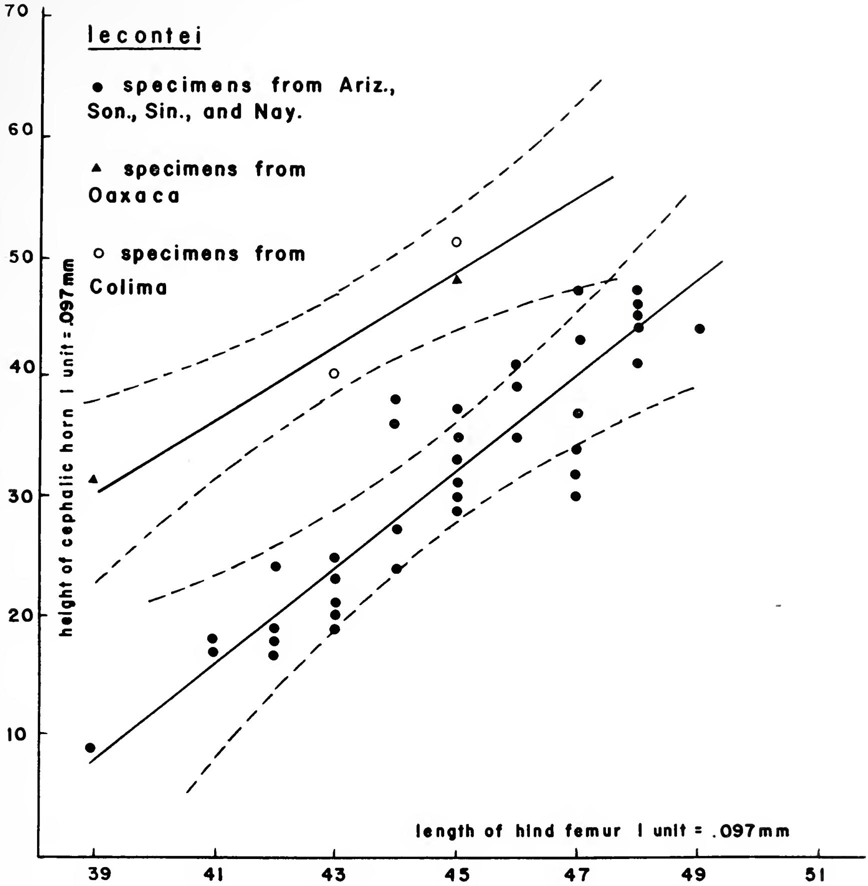

Fig. 8. *C. lecontei* n. sp., $a = 3.99$ for Arizona to Nayarit, 3.08 for Oaxaca and Colima. Interrupted lines indicate 95% confidence intervals for regression lines.

INTERSPECIFIC VARIATION IN HORN HEIGHT

It is not our purpose here to discuss the interesting theoretical implications of the species curve distributions. It should merely be noted in passing that the "rule of Lameere and Smith" (Huxley, 1932, pp. 212–216) is not at all adhered to in *Copris* (contrary to what Paulian [1935] states) but that each species falls along a curve (or two curves) of its own and that these curves are remarkably parallel (fig. 9). This is expressed mathematically in the relatively constant value of *a* (averaging 4.76) in the linear formula $y = ax + b'$ (table I). The points of origin of deviations are nearly isometric (fig. 10). This shows that there is a constant *average* proportion of horn-to-body size in all the species regardless of size and a more or less constant degree of allometry. It seems probable that the allometric nature of the horn size relationship is of selective advantage to the species, perhaps to maintain some sort of dominance hierarchy in random assemblages at food sources for the purposes of pairing off.

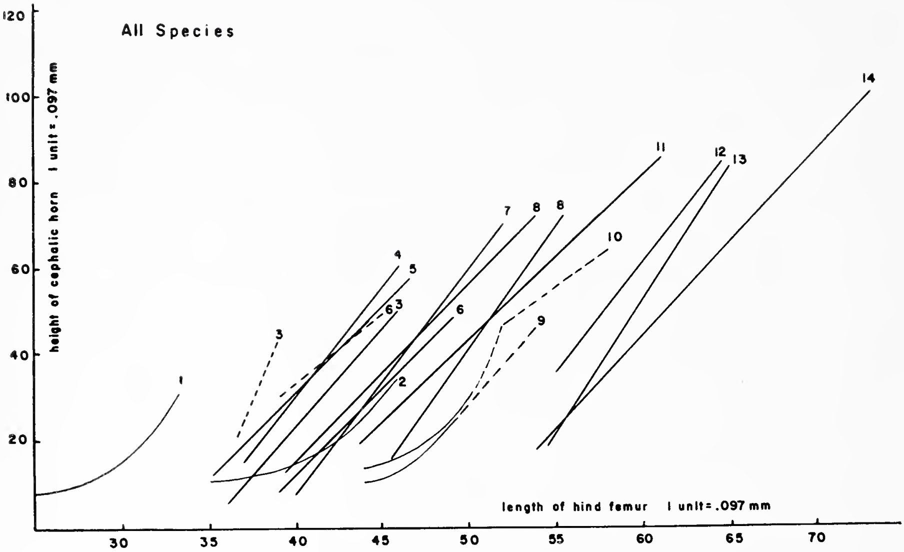

Fig. 9. Plot of horn height against femoral length; regression lines for all species measured. Interrupted lines are of relatively low reliability. Numbers refer to species as listed in table I.

There are no detectable consistent qualitative differences in horn shape or design between species to suggest in any way that the horn could have any species-recognition value. There are differences in horn design and these are very useful to the taxonomist, but these differences do not correlate with relationship or geographical distribution in any way (e.g., closely related sympatric species do not necessarily differ more strongly in horn design).

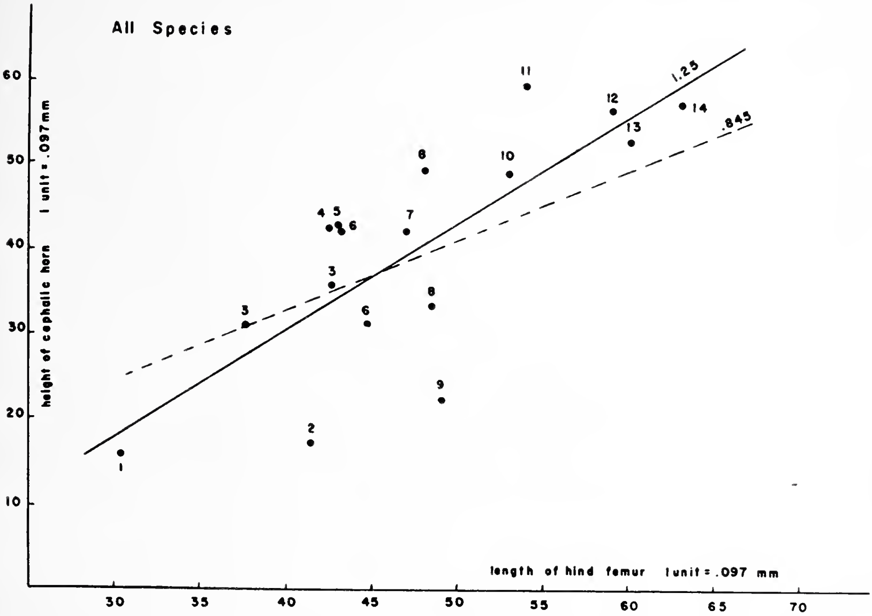

Fig. 10. Regression of mean height of head horn on mean length of hind femur for all species. Solid line represents regression of $\bar{y}$ on $\bar{x}$; interrupted line represents the line of constant proportionality (isometry). Further explanation in text. Numbers refer to species as listed in table I.

BIOLOGY

Notes on the nesting habits of five American species have been published. These will be briefly summarized below together with notes on the results of my own field observations on four species.

The available data indicate that the majority of the species of the genus feed on mammal dung, the only known exception being that of *C. gopheri* Hubbard, which feeds on the dung of the

Florida Gopher Tortoise. Aside from this, there is no evidence to indicate that any preference is shown for the dung of any particular species or type of feeder. There are scattered records of individuals occurring at carrion (these are mentioned in the systematic section under the particular species involved), but it must be borne in mind that these could be attracted to the gut contents of the carcass. There are a very few records of individuals coming to traps baited with fermenting malt, mushrooms, decaying meat, and fruit.

Insofar as I have been able to determine, the nidification behavior of the American species differs only in detail from that of *Copris hispanus* (L.) in Europe, as discussed by Fabre (1918), Siyazov (1914), and Lengerken (1954).

It appears, therefore, that biological differences between species generally do not reside in the nature of the food consumed or in the basic aspects of nidification. We may therefore expect that such differences are to be found in ecological tolerances to such factors as humidity, temperature, and so forth, so that the genus may be able to exploit the available dung food in all possible environments. One example of this may be provided by the habitat preferences shown by the two closely related species *incertus* Say and *lugubris* Boheman. The former is typical of the humid tropical forest fauna of the more elevated portions of the Veracruz region, exemplified by Jalapa and Fortín de las Flores, whereas the latter, in this region and in Oaxaca, is restricted to the open areas—the clearings in the forest and the sandy areas immediately along the sea coast (Gonzalo Halffter, personal communication).

There follow brief accounts of the nidification of seven American species the habits of which are at least partly known.

Copris fricator (Fabricius)

From my own observations in the Blue Ridge Mountains in May, 1959, the following outline of the life history of this species emerges.

Nidification is preceded by a period of adult feeding in the spring. Feeding always involves the digging of a small, shallow individual burrow about 4 cm. long beneath or beside a pile of cow dung. The burrow is filled with dung before feeding, the beetle grabbing small "armfulls" of dung and backing into the hole. Each individual of both sexes digs its own burrow independently.

Nidification begins towards the end of May in North Carolina and usually involves a pair of beetles of each sex acting in co-operation, although the female may begin the nest alone. Of 13 nests I uncovered in various stages of construction and provisioning, seven contained a male as well as the female. Of six later nests uncovered, containing completed brood ovoids, a male was present in only one, showing that the male usually departs after construction and provisioning is completed.

The completed nest is a large oval underground chamber located under the dung pile and with the measurements indicated in table II. The floor of the chamber is 5–12 cm. below the ground surface and is connected to the surface by a short passageway just wide enough to admit one beetle; this passageway is left open to the outside (fig. 82). Initially the nest is nearly filled by one large "cake" of dung which is "tended" by the female or pair wandering repeatedly over its surface. After an unknown period, the female begins cutting and shaping the brood ovoids from the dung cake (figs. 83–86). These measure about 2.5 cm. in diameter with one slightly longer vertical axis at the top of which is located a small spherical cavity containing one egg. The female evidently lays the egg and completes the ovoid before starting on the next one. The total number of ovoids seen in completed field nests varies from three to five. The larva on hatching begins to consume the inside of the ovoid, storing excrement in the characteristic coprine "hump" (an outpouching of the mid-gut). Emergence of adults in captivity from these ovoids completed in late May took place between 14 and 25 July. The continuous presence of the female in the nest was proved necessary to maintain the smooth, unblemished contours of the outside of the ovoids. Ovoids kept apart from the female soon became heavily overgrown with fungi and molds.

Lindquist (1933) indicates that the beetles overwinter singly as adults in very deep vertical burrows devoid of dung.

Ritcher (1945) described the third-stage larva of this species (under the name *tullius* Olivier).

Copris remotus Leconte

Lindquist (1935) gave an excellent account of the nesting habits of this species near Uvalde, Texas. Some of his numerical data are summarized in table II.

The points in which the nidification of this species appears to differ from that of *C. fricator* just discussed are as follows. The female apparently digs and provisions the nest alone; provisioning, with cow dung, takes one or two days. Each brood ovoid takes two

Table II. Summary of Data on the Nidification of Nine Species of *Copris*.

Species	Place	Source	Average dimensions of chamber (cm)	Average depth of bottom of chamber (cm)	Tunnel plugged	Number of brood-ovoids per nest	Average size of ovoids (cm)	Participation of male
hispanus	Provence	Fabre	10–12 × 6	20	Yes	Up to 5	4.0 × 3.4 × 3.4	to end of provisioning
"	Dalmatia	von Lengerken	9 × 7.5 × 6.5	14.5	Yes	Up to 5	4.0 × 3.6 × 3.3	to end of provisioning
"	Central Asia	Siyazov	8 × 7 × 5	70	Yes	± 5	4.5 × 4 × 4	to making of first ovoid
lunaris	captivity	Fabre	15 × 6	?	?	7–8	?	throughout
fricator	Kansas	Lindquist	3.79 × 2.8	9.78	?	?	?	?
"	NC, Va.	original	5.7 × 5 × 3.7	8.83	No	3–5	2.63 × 2.37 × 2.33	to start of ovoid formation
remotus	Texas	Lindquist	5 × 7.5 × 2.5	?	Yes	1–8 (av. 4–6)	2.5 × 2	none?
aspericollis	Guatemala	original	8 × 7 × 6	15	Yes?	?	?	at least to end of provisioning
minutus	Virginia	original	?	7	?	4	?	?
"	Kentucky	Ritcher	?	?	?	2–3	1.4 × 1.35	throughout?
gopheri	Florida	Hubbard	?	10–12.5 (beneath tortoise gallery)	?	1?	?	?
lugubris	Nicaragua	original	7.6 × 4.8 × 3.6	12.7	Yes	?	?	at least to end of provisioning
incertus	N. Zealand	Thomas	?	?	No?	2–7	1.8–2.5 diam.	to start of ovoid formation

to three days to construct and there may be up to eight ovoids per nest. The female plugs the ingress passageway with soil.

Under laboratory conditions embryonic development takes 5–10 days, the first instar 2–4 days, the second 2–5 days, the third 13–17 days, the pupa 12–37 days, for a total of 38–69 (average 49) days to complete development from hatching to adulthood. Eggs are obtained from 20 March to 10 October.

A reared female lived 644 days in captivity. Several females laid eggs over two seasons. Lindquist was able to get up to 12 nests from one female, with a total of 41 eggs. The normal appears to be 3–4 broods annually.

Copris aspericollis Gillet

I uncovered three burrows of this species under cow dung near Guatemala City on 22 July 1958. Two consisted merely of short burrows containing one female each and no dung. The third consisted of a chamber containing a dung cake and a male and female pair. No ingress tunnel could be detected, suggesting that it had been blocked with soil. Evidently, nidification in this species involves the participation of both sexes.

Copris minutus (Drury)

The only available data on this common species is provided by Ritcher (1945), who found larvae in balls of dung associated with one or two adults in a brood chamber, the number of balls being two or three. The nests are dug several inches deep in the soil under cow dung. Measurements are given in table II. The adults are usually found in the chambers with the ovoids even after the larvae have pupated. Third-stage larvae were found in April and June, pupae in July. Ritcher described the full-grown larva.

I found one nest of this species in the Blue Ridge Mountains of Virginia on 4 July, 1960, containing four brood ovoids and one female beetle.

Copris gopheri Hubbard

Hubbard's (1894) account is still the only one we have on this interesting species. He found nests in large numbers four or five inches below the floor of the nest chamber of the Gopher Tortoise near Cresent City, Florida. The brood ovoids are apparently made of tortoise dung. An important difference and apparently unique feature of this species is that the larva, when pupating, constructs a cocoon of excrement around itself. This is apparently necessary because of the friable nature of the tortoise dung. The study of the biology of this species is made extremely difficult by the enormous depth of the tortoise burrows.

Copris lugubris Boheman

I was able to uncover six burrows of this species in Nicaragua on 27 and 28 July, 1958. The important features of the nests are diagrammed in figs. 87 and 88 and measurements are given in table II. Only the preliminary, or dung-cake, stage was seen. Important points are that the ingress tunnel is blocked with loose soil, there is usually a cavity *under* the dung cake (a unique feature), and the male always accompanies the female in this stage of nest construction (digging and provisioning).

Copris incertus Say

An excellent account of this species in New Zealand, where it was introduced, is given by Thomas (1960). His account is similar to that given above for *C. fricator,* but the following points are worth noting.

On one occasion, three days after dung was exposed to beetles six burrows were dug up, four containing a female each and two containing a male and female pair. The dung cake remains intact for several weeks in the field. The egg cavity is made and the egg laid directly in the dung cake *before* the brood ovoid is cut and shaped around it. The particular process of oviposition has not been observed in the other species. Two to seven ovoids are made per nest. Development from egg to adult takes 57–70 (average 62) days in captivity. The larva and pupa are figured.

It is to be noted that there is no cavity under the dung mass as is seen in the very closely related *C. lugubris,* but that the spaces are over and around the mass, as in the other species seen.

Additional biological data taken from the labels attached to the collected material used in this revision are presented in the systematic section under the particular species involved.

TAXONOMY

The genus *Copris* Müller is completely isolated taxonomically from any other New World genus of Coprini and can easily be distinguished by the characters mentioned in the diagnosis. In the Old World, however, it shows close affinities with a number of genera, among which we may mention particularly *Pseudopedaria* Felsche (Africa), *Coptodactyla* Burmeister and *Arrowianella* Paulian (Australia). The customary grouping of coprine genera into ''subtribes'' (ending in the termination -ides) after Gillet (1911) is in my opinion so artificial that it should be abandoned.

The genus *Copris* has been recently divided into four subgenera (Balthasar, 1958), all the American species falling into the subgenus *Copris s. str.* A study of the American species, however, reveals a sharp division into two groups which would merit subgeneric distinction if the genus were purely American. As it is, it is more probable that this division represents a double invasion of North America by two ancestral Asian species, since it is not reflected in the Old World fauna. It is impossible, therefore, to erect formal categories for these two subdivisions; they have been treated as ''groups'' in the present work, each being named after the earliest described included species. Each of these groups are further divisible into subgroups, here called ''complexes'', of species which fall naturally together. There are seven such complexes, each containing a few species, some of which are extremely closely related and most of which are distributed in geographical ''chains'' (allopatrically).

Figure 11 summarizes the relationships of the species as interpreted here. In the *fricator* group, the *armatus* complex is considered the most primitive as it contains large, morphologically unmodified species (with the full complement of elytral striae, simple anterolateral angles, typical puncturation, etc.). It will be noted that the geographical distribution of the groups suggests that the center of evolution for the genus in the New World is the northern Mexican highland region and that species become more evolved as they radiate out from this center.

There is a further suggestion, derived from the close relationships between the species within the two groups, that the genus is at present rather actively speciating in the New World and may therefore be of rather recent immigration, probably from Asia via the Bering bridge. Certain Chinese species I have seen (undetermined) bear a striking similarity to *incertus* Say.

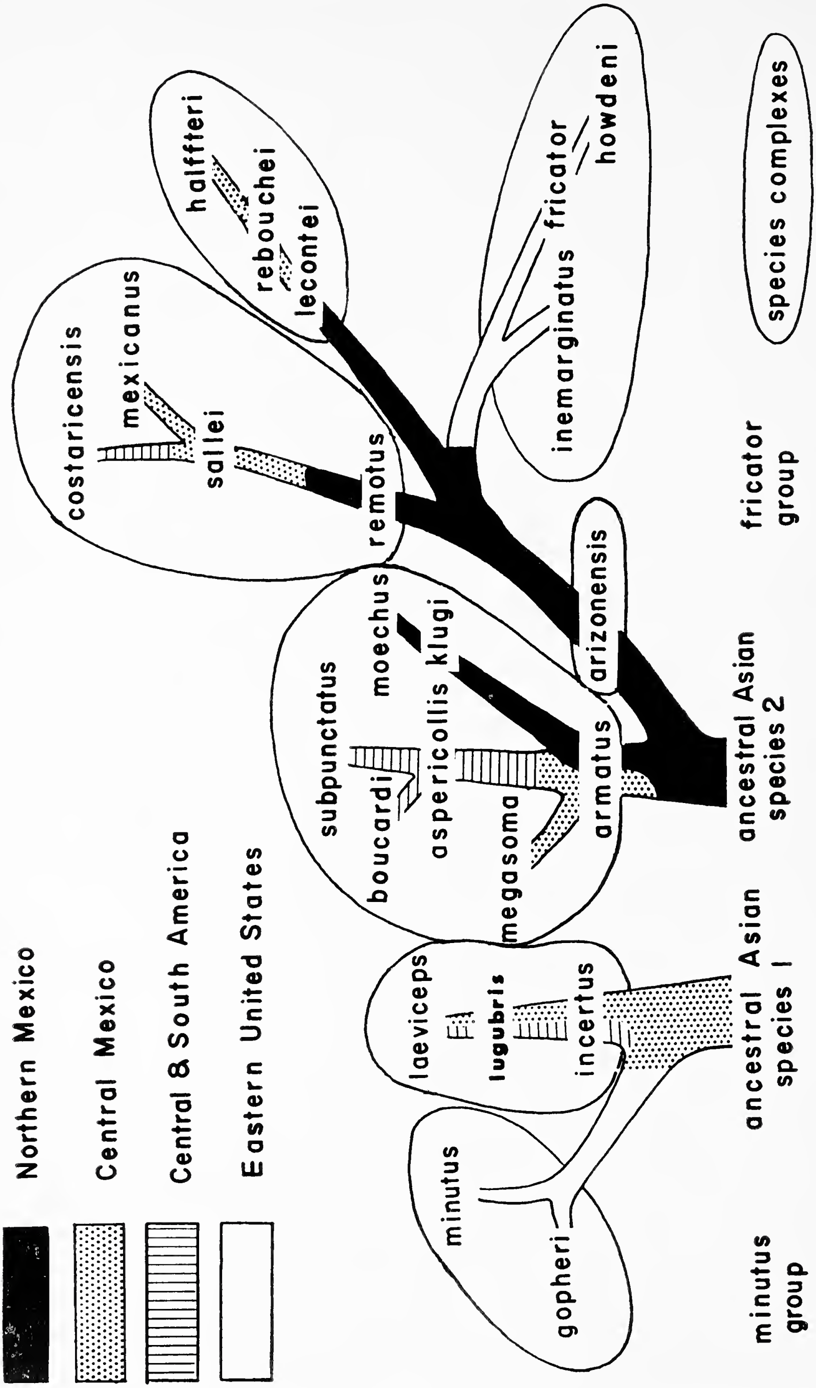

Fig. 11. Proposed relationships of the American species of *Copris*.

The fossil species *Copris pristinus* Pierce (1946), of the Upper Pleistocene (La Brea tar pits, California), is definitely a *Copris* and appears to be a true extinct species very close to *C. armatus* Harold but much larger, being in a size class with the giant *C. megasoma* Matthews and Halffter, which it also closely resembles. The latter two species are from central Mexico. I cannot place *C. pristinus* with greater accuracy at the moment, as I have not seen the original material.

Palaeocopris labreae Pierce, from the same deposits, cannot be placed anywhere at present and appears to be a composite of two genera.

GENUS *Copris* MÜLLER, 1764

Copris Müller, 1764, Fauna insectorum Fridrichsdalina, p. xi. Type, by subsequent designation, *Scarabaeus lunaris* Linnaeus (Curtis, 1832, British Entomology, pl. 414).

DIAGNOSIS. Head semicircular in outline, very strongly flattened, and completely margined above, its dorsal surface punctate, never wrinkled. Thorax below with a distinct oblique propleural carina and a longitudinal proepimeral carina (fig. 26, lpc, pc), a short transverse mesosternum with a median impunctate area, an obtusely angular meso-metasternal suture, and a parallel-sided median metasternal lobe devoid of long setae. Elytra with ten striae, of which at least eight are complete (including the one along the lateral carina). Abdomen with six visible sternites, all of which are distinct along the mid-line, not being fused together or overlapping. Fore tibia with four outer teeth or expansions, the proximal one very small. Hind tibia with a very prominent transverse carina close to the middle on its outer face.

KEY TO THE SPECIES OF THE GENUS COPRIS IN THE WESTERN HEMISPHERE BASED ON THE MAJOR MALES*

1. Male armed like a female, with a well developed, typical female head horn which is transverse, quadrate, and apically excavate (fig. 77); anterior margin of prosternum with a salient, bilobate median process (fig. 55). Guerrero .... *halffteri* Matthews.

   Male armed with a conical or slender horn; anterior margin of prosternum with a median process varying in shape but never bilobate, or without any median process .... 2.

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* The following species, the males of which are hornless, are not included in this key: *howdeni* Matthews and Halffter, *inemarginatus* Blatchley, and *laeviceps* Harold. *C. sallei* Harold, of which I have seen only females, is also not included.

2\. Median pronotal prominences, when present, transversely truncated; lateral pronotal carina absent; lateral pronotal inner margin evenly curved; pygidial margin incomplete, its edge effaced ventrally .... 3.

Median pronotal prominences rounded or acute; lateral pronotal carina present; lateral pronotal margin sinuate or slightly angulate anteriorly .... 6.

3\. Head with a horn-like tubercle behind the horn; forespur expanded distally, truncate (fig. 33); a tuft of long setae present on hind edge of median and posterior trochanters .... 4.

Head with only one horn-like prominence; forespur acute or bluntly rounded; trochanters without setae .... 5.

4\. Head horn arising approximately from middle of head surface; tubercle behind it erect or sometimes bent (never inclined) forward (fig. 64); dorsal edges of median pronotal prominences, when seen from the front, sloping down laterally at an angle of about 45° from horizontal. S. Mexico and Central America .... *lugubris* Boheman.

Head horn arising from before middle of head; tubercle behind horn inclined forward (fig. 63); dorsal edges of median pronotal prominences, when seen from the front, almost horizontal. Tamaulipas to Ecuador, Hawaii, New Zealand .... *incertus* Say

5\. Pronotum and elytral striae coarsely punctate; clypeus contrastingly more finely punctate than rest of head; a segment of anterior portion of 9th elytral stria present and coarsely punctate; proepimeron fully punctate. Eastern U. S. .... *minutus* (Drury)

Entire body very feebly punctate; elytral striae partially impunctate; 9th elytral stria present only posteriorly; proepimeron partly impunctate inwardly. Florida .... *gopheri* Hubbard

6\. Anterolateral angles of pronotum with the point made salient by an inward curve or emargination of the margin immediately behind it; 8th elytral stria nearly always complete. Smaller beetles (10–18 mm in length) .... 7.

Anterolateral angles of pronotum subquadrate, obtusely angled, or broadly rounded, occasionally acute in very highly developed specimens, never with a sharp inward curve of the margin immediately behind them. Larger beetles (14–29 mm in length) .... 13.

7\. Pronotum uniformly very densely punctate, the punctures separated by a distance roughly equal to their diameter (fig. 66); elytral interstriae distinctly and profusely punctate; head horn almost straight, slightly transversely dilated at apex in well developed individuals. Central and Northeast U. S., Southeast Canada ... *f. fricator* (Fabricius)

Pronotum not uniformly very densely punctate, the punctures separated by a distance equal to far more than their diameter on at least part of pronotum; elytral interstriae very finely punctate (appearing impunctate to the unaided eye) or quite impunctate. .... 8.

8. Median dorsal sulcus of pronotum and pronotal disc impunctate; median pronotal prominences laminar, well separated, with a deep depression between them, and parallel (fig. 76); pygidial margin incomplete, its inner border completely effaced ventrally (fig. 58); anterior prosternal margin with an acute, minute median tooth (fig. 54). Central Mexico .... *rebouchei* Harold.

Median dorsal sulcus of pronotum punctate or, if impunctate, then anterior prosternal margin is without an acute median tooth and inner border of pygidial margin is completed ventrally by a close-set row of punctures (fig. 59) .... 9.

9. Pygidial margin incomplete, its inner border completely effaced ventrally; median pronotal prominences closely approximated, parallel in direction, in developed individuals tending to become merged into a single bifurcate process receiving the head horn (fig. 80); anterior margin of pronotum forming a minute, downwardly directed median point. Chiapas and Central America ...... *costaricensis* Gahan

Pygidial margin nearly always complete; median pronotal prominences never merging and otherwise not as above 10.

10. Male with well developed, divergent median pronotal prominences, but with either no trace of any lateral prominences (fig. 79), or these represented by tubercles. Tamaulipas .... *remotus dicyrtus* Matthews and Halffter.

Male, if bearing well developed median pronotal prominences, also bears well developed, laminar lateral prominces ..... 11.

11. Clypeal teeth obtuse, relatively approximated, the margin between them excised at a distinct angle without any median notch; hind angles of head quadrate; median dorsal sulcus of pronotum not contrasting with rest of disc in punctuation; disc usually moderately punctate (fig. 75). S. Arizona and W. Coast of Mexico to Tehuantepec .... *lecontei* n. sp.

Clypeal teeth acute and remote, very small, the margin between them not appreciably excised, with or without a very shallow median notch; hind angles of head acute; median dorsal sulcus of pronotum coarsely umbilicopunctate in sharp contrast to the impunctate or very finely punctate elevated portions of disc .... 12.

12\. Median pronotal prominces remote and slightly divergent (fig. 78); forespur abruptly bent in very near apex, where it forms a dull point (fig. 43). S. Texas, N. Nuevo León .... *r. remotus* Leconte.

Median pronotal prominences very approximated, their outer edges converging forward (fig. 67); forespur curved inward and tapering near apex to a sharp point (fig. 44). Michoacán .... *mexicanus* Matthews and Halffter.

13\. Clypeal emargination very shallow, wide, and arcuate, without a median notch; forespur curved inward and tapering to a sharp point (fig. 39); median pronotal prominences closely approximated to form a single bifurcate process in well developed individuals (fig. 68); entire surface of pronotum regularly and usually densely punctate; 8th elytral stria complete. S. Arizona and New Mexico, W. Texas Chihuahua .... *arizonensis* Schaeffer.

Clypeal emargination broadly triangular, with a median notch, or absent; forespur rounded at the end or coming to a blunt point, curving downward a little but not inward appreciably; 8th elytral stria incomplete, disintegrating posteriorly or largely effaced .... 14.

14\. Median prominences of pronotum with the apices well separated, their outside edges divergent in well developed individuals .... 15.

Median prominences of pronotum closely approximated, their outside edges evenly convergent anteriorly .... 18.

15\. Anterior face of pronotum sparsely to moderately punctate; clypeus devoid of teeth .... 16.

Anterior face of pronotum coarsely granulate; clypeus obtusely bidentate .... 17.

16\. Median pronotal prominences with the apices obliquely flattened, their lower surfaces flat or slightly concave; clypeus entire, without any median notch (fig. 70). Michoacán .... *megasoma* Matthews and Halffter.

Median pronotal prominences conical, round in cross section; clypeus with a median notch (fig. 69). Central Mexico .... *armatus* Harold.

17\. Elytral striae appearing distinctly punctate to the unaided eye; apices of median pronotal prominences conical, round in cross section (fig. 74). Guatemala. *aspericollis* Gillet.

Elytral striae appearing impunctate to the unaided eye, the punctures obsolescent; apices of median pronotal prominences pyramidal, their lower surfaces flattened or slightly excavate (fig. 72.). Costa Rica, Panamá
subpunctatus Gillet.

18. Anterior face of pronotum sparsely to moderately punctate (fig. 71). Central Mexico .... *klugi* Harold.
Anterior face of pronotum granulate or asperate, or if partly punctate, then very densely so, the punctures with raised edges, imparting an asperate appearance to the surface 19.

19. Apices of median pronotal prominences pyramidal, abruptly and sharply turned upward when seen from sides (fig. 73); head horn evenly tapering when seen from front. Chiapas and Central America .... *boucardi* Harold.
Apices of median pronotal prominences blunt or conical, directed forward or evenly curving slightly upward when seen from sides (fig. 81); head horn, when seen from front or rear, expanded distally into transverse knob. Chihuahua and Durango .... *moechus* Leconte.

KEY TO THE SPECIES OF THE GENUS COPRIS IN THE WESTERN HEMISPHERE BASED ON THE MALES AND FEMALES

1. Lateral pronotal carina absent; lateral pronotal margin evenly curved; pygidial margin incomplete, the inner border effaced ventrally .... 2.
Lateral pronotal carina present; lateral pronotal margin sinuate or slightly angulate; pygidial margin complete or not .... 6.

2. Median and posterior trochanters with a tuft of long setae on the hind edge. Total length 13.5–19 mm .... 3.
Median and posterior trochanters without setae. Total length 8–13 mm .... 4.

3. ♂. (Forespur spatulate.) Occipital margin usually with a sharp transverse carina closely paralleling the marginal setigerous groove (fig. 24, toc). ♀. (Forespur tapering.) Anterior portion of pronotum without any transverse carina; very developed specimens with two low transverse gibbosities not followed by any intensification of the punctures. S. Mexico and Central America
lugubris Boheman.
♂. (Forespur spatulate.) Occipital margin usually with a dull transverse carina closely paralleling the marginal

setigerous groove. ♀. (Forespur tapering.) Anterior portion of pronotum, even in the least developed specimens, with two indistinct transverse carinae which are rounded and, especially in developed specimens, sinuate, with the disc immediately behind them abruptly and contrastingly densely punctate. Tamaulipas to Ecuador, Hawaii, New Zealand .... *incertus* Say.

4. Lateral pronotal margin finely serrate just behind anterolateral angle; prosternal-proepisternal suture distinctly carinate; pronotum and head completely devoid of gibbosities in both sexes. S. Mexico and Central America ...... *laeviceps* Harold.

Lateral pronotal margin not serrate; prosternal-proepisternal suture not carinate; pronotum sculptured or not; head usually with a horn-like process .... 5.

5. Pronotum and elytral striae coarsely punctate; a punctate segment of 9th elytral stria present at base of elytron; proepimeron entirely, evenly punctate; clypeus contrastingly more finely punctate than rest of head; forespur linear, rounded at the end (fig. 6). Eastern U. S. *minutus* (Drury).

Entire body very finely punctate; elytral striae partly impunctate; proepimeron largely impunctate inside posterior longitudinal proepimeral carina; forespur cresent-shaped, curving outward (fig. 35). Florida .... *gopheri* Hubbard.

6. Anterolateral angles of pronotum with the point made salient by an inward curve or indentation of lateral margin immediately behind them (sometimes indistinct), the margin often sharply sinuate anteriorly; 8th elytral stria nearly always complete. Total length 10–18 mm .... 7.

Anterolateral angles of pronotum subquadrate, obtusely angled, or broadly rounded, never with a sharp inward curve of margin immediately behind them. Total length 14–29 mm .... 17.

7. Pronotum uniformly very densely punctate, without smooth areas except at the very apices of prominences, if any ...... 8.

Pronotum with impunctate areas, or large areas with finer or sparser punctures than others .... 10.

8. Clypeal margin entire, slightly sinuate at most; elytral intervals appearing smooth, convex. Florida *inemarginatus* Blatchley.

Clypeus distinctly emarginate; elytral intervals appearing distinctly punctate to the unaided eye, moderately convex or flat; elytral striae crenulate, the punctures obsolescent 9.

9. Elytral interstriae moderately punctate, convex, the punctures separated by a distance equal to 1–3 times their diameter. Central and N. E. U. S. .... *fricator* (Fabricius).
   Elytral interstriae more densely punctate, flat, the punctures separated by a distance about equal to their diameter; both sexes always completely devoid of pronotal prominences. Florida .... *howdeni* Matthews and Halffter.
10. Pygidial margin incomplete, its inner border completely effaced ventrally (fig. 58) .... 11.
   Pygidial margin complete, its inner border entirely engraved, or incomplete but with median portion of inner border represented by close-set punctures (fig. 59) .... 13.
11. Median longitudinal sulcus of pronotum coarsely punctate and deeply impressed; anterior margin of pronotum forming a minute, downwardly directed median tooth; median coxae with some coarse punctures on outer faces. Chiapas and Central America .... *costaricensis* Gahan.
   Median longitudinal sulcus of pronotum shallow and impunctate or finely punctate, the punctures never umbilical; anterior margin of pronotum not forming any median tooth .... 12.
12. Anterior margin of prosternum with a minute, acute median tooth (fig. 54); basal part of disc and median longitudinal sulcus of pronotum quite impunctate. Central Mexico *rebouchei* Haròld.
   Anterior margin of prosternum without any median tooth (fig. 53) or with a very low broad lobe which may be truncate or bidentate apically; basal part of disc and median longitudinal sulcus of pronotum finely punctate in northern specimens. S. Arizona and W. Coast of Mexico to Tehuantepec .... *lecontei* n. sp.
13. Anterior margin of prosternum with a salient median process which is bilobed at the apex (fig. 55); base and median longitudinal sulcus of pronotum quite impunctate; a deep depression between median pronotal prominences in both sexes; ♂ with a typical female head horn. Guerrero *halffteri* Matthews.
   Anterior margin of prosternum without a salient, bilobed median process .... 14.
14. Forespur curved inward near the apex and tapering to a sharp point (figs. 40, 44) .... 15.
   Forespur straight and bluntly rounded at the apex, or abruptly bent inward very near apex and narrowing to a dull point (figs. 43, 45) .... 16.

15. Hind angles of head quadrate; ♂ with a broad triangular median emargination of clypeal margin; base of pronotum and median longitudinal sulcus finely punctate or impunctate, the puncturation gradually intensifying anteriorly. S. Arizona and W. Coast of Mexico to Tehuantepec .... *lecontei* n. sp.

Hind angles of head acute; ♂ with a very shallow, barely perceptible emargination and two remote, minute teeth on clypeal margin; base of pronotum impunctate except for median longitudinal sulcus, which is coarsely umbilicopunctate. Michoacán ...... *mexicanus* Matthews and Halffter.

16. Eighth elytral stria incomplete, effaced or at least partly disintegrating posteriorly; anterior pronotal margin with a minute, acute median tooth. Veracruz and Chiapas *sallei* Harold.

Eighth elytral stria complete; anterior pronotal margin without any median tooth; ♂ with a very shallow, arcuate median emargination of clypeal margin; base of pronotum impunctate or finely punctate, becoming abruptly coarsely punctate anteriorly in the depressions. Texas, Nuevo León, Tamaulipas .... *remotus* Leconte.

17. Eighth elytral stria complete; pronotal puncturation rather dense, umbilical, usually becoming sparser posteriorly, never asperate or granulate on the anterior face; ♀ head horn usually widely expanded distally; ♂ with a very shallow, arcuate clypeal emargination and curved, acute forespurs (when not worn). S. Arizona and New Mexico, W. Texas, Chihuahua .... *arizonensis* Schaeffer.

Eighth elytral stria incomplete, disintegrating posteriorly (sometimes almost complete); pronotal puncturation much less dense on disc; ♀ head horn either parallel-sided or narrowing apically; forespurs of both sexes straight and with blunt apices; ♂ clypeal emargination angular or absent .... 18.

18. Elytral striae appearing impunctate to the unaided eye, the punctures obsolescent, quite effaced on the 8th stria. Costa Rica, Panamá .... *subpunctatus* Gillet.

Elytral striae appearing distinctly punctate to the unaided eye .... 19.

19. Clypeal margin entire, devoid of teeth or emargination; ventral surfaces of median and posterior femora impunctate. Total length 28–30 mm. Michoacán *megasoma* Matthews and Halffter.

Clypeal margin with at least a small median notch, often also with two broad, low teeth or expansions; ventral surfaces of median and posterior femora with at least a few punctures distally. Size smaller, total length 14–25 mm .... 20.

20\. ♂. Clypeal margin very broadly, shallowly emarginate, with two very small teeth (often worn); anterior face of pronotum entirely punctate, the punctures large, umbilical, and often dense, not accompanied by pronounced asperation. ♀. Anterior face of pronotum with at least a few umbilical punctures along anterior margin interspersed among the dense rugosities or granules of the surface. Central Mexico to Chihuahua, in the mountains .... *klugi* Harold.

♂. Clypeal margin with a small, acute median notch and no marginal expansions, or anterior face of pronotum granular, asperate, or both punctate and asperate. ♀. Anterior face of pronotum uniformly densely granular or sparsely to moderately asperate .... 21.

21\. Clypeal margin with a small acute median notch and no salient teeth. ♂. Anterior face of pronotum punctate, with no rugosities. ♀. Anterior margin of prosternum usually with a quadrate median lobe; anterior face of pronotum sparsely to moderately asperate, never granulate. Central Mexico. .... *armatus* Harold.

Clypeal margin with two low, indistinct expansions; anterior face of pronotum granulate, usually densely so .... 22.

22\. Complete portion of 8th elytral stria fully punctate like the other striae; anterolateral angles of pronotum angulate, the angle very obtuse. Chihuahua, Durango *moechus* Leconte.

Complete portion of 8th elytral stria more feebly punctate than striae I–IV; anterolateral angles of pronotum broadly rounded (in undeveloped specimens). Chiapas and Central America .... 23.

23\. Basal part of pronotal disc impunctate, shiny. Chiapas, Guatemala, El Salvador .... *boucardi* Harold.

Basal part of pronotal disc profusely but shallowly punctate, dull. Guatemala .... *aspericollis* Gillet.

Group I. The *minutus* group.

Outer face of apical maxillary palpal segment convex. Lateral pronotal carina absent. Lateral pronotal margin evenly curved.

Male median pronotal prominences, when present, broadly transversely truncated. Complex punctures with minutely granular texture. Sternellum tending to be longitudinally carinate. Pygidial margin always incomplete. Male genital parameres slender, tapering to a fairly acute apex. Individuals are frequently incompletely pigmented. Five species.

Complex 1. The *incertus* complex.

Lateral pronotal margin finely and irregularly serrate just behind the anterolateral angles. Prosternal-proepisternal suture strongly carinate.

Three closely related species of tropical Mexico, Central America, and northeastern South America: *incertus* Say, *lugubris* Boheman and *laeviceps* Harold.

Copris incertus Say

Copris incerta Say, 1835, Boston Journ. Nat. Hist., I: 175 [type: Mexico; Museum of Comparative Zoology]; 1859, Complete Writings, ed. Le Conte, II: 649; Harold, 1869, Ann. Soc. Ent. France, ser. 4, IX: 494 (key); Bates, 1887, Biol. Cent.-Amer., Coleop. II, 2, p. 55 (distr.); Heyne and Taschenberg, 1908, Die exotischen Käfer, p. 64 (descr.); Pereira and d'Andretta, 1955, Pap. av. Dep. Zool. Secr. Agric., S. Paulo, XII: 261–263 (descr. and syn.); Matthews, 1959, Ciencia XIX(6–7): 135 (key and distr.); Thomas, 1960, N.Z. Journ. Sci., III (1): 8–14 (biol. and distr.).

Copris procidua Say, 1835, Boston Journ. Nat. Hist. I: 176 [type: Mexico; Museum of Comparative Zoology]; 1859, Complete Writings, ed. Le Conte, II: 649; Harold, 1859, Ann. Soc. Ent. France, ser. 4, IX: 495 (key); 1880, Stettiner Ent. Zeit. XLI: 27 (distr.); Blanchard, 1885, Trans. American Ent. Soc. XIII: 171 (distr.); Bates, 1887, Biol. Cent.-Amer., Coleop. II, 2, p. 54 (distr.); Schaeffer, 1906, Trans. American Ent. Soc. XXXII: 255 (key); Williams, 1929, Proc. Hawaiian Ent. Soc. VII(2): 210, 227, 237 (distr.); Pereira and d'Andretta, 1955, Pap. av. Dep. Zool. Secr. Agric., S. Paulo, XII: 260–263 (distr. and syn.); Matthews, 1959, Ciencia XIX(6–7): 135 (key and distr.).

Description of Male. *Head.*—Armed or not. Clypeus bidentate, clypeal teeth not at all prominent, margin between them broadly, angularly emarginate with a slightly deeper V-shaped median notch not cutting through margin. Posterior angles of genae subquadrate or slightly obtuse. Upper surface of head rather densely punctate, the punctures simple except for those behind horn (between eyes), which are coarse and granular. Posterior oblique carina absent. Occipital margin with transverse setigerous groove intact and paralleled by an incomplete, dull carina, which is sometimes absent. Demarcation between gula and submentum usually broadly V-shaped, sometimes rounded. *Thorax.*—Pronotum armed or not. Anterolateral angles obtuse, lateral margin just behind them irregularly serrate. Lateral margin evenly arcuate. Anterior margin of pronotum not forming any median point or angle. Median longitudinal sulcus deep, coarsely punctured. Puncturation of pronotum as follows: sparsely and very finely punctate, or impunctate, on disc, becoming a little more densely and deeply punctate on anterolateral lobes and anterior declivities, the punctures here simple; grossly umbilico-punctate, the punctures granular, along entire submargin (sparser laterally and anteriorly), along dorsal longitudinal sulcus, and in lateral fossae. Anterior prosternal margin with a rounded median tooth; sternellum concave with an indistinct median longitudinal carina, moderately punctate. Median lobe of metasternum with no coarse punctures; median longitudinal groove complete. *Elytra.*—8th stria obsolescent, effaced at base and for median third of elytral length, present intact only for a short length near base and behind posterior angle; 9th stria arising from 10th about halfway down elytron; 10th complete or disintegrating temporarily for median third of elytral length. Striae moderately punctate, the punctures not deep, round, little wider than striae, separated by a distance equal to more than their diameter. Interstriae slightly convex, sparsely and very finely punctate, appearing smooth. *Abdomen.*—Pygidium punctate only dorsally, the punctures granular; pygidium incompletely margined, inner edge of margin being effaced ventrally. *Anterior legs.*—Ventral surface of femur with coarse setigerous punctures on posterior longitudinal half, finely punctate on anterior. Forespur expanded and truncated distally. *Middle legs.*—Coxa with some indistinct punctures along median carina. Trochanter with a tuft of long setae arising from posterior margin. Ventral surface of femur very finely punctate, appearing smooth, except for a few setigerous punctures at distal end in some specimens. Tibia below with one distal seta tuft, above with 1–3 supplementary setae distally. *Posterior legs.*—Trochanter with a tuft of long setae arising from posterior margin. Ventral surface of femur without coarse punctures or with several coarse punctures at distal end. Tibia below with one distal seta tuft, above with 0–3 supplementary setae. *Total length.*—13.5–18.5 mm.

Male armament. The least developed male seen possessed neither a head horn nor any pronotal prominences. More developed specimens bear a slightly curved, tapering clypeal horn which is situated forward of the middle of the head (the more developed the horn the more anteriorly it is located), and an acute tubercle just behind it which is strongly inclined forward, almost recumbent (fig. 63). The median pronotal prominences are very low, approximated, and broadly, transversely truncated. The upper edges of the truncated faces, when seen from the front, are practically on a horizontal plane. The lateral pronotal prominences are low, conical, and directed upwards. The males never achieve a very high degree of secondary sexual development (compared to *lugubris*).

Description of Female. Similar to male, but differing in armament and in the following features: clypeal teeth more prominent, rounded, approximated, the notch between them deeper, more rounded; forespur not expanded distally, tapering to a blunt point; pronotum anteriorly more densely punctate; median and posterior tibiae with more seta tufts distally below (1–3) and more supplementary setae above (2–4). *Total length.*—13.5–18.5 mm.

Female armament. Head sometimes devoid of a horn in small specimens, with only an acute transverse cariniform process, but usually bearing a narrow transverse horn which is truncated and excavate apically. Median pronotal prominences quite different from the male's, indistinctly transversely carinate, the carinae visible even in undeveloped specimens close to the anterior margin. In large specimens these carinae are sinuate, their anterior faces moderately punctate, the disc behind them abruptly and contrastingly densely punctate. Lateral pronotal prominences absent.

Distribution. Fig. 12. This species has a remarkably extended distribution which appears to be made up of isolated populations. It is represented in numerous localities in the tropical forest of eastern Mexico north of Veracruz and in Yucatán at altitudes of 150–1360 m. (500–4500 ft.). It does not occur along the coast itself where it is replaced by the closely related *C. lugubris* Boh. To the south the species disappears completely (in collections) to show up again among some specimens collected by Nevermann on the lower reaches of the Reventazón in Costa Rica, where it appears to occur in association with *C. laeviceps* Harold. Thence it disappears again and we do not find it until we reach the Cordilleras of Colombia and Ecuador, where it occurs at altitudes of 1050–1800

m. (3500–5800 ft.). Blanchard and Horn mention this species (under the name *prociduus*) as occurring in Texas, but I have seen no reliable records to support this and in view of the nature of its habitat in Mexico I consider it highly unlikely that it occurs in the United States (other than in Hawaii), except perhaps as an occasional stray. Blanchard further mentions having seen a specimen from Guatemala.

In addition to the localities cited below, Pereira and d'Andretta give five additional Colombian, six additional Ecuadorean, and five additional Hawaiian localities which certainly refer to this species.

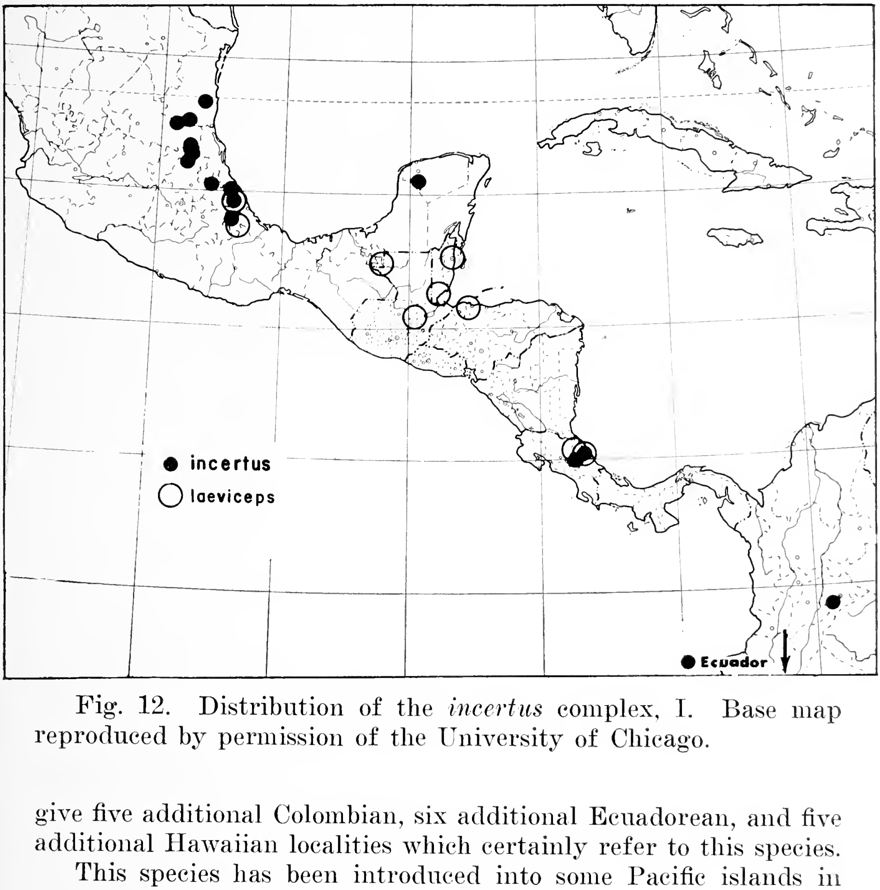

Fig. 12. Distribution of the *incertus* complex, I. Base map reproduced by permission of the University of Chicago.

This species has been introduced into some Pacific islands in order to reduce the amount of exposed cow dung, which serves as a breeding medium for several species of flies. It has become successfully established in Hawaii, Western Samoa, and New Zealand (Thomas, 1960).

Biology. Recorded from cow dung in Mexico and New Zealand and cow and horse dung in Hawaii. Nevermann in Costa Rica found it under human dung, in dried wood, and in undergrowth at night. There is one Hawaiian record of its occurrence on *Opuntia* cactus attacked by Fusarium disease. Nidification is discussed previously.

Remarks. I have examined three specimens from the Say material in the Harris collection at the Museum of Comparative Zoology which agree with Say's original description of *incerta*. All are females (Say's description was that of a female, as he suspected), two of them simply bear one very small label each with the number "51" on it while the third bears three labels: an old handwritten one with "*incerta* Say" and "Mexico" written on it, a newer handwritten one (Harris's?) with "type Mexico" on it, and likewise a very small one with the printed number "51". The latter specimen is here designated as **lectotype** of *incertus* Say.

This same collection also contains a single specimen bearing the name *procidua*. It is a male of the same species and agrees perfectly with Say's original description. It also bears three labels saying "*procidua* Say" and "Mexico", "type Mexico", and the number "53". Since this is the only male of this species in the collection, it is here considered to be the holotype of *prociduus* Say.

All these specimens belong to the same species and since the female was described first, this species (which has hitherto been called *prociduus* or *incertus* var. *prociduus*) must now bear the name *incertus*—engendering considerable nomenclatorial confusion, because the name *incertus* has consistently been applied to a closely related, very abundant species here considered as *lugubris* Boheman.

The separation of this species from the closely related *lugubris* Boheman and *laeviceps* Harold is discussed under the remarks pertaining to those two species.

Material Examined. 99 males, 106 females, including lectotype.

UNITED STATES: *Hawaii:* Mapulehu, Molokai; Maui.

MEXICO: *Hidalgo:* Chapulhuacán; *Puebla:* Necaxa; San Diego; Mesa de San Diego; Villa Juárez; *San Luís Potosí:* El Salto; Huichihuyan, 20 mi N Tamazunchale; Tamazunchale; *Tamaulipas:* 3 mi NW Acuña; Quintero; *Veracruz:* Banderilla; Barranca de Metlac; Córdoba; Fortín; Jalapa; Laguna de Tamihaua, 20 km N Tuxpan; Martínez de la Torre; Orizaba. *Yucatán:* Uxmal.

COSTA RICA: *Cartago:* Turrialba, 800 m (Schild), 1 ♂ (USNM); 31 May 1951 (O. L. Cartwright), 1 ♂ (USNM). *Limon:* Hamburgfarm, Reventazón, Plain of Limón, 21 Jul. 1931, 27 Jul. 1935, 21 May 1936 (F. Nevermann), 4 ♂♂, 6 ♀♀ (USNM).

COLOMBIA: *Cundinamarca:* Fusagasugá, 1800 m, 9 Sep. 1942 (F. J. Otoya), 6 ♂♂, 2 ♀♀ (USNM); 8 May 1946 (E. A. Chapin), 3 ♂♂, 2 ♀♀ (USNM).

ECUADOR: *Guayas:* Naranjal (F. Campos R.), 1 ♀ (USNM); *Los Ríos:* 21 Apr. 1938 (W. MacIntyre), 1 ♂ (OLC); *location undetermined:* Paramba, 3500 ft, Mar. 1897 (Rosenberg), 1 ♂ (BM); Lita, 1 ♂ (BM); San Rafael (F. Campos R.), 1 ♂ (USNM).

Copris lugubris Boheman

Copris lugubris Boheman, 1858, Eugenies Resa, Coleop., p. 42 [type: Galapagos I.; Naturhistoriska Ricksmuseum, Stockholm]; Waterhouse, 1877, Proc. Zool. Soc. London V: 82; Linell, 1898, Proc. United States Nat. Mus. XXI: 258; Felsche, 1901, Deutsche Ent. Zeitschr., p. 145; Mutchler, 1925, Zoologica V(20): 237; Van Dyke, 1953, Coleoptera of the Galapagos Islands, p. 122; Pereira and d'Andretta, 1955, Pap. av. Dep. Zool. Secr. Agric. S. Paulo, XII: 261 (synon.).

Description of Male. *Head.*—Armed. Clypeus bidentate, clypeal teeth relatively prominent, margin between them shallowly, angularly emarginate without any median notch. Posterior angles of genae subquadrate or obtuse. Upper surface of head largely impunctate basally, becoming moderately punctate on flattened portions and horn, punctures simple; in small specimens there are some granular punctures between the eyes. Posterior oblique carina obsolescent. Occipital margin with transverse setigerous groove complete, closely preceded by a sharp transverse carina which may be complete or interrupted at middle. Demarcation between gula and submentum a deep arc, usually with a median V-shaped area. *Thorax.*—Pronotum armed or not. Anterolateral angles obtuse, the lateral margin just behind them irregularly serrate. Lateral margin rather evenly arcuate without any pronounced angulation. Anterior margin of pronotum not forming any median point or angulation. Median longitudinal sulcus deep, coarsely punctured. Puncturation of pronotum as follows: sparsely and finely punctate on disc becoming a little more densely and deeply punctate on anterolateral surfaces and anterior declivity, the punctures simple here; grossly punctate, the punctures umbilical and granular, only along hind submargin (and occasionally along fore submargin), along the dorsal sulcus, and in the lateral fossae. Anterior prosternal margin with a prominent, rounded median tooth; sternellum somewhat concave but with an indistinct median longitudinal carina, moderately punctate. Median lobe of metasternum very finely punctate, with no coarse punctures; median longitudinal groove very indistinct anteriorly. *Elytra.*—8th stria obsolescent, effaced at base and median third of elytron, present integrally only for a short length near base and apically; 9th stria arising at anterior third of elytral length and continuing distally; 10th stria complete. Striae indistinctly punctate, the punctures not deep, round, little wider than stria, separated by a distance equal to more than their diameter over most of strial length. Interstriae very slightly convex, sparsely and very finely punctate, appearing smooth. *Abdomen.*—Pygidium moderately punctate dorsally, the punctures granular, becoming sparser ventrally; margin incomplete, effaced ventrally. *Anterior legs.*—Ventral surface of femur entirely punctate, the punctures coarser and setigerous on posterior longitudinal half. Forespur rather straight, expanded and truncate at apex (fig. 33). *Middle legs.*—Coxa faintly punctate along median carina. Trochanter with a single tuft of long setae arising from posterior edge. Ventral surface of femur sparsely and very finely punctate, usually with a few setigerous punctures distally. Tibia below with a single distal seta tuft, above without supplementary setae. *Posterior legs.*—Trochanter with a single tuft of long setae arising from posterior edge. Ventral surface of femur very sparsely and finely punctate. Tibia below with a single distal seta tuft, above usually without supplementary setae apically, sometimes with one or two. *Total length.*—13.5–18 mm.

Male armament. The least developed male seen possessed a head horn, albeit a very low one, on the posterior part of the clypeus and a barely evident tubercle close behind it. The pronotum showed traces of median prominences in the form of two approximated transverse tumosities and not a trace of any lateral prominences. With further development, the head horn elongates, becoming gently arcuate and slightly dilated apically in the most developed specimens. The horn is situated at about the middle of the head. Behind it is a prominent tubercle which is either erect or bent forward, but never inclined forward (fig. 64). The median pronotal prominences are broadly transversely truncate, closely approximate, their outer edges converging anteriorly in dorsal view. The upper edges of the truncated faces, when seen from the front, are very strongly sloping down to the sides at about a 45° angle from the horizontal or more. The lateral prominences are laminate, directed forward and upward, and parallel to the longitudinal axis when viewed from above.

Description of Female. Similar to the male, but differing in armament and in the following features: clypeal teeth more prominent and approximated, with a V-shaped median notch in margin between them. Forespur not expanded and truncate distally, narrowing slightly to a rounded apex. Pronotum anteriorly more densely punctate. Hind tibia above with 2–4 supplementary setae distally (fig. 50). *Total length.*—14–19 mm.

Female armament. Many females are completely unarmed, with only a short transverse carina on the head. The head horn, when developed, is much less transverse than is usual in the genus and is often quite high and narrow; it is excavate on the posterior surface. The median pronotal prominences in developed specimens are like those of a minor male, that is, low rounded tumosities; the lateral ones are absent. There is never an abrupt intensification of the dorsal pronotal puncturation just behind the median tumosities.

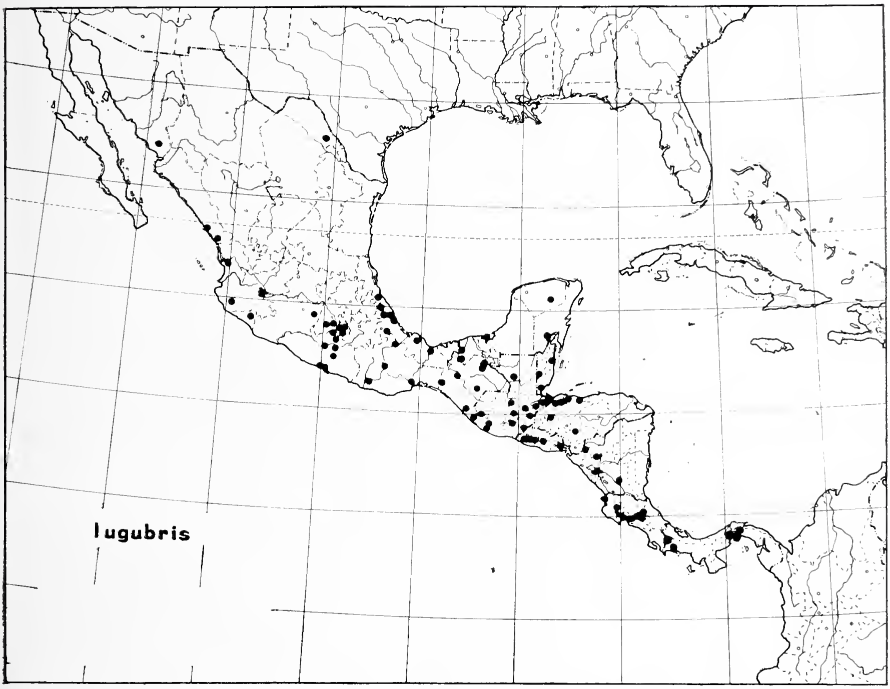

Fig. 13. Distribution of the *incertus* complex, II. Base map reproduced by permission of the University of Chicago.

Distribution. Fig. 13. Widely distributed throughout Southern Mexico and Central America to the Panama Canal at all altitudes up to 1500 m. (4500 ft.). In the northern part of its range it extends up along the coastline on both sides of Mexico, occurring along the Gulf Coast in the sandy area just behind the sea beach. A single specimen was taken surprisingly far inland in northern Coahuila and might be a stray. It has been recorded from Colombia, Ecuador and Hawaii, but I have seen no reliably labelled specimens from these areas and I believe all these records refer to the closely related *C. incertus* Say.

Biology. Some aspects of nidification have been discussed previously. The collected specimens bear the following data: at light, under cow dung, in a banana trap, in dead calf, on avocado. I have collected it under burro dung and human faeces. It appears to be most frequently collected at light. In Central America it is active throughout the year. In Central Mexico it is one of the only two species of coprophages occasionally encountered above ground during the dry season (G. Halffter, oral communication).

Remarks. This species has long gone under the name *incertus* Say. In the remarks under the species now bearing that name I pointed out that Say's types in the Museum of Comparative Zoology show that he did not have any specimens of this species. I have examined the type of *C. lugubris* Boheman in the Naturhistoriska Ricksmuseum, Stockholm, and have found it to be this species. *C. lugubris* is therefore its valid name.

C. lugubris may be told from *incertus,* to which it is closely related, by a number of characters in both sexes. Specific distinction is shown beyond doubt by the differences in the male secondary sexual characters, which never show intermediacy between the two forms. The female also shows very distinct differences in pronotal sculpturing (compare descriptions of female armament) and, because of the frequent occurrence of minor males in both species, it is actually often easier to separate the two species on the basis of the females. Additional, less reliable, differences are seen in the male genital parameres (which bear a minute dorsal hook at the apex in *incertus* (fig. 61) but not in *lugubris*) and, to a lesser extent, in the occipital margin of the head, which in *lugubris* usually bears a sharp transverse carina, whereas in *incertus* this carina is usually dull or absent altogether.

Material Examined. 303 males, 360 females.

MEXICO. *Campeche:* Ciudad del Carmen; *Chiapas:* Comitán; El Vergel (Volcán Soconusco); Escuintla; ?Finca "La Isla"; La Esperanza (Tapachula region); Las Cruces; Ocosingo; Pacific slope Cordilleras; Palenque; ?San José; ?Sta. Julia; Suchiate; Tapachula; Tuxtla Gutierrez; *Coahuila:* 10 mi. S. Allende; *Colima:* Colima; Volcán de Colima; *Distrito Federal:* México; *Guerrero:* Acapulco; Acuitlapán (nr. Cacahuamilpa); Balsas; Cacahuamilpa; Chilpancingo; 22 mi. N. Chilpancingo; El Margues, 28 km. W. Acapulco; Iguala; 3 mi. N. Mexcala; Taxco; Teloloapan; *Jalisco:* Chapala; Purificación; *Mexico:* Río San Jerónimo, 10 km. NE. Cacahuamilpa; Tenancingo; ?Tenayuca; Tonatico; *Michoacán:* San José Purua; *Morelos:* Cuautla; Cuernavaca; 10 mi. S. Cuernavaca; Jojutla; ?Oaxtepec; Yautepec; *Nayarit:* Tepic; 17 mi. NW. Tepic; *Oaxaca:* Amapa; Ixcatlán (W. of Tuxtepec); Oaxaca; 25 km. S. Oaxaca; Panixtlahuaca; Soyaltepec (N. of Tuxtepec); Tehuantepec; ?Valerio Trujano; *Quintana Roo:* Bacalar; *Sinaloa:* Escuinapa; Mazatlán; *Sonora:* Río Mayo; *Tabasco:* Teapa; Villahermosa; *Veracruz:* Atoyac; Coatepec; Cotaxtla; La Gloria, Cardel; Lake Catemaco; Minatitlán; Papantla; Presidio; Puente Nacional; Pureza, 5th RR. station Veracruz to Jalapa; San Andrés Tuxtla; San Carlos; San Martín, San Andrés Tuxtla; Tecolutla; Tlapacoyan; Tres Zapotes; Veracruz; *Yucatán:* Chichen Itzá.

GUATEMALA: *Alta Vera Paz:* Cacao Trece Aguas; Cobán; San Miguel Tucurú; *Baja Vera Paz:* Rabinal; San Jerónimo; *Chiquimula:* Chiquimula; *Guatemala:* Guatemala City; San José de Pinula; *Izabal:* Cayuga; Los Amates; *Jutiapa:* Laguna Atescatempa; *Petén:* La Libertad; ?Pacomón; *San Marcos:* San Marcos; *Suchitepéquez:* ?Finca El Cipres; Mocá; Variedades; *Zacapa:* Zacapa; *location undetermined:* Jocobo.

BELIZE: Belize; Benque Viejo; San Antonio; Punta Gorda.

EL SALVADOR: *La Libertad:* Santa Tecla; *La Unión:* La Unión; *San Salvador:* San Salvador; *San Vicente:* 49 Km. E. San Salvador; *Sonsonate:* Izalco; Sonsonate.

HONDURAS: *Atlántida:* La Ceiba; Tela; *Copán:* Copán; *Morazán:* Esc. Agr. Pan. Zamorano; *Santa Bárbara:* Choloma; Quimistán; *Tegucigalpa:* Tegucigalpa; *Yoro:* Progreso; *location undetermined:* Carmelina; Ruatan I.

NICARAGUA: *Chontales; Jinotega:* Jinotega; *Madriz:* Somoto; *Managua:* Managua; 8 mi N. Managua; San Antonio.

COSTA RICA: *Alajuela:* Grecia; *Guanacaste:* Las Cañas; Guanacaste; Piedra Negra; Santa Elena; *Heredía:* Santa Clara; *Puntarenas:* Las Loras nr. Puntarenas; Orotina; San Lucas I., Gulf of Nicoya; San Mateo; *San José:* Santa Ana; San Jose.

PANAMA: *Canal:* Alhajuelo; *Chiriquí:* David; Potrerillos; Volcán de Chiriquí; *Panamá:* La Chorrera; Chepo; Taboga I.; *location undetermined:* La Joya.

Copris laeviceps Harold

Copris laeviceps Harold, 1869, Ann. Soc. Ent. France, ser. 4, IX: 498 [type: San Andrés Tuxtla, Ver.; Museum d'Histoire Naturelle, Paris]; Bates, 1887, Biol. Cent.-Amer., Coleopt. II, 2, p. 54 (distr.); Matthews, 1959, Ciencia XIX (6–7): 135 (key and distr.).

Description of Male. *Head.*—Unarmed (with but a low conical process on the clypeus. Clypeus bidentate, clypeal teeth prominent, angular, the margin between them broadly angulate with a slightly deeper median V-shaped notch not cutting through margin. Posterior angles of genae obtuse. Upper surface of head very finely punctate, appearing impunctate, except for a dense transverse band of coarse umbilical and granular punctures extending between eyes. Posterior oblique carina absent. Occipital margin with transverse setigerous groove complete; marginal occipital carina paralleling setigerous groove very sharp and interrupted in middle. Demarcation between gula and submentum arcuate or subangulate. *Thorax.*—Pronotum unarmed. Anterolateral angles subquadrate. Lateral margin evenly curved, without angulations, indistinctly and irregularly serrate just behind anterolateral angles. Anterior margin of pronotum not forming any median point or angle. Median longitudinal sulcus impressed, complete, coarsely punctate. Puncturation of pronotum as follows: very finely punctate, appearing impunctate, except for the following areas, which are coarsely punctate, the punctures umbilical and granular: along entire submargin, on anterolateral lobes, in lateral fossae, in a narrow chain along entire median longitudinal sulcus, and forming two large patches just above lateral fossae on either side; these patches are isolated from all other coarse punctures except those of lateral fossae. Anterior prosternal margin with a low median salience; sternellum not very concave with a suggestion of a median longitudinal carina anteriorly, coarsely, closely punctate, the punctures granular and umbilical. Median lobe of metasternum with some coarse granular punctures anteriorly along sides; median longitudinal groove somewhat effaced anteriorly. *Elytra.*—8th stria arising close to base but not from it, disintegrating halfway down elytron, then resuming intact after hind angle; 9th stria arising from 10th anterior to the halfway point; 10th complete. Striae coarsely punctate, the punctures round, umbilical, separated by a distance equal to a little more than their diameter. Interstriae slightly convex, very finely punctate, appearing smooth. When seen from behind, elytral surface is bent, forming an indistinct, obtuse ridge running from hind angle to end of median suture; no striae cross this ridge. *Abdomen.*—Pygidium densely and coarsely punctate, the punctures granular; pygidial margin incomplete, becoming effaced ventrally. *Anterior legs.*—Ventral surface of femur coarsely punctate, the punctures setigerous, on posterior longitudinal two thirds, very finely punctate on anterior third. Forespur slightly expanded distally, rounded and curved down at apex. *Middle legs.*—Coxa with a few coarse punctures on outer face anteriorly near median carina. Trochanter without setae. Ventral surface of femur very finely punctate with a few coarse punctures distally. Tibia below with 1–2 distal seta tufts, above with 1–2 supplementary setae. *Posterior legs.*—Trochanter without setae. Ventral surface of femur coarsely punctate over most of distal half. Tibia below with one distal tuft, above with 1–3 supplementary setae. *Total length.*—11.5–12.5 mm.

DESCRIPTION OF FEMALE. Differs from the male only in having a parallel-sided or tapering forespur (instead of a distally expanded one). In worn specimens this difference is obliterated. *Total length.*—11–13 mm.

DISTRIBUTION. Fig. 12. Known from isolated localities from Jalapa, Ver., to the Reventazón River in Costa Rica. Appears to be an east coast lowland form and may occur throughout the "Mosquitia" coastal plain of Central America, a very poorly collected region. The localities given by Bates are all probably correctly attributed to this species.

BIOLOGY. Nevermann records the following data on his specimens from the Reventazón River and Plain of Limón, Costa Rica: under horse dung, human dung, in the undergrowth at night in the primeval forest ("nachts im Urwald am Gebüsch"), in iguana carcass, at light. Active throughout the year.

REMARKS. This species is very closely related to *incertus* Say and *lugubris* Boh., with which it shares the features characterizing the *minutus* group, plus several others such as the serrate lateral pronotal margin, broadened male forespur, and carinate prosternal-proepisternal suture characterizing the *incertus* complex. In addition, it shows distinctly closer affinities with *lugubris*, with which it shares the type of male genital parameres and sharp transverse occipital marginal carina. However, all the specimens I have seen may be easily told from both *incertus* and *lugubris* by the lack of setae on the posterior margin of the median and posterior trochanters; it differs also in the pronotal puncturation, showing an oval patch of coarse punctures on the sides of the pronotal disc, and in the carinate nature of the posterior elytral angles. All specimens are small in size and totally devoid of cephalic and pronotal armament.

Material Examined. 39 males, 26 females.

MEXICO. *Chiapas:* Tuxtla (O. W. Barret), 1 ♂ (USNM); *Veracruz:* Jalapa (Hoege), 2 ♂♂ (BM); Presidio, E of Zongolica, 1200 m., Jul. 1952 (G. Halffter), 1 ♂ (GH); *national record only:* (Bock), 1 ♂, 1 ♀ (USNM).

GUATEMALA: *Alta Vera Paz:* Cacao Trece Aguas, 26 Apr. (Barber and Schwarz), 2 ♀♀ (USNM); Cubilguitz [1050 ft., on road from Cobán to Petén, 10–20 Mar. 1880] (Champion), 1 ♀ (BM); Telemán [100 m, 13–18 May 1880] (Champion), 1 ♂ (BM); *Petén:* ?Pacomón, 2–8 Jun. 1923 (Harry Malleis), 1 ♂ (CAS); Piedras Negras, 1939 (H. M. Smith), 8 ♂♂, 8 ♀♀ (PAS); *national record only:* 1 ♂ (CAS).

BELIZE: Belize (F. C. Bowditch), 5 ♂♂, 3 ♀♀ (MCZ); M-tee Dist., 21 Mar. 1906 (F. C. Bowditch), 4 ♂♂ (MCZ); Punta Gorda, 10–20 Sept. 1906 (F. C. Bowditch), 1 ♀ (MCZ).

HONDURAS: *Atlántida:* Tela, Guaimas distr. [100 m.], 1, 10 May 1923 (T. H. Hubbell), 4 ♂♂, 3 ♀♀ (UMich, USNM).

COSTA RICA: *Limón:* Hamburgfarm, Reventazón, Plain of Limón, 8 May 1925, 29 Aug. 1926, 1 Aug. 1928, 1 Oct. 1932, 25 Jul. 1935, 21 May, 26 Jun. 1936 (F. Nevermann), 10 ♂♂, 8 ♀♀ (USNM); Guápiles, Sta. Clara, 250–300 m., May 1934 (F. Nevermann), 1 ♂ (USNM).

Complex 2. The *minutus* complex

Lateral pronotal margin not finely serrate anteriorly. Prosternal-proepisternal suture not carinate. Both sexes armed in the male manner.

Two closely related species of the Eastern United States: *gopheri* Hubbard and *minutus* (Drury).

Copris gopheri Hubbard

Copris gopheri Hubbard, 1894, Insect Life VI(4): 310 [type: Crescent City, Fla.: United States National Museum]; 1896, Proc. Ent. Soc. Washington III: 299–302 (distr. and biol.); Hamilton, 1896, Ent. News VII: 286 (biol.); Schaeffer, 1906, Trans. American Ent. Soc XXXII: 255 (key).

Description of Male. *Head.*—Armed. Clypeus with two low marginal expansions and a deeper median V-shaped emargination not cutting through margin. Posterior angles of genae quadrate. Upper surface of head very finely and sparsely punctate, appearing smooth, except occasionally for a band of granular punctures between eyes just behind horn. Posterior oblique carina absent. Occipital margin with transverse setigerous groove present only at sides; no marginal occipital carina. Demarcation between gula and submentum a flattened arc. *Thorax.*—Pronotum unarmed. Anterolateral angles subquadrate, lateral margin evenly arcuate. Lateral carina absent, represented by a tumosity below lateral fossae. Anterior margin not forming any median point. Median longitudinal sulcus visible on middle of disc, fine, impunctate. Puncturation of pronotum as follows: sparsely and very finely punctate over most of its surface with coarser granular and partly umbilical punctures on anterolateral lobes, usually along margins except median part of hind margin, which is mostly impunctate, in lateral fossae, and to a lesser extent on a patch situated on either side of mid-line dorsal to lateral fossa. Anterior prosternal margin with a very small, acute median tooth which is sometimes absent; sternellum only very slightly concave, with a trace of a longitudinal median carina anteriorly, coarsely umbilico-punctate. Median lobe of metasternum umbilico-punctate along edges anteriorly, median longitudinal groove more impressed posteriorly. *Elytra.*—8th stria with base and posterior half effaced, present only as an isolated impressed line; 9th stria arising from 10th somewhat before middle of elytral length; 10th stria disintegrating momentarily at hind angle. Striae moderately punctate, the punctures round and distinct basally, becoming effaced over most of strial length. Interstriae convex, sparsely and very finely punctate, appearing smooth. *Abdomen.*—Pygidium distinctly granular-punctate, the punctures finer ventrally, margin incomplete, totally effaced ventrally. *Anterior legs.*—Ventral surface of femur coarsely setigerous-punctate, the punctures reniform, except for an area along anterior edge, which is impunctate. Tibial forespur somewhat falciform, curving outwardly (fig. 34). *Middle legs.*—Coxa usually with two rows of granular punctures on outer face near median carina. Ventral surface of femur with a few coarse, reniform, setigerous punctures distally, elsewhere very finely punctate. Tibia below with 2–3 seta tufts distally, above without supplementary setae. *Posterior legs.*—Ventral surface of femur with a very few setigerous punctures distally or none, elsewhere very finely punctate. Tibia below with 2–4 setae distally, above without supplementary setae. *Total length.*—8–10 mm.

Male armament. Head with a low conical horn which is swollen at the base behind. Pronotum unarmed but with a broad, very indistinct, median transverse gibbosity and low tumosities on either side representing the usual pronotal prominences. Minor specimens possess but a low transverse carina on the head and no trace of any prominences on the pronotum.

Description of Female. Very similar to male. May sometimes be told by the deeper, more rounded clypeal emargination. *Total length.*—9–10 mm.

Female armament. Identical to that of male.

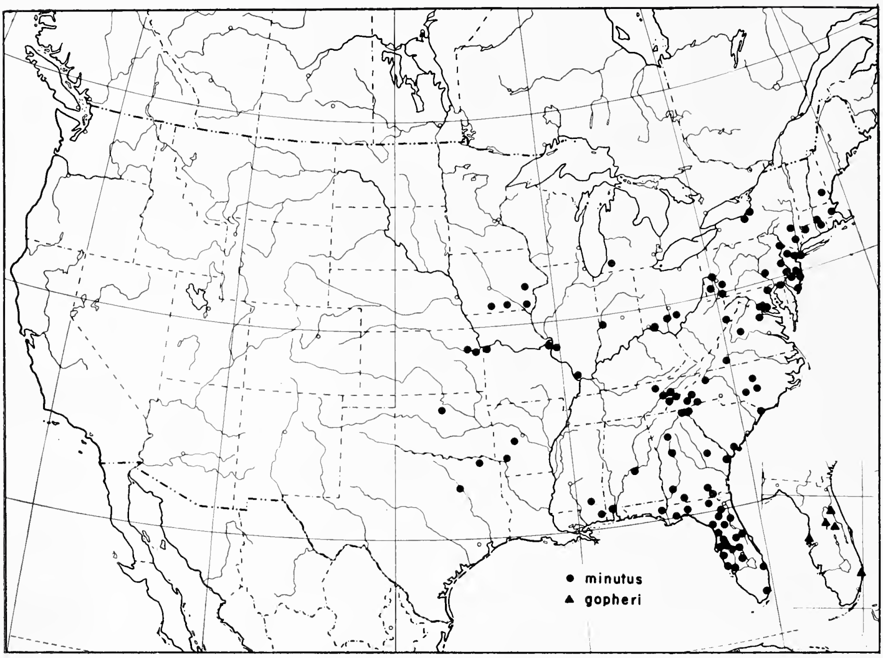

Fig. 14. Distribution of the *minutus* complex. Base map reproduced by permission of the University of Chicago.

Distribution. Fig. 14. I have seen specimens only from the southern part of the range of the Florida Gopher Tortoise in peninsular Florida, but Hubbard (1896) reports finding the species at De Funiak Springs in the extreme western part of the state. It is possible that it occurs throughout the range of the tortoise, but it has never been reported outside of Florida.

Biology. Inhabits the burrows of the Florida Gopher Tortoise as a coprophage. Nothing new has been added to the biological notes made by Hubbard (1894). It has occasionally been taken at light (Hamilton, 1896).

Remarks. Hubbard did not designate a type specimen for this species. The United States National Museum possesses one specimen of the original type series in the type collection (No. 1299). This specimen, bearing the label "Crescent City, Fla., H. G. Hubbard Coll.", had been entered as a type by Hubbard himself in 1896. It is here designated as **lectotype** of *Copris gopheri* Hubbard. There are, in addition, numerous other specimens from the type series in the National Museum (including some entered as "types" from the Hubbard and Schwarz collection in 1900) and elsewhere. These all bear the Crescent City label and, although not marked as such, may be considered paratypes.

This species is closely related to *minutus* (Drury) from which it differs in being less punctate and in having an outwardly curved forespur. It can immediately be told from *minutus* by examining the under surface of the prothorax just inside the longitudinal proepimeral carina. This area is impunctate in *gopheri* (and all other *Copris*) and fully punctate in *minutus* (a unique character). In addition, *minutus* shows a distinct anterior segment of the 9th elytral stria, this being absent in *gopheri*.

Material Examined. 16 males, 12 females (including lectotype).

UNITED STATES: *Florida:* Lake Co.: Leesburg, 2 Jul. 1938 (C. C. Goff), 1♀ (OLC); Palm Beach Co.: Lake Worth, 4♂♂, 4♀♀ (CM); Pinellas Co.: Tarpon Springs, 18 Apr. 1943 (Borys Malkin), 1♀ (OLC); Putnam Co.: Crescent City, 15 Jun. 1894 (H. G. Hubbard), 5♂♂, 4♀♀ (USNM); (Hubbard and Schwarz), 6♂♂, 2♀♀ (USNM, CAS); 15 Jul. (Fuchs), 1♂ (CAS).

Copris minutus (Drury)

Scarabaeus minutus Drury, 1770, Illus. Exot. Ins. I, pp. 78–79, pl. XXXV, fig. 6 [type: New York; British Museum (N. H.)].

Copris minutus, Horn, 1873, Trans. American Ent. Soc. IV: 42–51 (key and descr.); Schaeffer, 1906, Trans. American Ent. Soc. XXXII: 255 (key).

Scarabaeus silenus Fabricius, 1775, Syst. Ent. p. 21, No. 83 [type: America; British Museum (N. H.)].

Scarabaeus ammon Fabricius, 1781, Sp. Ins. I, p. 24, No. 105 [type: America; British Museum (N. H.)]; 1792, Ent. Syst. I, 1, p. 44, No. 147; Olivier, 1789, Ent. I, 3, p. 124, pl. 12, fig. 111; 1790, Encycl. méth. V, p. 161.

Copris ammon, Fabricius, 1801, Syst. Eleuth. I, p. 35, No. 25; Leconte, 1866, List of the Coleoptera of North America, p. 36.

Scarabaeus lar Fabricius, 1787, Mantissa Ins. I, p. 13, No. 124 [type: East India; lost. Co-types in Hunterian Collection, Glasgow]; Staig, 1931, The Fabrician Types of Insects in the Hunterian Collection at Glasgow University, pp. 50–52, pl. 15 (descr. of co-type).

Copris reflexus Panzer, 1794, Faunae Ins. Amer., p. 7 [type: ?].

Description of Male. *Head.*—Armed. Clypeus bidentate, clypeal teeth very broad, separated by a deep V-shaped median notch which cuts through margin. Posterior angles of genae quadrate. Upper surface of head sparsely and very finely punctate with genae, occasionally the sides of the clypeus, and a band between the eyes contrastingly, coarsely umbilico-punctate, the punctures granular. Posterior oblique carina absent. Occipital margin with setigerous groove present only at sides, where setae are very long; no marginal occipital carina. Demarcation between gula and submentum arcuate. *Thorax.*—Pronotum armed or not. Anterolateral angles subquadrate, lateral margin rather evenly curved. Lateral carina absent, represented by a longitudinal swelling just below lateral fossae. Anterior margin of pronotum not forming any median point or angle. Median longitudinal sulcus shallow, broad, complete, with coarse granular punctures. Punctuation of pronotum as follows: rather densely, coarsely punctate over entire surface, the punctures granular, finer on anterior declivities away from margin and on either side of dorsal sulcus. Anterior prosternal margin with a minute, acute median tooth; sternellum concave, with coarse granular punctures, sometimes with a trace of a median longitudinal carina anteriorly. Proepimeron evenly punctate over entire surface. Median lobe of metasternum with coarse granular punctures except along median line; median longitudinal groove distinct only posteriorly. *Elytra.*—8th stria incomplete, disintegrating beyond halfway point, but intact at the very base; 9th stria with a distinct, fully punctate segment close to base of elytron, then effaced for a short distance, arising again at about halfway point as usual, thereafter intact, occasionally the entire stria uninterrupted and fully punctate; 10th stria complete. Striae closely, coarsely punctate, the punctures round and separated by a distance approximately equal to their diameter. Interstriae convex and sparsely, very finely punctate, appearing smooth. *Abdomen.*—Pygidium densely, coarsely punctate, the punctures granular; pygidial margin incomplete, becoming effaced ventrally. *Anterior legs.*—Ventral surface of femur completely punctate, the punctures setigerous, reniform or oval. Tibia below often with a great reduction in the number of short ridges outside of median longitudinal carina. Forespur linear with a blunt apex curved downward and very slightly outward apically (fig. 36). *Middle legs.*—Coxa with a patch of dense, coarse punctures on outer face near longitudinal carina. Ventral surface of femur rather densely, coarsely setigerous-punctate over most or all of surface. Tibia below with 2–4 median distal seta tufts, above without supplementary setae. *Posterior legs.*—Femur and tibia as described for middle legs. *Total length.*—8–12.5 mm.

Male armament. Minor males bear a salient transverse carina on the head. With further development this grows into an acute horn which may be very long in some individuals and curved backward slightly near the apex. The base of the horn on either side posteriorly is climbed for about a third of its length by a prominent carina which appears to be a continuation of the fronto-clypeal suture; these carinae give the horn a swollen appearance at the posterior base (fig. 65). The sides of the horn are coarsely rugose basally. The pronotum is completely unarmed in poorly developed individuals; in better developed ones, the median prominences are seen to be approximated and very broadly truncated, their upper edges forming two median transverse carinae as in *lugubris* and *incertus*. The lateral prominences are at most low and conical, never achieving the laminate stage.

Description of Female. Very similar to male but usually distinguishable from it in armament and pronotal puncturation, the punctures of the anterior disc abruptly intensifying just behind the median transverse carinae. *Total length.*—9–12 mm.

Female armament. Head horn like that of less developed males, differing in being a little more transverse, very slightly truncate, and apically excavate on the posterior face. Median pronotal prominences very much like male's, but the transverse carinae are more curved in well developed specimens and approximated.

Distribution. Fig. 14. The eastern half of the United States in an area corresponding to the Lower and Upper Austral zones (except for the West Gulf and Mississippi Alluvial Plain sections), climbing a little into the Transition Zone in the mountains of North Carolina and Tennessee.

Biology. Some aspects of nidification have been discussed. Frequently collected under cow dung, also at light and coming to malt, butyric acid, and fungus baits (only one record of the latter).

Remarks. This species may immediately be told from all other American *Copris* by the uniformly punctate proepimeron. In all other species, the proepimeron is divided longitudinally by an indistinct carina (the posterior longitudinal proepimeral carina) (fig. 26 lpc), which sharply differentiates an outside, densely punctate area from an inside, almost impunctate one. Although traces of the carina are usually present in *minutus*, this sharp difference in puncturation is not seen and the entire proepimeron is rather uniformly, coarsely punctate. Similarly unique is the presence of a fully punctate anterior segment of the 9th elytral stria near the base of the elytron. This species and the closely related *gopheri* Hubbard are further distinguished by the similarity in armament between the males and females. The females, when developed, possess an acute horn of the male type, and not a truncate and apically excavate one as in all other American *Copris* showing sexual dimorphism.

For an analysis of the geographical variation in sexual dimorphic development in this species see p. 18.

Material Examined. 352 males, 208 females.

UNITED STATES: *Alabama:* Mobile; Montgomery; *Arkansas:* Garland Co.: Hot Springs; Hempstead Co.: Hope; Pike Co.: Highland; *Connecticut:* Litchfield Co.: Cornwall; Litchfield; Tolland Co.: Storrs; *District of Columbia:* Washington; Woodridge; *Florida:* Alachua Co.: Gainesville; Newman's Lake; Bradford Co.: Starke; Calhoun Co.: Clarksville; Charlotte Co.: Punta Gorda; Citrus Co.; Columbia Co.: High Springs; Suwanee Springs; Dade Co.: Miami; De Soto Co.: Arcadia; Fort Ogden; Hernando Co.: Brooksville; Highlands Co.: Archbold Biol. Sta., Lake Placid; Hillsborough Co.: Lutz; Tampa; Jefferson Co.: Monticello; Levy Co.: Waccasassa R., Gulf Hammock; Manatee Co.: Oneco; Marion Co.: Ocala; Orange Co.: Winter Park; Palm Beach Co.: Lake Worth; Pasco Co.: Dade City; Pinellas Co.: Largo; Tarpon Springs; Polk Co.: Fort Meade; Lakeland; 3 mi SW Lake Marion; Putnam Co.: Crescent City; Interlachen; 8 mi SE Interlachen; Suwannee Co.: 13 mi N O'Brien; Volusia Co.: Enterprise; Wakulla Co.; location undetermined: Natal; Stemper; *Georgia:* Atlanta; Baker Co.: Emory U. Field Sta., Newton; Chatham Co.: Savannah; Emanuel Co.: Swainsboro; Lamar Co.: Barnesville; Rabun Co.: Clayton; Spalding Co.: Experiment; Thomas Co.: Thomasville; Ware Co.:

Waycross; Okefinokee Swamp: Billys I.; location undetermined: The Rock; *Illinois:* Alexander Co.: Olive Branch; St. Clair Co.; *Indiana:* Terre Haute; *Iowa:* Appanoose Co.: Moulton; Decatur Co.: Leon; Henry Co.: Mt. Pleasant; Iowa City; *Kansas:* Doniphan Co.; Douglas Co.: Lawrence; Shawnee Co.: Topeka; *Maryland:* Baltimore; Cecil Co.: Blythedale; Prince George Co.: Branchville; *Massachusetts:* Hampden Co.: Wilbraham; Middlesex Co.: Cambridge; Framingham; Sherborn; *Michigan:* Van Buren Co.: Paw Paw; *Mississippi:* Forrest Co.: Cp. Shelby, nr. Hattiesburg; George Co.: Lucedale; "S. Miss."; *Missouri:* Kansas City; St. Louis; *New Hampshire:* Belknap Co.: Barnstead; *New Jersey:* Atlantic Co.; Burlington Co.: Bordentown; Moorestown; Riverton; Camden Co.: Clementon; Cape May Co.; Essex Co.: Newark; Morris Co.: Boonton; Ocean Co.: Island Beach, Barnegat Bay; Lakehurst; Orange Mts.; Sussex Co.: L. Lackwanna; *New York:* Brooklyn; Greene Co.; Long Island; Orange Co.: New Windsor; West Point; Oswego Co.: Oswego; Wayne Co.; *North Carolina:* Blue Ridge Parkway: Mile 277.7; Buncombe Co.: Black Mt.; Weaverville; Duplin Co.: Faison; Harnett Co.: Dunn; Henderson Co.: Mills River; 16 mi S Asheville; Moore Co.: Southern Pines; Polk Co.: Tryon; Raleigh; Transylvania Co.: Brevard; *Ohio:* Clermont Co.; Hocking Co.; Ross Co.; *Oklahoma:* Payne Co.; *Pennsylvania:* Allegheny Co.; Cumberland Co.: Lemoyne; Dauphin Co.: Deodate; Delaware Co.: Castle Rock; Fayette Co.; Northampton Co.: Easton; Philadelphia Co.: Frankford; Pike Co.; Pittsburgh; Washington Co.; Westmorland Co.: Jeanette; *South Carolina:* Beaufort Co.: Beaufort; Seabrooks I.; Okeegee R.; Horry Co.: Little River; Oconee Co.: Clemson College; Fish Hatchery; *Tennessee:* Great Smoky Mts. N. P.: Chilhowee Mts.; Morgan Co.: Burrville; Roane Co.; Sevier Co.: Gatlinburg; *Texas:* Dallas; Dallas Co.; Lamar Co.: Paris; *Virginia:* Arlington Co.: E Falls Church; Blue Ridge Parkway: Mile 162.6; Fairfax Co.: Falls Church; Frederick Co.: Fredericksburg; Nelson Co.; Shenandoah N. P.; *West Virginia:* Cheat Mts.

Group II. The *fricator* group.

Outer face of apical maxillary palpal segment flattened or longitudinally grooved. Lateral pronotal carina present. Lateral pronotal margin sinuate or angulate. Male median pronotal prominences, when present, rounded or acute. Complex punctures nearly always without a granular texture. Sternellum concave, not longitudinally carinate. Pygidial margin usually complete. Male genital parameres bluntly rounded at the apices. 19 species.

Complex 1. The *armatus* complex.

Posterior angles of head acute. Anterolateral angles of pronotum broadly rounded or angulate, lateral margin obtusely angulate, not sinuate. Forespur not appreciably bent or curved inward and with apex broadly rounded or obtusely pointed in both sexes. 8th elytral stria disintegrating posteriorly, often also effaced anteriorly. Pygidial margin complete. Large and robust beetles.

Seven species found in the mountains at moderate to very high altitudes in Mexico and Central America: *armatus* Harold, *megasoma* Matthews and Halffter, *klugi* Harold, *moechus* Leconte, *boucardi* Harold, *aspericollis* Gillet, and *subpunctatus* Gillet.

Copris armatus Harold

Copris armatus Harold, 1869, Ann. Soc. Ent. France, ser. 4, IX: 498 [type: Mexico, D. F. or Toluca, Méx.*; Museum d'Histoire Naturelle, Paris]; Bates, 1887, Biol. Cent.-Amer., Coleopt. II, 2, p. 54 (distr.); Gahan, 1894, Ann. Mag. Nat. Hist., ser. 6, XIV: 117 (distr.); Gillet, 1910, Not. Leyden Mus. XXXII: 3 (distr.); Matthews, 1959, Ciencia XIX(6–7): 136 (key and distr.).

Description of Male. *Head.*—Armed. Clypeus without teeth or marginal expansions, with a small triangular median notch not cutting inner edge of margin. Upper surface of head closely punctate, the punctures not umbilical, with posterior part of head between eyes and horn and behind them smooth. Posterior oblique carina present but not sharp. Occipital margin with transverse setigerous groove interrupted into three sections, the lateral sections displaced forward and partly overlapping the median one; no marginal occipital carina. Demarcation between gula and submentum arcuate. *Thorax.*—Pronotum armed. Anterolateral angles subquadrate or obtuse, lateral margin slightly angled out at origin of lateral carina. Lateral carina prominent, not issuing from margin anteriorly. Anterior margin of pronotum not forming any median point or angle. Median longitudinal sulcus complete, broadly impressed, and coarsely umbilico-punctate. Puncturation of pronotum as follows: finely to coarsely punctate over entire area, the punctures running together on inner surfaces of lateral prominences apically, the punctures simple except on the following areas, which are coarsely umbilico-punctate: posterior and lateral submargins, lateral fossae, along dorsal sulcus in an anteriorly widening

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* Harold gives the range ("patrie") of this species as: "de Mexico et de Toluca", without designating one of these as the type locality.

area, on anterior face in varying proportions, and in depressions between median and lateral prominences where in developed specimens the punctures become sparse, very large, and annular or cicatricial. Anterior prosternal margin with a median tooth which is nearly always truncate and usually quadrate (fig. 52); sternellum sparsely punctate. Median lobe of metasternum impunctate but somewhat wrinkled laterally; median longitudinal sulcus of metasternum with impressed portion ending somewhat short of anterior depression. *Elytra.*—8th stria incomplete, disintegrating at posterior angle; 9th stria arising about halfway down elytral length, occasionally barely visible more anteriorly as a faint, impunctate impressed line; 10th stria complete. Striae closely punctate, the punctures round and separated by a distance approximately equal to their diameter. Interstriae almost flat, very faintly punctate, appearing smooth. *Abdomen.*—Pygidium moderately, evenly umbilico-punctate, the punctures small; pygidial margin complete. *Anterior legs.*—Ventral surface of femur coarsely setiferous-punctate on posterior (upper) longitudinal half, more finely punctate on anterior half. Forespur only slightly curved inward apically, the apex broadly rounded. *Middle legs.*—Coxa with a few coarse setigerous punctures along outer edge, impunctate elsewhere. Proximal half of ventral surface of femur very finely punctate, distal half coarsely setigerous-punctate. Tibia with 2–3, usually two, distal seta tufts medially on ventral side. *Posterior legs.*—Ventral femoral surface punctate, the punctures becoming gradually coarser distally. Ventral distal seta tufts on tibia 1–3. *Total length.*—18.5–23 mm.

Male armament. In better developed individuals the head horn is long and evenly curved back, the outer pronotal gibbosities are laminate and the median ones prominent and approximated. In extreme developments, the very long head horn is bent back at about the middle and tapers to the apex (fig. 69), the median pronotal prominences are sharply conical, approximated, their apices divergent and directed horizontally in profile. The lateral pronotal prominences are directed slightly outward.

Description Of Female. Similar to male, differing only in armament and in the following features: clypeus with two very low rounded marginal expansions flanking median notch, clypeal margin broader and more reflexed than that of male. Head with short impressed lines (transverse punctures) behind horn and eyes. Median dorsal sulcus of pronotum present only on base, fine, sparsely punctate. Puncturation of pronotum as follows: evenly, finely punctate on disc and base, the punctures becoming coarser and more transverse anteriorly, their anterior edges becoming more raised into ridges, until on extreme anterior end of pronotum only the ridges remain, giving anterior face an asperate appearance. The punctures are umbilical only along posterior and lateral submargins, in lateral fossae, and a few along dorsal sulcus. *Total length.*— 19–24 mm.

Female armament. Normal for genus.

Distribution. Fig. 15. The Central Volcanic Range of Mexico at altitudes of 1830–3000 m. (6000–9800 ft.) The Central American localities given by Bates refer to other species.

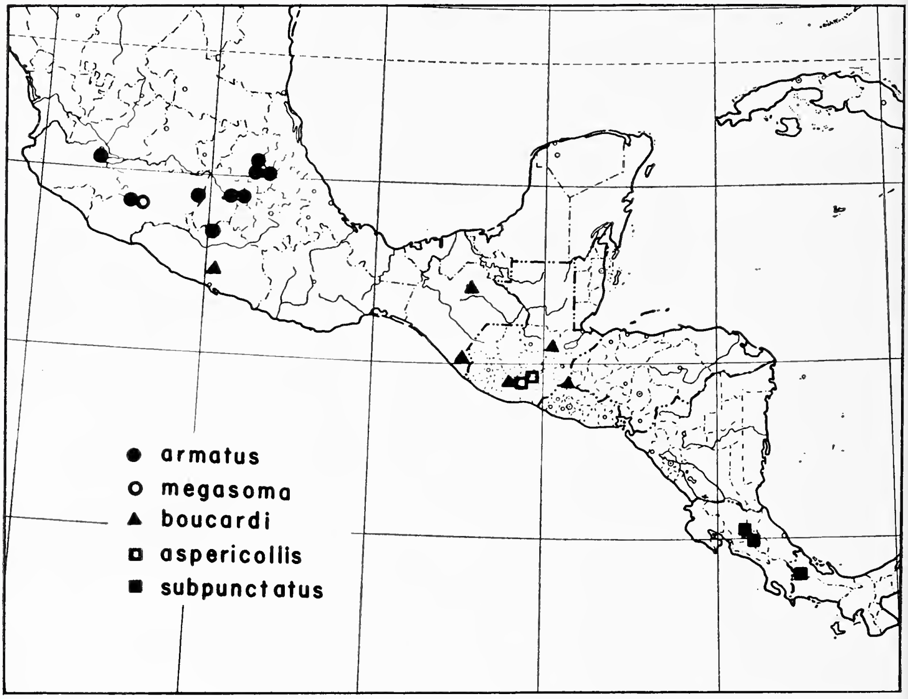

Fig. 15. Distribution of the *armatus* complex, I. Base map reproduced by permission of the University of Chicago.

Biology. Feeds on cow dung; otherwise nothing is known of its biology. Appears to be active throughout the rainy season of June–October and apparently has not been collected at light.

Remarks. Because of the punctate (not granulate) anterior pronotal surface in the male, this species could be confused only with *klugi* Harold in this complex. Major males differ very radically from this species in the nature of the median pronotal prominences, which are separated with the apices divergent in *armatus* and closely approximated and convergent in *klugi*. In addition, *armatus* is somewhat larger than *klugi* and usually bears a truncate median lobe on the anterior margin of the prosternum. The clypeal margin of the males is also totally different, being evenly rounded with a small median notch in *armatus*, remotely bidentate and broadly emarginate in *klugi*. The females of *armatus* are completely rugose on the anterior pronotal surface and the clypeal margin is practically devoid of expansions flanking the notch.

This species and the fossil *Copris pristinus* Pierce are closely related (see discussion on p. 35).

Material Examined. 45 males, 30 females.

MEXICO: *Distrito Federal:* México, 10 Aug. 1942 (C. Bolívar), 1 ♂ (GH); Villa de Guadalupe, México, 11 Jul. 1949 (G. Halffter), 1 ♂ (GH); *Guerrero:* Teloloapan, 15 Aug. 1957 (D. Douglas), 1 ♀ (GH); *Hidalgo:* Bosque del Chico (N of Pachuca), 29 Jul. 1953 (G. Halffter), 8 ♂♂, 10 ♀♀ (GH); Guerrero Mills (W. M. Mann), 1 ♂, 1 ♀ (MCZ); Real del Monte, Pachuca (Richardson), 1 ♀ (GH); San Miguel (W. M. Mann), 1 ♂ (USNM); 8 km. W. Tulancingo, 4 Aug. 1957 (W. W. Gibson), 1 ♂ (IR); *Jalisco:* 8 mi. S. Guadalajara, late Sep. 1954 (F. X. Williams), 1 ♂ (CAS); *México:* México-Morelia Rd. at border of Michoacán, 13 Sep. 1953 (V. Aguilar), 9 ♂♂, 2 ♀♀ (GH); Salazar [3000 m], Mar. 1952 (found dead), Aug. 1952, 10 Aug. 1953, 25 Jun. 1956 (G. Halffter), 4 ♂♂, 7 ♀♀ (GH); 9 Oct. 1953 (P. Avila, G. García), 1 ♂ (GH); Toluca [2640 m] (Sallé), 1 ♂, 1 ♀ (BM, PAS); *Michoacán:* Bosenchave Nat'l. Pk., 2400 m. 10 Oct. 1953 (Bolívar), 2 ♂♂ (GH); Corupo, 20 Jun. 1947 (T. H. Hubbell), 1 ♀ (USNM); Tancítaro, 6000 ft. 10 Jul. 1940 (Hoogstraal and Knight), 1 ♂ (CAS); 6600 ft., 19 Jul. 1940 (Hoogstraal and Knight), 1 ♀ (CAS); 6000 ft., 24 Jun. 1941 (Hoogstraal and Haag), 2 ♂♂ (CAS); 6500 ft., 28 Jun. 1941 (Hoogstraal and Haag), 3 ♂♂, 1 ♀ (CAS); 6500 ft., 18 Jul. 1941 (H. Hoogstraal), 2 ♂♂ (CAS); Zitácuaro, 15 Jun. 1957 (G. and V. Halffter), 1 ♂ (GH); *national record only:* (Lundholtz), 3 ♂♂, 6 ♀♀ (AMNH); (Sallé), 1 ♂, 1 ♀ (BM); 1 ♂, 3 ♀♀ (CAS).

Copris megasoma Matthews and Halffter

Copris megasoma Matthews and Halffter, 1959, Ciencia XVIII(9–10): 194–196 [type: Tancítaro, Mich.; California Academy of Sciences]; Matthews, 1959, Ciencia XIX(6–7): 136 (key and distr.).

Description of Male (holotype only). *Head.*—Armed. Clypeus with neither teeth nor emargination (median area of clypeal margin in holotype is damaged, but enough of margin remains to reveal no trace of any median notch or teeth). Upper surface of head closely punctate, the punctures simple, with impunctate areas at base of head and about eyes. Posterior oblique carina present. Occipital margin with setigerous groove in three partially overlapping sections; no marginal occipital carina. Demarcation between gula and submentum arcuate. *Thorax.*—Pronotum armed. Anterolateral angles rounded, lateral margin fairly straight. Lateral carina sharp, issuing from anterior angle in holotype (point of issuance of lateral carina usually depends on thoracic development). Anterior margin forming a distinct upwardly directed median angle with inner edge. Median longitudinal sulcus obsolescent, with a few simple punctures. Puncturation of pronotum as follows: base and disc glassy smooth, quite impunctate except for the umbilico-punctate submargin; entire area forward of a transverse line joining hind edges of lateral fossae densely punctate, the punctures umbilical only in lateral fossae and in depressions between median and lateral prominences; there is an impunctate area along mid-line on anterior surface of pronotum. Anterior prosternal margin devoid of any median tooth; sternellum rather flat; moderately punctate. Median lobe of mestasternum impunctate; median longitudinal groove complete. *Elytra.*—8th stria incomplete, disintegrating about halfway down elytron; 9th stria originating about halfway down elytron, but also present as a short, faint impunctate line near base of elytron; 10th stria complete. Striae closely, finely, and shallowly punctate, the punctures round or slightly transverse, separated by a distance equal to a little more than their diameter, strial lengths between punctures very fine and shallow. Interstriae almost flat, quite impunctate. *Abdomen.*—Pygidium rather sparsely and very finely punctate, completely margined. *Anterior legs.*—Ventral surface of femur with setigerous punctures on posterior longitudinal half, impunctate on anterior half. Forespur fairly linear, curved slightly downward and inward at apex, ending in a blunt, rounded apex. *Middle legs.*—Coxa impunctate except for a few small setigerous punctures along outer edge apically. Ventral surface of femur impunctate but with a few indistinct punctiform impressions apically. Tibia with two distal seta tufts below. *Posterior legs.*—Ventral surface of femur impunctate. Tibia with 1–2 distal seta tufts below. *Total length.*—28 mm.

Male armament. The head of the holotype bears a short, straight horn abruptly truncated at the apex (perhaps by wear, but the specimen on the whole is not particularly worn (fig. 70). The pronotum bears the usual four prominences, the two median ones situated far apart, slightly divergent and truncated when seen from above, obliquely flattened when seen from the front, the lower surfaces slightly concave. The two lateral prominences are laminate, not very developed, their upper edges sloping downward in lateral view.

Description of Female (allotype only). Similar to the male, but differing in armament and in the following features: anterolateral angles of pronotum more rounded, the lateral carina issuing considerably behind the angle. Puncturation of pronotum quite different, consisting of a dense granulation on the anterior face and lateral surfaces before the fossae, becoming asperate on anterior portion of disc, these asperations giving place to transverse punctures posteriorly, which fade out at about the transverse midline of the pronotum, the base of which is therefore completely impunctate and glassy smooth except for a row of umbilical punctures along the posterior submargin. The forespur is more worn, being evenly tapering from the base, only very slightly curved inward apically, the apex being more acute. Pygidium more faintly punctate. The entire insect is considerably broader in relation to its length than the male; this is particularly noticeable with regard to the pronotum. *Total length.*—29.5 mm.

Female armament. Normal for the genus.

Distribution. Fig. 15. Known only from the type locality at Tancítaro, Michoacán, 1800–1900 m. (5900–6300 ft.).

Biology. Unkown.

Remarks. This appears to be nearly the largest species of *Copris* in the world, being slightly exceeded in size only by the African *C. draco* Arrow, as far as I am aware. In appearance the specimens are reminiscent of large *Pinotus* and are equally robust. The only other species with which this one could be confused is *armatus* Harold. From *armatus* it differs in apparently not having any median notch in the clypeal margin, in the ventral femoral surfaces, which are quite impunctate, in the anterior margin of the prosternum, which does not bear any median lobe or tooth, in the completely impunctate pronotal disc, and, of course, in size, the largest *armatus* measuring but 24 mm. in total length. Its specific distinctness is also shown by the difference in the male median pronotal prominences, which are flattened at the apices in *megasoma*, conical and round in cross section in *armatus* (figs. 69, 70). It is closely related to the fossil *C. pristinus* Pierce.

Material Examined. Holotype and allotype.

MEXICO. *Michoacán:* Tancítaro, 1900 m, Jul. 1940 (Hoogstraal and Knight), 1 ♂ (CAS); 1800 m, 20 Jul. 1941 (Hoogstraal), 1 ♀ (CAS).

Copris klugi klugi Harold

Copris klugi Harold, 1869, Ann. Soc. Ent. France, ser. 4, IX: 498–499 [type: Oaxaca, Oax.; Museum d'Histoire Naturelle, Paris]; Bates, 1887, Biol. Cent.-Amer., Coleopt. II, 2, p. 54 (distr.); Matthews, 1959, Ciencia XIX(6–7): 136 (key and distr.).

Copris hintoni Saylor, 1933, Canadian Ent. LXV (10): 238–239 [type: Real de Arriba, State of Mexico, 6300 ft.; California Academy of Sciences]; Matthews and Halffter, 1959, Ciencia XVIII(9–10): 193 (synon.).

Description of Male. *Head.*—Armed. Clypeus with two remote, very small teeth, sometimes barely perceptible, and a very shallow median triangular notch not cutting through margin. Upper surface of head sparsely punctate along margin, the punctures not umbilical, rest of head very finely punctate, appearing smooth. Posterior oblique carina distinct. Occipital margin with transverse setigerous groove complete; no marginal occipital carina. Demarcation between gula and submentum slightly angulate. *Thorax.*—Pronotum armed. Anterolateral angles obtuse. Lateral margin curved inward slightly behind origin of lateral carina. Lateral carina sharp. Anterior margin not forming any median point or angulation. Median longitudinal sulcus complete, impressed, coarsely umbilico-punctate. Puncturation of pronotum as follows: entirely punctate, with no rugosities; finely punctate on base, the punctures becoming cicatricial then umbilical anteriorly in the depressions, more impressed but simple on outside of lateral prominences; punctures coarse and umbilical along posterior and lateral submargins, in lateral fossae, along dorsal sulcus in an anteriorly widening band, in depressions between median and lateral prominences, and on all anterior declivities, where punctures are moderately sparse, separated by more than their diameters except in very minor specimens, and not accompanied by any rugosity or asperation; sometimes these punctures on anterior surface are not umbilical. Anterior prosternal margin without any median tooth; sternellum sparsely punctate. Median lobe of metasternum finely to coarsely umbilico-punctate along edges; median impressed line complete. *Elytra.*— 8th stria incomplete, interrupted at hind angle;

9th stria arising halfway down elytral length; 10th complete. Striae closely punctate, the punctures transverse, separated by about their width. Intervals slightly convex, very finely punctate, appearing smooth. *Abdomen.*—Pygidium entirely margined, moderately, finely umbilico-punctate. *Anterior legs.*—Ventral surface of femur coarsely setigerously punctate except for a very finely punctate anterior area. Forespur parallel sided, curving sharply downward and inward apically, apex broadly rounded, occasionally acute. *Middle legs.*—Coxa impunctate or with a few fine punctures along median longitudinal carina. Ventral surface of femur finely punctate with some coarser setigerous punctures distally. Tibia below with 1–2 distal seta tufts. *Posterior legs.*—Ventral surface of femur finely punctate with at least a few reniform, usually setigerous, punctures distally. Tibia below with 2–3 distal seta tufts. *Total length.*—15–19 mm.

Male armament. In major individuals, the head horn is elongated and evenly curved, gradually tapering or linear, the median prominences are acute, closely approximated without merging, their outer edges evenly converging forward, and the lateral prominences are laminate as usual and are directed forward and slightly outward (fig. 71).

DESCRIPTON OF FEMALE. Similar to male but differing in armament and in the following features: clypeal teeth more prominent and rounded, the emargination between them narrower. Head surface more densely punctate. Occipital margin with transverse setigerous groove often interrupted. Pronotum with a deeply impressed, umbilico-punctate median longitudinal sulcus at base, rest of disc (except along the margin) finely punctate, becoming either coarsely umbilico-punctate or asperate and transversely pitted, or both, on anterior declivity; anterior declivity always with at least some umbilical punctures, especially at sides; posterior and lateral submargins and lateral fossae coarsely umbilico-punctate. Median and posterior tibiae below with 2–4 median seta tufts distally. *Total length.*—14–20 mm.

Female armament. Normal for the genus.

DISTRIBUTION. Fig. 16. Occurring throughout the Eje Volcánico Transversal and Sierra Madre del Sur at altitudes of 1500–2000 m. (5000–6500 ft.). The type locality is Oaxaca, Oax. (collected by Boucard) and I have seen specimens collected by Sallé from the state of Oaxaca. Since then it has not been collected so far south. Bates records it from Guatemala, but his determination needs confirmation.

BIOLOGY. Collected under cow dung; otherwise the biology is unknown. Active from May to August.

REMARKS. The numerous paratypes I have examined which bear the name *hintoni* Saylor are perfectly typical *klugi* in every respect. It appears that Saylor described his species through a misapplication of the name *klugi* to the species known as *boucardi* Harold, judging by his discussion. These two species may be confused because the males are armed in a very similar manner, but *boucardi* is always densely granulate on the anterior pronotal surface in the male, whereas *klugi* is punctate, a distinction which Harold overlooked in his original descriptions, preferring to use the fact that *klugi* is punctate on the median dorsal sulcus of the pronotum while the other species is not, a character which will also serve to distinguish them. Furthermore, they do not occur together. *C. klugi* might also be confused with *mexicanus* Matthews and Halffter and *sallei* Harold; however, the latter two species have sinuate anterior pronotal angles.

MATERIAL EXAMINED. 55 males, 60 females.

MEXICO: *Aguascalientes:* Aguascalientes, Aug. 1957 (G. Halffter), 1 ♀ (GH); *Guerrero:* Taxco, Jun. 1937 (Embury), 4 ♂♂ (CAS); *México:* Malinalco, 1780 m., Jul. 1946 (G. Halffter), 1 ♂ (GH); Real de Arriba, Temascaltépec, 6300 ft., 1931, 1932 (H. E. Hinton), 21 ♂♂, 19 ♀♀ (CAS); Tejupilco, Temascaltépec, 1932 (H. E. Hinton), 1 ♀ (CAS); Temascaltépec, Feb. 1931 (G. B. Hinton), 5 ♂♂, 9 ♀♀ (CAS); Tenancingo, 22 May 1956 (G. and V. Halffter), 3 ♂♂, 1 ♀ (GH); 10 km. S Villa Morelos, 26 August 1956 (G. and V. Halffter), 1 ♀ (GH); *Michoacán:* Tuxpan, 15 Jun. 1957 (G. and V. Halffter), 1 ♂ (GH); Zitácuaro, 15 Jun. 1957 (G. and V. Halffter), 4 ♂♂, 17 ♀♀ (GH); *Morelos:* Cuernavaca, 3 Aug. 1938 (L. J. L.), 1 ♂, 1 ♀ (OLC); Jul. 1957 (W. W. Gibson), 2 ♂♂ (IR); 27 Aug. 1957 (G. Halffter), 3 ♂♂, 2 ♀♀ (GH); 3 mi. NW Cuernavaca, 17 Jun. 1959 (H. E. Evans), 6 ♂♂, 5 ♀♀ (CU); Tepoztlán, 10 Jun. 1951 (G. Halffter), 1 ♀ (GH); *Oaxaca:* Capulálpam [2000 m.] (Sallé), 1 ♂ (BM); Juquila [2000 m.] (Sallé), 1 ♀ (BM); *Puebla:* 1 mi. N Atlixco, 29 Jun. 1955 (U. Ks. Mex. Exp.), 1 ♀ (UKs); *Veracruz:* Jalapa (Hoege), 1 ♀ (USNM).

Copris klugi sierrensis n. subsp.

Holotype: 3 mi. NE Santa María de los Angeles, Jalisco, Mexico, 17 July 1954 (R. H. Brewer), ♂; California Academy of Sciences.

DESCRIPTION. This form is distinguishable primarily by its proportionately smaller horn in the male. When the horn height is plotted against femoral length for all specimens of the species (fig. 6) it is seen that this form falls along a significantly different line from that followed by the more southern subspecies. This form differs further in that there is a faint sclerotized longitudinal band on the dorsal surface of the male parameres. The females are indistinguishable from *k. klugi.*

DISTRIBUTION. Fig. 16. The Sierra Madre Occidental from Jalisco to Chihuahua at altitudes of 1380–2600 m. (4500–8500 ft.). In Durango, where the closely related *moechus* Leconte occurs, *k. sierrensis* appears to undergo an altitude displacement by that species, *moechus* being found here at altitudes of up to 2300 m. (7500 ft.), whereas *k. sierrensis* is found only at 2500 m. or higher in this region.

BIOLOGY. Unknown.

REMARKS. Means for distinguishing this form from the closely related and sympatric *moechus* Leconte are discussed under the latter species. The females of *klugi* invariably show at least a few umbilical punctures amid the rugosities on the anterior pronotal face; this character is not shared by other females in the complex.

MATERIAL EXAMINED. 23 Males, 17 females.

MEXICO: *Chihuahua:* 20 mi. SW Camargo, 4500 ft. 13 Jul. 1947 (Michener), 1 ♂ (AMNH); Namiquipa (W. F. Foshag), 1 ♀ (USNM); *Durango:* 6 mi. NE El Salto, Durango Dist., 8500 ft., 10 Aug. 1947 (Gertsch), 1 ♂ (AMNH); Las Adjuntas, 8500 ft., 8 Jun. 1953 (R. K. Selander), 1 ♂ (IR); Otinapa, 8200 ft., 11 Aug. 1947 (Gertsch), 1 ♂ (AMNH); *Jalisco:* 8 mi. S. Guadalajara, 28 Sep. 1954 (F. X. Williams), 2 ♂♂ (IR); 3 mi. NE Santa María de los Angeles, 6200 ft., 17 Jul. 1954 (R. H. Brewer), 6 ♂♂, 3 ♀♀ (CAS); *Zacatecas:* ?Laguna Balderrama, 8200 ft., 7 Jul. 1954 (R. H. Brewer), 9 ♂♂ (CAS); Sain Alto, 7000 ft., 14 Aug. 1947 (Cazier), 1 ♂ (AMNH); 10 mi. NW Sombrerete, 7700 ft., 1 Jul. 1954 (R. H. Brewer), 1 ♂, 13 ♀♀ (CAS).

Copris moechus Leconte

Copris moecha Leconte, 1854, Proc. Acad. Nat. Sci. Philadelphia VII: 222 [type: Camp 14*; Museum of Comparative Zoology]; Leconte, 1858, Jour. Acad. Nat. Sci. Philadelphia, ser. 2, IV: 9–42 (distr.); Horn, 1873, Trans. American Ent. Soc. IV: 42–51 (key and descr.); Schaeffer, 1906, Trans. American Ent. Soc. XXXII: 255 (key).

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* I have not been able to determine the location of "Camp 14". This refers to the United States and Mexican Boundary Commission explorations of 1850–1853 during which one member of the expeditions, Dr. Thos. H. Webb, made "large collections . . . in the region between the Rio Grande and the Colorado River of California, chiefly in the valley of the Gila" (Leconte, 1858). Leconte in the

Copris clavicornis Matthews and Halffter, 1959, Ciencia XVIII(9–10) : 191–194 [type: 100 km W of Sta. Bárbara, Chih.; American Museum of Natural History]; Matthews, 1959, Ciencia XIX(6–7) : 136 (key and distr.). **New synonymy.**

Description of Male. *Head.*—Armed. Clypeus with two low angular teeth and a U- or V-shaped notch between them, not cutting through margin. Upper surface of head densely, evenly punctate, the punctures simple, with a basal impunctate area between eyes and horn, and behind both. Posterior oblique carina reduced. Occipital margin with transverse setigerous groove interrupted into three sections, the latter ones displaced forward and partly overlapping the median. Demarcation between gula and submentum arcuate. *Thorax.*—Pronotum armed. Anterolateral angles obtuse, lateral margin curved inward slightly behind origin of lateral carina. Lateral carina sharp, issuing from margin. Anterior margin not forming any median point or angle. Dorsal median longitudinal sulcus complete and impressed, sparsely umbilico-punctate. Puncturation of pronotum very variable, as follows: basal part of disc shallowly punctate, the punctures usually simple, or impunctate; rest of disc densely punctate, the punctures usually simple; posterior and lateral submargins, lateral fossae, and depressions between median and lateral prominences coarsely umbilico-punctate; the anterior surfaces may be entirely asperate (as in the holotype of *clavicornis*) or more usually both asperate and punctate, the punctures simple or umbilical, the rugosities and punctures always very dense (one specimen seen was densely umbilico-punctate over the entire pronotum, without asperation). Anterior prosternal margin with a broad, low, rounded median lobe (no median tooth); sternellum moderately punctate. Median lobe of metasternum impunctate but with some faint punctiform impressions laterally, or umbilico-punctate anteriorly; median longi-

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latter work places the type locality of *C. moechus* in Arizona, while Horn (1873) places it erroneously in Texas. However, a reading of the personal narrative of the leader of the Commission (Bartlett, 1854) reveals that two additional expeditions were carried out: one from the headquarters at the "Copper Mines" (Santa Rita del Cobre, Chih., now Santa Rita, N.M.) to Fronteras and Arispe, Sonora, the other from El Paso south to Chihuahua, Chih. and thence southeast to Saltillo, Coah., and Monterrey, N.L. Dr. Webb took part in both of these and it was almost certainly during the latter expedition, which passed right through the presently known range of *moechus*, that the type specimen was collected. This places the type locality in Chihuahua, probably near the capital, and this species cannot be considered as occurring within even the present boundaries of the United States.

tudinal impressed line complete. *Elytra.*—8th stria incomplete, disintegrating at posterior angle; 9th stria arising about halfway down elytron; 10th stria complete. Striae closely punctate, the punctures transverse, separated by a distance equal to about their width. Interstriae slightly convex, very finely punctate, appearing smooth. *Abdomen.*—Pygidium completely margined, densely umbilico-punctate. *Anterior legs.*—Ventral surface of femur densely and coarsely setigerous-punctate on posterior longitudinal half, finely punctate on anterior half. Forespur relatively straight and parallel-sided, bluntly rounded and somtimes slightly dilated apically. *Middle legs.*—Coxa finely punctate along median longitudinal carina, occasionally with a very few large setigerous punctures along outer edge. Ventral surface of femur finely punctate with a few coarser setigerous punctures distally. Tibia below with 1–2 distal median seta tufts. *Posterior legs.*—Ventral surface of femur finely punctate, more coarsely so distally, with or without stigerous punctures. Tibia below with 2–3 distal median seta tufts. *Total length.*—15.5–20 mm.

Male armament. In major males the head horn is elongated and slightly bent, dilated transversely at the apex, and the pronotal prominences are produced, the median ones closely approximated, acute, not at all divergent but not merging, and directed slightly upward, the lateral ones laminate and directed forward parallel to the long axis or slightly divergent (fig. 81).

Description of Female. Similar to male but differing in armament and in the following features: clypeal teeth rounded, more prominent, flanking a broader, U-shaped notch. Pronotum punctate on upper part of disc and sides below lateral carina, umbilico-punctate along posterior submargin and in lateral fossae, densely granulate or asperate elsewhere, especially on anterior declivity, which never shows any punctures or depressions. Median longitudinal sulcus impunctate and impressed only on superior part of disc. Both median and posterior tibiae with 2–3 distal seta tufts below. *Total length.*—13–21 mm.

Female armament. Normal for the genus.

Distribution. Fig. 16. The mountains of Southern Chihuahua and Northern Durango at altitudes of 1520–2420 m. (5000–8000 ft.).

Biology. Unknown.

Remarks. This species is extraordinarily variable in the puncturation of the anterior pronotal face in the male, which ranges all the way from being completely rugose (without punctures) to completely punctate. Of the more than 90 male specimens examined, however, only one was completely punctate (without asperation). Possibility for confusion exists in attempting to separate the punctate males of this species from *arizonensis* Schaeffer and

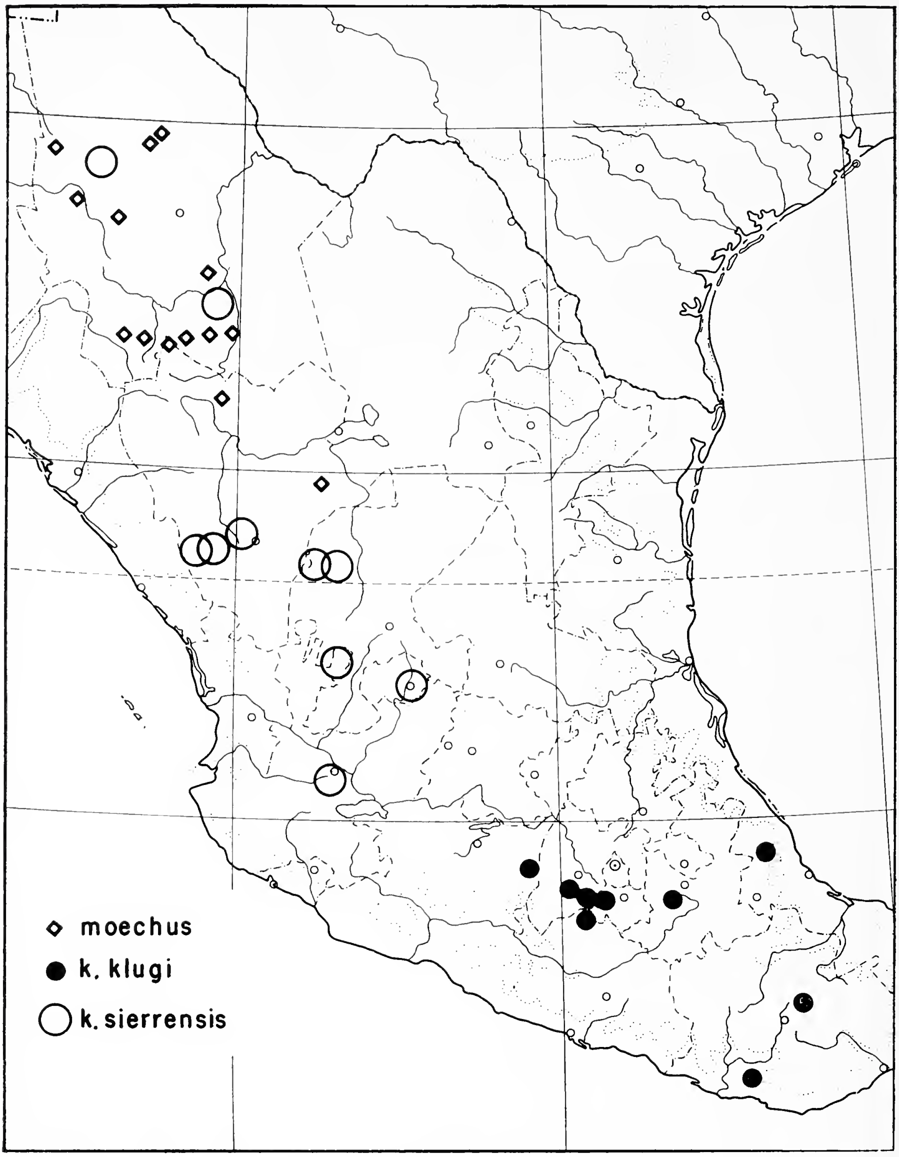

Fig. 16. Distribution of the *armatus* complex, II. Base map reproduced by permission of the University of Chicago.

klugi Harold, both of which occur in the same area. *C. arizonensis* may immediately be told by its very shallow, arcuate median clypeal emargination, acute forespur, and fully complete 8th elytral stria. With regard to the latter species, difficulty may be encountered, since *klugi* and *moechus* are very closely related. However, *klugi* is never rugose or asperate on the anterior pronotal surface, but usually relatively sparsely punctate (sometimes almost impunctate). *C. moechus,* when (very rarely) punctate exclusively here, is very densely so. There also appears to be a geographical or altitude separation between the two species; I have not seen both from the same locality. In Durango, the American Museum Expedition collected *moechus* exclusively at altitudes of up to 8000 ft. (2430 m.) and *klugi* exclusively at 8200 ft. (2500 m.) and higher.

Upon recently examining the type of this name I was very surprised to find that it belonged to this Mexican species, which had just been redescribed under the name *clavicornis* Matthews and Halffter. The common Arizona species which has gone under the name *moechus* for a very long time is here described as new under the name *lecontei* n. sp. There can be little doubt that the specimen in the Leconte Collection labelled as the type of this species actually is such, since it bears the number "14" corresponding with the type locality given as "Camp 14".

Material Examined. 93 males (including holotype) and 126 females.

MEXICO: *Chihuahua:* Agua Caliente, Sta. Bárbara Dist.; Buena Vista; Catarinas; Cuevas, Matamoros Dist.; Gaborachic; 8 mi. S Gallego; 12 mi. W Gran Morelos; 10 mi. N Jiménez; Madera; Madera Chic; 8 mi. W Matachic; Naica; Parral; 15 mi. E Parral; 2 mi. W Pedernales; Primavera; Salaices; San José Babicora; Santa Bárbara; Km. 36 Sta. Bárbara-Ojito; 63 mi. W Sta. Bárbara; Valle de Olivos; *Durango:* Encino; Las Puentes; San Isidro, Cuencamé Dist.

Copris boucardi Harold

Copris boucardi Harold, 1869, Ann. Soc. Ent. France, ser. 4, IX: 497–498 [type: Juquila, Oax.; Museum d'Histoire Naturelle, Paris]; Bates, 1887, Biol. Cent.-Amer., Coleop. II, 2, p. 54, 1889, Suppl., p. 387 (distr.); Matthews, 1959, Ciencia XIX(6–7): 136 (key and distr.).

Description of Male *Head.*—Armed. Clypeus with two barely perceptible teeth, the margin between them very shallowly emarginate with a slightly deeper median notch which is sometimes absent. Posterior angles of genae very acute. Upper surface of head closely punctate, the punctures simple, except for impunctate areas around eyes and behind horn. Posterior oblique carina developed, sharp. Occipital margin with transverse setigerous groove interrupted into three parts, the lateral sections displaced forward and partly overlapping median one. Demarcation between gula and submentum arcuate. *Thorax.*—Pronotum armed. Anterolateral angles subquadrate, margin behind them almost straight. Lateral carina sharp, not issuing from margin anteriorly. Anterior margin of pronotum not forming any median point or angle. Median longitudinal sulcus distinct, complete, umbilico-punctate at least anteriorly. Puncturation of pronotum as follows: very finely punctate, appearing smooth and shiny, over entire base; lateral surfaces shallowly punctate or ridged; anterior declivity and inside surface of lateral prominences granulate or asperate; posterior submargin, dorsal sulcus anteriorly and also sometimes for its entire length, lateral fossae, and cavities between median and lateral prominences (even in minor males) umbilico-punctate. Anterior prosternal margin variable, either without any median tooth, with a rounded one, or bidentate; sternellum moderately punctate. Median lobe of metasternum with a few punctiform impressions laterally and anteriorly; median longitudinal impressed line usually complete. *Elytra.*—8th stria incomplete, disintegrating about halfway down elytron; 9th stria arising about halfway down; 10th complete. Striae finely but distinctly punctate, the punctures round and separated by a distance equal to two or more times their diameter. Interstriae sparsely and very finely punctate, appearing smooth, and slightly convex. *Abdomen.*—Pygidium completely margined, moderately umbilico-punctate, the punctures small. *Anterior legs.*— Ventral surface of femur coarsely setigerous-punctate on posterior (upper) longitudinal half, impunctate on anterior half. Forespur straight in dorsal view, narrowing apically, the apex broadly rounded. *Middle legs.*—Coxa impunctate. Femur below distinctly setigerous punctate only at distal end, impunctate elsewhere. Tibia below with 1–2 distal seta tufts. *Posterior legs.*—Ventral surface of femur entirely finely punctate, without setigerous punctures. Tibia with 0–3 seta tufts distally below. *Total length.*—19–23.5 mm.

Male armament. Minor and medium males have median pronotal prominences which are approximated but not extremely so. Not until well developed males are examined is the characteristic nature of the median pronotal prominences seen. In these individuals, the median prominences are more or less pyramidal, very closely approximated, and directed sharply upwards (fig. 73). The head horn is gently curved, not bent, in some instances almost straight, and in other instances massive for most of its length when seen from the side, then abruptly narrowing apically. The lateral pronotal prominences are directed somewhat outward in dorsal view.

Description of Female. Similar to male, but differing in armament and in the following features: clypeal teeth more prominent, rounded and approximated, with a shallow notch between them. Dorsal longitudinal sulcus of pronotum impressed only basally or entirely very faint. Puncturation of pronotum as follows: impunctate on disc, shallowly punctate on rest of base, anterior half of pronotum densely granulate; umbilical punctures are present only along posterior submargin and in lateral fossae. *Total length.*—19–21 mm.

Female armament. Normal for the genus.

Distribution. Fig. 15. Found on the volcanoes of northern Central America and Chiapas at altitudes of 1000–1200 m. (3300–4000 ft.). The type locality is Juquila in southern Oaxaca and I have seen a female ascribable to this species from Omilteme, Guerrero (also cited by Bates), so it is probable that it occurs in Mexico south of the depression of the Río Balsas as well. The British Museum has two male specimens labelled "Venezuela", but this record is certainly erroneous.

Biology. Unknown.

Remarks. This species is very closely related to *aspericollis* Gillet occurring in the same area, minor males and females of the two species being difficult to distinguish (see key). These two species provide a good example of how two sympatric, closely related species may differ radically in male secondary sexual characters. The apices of the median pronotal prominences of *boucardi* are very closely approximated in developed males, those of *aspericollis* being quite widely divergent (figs. 73, 74). Its separation from the superficially similar *klugi* Harold is discussed in the remarks under the latter species.

Material Examined. 13 males, 16 females.

MEXICO: *Chiapas:* Ocosingo, 1200 m., Jun.–Sep. 1917 (M. del Toro), 1 ♂ (GH); Volcán de Tacaná (Coffee belt), 30 Sep. 1956 (V. Aguilar), 1 ♂, 2 ♀♀ (GH); 7500 ft., 4 Apr. 1939 (F. Brodkorb), 1 ♀ (USNM); *Guerrero:* Omilteme [W of Chilpancingo], 8000 ft., Jul. (H. H. Smith), 1 ♀ (BM).

GUATEMALA: *Alta Vera Paz:* Senahú [1000 m.] (Paul Haase), 2 ♀♀ (USNM); *Chimaltenango:* Capetillo [Valley between volcanoes Agua and Fuego, 17 Apr.–12 May, 1879] (Champion), 1 ♀ (BM); *national record only:* (Sallé) 1 ♂ (BM); 3 ♂♂ (AMNH, CAS).

EL SALVADOR: *Santa Ana:* Monte Cristo, 7–9 May, 1958 (O. L. Cartwright), 5 ♂♂, 9 ♀♀ (USNM).

Copris aspericollis Gillet

Copris aspericollis Gillet, 1910, Not. Leyden Mus. XXXII: 3 [type: Central America; Musée Royal d'Histoire Naturelle, Brussels]; Matthews, 1959, Ciencia XIX(6–7): 136 (key and distr.).

DESCRIPTION OF MALE. *Head.*—Armed. Clypeus with two very low teeth, the margin between them very shallowly emarginate with a deeper median notch not cutting through the margin. Upper surface of head strongly and densely punctate, the punctures shallow and simple, disappearing at extreme base of head, posterior oblique carina distinct. Occipital margin with transverse setigerous groove complete but somewhat bent at middle of each side. Demarcation between gula and submentum arcuate. *Thorax.*—Pronotum armed. Anterolateral angles subquadrate in developed specimens, rounded in undeveloped ones, lateral margin slightly inwardly curved behind origin of lateral carina. Lateral carina sharp, almost issuing from margin anteriorly. Anterior margin of pronotum not forming any point or angle medially. Median longitudinal sulcus very faint, almost wanting. Puncturation of pronotum as follows: upper part of disc almost impunctate, the longitudinal sulcus impunctate, rest of upper surface and lateral surfaces punctate, the punctures simple; anterior declivities densely and coarsely granulate or asperate; posterior submargin and lateral fossae umbilico-punctate. Anterior prosternal margin without any median lobe or with a rounded low one; sternellum densely punctate. Median lobe of metasternum with numerous punctiform impressions laterally and anteriorly; median longitudinal impressed line complete. *Elytra.*— 8th stria incomplete, disintegrating posteriorly; 9th stria arising about a third of the way down the elytral length; 10th complete. Striae on dorsal part of elytra distinctly punctate, the punctures slightly transverse and separated by a distance equal to once or twice their width; striae 7, 8, and 9 less punctate but the punctures can still be made out. Interstriae very slightly convex, impunctate. *Abdomen.*—Pygidium moderately umbilico-punctate, the punctures very small; pygidial margin usually complete, sometimes effaced at apex. *Anterior legs.*—Ventral surface of femur coarsely setigerous-punctate on posterior (upper) longitudinal half, more finely punctate on anterior half. Forespur almost straight in dorsal view, tapering slightly to a rounded apex, curved down at apical third. *Middle legs.*—Coxa impunctate. Femur below finely punctate, with a few, usually setigerous, coarse punctures distally. Tibia below with 2–3 distal median seta tufts. *Posterior legs.*—Femur like that of middle legs. Tibia with 1–2, usually one, seta tuft distally on ventral surface. *Total length.*—21–21.5 mm.

Male armament. The head horn is not very tapering but comes to a rather abrupt end, and is noticeably bent in the middle (fig. 74). The median thoracic prominences are slightly divergent and conical, their lower surfaces not flattened, and directed horizontally in lateral view. The lateral prominences are laminate, rather acute, and directed forward, their dorsal edges parallel in dorsal view.

Description of Female. Similar to male, but differing in armament and in the following features: clypeal teeth more prominent, rounded, and approximate, with a V-shaped notch between them. Pronotum more extensively granulate, the granules extending from face over sides and anterior surface of disc, which takes on an asperate appearance. Base of disc finely punctate; umbilical punctures are confined to posterior submargin and lateral fossae. Pygidium more finely punctate and always completely margined. *Total length.*—21–23.5 mm.

Female armament. Normal for the genus.

Distribution. Known only from the area around Guatemala City at altitudes of 340–1700 m. (1100–5600 ft.).

Biology. Feeds on cow dung. Some aspects of nidification are discussed on p. 31.

Remarks. This species is poorly represented in collections, probably reflecting the generally uncollected nature of Central America rather than any rarity of the species. I collected it in a cow pasture on the road southeast from Guatemala City, indicating that it probably is abundant in central Guatemala, but I did not encounter it again elsewhere in Central America. It is most closely related to *boucardi* Harold (see remarks under that species) and to *subpunctatus* Gillet, which it strongly resembles in habitus, being however much more strongly punctate than the latter species. It also differs from the latter in the shape of the male median pronotal prominences, which are conical in *aspericollis* and flattened at the apices in *subpunctatus*.

Material Examined. Seven males, seven females.

GUATEMALA: *Escuintla:* Escuintla [338 m., Feb. or Apr., 1881] (Champion), 1 ♂, 1 ♀ (BM); *Guatemala:* 18 km. SE Guatemala City, 610 m., 22 Jul., 1958 (Neff and Matthews), 1 ♂, 3 ♀♀ (EGM); S. José Pinula [1500–2000 m.] May, 1924 (W. M. Mann), 1 ♂ (USNM); *national record only:* 1 ♂, 1 ♀ (CAS); 3 ♂♂, 2 ♀♀ (MCZ).

Copris subpunctatus Gillet, new combination

Copris aspericollis var. *subpunctatus* Gillet, 1910, Not. Leyden Mus. XXXII: 3 [type: Costa Rica; Musée Royal d'Histoire Naturelle, Brussels].

Description of Male. *Head.*—Armed. Clypeus with two very low teeth, the margin between them very shallowly angular with a deeper central notch not cutting through the margin. Upper surface of head strongly and densely punctate, the punctures shallow and simple, except for an impunctate area at base of head and about the eyes. Posterior oblique carina distinct. Occipital margin with transverse setigerous groove complete but somewhat bent at middle of each side. Demarcation between gula and submentum arcuate. *Thorax.*—Pronotum armed. Anterolateral angles acute in developed specimens, subquadrate or rounded in less developed ones, lateral margin slightly inwardly curved behind the angle. Lateral carina sharp, not issuing from margin in developed specimens, almost issuing from it in less developed ones. Anterior margin of pronotum not forming any median point or angle. Median longitudinal sulcus very faint, obsolescent. Punctuation of pronotum as follows: upper part of disc almost impunctate, longitudinal sulcus impunctate; rest of upper surface of pronotum and lateral surfaces punctate, the punctures simple or, in developed specimens, umbilical on anterior part of disc; anterior declivities densely and coarsely granulate and asperate; posterior submargin and lateral fossae umbilico-punctate; in the most developed individuals, the cavities between the median and lateral prominences are grossly annular-punctate or cicatricial. Anterior prosternal margin with a broadly truncate or rounded median lobe; sternellum concave, densely punctate. Median lobe of metasternum impunctate or more usually with punctiform indentations along the edges anteriorly; median longitudinal groove complete. *Elytra.*—8th stria incomplete, disintegrating at posterior angle; 9th arising about a third of the way down elytron; 10th complete. Striae practically impunctate, the punctures represented by slight widenings of the fine strial line; stria 8 impunctate. Interstriae very slightly convex, impunctate. *Abdomen.*—Pygidium moderately umbilico-punctate, the punctures very small; pygidial margin usually complete, sometimes effaced at apex. *Anterior legs.*—Ventral surface of femur with coarse setigerous punctures on posterior longitudinal half, more finely punctate on anterior half. Forespur almost straight in dorsal view, tapering slightly to a rounded apex, curved downward for apical third. *Middle legs.*—Coxa impunctate. Ventral surface of femur finely punctate. Tibia below with 2–3 distal seta tufts. *Posterior legs.*—Femur as described for middle legs. Tibia below with 1–2, usually one, seta tuft distally. *Total length.*—17–24.5 mm.

Male armament. In extremely developed specimens, the head horn is massive and sharply bent in the middle, the disc is humped behind the median pronotal prominences, and these are divergent in dorsal view and directed slightly upward in lateral view (fig. 72), their lower surfaces being flattened or even slightly excavate. The lateral pronotal prominences are distinctly directed outward in dorsal view.

DESCRIPTION OF FEMALE. Similar to male, differing in armament and in the following features: clypeal teeth more prominent, rounded, and approximate, with a V-shaped notch between them; pronotum more extensively granulate, the granules extending from face over sides and anterior surface of disc, which takes on an asperate appearance; base of disc finely punctate; umbilical punctures are confined to posterior submargin and lateral fossae. Pygidium more finely punctate and completely margined. *Total length.*—22–25 mm.

Female armament. Normal for the genus.

DISTRIBUTION. Fig. 15. Known only from the environs of San José and Irazú Volcano, Costa Rica, and Chiriquí Volcano, Panamá, at altitudes of 1000–2000 m. (3300–6600 ft.).

BIOLOGY. Unknown. All specimens appear to have been collected at light, from October to June.

REMARKS. This is certainly one of the most striking and beautiful species of the genus, the male achieving an extreme in horn development and the reduced puncturation of the integument imparting a glossy sheen to the body surface. It is here elevated to species rank primarily because it differs from *aspericollis* Gillet in the shape of the male median pronotal prominences (see p. 133). Both sexes are most easily told from *aspericollis* by the obsolescent elytral strial punctures (I have seen no intermediate specimens), but in all other non-dimorphic characters it is apparently identical with the Guatemalan species.

Material Examined. 19 males, nine females.

COSTA RICA: *Alajuela:* Desengaño, 2000 m. (P. Biolley), 1 ♂ (CM); *Cartago:* Guayabillos, SW slope Irazú, 2200 m., Mar. 1933 (F. Nevermann), 2 ♂♂ (USNM); Irazú Volcano, 6–7000 ft. (H. Rogers), 1 ♀ (USNM); south slope, 2800–3000 m., Sep. 1931 (F. Nevermann), 1 ♂ (USNM); 1625 m., 15 May 1951 (O. L. Cartwright), 2 ♂♂ (USNM); Pacayas, SE slopes of Volcán de Irazú, 6000–6250 ft., 6 Oct. 1923 (Rehn and Lankester), 2 ♀♀ (PAS); *Heredía:* Río Sucio (H. Rogers), 1 ♂, 2 ♀♀ (AMNH, MCZ); *Limón:* Hamburgfarm, 30 Mar. (C. P. Dodge), 1 ♀ (MCZ); *San José,* 1000–1200 m., May 1921, 27 Apr. 1922, 1 Dec. 1923, 15, 18 May 1925, May, Dec. 1931, 18 Apr. 1932, 17 May 1933, 10 Jan., 15 Dec. 1934 (F. Nevermann), 11 ♂♂, 4 ♀♀ (USNM); 1160 m, Jun. 1943 (Biolley), 1 ♂, 2 ♀♀ (CM).

PANAMA: *Chiriquí:* Chiriquí, 2 ♂♂, 1 ♀ (CM).

Complex 2. The *arizonensis* complex.

Posterior angles of head acute. Anterolateral angles of pronotum obtusely angulate, the lateral margin not sinutate. Forespur with the apex acute and curved inward, strongly so in the male. 8th elytral stria complete. Pygidial margin complete.

One species found in the mountains of Chihuahua and bordering United States territory: *arizonensis* Schaeffer.

Copris arizonensis Schaeffer

Copris arizonensis Schaeffer, 1906, Trans. American Ent. Soc. XXXII: 254–255 [type: Huachuca Mts., Ariz.; United States National Museum]; Matthews, 1959, Ciencia XIX(6–7): 135 (key and distr.).

Description of Male. *Head.*—Armed. Clypeus with a broad, very shallow, arcuate emargination without any median notch. Upper surface of head evenly punctate on outer, flattened portions and on horn, impunctate elsewhere; the punctures are shallow and simple except often for some of those on genae, which are umbilical. Posterior oblique carina evident only directly behind eye. Occipital margin with transverse setigerous groove broken into three parts, the lateral ones displaced slightly forward. Demarcation between gula and submentum arcuate. *Thorax.*—Pronotum armed. Anterolateral angles obtuse, the lateral margin slightly angled out at origin of lateral carina. Lateral carina prominent, issuing from margin anteriorly. Anterior margin of pronotum not forming any median point or angle. Dorsal median longitudinal sulcus incomplete, faint, sometimes wanting. Entire pronotal surface regularly and densely umbilico-punctate, the punctures varying in size, being smallest on convex areas and largest in depressions; highly developed individuals tend to become impunctate on disc. Anterior prosternal margin with a very small median process which is sometimes bidentate; sternellum sparsely and grossly umbilico-punctate. Median lobe of metasternum umbilico-punctate, sometimes only along edges; median longitudinal impressed line usually complete. *Elytra.*—8th stria complete; 9th arising about a third of the way down elytron; 10th complete. Striae closely punctate, the punctures slightly transverse, separated by a distance approximately equal to their width. Interstriae almost flat, very faintly punctate, appearing smooth. *Abdomen.*—Pygidium rather densely and coarsely umbilico-punctate, completely margined. *Anterior legs.*—Ventral surface of femur grossly umbilico-punctate over most of its area, more finely punctate along anterior margin. Forespur curved inward at apex and tapering to a sharp point. *Middle legs.*—Coxa with scattered umbilical punctures on outer face. Ventral surface of femur punctate, the punctures setigerous and larger distally. Tibia with 1–2, usually two, distal seta tufts ventrally. *Posterior legs.*—Femur like that of middle legs. Tibia with 2–3 distal seta tufts ventrally. *Total length.*—14–20.5 mm.

Male armament. Minor individuals have the median pronotal prominences approximated but not merged. With further development they grow forward into a single bifurcate median process (fig. 68). The most developed individuals bear a long, evenly curved head horn which is slightly transversely clavate at the apex, and the median pronotal prominences are seen in side view to be very acute and directed slightly upwards, in dorsal view to be closely approximated with their outer edges parallel or very slightly directed outward. The lateral prominences are directed forward.

DESCRIPTION OF FEMALE. Similar to male, but differing in armament and in the following features: the low clypeal teeth are more closely approximated and the emargination between them is broadly angulate, with no median notch or a very feeble one. Surface of pronotum densely punctate over entire area, the punctures usually entirely umbilical, but some specimens have simple punctures on disc and sides, in which case the anterior area of disc is somewhat ridged. Forespur somewhat less bent apically and less acute than that of male. *Total length.*—15.5–22 mm.

Female armament. The head horn consists of a prominent transverse process which is apically excavate, its sides sharply divergent apically in front or rear view and recurved backwards in developed specimens. The least developed specimen seen bore a horn with its sides parallel; none were seen with a horn narrowing apically.

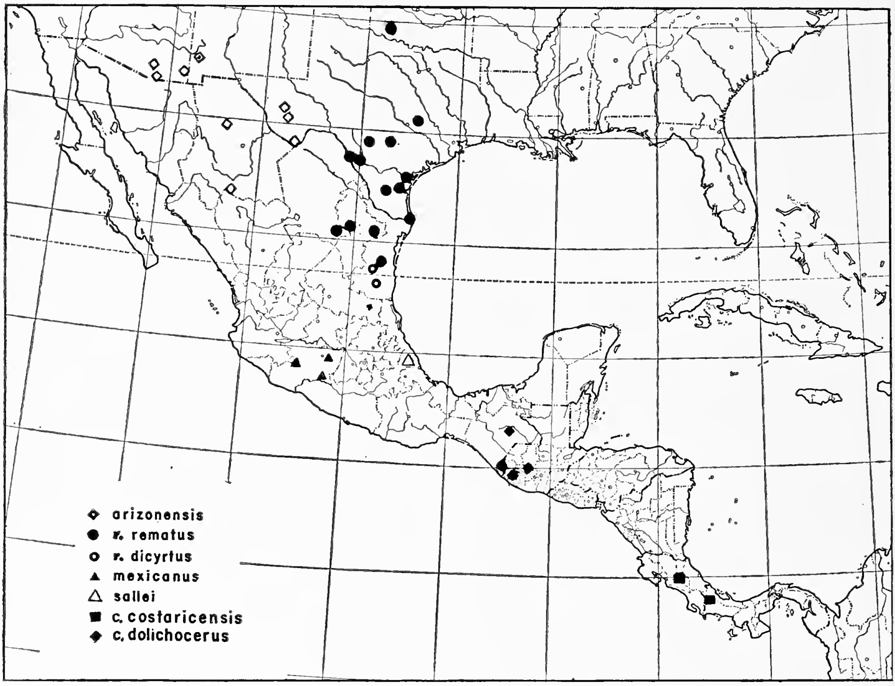

Fig. 17. Distribution of the *remotus* and *arizonensis* complexes. Base map reproduced by permission of the University of Chicago.

Distribution. Fig. 17. Known from the Huachuca and Chiricahua mountains of Arizona, the Continental Divide in southern New Mexico, the general region of the Davis and Chisos mountains of Texas, and two highland localities in Chihuahua, at altitudes of 1350–1900 m. (4500–6300 ft.). Perhaps occurring in all intervening highlands, which have not been collected very much.

Biology. Nothing at all is known of the biology of this species; all specimens for which the collecting method was specified were collected at light. It appears to be active from May to August.

Remarks. Schaeffer did not designate a holotype for this species. The type collection of the United States National Museum contains two specimens—a male (No. 42,570) and a female. These specimens were entered in 1929 from the Brooklyn Museum and recorded in the record book as cotypes; each bears the label "Huachuca Mts.". The male, a rather worn specimen, is here designated as **lectotype** of *Copris arizonensis* Schaffer.

This species stands alone among the American forms not so much because of unusual characters as because of a unique combination of characters found in other complexes. It shares with the *armatus* complex the large size and simple anterolateral angles, with the *remotus, fricator,* and *rebouchei* complexes the shape of the forespur and the complete 8th elytral stria, and with the *remotus* complex the shape of the male head. The shape of the female head horn is, however, quite unique.

Material Examined. 31 males (including lectotype), 22 females.

UNITED STATES: *Arizona:* Cochise Co.: Chiricahua Mts.; Chiricahua Mts., Cave Creek; Southwest Res. Sta. 5 mi. W. Portal; Chiricahua Mts., Painted Cyn Ranch; Huachuca Mts.; Huachuca Mts., Carr Canyon; Huachuca Mts., Garden Canyon; Huachuca Mts., Ramsey Canyon; Palmerlee; Pima Co.: Tucson; Santa Cruz Co.: Mt. Washington, Nogales; *New Mexico:* Grant Co.: Tyrone, 8 Aug. 1939 (K. Stager), 1 ♀ (AMNH); *Texas:* Big Bend Nat'l Pk.: Basin Area, 5400 ft., 18 May 1959 (Howden and Becker), 1 ♀ (HH); Brewster Co.: Alpine, 15–30 May, 15–30 Jun., 28 Jul., 1–15 Aug., 1926 (O. C. Poling, R. C. Casselbury), 5 ♂♂, 1 ♀ (AMNH); 25 Jul. 1936 (J. G. Gehring), 1 ♂ (MCZ); S. G. Ranch, 26 Jun., 1 ♀ (MCZ); Jeff Davis Co.: Davis Mountains, 28 Jun. 1946 (Van Dyke), 1 ♂, 2 ♀♀ (CAS).

MEXICO: *Chihuahua:* Parral, 16 Jul. 1947 (Spieth), 2 ♂♂ (AMNH); 15 mi. E Parral, 5500 ft., 15 Jul. 1947 (Cazier), 2 ♂♂, 1 ♀ (AMNH); Primavera, 5500–6000 ft., 30 Jun. 1947 (Cazier), 1 ♂ (AMNH); Sta. Bárbara, 6300 ft., 17 Jul. 1947 (Cazier), 1 ♂ (AMNH).

Complex 3. The *remotus* complex.

Posterior angles of head subquadrate or usually acute. Anterolateral angles of pronotum acute, the margin behind them sinuate. Median longitudinal sulcus of pronotum coarsely punctate. Forespur with the apex acute in both sexes. Median coxae with gross umbilical punctures on the outer face. Pygidial margin complete or not.

Four species found at low to moderate altitudes in Central and Eastern Mexico (and bordering United States territory) and Central America: *remotus* Leconte, *mexicanus* Matthews and Halffter, *sallei* Harold, and *costaricensis* Gahan.

Copris remotus remotus Leconte

Copris remotus Leconte, 1866, Proc. Acad. Nat. Sci. Philadelphia XVIII: 381 [type: Texas, near the Rio Grande; Museum of Comparative Zoology]; Horn, 1873, Trans. American Ent. Soc. IV: 42–51 (key and descr.); Harold, 1886, Berliner Ent. Zeitschr. XXX: 148 (descr.); Schaeffer, 1906, Trans. American Ent. Soc. XXXII: 255 (key); Lindquist, 1935, Circular U.S.D.A. No. 351, pp. 2–4 (biol.); Matthews, 1959, Ciencia XIX (6–7): 135 (key and distr.).

Description of Male. *Head.*—Armed. Clypeus with two remote, very small teeth, the margin between them curved inward in a broad, very shallow arc; no median notch. Posterior angles of genae acute. Upper surface of head entirely punctate, the punctures denser and simple along margin, sparser and umbilical on posterior part of genae and base. Posterior oblique carina reduced. Occipital margin with transverse setigerous groove broken into three parts, the median one devoid of setae. Demarcation between gula and submentum arcuate. *Thorax.*—Pronotum armed. Anterolateral angles acute, immediately followed by an indentation or erosion of margin, indistinct in some specimens; lateral margin angled out at origin of lateral carina. Lateral carina distinct, issuing from margin. Anterior margin usually not forming any median point, but sometimes forming a downwardly directed one and occasionally an upwardly directed one, formed by inner edge of margin. Median longitudinal sulcus distinct, broadly impressed, more coarsely punctured than rest of disc. Puncturation of pronotum as follows: elevated areas of base of pronotum impunctate or very finely punctate, the following areas abruptly, contrastingly, coarsely umbilico-punctate: posterior and lateral submargins, lateral fossae, dorsal longitudinal sulcus in an anteriorly broadening band, and all anterior declivities, including excavations between median and lateral prominences; median anterior face is often impunctate in an area of varying size about median line. Anterior prosternal margin without any median tooth; sternellum regularly, coarsely umbilico-punctate. Median lobe of metasternum coarsely umbilico-punctate anteriorly and laterally; median longitudinal groove present and complete. *Elytra.*—8th stria complete; 9th arising at anterior third of elytral length; 10th complete. Striae very coarsely, closely punctate, the punctures somewhat transverse and separated by a distance equal to once or twice their width. Interstriae convex, very finely punctate, appearing smooth. *Abdomen.*—Pygidium with margin complete, densely umbilico-punctate. *Anterior legs.*—Ventral surface of femur coarsely punctate on posterior longitudinal half, finely punctate on anterior, with some larger punctures along anterior margin. Forespur linear, somewhat broadened apically, the extreme apex bent inward to a dull point. *Middle legs.*—Coxa with scattered large umbilical punctures on outer face and a few smaller ones on inner face. Ventral surface of femur very finely punctate basally, with coarse setigerous punctures distally. Tibia below with 2–4 median seta tufts. *Posterior legs.*—Femur as described for middle legs. Tibia usually with up to six seta tufts arranged in an irregular row up the ventral surface. *Total length.*—12–15.5 mm.

Male armament. In major males, the head horn is long, evenly arcuate and tapers to a moderately sharp apex, the median pronotal prominences are two remote, slightly diverging, forwardly directed, blunt cones, the apices of which are sometimes a little obliquely compressed and separated from each other by a distance equal to their separation from the lateral prominences, which are laminate, directed forward and a little outward (fig. 78).

Description of Female. Similar to male, but differing in armament and in the following features: clypeal teeth more prominent and margin between them broadly angulate, not arcuate (there is no median notch, as in the male); nearly all females show a small downwardly directed point at middle of anterior pronotal margin; puncturation of pronotum similar to that of male, with abruptly contrasting smooth and coarsely punctate areas, but the crowded punctures on anterior part of disc and anterior declivity tend to be simple, rather than umbilical; dorsal longitudinal sulcus of pronotum is impressed basally and umbilico-punctate. *Total length.*—14–16 mm.

Female armament. The head horn is transverse but thick. The median pronotal transverse carinae are well separated by a punctate depression, the inner ends of the carinae being sometimes curved up to form two points.

Distribution. Fig. 17. Southern Texas, Nuevo León, and northern Tamaulipas in an area centering about the lower Rio Grande (Río Bravo) Valley at altitudes of sea level to 600 m.

(2000 ft.), with one (perhaps inexact) record from Saltillo, Coahuila, at 1589 m. (5200 ft.) and one specimen from Oklahoma. In addition, I have seen two specimens from "Aquilares", Arizona, a place I cannot find on any map. The presence of this species in Arizona is very doubtful.

BIOLOGY. Lindquist gives an excellent account of the nidification of this species, which is summarized on pp. 29–30. It comes to light and is found under cow dung.

REMARKS. The contrasting smooth and coarsely punctate areas on the pronotum serve to distinguish this species from all others which occur in the United States. For some reason it is confused with *lecontei* n. sp. in collections although the species are quite dissimilar and do not, apparently, occur together. Aside from showing the above mentioned characteristic, it is more coarsely punctate than *lecontei,* the males have a very shallow clypeal emargination, relatively blunt forespurs, a more sharply curved horn, and the median pronotal prominences are divergent. It is closely related to *costaricensis* Gahan, with which it shares the type of puncturation, but from which it may easily be distinguished by the complete pygidial margin.

MATERIAL EXAMINED. 25 males (including holotype), 17 females.

UNITED STATES: *Oklahoma:* Comanche Co.: Wichita N.F., 10 Sep. 1930 (T. H. Hubbell) 1 ♂ (USNM); *Texas:* Bexar Co.: San Antonio, 21 Dec. 1942 (E. S. Ross), 1 ♀ (CAS); Cameron Co.: Port Isabel, 23–27 Jun. 1956 (H. E. Evans and E. G. Matthews), 1 ♀ (EGM); Comal Co.: (C. Schaeffer), 1 ♂ (USNM); Dimmit Co.: Tex, Exp. Sta. Light trap, 4, 17 Mar., 12 Aug. 1933, 14 Mar., 24 Apr. 1934 (S. E. Jones), 4 ♂♂, 1 ♀ (OLC); Duval Co.: Realtos, Jul. 1939 (K. Stager), 2 ♀♀ (AMNH); Kleberg Co.: Kingsville (C. T. Reed), 2 ♂♂, 3 ♀♀ (CU); Lee Co.: Fedor, June, 1 ♂ (CM); Maverick Co.: Eagle Pass, May 1914, 1 ♂ (CM); Nueces Co.: Corpus Christi, 28 Jun. 1942 (E. S. Ross), 1 ♂ (CAS); Uvalde Co.: Sabinal, 9 Jun. 1910 (F. C. Pratt), 3 ♀♀ (USNM); Uvalde, 11 Apr., 24 Jun., 1 Aug. 1931 (A. W. Lindquist), 3 ♂♂, 1 ♀ (USNM); state record only: 8 ♂♂, 1 ♀ (USNM, CM).

MEXICO: *Coahuila:* Saltillo, 6 Dec. 1954 (J. Moncada), 1 ♀ (GH); *Nuevo León:* Monterrey. 6 Oct. 1946, 2 ♂♂ (GH); 5 Mar. 1955 (Alfonso Terraza), 1 ♀ (GH); 24 Mar. 1957 (B. Moscoso), 1 ♂, 1 ♀ (GH); Rancho Presa Nueva, Jun. 1934 (H. A. Howies), 1 ♀ (USNM); *Tamaulipas:* 8 mi E of Padilla, 19 Dec. 1941 (Cantrell-Friauf), 1 ♂ (USNM).

Copris remotus dicyrtus Matthews and Halffter new combination

Copris dicyrtus Matthews and Halffter, 1959, Ciencia XVIII (9–10) : 198–200 [type: Ciudad Victoria, Tamps.; United States National Museum]; Matthews 1959, Ciencia XIX(6–7): 135 (key and distr.).

Description. This subspecies is a southern form of the typical *remotus.* It differs from *r. remotus* only in the nature of the lateral pronotal prominences of the male, which are completely absent in the holotype (while the median prominences are well developed) and curiously reduced to tubercles in the other male, accentuating a tendency seen in the typical form. The other differences cited in the original description of *dicyrtus* have not stood up when additional specimens were found; consequently this form is here reduced to subspecies level.

Material Examined. Holotype and allotype, one additional male and two females.

MEXICO. *Tamaulipas:* Ciudad Victoria, 1, 3 Jun. 1950 (G. Halffter), 1 ♂, 1 ♀ (USNM); 47 km. S Ciudad Victoria, Rt. 1, km. 659, 900 ft., 5 Jul. 1948 (W. Nutting), 1 ♂, 2 ♀♀ (USNM).

Copris mexicanus Matthews and Halffter

Copris mexicanus Matthews and Halffter, 1959, Ciencia XVIII(9–10): 194–196 [type: Tancítaro, Mich.; California Academy of Sciences]; Matthews, 1959, Ciencia XIX(6–7) : 135 (key and distr.).

Description of Male. *Head.*—Armed. Clypeus bidentate, the teeth remote and very small, with a very shallow, obtuse median notch. Posterior angles of genae acute. Upper surface of head closely punctate except for base and area between eyes, which are smooth; some of punctures on genae are umbilical, the rest simple. Posterior oblique carina prominent but rounded. Occipital margin with transverse setigerous groove broken into three partially overlapping sections. Demarcation between gula and submentum arcuate with a suggestion of median angulation. *Thorax.*—Pronotum armed. Anterolateral angles subquadrate with point of angle made salient by an inward curve of lateral margin immediately behind it, the margin curving out again at origin of lateral carina. Lateral carina sharp. Anterior margin of pronotum not forming any median point or angle. Median longitudinal sulcus present only on disc proper, impressed, umbilico-punctate, the field of punctures broadening anteriorly. Puncturation of pronotum as follows: base and disc glassy smooth, impunctate except for dorsal sulcus and submargin, which are umbilico-punctate; entire submargin, lateral fossae, depressions between prominences, and median anterior face rather sparsely umbilico-punctate; no simple punctures on pronotum except for a few on outer surface of lateral prominences. Anterior prosternal margin without any median tooth; sternellum sparsely punctate. Median lobe of metasternum with umbilical punctures anteriorly and laterally; median longitudinal groove complete. *Elytra.*—8th stria complete; 9th arising at about anterior third of elytral length; 10th complete. Striae closely and distinctly punctate, the punctures transverse, separated by a distance about equal to their width. Interstriae slightly convex, impunctate. *Abdomen.*—Pygidium moderately umbilico-punctate, completely margined. *Anterior legs.*—Ventral surface of femur with coarse setigerous punctures on posterior longitudinal two thirds, very finely punctate on anterior third. Forespur linear to apical third, where it is curved downward and inward and tapers to a fairly acute point. *Middle legs.*—Coxa with a few large umbilical punctures on middle of outer face. Ventral surface of femur with many coarse setigerous punctures distally, some regularly distributed, fine punctures over rest of surface. Tibia below with 2–3 distal seta tufts. *Posterior legs.*—Femur as described for middle legs. Tibia below with 2–4 distal seta tufts arranged in a row along length of tiba. *Total length.*—16–16.5 mm.

Male armament. In the four specimens examined, the head horn is rather straight with the sides evenly tapering. The median pronotal prominences are acute and closely approximated, their outer edges evenly converging forward, their apices not turned upward in lateral view. The lateral pronotal prominences are laminate, not well developed, their dorsal edges sloping downward anteriorly in lateral view, parallel in dorsal view (fig. 67).

FEMALE. Unknown.

DISTRIBUTION. Fig. 17. Known only from three localities in Michoacán on the northern slope of the depression of the Río Balsas.

BIOLOGY. Unknown.

REMARKS. This species is closely related to *costaricensis* Gahan and *sallei* Harold. From the former it may be told by its complete pygidial margin and by the lack of an acute median tooth on the anterior pronotal margin. It differs further in that the median pronotal sulcus is less coarsely punctate than in *costaricensis* and the male median pronotal prominences apparently do not merge. It is difficult to estimate the degree of relationship of this species (known only from the males) to *sallei* Harold (of which I have seen only females). There is little doubt that they are distinct species, not only because of the difference in geographical distribution, but also because the *sallei* specimens I have seen differ from *mexicanus* in possessing blunt (not curved and acute) forespurs, a median tooth on the anterior pronotal margin, and an incomplete 8th elytral stria. None of these differences is associated with secondary sexual characters in this complex.

MATERIAL EXAMINED. Holotype, male paratype, and two additional males.

MEXICO: *Michoacán:* Tancítaro, 1800 m., 24 Jun. 1941 (Hoogstraal and Haag), 1 ♂ (CAS); Huétamo, 2100 m., 8 Jul. 1947 (T. H. Hubbell), 1 ♂ (UMich); Jct. Hwy. 4 and Huétamo rd. 15 mi. E of Morelia, 2100 m., 8 Jul. 1947 (T. H. Hubbell), 2 ♂♂ (USNM).

Copris sallei Harold

Copris sallei Harold, 1869, Ann. Soc. Ent. France, ser. 4, IX: 496–497 [type: Córdoba, Ver.; Museum d'Histoire Naturelle, Paris]; Bates, 1887, Biol. Cent.—Amer., Coleopt. II, 2, p. 54 (distr.); Matthews, 1959, Ciencia XIX(6–7): 135 (key and distr.).

DESCRIPTION OF MALE. Given by Baron von Harold as follows: Oblongus, clypeo obtuse bidentato, thoracis angulis anticis acutiusculis postice sinuatis, elytris fortiter punctato-striatis, punctis inter se approximatis. Mas: Cornu erecto fortiter et fere subangulatim recurvo; thorace quadridentato, dentibus mediis approximatis, sulci fortiter punctato et profundo usque ad basin prolongato divisis, foveolis lateralibus et excavationibus grosse umbilicopunctatis. . . . Long. 13–17 mill.

An illustration of a developed male specimen which, in my opinion, has been correctly determined to be this species is given by Bates (1887, plate 3, fig. 12, 12a). This figure shows the clypeal margin to be remotely bidentate, with the teeth minute and pointed, and the margin between them very shallowly, angularly emarginate; the hind angles of the head are acute; the forespur is straight, and the median pronotal prominences are approximated but not merging.

DESCRIPTION OF FEMALE. *Head.*—Armed. Clypeus with two prominent, subangular, approximated teeth separated by a shallow, rounded median notch not cutting through margin. Posterior angles of genae subacute. Upper surface of head outwardly densely punctate, the punctures umbilical on genae and on an area of clypeus on either side of horn, with a few or many umbilical punctures between eyes; rest of head impunctate. Posterior oblique carina sharp. Occipital margin with transverse setigerous groove broken into three parts. Demarcation between gula and submentum slightly angulate. *Thorax.*—Pronotum armed. Anterolateral angles acute, immediately followed by a sharp inward curve of margin. Lateral carina prominent, issuing from margin. Anterior margin of pronotum forming a small, downwardly directed median point. Median longitudinal sulcus deeply impressed, coarsely umbilico-punctate. Puncturation of pronotum as follows: Middle of disc and base impunctate; anterior face dorsally impunctate; posterior submargin and lateral fossae grossly annular-punctate; lateral and anterior submargins and anterior portion of sides of pronotum largely umbilico-punctate; anterior portion of disc densely punctate, the punctures round, cicatricial, or linear, simple or umbilical. Anterior prosternal margin devoid of a median tooth; sternellum grossly umbilico-punctate. Median lobe of metasternum with large umbilical punctures along sides; median longitudinal groove evenly impressed. *Elytra.*—8th stria incomplete, disintegrating or becoming effaced posteriorly; 9th stria arising at the anterior third of elytral length; 10th complete. Striae coarsely punctate, the punctures circular, subumbilical, and separated by a distance equal to once or twice their diameter. Interstriae slightly convex, impunctate. *Abdomen.*—Pygidium completely margined, moderately umbilico-punctate. *Anterior legs.*—Ventral surface of femur coarsely setigerous-punctate on posterior longitudinal half, impunctate on anterior. Forespur rather straight in dorsal view, somewhat expanded distally, ending in a bluntly rounded apex. *Middle legs.*—Coxa with some umbilical punctures on outer face. Ventral surface of femur impunctate basally, with some coarse setigerous punctures distally. Tibia below with 2–3 distal seta tufts. *Posterior legs.*—Femur and tibia as described for middle legs. *Total length.*—14.5–16 mm.

Female armament. Head horn low, gibbous, only slightly transverse, arcuately carinate apically. Median pronotal prominences in the form of two slightly curved, sharp transverse carinae separated at the midline by a small punctate depression which is a continuation of the median longitudinal sulcus. Lateral pronotal prominences obsolescent.

Distribution. Fig. 17. Known from only two localities: Córdoba (''Cordova''), Veracruz, and the state of Chiapas. Through the courtesy of the British Museum I was able to examine the specimens seen by Bates and recorded as belonging to this species in the Biologia Centrali Americana. As suspected, all but the specimens from Córdoba are *C. costaricensis* Gahan. This species has not been collected at Córdoba since Sallé visited the area almost a hundred years ago and it must be considered extraordinarily rare.

BIOLOGY. Unknown.

REMARKS. I have seen only two females which can be ascribed to this species. All other specimens I have seen bearing the *sallei* label have been referable to *costaricensis* Gahan, *lecontei* n. sp., or *mexicanus* Matthews and Halffter. The two specimens seen differ considerably in the degree of puncturation, the "Cordova" specimen being more heavily punctate. This specimen may be part of the original series collected by Sallé and used by Harold for his description, though it does not bear a paratype label. The others are presumably in the Paris Museum with the type. Both specimens I have seen are from the British Museum collection.

This species is evidently very close to *costaricensis* Gahan, differing only in apparently possessing blunt forespurs, an incomplete 8th elytral stria, and a complete pygidial margin. From *mexicanus* Matthews and Halffter it differs only in showing a small median tooth on the anterior pronotal margin (like *costaricensis*), blunt forespurs, and an incomplete 8th elytral stria. Until more specimens are collected the status of these three species must remain confused.

MATERIAL EXAMINED. Two females.

MEXICO: *Chiapas:* State record only, 1905 (Fry), 1 ♀ (BM); *Veracruz:* Córdoba (Sallé), 1 ♀ (BM).

Copris costaricensis costaricensis Gahan

Copris costaricensis Gahan, 1894, Ann. Mag. Nat. Hist., ser. 6, XIV: 116–117 [type: San Francisco de Guadalupe, Costa Rica, 1200 m.; British Museum (N. H.)]; Matthews, 1959, Ciencia XIX(6–7): 135 (key and distr.).

Copris furcillatus Felsche, 1910, Deutsche Ent. Zeitschr.: 345 [type: Chiriquí, Panamá; Dresden Museum]; Gillet, 1911, Ann. Soc. Ent. Belgique 55: 319 (synon.).

DESCRIPTION OF MALE. *Head.*—Armed or not. Clypeus with two very low teeth and a shallow triangular notch between them almost cutting through margin. Posterior angles of genae subquadrate. Upper surface of head coarsely punctate, the punctures umbilical between eyes, on either side of horn, and on genae, simple elsewhere. Posterior oblique carina sharp. Occipital margin with transverse setigerous groove broken into three parts. Demarcation between gula and submentum arcuate or slightly angulate. *Thorax.*—Pronotum armed or not. Anterolateral angles acute, immediately followed by a sharp indentation or curve of the margin, less evident in some specimens. Lateral carina sharp, issuing from margin. Anterior margin forming a small, downwardly directed median point, occasionally an upwardly (inwardly) directed one as well. Median longitudinal sulcus deeply impressed, coarsely umbilico-punctate. Puncturation of pronotum as follows: coarsely umbilico-punctate in all depressions and along margins; raised areas of pronotal base, prominences, and most of anterior declivities contrastingly impunctate; no simple punctures. Anterior prosternal margin without any median tooth; sternellum coarsely punctate. Median lobe of metasternum umbilico-punctate anteriorly and laterally; median longitudinal impressed line complete. *Elytra.*—8th stria complete; 9th arising at anterior third of elytron; 10th complete. Striae very coarsely punctate, the punctures circular, umbilical, and separated by a distance equal to about their diameter or up to three times their diameter, depending on the location. Interstriae convex, impunctate. *Abdomen.*—Pygidium with the margin incomplete, its inner border totally effaced ventrally, moderately umbilico-punctate. *Anterior legs.*—Ventral surface of femur coarsely setigerous-punctate on posterior longitudinal half, impunctate on anterior. Forespur curved downward or slightly inward at apex, tapering to a sharp point. *Middle legs.*—Coxa with some umbilical punctures on outer face. Ventral surface of femur impunctate basally, becoming coarsely setigerous punctate distally. Tibia below with two distal seta tufts. *Posterior legs.*—Femur as described for middle legs. Tibia below with 2–3 distal seta tufts. *Total length.*—12–16 mm.

Male armament. In minor and medium individuals the head horn is straight and the median pronotal prominences are closely approximated and parallel, but not merging. Major males bear a long, slightly bent head horn tapering to the apex, the median pronotal prominences are merged together into a single bifurcate process, the ends of which diverge in dorsal view and bend downwards in lateral view, and the lateral pronotal prominences are laminate, directed forward when seen from above, rounded apically when seen from the side (fig. 80).

Description of Female. Identical to male in every respect except in armament. *Total length.*—13–15.5 mm.

Female armament. Normal for the genus.

Distribution. Fig. 17. The highlands of Costa Rica and Panama at altitudes of 1000–1500 m. (3300–4900 ft.).

Biology. Nevermann has attached the following data to his specimens from San José, C.R.: on carcass of *Didelphis richmondi*, in garbage pit (Abfallgrube), at light (3 ♂♂, 2 ♀♀). Another collector has recorded it from cow dung. It appears to be active throughout the year in Costa Rica.

Remarks This species is easily told by its incomplete pygidial margin, the inner border of which is effaced ventrally. It is also the only known species with a sinuate lateral pronotal margin to be found in Central America. The major males are unique in the complex in that the median pronotal prominences are merged into a single bifurcate process. It is closely related to the enigmatical *sallei* Harold, the two specimens of the latter species that I have seen differing from *costaricensis* only in that the inner border of the pygidial margin is quite complete all the way around, the forespurs are blunt, and the 8th elytral stria is partly or totally effaced posteriorly. Both species show an acute median tooth on the anterior pronotal margin.

Material Examined. 13 males, eight females.

COSTA RICA: *Cartago:* Las Mercedes, Jul. 1921, 1 ♀ (USNM); *San José:* San José, 1000—1200 m., Oct. 1925, Oct. 1928, Jun. 1931, 20 Oct. 1932, 17 Apr. 1933, 17 May 1933, 4 Oct. 1934, 22 Oct. 1935, 7 Oct. 1932 (F. Nevermann), 6 ♂♂, 3 ♀♀ (USNM); 10 Jun. 1943, 1 ♀ (AMNH); 9 Mar. 1924, 1 ♂ (USNM); 15 May, 1924, 1 ♂ (USNM); *location undetermined:* Azahar de Carboga (Underwood), 1 ♂, 1 ♀ (CM); *national record only:* 1897 (Pittier), 2 ♂♂ (USNM).

PANAMA: *Chiriquí:* Potrerillos, 1 ♀ (CAS); Volcán de Chiriquí, 2500–4000 ft. [6–8 Jun. 1882] (Champion), 1 ♂ (BM).

Copris costaricensis dolichocerus n. subsp.

Holotype: Volcán de Tacaná, Chiapas, Mexico, 1 Oct. 1956 (V. Aguilar), ♂; United States National Museum.

Description. Differs from the typical subspecies only in the greater proportional length of the male cephalic horn. When the height of the male horn is plotted against the length of the hind femur on a graph (fig. 7), the specimens of this species are seen to fall into two lots and to follow different curves, corresponding to their geographical origin.

Distribution. Fig. 17. Chiapas and Guatemala at 1500–2000 m. I have ascribed the two known Guatemalan females to this subspecies purely on the basis of geographical distribution, as the females are not separable from the Costa Rican subspecies.

Biology. Unknown.

Remarks. This form is recognized on the basis of the same character distinguishing the subspecies of *klugi* and *lecontei*. Different horn-length allometric relationships in this genus suggest a fundamental (perhaps genetic) difference which is sometimes (but not in this case) reflected in other morphological characters.

Material Examined. Three males, seven females.

MEXICO: *Chiapas:* El Verjel, 6 Oct. 1939 (C. Bolívar), 3 ♀♀ (GH); Volcán de Tacaná (Coffe Belt), 1 Oct. 1956 (V. Aguilar), 3 ♂♂, 2 ♀♀ (USNM, GH).

GUATEMALA: *Quezaltenango:* San Isidro, 1500 m. [10–23 Sep. 1880] (Champion), 1 ♀ (BM); *Quiché:* Santa Cruz del Quiché, 13 Aug. 1947 (C. and P. Vaurie), 1 ♀ (AMNH).

Complex 4. The *rebouchei* complex.

Posterior angles of head quadrate. Anterolateral angles of pronotum acute, the margin behind them sharply sinuate. Median longitudinal sulcus of pronotum impunctate or very finely punctate. Forespur with the apex acute and curved inward in both sexes. Median coxae devoid of coarse punctures. 8th elytral stria complete. Pygidial margin complete or not. Complex punctures usually minutely granulate.

Three species found at low to moderate altitudes in Central and Western Mexico and bordering United States territory: *lecontei* n. sp., *rebouchei* Harold, and *halffteri* Matthews.

Copris lecontei lecontei **new species**

Holotype: Huachuca Mts., Arizona, ♂; United States National Museum.

Description of Male. *Head.*—Armed. Clypeus bidentate, the teeth not at all prominent, very obtuse, their inner edges meeting at a very broad angle forming the median emargination; no median notch. Upper surface of head densely punctate except for area between eyes, which is sparsely and very finely punctate or impunctate; all punctures simple. Posterior oblique carina sharp. Occipital margin with transverse setigerous groove broken into three sections which do not overlap. Demarcation between gula and submentum arcuate. *Thorax.*—Pronotum armed. Anterolateral angles with a salient point followed by a sharp inward curve of the margin, which is then angled out again at origin of lateral carina. Lateral carina sharp and prominent. Anterior margin of pronotum not forming any median point or angle. Median longitudinal sulcus deeply impressed, with a few punctures or impunctate. Puncturation of pronotum as follows: densely punctate over all dorsal and lateral surfaces, the punctures smaller and less dense, or sometimes absent, on disc, becoming more sparsely punctate on anterior declivities; punctures simple except for those of the following areas, which are coarse and umbilical: along entire submargin, a few along median longitudinal sulcus and median line of anterior face, in lateral fossae, and hollows between prominences. Anterior prosternal margin with a low, truncate median tooth; sternellum moderately umbilico-punctate. Median lobe of metasternum with shallow umbilical punctures along sides and anteriorly; median longitudinal groove complete to anterior pit. *Elytra.*—8th stria complete; 9th arising about one third of way down elytron; often a more anterior segment of 9th stria is present, not quite issuing from base or joining posterior section and not punctate; 10th stria complete. Striae coarsely crenato-punctate, the punctures very little deeper than the striae, round, separated by a distance equal to their diameters or less. Interstriae very slightly convex, sparsely, finely punctate, appearing smooth, or quite impunctate. *Abdomen.*—Pygidium rather densely, coarsely umbilico-punctate, the margin complete or rarely incomplete, the inner edge of margin being effacted ventrally (fig. 59). *Anterior legs.*—Ventral surface of femur with coarse setigerous punctures on posterior longitudinal half, impunctate on anterior half. Forespur straight and parallel-sided to apical third, where it takes a sharp bend inwards and tapers to a sharp point. *Middle legs.*—Coxa impunctate. Ventral surface of femur very sparsely and finely punctate or impunctate except distally, where the punctures are coarse and setigerous. Tibia below with three distal seta tufts. *Posterior legs.*—Like middle legs, but tibia below with a row of 4–5 seta tufts. *Total length.*—10–15.5 mm.

Male armament. Medium specimens bear a horn which is practically straight, the rearward curvature being barely perceptible (fig. 75). The horn of major specimens is gently arcuate and slightly expanded transversely at the apex. The pronotum bears four prominences as usual, the two median ones compressed, slightly upwardly directed, and approximated, but always with a punctate depression between them.

Description of Female. Similar to male, but differing in armament and in the following features: usually some umbilical punctures between eyes on upper surface of head; puncturation on

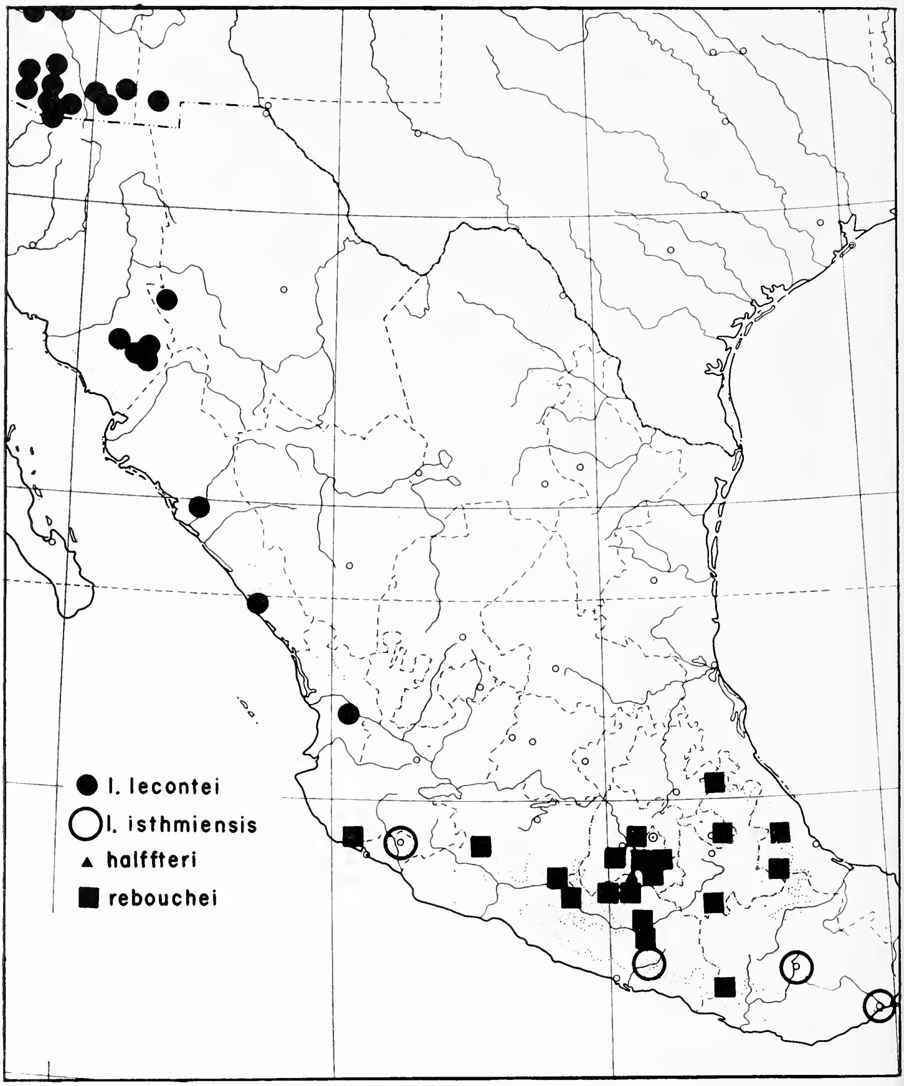

Fig. 18. Distribution of the *rebouchei* complex. Base map reproduced by permission of the University of Chicago.

anterior part of disc much denser and merging, the punctures umbilical only along submargins and in lateral fossae. *Total length.*—11–15 mm.

Female armament. Typical for the genus.

DISTRIBUTION. Fig. 18. Known from practically all the mountain ranges of southeast Arizona at altitudes of 2500 to 6000 ft. (760–1800 m.) but found most frequently at about 4000 ft. (1200 m.). There is one record each from the Animas Mts. of New Mexico and the Río Mayo in Chihuahua and there are several records from the Sierra de Alamos in southern Sonora at altitudes of but a few hundred metres. Thence there are isolated records down the west coast of Mexico to Nayarit at altitudes of sea level to 1500 m. (4900 ft.).

BIOLOGY. Unknown. In Arizona it is apparently most abundant in late summer.

REMARKS. The relationship of this species to *rebouchei* Harold is extremely close. This cannot be seen in the Arizona specimens, which are very different from *rebouchei*, being much more heavily punctate on the pronotum and the males bearing median pronotal prominences of a different type (figs. 75, 76). However, as we examine *lecontei* further south in Sinaloa and Nayarit we find it becomes increasingly less punctate and the median pronotal prominences become more laminate and remote, approaching both *rebouchei* and *l. isthmiensis* in form. *C. rebouchei* possesses an acute tooth on the prosternal margin (fig. 54), whereas in *lecontei* there is at most a rounded expansion or truncate process here, and in *rebouchei* the pygidial margin is always quite effaced medially, whereas in *lecontei* it is nearly always either engraved for its entire length or continued medially by a close-set row of punctures (fig. 59).

This species has been long familiar under the name *moechus* Leconte. A recent examination of the type of *moechus* revealed it to belong to a Mexican species hitherto bearing the name *clavicornis* Matthews and Halffter. As there were no synonyms available for this common species, it is here described as new and dedicated to the distinguished American systematist, J. L. Leconte.

MATERIAL EXAMINED. 244 males, 249 females.

UNITED STATES: *Arizona:* Cochise Co.: Carr Cyn, Huachuca Mts.; Lower Carr Cyn, Huachuca Mts.; Chiricahua Mts.; Huachuca Mts.; Mule Mts., Gilman Ranch, 8 mi. N Bisbee; Palmerly; 3 mi. E Portal; Ramsay Cn., Huachuca Mts.; San Bernardino Ranch; Texas Pass, Dragoon Mts.; Webb; SE end Whetstone Mts., Sands Ranch; Gila Co.: Globe; Base Pinal Mts.; Rice; Pima Co.: Baboquivari Mts.; Baboquivari Mts., Kitts Peak Rincón; Baboquivari

Mts., El Mirador Rch., 4 mi. NW Sasabe; Baboquivari Canyon, W. side Baboquivari Mts.; Brown's Canyon, E side Baboquivari Mts.; Elkhorn Ranch, E slope N end Baboquivari Mts.; Sycamore Canyon, N of Baboquivari Canyon, W side Baboquivari Mts.; Continental; Santa Catalina Mts.; Santa Rita Mts.; Santa Rita Mts., Old Parker Ranch; Sierritas, Black Dike Prospect; Tucson; Tucson, St. Xavier Mission; Santa Cruz Co.: Elgin; Nogales; Patagonia; Ruby; 21 mi. SE Ruby; Sonoita R., Patagonia; 25 mi. E Sonoita; Tumacacori Nat'l. Mon.; Yanks Spring, 4 mi. SE Ruby, Pajaritos Mts.; Washington Mts., nr. Nogales; Yavapal Co.: Prescott; *New Mexico:* Hidalgo Co.: Animas Mts., Double Adobe Ranch.

MEXICO: *Chihuahua:* Río Mayo, Aug. (Gentry), 1 ♂ (CAS); *Nayarit:* Tepic, 28 Jul. 1953 (C. and P. Vaurie), 2 ♂♂, 2 ♀♀ (AMNH); 27 Jul. 1954 (M. Cazier, W. Gertsch, Bradts), 1 ♀ (AMNH); *Sinaloa:* Culiacán, 250 ft., 21 Jul. 1959 (H. E. Evans), 2 ♂♂, 2 ♀♀ (CU); Mazatlán, 15–17 Sep. 1918, 1 ♂, 1 ♀ (USNM); 9 mi. N Mazatlán, 100 ft., 12–16 Jun. 1953 (R. K. Selander), 1 ♀; El Venadío [4.5 mi. N Mazatlán]*, 16 Jun. 1918 (J. A. Kusche), 41 ♂♂, 35 ♀♀ (USNM, CAS); *Sonora:* Agua Marina nr. Alamos, 20 Jul. 1955 (R. and O. Flint), 1 ♂ (EGM); Alamos, 29 Jul. 1940 (R. P. Allen), 1 ♂, 3 ♀♀ (CAS); 10 mi. W Alamos, 21 Jul. 1954 (M. Cazier, W. Gertsch, Bradts), 1 ♂ (AMNH); Minas Nuevas, 7 Aug. 1952 (C. and P. Vaurie), 15 ♂♂, 9 ♀♀ (AMNH); Río Mayo, Aug., 3 ♀♀ (CAS); Sta. Rosa Ranch, N of Navojoa, 2 Aug. 1952 (C. and P. Vaurie), 1 ♂, 2 ♀♀ (AMNH).

Copris lecontei isthmiensis n. subsp.

Holotype: Tehuantepec, Oaxaca, Mexico, 12 July 1955 (P. and C. Vaurie), ♂; American Museum of Natural History.

DESCRIPTION. The Oaxaca and Colima males of *lecontei* are sharply separated from the rest of the species by the greater proportional length of the cephalic horn. When the height of the cephalic horn is plotted against the length of the hind femur on a graph (fig. 8), it is seen that the specimens from these two states fall along a very different curve from that followed by the rest of the species. In appearance this subspecies is very close to *rebouchei* Harold, being distinguished only by the complete pygidial margin and absence of an acute prosternal process. *C. l. isthmiensis* is very

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* This locality is given as "Venodio" on the specimens. For its correct spelling and location I am indebted to E. J. Cantrell (unpublished information).

sparsely punctate on the pronotum in the male and the median pronotal prominences are remote and laminate as in *rebouchei.* Except in horn allometry, this form seems to merge imperceptibly with the northern subspecies.

Distribution. Colima, Guerrero, and Oaxaca at sea level to 1520 m. (5000 ft.). I have ascribed the single female from Jalisco to this subspecies arbitrarily, since the females are not distinguishable from the northern form.

Biology. Unknown.

Remarks. A poorly represented form, distinguishable from *rebouchei* Harold primarily by its completely margined pygidium. It could, with almost equal justification, be ascribed to *rebouchei,* since their horn allometry curves coincide (fig. 9). For the present, however, I prefer to attach greater weight to the morphological, rather than to the allometric, evidence.

Material Examined. Eight males, five females.

MEXICO: *Colima:* Colima, 18 Jun. 1943 (H. D. Smith), 1 ♀ (USNM); Volcán de Colima (L. Conradt), 3 ♂♂, 2 ♀♀ (USNM); state record only (L. Conradt), 2 ♂♂ (USNM); *Guerrero:* 10 mi. S Chilpancingo, 25 Jun. 1932 (Hobart Smith), 1 ♂ (PAS); *Jalisco:* Atenquique, 30 Jun. 1949 (W. D. Clarke), 1 ♀ (CAS); *Oaxaca:* Oaxaca, Jul. (Embury), 1 ♂ (CAS); 30 Jun. 1955 (P. and C. Vaurie), 1 ♀ (AMNH); Tehuantepec, 12 Jul. 1955 (P. and C. Vaurie), 1 ♂ (AMNH).

Copris rebouchei Harold

Copris rebouchei Harold, 1869, Ann. Soc. Ent. France, ser. 4, IX: 497 [type: Puebla, Pue.; Museum d'Histoire Naturelle, Paris]; Bates, 1887, Biol. Cent.—Amer., Coleopt. II, 2, p. 54, 1889, Suppl., p. 387 (distr.); Matthews 1959, Ciencia XIX (6–7): 135 (key and distr.).

Description of Male. *Head.*—Armed. Clypeus bidentate, the teeth moderately prominent in unworn specimens, broad, rounded, separated by a U-shaped median notch which does not cut through margin. Upper surface of head moderately punctate outwardly with basal and central portions impunctate; all punctures simple. Posterior oblique carina very sharp. Occipital margin with transverse setigerous groove interrupted into three non-overlapping portions; demarcation between gula and submentum a rounded, broad V. *Thorax.*—Pronotum armed. Anterolateral angles with the point made salient by a deep inward curve of margin immediately behind it, the margin then angled out at origin of lateral carina. Lateral carina very sharp. Anterior margin of pronotum not forming any median point or angle, or sometimes forming a very slight one. Median longitudinal sulcus shallow, fine, and impunctate. Pronotum impunctate except for the following areas, which are sparsely and coarsely umbilico-punctate: posterior and lateral submargins, including anterolateral lobes, lateral fossae, and hollows between median and lateral prominences; in addition, there are usually some scattered smaller umbilical punctures along anterior margin and mid-line of anterior face, including the hollow between median prominences; some shallow punctiform impressions on outside faces of lateral prominences. Anterior prosternal margin with a minute, acute median tooth (fig. 54); sternellum sparsely punctate. Median lobe of metasternum impunctate except for a few umbilical punctures along edges; median longitudinal groove fine but complete. *Elytra.*—8th stria complete, sometimes tending to disintegrate at the very base; 9th stria arising one-third the way down elytron; 10th complete. Striae coarsely crenato-punctate, the punctures round, scarcely deeper than the striae, separated by a distance equal to their diameter or less. Interstriae convex and impunctate. *Abdomen.*—Pygidium moderately umbilico-punctate, the margin incomplete, its inner border effaced ventrally. *Anterior legs.*—Ventral surface of femur with coarse setigerous punctures on posterior longitudinal half, impunctate on anterior half. Forespur parallel-sided for basal two thirds, then sharply bent inwards, almost at a right angle, tapering to a sharp point. *Middle legs.*—Coxa impunctate. Ventral surface of femur impunctate on basal half, with sparse setigerous punctures on apical half. Tibia below with two distal seta tufts. *Posterior legs.*—Femur as described for middle legs. Tibia below with a row of 3–4 median seta tufts. *Total length.*—12–15 mm.

Male armament. The head horn gradually tapers to an acute apex and is very slightly curved or practically straight. The pronotal prominences are all laminate, the median ones only slightly closer to each other than each is to the lateral prominence, and directed forward parallel to each other with a deep concavity between each (fig. 76). In lateral view the median prominences are rounded at the apex, the lateral ones acute as usual.

DESCRIPTION OF FEMALE. Similar to male, but differing in armament and in the following features: clypeal teeth more prominent and round, median notch often more rounded than that of male; pronotum impunctate at base of disc, becoming densely punctuate over most of dorsal and lateral surfaces, the punctures transverse and accompanied by ridges; anterior face impunctate; the punctures are umbilical only along margins and in lateral fossae. *Total length.*—11.5–15 mm.

Female armament. Normal for the genus.

DISTRIBUTION. Fig. 18. The Central Volcanic Range and the depression of the Río Balsas. In the western part of its range the species descends to sea level, occurring in the same areas as the closely related *lecontei*, n. sp., but over most of its range it occurs at altitudes of 430–1520 m. (1400–5000 ft.), with a single record at 3000 m. (9800 ft.).

BIOLOGY. Found under cow dung; otherwise its biology is unknown. Active throughout the rainy season.

REMARKS. This smooth and shiny species can always be told by its incomplete pygidial margin, the inner border of which is completely effaced for the median third or more of its length (fig. 58), and by the minute, acute median tooth on the anterior posternal margin. Its relationship to *lecontei* is discussed under the latter species.

MATERIAL EXAMINED. 63 males, 58 females.

MEXICO: *Guerrero:* Ajuchitlán; Altamirano (NE of Coyuca de Catalán); Apipilulco; Balsas; Cacahuamilpa; 25 km. N Chilpancingo; Iguala; 8 mi. N Iguala; 5 mi. S Iguala; Mexcala; Teloloapan; *Jalisco:* 3 mi. E Jaluco (43 mi. SW La Resolana); *México:* Salazar; Tejupilco, Temexcaltépec; *Michoacán:* El Sabino, Uruapan; Huétamo; *Morelos:* 7 km. S Alpuyeca; Cuautla; Cuernavaca; 10 mi. S Cuernavaca; 25 km. S Cuernavaca; Jojutla; ?Oxtepec; ?Progreso; Puente de Ixtla; Tepoztlán; ?Tequesquitengo; Valle de Morelos; Vista Hermosa, 15 km. S Cuernavaca; *Oaxaca:* Tepetlapa; *Puebla:* Km. 259 on Oaxaca Rd. (nr. Acatlán); Pahoatlán (nr. Huachinango); *Tlaxcala:* 21 mi. W Apizaco; *Veracruz:* Coatepec; Presidio.

Copris halffteri Matthews

Copris halffteri Matthews, 1959, Ciencia XIX(6–7): 133–134 [type: Cacahuamilpa, Gue.; United States National Museum].

DESCRIPTION OF MALE. *Head.*—Armed. Clypeus bidentate, the teeth prominent, rounded, approximated, separated by a U-shaped median notch not cutting through margin. Upper surface of head shallowly punctate only along edges, rest of surface being impunctate; punctures simple except for a few umbilical ones at hind edges of genae. Posterior oblique carina very prominent, short, curved backwards at inner end, abruptly cut off. Occipital margin with setigerous groove divided into three partially overlapping sections. Demarcation between gula and submentum arcuate. *Thorax.*—Pronotum armed. Anterolateral angles with the point made prominent by a sharp inward curve of margin immediately behind it, the margin then sharply angled out at origin of lateral carina. Lateral carina very sharp. Anterior margin of pronotum not forming any median point or angle. Median longitudinal sulcus of pronotum moderately impressed, fine, complete, and impunctate. Puncturation of pronotum as follows: entire base forward of submargin extremely faintly punctate, appearing impunctate, becoming more visibly punctate forward of a transverse line joining hind limits of lateral fossae, the punctures being shallow and somewhat cicatricial, becoming round and subumbilical only on anterolateral lobes, and abruptly disappearing on anterior declivity, which is therefore impunctate except for a few shallow punctures about the mid-line and along anterior margin; the punctures are umbilical along posterior and lateral submargins and in lateral fossae. Anterior prosternal margin with a median process of unique shape, being very salient, parallel-sided, and bilobate at apex, which is also slightly reflexed; sternellum concave, not longitudinally carinate, sparsely umbilico-punctate. Median lobe of metasternum impunctate, but wrinkled and with some faint punctiform impressions at edges; median longitudinal impressed line complete. *Elytra.*—8th stria incomplete, disintegrating beyond halfway point; 9th stria arising close to 10th a little forward of halfway point; 10th complete. Striae crenatopunctate, the punctures little wider and no deeper than the striae, separated by a little more than their diameter. Interstriae slightly convex, sparsely, regularly, and very finely punctate, appearing smooth. *Abdomen.*—Pygidium moderately and rather shallowly punctate, the punctures small and umbilical; pygidial margin complete. *Anterior legs.*—Ventral surface of femur coarsely setigerous-punctate on posterior longitudinal half, impunctate on anterior. Forespur straight and parallel-sided to near apex, where it makes a sudden, right-angled (or even a little acute-angled) inward bend, tapering to a sharp point (fig. 42). *Middle legs.*—Coxa impunctate. Ventral surface of femur very finely punctate on basal half, coarsely setigerous-punctate on distal half. Tibia below with three distal median seta tufts. *Posterior legs.*—Femur and tibia as described for middle legs. *Total length.*—14.5–15 mm.

Male armament. Male armed like a female. Head horn typical of the female in the genus, well developed, transverse, low, parallel-sided, truncate and excavate at the apex. Pronotum with the median prominences low, transverse, and cariniform, like those of a female, but quite narrow and separated by a deep, rounded median depression. The lateral prominences are low conical bumps (fig. 77).

Description of Female. Very similar to male, differing only in armament. *Total length.*—15 mm.

Female armament. Head horn like that of the male, but lower and more excavate at the apex. Median pronotal prominences in the form of much sharper transverse carinae which are longer and strongly curved, their inner ends turned up and forming prominent points separated by a depression which is smaller than that of the male; the notal surface is depressed behind these carinae. Lateral prominences as in male.

Distribution. Fig. 18. Known only from the type locality at Cacahuamilpa, Guerrero.

Biology. Found in cow dung, otherwise unknown.

Remarks. This species is truly remarkable and quite unique with regard to its male armament, which is of the female type. The prominent bilobate process of the median prosternal margin (fig. 55) is also unique. It may further be told from *rebouchei* Harold, which it otherwise closely resembles, by the complete pygidial margin (fig. 60). It was collected in association with some typical specimens of *rebouchei.*

It appears that a similar phenomenon may be observed in some Old World species of *Copris* (Balthasar, personal communication), where occasionally male individuals of known species may appear with female armament. In such cases these have been interpreted as being individual gynandromorphs rather than separate species. It is impossible that this could be the case here because, for one thing, the females also show the distinguishing characters of the bifurcate prosternal process and complete pygidial margin. It may well be, however, that the species arose from such individuals which were initially merely gynandromorphs.

Material Examined. Holotype, allotype, and male paratype.

MEXICO: *Guerrero:* Cacahuamilpa, 25 Aug. 1956 (G. and V. Halffter), 2 ♂♂, 1 ♀ (USNM, GH).

Complex 5. The *fricator* complex.

Posterior angles of head subquadrate or acute. Anterolateral angles of pronotum acute, the margin immediately behind them sinuate or emarginate. Entire pronotal surface coarsely and very densely punctate. Forespur with the apex acute in both sexes.

Eighth elytral stria complete. Pygidial margin nearly always complete.

Three species found at low to moderate altitudes in the Eastern United States and extreme southern Ontario: *inemarginatus* Blatchley, *fricator* (Fabricius), *howdeni* Matthews and Halffter.

Copris inemarginatus Blatchley

Copris inemarginatus Blatchley, 1918, Canadian Ent. L: 54–55 [type: Dunedin, Fla.; Purdue University, Lafayette, Indiana]; Wickham, 1919, American Journ. Sci., ser. 4, XLVII (281): 355–357 (fossil); Young, 1959, Coleop. Bul. XIII: 103–106 (fossil and distr.).

Description of Male. *Head.*—Armed with a very low horn. Clypeus without teeth or median notch, with a very slight median sinuation. Posterior angles of genae acute. Upper surface of head entirely punctate, all raised surfaces and basal portion of genae umbilico-punctate, outer portions with the punctures simple and merged together, forming irregular ridges; horn and area immediately around it impunctate. Posterior oblique carina absent. Occiptal margin with setigerous groove interrupted into three parts. Demarcation between gula and submentum irregular, with a slight median rearward extension of the setose submental area. *Thorax.*—Pronotum unarmed. Anterolateral angles obtuse with the point drawn out into a point or tubercle. Lateral margin slightly angulate at origin of lateral carina. Lateral carina not prominent, rounded, not issuing from margin. Anterior margin not forming any median point or angle. Median longitudinal sulcus visible on dorsal part of disc, fine, shallow, and impunctate. Puncturation of pronotum as follows: densely punctate over entire surface, the punctures shallow and often indistinct, simple on dorsal part of disc, cicatricial or umbilical elsewhere, separated by a distance equal to a little more than their diameter, and annular along the hind and lateral submargins. Anterior prosternal margin with two very minute teeth close together at the middle; sternellum coarsely umbilico-punctate. Median lobe of metasternum cicatrico-punctate along sides; medium longitudinal groove strongly impressed on posterior two-thirds of metasternum only, effaced anteriorly. *Elytra.*—8th stria complete; 9th arising about halfway down elytral length; 10th complete. Striae crenato-punctate, the punctures elongated, shallow, flanked by undulations of the interstrial margins which give the punctures a transverse appearance.

Interstriae strongly convex, very finely punctate, appearing smooth. *Abdomen.*—Pygidium completely margined, densely umbilicopunctate. *Anterior legs.*—Ventral surface of femur coarsely setigerous-punctate over most of area, more finely punctate along anterior margin basally. Forespur bent in apically and tapering abruptly to an acute apex. *Middle legs.*—Coxa with numerous umbilical punctures along median carina and a row of coarser setigerous ones along outer edge. Ventral surface of femur impunctate except for a few coarse setigerous punctures distally. Tibia below with 4–6 seta tufts arranged in a longitudinal row along most of tibial length. *Posterior legs.*—Femur as described for middle legs. Tibia with 6–8 seta tufts in a longitudinal row over most of length of tibia. *Total length.*—11–14 mm.

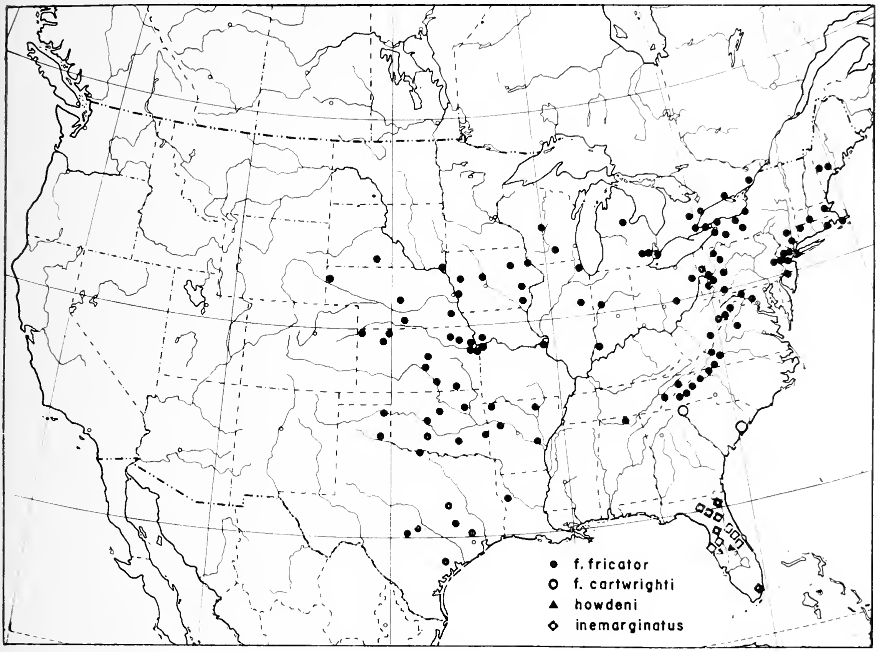


Fig. 19. Distribution of the *fricator* complex. Base map reproduced by permission of the University of Chicago.

Description of Female. Not differing in any external respect from the male. *Total length.*—12–15 mm.

Distribution. Fig. 19. Northern and Central Florida and Miami.

Biology. Found under cow dung. It is most active during the winter and spring from November to April. Blatchley records finding it under a dead turtle and at a porch light in January. Young (1959) describes it as highly characteristic of the scrub habitat in Florida.

Remarks. I believe this species to be an early offshoot from the stem leading to *fricator,* with which latter species it shares the characters here used to differentiate the *fricator* complex, but from which it differs primarily in retaining the very finely punctate elytral interstriae of the presumed ancestor in the *rebouchei* or *remotus* complexes. It is also easily distinguished by the clypeal margin, which lacks any teeth or emargination—a unique feature of this species. It differs further from *fricator* and *howdeni* in that the outer head punctures above are merged to form irregular grooves, in not showing the fine shagreening of interpunctural surfaces characteristic of those two species, and in not bearing a salient median tooth on the anterior prosternal margin; the under surface is also somewhat less densely punctate.

Material Examined. 68 males, 56 females.

UNITED STATES: *Florida:* Alachua Co.: Gainesville; High Springs; Dade Co.: Miami; Duval Co.: Jacksonville; Hillsborough Co.: Lutz; Tampa; Marion Co.: 4 mi. NW Dunellon; Orange Co.: Orlando; Osceola Co.: Kissimmee; Pinellas Co.: Dunedin; Putnam Co.: Interlachen; 8 mi. S Interlachen; Seminole Co.: Sanford; Suwannee Co.: 13 mi. N. O'Brien; Volusia Co.: Enterprise; location undetermined: Stemper; Weeki Wachee.

Copris fricator fricator (Fabricius)

Scarabaeus fricator Fabricius, 1787, Mant. Ins., p. 15, No. 140 [type: East India; Hunterian Collection, Glasgow]; 1792, Ent. Syst. I, 1, p. 54, No. 176; Olivier, 1789, Ent. 1, 3, p. 122, pl. 16, fig. 149; 1790, Enclycl. méth. V, p. 161.

Copris fricator, Fabricius, 1801, Syst. Eleuth. I, p. 45, No. 67; Gillet, 1911, Ann. Soc. Ent. Belgique LV: 314; Staig, 1931, The Fabrician Types of Insects in the Hunterian Collection at Glasgow University, pp. 48–50, pl. 14 (descr. of type); Arrow, 1931, Fauna of British India, Colept., Lamell. III, p. 107 (synon.).

Scarabaeus tullius Olivier, 1789, Ent. I, 3, pl. 11, fig. 98, pl. 19, fig. 88b [type: East Indies; Hope Mus., Oxford]; 1790, Encycl. méth. V, p. 159.

Copris tullius, Fabricius, 1801, Syst. Eleuth. I, p. 44, No. 65; Lansberge, 1886, Tijdschr. v. Ent. XXXIX: 16 (synon.); Gillet, 1911, Ann. Soc. Ent. Belgique LV: 290 (discuss. of synon.); Lindquist, 1933, Jour. Kansas Ent. Soc. VI(4): 1–9 (biol.).

Copris anaglypticus Say, 1823, Jour. Acad. Nat. Sci. Philadelphia III: 204 [type: United States; destroyed]; 1859, Complete Writings, ed. Leconte, II, p. 131; Horn, 1873, Trans. American Ent. Soc. IV: 42–51 (key and descr.); Schaeffer, 1906, Trans. American Ent. Soc. XXXII: 256 (key); Arrow, 1931, Fauna of British India, Coleopt., Lamell. III, p. 107 (synon.).

Description of Male. *Head.*—Armed or not. Clypeus bidentate, the teeth rounded, broad, and very low, often completely worn down, with a median V-shaped notch between them which cuts through the margin. Posterior angles of genae subquadrate. Upper surface of head entirely closely punctate, the punctures simple except at least some of those on genae, between eyes, and, in minor specimens, on upper part of clypeus. Surface between punctures often very finely shagreened. Posterior oblique carina absent. Occipital margin with transverse setigerous groove broken into several parts. Demarcation between gula and submentum arcuate. *Thorax.*—Pronotum armed or not. Anterolateral angles with the point made prominent by a sharp inward curve of margin immediately behind it, the margin then angled out at origin of lateral carina. Lateral carina well developed, sharp. Anterior margin of pronotum not forming any median point or angle. Median longitudinal sulcus obsolescent, visible as a shallow impunctate line over most of length of disc, or totally effaced. Pronotum entirely densely umbilico-punctate (many punctures not umbilical in well developed specimens), the punctures separated by a distance more or less equal to their diameter, smaller on anterior declivity, larger and annular along posterior submargin. Surface between punctures often very finely shagreened. To the naked eye the texture imparts a silky sheen to the pronotum. Prosternal-proepisternal suture not carinate; anterior prosternal margin with a salient median process which is usually quadrate, sometimes acute or rounded; sternellum with very large, shallow punctures. Median lobe of metasternum densely and shallowly umbilico-punctate, the punctures finer on middle; median longitudinal groove impressed on posterior two thirds, the anterior third very shallow. *Elytra.*—8th stria complete; 9th arising about halfway down elytral length, very close to 10th; 10th complete. Striae very shallow, broad, crenulated, with the punctures obsolescent or absent. Interstriae slightly convex, profusely and distinctly umbilico-punctate, the punctures small, setigerous, and separated by a distance equal to many times their diameter. Surface between punctures finely shagreened, especially along sides of elytra. Small specimens tend to a reduction in the size and number of interstrial punctures and to a more profuse shagreening. *Abdomen.*—Pygidium densely umbilico-punctate, the margin complete. *Anterior legs.*—Femur below entirely, densely umbilico-punctate. Forespur tapering to an acute point, curved inward and slightly downward for its apical third. *Middle legs.*—Coxa with a few small punctures along median longitudinal carina, rest of surface finely shagreened and often wrinkled. Ventral surface of femur entirely, coarsely punctate, the punctures reniform and setigerous. Tibia below with a row of up to eight median seta tufts over most of its length. *Posterior legs.*—Femur and tibia as described for middle legs. *Total length.*—10.5–18.5 mm.

Male armament. Very variable in development (but not in form), small specimens bearing no horns or gibbosities whatever, medium sized ones bearing a straight, evenly tapering and transversely flattened horn on the head, and two moderately approximated median pronotal prominences which are a little transversely carinate. The lateral prominences are represented by the usual conical bumps. Large specimens bear a long, rather straight, and usually distinctly clavate horn, the apex being transversely expanded and rounded. The median prominences are prominent rounded gibbosities which are approximated but always with a depression between them, and the lateral prominences are cariniform and not very prominent (fig. 66).

Description of Female. Very similar to male, differing only in armament (in specimens possessing it) and in the fact that the clypeal teeth are more rounded and prominent, the notch between them more U-shaped. Slightly worn minor females are quite indistinguishable from minor males. *Total length.*—12–18 mm.

Female armament. Normal for the genus.

Distribution. Fig. 19. The Eastern United States (penetrating into Canada along the northern shores of lakes Erie and Ontario) in an area corresponding to the Upper Austral (Carolinian) Zone, but descending well into the Lower Austral in the western part of its range. In the eastern part of its range, in the Appalachian Mountains, it climbs well into the Transition Zone. In Western North Carolina the subspecies does not appear to be found at altitudes lower than 2500 ft. (760 m.), nor south of Balsam and Sunburst. This is the northernmost of the American species and the only one definitely occurring in Canada, to my knowledge.

Biology. Found abundantly under cow dung and occasionally coming to light. Nidification is discussed on pp. 28–29.

Remarks. Specimens from Kansas, Oklahoma, Arkansas, Texas, Louisiana, and Missouri are characterized by a rather uniform small size and consequent low development of armament (fig. 3); this difference does not appear to be sharply set off from the rest of the populations (see more complete discussion on p. 19), nor is it accompanied by any other feature that I could find, and it appears doubtful that anything would be gained by introducing a subspecific name here.

It is regrettable that this species should undergo yet another name change, but there is no doubt that the specimen now considered to be the type of *Scarabaeus fricator* F. belongs to this species. Mr. R. A. Crowson was kind enough to compare some Pennsylvania specimens of this species with the type in the Hunterian Collection at Glasgow, whereupon he pronounced them identical. The synonymy of *fricator* and *anaglypticus* was actually pointed out by Arrow in 1931, a fact which seems to have been overlooked by everyone on this side of the Atlantic until recently and which would also have been overlooked by me if it had not been pointed out by Father F. S. Pereira and Mr. O. L. Cartwright.

There is still considerable doubt as to whether the specimen in Glasgow does indeed represent the type of *fricator* (Balthasar, personal communication) particularly as Olivier evidently considered the species *tullius* and *fricator* as being quite distinct. The Glasgow specimen was separated from its label for some time (Staig, 1931; Crowson, personal communication) and reunited with some doubt. Nevertheless, it appears to me on reading Olivier that the differences he mentions are sexual and not specific; there is no indication that he was aware that the type of *fricator* he described was actually a female (the Glasgow type is a female, an indication that it probably is the true type). Furthermore, it appears to me that in the interest of nomenclatorial stability the supposed Fabrician types in the Hunterian Collection should be accepted in the absence of any contradictory evidence; otherwise they would serve no purpose and the situation would remain confused for all time.

Material Examined. 182 males, 182 females.

CANADA: *Ontario:* Ancaster; Fisher Glen; Grimsby; Guelph; Leamington; Marmora; Pt. Pelee; Spencerville; Toronto; Trenton.

UNITED STATES: *Alabama:* Madison Co.: Monte Sano St. Pk.; *Arkansas:* Arkansas Co.: Arkansas R.; Benton Co.: Bentonville; Lawrence Co.: Imboden; Logan Co.: Cove Lake nr. Paris; *Connecticut:* Litchfield Co.: Cornwall; *Illinois:* Champaign Co.: Urbana; Cook Co.: Evanston; Dupage Co.: Lyons; Lake Co.: Libertyville; McHenry Co.: Algonquin; *Indiana:* Knox Co.: Vincennes; Lafayette; *Iowa:* Buchanan Co.: Independence; Clayton Co.: Guttenberg; Crawford Co.: Denison; Henry Co.: Mt. Pleasant; Johnson Co.: Iowa City; Polk Co.: Herrold; Pottawatomie Co.: Council Bluffs; Story Co.: Ames; *Kansas:* Cheyenne Co.; Douglas Co.: Lawrence; Ellsworth Co.: Ellsworth; Jackson Co.; Johnson Co.; Leavenworth Co.; McPherson Co.; Montgomery Co.; Norton Co.; Pottawatomie Co.: Onaga; Reno Co.: Medora, Sand Hills; Saline Co.; Sedgwick Co.: Wichita; Sheridan Co.; Wyandote Co.; *Louisiana:* Sabine Co.: Many; *Maine:* Kennebec Co.: Monmouth; Oxford Co.: Bethel; *Maryland:* Montgomery Co.: Forest Glen; Washington Co.: Hagerstown; *Massachusetts:* Barnstable Co.: Woods Hole; Hampden Co.: Chicopee, Ludlow, Wilbraham; Middlesex Co.: Concord; *Michigan:* Detroit: Highland Park; Livingston Co.: George Reserve; Midland Co.; Washtenaw Co.; *Missouri:* Clinton Co.: Lathrop; Jefferson Co.: Webster Groves; Kansas City; *Nebraska:* Brown Co.: Koshopah; Custer Co.: Ansley; Lancaster Co.: Bennet; Phelps Co.: Holdredge; Sioux Co.; *New Jersey:* Burlington Co.; Essex Co.: Newark, Orange; Middlesex Co.: New Brunswick; Morris Co.: Boonton; Passaic Co.: Clifton; Somerset Co.; Warren Co.: Phillipsburg; *New York:* Erie Co.: Hamburg; Long Island; New York City: Brooklyn, Queens; Niagara Co.: Olcott; Orange Co.: New Windsor; West Point; Oswego Co.: Oswego; Tompkins Co.: Ithaca; Ulster Co.; Wayne Co.; Westchester Co.: Yonkers; Wyoming Co.: Pike; *North Carolina:* Blue Ridge Parkway: Cumberland Knob Pk.; Miles 291.4, 339.2; Buncombe Co.: Weaverville; Haywood Co.: Sunburst; Jackson Co.: Balsam; *Ohio:* Columbiana Co.: Millport; Licking Co.: Newark; *Oklahoma:* Canadian Co.; Coal Co.: Cairo; Grady Co.: Ouachita Nat'l Forest; Payne Co.: Stillwater; Rogers Co.: Claremore *Pennsylvania:* Allegheny Co.; Beaver Co.: New Brighton; Fayette Co.: Ohiopyle; Forest Co.; Indiana Co.: Indiana; Jefferson Co.; Lawrence Co.: Slippery Rock; Northampton Co.: Easton, Wind Gap; Pittsburgh; Washington Co.; Westmoreland Co.: Jeanette; *Rhode Island:* Washington Co.: Watch Hill; *South Dakota:* Bennett Co.: Martin; Clay Co.: Vermillion; Union Co.: Elk Point; *Tennessee:* Greene Co.: Greeneville; Sevier Co.: Gatlinburg; *Texas:* Blanco Co.: Cypress Mills; Brazos Co.: College Station; Gillespie Co.: Fredericksburg; Hall Co.: 5 mi. W Memphis; Hemphill Co.: Canadian; Kerr Co.: Kerrville; Leon Co.: Peeler; Limestone Co.: Mexia; Montgomery Co.: Conroe; Victoria Co.: Victoria; Wichita Co.: Burkburnett, Red River; *Virginia:* Blue Ridge Parkway: Miles 162, 167, 210; Shenandoah Nat'l Pk., Mile 95; Washington Co.: Blacksburg; *West*

Virginia: Greenbrier Co.: White Sulphur Springs; Hardy Co.: Wardensville; Pendleton Co.: Cheat Mts.; *Wisconsin:* Madison; Wood Co.: Cranmoor.

Copris fricator cartwrighti Robinson, new combination

Copris cartwrighti Robinson, 1941, Trans. American Ent. Soc. LXVII: 131–132 [type: Cashiers Valley Road, Oconee Co., S. C., 16 Oct. 1934; United States National Museum].

DESCRIPTION. Differs from *fricator fricator* (F.) in that both sexes are always devoid of any cephalic or pronotal armament: the head horn is represented by a low transverse tumosity; the pronotum may be strongly convex in larger individuals but it never shows any distinct prominences or carinae. In addition, the elytral interstriae are somewhat more densely punctate than in *f. fricator* (see discussion below).

DISTRIBUTION. The mountainous portions of extreme northwestern South Carolina at over 2000 ft. altitude. One specimen from the coast at Charleston, S. C.

BIOLOGY. Found under cow dung. From the collected material it appears that this form is most active during the cooler months of the year. I could not find it in May, at a time when *f. fricator* was very active a little further north.

REMARKS. This form was described by Robinson as a distinct species distinguished from *fricator* by the absence of horns or thoracic protuberances. As we have seen, specimens of *fricator* often lack this armament, particularly in southwestern populations. A better character for distinguishing this form is the denser puncturation of the elytral interstriae, but even this does not serve to distinguish many individuals of *cartwrighti.* To be specific, in comparing 15 individuals of *cartwrighti* with an equal number of *fricator* from adjacent North Carolina populations, counting the number of punctures in a single row in 2 mm. of length at the middle of the left fourth interstria, the following ranges were obtained: *cartwrighti*—15–24 punctures, *fricator*—13–19 punctures. The means were 19.26 and 15.93 respectively. Adopting a criterion recommended by Mayr et al. (1953), one sees that these differences are below the conventional level of subspecific distinctness. The form would not merit recognition were it not for its apparent geographical separation from *f. fricator.* In May, 1959, in an attempt to determine the exact limits of the two forms, I collected under cow dung in Western North Carolina and extreme northwestern South Carolina in the type locality of this form. Unfortunately I was unable to find *cartwrighti*, but *fricator* was abundant in dung at an altitude of 2500 ft. and higher near Asheville, N. C., or about 55 air miles away from the *cartwrighti* locality. In the intervening distance neither form could be found at all at any altitude. The other closest records of *fricator* are at Balsam and Sunburst, N. C., at an approximately equal distance away. This sort of negative evidence is not conclusive, but it does suggest the presence of an hiatus between the ranges of the two forms, and until connecting specimens are proved to be present in the intervening areas it seems best to retain this form as a distinct subspecies, particularly as there is some evidence that *cartwrighti* is a winter form.

MATERIAL EXAMINED. Eight male and seven female paratypes, one additional specimen.

UNITED STATES: *South Carolina:* Charleston Co.: Charleston, May 1944 (R. Peters), 1 (USNM); Oconee Co.: Cashiers Valley Rd., 3, 16 Oct. 1934 (O. L. Cartwright), 5 ♂♂, 6 ♀♀ (OLC, USNM); [Walhalla Federal] Fish Hatchery, 28 Apr. 1939 (O. L. Cartwright), 2 ♂♂, 1 ♀ (OLC, USNM); Jocassee, 13 Jul. 1936 (O. L. Cartwright), 1 ♂ (OLC).

Copris howdeni Matthews and Halffter

Copris howdeni Matthews and Halffter, 1959, Ciencia XVIII (9–10): 200–202 [type: Oneco, Manatee Co., Fla.; United States National Museum].

DESCRIPTION OF MALE. *Head.*—Unarmed. Clypeus bidentate, the teeth approximated, very low, with a very shallow U- or V-shaped notch between them, not cutting through the margin. Posterior angles of genae subquadrate. Upper surface of head entirely, densely, evenly punctate, the punctures umbilical except along margin of clypeus. Posterior oblique carina absent. Occipital margin with transverse setigerous groove broken into several sections. Demarcation between gula and submentum variable, arcuate or broadly angulate, in one specimen forming a median V. *Thorax.*—Pronotum unarmed. Anterior angles with the point slightly expanded into a small rounded tooth. Lateral margin angled out at origin of lateral carina. Lateral carina evident but not sharp, running straight from margin to lateral fossa. Anterior margin of pronotum not forming any median point. Median longitudinal sulcus visible only on middle of disc, faint. Pronotum entirely, evenly, densely punctate, the punctures umbilical, separated by a distance equal to somewhat less than their diameter. Anterior prosternal margin with a distinct quadrate median tooth; sternellum only slightly convex, grossly umbilico-punctate. Median lobe of metasternum coarsely umbilico-punctate except along midline; median longitudinal groove complete. *Elytra.*—8th stria complete; 9th arising from 10th about halfway down elytron; 10th complete. Striae crenulate, broad, flat, devoid of punctures. Interstriae completely flat, densely and coarsely umbilico-punctate, the punctures separated by a distance equal to somewhat less than their diameter. *Abdomen.*—Pygidium very densely umbilico-punctate, the margin usually complete. *Anterior legs.*—Ventral surface of femur entirely, densely umbilico-punctate, the punctures smaller anteriorly. Forespur gradually narrowing to a point, the apex curved sharply inward and slightly downward. *Middle legs.*—Coxa with numerous umbilical punctures. Ventral surface of femur densely punctate over entire surface. Tibia below with 2–3 seta tufts and usually a row of seta insertions up its length. *Posterior legs.*—Femur and tibia as described for middle legs. *Total length.*—13–14 mm.

DESCRIPTION OF FEMALE. With the clypeal teeth slightly more prominent and the notch between them deeper, otherwise identical to male. *Total length.*—15 mm.

DISTRIBUTION. Fig. 19. Known from two localities in central Florida.

BIOLOGY. Unknown. All specimens were collected at light in the month of March.

REMARKS. This species and *f. cartwrighti* Robinson represent isolated southern populations apparently derived from *f. fricator* (F.). It differs in no respect from *fricator* specimens of similar size except in the coarsely and densely punctate, rugose, and absolutely flat elytral intervals. Its separation from *fricator* as a full species is based primarily on its geographical isolation and appears justified on the basis of the great ecological and climatic differences between its habitat and that of *fricator.*

MATERIAL EXAMINED. Four males (holotype and three male paratypes), one female.

UNITED STATES: *Florida:* Manatee Co.: Oneco, 23, 25 Mar. 1954, 26 Mar. 1955 (D. M. Anderson, W. W. Boyle, G. E. Ball), 4 ♂♂ (CU, USNM, GH, HH); Polk Co.: 3 mi. SW Lake Marion, 14 Mar. 1956 (H. Howden), 1 ♀ (HH).

LITERATURE CITED

Arrow, G. J. 1904. Sound production in the lamellicorn beetles. Trans. Ent. Soc. London 1904 (IV) : 709–750.

———. 1931. The Fauna of British India, Col. Lamell. III (Coprinae). Taylor & Francis, London.

———. 1951. Horned beetles, a study of the fantastic in nature. W. Junk, The Hague.

Balthasar, B. 1958. Eine neue Untergattung und einige neue Arten der Gattung *Copris* Geoffr. Acta Ent. Musei Nat. Prague XXXII : 471–480.

Bartlett, J. R. 1854. Personal narrative of explorations and incidents in Texas, New Mexico, California, Sonora, and Chihuahua connected with the United States and Mexican Boundary Commission during the years 1850, '51, '52, and '53. D. Appleton & Co., New York, vols. 1 and 2.

Bates, H. W. 1887–1889. Copridae *in* Biologia Centrali Americana, Coleoptera II, 2, pp. 53–55, Supplement p. 387.

Blackwelder, R. E. 1944. Checklist of the coleopterous insects of Mexico, Central America, the West Indies, and South America, pt. II. United States Nat. Mus. Bul. 185, p. 208.

Bowden, J. 1959. A note on the horn of the beetle *Dynastes centaurus* (F.). Journ. Ent. Soc. South Africa 22(1) : 78–87.

Burmeister, H. C. C. 1846. Genera quaedam insectorum. Burmeister et Strange, Berolini, no pag.

Butt, F. H. 1944. External morphology of *Amphimallon majalis* (Razoumovski) (Coleoptera, the European chafer). Cornell Univ. Agric. Exp. Sta. Memoir 266.

Champion, G. C. 1907. Itinerary of Mr. G. C. Champion's travels in Central America, 1879–1883. Ent. News 18 : 33–44.

Curtis, J. 1832. British Entomology, vol. IX, pl. 414.

Darwin, C. R. 1871. The descent of man, and selection in relation to sex. D. Appleton & Co., New York.

Erichson, W. F. 1847. Conspectus insectorum coleopterorum, quae in Republica Peruana observata sunt. Arch. Naturg. XIII(1) : 67–185.

Fabre, J. H. 1918. The sacred beetle and others. A. T. de Mattos translation. Dodd, Mead & Co., New York.

Fourcroy, A. F. 1785. Entomologia parisiensis. Via et Aedibus Serpentineis, Paris.

Geoffroy, E. L. 1764. Histoire abregée des insectes. Durand, Paris.

Gillet, J. J. E. 1911. Coleopterorum Catalogus, pars. 38. Scarabaeidae, Coprinae I. S. Schenkling, Berlin.

Halffter. G. 1952. Notas sobre el género *Phanaeus*. I. *Phanaeus quadridens* Say, 1835 (Col., Scarab.). Ciencia XII (3–4): 79–86.

Harold, E. de. 1869. Note sur quelques coprides du Mexique. Ann. Soc. Ent. France, ser. 4, 9: 493–512.

Hardenberg, C. B. 1907. Comparative studies in the trophi of Scarabaeidae. Trans. Wisconsin Acad. Sci. XV: 548–602.

Hope, F. W. 1837. The coleopterist's manual. Henry G. Bohn, London.

Horn, G. H. 1873. Notes on some genera of coprophagous Scarabaeidae of the United States. Trans. American Ent. Soc. IV: 42–51.

Hubbard, H. G. 1894. The insect guests of the Florida land tortoise. Insect Life VI (4): 302–315.

Huxley, J. 1932. Problems of relative growth. Methuen & Co., London.

Index to Map of Hispanic America, 1:1,000,000. Vol. I, Geographical names in Central America, 1943; Vol. II, Geographical names in Mexico, 1944. American Geographical Society. United States Gov't. Printing Office, Washington.

Kolbe, H. J. 1905. Über die Lebensweise und die geographische Verbreitung der coprophagen Lamellicornier. Zool. Jahr. Suppl. VIII: 475–594, 19 pls.

Lacordaire, T. 1856. Genera des Coléoptères, III. Paris.

Leng, C. W. 1920–1948. Catalogue of the Coleoptera of America North of Mexico, with suppl. 1–5. Mount Vernon, N. Y.

Lengerken, V. von. 1954. Die Brutfürsorge und Brutpflegeinstinkte der Käfer, 2nd. ed. Akad. Verlagsgesellschaft, Leipzig.

Lindquist, A. W. 1933. Amount of dung buried and soil excavated by certain Coprini (Scarabaeidae). Kansas Ent. Soc. Journ. 6(4): 109–125.

Lindquist, A. W. 1935. Notes on the habits of certain coprophagous beetles and methods of rearing them. United States Dept. Agr. Circ. 351.

Matthews, E. G. 1959. Nueva especie de *Copris* (Col., Scarab.) y clave para la determinación de las especies mexicanas. Ciencia XIX (6–7): 133–136.

Matthews, E. G. and **G. Halffter.** 1959. Nuevas especies americanas de *Copris* (Col., Scarab.). Ciencia XVIII (9–10): 191–204.

Mayr, E., E. G. Linsley and **R. L. Usinger.** 1953. Methods and principles of systematic zoology. McGraw-Hill, New York.

Mohr, C. O. 1930. Morphological comparisons of Coprinae, Aphodiinae, and Geotrupinae (Coleoptera, Scarabaeidae). Trans. Illinois State Acad. Sci. XXII: 263–284.

Müller, O. F. 1764. Fauna insectorum Fridrichsdalina. Frid. Gleditschii, Hafniae et Lipsiae.

Oliver, A, G. 1790 Encyclopédie méthodique, V. Panckoucke, Paris.

Paulin, R, 1935. Le polymorphisme des mâles de coléoptères. Exposés de Biométrie et de Statistique Biologique, VI. Hermann et Cie., Paris.

Pereira, P. F. S. and **M. A. V. d'Andretta.** 1955. Novos escarabeídeos e novas sinonímias (Col., Scarabaeidae). Pap. av. Dep. Zool. Secr. Agric. São Paulo 12: 261–263.

Pereira, P. F. S. and **A. Martínez.** 1956. Os gêneros de Canthonini americanos (Col., Scarabaeidae). Rev. Brasileira Ent. 6: 91–192.

Pierce, W. D. 1946. Fossil arthropods of California, 10. Exploring the minute world of the California asphalt deposits. Bul. So. California Acad. Sci. XLV (3): 122–130.

Ritcher, P. O. 1945. Coprinae of Eastern North America Kentucky Agr. Exp. Sta. Bul. 477.

Schaeffer, C. 1906. On *Bradycinetulus* and *Bolboceras* of North America, with notes on other Scarabaeidae. Trans. American Ent. Soc. XXXII: 254–256.

Siyazov, M. M. 1914. K biologii zhukov navoznikov (Coleoptera, Scarabaeidae). Russk. Ent. Obozr. 1913, XIII: 113–131.

Thomas, W. P. 1960. Notes on a preliminary investigation into the habits and life cycle of *Copris incertus* Say (Coprini: Coleoptera) in New Zealand. N. Z. Journ. Sci. 3(1): 8–14.

PLATES.

Plate I

Fig. 20. Granular umbilical puncture on pronotal submarginal of *C. incertus,* much enlarged.

Fig. 21. Granular setigerous puncture on metasternum of *C. incertus,* much enlarged.

Fig. 22. Umbilical puncture on pronotal submargin of *C. armatus,* much enlarged.

Fig. 23. Setigerous puncture on posterior margin of proepimeron of *C. armatus,* much enlarged.

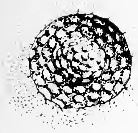
Fig. 24. Head of female *C. lugubris,* dorsal view.
toc—transverse occipital carina
tog—transverse occipital groove (entire)

Fig. 25. Head of female *C. rebouchei,* dorsal view.
poc—posterior oblique carina
tog—transverse occipital groove (divided into three parts)

Fig. 26. Ventral view of *C. fricator.*
lpc—longitudinal proepimeral carina
ml—median lobe of metasternum
pc—pleural carina
pp—prosternal-proepisternal suture

Fig. 27. Posterior view of inside of prothorax showing position of deeply sunken coxa, diagrammatic.
cx—coxa
stn—sternellum
trm—tergal remotor muscle, in two parts

Plate I



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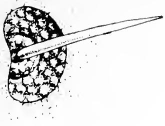

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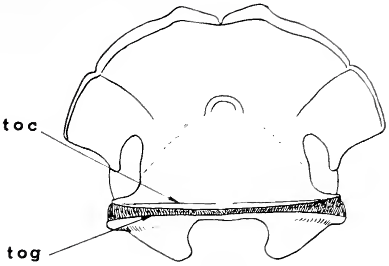

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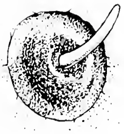

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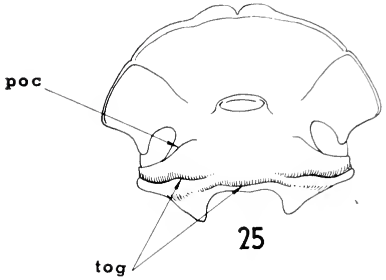

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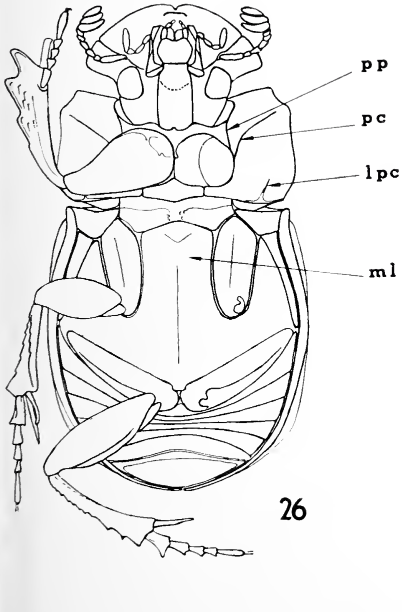

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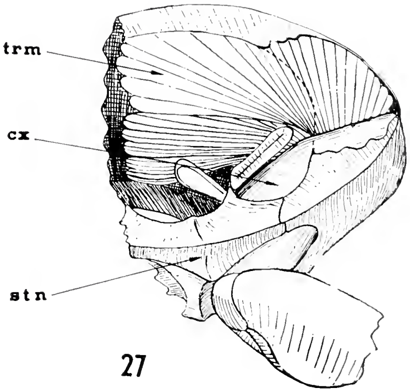

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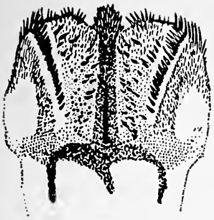
Plate II

Fig. 28. Labrum-epipharynx of *C. gopheri*, ventral view.
Fig. 29. Left mandible of *C. gopheri*, dorsal view.
  a. Same, in ventral view.
Fig. 30. Labium and left maxilla of *C. gopheri*, ventral view.
Fig. 31. Left maxilla of *C. gopheri*, dorsal view.
Fig. 32. Hypopharynx and ligula of *C. armatus*, three-quarter dorsal view. Positions of labial palpi represented by dotted outlines.

Plate II



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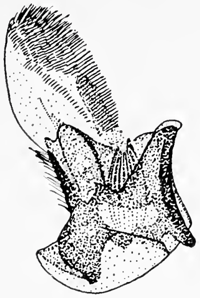

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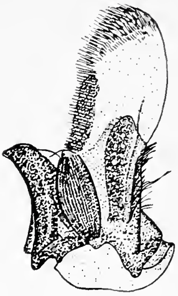

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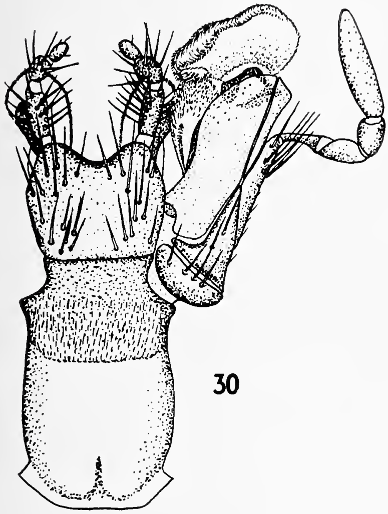

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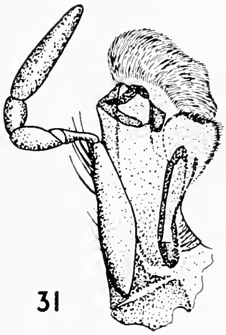

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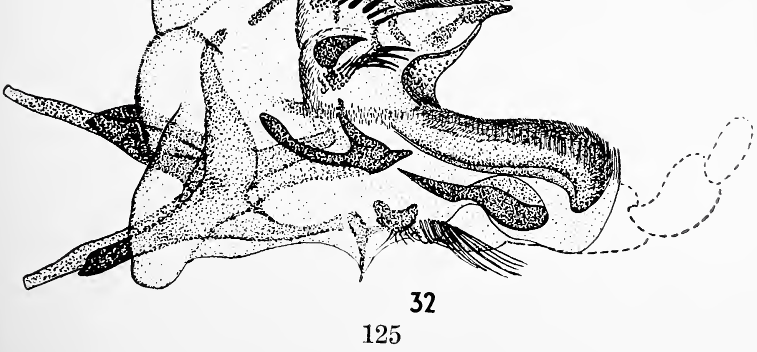

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Plate III

Figs. 33–48. Right tibial forespur in direct dorsal view.

Fig. 33. *C. lugubris*
34. *laeviceps*
35. *gopheri*
36. *minutus*
37. *armatus*
38. *klugi*
39. *arizonensis*
40. *lecontei*
41. *subpunctatus*
42. *halffteri*
43. *remotus*
44. *mexicanus*
45. *sallei*
46. *costaricensis*
47. *inemarginatus*
48. *fricator*

Fig. 49. Right hind tibia and tarsus of *C. fricator* in ventral view. *st*—ventral and distal seta tufts

Fig. 50. Right hind tibia and tarsus of *C. lugubris* in dorsal view. *ss*—supplementary setae

Figs. 51–57. Median processes of anterior margin of prosternum, much enlarged.

Fig. 51. *C. minutus*
52. *armatus*
53. *lecontei*
54. *rebouchei*
55. *halffteri*
56. *inemarginatus*
57. *fricator*

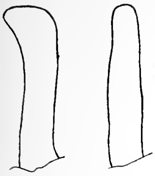
Figs. 58–60. Pygidia.

Fig. 58. *C. rebouchei,* pygidial margin incomplete.
59. *lecontei,* pygidial margin interrupted, completed by punctures.
60. *halffteri,* pygidial margin complete.

Fig. 61. Genital capsule of male *incertus* showing apical dorsal hook on paramere.

Fig. 62. Genital capsule of *lugubris* showing absence of apical hook.

Plate III



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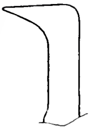

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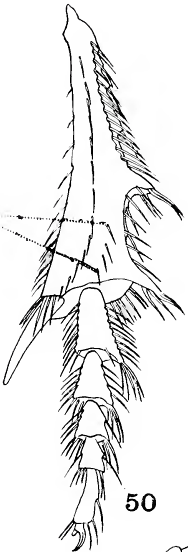

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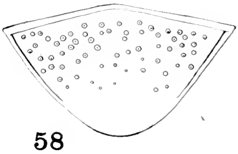

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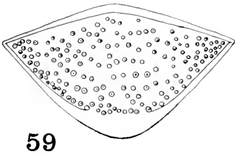

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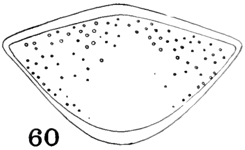

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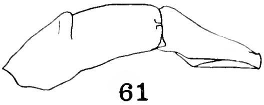

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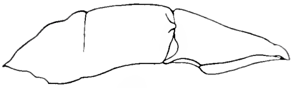

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Fig. 63. *C. incertus*, Jalapa, Ver.
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Plate IV

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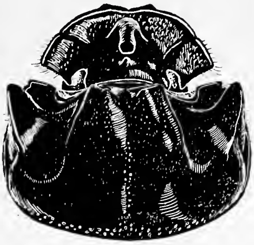

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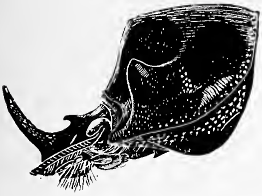

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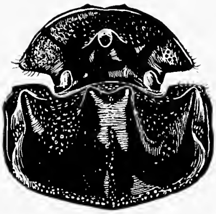

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Forebodies of major males in dorsal and lateral views.
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Fig. 71. *C. klugi,* Temascaltépec, Méx.

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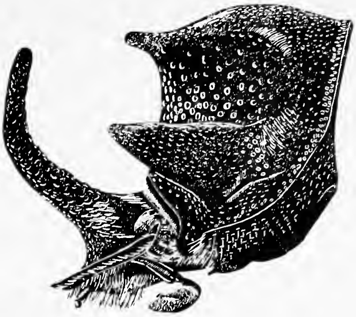

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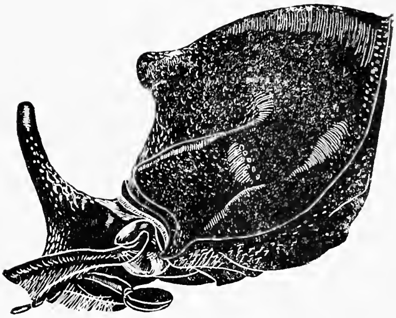

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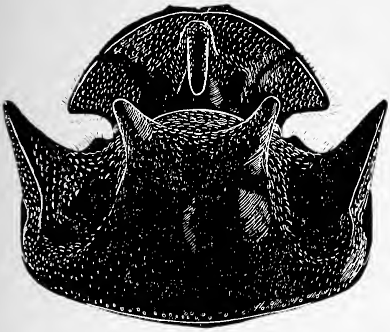

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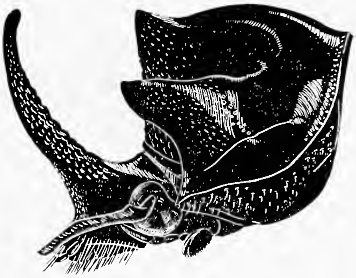

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Forebodies of major males in dorsal and lateral views.

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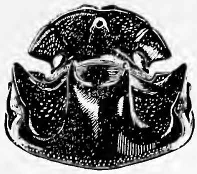

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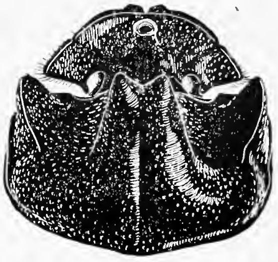

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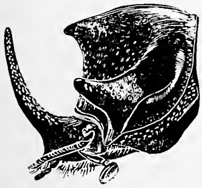

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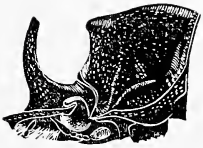

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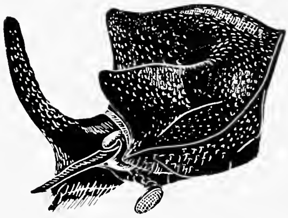

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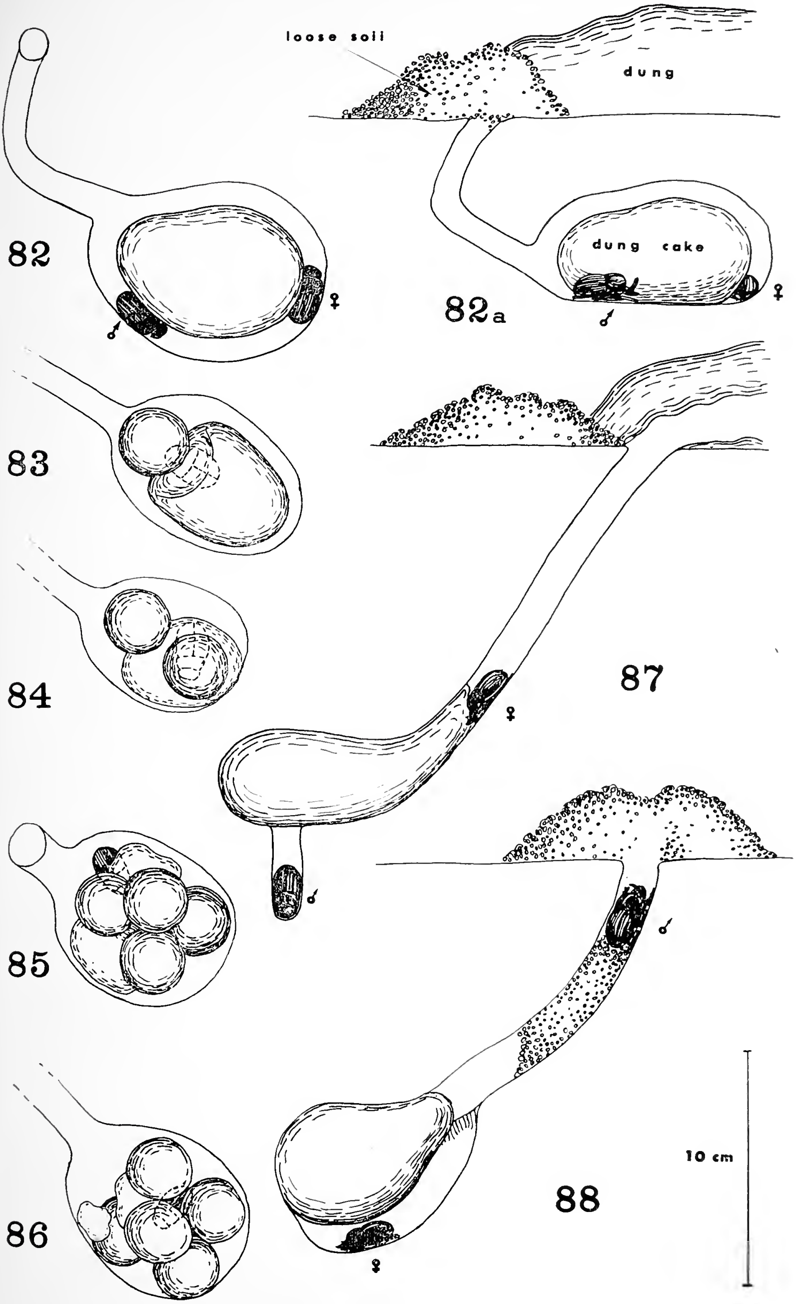

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New names in **bold face**; synonyms in *italics*.

ENTOMOLOGICA AMERICANA

A JOURNAL OF ENTOMOLOGY.

VOLUME XLII (NEW SERIES)
for 1962

PUBLISHED BY THE
BROOKLYN ENTOMOLOGICAL SOCIETY
1962

ENTOMOLOGICA AMERICANA

Vol. XLII (N.S.), for 1962

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ED. NOTE: Dr. E. G. Mathews wishes to gratefully acknowledge publication support from the Grace H. Griswold Fund of the Dept. of Entomology of Cornell University for his Revision of the Genus Copris that appeared in Volume 41 of Entomologica Americana. This publication was the result of a thesis submitted for the Doctor of Philosophy degree at Cornell University.

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VOL. XLII (NEW SERIES)

ENTOMOLOGICA AMERICANA

A JOURNAL OF ENTOMOLOGY.

PUBLISHED BY THE
BROOKLYN ENTOMOLOGICAL SOCIETY

Published for the Society by the
Business Press Inc.
N. Queen St. and McGovern Ave., Lancaster, Pa.
Subscription $6.00 Per Year
Date of Issue November 14, 1962

ENTOMOLOGICA AMERICANA

VOLUME XLII

A REVISION OF THE COSMOPTERIGIDAE OF AMERICA NORTH OF MEXICO, WITH A DEFINITION OF THE MOMPHIDAE AND WALSHIIDAE (LEPIDOPTERA: GELECHIOIDEA)[1]

By

Ronald W. Hodges[2]

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[1] Modified from a thesis submitted to the Graduate School of Cornell University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

[2] Entomology Research Division, A.R.S., U. S. Department of Agriculture, Washington 25, D. C.

INTRODUCTION

This study started as a generic review of the Cosmopterigidae (in the sense of the McDunnough, 1939, list) for the purpose of defining the Cosmopterigidae and Momphidae and assigning the North American genera and species to them. Study soon showed that it would be impossible to proceed as planned without first determining the species. This was done for the Cosmopterigidae, but the number of species in this family proved to be so large that it was not feasible to do the same for the Momphidae and Walshiidae (defined later). However, the type species of the genera of the North American and European Momphidae and Walshiidae have been examined, and a study made of the types of the described species of Walshiidae. Three major items form the body of this paper: 1) the definition of the Cosmopterigidae, Momphidae, and Walshiidae, 2) the revision of the Cosmopterigidae, and 3) the grouping of the North American species and genera (and some of the European genera) under the three families in an annotated list.

The revision of the Cosmopterigidae is at best preliminary, because many species and a few genera undoubtedly remain to be described from the United States. This can be exemplified by the results of an eleven day period of collecting in south-central Florida, where eleven species of cosmopterigids were collected, six of which are new, one of them representing a new genus. However, the keys and illustrations of the moths and of the male and female genitalia should enable a worker to determine whether his specimens have been described.

TERMS

The terminology for the external features of the adults follows Forbes (1923) with the exception of the wings. The numeral system for the venation (Fig. 11) follows Meyrick (1928). I have used ''dorsal'' margin for what is called the ''inner'' margin by many lepidopterists. In describing the maculation of the antennae, I have considered that they were held at right angles with the longitudinal axis of the body. The fraction following the antennae in the descriptions is the ratio of the length of the antenna to the length of the forewing. The alar expanse was determined by measuring the distance from the middle of the thorax to the apex of the wing and doubling this figure. Colors used to describe the patterns were as seen under incandescent illumination.

The male genitalia pose problems because the terminology given by Klots (1956) is based mainly upon the higher moths, Geometridae and Noctuidae. The Gelechioidea are a highly evolved group, and many of the structures are doubtfully homologous with those of the same name in other groups. I have attempted to apply the terms given by Klots whenever they seemed reasonable, but one must realize that a thorough morphological study of the genitalia of all of the Microlepidoptera is required before an accurate application of terms can be made. Where a structure seemed not to be homologous with a named one, I have given a descriptive phrase for it rather than coin a new term. Figure 28 illustrates the structures and their terminology. The terminology used for the female genitalia follows Klots and is illustrated in Figure 89.

Special Techniques

A ventral mount of the male genitalia with the valvae spread is desirable for the comparison of a maximum number of features. The genitalia of several of the cosmopterigids are difficult to maneuver into this position because of the relation of parts; however, it is often possible to obtain the desired results by the following procedure: after the genitalia have been stained and cleaned, the valvae are spread laterally with a pair of forceps; then, while holding the valvae apart, the apex of the aedeagus is pushed dorsally. This action should move the costae dorsolaterally and move the left brachium ventrally. At this point a small piece of glass is placed on top of the genitalia to hold the parts in the desired position. Caution must be exercised to prevent disarticulating the tegumen from the vinculum. The males of *Melanocinclis* are best mounted laterally or ventrolaterally.

The small size of the adult moths makes it desirable to mount them on minutens or small sized pins before the body has become dry (Hodges, 1959). They should never be glued on points because the scales, which are glued, come loose from the body with the result that the specimen drops off the point.

CLASSIFICATION

The moths discussed in this paper were placed in the Elachistidae until 1871 when Wocke placed many genera in a new family Lavernidae, without formally defining the group. In 1876, basing his classification primarily on wing venation, Wocke erected two monogeneric families, Batrachedrae (*sic*) and Cosmopterygidae, and placed the following genera in the Lavernidae: *Cyphophora, Laverna, Limnaecia, Ascalenia, Mompha* (*rhamniella*), *Stagmatophora, Pyroderces, Stathmopoda, Heinemannia, Blastodacna, Tebenna, Chrysoclista,* and *Psacaphora.* Meyrick (1909), also on the basis of venation, defined the Cosmopterigidae as follows: "I have come to the conclusion that the family *Elachistidae* as formerly understood by myself is heterogeneous, and includes forms of various origin. I use the family name *Cosmopterygidae* to include those genera with long sickle-shaped palpi, fore-wings lanceolate or linear, with veins 7 and 8 stalked, 7 to costa, hind-wings lanceolate or linear, with veins 2–5 separate, nearly parallel, 3 from before angle of cell, 6 and 7 more or less approximated towards base. Characteristic genera of this family are *Cosmopteryx, Stagma-*

tophora, *Limnoecia*, and *Mompha;* but *Elachista* itself does not belong here. I regard the family as a development of the *Oecophoridae*, and believe I have a complete series of transitional forms." Walsingham (1891), using Tineidae as an inclusive family, listed the West Indian genera considered by this paper under Cosmopteryginae, Laverninae, and Batrachedrinae, and in 1909 he grouped the Central American genera under Lavernidae. This concept is the same as Meyrick's Cosmopterygidae.

Spuler (1910) placed the European species in the new taxon Momphidae which was subdivided into the Momphinae and Cosmopteryginae. The Momphinae included *Pancalia, Stagmatophora, Mompha, Anybia, Ascalenia, Sorhagenia, Limnaecia, Cyphophora, Psacaphora, Tebenna, Chrysoclista, Spuleria, Heinemannia,* and *Blastodacna;* the Cosmopteryginae included *Tetanocentria. Batrachedra, Eustaintonia, Pyroderces, Stathmopoda,* and *Cosmopteryx.* Subsequent authors have used Cosmopterygidae, Momphidae, or Lavernidae, depending upon their concepts of priority and validity of the names.

Busck (1932) distinguished between two groups as follows: "The genus [*Teladoma*] belongs to the family Cosmopterygidae as distinguished from the Momphidae (Lavernidae). The two families have been confused and united under the former name by European and American authors, the writer included, but they have no close relationship and must be retained as separate families. This will be the subject of a forthcoming paper. The Momphidae have symmetrical male genitalia . . . and the *ostium* of the female not protruding beyond the body wall." This was the first time that characters other than the venation were used to define the two families, and Clarke (1941, 1955) followed Busck's definition in assigning genera to the Cosmopterigidae.

I do not believe that any of the preceding systems of classifying these moths is wholly satisfactory. When characters of the male and female genitalia are used in conjunction with characters of the venation and of the head, three relatively distinct groups are evident. The basic problem is to determine the sets of characters which can be used to define suprageneric categories. If the venation is used exclusively, then one classification is obtained. If the male genitalia are used, then another, and so on. It seems as though a natural classification is best obtained by a combination of sets of characters such as the male and female genitalia, the venation, the maxillary and labial palpi, the antennae, the nature of the scales on the head and other parts of the body, the shape of the wings, the setal patterns of the larvae, and the pupae. However, this has its problems. I have used several sets of characters in defining three groups; but when the characters seem to disagree as to probable relationship, I have turned to the male genitalia as the ultimate criterion. At present, adequate material of the immature stages is not available to work out a classification based upon their characters.

The Cosmopterigidae is defined as follows: head smooth-scaled; tongue developed, scaled; maxillary palpi folded over base of tongue; labial palpi recurved, smooth (or slightly rough) scaled, apex acute; antennae two-thirds to one, simple or ciliate, pecten present or absent, scape elongate. Metathoracic tibiae often with long dorsal scales. Forewings broadly lanceolate with apex rounded to lanceolate with apex acuminate; 11 or 12 veins present; 1b furcate basally; 1c present or absent, usually absent; 2 before end of cell; 7 and 8 stalked, 7 to costa; 11 from central area of cell. Hindwings broadly lanceolate and apex rounded to linear, cell open or closed; 4 to 8 veins present; 6 and 7 divergent, 7 to costa. Male genitalia asymmetrical; *valvae* latero-ventral or ventral; *costae* free or fused with *valvae* (in several genera right *costa* free, left *costa* free fused with *valva*), asymmetrical costal processes sometimes present but not in those forms having free *costae; tegumen* broad, heavily sclerotized; *uncus* and *socii* absent; *brachia* asymmetrical; *aedeagus* heavily sclerotized, usually ankylosed, *cornuti* present or absent; *juxta* and *transtilla* usually not recognizable; 7th and 8th abdominal segments specialized to form plates, rods, or valvae-like structures in several genera; abdominal hair pencils present or absent. Female genitalia: *corpus bursae* membranous; *ductus bursae* membranous or sclerotized; *signa* present or absent; *lamellae vaginales* forming a tube-shaped structure in several genera.

This definition includes a wide variety of forms whose common denominator is the male genitalia. It appears as though this group may have arisen from the Oecophoridae through a form which lacked the uncus and socii. This would explain the type of venation common to some cosmopterigids and oecophorids. The hindwing venation, used by Meyrick to define the Cosmopterigidae, is probably the result of convergence.

The second group is the Momphidae which is defined as follows: head smooth-scaled; tongue developed, scaled; maxillary palpi folded over base of tongue; labial palpi recurved, smooth-scaled, apex acute; antennae two-thirds to one, simple or ciliate, pecten present or absent, scape short or elongate. Metathoracic tibiae with long dorsal scales in some forms. Forewings lanceolate, apex rounded to falcate, often with raised scales; 9, 10, 11, or 12 veins present; 1b simple or furcate basally, 1c present or absent; 2 at or before end of cell; 5 separate or fused with 4; 7 and 8 stalked, 7 to costa; 11 from middle half of cell. Hindwings lanceolate to linear; 5, 6, 7, or 8 veins present; 1b simple or furcate basally; 1c present or absent; 2, 3, and 4 usually subparallel; 5 and 6 separate, connate or stalked; 7 to costa. Male genitalia: symmetrical; *valvae* simple or divided with *costae* free apically; *sacculus* often well developed and long; *aedeagus* not ankylosed, slender or stout, *cornuti* present or absent; *juxta* usually present, *furca* often highly developed as two plates; *transtilla* present or absent; *tegumen* broad, heavily sclerotized; *uncus* and *gnathos* present or absent (both may be present, one or other may be absent but not both); *socii* absent; arms of *gnathos* free or fused, often with a spined process. Female genitalia: *bursa copulatrix* membranous or sclerotized, *ductus bursae* sometimes with accessory diverticula, *signa* present or absent.

Two well marked groups are included in the preceding definition: *Mompha* and allies and *Blastodacna* and allies. In the former group the *costae* are usually separate from the *valvae* apically; the *juxta* is moderate; the *uncus* is present; and the *gnathos* is absent. In the latter group the *valvae* usually are simple; the *juxta* often has two large, separate lobes; the *uncus* is usually absent; the *gnathos* is present, and each *brachium* when present has a spined process. But, it is possible to follow a series of specimens, starting with *Batrachedra* and some closely related genera and continuing through *Zaratha pterodactylella* Wlk., which seem to link the two groups. For this reason I am including both in the Momphidae. It appears as though the Momphidae were derived from the same group which may have given rise to the Blastobasidae, Oecophoridae, and Elachistidae.

The third group, present in the old concept of Cosmopterigidae, is the Walshiidae. It is defined as follows: head smooth-scaled; tongue developed, scaled; maxillary palpi folded over base of tongue; labial palpi recurved, smooth-scaled, apex acute; antennae one-half to three-fourths, pecten present or absent, simple or ciliate, scape usually elongate, Metathoracic tibiae often with long or stout dorsal scales. Forewings lanceolate, apex rounded or acute, raised scales present or absent; 12 veins present; 1b furcate basally; 2 from three-fourths to five-sixths on cell; 2, 3, and 4 separate; 4 and 5 separate or connate; 6 separate or stalked with 7 and 8; 11 from one-half to two-thirds on cell. Hindwings lanceolate to linear; 8 veins present; 1b simple; 2, 3, and 4 equidistant, parallel;

4 and 5 approximate or connate; 6 and 7 stalked; veins in hindwing sometimes evanescent. Male genitalia: symmetrical to asymmetrical; *valvae* simple or complex, separate or fused ventrally; *aedeagus* large, heavily sclerotized, ankylosed, heavily sclerotized *manica* articulating with saccus; *transtilla* usually absent; tegumen narrow; *uncus* present, simple or bifid; *socii* and *gnathos* absent; ventral surface of *tuba analis* often lightly sclerotized; a short sclerotized lobe extending from *vinculum* at point of articulation with *tegumen; saccus* developed or not; eighth segment modified into plates, rods, or glandular structures in some genera. Female genitalia: *bursa copulatrix* membranous or scerotized; *signa* present or absent; *ostium* an opening in eighth sternite; eighth sternite simple or modified as an invagination around ostium; in some species seventh and eighth segments heavily sclerotized.

The Walshiidae form a natural group. For the present, however, I can not suggest a reasonable hypothesis as to their relationship with the other gelechioids.

MATERIAL EXAMINED

I wish to express my thanks to the following institutions and individuals for providing me with specimens (the letters in brackets indicate the abbreviations used in citing the location of specimens): United States National Museum [USNM], Cornell University [CU], American Museum of Natural History [AMNH], California Academy of Sciences [CAS], Los Angeles County Museum [LACM], University of California at Berkeley [UCB], Chicago Natural History Museum [CNHM], Illinois Natural History Survey [INHS], Michigan State University [MSU], University of Michigan [UM], Canadian National Collection [CNC], Museum of Comparative Zoology [MCZ], British Museum (Natural History) [BMNH], Dr. A. F. Braun [AFB], Mr. C. P. Kimball [CPK], Mr. M. O. Glenn [MOG], Dr. A. E. Brower [AEB], Dr. J. A. Powell [JAP], Dr. A. B. Klots [ABK], Dr. S. W. Frost [SWF], and Dr. J. G. Franclemont [JGF]. Material in my collection is indicated by [RWH].

REVISION OF THE COSMOPTERIGIDAE OF AMERICA NORTH OF MEXICO

Cosmopterygidae Wocke, *in* Heinemann, 1877 [1876]. Die Schmetterlinge Deutschlands und der Schweiz, 2: 520. Meyrick, 1909. Trans. Ent. Soc. London, 1909: 17. (*partim*).

Lavernidae Walsingham, 1909. Biologia Centrali-Americana. Insecta. Lepidoptera-Heterocera, 4: 1. (*partim*). Forbes, 1923. The Lepidoptera of New York and neighboring states, Cornell Univ. Agric. Exp. Sta. Mem., 68: 318. (*partim*).

Momphidae Spuler, 1910. Die Schmetterlinge Europas, 2: 381. (*partim*).

The description of the family is as given under the section on classification. The major point of separation of the Cosmopterigidae from the Oecophoridae and Momphidae is the asymmetry of the gnathos in the male genitalia; it differs from the Walshiidae by the absence of the uncus and by the broad tegumen.

Ten genera and 67 species are recognized in the North American fauna. Of this number four genera and 29 species are described as new. *Stagmatophora*, as determined by the type of the genus, does not occur in North America. *Eteobalea* has been proposed for our species formerly included in *Stagmatophora* except *ceanothiella* and *gleditschiaeella* which have been transferred to *Periploca* in the Walshiidae. *Pyroderces rileyi* is not congeneric with *P. argyrogrammos*, the type of the genus; therefore, *Sathrobrota* has been proposed for *P. rileyi* and a new species. On the basis of the male genitalia *Antequera* does not belong in the Cosmopterigidae; it appears to go with some of the heliodinids.

The types of all of the North American genera and specimens of all of our species with the exception of *Cosmopterix chalybaeella*, which I do not know, have been examined. Of *Anoncia orites* I have seen only a sketch of the genitalia of the type.

The larval habits of cosmopterigids are diverse. *Cosmopterix* larvae are leaf miners in plants of the Gramineae, Cyperaceae, Leguminosae, Convolvulaceae, and Urticaceae. The known larvae of *Eteobalea* are gall makers on *Trichostema* (Labiatae); the larva of *Limnaecia phragmitella* feeds on the seeds of *Typha* spp. (Typhaceae); the larva of *Triclonella pergandeella* draws the leaflets of *Desmodium* or *Clitoria* (Leguminosae) together and feeds on the upper surface of the leaf; the known larvae of *Anoncia* are leaf miners on *Lantanum* (Verbenaceae) and *Sphacele* (Labiatae); and the larvae of *Sathrobrota* are scavengers of plant materials.

Key to the Genera of Cosmopterigidae

1\. Labial palpi evenly curved 2
   Labial palpi angulate between second and third segments 4
2\. Labial palpi long, reaching well beyond vertex .... *Triclonella*
   Labial palpi short, not reaching beyond vertex 3
3\. Veins 3 and 4 of hindwing approximate or connate .... *Anoncia*
   Veins 3 and 4 of hindwing distant .... *Teladoma*
4\. Third segment of labial palpi rough-scaled .... *Melanocinclis*
   Third segment of labial palpi smooth-scaled 5
5\. Veins 2 and 3 of forewings approximate .... *Sathrobrota*
   Veins 2 and 3 of forewings not approximate 6
6\. Tongue short; second segment of labial palpi tufted ventrally .... *Eteobalea*
   Tongue moderate; second segment of labial palpi not tufted (in North American forms) 7
7\. Cell in hindwing closed .... *Limnaecia*
   Cell in hindwing open 8
8\. Veins 1–4 of hindwing developed .... *Tanygona, Cosmopterix*
   Veins 1–4 of hindwing evanescent .... *Eralea*

Key to the Genera of Cosmopterigidae based primarily on the Male Genitalia

1\. Eighth sternite forming two lobes 2
   Eighth sternite not forming two lobes, modified into rods, or with sclerotized patches 8
2\. Costae symmetrical 3
   Costae asymmetrical 6
3\. Costae free 4
   Costae partially fused to aedeagus 5
4\. Apex of left brachium more heavily sclerotized than base .... *Cosmopterix*
   Apex of left brachium not more heavily sclerotized than base .... *Eralea*
5\. Apices of brachia slender (Fig. 57) .... *Melanocinclis*
   Apices of brachia tapering more rapidly to apex, broader (Fig. 49) .... *Tanygona*
6\. Apex of left brachium blunt, heavily sclerotized .... *Eteobalea*
   Apex of left brachium acute 7
7\. Valvae linear .... *Sathrobrota*
   Valvae broad .... *Limnaecia*

8. Brachia fused distally .... *Teladoma*
   Brachia not fused distally 9
9. Brachia subequal in length .... *Triclonella*
   Right brachium reduced, much shorter than left brachium
   .... *Anoncia*

Cosmopterix Huebner
(Figs. 7, 17, 21, 87)

Cosmopterix Huebner, [1826]. Verzeichniss bekannter Schmettlinge (*sic*), 424.

Type: *Tinea angustipennella* Huebner, [1796]. Designated by Desmarest, *in* Chenu, Encyclopédie d'Histoire Naturelle. Papillons Nocturnes, 299, 1857.

Type: *Tinea zieglerella* Huebner, [1805–1810]. Designated by Walsingham, Biologia Centrali-Americana. Insecta. Lepidoptera-Heterocera, 4: 4, 1909.

Acceptance of the first type designation above would create confusion in a group which has been nomenclatorially stable for more than 100 years. This can be exemplified by the fact that Zeller, Snellen, Wocke, Clemens, Stainton, Walsingham, Durrant, Meyrick, Fletcher, Lower, Turner, Busck, Braun, and Bradley have described more than 130 species of *Cosmopterix* as defined by Walsingham. Therefore, I am drafting an appeal to the International Commission on Zoological Nomenclature requesting a *nomen conservandum* for *Cosmopterix* Huebner with *Tinea zieglerella* Huebner as type.

If one accepts the first type designation, then the following changes in our association of names with entities would have to be made: 1. *Cosmopterix* Huebner (= *Stathmopoda* Herrich-Schaeffer). This synonymy removes the name *Cosmopterix* from the Cosmopterigidae to the Heliodinidae. 2. Proposal of a new generic name for *Tinea zieglerella* Huebner. 3. Proposal of a new name for the group defined as the Cosmopterigidae in this paper. The better course would be to follow Walsingham's traditional type designation, which does not lead to confusion, in preference to Desmarest's type designation, which would result in a shift in concepts with concomitant confusion in the literature.

A second problem involves the identity of *Tinea zieglerella*. Earlier workers have associated *zieglerella* with *Gracillaria eximia* Haworth. However, instead of making *eximia* the junior synonym as it should be by reason of publication date (*zieglerella*, [1805–

1810]; *eximia*, [1828]), *eximia* has been treated as the senior synonym. It appears that early authors were more interested in having a name, *eximia*, which was connected with an organism than in having one, *zieglerella*, which was a *nomen inquirendum*. After careful study of the group, I affirm the association of the name *zieglerella* with the species which has been known as *eximia*, and I confirm the synonymy *zieglerella* Hubner (= *eximia* Haworth).

Cosmopteryx, Zeller, 1839. Isis von Oken, 32: 210. (Emendation). Duponchel, 1845. Catalogue Méthodique des Lépidoptères d'Europe, 373. Stainton, 1854. Insecta Britannica. Lepidoptera: Tineina, 228, pl. 7, ff. 4a-h. Frey, 1856. Die Tineen und Pterophoren der Schweiz, 257. Stainton, 1870. Natural History of the Tineina, 12: 2–9. Wocke, *in* Heinemann, 1877 [1876]. Die Schmetterlinge Deutschlands und der Schweiz, 2: 521. Snellen, 1882. Vlinders van Nederland, Microlepidoptera, 2: 867. Meyrick, 1895. Handbook of British Lepidoptera, 662. Meyrick, 1897. Proc. Linn. Soc. New South Wales, 22: 338. Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52: 534. Busck, 1906. Proc. U. S. Natl. Mus., 30: 707–713. Walsingham, 1909. Biologia Centrali-Americana. Insecta. Lepidoptera-Heterocera, 4: 4. Spuler, 1910. Schmetterlinge Europas, 2: 389, f. 152. Forbes, 1923. Lepidoptera of New York and neighboring states, Cornell Univ. Agric. Exp. Sta. Mem., 68: 331, f. 185. Busck, 1932. Proc. Ent. Soc. Washington, 34: 17, pl. 3, f. 1. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 63.

Cosmopterix, Fletcher, 1928. Catalogue of Indian insects, pt. 16: 1. Kuroko, 1960. Esakia, 1: 9, pl. 4, ff. 3, 5, and 6.

Head smooth-scaled; tongue scaled, well developed; maxillary palpi folded over base of tongue; labial palpi recurved, not reaching vertex, smooth, third segment slightly longer than second; antennae nearly one, simple, pecten usually present, scape long and enlarged distally. Upper surface of metathoracic tibiae usually with flat lying scales, some species with scale tufts preceding the white streaks.

Forewings elongate lanceolate, apex acuminate; 12 veins present; 1b furcate basally; 2 from three-fourths on cell; 2, 3, 4, and 5 parallel; 5 approximate or connate with 6, 7, and 8; 6, 7, and 8 stalked; 11 from three-fifths on cell. Hindwings linear, a tuft of scales on costal margin; 6 or 7 veins present; 1 weak or absent, 5 absent; 2, 3, and 4 equidistant, parallel; 6 and 7 stalked, 6 from

7 at three-fourths of wing.

Male genitalia: *valvae* lobate, arising ventrolaterally, symmetrical (asymmetrical in *C. victor*); *costae* free, connected to *anellus* and to base of *valvae; aedeagus* heavily sclerotized with a basal process and two flanges near line of juncture of basal process; *anellus* heavily sclerotized; *tegumen* narrow; *uncus* and *socii* absent; *brachia* separate, asymmetrical, left *brachium* heavily sclerotized distally, right *brachium* short, lightly sclerotized.

Female genitalia: *bursa copulatrix* membranous; two small sclerotized patches on *ductus bursae* before juncture with *corpus bursae* in several species; two *signa* usually present, sometimes absent or single; *lamellae vaginales* heavily sclerotized; *lamella antevaginalis* usually snowshoe-shaped, occasionally tubular; eighth tergite usually membranous.

Species of *Cosmopterix* occur on all the continents with the exception of Antarctica; however, they are most numerous in the subtropics and tropics. Most of the known species have a restricted distribution, but one species, *C. attenuatella* Wlk., occurs in the southern United States, the Antilles, the Canaries, Africa, India, and Australia.

McDunnough (1939) lists seventeen species and three synonyms for the North American fauna. Of these *C. lespedezae* and *C. floridanella,* among the synonyms, are good species; and *C. nigrapunctella* is a synonym of *floridanella*. *C. unicolorella* is a synonym of *C. montisella,* and *C. hermodora* is a synonym of *C. clemensella.* I have seen no specimens of *C. chalybaeella*; however, Mr. Bradley (*in litt.*) has confirmed that it was not *C. gracilens* or *montisella* with which I had associated the name. This does not preclude the possibility that *chalybaeella* may equal one of the described species, but it seems as though the better course is to treat it as a separate species. Twelve new species are described in the present paper, bringing the number of known species of *Cosmopterix* for our fauna to twenty-eight.

KEY TO THE SPECIES OF COSMOPTERIX BASED UPON THE MACULATION

1. Basal lines of forewings very broad, confluent 2
   Basal lines of forewings narrow, separate 3
2. Apical 2 segments of antennae white, 7 bronze, 1 white ... *nitens*
   Apical 4 segments of antennae white, 5 leaden, 5 white .... *molybdina*
3. Thorax without lateral white or silver-blue lines 4
   Thorax with lateral white lines 9

4. Forewings with subdorsal basal line ..... *bendidia*
Forewings without a subdorsal basal line 5
5. Thorax without white markings dorsally; forewings with basal silver-blue lines short and broad, dorsomedial line basad of costomedial one ..... *clandestinella*
Thorax with white markings; forewings with basal silver-blue lines narrow, costomedial line basad of dorsomedial one 6
6. Costomedial line from base almost to fascia ..... *opulenta*
Costomedial line short 7
7. Apex of antennae white; outer silver spots bounding fascia separate, costal spot offset apically 8
Apex of antennae brown; outer silver spots bounding fascia fused, not offset; dorsal surface of abdomen dark purplish ..... *pulchrimella*
8. Apical 8 segments of antennae white, remainder brown ..... *bacata*
Apical 3 segments of antennae white, 5 brown, 4 white, then brown ..... *gemmiferella*
9. Costomedial line from base of forewings 10
Costomedial line not from base of forewings 14
10. Fascia surrounding basal silver spots, extending basally to one-third ..... *quadrilineella*
Fascia not surrounding basal silver spots, starting at one-half 11
11. Fascia extending between outer silver spots as a narrow line ..... *floridanella*
Fascia extending between outer silver spots broadly and becoming wider beyond them 12
12. Apical segment of antennae gray or partly gray, 3 white, 6 gray, 1 white (or gray) 13
Apical 4 segments of antennae white, 3 brown ..... *minutella*
13. Apex of last antennal segment gray, apical 2 segments white, 1 brown, 1 white ..... *dicacula*
Apical antennal segment gray, 3 white, 6 gray ..... *dapifera*
14. Forewings olive-gray or light brown 15
Forewings dark olive-brown or brown 17
15. Apical 3 or 4 segments of antennae white, 5 brown, 1 white 1 brown, 5 white ..... *facunda*
Apex of antennae gray-brown or brown 16
16. Costal cilia beyond fascia concolorous with base of wing ..... *delicatella*
Costal cilia beyond fascia buff, not concolorous with base of wing ..... *fernaldella, ebriola, scirpicola*

17\. Forewings with a tuft of white scales in cilia; a small patch of silver-blue scales on dorsal margin at midpoint between fascia and apex .... *montisella*
Forewings (beyond fascia) with a blue-white line on dorsal margin to apex (occasionally this line somewhat incomplete) 18
18\. Apex of antennae brown 19
Apex of antennae white 21
19\. Apical segment of antennae partly brown .... *magophila*
Apical 2 segments of antennae brown 20
20\. Apical 2 segments of antennae brown, 2 white .... *attenuatella*
Apical 2-½ segments brown, 1-½ white .... *damnosa*
21\. Apical 3 or 4 segments of antennae white, 4 or 5 brown, 4 or 5 white, then brown .... *clemensella*
Antennal pattern different, usually second white area interrupted by a brown segment 22
22\. Costomedial line longer than dorsomedial line 24
Costomedial line shorter than dorsomedial line, or equal to it 23
23\. A white line on dorsal surface of metathoracic tarsi (2nd through 5th segments) .... *lespedezae*
Without a white line on dorsal surface of metathoracic tarsi .... *abdita*
24\. Outer silver-white spots bordered by black basally .... *inopis*
No black scales bordering outer silver-white spots .... *gracilens*

Key to the Species of Cosmopterix based upon the Male Genitalia

1\. Aedeagus linear (Fig. 26) .... *attenuatella*
Aedeagus sublinear or rounded 2
2\. Aedeagus sublinear; basal projection cylindrical, not expanded basally 3
Aedeagus with distinct swelling at some point; basal projection expanded basally 5
3\. Subcostal margin of valvae concave upward (in distal half), rising apically (Fig. 25) .... *bendidia*
Subcostal margin of valvae not concave upward in outer half 4
4\. Apex of left brachium curved (Fig. 23) .... *molybdina*
Apex of left brachium blunt (Fig. 24) .... *pulchrimella*

5. Apical area of costae expanded, edge blunt (Fig. 28) .... *clandestinella*
Apical area of costae not expanded, edge curved 6
6. Apex of left brachium elliptical, slightly expanded .. *lespedezae*
Apex of left brachium not elliptical, expanded or not expanded 7
7. Left brachium strongly expanded at some point 10
Left brachium linear, not strongly expanded 8
8. A distinct shoulder on costal projection (Fig. 38) .... *quadrilineella*
Without a distinct shoulder on costal projection (Fig. 37) ... 9
9. Left brachium broad at apex (Fig. 37) .... *opulenta*
Left brachium narrow at apex (Fig. 42) .... *bacata*
10. Apical half of left brachium offset in middle of heavily sclerotized portion (Fig. 36) .... *abdita*
Apical half of left brachium not offset in middle of heavily sclerotized area 11
11. Left brachium with a constriction immediately before apex (Fig. 39) 12
Left brachium without a constriction immediately before apex 15
12. Valvae quadrate distally (Fig. 39) .... *inopis*
Valvae rounded distally (Fig. 22) 13
13. Left brachium expanded before middle (Fig. 22) 14
Left brachium expanded at two-thirds (Fig. 30) .... *gracilens*
14. Apex of aedeagus one-half maximum width of aedeagus (Fig. 22) .... *nitens*
Apex of aedeagus one-fourth maximum width of aedeagus (Fig. 41) .... *gemmiferella*
15. Distal portion of aedeagus widest at base, tapering to apex (Fig. 32) 16
Distal portion of aedeagus not widest at base 21
16. Subcostal margin of valvae deeply concave, outer margin moderately straight (Fig. 32) .... *dapifera*
Subcostal margin of valvae not deeply concave, outer margin curved 17
17. Apical half of left brachium enlarged, apex blunt (Fig. 47) .... *floridanella*
Apical one-fourth to one-third of left brachium enlarged 18
18. Apex of left brachium blunt 19
Apex of left brachium pointed 20
19. Expansion of left brachium gradual (Fig. 33) .... *delicatella*
Expansion of left brachium abrupt (Fig. 34) .... *dicacula*

20\. Costal projection expanding gradually to widest point .... *magophila*
Costal projection expanding abruptly to widest point (Fig. 27) .... *montisella*
21\. Apex of left brachium blunt, slightly upturned dorsally (Fig. 31) .... *minutella*
Apex of left brachium tapering to apex 22
22\. A shoulder or slightly produced area at two-thirds on dorsal margin of costae (Figs. 40, 43) .... *clemensella, damnosa*
Dorsal margin of costae without a distinct angle (Figs. 45, 46) 23
23\. Apical one-half of left brachium tapering, convex up, to apex (Fig. 45) .... *fernaldella*
Apical one-half (or one-half to one-fourth) of left brachium tapering, concave up, to apex (Fig. 46) 24
24\. Dorsal expansion of left brachium with a sharp angle, tapering abruptly to apex (Fig. 46) .... *ebriola*
Dorsal expansion of left brachium without a sharp angle, tapering more gradually to apex (Fig. 44) .... *scirpicola*

Key to Species of Cosmopterix based upon the Female Genitalia

1\. Signum present 2
Signum absent .... *attenuatella*
2\. Base of lamella antevaginalis bifurcate (Fig. 96) .... *lespedezae*
Base of lamella antevaginalis rounded or truncate 3
3\. Ductus bursae with a small sclerotized area near juncture with corpus bursae (Fig. 102) 4
Ductus bursae without a small sclerotized area near juncture with corpus bursae 14
4\. Two signa 5
One signum .... *opulenta*
5\. Basal portion of lamella antevaginalis narrow, sharply constricted from distal portion 6
Basal portion of lamella antevaginalis broad, if narrow, gradually tapering 11
6\. Posterior edge of seventh sternite emarginate 7
Posterior edge of seventh sternite not emarginate .... *dapifera*
7\. Medial area of emargination produced, truncated (Fig. 102) .... *floridanella*
Medial area of emargination not produced, or, if so with a curved margin 8

8. Apophyses anteriores shorter than lamella antevaginalis 9
   Apophyses anteriores longer than lamella antevaginalis (Fig. 105) ..... *scirpicola*
9. Signa subcircular (Fig. 100) ..... *ebriola*
   Signa elliptical (Fig. 99) 10
10. Linear portion of lamella antevaginalis one-fourth or less entire length of lamella; sclerotized area around signa well defined ..... *clemensella*
   Linear portion of lamella antevaginalis one-third or more entire length of lamella; sclerotized area around signa poorly defined distally ..... *fernaldella*
11. Lamella antevaginalis truncated or rounded basally (Fig. 94) 12
   Lamella antevaginalis tapering basally (Fig. 107) ..... *gemmiferella*
12. Posterior edge of seventh sternite emarginate 13
   Posterior edge of seventh sternite not emarginate ..... *facunda*
13. Length of lamella antevaginalis more than three times maximum width (Fig. 103) ..... *inopis*
   Length of lamella antevaginalis approximately twice that of maximum width (Fig. 94) ..... *quadrilineella*
14. Lamella antevaginalis subelliptical (Fig. 92) ..... *pulchrimella*
   Lamella antevaginalis linear or hamate (Figs. 93, 101) 15
15. Lamella antevaginalis linear (Fig. 89) 17
   Lamella antevaginalis not linear (Fig. 93) 16
16. Greatest width of lamella antevaginalis in distal half ..... *montisella*
   Greatest width of lamella antevaginalis in basal half ... *bendidia*
17. Posterior edge of seventh sternite with medial area produced (Fig. 95) 18
   Posterior edge of seventh sternite with medial area not produced (Fig. 88) ..... *nitens*
18. Medial area of posterior edge of seventh sternite strongly produced (Fig. 95) ..... *clandestinella*
   Medial area of posterior edge of seventh sternite slightly produced (Fig. 89) ..... *molybdina*

Cosmopterix nitens Walsingham
(Figs. 22, 88, 135)

Cosmopteryx nitens Walsingham, 1889. Ins. Life, 1: 289. Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull.

U. S. Natl. Mus., 52: 535. Busck, 1906. Proc. U. S. Natl. Mus., 30: 712. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 63.

Tongue shining silver-yellow. Labial palpi bronze colored, paler basally and on inner surface of second segment. Antennae bronze colored; pecten present; ventral surface of scape white; apical two segments white, preceded by seven bronze, one white, then bronze colored segments. Forewings bronze colored basally and apically; an oblique, transverse silver-blue fascia at one-fourth, a transverse silver-blue fascia slightly beyond one-half, and another such fascia at three quarters; between outer bluish fasciae a straw colored one interrupted by a black dash near costal margin; a row of silver-blue scales along outer margin to apex of cilia; slightly paler than basal area. Hindwings dark fuscous-brown. Legs bronze colored; metathoracic tibiae with a dorsal white line from base to one-fourth; a white annulation at middle and at apex; first, second, and third tarsal segments tipped with white; fourth and fifth tarsal segments white.

Male genitalia: (Fig. 22) R.W.H. slide no. 949.

Female genitalia: (Fig. 88) R.W.H. slide no. 402.

Alar expanse: 8–10 mm.

Food plant: unknown.

Type: British Museum (Natural History).

Type locality: Southwest Texas.

Specimens examined: 5 ♂, 9 ♀. Alabama: Theodore, 2 ♀, June 12, 1917 [CU]; Leroy, 1 ♀, June 11, 1917 [CU]. Texas: no locality, 4 ♂, 6 ♀ [AMNH, USNM]; no locality, 1 ♀, March 2, 1886 [BMNH].

C. nitens can be separated from *C. molybdina* by the difference in color, bronze of *nitens* and leaden of *molybdina*, and by the two apical segments of the antennae being white. The male and female genitalic characters are given in the keys.

Cosmopterix molybdina, new species

(Figs. 28, 89, 136)

Head, thorax, forewings, abdomen, and legs shining lead colored. Labial palpi lighter (gray) basally. Antennae with pecten absent; apical four segments white, preceded by five lead colored, five white, then lead colored segments. Forewings not as shining as other surfaces; a broad bluish-silver fascia at one-fourth, one at one-half, and an oblique one at three-fourths; area between outer fasciae concolorous with wing or bright yellow-orange; a few white scales in cilia at apex. Hindwings dark fuscous. Legs unicolorous except for metathoracic tibiae having a white annulation at middle and apex.

Male genitalia: (Fig. 23) R.W.H. slide no. 845.

Female genitalia: (Fig. 89) R.W.H. slide no. 846.

Alar expanse: 9–10 mm.

Food plant: unknown.

HOLOTYPE: ♂, Bar Harbor, MAINE, July 13, 1936 (A. E. Brower), [CU Type No. 3815].

PARATYPES: 1♂, 6♀, same data as type with dates June 30, 1936, July 10 and 15, 1938 [AEB, MOG, RWH].

Other specimens examined: Berkeley Hills, back of U. of California, CALIFORNIA, 1♂, April 17, 1959 (C. W. O'Brien), [UCB].[1]

C. molybdina can be separated from *C. nitens* by the coloration: *molybdina* is leaden; *nitens* is bronze. The male genitalia can not be consistently separated from those of *C. pulchrimella*; however, the maculation of the insects is so different that there should be no cause for confusion.

Cosmopterix pulchrimella Chambers

(Figs. 24, 92, 137)

Cosmopteryx pulchrimella Chambers, 1875. Cincinnati Quart. Jour. Sci., 2: 231. Forbes, 1923. Lepidoptera of New York and neighboring states, Cornell Univ. Agric. Exp. Sta. Mem., 68: 332.

Cosmopteryx pulcherrimella Chambers, 1878. Bull. U. S. Geol. Geog. Surv. Terr., 4: 137. Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52: 535. Busck, 1906. Proc. U. S. Natl. Mus., 30: 709. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 63.

Tongue olive-buff, slightly darker at tip. Maxillary palpi silver-gray-green. Labial palpi olive-brown with white lines: one on ventral, inner, and outer surfaces of second segment; one on

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[1] This specimen agrees with the type series in nearly all aspects, and, if it had been collected in eastern North America, or, if the species were known by examples collected from localities between Maine and California, then I would have made it a paratype.

anterior and posterior surfaces of third segment. Antennae olive-brown; pecten present; ventral surface of scape white; scape with an anterior white line continued on shaft as a series of dots to one-half; apical two segments brown, preceded by two white, five brown, one white, one brown, then two or three white segments. Face silver-gray, vertex olive-brown with a white line above each eye. Thorax olive-brown, a medial white line sometimes present, width variable. Forewings dark olive-brown basally and distally; three blue-white lines in basal area; a bright orange to orange-brown fascia at one-half, bordered internally and externally by a silver-blue fascia; a white streak on costa beyond orange-brown fascia and another at apex of wing; a blue-white spot in middle of outer margin. Hindwings fuscous-brown, cilia lighter shade of same color. Abdomen brown dorsally, silver-blue-white laterally and ventrally, eighth segment brown. Legs dark olive-brown; metathoracic tibiae with blue-white at middle and apex; apices of first four tarsal segments blue-white; fifth tarsal segment blue-white.

Male genitalia: (Fig. 24) R.W.H. slide no. 546.

Female genitalia: (Fig. 92) R.W.H. slide no. 850.

Alar expanse: 7–8 mm.

Food plant: *Parietaria pennsylvanica* Muhl. and *Pilea pumila* (L.). Busck (1906) gives the following discussion of the larva (in turn the notes originated with Miss Murtfeldt): "Feeds on rickweed (*sic*) (*Pilea pumila*), a succulent little plant of the nettle family, with adhesive, but not urticating leaves; mining, twisting, and crumpling them.

"Larva yellowish white, subcylindrical.

"Head shining black, with the diversions defined by narrow white lines. Cervical shield broad, oblong, with fine white central line. The sutures are very deep, giving the larva a moniliform aspect.

"These larvae are not confined to one mine, but may be seen wandering over the leaves and stems, cutting in between the two cuticles of a leaf and covering it with transparent spots of various sizes. They change to pupa under a fold of the leaf or between the wrinkles or not infrequently on the surface of the ground, protected by a very slight dingy cocoon. There seems to be several broods in a season."

Type: Museum of Comparative Zoology.

Type locality: Covington, Kentucky.

Specimens examined: 90 ♂, 20 ♀. ARIZONA: Madera Canyon, 5,600 feet, Santa Rita Mountains, Santa Cruz Co., 4 ♂, 2 ♀, September 12, 1959 (R. W. Hodges), [CU, RWH]. FLORIDA: Siesta Key, Sarasota Co., 27 ♂, 4 ♀, January 28 through October 24 (C. P. Kimball), [CPK, RWH]; Homestead, 1 ♂, April 15, 1959 (D. O. Wolfenbarger), [CPK]. Georgia: Clarke Co., 5 ♂, April 5, 1924 (Richards), [ABK]. Illinois: Putnam Co., 12 ♂, 3 ♀, April 24 through September 5 (M. O. Glenn), [MOG]; Arlington Hts., 1 ♂, August 12, 1949 (A. L. McElhose), [CNHM]. Kansas: Onaga, 1 ♂?, "8/5 02" [MCZ]. Kentucky: L. Sandy R., Ellicott Co., 1 ♂, May 3, 1936 (Annette F. Braun), [AFB]. Minnesota: no locality, 1 ♂, August 15, 1903 [CU]. Missouri: Kirkwood, 4 ♂, 1 ♀, June 1 through July 29 (Murtfeldt), [CU]; no locality, 3 ♂, July 13 and 19 [USNM]; Columbia, 2 ♂ [AMNH]. New York: Monroe Co. 4 ♂, July 30 through August 13, 1949 (C. P. Kimball), [CPK]; Pelham, Westchester Co., 1 ♂, 2 ♀, July 23–27, 1954 (A. B. Klots), [ABK]; Rochester, 1 ♀, July 20, 1933 (A. B. Klots), [ABK]; Ithaca, Tompkins Co., 5 ♂, 1 ♀, May 19–27, 1931 (A. B. Klots), [ABK]; Ithaca, Six Mile Creek, Tompkins Co., 1 ♂, May 21, 1959 (R. W. Hodges), [RWH]. North Carolina: Highlands, Macon Co., 1 ♂, July 18, 1958 (R. W. Hodges), [RWH]; Maxton, 1 ♂, April 23, 1944 (A. B. Klots), [ABK]; no locality, 2 ♂ (Morrison), [USNM]. Ohio: Cincinnati, 4 ♂, May 12 through September 21 (Annette F. Braun), [AFB, USNM]; 9 ♂, 5 ♀, under rearing record B. 744, emerged from June 18 through August 15 (Annette F. Braun), [AFB, RWH].

C. pulchrimella can be separated from *C. clandestinella* by the presence of a medial white line and by the basal lines in the forewings being narrow as contrasted with short and broad ones in *clandestinella*. The apex of the left brachium being blunt in the male genitalia usually serves to separate *pulchrimella* from *C. molybdina*. In the female genitalia *pulchrimella* has a subelliptical lamella antevaginals, whereas those of *molybdina* and *clandestinella* are linear.

Cosmopterix bendidia, new species

(Figs. 25, 93, 138)

Tongue shining pale yellow. Labial palpi white; second segment with three olive-brown lines: one internal, one external, and one dorsal; third segment with an internal and an external brown line. Face shining dark ochreous with purple reflections; vertex dark olive-brown with a white line above each eye. Antennae with pecten present; dark brown; scape white on ventral surface and with an anterior white line, continued on shaft to one-half; segments 1–4, 10, and 12–14 (some specimens 12 or 12–13) white, others brown. Thorax dark olive-brown with tip of mesothorax silver-blue. Forewings dark olive-brown basally and apically; a bright yellow fascia at one-half; six silver-blue lines in basal area: one along costa from base to one-fourth tending dorsally, another slightly in from costa at one-third, a medial one costad of fold at one-fourth, a medial one dorsad of fold at one-third, a short one from base near dorsal margin, and one on dorsal margin from one-seventh to one-third; a narrow silver fascia bordering yellow fascia basally and two silver spots bordering fascia externally; a path of white scales in cilia costad of outer subcostal silver spot; a silver-blue line along dorsal margin to apex, starting beyond dorsal silver spot. Hindwings dark fuscous-brown. Abdomen dark brown dorsally, shining buff and silver ventrally. Legs shining buff basally, dark olive-brown distally; metathoracic tibiae with three silver-blue annulations: one basal, one medial, and one apical; a row of long setae on posterior surface on inner medial tibial spur; apices of tarsal segments pale gray.

Male genitalia: (Fig. 25) R.W.H. slide no. 541.

Female genitalia: (Fig. 93) R.W.H. silde no. 849.

Alar expanse: 6–8 mm.

Food plant: *Ipomoea* spp.

Holotype: ♂, Madera Canyon, 4,880 feet, Santa Rita Mts., Santa Cruz Co., Arizona, August 18, 1959 (R. W. Hodges), [CU Type No. 3795].

Paratypes: same data as type with date range from July 11–September 7, 12 ♂, 1 ♀, [CU, RWH]; Paradise, Cochise Co., Arizona (no date or collector), [USNM]; Homestead, Flordia, 1 ♂ February 24, 1959 (D. O. Wolfenbarger), [CPK]; Clarke Co., Georgia, 1 ♂, May 1929 (A. G. Richards), [ABK]; Hyattsville, Maryland, 3 ♀, bred from morning glory, one issued February 18, 1910, two issued March 1910 (A. B. [usck]), [USNM]; Montclair, New Jersey, 1 ♂, September 5 (W. D. Kearfott), [USNM]; Cincinnati, Ohio, 6 ♂, 3 ♀, under rearing record B. 2074 (on *Ipomoea*), 1 ♂, 1 ♀, emerged October 18, 1943, 1 ♀, emerged April 1944, others from July 4–22, 1944 (Annette F. Braun), [AFB]; Kerryville (*sic*) [Kerrville], Texas, 1 ♂, May 06 (F. C. Pratt), [USNM].

Other specimens examined: Oakland, New Jersey, 1 ♂, August 24, 1948 (C. P. Kimball), [CPK]; Monteagle, Tennessee, 1, June 21, 1930 (A. G. Richards), [CU].

C. bendidia can be distinguished from the other North American species of *Cosmopterix* by the presence of a subdorsal basal line on the forewings. No other species examined has this line.

Cosmopterix attenuatella Walker
(Figs. 26, 90, 139)

Gelechia attenuatella Walker, 1864. List of the specimens of the Lepidopterous insects in the collection of the British Museum, 30: 1019. Walsingham, 1891 [1892]. Proc Zool. Soc. London, 519, 545.

Cosmopteryx attenuatella, Walsingham, 1897. Proc. Zool. Soc. London, 105. Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52: 535. Busck, 1906. Proc. U. S. Natl. Mus., 30: 710. Walsingham 1907 [1908]. Proc. Zool. Soc. London, 265. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 63. Ghesquière, 1942. Annales du Musée du Congo Belge, C. Zoologie, Series 3 (2), Tome 7, Fascicle 1: 70.

‡ *Cosmopteryx lespediza* (*sic*) Dyar, 1901. Proc. Ent. Soc. Washington, 4: 478. (misidentification).

Cosmopteryx flavofasciata Wollaston, 1879. Ann. Mag. N. H., series 5, 3: 438. Staudinger and Rebel, 1901. Catalog Lepidopteren des Palaearctischen Faunengebietes, 2: 185.

Cosmopteryx mimetis Meyrick, 1897. Proc. Linn. Soc. New South Wales, 22: 339. Meyrick, 1909. Jour. Bombay Nat. Hist. Soc., 19: 417. Fletcher, 1921. Mem. Dept. Agric. India, Ent. Series, 6: 102.

Cosmopterix mimetis, Fletcher, 1928. Catalogue of Indian Insects, pt. 16: 4.

Cosmopteryx antillia Forbes, 1931. Jour. Dept. Agric. Porto Rico, 4: 356. **new synonymy.**

Tongue white to pale yellow. Labial palpi white; an internal and an external dark brown line on second and third segments; apex of third segment white. Antennae dark brown; pecten present, scape with ventral surface and an anterior line white; anterior white line continued on shaft as a series of dots to three-fifths; apical two segments brown, preceded by two white, five brown, one white, one brown, one white, then by brown segments. Face shining buff-gray, becoming darker dorsally; vertex dark olive-brown with three white lines, one above each eye and one medial. Thorax dark olive-brown with continuation of white lines on vertex. Forewings dark olive-brown basally and distally; five white lines on basal half; a yellow to yellow-brown fascia at one-half bordered internally by a silver fascia, externally by two silver spots, one subcostal and one subdorsal; a few black scales following silver fascia below costa; a white streak in costal cilia from outer costal spot; a white line along dorsal margin of wing from three-fourths to apex of cilia, interrupted in some specimens; cilia paler than base of wing. Hindwings gray. Abdomen shining gray dorsally with orange scales on medial area of several tergites; shining pale buff ventrally; last segment buff. Legs shining gray basally, brown distally; metathoracic tibiae with an oblique white line from base and one at two-thirds, apex white; tarsal segments shining gray on dorsal surface of segments one, two, three, and five, apices brown; a dorsal white line on prothoracic tibiae and segments one, two, three, and five of tarsi.

Male genitalia: (Fig. 26) R.W.H. slide no. 484.

Female genitalia: (Fig. 90) R.W.H. slide no. 926.

Alar expanse: 6½–8 mm.

Food plant: *Scirpus* sp.

Type: British Muséum (Natural History).

Type locality: Jamaica.

Specimens examined: 79 ♂, 6 ♀.

FLORIDA: Archbold Biological Station, Highlands Co., 4 ♂, 1 ♀, March 29–April 2, 1959 (R. W. Hodges), [RWH]; same locality, 1 ♂, January 8, 1960 (S. W. Frost), [SWF]; Hastings, 1 ♂, "19C" [MCZ]; Homestead, 10 ♂, 2 ♀, February 8–November 13, 1958 and 59 (D. O. Wolfenbarger), [CPK, RWH]; Chokoloskee, 1 ♂ [USNM]; Orlando, 7 ♂, February–April (G. G. Ainslie), [USNM]; Orlando, 1 ♂, August 17, 1945 (A. B. Klots), [ABK]; Royal Palm Park, 1 ♂, April 10, 1938 (F. E. Watson and L. J. Sanford), [AMNH]; Sarasota, 1 ♂, February 17, 1946 (Needham), [CU]; Siesta Key, Sarasota Co., 49 ♂, 3 ♀, dates in March, April, November, and December (C. P. Kimball), [CPK, RWH]; Winter Park, 1 ♂, July 27, 1933 (H. T. Fernald), [USNM]. TEXAS: Mercedes, 1 ♂, "1–7 1956" (Paul T. Riherd), [USNM].

See discussion under *C. lespedezae* concerning the synonymy of the two species.

C. attenuatella can be separated from *C. damnosa* by the characters given in the keys. The male genitalia with the linear aedeagus is distinct from the other species of North American *Cosmopterix*.

Cosmopterix clandestinella Busck
(Figs. 28, 95, 140)

Cosmopteryx clandestinella Busck, 1906. Proc. U. S. Natl. Mus., 30: 712. Barnes and McDunnough, 1917. Check list of the Lepidoptera of Boreal America, 152. Forbes, 1923. Lepidoptera of New York and neighboring states, Cornell Univ. Agric. Exp. Sta. Mem., 68: 333. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 63.

Tongue shining yellow-white. Labial palpi: second segment buff with a dorsal brown line; third segment brown with a broad, white dorsal line. Face pale silver-yellow with purple reflections; vertex olive-brown with a blue-white line above each eye. Antennae with pecten present; dark brown; scape white ventrally and with an anterior white line continued on shaft as a series of dots to three-fifths; ventral surface of shaft white to one-half; apical three segments white, preceded by five brown, three white, then brown segments (in some specimens apical four white, preceded by four brown, three white). Thorax dark olive-brown, no silver-blue markings, anterior surface of patagia with purple reflections. Forewings dark olive-brown basally and distally; three short, broad silver-blue lines in basal area, costal one narrower than medial ones; a yellow-orange fascia at one-half, bordered internally and externally by a series of black scales; a silver-blue fascia basad of yellow-orange fascia; beyond yellow-orange fascia a silver-blue spot extending from dorsal margin to middle of wing; a silver-blue spot offset apically from dorsal one below costal margin with a white streak extending from it into costal cilia; apical cilia white; a few silver-blue scales along dorsal margin in apical fourth. Hindwings dark fuscous. Abdomen shining dark ochreous dorsally, olive-brown laterally, shining white ventrally; last segment brown. Legs shining buff with purple reflections basally; dark olive-brown distally; metathoracic tibiae with three dorsal tufts of scales: one at one-third, two thirds, and apex; each tuft preceded by silver-blue scales; apex white to buff; penultimate and ultimate tarsal segments shining white.

Male genitalia: (Fig. 28) R.W.H. slide no. 400.

Female genitalia: (Fig. 95) A. Busck slide.

Alar expanse: 7–8 mm.

Food plant: *Panicum clandestinum* L. Busck (1906) gives the following description of the mine and larva: "The mine is an irregular longitudinal clear blotchmine with the frass ejected at one end. The larva is light green with short light hairs and with yellow head and thoracic shield. At maturity it assumes a brilliant wine-red color in three broad longitudinal stripes, and cuts a circular piece off of the epidermis of its mine, which it bends lengthwise and uses for a cocoon exactly like the genus *Cycloplasis* Clemens."

Type: United States National Museum.

Type locality: Washington, D. C.

Specimens examined: 23 ♂, 21 ♀. KENTUCKY: Powell Co., 1 ♂, 1 ♀, under rearing record B. 927, emerged May 28 and June 9, 1917 (Annette F. Braun), [AFB, USNM]; Natural Bridge, McCreary Co., 1 ♂, October 10, 1950 on *Panicum*, issued May 10, 1951 (Annette F. Braun), [AFB]. MARYLAND: Washington D. C., 6 ♂, 10 ♀, Busck rearing, emerged July 20, 1899, August 10, 1902, August 12, 1919, and July 1928 (August Busck), [USNM]; Hyattsville, 1 ♂, 4 ♀, Busck rearing, emerged August 1906 and August 9–11, 1913 [USNM]; Plummer's Id., 1 ♂, 1 ♀, June 3, 1914 (R. C. Shannon), [USNM]. MASSACHUSETTS: Woods Hole, 1 ♂, July 18, 1919 [CU]. NEW JERSEY: Caldwell, 1 ♂, 1 ♀, July 8, 1900 (W. D. Kearfott), [USNM]; Essex Co. Park, 1 ♂, June 22 (W. D. Kearfott) [USNM]. NORTH CAROLINA: Balsam, 2 ♂, July 14 and 22, 1911 (Annette F. Braun), [AFB]. OHIO: Clermont Co., 1 ♂, May 31, 1917 (Annette F. Braun), [USNM]; Cincinnatti, 1 ♂, 1 ♀, under rearing record B. 486, emerged August 2, 1909 (Annette F. Braun), [RWH]; same locality, 2 ♂, on *Panicum*, emerged May 29 and July 31, 1917 (Annette F. Braun), [USNM]; same locality, 1 ♂, June 7, 1908 (Annette F. Braun), [USNM]; same locality, 1 ♂, under rearing record B. 498, emerged August 3, 1909 (Annette F. Braun), [AFB]; same locality, 1 ♂, August 1, 1903 (Annette F. Braun), [USNM]; same locality, 1 ♀, under rearing record B. 486, emerged August 16, 1913 (Annette F. Braun), [USNM]; Conkle's Hol., Hocking Co., 1 ♂, on *Panicum clandestinum*, emerged April 2, 1944 (Annette F. Braun), [AFB]; Scioto Co., 1 ♀, on *Panicum*, emerged July 26, 1948 (Annette F. Braun), [AFB]. VIRGINIA: Falls Church, 1 ♂, June 2, 1914 (Heinrich), [USNM].

This species is closest to *C. pulchrimella* but may be easily distinguished from it by the absence of white markings on the thorax and the presence of broad silver-blue lines in the basal area of the forewings.

Cosmopterix montisella Chambers
(Figs. 27, 101, 141)

Cosmopteryx montisella Chambers, 1875. Cincinnati Quart. Jour. Sci., 2: 297. Chambers, 1878. Bull. U.S. Geol. Geog. Surv. Terr., 4: 137. Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52: 535. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 63.

Cosmopteryx monticella (*sic*) Busck, 1906. Proc. U. S. Natl. Mus., 30: 712.

Cosmopteryx unicolorella Walsingham, 1889. Ins. Life, 1: 291. **new synonymy**. Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52: 535. Busck, 1906. Proc. U. S. Natl. Mus., 30: 710. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 63.

Tongue shining buff. Labial palpi brown; second segment with three white lines: one ventral, one internal, and one external; third segment with an anterior and a posterior white line. Antennae brown; pecten present; ventral surface of scape white; an anterior white line on scape, continued on shaft as a series of dots to one-half or farther; apical four segments: three brown, one white; or, two brown, two white; or, one-half brown, three-and-one-half white. Apical four segments preceded by five brown, one white, one brown, two white, then brown ones. Face olive-brown with purple reflections; vertex dark olive-brown with three white lines, one above each eye and one medial. Thorax dark olive-brown with continuation of three white lines on vertex. Forewings dark olive-brown basally and apically; four white lines in basal area; a yellow-orange fascia at one-half; a silver-gray fascia bordering it inwardly; outwardly, yellow-orange fascia bordered by two silver-gray spots, one dorsal and one subcostal; subcostal spot offset apically from dorsal one; a white costal streak above subcostal spot; a broad white streak at apex of wing; a few silver-blue scales on dorsal margin midway between apex and dorsal spot. Hindwings fuscous. Abdomen brown and buff dorsally, brown with apices of segments silver ventrally. Legs silver-gray with purple reflections basally, brown distally; metathoracic tibiae with a dorsal line from base to one-half; a white annulation at two-thirds and one at apex; apices of tarsal segments buff to white.

Male genitalia: (Fig. 27) R.W.H. slide no. 537.

Female genitalia: (Fig. 101) R.W.H. slide no. 538.

Alar expanse: 10–13 mm.

Food plant: unknown.

Type: *montisella,* Museum of Comparative Zoology; *unicolorella,* British Museum (Natural History).

Type locality: *montisella,* Spanish Bar, Colorado; *unicolorella,* Siskiyou Co., California.

Specimens examined: 32 ♂, 17 ♀. ARIZONA: Madera Canyon, 4,880 and 5,600 feet, Santa Rita Mountains, Santa Cruz Co., 9 ♂, 9 ♀, July 9 through September 29, 1959 (R. W. Hodges), [CU, RWH]; same data except 4,400 feet, Pima Co., 1 ♀, October 6, 1959 [RWH]; Santa Catalina Mountains, Pima Co., 1 ♂, August 1, 1938 (Bryant), [LACM]; Palmerlee, 1 ♂ [USNM]. CALIFORNIA: Mt. Shasta City, Siskiyou Co., 9 ♂, July 2–18, 1958 (J. Powell), [UCB, RWH]; Davis Creek, Modoc Co., 1 ♀, July 11, 1957 (J. Powell), [RWH]; Bear Creek, Shasta Co., 3 ♂, July 27–28, 1871 (Walsingham), [USNM, BMNH]; Mt. Shasta, Siskiyou Co., 1 ♂, August 2 through September 1, 1871 (Walsingham), [BMNH]; Hatchet Creek, Shasta Co., 1♂, July 14–17, 1871 (Walsingham), [BMNH]. COLORADO: Mesa Verde Natl. Park, 1 ♂, July 24, 1941 (A. B. Klots), [ABK]; Rocky Mountain Natl. Park, 2 ♂, July 15, 1937 (A. B. Klots), [ABK]. ILLINOIS: Arlington Hts., 1 ♀, September 18, 1940 (A. L. McElhose), [CNHM]; Putnam Co., 1 ♀, August 27, 1956 (M. O. Glenn), [MOG]. MICHIGAN: Livingston Co., 1 ♀, July 1, 1947 (J. Newman), [RWH]; Ecorse, Wayne Co., 2 ♀, September 4, 1951 and September 10, 1949 (Ralph Beebe), [AMNH, UM]. NEW MEXICO: Little Tesuque Canyon, vic. Santa Fe., 1 ♀, July 27 through August 10, 1932 (A. B. Klots), [ABK]. NEW YORK: Ithaca, Six Mile Creek, 1 ♂, June 6, 1957 (J. G. Franclemont), [JGF]; Ithaca, 1 ♂, 1 ♀, July 5, 1924 and September 1, 1919 (W.T.M.F.), [CU]. OREGON: Glide, 1 ♂, August 19, 1954 (D. R. Davis), [DRD]. PENNSYLVANIA: New Brighton, 1 ♂, June 28, 1907 (Merrick), [USNM].

C. montisella can be separated from *C. clemensella* by the patch of silver-blue scales on the outer margin of the forewing. The keys will identify the species by the male and female genitalia.

This species has a tendency toward melanism which is expressed by the replacement of the yellow-orange fascia by scales concolorous with the basal area of the forewing. The specimen from Mesa Verde National Park is a melanic. Walsingham's species, *unicolorella,* is based on a melanic specimen of *montisella.* Mr. J. D. Bradley has very kindly sent me photographs of the male genitalia of the type of *unicolorella,* and they agree very well with those of *montisella.*

There is a moderate amount of variation in this species both in alar expanse and coloration; however, the characters emphasized in the keys have been diagnostic for the specimens seen.

Cosmopterix magophila Meyrick
(Figs. 29, 142)

Cosmopteryx magophila Meyrick, 1919. Exot. Micr., 2: 282. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 63.

Tongue shining pale buff. Labial palpi white, second segment with some black scales dorsally and ventrally, third segment with a black line on inner surface and one on outer surface. Antennae dark brown; pecten present; ventral surface of scape and shaft white; a white line on anterior surface of scape; apical one-half segment of shaft brown, preceded by three-and-one-half white, five brown, one white, one brown, one or two white, then brown segments. Face pale buff-bronze; vertex dark olive-brown with three white lines, one above each eye and one medial. Thorax dark olive-brown with continuation of three white lines on vertex. Forewings dark olive-brown basally and apically; four white lines in basal area; a yellow fascia at one-half; fascia bordered inwardly by two pale gold spots, costal one based of dorsal one; costal spot followed by a small patch of black scales; outwardly, fascia bordered by two pale gold spots; a white streak in costal cilia from outer costal gold spot; a white line along outer margin to apex of cilia. Hindwings dark fuscous. Abdomen dark fuscous, anal segment pale buff. Legs buff basally, brown distally; metathoracic tibiae white at base, middle, and apex; outer tibial spurs white on outer surface; tarsi white ventrally and at apices of segments.

Male genitalia: (Fig. 29) R.W.H. slide no. 480.

Female genitalia: Unknown.

Alar expanse: 7–8 mm.

Food plant: unknown.

Type: British Museum (Natural History).

Type locality: Southern Pines, North Carolina.

Specimens examined: 4 ♂. North Carolina: Maxton, 2 ♂, May 11 and 16, 1944 (A. B. Klots), [ABK]; Southern Pines, 1 ♂, ".18" (P.), [USNM]; same locality, 1 ♂, August 8–15 [USNM].

C. magophila can be distinguished from *C. clemensella* and *C. damnosa* by the outer one-half of the apical segment of the shaft of the antennae being brown; *clemensella* has the apex of the antennae white, and *damnosa* has the apical two-and-one-half segments of the antennae brown. The male genitalia of *magophila* are closest to *C. montisella;* here, the gradual expansion of the costal projection to the widest point will separate it from *montisella.*

Cosmopterix gracilens, new species

(Figs. 30, 143)

Tongue shining buff-white. Labial palpi white with an internal and an external olive-brown line. Antennae dark olive-brown; pecten present; scape with ventral surface and an anterior line white; anterior white line continued on shaft to two-thirds; apical four segments white, preceded by five brown, one white, one brown, two white, three-and-one-half brown, then by a series of segments one-half white and one-half brown. Face shining buff-yellow with purple reflections; vertex dark olive-brown with three blue-white lines, one above each eye and one medial. Thorax dark olive-brown with continuation of three lines on vertex. Forewings dark olive-brown basally and distally; four blue-white lines on basal one-half, costomedial line longer than dorsomedial line; a lemon-yellow fascia at two-thirds, preceded by a silver fascia not reaching costal margin; outwardly, yellow fascia bordered by a subcostal and a dorsal silver spot; one or two black scales following silver fascia costomedially, and one or two black scales preceding dorsal silver spot; a white streak in costal cilia from yellow fascia; a blue-white line along outer margin of wing from end of yellow fascia to apex of cilia; cilia concolorous with base of wing. Hindwings dark gray-brown. Legs golden basally, dark olive-brown distally; metathoracic tibiae with a white streak from base to one-fourth, an oblique white streak from middle spur, apex white, outer surface of outer tibial spurs white; metathoracic tarsi with a white streak at base of first segment, apex buff, other segments missing on this specimen.

Male genitalia: (Fig. 30) R.W.H. slide no. 933.

Female genitalia: no specimens available.

Alar expanse: 10 mm.

Food plant: unknown.

HOLOTYPE: ♂, Palmerlee, ARIZONA [USNM Type No. 66079].

C. gracilens can be separated from *C. inopis* by the absence of an internal black border before the outer silver spots on the forewings. The male genitalia of *gracilens* can be separated from those of *inopis* by the rounded outer margins of the valvae; the valvae of *inopis* have the outer margins quadrate.

Cosmopterix dapifera, new species

(Figs. 32, 91, 144)

Tongue shining white. Labial palpi white with two dark olive-brown lines on second and third segments, one internal and one external. Antennae with pecten present; olive-brown; scape white ventrally and with an anterior white line continued on shaft to one-sixth; apical segment of shaft dark, preceded by three white, six olive-brown, one gray, then olive-brown ones. Face shining buff; vertex pale olive-brown with three blue-white lines, one above each eye and one medial. Thorax pale olive-brown with five blue-white lines: one on outer margin of patagia, one on inner margin of patagia, and one medial. Forewings olive-brown (fading to pale olive-brown) basally and apically; four blue-white lines in basal area; a bright yellow-orange fascia from one-half to three-fourths bounded inwardly by two silver spots, one on dorsal margin and one medial; a few orange-brown scales preceding silver spots; a dorsal and a costal silver spot present within apical portion of fascia; some black scales usually preceding outer silver spots and succeding medial silver spot; a white line along dorsal margin from end of fascia to apex of cilia. Hindwings concolorous with basal area of forewings. Abdomen shining dark yellow-brown with purple reflections dorsally, ochreous basally. Legs shining buff or white; metathoracic tibiae with a brown line from base to middle and another from middle to slightly before apex; metathoracic tarsi olive-brown laterally.

Male genitalia: (Fig. 32) R.W.H. slide no. 542.

Female genitalia: (Fig. 91) R.W.H. slide no. 543.

Alar expanse: 8–9 mm.

Food plant: unknown.

HOLOTYPE: ♂, Madera Canyon, 4,880 feet, Santa Rita Mountains, Santa Cruz Co., ARIZONA, August 29, 1959 (R. W. Hodges), [CU Type No. 3797].

PARATYPES: same locality as type, 2♂, 1♀, July 19 and 24, September 5, 1959 [CU, RWH]; Clarke Co., GEORGIA, 1♂, April 4, 1929 (A. G. Richards), [ABK]; Monteagle, TENNESSEE, 1♂, June 12, 1930 (A. G. Richards), [CU].

This species can be separated from *C. minutella* by the antennal markings: the apical segment of *dapifera* is gray; that of *minutella* is white.

Cosmopterix delicatella Walsingham
(Figs. 33, 145)

Cosmopteryx delicatella Walsingham, 1889. Ins. Life, 1:290. Riley, *in* Smith, 1891. List of the Lepidoptera of Boreal America, 107. Kearfott, *in* Smith, 1903. Check list of the Lepidoptera of Boreal America, 116. Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52:535. Busck, 1906. Proc. U. S. Natl. Mus., 30:711. McDunnough, 1939. Mem. S. California Acad. Sci., 2:63.

Tongue shining pale yellow. Labial palpi gray-white; second segment with three brown lines: one on inner surface, one on outer surface, and one on dorsal surface. Antennae olive-brown, pecten present; scape with ventral surface and an anterior line white; apical two segments of shaft brown, preceded by two white, five brown, one white, one brown, one white, then brown segments. Face shining olive-brown with purple reflections, yellow at base of tongue; vertex olive-brown with three white lines, one above each eye and one medial. Thorax concolorous with vertex; white lines of vertex continuing on thorax. Forewings gray-olive-brown basally and distally; four blue-white lines in basal area; a yellow fascia at one-half bordered internally by two silver-gray spots, one costomedial and one dorsal, costomedial spot basad of dorsal one; externally, fascia extending between a dorsal silver-gray spot and a costal white streak; a white line along dorsal margin from end of fascia to apex of cilia; dorsal cilia concolorous with basal area or slightly paler than basal area. Hindwings dark fuscous. Abdomen gray-brown dorsally, shining buff ventrally. Legs shining buff basally, brown distally; metathoracic tibiae with a dorsal white line from base to one-third; an oblique white line from ventral surface to dorsal surface, starting at one-half and terminating at two-thirds; apex white; dorsal surface and apices of metathoracic tarsal segments white.

Male genitalia: (Fig. 33) R.W.H. slide no. 902.

Female genitalia: no specimens available.

Alar expanse: 8–9 mm.

Food plant: unknown.

Type: British Museum (Natural History).

Type locality: North Carolina.

Specimens examined: 33 ♂. Florida: Archbold Biological Station, Highlands Co., 2 ♂, March 27 and 29, 1959 (R. W. Hodges), [RWH]. Maryland: Washington, D. C., 1 ♂, July (A. Busck), [USNM]. Massachusetts: Barnstable, 25 ♂, June 1 through July 2, 1950–1952 (C. P. Kimball), [CPK, RWH]. Mississippi: Biloxi, 1 ♂, June 13, 1917 [CU]. North Carolina: Southern Pines, 3 ♂, August 1–15 [USNM]; no specific locality, 1 ♂, 1883 (Morrison), [BMNH].

An examination of the type of *C. quadrilineella* and comparison with more material indicates that the difference in the number of metallic spots, cited by Walsingham (1889), is not valid. Chambers' specimens are worn, and the outer costal spot is not plainly indicated. In *quadrilineella* the costomedial line starts at the base of the forewing. It starts at a point distant from the base in *delicatella*.

Cosmopterix dicacula, new species

(Figs. 34, 146)

Tongue white. Labial palpi white, a pale brown line on outer surface of second and third segments. Antennae brown; pecten present; scape with ventral surface and an anterior line white; white line continued on shaft to one-half; apex of shaft gray, preceded by two white, one brown, one white, three brown, one white, one brown, one white, one brown, one white, then brown segments. Face shining buff; vertex pale brown with three white lines, one above each eye and one medial. Thorax brown with continuation of white lines on vertex. Forewings olive-brown basally; four white lines in basal area, costomedial one from base to fascia; a yellow fascia at two-thirds; internally, fascia bordered by a subdorsal and subcostal silver spot; externally, fascia bordered by a subdorsal and a subcostal silver spot; inner, subdorsal silver spot preceded by a few black scales; inner, subcostal silver spot succeeded by a few black scales; a white streak in costal cilia from outer silver spot; a white streak in dorsal cilia from outer silver spot; a white line along dorsal margin from fascia to apex of cilia; remainder of apical one-fourth pale gray-brown; dorsal cilia pale gray in apical area, yellow-white below fascia. Hindwings pale gray. Legs buff basally, olive-brown distally; metathoracic tibiae with an oblique white streak at base, one at one-half, and one at five-sixths, apex white; tarsi with a discontinuous, dorsal white line, apices of segments white.

Male genitalia: (Fig. 34) R.W.H. slide no. 101.

Female genitalia: no specimens available.

Alar expanse: 7½ mm.

Food plant: unknown.

HOLOTYPE: ♂, Gainesville, FLORIDA, July 7, 1927, trap light (J. Speed Rogers), [CU Type No. 3800].

C. dicacula can be distinguished from *C. dapifera* by the antennae as stated in the key. In the male genitalia of *dicacula* the outer margin of the valvae is rounded, that of *dapifera* is relatively straight; the apex of the left brachium of *dicacula* is blunt, that of *dapifera* is pointed.

Cosmopterix lespedezae Walsingham

(Figs. 35, 96, 147)

Soc., 10: 198. Walsingham, 1891 [1892]. Proc Zool. Soc.
Cosmopteryx lespedezae Walsingham, 1882. Trans. American Ent.

London, 536, 548. *partim.* Walsingham, 1897. Proc. Zool. Soc. London, 105. (as synonym of *C. attenuatella*). Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52 : 535. (as synonym of *C. attenuatella*). Busck, 1906. Proc. U. S. Natl. Mus., 30 : 710. (as synonym of *C. attenuatella*). Walsingham, 1907 [1908]. Proc. Zool. Soc. London, 965. (as synonym of *C. attenuatella*).

‡*Cosmopteryx magophila* Braun, 1930. Trans. American Ent. Soc., 56 : 9. misidentification.

Tongue shining pale buff. Labial palpi olive-brown; second segment with three white lines: one internal, one external, and one ventral; third segment with an anterior and a posterior white line. Face shining buff-brown; vertex olive-brown with three silver-blue lines, one above each eye and one medial. Antennae dark olive-brown; pecten present; scape with an anterior white line, ventral surface white; shaft with white ventral surface to one-half and an anterior white line to two-thirds; apical four segments white, preceded by five brown, one white, one brown, then three white segments with brown on distal, posterior half (some specimens with four white, five brown, one white, one brown, two white, four brown, then four brown basally, white distally). Thorax olive-brown with five blue-white lines; one on outer margins of patagia, one on inner margins of patagia, and one medial. Forewings with basal and apical areas dark olive-brown; four silver-blue lines on basal half; a pale yellow fascia at one-half bordered basally by two silver spots and apically by two silver spots; a white streak in costal cilia beyond fascia; a white line from fascia to apex. Abdomen shining buff-brown dorsally, shining pale buff ventrally; last segment buff. Legs buff basally; metathoracic tibiae with a basal and a medial white streak, apex white; tarsi with a white annulation near base of first segment, apex of each segment pale gray.

Male genitalia: (Fig. 35) R.W.H. slide no. 482.

Female genitalia: (Fig. 96) R.W.H. slide no. 551.

Alar expanse: 7 ½–8 mm.

Food plant: *Desmodium* sp. Braun (1930) gives the following description of the larval habits: "The mine begins at the midrib, spreading outward and upward between two lateral veins in that part of the early mine adjacent to the lower of the lateral veins between which it lies, the parenchyma is left in narrow transverse bars, giving the mine a very characteristic aspect; as the mine increases, it extends beyond the confines of the two veins, with irregular projections and parenchyma all consumed. Pupa formed with the mine beneath the transverse bars, which are here lined with silk forming a tubular pupal chamber."

Type: United States National Museum.

Type locality: Unknown. The type bears the following labels: 1) "1189." 2) "*Cosmopteryx* on *Lespedeza,* Boll." 3) *Cosmopteryx lespedeza* Wlsm. Type." The specimen was in Riley's collection. It seems likely that the specimen came from Dallas, Texas the point of origin of much of the Boll material; however, this is not a certainty.

Specimens examined: 8 ♂, 7 ♀. Arkansas: Ozark National Forest, Stone Co., 1 ♂, 2 ♀, under rearing record B. 1643, emerged July 28, 1938 (Annette F. Braun), [AFB]. Connecticut: East River, 1 ♂, July 31, 1908 (Chas. R. Ely). [USNM]. Kentucky: Cumberland Falls, 2 ♂, 1 ♀, under rearing record B. 1315, emerged July 12, 1932 (Annette F. Braun), [AFB, RWH]; Cumberland Valley, Letcher Co., 1 ♂, June 27, 1933 (Annette F. Braun), [AFB]; Mammoth Cave, 1 ♂, 1 ♀, under rearing record B. 1315, emerged September 9 and 11, 1941 (Annette F. Braun), [AFB]; Yahoo Creek, McCreary Co., 1 ♂, 1 ♀, under rearing record B. 1315, emerged July 5, 1935, collected June 18, 1935 (Annette F. Braun), [AFB]. Ohio: Beaver Pond, Adams Co., 1 ♀, under rearing record B. 1315, emerged August 15, 1927 (Annette F. Braun), [AFB]. South Carolina: Clemson College, 1 ♀, leaf miner on legume, emerged August 27, 1933 (W. C. Nettles), [USNM].

C. lespedezae can be distinguished from *C. attenuatella* by the apex of the antennae being white in *lespedezae,* brown in *attenuatella.* The markings place *lespedezae* closest to *C. abdita;* however, the characters in the keys to the male and female genitalia will suffice to separate the two species.

Apparently, Walsingham did not have complete notes on *lespedezae* when he synonymized it with *attenuatella* because the differences in the antennal markings and the maculation of the forewings are more than adequate to separate *lespedezae* as a discrete species. Even though the distribution records are not complete, *lespedezae* appears to have a more northern range than does *attenuatella.* By Walsingham's indicating that *attenuatella* equaled *lespedezae,* an error in the identity of *attenuatella* occurred. Busck (1906) gave the characters of the type of *lespedezae* for *attenuatella*, and this definition was followed by subsequent workers. Mr. Bradley has made it possible for me to identify *attenuatella* by furnishing me with a sketch of the male genitalia. The type of genitalia is so characteristic of this species that there can be no doubt as to it identity.

Cosmopterix opulenta Braun
(Figs. 37, 104, 148)

Cosmopteryx opulenta Braun, 1919. Ent. News, 30: 260. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 63.

The description is quoted from Braun's paper (1919).

"Palpi white, outer and inner surfaces each marked with a black longitudinal line. Antennae grayish brown, becoming darker towards apex; with a conspicuous white line on anterior surface near base; last segment black, or sometimes merely black-tipped; next three preceding segments white; next three segments black; followed by a white, then a black, then a white segment [pecten present]. Head and thorax grayish brown, with three longitudinal white lines.

"Forewings brownish gray, or seal brown, with the basal half marked with five fine white longitudinal lines; one starting from base just within the costal edge diverges from the costa outwardly, extending about two-thirds through the basal brown area; a second extends along the extreme costa from the basal fourth almost or quite to the yellow fascia, becoming broader outwardly; a third along middle of wing from base to a little beyond the costo-basal streak; a fourth shorter streak below fold not attaining the base; a fifth white streak dorso-basal. Just beyond middle of wing, a yellow fascia. Four patches of metallic scales; the costal one of the inner pair limits the fascia inwardly, not touching the costa, and has a few black scales on its outer margin; dorsal patch placed farther back and with black scales on its inner margin; the yellow fascia extends between them and borders the inner side of the dorsal patch, sometimes almost to dorsal margin. Posterior pair of metallic patches almost opposite, attaining the margins, and limiting the yellow fascia outwardly, except in the middle of the wing where the fascia extends between and a little beyond them. Costal cilia immediately following the second costal metallic patch white; occasionally the yellow of the fascia is almost confluent with this white patch. Remainder of apical portion of wing and cilia of the basal brown ground color, except for a long white line extending from just beyond the yellow fascia to the tips of the apical cilia. Hind wings and cilia concolorous with fore wings. Legs gray streaked and banded with white. [Metathoracic tibiae with a longitudinal blue-white line extending from base to two-thirds or nearly to apex; this line moving from ventral surface to dorsal surface; apex blue-white.]

Male genitalia: (Fig. 37) R.W.H. slide no. 552.

Female genitalia: (Fig. 104) R.W.H. slide no. 539.

Alar expanse: 7½–9 mm.

Food plant: *Ambrosia psylostachya* DC. Braun (1919) gives the following description of the larval mine: ''The mines extend principally along the midrib, with irregular proections branching out on either side. The larva spins a cocoon on the densely pubescent under side of the leaf, constructed of silk, and the whitish pubescence of the leaf.''

Type: Annette F. Braun Collection.

Type locality: Rivera, Los Angeles County, California.

Specimens examined: 10♂, 2♀. ARIZONA: Madera Canyon, 4,400 feet, Santa Rita Mountains, Pima Co., 1♂, October 12, 1959 (R. W. Hodges), [RWH]. CALIFORNIA: Rivera, Los Angeles Co., 2♂, 1♀, under rearing record B. 589, emerged April 17, 1910 (Annette F. Braun), [AFB]. OKLAHOMA: Oklahoma City, 8♂, July 27 through September 4 (D. R. Davis), [DRD, RWH].

C. opulenta can be separated from *C. quadrilineella* by the absence of lateral thoracic lines. The presence of a single signum in the female genitalia serves to separate it from the other species of *Cosmopterix.*

Specimens from Arizona and Oklahoma are decidedly darker brown than those from California. In part this may be a result of fading of the California specimens; however, when the description was made, the specimens were relatively fresh.

Cosmopterix quadrilineella Chambers
(Figs. 38, 94, 149)

Cosmopteryx quadrilineella Chambers, 1878. Bull. U. S. Geol. Surv. Terr., 4: 95. Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52: 535. Busck, 1906. Proc. U. S. Natl. Mus., 30: 710. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 63.

Tongue white to light buff. Labial palpi gray-brown; second segment with three white lines: one ventral, one on inner surface, and one on outer surface; third segment with an anterior and a posterior white line; apex white. Face buff ventrally becoming gray-brown dorsally; vertex gray-brown with three white lines, one over each eye and one medial. Antennae brown; pecten present; ventral surface of scape white; an anterior white line continued on shaft to one-half; apical two segments brown, preceded by two white, five brown, one white, four brown, one white, then brown segments. Thorax brown with continuation of three white lines on vertex. Forewings with basal third and apical area dark gray-brown; four white lines in basal area; a yellow fascia from one-third to two-thirds with a medial extension to three-fourths; four silver patches in fascia; outer costal silver patch followed by a white streak in cilia; a white line from end of fascia to apex; cilia gray-brown. Hindwings fuscous. Abdomen brown with purple reflections dorsally, becoming ochreous ventrally. Legs brown; prothoracic legs with a white line from femur to apex of tarsus; tibiae with three oblique stripes; basal, medial, and apical; tarsi brown with a dorsal white line; metathoracic tibiae with a basal and a medial oblique white line; apex and spurs white; tarsi with a dorsal white line.

Male genitalia: (Fig. 38) R.W.H. slide no. 544.

Female genitalia: (Fig. 94) R.W.H. slide no. 848.

Alar expanse: 7–9 mm.

Food plant: unknown.

Type: Museum of Comparative Zoology.

Type locality: Bosque Co., Texas.

Specimens examined: 11♂, 21♀. ARIZONA: Madera Canyon, 4,880 and 5,600 feet, Santa Rita Mountains, Santa Cruz Co., 10♂, 20♀, July 10 through September 24, 1959 (R. W. Hodges), [CU, RWH]; same date except, Pima Co., 4,400 feet, 1♂, 1♀, October 10 and 26, 1959 [RWH].

C. quadrilineella can be separated from the other species of *Cosmopterix* by the fascia surrounding both of the basal silver spots.

Cosmopterix minutella Beutenmueller
(Figs. 31, 150)

Cosmopteryx minutella Beutenmueller, 1889. Ent. Americana, 5: 10. Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52: 535. Busck, 1906. Proc. U. S. Natl. Mus., 30: 711. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 63.

Tongue shining pale buff-yellow. Labial palpi white, a dorsal brown line on second segment, an internal and an external brown line on third segment. Antennae olive-brown; pecten present; scape with ventral surface and an anterior line white; anterior line continued on shaft to one-third or one-half; apical four segments white, preceded by three brown, one white, one brown, one white, and one brown segment. Face shining gray-brown; vertex olive-brown with three white lines, one above each eye and one medial. Thorax olive-brown with continuation of three white lines. Forewings with basal area olive-brown and with four white lines; fascia pale yellow, bordered by four silver spots; apical area buff-gray with a white line along dorsal margin. Hindwings pale fuscous. Abdomen ochreous dorsally, shining buff ventrally. Legs shining buff basally; metathoracic tibiae olive-brown with three white lines: one from base to one-third, one from base to three-fourths, and one from two-thirds to near apex; metathoracic tarsi with a brown annulation basally followed by a broad white annulation, then buff-brown and buff; segments two through five brown ventrally, buff dorsally.

Male genitalia: (Fig. 31) R.W.H. slide no. 893.

Female genitalia: no specimens available.

Alar expanse: 7–8 mm.

Food plant: unknown.

Type: United States National Museum.

Type locality: Central Florida.

Specimens examined: 6 ♂. FLORIDA: Archbold Biological Station, Highlands Co., 1 ♂, March 29, 1959 (R. W. Hodges), [RWH]; Everglades, 1 ♂, April 8–15 [USNM]; Homestead, 3 ♂, May 1 and November 2, 1959 (D. O. Wolfenbarger), [CPK]; Lakeland, 1 ♂, March 1913 (C. N. Ainslie), [USNM].

The costomedial line extending from the base of the forewing in *C. minutella* separates it from *C. attenuatella* and *C. damnosa* which have this line starting beyond the base of the wing. The shape of the left brachium in the male genitalia (Fig. 31) serves to distinguish *minutella* from the other North American species of *Cosmopterix*.

Cosmopterix abdita, new species

(Figs. 36, 151)

Tongue shining yellow-white. Labial palpi dark olive-brown; second segment with three white lines: one ventral, one on inner surface, and one on outer surface; third segment with a dorsal and a ventral white line; apex white. Antennae with pecten present; dark olive-brown; ventral surface of scape white; an anterior white line on scape continued on shaft as a series of dots to two-thirds; apical five segments white, preceded by five brown, one white, one brown, one white, then brown segments (in some specimens segments one through four, ten, and twelve white). Face shining brassy-white, vertex olive-brown, caudal margin dark olive-brown, a white line above each eye and a medial one. Thorax olive-brown with continuation of three white lines on vertex. Forewings dark olive-brown basally and distally; four silver-blue lines in basal area; an orange-brown or brown fascia at two-thirds, bounded by silver-blue fasciae; a white costal patch beyond orange-brown fascia; apex white; cilia concolorous with basal area of wing, becoming paler dorsally. Hindwings fuscous-brown, cilia slightly paler. Abdomen brown dorsally, becoming straw colored ventrally. Legs buff basally; metathoracic tibiae with a white annulation at middle and another at apex, a white line from base to one-fourth; apices of first three tarsal segments white, last two segments white; prothoracic legs with a dorsal white line on tibiae and tarsi.

Male genitalia: (Fig. 36) R.W.H. slide no. 405.

Female genitalia: no specimens available.

Alar expanse: 7–8 mm.

Food plant: unknown.

HOLOTYPE: ♂, Archbold Biological Station, Lake Placid, Highlands Co., FLORIDA, April 1, 1959 (R. W. Hodges), [CU Type No. 3794].

PARATYPES: same data as type, 5 ♂, March 27 through April 4 [RWH]; Homestead, FLORIDA, 3 ♂, September 23, 1958, February 8, 1959, and April 24, 1959 (D. O. Wolfenbarger), [CPK]; C[olumbia], MISSOURI, 1 ♂, no date or collector [AMNH]; Kirkwood, Missouri, 2 ♂, September 2 and 30, 1899 (Murtfeldt), [CU].

Other specimens examined: Everglades, FLORIDA, 2 ♂, 8–15 IV [USNM]; N. ILL[INOIS], 1 ♀, no date or collector [USNM].

Cosmopterix abdita can be distinguished from the other species of *Cosmopterix* by the left brachium being offset in the middle of the sclerotized area in the male genitalia. This species is close to *C. lespedezae* in maculation, and in questionable cases reference should be made to the genitalia.

Cosmopterix inopis, new species
(Figs. 39, 103, 152)

Tongue shining buff. Labial palpi dark olive-brown; second segment with three white lines: one ventral, one internal, and one external; third segment with a ventral and a dorsal white line; apex white. Antennae dark olive-brown; pecten present; scape with ventral surface white and with an anterior white line continued on shaft to one-half; apical four segments white, preceded by five brown, one white, one brown, one- and one-half white, then brown segments. Face buff-brown with purple reflections; vertex olive-brown with three white lines, one above each eye and one medial. Thorax dark olive-brown with continuation of three white lines on vertex and with a blue-white line on outer margin of patagia. Forewings basally and apically dark olive-brown; four blue-white lines in basal area; a bright yellow fascia bordered basally by a silver fascia and apically by two silver-purple spots; a white streak in costal cilia beyond fascia; a blue-white line from end of yellow fascia to apex of cilia; a yellow line extending along costa basally from fascia. Hindwings fuscous. Abdomen pale gray-yellow dorsally, buff ventrally. Legs buff basally, dark olive-brown distally; metathoracic tibiae with a blue-white streak from base to one-fourth, another from one-half to three-fourths, apex blue-white; outer surface of outer tibial spurs blue-white; tarsi shining pale buff-gray.

Male genitalia: (Fig. 39) R.W.H. slide no. 540.

Female genitalia: (Fig. 103) R.W.H. slide no. 996.

Alar expanse: 7–8 mm.

Food plant: unknown.

HOLOTYPE: ♂, Madera Canyon, 4,880 feet, Santa Rita Mountains, Santa Cruz Co., ARIZONA, September 23, 1959 (R. W. Hodges), [CU Type No. 3799].

PARATYPE: same locality as type, 1 ♂, September 2, 1959 [RWH].

Other specimens examined: Homestead, FLORIDA, 1 ♀, April 10, 1959 (D. O. Wolfenbarger), [CPK].

C. inopis can be distinguished from the other species of *Cosmopterix* by the quadrate distal portion of the valvae in the male genitalia.

Cosmopterix chalybaeella Walsingham

Cosmopteryx chalybaeella Walsingham, 1889. Ins. Life, 1: 289. Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52: 534. Busck, 1906. Proc. U. S. Natl. Mus., 30: 711. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 63.

C. chalybaeella is known only from the type which is in the British Museum (Natural History). I quote Walsingham's original description because no specimens are available.

"Antennae, brown, a white line along the side of the basal joint and running approximately through half their length; apex white, with two or more white rings, preceded by a dark band before it.

"Palpi, whitish, with a slender line of brown scales extending along the outer side of the apical joint.

"Head, brown, with central and lateral slender white lines running back over the thorax, which is also brown; face whitish.

"Fore-wings, brown, with two short rather broad silvery dashes at about one-fourth from the base, the first nearest the costa, commencing also nearest to the base; a very slender silvery line from the base along the dorsal margin; and a short oblique streak of the same color tending downwards from the costal margin towards the apex of the upper dash; beyond the basal half of the wing is the usual orange-yellow space, limited internally and externally by shining steel-gray metallic spots, the pair adjacent to the costa being much wider apart than the opposite pair, which are adjacent to the dorsal margin; there is a white streak in the costal cilia touching the upper and outer metallic spot, and a similar apical streak is continued a very short distance along the dorsal margin; cilia steel-gray, with a slight greenish tinge.

"Hind-wings and cilia, the same color.

"Legs, brownish; tarsal joints smeared and spotted with white.

"Exp. al., 6 mm.

"Habitat, Southwest Texas (Morrison).

"Type male, Mus. Wlsm."

According to Walsingham's description of the habitus of *chalybaeella*, it would key to the last couplets which include *C. inopis, C. lespedezae, C. gracilens,* and *C. abdita.*

Mr. Bradley (*in litt.*) states that the abdomen of the type is missing. He has compared some specimens which I thought might be *chalybaeella* with the type; however, in each instance the specimen was of another species.

Cosmopterix gemmiferella Clemens
(Figs. 41, 107, 153)

Cosmopteryx gemmiferella Clemens, 1860. Proc. Acad. Nat. Sci. Philadelphia, 10. Frey and Boll. 1876. Stettiner Ent. Zeit., 37: 214. Busck, 1903. Proc. Ent. Soc. Washington, 5: 197. Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52: 535. Busck, 1906. Proc. U. S. Natl. Mus., 30: 709. Forbes, 1923. Lepidoptera of New York and neighboring states, Cornell Univ. Agric. Exp. Sta. Mem., 68: 332. Braun, 1923. Trans. American Ent. Soc., 49: 115. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 63.

Tongue gray-brown. Labial palpi brown; a white line on inner surface of second segment, another on outer surface; a white line on anterior surface of third segment, another on posterior surface. Antennae brown; pecten present; scape with an anterior white line continued to middle of shaft as a series of dots; apical four segments white, preceded by five brown, four white, then by brown segments (series possibly three white, five brown, three white or three white, five brown, one white, one brown, and two white.) Face silver-gray with bluish highlights; vertex brown with three silver-blue lines, one above each eye and one medial. Thorax brown with continuation of medial line, lateral lines not present. Forewings brown on basal half and apical fourth; four silver-blue lines in basal area; a transverse silver fascia at one-half followed by an orange fascia (with age orange fading to pale yellow-brown); a silver patch at end of orange fascia from dorsal margin to middle of wing; another smaller silver patch more distad from middle of wing towards costa, white on costa at this point; a row of brown scales preceding outer silver patches; a silver-blue streak at tornal area; apex white; cilia concolorous with base of wing. Hindwings fuscous-brown. Abdomen brown dorsally, silver ventrally. Legs metallic bluish-brown on coxae, trochanters, and femora; tibiae and tarsi brown; metathoracic tibiae with a short white line on dorsal surface from base; a white annulation at middle of tibia; outer dorsal surface of tibial spurs white; apices of first, second, and fourth tarsal segments white; fifth tarsal segment white.

Male genitalia: (Fig. 41) A. Busck slide.

Female genitalia: (Fig. 107) R.W.H. slide no. 947.

Alar expanse: 9–12 mm.

Food plant: *Panicum dichotomum* L. According to Braun (1923) the habits of the larva are: "The larva mines the small basal leaves of *Panicum dichotomum* L., in the spring, eating out almost the entire substance of the leaf. Just before pupation, it enters one of the lower stem leaves, in which it makes a small inconspicuous mine, scarcely larger than the larva, but broadening at its anterior end toward the tip of the leaf, slightly inflated, and showing as a convexity on the upper surface of the leaf. Within this cavity, which is silk-lined, pupation takes place. Beyond the pupation chamber, the mine extends a short distance forwards, but is scarcely visible except at its end, where the epidermis is almost eaten through, permitting the emergence of the imago."

The statement in Forbes (1923) that the foodplant is *Ipomoea* is possibly based upon an earlier hypothesis of Busck; however, the larva of *C. gemmiferella* has never been recorded from *Ipomoea.*

Type: Academy of Natural Sciences, Philadelphia.

Type locality: Philadelphia.

Specimens examined: 25 ♂, 7 ♀. FLORIDA: Boulogne, U. S. Route 1 and St. Marys River, 1 ♂, April 1, 1936 (J. G. Franclemont), [CU]. ILLINOIS: Putnam Co., 1 ♀, June 30, 1940 (M. O. Glenn), [MOG]. KENTUCKY: Pine Knot, McCreary Co., 1 ♂, June 14, 1935 (Annette F. Braun), [RWH]; Pine Mt., Letcher Co., 1 ♂, June 21, 1933 (Annette F. Braun), [AFB]. MAINE: Augusta, 3 ♂, July 6 and 16 (A. E. Brower), [AEB]; Bar Harbor, 1 ♂, (A. E. Brower), [AEB]; Lincoln, 1 ♀, July 10 (A. E. Brower), [AEB]. MASSACHUSETTS: Boston, 1 ♂ [USNM]. NEW JERSEY: Essex Co. Park, 4 ♂, 1 ♀, June 7 through July 4 (W. D. Kearfott), [USNM, MCZ]. NEW YORK: East Aurora, 1 ♀, July 30, 1917 (W. Wild), [CU]. OHIO: Beaver Pond, Adams Co., 1 ♂, under rearing record B. 1079, emerged June 3, 1931 (Annette F. Braun), [AFB]; Cincinnati, 1 ♂, July 3, 1917 (Annette F. Braun), [AFB]; Clermont Co., 2 ♀, under rearing record B. 1079, emerged May 24 and 26, 1922 (Annette F. Braun), [AFB, USNM]; Mineral Springs, Adams Co., 1 ♂, June 27, 1931 (Annette F. Braun), [AFB]. PENNSYLVANIA: New Brighton, 2 ♂, July 12 and 17, 1907 [USNM]; Hazelton, 4 ♂, 1 ♀, July 2–27 (Dietz), [MCZ]; Oak Station, Allegheny Co., 1 ♂, June 23, 1913 (Fred Marloff), [CNHM]. VIRGINIA: Falls Church, 1 ♀, June 2 (A. Busck), [USNM]. QUEBEC: Knowlton, 1 ♂ (L. J. Milne), [CNC].

C. gemmiferella can be distinguished from *C. bacata* by the antennal markings; the former has a brown annulation interrupting the white area.

Cosmopterix bacata, new species
(Figs. 42, 154)

Tongue buff-brown. Labial palpi: second segment gold-buff dorsally, olive-brown ventrally; third segment olive-brown with an anterior and a posterior blue-white line. Antennae with pecten present; olive brown; scape with ventral surface and an anterior line white; apical eight segments of shaft white, preceding segments olive-brown. Face shining golden; vertex olive-brown with three blue-white lines, one above each eye and one medial. Thorax olive-brown with continuation of medial blue-white line of vertex

Forewings olive-brown basally and apically; four silver-blue lines in basal area; a transverse silver fascia at one-half followed by a broad orange fascia; a silver spot at end of orange fascia from dorsal margin to middle of wing; another, smaller silver patch more distad from middle of wing towards costa; white on costa at this point; a row of brown scales preceding outer silver spots; a silver-blue streak at tornal area; apex white; cilia concolorous with base of wing. Hindwings fuscous-brown. Abdomen brown dorsally, silver ventrally. Legs metallic bluish-bronze on coxae, trochanters, and femora; tibiae and tarsi brown; metathoracic tibiae with a short white line on dorsal surface from base; a white annulation at middle of tibiae; outer dorsal surface of tibial spurs white; apices of first, second, and fourth tarsal segments white; fifth tarsal segment white.

Male genitalia: (Fig. 42) R.W.H. slide no. 406.

Female genitalia: Unknown.

Alar expanse: 9–10 mm.

Food plant: Unknown.

HOLOTYPE: ♂, Leroy, ALABAMA, June 11, 1917 (J. C. Bradley), [CU Type No. 3816].

PARATYPE: Winter Park, FLORIDA, 1 ♂, May 1946 (A.B. Klots), [ABK].

C. bacata can be separated from *C. gemmiferella* by the apical eight segments of the antennae being white; in *gemmiferella* the apical three segments are white, preceded by five brown segments.

Cosmopterix damnosa, new species

(Figs. 43, 155)

Tongue shining pale buff. Labial palpi olive-brown; second segment with three white lines: one internal, one external, and one ventral; third segment with an anterior and a posterior white line. Antennae dark olive-brown; pecten present; scape with an anterior white line, ventral surface white; shaft with white ventral surface to one-half and an anterior white line to two-thirds; apical three segments brown, preceded by two white, five brown, one white, one brown, one white, then brown segments. Face shining buff-brown; vertex olive-brown with three silver-blue lines, one above each eye and one medial. Thorax olive-brown with five blue-white lines, one on outer margins of patagia, one on inner margins of patagia, and one medial. Forewings with basal and apical areas dark olive-brown; four silver-blue lines on basal half; a pale yellow fascia at one-half bordered basally by two silver spots and apically by two silver spots; a white streak in costal cilia beyond fascia; a white line from fascia to apex. Abdomen shining buff-brown dorsally, shining pale buff ventrally; last segment buff. Legs buff basally; metathoracic tibiae with a basal and a medial white streak, apex of each segment pale gray.

Male genitalia: (Fig. 43) R.W.H. slide no. 896.

Female genitalia: No specimens available.

Alar expanse: 7 mm.

Food plant: Unknown.

HOLOTYPE: ♂, Archbold Biological Station, Highlands Co., FLORIDA, March 27, 1959 (R. W. Hodges), [CU Type No. 3796].

This species can be distinguished from *C. lespedezae* by the apex of the antennae being brown in *damnosa*, white in *lespedezae*. It can be separated from *C. attenuatella* by the globose aedeagus.

Cosmopterix clemensella Stainton
(Figs. 40, 99, 156)

Cosmopteryx clemensella Stainton, 1860. Ent. Week. Int., 9:31. Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52:535. Busck, 1906. Proc. U. S. Natl. Mus., 30:9. Forbes, 1923. Lepidoptera of New York and neighboring states, Cornell Univ. Agric. Exp. Sta. Mem., 68: 332. McDunnough, 1939. Mem. S. California Acad. Sci., 2:63.

Cosmopteryx hermodora Meyrick, 1919. Exot. Micr., 2:282. **new synonymy.** Forbes, 1923. Lepidoptera of New York and neighboring states, Cornell Univ. Agric. Exp. Sta. Mem., 68:332. McDunnough, 1939. Mem. S. California Acad. Sci., 2:63.

Tongue buff-white. Labial palpi dark olive-brown; second segment with three white lines: one ventral, one on inner surface and one on outer surface; third segment with an anterior and a posterior white line. Antennae with pecten present; scape with ventral surface and an anterior line white; white line continued on shaft to three-fifths, in some specimens to inner white band; apical four segments white, preceded by five brown (or one white, one brown, two white), four white, then brown segments. Face shining buff-white; vertex olive-brown with three white lines, one medial and one above each eye. Thorax dark olive-brown with continuation of three lines on vertex. Forewings dark olive-brown basally and apically; four blue-white lines on basal half; a yellow-orange fascia at one-half, bordered inwardly by a silver band not reaching costal margin; outwardly, fascia bordered by a dorsal and a costal silver patch; fascia extending between outer silver spots; a white streak in costal cilia above outer costal spot; a blue-white line along dorsal margin of wing from end of fascia to apex of cilia; cilia concolorous with base of wing. Hindwings fuscous brown. Abdomen pale yellowish or yellow-brown dorsally, silver ventrally. Legs metallic silver-yellow basally, brown distally; metathoracic tibiae with blue-white at base, middle, and apex; tibial spurs blue-white with a ventral brown line; metathoracic tarsi brown basally, silver-blue distally; each segment tipped with silver-blue; a dorsal silver-blue line on segments one, two, three, and five.

Male genitalia: (Fig. 40) R.W.H. slide no. 556.

Female genitalia: (Fig. 99) R.W.H. slide no. 555.

Alar expanse: 6½–9 mm.

Food plant: *Carex* spp.

Type: *clemensella*, British Museum (Natural History); *hermodora*, British Museum (Natural History).

Type locality: *clemensella*, Pennsylvania (?); *hermodora*, Toronto, Canada.

Specimens examined: 39 ♂, 29 ♀. ILLINOIS: Putnam Co., 5 ♂, 1 ♀, June 16 through July 31 (M. O. Glenn), [MOG, INHS]. INDIANA: Spring Mill State Park, 3 ♂, 2 ♀, under rearing record B. 1934, emerged May 13–23, 1942 (Annette F. Braun), [AFB]. MAINE: Bar Harbor, 1 ♀, August 3, 1936 (A. E. Brower), [AEB]. MARYLAND: Plummer's Id., 1 ♀, May 30, 1916 (A. Busck), [USNM]; same locality, 1 ♂, June 23, 1920 (H. Barber), [USNM]. NEW HAMPSHIRE: no locality or date (A. Busck), [USNM]. NEW JERSEY: Essex Co. Park, 1 ♂, June 30 (Kearfott), [USNM]. NEW YORK: Blue Mt., Adirondacks, 1 ♂, 1 ♀, under rearing record B. 2105, emerged July 10, 1946 (Annette F. Braun), [AFB]; Ithaca, Tompkins Co., 1 ♂, July 12, 1928 (A. B. Klots), [ABK]; Slaterville Springs, Tompkins Co., 2 ♂, July 6, 1960 (R. W. Hodges), [RWH]; Wanakena, 1 ♂, under rearing record B. 2104, emerged July 1946 (Annette F. Braun), [AFB]; same locality, 1 ♂, 1 ♀, under rearing record B. 2103, emerged June 30 and July, 1946 (Annette F. Braun), [AFB]; Woodlands, 1 ♂, July 4, 1934 (A. B. Klots), [ABK]. NORTH CAROLINA: Nantahala Gorge, 2 ♂, 2 ♀, under rearing record B. 1706, emerged June 1–9, 1939 (Annette F. Braun), [AFB]. OHIO: Beaver Pond, Adams Co., 1 ♀, on *Carex*, emerged March 20, 1938 (Annette F. Braun), [AFB]; Cincinnati, 4 ♂, 10 ♀, June 21 through July 1 (Annette F. Braun), [AFB, USNM, RWH]; Cincinnati, 1 ♂, 2 ♀, under rearing record B. 999, emerged May 15–26 (Annette F. Braun), [AFB]; Clermont Co., 2 ♂, June 6, 1919 (Annette F. Braun), [CAS, RWH]; Clermont Co., 2 ♀, under rearing record B. 999, emerged May 14 and 17, 1929 (Annette F. Braun), [AFB]; Mineral Springs, Adams Co., 1 ♀, under rearing record B. 999, emerged June 3, 1931 (Annette F. Braun), [AFB]. PENNSYLVANIA: New Brighton, 5 ♂, June 20 through July 9 (H. D. Merrick), [USNM]; Harvey's Lake, 1 ♀, June 16 [USNM]. VERMONT: Sherburne Pass, 1 ♀, under rearing record B. 2108, emerged July 11, 1946 (Annette F. Braun), [AFB]. MANITOBA: Aweme, 1 ♂, July 9, 1924 (N. Criddle), [CNC]. ONTARIO: Toronto, 1 ♂, July 1922 (Parish), [USNM]; Toronto, 2 ♀, "7.16" and "5.7 16" (Parish), [BMNH].

C. clemensella can be separated from the other species of *Cosmopterix* by the characters given in the key based on maculation. The male genitalia of *C. damnosa* are not separable from some of *clemensella*. In this situation the two keys should be used in conjunction.

I have examined the female syntypes of *hermodora* and have seen a photograph of the lectotype male (selected by Clarke and to be published in the near future). The maculation and the genitalia fall within the range of variation observed in *clemensella;* thus, I consider *hermodora* a synonym of *clemensella.*

There is considerable variation in the shape of the distal half of the left brachium in the male genitalia. In some specimens it is broad almost to the apex; then it tapers abruptly to the apex. In other specimens this same structure begins to taper at the middle or outer third with the result that the apex is acute. In the female genitalia the *lamella antevaginalis* can be relatively broad, or, it can be narrow with an abrupt constriction at the basal third. Also, the length of the *apophyses anteriores* is between one and two times the length of the sclerotized portion of the eighth tergite. Males and females exhibiting the maximum amount of difference have been reared from *Carex,* and they make the same type of mine. Thus, I have concluded that *clemensella* is a single, variable species.

Cosmopterix scirpicola, new species

(Figs. 44, 105, 157)

Tongue shining buff-yellow. Labial palpi pale buff; a dorsal and a ventral olive-brown line on second segment; an internal and an external olive-brown line on third segment; apex white or olive-brown. Antennae with pecten present; olive-brown; scape white ventrally and with an anterior white line; shaft white ventrally to one-half, continuation of anterior white line to one-fourth; apical nine segments olive-brown, preceded by one white, then brown segments (or apical three brown, one white, five brown, one white, then brown). Face shining pale yellow becoming olive-brown dorsally; vertex olive-brown with three white lines, one above each eye and one medial. Thorax olive-brown with continuation of three white lines on vertex. Forewings: pattern and coloration as for *C. ebriola;* color slightly darker than that of *ebriola.* Hindwings fuscous. Legs shining buff basally, olive-brown distally; metathoracic tibiae with three oblique white stripes: one basal, one medial, and one apical; apices of tarsal segments one, two, four, and five buff.

Male genitalia: (Fig. 44) R.W.H. slide no. 478.

Female genitalia: (Fig. 105) R.W.H. slide no. 856.

Alar expanse: 10–11 mm.

Food plant: *Scirpus americanus.*

HOLOTYPE: ♂, Oklahoma City, OKLAHOMA, August 13, 1956 (D. R. Davis), [USNM Type No. 66080].

PARATYPES: same locality as type, 1 ♂, 2 ♀, July 16 through August 6 [DRD, RWH]; Archbold Biological Station, Highlands Co., FLORIDA, 1 ♂, March 27, 1959 (R. W. Hodges), [RWH]; Cedar Swamp, Champaign Co., OHIO, 1 ♂, on *Scirpus americanus,* emerged May 1934 (Annette F. Braun), [AFB]; Chicago, ILLINOIS, 1 ♀, June 30, 1909 (W. J. Gerhard), [CNHM]; Putnam Co., ILLINOIS, 1 ♀, June 8, 1954 (M. O. Glenn), [MOG]; Pautexaut (*sic*) [Patuxent] Research Refuge, Prince George Co., MARYLAND, *ex* culms of *Scirpus americanus,* emerged July 22, 1942 [USNM]; Putnam Co., Illinois, 1 ♀, June 8, 1954 (M.O.) Glenn), [MOG]; Sabine R. Ferry, opp. Orange, LOUISIANA, 1 ♂, June 20, 1917 [CU]; San Diego, CALIFORNIA, 1 ♂, August 29, 1923 [LACM].

C. scirpicola can be separated from *C. ebriola* and *C. fernaldella* by the dorsal surface of the left brachium tapering gradually to the apex (see Figs. 44, 45, 46 for comparison). The best point of separation is the comparative length of the *apophyses anteriores* in the female genitalia. In *scirpicola* the *apophyses anteriores* are longer than the *lamella antevaginalis;* they are shorter than the *lamella antevaginalis* in *ebriola* and *fernaldella.* The maculation offers no constant features for separating this species from *ebriola* and *fernaldella.*

Cosmopterix ebriola, new species

(Figs. 46, 100, 158)

Tongue shining buff. Labial palpi light buff to white; second segment with a ventral brown line, continued on inner surface of third segment; a brown line on outer surface of third segment;

apex of third segment white; a pale brown line on dorsal surface of second segment. Antennae with pecten present; brown; scape with ventral surface buff; an anterior white line continued on shaft to one-half; ventral surface of shaft white basally; apical nine segments brown, preceded by one buff, one brown, one buff, then brown segments (in a few specimens fourth segment buff instead of brown). Face shining ocher becoming darker and browner toward vertex; vertex brown with three white lines, one above each eye and one medial. Thorax buffy-olive with continuation of three lines on vertex. Forewings with basal half and outer third dark olive-buff; four white lines in basal area; an ochraceous-buff fascia from one-half to two-thirds, bordered inwardly by two silver spots—one dorsally and one costally; costal spot preceded by a row of darker scales and followed by a few black scales; fascia extending basad along costal margin to one-fourth, becoming paler; outwardly, fascia bordered by two silver spots, one dorsal and one costal; fascia extending apically between spots and along costal margin; a white line along dorsal margin of wing from end of fascia to apex of cilia; cilia fuscous brown. Hindwings fuscous-buff basally, brown distally; prothoracic tibiae and tarsi with a continuous dorsal white line; metathoracic tibiae with a dorsal white line from base to one-third; a second white line from base along ventral surface to one-half then moving dorsal to three-fourths; apex white; inner surface of tarsi white.

Male genitalia: (Fig. 46). R.W.H. slide no. 475.

Female genitalia: (Fig. 100). R.W.H. slide no. 851.

Alar expanse: 8–11 mm.

Food plant: unknown.

HOLOTYPE: ♀, Archbold Biological Station, Highlands Co., FLORIDA, March 30, 1959 (R. W. Hodges), [CU Type No. 3798].

PARATYPES: same locality as type, 12 ♂, 9 ♀, March 27 through April 4, 1959 [CU, USNM, BMNH, RWH]; Gainesville, FLORIDA, 1 ♀, July 8, 1927 (J. S. Rogers), [CU]; Hastings, Florida, 1 ♂, 1 ♀, "19C and 19a" [MCZ]; Punta Gorda, Florida, 2 ♂, 2 ♀, March 1940 (H. Ramstadt), [MOG]; Siesta Key, Sarasota Co., Florida, 1 ♂, May 1, 1960 (C. P. Kimball), [CPK]; Biloxi, MISSISSIPPI, 2 ♂, June 13, 1917 [CU].

Other specimens examined: Hastings, FLORIDA, 1 ♂, "19a" [MCZ]; Lakeland, Florida, 1 ♀, March 13 (C. N. Ainslie), [USNM]; Siesta Key, Sarasota Co., Florida, 2 ♀, April 26 and 29 (C. P. Kimball), [CPK, RWH].

Two females with the same type of genitalia as *ebriola* have the fascia almost concolorous with the basal area of the wing; there are more black scales distad of the silver spot; the silver spots are fused; the hindwings are darker; the median line on the vertex and thorax is absent; and the specimens are in general slightly melanic. However, these specimens fall within the range of variation of *ebriola* and do not appear to represent another species.

C. ebriola cannot be separated with confidence from *C. fernaldella* and *C. scirpicola* by the maculation. The female genitalia will serve to distinguish among them as follows: *ebriola* has subcircular signa and the *apophyses anteriores* shorter than the *lamella antevaginalis.* The latter character will separate it from *scirpicola;* the former character will separate it from *fernaldella.*

Cosmopterix fernaldella Walsingham
(Figs. 45, 97, 98, 159)

Cosmopteryx fernaldella Walsingham, 1882. Trans. American Ent. Soc., 10: 197. Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52: 535. Busck, 1906. Proc. U. S. Natl. Mus., 30: 711. Forbes, 1923. Lepidoptera of New York and neighboring states, Cornell Univ. Agric. Exp. Sta. Mem., 68: 332. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 63.

Tongue shining buff. Labial palpi pale buff; second segment with three brown lines: a faint dorsal one, one on inner ventral surface, and one on outer ventral surface; third segment with two brown lines, one inner surface and one on outer surface; apex white. Antennae with pecten present; brown; scape with ventral surface buff and an anterior buff line; anterior line continued to one-third; apical three segments brown, preceded by one buff, five brown, one buff, two brown, one buff, then brown segments (five brown, one buff, one brown in a few specimens). Face shining buff; vertex gray-brown with three white lines, one above each eye and one medial. Thorax gray-brown with continuation of three white lines. Forewings gray-brown basally and apically; four blue-white lines in basal area: one costal, two medial, and one dorsal; a pale yellow, orange, or orange-brown fascia at two-thirds bordered inwardly by two silver spots preceded by a few brown scales; a patch of black scales on outer margin of costal silver spot; outwardly, fascia bordered by two silver spots preceded by a few black scales; fascia sometimes extending distally between outer silver spots; a buff to white patch of scales in costal margin above outer silver spot;

a white line extending from middle of outer margin to apex; cilia concolorous with basal area. Hindwings light fuscous. Abdomen gray-brown dorsally, buff ventrally. Legs buff; metathoracic tibiae with three annulations: one basal, one medial, and one terminal; apices of tarsal segments whitish.

Male genitalia: (Fig. 45). R.W.H. slide no. 490.

Female genitalia: (Figs. 97, 98) R.W.H. slide nos. 854 and 883.

Alar expanse: 9–11 mm.

Food plant: *Carex* sp.

Type: United States National Museum.

Type locality: unknown.

Specimens examined: 34 ♂, 28 ♀. MAINE: Ashland, 1 ♂, 2 ♀, July 16, 31 (A. E. Brower), [AEB, RWH]; Augusta, 1 ♂, July 21, 1948 (A. E. Brower), [AEB]; Dennysville, 2 ♂, July 19 (A. E. Brower), [AEB]; Lincoln, 1 ♂, July 13 (A. E. Brower), [AEB]; Millinocket, 2 ♀, July 22 (A. E. Brower), [AEB]; Princeton, 1 ♂, 5 ♀, July 9–24, 1943 (A. E. Brower), [AEB]; T. 6, R. 7 (Patten), 1 ♂, 3 ♀, July 16–21 (A. E. Brower), [AEB]. MARYLAND: Washington, D. C., 1 ♀, May 1902 (A. Busck), [USNM]. MICHIGAN: Dickinson Co., 4 ♂, July 21–25, 1909 (W. W. Newcomb), [UM]; Black Lake, Presque Isle Co., 2 ♂, 1 ♀, leafminer on *Carex stricta*, emerged July 8 and 15, 1936 (Annette F. Braun), [USNM]; Burt Lake, Reese's Bog, Cheboygan Co., 11 ♂, 3 ♀, under rearing record B. 1975, emerged July 24, 1942 (Annette F. Braun), [AFB]; Gull Lake Biological Station, Kalamazoo Co., 1 ♂, 1 ♀, July 3 and 6, 1956 (R. W. Hodges), [MSU]. NEW JERSEY: Montclair, 2 ♂, 2 ♀, June 28 and July 1 (W. D. Kearfott), [USNM, MCZ]. NEW YORK: Ithaca, 1 ♂, July 17, 1931 [ABK]; Monroe Co., 3 ♂, 5 ♀, June 3 through July 11 (C. P. Kimball), [CPK]; The Shack, McLean Bogs Reserve, Tompkins Co., 2 ♂, 1 ♀, July 24, 1924 [CU]. PENNSYLVANIA: Hazelton, 1 ♂, 1 ♀, July 7 and 8, 1897 (Dietz), [MCZ]. ONTARIO: Ottawa, 1 ♂, 2 ♀, July 11–23 (C. H. Young), [CNC].

C. fernaldella cannot be consistently separated from *C. ebriola* and *C. scirpicola* by the maculation. The male and female genitalic characters given in the keys will separate them. Females from the central New York area differ from other populations in the nature of the posterior edge of the seventh abdominal sternite. This is not produced as much in the medial area as it is in specimens from other areas, but it seems to me that this is within the variation of the species rather than another species. The male genitalia of this population agree very closely with those from other areas.

Cosmopterix floridanella Beutenmueller
(Figs. 47, 102, 160)

Cosmopteryx floridanella Beutenmuller, 1889. Ent. Americana, 5: 10. Busck, 1902. Jour. New York Ent. Soc., 10: 98. Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52: 535. Busck, 1904. Proc. U. S. Natl. Mus., 27: 769. (as synonym of *C. fernaldella*). Busck, 1906. Proc. U. S. Natl. Mus., 30: 711. (as synonym of *C. fernaldella*). McDunnough, 1939. Mem. S. California Acad. Sci., 2: 63. (as synonym of *C. fernaldella*).
Cosmopteryx nigrapunctella Busck, 1900. Proc. U. S. Natl. Mus., 23: 235.

Tongue shining buff. Labial palpi buff; a brown line starting ventrolaterally on second segment, becoming lateral on third segment; a second brown line on internal surface of third segment. Antennae with pecten present; olive-brown; ventral surface of scape and shaft white; a white line on anterior surface of scape, continued on shaft to one-half; apical segment brown, preceded by three white, one brown, one white, three brown, one white, one brown, then a series of segments one-half white and one-half brown. Face shining ochreous; vertex pale olive-brown with three white lines, one above each eye and one medial. Thorax pale olive-brown with continuation of three lines on vertex. Forewings pale olive-brown basally and distally; basal area with four white lines; a pale yellow fascia at one-half, bordered inwardly and outwardly by two silver spots; a small patch of black scales preceding inner dorsal spot, and one succeeding inner costal spot; fascia extending between spots basally and apically; a white line along outer margin from apical extension of fascia to apex of cilia; a patch of buff scales in costal cilia starting at outer costal spot; outer cilia buff-brown. Hindwings pale fuscous. Abdomen ochreous dorsally, shining buff ventrally. Legs shining buff basally; metathoracic tibiae pale olive-brown with a basal white streak extending dorsally to one-third; a second white streak starting at one-sixth extending dorsally to two-thirds; apex white; tarsi shining buff on inner and dorsal surfaces, olive-brown externally.

Male genitalia: (Fig. 47) R.W.H. slide no. 476.

Female genitalia: (Fig. 102) R.W.H. slide no. 852.

Alar expanse: 8–11 mm.

Food plant: unknown.

Type: *floridanella,* United States National Museum; *nigrapunctella,* United States National Museum.

Type locality: *floridanella,* Central Florida; *nigrapunctella,* Palm Beach, Florida.

Specimens examined: 45 ♂, 9 ♀. FLORIDA: Hastings, 4 ♂ [USNM, MCZ]; Archbold Biological Station, Highlands Co., 24 ♂, 7 ♀, March 27 through April 4, 1959 (R. W. Hodges), [CU, RWH]; Delray Beach, P. B. Co., 1 ♂, April 22, 1957 (C. P. Kimball), [CPK]; Homestead, 1 ♀, April 16, 1959 (D. O. Wolfenbarger), [CPK]; Lakeland, 1 ♂, March 1913 (C. N. Ainslie), [USNM]; Orlando, 2 ♂, February 26 and 28, 1918 (G. G. Ainslie), [USNM]; Royal Palm State Park, 1 ♂, March 17, 1939 (J. C. Bradley), [CU]; Siesta Key, Sarasota Co., 9 ♂, January 18 through May 21 (C. P. Kimball), [CPK]. MARYLAND: Washington, D. C., 1 ♂, June (Aug. Busck), [USNM]. MISSISSIPPI: Biloxi, 1 ♂, 1 ♀, June 13, 1917 [CU].

C. floridanella can be separated from *C. fernaldella, C. ebriola,* and *C. scirpicola* by the costomedial line starting at or very near the base of the forewing; in the other species it starts farther from the base. The produced, truncated medial area of the posterior margin of the seventh sternite in combination with the sclerotized area in the *ductus bursae* in the female genitalia will separate *floridanella* from the other North American species of *Cosmopterix.*

Cosmopterix facunda, new species
(Figs. 106, 161)

Tongue gray-buff. Labial palpi (second segment of left palpus present) white with a dorsal and a ventral pale brown line. Antennae with pecten present; olive-brown; scape with ventral surface white and with an anterior white line; ventral surface of shaft white; white line on scape continued on shaft to one-half; apical four-and-one-half segments white, preceded by four-and-one-half olive-brown, one white, one brown, five white, then brown segments. Face dark gray-buff; vertex olive-brown with three white lines, one above each eye and one medial. Thorax olive-brown with continuation of white lines. Forewings pale olive-brown; a pale buff-yellow fascia at one-half; four blue-white lines in basal half; fascia bordered inwardly by two silver-white spots; costal one not reaching margin and followed by a small patch of black scales; dorsal silver spot starting beyond termination of costal one; a white costal line from fascia to one-fourth; fascia bordered outwardly by two silver-white spots, and extending between spots; a white dash in cilia costad of subcostal silver spot; a white line along dorsal margin beyond fascia to apex. Hindwings buff, cilia fuscous. Legs gray-buff basally, pale olive-brown distally; metathoracic tibiae with three annulations: one basal, one medial, and one terminal; apices of tarsal segments whitish.

Male genitalia: no specimens available.

Female genitalia: (Fig. 106) R.W.H. slide no. 900.

Alar expanse: 11 m.

Food plant: unknown.

HOLOTYPE: ♀, Brownsville, TEXAS, March 27, 1928 (F. H. Benjamin), [USNM Type No. 66081].

C. facunda can be separated from *C. delicatella*, *C. fernaldella*, *C. ebriola*, and *C. scirpicola* by the white apex of the antennae. The shape of the lamella antevaginalis, lacking the basal projection, in the female genitalia will serve to separate it from the same four species.

TANYGONA Braun
(Figs. 10, 16, 49, 108)

TYPE: *Tanygona lignicolorella* Braun, 1923. Original designation.

Tanygona Braun, 1923. Trans. American Ent. Soc., 49:115. McDunnough, 1939. Mem. S. California Acad. Sci., 2:63.

Head smooth-scaled; tongue scaled, moderate; maxillary palpi minute, not folded over base of tongue; labial palpi recurved, reaching apex, smooth-scaled, second segment shorter than third, apex acute; antennae five-sixths, pecten present, scape long and enlarged distally. Dorsal surface of metathoracic tibiae with long hairs.

Forewings lanceolate, acuminate; 12 veins present; 1b furcate basally; 2 and 3 before end of cell, 2 weak, 3 not reaching margin; 5 connate with 6, 7, and 8; 6, 7, and 8 stalked, 6 very short; 10 arising before 2; 11 from middle of cell. Hindwings linear; a tuft of scales on costal margin; 5 veins present; 1b simple; 2, 3, and 5 missing; 6 and 7 stalked; 6 short, not reaching margin.

Male genitalia: *valvae* narrow, *costae* separate, fused to *aedeagus; aedeagus* ankylosed, *cornuti* absent; *tegumen* heavily sclerotized; *uncus* and *socii* absent; *brachia* subequal, left one longer than right, tapering gradually to apex.

Female genitalia: *bursa copulatrix* membranous; *signa* present or absent; *lamellae vaginales* forming a cylinder.

Tanygona is closely related to *Cosmopterix.* However, the connection and partial basal fusion of the *costae* with the *anellus;* the narrow, almost linear *valvae;* and the gradually tapering, subequal *brachia* of the male genitalia of *Tanygona* serve to distinguish it from *Cosmopterix.*

Cosmopterix ipomoeae is transferred to *Tanygona* because the male and female genitalia agree with those of *T. lignicolorella* and not with any known species of *Cosmopterix.* However, the pattern of the forewings is the same as that of *Cosmopterix.*

KEY TO THE SPECIES OF TANYGONA BASED UPON THE MACULATION

1. Base of forewings dark olive-brown .... *ipomoeae*
   Base of forewings buff-brown .... *lignicolorella*

KEY TO THE SPECIES OF TANYGONA BASED UPON THE MALE GENITALIA

1. Valvae angulate (Fig. 49) .... *lignicolorella*
   Valvae not angulate (Fig. 48) .... *ipomoeae*

KEY TO THE SPECIES OF TANYGONA BASED UPON THE FEMALE GENITALIA

1. Signa present; lamellae vaginales forming a narrow tube (Fig. 109) .... *ipomoeae*
   Signa absent; lamellae vaginales forming a short, broad tube (Fig. 108) .... *lignicolorella*

Tanygona lignicolorella Braun

(Figs. 49, 108, 162)

Tanygona lignicolorella Braun, 1923. Trans. American Ent. Soc., 49: 116. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 63.

Tongue buff-white. Labial palpi buff-white with an incomplete brown line on internal and external surfaces of second and third segments; apices of second and third segments buff-white. Antennae brown basally, buff distally; an anterior and a posterior buff line on scape; these lines continued on shaft to two-thirds. Face shining buff-white with lavender reflections; a few brown scales anterior to eyes; vertex brown with three white lines, one above each eye and one medial. Thorax brown with continuation of three white lines from vertex. Forewings buff-brown; an oblique blue-white line extending from costa at one-fifth to fold at one-half; another oblique blue-white line from costa at one-half to dorsal margin at two-thirds; a narrow blue-white fascia at four-fifths; apex of wings brown-black; cilial scales at apex buff basally, brown-black terminally, buff-gray elsewhere. Hindwings buff, cilia paler. Abdomen gray-brown. Legs buff-white, brown on dorsal surface of prothoracic and mesothoracic tibiae.

Male genitalia: (Fig. 49) R.W.H. slide no. 668.

Female genitalia: (Fig. 108) R.W.H. slide no. 669.

Alar expanse: 7 ½–9 mm.

Food plant: Unknown.

Type: Collection of Annette F. Braun.

Type locality: Cincinnati, Ohio.

Specimens examined: 5 ♂, 2 ♀. Illinois: Putnam Co., 1 ♂, 1 ♀, July 12 and 17, 1959 (M. O. Glenn), [MOG]. Maryland: Plummer's Island, 1 ♂, July 1903 (A. Busck), [USNM]. North Carolina: Highlands, Macon Co., 1 ♂, August 4, 1958 (R. W. Hodges), [RWH]. Ohio: Cincinnati, 1 ♂, 1 ♀, July 5 and 16 (Annette F. Braun), [AFB]. South Carolina: Cherry Hill Recreation Area, 2000 feet, Route 107, Oconee Co., 1 ♂, August 7, 1958 (R. W. Hodges), [RWH].

T. lignicolorella can be distinguished from *T. ipomoeae* by the characters given in the keys and by comparison with the illustrations of the wings.

Tanygona ipomoeae Busck, new combination
(Figs. 48, 109, 163)

Cosmopteryx ipomoeae Busck, 1900. Proc. U. S. Natl. Mus., 23: 235. Dyar, 1901. Ent. Soc. Washington, 4: 478. Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52: 535. Busck, 1906. Proc. U. S. Natl. Mus., 30: 710. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 63.

Tongue buff-white. Labial palpi dark olive-brown. Antennae dark olive-brown; scape with an anterior white line continued on shaft to one-half; apical three segments white, preceded by five brown, one white, then brown segments. Face shining buff-brown on lower half, upper half of face and vertex brown. Thorax dark olive-brown with a medial blue-white line. Forewings dark olive-brown basally and distally; four narrow blue-white lines on basal half, subcostal one broken; a pale straw-colored fascia at three-fifths, bordered inwardly by two silver-white spots and outwardly by two silver-white spots, costal ones not reaching costal margin, dorsal ones on margin; a few black scales following costo-basal silver-white spot; a streak, concolorous with fascia, in costal cilia from outer spot; a buff-white line on dorsal margin from end of fascia to apex of wing; dorsal cilia slightly paler than base of wing. Legs shining buff-white basally, brown distally; prothoracic legs with a dorsal white line on tibiae and tarsi; metathoracic tibiae with an oblique white, with lavender reflections, streak from base to base of medial tibial spurs, then dorsad to one-half; apex white; apices of metathoracic tarsal segments white; inner surface of legs buff-white.

Male genitalia: (Fig. 48) R.W.H. slide no. 501.

Female genitalia: (Fig. 109) R.W.H. slide no. 903.

Alar expanse: 7–8 mm.

Food plant: *Ipomoea* sp. Dyar (1901) gives the following description of the larval habits of *ipomoeae:* "The larvae are leaf miners in 'morning glory' (*Ipomoea* sp.). The mine is an irregular series of blotches and lobes, usually elongate and several partly joined; taking all the parenchyma between the two epidermes, the skin strengthened by the web, so that the surface is wrinkly. Frass partly ejected, held to the leaf by a close web. . . . Spun a fine silken cocoon between leaves or in a folded leaf."

Type: United States National Museum. Only one of the two specimens which Busck mentions in the original description is in the Museum; I designate this specimen as the **lectotype**.

Type locality: Palm Beach, Florida.

Specimens examined: 1 ♂, 1 ♀. FLORIDA: Fort Lauderdale, 1 ♀, reared *ex* morning glory, emerged May 21, 1945 [USNM]; Palm Beach, 1 ♂, no date (Dyar), [USNM].

T. ipomoeae can be separated from T. *lignicolorella* by the characters given in the keys. It is likely that a genitalic preparation will be necessary to separate it from the species of *Cosmopterix.*

Eralea, new genus

ερως = love, ἁλέα = warmth

(Figs. 3, 18, 51, 110)

Type: *Eriphia albalineella* Chambers, 1878.

Head smooth-scaled; tongue scaled, well developed; maxillary palpi folded over base of tongue; labial palpi smooth-scaled, recurved, not reaching apex, second segment longer than third, apex acute; antennae two-thirds to three-fourths, pecten present, scape elongate and slightly swollen distally. Dorsal surface of metathoracic tibiae with long scales.

Forewings lanceolate, apex acute; 12 veins present; 1b furcate basally; 2 and 3 before end of cell; 6, 7, and 8 stalked, 8 weak; 10 opposite 2; 11 from middle of cell. Hindwings linear; a tuft of scales on costal margin; 8 veins present; 1b simple; 1, 2, 3, and 4 evanescent; 6 and 7 stalked, divergent.

Male genitalia: *valvae* lobate, rounded apically; *costae* separate, short, lobate; *tegumen* heavily sclerotized; *uncus* and *socii* absent; arms of *gnathos* separate, asymmetrical, left *brachium* longer than right one; *aedeagus* short, cylindrical, a basal process from dorsal surface, ankylosed.

Female genitalia: *bursa copulatrix* membranous; two *signa*, cornucopia shaped; *lamella antevaginalis* sclerotized, forming a plate in front of ostium; *apophyses* moderately short.

Eralea differs from *Stagmatophora* in the following characters: the second segment of the labial palpi of *Eralea* is longer than the third; in *Stagmatophora* the third segment is longer than the second. The second segment of the labial palpi of *Eralea* is not thickened ventrally; that of *Stagmatophora* is thickened ventrally. The scales on the dorsal surface of the metathoracic tibiae of *Eralea* are long and thin; those of *Stagmatophora* are normal. In the hindwings veins 1 through 5 are evanescent in *Eralea;* these veins are well developed in *Stagmatophora.* In the male genitalia of *Eralea* the *costae* are symmetrical and not fused with the *anellus;* those of *Stagmatophora* are asymmetrical and fused with the *anellus.* The female genitalia of the two genera are very similar, indicating their close relationship.

Two species of *Eralea* are known from the southern United States, one from Florida and one from Texas and Arizona. Future collecting will probably extend the known ranges of these species.

Key to the Species of Eralea based upon the Maculation

1. Vertex dark brown .... *striata*
   Vertex pale buff-white .... *albalineella*

Key to the Species of Eralea based upon the Male Genitalia

1. Ventral margin of costa concave .... *striata*
   Ventral margin of costa almost straight .... *albalineella*

Eralea albalineella Chambers, new combination
(Figs. 51, 110, 163)

Eriphia (?) *albalineella* Chambers, 1878. Bull. U. S. Geol. Geog. Surv. Terr., 4: 95.
Eriphia albalineella, Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52: 540.
Tanygona albalineella, Braun, 1923. Trans. American Ent. Soc., 49: 115. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 63.

Tongue white to pale gray. Labial palpi brown with a dorsal and a ventral buff line on second and third segments. Antennae buff, scape with a broad dorsoposterior brown line continued on shaft to one-third, a faint brown line on anterior surface of scape and basal part of shaft. Face and vertex buff-white, brown anterior to and dorsad of eyes, brown along cervical margin. Thorax brown with three blue-white lines, two lateral and one medial. Forewings brown-black; an oblique buff-white line from costal margin at base to dorsal margin at two thirds; a second starting from costal margin at one-half to middle of wing at three-fourths; and a short one in middle of wing at five-sixths; costal cilia buff; apical cilia buff basally, brown distally; dorsal cilia buff with some brown flecks. Hindwings buff, cilia gray. Legs shining buff; outer surface of metathoracic tibiae with a broad gray-brown streak from base to one-half, another from one-half to nine-tenths; metathoracic tarsi gray-brown on dorsal surface of first segment and basal half of second.

Male genitalia: (Fig. 51) R.W.H. slide no. 868.

Female genitalia: (Fig. 110) R.W.H. slide no. 869.

Alar expanse: 8–9 mm.

Food plant: Unknown.

Type: Museum of Comparative Zoology.

Type locality: Bosque Co., Texas.

Specimens examined: 1 ♂, 2 ♀. ARIZONA: Chiricahua Mts. near Portal, Cochise Co., 1 ♂, 1 ♀, July 5, 1939 (Annette F. Braun), [AFB]. TEXAS: [Bosque Co.], 1 ♀, "3/3" [MCZ].

The buff-white line from the base of the forewings of *albalineella* is narrower than the one of *E. striata.* This character, in combination with the pale vertex, will separate *albalineella* from *striata.*

Eralea striata, new species

(Figs. 50, 165)

Tongue white basally, gray distally. Labial palpi brown with a ventral white line on second and third segments. Antennae buff-white, scape brown except for an anterior white line, pecten brown, base of shaft pale brown. Face gray-brown with lavender reflections; two oblique white streaks, one from base of each antenna to base of tongue; vertex brown. Thorax brown; patagia white on inner and outer margins. Forewings buff-white to white; a broad white band from base of wing to dorsal margin at one-half; an oblique white line near base running from near costal margin to medial white band; a row of brown scales at apex of wing; cilia with pale brown flecks basally, buff-white distally. Hindwings pale fuscous. Legs buff-white; prothoracic legs with an anterior brown line; metathoracic tibiae with a brown streak from base to one-half, another from two-thirds to nine-tenths; metathoracic tibiae with brown on dorsal surface of first, second, and third segments.

Male genitalia: (Fig. 50) R.W.H. slide no 925.

Female genitalia: No specimens available.

Alar expanse: 8 mm.

Food plant: Unknown.

Holotype: ♂, Siesta Key, Sarasota, Co., Florida, May 13, 1960 (C. P. Kimball), [CU Type No. 3812].

Paratype: Oneco, Manatee Co., Florida, 1 ♂, May 19, 1953 (Paula Dillman), [CPK].

Melanocinclis, new genus

μέλᾰν = black pigment, κινκλίς = latticed gate

(Figs. 8, 15, 57, 116)

Type: *Melanocinclis lineigera, sp. nov.*

Head smooth-scaled; tongue scaled, well developed; maxillary palpi minute; labial palpi recurved, not reaching vertex, second segment longer than third and slightly thickened ventrally, third segment rough-scaled, apex acute; antennae three-fourths, pecten present, simple, scape long and broad. Metathoracic tibiae with long hairs on dorsal surface.

Forewings lanceolate, acuminate; 10 veins present; 2 and 4 absent; 1b furcate basally; 3 before end of cell, not reaching margin; 6, 7, and 8 stalked; 9 from end of cell; 10 before 3; 11 from middle of cell. Hindwings linear; a series of scales on costal margin; 4 veins present; 2, 3, 5, and 6 absent; 1b simple.

Male genitalia: *valvae* linear, expanded distally; *costae* separate, fused to *anellus; anellus* heavily sclerotized; *aedeagus* ankylosed, *cornuti* absent; *tegumen* heavily sclerotized; *uncus* and *socii* absent; *brachia* broad basally, aciculate distally, subequal in length.

Female genitalia: *bursa copulatrix* membranous; *signa* absent; *lamellae vaginales* forming an irregularly shaped tube; apophyses long.

Melanocinclis differs from *Tanygona* in the following characters: The third segment of the labial palpi is rough-scaled and shorter than the second segment; that of *Tanygona* is smooth and longer than the second segment. Veins 2 and 4 of the forewing of *Melanocinclis* are absent, whereas these veins are present in *Tanygona.* Vein 6 is absent in the hindwing of *Melanocinclis;* it is present in *Tanygona.* In the male genitalia the *brachia* of *Melanocinclis* are very slender apically; those of *Tanygona* are shorter and stouter. The configuration of the *lamellae vaginales* of *Melanocinclis* is irregular; the *lamellae vaginales* of *Tanygona* form a straight tube.

The paucity of specimens of the known species of *Melanocinclis* make it difficult to give an accurate statement as to the geographic range of the genus. *M. lineigera* occurs in Florida, and *M. nigrilineella* occurs in Texas and Arizona.

I am placing *E. nigrilineela* Chambers in *Melanocinclis* because the general facies agree very well with the type of the genus. Chambers (1878) was quite correct in questioning the generic placement of *nigrilineella.*

Key to the Species of Melanocinclis based upon the Maculation

1. Forewings dusted with tawny flecks .... *lineigera*
   Forewings dusted with black flecks .... *nigrilineella*

Key to the Species of Melanocinclis based upon the Male Genitalia

1. Right brachium with a lateral process (Fig. 57) .... *lineigera*
   Right brachium without a lateral process (Fig. 56) *nigrilineella*

Melanocinclis lineigera, new species
(Figs. 57, 116, 168)

Tongue white. Labial palpi white; basal half of second segment black, a few ventral black scales before apex; third segment with a black annulation at two-fifths and one at four-fifths; apex black. Antennae with pecten black; scape white with a black saddle on posterior surface, apex white; apical segment fuscous, preceded by one-and-one-half buff-white, one-and-one-half fuscous, one buff-white, one-half fuscous, one buff-white, one-and-one-half fuscous, two buff-white, four-and-one-half fuscous, *etc.* Face and vertex white, lower half of face dark gray with purple reflections, a few black flecks above eyes. Thorax white medially, black laterally, patagia white with tawny flecks laterally. Forewings white overlaid with tawny flecks; a broad oblique black band from base at costal margin to one-half at center; a second black band starting at one-half on costa running to apex of wing below costa; black dorsad of fold from base of wing to one-fourth, sometimes reaching margin; cilia with a black medial line and a fuscous terminal line from apex to a point parallel with dorsal margin. Hindwings shining gray. Abdomen brown-black with ochreous scales dorsally, buff ventrally. Legs shining white; metathoracic tibiae with an oblique black stripe at four-fifths, dorsal surfaces of spurs black, under certain light conditions; metathoracic tarsi with a broad black annulation on middle of first segment, black at apex of second segment and at base of third segment.

Male genitalia: (Fig. 57) R.W.H. slide no. 919.

Female genitalia: (Fig. 116) R.W.H. slide no. 781.

Alar expanse: 5½–6½ mm.

Food plant: *Pinus caribaea* Morelet.

Holotype: ♀, Archbold Biological Station, Highlands Co., Florida, March 31, 1959 (R. W. Hodges), [CU Type No. 3813].

Paratypes: same locality as type, 3 ♂, March 29 and April 4, 1959 [RWH]: Homestead, Florida, 2 ♂, February 9 and March 21, 1959 (D. O. Wolfenbarger), [CPK]; Lake City, Florida, 1 ♂, 1 ♀, reared *ex* Slash Pine cones, emerged February 7, 1951 (C. F. Spears), [USNM]; Siesta Key, Sarasota Co., Florida, 5 ♂, 5 ♀, March 31 through May 3, 1960 (C. P. Kimball), [CPK, RWH].

Other specimens examined: Homestead, Florida, 1 ♂, 2 ♀, February 8 and April 16, 1959 (D. O. Wolfenbarger), [CPK]; Siesta Key, Sarasota Co., Florida, 3 ♂, 2 ♀, February 25 through May 13 (C. P. Kimball), [CPK, RWH].

The tawny flecks on the forewings will separate *lineigera* from *M. nigrilineella.*

Melanocinclis nigrilineella Chambers, new combination.
(Figs. 56, 167)

Eriphia (?) *nigrilineella* Chambers, 1878. Bull. U. S. Geol. Geog. Surv. Terr., 4: 96. Chambers, 1880. Jour. Cincinnati Soc. Nat. Hist., 2: 204, f. 42.

Eriphia nigrilineella, Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52: 540. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 64.

Tongue white. Labial palpi white; second segment black to two-thirds, a few black scales ventrally before apex; third segment with a black annulation at two-fifths and another at four-fifths. Antennae buff-white, pecten ochreous, no pattern of black and white on specimen available. Head white, lower two-thirds of face gray with purple reflections, vertex with lavender reflections. Thorax black medially, white laterally. Forewings white with a light dusting of black flecks; a pattern of two oblique black bands as in *M. lineigera*, but basal one interrupted medially; black at end of fold; cilia white, heavily dusted with black at apex, a few black flecks between apex and dorsal margin, no markings dorsad of wing margin. Hindwings gray. Legs shining white; metathoracic tibiae with an oblique black stripe at four-fifths, dorsal surfaces of spurs black, under certain light conditions; metathoracic tarsi with a broad black annulation on middle of first segment, black at apex of second segment and at base of third segment.

Male genitalia: (Fig. 56) R.W.H. slide no. 921.

Female genitalia: no specimens available.

Alar expanse: 7 mm.

Food plant: unknown.

Type: Museum of Comparative Zoology.

Type locality: Bosque County, Texas.

Specimens examined: 2 ♂. ARIZONA: Madera Canyon, 4880 feet, Santa Rita Mountains, Santa Cruz Co., 1 ♂, June 30, 1959 (R. W. Hodges), [RWH]. TEXAS: Bosque Co., 1 ♂, no date [MCZ].

M. nigrilineella can be separated from *M. lineigera* by the black dusting on the forewings.

Eteobalea, new genus

εῑεός = true, βᾰλιός = spotted
(Figs. 2, 20, 53, 113)

Type: *Gelechia sexnotella* Chambers, 1878.

Head smooth-scaled; tongue scaled, moderately short; maxillary palpi folded over base of tongue; labial palpi recurved, reaching beyond vertex, first and second segments smooth dorsally, second segment tufted ventrally, third segment smooth, second and third segments subequal; antennae three-fourths, pecten present, simple.

Forewings broadly lanceolate, apex acute; 1b furcate basally, sometimes furcate distally; 2 from two-thirds; 2, 3, 4, and 5 equidistant, subparallel; 5 connate with 6, 7, and 8; 6, 7, and 8 stalked; 10 slightly before 3; 11 from two-fifths of cell. Hindwings lanceolate, apex acute; no tuft of scales on costal margin; 8 veins present; 1b simple; 2, 3, 4, and 5 equidistant, subparallel; 6 and 7 stalked, divergent.

Male genitalia: *costae* separate from *valvae;* right *costa* smaller than left one, partially fused with *aedeagus; valvae* lobate, slightly expanded distally; *aedeagus* shaped like a long-necked vase without a well defined base, ankylosed; *cornuti* absent; *tegumen* heavily sclerotized; *tuba analis* emerging between brachia; *tegumen* emarginate apically; left *brachium* larger than right one, apex enlarged, blunt.

Female genitalia: *lamellae vaginales* small, heavily sclerotized, mainly developed anterior to *ostium bursae* with a narrow band encircling posterior part of *ostium bursae; ductus bursae* slender, lightly sclerotized; *corpus bursae* lightly sclerotized; *signa* present.

Eteobalea differs from *Stagmatophora* (Figs. 58, 111) in the following characters: the second segment of the labial palpi is tufted ventrally in *Eteobalea;* rough-scaled in *Stagmatophora.* The second and third segments of the labial palpi are subequal in *Eteobalea*; the second segment is shorter than the third in *Stagmatophora.* In the male genitalia of *Eteobalea* the left *brachium* is large, the apex is blunt and slightly enlarged, the right *brachium* is a blunt lobe; in *Stagmatophora* the *brachia* are slender, subequal, and taper to the apices.

McDunnough (1939) lists six species in *Stagmatophora.* Of these *S. iridella, S. sexnotella,* and *S. wyattella* are transferred to *Eteobalea; S. niphochrysa* is a synonym of *iridella;* and *S. ceanothiella* and *S. gleditschiaeella* are transferred to *Periploca* in the Walshiidae. In addition one new species is described, bringing the number of known species for our fauna to four.

KEY TO THE SPECIES OF ETEOBALEA BASED UPON THE MACULATION

1. Forewings black with white spots 2
   Forewings brown or bronze 3
2. Hindwings light fuscous; base of tongue white, base of forewings usually black .... *sexnotella*
   Hindwings dark fuscous; base of tongue black; base of forewings white .... *wyattella*
3. Base of second segment of labial palpi bronze-black .... *enchrysa*
   Base of second segment of labial palpi white .... *iridella*

KEY TO THE SPECIES OF ETEOBALEA BASED UPON THE MALE GENITALIA

1. Apex of left brachium four or more times width of narrowest part of brachium (Fig. 52) .... *iridella*
   Apex of left brachium less than three times width of narrowest part of brachium 2
2. Apex of left brachium more than twice width of narrowest part of lobe (Fig. 55) .... *wyattella*
   Apex of left brachium less than twice width of narrowest part of lobe 3
3. Left brachium with a lobate medial projection (Fig. 54) .... *enchrysa*
   Left brachium without a medial projection (Fig. 53) *sexnotella*

KEY TO THE SPECIES OF ETEOBALEA BASED UPON THE FEMALE GENITALIA

1. Lamella postvaginalis subtriangular, lightly sclerotized; two, lightly sclerotized signa in form of triangular plates (Fig. 113) .... *sexnotella*
   Lamella postvaginalis not subtriangular, heavily sclerotized; signa heavily sclerotized 2
2. Lamellae vaginales irregularly margined with constriction before anterior termination; signa with irregular margins (Fig. 114) .... *wyattella*
   Genital plate and signa with smooth margins 3
3. Lamellae vaginales subreniform (on right side); signa one-third to one-half length of corpus bursae (Fig. 112) *iridella*
   Lamellae vaginales subquadrate; signa one-seventh to one-eighth length of corpus bursae (Fig. 115) .... *enchrysa*

Eteobalea sexnotella Chambers, new combination
(Figs. 53, 113, 197)

Gelechia sexnotella, Chambers, 1878. Bull. U. S. Geol. Geog. Surv. Terr., 4: 88. Hagen, 1884. Papilio, 4: 99. Riley, *in* Smith, 1891. List of the Lepidoptera of Boreal America, 102.

Mompha sexnotella, Busck, 1902. Jour. New York Ent. Soc., 10: 97. Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52: 543.

Stagmatophora sexnotella, Walsingham, 1907. Proc. U. S. Natl. Mus., 33: 219. Barnes and McDunnough, 1917. Check list of the Lepidoptera of Boreal America, 153. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 64.

Laverna sexnotella, Forbes, 1923. Lepidoptera of New York and neighboring state, Cornell Univ. Agric. Exp. Sta. Mem., 68: 324.

Tongue and maxillary palpi white. Labial palpi white with three black annulations: one at base of second segment, one at two-fifths and one at four-fifths on third segment. Face and vertex white, a fuscous line from base of each antenna to base of tongue, a row of black scales along posterior edge of eyes. Antennae: scape white on ventral surface and at apex, black on dorsal surface; shaft black with fuscous annulations, becoming white on outer third. Thorax black. Forewings black with six shining white spots; basal white spot broken in area of fold. Hindwings light fuscous. Abdomen dirty yellow, last segment fuscous. Legs black; metathoracic tibiae with three white stripes: one at one-fourth, one at two-thirds, and one apical; tarsal segments with white apices; base of first tarsal segment white.

Male genitalia: (Fig. 53) R.W.H. slide no. 830.

Female genitalia: (Fig. 113) R.W.H. slide no. 831.

Alar expanse: 8–14 mm.

Food plant: *Trichostema dichotomum* L., *T. suffrutescens* Kearney. The larva is a stem gall former.

Type: Museum of Comparative Zoology.

Type locality: Bosque County, Texas.

Specimens examined: 75 ♂, 31 ♀. Connecticut: East River, 1 ♂, August 6, 1907 (Chas. R. Ely), [USNM]; same locality, 8 ♂, July 8–21 [MCZ]; Putnam, 1 ♀, May 27, 1933 (A. B. Klots), [ABK]. Florida: Archbold Biological Station, Highlands Co., 2 ♂, 4 ♀, March 27 through April 2, 1959 (R. W. Hodges), [RWH]; same locality, 1 ♂, 1 ♀, July 15–31, 1948 (A. B. Klots), [ABK]; Georgiana, 1 ♂, 1 ♀, gall on *Trichostema dichotomum,* emerged

July 11, 1882 (Wm. Winfield), [USNM]; Longboat Key, Sarasota, 1 ♀, gall on *Trichostema suffrutescens,* emerged January 31, 1945 (J. G. Needham), [CU]; Oneco, 1 ♂, May 28, 1953 (Paula Dillman), [CPK]; Sarasota, 2 ♂, 1 ♀, February 1945 (J. G. Needham), [CU]; Siesta Key, Sarasota Co., 2 ♀, April 24 and May 4, 1960 (C. P. Kimball), [CPK]. KANSAS: Onaga, 1 ♀ [MCZ]. MARYLAND: Frederick, 3 ♂, June 11, 1906 [MCZ]; Hyattsville, 1 ♂, June (A. Bsk), [LACM]; Washington, D. C., 2 ♂, May 21, 1906 (Chas. R. Ely), [USNM]; same locality, 1 ♂, 1 ♀, May and June (A. Bsk), [USNM, MCZ]. MASSACHUSETTS: Barnstable, 8 ♂, 3 ♀, June 5 through July 24 (C. P. Kimball), [CPK]; Magnolia, 1 ♂, June 3, 1908 [USNM]; Martha's Vineyard, 2 ♂, "1–VI and VIII–23" (F. M. Jones), [USNM]. MISSISSIPPI: Biloxi, 1 ♂, June 13, 1917 [CU]; Ocean Springs, 1 ♂, June 28, 1921 (F. H. Benjamin), [USNM]. NEW HAMPSHIRE: Webster, 1 ♀, "6/190" [MCZ]. NEW JERSEY: Essex Co. Park, 3 ♂, August 2–16, 1906 (W. D. Kearfott), [USNM]; Ramsey, 1 ♂, August 19, 1909 [AMNH]. NORTH CAROLINA: Maxton, 7 ♂, 4 ♀, April 23 through August 31, 1944 (A. B. Klots), [ABK]: Southern Pines, 22 ♂, 4 ♀, May through August 31 [USNM]. OHIO: Clermont Co., 1 ♂, reared *ex* gall on *Trichostema dichotomum,* emerged June 1932 (Annette F. Braun), [AFB]; Fort Hill, Highland Co., 2 ♂, 2 ♀, under rearing record B. 1930, emerged June 19 through July 9, 1942 (Annette F. Braun), [AFB]. TEXAS: Bosque Co., 1 specimen, "11/9" [MCZ]. VIRGINIA: Great Falls, 1 ♂, 1 ♀, May 28, 1919 (A. Busck), [USNM]. ONTARIO: Dunrobin: 1 ♀, June 25, 1941 (G. A. Hobbs), [CNC]; Trenton, 1 ♀, June 14, 1908 (Evans), [USNM].

E. sexnotella can be distinguished from *E. wyattella* by the base of the tongue being white.

Eteobalea wyattella Barnes and Busck, new combination
(Figs. 55, 114, 198)

Stagmatophora wyattella Barnes and Busck, 1920. Contributions to the natural history of the Lepidoptera of North America, 4: 222. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 64.

Laverna wyattella, Forbes, 1923. Lepidoptera of New York and neighboring states, Cornell Univ. Agric. Exp. Sta. Mem., 68: 324.

Tongue black at base and on undersurface, white on upper surface and tip. Maxillary palpi gray. Labial palpi white with three black annulations: one at base of second segment, one at one-fifth, and one at four-fifths on third segment. Face and vertex shining white, a collar of black scales, a line of black scales from base of each antenna to base of tongue. Antennae: scape black with a few white scales at apex; shaft with alternating annulations of white and black scales, black at outer four-fifths, followed by alternating black and white. Thorax black. Forewings with shining black and white markings. Hindwings shining dark fuscous. Abdomen dark fuscous dorsally and ventrally on anterior portion of segments, ventral surface shining white. Prothoracic legs black with shining white on inner surface of tibiae, base and apex white; first tarsal segment with a broad black medial annulation; second with a white basal annulation extending distally on dorsal surface; third and fourth segments black; fifth segment white; mesothoracic and metathoracic legs with similar maculation but with more extensive white markings.

Male genitalia: (Fig. 55) R.W.H. slide no. 727.

Female genitalia: (Fig. 114) R.W.H. slide no. 833.

Alar expanse: 13–16 mm.

Food plant: unknown.

Type: United States National Museum.

Type locality: Palos Park, Illinois.

Specimens examined: 22 ♂, 7 ♀. ILLINOIS: Beverly H's, 1 ♂, August 21, 1909 (W. J. Gerhard), [CNHM]; Chicago, 1 ♂, August 14, 1912 [MCZ]; Edgebrook, 2 ♂, 2 ♀, July 15–27 (A. K. Wyatt), [USNM, CNHM]; Palos Park, 2 ♂, 1 ♀, July 15, 1911 (A. K. Wyatt), [USNM]; Putnam Co., 11 ♂, 4 ♀, July 7 through August 8 (M. O. Glenn), [MOG, RWH]. NEW YORK: Ithaca, Six Mile Creek, Tompkins Co., 3 ♂, July 26 through August 8 (J. G. Franclemont), [JGF]; same locality, 1 ♂, July 21, 1939 [CU]; Orient, Long Island, 1 ♂, August 22, 1936 (Roy L. Latham), [CU].

E. wyattella can be distinguished from *E. sexnotella* by the darker color of the hindwings and by the base of the tongue being black. The characters of the male and female genitalia are given in the keys.

Eteobalea iridella Busck, new combination
(Figs. 52, 112, 166)

Mompha iridella Busck, 1907. Proc. Ent. Soc. Washington, 8: 96.

Stagmatophora iridella, Barnes and McDunnough, 1917. Check list of the Lepidoptera of Boreal America, 153. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 64.

Stagmatophora niphochrysa Meyrick, 1930. Exot. Micr., 3: 546. **new synonymy.** McDunnough, 1939. Mem. S. California Acad. Sci., 2: 64.

Tongue, maxillary palpi, labial palpi, face, and vertex white. Antennae dark brown with light fuscous annulations along shaft. Thorax gold-brown, patagia white. Forewings gold-brown with white and metallic gold spots; cilia white at apex, light fuscous dorsally. Hindwings light fuscous, almost white at base. Legs gold-brown basally; metathoracic tibiae white with a brown annulation at one-half and another at four-fifths; tarsi white; a dorsal median brown patch on first segment; brown basally on second, third, and fourth segments; fifth segment brown. Abdomen brown with apices of segments light fuscous. Some specimens much darker, having gold-brown replaced by dark brown. In this form third segment of labial palpi sometimes brown except for white apex; and face, vertex, and thorax brown.

Male genitalia: (Fig. 52) R.W.H. slide no. 382.

Female genitalia: (Fig. 112) R.W.H. slide no. 381.

Alar expanse: 9–13 mm.

Food plant: unknown.

Type: United States National Museum.

Type locality: Claremont, California.

Specimens examined: 48 ♂, 30 ♀. ARIZONA: Mayer, 1 ♂, June 3, 1959 [MOG]. CALIFORNIA: Berkeley, 1 ♀, April 2, 1959 (D. D. Linsdale), [RWH]; Berkeley-U. of C., 1 ♂, 1 ♀, April 4, 1959 (Chemsack and Powell), [JAP]; Colfax, Placer Co., 1 ♂, April (A. H. Vachell), [USNM]; Gavilan Hills, 1 ♀, July 19, 1939 (C. R. Henne), [RWH]; Hastings Res. near Jamesburg, 1 ♂, May 3, 1958 (J. A. Powell), [JAP]; Loma Linda, 4 ♂, 3 ♀, February 17 through August 21 (G. R. Pilate), [AFB, USNM]; Los Angeles Co., 2 ♂, 2 ♀, August (Koebele), [CAS]; nine miles E. King City, Monterey Co., 1 ♂, March 29, 1959 (C. W. O'Brien), [JAP]; Olancha, Inyo Co., 1 ♂, "1–7·V" [USNM]; Oroville, 29 ♂, 18 ♀, May 29 through July 15 (H. H. Keifer), [CAS, RWH]; Palm Springs, 1 ♀, March 26, 1917 [AFB]; Sacramento, 2 ♂, July 12, 1933 (H. H. Keifer), [USNM]; San Diego, San Diego Co., 1 ♂, August 31, 1921 (E. Piazza), [USNM]; San Diego, 2 ♀, May 31, 1924 and August 30, 1921 [USNM]; Webber Creek nr. Camino, El Dorado Co., 3 ♂, June 25, 1959 (J. A. Powell), [JAP]. TEXAS: Fort Davis, 5000 ft., "5.28" [USNM]. WASHINGTON: Pullman, 1 ♂, July 12, 1898 (C. V. Piper), [USNM].

E. iridella can be distinguished from *E. enchrysa* by the base of the second segment of the labial palpi being white. See the comments under *enchrysa* for the diagnostic characters of the male and female genitalia.

Eteobalea enchrysa, new species

(Figs. 54, 115, 199)

Tongue slightly reduced, white. Maxilary palpi white. Labial palpi white, base of second segment burnished brown on outer surface, third segment with a black annulation at one-fourth and another at five-sixths. Antennae brown-black, undersurface and apex of scape white. Face and vertex white. Thorax brown, disc with purple reflections, patagia and collar burnished brown. Forewings burnished brown with irregular pattern of metallic lead colored spots from one-fourth to apex of wing, also along outer one-third of dorsal margin; a short subcostal white patch at one-fourth, another at one-half; a costal patch of white scales from two-thirds to five-sixths; cilia dark fuscous. Hindwings fuscous. Undersurface of all wings with white at apices. Abdomen gray-brown, apex of last segment white. Legs burnished gray-brown; metathoracic tibiae with a subdorsal, post medial, and apical white stripe on outer surface; inner surface white; apices of tarsal segments white.

Male genitalia: (Fig. 54) R.W.H. slide no. 474.

Female genitalia: (Fig. 115) R.W.H. slide no. 596.

Alar expanse: 13–16 mm.

Food plant: *Trichostoma lanatum* Ben.

HOLOTYPE: ♂, Cajon Valley, San Bernardino Co., CALIFORNIA, emerged June 30, 1938 (C. Dammers), [USNM Type No. 66082].

PARATYPES: 17 ♂, 9 ♀, same data as type, June 16 through July 20, 1938 [USNM, CU, LACM, MCZ, RWH].

E. enchrysa can be distinguished from *E. iridella* by the base of the second segment of the labial palpi being bronze-black; in *iridella* this area is white. In the male genitalia the apex of the left *brachium* of *enchrysa* is less than twice the width of the narrowest part of the *brachium;* in *iridella* this structure is four or more times the width of the narrowest part. The *signum* of the female genitalia of *enchrysa* is one-third to one-half the length of the *corpus bursae*; in *iridella* the signum is one-seventh to one-eighth the length of the *corpus bursae.*

Sathrobrota, new genus

σαθρός = decayed, βρωτήρ = eating

(Figs. 5, 13, 59, 117)

Type: *Batrachedra rileyi* Walsingham, 1882.

Head smooth-scaled; tongue scaled, moderately developed; maxillary palpi folded over base of tongue; labial palpi recurved, reaching beyond vertex, smooth-scaled, second segment thickened ventrally, third segment longer than second, apex acute; antennae two-thirds, simple, pecten present, scape enlarged for entire length, width equals one-half length. Metathoracic tibiae with long dorsal scales.

Forewings lanceolate, apex subfalcate; 12 veins present; 1b furcate basally; 2 and 3 approximate at base, parallel; 5, 6, 7, and 8 stalked; 10 almost opposite 2; 11 from two-thirds on cell. Hindwings sublinear; a series of scales on costal margin; 8 veins present; 1b simple; 2, 3, and 4 subparallel, arising equidistant; 5 present at margin; 6 and 7 stalked, divergent.

Male genitalia: *valvae* lanceolate, rounded apically, fused basally; right *costa* separate from *valva,* linear; left *costa* reduced; *aedeagus* ankylosed; *uncus* and *socii* absent; *brachia* heavily sclerotized, cylindrical, apices acute, left *brachium* longer than right one.

Female genitalia: *bursa copulatrix* membranous, *signa* small (if present); *lamellae vaginales* forming a cylinder.

Sathrobrota differs from *Pyroderces* (Figs. 62, 119) in the following characters: veins 2 and 3 in the forewings of *Sathrobrota* are approximate; distant in *Pyroderces.* In the male genitalia the right *costa* of *Sathrobrota* is free and linear; that of *Pyroderces* is stout and fused basally to the *aedeagus.* The *brachia* of *Sathrobrota* have acute apices; those of *Pyroderces* are blunt. In the female genitalia of *Sathrobrota* the *lamellae vaginales* are fused and are long and cylindrical; those of *Pyroderces* are short, encircling the *ostium.*

Two species of *Sathrobrota* are known to occur within the geographic limits specified by this paper. One, *S. rileyi,* is a scavenger which has been reared from rotten cotton bolls, corn husks, Milo maize, and the flower heads of castor bean and *Mesosphaerum rugosum.* The other species, *S. badia,* is also a scavenger; however, the hosts are different. They are peach mummies, loquat mummies, limes, grapefruit, cabbage, blossoms of cocoanut, bananas, infected cones of *Pinus* spp., and elm leaves. Unfortunately, the two species have been confused with the result that the literature is not to be trusted as to the identity of the species.

Walsingham's original description of *rileyi* states that the specimens were reared from cotton bolls, restricting the name to this species. It has been suggested that *S. stigmatophora* Walsingham was the second species of *Sathrobrota* which occurred in the United States, however, examination of the specimens determined as *stigmatophora* has revealed that they are *rileyi*. Also, the description of *stigmatophora* suggests that the name may be a synonym of *rileyi*. On this basis I have described the second species of *Sathrobrota* as new.

KEY TO THE SPECIES OF SATHROBROTA BASED UPON THE MACULATION

1. Outer surface of metathoracic tibiae brown basally and distally, median white streak with a dorsolateral row of brown scales .... *rileyi*
   Outer surface of metathoracic tibiae tawny before median annulation, brown beyond it, median annulation unicolorous .... *badia*

KEY TO THE SPECIES OF SATHROBROTA BASED UPON THE MALE GENITALIA

1. Apex of right costa blunt (Fig. 59) .... *rileyi*
   Apex of right costa acute (Fig. 60) .... *badia*

KEY TO THE SPECIES OF SATHROBROTA BASED UPON THE SEVENTH ABDOMINAL SEGMENT OF THE FEMALE

1. Posterior margin of seventh sternite emarginate (Fig. 117) *rileyi*
   Posterior margin of seventh sternite convex (Fig. 118) ...... *badia*

Sathrobrota rileyi Walsingham, new combination
(Figs. 59, 117, 169)

Batrachedra rileyi Walsingham, 1882. Trans. American Ent. Soc., 10: 198. Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52: 534.

Pyroderces rileyi, Durrant, 1912. Bull. Ent. Res., 3: 207, f. 3. (*partim*). Busck, 1917. Jour. Agric. Res., 9: 365, ff. 7 B, 8 E. (*partim*). Heinrich, 1921. Jour. Agric. Res., 20: 820. (*partim*). Forbes, 1923. Lepidoptera of New York and neighboring states, Cornell Univ. Agric. Exp. Sta. Mem., 68 : 327. (*partim*). McDunnough, 1939. Mem. S. California Acad. Sci., 2 : 64.

Tongue pale buff-white basally, yellow distally. Labial palpi white with tinge of buff; second segment with a broad tawny band on outer surface at one-fifth, a tawny annulation at three-fifths, apex tawny; third segment with three brown annulations: one postbasal, one medial, and one preapical. Antennae: pecten brown, scape buff-white with tawny dusting on dorsal surface, apex of scape pale, shaft white to buff-white ventrally and on distal half of each segment dorsally. Face buff-white, vertex pale tawny. Thorax pale buff-white overlaid with tawny. Forewings buff-white heavily overlaid with tawny, overlaid with fuscous on costal half of wing; a transverse series of black scales at one-fourth, another at one-half; an oblique brown streak in costal cilia before apex; two short brown lines forming an angle in dorsal cilia, apex of angle at apex of wing; cilia pale buff-brown. Hindwings fuscous-brown, cilia paler. Abdomen buff-white dorsally, cream-white ventrally. Metathoracic tibiae brown on outer surface; a short oblique white patch from ventral surface at base; an oblique white streak at one-half, interrupted dorsally by brown scales; apex white; middle portion of tibial spurs black; tarsal segments buff-white with brown basally on dorsal surface.

Male genitalia: (Fig. 59) R.W.H. slide no. 915.

Female genitalia: (Fig. 117) R.W.H. slide no. 1033.

Alar expanse: 9–12 mm.

Food plant: scavenger, recorded from the following materials: rotten cotton bolls, cotton seed, corn, Milo maize, stems of corn, corn husks, flowers of castor bean, flower heads of *Mesosphaerum rugosum*.

Type: British Museum (Natural History).

Type locality: Savannah, Georgia.

Specimens examined: 19 ♂, 19 ♀. ARIZONA: Yuma, Webster Co., 2 ♂, 3 ♀, reared from Milo maize, emerged October 10, 1922 (V. L. Wildermuth), [USNM]. ARKANSAS: Center Point, 2 ♂, 11–19 and 11–25, 1915 (C. M. Packard), [USNM]. GEORGIA: Columbus, 2 ♀, February 9 and March 29, 1915 [USNM]; Thomasville, 2 ♂, bred from cotton seed, no date (G. D. Smith), [USNM]. LOUISIANA: Baton Rouge, 3 ♂, 1 ♀, on corn, emerged September 15 through October 15, 1894 [USNM]; Monroe, 1 ♂, 1 ♀, from old cotton boll, emerged October 22 and 23, 1900 [USNM, RWH]. MARYLAND: Washington, 2 ♂, 4 ♀, no date (A. Busck), [USNM]. MISSISSIPPI: Batesville, 1 ♂, 1 ♀, 1–2–1915 [USNM]; Greenwood, 1 ♀, June 16, 1915 (J. M. Langston), [USNM]. TEXAS: Beeville, 1 ♂, issued from cotton bolls, November 21, 1895 [USNM]; Beeville, 1 ♂, corn husks, emerged September 13, 1895 [USNM]; Beeville, 2 ♀, April 25, 1896 [USNM, RWH]; Columbia, 2 ♀, from rotten cotton bolls, emerged December 25, 1879 (E. A. Schwarz), [USNM]; Corpus Christi, 1 ♂, September 21, 1943 (W. M. Gordon), [CU]; Smith Point, 1 ♂, from old bolls of cotton, emerged October 17, 1923 (L. J. Bottimer), [USNM]; Smith Point, flower heads of *Mesosphaerum rugosum*, emerged October 18, 1923 (L. J. Bottimer), [USNM]; Welasco, 1 ♀, reared from flowers of castor bean, emerged August 30, 1952 (P. T. Riherd), [USNM].

The characters given in the keys will serve to distinguish between *rileyi* and *S. badia*.

Sathrobrota badia, new species
(Figs. 60, 118, 170)

Pyroderces rileyi Busck, 1917. Jour. Agric. Res., 9: pl. 8, f. D. (misidentification.)

Tongue pale buff-white basally, yellow distally. Labial palpi white with tinge of buff; second segment with a broad tawny band on outer surface at one-fifth, a tawny annulation at three-fifths, apex tawny; third segment with three brown annulations: one postbasal, one medial, and one preapical. Antennae: pecten brown, scape buff-white with tawny dusting on dorsal surface, apex of scape pale, shaft white to buff-white ventrally and on distal half of each segment dorsally. Face buff-white, vertex pale tawny. Thorax pale buff-white overlaid with tawny. Forewings heavily overlaid with tawny; costa fuscous to one-half; pattern composed of black tipped scales preceded or followed by buff-white scales; a few black scales on costal margin at one-eighth; a broken transverse row of black scales at one-fourth, not reaching costal or dorsal margin; a subtriangular to quadrate patch of blackish scales at one-half in center of wing; a subcostal series of black scales from three-fifths to four-fifths; a row of dark brown scales along outer margin from tornus to apex of wing; a short brown cross at apex; cilia gray-brown. Hindwings fuscous. Abdomen buff-brown with lavender reflections dorsally, cream-white with some gray ventrally. Metathoracic tibiae tawny on basal two-fifths of outer surface, an oblique white streak from middle tibial spur, outer surfaces of distal half of tibiae dark brown, apex pale buff-white, tibial spurs white or pale buff-white with black at middle; tarsal segments dark brown basally on dorsal surface, pale apically.

Male genitalia: (Fig. 60) R.W.H. slide no. 1031.

Female genitalia: (Fig. 118) R.W.H. slide no. 595.

Alar expanse: 7½–11½ mm.

Food plant: scavenger, recorded from the following materials: pine cones infested by *Dioryctria* (Lepidoptera: Pyralidae), rust infected cones of *Pinus elliottii, Pinus palustris,* pods of *Cassia occidentalis,* peach mummy, mummy fossil of loquat, limes, grapefruit, bananas, cabbage, blossoms of cocoanut, and elm leaves.

HOLOTYPE: ♀. So. FLORIDA, in pine cones infested by *Dioryctria,* emerged June 16, 1931 (J. K. Small), [USNM Type No. 66083].

PARATYPES: same data as type, 3 ♂, 1 ♀, June 16–18, 1931 [USNM, RWH]; Santa Ana, Orange So., CALIFORNIA, 27 ♂, 28 ♀, reared from peach mummy, collected March 26, 1943, emerged April 1–16, 1943 (H. H. Keifer), [CAS, RWH, JAP]; Costa Mesa, California, 1 ♀, reared from peach mummy, collected November 10, 1942, emerged December 16, 1942 (Gammon), [CAS]; Cocoanut Grove, FLORIDA, 2 ♂, 4 ♀, from blossoms of cocoanut, May 16–23, 1916 (H. M. Matheson), [USNM, CU]; Miami, Dade Co., Florida, 6 ♂, 4 ♀, mummy fossil of loquat, July 1, 1910 [USNM]; Siesta Key, Sarasota Co., Florida, 10 ♂, 6 ♀, January 2 through May 11 (C. P. Kimball), [CPK, RWH, BMNH]; Archbold Biological Station, Highlands Co., Florida, 1 ♂, 1 ♀, April 2 and 4, 1959 (R. W. Hodges), [RWH]; WASHINGTON, D. C., 2 ♂, 2 ♀, reared from *Pinus palustris,* June 28 and July 14, 1917 (G. G. Hedgecock), [USNM, RWH]; Great Falls, VIRGINIA, 1 ♂, elm leaves, July 17, 1916 [USNM].

Other specimens examined: Mobile, ALABAMA, 1 ♀, April 19, 1922 (Dukes), [USNM]; Lake Alfred, FLORIDA, 1 ♂, larva in pod of *Cassia occidentalis,* August 9, 1929 (L. J. Bottimer), [USNM]; Matheson's Key, 1 ♂, 2 ♀, limes, May 1918 (G. F. Meznette), [USNM]; Osceola Natl. Forest, Baker Co., Florida, 1 ♂, reared from rust infected cones of *Pinus elliottii,* June 28, 1957 (E. P. Merkel), [USNM]; Palmetto, Florida, 1 ♀, cabbage, June 12, 1945 [USNM]; Royal Palm State Park, Florida, 1 ♀, no date (F. M. Jones), [USNM]; 3 miles S. Clarcona, Florida, bred from grapefruit, emerged September 25–30, 1930 (F. H. Benjamin), [USNM]; Siesta Key, Sarasota Co., Florida, 2 ♂, 5 ♀, December 1 through April 19 (C. P. Kimball), [CPK]; Boothville, LOUISIANA, 5 ♀, *ex* bananas, March 8, 1945 [USNM].

LIMNAECIA Stainton
(Figs. 1, 12, 63, 121)

Type: *Limnaecia phragmitella* Stainton, 1851. Monobasic.

Limnaecia Stainton, 1851. Suppl. Cat. Brit. Tineina, 4. Wocke, *in* Heinemann, 1877 [1876]. Die Schmetterling Deutschlands und der Schweiz, 2: 421. Staudinger and Rebel, 1901. Catalog der Lepidopteren des Palaearctischen Faunengebiets, pt. 2: 187. Spuler, 1910. Schmetterlinge Europas, 2: 384, f. 142. Forbes, 1923. Lepidoptera of New York and neighboring states, Cornell Univ. Agric. Exp. Sta. Mem., 68: 324, ff. 181, 194. Fletcher, 1928. Catalogue of Indian Insects, pt. 16: 18. Fletcher, 1929. Mem. Dept. Agric. in India, Ent. Ser., 11: 127. Diakonoff, 1954. Verh. Akad. Wet. Amsterdam, 50, no. 1: 74.

Laverna Stainton, 1854. Insecta Britannica. Lepidoptera: Tineina, 238. (*partim.*)

Limnoecia Meyrick, 1888. Trans. New Zealand Inst., 172. (emendation). Busck, 1901. Proc. Ent. Soc. Washington, 4: 421.

Anybia Meyrick, 1928. Revised Handbook of British Lepidoptera, 652. (incorrect association). Fletcher, 1928. Catalogue of Indian Insects, pt. 16: 19. (as synonym of *Limnaecia.*) Fletcher, 1929. Mem. Dept. Agric. in India, Ent. Ser., 11: 17, 127. (as synonym of *Limnaecia*).

Lymnaecia Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52: 537. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 64.

The synonymy given by Fletcher (1928) and cited with doubt by Diakonoff (1954) is not repeated. Study of the type species involved should be made before the list is accepted.

Head smooth-scaled; tongue scaled, well developed; maxillary palpi folded over base of tongue, slightly drooping; labial palpi recurved, reaching well beyond vertex, smooth-scaled, third segment longer than second, apex acute; antennae two-thirds to four-fifths, pecten present, ciliate in male, simple in female.

Forewings narrow, elongate, apex acute; 12 veins present; 1b furcate basally; 2 from two-thirds on cell; 2, 3, and 4 equidistant; 7 and 8 stalked; 10 from three-fourths on cell; 11 from two-fifths on cell. Hindwings narrow, elongate, apex acute; 8 veins present; 2 from three-fifths on cell; 2, 3, 4, and 5 equidistant; 5, 6, and 7 approximate; 6 and 7 diverging.

Male genitalia: *valvae* asymmetrical; costal area separate or heavily sclerotized and connected to valva; *aedeagus* short, ankylosed, basal process present; arms of *gnathos* separate, left *brachium* larger than right one, heavily sclerotized.

Female genitalia: *bursa copulatrix* membranous; *signa* present; *lamellae vaginales* forming a long heavily sclerotized tube; *apophyses anteriores* broad, heavily sclerotized; *apophyses posteriores* sinuate distally.

One species of *Limnaecia* is known to occur within the region considered by this paper; and it is reported by Meyrick (1928) to be found in Europe, North Africa, Australia, and New Zealand. He believed that it has been dispersed in the larval stage by being blown with the down of *Typha,* the food plant of the larva.

Limnaecia phragmitella Stainton
(Figs. 63, 121, 171)

Limnaecia phragmitella Stainton, 1851. Suppl. Cat. Brit. Tineina, 4. Spuler, 1910. Schmetterlinge Europas, 2: 384, pl. 89, f. 66. Forbes, 1923. Lepidoptera of New York and neighboring states, Cornell Univ. Agric. Exp. Sta. Mem., 68: 324.

Laverna phragmitella Stainton, 1854. Insecta Britannica. Lepidoptera: Tineina, 238. Stainton, 1870. Natural History of the Tineina, 11: 150–159, pl. 4.

Limnoecia phragmitella, Meyrick, 1895. Handbook of British Lepidoptera, 675. Busck, 1901. Proc. Ent. Soc. Washington, 4: 421.

Lymnaecia phragmitella, Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52: 537. Claassen, 1921. Typha Insects, Cornell Univ. Agric. Exp. Sta. Mem., 47: 487. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 64.

Tongue buff, apical one-third very lightly scaled. Labial palpi buff-white, a few pale brown scales on dorsolateral surface of first segment, second segment with a few pale brown scales subbasally and subapically, third segment with an internal and an external brown line. Antennae buff, ventral surface of scape with a few pale brown scales at base, scape with an anterior brown line continued on shaft as a series of dots to one-half. Face and vertex buff-brown. Forewings buff-brown with a medial brown spot at one-third, another brown spot at two-thirds, four or five pale brown spots on costal margin on apical one-third, a faint pale brown spot on dorsal margin near vertex, a pale brown spot on fold at two-thirds, internal brown spots encircled or partially bordered by white scales, costal spots bordered internally by white scales, a gray streak from inner medial dot to apex complete or partially developed, cilia shining buff. Hindwings gray-brown, cilia buff. Abdomen buff dorsally, buff-white ventrally. Legs buff to buff-brown, prothoracic tibiae gray-brown with a dorsal buff line.

Male genitalia: (Fig. 63) R.W.H. slide no. 597.

Female genitalia: (Fig. 121) R.W.H. slide no. 3.

Alar expanse: 15–20 mm.

Food plant: *Typha latifolia* L. and *T. angustifolia* L. Claassen (1921) gives the following discussion of the habits of the immature stages:

''The larvae restrict their work to the head of the plant, except occasionally when they bore into the stem to transform. The young larvae feed on the tender styles of the pistillate flowers, but as these grow larger and become dry, the larvae move farther inward and eat the seeds of the plant. As cold weather approaches, they migrate still farther inward, and finally locate near the rachis of the flower spike, where they often eat away the basal part of the little stalks which bear the seeds. The larvae spin an abundance of silk with which they tie the down, or pappus, together, thus keeping it from being torn off or blown away.

''The cat-tail heads which are infested by these larvae present a striking appearance. The silk spun by the larvae holds the downy material together and does not allow the seeds to escape, but the heads fluff out. . . .

''The larvae overwinter in the half-grown stage in the head of the plant, the fluffy material of the fruiting spike being their protection.

''In the latter part of May or early June the larvae attain their full growth. Then, in the midst of the downy material, the larvae spin their thin, tough, white cocoons and transform to the pupal stage. Many of the larvae, leaving the heads, go down and bore into the stem of the cat-tail plant, forming burrows which they line with silk; and there they pupate.''

Type: British Museum (Natural History).

Type locality: ? England.

Specimens examined: 100 ♂, 108 ♀. COLORADO: Watkins, Adams Co., 4 ♂, July 4 and 5, 1927 [CU]; Fort Collins, 1 ♀, July 19, 1930 (A. B. Klots), [ABK]; Fountain Valley School, Colorado Springs, 1 ♂, July 12–19, 1932 (A. B. Klots), [ABK]. ILLINOIS: Arlington Hts., 1 ♂, July 10, 1930 (A. L. McElhose), [CNHM]; Putnam Co., 3 ♂, 5 ♀, June 20 through July 25 (M. O. Glenn), [MOG, CNHM, INHS]. MARYLAND: Berwyn, 2 ♀, September 2, 1913 (P. L.

Boone), [USNM]; Twining, 1 ♀, October 1, 1899 (A. Busck), [USNM]; Washington, D. C., 10 ♂, 3 ♀, June through September 30 (A. Busck), [USNM, MCZ]. MASSACHUSETTS: Martha's Vineyard, 2 ♂, 6 ♀, July 25 through August 6 (F. M. Jones), [USNM, CPK]; Barnstable, 1 ♀, July 14, 1954 (C. P. Kimball), [CPK]; Nantucket, 1 ♀, July 19, 1945 (C. P. Kimball), [CPK]; Watertown, 1 ♀, on *Typha* sp., emerged May 7, 1921 (W. O. Ellis), [USNM]. MICHIGAN: Bath, Clinton Co., 9 ♂, 12 ♀, reared *ex Typha,* emerged June 25 through July 9, 1958 (R. W. Hodges), [RWH]; Isle Royale, Keweenaw Co., 1 ♂, July 27, 1957 (R. W. Hodges), [RWH]; Midland Co., 1 ♂, June 30, 1941 (R. R. Dreisbach), [CU]. NEW JERSEY: Anglesea, 1 ♂, no date or collector [MCZ]; Montclair, 7 ♂, 3 ♀, June 25 through July 10 (W. D. Kearfott), [USNM]; Newark, 3 ♂, 2 ♀, July 13 (A. J. Weidt), [USNM]; Oakland, 1 ♀, August 21, 1948 (C. P. Kimball), [CPK]; Short Hills, 1 ♂, 4 ♀, July 1, 1888 (Beutenmueller), [CU, USNM, MCZ]. NEW YORK: Buffalo, 1 ♂, July 2, 1905 [CU]; East Aurora, 1 ♀, July 20, 1912 [CU]; Ilion, 1 ♀, July 3, 1912 (H. McElhose), [CNHM]; Irving, 1 ♀, July 22, 1917 [CU]; Ithaca, 14 ♂, 12 ♀, June 26 through August 8 [CU]; Six Mile Creek, Ithaca, 1 ♀, August 10, 1956 (J. G. Franclemont), [JGF]; McLean Bogs Reserve, Tompkins Co., 1 ♂, 23 ♀, July 17–22 (J. G. Franclemont), [CU, JGF]; Mattituck, Long Island, 1 ♂, July 6, 1933 (Roy Latham), [CU]; Minetto, Oswego Co., 5 ♂, 1 ♀, June 22–24, 1938 (W. T. M. Forbes), [CU]; New Windsor, 1 ♀, no date given [USNM]; Orient, Long Island, 3 ♂, 1 ♀, May 12 through June 16, 1934 and September 9, 1934 (Roy Latham), [CU]; North Collins, 10 ♂, 10 ♀, June 27 and 28, 1938 (W. T. M. Forbes), [CU]; Riverhead, Long Island, 1 ♀, July 1, 1934 (Roy Latham), [CU]; Rochester, 1 ♀, July 8, 1933 (A. B. Klots), [ABK]. OHIO: Cincinnati, 1 ♂, reared, emerged June 10, 1922 (Annette F. Braun), [CAS]. PENNSYLVANIA: Germantown, 1 ♂, June 21 [MCZ]; Hazelton, 5 ♂, 1 ♀, June 8 through 24 (Dietz), [USNM, MCZ]; Mt. Airy, 1 ♂, 1 ♀, June 25 [USNM, MCZ]; Oak Station, Alleghany Co., 3 ♂, June 25 through July 1 (Fred Marloff), [USNM, CNHM]. ONTARIO: Charlton, 1 ♀, July 25, 1932 (H. S. Parish), [CU]; Geraldton, 1 ♀, July 14–19, 1955 (A. B. Klots), [ABK]; Ottawa, 1 ♂, July 4, 1925 (C. H. Curran), [CNC]; Ottawa, 1 ♀, July 14, 1931 (C. H. Young), [CNC]; Toronto, 1 ♀, June 1, 1931 (H. S. Parish), [CU]; Trenton, 1 ♀, July 16, 1907 (Evans), [USNM]. QUEBEC: St. Johns, 1 ♀, July 1, 1915 (W. Chagnon), [USNM].

Comparison with the illustration of the wings of *L. phragmitella*

(Fig. 171) should suffice to separate this species from the other cosmopterigids.

This species appears to be very local and usually does not fly far from its breeding area.

TELADOMA Busck
(Figs. 9, 14, 61, 120)

Type: *Teladoma helianthi* Busck, 1932. Original designation.

Teladoma Busck, 1932. Proc. Ent. Soc. Washington, 34: 17. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 63.

Head smooth-scaled; tongue short, scaled; labial palpi smooth-scaled, recurved, reaching vertex, slightly tufted on ventral surface of second segment, second segment longer than third, apex of third segment acute; antennae one-half to two-thirds, pecten present, composed of many scales, ciliate in male, simple in female. Dorsal surface of mesothoracic and metathoracic tibiae with long scales.

Forewings lanceolate; 10 veins present; 1b furcate basally; 2 and 3 absent; 4 and 5 connate; 7 and 8 stalked, 7 to costa; 11 from middle of cell. Hindwings sublanceolate to linear; 8 veins present; 1 weak; 2, 3, and 4 arising equidistant; 6 and 7 parallel basally, slightly diverging distally.

Male genitalia: *aedeagus* linear; *cornuti* absent; *aedeagus* armed externally with a large spine; *tegumen* heavily sclerotized with lateral lobes; arms of *gnathos* fused to form a spine; *uncus* and *socii* absent.

Female genitalia: *lamellae vaginales* united to form a projecting tube; *signa* absent; *ductus bursae* not sclerotized; *apophyses anteriores* united at base.

Paratheta astigmatica Meyrick is transferred to *Teladoma* on the basis of a male paratype in the United States National Museum, and two new species are described, bringing the number of species known from North America north of Mexico to four. There is a specimen of another new species in the Cornell Collection; however, its condition is too poor to warrant description. The distribution records of the known species indicate that the genus has its center of distribution in the Midwest and Southwest with a probable extension into Sonora and Chihuahua.

KEY TO THE SPECIES OF TELADOMA BASED UPON THE MACULATION

1. Forewings buff-gray 2
   Forewings gray 3

2. Hindwings brown; discal spot of forewings absent .... *astigmatica*
   Hindwings gray to gray-brown; discal spot of forewings present .... *helianthi*
3. Hindwings sublanceolate; tendency to have spots above fold on forewings (Fig. 174) .... *murina*
   Hindwings linear; no tendency to have spots on forewings *incana*

Key to the Species of Teladoma based upon the Male Genitalia

1. Lateral projections of tegumen asymmetrical 2
   Lateral projections of tegumen symmetrical (Fig. 65) .... *astigmatica*
2. Gnathos slender, apex recurved 3
   Gnathos stout, apex straight (Fig. 61) .... *helianthi*
3. Projection on left side of tegumen single (Fig. 64) .... *incana*
   Projection on left side of tegumen double (Fig. 66) .... *murina*

Teladoma helianthi Busck

(Figs. 61, 120, 172)

Teladoma helianthi Busck, 1932. Proc. Ent. Soc. Washington, 34: 17. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 63.

Head, thorax, and forewings covered with light gray scales with flecks of darker gray on them. Labial palpi short, apex of second segment gray. Forewings generally unicolorous, costal margin darker, sometimes with a dark gray spot above end of fold. Hindwings gray. Abdomen gray-brown dorsally, pale gray ventrally. Legs pale gray basally, dark gray distally; metathoracic tibiae with dense covering of long pale scales dorsally; apices of tarsal segments pale gray.

Male genitalia: (Fig. 61) A. Busck slide.

Female genitalia: (Fig. 120) A. Busck slide.

Alar expanse: 6–12 mm.

Food plant: *Helianthus* and *Xanthium*.

Type: **Lectotype**, present designation. ♂, East St. Louis, ILLINOIS, reared from sunflower leaves, emerged June 30, 1930 (Satterthwait), [USNM].

Type locality: East St. Louis, Illinois.

Specimens examined: 19 ♂, 11 ♀. CALIFORNIA: San Diego, 1 ♂, July 28, 1923 [LACM]. ILLINOIS: East St. Louis, 14 ♂, 11 ♀, reared from sunflower leaves, emerged June 23 through August 25, 1930

(Satterthwait), [USNM]. Oklahoma: Oklahoma City, 3 ♂, August 2–21, 1955 (D. R. Davis), [DRD]. Texas: Devers, 1 ♂, June 21, 1917 [CU].

T. helianthi and *T. astigmatica* are similar in respect to maculation; however, the presence of a discal spot in *helianthi* will usually separate them. The stout *gnathos* and asymmetrical projections of the *tegumen* will separate *helianthi* from the other species of *Teladoma*.

Teladoma astigmatica Meyrick, new combination
(Figs. 65, 173)

Paratheta astigmatica Meyrick, 1928. Exot. Micr., 3: 467. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 77. Clarke, 1941. Proc. U. S. Natl. Mus., 90: 39.

Maculation as for *T. helianthi,* the general facies slightly browner than *helianthi.* Labial palpi and distal portion of legs pale gray.

Male genitalia: (Fig. 65) R.W.H. slide no. 979.

Female genitalia: no specimens available.

Alar expanse: 12–12 ½ mm.

Food plant: unknown.

Type: British Museum (Natural History).

Type locality: Bent, 7,000 ft., New Mexico.

Specimens examined: 1 ♂. Texas: Fort Davis, 5,000 feet, 1 ♂, "10.27" [USNM].

T. astigmatica can be distinguished from the other species of *Teladoma* by the symmetrical projections of the *tegumen* in the male genitalia.

Teladoma murina, new species
(Figs. 66, 174)

Head, thorax, forewings, abdomen, and legs dark gray. Maculation as for *T. helianthi.* Forewings often with a median gray-brown spot above middle of fold and another above end of fold, a few gray-brown scales at two-thirds on fold.

Male genitalia: (Fig. 66) R.W.H. slide no. 990.

Female genitalia: no specimens available.

Alar expanse: 8–9 ½ mm.

Food plant: unknown.

Holotype: ♂, Peña Blanca Canyon, Santa Cruz Co., Arizona, August 26, 1959 (R. W. Hodges), [CU Type No. 3804].

Paratypes: same locality as type, 7 ♂, August 24 and 26, 1959 [CU, RWH, USNM].

The mouse-gray color and presence of spots on the forewings will separate *murina* from *T. incana.* In the male genitalia the double projection on the left side of the tegumen will separate *murina* from *incana.*

Teladoma incana, new species

(Figs. 64, 175)

Head, thorax, forewings, abdomen, and legs dark gray. Second segment of labial palpi with a subapical annulation of dark gray followed by paler gray at apex. Forewings immaculate.

Male genitalia: (Fig. 64) R.W.H. slide no. 1005.

Female genitalia: no specimens available.

Alar expanse: 8 mm.

Food plant: unknown.

Holotype: ♂, Putnam Co., Illinois, July 10, 1959 (M. O. Glenn), [USNM Type No. 66084].

T. incana can be separated from *T. murina* by the lack of markings on the forewings and the narrower hindwings. The single projection on the left side of the *tegumen* and the long slender *gnathos* in the male genitalia will distinguish *incana* from *murina.*

TRICLONELLA Busck

(Figs. 6, 11, 67, 123)

Type: *Triclonella pergandeella* Busck, [1901]. Original designation.

Triclonella Busck, 1900 [1901]. Jour. New York Ent. Soc., 8: 236. Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52: 525. Kearfott, *in* Smith, 1903. Check list of the Lepidoptera of Boreal America, 114. Busck, 1908. Proc. U. S. Natl. Mus., 35: 203. Walsingham, 1912. Biologia Centrali-Americana, Lepidoptera-Heterocera, 4: 136. Walsingham, 1915. *ibid.*, 422. Busck, 1914. Proc. U. S. Natl. Mus., 47: 32. Barnes and McDunnough, 1917. Check list of the Lepidoptera of Boreal America, 161. Meyrick, *in* Wytsman, 1922. Genera Insectorum, 180: 22. Forbes, 1923. Lepidoptera of New York and neighboring states, Cornell Univ. Agric. Exp.

Sta. Mem., 68: 249. Fletcher, 1929. Mem. Dept. of Agric. in India, Ent. Ser., 11: 230. Busck, 1932. Proc. Ent. Soc. Washington, 34: 17. Gaede, *in* Bryk, 1938. Lepidopterorum Catalogus, pt. 88: 21. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 77. Clarke, 1941. Proc. U. S. Natl. Mus., 90: 269.

Head smooth-scaled; tongue scaled, well developed; maxillary palpi folded over base of tongue; labial palpi recurved, slender and smooth scaled, second and third segments subequal in length, apex acute; antennae with pecten, ciliate in male, simple in female.

Forewings elongate, apex rounded or acute; 12 veins present; 1b furcate basally; 2–6 separate; 7 and 8 stalked, 7 to costa before apex; 11 arising before middle of cell. Hindwings elongate, apex rounded or acute, slightly narrower than forewings; 8 veins present; 1b furcate basally; 3 and 4 stalked; 5 connate or approximate to 3 + 4; 6 and 7 arising parallel, diverging distally, 7 to costal margin before apex.

Male genitalia: *valvae* lobate with a costal process arising near base, inner faces with long setae; *juxta* weakly developed; *tegumen* heavily sclerotized; *aedeagus* long, cylindrical; *cornuti* present or absent; *uncus* and *socii* absent; *brachia* asymmetrical, subequal in length.

Female genitalia: *lamella antevaginalis* heavily sclerotized, asymmetrical; *ductus bursae* sclerotized or not; *bursa copulatrix* lightly sclerotized; *signum* absent; *apophyses anteriores* shorter than apophyses posteriores.

Busck (1901) proposed *Triclonella* for *pergandeella* and *villella,* and he placed the genus in the Oecophoridae. In 1908 he transferred *villella* to *Holcocera* in the Blastobasidae and at the same time transferred *determinatella* from *Oecophora* to *Triclonella,* and in 1932 he transferred *Triclonella* from the Oecophoridae to the "Cosmopterygidae." Clarke (1941) confirmed Busck's transfer of the genus to the "Cosmopterygidae" and transferred *antidectis* from *Epicallima* to *Triclonella.* In the present paper two new species of *Triclonella* are described, bringing to five the number of species recognized as occurring in North America north of Mexico.

KEY TO THE SPECIES OF TRICLONELLA BASED UPON THE MACULATION

1. Base of forewings yellow-ocher 2
   Base of forewings dark brown 4
2. Outer third of forewings gray to black 3
   A costal and a dorsal gray triangle at one-half, followed by an orange-brown patch of scales (Fig. 177) .... *antidectis*

3. A small patch of brown scales at three-fourths .... *xuthocelis*
   No brown scales on outer third .... *pergandeella*
4. Basal fourth of forewings dark brown .... *determinatella*
   A few rows of brown to orange-brown scales at base of forewings *bicoloripennis*

KEY TO THE SPECIES OF TRICLONELLA BASED UPON THE MALE GENITALIA

1. Cornuti present in vesica of aedeagus 2
   Cornuti absent in vesica of aedeagus 4
2. Two or more cornuti 3
   With a single cornutus .... *antidectis*
3. Two cornuti, one medial and one distal (Fig. 67) *pergandeella*
   Four or five cornuti, three or four postmedial and one distal (Fig. 68a) .... *xuthocelis*
4. Valvae with a distinct shoulder in saccular area (Fig. 70) *determinatella*
   Valvae without a distinct shoulder in saccular area (Fig. 71) *bicoloripennis*

KEY TO THE SPECIES OF TRICLONELLA BASED UPON THE FEMALE GENITALIA

1. Ductus bursae sclerotized (Fig. 123) 2
   Ductus bursae not sclerotized (Fig. 124) .... *determinatella*
2. Ductus bursae evenly sclerotized 3
   One side of ductus bursae more heavily sclerotized (Fig. 123) *pergandeella*
3. Ductus bursae broad at posterior extremity (Fig. 122) *antidectis*
   Ductus bursae narrow before juncture with lamella antevaginalis (Fig. 125) .... *xuthocelis*

Triclonella pergandeella Busck
(Figs. 67, 123, 176)

Triclonella pergandeella Busck, 1900 [1901]. Jour. New York Ent. Soc., 8: 237. Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52: 525. Busck, 1908. Proc. U. S. Natl. Mus., 35: 203. Barnes and McDunnough, 1917. Check list of the Lepidoptera of Boreal America, 161. Meyrick, *in* Wytsman, 1922. Genera Insectorum, 180: 22. Forbes, 1923.

Lepidoptera of New York and neighboring states, Cornell Univ. Agric. Exp. Sta. Mem., 68: 249. Busck, 1932. Proc. Ent. Soc. Washington, 34: 17. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 77. Clarke, 1941. Proc. U. S. Natl. Mus., 90: 269.

Tongue pale brown basally, white distally. Maxillary palpi white ventrally, black dorsally. Labial palpi black; second segment with an anterior lateroventral and an exterior lateroventral white line, dorsal surface dusted with white scales; third segment with an anterior white line, posterior surface dusted with white scales. Antennae black; scape with ventral surface white; an anterior and a posterior white line, each continued on shaft as a series of dots. Face gray-brown, anterior edge of eyes bordered by a row of black scales followed by a few white ones; vertex gray-brown centrally, a fascicle of brown scales above posterior edge of eyes; a row of white scales above each eye. Thorax yellow-ocher. Forewings yellow-ocher on basal two-thirds, followed by a row of white scales, then a dorsal patch of black scales; outer one-third covered with black scales tipped gray; anterior edge of costa gray-brown basally; a patch of white scales above tornus; a row of white scales on costal margin from two-thirds to apex; cilia on outer margin light gray with a few white scales. Hindwings pale gray. Abdomen dark gray, last segment yellow-brown. Legs brown, darker distally; prothoracic tibiae with two anterior white lines; mesothoracic tibiae with a few white scales at apex; metathoracic tibiae with a medial and an apical white annulation, apices of tarsal segments white, base of first tarsal segment white.

Male genitalia: (Fig. 67) R.W.H. slide no. 617.

Female genitalia: (Fig. 123) R.W.H. slide no. 618.

Alar expanse: 10–13 mm.

Food plant: *Desmodium* spp., *Lespedeza hirta* (L.), *Clitoria mariana* L. The habits of the larva are quoted from Busck (1901):

"The larva feeds on the common tick-trefoil, *Meibomia* [*Desmodium*] *dillenii*. . . .

"The eggs are laid singly on the underside of a leaflet and the larva lives in a roomy inclosure between two leaflets spun together. When full grown it is about 12 mm. long, cylindrical, slightly depressed and tapering fore and back. . . . When younger, the larva is of a much lighter appearance, the yellow predominating. It is very agile and runs quickly forwards or backwards and lets itself fall on a silken thread, if the leaves are not carefully handled. When ready to pupate it enlarges its cell by adding the third leaflet, and suspended by a slight web a thin white half-transparent oval cocoon is spun inside the cell, in which the larva transforms to a rather robust light brown pupa.

"There are two or three overlapping generations yearly in this locality, the moth issuing late in June and late in August and sometimes again late in September.

"The species over-winter as imago."

Type: United States National Museum.

Type locality: District of Columbia.

Specimens examined: 30 ♂, 9 ♀. ALABAMA: Camp Rucker, Ozark, 4 ♂, March 25–28, 1943 (J. G. Franclemont), [CU]. FLORIDA: Gainesville, 1 ♂, March 9, 1927 (D. M. Bates), [UM]; Lake Alfred, 1 ♀, May 29, 1929 (L. J. Bottimer), [USNM]; Winter Haven, 2 ♂, under rearing record B. 128, on *Clitoria fragrans*, emerged July 26 and 28, 1929 (L. J. Bottimer), [USNM]. KENTUCKY: Natural Bridge, 2 ♂, May 18, 1929 (Annette F. Braun), (RWH); Pine Mt., Letcher Co., 1 ♂, 2 ♀, under rearing record B. 1370, emerged July 1 and 5, 1933 (Annette F. Braun), [AFB]; Pine Mt., Harlan Co., 1 ♀, under rearing record B. 1370, emerged July 22, 1932 (Annette F. Braun), [AFB]; Pine Mt., Bell Co., 1 ♂, under rearing record B. 1370, emerged July 22, 1937 (Annette F. Braun), [AFB]. MARYLAND: Washington, D. C., 11 ♂, 5 ♀, reared from *Desmodium*, emerged June 30 through August 25 (A. Busck), [USNM, MCZ, CU]; Forest Glen, 1 ♀, July 16, 1914 (O. Heideman), [USNM]; Hyattsville, 1 ♂, August 1906 (Aug. Busck), [LACM]. NORTH CAROLINA: Highlands, Macon Co., 1 ♂, July 15, 1958 (R. W. Hodges), [RWH]; Southern Pines, 1 ♂, "1–7:IV" [MCZ]. SOUTH CAROLINA: Cherry Hill Recreation Area, Route 107, 2000 feet, Oconee Co., 1 ♂, September 4, 1958 (R. W. Hodges), [RWH]. TENNESSEE: Monteagle, 3 ♂, August 31, 1929 and August 20, 1930 (Richards), [CU]. TEXAS: [Dallas], 1 ♂, April 23 (Boll), [USNM].

T. pergandeella can be distinguished from *T. xuthocelis* by the absence of brown scales in the outer third of the forewings. The presence of two *cornuti* in the *vesica* of the *aedeagus* of the male genitalia will separate it from *xuthocelis* which has four or five *cornuti* in the *vesica*.

Triclonella xuthocelis, new species

(Figs. 68, 68a, 125, 177)

Tongue white. Maxillary palpi white ventrally, black dorsally. Labial palpi black; second segment with an interior lateroventral and an exterior lateroventral white line, dorsal surface dusted with white scales; third segment with an anterior white line, posterior surface dusted with white scales. Antennae black, scape with ventral surface white and with an anterior and a posterior white line, each continued on shaft as a series of dots. Face gray, anterior edge of eyes bordered by a row of black scales followed by a few white ones, vertex gray centrally, a fascicle of brown scales above posterior edge of eyes, a row of white scales above each eye. Thorax yellow-ocher. Forewings yellow-ocher from base to two-thirds, outer third composed of gray scales tipped with black, a row of white scales on dorsal half at point of contact of two colored areas, then a small area of black scales, a small patch of yellow-brown scales at three-fourths preceded by some scattered white scales, cilia on outer margin pale gray. Hindwings gray. Abdomen shining gray; male with a few whitish scales from margin of eighth tergite. Legs gray basally; prothoracic and mesothoracic legs black distally with two dorsal white lines on tibiae; metathoracic tibiae gray with three oblique white streaks: one from base, one at one-half, and one apical; tarsal segments pale gray, apices white, base of first segment white.

Male genitalia: (Figs. 68, 68a) R.W.H. slide nos. 616 and 583.

Female genitalia: (Fig. 125) R.W.H. slide no. 584.

Alar expanse: 13–16 mm.

Food plant: unknown.

HOLOTYPE: ♂, Madera Canyon, 4880 feet, Santa Rita Mountains, Santa Cruz Co., ARIZONA, August 27, 1959 (R. W. Hodges), [CU Type No. 3802].

PARATYPES: same locality as type, 96 ♂, 82 ♀, June 30 through September 23, 1959 [CU, RWH, USNM, BMNH, LACM, CAS, AFB]; same locality as type, except elevation, 5,600 feet, 1 ♂, September 3, 1959 [RWH]; Southwest Research Station of AMNH, Cave Creek Canyon, 5400 ft., Chiricahua Mts., Cochise Co., ARIZONA, 1 ♂, June 16, 1958 (J. M. Burns and S. N. Burns), [UCB].

There are 24 poor specimens from Madera Canyon. These are not included among the paratypes.

T. xuthocelis can be separated from *T. pergandeella* by the characters stated under *pergandeella*. Superficially, *xuthocelis* is closest to *T. xanthota* Walsingham described from Amula, Guerrero, Mexico. Mr. Bradley has compared some of the material of *xuthocelis* with the type of *xanthota*. He feels that they are close but distinct. He states concerning the female genitalia, "They are very similar: there is little difference in the *ostium:* there is a difference in the sclerotization in the *ductus bursae* (*cestum*), in *xanthota* it is not broadened and expanded as it curves before inception of the *bursa copulatrix.*"

This species came commonly to "black light" during the summer of 1959; however, it was noted that almost all of the specimens were taken at a light which was near the probable breeding area. A light situated about one-hundred-fifty feet farther from the area attracted few specimens. It would seem that Busck's (1901) earlier hypothesis about the flight habits of *T. pergandeella* holds for another species in the genus.

Triclonella antidectis Meyrick
(Figs. 69, 122, 178)

Epicallima antidectis Meyrick, 1914. Exot. Micr., 1: 218. Barnes and McDunnough, 1917. Check list of the Lepidoptera of Boreal America, 161.

Schiffermulleria antidectis, McDunnough, 1939. Mem. S. California Acad. Sci., 2: 77.

Triclonella antidectis, Clarke, 1941. Proc. U. S. Natl. Mus., 90: 270.

Tongue white. Maxillary palpi white ventrally, black dorsally. Labial palpi black; second segment with an interior lateroventral and an exterior lateroventral white line, dorsal surface dusted with white scales; third segment with an anterior white line, posterior surface dusted with white scales. Antennae black; ventral surface of scape white; scape with an anterior white line continued on shaft to one-half; segments of distal half of shaft white on basal half, black on distal half. Face gray-brown, a row of white scales before eyes. Thorax yellow-ocher. Forewings concolorous with thorax to one-half, followed by a costal and a dorsal gray triangle, sometimes meeting to form a fascia; a row of brown scales along costal margin followed, medially, by a row of white and then a row of brown scales; a costal patch of white to buff scales beyond gray triangular area; rest of costal third of wing orange-brown; cilia paler than apical area; becoming gray at tornus. Hindwings pale gray. Abdomen dark gray dorsally, buff on medial portion of ventral surface. Legs pale gray basally; prothoracic legs black distally, two white lines on dorsal surface of tibiae, apices of first, second, third, and fifth tarsal segments white; mesothoracic legs dark gray-brown distally with some areas of white; metathoracic legs buff-white distally.

Male genitalia: (Fig. 69) R.W.H. slide no. 533.

Female genitalia: (Fig. 122) R.W.H. slide no. 534.

Alar expanse: 11–12 ½ mm.

Food plant: unknown.

Type: British Museum (Natural History).

Type locality: Nogales and Patagonia Mts., Arizona.

Specimens examined: 13 ♂, 2 ♀. ARIZONA: Nogales, 1 ♂, "6 · 03" [USNM]; Madera Canyon, 4,880 feet, Santa Rita Mountains, Santa Cruz Co., 9 ♂, 2 ♀, July 14 through August 9, 1959 (R. W. Hodges), [CU, RWH]; same locality, 5,600 feet, 1 ♂, July 30, 1959 [RWH]; Patagonia Mts., 1 ♂, "4 · 03" [USNM]; Redington, 1 ♂, [USNM].

T. antidectis can be separated from the other species of *Triclonella* by the three rows of scales which are brown, white, then brown, along the costal margin of the forewings.

Triclonella determinatella Zeller
(Figs. 70, 124, 179)

Oecophora determinatella Zeller, 1873. Verh. zool-bot. Ges. Wien, 23: 289. Chambers, 1878. Bull. U. S. Geol. Geog. Surv. Terr., 4: 159. Dyar, 1902 [1903]. List of the Lepidoptera of North America, Bull. U. S. Natl. Mus., 52: 525.

Triclonella determinatella, Busck, 1908. Proc. U. S. Natl. Mus., 35: 203. Forbes, 1923. Lepidoptera of New York and neighboring states, Cornell Univ. Agric. Exp. Sta. Mem., 68: 249. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 77. Clarke, 1941. Proc. U. S. Natl. Mus., 90: 270.

Oecophora australisella Chambers, 1875. Cincinnati Quart. Jour. Sci., 2: 114. Chambers, 1877. Can. Ent., 9: 24.

Tongue gray-brown basally, pale gray distally. Maxillary palpi brown, a few white scales dorsally. Labial palpi black; second segment with two white lines, one ventrolateral internally and one venterolateral externally, a few white scales at apex on inner surface; third segment with an anterior white line. Antennae black, scape with an anterior and a posterior row of white scales, continued on shaft to apex. Face and vertex dark brown, a few white scales in front of eyes, and a fascicle of white scales above posterior angle of eyes. Thorax dark brown. Forewings brown basally followed by a shining straw colored (some brown) fascia, very pale basally; an irregular gray-black fascia from one-half to three-fourths; then a gray fascia, almost white at costa; a circular patch of shining straw colored scales at two-thirds; apical fourth composed of gray scales tipped with black, pale basally (white on costa), dark apically; cilia gray with black or dark gray flecks. Hindwings pale gray. Abdomen fuscous, last segment with some buff scales. Legs fuscous basally; prothoracic tibiae and tarsi black with a dorsal white line; metathoracic tibiae with white at base, middle, and apex; tarsi fuscous, paler at apices of segments.

Male genitalia: (Fig. 70) R.W.H. slide no. 1000.

Female genitalia: (Fig. 124) R.W.H. slide no. 924.

Alar expanse: 9 ½–11 mm.

Food plant: unknown.

Type: Museum of Comparative Zoology.

Type locality: Dallas, Texas.

Specimens examined: 28 ♂, 9 ♀. FLORIDA: Gainesville, 2 ♀, May 10 and June 29, 1927 (J. Speed Rodgers), [CU]; Weeki Wachee Springs, Hernando Co., 1 ♂, March 14, 1955 (J. F. May), [CPK]. ILLINOIS: Putnam Co., 3 ♂, 1 ♀, June 8–12 and September 11 (M. O. Glenn), [USNM, RWH]. KANSAS: Onaga, 1 ♂, "25 · VI" [MCZ]. KENTUCKY: no locality, 4 ♂, 1 ♀ (Chambers), [MCZ]. LOUISIANA: Natchitoches ph., 1 ♀, "VIII" (G. Coverdale), [USNM]. Missouri: Kirkwood, 3 ♂, "9/30 04" (Murtfeldt), [CU]; 2 ♂, W. St. Louis, 1 ♀, VIII · 04 (Aug. Busck), [USNM]. OKLAHOMA: Tenkeller Lake, Cookson, 4 ♂, August 25 through September 4 (D. R. Davis), [DRD]. TEXAS: Brownsville-Los Borregos, 1 ♂, 2 ♀, June 5, 1904 (H. S. Barber), [USNM]; Fedar, 3 ♂, "4 · 1 · 17" Kerrville, 1 ♂, 1 ♀ (F. C. Pratt), [USNM]; Kerrville, 2 ♂, April [USNM]; San Benito, 1 ♂, March 24–30 [USNM].

T. determinatella can be distinguished from the other species of *Triclonella* by the presence of a circular patch of shining straw-colored scales at two-thirds on the forewings.

Triclonella bicoloripennis, new species
(Figs. 71, 180)

Tongue white. Maxillary palpi white with a dark brown dorsal line. Labial palpi: first segment white with scattered gray scales (second and third segments missing). Antennae dark brown to black, ventral surface and an anterior line white. Face gray-brown becoming darker dorsally, a streak of white scales from base of each antenna to base of tongue; vertex dark gray-brown with a few white scales arising above dorsal margin of eyes. Thorax brown. Forewings brown on costal margin to three-fifths; apical fourth brown; a dorsal triangular brown patch at one-half; remainder of wing various shades of straw-brown. Hindwings fuscous. Prothoracic legs pale gray-brown basally, darker distally; apices of tarsal segments white (other legs missing).

Male genitalia: (Fig. 71) R.W.H. slide no. 923.

Female genitalia: no specimens available.

Alar expanse: 7 ½ mm.

Food plant: unknown.

HOLOTYPE: ♂, Corpus Christi, Texas, September 21, 1943 (W. M. Gordon), [CU Type No. 3803].

T. bicoloripennis can be distinguished from the other species of *Triclonella* by the presence of a few rows of brown scales at the base of the forewings. In the male genitalia the absence of *cornuti* in the *vesica* of the *aedeagus* and the absence of a shoulder in the saccular area will separate *bicoloripennis* from the others.

ANONCIA Clarke

(Figs. 4, 19, 72, 126)

Type: *Hypatopa conia* Walsingham, 1907. Original designation. *Anoncia* Clarke, 1941. Proc. U. S. Natl. Mus., 90: 268. Clarke, 1942. Can. Ent., 74: 17.

Head smooth-scaled; tongue scaled, moderately developed; maxillary palpi folded over base of tongue; labial palpi recurved, second segment rough-scaled and longer than third, apex acute; antennae one-half to two-thirds, pecten present, ciliate in male, ciliate or simple in female.

Forewings elongate ovate, apex acute; 12 veins present; 1b furcate basally; 2–5 equidistant at base; 2 from near angle; 7 and 8 stalked; 11 arising before middle of cell. Hindwings narrower than forewings, anal area moderate; 8 veins present; 1b developed basally; 2 from three-fourths on cell; 3 and 4 connate or stalked; 5, 6, and 7 equidistant; 6 and 7 parallel, 7 slightly sinuate.

Male genitalia: *valvae* broad, ventral; costal processes from base of *valvae; aedeagus* heavily sclerotized, ankylosed; *cornuti* absent; a basal process in *aedeagus; tegumen* heavily sclerotized, emarginate dorsally; *uncus* absent; arms of *gnathos* separate, left one larger than right.

Female genitalia: *corpus bursae* not sclerotized; *signa* present or absent; *ostium* dorsal in some species; *apophyses anteriores* fused at base.

Clarke (1941) proposed *Anoncia* for several species which had been placed in *Hypatopa* and *Borkhausenia.* In 1942 he transferred *B. longa* and *B. leucoritis* to *Anoncia* and described *A. mentzeliae,* bringing the number of species to ten. Upon examination of the genitalia of the paratypes of *A. conia* and of the material which Heinrich (1921) figured, it is evident that he illustrated the genitalia of an undescribed species and not those of *conia*. *A. marinensis* is a synonym of *conia*, and *mentzeliae* is a synonym of *leucoritis*. I am describing nine new species of *Anoncia*, bringing the total number of known species to seventeen. It is unfortunate that some of the species are described from unique specimens; however, where a series of specimens of a species exists, several genitalic preparations have been made; and they serve to reinforce the fact that within a species of this genus there is very little genitalic variation. Mr. Bradley has sent me a sketch of the genitalia of *H. orites;* it is an *Anoncia*, but I can not recognize the species.

Most of the material in collections is from Arizona and California. It is reasonable to assume that future collecting will show that members of the genus are found from Texas to the West Coast and north and south of this region.

Key to the Species of Anoncia based upon the Maculation

1\. Fascia on basal half of forewings 2
Fascia absent on basal half of forewings 6
2\. Forewings white overlaid with dark brown .... *alboligula*
Forewings gray-white or buff-white overlaid with brown 3
3\. Fascia oblique, farther from base dorsally than costally *nebritis*
Fascia transverse or convex 4
4\. Fascia with buff-brown in center .... *diveni*
Fascia unicolorous 5
5\. Spot at end of cell confluent with a tornal brown area .... *fasciata*
Area costad of tornus not heavily covered with brown scales .... *porriginosa*
6\. Forewings creamy white; a brown discal spot; a few brown scales above tornus, around apex, and outer margin of wing .... *leucoritis*
Forewings not creamy white 7
7\. Forewings and head overlaid with brown or black 8
Forewings very lightly overlaid with brown; head buff-white .... *longa*
8\. Forewings gray-white or buff-white overlaid with gray or brown 9
Forewings white overlaid with dark brown .... *piperata*
9\. Forewings gray-buff heavily overlaid with brown; costal margin dark gray-brown .... *furvicosta*

Forewings gray-white or buff-white; discal spot small; if discal spot large, forewings buff-white 10
10. Forewings buff-white overlaid with brown 11
Forewings gray-white overlaid with brown 13
11. Forewings heavily overlaid with brown; cilia of pecten with brown before apices .... *episcia*
Forewings lightly overlaid with brown; cilia of pecten unicolorous 12
12. Discal spot large .... *nocticola*
Discal spot very small .... *callida*
13. Head heavily overlaid with brown *conia, sphacelina, brunneipes*
Head lightly overlaid with brown, almost white .... *glacialis*

KEY TO THE SPECIES OF ANONCIA BASED UPON THE MALE GENITALIA

1. Basal processes on left valva stout (Fig. 80) 2
Basal processes on left valva slender (Fig. 73) 13
2. Basal process on left valva heavily sclerotized, curved 3
Basal process or processes on left valva lightly sclerotized, lobate 7
3. Basal process on right valva short or absent 4
Basal process on right valva heavily sclerotized, one-half length of valva (Fig. 84) .... *callida*
4. Left brachium sickle-shaped (Fig. 86) 5
Left brachium slender (Fig. 81) .... *nebritis*
5. Valvae deltoid (Fig. 80) 6
Valvae not deltoid (Fig. 86) .... *leucoritis*
6. Aedeagus angulate at one-half or two-thirds (Fig. 80) *furvicosta*
Aedeagus curved, not angulate (Fig. 79) .... *longa*
7. Three teeth on right side of aedeagus at two-thirds ... *glacialis*
No teeth on right side of aedeagus 8
8. A dorsal projection on left brachium (Fig. 83) .... *diveni*
Without a dorsal projection on left brachium 9
9. Two basal processes on left valva 11
One basal process on left valva 10
10. Basal process on left valva one-half length of that on right valva (Fig. 76) .... *alboligula*
Basal process on left valva equal to or longer than that of right valva (Fig. 85) .... *porriginosa*
11. Costobasal process of left valva longer than medial one *episcia*
Costobasal process of left valva shorter than medial one 12
12. Right costal process single, tapering gradually to apex (Fig. 78) .... *piperata*

Right costal process bifid (Fig. 82) .... *fasciata*
13. Left brachium slender, "L" shaped (Fig. 73) .... *sphacelina*
Left brachium stout, not "L" shaped 14
14. Left brachium sickle-shaped (Fig. 75) .... *brunneipes*
Left brachium not sickle-shaped (Fig. 72) .... *conia*

Anoncia conia Walsingham
(Figs. 72, 126, 181)

Hypatopa conia Walsingham, 1907. Proc. U. S. Natl. Mus., 33:212.
Borkhausenia conia, Busck, 1908. Proc. U. S. Natl. Mus., 35:204. Barnes and McDunnough, 1917. Check list of the Lepidoptera of Boreal America, 162. Heinrich, 1921. Jour. Agric. Res., 20:815. McDunnough, 1939. Mem. S. California Acad. Sci., 2:77.
Anoncia conia, Clarke, 1941. Proc. U. S. Natl. Mus., 90:269. Clarke, 1942. Can. Ent., 74:17.
"Borkhausenia" marinensis Keifer, 1935. Monthly Bull. Dept. Agric. California, 24:215, pl. II, ff. 5A–5E. **new synonymy.**
Borkhausenia marinensis, McDunnough, 1939. Mem. S. California Acad. Sci., 2:77.
Anoncia marinensis, Clarke, 1941. Proc. U. S. Natl. Mus., 90:269. Clarke, 1942. Can. Ent., 74:17.

Head, thorax, forewings, and legs gray-white overlaid with gray-brown. Labial palpi heavily overlaid with gray-brown, apex of second segment gray-white, base and apex of third segment gray-white. Antennae ciliate in male, simple in female, cilia of pecten gray-brown before apex, apex gray-white. Forewings light on most of discal cell (some specimens are dark on discal cell), an oblique dark band through cell at two-fifths, a dark dash on fold at one-half, cilia with a pale median line. Hindwings shining gray, basal half of cilia darker than distal half. Abdomen unicolorous gray-white. Legs darker colored distally, apices of tarsal segments pale.

Male genitalia: (Fig. 72) R.W.H. slide no. 1015.

Female genitalia: (Fig. 126) R.W.H. slide no. 996.

Alar expanse: 13–17½ mm.

Food plant: *Sphacele calycina* Bentham. Kiefer (1935) gives the following discussion of the larval habits: "The larva of this species is much like the one described above [*A. sphacelina*]. It is a miner in *Sphacele* leaves. The mine apparently originates near the base of the leaf on the underside by the midrib, but soon appears above as a brown area, its shape somewhat determined by the angle of the lateral ribs when the larva is young. The frass is spun against the lower epidermis. The larva may mine in several leaves during its lifetime. The cocoon is oval and rather loosely woven.''

Type: *conia,* British Museum (Natural History); *marinensis,* California Academy of Sciences.

Type locality: *conia,* Lake County, Blue Lake, California, Siskiyou County, Mount Shasta, California; *marinensis,* Phoenix Lake, Marin County, California.

Specimens examined: 6 ♂, 7 ♀. CALIFORNIA: Mt. Shasta, Siskiyou Co., 3 ♂, 1 ♀, August 2 through September 1, 1871 (Walsingham), [USNM]; Phoenix Lake, Marin Co., 2 ♂, 3 ♀, larva on *Sphacele calycina,* emerged June 26 through July 1, 1927 and May 12, 1934 (H. H. Keifer,), [AFB, RWH]; Riverside, 2 ♀, July 7 and 8, 1933 (H. H. Keifer), [RWH]; Shingle Springs, El Dorado Co., 1 ♂, 1 ♀, May 27, 1931 (H. H. Keifer), [RWH].

A. conia cannot be separated from *A. sphacelina* and *A. brunneipes* by the maculation. (See the statement under *brunneipes* for the characters separating *conia* from *sphacelina* and *brunneipes* by the male genitalia.) In the female genitalia the *ostium* of *conia* is dorsolateral; that of *sphacelina* is ventrolateral. The female of *brunneipes* is unknown.

Anoncia sphacelina Keifer
(Figs. 73, 127, 182)

''*Borkhausenia*'' *sphacelina* Keifer, 1935. Monthly Bull. Dept. Agric. California, 24: 214, pl. V.

Borkhausenia sphacelina, McDunnough, 1939. Mem. S. California Acad. Sci., 2: 77.

Anoncia sphacelina, Clarke, 1941. Proc. U. S. Natl. Mus., 90: 269. Clarke, 1942. Can. Ent., 74: 17.

Head, thorax, and forewings gray-white overlaid with gray-brown flecks. Labial palpi heavily overlaid with gray-brown, second segment darker than third; apex of second segment and base and apex of third segment gray-white. Antennae ciliate in male, simple in female; cilia of pecten gray-brown before apex. Forewings pale dorsad of fold and generally in discal cell, a faint line in middle of cilia. Hindwings gray-buff, cilia darker basally. Abdomen light ochreous dorsally, pale buff ventrally. Prothoracic and mesothoracic legs gray-white heavily overlaid with gray-brown, metathoracic legs buff-white lightly overlaid with gray-brown, apices of tarsal segments pale.

Male genitalia: (Fig. 73) R.W.H. slide no. 993.

Female genitalia: (Fig. 127) R.W.H. slide no. 994.

Alar expanse: 16½–17½ mm.

Food plant: *Sphacele calycina* Bentham. Keifer (1935) gives the following discussion of the larva and pupa of *sphacelina:*

''The dark brown larvae of this moth form a very conspicuous and characteristic globular chamber amongst bunched leaves, and then mine into these leaves. Pupation takes place within this chamber.

''The pupa is about 6 mm. long, widest at first abdominal segment, glabrous, dark brown. Wings and antennae extending over onto sixth segment. No movable segments. Genital opening in a groove in center of an elevated area; cremaster absent, hooked hairs present.

''Larval length about 12 mm. Head ochreous, black on margins and sides. Prothoracic shield ochreous, black on lateral and posterior ⅔. Suranal plate black. Tubercles small. Body very dark reddish-brown, intersegmental areas of thorax white; flattened dorso-ventrally. About 20–28 biordinal crochets on anterior prolegs, broken outwardly; posterior prolegs with sixteen crochets.''

Type: California Academy of Sciences.

Type locality: Three miles west of Shingle Springs, El Dorado Co., California.

Specimens examined: 3 ♂, 3 ♀. California: Shingle Creek, El Dorado Co., 3 ♂, 3 ♀, reared from *Sphacele calycina*, collected April 17–20, 1934 and May 5, 1935, emerged April 28 through May 28 (H. H. Keifer), [AFB, RWH].

A. sphacelina cannot be separated from *A. conia* and *A. brunneipes* by the maculation. The ''L'' shaped left arm of the *gnathos* in the male genitalia of *sphacelina* will separate it from the known species of *Anoncia.*

Anoncia brunneipes, new species

(Figs. 75, 183)

‡ *Borkhausenia conia,* Heinrich, 1921. Jour. Agric. Res., 20: 815, pl. 97. (misidentification.)

Head, thorax, and forewings gray-white overlaid with brown. Labial palpi paler dorsally on second and third segments, first segment without brown overlay, apex of second segment gray-white, base and apex of third segment gray-white, a few very dark scales on anterior surface of third segment. Antennae ciliate in male, female unknown, cilia of pecten brown before apex. Forewings almost uniformly overlaid with brown, a small brown spot at two-fifths in cell, one at end of cell, and one at one-half on fold. Hindwings gray-brown. Abdomen buff-gray. Legs buff-white, prothoracic and metathoracic legs heavily overlaid with brown, metathoracic legs with a few pale brown scales, last segment of metathoracic tarsi brown.

Male genitalia: (Fig. 75) Carl Heinrich slide.

Female genitalia: no specimens available.

Alar expanse: 16 mm.

Food plant: unknown.

Holotype: ♂, San Diego, California, June 20, 1911 (W. S. Wright), [USNM Type No. 66085].

Paratypes: same locality as type, 3 ♂, June 18 and 20, 1911 [USNM].

A. brunneipes cannot be distinguished with certainty from *A. conia* and *A. sphacelina* by the the maculation. It can be separated from *sphacelina* by the stout left *brachium*, that of *sphacelina* is slender and ''L'' shaped; the left *brachium* of *brunneipes* has two parts, of which the larger one is sickle-shaped. The left *brachium* of *conia* is single, and it is not sickle-shaped.

Anoncia glacialis, new species

(Figs. 74, 184)

Head white overlaid with dark gray. Thorax, forewings, and legs gray-white overlaid with dark gray. Labial palpi heavily overlaid with dark gray, apex of second segment white, base and apex of third segment white. Antennae ciliate in male, female unknown, cilia of pecten dark gray before apex. Forewings darker along costa, remainder of wings rather uniformly dusted with dark gray. Hindwings buff-gray apically, paler basally; cilia with a faint median line. Prothoracic and mesothoracic legs darker than metathoracic pair, apices of tarsal segments gray-white.

Male genitalia: (Fig. 74) R.W.H. slide no. 995.

Female genitalia: no specimens available.

Alar expanse: 15 ½ mm.

Food plant: unknown.

Holotype: ♂, Riverside, California, July 8, 1933 (Keifer), [CU Type No. 3811].

A. glacialis can be separated from *A. conia, A. sphacelina,* and *A. brunneipes* by the head being lightly overlaid with brown; in the latter three species the head is heavily overlaid with brown.

The presence of three teeth on the right side of the *aedeagus* at two-thirds in the male genitalia will distinguish the male of this species from the males of the other species of *Anoncia.*

Anoncia fasciata Walsingham
(Figs. 82, 129, 185)

Hypatopa fasciata Walsingham, 1907. Proc. U. S. Natl. Mus., 33: 213.

Borkhausenia fasciata, Barnes and McDunnough, 1917. Check list of the Lepidoptera of Boreal America, 162. Heinrich, 1921. Jour. Agric. Res., 20: 815. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 77.

Anoncia fasciata, Clarke, 1941. Proc. U. S. Natl. Mus., 90: 269. Clarke, 1942. Can. Ent., 74: 17.

Head, thorax, forewings, and legs gray-white heavily overlaid with brown. Labial palpi gray-white at apex of second segment and at base and apex of third segment. Antennae ciliate in male, female unknown, cilia of pecten brown before apex, apex gray-white. Forewings with a brown fascia at one-third, preceded by a narrow gray-white fascia; a brown discal spot, a brown spot at end of cell, and one on fold at one-half; basal half of cilia overlaid with brown, distal half with brown flecks; a faint postmedial line and a faint subterminal line in cilia. Hindwings gray-brown, cilia with a faint antemedial line. Abdomen buff-white. Legs becoming paler from prothoracic through metathoracic pairs, outer tibial spurs of metathoracic legs dark, metathoracic tibiae with a pale annulation at one-half and another at apex, apices of tarsal segments pale.

Male genitalia: (Fig. 82) A. Busck slide.

Female genitalia: (Fig. 129) R.W.H. slide no. 1012.

Alar expanse: 13–16 ½ mm.

Food plant: unknown.

Type: British Museum (Natural History).

Type locality: Head Noyo River, Mendocino County, California; past Little Lake; Lake County, Blue Lake; Colusa County, North Fork Cache Creek.

Specimens examined: 3 ♂. California: Head of Noyo River, Mendocino Co., 1 ♂, June 8–11, 1871 (Walsingham), [USNM]; past Little Lake, Mendocino Co., 2 ♂, June 12, 1871 (Walsingham), [USNM].

See discussion under *A. porriginosa* for characters separating the two species.

Anoncia porriginosa, new species
(Figs. 85, 186)

Head, thorax, forewings, and legs gray-white heavily overlaid with brown. Labial palpi with gray-white at apex of second segment and at base and apex of third segment. Antennae ciliate in male, female unknown, cilia of pecten with brown before apex. Forewings with a brown fascia at one-third, preceded by a narrow gray-white band; a small brown discal dot, another at end of discal cell, and one at one-half on fold. Hindwings gray-brown, a faint antemedial line in cilia. Abdomen buff-white overlaid with brown. Metathoracic tibiae and tarsi buff-white, apices of tarsal segments pale.

Male genitalia: (Fig. 85) R.W.H. slide no. 1029.

Female genitalia: no specimens available.

Alar expanse: 13–15 mm.

Food plant: unknown.

Holotype: ♂, Claremont, California (Metz), [USNM Type No. 66086].

Paratypes: same data as type, 5 ♂, [USNM, RWH].

A. porriginosa can be separated from *A. fasciata* by the absence of a brown patch above the tornus. In the male genitalia there is one basal process on the left *valva* of *porriginosa*, two on the left *valva* of *fasciata*. The right basal process of *porriginosa* is single, that of *fasciata* is bifid.

Anoncia alboligula, new species
(Figs. 76, 187)

Head, thorax, forewings, and legs white overlaid with dark brown. Tongue white. Labial palpi dark brown on outer surface of second segment, apex of second segment white, base and apex of third segment broadly white. Antennae ciliate in male, female unknown, cilia of pecten gray-brown before apex, anterior surface and apex of scape white. Forewings with a broad brown fascia at one-third, preceded by a white one; a dark brown dash at one-half on fold; pale gray-brown dusting on cilia at apex; cilia with a postmedial and a subterminal gray-brown line. Hindwings gray-brown, a faint basal line in cilia. Abdomen buff-white dorsally, white ventrally. Apices of tarsal segments white.

Male genitalia: (Fig. 76) R.W.H. slide no. 1027.

Female genitalia: no specimens available.

Alar expanse: 13 mm.

Food plant: unknown.

HOLOTYPE: ♂, Olancha, Inva (*sic*) [Inyo] Co., CALIFORNIA, June 24–30 [USNM Type No. 66087].

The combination of white forewings and a fascia on the basal half of the forewings separates *alboligula* from the other species of *Anoncia*. In the male genitalia the single lobate basal process of the left valva being one-half the length of the process of the right valva will separate *alboligula* from *A. porriginosa* and *A. fasciata*.

Anoncia nebritis, new species

(Figs. 81, 132, 188)

Head, thorax, and forewings gray-white overlaid with brown. Labial palpi heavily overlaid with brown, apex of second segment gray-white, base and apex of third segment gray-white, a few gray-white scales on inner surface of second segment, gray-white scales general on third segment. Antennae ciliate in male and female, median gray color of cilia of pecten blending gradually into gray-white of extremities, scape gray-white at base and apex. Forewings brown on costa to two-thirds, an oblique fascia at one-half from costal margin to dorsad of fold, a brown blotch at one-fourth from costa to fold or slightly beyond it. Hindwings dark gray. Abdomen ochreous dorsally, buff-white ventrally. Legs gray-white overlaid with brown on coxae, trochanters, and femora; buff-white overlaid with brown on tibiae and tarsi; dorsal surface of metathoracic tibiae with long buff-white scales; metathoracic tibiae with a subbasal, medial, and apical buff-white annulation; apices of tarsal segments buff-white.

Male genitalia: (Fig. 81) R.W.H. slide no. 985.

Female genitalia: (Fig. 132) R.W.H. slide no. 986.

Alar expanse: 9½–11 mm.

Food plant: unknown.

HOLOTYPE: ♂, Madera Canyon, 4,880 feet, Santa Rita Mountains, Santa Cruz Co., ARIZONA, July 12, 1959 (R. W. Hodges), [CU Type No. 3807].

PARATYPES: same locality as type, 3 ♂, 1 ♀, July 11–25, 1959 [CU, RWH].

The oblique fascia on the forewings will separate *nebritis* from *A. diveni, A. fasciata,* and *A. porriginosa.* In the male genitalia the heavily sclerotized basal process on the left valva will separate *nebritis* from the same three species. In *nebritis* the basal process on the left valva is lightly sclerotized and lobate.

Anoncia diveni Heinrich
(Figs. 83, 134, 189)

Borkhausenia diveni Heinrich, 1921. Jour. Agric. Res., 20: 814, pl. 96, ff. C–F. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 77.

Anoncia diveni, Clarke, 1941. Proc. U. S. Natl. Mus., 90: 269. Clarke, 1942. Can. Ent., 74: 17.

Head, thorax, forewings, and abdomen gray-white overlaid with brown. Labial palpi heavily overlaid with brown on basal half of second segment and at middle of third segment. Antennae ciliate in male, simple in female, cilia of pecten unicolorous. Forewings brown on costa at base, a brown fascia at two-fifths, buff-brown scales in middle of fascia, scattered brown and buff-brown scales on apical half of wing. Hindwings gray-brown. Legs heavily overlaid with brown; mesothoracic and metathoracic tibiae with gray-white, almost white, annulations at one-third, two-thirds, and apex; apices of first two tarsal segments of prothoracic and mesothoracic legs gray-white; apices of first, second, third, and fifth tarsal segments of metathoracic legs gray to buff-white.

Male genitalia: (Fig. 83) Carl Heinrich slide.

Female genitalia: (Fig. 134) R.W.H. slide no. 10001.

Alar expanse: 12–13 mm.

Food plant: *Lantana horrida.* According to Diven (note accompanying specimens), "Larvae making a narrow blotch mine at the edge of the leaf and curling the edge near base, pupating within the mine." Heinrich's (1921) description of the larva and pupa is as follows:

"The larva when full-grown is 7.5 to 9 mm. long; white, with the thoracic segments and the anterior portion of the first abdominal segment a brilliant wine-red: in fully fed specimens there is often a pinkish suffusion on the dorsum of the abdominal segments; thoracic shield yellow, posteriorly and laterally edged with dark brown; anal shield pale yellow, other chitinized portions of thoracic segments dark brown; thoracic legs blackish brown, paler on inner sides; body tubercles deep brown, minute; setae pale, slender, moderately long; crochets of prolegs dark brown, 24 to 26, biordinal and in a circle broken outwardly; spiracles pale yellow, small, round, inconspicuous; no anal fork; head pale yellow with a dark brown band on each side, extending from the ocelli to the lateral incision of the hind margin; ocellar pigment black, continuous under the ocelli.

"The pupa is rather stout and short, 1.5 to 2 mm. wide by 4.5 to

5 mm. long; pale yellow-brown; smooth; caudal end rounded; cremaster absent; wings and antennae extending to anterior margin of sixth abdominal segment; labial palpi clearly defined but small, *not* extending to proximolateral angles of maxillae; between genital and anal openings a divided, blackish, chitinized rise, without spines, hairs, or other armature.''

Type: United States National Museum.

Type locality: Brownsville, Texas.

Specimens examined: 2 ♂, 2 ♀. TEXAS: Brownsville, 2 ♂, 2 ♀, collected on *Lantanum horrida,* April 22, 1919, emerged April 30 and May 5, 1919 (Diven), [USNM].

A. diveni can be separated from the other species of *Anoncia* by the presence of buff-brown scales in the center of the fascia.

Anoncia episcia Walsingham
(Figs. 77, 190)

Hypatopa episcia Walsingham, 1907. Proc. U. S. Natl. Mus., 33: 211.

Borkhausenia episcia, Barnes and McDunnough, 1917. Check list of the Lepidoptera of Boreal America, 162. Heinrich, 1921. Jour. Agric. Res., 20: 815. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 77.

Anoncia episcia, Clarke, 1941. Proc. U. S. Natl. Mus., 90: 269. Clarke, 1942. Can. Ent. 74: 17.

Head, thorax, forewings, and legs buff-white heavily overlaid with brown. Labial palpi buff-white at apex of second segment and at base and apex of third segment. Antennae ciliate in male, female unknown, cilia of pecten gray-brown before apex. Forewings with a small brown discal spot, a brown spot at end of cell, and one at one-half on fold. Hindwings gray-brown. Metathoracic legs less heavily overlaid with brown than prothoracic and mesothoracic legs, apices of tarsal segments pale.

Male genitalia: (Fig. 77) R.W.H. slide no. 1011.

Female genitalia: no specimens available.

Alar expanse: 13 mm.

Food plant: unknown.

Type: British Museum (Natural History).

Type locality: Sonoma County, Russian River, California; Mendocino County, head of Noyo River, California; past Little Lake, Mendocino Co., California.

Specimens examined: 1 ♂. CALIFORNIA: Dry Creek, Sonoma Co., 1 ♂, May 20–21, 1871 (Walsingham), [USNM].

A. episcia can be separated from *A. nocticola* and *A. callida* by the pecten being brown before the apex and by the forewings being heavily overlaid with brown. In the male genitalia of *episcia* the basal process of the right *valva* is longer than the *valva;* that of *callida* is one-half the length of the *valva.*

Anoncia callida, new species

(Figs. 84, 191)

Head, thorax, forewings, and legs buff-white overlaid with dark gray. Labial palpi heavily overlaid with dark gray, apices of segments white. Antennae ciliate in male, female unknown, cilia of pecten unicolorous. Forewings irregularly overlaid with dark gray, darkest along costa at base of wings; a dark gray spot at end of cell. Hindwings buff-gray. Apices of tarsal segments white or buff.

Male genitalia: (Fig. 184) R.W.H. slide no. 582.

Female genitalia: no specimens available.

Alar expanse: 17½ mm.

Food plant: unknown.

HOLOTYPE: ♂, Madera Canyon, 4,880 feet, Santa Rita Mountains, Santa Cruz Co., ARIZONA, July 17, 1959 (R. W. Hodges), [CU Type No. 3805].

The buff-white forewings which are evenly and lightly overlaid with brown will separate *callida* from the other species of *Anoncia.* In the male genitalia the combination of the basal processes of both *valvae* being heavily sclerotized and moderately long will separate the male of *callida* from the males of the other species of *Anoncia.*

Anoncia piperata, new species

(Figs. 78, 192)

Head, thorax, forewings, and legs white overlaid with dark brown. Labial palpi: second segment white dorsally and at apex, base and apex of third segment white. Antennae ciliate in male, female unknown, cilia of pecten brown before apex. Forewings irregularly dusted with brown, cilia white with a postmedial and a subterminal line. Hindwings buff-gray, cilia with a basal line and a faint antemedial line around apex. Legs heavily overlaid with brown, apices of tarsal segments white.

Male genitalia: (Fig. 78) R.W.H. slide no. 473.

Female genitalia: no specimens available.

Alar expanse: 20 mm.

Food plant: unknown.

HOLOTYPE: ♂, Smoky Valley, 6,200 feet, Tulare Co., CALIFORNIA, 6-8-44 (C. Henne), [USNM Type No. 66088].

The white forewings overlaid with brown will separate *piperata* from the other species of *Anoncia.* The key based on the male genitalia will serve to distinguish *piperata* from the other species of *Anoncia.*

Anoncia leucoritis Meyrick
(Figs. 86, 130, 193)

Borkhausenia leucoritis Meyrick, 1927. Exot. Micr., 3: 381. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 77.

Anoncia leucoritis, Clarke, 1942. Can. Ent., 74: 17.

Anoncia mentzeliae Clarke, 1942. Can. Ent., 74: 18. **new synonymy.**

Head, thorax, forewings, and legs pale buff-white, almost white. Antennae ciliate in male and female, cilia of pecten unicolorous. Forewings with a patch of brown scales above tornus, a few brown scales in middle and at end of cell, very few scales with brown flecks in cilia. Hindwings buff-gray, cilia with a faint antemedial line at apex. Abdomen buff. Distal segments of legs overlaid with brown, prothoracic pair darker than mesothoracic pair, mesothoracic pair darker than metathoracic pair, apices of tarsal segments pale.

Male genitalia: (Fig. 86) August Busck slide.

Female genitalia: (Fig. 130) J.F.G. Clarke slide no. 3203.

Alar expanse: 16–19½ mm.

Food plant: *Mentzelia laevicaulis* (Dougl.) T. and G. Accord-to Clarke (1942), "The larva of *mentzeliae* feeds in the immature ovaries of the food plant. Pupation occurs in a loosely constructed cocoon within the ovary."

Type: *leucoritis,* British Museum (Natural History); *mentzeliae,* United States National Museum.

Type locality: *leucoritis,* Alpine, Texas, 7,500 feet; *mentzeliae,* Snake River, Whitman County, Washington, opposite Clarkston.

Specimens examined: 9 ♂, 7 ♀. TEXAS: Alpine, 5,000 feet, 1 ♂, "5.27" [USNM]. WASHINGTON: Snake River opp. Clarkston, Whitman Co., 7 ♂, 6 ♀, reared from *Mentzelia laevicaulis,* emerged August 7–23, 1940 (J. F. G. Clarke), [USNM]; Walla Walla, 1 ♂, 1 ♀, June 27, 1925 (H. P. Lanchester), [USNM].

A. leucoritis can be separated from *A. longa* by the color; *leucoritis* is creamy white; *longa* is buff-white. And, by the alar expanse, that of *leucoritis* is 16–19½ mm., that of *longa* is 23–26 mm. The *valvae* of the male genitalia of *leucoritis* are not deltoid; those of *longa* are deltoid. In the female genitalia the *ostium* opens dorsally in *longa*, laterally in *leucoritis*.

Anoncia longa Meyrick

(Figs. 79, 133, 194)

Borkhausenia longa Meyrick, 1927. Exot. Micr., 3: 381. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 77.

Anoncia longa, Clarke, 1941. Proc. U. S. Natl. Mus., 90: 269. Clarke, 1942. Can. Ent., 74: 17.

Head, thorax, abdomen, wings, and legs buff-white. Antennae ciliate in male and female, cilia of pecten unicolorous. Forewings with pale ochreous dusting on costa; a tawny discal spot, a tawny spot at end of cell, and one on fold at two-thirds; a light tawny to ochreous dusting on outer third. Hindwings overlaid with tawny in some specimens. Prothoracic legs overlaid with tawny in one specimen.

Male genitalia: (Fig. 79) A. Busck slide.

Female genitalia: (Fig. 133) R.W.H. slide no 1007.

Alar expanse: 23–26 mm.

Food plant: unknown.

Type: British Museum (Natural History).

Type locality: Alpine, Texas, 7,500 feet; Dividend, Utah.

Specimens examined: 3 ♂, 1 ♀. ARIZONA: Paradise, Cochise Co., 1 ♂, September [USNM]; Prescott, 1 ♂, 1–7·X [USNM]. UTAH: Dividend, 1 ♂, "7.27" [USNM]; Eureka, 1 ♀, August 18, 1911 (Tom Spalding), [USNM].

See the discussion under *A. leucoritis* for the points of separation between the two species.

Anoncia furvicosta, new species

(Figs. 80, 131, 195)

Head and thorax gray-buff heavily overlaid with dark gray-brown. Labial palpi with apex of second segment white, a few white scales at base of third segment. Antennae ciliate in male and female, cilia of pecten slightly darker before apex. Forewings buff-brown; dark gray-brown, almost black, on costa from base to three-fourths; a dark gray-brown discal spot; a dark gray-brown spot at end of cell; a series of subterminal spots of same color on outer margin and beyond costal band; cilia concolorous with wing. Hindwings dark gray. Abdomen buff-brown dorsally, gray ventrally, last segment buff. Legs buff-brown, apices of tarsal segments buff.

Male genitalia: (Fig. 80) R.W.H. slide no. 981.

Female genitalia: (Fig. 131) R.W.H. slide no. 982.

Alar expanse: 14–21 mm.

Food plant: unknown.

HOLOTYPE: ♂, Madera Canyon, 4,880 feet, Santa Rita Mountains, Santa Cruz Co., ARIZONA, July 12, 1959 (R. W. Hodges), [CU Type No. 3806].

PARATYPES: same locality as type, 56 ♂, 19 ♀, July 11–23, 1959 [CU, RWH, USNM, BMNH, LACM, CAS, AFB].

The large size and heavy overlay of dark gray-brown of the forewings of *furvicosta* will separate it from *A. nocticola*. The angulate *aedeagus* in combination with the heavily sclerotized basal process on the left *valva* will separate the male of *furvicosta* from the males of the other species of *Anoncia*.

Anoncia nocticola, new species

(Figs. 128, 196)

Head, thorax, forewings, and legs buff-white overlaid with brown. Labial palpi buff-white at apex of second segment and at base and apex of third segment. Antennae ciliate in female, male unknown, cilia of pecten unicolorous. Forewings with a large discal spot, brown flecks not forming a pattern. Apices of tarsal segments buff-white.

Male genitalia: no specimens available.

Female genitalia: (Fig. 128) R.W.H. slide no. 1026.

Alar expanse: 10½ mm.

Food plant: unknown.

HOLOTYPE: ♀, Madera Canyon, 4,880 feet, Santa Rita Mountains, Santa Cruz Co., ARIZONA, August 3, 1959 (R. W. Hodges), [CU Type No. 3808].

A. nocticola can be separated from *A. nebritis* by the absence of a fascia in the forewing. Sternites two through five of the female of *nocticola* are lightly sclerotized; these sternites are not sclerotized in the female of *nebritis*.

Anoncia orites Walsingham

Hypatopa orites Walsingham, 1907. Proc. U. S. Natl. Mus., 33: 213.

Borkhausenia orites, Barnes and McDunnough, 1917. Check list of the Lepidoptera of Boreal America, 162. Heinrich, 1921. Jour. Agric. Res., 20: 815. McDunnough, 1939. Mem. S. California Acad. Sci., 2: 77.

Anoncia orites, Clarke, 1941. Proc. U. S. Natl. Mus., 90: 269. Clarke, 1942. Can. Ent., 74: 17.

I quote Walsingham's original description because I have seen no specimens.

"*Antennae* brownish gray; basal joint pectinate.

Palpi strongly recurved to the back of the head above; grayish white, much dusted with brownish fuscous, especially on the outer side of the median joint.

Head grayish white, sprinkled with fuscous.

Thorax grayish white, suffused and sprinkled with brownish fuscous.

Forewings grayish white, suffused and sprinkled with brownish fuscous; the central portion of the wing, on which is exhibited a dark discal shade-spot is an elongate dark streak in the fold, and a dark shade at the end of the fold is a little less obliquely placed in relation to a spot at the end of the cell; the apex and termen show slight pale interruptions in the dark shading, which gives the appearance of a series of ill-defined marginal shade-spots extending through the whitish gray cilia; the whole wing has thus a mottled and speckled appearance, the white ground-color showing chiefly before and beyond the discal spot, and in two rather oblique marks pointing to the flexus beneath the basal half of the fold.

Alar expanse—16 mm.

Hindwings shining, grayish brown; cilia brownish ochreous.

Abdomen pale brownish ochreous.

Legs pale brownish ochreous."

Food plant: unknown.

Type: British Museum (Natural History).

Type locality: Mount Shasta, Siskiyou County, California.

ANNOTATED LIST OF THE NORTH AMERICAN COSMOPTERIGIDAE, WALSHIIDAE, AND MOMPHIDAE

The list of the Cosmopterigidae follows the arrangement presented in the systematic part of this paper. Synonyms are indicated by italics.

The list of the Walshiidae gives the generic citations and type designations. The types of Chambers' Cosens', Busck's, and Forbes' species have been examined; and authentic specimens of Braun's and Clemens' species have been seen. Thus, the arrangement of genera and species is based on a study of all the North American species. In addition lectotypes of Chambers' species are designated whenever it is necessary. *Ascalenia,* a European genus, is included.

The list of the Momphidae gives generic citations and type designations. Types of the genera have been examined; therefore, the generic synonymy and the arrangement of the genera should not have to be materially changed.

COSMOPTERIGIDAE

Cosmopterix Huebner, [1826]
  nitens Walsingham, 1889
  molybdina, *sp. nov.*
  pulchrimella Chambers, 1875
  bendidia, *sp. nov.*
  attenuatella Walker, 1864
    flavofasciata Wollaston, 1879
    antillia Forbes, 1931
    mimetis Meyrick, 1897
  clandestinella Busck, 1906
  montisella Chambers, 1875
    unicolorella Walsingham, 1889
  magophila Meyrick, 1919
  gracilens, *sp. nov.*
  dapifera, *sp. nov.*
  delicatella Walsingham, 1889
  dicacula, *sp. nov.*
  lespedezae Walsingham, 1882
  opulenta Braun, 1919
  quadrilineella Chambers, 1878
  minutella Beutenmueller, 1889

abdita, *sp. nov.*
inopis, *sp. nov.*
chalybaeella Walsingham, 1889
gemmiferella Clemens, 1860
bacata, *sp. nov.*
damnosa, *sp. nov.*
clemensella Stainton, 1860
  hermodora Meyrick, 1919
scirpicola, *sp. nov.*
ebriola, *sp. nov.*
fernaldella Walsingham, 1882
floridanella Beutenmueller, 1889
  nigrapunctella Busck, 1900
facunda, *sp. nov.*

TANYGONA Braun, 1923
lignicolorella Braun, 1923
ipomoeae Busck, 1900

ERALEA, *gen. nov.*
albalineella Chambers, 1878
striata, *sp. nov.*

MELANOCINCLIS, *gen. nov.*
lineigera, *sp. nov.*
nigrilineella Chambers, 1878

ETEOBALEA, *gen. nov.*
sexnotella Chambers, 1878
wyattella Barnes and Busck, 1920
iridella Busck, 1907
  niphochrysa Meyrick, 1930
enchrysa, *sp. nov.*

SATHROBROTA, *gen. nov.*
rileyi Walsingham, 1882
badia, *sp. nov.*

LIMNAECIA Stainton, 1851
phragmitella Stainton, 1851

TELADOMA Busck, 1932
  helianthi Busck, 1932
  astigmatica Meyrick, 1928
  murina, *sp. nov.*
  incana, *sp. nov.*

TRICLONELLA Busck, 1901
  pergandeella Busck, 1901
  xuthocelis, *sp. nov.*
  antidectis Meyrick, 1914
  determinatella Zeller, 1873
  bicoloripennis, *sp. nov.*

ANONCIA Clarke, 1941
  conia Walsingham, 1907
    marinensis Keifer, 1935
  sphacelina Keifer, 1935
  brunneipes, *sp. nov.*
  glacialis, *sp. nov.*
  fasciata Walsingham, 1907
  porriginosa, *sp. nov.*
  alboligula, *sp. nov.*
  nebritis, *sp. nov.*
  diveni Heinrich, 1921
  episcia Walsingham, 1907
  callida, *sp. nov.*
  piperata, *sp. nov.*
  leucoritis, Meyrick, 1927
    mentzeliae Clarke, 1942
  longa, Meyrick, 1927
  furvicosta, *sp. nov.*
  nocticola, *sp. nov.*
  orites Walsingham, 1907

WALSHIIDAE

ASCALENIA Wocke, *in* Heinemann, 1877 [1876]. Schmetterlinge Deutschlands und der Schweiz, 2: 421.
  TYPE: *Laverna vanella* Frey, 1860. Monobasic.
  vanella Frey, 1860

PERIPLOCA Braun, 1919. Ent. News, 30: 261.
TYPE: (*Periploca purpuriella* Braun, 1919) = *Elachista concolorella* Chambers, 1875. Monobasic.
concolorella Chambers, 1875
purpuriella Braun, 1919
ceanothiella Cosens, 1908
gleditschiaeella Chambers, 1876
nigra Hodges, 1962
atrata Hodges, 1962
fessa Hodges, 1962
facula Hodges, 1962
laeta Hodges, 1962
funebris Hodges, 1962
cata Hodges, 1962
gulosa Hodges, 1962
mimula Hodges, 1962

WALSHIA Clemens, 1864. Proc. Ent. Soc. Philadelphia, 2: 418.
TYPE: *Walshia amorphella* Clemens, 1864. Monobasic.
particornella Busck, 1909
amorphella Clemens, 1864
miscecolorella Chambers, 1875
miscecalonella Chambers, 1875. *lapsus calami.*
dispar Hodges, 1961
similis Hodges, 1961
exemplata Hodges, 1961

PERIMEDE Chambers, 1874. Can. Ent., 6: 51.
TYPE: *Perimede erransella* Chambers, 1874. Monobasic.
erransella Chambers, 1874
falcata Braun, 1919
ricina Hodges, 1962
battis Hodges, 1962
latris Hodges, 1962

AEAEA Chambers, 1874. Can. Ent. 6: 73.
TYPE: *Aeaea ostryaeella* Chambers, 1874. Monobasic.
ostryaeella Chambers, 1874
quadricristatella Chambers, 1879

CHRYSOPELEIA Chambers, 1874. Can. Ent., 6: 72.
TYPE: *Chyrsopeleia purpuriella* Chambers, 1874. Monobasic.
purpuriella Chambers, 1874.

Lectotype: ♂, bearing following labels: 1) Type, 1358. 2) Kentucky, Chambers. 3) 96. 4) male Genitalia Slide 871, Ronald W. Hodges. 5) MCZ slide 792; Museum of Comparative Zoology.

STILBOSIS Clemens, 1860. Proc. Acad. Natl. Sci. Philadelphia, 12: 170.
TYPE: *Stilbosis tesquella* Clemens, 1860. Monobasic.
tesquella Clemens, 1860
quinquicristatella Chambers, 1880

AMAUROGRAMMA Braun, 1919. Ent. News, 30: 261.
TYPE: *Amaurogramma extensa* Braun, 1919. Monobasic.
extensa Braun, 1919

SORHAGENIA Spuler, 1910. Schmetterlinge Europas, 2: 384.
TYPE: *Elachista rhamniella* Zeller, 1839. Monobasic.
Cystioecetes Braun, 1915. Can. Ent., 47: 194.
TYPE: *Cystioecetes nimbosus* Braun, 1915. Monobasic.
rhamniella Zeller, 1839
nimbosa Braun, 1915

ITHOME Chambers, 1875. Can. Ent., 7: 93.
TYPE: *Ithome unimaculella* Chambers, 1875. Monobasic.
Eriphia Chambers, 1875. Can. Ent., 7: 55; preoccupied.
TYPE: *Eriphia concolorella* Chambers, 1875. Monobasic.
concolorella Chambers, 1875
unimaculella Chambers, 1875
quinquepunctata Forbes, 1931
lassula Hodges, 1962
edax Hodges, 1962
ferax Hodges, 1962

MOMPHIDAE

MOMPHA Huebner, 1816 [1826]. Verzeichniss Bekannter Schmettlinge (*sic*), 414.
TYPE: *Tinea conturbatella* Huebner, [1818–1819]. Designated by Walsingham and Durrant, Ent. Mo. Mag., 45: 173, 1909.
Anybia Stainton, 1854. Insecta Britannica. Lepidoptera: Tineina, 244.

Type: *Tinea langiella* Huebner, [1801]. Monobasic. [= *Alucita epilobiella* Roemer, 1794].

Cyphophora Herrich-Schaeffer, [1853]. Systematische Bearbeitung der Schmetterlinge von Europa, 5 : 45 ; 6 : pl 13, ff. 7–9.
Type: *Elachista idaei* Zeller, 1839. Monobasic.

Laverna Curtis, 1839. British Entomology, 16 : expl. for pl. 735.
Type: *Laverna ochraceella* Curtis, 1839. Monobasic.

Leucophryne Chambers, 1875. Can. Ent., 7 : 210.
Type: *Leucophryne tricristatella* Chambers, 1875. Monobasic.

Lophoptilus Sircom, 1848. Zoologist, 6 : 2037.
Type: *Lophoptilus staintoni* Sircom, 1848. Monobasic.

Psacaphora[1] Herrich-Schaeffer, [1853]. Systematische Bearbeitung der Schmetterlinge von Europa, 5 : 48 ; 6 : pl. 13, ff. 22–24.
Type: *Tinea schrankella* Huebner, [1800–1805]. Designated by Walsingham and Durrant, Ent. Mo. Mag., 45 : 155, 1909.

Wilsonia Clemens, 1864. Proc. Ent. Soc. Philadelphia, 2 : 428.
Type: *Wilsonia brevivitella* Clemens, 1864. Monobasic.

albella Chambers, 1875
albapalpella Chambers, 1875
bifasciella Chambers, 1876
brevivittella Clemens, 1872
  oenotheraevorella Chambers, 1880
  oenotheraeseminella Chambers, 1876
stellella Busck, 1906
circumscriptella Zeller, 1873
pecosella Busck, 1907
bottimeri Busck, 1940
capella Busck, 1940
coloradella Chambers, 1877
definitella Zeller, 1873
  unicristatella Chambers, 1875
ignobilisella Chambers, 1875
claudiella Kearfott, 1907
minimella Chambers, 1880
murtfeldtella Chambers, 1875
  albocapitella Chambers, 1875
  grissaeella Chambers, 1875
  obscurusella Chambers, 1875
  parvicristatella Chambers, 1875

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[1] It seems to me as though some of the species described in *Psacaphora* do not belong in the genus *Mompha*. Future study will probably indicate that they should be placed in a separate genus.

unifasciella Chambers, 1876
rufocristatella Chambers, 1875
punctiferella Busck, 1906
nuptialis Meyrick, 1922
conturbatella Huebner, [1818–1819]
bicristatella Chambers, 1879
purpuriella Busck, 1909. new combination.
edithella Barnes and Busck, 1920. new combination.
terminella Westwood, 1851
  engelella Busck, 1906
deceptella Braun, 1921. new combination.
sexstrigella Braun, 1921. new combination.
annulata Braun, 1923. new combination.
difficilis Braun, 1923. new combination.
communis Braun, 1925. new combination.
argentimaculella Murtfeldt, 1900
luciferella Clemens, 1860
cephalanthiella Chambers, 1871
metallifera Walsingham, 1882. new combination.
tricristatella Chambers, 1875. new combination.
  grandisella Chambers, 1875
  subiridescens Walsingham, 1882
passerella Busck, 1909. new combination.
eloisella Clemens, 1860
  magnatella Zeller, 1873
  oenotheraeella Chambers, 1875
  lyonetiella Chambers, 1875

SYNALLAGMA Busck, 1907. Ent. News, 18 : 277.
TYPE : *Synallagma busckiella* Engel, 1907. Monobasic.
busckiella Engel, 1907

HOMALEDRA Busck, 1900. Proc. U. S. Natl. Mus., 33 : 236.
TYPE : *Homaledra heptathalama* Busck, 1900. Original designation.
heptathalama Busck, 1900
sabalella Chambers, 1880

BATRACHEDRA Herrich-Schaeffer, [1853]. Systematische Bearbeitung der Schmetterlinge von Europa, 5 : 54 ; 6 : pl. 9, ff. 18–21.
TYPE : *Ornix turdipennella* Treitschke, 1833. Monobasic. [= *Gracillaria praeangusta* Haworth, [1828]]. [I do not know *Ornix turdipennella* Kollar, 1832. Beitraege zur Landeskunde

Oesterreichs unter der Enns (Wien), 2: 99. (This paper has not been seen.)]

praeangusta Haworth [1828]
 pulvella Chambers, 1876
 clemensella Chambers, 1877
striolata Zeller, 1873
concitata Meyrick, 1928
salicipomonella Clemens, 1867
mathesoni Busck, 1917
knabi Walsingham, 1909
 enormis Meyrick, 1928. **new synonymy.**
linaria Clark, 1957
(?) trichella Busck, 1908
 concors Meyrick, 1916. **new synonymy.**

AETIA Chambers, 1880. Jour. Cincinnati Soc. Nat. Hist., 2: 186.
 TYPE: *Aetia bipunctella* Chambers, 1880. Monobasic.
 Chaetocampa Busck, 1926. Jour. Agric. Res., 33: 804. **new synonymy.**
 TYPE: *Chaetocampa crotonella* Bottimer, 1926. Monobasic.
bipunctella Chambers, 1880
 crotonella Bottimer, 1926. **new synonymy.**

BLASTODACNA Wocke, *in* Heinemann, 1877 [1876]. Schmetterlinge Deutschlands und der Schweiz, 2: 428.
 TYPE: *Alucita hellerella* Duponchel, [1838]. Designated by Fletcher, Catalogue of Indian Insects, pt. 16: 25, 1928.
 Spuleria Hofman, 1897. Iris, 10: 230.
 TYPE: *Tinea aurifrontella* Huebner, [1832]. Monobasic.
curvilineella Chambers, 1872
bicristatella Chambers, 1875
 Lectotype: ♂, bearing following labels: 1) Type, 1459. 2) Chambers, Canada. 3) *Gelechia bicristatella,* Canada, Cham. 4) Elachistid, AB Oct. 1902. Museum of Comparative Zoology.
 placendiella Busck, 1908. **new synonymy.**
 sublustris Meyrick, 1922. **new synonymy.**

CHRYSOCLISTA Stainton, 1854. Insecta Britannica. Lepidoptera: Tineina, 240.
 TYPE: *Phalaena linneella* Clerck, 1759. Designated by Fletcher, Catalogue of Indian Insects, pt. 16: 25. 1928.
linneella Clerck, 1759
villella Busck, 1904
cambiella Busck, 1915. new combination.

ACKNOWLEDGEMENTS

The work forming the basis of this paper was done at Cornell University. I wish to express my gratitude to Dr. J. G. Franclemont for his guidance and critical review of the manuscript. Drs. J. W. Wells and D. Pimentel have reviewed the manuscript and have aided me in many other ways. I also express my thanks to Dr. J. F. Gates Clarke, Curator of Insects, United States National Museum; Dr. Annette F. Braun; and Mr. J. D. Bradley, Department of Entomology, British Museum (Natural History) for their interest in my work, for their willingness to answer numerous questions and for furnishing crucial specimens.

Grateful acknowledgement is made to the Grace H. Griswold Fund of the Department of Entomology of Cornell University for assuming the cost of engraving the plates.

LITERATURE CITED

Braun, A. F. 1919. Notes on Cosmopterygidae, with descriptions of new genera and species (Microlepidoptera). Ent. News, 30: 260–264.

———. 1923. Microlepidoptera: notes and new species. Trans. American Ent. Soc., 49: 115–127.

———. 1930. Notes and new species of Microlepidoptera from the mineral springs region of Adams County, Ohio. Trans. American Ent. Soc., 56: 1–17.

Busck, A. 1900 [1901]. New American Tineina. Jour. New York Ent. Soc., 8: 234–248.

———. 1906. A review of the American moths of the genus Cosmopteryx Huebner. Proc. U. S. Natl. Mus., 30: 707–713.

———. 1908. A generic revision of American moths of the family Oecophoridae, with descriptions of new species. Proc. U. S. Natl. Mus., 35: 187–207.

———. 1932. Description of a new cosmopterygid leaf miner (Lepidoptera) on Helianthus. Proc. Ent. Soc. Washington, 34: 17–20.

Chambers, V. T. 1878. Descriptions of new Tineina from Texas, and others from more northern localities. Bull. U. S. Geol. Geog. Surv. Terr., 4: 79–106.

Clarke, J. F. G. 1941. Revision of the North American moths of the family Oecophoridae, with descriptions of new genera and species. Proc. U. S. Natl. Mus., 90: 33–286, pl. 1–48.

———. 1942. A synopsis of the genus Anoncia, with one new species (Cosmopterygidae; Lepidoptera). Can. Ent., 74: 17–19.

————. 1955. Catalogue of the type specimens of Microlepidoptera in the British Museum (Natural History) described by Edward Meyrick. Norwich: Jarrold and Sons, Ltd., vol. 1.

Diakonoff, A. 1954. Microlepidoptera of New Guinea Part 4. Verh. Akad. Wet. Amsterdam, 50: 1–191.

Dyar, H. G. 1901. Notes on the winter *Lepidoptera* of Lake Worth, Florida. Proc. Ent. Soc., Washington, 4: 446–485.

Flecher, T. B. 1928. Catalogue of Indian Insects. pt. 16. Cosmopterygidae. Calcutta, Govt. India Centr. Pubn. Branch.

Forbes, W. T. M. 1923. The Lepidoptera of New York and neighboring states. Cornell University Agric. Exp. Sta. Mem., 68: 1–729, ff. 1–439.

de Gray, T., Lord Walsingham. 1889. Steps towards a revision of Chambers' Index, with notes and descriptions of new species. Insect Life, 1: 287–291.

————. 1891 [1892]. On the Micro-Lepidoptera of the West Indies. Proc. Zool. Soc. London, 492–549.

————. 1909–1915. Biologia Centrali-Americana. Insecta. Lepidoptera-Heterocera, vol. 4.

Heinrich, C. 1921. Some Lepidoptera likely to be confused with the Pink Bollworm. Jour. Agric. Res., 20: 807–836.

Hodges, R. W. 1959. A method of preparing fresh Microlepidoptera for spreading. The Lepidopterists' News, 12: 205.

Keifer, H. H. 1935. California Microlepidoptera VII. Monthly Bull. Dept. Agric. California, 24: 195–218, pl. 1–5.

Klots, A. B., *in* Tuxen, S. L. (ed.). 1956. Taxonomist's glossary of genitalia in insects. Copenhagen, Ejnar Munksgaard. Lepidoptera, pp. 97–111, ff. 121–132.

McDunnough, J. 1939. Check list of the Lepidoptera of Canada and the United States of America. Part 2: Microlepidoptera. Mem. S. California Acad. Sci., 2: 1–171.

Meyrick, E. 1909. Descriptions of Micro-Lepidoptera from Bolivia and Peru. Trans. Ent. Soc. London, 1909: 13–43.

————. 1929. A revised handbook of British Lepidoptera. London: Watkins and Doncaster, pp. 1–914.

Spuler, A. 1910. Die Schmetterlinge Europas. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung, vol. 2.

Wocke, M., *in* Staudinger, O. and M. Wocke. 1871. Catalog der Lepidopteren des Europaeischen faunengebiets. Dresden: Staudinger, pp. 1–426.

————, *in* Heinemann, O. von. 1877 [1876]. Die Schmetterlinge Deutschlands und der Schweiz. Braunschweig: Schwetschke und Sohn, vol. 2, pt. 2.

ADDENDA

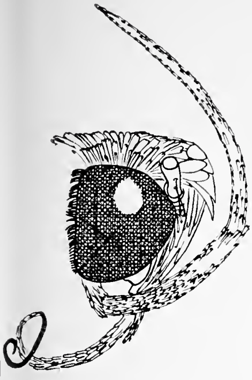
The following additions have been made since the writing of this paper: 1. The type specimens of *Sathrobrota rileyi* Walsingham and *Sathrobrota stigmatophora* Walsingham have been examined by Mr. Bradley; and according to the diagnostic characters of *rileyi*, *stigmatophora* is the same as *rileyi* (new synonymy). 2. *Anoncia aciculata* Meyrick occurs in the geographic area of this paper. Clarke (in press) illustrates the male genitalia and the habitus of the type. 3. I have seen another species of *Antequera* as well as more material of Cosmopterigidae from the Old World tropics, and because of this, now retain this genus in the family. The male and female genitalia, venation, and lateral view of the head are given in Clarke (1941, Proc. U. S. Natl. Mus., 90: 33–286).

PLATES

Explanation of the Figures

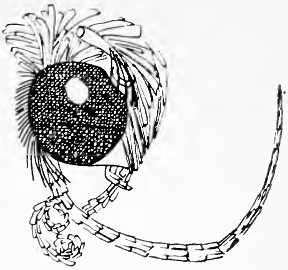
Figures 1–10. Lateral view of heads of genera of Cosmopterigidae.

Fig. 1. *Limnaecia* Stainton(*Limnaecia phragmitella* Stainton).
Fig. 2. *Eteobalea, gen. nov.* (*Eteobalea sexnotella* Chambers).
Fig. 3. *Eralea, gen. nov.* (*Eralea albalineella* Chambers).
Fig. 4. *Anoncia* Clarke (*Anoncia conia* Walsingham).
Fig. 5. *Sathrobrota, gen. nov.* (*Sathrobrota rileyi* Walsingham).
Fig. 6. *Triclonella* Busck (*Triclonella pergandeella* Busck).
Fig. 7. *Cosmopterix* Huebner (*Cosmopterix zieglerella* Huebner).
Fig. 8. *Melanocinclis, gen. nov.* (*Melanocinclis lineigera,* sp. nov.).
Fig. 9. *Teladoma* Busck (*Teladoma helianthi* Busck).
Fig. 10. *Tanygona* Braun (*Tanygona lignicolorella* Braun).

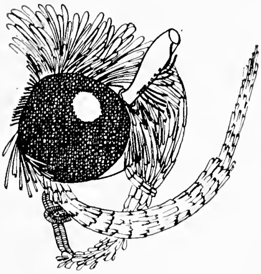


1. LIMNAECIA

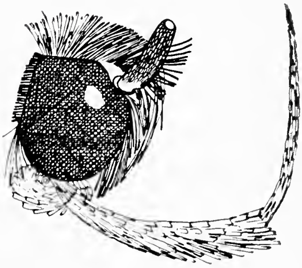
2. ETEOBALEA



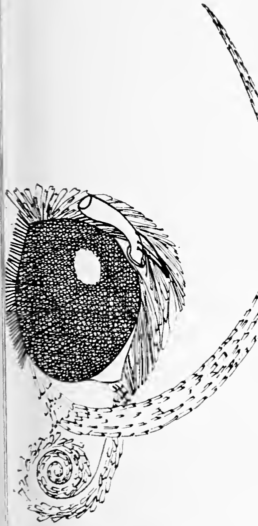
3. ERALEA



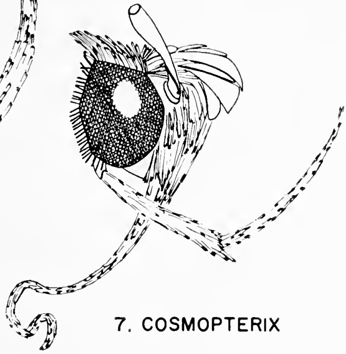
4. ANONCIA



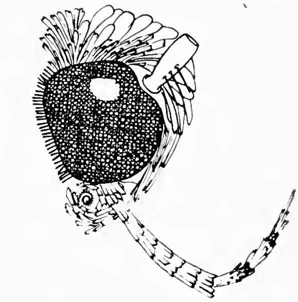
5. SATHROBROTA



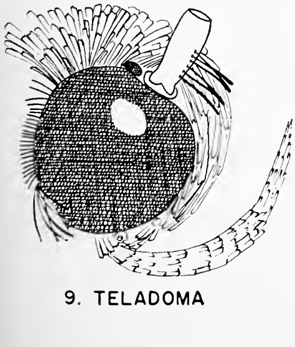
6. TRICLONELLA



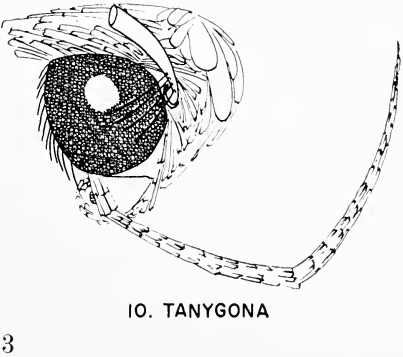
7. COSMOPTERIX



8. MELANOCINCLIS



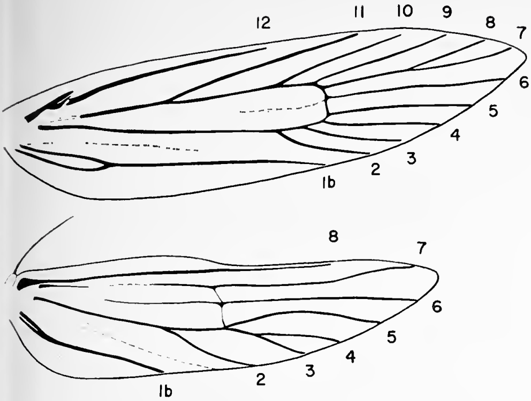
9. TELADOMA



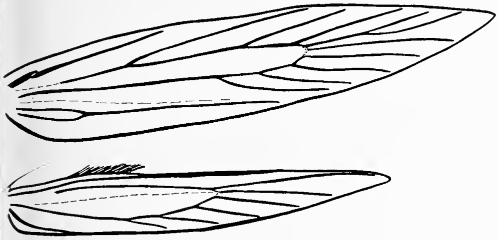
10. TANYGONA

Figures 11–20. Venation of genera of Cosmopterigidae.

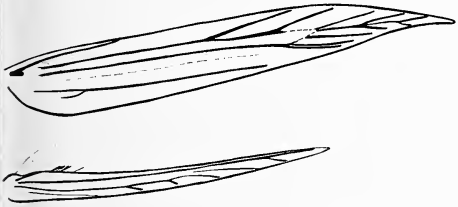
Fig. 11. *Triclonella* Busck.
Fig. 12. *Limnaecia* Stainton.
Fig. 13. *Sathrobrota, gen nov.*
Fig. 14. *Teladoma* Busck.
Fig. 15. *Melanocinclis, gen. nov.*
Fig. 16. *Tanygona* Braun.
Fig. 17. *Cosmopterix* Huebner.
Fig. 18. *Eralea, gen. nov.*
Fig. 19. *Anoncia* Clarke.
Fig. 20. *Eteobalea, gen. nov.*



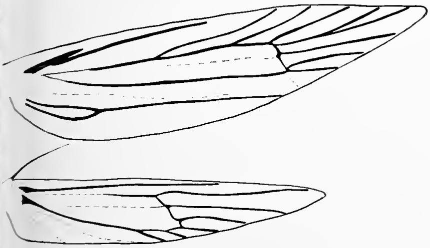
11. TRICLONELLA



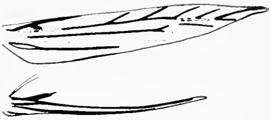
12. LIMNAECIA



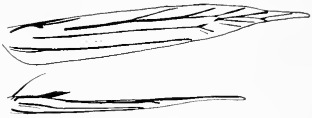
13. SATHROBROTA



14. TELADOMA

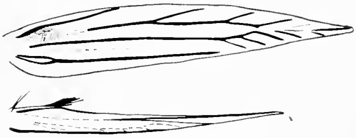


15. MELANOCINCLIS

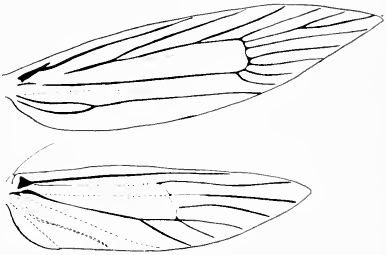


16. TANYGONA

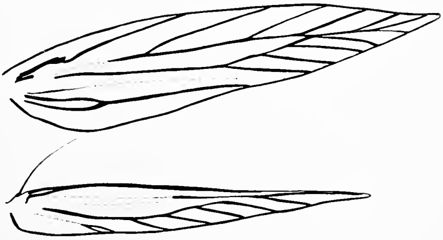
17. COSMOPTERIX



18. ERALEA



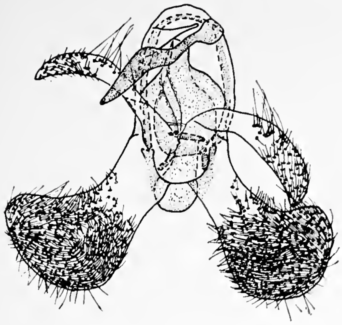
19. ANONCIA



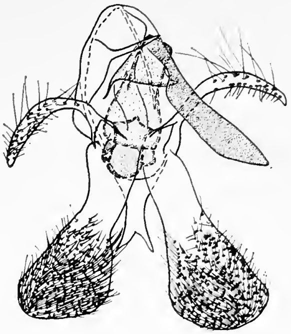
20. ETEOBALEA

Figures 21–28. Ventral view of male genitalia of species of *Cosmopterix*.

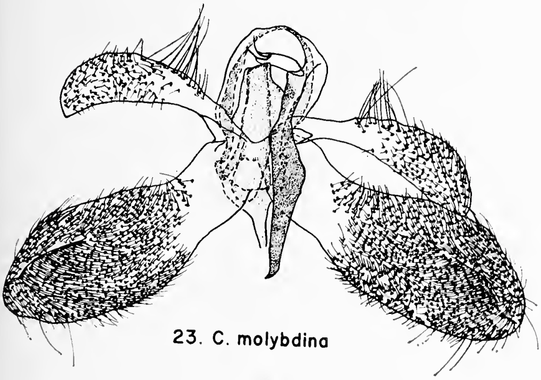
Fig. 21. *Cosmopterix zieglerella* Huebner.
Fig. 22. *C. nitens* Walsingham.
Fig. 23. *C. molybdina, sp. nov.*
Fig. 24. *C. pulchrimella* Chambers.
Fig. 25. *C. bendidia, sp. nov.*
Fig. 26. *C. attenuatella* Walker.
Fig. 27. *C. montisella* Chambers.
Fig. 28. *C. clandestinella* Busck.



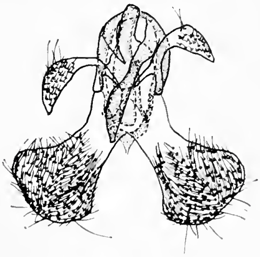
21. C. zieglerella



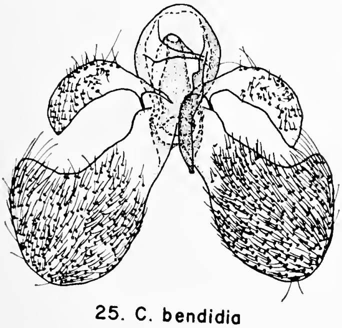
22. C. nitens



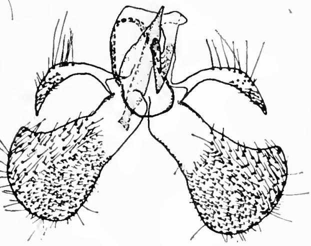
23. C. molybdina



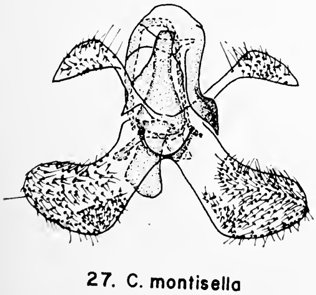
24. C. pulchrimella



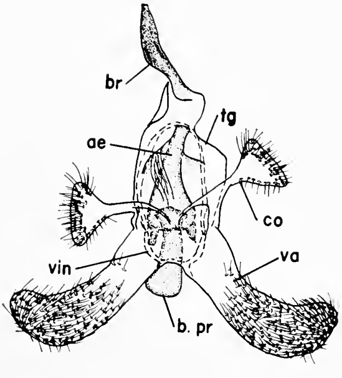
25. C. bendidia



26. C. attenuatella



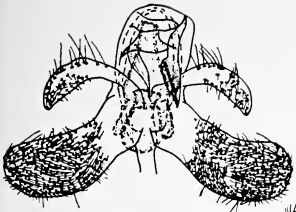
27. C. montisella



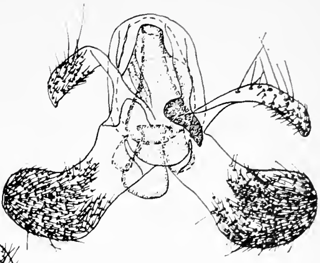
28. C. clandestinella

Figures 29–38. Ventral view of male genitalia of species of *Cosmopterix*.

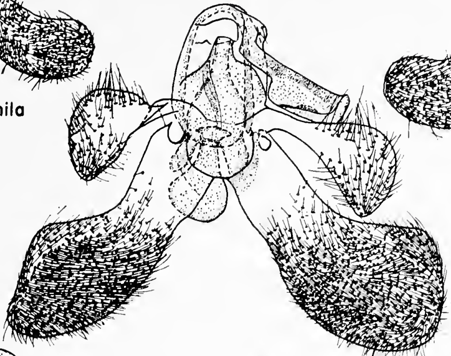
Fig. 29. *Cosmopterix magophila* Meyrick.
Fig. 30. *C. gracilens, sp. nov.*
Fig. 31. *C. minutella* Beutenmueller.
Fig. 32. *C. dapifera, sp. nov.*
Fig. 33. *C. delicatella* Walsingham.
Fig. 34. *C. dicacula, sp. nov.*
Fig. 35. *C. lespedezae* Walsingham.
Fig. 36. *C. abdita, sp. nov.*
Fig. 37. *C. opulenta* Braun.
Fig. 38. *C. quadrilineella* Chambers.



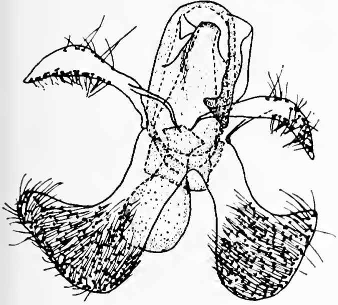
29. C. magophila



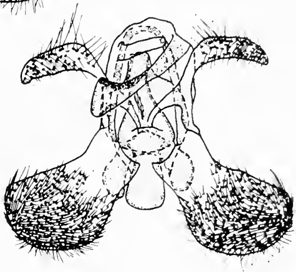
30. C. gracilens



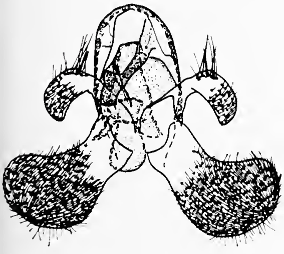
31. C. minutella



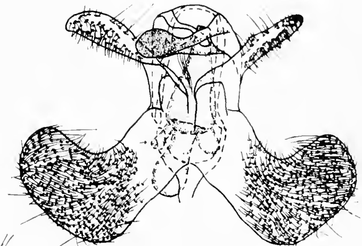
32. C. dapifera



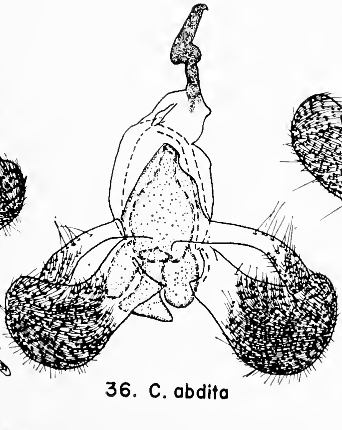
33 C delicatella



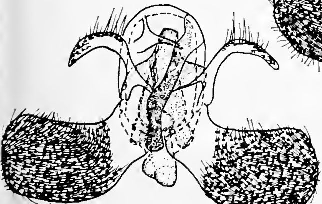
34. C. dicacula



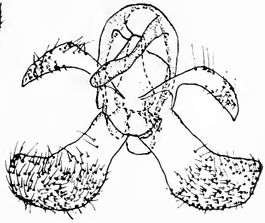
35. C. lespedezae



36. C. abdita



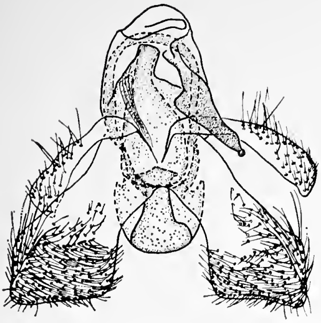
37. C. opulenta



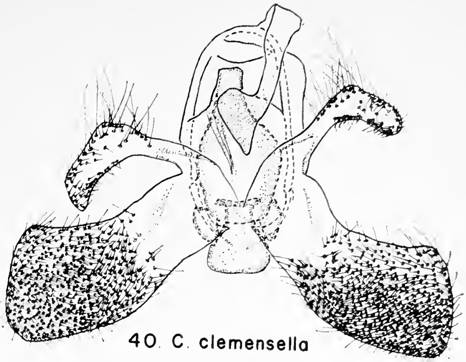
38. C. quadrilineella

Figures 39–44. Ventral view of male genitalia of species of *Cosmopterix.*

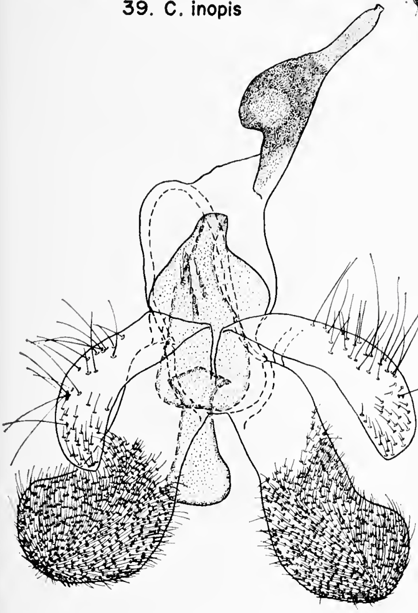
Fig. 39. *Cosmopterix inopis, sp. nov.*
Fig. 40. *C. clemensella* Stainton.
Fig. 41. *C. gemmiferella* Clemens.
Fig. 42. *C. bacata, sp. nov.*
Fig. 43. *C. damnosa, sp. nov.*
Fig. 44. *C. scirpicola, sp. nov.*



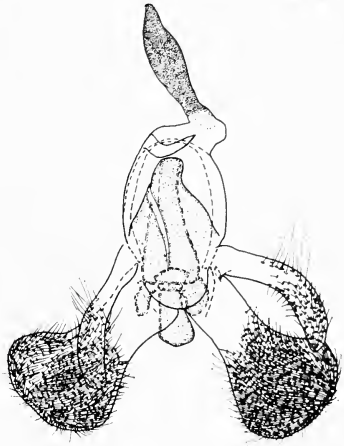
39. C. inopis



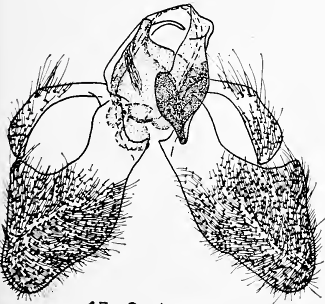
40. C. clemensella



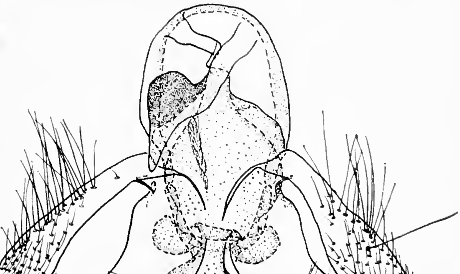
41. C. gemmiferella



42. C. bacata



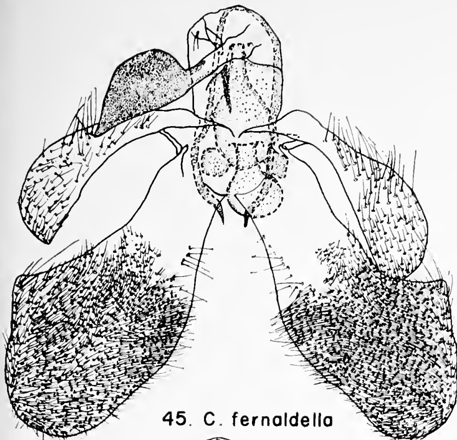
43. C. damnosa



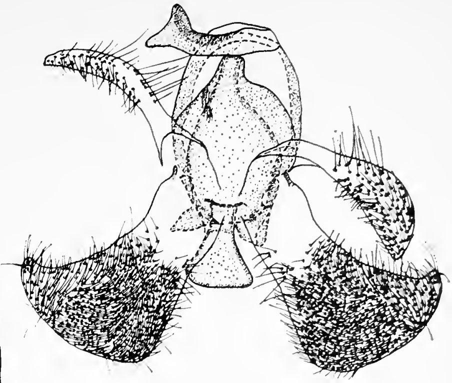
44. C. scirpicola

Figures 45–53. Ventral view of male genitalia of species of *Cosmopterix*, *Tanygona*, *Eralea*, and *Eteobalea*.

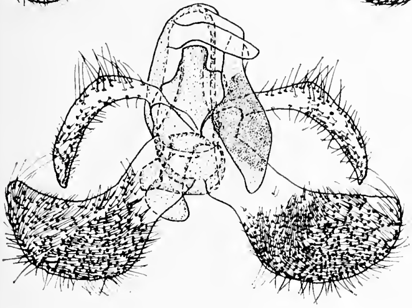
Fig. 45. *Cosmopterix fernaldella* Walsingham.
Fig. 46. *C. ebriola, sp. nov.*
Fig. 47. *C. floridanella* Beutenmueller.
Fig. 48. *Tanygona ipomoeäe* Busck.
Fig. 49. *T. lignicolorella* Braun.
Fig. 50. *Eralea striata, sp. nov.*
Fig. 51. *E. albalineella* Chambers.
Fig. 52. *Eteobalea iridella* Busck.
Fig. 53. *E. sexnotella* Chambers.



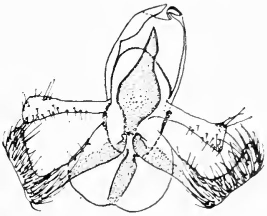
45. C. fernaldella



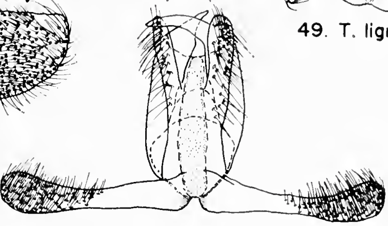
46. C. ebriola



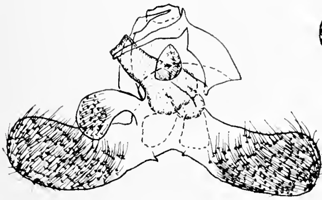
47. C. floridanella



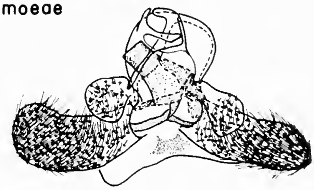
49. T. lignicolorella



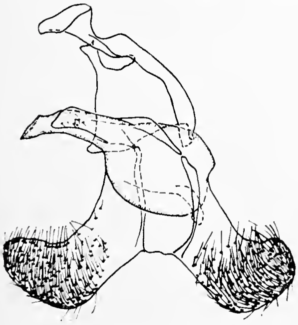
48. T. ipomoeae



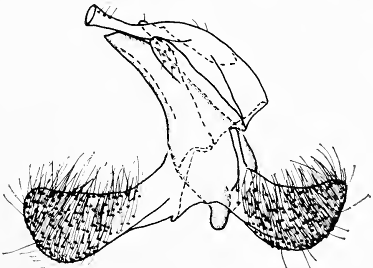
50. E. striata



51. E. albalineella



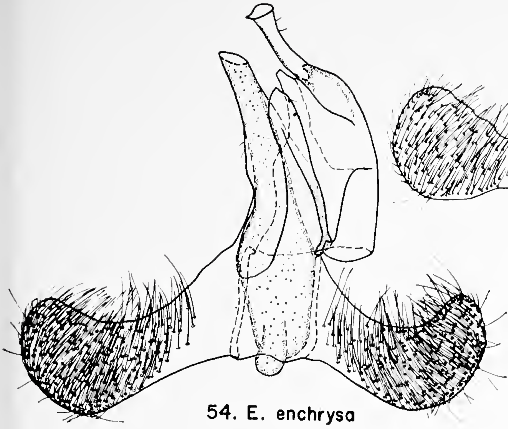
52. E. iridella



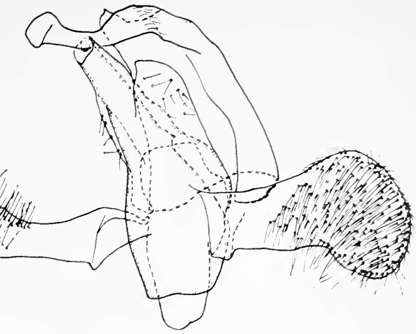
53. E. sexnotella

Figures 54–60. Ventral view of male genitalia of species of *Eteobalea*, *Melanocinclis*, *Stagmatophora*, and *Sathrobrota*.

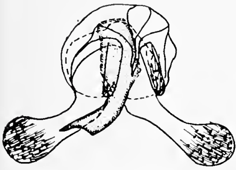
Fig. 54. *Eteobalea enchrysa, sp. nov.*
Fig. 55. *E. wyattella* Barnes and Busck (left valva upside down).
Fig. 56. *Melanocinclis nigrilineella* Chambers.
Fig. 57. *M. lineigera, sp. nov.*
Fig. 58. *Stagmatophora heydeniella* Fischer von Roeslerstamm.
Fig. 59. *Sathrobrota rileyi* Walsingham.
Fig. 60. *S. badia, sp. nov.*



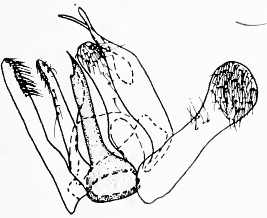
54. E. enchrysa



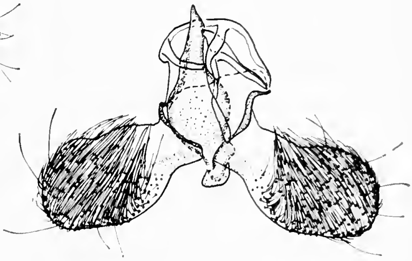
55. E. wyattella



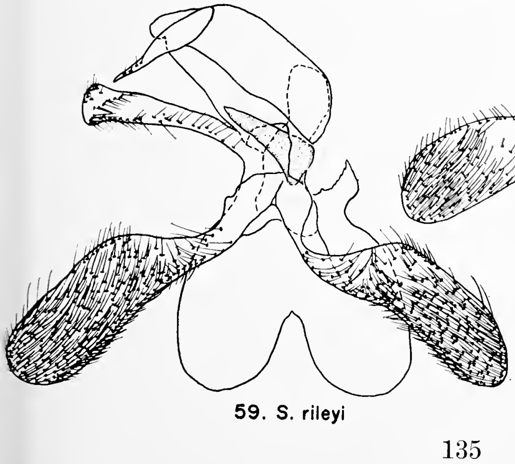
56. M. nigrilineella



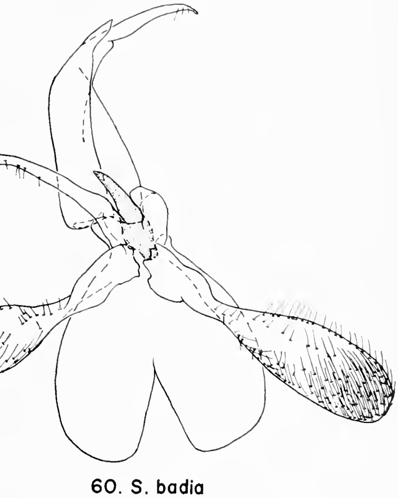
57. M. lineigera



58. S. heydeniella



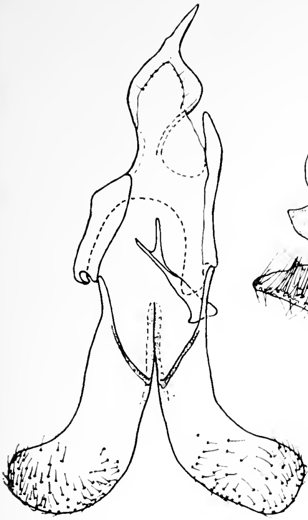
59. S. rileyi



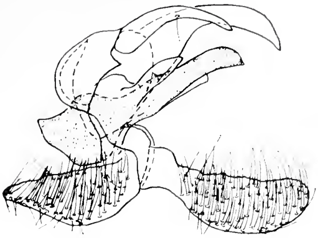
60. S. badia

Figures 61–66. Ventral view of male genitalia of species of *Teladoma*, *Pyroderces*, and *Limnaecia*.

Fig. 61. *Teladoma helianthi* Busck.
Fig. 62. *Pyroderces argyrogrammos* Zeller.
Fig. 63. *Limnaecia phragmitella* Stainton.
Fig. 64. *Teladoma incana, sp. nov.*
Fig. 65. *T. astigmatica* Meyrick
Fig. 66. *T. murina, sp. nov.*

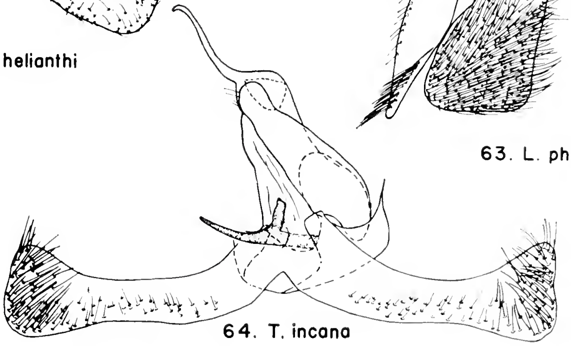


61. T. helianthi



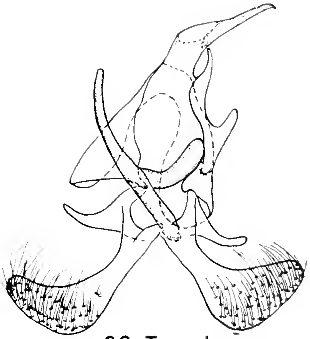
62. P. argyrogrammos

63. L. phragmitella



64. T. incana

65. T. astigmatica

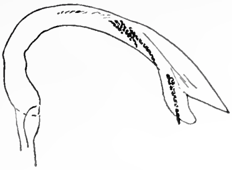


66. T. murina

Figures 67–71. Ventral view of male genitalia of species of *Triclonella*.

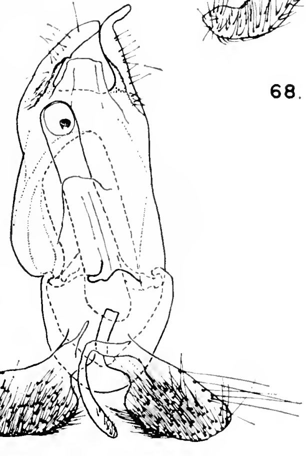
Fig. 67. *Triclonella pergandeella* Busck.
Fig. 68. *T. xuthocelis, sp. nov.*
Fig. 68a. *T. xuthocelis, sp. nov.*, aedeagus.
Fig. 69. *T. antidectis* Meyrick.
Fig. 70. *T. determinatella* Zeller.
Fig. 71. *T. bicoloripennis, sp. nov.*

67. T. pergandeella

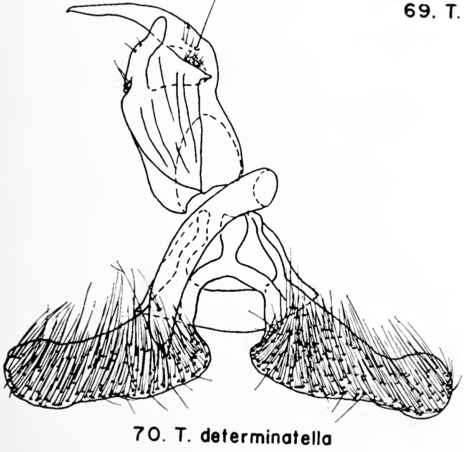


68a.

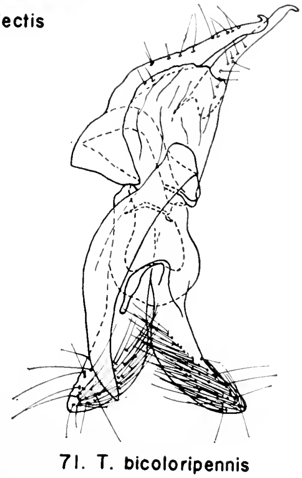
68. T. xuthocelis



69. T. antidectis



70. T. determinatella



71. T. bicoloripennis

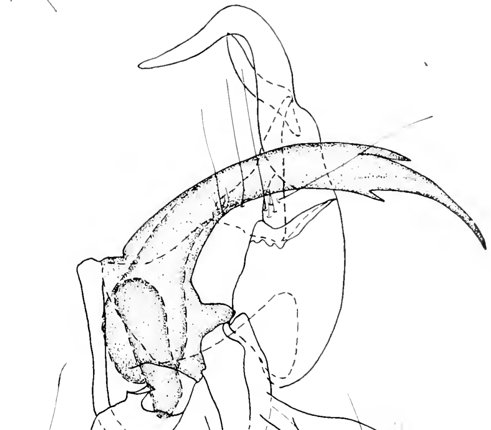
Figures 72–75. Ventral view of male genitalia of species of *Anoncia*.

Fig. 72. *Anoncia conia* Walsingham.
Fig. 73. *A. sphacelina* Keifer.
Fig. 74. *A. glacialis, sp. nov.*
Fig. 75. *A. brunneipes, sp. nov.*

72. A. conia

73. A. sphacelina

74. A. glacialis

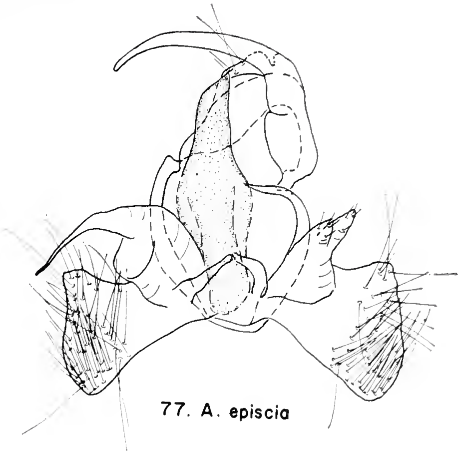


75. A. brunneipes

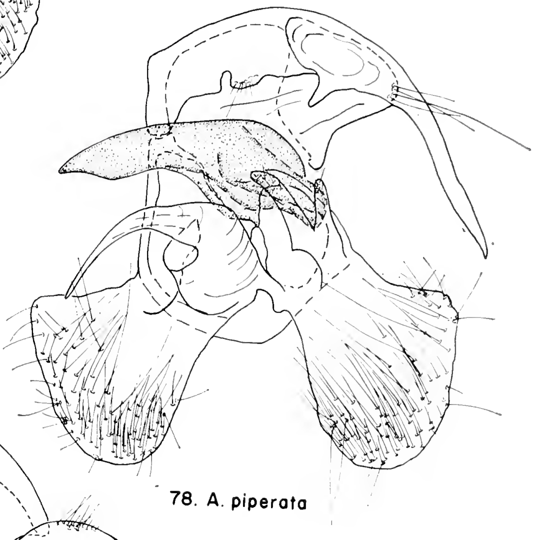
Figures 76–79. Ventral view of male genitalia of species of *Anoncia.*

Fig. 76. *Anoncia alboligula, sp. nov.*
Fig. 77. *A. episcia* Walsingham.
Fig. 78. *A. piperata, sp. nov.*
Fig. 79. *A. longa* Meyrick.

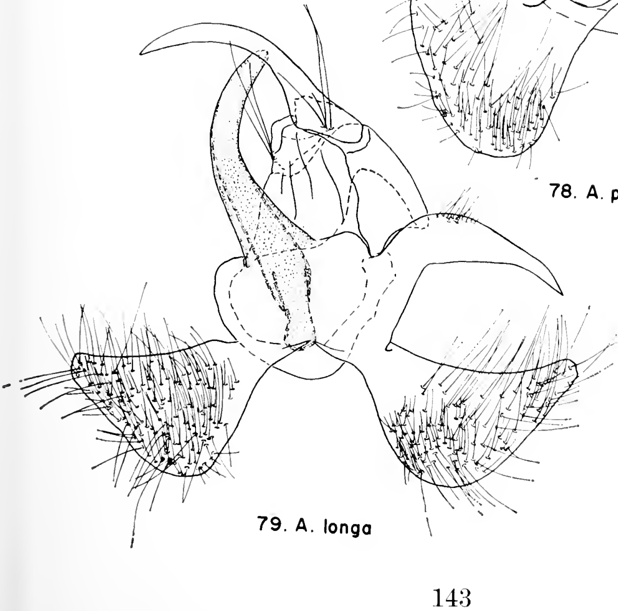
76. A. alboligula



77. A. episcia



78. A. piperata

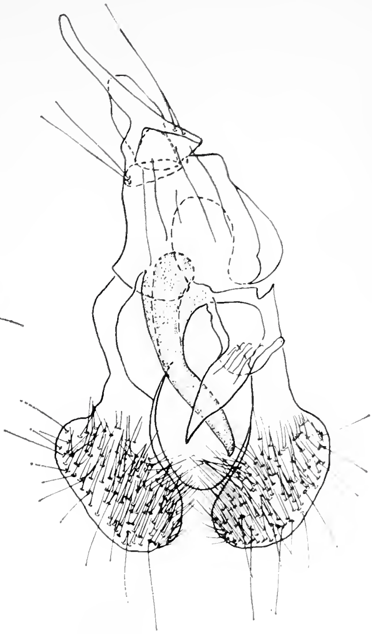


79. A. longa

Figures 80–84. Ventral view of male genitalia of species of *Anoncia*.

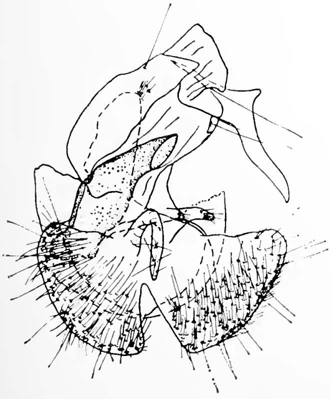
Fig. 80. *Anoncia furvicosta, sp. nov.*
Fig. 81. *A. nebritis, sp. nov.*
Fig. 82. *A. fasciata* Walsingham.
Fig. 83. *A. diveni* Heinrich.
Fig. 84. *A. callida, sp. nov.*

80. A. furvicosta

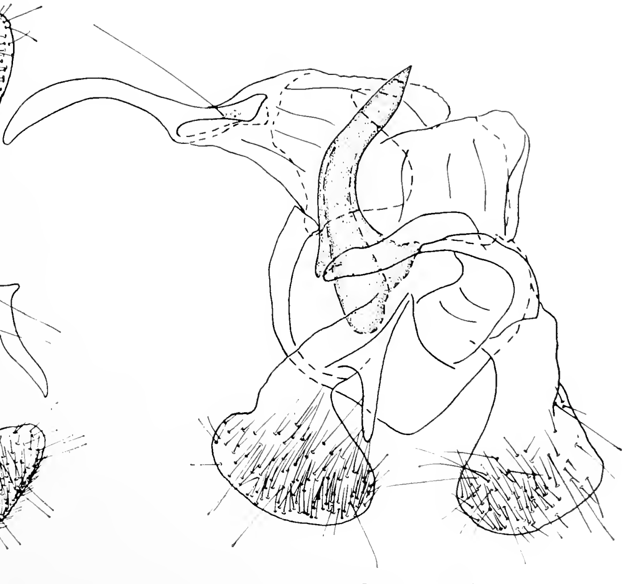


81. A. nebritis

82. A. fasciata



83. A. diveni



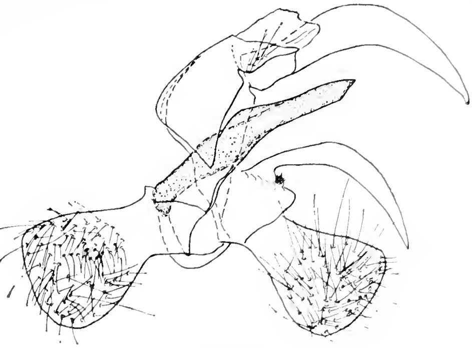
84. A. callida

Figures 85, 86. Ventral view of male genitalia of species of *Anoncia.*

Figures 87–91. Ventral view of female genitalia of species of *Cosmopterix.*

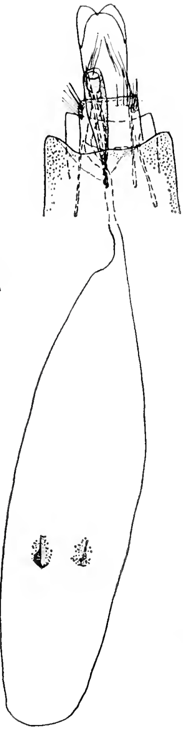
Fig. 85. *Anoncia porriginosa, sp. nov.*
Fig. 86. *A. leucoritis* Meyrick.
Fig. 87. *Cosmopterix zieglerella* Huebner.
Fig. 88. *C. nitens* Walsingham.
Fig. 89. *C. molybdina, sp. nov.*
Fig. 90. *C. attenuatella* Walker.
Fig. 91. *C. dapifera, sp. nov.*

85. A. porriginosa

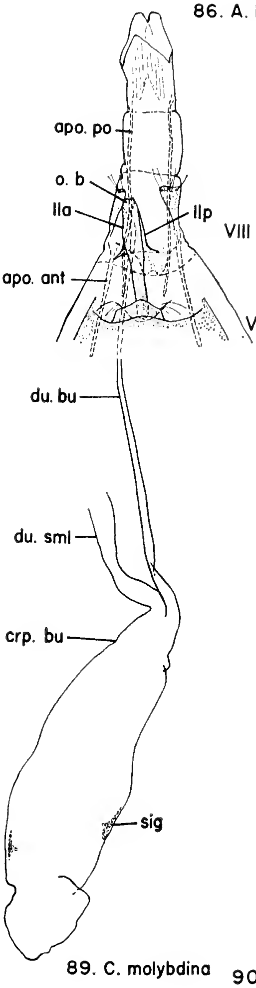


86. A. leucoritis

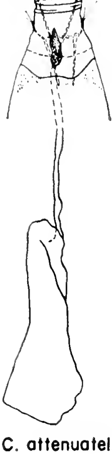
87. C. zieglerella



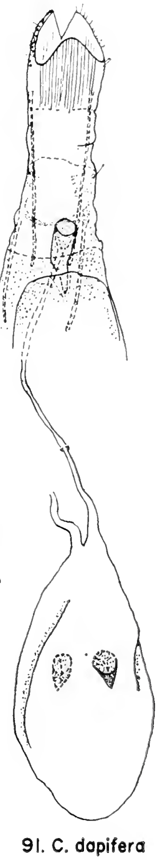
88. C. nitens



89. C. molybdina



90. C. attenuatella



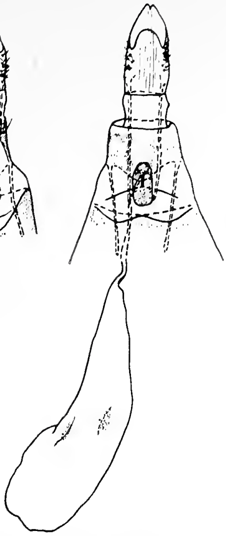
91. C. dapifera

Figures 92–100. Ventral view of female genitalia of species of *Cosmopterix*.

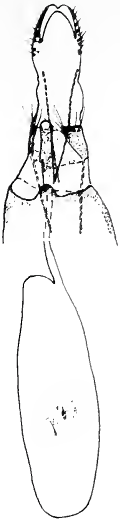
Fig. 92. *Cosmopterix pulchrimella* Chambers.
Fig. 93. *C. bendidia, sp. nov.*
Fig. 94. *C. quadrilineella* Chambers.
Fig. 95. *C. clandestinella* Busck.
Fig. 96. *C. lespedezae* Walsingham.
Fig. 97. *C. fernaldella* Walsingham.
Fig. 98. *C. fernaldella* Walsingham.
Fig. 99. *C. clemensella* Stainton.
Fig. 100. *C. ebriola, sp. nov.*

92. C. pulchrimella

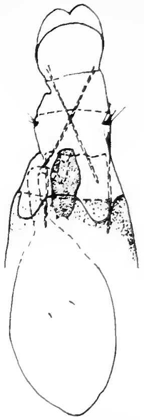
93. C. bendidia



94. C. quadrilineella



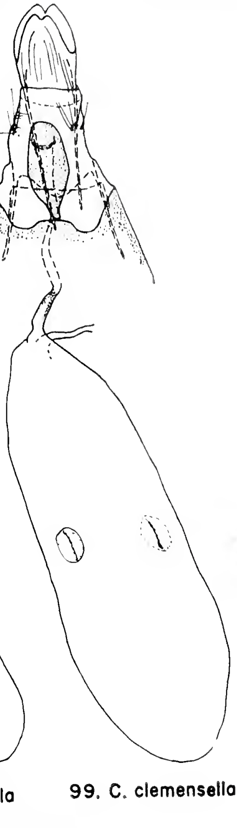
95. C. clandestinella



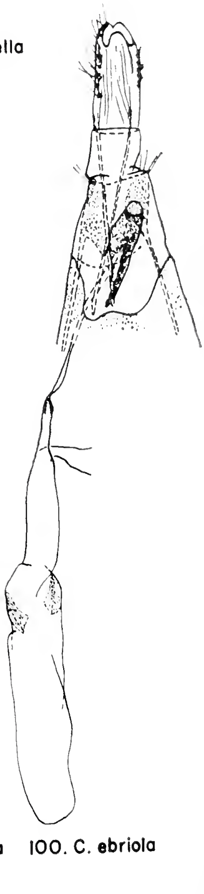
96. C. lespedezae

97. C. fernaldella

98. C. fernaldella



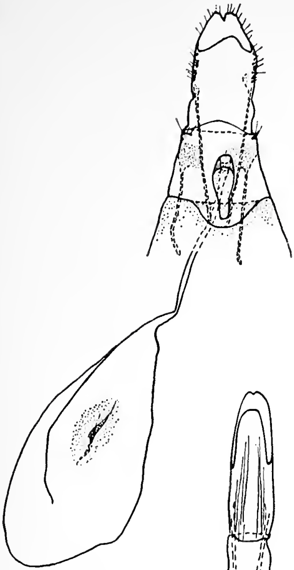
99. C. clemensella



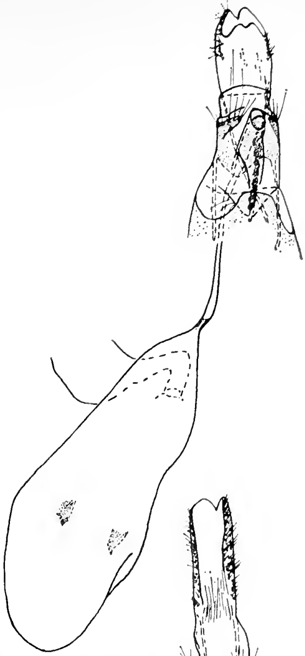
100. C. ebriola

Figures 101-107. Ventral view of female genitalia of species of *Cosmopterix.*

Fig. 101. *Cosmopterix montisella* Chambers.
Fig. 102. *C. floridanella* Beutenmueller
Fig. 103. *C. inopis, sp. nov.*
Fig. 104. *C. opulenta* Braun.
Fig. 105. *C. scirpicola, sp. nov.*
Fig. 106. *C. facunda, sp. nov.*
Fig. 107. *C. gemmiferella* Clemens.

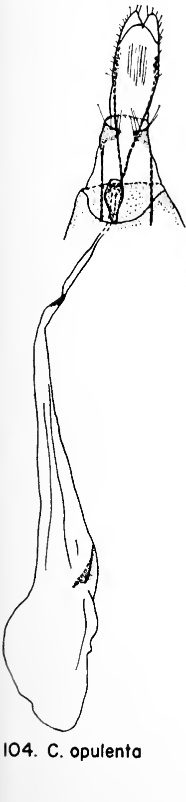


101. C. montisella

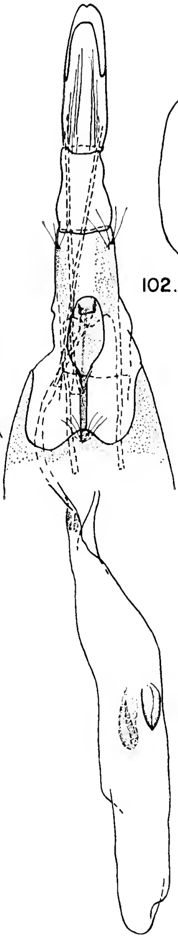


102. C. floridanella

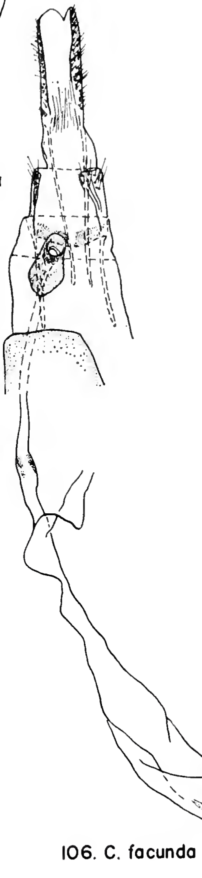
103. C. inopis



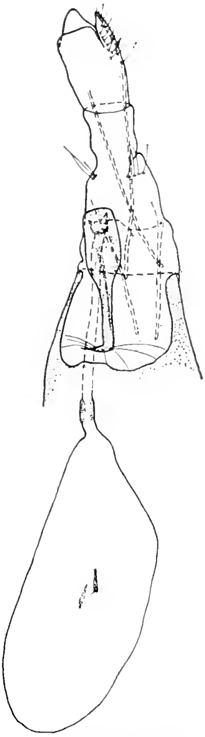
104. C. opulenta



105. C. scirpicola



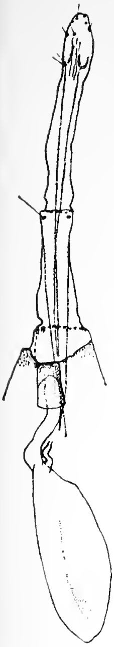
106. C. facunda



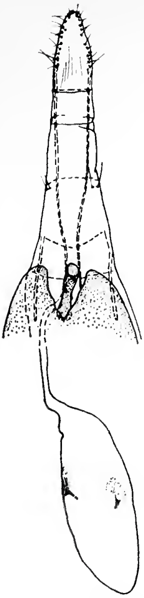
107. C. gemmiferella

Figures 108–115. Ventral view of female genitalia of species of *Tanygona*, *Eralea*, *Stagmatophora*, and *Eteobalea*.

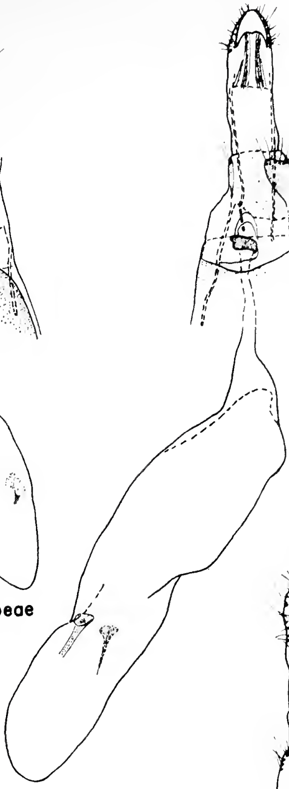
Fig. 108. *Tanygona lignicolorella* Braun.
Fig. 109. *T. ipomoeae* Busck.
Fig. 110. *Eralea albalineella* Chambers.
Fig. 111. *Stagmatophora heydeniella* Fischer von Roeslerstamm.
Fig. 112. *Eteobalea iridella* Busck.
Fig. 113. *E. sexnotella* Chambers.
Fig. 114. *E. wyattella* Barnes and Busck.
Fig. 115. *E. enchrysa, sp. nov.*



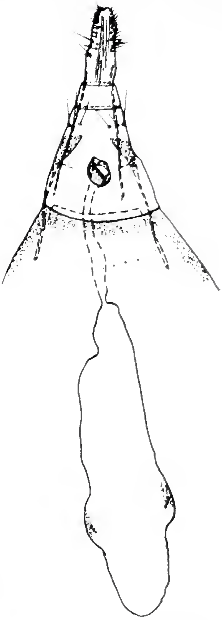
108. T. lignicolorella



109. T. ipomoeae



110. E. albalineella



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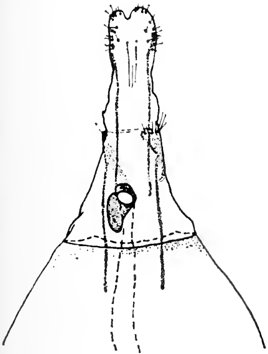

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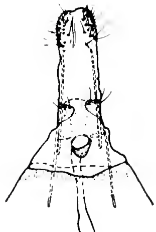

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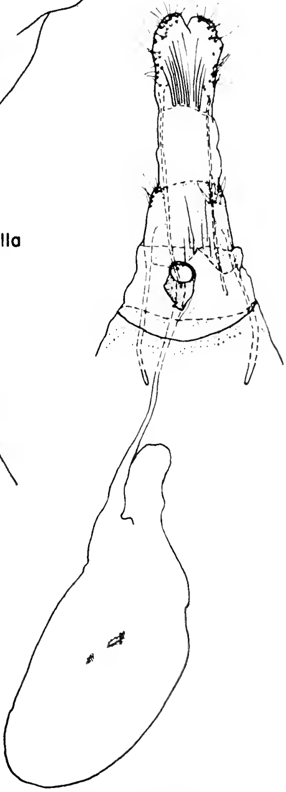

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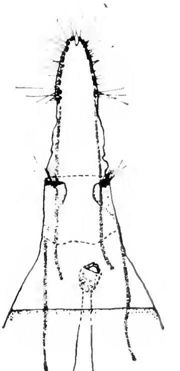

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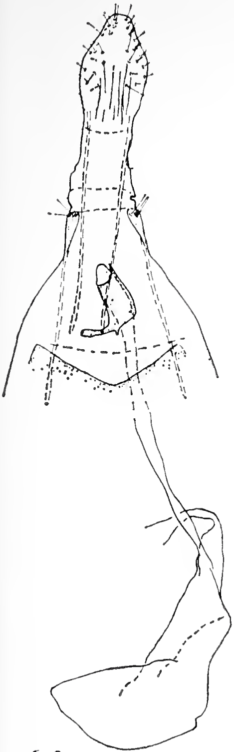

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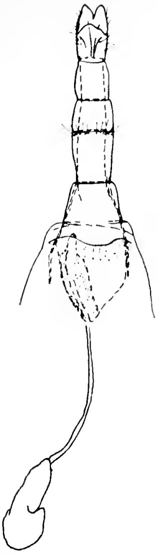

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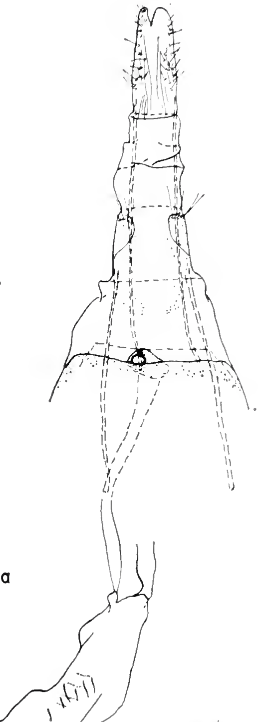

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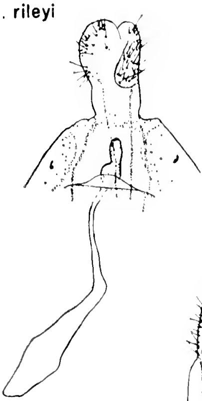

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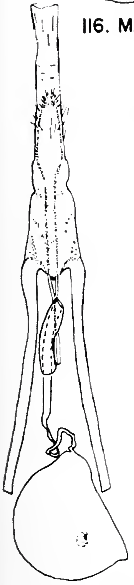

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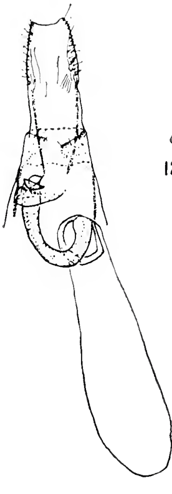

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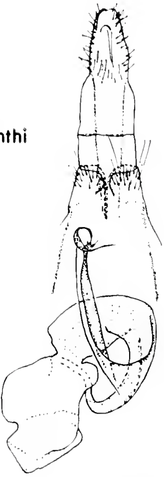

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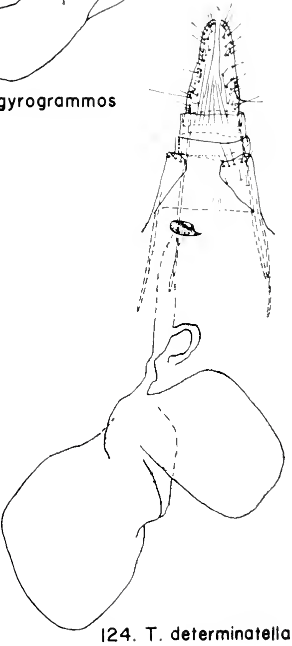

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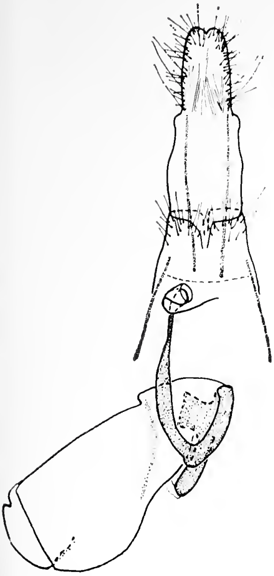

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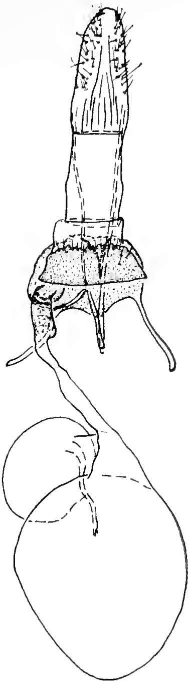

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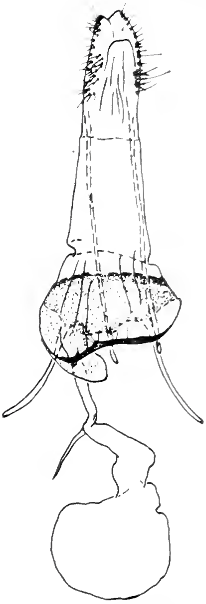

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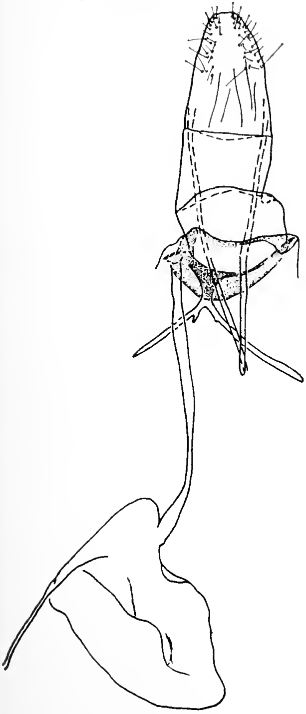

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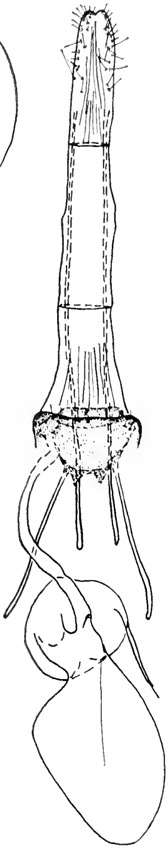

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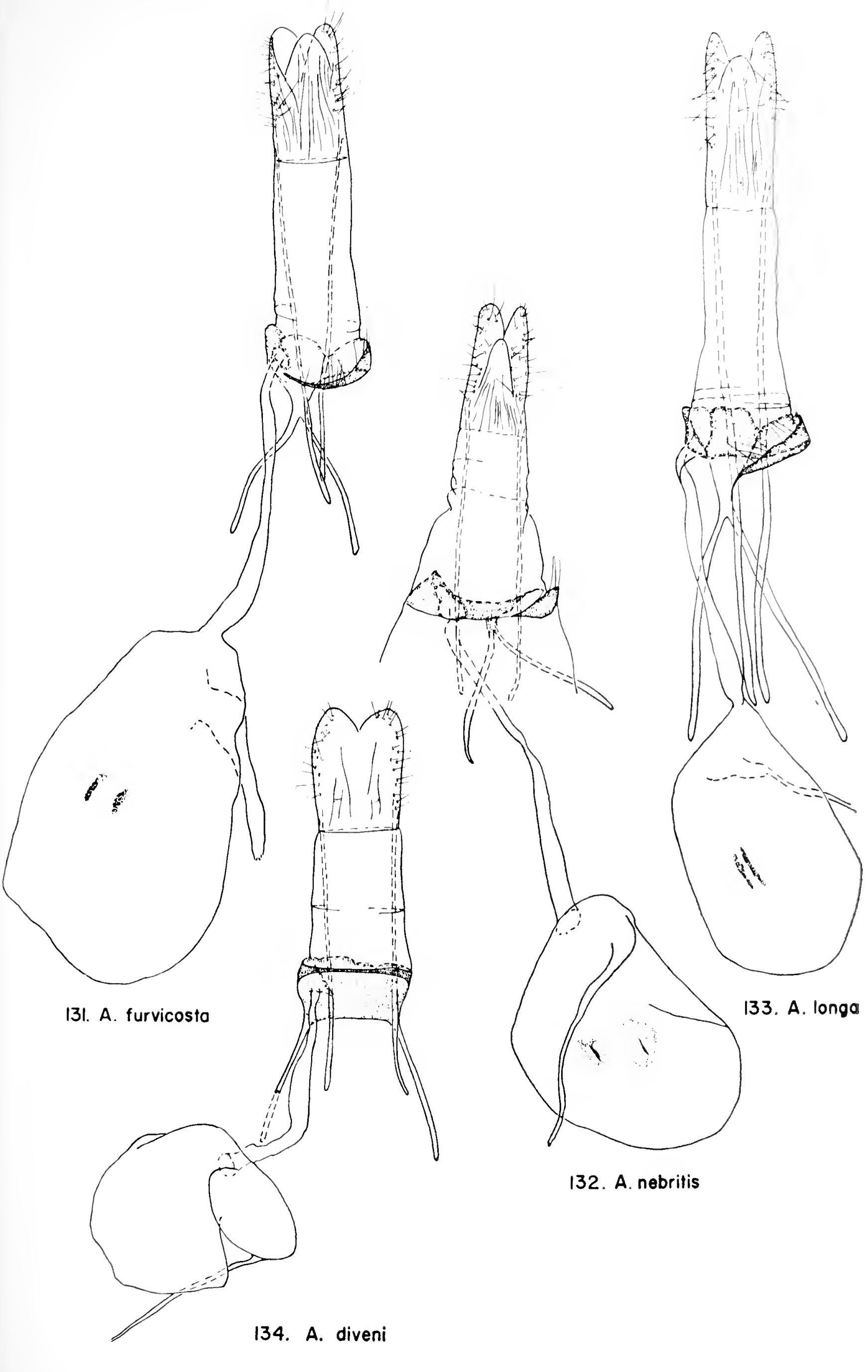

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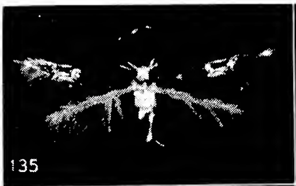
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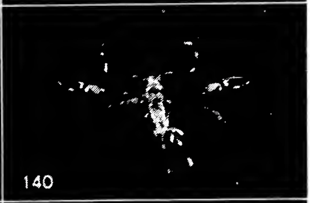
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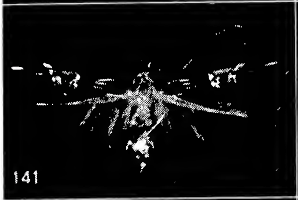
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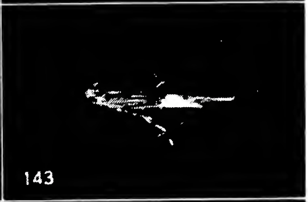
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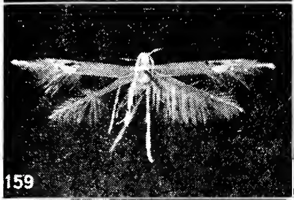
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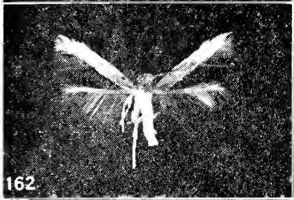
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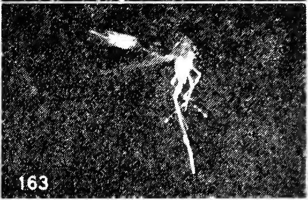
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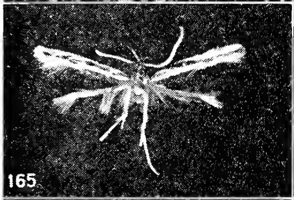
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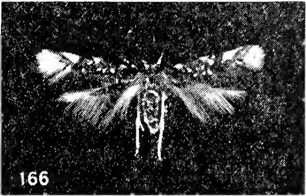
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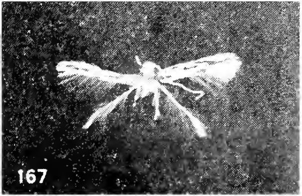
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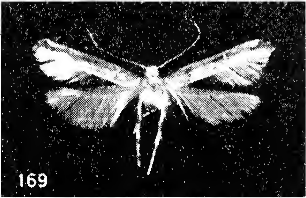
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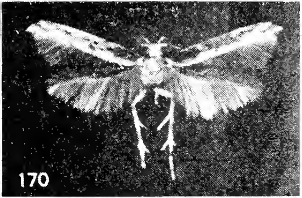
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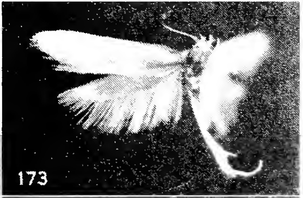
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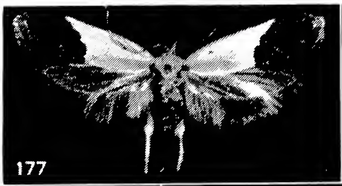
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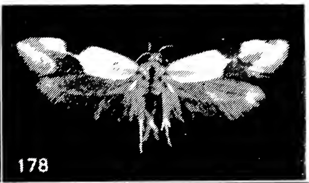
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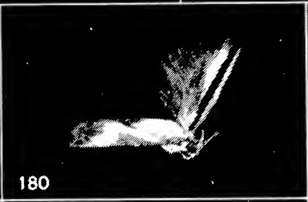
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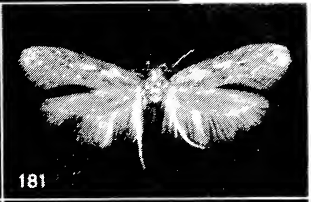
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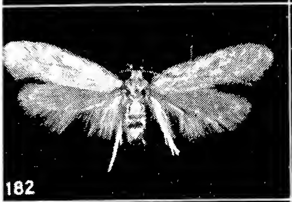
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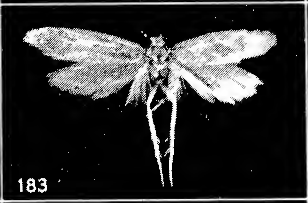
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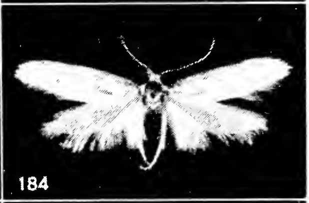
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ENTOMOLOGICA AMERICANA

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VOLUME XLIII (NEW SERIES)
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1872

PUBLISHED BY THE
BROOKLYN ENTOMOLOGICAL SOCIETY
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ENTOMOLOGICA AMERICANA

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Published for the Society by the
Business Press Inc.
N. Queen St. and McGovern Ave., Lancaster, Pa.
Subscription $6.00 Per Year
Date of Issue March 23, 1964

ENTOMOLOGICA AMERICANA

VOLUME XLIII

THE BIOLOGY AND ECOLOGY OF THE RHYPAROCHROMINAE OF NEW ENGLAND (HETEROPTERA: LYGAEIDAE). PART I[1]

By

MERRILL HENRY SWEET[2]

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THE GENERAL DISCUSSION

THE SPECIES ACCOUNTS

---

[1] A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Connecticut.

[2] Department of Biology, Texas A & M University, College Station; formerly at University of Connecticut, Storrs.

INTRODUCTION

Very little is known of the biology and ecology of the subfamily Rhyparochrominae, a taxon which includes over half of the members of the hemipterous family Lygaeidae. Since the Lygaeidae comprises a large family of insects, probably second in size to the Miridae among the Heteroptera, this is an unfortunate gap in our knowledge. For this reason, the present study was undertaken upon the New England rhyparochromine fauna. Of a total known lygaeid fauna of 65 species, 42 or 66% belong to the Rhyparochrominae. Of these I have been able to work with 39 species. Although restricted in scope to New England, this fauna, for the most part, is found throughout the eastern half of northern United States and southern Canada. A few rare species are included which while not as yet known from New England, are described from northeastern North America and may eventually be found in New England.

During the study only one new species was discovered in New England (Sweet 1963). This points up the maturity of the taxonomic knowledge and as Slater (1952) emphasized, biological studies should develop from such a taxonomically well-known fauna. The accompanying chart (Table 1) demonstrates the decline of new species descriptions as the New England fauna became better known. This diminution occurred despite the presence of several hemipterists who were intensively working on the New England fauna. It must be pointed out, however, that several species probably are not conspecific with the Central American populations from which they were originally described by Distant (1882, 1893).

TABLE I

DESCRIPTION OF SPECIES OF LYGAEIDAE FROM NEW ENGLAND

Date	Species	Date	Species
1758–1800	7	1881–1900	10
1801–1820	4	1901–1920	6
1821–1840	11	1921–1940	2
1841–1860	4	1941–1950	2*
1861–1880	11	1951–1963	1

* recognized but carried under incorrect names

While many studies have been made on particular insect species for reasons of economic importance, size and color, abundance, or laboratory availability, relatively few intensive studies have been made on the biology and ecology of larger taxonomic units. This is especially true of groups of little or no economic importance. Miller (1956) was essentially correct in stating, "There is not a great deal of knowledge about the ecology of the Lygaeidae, or about their developmental stages, except those species economically important."

This lack of work is especially true in the Rhyparochrominae, as there are only a few species which have proven to be minor economic pests, chiefly on strawberries in the United States and peanuts in Africa (Sweet 1960). But as will be later discussed, this group is actually of considerable ecological importance as feeders on ripe fallen seeds. It is not surprising that conventional collecting yields very few of these insects as the species are small, somber in coloration, and for the great part, live on the ground, usually hidden in the litter layer. As a result, as Butler (1923) said in discussing the English fauna, ". . . very little is known of the life-history of the various species and it will be seen that this sub-family affords abundant scope for investigation, and raises many interesting questions."

While one cannot entirely disagree with Miall (1895) who long ago emphasized that a biological study is best pursued exhaustively on a single species at a time, it nevertheless seems advantageous when confronted with a group about which so little is known, to employ a broader approach. Such an approach yields results in direct relation to the availability of material and collecting fortune and permits a gathering of data on relatively rare or local species as well as a fair amount of information on common species. In this fashion, the overemphasis on common species, which so highly colors most ecological studies as emphasized by Andrewartha and Birch (1954), is at least partly avoided. Moreover, such a broad study allows a comparative, essentially biosystematic approach to the ecology and biology of the various species, which provides important data for systematic studies especially on closely related species. Such an approach also makes possible a consideration of the engrossing problem of the adaptive integration of the various species which occupy a similar functional niche, in this case, seed feeding. This problem is especially interesting among the rhyparochromines because frequently a number of species will occur together in the same biotope, feeding on the same seeds. These considerations in turn lead to the question of why one species is common, another uncommon.

It may therefore be said that this paper proposes to ascertain the biological identity of the various species. It is not an attempt to solve any general biological problem *per se.* Of course it is realized that the study raises a great many more problems than it solves, but it is hoped that this study will form a framework which will stimulate further investigations by indicating desirable lines of research. It is especially to be hoped that amateur interest may be eventually stimulated to provide the local biological work which has already proven so successful in the British Islands. It will be invaluable to have the present results tested over the whole range of the insect, especially toward the center of its range. Moreover some of the hypotheses given to explain some data sets will need careful experimental proof.

In several other heteropterous families some rather similar biological studies of varying degrees of intensity have been made such as those by Hungerford (1920) on the Nearctic aquatic Hemiptera, Readio (1927) on the Nearctic Reduviidae, Bailey (1951) on the New England Tingoidea, and Kullenberg (1944) on the Swedish Miridae. There are several general surveys: Butler (1923) on the British Heteroptera, Blatchley (1926) on Heteroptera of eastern North America, Weber's biology of the Hemiptera (1930), and Southwood and Leston's (1959) valuable updating summary of the British Heteroptera. Miller's (1956) biology of the Hemiptera, is better considered as being essentially a survey of the biology of the Reduviidae.

In the Lygaeidae, important papers are Pfaler-Collander's two contributions (1936, 1941) on the life cycles and chromosome configurations of the Finnish Heteroptera. Very important is the recent work of the Putshkovs (1956), Putshkova (1956), and Putshkov (1958) on the eggs and nymphs of the Lygaeidae. Also important is an unpublished master's thesis by Slater (1947) on the biology and taxonomy of the immature stages of the Lygaeidae of Illinois.

Unlike Readio's study of the Reduviidae the present work contains no keys or descriptions. For these the reader is referred to the work of Barber (1917a, 1918a, 1918c, 1923, etc.), Blatchley (1926), Torre-Bueno (1946), and the forthcoming picture guide on Heteroptera by Slater and Baranowski. In addition, a key to the Nearctic genera of nymphs is given by Sweet and Slater (1961).

The present paper is divided into two sections, one the general discussion and another the individual species. In the general section the information common to the subfamily is discussed and the data on the species are collated.

Under each species the information may be readily separated into three categories. The first section includes the distribution, the environment, and abundance; the second treats the general biology including such phenomena as dispersion, wing polymorphism, protective coloration, and behavior, predation, parasitism, food-seeds, and feeding and mating behavior; the third includes bionomic data on phenology, seasonal cycle, diapause, life cycle, longevity, and reproduction, including oviposition habits.

ACKNOWLEDGEMENTS

This is a pleasant opportunity to express my warm gratitude to those who have aided me in this study: especially to Dr. James A. Slater of the University of Connecticut, my major adviser, who suggested and guided the study, helped me in numerous and invaluable ways, and assisted greatly with the literature; the members of my graduate committee, Dr. Norman T. Davis, Dr. Ralph M. Wetzel, of the same institution, and Dr. James B. Kring of the Connecticut Agricultural Experiment Station in New Haven for advice and patient guidance of my graduate program; the late Dr. W. H. Camp of the University of Connecticut and Mr. John Czar formerly of the same institution for advice and assistance on plant identification; Mr. H. Lincoln Foster for plant identifications and initially encouraging me to pursue biological studies; Mr. Peter D. Ashlock of the University of California for advice and unpublished habitat and distribution notes; Mr. and Mrs. Robert E. Moore for their aid in field work; Dr. John Lattin of Oregon State University, Dr. Richard C. Froeschner and Dr. Jon Herring of the United States National Museum for the loan of lygaeid specimens; Dr. C. W. Sabrosky of the United States National Museum and Dr. Paul R. Arnaud, Jr. of the American Museum of Natural History for the identification of tachinid flies; Dr. John Rankin, Jr. for the use of laboratory facilities at the Noank Marine Research Laboratory in 1957; Miss Roberta Smith of the University of Connecticut Library for her invaluable assistance in acquiring rare literature; and to my wife, Janice Readio, who assisted me immeasurably in collecting, typing, filing, and in many other ways. I must give thanks also to many other people who abetted my work in various ways.

Finally, I acknowledge most gratefully three National Science Foundation cooperative graduate fellowships granted to me during 1959 to 1962, without which this thesis could not have reached its present form.

MATERIALS AND METHODS

The distributions of the genera and species were obtained from the literature as compiled in the forthcoming Catalogue of the Lygaeidae (Slater, in prep.). Further range extensions and corrections were gathered by examining collections at the United States

National Museum, at the University of Connecticut, and by personal communications and collecting.

As the rhyparochromines are relatively easy to rear and handle (Sweet 1960), equal emphasis was placed upon field and laboratory work, so that an integrated approach could be utilized. This approach was particularly valuable in resolving the life histories. Moreover, in contrast to herb level insects like the Miridae (Kullenberg 1944), the cryptic ground level biotope of the rhyparochromines necessitated extensive laboratory work, since the natural behavior, feeding habits, and oviposition could not be observed in the field.

Field Work

Near Storrs, Noank, and Canaan, Connecticut, field populations of the species were followed in detail through seasonal cycles by weekly or biweekly sampling during the study period from the summer of 1957 to 1962. During the same period a series of field trips through New England were undertaken to study the ecology of the more boreal species, and to compare the local populations which were studied in detail against other populations in New England. Field trips were made to Cape Cod, Massachusetts, Maine, the White Mountains of New Hampshire, and sites between as noted in the species discussions, and also to the Adirondacks in New York, New Jersey, and the Great Smoky Mountains in the southern Appalachians (North Carolina and Tennessee).

The habitats studied are described under the individual species, and discussed in the general sections. The communities studied include spruce-fir (montane and coastal), alpine, northern hard woods, hemlock-birch, oak-hickory, pine barren, and subclimax forest types; succession stages from bare soil and ruderal associations through old fields to forests, including ecotones; special habitats as swamps, bogs, salt marsh, sand dunes, alluvial sites, beach and stream wash litter, and other sites. Valuable and useful studies upon plant associations in or near southern New England are found in Nichols (1913a, 1913b, 1914), Conard (1935), and Bromley (1935).

Since this is essentially an autecological study, the biotope or microhabitat of the species was emphasized, and the habitat viewed from this aspect. For an animal ecologist investigating the field ecology of a certain species it is in most instances impractical and of little meaning to make exhaustive quadrate studies of the plant communities and the physical parameters and a best compromise suited to the problem should be adopted (Elton and Miller 1954).

A relatively large number of sites were investigated in this study and the discussion under the species usually represents the essence of these observations, with emphasis placed on habitat sites where the species was found most abundantly. For most species this method yielded a consistent picture of their ecological distributions. At each site the topography, vegetation aspect, plant association and sere, the estimated habitat age, and at the biotope level, the exposure, soil type, litter, moisture level and temperature were noted. Wintering populations and habitat choice changes were described.

Under topography is included the type of land form, slope, drainage and elevation. The vegetation structure classification is the simple one proposed by Elton and Miller (1954). The plant associations are described in terms of the more abundant species around the immediate biotope in each of the vertical community strata. Exposure indicates the amount and kind of shading of the biotope, and the direction and degree of slope of a site. The soils were discriminated on the proportion of humus and sand, and whether it was mull soil, with a sharp discrimination between the litter layer and the soil or a mor soil with no such distinction. The litter was described in terms of source, depth, consistency, and presence of visible seeds.

The temperature of the ground layer was measured by means of a thermistor-thermometer Model 8410 Yellow Springs Instrument Co. which measured -4 to 37°C plus or minus 1% of scale range. An ordinary thermometer was used for extreme temperature levels. At first for moisture levels water evaporation methods were used but aside from being laborious and not allowing rapid comparisons of many habitats gave results which varied greatly with soil and litter types with the same apparent moistness. Moreover the rhyparochromines select a definite level in the moisture gradient through the litter. Such an exact layer is difficult to measure. For this reason a 0 to 10 scale was devised with 0 extreme dryness, 10, oversaturated conditions and with 4 to 6 representing mesic conditions. This method allowed ready comparisons of different sites, and afforded a useful index.

The winter conditions at the different local sites were noted, especially the snow retention period which gave an estimate of the exposure and microclimate of a site.

As these insects are almost exclusively restricted to the ground, a specialized type of collecting had to be utilized. The collecting or sampling technique which was found to be the most effective and replicable was to search through a square meter of ground litter, collecting and counting the rhyparochromines. Barber (1928b) described this method thus: ''As my method of collecting was rather unusual, it deserves a bit of explanation. My operation was very much like a busy hen, scratching and searching for her juicy morsels among the dead leaves.'' Since the rhyparochromines are mostly at the interface between the litter and the ground, at the margin of clumps or upon open ground it was difficult to sample them adequately with a Berlese funnel, a difficulty which was compounded by the very rapid running reaction of most species when disturbed. Moreover the population distribution in a habitat is often highly discontinuous and only by judicious sampling could the abundance of the species be estimated. A prime advantage of this method is that it allows samples to be made over a great many areas and the results are comparable insofar as the collecting method was uniform. Coulianos (1961) used this same method and found it the most suitable for studying populations of *Nithecus jacobeae* (Schill.). As mentioned by Coulianos a major drawback is that it is extremely time consuming and only a few samples can be made in a day. This was partly offset by combining spot checks of a few square feet with the square meter counts. Another problem was that the habitats or biotopes presented different collecting conditions. The accuracy of this method is difficult to estimate but results gained are comparable as minimum densities. Errors would result from escape from the square meter area, and concealment of the insects by color, size, or in litter crevices. Careful collecting helped to reduce this uncertainty. An initial rapid scanning yields the larger long legged species which live on the litter or in very loose litter and which quickly flee. Rarely a few individuals were swept from the herb layer. At any rate this sampling technique should be considered only as an index of the abundance, a problem shared by nearly all population sampling techniques (Morris 1961).

The insects were collected live and placed in small specimen containers which were interchangeable with the aspirator. The containers were carried in a convenient collecting bag which had individual container compartments. Because of the water requirements of these species, a moist piece of cotton or like was placed in each container to prevent desiccation. With woodland species care had to be taken to prevent overexposure to sunlight which proved fatal to the insects. Night collection at a lighted sheet in different habitats yielded possible dispersal records.

Along with the insects, samples of seed bearing litter were collected. In the field, the avoidance behavior, flight, death feigning, and particularly the relation between coloration and the background was studied. Ant mimicry behavior and association with ants was especially noted.

LABORATORY WORK

As described previously (Sweet 1960), these insects can be reared readily in petri dishes or other containers upon seeds and water alone. Both plastic and glass dishes were used, but plastic "disposable" dishes were preferable for general convenience and because their surfaces provide a surface upon which the insects can more readily right themselves. Water was provided in a vial stoppered with cotton. Sunflower seeds were standardly used as a food. Under these conditions, the humidity level in the petri dish was saturated but with very little free water surfaces. These conditions are similar to the conditions of a dense litter layer (Cloudsley-Thompson 1956, Southwood 1962a). An important advantage of the shallow petri dishes is that the insects may be readily observed and counted especially when using a dissecting microscope. Both clean culture and "dirty" culture techniques were used. Dirty technique which approximates field conditions with the introduction of soil and litter was found to be a much more effective method of rearing most species, and various behavioral aspects of oviposition and feeding were not evoked under "clean" conditions. Under clean conditions methyl cellulose sheets were provided as a substrate. Clean cultures were advantageous in allowing readier observation of the insects and facilitated egg counts in those species which will lay eggs in methyl cellulose. Dirty cultures, however, also usually introduced mites, Collembola and psocids into the rearing room. One problem which was troublesome and difficult to control was the presence of the small granary mites *Tyroglyphus* spp. which were continually reintroduced from other rooms in the laboratories. Also troublesome were molds (*Penicillium* and *Aspergillus*) which necessitated periodical changing of the cultures.

The majority of the rearings were carried out at room temperature which averaged 75°F. and varied from 68° to 85° with a few exceptional extremes. Weekly temperature records were kept with a tempscribe (Bacharach Industrial Inst. Co.). Whenever possible the insects were reared where the photoperiod conditions were known such as a normal daylight room. Photoperiods were set with the use of an Intermatic Timeall Model A211–4, Intern. Register Co. Constant temperature rooms (77°F.) were used with photoperiods set at a equinoctal (12 hours) and long day (15 hours). Both cold room (36°F.) and the refrigerator (−7°C.) were used for studies on diapause conditions. Long photoperiods were also used in cold rooms to restrict the test to the cold factor alone.

The stadia were determined by isolating newly molted nymphs in a petri dish, or large vial, and by recording the development in culture. A stop watch was used to time aspects of mating behavior. Parasites were isolated and kept alive on sugared water.

Nymphs and eggs were preserved in KAAD (Peterson 1955), transferred to 70% alcohol, or directly in Carnoy's fixative (Isopropyl) as suggested by Ueshima and Ashlock (*in litt.*).

Feeding habits were studied by isolation of an insect with seeds of different species, or with a combination of seeds. It is very easy to ascertain which seeds had been fed on by the formation of minute salivary fluid cones on the surface of the seed (Miles 1959).

In the discussions of mating behavior, oviposition, etc., if no mention is made of the number of observations, the behavior pattern was observed frequently, at least 20 times. In deriving the ratio of maropters to brachypters, the sample size numbered at least 100 insects.

Systematic Review

Unfortunately, the tribal classification of the Rhyparochrominae has been in a state of flux due to both systematic and nomenclatoral changes. The system used here is that of Slater and Sweet (1961), as modified by recent work by Ashlock (in press), and Sweet (unpublished).

The 42 recorded species of Rhyparochrominae from New England are distributed among 22 genera, an average of 1.7 species per genus. This is considerably smaller than the general number of insect species per genus of 4.23 in a somewhat equivalent area, Britain (Elton 1946). The maximum number of species per genus is in *Ligyrocoris* with four species.

Of the 13 presently recognized tribes, 10 are present in New England, but the representatives of at least one of these, the Stygnocorini, are European introductions (Barber 1948b, Lindberg 1958) and one or both of the Megalonotini genera are introduced (Slater and Sweet 1958). The salient difference between the Nearctic and the Palearctic fauna is the predominance of the Myodochini in the Nearctic and the concomitant restriction of the other tribes (Slater 1952). Thus, in New England, many of the other tribes have only one or two, often introduced, genera. Quite the converse is true in the Palearctic where the Myodochini are represented by only three genera. The representation of the tribes in New England is outlined in Table 2, along with the representation in an equivalent temperate Palearctic region, Britain.

Table 2

Size of the Tribes of the Rhyparochrominae of New England and Britain

	New England		Britain	
Tribe	Genera	Species	Genera	Species
Plinthisini	1(3%)	1(2%)	1(4%)	1(2%)
Antillocorini	1(3%)	2(5%)	1(4%)	1(2%)
Lethaeini	2(7%)	2(5%)	——	——
Ozophorini	1(3%)	1(2%)	——	——
Stygnocorini*	1(3%)	2(5%)	3(13%)	6(11%)
Drymini	3(10%)	7(16%)	6(25%)	20(39%)
Myodochini	14(47%)	19(45%)	1(4%)	2(4%)
Rhyparochromini	1(3%)	2(5%)	5(21%)	11(21%)
Megalonotini*	2(7%)	2(5%)	2(8%)	5(10%)
Gonianotini	4(13%)	4(10%)	5(21%)	6(11%)

*introduced from Europe

Several other rare species from contiguous areas may eventually be found in New England, and are accordingly included in the list of species. *Sphaerobius quadristriatus* Barber a distinctive species, is known only from the New Jersey pine barrens (Barber 1911) and *Gastrodes walleyi* Usinger is known only from a single collection in Ontario, Canada (Usinger 1938).

On the other hand, several species presently listed from New England were not found during the present study. *Pachybrachius bilobatus* (Say) is known from a single collection at New Haven, Connecticut which represents its most northerly record, and probably represents a northward irruption. *Eremocoris setosus* Blatchley, another southern species, is not recorded from Connecticut or New Jersey, but is recorded from Long Island, New York and Massachusetts (Barber 1928c) so it has a greater likelihood of occurring in the New England fauna. *Exptochiomera nana* Barber, has never been collected again since the original collection by Frost at Framingham, Massachusetts, and may represent an adventitious species (see Species Discussion).

EUROPEAN INTRODUCTIONS

A number of European species have been recorded from northeastern North America which have not been recovered since the original collections. As Barber (1918b) noted, a single male specimen of *Microtoma atrata* (Goeze), which is plainly labeled R.I., exists in the Uhler collection at the United States National Museum. If this locality datum is correct the species was introduced but apparently did not establish itself. Both *Pachybrachius luridus* Hahn and *P. fracticollis* (Schilling) were collected at Montreal, Canada by J. I. Beaulne in May, 1915 (Parshley 1923) but have not been recorded since then despite Moore's (1950) intensive collecting in this area.

The following species have established themselves in North America and are discussed under the appropriate headings: *Stygnocoris pedestris* (Fallen), *S. rusticus* (Fallen), *Megalonotus chiragrus* (Fabr.) and perhaps *Sphragisticus nebulosus* (Fallen). It is perhaps significant to note that these are also the only Nearctic representatives of the tribes Stygnocorini and Megalonotini respectively.

List of the Species

This checklist includes all species recorded and likely to be found in the New England Rhyparochrominae fauna. The starred species were not studied.

Myodochini

Myodocha serripes (Olivier)
Heraeus plebejus Stål
Pachybrachius basalis (Dallas)
Pachybrachius albocinctus Barber
Pachybrachius bilobatus (Say)
Cnemodus mavortius (Say)
Pseudocnemodus canadensis (Provancher)
Sphaerobius insignis (Uhler)
**Sphaerobius quadristriatus* Barber
Ligyrocoris diffusus (Uhler)
Ligyrocoris depictus Barber
Ligyrocoris sylvestris (Linnaeus)
Ligyrocoris caricis Sweet
Zeridoneus costalis (Van Duzee)
Perigenes constrictus (Say)
Ptochiomera nodosa Say
Sisamnes clavigera (Uhler)
Carpilis consimilis Barber
**Exptochiomera nana* Barber
Kolenetrus plenus (Distant)

Plinthisini

Plinthisus americanus (Van Duzee)

ANTILLOCORINI
- *Antillocoris minutus* (Bergroth)
- *Antillocoris pilosulus* (Stål)

LETHAEINI
- *Cryphula trimaculata* (Distant)
- *Xestocoris nitens* Van Duzee

OZOPHORINI
- *Ozophora picturata* Uhler

STYGNOCORINI
- *Stygnocoris rusticus* (Fallen)
- *Stygnocoris pedestris* (Fallen)

DRYMINI
- *Drymus unus* (Say)
- *Drymus crassus* Van Duzee
- *Scolopostethus diffidens* Horvath
- *Scolopostethus atlanticus* Horvath
- *Scolopostethus thomsoni* Reuter
- *Eremocoris ferus* (Say)
- **Eremocoris setosus* Blatchley
- **Gastrodes walleyi* Usinger

RHYPAROCHROMINI
- *Peritrechus fraternus* Uhler
- *Peritrechus paludemaris* Barber

MEGALONOTINI
- *Megalonotus chiragrus* (Fallen)
- *Sphragisticus nebulosus* (Fallen)

GONIANOTINI
- *Emblethis vicarius* Horvath
- *Trapezonotus arenarius* (Linnaeus)
- *Delochilocoris umbrosus* (Distant)
- *Malezonotus fuscosus* Barber

GENERAL DISCUSSION

DISTRIBUTION

Only a brief consideration of the distribution of the New England Rhyparochrominae is attempted here. The distribution or range of a species can be considered either in terms of its faunal affinities which may indicate the origins of a fauna, or it may be correlated with climatic conditions, i.e., as a function of a species' ecological requirements (Hesse, Allee, and Schmidt 1951). This is also the essential difference between a biotic province and a life zone respectively (Kendeigh 1954). Darlington (1957) strongly criticized any emphasis upon ecological distribution, for the ecology, while important, is not the basis of zoogeography. Darlington's criticisms are entirely valid, but certainly upon the species level, a knowledge of the ecological requirements of a species allows an interpretation to be made of its distribution, especially in the absence of pronounced barriers. In the Rhyparochrominae, however, there appears to be a reflection between faunal affinity and climatic distribution.

Faunal Relations

Horvath (1908) discussed the origins of the Holarctic heteropteran fauna, and concluded that the majority of the genera were of Palearctic origin. Slater (1952) discussed the faunal origins of the Iowa and Illinois lygaeid faunas and pointed out the relatively large representation of the Myodochini in the Nearctic as compared with the Palearctic (see Systematic Review).

In contrast to the many other animal groups, a considerable majority, 20 of 28 (72%) of the native rhyparochromine genera of northeastern North America are derived from the Neotropical Region or are largely restricted to the Nearctic Region.

Holarctic Element—9 genera (32%)

Plinthisus, Drymus, Scolopostethus, Eremocoris, Gastrodes, Peritrechus, Trapezonotus, Emblethis, Sphragisticus. Most of these genera are much better represented in the Palearctic Region from which they are probably derived. Some genera are about equally abundant, given the difference in area, and may more properly constitute the Holarctic element. These include *Eremocoris* and *Trapezonotus.* The largely western *Gastrodes* alone appears to have its distributional center in the western Nearctic (Usinger 1938). It is an open question as to whether the monotypic *Sphragisticus* is part of the Holarctic element (Horvath 1908) or is an introduced species (Blatchley 1926). It is known from Siberia (Slater, Catalogue) and Fairbanks, Alaska (James A. Slater Collection) so it may possibly represent a relatively new natural element in the fauna. At any rate, if it was introduced by man, it is a very old introduced species, and had spread throughout the country by the late 19th century. It is noteworthy that other genera with Holarctic distributions have either speciated extensively—*Eremocoris, Drymus, Scolopostethus, Peritrechus,* and *Plinthisus,* or are also found in the highlands of Central America—*Emblethis* and *Trapezonotus*. The monotypic *Sphragisticus* (Ashlock *in litt.*) has not been recorded from Mexico or the southeastern United States.

It is most interesting that the extensive genus *Drymus* with 17 species in the Palearctic, has its only two Nearctic species restricted to the eastern half of North America, not the western half as is the rule with other Holarctic rhyparochromine genera. As it is an inhabitant of deciduous forests, this genus may reflect the general restriction of the mixed mesophytic deciduous woodlands to eastern North America. In this same vein, it should be noted that the Drymini which in New England are characteristic of the more mesic sites, especially woodlands, are the most richly represented Holarctic element. *Plinthisus americanus* is also a woodland species, and *Peritrechus* with one species in salt marshes, the other often in flood wash, exhibits considerable humidity tolerance. The Holarctic *Ligyrocoris sylvestris* is a Taiga-*Sphagnum*-cool margin species. If the migration route between the Nearctic and Palearctic was most easily traversed during Cenozoic times by organisms adapted to temperate, mesic conditions (Ross 1962), then this may be reflected by the preponderance of such forms in the Holarctic Rhyparochrominae fauna.

NEARCTIC ELEMENT—6 genera (22%)

Carpilis, *Zeridoneus*, *Sphaerobius*, *Pseudocnemodus*, *Malezonotus*, "*Delochilocoris*." These Nearctic genera belong to the Myodochini and Gonianotini only, and at least three more western Nearctic genera of Gonianotini are as yet undescribed (Ashlock *in litt.*). All these gonianotine genera are endemic except *Trapezonotus*, and may represent an old Nearctic faunal element.

NEOTROPICAL ELEMENT—13 genera (46%)

Myodocha, *Heraeus*, *Pachybrachius*, *Cnemodus*, *Ligyrocoris*, *Perigenes*, *Ptochiomera*, *Sisamnes*, *Exptochiomera*, *Antillocoris*, *Cryphula*, *Xestocoris*, and *Ozophora*. This group includes genera which are much more richly represented in the Neotropics and are represented by only a few or a single outlier cool temperate species. Included are all the Antillocorini, Lethaeini, Ozophorini and most of the Myodochini. Only *Ligyrocoris sylvestris* extends into the Palearctic.

It is probable that the Nearctic myodochine genera will eventually be shown to have Neotropical foci. In this respect it may be significant that very few of these genera with Neotropical or Nearctic affinities occur in California.

INTRODUCED ELEMENT—2 genera

Stygnocoris, Megalonotus. This group includes genera which show the spread phenomena of introduced taxa (Lindroth 1957). They were originally collected near the coastline, and have been progressively spreading in distribution. As mentioned earlier, *Sphragisticus* may possibly belong to this group, but if so, it is an older introduction.

To summarize, it may be said of the New England fauna that the representation of the Myodochini, the Ozophorini, Antillocorini, and Lethaeini shows Neotropical or Nearctic affinities: the representation of Drymini, Plinthisini, Rhyparochromini, and Megalonotini, shows a largely Holarctic-Palearctic affinity, and the gonianotine representation appears to be equally Nearctic and Palearctic in affinity.

It is important to note that no strong relationship is presently discernible among the rhyparochromines between the eastern Palearctic and eastern North America, which may result (Horvath 1908) from our extremely poor knowledge of the fauna of the eastern Palearctic. *Drymus,* however, may represent such a relationship as it is restricted to the eastern half of North America. No rhyparochromine genus exhibits the converse peculiar distribution of *Thyreocoris* which is extensively represented in North America and otherwise found only in Europe (China 1930).

BIOTIC ASSOCIATION

Southwood and Johnson (1957) would limit the term "distribution" to the ecological areas or local places where a species occurs and define the total extent of a species as its range. However, in general biological use distribution and range are used nearly synonymously (Hanson 1962) and I prefer to use *ecological distribution* as a less confusing way to make the former distinction. Andrewartha and Birch (1954) emphasize a close relation between abundance and distribution and that they represent different facets of the same ecological problem. While not defining the term, Andrewartha and Birch clearly use distribution in the usual sense, although emphasizing range fluctuations with ecological fluctuations. This concept of distribution is closely related to biotic divisions based upon climatic factors as the life zones (Merriam *et al.* 1910, Muesebeck and Krombein 1952). The life zone is conceptually distinct not only from geographical distribution in the sense of Darlington (1957) but also from the biotic province which incorporates origin as well as climate (Dice 1943). For this reason, along with its overemphasis upon temperature, the Merriam life zone system has been heavily criticized especially in western North America

(Daubenmire 1938, Kendeigh 1954) but is quite useful for eastern North America (Monroe 1956).

The following is a brief summary of the equivalent systems. New England is divided into at least three chief zones.

1. *The Carolinian* or upper austral zone of Merriam is defined by mean summer temperature isotherms of 72 to 79°F. It covers the southern part of New England, and is roughly equivalent to the beech-maple association (Munroe 1956), and the oak-hickory association (Bromley 1935, Braun 1950) or the southern hardwoods biotic province (Dice 1943). Along the southern New England coast and in pockets inland especially on the southeastern portion is an edaphic open xeric association of pitch pine (*Pinus rigida*) which constitutes an outlier of the pine barren association of Long Island (Concord 1935, Fernald 1925, Nichols 1913a). This association which reflects the poor soil and more oceanic climate is recognized here.

2. *The Alleghenian* or transition zone of Merriam occupies the major part of New England, the remainder except the higher elevations and northern Maine. It is nearly equivalent to the hemlock-white pine-northern hardwoods forest (Braun 1950) or province (Dice 1944). Merriam distinguished it by the summer isotherms of 64 to 72°F.

3. *The Canadian* province of the boreal zone which is distinguished by summer isotherms of 57 to 64°F., is characterized by the presence of spruce and fir. Munroe (1956) considered the mountain spruce forests of New England and the coastal spruce forests of the shore of Maine to be part of the Alleghenian province because red spruce not white spruce formed the dominant species. However, many Canadian zone species are present in this fauna and the higher summits are noted for their isolated alpine areas (Forbes 1923, Dansereau 1957). For this reason the Canadian zone of Merriam is recognized here in northern New England and on the higher elevations. It corresponds to the red spruce-balsam fir association of Braun (1950).

The biotic regions based on vegetation climax (Clements 1916, 1936) happen to correspond to Merriam's life zones (Munroe 1956). However, the climax association concept has been strongly criticized especially by Whittaker (1953) among other authors as being artificial since the individual species have separate requirements and distributions and only by coincidence, occur together as associations. Nevertheless, this classification appears to work in northeastern North America (Kendeigh 1954, Monroe 1956) and provides a marker system for biotic distributions.

Species Distribution

Against this background the distribution of rhyparochromine species may be considered. Munroe (1956) in his excellent analysis of the patterns of distribution exhibited by Canadian insects provides a system which may be used with some modifications. He distinguishes ten range types with various subdivisions: (1) eastern, (2) northeastern, (3) central, (4) western, (5) northwestern, (6) boreal, (7) subarctic, (8) arctic, (9) combined ranges, (10) introduced species. Of these, only the eastern, boreal, combined, and introduced types pertain here. No known rhyparochromines exhibit northeastern, subarctic, or arctic distribution patterns.

Only *Gastrodes walleyi* may belong to the boreal range which extends across the Laurentian shield, and does not enter the United States, but as many boreal forms of this region occur on Mount Washington, New Hampshire and Mount Katabdin, Maine, this species may occur in New England (see *Gastrodes*).

The introduced ranges include *Stygnocoris rusticus, S. pedestris,* and *Megalonotus chiragrus.* These species are characterized (Lindroth 1957, Munroe 1956) by not following any simple geographic pattern and their extent is determined by their place of introduction and rate of spread. At least with the two species of *Stygnocoris*, this does not appear to be entirely so, as these species occur in New England as northern forms Moreover, they are rare or absent in southern Connecticut despite being abundant in the northwestern highlands of that state. However, in Europe they appear to have a wider north-south distribution. *Megalonotus* is presently known in the east only from Connecticut and Cape Cod, Massachusetts but has a wide range on the west coast from British Columbia south to mid-California (Scudder 1961, Ashlock *in litt.*, Van Duzee 1923). Rather than by ballast transport (Lindroth 1957), Slater and Sweet (1958) suggested *Megalonotus* was introduced in produce. *Trapezonotus distinguendus* was found established in Newfoundland (Lindberg 1958), but not elsewhere.

The ranges of the other species fall into Munroe's eastern and combined range types. Munroe distinguished the different subdivisions of the eastern type upon the extent of their penetration into Canada. A similar division follows for the New England fauna. The eastern ranges correspond to the extent of the eastern forest biome.

With due respect to our poor knowledge of the ranges of the rhyparochromines, a number of types can be distinguished. The distribution patterns roughly correspond to the faunal regions. The subdivisions which follow are only pigeon holes into which a given species may but approximately fit. The range types are sorted into four main categories: Austral, Intermediate, Boreal, and west-extended (Combined) ranges.

AUSTRAL RANGES

Type 1..—a distinctly southeastern distribution which barely attains the extreme southern New England coastal area, but usuallly extends south into Florida or the subtropics. It represents a Carolinian fauna, and corresponds to Munroe's type E_1: *Pachybrachius albocinctus, P. bilobatus, Ptochiomera nodosa, Cryphula trimaculata, Ozophora picturata, Antillocoris pilosulus, Eremocoris setosus.*

Type 2. —also largely southern in distribution, but extends into middle New England and often southern Quebec. It then attains the transition zone, and corresponds to type E_2 of Munroe: *Pachybrachius basalis, Cnemodus mavortius, Myodocha serripes, Heraeus plebejus, Drymus crassus.*

Type 3. —included here is *Peritrechus paludemaris* which is limited to the eastern coastline, in this case, an Austral distribution. If it were more northern it would fall in Munroe's type $E_{4(a)}$.

INTERMEDIATE RANGES

Type 4. —includes species limited to the northeastern coast plain approximating the pine barrens area, or in part, barely attaining New England. *Malezonotus fuscosus, Sphaerobius quadristriatus, Scolopostethus atlanticus,* (*Exptochiomera nana?*).

Type 5. —found throughout New England and extensively into Canada and reaches south into the middle Atlantic states. It appears to correspond somewhat to type E_3 of Munroe. It is mainly an Alleghenian distribution with a considerable western extention to Missouri and Colorado: *Drymus unus, Antillocoris minutus, Eremocoris ferus.*

BOREAL DISTRIBUTIONS

Type 6. —restricted to northeastern North America, not found south of northern New Jersey, nor west of the Appalachians: *Carpilis consimilis, Plinthisus americanus, Ligyrocoris caricis.*

Type 7. —a montane distribution from New England into the southern Appalachians, but is not found west of these mountains. Only *Ligyrocoris depictus.*

Type 8. —a northern distribution from the Great Plains into New England, and south along the Appalachians. It approaches somewhat Munroe's type E_5: *Zeridoneus costalis, Xestocoris nitens.*

COMBINED RANGES—WESTERN EXTENSIONS

Type 9. —a boreal distribution across the entire United States, not occurring south of New Jersey except the first two which occur in the southern Appalachians of North Carolina. It parallels Munroe's type CO_2. *Pseudocnemodus canadensis, Scolopostethus thomsoni, Ligyrocoris sylvestris, Sphaerobius insignis, Trapezonotus arenarius,* and it appears, *Stygnocoris rusticus* and *pedestris.*

Type 10. —a mainly southwestern distribution barely attaining New England. It corresponds to Munroe's type CO_2: *Sisamnes clavigera.*

Type 11. —an intermediate range across the continent from Canada south to Virginia. It is rather similar to Merriam's transition life zone: *Ligyrocoris diffusus, Perigenes constrictus,* and *Peritrechus fraternus.*

Type 12. —disjunct montane populations in the east and the west and in Guatemala: *Kolenetrus plenus.*

Type 13. —possessing a very wide transcontinental distribution: *Emblethis vicarius, Sphragisticus nebulosus, Delochilocoris umbrosus.*

It is instructive to note that the species that exhibit Austral type distributions 1 and 2 are largely of Neotropical affinities. The species largely restricted to the northeastern part of North America (types 4, 6, 7, 8, and also 12) are mainly of Nearctic affinities. Many species with transcontinental distribution (types 9 and 13) belong to genera with Holarctic affinities. Several of the species show a disjunct distribution pattern and are presently also known from the Guatemalan Highlands: *Kolenetrus plenus, Delochilocoris umbrosus, Emblethis (vicarius?), Cryphula trimaculata.* Of these, only *Kolenetrus plenus* and *Delochilocoris umbrosus* are entirely temperate in distribution in North America. It is true that these populations probably are not conspecific in each case, but they are at least very closely related as is *Carpilis consimilis* which was not distinguished from the western *ferruginea* until 1953 (Barber 1953). The range of *Kolenetrus,* however, has been considerably expanded recently by new records and appears to be present throughout the mountains of western United States.

In this same connection it is noteworthy that a great many other species or closely related species do not show a east-west disjunct pattern between eastern and western North America. This situation is similarly true with mesic plants (Braun 1955) and only xero-mesophytes of wide distributions established disjunct east-west and Guatemalan distributions during the Pleistocene glaciations. Similarly, the rhyparochromines with such disjunct distributions are adapted in New England to relatively xeric conditions.

Of course, further collecting might modify this considerably. The rhyparochromines have been very poorly collected and their distributions cannot be understood in the same manner as are those of vertebrate and butterfly species.

Ecology

While they are with few exceptions largely restricted to the ground layer, the rhyparochromines are found in a large and varied series of habitats, ranging from beach wrack to alpine balds, and from raw early succession areas to mature climax forests. This broad ecological distribution attests to their domination of the fallen seed ecological niche. On the significance of the litter biotope, Elton and Miller (1954) remark, ''In spite of its narrow vertical depth, the ground zone is probably the most important and certainly the most complex of the strata.''

Each species has a definite ecological distribution, some narrow, others broad. The particulars upon the individual species including descriptions of biotopes and habitats are to be found under the species discussions.

In contrast or apparent contrast to other animal groups I have found only a few of the species to be rare. Usually, an apparent rareness, such as is indicated in the literature, actually reflects instead a specificity to certain habitats. Couple this with the infrequency of ground level collecting by entomologists, and consider the small size and obscure coloration of most of the rhyparochromines, it then becomes understandable that so little is known about these insects. Likewise a restriction to disturbed, ruderal habitats or a tendency to occasionally climb into the plant material yields an overestimate of the abundance of these species. It follows from this that any estimation of the abundance of a species is quite difficult to make and must be related to its habitat selection. Of course, rareness itself may be interpreted in terms of strict ecological requirements, and a species may be abundant in terms of total numbers either through a large ecological amplitude or an abundance within a common habitat.

One of the most striking features is the frequent association of a number of species together in a given habitat, in the same ground biotope, and most of them feeding on the same seeds. This is of considerable interest in terms of niches and competition, and will be returned to after a general consideration of the species (see Competition).

A major outline of a habitat classification is provided by Elton and Miller (1954). Of their six habitat systems, two pertain here, the terrestrial and the aquatic-terrestrial transition. They further divide the terrestrial system into formation-types based on vegetation cover: (1) open ground (life form under 6 inches), (2) field type (herbaceous, seldom exceeds 6 feet), (3) scrub type, and (4) woodland type. They also suggest four modifiers: (1) broad leaved forest vs. conifer, (2) mixed broadleaf and conifer, (3) "edge," and (4) rotation arable. The formation-types are similarly divided into vertical strata: (1) subsoil and rock, (2) topsoil, (3) ground layer (including litter), (4) field layer, high or low, (5) low canopy, (6) high canopy, and (7) air above the vegetation. Of these layers, only the field and especially the ground layer pertains here. If this classification seems obvious, the authors emphasize that no usable system for classifying habitats had been so proposed, and that taxonomists, naturalists, and even ecologists have been very negligent about reporting such data, in contrast to elaborate plant censuses which abound in the journals. Elton and Miller (1954) furthermore stress that ". . . direct and limited connections between animals that depend on particular plant species are not, as formerly supposed, the dominant situation determining the composition of the community. . . ." These workers, like Tansley (1939), proposed that habitats for animal populations be based on the structural aspects rather than the phytosociology. Moreover, detailed floristics were considered beyond the scope and labor capacity of an ordinary worker.

This formation classification is an especially useful index here because of the overriding influence of the vegetation type upon the ground layer. With increasing plant cover the litter conditions change from the extremely variable conditions of a barren site with its great diurnal temperature extremes and surface droughts to the moderate mesic conditions of the deep litter of a climax forest with its small variation in temperature and moisture (Geiger 1950, Cloudsley-Thompson 1962, Dansereau 1957). The litter type and consistency is directly controlled by the type of leaf-fall, a difference best seen in the contrast between broad-leaved and coniferous forest with their mull and mor soils respectively (Murphy 1953).

In order to make more intelligible the ecological distribution of the rhyparochromines, several additional factors need to be considered. The litter layer under oak-hickory forests is entirely different in consistency and history than maple or birch litter, for the oak litter is coarse and stiff and tends to form a deep layer, especially on dry slopes and the acid leaves decay slowly. The softer foliage of birch and maple compresses readily, decomposes more rapidly and forms a very different physical type of litter (Murphy 1953). The scrub habitats do not form for the rhyparochromines a habitat type distinct from woodlands.

Especially in open ground and field type habitats, a number of important edaphic factors strongly influence the vegetation types and the distribution of the rhyparochromines. The type of slope and exposure is important, for south exposures are considerably warmer and more xeric (Cooper 1961). Whether the soil is sandy, gravelly, rocky or a mature loam, and whether it is overdrained or mesic or poorly drained is very important, for these edaphic conditions strongly influence the type of plant cover and succession. In turn, of course, this influences the temperature, moisture and litter conditions of the ground layer. Although Elton and Miller state that attention to succession is unnecessary, very different litter conditions prevail at different times and under xerosere or mesosere succession. The arable rotation formation is essentially a rapid type of mesic succession.

Burges (1960) emphasizes, that with all the interest in the structural and vegetation changes in succession, it is remarkable that the essential parameter of any changing system, time, has seldom been mentioned. For example, and in contrast to "arable rotation" and other mesic successions the sparse vegetation, usually an *Andropogon scoparius* association, of an overdrained xeric slope forms a long persisting stage. Blizzard (1931) described such a succession stage on Long Island, N. Y., which was still persisting after 30 years without any outside interference. The rate of succession is an important factor in the biology of the rhyparochromines as will be discussed under dispersion.

The time factor can be estimated in part from the type of plant cover, litter, and soil in conjunction with discussions in the literature of such habitats, and also through the changes visible in the habitats over the five to eight years that some of the populations have been under observation.

HABITAT CLASSIFICATION

Any habitat classification becomes difficult because of the extensive mosaic of types under disturbed conditions. The habitats considered here are pure types which may be closely contiguous.

In the following classification, the rhyparochromines are divided into ecological groups based on the factors mentioned in the previous sections. There is, of course, considerable overlap with some species. Moreover, being mobile, the insects are sometimes found sporadically in other habitats. These variations and more detailed discussions of the biotopes are found under the individual species. The number after the habitat type indicates the approximate litter moisture level. The species are listed in their approximate order of abundance in the habitat type. Rare species are starred.

I. Woodland formation type—includes shrub formation.
  A. Mesic forests- deciduous.
    1. Climax maple-beech in heavy mull (8):
    Drymus crassus V.D.
    2. Light subclimax black birch-maple-oak-red, maple (6–8), often an elevated flood plain forest:
    Drymus unus, Ozophora picturata, Eremocoris ferrus; and on the coastal plain with the shrubs *Vaccinium* and *Viburnum*: *Scolopostethus atlanticus* and *Antillocoris minutus.*
    3. Gray birch or white birch subclimax forest (6–8):
    Scolopostethus diffidens, Antillocoris minutus, Eremocoris ferus, Drymus unus.
  B. Xerophytic oak-hickory forest (4–5):
    Ozophora picturata.
  C. Coniferous forest or mixed with white birch.
    1. Climax hemlock or red spruce often with white birch mixed in (7–8):
    Scolopostethus diffidens, Eremocoris ferus, Plinthisus americanus, sometimes *Drymus unus.*
    2. Pure white pine (northern) or pitch pine (lygaeids rare) also see field edge habitats, II F 1.

II. Field type.
  A. Mesic edge of woodland, rank herbs shaded.
    1. Edge of spruce-northern hardwoods association (6–8):
    Scolopostethus thomsoni.-A, *Stygnocoris pedestris, Ligyrocoris sylvestris.*
    2. Edge of southren oak-hickory woodland (6–8):
    Myodocha serripes, Heraeus plebejus, Pachybrachius basalis (uncommonly), *Drymus unus.*
  B. Mesic rank forb habitat or meadow (5–8):
    Pachybrachius basalis, Myodocha serripes, Heraeus plebejus, Stygnocoris pedestris, Stygnocoris rusticus, Zeridoneus costalis.
  C. Rotation arable—mesic gardens and fallow plowed fields; some new flood plain sites (4–6):
    Ligyrocoris diffusus, Sphragisticus nebulosus, Pachybrachius basalis.
  D. Ruderal habitats often with considerable bare ground- roadsides and vacant lots, poor soils.
    1. New succession—xeric (2–3);
    Ligyrocoris diffusus, Megalonotus chiragrus, Delochilocoris umbrosus.
    2. Later succession—more mesic (4–5):
    Pachybrachius basalis (with *Panicum*), *Perigenes constrictus,*

    Zeridoneus costalis.
  - E. Old xerosere successions—long lasting.
    - 1. *Andropogon* association with considerable exposed ground (1–2):
      *Cnemodus mavortius, Sphaerobius insignis, Emblethis vicarius, *Sisamnes clavigera.*
    - 2. Old overdrained sparse fields; also includes dry montain balds (1–3):
      Xestocoris nitens, Pseudocnemodus canadensis, Carpilis consimilis, Trapezonotus arenarius, Kolenetrus plenus.
    - 3. Low *Vaccinium* scrub, old sites (2–4):
      Ligyrocoris depictus, Pseudocnemodus canadensis, Trapezonotus arenarius.
  - F. Dry sparse woodland margins and glades (3–5).
    - 1. Southern: oak-hickory edge or pitch pine:
      Cryphula trimaculata, Pachybrachius basalis.
    - 2. Northern: white pine, *Betula populifolia,* edge. All of lygaeids of II E 2 and 3.
  - G. Alpine cool meadows (7–8), Krummholz.
    Eremocoris ferus, Trapezonotus arenarius.
- III. Open formation largely under six inches in height.
  - A. Xeric sites.
    - 1. Dry sandy sites—dunes (1):
      Emblethis vicarius, Ptochiomera nodosa.
    - 2. Dry cropped pastures (2–3):
      Delochilocoris umbrosus.
    - 3. Old dry slopes—with very sparse but complete vegetation (1–2):
      *Trapezonotus arenarius, *Malezonotus fuscosus.*
  - B. Mesic sites.
    - 1. Rotation arable—new fallow fields or road cuts with litter:
      Ligyrocoris diffusus, Sphragisticus nebulosus, Zeridoneus costalis, Peritrechus fraternus.
    - 2. Litter of sea or lake strands (2–8):
      Peritrechus fraternus and sometimes lygaeids of II A 2 and II D 2.
- IV. Aquatic transition.
  - A. Salt marsh (9–10).
    Peritrechus paludemaris.
  - B. *Carex stricta-Scriptus* marsh margin (10).
    Ligyrocoris caricis, Pachybrachius albocinctus, Scolopostethus thomsoni-B.

It is immediately observable that the considerable majority (78%) of the New England rhyparochromines are open habitat species, even the aquatic transition species, and that 50% of these in turn display a xerophilous and thermophilous habitat preference. This confirms similar results by Penth (1952) upon the German fauna, Putshkov and Putshkova (1956) on the Russian fauna and Strawinski (1959) on the Polish fauna.

The dominance of the Drymini in mesic wooded habitats is especially apparent, as is the restriction of the Plinthisini, the Ozophorini, and the Antillocorini to woodlands, and the converse rarity of Myodochini, Rhyparochromini, Megalonotini, and Gonianotini in wooded areas. Several myodochines inhabit rather moist sites, but none were found under closed canopies except during hibernation periods. Even *Ligyrocoris sylvestris* penetrates only into half open spruce-sphagnum areas. The Megalonotini and the Gonianotini are all xeric adapted forms.

The one area which was particularly non-productive of Lygaeidae was the shrub level formation which has suppressed or eliminated the herbaceous vegetation. Penth (1952) found essentially the same thing when she recorded a complete absence of Lygaeidae in the shrub stage in Germany. This may be the result of a lack of seeds in such a community when the shrubs are too young to produce seeds.

Even in those species which are adapted to the wetter or mesic habitats, greater population densities occurred in the drier microclimates such as on a slight woodland slope or elevation, or upon the top and sides of a *Carex* clump. No rhyparochromines were found on wet clayey soil. Indeed, the species which occur in aquatic transistion habitats were much more frequently swept from seed heads than the purely terrestrial species. The same appears to be true of the European wet habitat rhyparochromines *Pachybrachius luridus* and *P. fracticollis* (Krogerus 1960) and *Acompus rufipes* (Wolff) (Cobben 1953). However, no distinct diel rhythms or nocturnal movements into the field layer were found by night sweeping. The few species that left the ground layer did so during daylight periods to feed on ripe seeds. Aside from the marsh species mentioned the only rhyparochromines occasionally swept were *Stygnocoris rusticus* and *pedestris, Ligyrocoris diffusus* and *sylvestris, Zeridoneus costalis,* and *Drymus unus. Ptochiomera nodosa* however, displayed in the laboratory a distinct endogenous crespuscular activity rhythm (see *Ptochiomera* discussion), but was not swept in the field. It would seem then that most migrations from the litter biotope may involve purely migratory or dispersal movements.

A preference for open xeric environments also exposes the insects to great temperature extremes (Allee, *et al.* 1949, Cloudsley-Thompson 1962). This is particularly so in species adapted to open ground, *Sphaerobius insignis*, *Cnemodus mavortius*, and especially the sand loving lygaeid, *Emblethis vicarius.* With these insects, the substrate temperatures frequently reached 50°C. The early instar nymphs of these species are restricted to denser litter sites. Under these high temperatures the long legged myodochines were seen to distinctly raise themselves high on their legs and rarely remained still for long. This behavior combination is effective in cooling desert tenebrionids (Cloudsley-Thompson 1956) and dune grasshoppers (Chapman *et al.* 1926). In contrast such mesic woodland species as *Drymus* spp. are unable to survive brief exposures to full mid-summer sunlight.

While all the rhyparochromines chiefly frequent the ground biotope, they may be divided into two groups—those which secrete themselves under litter, and those which usually walk upon the litter and are only occasionally found in the litter. These insects, while in the same general biotope, will be exposed to somewhat different microclimatic conditions (Cloudsley-Thompson 1962). Those which hide in dense litter remain in somewhat more equitable conditions than those which may be abroad upon the open ground (Waterhouse 1955, Barnes and Barnes 1954).

These open hot xeric environments are unfavorable severe habitats (Allee *et al.* 1949) and a specialized fauna inhabits such sites (Cloudsley-Thompson 1962). If so, why the concentration of rhyparochromines in such habitats? The answer probably lies in the litter conditions and also explains the greater abundance of mesic species in the slightly drier microhabitats. In xeric habitats, the litter is overdrained and dries out very quickly after a rain. As a result the litter breaks down slowly and tends to accumulate with little change, in contrast to moister habitats where the activities of fungi, bacteria and other organisms are very evident (Murphy 1953, Burges 1960). Similarly, an examination of the drier habitats shows a much larger accumulation of viable seeds, which are both prevented from sprouting and protected from attacks by fungi by the overdrained conditions, in considerable contrast to wetter conditions where the seeds are difficult to find. A similar explanation is usually given to explain the persistence of desert seeds for very long periods of time. In correlation, the Lygaeidae like the seed feeding Tenebrionidae appear to be especially abundant and numerous of species in arid areas. Finally wet sites usually have rather compressed litter with relatively few large crevices and may provide an unsuitable "place to live" (Andrewartha and Birch 1954). It is speculative to attribute the habitat preferences to an innate thermophily or xerophily.

The sporadic reappearance of many rhyparochromines outside of their usual habitats as in the *Peritrechus* dominated wash litter habitat, is readily understandable for the wash contains a large abundance of loose ripe seeds. Moreover the wash litter usually possesses a remarkable variety of microclimatic conditions.

From the point of view of succession (Clements 1916, Dansereau 1957) the habitats listed may be treated as two series, a xerosere and a mesosere succession. These are both secondary successions, but the slow xerosere succession partakes of some of the aspects of a primary succession. The aquatic transition would form essentially a serclimax in the primary hygric succession. The terrestrial succession stages converge into the different climatic climaxes of northern and southern New England. The exact sequences of some dry site succession stages has not been completely understood (Conard 1935) but the general sequence is clear.

The xerosere succession would begin with open formation sand or close-cropped old pasture (III A 1 and III A 2), may lead to a slow changing low vegetation (II A 3) or ruderal vegetation (II D) and then to dry field stages (II A 2 and II A 3) and to dry oak-hickory (I A) or pitch pine forests. No rhyparochromines were found in pure pitch or white pine litter. The rotation arable sequence leads from open humus soil as in gardens (III B I), and very rapidly attains mesic field stages (III B 3 and III B 2) and then to light mesic forests (I A 3 and I A 2) and to climaxes (I A 1 or I C).

Since New England falls entirely within the forest biome, an obvious questions is, where did these many inhabitants of dry, warm open sites live before the clearing of the forest and the establishment of the present habitat mosaic? Bromley (1935) cited considerable evidence which indicated that the pre-colonization forests were open, with considerable illumination, grass pasturage and open areas due to the influence of the Indians. Furthermore he showed that a number of coastal sites, by earliest records, had in historical times never been forested because of their overdrained xeric soil conditions operating perhaps in partial conjunction with fire. Moreover, between 1820 and 1850, southern New England was about 80% deforested.

Lindroth (1957) considered this extensive deforestation of the eastern United States of major importance in the establishment of European species of plants and animals which were preadapted to the newer man-made habitats by their origin in the Palearctic steppes. Similarly, plants of Midwestern steppe origin had expanded eastward into these new habitats. However, many of these organisms which are centered in the Midwest had always existed in the east as subclimax species, and had merely expanded *in situ* with the expansion of subclimax habitats (Dansereau 1957, Ross 1962). Moreover, during the post-Pleistocene xerothermal maximum the natural prairie apparently extended east in patches to southern New York (Raup 1937, Braun 1955).

Since a number of open habitats exist upon barren, exposed mountain balds, as permanent serclimaxes (Dansereau 1957), it is evident that these areas would also form minor centers of dispersal into the new subclimax areas (Bromley 1935).

The European introductions form an obvious source, and the established species *Megalonotus chiragrus* and *Sphragisticus nebulosus* (if introduced) are both adapted to dry new ruderal habitats. The former is associated with similarly introduced bachelor's buttons (*Centaurea cyanus* L.) (Slater and Sweet 1958) and the latter is nearly always found along garden margins and waste sites, but neither are particularly abundant (except locally) in competition with the native myodochine fauna.

The two species of *Stygnocoris* which are adapted to well vegetated rank habitats are very abundant from northwestern Connecticut northward, and are well established in natural habitats. Their success, it *appears*, may in large part be due to the presence of an open niche for a feeder on composite seeds in rank habitats in northern New England.

From their present distribution and adaptation to the bald serclimax, *Carpilis consimilis, Ligyrocoris depictus*, and *Xestocoris nitens* may have spread into the subclimax from eastern centers. Most of the remaining dry area species (II C and II D) all extend out into the Great Plains where the xeric associations are climax types, and perhaps had expanded westward, or were part of the original subclimax. *Sisamnes clavigera,* which is known from very few eastern records appears to be an example of the former possibility.

The remainder are adapted to habitats which indicate their continuous presence in New England but many here also are known into the Midwestern plains area. It may be said finally that the influence of man has greatly extended the abundance and variety of the Rhyparochrominae of New England.

DISPERSION

Fortunately, this subject has recently been under intense study and review (Southwood 1960, 1961b, 1962a, 1962b, Schneider 1962, Johnson 1960a, 1960b, Brinkhurst 1958, 1959) so that the present data can be compared to other work. Southwood (1962a, 1962b) has brought together evidence to show that high flight activity is characteristic of denizens of temporary habitats and indicates active dispersion or migration from habitat to habitat.

MIGRATION

There is considerable confusion in the use of this word (Urquhart 1958, Kennedy 1961, Schneider 1962) due to its association with bird migration. Southwood (1962) would use it for any directional dispersal movement from habitat to habitat not connected with normal movement within an animal's habitat. The latter type of dispersal movement Southwood designates as trivial. Schneider would rather call Southwood's migration ''lateral displacement movement.''

Johnson (1960a, 1960b, 1962) has shown that the mass dispersal or exodus movements of insects are undertaken by teneral adults. Schneider (1962), however, gives examples to show that not all migrational movements are of this type, and Johnson (1960b) acknowledged that other types are possible but are possibly associated with reproductive cessation. Southwood and Johnson (1957) and Southwood (1962a) state that frequently an exodus occurs in early May. In the Heteroptera, especially, these flights are diurnal because of the high temperature flight thresholds for heteropterans as compared to Lepidoptera or Diptera (Southwood 1962a). This dispersal movement is especially marked in woodland insects from concealing habitats (Southwood and Johnson 1957). The bright illumination of the woodlands in spring may also work in conjunction with a post diapause (sexually teneral) flight propensity as indicated by a strong positive phototaxis. The behavior changes which occur in the development of dispersal phase or period are reviewed by Kennedy (1961) and interpreted in terms of developmental changes in thresholds: during dispersal, low thresholds for a positive response to light (Johnson 1960a); high thresholds, vegetative behavior, resulting in straight line flights. Since in the Heteroptera the predominant mode of locomotion is walking, not flying, trivial motions are largely of this type (Southwood 1962a). In some taxa as among mirids, short flights (called by Southwood ''flits'') are also of this type. As the Rhyparochrominae are largely restricted to the ground layer, and rarely ''flit,'' most captures in flight, are with little doubt migrational movements.

With the long series of flight data accumulated by suction and light traps at Rothamsted, Southwood (1960) was able to analyze the flight activity of the Heteroptera, and compare it with the habitat preferences of the species. He found that in the light traps in southern England the lygaeoid families made up only 0.002% of the total catch while the Miridae comprised 97%. In contrast, the suction traps yielded 18% Lygaeidae, which signified a diurnal flight disperson behavior. In striking contrast, the yields at lights in tropical Africa (Southwood 1961a, 1962a) were largely lygaeoids, and the Lygaeidae in each case considerably outnumbered the Miridae at lights.

Southwood considered the flight records from temperate North America similar to those obtained in England. However as Torre-Bueno (1914) long ago noted, there is a striking difference in light response between the European and American fauna, especially in the Lygaeidae. This may reflect a systematic difference in the fauna as the lygaeids recorded at lights (L in Table 4) are predominantly Myodochini and Ozophorini, and very few (in New England none) of the other tribes were recorded at lights. The records of *Emblethis, Sphragisticus,* and *Peritrechus* are from much more southern localities.

Thomas (1938) noted this striking disparity between light trapping and the abundance of lygaeids in the fields of southern England. It is possible to interpret this difference in terms of high temperature thresholds in most lygaeids for flight. As China (1930) noted, "the decrease in activity producing a slower rate of metabolism of most Heteroptera at the moderately low temperatures usually experienced in Britain, is very obvious. The British collector rarely sees his quarry flying and when visiting the continent or even the Channel Islands, is surprised to see many species take to flight at the slightest disturbance."

In this respect, then, it is of considerable interest that the few flight captures recorded by Southwood (1960) are to a surprising extent members of the generally cool-adapted Drymini, and no mid-summer flight was recorded, only early spring post-hibernation flights, when temperature conditions would be as low as any during the summer. Moreover, it was shown that these were definitely dispersing and do not represent short flits as in many mirids.

Similar post hibernation flights in April and May were observed during this study in *Eremocoris ferus* and *Antillocoris minutus* respectively. As cool adapted forest or forest edge species, their activity in early spring correlates with the period of sunny forest floor conditions before the forest leaves emerge to shade the forest litter.

It does not appear to me that the data on flight activity presented by Southwood (1960) on the lygaeids is especially illustrative of his otherwise reasonable theory (1962a) that such activity should reflect habitat type. The lygaeids listed from southern England (Southwood 1960) as mentioned earlier are mostly cool adapted Drymini (*Drymus sylvaticus* (Fab.), *Scolopostethus affinis* (Schill.), *S. thomsoni* (Reuter) and *Taphropeltus contractus* (H.-S) which from the published habitat data have come from mesic woodland or woodland edge habitats. Only *Peritrechus lundi* (Gmelin) appears to be a denizen of temporary habitats. Moreover in his listing of world representatives, he wrongly placed *Antillocoris* spp., a woodland insect, as a denizen of temporary habitats. In contrast, a great representation of species of temporary habitats is not listed. It would appear then that flight activity should also be used cautiously, consideration given not only to abundance, but to the mode of habitat migration. However, if Johnson (1960a) is correct, all normal macropters should disperse.

Other evidence for dispersion in the New England species is given in Table 4. This evidence includes, aside from the light collections (L), beach wash collections (B), which, with high probability indicate dispersals over water (Torre-Bueno 1915, 1927, Parshley 1917a); airplane sampling (A) by Glick (1939) and Glick and Noble (1960); and the diurnal observations (D) just mentioned. Under any conditions, the flight activity levels are difficult to assess, but this evidence can at least be compared with the habitat data. The light collections in this study were all made in mid-summer and early autumn and represent a summer dispersion. A rhythmn of seasonal habitat migration is described under the discussion of *Myodocha.*

BRACHYPTERY

Perhaps the most interesting information stems from the remarkable wing polymorphism exhibited by many rhyparochromines. Brinkhurst (1958, 1959) was able to associate brachyterism with the life cycles and habitat preferences of a number of British Gerridae.

Since the brachypters are flightless, they must be restricted to a given environment. It cannot be so simply assumed, however, that the macropters will disperse, for while long winged, many corixids and notonectids are flightless (Young 1961) as is *Ilyocoris cimicoides* (L.) (Poisson 1924). Moreover as Caswell (1960) was able to demonstrate with the bruchid *Callosobruchus maculatus* (F.) there may be a flight polymorphism in the fully winged individuals. This uncertainty in fully macropterous forms is in part alleviated by the actual flight records mentioned earlier. Wing polymorphism to be biologically meaningful infers a functional significance—flight, to the macropterous form. If teneral dispersion (Johnson 1960a) theory holds, all the macropters presumably should disperse in such a population.

While Southwood (1962a) does not say, as Brinkhurst (1959) suggested, that brachyptery is restricted to inhabitants of permanent habitats *per se,* he did state that brachyptery would be "geared, by natural selection, to the frequency of change of the habitat: the more temporary the habitat, the more obligatory migratory individuals and vice-versa." Lindroth (1949) and Darlington (1943) discussed a similar relationship among beetles on mountains and islands which would apply to permanent habitats (Southwood 1962a). Lindroth (1957) used the high incidence of macroptery as one of his criteria of the spread of an introduced species. Other evidence of wing polymorphism is discussed by Southwood (1962a).

Under certain circumstances species of permanent habitats will be macropterous because their life history involves a change of habitat, as in many Orthoptera, for oviposition and feeding sites; or the food supply is inconstant in the permanent habitat and the insect has no resting stage. In this latter fashion Southwood (1962a) explained the macropterous condition in the pyrrhocorid *Dysdercus* which is arboreal, feeding on the seeds of Malvales. Since the seeds ripen and are available for only a short time, the *Dysdercus* fly to various feeding sites with available seeds.

Since the Rhyparochrominae are also seed feeders, at first thought this same condition would seem present, except for an important difference. The Rhyparochrominae feed on fallen seeds which may remain continuously present and the insects are at least oligophagous (Sweet 1960). Moreover, in New England, the short warm period limits the period for feeding.

For the purpose of the present study the degree of brachyptery of the New England populations may be expressed in a scale from 1 to 4 (Table 4). Full macroptery is indicated by 1; over 15% macropters, 2; 15–5% macropters, 3; macropters rare or apparently absent, 4. It is immediately apparent that a large variety of combinations are present.

RELATION TO HABITAT

Southwood (1962a) would consider permanent habitats to include "rivers, lakes, perennial plants including trees of climax vegetation such as woodlands, salt marshes, heathlands and marshes fringing lakes and rivers." In contrast temporary habitats would include dung, carrion, fungi, plant debris (i.e. logs, straw, hot beds) and annual and perennial plants of seral communities (e.g. wastelands, fields). He furthermore noted that semi-arid plants (xerophytes) are characteristic of temporary habitats.

If we thus distinguish the permanent habitats from the temporary ones, the permanent habitats will include the aquatic transition stages and climax habitats only: the subclimax seral field stages, including edges, are all temporary habitats (Dansereau 1957). In Table 4 the species are listed with P representing permanent habitats, and T temporary habitats.

The relationship between brachyptery and habitat permanence is summarized on Table 3.

If we consider the few species (26%) characteristic of permanent habitats (Permanent I), a remarkable percentage, 50% are macropterous. Even if the aquatic transition species, *Pachybrachius albocinctus* and *Peritrechus paludemaris* are discarded because these species may undergo habitat migrations, the percentage of macroptery remains 38 (Permanent II). However, the remaining three species each have special biological aspects which may make understandable their macropterous conditions. *Drymus unus* and especially *Eremocoris ferus* have a very wide ecological distribution and are found in subclimax forests and edges. *E. ferus* ranges from high alpine areas to shaded beach wash and coastal *Myrica* shrubs, and indeed the biological success of this species may render unnecessary the advantage of brachyptery. *Ozophora picturata* of the oak-hickory association belongs to a large genus of which all known species are macropterous and may fly very readily. The defense behavior of this species may involve its frequent use of "flits".

TABLE 3

Relation Between Macroptery and Habitat Permanency

Habitat	Percentage of Macroptery			
	100%	< 15%	15–6%	> 5%
Permanent I	5(50%)	——	2(20%)	3(30%)
Permanent II	3(38%)	——	2(24%)	3(38%)
Temporary	13(46%)	5(18%)	5(18%)	5(18%)
Type 1	12(92%)	——	1(08%)	——
Type 2	1(6%)	5(33%)	4(27%)	5(33%)

Among the brachypters of permanent habitats, two, *Scolopostethus diffidens* and *Antillocoris minutus* have a frequent production of macropters, and, in accordance, both may occur in subclimax

Betula populifolia litter, and *Antillocoris* in fact sometimes is found sporadically in some cool meadows, then always macropterous. Southwood (1960) listed the habitat of *Antillocoris minutus* and *A. pilosulus* to be temporary. However, the habitat of the macropterous *A. pilosulus* in Florida and North Carolina (forest edge litter) does not agree with this placement. The frequency of *Antillocoris* in air trapping is undoubtedly the result of its small size which allows it to be lofted high by winds during the dispersal phase. The three species with a very low level of macroptery, *Drymus crassus, Plinthisus americanus,* and *Ligyrocoris caricis* are all found in climax or serclimax habitats.

When the many rhyparochromines (74%) of temporary habitats are considered, in the sense of Southwood (Table 3, Temporary) it is seen that only a minority (46%) are completely macropterous, which is again, seemingly unaccountable. But if one considers what is rarely mentioned by ecologists (Burges 1960), the time element involved in the succession rates, a quite different pattern emerges (see Ecology). Compared to the annual life of an insect the decades in which some xeroseres undergo succession (Blizzard 1931) is a very long time. Type 1 (Table 3) includes the rapid mesosere and bare ground (rotation arable, ruderal, etc.) succession habitats which rarely last more than a year or two. In complete correlation 92% of the rhyparochromines of such habitats are totally macropterous and the only exception is the introduced *Stygnocoris rusticus* which may not be exploiting its natural habitat. Type 2 (Table 3) includes the slow progressing xerosere successions, and is again in close correlation with 94% of the species exhibiting brachyptery. The bionomics of the sole apparent exception, *Kolenetrus plenus,* is not well understood. The three levels of brachyptery proportions also correspond to habitat permanence within Type 2 habitats. Those species with a large percentage of macropters (2) are members of the *Andropogon* association which often constitutes a relatively short-lived habitat in the open xerosere series. In contrast, those species with rare macropters (4) are frequently found in sparse numbers in serclimax grassy or *Vaccinium* scrub bald habitats but extend (in greater abundance) into morainic lowland sites. The sole exception is *Sisamnes* in the *Andropogon* association whose range, however, is mostly western. Moreover the rareness of *Sisamnes* may stem from a consequent poor adaptation to the habitat mosaic of New England. Those species with intermediate brachyptery are also found in serclimaxes, but are even considerably more numerous in the lowland temporary habitats.

It appears then that a good correlation exists between the proportions of brachypters and the habitat permanency. Lack of exact habitat ages precludes a closer comparison, but it should be noted the proportion of brachypters in some species especially abundant in climax forest may be higher than some other species upon xeric field succession slopes, i.e., there is a complete overlap between permanent and temporary habitat as defined by Southwood. The overlap was explained as with water beetles (Jackson 1928) in terms of the total habitat and distribution range.

Nevertheless since southern New England was once almost completely denuded of forests (Bromley 1935), and the dry sites on outcrops and morainic slopes are quite discontinuous, a perfect mosaic of favorable habitats for different species is present. As Parshley (1920b) said, on finding brachypterous *Microvelia* in pools on Mt. Greylock, Massachusetts, "The common occurrence of several species of this genus in such isolated situations indicates the importance in the economy of the race of the fully winged phase, which must appear in sufficient frequency to provide for a favorable rate of dispersal."

Relation of Dispersion to Habitat

Despite the misgivings expressed about the lygaeid flight records (in southern England) there appears to be a good correlation between temporary habitats and dispersal records, when one discounts the tribes which despite their abundance are rarely or never found at lights, especially the Gonianotini, Megalonotini and temperate Drymini, Stygnocorini and Plinthisini and considers the Myodochini alone (Table 4). In excellent correlation all the myodochines of short-lived temporary (T_1) habitats have been collected at lights, including the marsh dwelling *Pachybrachius albocinctus*. Only a few dispersal records on the other hand are available for the species of the T_2 xerosere habitats and these are mostly the inhabitants of the newest almost ruderal *Andropogon* type habitats, which species also have a high percentage of macropters. Even among the other tribes, the various existing dispersal records are of species of temporary habitats except with the spring-dispersing *Eremocoris* and *Antillocoris* and *Ozophora* which very frequently flies despite its permanent type habitat. Dispersal among the other tribes may be of mainly a diurnal type. The apparent difference in reaction to light among these tribes in eastern North America would be a significant area of research.

Southwood (1962a) has grouped migratory variability into two categories, obligatory and facultative. In the first the species is obligatorily dimorphic, i.e., under genetic control; in the second, the migratory response is facultative, and triggered by certain environmental conditions, such as crowding, or habitat changes. The latter is an especially ideal adaptation to temporary environments. In the second category Johnson's teneral migration period may be modified to include other non-sexual periods (Johnson 1960b).

It is difficult to apply this system to the present taxon for not enough is known about what promotes dispersal, nor was any work done upon the proportion of obligatorily dispersing individuals in a population of macropters. However, most of the fully macropterous species are probably of the facultative type. Among the brachypterous species, the type would depend on whether the macropterous condition is genetically obligatory; or also requires an environmental stimulus, and so, is facultative. For this a fuller discussion of wing polymorphism is required.

Wing Polymorphism

Fully half (51%) of the Rhyparochrominae of New England have brachypterous forms (Table 4). As described in the previous discussion on dispersal the proportion of brachyptery was noted (Table 4) from 1 (macropterous) to 4 (nearly entirely brachypterous).

In nearly all species the brachypterous form is distinct with very few intergrades between it and the macropter. Several different types of brachyptery exist. In 15 (75%) of the brachypterous species the entire wing is shortened, and the membrane is reduced in extent and slightly overlaps. *Trapezonotus arenarius* (see Species Discussion) exhibits a sexual dimorphism in that the female shows a more plastic expression of brachyptery. *Scolopostethus thomsoni* shows a considerable non-sexual variation in degree of brachyptery (Butler 1923, Southwood 1961b). In *Ligyrocoris sylvestris, depictus,* and *caricis* the membrane is not so reduced (submacropterous) but no macropterous forms were found.

The five remaining species have quite different types of brachyptery. *Antillocoris minutus* is unusual in that it has three distinct types of wing development, the macropter, the "normal" brachypter, with the wing reduced, and a subbrachypterous form with the corium truncated and the membrane lost (see *Antillocoris*).

Drymus crassus has rather coleopteroid hemelytra, and the hind wings are reduced. The corium is elongated and the membrane is narrowed and reduced although attaining the apex of the abdomen. In an occasional female the membrane was slightly shorter. In *Plinthisus americanus,* although the corium is also elongated and the claval suture indistinct, the membrane is reduced but overlaps. In *Carpilis consimilis* the membrane is reduced to a very thin non-overlapping fringe. Finally in *Sisamnes clavigera* the membrane is altogether absent as in *Antillocoris* and the corium somewhat truncated. It is significant that *Drymus crassus* and *Plinthisus* with their coleopteroid type of brachyptery were rarely found outside of climax forests.

The obvious question, as Butler (1923) asked, is why the varieties of hemelytral development? Indeed, the question may be restated to ask why does the development of the brachyptery extend beyond a flight polymorphism as in some aquatic Corixidae and Notonectidae (Young 1961)? A flight polymorphism of this type would be sufficient to insure that the favorable habitats remain populated especially if a dispersal flight is obligatory in teneral macropters as Johnson suggests.

As Darwin (1859, pp. 111, 346) long ago proposed, such wing reductions could result from natural selection to allow the most economical growth, when flight became of no selective value. It therefore follows that if a large scale dispersal away from a habitat is no longer a selective advantage, but instead only a certain low percentage is required, a disruptive selection (Ross 1962) could operate. This could bring about an evolutionary progression from little or no structural dimorphism to the most extreme, but economical dimorphism between the macropter and the brachypter. It would then also follow that only under long continuing selection would the extreme dimorphism result, and it then becomes relevant that the rhyparochromines with extreme brachypters are denizens of some of the most permanent habitats in eastern North America.

Brinkhurst (1959) in this connection, considered the selective advantage of the brachypter of *Gerris odontogaster* (Zett.) to be at least 5% over the macropter to overcome a lethal condition.

Hormone Control

Southwood (1961b) in reasoning from Wigglesworth's experimental work (1952) with *Rhodnius* has proposed that a brachypterous form is either a neotenic (juvenile) expression (methathetely) produced by an excess of juvenile hormone, or is paedogenetic and results from a depression of the juvenile hormone level leading to a last instar with adult characters (prothetely). Since all the rhyparochromines studied have five full instars, and are heavily sclerotized, all then would represent some expression of metathetely.

Southwood (1961b) proposed that cold temperatures promoted metathetely by lengthening the exposure of the last instar to juvenile hormones, and cites evidence to show that in many species the brachypter is associated with northern distributions and with mountain populations. He considered most important as experimental evidence Brinkhurst's (1958, 1959) demonstration that the exposure of the eggs of *Gerris odontogaster* (Zett.) to warm temperatures produced macropterous adults. However, this cannot be considered as being metathetelous in the sense that the effect of the juvenile hormone is extended in the last instar.

Southwood (1961b) further considered the reduction in ocelli size (Butler 1923) as another neotenic expression. Only *Cnemodus* among the New England rhyparochromines lacks ocelli. This, however, occurs both in the macropter and the brachypter. In *Plinthisus americanus* the macropter has distinctly larger ocelli. There appears to be little difference in size in the other species. If the ocelli are important in flight behavior, their quoted reduction in the brachypters may also correlate with their reduced selective value.

While, like much growth phenomena, the wing shortening is under hormonal control (Wigglesworth 1952, 1954), it appears somewhat debatable to interpret all brachypters as simple general neoteny, since the rhyparochromine brachypters are very similar otherwise to the macropters and the wings are usually nearly identical in structure and only reduced in size, i.e., it is not a wing pad in structure or an intermediate structure. Moreover, a complete gradation exists between wing muscle loss and very short wings, and an all or nothing tissue response in different species would produce a more abrupt and nymphoid wing distribution as in the *Rhodnius* seventh instar adult (Wigglesworth 1954). The close relation between habitat permanence and brachyptery would suggest a selection control rather than environmental cold control suggested by Southwood (1961b).

The various and diverse modifications of the brachypterous wings, of which a few simple examples among the rhyparochromines have been given here, would further illustrate a selective and adaptive procession. It may be more accurate and useful then to consider selection as utilizing a variable hormone threshold to effect a brachypterous condition. Given a cold habitat, selection may then possibly utilize the normally lengthened last stadia to operate a hormone balance or threshold mechanism.

Latitudinal Relationship

Since Southwood (1961b) suggests that the metathetelic macropters would be more abundant at the southern limit of the species range, the distribution patterns should be considered. In the Rhyparochrominae such a relationship was not seen, and on the contrary, the brachypterous species with more northern distributions were almost entirely brachypterous and the macropters occurred near the center of the species distribution, not at the southern limits, while the brachypterous species of more southern distribution appeared to have an ample representation of macropters in Connecticut. *Sisamnes clavigera* is a possible exception as all specimens of this species ever collected in the northeastern United States have been brachypterous, but rearing under many conditions failed to yield the macropter.

Despite both areas having a north temperate location, the generally continental climate of northeastern North America produces very warm mid-summer temperatures in contrast to the moderate Atlantic climate of western Europe, and open land areas (Cloudsley-Thompson 1962) become very hot and dry. Since many brachypterous rhyparochromines favor such habitats, the actual development period, especially of the last instar, occurs under very hot field conditions. Yet these progeny are as brachypterous as those reared under cooler laboratory conditions. Moreover both slow-developing and rapid-developing species may be brachypterous or macropterous.

There appears, nevertheless, to be a definite correlation between species of northern distributions and wing polymorphism. The incidence of brachypters among boreal species is 11 of 14 species (79%); and among intermediate ranges 4 of 13 species (31%); and among austral ranges 5 of 14 species (36%).

This correlation, however, may stem more from the habitat permanency of these particular boreal species than from their distribution. Most of these boreal northern species are found in semipermanent or serclimax habitats, usually hot in summer. Indeed, this group may represent the element most closely adapted to New England climatic conditions, while most of the other species which have their main distribution centers elsewhere are adapted to temporary subclimax associations. This situation is common in subclimax associations (Ross 1962).

Moreover the relationship in terms of total latitudinal range limits is the direct converse of what Southwood predicted—the northern species at their austral limits are nearly entirely brachypterous, and most southern and intermediate species macropterous near their boreal limits. From the standpoint of selection this pattern would be expected.

Other Environmental Factors

On more general grounds, if metathetely were based on hormone control such as suggested by Southwood many detrimental conditions should favor the production of the brachypters by lengthening the last instar through low food levels or through excessive cooling. If purely genetic considerations are involved, a rare gene combination for macroptery would be more possible under heavy densities. Macroptery arising from a crowding stimulus would produce a similar result. Thus macroptery development and dispersal would occur at optimal times; brachyptery and contraction at inoptimal conditions.

In a permanent or semi-permanent environment, this situation is reasonable, for the brachypters would insure survival of a population; and dispersal would occur when optimal conditions for colony establishment or ecesis may exist in other habitats.

LABORATORY WORK

First it should be emphasized that all the species were reared under laboratory conditions in environments considerably warmer or cooler than field conditions, and several species were deliberately reared under hot conditions in an effort to obtain the rare macropterous forms. Moreover, the stadia could be considerably accelerated or delayed by temperature and food conditions. The Heteroptera moult only 5 (rarely 4) times and the stadia may be greatly varied by starvation, or, in a few species, a superabundance of food. If cool conditions can lengthen the stadia and increase the exposure to the juvenile hormone, which assumes that the action of juvenile hormone is not equally affected by cooling, then the lengthening of a late stadia may similarly extend the exposure to juvenile hormone, but, moreover, without a concomitant reduction in the rate of action of the hormone.

It is then significant that in nearly all of many hundreds of laboratory cultures no change in the proportion of macropters as compared to field populations was observed. The single exception was *Carpilis consimilis* where rearing under heavy density conditions did apparently promote the appearance of the macropters much as in the leaf hopper *Nitaparavala* (Kisimoto 1956). On the contrary the pattern usually appears to be under genetic control with little if any phenotypic plasticity, e.g., the penetrance of the gene was complete under the varied and different laboratory conditions.

These results then do not support among rhyparochromines the juvenile hormone hypothesis of Southwood, and the production of the macropters appears to be usually genetically controlled, e.g., controlling the wing anlage thresholds to the action of the juvenile hormone without phenotypic variability.

It is realized that other obscure triggering factors not present in the artificial laboratory conditions may be involved. It might be significant that whenever one of the rarer macropters of *Plinthisus* and *Carpilis* was found in the field it appeared among an unusually heavy population of the species. Moreover whenever a sparse population of a Type 3 brachypter was found it was *usually* composed almost entirely of brachypters. To what extent this results from lack of crowding, or the infrequency of chance rare gene combination, is uncertain and certainly deserves intensive work.

While brachyptery does not then appear to be controlled in the New England Rhyparochrominae by nutritional factors, there may be a relation between habitat productivity and brachyptery. There is a predominance of brachypterous rhyparochromines in xerosere (T_2) habitats which frequently approach a serclimax in their permanence. Now the reason for the slowness or failure of these habitats to develop to climax is attributed to poor overdrained soil which renders the biological productivity of these areas low. The vegetation of such sites is accordingly very sparse and low, and represents a low biomass productivity.

Recalling that the evolution of brachyptery represents a selection for metabolic economy, in contradiction with flight dimorphism *per se*, and that the rhyparochromine populations are frequently sparse in these severe habitats, it would appear that there would be strong selection for the most economical development to the adult in these habitats of nearly permanent but low productivity.

Because so many of the brachypterous species have univoltine life cycles with obligatory diapauses, it was difficult to do crossmatings of the wing types and yield genetic proof for the pterygopolymorphism, as done by Poisson (1924) and Brinkhurst (1958, 1959).

It was possible to show that a few macropters will result from brachypter × brachypter matings in *Trapezonotus arenarius, Pseudocnemodus canadensis, Cnemodus mavortius, Cryphula trimaculata, Scolopostethus atlanticus, S. thomsoni, and S. diffidens* (see Species for details).

In *Antillocoris minutus*, as in *Eremocoris ferus* and *Myodocha serripes* fertilization occurred before the post hibernational flight by the macropters. In *Antillocoris*, a univoltine species, the progeny of random mated macropters were nearly all normal brachypters, and all the subbrachypters yielded only subbrachypterous progeny (see *Antillocoris*).

As Southwood (1962a) emphasized, dispersal patterns and brachyptery should be interpreted as methods of surviving an unfavorable period, and that "the type of habitat change has been of profound importance in determining the evolution of methods of surviving such environmental change by the Arthropoda." To discuss this, the life histories need consideration.

SEASONAL CYCLES

In a cold temperate climate such as New England's, the life cycles of the various rhyparochromines must be adapted to the seasonal fluctuations and synchronized to allow survival over the adverse winter and sometimes, the late summer periods. As summarized by Andrewartha (1952) and Lees (1955), it has long been known that arthropods adapt to seasonal ecological stress by going into a state of diapause, that is, a cessation or retardation of growth, metabolism, and reproductive activity, a state which is largely independent of the ambient temperatures. Quiescence, in contrast, is directly controlled by the ambient conditions and upon return to favorable conditions the insect will develop, etc., without delay.

As Andrewartha (1952) and Bonnemaison (1945) have stressed, diapause functions chiefly as a timing mechanism to ensure that the insects will become active only during favorable periods and will not respond to brief variations during unfavorable conditions, such as an unusually warm period during autumn or spring.

In this study only the general outlines of the seasonal cycles and diapause were traced and no attempt was made to establish in detail the optimum conditions for diapause development or the precise conditions which initiate facultative diapause. It should be added that since many of the species have a considerable north-south distribution, the seasonal cycles and diapause may show some geographical variation (Musaki 1961, de Wilde 1962). In a few species data from North Carolina and Florida could be included. The seasonal patterns given are characteristic of the New England Rhyparochrominae.

The aspects of the seasonal cycles considered here (Table 4) include generations a year, the overwintering state, type of diapause, diapause intensity, and periods of nymphal development and oviposition. Details of the phenology, diapause conditions, photoperiodicity, etc., are given under the individual species.

All the rhyparochromines were either univoltine or bivoltine, and in a few species, *Pseudocnemodus canadensis* and *Peritrechus fraternus,* both conditions prevailed. As usual (Lees 1955) most of the univoltine species have obligatory diapause states. Diapause occurred only in the adult or egg state, and there were no examples of nymphal diapause as in *Reduvius personatus* (L.) (Readio 1931). In both the egg or adult diapause the diapause was either obligatory or facultative.

There were several types of facultative diapause. The most common involved a photoperiodic response resulting either in retarding reproductive development (gonadotropic disassociation) or in the production of diapausing eggs. In several species which laid diapause eggs, the adults remained in reproductive diapause until an autumnal short day or cold stimulus induced oviposition. These species are designated with a "+";—designates no summer diapause period.

In all cases when evidence was gathered (see Species Discussions) the factor initiating a bivoltine facultative diapause was photo-period much as predicted by de Wilde (1962).

The diapause intensity could be measured by the reaction of the diapausing adults or eggs to continuous warmth. In some, diapause was completed within two months (1) or was absent (0). In others, it was broken after two or three months in warmth (2) or was not completed in warmth before death and a cold exposure was obligatory (3). The numbers classify the species in this scheme on Table 4. In most species the diapause development was completed by prolonged cold exposure (4°C.) in a cold room.

Of the 38 species, 15 (40%) overwinter as eggs. This is an unusual percentage as compared with the north European fauna where only three species of *Stygnocoris* and *Ligyrocoris sylvestris,* itself a myodochine, overwinter as eggs (Pfaler 1936, Southwood and Leston 1959). This may, as in the nocturnal response of myodochines and ozophorines to light, stem in part from a taxon difference as all of the cold adapted boreal myodochines (10 of 17 species) diapause as eggs. However *Plinthisus americanus* and both species of *Drymus* also diapause as eggs, yet all of the European species of *Drymus* and *Plinthisus* whose overwintering condition is known overwinter as adults (Pfaler 1936, Southwood and Leston 1959). It is perhaps significant that the two introduced rhyparochromines which have very successfully invaded the natural (?) habitats in New England are the egg-overwintering species of *Stygnocoris.* Rather than a response to a more continental climate, the prevalence of egg overwintering may possibly reflect an arid subtropical origin of the Myodochini where estivation through dry periods might occur in the egg state, preadapting the eggs to winter diapause.

Egg diapause intervenes in at least three different stages of embryonic development. (1) During early development before much development has occurred—most of the species. These all have strong diapauses except *Perigenes constrictus,* and *Kolenetrus plenus.* (2) During late anatrepsis at the "diapause" stage—*Ligyrocoris diffusus,* and (3) in late katatrepsis, with the embryo nearly fully developed—*Stygnocoris rusticus* and *pedestris* and some eggs of *Drymus unus.* It is then significant that *Stygnocoris* and *Ligyrocoris diffusus,* and especially *Drymus,* considering their mesic habitats, hatch much earlier than most other egg-diapausing species which must complete egg development during the spring.

In the species *Ligyrocoris diffusus* and *Drymus unus*, an intense cold exposure of some adults in late autumn destroyed the diapause producing factor in the adults and nondiapause eggs were laid.

Of the remaining 23 species which overwinter as an adult, 7 or 8 are univoltine (*Antillocoris pilosulus* appears to belong to this type). The remainder are bivoltine. The diapause intensity among these species varies considerably (see Table 4). The boreal *Antillocoris minutus* and *Xestocoris nitens* have especially intense dispause states. The more austral species exhibit a weaker diapause, especially *Sisamnes clavigera, Heraeus plebejus,* and *Cnemodus mavortius.* In four bivoltine species *Myodocha serripes, Ptochiomera nodosa, Peritrechus fraternus,* and *Malezonotus fuscosus,* the diapause state was not broken except under long daylight condition, and after 4–5 months (see Species Discussions).

A progression then may be traced in cumulative adaptations to a cold environment, which allows us to group the various species into several seasonal cycle types.

SPECIES GROUPS

Type 1.—this corresponds to the *sommertypus* of Pfaler (1936). These species are univoltine, with an obligative strong diapause and overwinter as an egg. There are two subgroups. The first lays eggs shortly after becoming adult, and the eggs are exposed to warm conditions, often for several months before winter begins, especially the first two species.

Ligyrocoris depictus, L. caricis, L. sylvestris, Carpilis consimilis, and *Plinthisus americanus.*

In the other subtype, the adults do not lay eggs until autumn and require a cold stimulus for its initiation.

Stygnocoris rusticus, S. pedestris, Drymus unus, D. crassus, and *Kolenetrus plenus.*

Type 2.—these species have an obligative univoltine adult diapause. In the first three cold exposure was obligatory to complete diapause:

Antillocoris minutus, Xestocoris nitens, and *Peritrechus paludemaris. Scolopostethus diffidens, S. atlanticus, Trapezonotus arenarius,* and *Cryphula trimaculata.*

In all the species except the early developing *Trapezonotus,* the new adults did not appear until after July 10 or later. There is a possibility that *Peritrechus paludemaris,* an austral species, has a facultative diapause determined in an early instar.

Type 3.—these species are bivoltine with a facultative diapause as an egg. The first two species lay diapause eggs immediately, while the other three have a brief photoperiodic reproductive pause until autumn short day conditions:

Pseudocnemodus canadensis, Sphaerobius insignis; Zeridoneus costalis, Perigenes constrictus, and *Ligyrocoris diffusus.*

Type 4.—these species have a facultative bivoltine diapause in the adult stage. The first two become adult remarkably late in the year. The next two species did not break diapause except under long day conditions:

Ptochiomera nodosa, Sisamnes clavigera, Myodocha serripes, Malezonotus fuscosus, Heraeus plebejus, Pachybrachius basalis, Cnemodus mavortius, Peritrechus fraternus, Megalonotus chiragrus, Sphragisticus nebulosus, and *Emblethis vicarius.*

Type 5.—here is included a species with a facultative univoltine (usually) life cycle and a weak diapause.

Ozophora picturata.

Type 6.—the following bivoltine species have no apparent diapause, and overwinter through quiescence. This corresponds to the *mischtypus* of Pfaler (1936).

Pachybrachius albocinctus, Eremocoris ferus, and *Scolopostethus thomsoni.*

It is significant that only in the non-diapausing *Eremocoris ferus* were a few nymphs ever found overwintering.

A final aspect of the seasonal cycles is the period of nymphal development and of oviposition. In part, of course, this corresponds closely to the univoltine-bivoltine divisions, but differs in detail and subdivides the other seasonal cycle categories already mentioned.

In Type 1 and 3, which overwinter as eggs, the species can be distinguished into early maturing (by late June) and late maturing groups (later, usually much later, than late June). These species directly utilized a spring fallen seed source without prior spring depletion by adults.

EARLY MATURING.—(univoltine)—*Ligyrocoris depictus, L. caricis, Kolenetrus plenus;* (bivoltine)—*Ligyrocoris diffusus, Perigenes constrictus, Zeridoneus costalis, Sphaerobius insignis, Pseudocnemodus canadensis* (part).

LATE MATURING.—(univoltine)—*Ligyrocoris sylvestris, Carpilis consimilis, Plinthisus americanus, Stygnocoris rusticus, S. pedestris, Drymus unus, D. crassus;* (bivoltine)—*Pseudocnemodus canadensis* (part).

The next group includes those which overwinter as adults—types 2, 4, 5, and 6—and thus have a spring feeding and oviposition period followed and overlapped by the nymphal feeding period. Here early maturing adults (by June 21), mid-summer adults (by July 15), and late maturing adults (after July 15) may be distinguished. The bivoltine species have a second feeding period in late summer, and these feeding groups overlap broadly. In contrast to the egg dispause species there is little or no fall feeding.

Early Maturing Adults.—(by June 21)—(univoltine)—*Trapezonotus arenarius* (part); (bivoltine)—*Emblethis vicarius, Peritrechus fraternus, Megalonotus chiragrus, Pachybrachius basalis, Sphragisticus nebulosus.*

Mid-Summer Adults.—(by July 15)—(univoltine)—*Antillocoris minutus, Scolopostethus diffidens, S. atlanticus, Trapezonotus arenarius* (part), *Peritrechus paludemaris;* (bivoltine)—*Malezonotus fuscosus, Myodocha serripes, Heraeus plebejus, Cnemodus mavortius, Scolopostethus thomsoni, Eremocoris ferus.*

Late Summer Adults.—(after July 15)—(univoltine)—*Xestocoris nitens, Cryphula trimaculata;* (bivoltine)—*Pachybrachius albocinctus, Sisamnes clavigera, Ptochiomera nodosa, Ozophora picturata.*

While some species simply become sexually mature in spring at different rates or have different temperature responses, in a few such as *Myodocha serripes* the photoperiod control continues to operate in the spring. In others, especially and significantly the woodland Drymini, but also *Xestocoris nitens* and *Cryphula trimaculata,* although the adults mate in early spring and oviposition can occur under short photoperiods, the nymphs appear in the field very late. It seems most probable that this is the result of the cool forest conditions throughout the spring which cause a very slow egg development. In *Xestocoris* and *Cryphula* a similar explanation may be warranted for the eggs of these species develop especially slowly.

Relation to Distribution

As might be expected some good correlation exists. All the species of Type 1 (univoltine egg diapause) except the *Drymus* spp. have boreal distributions. Among the species of Type 2 (univoltine, adult diapause) all but *Peritrechus paludemaris* and *Cryphula trimaculata* have generally boreal ranges and *Scolopostethus atlanticus* is intermediate. In Type 3 (egg diapause, adult bivoltine) all species are boreal or intermediate in range. In Type 4 and 5 none of the species have boreal ranges, and those with the weakest diapause are among the austral element except *Ptochiomera.*

The species of Type 6 (no diapause) appear unusual in that while one of the species is austral, the other two have ranges which extend far north. These latter two, *Eremocoris ferus* and *Scolopostethus thomsoni,* are cold adapted and perhaps like the arctic midge larvae that are merely quiescent (Lees 1955) no synchronization is required for survival. Indeed, these are entirely successful species.

Relation to Systematics

Lees (1955) said, that while some general trends can be ascertained in systematic relationships, in most short-lived insects there is little constancy in the stage of arrest. This, he emphasized, indicates that the diapause states had evolved independently, and their selective value is little affected by the stage in which it occurs. This last consideration does not appear to be entirely true, for all the cold-adapted Myodochini genera have evolved an egg diapause and many independently, it appears, but on the other hand, apparently none of the extensive Palearctic fauna of Gonianotini, Megalonotini, and Rhyparochromini have evolved an egg diapause. Such an egg diapause was found elsewhere only in *Stygnocoris* and in the Nearctic *Drymus* and *Plinthisus americanus*. Within the Myodochini all the members of the related New England *Ligyrocoris* group including *Zeridoneus*, *Sphaerobius*, and *Perigenes* diapause as an egg. This certainly must indicate a systematic relationship to diapause evolution.

Relation to Ecology and Brachyptery

As noted earlier, there is a direct correlation between habitat permanence and brachyptery, and it was suggested that this faunal element, since it is essentially composed of climax or serclimax species, was closely adapted to the New England climate. The life cycles further bear this out: most (77%) of the strictly univoltine species with an obligative diapause are largely brachypterous, indicating at least a semi-permanent environment. In converse, of the bivoltine species, only 29% are brachypterous.

Actually overwintering as an egg also is a definite biological risk, requiring that a permanent habitat for the next year be present at the place of oviposition. There is again a correlation of 67% between permanent habitats and egg diapause and the exceptions are all bivoltine species except the introduced *Stygnocoris*. *All* the brachypterous species which overwinter as eggs are found in permanent habitats. Most of the species, 12 of 13 (93%), with a low level of macropters (Type 3 and 4) are univoltine or mostly so (*Pseudocnemodus*). *Sisamnes* again is the only exception. All the species with unusual types of brachyptery (see Brachyptery) are univoltine.

As was discussed earlier, the serclimax or semipermanent vegetation is usually sparse and poor, indicating a low biomass productivity, and it was proposed that brachyptery may function as an economical adaptation. Also, this may conversely explain the fair abundance of macropters in similarly permanent, but seed-productive woodlands.

It therefore appears possible that univoltinism could represent a similar adaptation to a poor environment, and again a good relation exists. Of the seven species found on the dry sparse serclimax, *all* are univoltine. *Malezonotus* may represent an exception as the single station, although temporary, resembles a serclimax. An adaptation to low biomass productivity may be as important a factor in the evolution of brachyptery as an adaptation to climax permanent habitats. These poor open habitats may become very hot, as hot as an open ruderal site. In the northern open *Andropogon* association, in a more productive habitat, a bivoltine life cycle can be afforded as in *Sphaerobius.*

A univoltine life cycle may be prolonged over most of the summer or the peak developmental period placed early or late in the summer. In *Xestocoris,* a boreal species, and *Cryphula,* an austral species, the univoltine generations do not appear until mid-July; *Ligyrocoris depictus* and *L. caricis* become adult in late May and early June and *Carpilis* becomes adult from late June to late July.

A bivoltine life cycle on the other hand must be dependent on a seed source early in the year, usually fallen seeds from the previous year, and also upon new fallen seeds in late summer. In *Ligyrocoris diffusus,* at least, an active migration period exists at the time of the early new adults to seek out food sources. This need correlates with the frequent occurrence of the bivoltine myodochines at lights, and the macropterous condition of many bivoltine rhyparochromines.

It is then apparent that a strong relationship exists, as Southwood (1926a) predicted, among the ecological requirements, habitat permanency, migration, brachyptery, and the seasonal life histories. It is moreover apparent, that there are definite assemblages of species in the different habitats. But before we can consider these, other aspects of their general biology should be considered.

PROTECTIVE COLORATION AND BEHAVIOR

This subject certainly forms an important part of the ecology of the rhyparochromines. However, it is difficult to generalize from human perceptions on the nature and function of color and movements (Cott 1940, Klopfer 1962) to the perceptive realm of vertebrate and invertebrate predators and also parasites. It is extremely difficult to observe predation on the ground layer, and caged predators and prey are unlikely to represent the natural or open ecological situation (Cott 1940).

TABLE 4

Summary of Various Biological Information

Species	Macroptery	Habitat	Dispersion	Generations	Overwintering Form	Diapause	Summer Diapause	Diapause Intensity
M. serripes	1	T_1	LD	2	A	F	–	3
H. plebejus	1	T_1	L	2	A	F	–	1
Pa. basalis	1	T_1	LBA	2	A	F	–	2
Pa. albocinctus	1	P	LA	2	A	H	–	0
C. mavortius	2	T_2	L	2	A	F	–	1
P. canadensis	3	T_2	B	1(2)	E	F	–	3
S. insignis	2	T_2	—	2	E	F	–	3
L. diffusus	1	T_1	LB	2	E	F	+	2
L. depictus	4	T_2	—	1	E	O	–	3
L. sylvestris	4	T_2	—	1	E	O	–	3
L. caricis	4	P	—	1	E	O	–	3
Z. costalis	1	T_1	L	2	E	F	+	3
P. constrictus	1	T_1	LA	2	E	F	–	2
Pt. nodosa	2	T_1	LA	2	A	F	+?	3
S. clavigera	4	T_2	—	2	A	F	+?	1?
C. consimilis	4	T_2	—	1	E	O	–	3
K. plenus	1	T_2	B	1	E	O	+	2
P. americanus	4	P	—	1	E	O	–	3
A. minutus	2	P	D	1	A	O	–	3
A. pilosulus	1	P	AL	1	A	O	?	3
C. trimaculata	3	T_2	—	1	A	O	–	2
X. nitens	3	T_2	—	1	A	O	–	3
O. picturata	1	P	L	1(2)	A	F	–?	1
St. rusticus	2	T_1	—	1	E	O	+	3
St. pedestris	1	T_1	—	1	E	O	+	3
D. unus	1	P	—	1	E	O	+	3
D. crassus	4	P	—	1	E	O	+?	3
S. diffidens	3	P	—	1	A	O	–	2
S. atlanticus	2	T_2	—	1	A	O	–	2
S. thomsoni	2	T_2	—	2	A	H	–	0
Er. ferus	1	P	DB	2	A	H	–	0
P. fraternus	1	T_1	L	1(2)	A	F	–	3
P. paludemaris	1	P	—	1	A	O	–	3

Species	Macroptery	Habitat	Dispersion	Generations	Overwintering Form	Diapause	Summer Diapause	Diapause Intensity
M. chiragrus	1	T_1	D	2	A	F	–	2
S. nebulosus	1	T_1	L	2	A	F	–	2
Em. vicarius	1	T_1	LB	2	A	F	–?	3
T. arenarius	3	T_2	—	1	A	O	–	3
D. umbrosus	2	T_1	A	2	A	F	–	2
M. fuscosus	4	T_2	B	2	A	F	–	3

Macroptery: 1—macropterous, 2—>15% macropterous, 3—15–5% macropterous, 4—<5% macropterous
Habitat: P—permanent, T_1—brief temporary, T_2—persisting temporary
Dispersion: L—lights, B—beach wash, A—airplane sampling, D—diurnal
Generations: number per year; overwintering form, A—adult, E—egg
Diapause: F—facultative, O—obligative, H—quiescence
Summer diapause: +; diapause intensity, 3—strong, 2—moderate, 1—weak, 0—none

The apparent colors, forms, and motions of the rhyparochromines vary remarkably, a variation which must stem from some selective basis, although the patterns can also reflect a systematic relationship especially in the coloration of the nymphal forms. Significantly the coloration pattern nearly always correlates with the field behavior of these animals. Moreover, there has been some impressive recent experimental work on the effectiveness of lepidopteran mimicry (Brower 1958, Sheppard 1959) and on predation by jays and toads (Brower 1959, Brower and Westoff 1960). Isely (1938) was able to show the value of protective coloration in grasshoppers against predators. Cott (1940) effectively amassed a great deal of evidence in support of protective coloration and behavior. It therefore would appear reasonable to consider the variable protective patterns of the rhyparochromines as important biological factors and also important in evaluating the problem of several species existing in the same habitat.

ODORS

In any consideration of the meaning of the protective coloration, a paramount factor is the presence, as in most Heteroptera, of odorous or repellent glands in all the species, both nymphs and adults. In all the species and all instars the insects have a burning acrid taste which is quite independent of variations in the odors of the insects. The burning sensation of a minute first instar is quite remarkable. With few exceptions the odor of the rhyparochromines is the heavy ''buggy'' odor so frequently associated with Pentatomidae. The exceptions, however, were remarkably different. In the lethaeines *Xestocoris nitens*, *Cryphula trimaculata*, and *Antillocoris minutus*, the odor was strongly reminscent of the peculiar *Tapinoma* ant odor. *Eremocoris ferus* and at least one population of *Scolopostethus thomsoni* have a distinctly sweet fruity odor. It is noteworthy that the acrid taste remained constant although the odor varied. Significantly, from an evolutionary point of view, in *Cryphula*, *Xestocoris*, and *Antillocoris* both the nymphs and adults, with their quite independently derived scent glands, shared the same peculiar odors, while in *Eremocoris* and *Scolopostethus* the adults and nymphs had different odors.

There is a distinct and remarkable type of scent gland in nymphs which possess the Y-suture described by Slater and Sweet (1960). The anterior gland between terga III and IV is white and apparently of a tubular nature, in contrast to the bright orange walls of the posterior two scent glands and the adult metathoracic glands. In groups without a Y-suture, the anterior gland when present, resembles the posterior two. The anterior gland is absent in the Gonianotini and in *Antillocoris*. The Y-suture is present in every instar except the first and thus allows the first and second instars to be distinguished in species with the Y-suture. It is apparent that the significance of these different scent glands should be pursued further.

Remold (1962) has effectively and clearly shown that the scent gland secretion of various heteropterans not only repels, but acts as a temporary paralytic poison upon ants and carabid beetles. The action is that of a nerve poison, and may paralyze an ant (*Lasius*) for 15 minutes. He found that various lygaeids utilize all the known methods among the Heteroptera for distributing the secretion. Some spread it over their own bodies (nymphs of *Nysius* and *Henetaris*), place the secretion with their legs or tarsi directly on the aggressors (*Lygaeus* nymphs, *Geocoris*), or release it slowly as a protective odor (*Lygaeus* adults), but all 17 rhyparochromines representing 6 tribes investigated by Remold spray the secretion directly at the aggressors.

In the present study, none were seen to spread the secretion with their legs. For the most part, the species did not release their odor until handled. Indeed, some, for example *Antillocoris,* do not release the odor until nearly crushed. *Cnemodus,* and especially *Eremocoris ferus,* release their odors very readily, but none release the odor a little at a time as do *Spilostethus saxatilis* (Scop.) and *L. equestris* (L.) (Remold 1962). With the effectiveness of the scent gland secretions against ants and beetles established, their significance against vertebrates should be followed up. Since, unlike many aposematic plant-living Heteroptera, most adult rhyparochromines are procryptic in coloration, it may be that the odor itself may at least function as a warning to mammal insectivores, notably shrews as Rothschild (1962) suggests. She also points out that since bird and lizard predators do not use smell to locate prey, the procryptic coloration may protect against birds, and the odor against the color blind, smell-sensitive mammals. She quotes an example of a coati-mundi which refused to eat procryptically colored pentatomids.

The situation is rendered more complex by the nymphs frequently being colored quite differently from the adults, and each must be considered separately. First the general color characteristics should be mentioned. These however should be considered with care as they may show considerable systematic relationships especially in the first instars. Of course such resemblances may reflect a biological similarity

Among nearly all myodochines, despite the diverse appearance of the adults, the first instars are pale yellow with a narrow red band across the abdomen. This pattern is also shared by the ozophorine, *Ozophora picturata.* The first instars of the two Megalonotini have a yellow band on the first two segments of an otherwise red abdomen. In all known Gonianotini except *Emblethis,* the first instars are deep red but the later instars are deep black. In the remaining species the color of the first instar varies from red to pink.

The color patterns may be grouped into three categories: (1) procryptic or concealing coloration, (2) ant mimicry, (3) aposematic or warning coloration. It is not clear which category some nymphs fall in, partly because white lateral spots on the mid-abdomen may also be interpreted as a disruptive coloration, and partly because the succeeding instars may progressively differ from earlier to late instars. For details see the individual species discussions.

PROCRYPTIC COLORATION

In nearly all species the adults possess a very evident procryptic type coloration which lends to the subfamily a brown, somber, ''sparrow-like'' mien, which has contributed to our poor knowledge of the taxon.

Nymphs exhibiting procryptic coloration include the black nymphs of the Megalonotini and most Gonianotini, *Emblethis, Carpilis, Perigenes, Ozophora, Pachybrachius, Zeridoneus, Ligyrocoris diffusus,* and the last instar nymphs of *Eremocoris;* the nymphs of *Stygnocoris pedestris* and *Kolenetrus plenus* have disruptive procryptic color, and *Myodocha* nymphs are longitudinally striped.

The species with procryptic coloration fall into several behavior groups. The Gonianotini, the Megalonotini, and *Carpilis, Sisamnes* and *Kolenetrus* of the Myodochini tend to hide in narrow crevices and run agilely and rapidly from one crevice to another, rather like a roach. The coloration of *Emblethis* closely matches its sandy habitat and it moves in short rapid bursts, stopping frequently, which renders it difficult to see.

The other group includes the long-legged, rapid running adult myodochines of open places which are not ant mimics such as *Ligyrocoris, Zeridoneus,* and *Perigenes.* The third group includes the species of rank habitats and loose litter, and which accordingly may have generalized legs such as *Peritrechus fraternus, Stygnocoris* spp., *Drymus, Pachybrachius, Antillocoris,* and also a few long-legged myodochines like *Myodocha.* Some species of rank habitats characteristically move slowly and deliberately, in contrast to the roach-like scurry of the gonianotines. These include *Myodocha, Heraeus, Antillocoris, Peritrechus paludemaris,* and *Plinthisus americanus.*

ANT MIMICRY

This may be a more controversial category to interpret, but it is especially marked in the nymphs of some species. In others, both nymphs and adults, the appearance of ant mimicry ''grades'' into procryptic disruptive coloration. Field observations, however, are invaluable here, for the ant mimics move with an exaggerated jerky hesitant gait much like ants. The species are listed in order of resemblance to ants.

Adults.—*Sphaerobius insignis, Cnemodus mavortius, Pseudocnemodus canadensis, Eremocoris ferus, Scolopostethus* spp.

Nymphs.—above, but only early instars of *Eremocoris* and late instars of *Scolopostethus, Pachybrachius albocinctus, P. bilobatus, Ligyrocoris depictus, L. sylvestris, L. caricis,* and up to fourth instars of *L. diffusus.*

The most remarkable ant mimic is *Sphaerobius insignis.* Frequently this insect was overlooked in the field for it ran actively about and was very difficult to distinguish from a large *Formica* ant. This species is of considerable interest for it is polymorphic in color (see *Sphaerobius*) with few intermediates, and so resembles both black and red ants. The fifth instars, however, are all red, not black, and were the better mimics. Such dimorphism (Sheppard 1959) which is adapted to two models should greatly enhance the protection from mimicry resemblance.

Nearly its equal as a mimic although much larger is *Cnemodus mavortius.* The adults, especially the brachypters, resemble huge black ants, the nymphs, red ants.

In the other mimics the resemblance is not so striking, but frequently this is not necessary with many predators, as only a general resemblance is required (Klopfer 1962).

To a certain extent the predominance of myodochine ant mimics may result from the predominance of these preadapted long-legged, rapid running forms in open dry habitats. These habitats are especially favored by ants.

The ''mimicry'' by *Eremocoris* and *Scolopostethus* is of a different sort. These species tend to form loose aggregates under litter in favorable biotopes, and frequently, disturbing the litter causes the whole group to ''boil up'' and actively run in all directions as when an ant nest is disturbed. A difficulty is that the ant resemblance is not so obvious although the color pattern is very clearly marked in these genera. However, if this is a defense against bird predation, the constricted rapid moving aspect of the insects may form a simple sign stimulus so frequent in bird behavior (Klopfer 1962).

The obvious question is, if this is mimicry, is it Batesian or Mullerian. It is realized that the two types may grade into each other (Huheey 1961). While it may be assumed that the Rhyparochrominae *may* be distasteful because of their scent glands (Remold 1962), no conclusion can be drawn until the potential predators are determined, along with their reaction to the taste of the rhyparochromines. The difficulty with a Mullerian interpretation might be the absence of clearly marked warning coloration schemes among other non-ant mimic rhyparochromines. If it is Batesian the abundance levels as compared to the ants is often remarkably high which would allow, say, some bird predator to see through it. The final aspect, which may suggest a combined Batesian-Mullerian explanation, lies in the remarkable tendency for the nymphs to be ant mimics, the adults procryptic. Moreover, some of the nymphs appear to be aposematic. The possibility suggests itself that the nymphs may form a Mullerian assemblage with ants, the adults, a

Batesian assemblage. The different position of the scent glands in the nymphs and adults may be significant here.

The red aposematic coloration would here, of course, be meaningful only to a bird predator, as the mammals are color-blind and most arthropods would not perceive red, and in which case the insect *may* appear black. These are all nymphs. The brightest and most conspicuous are the striking red nymphs of *Drymus* spp. and *Stygnocoris rusticus.* The nymphs of *Ptochiomera* and *Sisamnes* are similar, a bright contrasting red and white. Finally, the most generalized rhyparochromines have bright light pink nymphs—*Plinthisus, Antillocoris, Cryphula, Xestocoris* as well as *Peritrechus fraternus.* It is noteworthy that all are loose litter dwellers, and none are long-legged runners or crevice seekers.

Only four species are known to feign death: the two *Stygnocoris, Eremocoris ferus,* and *Drymus unus.* In *Stygnocoris* this is especially noticeable for when disturbed while feeding above the ground level on composites, the insects will freeze and drop to the ground.

Predators and Parasites

Predators

As mentioned in the preceding section, very little is known about the natural predators of the Rhyparochrominae. Enough, however, is known to indicate a large number of predators. Thomas (1955) considered the important predators in England to be nabids, anthocorids and the centipede, *Lithobius.* Wilson (1938) has found that *Pachybrachius bilobatus* and *P. vinctus* are preyed upon by lizards (*Anolis* spp.) in Puerto Rico. Knowlton and Nye (1946), and Knowlton (1944) working in Utah, found that a number of rhyparochromine species were fed upon by the sage sparrow, *Amphispiza nevadensis* (Ridgway). Knowlton, Maddock and Wood (1946) in Utah found rhyparochromines in the diet of the sagebrush swift lizard, *Sceloporus graciosus graciosus* (Baird and Girard). Miller (1956) reports that certain African lizards consumed *Dieuches* sp.; Corby (1947) found *Gryllodes sigillatus* Walker feeding on adults and eggs of *Elasmolomus sordidus* (Fab.).

I have found *Ptochiomera nodosa* being preyed on by *Geocoris uliginosus* (Say); *Pseudocnemodus canadensis* by *Geocoris limbatus* Stål; *Myodocha serripes, Cnemodus mavortius, Zeridoneus costalis* by *Melanolestes picipes* (H.-S.) but *not* by *Nabis roseipennis* Reuter from the same environment. *Trapezonotus* is preyed on by all stages of *Pagasa fusca* (Stein). In the laboratory the eggs of various lygaeids were readily fed on by roaches. A few other examples are given under the species, but this in no wise is adequate, and merely shows that the rhyparochromines are preyed on by a large assortment of predators, and it appears unlikely, as Thomas (1955) thought, that the rhyparochromines suffer an unusually low natural mortality.

Probable predators are wasps of the sphecid genera *Diploplectron* Fox and *Dryndella* Spinola, both members of the subfamily Astatinae, Williams (1946) found that *Diploplectron* provisioned its nests with nymphs of *Emblethis vicarius, Megalonotus chiragrus,* and *Sphragisticus nebulosus.* Parker (1962) notes that there is no apparent host specificity, but rather a size specificity for Heteroptera, the larger astatines capturing pentatomids, coreids, cydnids, or scutelleroids; the smaller, lygaeids. It appears of some interest that these Heteroptera are all from the Trichophora section of the Pentatomomorpha. Evans (1958) describes the hunting procedure of the wasps as follows, ''The female hunts its prey in weedy areas and is often seen crawling up and down plant stems. When a bug is located the wasp grasps it and stings it to immobility.''

As emphasized by Wheeler (1910) and Remold (1962), ants form the most abundant and active arthropod predators, especially at the ground level. Remold found that although the different heteropterans, including rhyparochromines, were attacked by various ants, the ants were warded off by the temporary paralyzing action of the scent gland secretion. Moreover the secretion also acts as a general repellent. Further work is needed to evaluate the actual effectiveness of the secretion in the field, and to what extent the insects are preyed upon by ants. At any rate this defense mechanism would make understandable the coexistence of large populations of lygaeids with ants, and, in turn, also the evolution of ant mimicry among lygaeids and other Heteroptera.

Parasites

There are only a few records of parasitism among the rhyparochromines. Tachinid flies are known to parasitize *Scolopostethus thomsoni* and *Eremocoris plebejus* (Fall.) in Germany (Michalk 1935b, 1938a). The tachinid parasite of the *Eremocoris* was determined as *Cinochira atra* Zett. (Michalk 1938a), and a species of Chalcididae as also recorded from this species (Michalk 1940). A scelionid parasite has been recorded from the eggs of *Gastrodes grossipes* (DeGeer) (Nageli 1933). Michalk (1938b) found *Scolopostethus affinis* (Schill.) parasitized by the larvae of the mite, *Allothrombium.* I have found *Thrombidium* mites on *Myodocha serripes* and *Scolopostethus diffidens.*

Various rhyparochromines were found to be parasitized by tachinid flies of the genera *Catharosia* and *Petia* (= *Procatharosia*). A fairly large complex of *Catharosia* species appears to be involved. Dr. Paul H. Arnaud, Jr. (*in litt.*) is presently revising these genera.

A more detailed presentation of the biology of the flies will be given in a later contribution as a considerable number of new species appears to be involved.

A general outline may be sketched. Parasitism occurs at least by the late instars, but the parasite does not leave until the host becomes adult. The parasites leave by either pushing through the ovipositor in the female or through the conjunctiva between the genital capsule and segment eight in the male. The larva crawls a short distance away usually to a wetter site and pupates. Pupation usually takes approximately a week. Ashlock (*in litt.*) was able to rear *Catharosia lustrans* from a new species of *Eremocoris.* The fly developed very rapidly and was reared through its entire life history between April 9 and May 4. Neither of us have observed the type of oviposition by which tachinids are classified biologically.

The catharosines were usually reared in the spring or fall, and very few were found in the summer generation of bivoltine lygaeids. A parasitized female can be readily recognized because it is nonreproductive.

The life cycle of the catharosines varies with whether the host species overwinters as an egg or an adult. If in a species which diapauses over the winter as an adult, the parasite overwinters in the hibernating host. If the host overwinters as an egg, then the parasite leaves the lygaeid host in the autumn.

The following lygaeids were found parasitized by *Catharosia* spp.:

Host adult (*and parasite*) *overwintering.—Heraeus plebejus, Pachybrachius basalis, P. albocinctus, P. bilobatus, Cnemodus mavortius, Ptochiomera nodosa, Cryphula trimaculata, Peritrechus fraternus,* and *P. paludemaris.*

Host egg overwintering.—Pseudocnemodus canadensis, Sphaerobius insignia, Ligyrocoris diffusus, L. depictus, Zeriodoneus costalis, and *Perigenes constrictus.*

Only one species, *Catharosia nebulosa* (Coq.) was determinable, (Arnaud *in litt.*) but the remarkable size range of the host species and corresponding variation in the size of the parasites, along with the quite different methods of overwintering of populations from adult or egg overwintering hosts, suggests that the species concept of *C. nebulosa* may be too broad, and warrants further studies.

Hibernating *Pachybrachius albocinctus* were also parasitized by a different tachinid, *Alophorella aeneoventris* (Will.). *Emblethis vicarius* was found parasitized by another catharosine, *Petia* (= *Procatharosia*) ? calva Coq., and Ashlock (*in litt.*) informs me that in California he too reared *Petia* from *Emblethis.* Moreover, the *Procatharosia* parasitized *Emblethis* were among and near myodochines which were parasitized by *Catharosia,* which further suggests a parasite-host specificity. *Petia* overwinters in its host, *Emblethis vicarius.*

Both Sabrosky and Arnaud doubt (*in litt.*) that the tachinids could have such a narrow host range as appears to be indicated by these results. However, from the converse view, the parasitism of the rhyparochromines is very narrow as each species appears to have a specific catharosine parasite. This exploitation by a single taxon of parasites has a parallel in the Miridae which are almost exclusively parasitized by euphorine Braconidae (Leston 1961). The Catharosini are so far known only from the Lygaeidae, and these observations constitute the first host records (Arnaud *in litt.*).

Of the total rhyparochromine fauna of 40 species, tachinid parasites were found in 16 (40%). Of these hosts 12 (75%) were myodochines which is a significant proportion as the Myodochini (Table 1) comprise only 47% of the fauna.

However, another important correlation is that no lygaeids of closed canopy habitats were so parasitized, and nearly all Myodochini are found in open habitats. It could be that the western species of *Eremocoris* investigated by Ashlock (*in litt.*) is an open area inhabitant like some European *Eremocoris.* Since *Eremocoris plebejus* is typically found in open habitats (Penth 1952), and the Catharosini are known from Europe (Arnaud *in litt.*), but without hosts, the determinations given by Michalk (1938a) should be checked.

Since parasites form a major population control factor, it is interesting to relate the distribution of hosts to Gause's (1934) statement, "When a new habitat is first colonized there is a strong probability that its normal predators, including parasites, will be absent and during the first period after colonization, the population (of the host), if the reproduction rate is sufficiently high, will build up quickly."

The first aspect is that the inhabitants of permanent habitats with the significant exception of the salt marsh species *Peritrechus paludemaris* and the marsh edge species, *Pachybrachius albocinctus,* were not parasitized. Parasitism was most pronounced among myodochines of temporary habitats especially the newest habitats. In populations of *Ligyrocoris diffusus, Zeridoneus, Pachybrachius,* and *Cnemodus,* the parasites were found only in well-established colonies, never in new small populations.

There is obviously a great need here for further study of predation and parasitism especially its role in population control. Information on prey or host seeking and capture is needed to interpret protective coloration and competition among the rhyparochromines.

Feeding Habits

A general account of feeding habitats of the Lygaeidae was given earlier (Sweet 1960) in which it was shown that the Rhyparochrominae like most other Lygaeidae were seed feeders and not predacious. Therefore, only the recent literature is reviewed here. Thomas (1955) investigated the feeding habitats of a number of rhyparochromines. He found that the insects would feed on buds, moss, dead and dying insects, and concluded that materials of this sort formed the food sources of the Rhyparochrominae. Moreover, he noted that the Rhyparochrominae laid only few "batches" of eggs and concluded from this that the Rhyparochrominae with their biological success in their protected environment, needed only a low reproductive capacity.

Putshkov and Putshkova (1956) and Putshkov (1956) found that most of the Lygaeidae were seed feeders, and their reproductive potential was not low, but high. The work of Johansson (1858a, 1958b) effectively explains the disparity. He showed that in *Oncopeltus fasciatus* (Dallas), the *corpora allata* hormone production was controlled by seed feeding, for starving or placing the insect on a diet without seeds cuts off egg production. I have similarly found that on lettuce and other green material only a few eggs were laid, in contrast to the heavy egg production when fed on sunflower and other seeds.

Beck, Edwards, and Medler (1958) found that *Oncopeltus* could not be reared readily upon a defined diet *per se*, for the insect needs to pierce through a milkweed seed coat to stimulate normal feeding. The seed coat thus appears to be very important, as some rhyparochromines react to seed coats, others do not. Most species, however, fed normally on a hulled sunflower seed.

The general behavior of the insects during feeding is much as described by Feir and Beck (1963) for *Oncopeltus* and in *Leptoglossus* (Koerber 1963). As in most Heteroptera the labium bends on its joints to allow feeding, and frequently the labium is entirely removed and feeding occurs by the stylets alone as in *Leptoglossus* (Koerber 1963). After a feeding period, as noted by Feir and Beck, a rhyparochromine always seeks out and imbibes free water.

Salivary fluid

Miles (1959) showed that *Oncopeltus fasciatus* like several pentatomids and coreids and all Homoptera secretes a salivary fluid which coagulates to form a sheath. In contrast, this fluid is absent in the Miridae, Tingidae, and predacious Hemiptera such as the Anthocoridae, Nabidae, and Reduviidae (Sweet, unpublished). He thought the function of this sheath was to seal the stylet entrance and line the bores to avoid wastage of the salivary-food solution.

Saxena (1963), however, has shown that in the pyrrhocorid *Dysdercus*, the sheath fluid is deposited only when piercing a tough barrier. He found no loss of salivary fluid from the junction of the labium with the seed whether the sheath was present or absent. From the feeding behavior and conditions of sheath deposition, Saxena concluded that the sheath functions to affix and stabilize the beak during piercing, and unlike *Oncopeltus* (Miles 1959), it was not deposited along the path of the stylets in the seed. Saxena was also able to show that the salivary fluid in *Dysdercus* did not preorally digest the seed kernel. Instead, a suspension was formed along the path by the mechanical action of the stylets. Miles (1959) on the other hand thought preoral digestion occurred in the salivary fluid-filled feeding bores. Saxena suggested that the rapid saliva ejection-ingestion process of *Dysdercus* also occurs in *Oncopeltus* and thought Miles' conclusions need further validation. Saxena moreover demonstrated that digestion occurred entirely within the gut in *Dysdercus*. This resolves the dilemma imposed by the slow action time of the enzymes *in vitro* as was observed by Nuorteva (1958) and Baptist (1941).

I can only add that the salivary sheath cone was not formed when feeding on the freshly broken sunflower kernel but was formed upon the thin membrane (true seed coat) that surrounds the seed. Upon hard substrates the salivary cones may be deposited on bores already made, even upon a cone already present to the extent that as many as five cones have been observed on top of one another at a feeding site in *Pachybrachius basalis* cultures. Cone formation may then be inhibited by a direct food or water stimulus rather than stimulated by surface hardness as Saxena suggested. At any rate, the salivary cone is more than a mere fleck of dried saliva as thought by Koerber (1963).

I found the salivary sheath fluid in all the Rhyparochrominae studied and throughout the Lygaeidae, including the predacious Geocorinae. Moreover, the predacious asopine Pentatomidae (*Podisus, Perillus*) secreted this fluid very copiously. Alydids and rhopalids which can also be reared on sunflower seeds, similarly secrete a sheath fluid. It will be most interesting to trace further the presence of this fluid, which Miles (*in litt.*) considers to be strictly homologous in the Homoptera and the Pentatomomorpha.

Food Plants

In my 1960 paper I implied that the Lygaeidae were unusual in their seed feeding habits, but it appears that this tendency is wide spread, especially in the Trichophora families, the Pyrrhocoridae, Rhopalidae, Alydidae, Stenocephalidae, (Southwood and Leston 1959), and common in the Pentatomidae and Coreidae (Leston *in litt.*). Nevertheless, the term "seed bugs" is still applicable, as this family is, in general, highly adapted to feeding on fallen loose seeds.

As stated previously (1960), the rhyparochromines are rather oligophagous on seeds which makes the task of ascertaining their preferred seeds, if any, difficult. Some definite patterns emerge. *Pachybrachius basalis* is very partial to *Paspalum* and *Panicum* seeds, *P. albocinctus* to *Carex* and *Scriptus* seeds; *Peritrechus* to *Panicum,* but also many others, also *P. paludemaris* for *Spartina* seeds; *Myodocha* showed a preference for *Hypericum* and strawberry seeds; *Pseudocnemodus* for *Vaccinium* and *Festuca; Cnemodus, Sphaerobius,* and *Sisamnes* for *Andropogon* seeds; *Carpilis* for *Veronica* seeds; *Zeridoneus, Ligyrocoris diffusus, L. depictus,* and *L. sylvestris* for composite seeds, especially *Rudbeckia,* the latter also for *Betula* and *Tsuga* seeds; *L. caricis* for *Carex* seeds; *Ptochiomera* for *Rumex* seeds, etc.; *Ozophora* for *Aster* seeds; *Plinthisus* for *Tsuga, Picea,* and *Betula* seeds; both species of *Stygnocoris* for composite seeds, especially *Tanacetum; Cryphula* for *Panicum* and other grass seeds; *Xestocoris* for *Festuca, Danthonia,* and *Andropogon* seeds; *Antillocoris* for *Betula populifolia* seeds; *Trapezonotus* for many seeds especially *Vaccinium; Megalonotus* for *Centaurea; Sphragisticus* for *Rumex* and *Agropyron* seeds; *Drymus* spp. for *Aster seeds; Eremocoris* has a very wide seed range; *Scolopostethus atlanticus* for *Vaccinium* and *Viburnum* seeds; *Scolopostethus diffidens* for *Betula, Tsuga,* and *Picea* seeds; *S. thomsoni* A for *Rumex* seeds, etc.; *S. thomsoni* B for *Carex* seeds; *Emblethis* for *Andropogon, Carex,* and composite seeds.

There is *not* any well-marked host specificity, but frequently as shown above there are preferences for certain seeds from the native habitat that may help to explain niche overlaps in the natural habitats. Frequently, in additions of these seeds may ameliorate the high mortality in the first instar. The later instars of most species as Putshkov (1956) found, are practically polyphagous on seeds although often retaining a preferential for a particular species of seed. This preferential was repeatedly observed in the feeding behavior.

While I earlier (1960) could find no reference to insect predation among the rhyparochromines it has recently been found that the genus *Mizaldus* preys on beetles and on meal worms in grain respectively (Miyamoto 1955, Slater and Carayon 1963). As the latter authors point out, these insects may also feed on seeds much as does *Geocoris* (Sweet 1960). Poppius and Bergroth (1921) report that *Xenydrium formiciforme* Berg. is a predator on eggs and larvae of the ponerine ant *Ectatomma ruida* Roy. However it is not clear whether this was inferred from ant mimicry as at that time mimicry was considered closely associated with predation on ants (Wheeler 1910) and predation assumed.

Eyles (*in litt.*) has been able to show that *Scolopostethus decoratus* may, when starving, attempt to feed on animal food, but makes poor growth and oviposits very little upon such a diet.

In my earlier paper (1960) I neglected to mention that when starving or in thirst, some of the species will attempt to scavenge upon dead or dying insects. However there was no oviposition, no or little nymphal growth, and great mortality even when an abundant supply of dead insects was kept available. The species which expressed such scavenging behavior were: *Pachybrachius basalis, Pseudocnemodus canadensis, Cryphula trimaculata, Ozophora picturata, Stygnocoris pedestris,* and *Eremocoris ferus.* It should again be emphasized that these insects made no attempt to attack live prey, nor did they feed on the eggs of other rhyparochromines.

SYMBIONTS

It has been known since the early work of Glasgow (1914) that the phytophagous Heteroptera of the group Trichophora, including pentatomoid, lygaeoid, and coreoid families, all have bacterial caecae or mycetomes connected to or associated with the posterior or fourth part of the mid-intestine. Other heteropterous families may have different types of mycetomes. This subject including the transmission of the symbionts has been reviewed by Carayon (1952).

In some Pentatomidae the symbionts are smeared on the surface of eggs and the new hatched nymphs become contaminated by feeding on this after hatching. In others, as shown by Glasgow (1914), the infection occurs in the embryo. Among the Rhyparochrominae there does not appear to be any work upon the transmission but in other lygaeids as *Ischnodemus sabuleti* Fallen and *Nysius* spp. (Schneider 1940) the infection occurs within the egg before shell formation.

In no instance when hatching was observed were the new nymphs ever observed to feed on the surface of the egg shell. Detailed work on this important biological subject was considered beyond the scope of the present study. Nevertheless all the rhyparochromines in the present study had the fingerlike groups of bacterial caeca as described by Glasgow (1914). As he indicated, but never carried through, the caeca configurations are species-specific and each species is inhabited by bacteria which are apparently host specific (at least in form). Clearly, a careful study of the anatomy of the caecae, the types and relation of the bacteria to the host, and the methods of transmission should prove of great value in elucidating evolutionary patterns among the Lygaeidae, and of course, in other families.

As indicated by Glasgow (1914), the presence of the caeca are somehow related (in the Pentatomomorpha) to a phytophagous feeding habit, as the predacious species lack them. Slater and Carayon (1963) have shown that the presence of bacteria is unstable in the predacious rhyparochromine *Mizaldus*.

Economic Importance

While it is true that very few (none in New England) of the rhyparochromines are economic pests, these insects may be of some economic importance as beneficial insects, especially those species adapted to field and garden habitats. It follows from their frequent high populations, ground level biotope, and seed feeding habit that these insects must be an important ecological factor in the destruction of fallen seeds and fill an important niche in the natural biota. This destruction would result not only from feeding but in piercing the seed coat, for probably fungal pathogens such as *Fusarium* and *Pythium* may more readily gain entrance. Moreover seeds deeply planted as in conventional agriculture would not be disturbed, while weed seeds on the surface of the ground would be susceptible to the ground living seed bugs. Thus for the most part such seed feeding would be beneficial.

Behavior

Seed Defense

Many of the rhyparochromines exhibited remarkable behavior patterns relating to seeds. It was in the observation of this behavior that the function of the fore-femora became evident. Only under what would be called dirty culture conditions could this repertoire be expressed, and sometimes only over certain seeds and when the bugs were allowed to become hungry.

This behavior was displayed in essentially two ways. In the first, and this appears to be common to all Rhyparochrominae, the seeds are dragged or moved from exposed open sites into protected sites. This is very likely a thigmotactic response, the insects responding positively to contact with the substrate around them. Perhaps the function of the long abdominal and head trichobothria is to sense such contact, much after the analogous example of a mouse's vibrissae. Tullgren (1918) thought these hairs may be auditory organs, but so far no evidence is at hand for such a function. A thigmotactic function is consistent with modern concepts of orientation in arthropods (Fraenkel and Gunn 1940, Carthy 1958).

This behavior was long ago noted in *Elasmolomus sordidus* by

Maxwell-Lefroy (1909) who wrote, it has "been found to infect threshing floors and to carry off the wheat grains to the margins of the floor and hide them. What nourishment they can extract from a dry wheat grain seems doubtful, unless their salivary excretion has solvent powers, but they carry off the grain so abundantly that the cultivators require to collect them again every morning." Ashlock (1958) observed one individual of *Ligyrocoris latimarginatus* to pick up a seed between its fore legs and run with it. In clean cultures such a use of the fore legs was never observed. The insects would sense a seed, feed on it for a variable period, and then drag the seed by the labium, if large, or suspend it under the body affixed to the labium, if small, and carry it to shelter. But if the culture was full of litter and obstacles, the fore legs were clearly observed to aid in moving the larger seeds. The fore legs were placed over the seed and the seed was lifted over the obstacle. From the diverse and varied shapes and sizes of fore femora in the Lygaeidae, such a tool-like function may have been expected. But in no case was the seed observed actually being carried in this position.

The second behavior response is one of direct defense. This frequently approaches a territorial sort of behavior, and is such at least in *Pachybrachius bilobatus.* Only in certain species was such an extreme intraspecific competition behavior seen, although it may perhaps be elicited in all species under the proper conditions. In its most simple form as seen in most species, the seed is kept out of the aggressor's reach by the defender keeping himself between the seed and the aggressor. The several successive stages of seed defense behavior are as follows: a vigorous wagging of the antennae as in *Eremocoris* and *Drymus;* then, a defense dash at the aggressor; and a clash with wildly flailing legs and antennae as in *Ligyrocoris diffusus* and *Scolopostethus diffidens;* finally the defense behavior reaches its highest expression in *Pachybrachius* when the fore femora are spread stiffly and the two, the aggressor and the defender, stand upright with antennae and legs flailing. This final behavior pattern was only observed in *Pachybrachius basalis, P. bilobatus,* and (?) *Sisamnes contractus* (Dist.) (= *Exptochiomera antennata* V. D.). In *P. bilobatus* the seed defense or territoriality is involved in sexual behavior, and the males which are considerably larger than the females defend the seeds from other males.

It is significant that the species which display this defense behavior most vigorously are also those species which frequently exist in high local abundances in the natural habitat. These behavior patterns may play an important role in intraspecific and interspecific competition.

A remarkable aspect is the ability of the rhyparochromines to relocate a particular seed after a defense display. The behavior patterns are described in detail under the individual species.

Mating Behavior

The individual species accounts should be consulted for details but, several basic mating behavior types are present: (1) Those which involve a shaking dance by the male. In these species there is a stridulitrum (c.f. Ashlock and Lattin 1963) on the abdomen and a plectrum on the hind femora: *Ligyrocoris* spp., *Sphaerobius insignis, Zeridoneus costalis.* (2) Male employs a fore femora activity, (stridulation?) and vibrating antennae: *Pseudocnemodus canadensis.* (3) The male recognizes the female before contact, and leaps suddenly on her: *Stygnocoris* species, *Sphragisticus nebulosus, Megalonotus chiragrus,* and *Plinthisus americanus.* (4) The male vibrates the antennae rapidly near the female and climbs upon her deliberately: *Pachybrachius basalis, P. albocinctus, Myodocha serripes, Heraeus plebejus,* and most other species. The known species which employ the dance and stridulating behavior are all long legged myodochines of open habitats.

Cleaning Behavior

Another interesting behavior pattern involves cleaning behavior. This is readily elicited by shaking the bugs with debris, but also occurs frequently after feeding. First the labium is pulled through the fore tibial cleaning brushes, and then the antennae are similarly cleaned. Second, the fore tibia are rubbed together, and then one of the tibial brushes is brushed against the maxillary plate (lorum), and the first labial segment. With each fore tibial stroke the labium is partly opened. Thereafter the fore tibia are rubbed against the mesotibia and the meso- upon the metatibia. The metatibia and tarsi are next rubbed against the sides of the abdomen, and frequently with each other. Often at this point the genitalia are groomed. Frequently this sequence is repeated rapidly on each side always beginning with several strokes against this particular site on the base of the labium. This grooming behavior has been observed in second to fifth instar lygaeids as well as in the adults.

Parsons (1958) has summarized the literature on the presence of large cephalic glands in water bugs and described a similar gland in *Gelastocoris.* These glands have been found in the pyrrhocorids *Dysdercus* (Macgill 1947), *Pyrrhocoris* (Bugion and Popoff); and the lygaeids, *Oncopeltus* (Linder and Anderson 1955), and *Mizaldus, Ischnodemus* and *Dimorphopterus* (Slater and Carayon 1963).

Except in *Gelastocoris* (Parsons 1958) the glands in aquatic Heteroptera and *Pyrrhocoris* open on the margin of the maxillary plates at the base of the labium or at the labium. In the lygaeids, *Oncopeltus* and *Mizaldus,* the orifices of the glands open in the preoral cavity. I have found similar glands in several other rhyparochromines.

According to Parsons (1958) three functions have been suggested for these glands: (1) subduing prey; (2) defense against predators; or, (3) excretory organs. The last was shown to be untenable and in *Gelastocoris,* the posterior position of the glands made unlikely any poisonous action. Slater and Carayon suggested that the glands in *Mizaldus* secreted a toxic substance that paralyses the prey.

Both *Dysdercus* and *Oncopeltus* exhibit the same sort of cleaning and grooming behavior seen in the rhyparochromines, and repeatedly stroke their fore tibia against the maxillary plate-labial segment one region.

It is here suggested that the secretion of the cephalic gland is spread over the body during the grooming process. It would be most interesting to ascertain the exact role of this secretion. Perhaps the secretion has a species-specific odor which has a role in sexual and aggregational activities.

Nymphal Development and Reproduction

In this section are considered the essentially developmental and reproductive aspects of the life history. All the New England species are oviparous. Carayon (1961), however, has found that the African rhyparochromine *Stilbocoris* is ovoviviparous.

Nymphal Instars

As in other Heteroptera (Southwood and Leston 1959, Weber 1930) all the species have five distinct instars and none have the exceptional four instars associated with prothetely as in *Dolichonabis limbatus* (Dahl.) (Southwood 1961b). The instars may readily be distinguished by the relative development of the wing pad (Gulde 1919, Slater 1951, Putshkov 1958, Southwood and Scudder 1956). As Slater (1951) indicated, the first and second instars are frequently difficult to distinguish. The difference in length of the meso- and metathoracic segments used by Southwood and Leston (1959) is often difficult to ascertain and is not invariable (Putshkov 1956). In many rhyparochromines especially those of the tribes Myodochini and Ozophorini, the first and second instars undergo a striking change in color. Moreover the Y-suture is always absent in the first instar. In *Eremocoris ferus, Scoloposte-*

thus atlanticus, and *Malezonotus fuscosus* the first instars have pale terminal antennal segments.

The changes in color in Palearctic lygaeid species during the nymphal ontogeny are summarized by Putshkov (1956). The color patterns have already been alluded to under protective coloration, and only the ontogenetic changes are considered here. According to Putshkov most of the species of the other subfamilies differ from the Rhyparochrominae (except *Emblethis* and *Gonianotus*) in that the body is generally pale colored and the basic color pattern appears in the second instar. In the Rhyparochrominae with the exception of *Emblethis* and *Gonianotus* the nymphs are either dark or contrastingly colored with the head and thorax dark, the abdomen light. Putshkov distinguished four types of color changes each beginning with a red or pink first instar nymph. These four groups are largely adaptable to the New England fauna especially in genera also present in the Palearctic. A fifth type distinguished by Putshkov includes species with a pale band on abdominal segment one to three in the first instar. This band gradually disappears in later instars. Only *Megalonotus* and *Sphragisticus* show this color pattern in New England. For most of the Myodochini and the known Ozophorini a sixth type must be noted. In this type the first instar is pale yellow with a narrow red band across segment four. In the second instar there is an abrupt color change. This includes all the New England Myodochini except *Perigenes* which has a dark red first instar and *Kolonetrus* which is unique with an entirely pale yellow abdomen.

Into Putshkov's four types the other New England genera fit as follows: (1) Coloration remains nearly unchanged through nymphal development: *Xestocoris, Plinthisus, Antillocoris, Drymus, Stygnocoris.* (2) Coloration becomes more complex but not black: *Cryphula, Peritrechus, Scolopostethus, Eremocoris, Perigenes.* (3) Coloration becomes lighter—no Nearctic rhyparochromine fits here except perhaps some specimens of *Drymus.* (4) Coloration becomes a deep black although the subcuticular layer remains red. These lack the Y-suture and include the megalonotines *Megalonotus* and *Sphragisticus* as well as the gonianotines *Malezonotus, Delochilocoris,* and *Trapezonotus.*

As summarized by Putshkov there are very few structural changes during development in the Lygaeidae, each instar differing mostly in allometric changes in head size and appendage length, the head decreasing in relative size, and the appendages increasing in length, but to a variable extent, resulting in long legged and short legged genera. There is often an increase in pilosity and on the head there is frequently an increase in major setae. However, in the first instar, much as in lepidopterous larvae (Fracker 1915) only the primary long setae (head trichobothria) are present like the abdominal trichobothria. Aside from the Y-suture appearing in the second instars and the appearance of a vestigial scent gland plate between segment three and four in *Antillocoris,* the various structures remain largely unchanged in nymphal ontogeny. The spiracles and trichobothria and sutures are much as they are in the adult. The known lygaeid nymphs are distinctive, compared to the Coreidae and Pentatomidae, in that their generalized smooth abdominal cuticle nearly always (except Malcinae) lacks spines and protuberances and rarely has punctures (Putshkov 1956), never in the Rhyparochrominae.

Nymphal Development

The details of the development periods are discussed under the individual species. There is no obvious relationship of development rate to size, the minute species of *Antillocoris* only 2 mm. long takes approximately five weeks to reach maturity, a period much longer than that of the large species of the *Ligyrocoris* group or the largest rhyparochromines in New England *Perigenes* and *Cnemodus* which are 8 to 9 mm. long.

In general, as indicated under the seasonal cycle discussion, the development rates show adaptations to the habitat type and the type of seasonal cycles.

The relation to temperature is only partial. Forest species develop fairly slowly in the egg state, but in the laboratory and during nymphal development in the field, growth proceeds rapidly. Xerothermic species like *Carpilis* and *Xestocoris* develop slowly while the cool adapted *Eremocoris* develops rapidly both in the field and laboratory.

Species adapted to diversified forb habitats with a large seed production (these are all short lived subclimax habitats) have rapid life cycles which take only about three or four weeks and such species usually have bivoltine seasonal cycles. On the other hand species of habitats with low productivity, that is, the sparse open barren old sites, develop more slowly as do *Carpilis* and *Xestocoris* and are univoltine. These development patterns hold under laboratory conditions of similar food and temperature, are not related to size, and so indicate a genetic difference.

Reproduction

A similar relationship is apparently present in the reproductive capacities as measured by oviposition capacity in the laboratory. However data on this aspect must always be treated with some skepticism because of the close control that seed feeding holds over egg production (See Feeding Habits). In the natural habitat, given this physiological mechanism, egg production would be controlled by the availability of seed food. However *r*, the intrinsic rate of increase or the reproductive rate (Andrewartha and Birch 1954) under optimum conditions is fairly high as shown by Putshkov and Putshkova (1956) rather than low, in the order of a few tens of eggs as thought by Thomas (1955). Thomas' data, as indicated under feeding habits, is readily replicated by transferring these insects from seeds to foliage diet. Indeed the egg production figures given by Putshkov and Putshkova (1956) appear a little low (55–85), but as the authors state, this may result from the short term study in the rearing cages.

Nevertheless laboratory fecundity cannot be assumed in the field, where not only food availability (Johannson 1958b), but incidence of feeding, weather, predation and the like would adversely affect fecundity. Density factors may be involved (Watt 1962) and this was apparent in *P. bilobatus* (see in Species Discussions). It was repeatedly observed that the total number of eggs laid per female in mass culture was much less than the fecundity found in individual rearings.

Nevertheless, if these uncertainties are assumed to cancel out, insofar as species differences are concerned, there were distinct differences in the reproductive rates among the species. In general the rapid developing species of temporary habitats had higher oviposition rates than slow developing species of permanent habitats. However the relation also seems to partly involve size (as expressed by length), the larger species laying a larger number of eggs.

Among the larger myodochines (over 4 mm. long) the mean oviposition rate in the laboratory was 168 to 273 eggs, while the smaller species (under 4 mm.) averaged 70 to 130 eggs, and the rate per day was 6–7 eggs as compared with 3–4 eggs a day in the smaller species. However the smaller species are usually adapted to habitats with low productivity. Similarly the three gonianotines *Trapezonotus, Malezonotus,* and *Delochilocoris* averaged 3–4 eggs a day, and at least the first two are characteristic of sparse habitats. But *Drymus unus* and *Pachybrachius basalis* which are close to the above in size were found to lay a mean of 150 and 170 eggs each and each inhabit seed-rich habitats, the former in permanent woodland habitats, the other in temporary habitats.

Several other factors influence egg productivity. When the virgin females are sexually isolated in most species their egg productivity is greatly reduced. The sole exception is *Heraeus plebe-*

jus which would lay eggs freely whether mated or not. Among the species two conditions may be distinguished. In the first no eggs whatever were laid. These species include *Pachybrachius basalis, P. albocinctus, Cnemodus mavortius, Sphaerobius insignis, Perigenes constrictus, Plinthisus americanus, Xestocoris nitens, Antillocoris minutus, A. pilosulus, Drymus unus, Delochilocoris umbrosus, Malezonotus fuscosus, Emblethis* and perhaps the two species of *Stygnocoris.* Among the remaining species from none to a few eggs were laid by sexually isolated females. These species include *Myodocha serripes, Ligyrocoris diffusus, L. depictus,* and *L. caricis, Zeridoneus costalis, Sisamnes clavigera, Carpilis consimilis, Cryphula trimaculata, Ozophora picturata, Peritrechus fraternus, Trapezonotus arenarius, Scolopostethus thomsoni, S. diffidens, Eremocoris ferus,* and *Megalonotus chiragrus.*

Logically, such oviposition control would be of considerable adaptive significance, for it would conserve resources and prevent the metabolic waste of unfertilized eggs. In correlation the virgin females lived a much longer time than the fertilized ovipositing females. For example in *Myodocha serripes* a virgin female lived for over a year while the normal adult life span is about 5 weeks. (See species discussions for further examples.)

Another important factor is the availability of an appropriate substrate for oviposition. In many species such as in *Ligyrocoris diffusus,. Pseudocnemodus canadensis,* and *Emblethis vicarius* the egg production is sharply decreased if it is not provided with a methyl cellulose, cotton or soil substrate for oviposition.

Eggs and Oviposition

Southwood (1956) summarized the knowledge of the eggs of the terrestrial Heteroptera and discussed the phylogenetic significance of the different egg types. Like Pentatomomorpha eggs in general, the eggs of the Lygaeidae lack a true operculum and have an anterior ring of micropylar processes which serves for both sperm passage and air exchange. An egg-burster is always present. This is a small spine surrounded by a chitinized area on the embryonic vertex. The egg burster is inconspicuous in the Lygaeidae and best seen on the shed embryonic cuticle. The Lygaeoidea, with the exception of the Cleradini (sensu Stål) (Sweet, unpublished), never have a true pseudoperculum as in the Pentatomidae, although this condition is approached in *Piesma* (Southwood 1956, Putshkova 1956).

Corby (1947) and Putshkova (1956) have described a thin polygonal area on the anterior end of the egg within the ring of micropylar processes. Each side of the polygon corresponds to a micropylar process and the cleavage of the eclosion rupture begins at the grooves which extend from each corner of the polygon. A micropylar process may be absent but the side of the polygon remains. Putshkova (1956) found that the cleavage pattern corresponds to the various egg types. Eggs with rounded anterior ends usually split laterally along one or two sides and the cleavage curves ventrally. In eggs with flattened anterior ends, the cleavages may radiate from all the grooves to the central polygon. The exact type of cleavage or bursting is species specific (Putshkova 1956) and although there may be some variation, especially in lygaeoid type eggs, it is however not entirely correct to state that the chorion splits irregularly at ecdysis (Andre 1934, Southwood 1956).

In most species, the micropylar processes show a considerable variation in number except in most of those species with four micropylar processes. The number of processes varies from 3 to 12 in the known Rhyparochrominae and are always located close together in a ring. It would appear from the variation of 5 to 9 in some species that the number of sides in the central polygon also varies.

As in the eggs of *Myrmus miriformis* Fallen (Woodward 1952), egg development was in all cases apparently independent of free water absorption. However, in a dry atmosphere, the eggs, especially those eggs which diapause, may desiccate, and at least a humid atmosphere was frequently necessary to prevent such dessication. The eggs of different species varied in their resistance to drying. This difference was frequently expressed in the moistness of the preferred oviposition substrate. In the normal ground level biotope, the favorable microclimatic condition of humid still air and reduced evaporation rate prevents undue dessication (Southwood 1956). Similar conditions exist in a closed petri dish as the humidity is high but free moisture is lacking. No water uptake was observed in semidesiccated eggs placed on a moist substrate.

The process of development and hatching is much as described by Southwood (1956). Lygaeid egg chorions are transparent and particularly convenient for observing their development. Southwood (1956) and Corby (1947) noted that the embryonic cuticle actually represents the first true instar. However, in this paper, the first instar refers to the first actively moving or normal instar. The embryonic cuticle in all cases was shed after complete emergence from the egg. The posterior apex of the embryonic cuticle sticks usually to the edge of the cleavage in the egg shell, or to the substrate a short distance away from the egg.

Putshkova (1956) has studied in detail the eggs of Palearctic Lygaeidae and constructed a key based upon egg types and oviposition. In a later contribution, I hope to present a similar and complementary study of the Nearctic lygaeid eggs. I wish to discuss here only those aspects which may pertain to the ecology of the various species.

Putshkova (1956) found lygaeid eggs to be quite diverse in form and she distinguished six types of eggs, four of which were also applicable to other heteropteran families. These types were named: lygaeoid, aphanoid, oxycarenoid, piesmoid, berytoid, and macroparoid eggs. Kullenberg (1944) could find no systematic meaning in the egg types of the Miridae and considered the differences present to represent specific adaptations to the site and manner of oviposition. While some similar adaptability is shown among the Lygaeidae, Putshkova's egg types appear to have some systematic significance but not at the high level of significance suggested by Reuter (1910) for egg types. All the aphanoid type eggs were found only among the Rhyparochrominae, and in none of the other lygaeid subfamilies was this particular type of egg found.

On the other hand, a few rhyparochromine species have eggs whose forms place them in certain other categories (Putshkova 1956). Among the New England Rhyparochrominae only two of Putshkova's egg types were distinguished, the aphanoid and piesmoid. The aphanoid eggs are elongate-cylindrical and one side, the ventral, is flattened or concave, the opposite side, convex. Most are roughly "cucumber-shaped". The piesmoid type eggs are elongate with the anterior end flattened and the posterior end somewhat pointed. Putshkova, however, states that rhyparochromine eggs really only approach the piesmoid type. This type is illustrated by Southwood (1956). Actually these two types were not precisely exclusive, as some aphanoid eggs approach the piesmoid type. Moreover, the aphanoid eggs differ considerably and can be further subdivided. Both types are basically similar with the similar micropylar processes grouped relatively close together on top of the egg and have the venter concave. Putshkova classified several rhyparochromines as having lygaeoid type eggs, but at least in the case of *Sphragisticus,* the eggs I examined had a definite ventral curvature which is thicker in the middle and could not be clearly distinguished from the aphanoid type egg. The lygaeoid type, I think, should be limited to the oval almost football shaped egg with a wide circle of many micropylar processes. This distinctive egg type is characteristic of the subfamily Lygaeinae *sensu stricto.* Putshkova places the eggs of *Gastrodes* among the berytinoid type eggs. This type has longitudinal ribs along the side, but the anterior end is not flattened.

We may distinguish the following types of eggs among the New England Rhyparochrominae.

Piesmoid type eggs

Group one.—eggs with the anterior end strongly flattened, so that a marginal rim appears to be present. These eggs have a smooth chorion which is fluted: *Plinthisus americanus, Carpilis consimilis, Ptochiomera nodosa, Sisamnes clavigera.* The eggs of *Ischnocoris* and *Acompus* are also of this type.

Group two.—eggs with the anterior end flattened but a distinct rim is not evident: *Peritrechus fraternus, Pachybrachius basalis, Kolenetrus plenus, Ligyrocoris caricis.* Putshkova found *Peritrechus nubilis* and *geniculatus* to be of this type but not *P. sylvestris.*

Aphanoid type eggs

Group one.—eggs without setules. Eggs of this group vary from being quite short to rather elongate. The shorter ones are thickly cylindrical and show only a slight curvature. They are listed from relatively shorter to longer as follows: *Xestocoris nitens, Cryphula trimaculata, Antillocoris minutus, Stygnocoris rusticus* and *S. pedestris, Eremocoris ferus, Scolopostethus thomsoni, S. diffidens, S. atlanticus, Sphragisticus nebulosus, Heraeus plebejus, Pachybrachius albocinctus, Myodocha serripes, Cnemodus mavortius.*

Group two.—eggs covered with chorion setules or ''nap''. This chorionic investiture varies from sparse to thick and dense: *Ligyrocoris depictus, L. diffusus, L. sylvestris, Sphaerobius insignis* Uhler, *Zeridoneus costalis, Perigenes constrictus, Pseudocnemodus canadensis, Ozophora picturata, Megalonotus chiragrus* (this genus has remarkable ''tack-like'' processes), *Trapezonotus arenarius, Delochilocoris umbrosus, Malezonotus fuscosus, Emblethis vicarius, Drymus unus,* and *D. crassus.*

SYSTEMATIC RELATIONSHIPS

There is a diversity of egg types among the Myodochini, the largest tribe. The only similarity is the relatively elongated shape of their eggs. In contrast, the Lethaeini, Antillocorini, Stygnocorini, and in general, the Drymini, all have eggs proportionally shorter than the Myodochini eggs. All Gonianotini have setulose eggs.

These similarities are in large part related to the oviposition habitats of the species and may reflect common adaptive similarities. This is especially true of the setulose investiture. While our two species of *Drymus* resemble the Palearctic *D. brunneus* in having setulose eggs, *D. sylvestris* has perfectly smooth eggs. Moreover, *D. brunneus* belongs to the same subgenus as *sylvestris* (*Sylvadrymus*) while our species represent *Drymus sensu stricto.* While all our species of *Scolopostethus* have smooth chorions like the Palearctic *S. pilosulus* and *S. lethierryi* Jak., *S. affinis* Schill. and *S. decoratus* Hahn have setulose eggs. *Eremocoris podagricus* also has setulose eggs while those of our *E. ferus* are smooth. A similar situation is found in the eggs of *Peritrechus* and *Rhyparochromus* (= *Raglius*) (Putshkova 1956). The piesmoid type reappears independently in the Myodochini, Rhyparochromini, Stygnocorini, and Drymini.

OVIPOSITION SITES

As described by Putshkov (1956) most of the Lygaeidae and all the Rhyparochrominae lay their eggs singly although a small pile of eggs is sometimes formed in some species. Only *Heterogaster* always lays a mass of eggs which are cemented together with a copious secretion (Putshkov 1956).

When selecting a place for oviposition, the females investigate a site with the antennae, sometimes the labium, and subsequently carefully and repeatedly probe it with the ovipositor. These insects possess a remarkable and delicate control over the movements of the ovipositor and can work it into various kinds of substrates and crevices. In soft material the apex of the abdomen may be submerged during oviposition. It is noteworthy that the apex of the ovipositor has a series of erect stiff hairs and the repeated probing and pushing probably represent trials toward stimulating these sensory hairs equally. The actual process of oviposition lasts at least several minutes.

The type of substrate preferred by the different species corresponds in large part to the oviposition behavior and egg type. Southwood (1956) classified the oviposition types in the Heteroptera into four loose categories and criticized Michalk's (1935a) over-rigid ten categories. All rhyparochromine egg sites fall into Southwood's category of semi-exposed egg sites "e.g., in the soil, under rocks, amongst fallen leaves, in axils of stems. . . ." The soft lygaeid ovipositor precludes oviposition into plant material (Putshkova 1956), but allows a definite placement of eggs into crevices, surface pilosities, soil, and even into rather tight substrates. Butler (1923) was then incorrect in referring to the lygaeid ovipositor as being "saw-like" with the single known exception of *Ischnodemus sabuleti* Fallen.

According to Putshkova some species do not attach their eggs to the substratum but lay them free or at random. The chorion is usually smooth and the eggs fall readily into fissures between bits of litter and the ground. On the other hand, eggs which are covered with different kinds of nap, or chorionic investiture are frequently laid on pubescent, hairy or similar substrates. However, as Putshkova notes, in some species the smooth eggs are laid in different fashions.

The elongate piesmoid eggs with pointed apices and flattened anterior ends, were usually laid into firm substrates, either into wet or dry litter. These eggs were frequently forced into the tight cotton stoppers of the water vials (*Pachybrachius basalis, Carpilis consimilis, Peritrechus fraternus, Ligyrocoris caricis*). In the other species the eggs were laid into the parenchyma of plant stems or narrow grass culms, or otherwise into cotton stoppers or loose litter. The elongate egg form would appear to facilitate oviposition in firm substrates. However, the thicker aphanoid eggs of *Sphragisticus nebulosus* are similarly laid. The slighter egg curvature of *Sphragisticus* may correspond to its habit of laying eggs into the parenchyma of fallen herb stems (Putshkova 1956). *Plinthisus* oviposits into the tight crevices of hemlock and spruce litter, frequently placing the eggs into hollow needles. The eggs of *Sisamnes* also stick by a cement layer to the substrate in which they are laid.

The other species which lay smooth, but aphanoid eggs fall into three groups. The first are those which oviposit directly into loose litter and lay eggs which are free and sift readily into crevices. These include the short, thick eggs of *Cryphula, Xestocoris, Antillocoris, Eremocoris,* and *Scolopostethus.* The latter three are woodland species which preferably lay their eggs in moist litter, or, in the laboratory on loose cotton. The eggs of *Scolopostethus,* as shown by Putshkov have leathery egg shells which give readily on slight pressure, in contrast to brittle chorion typical of the other species.

The second group includes those which lay eggs with a considerable cement layer, and the eggs are stuck to the litter or soil of the oviposition site and to each other. These include the eggs of *Stygnocoris* which also are diapause eggs. Since all heteropteran eggs are apparently laid with a cement layer from the accessory glands (Southwood 1956), it appears that the cement coating must differ considerably among the different species. The eggs of these latter two groups, if no substrate is available, are laid ''at random''.

The species of the third group lay their eggs into the ground or into tight crevices and the eggs are relatively elongate. These are all myodochines and include *Pachybrachius albocinctus, Myodocha serripes, Heraeus plebejus,* and *Cnemodus mavortius.* The first three species prefer a fairly moist substrate for oviposition.

All the eggs which have "nap" are laid and affixed upon definite substrata. These eggs are all aphanoid in contrast to the piesmoid egg *per se* (of *Piesma*) which also have a nap-like surface and are laid upon leaf epidermis. As mentioned, the rhyparochromine piesmoid eggs are laid into tight crevices or into soft parenchyma. All the setulose surfaced eggs stick tightly to the substrate, but the sticking appears to be accomplished more by the cement layer, and the setulose surface apparently prevents ready dislodging, especially on a fibrous substrate as on plant fuzz or pilosity. The setulose surface probably abets sticking to a rough surface as to sand grains. While there is a broad behavioral overlap there are different oviposition preferences among the species. These oviposition sites may be classified into three general categories: (1) on plant fuzz or crevices, and (2) in loose fine litter on ground, and (3) under small surface objects. Accepting a considerable plasticity within a species, species may be classified by their preferred oviposition sites. Because of this plasticity the preferential of a few of the species might be misinterpreted.

The species which prefer to lay their eggs in crevices or plant fuzz may also lay their eggs shallowly in the soil but rarely lay their eggs deeply into the ground. Frequently the eggs of this group are laid near or on fallen seeds or seed capsules as Putshkova notes. These include *Malezonotus fuscosus, Delochilocoris umbrosus, Pseudocnemodus canadensis,* and frequently the summer generation eggs of *Ligyrocoris diffusus, Zeridoneus costalis,* and *Perigenes constrictus. Ozophora picturata, Drymus unus,* and *D. crassus* lay their eggs in crevices in leaf mold but could be placed as readily in the second type. The eggs of *Drymus* species like *Stygnocoris* have a heavy cement coat and are frequently found stuck together in a group of two or three eggs.

The second type of site, ground deposition, actually would include all the species, since both of the other types frequently overlap this type. However, certain species especially manifest this habit and lay their eggs quite deeply in loose soil. In the laboratory these species especially prefer to lay their eggs into deep mounds of dry cotton or methyl cellulose. In ovipositing, species of this group commonly oviposit in a vertical position with spread legs, and also often work the apex of the abdomen into loose soil as well. These species include *Ligyrocoris diffusus, L. depictus,* and *L. sylvestris, Zeridoneus costalis, Sphaerobius insignis, Perigenes constrictus,* and *Emblethis vicarius.*

The third type are those which lay their eggs preferably under small objects. These species show little inclination to lay their eggs into cotton or methyl cellulose, and never deeply, and more frequently will lay their eggs in narrow crevices or in plant fuzz. These species are readily recognized for they predominantly lay their eggs directly backward with the body horizontal, and show very little vertical displacement. These species include: *Trapezonotus arenarius, Megalonotus chiragrus* and frequently also *Malezonotus* and *Delochilocoris.*

In no case was a hole observed dug into the sand for oviposition as Weber (1930) illustrates for *Rhyparochromus pini* (L.). Nor were the fore legs ever observed being used to help dig such a hole as he suggested. Southwood and Leston (1959) also note that this species lays its eggs deeply.

While *Drymus* spp. and *L. sylvestris* lay their eggs in mesic or moist sites, all the other species with setulose eggs are typical inhabitants of drier locations where the exact egg placement and lodgement may be important in ensuring proper microclimatic conditions for development. This general relationship is also true of the Palearctic species as was shown by a comparison of Putshkova's egg descriptions with the ecological data of Penth (1954) and Southwood and Leston (1959).

The eggs of this type, especially of *Emblethis, Sphaerobius,* and *Malezonotus,* when laid in the soil, become densely covered with sand grains and litter which makes the eggs difficult to locate in the cultures. It would be most interesting to compare the oviposition habits with egg parasitism which undoubtedly occurs. It would seem that the thick layer of attached sand grains and deep oviposition of individually laid eggs should lower the parasitism rate.

It would appear then, from the different types of oviposition sites and also from the large percentage which diapause (see Seasonal Cycles), that such adaptations should result in different reactions of the species to weather vicissitudes and perhaps, to parasite and predation pressures.

Competition

Now that a general review of the biology of the New England Rhyparochrominae has been completed, the ecological relationships among the species may be considered. It was mentioned earlier that frequently there were characteristic assemblages of rhyparochromine species. Since each of these species is apparently oligophagous on seeds it would appear that these species assemblages are living together in the same functional niche in the same ground level biotope. The standard question which then presents itself is are these species really in the same niche and in direct competition? It should be kept in mind that the following discussion is largely exploratory as a great deal of quantitative data and careful study is required to approach an accurate understanding of competition.

The question of competition is of course an important one, one which forms a major foundation of evolutionary theory (Darwin 1859, Crombie 1947), of modern systematic thinking on speciation (Mayr 1942, Lack 1947, Brown and Wilson 1956), as well as a fundamental ecological concept (Gause 1934, Hutchison and Deevy 1949, Allee *et al.* 1949, Hardin 1960). Recently the concept has been attacked by Andrewartha and Birch (1954) and some phases are presently in a state of flux (Slobodkin 1961, Klopfer 1962) although the basic principles and implications of competition as laid out by Darwin (1859) are entirely valid (Kendeigh 1961). Much of the controversy has revolved around the basic unit of thought upon competition, the niche. Since these considerations are basic to any interpretation of the biology and ecology of a taxon (Lack 1944), it is apropos to the present discussion to review the concepts involved.

THE NICHE

When originally proposed independently by Grinnell (1917, 1924, 1928) and Elton (1927) the concept of the niche was given similar but distinctly different meanings (Clarke 1954). Grinnell conceived of it as a habitat niche, a discrete spatial and distributional unit occupied by a species, and to which the species was held by structural and instinctive factors. Elton defined it more in terms of an animal's position in a trophic hierarchy, or its functional place in a community. The common European use of the word biotope corresponds very closely to the spatial aspect of Grinnell's concept, and forms the unit equivalent of a species in a habitat analysis (Hesse, Allee and Schmidt 1951). Elton's definition along with the instinctive and structural aspects forms the ecological niche or the present functional role concept of the niche.

From this original structuring of space and function, the niche has been interpreted in terms of competition (Gause 1934) which led to the formulation of Gause's Law which stated that two species with the same ecology cannot persist in the same region, i.e., no two species can occupy the same niche. Although applicable to many species this concept has presented some difficulties when applied to several natural situations (Ross 1957, 1962) perhaps because of the then-prevailing concept of the niche. This has led to an operational definition in which an ''ecological niche or space is that space which no two species can continue to occupy for an indefinitely long period of time'' (Slobodkin 1961). Slobodkin further stated "if two species persist in a particular region it can be taken as axiomatic that some ecological distinction must exist between them, and that their ecological niches, in the restricted sense, do not coincide." Thus Hardin (1960) could erect this concept into an exclusion principle based on competition.

This concept, and especially that of competition, has been sharply attacked (Andrewartha and Birch 1954, Birch 1957 and Andrewartha 1961) as not applicable to ordinary "rare" species or in large areas which regularly suffer great ecological changes.

Moreover the size of the niche has become disconcertingly small in many situations. Hutchison (1959) reviewed the size ratio of trophic characters in ecologically overlapping species and obtained the ratio of 1.2 to 1.4 which he explained as an example of character displacement in feeding habits. However Klopfer and McArthur (1961) found that in some tropical mixed flocks of birds, the ratio was actually unity between some species. This they explained as resulting from extremely stereotyped behavior patterns. Park (1954) showed that only a small difference in environment adaptation to temperature and humidity separated two species of tenebrionids. Andrewartha (1961) called attention to the remarkably long time of 6 months to several years for the competition between the beetles to come to completion, and considered the situation impossible in nature with insects of one generation a year in an extremely variable climate. Ross (1957) cited the example of six *Erythroneura* leaf hoppers on the same host plant and explained this situation (1962) on the basis of different microclimatic optima within the context of seasonally and locally variable weather conditions. These conditions produced an ecological oscillation among the species as the first one and then another is favored. In this context, then, the exclusive niche may be the small difference in climatic optima between these species (Slobodkin 1961). This appears far from the trophic role of Elton's definition of the niche.

Indeed the competitive niche concept is applicable with difficulty to preclimax species especially those which invade a habitat only briefly and are termed by Hutchinson (1951, 1953) as "fugitive" species. Such niches if so defined would have a large open or escape aspect and competition can scarcely be understood in such a species (Slobodkin 1961). Slobodkin admits these difficulties and states, "It is true that some field situations are difficult to explain in such a way as to conform to the Gause axiom and that occasionally the explanations are quite frankly speculative. The abandonment of the Gause axiom however, is equivalent to abandoning the concept of competition, and competition is the only reasonable mechanism developed to explain the generally homeostatic properties of the natural world.''

It is not in the scope of the present paper to evaluate this controversy except to cite Watt's (1962) criticism of the tendency of ecologists to believe in *a priori* models without empirical testing. In such controversies, the reality usually lies between the semantic poles and is fairly complex (Allee *et al.*, pg. 729). For this reason the interpretation of Ross (1962) may present the most balanced judgement of niches and competition.

COMPETITIVE RELATIONS

In species of the same community Ross (1962) makes the standard ecological distinctions among exploitation, mutualism and coexistence, and among different trophic levels. However he distinguishes between direct and indirect competition for the same commodity. In direct competition the organisms feed side by side, simultaneously and in the same fashion on the same food. If some significant difference exists in the site, time or method of feeding, Ross considers this situation indirect competition, for these organisms, contrary to the common conception, do not avoid competition for potentially each species reduces the nutrition available to other species. This is a logical extension of the same reasoning which led Slobodkin (1961) to disagree with Hutchinson's concept (1957) that a nocturnal organism occupies an entirely different niche than its diurnal counterpart. Slobodkin reasoned that these species were actually in competition, i.e., in the same niche since each utilizes the same fixed energy source of which any depletion results in a diminished supply available to other competitors.

Competition then is indirect for the present purposes under the following conditions. (1) Host seed preferences differ even though there may be a complete overlap, (2) seasonal cycles distribute the feeding stages of different species in different periods of the year. For example, the orthopterans *Arphia sulphurea* and *A. xanthoptera* exist in similar habitats but the former overwinters as a nymph, and the latter as an egg. In different lygaeid species the time of oviposition and whether overwintering occurs as an egg or an adult is important. (3) Size differentials are usually cited, and may involve, among rhyparochromines, an ability to move and defend seeds or the ability to penetrate and feed on the seeds with their stylets.

Direct competition occurs when either of two conditions or maxims are met (Ross 1962): ''(1) If populations over the entire community range are at levels producing interspecific competition, coexistence will be possible only for species best adapted to some recurring variant of the ecological pattern of the community. (2)

If populations are habitually or locally below levels producing interspecific competition, any number of potentially but not actually competing species may coexist.''

Conceivably both of the above conditions can operate on a given population. The first situation has already been discussed in terms of unstable niches. The second situation is an important one upon which biological control is largely predicated (Glen 1954) in which a combination of inanimate environment resistance together with predation-parasite pressure reduces insect populations well below the carrying capacity of the nutrition available. This situation is characteristic of normal complex communities (Smith 1935, Glen 1954, Andrewartha and Birch 1954). It should be mentioned that along with standard predator-parasite-disease factors, host resistance in plants (Dethier 1947, 1954, Fraenkel 1959) is surely an important factor involved in the controlling of the insect populations.

In most situations the survival of a species requires adaptations to an inclement and variable climate which involves the seasonal cycle, diapause, cold hardiness, migration, and egg sites. There need also be adaptations to predators and parasites (Cott 1940, Klopfer 1962) which would include protective coloration and behavior, concealment habits, density patterns. Obviously such adaptations also influence the competitive relationship among different species. In this context, among the Rhyparochrominae the procryptic, warning (?) and ant mimicry coloration, repellent odors, and protective behavior takes on relevance, as do the seasonal cycle and brachyptery phenonema.

Since all of the above attributes strongly affect the competitive survival of a species, they should (Klopfer 1962) be considered as a component of the niche of a species and utilizable in analyzing an apparent niche that contains several species. Ross (1962) emphasizes that survival adaptions *per se* may be difficult to distinguish from the adaptations supposedly arising from niche segregation (Lack 1947). Brower L. (1958) suggests that many apparent host selections or ranges may instead represent behaviorial adaptations to predation pressure upon procryptic insects. Such adaptations would render predator learning more difficult in the mosaic distribution of the plant forming the background. Reasoning along similar lines Slobodkin (1961) suggests that conceivably several species could inhabitat the same (?) apparent niche if mutual survival is enhanced. It follows then that such a symbiotic-like arrangement could involve several species with different procryptic patterns or behavior, especially where the reproductive rate barely exceeds predator pressure so that food competition is low. This is analogous to the explanation given to polymorphic color patterns, especially in mimicry, in which predator learning is rendered more complex (Sheppard 1958).

The problem posed by the many rare species as emphasized by Darwin (1859) and Andrewartha (1961) are hardly treated by population workers and indeed are almost jocularly dismissed by Slobodkin (1961) as due to "exogenous" factors without explaining the limitations or acknowledging that many of these possible factors are not based on competition. Kendeigh (1961) suggested that the competitive niche concept can be extended to such organisms and others of densities lower than carrying capacity by postulating occasional high abundance levels when competition will then establish the niche restriction of the species along the lines suggested by Lack (1947). Obviously care must be taken in assessing abundance in relation to the niche size. No attempt is here made to compare the abundance levels of the different seed feeding rhyparochromines in different communities with the species abundance distribution formulae developed by McArthur (1957). While the rhyparochromines qualify as a uniform trophic level, it is better to take the entire seed feeding trophic level into consideration, if competition of this sort is to be considered.

SIGNIFICANCE

Thus one can readily see the complexity involved in assessing competition and niche definition, especially in sympatric competitors. As Klopfer (1962) said, it has become a routine exercise for ecologists to demonstrate feeding differences in sympatric species, or other differences that place the species in different niches.

For the insects studied here the question which appears is, what differences? For all the rhyparochromine studied here are biologically distinct from each other, even those of the same genus. As Slobodkin admitted, often any biological difference ascertained are assumed *a priori* to account for the niche differences in species of different appearance. Such thinking is tautological since it has been repeatedly shown that morphological evolution itself is adaptive (Lack 1944, 1947). Moreover as Ross (1962) and Andrewartha (1961) emphasized, a species, when evolving, is bound to become biologically differentiated in some way. Thus most of the demonstrations of niche differences among species in the same habitat have been purely hypothetical since "what is not yet clear is the degree of ecological difference required to permit coexistence, and we are not even sure how this difference should be measured (Slobodkin 1961)."

It then appears from this uncertainty and the various relationships possible (Ross 1962) that it would be difficult to accurately evaluate competitive relationships even in very well studied groups. For the present discussion then, it is best to point out the differences among the coexisting species of rhyparochromines. It must be emphasized that not enough is known about the causes of natural mortality, etc., to do more. It is assumed that the ecological segregation already observed evolved from former competitive situations (Lack 1947).

Genera

The best evidence for possible ecological displacement is in the distribution of related species in a genus. However generic size in New England rhyparochromines is relatively small and most genera are represented by only a single species. To further evaluate this aspect, the same sort of study needs to be done in a warm species-rich southern climatic area.

Only six genera have more than one species present in New England. *Ligyrocoris* with four, *Pachybrachius* with two, *Peritrechus* with two, *Drymus* with two, *Scolopostethus* with three (or four) and *Stygnocoris* with two. Only in the case of *Stygnocoris* were species of the same genus found together in the same habitat, and *Stygnocoris* species were much more frequently found separated than together. The species differ as follows: In *Ligyrocoris, L. diffusus* is typical of open ruderal habitats; *L. depictus* of dry sparse bald habitats; *L. sylvestris* of northern cool woodland margins; *L. caricis* of a *Carex stricta* aquatic transition habitat. In *Pachybrachius*, while *P. albocinctus* inhabits aquatic transition, *P. basalis* is found under rank, often ruderal vegetation. The three species of *Scolopostethus* are found as follows: *S. diffidens* in climax or subclimax forest of white birch-hemlock; *S. atlanticus* is geographically separate and found in a mature shrub and red maple community, and *S. thomsoni* varies from aquatic transition to moist roadsides and meadows with scattered trees. In *Drymus, D. unus* is found in aster-rich subclimax deciduous woodlands, *D. crassus* in mature climax woodlands. In *Peritrechus, P. fraternus* is usually found in beach wash; *P. paludemaris* in salt marshes. *Stygnocoris pedestris* is often found on woodland margins and grass dominated habitats while *S. rusticus* is especially abundant under tall forb habitats.

Species Assemblages

Because of the importance of the steady state condition in Gausian competition, the species assemblages fall into two groups: inhabitants of short-lived habitats and of long-lived habitats. While such short-lived (T_1) habitats should be of the type characteristic for fugitive species, they also yield the highest abundance of rhyparochromines, presumably because of the abundance of fallen seeds and perhaps a lack of population density controls. Competitive conditions presumably exist briefly under these conditions. The pattern then is a rapid succession of species whose habitats broadly overlap and should partly compete at times. These species generally show rather catholic feeding habitats and have higher reproductive potentials under similar conditions than most permanent habitat species. The species of this group can hardly be conceived of as species assemblages as the associations are sporadic and brief. Each of the species does select a fairly definite habitat and the species may be organized into a succession scheme (see Ecology). It is not clear whether these species succeed by competition or habitat choice.

An important and interesting aspect is that the two introduced megalonotines *Megalonotus* and (?) *Sphragisticus* apparently compete rather poorly with the native rhyparochromine fauna, and are found in rather restricted man-influenced habitats in New England. *Sphragisticus* is nearly always found around gardens and in ruderal habitats, but even then much less abundantly than *Ligyrocoris* and *Pachybrachius* at the same sites. *Megalonotus* was nearly always restricted to patches of the European plant, *Centaurea. Trapezonotus arenarius,* if introduced, does not show the wide ecological range of the Palearctic species (Southwood and Leston 1959, Penth 1952).

In the seed-rich litter habitat, *Peritrechus fraternus* was dominant over the other rhyparochromines which invaded briefly—*Pachybrachius basalis, Perigenes, Heraeus.* One species, *Delochilocoris umbrosus,* has the most sporadic ecological distribution of all and occurred briefly in a large variety of open habitats and only once was found in any abundance in a peculiar thin wash habitat. Of all the rhyparochromines studied it appears to best fit the fugitive species concept of Hutchinson (1953) as it simply did not appear to compete well with the other rhyparochromines for long. In a sense all of the species of temporary habitats may be considered fugitive species (Slobodkin 1961).

The second broad group comprises the species of permanent (P) and semipermanent (T_2) habitats (see Table 4). In this group the long persistence of the species allows discrimination of definite species assemblages which are present year after year and indicate a steady state relationship, especially since the majority of the individuals of such populations are flightless. While a particular assemblage will remain present, the exact species composition of the assemblage varies, especially on a north-south pattern, and component species may vary in relative abundance from site to site.

NORTHERN WOODLAND ASSEMBLAGES

Eremocoris ferus, Scolopostethus diffidens, and characteristically, *Plinthisus americanus* compose this group. It is especially characteristic of mixed deciduous conifer woodlands. All species feed on *Tsuga* and birch seeds. *Plinthisus* was most abundant relative to the other species in pure *Tsuga* or *Picea* woodlands.

On the trophic level the species differ in that *Plinthisus* has one yearly generation and lays diapause eggs in autumn: *Scolopostethus* is also univoltine but diapauses as an adult and has a single early summer feeding period. *Eremocoris* feeds and oviposits throughout the summer. Moreover *Eremocoris* is about twice the size (5.2–6.0 mm.) of *Scolopostethus* (3–3.5 mm.). The life cycles differ as *E. ferus* hibernates, the others diapause over the winter. *Plinthisus* has procryptic coloration, the others are flash type ant mimics. All hide under litter but the drymines run rapidly when disturbed while *Plinthisus* moves slowly. *Eremocoris* is macropterous with a relatively wide distribution. The others are brachypterous and restricted in distribution.

Drymus unus was found only in deciduous margins, *D. crassus* in rich climax deciduous forests. Both species of *Drymus* have one generation a year, overwinter as an egg, and the nymphs are bright red (warning coloration?).

MIDDLE WOODLAND ASSEMBLAGES

This is a similar group except that *Plinthisus* drops out and *Antillocoris minutus* appears. This species is procryptic, slow moving, and minute (1.8–2.2 mm.) but with a life cycle similar to *Scolopostethus. Drymus unus* is also a regular member and differs from the other species in that like *Plinthisus* it has a fall feeding and oviposition period with diapause eggs being produced. It moreover prefers aster seeds to birch seeds.

SOUTHERN WOODLAND ASSEMBLAGES

This group is characteristic of a *Vaccinium-Viburnum-Acer rubrum* community. *Eremocoris ferus* and *Antillocoris minutus* are again members. *Scolopostethus diffidens* is replaced by *S. atlanticus* which has a similar life history. Both species feed on *Vaccinium* and *Viburnum* seeds. *D. unus* is abundant, and *Ozophora picturata* is present. *Ozophora* has a late summer reproductive period which coincides with the second generation of *Eremocoris ferus.* At this time *Scolopostethus* and *Drymus* feed little, although *Drymus* has an autumn feeding period. *Ozophora* is procryptic and rapid moving both as adults and nymphs in contrast to the other species which are self-concealing forms. Moreover *Ozophora* is larger (6.0–6.5 mm.) and is more characteristic of but less abundant in dry oak-hickory forests where the other species do not occur.

Aquatic Transition Assemblage

This group which includes *Ligyrocoris caricis, Pachybrachius albocinctus* and *Scolopostethus thomsoni* is characteristic of the *Carex stricta* community along the shore of Pink Ravine at Storrs, Connecticut. All three species feed on seeds of *C. stricta,* a clump (stool) forming sedge with cover at its base. On the trophic level, *P. albocinctus* is not represented by nymphs until after July 10 at which time *L. caricis* is already midway through its oviposition period and producing diapause eggs. *P. albocinctus* moreover develops here largely on the seeds of the tall bullrush *Scirpus.* Both myodochines climb the plants frequently to feed, but *S. thomsoni* which has a bivoltine life cycle which begins a month earlier than *Pachybrachius,* was not observed to do this. Comparing the climatic adaptations, *L. caricis* diapauses as an egg through late summer and winter, and is not dependent upon equitable late summer conditions as is *P. albocinctus.* The late life cycle of *P. albocinctus* may reflect its southern distribution as is the case in aquatic Odonata of tropical derivation which become active only during the warmest part of the season (Kennedy 1927). On the protective level, *P. albocinctus* is macropterous and flies readily, the others are brachypterous and restricted to the location. Both *Ligyrocoris* and *Pachybrachius* have ant mimicking nymphs but the ant resemblance is more pronounced in *P. albocinctus.*

In *Scolopostethus thomsoni* the color pattern appears disruptive rather than ant-mimicking. In this same community feeding on the same seeds are several other non-rhyparochromine lygaeids, *Cymus discors* Horvath, *Cymus luridus Stål,* and occasionally, *Cymus robustus* Barber, and *Oedancala dorsalis* (Say). These species are competitive in the sense that they reduce the available seed supply. However, they are rarely found on the ground where the rhyparochromines are concentrated, and may then be considered as being in a separate ecological niche.

Sparse Old Field or Bald Assemblage

This assemblage includes *Xestocoris nitens, Carpilis consimilis, Pseudocnemodus canadensis, Ligyrocoris depictus,* and *Trapezonotus arenarius* and is characteristic of dry sparse bald habitats. At any given site one of the species may be absent or infrequent. *Xestocoris* is the most abundant and characteristic species.

On the trophic level *Xestocoris* is predominantly a grass seed feeder. *Carpilis* will also feed on *Veronica* seeds, and *Trapezonotus, L. depictus* and *Pseudocnemodus* feed on composite and *Vaccinium* seeds as well.

The myodochine species all overwinter as eggs, but *L. depictus* emerges early and grows rapidly, becoming adult in early to late June. *Pseudocnemodus* is intermediate becoming adult around June 21. *Carpilis* however develops slowly and does not become adult until mid-July. These species begin ovipositing shortly after becoming adult. Some individuals of *Pseudocnemodus,* however, are bivoltine, rather than univoltine.

The other two species overwinter as adults. *Trapezonotus* maturates early and produces diapausing adults by mid-July. At this time *Xestocoris* is ovipositing and nymphs are still only up to the third instar. The slower cycle of *Xestocoris* synchronizes its feeding period with the ripening of the seeds of *Festuca* spp. Thus the feeding periods are distributed differently among the species.

On the climatic adaptation level, all species are univoltine or nearly so. The myodochines overwinter as eggs, the other species as adults. In the laboratory the eggs of *Xestocoris* are laid in loose litter while those of *Trapezonotus* are placed in glumes and crevices. *Pseudocnemodus* lays its eggs deeply in loose litter, while *Carpilis* and *L. depictus* push their eggs into the ground and tight crevices. *L. depictus* and *Pseudocnemodus* are found in an open microhabitat on the litter, while the other species keep under the litter. On the protective level, the adults and nymphs of *Pseudocnemodus* and the nymphs of *L. depictus* are ant mimics. The remainder have procryptic coloration: *Xestocoris* is a glossy brown; *Trapezonotus,* a mottled brown; and *Carpilis* is a contrasting pale gray and black. *L. depictus* and *Pseudocnemodus* run rapidly on the litter when disturbed while the other species seek cover. These species thus present a varied assemblage of forms, colors, and escape reactions to potential predators.

Pseudocnemodus and *L. depictus,* were parasitized by tachinids while the others were not. At Warrensburg, New York, *Konenetrus plenus* was found with this assemblage. It also feeds on *Festuca* seeds and has a nymphal development like *Pseudocnemodus.* It is contrastingly colored to break up the body pattern. It has one yearly generation with diapause over the winter as an egg.

In southern New England at Noank, Connecticut *Xestocoris* is largely replaced by *Cryphula,* and perhaps *Trapezonotus* is replaced by the rather rare *Malezonotus* when the latter occurs. The latter relationship is speculative, but the *Xestocoris-Cryphula* exchange is well marked. These species rarely occur together in the same habitats. The seasonal cycle of *Crypula trimaculata* is nearly identical to that of *Xestocoris nitens*. *Malezonotus* is bivoltine rather than univoltine. *Sphaerobius* and *Cnemodus* are also never found together since the former is northern, the latter southern. These remarkable ant mimics are characteristic of dry *Andropogon* communities with considerable interspaces. They frequently form unispecific populations. They are each parasitized by different species of tachinids.

Thus it is seen in the foregoing analysis of the assemblages that the various species are quite different from one another. The exact meaning of the differences must await studies which can establish what precisely controls the population sizes. In most cases despite the abundance of these insects I doubt that the controlling factor is food as there are simply too many seeds produced and available. Further study of these complexes should yield valuable information on their population structures.

Speciation

Lack (1944, 1947) has interpreted the habitat distinctions among sympatric species as steming from former isolation speciation and competitive interactions. The present species are derived from various sources and have migrated into once-glaciated New England.

Since the New England fauna includes several zoogeographical elements, the habitat specificities may have derived from competitive interaction during the faunal mingling of diverse elements (Ross 1962). It may be illuminating to compare the habitat range of the related species from the center of the distribution of the genera with the New England representatives. The habitat ranges may be restricted in New England as a result of such a competitive mingling.

If the species distribution and feeding patterns are interpreted as Kohn and Orians (1962) suggest, the speciation pattern in the Rhyparochrominae is horizontal and habitat-specific as with small mammals and not related to host plants and vertical stratification which results in high speciation. This interpretation would also help explain the lower speciation level of the Lygaeidae as compared with the Miridae.

Conclusions

1. It has been shown that the species of Rhyparochrominae exhibit a well marked ecological distribution.
2. There is a close relation between habitat permanency and the phenomena of brachyptery or flightlessness, and between macroptery, temporary habitats, and dispersal records.

3. Certain correlations were evident among habitat selection, zoogeographical origin, and systematics.
4. The life cycles are strongly structured, and adapted to the habitat types. Either one or two generations are present and diapause occurs in the egg or the adult.
5. A variety of protective coloration and behavior patterns are noted, and related to the habitat background. Many of the species are ant mimics.
6. Many species especially of temporary habitats are parasitized by the tachinids *Catharosia* and *Petia* (= *Procatharosia*). The parasites' overwintering patterns are adapted to the hosts'.
7. While oligophagous on seeds, many species show distinct preference for the seeds of certain species.
8. Many of the species possess a remarkable seed defense behavior and also actively move seeds about to more protected sites, often with aid of the fore femora.
9. The mating behavior of the different species vary from simple to complex with stridulatory devices occurring in some species.
10. Development rates vary among the species and the variation is largely independent of food and temperature and correlates with life cycle whether univoltine or bivoltine and the productivity of the habitat.
11. Reproductive rates can be varied directly with seed supply, and reproduction ceases on foliage diets. Total productivity in the laboratory appears to vary with habitat productivity and size.
12. Ontogenetic changes during nymphal development in color and appendage allometry occurs.
13. Several types of eggs are discerned and the different types in large part correlate with oviposition habits although some systematic relationships seem present.
14. The biology and ecology of the species are considered in relation to competition theory. Species assemblage are shown to be very different among themselves and each species may be considered as being in different niches in the narrow Gausian sense.
15. Species of all habitat assemblages are generically distinct.

THE SPECIES ACCOUNTS

TRIBE MYODOCHINI

Myodocha serripes (Olivier)

This species is easily recognized by its strikingly elongated head and is better known than most other rhyparochromines. Many workers have been impressed by its apparent ''predacious'' appearance and in the early literature *Myodocha* was even placed in the Reduviidae (Spinola 1837, Kirby 1837). Barber (1932) thought the species was at least in part predacious. Blatchley (1926) compared it to the carabid beetle *Casnonia pennsylvania* (L.) and surmised that the long slender necks of both species had developed through reaching into crevices. Later workers, as summarized by Sweet (1960), have found it to be phytophagous. I have little positive evidence about the adaptive significance of the elongated head, except that I have frequently observed the insect probing inside the fallen seed capsules of St. Johnswort (*Hypericum* spp.) and the whole head may enter into the capsule. However, many rhyparochromines do this, and this answer can only be suggestive. Actually, the significance of the long ''neck'' may probably be better sought among tropical species of *Myodocha* which have much longer necks—which inspired Stål (1862) to name one species *giraffa*.

Myodocha serripes represents the most northern extension of *Myodocha*, a predominantly Central American genus of seven species. *M. serripes* has the widest known distribution of any of these species but this may be largely a result of more thorough collecting and the distribution patterns of the Neotropical species will undoubtedly be extended. In fact, the genus is already known from Ecuador (Campos 1925) and southern Brazil (Slater, *in litt.*).

In southern Florida, *M. serripes* is replaced by an entirely different species, the endemic *M. annulicornis* Blatchley. Unfortunately no records of *Myodocha* are at hand from northern Florida and Georgia. *M. serripes* is recorded (Slater, Catalogue) north to Quebec and Minnesota, west to Colorado and Texas, and south to Louisiana and South Carolina. Brimley (1944) found the species only to the west of Raleigh, North Carolina, and not on the low coastal plain. While Moore (1950) collected it in Quebec and Parshley (1917b) recorded it from Maine to New Hampshire, I found it extremely uncommon from the northwestern highlands of Connecticut northward.

Environment

As Uhler (1876, 1878, 1884) early noted, *M. serripes* overwinters in woodlands and moves into field habitats during the spring. The autumn migration is quite marked and begins in Connecticut in late August (first date, August 25) well before the advent of cold weather. This migration continues throughout September and into October as the nymphs mature in the fields. The movement into woodlands extends very little beyond the forest side of the ecotone between field and forest. Within woodlands of appreciable extent relatively few specimens are found. A definite preference is shown for a light woodland of mixed black birch, red maple, and red oak. The litter beneath such a combination is of medium looseness (4–6 inches deep), and moderately moist in contrast with the dry loose litter of oak alone or the very tight litter as of conifers and *Betula populifolia* Marsh. Despite the great abundance in the area studied of pure oak litters, no colonies are found in them, while five separate overwintering colonies were found in the mixed litter type, to one of which *Myodocha* returned for four successive years. Dowdy (1955) also found *Myodocha* hibernating in a climax oak hickory forest in Missouri under rocks and logs, often in large colonies. I never collected the insect under rocks and logs but rather in litter along such objects. In the hibernating areas the bugs are found aggregating in groups of from 2–3 to as many as 25 in a square of four inches. They are not found clustered tightly together, but merely near each other. I could distinguish no conditions in the hibernation loci different from surrounding microhabitats.

In May when the adults disperse into field habitats they are found in many types of field habitats but in June and later, especially as the ground becomes warmer and drier, the habitat distribution becomes much more limited. This species is found most abundantly in relatively new habitats such as fallow fields, gardens, or embankments which are colonized by a dense, species-rich association of forbs 1–2.5 feet in height. These forbs include such species as *Achillea millefolium, Chrysanthemum leucanthemum, Arthemis* sp., *Ambrosia artemisiifolia, Solidago* spp., *Rumex* spp., *Galium* spp., and especially *Hypericum* spp. and *Fragaria.* These habitats persist at most only 2–3 years, and accordingly, only once have I collected *Myodocha* two years in succession in the same habitat. The very sparse first stages of plant succession are avoided, as are the more xeric hillsides characterized by morainic gravelly soil. Occasionally a few nymphs are found along an ecotone of southern exposure and it is noteworthy that when this occurs, *Hypericum* is usually present. The preferred habitats are also characterized by a brown, friable, and moderately (5–7) moist soil which is semi-shaded by the plants, and is covered with a thin litter of broken stems. Litter temperature during the hottest days never exceeds 32°C. Under apparently optimum conditions the population may reach 25 per square meter. More often, the population is about 5–8 per square meter. It is difficult to follow a population increase as the populations are quite unstable. While the species may certainly be considered common, its abundance is more accurately a reflection of the abundance of relatively new forb covered habitats. At no time was *Myodocha* found off the ground on the plants. No specimens of *Myodocha* could be collected by sweeping at night.

There are several literature records of the summer generation. *Myodocha* sometimes becomes a pest of strawberries in a habitat which is probably similar to natural rank forb habitats (Osborn 1900, Bryson 1939, Neiswander 1944). Walkden and Wilbur (1944) collected the species in alfalfa fields in Kansas. Torre-Bueno (1929a) sifted the species from grass piles in Massachusetts. Wray and Brimley (1943) found specimens of *Myodocha* in the pitcher plants, *Sarracenia flava* L. and *S. purpurea* L.

At Naranja, Florida, I found second and third instars of the closely related *Myodocha annulicornis* Blatchley in a rank forb habitat at the margin of an avocado grove, a habitat very similar in aspect to those favored by *M. serripes*.

General Biology

The dispersion of the species may occur at night as it has been frequently collected at lights (Summers 1891, Tucker 1907, Torre-Bueno 1908, Barber 1923, Froeschner 1944). I collected the species in early June at lights which may mean the species disperses as teneral adults at the end of the first generation (see General Discussion), and also in late August which may represent the autumnal hibernation migration of the second generation. As spring nights are quite cool during the vernal movement back into the fields, it may be relevant that I observed a male *Myodocha* to fly across a field flitting from the top of one herb to another on May 8. Females can be induced to fly throughout the summer, even during oviposition periods. It is noteworthy that all species of the genus *Myodocha* are entirely macropterous.

When presented in the laboratory with a light or dark background *Myodocha* persistently comes to rest upon the dark one. In the field, the insect blends very well into the dark, stem-strewn surface of its habitat. Its movements further suggest a reliance on protective coloration as it normally moves rather deliberately and slowly. Its color pattern is a good example of disruptive coloration as the three white spots, one at the apex of the membrane, the others at the apex of the corium, the elongated shining head, and the yellow legs with the dark apices of the long fore femora, together serve to break up the form of the insect and blend it into the background. The second to fifth instars show protective coloration of a very different sort. These nymphs are unusual among the Rhyparochrominae in possessing three longitudinal dark bands that extend the length of the abdomen which is otherwise a pale yellow. The bands blend the nymph into the background litter of stems in the summer habitat. When disturbed, *Myodocha* moves very rapidly, its long legs abetting its movement over the rough litter.

No insect parasites emerged from 123 specimens collected. *Nabis ferus* (L.) and *Melanolestes picipes* (H.–S.) fed readily on *Myodocha* adults.

In the laboratory, the bug readily feeds on various seeds from the field litter of its habitat. A strong preference is shown for *Hypericum* sp. and *Fragaria* seeds, but seeds of *Taraxacum, Achillea, Erigeon, Aster* spp., *Potentilla canadensis* L., *Rumex crispus* L., *Aquilegia canadensis* L., and *Paspalum muhlenbergii* Nash, are readily fed on. Other grass seeds than *Paspalum* are, in general, avoided. I never observed this species ever to make any overt move toward aphids, beetle larvae, sow bugs, nor to scavenge on a dying or dead bug as does *Pachybrachius basalis.* Neiswander (1944), Osborn (1900) found this species to seriously injure everbearing varieties of strawberries by causing the berries to become soft and covered with a mold. In the laboratory it is observed that the feeding is largely restricted to the achenes on the surface of the fruit, and the fruit is pierced only occasionally, and infrequently when water is present. The older nymphs when placed with lettuce grow slowly but in the absence of seeds the adults do not oviposit. It seems very likely that when the strawberry fruit is pierced in search of water, the wound allows the entrance of infection hypha which cause the damage recorded by Neiswander (1944). Without water *Myodocha* dehydrates and dies in a day.

Myodocha does not exhibit a complex ''seed territoriality'' behavior with a threatening stance. Seeds, if large, are dragged to secluded sites. If the seeds are small, as with *Hypericum* seeds, the seeds are carried at the end of the labium and beneath the body. Once when a seed was lodged in some methyl cellulose a female used a three quarters open fore leg draped over the seed to dislodge it. This suggests that the fore legs as in other species may have this function in the natural habitat.

This species mates quite infrequently and the courtship behavior was only briefly observed. The male apparently does not recognize the female until after contact, and even then only after repeated contacts. When excited, the male vibrates his antennae very rapidly, protrudes his genital capsule, and attempts to climb upon the female who usually evades him. It is noteworthy that the male spends a good deal of time "grooming" himself. The males have a long spur on the fore femora which may function in the mating behavior.

Life History

Myodocha serripes has a bivoltine life cycle as Neiswander (1944) predicted. The adults overwinter (Blatchley 1895, Wirtner 1905, Torre Bueno 1908, 1925, Dowdy 1955). Blatchley (1926) states that the fourth and fifth instar nymphs may also overwinter. In New England, however, I have found only the adults overwintering. The adults appear in the fields in May at Storrs, Connecticut with the earliest date May 10. The observed phenology at Storrs is as in Table 5.

The percentage of adults in the field in September is of little significance as the adults migrate into woodlands from August 25 on. The two generations overlap, as the early instars of the second generation and ovipositing females of the first generation occur together with late instar nymphs of the first generation. Adults collected in late August and September were in reproductive diapause.

TABLE 5

Phenology of *Myodocha serripes*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adults
June 1	——	——	——	——	——	100%
June 13	——	30%	——	——	——	70%
June 19	6.2%	62.5%	21.3%	——	——	10%
June 28	——	12.5%	45%	25%	12.5%	5%
July 6	10%	——	——	——	10%	80%
July 15	12%	38%	23%	1%	9%	17%
Aug. 3	10%	20%	20%	——	20%	30%
Aug. 20	——	——	5%	20%	45%	30%
Aug. 31	——	——	1%	29%	45%	25%
Sept. 20	——	——	——	10%	34%	56%
Oct. 10	——	——	——	——	50%	50%

The late summer cessation of reproductive activity and migration into woodlands well before the advent of cooler weather suggests that the diapause state is initiated by a short photoperiod. Members of a population sample collected on March 21 were in reproductive diapause. As fertilization occurs during the spring, the function of photoperiod could be assessed. When kept under equinoctal daylight (12 hours) the females remained in reproductive diapause. Under long day (16 hours) an aliquot of overwintered adults came out of diapause after 16 days and reproduced several months before the field and greenhouse populations. It is noteworthy that copulation occurs quite independently of reproduction and that the males do not exhibit reproductive control by photoperiod under these conditions.

In the fall a somewhat different situation exists. When populations from late July and early August are brought into the laboratory and kept under long daylight they do not enter into the facultative diapause. However, when exposed to long photoperiod (16 hours) or exposed independently to cold the insects did not come out of diapause. The diapause was a strong one, and if left in warmth during the autumn, the insects died without reproducing in the laboratory. Only after a combined cold-long photoperiod exposure could diapause be broken. The exact day length which initiates diapause was not ascertained, but the field evidence appears to indicate that it is less than the summer solstice (15 hours 15 minutes at 42° latitude), and is near 14 hours for this day length coincides with the earliest (May 15) and latest (early August) occurrence of gravid females.

In the laboratory, the mean stadii and extremes were as in Table 6.

Neiswander (1944) stated that under experimental conditions the newly hatched nymphs reached the adult stage in from 19 to 25 days, and that under field conditions probably twice this period was required for development. The phenology data indicates that in field conditions at Storrs, Connecticut, one month or a little more is required for this development period. The laboratory life cycle happens to be in essential agreement with this interval, rather than more rapid as is usual in other species. My longer development periods than Neiswander may result from the more moderate (75°F.) laboratory temperatures against higher field temperatures.

I was unable to determine the precopulatory or preoviposition period of a non-diapause female. Release from diapause under long photoperiod (16 hours) took 13 days as measured by oviposition time. As remarked under diapause, oviposition began by mid-May and continued normally until death in mid-June. If the fe-

TABLE 6

Stadia of *Myodocha serripes*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
10.5	7	7	7	7	10	37
(10–12)	(6–9)	(6–10)	(6–10)	(6–10)	(8–12)	(27–41)

male is not fertilized she may live for a very long time without laying eggs. One virgin female collected April 14 remained alive until April 29 of the next year without laying any eggs. Under 16 hour illumination, other virgin females sometimes laid a few (mean 9.4 (0–26)) eggs. The mean normal fecundity in the laboratory was 107 eggs, the range 55 to 161. The rate varied from 4.5 to 10.1 eggs a day (mean 6.8).

Contrary to Neiswander (1944) the eggs are not laid at random. The female carefully examines a site with her antennae and then probes it repeatedly with her ovipositor. This may be repeated several times until a suitable location is found. In the laboratory, the smooth, unadorned, elongate eggs were laid singly into the soil, crevices in litter, under small stones, and into methyl cellulose and cotton.

Heraeus plebejus Stal

The genus *Heraeus* differs from *Myodocha* primarily in that the head is only constricted behind the eyes rather than elongated into a slender "neck." Its appearance similarly suggested to Barber (1923) that the species was at least partly predacious. In view of the apparent close taxonomic relationship of these genera, it is perhaps significant that *H. plebejus* shows distributional, ecological, and bionomic similarities to *Myodocha serripes.*

H. plebejus appears to be the only species of the 10 known which is adapted to a cool temperate climax. Most of the other species, insofar as is known, are found in Central America and the West Indies. Only one, *H. cincticornis* Stål is recorded from South America (Bolivia and Argentina) and another, *H. pacificus* Barber is endemic to the Galapagos. *H. plebejus* has a wide range, extending north to Quebec, south to Florida, Bahamas, and Haiti, and west to Kansas and Arizona (Slater, Catalogue).

In New England, I found the species to have a scattered and spotty local distribution, and did not collect the insect north of Connecticut and Rhode Island. Parshley (1926) had no records of the species north of Massachusetts. Blatchley (1926) considered it scarce in Indiana, especially northward. Moore (1944, 1950) however has recorded the species from Quebec. Nevertheless, *H. plebejus* is at the northern fringe of its range in southern New England. Consequently, the biology of this species should eventually be amplified by work nearer to the center of its distribution.

Environment

Several authors found *Heraeus* to overwinter as an adult: concealed in moss in January near Buffalo, New York (Van Duzee 1894); sheltering under boards and other loose objects (Barber 1923); and under stones in December (Torre-Bueno 1910). In Florida, Blatchley (1926) captured numerous specimens in winter by beating Spanish moss and the dead leaves of the cabbage palmetto.

In Connecticut there is an annual movement to woodlands in early autumn to hibernate and a redispersal in spring into open habitats, as in *Myodocha*. While these two species are rarely found together in summer habitats, they frequently hibernate together. In fact every hibernation capture of *Heraeus* in late fall has been with *Myodocha* at edges of light mesic woodlands. The earliest fall record in woodlands is September 9, and only nymphs and very few adults remain in the summer habitats during September. In the spring, the species reappears in open mesic habitats, but very infrequently re-establishes itself in the same locale occupied the previous year.

Of course, this temporary presence in a habitat in part results from the scarcity and the dispersal pattern of the species, but also and perhaps more important is its preference for a particular open, mesic, rank forb type of habitat. It is also found along streams and shaded ecotones between woodlands and fields or marshes. Torre-Bueno's (1910, 1924, 1925) records of *Heraeus* from near swampy areas, and perhaps Hussey's (1922) collection of it in a sassafrass strip between white pine and black oak communities correspond to these observations.

In the summer habitats, only four large colonies of *Heraeus* with nymphs were found. More frequently, only a few specimens are found at a site. These favorable habitats are all open relatively moist ecotones between fields and marshes or mesic woodlands. They agree in having moist soil (8–9), dark with humus, which is shaded by the herbs and so remains relatively cool (no more than 75° F.) on hot days. As I was fortunate enough to visit each of these areas earlier, the colonies definitely persisted for only one year. Two of the habitats were similar, as ecotone of rank forbs between a drier field slope and a marsh stream with woodlands 30–50 feet away. The plant association consisted of various tall grasses, the rank forbs *Impatiens biflora* Walt, *Eupatorium purpureum* L., *E. perfoliatum* L., *Galium* sp., *Bidens laevis* (L.), *Solidago patula* Muhl., *Solidago* sp., and in one area, a few young *Sambucus canadensis* L. The third habitat was on the edge of a butternut-maple-oak wood with a drier field above it, and the fourth favorable habitat was at Rocky Neck State Park, Connecticut where the insects were found among rank tall grasses leading down a slope toward a sheltered salt marsh, but well above and away from the influence of the salt level.

Among the various locations where *Heraeus* occurred in low abundance, several may be mentioned. One was a thick strand of flood litter on a partly shaded bank at Mansfield Center, Connecticut. Here, in the seed-rich litter, it occurred with three other rhyparochromines, and it was significant that in the drying litter *Heraeus* occupied the wettest level while the other species occupied drier levels. At Noank, Connecticut a surprisingly dry habitat (soil 4–5), was a sandy roadside with scattered clumps of *Andropogon scoparius*. As mentioned earlier, a study at the center of its range should be made, as I have found it in June upon the cool grassy balds at 5,000 feet on Mt. Pisgah and Mt. Mitchell, North Carolina in the Great Smoky Mountains, as well as in roadsides in the valleys at 1,000 feet.

Not only does *Heraeus* have a scattered scarce overall distribution, but it is found in populations of low densities, usually 1–3 per square meter, at most, 8 per square meter, and the total colonies are of small size, covering no more than 10–20 square meters.

General Biology

The seasonal movements and preference for a relatively short lived seral stage, suggests that the bug readily disperses, which correlates with its entirely macropterous condition. *H. plebejus* may migrate at night at it has been taken at lights in New York by Torre-Bueno (1908) on July 17, 1907, and subsequently (1930). Blatchley (1926) collected it on March 15 and October 27 at Dunedin, Florida. I collected the species at lights July 10, 1957 at Noank, Connecticut and July 25, 28, 1960 at Storrs, Connecticut. Another species of this genus, *H. guttatus* was captured in Puerto Rico at lights (Ramos 1946). The species may be capable of larger dispersal movements at Glick (1939) captured this species up to an altitude of 1,000 feet over Louisiana.

Like *Myodocha,* the adult *Heraeus* has a dark color pattern with white pattern-breaking markings on the lateral margin of the corium and apex of the membrane. The bug ordinarily moves slowly and deliberately and blends well into its natural habitat. The nymphs are conspicuously colored with a white band along the Y-suture which gives a good impression of ant mimicry when the insect runs. When the nymph is motionless, however, the color pattern breaks up the form and renders it difficult to see. The first instar has a longitudinal mesal red band as well as the usual transverse red band across the yellow abdomen which is typical of the Myodochini.

Unlike *Myodocha, Heraeus* is parasitized by the tachinid *Catharosia nebulosa* (Coq.). All individuals were reared from diapausing adults of *Heraeus.* The parasites emerged from the host in the laboratory at the same time that *Heraeus* ordinarily breaks diapause. Thus the parasite overwinters in the host bug.

Feeding was not observed in the field. In the laboratory aside from sunflower seeds, it feeds upon various small seeds: *Galium* sp., and *Monarda* sp. from its habitat, and also upon small composite seeds and grass (*Festuca* and *Andropogon*) seeds. It would seem to be a general seed feeder but more critical work needs to be done. I have reared it through the life cycle only on sunflower seeds on which the bug feeds very readily. However the mortality on this seed is very high (90%), most (ca. 70%) dying in the first instar. *H. plebejus* dehydrates and dies very quickly away from water.

While I frequently observed mating end to end, I have not been able to record courtship or initiation of mating. Nor did this species show any manifestation of seed possession or aggressive display as in many other rhyparochromines. These seeds are moved to more secluded places for feeding.

Life History

Heraeus plebejus has two generations a year. The earliest overwintered adults were collected in late spring (June 7 and 9) and were already gravid and laying eggs. Blatchley (1926) collected the bug on March 15 in Indiana. Only one population was followed as it developed. Its phenology is given in Table 7.

On July 25 some new females of the first generation were gravid. However, all adults of the second generation were in reproductive diapause. When brought into the laboratory, they remained in diapause until October 10 or later. Evidently the diapause is not a strong one and the adults become reproductive after only two or three months in warmth. This short cessation, however, serves to suspend reproductive activity until after the advent of cold weather. It is interesting that the females of the first generation, when sexually isolated, would survive until October but did *not* go into reproductive diapause like the second generation. One was mated with a second generation male which broke diapause in early October and a few fertile eggs were produced. This reproductive cessation is probably initiated by a short photoperiod as in *Myodocha*.

TABLE 7

Phenology of *Heraeus plebejus*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
June 7	——	——	——	——	——	100%
June 21	11%	11%	34%	22%	11%	11%*
July 5	——	——	10%	20%	40%	30%
July 25	——	——	——	——	23%	77%
Aug. 2	30%	20%	15%	——	——	35%
Aug. 20	——	10%	15%	40%	30%	5%
Sept. 11	——	——	5%	15%	25%	65%

* new adults

The life cycle in the laboratory correlates with the field notes. The stadia were measured accurately only up to the third instar. Beyond that, too few developed and too erratically to give a meaningful average.

TABLE 8

Stadia of *Heraeus plebejus*

Walmer 12-2

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
10	9	10	11	5	8	53
(9.5–11)	(7–13)	(8–12)	(8–13)	——	(5–14)	(42–68)

The adult longevity varies with generation, of course, and for the summer generation it is two months, and for the winter generation (overwintered), nine months or, in laboratory warmth, four months.

One female after breaking diapause on October 18 laid 455 eggs at a rate of 7.6 eggs a day over two months. The number of eggs per female varied from 30 to the above figure but the sample is too small to give an accurate average fecundity. Egg production occurs regardless of fertilization. The mean preovipositional period of four virgin females was 18 days.

A female mates repeatedly any time during her reproductive period, but one mating suffices to fertilize all eggs to be laid. The smooth elongate eggs are laid singly in the laboratory into loose substrates as sand, loose soil, wet or dry cotton or methyl cellulose and are not laid at random or loose in the culture dish. The female searches assiduously, prior each egg laying, for a proper site.

LIGYROCORIS Stal

In New England four species of the genus *Ligyrocoris* occur, one of them described only recently (Sweet, 1963). There is some controversy concerning the limits of this genus as some authors (Van Duzee 1914, Ashlock 1957, Ashlock and Lattin 1963) have questioned whether the possession of the lunate or stigose abdominal vitta (stridulitrum of Ashlock and Lattin 1963) indicates a natural genus. Nevertheless the four closely related species treated here should remain nomenclaturally unaffected by any further generic changes because among them is the type species for the genus, *Ligrocoris sylvestris* (Linn.).

As *sylvestris* and *diffusus* Uhl. were confused by synonymy, and *depictus* Barb. not yet recognized, American literature prior to Barber's 1921 revision of the genus must be used with great caution.

Distribution

At present the genus includes two subgenera, *Pseudopamera* Dist. and *Ligyrocoris* Stål. *Pseudopamera,* originally established as a separate genus, includes nine species and is restricted to southwestern North America and Central America. *Ligyrocoris* (*sensu stricto*) includes fourteen species and while also apparently centered in Central America, has a much wider distribution. Although several species of *Ligyrocoris* extend to South America and the West Indies, the present complex of species is apparently adapted to a temperate climate.

While sympatric in New England, the ranges of the four species to be considered differ greatly; *L. sylvestris* is evidently a boreal form (Krogerus 1960) and is widely distributed over the north Holarctic region. The very closely related *L. depictus* Barb. occurs from Quebec south along the Appalachians to North Carolina. *L. diffusus* Uhl. extends across North America, roughly between the

38th and 50th parallels and broadly overlaps on the southern limits of *L. sylvestris.* The fourth species, *L. caricis* Sweet is so far limited to one locality each from Connecticut and Maine. The origin of this pattern of distribution and overlap poses an intriguing problem, but an analysis must await a better knowledge of the range of the species, especially in southeastern and southwestern United States.

Ligyrocoris diffusus Uhler

This is one of the most abundant and widespread of the rhyparochromines studied. Its range extends as far north as Newfoundland (Lindberg 1959), and the north shore of the Gulf of St. Lawrence (Walley 1932); west to British Columbia and California (Barber 1921); and south to Missouri (Froeschner 1944) and North Carolina (Barber 1921). Blatchley (1926) noted that it was frequent in the northern counties of Indiana, but had not been taken in southern Indiana. Slater (1952) said that *diffusus* is one of the most common members of the subfamily in the midwest, but scarce in southern Illinois.

Over this wide range the species exhibits some variation in size and darkness and may eventually be separated into subspecies. Specimens from northern New England and the Adirondacks are definitely smaller and duskier, but the differences overlap greatly those of specimens from Connecticut. As the specimens from Connecticut closely resemble those from the Midwest it may be that these represent a large western population that has moved eastward with the creation of extensive open habitats in eastern United States. While it is true that Barber (1921) could say that he had never seen a brachypterous form of this species, wing lengths are not uniformly the same. Smaller female specimens from the northern and western limits of its range frequently exhibit a slightly shorter hemelytra which, while exceeding tergum seven, does not exceed tergum eight, the apex of the abdomen. The hind wing in each is slightly shorter than the hemelytra at rest. In a very few males the membrane may not quite attain the apex of tergum seven, the apical segment. These slightly brachypterous forms also have a narrower pronotum with a proportionally larger anterior lobe.

Environment

This species is abundant throughout New England, but it is ecologically restricted and its abundance is in large part an expression of the abundance of its preferred habitats. While in reality it is primarily a ground-living insect, it frequently ascends plants to feed on seeds, and so has often been recorded as collected by sweeping which greatly contributes to its ''abundance.'' Sweeping and ground collecting each produces a very different impression of the species' habitat preferences. Hussey (1922) in Michigan said it was abundant in fields, especially on goldenrod and ragweed. Blatchley (1926), in Indiana, swept it from ''tall grasses and other herbage along margins of wet meadows and marshes.'' Froeschner (1944) in Missouri swept it from weedy fields and open woods between July 1 and October 15. Hendrickson (1930) in his study of insect populations in relatively undisturbed prairie communities in Iowa made more detailed observations. He swept *diffusus* from all communities, and found it common to numerous in both climax and subclimax grasslands, but absent from wetter consocies. Significantly, he noted *diffusus* as especially numerous on *Andropogon furcatus* associes where herbacious plant flowers attracted many of this species. Lindberg (1958) however stated that the species was found in Newfoundland in humid localities, along margins of lakes and pools, on wet meadows, and *Sphagnum* bogs.

In New England, this species is typical of open disturbed habitats, roadsides, as well as old fields with many forbs present, especially composites. In the latter habitat *diffusus* is frequently collected by sweeping, for it prefers the seeds of certain composites such as *Chrysanthemum leucanthemum* L., *Solidago* spp., *Tanacetum vulgare* L., and especially *Rudbeckia serotina* Nutt. In late summer when the seeds are ripe the insects will congregate on the ripe seed heads. In such a site where it is readily collected and appears abundant, ground sampling will frequently indicate a lower overall abundance at this site than at a nearby waste habitat. Indeed, *diffusus* will be apparently absent from the tall forb habitats earlier in the year, when abundant in other habitats.

Barber (1928b) found it under ground cover and Procter (1946) said it was to be looked for under boards, etc. These notes do little justice to the great predominance of this species on the ground. Nearly all collections of *diffusus* have been in relatively open unshaded habitats, especially on level exposed areas. In general the population density of *diffusus* decreases as the herbacious level becomes more dense and shades the ground surface. The greatest densities occur in areas with pioneer stages of herbacious vegetation frequently in ruderal communities on poor sandy soil which are aptly described as wastelands. Frequently the margins of cultivated fields and recently fallow fields support high densities of this insect. Plants found in such preferred sites usually include *Ambrosia artemisifolia* L., *Silene* spp., *Daucus carota* L., *Agropyron repens* (L.), *Potentilla recta* L. and *P. canadensis* L., *Rumex ace-*

tosella L., *Panicum* spp., *Polyganum* sp., *Stellaria* sp., *Chrysanthemum leucanthemum* L., *Tanacetum vulgare* L., *Oenothera* spp., *Verbascum thapsus* L., *Erigeron* sp.; in short many of the rapidly invading plants which are commonly called weeds. In sparser areas abundances may reach 30–50 per square meter. By far the most favorable site was a corn field 40 by 150 meters, left fallow for a year. The ground was heavily littered with corn husks, stalks, and cobs, fallen stems of grasses and composites, and in mid-June had a heavy population of 50–70 adults and fifth instars of *diffusus* per square meter.

Areas nearly or completely devoid of plants are not colonized unless a good deal of litter is present. Also, as the proportion of grass to forbs increases, the numbers of *L. diffusus* decreases. I never swept this species from grass, and it is completely absent from the dry *Festuca-Andropogon-Cladonia* habitats.

The great majority of collections of *diffusus* are from habitats with but a thin sparse layer of litter, which, in the open conditions prevailing, is very dry. Surface soil on the moisture scale varies from 1 to 4 with an average dryness of 2.5. As is to be expected such habitats are very hot in early afternoon, with surface soil temperatures up to 140°F. This strong insolation very likely accounts at least in part for the rapid spring development of this species as compared wth many other rhyparochromines.

In autumn when diapause eggs are laid, a definite change in habitat preference occurs as the weather becomes cooler. The adults are then frequently found in more shaded marginal areas than during the summer, and the soil moisture level is usually 5–6. It is important to note, however, that such areas in the following spring are unshaded, quite warm (80°F.) and drier (3–5) at midday as the leaves are small and herbs have fallen during the winter leaving a seed rich litter.

For over five years several new fields in Storrs, Noank, and Canaan, Connecticut were left fallow and in the invasion, expansion and subsequent decline of populations of *diffusus* could be followed. This sequence strongly shows a peak abundance at an early sere succession stage and subsequent tapering off as herbs, especially grasses, more thickly cover the ground.

General Biology

As the herbs grew and filled in the habitats open in early spring, the later instars and new adults often dispersed into surrounding, more sparsely vegetated, xeric areas. (Frequently adults and older nymphs dispersed into nearby flood wash litter along river banks). In late June and early July populations appear in habitats—frequently very new—which earlier did not have *diffusus* present. This, combined with its ubiquitous presence in fallow fields, indicates that it is a rapidly dispersing species. It has been collected at lights (Torre-Bueno 1930) but apparently much less frequently than might be anticipated from its abundance. *L. diffusus* is one of the most abundant species found in beach wash (Torre-Bueno 1915, 1927, Parshley 1917a). Torre-Bueno suggested that such insects were on dispersal flights which happened to lead over water. The nearly total macroptery attests to the importance of dispersal in this species. It would be interesting to see if the slightly shorter wing forms have reduced flight or dispersal ability.

Two female specimens were collected above the tree line at 5,400 and 5,500 feet respectively on the roadside of Mt. Washington, New Hampshire on August 9, 1961 and had probably dispersed there from the valley floor where the species was abundant along road sides.

As in many "weedy" fields which apparently had no *diffusus* present earlier in the year it is probable that these were dispersing adults.

The mottled brown coloration of *L. diffusus* allows it to blend well with the thin litter and sandy soil of its preferred habitats. As it is not a sub-litter inhabitant and often lives in areas normally with little litter, its main defense is to run and freeze near some object or to crawl into loose litter. The nymphs of instars two to five are fuscous with the abdomen marked with small white spots. The second to fourth instars have a lateral white band along the suture between the third and fourth segments, which, when the nymph runs gives a definite impression of ant mimicry.

Balduf (1939) found *L. diffusus* preyed on by *Phymata pennsylvanica* Melin which gains significance when it is recalled that *Phymata* waits in ambush on flowers. I have fed *diffusus* to *Nabis ferus* (L.), *Pagasa fusca* (Stein), and *Melanolestes picipes* (H.-S.).

I have found *diffusus* parasitized by a small undescribed tachinid of the genus *Catharosia*. The degree of parasitism was low (less than 5%), and only a few *diffusus* populations yielded any tachinids.

As mentioned earlier (Sweet 1960) *L. diffusus* is fairly unusual among the rhyparochromines for it does on occasion climb into plants to feed on ripening composite seed heads. *Rudbeckia serotina* Nutt. was by far the most preferred host plant. When observed feeding in the field on a seed head, the insect had pierced the achene through near the pappus, and the usual pumping motions of the head indicated its feeding. Such feeding has been observed on *Tanacetum vulgare* L., *Chrysanthemum Leucanthemum*

L., and *Solidago* spp. This feeding on seed heads explains the relatively late date of recorded collections: July 23 (Hendrickson 1930), July 1 (Froeschner 1944), July 15 (Procter 1946), and July 11 (Blatchley 1926), which corresponds to ripening of composite seed heads.

In the field the nymphs feed on fallen seeds of the previous year as indicated by several rearings of the insects on litter from the collection locality. By laboratory observations it was found that the nymphs and adults feed on the seeds of *Rumex acetosella, Rumex* sp., *Polyganum* sp., *Potentilla recta, P. canadensis, Fragaria virginiana* Duchesne, *Acer rubrum* L., *Medicago* sp., *Trifolium* spp., *Monarda* sp., and some other unidentifiable seeds, but grass seeds and *Daucus carota* seeds did not elicit a feeding reaction, which correlates with the absence of *diffusus* on these plants. The most vigorous feeding response was toward *Rudbeckia* and sunflower seeds. In general, *L. diffusus* should be considered as oligophagous on seeds, especially of the Compositae. In this connection, it may be relevant to note that *Rudbeckia serotina* is noted by Fernald (1950) as a most aggressive Great Plains species which has rapidly spread eastward with the clearing of the forests. The midwestern population of *L. diffusus* may have moved east in company with *Rudbeckia.*

There are several other references in the literature which mention the presence of *diffusus* on a plant but these do not indicate definite feeding. Phillips (1951) found it on sour cherry in orchards; Adam (1915) collected it on *Lepachys* (= *Ratibida* sp.), the prairie coneflower; Forbes (1905) found it on corn silk. Vestal (1913) described *diffusus* as a non-selective plant feeder. In the field *diffusus* was never observed to feed on any part of the plant other than the seeds. It fed readily on lettuce for water but no eggs were produced. With the addition of a vial of water such "feeding" was greatly reduced. The addition of seeds brought about egg production; the removal, a cessation in egg production.

L. diffusus was reared through several generations on *Rudbeckia* seeds and numerous times on sunflower seeds. The culture results were quite variable, very likely because of disease interference. Yet nymphs of any instar could be reared quite easily to adults which oviposited vigorously in culture. However nymphs reared from the eggs, suffered very high mortality on the same food. Most of the mortality occurred during the earlier instars.

Not only was this species in no way observed as actively predacious, but it did not probe at a dead or dying insect as shown by an absence of any cones of salivary sheath fluid on the dead insects. It is therefore interesting that Slater (*in litt.*) found one feeding on a large black aphid.

Like other rhyparochromines *diffusus* fares badly away from water, thus it is interesting to speculate on the source of water available in its dry habitat. Vegetation is an obvious choice, but dew, which condenses heavily in such open habitats is very likely quite important.

In various dry habitats *diffusus* was found active until early afternoon on very hot days, when, the insect retreated into clumps of litter in late afternoon. I frequently observed that the nymphs had slightly shrunken abdomens by late afternoon and specimens from the field at this time did not feed unless water was provided, in contrast with those collected in the forenoon which fed readily on sunflower seeds. This would indicate, then, that the insects were dehydrated. It also strongly suggests that dew is the important water source, especially as free water was much preferred to water from plant tissues in the laboratory. When in thirst, however, *L. diffusus* will pierce nearly any green plant in search of water.

As in other members of this genus and the related *Zeridoneus* a fertile male reacts to a receptive female with a sort of courtship dance which probably involves stridulation. The peculiar jerky movements of an excited male are produced by a rocking of the body back and forth while at the same time the male jerkily moves forward and moves his antennae in an uneven tapping or shaking fashion.

The male does not react unless he comes in contact with the female, in contrast with some other rhyparochromines which react to the female before actual contact. The female usually resists the excited male by turning on him with rapidly vibrating antennae which is an annoyance signal, and moving away a short distance. This may be repeated several times as the male endeavors to mount her from the side. Finally the female may become quiet and the male, still continuously jerking, mounts her, usually on the right side. The extruded pygophore is turned over 180° and placed upon the apex of the female's abdomen. At this point the female may release the ovipositor and the claspers, which work like little claws, then grip the apex of the ovipositor, and copulation ensues. The male swings away into an end to end position. With considerable pulling and pulsating the male slowly forces the aedeagus into the genital chamber and the spermatheca. The slow course of intromission can be observed readily as the spines of the conjunctiva are clearly visible through the semi-transparent valvulae of the ovipositor. Length of copulation varies from 1 to 4 hours.

Repeated attempts to cross *L. diffusus* wth the other species of

Ligyrocoris, showed that the males, except *caricis,* reacted with the various females in very similar fashion, but that the female after a few usually preliminary circlings became extremely excited if the male was of another species and she ran *very* rapidly and ''frantically'' about the dish as the alien male jerkily ''danced'' about. In only one case, a *diffusus* female of the second generation mated with a *sylvestris* male, when the male was dropped suddenly beside the female. The male made copulation before the female could react to it. Repeated attempts to duplicate this have failed, and it seems highly unlikely that this would occur in the unconfined natural environment where ecological factors also keep the species apart. Neither *L. caricis* male nor *Zeridoneus* male seemed to recognize the *diffusus* female, but *L. diffusus* male was very interested in the tiny *caricis* female, but on the other hand, was not stimulated by a *Zeridoneus* female.

The annoyance waggling of the antennae mentioned earlier plays an important part in the ''seed possession'' behavior which is strongly developed in *diffusus.* By starving the insects for a few days this behavior can be readily elicited. When first disturbed by an intruder, the insect (usually female) simply places itself between the intruder and the seed. Further intrusion results in a rapid alternate waggling of the antennae and vigorous attempts to keep the intruder away by kicking at it with the hind legs. If this fails the seed possesser will leave the seed and rapidly charge on the intruder flailing at it with antennae and fore legs. The fore legs are not spread as in *Pachybrachius,* but two may flail at and ''fight'' one another actively until one ceases to intrude. The insect may return to the seed, carefully search it over with its labium until the original feeding hole is found, and resume feeding.

Life History

L. diffusus, in New England, overwinters as an egg and has two generations a year. The statement by Forbes (1905) that it overwinters as an adult and Torre-Bueno's collection (1924) of the species in New York by sifting in December are very likely the result of the cold hardiness of *diffusus.*

It lays eggs until very late in fall, and the latest ovipositing females were collected on November 10, 1959 and a male as late as November 29, 1960.

The eggs hatched in spring at a staggered rate, for while some appeared as early as April 25, 1960 first instars continued to be present on May 14, 1960 and May 27–29, 1959 when some nymphs were already just becoming adults. Thus all instars would be found in the field in May although the mode instar changes, as shown by the instar distributions in Table 9.

In the first generation adults, mating was observed in the field on June 24. The adults from July 10 on represent the second generation. The adults of this second generation remain sexually immature until the last week of August. It is interesting that in a cool valley at the base of Mt. Washington, New Hampshire the second generation appeared much later and in late July as only first to third instar nymphs were present, and first instars were still present on August 3. Last instar nymphs of the second generation were found as late as August 26 in Storrs, Connecticut and September 8, in Canaan, Connecticut and evidently occur much later in New Hampshire.

TABLE 9

Phenology of *Ligyrocoris diffusus*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
Apr. 29	93%	7%	——	——	——	——
May 7	50%	35%	10%	5%	——	——
May 17	——	13%	50%	25%	12%	——
June 9	——	——	10%	15%	35%	40%
June 16	——	——	——	——	20%	80%
June 22	——	——	——	——	——	100%
June 28	50%	30%	——	——	——	20%
July 5	55%	30%	15%	——	——	——
July 10	24%	35%	17%	15%	8%	1%
July 17	5%	5%	10%	30%	35%	15%
July 27	——	——	5%	20%	35%	40%
Aug. 7	——	——	——	15%	25%	60%
Aug. 26	——	——	——	——	8%	92%
Sept. 10	——	——	——	——	——	100%

As the second generation adults do not become reproductively active in the field until late August or the beginning of September, this indicates that the early maturing adults are in a reproductive diapause for a period of a month or more, in sharp contrast with the rapid attainment of reproductive activity (6–8 days) in the first generation. This is then not an immature state in the sense of a normal pre–reproductive period as the late fifth instar nymphs at Storrs, Connecticut and the late developing population from New Hampshire all attained reproductive activity at the same time as the earlier developing individuals in the southern New England populations.

These events, including the assumption of reproductive activity between August 29 to September 6, occur well before the advent of cold weather and also in field populations exposed to normal day length in the laboratory. Moreover the second generation colonies when reared under long photoperiod in the laboratory, laid non-diapause eggs in early and mid-August. These results indicate that a photoperiodic response is involved in this seasonal cycle. However the reaction of the first generation to short photoperiods has not been tested. These results may be most readily explained as follows. There is no reproductive diapause under summer solstice long photoperiods (15.5 hours) when the first generation matures. In shorter photoperiods from late July (14 hours) to late August, the adults remain in diapause. After late August (13.5 hours) diapause eggs are laid.

The picture which emerges is a species very finely adjusted to its environment. Its bivoltine life cycle coupled with actively dispersing macropterous forms allows it to readily fill the transient sere it prefers, and egg production in the fall allows the females to make use of the ripening composite seeds, and place the diapause eggs around the site of such plants. The emerging nymphs can make use of the fallen seeds before the seeds sprout or succumb to molds.

The diapause eggs are darker and slightly larger (ave. 1.07 mm.) than non-diapause eggs (ave. 0.98 mm.). The diapause eggs develop until the eye spots are visible through the chorion. At this time, coincidentally at the blastokinetic stage Wheeler (1893) termed diapause, physiological diapause intervenes. The diapause is a fairly strong one, but its strength differs in various females when the eggs are left in warmth; in some females, a few eggs would resume development in two weeks; in other females, none would hatch until 60 to 150 days later. Eggs from adults collected in Laconia, New Hampshire did not develop at all in warmth, but required a cold exposure. Diapause development occurs in cold (35°F.). Nymphs hatched from the diapause eggs of April 14 after restoration to warmth March 21. The development, however, was irregular, and some eggs did not hatch until early May. This variability correlates with the field observations of apparent staggered egg hatching. It would seem that this would be an excellent physiological mechanism to scatter the risk of hatching during unfavorable weather conditions. Since a few eggs of a few females did hatch early, it is interesting that several third instars were collected in early October and certainly represent a field example of an early diapause release. It may then be that three generations will be present further south.

Two females which were collected at the late dates of November 8, 1959 and November 10, 1960 each laid 50–60 eggs all of which did *not* diapause. This indicates that the exposure to cold had broken the diapause initiating phenomenon in the female *before* the eggs were formed.

TABLE 10

Stadia of *Ligyrocoris diffusus*

Egg*	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
10.0 (7–12)	7.6 (6–8)	6.6 (3–11)	4.5 (3–6)	6.7 (3–10)	8.2 (5–9)	30.6 (22–40)

*Generation 1

In the laboratory the stadia (in days) are quite variable (Table 10). The more rapid development always occurs in nymphs taken from field and slower development occurs in nymphs which are reared from eggs in the laboratory. The life span of the adults varies with the generation and mating. Fertilized females live 19 to 31 days, males and unfertilized females, 45 to 75 days. In the second generation with its brief diapause period fertilized females live longer, 44 to 78 days, unfertilized adults 60 to 85 days.

The precopulatory and preoviposition period for the female is eight days, and the precopulatory period for the male is four to seven days. There is no marked difference in egg productivity in females of each generation. The productivity varies in 26 mated females from 51 to 325 eggs (mean 166.5).

In 11 unmated females the number varies from none to 29 eggs. In some sexually isolated females of both generations, a few eggs are laid at the beginning of the normal oviposition period. Laying soon ceases and the abdomen of the virgin females becomes very distended. Dissection showed well developed eggs. The egg-laying stimulus is probably copulatory as the following two experiments illustrate: (1) a twelve day old virgin female when mated with a three day old immature male immediately laid a normal, but infertile complement of 29 eggs in three days, after which the female ceased laying eggs and once again became swollen; (2) a virgin female mated with a very old male (45 days) produced a normal 170 but infertile complement of eggs. This suggests that the male may transmit some substance to the female which induces oviposition, and which was in low quantity in the new male, but present in the old male which apparently was infertile.

The females lay their eggs singly into litter, on grass culms, hollow stems, and in soil, especially loose sandy soil. The eggs are cylindrical, slightly curved (cucumber-shaped) and beset with tiny clubbed hairs. Small sand grains and other debris cling to the egg, concealing it. Wet substrates are shunned unless no others are present. The females prefer to lay their eggs deeply into sand or such loose dry substrates as cotton and methyl cellulose, and will even work their abdomens into the substrate to insure deep placement of the eggs. On sand the females spread their legs wide, tilt their abdomen to 80° from the horizontal, and work their entire abdomen into the sand. After each egg is laid the female makes several jabbing movements which tumble sand into the oviposition site. Egg production becomes much retarded and reduced when no suitable substrate is provided. Such females become greatly swollen and egg production may entirely cease.

Ligyrocoris depictus Barber

This species, which was not recognized until 1921, very strongly resembles *sylvestris* and differs from it chiefly in coloration and slightly different labial segment ratios. From the type localities of New Jersey, Massachusetts, and New York it has been found north to Quebec (Moore 1950) and Maine (Procter 1946). I have further found the species in Connecticut, New Hampshire, and also in the Great Smoky Mountains of North Carolina. It has an Appalachian distribution. It is to be noted that the specimens from lowland habitats—New Jersey and Storrs, Connecticut—are much the same in size and coloration, while the specimens from the mountainous areas are larger and darker and more nearly resemble *sylvestris.* The habitat selection of this species is entirely different from that of *L. sylvestris,* and the two were never found together.

Environment

Despite the apparent rareness of *L. depictus*, it is actually a fairly common species on mountain bald habitats with *Xestocoris nitens* V.D., *Carpilis consimilis* Barb., and *Trapezonotus arenarius* L. It is also found on similar lower slopes where ericaceous shrubs, principally *Vaccinium angustifolium* Ait. along with *Danthonia spicata* (L.), *Aristida dichotoma,* and open grasses form a relatively permanent, long persisting open habitat.

The habitats of the balds varies from low dense ericaceous shrubs mostly *Vaccinium* on Mt. Everett and Mt. Greylock in Massachusetts, to grass, blueberry, and lichen margins around large open rock outcrops among scrub oak (*Quercus licifolia* Wang.) on Canaan Mountain, Connecticut and to a nearly pure grass and sedge herb layer around *Rhododendron catawbiense* Michx. clumps on Andrew's Bald, Clingman's Dome, North Carolina. In Storrs it was found in an old open habitat dominated by fine leaved *Festuca capillata* community. At Canaan it was also found in a *Festuca-Gnaphalium-Vaccinium* community surrounded by white pine, as well as some essentially disclimax old ecotones between pastures and woodlands on xeric morainic hillsides.

These habitats for the most part have in common a xeric, open aspect, a relatively open vegetation community with a growth of low ericaceous shrubs. In each the soil is sandy, gray, and very poor with a considerable lichen (*Cladonia*) flora present. These exposed habitats become quite warm (105°F.) on the ground at mid-day in summer but not as hot as in *diffusus* habitats. In the late summer or aestival period these sites become extremely dry.

The species is always present in relatively low densities of 3–10 per square meter and reached the latter density on Canaan Mt. balds.

Barber (1928b) collected the species in apparently similar open dry habitats in the Adirondacks. Torre-Bueno (1925), however, swept *L. depictus* from bunch grass in a marshy place. This record might possibly refer to L. *caricis* (see *L. caricis*). Procter (1946) found it on *Atriplex patula* on Mt. Desert Island, Maine.

General Biology

As all known specimens are brachypterous or submacropterous, the macropterous forms must be produced at rare intervals, if at all, and dispersion would be rather limited which correlates with the relative permanency of the habitat.

This is a very rapid moving and agile insect which is difficult to collect. When disturbed its escape response is to run rapidly for a considerable distance. It does not actively seek refuge in litter crevices, and would come to rest as often in the open as in some coarse loose litter. When found in the field it was *upon* the ground litter and not concealed in it.

In the resting position the brown and black coloration of the adults appears clearly procryptic. The rather light coloration of this species, in contrast to *diffusus,* and the more linear effect of the mesal zone of dark coloring presumably better blends this species into its usual dry *Vaccinium*—grass habitats, similar to other grass community insects. The nymphs are similar to *diffusus* except that the white band between segment three and four is pronounced in the last instar as well as in the earlier instars. When running with their characteristic jerky gait, a definite ant mimicry effect is apparent.

Only one population found near Mt. Greylock, Massachusetts yielded *Catharosia* tachinid parasites. The nymphs at least were definitely fed on by *Pagasa fusca* (Stein) nymphs.

Although *Rudbeckia* was *not* found in the habitat of *depictus,* the seeds elicit a strong feeding response in the insect, as do sunflower seeds. It also feeds on the seeds of *Vaccinium, Betula populifolia* L., and *Gnaphium,* but is negative to *Centaurea* seeds. Apparently *Rudbeckia* seeds have a definite odor for when a few are introduced into the culture dish, the *Ligyrocoris* nymphs present become quite excited and search vigorously until the seeds are found. There was only some cursory probing at fescue and *Panicum* seeds which were the major seed component in the litter of several habitats.

Seed possession behavior is similar to that of *diffusus*, but much more vigorous. Here the third to fifth instar nymphs were also observed to express this behavior. A fifth instar nymph usually effectively dislodges third and fourth instars from a seed by swarming over it with flailing legs and wagging antennae. The possessor often clings flat over the seed when under such an attack.

The mating behavior is similar to that of *L. diffusus. L. depictus* is a much more active and vigorous species. The shaking dance was timed at 3.2 motions per second. While a strong avoidance reaction is present which would preclude field matings, prolonged enclosure is also negative. Virgin females of *depictus* were reared with *diffusus* males from third instar on, and kept together in a four inch petri dish without any cross mating occurring.

Life History

This species has but one generation a year and lays eggs which diapause through the late summer and winter to hatch the next spring. It appears evident that this life cycle corresponds to a moist spring and early summer, with dry conditions in late summer, often a severe drought. This climate pattern is strongly accentuated in the open, overdrained habitat of this species.

The available phenological record is rather heterogeneous. While first and second instars were collected May 17 at Storrs, Connecticut, those collected May 20 and May 21 at Mt. Everett and Canaan Mt. were third and fourth instars. Second instars were collected May 28 at a cool location on Canaan Mt. Fifth instars were found with third and fourth instars May 28 on a warmer slope. In the laboratory and field adults become mature between June 8 and June 25. Instar ratios obtained are too variable and represent too many different small populations to form a meaningful phenological sequence. For example, third instars were present until June 10 in some localities. This variability suggests that staggered hatching occurs here as in *diffusus.*

Oviposition begins between June 6 and June 21 and continues until mid-July and early August. The eggs are laid in a state of strong diapause which commences in early anatrepsis when the egg is still white. The eggs of one female began to show some development from early August on—these eggs malfunctioned and died before completing anatrepsis. Another female's eggs in contrast showed no development whatever until October 1 when they all quickly began to develop, but only to early anatrepsis, if at all. I was unable to get adequate hatching under 35°F. conditions, and in the spring, of 311 eggs, three-quarters of them developed, one-half to katatrepsis, but only one hatched.

The stadia in days of field collected instars reared on sunflower seeds were as in Table 11.

TABLE 11

The Stadia of *L. depictus*

Instar 2	Instar 3	Instar 4	Instar 5
4	4	5.5 (4–7)	7.0 (5–9)

This development rate is much more rapid than in the field populations. The longevity of the adults in the laboratory varies from 36–75 days, the average being 60.1 days. Most died by early August, but a few lingered longer in the laboratory, one to August 21.

Preoviposition period ranges from 10–13 days (ave. 11.5). I could not induce four old virgin females (32–45 days) to mate which suggests a *post* copulatory period.

Ligyrocoris sylvestris (Linnaeus)

This boreal species is one of the few rhyparochromines with Holarctic distribution. Its distribution largely coincides with the taiga biome, and it is absent from the areas of western Europe with an Atlantic climate. It was found from Lappland south into the boreal coniferous zone in the Alps (Hedicke 1942), the Pyrenees at 1,600 meters (5,248 ft.) (Wagner 1958), the Caucasus (Kiritshenko 1918), and Bulgaria (Strawinski 1961). It extends east through Siberia and Alaska and across North America to Newfoundland, and south to New Jersey, northeastern Illinois, South Dakota, and in the mountains to Colorado, Idaho, and British Columbia (Slater, Catalogue).

It is, however, conspicuously absent from the highlands of Scotland where suitable habitats appear to be present. Since disjunct populations occur in the Caucasus and the Pyrenees it is probable that land connection was broken between Britain and the continent before *L. sylvestris* reached this area. Since *sylvestris* is a boreal species, it is possible that it represents a post-Wisconsin glaciation introgression of *Ligyrocoris* into the Palearctic region.

As may be anticipated in a species so widespread, considerable variation exists. Horvath (1901) noted that specimens from Siberia had much darker femora than the European representatives. Specimens examined from Anchorage and Fairbanks, Alaska were considerably smaller and lighter colored than the New England population. In *L. diffusus* the northern New England specimens are usually smaller and dingier with weaker hemelytral fascia. It therefore may seem that by parallel both *L. diffusus* and *L. sylvestris* are smaller and lighter at the northern extreme of its range. Since the dingy *diffusus* populations occur where the ranges of *diffusus* and sylvestris overlap, another interpretation is conceivable. This may be an example of overlap of two related species (Blair 1955) which is described as character displacement (Brown and Wilson 1956).

L. sylvestris in New England is fairly common in the appropriate habitats in the North but becomes extremely scarce in Connecticut and only a few specimens were collected in the northwestern highlands at Canaan and Norfolk, Connecticut. According to Parshley (1917) it reaches the New England transition zone from the north. Barber (1921) noted the species as very uncommon in New Jersey, and Slater found records of *sylvestris* only from the northeastern corner of Illinois (1952). It is therefore most interesting that Froeschner (1944) records it from Missouri and refers to it as a ". . . so-called northern species (which) has been taken as far south as the southern border, where it occurs along with many of the more truly (*sic*) southern species.'' Could this possibly be a disjunct Ozarkian population which has adapted to a warmer habitat? Or, may it represent another species?

Environment

In New England *sylvestris* is found limited to cool, mesic, and semishaded habitats along north exposed ecotones between meadows or bogs and beech-maple-birch or spruce-fir woodlands. It is always found in the field aspect side of the ecotone, never in the closed canopy forest. This field formation is one to two feet in height, of medium density and is characteristically dominated by forest type mesophytes as *Festuca obtusa* Bicher, *Carex* spp., *Aster acuminatus* Michx., *A. lateriflorus* (L.), *Solidago caesia* L., and *Dryopteris spinulosa* (Muell.). The ground biotope usually has only a thin litter layer on the mesic soil (moisture 5–7).

A few specimens were swept from composites as in *L. diffusus*. There is a clear ecological separation between *diffusus* and *sylvestris*. On the exposed drier portion of an open slope, only *L. diffusus* is collected. But as the more mesic ecotone is approached, *diffusus* drops out and the sparse population of *sylvestris* appears. The same phenomenon was noted by Slater (*in litt.*) at the Moosehorn National Wildlife Refuge, Maine and at Lake George, New York. The close contiguity of these populations adds more credence to the species difference accentuation hypothesis mentioned previously.

L. sylvestris was found in several sphagnum-black spruce-larch bogs in Maine and in *Myrica gale* L., at the margin of black spruce, at Norfolk, Connecticut. The other Connecticut collection was in an alder swamp at Canaan, Connecticut. These bog-type ground habitats were, of course, nearly hygric with moisture levels at 1–2. The abundance here was 1–2 per square meter, and this was the only rhyparochromine found in these habitats.

Uhler (1875) described it from wild grassy spots adjacent to *Sphagnum* swamps and in high mountains in North Carolina. These North Carolina records, however, *may* refer to *L. depictus*.

The extensive European literature indicates a very similar habitat type. Stŷs (1960) collected it in birch litter and sphagnum in a coniferous forest in Czechoslovakia. Sahlberg (1920) in Sweden and Stichel (1925) in north Germany collected it on the ground in coniferous woods. Pfaler (1936) found it regularly on the margin of spruce woods in Finland. Hedicke (1942) records it in coniferous woods in high alpine areas in the Alps. Wagner (1958) swept it from alpine fields in the Pyrenees. Krogerus (1932, 1960) however describes it in Finland as an ubiquitous species found in *Calluna* healthlands, *Festuca-Elymus* open associations, spruce and pine woodland margins, and birch-alder associations. It appears from Krogerus' data, that *L. sylvestris* has a wider ecological amplitude in high latitudes in Europe than at lower latitudes there and in New England. This is perhaps to be expected, and the ecological range of the species in northern parts of North America may be similarly broader. However, it remains possible that in Europe, in the absence of competition with other *Ligyrocoris* species, *L. sylvestris* may assume a wider ecological range, much as have many introduced species when released from competition with congeners (Elton 1958, Ross 1962).

General Biology

As all the specimens available from New England are brachypterous, the macropters and submacropters must be rare which would place an important limitation on dispersal in the discontinuous mosaic of favorable habitats in the southern portion of its range. It is therefore significant that in Europe, according to Reuter (1875), long winged forms are found southward, short winged forms northward, which may correlate with a discontinuum of favorable habitats in the southern part of its European range. At any rate, many of the habitats, especially bog margins, would be long lasting habitats.

The behavior and movements of this species are similar to *depictus.* The darker and more sharply contrasting hemelytral coloration of *sylvestris* forms a disruptive type coloration which conforms to the mosaic of dark substrate and light leaves in its mesic ecotone habitat.

In the laboratory immediately on introduction *sylvestris* feeds on the seeds of *Aster* spp., *Solidago caesia* L., *Betula populifolia* Marsh, *B. alba* L., and *Tsuga canadensis* L., all from its habitat, but not on *Festuca obtusa* Bichler. It oviposits when feeding on these seeds. It appears especially attracted to sunflower seeds.

It has been recorded from a number of plants, especially in Europe, but it is not at all certain that these records represent feeding: goldenrod (*Solidago* sp.) in Indiana (Blatchley 1926), *Ledum palustre* and *Betula nana* (Sahlberg 1920, Stichel 1925), and *Myrica gale* (Stichel 1926).

Mating behavior and seed defense behavior is similar to *L. depictus,* but less vigorous in execution. While the males will mate with already fertilized young females, the older actively ovipositing females would not permit copulation.

Life History

Jensen-Haarup (1912) cited *L. sylvestris* as over-wintering as an adult. Pfaler (1936) refuted this and found that *sylvestris* overwintered as an egg and had a single generation in Finland. The nymphs are present from June 15 to July 15. Immature adults appear in early July, and oviposit from late July to the end of August. Prohaska (1923) found both adults and nymphs in equal numbers on July 18 and 25 in moist meadows in Austria.

In New England a nearly identical pattern to Pfaler's was obtained at Laconia, New Hampshire. Very few last instar nymphs (4%) were found with the adults in late July, and oviposition in the laboratory continued through August. Slater (*in litt.*) found fourth and fifth instars as late as August 18 in Maine.

In light of this cycle it is most interesting that Strawinski (1960) reported *sylvestris* in Bulgaria as overwintering as an adult. Moreover in the population of *L. sylvestris* in Missouri, Froeschner (1944) reported adults from as early as May 24 to as late as October 19. Either this population is not *L. sylvestris* as mentioned earlier, or it may represent an adaptation of a southern disjunct population to a longer, warmer season.

The onset of diapause occurs in early anatrepsis when the egg is still white. When left in warmth, development occurs slowly and some eggs during late September and October become pink colored at late anatrepsis, and a few later slowly reach katatrepsis. These eggs uniformly died without hatching. Some viable eggs never developed. Cold exposure (20° and 34°F.) for several months did not permit hatching, although the eggs developed to katatreptic position. Only a long cold exposure (September 12 to April 30) yielded any nymphs (28% hatched).

Only data on oviposition is available. The fecundity in the laboratory is high: the mean, 272 eggs; the range, 161–475 eggs. Both moist and dry substrates are readily oviposited into, and no preference is discerned except for a loose substrate. The eggs are beset with hairs and cling to the substrate.

Ligyrocoris caricis Sweet

This is the only new species discovered during the present study on the New England Rhyparochrominae (Sweet 1963). This slender small species was found only at Pink's Ravine Pond near Storrs, Connecticut, and was collected on Mt. Desert Island, Maine (Great Health) by F. B. Shaw. It is very unlikely that its distribution is this limited and it should be found in suitable habitats at other locations at least in the northeastern United States.

Environment

As mentioned earlier (Sweet 1963), the habitat of this species is entirely different from its close relatives. It is found among the outcropping stones and stool-tussocks of *Carex stricta* Lam. at the margin of Pink's Ravine Pond, an artificial but dystrophic pond with dark humus-colored water. This is a rather limited area only about 50 yards long. The plant community is the typical transition from a wet red maple forest through shrubs to the emergent pond vegetation. Shrubs of *Cletha alnifolia* L., *Rosa carolinianum* L., and *Cephalanthus occidentalis* L., form the shrub layer. In the open area, other shore herbs are *Scirpus* sp., *Hypericum* sp., *Drosera rotundifolia* L., and emergent further out, *Alisma* sp., *Sparganium* sp., and *Sagittaria* sp. Around the bases of the *Carex* stools and rocks are a few scattered patches of the bog moss *Sphagnum* sp. This association approaches the *Caricetum strictae* of Conrad (1935). *L. caricis* is collected chiefly in the open area on the *substratum*, on the *Carex* stools, at the edges of rock outcrops, and on fallen *Carex* litter at the water's edge. During early June at all times of the day adults and last instar nymphs are frequently found feeding on the *Carex* heads on the seeds. By late June and early July the seeds have largely fallen and the insects are then restricted to the ground level and rarely could be swept. At this same time, the adults are occasionally found in the mixture of *Sphagnum* and leaf litter beneath the shrubs.

The biotope of *caricis* then varies from open exposures to semishade in *Carex* clumps or in the shrub margin. The moisture level is, of course, saturated to very wet (9–10) and the temperatures moderate 62° to 76°F. in late June.

The population level of *L. caricis* remained approximately the same from 1960 to 1962, despite the draining of the entire artificial pond in August of 1961 which left the area dry for several weeks. The population as sampled reaches a peak in mid-June and declines steadily until late July when none could be found. The abundance at its peak was 5–6 per square meter of *Carex* tussock, or 1–2 per square meter of straight area and declined to less than 1 per square meter of tussock by July 10.

It was found with *Scolopostethus thomsoni* and *Pachybrachius albocinctus* Barb. (see Competition Discussion).

As mentioned under *L. depictus*, Torre-Bueno's (1925) collection of *L. depictus* from sedges in New York may very well represent this species. Moreover, the extent of the hemelytral fascia in *L. caricis* is variable and some individuals may be keyed out as *L. depictus* in Barber's 1921 key (Sweet 1963). The association of *Scolopostethus "atlanticus"* (=*"thomsoni"*) with Torre-Bueno's *depictus* is also similar to the present association.

General Biology

It is clear that this species must have considerable difficulty in colonizing new habitats as all of the specimens collected or seen were brachypterous or submacropterous, and incapable of flight. When collected or disturbed on *Carex* heads the insects either dropped or ran down the stalks to the ground layer, and at no time attempted flight. Collecting at night by lights at this location drew *Pachybrachius albocinctus,* but not *L. caricis.* Yet Pink's Ravine pond is definitely an artificial one and is of no great age.

This is an extremely rapid moving insect and, in its speed, very similar to *L. depictus,* a much larger species but its closest relative (Sweet 1963).

In the field it appears that the narrow form of this species (much narrower than other *Ligyrocoris*), along with the pale margin of the hemelytra which increases the apparent slimness, may be a camouflaging adaptation to the narrow leaves of the *Carex* as in many other grass and sedge feeding insects. Otherwise the coloration is a procryptic fuscous and black.

The nymphs are clearly ant mimics with a broad white band across their fuscous and white spotted abdomens. This mimicry is especially apparent in their rapid jerky movements when disturbed.

While these insects pass their entire nymphal life history on *Carex* seeds, they feed quite readily on sunflower seeds. Indeed such is the low fertility of the *Carex* seeds brought into the laboratory that it is safer to rear the species largely on sunflower seeds, although they can be reared readily on the sedge seeds.

Mating behavior is, in general, similar to that of the other species. The male courts the female with a jerky dance which is probably a stridulation dance as discussed under *diffusus.* In the mating patterns, there are some significant differences. First the male is much less excitable than in the other species and requires a number of contacts with a female before any sexual response is elicited. Second, the female takes a much more active role in the courtship pattern. When contacting a male, and before the male shows any recognition, the female in each case advances shortly on the male, her antennae wagging rapidly. This prior advance was not seen in the other species. After three or four such advances the male, which has moved but little, suddenly begins the courtship dance whereon the receptive female quiets a little and usually after two or three attempts which the female repels in the fashion of *diffusus* the male will accomplish copulation. As in *diffusus* the male jerks continuously and vibrates the antennae rapidly when initiating copulation. One copulation lasted 2 hours 15 minutes. As in *L. diffusus,* copulation may occur repeatedly in the young female, but an old female (in this case over 20 days old) would not mate. Males caged together would occasionally advance on one another. A female which lost its antennae was unable to recognize the males and never copulated as in *L. diffusus.*

It is rather interesting that although the males of the other species of *Ligyrocoris* reacted with the different female species, they showed no response to *L. caricis* females and nor did *L. caricis* males react to females of other species. However, the introduction of the male of another species with *L. caricis* stimulated a very obvious avoidance reaction, in which the female raced to and fro across the dish despite the quietude of the alien male.

As in *diffusus* the wagging antennae indicates ''annoyance'' during feeding when intruded on by another individual. Often the insects would run about with the small *Carex* seeds suspended on the end of the labium when it was folded under the body.

Life Cycle

As in *L. sylvestris* and *L. depictus,* there is one generation a year with a long diapause as an egg. Partly due to the high water table in May, and perhaps because of their small size, I could not find the early instars in the field. The observed phenology is as in Table 12.

TABLE 12

Phenology of *Ligyrocoris caricis*

Date	Instar 3	Instar 4	Instar 5	Adult
May 29	25%	75%	——	——
June 8	——	67%	33%	——
June 12	——	——	100%	——
June 25	——	——	84%	16%
June 28	——	——	44%	56%
July 11	——	——	——	100%

Diapause intervenes in early anatrepsis when the egg is white. No further development occurs in the laboratory indicating a strong diapause. I was unable to break diapause with cold exposures of two to four months at 4° C. As the species oviposits shortly after becoming adult, egg diapause in the field must last as in *L. depictus* through the summer as well as through the winter. Such a seasonal cycle may not only be adapted to the host sedge plant, but may also serve to allow a late summer drought period. Such a rapid life cycle may also adapt this species to a much shorter summer season. It may be conjectured that this species will be found much farther north and indeed some of the records of *L. diffusus* as Lindberg's (1958) from Newfoundland may represent this species.

Since only the late instar nymphs were found the stadia are not available except for the last instar. It averaged 6.8 days, and ranged from 6-7 days. The male and fertilized female longevities are similar: mean, 33.0 days, range 31–36 days. A virgin female lived longer, 48 days.

The precopulatory and preoviposition periods are nearly the same, 5.0 and 5.5 days respectively, as oviposition occurs shortly after fertilization. The average fecundity of four females is 133 eggs (range, 125–151 eggs). The oviposition period is from mid or late June to late July. The eggs are laid singly at the rate of 4.8 a day. The rate could be varied by not providing an appropriate substrate to oviposit into. The female would retain its eggs for a few days and become quite swollen, and then would lay a large complement of 10–11 eggs.

The eggs are slender and smooth, not beset with knobbed hairs as in *L. diffusus* and do not stick to objects. They are laid preferably on loose wet methyl cellulose, wet soft *Carex* debris, and not on dry substrates as in *L. diffusus* and *L. depictus*.

To Be Continued

PRINTED BY BUSINESS PRESS, INCORPORATED

ENTOMOLOGICA AMERICANA

A JOURNAL OF ENTOMOLOGY.

VOLUME XLIV (NEW SERIES)
for 1964

PUBLISHED BY THE
BROOKLYN ENTOMOLOGICAL SOCIETY
1964

ENTOMOLOGICA AMERICANA

Vol. XLIV (N.S.) 1964

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VOL. XLIV (NEW SERIES)

ENTOMOLOGICA AMERICANA

A JOURNAL OF ENTOMOLOGY.

PUBLISHED BY THE

BROOKLYN ENTOMOLOGICAL SOCIETY

1872

PUBLICATION COMMITTEE

JAMES A. SLATER, EDITOR

GEORGE S. TULLOCH JOHN HANSON

Published for the Society by the
Business Press Inc.
N. Queen St. and McGovern Ave., Lancaster, Pa.
Subscription $6.00 Per Year
Date of Issue December 29, 1964

ENTOMOLOGICA
AMERICANA

VOLUME XLIV

THE BIOLOGY AND ECOLOGY OF THE RHYPAROCHROMINAE OF NEW ENGLAND (HETEROPTERA: LYGAEIDAE). PART II[1]

By

Merrill Henry Sweet[2]

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In Part I the ecology of the Rhyparochrominae was discussed in general and six of the species were taken up. In the present and final part the remaining rhyparochromine species of New England are considered.

Attention should be called to the recent work of Eyles (1963a, b, c, d) upon the biology of nine British rhyparochromine species which came too late to be included in Part I.

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[1] A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Connecticut.

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Zeridoneus costalis (V. D.)

Zeridoneus differs from *Ligyrocoris* in lacking an abdominal stridulatory area. At present the genus contains only two species. However as shown by Ashlock and Lattin (1963), *Z. costalis,* along with such *Ligyrocoris* species as *L. latimarginatus* Barb., *L. litigiosus* Barb., *L. obscurus* Barber (and perhaps a few others) forms a rather compact group of species that are similar in general structure and type of aedeagus. Under high magnification the epidermal cells of the normal stridulatory area in *Z. costalis* are clearly aligned in raised parallel rows essentially similar to the much more distinct condition in *Ligyrocoris.*

Even with the potential inclusion of these other species, *Zeridoneus* has a distinctly Nearctic distribution. The other known species, *Z. knulli* Barb., was described from western Texas (Barber 1948a). Of the species of *Ligyrocoris* related to *Zeridoneus, L. obscurus* is known from the eastern United States in a narrow band from Maryland to Kansas; *latimarginatus* Barber from the northwest Pacific coast of United States; and *litigiosus* from Florida to Arizona and Mexico (Barber 1921).

Zeridoneus costalis itself is a north temperate species found in the eastern half of northern North America from Alberta and Manitoba to Quebec and south to Iowa, northern Illinois, southern New England (Slater, Catalogue), and also in the highlands of North Carolina (Brimley 1944). It may be significant that the ranges of the above species, for the most part, are allopatric. Froeschner (1944) recorded a specimen of *Zeridoneus* from Missouri, but stated that Barber was uncertain whether it was *Zeridoneus costalis* as it differed considerably in color. This specimen may represent a relict Ozarkian population or a separate species.

While *Z. costalis* is generally considered rare (Blatchley 1926, Slater 1952), in Connecticut I found it to be of average abundance compared to other rhyparochromines.

Environment

Zeridoneus is found in open field habitats in relatively early succession stages, but the general aspect of these habitats varies considerably. It is found at such ruderal sites as vacant lots and road sides, on flood plain pastures, along the disturbed field side of mesic woodland ecotones, in tall herb fields, and even in some small drying marshes. These sites vary in exposure from completely open to semi-shaded. It is clear, however, that *Zeridoneus* has a mesic (5–6) ground layer biotope preference, and even in the drier open habitats it is found in relatively moister sites than *L. diffusus,* such as in the margin of litter of a thick grass pile, in the shade of a *Panicum* clump, or near a riverside. It is never found on dry, well drained slopes such as those dominated by *Festuca, Stipa,* or *Andropogon.* The highest populations (20 per square meter) of *Zeridoneus* were found on several newly abandoned gardens in the semi-shade of a woodland margin, among the pioneering plants *Panicum* spp., *Agropyron repens* (L.), *Rumex obtusifolium* L., *Chenopodium album* L. and other forbs.

At more ruderal sites, *Zeridoneus* is frequently found in moderate abundances (6–8 per square meter) at the base of *Panicum* sp., *Potentilla recta* L., *Centaurea, Cichorium intybus* L., *Chrysanthemum leucanthemum* L., *Daucus carota* L., *Plantago* sp., and other rank plants.

While the vegetation cover varies from complete to areas with considerable bare soil, the greater abundances are found in the more sparsely covered disturbed sites, or where the general cover is quite short, under 6 inches, interspersed with larger grass clumps. The soil is sandy or loamy, frequently dark, reflecting the relatively mesic sites. The litter layer is usually sparse, except where once it was artificially piled and provided a habitat for *Zeridoneus* in a site otherwise dominated by *Ligyrocoris diffusus.*

Although *Zeridoneus* was not swept from plants in the favorable habitats, it was swept in small numbers at sites where it was not found on the ground layer. Slater (*in litt.*) swept it from tall rank herbs near Lake George, New York but also did not find it on the ground. (Only adults were collected by sweeping.) According to Blatchley (1926) Barber collected a specimen from high weeds along the bank of a stream in the Adirondacks. Barber (1928b) collected it on a semi-xeric hillside in the Adirondacks and, significantly, described the habitat as adjoining a woodland. Hendrickson (1930) collected it in a *Stipa-spartea- Andropogon scoparius* association and a *Bouteloua curtipendula* association in Iowa.

While the former Iowa community is a climax association (Hendrickson 1930), in the northern and eastern parts of the range of *Zeridoneus* the climax is forest. Thus in the eastern part of its range, *Zeridoneus* is a subclimax species inhabiting open mesic disturbed habitats which are relatively short lived.

General Biology

Zeridoneus is a completely macropterous species. This correlates with its temporary habitat preferences. While there are no recorded light captures, it was frequently observed in the laboratory that new adults are especially active in the evening after sundown and fly readily to nearby lights.

This is another rapid moving long legged myodochine which when disturbed responds by actively running instead of taking refuge in litter. It is usually found on the ground or litter and infrequently in other than loose thin litter. Its dark coloration blends into the more mesic habitats but renders it conspicuous in some of the sandier habitats. The nymphs are darker than are those of *Ligyrocoris* which they strongly resemble. As in *Ligyrocoris,* the running nymphs mimic ants.

A few tachinid parasites of the genus *Catharosia* were reared from the second generation of this species. They emerge shortly after the host becomes adult. The late developing instars that were collected as late as September 21 were all parasitized by *Catharosia.*

This insect utilizes a wide range of ripe food seeds. In the field adults were occasionally observed on the plants feeding on ripe seeds of *Carex lupulina* Muhl., *Potentilla recta* L., *Cichorium intybus* L., and *Chrysanthemum lecucanthemum* L. In the laboratory they feed on these seeds, especially those of *Potentilla;* and also on the hedge-nettle *Stachys* sp., *Festuca* sp., *Rudbeckia* sp., and sunflower seeds. It displays the strongest response to *Rudbeckia* and *Potentilla.* It does not appear to recognize as food the seeds of *Paspalum* sp., *Panicum muhlenbergii* Nash, *Solidago* sp., *Chenopodium alba* L., or *Hypericum* sp. It is readily reared on sunflower seeds from egg to adult. The mortality is lower and the rate of development more rapid when *Potentilla* seeds are added. Nymphs as young as the second instar can pierce the thick sunflower seed coat and feed on the kernel.

The seeds are frequently dragged to more protected sites under methyl cellulose in the laboratory, but no seed defense behavior was observed. Like *Perigenes,* the male smeared its defecations in a thin line, but no associated odor was perceived.

The mating behavior is rather similar to that of *Ligyrocoris* and may constitute additional evidence of the close relationship between these two genera. After contacting a sexually receptive female, the male may become sexually excited. It responds by moving in short bursts on high stiff legs; the abdomen shakes back and forth at the rate of 2 or 3 times a second; and the distal three antennal segments are vibrated rapidly in a horizontal plane and at a right angle to the body and the antennal scape. With this courtship "dance" the male advances on the female frequently touching her with his vibrating antennae. The male often follows a circular path around the female in his attempt to mate with her. Initially, the female, in several trials, gave a quick brief jerk of her legs similar to the male's shaking and actually advanced toward the male. Only in a very few trials was the male observed to complete mating, in the same fashion as described in *Ligyrocoris diffusus*. In 90% of the trials the female decamped. An interesting aspect is that in a culture with eleven pairs of these insects, one male was responsive to only one of the females and would dance only when contacting her, and one other male was responsive to one other female. The excitement of a male may spread by contact to other males, causing them to begin "dancing." When caged alone an unmated male will spontaneously begin to dance despite the absence of a stimulus from the female. This qualifies as a "spontaneous release" of the behavior pattern. When several virgin males are isolated together one male may dance briefly on contact with another male. This release in isolation was not observed in *Ligyrocoris*. Finally, despite the faintness of the stridulitrum, it is possible that these insects may stridulate by the shaking movements of the abdomen as was postulated also in *Ligyrocoris*.

When placed with other large myodochine species such as *Pachybrachius*, *Cnemodus*, and *Pseudocnemodus*, no reaction was elicited from sexually active males or from the alien females. It is therefore significant that while males of *Zeridoneus* did not react to females of *Perigenes*, *Ligyrocoris depictus*, and *L. diffusus*, the females of these genera gave a strong avoidance reaction to the presence of the *Zeridoneus* males. This may further substantiate the apparent close relationship of these genera.

Life History

While the bivoltine seasonal cycle with an egg diapause is similar to that of *Ligyrocoris*, the precise phenology is different. The phenology at Storrs, Connecticut is shown on Table 13.

Adults were found *en copulo* in the field September 9. Ovipositing females of the first generation were found after July 11 and the second generation after September 9.

The reproductive pause from mid-June to early July cannot be considered merely as an immature period, for in the second generation oviposition occurs shortly after this generation becomes adult. The result is that the second generation occurs largely in August, which is about a month later than in *Ligyrocoris*.

This data suggests that reproductive activity occurs during shortening photoperiods and during long photoperiods non-diapause eggs are laid while in short photoperiods diapause eggs are laid. While no experiments were performed, this hypothesis explains the occurrence of 26% non-diapause eggs in two second generation females which were forced to early maturity under the prevailing photoperiod in the laboratory by August 18. This aspect is discussed later.

Autumn eggs entered diapause in early anatrepsis. The diapausing eggs never broke diapause in warmth and died in mid-winter. Short cold exposures of 1 to 6 weeks and three months did not terminate diapause. Diapause was broken by cold exposures (35°F.) of 192 and 212 days (six to seven months). Unlike other species, the majority of the diapause-released eggs developed nearly in unison and the hatching was only weakly staggered, with a few of the eggs hatching later.

TABLE 13

Phenology of *Zeridoneus Costalis*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
May 27	73%	20%	7%	——	——	——
June 10	——	——	20%	20%	45%	15%
June 18	——	——	——	18%	32%	50%
July 5	——	——	——	——	9%	91%
July 12	——	——	——	——	——	100%
July 27	72%	——	——	——	——	28%
Aug. 7	——	25%	40%	15%	——	20%
Aug. 18	2%	8%	22%	35%	23%	10%
Sept. 3	——	——	——	——	15%	85%
Sept. 20	——	——	——	——	10% *	90%

* parasitized

It would seem that the later eclosion of *Zeridoneus* eggs in the field than those of *Ligyrocoris* of almost contiguous habitats stems from the earlier onset of diapause and consequent longer spring development. Moreover *Zeridoneus* eggs are laid in cooler more shaded biotopes than *Ligyrocoris* which would become warmer later in spring.

The rapid field development of the stadia of laboratory reared specimens is reflected in Table 14.

After release from diapause the overwintered eggs develop in 14 to 17 days. Adults of the spring generation persist until mid-August and the average longevity is 47 days (range 35–57 days) in the laboratory. In the autumnal or second generation the adults, presumably since they become reproductive earlier, live for a shorter period in the laboratory (mean, 34.5; range, 28–39 days). The insects are relatively cold hardy, and persist in the field until as late as November 6. This field longevity is distinctly longer than that found in laboratory specimens, undoubtedly because of the cooler field temperatures. Cold exposure of the adult females for a week does not affect the egg diapause condition.

TABLE 14

Stadia of *Zeridoneus costalis*

Egg*	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
11.0 (11–12)	4.2 (4–5)	4.9 (4–6)	5.0 (4–6)	5.6 (5–7)	6.7 (5–10)	36.5 (32–45)

* Generation 1

Virgin females have a much longer adult life span in probable correlation with their low reproduction activity (mean 57 days, range 43–71 days).

As noted under the diapause discussion, the preoviposition periods of the spring and summer generation are quite different. The first generation adults do not become sexually active until the first week in July, and the precopulatory and preoviposition periods vary accordingly and average 20 days. In the second generation the precopulatory period is as short as 3 days, the preovipositional period 4 days in the field adults which have become mature from August 29 on. However, adults reared to maturity under prevailing daylight earlier than mid-August likewise did not become mature until the first week of September. This oviposition pattern may be readily explained by a photoperiodicity mechanism with the critical points after the summer solstice (15 hours) and in late August (13.5 hours).

The fall and spring generations have similar laboratory fecundities which vary from 99 to 231 eggs (mean 164). The eggs are laid at the rate of 5.5–8.7 eggs a day (mean 6.4). Sexually isolated females laid none or very few eggs (0–20, mean 7.3). One female, however, laid 50 eggs at the rate of 2.2 eggs a day.

Like *Ligyrocoris diffusus*, the rounded cylindrical eggs are covered with a layer of short fine hairs and the eggs similarly cling to debris. They are laid singly into litter crevices, into fallen ripe seed heads and sepals of *Potentilla* flowers (from which they could not be shaken), in hollow stems, and into dry loose soil or litter. The female spends considerable time probing at a site before ovipositing. This is apparently related to a definite spatial contact requirement for oviposition. A gradient of sand grain sizes was formed by shaking sand in a petri dish. On such a gradient, the female selectively laid her eggs in a zone of sand particles which were similar in size (and in interspace) to *Zeridoneus* eggs.

Perigenes constrictus (Say)

Only the more recent literature can be accurately associated with *Perigenes constrictus,* as this large dark species was thoroughly confused in the literature with *Zeridoneus costalis* (Say) and *Ligyrocoris abdominalis* Guerin (Heidemann 1903, Van Duzee 1909) which it superficially resembles.

As presently defined *Perigenes* Dist. contains two other species; *P. dispositus,* the type, from Guatemala, and *P. similis* from the southeastern United States. *P. constrictus* is a northern species and the southern records are undoubtedly referable to *L. abdominalis* Guer. (Barber 1914b, Van Duzee 1914). It is recorded from Quebec and South Dakota south to North Carolina and Texas, and also from Colorado, California, and Alaska (Slater, Catalogue). The great majority of the records are from the central and eastern United States. In the Midwest its range apparently broadly overlaps that of the more southern *P. similis.* While Slater (1952) reported it as relatively common in Illinois and Iowa, Froeschner (1944) found it uncommon in Missouri and *similis* to be the much more abundant species. Blatchley (1895) considered it rare in Indiana. In New England, I collected it only in Connecticut, and only a few temporary populations were found. It appears to be more common along the coast. It cannot then be considered a particularly common species, but its large size and ruderal habitat preference would cause it to be more frequently collected than indicated by its abundance after precise collecting.

Environment

P. constrictus is typically collected in exposed, level ruderal habitats in vacant lots, roadsides, and newly fallow fields. In general it is found in a slightly later seral stage than *L. diffusus,* and in a community of rank forbs and grasses such as *Angropyron repens* L., *Chenopodium album* L., *Erigeron canadensis* L., *Ambrosia artemsiifolia* L. The herb layer is usually two to three feet in depth.

This is a distinctly more mesic habitat type than that of *L. diffusus.* The ground biotope is shaded from direct sunlight by the field layer, and little litter is present on the ground. The soil is usually a loam or sandy loam, moderately dry (3–5), and the soil temperature moderate. Only once was the species swept from low ruderal forbs.

An exceptional occurrence was the presence of nymphs in a wash habitat at Mansfield, Connecticut along with a number of other rhyparochromines. However in this favorable seed-filled habitat, *Perigenes* was found in a zone of moisture and temperature which approximated the more normal habitats.

The abundance of this species varied from one or two to as many as 20 per square meter at one favorable habitat in a vacant lot at Noank, Connecticut which was dominated by *Agropyron repens* L. At none of the sites in Connecticut was the species collected more than two years in succession, and this only with fall ovipositing adults and the resultant spring generation.

The available habitat notes largely confirm this habitat choice: Hussey (1922) collected it on Indiana sand dunes area on ragweed, and found another on sand by a road. Torre-Bueno (1910) collected it from short grasses in New York, and Blatchley (1926) records sweeping it from herbage along streams and on mulleins in June and July, in sphagnum moss in August, and under logs in November. Froeschner (1944) collected it among weeds in a low marshy field. Dowdy (1947) collected it from the herb layer in a oak-hickory forest margin.

General Biology

In correlation with its preference for temporary habitats, *Perigenes* is entirely macropterous. While it has not been previously recorded from lights, I have collected three specimens during early July at lights at Noank, Connecticut. *Perigenes similis* has been collected at lights in Missouri by Froeschner (1944), and in Florida by Hussey (1952). Glick and Noble (1961) collected *P. constrictus* (?) by airplane at 200 feet in Louisiana.

This large species is procryptically colored, its dark fuscous coloration blending into the dark loam substrate of many of its habitats. Occasionally, however, it is found on lighter sandy loam on which it is very conspicuous, especially when moving. The later instar nymphs are similarly colored a dark fuscous, the abdomen patterned with minute pale spots. This is a *relatively* slow moving heavy-bodied myodochine, and appears to rely on its coloration and concealment in its rank plant habitat. It shows little tendency to take cover under litter or debris.

A *Catharosia* tachinid fly parasitizes *Perigenes*. All parasites were reared from the second generation *Perigenes*, and emerged shortly after the host became adult. This early emergence correlates with the egg overwintering diapause condition of this species. The rate of parasitism is low, under 10%. No predators were ascertained.

While this species is readily reared on sunflower seeds from any field-collected nymphs, only a few first instar nymphs, despite active feeding, develop past the first or second instar. Those that did were reared through the life cycle. This species feeds on the seeds of *Chrysanthemum leucanthemum* L., *Ambrosia* sp., a grass (*Agropyron repens*), *Rudbeckia* seeds, and probably feeds on many others.

No expression of seed territorially was elicited from *Perigenes*. Unfortunately the mating behavior was not observed. The males, however, possess an unique peculiar odor which is associated with their defecations. Moreover, when defecating, the male, as the drop is released, moves forward a few steps and smears a long streak of the odorous material. Presumably the odor and the smearing behavior play a part in this species's mating behavior. This odor is very persistent, and several dishes still retained the odor after four years.

Life History

While Blatchley (1895, 1926) considered this species to overwinter as an adult in Indiana, it actually overwinters as an egg, but the adults are cold resistant and persist until late in autumn. Blatchley recorded specimens ''under logs'' in November and on December 10. I have taken actively ovipositing females as late as November 16. There are two generations a year but the non-diapause spring generation was indeed scarce. Only in the second generation was *Perigenes* found in any numbers.

The available phenology at Storrs, Connecticut is as given in Table 15.

While this life cycle parallels that of *Ligyrocoris diffusus*, the second generation occurs later in the summer. Probably a similar photoperiodicity is involved.

The onset of diapause occurs in early anatrepsis. Unlike *diffusus* cold exposure does not affect the female's capacity to lay diapause eggs. The strength of the diapause condition is quite variable. A few eggs develop within a month in warmth after being laid and a few others continue to come out of diapause all through the winter. About two-thirds of the eggs, however, never develop in warmth. When placed in cold (35°F.) for five months, the eggs hatch readily but again at staggered intervals, which suggests a protective spreading out of the spring eclosion. Once diapause terminates egg development occurs rapidly. In thirteen days after removal from cold, first instars hatched.

TABLE 15

Phenology of *Perigenes constrictus*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
May 18	——	33%	67%	——	——	——
May 26	——	——	50%	50%	——	——
June 9	——	——	——	——	50%	50%
June 20	——	——	——	——	——	100%
July 12	——	——	——	——	——	100%
July 15	5%	15%	35%	20%	——	25%
Aug. 20	——	——	10%	16%	30%	44%
Aug. 28	——	——	——	12%	44%	44%
Sept. 15	——	——	——	——	——	100%

The stadia in Table 16 are based on rather small samples and no averages are given.

Spring adults lived in the laboratory until late July and early August and averaged 45 days (34–56 days). The fall generation lives longer, averaging 76 days (60–82 days).

TABLE 16

Stadia of *Perigenes constrictus*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
12(?)	6	6–7	6	6–7	7–8	45

The reproductive capacity is very great, averaging 268 eggs (184–330) which are laid at a rate of 7 to 8.5 eggs a day. The eggs are laid singly when an appropriate substrate is available or in batches of 8–10 when a substrate is withheld. The eggs are preferably laid in dry substrates, and like *Ligyrocoris* the eggs are oviposited deeply into the substrate of methyl cellulose, cotton, or sand. These eggs do not cling to the litter or sand. Even into firm sand the female was able to oviposite. Two virgin females laid no eggs.

Sphaerobius insignis Uhler

Among the rhyparochromines of New England, *Sphaerobius* is the most remarkable ant mimic. Three species are presently placed under *Sphaerobius,* but Slater (*in litt.*) informs me that the type, *S. gracilis* Uhler from St. Vincent Island does not appear to be congeneric with *S. insignis.* It is unfortunate then that Van Duzee (1917) fixed *gracilis* as the type, not the well known *insignis.* The third species, *quadristriatus* Barber, was placed close to *insignis.* Bearing this situation in mind, we may consider *"Sphaerobius"* in the sense of *insignis,* to be a purely Nearctic genus.

The two species are quite different in distribution. *S. quadristriatus* is known at present only from New Jersey. Other records refer to *insignis. S. insignis* has a northern or boreal distribution across North America from Newfoundland to British Columbia, and south to northern New York, Connecticut, Iowa, and in the western mountains to Colorado (Slater, Catalogue). In New England, *insignis* is found only as far south as northwestern Connecticut, and moreover, is scarce south of the northern tier of New England states.

Environment

Like *Cnemodus* this species is especially common on open dry barren sites among sparse clumps of the grass *Andropogon scoparius* Michx. It is frequently found on roadsides and railroad right-of-ways which are dominated by the above association. It is not found at all in ruderal sites dominated by new field forbs. Truly remarkable abundance levels (up to 60 per square meter) were found in an andropogonetum association along a railroad right of way in the southern Adirondacks near Warrensburg, New York. The soil on such open xeric sites is overdrained and very dry (1–2), and during the day becomes very hot (up to 50°C.). It was observed at several sites that in the early morning and late afternoon, the insects were found in the open bare areas, and as the day progressed became restricted to the litter of the *Andropogon* clumps.

When the ground cover becomes completely filled in by other grasses, the abundance of the insect is much lower (1–5 per square meter). At a site in Canaan, Connecticut a definite gradient in abundance was traced from a filled-in margin to a bare soil area. It is clear that these habitats are essentially temporary. The poor overdrained gravelly soil, however allows only a very slow succession to proceed.

Hendrickson (1930) found *Sphaerobius* to be very abundant in a climax prairie association of *Andropogon* and *Stipa.* It may be that the eastern populations represent an influx of a western population, but Lindberg (1958) reports that it was found in Newfoundland on open swampy ground with *Carex* and *Sphagnum* near the seashore. It is evident that much more field work needs to be done over the entire range.

General Biology

The populations studied consisted of a majority of brachypterous (flightless) adults with a minority (ca. 20%) of macropters. No relation appears to exist, however, between population density and macroptery. It is evident from the natural situation that the production of macropters is sufficient to maintain *Sphaerobius* in the scattered mosaic of suitable sites. It would be interesting to see whether north midwestern populations in presumably widespread permanent habitats exhibit a lower frequency of macroptery.

Sphaerobius exhibits a most interesting color polymorphism which is unique among the rhyparochromines studied. In large populations about 50% consisted of dark individuals, most of the remainder of light tan individuals, and a few intermediates. This is not a generation or developmental change in color as in many mirids (Kullenberg 1944), for the final color pattern develops shortly after molting. There is no apparent relation of color to sex or brachyptery.

The ant mimicry effect is gained by transverse white bands on the corium, a narrow swollen thorax and a somewhat myrmeform head. The nymphs are yellow-brown in color with white markings on the abdomen, and the abdomen is narrowed near the junction with the thorax. The mimicry effect is greatly emphasized by an irregular ant-like gait when running. The effect of this combination in the field is of a population of very large black, red, yellow-red, and smaller yellow ants (the earlier instars). The only ant found anywhere near the adult range was the much smaller *Formica rufa,* and the lygaeids were frequently as abundant or much more abundant than the ants at a given site. The ant mimicry effect was noted by Barber (1922) and Parshley (1921) who also noted an association with ants. Such an association, however, is inevitable in the dry habitats preferred by *Sphaerobius.*

Sphaerobius is parasitized by *Catharosia* tachinid flies. Parasitism appears to occur during the late instars and emergence occurs from the adults. There is no diapause, the fly emerging a short time after the insect becomes adult, which correlates with the egg diapause in *Sphaerobius.*

Sphaerobius feeds on the seeds of the grasses *Andropogon scoparius, Panicum* sp. and *Paspalum* sp. It feeds readily in the laboratory on sunflower seeds on which it can be reared very easily.

Seeds are defended by quick rushes with flailing antennae, and annoyance is shown by rapid antennal wagging.

The courtship pattern in *Sphaerobius* involves a rapid shaking jerking motion by the male when approaching the female much as in *Ligyrocoris* and *Zeridoneus*. It is therefore interesting that *Sphaerobius*, like *Ligyrocoris* also has a faint striated area (or stridulitrum) on the sides of abdominal segments three to four (Ashlock and Lattin 1963). The remaining mating process is much as in *Ligyrocoris*.

Life Cycle

Sphaerobius insignis has a bivoltine seasonal cycle with a facultative egg diapause. Only a general description can be given here as much of the quantitative data on this species was lost. The phenology at Canaan, Connecticut is as follows: Early instar nymphs were found as early as mid-May, but third and fourth instars were present as late as mid-June, apparently from a staggered eclosion. The first generation adults appeared in mid-June and oviposition began in late June. The late maturing nymphs became adult by early July. In late July at Warrensberg, New York, second generation nymphs of all instars were present.

As in *Ligyrocoris depictus* there is no mid-summer reproductive pause, and the oviposition of diapause eggs begins in August after a brief precopulatory period. Fourth and fifth instars were found as late as mid-August. Diapause occurs during early anatrepsis, and is a strong one. The diapause is probably under photoperiodic control since several second generation cultures laid non-diapause eggs under long photoperiods. A few eggs broke diapause after several months but nearly all required cold exposure of several months to terminate the diapause state.

This bivoltine seasonal cycle is unusual for a rhyparochromine with a northern distribution. Very probably this is made possible by the generally hot exposed habitats selected by *Sphaerobius*.

Sphaerobius has a very high reproductive capacity, and in the laboratory the fecundity varies from 180 to 350 eggs per female. Sexually isolated females laid no eggs. The eggs are curved-cylindrical with rounded ends and heavily and densely beset with hairs. The eggs stick to objects and become densely covered with sand grains and debris when laid in the ground. An egg is laid after a careful examination of the site. The eggs are laid singly in loose fine litter into soft ground, and into methyl cellulose and cotton. The eggs are not laid on wet substrates or bare substrates.

Sphaerobius quadristriatus Barber

I have not been able to find this most interesting and apparently very rare species which was described from Lakehurst, New Jersey by Barber in 1911. From the type locality and a history similar to *Malezonotus fuscosus* it is very likely that *S. quadristriatus* is one of the endemic pine barren forms (see *Malezonotus*). The three known males were all brachypterous, and collected on July 4 and September 7, 1909.

Pachybrachius Hahn

This large and cosmopolitan genus is known from all zoogeographical regions, especially from tropical areas. Presently 71 species are placed in this genus, but many do not belong here, for the genus was a convenient one for placing new myodochine species, especially under the name *Pamera*. Scudder (1962), for example, has moved many species into several other genera.

In New England three species are recorded, *basalis*, *albocinctus*, and *bilobatus*, each of which represents a different northern extension in New England. Only the former two were found in the course of this study. Eventually two others might be found, the European *P. fracticollis* and *P. luridus* which may have been successfully introduced into Canada as both species are adapted to boreal swamps and sphagnum bogs (Krogerus 1960, Southwood and Leston 1959, *et al.*), a niche which is apparently unfilled in Canada.

One other species, *occultus* Barber, occurs in the western United States, in Idaho, Montana, and Colorado. Ashlock (*in litt.*) says the genus *Pachybrachius* does not occur in California.

Pachybrachius basalis (Dallas)

This species is one of the most abundant rhyparochromines in New England. It is distributed in eastern North America north to Quebec and Minnesota, west to Iowa and New Mexico, and south to Texas and south Florida (Slater, Catalogue). Uhler's (1894) record of it from Grenada in the West Indies is probably incorrect in the light of the otherwise known distribution. It is found more abundantly in the southern parts of New England than farther north.

Environment

P. basalis also appears to have perhaps the largest ecological range among the New England rhyparochromines, which considerably magnifies its apparent abundance. While it is occasionally found hibernating in late autumn with *Myodocha* and *Heraeus* in light woodland sites, it is definitely an insect of field habitats. It is found from relatively moist mesic streamside meadows with rank plants to fairly dry upland old fields. Its greatest abundances are reached on rank hillsides and roadsides covered with the large coarse panic grass, *Panicum* spp. It is commonly collected at ruderal sites and along garden margins. Uhler (1876) recorded it from wheat and grass fields in spring and summer, and Blatchley (1895) found it rather common on the borders of cultivated fields. This wide ecological amplitude is further shown by the collection of it in a small marsh in Michigan (Hussey 1922). Indeed such is the variety of habitat types in New England that it frequently appears that two species are involved since the wet site populations are distinctly larger and darker than the dry slope populations. However the two forms interbreed readily in the laboratory, intergrade completely with each other when insects from all habitats are compared, and have the same sort of life cycle, so these population types are perhaps comparable to ecophenotypes. It appears that these forms may be what Blatchley (1926) was considering when he separated a smaller *curvipes* Stål from a larger *basalis*. Barber (1953b) synonymized the two.

It is easier to state where *P. basalis* was *not* found. It was not found on dry very old fields especially those with north exposures; on hot exposed open ground; nor in ericaceous scrub, and uncommonly in woodland glades and margins. It was never swept from vegetation. A few were sometimes found in flood wash with *Peritrechus fraternus*.

In Florida it was found in grass clumps in the slash pine-palmetto association, but was not found in ruderal sites as these appeared to be preempted by other rhyparochromines especially *P. bilobatus*. As Blatchley noted, only the smaller form appears to be present in Florida perhaps for the above reason.

The ground biotope was then always at least semishaded by the herbaceous vegetation. Soil moisture estimates ranged from 3 to 8, and litter temperatures were rarely over 30°C.

Among the tall *Panicum* grass clumps the abundance frequently attains 60–70 per square meter, while the lowest abundances (1–3 per square meter) are in the more xeric sites with a shorter grass. It is significant that the most favored habitats are relatively short lived succession stages.

Overwintering largely occurs *in situ,* although some appear along woodland margins in autumn, a few move even into woodlands.

General Biology

In agreement with its preference for early succession stages, *P. basalis* is entirely macropterous. In probable dispersal, it has been collected at lights (Tucker 1907, Torre-Bueno 1914, Froeschner 1944). Torre-Bueno (1927) found it washed up in beach drift on Long Island. Glick (1939) collected it by airplane at 1,000 feet over Louisiana.

In general form, *Pachybrachius basalis* is fairly generalized, and is not an especially fast runner, nor does it conceal itself among the tangled litter of stems and grass. The coloration is distinctly procryptic, a dull brown with a few light flecks on the hemelytra to break up the pattern. The nymphs display a disruptive color pattern in the later instars, and are pale yellow and red in the earlier instars.

P. basalis is extensively parasitized by the tachinid *Catharosia.* The parasite was reared only from the second or summer generation. The parasite overwinters in the host *Pachybrachius.*

P. basalis is especially partial to feeding on grass seeds, especially *Panicum* spp. and *Paspalum* spp.; it also feeds on *Festuca* spp., *Bromus* sp., *Andropogon scoparius* Michx, *Poa* spp., but ignores these and various forb seeds when *Panicum* or *Paspalum* seeds are present. It would feed sparingly on *Oenothera* and *Rumex* seeds, and could be reared from field first instars on sunflower seeds. However, the mortality of the laboratory reared first instars is very high when reared on sunflower seeds alone. *P. basalis* does not show any feeding reaction to pepper grass (*Lepidium* sp.), *Hypericum* sp., *Aquilegia canadensis* L., *Chenopodium albus* L. or various small composite seeds. As *Panicum* is an enormous genus with many large and small species, this grass was present in most of the habitats. Torre-Bueno (1946) mentions *P. basalis* as being found on strawberries, but I was unable to rear even late instars upon this plant or its seeds. An excellent and effective rearing technique is a mixture of *Paspalum* and sunflower seeds. The presence of a few *Paspalum* (or *Panicum*) seeds circumvents much of the first instar mortality. It is noteworthy that the labium or beak of this species is unusually short, and probably correlates with the small size of the preferred grass seeds.

Only with *Panicum* and *Paspalum* seeds could the remarkable seed defense behavior of this species be elicited. The seeds are frequently picked up with the labium and moved to a more protected site for feeding. When intruded on by another, a feeding bug endeavors to keep the seed away from the intruder. If the aggressor persists, the defender flutters or rapidly flicks its antennae back and forth through a 35° arc directly above its head. If this fails to dissuade the aggressor, the defender then ceases feeding, and with the antennae continuing to flutter, it quickly advances on the intruder. On contacting the intruder, the defender rapidly flails his legs. Usually the intruder decamps at this point. If not, the defender spreads its fore femora wide, holding them stiffly at right angles to the body, and rears up on its hind and middle legs. The intruding *Pachybrachius* immediately responds with a similar posture, and the two advance on each other, and rise into a vertical biped position on their hind legs. Through this encounter the insects vigorously flail their fore tibia, and middle legs, and flutter the antennae very rapidly until one insect topples over. When this happens they immediately desist, and the loser, which in the observed cases was always the intruder, decamps. If the insects are hungry, this activity may be repeated again and again by the same insects. In no apparent way was any harm done to either insect. Of considerable phylogenetic interest is the similarity of the total defense pattern to that of *P. bilobatus*. In *P. basalis* both sexes are involved and there is no association with sexual behavior, although in *P. basalis* the male may, and does, take advantage of the female's passive feeding posture.

The mating behavior appears to be simple. A male responds to an appropriate female on contact by rapidly vibrating his antennae. If the female remains still the male usually attempts to mount, whereupon the female gives a rapid ''annoyance'' fluttering of her antennae. If the male at this point succeeds in mounting, he rapidly vibrates his antennae upon her head, and if the female is receptive, copulation is quickly accomplished. The male then drops off into an end to end position. More often the female dislodges the male, and decamps or may continue to stand him off with her antennae fluttering, especially if she is feeding on a seed, and the male may again attempt to mount the female. Certainly, at least under the laboratory conditions, the male's chances of mating with the female are greatly enhanced when she is feeding on a seed.

Life History

P. basalis in New England has a bivoltine seasonal cycle with a faculative adult diapause. Fertilization occurs in early spring as most females collected in April were fertilized, while those collected before March 20 were not. A pair was found *en copulo* in the field on March 29. However, as in *Myodocha*, the earliest nymphs are not found until early June and only the fourth instar was attained by June 23. Some first generation adults, however, appear before July 1, and a few first generation fifth instars were present as late as July 17. With this maturation variability and especially given the long oviposition period of one to two months, the second generation nymphs were of considerably different age ranges in different local populations. Thus, second generation first instars were found from July 14 to September 9, and second generation fifth instars as late as November 1. However, many of the late autumn nymphs were parasitized. The observed overall phenology at Storrs is given in Table 17.

TABLE 17

Phenology of *Pachybrachius basalis*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
May 15	——	——	——	——	——	100%
June 1	——	10%	——	——	——	90%
June 15	15%	15%	30%	——	——	40%
July 3	15%	20%	15%	10%	10%	30%
July 17	6%	——	9%	12%	33%	40%
Aug. 5	12%	10%	3%	15%	15%	45%
Aug. 19	——	5%	35%	30%	2%	28%
Sept. 5	8%	8%	12%	12%	47%	13%
Sept. 15	——	——	5%	5%	40%	50%
Oct. 1	——	——	1%	3%	11%	85%
Oct. 15	——	——	——	2%	10%	88%
Nov. 1	——	——	——	——	5%	95%

The second generation adults, which appear from mid-August on, enter diapause under field conditions and overwinter. This is a facultative diapause because it did not appear when the second generation was reared under long day (15 hour) conditions. The converse, rearing the first generation under deliberate short day conditions, was not attempted. However, such a photoperiod relationship renders comprehensible early spring cultures in which the first generation was forced to maturing in the laboratory (normal spring daylight) before early June. These cultures went directly into diapause. The diapause state is only moderately strong and is spontaneously broken under laboratory conditions in late October or early November in adults reared in August. Adults which became mature in September did not break diapause in the laboratory until January. The first generation which went directly into diapause in June became reproductive by mid-August. The period of reproductive cessation averaged two months and varied from 45 days in summer to three months in autumn.

P. basalis population collected at Cherokee and Roam Mt., North Carolina displayed a similar seasonal periodicity and a *P. basalis* population from south Florida collected November 19 at Naranja, was in a state of reproductive diapause similar to the northern populations and similarly required a period of warm laboratory conditions, but here only a five week interval was required to break reproductive cessation. Photoperiods in the late fall were long because of the lighting conditions prevalent in the laboratory.

In the laboratory, on a sunflower seed diet alone, the stadia of the surviving nymphs are variable and unusually prolonged growth rates similar to nymphs captured in the field are obtained on mixed sunflower—*Panicum* grass seeds. The stadia information on this diet under room temperatures are given in Table 18.

TABLE 18

Stadia of *Pachybrachius basalis*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
9.6 (7–12)	7.1 (6–9)	6.3 (5–8)	5.4 (4–7)	6.6 (4–8)	8.0 (6–10)	43.5 (38–51)

The longevity of laboratory summer generations varied from 34–52 days (mean 44). April collected adults survived 26–58 days (mean 39). Diapausing adults in warmth lived 2.5 to 7 months (mean 5). The longevity is then clearly related to reproductive activity.

P. basalis has a fairly long preoviposition period (first generation) of about a week. In the laboratory 62 to 210 eggs (mean 108) per female were laid. In adults which are allowed to complete diapause under warm conditions the fecundities are much lower, varying from 7 to 36 eggs. The eggs are laid singly at the rate of 6–7 per day. Ten sexually isolated females laid no eggs, but one spring female laid 9 eggs. Oviposition occurs freely with sunflower seeds alone, although complete rearing was rare on this diet.

The female investigates each oviposition site first with her antennae, and then with her ovipositor. The eggs are oviposited into crevices, soil, and rather tight wet or dry cotton, even into parenchyma of herb stems and the inner coat of sunflower seeds. The eggs are long, slender, with the apical end somewhat pointed, the anterior flattened, and the chorion apparently has no sticking mechanism. This shape appears adapted for oviposition into firm substrates.

Pachybrachius albocinctus Barber

This species was only recently described (Barber 1953a) as it has been much confused with *P. bilobatus* or following Stål (1862), was erroneously called *P. servillei* Guérin. It may be easily distinguished from *P. bilobatus* by the basal white band on the terminal antennal segment.

Like *P. bilobatus, P. albocinctus* has a remarkably broad distribution throughout the American tropics but extends somewhat farther north to Illinois, Michigan, Ohio, and New York, and is here recorded from Connecticut. Its presence in Connecticut, then, is at the northern edge of its range. A population of this species has been present for at least eight years in Storrs, Connecticut (Slater, *in litt.*) so a permanent population appears to be established.

Environment

This species is closely adapted to wet habitats. Froeschner (1944) collected the species from shrubs and weeds near water and considered it not uncommon in Missouri. Blatchley (1926) mentions sweeping it from low moist ground, and beating it from Spanish moss in Florida. Not surprisingly, then, Wray and Brimley (1943) recovered this species from pitcher plants (*Sarracenia*) in North Carolina. In Florida the relation of the species to water margins was striking and effectively isolated *albocinctus* from *bilobatus* which was found in much drier sites.

In New England *P. albocinctus* was found only at two stations near Storrs, Connecticut. At Pink Ravine (in Storrs), it was found abundantly with *Ligyrocoris caricis* in the *Carex stricta-Scirpus* sp. community on the margin of the pond, frequently above standing water (see *L. caricis* for a description of this habitat). In this community adults of *albocinctus* are frequently swept with *Ligyrocoris* from the early maturing clump-forming *Carex* where they are feeding on the seeds. Much more frequently both adults and nymphs are found feeding on the seeds of the non-clump forming *Scirpus* sp. which matures considerably later. However, only a minority occur on the plants; the majority are found on the ground at the base and in the clumps of *Carex,* frequently even on mud and wet plant debris. The substrate moisture level is very saturated (10) and the temperature moderate. The abundance was low (1–3 per square meter of *Carex* clumps) in spring and rose to about 20–30 per square meter in late summer. These abundances are only approximate because of the counting difficulties encountered in this habitat.

General Biology

P. albocinctus is completely macropterous and when provoked readily takes flight from a *Scirpus* seed head. It was taken by airplane, presumably dispersing, at 200 feet in Louisiana (Glick 1939). It was taken at lights (Barber 1954) and I have frequently collected it at a lighted sheet in July and August. The ability of this species to disperse is perhaps best attested to by its broad distribution not only in continental areas but also throughout the West Indies.

The adults are procryptically colored brown and tan, as is frequent in species living in rank sites. The terminal antennal segment has a basal white band which is especially conspicuous when the resting insects move the antennae to and fro against the dark background of the marsh habitat. Such a band (Cott 1960) is usually interpreted as a device to distract a predator's attention. In contrast, the nymphs, except the first instar, are conspicuous ant mimics with the ''petiole'' formed by white patches upon the anterior abdominal area.

P. albocinctus was found parasitized by a tachinid fly *Alophorella aeneoventris* (Will.) a parasitism which is unusual in that it does not involve *Catharosia.* Sabrosky (*in litt.*) tells me that Dr. Medler has reared a species of this tachinid genus from a mirid bug, *Lygus* spp. The parasites were recovered from specimens of *P. albocinctus* which were found hibernating in late November. The parasites emerged only after a long interval in the laboratory, and so apparently were overwintering in the host bug. *Catharosia* was also reared from *P. albocinctus* collected in Florida.

The adults and all instars feed upon the seeds of *Jussiacea.* The insects could be readily reared in the laboratory on sunflower seeds. For some unknown reason, feeding turned the seeds to a bright green color.

No seed defense behavior was observed in *P. albocinctus.* The mating behavior is as follows: When introduced to a female the male does not overtly respond until he comes in contact with her. However, the female seeks out the male in each case and responds first by rapidly vibrating her antennae. After about 12 seconds the male responds by similarly vibrating his antennae. It is noteworthy that the white antennal band is very conspicuous when so vibrated, which suggests another, perhaps true, function to the white band. After a remarkably long time of such face to face antennae vibrating (45 seconds) the male slowly climbs upon the passive female's right side and vibrates his antennae close to the female's head. The pygophore is extruded, and with the male's claspers (parameres) working he moves the pygophore up and down the side of the lateral side of the abdomen. If the female does not release her ovipositor, the male decamps. Again, the female may seek out the male, and the procedure be repeated. If effective, the female raises her abdomen high, and releases her ovipositor which is then clasped by the male's parameres; in this position each sex is at a considerable angle with the left sides tilted down, a relation which persists when the male drops off into an end to end position. During the initiation of copulation the male suddenly flickes his antennae several times through a 45° arc. This flick is the essential component of the rapid up and down antennal fluttering, the "annoyance" signal of *P. basalis*. Copulations last from 1 hr. 45 min. to 2 hr. 30 min. *P. albocinctus* is completely isolated sexually from *P. basalis* and other large myodochine genera, apparently by a complete nonrecognition.

Life History

In Connecticut, *P. albocinctus* has a bivoltine seasonal cycle with no diapause intervention. The earliest nymphs, however, are not found until late June, and, largely third and fourth instars are found in the field as late as July 25. First generation fifth instars are found as late as August 28. Adults of the new generation appear in early August, rarely in the last week of July. The second generation appears in mid-August, and new adults appear in late September. Many nymphs are still present on the latter date but these are presumably killed by the advent of cold weather as only the adults are found overwintering. It is clear that this seasonal cycle is barely adequate to allow the completion of two generations. There is also no reproductive diapause in the adults whether reared in the laboratory or taken from the field, and reproductive cessation is established by cold dormancy. The overwintered females collected in early spring were unfertilized.

The life cycle in the field took approximately 7 weeks, in the laboratory about 6 weeks. A considerable increment of warmth seems required as the early spring adults would readily oviposit in the laboratory. The tardiness of the spring generation is probably best explained by the cool substrate conditions, since laboratory behavior indicates that eggs are laid in the moist substrate and egg development is relatively slow (11–13 days) even under the warmer laboratory conditions. The laboratory stadia based on the progeny of three females are given in Table 19. Nymphal development occurs much more rapidly and with a much smaller mortality rate on a mixture of *Scripus-Carex* and sunflower seeds than on sunflower seeds alone. The longevity in the laboratory of two mated females was 57 and 74 days of two virgin females 71 and 76 days and of two males, 43 and 45 days.

TABLE 19

Stadia of *Pachybrachius albocinctus*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
12 (11–13)	10.4 (7–18)	9.5 (9–10)	8.5 (6–12)	8.3 (5–11)	8.4 (6–10)	52.6 (45–58)

The precopulatory period is 6–8 days and oviposition occurs 1–2 days later in mated females. Unmated females of the summer generation lay no eggs. The fecundity of 5 females varies from 82 to 231 eggs (mean 140). From 2 to 10 eggs (mean 5.2) are laid daily.

The insects oviposit on wet substrates, but dry substrates are acceptable if no wet ones are present. The eggs are frequently forced into very tight wet cotton stoppers. In correlation, the eggs are smooth, slender, and somewhat pointed at the posterior end.

Pachybrachius bilobatus (Say)

This dominant and widespread species is known from throughout the American tropics north to Missouri, Pennsylvania, New Jersey, and has been recorded once from New Haven, Connecticut (Barber 1953b). It was not found in New England in the present study, but from its habitat preferences in Florida, it is to be searched for in warm ruderal sites, dry lawns and gardens, a fact which, along with its propensity to occasionally climb into vegetation and thus be swept, has led to its ready collection.

While a Florida population has been reared readily on sunflower seeds, I will not discuss this species in much detail as it has been recorded as a pest of strawberries along with *P. vinctus* (Sweet 1960, for references) and undoubtedly economic entomology workers will work out its biology in closer detail.

For the present discussion, it is most interesting to note that this species exhibits an elaborate seed defense behavior in part similar to *P. basalis,* but also a distinct sexual element is involved. When a few seeds are available some of the males station themselves by the seeds, only occasionally feeding, and drive away other males, nymphs, and some females. But if an appropriate female approaches, she is allowed to feed on the seed and the male attempts to copulate, mounting her and rapidly vibrating his antennae against her head. Usually the female would rapidly wag her antennae in ''annoyance'' as in *basalis* and decamp. Occasionally copulation would ensue, instead, if the female was receptive.

When nymphs or some females intrude on the seed they are repulsed by the male who advances on the intruder and touches it with his antennae which are held stiffly and vibrated rapidly in a very slight plane. Once when a dominant male returned to a seed, after he had copulated with a female, he dislodged four insects, a weak male, a female, a third and fifth instar which were feeding on the seed, by climbing upon the back of each and `employing this slight but rapid antennae vibration.

The territorial limits of this seed possession extends to about 1 cm. from the seed and frequently the defending male is at the outskirts of this zone, not on the seed. When a male intrudes, he is repulsed with great vigor and sometimes chased across the rearing dish. In several such chases the dominant male became, so to speak, lost. Thereupon a formerly recessive male took over the defense of the seed, and attempted to copulate with a female. Later the dominant male returned to this particular seed, despite the presence of other similar seeds, and touched the smaller male with his vibrating antennae in the usual manner. This time a different result ensued. The small male clung close to the seed and would not dislodge, whereupon the dominant male suddenly began to flutter his antennae rapidly and stiffly spread his fore femora wide much as in *P. basalis.* The small male almost simultaneously likewise spread his fore femora and fluttered his antennae. The two males reared upon their hind legs and clashed for 5–8 seconds with flailing mid legs and fore tibia and very rapidly fluttering antennae. Suddenly both desisted, and began to clean their antennae. This appears to be displacement behavior. The large male then resumed possession of the seed.

This behavior is described for it illuminates an unusual sexual dimorphism, for the males of *P. bilobatus* while variable in size among themselves are usually larger than the females, an unusual situation among insects (Darwin 1871, p. 628). Among mammals the greater size of the male is explained as a result of intraspecific selection among males in competition for females (Darwin 1871, p. 831, Simpson 1951, p. 86), and a similar explanation seems apparent here as among stag beetles (Darwin 1871, p. 628).

Also of considerable interest is that cultures with many competing males and resultant continuous agitation, underwent a great population decrease which was prevented in one culture by removing the adults. Clearly this species would be an excellent subject for a study of a possible stress syndrome.

Wilson (1938) found *P. bilobatus* parasitized by a fungus *Beauveris bassiana* (Bals.) and preyed on by three species of lizards in Puerto Rico; *Anolis klugii* Barbour, *Anolis stratulus* Cope, and *Anolis cristabellus* Dumeril and Bibron.

Pseudocnemodus canadensis (Provancher)

This monotypic genus bears a pronounced resemblance to *Cnemodus. Pseudocnemodus canadensis* has a boreal Nearctic distribution from Quebec to British Columbia, south to Iowa, northern Indiana, southern New England and New York, and in the Appalachian Mountains to North Carolina (Slater, Catalogue). It appears to be scarce in Iowa and Illinois (Slater 1952). Torre-Bueno (1912) considered it to be a ''pretty common and widespread species'' in New York.

Environment

In New England *Pseudocnemodus* is typically found on dry overdrained slopes which have a sparse but complete ground cover especially on dry edge habitats between forests and an old fields. Such areas are dominated by low bunch-forming grasses such as *Festuca rubra* L., *Andropogon scoparius* Michx., and *Aristida dichotoma Michx.* Open patches of the low blueberry *Vaccinium augustifolium* Ait. also form a common habitat.

These sites have rather uniformly gravelly dry soils, with the interspaces between the grass clumps filled with fallen litter, *Cladonia* and *Polytricum. Xestocoris nitens, Carpilis consimilis, Trapezonotus arenarius,* and *Lygaeospilus tripunctatus* (Dallas) are seed feeding insects that frequently occur with *Pseudocnemodus.* The ground biotope, at the bases of the grass clumps or *Vac-*

cinium low scrub, is relatively dry (2–3) and becomes quite hot (up to 48°C. during mid-day).

While these field habitats do form an early seral stage, much dry overdrained sites only slowly undergo succession. In at least one such area a population of *Pseudocnemodus* was present continuously for at least nine years (Slater, *in litt.*). However, the serclimax *Vaccinium* scrub habitats of exposed rock faces forms a practically permanent habitat. The abundance of the insect is usually fairly low, in the order of 3 to 8 per square meter, more rarely as much as 16 to 20 per square meter. Hendrickson (1930) who found it in a number of climax associations, similarly did not find it numerous.

The locality at Vernon, British Columbia was a site dry in summer and cool in winter, and very different from the wet and equitable coastal climate (Parshley 1919).

General Biology

Since all the field populations are largely brachypterous the presence of *Pseudocnemodus* in a mosaic of scattered favorable habitats indicates a sufficient production of dispersing macropters. Dispersing adults are indicated by the large numbers of individuals, all macropterous, washed up on ocean beaches on Long Island (Torre-Bueno 1915, 1927).

This long legged myodochine is an alert rapid-moving insect and shows little tendency to hide under the litter. Both the adults and especially the reddish nymphs display a relatively weak ant mimicking appearance and behavior. A pale lateral margin to the hemelytra and the pale humeral angles heighten the narrow shape of the insect which blends it into the dry grass background.

Several populations were intensively parasitized by *Catharosia* tachinid flies. One population of *Pseudocnemodus* at a considerable density of 10 per square meter was 94% parasitized, a factor which may have led to the extinction of this population in contrast to the very long lasting population mentioned earlier where parasitism was never found over six years. The tachinids emerged after the *Pseudocnemodus* nymphs became adult. Only one of many pupae yielded a fly, which may indicate a pupal diapause condition, which correlates with the egg diapause of *Pseudocnemodus.*

In the laboratory *Pseudocnemodus* rears readily on sunflower seeds. It expresses a strong feeding reaction to *Vaccinium* and *Gaylussacia* seeds. It also feeds on the seeds of *Festuca rubrum, Hedeoma* sp., *Solidago, Aquilegia canadensis, Betula populifolia,* and *Rumex obtusifolia.* It appears then, on this evidence, to have a large potential seed feeding range. It also will scavenge on nearly dead or dead adults but no active cannabalism or predation was observed nor indicated.

No seed feeding defense was observed. The insects drag the seed to more protected sites beneath loose litter.

Ashlock and Lattin (1963) have described an interesting large stridulatory area (stridulitrum) along the side of the pronotum. This stridulitrum occurs also in the nymphs. The plectrum is an irregular row of small tubercules along the inside of the fore femora. This mechanism occurs in both females and males. Ashlock and Lattin note that when irritated, this species moves its femora rapidly up and down next to its body. These authors heard no sounds but assumed that if produced the sounds are inaudible.

This stridulatory area may also play a role in the mating behavior of the male. When placed with a receptive female, the male responds to the female before contacting her. The male's response is shown by his rapidly vibrating antennae, and by a peculiar awkward-appearing partial spreading and closing of the fore femora. This spreading at first was thought to be a display of the shiny inner surface of the fore femora but further study showed that this maneuver effectively rubs the fore femoral plectrum over the stridulitrum. No similar motions were observed in the female, however. If receptive, the female briefly approaches the male and also vibrates her antennae, and the antennae of the pair meet. From this position the male slowly rotates into a parallel position to the female and mounts her. Once upon the female, the male loosely taps the female's head with his vibrating antennae. Copulation is effected and the male drops off into a reversed (end to end) position. Copulation lasts from 44 minutes to at least several hours. One pair mated at least five times, but a single mating is sufficient to fertilize an entire egg complement.

Life History

Pseudocnemodus canadensis diapauses over the winter as an egg. Both uni- and bivoltine conditions occur. The earliest first instar nymphs were found in the field May 24, but the first instars occurred as late as June 10, at which time third and fourth instars also were found. This variability indicates staggered hatching, which agrees with the artificially over-wintered eggs, which exhibit a very variable rate of hatching. This situation is of considerable significance, for those insects which became adult in the field shortly after mid-June went on to lay non-diapause eggs, while those which became adult after June 31 uniformly laid diapause eggs. This interesting situation is true in both field and laboratory populations. *Pseudocnemodus* populations such as one on a cool north side of a drumlin are entirely of this late developing type, while the several populations with bivoltine females (mixed with late developing univoltine individuals) are found in considerably warmer sites. Unfortunately this situation was not followed up, as the nymphs could not be forced to early maturity in the laboratory under short daylight conditions. This situation could not result from temperature conditions as the peak in field temperatures came in late July and early August, and only diapause egg laying adults are present, and the lower laboratory temperatures also yielded diapause adults. The most logical explanation is that under the solstice long day conditions, the insects are stimulated to produce non-diapause eggs. Another factor possible may be a genetic factor which allows a more rapid development and also sensitivity to long day conditions. At any rate there are two phases of diapause egg oviposition, one in summer from July to late August, another by the partial second generation from mid-August into September. Both first and second generation eggs were artificially overwintered and diapause broken at 4°C. after 5 months of cold. Diapause occurs during early anatrepsis. The total life cycle varies from a month to a month and a half, and second generation fifth instars are found as late as September 10. The overall phenology is given in Table 20. Bear in mind that local populations may differ greatly in the instar ratios due to microclimatic differences and staggered hatching, etc.

TABLE 20

Phenology of *Pseudocnemodus canadensis*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
May 24	100%	——	——	——	——	——
June 1	40%	40%	20%	——	——	——
June 10	8%	44%	36%	8%	4%	——
June 22	——	20%	35%	25%	15%	5%
July 2	——	2%	16%	25%	32%	25%
July 18	——	2%	3%	5%	20%	70%
July 28	——	——	——	2%	8%	90%
Aug. 18	4%	4%	8%	14%	10%	60%
Sept. 5	——	——	——	2%	11%	87%
Sept. 27	——	——	——	——	——	100%

The stadia given in Table 21 are based largely on nymphs captured in the field and reared in the laboratory. Because only a few populations with non-diapausing adults could be found, the egg and first instar stadia are represented by only two records each. After removal from cold the few eggs which immediately developed hatched in 15 days. The adult life span in the laboratory varies from 35–75 days. The average longevity of ovipositing females was 49 days, considerably less than virgin females (69 days) or males (59 days).

TABLE 21

Stadia of *Pseudocnemodus canadensis*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
——	——	5.0	7.7	6.0	8.8	40
(12–15)	(6–7)	(5–7)	(6–9)	(5–7)	(7–11)	(38–48)

There is no summer reproductive diapause and oviposition of diapause eggs ensues after a preoviposition period of about 14 days. From 79 to 280 eggs per female were laid (mean 154). When an unsuitable oviposition substrate was provided the egg production was drastically reduced to only 1 to 25 eggs. Virgin females laid from none to only 19 eggs (mean 6.1) over a two or three month period.

The eggs are of average size, cylindrical with rounded ends and densely covered with very short minute tubercules. The eggs are preferably laid deeply in fine loose dry litter debris, which sticks to the eggs, covering them up, and effectively conceals their presence.

Cnemodus mavortius Say

This striking large black myodochine is exceptional in that both the macropterous and the brachypterous forms lack all visible traces of ocelli. Its generic name, which means "well-legged," (Grover 1876), aptly describes the general appearance of this insect.

Four other species are presently known in the genus. Berg (1879, 1894) described *albimaculus* from Argentina and Uruguay and *multifarius* from Bolivia. Blatchley (1924) discerned a separate species, *hirtipes*, which is apparently endemic to Florida. However, the validity of the fourth species, *inflatus*, which was described from North Carolina by Van Duzee (1915) has been questioned by Froeschner (1944). Froeschner found that populations of *C. mavortius* in Missouri exhibited a large range of structural variation, largely associated with pronotal changes associated with brachyptery and considered *inflatus* to represent an extreme form. Torre-Bueno (1946) disagreed, and considered the structural differences between the two forms of rather great magnitude and as indicating species differences. My own work on Connecticut populations of *C. mavortius* agrees with Froeschner's observation that there is a rather striking variation in total size and pronotal shape in relation to brachyptery but there is also a sexual dimorphism involved, as the males are variable in size, and both *mavortius* and *inflatus* types can be distinguished. Since I have not seen the type of *inflatus,* this form cannot yet be synonymized.

Cnemodus mavortius has a generally southern range from Georgia and Texas north to Iowa, Indiana, New York, southern New England, Nantucket Island, Massachusetts and also along the coast as far north as Maine. In New England I have found the species fairly frequently at a number of sites in southeastern New England, but not at all north of northwestern Connecticut. It appears to be uncommonly collected (Froeschner 1944, Slater 1952). However this can be accounted for by the habitat specificity of this insect.

Environment

Cnemodus mavortius in Connecticut is highly specific to fully exposed old overdrained morainic sites dominated by *Andropogon scoparius,* especially where considerable areas of bare gravelly soil are present. Several old abandoned gravel pits with such a sparse cover of *Andropogon* formed a very typical habitat. In a few habitats the plant cover although short completely covered the ground. The soil is always dry (1–2), sandy or gravelly, with a sparse litter of fallen culms around the *Andropogon* clumps. The surface soil temperatures frequently become very high (55° C.) at these sites, and the insects at such times are frequently observed perched on bits of litter and noticeably very high on its legs as is usual with species found in such hot habitats (Cloudsley-Thompson 1962). The thermophily of this species is especially well shown in the laboratory as the insects will thickly cluster close to a source of warmth. It was never swept from plants and never found on the grass stems as is *Nithecus jacobeae* (Schill.) when it is exposed to high temperatures (Coulianos 1961).

Cnemodus is found abundantly (up to 25–35 per square meter) at sites where considerable bare soil is present, and less abundantly (1–3 per square meter) in more closed over habitats. It is apparent that *Cnemodus* is a highly thermo- and xerophilous insect which inhabits a early succession stage on xeric old fields with poor soils. Such habitats, however, while obviously temporary are very long enduring (Blizzard 1931, Conard 1935) and may persist in such an open state for many decades.

The insect is found in refuge in thick *Andropogon* clumps for hibernation, especially in clumps close to the margin of a field. Such an overwintering site may be meant by Blatchley (1926) when he described its habitat as ''beneath dead leaves on the wooded slopes of streams.'' This is a very different sort of habitat from the xeric hot habitats where *Cnemodus* is found in Connecticut. Several authors record it as overwintering in wooded areas (Uhler 1875, Blatchley 1895, Froeschner 1944).

General Biology

The populations of *Cnemodus* studied in Connecticut are largely brachypterous, especially those in restricted populations. In the larger populations a variable percentage of macropters are found. Since the habitats described are fundamentally temporary although long enduring, it is therefore apparent that a sufficient production of macropters does occur so as to allow dispersal to new habitat types. Sometimes, however, as at a renewed gravel pit near Storrs, Connecticut a population of brachypters was but a short distance away and dispersal to this new habitat more likely occurs via the ground. *Cnemodus* was collected at lights (Torre-Bueno 1933) and so the macropters may disperse at night. *Cnemodus hirtipes* of Florida has also been collected at lights (Blatchley 1926). It would be interesting to ascertain if the absence of ocelli in any way affects the dispersal ability of this species. The prevalence of brachyptery may help explain its spotty local distribution in available habitats.

In the field and the laboratory the adults of *Cnemodus* give an immediate impression of being huge black ants. This resemblance to ants is intensified by the jerky movements of this rapid moving insect. Also noteworthy is that the brachypters more closely resemble ants than the macropters. *Cnemodus* is by far the largest (in length) of the rhyparochromines of New England and is also much larger than the largest ant (*Camponotus pennsylvanicus*) and very much larger than the common black *Formica*. Therefore, the ant mimicry resemblance is a general one and not based on a single model. The nymphs, far more than the adults, are striking ant mimics. Instead of black the nymphs are reddish with white lateral patches along the abdominal Y-suture immediately posterior to the thorax, which helps to create the impression of a petiole as the pronotum and posterior part of the abdomen are swollen in appearance. The development of mimicry appearance is gradual, the effect heightening with each instar after the first instar which itself is yellowish with a red abdominal crossband as in other myodochine first instars. In effect, then there is a polymorphic ant mimicking population with the adults and nymphs having different colors. Certainly, against the pale soil and dry brown vegetation of the *Andropogon* community, these insects, especially the black adults, stand out conspicuously. Berg (1879, 1884) described similar ant mimicry in both adults and fifth instar nymphs of *Cnemodus albimaculus* Berg.

Cnemodus is very frequently parasitized by *Catharosia* tachinid flies especially when the *Cnemodus* population density is relatively high. The parasitism appears to occur during the later instars. The parasites all emerged from the adults only. Parasitized female *Cnemodus* can be recognized readily in the laboratory because they are non-reproductive. The parasite diapauses through the winter *in* the host as the parasite emergence does not occur until during the winter from the fall adults which were kept in warmth or in spring from the overwintered adults. Normal adults become reproductive in a brief time, while the parasitized adults continue on as if they were in reproductive diapause.

Cnemodus feeds on *Andropogon* seeds in the laboratory, but was never swept from *Andropogon* seed heads, and probably feeds only on the fallen seeds in the field. There was some feeding on *Oenothrea* sp., *Acer rubrum* and *Quercus alba* seeds. An especially strong feeding reaction was shown to ripe *Rumex acetosella* seeds, but it did not feed on *Panicum* and *Agropyron* grass seed, and on various other composites. Yet it feeds readily on sunflower seeds, both hulled and unhulled.

No active seed defense behavior is exhibited aside from keeping a seed out of the reach of another individual by placing its body between the seed and the intruder. The seeds are carried on the labium to more protected litter sites. The seeds are located largely by probing with the labium. When feeding the antennae are characterically held at right angles to the body.

Although the insects were frequently observed mating, the courtship behavior was not observed despite continued attempts. At least it may be said that a receptive pair reacts rather slowly to each other and no apparent reaction occurs for several hours before mating. Copulation lasts at least two hours in the usual reversed position, and may be repeated several times, but only one mating is sufficient to fertilize the entire egg complement.

Two generations a year are present in Connecticut, and the adults overwinter. Copulation occurs in the field in late April and May and the fertilized females oviposit immediately on being brought into the laboratory, but the earliest nymphs were not found in the field until mid-June. The phenology at Storrs, Connecticut is given in Table 22. Oviposition occurs over a period of several months and the second generation considerably overlaps the first. Last instar nymphs which are found later than October 10, are very frequently parasitized.

TABLE 22

Phenology of *Cnemodus mavortius*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
June 1	——	——	——	——	——	100%
June 25	10%	30%	20%	——	——	40%
July 10	15%	15%	30%	20%	10%	10%
July 27	——	——	——	10%	20%	70%
Aug. 10	——	20%	25%	——	——	55%
Sept. 1	5%	9%	26%	14%	9%	37%
Sept. 17	——	——	5%	10%	15%	70%
Oct. 10	——	——	——	——	10%	90%
Nov. 1	——	——	——	——	2%	98%

There appears to be a relatively weak diapause mechanism, and in the field adults of the second generation are non-reproductive. This quiescence is ordinarily broken readily and most individuals become reproductively active in the laboratory in early October. However the progeny of a forced third generation was in a much stronger diapause state and did not become reproductive after three to five months.

Since the general distribution of this species is to the south of New England, it may be hypothesized that this curious increase in diapause strength may represent the normal seasonal cycle further south under a longer season with a shorter late autumn photoperiod. The weaker diapause state of the second generation in Connecticut under equinoctal conditions may represent a developing adaptation to north temperate conditions. It is significant that a few *Cnemodus* did *not* break diapause in October as did the great majority of the specimens.

The stadia of instars 2 to 5 given in Table 23 were obtained by rearing field collected nymphs in the laboratory. When reared from eggs on sunflower seeds the stadia were greatly prolonged as seen in the data on instar 1. The life span of the nondiapause adults in the laboratory was long, averaging 67 days (range 35–87). The diapause period of second generation adults averaged 35 days and the adult life span averaged 103 days. Forced third generation adults in diapause lived from 60 to 168 days (mean 97).

TABLE 23

Stadia of *Cnemodus mavortius*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
11.3 (8–14)	15.2 (12–26)	8.4 (4–8)	6.5 (4–9)	6.0 (4–9)	8.4 (5–11)	52 (39–67)

The preoviposition period was 10 days in two non-diapause females. The individual fecundity in the laboratory of 19 females varied from 54 to 280 eggs (mean 128) on a sunflower seed diet. Twelve unmated females laid no eggs. The eggs are elongate and smooth without any spines or sticking mechanism.

The females oviposit in dry substrates, such as litter crevices, sand, or in other loose material such as cotton and methyl cellulose. Rarely the eggs were laid in wet stoppers. Egg production is drastically reduced when a proper loose substrate is lacking.

Ptochiomera nodosa Say

Ptochiomera nodosa is a bizarre little species as its antennae are greatly enlarged, especially the third segment. In this respect it is most closely related to *Sisamnes* Dist. Formerly Barber (1928a) included in *Ptochiomera* various species now distributed in three other genera which are closely related (*Ptochiomera* Say, *Sisamnes* Dist., *Carpilis* Stål, and *Exptochiomera* Barber). *Prytanes* Distant also belongs to this complex (Barber 1954). Later Barber (1935a) recognized the diversity of this group of short legged small myodochines and considered the above genera as distinct, and restricted *Ptochiomera* to the monotype, *nodosa* Say.

Since many early European workers used the emendation of *Ptochiomera*, *Plociomera*, to refer to myodochines in general, there are various other species now listed under the name *Ptochiomera* (Slater, Catalogue).

The genus is Neotropical as well as Nearctic for I have observed an undescribed species from Venezuela in the United States National Museum. *Ptochiomera nodosa,* itself, is distributed over the southern part of the United States from Florida and northern Mexico north to Iowa, Indiana, and Massachusetts. It is here recorded for the first time from Connecticut. Blatchley (1926) noted that this species was common in the southern tier of counties in Indiana, but scarce in the north counties. Slater (1952) noted it only from the southern counties of Illinois and the extreme southeast of Iowa. Froeschner (1944) stated that it is abundant in Missouri, and Uhler (1876) found it to be common in Maryland. In New England I found the species only along the extreme southern coast along Long Island Sound at Noank, Rocky Neck, and New Haven, Connecticut. The Massachusetts record is from Woods Hole (Parshley 1917).

Because of the relative scarcity of *P. nodosa* in Connecticut the following discussion is rather limited.

Environment

Nearly all my collections of this species have been along road sites and parking lots except for a few found along the margin of a lawn next to a beach at New Haven. At these sites it was narrowly confined to the dry thin litter along the sharp edge between the ruderal plants and the open road, lot, or beach. It was never found where the vegetation thickened, and formed a continuous cover, nor under dry litter in open areas, nor where the litter was at all moist. In southern Florida I found this species in essentially similar biotopes along the margins of open fields and roadsides. The soil was always light colored and sandy or gravelly and mixed with bits of grass litter. The temperatures at mid-day were often high and measured between 110–140° F. in the litter area but considerably lower than on the open ground. Of course, the litter and and ground were quite dry (1–3) at all stations. The vegetation consisted of the usual ruderal plants, chiefly *Agropyron repens, Poa annua* L., *Digitaria sanguinalis* (L.), *Rumex obtusifolia* L., *Silene* sp., *Potentilla pumila* Poir., *Lepidium virgineum* L., *Brassica* sp., with *Agropyron* the usual dominant species.

Clearly these habitats are at best very temporary habitats which would rapidly undergo succession except for man's activities which cause the roadside community to conceivably be a sort of disclimax. But even among ruderal communities, this marginal biotope is especially short lasting. *P. nodosa* was not found for several years in succession at any sites except the one at Noank where it was found in the summers of 1957 and 1958.

Some authors have mentioned *P. nodosa's* abundance in the southern states but at its northern fringe in Connecticut it is represented at most sites by only a few specimens an abundance level of less than 1–2 per square meter. The only exception was at a parking lot in Noank where it was sometimes found at 20–30 per square meter. At this site the insects appeared to be distinctly gregarious and formed close groups of 10–20 which clung closely to the base of the small dried thin grass tufts. In the laboratory a similar tendency was found and the nymphs and adults would congregate under a bit of litter.

The habitat notes in the literature appear to bear this observation out. Blatchley (1895, 1926) found the species beneath chunks and rubbish and at the bases of tufts of grasses along the margin of open cultivated fields and road sides. He also observed that it overwintered at these same sites. Froeschner (1944) found it under logs, boards, rocks, and grass clumps in Missouri. Perhaps the oddest reference is that of Wirtner (1905) who said, ''Klages tells me that he finds it abundantly on the mushrooms on trees.''

General Biology

In the brachypterous form the hemelytral membranes slightly overlap and just attain the anterior margin of tergum seven. Despite the essentially temporary nature of the habitat of this species both macropters and brachypters were always found in about equal proportions. Clearly this level of macroptery must allow sufficient dispersal capacities to colonize such temporary habitats. In this respect it is significant that whether colonies begin with brachypterous or macropterous forms both yield progeny of approximately equal proportions of brachypters and macropters. Uhler (1876) stated that the short winged form was found in the granitic and primitive areas in Maryland but was full winged in the newer and more southern portions of this region and in the southern states was always long winged. Blatchley (1926) disagreed and wrote that the species was fully one-half brachypterous in Florida. I have observed much the same in south Florida and Texas. But Uhler's observations may eventually still be significant in the relation of such macroptery and brachyptery to permanent and temporary habitats.

Dispersal may occur at night as it was collected at lights (Froeschner 1944, Barber 1953a). Glick (1939) collected this species at 3,000 feet over Louisiana.

The adult coloration, with a pale corium and posterior pronotum, and dark head and antennae blends the species readily into the light background of its habitat. When given a choice between dark earth and dry sand litter mixture, the adults come to rest on the light surface, and generally avoid the dark surfaces. The nymphs of instars two to five are bright red and white, very similar to *Sisamnes clavigera* nymphs, and so would appear conspicuous to bird predators. If so, this coloration is aposematic.

The gregarious habit of this species may protect it from such a predator as *Geocoris uliginosus* Say which actively preyed on the smaller nymphs of *Ptochiomera* in the laboratory and in the field at Noank, Connecticut. The *Geocoris* definitely showed an avoidance reaction when it came on a group of *Ptochiomera* adults and nymphs. Such an aggregation is quiet and only by vigorously disturbing it would the insects move about. This is significant for the *Geocoris* was found to react especially to movements. Disturbing and dispersing this field colony of *Ptochiomera* brought about predation by *Geocoris* adults and nymphs which were abundant at this site.

The only parasite was a catharosine tachinid recovered from a male *Ptochiomera* collected in Georgia in December of 1961 by D. E. Leonard.

It is interesting that a distinct diurnal rhythm is present. Colonies from Connecticut and Florida both exhibited this behavior. This behavior was followed daily from March 15 to April 21. It has no relation to artificial illumination, darkness, or to variation in room temperature (68–78° F.). During the day a large colony of about 200 insects kept refuge in a pile of methyl cellulose. Between 4:20 and 4:35 P.M. the insects began to come out of the pile. By 5:25 to 5:45 they were out in large numbers and climbing the sides of the container very actively. This activity continued to increase and reached a peak at about 9:30 to 10:00 when some macropters attempted flight. Both macropters and brachypters and even the early instar nymphs were very active. At 11:15 the numbers were noticeably decreased, at about 11:45 only a few were out, and between 12:15 and 12:50 all disappeared again into the pile. This species then exhibits a crepuscular and early evening activity rhythm, but not an auroral activity period. *Exptochiomera dissimilis* Barber from south Florida exhibits a quite similar rhythm.

Ptochiomera feeds on seeds of *Rumex acetosella, R. obtusifolia, Agropyron repens, Plantago*, and is especially attracted to sunflower seeds. It is reared very readily and often with little mortality on the sunflower seeds. Some colonies, however, sometimes exhibit a considerable mortality in the earlier instars. There is no scavenging on dying insects even in starving individuals. Despite the xeric habitat preference it could not be kept alive even overnight without water.

As with other rhyparochromines these insects move seeds about and carry or drag them into the litter. When annoyed, the insects wag their antennae rapidly. This is true both when a male attempts to copulate with a nonresponsive female and when an intruder disturbs *Ptochiomera* feeding on a seed.

Copulation occurs in the usual reversed position. The courtship behavior was not observed except that the male's antennae quiver very rapidly on contact with a female.

The heavy antennae of both *Sisamnes* and *Ptochiomera* are used to help lift the insect above the substrate and so aid the short legs in the righting response. Probably the natural sandy habitat may make righting somewhat difficult and the antennae assist such a movement.

Life History

Uhler (1876) noted that this species overwinters as an adult and was among the first insects to become active in the spring in Maryland. There is not much evidence on hand and the life cycle is not adequately understood in the earlier part of the year. The life cycle appears very similar to that of *Sisamnes* in Connecticut, and the nymphs occur late in the summer.

The observed phenology is as in Table 24, but very few *Ptochiomera* were found before August 15.

TABLE 24

Phenology of *Ptochiomera nodosa*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
July 18	——	——	——	——	——	100%
July 25	8%	11%	——	——	——	81%
Aug. 5	——	——	10%	23%	——	67%
Aug. 19	16%	21%	11%	——	16%	36%
Sept. 3	6%	——	25%	32%	12%	25%
Sept. 11	10%	30%	10%	10%	25%	15%
Sept. 30	——	——	8%	8%	19%	65%
Oct. 27	——	——	——	11%	11%	78%

Oviposition in field adults occurred from July 30 to September 11, and mating was observed in the field on July 28.

The evidence for two generations hinges on the occurrence of late instar nymphs in early August and the distinct break in the nymphal ratios on August 19. Unfortunately these late instar nymphs of early August were not isolated, and it is not known whether they became reproductive or not. All other nymphs from late August on, when reared, go directly into diapause and do not reproduce. The only, and significant exception, were the nymphs and adults collected on October 20 and October 27 which became reproductive after being brought into the laboratory. This is exactly the same pattern of cold release (?) found in *Sisamnes.* In *Ptochiomera,* however, the second generation extends even later into the autumn.

Froeschner (1944) similarly recorded in Missouri a late occurrence of nymphs from August 11 to October 3. It is possible that this late sequence of generations is a primary limitation on the northward spread of this species. At this same time in November and December in southern Florida and Georgia, only adults were found and Blatchley (1926) observed that the adults overwintered at Dunedin, Florida. Collections from Florida became reproductive at Storrs in December and January.

So readily do the cold exposed insects leave diapause that this increases the probability that an earlier generation occurs. It is possible that a long photoperiod after a diapause period brings about sexual activity. Considerably more work remains to further elucidate this life cycle. At any rate this life cycle appears adapted, in Connecticut, to a late summer production of ripe seeds.

The stadia are derived from relatively few observations and given in table 25.

TABLE 25

Stadia of *Ptochiomera nodosa*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
10 (9–12)	6	7	6–7	7	9 (8–11)	41–47

Under diapause conditions in warmth the adults live 67–235 days (average 171). It is not known whether the sexually isolated adults lay eggs or not.

The fecundity varies from 66–230 eggs (average 131) including data from adults from Florida. The smooth eggs are laid in litter, in methyl cellulose, are very well concealed, but do not stick to the litter as do those of *Sisamnes.*

Sisamnes clavigera (Uhler)

The genus *Sisamnes* at present contains three species. The type species *contractus* Dist. was described from Guatemala and is also known from Arizona and Florida. *S. annulicollis* was described by Berg (1879) from Brazil and Argentina. The species present in New England is clearly a temperate zone species and ranges from Massachusetts west to Idaho and New Mexico and south to Texas and North Carolina. Uhler (1876) mentions *S. clavigera* as being more abundant in the western states. From the published records the species appears to be especially rare in eastern United States despite more intensive collecting. It was not recorded from Connecticut and Massachusetts until 1922 (Parshley 1922).

Sisamnes clavigera is apparently unique among the Myodochini for it possesses thickened scale-like body hairs much as do the other lygaeids *Slaterellus* and *Chauliops* (Drake and Davis 1960) and *Heinsius* (Slater and Sweet 1963). In all these genera the ''scale'' appears to be a waxy exudate for it melts when heated. Also remarkable are the peculiar stiff hairs on the clavate terminal antennal segment of *Sisamnes clavigera*.

Environment

The only meaningful habitat note is that of Torre-Bueno (1924) who found several specimens running rapidly among dry leaves near a clump of small yellow birches in Amherst, Massachusetts. Froeschner (1944) considered the species scarce in Missouri and found it under rocks, logs, boards, and at the base of mullein leaves.

My own collection records are at variance with those of Torre-Bueno, but since I have collected this scarce species only a few times near Storrs, Connecticut, I obviously cannot give an accurate picture of its habitat preferences. The site where it was first collected (in 1958) was in an old sand pit on a gentle, south-facing small slope. The vegetation consisted of scattered clumps of *Andropogon scoparius* and a few other withered plants and lichens (*Cladonia*). The grass clumps were widely spaced with a thin loose dry litter of grass culms and seeds on the exposed ground between the clumps. The soil was a very dry grey-brown sand (moisture level 1–2). The site was obviously, from the size of clumps and the accumulation of lichens and litter, rather old and had been undisturbed for some time. Because of the over drained sandy soil, succession had evidently proceeded slowly. Temperature measurements were not taken as the site was discovered in autumn but it was evident from the open exposure that this was a warm slope. When first found on October 10 the insects were dispersed over the slope and a few were even found in an adjoining ruderal roadside. The density was 4–6 per square meter. Later checks after a period of cold weather seemed to indicate that the population was decreasing. However, on November 5, a cluster of 25 of the insects was found within six square inches in a small accumulation of litter between the grass clumps, and another smaller group of 8 insects was similarly found about ten yards away. The apparent population reduction probably resulted from the aggregating of the insects. While several other lygaeid species, *Emblethis vicarius, Peritrechus fraternus,* and *Cnemodus mavortius* were found hiberating within the clumps of *Andropogon, Sisamnes* was found in the much drier and semi-open intervals between the clumps. Unfortunately this population and site could not be further studied for the habitat was destroyed in late November when this portion of the sand pit was bulldozed. Although a single male specimen was found on the fringe of the area in the following May, despite continued search the population seemed to be eliminated until two years later in August, 1961 when a small colony was found about 125 yards from the original site.

This was a much newer habitat although in general similar to the original site in soil and exposure. The vegetation consisted of a ground cover of *Potentilla canadensis* L. and a few scattered young clumps of *Andropogon scoparius* and some scattered St. Johnswort (*Hypericum*) and a few thin grasses. The ruderal aspect of this association were also indicated by the presence of *Poa pratensis* and *Ligyrocoris diffusus* Uhl. The biotope of *Sisamnes* was in the ground litter at the base of the plants. In this habitat the abundance of the insect was only 2–3 per square meter over a small ten square meter area. As this biotope was adjacent to open sandy biotopes with sparse litter, the litter temperatures were compared. At 1:30 on August 24 the sandy areas where *Emblethis vicarius* and *Geocoris bullatus* occurred had litter temperatures of 45° C., while the temperature of the *Sisamnes* biotopes was 35° C. Unfortunately, once again, the habitat was destroyed in the following autumn.

In the original habitat, *Sisamnes clavigera* occurred with four other chiefly brachypterous species, *Geocoris limbatus, Cnemodus mavortius, Pseudocnemodus canadensis,* and *Carpilis consimilis,* of which the last two were much less abundant.

This species is evidently rare in Connecticut. Many similar habitats were searched with no success. Along with its ecological restriction and rareness, this small insect possesses a remarkable camouflaging coloration which would render it much less frequently collected. The apparent preference of this species for dry sparse habitats suggests that the center of distribution of *Sisamnes* is in the drier western areas such as, perhaps Colorado, from where it was first described by Uhler (1895). At the United States National Museum nearly all the specimens are from the western United States and include a few macropterous individuals.

General Biology

S. clavigera is almost entirely brachypterous and although Barber (1953) stated that the macropterous form exists, all specimens collected and reared in Connecticut were uniformly brachypterous without a trace of the membrane. Unlike *Carpilis,* high laboratory densities did not promote the appearance of the macropterous form, nor did mass rearings at the relatively high temperature of 35° C. The rareness of this species in Connecticut is probably in part the consequence of its poor dispersal powers in utilizing the discontinuous mosaic of favorable but temporary habitats.

The adult of this small, short legged species is entirely gray with a pattern of pale blotches. It blends remarkably well with the background coloration of the sparse dry litter of the area where it was collected. Indeed in the laboratory on a substrate from the natural habitat it often could not be seen until disturbed. In correlation with this effective camouflage it usually takes a great deal of agitation to induce *Sisamnes* to move about. When thus stimulated it only runs to the next concealing crevice and again becomes quiescent. It does not, however, exhibit a death feigning response. When given a choice between various kinds of substrate it invariably comes to rest on sand with bits of litter, often concealing itself beneath small leaf particles.

The later instar nymphs are, in contrast, apparently aposematically colored a contrasting red and white, in a pattern quite similar to that of *Ptochiomera nodosa* Say.

No parasites were reared, although other lygaeid species present in the same habitat were heavily parasitized.

In the laboratory, *S. clavigera* is easily reared on sunflower seeds. A colony was kept through four generations before it died out. Of the seeds available in its habitat, *Sisamnes* fed readily on *Andropogon scoparius* seeds and also fed on *Hypericum* and *Potentilla* seeds.

If the seeds are placed in an exposed position as on methyl cellulose, they are dragged under the litter or substrate by the insects. In the supposedly congeneric *Sisamnes contractus* from Florida, an aggressor releases a territoriality response from a defender *S. contractus* which is very similar to the behavior observed in *Pachybrachius* where the forelegs are held sideways and the insect rears up on its hind legs. The antennae also wag alternately very rapidly. While no such elaborate display was observed in *S. clavigera*, a similar annoyance waggle response is released from the defender when another insect attempts to feed on a seed "in possession" of the defender. This behavior was also observed in the fifth instars.

The sexes do not appear to recognize each other until contact is made. Copulation occurs only after a considerable period (at least several hours) together and after many attempts by a male. When the male becomes excited he taps the female lightly and rapidly with his antennae and presently climbs upon her and attempts to mate with her. If the female is receptive she becomes passive with her antennae held low close to the substrate and she release her ovipositor. If she is not receptive, the antennae are alternately wagged rapidly back and forth at a high angle.

Life History

While I do not have definite field evidence on whether this species has one or two generations a year, there is enough supporting evidence to indicate that there are very probably two generations a year. The observed phenology at Storrs is as in Table 26.

TABLE 26

Phenology of *Sisamnes clavigera*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
Aug. 26	8%	15%	47%	15%	——	15%
Sept. 16	——	——	——	10%	45%	45%
Oct. 14	——	——	——	4%	20%	76%
Nov. 1	——	——	——	——	——	100%
May 16	——	——	——	——	——	100%

It may be added that Froeschner (1944) in Missouri found adults on April 22, July 14, and September 18, and a fifth instar September 24.

All the adult females when collected in the field were in reproductive quiescence or diapause. Unfortunately the few adults collected in August and May were all males. Dissection of several females from the field in October showed immature, non-active ovaries. Furthermore when two replicates were reared in warmth under autumn (normal) short daylight conditions no reproductive activity occurred, and the adults died without copulating or laying any eggs (40–74 days). In contrast, those reared under long day laboratory illumination (over 15 hours) began ovipositing (in 4 replicates) between 18 and 21 days. This is only slightly longer than the normal preoviposition period of 13.6 days (12–15 days). Unfortunately, it must be emphasized that the role of cold was not taken up. Those reared under normal daylight had not been exposed to cold. Those reared under long daylight had been exposed to the considerably cooler temperatures of October 14 and after. Therefore it is not known whether long photoperiod or cold was the releasing factor. The species may be reared continuously under long photoperiod conditions. It is probable that short photoperiods bring about reproductive diapause.

From the short preoviposition period, the rapid release from diapause and the developmental period in the laboratory, it would appear that ample time is available for two generations a year, especially as the apparent second generation develops so late in the year that fifth instars appear after August 26.

The laboratory stadia in days are as given in Table 27.

The salient aspect is the relatively slow egg development. This development period is long enough to explain the late appearance of nymphs of the second generation. If it may be assumed that only the adults can overwinter at the northern limits of the species, it is probable that the northern extent of the distribution of *S. clavigera* may be determined by a warm season long enough to allow it to pass through two generations successfully. The mean adult longevity in the laboratory is 90 days and varies from 41 to 148 days.

TABLE 27

Stadia of *Sisamnes clavigera*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
16.3 (14–22)	6.3 (5–7)	6.5 (5–8)	7.8 (6–11)	7.3 (5–9)	8.6 (6–12)	53 (41–69)

As already mentioned, the preoviposition period is 13.6 days with a variation of 12 to 15 days. As these insects are slow to react sexually, it is difficult to determine the precopulatory period. When the male and females were left together it was clearly less than 13 days, but when daily two hour trials of introduction of males to virgin females were used, frequently the females would lay a few infertile eggs before copulation. That is, the precopulatory period appeared longer than the preoviposition period. Perhaps a more sensitive test is the male's response to a female. Twice, a male made no recognition response to a virgin female less than 6 days old but became excited when exposed to a 7 day old female.

Egg productivity is 3–4 eggs per day with mean total productivity of 130 and varies from 78–235 eggs. These figures appear low compared to the longevity of the insects and the number of eggs laid in small cultures. Virgin females in this species lay very few eggs (2–6), or none, in their life span.

While the slender eggs are not beset with hairs they are adhesive when first laid and become closely covered with dust and sand grains which effectively conceal the eggs. The eggs are laid singly mainly into the soil and crevices. Very few are laid in methyl cellulose or wet cotton.

Carpilis consimilis Barber

The genus *Carpilis*, with three known species, is entirely Nearctic in distribution. The type species *ferruginea* was described by Stål from Texas and later recorded by Uhler (1876, 1894) from New Mexico and Lower California. It was not until 1953 that Barber discerned that the northeastern population represented a separate species, *consimilis*. The third species, *barberi*, was described by Blatchley (1926) from Florida. The northeastern species, *C. consimilis*, has a relatively restricted known range from southern Quebec south to Long Island (New York) and northern New Jersey. As comparable ecological conditions exist along the Appalachians it seems entirely probable that *consimilis* will eventually be found as far south as the grassy mountain balds of the southern Appalachians. Nevertheless, the three known species are apparently widely separated from one another. It may be that the quite similar eastern and western species evolved from populations isolated during Pleistocene times. The third species, *barberi*, is endemic to Florida, but is not the usual Florida endemic (c.f. Hubbell 1961) for it apparently occurs in south, not north, Florida. It should be added that *Carpilis* is very closely related to *Prytanes* Dist. (Barber 1954) which includes a Cuban species along with two described by Distant (1993) from Central America.

Environment

As is generally true of brachypterous species, populations of *Carpilis* usually persist in the same locations from year to year, and do not readily invade new pioneer habitats. Nevertheless, most of the habitats where *consimilis* was collected were basically open temporary habitats eventually to yield in succession to forest vegetation. Therefore, it would appear that this species violates the restriction to climax habitats of brachypterous species (c.f. Southwood 1962). The important element, however, is the time factor involved; *Carpilis* is restricted to environments which become invaded by woody plants relatively slowly because of the overdrained nature of the soil.

These environments may be considered to be of two types. One includes overdrained xeric slopes, usually morainic structures, which undergo succession relatively slowly. The other consists of dry wind-swept mountain balds where the available soil is much too thin and dry to give sustenance to any but scattered trees. This is a very long lasting habitat, which should be considered a serclimax somewhat resembling a savanna woodland (Dansereau 1957).

Such serclimax habitats were found on Canaan Mountain, Connecticut and Mt. Greylock, Massachusetts. The scattered, stunted trees of these habitats are predominantly of *Quercus ilicifolia* Wang, *Q.. prinus* L., with some dwarfed white pine (*Pinus strobus* L.), quaking aspen (*Populus tremuloides* Michx.) and low shrubs of *Vaccinium angustifolium* Ait., *V. vacillans* Kalm, *Gaylussacia baccata* (Wang.), and *Aronia melanocarpa* (Michx.) are present. The biotope of *Carpilis consimilis* in this habitat is in the litter beneath the low plants around and in the crevices of the exposed rock outcrops.

The low vegetation consists of *Vaccinium angustifolium* Ait., the graminoids *Festuca rubra* L., *F. capillata* Lam., *Danthonia compressa* Augt., *Panicum* spp., *Bromus kalmii* Grey, *Juncus greeni* O. and T., a few forbs such as *Solidago squamosa* Muhl., and some coarse mosses, mostly *Polytrichum piliferum*, and *Cladonia* lichens. *Carpilis* is often found in this environment with several other lygaeids especially *Xestocoris nitens* and *Lygaeospilis tripunctatus* (Dallas) but it is the least abundant of these, and occurs in abundances of 1–4 per square meter.

The other habitat type is found on dry overdrained morainic sites which support a definitely pioneer type vegetation of sparse clump-forming grasses with semi-open interstices among the clumps. Such overdrained sites with poor gravely to sandy soils are usually found on slopes of eskers and drumlins. With such conditions, the ground litter is quite dry (2–3).

It was noted repeatedly that *Carpilis* is rarely found on very hot exposed slopes, but more frequently on the cooler, but dry, north facing slopes and in the temperature gradient of ecotones and margins of occasional trees and shrubs which were establishing themselves on south exposed sites. As this old field type is particularly favorable for the ecesis of *Pinus strobus* L., *Carpilis* is frequently found in a particular edaphic zone around this tree. But the relation is apparently only an edaphic one as *Carpilis* is similarly found around *Betula populifolia* Marsh, *B. papyrifera* Marsh, *Populus tremuloides* Michx., *Vaccinium corymbosum* L., *Spirea latifolia* (Ait.), *Quercus*, and others. The herbaceous vegetation of such habitats usually consists of the grasses *Festuca rubra* L., *Festuca elatior* L., *Danthonia spicata* (L.), *Panicum* sp., and *Andropogon scoparius* L. which form tussocks, producing interstices with a dry litter of seeds and debris and often with a considerable growth of xeric mosses and lichens. The forbes *Veronica officinalis* L. and *V. serpyllifolia* L., *Potentilla canadensis* L., and *Rubrus villosus* Ait. are frequently present. These interstices form the biotope of *Carpilis*. The habitat described by Barber (1928b) at Indian Lake in the Adirondacks seems quite similar. The temperature preferences in the field could be effectively studied at sites where the preferred biotopes was limited to a narrow ecotone. Such an ecotone at Canaan, Connecticut was found between a pine wood lot and a close-cropped poor pasture on a drumlin. The litter temperature readings (average) were: shaded pine forest edge litter, 66° F.; ecotone biotope favorable to *consimilis*, 95° F.; exposed pasture, 120° F.

While moranic structures are common throughout southern New England, *Carpilis* was not found near the Long Island Sound coast and becomes progressively more common northward. This distribution parallels that of white pine in contrast to pitch pine (*Pinus rigida* Mill.) which predominates on such sites near the coast. Habitats of this sort are relatively abundant across central New England and northern New York, an area frequently called the white pine region (Bromley 1935), and where *Carpilis* was collected at Warrensville, New York; Canaan, Connecticut; Great Barrington, Massachusetts; Northampton, Massachusetts; and other sites. In these temporary but long lasting habitats I have often found the species in abundances of 10–15 per square meter. By no means should this species be considered rare, but rather as an ecologically restricted species whose habitat renders it infrequently collected by conventional means.

The northern and especially the western limit of the range of this species are rather poorly known. It was not found in the present study on high cool but also humid elevations at Mount Washington, New Hampshire; Mt. Greylock, Massachusetts; and Mt. Monadanock, New Hampshire; nor in the relatively moist environments of the lowlands of the Green Mountains of New Hampshire and along the coast of Maine. It was, however, collected from Maine at Orono by Parshley (1917b) and by Procter (1946) on Mount Desert Island. As the species was collected in southern Quebec by Provancher (1886) and Moore (1944), it would appear that the species might be found west of Michigan and central Canada along the southern margin of the Laurentian shield where equivalent ecological conditions occur (Monroe 1956). Of especial interest is that Torre-Bueno (1912) collected it in a marsh by sweeping at Yaphank, Long Island, New York, for I have never collected the species in or near a marsh, or by sweeping, or in the pitch pine community which dominates on Long Island.

Despite the great predominance of brachypterous forms, this species must evidently disperse enough to invade and persist in the dry old field habitats that undergo succession rather slowly. Eventually, as I was able to observe in several habitats, sucession does proceed and eliminate the *Carpilis* colonies.

General Biology

In this small species the macropterous form is very rare, and most field populations yield entirely brachypterous samples. Only two macropters were found in five years of fairly intensive collecting. It is therefore interesting that there is partial evidence suggesting that the occurrence of the macropterous form is related to high densities. In 41 cultures of low density rearing, all progeny were brachypterous both when reared from field nymphs or overwintered eggs, except in the one relatively high density culture reared from overwintered eggs of brachypterous parents. In the culture, of 25 insects, 3 (two male, one female) or 12% were macropters. This hypothesis would seem supported by the occurrence of the two field macropters among an exceptionally dense field population (Slater *in litt.*). However this may be simply due to chance in large populations. Rearing *C. consimilis* under different temperature regimes (15° to 30° C) at low densities did not produce any macropterous forms (see discussion of wing polymorphism).

The habitus of *Carpilis* is rather unlike that of most myodochines as it is a short legged, sublitter inhabiting species which moves relatively slowly in contrast to the many long legged myodochines. The nymphs are protectively colored dark to light grey for concealment, and are *not* ant mimics. The darkness of the abdominal cuticle varies with the sizes of the abdomen, becoming lighter in swollen nymphs about to molt. In the first instar, however, the abdomen is yellow with a thin red transverse band like other myodochines. The adults might seem to be conspicuous in nature as their white hemelytra contrast with the otherwise black body, but in the light grass, seed litter, and debris, the insects appear to blend in readily when quiet.

No parasites have been recovered in insects captured in the field, nor have any predators been observed.

Carpilis feeds on many available seeds in its habitats. It feeds on *Betula, Panicum* sp., and *Festuca* seeds, but does not feed on pine seeds, nor on *Andropogon scoparius* seeds. It was reared on sunflower seeds (Sweet 1960) and *Betula populifolia* and *Veronica* spp. seeds. Survival from the egg is much enhanced with the inclusion of *Veronica* seeds, while a much higher mortality results when it is fed on sunflower seeds alone. The species survives only about 6–12 hours without water. In their relatively dry habitats water is presumbly acquired from plants and dew.

Carpilis, like *Ptochiomera* and *Sisamnes,* uses its antennae to raise the body in the righting response, which may suggest the functional significance of the short stout antennae. No seed territoriality or any brandishing of the fore femora was observed. *Betula, Panicum,* and *Veronica* seeds are transported from exposed positions to sites under debris or methyl cellulose. The seeds are dragged by the labium and several times when a seed was caught in the litter, the fore legs were used to dislodge it, but whether the tarsi or femora were used could not be determined. In the males the fore tibia is armed with a strong spine but no function could be discerned for it. It may have some mating function.

At no time are the males highly reactive to the females and there is no pronounced courtship. The female responds to the presence of a male by rapidly ''wagging'' her antennae. When very receptive, she sometimes actively advances on the male. The male climbs upon the female from any angle, grips her firmly with his fore tarsi and presses the apices of his antennae against her head as she continues to wag her antennae. If receptive, copulation ensues; if not, the male is dislodged by the female with rapid, convulsive side to side jerks of her body. Copulation lasts from three-quarters of an hour to four and a half hours during which time the pair usually conceals itself under the debris. The coiled vesica of the aedeagus is very long (Ashlock 1957). Nevertheless, it entirely enters the equally long spermathecal duct. In separating, the insects walk away from one another, pulling at the substrate. Because the straightened vesica is three times as long as the male's body it frequently becomes caught in debris especially when a pair is startled while separating. Perhaps because of its great length the vesica does not snap back into place as is usual, but recoils slowly. The male tilts forward upon antennae and fore and middle legs, and uses the hind tarsi to help settle the coils back into place. Later the male may mate again. Sometimes, however, the aedeagus does not recoil and it is dragged along behind the male and eventually becomes entangled which results in the death of the insect.

Life History

Carpilis consimilis has a univoltine life cycle and overwinters as an egg with a strong obligative diapause. Evidently, the life cycle of the species is adapted to a cold temperate climate with a relatively short summer. The entire life cycle is passed in the same habitat.

Because of the relatively infrequent occurrence of *Carpilis* around Storrs, Connecticut, only a rough phenological outline can be drawn. Table 28 represents a summary of data from Canaan, Connecticut.

Adults were observed copulating in the field as early as July 24 in Canaan.

It appears evident, as compared with other egg-diapause species, that eclosion in *Carpilis* occurs relatively late in spring. This probably results from the early onset of diapause in egg development, which necessitates that egg development occur largely during spring after the ground temperatures have risen. Under the warmer laboratory conditions such eggs hatch much earlier in the spring and the life cycle is then accelerated.

TABLE 28

Phenology of *Carpilis consimilis*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
June 1	33%	67%	——	——	——	——
June 10	——	60%	40%	——	——	——
June 13	——	10%	90%	——	——	——
June 21	——	——	50%	50%	——	——
July 1	——	——	——	100%	——	——
July 7	——	——	——	50%	50%	——
July 12	——	——	——	33%	67%	——
July 18	——	——	——	9%	86%	5%
July 26	——	——	——	——	15%	85%
Aug. 5	——	——	——	——	7%	93%
Aug. 18	——	——	——	——	——	100%

The eggs of *C. consimilis* possess a strong diapause as none of the eggs develop spontaneously under room temperatures. While the eggs may survive at least −15° C. and obviously much colder temperatures in the field, only moderate cold temperatures are required to break diapause. A detailed analysis of diapause requirements was not attempted, but the following conditions were noted. Diapause was broken at 0° C. and 12° C. with cold exposures of 199 to 250 days. Shorter cold periods of 28 to 127 days were unsuccessful except for one of 51 days where 9% of the eggs broke diapause, but only after abnormally long developmental periods of 38 to 50 days as compared with the normal (average) egg development period of 17 days.

There is no pronounced reproductive pause, and oviposition follows directly after maturity is reached. It appears conceivable that the austral limits of the species are in part determined by the ability of the eggs to survive prolonged exposure to warmth, for the longer the warm season, the sooner the adults mature and begin egg-laying. The crucial question then becomes whether enough eggs will survive to ensure the next annual generation. Of course the cold requirement must be met, but selection may probably vary this need. The obligative diapause, univoltine seasonal cycle relationship is more demanding. Several tests were made at 60 and 90 day pre-cold periods with cold periods of 80, 127, and 199 days. None of these eggs hatched, and the best survival when the eggs were placed in cold shortly (2–20 days) after being laid. In fact, many of the old eggs died in room conditions before being placed in cold. Eventually all die if left too long in warmth. This relationship then very well might form the major factor limiting the austral distribution of this species. Clearly this situation warrants more detailed study.

Under laboratory conditions the stadia in days are as in Table 29.

TABLE 29

Stadia of *Carpilis consimilis*

Egg*	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
17.5 (6–26)	7.0 (7)	8.3 (5–12)	9.0 (6–13)	7.6 (5–12)	12.1 (7–23)	61.5 (48–83)

* period after return to warmth

As usual, development occurs more rapidly in the laboratory than in field populations. No significant difference was found in the longevity of males and females or whether mated or not. The average longevity was 54.4 days and varied from 23–65 days. Some field adults survive in the laboratory until early December, but the majority die during October.

The precopulatory period of the male and female is not precisely determined but is less than nine days. The preoviposition period is eleven days.

Egg productivity is markedly less than in other rhyparochromines and varies from 40–147 eggs (mean, 70 eggs) in mated females. The variation results from differing longevity, as on a per day basis the productivity ranged from 2.2 to 3.3 (mean 2.6). Sexually isolated females lay from none to 21 eggs. Such females become very swollen with eggs. Withdrawal of seeds caused a cessation of reproduction, so oviposition in the field must be also related to the availability of seeds. When a substrate for oviposition was not provided, egg production was greatly curtailed, and two fertile females laid only 26 and 38 eggs.

The smooth narrow somewhat pointed eggs are laid singly deep into the soil, or into crevices as the axils of seeds of *Veronica*, in hollow stems, often pressed into soft pith, into heavy tomentosity and other plant debris. In the laboratory *Carpilis* also oviposits into methyl cellulose, and cotton both wet and dry, but prefers dry substrates. The eggs do not cling to the substrate as in many other rhyparochromines. Considerable time and care is spent by the female selecting individual oviposition sites. Such care may be related to the long diapause state of the eggs, for the eggs must be laid in safe locations.

Exptochiomera nana Barber

This unique and apparently very rare species was described from a damaged specimen which was collected December 13, 1913 by Mr. C. A. Frost in Framingham, Massachusetts.

Mr. Frost indicated (*in litt.*) that he had indeed collected this specimen at Framingham, but discussed at length another new species *Blissus breviusculus* Barb. which together with *Exptochiomera nana* he had sent to Dr. Walther Horn in Germany, who had then sent the specimens on to Mr. Barber. Unfortunately, at this juncture, Mr. Frost died, before I could take further advantage of this eminent coleopterist's clear memory. Despite continued search at Mr. Barber's urging, Mr. Frost had been unable to obtain any other specimens.

Among the Myodochini this species is unusual because the anterior lobe of the pronotum, instead of being smoothly rounded, is delicately carinate. The sole known specimen is macropterous. Barber expressed some doubt whether this species actually belonged in *Exptochiomera.* Slater (*in litt.*) has examined the type and remarks that it may be related to the oriental genus *Suffenus* Dist. Even whether it is a myodochine is open to question as the spiracle positions are not known.

It is a possibility then that this species may be adventive in Massachusetts, perhaps introduced from the Orient or possibly from the Neotropical region where the large genus *Exptochiomera* is concentrated. Its occurrence in the field in December, however, would seem to indicate that at least some adaptation to cold was present.

Kolenetrus plenus Distant

As it is presently understood, this species and monotypic genus has a discontinuous known distribution in the mountainous areas of North America. It was originally described from the mountains of Guatemala, and has been recorded from the Huachuca Mountains of Arizona, northern New York, New England (Barber 1918b), Quebec (Moore 1950), Ontario (Criddle 1922), and recently from British Columbia (Scudder 1961). Father C. V. Reichart (*in litt.*) has collected the species at Chateau, Montana. I have collected this species from the Great Smoky Mountains in North Carolina.

However, a species complex may be involved. I have examined material collected in Guatemala (by Champion), from Arizona, Utah, and from eastern North America, and these populations although certainly closely related, appear quite different, and the whole complex should be carefully restudied. As noted by Distant (1893) *K. plenus* males from Guatemala have black femora, tibial bases, and first antennal segments and are brachypterous with the membrane barely reaching tergum seven. In the eastern populations the sexes are dimorphic in color, much as is *Trapezonotus.* In the male, the black areas mentioned are yellow-brown (ochraceous) in color, and the membrane almost reaches the apex of the abdomen. In the female these black areas are distinctly infuscated, but not as dark in the Guatemalan males. Moreover, the propleural punctures are fewer and larger in the Guatemalan specimens. It is apparent, then, that this discussion may refer to quite another species or subspecies than Distant's *plenus.*

In the northeastern United States this species becomes more common northward toward the mountainous areas, especially in the Adirondacks. Its distribution, however, is very spotty, and I consider it one of the more uncommon species in New England.

Environment

In New England this species is ecologically quite restricted and is predominantly found in relatively xeric, but cool sites. Since the more boreal habitats are also often more moist, this species was infrequently found in northern New England. In this respect its distribution parallels *Carpilis,* but it is even less frequently found. However, it does occur in northern New England. Barber (1918b) records it from Mt. Washington, New Hampshire, and Moore collected it on Peaks Island, Maine, in Portland Harbor Bay (Parshley 1920).

It was found most abundantly at a site near Warrensburg, New York, in the southern Adirondacks which may combine the favorable ecological aspects of other sites where it occurred less abundantly. This was an old dry field partly invaded by white pine. Along one side of the field ran an esker moraine which had only a thin scattered vegetation of the grass *Andropogon scoparius* along with a few small pines which had been planted. There were considerable interspace areas of bare dry gravelly ground between the grass clumps. Clearly this was a pioneer type habitat, but judging from the planted pines and the accumulation of *Cladonia* lichens and litter around the clumps, the habitat had persisted for a long time. At one side a clump of *Spirea latifolia* (Ait.) had established itself, and part of the clump had been cut down and piled by the landowner. In this habitat the biotope of *Kolenetrus* was in the thin layer of pine needles mixed with a short grass which formed a fringe or ecotone between the white pine dense litter and the open areas. It was also found in the shade of the dry pile of *Spirea* stems and at the margin of a clump of *Betula populifolia.* Here it coexisted with *Carpilis consimilis, Xestocoris nitens*, and *Trapezonotus arenarius.* In this habitat its abundance reached as high as 15 per square meter. It was found about Storrs in far fewer numbers, less than 1–2 per square meter, in dry old north facing fescue fields slowly being invaded by woody plants such as sweet fern (*Comptonia perigrina* (L.)), *Vaccinium pennsylvanium,* and *Quercus* spp. It is perhaps significant that this species although it was frequently found with *Carpilis*, was never collected in bald-type mountain habitats except for one specimen collected at 5,000 feet on the edge of Andrew's Bald, Clingman's Dome, North Carolina. On this bald, which was dominated by sedges and fescue grasses, it was found on the margin of

Rhododendron catawbiense E.L.Br. litter. At the Great Smoky National Park it was also collected along a gravelly roadside near Suco Bald at 4,500 feet.

The essential requirements of this species would appear to be xeric (2–3) habitat which is cool and partly shaded, as an old field ecotone, a combination which was not commonly found. These requirements in large part explain the scarcity of this species.

Scudder (1961) collected *K. plenus* in a quite different habitat among *Juncus* tufts at the edge of Westwick Lake, Cariboo, British Columbia. Scudder further notes that *Kolenetrus* appears very similar to *Acompus* which in Europe occurs in this sort of habitat. Torre-Bueno (1922), it should be added, collected *Kolenetrus* in a bog in Massachusetts.

The specimens from Guatemala were collected by Champion from the Quichė Mountains and at Quezaltango between 7,000 and 9,000 feet (Distant 1893). This altitude is above the cloud forest (4,500–7,000 feet) at a temperate level variously dominated by temperate-type coniferous or broad leaved forests (Standley and Steyermark 1946).

General Biology

All the specimens seen from eastern North America are macropterous (female) or submacropterous (male). Actually the male's wing is proportionally as long as the female's, but tergum seven is exceptionally long in the male *Kolenetrus* which causes the wing to appear submacropterous. The specimens appear capable of flight. According to Parshley (1917) this species was freshly washed up in ocean litter on Beach Bluff, Massachusetts, and because of the on shore wind he thought it clearly had to be flying over the water at that time.

K. plenus appears to possess disruptive coloration, with a clear contrast between the black-bronzed head and pronotum, and the half pale, half fuscous hemelytra; but when moving it is quite conspicuous. The nymphs have the abdomen cross banded in a pattern similar to that of *Stygnocoris pedestris,* which is frequently found in similar habitats.

No predators or parasites are yet known.

The natural food seeds of this species are not known. It does feed readily on sunflower and *Betula populifolia* seeds. It feeds very little during the essentially aestival diapause period of late summer which complicated attempts to elucidate feeding preferences.

No seed defense behavior was observed. Mating behavior was not observed except that the copulating pairs are secretive and take refuge under litter. Observed copulations last from 1 hour 43 minutes to at least 3 hours 30 minutes.

Life History

The life cycle of this insect is not clearly resolved. It has one generation a year with the phenology in table 30 based on very small samples.

TABLE 30

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
June 7	——	20%	40%	40%	——	——
June 22	——	——	——	33%	67%	——
July 7	——	——	——	14%	29%	57%
July 17	——	——	——	——	50%	50%
July 28	——	——	——	——	——	100%

No adults were collected from September 1 on. Therefore the method of overwintering could not be directly observed in the field and correlated with the field populations brought into the laboratory. The laboratory populations clearly were in an obligative state of reproductive inactivity in late summer in so far as oviposition was concerned. However, on July 27 in the field and on August 5 in the laboratory copulation was observed. But no eggs were laid. When left at room temperatures the insects came out of diapause in late November, laid a few eggs, and died. Moreover, these eggs did not go into diapause and most hatched readily. On this basis it would appear that the insect overwinters as an adult as this situation frequently occurs in overwintering adults which may complete diapause in warmth. However, in no other rhyparochromine species with a single generation and which obligatively overwinter as an adult was copulation observed in the field or laboratory in late summer. But a somewhat similar preoviposition copulation period exists in *Stygnocoris* and *Drymus* which overwinter as eggs. A replicate of seven *Kolenetrus* adults were placed in cold (3° C.) for 18 hours on September 23. One male and a female were removed. The other adults were left in cold for a longer time but died. The female after four days laid 14 eggs which were put in the cold room on October 15 and removed April 16, 1961 after 183 days. Of the 14 eggs, eleven developed, and one hatched, which at least indicates that the eggs have the capacity to overwinter, even if in a quiescent rather than diapause state. The best interpretation of this abnormal laboratory data, and the field evidence is that the eggs overwinter and the adults, like *Stygnocoris* and *Drymus* need a cold exposure to initiate oviposition.

The stadia of table 31 are based again on rather limited samples, the earlier instars on laboratory hatched eggs, the later instars on field nymphs reared in the laboratory. None were reared completely through the life cycle.

TABLE 31

Stadia of *Kolenetrus plenus*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
16	9	10?	7	7	8	57?

The slow development of the eggs is noteworthy.

Longevity of the adults averaged 125 days (range 82–164) in the laboratory. In one female in which the first copulation was observed, the eggs were laid after a preoviposition period (?) of eight days.

As indicated above, the data on reproduction is quite abnormal. The females which came out of diapause laid few eggs (average 18.5, range 14–21) over 14–20 days. The poor fecundity may be the result of metabolic wastage from keeping the adults in warmth for so long a period, as is the case in *Stygnocoris* and *Drymus*.

The eggs are smooth and slender and have the anterior ends flattened. Most are laid in the tight crevices in the litter and into methyl cellulose. Several are pressed into the tight wet cotton stopper.

TRIBE PLINTHISINI

Plinthisus americanus (Van Duzee)

P. americanus (V.D.) is here raised from synonymy with *P. compactus* (Uhler). Barber (1918d) carefully compared the types of *P. americanus* described by Van Duzee (1910) from Tyngsboro, Massachusetts and *P. compactus* described by Uhler (1904) from La Vegas, New Mexico and considered them to be conspecific. They are very similar, but a striking sexual dimorphism suggested that the species were distinct. In the eastern population, while the males have a nearly nude hemelytra, the females have the hemelytra densely investitured with long erect hairs, similar to the pronotum. In the western population, however, both sexes have nearly nude hemelytra. The species can be separated as in the following couplet which may be added to Barber's 1918 key (1918d).

1. Hemelytra of female nude; male with a nearly feature-less internal surface of tergum seven; paramere with basal lobe small, nearly pointed; paramere apex long and slender; spermathecal duct with only a narrow rim of sclerotization just beneath the bulb; female with sutures on tergum 8 diverging cephalad and not meeting ...... *compactus* (Uhler)

1a. Hemelytra of female densely pilose; male with a circular apodeme on inner surface of tergum seven which receives genital capsule at rest; paramere with a large rounded basal lobe; spermatheca with a broad sclerotized band on the duct just proximal to the bulb; females with sutures on tergum 8 converging and meeting cephalad .... *americanus* (V.D.)

The disjunct presence of such closely related species in eastern North America and southwestern United States probably indicates a long isolation (Ross 1962).

The other three known American species are recorded from the western United States and Ashlock informs me (*in litt.*) that actually a large complex of *Plinthisus* exists there. So far *americanus* is known only from Quebec and Ontario south to northwestern Connecticut. It will probably be found southward along the Appalachians. The southwestern form is also found in Arizona (Banks 1910) and was collected in a *Neotoma* nest in California (Torre-Bueno 1946).

The genus *Plinthisus* itself is nearly world wide, and the only major zoogeographical region without any recorded species is South America. There is a heavy concentration of species (43 to 62) in the Palearctic (mostly Mediterranean region) but recent work on the Ethiopian fauna rather suggests that the distribution of *Plinthisus* may more closely parallel the presence of hemipterists. Nevertheless only a few of the species are found in north temperate areas. It is therefore of interest that *P. americanus* is adapted and restricted to a north temperate climate.

Environment

P. americanus is a forest species found in the litter biotope beneath hemlock (*Tsuga canadensis*), hemlock-birch (*Betula papyrifera*), spruce-fir (*Picea rubrum-Abies balsamea*) forest associations, but rarely in white pine litter. The heaviest densities (20–25 per square meter) are found in *Tsuga* litter. Litter that is relatively loose and on a slightly drier than average slope is more favorable than the tightly packed litter common to coniferous forests. The litter is always a typical mor type and the soil a grey podsol. In favorable biotopes the litter has a mesic moisture level of 4–6. *Plinthisus* is absent from wet sites with considerable accumulation of mosses, typical of many spruce forests and also is rare in very dry red spruce litter on mountain tops. It is frequently found with *Eremocoris ferus* and *Scolopostethus diffidens*, especially where a considerable admixture of *Betula papyrifera* L. is present. The herbacious level, as is typical of coniferous forests, was absent or insignificant. Within the wide spread forests of this type, *Plinthisus* displays a discontinuous ecological distribution in relation to the variable litter and slope types. In northern New England, it is more abundant in valley forests than in the mountain forests. Its abundance is frequently quite low, 2–4 per square meter, but occasionally up to as much as 20–25 per square meter.

General Biology

Macropters are very rare in this species, and only two were found in the course of the study. This correlates with the permanence of its climax forest habitat. The only specimen of *Plinthisus* collected by Ashlock (*in litt.*) was a macropterous male. This becomes significant for it was collected in white pine litter which is apparently a rather unfavorable habitat for *Plinthisus*, and the macropter may represent a dispersing individual.

Like all brachypterous species of *Plinthisus, P. americanus* is a small, oval, shiny brown insect. It is a sublitter form, keeping to cover under the debris, and it usually remains quite still when the litter is disturbed and the insect must be directly disturbed before it moves to seek cover elsewhere. It does not feign death, however. Its color blends well into the background litter and it requires careful search especially where the densities are low.

Plinthisus feeds very readily on the fallen seeds of *Tsuga* *canadensis, Betula papyrifera, B. populifolia,* and *Picea rubra.* It also feeds readily on sunflower seeds. Like many forest rhyparochromine species it can survive only about 4–6 hours in a dry enclosure.

Plinthisus actively moves the seeds into interstices in loose litter for feeding. Since *Plinthisus* shows a marked sociability in the field and often aggregates in a particular litter clump in the laboratory, the seeds are often found grouped together. Frequently these litter mounds were bound together with (?) mycelia strands. On several occasions *Plinthisus* was observed moving the large (compared to the insect) *Tsuga* seeds. It first feeds on the seed and then proceeds to drag the seed with its labium. When the seeds became caught in the litter, the insect places its fore femora over the seed, dislodges the seed, and resumes dragging. When enclosed with *Eremocoris ferus* and *Scolopostethus diffidens,* this behavior becomes much more accentuated, as the *Plinthisus* endeavors to protect the seeds from the *Eremocoris* which displays an equal readiness to feed on the *Tsuga* seeds.

In the mating behavior, the male leaps suddenly on the female and apparently senses her without any prior contact. Copulation lasts from 5 to 8 hours and is often repeated.

Life History

Plinthisus americanus has a univoltine life cycle with an obligative egg diapause. The earliest nymphs were found in mid-June in the third instar, and fifth instars were found as late as July 27. This evidently indicates a late eclosion period, which would correlate with the fool forest floor environment. There apparently is a fairly long preoviposition period of 17–21 days as oviposition begins in early to mid-August. Laboratory conditions, however, may greatly curtail egg production. When hemlock seeds were included, the fecundities were more uniform and higher.

The eggs are laid from late summer until winter intervenes, and diapause in early anatrepsis. I was unable to completely break the strong diapause. However, after six months exposure to moderate cold (4° C.) egg development to katatrepsis occurs, but no hatching.

Fecundities of from 45–97 eggs per female (mean, 67) are recorded. Four sexually isolated females lay no eggs. The longevity of the adults in the laboratory varies from 30 to 101 days (mean 62).

The eggs are laid into the forest litter, pressed into small crevices in the substrate. The eggs are narrow, somewhat pointed on the posterior end, the anterior end is flattened and the sides are slightly fluted.

TRIBE ANTILLOCORINI

Antillocoris minutus (Bergroth)

The tribe Antillocorini as recently established by Ashlock (in press) includes a number of genera of minute Lygaeidae. The species of *Antillocoris* themselves are about 2 mm. in length. The genus includes 6 species, 3 of these occur in Central America or the West Indies and one reaches South America. Many more species will probably be described when the Neotropical fauna is better known. The other three species are found in the eastern United States, each with a different latitudinal distribution (Barber 1952). *A. discretus* Barb. was recently (Barber 1952) described from the Gulf Coast area from Florida to Texas with one isolated record from southern New Jersey. *A. pilosulus* is found throughout the southeastern United States north to New Jersey and Missouri. The third species, *A. minutus,* is a northern species, occurring from eastern Canada south to New Jersey and Missouri. Southern records of *minutus* refer to the two southern species (Barber 1952). While the two southern species are entirely macropterous, *A. minutus* is pterygopolymorphic.

Environment

Antillocoris minutus is a common although infrequently collected inhabitant of forest litter. It is often abundant in litter beneath gray birch (*Betula populifolia* Marsh) and white birch (*Betula papyrifera* Marsh) where it may attain densities of 50–80 per square meter. *A. minutus* is also found in lesser abundances (up to 20 per square meter) in hemlock (*Tsuga canadensis*) litter, and in *Vaccinium-Viburnum-* maple litter. In all of these forest habitats it is frequently associated with the rhyparochromines *Scolopostethus* spp., *Eremocoris ferus* and *Drymus unus* (see Competition discussion).

However, the species was never collected in oak-hickory forests and rarely in very mesophytic deciduous forests. Occasionally it is found in various marginal type habitats but in low abundances (1–5 per square meter) as in vole runs in heavy grass meadows, or at the base of sedge clumps in marshes. In spring after the post-hibernation flight it frequently occurs in various habitats, then apparently suitable, but which dry out later, and the species disappears.

In the favored biotopes of *A. minutus*, the litter is well-drained but relatively mesic (moisture 5–8) and the temperatures vary from 71° to 82° F. at midday in July. The litter layer varies from 2 to 10 inches deep and contains many small seeds. Sometimes the litter accumulates between clumps of a fine leaved grass. The soil is usually a mull litter on a sandy loam or in hemlock forests, a grey podsol. In nearly all habitats its ground layer biotope is completely shaded from direct illumination. In southern Connecticut *A. minutus* occurs frequently on cool north-facing slopes which are also favorable to *Betula*-hemlock communities.

The few habitat notes in the literature largely confirm a woodland habitat selection. Torre-Bueno (1924, 1929a) sifted it from moss in dense woodlands, and from sphagnum and leaves near a swamp edge (Torre-Bueno 1925). Barber (1923) says it is a common species among dead leaves in damp situations.

A. minutus occurred at several forest sites for at least five years in succession and overwintered in these same habitats.

General Biology

In marginal habitats only macropterous specimens are collected. These probably result from post-hibernation migration flights. In favorable habitats where it occurs year after year the large majority of the population is brachypterous. At one area for two years in succession the percent of macropters diminished sharply from early spring to late summer. There are no good records of *A. minutus* at lights.

A. minutus is unique among New England rhyparochromines in possessing two distinct brachypterous forms. In one, the brachypter, the hemelytra are merely abbreviated as is usual, but in the other, the subbrachypter, the membrane is absent and the margin of the corium is truncated. Since the species is univoltine, little could be done to resolve the nature of this interesting wing polymorphism. From one large population with an exceptional number of macropters present the spring females were isolated. The females were already mated and only the resultant progeny were examined. The results are interesting as shown in Table 32.

TABLE 32
The wing development of the progeny of *Antillocoris* females

Parental Females	Progeny
5 subbrachypters	134 subbrachypters
4 brachypters	120 brachypters
8 macropters	191 brachypters
1 macropter	37 brachypters, 8 macropters

Since this is the same population, random mating was probable. The data on the progeny permit a few deductions. First, that the laboratory environment did not affect the appearance of the subbrachypterous phenotype since the conditions were nearly identical. But all the macropterous females but one yielded only brachypters and the brachypters, only brachypters. The meaning of these data is unclear: a maternal factor may be involved and/or a switch gene for brachyptery and macroptery as in *Gerris* (Brinkhurst 1959). This certainly warrants more work.

A. minutus is one of the least conspicuous of all the New England lygaeids and its abundance must be considerably underestimated. The adult is dark brown in color and characteristically moves slowly and deliberately like many woodland lygaeids. When touched it runs rapidly for a short distance then suddenly resumes its deliberate gait. Its small size allows *minutus* to conceal itself in small crevices such as in rolled up birch leaves. The nymphs however are very conspicuous. They are a distinct pale pink color.

Both nymphs and adults possess a peculiar scent gland odor resembling *Tapinoma* ant odor. The nymphs of *Antillocoris* lack the anterior scent gland. The scent gland secretion is released only under very rough treatment. The predators or parasites of *A. minutus* are not known.

In the laboratory *Antillocoris* feeds readily on seeds of *Betula populifolia, Betula papyrifera, Tsuga canadensis* and probably other seeds as its feeds on sunflower seeds. It can be reared very easily on a sunflower-birch seed mixture. No seed defense behavior was observed. Beyond the male vibrating his antennae at the approach of a female, the mating behavior was not observed.

Life History

A. minutus is univoltine and has an obligative adult diapause. Its seasonal cycle begins in mid-June and is completed by late July as shown in Table 33.

Adults collected in late April and early May lay eggs in the laboratory within 2 to 5 days and many adults are already fertilized by this time. Since the nymphs do not appear until much later it is probable that under cool and shaded litter conditions in spring the eggs develop slowly as in *Xestocoris* and *Scolopostethus diffidens.* A long photoperiod stimulus is apparently not necessary as in *Myodocha* since *A. minutus* matures under a 12 hour photoperiod. The diapause condition is a strong one and very few individuals complete diapause development under warm conditions. In one culture a female broke diapause after a long dormant period of 254 days but laid only 19 eggs. This is unusual, for most adults live under warm conditions only until December to February and die without reproducing. Photoperiod seems to have no effect on the seasonal cycle and diapause is completed under cold conditions.

The stadia given in Table 34 are based on cultures reared on a gray birch—sunflower seed mixture. Poor growth is made on sunflower seeds alone.

TABLE 33
Phenology of *Antillocoris minutus*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
June 8	—	—	—	—	—	100%
June 18	5%	20%	—	—	—	75%
June 28	10%	30%	25%	5%	—	30%
July 9	10%	20%	40%	20%	5%	5%
July 18	—	—	25%	45%	30%	—
July 26	—	—	—	16%	42%	42%
Aug. 13	—	—	—	3%	7%	90%
Aug. 26	—	—	—	—	2%	98%
Sept. 10	—	—	—	—	—	100%

TABLE 34
Stadia of *Antillocoris minutus*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
11.0 (9–15)	7.0 (5–10)	6.0 (5–8)	7.1 (6–9)	7.8 (7–10)	10.4 (9–12)	53.0 (46–62)

The egg productivity of field collected adults ranges from 34 to 158 eggs with an average of 94 eggs per female and the eggs are laid at a rate of 2 to 6 a day. Eight spring collected virgin females laid no eggs whatever. At least one field female was non-reproductive as late as June 7, and oviposited only after fertilization. The eggs are oviposited singly in wet substrates such as the stopper of the water vial or damp litter. The eggs are smooth, unadorned, rather short and thick, and slightly curved on the ventral side. They do not stick to the substrate.

Antillocoris pilosulus (Stål)

This species reaches the northern limit of its range in southern New England and Barber (1952) cited it as only extending north to southern New Jersey. However Barber (1923) recorded it from Massachusetts. The species of *Antillocoris* are similar, and literature records must be used with care.

I was able to collect only 3 specimens of what are apparently *A. pilosulus* in Connecticut. These were collected July 28, 1957 at Noank, Connecticut which is on the Long Island Sound coast. The habitat was an open area heavily invaded by shrubs. The precise biotope was in thick litter beneath the bayberry *Myrica pensylvanica* Loisel.

In the Great Smoky Mountains of North Carolina, 8 adults were collected on June 6 and 7, 1960. Three specimens were found in the litter of the shrub, *Rhododendron catawbiense* at 5,600 feet at Andrew's Bald, a grassy bald on Clingman's Dome, North Carolina. The other five specimens were collected in leaf litter along a mesophytic woodland edge in the valley at 2,000 feet near Cherokee, North Carolina. These habitats were relatively moist and shaded much like the habitat of *Antillocoris minutus.*

In the literature *A. pilosulus* was swept from grasses in a dry cranberry bog in New Jersey (Torre-Bueno 1912) and Blatchley (1926) collected it from beneath stones in a pasture in Indiana. Wray and Brimley (1943) found it in the pitcher plant (*Sarracenia purpurea* L.). It has been collected at lights in Missouri (Froeschner 1944) and Glick (1939) found what was probably *A. pilosulus* up to 5,000 feet in the air over Louisiana. This aerial collection included two nymphs so the occurrence might be accidental due to strong winds and the insect's small size.

The adults collected in Connecticut in late July, like *minutus*, were in a state of dispause, did not become reproductive in the laboratory and died in October.

The insects feed readily on sunflower seeds. The adults from North Carolina also fed on sunflower seeds and two surviving females laid a total of 37 eggs. Only 2 adults, a male and a female, were reared through and the did not become reproductive.

In southern Florida at Naranja, *A. discretus* Barb. was collected in mesic leaf litter under an old overgrown avocado tree. This indicates a considerable similarity in the general habitat of these three species of *Antillocoris.*

TRIBE LETHAEINI

Cryphula trimaculata (Dist.)

According to Scudder (1962) the correct name of the single species of *Cryphula* in northeastern North America is *trimaculata* (Dist.) not *parallelogramma* Stål. *C. parallelogramma*, the type of the genus, is a small dark species known from Texas and Arizona. *C. trimaculata* was described by Distant (1882) from specimens collected in the highlands of Guatamala. If these widely separated populations represent one and the same species, *trimaculata* has a wide distribution from southern New England west to Colorado and Texas and south to Guatemala. However it should be understood that this discussion may refer to a new species (or subspecies) closely related to *Cryphula trimaculata* of Guatemala since a Guatemalan male specimen before me differs from New England specimens in size, puncturation and color.

The genus *Cryphula* includes seven described species of which five occur in the United States and three in South America as well as Central America. However specimens from various collections indicate that species of *Cryphula* range throughout the Neotropical Region and this genus is quite probably Neotropical in origin.

In New England I find *Cryphula* limited to the southern portion from Cape Cod to southwestern Connecticut. Although it is relatively abundant at Storrs, Connecticut I could not find the species in northwestern Connecticut and northward.

Environment

Cryphula trimaculata is a ground litter inhabitant of long lasting old fields vegetated with perennial bunch grasses such as *Andropogon scoparius, Festuca rubra* L., *Panicum* spp., a plant association described under *Cnemodus mavortius* with which *Cryphula* frequently occurs. Its habitat range extends to woodland margins and grassy glades in relatively xerophytic oak-hickory forests, but it is not a woodland species like *Ozophora picturata* and it nearly always occurs on the field side of woodland ecotones.

This plant association dominates exposed areas on dry overdrained gravelly slopes for considerable periods of time. The biotype of *Cryphula* is in ground litter at the bases and in the interstices between the grass clumps. The surface soil is usually quite dry (1-2) sometimes, in edge areas relatively mesic (4–6). The biotope temperatures at midday in August range from around 28° to 35° C. much less than fully exposed soil nearby (excess of 50° C.).

The abundance of the species where it occurs is usually about 6–10 per square meter and in favorable habitats under *Panicum* sp. it reaches 30–40 per square meter.

Blatchley (1926) reported sweeping adults and nymphs of this species from the flowers of redhaw (*Crataegus punctata* Jacq.). Barber (1923) noted *Cryphula* as another species found in sifting dead leaves or beneath stones and sticks on the ground. Barber (1918c) also collected *C. abortiva* Barber and *C. nitens* by shifting among dead leaves.

In general, *Cryphula trimaculata* appears ecologically similar to the other lethaeine species, *Xestocoris nitens.* While *Xestocoris* also is an inhabitant of semi-permanent grass habitats, it is rarely found with *Cryphula. Cryphula* may ecologically replace *Xestocoris* in southern New England where, perhaps in competitive exclusion, *Xestocoris* occurs on north-facing slopes on dry *Festuca* habitats as described under *Carpilis. Cryphula,* on the other hand, is much more frequently found on south-facing slopes, and more mesic margins of woodlands than is *Xestocoris.* And perhaps as a consequence of this, *Cryphula* is frequently found with *Pachybrachius basalis* under *Panicum* spp. in mesic habitats where *Xestocoris* is rarely found.

More work is needed both to the north and to the south to see whether these species are really ecological equivalents and if any character (ecological) displacement is occurring where the ranges of the species overlap. With *Xestocoris,* the ecological amplitude appears greater in more northern habitats than at Storrs, Connecticut but this may simply reflect more restricted microclimatic conditions in southern New England.

In southern Florida at Naranja, I collected a small rather infuscated form of this species in short grasses in a palmetto—slash pine habitat. The general aspect of this open association is similar to some habitats of *Cryphula* in southern New England.

General Biology

Like *Xestocoris, Cryphula trimaculata* is wing polymorphic and roughly 10% of the field populations are macropterous, the percentage varying from one population to another, but with the brachypter always the much more abundant form. This wing condition correlates with the relatively long-lasting dry habitat of this species. The presence of the macropter correlates with the frequent occurrence of *Cryphula* in the scattered mosaic of favorable habitats. There apparently are no dispersal records for this species. However, field observations show a larger proportion of *Cryphula* along woodland margins in autumn than in midsummer which may indicate some small scale movements to more protected hibernacula. Dowdy (1955) collected this species overwintering in oak-hickory forest in Missouri.

Cryphula is a small brownish insect blotched with pale lines and areas. This procryptic coloration blends very well with the dry grass litter background. This insect is short-legged and flattened and does not run far when provoked, but scurries to the nearest crevice to hide. It frequently takes direct contact to provoke the insect, but *Cryphula* does not feign death. In the laboratory it conceals itself under bits of leaves and avoids white substrates. The function of the remarkable iridescent sheen of the integument and the iridescent patches on the vertex of the head is not understood.

There is a very low percentage (less than 2%) of parasitism by an undescribed species of *Catharosia*. The parasite overwinters in the diapausing host.

Cryphula feeds readily on sunflower seeds, oviposits abundantly, and can complete its development on this seed, although the mortality is high. However, it definitely prefers to feed on seeds of *Panicum* spp. and is easily reared on this seed. It also feeds on seeds of fescue, millet, and strawberry and probably feeds on other seeds as well. Under hunger stress this species will scavenge on dead and dying *Cryphula* specimens.

The seeds of *Panicum* are dragged about to sheltered locations for feeding. The seeds are impaled on the labium and dragged about under the insect. When the seed catches on the litter the insect lifts the seeds over the obstacle with the combined action of its fore and middle legs.

In its mating behavior, the male approaches a receptive female which it apparently recognizes before actual contact. The antennae are alternately moved up and down with a quick flick at the end of each beat. After contacting the female the male jerks his body from side to side with a very brief pause after each movement. He climbs on the female, flicking her head with these antennal movements and accomplishes copulation in an end to end position. It may be relevant that in all eight observed copulations the female was feeding on a seed.

Life History

Despite its southern distribution, *Cryphula* has an univoltine seasonal cycle with an obligative adult diapause. Dowdy (1955) noted that this species overwinters as an adult. The nymphs do not appear until rather late in the season at Storrs, Connecticut as shown in Table 35.

TABLE 35
Phenology of *Cryphula trimaculata*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
June 20	——	——	——	——	——	100%
July 3	25%	30%	15%	——	——	30%
July 20	11%	28%	22%	11%	11%	17%
Aug. 6	——	4%	16%	32%	48%	——
Aug. 22	——	——	7%	7%	26%	60%
Sept. 5	——	——	——	——	25%	75%
Sept. 25	——	——	——	——	9%	91%
Oct. 10	——	——	——	——	——	100%

As early as May 26 some females are already fertilized. Active mating and oviposition were observed in field populations at Storrs, Connecticut on June 18 and 19, 1962.

To test for photoperiod response a population of early spring adults not yet reproductive was divided into two groups and cultured under photoperiods of 12 and 15 hours. Under both long and short photoperiods the cultures became reproductively active at the same time. Moreover the progeny of each culture went into reproductive diapause, showing the obligative nature of the diapause. The duration of the diapause state was also not affected by these photoperiodic conditions.

Most cultures which are kept in the laboratory in autumn under warm conditions do not become reproductive. The few that do are all collections which were exposed to cool field conditions of early November. However, only certain individuals are released from diapause and these after diapause periods varying from 16 to 98 days, after which the ovipositing females live 28 to 42 days. These females lay very few eggs (13–28 eggs) at a rate of less than one a day.

The normal fecundity of *Cryphula* in spring is from 84 to 128 eggs (mean, 98). Adults collected in late April begin ovipositing in about a week. Unmated females lay from none to 41 eggs (mean 26). The longevity of diapausing adults ranges from 97 to 219 days.

The stadia which are given in Table 36 are not completely worked out and for the later instars only the range is given. The egg development given is for 80° F. (room temperature) and is relatively slow. Eggs incubated at 67° F. developed even more slowly, taking from 34 to 39 days to hatch. The late occurrence of nymphs is probably best accounted for by prolonged egg development under spring ground temperatures.

The eggs are rather short and thick with a smooth chorion which does not stick to objects or to other eggs. The eggs are oviposited singly in cotton and under bits of litter.

TABLE 36
Stadia of *Cryphula trimaculata*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
26.3	9.2	9.0	9.4			
(16–39)	(7–12)	(8–10)	(8–10)	(10–12)	(10–12)	(60–62)

Xestocoris nitens (Van Duzee)

Xestocoris is a small genus of three species. One, *X. collinus* Dist. is known from Guatemala and Panama. The second, *uhleri* (Dist.), is known from Grenada, West Indies. The third, *nitens*, has a northern distribution from Quebec west to Iowa and south to Massachusetts and New York (Slater, Catalogue), and I have collected the species in the high elevations of the southern Appalahians in the Great Smoky Mountains National Park, North Carolina. *X. collinus* has on several occasions been intercepted on orchids, *Oncidium* sp. and *Cattleya bouringiana* from Panama (Swezey 1945).

From the literature, *Xestocoris* would appear to be an extremely rare species, but again such a "rareness" is more the result of its habitat choice and ground layer biotope. It was only recently found west of New York in Illinois and Iowa (Slater 1952).

Environment

Xestocoris is a characteristic species of dry (2–3) overdrained morainic old fields with a long persisting sparse, low vegetation of clump forming grasses such as *Andropogon scoparius*, *Festuca rubra* L., *F. capillata* Lam, and *Danthonia spicata* (L.). In southern New England it is usually found on north-facing exposures. Similarly it is common on mountain balds in the sparse vegetation among rock outcrops. It is frequently found in dry edge habitats between a field and forest, especially on the margin of the dry soil indicator, white pine (*Pinus strobus*). It is *not* found in very barren open hot habitats with a considerable amount of bare soil, but only where the vegetation forms a closed ground biotope of litter and lichens between the grass clumps. Its abundance in some lowland fields is as much as 25–30 per square meter and on mountain sites, 15–20 per square meter, but it is usually found in densities of about 5 per square meter.

I never found *Xestocoris* in wet habitats from where it was reported by Barber (1923) and Blatchley (1926). Torre-Bueno (1929a) collected it by sifting grass piles in Massachusetts.

It hibernates *in situ*, and frequently forms large hibernating aggregations at the base of a single grass clump which is no way distinguishable from other neighboring clumps. This tendency to aggregate is also shown in the laboratory for a group of insects will cluster together in one corner of the rearing dish, especially under cool conditions.

General Biology

The great majority of the specimens are brachypterous which correlates with the semi-permanent habitat perference of *Xestocoris*. The resultant low dispersal rate, however, must be sufficient to readily colonize such areas. Dispersal apparently occurs in the spring, as is indicated by the nearly complete disappearance of macropters from several habitats through the spring. Movement from the localized hibernacula occurs in early spring and this also actually constitutes an active dispersal movement but not by flight as most individuals are brachypterous.

Xestocoris is a small insect with a generalized body shape and short legs. It keeps to cover at the base of grass clumps in the fallen grass litter and lichens. When disturbed the insect's immediate reaction is to conceal itself again. Its dark shiny coloration against the light litter does not appear to be especially procryptic except when it is concealed in dark crevices at the base of the plants. The nymphs are pale pink in color, and the late instars are quite conspicuous in the field.

No predators or parasites were found. Its chemical defense should be interesting as this species in both nymphs and adults (like *Antillocoris* and *Cryphula*) has a heavy odor very similar to the odor of the ant *Tapinoma*. There is a possibility that *Xestocoris* is avoided by ants as the odor of *Tapinoma* repels other ants (Wheeler 1910).

This is one of the few species which suffers a heavy mortality in the shift from field diet to sunflower seeds. It does not do well on this seed and could only be reared by adding *Festuca* seeds. It feeds readily on *Festuca rubra, F. capillata, Andropogon scoparius, Paspalum muhlenbergia* (Nash) and *Danthonia* seeds.

It does *not* feed readily on *Vaccinium* or various composite seeds. While it will feed, if forced by starvation, on non-grass seeds such as sunflower seeds, it strongly prefers grass seeds. Its water needs are large, despite the xeric environment preference and it dies quickly without water.

Although the seeds are moved about to safer sites, no seed defense was observed. Nor could the mating behavior be observed beyond a male responding to a receptive female by rapidly vibrating his antennae.

Life History

Xestocoris nitens has a univoltine seasonal cycle and an obligative adult diapause. As shown in Table 37 the phenology in Connecticut is late. The early instar nymphs are not found in Storrs, Connecticut until early July, and fifth instars are found from mid-August to early October. Oviposition begins at least by mid-June and continues until early August. However, oviposition apparently is not correlated with a photoperiod response since long or short day photoperiods do not affect oviposition time in the laboratory, and oviposition occurs under short (12 hour) photoperiods.

TABLE 37
Phenology of *Xestocoris nitens*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
June 1	——	——	——	——	——	100%
June 20	——	——	——	——	——	100%
July 1	22%	——	——	——	——	78%
July 17	12%	25%	25%	——	——	38%
July 29	——	17%	32%	17%	17%	17%
Aug. 15	——	——	18%	55%	18%	9%
Aug. 30	——	——	6%	22%	50%	22%
Sept. 15	——	——	——	2%	18%	80%
Oct. 7	——	——	——	——	4%	96%
Oct. 25	——	——	——	——	——	100%

The stadia as given in Table 38 are based on laboratory rearing on mixed fescue-sunflower seeds. The life cycle is especially characterized by a relatively long egg development period in the laboratory of 16 days which may in part explain the late occurrence of nymphs. As already indicated the apparent preoviposition period after winter ends is long, at least two months. However, the precopulatory period is much shorter as adults collected April 27 were found mating May 1st in the laboratory.

The late cycle is probably related to a late maturation since maturation is speeded by bringing the overwintered insects into the warm laboratory.

This late seasonal cycle closely coincides with the major seed food plant of *Xestocoris,* the fescue grass, which in Connecticut in early July ripens its seeds. Thus the nymphs develop during the period when the host plant seeds are abundant.

The diapause is a relatively strong one and is broken only occasionally under warm laboratory conditions after a long dispause development of three or four months. The life cycle from egg to adult takes from seven to eight weeks in both the field and laboratory.

The fecundity in the laboratory is relatively low. On a mixed sunflower-*Festuca* seed diet, only 40 and 62 eggs were laid by two females. These eggs were oviposited at a rate of 2–4 eggs a day. Sexually isolated virgin females lay no eggs. A substrate factor is apparently involved as egg production is greatly reduced (to 10–20) when a suitable oviposition substrate is unavailable.

The eggs are smooth, and thickly cylindrical with rounded ends. They are laid in crevices between culms, between the culm and a grass stalk, and into loose dry litter. They may also be laid in dry methyl cellulose, but are not laid on wet surfaces.

TABLE 38
Stadia of *Xestocoris nitens*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
16.0 (14–17)	9.3 (8–11)	10.0 (8–12)	10.3 (8–12)	9.2 (8–10)	11.5 (10–13)	61.0 (49–72)

TRIBE OZOPHORINI

Ozophora picturata Uhler

O. picturata is the only representative in New England of the largely tropical tribe Ozophorini. The essentially Neotropical genus *Ozophora* contains 21 known species, 18 apparently restricted to an area approximating the Carribean Province of Good (1953). Only two species are known from South America, but this probably indicates once again our very poor knowledge of the South America lygaeid fauna. Two species, *O. reperta* and *O. trinotata* appear to be endemic to Florida.

Not only does *O. picturata* represent the northern limit of the genus, but it is also the most widely distributed species if the literature is to be taken at face value. It occurs north to Massachutts and Ontario, west to Iowa, Arizona, and perhaps California, and south to Mexico, Guatemala, Dominica, and Grenada (Slater, Catalogue). Some doubt, however, should be reserved for the Carribean records. The *Ozophora* species are closely related and need careful study.

According to Slater (1952), while *O. picturata* is a common insect in the southern states it is very uncommon in Iowa and Illinois. There is some diversity of opinion about its abundance, which may be linked to its distribution. Uhler (1876) remarks that it ''is very rare near Baltimore, in spots with rank growth late in July.'' Barber (1923) and Torre-Bueno (1925) said that it is frequently taken in New York by a sifting among dead leaves in late fall or sheltering under boards. Blatchley (1926) described it as ''scarce throughout Indiana under logs, low marshy places, or herbage.'' He also collected it as far south as the Everglades National Park, and considered it the least common species of *Ozophora* in Florida. In New England, I found *O. picturata* common along the coast of southern Connecticut at Noank and New Haven and fairly abundant at Storrs, Connecticut. But at Canaan, Connecticut in the highlands it is either absent or at least so scarce that I was unable to collect it. Slater (in litt.) collected a specimen at Camden Hills, in southern Maine.

Environment

In Connecticut, *O. picturata* shows no evident seasonal change of habitat. It is found in the same habitats from season to season and year to year. This species is strictly an inhabitant of forest floors, ranging from climax oak-hickory forests to shrubby consolidation seres. It is never collected in open habitats, but only where the litter layer is shaded.

At Storrs, Connecticut *Ozophora* occurs in the thick loose litter of well-drained mesophytic oak-hickory forests, usually on moderate slopes. In relation to the life history of the insect this community forms a relatively permanent habitat. It appears to be of some interest too, that this rhyparochromine is the only seed feeding lygaeid found in the oak-hickory forest community which forms the climax community in much of the eastern United States (Braun 1950). In such habitats in southern New England, however, its density is never high, usually about 1–3 per square meter. This average holds quite constant over large tracts of oak forest in eastern Connecticut. Forests with maple, grey or black birch admixtures do not usually alter the counts. In this habitat the species is found most abundantly in the drier, well drained duff while depressions and spots with wetter litter rarely harbor the species.

Ozophora is much more abundant in several shrub communities at Noank, Conn. The plant community of this sere consists of a few *Acer rubrum* L., with a dense shrub understory of *Vaccinium corymbosum* (L.) and *Viburnum dentatum* L. and with a herb layer largely of *Aster* spp., *Rhus toxicodendron* L. and the fern, *Dennstaedtia punctilobula* (Michx). In the mesic leaf litter under the above plants *O. picturata* is found in a density of 20–25 per square meter along with the rhyparochromines *Eremocoris ferus*, *Scolopostethus atlanticus*, and *Antillocoris minutus*.

At Noank, in the extensive dense sumac community (*Rhus typhina* L., *R. glabra* L., *R. toxicodendron* L., *Smilax* spp.) so typical of the shrub sere of old fields along the Connecticut coast, there is a sparse population especially beneath occasional scattered black cherry trees (*Prunus serotina* Ehrh.). On Ram Island at Noank in dry litter beneath a pure strand of bayberry (*Myrica pensylvanica* Loisel.), first and second instars were found along with adults of *Eremocoris ferus*.

In addition to occurring in a closed oak-hickory forest *Ozophora* is also found in the more open white oak forest with considerable short grass growing between the trees. It occurs here in abundances of 1–2 per square meter.

The chief factors which distinguish the litter of the foregoing habitats is a general dryness of about 4–5, considerable shade, and a litter depth of at least two inches, usually more. The texture of the litter is important as *Ozophora* is always found in coarse, loose mull litter which characterizes the litter formed by oaks in contrast to most other trees. Both *Vaccinium* and *Myrica* also form a fairly loose but finer litter. Dry oak-hickory slopes are frequently found on well drained south slopes of moraines in southern Con-

The Committee on Publications of the Brooklyn Entomological Society regrets to announce that it is compelled to suspend publication of Entomologica Americana with the present volume.

The editor wishes to take this occasion to thank contributors and readers who have been so cooperative and pleasant during his tenure as editor.

It is the hope of your editor that this old and distinguished journal will be reactivated in the future so that it can once again serve those interested in the Science of Entomology.

J. A. Slater

necticut. The soil is usually of overdrained sand and gravel. But where the litter is thick and the uppermost layers dry, the soil may vary considerably in moisture.

Forest litter temperatures are moderate in summer with recorded litter temperatures never over 75° F. Since the forest community inhabited by *picturata* extends much farther north than does *picturata* and the relative abundance of the insect drops very rapidly north from the coast in Connecticut, it is probable that temperature determines the northern limits of the distribution of this species. To explore this hypothesis, the resistance of *picturata* to cold stress must be studied.

As already mentioned, populations of *Ozophora* in Connecticut tend to be thin, usually 1 or 2 per square meter, and occasionally up to 20 per square meter. There is apparently little tendency to aggregate, and the populations are dispersed fairly evenly over large areas. In 38 square meter counts on an oak-hickory hillside at Mansfield, Connecticut an average abundance of 2 per square meter was obtained with extremes of 0–4 per square meter. This density pattern was repeatedly observed in oak-hickory associations. Dowdy (1947) collected ten specimens in a 10.8 square feet sample on August 14 in Missouri in oak-hickory litter.

Available habitat notes largely confirm the forest preference of *Ozophora*. Torre-Bueno (1912) beat the species from oak at Yaphank, Long Island, New York in a pine-scrub oak roadside area. Froeschner (1944) collected it from May 11 to August 2 under rocks and logs in Missouri. Dowdy (1947) recovered it from forest litter during an ecological study of an oak-hickory forest at Jefferson, Missouri. Other habitat notes are as follows. Gaines (1933) collected it in a trap in a cotton field in Texas, and Hussey (1954) caught the species in a baited malt trap in a cotton field in Georgia. Linsdale and Trevis (1951) reported collecting the species in Monterey Co., California with *O. depicturata* Barb. in the nest of *Neotoma fuscipes,* the dusky footed wood rat.

General Biology

O. picturata often inhabits a climax association which is surely a permanent habitat. Yet these insects are entirely macropterous as are all known members of the genus *Ozophora*. Several aspects of the behavior of these insects may explain the importance of macroptery. This fast moving rhyparochromine which is extraordinarily difficult to catch, may frequently "flit," to use Southwood's term (1961) to evade capture. These insects are known to fly at night and come to lights (Blatchley 1926). Torre-Bueno (1912) captured three by lantern on Long Island on September 24, 25, and

I captured three adults August 20, 1958 at Noank, Connecticut and September 10, 15, 1961 at Storrs, Connecticut. Other species of *Ozophora* also have been captured at lights. According to Barber (1954) *O. atropicta* was collected at lights in Puerto Rico by Ramos (1946) and *O. pallescens* was taken at lights in Puerto Rico by Wolcott (1941). Barber (1939) records specimens of *O. quinquemaculata* taken at lights, and Blatchley (1926) collected *O. trinotata* at lights in Florida. Dispersal flights may be an essential part of the life cycle of this insect, but with little change of habitat. Myers (1926) found *Ozophora* in beach drift litter in Massachusetts.

The selection value of dispersion and protection, then, may be factors which outweigh the advantage which can result from brachyptery.

The coloration of this insect, both adults and nymphs, which is a light brown mottled with off-white areas, blends it very closely into its leaf litter habitat. Like many other members of the genus, *O. picturata* has a white ring around the basal one half of the terminal antennal segment. The nymphs also have the last segment entirely pale. Against the dark leaf litter, these white rings are very conspicuous as the resting insect slowly moves its long antennae to and fro. It seems quite apparent that such a white antennal segment serves to distract the attention of a predator such as a bird from the bug's exact location (Cott 1940). No predators or parasites are as yet known from this species.

Like other rhyparochromines *O. picturata* is a seed feeder (Sweet 1960). It feeds very readily on hulled sunflower seeds and the adults will pierce the hard shell to reach the kernel. It also feeds in the laboratory on seeds of *Aster cordifolius* L., *A. lateriflorus* (L.), *Aster* spp., *Betula populifolia* L., *B. lenta* L., on blueberry seeds (*Vaccinium corymbosum* L.), and on grass (*Panicum*) seeds. It does not feed on acorns, of either white or red oaks, even if hulled. It then appears that the sparse distribution of *Ozophora* in oak forests may reflect the rather poor herb layer which develops on the deep litter of the dry oak slopes. I was able to rear this species on sunflower seeds through four generations. With each generation, however, as is commonly the case, the mortality becomes greater. No pure food rearing was attempted with *Aster* seeds. Occasionally, when starving, the insects will scavenge on dead and dying individuals, but very inefficiently.

Ozophora in its normal activities moves slowly and deliberately much like *Myodocha* and *Antillocoris*. It constantly taps the ground with its long antennae as it walks. When excited, as Torre-Bueno noted (1912), it runs very rapidly and with great agility. If caged in overdense numbers the insects become very excited and active and no mating or sustained feeding was observed. This was true both during day and night. Under these conditions mortality became very high and reproduction low. Seed defense behavior was not observed in this insect.

I have not been able to observe the entire sequence of mating in this species. I have observed, however, the initial response of an excited male to the female. The male showed no response to the female until he touched her. He turned, approached the female, and touched his vibrating antennae against hers. Then suddenly the male lunged for the female, and the insects tumbled actively with antennae and legs moving rapidly, and just as suddenly stopped and ignored one another. They mate more than once, and were found mating both by day and by night. Copulation lasted for 1½ to 3½ hours in the laboratory.

Life History

O. picturata overwinters as an adult. Blatchley (1895) collected it in Indiana on December 3 in a log on a sandy forest hillside. Torre-Bueno (1925) collected it by sifting leaves in winter. Dowdy (1955) collected the adults hibernating in oak-hickory litter. *O. picturata* hibernates in the same habitats in which it completes its life cycle. There appears to be very little change in population density from late fall to early spring in oak-hickory habitats which would suggest that winter mortality is low. The species, however, becomes quite scarce in late May and early June, but enough collections were made to show that the species in the field does not lay eggs until relatively late in the summer. The phenology given in Table 39 begins then on July 1 at Storrs, Connecticut. Only adults are found earlier.

At Noank, Connecticut while last instar nymphs are found as early as July 17, 1958, much later in the year on September 7, there were 20% fourth, 30% fifth, and 50% adults. This may represent a partial second generation at Noank since a few third instars were found September 20 at Storrs (see below). This late seasonal cycle may reflect the same southern distribution of this species as is illustrated by *Pachybrachius albocinctus.*

Adults collected after mid-July remain reproductively inactive for two to three months. After this period in the laboratory at room temperature the insects spontaneously come out of this weak reproductive diapause, and no cold treatment is required. The field data indicates that there is apparently only one prolonged generation at Storrs with the females laying eggs over a considerable period, as is shown by the occurrence of third instars as late as August 15. This reproductive pattern is similar to that of

Cryphula trimaculata and *Xestocoris nitens*. Similar to *Cryphula*, the cycle may be hastened by ''forcing'' earlier in the laboratory. But while *Cryphula* remains in obligate diapause, the first generation *O. picturata* in the laboratory becomes sexually mature in about 18 days during June, and can be mated with field overwintered males of the previous generation. This contrasts with adults reared later in the year from nymphs collected in July and August and the second generation and laboratory adults. These late summer adults remain in reproductive diapause for at least several months. The only significant apparent difference between the two sets of laboratory populations is day length. It may be hypothesized than that shorter day lengths bring about a facultative reproductive diapause in *O. picturata* which may be broken by cold exposure or several months time in warm temperatures. This explanation seems to best fit the available data. It is apparent, too, that a relatively high ambient temperature must be attained for reproduction to occur, for the insects may be forced in April, yet nymphs are not found in the field at Storrs until July 1. The slower spring increase in ground temperatures of woodlands compared to field (Geiger 1950) would also delay development. It is highly probable that two generations a year occur in southern parts of its range and perhaps a partial second at Noank, Connecticut. (Froeschner (1944), in fact, found late instar nymphs on June 21 in Missouri).

The stadia in Table 40 represent cultures at room temperature (75–80° F) on a sunflower seed diet.

TABLE 39
Phenology of *Ozophora picturata*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
July 1	100%	——	——	——	——	——
July 9	——	100%	——	——	——	——
July 13	——	40%	60%	——	——	——
July 17	25%	25%	50%	——	——	——
July 25	——	——	50%	50%	——	——
Aug. 6	——	10%	10%	20%	50%	10%
Aug. 15	——	——	10%	25%	40%	25%
Aug. 24	——	——	——	5%	60%	35%
Sept. 1	——	——	——	——	15%	85%
Sept. 10	——	——	——	——	5%	95%
Sept. 15	——	——	——	——	——	100%

TABLE 40
Stadia of *Ozophora picturata*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
12.5 (10–17)	8.5 (6–10)	8.2 (5–10)	5.6 (5–8)	8.3 (6–11)	8.0 (6–11)	51.1 (27–63)

The longevity of the adults, especially the female, depends on time of generation and whether mating had occurred or not. Mated females live 53–65 days in a forced generation while two unmated females lived 130 and 145 days. A normal generation, however, overwinters and lives nearly a year. One spring female lived 60 days in the laboratory. Overwintered adults are found as late as June 21 at Storrs, Conn.

Sexually isolated females lay no or very few eggs. Of thirteen virgin females, only three produced a few eggs (average 5.7 eggs). In contrast, mated females in the laboratory lay 88–135 eggs. As there is one generation a year in Connecticut, the normal precopulatory and preovipositional periods are difficult to determine. However in the forced early summer culture the preovipositional period is 18 days. Some of the winter forced cultures are very irregular in oviposition time and rates. Starvation effectively halts egg production.

O. picturata in the laboratory oviposits in dry material such as fine litter, methyl cellulose, and similar materials and in wet substrates only if no other is available. The cucumber-shaped eggs are covered with fine knobbed hairs which effectively fasten the eggs to fibrous and flaky substrates.

TRIBE STYGNOCORINI

Stygnocoris Douglas and Scott

The eleven species included in the genus *Stygnocoris* are restricted to the western Palearctic, except for two, *S. rusticus* and *pedestris* which have been introduced into North America. These species were probably introduced through ballast dumped by shipping vessels (Lindroth 1947). This is evident because both species show a spread pattern, first appearing in northeastern North America, and later being found at more southern and western localities.

Of the European rhyparochromines, these two species are unusual in having a winter egg diapause (Pfaler 1936, Putshkova 1956). Diapausing eggs seemingly have a greater probability than do adult insects of surviving transport from Europe to North America, because adult rhyparochromines at least in New England show little tolerance to water stress. It may also be significant for the establishment of the species that in contrast to European rhyparochromines, many rhyparochromines in New England overwinter in the egg state.

Eyles (1963b) found *S. fuligineus* to be the most common of the English species of *Stygnocoris* at the Imperial Field Station, Sunninghill, Berkshire and intensively studied the biology of this species. The other species *S. pedestris* and *S. rusticus* were apparently rare in the area and Eyles suggested that their habitats did not overlap with that of *fuligineus.*

Stygnocoris rusticus Fallen

This eastern Palearctic species shows a definite spread pattern. It was first collected in northern New York by Torre-Bueno (Heidemann 1908) and in Quebec, Canada (Horvath 1909). Despite intensive collecting, Parshley (1917b) did not find this species in New England until Moore collected it in 1918 in Maine (Parshley 1920a, 1922). It was collected in Nova Scotia at Truro in 1913 (Barber 1918c, Parshley 1923), and in British Columbia (Downes 1924). Barber (1948b) reported that Esselbaugh collected the species at Duckabush, Washington, and Slater (1952) collected the species in northern Illinois.

The present study indicates that *S. rusticus* is now fairly abundant throughout northern New England. Its distribution southward may be limited by climatic factors for there is a rather sharp change in abundance from common in the cooler highlands of northwestern Connecticut to scarce at the lower elevations at Storrs and it is either absent or very rare along the southern coast of New England. These localities are separated by distances of only 40 to 70 miles and this pattern showed no significant changes for at least six years.

Environment

In New England *S. rusticus* inhabits mesic open field habitats supporting an abundance of tall forbs such as *Saponaria officialis* L., *Solidago canadensis, Solidago* spp., *Daucus carota* L., *Geranium maculatum* L., *Ranunculus acris* L., *Silene* spp., and *Potentilla fructicosa* L. This association is characteristic of a later state of arable succession on mesic loamy soils.

Normally the biotope of *S. rusticus,* especially during nymphal development, is on the ground. Under the tall forbs, the ground is shaded and relatively mesic (4–6) in midsummer. In early spring before the herbs have grown up, this biotope is more exposed to isolation. In late summer, the species is frequently found on the ripening seed heads of certain plants, especially *Tanacetum vulgare* L. At any one time, however, most of the population is on the ground. In such a habitat *S. rusticus* is found in its greatest abundance, attaining 25–30 per square meter.

It is found in much lesser abundances in a variety of open habitats more dominated by grasses, such as in new roadside associations, and is taken infrequently along woodland margins. *S. pedestris* is frequently found with *S. rusticus* and in the laboratory will feed on the same seeds, but *S. pedestris* is least frequent in the tall forb old field habitat and is more abundant along wooded margins and ruderal sites. The pattern indicates that while the biotopes of these species overlap they do not coincide. The abundance of these two species of *Stygnocoris* varies from year to year. In 1957 both species were abundant, but in 1960 both species were rather scarce, and in 1962 both were relatively common again.

In the extensive European literature on this species, there are various brief habitat notes. It was collected from and under heather (*Calluna, Erica*) (Scholtz 1847, Saunders 1892, Stichel 1925), from furze (Halbert 1935), from *Pulicaria dysenterica* (Douglas and Scott 1865, Butler 1923), from *Tanacetum* (Prohaska 1923, Smrezynski 1954, Forster 1955), under *Thymus* and *Potentilla* (Duda 1885, Stichel 1925), from *Achillea millefolium* (Beer et al. 1935, Feige and Kuhlhorn 1938). Barber (1948b) also recorded this species as abundant on *Achillea* at Montreal, Canada. Woodroffe (1955) collected *rusticus* on cindery ground in large numbers with nymphs under *Cerastium vulgatum.*

Nearly all of these plants from which *S. rusticus* has been collected are meadow or open habitat species. Piasecka (1960) considered the species characteristic of meadows in Czechoslovakia. Hedicke (1942) said that the species occurs in Switzerland under vegetation hummocks at edges of fields. Southwood and Leston (1959) characterized its habitat as dry sandy places with plenty of flowers and stated that *S. rusticus* is now rarer in Britain than it was 50 years ago.

In North America, Barber (1922) took it in "moss" in New York. Procter (1938, 1946) collected it near bogs and water on Mt. Desert Island, Maine.

General Biology

S. rusticus differs from *S. pedestris* in being pterygopolymorphic but its habitat selection in New England is for the temporary habitats described instead of long persisting habitats inhabited by most indigenous pterygopolymorphic rhyparochromines. It is however dangerous to speculate on the natural habitat of an introduced species which may be exploiting an open niche in New England. Moreover, the persistence of the species is enhanced by the overall continuation of such forb habitats by agricultural activities. Its occurrence in the long persisting heath habitats as well as tall forb habitats in Europe may indicate a different habitat selection. Again, *S. rusticus* originally may be a savanna species of eastern Europe (Lindroth 1957).

Stehlik (1952) suggests that the macropter is more abundant at high elevations in Czechoslovakia. Weber (1930) quotes Sahlberg (1868b) as believing that the brachypters are less sensitive to cold and penetrate further into the North than the macropters.

S. rusticus is a medium sized rhyparochromine, generalized in shape with short legs. It runs actively but not rapidly, and shows no special tendency to hide in narrow crevices. Its uniform dark grey coloration blends well into the dark substrate of its tall forb habitat. The nymphs however have bright red abdomens like nymphs of *Drymus* and seem very conspicuous in comparison with the adults. When disturbed while feeding on a seed head the insects feign death and drop to the ground. After a few seconds the insects recover and crawl away.

No parasites are as yet known for this species. Thomas (1955) stated that the damsel bugs *Nabis major, N. minor,* and *N. mirmicoides,* the centipede *Lithobius,* and the ant *Formica rufa* prey on *S. rusticus.*

At least some of the forbs mentioned earlier from which *rusticus* has been swept are probably food plants. *S. rusticus* feeds on seeds of bitter buttons (*Tanacetum vulgare* L.), yarrow (*Achillea mille-*

folium), *Solidago* spp., and several undetermined fallen seeds. Woodroffe (1955) found it in large numbers under *Cerastium vulgatum* and surmised that this is a host plant. Its significance is not clear, but Waddell (1951) stated that *rusticus* survived a testing period on a sweet cherry cover crop. It is definite that in the field the nymphs feed on ripe fallen seeds from the previous year and the insect does not climb on the plant to feed on the seeds until early autumn when oviposition takes place. The nymphs are readily reared to adults on sunflower or *Tanacetum* seeds.

S. rusticus sometimes carries and drags small seeds about in the petri dishes to more protected locations, but no seed defense behavior was observed. In the mating behavior the male senses the female well before actual contact, raising his antennae stiffly toward the female. When near enough the male springs suddenly on the female. He taps the females' head with a slow alternate slapping movement. If receptive, the female becomes quiescent, and exposes her ovipositor which is then gripped by the male's parameres. The male slides off the female into the normal end to end copulation position. Several females at this point become cataleptic for several minutes. Later the female recovers and actively runs about, the male running backward in unison.

When the female is not receptive to the male she wags her antennae rapidly back and forth directly over her head while trying to dislodge the tapping male. One male, after leaping on the female, gripped one of her antennae with both forelegs before tapping her head. This occurred twice in succession and again when the excited male leaped on another male. This is the only time the swollen forelegs were ever observed being used during mating behavior by any rhyparochromines. Since this species frequently lacks one of its antennae, this may be the reason.

Copulation lasts for a long time in the laboratory, often for 10–12 hours and is repeated frequently. In the field *rusticus* individuals are very frequently found mating both on the *Tanacetum* seed heads and on the ground and running up and down the stems while *en copulo*. Even when disturbed by collecting, the mating pairs rarely separate.

Life History

S. rusticus has a univoltine seasonal cycle with an obligative egg diapause (Pfaler 1936). Several authors (Scholtz 1847, Stehlik 1952, Massee 1960) state that this species overwinters as an adult but these records were probably late autumn adults as the insects are cold hardy and have been collected as late as December 3 in New England.

The eggs evidently hatch in late May and the observed phenology at Canaan, Connecticut is given in Table 41.

TABLE 41
Phenology of *Stygnocoris rusticus*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
May 28	80%	20%	——	——	——	——
June 5	30%	65%	5%	——	——	——
June 11	——	40%	50%	10%	——	——
June 20	——	5%	45%	42%	7%	1%
June 30	——	——	8%	20%	27%	45%
July 5	——	——	——	10%	30%	60%
July 15	——	——	——	——	5%	95%
July 20	——	——	——	——	——	100%

Mating occurs in the field continually from late July to October. Oviposition, however, does not begin until after mid-September. It is clear then that there is an extended period of nonreproduction. Such adults collected in the summer and kept in the laboratory remain in this state, dying in midwinter. Adults collected after mid-September are normally reproductive. Exposing the insects to short photoperiods (12 hours) does not affect the condition. When two cultures were exposed to cold room temperatures (36° F.) in mid-September oviposition was stimulated. However one culture which was exposed to cold for 18 days in late October did not become reproductive. The adaptation of *S. rusticus* to cool conditions is shown by its moving around and mating under cold room (6° C) conditions.

The egg diapause is strong, and does not terminate under warm laboratory conditions and the eggs die. Three aliquots of eggs kept under moderate (36° F.) conditions for four months also did not hatch. The eggs diapause in the katatreptic embryonic phase as a well-developed embryo.

It appears probable that the southward distribution of *S. rusticus* is limited by the capacity of this insect to survive such a long summer nonreproductive period and then to oviposit vigorously in autumn.

The stadia given in Table 42 are based on field collected nymphs reared to adults on sunflower seeds. Since only three to five records per stadium are available only the range is given. The longevity of adults in the period of reproductive quiescence varies from 36 to 130 days (mean 84).

The precopulatory period was not determined. The oviposition period lasts about two months from mid-September to November. Thomas (1955) stated that only a few batches of 10 eggs are laid. This undoubtedly results from depriving the insects of seeds. The reproductive rate of *rusticus* is actually much higher. The fecundity in the laboratory of 54–128 eggs (mean 98) is also probably low.

TABLE 42
Stadia of *Stygnocoris rusticus*

Instar 2	Instar 3	Instar 4	Instar 5
6	5–7	8	10–13

The eggs are relatively short and smooth with no spines. The eggs are coated with a cement layer that sticks the eggs to the substrate and to each other. Michalk (1935b) described and figured the eggs and referred to them as the horizontal agglutinent type. The eggs are laid singly in loose moist substrates as wet cotton and moist soil, and sometimes a group of eggs stuck together resulted, perhaps forming the ''groups'' mentioned by Putshkova (1956). Such a ''batch'' however is not laid at one time.

Stygnocoris pedestris (Fallen)

The history of *S. pedestris* in North America parallels that of *S. rusticus.* It has a similar western Palearctic distribution, and very probably has been introduced into North America. Gibson (1917) first recorded this species from North America from specimens collected in 1913 at Truro, Nova Scotia. It was a little later recorded from upper New York State and Cape Breton Island (Barber 1918, Parshley 1919). Parshley (1917b) however did not record the species in New England in his check list despite his intensive collecting. Scudder (1961) recorded this species from British Columbia. It is possible that *S. pedestris* has been introduced twice into North America by ballast, once each on the east and west coasts of North America.

Although there are no further records of it in the literature, *S. pedestris* is very abundant throughout northern New England.

Even more so than in *S. rusticus,* there is a pronounced change in abundance toward the southern coast of New England. In the northwestern highlands of Connecticut, *S. pedestris* is extremely abundant, one of the most common lygaeid species. In eastern Connecticut at Storrs, it was very rare and only 2 individuals were collected in six years, and along the southern coast, none.

Environment

In northern New England this species has a rather wide ecological distribution and is the only introduced species that has invaded natural New England environments. The other three presumably introduced species *S. rusticus, Megalonotus* and *Sphragisticus* inhabit disturbed areas only.

The habitat of *S. pedestris* ranges from woodland margins to disturbed roadside areas. In open fields with a greater dominance of grasses and with fewer tall forbs it frequently occurs with *S. rusticus. S. pedestris* inhabits relatively mesic litter (moisture 3 to 6) on the edge of forests of *Tsuga canadensis, Pinus strobus, Juniperus virginiana, Fagus grandentata, Betula* spp., *Acer* spp., and in general along northern hardwood forest margins as well as in open fields and roadsides. It also occurs along the margin of *Picea rubens* in both highland forests in New Hampshire, and coastal *Picea* forests in Maine. It is not, however, a forest species and does not penetrate far into forests and is usually found on the field side of a forest-field ecotone. It occurs in low abundance of 3–5 per square meter in a few *Vaccinium* balds on Mt. Greylock, Massachusetts and at Laconia, New Hampshire. It is never found in the xeric sparse grass habitat favored by many New England rhyparochromines, nor in oak-hickory forests. While its normal biotope is on the ground and the nymphs are never found off the ground, the adults like those of *S. rusticus* sometimes climb up the plants in autumn to feed on the ripe seeds. It was swept from pearly everylasting, *Anaphalis margaritacea* L., *Spirea tormentosum* L. *Tanacetum vulgare* L.

Beneath *Anaphalis* and in the margin of juniper litter it reaches an abundance of 50 to 80 per square meter. It is found in lower abundances of 10 to 20 per square meter in the other habitats. Over the five year study, its numbers did not fluctuate as much as did those of *S. rusticus* but in the same years that *S. rusticus* was rare, *S. pedestris* was also less abundant.

The European literature indicates a similar habitat choice. *S. pedestris* is very abundant in England (Butler 1923, Southwood and Leston 1959), although Eyles (1963b) found it scarce at the Imperial Field Station at Sunninghill, Berkshire, England. It has been frequently found in leaves and moss litter (Lethierry 1869, Saunders 1892, Marchal 1898, Nicholson 1935, Leston and Southwood 1961), in *Calluna-Erica* heath (Scholtz 1847, Sahlberg 1868, 1920, Becker 1886, Stichel 1925, Stys 1960). Piasecka (1960) noted it in meadows near woodlands. Lambertie (1906) found it on *Salix,* but this is probably accidental. Krogerus (1960) found it numerous in southwest Finland in moss, in *Ledum-Calluna* heath and as extending north to 62°5″. Southwood and Leston (1959) recorded *S. pedestris* in England as being found on dry sand chalk or light soils with good vegetation cover.

Lindberg (1958) recorded *S. pedestris* on Newfoundland under stones on grass verges, on shingle overgrown with grass and on the seashore.

As mentioned under *S. rusticus* the biotope of *S. pedestris* overlaps on that of *S. rusticus.* However, it is not clear whether either of these species is displacing any native rhyparochromines unless it be species like *Myodocha, Heraeus, Zeridoneus,* and *Pachybrachius basalis.* These are all myodochines of relatively mesic habitats, but all are biologically quite different from the species of *Stygnocoris* in their different seasonal cycles, distributions, food plants, and behavior.

General Biology

S. pedestris, unlike *S. rusticus,* is entirely macropterous (Southwood and Leston 1959). It is probable that this wing condition correlates with the wide ecological distribution of *S. pedestris* and the occurrence of the species in temporary roadside habitats. There appear to be no records that can definitely be attributed to dispersal.

S. pedestris is one of the smaller rhyparochromines, being only about 2.7 mm. in length, considerably smaller than *S. rusticus.* Its procryptic coloration is black and dark reddish brown; the legs are inconspicuously pale. It is generalized in shape with short legs and is not a rapid runner, but conceals itself in the litter debris of stems, leaves, and grass of its biotope. The nymphs are conspicuous with the abdomen banded, pale and red and are quite different in coloration from the nymphs of *rusticus.*

Frequently when disturbed, it feigns death. On *Tanacetum* even when mating *pedestris* will feign death and fall to the ground. After about 10–15 seconds it recovers and conceals itself. During this death feigning period it does not respond to a touch stimulus.

Eyles (1963a) found an overwintering individual of *S. pedestris* parasitized by *Alophora pusilla* Mieg, a parasite also known from the hemipterous *Chilacis* and *Cydnus.* *S. fuligineus,* that Eyles (1963a) investigated intensively, is attacked by the fungi *Poecilomyces* and *Entomophthora.* No predators are known.

S. pedestris has been found in nests of the ants *Myrmica scabrinodis* and *M. miruginodis* (Donisthorpe 1927) and of *Formica rufa* (Reclaire 1932). These records are probably accidental, resulting from the ground layer habitat and abundance of the species.

S. pedestris feeds on the seeds of *Tanacetum vulgare* L., *Anaphalis margaritacea* (L.,) *Spirea tormentosum* L. and *S. latifolia* (Ait.), *Aster novaeangliae* L., *Solidago* spp., *Betula populifolia,* and a number of other unidentified fallen seeds. When starving the insects will scavenge on dead and dying insects but cannot subsist on this diet and soon die. No seed defense behavior was observed in this species.

In the mating behavior, like *S. rusticus,* the male senses the female usually before actual contact. When a female is near, the male springs suddenly on the back of the female, turns into a position parallel to the female and begins to tap her head with alternate rapid movements of his antennae. The tapping is more rapid and has a smaller arc of movement than in *S. rusticus.* Under the tapping the female quiets and releases her ovipositor and copulation begins. In three cases after the male swings off the female to assume the end to end position, there is a cataleptic pause affecting both sexes which lasts about 30 seconds. After moving to the end to end position there is some pulling and pulsating between the male and female until abruptly the pair move together with the male running rapidly backwards.

Copulation lasts from 3 to 11 hours and is repeated frequently over a period of three months from July to October. Many copulating pairs are found in the field at this time which correlates with the long copulation period in the laboratory.

Life History

Like *S. rusticus, S. pedestris* has an univoltine life cycle with an obligative egg disapause (Pfaler 1936). There is also an extended adult reproductive diapause in late summer.

Eclosion occurs in May, and the earliest nymphs are found in late May. The observed phenology at Canaan, Connecticut is as given in Table 43. In northern New England a few fifth instars were found as late as August 20.

The long preoviposition period of the Canaan population lasts until late September although copulation occurs from at least late July and through the autumn oviposition period. Adults which are collected after September 26 actively oviposit. Females brought into the laboratory do not oviposit as do the field adults but remain in a nonreproductive condition until death in late autumn and early winter. A few of these fertilized females laid a few (2–17) eggs, but such ovipositing soon ceased.

The long prereproductive period is not affected by photoperiodic conditions. Adults reared in the laboratory under short, long, normal (decreasing), and even increasing photoperiods, remained in diapause.

TABLE 43

Phenology of *Stygnocoris pedestris*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
May 28	83%	17%	——	——	——	——
June 7	55%	35%	10%	——	——	——
June 15	21%	40%	33%	6%	——	——
June 22	——	5%	25%	43%	17%	10%
July 4	——	——	——	3%	12%	85%
July 15	——	——	——	——	2%	98%
July 20	——	——	——	——	——	100%

Exposure of three cultures of adults to repeated cold (6° C.) exposures of 7–24 hours each in August did not stimulate oviposition. However, exposing adults of four cultures collected in summer to low temperatures in September did stimulate oviposition. These colonies normally would not have become reproductive. However, it is noteworthy that the oviposition rate fell off rapidly in the laboratory except in one colony that was reared in a cool office. The rearing room temperature may have been too high for optimal oviposition. It is possible that both cold and short photoperiods are required.

There is also a definite acclimation because adults exposed to 6° C. in August are immobilized but adults in late November move actively about at temperatures barely above freezing (2°–3° C.). The records of *S. pedestris* overwintering as an adult (Scholz 1847, Butler 1923, Murray 1936, Michalk 1938b, Massee 1960) undoubtedly are late autumn collections reflecting the cold resistance of this species, or perhaps may represent a confusion with *S. fuligineus* which does overwinter as an adult (Pfaler 1936).

Although *S. fuligineus* overwinters as an adult, Eyles (1963b) states that it does not have a diapause state. Yet his data indicates that *S. fuligineus* is not reproductive (immature) for periods of two to three months in summer which suggests that a reproductive diapause is involved in this species.

The eggs diapause either in early anatrepsis or late katatrepsis. Some eggs kept in warmth will develop to late katatrepsis, but no further. Normal diapause eggs will not hatch kept at room temperatures. Both egg stages overwinter at 6° C. and complete diapause development at this temperature.

Non-diapause eggs were obtained from two females collected on November 27 and which had been exposed to low field temperatures. The eggs which were placed in the cold room remained undeveloped, but the eggs left in warmth developed and hatched in 16 to 23 days (mean 19 days.) This indicates that as in *L. diffusus* the diapause-producing mechanism was broken in the female before oviposition. However, the egg development period of these eggs was considerably longer than in diapause eggs which have completed diapause development.

The stadia of immature forms are given in Table 44. The shorter stadia figures apply to the more rapid development of the nymphs collected in the field and reared in the laboratory. The longer stadia apply to nymphs reared in the laboratory from eggs. The egg incubation period indicates the time from the day the eggs were moved out of the cold room until they hatched. This is probably not comparable to a normal egg development period.

TABLE 44
Stadia of *Stygnocoris pedestris*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
10.3 (8–12)	5.7 (3–9)	4.8 (3–9)	6.0 (3–10)	5.9 (4–10)	10.0 (4–15)	42 (28–63)

The longevity of nonreproductive adults in the laboratory ranged from 52–144 days (mean 77). Only a single exceptional female lived 144 days. The mean represents the usual longevity.

In the field at Canaan, Connecticut, adults were found as late as November 28. The laboratory longevities are consistently shorter than in the field probably due to warmer temperatures. Cooler summer temperatures also probably prolong the adult longevity in northern New England.

Since the nonreproductive period in the field is approximately 60–70 days in Canaan, Connecticut (in southern New England), and only about 30 days in northern New England, the sudden drop off in abundance toward the Connecticut coast becomes more understandable. The southward distribution of *S. pedestris* is most likely limited by its capacity to endure a long summer nonreproductive period. Adults forced from eggs hatched in early April failed to survive the summer.

The precopulatory period was not determined but is no longer than two weeks. Copulation occurs freely from mid-July on. The preoviposition period is largely determined by the environment. Due to the interference of reproductive diapause, the fecundity figures of ovipositing adults is sketchy, ranging from 20 to 81 (mean 48) which is probably much too low, judging from oviposition rates for a few days (5–7) and the length of the oviposition period in the field (late September to mid-November).

The eggs are laid singly, preferably into moist substrates as the cotton stopper of the water vial or damp loamy soil. The eggs like *S. rusticus* are relatively short and smooth, and covered with a cement layer that sticks the eggs to soil particles and litter and sticks the eggs together.

TRIBE DRYMINI

DRYMUS Fieber

This well-named genus is characteristic of forest habitats both in North America and in Europe (Leston and Southwood 1959.) Two Nearctic species are known, *D. unus* and *D. crassus.* Recently the genus has been divided into two subgenera, the typical subgenus, and *Sylvadrymus* (Le Quesne 1956). Despite having, at most, only a sparse pubescence instead of long erect hairs on the tibia, the remarkable expanded parandria of the genital capsules place both *D. unus* and *D. crassus* in the typical subgenus. Moreover, and unlike the European *Drymus sensu stricto,* the puncturation of the anterior lobe of the pronotum is only slightly finer than the posterior lobe's and hardly so in *D. crassus.*

As remarked under the distribution discussion, although *Drymus* is found throughout the Palearctic with 17 species, the two Nearctic species are restricted to eastern North America. Since a number of the species are not yet placed, the distribution of the subgenera cannot be discussed except to say that both occur in Europe, and only *Drymus sensu stricto* in the Nearctic.

Although all the European species are recorded as over-wintering as adults (Pfaler 1936, Southward and Leston 1959), both of the Nearctic species, at least in New England, overwinter as eggs. However Putshkova (1956) states that *D. brunneus* lays winter eggs in Russia, although in the key she notes "eggs in spring." Under the discussion of *D. unus* the seasonal cycle of *D. brunneus* is discussed further in light of the recent observations of Eyles (1963).

Drymus contains both macropterous and pterygopolymorphic species. Woodroffe (1963) found that the English species of *Drymus* and *Sylvadrymus* form two parallel series based on wing development. In *Sylvadrymus, sylvaticus F.* is macropterous, *ryei* (D.S.) is submacropterous and *brunneus* is brachypterous and all three species may be found together. Similarly in *Drymus* (*sensu stricto*), *pilipes* (Fieb.) is macropterous, *latus* largely submacropterous and *pilicornis* brachypterous and these species are also found together.

Drymus unus (Say)

D. unus is known from Quebec and Iowa south to North Carolina and Texas, which approximates the extent of the eastern deciduous forest biome. Uhler (1895) also mentions this species from Colorado and lower California, but these records must be further confirmed, especially as there are several western species of *Eremocoris* which bear a slight resemblance to *Drymus*, and there are no subsequent records.

Like most forest floor Rhyparochrominae there are few records of this species in contrast to its actual abundance in New England. Indeed, this appears to be the first published record of *D. unus* from Connecticut. Slater (1952) noted it as scarce in Iowa and Illinois.

Environment

D. unus is a common and characteristic inhabitant of the forest litter of light mesic woodlands. While it does occur in climax forests, it is much more abundant in light subclimax forests. It is abundant where black birch and red maple are associated with oak and hickory, but rare in the thick litter of dry oak slopes or in climax sugar maple-beech forest. In the heavy deciduous forest *D. unus* is replaced by *D. crassus*. *D. unus* is also apparently more abundant in edge habitats. Where abundant, it may even be found on the field side of forest edges, providing the substrate is mesic and shaded by rank herbs. Frequently it is found beneath isolated trees in open fields.

In such favorable habitats its abundance may attain 40 per square meter. It occurs in intermediate abundance of 5–10 in both birch and hemlock forests associated with *Scolopostethus diffidens*, and *Eremocoris ferus*, and also in *Vaccinium* litter with *Scolopostethus atlanticus*. A few specimens were collected at one exceptional habitat, a hummock in an open brackish salt marsh.

In the biotopes of *D. unus* the herb layer is thin, averaging a foot in height, and usually includes several species of *Aster*, *Mitella diphylla* L., *Smilacina racemosa* Morang., *Anemone quinquefolia* L., *Solidago bicolor*, *Dryopteris spinulosum*, other herbs and tree seedlings. *D. unus* is abundant in biotopes of fine friable mull litter as beneath birch and maple, and rare in dry loose oak litter.

The soil is nearly always a dark humus and mesic (moisture, 5–6). The chief limiting factors of this species are its mesic requirements. It is never found in habitats with ground temperatures over 26° C. In one area where it invaded the rank edge of a small field, the ground biotope was 24° C. while the air temperature above the herbs was 36° C. When exposed for a few minutes to this higher air temperature, *Drymus* quickly succumbed. *D. unus* is also infrequent in very wet habitats such as swamps and extremely mesophytic forests.

D. unus is closely restricted to its litter biotope and only rarely is swept from plants, these woodland Compositae in late autumn.

It frequently remains in a habitat for several years, and in one black birch oak habitat it was continuously present for at least nine years. In more marginal sites, such as along ecotones, its occurrence is only temporary.

It was collected by sifting under alders (Smith 1910), from grass piles (Torre-Bueno 1929a), and under stones and boards on Mt. Desert Island, Maine (Procter 1946). Dowdy (1955) collected *D. unus* in an oak hickory woodland, and Blatchley (1895, 1926) found it in shelter under a rail near the border of an upland wood.

General Biology

It would appear that the entirely macropterous *D. unus* inhabits forest areas which are habitats as permanent as any of the habitats of the xeric-adapted brachypterous lygaeids. However, it is especially abundant in edge and glade habitats and it readily colonizes isolated patches of forest. Full macroptery and ready dispersal is probably a definite advantage in a mosaic of subclimax woodlands or, in a more homogeneous forest condition, it would allow the ready invasion of new habitats such as river bottoms and glade openings in forests.

The adults of *Drymus* are a deep dark red-brown and dull black which effectively conceals the insect on the forest floor. This pattern is especially effective since *D. unus* readily feigns death. In death feigning, the antennae and the legs are rigidly held close to the body. When it is disturbed on a low herb, it feigns death and falls directly to the ground. Shortly afterwards it quickly seeks refuge under bits of litter, but does not run rapidly as do the long-legged lygaeids. The nymphs, in contrast, are a very bright red against the forest floor which would make them conspicuous to bird predators such as towhees or catbirds probing the leaf litter floor.

D. unus does not feed on acorns, ash, willow, or maple seeds, but rather strongly prefers the seeds of small composites, especially the woodland asters. It could sometimes be found feeding on the dried seed heads of this plant in autumn as late as November 18 with the air temperature at 6° C. It also feeds on the seeds of *Solidago* spp. and *Spirea latifolia* and is readily reared on *Betula* seeds as well as sunflower and Aster seeds. The nymphs feed on the fallen ripe *Aster*, etc., seeds of the previous year while the ovipositing adults feed on the newly fallen seeds. Thus the seasonal cycle of this insect correlates with the fall seed production of the host composites.

When hungry the insects readily carry or drag the seeds about. When disturbed during feeding, the insect endeavors to protect its position by maneuvering itself between the aggressor and the seed and by wagging its antennae. No further seed defense behavior was observed, except that the defender, with its hind legs, may push away the aggressor.

In courtship, the male recognizes the female apparently only on contact. In every instance observed, the male advances on a female which is feeding. This may simply be an occasion when the female remains still. The male's excitement is shown by its rapid agitation in moving around and in climbing upon the female. The female frequently dislodges the male by jerking her body sharply from side to side, or earlier she may keep him away with her hind legs. If the female is passive, the male vibrates his antennae on the female's head. The male's antennae which are held parallel and close together with the apical joint bent slightly down, are vibrated very rapidly with a barely discernible plane of movement.

Life History

D. unus has a univoltine seasonal cycle and diapauses over the winter as an egg. The phenology at Storrs, Connecticut is given in Table 45. This is a pooled phenology from summer of 1957 to spring of 1963.

The first instars were found as early as May 19, but could also be found as late as June 15 at which time third, and fourth instars were present. This probably indicates that eclosion is staggered over a long period.

TABLE 45
Phenology of *Drymus unus*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
May 19	85%	15%	——	——	——	——
May 30	25%	63%	12%	——	——	——
June 10	12%	40%	42%	6%	——	——
June 19	——	4%	36%	53%	7%	——
June 27	——	——	3%	52%	45%	——
July 5	——	——	——	16%	78%	6%
July 18	——	——	——	1%	38%	61%
July 27	——	——	——	——	2%	98%
Aug. 4	——	——	——	——	——	100%

Copulation occurs from August to October. However, oviposition does not occur until after the advent of cold weather. In the laboratory under both long and short day photoperiods and in warmth (ca. 25° C.) there is either no or a greatly delayed and diminished oviposition in most adults captured before mid-September. In most adults collected after this time oviposition in the laboratory is rapid and plentiful. This is probably in response to cold nights. Repeatedly exposing several summer reared colonies to cold room (5° C.) conditions stimulated increased oviposition. The cold room was continuously illuminated to simulate long day conditions. However, photoperiod cannot be ruled out, short days may further promote the basically cold stimulated oviposition.

D. unus is remarkably adapted to cool conditions and even oviposits under cold room (5° C.) conditions. It was observed on November 6, at dusk, feeding and mating on seed heads at an air temperature of 6° C. Ovipositing females have been collected in the field in late autumn as late as December 24. This late oviposition period and cold hardiness explains the over-wintering records in the literature, as these are all late November or December records (Blatchley 1895, 1926, Torre-Bueno 1925, Barber 1928d, Dowdy 1955).

At this point it is important to compare the seasonal cycle of *D. unus* with the European *D. brunneus*. Eyles (1963b) suggests that in England, *D. brunneus* overwinters in three stages, as adults, eggs or nymphs. However I see no clear evidence that the nymphs overwinter. Even so if *D. brunneus* overwinters in two stages as either immature females or eggs then there must be two reproductively isolated populations as the species is obligatorily univoltine. This would imply that two sibling species are involved with quite different seasonal cycles and the corresponding physiological adaptations.

Perhaps a more probable interpretation of the data is that *D. brunneus* like *D. unus* is cold hardy, oviposits in autumn, and persists into winter. Perhaps a few survive to also oviposit in the early spring. This would be similar to the pattern in *D. unus*. Moreover the nonreproducing adults of *D. brunneus* in Eyles's insectary parallel the reaction of *D. unus* which did not oviposit under warm laboratory conditions outlined earlier.

The oviposition period is long, and in the laboratory was continued in some normal, cold exposed and fall collected specimens until early January. Since *Drymus unus* ranges as far south as North Carolina and Texas, it appears entirely possible that in the more southern areas the normal oviposition period may fall during the prevailing mild winter period. The laboratory evidence indicates that this is within the insect's physiological capacity. Summer reared *Drymus* kept in warmth frequently begin laying a few eggs after October 15. This continues sporadically through the autumn and winter and in one case continued until as late as March 10. If this seasonal cycle is present further south, it follows that the southern limit of the distribution of *D. unus* may be determined by the capacity of the insect to survive a very long summer reproductive diapause. *Drymus* nymphs which are forced to early maturity in the laboratory by early June rarely survive past late September, which would tend to support this hypothesis.

The egg diapause occurs in early anatrepsis in most eggs, but some attain katatrepsis and remain in that state. As in *Ligyrocoris diffusus,* when the females are exposed to considerable cold, i.e. in adults collected during late November, from 10% (November 5) to 40% (November 26) of the eggs do not enter diapause, but hatch directly in the laboratory. This indicates that cold exposure affects the diapause forming mechanism in ovarian egg development. Such late eggs, then, must normally "hibernate" over the winter.

The entire nymphal life cycle takes about a month and a half in the field, and is shortened to a little more than a month in the laboratory. Part of the explanation for the apparently variable ecolsion and development rate in the field probably resides in the changing microclimate with the ground layer exposed and sunny in early spring, but shaded when the canopy develops in late May.

TABLE 46
Stadia of *Drymus unus*

Instar 1	Instar 2	Instar 3	Instar 4	Instar 5
7.6 (5–9)	6.0 (5–9)	6.8 (5–9)	7.8 (6–9)	9.4 (7–13)

The stadia given in Table 46 are derived from rearing field collected nymphs. Egg development period is not available. The first stadium is based on laboratory hatched first instars. These could not be reared past the third instar. As mentioned earlier, the adults are long-lived and the average longevity in the laboratory of adults reared in the laboratory ranges from 62 to 238 days (mean 116 days). There is no marked difference between mated and unmated females or males.

Egg production in the laboratory is highly variable. In normal cold exposed field collected females 120–250 eggs (mean 131) are recorded. About half of the females which were not exposed to cold, later laid a few fertile eggs, (6–38 eggs (mean 24)). The eggs are laid singly in the laboratory at a rate of 2–7 eggs (mean 3.2) in normal females. Three sexually isolated virgin females which were reared in mid-summer when given a cold exposure laid no eggs in contrast to the control fertilized females which laid 36–85 eggs.

The eggs are laid singly after some probing for an oviposition site. The eggs are laid on wet or dry substrates and are deeply imbedded. The eggs are relatively short and fat and covered with fine nap like those of *D. crassus.* The eggs stick to each other and to the substrate by a cement secretion. Eggs which will diapause become quite dark in comparison to the few non-diapause eggs.

Drymus crassus Van Duzee

This is a much larger species than *D. unus.* It is recorded from a slightly more restricted range which corresponds closely to the deciduous forest biome. It is known from North Carolina to Texas north to South Dakota, Iowa, and New York (Slater, Catalogue). I have collected it in Connecticut and also in Maine in the coastal Acadian spruce zone.

Environment

Drymus crassus has the most mesic habitat preference of the various rhyparochromines. It is only found in mature leaf mold sites beneath mesophytic forests, especially on north exposures. It is not found in oak-hickory forests or younger subclimax associations, but is found in maple-beech, hemlock-white birch-maple, and red spruce (coastal Acadian) litter. In New England it accordingly does not exhibit a southern type distribution, but rather reflects the distribution of mesic habitats. It has been infrequently collected, probably because of this habitat choice, and partly because of its low density (2–6 per square meter) in such dense mull litter. Its extreme mesic requirements demand even greater care in collecting than *D. unus* to avoid exposing the insects to sunlight. The litter, while very mesic in type, is at 8–9 moisture level, not water-soaked or hygric. Most noteworthy is that *D. crassus* is rarely found with *D. unus* despite the presence of large populations of *D. unus* nearby. Blatchley (1926) reported finding it on a densely wooded slope in Indiana, a habitat suggesting those reported here from New England.

General Biology

Drymus crassus at first appears macropterous but it actually displays an unusual type of wing polymorphism. In the flightless form the corium is elongated and the membrane although it attains the apex of the abdomen, is narrowed, and only partly overlaps the other membrane. The hind wing is considerably reduced in length and barely reaches past the end of the commissure. As the corium appears thick and heavily sclerotized, the wing takes on a distinctly coleopteroid appearance. This condition forms a logical intermediate to the remarkable tropical coleopteroid forms. Only one macropter was seen among 52 specimens.

This largely flightless condition correlates well with the permanent climax forest habitat of *D. crassus.* The presence of the macropter must have enabled the spread of this species into mesic habitats in areas like Canaan Mountain, Connecticut which was completely deforested at one time.

As in *D. unus,* the dark coloration of the adults form a procryptic coloration, but the nymphs are bright red and conspicuous on the leaf mold. Is this a warning coloration for bird predators? When disturbed in the field the adults, like *D. unus,* frequently feign death. Care must therefore be taken in searching for these insects as the adults blend in very well with the background.

These insects feed on *Aster* spp. seeds, birch (*Betula papyrifera* L.), and very readily on sunflower seeds.

Mating occurs in the usual reversed position in late summer and autumn, but courtship was not observed. However there apparently is complete reproductive isolation between the *Drymus* species as three *Drymus unus* females enclosed with 5 *Drymus crassus* males were not inseminated.

Life History

The seasonal cycle is similar to *D. unus,* with one generation a year and an obligative overwintering diapause in the egg state. The phenology is rather sketchy: on July 14, at Storrs, one fourth, and three fifth instars were collected; July 26, seven fifth instars, three adults; August 4, one fifth instar and seven adults; and from August 15 on, all were adults. The stadia are not known.

The diapause situation appears to be very similar to *D. unus.* The population collected in late July mated readily but produces no eggs whatever throughout autumn in the laboratory under short day periods. Adults collected later in August laid a few eggs, but from September 14 on, diapause eggs are laid readily. The eggs diapause in early anatrepsis. None could be released from diapause by moderate cold (4° C.) exposures of five months. Fertile eggs are easily told from unfertilized eggs because the egg shell becomes dark and horn colored in fertile eggs.

There are, then, two sorts of diapause states operating as in

D. unus, a late summer oviposition inhibition and an overwintering egg diapause. It is probable that the very late autumn "overwintering" insects reported by Torre-Bueno (1925) and Barber (1928d) represent cold resistant insects as in *D. unus.* It may oviposit throughout the winter further south.

The eggs are laid at a relatively low rate of 2–4 per day, and total egg productivity ranges from 49–93, which appears to be a little low, but may correlate with the permanent habitat, as this is a relatively large rhyparochromine.

The large thick eggs are preferably laid on moist substrates, and a loose substrate is preferred. Like the eggs of *D. unus,* the eggs of *D. crassus* are beset with minute spinules.

Scolopostethus Fieber

This Holarctic genus includes 20 species of which 16 are known from the Palearctic, 4 from the Nearctic, (*S. thomsoni* is found throughout the Holarctic region). Horvath (1893) thought that *S. thomsoni* may have been introduced into North America. It is more probable that this species occurs naturally in North America.

In the eastern United States 3 species occur, one, *S. atlanticus,* is restricted to the eastern United States. In the western United States are two other species, one of which, *S. tropicus* extends south to Guatemala from where it was described by Distant (1882).

The species of eastern North America are adequately distinguished by Barber's (1918e, 1923) keys to the species, but care must be used for some populations of *S. thomsoni* resemble *S. atlanticus* in the coloration of the hind femora and the reduction and absence of the proximal spines on the fore femora.

Eyles (*in litt.*) has crossed several of the English species and obtained progeny which were sterile. I have been unable to cross *S. diffidens* with *S. atlanticus* or with *S. thomsoni* (*Carex* population).

Eyles (1963b) has studied the life histories of four species of *Scolopostethus, S. thomsoni* Reut., *S. affinis* (Schill.), *S. decoratus* (Hahn) and *S. grandis* (Horv.) and concluded that the species are univoltine and have no diapause, overwintering in a quiescent state. However, it must be noted that the new adults remained immature for a rather long period, especially *S. decoratus,* suggesting that a reproductive diapause may be involved.

Scolopostethus diffidens Horvath

S. diffidens has a boreal distribution across North America and extends south to British Columbia and northern California. It is much more abundant in northern New England than southern New England and apparently does not occur along the coast between Cape Cod, Massachusetts and New Haven, Connecticut.

Environment

S. diffidens is a sylvan species typical of northern birch-coniferous forests. It is restricted to and abundant in the litter beneath grey birch (*Betula populifolia* Marsh), white birch (*Betula papyrifera* Marsh), hemlock (*Tsuga canadensis* L.) and red spruce (*Picea rubens* L.). *S. diffidens* is found in either pure or mixed stands of these trees. Its presence in southern New England largely parallels the presence of this forest assemblage. The forest herb layer is frequently absent and is of no apparent significance in the ecology of this insect, except occasionally, as an edaphic factor. The spruce and hemlock forests form climax assemblages but the birches, especially gray birch, are subclimax. However, these are long persisting subclimaxes in terms of this insect's life cycle.

These trees often form extensive stands, and the edaphic effects of the varying forest floor conditions are readily observed. Where the litter is thin and tightly packed, as commonly occurs under pure coniferous stands, *S. diffidens* is scarce. In rougher spots where small twigs and herbs create a looser litter, the species is more abundant. The same effect occurs when the litter is of mixed conifer-birch leaves, or completely of birch.

Slightly drier spots also favors *diffidens* and very wet litter is unfavorable. The very dry litter of some of the mountainside *Picea* forests is also a rather unfavorable habitat for *S. diffidens.*

In general, thick loose dry-mesic (5–7) litter with many fallen seeds from the trees forms the most favorable biotope for this species. Its abundance is frequently extremely high in such biotopes, attaining at least 130 per square meter. *S. diffidens* frequently occurs in clusters which indicates a definite sociability effect which is apparently unrelated to edaphic factors.

Temperature conditions are moderate in the litter because of the shade, rarely exceeding 26° C. at midday, even in sun flecks. Although gray birch is abundant in southern New England it is only on north or east exposed slopes under old stands that *S. diffidens* occurs. On such slopes the snow cover lasts until rather late retarding the warming of the ground biotope. There are no observable seasonal population movements.

Populations of *S. diffidens* were found year after year in the same habitat and at three sites for six years in succession. As discussed under Competition, *diffidens* is one of an assemblage of seed feeding rhyparochromines in this habitat.

Despite the abundance of *S. diffidens* in its habitat, there are very few records of it in the literature. Both Blatchley (1926) and Barber mention it as being collected under dead leaves.

General Biology

In correlation with its climax or long persisting habitat, *S. diffidens* is pterygopolymorphic with only about 10% of the populations macropterous. Although there are no definite dispersal records, during the spring there is a definite decline in the abundance of the macropterous form. Brachypter × brachypter matings yield a few macropterous as well as brachypterous progeny.

These small rhyparochromines are brightly marked with white, tan and black with conspicuous white spots in the lateral corners of the hemelytral membranes. The nymphs of the later instars also have their reddish abdomens laterally marked with white areas. Although these color patterns do not appear very ant-like, when a cluster of these insects are disturbed the sudden boiling up of the insects and their rapid jerky running produces a very definite ant-like effect. This interpretation of the protective coloration and behavior may also explain the sociability effect mentioned earlier. Such an ant mimicry effect has also been noted by European workers in *S. affinis* Schill. (Wassman 1889, 1894, Gulde 1937), *S. pictus* (Marchal 1898, Butler 1923) and *S. pseudograndis* (Singer 1952).

Despite its existence in large populations, no insect parasites have been reared from *S. diffidens.* Several fifth instar nymphs had red mites (near *Thrombidium*) attached to them in the field. No predators are as yet known.

S. diffidens is readily reared on the seeds of the trees mentioned earlier, white and gray birch, hemlock and red spruce. It also feeds readily on sunflower seeds but suffers a very high mortality.

The seed defense behavior of this species is easily elicited by presenting seeds after allowing a colony to become hungry. The insects clash over seeds by pushing and flailing at each other with their antennae and fore tibiae. Neither the fore femora nor the beak are used in this behavior. After repelling the aggressors, the insect pierces the seed, and drags it with its beak to a more protected site for feeding.

The mating behavior was not observed in detail, but a male after touching the female climbs or leaps quickly on her and begins vibrating his antennae on her head. Mating lasts for at least 2 hours and the adults move about readily in the end to end position, with the male running backwards.

Life History

Scolopostethus diffidens has an univoltine seasonal cycle with an obligative adult diapause. Although the females are fertilized in early spring, some as early as March 26, the nymphs do not appear until June. The phenology of *S. diffidens* at Storrs is given in Table 47. These insects are quite cold hardy and are found actively moving about in the field directly after the snow melts. Such adults are not yet sexually active and the females are unfertilized.

TABLE 47

Phenology of *Scolopostethus diffidens*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
June 1	——	——	——	——	——	100%
June 11	20%	——	——	——	——	80%
June 19	45%	15%	5%	——	——	35%
June 27	20%	30%	25%	20%	——	5%
July 9	3%	7%	25%	35%	25%	5%
July 17	——	5%	10%	25%	35%	25%
July 25	——	——	——	5%	15%	80%
Aug. 7	——	——	——	——	7%	93%
Aug. 21	——	——	——	——	——	100%

Climatic effect on the phenology is clearly apparent. On August 10, 1960, on the cool northside of Canaan Mountain in the northwestern Connecticut highlands, the instar ratios were IV : 5% V : 20%, and adult : 75%. In the White Mountains of New Hampshire, the instar ratios on August 12, 1961 were III : 5%, IV : 20%, V : 50%, and adult : 25%.

The late occurrence of nymphs is evidently a temperature effect affecting egg development because females dissected in early April have fully developed eggs in their ovaries. Females collected in late April and early May lay eggs in the field in the specimen bottles shortly after being captured. Photoperiod control is not involved. Colonies collected in early March and kept in 12 and 15 hour photoperiods became reproductive simultaneously.

The adult reproductive diapause condition is relatively strong and only a few individuals live long enough to spontaneously break or complete diapause development under warm laboratory conditions. Again photoperiod conditions have no apparent effect on the diapause state. The longevity of the diapausing adults under warm laboratory conditions varied from 91–220 days (mean 175 days). Diapause is not broken until January or February after about 190 days of adult diapause and such few adults lived only 15 to 25 days. Exposing the insects to brief one month cold exposures of 6° C. did not terminate diapause.

TABLE 48

Stadia of *Scolopostethus diffidens*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
9.7 (9–11)	4.3 (3–5)	4.6 (3–7)	4.4 (3–6)	6.0 (5–7)	7.6 (6–10)	37.0 (34–46)

The stadia in Table 48 are derived from spring cultures reared on mixed sunflower—gray birch seed mixture. Development is very rapid in the laboratory, definitely faster than in the field, probably because of cooler field conditions. Such forced spring cultures become adult by late May and early June. The diapausing adults of these cultures begin dying in the laboratory in late August. It appears possible that the southern limits of this species is determined by its inability to survive the long summer in the diapause state.

The spring precopulatory period is very short but in cultures collected in March after the snow melts the pre-oviposition period in the laboratory is about 7 days. The normal fecundity in the laboratory ranges from 94–184 eggs (mean 132 eggs). The eggs are laid at a rate of 4–5 a day. Very few eggs (15, 18, and 27) were laid by three females released from diapause in midwinter. Three sexually isolated females laid 24, 43, and 49 eggs.

The smooth, relatively stubby cucumber-shaped eggs are laid loose in dry substrates and do not stick to the substrate. Wet substrates are utilized only when no other is available.

Scolopostethus atlanticus Horvath

I am using Barber's written concept of *atlanticus* (Barber 1918,

1923) despite some question as to the status of the species (Lattin, *in litt.*). Horvath (1893) probably had this clearly marked eastern species in mind when he described *atlanticus.* In practice however Barber himself at the United States National Museum frequently and erroneously named specimens of *S. thomsoni* and *S. diffidens* as *S. atlanticus.* For this reason many if not most of the distribution records of *atlanticus* are incorrect. I have seen definite specimens of *atlanticus* only from New Jersey, Long Island, New York, southeastern Connecticut and on Cape Cod at Wood's Hole Massachusetts. This is a typical pine-barren type distribution. The specimens of "*atlanticus*" seen from middle and northern New York (Torre-Bueno 1917, Barber 1923), and from British Columbia (Parshley 1919) are all referable to *S. thomsoni* and should be deleted as records of *S. atlanticus.*

S. atlanticus is clearly distinguished from *S. thomsoni* by several characters in addition to those used by Barber. In the male of *S. atlanticus* the large fore femoral spine is oddly bent rather than straight, and the parameres of *S. atlanticus* are only slightly curved as in *S. diffidens* rather than strongly curved as in all populations of *thomsoni* seen. In both sexes of *atlanticus* the adult scent gland evaporatorium covers about 3/5 of the metapleuron similar to *S. diffidens* while in *S. thomsoni* the evaporatorium covers less than ½ of the metapleuron. It appears that *S. atlanticus* may actually be most closely related to *S. diffidens.*

Environment

The only habitat note in the literature that is definitely referable to *S. atlanticus* is Barber's collection of it under huckleberries in New Jersey (Blatchley 1926). These same specimens are in the U.S. National Museum.

I have been able to find only one good station for *atlanticus.* This is a habitat at Noank, Connecticut. A few specimens were also collected at Storrs, Connecticut with *S. diffidens.*

The Noank habitat is a mixed *Vaccinium corymbosum—Viburnum dentatum* tall shrub community with an emerging overstory of *Acer rubrum.* The herb layer consists mostly of a heavy growth of the hay-scented fern *Dennstaedtia punctilobula, Aster* spp., and a few undetermined grasses.

The biotope of *S. atlanticus* is in the shaded mesic litter beneath the *Vaccinium* and *Viburnum* where it coexists with *Ozophora picturata, Eremocoris ferus, Antillocoris minutus,* and *Drymus unus.* The litter varies from relatively moist (7) to mesic (4) and *atlanticus* is concentrated in the better drained and drier spots. As the ground layer is shaded, the litter temperatures are moderate. In late summer in 1957 *S. atlanticus* was the third most abundant species with 20–30 insects per square meter, but in successive years as the maples shaded out the shrubs, the abundance of the other rhyparochromines dropped leaving *S. atlanticus* as the most abundant species but with only about 10 insects per square meter. *S. atlanticus* was present in the same biotope for six successive years.

General Biology

Although Barber (1918e) thought *S. atlanticus* was entirely macropterous, the population at Noank is polymorphic and consisted mostly (75%) of brachypters. Not enough is known about this species to evaluate the relation of its wing condition to its normal habitat, except to note that its six years persistence at the Noank habitat is typical of pterygopolymorphic species.

This brighly marked species behaves like *S. diffidens* in the field and appears to be an even better ant mimic than *S. diffidens.* The nymphs unlike either *S. diffidens* or any of the populations of *thomsoni* also have the tips of their fourth antennal segments pale white as in the early instars of *Eremocoris ferus,* which probably serves to distract predators.

S. atlanticus feeds on the seeds of *Vaccinium* and *Viburnum* and also a number of small unidentified seeds in the litter from the field. It probes the litter with its labium until a seed is sensed and then proceeds to pierce the seed. It frequently drags the seeds with its labium to more protected locations for feeding. Like *S. diffidens,* when hungry, the adults of *atlanticus* clash over the seeds, flailing at each other with their legs and antennae.

Life History

Like *S. diffidens, S. atlanticus* is univoltine with an obligative adult diapause. Despite the warmer coastal climate at Noank than at Storrs, the seasonal cycle is no earlier. The observed sketchy phenology is given in Table 49.

Adults which are captured in spring have a long oviposition period in the laboratory which correlates with the late presence of nymphs and the overlap of old and young adults in July in the field. These new adults remain in reproductive diapause in laboratory warmth until midwinter.

The late occurrence of first instars has apparently no relation to photoperiod. Adults collected in late March and allowed to become mature under 12 and 15 hour photoperiods do so simultaneously. As in *S. diffidens,* a temperature response is probably involved. Bringing the adults into the laboratory forces the seasonal cycles several months ahead of the field population's cycle.

The diapause state is a moderately intense one and only a few adults survive under warm laboratory conditions to spontaneously complete diapause development in January. In cultures forced to maturity several months ahead of the field populations the few surviving adults become reproductive in November instead. This is a diapause period of five months. Such adults which complete diapause development in warmth live only a month as compared with spring adults which live two or three months or until as late as the middle of July.

The stadia are inadequately worked out and only the single figures available are given in Table 50. The adult longevity is at least a year as *atlanticus* is a univoltine species and the generations overlap.

TABLE 49
Phenology of *Scolopostethus atlanticus*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
May 25	—	—	—	—	—	100%
June 9	20%	—	—	—	—	80%
June 20	25%	20%	10%	—	—	45%
July 16	5%	15%	25%	25%	20%	10%
Aug. 5	—	—	10%	15%	35%	40%
Aug. 18	—	—	—	—	10%	90%
Aug. 28	—	—	—	—	—	100%

TABLE 50
Stadia of *Scolopostethus atlanticus*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
10	5	4	4	8	12	43

Some females are already fertilized by April 22, but eggs are not laid until after 6 days in the laboratory. A sexually isolated unmated female laid only 4 eggs. The fecundity in the laboratory is largely due to the extended oviposition period. One female laid 208 eggs at an average rate of 5 eggs a day over about 40 days.

The eggs are similar to those of *S. diffidens* and are laid at random or pressed into crevices in the litter. The eggs do not stick to each other and are often laid into wet substrates.

Scolopostethus thomsoni Reuter

Such is the biological and morphological diversity of the New England populations of *thomsoni* that this study is inadequate and a more detailed study will be needed to understand this species. It is not clear whether the various populations represent different species, ecophenotypic groups, or genetic aggregates separated by ecological barriers. No attempt was made to study mating reactions among the different populations. Eyles (1963, *in litt.*) also has found considerable diversity in the habitats of *S. thomsoni* in Europe. He has intensely studied several populations of this species in England.

In North America *thomsoni* has a generally northern distribution and is known in high altitudes south to New Mexcio. I have collected it on a cool grassy bald at 6,000 feet on Roan Mountain, North Carolina. There are specimens from Anchorage, Alaska in the United States National Museum and *thomsoni* is recorded from Lappland and Siberia in the Palearctic as well as from Algeria and Morocco. This wide spread distribution and its far northern extension along with the biological diversity of *S. thomsoni* in North America makes it seem likely that *thomsoni* is one of the few lygaeids with a Holarctic distribution. It is conceivable that both native and introduced populations may be present in New England.

Environment

The population studied in New England may be separated into three or four groups. The first includes the common *Scolopostethus* found around sedge "stools" (*Carex stricta* Lam.) in marshes sometimes with *Ligyrocoris caricis* and *Pachybrachius albocinctus*. (See under *L. caricis* for a description of this habitat at Storrs, Connecticut). This habitat agrees closely with that described by Torre-Bueno (1917) for his "*atlanticus.*" He considered this the most common *Scolopostethus* in New York and swept it in large numbers from sedges. His records undoubtedly refer to this population of *S. thomsoni.* This is an unusually wet habitat for a *Scolopostethus* species and sometimes individuals are seen running across water on bits of litter between the sedge clumps. This form was collected in large numbers in flood wash left by high water at Mansfield Center, Connecticut. This area contains extensive stands of sedges under which occurs this *Scolopostethus.* It was also collected in marshes at Norfolk and Canaan, Connecticut. This is the population that may key down to *S. atlanticus* because the hind femora are pale and the proximal small spines on the fore femora are often reduced or absent.

Although it is commonplace for northern species to occur at their southern limits in marsh or bog habitats (Allee *et al.*, 1949), there are no equivalent *Carex* habitat records in the European literature.

The remaining populations of *S. thomsoni* are collectively referred to as thomsoni "B" in the general discussion. Actually it too consists of at least two groups here termed "B" and "C." The second group "B" is found in northern New England in mesic roadside habitats, often among rank forbs and along woodland margins and sandy flood plains. This habitat probably corresponds to the collections of *S. thomsoni* in roadside trash near Buffalo, New York (Van Duzee 1894) and resembles the typical habitat in Europe where *thomsoni* is found abundantly on nettles (*Urtica*) (Southwood and Leston 1959). However, there are no records of *thomsoni* on nettles (*Urtica*) in North America, nor have I found *thomsoni* on or about *Urtica* in New England despite specific search. *S. thomsoni* "B" is the most contrastingly colored population, and is the most clearly "thomsoni." However some individuals have the proximal fore femora spines reduced, especially in several populations found in Connecticut on a sandy flood wash plain. Populations in northern New England fall definitely into Barber's concept of *thomsoni*.

In a habitat at Laconia, New Hampshire *S. thomsoni* was found abundantly with *Ligyrocoris diffusus* and *Trapezonotus arenarius*. In a transect at Laconia from a ruderal roadside to a white birch stand the numbers of *S. thomsoni* "B" dropped off sharply and were completely replaced by *S. diffidens* in birch litter.

The third population "C" is a little larger and lighter in color and was found at Gorham, New Hampshire, in grasses under and near birch trees but not in thick birch litter. The nymphs of this form are also lighter in color. This habitat is similar to the grass-birch habitat found for *thomsoni* in Oslo, Norway by Eyles (1963b, *in litt.*).

Several other habitat notes bring out the diversity of the habitat of *S. thomsoni* in Europe. In Switzerland Hedicke (1942) notes it in wood and field edges. In England, Southwood and Leston (1959) list it from damp meadows, wastelands, woodland clearings, parks and gardens. Stys (1960) records it in Czechoslovakia on *Calluna*, in birch litter and *Sphagnum* as well as *Urtica*. Lindberg (1958) records it in Newfoundland from many localities in sifting among leaves and dry grass, on vegetation, in humid and shady locations in woods and on shores. In Canada, *thomsoni* was collected in humus under pine trees (Brown 1934). One point clear about the habitats of *S. thomsoni* is that although they are usually open, they are wet sites with an abundant herbaceous growth.

General Biology

All populations of *S. thomsoni* studied are pterygopolymorphic, but none have the low number of macropters (4.2%) reported by Eyles (1963b) for the nettle population of *S. thomsoni.* Forster (1955) also notes that the macropters are very rare. There is some variation among the New England populations but these all have at least 10% macropters. The meaning of the flightless condition is not apparent in those populations existing in rather temporary habitats, but the population of *thomsoni* "A" is certainly inhabiting a long persisting serclimax type of habitat along pond edges. The presence and abundance of *S. thomsoni* on nettles, a forb of temporary habitats, seems to be an exception to the relationship between macroptery and temporary habitats. Of course if the nettles are very abundant only a small dispersal rate would be necessary for migratory purposes. Southwood (1960) noted that *S. thomsoni* in England is probably a day flier, and Eyles (1963b) collected only two females in air suction traps.

Although the other two species of *Scolopostethus* are definite ant-mimics the field appearance of *S. thomsoni* and its smoother, less jerky run, does not appear ant-like. The coloration pattern appears disruptive, especially the macropter, in which the membrane is almost entirely white.

Like *E. ferus* some populations of *S. thomsoni* possess a sweet aromatic scent gland odor quite unlike the usual "buggy" odor. This odor is present in the sedge *Scolopostethus* and in a Laconia "B" population. However population "C" from Gorham, New Hampshire does not possess this odor nor does a "B" habitat type form from Camden Hills, Maine. Some populations studied earlier were not tested for this characteristic. This variation underlines the diversity of "*S. thomsoni.*"

No predators or parasites were observed in this study. According to Thomas (1955) in England *S. thomsoni* is the prey of *Nabis major, N. mimicoides, Lithobius* sp. and *Formica rufa* L. *S. thomsoni* is parasitized by a tachinid (Southwood and Leston, 1959) and Eyles (1963a) found 7 specimens parasitized by *Cirochira atra* Zett. which also parasitized *S. decoratus. S. thomsoni* is also attacked by a fungus, *Entomophthora* sp. (Eyles 1963a).

In the European literature *S. thomsoni* is repeatedly reported to feed on nettles (Puton 1896, Butler 1923, Brown 1925, Murray 1935, Feige and Kulhorn 1938, Hedicke 1942, Franz 1943, Shaw 1945, Forster 1955, Southwood and Leston 1959, Stys 1960, Eyles 1963b). Eyles definitely showed that the insects feed on the seeds of the nettles. *S. thomsoni* has also been collected from *Mentha* sp. (Puton 1894) and *Tanacetum* blossoms (Prohaska 1923). Eyles

(1963b) found that the larger part of the population is on the nettle plant, not on the ground. Although Torre-Bueno (1917) swept *thomsoni* ''A'' on sedges, I found less than 10% of the total population ever actually on the sedges, and the other populations are restricted to the ground.

The feeding habits of the New England *S. thomsoni* reflect the population diversity already seen. The sedge population feeds on *Carex* and *Scirpus* seeds to the exclusion of other seeds offered it. Nymphs reared from eggs on a *Carex*-sunflower seed mixture fed exclusively on *Carex* seeds ignoring the sunflower seeds unless starving. In contrast populations of ''B'' *thomsoni* feed readily on a larger variety of seeds, including sunflower seeds. A ''B'' population at Canaan, Connecticut feeds on seeds of *Oenothera, Rumex* and *Mentha*. Populations from northern New England feed on *Rudbeckia, Tsuga* and *Betula* seeds.

Specimens of *S. thomsoni* clash intraspecifically over the seeds as do the other two species, and drag the small seeds about or suspend them under their body on the beak. The Canaan population also somehow attaches the *Oenothera* seeds to the sides and top of the glass rearing dish. On at least ten occasions a *thomsoni* which was not feeding on the seed drove away another *Scolopostethus* approaching the seed. Several times the fore femora were raised at the appearance of an aggressor. This behavior pattern was not observed in the other populations.

Life History

Although Eyles (1963b) detected only one generation a year in *S. thomsoni* in England, the populations in southern New England are bivoltine. Although population ''C'' from Gorham, New Hampshire probably overwinters as adults and late instars as does *S. thomsoni* in England (Forster 1955, Eyles 1963b), the only overwintering form found in populations ''A'' and ''B'' in Connecticut is the adult.

No phenology table can presently be given for *S. thomsoni* because no one population could be sampled through the entire year and the different populations are not ecologically or climatically equivalent. Some comparative notes can be given, however. The nymphs of *thomsoni* ''A'' population at Storrs do not appear until early June, but in the *thomsoni* ''B'' population of the sandy flood plain at Canaan, Connecticut, first instar nymphs are present in the middle of May and become adult in late June. The new adults of the *thomsoni* ''A'' population appear in the middle of July. This difference may result from the different insolation levels of these habitats.

Instead of remaining "immature" as does the English *S. thomsoni,* the first generation of Connecticut populations both in the laboratory and in the field become reproductive after a preoviposition period of 8 to 10 days. This is also true of a *Laconia* population "B" in late July and early August and a Gorham, New Hampshire population "C" in mid-August.

The second generation of both "A" and "B" populations of *S. thomsoni* remains nonreproductive or immature. This however is not true of the late August Gorham "C" population in which the new adults in September become reproductive in the laboratory and produce a third generation. In contrast, late August adults of Camden Hills "B" population do not become reproductive.

Therefore only population "C" lacks a reproductive diapause mechanism and overwinters in a quiescent state. That the other populations have a facultative reproductive diapause and not merely an "immature" period is shown by the short preoviposition period of the first generation in contrast to the long reproductive diapause of the second generation. Because this occurs in the laboratory under warm conditions the diapause condition is probably a photoperiod response. This would account for a few apparently first generation adults which go directly into diapause. Since the English climate is cooler, the univoltine condition may not be obligative but facultative, the single generation becoming adult in late summer.

The diapause state under warm laboratory conditions is broken by only part of the population in January and so lasts at least four months.

The table of stadia given here (Table 51) is based on the *Scolopostethus* "A" population on *Carex* seeds. Under laboratory conditions development occurs more rapidly than in Eyles's work probably because of the higher room temperature (78° F.).

TABLE 51
Stadia of *Scolopostethus thomsoni*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
10.0 (8–12)	5.8 (4–7)	5.0 (3–7)	4.7 (4–5)	5.3 (4–7)	6.8 (5–10)	39 (31–50)

As already mentioned the preoviposition period of the first generation is 8–10 days. After being brought into the laboratory in spring on April 14, the flood plain population "B" females are already fertilized and oviposition begins immediately. Females from the *Scolopostethus* "A" population are not fertilized at this time.

As in *S. thomsoni* in England virgin females of the *Carex* population laid a few eggs (7–20, mean 16). The fecundity varied from 104 to 250 eggs laid at an average rate of 6 a day in the *thomsoni* "B" population.

The eggs are similar to those of the other *Scolopostethus*. They are laid in substrata available. Population "A" definitely prefers to lay the eggs in wet substrates while the other two populations lay eggs in both dry and wet substrates. The wet substrate preference correlates with the wet habitat of *thomsoni* "A." Eyles (1963b) found eggs of the nettle population laid in the perianth of the nettle seed heads.

Eremocoris ferus (Say)

The genus *Eremocoris* includes 30 species, of which 11 are Nearctic, 16 Palearctic, 2 Oriental but from high elevations in India, and 1 in the Ethiopian region. This is in general then a Holarctic distribution. One species *angusticollis* Jak. from Siberia was judged by Horvath (1883) to be close to *E. ferus*.

In the eastern United States there are three species recorded of which two are southeastern in distribution. *E. ferus* has the widest distribution and occurs completely across North America from Newfoundland and Hudson's Bay to British Columbia and south to California, Texas, Louisiana, and South Carolina. (Slater, Catalogue). There appear to be no records from the extreme southeastern United States. Nevertheless, this is a very broad distribution indeed.

Unfortunately it was not realized until the present moment of writing that Blatchley's (1926) Barber's (1928c) and Torre-Bueno's (1946) concepts of *Eremocoris ferus* are composite and *ferus* actually includes two distinct species. One species is northern, the other southern.

The two species can be easily distinguished. The northern species has the hind tibia nearly nude except for two rows of small moveable spines; the body, including the abdomen is almost nude; and the labium attains only the metasternum or the mesocoxae. The southern species has the hind tibia densely covered with many fine erect long setae; the body is rather pilose, especially the abdomen; and the labium attains the hind margin of the metacoxae, or the abdomen. The last instar nymphs may also be told apart by the setae of the hind tibia and the length of the labium. The color patterns of these two species are very similar, and the southern species is slightly smaller.

Within the study area the northern species occurs south to Canaan and Storrs, Connecticut but not to Noank and New Haven, Connecticut. The southern species occurs at Noank and Storrs but not in Canaan and farther north. Specimens before me from Quebec are all the northern species. This is not a subspecies pattern because the two specific forms coexist as separate populations with no evident overlap at Storrs, Connecticut. Indeed, the southern *ferus* in Connecticut differs only slightly from specimens of *ferus* from Texas.

Since *ferus* is one of Say's species the types of which were destroyed and a lectotype has not been selected for *E. ferus*, it is not certain which species should carry the name *ferus*. Although Say gave ''the Union'' for the locality of *E. ferus*, the austral species is probably the one that he described, and the boreal form is the new species. The name *borealis* Dallas presently a synonym of *ferus* may refer to the northern species.

Environment

In the discussion on wing polymorphism *E. ferus* is noted as having a very wide ecological distribution. The resolution of *E. ferus* into two species is reflected in their more restricted ecological distributions, although the variety of habitats exploited by each is still considerable.

The two species are similar in that both inhabit shaded or cool habitats and are restricted to loose ground litter except during spring dispersal flights.

The northern species, like *Scolopostethus diffidens* is a common inhabitant of the litter beneath the northern forest trees hemlock (*Tsuga canadensis*), spruce (*Picea rubens*), and birches (*Betula papyrifera, B. lutea* Michx. and *B. populifolia*). Drake's (1922) record of it under yellow birch (*Betula lutea*) probably refers to this species. It is also found in open but cool habitats at high elevations. Adults were collected on the alpine area on Mt. Washington at 6200 and 6000 feet. A little lower, at 5500 it was collected in *Vaccinium* heath with *Trapezonotus arenarius*. At lower elevations it is frequently found in forest edge habitats. At Storrs, Connecticut it is found in several cool ravines where hemlock stands exist, and is much less abundant and widespread than farther north.

The ecological distribution of the southern species is more heterogenous and difficult to characterize. It occurs at Noank, Connecticut in the litter under *Vaccinium corymbosum* (L.), *Viburnum dentatum* L. with *Scolopostethus atlanticus* (see *Ozophora* for a description of this habitat), under the litter of arbor vitae (*Thuja occidentalis* L.), and under bayberry (*Myrica pensylvanica* Loisel). Under gray birch (*B. populifolia*) at Storrs, it is much less abundant than the northern species is under this same subclimax tree at Canaan, Connecticut. In small scattered groups it occurs in light mesophytic woodlands of *Acer rubrum* L. and *Betula lenta* L. with *Drymus unus*. It is even occasionally found along shaded beach strands, or the litter under roof eaves. The species does not occur in open dry grassy habitats, or among rank forbs, or in xeropyhtic oak-hickory forests.

The litter of austral *ferus* is usually drier (4–8) than the boreal *ferus* which sometimes, as on Mt. Washington, New Hampshire occurs in completely water-soaked (10) sedge-sphagnum environments. The driest habitats of the boreal *ferus* are some well drained hemlock slopes (4).

For the northern form the soil and litter varies from the gray podsol soil—mor litter under hemlock and spruce to brown mull soil with a deep leaf litter under birches. For the southern form the litter is usaully loose and well drained, soil variable. In both the presence of field colonies corresponds to small edaphic changes, but as in *Scolopostethus* a degree of gregariousness is apparent.

Both species are occasionally found in great abundance within their preferred habitats. The northern *ferus* occurs in a density up to 50–60 per square meter in *Picea-Betula* litter, and the southern form in a similar abundance in *Vaccinium-Viburnum* litter. Most of the available habitat notes, judging from their distribution, refer to the austral species.

Torre-Bueno (1929a) collected *E. ferus* around a marsh under cattails. The species was found under cover in upland woods and in the summer on the ground in sandy places (Blatchley 1926). Froeschner (1944) noted that *ferus* is uncommon in Missouri and found in weedy fields.

General Biology

Both species are completely macropterous. At least the southern form flies readily in dispersal flights. There is a definite spring migration phase which takes place the first warm days in early spring. This dispersal occurs during the day and can be easily sampled by inspecting sheets hung up to dry at homes near woodlands. The dispersing *Eremocoris* are attracted to the large white sheets. Other records demonstrate that *Eremocoris* disperses. Torre-Bueno (1914, 1915) and Myers (1926) found *Eremocoris* in large numbers washed up in beach litter. Glick (1939) collected *E. ferus* in the air at 200 feet over Louisiana.

Eremocoris ferus is not only found very frequently with *Scolopostethus,* but like it, displays a ''flash'' type ant mimicry when disturbed in the field. However, *Eremocoris* is twice (6 mm.) the size of *Scolopostethus.* The boreal form is found only with *S. diffidens,* the austral with *S. atlanticus* and *S. diffidens.* The northern form is much more definitely associated with *Scolopostethus.* The nymphs of instars one to four are also ant-like because the red abdomen has a transverse white band across the anterior abdominal segments. The fifth instar is dark colored. *E. ferus* feigns death for a brief period of 10–20 seconds when disturbed directly.

The scent gland odor of *Eremocoris* is not the usual ''buggy'' odor but a strong sweet aromatic odor which is readily released at slight disturbances. This odor is similar to that found in some populations of *S. thomsoni* but not in the *Scolopostethus* with which *Eremocoris* is often associated. The nymphs have the usual ''buggy'' odor.

As yet no parasites or predators are known. Ashlock (*in litt.*) has reared a *Catharosia* from an undescribed western species of *Eremocoris.* There are many references in the European literature relating *Eremocoris abietis* (L.) (Puton 1876, Wassmann 1889, 1894, Gulde 1937, Franz 1943, et al.) to ants. I have found no unusual relationships between the eastern *Eremocoris* and ants.

Both species are usually found in litter devoid of plant material, and feed on the fallen seeds from the trees or shrubs. The northern form feeds on seeds of *Betula* spp., *Tsuga,* and *Picea.* The southern form feeds on seeds of *Myrica, Vaccinium, Gaylussacia* and *Thuja,* and in the laboratory also on the seeds of *Tsuga* and *Betula.*

The insects actively drag seeds about in the rearing dish to protected sites for feedings, so that the seeds are frequently brought together in a small area under a bit of litter where the bugs aggregate. The seed possession behavior is well developed in the adults and a feeding *Eremocoris* endeavors to keep the seed away from other insects. Several times an adult would even climb to the underside of the top of the cage and suspend the seed on the end of its labium. The nymphs are more tolerant and several may feed together on the same seed.

Only data on the mating behavior of the southern species is available. The male, on sensing by contact a receptive female will slowly approach her. The apical three antennal segments are held at a right angle to his body and parallel to the floor, and the male vibrates his antennae very rapidly. The antennae vibrate in a small horizontal plane on the joint between the first and second antennal segments. The antennae are vibrated in bursts while the male climbs on the female and effects copulation. The male drops off into the usual end to end position. When approached by a male a female easily decamps or merely holds the male off with repulsing movements of her hind legs. Copulation is accomplished most frequently while the female is feeding. Copulation lasts for at least several hours. Although it may be repeated, copulation does not occur with the frequency observed in several rhyparochromines such as in *Stygnocoris.*

Although no deliberate mating experiments could be run, by accident two occurred during experiments to determine prereproductive periods. A boreal *ferus* male from Canaan, Connecticut was placed with a 25 day old austral female from Storrs, Connecticut. After 28 days the female died after having laid only four infertile eggs. This small fecundity is typical of unmated females. This same male was then placed with a teneral virgin austral female and after 20 days only six infertile eggs were produced. An austral male was then supplied and normal oviposition ensued.

In the other case a boreal male from Laconia, New Hampshire was placed with two unfertilized austral females from Storrs, Connecticut. As before, one female produced only 7 infertile eggs. The other female however, produced a total of 65 eggs of which 42 did not develop. The 23 hybrid progeny could not be reared past the third instar.

Since I failed to recognize that two species were involved at the time, these peculiar results were merely dismissed as due to abnormal males, despite the males' healthy appearance and behavior, and despite normal reproduction in the source cultures. These results need substantiating, but as they stand, indicate a significant degree of reproductive isolation between the boreal and austral forms.

Life History

Most of my data refers to the southern species, but enough is available on the northern species to show that the life histories are similar. Both are bivoltine, have no diapause mechanism, and overwinter in a quiescent state as adults, and in a few cases, as nymphs of the last three instars. Cool temperatures in autumn bring about a cessation of reproductive activities in late autumn although nymphal development continues. As a result early instars are not present in the population at the advent of cold weather. As usual in drymines, the adults are quite cold hardy and move about and feed under 6° C. conditions. It is not known whether or not the females may survive the winter already fertilized. Two females collected on March 12 and isolated, laid fertilized eggs, but copulation begins very early in spring so this is inconclusive.

The phenology given in Table 52 is for the population of the southern species at Storrs, Connecticut. The northern species at Canaan shows a similar although later phenology but is incomplete and so not given here. The two generations completely overlap in August and September. Different small populations of the austral *ferus* vary completely in their instar composition in late summer during the second generation because of differences in the colonizing of new habitats and the maturation of the females. The figures then represent a pooling of the data for the populations.

When brought into the laboratory any time from spring to autumn the adults become or remain reproductive. *E. ferus* can be readily reared on sunflower seeds but suffers a very high mortality especially in the early instars (Sweet 1960). Mixing birch or hemlock seeds with sunflower seeds greatly reduces the mortality in the early instars. Under high densities there is a clear-cut fall off in oviposition and frequency of copulation and increased mortality, despite food availability.

TABLE 52
Phenology of *Eremocoris ferus*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
Apr. 15	——	——	——	1%	4%	95%
May 15	——	——	——	——	2%	98%
June 1	20%	5%	——	——	1%	74%
June 15	30%	20%	15%	——	——	35%
June 25	5%	30%	45%	15%	5%	——
July 7	10%	20%	20%	30%	10%	10%
July 20	——	——	10%	20%	50%	20%
Aug. 15	20%	20%	15%	10%	10%	25%
Sept. 7	15%	10%	15%	20%	20%	20%
Sept. 21	10%	5%	10%	10%	15%	50%
Oct. 7	——	——	5%	5%	15%	75%
Oct. 22	——	——	——	3%	7%	90%

The stadia given in Table 53 again is for the austral form only, and represents the first generation reared in the laboratory at room temperature on a mixed birch-sunflower seed diet. Nymphs brought in from the field and reared grew faster than the averages given.

TABLE 53
Stadia of *Eremocoris ferus*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
9.8 (7–11)	6.0 (5–10)	5.6 (5–7)	6.4 (5–8)	7.4 (5–11)	7.9 (5–11)	46.0 (35–58)

The nymphs with swollen abdomens feed very little and remain quiescent. Five newly moulted fifth instar nymphs of the northern species were allowed to feed on *Tsuga* seeds for twenty-four hours and then isolated with no food. By this time the abdomens were fully distended. After five to six days all moulted into normal sized adults. This clearly indicates that the feeding period can be restricted to a short period during the stadium. The adult longevity varied from 28 to 112 days (mean 71). The larger extreme was an exceptional female which, however, laid no eggs for the last 42 days of her life span.

The normal preoviposition period is 10.5 days (range 10–12). The precopulatory period could not be determined precisely; it is no longer than the preoviposition period. After being brought into the laboratory in March, 5 to 11 days (mean 8) days elapsed before oviposition occurs, although copulation in some cases had already occurred in the field. Adults collected in late February are not fertilized.

The fecundity is high and varies from 148 to 291 eggs (mean 198) and is probably higher. Only one mating is necessary to fertilize the entire complement. Unmated sexually isolated females of both the austral and boreal forms lay from none to 11 eggs (mean 5.6). The eggs are laid singly at the rate of 4 to 6 a day. The eggs are typical drymine eggs rather stubby and cucumber shaped, with no spinules or any sticking mechanism. They are laid in loose litter, sand, cotton, both wet and dry with a distinct preference for dry substrates.

Eremocoris setosus Blatchley

Blatchley (1926) described this species from a manuscript of Barber's as a distinct species. Barber (1928e) described *setosus* as a subspecies of the European *E. plebejus* Fallen distinguished by its even denser coating of long soft hairs. If *setosus* is a distinct subspecies of *plebejus* this would be a remarkable disjunct distribution.

Although Barber (1928e) recorded specimens of this southeastern species from Tyngsboro, Massachusetts and Long Island, N.Y., I have been unable to locate the species is New England. There is also a record from Montreal, Canada (Moore 1950), but otherwise, *setosus* is restricted to the southeastern seaboard.

Barber (1928e) found *setosus* abundant near Vienna, Virginia in sifting dead leaves in or about the woods. Blatchley (1926) took the species in Indiana from beneath logs on slopes of upland wooded pastures, and swept it from boneset and other Compositae.

Gastrodes walleyi Usinger

The genus *Gastrodes* includes 9 species, five in the Nearctic, three in the Palearctic, and one in the Oriental Region at Macao. Of the Palearctic species, one is restricted to Japan and northern China, and the other two are widespread Palearctic species. Four of the Nearctic species are restricted to western North America. The fifth and only eastern Nearctic species *G. walleyi* was described by Usinger (1938) from a single mutilated specimen collected by G. Beaulieu on July 1, 1914 at Ottawa, Ontario, Canada. This locality makes it probable that *G. walleyi* occurs in northern New England. It is evidently quite rare as it has not been collected again since the first collection and Kelton (*in litt.*) at the Canadian Entomology Research Institute, Ottawa, Canada has been so far unsuccessful in locating the species.

The available records indicate that the species of *Gastrodes* feed in the trees on the seeds on conifers. The two common European species have been studied (Nageli 1933, Aitkens 1936, Pfaler 1936, Southwood and Leston 1959). *G. abietum* (Bergr.) is specific to Norway spruce (*Picea abies* L). while *G. grossipes* is abundant on Scots pine (*Pinus sylvestris* L.). *G. conicola* was collected in California on resinous mature cones of the digger pine (*Pinus sabiniana* Dougl.) (Usinger 1933). The rarity of *walleyi* may be in part explicable by Usinger's note on *G. conicola:* "No specimens had ever been found during previous years of collecting nor, upon diligent search were any specimens later found to occur in the foliage or in old cones of previous seasons."

It is probable then, that *G. walleyi* will be found on a coniferous host, feeding on the seeds. I have searched without success in Maine and New Hampshire for it on the new and old cones of *Pinus strobus* L., *Pinus rigida* (Mill.), *Picea rubens* Sarg., *Picea mariana* (Mill.), *Picea glauca* (Moench.), *Picea abies* (L.), *Abies* *balsamea* (L.), *Larix laricina* (DuRoi and *Tsuga canadensis* (L.), but it probably occurs on one of these hosts. *Pinus banksiana* Lamb. is another possibility.

TRIBE RHYPAROCHROMINI

Peritrechus Fieber

This large genus has a Holarctic distribution with the majority of the species in the Palearctic region. Of 26 species, 22 are from the western Paleactic, but apparently none are recorded from the eastern Palearctic—China, Japan, and Korea. This apparent faunal break in the eastern Palearctic is probably a collecting gap as a number of European species range quite far north, and four, *P. angusticollis* Sahlb., *P. convivus* Stål, *P. distinguendus* Flor, and *P. geniculatus* Hahn, are recorded from "Siberia" (Slater, Catalogue). Lindberg (1958) reported a colony of *distinguendus* on Newfoundland and considered it to have been introduced there by way of ballast from European ships.

Of the four Nearctic species, two are western, one is widespread, and the other is limited to the eastern sea board. It is reasonable to consider the genus as a Palearctic one which has spread into the Nearctic region.

Peritrechus fraternus Uhler

Peritrechus fraternus is a widespread species recorded from Mexico and lower California north to British Columbia and Alberta and east to Quebec and New Hampshire, but in the eastern United States it is not recorded south of New Jersey (Slater, Catalogue) except in the mountains of North Carolina at Spruce Pine (Brimley 1938). I have collected the species in the same county, Mitchell, at 6,000 feet on Roam Mt., North Carolina. It appears then that the eastern and western populations have a quite different north-south extent. It would be important to ascertain if a species complex may be involved. Since the type material of *P. fraternus* was originally described by Uhler (1871) from Massachusetts, it is very probable that, whatever the species situation may be, the population in New England represents this species.

Environment

While it is ecologically restricted, *Peritrechus fraternus* is one of the more common species of rhyparochromines in southern New England. The great majority of the collections of this species are from wash litter communities. Since the wash litter is a concentration point for various seeds, it forms a favorable habitat. The species is found in strand wash at the high tide mark along the ocean shore at Rocky Neck and Noank, Connecticut and at Woods Hole and Brewster's Point, Massachusetts; in litter along the shore of Lake Cayuga, New York, and Twin Lakes, Connecticut; and in the flood wash of various streams. In the salt water beach wash it is found only at the highest strand levels, above the level dominated by the sand flea *Orchestia,* where the substrate moistness is mesic, about 5–6, and the salt content is low. At Brewster's Point it is also found on the high beach in wind blown litter at the bases of seaside goldenrod (*Solidago sempervirens* L.), beach rose (*Rosa rugosa* Thunb.), beach plum (*Prunus maritima* Marsh.), beach pea (*Lathyrus japonicus* Willd.), and poison ivy (*Rhus radicans* L.). In similar inland litter aggregations, especially where large litter layers are deposited, this species attains very dense populations at some sites, up to 86 per square meter, although at others as low as less than 1 per square meter. Such low abundances are usually in old litter lines, the highest in fresh litter deposited during spring flooding. Open or semi-open areas are favored and heavily shaded strands contain very few *Peritrechus.* Nearly always, probably because of the nature of the site of litter deposition, the soil is sandy or gravelly. Repeatedly *Peritrechus* concentrates in a mesic zone of intermediate moisture (4–6) and temperature (70–90°F.) in the litter. At times such favorable aggregations of seeds attracts other rhyparochromines such as *Perigenes constrictus, Heraeus plebejus, Pachybrachius basalis,* and *Scolopostethus thomsoni* (A), but always in the strand litter biotope *Peritrechus* is dominant. It also occurs in the similar aggregations of dry litter along some new roadsides. Sometimes it is found in low densities in new sandy often ruderal habitats, but here, it is always an infrequent member of this community which is usually dominated by rhyparochromines such as *Ligyrocoris diffusus, Pachybrachius basalis,* and *Emblethis vicarius.* Occasionally I found this species on small rises and hummocks in salt marshes along with *Peritrechus paludemaris* Barb. (see *P. paludemaris* for further discussion).

On Roam Mountain, North Carolina, I collected a population at 6,000 feet on an open cool bald dominated by *Rumex acetosella* and fescue grass *Festuca* spp. While the area had been maintained in this condition by man's activities, the habitat is so very different from the New England habitats that the question must be raised as to whether or not this mountain population is conspecific with the new England population. Perhaps it is a latitudinal variation in habitat selection. Since this mountain population is slightly larger and darker but otherwise very similar to the New England population it is unfortunate that I was unable to cross the two populations because of diapause interference.

At inland sites, *Peritrechus* overwinters in the same habitats in which it matures, but along the seashore there is a definite retreat nearby to drier, more protected sites away from the strand margin.

Many of the following notes in the literature are too generalized to compare with my findings. Van Duzee (1894) collected it hibernating under dead leaves. He (1914) also collected what is supposedly this species on low flatland between the bay and the Pacific Ocean at San Diego, California. Smith (1910) collected it in a cranberry bog. Blatchley (1895, 1926) considered it scarce in Indiana and collected it under chips and dead leaves in fall, and under stones and other cover in winter. A habitat perhaps related to the wash litter is the drop seed habitat in which Walkden and Wilbur (1944) found *Peritrechus* is Kansas. Froeschner (1944) lists it as common in Missouri under rocks, logs, and in grass clumps.

The strand and flood litter habitats, while their general presence is a permanent situation, the individual aggregations of litter, especially on floodwash sites, are temporary biotopes.

General Biology

P. fraternus is entirely macropterous, and no brachypterism is known as is apparently true of the other species of the genus. It is not surprising that it is entirely macropterous, with such an obvious requirement to disperse to new habitats.

The species may disperse, at least on occasion, at night for Hussey (1922) collected 30 at a lighted sheet at Devil's Lake, North Dakota. Knowlton (1960) collected it in Utah at lights. Froeschner (1944) notes that in Missouri it may sometimes come in numbers to light.

As is so frequent among lygaeids the nymphs and adults are quite differently colored. The adults are dark black and mottled brown and blend extremely well, when quiet, into the litter and sand. However, all nymphal instars are a rather bright pale reddish color which may render them conspicuous to bird predators.

When disturbed these insects move rapidly and agilely hide under some concealing object. They may ''freeze'' but do not feign death like *Eremocoris* and *Stygnocoris*. Their normal movements are fairly quick and active in contrast to *Peritrechus paludemaris.* These insects are prone to aggregate together under a bit of litter cover, and are reared much more readily in the laboratory if cover like crumpled methyl cellulose is provided.

I have not discerned any known predators although it may clearly be subject to predation by the large numbers of predatory carabid and staphylinid beetles in the wash litter. Parasitism by *Catharosia* sp. tachinid flies is very low; one male specimen of a long series of adults and nymphs from Rocky Neck, Connecticut was found parasitized.

When litter from its biotope is brought into the laboratory along with it, *P. fraternus* oviposits readily and is easily reared to maturity on the seeds contained in the litter. This is equally true if the other arthropods are either present or killed by baking. Among the profusion of seed species, seeds of *Panicum* spp. are distinctly preferred; other seed species are probed at, but are not fed on except for some *Solidago* seeds. On sunflower seeds growth is excellent with little mortality up to the fourth and fifth instars when growth becomes quite slow and the mortality very great. While the water requirements are high, *P. fraternus* may survive for as long as 24 hours without water.

When *Panicum* seeds are placed on a sheet of methyl cellulose, they are subsequently dragged by the insects to concealed positions beneath the sheet. As in *L. diffusus* this species exhibits a definite defense reaction or display when one individual intrudes on another which is feeding. The defender first wags its antennae rapidly and alternatly, and endeavors to position its body between the intruder and the seed. If this fails to discourage the intruder, the defender either drags the seed away, or it ceases to feed, and, with antennae wagging and fore legs flailing, it charges the intruder. The intruder may move away or persist, in which event the charge is repeated. In each observation the defender wins. It is remarkable that after such a scuffle, which may carry the insect two or four inches away from a seed, the exact same seed—among many—will be searched out and the exact same hole previously drilled is found.

Because of the intense diapause of this species and the essentially univoltine life cycle of much of the population, mating behavior could not be extensviely studied. The male becomes sexually excited when a female comes near, and recognizes her without touching her with his antennae. Recognition is shown by the male's extending his motionless antennae towards the female. The male advances by suddenly leaping on the female, and positioning himself parallel to the female and tapping her head with his rapidly vibrating antennae. In most observed encounters the female escaped the male. Under caged conditions there may frequently be 4–6 males around a female. On several occasions in the field similar aggregations were found. Occasionally a male would leap upon a male. A male which had matured before the diapause point, is sexually excited by diapausing females of both *P. fraternus* and *P. paludemaris.* After advancing several times, however, the male lost interest in the diapausing females, while fertile females continue to elicit a reaction.

Life History

Peritrechus fraternus was observed to overwinter by Van Duzee (1894), Blatchley (1895, 1926) and Froeschner (1944). The observed phenology at Storrs is as in Table 54.

It is significant that some early instars occur in the middle of July, for they represent a partial second generation. Ordinarily these nymphs might be thought of as progeny from an adult which lived exceptionally long. However, it was found that the insects which become adult in late June or early July (at least before July 9) become sexually reproductive and lay a small number of eggs until after about July 15 when such egg laying ceases. The adults which mature near this time go directly into reproductive diapause. The best hypothesis appears to be that some photoperiod effect initiates diapause. Most of a given population in New England does not undergo a partial second generation especially at inland sites. At a Rocky Neck salt marsh margin a considerable number did in 1960 (see *paludemaris* for further discussion).

The phenology given in table 54 is pooled from the populations studied at Noank, Rocky Neck, and Mansfield, Connecticut. However, one population progressed differently. At Storrs, Connecticut, on a grassy, south facing roadside bank strewn with debris, a population entirely of fifth instar nymphs was found on September 10, 1958. These became diapausing adults in mid- and late September. This may represent the partial second generation.

The diapause condition is an intense one and is not broken by short cold exposures (one month), photoperiod conditions, or elevated temperatures (32°C.). The cultures do not survive longer cold exposures, nor does diapause development complete itself during the winter in laboratory warmth as in other species. Only the few cultures which survive in the laboratory until middle April become reproductive which is nearly the same time as the field populations. It thus appears that diapause development will go to completion in this species over a long period of warmth. The occurrence of the partial second generation in early maturing adults suggests that the diapause state is initiated by shorter or shortening photoperiods, but no experimental proof is at hand.

The stadia in table 55 are rather variable in later instars especially those that feed on sunflower seeds. The very prolonged development of some nymphs is presumably abnormal and results from some limitation in the caged conditions. Nymphs brought in from the field and reared develop much more rapidly. If *Panicum* seeds are provided, the newly hatched nymphs develop much more normally and with a smaller mortality. The earlier instars, however, develop equally well on sunflower seeds as *Panicum* seeds.

TABLE 54
Phenology of *Peritrechus fraternus*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
Mar. 15– Apr. 27	——	——	——	——	——	100%
June 1	8%	23%	15%	——	——	54%
June 11	5%	9%	38%	28%	——	20%
June 24	——	21%	32%	35%	12%	——
July 3	——	——	7%	13%	35%	45%
July 11	——	21%	43%	15%	——	21%
July 16	——	——	——	4%	22%	74%
July 25	——	——	——	6%	29%	65%
Aug. 5	——	——	——	——	2%	98%
Aug. 10 *on*	——	——	——	——	——	100%

The average longevity of non-diapause adults is 52 days. The diapause adults in the field live through the summer and winter to spring and die in June. Those kept in warmth frequently live nearly that long (278 days) but most die before early spring without laying any eggs.

With the few adults which mature before diapause conditions set in, the preoviposition period is about 4 days.

Adults collected on April 15 are already reproductively active, mating, and contain ripe ova. Eggs are laid by spring adults a few days after being brought into the laboratory. The early spring females laid in the laboratory from 84–386 eggs (average 193). The partial second generation females laid 78–104 eggs (average

83). The rate per day is 6.1 and varies from 4–8.6 eggs. Most sexually isolated virgin females which overwintered laid no eggs except for one female which laid 79 at a low rate of 2 per day. The two virgin females which became adult at the time that the partial second generation females became reproductive, laid no eggs and later went directly into diapause.

The eggs are laid singly into litter crevices, hollow stems, dry soil, and in tight cotton and methyl cellulose. The females spend a considerable time selecting oviposition sites. The elongate smooth eggs are sticky when laid and stick tight into crevices, to litter fragments, glass, and to methyl cellulose. The eggs often are completely covered with grains of sand and litter fragments, which renders them difficult to see.

TABLE 55

Stadia of *Peritrechus fraternus*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
7.2 (6–9)	5.3 (4–7)	5.9 (4–8)	6.6 (5–8)	7.7 (5–11)	12.2 (6–18)	43.5 (27–70)

Peritrechus paludemaris Barber

Barber (1914b) noted this species as being very closely related to *fraternus,* but many species of the genus *Peritrechus* are rather similar appearing, and actually *paludemaris* is quite different. Barber used the relation between the distance across the anterior angles of the pronotum and the width of the head to distinguish the species. In practice this character is difficult to use and resulted in some misidentifications. *P. paludemaris* is considerably larger, the membrane is mostly fuscous, and the antennae are much longer, especially the fourth antennal segment which is one and a half times as long as the third segment.

P. paludemaris is found along the eastern sea board from Massachusetts to Florida (Barber 1914b). As there is a specimen in the Slater Collection from Biloxi, Mississippi, it is probable that this species is also found all along the Gulf Coast as well. The species is here recorded for the first time from Connecticut.

Environment

In the literature all records of this species are from salt marshes

(Barber) 1914a, 1923, 1928d, Blatchley 1926) or seashores (Torre-Bueno 1931, 1946) of Massachusetts, New York, Maryland, and Florida. I collected this species in brackish and salt marshes at Rocky Neck State Park, Connecticut, and at Hammonasett State Park, Connecticut. The preferred biotope of this species is in the litter of the slightly raised hummocks in salt marshes. The marsh grass is composed largely of a single species, *Spartina patens* (Ait.) and some *Distichlis spirata* (L). on the hummocks. Other plants frequently on the hummocks are *Hibiscus palustris* L., *Aster subulatus* Michx., *Pluchea purpurascens* (Sw.), and in a brackish area, *Spirea latifolia* (Ait.). The ground moisture level of course is saturated (10), but the exposed litter is quite dry and grades off towards the ground. *P. paludemaris* is found at the narrow litter zone between these extremes. Temperatures are moderate, and measured at 78° F. *P. paludemaris* is never found on the mucky surface of the salt marsh flat, but on the hummocks which protrude slightly above the high tide level.

In late autumn at Rocky Neck and at New Haven, Connecticut, several adults were found sheltered under *Andropogon scoparius* clumps a short distance (about 50 and 75 yards respectively) from the salt marsh. At the same time no *paludemaris* could be found in the marsh, despite careful search. This suggests that *P. paludemaris* may migrate away from the marshes to more protected sites in the autumn.

The abundance of *P. paludemaris* is always relatively low compared to the numbers in which *fraternus* frequently occurs, and is quite discontinuous, some nearly identical hummocks with, others without insects. The greatest abundance is reached in mid-June when the population consists of early instars at abundance of 4–5 per square meter on certain hummocks. Usually the abundance is considerably less than 1 per square meter.

This is the only lygaeid found on low hummocks far out in the salt marsh. In sites which are higher, drier and closer to the land margin of the marsh, *P. fraternus* often appears during July. During June in 1961 and 1962 at Rocky Neck, *P. paludemaris* was the only lygaeid on the salt marsh, and even the litter along the margin did not harbor *P. fraternus* which was abundant at other wash sites. However in July of 1960, 1961, and 1962 *P. fraternus* appeared on the drier hummocks and along the margins. As explained under *P. fraternus,* this apparently represents the partial second generation of *P. fraternus.*

General Biology

There probably is a seasonal shift from hibernation sites to the salt marshes, as indicated earlier. The precarious water level of the salt marsh must impose a hazard which may outweigh any advantage of brachyptery in the essentially permanent habitat of the salt marsh.

P. paludemaris is similarly colored to *fraternus* although a shade lighter, but behaves quite differently. While *fraternus* moves rapidly in a scurrying fashion to take refuge under bits of debris, *paludemaris* moves much more slowly and deliberately, and hurries in short bursts of speed much like *Myodocha* and *Antillocoris.* It is much less active in taking refuge under objects. This difference in movements extends to the nymphs, which are quite different in appearance from the nymphs of *fraternus.* *P. paludemaris* nymphs are very densely pilose which gives them a grayish red color, and have a broad black band extending down the middle of the head and thorax. The pilosity may protect the nymphs from submergence at high tide.

One tachinid parasite of the genus *Catharosia* was bred from this species. No predators are known. It has not been collected at lights.

While this species feeds readily on sunflower seeds, its natural food are the seeds of *Spartina patens* (Ait.) and probably of other salt marsh plants. No seed defense or mating behavior was observed.

Life History

Just enough information is gathered to show that this species is univoltine, with an obligative diapause. The observed phenology is as in Table 56.

TABLE 56
Phenology of *Peritrechus paludemaris*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
May 25	——	——	——	——	——	100%
June 10	56%	44%	——	——	——	——
June 28	——	25%	50%	25%	——	——
July 11	——	——	25%	75%	——	——
July 26	——	——	——	——	33%	67%
Aug. 8	——	——	——	——	——	100%

Oviposition clearly begins at least by late May. All adults are in a obligative diapause which is unaffected by rearing the late instars under short (12 hours) or long (16 hour) photoperiods. I could not break the diapause with either photoperiods, with elevated temperatures (32°C.) or a cold exposure of one month. In warmth the diapausing adults live until early spring.

The available stadia based on a small sample are as in Table 57.

TABLE 57
Stadia of *Peritrechus paludemaris*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
——	——	6	7	8–9	10–11	——

Since no females were found in spring and diapause was not broken, no reproductive data is available.

TRIBE MEGALONOTINI

Megalonotus sabulicolus (Thomson)

This introduced Palearctic species has been carried in previous American literature (including Part I of this paper) under the name *M. chiragrus* (Fabricius). There has been little agreement among European workers on the status of *sabulicolus,* and Slater and Sweet (1958) following several European authors, considered *M. sabulicolus* as one of the many color forms of the variable species *M. chiragrus* (c.f. Stichel 1925).

Southwood (1963) and Roubal (1963), however, have presented evidence to show that *M. chiragrus* and *M. sabulicolus* are two distinct species not merely color varieties. The two can be distinguished by size, width of pronotum, length of antennae, paramere shape, and prevalence of brachyptery. *M. chiragrus* is larger with longer antennae and is usually brachypterous.

As Southwood (*ibid*) rightly points out, the two forms are not subspecies since their ranges greatly overlap. Subspecies cannot be sympatric without intergrading, and Southwood found no or little intergrading between *chiragrus* and *sabulicolus* in England.

The available literature (Slater, Catalogue) indicates that the two forms are sympatric over much of Europe, with records of *sabulicolus* concentrated around the Mediterreanean. Hoberlandt (1955) in discussing the distribution of *M. chiragrus* in Turkey, designated the distribution of *M. chiragrus* as Euro-siberian and *M. sabulicolus* as Holomediterranean. He indicated that *chiragrus* has a more northern distribution and is found at higher altitudes in the south Palearctic than *sabulicolus*. It is noteworthy that the type locality of *sabulicolus* is in Sweden at the northern limit of the range of *sabulicolus*.

According to Southwood (*ibid*), although there is some habitat overlap, in England the two species are ecologically distinct and *sabulicolus* is limited to sandy habitats in southern England. Since the differences are not exclusive, Southwood (*ibid*) raises the possibility these may be forms; environmental selection favoring a *sabulicolus* genotype in sandy habitats. A similar close relationship is shown among *Scolopostethus* species and Southwood reasons by analogy with Eyles's (1963, *in litt.*) breeding work on *Scolopostethus*, that these forms of *Megalonotus* are good species. Moreover, if these are ecological forms, more variability in response to ecological conditions would be expected than Southwood indicates for the English populations.

This species pattern has a close parallel in *Ischnodemus sabuleti* (Fallen) and *I. quadratus* Fieber which ecologically displace one another (character displacement) over a broad zone of overlap where *sabuleti* is restricted to wet habitats, *quadratus* to dry habitats (Slater 1960). When considered in this light, the ecological distribution of the *chiragrus* complex should prove interesting since the area of sympatry is very large and many forms are described.

The question that arises is the identity of the introduced *Megalonotus* in North America and how it relates to the *chiragrus-sabulicolus* problem. The evidence for the introduction of *Megalonotus* into eastern North America on produce is given by Slater and Sweet (1958). Scudder (1961) considered ballast to be the probable mode of introduction of *Megalonotus* on the Pacific coast of North America. Scudder (ibid) noted that most of the British Columbia material is referable to *M. chiragra sabulicola*.

Since 1958 I have found several additional populations of *Megalonotus* in Connecticut and one at Brewster, Cape Cod, Massachusetts. On the basis of the coloration of the antennae and hind tibiae by which *sabulicolus* and *chiragrus* were originally recognized, both *sabulicolus* and *chiragrus*-like patterns occur in all the New England populations. But on the basis of the other characters given by Southwood (1963) all the New England populations clearly pertain to *M. sabulicolus* not *chiragrus*. However obvious and useful, the color variability of the antennae is so great, as is shown by the multiplicity of forms (Stichel 1925), that errors can easily result.

The delimiting of the species in North America to *sabulicolus* further verifies that it was introduced into North America since *sabulicolus* is limited to the western Palearctic. The genus *Megalonotus* itself with 20 described species is concentrated in the Mediterrean region of the west Palearctic, with only *chiragrus* itself having a Palearctic distribution. Since *M. chiragrus* is the most common species in England, and *M. sabulicolus* is known there from only a few localities, it is probable that the New England population came from continental Europe as suggested by the produce records (Slater and Sweet 1958).

If *M. sabulicolus* is possibly a sandy area genotype or ecophenotype of *chiragrus* one would expect the species to occur in New England and British Columbia in different forms in sandy or nonsandy habitats. All but one of the populations found in southern New England occur in sandy or gravelly habitats. Each of these populations closely fits Southwood's description of *sabulicolus* and is completely macropterous. A population on Cape Cod near Brewster, Massachusetts occurs on a steep hillside covered with a low grass and partly shaded by pitch pines (*Pinus rigida* Mill.). The population from this quite different habitat is definitely *sabulicolus* in morphological characters although 70% of the population has the third antennal segment dark as in *chiragrus*. Three of nine Cape Cod males examined also have a cryptic form of brachyptery in which the forewing membrane almost attains the apex of the abdomen, but the hind wings are short, reaching only tergum six. According to Southwood *M. sabulicolus* is *usually* macropterous while *chiragrus* is clearly brachypterous.

It also may be significant that unlike *Stygnocoris, Megalonotus* was not found along the northern coast of New England from northern Massachusetts north to Maine despite repeated search for it among its host plant *Centaurea*. It is possible that the Holomediterranean adaptation of *sabulicolus* may limit it to southern New England.

The New England populations of *M. sabulicolus* should be kept under observation to see if it extends its range and whether the *M. chiragrus* genotype will emerge. At present, the evidence from the New England population indicates that *M. sabulicolus* is retaining its European characteristics. Its release from competition with *chiragrus* and other *Megalonotus* species is another factor but it may be offset by competition with the native rhyparochromine fauna.

Environment

Several of the habitats of *M. sabulicolus* at Noank and Canaan, Connecticut were described by Slater and Sweet (1958). Subsequently other sites were found as mentioned earlier. Except for the Cape Cod habitat described before, these new sites are sandy ruderal areas where the star thistle or bachelor's buttons (*Centaurea* spp.) grows. The association of *sabulicolus* with *Centaurea* is very close and the insects are found in the litter about the base of these plants. These all constitute disturbed habitats often roadsides and with the possible exception of the Cape Cod colony, *Megalonotus* is not found in natural habitats.

Interestingly, *Centaurea* itself is not only introduced from Europe but like *Megalonotus* also has its distributional center in the Mediterranean region (Fernald 1950).

These habitats are all hot dry sites with the ground between the plants open to direct insolation. This is especially true of the site at Canaan in the cooler northwestern highlands.

It was noted at Canaan (Slater and Sweet 1958) that the large population dropped off rapidly in numbers in late autumn. Repeated observations over six years show that this results from a decimation of the population at the advent of cold weather. Only a few adults survive the winter to start the population going the next spring. The adults overwinter in litter at the base of *Centaurea.*

The European records given in Slater and Sweet (1958) are mostly from England and Finland and probably refer to *M. chiragrus* itself. Scudder (1961) notes that what is probably *sabulicolus* is abundant on boulevards in Vancouver, British Columbia. Ashlock (*in litt.*) notes *chiragrus* as abundant in California and feeding on strawberries. The species is apparently much more abundant on the west coast than the east coast.

These hot sandy sites are all temporary habitats which exist in one place for only a few years although such a habitat may be maintained longer by repeated disturbances along a roadside or on a shifting flood plain. The Cape Cod habitat forms an exception for it appears to be a long persisting habitat.

General Biology

The largely macropterous condition of *sabulicolus* correlates with its occurrence in temporary sandy habitats. The few cryptic submacropters from Cape Cod is an interesting development and should be kept under observation as mentioned earlier. If selected for, this population may eventually become brachypterous.

The only available dispersal record is the collection of 117 specimens of *Megalonotus* in a flight trap in 1931 in Oregon.

The mottled brown and black pattern of the adults of this hairy medium sized (5 mm.) rhyparochromine blends it effectively into the sandy background of its biotope but the black nymphs are much more conspicuous. This insect has a rather flattened shape and despite its average sized legs it runs rapidly to take cover under bits of litter when disturbed.

Williams (1946) in California found *Megalonotus* along with *Emblethis* to be the prey of the astatine sphecid wasp *Diplopectron*. Several bugs were placed in a cell in the wasp nests which were built in sandy soil. No other parasites or predators are recorded for *M. sabulicolus*.

The natural food plant seeds were those of *Centaurea*. The insect is never found on the composite heads but feeds on the fallen seeds. In the laboratory it will also feed and oviposit on *Oenothera* sp. and sunflower seeds both hulled and unhulled. Much better growth is had on a sunflower-*Centaurea* seed mixture.

The insect actively drags or carries *Centaurea* and *Oenothera* seeds about by its beak to more sheltered sites for feeding. This was observed in the field as well as in the laboratory.

In the mating behavior, the male responds to a receptive female by rapidly vibrating his antennae and advancing on the female with a hesitant jerky movement. The male mounts the female, aligns himself parallel and vibrates his antennae rapidly on her head. After effecting copulation the male swings into an end to end position. Copulation lasts for at least two hours.

Life History

According to Pfaler (1936) *M. chiragrus* in Finland overwinters as an adult and has two generations a year. Similarly, the New England population of *sabulicolus* is bivoltine and has an adult diapause.

At Canaan, the few overwintered adults lay their eggs in May and early June. The phenology at Canaan is given in Table 58.

At Storrs the phenology is advanced by about three weeks so that only late instars are present in early September before the advent of cold weather. In Canaan much of the second generation especially the nymphs are apparently killed by cold weather.

The two generations overlap considerably, diapausing adults occurring in the field as early as August 10 and some first generation adults lay eggs through August. Second generation adults go directly into an intense diapause state. Of twenty cultures only four individuals in one spontaneously broke diapause after 132 days under warm laboratory conditions. A brief 30 day exposure to 6°C. did not affect the diapause state, nor did long photoperiods in December. Adult longevity in the diapause state in laboratory warmth ranged from 125 to 185 days (mean 132 days). Such adults which broke diapause oviposited only a few eggs (17–26) and the resulting nymphs could not be reared past the second instar.

No experimental work with photoperiodism was made on the diapause mechanism. The second generation diapause state occurs under warm conditions in field and laboratory. Reasoning from the condition in other bivoltine species, the diapause is probably facultative, based on photoperiod. Even when forced by early rearing the cultures did not produce second generation eggs until early July. The preoviposition period of summer adults maturing normally in July was only 5–7 days, but in a culture forced to maturity by June 16 it was 16–19 days.

TABLE 58
Phenology of *Megalonotus sabulicolus*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
May 20	——	——	——	——	——	100%
June 7	50%	30%	——	——	——	20%
June 25	——	20%	30%	40%	7%	3%
July 6	——	——	10%	15%	45%	30%
July 28	10%	10%	5%	——	15%	60%
Aug. 16	14%	14%	15%	10%	19%	28%
Sept. 13	5%	5%	10%	15%	25%	40%
Sept. 25	——	——	——	1%	19%	80%
Oct. 15	——	——	——	——	5%	95%
Nov. 1	——	——	——	——	——	100%

The stadia given in Table 59 are derived from both first and second generations on a *Centaurea*-sunflower seed mixture. While field collected nymphs can be reared on sunflower seeds, nymphs hatched from eggs in the laboratory could not be reared on sunflower seeds. The normal longevity in the laboratory ranged from 25 to 49 days.

The fecundity in the laboratory is high, in eight females ranging from 129 to 215 eggs (mean 167). The eggs are laid at an average rate of 8.1 eggs a day (range 3–11 eggs). Four sexually isolated unmated females laid from none to 27 eggs (mean 18 eggs).

The eggs of *Megalonotus* are remarkable because of their peculiar tack-like processes which attach the eggs to plant fuzz, ground litter, and sand. A cementing substance is also involved. The eggs are oviposited into available loose dry substrates. Wet substrates are avoided.

TABLE 59

Stadia of *Megalonotus sabulicolus*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
10.3	4.5	4.8	5.0	6.4	8.4	37.0
(9–11)	(3–7)	(3–8)	(4–6)	(4–10)	(5–13)	(27–45)

Sphragisticus nebulosus (Fallen)

The genus *Sphragisticus* is apparently monotypic. Ashlock (*in litt.*) tells me that *simulans* which Barber (1918c) described in *Sphragisticus* actually belongs in the tribe Gonianotini not Megalonotini and therefore cannot be a *Sphragisticus.*

Sphragisticus nebulosus has a wide North Holarctic distribution. As stated in Part I, it is not clear whether *Sphragisticus* is an introduced species or one of the few Holarctic species. If it is a Holarctic species as thought by Horvath (1909) it is the only Nearctic representative of the tribe Megalonotini. Moreover, there are no relict populations of *Sphragisticus* in Mexico or Guatemala in contrast to other Holarctic lygaeid genera and to the relict populations of *Sphragisticus* in Algeria and the Caucasus in the Palearctic.

If it is an introduced species, it is an early introduction since Say recorded the species from North America in 1831. Its far northern distribution from Lappland to Eastern Siberia (Jurinskij 1926) suggests that it could have made the transit from the Palearctic to the Nearctic. In the Nearctic it is only recorded as far north as British Columbia and Quebec, but I have seen a specimen from Fairbanks, Alaska (Univ. of Conn. Coll.). It is conceivable that *Sphragisticus* may have in late Pleistocene times spread naturally into the Nearctic which may account for the apparent lack of distinction between the Nearctic and Palearctic populations. A study of the population variability throughout the Holarctic may resolve this question.

In the Nearctic *Sphragisticus* has a distinctly northern distribution, and in the east is not recorded south of New Jersey and Missouri (Slater, Catalogue). While Hussey (1922) found it common in Michigan, Froeschner (1944) considered it scarce in Missouri and Slater (1952) had no records of it from southern Illinois.

Environment

In New England *Sphragisticus* is largely restricted to disturbed habitats such as ruderal areas and along the edges of cultivated fields. It does not penetrate into natural habitats except in naturally disturbed areas, as a sandy flood plain which is in early succession. Penth (1952) in a thorough study of Heteroptera populations in different associations at Mainz, Germany, found *Sphragisticus* similarly limited to disturbed ruderal habitats along roads and field edges.

An arable habitat with considerable bare soil and litter does not support *Sphragisticus* populations as large as slightly latter succession stages where low often prostrate pioneer forbs have invaded the area. In later plant succession stages when the ground is filled in with taller forbs which shade the ground, *Sphragisticus* drops out. The plant associations of such favorable habitats typically includes *Angropyron repens, Stellaria media* (L.), *Cerastium vulgare* (L.), *Lepidium virginicum* L., *Capsella bursa-pastoris* (L.), *Polygonum* spp., *Silene* spp., *Specularia perfoliata* (L.), *Chenopodium album* L., *Rumex crispus* L. and others.

The soil of favorable areas varies from a light loam to sand, and none were found in clayey or wet soils. The litter layer is frequently very sparse except along field margins. In such open areas with low forbs the sun shines directly on the ground creating a dry hot microenvironment.

In the most favorable habitats the abundance of the insect reaches 20–25 per square meter, but is more frequently around 5–10 per square meter. *Sphragisticus* apparently does not compete particularly well with the native rhyparochromine species such as *Ligyrocoris diffusus, Pachybrachius basalis, Zeridoneus costalis* and *Emblethis vicarius* and is nearly always the least abundant when the species occur together, except in the narrow succession stage just described.

The invasion, rise and disappearance of *Sphragisticus* was observed several times in fallow fields in Noank and Canaan, Connecticut. It was rarely found for more than two years in a fallow field, except along edges maintained by cultivation.

The literature on *Sphragisticus* is larger than usual because of its occurrence in cultivated fields, and several host plant records are given under the general biology which substantiates this habitat selection. *Sphragisticus* was found in large numbers in fields in autumn in Minnesota (Lugger 1900). It has been frequently recorded from cultivated fields (Bruner 1891, Bruner and Barber 1894, Forbes 1900, 1905, Barber 1923). Blatchley (1926) said that it is quite common in Indiana in rubbish; around sandy fields, especially where melons have been cultivated.

General Biology

Sphragisticus is entirely macropterous which correlates with the temporary nature of the arable field habitats. There are no dispersal records from New England, but Froeschner (1944) collected a specimen at lights in Missouri.

The coloration of adult *Sphragisticus* is a mottled black and light brown which blends very well into the light, often sandy soils of its preferred habitats. The nymphs like the nymphs of *Megalonotus* and most Gonianotini are shiny black and appear much more conspicuous than the adults. The insect is flattened with short legs and when disturbed it scurries rapidly to cover under bits of litter. It sometimes freezes after a brief run as does *Emblethis vicarius*.

There are as yet no known predators or parasites, except for Williams' (1946) record of it as one of the lygaeids utilized by the sphecid wasp *Diplopectron* to provision its larval cells.

This insect feeds in the laboratory on the seeds of *Oenothera* sp., *Rumex* spp., *Chenopodium album*, *Verbascum thapsus*, and a number of unidentified seeds from the ground litter. The insect feeds readily on sunflower seeds.

Several notes in the literature indicate probable host plants. Bruner (1891) in Nebraska recorded it from sugar beets, grape vines and on the white pigweed (*Chenopodium album* L.). Bruner and Barber (1894) named it the "clouded weed bug" and said it was partial to *Amaranthus*, *Chenopodium*, purslane (*Portulaca oleracea* L.) and stink-grass (*Eragrostis megastachya* (Koel.). Forbes (1905) noted that *Chenopodium album* is its favorite food plant and it damages corn. Blatchley (1934) collected it under *Amaranthus* in California. Larson and Hinman (1932) stated that it is injurious in pea fields in Oregon. Hussey (1922) collected it on ragweed (*Ambrosia* sp.) in Michigan.

In the laboratory mating occurs infrequently because the females repeatedly repulse the males. Copulation eventually does occur, but it is difficult to observe the mating behavior to completion. In 21 trials involving different males and females at different times, the female did not open her ovipositor and dislodged the male.

The male senses the female before actual contact and responds by turning his body and head toward her and holding his antennae stiffly erect at 60° angle from horizontal. When about a centimeter away the male suddenly leaps upon the female, who immediately attempts to dislodge the male. The male quickly orients himself parallel to the female and places the tips of his antennae on the female's head. The antennae which are held stiffly and slightly convergent apparently are not vibrated, but instead are moved slowly over a small radius on the female's head. During this time the pygophore is extruded, rotated 180°, and pressed against the tip of the female's abdomen. In this position the parameres move like tiny jaws against the ovipositor. When sexually excited by a female the male will leap on other males and even on the female's cast exuviae. Copulation lasts at least one and one-half hours in the usual end to end position.

Life History

Sphragisticus in Connecticut is bivoltine and the adults overwinter in a state of reproductive diapause. It was observed to overwinter as an adult (Scholtz 1847, Forbes 1905, Blatchley 1926) and lay eggs in spring (Pfaler 1936). The phenology given in Table 60 is for the seasonal cycle at Canaan, Connecticut on a hot sandy field which warms up earlier than most other sites. There is an overlap of old spring adults and new adults in late June, and in August there is an another overlap of ovipositing first generation adults with diapausing second generation adults.

TABLE 60
Phenology of *Sphragisticus nebulosus*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
May 10	—	—	—	—	—	100%
May 25	20%	—	—	—	—	80%
June 2	15%	15%	10%	—	—	60%
June 15	—	10%	15%	25%	30%	20%
July 3	—	—	—	—	5%	95%
July 31	10%	10%	5%	—	—	75%
Aug. 20	—	—	5%	15%	45%	35%
Sept. 15	—	—	—	5%	25%	70%
Oct. 3	—	—	—	—	10%	90%
Oct. 20	—	—	—	—	—	100%

Second generation adults brought in the laboratory in mid-August remain in an intense state of reproductive diapause, and did not break diapause in midwinter. Adults collected in late October and November for the most part also remained in diapause but a few spontaneously broke diapause and laid eggs in December.

Little work could be done on the diapause mechanism, but the available data fits the facultative diapause pattern found in other species in which short photoperiods bring about reproductive cessation. Since *Sphragisticus* extends to the far north it is probably univoltine under those conditions.

The available data is somewhat diverse, but suggests a pattern as in *Pachybrachius basalis*. The normal prereproductive period is about 5–9 days. One culture of new adults collected July 3 were ovipositing by July 9. In contrast several cultures reared to adults in the laboratory on June 23 did not become reproductive until mid-August. This may account for some of the late nymphs found in the field. On October 3 some very late fifth instar nymphs were collected with diapausing adults. The adults remained in diapause, but the 4 new adults reared from the nymphs began laying eggs after 17 days. The data is not sufficient for any further interpretation but indicates an interesting problem to resolve.

The stadia given in Table 61 are based on laboratory rearing of field-collected early instars on sunflower seeds. Only four to seven measurements of each of the stadia are available.

TABLE 61

Stadia of *Sphragisticus nebulosus*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
9.5 (9–10)	5.7 (5–7)	5.5 (4–7)	5.7 (4–7)	7.3 (5–9)	10.1 (9–13)	43.0 (36–53)

The laboratory longevity of the adults of the first generation is long and varies from 42 to 70 days (mean 59 days). While this is probably longer than the field longevity, it accounts for the overlapping of generations in the field.

The scant data available indicates that this species has a high reproductive potential. Two females laid 157 and 224 eggs. The eggs are laid at a rate of 6–7 a day. Six unmated females laid from none to 23 eggs (mean 18).

The eggs are smooth and elliptical in shape with only a slight ventral curvature. This shape is generally convergent toward a lygaeoid type egg (Putshkova 1956). The eggs are oviposited into the parenchyma of stems (Putshkova, *ibid*) and into litter, crevices and into tight cotton stoppers. Both wet and dry substrates are utilized although dry is preferred.

TRIBE GONIANOTINI

Emblethis vicarius Horvath

The genus *Emblethis* includes a large number of Palearctic species, but apparently only one Nearctic species, *E. vicarius*. However, the Palearctic species are rather similar in appearance. Various specimens identified as *vicarius* from different Nearctic localities were run through Wagner's (1958) key to the European *Emblethis*. These Nearctic specimens keyed out near different Palearctic species. It appears probable that *E. vicarius* is actually a species complex.

The distribution of *Emblethis* is from the highlands of Guatemala north to British Columbia and Quebec. The specimens from northeastern North America appear distinctly larger and darker. Since Horvath's type specimens (a lectotype, Slater, *in litt.*) comes from eastern North America the form discussed here is *E. vicarius*.

Environment

Emblethis may be aptly called the ''sandbug'' for it is very characteristic of, and largely restricted to open sandy habitats (Uhler 1876, Hart 1907, Torre Bueno 1910, *et al.*). Walkden and Wilbur (1944) found it frequent on overgrazed pastures in Kansas. Lugger (1900) found it in large numbers in fields with *Sphragisticus*. It has been collected along sandy beaches in Long Island (Torre Bueno 1915) and in Florida (Barber 1914b). Hendrickson (1930) recorded it from prairie associations of *Stipa spartea-Andropogon scoparius* and *Andropogon scoparius-Boutelona curtipendula* found on dry steep hill sides and bluffs. Blatchley (1934) collected it under *Amaranthus* in southern California. The Guatemala specimens were collected in the temperate zone at 7500 feet at Ostuncalco (Distant 1882).

In New England *Emblethis* is found naturally along sandy beaches above the high tide line, usually about and under thin patches of litter. In inland areas similar but artificial areas are created in gravel pits, parking lots, sandy fields and roadsides and populations of *Emblethis* are very frequent in such areas.

As a characteristic species of dry sandy areas, *Emblethis* is the best example of the ability of lygaeids to survive high temperatures. *Emblethis* is frequently found out on the hot open sand or under the very thin litter. Measurements with a thermistor confirms its resistance to heat. Probes placed next to the insect in the field regularly measure from 43° to 50° C. On the very hot sand over 50° C. the insect does not remain still for long but moves from one small bit of litter to another. These small bits are equally hot but are poor heat conductors. Frequently it stands high on its hind legs to avoid the heated ground. But on sand of 45° C. it could "freeze" for 25–30 seconds. The nymphs are apparently less resistant to heat and under intense illumination keep to shaded cover under litter or around the bases of plants such as *Andropogon* clumps. In the evenings or on cloudy days the nymphs also run about on the open sand. Despite the dryness of their habitat (1), the insects will die in 24 hours without water.

In the sandy habitat of *Emblethis* the plants which are often present are xerophytic pioneers such as *Andropogon scoparius* Michx., *Eragrostis pectinacea* (Michx.), *Hypericum perfolium* L., *Rumex acetosella* L., *Potentilla* spp., *Trifolium arvense* L., *Carex* sp. Sometimes, such as on beaches, the plant association is non-existent and the insect live in the dry litter with no green plants present.

The abundance varies greatly from one site to another. It reaches 40–50 per square meter at a few places such as a sandpit at Storrs, Connecticut. More usually it is 10–15 per square meter. While beaches form long persisting habitats, the patches of seed bearing litter do not. In inland areas, sandpits and sandy fields are certainly temporary habitats. Although later succession may proceed rather slowly because of the xeric soil conditions, early succession proceeds rapidly.

General Biology

The completely macropterous condition of this species correlates with the temporary nature of its habitat. In New England it has not been collected at lights as in Missouri (Froeschner 1944). Torre-Bueno (1910, 1915) found *Emblethis* washed up in beach wash and he deduced from the wind conditions that it had been flying over water.

Emblethis has a remarkably effective procryptic coloration. The adults are mottled brown with dark punctures and rather broad and flattened in shape. There is considerable variation in color in the same population from pale brown to dark brown. The color variation has no relation to the age of non-teneral insects. The nymphs are similarly colored, but show less variation in color. *Emblethis* infrequently conceals itself under litter and is often found quiescent on the open sand. When disturbed, like other similarly colored animals such as the piping plover (*Choradius melodus*) it moves in rapid bursts, suddenly freezes, and seems to literally vanish into the sand as the eye is carried past it.

A few predators are known. Knowlton, Maddock and Wood (1946) found 79 specimens of *Emblethis* in the stomach of the lizard *Scoloporus graciosus graciosus* (Baird and Girard) in Utah. Williams (1946) found *Emblethis* adults and nymphs among the lygaeids used by the astatine sphecid wasp *Diploplectron* to provision its nests.

Emblethis vicarius is parasitized by the catharosine tachinid *Petia* (= *Procatharosia calva* Coq.). In mixed associations of *Emblethis, Cnemodus, Pseudocnemodus* and *Pachybrachius, Catharosia* itself was found only in the myodochines, *Petia* in *Emblethis*. Ashlock informs me (*in litt.*) that he has taken *Petia* from *Emblethis* in California. This suggests that there may be a definite host specific relationship. The parasite overwinters in the host *Emblethis* and emerges in late autumn and early winter from the hosts which are kept at room temperature.

In the laboratory *Emblethis* feeds on seeds of *Andropogon scoparius, Bromus* sp., *Chenopodium album* L., *Solidago* sp., *Stellaria media* (L.), *Rumex acetosella, R. obtusifolia* L., *Lechea villosa* Ell., *Oenothera* sp., *Hieracum* sp. and other unidentifiable fallen seeds, but does not feed on *Panicum* sp. and *Paspalum* sp. Sunflower seeds are fed on but the nymphs grow slowly. More rapid growth occurred on a mixture of fallen seeds from the field. The first instar nymphs showed a strong feeding reaction to *Oenothera* and *Rumex obtusifolia*. One adult pierced the bracts and the carpels before reaching and penetrating the seed of *Rumex obtusifolia*. At the point of contact with each succeeding structure the salivary sheath cone was laid down.

There are several host association records from the economic entomology literature: In Nebraska on sugar beets (Bruner 1891), as a general weed feeder and on *Chenopodium album* L., and roots of *Eragrostris major* Host (= *E. megastachya* Koel.) (Bruner and Barber 1894, Forbes 1900). No seed defense behavior was observed.

The mating behavior is not known in detail since *E. vicarius* mates infrequently in the laboratory. An active male on contact with a receptive female vibrates his antennae rapidly. After climbing on the female he aligns himself parallel and taps his antennae rapidly on the female's head. Copulation occurs in the end to end position. In one instance it lasted 6.5 hours.

Life History

In southern New England *Emblethis vicarius* is bivoltine and overwinters as an adult. Because of its open sandy habitat *Emblethis* begins ovipositing early and the first instars are collected in early March as given in Table 62. The first and second generations overlap considerably in July.

The entire first generation apparently becomes reproductive. Second generation adults, which appear as early as July 30 do not become reproductive but remain in an intense diapause state. Thus ovipositing first generation and diapausing second generation adults are found in the field simultaneously in early August.

TABLE 62
Phenology of *Emblethis vicarius*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
Apr. 15	——	——	——	——	——	100%
May 10	30%	——	——	——	——	70%
May 22	25%	12%	8%	——	——	55%
May 29	15%	35%	35%	10%	——	5%
June 7	5%	20%	50%	15%	10%	——
June 16	——	10%	30%	35%	15%	10%
July 9	27%	15%	3%	——	35%	20%
July 30	26%	18%	23%	18%	5%	10%
Aug. 13	5%	10%	10%	20%	25%	30%
Aug. 25	——	——	5%	10%	40%	45%
Sept. 7	——	——	——	5%	20%	75%
Sept. 20	——	——	——	——	15%	85%
Oct. 15	——	——	——	——	——	100%

The diapause state is not usually broken at room temperatures. In an exceptional case, a male and a female which lived 224 and 227 days respectively in the laboratory became sexually reproductive March 15 but died a few days later. A facultative diapause under photoperiod control is probable in which long photoperiods promote reproduction, short initiate diapause. Long photoperiods and warm conditions did not affect the diapause condition in

December.

The stadia given in Table 63 are mostly derived from rearing field collected nymphs on sunflower seeds and seeds from the natural habitat. A few can be reared entirely through their life cycle on mixed field seeds and sunflower seeds, but sunflower seeds alone are successful although first instars from the field are readily reared on sunflower seeds. The growth rate is probably slower than under hot field conditions.

TABLE 63
Stadia of *Emblethis vicarius*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
9.7 (9–10)	6.2 (6–7)	6.3 (5–7)	6.2 (5–8)	8.5 (6–10)	9.5 (7–13)	46.0 (36–52)

Longevity of the non-diapause adults in the laboratory varies from 24 to 48 days (mean 31). Diapausing adults live a long time under laboratory room temperatures (134 to 233 days). However, the adults feed all winter long.

The preoviposition period of first generation adults is about 10 days. Overwintered adults brought in from the field in March became reproductive in 15–18 days.

The fecundity is high, and in six females it ranged from 150 to 218 eggs (mean, 181 eggs). Unmated and sexually isolated females laid no eggs. The eggs are laid singly at a rate of 6 to 11 per day (mean 8). Lack of a proper substrate greatly inhibits oviposition reducing it to only 15–35 eggs. Provided with sandy substrate, oviposition occurs copiously as shown in the fecundity figures just given.

The eggs are cucumber shaped and beset with fine short setules. After considerable probing and testing with both antennae and ovipositor, the eggs are oviposited into the sand or under small pebbles and bits of litter on the sand. The female employs a more horizontal placement of the eggs than in myodochines like *Ligyrocoris diffusus* and rarely releases the ovipositor to the extent of *Ligyrocoris*. Partly because of the setules but more from a cement layer, the sand and pieces of litter densely cling to the eggs effectively concealing the eggs and making them hard to count as well. The eggs are laid in dry substrates, never in moist substrates.

Trapezonotus arenarius (L.)

Trapezonotus has a Holarctic distribution with nine known species in the Palearctic, and four in the Nearctic region. One species, *arenarius,* is presumably common to both regions. In both regions the genus has a large north-south distribution, extending south to North Africa and the Middle East in the Palearctic and into Panama in the Nearctic. *T. arenarius* (L.) has an exceptionally wide-spread distribution and is the only species which reaches eastern North America. It is found in the Palearctic south to the Madeira Islands, Morocco and Turkey, north to Lappland in Europe and east to Siberia, China and Kamchatka (Slater, Catalogue). However, *T. arenarius* in the Nearctic region appears to have an entirely different southern limitation. It occurs only from British Columbia east through Manitoba to Quebec and is recorded in the United States only in the highlands of New England and northern New York. It is not recorded from the western United States and is the only species of *Trapezonotus* in Canada. The other species of *Trapezonotus* have a montane distribution in the southwestern United States, and one, *T. caliginosus* Dist., extends south from Arizona into the high mountains of Guatemala and Panama. *T. vandykei* V.D. was collected at 10,000 feet in Colorado, and represents the apparent northern limits of the Nearctic group aside from *T. arenarius.*

Blatchley (1926) believed *T. arenarius* to be an introduced species and Seidenstucker (1951) apparently agreed with the judgment. However, certain aspects of the biology and ecology of this species to be discussed suggest that *T. arenarius* is not an introduced species, and indeed rather raises the question of the supposed identity of the Nearctic and Palearctic populations. Certainly the European population is very similar to the North American, and the question revolves upon whether the North American "*arenarius*" is a vicariant species (Ross 1962) or a subspecies. In this respect, certainly populations from northeast Asia should be studied. The extremes overlap, but the New England *arenarius* appears smaller than the European *T. arenarius:* New England male, 4.36 (4.22–4.55) to European 4.5 (Seidenstucker 1951).

The European *arenarius* was described by Seidenstucker (1951) as being constantly macropterous except for very few brachypterous forms from the Alps. Yet the North American population is largely brachypterous. As Lindroth (1957) emphasized, introduced species are largely macropterous in their early stages of establishment and generally are restricted to coastal areas. In

New England and New York, *T. arenarius* is not found along the coast but only in the highlands, and is quite scarce in southern New England. Lindberg (1958) did not find *T. arenarius* in Newfoundland, but did find that the European *T. distinguendus* (Flor) had established itself along the shore.

Even species presently recognized in the *arenarius* complex (Seidenstucker 1951) have been questioned as being only ecological ''forms'' and the various differences in the claspers, etc., were considered the result of allometric growth in these forms (Southwood and Leston 1959). It is clear that this European complex requires a careful biological study before the status of American populations can be understood. Our species keys out to *T. arenarius* in Seidenstucker's key.

Along with the different distributions of the Palearctic and Nearctic populations, the habitat preferences are apparently different. In the extensive European literature *T. arenarius* is recorded from a large variety of habitats. Southwood and Leston (1959) described *arenarius* (*sensu lato*) in England as inhabiting sand dunes, heaths, light sandy soils, dry woodlands, chalk soils, but as usually absent from damp soils. Seidenstucker (1951) gave a similar habitat range for *arenarius* (*sensu stricto*) in Germany and noted a definite preference for humosere rather than heath and sandy soils, and often light woods. He considered this broad habitat range the explanation for its widespread distribution through cultivated regions. Krogerus (1932) found it to be a xerophilous species common on sandy littoral areas in Finland. The North American population is not found in sandy dune shore areas or in dry woods. Nor is there any relation to agricultural practice, in fact, quite the opposite. These differences seem to make it advisable to treat the two populations as distinct, and only briefly consider the literature on the European *T. arenarius*.

Environment

In general, *Trapezonotus* is a species of open upland habitats. It is found most abundantly in northern New England and northern New York. In southern New England it is found on several north facing drumlin slopes about Storrs, and in northwestern Connecticut on the summit balds of Canaan Mountain. Toward the north the species is found in a greater variety of habitats, from dry roadsides near Gorham, New Hampshire to the alpine meadows on Mount Washington at 5,300 feet.

The exposure of these habitats is always largely open, often on a slope. The soil is nearly always poor and gravelly, and is overdrained. These dry sites (2–3) at lower elevations support a sparse short vegetation which varies from fescue (*Festuca capillata* Lam.) dominated areas of short grasses, to old bare areas with clumps of *Andropogon scoparius* with the xeric lichens (*Cladonia*) and the mosses (*Polytricum pilifera*) in the wide interstices. On higher elevations *Trapezonotus* is found in the short (6 inches to 1 and one half foot) dense *Vaccinium pennsylvanica* scrub, especially along the bed rock outcrop areas which are dominated by scattered xerophytic oak *Quercus ilicifolia.* On Mt. Washington, New Hampshire, adults, and fourth and fifth instar nymphs are found above the three line at 5,300 feet in a *Vaccinium* patch in an alpine sedge-grass-meadow. This was, of course, much more moist (6–7) than the other habitats mentioned, and with a more uniform ground coverage. Brindley (1935) collected *arenarius* at 6,000 feet in the Alps.

The biotope proper is the thin litter layer especially at the margins of bare or nearly bare areas. It is rare in completely barren sites or in dense ground-covering vegetation, and never where the herbs are over a foot or two in height. Thus, its distribution is quite discontinuous at a given site, and the abundance is usually about 1–3 per square meter or less. At some outcrop margins in *Vaccinium* cover, it is found at 5–7 per square meter density, and at one favorable barren site at Storrs as high as 17 per square meter. In these habitats it is often found with the other seed bugs: *Xestocoris nitens, Carpilis consimilis, Kolenetrus plenus, Ligyrocoris depictus,* and *Pseudocnemodus canadensis.*

In overwintering, *Trapezonotus* moves a short distance into marginal areas of deeper vegetation where I found them hibernating in groups of two or three. The European *Trapezonotus* is recorded as hibernating in large colonies in moss (Rieber and Puton 1876, Oliver 1904).

General Biology

As already mentioned the Nearctic population of *T. arenarius* is largely brachypterous, and the samples before me are only 11% macropterous. In this population there is also a sexual difference in wing polymorphism in *T. arenarius* with the condition in the female evidently more plastic. The relationship is summarized in Table 64.

This low proportion of macropters correlates with the long lasting nature, often of a serclimax type, of the habitats of this species. Nevertheless several of the habitats especially several roadsides near Gorham, New Hampshire and at Camden Hills, Maine, are nearly ruderal in aspect and appear to be rather short lived sites. So it is apparent that the low proportion of long winged females must be adequate to colonize such an area.

One such probable colonization was observed at a site studied at Storrs, Connecticut for five years. In 1958 the species here was absent or at least very rare, for this site was searched closely and carefully for another rather uncommon rhyparochromine in the Storrs area. In 1959 several females were found in May, and during the summer the population increased rapidly to 17 per square meter in some microhabitats. In the subsequent year, 1960, it had dropped to but 1–2 per square meter and despite very careful search it could not be found in 1961 and 1962. Over this time the plant community changed hardly at all. A very similar decline affected another population about four miles away, but the density here was much lower.

TABLE 64

Brachyptery patterns in *Trapezonotus arenarius*

Sex	1	2	3	4
Male	94%	——	6%	——
Female	8%	41%	22%	29%

"1" wing attains tergum 6; "2," wing to margin of tergum 7; "3," wing to middle of tergum 7; "4," macropter.

Both the shining black late instar nymphs and the brown and black patterned adults apparently have procryptic coloration. The amount of pigmentation varies considerably, but is not related to populations or age changes. In the laboratory these short legged insects strongly prefer samples of litter from the habitat and rarely venture on white or unsheltered backgrounds. In the litter the insects are very cryptic and quickly take refuge under bits of litter and in rolled leaves. Considerable disturbance of the litter is required to alarm them into movement, which, roach fashion, is quickly to the next crevice. When the first instars are put into a dish provided with only methyl cellulose, they are extremely active and crawl continuously around. But when litter is provided they actively seek "refuge" in the litter and become very quiet. In fact when the litter is comprised of rolled *Gaylussica* or *Vaccinium* leaves, it is nearly impossible to determine their numerical presence in the field.

No parasites were reared from *Trapezonotus*. The adults and all instars are actively preyed on by the nabid *Pagasa fusca* (Stein) which is fairly abundant in the same habitats as *Trapezonotus*. When some litter was brought into the laboratory with adults of *Trapezonotus* in early April it contained the eggs of the nabid as well. The tiny first instar nabids agilely climbed on top of adult *Trapezonotus* and pierced them through the back of the head with their stylets. The *Trapezonotus* quickly succumbed and the diminutive nabid proceeded to feed. The nabids were reared up to the third instar in this fashion.

Gronblom (1946) found that in Europe, the "Grabwespe" *Astata stigma* Panz. provisioned its nest with *T. arenarius*. This sphecid is of the same subfamily, the Astatinae, as are the Nearctic wasps which prey on Lygaeidae.

In its feeding habits this species is evidently nearly omnivorous on seeds. When exposed to sunflower seeds it reacts very rapidly and feeds within a few seconds. During its feeding I have never observed the distal two labial segments to be bent or removed as in other lygaeids. The seeds are pierced very rapidly compared to other lygaeids. It feeds in the laboratory also on seeds of *Festuca* sp., *Solidago* sp., *Vaccinium pennsylvanicum*, *Gaylussica*, and *Betula* spp. It does not react, however, to *Panicum* or *Paspalum* seeds. *Trapezonotus* is reared very readily from field nymphs or from the eggs through to the adult on sunflower seeds, but in some colonies the mortality is very high in the first instar. Cobben (1953) found *Trapezonotus* feeding on the seeds of *Erodium circutarium* L'Herit.

No seed defense behavior was observed. The seeds are often dragged by the beak into litter refuges.

T. arenarius, like all other known members of the genus known to me (11 of the 14 species) except the monotypic subgenus *Gnopherus* is sexually dimorphic: the females have entirely black antennae and legs while the males have the fore legs, basal two-thirds of the mid and hind femora and the basal antennal segment orange-brown (ferrugineous). However, no functional significance of this dimorphism was observed.

Courtship as such is very brief. When placed with a female the male randomly comes in contact with her. The first response of the male is to freeze, extend his antennae, and extrude his genital capsule. When the male touches the female again with his outstretched antennae, he may suddenly leap upon her. He immediately begins tapping her head with his very rapidly vibrating antennae, and pressing his revolved genital capsule against the females ovipositor area. If the female is receptive in the next moment the male slides off and goes into the reversed copulatory position. If not receptive the female decamps. The whole process may take only four seconds. Mating lasts from two and a half to five and one quarter hours. The male for the first hour or two appears semi-paralyzed and the female literally drags him about. Later the male becomes more active and walks backwards with the female. Copulation reoccurs frequently in the laboratory, and at least six copulations were observed with one female. However, only one mating is required to fertilize a female's entire complement of eggs.

No male reacts to another male, nor did the sexually active males react to diapause females present in the field at the same time. The single very long lived female mentioned earlier also failed to elicit any response from the males which came out of diapause in October.

Life History

T. arenarius has a univoltine life cycle with an obligative adult diapause. The phenology observed at Storrs in 1960–1961 is as in Table 65.

TABLE 65
Phenology of *Trapezonotus arenarius*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
May 13	—	—	—	—	—	100%
June 7	9%	9%	18%	9%	—	55%
June 12	10%	20%	30%	10%	10%	20%
June 23	—	5%	28%	43%	21%	3%
July 1	5%	5%	10%	25%	35%	20%
July 8	—	7%	9%	22%	53%	9%
July 17	—	—	2%	8%	30%	60%
July 29	—	—	—	2%	10%	88%
Aug. 15 *on*	—	—	—	—	—	100%

In northern New England, late instars are found considerably later, and at Gorham, New Hampshire and Laconia, New Hampshire on August 12 and 15 respectively, fifth instars still compose 33% and 25% of the populations found.

The new adults are in a state of obligative diapause. They feed very little in late summer and may go without food for several weeks or water for several days.

They remain in this strong diapause condition until late autumn or winter when some colonies complete diapause, mate, lay a few eggs, and die. It appears from the data that a sudden high temperature elevation is the best explanation for the diapause break for photoperiod conditions caused no change, and all colonies of a given year either break or remain in diapause. The change correlates with the temperature records, which show that in 1957 and 1959 the rearing room became briefly overheated, exceeding 105°F. and diapause terminated shortly after this event. In the other years the temperature remained at least between 65°F. and 85°F. extremes. Leonard (*in litt.*) similarly has found that high temperature releases *Blissus* spp. from diapause in late autumn.

The stadia of nymphs reared in the laboratory are as in Table 66. This appears to parallel the field development and is perhaps somewhat slower. The last two stadia are considerably longer, which agrees with the late field occurrence of last instar nymphs. The longevity of the overwintered adults was quite long, and the generation overlap was complete, with some ovipositing females present along with new diapause adults.

TABLE 66

Stadia of *Trapezonotus arenarius*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
11.6 (10–13)	6.3 (5–8)	6.4 (5–9)	6.8 (6–9)	9.4 (8–14)	11.1 (9–15)	50.0 (46–59)

Overwintered adults live in the laboratory usually until between July 1 and July 30, but an unusual female lived 236 days after being brought into the laboratory on May 28. It ceased to oviposite about July 9, but remained alive like normal males until January 1. This represents a total longevity of a year and a half. Most interesting is the nature of the cessation in oviposition in this female. When left in warmth the adult lives either until diapause is broken or dies in midwinter. None survived past January 27. It is clear, then, from this longevity data that the southward spread of this species (or population) may be limited by a requirement for a long cold diapause period.

As stated earlier this species has a long oviposition period. Colonies collected on April 19 and 23, however, while copulation occurred at this time, did not begin ovipositing until May 4. Colonies collected on May 15 and May 21 were ovipositing and the females contained fully developed eggs. The oviposition period is long, approximately 50–55 days, but probably less in the field due to natural mortality. In perhaps inverse correlation the rate of oviposition in the laboratory is low and averages 2.8 eggs per day (2–4 a day), so that the total fecundity is 58–141 eggs (average 97), which is fairly similar to other rhyparochromines with shorter oviposition periods. For this reason the rapid population increase in 1960 is most interesting for it may imply a high survival rate in that particular population.

In those colonies which broke diapause, only 16–25 eggs (average 19) are laid, at a rate of less than 1.2 eggs a day. The nymphs of these eggs appear unusually weak and die off rapidly without developing in direct contrast to the spring colonies. Three virgin females which broke diapause in October laid in all, 17 eggs (average 5.4).

When given a choice, oviposition occurs into dry substrates, but *T. arenarius* will lay its eggs on wet cotton if no other is provided. When ovipositing this species does not prefer deep contact with the substrate, but lays its eggs singly near the margins, and lays eggs under stones, twigs, seeds, into leaf crevices, hollow stems, and into loose dry litter. The short thick eggs are beset with hairs which cling to objects and debris and further conceal the eggs.

Delochilocoris umbrosus (Dist.)

This species has had a variegated generic history, and is listed under a variety of names. It was originally described by Distant (1893) in the preoccupied genus *Dorachosa* and Bergroth (1893) substituted *Delochilocoris* for *Dorachosa.* Horvath (1908) however, made *Delochilocoris* a synonym of *Aphanus* Lap. Most of the records are listed under this name. Uhler, unfortunately, mistook this species for *Microtoma carbonaria* Rossi (Barber 1918b). According to Britton (1938), the 1920 record of *Rhyparochromus plenus* from Connecticut refers to this species. It was found that *Rhyparochromus* should replace *Aphanus* (China 1943), Ashlock (1960) resurrected *Delochilocoris* and returned *umbrosus* to it, but it has recently been discerned that *umbrosus* must be placed in a new genus distinct from the type species, *illuminatus* Dist. (Slater, Ashlock, and Sweet *in prep.*). Thus the literature references are confusing.

Both of these species belong to the series of gonionotine genera endemic to the Nearctic. "*D.*" *umbrosus* has a wide distribution and is recorded from southern New England and Ontario, west to Colorado and California, and south through Florida and Mexico to Guatemala and Panama, the latter three being the type localities. In Central America it was collected by Champion in the temperate highlands at 8,000 feet in the Quiché Mts. at Ostuncalco, Guatemala, and between 4,000–6,000 feet on the Volcán de Chiriqui in Panama (Distant 1893). It is interesting that while *illuminatus* attains only the extreme warm temperature tier of southern states, it is also not recorded south of Guatemala.

Blatchley (1926) states that while *umbrosus* is frequently found in southern Indiana, it was not found in the northern counties. Both Barber (1923) and Froeschner (1944) commented on the general scarcity of this species. I have found it only in southern New England and also to be one of the more infrequent species. For this reason the following discussion is relatively limited.

Environment

Its relative scarcity is apparently not due to a restriction to an uncommon habitat for *umbrosus* is found in a diversity of habitats. Nevertheless these habitats are generally characterized as fully exposed open subclimax areas, which are not particularly old sites. The ground level biotope is usually dry and moisture level ranges from 2–4, and litter layer is rather sparse. Both adults and nymphs are found in the following habitats: temporary new fields dominated by pioneer weedy plants; on a sandy flood plain in *Oenothera* and *Verbascum thapsus* L. litter; in dry pastures on mullein leaves (*Verbascum thapsus*) and at the edges of rock outcrops; and in mullein leaves and grass (*Agropyron repens* (L.) at a sandy ruderal site. One ovipositing female was collected at 1,800 feet on exposed rock ledges on Canaan Mountain. In all these sites the species occurs in low abundances of 1–2 per square meter, at most. At one site in Mansfield Center, Connecticut on July 12, 1957, it was found in the greatest abundance (6–7 per square meter) and in all nymphal stages. This was a flood wash area at the base of a sandy scree from a sand pit. The gravelly ground supported a low ruderal vegetation, and was thinly covered with light dry flood debris. Also present on the ground in this habitat were the lygaeids *Emblethis vicarius, Ligyrocoris diffusus, Peritrechus fraternus,* and a few *Megalonotus sabulicolus.* At each of the above sites, *umbrosus* was associated with different lygaeid species, which reflects the ecological diversity of the habitat selection of *Delochilocoris.*

The various habitat notes in the literature agree with the observed findings and *appear* to be in open areas. Blatchley (1926) collected it in spring and summer in Indiana by sweeping low herbage, more commonly in sandy localities. He found it hibernating beneath logs, chunks and leaves of mullein (1895). Vestal (1913) collected it in Illinois under a board at the edge of a field. Forbes (1905) found it in corn fields apparently on husks and hibernating under bark. Froeschner (1944) found it ''hibernating in grass clumps, or under rocks, logs or mullein leaves.'' Walkden and Wilbur (1944) collected the species in native hay habitats of brome grass and blue grass in Kansas. Gillette and Baker (1895) collected it under stones in Colorado and Rainwater (1941) recovered it from Spanish moss in Louisiana and South Carolina.

Nearly all of the *D. umbrosus* habitats are apparently of recent origin and temporary nature. At not one site, even the most favorable one, was the species found in a subsequent year. In two weedy field sites which were carefully collected earlier, the occurrence of the species apparently represented a new migration into the site. The ''native hay'' habitats in Kansas (Walkden and Wilbur 1944). however, would be a climax prairie association rather than a new subclimax.

General Biology

Such utilization of newer subclimax communities makes understandable the completely macropterous condition of this species. Several references may refer to its ability to disperse. Glick (1939) collected it 200 feet in the air in Louisiana. Caudell (1902) found it on mountain snow in Colorado. It has not been collected at lights.

When disturbed in the field, this black, rapid-moving insect runs but a short distance and takes cover in the nearest crevice. This protective behavior is reflected in the flattened shape of the insect. Perhaps the black coloration may enhance the shadow effect in such crevices. At any rate, it is frequently found in light background habitats and both the adults and the equally black nymphs are very conspicuous when disturbed, and the contrast would be apparent to both color blind and color perceiving predators. No parasites or predators are yet known. However Billings and Glen (1911) found it infected with a *Sporotrichum* fungus.

In the laboratory it fed readily on sunflower seeds and could be completely reared from egg to adult. It also feeds on seeds of the mullein, *Verbascum thapsus*, grasses, *Agropyron repens, Panicum* sp., and a number of unidentified composite seeds collected in wash litter.

No seed defense behavior was elicited, perhaps because in the laboratory only small populations were available. Seeds are, however, moved to more protective sites.

Mating behavior was observed only in the male courtship behavior. The male or female consistently decamps before copulation is completed. In contrast to other species the female apparently does not show an avoidance reaction, and it is the male which usually decamps. Since the available material is rather old by middle June, it may have been too late for normal copulation. Four similar trials were made, and the following sequence was observed repeatedly. At any point the male may decamp. The sequence is always repeated.

If the sexes come close to each other during random movements, the male may perceive the female without actually touching her and extend his antennae toward her. Or, the male may directly touch the female by accident. The female may become passive or more often turn and face the male, and touch antennae. The male frequently decamps or becomes passive at this point. If not, the male becomes sexually stimulated and vibrates his antennae rapidly with the distal three segments held horizontal and at right angles to the scape. The male moves upon the female with slight shaking movements reminescent of *Ligyrocoris* and protrudes and revolves the pygophore. The response of the female is to become very passive, but as the male climbs upon the female from the side, she may place her hind leg across the male's head. Once on the female the male's antennae are held parallel and tapped on the female's head. The pygophore, with the claspers working, is moved back and forth in the area of the ovipositor. In no case did the female release the ovipositor and allow copulation. Frequently the females were observed to touch antennae and quiver them briefly, and become quiet.

Life History

D. umbrosus overwinters as an adult (Blatchley 1895, 1926, Froeschner 1944). It has not been definitely ascertained whether there are two generations or a very long single generation. The data pattern resembles *Peritrechus fraternus,* and it is very probable that two generations are involved. The observed phenology at Storrs is as in Table 67.

In the laboratory, the overwintered adults live until late June and early July, and July 2 is the latest date of oviposition. It seems that very few adults can survive that long in the field. Along with this, the late occurrence of early instars in mid-July, and fifth instars on September 8 strongly suggests that two generations are involved, especially as oviposition occurs in May and fifth instars are found as early as June 17.

If so, the pattern is very similar to *Peritrechus* for in the laboratory cultures, the new adults, which are not obtained until late

July, are in reproductive diapause. Also, adults reared from nymphs collected on July 14 in the field were in diapause. If so the diapause may be similarly governed by a photoperiod stimulus.

The diapause is a strong one, and is not broken by cold exposures. The diapausing adults survive as late as mid-winter and die without coming out of diapause. The average longevity of such diapausing adults was 148 days, the range (73–184 days).

The stadia in days are as given in Table 68. A few first instars lived 27 days and then died, despite feeding.

TABLE 67
Phenology of *Delochilocoris umbrosus*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
May 31	——	——	——	——	——	100%
June 17	——	——	33%	——	33%	34%
July 10	——	——	——	——	50%	50%
July 14	6%	18%	12%	18%	18%	28%
Aug. 4	——	——	10%	15%	25%	50%
Sept. 8	——	——	——	——	37%	63%
Oct. 2	——	——	——	——	——	100%

TABLE 68
Stadia of *Delochilocoris umbrosus*

Egg	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Total
9.6 (9–10)	9.2 (8–10)	8.5 (7–10)	6.3 (6–7)	8.0 (6–10)	10.4 (7–14)	54.3 (46–62)

Oviposition of fertile eggs occurs from May 9 to June 2. The average fecundity is 123 eggs (93–152 eggs). The eggs are laid at a rate of 3.5 eggs a day, but one female over a week laid eggs at 5.9 a day. Oviposition ceases when seeds are removed. Sexually isolated females do not lay any eggs.

Oviposition is always on a dry site, and into some sort of loose substrate. Loose dry soil is preferred over methyl cellulose, and there is a strong tendency to lay the eggs under objects like twigs, pebbles and seeds. Even into methyl cellulose and litter the eggs are oviposited in a relatively horizontal plane rather than vertically as in *Ligyrocoris.* The short eggs are beset with small spines and cling to litter, obscuring the eggs. In this respect it is interesting that after oviposition, the female usually moves the ovipositor back and forth which further covers the eggs with minute bits of litter.

Malezonotus fuscosus Barber

The Nearctic genus *Malezonotus* is predominantly western in distribution, with five of the seven species restricted to the area west of the Great Basin—none are as yet known from the Rocky Mountain ranges. Although Ashlock (1958) mentioned only one species, *M. angustatus,* as being found outside a mountainous area, the remaining two are low-land species. *M. rufipes* has a wide distribution from southeastern Arizona through the southern United States to Virginia. *M. fuscosus,* itself, has the most restricted distribution and was known only from New Jersey, and Long Island (Ashlock 1958, *in litt.*).

Malezonotus fuscosus is here recorded for the first time from Connecticut. This apparently represents the first collection of the species since Barber (1918c) collected the type series in 1916 in Lakehurst, New Jersey. A few were collected earlier: Barber (1914a) states that the records of *Malezonotus fuscosus* (as *rufipes*) listed in *The Insects of New Jersey* (Smith 1910) are based on two specimens which he collected at Lakehurst. The sole other specimen was collected in 1915 at Fire Island Beach on Long Island, New York by Torre-Bueno (Barber 1918c).

M. fuscosus was collected in east central Connecticut at a single station near Mansfield Center, in an area which is largely dominated by an outlier pine barren community. This New Jersey-Long Island-southeastern New England distribution is similar to many plant species which are endemic to the coastal pine barren formation (Nichols 1913a, Transeau 1913, Fernald 1925, 1933, Conard 1935 and Braun 1955).

Environment

This single station is a south-exposed slope of a small hill, the top of which is covered with a stand of *Pinus rigida.* The overdrained dry soil of this slope for the most part supports an *Andropogon* community except along an especially dry margin between the andropogonetum and a fescue field. This marginal ridge area supports a very sparse plant cover of small thin grasses *Festuca capillata* L. and *Eragrostis pilosa* (L.) (?), lichens (*Cladonia*), and a number of small low forbs, *Sericocarpus asteroides* (L.), *Hier-*

acium scabrum Michx., *Solidago odora* Ait., *Potentilla canadensis* L., *Antennaria capillatum*, and some *Rubrus villosus* L. This small rim-like area, but 10 × 40 meters in extent, is the habitat of *M. fuscosus.* Very few specimens could be found outside this area in the marginal *Andropogon* association.

While the habitat appears to be a moderately old one from the presence of a heavy growth of lichens, it may be in part maintained from *Andropogon* ecesis because the late summer mowing of the fescue field also covers this barren spot. This mowing, however, hardly affects the sparse low vegetation of the site. The poor soil and litter is very dry (2) and the sun-exposed ground temperatures reach at least 135° F. The soil, while sandy, is rather dark which may represent charcoal from an old burn. The abundance of *Malezonotus* is low and varies from 0.1 per square meter in spring to 2–4 per square meter in mid-summer. The population is highly discontinuous and consists of small groups scattered here and there in the area. It is the only rhyparochromine in this dry area despite a rich myodochine fauna in neighboring biotopes. Both of Barber's collections (1914a, 1918c) of *Malezonotus* at Lakehurst, New Jersey were under huckleberry (*Gaylussacia buccata* L.) but none could be found under nearby *Gaylussacia* cover at the Connecticut station. The collection under huckleberry may indicate at least an open site on the pine barrens.

Other species of *Malezonotus* apparently occur in open habitats also: *M. rufipes* (Stål) (as *sodalicus* (Uhl.)) was collected in numbers, hibernating under *Andropogon* (Froeschner 1944); and *M. sodalicus* has been noted as common in strawberry fields in British Columbia (Parshley 1919); and *M. angustatus* was collected under dried cattle droppings in a pasture (Downes 1924).

General Biology

M. fuscosus appears to be most closely related to *M. rufipes* (Ashlock 1958) so it is interesting that nearly all *fuscosus* specimens are brachypterous and *rufipes* is entirely macropterous. All reared specimens are brachypterous. The only known macropter of *fuscosus* is the specimen collected in beach wash up on Long Island by Torre-Bueno. Presumably this may indicate dispersal over or near the ocean. As the site described earlier is essentially a temporary one, although apparently a long persisting stage, this low production of macropters must be sufficient to maintain this rare species. However, its rareness may stem in part from a low vagility coupled with a particular habitat selection.

When disturbed, *M. fuscosus* is an extremely rapid moving insect especially in relation to its small body and medium length legs.

Like *Trapezonotus* it hides closely under small chips, etc., and will not move until directly disturbed. Its dark fuscous color blends in well with the soil of its biotope. The late instars are shining black. This insect is very nervous and active in its normal movements, and constantly vibrates its antennae. Ashlock noted (1958) that *M. angustatus* was difficult to observe because of its great activity.

Malezonotus fuscosus feeds readily on a variety of small seeds: *Antennaria capillata, Carex* sp., *Sericocarpus asteroides, Hieracium* sp., *Eragrostris* sp., *Festuca capillata* L., *Solidago odora* Ait., *Potentilla canadensis* L., *Rumex acetosella* L., *Panicum* sp., *Aquilegia canadensis* (L.), and sunflower seeds. The insects oviposit readily on the seed diet and could be reared very readily from field-collected second instars. However very slow development occurred in nymphs hatched in the laboratory and only a few attained the third instar. I could not promote growth with different seeds, nor with green material from the habitat. Ashlock (1958, *in litt.*) records a similar difficulty in attempting to rear *Malezonotus angustatus* V.D.

The seeds are often dragged by the beak to more protected sites for feeding. No seed defense behavior was observed which may be related to the low laboratory culture abundances.

As in *Trapezonotus*, the sexes are dimorphic in coloration, the males having distinctly orange fore femora, the female dark legs. The significance is not evident in the observed mating behavior. The male does not respond until after he comes in contact with the female. The sexual response of the male is to vibrate his antennae very rapidly, holding with the terminal three segments horizontal and at right angles to the body and the scape. Next the male advances on the female with slow somewhat jerky movements. If the female remains passive the male climbs upon her and proceeds to vibrate his antennae close to her head and places the revolved genital capsule over the apex of the ovipositor. This is similar to the actions of *Delochilocoris* but the movements are much more nervous and hesitant. Mating is frequently repeated.

Ashlock (1958) reports mating frequent in *M. angustatus* and that they mate in an obtuse angle. *M. fuscosus* may or may not rest in an obtuse angle. When the pair is moving the male is clearly directly behind the female.

Life History

M. fuscosus has a bivoltine life cycle with a facultative but strong diapause, and overwinters as an adult.

The *available* phenology is as in Table 69. Barber's collections were both in early spring, March and April, and the insects presumably were in hibernation.

The adults collected in June actively oviposit as do the first generation adults in August. However, the second generation uniformly enters into a diapause which I could not break with a cold exposure. The diapause is not related to feeding as the fall adults feed readily and become quite fat, so that the abdominal conjunctiva are exposed. Dissection, however, showed immature ovaries. A most interesting aspect of the diapause is that there is very little mortality in warmth and the adults, although in reproductive diapause, are active all winter in the laboratory, and a number live until early summer. Diapause was broken in an aliquot in the spring by placing the insects in a long photoperiod (15 hours) room. While a relation between diapause and photoperiodicity is suggested by the evidence, further experimental work is needed. Diapause was not broken until after 47 days of long day illumination.

TABLE 69
Phenology of *Malezonotus fuscosus*

Date	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
June 10	——	——	——	——	——	100%
July 9	——	——	——	20%	60%	20%
Aug. 11	——	5%	10%	20%	40%	25%
Sept. 20	——	——	——	——	——	100%

Only the egg development period of 15 days is available. The very long stadia of laboratory-hatched nymphs are abnormal and not included. Some remained as first instars for as long as 28 days. The field evidence indicates a total development period of approximately 40 days.

The longevity of two adults which overwintered in warmth was remarkably long; female 323 days; male, 453 days. The overwintered adults, however, from the field die in late June and early July.

The fecundities are 58, 68, and 102 eggs which are laid at a rate of 3–4 per day. Deprivation of seed food causes oviposition to cease. One virgin female laid no eggs.

The eggs are laid in the laboratory in seed heads of *Antennaria* and *Solidago,* in grass culms, in heavy plant pilosity and in other litter crevices. It lays eggs sparingly in methyl cellulose, and preferred plant debris crevices and fuzz.

Literature Cited

Adam, C. C. 1915. An ecological study of prairie and forest invertebrates. Bull. nat. Hist. Surv. 11: 31–280.

Aitkins, A. E. 1936. The "Spruce Cone Bug" *Gastrodes abietis* Linn. (Hemiptera: Heteroptera: Lygaeidae). Ent. mon. Mag. 72: 139–49.

Allee, W. C., A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. 1949. Principles of Animal Ecology. W. B. Saunders & Co., Philadelphia.

Andre, E. 1874. Description de fourmis d'Europe pour servir a l'etude des etude de myrmecophiles. Rev. Mag. Zool. (3): II: 152–335.

Andre, F. 1934. Notes on the biology of *Oncopeltus fasciatus* (Dallas). Iowa St. Coll. J. Sci. 9: 73–87.

Andrewartha, H. G. 1952. Diapause in relation to ecology. Biol. Rev. 27: 50–107.

————. 1961. Introduction to the study of animal populations. U. of Chicago Press, Chicago.

Andrewartha, H. G. and L .C. Birch. 1954. The distribution and abundance of animals. U. of Chicago Press, Chicago.

Ashlock, P. D. 1957. An investigation of the taxonomic value of the phallus in the Lygaeidae (Hemiptera-Heteroptera). Ann. ent. Soc. Amer. 50: 407–426.

————. 1958. A revision of the genus *Malezonotus* (Hemiptera: Heteroptera). Ann. ent. Soc. Amer. 51: 199–208.

————. 1960. New synonymies and generic changes in the Lygaeidae (Hemiptera-Heteroptera). Proc. biol. Soc. Wash. 73: 235–238.

Ashlock, P. D. and J. D. Lattin. 1963. Stridulatory mechanisms in the Lygaeidae with a new American genus of Orsillinae (Hemiptera: Heteroptera). Ann. ent. Soc. Amer. 56: 695–701.

Azam, J. 1893. Premiere liste des Hemipteres des Basses-Alpes. Digne. Chaspoul, Constans et ve Barbaroux Place de l'Eveche.

Bailey, N. S. 1951. The Tingoidae of New England and their biology. Ent. amer. 31: 1–140.

Balduf, W. V. 1939. Food habits of *Phymata pennsylvanica americana* Melin (Phymatidae, Hemiptera). Ann. ent. Soc. Amer. 34: 204–214.

————. 1943. New food records of entomophagous insects. Ent. News 54: 12–15.

Banks, N. 1910. Catalogue of the Nearctic Hemiptera-Heteroptera. Amer. Ent. Soc. Philadelphia. P. C. Stockhaussen, Philadelphia.

Baptist, B. A. 1941. The morphology and physiology of the salivary glands of Hemiptera-Heteroptera. Quart. J. micro. Sci. 82: 91–139.

Barber, H. G. 1911. Descriptions of some new Hemiptera-Heteroptera. J. N.Y. ent. Soc. 19: 23–31.

————. 1914a. New Hemiptera-Heteroptera with comments upon the distribution of certain known species. J. N.Y. ent. Soc. 22: 164–171.

————. 1914b. Insects of Florida. II. Hemiptera. Bull. Amer. Mus. nat. Hist. 33: 495–535.

————. 1917. Synoptic keys to the Lygaeidae (Hemiptera) of the U.S. Pt. 1. Psyche, Camb., Mass. 24: 129–135.

————. 1918a. Synoptic keys to the keys to the Lygaeidae of the United States. Pt. II. Psyche, Camb., Mass. 25: 71–88.

————. 1918b. Concerning Lygaeidae.—No. 1. J. N.Y. ent. Soc. 26: 44–46.

————. 1918c. Concerning Lygaeidae.—No. 2. J. N.Y. ent. Soc. 26: 49–66.

————. 1918d. The genus *Plinthisus* Latr. (Lygaeidae, Hemiptera) in the United States. Proc. ent. Soc. Wash. 20: 108–111.

————. 1918e. Corrections to ‘‘New York Scolopostethi’’ (Family Lygaeidae: Heter.). Ent. News 29: 51–52.

————. 1921. Revision of the genus *Ligyrocoris* Stål (Hemiptera, Lygaeidae). J. N.Y. ent. Soc. 29: 100–114.

————. 1922. Collecting Hemiptera in the Adirondacks. J. N.Y. ent. Soc. 30: 110–111.

————. 1923. Family Lygaeidae (*in* Britton, W. E.). Guide to the insects of Connecticut. Part. IV. The Hemiptera or sucking insects of Connecticut. Connecticut State Geol. and Nat. Hist. Surv., Bull. No. 34: 708–737.

————. 1928a. Revision of the genus *Ptochiomera* Say (Hemiptera, Lygaeidae). J. N.Y. ent. Soc. 36: 175–177.

————. 1928b. Some quantitative results in collecting Hemiptera. Ent. News 39: 193–194.

————. 1928c. The genus *Eremocoris* in the Eastern United States, with a description of a new species and a new variety (Hemiptera-Lygaeidae). Proc. ent. Soc. Wash. 30: 59–60.

————. 1928d. *In* Leonard: a list of the insects of New York Mem. Cornell agric. Exp. Sta. 101: 1–1121.

————. 1939. Insects of Porto Rico and the Virgin Islands-Hemiptera-Heteroptera (excepting Miridae and Corixidae). Sci. Surv. P. Rico. *14:* 263–441.

————. 1947. The family Lygaeidae (Hemiptera-Heteroptera) of the island of Cuba and the Isle of Pines. Mem. Soc. cubana, Hist. nat. 19: 55–75.

————. 1948a. Lygaeidae collected in western Texas, with a new *Lygaeospilus* from California. Ohio J. Sci. 48: 66–68.

————. 1948b. New records for *Stygnocoris rusticus* Fallen. Bull. Brooklyn ent. Soc. 43: 31.

————. 1952. The genus *Antillocoris* Kirk. in the United States (Hemiptera-Lygaeidae). Bull. Brooklyn ent. Soc. 47: 85–87.

————. 1953a. A second revision of the genus *Ptochiomera* Say and its allies (Hemiptera, Lygaeidae). Proc. ent. Soc. Wash. 55: 19–27.

————. 1953b. The genus *Pachybrachius* in the United States with the description of two new species (Hemiptera: Lygaeidae). J. N.Y. ent. Soc. 60: 211–220.

————. 1954. A report on the Hemiptera-Heteroptera from the Bimini Islands, Bahamas, British West Indies. Amer. Mus. Novit. No. 1682: 1–18.

Barnes, B. M. and R. D. Barnes. 1954. The ecology of the spiders of maritime drift lines. Ecology 35: 25–35.

Beck, S. D., C. A. Edwards, and J. T. Medler. 1958. Feeding and nutrition of the milkweed bug *Oncopeltus fasciatus* (Dallas). Ann. ent. Soc. Amer. 51: 283–288.

Becker, M. A. (Ed.). 1886. Hernstein in Niederosterreich, sein Gutsgebiet und das Land in weiteren Umkreise. III. Fauna des Gebietes. pp. 465–711. Alfred Holder Wein. (original not seen)

Beer, C., G. Feige, A. Frank H. Haupt, G. Jauner, F. Kuhlhorn, F. Maass, G. Muller, and O. Rapp. 1935. Beitrage zur Fauna Thuringens 1. Hemiptera, Halbflugler. Heteroptera, Wanzen, und Homoptera, Cicaden. *In* Die Natur der Mitteldentschen Landschaft Thuringen, pp. 1–56. Otto Rapp, Erfust. (original not seen)

Berg, C. 1879. Hemiptera Argentina Eumeravit Speciesque Novas. Pauli E. Coni. Bonariae.

————. 1884. Addenda et emendanda ad Hemiptera Argentina. An. Soc. Cient. Argentina 16: 97-118, 166–176. (original not seen)

Bergroth, E. 1893. Notes synonymies sur quelques Lygaeidae (Hemiptera). Ann. Soc. ent. Fr. 62: 225.

Billings, F. H. and P. A. Glenn. 1911. Results of the artificial use of the white-fungus disease in Kansas. Bull. U.S. Bur. Ent. 107: 1–58.

Birch, L. C. 1957. The meanings of competition. Amer. Nat. 91: 5–18.

Blair, W. F. 1955. Size difference as a possible isolation mechanism in *Microhyla.* Amer. Nat. 89: 297–300.

Blatchley, W. S. 1895. Notes on the winter insect fauna of Vigo County—II. Psyche, Camb., Mass. 7: 267–270.

————. 1926. Heteroptera or true bugs of eastern North America, with especial reference to the faunas of Indiana and Florida. Nature Publish. Co., Indianapolis.

————. 1934. Notes on a collection of Heteroptera taken in winter in the vicinity of Los Angeles, California. Trans. Amer. ent. Soc. 60: 1–16.

Blizzard, A. W. 1931. Plant sociology and vegetational change on High Hill, Long Island, New York. Ecology 12: 208–231.

Bonnemaison, L. 1945. Arrtets de developpement et diapause. Ann. Epiphyt. 11: 19–56.

Braun, E. L. 1935. The vegetation of Pine Mountain, Kentucky: an analysis of the influences of soils and slope exposures as determined by geographical structure. Amer. Midl. Nat. 16: 517–565.

————. 1950. Deciduous forests of eastern North America. Blakiston Co., Philadelphia.

————. 1955. The phytogeography of unglaciated eastern United States and its interpretation. Bot. Rev. 21: 297–375.

Brimley, C. S. 1938. The insects of North Carolina. N. Car. Dept. Agr. Div. Ent., Raleigh .

————. 1944. Supplement to insects of North Carolina. N. Car. Dept. Agr. Div. Ent., Raleigh.

Brindley, M. D. 1935. Notes on the vertical distribution of some Heteroptera in the Austrian Alps. Ent. mon. Mag. 71: 260–261.

Brinkhurst, R. O. 1958. Alary polymorphism in the Gerroidea (Hemiptera-Heteroptera). J. anim. Ecol. 28: 211–230.

————. 1959. Alary polymorphism in Gerroidea (Hemiptera-Heteroptera). Nature, Lond. 182: 1461–1462.

Britton, W. E. 1938. Additions to the checklist of the insects of

Connecticut. Bull. Conn. geol. nat. Hist. Surv. No. 60: 1–169.

Bromley, S. W. 1935. Forest types of southern New England. Ecol. Monogr. 5: 61–89.

Brower, J. VZ. 1958. Experimental studies of mimicry in some North American butterflies. I. *Danaus plexippus* and *Limenitis archippus archippus*. Evolution 12: 32–47.

Brower, L. P. 1958. Bird predation and food plant specificity in closely related procryptic insects. Amer. Nat. 92: 183–187.

Brower, L. P., J. VZ. Brower and P. W. Westcott. 1960. Experimental studies of mimicry. 5. The reactions of toads (*Bufo terrestris*) to bumblebees (*Bombus americanorum*) and their robberfly mimics (*Mallophora bomboides*) with a discussion of aggressive mimicry. Amer. Nat. 94: 343–356.

Brown, J. M. 1925. Hemiptera from North-east Yorkshire. Naturalist 1925: 113–116.

Brown, W. A. 1934. A contribution to the insect fauna of Timagami. Can. Ent. 66: 220–231.

Brown, W. L., Jr. and E. O. Wilson. 1956. Character displacement. Syst. Zool. 5: 46–64.

Bruner, L. 1891. Notes on beet insects. Insect life 3: 229–230.

Bruner, L. and H. G. Barber. 1894. Experiments with infectious diseases for combating the chinch bug. Bull. Neb. agric. Exp. Sta. 6: No. 34: 143–161.

Bryson, H. R. 1939. Insect Pest Surv. Bull. U.S. 19: 153.

Burges, A. 1960. Time and size as factors in ecology. J. Anim. Ecol. 29: 1–14.

Butler, E. A. 1923. A biology of the British Heteroptera. H. F. C. Witherby, London.

Campos, F. 1925. Neuva Contribucion al estudio de los Rincotos Heteropteros del Ecuador. Nos. 19–20: 43–67. Rev. Col. Rocafuerte.

Carayon, J. 1952. Le mecanismes de transmission hereditaire des Endosymbiontes chez les Insectes. Tijdschr. Ent. 95: 111–142.

————. 1961. La viviparite chez les Heteropteres. XI. Intern. Kongr. Ent. 1: 711–714.

Carthy, J. O. 1958. An introduction to the behavior of invertebrates. George Allen & Unwin, London.

Caswell, G. H. 1960. Observations on an abnormal form of *Callosobruchus maculatus* (F.). Bull. Ent. Res. 50: 671–680.

Caudell, A. W. 1902. Some insects from the summit of Pikes Peak, found on snow. Proc. ent. Soc. Wash. 5: 74–82.

China, W. E. 1930. The origin of the British heteropterous fauna. Soc. biogeog. 3: 77–90.

————. 1943. The generic names of the British Hemiptera-Heteroptera, with a check list of the British species. Spec. Publ. R. ent. Soc. Lond.

Chapman, L. N., J. K. Michel, K. R. Parker, G. E. Miller and E. G. Kelly. 1926. Studies in the ecology of sand dune insects. Ecology 7: 416–426.

Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. Publ. Carneg. Instn. No. 242.

————. 1936. Nature and structure of the climax. J. ecol. 24: 252–284.

Cloudsley-Thompson, J. L. 1956. Studies in diurnal rhythms. VI. Bioclimatic observations in Tunisia and their significance in relation to the physiology of the fauna, especially wood lice, centipedes, scorpions and beetles. Ann. Mag. nat. Hist. 9(12): 305–329.

————. 1962. Microclimates and the distribution of terrestrial anthropods. Ann. Rev. Ent. 7: 199–222.

Cmoluchowa, Alicja. 1960. Observations on Hemiptera-Heteroptera of the botanical garden of the Maria Curie-Skodowska University Lublin. Ann. Univ. Marie-Curie-Skodowski (C) 15: 161–175.

Cobben, R. H. 1948. Wantsen in hun milieu. Maandbl. Overd. Nathist. 37: 75–82.

————. 1953. Bemerken zur Lebenweise Einiger Hollandischen Wanzen (Hemiptera-Heteroptera). Tijdschr. Ent. 96: 169–198.

Conard, H. S. 1935. The plant associations of central Long Island. Amer. Midl. Nat. 16: 433–516.

Cooper, A. W. 1961. Relationships between plant life-forms and microclimate. Ecol. Monogr. 31: 31–59.

Corby, G. H. 1947. *Aphanus* (Hem., Lygaeidae) in stored groundnut. Bull. ent. Res. 37: 609–617.

Cott, H. B. 1940. Adaptive coloration in animals. Oxford University Press, New York.

Coulianos, C.-C. 1961. Microclimatic effects upon the behavior of *Nithecus jacobeae* (Schill.) (Hem. Het. Lygaeidae). Opusc. Ent. 26: 41–52.

Criddle, N. 1922. The entomological record, 1921. Rept. ent. Soc. Ont. 52: 57–70.

Crombie, A. C. 1947. Interspecific competition. J. Anim. Ecol. 16: 44–73.

Dansereau, P. 1957. Biogeography. Ronald Press, New York.

Darlington, P. J. 1943. Carabidae of mountains and islands: data on the evolution of isolated faunas and on the atrophy of wings. Ecol. Monogr. 13: 37–61.

————. 1957. Zoogeography: the geographical distribution of animals. John Wiley & Sons, New York.

Darwin, C. 1859. The origin of the species. (Modern Library Reprint. Random House, New York.)

————. 1871. The descent of man and selection in relation to sex. Random House, New York.

Daubenmire, R. F. 1938. Merriam's life zones of North America. Quart. Rev. Biol. 13: 327–332.

Dethier, V. 1947. Chemical attractants and repellants. Blakiston Co., Philadelphia.

————. 1954. Evolution of feeding preferences in phytophagous insects. Evolution 8: 33–54.

Dice, C. R. 1943. The biotic provinces of North America. Univ. Michigan Press, Ann Arbor.

Distant, W. L. 1882. Insecta Rhynchota Hemiptera-Heteroptera. Vol. 1. Lygaeidae. Biol. cent.-amer. 173–220.

————. 1893. Hemiptera-Heteroptera. I. Suppl. Biol. cent.-amer.: 378–462.

Dobsik, B. 1950. Prispevek k Podanai Plostic CSR Contribution a la Connaisauce des Heteropteres De CSR IV. Ent. Listy 13: 36–40.

Donisthrope, J. K. 1927. The guests of British ants, their habits and life histories. George Routledge and Sons, London.

Douglas, J. W. and J. Scott. 1865. The British Hemiptera. Vol. 1. Hemiptera-Heteroptera. Ray Society. Robert Hardwicke, London.

Dowdy, W. W. 1947. An ecological study of the Arthropoda of an oak-hickory forest with reference to stratification. Ecology 28: 418–439.

————. 1955. An ecological study of Arthropoda with reference to hibernation. Ann. ent. Soc. Amer. 48: 76–83.

Downes, W. 1924. New records of Hemiptera from British Columbia. Proc. ent. Soc. Brit. Col. 1924: 27–33.

————. 1927. A preliminary list of the Heteroptera and Homoptera of British Columbia. Proc. ent. Soc. Brit. Col. 1927: 1–22.

Drake, C. J. 1922. Heteroptera in the vicinity of Cranberry

Lake. Tech. Publ. N.Y. St. Coll. For. No. 16. Vol. 14: 54–86.

Drake, C. J. and N. T. Davis. 1959. A new subfamily, genus, and species of Lygaeidae (Hemiptera-Heteroptera) from Australia. J. Wash. Acad. Sci. 49: 19–26.

Dubois, M. 1888 (1889?). Catalogue des Hemipteres de la Somme. Mem. Soc. linn. Nord. 7: 97–178. (not seen in original)

Duda, L. 1885. Beitrage zur Kenntniss der Hemipteren-Fauna Bohmens. Wien ent. Ztg 4: 33–38, 67–70, 99–100, 169–172, 209–212, 237–240, 257–266, 293–294. Lygaeids: 140, 169–172, 209–212. (not seen in original)

Elton, C. 1927. Animal ecology. Macmillan Co., New York.

————. 1946. Competition and the structure of ecological communities. J. Anim. Ecol. 15: 54–68.

————. 1958. The ecology of invasions by animals and plants. Methuen & Co., London.

Elton, C. and R. S. Miller. 1954. The ecological survey of animal communities: with a practical system of classifying habitats by structural characters. J. Ecol. 42: 460–496.

Evans, H. E. 1958. Ethological studies on digger wasps of the genus *Astata* (Hymenoptera: Sphecidae). J. N.Y. ent. Soc. 65: 159–185.

Eyles, A. C. 1963a. Some notes on natural enemies of Lygaeidae. Ent. mon. Mag. 99: 226–227.

————. 1963b. Life histories of some Rhyparochrominae (Heteroptera: Lygaeidae). Trans. Soc. Brit. Ent. 15: 135–166.

————. 1963c. Descriptions of the immature stages of five Rhyparochrominae (Heteroptera: Lygaeidae). Trans. Soc. Brit. Ent. 15: (In Press)

————. 1964d. Feeding habits of some Rhyparochrominae (Heteroptera: Lygaeidae) with particular reference to the value of natural foods. Trans. R. ent. Soc. Lond. 114: (In Press).

Feige, C. and F. Kuhlhorn. 1938. Die Wanzen (Hemiptera-Heteroptera) von Eisleben und Umgegend. Z. Naturw. 92: 100–122.

Feir, D. and S. D. Beck. 1963. Feeding behavior of the large milkweed bug *Oncopeltus fasciatus*. Ann. ent. Soc. Amer. 56: 224–229.

Fernald, M. L. 1925. Persistence of plants in unglaciated areas of boreal America. Mem. Gray. Herb. No. 2.

————. 1933. Recent discoveries in the Newfoundland flora. Rhodora 35: 1–16.

————. 1950. Gray's manual of botany. American Book Co., New York.

Ferrari, P. M. 1874. Hemiptera agri Ligustici. Ann. Mus. Stor. nat. Genova (Ser. 1) 6: 116–208. (not seen in original)

Fewkes, D. W. 1961. Diel vertical movements in some grassland Nabidae (Heteroptera). Ent. mon. Mag. 97: 128–130.

Flor, G. 1860. Die Rhynchoten Livlands in Systematischer Folge beschrieben. Arch. Naturk. Liv.-, Ebst- u. Kurl. (2) III: 1–825. (not seen in original)

Forbes, S. A. 1900. 21st report of the state entomologist on the noxious and beneficial insects of the state of Illinois. Hack & Anderson, Chicago.

————. 1904. The more important insect injuries to Indian corn. Bull. Ill. agric. Exp. Sta. 95: 331–339.

————. 1905. 23rd report of the state entomologist on the noxious and beneficial insects of the state of Illinois. R. R. Donnelley & sons, Chicago.

Forbes, W. T. M. 1923. Lepidoptera of New York and neighboring states. Part I. Mem. Cornell Agric. Exp. Sta. No. 68: 1–729.

Forster, H. 1955. (Part in 1956). Die Wanzen der Umgebung von Aselage im Kreise Meppen. Beitr. Naturk. Niedersachs. 8: 19–23, 50–54, 120–121; 9: 28–38. Sonderdruck aus Beitrage zur Naturkunde Niedersachsens 8: 19–23, 50–54, 120–121; 9: 28–38.

Fracker, S. B. 1915. The classification of Lepidopterous larvae. Univ. Ill. Biol. Monogr. 2: 1–169.

Fraenkel, G. S. 1959. The raison d'etre of secondary plant substances. Science 129: 1466–1470.

Fraenkel, G. S. and D. L. Gunn. 1940. The orientation of animals. Clarendon Press, Oxford.

Franz, H. 1943. Die Landtierwelt der Mittleren Hohen Tauern. Einbeitrag zur tiergeographischen und Soziologischen erarschung der Alpen. Denkschr. Akad. Wiss. Wien 167: 1–552.

Froeschner, R. C. 1944. Contributions to a synopsis of the Hemiptera of Missouri. Pt. III. Am. Midl. Nat. 31: 638–683.

Gaines, J. C. 1933. Trap collections of insects in cotton in 1932. Bull. Brooklyn ent. Soc. 28: 47–54.

Gause, G. F. 1934. The struggle for existence. Williams & Wilkens, Baltimore.

Geiger, R. 1950. The climate near the ground. (Transl. by Milroy N. Stewart *et al.* of "Das Klima der Bodennahen Luftschicht"). Harvard Univ. Press, Cambridge, Mass.

Gibson, A. 1917. The Entomological Record. 47th Annual Report. Rep. ent. Soc. Ont. No. 36: 137–171.

Gillette, C. P. and C. F. Baker. 1895. A preliminary list of the Hemiptera of Colorado. Bull. Colo. agric. Exp. Sta. 31: Tech. Ser. No. 1: 1–137.

Glasgow, H. 1914. The gastric caeca and the caecal bacterial of the Heteroptera. Biol. Bull. Wood's Hole 26: 101–139.

Glen, R. 1954. Factors that affect insect abundance. J. Econ. Ent. 47: 398–405.

Glick, P. A. 1939. The distribution of insects, spiders, and mites in the air. Tech. Bull. U.S. Dep. Agric. No. 673: 1–150.

Glick, P. A. and L. W. Noble. 1961. Air borne movement of the pink bollworm and other arthropods. Tech. Bull. U.S. Dep. Agric. No. 1255: 1–20.

Glover, T. 1876. Manuscript notes from my journal or illustrations of insects native and foreign. Order Hemiptera, suborder Heteroptera, or Plant Bugs. Washington.

Good, R. 1953. The geography of the flowering plants. Longmans, Green & Co., New York.

Gredler, V. M. 1870. Rhynchota Tirolensia I: Hemiptera Heteroptera (Wanzen). Abh. zool.-bot. Ges. Wien. (original not seen)

Grinnell, J. 1917. Field tests of theories concerning distribution control. Amer. Nat. 51: 115–128.

————. 1924. Geography and evolution. Ecology 5: 225–229.

————. 1928. Presence and abundance of animals. Univ. California Chron. 30: 429–450.

Gronblom, T. 1946. *In*-Monatsversammlung 8. III. 1946. Ann. Ent. Fenn. 12: 33–34.

Gulde, J. 1919. Die Larven-Stadien der Asopiden. Dtsch. ent. Z. 1919: 45–55.

————. 1921. Die Wanzen (Hemiptera Heteroptera) der Umgebung von Frankfurt a M. un des mainzer Beckens. Frankfurt. Abh. senckenb. naturf. Ges. 37: 329–503.

————. 1937. Die Wanzen Mitteleuropas. Hemiptera Heteroptera Mitteleuropas. V. Teil 2: 105–222.

Halbert, J. N. 1935. A list of the Irish Hemiptera (Heteroptera and Cicadina). Proc. R. Irish Acad. 42 (B): 211–318.

Hanson, H. C. 1962. Dictionary of ecology. Philosophical Library, New York.

Hardin, G. 1960. The competitive exclusion principle. Science 131: 1292–1297.

Hart, C. A. 1907. On the biology of the sand areas of Illinois. Pt. III. Zoological studies in the sand regions of the Illinois and Mississippi River Valleys. Bull. Ill. Lab. nat. Hist. 7: 195–272.

Hedicke, H. 1942. Heteroptera (Insekten). *In* P. Brohmer, P. Ehrman, G. Ulmer, *et. al.* Tierwelt Mitteluer. 4: 3: 1: Section X: 15–113.

Heidemann, O. 1903. Remarks on *Ligyrocoris constrictus* Say and descriptions of *Perigenes fallax,* a new species. Proc. ent. Soc. Wash. 5: 155–157.

————. 1908. (Note on *Stygnocoris* in North America). Proc. ent. Soc. Washington 10: 14.

Hendrickson, G. O. 1930. Studies on the insect fauna of Iowa prairies. Iowa St. Coll. J. Sci. 4: 49–179.

Hesse, R., W. C. Allee and K. P. Schmidt. 1951. Ecological animal geography. John Wiley & Sons, New York.

Hinman, F. G., and A. O. Larson. 1935. Insects collected in flight traps in the Willamette Valley Oregon, 1931, 1932. Ent. News 46: 147–153.

Hoberlandt, L. 1955. Results of the zoological scientific expedition of the national museum in Praha to Turkey. 18. Hemiptera IV Terrestrial Hemiptera-Heteroptera of Turkey. Acta Ent. Mus. Nat. Pragae 1955. Suppl. #3: 1–264.

Horvath, G. 1883. Revision du genre *Eremocoris* Fieb. Rev. Ent. Caen. 2: 1–12.

————. 1893. Les *Scolopostethus americanus.* Rev. Ent. Caen. 12: 238–241.

————. 1901. Hempitera. Zool. Ergebn. drit. asiat. Forshr. Grafen Engen Zichy. 2: 245–274.

————. 1908 (1909). Les relations enter les faunes Hemipterologique de l'Europe et de l'Amerique du Nord. Ann. hist.-nat. Mus. hung. 6: 1–14.

Hubbell, T. H. 1961. Endemism and speciation in relation to Pleistocene changes in Florida on the southeastern coastal plain. Proc. XI Int. Cong. Ent. Wein 1960: 1: 466–469.

Huheey, J. E. 1961. Studies in warning coloration and mimicry. III. Evolution of Mullerian mimicry. Evolution 15: 567–568.

Hungerford, H. B. 1920. The biology and ecology of aquatic and semi-aquatic Hemiptera. Kans. Univ. Sci. Bull. 11: 1–256.

Hussey, R. F. 1922. Hemiptera from Berrien County, Michigan. Occ. Pap. Mus. Zool. Univ. Mich. No. 118: 1–39.

————. 1952. Food plants and new records for some Hemiptera in Florida. Florida Ent. 35: 117–118.

————. 1954. Concerning the Floridian species of *Fulvius* (Hemiptera, Miridae). Florida Ent. 37: 19–22.

Hutchinson, G. E. 1951. Copepodology for the ornithologist. Ecology 32: 571–577.

————. 1953. The concept of pattern in ecology. Proc. Acad. nat. Sci. Philad. 105: 1–12.

————. 1957. "Concluding remarks." Cold Springs Harbor Symposia on Quantitative Biology 22: 415–427.

Hutchinson, G. E. and E. S. Deevey, Jr. 1949. Ecological studies on animal populations. *In* Survey of Biological Progress. Vol. 1: 325–359, Academic Press, New York.

Isely, F. B. 1938. Survival value of acridian protective coloration. Ecology 19: 370–389.

Jensen-Haarup, A. C. 1912. Dansmarks Fauna: Taeger (Hemiptera: Heteroptera). G. E. C. Gads, Forlag-Kobenhavn.

Johansson, A. S. 1958a. Hormonal regulation of reproduction in the milkweed bug, *Oncopeltus fasciatus* (Dallas). Nature, Lond. 181: 198–199.

————. 1958b. Relation of nutrition to endocrine-reproductive functions in the milkweed bug *Oncopeltus fasciatus* (Dallas) (Hemiptera: Lygaeidae). Nytt Mag. Zool. 7: 1–132.

Johnson, C. G. 1960a. A basis for a general system of insect migration and dispersal by flight. Nature, Lond. 186: 348–350.

————. 1960b. The present position in the study of insect dispersal and migration. Rep. Seventh Commonw. Ent. Conf. 1960: 140–145.

————. 1962. A functional approach to insect migration and dispersal and its bearing on future study. Proc. XI Int. Congr. Ent. Wein, 1960. 3: 50–53.

Johnson, C. W. 1930. A list of the insect fauna of Nantucket, Massachusetts. Publ. Nantucket Maria Mitchell Assoc. 3: 1–714.

Jordan, K. H. C. 1937. Zur Biologie von *Eremocoris abietis* einer myrmecophilen Heteroptera. Stettin. ent. Ztg 98: 23–33.

————. 1940. Die Heteropteren fauna der Oberlausitz und Ostsachsens. Isis Budissina 14: 96–156.

Jurinskij, T. 1926. Contributions a la fauna des Hemipteres de la Siberie orientale. Rev. russe Ent. 19: 229–231.

Kendeigh, S. C. 1954. History and evaluation of various concepts of plant and animal communities in North America. Ecology 35: 152–171.

————. 1961. Animal ecology. Prentice-Hall, Englewood Cliffs, N.J.

Kennedy, C. H. 1927. The metabolic gradient of the group or the ecological factors in zoogeographical distribution. Bull. ecol. Soc. Amer. 8: 7.

Kennedy, J. S. 1961. A turning point in the study of insect migration. Nature, Lond. 189: 785–791.

King, K. H. C. 1933. Some ants and mymecophilous insects from Toronto. Canad. Ent. 24: 100–103.

Kirby, W. 1837. The insects *in* Richardson's Fauna Doreali-Americana, Vol. IV. Joseph Fletcher, Norwich. (original not seen)

Kiritshenko, N. A. 1918. Hemiptera-Heteroptera Faunae Caucasicae Pars. 1. Mem. Mus. Caucase (A) 6: 1–177. (original not seen).

Kisimoto, R. 1956. Effect of crowding during the larval period on the determination of the wing form of an adult plant hopper. Nature, Lond. 178: 641–642.

Klopfer, P. H. 1962. Behavioral aspects of ecology. Prentice-Hall, New York.

Klopfer, P. H. and R. A. McArthur. 1961. On the causes of tropical species diversity, niche overlap. Amer. Nat. 95: 223–226.

Knowlton, G. F. 1944. Observations on the feeding of some predacious Hemiptera. Proc. Utah Acad. Sci. 21: 57–59.

————. 1960. An unusual flight of Hemiptera in southern Utah. Proc. Utah Acad. Sci. 37: 53–54.

Knowlton, G. F., D. R. Maddock and S. L. Wood. 1946. Insect food of the sage brush swift. J. econ. Ent. 39: 382–383.

Knowlton, G. F. and W. P. Nye. 1946. Some insect food of the sage sparrow. J. Kans. ent. Soc. 19: 139.

Koeppe, C. E. and G. C. De Long. 1958. Weather and climate. McGraw Hill, New York.

Koerber, T. W. 1963. *Leptoglossus occidentalis* (Hemiptera, Coreidae), newly discovered pest of coniferous seed. Ann. ent. Soc. Amer. 56: 229–234.

Kohn, A. J. and G. H. Orians. 1962. Ecological data in the classification of closely related species. Syst. Zool. 11: 119–127.

Koppany, T. and E. S. Wolcsanky. 1956. Biozonologische Untersuchungen im Insektenbestand der Wieden-und Wiesentypen des Hortobagy. Acta zool. Acad. Sci. Hung. 2: 359–378.

Krogerus, R. 1932. Uber die Okologie und Verbreitung der Arthropoden der Triebsandgebiete an den Kusten Finnlands. Acta zool. fenn. 2: 1–308.

————. 1960. Okologische studien uber mordische Moor Arthropoden. Comment. biol. Helsigf. 21: 1–238.

Kullenberg, B. 1946. Studien über die Biologie der Capsiden. Zool. Bidrag, Uppsala 23: 1–522.

Lack, D. 1944. Ecological aspects of species-formation in passerine birds. Ibis 86: 260–286.

————. 1946. Competition for food by birds of prey. J. Anim. Ecol. 15: 123–129.

————. 1947. Darwin's finches. Cambridge Univ. Press, Cambridge, England.

Lambertie, M. 1906. Note sur divers Hemipteres nouveaux ou rares pour la Gironde. P. V. Soc. linn. Bordeaux 61: xvii–xx. (original not seen)

Larson, A. O. and F. G. Hinman. 1932a. A list of insects collected in moss and lichens on oak trees near Corvallis, Oregon. Proc. ent. Soc. Wash. 34: 43–44.

————. 1932b. Insects found on pea fields in the Willamette Valley, Oregon, after harvest. J. econ. Ent. 25: 971–976.

Lees, A. D. 1955. The physiology of diapause in arthropods. Cambridge University Press, Cambridge.

LeQuesne, W. J. 1951. Notes on some Lygaeidae (Hem.) in the Oxford District. Ent. mon. Mag. 87: 287.

————. 1956. An examination of the British species of *Drymus* Fieber (Hem., Lygaeidae) with a new subgenus and an addition and a generic reassignment in the British List. Ent. mon. Mag. 92: 337–341.

Leston, D. 1953 The eggs of Tingitidae (Hem.) especially *Acalypta parvula* (Fallen). Ent. mon. Mag. 89: 132–134.

Leston, D. 1961. Observations on the mirid (Hem.) hosts of Braconidae. Ent. Mon. Mag. 98: 65–71.

Leston, D. and T. R. E. Southwood. 1961. New country records of Hemiptera-Heteroptera. Ent. mon. Mag. 97: 32–33.

Lethierry, L. 1869. Catalogue des Hemipteres du departement du Nord. Mem. Soc. Sci. Lille (3) VI: 307–374.

Lindberg, H. 1941. Die Hemipteren der Azorischen Inseln. Comment. biol. Helsigf. 8: 1–32.

————. 1953. Hemiptera Insularum Canariensium (Systematic, Okologie und Verbreitung der Kanarischen Heteropteren und Cicadinen. Comment. biol. Helsigf. 14: 1–304.

————. 1958. Hemiptera Heteroptera from Newfoundland, collected by the Swedish-Finnish expedition of 1949 and 1951. Acta zool. fenn. 96: 1–25.

————. 1960. Hemiptera from the Azores and Madeira. Bol. Mus. munic. Funchel 13: 85–94.

Linder, F. J. and J. M. Anderson. 1955. Structure and histochemistry of the maxillary glands in the milkweed bug *Oncopeltus fasciatus* (Hemiptera). Anat. Rec. 122: 489.

Lindroth, C. H. 1949. Die Fennoskandischen Carabidae, Eine tiergeographische Studie, Pt. 3. Medd. Goteborgs mus. zool. 122: 1–911.

————. 1957. The faunal connections between Europe and North America. John Wiley & Sons, New York.

Linsdale, J. M., and L. P. Tevis, Jr. 1951. The dusky-footed wood rat. A record of observations made on the Hastings Natural History Reservation. U. Calif. Press; Berkeley and Los Angeles.

Lugger, O. 1900. Hemiptera or bugs destructive in Minnesota. *In* 6th Ann. Rept. of the Entomologist of the State Experiment Station of U. of Minn. to the Gov. for the year 1900. Bull. Minn. agric. Exp. Sta. 69: 1–259.

MacArthur, R. H. 1957. On the relative abundance of bird species. Proc. nat. Acad. Sci. 43: 293–295.

MacGill, E. J. 1947. The anatomy of the head and mouth-parts of *Dysdercus intermerius* Dist. Proc. zool. Soc. Lond. 117: 115–128.

Marchal, G. 1898. Premieres notes sur les Hemipteres de Saone-et-Loire. Bull. Soc. Hist. nat. Autun 11: 557–606. (original not seen)

Masaki, S. 1961. Geographic variation of diapause in insects. Bull. Fac. Agric. Hirosaki Univ. No. 7: 66–98.

Massee, A. M. 1954. The Hemiptera-Heteroptera of Kent. Trans. Soc. Brit. Ent. 11: 245–280.

————. 1956. Hemiptera-Heteroptera associated with fruits and hops. J. Soc. Brit. Ent. 5: 179–186.

————. 1960. The Hemiptera-Heteroptera, plant bugs in the parish of East Malling, Kent. Trans. Kent Field Club 1960: 83–106.

Maxwell-Lefroy, H. 1909. Indian insect life. Thacker, Spink & Co., London.

Mayr, E. 1942. Systematics and the origin of species. Columbia Univ. Press, New York.

McAtee, W. L. 1927. Notes on "Heteroptera or true bugs of eastern North America." Bull. Brooklyn ent. Soc. 22: 267–281.

Merriam, C. H., V. Bailey, E. W. Nelson and E. A. Preble. 1910. Zone map of North America. Biol. Surv. U.S. Dept. Agric., Washington.

Miall, L. C. 1895. The natural history of aquatic insects. MacMillan & Co., London.

Michalk, O. 1935a. Zur Morphologie und Ablage der Eier bei den Heteropteran sowie uber ein System der Eiablagetypen. Dtsch. ent. Z. 1935: 148–175.

————. 1935b. Neue Beobachtungen uber Wanzenfliegen und das eindringen der Fliegenlarven in den Wirt (Dipt. Tachin.). Mark. Tierwelt 1: 129–140.

————. 1938a. Neue entoparasiten der Palearktischen Heteropteran. Arb. Phys. Angew. Ent. Berl. 5: 255–260.

————. 1938b. Heteropteren der Leipzig. S. B. naturf. Ges. Lpz. 63–64: 15–188. (original not seen)

————. 1940. Weiter Heteropteren-Schmartozer. Ent. Z. 54: 162–168. (original not seen)

Miles, P. W. 1959. The salivary secretions of a plant-sucking bug, *Oncopeltus fasciatus* (Dall.) (Heteroptera: Lygaeidae)-I. The types of secretion and their roles during feeding. J. Ins. Physiol. 3: 243–255.

Miller, N. C. E. 1956. The biology of the Heteroptera. Leonard Hills, London.

Miyamoto, S. 1955. *Mizaldus lewisi* Distant attacking beetles. Pulex, No. 6: 27.

Monguillon, E. 1932. Catalogue des Hemipteres du department de la Sarthe, principalement des environs du Mans. Soc. Arts Mans 15: 217–254.

Monroe, E. 1956. Canada as an environment for insect life. Canad. Ent. 88: 372–476.

Montandon, A. F. 1893. Lygaeidae exotiques notes et descriptions d'especes nouvelles. Ann. Soc. ent. Belg. 37: 399–406.

Monteith, J. L. 1960. Micrometerology in relation to plant and animal life. Proc. Linn. Soc. Lond. 171: 71–82.

Moore, G. A. 1944. A list of Hemiptera taken at Hudson Heights, Quebec. Canad. Ent. 76: 40–44.

————. 1950. Check-list of Hemiptera of the province of Quebec. Contr. Inst. Biol. U. Montreal. No. 26: 1–49.

Morley, C. 1905. The Hemiptera of Suffolk. Plymouth.

Morris, R. F. 1961. Sampling insect populations. Ann. Rev. Ent. 5: 243–264.

Muesebeck, G. F. W. and H. K. Townes. 1952. Hymenoptera of America north of Mexico. Synoptic Catalog. U.S.D.A. Agric. Monog. No. 2.

Muller, G. 1919. Beitrage zur Rhynchoten fauna Thuringens. Ent. Mitt. 8: 142–149. (original not seen)

————. 1931. Hemiptera-Heteroptera des Harzes. Dtsch. ent. Z. 1931: 65–112.

Murray, J. 1935. Dumfriesshire Hemiptera-Heteroptera in 1934. Ent. mon. Mag. 71: 164.

————. 1936. Dumfriesshire Hemiptera-Heteroptera. Ent. mon. Mag. 72: 96.

Murphy, P. W. 1953. The biology of forest soils with special reference to the mesofauna or meiofauna. J. Soil Sci. 4: 155–193.

Musaki, S. 1961. Geographical variation of diapause in insects. Bull. Fac. Agric. Hirosaki Univ. No. 7: 66–98.

Myers, J. G. 1926. Heteroptera in ocean drift. Psyche, Camb., Mass. 33: 110–115.

Myers, J. G. and G. Salt with an appendix by N. Banks and H. G. Barber. 1926. The phenomenon of myrmecoidy, with new examples from Cuba. Trans. ent. Soc. Lond. 2: 427–436.

Nageli, W. 1933. *Gastrodes.* Mitt. schweiz. ZentAnst. forstl. Versuchsw. 18: 193–280. (original not seen)

Neiswander, R. B. 1944. Insect pests of strawberries in Ohio. Bull. Ohio agr. Exp. Sta. 651: 1–37.

Nichols, G. E. 1913a. The vegetation of Connecticut. I. Phytogeographical aspects. Torreya 13: 89–112.

————. 1913b. The vegetation of Connecticut. II. Virgin forests. Torreya 13: 199–220.

————. 1914. The vegetation of Connecticut. III. Plant societies on uplands. Torreya 14: 167–194.

Nicholson, G. 1935. Bugs, with special reference to the Epping forest forms. Essex Nat. 21: 169–185.

Nuortava, P. 1958. Die Rolle der Speichelsekrete in Wechselverhaltnis zwischen Tier und Nahrungspflanze bei Homoptera und Heteropteren. Ent. exp. and appl. 1: 41–49.

Oliver, E. 1904. Faune de l'Allier: Hemipteres. Moulins: 31–62. (original not seen)

Osborn, H. 1900. Remarks on the hemipterous fauna of Ohio with a preliminary record of species. *In* 8th Annual Report. Rep. Ohio Acad. Sci. 1900: 60–74.

Osborne, H. and C. J. Drake. 1922. An ecological study of the Hemiptera of the Cranberry Lake Region, N.Y. Tech. Publ. N.Y. St. Coll. For. No. 16 Vol. 14: 54–86.

Park, T. 1964. Experimental studies of interspecific competition. II. Temperature humidity, and competition in two species of *Tribolium*. Physiol. Zool. 27: 177–238.

Parker, F. D. 1962. On the subfamily Astatinae, with a systematic study of the genus *Astata* of America north of Mexico (Hymenoptera: Sphecidae). Ann. ent. Soc. Amer. 55: 643–659.

Parshley, H. M. 1914. List of the Hemiptera-Heteroptera of Maine. Psyche, Camb., Mass. 21: 139–149.

————. 1917a. Insects in ocean drift. I. Hemiptera Heteroptera. Canad. Ent. 49: 45–48.

————. 1917b. Fauna of New England. 14. List of the Hemiptera-Heteroptera. Occ. Pap. Boston Soc. nat. Hist. 7: 1–125.

————. 1918. New England Hemiptera-Heteroptera. New records. Canad. Ent. 51: 70–72.

————. 1919. On some Hemiptera from western Canada. Occ. Pap. Mus. Zool. Univ. Mich. No. 71: 1–35.

————. 1920a. Hemiptera from Peaks Island, Maine, collected by Mr. G. A. Moore. Canad. Ent. 52: 80–87.

————. 1920b. Ethological remarks on some New England water-striders (Hemiptera). Bull. Brooklyn ent. Soc. 15: 67–70.

————. 1921. A report on some Hemiptera from British Columbia. Proc. ent. Soc. British Columbia (Syst. Ser.), 18: 13–24.

————. 1922. New England Hemiptera-Heteroptera. New records. II. Canad. Ent. 53: 233–239.

————. 1923. Records of Nova Scotian Hemiptera-Heteroptera. Proc. Acadian ent. Soc. 1922: 102–108.

Parsons, M. C. 1958. Cephalic glands in *Gelastocoris* (Hemiptera). Psyche, Camb., Mass. 65: 99–107.

Penth, M. 1952. Zur Oekologie der Heteropteren des Mainzer Sandes. Zool. Jb. Syst. 81: 91–121.

Peterson. A. 1955. A manual of entomological techniques and methods. Edwards Brothers, Ann Arbor, Michigan. Eighth edition.

Pfaler, E. V. 1936. Lebenzyklen der Lygaeiden (Hemiptera). Notul. ent., Helsingf. 16: 65–85.

Pfaler-Collander, E. V. 1941. Vergleichend-Karyologische untersuchungen an Lygaeiden. Acta zool. fenn. 30: 1–119.

Phillips, J. H. H. 1951. An annotated list of Hemiptera inhabiting sour cherry orchards in the Niagara Peninsula, Ontario. Canad. Ent. 83: 194–205.

Piasecka, J. 1960. Hemiptera-Heteroptera found on the meadows of Janow Lubelski situated in the close vicinity of forests. Ann. Univ. Marie Curie-Sklodowski (C) 15: 89–109.

Picco, L. 1908. Contributo allo studio della fauna entomologica Italiana elenco sistematica degli. emitteri finora raccolti nella provincia di Roma. Boll. Soc. ent. ital. 40: 10–105. (original not seen)

Poisson, R. 1924. Contributions a l'etude des Hemipteres aquatigues. Bull. biol. 58: 49–305.

Procter, W. 1938. Biological survey of the Mount Desert Region. Pt. VI. The insect fauna. Wistar Instit. Anat. Biology, Philadelphia.

————. 1946. Biological survey of the Mount Desert Region. Part VII. The insect fauna. Wistar Inst. Anat. Biology, Philadelphia.

Prohaska, K. 1923. Beitrag zur Kenntnis der Hemipteren Korntens. Klagenfurt: 32–101.

Provancher, A. L. 1886. Petite faune Entomologique du Canada et particulierement de la Province de Quebec. Cinquieme order, les Hemipteres. Vol. 3: 1–205.

Puton, A. 1876. Notes pour servir a l'etude des Hemipteres. Ann. Soc. ent. Fr. 6: 275–290.

————. 1894. Hemipteres nouveaux et notes diverses. Rev. Ent., Caen. 13: 114–116.

————. 1896. Hemipteres nouveaux. Rev. Ent., Caen. 15: 232–234.

Putshkov, V. G. 1956. Basic trophic groups of phytophagous, hemipterous insects and changes in the character of their feeding during the process of development. Zool. Zh. 35: 32–44.

————. 1958. Larvae of Hemiptera-Heteroptera. I. Lygaeidae. Rev. russe Ent. 37: 392–413.

Putshkov, V. G. and L. V. Putshkova. 1956. A key to the eggs and larvae of Hemiptera-Heteroptera injurious to crops. Trud. vseross. Ent. Obshch. 45: 218–342.

Putshkova, L. V. 1956. The eggs of Hemiptera-Heteroptera. II. Lygaeidae. Rev. russe Ent. 35: 262–284.

Rainwater, C. F. 1941. Insects and spiders found in Spanish moss, gin trash and woods trash and on wild cotton. Insect Pest Surv. Bull. U.S. E-528: 1–20.

Ramade, F. 1960. Contribution a l'etude des Rhynchotes Heteropteres terrestres de Provence. Ann. Soc. ent. Fr. 129: 201– .

Ramos, J. A. 1946. The insects of Mona Island (West Indies). J. Dep. Agric. P. R. 3C: 1–74.

Rasche, H. H. 1958. Temperature differences in Harvard forest and their significance. Harv. For. Pap. 1: 1–153.

Raup, A. M. 1937. Recent changes of climate and vegetation in southern New England and adjacent New York. J. Arnold Arbor. 18: 79–117.

Readio, P. A. 1927. Studies on the biology of the Reduviidae of America north of Mexico. Univ. Kans. Sci. Bull. 17: 1–291.

————. 1931. Dormancy in *Reduvius personatus* (L.). Ann. ent. Soc. Amer. 24: 19–39.

Reclaire, A. 1932. Nuamlijst der in Nederland en het omliggend gebied waargenomen watsen (Hemiptera-Heteroptera). Tijd. schr. Ent. 75: 59–258.

Reibur, F., and A. Puton. 1876. Catalogue des Hemipteres-Heteropteres de L'Alsace et de la Lorraine. Bull. Soc. Hist. nat. Autun 16: 51–88. (original not seen)

Remold, H. 1962. Uber die biologische bedeutung der Duftdrüsen bei den Landwanzen (Geocorisae). Z. vergl. Physiol. 45: 636–649.

Reuter, O. M. 1874. Remarques synonymiques sur quelques Heteropteres. Ann. Soc. ent. Fr. 4: 559–566.

————. 1875. Remarques sur le polymorphisme des Hemipteres. Ann. Soc. ent. Fr. 5: 225–236.

————. 1880a. Nya bidrag tilt abo och Alands Skargards Hemiptera-fauna. Medd. Soc. Fauna Fl. fenn. 5: 158–236.

————. 1880b. Fran Dalaro: September (1880) entomologisk Skizz. Ent. Tidskr. 1: 201–208.

————. 1881. Analecta Hemipterologica zur Artenntniss Synonymie und geographischen Verbreitung der Palearctischen Heteropteren. Berl. ent. Z. 25: 155–196.

————. 1909. Charakteristik und Entwickelungsgeschichte der Hemipterenfauna (Heteroptera, Auchenorrhynchia und Psyllidae) der Palaearktischen Coniferen. Acta. Soc. Sci. fenn. 36: 129 pp.

Reuter, O. M. 1910. Neue Beiträge zur Phylogenie und Systematik der Miriden nebst einleitenden Bemerkungen über die Phylogenie den Heteropteren-familien. Acta Soc. Sci. Fennicae 37: 1–171.

Rosenfield, A. H. 1911. Insects and spiders in Spanish moss. J. econ. Ent. 4: 398–409.

Ross, H. H. 1957. Principles of natural coexistence indicated by leaf hopper populations. Evolution 11: 113–129.

————. 1962. A synthesis of evolutionary theory. Prentice-Hall, London.

Rothschild, M. 1961. Defensive odors and Mullerian mimicry among insects. Trans. R. ent. Soc. Lond. 113: 101–121.

Roubal, J. 1963. (Revision of Megalonotus). Acta Ent. Mus. Prague 36 (In Press).

Sahlberg, R. F. 1848. Monographia Geocorisarum Fenniae Helsingforsiae, Frenckelliana.

————. 1868a. Hemiptera, samlade i Tornea Lappmark ar 1867 och uppraknade. Medd. Faun. Fl. fenn. 9: 221–233.

————. 1868b. Bidrag till Kannedomen om Finlands Dimorpha Insekt-arter. Medd. Fauna Fl. fenn. 9: 199–220. (original not seen)

————. 1881. Enumeratio Hemipterorum Gymnoceratorum Fenniae. Medd. Soc. Fauna Fl. fenn. 7: 1–109.

————. 1920. Enumeratio Hemipterorum Heteropterorum Faunae Fennicae. Bidr. Finl. Nat. Folk. 79: 1–227.

Sanders, E. 1892. The Hemiptera Heteroptera of the British Islands. L. Reeve & Co., London.

Saxena, K. 1963. Mode of injestion in a heteropterous insect *Dysdercus koenigii* (F.) (Pyrrhocoridae). J. Insect. Physiol. 9: 47–72.

Schneider, F. 1962. Dispersal and migration. Ann. Rev. Ent. 7: 223–242.

Schneider, G. 1940. Beitrage zur Kenntnis der symbiontischen Einrichtungen der Heteropteren. Z. Morph. Okol. Tiere 36: 599–614.

Scholtz, W. 1847. Prodromus zu einer Rhynchoten Fauna von Schlesien. Uebersicht der Arbeiten und Veranderungen der Schlesischen Gesellschaft fur vaterland Kulture im Jahr. 1846: pp. 104–164. (original not seen)

Schumacher, F. 1911. Beitrage zur Kenntnis der Rhynchoten fauna Deutschlands iii. Dstch. ent. Z. 16: 671–680.

Schwoerbel, W. 1957. Die Wanzen und Zikaden des Spitzberges bei Tubingen, eine Faunistisch-Okologische Untersuchung (Hemipteroidea: Heteroptera und Cicadina = Homoptera Auchenorrhyncha). Z. Morph. Okol. Tiere 45: 462–560.

Scudder, G. G. E. 1961. Some Heteroptera new to British Columbia. Proc. ent. Soc. B.C. 58: 28–29.

————. 1962. The world Rhyparochrominae (Hemiptera: Lygaeidae). I. New synonymy and generic changes. Canad. Ent. 94: 764–773.

Seidenstucker, G. 1951. *Trapezonotus desertus* n. sp. eine deutsche Lygaeidan-Art (Heteroptera). Senckenbergiana 32: 79–85.

Shaw, H. K. A. 1945. Additions to the list of Bedfordshire Hemiptera-Heteroptera. Ent. mon. Mag. 81: 183–185.

Shelford, V. E. 1913. Animal communities in temperate America as illustrated in the Chicago region. University of Chicago Press, Chicago.

Sheppard, P. M. 1959. The evolution of mimicry; a problem in ecology and genetics. Cold Springs Harbor Symposia on Quantitative Biology 24: 131–140.

Simpson, G. G. 1953. The major features of evolution. Columbia Univ. Press, New York.

Singer, K. 1952. Die Wanzen (Hemiptera-Heteroptera) des unteren Maingebietes von Hanau bis Wurzburg mit einschuluzz des spessarts. Mitt. naturw. Mus. Aschaffenb. 5: 1–128.

Slater, J. A. 1947. The biology and immature taxonomy of the Lygaeidae of Illinois (Hemip.-Heteroptera). Unpublished Master's thesis. University of Illinois, Illinois.

————. 1952. An annotated list of the Lygaeidae of Iowa and Illinois (Hemiptera: Heteroptera). Proc. Iowa Acad. Sci. 59: 521–540.

————. 1957. Nomenclatural considerations in the family Lygaeidae (Hemiptera-Heteroptera). Bull. Brooklyn ent. Soc. 52: 35–38.

————. 1960. A reconsideration of the status of the *Ischnodemus sabuleti* complex (Hem., Lygaeidae). Ent. mon. Mag. 96: 18–19.

Slater, J. A. and J. Carayon. 1963. Ethiopian Lygaeidae IV: A new predatory Lygaeid from Africa with a discussion of its biology and morphology (Hemiptera: Heteroptera). Proc. R. ent. Soc. Lond. (A) 38: 1–44.

Slater, J. A. and M. H. Sweet. 1958. The occurrence of *Mega-*

lonotus chiragra (F.) in the eastern United States with notes on its biology and ecology. Bull. Brooklyn ent. Soc. 53: 102–107.

Slater, J. A. and M. H. Sweet. 1963. Australodemus, a new genus of Blissinae from Australia, with a description of a new species of Heinsius (Heteroptera: Lygaeidae). J. Queensland ent. Soc. 2: 51–55.

Slobodkin, L. B. 1961. Growth and regulation of animal populations. Holt, Rinehart & Winston, New York.

Smith, H. S. 1935. The role of biotic factors in the determination of population densities. J. econ. Ent. 28: 873–898.

Smith, J. B. 1910. The insects of New Jersey. Rep. N.J. Mus. 1910: 1–888.

Smreczynski, S. 1954. Materialy do fauny pluskwiakow (Hemiptera) Polski materiaux pour la fauna d'Hemipteres de Pologne. Polsk. Akad. Nank Inst. zool. Fragm. faun.

Southwood, T. R. E. 1956. The structure of the eggs of the terrestrial Heteroptera and its relationship to the classification of the group. Trans. R. ent. Soc. Lond. 108: 163–221.

————. 1960. The flight activity of Heteroptera. Trans. R. ent. Soc. London 112: 173–220.

————. 1961a. Notes on light trap catches of Heteroptera made in the tropics. Ent. mon. Mag. 96: 114–117.

————. 1961b. A hormonal theory of the mechanism of wing polymorphism in Heteroptera. Proc. R. ent. Soc. Lond. 36: 63–66.

————. 1962a. Migration of terrestrial arthropods in relation to habitat. Biol. Rev. 37: 171–214.

————. 1962b. Migration—an evolutionary necessity for denizens of temporary habitats. Proc. Int. Congr. Ent., XIth, Wein (1960) 3: 54–58.

————. 1963. *Megalonotus sabulicola* (Thomson, 1870) (Hem., Lygaeidae) in Britain. Entomologist 96: 124–126.

Southwood, T. R. E. and C. G. Johnson. 1957. Some records of insect flight activity in May 1954, with particular reference to the massed flights of Coleoptera and Heteroptera from concealing habitats. Ent. mon. Mag. 93: 121–126.

Southwood, T. R. E. and D. Leston. 1959. Land and water bugs of the British Isles. Frederick Warne & Co., London.

Southwood, T. R. E. and G. G. E. Scudder. 1956. The immature stages of the Hemiptera-Heteroptera associated with the sting nettle (*Urtica dioica* L.). Ent. mon. Mag.

92: 313–325.

Spinola, M. 1837. Essai sur des Genres D'Insectes appartennants a L'ordre des Hemipteres Linn. ou Rhyngotes, Fab. et a la section Heteropteres, Dufour. Genes Chez Yves Gravier, Imprimeur Libraire, Paris. (original not seen).

Stål, C. 1862. Hemiptera Mexicana, enumeravit speciesque novas descripsit. Stettin ent. Ztg 23: 81–118, 273–281, 289–325, 437–462.

Standley, P. C. and J. A. Steyermark. 1946. The vegetation of Guatemala, a brief review: *In* Plants and plant science in Latin America. Editor: Verdoorn, F. Chronica Botanica; Waltham, Mass.

Stehlik, J. 1952. The fauna of the Heteroptera of the mountain, High Jesenik. Cas. morav. Musea zem. 37: 132–248.

Stichel, W. 1925. Illustrierte Bestimmungs Tabellen der Deutschen Wanzen. Pt. 3: 59–90. Berlin Verlagnaturwissen schaftlicher Publikationen. Dr. W. Stichel. Berlin-Harmsdorf.

————. 1926. Heteroptera of Estonian moors. *In* Dampf. S. B. Natf. Ges. Univ. Tartus 33: 92–97.

Strawinski, K. 1950. On the biological dependency of Hemiptera-Heteroptera on trees and shrubs. Ann. Univ. Marie Curie-Sklodowska (C) 5: 65–87.

————. 1956. Insekten der ordnung Heteroptera in der biocaenose im Urwalds von Bralowierza. Roezniki Nauk Lesnych 14: 1–121.

————. 1957. Hem.-Heteroptera aus der Krautschicht einiger Waldbestande der Umgegend von Wandzin. Ann. Univ. Marie Curie-Sklodowska (C) 12: 103–113.

————. 1959. A faunistic survey of Hemiptera-Heteroptera occurring in the "steppe" reservation near Grodek. Ann. Univ. Marie Curie-Sklodowska (C) 14: 1–28.

————. 1960 (1961). Hemiptera-Heteroptera found under stones. Ann. Univ. Marie Curie-Sklodowska (C) 15: 1–19.

Stys, P. 1960. Die Wanzenfauna des Moorgebietes Soos in Bohmen (Heteroptera). Acta Univ. Carolinae—Biol. Suppl. 1960: 83–133.

Summers, H. E. 1891. The true bugs, or Heteroptera, of Tennessee. Bull. Tenn. agric. Expt. Sta. 4: 75–96.

Sweet, M. H. 1960. The seed bugs: a contribution to the feeding habits of the Lygaeidae (Hemiptera: Heteroptera). Ann. ent. Soc. Amer. 53: 317–321.

————. 1963. A new species of *Ligyrocoris* Stål with a key to the northeastern species (Hemiptera: Lygaeidae). Psyche, Camb., Mass. 70: 17–21.

Sweet, M. H. and J. A. Slater. 1961. A generic key to the nymphs of North America Lygaeidae (Hemiptera-Heteroptera). Ann. ent. Soc. Amer. 54: 333–340.

Swezy, O. H. 1945. Insects associated with orchids. Proc. Haw. ent. Soc. 12: 343–403.

Tansley, A. G. 1939. The use and abuse of vegetational concepts and terms. Ecology 16: 284–307.

Taylor, L. R. 1960. The distribution of insects at low levels in the air. J. anim. Ecology 29: 45–63.

Thomas, D. C. 1938. A list of Hemiptera-Heteroptera in Hertfordshire with notes on their biology. Trans. Herts. nat. Hist. Soc. Fld. Cl. 20: 314–327. (fide Southwood 1956a)

————. 1955. Notes on the biology of some Hemiptera Heteroptera. IV. -Lygaeidae. Entomologist 88: 145–152.

Thomson, B. F. 1958. The changing face of New England. The Macmillan Co., New York.

Torre-Bueno, J. R. de la. 1908. Hemiptera-Heteroptera of Westchester County, N.Y. J. N.Y. ent. Soc. 16: 223–238.

————. 1910. Westchester Heteroptera—II. Additions, corrections, and new records. J. N.Y. ent. Soc. 18: 22–23.

————. 1912. Three days in the pines of Yaphank. Records of captures of Hemiptera Heteroptera. Canad. Ent. 44: 209–213.

————. 1914. Phototropism in Hemiptera. Bull. Brooklyn ent. Soc. 9: 90–96.

————. 1915. Heteroptera in beach drift. Ent. News 26: 274–279.

————. 1917a. New York Scolopostethi (Family Lygaeidae: Heteroptera). Ent. News 28: 65–68.

————. 1917b. *In* Proceedings of meetings of Bull. Brooklyn Ent. Soc. Bull. Brooklyn Ent. Soc. 12: 46.

————. 1918. Some Heteroptera from the Parry Sound District, Ont. Canad. Ent. 50: 24–25.

————. 1924. On a few Heteroptera from Massachusetts. Bull. Brooklyn ent. Soc. 19: 48–51.

————. 1925. Some winter bugs. Bull. Brooklyn ent. Soc. 20: 70.

————. 1927. Comment on insects in ocean drift or tide line. Bull. Brooklyn ent. Soc. 22: 158–162.

————. 1929a. On some New England Heteroptera. Bull. Brooklyn ent. Soc. 24: 310–313.

———. 1929b. A few late spring bugs. Bull. Brooklyn ent. Soc. 24: 221.

———. 1930. Bugs at light. Bull. Brooklyn ent. Soc. 25: 101.

———. 1931. Heteroptera collected by G. P. Engelhardt in the south and west—II. Bull. Brooklyn ent. Soc. 26: 135–139.

———. 1933. Records of Connecticut Heteroptera. Bull. Brooklyn ent. Soc. 28: 36.

———. 1940. Biological notes on Arizona Heteroptera. Bull. Brooklyn ent. Soc. 30: 62.

———. 1946. A synopsis of the Hemiptera-Heteroptera of America north of Mexico. Part III. Family XI. Lygaeidae. Ent. amer. 26: 1–141.

Townsend, C. H. T. 1891. Hemiptera collected in southern Michigan. Proc. ent. Soc. Wash. 2: 52–56.

Transeau, E. N. 1913. The vegetation of Cold Spring Harbor, Long Island. The littoral successions. Plant World 16: 89.

———. 1935. The prairie peninsula. Ecology 16: 423–437.

Tucker, E. S. 1907. Some results of desultory collecting of insects in Kansas and Colorado. Kans. Univ. Sci. Bull. 4: 52–112.

Tullgren, A. 1918. Zur morphologie und Systematik der Hemipteren-1. Uber das vorkommen von s.g. Trichobothrien bei Hemiptera-Heteroptera und ihr mutmassliche Bedeutung fur das Heteropteren system. Ent. Tidjkr. 39: 113–133.

Uhler, P. R. 1871. Notices of some Heteroptera in the collections of Dr. T. W. Harris. Proc. Boston Soc. nat. Hist. 14: 93–104.

———. 1876. List of Hemiptera of the region west of the Mississippi River, including those collected during the Hayden explorations of 1873. Bull. U.S. geol. geog. Surv. Terr. 1: 269–361.

———. 1877. Report upon the insects collected by P. R. Uhler during the explorations of 1875, including monographs of the families Cydnidae and Saldidae, and the Hemiptera collected by A. S. Packard, Jr., M. D. Bull. U.S. geol. geog. Surv. Terr. 3: 355–475.

———. 1878. On the Hemiptera collected by Dr. Elliott Cones USA, in Dakota and Montana during 1873–4. Bull. U.S. geol. geog. Surv. Terr. 4: 503–512.

———. 1884. *In:* Kingsley: Riverside Natural History Vol. 2: Hemiptera section: 204–293.

———. 1894. Observations upon the Heteropterous Hemiptera of lower California, with descriptions of new species. Proc. Calif. Acad. Sci. (2) 4: 223–295.

———. 1904. List of Hemiptera-Heteroptera of Las Vegas, Hot Springs, New Mexico, collected by Messrs. E. A. Schwarz and Herbert S. Barber. Proc. U.S. nat. Mus. 27: 349–364.

Urquhart, F. A. 1958. Discussion of the use of the word "migration" as it relates to a proposed classification for animal movements. Contr. R. Ont. Mus. Zool. No. 50: 1–11.

Usinger, R. L. 1933. A new species of *Gastrodes* from California (Lygaeidae-Hemiptera). Pan-Pacific Ent. 9: 127–128.

———. 1938. Review of the genus *Gastrodes* (Lygaeidae, Hemiptera). Proc. Calif. Acad. Sci. 23: 289–301.

Van Duzee, E. P. 1888. Mimicry in Hemiptera. Psyche, Camb., Mass. 10: 27–28.

———. 1894. A list of the Hemiptera of Buffalo and vicinity. Bull. Buffalo Soc. nat. Sci. 5: 167–216.

———. 1909. Synonymical and descriptive notes on North American Heteroptera. Canad. Ent. 41: 369–375.

———. 1910. Descriptions of some new or unfamiliar North American Hemiptera. Trans. Amer. ent. Soc., 36: 73–88.

———. 1914. A preliminary list of the Hemiptera of San Diego County, California. Trans. San Diego Soc. nat. Hist. 2: 1–57.

———. 1915. New genera and species of North American Hemiptera. Pomona Jour. Ent. Zool. 7: 109–121.

———. 1917. Catalogue of the Hemiptera of America north of Mexico. Univ. Calif. Publ. Ent. 2: 1–902.

———. 1923. Our First *Rhyparochromus* (Hemiptera: Lygaeidae). Pan-Pacif. Ent. 5: 47.

Verdcourt, B. 1950. Further records of Bedfordshire Hemiptera-Heteroptera. Ent. mon. Mag. 86: 6–8.

Vestal, A. G. 1913. An associated study of Illinois sand prairie. Bull. Ill. nat. Hist. 10: 1–96.

Wagner, E. 1954. Die Europaischen Arten der Gattung *Emblethis* Fieb. (Hem. Het. Lygaeidae). Opusc. Ent. 19: 225–231.

———. 1958. Deuxime contribution a la fauna des Hemipteres Heteropteres de France. Vie et Milieu 9: 236–247.

Waddell, D. B. 1951. A preliminary list of the Hemiptera of the Kootenay Valley. Proc. ent. Soc. B. C. 48: 93–96.

Walkden, D. and O. Wilbur. 1944. Insects and other Arthropods in pasture grasses, waste lands, and forage crops. Manhattan, Kans. 1937–1940. J. Kans. ent. Soc. 17 : 128–143.

Walley, G. S. 1929. Two new species of *Eremocoris* with notes and a key to the species of *Peritrechus* (Hemip., Lygaeidae). Canad. Ent. 61 : 41–44.

————. 1932. A second report on Hemiptera from the north shore of the Gulf of St. Lawrence. Canad. Ent. 64 : 152–155.

Waterhouse, F. L. 1955. Microclimatological profiles in grass cover in relation to biological problems. Quart. J. R. met. Soc. 81 : 63–71.

Watt, K. E. F. 1962. Use of mathematics in insect ecology. Ann. Rev. Ent. 7 : 243–260.

————. 1962. Use of mathematics in population ecology. Ann. Rev. Ent. 7 : 243–260.

Wassman, E. 1889. Ueber einige myrmekophile Heteropteren. Dstch. ent. Z. 1889. : Heft I : 191–192.

————. 1894. Kritisches Verzeichness der myrmekophilen un termitophilen Arthropoden. Felix L. Dames, Berlin.

Weber, H. 1930. Biologie der Hemipteren. Berlin.

————. 1941. Beitrag zur Kenntniss der Hemipteren-faune der Nordseeinsel Amrum. Kiel. Meeresf. 4 : 109–158.

Wheeler, W. M. 1893. A contribution to insect embryology. J. Morph. 8 : 1–16.

————. 1910. Ants, their structure, development and behavior. Columbia University Press, New York.

Whittaker, R. H. 1953. A consideration of climax theory: the climax as a population and pattern. Ecol. Monogr. 23 : 47–78.

Wigglesworth, V. B. 1952. Hormone behavior and the control of metamorphosis in *Rhodnius prolixus* (Hemiptera). J. exp. Biol. 29 : 620–631.

————. 1954. The physiology of insect metamorphosis. Cambridge Univ. Press, Cambridge, Mass.

Wilde, J. de. 1962. Photoperiodism in insects and mites. Ann. Rev. Ent. 7 : 1–26.

Williams, F. X. 1946. Two new species of Astatinae, with notes on the habits of the group (Hymenoptera: Sphecidae). Proc. Hawaii ent. Soc. 12 : 641–650.

Wilson J. W. 1938. Notes on *Pamera* populations on various types of plant communities in the vicinity of Plant City. Florida Ent. 21 : 28–40.

Wirtner, P. M. 1905. Preliminary list of the Hemiptera of western Pennsylvania. Ann. Carneg. Mus. 3: 183–232.

Wolcott, G. N. 1936. Insectae Borinquenses. A revised annotated check-list of the insects of Puerto Rico. With a host plant index by J. Otero. J. Dep. Agric. P. R. 20: 1–627.

————. 1941. A supplement to "Insectae Borinquenses." J. Dep. Agr. P. R. 25: 33–158.

————. 1951. The insects of Puerto Rico. J. Dep. Agric. P. R. (1948) 32: 1–975. (Hemiptera in Part I, pp 1–244, dated 1950 but published 1951).

Woodroffe, G. E. 1955. The Hemiptera-Heteroptera of some cinder-covered waste land at Slough, Buckinghamshire. Entomologist 88: 10–17.

————. 1961. *Drymus pilicornis* (Muls.) (Hem., Lygaeidae): at Bald Hill, Oxon. Ent. mon. Mag. 97: 200.

————. 1963a. Some recent captures of Hemiptera-Heteroptera. Ent. mon. Mag. 98: 207.

————. 1963b. The identity of the British *Eremocoris* Fieber (Hem., Lygaeidae). Ent. mon. mag. 98: 262–263.

Woodward, T. E. 1952. Studies on the reproductive cycle of three species of British Heteroptera, with special reference to the overwintering stages. Trans. R. ent. Soc. Lond. 103: 171–218.

Wray, D. L., and C. S. Brimley. 1943. The insect inquilines and victims of pitcher plants in North Carolina. Ann. ent. Soc. Amer. 36: 128–137.

Young, E. C. 1961. Degeneration of flight-musculature in the Corixidae and Notonectidae. Nature, Lond. 189: 328–329.

Zetterstedt, J. W. 1840. Insecta Lapponica Descripta. Sumtibus Leopolde Voss, Lipsiae. (original not seen)

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