Quaestiones entomologicae

A periodical record of entomological investigations, published at the Department of Entomology, University of Alberta, Edmonton, Canada

VOLUME V 1969

CONTENTS

Quaestiones entomologicae

A periodical record of entomological investigations, published at the Department of Entomology, University of Alberta, Edmonton, Canada.

VOLUME V NUMBER 1 JANUARY 1969

QUAESTIONES ENTOMOLOGICAE

A periodical record of entomological investigations published at the Department of Entomology, University of Alberta, Edmonton, Alberta.

Volume 5 Number 1 13 January 1969

CONTENTS

Book Review

GRESSITT, J. LINSLEY (editor). 1967. Entomology in Antarctica. American Geophysical Union. Library of Congress Catalogue No. 67-62159. Volume 10, xii + 395 pp., many figs. and photographs. $17.00 U.S.A.

This book has a large informative introduction by the editor, and then is divided into two major sections, Systematics and Ecology, for the text.

The Introduction contains five parts as follows: History of Entomological Explorations in Antarctica; Zoogeographical Summary; The Fossil Record; Dispersal; and Classification.

Entomological exploration began in 1897-1899 with the "Belgica" Expedition under de Gerlache and is continuing today. The "Belgica" Expedition brought back specimens of three species of springtails, a wingless midge, specimens of six species of mites, a tick, and specimens of four species of chewing bird-lice. Up to and including 1967, Gressitt lists 130 species and subspecies (a few are uncertain identifications or records) of terrestrial arthropods in 68 or 69 genera belonging to 29 families in 10 orders, and states that more new species will be found. Only one marine mite is mentioned by him. The distribution of each species is given with the list in tabulated form. The Zoogeographic Summary is short but clear. The Fossil Record is one beetle, *Grahamelytron crofti* Zeuner, of doubtful family association, and a few insect wing fragments. Gressitt states that the main dispersal methods available to insects appear to be winds and birds. The short Classification at the end of the Introduction is but a key to the orders and some families and seems a bit out of place. I feel that it should have been completed to include all the known arthropod fauna of Antarctica. It is not very useful in its present form.

The Systematics section treats the Acarina, Collembola, Mallophaga, Anoplura, and Diptera.

The Acarina are represented by 94 species in the suborders Mesostigmata (mesostigmatic and nasal mites); Metastigmatia (ticks); Prostigmata (marine and terrestrial trombidiform mites), Astigmata (sarcoptiformes), and the Cryptostigmata (oribatid mites). Hunter discusses the mesostigmatic families Rhodacaridae and Laelapidae. He provides neither key nor diagnoses for all the species. Wilson discusses the remaining mesostigmatic families Rhinonyssidae and Halarachnidae (nasal mites) and the metastigmatic Ixodidae (ticks). He provides diagnoses and drawings for the mites, and keys, diagnoses, and drawings for the ticks. There are no new species noted. Strandtmann discusses the terrestrial prostigmatic mites. He provides a key to all the Antarctic species of free-living mites. Brief diagnoses are provided for the eight previously known species and detailed diagnoses and illustrations are provided for the 14 new species. The known distributions are cited. Newell discusses the marine prostigmatic mites, the Halacaridae. Twenty-eight species are recorded from south of 60° south latitude. One new species is described and illustrated. Keys are provided for all the genera and species, and illustrations for the above mentioned species. Newell gives an interesting account of the family Halacaridae in the polar regions. Atyeo and Peterson discuss the astigmatic mites, which are represented by Procotophyllodidae and Avenzoariidae. Some illustrations are provided. Keys are provided for all genera and species. Wallwork discusses the cryptostigmatic mites. He lists 18 species and subspecies, three of which are new and provides a key to the species. He discusses briefly the endemic continental, the South American, and the circum-Antarctic - Sub-Antarctic elements of the Oribatidae.

The Collembola are represented by 17 species, three of which are new, in 13 genera of four families in two suborders. Wise provides a key to the species and illustrations of diagnostic characters of the new species. He discusses the history of collections of Collembola in Antarctica, and distribution and origin of this fauna.

The Mallophaga and Anoplura are discussed together, but in two parts. The first, by Clay, is a short paper on those Mallophaga parasitic on penguins. A key is provided to all the known species. The second paper, by Clay and Moreby, provides keys and locality lists of Mallophaga and Anoplura.

Wirth and Gressitt end the Systematic section with the Chironomidae. They discuss the two known species, one of which is apterous, the other winged. Data on distribution are given.

The Ecology section provides data on the biology and distribution of selected species. Janetscheck introduces this section with a broad, but thorough, discussion of Arthropod ecology of south Victoria land, and a specific discussion on growth and maturity of a springtail, *Gomphiocephalus hodgsoni* Carpenter, from the same region. Many graphs, charts and photographs are included. Gressitt and Shoup follow with a discussion of the ecology of several free-living mites in the north Victoria land, and Gless with short notes on the biology of another mite, again from the same region. Wise and Shoup discuss some Collembola distributions in relation to transects at Cape Hallett, and Tilbrook discusses arthropod ecology in the Maritime Antarctic. Strong discusses the ecology and habits of the free-living arthropods at Palmer Station, Anvers Island, and Gressitt follows with notes on arthropod populations in the south Shetlands, the Antarctic peninsula, and south Orkneys area. Murray, Orton, and Cameron end the book with a very short paper on the only Antarctic flea, covering distribution, taxonomic description and biology.

As the editor states in the Preface, "This volume is the first extensive assemblage of studies on the entomology of Antarctica." This is true, and it is well done. However, with just a little more planning, it could have been even better. For instance, the division of the information about the Mallophaga and Anoplura into two papers is needless and wasteful. The figures for both papers are at the end of the second paper, and not with their respective ones. The division apparently came as a late afterthought, with the result that there is a problem in the key to the mallophagan genera, and a taxonomic problem. The genus *Austrogoniodes* Harrison (1937) is not provided for in the key to the mallophagan genera in the second paper, and two new species described by Clay in the first paper, *A. gressitti* Clay 1967, and *A. keleri* Clay 1967 are in the second paper as *A. gressitti* Clay n. sp., and *A. keleri* Clay n. sp., despite the fact that they were described in the first paper.

Some of the ecology papers could have been joined together, such as those by Strong and Gressitt, to make the information more useful and to thus avoid some contradictions. For instance, Strong writes that the eggs of *Tydeus tilbrooki* Strandtmann (1967) have not yet been encountered (page 371), yet Gressitt describes them (page 382).

I feel that there should have been some discussion of the single Antarctic flea in the Systematic section.

It is interesting to note that only one of the acarologists (Newell) mentions the publication by Dalenius, The Acarology of the Antarctic Regions, *in* Biogeography and Ecology in Antarctica (van Mieghem and van Dye, editors), Junk, The Hague, 1965.

As Gressitt gave a good coverage in the Introduction on the history of Antarctic entomology, I feel that there is some unnecessary repetition in several of the systematic papers. However, for separate papers in standard scientific journals, the introductory history for each group would have been well placed. I think that some of the ecology titles should have read "Habitats" rather than "Ecology".

The book lacks an index, and for the ecological parts this is sorely needed, as there is overlap of discussion of many species.

The proof reading for Entomology of Antarctica was well done; most of the illustrations, figures and graphs are of high quality, though some small graphs are a little "busy" while others are unnecessarily large and with little information. The printing is clear and of a pleasant reading size. The binding is well done with cloth, and the paper is high gloss kaolin (which might not be a good feature in humid climates).

I believe that this book is worthwhile in spite of the above mentioned shortcomings and should get wide circulation. The price, I think, is a little too high.

The value of this book to biologists will increase significantly when it becomes possible to compare the Antarctic insect fauna with its Arctic counterpart. This will be possible when the systematic and ecological work done under the program "Studies on Arctic Insects" by the Canadian government is completed and published.

Robin Leech

NEW DISTRIBUTIONAL RECORDS FOR CANADIAN SOLDIER FLIES (DIPTERA: STRATIOMYIDAE)

PART I. BERIDINAE AND SARGINAE

M.W. McFADDEN
Department of Entomology
Washington State University
Pullman, Washington 99163

Quaestiones entomologicae
5 : 5-7 1969

New distribution records in Canada and Alaska are presented for the following species of Stratiomyidae: Allognosta fuscitarsis, A. obscuriventris, A. brevicornis, Actina viridis, Beris californica, Exodontha luteipes, Sargus bipunctatus, S. cuprarius, S. decorus, S. viridis, S. lucens, Microchrysa polita, *and* M. flavicornis.

Except for the contributions of Strickland (1938, 1946), James (1951), and James and Huckett (1952), information on the distribution of Stratiomyidae in Canada and Alaska has not been revised since Curran's synopsis (1927).

Work in progress on a revision of the Stratiomyidae of Alaska and Canada has revealed the following new records.

SUBFAMILY BERIDINAE

Allognosta fuscitarsis (Say)

Previously recorded from Nebraska to Quebec; the new records include specimens collected from Manitoba and Nova Scotia and indicate that the range of this species covers the eastern half of Canada.

Allognosta obscuriventris (Loew)

The species, previously known only from Ontario and Quebic, is now known to occur in Manitoba and Nova Scotia and apparently is sympatric with *A. fuscitarsis.*

Allognosta brevicornis Johnson

All previous records for the species have been from the northeastern section of the United States. New records show that its range can be extended in Canada to include Quebec, Ontario, Alberta, and British Columbia.

Actina viridis (Say)

Previously known to occur in Canada from Newfoundland to Alberta; new records from Nova Scotia, New Brunswick, and British Columbia confirm that this species extends from coast to coast.

Beris californica James

The species was not previously recorded from Canada or Alaska but is now known to occur in the southern portion of British Columbia. It has also been recorded from Vancouver Island.

Exodontha luteipes (Williston)

The species has been recorded from Vermont and New Hampshire in the northeastern United States and from Idaho in the northwest. It is now known to occur in the provinces of Alberta and British Columbia.

SUBFAMILY SARGINAE

Sargus bipunctatus (Scopoli)

Previously known only from the states of Oregon and Washington where it was originally introduced (James 1960), the species has now extended its range to include southeastern British Columbia.

Sargus cuprarius (Linnaeus)

In Canada, the species is known to occur from Quebec westward to British Columbia. Specimens collected from Nova Scotia indicate that the range now extends from coast to coast.

Sargus decorus Say

The species has been reported as having a range extending from Alaska to the province of Quebec. With new records from Nova Scotia and New Brunswick, the range now extends from coast to coast.

Sargus viridis Say

Previously known to occur in Alaska, its range extended eastward to the province of Quebec. New records from New Brunswick indicate that the range actually extends from coast to coast in Canada.

Sargus lucens Loew

The species has not been previously reported to occur in Canada. All new records are from the province of Ontario.

Microchrysa polita (Linnaeus)

The species is reported to have a range extending from coast to coast in Canada. The single new record is from the province of New Brunswick which serves to verify the fact that the species is established in the Atlantic provinces.

Microchrysa flavicornis (Meigen)

The species, previously known to have a range extending from the state of Washington to the province of Newfoundland, is now known to occur in the provinces of Saskatchewan, Alberta, and British Columbia.

REFERENCES

Curran, C.H. 1927. Synopsis of the Canadian Stratiomyidae (Diptera). Trans. R. Soc. Can. 21 : 191-228.

James, M.T. 1951. The Stratiomyidae of Alberta (Diptera). Proc. ent. Soc. Wash. 53(6) : 342-343.

James, M.T. 1960. The soldier flies or Stratiomyidae of California. Bull. Calif. Insect Survey 6(5) : 79-122.

James, M.T. and H.C. Huckett. 1952. The Diptera collected by I.O. Buss in southwestern Yukon Territory during the summer of 1950. Can. Ent. 84(9) : 265-269.

Strickland, E.H. 1938. An annotated list of Diptera of Alberta. Can. Res. D. 16 : 175-219.

Strickland, E.H. 1946. An annotated list of Diptera of Alberta. Additions and corrections. Can. Res. D. 24 : 157-173.

EFFECTS OF POPULATION DENSITY ON *CIMEX LECTULARIUS* L.

MONIB SAYED TAWFIK
Department of Entomology
University of Alberta, Edmonton.

Quaestiones entomologicae
5 : 9-14 1969

In C. lectularius, *population density affects fecundity and the duration of the nymphal stadia, the preoviposition period, and life, apparently through a contact stimulus. The effects reach optima at a population density of 4 to 8 insects/cm^2.*

Many studies have been made of the environmental factors that influence development and behavior of *C. lectularius*. Also, quantitative studies of natural populations have been conducted by Mellanby (1939) , Omori (1941), and Johnson (1942). Although the effect of population density on the physiology and ecology of many insects has received much attention, no detailed investigations have been carried out on *C. lectularius*. High population density, or overcrowding, is often accompanied by a shortage of food. The effect of food quantity free from the effect of population density was studied (Tawfik 1968). The aim of this study is to separate the effect of density itself from that of food quantity.

Overcrowding has a detrimental effect on insects in various ways; slower growth rate, increased mortality, smaller adults, and lower fecundity (Pearl and Parker 1922, Chapman 1928, Shannon and Putnam 1934, Bodenheimer 1938 and 1955, MacLagen and Dunn 1936, Crombie 1942, Robertson and Sang 1944, Terzian and Stahler 1949, Bar-Zeev 1957, Wada 1965). Most investigators have attributed the effect mainly to the mechanical disturbance of insects by each other. Some have demonstrated that most of these effects are dependent on the quantity and quality of food.

METHODS

Density ranging between 2 and 128 insects per surface area of 8 cm^2 of a piece of folded filter paper (2 x 2 cm) in 2 x 7 cm specimen tube was studied. Relating the density to the surface area of the folded filter paper is more important than relating it to the volume of the specimen tube because bedbugs are dorso-ventrally flattened, always aggregate on the surface of the folded filter paper, and thus essentially live in a two dimensional habitat. Data representing a density equal to 1 per 8 cm^2 was taken from Tawfik (1968) when the insects were fed till engorgement every 2 days. Eggs were taken from the standard culture and put in 4 x 4 x 1.5 cm plastic boxes. First instar nymphs were taken as soon as they hatched and were put in 7 x 2 cm specimen tubes together with 2 x 2 cm folded filter paper. Eight experiments were conducted in which the numbers of nymphs per tube were 2, 4, 8, 16, 32, 64, and 128 respectively (i.e. 0.25, 0.5, 1, 2, 4, 8, and 16/cm^2). In all the experiments the insects were allowed to feed on the second day after hatching and twice every week thereafter. For feeding, the insects from each tube were transferred to a 4 x 4 x 1.5 cm plastic box and were allowed to feed on human blood through organdie which covered a 3 cm diameter hole in the lid of the plastic box. Observations were carried out daily and the effects of the population density on the duration of the nymphal stadia, preoviposition period, fecundity, longevity, and mortality rate were studied.

With a constant food supply for the insects in all the experiments, the effect of population density could be due to either visual stimulus, olfactory stimulus, contact stimulus or combinations of these stimuli. All the experiments were conducted in the dark and the insects were exposed to the light only for ten minutes for examination to rule out the visual stimulus. An additional experiment was conducted to test whether the effect of population density is due to an olfactory or a contact stimulus. In this experiment 40 plastic boxes, similar to those used for feeding, were used. The lids of each 2 were glued together forming a combination of 2 chambers separated by the organdie on the inside of the lids. In one of these chambers a single first instar nymph was put with a piece of folded filter paper. In the other chamber 64 first instar nymphs were put. The insects were fed twice every week on human blood and the effect on the duration of the nymphal stadia of the single nymph was recorded. After the fifth moult two insects of opposite sex were put in one chamber instead of one insect and the effects on preoviposition period, fecundity, and longevity were studied. All the experiments were done at 80 F and 75% relative humidity.

On the Duration of the Nymphal Stadia

The effect of population density on the duration of the nymphal stadia is shown in fig. 1. Population density does not show a clear effect on the duration of the first nymphal stadium as this ranges between 3.6 and 4 days. On the other hand, the duration of the other four stadia decreased with the increase of population density. Olfactory stimulus does not seem to be involved in the effect on the duration of the nymphal stadia because there is no significant difference between the results of the experiment with the double chamber combination and those at density 1 and 2 (fig. 1).

On the Duration of the Preoviposition Period

The results are shown in fig. 2. Increasing the population density appears to decrease the minimum duration of the preoviposition period but beyond density 32 has no significant effect. Olfaction has no effect on the duration of the preoviposition period; the value obtained in this experiment does not show a significant difference from that when the population density was either 2 or 4.

On Fecundity

The relationship between the number of eggs laid per female and the population density is shown in fig. 3. Population density of 2 or 4 does not have a significant effect on the number of eggs laid per female. On the other hand, increasing the population density causes an increase in the number of eggs laid per female. This increase in the number of eggs reached a maximum when the population density was 64 and then decreased again. As shown in fig. 3, the number of eggs laid per female per day in the different population densities ranged between 2.1 and 2.4. Fig. 3 also shows that there is no olfactory stimulus involved in the effect of the population density on fecundity of the females.

On Longevity of the Adult Stage

Fig. 4 shows the effect of population density on the longevity of the adult stage. The longevity of both the female and the male increases with the increase in the population density. This increase in longevity reaches a maximum at a population density of 32 and then decreases with further increase in population density. There is no olfactory stimulus involved in the effect of population density on the longevity of the females or the males (fig. 4).

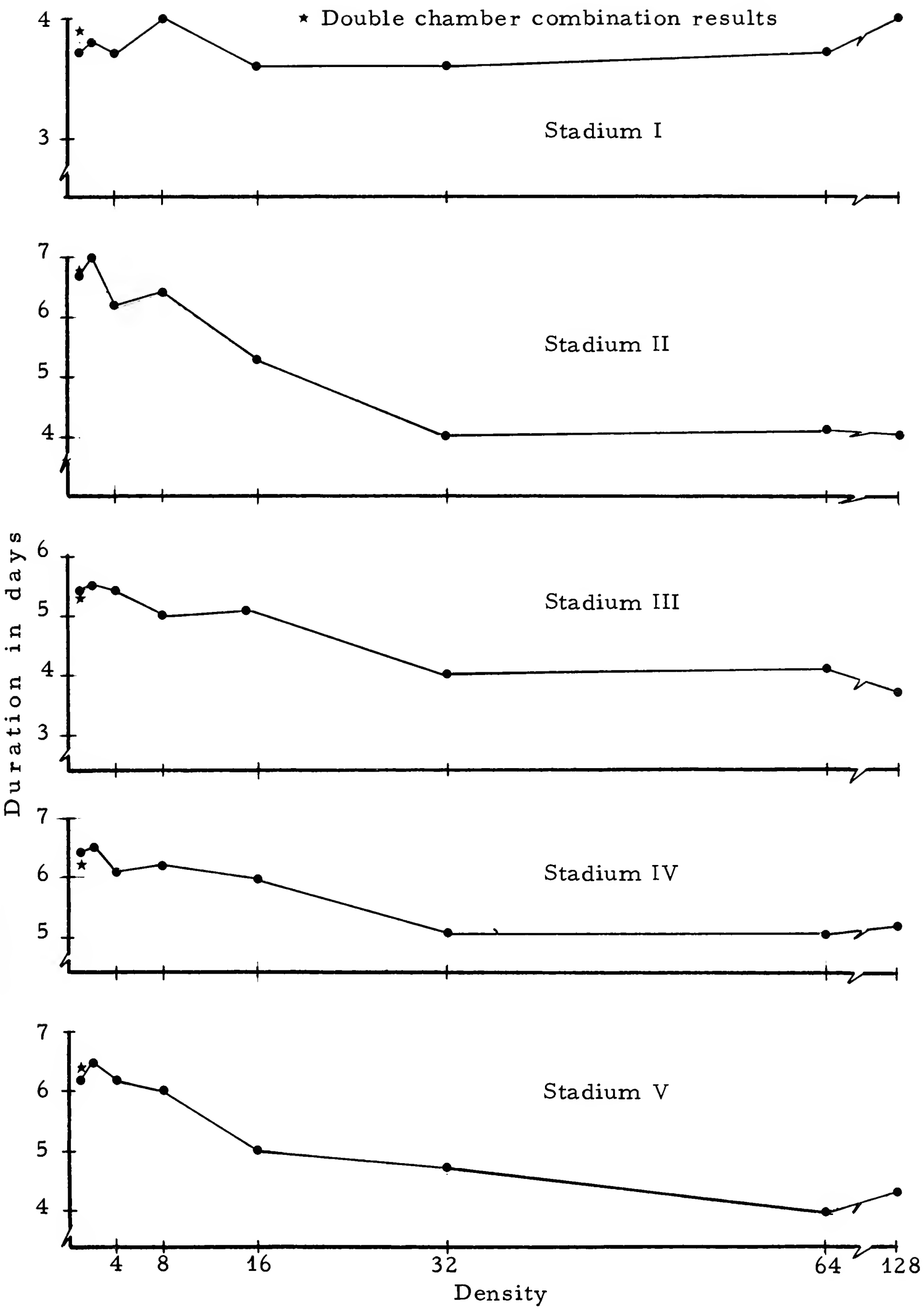


Fig. 1. Effect of population density of *C. lectularius* on the duration of the nymphal stadia.

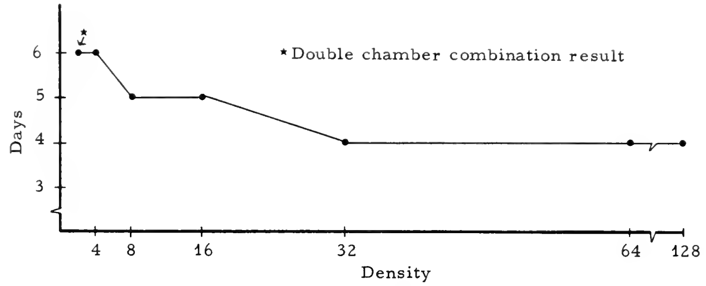


Fig. 2. Effect of the population density of *C. lectularius* on the duration of the preoviposition period.

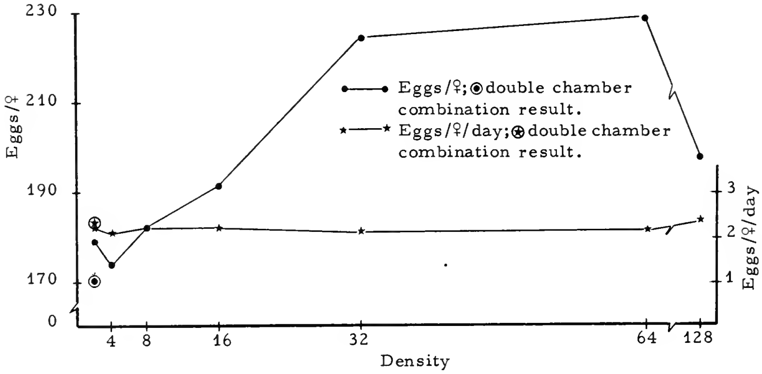


Fig. 3. Effect of population density of *C. lectularius* on the number of eggs laid per female and the number of eggs laid per female per day.

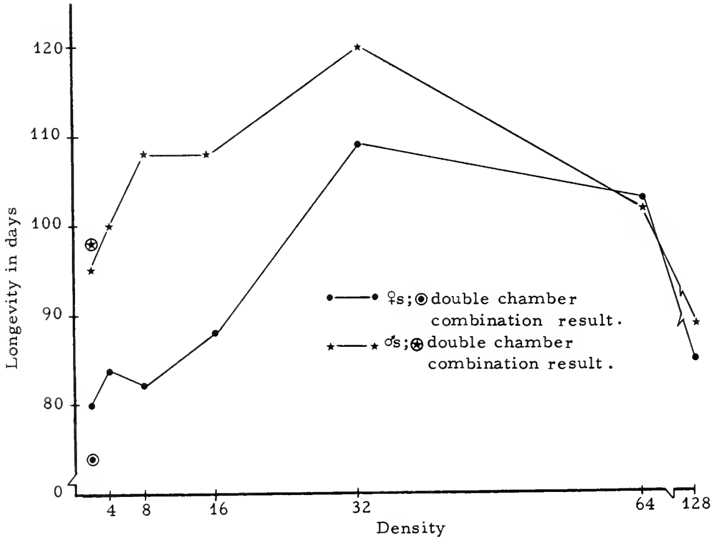


Fig. 4. Effect of the population density of *C. lectularius* on the longevity of males and females.

On Mortality Rate

Table 1 shows the effect of the population density on the percentage of mortality in the different instars of *C. lectularius*. Increasing the population density beyond 8 causes a decrease in the percentage of insects that reach the adult stage.

TABLE 1. Effect of population density on the percentage mortality in the different instars of *C. lectularius*.

Density	Percentage of the total died as					
	Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
1	0	0	0	0	0	-
2	0	0	6.6	3.3	0	91.1
4	0	2.5	0	2.5	2.5	92.5
8	0	2.5	2.5	0	0	95.0
16	0	0	6.2	9.4	3.1	81.3
32	0	5.0	6.2	5.0	5.0	78.8
64	0	5.5	11.7	6.3	2.3	74.2
128	1.6	9.4	18.0	9.4	6.2	55.4

DISCUSSION

From these investigations the effect of population density on *C. lectularius* was apparent and it was clear that neither a visual stimulus nor an olfactory stimulus was involved in that effect. The effect of population density on the duration of the nymphal stadia, preoviposition period, fecundity, and longevity reaches an optimum at a population density of 32 to 64 insects per 2 cm^2 folded filter paper in 2 x 7 cm specimen tube. Population density seems to influence the bedbug through the stimulations of increased mutual contact. This influence was also suggested for mosquito larvae by Bar-Zeev (1957) and Shannon and Putnam (1934). However, Wada (1965) claimed that the situation seemed to be more complex and that neurophysiological processes might be involved. Duration of the nymphal stadia and the preoviposition period in the females decreased with the increase of population density. It is difficult from these experiments to specify the manner in which population density produces its effect through increased mutual contact. It seems that increasing the population density may increase the temperature of the microclimate as *C. lectularius* is always found in aggregates. This increase in the temperature may cause the decreases in the duration of the nymphal stadia and the preoviposition period.

Neurophysiological processes may also be involved, but more experiments are required to prove that. Such experiments should relate population density to endocrine activity, moulting, and reproductive functions. Although the number of eggs laid per female increased with the increase in population density to a maximum when the density was 64, it seems that this effect on fecundity resulted from the effect of population density on longevity of the adult stage rather than the effect of population density on fecundity, since there was no significant difference in the number of eggs laid per female per day at the different population densities.

ACKNOWLEDGMENTS

I am indebted to Professor B. Hocking, Department of Entomology, University of Alberta, for his guidance and stimulating discussions during the course of this work. I am grateful to the late Dr. R.L. Usinger of the University of California, Berkeley, who was my external examiner. I also wish to acknowledge the financial assistance of the U.S. Army Grant No. 63-G83 (Hocking trust) which made this study possible.

REFERENCES

Bar-Zeev, M. 1957. The effect of the density of the larvae of a mosquito and its influence on fecundity. Bull. Res. Coun. Israel (B), 6B: 220-228.

Bodenheimer, F.S. 1938. Problems of animal ecology. Oxford University Press, London.

Bodenheimer, F.S. 1955. Precis d'ecologie animale. Payot, Paris.

Chapman, R.N. 1928. The quantitative analysis of environmental factors. Ecology 9 : 111-122.

Crombie, A.C. 1942. Effect of crowding upon the oviposition of grain infesting insects. J. exp. Biol. 19 : 311-340.

Johnson, C.G. 1942. The ecology of the bedbug, *Cimex lectularius* L., in Britain. J. Hyg. Camb. 41 : 345-461.

MacLagen, D.S. and E. Dunn. 1936. The experimental analysis of the growth of an insect population. Proc. roy. Soc. Edinburgh 55: 126-139.

Mellanby, K. 1939. The physiology and activity of the bedbug (*Cimex lectularius* L.) in a natural infestation. Parasitology 31 : 200-211.

Omori, N. 1941. Comparative studies on the ecology and physiology of common and tropical bedbugs, with special references to the reactions to temperature and moisture. J. med. Ass. Formosa 60(4) : 555-729.

Pearl, R., and S.L. Parker. 1922. Experimental studies on the duration of life. Data on the influence of density of population on the duration of life in *Drosophila*. Amer. Nat. 56 : 312-321.

Robertson, F.W. and J.H. Sang. 1944. The ecological determinant of population growth in *Drosophila* culture. Proc. R. ent. Soc. Lond. 132 : 258-277.

Shannon, R.C. and P. Putnam. 1934. The biology of *Stegomyia* under laboratory conditions. (1) The analysis of factors which influence larval development. Proc. ent. Soc. Wash. 36 : 185-216.

Tawfik, M.S. 1968. Effects of the size and frequency of blood meals on *Cimex lectularius* L. Quaest. ent. 4(3) : 92-111.

Terzian, L.A. and N. Stahler. 1949. The effects of larval population density on some laboratory characteristics of *Anopheles quadrimaculatus* Say. J. Parasit. 35 : 487-498.

Wada, Y. 1965. Effect of larval density on the development of *Aedes aegypti* (L.) and the size of adults. Quaest. ent. 1(4) : 223-249.

A REVISION OF THE GENERA *PHILOPHUGA* MOTSCHOULSKY AND *TECNOPHILUS* CHAUDOIR WITH NOTES ON THE NORTH AMERICAN CALLIDINA (COLEOPTERA: CARABIDAE)

DAVID J. LARSON
Department of Biology
University of Calgary,Calgary, Alberta

Quaestiones entomologicae
5 : 15-84 1969

A taxonomic revision of the species of the North American genera Philophuga *Motschoulsky and* Tecnophilus *Chaudoir is presented. Four species and four subspecies of* Philophuga *are recognized. The taxa* Philophuga horni *Chaudoir and* Philophuga amoena *LeConte are grouped with* P. viridis *Dejean to form a polytypic species, and* P. viridis klamathea *new subspecies is described.* Infernophilus *new genus, is erected to contain the species* castaneus *Horn, formerly included in* Philophuga. *The following names are synonymized for the first time:* P. lauta *Casey (=* P. viridis viridis *Dejean),* P. canora *Casey (=* P. viridis amoena *LeConte),* P. obscura *Casey (=* P. viridis amoena *LeConte),* P. cobaltina *Casey (=* P. viridis horni *Chaudoir),* P. uteana *Casey (=* P. viridis horni *Chaudoir). The name* Tecnophilus pilatei *Chaudoir is removed from synonymy to the name of a species. Two subspecies of a second species of* Tecnophilus *are recognized;* T. c. croceicollis *Menetries and* T. c. peigani *new subspecies.*

Geographical variation among the populations of Philophuga viridis *Dejean and* Tecnophilus croceicollis *Menetries is analyzed.*

The structure of the female stylus is described for the Callidina *and the variation pattern of this sclerite is used to erect a classification of the North American species of this group.*

The method of oviposition and the habitats of the adults are described, as well as the larvae of Philophuga viridicollis *and* Tecnophilus croceicollis.

My interest in this group of carabids began with the discovery of specimens of *Tecnophilus croceicollis* Menetries in southern Alberta. Examination of specimens of *T. croceicollis* from other localities indicated that considerable geographic variation was exhibited by specimens belonging to this species, and also suggested to me that the genus *Tecnophilus* contained more than the one recognized species. I decided to include the genus *Philophuga* in this study because of the similarities in both morphological characteristics and distribution patterns shown by members of the genera *Philophuga* and *Tecnophilus*. I undertook a cursory study of the subtribe Callidina to elucidate the relationship between these two genera, and their relationships to the genus *Callida*.

The complexity of the tribe Lebiini has led many authors to divide it into subtribes. The concept of the supra-generic grouping, the Callidina, was first introduced by Chaudoir (1872). Chaudoir's *Callidides* was a heterogeneous assemblage of lebiine genera which included some genera not belonging here, and excluded others, such as *Philophuga*, previously described by Motschoulsky 1859, which are certainly callidines. When Chaudoir (1877) later described *Tecnophilus*, a callidine genus in even the strictest sense, he placed it in his unspecified grouping *Mimodromiides.*

Horn's (1882) synopsis of the tribe Lebiini was the next, and last comprehensive work on the North American Callidina. Although Horn did not recognize any formal subtribal groupings, he did indicate that a close relationship existed between *Callida*, *Philophuga* and *Plochionus*. Without reference to the genitalic structures, Horn described *castanea* as a member of *Philophuga*. He also suggested that a relationship may exist between *Tecnophilus* Chaudoir and *Euproctus* Solier (= *Euproctinus* Leng and Mutchler) and that these two genera are rather separate from *Callida.*

Since Horn's time, the only work on a large group of North American lebiines has been Madge's (1967) revision of *Lebia* Latreille.

Casey (1913 and 1924) described six species of *Philophuga*, five of which are here regarded as conspecific with previously described species.

Jeannel (1942 and 1949) treated the lebiine faunas of France and Madagascar respectively. He recognized the formal grouping Callidinae but did not present any truly diagnostic characters.

Recently, two major works by Jedlička (1963) and Habu (1967) have appeared, dealing with the Asian Lebiini. Habu presents the best subtribal classification yet proposed, based largely on the structure of the legs, mandibles and female ovipositor. Habu's definition of the Callidina is followed in part in this study.

MATERIALS, METHODS, AND TAXONOMIC CHARACTERS

Materials

I have examined over 1200 specimens of adults and larvae of the genera *Philophuga* and *Tecnophilus* in the course of this study. Most of these specimens were obtained on loan from various museums in Canada and the United States. Many specimens of *Tecnophilus* were collected by myself on a number of field trips to southeastern Alberta, and on an extended trip through southwestern United States. Larvae were reared in the laboratory from eggs laid by captive adults.

Following the description and discussion for each species and subspecies, a list of the localities from which specimens have been examined is presented. The localities are listed alphabetically, in the following order: country, province or state, county and specific locality. Following this, the collector's name and the museum in which the specimen is stored are listed in parentheses.

Abbreviations for museums from which specimens were seen, are as follows: AMNH - American Museum of Natural History; Car. M. - Carnegie Museum; CAS - California Academy of Sciences; CNC - Canadian National Collection, Ottawa; CNHM - Chicago Natural History Museum; CU - Cornell University; DAL - Canada Department of Agriculture Research Station, Lethbridge, Alberta; INHS - Illinois Natural History Survey; IUM - University of Idaho; KUM - University of Kansas; MUB - University of Montana, Bozeman; MCZ - Museum of Comparative Zoology; OUM - Oregon State University; SJSC - San Jose State College, California; UASM - University of Alberta, Strickland Museum; USNM - United States National Museum; and WUM - University of Washington, Seattle.

Methods

General

Observation and comparison were the methods used (Ball 1966). Observations were made of both morphological and biological features of both preserved and living specimens of the subtribe Callidina. Using these observations, comparisons were made between different population samples in order to ascertain similarities and differences. Most observed characteristics were compared independently and were weighed subjectively depending upon the circumstances. That is, in one situation a given character may have been regarded as possessing no discriminatory value, while in another situation it may have been judged important. However, in dealing with variation in one species, *Tecnophilus croceicollis*, several characters were compared simultaneously and the weights for each of these characters were calculated according to their individual statistical discriminatory value, regardless of other considerations.

Criteria for Species, Subspecies and Genera

The multi-dimensional definition of the species (Mayr 1963) has been used as the underlying basis for the taxonomy in this study. The taxa assigned to the species category are less arbitrary than taxa assigned to lower or higher categories, hence the species category forms the basis around which a classification is built. Because it is difficult to make the necessary tests on a population to prove the principal criterion for recognizing a species, that is, genetical isolation from other such groups, this information must be obtained indirectly.

In this study, evidence interpreted as indicating specific identity, is provided by: forms which overlap geographically but do not intergrade in their diagnostic characters in the area of overlap; and allopatric forms in which geographically intermediate specimens do not show intermediate states in their diagnostic characters. For example, the two species *Tecnophilus croceicollis* Menetries and *T. pilatei* Chaudoir are primarily allopatric, and their members can be consistently distinguished from one another on the basis of several characters. However, in the vicinity of Brownsville, Texas, the ranges of these two species overlap, yet the diagnostic characters still hold and permit complete segregation of members of each of these species. I assume that maintenance of these differences is the result of reproductive isolation between these two groups.

I have recognized subspecies only in cases of concordant non-clinal variation in two or more characters. I have not recognized populations along, or at the end of clines as being subspecifically distinct. Rather an attempt has been made to point out such clines and to describe them when they have been recognized (Mayr, Linsley, and Usinger 1953). In one species, *Tecnophilus croceicollis* Menetries, clinal variation occurs in many characteristics; however, two subspecies of this species have been recognized. The new subspecies, *T. c. peigani*, was recognized because a number of characters, many of which varied clinally, showed a sharp change through a relatively short distance to produce two forms which were remarkably different in general appearance, and could be readily distinguished from one another.

A genus has been defined as "a systematic category [= taxon] including one species or a group of species of presumably common phylogenetic origin, which is separated from other similar units by a decided gap" (Mayr, Linsley, and Usinger 1953). However, the gap necessary to distinguish between groups of species belonging to different genera cannot be objectively defined. Rather, this must be decided by the taxonomist on the basis of his knowledge and experience in the group. Consistency in deciding the nature and size of the gap (degree of morphological difference) required to separate related genera is imperative in producing a uniform and workable classification.

In this study, I have recognized the previously described genera, *Callida*, *Philophuga* and *Tecnophilus*, and have used the degree of morphological difference between these three genera as a guideline by which to recognize other genera within this subtribe. The species *Philophuga castanea* Horn differs from the other species included in the genus *Philophuga* by at least as much as these species differ from the species included in the genera *Callida* and *Tecnophilus*. For this reason, I removed *castanea* from *Philophuga* and proposed the new genus *Infernophilus* to contain it. Recognition of *Infernophilus* is consistent with the maintenance of *Callida, Philophuga* and *Tecnophilus* as distinct genera.

Morphological Methods

To examine characters of the wings and of the genitalia, the specimens were first relaxed by placing them in boiling water for five to ten minutes. After this time, the specimens were sufficiently pliant to allow the elytra to be lifted so that the hind wings could be examined. This was adequate to determine the relative size of the wings. However, in cases where it was necessary to study the pigmentation of the wings, the hind wing was removed by breaking it off near the base. The wing was unfolded and first studied in water, then flattened out and glued to a card which was pinned beneath the specimen.

Male and female genitalia were removed from the relaxed specimens by breaking the supporting membranes around the genitalia with a hooked insect pin. The genitalia were removed with a pair of fine forceps. After dissection, the genitalia were placed in cold 10% KOH and allowed to stand overnight to clear the sclerites. The male genitalia were then examined with a binocular microscope. It was necessary to mount the female genitalia on slides and examine them with a compound microscope at higher magnification.

Preservation of Larvae

To prevent distortion and discoloration of specimens, larvae were killed by dropping them directly into gently boiling water. They were quickly removed and preserved in 70% ethanol. This method of killing extends the larvae to their maximum length and preserves color and hence facilitates later study.

Rearing Methods

Adult specimens of *Tecnophilus* were reared in the laboratory to obtain eggs and larvae. After collection, five or six specimens were placed in each jar, where mating readily occurred. After mating, the females were removed and isolated in small jars which contained soil a half inch deep and several twigs that permitted the insects to climb. Pieces of mealworm were added for food, and water was sprinkled into the jar weekly.

If adequate food and moisture were provided, the females began to oviposit within a week after mating. The eggs were removed as they appeared, and were placed on a moistened blotter in a petri dish where they were left until hatching occurred. Newly emerged larvae were isolated in small vials and were fed pieces of various soft-bodied insect larvae. High humidity was maintained by placing a piece of moistened blotting paper in the neck of the vial. Mortality was high, but a number of larvae were reared to the second and third instars.

Measurements and Ratios

Measurements were made of representative specimens of all species and subspecies dealt with in this study. Although they did not provide diagnostic characters for any species, measurements and the ratios derived from them were valuable in the analysis of intra-specific variation. A micrometer eyepiece in a Wild M5 stereoscopic microscope at a magnification of X 50 was used for these measurements.

The total length (TL) of adult specimens was obtained by the addition of three measurements: the length of the head from the anterior margin of the clypeus to the mid-point of the occipital groove (LH); the length of the pronotum along the mid-line (LP); and the length of the left elytron from the apex of the scutellum to the apex of the elytron (LE). Total length (LH + LP + LE) obtained in this way was not affected by contraction or curvature of the specimen. Other measurements taken of adult specimens and their abbreviations are: Width of pronotum (WP) - width across widest point of pronotum; maximum width of head (WH_1) - width of head across eyes; width of head between eyes (WH_2) - minimum width of frons between eyes. Measurements taken of larval specimens are: Width of head (WH) - width across widest part of head capsule; width of pronotum (WP) - width across widest part of pronotum; total length (TL) - one measurement of length from the anterior margin of the nasale to the posterior margin of abdominal segment 10. All ratios used in the text are derived from the above measurements, and are expressed in terms of the above abbreviations.

Analysis of Variation

Specimens from populations that differ slightly and possibly discordantly in a number of characters, may be assigned to the correct population by means of the discriminant function. In the study of such groups, the traditional methods of taxonomy, observation and comparison, do not work well for the mind is incapable of making the numerous summated judgments required.

The discriminant function used in this study has been developed by Fisher (1936) and outlined by Stanley (McGill University unpublished MS). The method has been used or discussed by Goulden (1952) and Bigelow and Reimer (1954).

Interpretation of the discriminant function is similar to that used for the hybrid index (Freitag 1965). Using this method, a specimen which deviates from the other members of its population in only one or a small percentage of its total characters, is still assigned to its correct population because of its greater overall similarity to members of that population. This reduces the possibility of mis-identification due to the over-weighting of one character.

Illustrations

Illustrations are presented to augment descriptions. These were prepared with the aid of an ocular grid in a stereoscopic microscope.

The male genitalia have been illustrated for many species even though they usually present few useful characters. Stippling has been used to indicate the folding pattern of the endophallus but as this folding pattern varies with small changes in inversion, it should not be considered as important in identification.

The slender sub-apical spines on the stylus of the female ovipositor have been included in illustrations of the styli. Both dorsal and ventral spines have been shown as though they occurred in the same plane, as this is the way they appear when the stylus is cleared in potassium hydroxide and mounted on a microscope slide.

Distribution maps are presented for all species and subspecies. Also maps summarizing data on intra-specific variation in the species *Philophuga viridis* and *Tecnophilus croceicollis* are included.

Taxonomic Characters

Taxonomic Characters of Adults

Color. - Within the Callidina, color is useful in the identification and classification of species, and to a limited extent, genera. Non-metallic colors are described by the terms yellow, testaceous (brownish-yellow), rufous (reddish), brown, piceous and black. The color black often has a metallic sheen associated with it. Metallic colors are usually blue or green. To describe variation in certain species, intermediate colors are designated in terms such as blue-green (green predominant) or greenish-blue.

External morphology. - Punctation and vestiture of the body, while extremely useful for the recognition of species and subspecies with *Philophuga* and *Tecnophilus*, are difficult characters to interpret and quantify. As the setae composing the dorsal vestiture of the body are situated in usually distinct punctures, the punctation of the body often gives an indication of the vestiture. However, in specimens from certain populations, the body is deeply punctate, but the punctures do not bear setae, or bear very inconspicuous setae. Care must be taken to avoid confusing these specimens with normally setose specimens that have been rubbed. The depth and density of the punctures in the elytral striae and on the elytral intervals are important for identification.

To describe the depth of punctation of the body and the depth of the impression of the elytral striae, the terms lightly, moderately and coarsely have been used. These terms are strictly comparative, and have been avoided as much as possible in keys. However, they have been used in descriptions in a comparative sense. Similarily, the terms sparse, moderate and dense have been used to describe vestiture.

The shape of the head shows both intra- and inter-specific variation. Differences in the convexity of the eyes and the constriction of the neck present characteristic forms for certain species. For all species, values for the ratio of the width of the head across the eyes to the minimum width of the head between the eyes has been presented in an attempt to quantify differences in eye convexity. This ratio is not diagnostic of any species but it provides an index of the head shape.

The post-ocular pinch is an impression just behind the posterior dorsal margin of the eye. This pinch is evident but small in most of the Callidina. However, in some of the neotropical species of *Callida* and in some species of *Cymindis* this pinch is very strongly developed.

The mouthparts were not found to provide any characters useful for species recognition. They are of value at the generic level, but even here their importance has been overestimated in past works.

The shape of the pronotum is of appreciable diagnostic value. In *Philophuga*, differences in pronotal shapes between related species are often slight and may be within the range of normal intra-specific variation. In *Tecnophilus* the shape of the pronotum is much more characteristic of a species, and is usually rather constant within a population sample. The pronotum has been illustrated for most species and subspecies.

The wings present several characters which are considered very important in *Philophuga*. Wing reduction occurs in this genus and has been used to distinguish between several subspecies of *viridis*. Also, the degree to which the membranous areas of the wings are pigmented is useful in the recognition of certain species. The wing venation was not found to offer any characters of diagnostic value at either the specific or generic levels.

Habu (1967) made extensive use of the structure of the legs in his classification of the Japanese Lebiini. In the present study, only two characteristics of the legs have been used: the structure of tarsal article 4; and the structure of the tarsal claws. Two forms of tarsal article 4 are found among the Nearctic Callidina, the bilobed form and the emarginate form. These are illustrated in figs. 28 and 29 respectively. The tarsal claws of members of the genus *Tecnophilus* are simple, while members of the other North American callidine genera possess pectinate claws.

Characteristic arrangements of setae on the ventral surface of the abdomen provide useful characters for the recognition of two genera. The usual arrangement of setae is: visible sterna 2 to 5 each with a pair of medial setae, sternum 6 with one to three pairs of anal setae. However, members of the genus *Plochionus* bear, in addition to the above-mentioned setae, a distinctive arrangement of setae on the lateral margins of sterna 4, 5 and 6 (fig. 26). Members of the genus *Infernophilus* lack the lateral setae, but sternum 6 possesses a pair of dense brushes of setae (these brushes are much denser in the male than in the female, fig. 27).

Male genitalia. - The structure of the male genitalia is rather consistent within the species of *Philophuga* and *Tecnophilus*. The aedoeagus (intromittent organ, see Torre-Bueno 1962) is slightly arcuate, with a prominent rounded apex. The basal piece, the portion of the aedoeagus surrounding the basal orifice, varies slightly, but is of minor taxonomic importance. The endophallus is usually unarmed and possess only poorly defined spiculate fields. However, the genitalia of *Infernophilus* shows a number of peculiarities.

Female ovipositor. - The structure of the apical article of the stylus is of great importance in determining subtribal affinities. Basically, the stylus is rectangular in shape, lightly sclerotized and with a setose apical margin. In *Tecnophilus pilatei* Chaudoir (fig. 55), and *Callida decora* Fabricius (fig. 50), the outer apical corner of the stylus is greatly produced. In *Infernophilus* (fig. 57) the apex of the stylus is broadly rounded and in *Plochionus* (figs. 45, 46) the apex is sharply pointed with a tassel-like arrangement of setae. Small slender spines are scattered over the surface of the stylus but were found to be of little taxonomic value.

Taxonomic Characters of Larvae

As larvae representing only a few of the species of the *Callidina* have been seen, the variation and distribution of the taxonomically important characters within the subtribe are unknown.

Color. - Color is of considerable value in recognizing the larvae of certain genera. The terminology used to describe color is presented under taxonomic characters of adults.

External morphology. - Most of the characters and terminology used are taken from Van Emden (1942).

The subtribal character of the presence of a soft membranous pulvillus between the tarsal claws is difficult to observe in some specimens; hence this structure must be sought for with care.

The dorsal surface of the maxilla of *Plochionus* possesses short dense setae (fig. 8). This surface is glabrous or covered with very short stout sensilla in the larvae of the other callidine genera.

The shapes of the pronota of *Philophuga* (fig. 9) and *Tecnophilus* (fig. 10) have been used to separate the larvae of these two genera. The number of articles in the cerci of 2nd and 3rd instar larvae also separates these two genera, but because this character could not be used to separate the larvae of all instars, it was not used in the key to genera.

TAXONOMY - THE SUBTRIBE CALLIDINA

This subtribe may be defined as follows:

Adult. - Lebiini with the following characteristics: labrum transverse, with six setae along anterior margin; mandible widened toward base, usually with scrobe; labial palpus with penultimate article bisetose, apical article securiform or at least tumid (less in female than in male) and truncate apically; ligula bi- or plurisetose apically, paraglossae not or but slightly extending beyond ligula; mentum usually with a tooth; fore tarsus of male with various number of articles bearing ventral adhesive scales, such scales frequently present on some articles of middle tarsus; tarsal article 4 bilobed, emarginate or simple; prothorax not lobed behind; male genitalia with smaller paramere bilobed apically; female stylus with setose apex.

Larva. - Head approximately quadrate; epicranial suture wanting, lateral sutures meeting medially at cervical margin; adnasale prominent, covering base of mandibles; nasale broad and prominent, entire or variously emarginate apically; antenna shorter than mandible, article 3 about twice length of article 1, and bearing a short sensory papilla distally; mandible bisetose externally, with reduced or obsolete retinaculum, penicillus present; maxilla without an inner lobe, palpiger evident; labium with a pair of prominent apical setae; leg with two equal claws, claws simple or toothed basally; pulvillus present, conspicuous or not; tergites margined anteriorly; abdominal segment 10 with a pair of protrusible vesicles, each bearing a semicircular row of crochets; cerci of four or five articles.

This definition of the Callidina is based upon the limited lebiine fauna of the United States. In this region, the genera *Callida* Latreille and Dejean, *Cylindronotum* Putzeys, *Lecalida* Casey, *Onota* Chaudoir, *Philophuga* Motschoulsky, *Plochionus* Wiedemann, *Tecnophilus* Chaudoir, and *Infernophilus* new genus may be assigned to the Callidina.

As defined here, this subtribe is more restricted than conceived by either Chaudoir (1872) or Habu (1967). Habu regarded the shape of the mandibles, the form of the tarsi and the structure of the female ovipositor as the principal subtribal characters. The structure of the tarsus does not unite the Nearctic genera of the Callidina. *Callida* possesses dilated tarsi (fig. 28) which Habu regards as characteristic of this subtribe. However, the closely related genus *Philophuga*, has only the stout form of tarsus (fig. 29) and members of the genus *Tecnophilus* possess almost slender tarsi. Both stout and dilated tarsi are found in the genus *Plochionus.*

Habu recognizes three forms of female ovipositor among the Japanese Callidina. These are as follows: (a) hemisternites transverse, apical segment of stylus long and pubescent apically (figs. 44-57); (b) hemisternites transverse, apical segment of stylus without terminal setae; (c) hemisternites not transverse, apical segment of stylus without pubescence but with slender spines near apical angle (fig. 43). In the Nearctic fauna, no genus occurs which possesses type "b" ovipositor, so I have not been able to determine the relationship between this form of ovipositor and type "a" ovipositor. Members of *Euproctinus* Leng and Mutchler possess type "c" ovipositor (fig. 43). As this genus differs from the North American callidines on the basis of the female ovipositor and larval characteristics, I exclude it from the Callidina. Because *Euproctinus* cannot be assigned to any of the presently recognized subtribes, a new subtribe may have to be proposed to receive it.

The unique brush-like stylus forms an excellent subtribal character for the Callidina, for while the structure shows considerable variation among the genera, the basic form remains recognizable. No other character examined has shown as great a diagnostic value within this group at the subtribal level.

LARVAE

The larvae of few species of the tribe Lebiini have been described. This may be the result of at least two factors which make it difficult to obtain the requisite specimens: adults of many species are rarely collected; and the species of at least one genus, *Lebia* Latreille, have a complex developmental cycle (Lindroth 1954, Madge 1967).

Key to the Larvae of the North American Subtribes of Lebiini *(modified from van Emden 1942)*

1\. Retinaculum of mandible vestigial or absent; or if well developed, the cervical groove and keel are present; antenna with article 1 longer than article 3 2

1'. Retinaculum well developed, projecting by more than a third of width of mandible just apicad of retinaculum; head without cervical groove or keel; antenna with article 1 shorter than article 3; tarsal claws toothed or simple . . . . Dromiina

2(1). Tarsus without a pulvillus; tarsal claws with or without a basal tooth, but if tooth present, head with a cervical groove 3

2'. Tarsus with a soft unpaired but more or less bilobed pulvillus between claws; retinaculum vestigial or absent; head without cervical groove; epicranial suture very short or almost absent 5

3(2). Retinaculum distinct; cervical groove and keel present except if antennal article 1 is longer than article 3; maxillary stipes rather slender, almost or fully three times as long as wide . . . . Coptoderina

3'. Retinaculum small, vestigial or absent; cervical groove absent; antennal article 1 shorter than 3; maxillary stipes robust, at most twice as long as wide 4

4(3). Ligula and its two setae well developed; epicranial suture present though short in some species; cercus of 5-7 articles (but of four articles in at least some first instar specimens) . . . . Cymindina

4'. Ligula and its two setae minute or absent; epicranial suture absent; cercus with at most four articles . . . . Lebiina

5(2). Anterior margin of abdominal tergites with margined border . . . . Callidina

5'. Anterior margin of abdominal tergites without margined border . . . . *Euproctinus* Leng and Mutchler

The Callidina, Cymindina and Lebiina show a number of common features that distinguish these groups from the Dromiina and Coptoderina. However, I do not intend to propose a classification based on characteristics of lebiine larvae. Rather, the known larvae were examined to determine if their characteristics substantiated the generic separations proposed in the Callidina on the basis of characters of adults. Where larvae were available, their characters supported the adult classification.

Key to the known Larvae of the Nearctic Genera of the Subtribe Callidina

1\. Anal vesicles of abdominal segment 10 bearing crochets 2

1'. Anal vesicles of abdominal segment 10 without crochets . . . . *Onota* Chaudoir

2(1). Maxilla with dorsal pubescence in addition to the usual fixed setae (fig. 8); nasale narrow, without a deep medial incision (fig. 7) . . . . *Plochionus* Weid. p. 25

2'. Maxilla glabrous except for usual fixed setae and short stout sensillae; nasale broad, with a deep medial emargination (figs. 11-14) 3

3(2). Pronotum quadrate (fig. 9) *Philophuga* Mots. p. 25

3'. Pronotum conical, widest basally and narrowing anteriorly (fig. 10) . . . . *Tecnophilus* Chaud. p. 26

Plochionus Wiedemann 1823

Larvae of only *P. timidus* Haldeman 1843 have been seen. The following description is based on five specimens from Kirkwood, Missouri (29/VI/1892, USNM).

Description. - Values for ratios and measurements are: TL, 2nd instar 5.9-7.4 mm; 3rd instar 8.9-10.4 mm; WH/LH, 2nd instar 1.30-1.36, 3rd instar 1.24-1.28; WP/WH, 2nd instar 1.20-1.24, 3rd instar 1.25.

Color whitish, head and anterior portion of pronotum yellow; nota two and three, legs, and abdominal tergites testaceous, without metallic lustre; sternites and pleurites testaceous-yellow.

Head broad, more or less quadrate, but somewhat rounded laterally; nasale convex with a prominent relatively narrow tri- or quadridentate medial tooth (fig.7); medial suture present but very short, divided into paired sinuate lateral sutures a short distance anterior to cervical margin, cervical border narrow.

Antenna shorter than mandible, with four articles; article 1 broad, about one half length of article 3; article 4 narrow, broadly rounded apically; article 3 with a minute subapical sensillum; subapical setae on articles 3 and 4 only.

Mandible relatively short, slightly and unevenly arcuate, with two external setae; retinaculum minute, rounded and blunt apically; internal apical half of mandible expanded and plate-like; penicillus present at base.

Maxilla (fig. 8) hairy above, with internal dorsal row of short stiff setae; ventral surface glabrous except for usual long setae; internal lobe absent; palpiger well developed, terminal article of palpus conical and pointed apically; median lobe with two articles, distal article very small.

Labium with medial pair of setae subapical and dorsal, ventral pair of setae also present; palpi of two articles, glabrous, apical article elongate, conical.

Prothorax transversely rectangular, broader and longer than head; lateral margin narrow and faint.

Legs with tarsal claws toothed at base and equal; pulvilli present but inconcpicuous.

Anterior margins of tergites and nota strongly margined; tergites entire; ventral sclerites consisting of a ventrite and three pairs of lateral postventrites, all lightly sclerotized and poorly delimited.

Abdominal segment 10 with a pair of protrusible anal tubes, each bearing a semicircular row of crochets; cerci elongate, slender, with five articles in 2nd and 3rd instar larvae (1st instar larvae not seen).

Discussion. - The larva of *Plochionus* stands apart from the known larvae of the other North American callidine genera on the basis of its setose maxillae, and toothed tarsal claws. Consequently, the position of this genus among the North American Callidina is unclear, and probably cannot be settled until the Neotropical genera are better known.

Philophuga Motschoulsky 1859

In this genus, the larvae of *P. viridicollis* LeConte and *P. viridis amoena* LeConte are known. As only first instar larvae of *viridis*, and second and third instar larvae of *viridicollis* were available, I was not able to find characters that would distinguish between the two species with any degree of certainty. Because of this, a key is not provided, and only the larva of *viridicollis* is described below.

Philophuga viridicollis LeConte 1848

A third instar larva, two pupae, an associated adult and a number of exuviae of *viridicollis* were seen (Rocky Ford, Colorado, Aug. 17, 1915, Hamilton Coll., USNM). Van Emden (1942) included this material under *Callida*, as *C. purpurea* Say.

Description. - Values for ratios and measurements of 12 larvae and exuviae are: TL, 3rd instar 9.1 mm; WH/LH, 3rd instar 1.18-1.22 (X = 1.20), 2nd instar 1.15-1.20 ($\bar{X}$ = 1.18); WP/WH, 3rd instar 1.18.

Color whitish; head testaceous; body sclerites brown to piceous with a metallic green or violaceous sheen.

Head (fig. 11) broad, almost quadrate with hind angles broadly rounded; frontal piece broad; sinuate lateral sutures meeting medially at cervical margin, median suture absent; nasale very broad, deeply incised medially, lateral portions tridentate; cervical margin narrow; ocelli six, strongly pigmented.

Antenna slightly shorter than mandible, of four articles; article 4 narrow, subequal in length to article 3, article 1 short; article 3 with a small subapical sensillum; subapical setae on articles 3 and 4 only.

Mandible slender and arcuate, with two lateral setae; retinaculum small and inconspicuous; basal penicillus present.

Maxilla with an internal dorsal row of stout setae plus usual long fixed setae, otherwise glabrous above; inner lobe absent; palpi with well developed palpiger, terminal article narrow and pointed.

Labium broad, bisetose apically, also with a pair of subapical ventral setae; palpi of two articles, glabrous.

Prothorax transversely rectangular (fig. 9), wider than head; lateral margin strong and complete.

Legs with equal simple claws; pulvilli present.

Tergites entire, with strong anterior borders; lateral margins of meso- and metanota angular; ventral sclerites consisting of a ventrite and three pairs of lateral postventrites.

Cerci with five articles in second and third instars, only subapical setae present; abdominal segment 10 with a pair of eversible anal tubes, each bearing a semicircular row of crochets.

Discussion. - Van Emden (1942), who saw some larval specimens of *Callida*, keyed *Callida* and *Philophuga* to the same couplet, stressing their similarities especially in the shape of the nasale, number of articles in the cerci, and the shape of the tarsal claws. Larval characteristics apparently confirm the close relationship suggested for these two genera by adult characteristics.

Tecnophilus Chaudoir 1877

The larvae of both subspecies of *Tecnophilus croceicollis* Mén. are known. They were obtained by rearing from adults collected at the following localities: junction of the Lost and Milk Rivers, Alberta (*T. c. peigani* n. ssp.); Cuddeback Lake and Alviso, California (*T. c. croceicollis* Mén.).

Description. - Values for ratios and measurements are presented in table 1. The first instar larva of *T. croceicollis* Men. is illustrated in fig. 6.

TABLE 1. Variation in dimensions and ratios among the larvae of *Tecnophilus croceicollis* Ménétriés.

Locality	No. of specimens	Instar	Width/length of head		Width pronotum/ width of head		Width of head (mm)	
			Range	Mean	Range	Mean	Range	Mean
Newark,	15	1	0.93-1.04	(0.97)	1.07-1.20	(1.14)	0.52-0.54	(0.52)
Calif.	6	2	0.97-1.03	(0.98)	1.14-1.31	(1.22)	0.62-0.70	(0.68)
	1	3	1.00		1.17		0.96	
Cuddeback	6	1	0.93-1.04	(0.98)	1.16-1.20	(1.17)	0.48-0.50	(0.50)
Lake, Calif.	2	3	0.94-0.98	(0.96)	1.16-1.18	(1.17)	0.90-0.96	(0.94)
Jct. Lost &	13	1	0.96-1.04	(0.97)	1.13-1.29	(1.19)	0.48-0.54	(0.51)
Milk Rivers,	2	2	0.91-0.93	(0.92)	1.24-1.38	(1.31)	0.78-0.84	(0.81)
Alberta	1	3	0.96		1.25		0.88	

Color whitish; head capsule and in many specimens prosternum and anterior half of pronotum yellow; remaining sclerites and appendages piceous, with at least a faint metallic green cast.

Head rectangular (figs. 12-14); frontal piece broad, medial suture wanting, sinuate lateral sutures meeting medially just anterior to cervical margin; nasale broad, deeply cleft medially, lateral pieces shallowly bifid; posterior constriction of head varied; cervical margin narrow; ocelli six, strongly pigmented.

Antenna shorter than mandible, with four articles; article 1 short, broad, about one half length of article 3; article 4 narrow, widening apically where broadly rounded; subapical setae on articles 3 and 4 only; small sensillum on article 3.

Mandible slender, with two lateral setae; retinaculum small, but evident; basal penicillus present.

Maxilla with internal dorsal row of short, stiff setae and scattered long external setae, otherwise glabrous; palpiger distinct; palpus with three articles, article 3 short, narrow; inner lobe absent; outer lobe with two articles, article 2 very short and narrow, basal article with a single preapical seta.

Labium bisetose apically, also with a pair of ventral setae; palpi with two articles, terminal article short and narrow, pointed apically.

Prothorax somewhat conical (fig. 10), widest basally and narrowing anteriorly to about width of base of head; variously margined laterally.

Legs with equal simple claws; pulvilli present but reduced.

Tergites and nota margined anteriorly; ventral sclerites consisting of a ventrite and three pairs of postventrites.

Cerci of four articles in all instars; abdominal segment 10 with a pair of eversible vesicles, each bearing a semicircular row of crochets.

Discussion. - I was unable to find characters to distinguish between the larvae of *T. c. croceicollis* and *T. c. peigani*. Table 1 summarizes variation in measured characteristics and ratios among larvae from three localities.

The larvae of *Tecnophilus* are similar to those of *Philophuga*, but they can be distinguished from one another by the character presented in the key. Also, larvae of all instars of *Tecnophilus* have cerci of only four articles. In *Philophuga*, on the other hand, the first instar larvae have cerci of four articles while later instars have cerci of five articles. These differences do not contradict the separation of *Tecnophilus* and *Philophuga* at the generic level.

ADULTS

Characteristics common to all members of the subtribe Callidina, are presented in the taxonomy section. Below is a key to the adults of the North American genera of the subtribe Callidina. Following the key, the genera *Philophuga*, *Infernophilus* and *Tecnophilus* are discussed in detail. I have not had the opportunity to examine the other genera in detail, as the majority of their members are neotropical. Hence any remarks about the latter group are tentative.

Key to the Adults of the North American Genera of the Subtribe Callidina
(modified from Ball 1963)

1. Mandible broadly expanded, without scrobe .... *Onota* Chaudoir
1'. Mandible with scrobe 2
2(1). Mentum without a tooth; width of pronotum less than maximum width of head .... *Cylindronotum* Putzeys
2'. Mentum with a tooth; width of pronotum greater than width of head............. 3
3(2). Lateral margin of abdominal sternum 4 with one seta, sternum 5 with two setae, and sternum 6 with one seta (fig. 16); hind femur broad.......... *Plochionus* Wiedemann
3'. Lateral margin of abdominal sterna 4, 5 and 6 without such arrangement of long setae; hind femur slender 4
4(3). Tarsus with fourth article bilobed (fig. 28) 5
4'. Tarsus with fourth article at most emarginate (fig. 29)........................ 6
5(4). Elytra metallic green or blue; pronotum elongate and slender, lateral grooves narrow. .... *Callida* Latreille and Dejean

5'. Entire body rufo-piceous, without metallic color; pronotum with lateral grooves broad .... *Lecalida* Casey

6(4). Tarsal claws pectinate 7

6'. Tarsal claws simple .... *Tecnophilus* Chaudoir, p. 38

7(6). Color dark with metallic blue or green sheen; abdominal sternum 6 with at most four pairs of anal setae .... *Philophuga* Motschoulsky, p. 24

7'. Color brown, non-metallic; abdominal sternum 6 with at least six pairs of moderate to long setae in female, distinct anal brushes present on male (fig. 27)................ .... *Infernophilus* new genus, p. 37

Philophuga Motschoulsky 1859

Philophuga Motschoulsky 1859 - 140.

Philopheuga Bates 1883 - 202.

Glycia LeConte 1851, not Chaudoir 1842.

Type species - *Philophuga cyanea* Motschoulsky 1850 (= *P. viridis* Dejean), here designated.

The diagnostic features of this genus are presented in the key. Other characteristics, common to all species of *Philophuga*, are given in the following description.

Description - Beetles 5.5-10.0 mm in length. Color various, but at least elytra and abdominal sterna dark with a metallic blue or green sheen; antennae black with articles 1 to 3 and base of 4 pale, at least on ventral surface.

Head with eyes prominent, convex; at least a faint post-ocular pinch present. Genae variously narrowed behind, neck evident. Labrum slightly emarginate medially; clypeus with a single seta on each side. Frons with indistinctly defined, rugose frontal furrows; punctate, at least laterally and posteriorly. Antennal articles 1 to 3 and base of 4 glabrous or very sparsely and finely hairy; remaining articles pubescent. Maxillary palpus with fusiform terminal article. Labial palpus with penultimate article bisetose; terminal article securiform (narrower in female). Ligula bisetose. Mentum with a prominent margined tooth.

Pronotum varied in shape; sides usually evidently sinuate behind; disc transversely rugose, best developed laterally; posterior lateral setae present or absent.

Tarsal articles glabrous or sparsely hairy above, moderately setose beneath; article 4 emarginate; claws pectinate; male with articles 1 to 4 of front and middle tarsi bearing two rows of scales beneath.

Elytra completely margined basally and apically. Hind wings full or reduced.

Abdominal sterna 3 to 5 with a pair of medial setae; sternum 6 with one to four pair of anal setae (male with usually one less pair of setae than female); sterna 4 to 6 without long lateral setae.

Male genitalia on right side in repose, left paramere large; aedoeagus tube-like,with apical orifice opening slightly to left of midline of aedoeagus; endophallus unarmed.

Female styli of typical callidine form.

Discussion. - Some members of this genus are superficially very similar to certain of the species included in the genus *Callida* (for example *Philophuga viridis amoena* LeConte and *Callida purpurea* Say; and *Philophuga brachinoides* Bates and *Callida decora* Fab.), and can often be recognized only on the basis of the character presented in the key. Even in the structure of tarsal article 4, *C. purpurea* very closely approaches the condition found in members of *Philophuga*. Perhaps when the species of *Callida* are studied in more detail, it will be found necessary to include *Philophuga* in *Callida*, as a subgenus (a parallel situation occurs in the two subgenera of *Plochionus* Weidemann which are separated by differences in the structure of tarsal article 4). However, in this study the status of *Philophuga* as a distinct genus is maintained

Distribution.- The species of *Philophuga* occur in the semi-arid and arid regions of western North America.

Key to the Species of *Philophuga* Motschoulsky

1. Pronotum rufous, contrasting with black head............ *brachinoides* Bates, p. 30
1'. Pronotum and head concolorous, black with a metallic blue or green sheen........ 2
2(1). Hind wings constantly full, membranous areas distinctly pigmented (fig. 23); hind angle of pronotum with a setiferous puncture 3
2'. Hind wings reduced, without reflexed apex, or if full, membranous areas not or only lightly pigmented; hind angle of pronotum with or without a setiferous puncture .. .. *viridis* Dejean, p. 34
3(2). Head and pronotum with metallic green lustre, contrasting with blue elytra, or elytra also green; elytral striae shallowly impressed; intervals flat, finely punctate.......... .... *viridicollis* LeConte, p. 31
3'. Head and pronotum with metallic blue or blue-green lustre, similar in color to elytra and not contrasting; elytral striae deeply impressed; intervals convex, finely to moderately coarsely punctate.............................. *caerulea* Casey, p. 33

Philophuga brachinoides Bates 1883

Philopheuga rachinoides Bates 1883 - 202. *Type locality* - Cerro de Plumas, Veracruz (Selander and Vaurie 1962), Mexico. Blackwelder 1944 - 62 (*Philophuga*).

Description. - Values for ratios and measurements for five specimens are: TL 6.8-7.8 mm (7.2); LE/LP 2.70-2.86 (2.75); WP/LP 1.18-1.28 (1.24); WH_1/WH_2 1.41-1.48 (1.45).

Color of prothorax, mesothorax, femora and antennal articles 1 to 3 and base of 4 rufous; remainder of body piceous to black with a metallic blue lustre.

Microsculpture obsolete on frons and disc of pronotum; strong on elytra, isodiametric medially, slightly stretched laterally.

Eyes prominent; post-ocular pinch faint. Genae strongly constricted behind, forming relatively narrow neck. Labrum broadly but shallowly emarginate. Clypeus micropunctate. Frons smooth and shiny medially, deeply but sparsely punctate posteriorly and laterally; frontal furrows short, deep, confluently punctate.

Prothorax (fig. 33) rounded laterally, sinuate before prominent though obtuse hind angles; front angles rounded, not or only slightly protruding; hind angle on each side bearing a setiferous puncture; disc glabrous, transversely rugose. Prosternum with very short fine setae. Metasternum with scattered moderately long fine setae.

Elytral striae clearly impressed medially on disc, effaced apically and in some specimens also laterally; discal striae finely punctate, punctures coarser basally and laterally; intervals slightly convex, each bearing an irregular row of fine punctures. Wings full, densely pigmented.

Abdominal sternum 2 with a small medial patch of setae; remaining sterna with very short sparse setae; abdominal sternum 6 with two pairs of anal setae in male, and three pairs in female.

Aedoeagus elongate, slender. Female stylus as in fig. 54.

Discussion. - This species very closely resembles *Callida decora* Fab. in color. It is the only species of *Philophuga* with pale legs and thorax.

Distribution. - I have seen only five specimens of this species from the following locality (fig. 60).

MEXICO, Oaxaca, Rte. 190, 21.7 miles SE Nochixtlan, 7200'. March 24, 1966 (Ball and Whitehead, UASM).

Philophuga viridicollis LeConte 1848

Cymindis viridicollis LeConte 1848 - 188. *Lectotype* - (here selected) female, labelled as follows: green disc, *Glycia viridicollis* Lec., Type 5821 MCZ, *Philophuga viridicollis* (Lec.).

Philophuga subcordata Chaudoir 1877 - 246. Holotype not seen. *Type locality* - "Mexique".

Philophuga purpurea Chaudoir 1877 - 245, not Say 1823.

Description. - Values for ratios and measurements of 40 specimens are: TL 7.1-9.6 mm; LE/LP 2.77-3.13 (2.98); WP/LP 1.07-1.29 (1.19); WH_1/WH_2 1.42-1.54 (1.47).

Color of head, pronotum and ventral parts of thorax and abdomen shiny metallic green or blue-green; elytra duller, blue or rarely in some specimens green; legs, epipleura and lateral portions of abdominal sterna piceous to black; antennae with articles 1 to 3 and base of 4 pale, at least on ventral side, outer articles black; palpi dark, with apex of terminal articles pale.

Microsculpture more or less effaced on head; lightly impressed and transverse on pronotum; finely granular on elytra, rarely slightly stretched.

Head with basal constriction gradual, neck evident; eyes prominent, convex. Labrum slightly emarginate. Clypeus smooth and shiny, irregularly and finely punctate; frons shiny, often with faint transverse rugae, sparsely but deeply punctate posteriorly and laterally; frontal furrows broad, poorly delimited, confluently punctate and longitudinally rugose; genae behind and below eyes with short sparse setae; labial palpus with terminal article very broadly dilated in male, less so in female.

Pronotum (fig. 31) narrow, broadest in apical third, rounded laterally with a faint sinuation before hind angle; hind angle obtuse and somewhat rounded, bearing a setiferous puncture; front angle rounded, slightly protruding; base clearly margined, at least laterally; prosternum and proepisternum sparsely punctate; prosternal punctures bearing very short fine setae. Metasternum punctate laterally, sparsely setose medially.

Elytra elongate, subparallel; striae fine, often only very faintly impressed apically, moderately punctate, punctures deeper and denser in basal half; intervals flat, with an irregular row of faint punctulae in each. Wings fully developed, strongly pigmented.

Abdominal sterna with fine setiferous punctures medially; abdominal sternum 6 with two pairs of anal setae in female and three pairs in male.

Male genitalia (fig. 15) with aedoeagus slightly arcuate dorsally; basal piece flattened, bent somewhat to right. Female stylus as in fig. 51.

Variation. - No marked pattern of variation was noticed for this species. These characters were observed to vary within a single population sample: shape of the pronotum, microsculpture of frons and pronotum, and the depth of the elytral striae. The color of the head and the pronotum varies from metallic green to blue-green, but remains sufficiently green to contrast conspicuously with the blue elytra. This color contrast is lost in the few specimens that possess greenish elytra. Color, however, is the most reliable character for separating *viridicollis* from the markedly similar *caerulea.*

Discussion. - I have seen two specimens of *viridicollis* from the following California localities: San Francisco (Hopping, CAS); Needles (CAS). As no specimens of this species have been seen from Arizona and western New Mexico, these specimens may have been accidently mislabelled. The two species *viridicollis* and *caerulea* appear to be almost completely allopatric (see discussion under *caerulea*).

Notes on synonomy. - Say's (1823) original description of *Callida purpurea* and *C. viridipennis* (both originally assigned to *Cymindis*) stated that article 4 of the tarsus was bilobed for these two species, thereby confirming their position in *Callida.* However, Chaudoir (1877) applied the name *purpurea* Say to specimens of *Philophuga viridicollis* LeConte, and relegated the name *viridicollis* LeConte to synonymy. Horn (1882), after receiving identified specimens of *Philophuga* from Chaudoir, noticed this confusion and corrected it by placing *purpurea* Say in the genus *Callida*, and reinstating *viridicollis* in *Philophuga.* In the same paper, Horn suggested that *subcordata* Chaudoir was probably a synonym of *viridicollis* LeConte. Leng (1920) followed Horn's suggested synonymy, and although the type of *subcordata* Chaudoir has not been seen in this study, this synonymy is followed here.

Specimens of the species *viridicollis* LeConte and *caerulea* Casey have been confused with one another. LeConte's collection contains specimens of both of these species under the name *viridicollis.*

Distribution. - The species *viridicollis* is found in the southern Great Plains, from Kansas and eastern Colorado south into eastern New Mexico, Texas (excluding the Edwards Plateau), northeastern Mexico and possibly California – but see above (fig. 58). I have examined over 260 specimens of this species from the following localities:

United States - ALABAMA: one specimen labelled "Ala." (WUM). COLORADO: Otero Co., Rocky Ford (Hamilton, USNM). KANSAS: Ellsworth Co., (Martin, KUM); Kiowa Co., (Woodruff, KUM); Reno Co., (Hopping, CAS); Sumner Co., (USNM). NEW MEXICO: Lincoln Co., Ramon (Ball, UASM); Roosevelt Co., Portales (IUM), Water Canyon (Shaw, CU). OKLAHOMA: Oklahoma Co., Oklahoma City (Grant, CAS), Stillwater (Whitaker, MCZ). TEXAS: Atascosa Co., Pleasanton (White, CNHM); Bee Co., Beeville (Tucker, USNM); Bexar Co., San Antonio (CAS, CUM, USNM); Blanco Co., Cypress Mill (USNM); Brewster Co., Alpine (CAS, USNM), Big Bend Nat'l Park (Becker & Howden, CNC), Horse Canyon (Becker & Howden, CNC), Marathon (Malkin, CNHM); Brooks Co., Falfurrias (Beer, Martin, CAS, KUM); Cameron Co., Brownsville (Glick, USNM), Bruni (Martin, CAS), Childress Co., Childress (Mitchell, USNM); Comal Co., New Braunfels (CAS, MCZ, USNM); Culberson Co., Van Horn (Barr, IUM); Denton Co., Denton (Bishop, USNM; Duval Co., San Diego (USNM); Frio Co., Pearsall (Tucker, USNM); Hardeman Co., Quanah (Morrill, USNM); Hemphill Co., Canadian (Mann, USNM); Hidalgo Co., Edinburg (CUM, USNM); Jeff Davis Co., Davis Mts. (CAS), Ft. Davis (Ball, CAS, UASM); Karnes Co., Kenedy (Marlatt, USNM); Kerr Co., Kerrville (Becker & Howden, CNC); Kleberg Co., Kingsville (Reed, CUM); LaSalle Co., Cotulla (USNM); Lubbock Co., (Manis, IUM); Nueces Co., Corpus Christi (CNHM, USNM); Presidio Co., Marfa (Scullen, Wickham, MCZ, OUM, USNM); Randall Co., Canyon (Stephenson, KUM); Terrell Co., Dryden (Ball, UASM), Sanderson (Martin, Mason, CAS, CNC); Travis Co., Austin (Darlington, Martin, Pinkus, CAS, MCZ, USNM); Uvalde Co., Sabinal (Pratt, USNM), Uvalde

(CAS, CNC, USNM); Val Verde Co., Comstock (Barr, IUM), Del Rio (CAS, CNC, USNM), Devils River (Schwarz, USNM); Victoria Co., Victoria (USNM); Ward Co., Monahans (Larson, UASM); Webb Co., Laredo (Martin, Werner, CAS, UASM).

Philophuga caerulea Casey 1913

Philophuga caerulea Casey 1913 - 174. *Holotype* - female labelled as follows: Ariz., Casey bequest 1925, Type USNM 47668, *caerulea* Casey.

Calleida viridis Chevrolat 1825 - 155 (not Dejean 1831). *Type locality* - Las Vigas, Veracruz, Mexico.

Description. - Values for ratios and measurements for ten specimens from Arizona are: TL 7.46-9.02 mm (8.36 mm); LE/LP 2.73-3.07 (2.94); WP/LP 1.12-1.26 (1.18); WH_1/WH_2 1.44-1.57 (1.49).

Color of dorsal surface uniformly metallic blue or greenish-blue; head and pronotum more shining than elytra but of about the same hue; epipleura rufo-piceous; legs piceous to black; antennal articles 1 to 3 and base of 4 pale, at least on ventral side, outer articles black; palpi dark with apices of terminal articles paler.

Microsculpture obsolete on frons and disc of pronotum; on elytra isodiametric and finely granular medially, slightly stretched laterally.

Head as in *viridicollis*; short sparse setae present on genae behind and below eyes.

Pronotum (fig. 32) varied in shape with seta present near each hind angle. More constricted basally than in specimens of *viridicollis*, with a longer more evident lateral sinuation; posterior lateral impressions slightly broader; lateral reflexion narrower.

Elytral striae clearly impressed, moderately punctate; intervals slightly convex, distinctly punctate, punctures stronger than in *viridicollis*. Hind wings fully developed; distinctly pigmented (fig. 23).

Male genitalia as in fig. 16. Female stylus similar to that of *viridicollis.*

Variation. - Size was the only character observed to vary geographically. Specimens from the southeastern portion of the range of *caerulea* tend to be noticeably smaller than specimens from other populations. The mean length for a sample of five specimens from Las Vigas, Veracruz, was 6.92 mm (range 6.74-7.22 mm), while the mean of a sample of ten specimens from Arizona was 8.36 mm (range 7.46-9.02 mm). Too few specimens from intermediate localities were available to determine if this variation was clinal.

Discussion. - *Philophuga caerulea* strongly resembles *viridicollis*, and differs little from this species aside from the characters presented in the key. In the United States, these two species are allopatric and are readily separated from one another. However, in Mexico the distributions are too incompletely known to determine if this geographical separation is maintained. A specimen from Monterrey, and two specimens from Monclova, Mexico, resemble *viridicollis* in color, but *caerulea* in the convexity of the elytral intervals and the depth of the striae. Perhaps when more specimens are available from Mexico, it will be necessary to treat these two species as well marked subspecies.

Distribution. - I have examined 92 specimens of this species from the following localities (fig. 58):

Mexico - AQUASCALIENTES: Aquascalientes (Hendrichs); CHIHUAHUA: Chihuahua (Wickham, MCZ); COAHUILA: Monclova (Schwarz, USNM); JALISCO: Guadalajara (MCZ, UASM); MEXICO: Lerma (Ball, UASM); Presa del Angulo (Hendrichs); Toluca (Bowditch, MCZ); Valle de Bravo (Hendrichs); NUEVO LEON: Monterrey; PUEBLA: Tlachichuca (Ball, UASM); TAMAULIPAS: "Mesa Gonzales" (= Gonzales) (CAS); VERACRUZ: Las Vigas (Hoege, MCZ, USNM); ZACATECAS: Sombrerete (Evans, UASM).

United States - ARIZONA: Cochise Co., Huachuca Mts. (CAS, USNM); Tombstone (UASM); Gila Co., Pinal Mts. (USNM); Santa Cruz Co., Nogales (CAS, CNHM); Patagonia (CNHM, MCZ); Sonoita (CAS, KUM); Sta. Rita Mts. (CAS, MCZ, UASM).

Philophuga viridis Dejean 1831

Cymindis viridis Dejean 1831 - 325. *Type locality* - California. Holotype not seen. Motschoulsky 1859 - 144 (*Philophuga*); Horn 1882 - 144 (*Philophuga*); Leng 1920 - 67. Hatch 1953 - 157 (not Chevrolat 1835 - 155).

This is the most varied species of *Philophuga*, containing four well defined subspecies. Characteristics common to all subspecies of *viridis* are presented in the following description.

Description. - Values for ratios and measurements are presented separately under each of the following four subspecies.

Color varied, ranging from dull black with a faint metallic blue sheen to bright metallic blue or green; palpi, legs and outer antennal articles piceous to black; antennal articles 1 to 3 and base of 4 pale, at least on ventral surface.

Microsculpture varied; effaced on frons and disc of pronotum in many specimens; isodiametric or slightly transverse on elytra, faintly impressed to granular.

Dorsal surface of body glabrous or setose; frons and disc of pronotum punctate.

Pronotum varied in shape; with or without a seta near each hind angle.

Elytra relatively short, oval, with greatest width in apical half. Hind wings varied in development, with reflexed apex or reduced to a small scale; when fully developed, membranous areas only lightly pigmented.

Male genitalia with aedoeagus short, slightly arcuate; basal piece curved (fig. 17).

Female stylus as in figs. 52 and 53.

Geographical variation and subspecies. - The species *Philophuga viridis* Dejean ranges widely in the semi-arid and cold desert regions of western North America, from the prairies of southern Canada west to Washington and Oregon, and south to northern New Mexico, Arizona, and California. Over this range, color, vestiture, wing development, and the presence of the posterior-lateral prothoracic setae vary. Data on variation in these characters is summarized in a pie diagram map (fig. 1) and in table 2. Four subspecies are recognized, based on variation in these characters.

On the eastern side of the Rocky Mountains, and in British Columbia, Washington, and northern Oregon, populations possessing the following characteristics occur: the posterior-lateral setae of the prothorax are absent; the wings are fully developed; the dorsal surface of the body is glabrous; and the color is a dark blue-black. Associated with the absence of the posterior-lateral setae, the pronotum tends to be less sinuate laterally, with more obtuse hind angles than in specimens that possess the setae. The name *viridis amoena* LeConte applies to specimens with these characteristics.

To the west of the Rocky Mountains, a population centering around the Great Basin occurs. This subspecies, *v. horni* Chaudoir, differs from the neighboring *v. amoena* by possessing a posterior-lateral seta on each hind angle of the pronotum, and by being bright metallic green or blue in color. The hind angles of the pronotum are more distinct than in *v.*

amoena and the lateral margins are more sinuate posteriorly.

TABLE 2. List of localities from which specimens of *Philophuga viridis* Dejean were used to compile pie-diagram map (fig. 1).

Map symbol	Locality	No. of specimens
A	Southern British Columbia	4
B	Southern Alberta	24
C	Southern Saskatchewan	3
D	Southern Manitoba	15
E	Valley Co., Montana	1
F	Lake Co., Montana	1
G	Lewis & Clark, and Missoula Cos., Montana	11
H	Musselshell Co., Montana	1
I	Gallatin Co., Montana	6
J	Bighorn Co., and Yellowstone National Park, Wyoming	6
K	Carbon and Laramie Cos., Wyoming	4
L	Delta and Garfield Cos., Colorado	2
M	Boulder, Jefferson, and Larimer Cos., Colorado	5
N	Chaffee, El Paso, Park and Teller Cos., Colorado	8
O	La Plata Co., Colorado	2
P	Sapello, San Miguel Co., New Mexico	1
Q	Coconino Co., Arizona	7
R	Washington Co., Utah	1
S	Soldier Summit, Utah Co., Utah	1
T	Touele Co., Utah	12
U	Esmeralda Co., Nevada	2
V	White Pine Co., Nevada	1
W	Washoe Co., Nevada	13
X	Humbolt Co., Nevada	1
Y	Ada, Canyon, Owyhee, and Payette Cos., Idaho	8
Z	Blaine, Cassia, Lincoln, Twin Falls Cos., Idaho	13
a	Bannock and Lake Cos., Idaho	2
b	Clark and Lemhi Cos., Idaho	2
c	Adams and Nez Perce Cos., Idaho	4
d	Grant Co., Washington	3
e	Seattle, Washington	2
f	Wasco Co., Oregon	3
g	Baker Co., Oregon	16

TABLE 2. (cont.).

Map symbol	Locality	No. of specimens
h	Harney, Lake, and Malheur Cos., Oregon	10
i	Klamath Co., Oregon	5
j	Jackson Co., Oregon	3
k	Yreka, California	1
l	Lassen, and Modoc Cos., California	8
m	San Francisco, California	96
	TOTAL	308

Although *amoena* and *horni* are consistent in their characters over the major portion of their respective ranges, two areas of intergradation occur; along the Rocky Mountains, and in the northwestern states. In the Rocky Mountains intergradation is most pronounced around low passes. I have seen two typical specimens of *amoena* from Pocatello and Salmon, Idaho. A specimen from Dubois was colored like *horni* but lacked the posterior-lateral prothoracic setae. All other specimens seen from Idaho were typical *horni*. Some specimens from the eastern side of the continental divide in southwestern Montana and northwestern Wyoming show *horni* characteristics. One of the six specimens seen from Gallatin Co., Montana, possessed posterior-lateral pronotal setae. One specimen of the six seen from Yellowstone National Park had the coloration of *horni.*

A similar situation in which the mountains do not form a complete barrier to genetic interchange, occurs in western Colorado and eastern Utah. On the eastern slopes of the Rocky Mountains in Colorado, some specimens of *amoena* show a brighter metallic blue or green coloration, most obvious along the frontal grooves of the head and the lateral margins of the prothorax. Specimens from localities to the south and west in Colorado show a higher incidence of bright coloration until all specimens seen from Utah, Arizona and New Mexico show the *horni* coloration. The posterior-lateral prothoracic setae tend to be absent from populations of *horni* colored beetles in eastern Utah, western Colorado and in New Mexico. Some specimens of *horni* from as far west as Salt Lake City, Utah, lack these setae even though the pronotum has the characteristic shape for *horni*. In this region, the bright coloration of *horni* seems to pass through or around the southern Rocky Mountains and occurs with limited frequencies in populations on the eastern slopes of the mountains. The *amoena* characteristic, the absence of the posteior-lateral pronotal setae, tends to occur in populations of *horni* as far west as Touele Co., Utah.

The situation in the northwestern states is similar. The subspecies *amoena* is found in the north and western portions of Washington and Oregon. One of the four specimens I have seen from southern British Columbia is typical *horni* while the remaining specimens are *amoena*. Even more surprising are two specimens of *horni* labelled Seattle, Washington (O.B.J.), while all other Washington specimens may be assigned to *amoena*. On the validity of O.B. Johnson's labels, Hatch (1950, p. 21) stated "But if he (O.B. Johnson) believed that a given species occurred in the vicinity of Seattle, he would not hesitate, according to Professor Kincaid, to put a Seattle label on any specimen that came to hand regardless of its exact point of origin." However, a specimen with *horni* characteristics from southern British Columbia does not permit me to discount the possibility that *horni* does occur in the Seattle region. Hybrid specimens have been seen from Baker and Wasco Counties, Oregon.

The separation of *amoena* and *horni* may be primarily ecological. Specimens of *amoena* are found on short-grass prairie in southern Alberta, and seem to occur in regions where grassland is prevalent. The subspecies *horni* seems to be found in regions of desert scrub vegetation.

The third subspecies, *v. klamathea* new subspecies, is known from only a small area in south-central Oregon and northern California. In coloration and the shape of the pronotum (the posterior-lateral setae are present), this subspecies resembles *horni*. However, it is readily distinguished from the latter by the presence of sparse vestiture on the dorsal surface of the body and by the reduced hind wings which are represented by no more than small scales. On the basis of these two characters, *klamathea* is quite distinct from *horni*. Nevertheless some introgression does occur. One macropterous specimen was collected along with four micropterous beetles in a series from Klamath Co., Oregon. All specimens from the neighboring Lake Co. to the east are macropterous but some specimens show traces of fine vestiture on the elytral intervals and on the genae below the eyes (such specimens have been scored as being glabrous in pie-graph map (fig. 1). The subspecies *klamathea* does not show any signs of intergrading with *amoena* to the north.

The fourth subspecies, *v. viridis* Dejean, appears to be isolated in the vicinity of San Francisco Bay and Sonoma Co., California. Its characteristics are: hind wings reduced to a small scale; vestiture present on dorsum; color black to dull blue-black, rarely bright blue or green; posterior-lateral setae of pronotum absent from most specimens (94%); however, the lateral margin of the thorax is sinuate and the hind angles are distinct though obtuse. The basal border of the elytra tends to be more sinuate internally in micropterous than in macropterous specimens. Also, this sinuation is usually stronger in *viridis s. str.* than in *klamathea*. These two subspecies also differ in some characteristics of the elytral striae and microsculpture. These differences are described below.

The geographically isolated position of *v. viridis* in conjunction with the differences mentioned above, suggest that *viridis* and *klamathea* may actually be specifically distinct. However, some instability in the diagnostic characters of color and the presence of the posterior-lateral pronotal setae cause me to consider these populations to be conspecific, at least until better evidence to the contrary is discovered.

Key to the Subspecies of *Philophuga viridis* Dejean

1. Hind wing reduced, much shorter and narrower than a single elytron 2
1'. Hind wing full, with reflexed apex 3
2(1). Hind angle of pronotum lacking setiferous puncture in most specimens (fig. 37); elytral striae finely impressed, outer striae often obsolete and represented by a row of fine punctures . . . . *v. viridis* Dejean, p. 38
2'. Hind angle of pronotum with a setiferous puncture (fig. 36); elytral striae clearly im-

pressed, outer striae distinct almost to apex....... *v. klamathea* new subspecies, p. 40

3(2). Hind angle of pronotum with a setiferous puncture (fig. 35). . *v. horni* Chaudoir, p. 41

3'. Hind angle of pronotum without a setiferous puncture (fig. 34) ....
.... *v. amoena* LeConte, p. 42

Philophuga viridis viridis Dejean 1831

Cymindis viridis Dejean 1831 - 325. *Type locality* - California. Type specimen not seen (not Chevrolat 1835 - 155).

Callida cyanea Motschoulsky 1850 - 36. *Type locality* - San Francisco, California. Type specimen not seen.

Philophuga lauta Casey 1913 - 175. *Holotype* - male, labelled as follows: Cal., Casey bequest 1925, Type USNM 47670, *lauta* Csy. New Synonymy.

Description. - Values for ratios and measurements of fifty-two specimens are: TL 5.7-7.5 mm (6.8 mm); LE/LP 2.39-2.80 (2.59); WP/LP 1.10-1.29 (1.21); WH_1/WH_2 1.41-1.54 (1.46).

Color dark, ranging from dull black to metallic blue or green; palpi and legs dark piceous to black; abdomen piceous to black.

Microsculpture varied; isodiametric to slightly transverse on frons, obsolete in many specimens; on disc of pronotum lightly impressed, transverse; isodiametric, faintly impressed to granular on elytra.

Body setose dorsally; evident setae present on frons behind and below eyes, on disc of pronotum and on at least odd numbered elytral intervals.

Head broad, genae broadly rounded laterally; postocular pinch faint; frons with setiferous punctures best developed posteriorly and laterally, also micropunctate.

Pronotum varied (fig. 37); lateral margins rounded, each with a long sinuate posterior constriction; sides subparallel or slightly converging behind; front angles rounded, slightly protruding; hind angles prominent but obtuse; most specimens without posterior lateral setae (setae present in 6% of specimens examined); lateral margin narrow, widening toward hind angles; disc with sparse setiferous punctures, deeper and denser posteriorly and laterally.

Elytra relatively short, oval, with greatest width in apical half; shoulders broadly rounded, basal margin with strong anterior convexity; striae lightly impressed, finely punctate, outer striae often incomplete before apex, stria 8 represented by a row of punctures in many specimens; intervals flat to slightly convex, with an irregular row of small punctures in each. Hind wings reduced, represented by a small scale.

Abdominal sterna sparsely and finely setose; sternum 6 bearing one pair of anal setae in the male or two pairs in the female.

Male genitalia (fig. 17) with aedoeagus short, apex short; basal piece strongly curved.

Female stylus as in fig. 52.

Distribution. - Localities from which specimens of this subspecies have been collected are indicated in fig. 59. I have examined 96 specimens of this subspecies from the following localities:

CALIFORNIA: Alameda Co., Grizzly Peak (Van Dyke, CAS); San Francisco Co., Lake Merced (Van Dyke, CAS), San Francisco (Blaisdell, Van Dyke, CAS, MCZ, USNM); Sonoma Co., Eldridge (CAS, USNM).

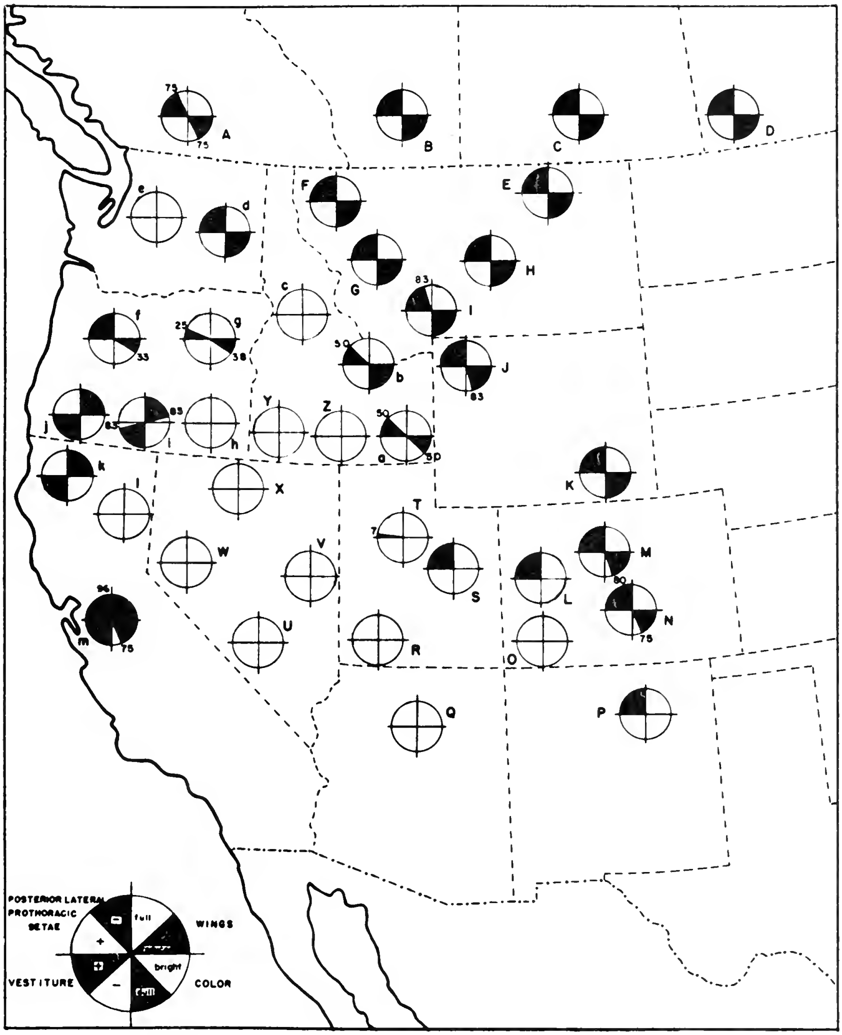


Fig. 1. Pie-diagram map illustrating geographic variation in four characteristics: wing development; color; vestiture; and presence of posterior-lateral prothoracic setae, of selected population samples of *Philophuga viridis* Dejean. A number external to a quadrant, indicates the percentage of specimens of that sample that show the black phase of the character. Localities represented by each pie-diagram are listed in Table 2.

Philophuga viridis klamathea new subspecies

Holotype - male, Klamath Falls, Oregon (Van Dyke, CAS).

Allotype - female, Medford, Oregon (USNM).

Paratypes are from the following localities:

CALIFORNIA: "CaL" (MCZ, WUM); Siskiyou Co., Yreka (USNM); OREGON: "Or." (USNM); Jackson Co., Ashland (Stephen, OUM), Colestine (Bishop, OUM), Medford (USNM); Klamath Co., (CNHM).

The diagnostic characteristics of this subspecies are presented in the key and in the discussion of variation under *Philophuga viridis.*

Description. - Values for ratios and measurements of ten specimens are: TL 6.56-8.00 mm (7.03 mm); WP/LP 1.16-1.29 (1.22); WH_1/WH_2 1.37-1.50 (1.45).

Color bright metallic blue or green. Antennal articles 1 to 3 and base of 4 pale, outer articles black.

Microsculpture highly effaced on head and pronotum, these areas shiny; irregularly isodiametric or faintly stretched on elytra, lightly impressed and shiny in many specimens.

Body setose dorsally. Setae evident on head behind and below eyes; on disc of pronotum most conspicuous along posterior-lateral margins; on disc of elytra forming an irregular row in at least odd numbered intervals. Ventral portions of body also with short evident setae.

Shape of head similar to *v. horni*; eyes convex, neck evidently constricted.

Pronotum as in fig. 36, but in some specimens somewhat narrower with sides more strongly constricted behind; differing from *v. viridis* by narrowness with greater lateral sinuation; posterior-lateral angles each bearing a setiferous puncture.

Elytra oval, narrowed basally; basal margin strongly sinuate; striae clearly impressed on disc, outer striae evident almost to apex, strongly punctate; intervals varied, flat to convex, deeply punctate.

Male genitalia similar in shape to that of *v. viridis*. Female stylus as in fig. 53.

Variation. - The following characteristics were observed to vary; shape of pronotum; density of vestiture; microsculpture, and depth of impression of elytral striae. As few specimens of this subspecies were available, I was unable to determine the pattern of variation in any of these characters. Variation was most evident among specimens from localities near the periphery of the range of *klamathea*, indicating that hybridization with *horni* may in part at least be responsible for this variation.

Relationships. - This subspecies is intermediate between *viridis s. str.* and *horni* in the diagnostic characters presented in fig. 1. However, on the basis of its peculiar combination of characteristics, and the apparently isolated geographical position it occupies, I chose to recognize this form as a subspecies.

Etymology. - This name is the latinized form of part of the name of the type locality - Klamath Falls, Oregon.

Disposition of type material. -The holotype has been deposited in the California Academy of Sciences. The allotype is in the United States National Museum. Paratypes have been deposited in the Chicago Natural History Museum (4 specimens), Museum of Comparative Zoology (1), Oregon State University (2), United States National Museum (2) and the University of Washington (3).

Distribution. - *Philophuga viridis klamathea* is known only from southwestern Oregon and northern California (fig. 59).

Philophuga viridis horni Chaudoir 1877, new combination

Philophuga horni Chaudoir 1877 - 245. *Type locality* - Nevada.

Philophuga uteana Casey 1924 - 92. *Holotype* - male, labelled as follows: Stockton, Utah, IV/7/04, Tom Spalding, Casey bequest 1925, Type USNM 47673, *uteana* Csy. New Synonymy.

Philophuga cobaltina Casey 1924 - 91. *Holotype* - male, labelled as follows: Trout Creek Juab Co., Utah, VII/4/22. Tom Spalding, Casey bequest 1925, Type USNM 47672, *cobaltina* Csy. New Synonymy.

Description. - Values for ratios and measurements of ten specimens are: TL,7.02-8.24 mm (7.58 mm); LE/LP, 2.77-2.93 (2.83); WP/LP, 1.21-1.27 (1.24); WH_1/WH_2, 1.38-1.50 (1.45).

Color shiny metallic blue or green. Antennal articles 1 to 3 and base of 4 pale, outer articles black.

Microsculpture absent or highly effaced on head and pronotum; strong on elytra, isodiametric medially showing tendency to become strethced and arranged in transverse rows laterally.

Body glabrous dorsally; even head below eyes without setae.

Head with eyes large, strongly convex; genae constricted posteriorly forming evident neck.

Pronotum as in fig. 35; lateral margin with long sinuation towards hind angle; hind angles prominent though somewhat obtuse, each bearing a setiferous puncture.

Elytra with greatest width in apical half but not strongly narrowed basally; basal border only slightly sinuate; elytral striae clearly impressed, moderately to coarsely punctate; intervals slightly to strongly convex, finely to coarsely punctate. Hind wings fully developed.

Male with three, female with two pair of anal setae on abdominal sternum 6.

Male genitalia similar to that of *v. viridis*. Female stylus as in *v. klamathea.*

Distribution. - This subspecies occurs throughout the Great Basin province, and extends a little outside of this region especially in the north (fig. 59). I have seen more than 90 specimens from the following localities:

United States - ARIZONA: Coconino Co., Flagstaff (USNM), Pinal Mts. (CU), Williams (Wickham, USNM). CALIFORNIA: Lassen Co., Bridgeport (Wickham, USNM), Hallelujah Junction (Westcott, UASM), Susanville (Martin, CAS), Modoc Co., Davis Creek (Fox, CAS), Hackmore (Van Dyke, CAS). COLORADO: La Plata Co., Pagosa Springs (Bowditch, MCZ); IDAHO: Ada Co., Nampa (Barr, IUM), Regina (Barr, IUM); Adams Co., Martin (Houk, WUM), Mesa (IUM); Bear Lake Co., Bear Lake (AMNH); Blaine Co., Carey (Hewitt, IUM), Crystal Ice Cave (Westcott, IUM), Magic Reservoir (Barr, IUM); Canyon Co., Caldwell (Barr, IUM), Parma (WUM); Cassia Co., Elba-Basin Pass (Stecker, SJSC), Malta (Henry, IUM), Rupert (Shull, IUM); Clark Co., Dubois (Penrose, UASM); Lincoln Co., Richfield (Barr, IUM); Nez Perce Co., Lewiston (Shull, IUM, USNM); Owyhee Co., Bruneau (Fillmore, IUM), Jordan Valley (Henry, IUM), Reynolds (Hewitt, IUM); Payette Co., Payette (Shull, IUM); Twin Falls Co., Hollister (Fox, IUSNM), Twin Falls (Homan, IUM). NEVADA: Esmeralda Co., Lida (O'Brien, UASM); Humbolt Co., Winnemucca (Barr, IUM); Washoe Co., Reno (Wickham, CAS, MCZ, USNM), Steamboat Springs (Van Dyke, CAS), Verdi (Blaisdell, CAS); White Pine Co., Ely (Van Dyke, CAS). OREGON: Baker Co., Baker (Van Dyke, CAS, WUM), Durkee (WUM), Pleasant Valley (Fender, WUM), Sparta (Van Dyke, CAS), Wallowa Mts. (Van Dyke, CAS), Harney Co., Frenchglen (Malkin, WUM), Tencent Lake (Malkin, CNHM, WUM); Lake Co., Hart Mtn. Antelope Refuge (Nelson, OUM); Malheur Co., Harper (OUM), Rome (CAS, OUM). NEW MEXICO: San Miguel Co., Sapello (Ball, UASM); UTAH: Touele Co., Stanisbury I. (USNM), Stockton (Spalding,CAS,MCZ); American Fork (H & S, USNM); Washington Co., St. George (AMNH). WASHINGTON: King Co., Seattle (O.B.J., WUM).

Philophuga viridis amoena LeConte 1848, new combination

Cymindis amoena LeConte 1848 - 188. *Lectotype* - (here selected) female, labelled as follows: green disc, *amoena* LeC., Type 5822 MCZ, *P. amoena* (LeC.).

Philophuga canora Casey 1913 - 174. *Holotype* - female, labelled as follows: Tex., Casey bequest 1925, Type USNM 47669, *canora* Csy. New Synonymy.

Philophuga puella Casey 1913 - 176. *Holotype* - male, labelled as follows: Boulder Co., Colo., Casey bequest 1925, Type USNM 47671, *puella* Csy. New Synonymy.

Philophuga obscura Casey 1924 - 91. *Holotype* - female, labelled as follows: N.Y., Casey bequest 1925, Type USNM 47674, *obscura* Casy. New Synonymy.

Description. - Values for ratios and measurements of ten specimens are: TL 7.20-8.32 mm (7.52 mm); LE/LP, 2.68-2.90 (2.80); WP/LP, 1.18-1.24 (1.21); WH_1/WH_2, 1.28-1.46 (1.40).

Color black (elytra piceous in some specimens) with a dull metallic blue sheen on disc of pronotum and elytra; very rarely with faint blue-green sheen, usually restricted to frontal furrows and lateral margins of pronotum. Antennae with articles 1 to 3 and base of 4 pale, at least ventrally.

Body glabrous dorsally; glabrous even laterally behind and below eye.

Head broad; eyes flattened, somewhat reduced; neck broad. Antennae with outer articles relatively short and stout.

Pronotum (fig. 34) convex; sides slightly rounded and only shallowly sinuate posteriorly; hind angles broadly rounded and lacking setiferous puncture on each side; front angles rounded, not or only slightly protruding; lateral margin narrowly and uniformly reflexed.

Elytra relatively convex, elongate oval, with greatest width in apical third; shoulders broad, basal border slightly sinuate interiorly; striae finely impressed, finely to moderately punctate; intervals faintly convex basally, flat apically, sparsely and finely punctate.

Abdominal sternum 6 with one pair of anal setae in male, and two pairs in female.

Male genitalia as in *v. viridis*.

Female stylus as in the other subspecies of *viridis.*

Variation. - Hybridization between *v. amoena* and *v. horni* has been discussed above. Some variation has been observed in the eastern portion of the range of *amoena.* Here, hybridization with *horni* would not occur.

Only a single female specimen has been seen from Kansas. It differs from the more typical western and northern specimens of *amoena* by a greenish-blue cast dorsally, and by a strongly rounded pronotum with a strong lateral reflexion, narrow anteriorly and broadening behind. The single female specimens seen from Nebraska has a normally proportioned pronotum, but the elytral striae are rather coarsely punctate, and the elytral intervals are convex and coarse punctate.

Distribution. - This species occurs primarily on the Great Plains east of the Rocky Mountains, and along the northern periphery of the Great Basin (fig. 59).

Canada - ALBERTA: Lethbridge (Larson, UASM); Lost River nr. Onefour (Larson, UASM); Medicine Hat (Carr, Pepper, CAS, CNC, CU, UASM); Milk River (Pepper, CNC); Ralston (Ball, UASM); Taber (White, DAL). BRITISH COLUMBIA: Mts. between Hope and Okanagan (Bowditch, MCZ); "Van." (= Vancouver?) (MCZ). MANITOBA: Aweme (Criddle, White, AMNH, CAS, CNC, CU, DAL, USNM); Brandon (AMNH, USNM); SASKATCHEWAN: Cypress Hills (Ball & Lindroth, UASM); Roche Percee (Criddle, CNC); Saskatoon (McMillan, CNC).

United States - COLORADO: Boulder Co., Nederland (Stainer, CNC); Chaffee Co., Buena Vista (Wickham, USNM); Delta Co., Paonia (Van Dyke, CAS); El Paso Co., Colorado Springs (Soltau, Wickham, MCZ, USNM); Garfield Co., Glenwood Springs (AMNH); Jefferson Co., Denver (Soltau, USNM); Mesa Co., Grand Junction (Titus, USNM); Park Co., Trout Creek Pass (Beamer, KUM), Wilkerson Pass (White, KUM); Teller Co., Florissant (Bowditch, MCZ). IDAHO: Bannock Co., Pocatello (Bruner, USNM); Lemhi Co., Salmon (Wakeland, IUM); KANSAS: "Ks." (MCZ); MONTANA: Gallatin Co., (MUB); Lake Co., (MUB); Lewis and Clark Co., Helena (many collectors, CAS, MCZ, USNM); Missoula Co., Missoula (MUB); Musselshell Co., (MUB); Valley Co., Hinsdale (MUB); NEBRASKA: "Neb." (MCZ); OREGON: Wasco Co., Maupin (Van Dyke, CAS), Warm Springs Indian Reserve (WUM); WASHINGTON: Grant Co., Dry Falls (Burnes, WUM), Grand Coulee (MCZ), Soap Lake (Hatch, WUM); WYOMING: Bighorn Co., Bighorn Mts. (Edwards, SJSC); Carbon Co., Rawlins (AMNH); Laramie Co., Cheyenne (Soltau, USNM); Yellowstone National Park (Hatch, Van Dyke, CAS, WUM).

Infernophilus new genus

Type species. - Philophuga castanea Horn 1882, here designated.

The species *I. castaneus* Horn was described originally as a member of the genus *Philophuga*, but it differs in several important details from the other species included in that genus. Further, this species cannot be included in any other known callidine genus. For these reasons, the genus *Infernophilus* is established to include *castaneus.*

The most striking external features of this genus are indicated in the preceding key. Another remarkable feature is the orientation of the male genitalia. In repose, the aedoeagus is on its left instead of on its right side; the latter is the usual position among the members of the Lebiini. Associated with this, the parameres are reversed. They are of the typical form for the Callidina, but the large paramere is on the right rather than on the left side of the aedoeagus. Also, the apical orifice opens dorso-laterally to the right. I know of no other North American callidine, or even lebiine, that shows a similar condition. As no intermediate stages are known between the normal and the reversed position of the genitalia, it seems plausible that the initial 180° rotation arose in a single step. Other modifications such as the reversal of the parameres and the shift of the apical orifice may have been secondary.

Etymology. - The name is derived from the Latin noun *infernus* - m., hell; and the Greek *philia* - fondness. The name refers to the hot desert region in which this insect is found.

Infernophilus castaneus Horn 1882

Philophuga castanea Horn 1882 - 144. *Type locality* - Kern Co., California. Leng 1920 - 67. Csiki 1932 - 1462.

Description. - Values for ratios and measurements for fourteen specimens are: TL 7.9-9.1 mm (8.6 mm); LE/LP 2.62-2.84 (2.74); WP/LP 1.07-1.25 (1.17); WH_1/WH_2 1.46-1.56 (1.52).

Color brown; elytra and abdomen darker brown to piceous.

Microsculpture on frons isodiametric, but effaced on most specimens; obsolete on disc of pronotum; isodiametric on elytra, but partly effaced and shiny. Body sparsely setose above.

Head with eyes prominent, convex. Genae broad behind eyes, with faint postocular pinch; narrowing posteriorly to form an evident neck. Labrum slightly emarginate. Clypeus with a single seta on each side; sparsely punctulate medially. Frons with poorly defined rugose frontal furrows; sparsely punctate medially with deeper setiferous punctures posteriorly and laterally. Antennae with articles 1 to 3 and base of 4 sparsely hairy; remaining articles pubescent. Maxillary palpus with terminal article cylindrical. Labial palpus with penultimate article bisetose; terminal article securiform (narrower in female). Ligula bisetose. Mentum with a prominent margined tooth.

Pronotum (fig. 30) varied in shape; lateral sinuation long, lateral margins subparallel toward base; hind angles obtuse, with setiferous puncture present; base slightly sinuate laterally; frontal angles broadly rounded, slightly protruding; posterior lateral impressions indistinctly limited and continuous with broad lateral grooves; lateral margins uniformly reflexed; disc transversely rugose laterally.

Tarsal articles sparsely hairy above, densely setose beneath; article 4 emarginate; basal article of middle and hind tarsi with faint median dorsal groove; claws pectinate; male with articles 1 to 3 of front tarsus and articles 1 and 2 of middle tarsus bearing two rows of scales beneath.

Elytra completely bordered both apically and basally; striae clearly impressed and well defined to apex, lightly punctate; intervals broadly convex, bearing small irregular setiferous punctures; odd-numbered intervals and apex of even numbered intervals with an irregular row of larger setiferous punctures. Hind wings fully developed.

Abdominal sternum 6 of male with a paired brush of setae along hind margin (fig. 27); in female brush reduced and in some specimens it is represented by as few as six pairs of moderate to long setae.

Male genitalia (figs. 21-22) with reversed parameres; endophallus with a field of short spines.

Stylus of ovipositor (fig. 57) short, broad; broadly rounded apically, sparsely setose.

Distribution. - I have examined fifteen specimens of this species from the following localities (fig. 61).

CALIFORNIA: Kern Co. (AMNH); Mono Co., Bridgeport (O'Brien, UASM, Coleville (O'Brien, CAS, DAO, UASM); San Diego Co., (USNM). NEVADA: (AMNH, USNM).

Biology. - Several specimens in a series taken at Coleville, California (July 6-10, 1966) were slightly teneral.

Tecnophilus Chaudoir 1877

Tecnophilus Chaudoir 1877 - 240. *Type species* - *Calleida croceicollis* Ménétriés 1843, here designated.

Philotecnus LeConte 1851 - 175, not Mannerheim 1837 - 42. *Type species* - *Philotecnus nigricollis* LeConte 1851 (= *T. croceicollis* Ménétriés), here designated.

This is a small genus closely related to *Philophuga*. Aside from the characters presented in the key to Callidina, the adults can be recognized on the basis of the cordate pronotum and the usually dense vestiture of the body.

Characteristics common to all species of *Tecnophilus* are given in the following description.

Description. - Beetles 5.7 to 8.0 mm in length. Color various, but elytra always metallic blue or green. Basal three articles of antenna similarly colored to outer articles.

Body variously punctate and setose dorsally; ventral portions of body moderately to densely setose.

Eyes prominent, of various convexity; hairy or glabrous. Labrum truncate apically with slight medial elevation. Frontal furrows shallow, broad, deeply punctate. Frons punctate.

Antennal articles 1 to 3 and base of 4 hairy; outer articles pubescent. Maxillary palpus with fusiform terminal article. Labial palpus with terminal article securiform; penultimate article bisetose. Ligula bisetose. Mentum with a prominent margined tooth.

Pronotum cordate, with strong posterior-lateral sinuations; lateral setae present; hind angles lacking setiferous punctures.

Tarsal articles slender; article 4 at most emarginate; hairy dorsally; tarsal claws simple (in some specimens may be minutely serrulate); articles 1 to 3 of front tarsi, and 2 and 3 of middle tarsi of male bearing two rows of scales beneath.

Elytra parallel sided or oval; completely margined both basally and apically; striae evident and punctate; intervals variously punctate. Hind wings fully developed.

Abdominal sterna 3, 4 and 5 with a pair of medial setae; sternum 6 with at most three pairs of anal setae; sterna 4 to 6 without long lateral setae.

Male genitalia on right side in repose. Left paramere large; right paramere smaller, bilobed apically. Aedoeagus simple, tube-like, with apical orifice opening somewhat laterally to the left; endophallus unarmed.

Female stylus with densely setose apex.

Discussion. - Chaudoir (1877) separated *Tecnophilus* from his Callidides on the basis of the structure of the ligula and paraglossae, and placed the genus in his Mimodromiides. However, Horn (1881) carefully studied the ligula and paraglossae of the Lebiini and concluded that they were of little value in defining groups of higher rank than the genus, and even here he suggested that they be used with caution. *Tecnophilus* is certainly a callidine in the sense used here.

Many of the peculiar features of *Tecnophilus*, such as the simple tarsal claws, slender tarsi, cordate pronotum and setose body, may be regarded as adaptations to a terrestrial mode of life.

Distribution. - The members of this genus are found in alkaline or saline situations in western North America.

Key to the Species of *Tecnophilus* Chaudoir

1. Apex of femur infuscated and contrasting with the otherwise rufous legs .... *pilatei* Chaudoir, p. 45

1'. Femur concolorous, rufous to black; or if femur rufous and infuscated apically, tarsi also infuscated .... *croceicollis* Ménétriés, p. 46

Tecnophilus pilatei Chaudoir 1877

Tecnophilus pilatei Chaudoir 1877 - 239. *Type locality* - Texas. Horn 1882 - 137. Leng 1920 - 67. Csiki 1932 - 1462.

Specimens of this species can be readily recognized by possession of the infuscated apices of otherwise rufous femora. Also, the elytral striae are much more coarsely punctate than in *croceicollis.*

Description. - Values for ratios and measurements of ten specimens are: LE 4.44-4.76 mm (4.56 mm); WP/LP 1.06-1.15 (1.10); WH_1/WH_2 1.61-1.70 (1.65).

Color of head and thorax rufous; abdomen piceous medially, paler laterally; elytra metallic blue or green, often with rufinistic background; antennae and palpi pale; legs pale except for conspicuous infuscated apical spot on femur.

Microsculpture obsolete on head; lightly impressed, transversely stretched on disc of pronotum; isodiametric but shallowly impressed on elytra.

Body densely pubescent, both dorsally and ventrally.

Head narrow, with temporal region strongly constricted; eyes very convex and protruding, glabrous.

Pronotum (fig. 38) narrow; sides slightly rounded laterally, relatively shallowly sinuate behind; front angles rounded, not protruding; hind angles obtuse, broadly rounded; lateral reflexion narrow.

Tarsal article 4 deeply emarginate, almost bilobed but not bearing dense setiferous pads beneath.

Elytra elongate, parallel sided; striae moderately impressed medially on disc, becoming obsolete laterally; striae with very coarse often confluent punctures, deepest in basal half but also evident apically; intervals flat; basal margin strongly sinuate internally; apex obliquely truncate and slightly sinuate.

Abdominal sternum 6 of male with two pairs of anal setae, with three pairs in female.

Male genitalia as in fig. 18; aedoeagus slightly arcuate, apex elongate.

Female stylus (fig. 55) with external apical angle greatly produced.

Relationships. - Specimens of the species *pilatei* superficially resemble Texas specimens of the species *croceicollis*. However, the strikingly different styli of the female ovipositor and the elongated apex of the male genitalia, associated with the external characteristics mentioned above, consistently separate specimens of these two species. The species *pilatei* is isolated from the *croceicollis* complex.

Distribution. - I have seen specimens of this species only from localities along the Gulf Coast of Texas (fig. 62). I examined 140 specimens from the following localities:

TEXAS: Aransas Co., Goose Island State Park (Larson, UASM), Brazori Co., Freeport (Evans, UASM); Cameron Co., Brownsville (UASM, USNM), Port Isabel (Ball, UASM), Cedar Lane (Shaw, KUM); Nueces Co., Corpus Christi (Hubbard & Schwarz, USNM).

Tecnophilus croceicollis Ménétriés 1843

Calleida croceicollis Menetries 1843 - 54. *Type locality* - California.

The most diagnostic characteristic of this highly variable species is presented in the preceding key to the species of the genus *Tecnophilus*.

Description. - Values for ratios and measurements of selected population samples are presented in tables 6 to 10.

Color highly varied; head and pronotum black to rufous with head always same color or darker than disc of pronotum; appendages black to rufous, femur uniformly colored, or if rufous and infuscated apically, tarsus and clypeus also infuscated; elytra black to piceous with metallic green, blue or purple sheen.

Vestiture varied, but even in least setose specimens setae present on head behind and below eyes, along lateral margins of pronotum and on at least odd numbered elytral intervals; dorsal vestiture of most specimens quite conspicuous.

Microsculpture obsolete on frons; on pronotum consisting of partially effaced transverse meshes; on elytra isodiametric but shallowly impressed and shiny on many specimens.

Head with neck variously constricted; eyes of various size and convexity (figs. 24 and 25).

Pronotum varied; more rounded laterally and more constricted behind than in *pilatei* (figs. 39-42).

Elytra with basal border shallowly sinuate; apex truncate or slightly sinuate; striae finely to moderately punctate, never as coarsely punctate as in *pilatei*.

Aedoeagus of male genitalia (figs. 19 and 20) short, arcuate, with short apex.

Female stylus (fig. 56) with apex truncate, not produced.

Geographical variation and subspecies. - The complex geographical variation displayed by this species makes it very difficult to organize the available population samples into well defined subspecies. Clinal variation occurs in several characteristics, and the general pattern of variation is discordant. Geographically terminal populations are comprised of individuals easily distinguished by distinctive combinations of characters, but specimens from intermediate areas are often difficult to associate with the terminal groups. However, as is shown below, it is possible to distinguish two groups of subspecific rank.

The pattern of variation of each character is described below, and this section is concluded with a summary of this information.

Color. - Over much of the range of *croceicollis*, the basic color pattern is as follows: elytra metallic blue or green; head, pronotum, and legs rufous; abdominal sterna piceous. However, considerable variation in color of each of these body parts occurs.

Data on variation in the color of the elytra among selected population samples of the species *croceicollis* are presented in table 3. Briefly, the color of the elytra varies in the following way: populations from the vicinity of San Francisco Bay, and from the Central Valley of California, possess dark blue or purple elytra; populations from southern California, Arizona, Nevada, and southern Utah generally have blue elytra, with a very small percentage of the specimens possessing greenish-blue or green elytra. The incidence of green elytra increases southwardly along the Gulf of California, and eastwardly through New Mexico, until green or blue-green is the predominant color in Texas populations. All specimens seen from Wyoming and Alberta show dark blue elytra. West of the Rocky Mountains in Idaho and northern Utah, the color of the elytra is highly varied.

Data on variation in the color of the head and pronotum are presented in tables 4 and 5. In specimens that show infuscation of the head and pronotum, the head is always the same color or darker than the disc of the pronotum. All specimens that have been seen from Mexico, and the United States from southeastern California east to Texas, and north to central Colorado, Utah, and Nevada, possess rufous heads and pronota. Specimens from the eastern side of the Rocky Mountains from northern Colorado to southern Alberta, possess black heads and pronota. I have not seen any specimens from Colorado that were intermediate between the black color of northern specimens, and the rufous color of specimens from southern localities. This suggests that no hybridization occurs between specimens belonging to these two different color classes in this region. However, west of the Rocky Mountains in Idaho and northern Utah, specimens of *croceicollis* are highly varied in color, with the color ranging from entirely black to rufous with only a light infuscation of the tarsi and the clypeus. This variability in color probably results from hybridization between the black members of the northern population, and rufous colored specimens which occupy the Great Basin. Similar variation in color occurs among populations in the Central Valley of California. Many specimens occurring around San Francisco Bay are black in color. Specimens from further inland tend to be paler, and specimens from the southern end of the San Joaquin Valley are almost as pale as specimens from the Mojave Desert. This evidence suggests that there is gene flow from the Mojave Desert, into the San Joaquin Valley.

TABLE 3. Geographical variation in color of elytra of *Tecnophilus croceicollis* Ménétriés.

Locality	Number of specimens	Purple	Blue	Blue-green	Green
Alberta	52	9	38	9	-
Wyoming	7	-	7	-	-
Idaho	5	1	1	2	1
San Francisco Bay, California	39	34	4	1	-
Central Valley, California	29	9	13	7	-
Cuddeback Lake, California	65	-	15	38	12
Arizona	32	-	13	18	-
Texas	38	-	1	12	25
Sinaloa, Mexico	8	-	-	-	8

TABLE 4. Geographical variation in color of head of *Tecnophilus croceicollis* Ménétriés.

Locality	Number of specimens	Black	Piceous	Rufous
Alberta	52	52	-	-
Wyoming	7	7	-	-
Idaho	5	2	3	-
San Francisco Bay, California	39	30	8	1
Central Valley, California	41	4	28	9
Cuddeback Lake, California	65	-	-	65
Arizona	32	-	-	32
Texas	38	-	-	38
Sinaloa, Mexico	8	-	-	8

TABLE 5. Geographical variation in color of pronotum of *Tecnophilus croceicollis* Ménétriés.

Locality	Number of specimens	Black	Piceous	Rufous
Alberta	52	52	-	-
Wyoming	7	7	-	-
Idaho	5	1	1	3
San Francisco Bay, California	39	9	16	14
Central Valley, California	41	1	4	36
Cuddeback Lake, California	65	-	-	65
Arizona	32	-	-	32
Texas	38	-	-	38
Sinaloa, Mexico	8	-	-	8

Vestiture. - Specimens from southeastern Alberta, and from southeastern California and the neighboring portion of Arizona, possess very short sparse setae. Over the remainder of the range of *croceicollis*, specimens are moderately setose, or in southern New Mexico and along the Rio Grande in Texas, specimens are very densely setose.

Measurements and ratios. - Five measurements were taken of specimens of *Tecnophilus croceicollis.* Various combinations of these measurements were made up to produce four ratios to map out the general shape of the insects and to quantify observed differences in habitus between members belonging to different populations of this species. Values for measurements and ratios of four population samples of the species *croceicollis* are presented in tables 6 to 10. Data are given for only four population samples, as these four are the only homogeneous samples available of sufficient size to yield statistically significant results. The analysis of variation which follows is based on these four samples.

Below, the pattern of variation shown by each of these characters is discussed separately.

Length of elytra (table 6). - This measurement is taken as giving an index of the size of the beetle. The largest specimens seen were from coastal localities (Brownsville, Texas, $\bar{X} = 4.38$ mm; Newark, California, $\bar{X} = 4.21$ mm). Specimens from intermediate inland localities were smaller (Cuddeback Lake, California, $\bar{X} = 4.03$) and the smallest specimens seen were from northern inland localities (Lost River Ranch, Alberta, $\bar{X} = 3.73$ mm).

Width of pronotum/length of pronotum (table 7). - The population sample with the highest mean value for this ratio is from Newark, California ($\bar{X} = 1.22$). The sample from Cuddeback Lake, California has the lowest mean value for this ratio ($\bar{X} = 1.14$). Population samples from Brownsville, Texas and Lost River Ranch, Alberta possess intermediate mean values, and do not differ significantly between themselves.

TABLE 6. Geographical variation in length of elytra (mm) among selected population samples of *Tecnophilus croceicollis* Ménétriés.

Locality	N	Range	Mean	S.E.	S.D.	C.V.%
Newark, Cal.	40	3.83 - 4.57	4.21	0.03	0.20	4.75
Cuddeback Lake, Cal.	64	3.64 - 4.48	4.03	0.03	0.22	5.71
Brownsville, Texas	20	3.92 - 4.77	4.38	0.06	0.25	5.71
S.E. Alberta	38	3.30 - 4.28	3.73	0.04	0.23	6.17

TABLE 7. Geographical variation in the ratio width of pronotum/length of pronotum among selected population samples of *Tecnophilus croceicollis* Ménétriés.

Locality	N	Range	Mean	S.E.	S.D.	C.V.%
Newark, Cal.	40	1.16 - 1.32	1.22	0.01	0.04	3.28
Cuddeback Lake, Cal.	64	1.06 - 1.25	1.14	0.01	0.04	3.51
Brownsville, Texas	20	1.15 - 1.23	1.18	0.01	0.02	1.69
S.E. Alberta	38	1.13 - 1.25	1.19	0.01	0.03	2.52

Length of elytra/length of pronotum (table 8). - The pattern of variation shown by this character is similar to the pattern of variation shown by the length of the elytra. The samples with the largest mean values are from coastal localities while samples from inland and northern localities possess smaller mean values for this ratio.

Width of pronotum/maximum width of head (table 9). - The pattern of variation in this character is similar to the pattern of variation shown by the character width of pronotum/length of pronotum. The sample from Newark, California possesses the greatest mean value for this ratio ($\bar{X}$ = 1.18) while the sample from Cuddeback Lake, California has the smallest mean value ($\bar{X}$ = 1.10). The means for the samples from southeastern Alberta and from Brownsville, Texas are identical in value to one another ($\bar{X}$ = 1.14) and are intermediate between the mean values for the two California population samples.

Maximum width of head/minimum width of frons between eyes (table 10). - The sample with the largest mean value for this ratio is from Brownsville, Texas ($\bar{X}$ = 1.63). This is followed in descending order by the samples from Cuddeback Lake, California ($\bar{X}$ = 1.54). Newark, California ($\bar{X}$ = 1.45), and southeastern Alberta ($\bar{X}$ = 1.41). The value for this ratio becomes smaller for samples from east to west and from south to north.

The above five characters show several different patterns of variation. Because it is difficult to justify the weighting of any one of these characters above the other four in any given comparison of population samples, all characters were used simultaneously to develop discriminant functions to compare population samples with one another. For each comparison of a pair of population samples, a weight was calculated for each character used. The calculation was such that the value of the weight depended upon the discriminatory value of the character in that comparison (see Stanley MS for details on calculation). That is, if a character can separate members of two populations consistently, that character has a higher weighting coefficient than a character that gives inconsistent separations.

For the sake of brevity in the following discussion the population samples used in the comparisons are designated alphabetically, as follows:

A = Brownsville, Texas
B = Cuddeback Lake, California
C = Newark, California
D = Lost River Ranch, Alberta

Not all possible combinations of population comparisons were made. The Brownsville, Texas population sample was not compared with the population sample from Newark, California because both of these populations were independently compared with the geographically intermediate population sample from Cuddeback Lake, California. Thus, the A versus C comparison was made indirectly. Similarly, an indirect comparison between Newark, California (C) and Lost River Ranch, Alberta (D) was made. The populations of *croceicollis* in the central valley of California appear to be effectively isolated to the north and east by the Klamath Mountains and Sierra Nevadas respectively. This means that any genetical connection between these two populations would have to be indirect, through southern California. For this reason, the population sample from Cuddeback Lake was also taken as being intermediate between these two populations.

TABLE 8. Geographical variation in the ratio of length of elytra/length of pronotum among selected population samples of *Tecnophilus croceicollis* Ménétriés.

Locality	N	Range	Mean	S.E.	S.D.	C.V.%
Newark, Cal.	40	2.76 - 3.06	2.92	0.01	0.08	2.74
Cuddeback Lake, Cal.	64	2.65 - 3.11	2.84	0.01	0.08	2.82
Brownsville, Texas	20	2.84 - 3.09	2.95	0.02	0.08	2.71
S.E. Alberta	38	2.59 - 2.82	2.71	0.01	0.06	2.21

TABLE 9. Geographical variation in the ratio of width of pronotum/maximum width of head among selected population samples of *Tecnophilus croceicollis* Ménétriés.

Locality	N	Range	Mean	S.E.	S.D.	C.V.%
Newark, Cal.	40	1.09 - 1.24	1.18	0.01	0.03	2.54
Cuddeback Lake, Cal.	64	1.03 - 1.16	1.10	0.01	0.04	3.64
Brownsville, Texas	20	1.08 - 1.20	1.14	0.01	0.03	2.63
S.E. Alberta	38	1.07 - 1.18	1.14	0.01	0.03	2.63

TABLE 10. Geographical variation in the ratio of maximum width of head/minimum width of head between eyes among selected population samples of *Tecnophilus croceicollis* Ménétriés.

Locality	N	Range	Mean	S.E.	S.D.	C.V.%
Newark, Cal.	40	1.40 - 1.53	1.45	0.01	0.03	2.07
Cuddeback Lake, Cal.	64	1.49 - 1.63	1.54	0.01	0.03	1.95
Brownsville, Texas	20	1.57 - 1.67	1.63	0.01	0.03	1.84
S.E. Alberta	38	1.31 - 1.48	1.41	0.01	0.03	2.13

Comparisons between pairs of populations were made in the following way. A $\overline{Z}_i$ value (the sum of the mean character values multiplied by their individual weighting coefficients) was calculated for each of the two population samples compared. An axis was plotted on a map joining the localities from which these population samples were obtained. Using the weighting coefficient calculated for the original comparison, $\overline{Z}_i$ values were calculated for samples from geographically intermediate localities that lay along the axis and these $\overline{Z}_i$ values were plotted on a map. Where the $\overline{Z}_i$ value obtained from geographically intermediate population samples was equal to or approached the mid-point value, a transverse line was drawn across the axis. This transverse line theoretically divided members of the two populations and their associated specimens from one another. If the position in which this transverse line occurred was concordant with a change in the state of one or more other characters such as color, the populations separated by this line were considered to be subspecifically distinct.

A summary of the population comparisons that have been made is presented below. Table 11 gives the weighting coefficients and the calculated $\overline{Z}_i$ values of the population samples used for each set of comparisons.

TABLE 11. Summary of calculated weighting coefficients (W*) and $\overline{Z}_i$ values obtained for each comparison of a pair of population samples of *Tecnophilus croceicollis* Ménétriés.

Comparison										% overlap	
I	vs II	W_1	W_2	W_3	W_4	W_5	$\overline{Z}_I$	$\overline{Z}_{II}$	Mid-point Z_i value	Ob-served	Calcu-lated
A	B	0.715	0.105	0.845	-0.135	-0.489	1.721	1.613	1.667	25	44
A	D	-	-0.053	3.643	1.165	-	9.102	8.090	8.596	0	30
B	C	-0.489	-0.029	0.715	0.707	0.038	0.673	0.568	0.621	9.8	44
B	D	-.3.281	-0.223	2.023	1.396	3.768	6.611	6.209	6.410	0	22

W_1 to W_5 are weighting coefficients for characters X_1 to X_5 respectively, where character X_1 = WP/LP; X_2 = LE mm; $X_3 = WH_1/WH_2$; X_4 = SE/LP; and $X_5 = WP/WH_1$.

Population samples have been designated alphabetically as follows: A = Brownsville, Texas; B = Cuddeback Lake, California; C = Newark, California; and D = Lost River Ranch, Alberta.

Brownsville, Texas versus Cuddeback Lake, California (Comparison A-B). - Calculated $\overline{Z}_i$ values for population samples from Brownsville, Texas, Cuddeback Lake, California and for specimens from intermediate localities are presented in table 12, and are plotted on a map in fig. 2. The line transverse to the A-B axis separates populations with $\overline{Z}_i$ values above the mid-point value. This line is not concordant with that of any other character observed to vary between the two populations.

TABLE 12. $\overline{Z}_i$ values calculated for selected population samples of *Tecnophilus croceicollis* Ménétriés from the discriminant function developed for the Brownsville, Texas (A) vs Cuddeback Lake, California (B) populations comparison (mid-point $\overline{Z}_i$ value is 1.667).

		Comparison A vs B		
Map symbol	Locality	Number of specimens	Range	$\overline{Z}_i$
	TEXAS			
A	Brownsville	20	1.667 - 1.799	1.721
b	Mission	1	1.698	1.698
c	Pecos	2	1.782 - 1.800	1.791
d	Fabens	5	1.726 - 1.786	1.743
	NEW MEXICO			
e	Alamogordo	1	1.759	1.759
f	Lordsburg	7	1.716 - 1.886	1.782
g	Fort Wingate	1	1.606	1.606
h	San Juan Valley	2	1.655 - 1.736	1.695
	Coolidge (?)	5	1.605 - 1.668	1.630
	ARIZONA			
i	San Bernardino	2	1.718 - 1.725	1.722
j	Tuscon	1	1.669	1.669
k	Globe	1	1.752	1.752
l	Winslow	5	1.592 - 1.664	1.631
m	Tempe	1	1.678	1.678
n	Palomas	1	1.617	1.617
o	Welton	5	1.605 - 1.696	1.659
	CALIFORNIA			
B	Cuddeback Lake	64	1.541 - 1.701	1.613

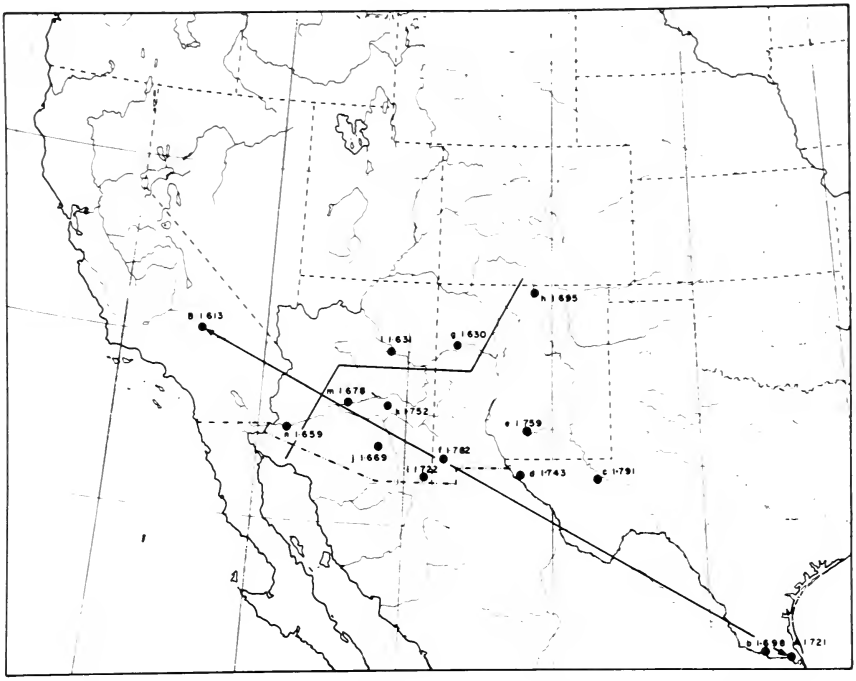


Fig. 2. Plotted mean Z_i values of selected population samples of *Tecnophilus croceicollis* Ménétriés used in the comparison of populations from Brownsville, Texas (A) to Cuddeback Lake, California (B). The mid-point Z_i value equals 1.667. Association of letters and locality names are made in Table 13.

Brownsville, Texas versus Lost River Ranch, Alberta (Comparison A-D). - Calculated $\overline{Z}_i$ values for the two population samples compared and for specimens from intermediate localities are presented in table 13 and are plotted on a map in fig. 3. The transverse line representing the position in which mid-point values are expected to occur extends across northern Colorado. This line is concordant with a change in color and a change in eye shape.

Cuddeback Lake, California versus Newark, California (Comparison B-C). - Calculated $\overline{Z}_i$ values are presented in table 14 and fig. 4, in the same way as above. The discriminant function gives poor separation of specimens from the two populations used in the original comparison. It provides even poorer separation of specimens from intermediate localities. Specimens with intermediate $\overline{Z}_i$ values are found in the northern portions of the San Joaquin Valley and this change is not concordant with a change in the state of any other character. Like color, $\overline{Z}_i$ values vary clinally.

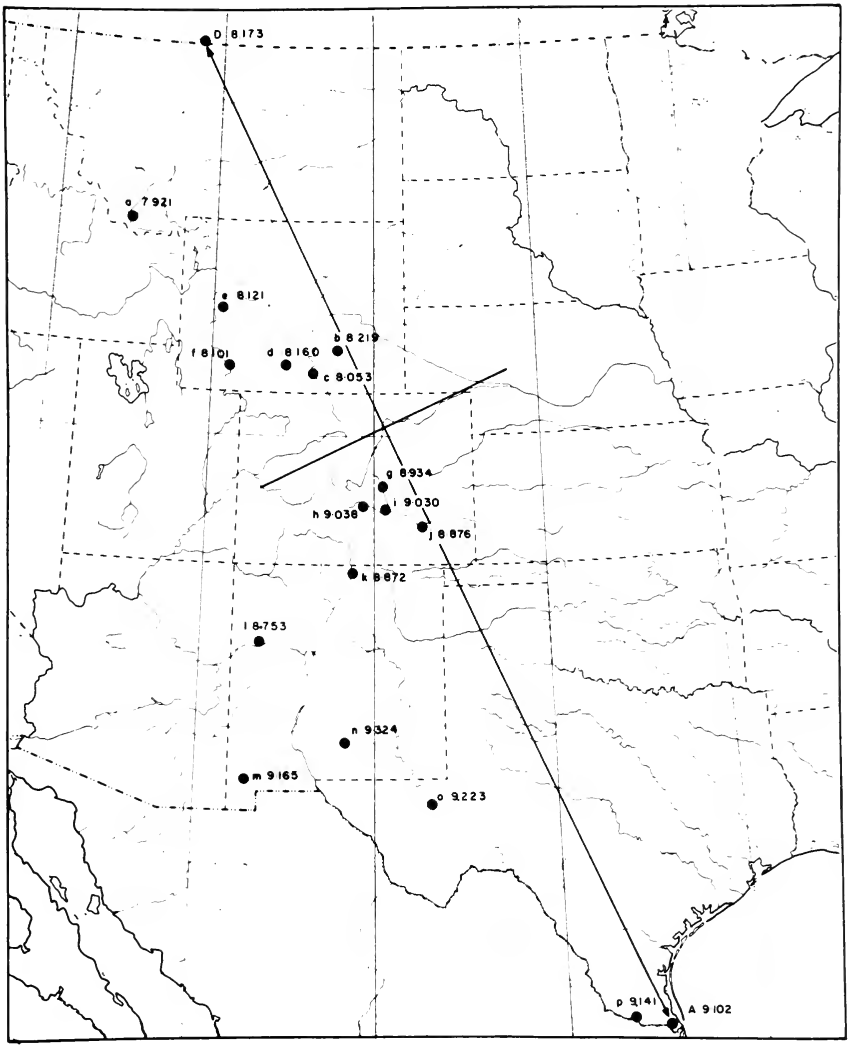


Fig. 3. Plotted mean Z_i values of selected population samples of *Tecnophilus croceicollis* Ménétriés used in the comparison of populations from Brownsville, Texas (A) to Lost River Ranch, Alberta (D). The mid-point Z_i value equals 8.596. Association of letters and locality names are made in Table 14.

TABLE 13. $\overline{Z}_i$ values calculated for selected population samples of *Tecnophilus croceicollis* Ménétriés from the discriminant function developed for the Brownsville, Texas (A) vs Lost River Ranch, Alberta (D) populations comparison (mid-point $\overline{Z}_i$ value is 8.596).

Map symbol	Locality	Number of specimens	Range	$\overline{Z}_i$
	ALBERTA			
D	Lost River Ranch	38	7.783 - 8.379	8.173
	MONTANA			
a	Dillon	1	7.921	7.921
	WYOMING			
b	Medicine Bow	1	8.249	8.249
c	Saratoga	2	7.974 - 8.133	8.053
d	Creston	2	8.110 - 8.210	8.160
e	Pinedale	1	8.121	8.121
f	Green River	1	8.101	8.101
	COLORADO			
g	Colorado Springs	2	8.769 - 9.099	8.934
h	Florence	1	9.038	9.038
i	Pueblo	1	9.030	9.030
j	La Junta	1	8.876	8.876
	NEW MEXICO			
k	San Juan Valley	2	8.618 - 9.124	8.872
1	Ft. Wingate	1	8.465	8.465
m	Lordsburg	7	9.031 - 9.457	9.165
n	Alamogordo	1	9.324	9.324
	TEXAS			
o	Reeves Co., Pecos	2	9.150 - 9.296	9.223
p	Mission	1	9.141	9.141
A	Brownsville	20	8.967 - 9.291	9.102

Cuddeback Lake, California versus Lost River Ranch, Alberta (Comparison B-D).-Calculated $\overline{Z}_i$ values are presented in table 15 and fig. 5 in the manner outlined above. In this case, the transverse line representing the approximate location of specimens possessing mid-point $\overline{Z}_i$ values, is in northern Utah. $\overline{Z}_i$ values for specimens collected from localities in close proximity to this line, tend to intergrade into each other. Color and vestiture also change through this region.

Summary. - Because of lack of concordance in the variation patterns among the characters studied, the population samples A, B and C are considered to be consubspecific. However, several characteristics differentiating population samples A and D change in the same area. Also, several characteristics differentiating population samples B and D change in the same area. I conclude therefore, that population sample D and specimens associated with it are subspecifically distinct from samples A, B and C and their associated specimens.

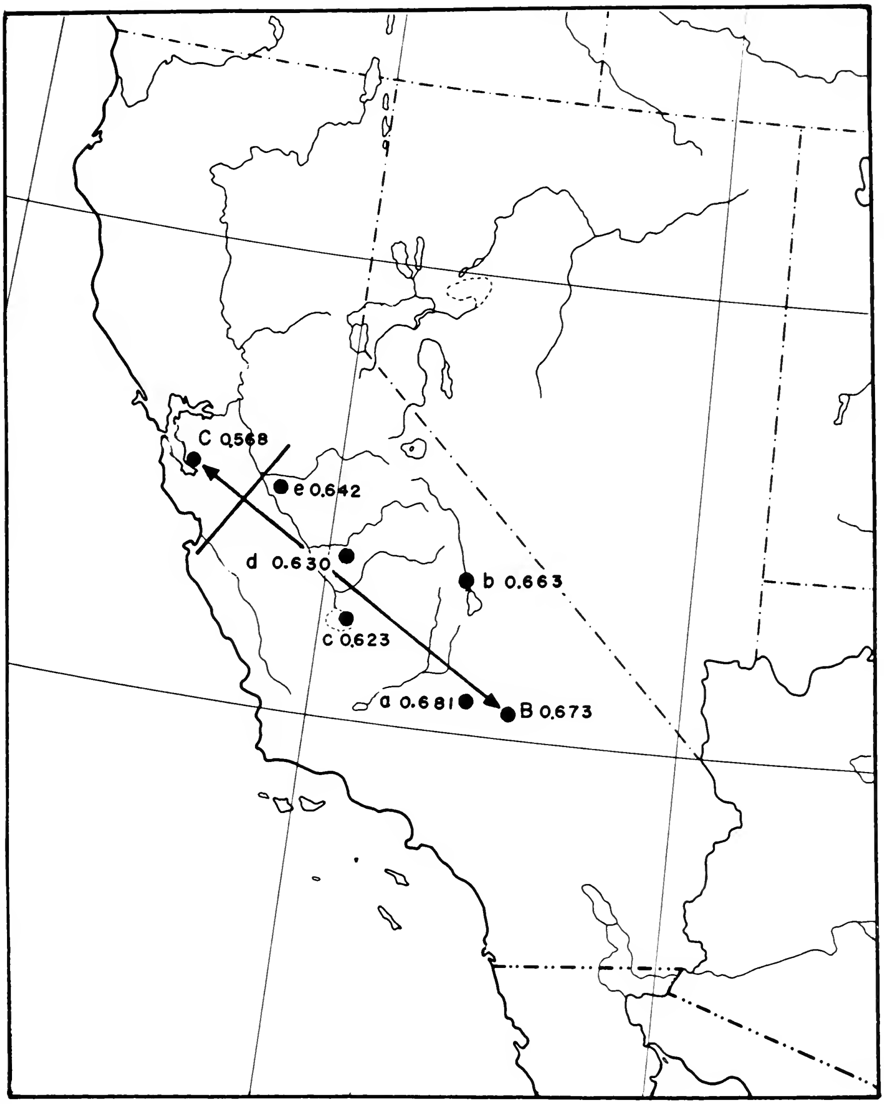


Fig. 4. Plotted mean Z_i values of selected population samples of *Tecnophilus croceicollis* Ménétriés used in the comparison of populations from Cuddeback Lake, California (B) to Newark, California (C). The mid-point Z_i value equals 0.621. Association of letters and locality names are made in Table 15.

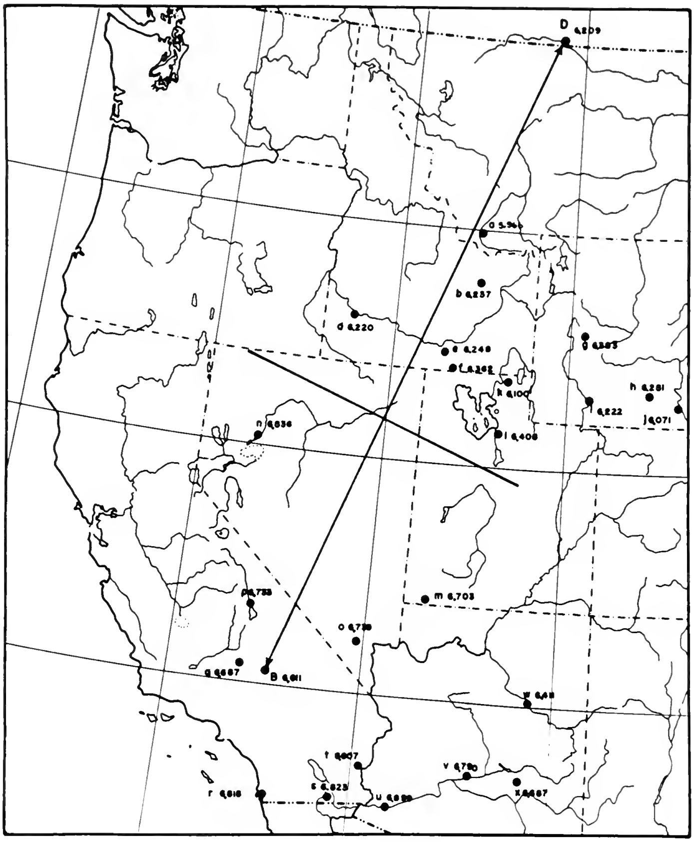


Fig. 5. Plotted mean Z_i values of selected population samples of *Tecnophilus croceicollis* Ménétriés used in the comparison of populations from Cuddeback Lake, California (B) to Lost River Ranch, Alberta (D). The mid-point Z_i value equals 6.410. Association of letters and locality names are made in Table 15.

TABLE 14. $\overline{Z}_i$ values calculated for selected population samples of *Tecnophilus croceicollis* Ménétriés from the discriminant function developed for the Cuddeback Lake, California (B) vs Newark, California (C) populations comparison (mid-point $\overline{Z}_i$ value is 0.621) (fig. 4).

		Comparison B vs C		
Map symbol	Locality	Number of specimens	Range	$\overline{Z}_i$
B	Cuddeback Lake	64	0.622 - 0.773	0.673
a	Koehn Lake	7	0.645 - 0.780	0.681
b	Lone Pine	3	0.632 - 0.690	0.663
c	Kings Co.	4	0.594 - 0.649	0.623
d	Fresno Co.	4	0.605 - 0.656	0.630
e	Merced Co.	3	0.624 - 0.653	0.642
C	Newark	40	0.492 - 0.648	0.568

TABLE 15. $\overline{Z}_i$ values calculated for selected population samples of *Tecnophilus croceicollis* Ménétriés from the discriminant function developed for the Cuddeback Lake, California (B) vs. Lost River Ranch, Alberta (D) populations comparison (mid-point $\overline{Z}_i$ value is 6.410).

Map symbol	Locality	Number of specimens	Range	$\overline{Z}_i$
	ALBERTA			
D	Lost River Ranch	38	5.926 - 6.308	6.209
	MONTANA			
a	Dillon, Beaverhead Co.	1	5.966	5.966
	IDAHO			
b	Howe	1	6.237	6.237
c	Viola	1	5.710	5.710
d	Grandview	1	6.220	6.220
e	Malta	1	6.248	6.248
f	Strevell	1	6.362	6.362
	WYOMING			
g	Pinedale	1	6.383	6.383
h	Creston	2	6.235 - 6.267	6.251
i	Green River	1	6.222	6.222
j	Saratoga	2	6.052 - 6.099	6.071
	UTAH			
k	Logan	1	6.100	6.100
l	Salt Lake City	6	6.267 - 6.488	6.408
m	St. George	5	6.510 - 6.866	6.703
	NEVADA			
n	Humbolt Lake	2	6.403 - 6.669	6.536
o	Las Vegas	2	6.651 - 6.827	6.739
	CALIFORNIA			
p	Lone Pine	3	6.567 - 7.056	6.733
q	Koehn Lake	7	6.499 - 6.804	6.687
B	Cuddeback Lake	64	6.421 - 6.871	6.611
r	San Diego	2	6.494 - 6.536	6.515
s	El Centro	3	6.690 - 6.906	6.823
t	Palo Verde	4	6.411 - 6.719	6.607
	ARIZONA			
u	Welton	5	6.489 - 6.982	6.699
v	Tempe	3	6.724 - 6.866	6.790
w	Winslow	5	6.410 - 6.537	6.411
x	Globe	1	6.657	6.657

Key to the Subspecies of *Tecnophilus croceicollis* Menetries

1. Specimens from California .... *c. croceicollis* Menetries

1'. Specimens from localities other than California 2

2(1). Color of head, pronotum and legs rufous; eyes large and convex (fig. 25). .... *c. croceicollis* Men., p.60

2'. Color not as above; if head, pronotum and legs basically rufous in color, at least tarsi, clypeus and frons between eyes somewhat infuscated: eyes small and flat (fig. 24). .... *c. peigani* new subspecies, p. 61

OR

2a(1). Specimens from west of Rocky Mountains 3

2a'. Specimens from east of Rocky Mountains 4

3(2). $(-3.281)WP/LP + (-0.223)LE + (2.023)WH_1/WH_2 + (1.396)LE/LP + (3.768)WP/WH > 6.410$ .... *c. croceicollis* Men.

3'. “+“+“+“+“ < 6.410 .... *c. peigani* n. ssp.

4(2). $(0)WP/LP + (-0.053)LE + (3.643)WH_1/WH_2 + (1.165)LE/LP + (0)WP/WH > 8.596$ .... *c. croceicollis* Men.

4'. “+“+“+“+“ < 8.596 .... *c. peigani* n. ssp.

Tecnophilus croceicollis croceicollis Ménétriés 1843

Calleida croceicollis Ménétriés 1843 - 54. *Type locality* - California.
Callida chloridipennis Motschoulsky 1850 - 39. (from Horn 1882)
Philotecnus nigricollis LeConte 1851 - 176. *Type locality* - San Jose, California.
Philotecnus ruficollis LeConte 1851 - 176. *Type locality* - San Diego, California.
Tecnophilus glabripennis Chaudoir 1877 - 242. *Type locality* - Nevada.

Specimens of this subspecies may best be recognized on the basis of the combination of characters presented in the key to subspecies of *croceicollis*.

Description. - Values for ratios and measurements of selected population samples of this subspecies are presented in tables 6 to 10.

Color varied in specimens from the Central Valley of California; head, pronotum and legs basically rufous with at least some infuscation and in some specimens these parts are black; elytra dark blue or purple. Specimens from remainder of range with head, pronotum and legs uniformly rufous; elytra blue to green.

Microsculpture lightly impressed or obsolete on head and disc of pronotum; varied on elytra from granular to lightly impressed and shiny.

Head with eyes large and convex (fig. 25). Antenna relatively long and slender.

Pronotum varied in shape (figs. 39 to 41); not so cordate as in *peigani*.

Elytra varied in shape, short and oval in some specimens to more elongate and parallel sided; striae evidently impressed and distinctly punctate; intervals flat to convex, variably punctate.

Male genitalia as in fig. 19. Similar to that of *T. pilatei* but with a shorter apex.

Female stylus (fig. 56) truncate apically, not produced.

Discussion. - The high degree of variation shown by this subspecies has led past authors to describe a number of species, or to regard *croceicollis* as a single highly variable species.

Notes on synonymy. - The name *pilatei* Chaudoir is not a synonym for *croceicollis* Menetries as is shown above.

Mexico - DURANGO: Durango (Emburg, CAS); SINALOA: El Camaron (Ball, UASM).

United States - ARIZONA: Cochise Co., San Bernardino Ranch (Snow, UASM); Gila Co., Globe (USNM); Navajo Co., Winslow (USNM); Pima Co., Tucson (MCZ); Yuma Co., Palomas (CU), Wellton (CU). CALIFORNIA: Alameda Co., Bay Farm Island (Barr, Dahl, CAS, IUM, MCZ), Newark (Tyson, UASM); Butte Co., Oroville (Kelfer, CAS); Contra Costa Co., Antioch (Rose, CAS), Brentwood (Van Dyke, CAS), Vine Hill (Blaisdell, CAS); Fresno Co., Mendota (MCZ); Imperial Co., El Centro (Hanson, Van Dyke, CAS, CU, WUM); Palo Verde (Barr, IUM); Inyo Co., Lone Pine (Van Dyke, CAS) Panamint Valley (USNM), (Nunenmacher, CNHM); Kern Co., Koehn Lake (Erwin, UASM); Kings Co., (CNHM); Lassen Co., (Nunenmacher, CNHM); Merced Co., Los Banos (O'Brien, Van Dyke, CAS, UASM); Orange Co., Seal Beach (Gillogly, CAS); Riverside Co., Coachella (Van Dyke, CAS); San Bernardino Co., Barstow (Hayward, MCZ), Cuddeback Lake (Larson & Sharp, UASM); Needles (Kusche, CAS); Santa Clara Co., Alviso (Erwin, Larson & Sharp, UASM); San Diego Co., San Diego (CAS); San Joaquin Co., Weston (Van Dyke, CAS); San Mateo Co., San Mateo (Nunenmacher, Van Dyke, CAS, CNHM); Solano Co., Benica (Car. M); Sonoma Co., Glen Ellen (Kusche, CAS, CNC); Stanislaus Co., Patterson (Ross, CAS); Yolo Co., Davis (Erwin, Hatch, Car. M., UASM, WUM); Yuba Co., Marysville (Van Dyke, CAS). COLORADO: Bent Co., La Junta (Hayward, MCZ); El Paso Co., Colorado Springs (Soltau, USNM); Freemont Co., Florence (Soltau, USNM); Pueblo Co., Pueblo (Soltau, USNM). NEVADA: Churchill Co., Humbolt Lake (Wickham, USNM); Clark Co., Las Vegas (Barr, Johnston, CNC, IUM); Pershing Co., Lovelock (Baker, SJSC). NEW MEXICO: Hidalgo Co., Lordsburg (Howden, CNC); McKinley Co., Ft. Wingate (Dow, CAS); Otero Co., Alamogordo (Wickham, USNM); Taos Co., San Juan Valley (Bowditch, MCZ). TEXAS: Cameron Co., Brownsville (many collectors, CNC, INHS, MCZ, UASM, USNM); El Paso Co., Fabens (Howden, CNC); Hidalgo Co., Mission (Gurney, USNM); Reeves Co., Pecos (Johnston, CNC), Pecos River? (Odenbach, USNM). UTAH: Washington Co., St. George (AMNH, CAS, MCZ, USNM).

Tecnophilus croceicollis peigani new subspecies

Holotype - male, Milk River near junction with Lost River, Lost River Ranch, Alberta (12 V/1965, Getty & Larson, CNC).

Allotype - female, same locality (CNC).

Paratypes. - All other specimens from Alberta have been labelled as paratypes (see below for list of localities).

The diagnostic characteristics of this subspecies are presented in the above key, and in the discussion of geographical variation in *T. croceicollis.*

Description. - Values for ratios and measurements of this subspecies are presented in tables 6 to 10.

Color black, with elytra and in some specimens disc of pronotum with dull metallic blue or blue-green lustre; appendages black or piceous (see following discussion for variation in color).

Microsculpture lightly impressed or obsolete on head and disc of pronotum; isodiametric and coarse on elytra.

Vestiture very short and sparse on specimens from Alberta. Specimens from more southerly localities moderately setose.

Head broad; eyes small and little convex (fig. 24). Antenna shorter and stouter than in *c. croceicollis*.

Pronotum strongly cordate (fig. 42), lateral margins strongly constricted behind, lateral reflexion narrow.

Elytra short and oval, with greatest width in apical half; striae deeply impressed and evidently punctate; intervals convex, each bearing an irregular row of coarse punctures.

Male genitalia (fig. 20) and female stylus similar to *c. croceicollis.*

Variation. - Vestiture and color vary over the range of this subspecies. Specimens from the eastern side of the Rocky Mountains are black or at least dark piceous in the color of the head and pronotum. Specimens with this coloration have also been seen from eastern Idaho and extreme northern Utah. However, specimens from central and western Idaho and the Salt Lake region of Utah are much paler in color. In specimens from these regions, the ground color of the head, pronotum and legs is usually rufous, with at least some infuscation occurring on the legs, clypeus and the frons between the eyes. This tendency towards pale coloration in specimens of *peigani* from Idaho and Utah is probably a result of hybridization with *c. croceicollis.*

Specimens of *peigani* from Alberta appear to be almost glabrous dorsally because of the greatly reduced length of the setae. Over the remainder of the range, the dorsal pubescence is longer and quite distinct.

Etymology. - The subspecific name is the latinized form of the word Peigan, the name of a tribe of Indians of the Blackfoot Confederation, which inhabited the prairies of southern Alberta. Confusion exists as to the correct spelling of this name, but the Edmonton office of the Canadian Government Department of Indian Affairs accepts "Peigan" as the correct spelling.

Disposition of type material. - The holotype and allotype have been deposited in the Canadian National Collection, Ottawa. Paratypes have been deposited in California Academy of Sciences, Canadian National Collection, Museum of Comparative Zoology, University of Alberta, Strickland Museum, and the United States National Museum.

Distribution. - Localities from which specimens of *peigani* have been collected are plotted in fig. 63. I have seen 73 specimens of this subspecies from the following localities.

Canada - ALBERTA: Forty Mile Coulee, 5 miles north Etzikom (Getty, Larson, Whitehead, UASM); Milk River near junction with Lost River, Lost River Ranch (Ball, Erwin, Freitag, Getty, Larson, CAS, CNC, MCZ, UASM, USNM); Picture Butte (Getty & Larson, UASM).

United States - COLORADO: "Col." (USNM). IDAHO: Butte Co., Howe (Barr, IUM); Cassia Co., Malta (Henry, IUM); Strevell (Barr, IUM); Owyhee Co., Grandview (Furniss, IUM). MONTANA: Beaverhead Co., Dillon (Jellison, MUB). UTAH: Cache Co., Logan (Henderson, CAS); Davis Co., (Stafford, USNM); Salt Lake Co., Salt Lake City (J.B., Henderson, Huelleman, Klages, Car. M., IUM , WUM). WYOMING: Carbon Co., Medicine Bow (AMNH), Saratoga (Bryant, CAS); Sublette Co., Pinedale (Alexander, MCZ); Sweetwater Co., Creston (Bryant, CAS), Green River (Bowditch, MCZ).

BIOLOGY

Although little is known of the biology of beetles of the subtribe Callidina, members of many of the species and genera appear to be at least partly arboreal. Habu (1960, 1967) summarized what is known of the biology of members of the genus *Callida.* Generally, these insects are arboreal predators, feeding mostly on lepidopterous larvae. These insects do not show any of the parasitic adaptations possessed by the members of the genus *Lebia.*

What I have observed of the biology of the genera *Tecnophilus* and *Philophuga* is presented below.

Biology of *Tecnophilus* Chaudoir

The biology of these insects is poorly known. Adults of this genus tend to be more terrestrial than are adults of any of the other North American callidine genera. This is reflected in the slender legs and tarsi, setose body and the cordate prothorax of *Tecnophilus*; characters which are often found in terrestrial carabids, but seldom found in arboreal forms.

Adults are found on saline or alkaline soils in eroding areas. Table 16 presents some of the physical characteristics of the top six inches of the soils on which these insects have been collected. The high soil salinity and the arid conditions in regions in which members of the genus *Tecnophilus* occur, suggests that desiccation may be an important factor with which these insects must contend. During relaxation of specimens prior to dissection, I noticed that the dried tissues were quite impermeable to water. Immersion in near-boiling water for periods of fifteen minutes to half an hour was not sufficient to soften the abdominal membranes enough to permit the genitalia to be withdrawn easily. This is a longer time than is required to relax most species of carabids. This impermeability may be an adaptation to resist desiccation under arid conditions.

In southeastern Alberta, specimens of *Tecnophilus croceicollis peigani* are usually found along the bases of south facing coulees, where considerable erosion has occurred and alluvial fans have been deposited. These fans are composed of a clay-sand soil which bakes and cracks extensively when dry. The sparse vegetation consists principally of *Bouteloua gracilis* (Lag.) H.B.K., *Atriplex nuttalli* Wats., *Opuntia* spp., *Mamillaria vivipara* Haw., and *Erigonum flavum* Nutt. A more complete description of the region is presented by Lewin (1963).

On sunny days in May and early June, specimens of *c. peigani* were found running over the surface of the ground, or climbing on very low vegetation. Infrequently specimens have been taken under cover or from cracks in the ground. At this time, the insects are often found in copulation, and mating occurs readily among captured specimens. Fertile females collected at this time and brought into the laboratory, usually laid eggs within a week or two. Larvae emerging from these eggs were reared as far as the third instar on the following foods: larvae of several species of curculionids, wheat stem sawfly larvae, wax moths, meal worms, and ant larvae and pupae. Mortality was high on all of these foods.

This subspecies probably hibernates in the adult stage, for one specimen from Green River, Wyoming (20-27/VII/1877), was teneral, indicating that emergence from the pupal stage occurs during the middle of the summer. All specimens are fully winged but flight has not been observed.

The habitats in which specimens of *c. croceicollis* were found, vary over the wide range of this subspecies. The most consistent features of the habitats are saline eroding soils and sparse vegetation.

In the vicinity of San Francisco Bay, beetles have been collected on salt flats, usually in areas dominated by plants of the genus *Salicornia*. During the winter months, these insects are found near or at the surface of the soil, under the *Salicornia* mats or other loose cover (Erwin, pers. comm.). However, on July 5, 1966 (Alviso, California, Larson & Sharp, collectors) seven specimens were collected at depths of four to eight inches in the sandy soil beneath *Salicornia* plants. The beetles were on the upper surface of the clay hardpan, and in company with specimens of *Amara stupida* LeConte and *Pristonychus complanatus* Dejean.

The two teneral specimens that I have seen from the central valley of California (Marysville, Yuba Co., VI/1908; and Mendota, Fresno Co., V-VIII) suggest that the larval stage occurs during the spring and summer in this region.

Specimens of *c. croceicollis* have been collected from the margins of several alkaline playas in the Mojave Desert of southeastern California. A long series of beetles collected at Cuddeback Lake (June 30, 1966, Larson & Sharp) was found among the buried portions of the crowns of bur sage (*Franeria dumosa* Grey) at depths of three to ten inches. Specimens collected at the neighboring Koehn Lake in the spring (April 10, 1965, Erwin) were found at the surface of the soil, under loose cover. I have seen teneral specimens from Lone Pine, California (20/V/1937). The larval stage probably occurs in the early spring as this is the season of greatest rainfall in the Mojave Desert.

All long series of *c. croceicollis* that I have seen from Texas, have been collected at light. I do not know the habitat of this insect in Texas, but it appears to occur only in inland localities and not along the Gulf Coast. On the other hand, *T. pilatei* is found primarily along the coast and only for a short distance inland. A mixed series of both of these species was collected at light in Brownsville, Texas (May 1967).

Outside of Texas, I have seen only one specimen of *croceicollis* (s.e. California) labelled as being collected at light.

Most specimens of the species *pilatei* have been collected at light. However, some at least have been collected by sweeping vegetation along sea beaches (Port Isabel, Ball).

In order to obtain the larvae of *Tecnophilus*, I maintained adults of *c. croceicollis* and *c. peigani* alive. The method of oviposition was observed, and was found to proceed as follows for both subspecies: when ready to lay an egg the female collected a small ball of soil particles on the apex of her abdomen. These particles were first loosened with the mandibles then picked up singly with the apex of the abdomen to which they adhered, probably by means of an adhesive substance produced by the accessory glands. When sufficient material was collected, the female climbed some object such as a twig. When she had climbed to a height of several inches, the beetle turned and faced downward. The abdomen was pressed against the twig, and a drop of fluid was released. The abdomen was then moved away from the twig, drawing the drop of fluid out until it hardened into a silk-like strand. This strand was formed partly by the movement of the abdomen, and partly by means of an apposable motion of the styli. When the thread reached a length of about 1 to 6 mm, the female injected an egg into the ball of soil particles that she still carried on the apex of her abdomen. The egg and soil covering were then released, and were left dangling in the air, suspended from the twig by means of the silken thread. The egg remained suspended in this way until the larva hatched.

This method of oviposition may be related to the peculiar form of stylus that is found in members of the Callidina. *Philophuga viridis amoena*, which possesses a similar form of ovipositor, lays its eggs in the same way. This form of egg laying could certainly be a valuable adaptation for desert species, for it would protect the eggs to some extent from most predators, flash floods, and soil erosion. On the other hand, it would make the eggs more susceptible to desiccation. As the rest of the members of the Callidina possess this form of ovipositor, and are more or less arboreal, this form of egg laying was probably an adaptation to an arboreal existence, and has secondarily proved useful to desert dwelling species.

TABLE 16. Some physical characteristics of soils on which specimens of *Tecnophilus croceicollis* Ménétriés have been collected.

Locality	Number of soil samples	pH	Electrical conductivity	$CaCO_3$	Na	Cl	Texture
Lost River, Alberta	5	8.1-8.4	0.9-6.0	high	high	trace	packed clay-sand
Alviso, California	2	4.0-4.4	16+	-	extremely high	200+	friable sand
Cuddeback Lake, California	1	7.5	15.0	high	extremely high	200+	sand
Rockport, Texas	1	8.1	8.0	-	very high	180	friable sand

Biology of *Philophuga* Motschoulsky

As I have collected few specimens of the genus *Philophuga*, I know little of the habits of these insects. In general, members of this genus occur in arid and semi-arid regions of western North America. They are not usually found in saline situations as are members of the genus *Tecnophilus*, and they appear to be much more arboreal than the latter, for specimens of *Philophuga* are often found on vegetation.

In southern Alberta, specimens of *P. viridis amoena* are found in the same general region as are specimens of *T. croceicollis peigani*. However, rather than occurring along the bases of coulees in regions of baked soil and sparse vegetation, they are usually found on short grass prairie.

Many of the specimens of *P. viridis horni* that I have examined, are associated with labels indicating that they have been collected on vegetation, usually *Artemisia* or *Atriplex*. I know nothing of the biology of the other subspecies of *viridis* except that most specimens of *v. viridis* that I have examined were collected during the month of December.

The labels associated with many adult specimens of *P. viridicollis* indicate that the beetles were collected on vegetation. Four specimens of this species collected at Monahans, Texas (Larson & Sharp, June 12,1966) were found on a short legume, in leaf rolls made by a lepidopterous larva. Larvae of *viridicollis* have been collected at Rocky Ford, Colorado (Hamilton, USNM) feeding on the larvae of *Ancylis comptana* W. & R. (Lepidoptera : Olethreutidae). Teneral adults of this species have been collected from April 28 to July 5.

Specimens of *P. brachinoides* have been collected in bromeliads (Ball & Whitehead).

I have not seen any records of specimens of the genus *Philophuga* collected at light.

In this genus, oviposition has been observed only for the subspecies *viridis amoena*. It proceeds in the same way as outlined under *Tecnophilus croceicollis.*

PHYLOGENY

The following discussion is an explanation of the rationale used to construct the phylogenetic diagram presented in table 17. In order to construct this model, two assumptions had to be made: (a) it is possible to discover those characteristics that are widespread in the group due to common ancestry, and to distinguish these from similar characteristics that have resulted from convergence (Cain & Harrison 1960); and (b) the rate of evolution has been uniform throughout the group, so that the degree of difference between two taxa is directly proportional to the length of time for which the two ancestral stocks have been isolated. These assumptions are necessitated by the complete lack of fossil evidence.

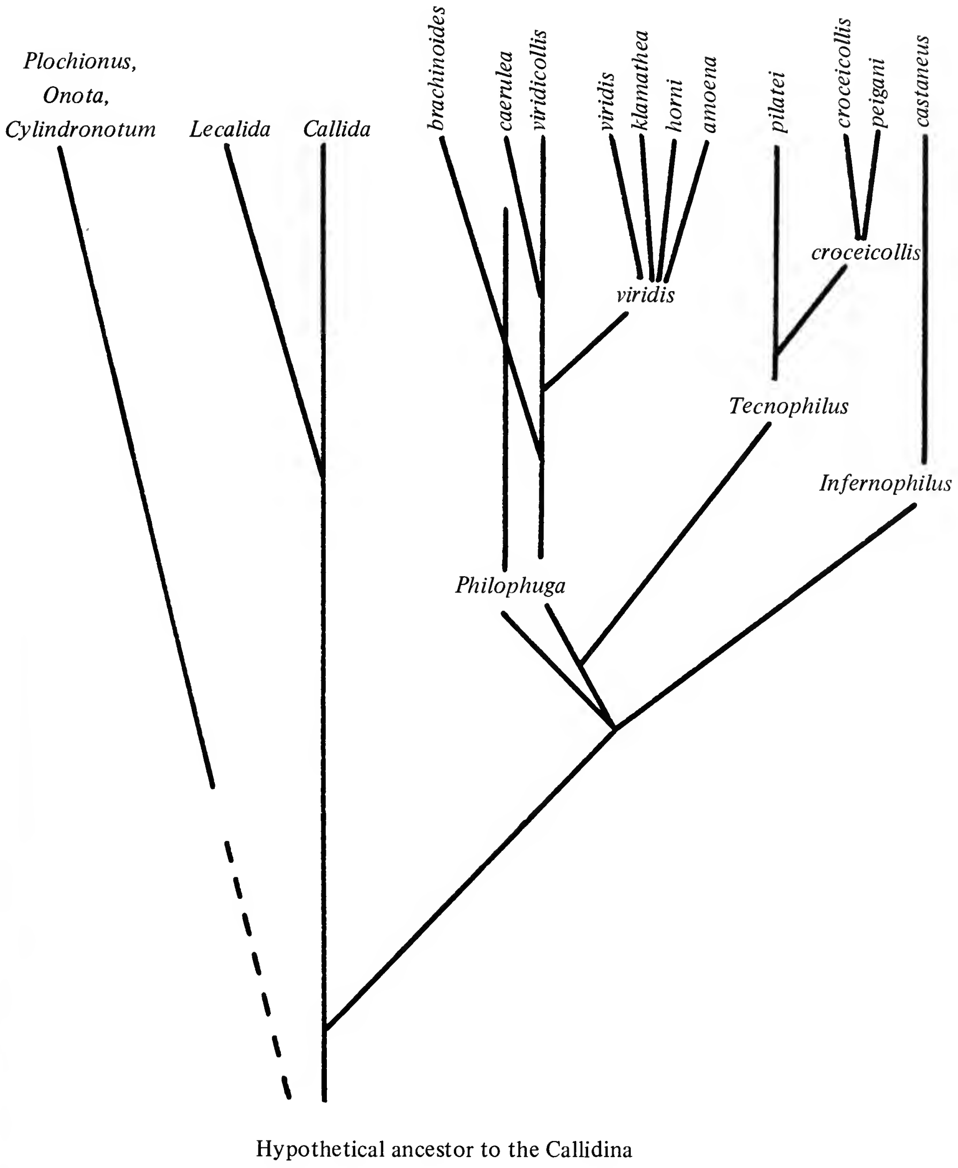
Based on these considerations, the following hypothetical model of the evolution of the North American Callidina is presented. The ancestral stock was probably arboreal, and possessed the following characteristics: color of elytra metallic blue or green, color of remainder of body rufous to black; dorsal surface of body glabrous; labial palpus with terminal article securiform, penultimate article bisetose; ligula bi- or pluri-setose;prothorax broad, with wide lateral reflexion; legs stout, with tarsal article 4 bilobed, claws pectinate, ventral surface of tarsal articles 1 to 4 of front and middle tarsi of male bearing two rows of scales beneath; elytra completely bordered basally and apically, striae evident and punctate, intervals flat or slightly convex; hind wings fully developed and lightly pigmented; abdominal sterna 4, 5, 6 lacking lateral setae, sternum 6 with a small number of anal setae (probably three pairs or less); male genitalia on their right side in repose, with left paramere large; endophallus armed or unarmed; female stylus rectangular, lightly sclerotized, with a setose apical margin.

An early differentiation of the basic callidine stock may have given rise to the ancestor of the *Plochionus-Onota-Cylindronotum* lineage. This group differs in many details from the remaining members of the North American Callidina, and has been included in the Callidina largely on the basis of the structure of the female ovipositor. The structure of the ovipositor as well as other external features of this group may resemble the condition found in the hypothetical callidine ancestor simply through convergence. If this is the case, the Callidina represents a grade, resulting from parallel adaptation to a common way of life, an arboreal habitat. As mentioned above, the affinities of this group are obscure and probably are among the poorly understood neotropical fauna. For this reason, this group will not be considered further.

A later differentiation of the ancestral stock of the Callidina probably gave rise to the genera *Callida* and *Lecalida* with very little additional modification. The genera *Philophuga, Infernophilus* and *Tecnophilus* are closely related, and were probably derived from a common stock. This stock differentiated from the main *Callida* lineage by acquiring slender legs (tarsal article 4 not bilobed, but only shallowly emarginate) and a setose body.

The most distinctive of these three genera is the genus *Infernophilus*. For this reason, the ancestor to the genus *Infernophilus* may have diverged from the *Philophuga-Tecnophilus*

TABLE 17. Hypothetical phylogeny of the endemic North American genera of the subtribe Callidina and their included species.



stock early in its history, in order to permit the *Infernophilus* stock sufficient time to acquire the characteristics listed below. This genus exhibits a peculiar form of male genitalia which has undergone 180° rotation. The mechanism which brought this reversal about is unknown, but it seems reasonable to postulate that the initial change involved a 180° shift in the orientation of the aedoeagus. The reversal of the parameres may have accompanied this initial reversal of the aedoeagus or they may have rotated at a later date. In this genus, other peculiar characters include the anal brushes, the non-metallic elytra, and the short, rounded female styli.

The stocks giving rise to *Philophuga* and *Tecnophilus* separated sometime after the separation of the *Infernophilus* stock. The stock giving rise to the genus *Philophuga* remained essentially unmodified after this point, but the stock ancestral to *Tecnophilus* acquired simple tarsal claws, a more cordate pronotum, and a more densely setose body.

The stock giving rise to the genus *Philophuga* probably possessed the following characters, as these are the most widespread characteristics in species of this genus: color of entire body except for basal antennal articles, black with a metallic blue or green lustre dorsally; body sparsely setose; pronotum sub-cordate, bearing posterior-lateral seta on each hind angle; elytra elongate and more or less parallel sided, with greatest width in apical half; hind wings fully developed, lightly pigmented.

An early derivative of this stock gave rise to the ancestor to the *viridis* complex. This stock was characterized by shorter, more oval shaped elytra and by a more cordate pronotum. The stock giving rise to *viridis* has undergone considerable recent diversification to give rise to the four extant subspecies. These four subspecies may have developed simultaneously from four isolated populations, as no subspecies is strikingly distinct.

The other ancestral stock of the genus *Philophuga* gave rise to the extant species *viridicollis, caerulea* and *brachinoides*. The ancestor to these species possessed deeply pigmented wings and elongate elytra. This stock gave rise first to the uniquely colored species *brachinoides* which also differs from the other two species in this group by having a more cordate pronotum, and also possesses several patches of setae on the ventral surface of the body. The two extant species *caerulea* and *viridicollis* are the result of relatively recent diversification in the ancestral stock.

The ancestral stock of the genus *Tecnophilus* may have divided early in its history to give rise to the species *pilatei* and *croceicollis*. Recent differentiation has produced two subspecies and a great deal of geographical variation in the species *croceicollis*.

ZOOGEOGRAPHY

The subtribe Callidina is represented in all major zoogeographical regions of the world. However, the greatest diversity in both numbers of genera and species occurs in tropical and subtropical areas. Only two genera contain members in both the Old and New Worlds. The majority of the species included in the genus *Plochionus* are restricted to the New World, but the species *Plochionus pallens* Fabricus has been widely distributed by commerce, and is now almost cosmopolitan. Only the genus *Callida* is represented naturally in Asia, the Americas and perhaps Africa (but see Jeannel 1949).

At present, the range of the genus *Callida* is disjunct. The majority of the American species occur in the tropics, but some species in eastern North America extend north into the southern portion of the cold temperate region. No members of the genus *Callida* occur in western North America, hence the New World species of *Callida* are separated from the oriental members of this genus by a wide geographical gap of apparently unsuitable habitat.

In western North America, the genera *Lecalida, Philophuga, Infernophilus* and *Tecnophilus*, replace the genus *Callida.*

Many of the morphological and biological adaptations shown by members of the subtribe Callidina, are adaptations for an arboreal existence. It then seems reasonable to assume that present and past distributions of these insects have paralleled the distributions of floral types that have provided suitable habitats.

While no fossil record is available for this group of carabids, adequate fossils have been discovered to enable us to extrapolate the movements of Tertiary floras in North America. Thus, it is necessary to review the events influencing floral dispersal in western North America during the Tertiary and Pleistocene in order to reconstruct the history of the callidine genera which are endemic to this region.

The following review is based largely on a paper by Axelrod (1959). Other papers from which this brief review is drawn are: Axelrod 1948, 1950, 1957, 1958; Blackwelder 1948, 1954; Cohn 1965; Dillon 1956; King 1958; MacGinitie 1958, and Martin 1958.

During the early Cenozoic, three geofloras were found in western North America. The southern portion of the continent was occupied by the broad-leaved evergreen Neotropical-Tertiary Geoflora, while the northern and central portions were covered by the temperate Arcto-Tertiary Geoflora of mixed deciduous hardwoods and conifers. Between them, in central southwestern North America, small areas of semi-arid vegetation of the Madro-Tertiary Geoflora were making their initial appearances.

The Eocene environment was one of low relief and low altitude, and the climate was warm and humid. These conditions permitted widespread distribution and migration of plants, and during this time, the Neotropical-Tertiary Geoflora moved northward along the Pacific coast into Alaska, and to or near the Canadian border interiorly. This Geoflora was dominated by broad-leaved evergreens of tropical families and genera which now find their closest counterparts in subtropical forests such as those presently found from southern Mexico to Panama, and in southern Asia, where annual rainfall is high and the climate is uniformly warm. The Coast Ranges and the eastern Cordilleras did not exist at this time, and the desert flora that now occupies the intervening region was not then in existence.

The cooler, drier climate following the Eocene gradually restricted the Neotropical-Tertiary Geoflora southward, and coastward where it persisted in warm coastal valleys of California and Oregon until into the Miocene, with a few relicts surviving into Pleistocene times. No plants in the United States today represent direct descendants from this flora. However, some genera and species were secondarily derived from it. These derivatives represent subtropic to warm temperate groups that became adapted to the expanding dry subtropical and warm temperate areas of southwestern North America.

During the early Tertiary, the Arcto-Tertiary Geoflora had a holarctic distribution at high and middle latitudes, and probably was continuous across the Bering Land Bridge that was present during early Eocene times. In western North America, three principal elements comprised this Geoflora: the western American element consisting of species related to present day dominants of the coastal and mountain forests; the eastern North American element consisting of deciduous hardwoods related to those of present eastern North America; and the East Asian element consisting of mixed deciduous forest species which are no longer native to North America, or have a discontinuous distribution in eastern North America and eastern Asia.

Species of these three elements were mixed in a forest of a rather generalized floristic composition. However, the Geoflora was not homogeneous throughout its area. It was composed of several forest types, depending upon geographical occurrence and climatic conditions. In response to gradual development of increasingly more emergent continents following early Tertiary, and to the accompanying trend toward lower temperature, this Geoflora gradually migrated southward from near the Canadian border where it occurred in the early Eocene, to central Nevada and northern California by the middle Oligocene. During the Miocene and early Pliocene, the increasing aridity further restricted this flora to more humid coastal and upland sites. Species belonging to the eastern North American and eastern Asian elements were rapidly reduced in western North America during the late Tertiary due to the reduction in summer rains brought about by uplifts in the coast ranges and Sierra Nevadas. Only a few of these forms lingered on into the late Pliocene in the mild coastal strip from central California north, becoming extinct here in the early part of the Pleistocene.

The species now dominating the western coniferous forests represent the surviving western American element of the old Arcto-Tertiary Geoflora. In the west, its species became adapted to a climate which was typified by winter rain and summer drought. Its major communities were differentiated chiefly in the latter Pliocene when important topographical changes such as the rise of the Sierra Nevada and the coast ranges produced more diverse climates.

The Madro-Tertiary Geoflora which originated in southwestern North America, was comprised of small-leaved, drought-deciduous, sclerophyllous plants. These plants were derived primarily from the Neotropical-Tertiary Geoflora and to a lesser extent from the Arcto-Tertiary Geoflora in response to the expanding dry climate. Fossil plants, apparently ancesteral to Madro-Tertiary species have been discovered in late Cretaceous and Paleocene floras of southwestern North America. This Geoflora had come into existence by the middle Eocene, and spread over the southwestern part of the continent during succeeding epochs as dry climates expanded. Part of the desert flora as well has been derived from this Geoflora.

In the middle Pliocene, the rapid expansion of dry climates almost completely eliminated woodland and chaparral from the lowlands of the present desert regions. In the later Pliocene and Pleistocene, the rapidly rising Cascades, Sierra Nevada and more easterly mountain ranges brought a drier climate to their lee, and a desert flora came into existence. Its species were derived from those represented in the Geofloras that dominated the area earlier in the Pliocene. The colder Great Basin received increments from the surviving Arcto-Tertiary Geoflora; the Sonoran and Mojave Deserts from the Madro-Tertiary Geoflora.

Considering the present distribution of the genus *Callida*, it seems that the coniferous forests, semi-arid regions and colder climates of northern and western North America provide unsuitable habitats for the species of this genus, and effectively isolate the few Asian species of *Callida* from the diverse American fauna. This distribution suggests that a faunal connection between Asia and North America occurred in the past.

The Bering Land Bridge which existed during Eocene times was probably forested by elements of the Arcto-Tertiary Geoflora, which at this time had a holarctic distribution at high latitudes. This would provide a pathway through which the ancestors of the Oriental species of *Callida* could disperse from the New World. At this time, the ancestral stock of *Callida* was probably trans-continental in North America. Following the Eocene, cooler climates restricted the Arcto-Tertiary Geoflora southward, away from the Bering region, permanently isolating the American and Asian callidine faunas. The latest at which this separation could have occurred was the Oligocene or the early Miocene. During the Miocene and Pliocene epochs, increasing aridity in western North America gradually eliminated much of the deciduous element of the Arcto-Tertiary Geoflora from this region, and with this sector of the flora, the ancestral species of *Callida* were restricted to the eastern and southern portions of the continent.

With the expansion of dry climates and the Madro-Tertiary Geoflora during the late Tertiary, a stock of the ancestral *Callida* developed adaptations for a more terrestrial existence, and occupied the semi-arid and arid regions of the west.

The descendants of this stock, *Philophuga, Tecnophilus*, and *Infernophilus*, more closely resemble eastern North American species of *Callida* than they do Mexican species. Hence, they were probably derived from the Arcto-Tertiary fauna, rather than from a Neotropical-Tertiary ancestor. On the other hand, the genus *Lecalida* resembles many of the Mexican species of *Callida*, and may be a northern extension of this group into the North American deserts. Thus, it is probably derived from a Neotropical-Tertiary ancestor.

The time and place of origin of the genus *Infernophilus* are obscure, for I know nothing of the habits of this genus and hence cannot trace the development of the necessary habitat.

After acquiring the basic terrestrial adaptation of slender legs, the ancestral stock of *Philophuga* has persisted with little modification. The derivative stock giving rise to *Tecnophilus* has acquired a number of specializations. This stock was derived from the stock ancestral to *Philophuga* probably during the Pliocene, as increased aridity resulted in the production of suitable habitats in the form of large salt flats and alkaline playas.

During the early Pliocene, the environment of western North America was one of low relief, and extensive plains covered much of this region. Mountains were not effective barriers at this time. During this period, the ancestral stock of *Philophuga* may have ranged widely throughout this area. Crustal unrest and the renewed mountain building processes of the later Pliocene probably isolated populations that evolved into the ancestors of *brachinoides, viridis* and *caerulea-viridicollis.*

The subspecies of *viridis* and the species *caerulea* and *viridicollis* do not appear to be completely separated from one another at present by geographical barriers such as mountains. The isolations that led to the evolution of these groups probably developed during glacial periods of the Pleistocene when mountain glaciers separated populations in the northern deserts and increased rainfall resulted in expanding forests which produced ecological barriers in the southern deserts.

At this time, the same factors isolated populations of *Tecnophilus croceicollis*, and produced the geographical variation now shown by this species. I do not know what factors led to the isolation of *croceicollis* and *pilatei*. Perhaps *pilatei* was isolated on the Gulf Coastof Texas, and the presence of *croceicollis* in Texas is the result of a recent invasion from the west.

Floral movements have profoundly influenced the distribution and evolution of the Callidina. Thus, the endemic callidine fauna now found in western North America is the result of climatic, geological and resulting floral changes which have occurred in this region in Terteary times.

ACKNOWLEDGEMENTS

It is a pleasure to acknowledge the contributions of the following people and to extend my thanks to them.

G.E. Ball, my supervisor, was most helpful with his kind assistance and guidance during the course of this study. The National Research Council of Canada provided financial support through Grant No. NRC-A1399, held by G.E. Ball. Much of the Mexican material reported above was collected in the course of an expedition financed by the National Science Foundation through Grant GB 3312, also held by Ball.

B. Hocking and D.A. Boag, members of my committee, read and criticized the manuscript.

My wife, Margaret Larson, offered many valuable suggestions and much encouragement.

My colleagues, J. Barron, T.L. Erwin, R. Freitag and D.R. Whitehad contributed many ideas in the discussions I had with them. Richard Freitag examined Casey's and LeConte's type material for me.

Specimens of *Tecnophilus*, both preserved and living, were provided by T.L. Erwin, D. Kavanaugh and W. Tyson. Mr. W. Sharp accompanied me on a collecting trip through western United States and assisted me in the collection of many specimens. My friend, Mr. R. Getty, collected many specimens of *Tecnophilus croceicollis* in southern Alberta.

G.A. Hobbs, N.D. Holmes, Ruby I. Larson, C.E. Lilly, and R.W. Salt and many others of the Canada Department of Agriculture Research Station, Lethbridge, Alberta, did much to stimulate my interest in entomology and to provide continued encouragement. A.L. Lagler of that institution wrote the computer program for the analysis of variance used in this study. E.T. Gushul assisted in the preparation of the illustrations.

I thank the following individuals for lending me material in their care: R.T. Allen, Illinois Natural History Survey; N. Anderson, University of Montana; W.F. Barr, University of Idaho; E.C. Becker, Canada Department of Agriculture, Ottawa; P.J. Darlington, Jr., Museum of Comparative Zoology; H. Dybas, Chicago Natural History Museum; M.H. Hatch, University of Washington; H.B. Leech, California Academy of Sciences; L.L. Pechuman, Cornell University; P. Spangler, United States National Museum; P. Vaurie, American Museum of Natural History; and G.E. Wallace, Carnegie Museum.

REFERENCES

Axelrod, D.I. 1948. Climate and evolution in western North America during middle Pleocene time. Evolution 2 : 127-144.

Axelrod, D.I. 1950. Evolution of desert vegetation in western North America. Publ. Carneg. Instn. 590 : 215-306.

Axelrod, D.I. 1957. Late Tertiary floras and the Sierra Nevadan uplift. Bull. geol. Soc. Amer. 68 : 19-46.

Axelrod, D.I. 1958. Evolution of the Madro-Tertiary Geoflora. Bot. Rev. 24 : 433-509.

Axelrod, D.I. 1959. Geological history. *In* Munz and Peck, A California flora. University of California Press, Los Angeles, Calif. 1681 pp.

Ball, G.E. 1963. Carabidae, Fascicle 4. *In* Arnett, R.H. The beetles of the United States (A manual for identification). The Catholic University of America Press, Washington, D.C. 55-210, 58 figs.

Ball, G.E. 1966. A revision of the North American species of the subgenus *Cryobius* Chaudoir (*Pterostichus*, Carabidae, Coleoptera). Opusc. ent., Suppl. 28, 166 pp.

Bates, H.W. 1883. Biologia Centrali-Americana, Insecta, Coleoptera, Carabidae, Cicindelidae suppl., 1(pt. 1) : 153-256, plates vi-xii.

Bigelow, R.S., and C. Reimer. 1954. An application of the linear discriminant function to insect taxonomy. Can. Ent. 86(2) : 69-73.

Blackwelder, E. 1948. The Great Basin. 1. The geological background. Bull. Univ. Utah geol. Ser. 38(20), 16 pp.

Blackwelder, E. 1954. Pleistocene lakes and drainage in the Mojave region of southern California. Bull. Calif. Min. Bur. 170 : 35-40.

Blackwelder, R.E. 1944. Checklist of the Coleopterous insects of Mexico, Central America, the West Indies, and South America. Part 1. U.S. Natl. Mus. Bull. 185, 188 pp.

Cain, A.J. and G.A. Harrison. 1960. Phyletic weighting. Proc. zool. Soc. Lond. 135 : 1-31.

Casey, T.L. 1913. Studies in the Cicindelidae and Carabidae of America. *In* Casey, T.L. Memoirs on the Coleoptera. IV. New Era Printing Company, Lancaster, Pa., 192 pp.

Casey, T.L. 1924. Additions to the known Coleoptera of North America. *In* Casey, T.L., Memoirs on the Coleoptera XI. New Era Printing Company, Lancaster, Pa., 347 pp.

Chaudoir, M. de. 1842. Description de quelques genres nouveaux de la famille des carabiques. Bull. Soc. Imp. Nat. Moscou. 15 : 832-857.

Chaudoir, M. de. 1872. Monographie des callidides. Ann. Soc. ent. Belg. 15 : 97-204.

Chaudoir, M. de. 1877. Genres nouveaux et especes inedites de la famille des carabiques. Bull. Soc. Imp. Nat. Moscou 52 : 188-268.

Chevrolat, L.A.A. 1835. Coléoptères du Mexique, fasc 5. Strasbourg, 50 pp.

Cohn, T.J. 1965. The arid-land katydids of the North American genus *Neobarrettia* (Orthoptera: Tettigoniidae): Their systematics and a reconstruction of their history. Misc. Publ. Mus. Zool. Univ. Mich. 126, 179 pp.

Csiki, E. 1932. Harpalinae VII. *In* Junk, W., and S. Schenkling (editors). Coleopterorum Catalogus 11. Berlin and s'Gravenhage. 1279-1598.

Dejean, P.F.M.A. 1831. Species general des coléoptères de la collection de M. le compte

Dejean. Vol. V. 883 pp. Paris.

Dillon, L.S. 1956. Wisconsin climate and life zones in North America. Science 123 : 167-176.

Emden, F.I. van. 1942. A key to the genera of larval Carabidae. Trans. R. ent. Soc. Lond. 92: 1-99, 100 figs.

Fisher, R.A. 1936. The use of multiple measurements in taxonomic problems. Ann. Eug. London 7 : 179-188.

Freitag, R. 1965. A revision of the North American species of the *Cicindela maritima* group with a study of hybridization between *Cicindela duodecimguttata* and *oregona*. Quaest. ent. 1(3) : 87-170.

Goulden, C.H. 1952. Methods of statistical analysis. J. Wiley & Sons, Inc., New York. 467 pp.

Habu, A. 1960. *Callida* species of Japan (Coleoptera, Carabidae). Bull. Nat. Inst. Agr. Sci.(C) 12 : 155-169.

Habu, A. 1967. Fauna Japonica: Carabidae Truncatipennes group (Insecta: Coleoptera). Tokyo Electrical Engineering College Press Tokyo. 338 pp., 27 plates.

Hatch, M.H. 1950. An account of the life of Orson Bennett Johnson. *In* Studies honoring Trevor Kincaid, 11-28.

Hatch, M.H. 1953. The beetles of the Pacific northwest. Univ. Wash. Publ. Biol. 16 : 340 pp.

Horn, G.H. 1881. On the genera of Carabidae, with special reference to the fauna of Boreal America. Trans. Amer. ent. Soc. 9 : 91-196, 10 plates.

Horn, G.H. 1882. Synopsis of the tribe Lebiini. Trans. Amer. ent. Soc. 10: 126-183.

Jeannel, R. 1942. Coléoptères Carabiques, 2me partie. Faune de France 40: 573-1173, figs. 214-368. Paris.

Jeannel, R. 1949. Coléoptères carabiques de la Region malgache (troisieme partie). Faune de l'Empire francais, vol. XI, 767-1146, figs. 365-548.

Jedlička, A. 1963. Monographie der Truncatipennen aus Ostasien. Lebiinae-Odacanthinae-Brachyninae (Coleoptera, Carabidae). Ent. Abh. Ber. Mus. Tierk. Dresden 28 : 269-579.

King, P.B. 1958. Evolution of modern surface features of western North America, p. 3-60. *In* C.L. Hubbs, (ed.), Zoogeography. Amer. Assoc. Adv. Sci. Symp., Washington, D.C.

LeConte, J.L. 1848. A descriptive catalogue of the geodephagous Coleoptera inhabiting the United States east of the Rocky Mountains. Ann. Lyc. Nat. Hist. New York 4: 173-474.

LeConte, J.L. 1851. Descriptions of new species of Coleoptera from California. Ann. Lyc. Nat. Hist. New York 5 : 125-184.

Leng, C.W. 1920. Catalogue of the Coleoptera of America, north of Mexico. Mount Vernon, N.Y., 470 pp.

Lewin, V. 1963. The herpetofauna of southeastern Alberta. Canad. Fld. Nat. 77(4) : 203-214.

Lindroth, C.H. 1954. Die larve von *Lebia chlorocephala* Hoffm. (Col. Carabidae). Opusc. ent. 20 : 10-34.

MacGinitie, H.D. 1958. Climate since the late Cretaceous. *In* C.L. Hubbs (ed.), Zoogeography. Amer. Assoc. Adv. Sci. Symp., Washington, D.C., 61-79.

Madge, R.B. 1967. A revision of the genus *Lebia* Latreille in America north of Mexico (Coleoptera, Carabidae). Quaest. ent. 3(3) : 139-242.

Mannerheim, C.G. von. 1837. Memoire sur quelques genres et especes de carabiques. Bull. Soc. Imp. Nat. Moscou. 10(2) : 3-49.

Martin, P.S. 1958. Pleistocene ecology and biogeography of North America. *In* C.L. Hubbs (ed.), Zoogeography. Amer. Assoc. Adv. Sci. Symp., Washington, D.C., 375-420.

Mayr, E. 1963. Animal species and evolution. The Belknap Press of Harvard University Press, Cambridge, Mass. 797 pp.

Mayr, E., E.G. Linsley, and R.L. Usinger. 1953. Methods and principles of systematic zoology. McGraw-Hill Book Co., Inc., New York. 336 pp.

Ménétriés, M. 1843. Sur un envoi d-insectes de la cote N.O. d'Amerique. Bull. Acad. Imp. Sci. St. Petersbourg Phys.-Math. 2 : 49-64.

Motschoulsky, V. von. 1850. Die Käfer Russlands, 9 pp. Moscou.

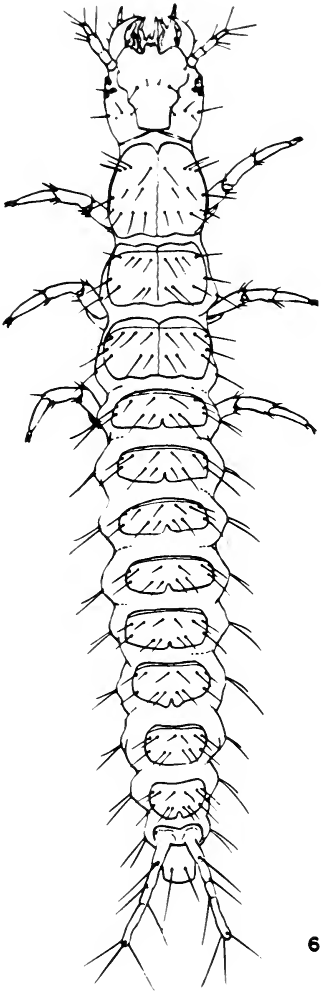
Motschoulsky, V. von. 1859. Coléoptères nouveaux de la Californie. Bull. Soc. Imp. Nat. Moscou 32(2) : 122-185.

Say, T. 1823. Descriptions of coleopterous insects collected in the late expedition to the Rocky Mountains, performed by order of Mr. Calhoun, Secretary of War, under the command of Major Long. J. Acad. nat. Sci. Philad. 3(1) : 139-216.

Selander, R.B., and P. Vaurie. 1962. A gazetteer to accompany the "Insecta" volumes of the "Biologia Centrali-Americana". Amer. Mus. Novit. no. 2099. 70 pp.

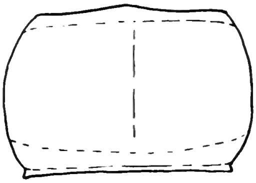
Stanley, J. The discriminant function. A mathematical method for the taxonomic separation of species. MS.

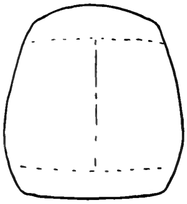
Torre-Bueno, J.R. de la. 1962. A glossary of entomology. Brooklyn Entomological Society, Brooklyn, N.Y. 336 pp.


6

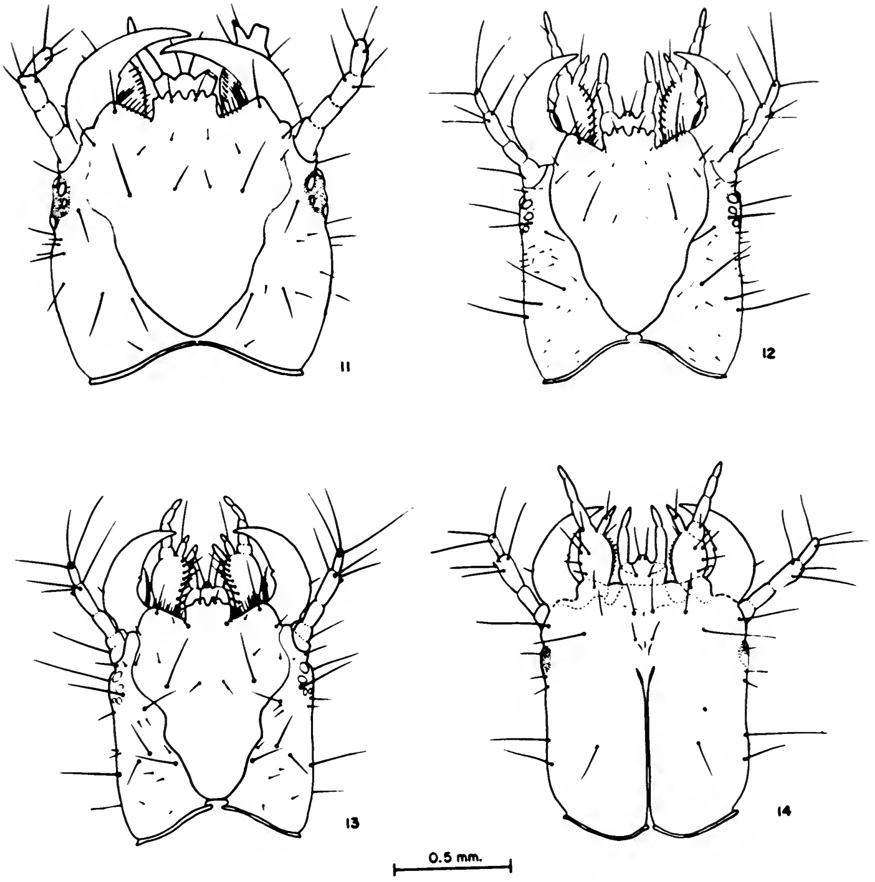

7


8

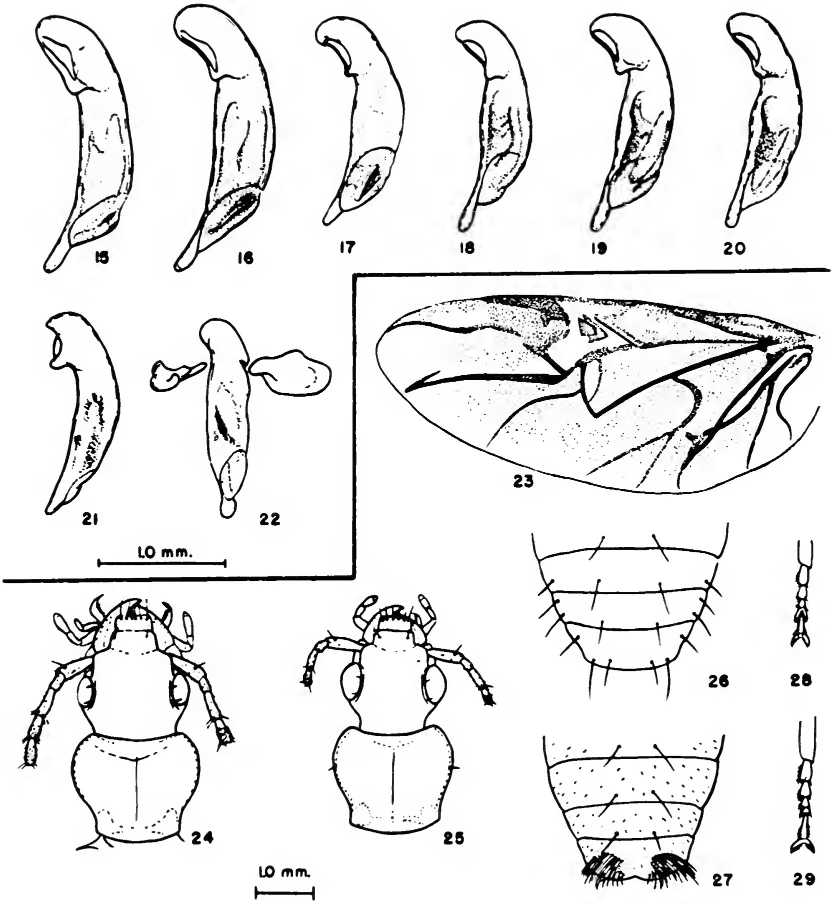

9


10

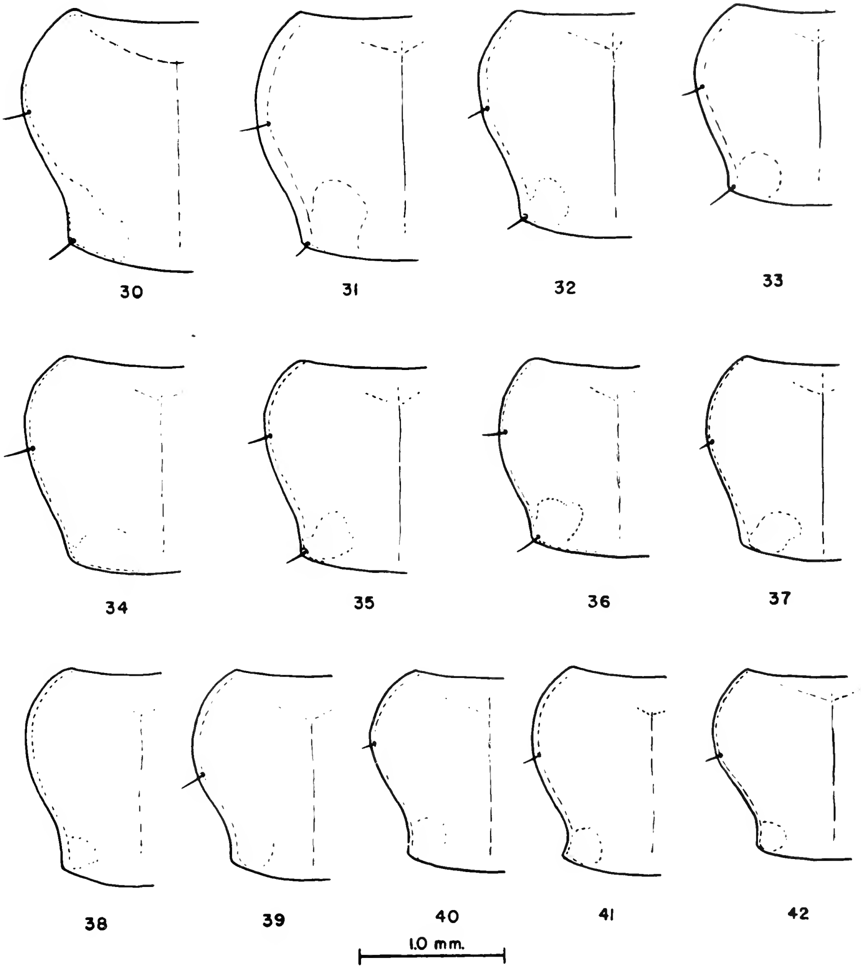
Figs. 6-10. 6. Larva of *Tecnophilus croceicollis croceicollis* Ménétriés, first instar (Newark, California). 7. Nasale and mandibles of *Plochionus timidus* Haldeman. 8. Maxilla of *Plochionus timidus* Haldeman. 9. Pronotum of larva of *Philophuga viridicollis* LeConte, third instar, dorsal aspect. 10. Same of *Tecnophilus croceicollis* Ménétriés.



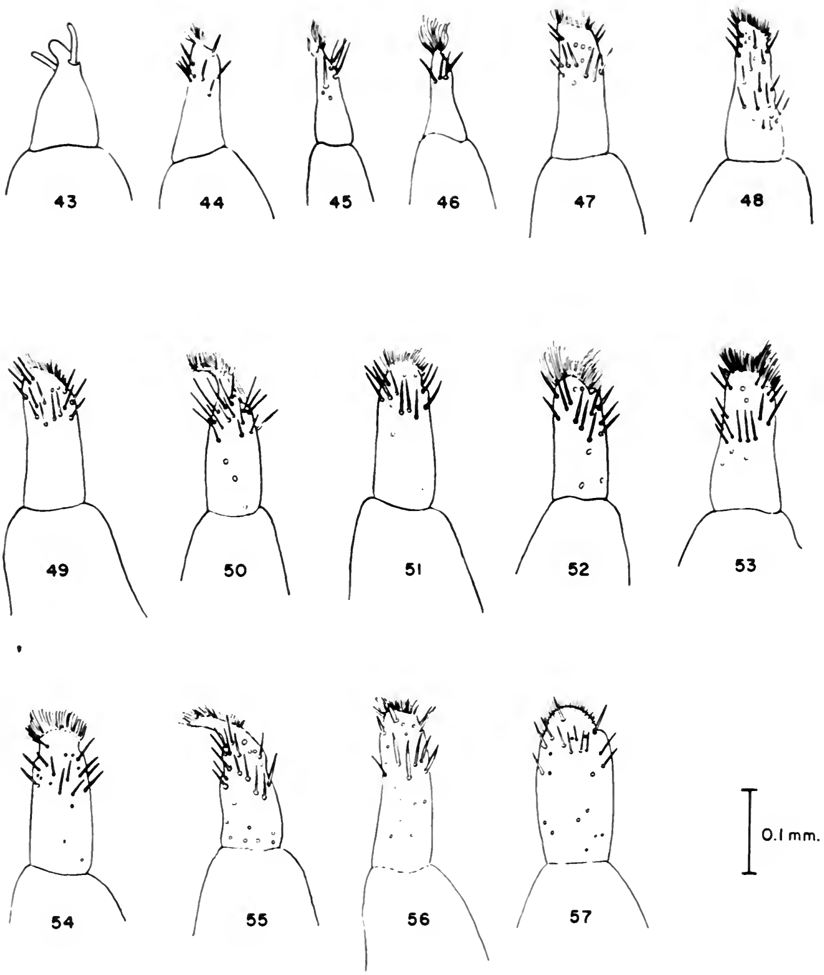
Figs. 11-14. Head capsule, third instar larva. 11. *Phophuga viridicollis* LeConte. 12. *Tecnophilus croceicollis croceicollis* Ménétriés. 13. *Tecnophilus croceicollis peigani* new subspecies, dorsal aspect. 14. Same, ventral aspect.



Figs. 15-29. 15. Male genitalia of *Philophuga viridicollis* LeConte, lateral aspect. 16. Same of *Philophuga caerulea* Casey. 17. Same of *Philophuga viridis viridis* Dejean. 18. Same of *Tecnophilus pilatei* Chaudoir. 19. Same of *Tecnophilus croceicollis croceicollis* Ménétriés. 20. Same of *Tecnophilus croceicollis peigani* new subspecies. 21. Same of *Infernophilus castaneus* Horn, dorsal aspect, parameres included. 23. Left wing of *Philophuga caerulea* Casey. 24. Head and pronotum of *Tecnophilus croceicollis peigani* new subspecies, dorsal aspect. 25. Same of *Tecnophilus croceicollis croceicollis* Ménétriés (Brownsville, Texas). 26. Abdomen of *Plochionus timidus* Haldeman, ventral aspect. 27. Same of *Infernophilus castaneus* Horn. 28. Front tarsus of *Callida decora* Fabricius. 29. Same of *Philophuga viridicollis* LeConte.



Figs. 30-42. Pronotum, left half, dorsal aspect. 30. *Infernophilus castaneus* Horn (Coleville, California). 31. *Philophuga viridicollis* LeConte (Monahans, Texas). 32. *Philophuga caerulea* Casey (Nogales, Arizona). 33. *Philophuga brachinoides* Bates (Nochixtlan, Oaxaca). 34. *Philophuga viridis amoena* LeConte (Medicine Hat, Alberta). 35. *Philophuga viridis horni* Chaudoir (Stockton, Utah). 36. *Philophuga viridis klamathea* new subspecies (holotype, Klamath Fall, Oregon). 37. *Philophuga viridis viridis* Dejean (San Francisco, California). 38. *Tecnophilus pilatei* Chaudoir (Brownsville, Texas). 39-41. *Tecnophilus croceicollis croceicollis* Ménétriés: 39. Brownsville, Texas; 40. Cuddeback Lake, California; 41. Alviso, California. 42. *Tecnophilus croceicollis peigani* new subspecies (paratype, Lost River Ranch, Alberta).



Figs. 43-57. Right stylus of female ovipositor, dorsal aspect. 43. *Euproctinus trivittatus* LeConte. 44. *Onota floridana* Horn. 45. *Plochionus amandus* Newman. 46. *Plochionus timidus* Haldeman. 47. *Callida punctata* LeConte. 48. *Callida viridipennes* Say. 49. *Callida purpurea* Say. 50. *Callida decora* Fabricius. 51. *Philophuga viridicollis* LeConte. 52. *Philophuga viridis viridis* Dejean. 53.*Philophuga viridis klamathea* new subspecies. 54. *Philophuga brachinoides* Bates. 55. *Tecnophilus pilatei* Chaudoir. 56. *Tecnophilus croceicollis croceicollis* Ménétriés. 57. *Infernophilus castaneus* Horn.

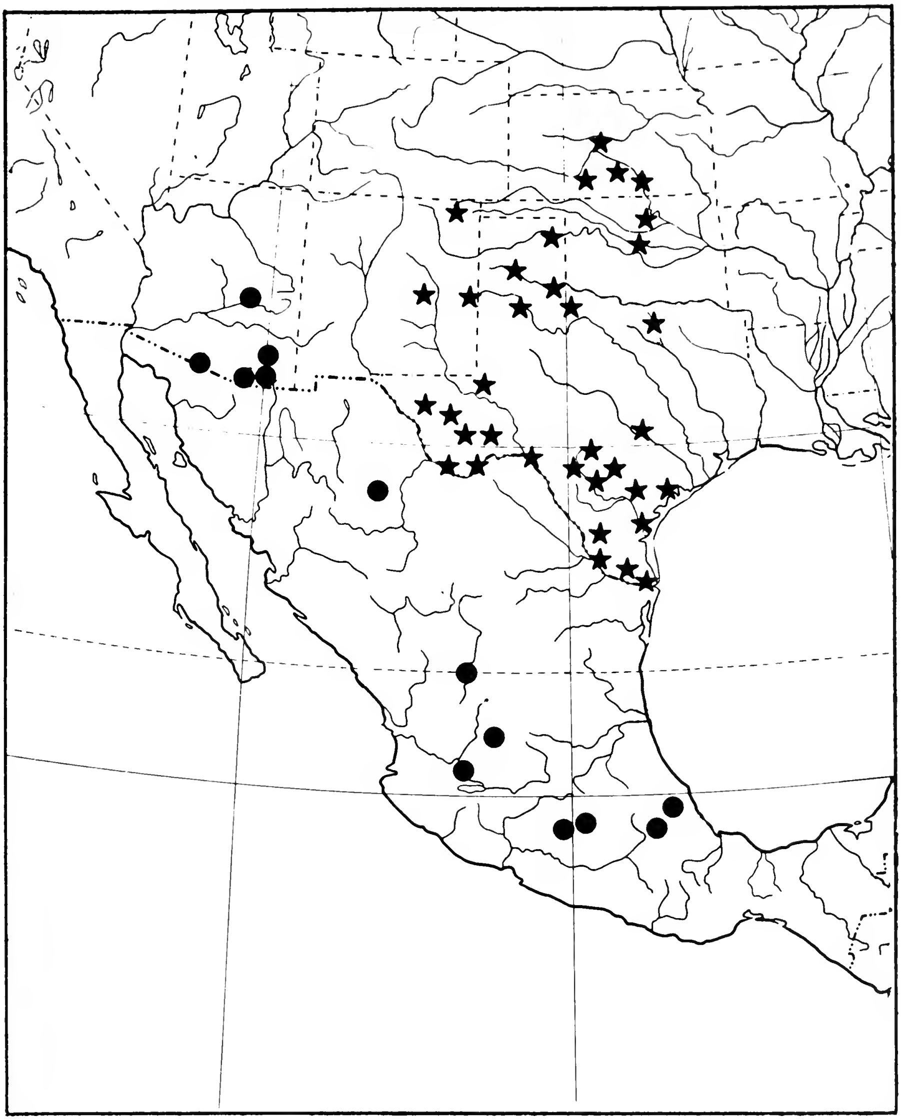


Fig. 58. Distribution of *Philophuga viridicollis* LeConte (★), and *Philophuga caerulea* Casey (●).

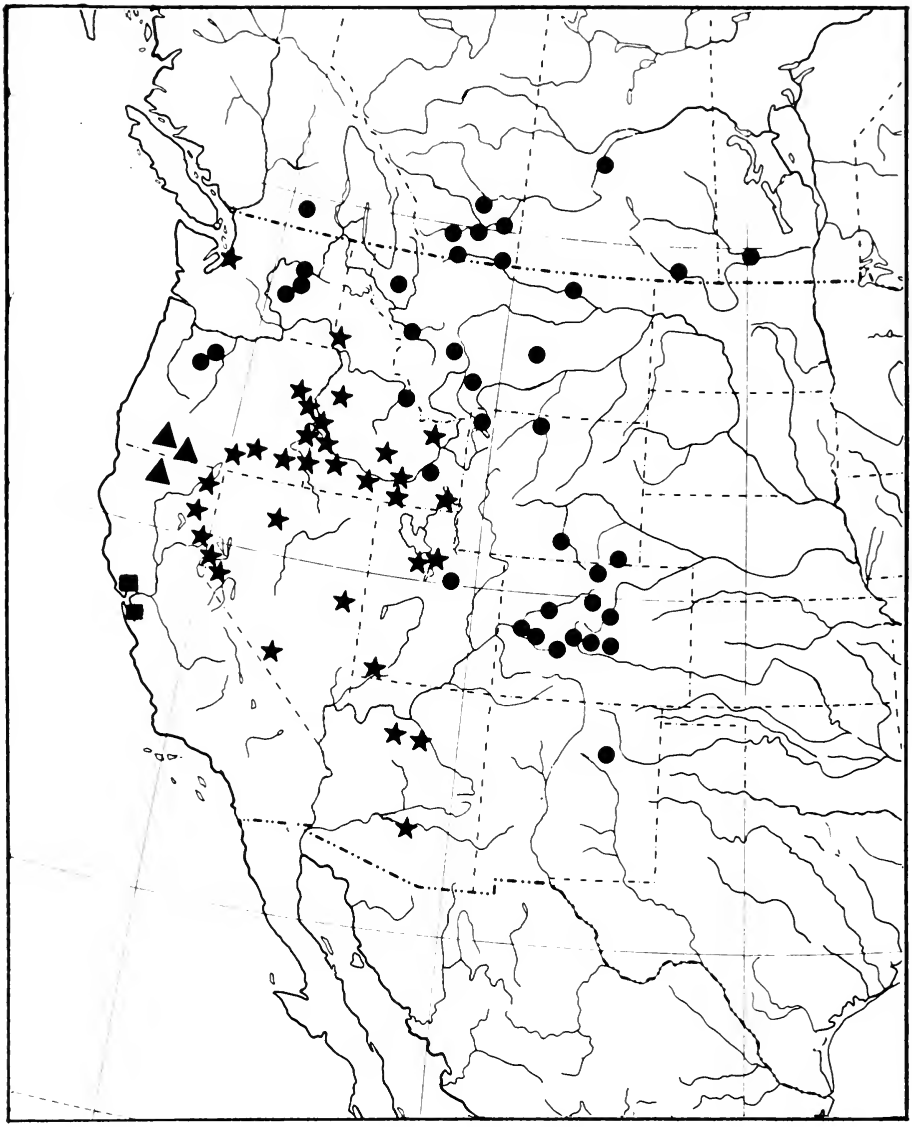
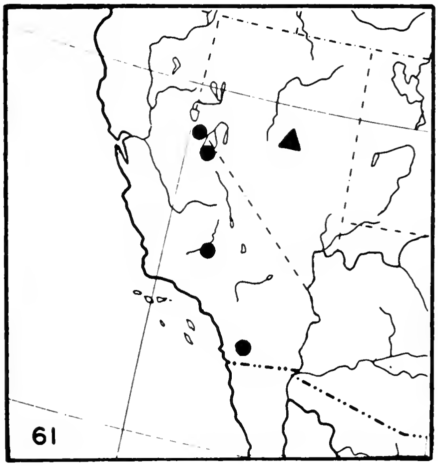


Fig. 59. Distribution of the subspecies of *Philophuga viridis* Dejean: ■ , *v. viridis* Dejean; ▲ , *v. klamathea* new subspecies;★*v. horni* Chaudoir, *v. amoena* LeConte.



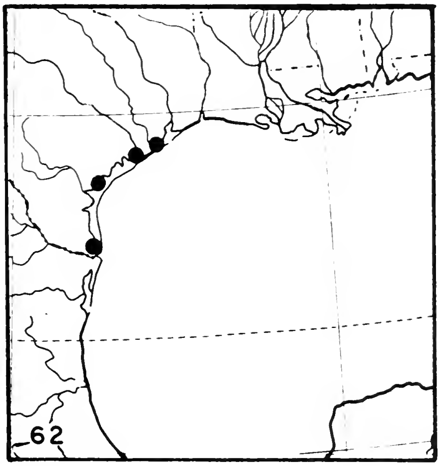


Fig. 60. Distribution of *Philophuga brachinoides* Bates. Fig. 61. Distribution of *Infernophilus castaneus* Horn. ▲ represents a state locality only. Fig. 62. Distribution of *Tecnophilus pilatei* Chaudoir.

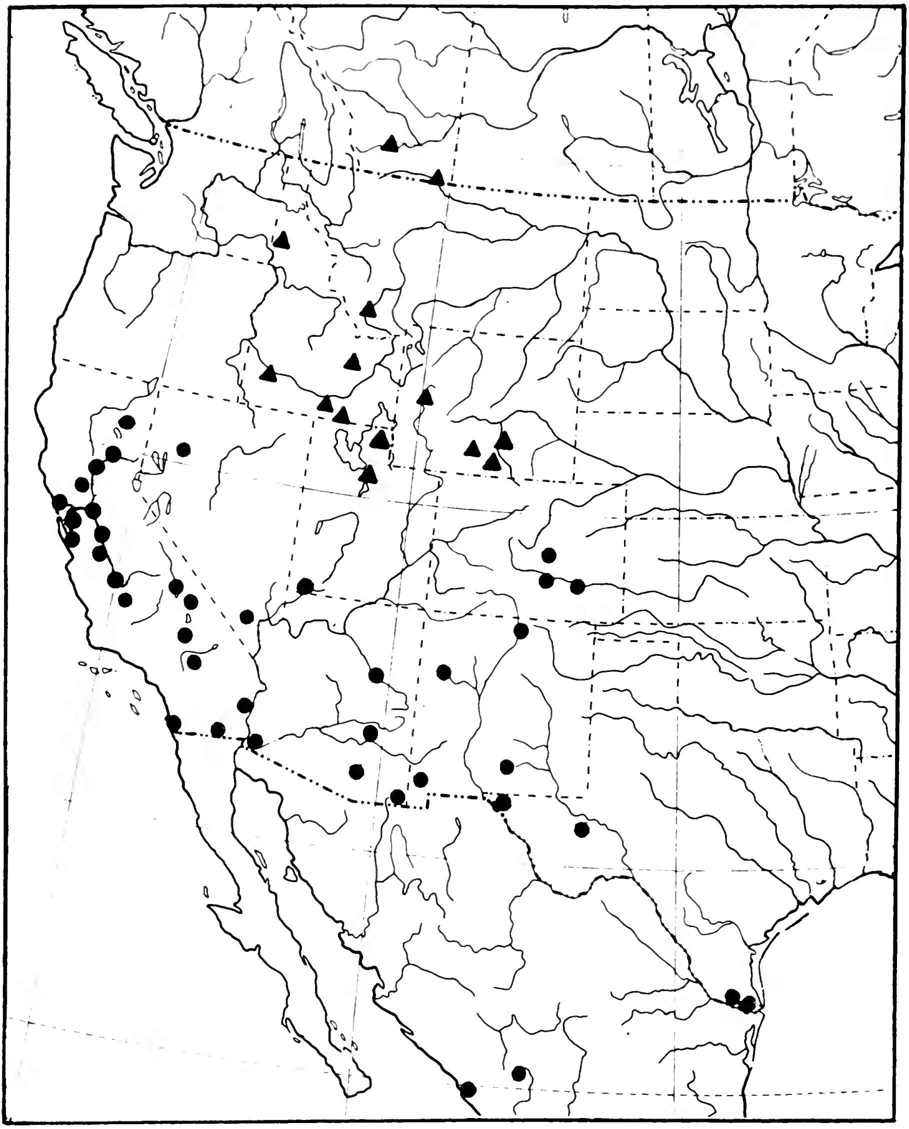


Fig. 63. Distribution of the subspecies of *Tecnophilus croceicollis* Ménétriés: ● *croceicollis croceicollis* Ménétriés; ▲ *croceicollis peigani* new subspecies.

Quaestiones entomologicae

A periodical record of entomological investigations, published at the Department of Entomology, University of Alberta, Edmonton, Canada.

VOLUME V NUMBER 2 APRIL 1969

QUAESTIONES ENTOMOLOGICAE

A periodical record of entomological investigations published at the Department of Entomology, University of Alberta, Edmonton, Alberta.

Volume 5 Number 2 April, 1969

CONTENTS

Book Review

COBBEN, R. H. 1968. Evolutionary trends in Heteroptera. Part I. Eggs, architecture of the shell, gross embryology and eclosion. 475 pp, 316 Figs. Centre for Agricultural Publishing and Documentation, Wageningen, Holland. $16.50 U. S.

This is the first of a series of three volumes by Cobben on the phylogeny of the supra-generic taxa of the Heteroptera, and there will be many biologists awaiting the next two volumes.

Cobben approaches the phylogeny of the Heteroptera on a wide front and this can best be summed up by a quotation from the page preceding the preface, "In its best practice, taxonomy is a wonderfully promising area of synthesis for all biological knowledge."

In this volume Cobben has examined the oviposition stance of the female, the detailed structure of the egg and the embryogenesis of as many species of Heteroptera as there was material available.

As might be expected in such a detailed study as this, many new characters of taxonomic value came to light. These, along with previously used characters have all been utilized in synthesizing a phylogenetic scheme which forms the basis for the next two volumes.

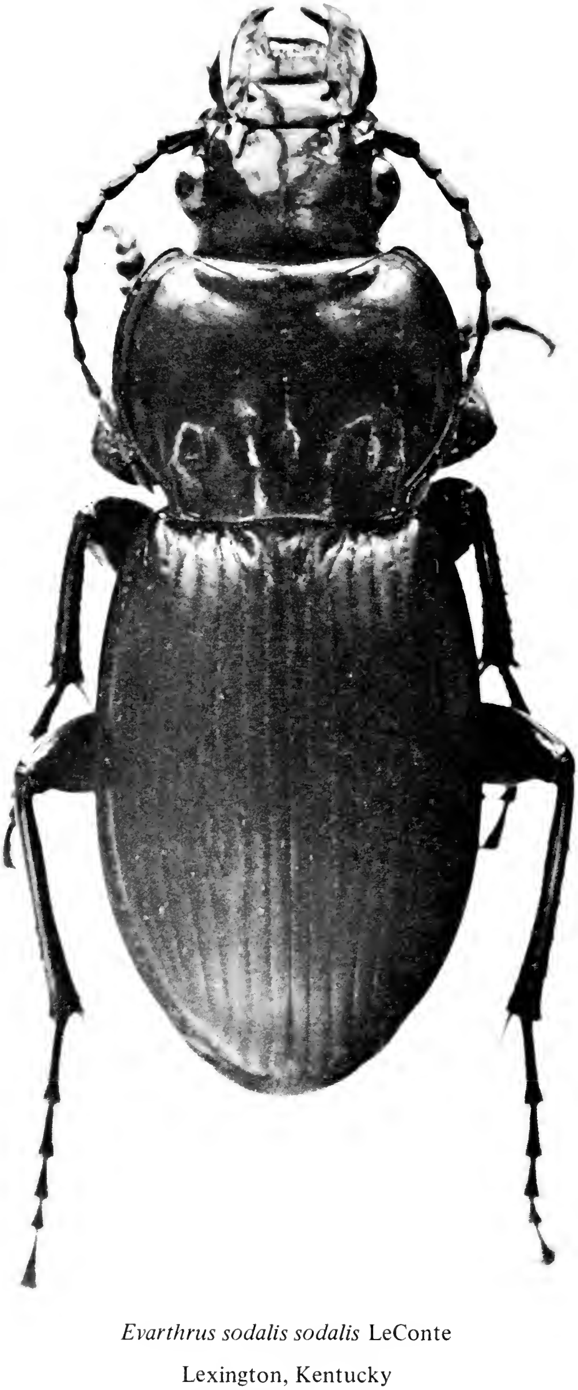
Cobben's work on the chorion of the eggs is in such detail that little of previous descriptions can be homologized to the structures he shows. Of particular interest are the "airo-static inner layer" of the Geocorisae chorion and the "porous inner layer" of that of the eggs of Saldidae. These structures along with other porous structures act as a plastron.

The importance that Cobben attaches to the Leptopodoidea is obvious from the arrangement of the contents of the volume. The first chapter is devoted entirely to the eggs of this family. The other families are dealt with in the second chapter. For each family the literature, material used, egg shape, oviposition behaviour, chorion, embryogenesis and eclosion are discussed in turn, enabling detailed information to be extracted rapidly. Chapter III is devoted to evaluating the egg characters. Chapter IV is a preliminary discussion of the phylogeny of the suborder with a short review of the investigations that will be reported in the other volumes. There is an excellent summary. The book will no doubt become a standard reference text on Heteroptera.

Although the book has been well produced it is surprising in a work of this nature that the abbreviations of morphological terms are not given in the text when the structure is referred to in a figure. Another disturbing feature is that the scales on the figures have not been given any absolute value, although they are probably in millimeters. Proof reading is good apart from some minor spelling mistakes and a series of transpositions in the caption of Figure 273. The line figures throughout the volume are of high standard and are explicit, as are the transmission and scanning electronmicrographs.

If the next two volumes of this series maintain the high quality of the first, then Cobben will have made a significant contribution to the understanding of Heteropteran biology and phylogeny. His approach is one that future taxonomists might well emulate.

D. A. Craig
Department of Entomology
University of Alberta



Evarthrus sodalis sodalis LeConte

Lexington, Kentucky

Photograph by J. Scott

A REVISION OF THE SPECIES OF THE GENUS *EVARTHRUS* LECONTE

(COLEOPTERA:CARABIDAE)

RICHARD FREITAG
Department of Biology
Lakehead University
Port Arthur, Ontario

Quaestiones entomologicae
5 : 89-212 1969

Within the genus Evarthrus, *three subgenera, 43 species, and five subspecies are recognized. The genus* Evarthrus *is described, and evidence is presented which removes* Evarthrus *as a unit from the* Pterostichus *complex to a position near the genus* Molops *in the tribe Pterostichini. A key to the species and subspecies is given. Each subgenus, species group, and species is described and synonymies are listed. The distribution of each species is presented by locality records and distribution maps. Structures which are used in identification are illustrated.*

The subgenus Fortax *comprises six species of which one,* iuvenis, *is described as new. One genus group name and six species names are reduced to synonymy.*

The subgenus Cyclotrachelus *includes 12 species, of which five,* fucatus, macrovulum, texensis, parafaber, *and* levifaber *are described as new. Six species names are listed as synonyms.*

The subgenus Evarthrus *includes 25 species of which seven are new. The species* sodalis *LeConte and* torvus *LeConte are polytypic. Five genus group names and 26 species names are relegated to synonymy.*

A phylogeny is postulated for the subgenera, species groups and species. The geographical distribution of the genus is discussed.

The endemic flightless Pterostichini of eastern North America are arrayed in a series of supraspecific taxa each of which is more or less easily defined; however, the relationships of these groups are at best uncertain. The most diverse of these groups is the genus *Evarthrus*, a complex of species included by some (Csiki, 1930; Lindroth, 1966) in the genus *Pterostichus*, and by others (Casey, 1918) treated as a group of related genera. (Ball, 1967 drew attention to this problem). I decided to attempt to solve these problems of relationships and classification, but learned in the initial stages of the study that I would first have to undertake a revision of the species. The results of this investigation are presented in this paper.

The revision is based on a study of adult specimens. The species were defined on the basis of evaluation of morphological and geographical evidence. Names were applied on the basis of study of the relevant type material. Sixteen species names were found to be junior synonyms, and 13 previously undescribed species were discovered and named.

In addition to the formal taxonomic treatment of this group, I have presented my views on the phylogeny and geographical distribution of the extant species.

MATERIALS AND METHODS

Materials

The material examined consisted of 7,600 adult specimens, which included the type specimens of Casey and LeConte. I have also briefly examined external structures and male genitalia of species of an additional 35 Nearctic and Palearctic subgenera of *Pterostichus* Bonelli, and of *Abaris* Dejean, *Pseudabarys* Chaudoir, *Oxycrepis* Reiche, *Cratocerus* Dejean, *Catapiesis* Brullé, *Abax* Bonelli, *Molops* Bonelli, *Percus* Bonelli, *Lesticus* Dejean, *Piesmus* LeConte, *Stomis* Clairville and *Myas* Dejean.

Names of individuals and institutions from which material was borrowed are abbreviated in the text as follows: AMNH – American Museum of Natural History; ANSP – Academy of Natural Sciences; AU – Auburn University; BM – British Museum (Natural History); CAS – California Academy of Sciences; CM – Carnegie Museum; CNC – Canadian National Collection; CNHM – Chicago Natural History Museum; CU – Cornell University; DL – David Larson; DRW – D. R. Whitehead; FDPI – Florida Division of Plant Industry; GEB – G. E. Ball; INHS – Illinois Natural History Survey; ISU – Iowa State University; KLE – Kansas State University; MCZ – Museum of Comparative Zoology; MHNP – Museum d'Histoire Naturelle, Paris; MSU – Montana State University; NCSU – North Carolina State University; RCG – R. C. Graves; RF – R. Freitag; RTB – R. T. Bell; RU – Rutgers University; TAM – Texas A & M University; TCB – T. C. Barr; TE – T. Erwin; TH – T. Hlavac; UA – University of Arkansas; UASM – University of Alberta Strickland Museum; UK – University of Kansas; UL – University of Louisville; UMMZ – University of Michigan Museum of Zoology; UP – Purdue University; USNM – United States National Museum; UW – University of Wisconsin; VMK – V. M. Kirk.

Methods

General methods

By making comparisons among their characteristics, specimens were sorted into demes, subspecies, species, and species groups according to degree of similarity and difference. The characteristics used were arbitrarily weighed, and the same characteristics were given different weights in different situations. The relationships revealed by these comparisons were interpreted and the evolution of the species and species groups was then inferred.

Characters of adults

Some structures which are used in the identification of the species of *Evarthrus* are discussed below to facilitate their use in the text.

The lines of microsculpture of the integument of the dorsal surface are almost effaced, disoriented, and do not form meshes in specimens of some species. In specimens of other species the lines are close together and sinuate, but they do not form meshes. More frequently meshes are formed and are amorphic or isodiametric. The interspaces are flat or raised and bead-like. The lustre of the integument correlated with the microsculpture is as follows: shiny in the absence of meshes; dull with isodiametric meshes and flat interspaces; matte or velvet with isodiametric meshes and bead-like interspaces; iridescent with dense sinuate parallel lines. Females are always duller than males of the same species.

The frontal grooves of the head are usually of a particular shape, and are useful in recognizing specimens of a number of species. The grooves are straight, or crescent-shaped with the convexity directed medially or laterally (figs. 70-71).

The number of setae on the penultimate article of the labial palpus is useful in delimiting species. Two dorsal "primary" setae are always present near the halfway point of the article. Three "secondary" setae are also present. One is apical, and arises from the ventral side of the article. Another is near the apical end of the article. It is dorsolateral and directed dorsolaterally. In a complementary position is the third seta. It is also near the apical end of the article on the dorsomedial side and is directed dorsomedially. The truly apical seta occurs more frequently than the other "secondary" setae but it is not always present. Other setae occasionally occur here and there near the "primary" setae (figs. 66-69). Horn (1881) noted that the number of setae on the labial palpus are not constant in *Evarthrus* and suggested that two groups may be recognized: a group with bisetose labial palpi and a group with plurisetose labial palpi.

The mandibles of the type species, *sigillatus* Say, are illustrated (fig. 72).

Details of form and structure of the pronotum are useful in recognizing subgenera and species. The general outline of the pronotum ranges in form from rectangular to cordiform (figs. 1-62). Another useful structure is the shape of the basal lateral fovea, which is punctiform (figs. 1-7), monostriate or bistriate (figs. 8-20, 21-62). The position of the basal lateral seta is on (figs. 8-20), or beside the lateral bead (figs. 1-7 and 21-62). The lateral bead in specimens of a few species is broad posteriorly, but in most species it is narrow posteriorly as in fig. 25. The prosternal process which projects posteriorly between the front coxae has a longitudinal medial groove. This groove is deep or shallow. The apex of the prosternal process is or is not marginate.

At least four setae are present on the anterior face of the middle femur and always in the same positions. A proximal pair of setae are located near the ventral side of the femur, and a distal pair near the dorsal side. In specimens of some species additional setae usually occur near either pair. The total number of setae ranges from four to eleven in the genus and seems to be a good character for grouping species (figs. 74-76). Setae are absent from the lateroventral margin of the claw bearing tarsal articles in specimens of four species of the subgenus *Fortax.*

I have used the term "last abdominal sternum" in the text. This is morphological sternum VII, which is the apparent sternum VI in beetles (sternum 1 has disappeared).

The male genitalia are very important structures in defining species and species groups. In fact, it would be exceedingly difficult to recognize and classify the species of *Evarthrus* without reference to these structures. Two parameres and a median lobe which contains an internal sac constitute the external male genitalia. The median lobe is a tube with a central bend. The portion of the lobe posterior to the bend is referred to here as the apical half, and that anterior to the bend the basal half. The lobe is always bent dorsoventrally with the convexity directed dorsally. In specimens of some species the apical half of the median lobe is bent laterally. The posterior extremity of the median lobe is flattened and heavily sclerotized, and is called here the apical blade. The posterior edge of the apical blade is the apex. Within the median lobe is a membranous sac known as the internal sac, which is everted during copulation. In studying this organ the following technique was used: the beetle was relaxed in boiling water; then by inserting a pair of fine forceps into the end of the abdomen the genitalia were grasped and pulled out; these structures were cleared in a hot 10% solution of potassium hydroxide for about 10 minutes and then washed in water; the internal sac was everted by gently pulling the sac through its open end with a pair of fine forceps. In specimens of some species the internal sac bears serrulate fields and an apical sclerite (the sclerite is apical when the sac is everted). The shape of the apical sclerite is commonly used for grouping species as well as separating closely related species. The shape of the whole everted internal sac is probably of taxonomic value but I have not used it here. Joined to the left and right sides of the basal portion of the median lobe near the anterior end are the parameres. The left paramere is broad and somewhat disc shaped in all of the known species of the genus. The right paramere varies in form among the species of the genus but does not vary interspecifically.

The sclerites of the female ovipositor exhibit slight variation. With the exception of the stylus they do not provide taxonomically useful features. Fig. 73 is a drawing of the ovipositor and bursa of *sigillatus*. The bursa copulatrix is short, and the anterior end is a flat, lightly sclerotized plate, which has a marked anteriorly-directed central mound. A small dark sclerite rests on the tip of the mound and is joined to the base of the spermathecal duct. The common oviduct enters the bursa beside the sclerite. A long accessory gland is joined to the spermathecal duct. The spermatheca is a simple sausage-shaped sac. The pygidial reservoir is rather large and it has a short thick duct which appears to open externally near the posterior end of the gonangulum. The pygidial gland duct is short and narrow. The stylus is typical of the genus. Slight variation in the form of the stylus occurs throughout the genus and is referred to in the text.

Measurements

The range of body size for each species was determined. A calibrated eyepiece in a Wild M5 stereoscopic binocular microscope was used. The body length is indicated by the sum of three measurements: length of head – distance from the base of the mandible to the hind margin of the eye; length of pronotum – distance between the anterior margin of the pronotum to the margin behind the basal angle; length of elytra – distance from the apex of the scutellum to the apical tip of an elytron. The widths of the head, pronotum, and abdomen are defined as follows: head – maximum distance behind the eyes dorsally; pronotum – maximum transverse distance; abdomen – maximum transverse distance across both elytra.

Illustrations and maps

The drawings were made with the aid of a Wild drawing tube, on the M5 stereo microscope.

Distribution maps are given for all species. Most maps comprise the distributions of species of a single species group.

Criteria for species and subspecies

Two forms with overlapping ranges are regarded as distinct species if they do not intergrade in at least one morphological character. If a clinal series of intermediate populations is intercalated between two morphologically distinct populations that are widely allopatric the entire complex is treated as a single variable species, but subspecific names are not assigned. Subspecies are recognized only in cases of steep clinal variation in at least one characteristic.

BIOLOGY

Little is known about the biology of this genus. Probably the members are omnivorous, as are most Carabidae. I have found spores of fungi in the gut of *E. faber* Germar, and ant remains in the gut of *E. sodalis colossus* LeConte.

All of the species are flightless: not only are the hind wings of all individuals atrophied, but the metathorax is reduced, and the elytra are fused along the suture. It is not surprizing, therefore, that geographical variation is marked, that most of the species have restricted ranges, and that closely related species are often allopatric – facts which indicate restricted powers of dispersal.

Members of the genus inhabit deciduous forests or open country. Those species which occur in open places are northern and western in distribution. Conversely, the ranges of the more numerous forest species are generally southern and east of the Mississippi River.

TAXONOMY

The Genus *Evarthrus* LeConte

Characteristics

Adults. – small to large Pterostichini (see Ball, 1966 for characterization of tribe); color of body black, legs usually black sometimes red; penultimate article of labial palpus plurisetose (usually) or bisetose; pronotum rectangular to cordate, basal lateral fovea of pronotum bistriate, monostriate, or a single puncture, always distinctly impressed; basal lateral seta of pronotum on lateral bead or beside it; elytron with seventh interval usually raised at base, 1-5 punctures on medial side of third interval; hind wings absent; metepisternum short, with lateral margin equal in length to anterior margin; article five of tarsus usually with a row of setae on each ventrolateral margin; venter impunctate, usually slightly rugose; females with two setae on last sternum of abdomen; eversion of internal sac of median lobe of male genitalia usually to right, less often dorsoapical, and rarely to left. Larva – Pterostichini; antenna with five articles; urogomphi short, terete, curved toward each other (Van Emden, 1942, and Böving and Craighead, 1930).

Type species. – *Evarthrus sigillatus* Say, 1823a (designated by Lindroth, 1966:473).

The species of *Pterostichus* Bonelli resemble species of *Evarthrus*, but in the former group the lateral areas of the ventral surface of the body are usually punctate, the eversion of the internal sac is to the left or dorsal, the females have usually four to eight setae on the last abdominal sternum, exceptionally two in some individuals and the larvae have four antennal articles and long multinodose urogomphi.

Some species of *Pseudabarys* and *Abaris* vaguely resemble species of *Evarthrus* in having a plurisetose penultimate labial palpus and a single puncture in the third interval of an elytron. Their general habitus is different, however. Species of *Abaris* have pectinate claws, and the internal sac seems to be telescopic rather than of the eversion type.

Members of the genus *Evarthrus* are like those of *Molops*. They have the following characteristics in common: Adult – similar body shape particularly the pronotum; ventral side of body not punctate; elytron usually with seventh interval raised at base; and setae usually present on each lateroventral side of the last tarsal article. Larvae – antenna with five articles. Specimens of *Molops* differ by having a ninth elytral interval which is lateral to the umbilicate series, setae on the dorsal side of the last tarsal article, and four setae on the last abdominal sternum of the females. The larvae of *Molops* and *Evarthrus* differ in characteristics of the urogomphi.

Schuler (1962, 1963a, 1963b) has studied the taxonomic importance of the spermatheca of female carabids. He points out that the spermatheca of *Molops* is a simple sac while that of *Pterostichus* is not. The spermatheca of *Evarthrus* is also a simple sausage-shaped sac, like that of *Molops*. This similarity may not be in itself important, but it adds to the characters that *Evarthrus* and *Molops* share.

Basford *et alii* (1968) used immunological techniques to investigate the classification of the Adephaga. Among other species of carabids, they studied *Evarthrus sodalis* LeConte and *Pterostichus chalcites*. They found the samples of these two species to be markedly different from one another, and this in itself could be accepted as additional evidence to support the ranking of *Evarthrus* as generically distinct from *Pterostichus*. However, this evidence is of doubtful value because the other results obtained are at such variance with the generally accepted classification. Indeed, these authors write that "(6) the distinct position of the genus *Harpalus* and the failure of the immunological results to cluster other Harpalinae with them suggested that, within the Carabidae, large amounts of random molecular variation exist (1968:405)."

I believe that the treatment of *Evarthrus*, *Pterostichus*, and *Molops* as separate genera in the tribe Pterostichini is justified. Simpson (1961) points out that criteria derived from relative divergence apply to the ranking of taxa. and he suggests several criteria of which one is as follows: in a group of related taxa it is desirable that differences between most similar taxa should be approximately equal. In addition to this the general feeling among taxonomists is that taxa of the same rank should have the same amount of diversity.

In treating *Evarthrus*, *Pterostichus*, and *Molops* as separate genera both of the above criteria are followed. The differences among the three genera are approximately the same in numbers of weighted characteristics, which are widespread in each genus. Each of the taxa contain many species, although *Pterostichus*, as regarded here, is the most diverse. The genus *Evarthrus* is a polythetic group, but nevertheless such groups are acceptable in taxonomic practice.

Subgenera and Species Groups

On the basis of similarities and differences of external structures and male genitalia the species are grouped into three subgenera. The species of each subgenus are arranged in species groups. The subgenus *Fortax* Motschulsky includes six species which constitute two species groups. The subgenus *Cyclotrachelus* Chaudoir contains 12 species which are arranged in three species groups. Twenty-five species are included in the subgenus *Evarthrus* and are placed in ten species groups. The names of most of the species groups are based on the name of the first described species contained in each. Two species groups have been given the names of the most well known species included in each: the *spoliatus* group and the *ovulum* group. The *gigas* group is so named because it includes *E. gigas* Casey, which was designated as the type species of *Megasteropus* Casey.

Key to the species and subspecies of the Genus *Evarthrus* LeConte

1 Plica of elytron present 2

– Plica of elytron absent .... *E. gravesi* new species, p. 167

2(1) Basal setae of pronotum in lateral bead (figs. 8-20); basal foveae of pronotum monostriate 3

– Basal setae of pronotum beside lateral bead (figs. 1-7, 21-*61); basal foveae of pronotum punctiform *OR* bistriate 15

3(2) Gula with anterior end flanked by raised knobs (fig. 63); body longer than 17.7 mm .... *E. unicolor* Say, p. 110

– Knobs absent; body shorter than 17.7 mm 4

4(3) Prosternal process with longitudinal groove deep and sharply defined 5

– Prosternal process with longitudinal groove shallow and not sharply defined ... 9

5(4) Penultimate article of labial palpus with two medial and two apical setae; pronotum circular (fig. 20); front tarsi of males with ventral rows of cup-like scales .... *E. faber* Germar, p. 125

– Penultimate article of labial palpus with two medial setae only; pronotum cordiform *OR* sides not produced (figs. 15-16, 18-19); males with typical scales on front tarsi 6

6(5) Pronotum with basal angles sharp and produced (figs. 15-16); microsculpture open and not dense 7

– Pronotum with basal angles broadly rounded and not produced (figs. 18-19), microsculpture open but dense 8

7(6) Frontal grooves crescent-shaped, widely separated, and oblique (fig. 71); range, Florida and Georgia .... *E. ovulum* Chaudoir, p. 118

– Frontal grooves straight, closer together, and more parallel (fig. 70); range, Mobile, Alabama area .... *E. alabamensis* Casey, p. 117

8(6) Basal foveae of pronotum with almost effaced long and shallow anterior extensions that together form a lyre-shaped figure; pronotum oval shaped because of gradual constriction of anterior half (fig. 18); range, Mobile, Alabama area .... *E. parafaber* new species, p. 122

---

*In a few specimens one seta on one side in bead.

– Basal foveae of pronotum without long anterior extensions; pronotum cordiform (fig. 19); range, Georgia, South Carolina, and North Carolina . . . . *E. levifaber* new species, p. 123

9(4) Pronotum cordiform (figs. 14, 17) 10

– Pronotum more oval (figs. 9-13) 12

10(9) Range, Georgia, Mississippi, and Tennessee; pronotum with basal sinuations elongate (fig. 14); males with obsolete punctures in elytral striae . . . . *E. vinctus* LeConte, p. 115

– Range, southern Alabama, Mississippi and Texas; pronotum with shorter basal sinuations; (fig. 17) males with large punctures in elytral striae 11

11(10) Range, northeastern Texas; male with apex of median lobe broader (fig. 95 e-g) . . . . *E. texensis* new species, p. 121

– Range, coastal Alabama and Mississippi; male with apex of median lobe narrower (fig. 95 a-c) . . . . *E. macrovulum* new species, p. 119

12(9) Range, east of the Appalachian Mountains 13

– Range, south and west of the Appalachian Mountains 14

13(12) Range, eastern South Carolina north to Maryland; male with apex of median lobe evenly rounded . . . . *E. spoliatus* Newman, p. 113

– Range, western South Carolina southward; male with apex of median lobe truncate . . . . *E. brevoorti* LeConte, p. 114

14(12) Range, northern Georgia, northern Alabama, Tennessee, Kentucky, Ohio, West Virginia, western Pennsylvania; apex of median lobe of male evenly rounded; pronotum of male glossy, microsculpture varying from open and sparse to obsolete . . . . *E. fucatus* new species, p. 111

– Range, northern Georgia, northern Alabama, south to Florida, southern Alabama and southern Mississippi; apex of median lobe of male truncate; pronotum of male semi-glossy, microsculpture open but dense . . . . *E. brevoorti* LeConte, p. 114

15(2) Basal foveae of pronotum punctiform (figs. 1-7) 16

– Basal foveae of pronotum bistriate (figs. 21-61) 21

16(15) Apex of prosternal process marginate . . . . *E. hernandensis* Van Dyke, p. 101

– Prosternal process not marginate 17

17(16) Pronotum with incomplete marginal groove between lateral setae (fig. 2) . . . . *E. morio* Dejean, p. 102

– Pronotum with complete marginal groove between lateral setae 18

18(17) Pronotum with basal setae near basal angles (figs. 3-4) . . . . *E. laevipennis* LeConte, p. 103

– Pronotum with basal setae in front of basal angles (figs. 5-7) 19

19(18) Pronotum with anterior transverse impression complete (fig. 5) . . . . *E. approximatus* LeConte p. 106

– Transverse impression incomplete (figs. 6-7) 20

20(19) East of the Appalachian Mountains, in North Carolina, and Virginia . . . . *E. iuvenis* new species, p. 107

– West and South of the Appalachian Mountains, in Indiana, Illinois, Ohio, Michigan, Tennessee, Mississippi, Alabama, Georgia .... *E. obsoletus* Say, p. 108

21(15) Elytron with 3-5 setae in third interval 22

– Elytron with one seta in third interval, occasionally one or two setae on one elytron and two setae on the other 26

22(21) Pronotum quadrate with smooth lateral margins (fig. 37); range, east of the Mississippi River .... *E. hypherpiformis* new species, p. 145

– Pronotum more cordate *OR* quadrate with lateral crenulations (figs. 54, 57-58); range, west of the Mississippi River 23

23(22) Elytra with striae almost impunctate .... *E. substriatus* LeConte, p. 156

– Striae distinct and deeply punctate 24

24(23) Pronotum 6-8 mm wide, quadrate, with lateral crenulations, particularly in basal sinuation (fig. 58) .... *E. gravidus* Haldeman, p. 163

– Pronotum less than 6 mm wide, more cordiform without lateral crenulations (figs. 53, 57)... 25

25(24) Elytra dull; range, Oklahoma, Texas .... *E. torvus deceptus* Casey, p. 160

– Elytra glossy; range, Iowa, Minnesota, South Dakota ....
.... *E. iowensis* new species, p. 154

26(21) Pronotum with anterior transverse impression obsolete medially 27

– Pronotum with anterior transverse impression complete and clearly impressed *OR* complete with short interruptions 36

27(26) Middle femur with four setae on anterior face, occasionally four setae on one femur and five on other 28

– Five or more setae on anterior face of both middle femora 29

28(27) Median lobe of male strongly arcuate and apical blade short with edges only slightly bent (fig. 100); body length 11.4 – 15.4 mm; legs always black; pronotum (fig. 22); in Arkansas elytral intervals with micropunctures indistinct; range, Arkansas, Oklahoma .... *E. whitcombi* new species, p. 129

– Median lobe of male moderately arcuate and apical blade long with edges strongly bent (fig. 99); total length 9.02 – 12.3 mm; legs black *OR* ferrugineous; pronotum (fig. 21); in Arkansas elytral intervals with distinct micropunctures; range, Arkansas, Iowa, Kansas, Missouri, Nebraska, Oklahoma, Pennsylvania, South Dakota ....
.... *E. incisus* LeConte, p. 127

29(27) Elytron with striae almost effaced; first three anterior umbilicate punctures with slight mounds between them .... *E. substriatus* LeConte, p. 156

– Elytron with striae distinct, higher ridges present between first three umbilicate punctures 30

30(29) Body length 11.2 – 13.9 mm; pronotum (fig. 53); range, Iowa, Minnesota, South Dakota .... *E. iowensis* new species, p. 154

– Body longer than 13.9 mm 31

31(30) Pronotum with longer constriction before basal angles which are about 90° or less (figs. 45–47, 52); range, mainly west of the Mississippi River 32

– Pronotum with basal angles shorter and greater than 90° (figs. 38-44, 48-51); range, mainly east of the Mississippi River *AND* eastern Iowa and Arkansas 33

32(31) Pronotum with basal angles laterally prominent; basal foveae more V-shaped than U-shaped, relatively short and inner edge anteriorly not markedly deflected laterally (figs. 45-47); range, mainly west and southwest of the Missouri River *AND* western Iowa . . . . *E. sodalis colossus* LeConte, p. 146

– Pronotum with basal angles less produced laterally (fig. 52); basal foveae more U-shaped than V-shaped, relatively longer and anterior end of inner edge deflected laterally; range, Illinois, Iowa, Missouri, South Dakota, Wisconsin . . . . *E. alternans* Casey, p. 153

33(31) Range, Arkansas; pronotum with basal angle obtuse (fig. 49) . . . . *E. parasodalis* new species, p. 150

– Range, north and east of Arkansas; specimens near Arkansas have pronotum with more distinct sinuation and basal angles more acute (figs. 38-44, 50-51) 34

34(33) Elytra of male with microsculpture stretched transversely; pronotum (fig. 48); range Alabama, Tennessee . . . . *E. sodalis lodingi* Van Dyke, p. 146

– Elytra of males with microsculpture isodiametric 35

35(34) Pronotum with basal angles round, and more obtuse in southern Pennsylvania (figs. 38-44); range, New York west to Iowa, and Minnesota south to northern Mississippi . . . . *E. sodalis sodalis* LeConte, p. 146

– Pronotum with basal angles sharp in south Pennsylvania and more obtuse in Virginia (figs. 50-51); range, southern Pennsylvania, Virginia, Maryland, southern New Jersey . . . . *E. furtivus* LeConte, p. 152

36(26) Apex of prosternal process with apical setae 37

– Prosternal process without setae 40

37(36) Pronotum with sides slightly sinuate near base, basal angles slightly obtuse and prominent (figs. 35-36) 38

– Pronotal sinuation obsolete, basal angles very obtuse, broadly rounded, not prominent (figs. 33-34) 39

38(37) Pronotum quadrate, margin slightly expanded near base (fig. 36); elytra dull, particularly in females; elytron of female with stria 8 and marginal groove widely separated; range, southern Arkansas, northern Louisiana, western Mississippi and northeastern Texas . . . . *E. nonnitens* LeConte, p. 144

– Pronotum with sides more acutely sinuate near base, margin more broadly expanded near base (fig. 35); elytra slightly glossy; elytron of female with stria 8 and marginal groove approximate; range, southeastern Texas . . . . *E. engelmanni* LeConte, p. 142

39(37) Pronotum at widest point 4-5 mm; body length 10.3 – 15.9 mm; legs black or red; pronotum more rectangular than circular (fig. 33); males almost always with flat elytral intervals . . . . *E. seximpressus* LeConte, p. 139

– Pronotum at widest point 5.5 – 6.5 mm; body length 14.6 – 18.7 mm; legs black only; pronotum more circular than rectangular (fig. 34); males almost always with convex elytral intervals . . . . *E. alabamae* Van Dyke, p. 141

40(36) Middle femur with four setae on anterior face *AND* pronotum typically cordiform, strongly constricted posteriorly (fig. 21) . . . . *E. incisus* LeConte, p. 127

– Middle femur with more than four setae on anterior face *OR* pronotum not as in fig. 21 41

41(40) Range, east of the Mississippi River 42

– Range, west of the Mississippi River 47

42(41) Pronotum moderately sinuate near base (fig. 44); range, Tishomingo County, Mississippi . . . . *E. sodalis sodalis* LeConte, p. 146

– Pronotum more quadrate, less sinuate near base (figs. 23-32) 43

43(42) Range, Florida east of the Suwannee River and coastal Georgia 44

– Range, other than above 45

44(43) Pronotum with the width of deplanate area between lateral ridge and disc nearly even throughout (fig. 23); body length 14.8 – 17.6 mm: elytron with two setae, in seventh stria near plica . . . . *E. blatchleyi* Casey, p. 131

– Pronotum with deplanate area broad near base (fig. 24); body length 13–15 mm; elytron with one seta, rarely two, in seventh stria near plica . . . . *E. floridensis* new species, p. 132

45(43) Range, mainly east of the Appalachian Mountains and southeastern Alabama, Florida west of the Suwannee River, eastern Tennessee*, Pennsylvania west to Pittsburg; Pennsylvania specimens with laterally arcuate and glossy elytra; pronotum (figs. 25-28); male genitalia (fig. 103) . . . . *E. sigillatus* Say, p. 133

– Range, west of the Appalachian Mountains, Pennsylvania specimens with parallel and dull elytra; pronotum (figs. 29–32) 46

46(45) Pronotum bell-shaped (fig. 29); range, coastal Alabama and Mississippi . . . . *E. sinus* new species, p. 136

– Pronotum rectangular (figs. 30-32); range, north of *E. sinus* . . . . *E. convivus* LeConte, p. 137

47(41) Body length 9.5 – 14.5 mm 48

– Body longer than 14.5 mm 52

48(47) Elytra with striae almost effaced; range, Mexico, Texas, New Mexico . . . . *E. substriatus* LeConte, p. 156

– Elytra with distinct impressed striae 49

49(48) Umbilicate series with first three anterior punctures small and separated from one another by low raised areas; pronotum strongly constricted at base (fig. 55) 50

– Umbilicate series with first three anterior punctures of normal size separate from one another by normal ridges; pronotum less strongly constricted at base (figs. 53, 57) 51

50(49) Plica large; last abdominal segment with prominent dorsal knob that fits onto plica, especially distinct in females (fig. 77); elytra markedly sinuate posteriorly (fig. 78) . . . . *E. substriatus* LeConte, p. 156

– Plica small; knob obsolete (fig. 79); elytra not markedly sinuate (fig. 80) . . . . *E. constrictus* Say, p. 158

*The geographic ranges of *convivus* and *sigillatus* are approximate in eastern Tennessee. For certain identification of specimens occurring in this region, examine the male genitalia.

51(49) Elytra dull; range, Oklahoma, Texas . . . . *E. torvus deceptus* Casey, p. 160

– Elytra glossy; range, Iowa, Minnesota, South Dakota . . . . *E. iowensis* new species, p. 154

52(47) Pronotum slightly or moderately constricted near base, sides not prominent (figs. 49, 56–58) 53

– Pronotum more strongly constricted near base, sides convex (figs. 45–47, 54, 59, 61) 56

53(52) Pronotum with posterior angles not prominent (fig. 49); range, Arkansas . . . . *E. parasodalis* new species, p. 150

– Pronotum with posterior angles more prominent 54

54(53) Pronotum quadrate, lateral margin crenulate particularly in basal sinuation, basal foveae not complete (fig. 58) . . . . *E. gravidus* Haldeman, p. 163

– Pronotum less quadrate and more constricted near base, lateral margin smooth or with indistinct crenulations, basal foveae complete (figs. 56–57) 55

55(54) Elytra dull; pronotum smooth (fig. 57) . . . . *E. torvus deceptus* Casey, p. 160

– Elytra glossy; pronotum rugose (fig. 56) . . . . *E. torvus torvus* LeConte, p. 160

56(52) Elytra with striae very shallow, almost effaced, impunctate, sometimes represented by a series of extremely shallow dashes rather than continuous lines, intervals always flat; pronotum (figs. 54, 60) 57

– Elytra with striae deeper, punctate, and sometimes represented by a row of punctures or distinctly impressed dashes; intervals flat or convex; pronotum (figs. 45–47, 59, 61) 58

57(56) Very large species; body length 19.4 – 23.8 mm; range, Texas . . . . *E. gigas* Casey, p. 165

– Smaller; body length 9.5 – 14.5 mm; range Mexico, Texas, New Mexico . . . . *E. substriatus* LeConte, p. 156

58(56) Elytron with scutellar stria long and always separated from stria 2; first complete stria (stria 2) begins at basal seta (fig. 65); elytra of females with intervals completely flat; stria 7 with four to five setae near apex; pronotum (fig. 61) . . . . *E. heros* Say, p. 166

– Elytron with scutellar stria always joined to stria 2 and base of stria 2 indicated near basal seta or absent (fig. 64), elytra of females with raised intervals and striae more impressed, stria 7 with two to three, rarely four, setae near apex; pronotum (figs. 45–47, 59) 59

59(58) Elytra of males with transversely stretched microsculpture, pronotum with base of basal foveae straight (fig. 59). . . . . *E. sallei* LeConte, p. 165

– Elytra of males with isodiametric microsculpture, pronotum with the base of the basal fovea curved (figs. 45–47) . . . . *E. sodalis colossus* LeConte, p. 146

The Subgenus *Fortax* Motschulsky

Fortax Motschulsky, 1865:246. – Ball, 1960:129. TYPE SPECIES – *Evarthrus morio* Dejean, 1828 (here designated).

Ferestria Leng, 1915:576. TYPE SPECIES – *Evarthrus laevipennis* LeConte. 1848 (designated by Leng, 1915:576).

Characteristics. – The following combination of characteristics is diagnostic for the subgenus *Fortax*: species of small size (body length 7.1 – 12.8 mm); penultimate article of labial palpus bisetose (usually) to quadrisetose; pronotum with sides strongly constricted posteriorly, posterior lateral foveae each completely punctiform or punctiform posteriorly with short anterior extension, posterior lateral setae situated beside lateral bead (figs. 1–7); middle femur with four setae on anterior face (fig. 74); last tarsal article with or without setae on lateroventral margins; eversion of internal sac of median lobe of male genitalia dorsoapically or ventrally on left side of median lobe.

The absence of setae on the ventral side of the last tarsal article and the left ventral eversion of the internal sac are characteristics found in the subgenus *Fortax* but not in the subgenera *Cyclotrachelus* and *Evarthrus*.

The two species groups in *Fortax* are the *morio* group and the *obsoletus* group.

The *morio* Group

Characteristics. – Pronotum with basal lateral foveae punctiform posteriorly, briefly and shallowly extended anteriorly; basal seta situated near basal angle; claw-bearing article of tarsus without setae on lateral ventral margins.

This group includes the species *hernandensis* Van Dyke, *morio* Dejean and *laevipennis* LeConte. The members of this group are found on the Gulf Coastal Plain and on the Piedmont in the southeastern United States.

Evarthrus hernandensis Van Dyke, 1943

Figures 1, 66, 74, 81, 125

Evarthrus (Ferestria) hernandensis Van Dyke, 1943:26. HOLOTYPE, male, labelled as follows: "Brooksville Fla I–20. 30/40; Van Dyke Collection; HOLOTYPE No. 5308 Evarthrus hernandensis Van Dyke". CAS. ALLOTYPE, labelled as follows: "Brooksville Fla I–20. 30/40; Van Dyke Collection; Allotype No. 5309 Evarthrus hernandensis Van Dyke." CAS. TYPE LOCALITY, near Brooksville, Hernando County, Florida. Blackwelder and Blackwelder, 1948:3 (*Ferestria*).

Recognition. – The following combination of characteristics is diagnostic for *hernandensis*: prosternal process with marginate apex; elytra with strongly convex intervals and deep striae; eversion of internal sac left and ventral around median lobe; stylus of female ovipositor elongate and narrow. The species *morio* is similar to *hernandensis* but is distinguished by the absence of a raised margin at the apex of the prosternal process and an incomplete groove along the lateral margin of the pronotum.

Description. – Body length 8.1 – 9.3 mm. Form small, short and robust.

Microsculpture of head between eyes and intervals of elytra isodiametric meshes, or highly sinuous, entwined lines. Disc of pronotum with microsculpture usually effaced, or of sinuous lines.

Head glossy; frontal grooves short, shallowly impressed, and not sharply defined, parallel or slightly oblique. Penultimate article of labial palpus with two medial setae (fig. 66).

Pronotum glossy; form circular in outline as in fig. 1; disc convex laterally but flattened in center; sides produced, constricted slightly anteriorly and strongly posteriorly, not sinuate near posterior margin; posterior angles obsolete, very broadly obtuse; anterior transverse impression incomplete, impressed laterally only; basal lateral foveae deep and punctiform posteriorly, short and shallow anteriorly. Prosternal process with marginate apex, and medially with short, distinctly impressed longitudinal groove.

Elytra glossy, slightly sinuate apically; intervals strongly convex; striae deep anteriorly, obsoletely or indistinctly punctate posteriorly; stria 7 with apical end distinctly impressed, obsolete anteriorly.

Male genitalia (fig. 81) with median lobe strongly arcuate, angle approximately right; apical blade spatulate and slightly deflected dorsally. Right paramere fairly short, slightly tapered apically, not extending to apical half of median lobe. Eversion of internal sac to left, around left and ventral sides of median lobe; apical sclerite absent, dark serrulate fields present apically on finger-like projections. The genitalia of two males were studied in detail.

Stylus of female ovipositor elongate and narrow.

Geographical distribution (fig. 125). – This species is found in western peninsular Florida. I have seen six specimens from the following localities.

United States – FLORIDA: Citrus County: (CAS). Hernando County: Brooksville (CAS). Hillsborough County: Tampa (ANSP, MCZ, USNM). Marion County: Juniper Springs (FDPI).

Evarthrus morio Dejean, 1828

Figures 2, 82, 125

Feronia (Steropus) morio Dejean 1828:302. TYPE, Labelled as follows: "morio M. in America borealis", MHNP. TYPE LOCALITY, Alma, Georgia (here selected). LeConte, 1848:355 (*Broscus*). – LeConte, 1852:231 (*Evarthrus*). – LeConte, 1863a:8. – Motschulsky, 1865:264 (*Fortax*). LeConte, 1873:319 (*Evarthrus*). – Schaupp, 1880:49. – Casey, 1918:364 (*Ferestria*). – Leng 1920:57. – Csiki, 1930:674 (*Pterostichus*).

Pterostichus (Pterostichus) (Sect. *Fortax*) *dejeanellus* Csiki, 1930:674.

Evarthrus (Ferestria) taurus Van Dyke, 1943:25. HOLOTYPE, labelled as follows: "Punta Gorda Fla. 2.5–12.40; Van Dyke Collection". CAS. ALLOTYPE, labelled the same as holotype. CAS. TYPE LOCALITY – near Punta Gorda, Fla. NEW SYNONYMY. – Blackwelder, 1948:3 (*Ferestria*).

Recognition. – the following characteristics are diagnostic for *morio*: pronotum with incomplete lateral grooves, absent between the lateral and basal setae, and complete anterior impression; prosternal process with apex unmargined; eversion of internal sac of male genitalia to the left and around left and ventral sides of median lobe. The species *laevipennis* is similar to *morio* but has crescent-shaped frontal grooves on the head, pronotum with complete lateral grooves, and the male genitalia are different (fig. 82 cf. fig. 83).

Description. – Body length 7.7 – 10.2 mm. Form robust.

Microsculpture of head between eyes, disc of pronotum and elytral intervals with sinuous lines often entwined forming amorphic or isodiametric meshes and partially effaced.

Head glossy; frontal grooves short, shallowly and broadly impressed, not sharply defined, slightly oblique. Penultimate article of labial palpus with two to four setae.

Pronotum glossy; form subcordiform in outline as in fig. 2; disc moderately convex; sides produced, constricted slightly anteriorly and strongly posteriorly, obsoletely sinuate in front of posterior angles; posterior angles obsolete, very broadly obtuse; anterior transverse impression complete; basal lateral foveae deep posteriorly, short and shallow anteriorly. Prosternal process with unmargined apex; longitudinal groove short and distinctly impressed. First articles of middle and hind tarsi with lateral grooves.

Elytra glossy, slightly sinuate apically; intervals completely flat or slightly raised and convex; striae 1 to 5 obsolete or distinctly impressed; striae 6 and 7 obsolete, obsoletely or indistinctly punctate.

Male genitalia (fig. 82) with median lobe strongly arcuate, angle approximately right; apical blade spatulate. Right paramere narrow apically and extending to apical half of median lobe. Eversion of internal sac to left and when everted, curled closely around left and ventral sides of median lobe; apical sclerite absent; serrulate field present apically. The genitalia of four males were studied in detail.

Stylus of female ovipositor average size for the *morio* group.

Variation. – The striae and intervals of the elytra vary. A few individuals have distinctly impressed and punctate striae and slightly raised and convex intervals. Generally, however, the striae are obsoletely impressed and the intervals are flat.

Notes on synonymy. – Van Dyke proposed the name *taurus* for the species. He wrote that the presence of the marginal groove of the pronotum was characteristic of *morio* Dejean. The groove is, in fact, absent in *morio* but it is present in the similar species *laevipennis* LeConte.

Collecting notes. – H. J. Weems, Jr. has collected this species in oak leaf litter.

Geographical distribution (fig. 125). – This species ranges from southwestern Florida to southern Georgia. I have seen 115 specimens collected in the following localities.

United States – FLORIDA: Alachua County: Archer (FDPI); Gainesville (CNC, FDPI, UMMZ); High Springs (UMMZ); Micanopy (UMMZ); Newnan's Lake (FDPI, UMMZ); University Farm (UMMZ); Warren's Cave (UMMZ). Baker County: Glen St. Mary (FDPI); Macclenny (FDPI). Charlotte County: Punta Gorda (CAS). Citrus County: (CAS). Collier County: Naples (CAS). Dixie County: Cross City (UMMZ). Duval County: Jacksonville (AMNH). Hernando County: Brooksville (CAS). Hillsborough County: Tampa (ANSP, MCZ, USNM). Jackson County: Florida Caverns State Park (FDPI). Manatee County: Bradenton (GEB); Manatee (UMMZ). Orange County: Winter Park (CU). Palm Beach County: Boynton (CAS); Lake Worth (AMNH), Putnam County: Camp Rosa, Bostwich (FDPI); Crescent City (USNM); Florahome (UMMZ); Welaka (CU). Suwanee County: Wellborn (UMMZ). Volusia County: Enterprise (ANSP, RU, USNM). County not determined: North Smyrna (CAS). GEORGIA: Bacon County: Alma (UMMZ). Bryan County: Lanier (UMMZ).

Evarthrus laevipennis LeConte, 1848

Figures 3–4, 83, 125

Broscus (Cephalotes) laevipennis LeConte, 1848:354. LECTOTYPE (here selected) a female, labelled as follows: "orange disc; Type 5627; E. laevipennis Lec." MCZ. TYPE LOCALITY, Georgia. – LeConte, 1852:231 (*Evarthrus*). – LeConte, 1863a:8. – LeConte, 1873: 319. – Schaupp, 1880:49. – Leng, 1915:577 (*Ferestria*). – Casey, 1920:193. – Leng, 1920:57. – Csiki, 1930:674 (*Pterostichus*). – Löding, 1945:16 (*Ferestria*).

Evarthrus acutus LeConte, 1852:231. LECTOTYPE (here selected) a female, labelled as follows: "orange disc; Type 5626; E. acutus Lec." MCZ. TYPE LOCALITY, Louisiana. NEW SYNONYMY. – LeConte, 1863a:8 (*Evarthrus*). – LeConte, 1873:319. – Schaupp, 1880:49. – Leng, 1915:577 (*Ferestria*). – Leng, 1920:57. – Csiki, 1930:674 (*Pterostichus*).

Evarthrus ovulum; Horn, 1875:126 (not Chaudoir).

Ferestria nanula Casey, 1918:364. HOLOTYPE, female, labelled as follows: "Mobile Ala; CASEY bequest 1925; TYPE USNM 47111; nanula Csy." USNM. PARATYPE, female, labelled as follows: "Mobile Ala; CASEY bequest 1925; nanula – 2 PARATYPE USNM 47111." USNM. NEW SYNONYMY. – Casey, 1920:192 (*Ferestria*). – Leng, 1920:57. – Csiki, 1930:674 (*Pterostichus*). –Löding, 1945:16 (*Ferestria*).

Ferestria simiola Casey, 1920:192. HOLOTYPE, female, labelled as follows: "Mobile Ala; CASEY bequest 1925; TYPE USNM 47112; simiola Csy." USNM. NEW SYNONYMY. – Leng and Mutchler, 1927:10 (*Ferestria*). – Csiki, 1930:674 (*Pterostichus*).

Ferestria seminola Löding, 1945:16 (misspelling for *simiola* Casey).

Ferestria castigata Casey, 1920:192. HOLOTYPE, male, labelled as follows: "Mobile Ala; H. P. Löding; male; CASEY bequest; TYPE USNM 47110; castigata Csy." USNM. PARATYPE, female, labelled as follows: "Mobile Ala.; CASEY bequest 1925; castigata – 2 PARATYPE USNM 47110. NEW SYNONYMY. – Leng and Mutchler, 1927:10 (*Ferestria*). – Csiki, 1930:674 (*Pterostichus*). – Löding, 1945:16 (*Ferestria*).

Ferestria bullata Casey, 1920:193. HOLOTYPE, female, labelled as follows: "Mobile Ala. H. P. Löding, CASEY bequest 1925; TYPE USNM 47113; bullata Csy." USNM. NEW SYNONYMY. – Leng and Mutchler, 1927:10 (*Ferestria*). – Csiki, 1930:674 (*Pterostichus*). Löding, 1945:16 (*Ferestria*).

Evarthrus (Ferestria) morio; Van Dyke, 1943:26 (not Dejean).

Ferestria acuta; Löding, 1945:16 (not LeConte).

Recognition. – Specimens of *laevipennis* are distinguished by the following combination of characteristics: head with sharply defined, crescent-shaped frontal grooves, oblique, and widely separated. Pronotum with complete lateral grooves between the lateral and basal setae; prosternal process shallow and broadly impressed or obsolete; internal sac everts apicodorsally and to the left. Specimens of *morio* and *laevipennis* can be confused. However, they are distinguished by a number of differences in structures that are described in the recognition section of *morio*.

Description. – Body length 7.1 – 9.0 mm. Form relatively slender for the *morio* group. Microsculpture of head between eyes, disc of pronotum, and intervals of elytra, comprised of generally effaced sinuous lines.

Head glossy; frontal grooves sharply defined, crescent-shaped with convexity directed laterally, oblique and widely separated. Penultimate article of labial palpus with two medial setae.

Pronotum glossy; form subcordiform or cordiform in outline as in figs. 3 and 4; disc moderately convex; sides produced, constricted slightly anteriorly and strongly posteriorly, obsoletely sinuate in front of posterior angles when posterior angles obsolete (fig. 3) , distinctly sinuate when angles distinct (fig. 4); posterior angles obsolete and broadly rounded or produced and acute; anterior transverse impression complete or absent medially; basal lateral foveae deep and short. Prosternal process with shallow and broadly excavated or obsolete longitudinal groove. First articles of middle and hind tarsi with lateral grooves.

Elytra glossy, obsoletely sinuate apically; intervals completely flat or slightly raised and slightly convex; striae obsolete and impunctate or distinctly impressed and punctate, 6 and 7 always obsolete and impunctate.

Male genitalia (fig. 83) with median lobe strongly arcuate, angle slightly obtuse; apical blade slightly tapered and evenly rounded at apex. Right paramere narrow apically and extending to apical half of median lobe. Eversion of internal sac dorsoapically and when everted, dorsoapically and to left; apical sclerite absent; dark serrulate field apically. The genitalia of four males were studied.

Stylus of female ovipositor short, tapered apically and slightly sinuate preapically.

Geographical variation. – Individuals from southern localities are characterized by obsolete basal angles of the pronotum, distinctly impressed and complete anterior transverse impression of the pronotum (fig. 3), and elytra with completely flat intervals and obsolete striae. In central areas of the species range populations are composed of some individuals with the above characters, and some with more distinct basal angles of the pronotum, an incomplete anterior transverse impression, and more or less raised intervals and impressed punctate striae of the elytra. Specimens of northern localities have produced, sharp angles of the pronotum, an incomplete anterior transverse impression (fig. 4), and elytra with somewhat raised intervals and distinctly impressed and punctate striae. Because of the apparent clinal nature of the changes in these structures, I believe northern and southern populations, although distinct, do not merit subspecific status.

Notes on synonymy. – LeConte was not aware of the geographic variation in *laevipennis.* In 1848 he proposed the name *laevipennis* for the northern form, and in 1852, he recognized the southern form as a separate species to which he gave the name *acutus.*

Casey provided the names *nanula*, *simiola*, *castigata*, and *bullata*, the types of which are of the average form of *laevipennis* found in Mobile, Alabama.

Collecting notes. – D. Larson and I collected specimens of *laevipennis* near Grey, Georgia, in deciduous forest in leaf litter.

Geographical distribution (fig. 125). – This species inhabits the Gulf Coastal Plain and southern Piedmont. I have seen 343 specimens from the following localities.

United States – ALABAMA: Baldwin County: (UASM). Barbour County: Eufaula (USNM), Clark County: Salt Mountain, six miles south of Jackson (UMMZ). Colbert County: Tuscumbia Mountains, southwest of Tuscumbia (UMMZ). Elmore County: Wetumpka (USNM). Houston County: Chatahoochee State Park (GEB). Lee County: Auburn (CAS, KSU, VMK), Madison County: Monte Sano State Park (CAS), Mobile County: Alabama Port (GEB); Citronelle (CAS); Grand Bay (AMNH); Mobile (AMNH, CAS, CNC, CU, MCZ, UASM, USNM); Mount Vernon (CU). Randolph County: Wadley (USNM). Tallapoosa County: Alexander City (KSU). County not determined: Dog River (UK); FLORIDA: Jefferson County: Monticello (UMMZ). Liberty County: Camp Torreya (CU, UMMZ); Torreya State Park (FDPI). GEORGIA: Cobb County: Austell (CAS). Hall County: White Sulfur Springs (UMMZ). Jones County: seven miles south of Gray (RF). Rabun County: (USNM); Clayton (USNM); Pinnacle Park (USNM). MISSISSIPPI: George County: Lucedale (CU). Greene County: Leaf (CU). Jackson County: Ocean Springs (CU). Lamar County: Lumberton (CU). Perry County: New Augusta (CU); Richton (CU). Stone County: Wiggins (CU). SOUTH CAROLINA: Greenville County: Greenville (USNM); 17 miles west of Spartenburg (DL). Oconee County: CCC Camp f2 (CAS); Clemson (GEB); Clemson College (CAS, USNM). Pickens County: Nine Times (RCG).

The *obsoletus* Group

Characteristics. – Penultimate article of labial palpus with two medial setae. Pronotum cordiform in outline; basal lateral foveae completely punctiform with no anterior extensions; basal seta situated in front of the basal angle. Prosternal process with obsolete medial longitudinal groove. Claw-bearing tarsal article usually with setae on lateroventral margins. Right paramere of male genitalia elongate.

This group is generally distributed north of the *morio* group in regions of the Piedmont flanking the Appalachian Mountains (fig. 126).

Evarthrus approximatus LeConte, 1848

Figures 5, 84, 126

Broscus (Cephalotes) approximatus LeConte, 1848:354. LECTOTYPE (here selected) a female, labelled as follows: "pink disc; Type 5628; E. approximatus Lec." MCZ. TYPE LOCALITY, Pennsylvania. – LeConte, 1852:231 (*Evarthrus*). – LeConte, 1863a:8. – LeConte, 1873:319. – Schaupp, 1880:49. – Leng, 1920:57 (*Ferestria*). – Csiki, 1930: 674 (*Pterostichus*). – Brimley, 1938:120 (*Ferestria*).

Recognition. – This species is characterized by the combination of a complete anterior transverse impression of the pronotum, male genitalia, and geographical range restricted to areas east of the Appalachian Mountains. Specimens of *approximatus* are distinguished from those of *obsoletus* by the less arcuate median lobe of the male genitalia. These very similar species are allopatric in relation to one another.

The species *iuvenis* resembles *approximatus* but is distinguished by an incomplete anterior transverse impression of the pronotum.

Description. – Body length 8.4 – 10.9 mm. Form average for *obsoletus* group.

Microsculpture of head between eyes and disc of pronotum completely effaced. Microsculpture at intervals of elytra effaced or consisting of indistinct isodiametric meshes. Micropunctures present on head and pronotum.

Head glossy; frontal grooves sharply defined, crescent-shaped with convexity directed laterally, oblique and widely separated.

Pronotum glossy; cordiform in outline as in fig. 5, disc moderately convex; sides produced, constricted slightly anteriorly and strongly posteriorly, obsoletely sinuate in front of posterior angles; posterior angles obsolete; anterior transverse impression complete. Lateroventral margin of last article of tarsus with setae.

Elytra glossy; obsoletely sinuate apically; intervals slightly raised and slightly convex; striae clearly impressed and indistinctly punctate.

Male genitalia (fig. 84) with median lobe strongly arcuate, angle approximately right, apical half deflected to right; apical blade evenly rounded at apex and slightly deflected dorsally. Right paramere tapered apically, long, extending to apical half of median lobe. Eversion of internal sac apical and to left; apical sclerite absent, serrulate fields present apically. The genitalia of three males were studied in detail.

Stylus of female ovipositor tapered apically and sinuate preapically.

Geographical distribution (fig. 126). – This species is found in North Carolina, Virginia and Washington, D. C. According to LeConte, it also occurs in Pennsylvania, but I have not been able to verify this record. I have seen 41 specimens collected in the following localities.

United States – DISTRICT OF COLUMBIA: Washington (ANSP, CAS, MCZ, UK, USNM). NORTH CAROLINA: Guilford County: High Point (USNM). Arlington County: Rosslyn (UASM, USNM). Fairfax County: (USNM); Blackpond (USNM): Herndow (USNM). Giles County: Mountain Lake (UMMZ). Henrico County: Richmond (AMNH).

Evarthrus iuvenis new species

Figures 6, 85, 126

Recognition. – The internal sac of the median lobe of *iuvenis* everts to the left and curls ventrally on the left side of the median lobe. This feature alone sets *iuvenis* apart from the similar *obsoletus*. Also *obsoletus* inhabits areas west of the Appalachian Mountains, while *iuvenis* occurs east of that mountain range. Another diagnostic characteristic of *iuvenis* is the shape of the median lobe of the male (fig. 85).

Description. – HOLOTYPE, male, labelled as follows: "24 miles north of Roanoke, Virginia Blue Ridge Parkway 21 October 1962 leg. D. R. Whitehead; HOLOTYPE Evarthrus iuvenis R. Freitag (red label)." MCZ.

Body length 10.3 mm; width 4.1 mm. Form robust. Microsculpture effaced on head between eyes and disc of pronotum. Isodiametric meshes on intervals of elytra.

Head glossy; length 1.2 mm; width 2.5 mm; frontal grooves sharply defined, crescent-shaped with convexity directed laterally, oblique toward one another, and widely separated.

Pronotum glossy; length 2.8 mm, width 3.4 mm; form cordiform in outline as in fig. 6; disc moderately convex; sides produced, constricted slightly anteriorly, strongly posteriorly, obsoletely sinuate in front of posterior angles; posterior angles obsolete; anterior transverse impression absent medially. First articles of middle and hind tarsi with lateral grooves; lateroventral margins of claw-bearing article of tarsus with setae.

Elytra glossy; length 6.2 mm, width 4.1 mm; slightly sinuate apically; intervals slightly convex; striae clearly impressed and indistinctly punctate.

Male genitalia (fig. 85) with median lobe slightly arcuate; apical blade narrow and evenly rounded at apex, deflected dorsally and to right; right paramere with markedly tapered apical half, extending to apical half of median lobe; eversion of internal sac to left and in everted position curled ventrally around median lobe on left side; apical sclerite absent, serrulate fields present apically.

ALLOTYPE, female labelled as follows: "Raleigh, N. C., April 14'49 H. F. Howden; under board; near 1043 (yellow label) loan from CNC; ALLOTYPE Evarthrus iuvenis. R. Freitag". CNC.

Body length 11.1 mm; width 4.8 mm. Form same as in holotype.

Microsculpture of head between eyes and disc of pronotum consists of partially entwined lines. Intervals of elytra with isodiametric microsculpture.

Head slightly glossy; length 1.4 mm, width 3 mm.

Pronotum, form same as in holotype; length 3 mm; width 3.8 mm.

Elytra slightly glossy; intervals flat; striae distinctly impressed and clearly punctate; length 6.7 mm; width 4.8 mm.

Stylus of ovipositor short and tapered apically, slightly sinuate preapically.

Variation among paratypes (six males, seven females, North Carolina, Virginia). – Total length 9.8 – 12.8 mm. The basal angles of the pronotum are slightly produced and sharp in six specimens. The last tarsal article may or may not have setae on the ventral side. The apical blade of three males is half the width of that of the holotype, while that of the other three is approximately the same width as that of the holotype. In other respects the paratypes resemble the holotype and allotype.

Derivation of specific name. – The word *iuvenis* is a Latin noun, meaning warrior. I have given the name to this species because its members seem warrior-like, robust and large in size for the subgenus *Fortax*.

Disposition of type material. – The holotype is in the MCZ. The allotype was returned to the CNC. The paratypes are deposited in the collection of CAS, DRW, RCG, RTB, UASM, UMMZ, and USNM.

Collecting notes. – This species is found in leaf litter in forested places.

Geographical distribution (fig. 126). – *Evarthrus iuvenis* is known from western Virginia and North Carolina. I have seen eight specimens from the following localities.

United States – NORTH CAROLINA: Stokes County: Hanging Rock State Park (RTB). Wake County: Raleigh (CNC). VIRGINIA: Bland County: Summit of Walker Mountain (UMMZ). Campbell County: (USNM). Floyd County: (UASM); Buffalo Mountain, five miles southeast of Willis (DRW). Rocky Knob Recreation Area, Blue Ridge National Parkway (RCG). Giles County: Cascades (TCB); Mountain Lake (RTB). Nelson County: (USNM). Roanoke County: Blue Ridge Parkway, 24 miles north of Roanoke (MCZ).

Evarthrus obsoletus Say, 1823

Figures 7, 86, 126

Feronia obsoleta Say, 1823a:57. Type lost. Type Locality – Indiana (here selected). – Say, 1834:424 (*Feronia*). – LeConte, 1848:354 (*Broscus*). – LeConte, 1852:231 (*Evarthrus*). – LeConte, 1863a:8. – LeConte, 1873:319. – Schaupp, 1880:49. – Blatchley, 1910:91 (*Pterostichus*). – Casey, 1918:364 (*Ferestria*). – Casey, 1920:193. – Leng 1920:57. – Csiki, 1930:674 (*Pterostichus*). – Löding, 1945:16 (*Ferestria*).

Recognition. – The shape of the median lobe of the male is markedly arcuate, and differs strongly from that of *approximatus* and *iuvenis* (fig. 86 cf. figs. 84 and 85). The species *obsoletus* alone in this group occurs to the west and south of the Appalachian Mountains.

Description. – Body length 7.9 – 9.9 mm. Form average for *obsoletus* group.

Microsculpture of head between eyes of obsolete sinuous impressions or completely effaced. Microsculpture of disc of pronotum and intervals of elytra completely effaced.

Head glossy; frontal grooves sharply defined, slightly curved, with convexity directed laterally, oblique toward one another and widely separated.

Pronotum glossy, cordiform in outline, as in fig. 7; disc moderately convex; sides produced, constricted slightly anteriorly and strongly posteriorly; posterior angles obsolete; anterior transverse impression incomplete, impressed laterally only. First articles of middle and hind tarsi with lateral grooves; last article of tarsus with setae on lateroventral margin.

Elytra glossy; obsoletely sinuate apically; medial intervals highly convex, lateral intervals flatter; striae deeply impressed, indistinctly punctate.

Male genitalia (fig. 86) with median lobe strongly arcuate, angle slightly obtuse; apical blade deflected to right, left edge deflected dorsally, evenly rounded at apex. Right paramere tapered apically, long, extended apically well beyond halfway point of median lobe. Eversion of internal sac apical and to left; apical sclerite absent; serrulate fields present apically. The genitalia of three males were examined.

Stylus of female ovipositor pointed at apex, tapered apically.

Notes on synonymy. – Say (1834) wrote that this species occurred in Indiana. For this reason I have selected Indiana as Type area. This species was identified by the original description.

Collecting notes. – This species is found in deciduous forests in damp leaf litter.

Geographical distribution (fig. 126). – This species ranges from southern Alabama north to Michigan west of the Appalachian Mountains. I have seen a total of 131 specimens.

United States – ALABAMA: Bibb County: The Sinks (UMMZ). Cherokee County: Leesburg (UMMZ). Colbert County: (USNM); Barton (CAS). Fayette County: Berry (GEB). Jackson County: Paint Rock (UMMZ). Madison County: Monte Sano State Park (CAS, CNHM, UASM). Mobile County: Mobile (CAS). Monroe County: Claiborne (UMMZ). Randolph County: Wadley (USNM). St. Clair County: Blount Mountains (GEB). Talladega County: Talladega (UMMZ). Tuscaloosa County: Hurricane Creek, near Peterson (GEB). Hurricane Creek, seven miles north of Tuscaloosa (RF); Lock 14 (CAS); Tuscaloosa (GEB); University (UMMZ). County not determined: National Forest (CAS, USNM); Tumblin Gap (USNM). GEORGIA: Cherokee County: Galt's Lodge (TCB). Fulton County: Silver Lake (USNM). Morgan County: four miles north of Madison (DL, RF); Madison (UMMZ). ILLINOIS: Cook County: Palos Park (UMMZ). Vermilion County: Camp Robert Drake, near Fairmount (RTB). Washington County: Dubois (UMMZ). INDIANA: Crawford County: (CNHM). Fulton County: (CAS). Monroe County: Bloomington (UMMZ). KENTUCKY: Fleming County: Blue Briar Springs (GEB). MICHIGAN: Washtenaw County: Cady's Woods, Ann Arbor (UMMZ). MISSISSIPPI: Lauderdale County: Meridian (UMMZ). Pontotoc County: Pontotoc (UMMZ). NORTH CAROLINA: Cherokee County: Murphy (CAS). OHIO: (CAS). TENNESSEE: Blount County: Chilhowee Mountains (CNC); Great Smoky Mountains National Park (CNC). Cumberland County: Grassy Cove (CAS). Hamilton County: Chattanooga (UMMZ). Lauderdale County: South Fulton (UMMZ). Morgan County: Burrville (UMMZ); Deer Lodge (USNM); Environs (CNHM). Obion County: Obion (UMMZ). Sevier County: Elkmont (USNM). County not determined: Cades Cove, Blounto (MCZ); Cedar Glade Area (USNM); Cove Mountain Trail (TCB).

The Subgenus *Cyclotrachelus* Chaudoir

Cyclotrachelus Chaudoir, 1838:27. Casey, 1918:348. – Van Dyke 1943:27. – Ball 1960: 129. TYPE SPECIES – *Molops faber* Germar, 1824 (here designated).

Evarthrus roticollis Casey (designated type species by Casey, 1918:348).

Characteristics. – The subgenus *Cyclotrachelus* is distinguished from the other subgenera of *Evarthrus* by the following combination of characteristics: pronotum with sides strongly constricted posteriorly, posterior lateral foveae monostriate, posterior lateral setae situated on bead (figs. 8–10), anterior transverse impression incomplete and impressed laterally only; middle femur with four setae on anterior face except for that of the species *unicolor* which has up to seven; eversion of internal sac of median lobe of male genitalia dorsoapical, internal sac not curled ventrally in everted position; right paramere of male genitalia without "elbow" at bend, and only slightly tapered apically. The styli of female ovipositor short and broad, in a few species sinuate preapically and tapered apically. With the exception of the right paramere all the above characteristics are present in each species of this subgenus. The species *levifaber* has an elbow in the right paramere.

The three species groups in *Cyclotrachelus* are: the *spoliatus* group, the *ovulum* group, and the *faber* group.

Notes on synonymy. – Casey's designation of *E. roticollis* Casey as type species was incorrect because this name was not included with the original description of *Cyclotrachelus*.

The *spoliatus* Group

Characteristics. – Pronotum almost circular in dorsal aspect and basal angles broadly obtuse; longitudinal groove of the prosternal process usually shallow, but if deep not sharply defined; internal sac of the median lobe of the male genitalia without apical sclerite, with serrulate fields apically.

This group includes the following species: *unicolor, fucatus, spoliatus,* and *brevoorti.* Members of these species inhabit the Coastal Plain and Piedmont regions of southeastern United States.

Evarthrus unicolor Say, 1823

Figures 8, 63, 67, 87, 127

Feronia unicolor Say, 1823a:40. Type lost. TYPE LOCALITY, Georgia (here selected). – LeConte, 1848:352 (*Feronia*). – LeConte, 1852:230 (*Evarthrus*). – LeConte, 1863a:8. – LeConte, 1873:319. – Schaupp, 1880:49. – Casey, 1918:349 (*Cyclotrachelus*). – Leng, 1920:56. – Csiki, 1930:672 (*Pterostichus*). – Löding, 1945:15 (*Cyclotrachelus*).

Recognition. – The large body size, four to six setae on the penultimate article of the labial palpus (fig. 67), raised knobs flanking the anterior end of the gula, and dark apical serrate field in the internal sac of the median lobe of the male genitalia, combined, distinguish specimens of *unicolor* from those of the similar species *fucatus*, *spoliatus* and *brevoorti.* The species *fucatus* is further distinguished by frontal grooves of the head that are oblique to one another and a subcordiform glossy pronotum. All specimens of *brevoorti* are smaller than those of *unicolor.* The species *spoliatus* and *unicolor* are allopatric, and can also be distinguished by structural features of the male genitalia (fig. 87 cf. fig. 89).

Description. – Body length 17.7 – 22.0 mm. Form parallel and elongate.

Microsculpture of head between eyes, pronotal disc, and elytral intervals with lines distinctly impressed, highly sinuous and entwined, often forming isodiametric or amorphic meshes.

Head dull or slightly glossy; frontal grooves deeply impressed, straight, and parallel to one another. Penultimate article of labial palpus with four to six setae. Anterior end of gula flanked by raised knobs (fig. 63).

Pronotum dull or slightly glossy; form as in fig. 8; disc moderately convex; sides slightly constricted anteriorly, strongly constricted posteriorly, and moderately sinuate in front of posterior angles; posterior angles right or slightly obtuse and produced; anterior transverse impression incomplete; basal foveae of average length and moderately impressed. Longitudinal groove in prosternal process shallow or deep. Anterior face of middle femur with four to seven setae.

Elytra dull or slightly glossy, sinuate apically; intervals usually flat, occasionally slightly raised; striae shallowly impressed, small punctures confined to anterior two-thirds, impunctate posteriorly.

Male genitalia (fig. 87) with median lobe strongly arcuate, angle approximately right; apical blade produced, of average width to relatively broad, apex evenly rounded: right paramere typical *Cyclotrachelus* form, not reaching apical half of median lobe; eversion of internal sac apicodorsal and to the right; internal sac with a dark serrate field apically, apical sclerite absent. The male genitalia of three specimens were examined in detail.

Stylus of female ovipositor short, broad, and evenly rounded at tip.

Notes on synonymy. – This species was identified by the original description, and by an examination of the LeConte *unicolor* specimen in the LeConte Collection. I have selected Georgia as type locality because many *unicolor* specimens which I have seen are from Georgia.

Geographical distribution (fig. 127). – This species inhabits the Gulf Coastal Plain and southern Piedmont. I have seen 18 specimens from the following localities.

United States – ALABAMA: Cherokee County: Leesburg (UMMZ). Lee County: Auburn (AU, UMMZ). FLORIDA: Jackson County: (FDPI). GEORGIA: Dodge County: Chester (CAS, CU). Dooley County: Umadilla (UMMZ), Morgan County: Madison (UMMZ). Upson County: (MCZ, USNM).

Evarthrus fucatus new species

Figures 9, 88, 127

Recognition. – The following three characters combined are diagnostic for the species *fucatus*: subcordiform pronotum; highly glossy dorsum, and form of male genitalia. Although there are striking similarities among *fucatus*, *spoliatus*, and *brevoorti* they differ in the following respects.

The species *fucatus* and *spoliatus* are allopatric. Specimens of *fucatus* have a subcordiform pronotum, and sometimes three setae on the penultimate article of the labial palpus, while *spoliatus* specimens have a more circular pronotum and always two setae on the penultimate article of the labial palpus. In addition the frontal grooves of the head are oblique in *fucatus* and parallel in *spoliatus*.

There is some overlap in the distributions of *fucatus* and *brevoorti*. Specimens of *fucatus* normally have a more cordiform pronotum. However the most distinguishing character is the male genitalia. The apex of the median lobe of *fucatus* is evenly rounded, but is truncate in *brevoorti*.

Description. – HOLOTYPE, male, labelled as follows: "Cherokee Co., Ala. Leesburg VII – 25 – 1929 54. T. H. Hubbell; loan from UMMZ; HOLOTYPE Evarthrus fucatus R. Freitag (red label)." UMMZ.

Body length 14.1 mm; width 5.7 mm. Form typical of this group, with robust pronotum.

Microsculpture of head between eyes, disc of pronotum, and elytral intervals, with highly sinuous dense and closely entwined lines, often forming amorphic meshes.

Head glossy; length 1.7 mm, width 3.4 mm; frontal grooves straight, deep and sharply defined, oblique and widely separated; penultimate article of labial palpus with three setae, two medial and one apical.

Pronotum with disc glossy; length 3.9 mm, width 4.6 mm; subcordiform (fig. 9); disc moderately convex; sides slightly constricted anteriorly and markedly constricted posteriorly, obsoletely sinuate in front of posterior angles; posterior angles not produced and broadly obtuse; anterior transverse impression absent medially; median longitudinal impression slightly deeper at either end; basal foveae deepest at bend, of average length. Longitudinal groove of prosternal process broad, indistinct and very shallowly impressed. Anterior face of middle femur with four setae.

Elytra glossy; length 8.5 mm, width 5.7 mm; obsoletely sinuate apically; intervals moderately raised but slightly flattened; striae deep with indistinct punctures in apical half, punctures obsolete in apical third.

Male genitalia (fig. 88) with median lobe strongly arcuate, angle slightly acute; apical blade moderately produced, slightly tapered apically, and evenly rounded; right paramere typical *Cyclotrachelus* form and of average length reaching apical half of median lobe, eversion of internal sac apicodorsal and slightly to right; internal sac with apical serrulate field; apical sclerite absent.

ALLOTYPE, female, labelled as follows: "Monte Sano State Park, ALABAMA 7-VI-1960 B. Benesh; CNHM 1965 Bernard Benesh General Coleop. Coll.; ALLOTYPE Evarthrus fucatus R. Freitag". CNHM.

Body length 14.3 mm, width 8.9 mm. Form same as in holotype.

Microsculpture of head between eyes and disc of pronotum same as in holotype. Elytra with microsculpture mainly composed of amorphic or isodiametric raised meshes that appear beady.

Head glossy; length 1.7 mm, width 3.2 mm.

Pronotum, shape, same as in holotype; length 3.7 mm, width 4.7 mm.

Elytra not highly glossy; intervals slightly convex, almost flat; striae deep and obsoletely punctate anteriorly, impunctate posteriorly; length 8.9 mm, width 5.7 mm.

Stylus of ovipositor obsoletely sinuate preapically and tapered apically.

Derivation of specific name. – The name *fucatus* is a Latin adjective which means deceitful and has been given this species because of the remarkable similarity of its members to those of *spoliatus.*

Variation among paratypes (19 males, 13 females, Georgia, Alabama, Tennessee, West Virginia, Pennsylvania, Ohio, CM, CNHM, UASM, UMMZ, USNM). – Total length 12.0 – 14.6 mm. The penultimate article of the labial palpus bears two or three setae. A minimal amount of variation is evident in coloration and structural features among the paratypes which resemble closely the holotype and allotype. The male genitalia of five specimens were examined in detail.

Disposition of type material. – The holotype and allotype are in the collections of the UMMZ and CNHM, respectively. The paratypes are in the collections of the following institutions: CM, CNHM, UASM, UMMZ, and USNM.

Collecting notes. – Specimens of *fucatus* have been collected in deciduous forest in leaf litter.

Geographical distribution (fig. 127). – This species inhabits the Piedmont on the western and southern sides of the Appalachian Mountains. I have seen 41 specimens collected in the following localities.

United States – ALABAMA: Cherokee County: Leesburg (UMMZ). Madison County: Huntsville (UMMZ); Monte Sano State Park (CNHM, UASM). GEORGIA: Floyd County: Armuchee (UMMZ). KENTUCKY: Edmonson County: near Hist. Ent. (TCB); Mammoth Cave (TCB). OHIO: Hamilton County: Cincinnati (UMMZ). PENNSYLVANIA: Allegheny County: Pittsburg (CM). Westmoreland County: Jeanette (CM). TENNESSEE: Cumberland County: Grassy Cove (UMMZ). Hamilton County: Signal Mountain (UMMZ). Montgomery County: Clarksville (USNM). Morgan County: Burrville (CNHM). WEST VIRGINIA: Marion County: Fairmount (CM).

Evarthrus spoliatus Newman, 1838

Figures 10, 89, 127

Feronia spoliata Newman, 1838:386. TYPE, male, labelled as follows: "Type H. T.; Ent. Club. 44–12; J. Ingall, Canada." BM. TYPE LOCALITY, Southern Pines, N. C. (here selected).

Evarthrus rotundatus LeConte, 1852:230. LECTOTYPE (here selected) a female, labelled as follows: "Va; rotundatus 2". MCZ. NEW SYNONYMY. – LeConte, 1863a:8 (*Evarthrus*). – LeConte, 1873:319. – Schaupp, 1880:49. – Casey, 1918:349 (*Cyclotrachelus*). – Leng, 1920:56. – Csiki, 1930:671 (*Pterostichus*). – Brimley, 1938:119 (*Cyclotrachelus*). – Löding, 1945:14.

Evarthrinus (Evarthrops) pinorum Casey, 1920:198. HOLOTYPE, male, labelled as follows: "Southern Pines, A. H. Manee. NC.; CASEY bequest 1925; TYPE USNM 47135; pinorum Csy". USNM. TYPE LOCALITY, Southern Pines, N. Carolina. NEW SYNONYMY. – Leng and Mutchler, 1927:10 (*Evarthrinus*). – Csiki, 1930:673 (*Pterostichus*). – Brimley, 1938:119 (*Evarthrinus*).

Recognition. – The combination of geographical distribution, generally parallel frontal grooves on the head, and form of the median lobe of the male genitalia is characteristic of *spoliatus*. The differences among *spoliatus*, *fucatus* and *unicolor* have been discussed in connection with the recognition of the last two species. The remaining species in this group, *brevoorti*, can also be mistaken for *spoliatus*. The frontal grooves of the head are parallel in *spoliatus* and oblique in *brevoorti*, and the apex of the median lobe is rounded in *spoliatus*, truncate in *brevoorti*.

Description. – Body length 12.8 – 15.8 mm. Form elongate.

Head between eyes, disc of pronotum, and elytral intervals, with lines of microsculpture dense, highly sinuous, entwined, forming amorphic raised meshes.

Head moderately or slightly glossy. Frontal grooves broadly but deeply impressed, normally with a slight bend the convexity of which is directed medially. Penultimate article of labial palpus with two setae.

Pronotum with slightly glossy disc; form as in fig. 10; disc moderately convex; sides moderately constricted anteriorly, more strongly so posteriorly, and distinctly sinuate in front of posterior angles; posterior angles slightly to broadly obtuse, and slightly produced; basal foveae moderately impressed. Longitudinal groove in prosternal process shallow. Middle femora each with four setae on anterior face; occasionally four setae on one middle femur and five or six on opposite one.

Elytra dull or slightly glossy; slightly sinuate apically; intervals slightly raised and flat; striae shallow or moderately impressed with small punctures anteriorly, impunctate posteriorly.

Male genitalia (fig. 89) with arcuate median lobe, apical half deflected to right; apical blade slightly tapered apically and apex evenly rounded; right paramere short and rather stout; internal sac with serrulate field apically, apical sclerite absent. Elongate, left lateral sclerotized flap of median lobe near opening of invaginated internal sac extending onto basal half of sac when everted; eversion of internal sac apicodorsal and to right. The genitalia of four males were studied in detail.

Stylus of female ovipositor tapered apically and slightly sinuate behind apex.

Notes on synonymy. – I have selected Southern Pines as the type locality because *spoliatus* specimens have been collected there. Also, it is centrally located in the species range. The name Canada on the label of the type specimen indicates the country of the collector, J. Ingall. The type specimens of *rotundatus* LeConte and *pinorum* Casey are average specimens of *spoliatus*.

Collecting notes. – V. M. Kirk collected specimens of *spoliatus* in litter on the ground in deciduous forest.

Geographical distribution (fig. 127). – This species is found on the Piedmont and Coastal Plain west of the Appalachian Mountains from District of Columbia south to South Carolina. I have seen 61 specimens from the following localities.

United States – DISTRICT OF COLUMBIA: Rock Creek (USNM, CNHM). NORTH CAROLINA: Duplin County: Faison (CNC). Durham County: Durham (USNM). Franklin County: Louisburg (CNC) Moore County: Pinehurst (MCZ): Southern Pines (USNM). New Hanover County: Wilmington (USNM). Orange County: Chapel Hill (CAS, CU). Union County: (GEB). Wake County: Raleigh (CNC). SOUTH CAROLINA: Bamberg County: Bamberg (VMK). Darlington County: Darlington (UMMZ). Florence County: Florence (GEB, VMK); Scranton (UMMZ); Three miles east of Florence (GEB). Sumter County: Sumter (GEB). VIRGINIA: County not determined: Virginia (CAS).

Evarthrus brevoorti LeConte, 1848

Figures 11–13, 90–91, 127

Feronia (Pterostichus) brevoorti LeConte, 1848:352. LECTOTYPE (here selected) a male, labelled as follows: "orange disc: Type 5625; E. spoliatus (Newm). Brevoorti Lec." MCZ. TYPE LOCALITY, Alabama. – LeConte, 1852:230 (*Evarthrus*). – LeConte, 1863a:8. – LeConte, 1873:319. – Schaupp, 1880:49. – Leng, 1920:57. – Csiki, 1930:671 (*Pterostichus).*

Evarthrus spoliatus; LeConte, 1873:319 (not Newman). – Schaupp, 1880:49. – Csiki, 1930:671.

Recognition. – The most distinctive feature of this species is the truncate apex of the median lobe of the male. Additional characteristics of this species have been mentioned above in connection with recognition of *unicolor*, *spoliatus*, and *fucatus*.

Description. – Body length 10.4 – 16.3 mm. Form typical of the *spoliatus* group. Head between eyes, disc of pronotum, and elytral intervals, with lines of microsculpture highly sinuous, entwined and usually forming amorphic meshes.

Head slightly or markedly glossy. Frontal grooves sharply defined, straight, slightly oblique. Penultimate article of labial palpus with two to four setae.

Pronotum with disc slightly or markedly glossy; form as in figs. 11–13; disc moderately convex; sides produced medially, constricted posteriorly slightly or moderately sinuate in front of posterior angles; posterior angles slightly produced, broadly obtuse; basal foveae moderately impressed. Longitudinal groove in prosternal process shallow and poorly defined or obsolete. Front face of middle femur with four setae.

Elytra slightly glossy and usually iridescent; slightly sinuate apically; intervals raised and weakly convex; striae deep, distinctly punctate anteriorly, obsoletely punctate or impunctate posteriorly.

Male genitalia (figs. 90–91) with median lobe arcuate, angle slightly obtuse, and apical half slightly deflected to right, apex truncate and often with a short, right, lateral spine; right paramere broad and reaching apical half of median lobe; internal sac with dark serrulate fields basally and very light, highly folded, serrulate fields apically; apical sclerite absent. Eversion of internal sac apicodorsal. The genitalia of nine males were studied in detail.

Stylus of female ovipositor sinuate preapically and tapered apically.

Geographical variation. – Individuals from coastal populations are generally somewhat larger in body size and slightly duller than those of inland areas. In some males the median lobe has a short spine jutting out of the right side of the apical blade (fig. 91). The pronotum varies slightly in form, but there is no geographical pattern to the variation.

Collecting notes. – Specimens of *brevoorti* are found in forested areas. H. V. Weems, Jr. collected a specimen in leaf mold on a bank of a stream in Florida. They are also found in rotting logs.

Geographical distribution (fig. 127). – This species is found on the Gulf Coastal Plain and southern Piedmont. I have seen 92 specimens from the following localities.

United States – ALABAMA: Clarke County: Salt Mountain, six miles south Jackson (UMMZ). DeKalb County: Mentone (GEB). Lee County: Auburn (AU). Mobile County: Alabama Port (GEB); Calvert (CAS, NCSU); Mobile (CAS, CU, MCZ, UMMZ, USNM). Perry County: Felix (UMMZ). FLORIDA: Liberty County: Camp Torreya (UMMZ); Torreya State Park (FDPI). GEORGIA: Cobb County: Austell (CAS). Floyd County: 2 mi. s. Armuchee (UMMZ). Fulton County: Atlanta (CAS). MISSISSIPPI: Choctaw County: Little Mountain Camp Ground (RCG). George County: Lucedale (CU). Jackson County: Ocean Springs (CU); Pascagoula (CU). Oktibbeha County: State College (CAS). Wayne County: Waynesboro (UMMZ). County not determined: Oneca Springs (CU). SOUTH CAROLINA: Oconee County: Clemson (CAS, GEB); Clemson College (AMNH, USNM). Pickens County: Kedwee River (RCG). Saluda County: Saluda (UMMZ).

The *ovulum* Group

Characteristics. – Small to medium size beetles; pronotum cordate with basal angles produced, relatively sharp and slightly obtuse; apical sclerite present in internal sac of median lobe.

This group includes the following species: *macrovulum, texensis*, *ovulum*, *alabamensis* and *vinctus*.

The group occurs on the Coastal Plain, except for the species *vinctus*, which lives in the higher altitudes of northern Georgia and western North Carolina, and in the Great Smoky Mountains.

Evarthrus vinctus LeConte, 1852

Figures 14, 92, 128

Evarthrus vinctus LeConte, 1852:232. LECTOTYPE (here selected) a female, labelled as follows: "orange disc; Type 5623; E. vinctus Lec." MCZ. TYPE LOCALITY, Nakutshi Valley, Habersham Co., Georgia. – LeConte, 1863a:8 (*Evarthrus*). – LeConte, 1873:319. – Schaupp, 1880:49. – Casey, 1918:350 (*Cyclotrachelus*). – Leng, 1920:57. – Csiki, 1930:672 (*Pterostichus*).

Recognition. – The following characters of this species combined are diagnostic: sharply defined and oblique frontal grooves of the head; elongate and deeply impressed basal foveae of the pronotum; very shallow longitudinal groove in the prosternal process; very convex and iridescent intervals of the elytra in the males; obsoletely punctate or impunctate elytral striae; and male genitalia (fig. 92).

Specimens of *vinctus* and those of its congeners in the *ovulum* group are similar in appearance. The impunctate or obsoletely punctate elytral striae are characteristics of *vinctus* and distinguish specimens of this species from those of *alabamensis, macrovulum, texensis* and *ovulum.*

Description. – Body length 8.5 – 11.1 mm. Form typical of this group.

Microsculpture on head between eyes with slightly sinuous, entwined lines, and raised amorphic meshes. Disc of pronotum with microsculpture same as that on head but occasionally partially effaced. Microsculpture of elytral intervals same as that on head only more stretched transversely and slightly effaced.

Head slightly or markedly glossy. Frontal grooves deep, sharply defined and oblique. Penultimate article of labial palpus with two or three medial setae.

Pronotum slightly or markedly glossy; form cordiform as in fig. 14; disc slightly convex; sides slightly constricted anteriorly and strongly constricted posteriorly, very broadly sinuate in front of posterior angles; posterior angles prominent, slightly obtuse; anterior transverse impression incomplete, very rarely complete, impressed laterally only; basal foveae elongate, sharply impressed throughout, deep posteriorly, crescent-shaped with convexity directed medially. Prosternal groove distinct or obsolete, but always very shallow. Four setae on front face of middle femur.

Elytra highly glossy and slightly iridescent in males, slightly glossy and slightly iridescent in a few females; intervals moderately to strongly convex in males, slightly convex in females; striae deeply impressed and obsoletely punctate or impunctate.

Male genitalia (fig. 92); angle of median lobe slightly obtuse, apical half deflected to right, apical blade moderately tapered apically and evenly rounded; right paramere of average length extending to apical half of median lobe, shape typical of *Cyclotrachelus*, eversion of internal sac to right and slightly dorsal of median lobe, and a basal bulbous serrulate field directed to left; internal sac with serrulate field basally and apically, preapical sclerite lightly sclerotized, large and hemispherical. The genitalia of two males were studied in detail. Stylus of female ovipositor short with preapical, lateral sinuation, and tapered apically.

Collecting notes. – Members of this species inhabit leaf litter of forests (information obtained from locality label).

Geographical distribution (fig. 128). – This species is found in the high Piedmont of northern Georgia, western South Carolina and eastern Tennessee. I have seen 29 specimens from the following localities.

United States – GEORGIA: Rabun County: Black Rock Mountain (CU); Clayton (AMNH, CAS, CU, MCZ, UMMZ, USNM). Rabun – Towns Co. line, Appalachian Trail, 1-2 mi. s. Dicks Ck. Gap, 3000-4000' (TCB). Towns – White Co. line, Rt. 75-17, Appalachian Trail, Unicoi Gap, 2950' (TCB). NORTH CAROLINA: eight miles northeast of Highlands (RTB). SOUTH CAROLINA: Oconee County: Walhalla (CAS). County not determined: Walnut Creek Gap, Cowee Mountains (RTB). TENNESSEE: Clingman's Dome, Great Smoky Mountains National Park (DRW).

Evarthrus alabamensis Casey, 1920

Figures 15, 70, 93, 128

Evarthrus constrictus Bates, 1882:80 (not Say, 1823b). TYPE, female, labelled as follows: "Type H. T.; Mexico Sallé Coll.; B. C. A. Col. I. 1. Evarthrus constrictus Bates; Evarthrus constrictus Bates." BM. NEW SYNONYMY. – Horn, 1886:9. – Blackwelder and Blackwelder, 1948:2.

Evarthrinus (Evarthrops) alabamensis Casey, 1920:198. HOLOTYPE, male, labelled as follows: "Allen Ala los; CASEY bequest 1925; TYPE USNM 47136; alabamensis Csy." USNM. TYPE LOCALITY, Allen, Alabama. – Leng and Mutchler 1927:10 (*Evarthrinus*). – Csiki, 1930:673 (*Pterostichus*). Löding, 1945:16 (*Evarthrinus*).

Evarthrinus (Evarthrops) lilliputicus Casey, 1920:199. HOLOTYPE, male, labelled as follows: "Mobile Ala. VII–17 H. P. Löding; CASEY bequest 1925; TYPE USNM 47137; lilliputicus Csy." USNM. PARATYPE, female, labelled as follows: "Mobile, Ala. II–5–15. H. P. Löding; CASEY bequest 1925; lilliputicus – 2 PARATYPE USNM 47137." USNM. NEW SYNONYMY. – Leng and Mutchler 1927:10 (*Evarthrinus*). – Csiki, 1930: 673 (*Pterostichus*). – Löding, 1945:16 (*Evarthrinus*).

Pterostichus batesellus Csiki, 1930:671. – Blackwelder and Blackwelder, 1948:1 (*Evarthrus*). New name for *constrictus* Bates, not Say, 1823b.

Recognition. – Specimens of this species are most easily recognized by their glossy pronota and dull elytra. Other diagnostic characters are: distinctly impressed straight frontal grooves (fig. 70); shape of the pronotum (fig. 15); and form of male genitalia (fig. 93).

This species, *macrovulum, texensis* and *ovulum* are separable by a number of characters that are given in the recognition sections of the last three species. However individuals of the species *parafaber* may also be mistaken for those of *alabamensis*. These can be distinguished by several characters. Specimens of *alabamensis* have: a cordiform pronotum with produced basal angles and glossy disc with partially effaced microsculpture; and moderately impressed elytral striae with distinct punctures. In contrast specimens of *parafaber* have: an oval pronotum with more parallel sides, recessed basal angles, and a semi-glossy disc with dense, closed, slightly transversely stretched meshes comprising the microsculpture; and deeply impressed elytral striae with coarse and broad indistinct punctures. In addition the male genitalia are diagnostic (fig. 96).

Description. – Body length 8.8 – 12.6 mm. Form of body typical of *ovulum* group. Head between eyes and disc of pronotum with lines of microsculpture sinuous, entwined and forming open meshes. Microsculpture of elytral intervals with isodiametric, raised and beady meshes in females, flatter in males.

Head glossy; frontal grooves (fig. 70) straight, sharply defined, slightly oblique and moderately separated. Penultimate article of labial palpus with two medial setae.

Pronotum (fig. 15) with disc glossy; sides strongly constricted posteriorly and very broadly sinuate in front of hind angles; posterior angles small, prominent and slightly obtuse; anterior transverse impression only impressed laterally, absent medially; basal foveae moderately impressed. Prosternal process with deep and sharply defined longitudinal groove. Anterior face of middle femur with four setae.

Elytra dull in females, slightly glossy in males; intervals moderately convex in males, distinctly flatter in females; striae moderately impressed in males shallow in females; punctures of striae coarse in males, small and distinct in females, obsolete posteriorly in both sexes. First articles of middle and hind tarsi with lateral grooves.

Median lobe (fig. 93) of male genitalia strongly arcuate, angle almost right; apical blade short, broad, almost truncate; right paramere of average length, just short of reaching apical half of median lobe; eversion of internal sac dorsoapical and slightly to right; apical sclerite of internal sac with two horns – one fairly tapered and one other broad and blunt and more like a serrulate field than a sclerite. The genitalia of three males were studied in detail.

Notes on synonymy. – The type specimen of *lilliputicus* Casey is an average male of *alabamensis*. The name *constrictus* cannot be used because it is a junior homonym of *constrictus* Say.

Geographical distribution (fig. 128). – This species is known only from Mobile County, Alabama. I have seen 87 specimens from the following localities.

United States – ALABAMA: Mobile County: Citronelle (CAS); Grand Bay (USNM); Mobile (CAS, CNC, CU, MCZ, NCSU, USNM); Spring Hill (CAS, USNM).

Evarthrus ovulum Chaudoir, 1868

Figures 16, 71, 94, 128

Feronia (Evarthrus) ovulum Chaudoir, 1868:52. TYPE, female, labelled as follows: "Steropus picipes, Sturm, Georgetown". MNHP. – LeConte, 1873:319 (*Evarthrus*). – Schaupp, 1880:49. – Leng, 1920:57 (*Ferestria*). – Csiki, 1930:674 (*Pterostichus*).

Recognition. – The diagnostic characters are a combination of crescent-shaped frontal grooves; sharp basal angles of the pronotum; deep short groove of the prosternal process; form of the median lobe and sclerite of the internal sac of the male genitalia; and small body size. Specimens of *ovulum* can be confused with specimens of three other small species of *Cyclotrachelus*. This species is most similar to *macrovulum* and *texensis*, but in specimens of the last two species the prosternal process is shallowly grooved. The three are also distinguished by differences in the shape of the median lobe and apical sclerite of the internal sac (fig. 94 cf. fig. 95a–d and 95e–h). In addition these species are allopatric.

The smaller body size, glossy elytra, crescent-shaped frontal grooves and male genitalia distinguish *ovulum* from *alabamensis*. Further, the two species are allopatric.

Description. – Body length 8.5 – 11.0 mm. Form narrow but rather typical of the *ovulum* group.

Head between eyes with microsculpture composed of highly sinuous, entwined or sparse lines. Microsculpture of disc of pronotum same as on head but generally effaced. Elytral intervals with isodiametric meshes, partially effaced in males.

Head between eyes, glossy; frontal grooves (fig. 71) sharply defined, oblique, crescent-shaped with bend produced laterally, widely separated. Penultimate article of labial palpus with two to four setae.

Pronotum (fig. 16) glossy; sides strongly constricted posteriorly and moderately sinuate in front of hind angles; posterior angles small, prominent and slightly obtuse; anterior transverse impression incomplete, impressed laterally only; basal foveae moderately impressed.

Prosternal process with deep and sharply defined longitudinal groove deepest near apex. Anterior face of middle femur with four setae.

Elytra glossy in males and slightly duller in females; intervals not markedly convex; striae of average depth, coarsely punctate anteriorly and impunctate posteriorly; umbilicate series markedly impressed.

Male genitalia (fig. 94) with median lobe strongly arcuate, angle slightly obtuse; apical blade short and broadly rounded at apex; right paramere of average length reaching halfway point of median lobe; eversion of internal sac dorsoapical and slightly to right; apical sclerite of internal sac U-shaped with horn-like projections narrow, sturdy, and slightly curved. The genitalia of three males were studied in detail.

Stylus of female ovipositor evenly rounded apically without preapical sinuations.

Notes on synonymy. – Chaudoir thought the type locality of *ovulum* was Georgetown, South Carolina. Georgetown, Georgia is closer to the range of this species and it is more likely the correct type locality.

Collecting notes. – This species has been collected in pine forests of Florida and Georgia. Specimens have also been found under bark and caught in malt bait traps

Geographical distribution (fig. 128). – *Evarthrus ovulum* inhabits Florida and southern Georgia. I have seen 29 specimens collected in the following localities.

United States – FLORIDA: Alachua County: Gainesville (FDPI). Baker County: Glen St. Mary (FDPI); Macclenny (FDPI). Gadsden County: Quincy (FDPI). Leon County: Tallahassee (CNHM, CNC, USNM). GEORGIA: Thomas County: Thomasville (ANSP). Toombs County: Lyons (UMMZ).

Evarthrus macrovulum new species

Figures 17, 95a–d, 128

Recognition. – The following combination of characters is diagnostic for specimens of *macrovulum*: crescent-shaped frontal grooves on the head; sharp basal angles of the pronotum; very shallow longitudinal groove in prosternal process; glossy pronotum and elytra, and very short right paramere of the male genitalia (fig. 95). This species, *texensis, alabamensis*, and *ovulum* are remarkably similar.

The differences between *macrovulum* and *ovulum* are given in the diagnosis of the latter species.

The frontal grooves of the head of *macrovulum* are distinctly crescent-shaped and oblique but they are straight and more parallel in *alabamensis*. A glossy pronotum and equally glossy elytra is characteristic of *macrovulum* and contrasts with the combined glossy pronotum and dull elytra of *alabamensis*. In addition *macrovulum* has a shallow groove in the prosternal process while it is deep in *alabamensis*. Males of the species can be separated by characteristics of the genitalia (fig. 93 cf. fig. 95a–d).

The species *texensis* is the only representative of *Cyclotrachelus* occurring to the west of the Mississippi River. Structurally, specimens of *texensis* closely resemble specimens of *macrovulum*, but they differ in details of the male genitalia (figs. 95a–c; cf. figs. 95e–g).

Description. – HOLOTYPE, male, labelled as follows: "Mobile, Ala XI–11–39; Van Dyke Collection; HOLOTYPE Evarthrus macrovulum R. Freitag (red label)." CAS.

Body length 10.8 mm, width 4.1 mm. Form average for group.

Head between eyes and disc of pronotum with microsculpture composed of isolated sinuous lines or effaced. Microsculpture of elytral intervals sinuous, closely entwined lines often forming amorphic meshes, and partially effaced.

Head glossy; length 1.8 mm, width 2.3 mm; frontal grooves sharply defined, oblique, crescent-shaped with lateral bend, and widely separated. Penultimate article of labial palpus with two medial setae.

Pronotum glossy on disc; length 2.8 mm, width 3.4 mm; form as in fig. 17; greatest width slightly anterior to transverse mid-line; disc moderately convex; sides strongly constricted posteriorly, and moderately sinuate in front of posterior angles; posterior angles small, prominent and slightly obtuse; anterior transverse impression incomplete, impressed laterally only; median longitudinal impression shallow throughout; basal foveae deepest posteriorly. Prosternal process with shallow longitudinal groove. Middle femur with four setae on anterior face.

Elytra glossy; length 6.2 mm, width 4.1 mm; intervals rather flat; striae shallow, distinctly but not coarsely punctate anteriorly, and impunctate posteriorly; umbilicate series deeply impressed. First articles of middle and hind tarsi with lateral grooves.

Male genitalia as in fig. 95a–d with median lobe strongly arcuate, apical blade short and evenly rounded at apex; right paramere short, not reaching apical half of median lobe; eversion of internal sac dorsoapical and slightly to right; apical sclerite of internal sac with two horns, one blunt and one sharp and twisted.

ALLOTYPE, female, labelled as follows: "Mobile Ala XII-1-39; Van Dyke Collection; ALLOTYPE Evarthrus macrovulum R. Freitag (green label)." CAS.

Body length 11.4 mm, width 4.4 mm. Form as in holotype.

Microsculpture of head between eyes and pronotal disc same as in holotype. Elytral intervals with microsculpture less effaced than that of holotype, formed by close and distinct closed amorphic meshes.

Head length 1.8 mm, width 2.5 mm.

Pronotum shape as in holotype; length 2.9 mm, width 3.6 mm.

Elytra slightly duller than holotype; length 6.8 mm, width 4.4 mm; sides more parallel posteriorly than those of holotype. Stylus of ovipositor tapered slightly toward apex.

Derivation of specific name. – This species name suggests that specimens of *macrovulum* are large and like *ovulum* in appearance. Specimens of *macrovulum* are not necessarily longer but appear more robust than those of *ovulum*.

Variation among paratypes (91 males, 89 females, Mobile, Alabama. CAS). – Slight and inconsequential. Total length, 8.5 – 11.8 mm. The genitalia of three males were examined in detail.

Disposition of type material. – The holotype and allotype are in the collection of the CAS. One paratype is in the UASM collection, and the others are in the collection of CAS, and RCG.

Geographical distribution (fig. 128). – This species is known from southern Alabama and southern Louisiana. I have seen 182 specimens from the following localities.

United States – ALABAMA: Baldwin County: Fairhope (CAS). Mobile County: Mobile (CAS). LOUISIANA: Saint Tammany County: Slidell (RCG). County not determined: Hart (CAS).

Evarthrus texensis new species

Figures 17a, 95e–h, 128

The following combination of characters is diagnostic for specimens of *texensis*: crescent-shaped frontal grooves on the head; very shallow longitudinal groove in prosternal process; broadly rounded apex of the median lobe of the male, length of right paramere, and shape of the apical sclerite of the internal sac.

Recognition. – The differences between the very similar species *macrovulum* and *texensis* are described in the recognition section of the former species.

Description. – HOLOTYPE, male, labelled as follows: "U. S. A., TEXAS, Tyler Co. 12 mi. W. Kirbyville, Rte. 1013 XII–6–68 G. E. Ball; HOLOTYPE Evarthrus texensis R. Freitag (red label)." MCZ.

Body length 7.5 mm, width 3.3 mm. Form average for group.

Microsculpture of head between eyes and disc of pronotum almost effaced; microsculpture of elytra composed of isodiametric meshes.

Head glossy; length 1.0 mm, width 1.6 mm; frontal grooves sharply defined, oblique, crescent-shaped, and widely separated. Penultimate article of labial palpus with two medial setae.

Pronotum glossy on disc; length 1.8 mm, width 2.6 mm; form as in fig. 17a; greatest width anterior to transverse mid-line; disc moderately convex, sides strongly constricted posteriorly, and moderately sinuate in front of posterior angles; posterior angles small, prominent and slightly obtuse; anterior transverse impression incomplete, impressed laterally only; median longitudinal impression moderately impressed; basal foveae deepest posteriorly; prosternal process with shallow longitudinal groove. Middle femur with four setae on anterior face. First article of middle and hind tarsi with faint lateral grooves.

Elytra slightly duller than head and prothorax; length 4.7 mm, width 3.3 mm; intervals slightly convex; striae moderately impressed, distinctly punctate anteriorly, impunctate posteriorly; umbilicate series deeply impressed.

Male genitalia as in fig. 95e–g with median lobe strongly arcuate, apical blade short and broadly rounded at apex; right paramere almost reaching apical half of median lobe; eversion of internal sac dorsoapical and to right; apical sclerite of internal sac with two horns, one very broad and blunt and one sharp and twisted (fig. 95h).

ALLOTYPE, female, labelled as follows: "USA., TEXAS, Tyler Co. 12 mi. W. Kirbyville Rte. 1013 XII–6–1968 G. E. Ball; ALLOTYPE Evarthrus texensis R. Freitag (green label)." MCZ.

Body length 8.4 mm, width 3.6 mm. Form as in holotype.

Microsculpture of head between eyes, pronotal disc, and intervals of elytra same as in holotype.

Head length 1.0 mm, width 1.8 mm.

Pronotum shape as in holotype; length 2.4 mm, width 2.9 mm.

Elytra length 5.0 mm, width 3.6 mm. Stylus of ovipositor tapered slightly toward apex.

Derivation of specific name. – This species has been named *texensis* since it is known only from Texas.

Variation among paratypes (four males, one female, Orange Co., Jasper Co., Tyler Co., Texas). – Total length, 7.0 – 9.2 mm. The genitalia of four males were examined.

Disposition of type material. – The holotype and allotype are in the MCZ collection and the paratypes are in the collections of CAS, UASM, and USNM.

Geographical distribution (fig. 128). – This species is known from eastern Texas. I have seen seven specimens from the following localities.

United States – TEXAS: Orange County nr. Lakeview. Jasper County: Rte. 63, 11 mi. N. Jasper. Tyler County: Rte. 1013, 12 mi. W. Kirbyville.

The *faber* Group

Characteristics. – Small to medium size beetles; pronotum circular to subcordate, with basal angles recessed and broadly obtuse; longitudinal groove of prosternal process long, deep and sharply defined; dark apical sclerite present in internal sac of median lobe of male genitalia.

The species included in this group are *faber*, *levifaber* and *parafaber*. All of these are found only on the Coastal Plain of southeastern United States.

Evarthrus parafaber new species

Figures 18, 96, 129

Recognition. – This species is distinguished from its relatives by the following combination of characters: frontal grooves of head fairly straight, slightly oblique in relation to one another; pronotum with sides not produced, basal angles almost obsolete; long deep, and sharply defined longitudinal, medial groove in prosternal process; and form of male genitalia. This species can be confused with most members of the *ovulum* group but is distinguished by the obsolete posterior angles of the pronotum. There is no overlap in the geographical ranges of the closely related species *parafaber*, *faber* and *levifaber*. Specimens of *faber* are distinguished from those of *parafaber* by their larger size, four setae on the penultimate article of the labial palpus, shape of the pronotum, and details of the male genitalia. The smaller species *levifaber* also resembles *parafaber* in habitus, but it has a pronotum with markedly produced sides that contrast with the more parallel sides of that of *parafaber*. Furthermore there are striking differences in the structures of the male genitalia of these two species (fig. 96 cf. fig. 97).

Description. – HOLOTYPE, male, labelled as follows: "Mobile, Ala XI–4–39; Van Dyke Collection; HOLOTYPE Evarthrus parafaber R. Freitag (red label)." CAS.

Body length 9.2 mm, width 3.8 mm. Form average for *faber* group.

Microsculpture of head between eyes with lines dense, highly sinuous or closed and forming bead-like meshes. Disc of pronotum with impressions of microsculpture highly sinuous or closed meshes slightly stretched transversely. Microsculpture of elytral intervals composed of isodiametric meshes.

Head semi-glossy; length 1.1 mm, width 2.1 mm; frontal grooves sharply defined, slightly curved but not crescent-shaped, widely separated. Penultimate article of labial palpus with two medial setae.

Pronotum with disc semi-glossy; length 2.7 mm, width 3.1 mm; form as in fig. 18; greatest width slightly anterior to transverse midline; disc moderately convex; sides slightly prominent laterally, moderately constricted anteriorly and strongly constricted posteriorly, slightly sinuate in front of posterior angles; posterior angles almost obsolete, widely obtuse and recessed; anterior transverse impression incomplete, impressed laterally only; median longitudinal impression distinctly deeper at both ends; basal foveae deep posteriorly, shallow and elongate anteriorly. Prosternal process with long, deep, sharply defined medial, longitudinal groove. Middle femur with four setae on anterior face.

Elytra semi-glossy; length 5.4 mm, width 3.8 mm; markedly sinuate apically; intervals slightly convex; striae moderately impressed and coarsely punctate in anterior half, obsoletely punctate apically.

Male genitalia as in fig. 96 with angle of median lobe almost right, apical blade short and slightly produced medially and deflected ventrally; right paramere not reaching apical half of median lobe; eversion of internal sac dorsoapical and slightly to right; apical sclerite of internal sac with two horns, one blunt, one sharp and twisted.

ALLOTYPE, female, labelled as follows: "Mobile Ala XI–4–39; Van Dyke Collection; ALLOTYPE Evarthrus parafaber R. Freitag (green label)." CAS.

Body length 9.5 mm, width 4.1 mm. Form as in holotype.

Microsculpture of head between eyes with distinct closed meshes. Microsculpture of disc of pronotum and intervals of elytra same as in holotype.

Head, length 1 mm, width 2.1 mm.

Pronotum shape as in holotype; length 2.7 mm, width 3.7 mm.

Elytra shape, intervals and striae same as in holotype; length 5.7 mm, width 4.1 mm.

Stylus of ovipositor short and broad, not sinuate apically.

Derivation of specific name. – This species is closely related to *faber*, which is what the name *parafaber* suggests.

Variation among paratypes (29 males, 26 females, Mobile, Ala. CAS). – Total length, 9.8 – 12.8 mm. Variation in color is moderate in the elytra ranging from light rufopiceous to deep piceous. Other parts of the body vary slightly from those of the type specimens. The genitalia of two males were carefully examined.

Disposition of type material. – The holotype, allotype, and 53 paratypes are in the collection of the CAS. Two paratypes are in the UASM collection.

Geographical distribution (fig. 129). – This species is known only from the type locality. I have seen 57 specimens.

United States – ALABAMA: Mobile County: Mobile (CAS, UASM).

Evarthrus levifaber new species

Figures 19, 97, 129

Recognition. – Specimens of *levifaber* are characterized by a combination of the following features: penultimate article of labial palpus bisetose; straight frontal grooves; slightly cordiform pronotum with produced sides; right paramere of male genitalia with distinct elbow; and apical sclerite of internal sac crescent-shaped. Characters that distinguish *levifaber* and *parafaber* are presented in the recognition section of the latter species. The species *levifaber* and *faber* are allopatric. The four setae on the penultimate article of the labial palpus, inwardly curved frontal grooves of the head, and male genitalia of *faber* distinguish it from *levifaber*. Furthermore the pronotum of *faber* is circular but in *levifaber* this sclerite is more cordiform.

Description. – HOLOTYPE, female, labelled as follows: "Camden S. C.; Roland Hayward Coll.; HOLOTYPE Evarthrus levifaber R. Freitag (red label)." MCZ.

Body length 10.1 mm, width 4.2 mm. Form robust. Head with microsculpture composed of highly sinuous entwined lines occasionally forming amorphic meshes. Disc of pronotum and elytral intervals with microsculpture same as head except amorphic meshes raised.

Head glossy; length 1.2 mm, width 2.5 mm; frontal grooves sharply defined and straight, slightly oblique toward one another. Penultimate article of labial palpus with two medial setae.

Pronotum with semi glossy disc; length 2.7 mm, width 3.5 mm; form as in fig. 19; disc moderately convex; sides broadly rounded and prominent, slightly constricted anteriorly and strongly constricted posteriorly, obsoletely sinuate in front of posterior angles; posterior angles not prominent and broadly rounded; anterior transverse impression incomplete, impressed laterally only; median longitudinal impression slightly deeper at posterior end; basal fovea deep posteriorly, moderately deep and short anteriorly. Prosternal process with long, deep, sharply defined longitudinal groove. Middle femur with four setae on anterior face.

Elytra semi-glossy; length 6.2 mm, width 4.2 mm; margin at shoulder broad; apex distinctly sinuate; intervals slightly convex; striae moderately impressed and distinctly punctate anteriorly, impunctate posteriorly.

Stylus of ovipositor short and broad, not sinuate apically.

ALLOTYPE, male, labelled as follows: "Ga.; Horn Coll H536; ALLOTYPE Evarthrus levifaber R. Freitag (green label)". ANSP.

Body length 9.1 mm, width 3.7 mm. Form same as in holotype.

Microsculpture of head between eyes and disc of pronotum same as in holotype. Microsculpture of elytra with sinuous lines that often form longitudinally stretched meshes.

Body mainly rufopiceous, antennae, palpi, legs and epipleura light rufopiceous.

Head glossy; length 1.1 mm, width 2.2 mm.

Pronotum shape same as in holotype; length 2.5 mm, width 3.0 mm.

Elytra glossy, appearance velvet; intervals more convex and striae more impressed than in holotype; length 5.5 mm, width 3.7 mm.

Genitalia (fig. 97) with strongly arcuate median lobe, particularly apical half, apical blade elongate, narrow, and evenly rounded at apex; right paramere with produced elbow, tapered apically and extended to apical half of median lobe; eversion of internal sac apicodorsal and to right; apical sclerite of internal sac dark and C-shaped.

Derivation of specific name. – Specimens of this species appear to be lighter in weight than those of the closely related species *faber*, which is implied in the name *levifaber*.

Variation among paratypes (three males, one female, Georgia, South Carolina, North Carolina, ANSP, MCZ and UASM). – Total length, 11.1 – 13 mm. Except for one teneral male the coloration of the paratypes is approximately the same as that of the holotype and allotype, and similar in all other respects. The genitalia of one male was examined in detail.

Disposition of type material. – The holotype and allotype are in the collection of the MCZ and ANSP respectively. The paratypes are in the collection of MCZ, ANSP, and UASM.

Geographical Distribution (fig. 129). – I have seen six specimens from the following localities.

United States – GEORGIA: (ANSP, UASM). NORTH CAROLINA: (MCZ). SOUTH CAROLINA: Kershaw County: Camden (MCZ).

Evarthrus faber Germar, 1824

Figures 20, 68, 98, 129

Molops faber Germar, 1824:23. Type not seen. TYPE LOCALITY, "*America septentrionali* (Kentucky)," [this locality is probably incorrect]. – LeConte, 1848:353 (*Steropus*). – LeConte, 1852:230 (*Evarthrus*). – LeConte, 1863a:8. – LeConte, 1873:319. – Schaupp, 1880:49. – Casey, 1918:349 (*Cyclotrachelus*). – Leng, 1920:56. – Csiki, 1930:671 (*Pterostichus*).

Feronia tenebricosa Dejean, 1828:301. Type seen by C. H. Lindroth (1955). TYPE LOCALITY, "l'Amerique septentrionale." MHNP. – Chaudoir, 1838:30 (*Cephalotes*). – LeConte, 1848:353 (*Steropus*). – LeConte, 1868a:8 (*Evarthrus*). – LeConte, 1873:319. – Casey, 1918:349 (*Cyclotrachelus*). – Leng, 1920:56. – Csiki, 1930:671 (*Pterostichus*).

Feronia spoliatus; LeConte, 1848:353 (not Newman). – LeConte, 1852:230. – LeConte, 1863a:8.

Cyclotrachelus roticollis Casey, 1918:349. HOLOTYPE, male, labelled as follows: "Fla; CASEY bequest 1925; TYPE USNM 47108; Cyclotrachelus roticollis Csy." USNM. TYPE LOCALITY, Dunedin, Florida. PARATYPES, two males, labelled as follows: "Dunedin; Fla. W. S. B. coll. 3–23 1913 and 17–7 2–15; roticollis – 2 and – 3 PARATYPE USNM 47108." NEW SYNONYMY. – Casey, 1924:78 (*Cyclotrachelus*). – Leng, 1920:56. – Csiki, 1930:671 (*Pterostichus*).

Cyclotrachelus fallaciosus Casey, 1924:77. HOLOTYPE, male, labelled as follows: "Dunedin, Fla. W. S. B. coll. 4–5–1915; TYPE USNM 47109; fallaciosus Csy." USNM. NEW SYNONYMY. – Leng and Mutchler, 1927:10 (*Cyclotrachelus*). – Csiki, 1930:671 (*Pterostichus*).

Recognition. – The following combination of characters is diagnostic of the species *faber*: penultimate article of labial palpus with four setae, frontal grooves on head crescent-shaped with the convexity directed medially; sides of pronotum strongly arcuate; long, deep, sharply defined longitudinal groove in prosternal process; cup-like scales on the ventral side of the front tarsi of the males; and details of the male genitalia.

The differences among the closely related species *faber*, *levifaber*, and *parafaber* are described in the recognition sections of the last two species.

Description. – Body length 8.5 – 11.1 mm. Form robust and typical of the *faber* group. Head between eyes, disc of pronotum, and intervals of elytra with lines of microsculpture distinctly impressed, very dense, and sinuous, forming raised amorphic meshes.

Head glossy, dull or slightly glossy; frontal grooves moderately impressed, crescent-shaped with convexity directed medially, and moderately separated. Penultimate article of labial palpus with two medial and two apical setae (fig. 68).

Pronotum dull or slightly glossy; form of sides circular in outline, as in fig. 20; disc markedly convex; sides moderately constricted anteriorly and strongly constricted posteriorly, slightly sinuate in front of posterior angles; posterior angles broadly obtuse; anterior transverse impression incomplete, impressed laterally only; basal foveae deep posteriorly, and often anterior end very shallowly extended onto anterior half of disc. Prosternal process with long, deep, sharply defined longitudinal groove. Middle femur with four or five setae on anterior face. Males with even rows of cup-like scales on ventral side of front tarsi.

Elytra dull or slightly glossy; margin near shoulder slightly narrow; sinuate apically; intervals slightly convex; striae deeply impressed and distinctly punctate anteriorly and on disc, impunctate posteriorly.

Male genitalia (fig. 98) with moderately arcuate median lobe, apical portion more acute, apical blade resembling a two-edged sword with produced medial apex; right paramere short, not extended to apical half of median lobe, shape typical of *Cyclotrachelus* with recessed elbow and not strongly tapered apically; eversion of the internal sac apicodorsal and to right; internal sac with light basal serrulate field and darker apical serrulate field, apical sclerite dark and C-shaped. The male genitalia of three specimens were examined in detail.

Stylus of female ovipositor short, broadly rounded apically.

Variation. – The number of setae on the front face of the middle femur varies from four to five, but there is no geographical pattern to the variation.

Notes on synonymy. – In the MNHP collection there are six specimens of the species determined as *faber* Germar, the first of which bears the label *tenebricosa m.* which was written by Dejean. The specimen was probably given to him by Joseph E. LeConte with whom Dejean traded specimens.

The type specimens of *roticollis* Casey and *fallaciosus* Casey are average specimens of *faber*.

Collecting notes. – Specimens of this species have been found in leaf litter (label data). The gut of one specimen contained a mixture of sand and fungus zygotes, which were identified by Dr. L. L. Kennedy.

Geographical distribution (fig. 129). – This species inhabits Florida and southern Georgia. The New York and Ohio records are certainly incorrect. I have seen 132 specimens collected in the following localities.

United States – FLORIDA: Alachua County: Archer (FDPI); Gainesville (UMMZ): High Springs (UMMZ): R.–24–E T–10–S (UMMZ). Baker County: Glen St. Mary (FDPI). Brevard County: Melbourne (USNM). Calhoun County: near Clarksville (CNC). Charlotte County: Punta Gorda (CAS, CNHM). DeSoto County: Arcadia (GEB, UMMZ); Fort Ogden (CNC). Dixie County: Cross City (UMMZ); Shamrock (CAS). Duval County: Jacksonville (USNM). Gadsden County: Quincy (FDPI). Hendry County: LaBelle (CU). Hernando County: Brooksville (CAS, UMMZ). Lee County: Fort Myers (CNC). Leon County: (CU); Tallahassee (CNC, UMMZ). Liberty County: Camp Torreya (UMMZ). Manatee County: Bradenton (CAS). Marion County: (ANSP); Ocala (CNC); Ocala National Forest (UMMZ). Monroe County: Big Pine Key (UMMZ). Okaloosa County: Delaco (UMMZ). Orange County: Winter Park (MCZ). Osceola County: Deer Park (MCZ); Kissimmee (AMNH). Pasco County: Elfers (CNC). Pinellas County: Dunedin (AMNH, CAS): St. Petersburg (AMNH). Polk County: Lakeland (USNM). Sarasota County: Sarasota (USNM). Seminole County: Sanford (MCZ). Walton County: DeFuniak Springs (UMMZ). County not determined: Fringers (USNM); Iuka Island (USNM); North Smyrna (CAS); 15 miles south of Wadky (CNC). GEORGIA: Camden County: Kingsland (UMMZ); St. Mary's (MCZ). Decatur County: Faceville (UMMZ). NEW YORK: Westchester County: Peekskill (CU). OHIO: (CMNH).

The Subgenus *Evarthrus* LeConte

Evarthrus LeConte, 1852:225, TYPE SPECIES – *Evarthrus sigillatus* Say, 1823a (designated by Casey, 1918:322).

Anaferonia Casey, 1918:341. TYPE SPECIES – *Evarthrus constrictus* Say, 1823b (designated by Casey, 1918:321).

Megasteropus Casey, 1918:350. TYPE SPECIES – *Megasteropus gigas* Casey, 1918 (designated by Casey, 1918:322).

Eumolops Casey, 1918:351. TYPE SPECIES – *Eumolops sexualis* Casey, 1918 (designated by Casey, 1918:322).

Evarthrinus Casey, 1918:357. TYPE SPECIES – *Evarthrus deceptus* Casey, 1918 (here designated).

Evarthrops Casey, 1920:194. TYPE SPECIES – *Evarthrus furtivus* LeConte, 1852 (here designated).

Characteristics. – Penultimate article of labial palpus with three (rarely) or five to seven setae; pronotum with sides parallel or constricted posteriorly, posterior lateral foveae bistriate, posterior lateral setae usually beside bead (figs. 21–61), but in *gravesi* on bead; middle femur with 4–11 setae on anterior face; last tarsal article with setae on ventral side; eversion of internal sac of median lobe of male genitalia right.

Notes on synonymy. – Casey established the above genera and subgenus *Evarthrops* on characters which are common throughout the subgenus *Evarthrus*. The description of *Anaferonia* provided by Casey can be applied to most species groups in the subgenus *Evarthrus*. He established *Megasteropus* on features such as size of head and impunctate striae of elytra. I do not accept these as generic or subgeneric characters. He separated *Eumolops* from *Evarthrus* mainly because of differences in the form of the last article of the maxillary palpus, a characteristic which varies intraspecifically throughout *Evarthrus*. Casey believed that species with three punctures on the third interval of the elytron constituted a separate genus which he named *Evarthrinus*. This characteristic is present in a number of unrelated species in the subgenus *Evarthrus*.

The following species groups compose the subgenus *Evarthrus*: the *incisus* group, the *blatchleyi* group, the *sigillatus* group, the *seximpressus* group, the *hypheripiformis* group, the *sodalis* group, the *substriatus* group, the *torvus* group, and the *gigas* group.

The *incisus* Group

Characteristics. – Penultimate article of labial palpus with five setae. Pronotum cordiform in outline; anterior transverse impression usually absent medially, complete in a few specimens. Prosternal process with longitudinal groove shallow. Middle femur with four setae on anterior face. Median lobe of male genitalia with hump medially on ventral surface; pigmented apical sclerite in internal sac; right paramere very short.

The species *incisus* and *whitcombi* are included in this group, which is represented on the Great Plains from Arkansas and Oklahoma north to South Dakota.

Evarthrus incisus LeConte, 1848

Figures 21, 99, 130

Feronia (Molops) incisa LeConte, 1848:345. LECTOTYPE (here selected) a male, labelled as follows: "green disc; Type 5620; E. incisus Lec." MCZ. TYPE LOCALITY, Missouri Territory. – LeConte, 1852:232 (*Evarthrus*). – LeConte, 1863a:8. – LeConte, 1873: 319. – Schaupp, 1880:49. – Casey, 1918:348 (*Anaferonia*). – Leng, 1920:56. – Csiki, 1930:671 (*Pterostichus*).

Feronia (Molops) lixa LeConte, 1848:346. LECTOTYPE (here selected) a female, labelled as follows: "green disc; Type 5622; E. lixa LeC; abdominalis 3". MCZ. TYPE LOCALITY, near Long's Peak. – LeConte, 1863a:8 (*Evarthrus*). – LeConte, 1873:319. – Schaupp, 1880:49.

Feronia (Molops) abdominalis LeConte, 1848:347. LECTOTYPE (here selected) a male, labelled as follows: "green disc; Type 5621; E. abdominalis Lec." MCZ. TYPE LOCALITY, near Long's Peak. – LeConte, 1852:232 (*Evarthrus*). – LeConte, 1863a:8. – LeConte, 1873:319. – Schaupp, 1880:49. – Casey, 1918:347 (*Anaferonia*). – Leng, 1920:56. – Csiki, 1930:671 (*Pterostichus*).

Anaferonia distincta Casey, 1918:342. HOLOTYPE, male, labelled as follows: "Ia; CASEY bequest 1925; TYPE USNM 47103; distincta Csy." USNM. TYPE LOCALITY, Iowa. NEW SYNONYMY. – Leng, 1920:56 (*Anaferonia*). – Csiki, 1930:671 (*Pterostichus*).

Anaferonia iowana Casey, 1918:347. HOLOTYPE, male, labelled as follows: "Ia; CASEY bequest; TYPE USNM 47107; iowana Csy." USNM. TYPE LOCALITY, Iowa. NEW SYNONYMY. – Leng, 1920:56 (*Anaferonia*). – Csiki, 1930:671 (*Pterostichus*).

Anaferonia fausta Casey, 1918:348. HOLOTYPE, male, labelled as follows: "Penn; CASEY bequest 1925; TYPE USNM 47104; fausta Csy." USNM; PARATYPE, male, labelled as follows: "Penn; CASEY bequest 1925; fausta –2; PARATYPE USNM 47104. USNM. TYPE LOCALITY, Pennsylvania. NEW SYNONYMY. – Leng, 1920:56 (*Anaferonia*). – Csiki, 1930:671 (*Pterostichus*).

Recognition. – Specimens of this species are easily confused with specimens of *whitcombi*, but they are distinguished by their smaller size and by differences in male genitalia (fig. 99 cf. fig. 100). In Arkansas the micropunctures in the elytral intervals are distinct in specimens of *incisus* but indistinct in specimens of *whitcombi*.

Description. – Body length 9.0 – 12.3 mm. Form robust anteriorly, average for *incisus* group.

Microsculpture of head between eyes and disc of pronotum effaced. Intervals of elytra with isodiametric meshes forming microsculpture, occasionally almost effaced; integument of dorsum glossy.

Head with frontal grooves distinctly but not deeply impressed, straight or slightly curved, usually oblique but occasionally parallel toward one another, not widely separated.

Pronotum form as in fig. 21; disc moderately convex; sides slightly constricted anteriorly, strongly constricted posteriorly, short and slightly sinuate in front of posterior angles; posterior angles small, produced, slightly obtuse; anterior transverse impression usually incomplete, in a few specimens complete with medial portion obsolete or interrupted; basal lateral foveae with sides usually continuous near base, separated in a few specimens.

Elytra obsoletely sinuate apically; intervals of average convexity or flattened, striae moderately impressed, indistinctly or obsoletely punctate in anterior half, obsoletely punctate apically.

Male genitalia (fig. 99) with median lobe slightly arcuate, angle broadly obtuse, low median ventral hump present; apical blade elongate with apical lateral edges strongly deflected dorsally, apex evenly rounded; right paramere short, broadly rounded at apex, not extended to apical half of median lobe; internal sac with serrulate field apically, apical sclerite dark elongate and slightly curved basally. The genitalia of five males were studied in detail.

Stylus of female ovipositor narrow, gradually tapered apically.

Geographical variation. – Individuals of *incisus* have red or black legs. Red legs are common in Nebraska and appear occasionally throughout the rest of the species range.

Notes on synonymy. – The lectotypes of *abdominalis* and *lixa* LeConte are average specimens of *incisus*. The type specimen of *distincta* Casey has a basal fovea of the pronotum with the sides continuous posteriorly, and is average for this species in most other structures. The type specimens of *fausta* and *iowana* Casey are normal *incisus* specimens.

Collecting notes. – D. L. Larson and I collected specimens of *incisus* in leaf litter of deciduous forest near Morrilton, Arkansas. Some of the specimens were taken at the soil surface beneath moist leaf litter and some were in the litter itself.

Geographical distribution (fig. 130). – This species inhabits the central states from Kansas and Arkansas north to Illinois and South Dakota. The Pennsylvania record is probably incorrect. I have seen 222 specimens collected in the following localities.

United States – ARKANSAS: Carroll County: Eureka Springs (INHS). Conway County: six miles south of Morrilton (DL, RF). Johnson County: ten miles east of Ozark (DL, RF). Madison County: 45 miles east of Fayetteville (RF). Marion County: (USNM); Buffalo River State Park (CU). Pope County: (UA). Washington County: Cove Creek (CU, DL, RF); Devil's Den State Park (RTB); Fayetteville (UA). ILLINOIS: Knox County: Galesburg (INHS). Piatt County: Robert Allerton Park, Monticello (RTB). IOWA: Johnson County: Iowa City (MCZ, UASM, USNM). KANSAS: Dickinson County: (CNHM). Wabaunsee County: McFarland (USNM). MISSOURI: Carter County: Van Buren (UMMZ). Crawford County: Onandaga Cave (UMMZ). NEBRASKA: Douglas County: Omaha (CAS). Fillmore County: (USNM). Red Willow County: McCook (USNM). OKLAHOMA: Comanche County: Wichita National Forest (CAS, UMMZ). Oklahoma County: (CAS). PENNSYLVANIA: Allegheny County: (CAS, CNC, USNM). SOUTH DAKOTA: Hutchinson County: Menno (VMK). Yankton County: Yankton (VMK).

Evarthrus whitcombi new species

Figures 22, 100, 130

Recognition. – Several characteristics, previously described in connection with the recognition of *incisus*, distinguish specimens of *whitcombi* from those of *incisus*. Both *incisus* and *whitcombi* can be mistaken for specimens of the somewhat similar species *substriatus* or *iowensis*. Individuals of *substriatus* are distinguished by a large elytral plica and distinct dorsolateral knob on the last abdominal segement that fits onto the plica (fig. 77). Specimens of *iowensis* are characterized by having five or six setae on the anterior face of the middle femur, which contrasts with the four setae on the same structure of *incisus* and *whitcombi*.

Description. – HOLOTYPE, male, labelled as follows: "Hot Springs, Ark. X–1–39; Van Dyke Collection; HOLOTYPE Evarthrus whitcombi R. Freitag (red label)." CAS.

Body length 13.4 mm, width 5.7 mm. Larger and more robust than specimens of *incisus* LeC.

Head between eyes and disc of pronotum with microsculpture composed of highly sinuous lines, entwined, but rarely forming meshes. Microsculpture of elytral intervals with isodiametric meshes. Integument of dorsum slightly glossy.

Head length 1.5 mm, width 3.3 mm; frontal grooves distinctly but broadly impressed, straight, parallel to one another.

Pronotum length 3.8 mm, width 4.6 mm; shape cordiform in outline as in fig. 22; disc moderately convex, somewhat flattened medially; sides constricted slightly anteriorly, strongly posteriorly, briefly sinuate in front of posterior angle; posterior angles small, produced, slightly obtuse; anterior transverse impression absent medially; basal lateral foveae with sides not continuous near base. First articles of middle and hind tarsi with lateral grooves.

Elytra 8.1 mm in length, width 5.7 mm; sides parallel, slightly sinuate apically; intervals of low convexity almost flat; striae moderately impressed anteriorly, punctate anteriorly, indistinctly or obsoletely impressed posteriorly.

Male genitalia (fig. 100) with median lobe moderately arcuate, and with marked median ventral hump; apical blade short and deflected to right, edges of apex not deflected dorsally; right paramere short, apical half evenly tapered to apex; internal sac serrulate apically, apical sclerite very dark with broad tooth apically and hook basally.

ALLOTYPE, female, labelled as follows: "Hot Springs Ark. X–1–39; Van Dyke Collection; ALLOTYPE Evarthrus whitcombi R. Freitag (green label)." CAS.

Body length 14.0 mm, width 5.7 mm. Form same as in holotype.

Head between eyes and disc of pronotum with highly sinuous dense, entwined lines comprising microsculpture. Intervals of elytra with isodiametric meshes forming microsculpture.

Head dull; length 1.7 mm, width 3.5 mm.

Pronotum dull, form same as in holotype; length 3.7 mm, width 4.8 mm.

Elytra dull; intervals somewhat flattened; striae moderately impressed, distinctly punctate anteriorly, indistinctly or obsoletely punctate posteriorly; length 8.7 mm, width 5.7 mm.

Stylus of ovipositor narrow, gradually tapered apically.

Derivation of specific name. – This species is named in honour of Dr. W. H. Whitcomb, formerly Professor of Entomology, University of Arkansas, who has made important contributions in the field of terrestrial arthropod biology.

Variation among paratypes (five males, eight females, Ark., Okla.). – Body length 11.4 – 15.4 mm. The genitalia of two males were examined.

Disposition of type material. – The holotype and allotype are in the collection of the CAS. The paratypes are in the collection of AMNH, CAS, CNHM, INHS.

Geographical distribution (fig. 130). – This species inhabits eastern Oklahoma and southern Arkansas. I have seen 15 specimens from the following localities.

United States – ARKANSAS: Garland County: Hot Springs (CAS, INHS, UASM). Logan County: Mount Magazine (CNHM). County not determined: Southwest (AMNH). OKLAHOMA: LeFlore County: Page (UMMZ). McCurtain County: Beavers Bend State Park (UMMZ).

The *blatchleyi* Group

Characteristics. – Penultimate article of labial palpus with five setae (fig. 69), pronotum quadrate with obtuse basal angles; prosternal process with deep, medial, longitudinal groove; middle femur with four setae on anterior face; male genitalia with median lobe slightly arcuate; right paramere short and broad; internal sac very lightly sclerotized or with serrulate field apically.

The group is composed of the species *blatchleyi* and *floridensis* whose collective range includes Florida, and southern and eastern Georgia.

Evarthrus blatchleyi Casey, 1918

Figures 23, 69, 101, 131

Evarthrus blatchleyi Casey, 1918:360. HOLOTYPE, male, labelled as follows: "Dunedin Fla. W. S. B. coll. 3-22-18; CASEY bequest 1925; TYPE USNM 47122; blatchleyi Csy." USNM, PARATYPES, two females, labelled as follows: "Dunedin Fla. W. S. B. coll. 3–18–16 and 3–14–16; CASEY BEQUEST 1925; blatchleyi –2 and –3 PARATYPE USNM 47122." USNM. – Leng, 1920:57 (*Evarthrus*). – Csiki, 1930:673 (*Pterostichus*).
Evarthrus americanus; LeConte, 1852:228 (not Dejean). – LeConte, 1863a:8. – LeConte, 1873:318. – Leng, 1915:577. – Leng, 1920:57.

Recognition. – The following combination of characteristics is diagnostic of this species: clearly impressed basal foveae of the pronotum, width of lateral bead of pronotum even throughout length, elongate apical blade of median lobe of male genitalia, and relatively large body size.

Specimens of *blatchleyi* are normally larger than specimens of the similar species *floridensis*. They are further distinguished by differences in the male genitalia (fig. 101 cf. fig. 102).

Description. – Body length 14.8 – 17.6 mm. Form broad with parallel sides.

Head between eyes and disc of pronotum with microsculpture composed of extremely tiny, densely distributed, amorphic meshes. Microsculpture of elytral intervals forming raised, bead-like isodiametric meshes. Micropunctures present on head between eyes. Integument of dorsum slightly glossy.

Head with frontal grooves deep, sharply defined, straight or slightly curved with convexity directed medially, parallel to one another.

Pronotum somewhat quadrate in outline as in fig. 23; disc slightly convex anteriorly, flatter posteriorly, sides constricted moderately anteriorly and slightly posteriorly, sinuation in front of basal angles obsolete or absent; posterior angles not produced but not broadly rounded, slightly obtuse; anterior transverse impression complete and distinctly impressed; basal lateral foveae with sides not continuous near base, inner side with extension from base toward middle longitudinal line; width of lateral bead even throughout.

Elytra slightly sinuate apically; intervals flat or slightly raised, striae moderately or shallowly impressed, punctate anteriorly, impunctate posteriorly.

Male genitalia (fig. 101) with median lobe slightly arcuate, angle broadly obtuse; apical blade elongate and narrow, deflected dorsally and to left, apex evenly rounded; right paramere short and broad, not extended to apical half of median lobe; internal sac serrulate apically, apical sclerite light amorphic. The genitalia of six males were examined.

Stylus of female ovipositor slightly tapered apically, broadly rounded at apex.

Collecting notes. – This species is found in open disturbed places. G. E. Ball collected specimens with a pitfall trap in an orange grove near Oneco, Florida.

Geographical distribution (fig. 131). – This species ranges from southwestern Florida to southeastern Georgia. I have seen 88 specimens from the following localities.

United States – FLORIDA: Alachua County: Gainesville (FDPI), (UMMZ); Newnan's Lake (UMMZ); Route 18 east (FDPI). DeSoto County: Arcadia (UMMZ). Duval County: Jacksonville (AMNH, CAS, CNHM, MCZ). Highlands County: Hammock State Park (GEB). Hillsborough County: Tampa (ANSP). Lee County: Fort Myers (UP). Manatee County: Oneco (GEB). Marion County: Ocala National Forest (UMMZ). Orange County: Orlando (GEB). Osceola County: Kissimmee (AMNH). Pasco County: Elfers (CNC). Pinellas County: Dunedin (UP). Putnam County: Welaka (UMMZ). Suwannee County: Wellborn (UMMZ). GEORGIA: Bryan County: Lanier (UMMZ). Camden County: Kingsland (UMMZ). Charlton County: Billy's Island, Okefenokee Swamp (CU). Ware County: Waycross (UMMZ).

Evarthrus floridensis new species

Figures 24, 102, 131

Recognition. – The combination of the flattened area between the basal fovea and margin of the pronotum, and unique shape of the apical blade of the median lobe of the male (fig. 102) sets this species apart from the closely similar species *blatchleyi*. Specimens of another species, *sinus*, also resemble specimens of *floridensis* but these two groups are allopatric and possess different male genitalia (fig. 102 cf. fig. 104) among other distinguishing features.

Description. – HOLOTYPE, male, labelled as follows: "Winter Park. 2–15–28 Fla.; John George Gehring Collection; HOLOTYPE Evarthrus floridensis R. Freitag (red label); loan from MCZ." MCZ.

Body length 13.1 mm, width 5.3 mm, sides parallel, not robust.

Head between eyes and disc of pronotum with microsculpture formed of highly sinuous, densely distributed lines, occasionally forming amorphic meshes. Elytral intervals with amorphic or isodiametric meshes composing microsculpture. Integument of dorsum slightly glossy.

Head length 1.7 mm, width 3.6 mm; frontal grooves deep and sharply defined, slightly curved with convexity directed medially.

Pronotum length 3.7 mm, width 4.6 mm; form quadrate in outline as in fig. 24; disc quite convex; sides not prominent, slightly constricted anteriorly and posteriorly, not sinuate in front of posterior angles; posterior angles not prominent, slightly obtuse and broadly rounded; anterior transverse impression complete and clearly impressed; basal lateral foveae not continuous posteriorly, inner groove with extension from base toward median longitudinal impression; lateral bead wider near basal foveae, and area between bead and foveae flat.

Elytra length 7.7 mm, width 5.3 mm, sides parallel, slightly sinuate apically; intervals almost flat; striae distinctly but not deeply impressed, indistinctly punctate anteriorly, impunctate posteriorly.

Male genitalia (fig. 102) with median lobe slightly arcuate, angle broadly obtuse; apical blade with ridge on ventral side, apex deflected dorsally; right paramere short and broad, not extended to apical half of median lobe; internal sac serrulate near apex, apical sclerite not present.

ALLOTYPE, female, labelled as follows: "Winter Park 2.15.28 Fla,; John George Gehring Collection; ALLOTYPE Evarthrus floridensis R. Freitag (green label); loan from MCZ." MCZ.

Body length 14.7 mm, width 6.1 mm. Form same as in holotype.

Microsculpture of head between eyes, disc of pronotum and intervals of elytra same as in holotype; integument of dorsum slightly glossy.

Head length 1.9 mm, width 3.6 mm. Pronotum form same as in holotype; length 4.1 mm, width 5.1 mm. Elytra length 8.7 mm, width 6.1 mm. Stylus of ovipositor gradually tapered apically.

Derivation of species name. – The name *floridensis* was given to this species because its members are known from Florida only.

Variation among paratypes (18 males, 13 females, Fla.). – Total length 13.0 – 15.0 mm. The genitalia of five males were examined and no variation was observed.

Disposition of type material. – The holotype and allotype are in the collections of the MCZ. Two paratypes are in the UASM collection and the others are in the collections of the CU and MCZ.

Geographical distribution (fig. 131). – This species is endemic to Florida. I have seen 46 specimens from the following localities.

United States – FLORIDA: Orange County: Winter Park (CU, MCZ, UASM). Osceola County: Deer Park (MCZ); Kissimmee (AMNH). Seminole County: Sanford (MCZ). Volusia County: Enterprise (CAS). Counties not determined: Haw Creek (USNM); North Smyrna (CAS).

The *sigillatus* Group

Characteristics. – Pronotum quadrate with obtuse and broadly rounded basal angles; male genitalia with median lobe moderately or strongly arcuate, right paramere tapered apically and slightly to markedly elongate.

The *sigillatus* group is composed of the species *sigillatus*, *sinus* and *convivus*. This group occupies the eastern side of the Mississippi River Valley, Piedmont and Coastal Plain areas.

Evarthrus sigillatus Say, 1823

Figures 25–28, 72–73, 103, 131

Feronia sigillata Say, 1823a:42. Type lost. TYPE LOCALITY, Mr. R. Haines farm, Germantown (Pa.). – LeConte, 1848:350 (*Feronia*). – LeConte, 1863a:8 (*Evarthrus*). – LeConte, 1873:318. – Schaupp, 1880:49. – Leng, 1920:57. – Leonard, 1926:222. – Brimley, 1938:119.

Feronia (Omaseus) vidua Dejean, 1828:278. Type seen by C. H. Lindroth (1955). MNHP. TYPE LOCALITY, l'Amerique Septentrionale. – LeConte, 1848:350 (*Feronia*). – LeConte, 1852:228 (*Evarthrus*). – LeConte, 1863a:49. – Leng, 1920:57. – Csiki, 1930:675 (*Pterostichus*).

Feronia (Abax) americana Dejean, 1828:392. TYPE, male, labelled as follows: "americanus m." MHNP. TYPE LOCALITY, "l'Amerique Septentrionale." NEW SYNONYMY. – Schaupp, 1880:49 (*Evarthrus*). – Casey, 1918:361. – Csiki, 1930:673 (*Pterostichus*).

Feronia orbata Newman, 1835:386. TYPE, female, labelled as follows: "Type H. T.; Ent. Club. 44-12; J. Ingall Canada; Feronia Latreille orbata Newman Ent. Mag. V.386." BM. NEW SYNONYMY. – Motschulsky, 1865:261 (*Evarthrus*). – Leng, 1920:57. – Csiki, 1930:673 (*Pterostichus*).

Evarthrus breviformis Casey, 1918:360. HOLOTYPE, female, labelled as follows: "Southern Pines; A. H. Manee. NC; CASEY bequest 1925; TYPE USNM 47120; breviformis Csy." USNM. TYPE LOCALITY, Southern Pines, N. Carolina. NEW SYNONYMY. – Leng, 1920:57 (*Evarthrus*). – Csiki, 1930:673 (*Pterostichus*). – Brimley, 1938:119 (*Evarthrus*).

Evarthrus montanus Van Dyke, 1926:116. HOLOTYPE, male, labelled as follows: "Black Mts. NC VII. 1902; collector E. C. Van Dyke; Van Dyke Collection." ALLOTYPE, labelled the same except for "Black Mts. NC VI.1902." CAS. TYPE LOCALITY, in the valley at the base of the Black Mountains, North Carolina. NEW SYNONYMY. – Csiki, 1930:673 (*Pterostichus*). – Leng and Mutchler, 1933:13 (*Evarthrus*).

Pterostichus (Pterostichus) (Sect. *Evarthrus*) *carolinensis* Csiki, 1930:673. NEW SYNONYMY. – Leng and Mutchler, 1933:13 (*Evarthrus*). – Brimley, 1938:119.

Recognition. – The following combination of characters separates specimens of *sigillatus* from specimens of all similar species of *Evarthrus*: pronotum quadrate, sides not strongly constricted posteriorly; basal angles slightly or broadly obtuse, not prominent, evenly rounded; male genitalia, with left side of apex of median lobe sharply deflected dorsally, internal sac with characteristic apical sclerite; range mainly east of the Appalachian Mountains.

Specimens of *sigillatus* in western areas of the range can be confused with *convivus* individuals. It is usually necessary to compare the male genitalia for a certain identification. The right paramere is long and tapered in *convivus* but short and broader in *sigillatus* (fig. 103 cf. fig. 105).

Specimens of *blatchleyi* resemble those of *sigillatus* in North and South Carolina. These can be distinguished as follows: basal fovea of the pronotum of *blatchleyi* simply and clearly impressed, but it is more complex in *sigillatus* (fig. 23 cf. figs. 25-28); apical blade of median lobe of male in *blatchleyi* is elongate, narrow, and evenly deflected dorsally and to the left, but it is short, broader, and left side of apex sharply deflected dorsally in *sigillatus* (fig. 101 cf. fig. 103).

Description. – Body length 13.4 – 18.3 mm. Form narrow with sides of elytra somewhat convex or broad with parallel sides of elytra.

Microsculpture of head between eyes and disc of pronotum with highly sinuous, entwined lines, often forming amorphic meshes, usually partially effaced. Intervals of elytra with microsculpture formed by amorphic or isodiametric meshes. Integument of dorsum markedly glossy, elytra dull in some specimens.

Head with frontal grooves fairly deep and sharply defined, usually short with middle bend, convexity directed medially, or straight and slightly oblique to one another. Penultimate article of labial palpus with four or five setae.

Pronotum shape somewhat variable but essentially quadrate as in figs. 25-28; disc of average convexity; sides not strongly produced, usually fairly parallel, slightly constricted anteriorly and posteriorly, sinuation in front of basal angle slight or absent; posterior angles not produced, obtuse and broadly rounded; anterior transverse impression complete and distinctly impressed, basal lateral foveae with sides continuous or not posteriorly, inner side with interrupted extension from base toward middle longitudinal line; lateral bead slightly broader posteriorly. Prosternal process with deep, sharply defined longitudinal groove. Middle femur with four to six setae on anterior face.

Elytra slightly sinuate apically; intervals slightly raised or flat; striae distinctly and moderately impressed, punctate anteriorly, obsoletely punctate or impunctate posteriorly.

Male genitalia (fig. 103) with median lobe moderately arcuate, angle distinctly obtuse; apical blade elongate, left corner of apex deflected dorsally; right paramere short not extending to apical half of median lobe, fairly broad, with slight tapering apically; internal sac with serrulate field apically, apical sclerite light, amorphic plate with darker basal tooth. The genitalia of 22 males were examined in detail.

Stylus of female ovipositor with relatively parallel sides and broadly rounded apex.

Geographical variation. – This is one of the most variable species of *Evarthrus*. The variable features which I have noted are: the shape of the pronotum, shape of the elytra, glossiness of the elytra and form of the male genitalia. In northern areas of the species range, in Pennsylvania for example, the pronotum is fairly rectangular in outline (fig. 25), elytra are produced laterally and slightly glossy. At higher altitudes in western North Carolina the pronotum is more elongate and the sides are more sinuate in front of the posterior angles (fig. 26). The shape and glossiness of the elytra are the same as those of specimens in Pennsylvania. On the Piedmont and Coastal Plain regions of North and South Carolina, Georgia, Florida panhandle and eastern Alabama, the pronotum is relatively broader, without sinuate sides in front of the posterior angles (figs. 27–28), and the sides of the elytra are more parallel and surface of the elytra are duller than those of specimens further north in Pennsylvania or at higher elevations. These three morphologically distinct populations are linked by populations with intermediate structures that intergrade clinally.

Notes on synonymy. – The species *sigillatus* was identified by the original description. The type specimen of *vidua* Dejean resembles *sigillatus* specimens from northern limits of this species range. The type specimen of *americana* Dejean is a *sigillatus* specimen of the form that occurs in central and eastern North and South Carolina. The type specimen of *orbata* Newman is a *sigillatus* specimen of the kind that composes populations in Pennsylvania and Virginia. The type of *breviformis* Casey is a *sigillatus* specimen of the sort found in eastern and southern North Carolina. The type specimen of *montanus* is a *sigillatus* specimen of the average form which inhabits western North Carolina. Csiki lumped *Evarthrus* and *Pterostichus* which brought into one genus the names *montanus* Motschulsky and *montanus* Van Dyke. The new name *carolinensis* Csiki was created to replace *montanus* Van Dyke.

Collecting notes. – This species is found in leaf litter of deciduous forests as well as under cover in open places such as pastures.

Geographical distribution (fig. 131). – *Evarthrus sigillatus* ranges from the Florida panhandle to southern New York primarily east of the Appalachian Mountains. I have seen 432 specimens collected in the following localities.

United States – ALABAMA: Lee County: Auburn (AU, CAS, MCZ). Randolph County: Wadley (USNM). Tallapoosa County: Alexander City (AU). DISTRICT OF COLUMBIA: Piney Bridge (CNHM); Washington (USNM). FLORIDA: Jackson County: Grand Ridge (FDPI). Leon County: Tallahassee (FDPI, UMMZ). Liberty County: Camp Torreya (UMMZ); Rock Bluff (UMMZ). GEORGIA: Camden County: Kingsland (UMMZ). Liberty County: Riceboro (UMMZ). Morgan County: four miles north of Madison (DL); Madison (UMMZ). Rabun County: Clayton (AMNH, UMMZ, USNM). County not determined: Wilson Gap (CU). MARYLAND: Ann Arundel County: Odenton (CU); Baltimore (CAS). Harford County: Edgewood (CU). Montgomery County: (USNM). County not determined: Yellow Springs (RTB). MASSACHUSETTS: Middlesex County: Woburn (USNM). NEW JERSEY: Bergen County: Hillsdale (MCZ, USNM); Palisades (USNM); Ramsey (AMNH). Essex County: Newark (AMNH); South Orange (USNM). Hudson County: Arlington (USNM). Morris County: Boonton (USNM); Chester (AMNH); Lake Hopatcong (MCZ). Passaic County: Oak Ridge (USNM). Somerset County: Bound Brook (USNM). Sussex County: Hopatcong (AMNH); Sparta (DRW). Counties not determined: Dundsel (MCZ); Durh. P. (USNM); Fulerton (CU); Lahaway (USNM); Springdale Park (USNM). NEW YORK: Nassau County: Sea Cliff (MCZ). Rockland County: Bear Mountain (CAS, UASM). NORTH CAROLINA: Buncombe County: (GEB); Asheville (MCZ); Black Mountains (AMNH, CAS, CNHM, MCZ, USNM). Burke County: Linn Falls (USNM). Catawba County: Hickory (CNC). Haywood County: Crestmont (UMMZ); Lake Junaluska (FDPI); Mount Sterling (UMMZ). Henderson County: 5 mi. north of Bat Cave (AMNH); Hendersonville (USNM); Mills River (CNC). Jackson County: Dillsboro (AMNH). Madison County: Hot Springs (USNM). McDowell County: Marion (MCZ). Mecklenburg County: Charlotte (MCZ). Moore County: Southern Pines (CAS, KSU, MCZ, RTB, UW). Orange County: Chapel Hill (CU). Polk County: Tryon (MCZ). Randolph County: Julian (MCZ). Robeson County: Lumberton (UMMZ). Wake County: Raleigh (CNC, NCSU, USNM). Wilkes County: Wilkesboro (CU, USNM). Counties not determined: Beaver Creek (NCSU); Black Camp Gap (TCB); Graybeard Mountain (AMNH); Morrison Mountain (USNM); Mount Pisgah (USNM); Peano Rendezvous (GEB)

Round Knob (USNM); Stony Creek (RTB). PENNSYLVANIA: Bucks County: (RU) Cumberland County: Enola (MCZ). Fayette County: Uniontown (CAS). Montgomery County: Whitemarsh (USNM). Northampton County: Easton (CAS, CNHM, TE, UASM); Wind Gap (CNHM). Philadelphia County: Frankford (USNM); Germantown (ANSP); Mount Airy (CAS, RU); Philadelphia (MCZ). Counties not determined: Abbotsford (MCZ); Angord (CAS); Fernwald (CNHM; Inglenook (CAS); Lehigh Gap (USNM); Rockville (MCZ); Water Gap (AMNH); Wissahickon Creek (RU). SOUTH CAROLINA: Beaufort County: Hardeeville (UMMZ). Berkeley County: Goose Creek (UMMZ). Colleton County: Round O (UMMZ). Darlington County: Hartsville (UMMZ). Florence County: Florence (GEB); Scranton (UMMZ). Greenville County: Greenville (UMMZ). Greenwood County: Greenwood (UMMZ). Kershaw County: Camden (MCZ, UMMZ). Oconee County: CCC Camp F–2 (CAS); Clemson College (USNM). Richland County: Columbia (UMMZ). Saluda County: Saluda (UMMZ). County not determined: Meredith (CAS). TENNESSEE: Blount County: Chilhowee Mountain (CNC). Carter County: Roan Mountain (UMMZ). Cocke County: French Broad River (MCZ). Knox County: Knoxville (CNC). McMinn County: 1.5 mi. north of Athens (UMMZ). Morgan County: (CNHM); Deer Lodge, Environs (CNHM). Sevier County: Gatlinburg (UMMZ, USNM). Counties not determined: Crabtree (CU); Great Smoky Mountains National Park (CNC); Unaka Mountains (ANSP); Unaka Springs (RTB). VIRGINIA: Arlington County: Rosslyn (MCZ). Bedford County: Blue Ridge National Parkway (RCG). Fairfax County: (ANSP, USNM); Dead Run (USNM). Nansemond County: Cypress Chapel (UMMZ). Counties not determined: Black Pond (USNM); Diamond Springs (USNM); Great Falls (USNM); Stony Man Mountain (MCZ).

Evarthrus sinus new species

Figures 29, 104, 131

Recognition. – The following combination of characteristics is diagnostic for this species: pronotum with sides more constricted anteriorly than posteriorly, not sinuate in front of posterior angles; lateral bead rather broad posteriorly; male genitalia with strongly arcuate median lobe and narrow parameres; coastal or near coastal distribution. The species which are most similar in external structural characteristics to *sinus* are *blatchleyi* and *floridensis*. The geographical ranges of *sinus* and the last two species are different. However specimens of these species can also be easily separated by differences in their male genitalia (figs. 101, 102, 104).

Description. – HOLOTYPE, male, labelled as follows: "Alabama Port, Mobile Co. Ala. June 6, 1950 Ball-Wilson; HOLOTYPE Evarthrus sinus R. Freitag (red label)." MCZ. Body length 13.7 mm, width 5.7 mm. Form approximately parallel at sides.

Head between eyes, disc of pronotum, and intervals of elytra with microsculpture consisting of sinuous, entwined, dense lines often forming amorphic meshes.

Head glossy; length 1.7 mm, width 3.3 mm; frontal grooves distinctly and sharply impressed; slightly curved away from one another posteriorly. Penultimate article of labial palpus with five setae, three medial and two apical.

Pronotum moderately glossy; length 3.9 mm, width 4.8 mm; shape somewhat cordiform in outline as in fig. 29; disc of average convexity, sides more constricted anteriorly than posteriorly, not sinuate in front of posterior angles; posterior angles not produced, obtuse and broadly rounded; anterior transverse impression complete and deeply impressed; basal lateral foveae with sides not continuous posteriorly, inner side with extension from base toward middle longitudinal line; lateral bead distinctly broader posteriorly. Prosternal process with deep, sharply defined longitudinal groove. Middle femur with four setae on anterior face.

Elytra slightly glossy, somewhat velvety in appearance; length 8.1 mm, width 5.7 mm; slightly sinuate apically; intervals almost flat; striae moderately impressed, distinctly punctate anteriorly, obsoletely punctate posteriorly.

Male genitalia (fig. 104) with median lobe strongly arcuate, angle approximately right; apical blade fairly short, round at apex, and deflected to right; right paramere of average length just extended to apical half of median lobe, distinctly tapered apically, apex narrow; internal sac with serrulate field apically, apical sclerite light amorphic plate with serrulate basal portion.

ALLOTYPE, female, labelled as follows: "Alabama Port, Mobile Co. Ala. June, 6, 1950 Ball-Wilson; ALLOTYPE Evarthrus sinus R. Freitag (green label)." MCZ.

Body length 13.9 mm, width 5.8 mm. Form same as in holotype.

Microsculpture on head, pronotum and elytra same as in holotype. Head glossy; length 1.7 mm, width 3.3 mm. Pronotum glossy; form same as in holotype; length 3.7 mm, width 4.7 mm. Elytra slightly glossy; length 8.4 mm, width 5.8 mm. Stylus of ovipositor with somewhat parallel sides, apex evenly rounded.

Derivation of specific name. – This species is given the name *sinus*, a latin noun meaning gulf, because its members live in the vicinity of the Gulf Coast.

Variation among paratypes (five males, nine females, Mississippi, Alabama). – Total length 13.1 – 15.9 mm. The variation in the features which I examined is no greater than that between the holotype and allotype. The genitalia of five males were examined.

Disposition of type material. – The holotype and allotype are in the collections of the MCZ. The paratypes are in the following collections: CAS, CU, GEB, MCZ, UASM, UMMZ, USNM.

Collecting notes. – This species has been collected in pine-oak coastal forest by G. E. Ball.

Geographical distribution (fig. 131). – This species is represented on the Coastal Plain of Alabama and Mississippi. I have seen 19 specimens from the following localities.

United States – ALABAMA: Mobile County: Alabama Port (GEB); Mobile (CAS, MCZ, UASM, USNM). MISSISSIPPI: George County: Lucedale (CU). Harrison County: Gulfport (UMMZ). Perry County: Richton (CU).

Evarthrus convivus LeConte, 1852

Figures 30–32, 105, 131

Evarthrus convivus LeConte, 1852:229. LECTOTYPE (here selected) a male, labelled as follows: "orange disc; Type 5654, E. orbatus (Newm) conviva LeC." MCZ. TYPE LOCALITY, Alabama. – LeConte, 1863a:8 (*Evarthrus*). – LeConte, 1873:318. – Schaupp, 1880: 49. – Leng, 1920:57. – Csiki, 1930:673 (*Pterostichus*). – Löding, 1945:16 (*Evarthrus*).

Feronia (Pterostichus) orbata; LeConte, 1848:348 (not Newman).

Evarthrus orbatus; LeConte, 1852:229 (not Newman). – LeConte, 1863a:8. – LeConte, 1873:318. – Schaupp, 1880:49. – Blatchley, 1910:101. – Löding, 1945:16.

Evarthrus sigillatus; LeConte, 1852:228 (not Say). – Blatchley, 1910:101. – Casey, 1918: 359. – Löding, 1945:16.

Evarthrus sigillatus parallelus Casey, 1918:359. HOLOTYPE, male, labelled as follows: "Ind; CASEY bequest 1925; TYPE USNM 47119, parallelus Csy." USNM. TYPE LOCALITY, Indiana. NEW SYNONYMY. – Leng, 1920:57 (*Evarthrus*). – Csiki, 1930:674 (*Pterostichus*). – Löding, 1945:16 (*Evarthrus*).

Pterostichus (Pterostichus) (Sect. *Evarthrus*) *sigillatus*; Csiki, 1930:674 (not Say).

Recognition. – A combination of flat and dull elytral intervals, male genitalia with an elongate and narrow right paramere and C-shaped sclerite of the internal sac, and geographic distribution west and southwest of the Appalachian Mountains, is characteristic of *convivus*.

The species *sigillatus* and *convivus* are for the most part allopatric but their ranges overlap in western Pennsylvania and eastern Tennessee. In Pennsylvania *convivus* specimens have decidedly more parallel sides and are duller than those of *sigillatus*. The distinction between these two species is more obscure in eastern Tennessee and indeed it is usually necessary to examine the male genitalia for a certain identification.

The closely related species *sinus* and *convivus* are distinguished by the basal lateral foveae of the pronotum (fig. 29 cf. figs. 30–32) male genitalia (fig. 105), and geographical range.

Description. – Body length 11.6 – 19.2 mm. Form typical of *sigillatus* group.

Head between eyes with highly sinuous lines and amorphic meshes or meshes alone composing microsculpture. Disc of elytra with highly sinuous lines, usually very densely distributed, forming microsculpture. Microsculpture of intervals of elytra with highly sinuous lines and raised bead-like meshes.

Head moderately glossy; frontal grooves fairly deep and sharply defined, with middle bend, convexity directed medially. Penultimate article of labial palpus with five setae.

Pronotum moderately glossy; shape quadrate as in figs. 30 – 32; disc of average convexity or slightly flatter; sides not strongly produced, slightly constricted anteriorly and posteriorly, obsoletely sinuate in front of posterior angles; posterior angles not produced, obtuse and broadly rounded; anterior transverse impression complete and distinctly impressed; basal lateral fovea with sides continuous or not posteriorly, inner side with interrupted extension from base toward median longitudinal impression; lateral bead slightly broader posteriorly. Prosternal process with deeply or shallowly impressed longitudinal groove. Middle femur with four to five setae on anterior face.

Elytra dull, matte, slightly sinuate apically; intervals flat or almost flat; striae not deeply impressed, distinctly punctate anteriorly, indistinctly or obsoletely punctate posteriorly.

Male genitalia (fig. 105) with median lobe strongly arcuate, angle slightly obtuse; apical blade short, evenly rounded at apex, curved to right; right paramere elongate, apical half narrow, extended to apical half of median lobe; internal sac with serrulate field apically, apical sclerite distinctly C-shaped. The genitalia of 26 males were examined.

Stylus of female ovipositor slightly tapered apically.

Geographical variation. – Body size is notably variable. Tiny specimens are uncommon and appear sporadically throughout the range. In contrast giant forms are rather common in northeastern Alabama and in all directions from that region the body size decreases clinally. In other characteristics variation is minimal and specimens in Mississippi are grossly similar to those at the other end of the range in Pennsylvania or Illinois.

Notes on synonymy. – The type specimen of *parallelus* Casey is a slightly smaller than average *convivus* specimen.

Collecting notes. – D. J. Larson and I have taken some specimens in leaf litter in mixed pine and deciduous forests in Mississippi.

Geographical distribution (fig. 131). – This species ranges from the Mississippi River east to the Appalachian Mountains and from southern Alabama north to Illinois and western Pennsylvania. Some populations occur beside the Mississippi River in Louisiana. I have seen 491 specimens from the following localities.

United States – ALABAMA: Bibb County: The Sinks (UMMZ). Blount County: Blount Springs (CM). Cherokee County: Leesburg (UMMZ). Clarke County: six miles south of Jackson (UMMZ). Conecuh County: Brooklyn (TCB). DeKalb County: Desoto State Park (CAS). Franklin County: Russellville (GEB). Jackson County: Point Rock (UMMZ); Sand Mountain, Bryant (UMMZ). Madison County: Huntsville (UMMZ); Monte Sano (CNC, UMMZ). Marengo County: south of Demopolis (UMMZ). Mobile County: (CAS); Chickasaw (CU); Mobile (ANSP, CAS, MCZ); Mount Vernon (CU); Spring Hill (CAS). St. Clair County: Blount Mountains (GEB). Talladega County: Talladega (UMMZ). Tuscaloosa County: Lock 14 (CAS); Peterson (GEB); Talladega State Forest (GEB); Tuscaloosa (GEB, UMMZ); Windham Springs (GEB). ILLINOIS: Alexander County: Cache River (RTB); Olive Branch (CAS, CNHM). Cass County: Virginia (CU). Champaign County: Urbana (CNHM, MCZ, RTB). Clark County: Martinsville (UMMZ). Coles County: Fox Ridge State Park (RTB). Vermilion County: Kickapoo State Park (RTB). Washington County: Dubois (INHS). County not determined: Bottoms (INHS). INDIANA: Crawford County: (UP). Clark County: (CAS, UP). Elkhart County: Goshen (UMMZ). Floyd County: (UP, MCZ). Gibson County: Oakland City (UMMZ). Greene County: (UP). Hendricks County: Stilesville (CAS). Jefferson County: Clifty Falls State Park (GEB). Knox County: (CAS). LaGrange County: Lagrange (UMMZ). Marion County (UASM). Monroe County: Bloomington (UMMZ). Montgomery County: (UP). Putnam County: (UP). St. Joseph County: Mishawaka (UMMZ). Starke County: Bass Lake (CNHM). Tippecanoe County: LaFayette (UMMZ). County not determined: Turkey Run (INHS). KENTUCKY: Barren County: Cave City (USNM). Edmonson County: Mammoth Cave National Park (TCB). Hardin County: Fort Knox (GEB). Jefferson County: Anchorage (UL); Prospect (UL). Jessamine County: (GEB). Wayne County: Wolf Creek Lake (UL). County not determined: Sleepy Hollow (UL). LOUISIANA: East Baton Rouge County: Baton Rouge (UMMZ). St. Tammany County: Covington (USNM). MISSISSIPPI: Adams County: Natchez (CAS, USNM). Calhoun County: Vardaman (UMMZ). Clairborne County: Edwardsville (RCG). Forrest County: Hattiesburg (AMNH). George County: Lucedale (CU). Granada County: Dubard Station (UMMZ). Greene County: Leakesville (CU). Lauderdale County: five miles south of Toomsuba (DL, RF); Meridian (UMMZ). Perry County: Richton (CU). Simpson County: (UMMZ). Tishomingo County: Iuka (UMMZ). Counties not determined: North Augusta (CU); six miles east of Iuka (FDPI). OHIO: Adams County: (UMMZ). Allen County: Lima (UMMZ). Brown County: Russelsville (CU). Cuyahoga County: Cleveland (MCZ, UMMZ). Darke County: Beamville (RU, UMMZ). Hamilton County: Cincinnati (UMMZ). Licking County: West Alexandria (RTB). Preble County: Eaton (UMMZ). PENNSYLVANIA: Allegheny County: (CM, CU); Fair Oaks (CM); Millvale (CM); Pittsburgh (CAS, CM); Wall (CM, UK). Fayette County: Dunbar (CM); Union Town (CAS, MCZ, UMMZ, USNM). Westmoreland County: Jeanette (CM). County not determined: Allegheny (ANSP, MCZ, UK, USNM). TENNESSEE: Knox County: 25 miles south of Knoxville (AMNH). Lake County: Gray's Landing (RTB). Lauderdale County: South Fulton (UMMZ). Morgan County: Burrville (CNHM, CU). Obion County: Obion (UMMZ). WEST VIRGINIA: Monongalia County: Greer (GEB). Taylor County: Grafton (USNM). Webster Springs (MCZ).

The *seximpressus* Group

Characteristics. – Penultimate article of labial palpus with five setae, two medial and three apical. Pronotum more or less quadrate in outline; anterior transverse impression complete and distinct throughout. Prosternal process with setae on apex. Middle femur with five to seven setae on anterior face (fig. 75). Prosternal process with longitudinal groove shallow, but sharply defined. Male genitalia with median lobe moderately arcuate; internal sac with apical sclerite light with darker oval basal portion; right paramere markedly tapered apically.

This group includes the species *seximpressus*, *alabamae*, *engelmanni*, and *nonnitens*. They occur on the Gulf Coast in Texas, Louisiana, Mississippi, Alabama, the Ozark Plateau, and Mississippi Valley north to Wisconsin.

Evarthrus seximpressus LeConte, 1848

Figures 33, 75, 106, 132

Feronia (Pterostichus) seximpressa LeConte, 1848:350. LECTOTYPE (here selected) a male, labelled as follows: "dark green disc; Type 5653; E. seximpressus LeConte." MCZ.

TYPE LOCALITY, Rocky Mountains near Long's Peak. – LeConte, 1852:228 (*Evarthrus*). – LeConte, 1863a:8. – LeConte, 1873:318. – Schaupp, 1880:49. – Blatchley, 1910:100. – Casey, 1918:361. – Leng, 1920:57. – Csiki, 1930:673 (*Pterostichus*). – Löding, 1945:16 (*Evarthrus*).

Evarthrus rubripes Casey, 1918:359. HOLOTYPE, male, labelled as follows: "Mo.; CASEY bequest 1925; TYPE USNM 47121; rubripes Csy." USNM. TYPE LOCALITY, Saint Louis, Missouri. PARATYPE, female, labelled as follows: "Ia; CASEY bequest 1925; rubripes – 2; PARATYPE USNM 47121." USNM. TYPE LOCALITY, Keokuk, Iowa. NEW SYNONYMY. – Leng, 1920:57 (*Evarthrus*). – Csiki, 1930:673 (*Pterostichus*).

Recognition. – The species *seximpressus* is distinguished from other species of the *seximpressus* group by the following combination of characteristics: body size relatively small; pronotum (fig. 33) more quadrate than circular in outline, posterior angles obsolete, lateral bead broad near base; male genitalia with apical blade of median lobe relatively narrow and evenly rounded at apex (fig. 106).

Description. – Body length 10.3 – 15.9 mm. Form relatively less robust than other species of the *seximpressus* group.

Microsculpture on head between eyes with markedly sinuous lines and amorphic meshes. Disc of pronotum with microsculpture formed of highly sinuous lines. Microsculpture of elytral intervals with amorphic or isodiametric meshes.

Head slightly or moderately glossy; frontal grooves fairly deep and distinct, with slight middle bend, posterior halves directed laterally. Penultimate article of labial palpus with five setae.

Pronotum moderately or slightly glossy; shape quadrate, as in fig. 33; disc of average convexity; sides produced, slightly constricted anteriorly and posteriorly, not sinuate in front of posterior angles; posterior angles not produced, obtuse and broadly rounded; anterior transverse impression complete and distinctly impressed; basal fovea with sides continuous or not posteriorly; lateral bead much broader posteriorly. Prosternal process with longitudinal groove distinctly but not deeply impressed. Legs red or black; middle femur with five or six setae on anterior face (fig. 75).

Elytra usually dull, slightly glossy in a few specimens; slightly sinuate apically; intervals flat or almost flat; striae not deeply impressed, distinctly punctate anteriorly, impunctate or obsoletely punctate posteriorly.

Male genitalia (fig. 106) with median lobe moderately arcuate, angle clearly obtuse; apical blade evenly rounded at apex, very slightly deflected to right; right paramere distinctly tapered apically, not extended to apical half of median lobe; internal sac with serrulate field apically, apical sclerite light amorphic plate. The genitalia of four specimens were examined in detail.

Stylus of female ovipositor slightly tapered apically.

Geographical variation. – Leg color varies from red to black. Specimens with red legs are most abundant in Wisconsin and northern Arkansas but they are uncommon throughout the rest of the range of this species.

Notes on synonymy. – The type specimen of *rubripes* Casey is an average, red-legged *seximpressus* specimen.

Collecting notes. – Specimens of *E. seximpressus* have been collected under cover in pastures.

Geographical distribution (fig. 132). – This species inhabits eastern areas of the Great Plains, and the Mississippi Valley, from Oklahoma or possibly Texas in the south, north to Michigan, Indiana and possibly western Pennsylvania. I have seen 451 specimens from the following localities.

United States – ARKANSAS: Benton County: Rogers (KSU). Bradley County: (UA); Pine Oak Woods (UA). Conway County: (UA). Garland County: Hot Springs (CAS). Hempstead County: Hope (CAS, MCZ, UMMZ). Lawrence County: (CAS). Searcy County: Leslie (CAS). Sebastian County: Greenwood (INHS). Washington County: (INHS, UA); Cove Creek, 27 miles from Fayetteville (DL); Cove Creek Valley (UA); Devil's Den State Park (RTB). Yell County: (UA). ILLINOIS: Adams County: Camp Point (INHS). Champaign County: (INHS); Urbana (INHS). DeKalb County: Hinckley (UP). Hardin County: Shane Landing (RTB). McHenry County: Harvard (RCG). Macoupin County: Chesterfield (RTB). Peoria County: Hanna City (INHS). Richland County: Wabash Valley (CM, MCZ). Rock Island County: Rock Island (UMMZ). County not determined: Grand Detour (CNHM). INDIANA: Greene County: (UP). Knox County: (UP). Marion County: (UP). Putnam County: (UP). IOWA: Davis County: (UMMZ). Henry County: Mount Pleasant (MCZ, MSU). Johnson County: Iowa City (CNC, MCZ, USNM); Solon (USNM). Polk County: Des Moines (ISU). Pottawattomie County: Council Bluffs (CAS, USNM). Story County: Ames (ISU). KANSAS: Clay County: (ANSP, CAS, UMMZ, USNM). Doniphan County: Wathena (USNM). Douglas County: (MCZ, UK, USNM); Lawrence (ANSP, CAS, CNC, UMMZ, UW). Pottawatomie County: Onaga (KSU). Riley County: Manhatten (KSU); Popenoe (KSU, USNM). Shawnee County: Topeka (KSU, USNM). Woodson County: two miles east of Yates Centre (DL). Wyandotte County: Argentine (AMNH, RU). MICHIGAN: Lenawee County: Adrian (MCZ). MINNESOTA: Houston County: Caledonia (KSU). MISSOURI: Buchanan County: St. Joseph (MCZ, USNM). Camden County: Camdenton (UMMZ). Carter County: Van Buren (UMMZ). Greene County: Willard (ANSP, MCZ, UASM). Jackson County: Kansas City (UK). Jefferson County: Kimmswick (UMMZ). Miller County: Ozark Lake (CAS). Polk County: Aldrich (CU). St. Louis County: St. Louis (CAS, CM, USNM). Taney County: Branson (CAS). County not determined: Bolival (CAS). NEBRASKA: Douglas County: Omaha, Child's Point (CAS). Lancaster County: Lincoln (CAS). OKLAHOMA: Cleveland County: (CAS); Norman (CAS). Latimer County: (CAS). LeFlore County: Page (UMMZ). Lincoln County: east of Stroud (TCB). Marshall County: Lake Texoma State Park (TE). Rogers County: Catdosa (CNHM). Tulsa County: Tulsa (CAS). Wagoner County: Cornell (UMMZ). PENNSYLVANIA: Westmoreland County: Jeanette (CM). TEXAS: Brazos County: College Station (INHS). WISCONSIN: Dane County: (UW); Madison (CU, UW). Dodge County: Beaver Dam (CAS, KSU, MCZ, UMMZ). Milwaukee County: Milwaukee (UW). Vernon County: Westby (USNM). County not determined: Wingra Lake (UW).

Evarthrus alabamae Van Dyke, 1926

Figures 34, 107, 132

Evarthrus vagans alabamae Van Dyke, 1926:118. HOLOTYPE, male labelled as follows: "Mobile, Ala. III.08; Van Dyke Collection." CAS. ALLOTYPE, labelled as follows: "Mobile, Ala. II.26.1901. H. P. Löding; Van Dyke Collection." CAS. NEW STATUS. – Csiki, 1930:673 (*Pterostichus*). – Leng and Mutchler, 1933:13 (*Evarthrus*). – Löding, 1945:16.

Evarthrus lodingi; Löding, 1945:16 (not Van Dyke).

Recognition. – The circular pronotum is diagnostic of *alabamae* and distinguishes it from the closely related species *seximpressus* which has a more rectangular pronotum. Characteristics of the male genitalia of *alabamae* and *seximpressus* also distinguish these species from one another (fig. 106 cf. fig. 107).

Description. – Body length 14.6 – 18.7 mm. Form robust, particularly the pronotum. Head between eyes and disc of pronotum with highly sinuous lines and amorphic meshes composing microsculpture. Intervals of elytra with microsculpture formed by a combination of raised amorphic and isodiametric meshes.

Head slightly or moderately glossy; frontal grooves of average depth, distinct, with slight middle bend, posterior halves directed laterally. Penultimate article of labial palpus with five setae.

Pronotum slightly or moderately glossy; shape somewhat circular in outline as in fig. 34. Disc of average convexity; sides strongly produced, moderately constricted anteriorly and posteriorly, not sinuate in front of posterior angles; posterior angles not produced, obtuse and broadly rounded; anterior transverse impression complete and deeply impressed; basal foveae with sides continuous or not posteriorly; lateral bead much broader posteriorly. Prosternal process with longitudinal groove distinct but not deep. Middle femur with five or six setae on anterior face.

Elytra dull or slightly glossy; slightly sinuate apically; intervals almost flat or strongly convex; striae of average depth, distinctly punctate anteriorly indistinctly punctate posteriorly.

Male genitalia (fig. 107) with median lobe moderately arcuate, angle clearly obtuse; apical blade rather broad, apex broadly rounded; apex with lateral edges deflected dorsally; right paramere distinctly tapered apically, extended to approximately halfway point of median lobe; internal sac with serrulate field apically; apical sclerite light amorphic plate, with darker elliptically-shaped basal portion. The genitalia of six males were examined in detail.

Stylus of female ovipositor slightly tapered apically.

Variation. – Body size and convexity of elytral intervals are somewhat variable, but there is no apparent geographical clinal pattern in the variation.

Two specimens from Oakhurst, Texas and two from Livingston, Texas are smaller than the average *alabamae* specimen (e.g. from Mobile, Alabama). They vaguely resemble *engelmanni*. However the *alabamae* characters are evident, e.g. very round basal angles of the elytra and broader apical blade of the male phallus. These appear to be variants of *alabamae* and that is how I regard them.

Collecting notes. – Specimens of *alabamae* are found in pine-oak woods, in leaf litter. G. E. Ball collected specimens of this species along with specimens of *E. sinus* in pine-oak coastal forest.

Geographical distribution (fig. 132). – This species inhabits the Gulf Coastal Plain from Alabama west to Texas. The Kansas and northern Arkansas records are probably wrong. I have seen 163 specimens from the following localities.

United States – ALABAMA: Mobile County: Alabama Port (GEB); Grand Bay (ANSP); Mobile (AMNH, ANSP, AU, CAS, CU, KSU, MCZ, UMMZ, USNM, UW). ARKANSAS: Bradley County: Pine Oak Woods (UA). Lawrence County: Imboden (CNHM, MCZ, USNM). KANSAS: Clay County: (CNHM). LOUISIANA: Caddo County: Shreveport (CAS). Jefferson Davis County: Lake Arthur (CAS). Natchitoches County: Natchitoches (UMMZ); Vowell's Mill (USNM). County not determined: Hart (CAS). MISSISSIPPI: Harrison County: Gulfport (CU); Handsboro (FDPI, UMMZ). Jackson County: Pascagoula (USNM). TEXAS: Harrison County: Marshall (UMMZ). Polk County: five miles east of Livingston (AMNH); Livingston (AMNH). San Jacinto County: two miles east of Oakhurst (AMNH). Travis County: Austin (MCZ).

Evarthrus engelmanni LeConte, 1852

Figures 35, 108, 132

Evarthrus engelmani LeConte, 1852:228. LECTOTYPE (here selected) a male, labelled as follows: "Tex; engelmani 2." MCZ. TYPE LOCALITY, Texas. – LeConte, 1858:28 (*Evarthrus*). – LeConte, 1863a:8. – LeConte, 1873:318. – Schaupp, 1880:49. – Leng, 1920:57. – Csiki, 1930:673 (*Pterostichus*).

Evarthrus vagans; Schaupp, 1880:49 (not LeConte). – Csiki, 1930:673 (*Pterostichus*). – Löding, 1945:16 (*Evarthrus*).

Recognition. – The combination of the produced sides, produced posterior angles, and posterior widening of the lateral bead of the pronotum is diagnostic of specimens of *engelmanni*. These features distinguish *engelmanni* from *nonnitens*.

Description. – Body length 12.6 – 19.1 mm. Form average for the *seximpressus* group. Head between eyes and disc of pronotum with highly sinuous lines and amorphic meshes composing microsculpture. Microsculpture of intervals of elytra formed by bead-like isodiametric meshes.

Head slightly or moderately glossy; frontal grooves moderately deep, distinct, straight or with slight middle bend, posterior halves directed laterally. Penultimate article of labial palpus with five setae.

Pronotum slightly glossy; shape somewhat quadrate in outline as in fig. 35 with disc of average convexity; sides strongly produced, moderately constricted anteriorly and posteriorly, distinctly sinuate in front of posterior angles; posterior angles small, more or less produced, slightly or broadly obtuse; anterior transverse impression complete and deeply impressed; basal lateral fovea with sides usually continuous posteriorly; lateral bead much broader posteriorly than anteriorly. Prosternal process with longitudinal groove moderately or deeply impressed. Middle femur with five or six setae on anterior face.

Elytra dull, slightly sinuate apically; intervals flat or slightly convex; striae not deep, indistinctly punctate anteriorly, obsoletely punctate or impunctate posteriorly.

Male genitalia (fig. 108) with median lobe moderately arcuate, angle clearly obtuse; apical blade broad with broadly rounded almost truncate apex; lateral edges of apex not strongly deflected dorsally; right paramere very narrow apically, not extended to halfway point of median lobe; internal sac with serrulate field apically, apical sclerite light amorphic plate with dark elliptical basal portion. The genitalia of eleven males were examined.

Stylus of female ovipositor moderately tapered apically.

Geographical variation. – The pronotum is variable, which sometimes makes it difficult to separate *engelmanni* from the three other species in the *seximpressus* group. For example several specimens from College Station, Texas are very much like *seximpressus* but they all have a sinuation in front of the posterior angles of the pronotum which is characteristic of *engelmanni*. Other specimens of *engelmanni* resemble individuals of *nonnitens* in pronotal features but are distinguishable by their male genitalia.

Notes on synonymy. – I believe LeConte named this species after George Engelmann, 1809 – 1844, a physician in St. Louis and eminent botanist. This is probably why LeConte changed the name *engelmani* (1852) to *engelmanni* in subsequent publications.

Collecting notes. – Specimens of *engelmanni* have been collected in forests (label data).

Geographical distribution (fig. 132). – This species inhabits eastern Texas. The El Paso record is surely not correct. I have seen 69 specimens from the following localities.

United States – TEXAS: Bastrop County: Bastrop State Park (CNC). Brazos County: (MCZ); College Station (MCZ, TAM). DeWitt County: Cuero (AMNH). El Paso County: El Paso (CM). Goliad County: (USNM). Grimes County: (TAM). Harris County: Houston (CM). Madison County: (TAM). Tarrant County: east of Fort Worth (KSU). Travis County: Austin (MCZ). Victoria County: Victoria (USNM). County not determined: Fedor (CAS, CM).

Evarthrus nonnitens LeConte, 1873

Figures 36, 109, 132

Evarthrus nonnitens LeConte, 1873:320. LECTOTYPE (here selected) a female, labelled as follows: "red disc; Red River; Type 5656; E. nonnitens LeC." MCZ. TYPE LOCALITY, Red River, Louisiana. – Schaupp, 1880:49 (*Evarthrus*). – Casey, 1918:362. – Leng, 1920:57. – Csiki, 1930:673 (*Pterostichus*).

Evarthrus enormis Casey, 1918:361. HOLOTYPE, female, labelled as follows: "Tex; CASEY BEQUEST 1925; TYPE USNM 47125; enormis Csy." USNM. TYPE LOCALITY, Houston, Texas. NEW SYNONYMY. – Leng, 1920:57 (*Evarthrus*). – Csiki, 1930:673 (*Pterostichus*).

Recognition. – Specimens of *nonnitens* are characterized by the combination of the extremely matte surface of the elytra, somewhat flattened disc of the pronotum, and relatively narrow posterior portion of the lateral bead of the pronotum.

Individuals of *nonnitens* can be confused with specimens of *seximpressus* and *engelmanni*. The duller elytra of *nonnitens* usually distinguishes it from both *engelmanni* and *seximpressus*. In addition specimens of *nonnitens* and *engelmanni* can be distinguished from one another by the difference in widths of the basal part of the lateral bead of the pronotum (fig. 35 cf. fig. 36). Also *seximpressus* does not have a produced basal angle of the pronotum while *nonnitens* has. The relative width of the apex of the median lobe of the genitalia is also a reliable feature for separating these species (fig. 109 cf. figs. 106 and 108).

Description. – Body length 13.7 – 16.9 mm. Form average for the *seximpressus* group. Head between eyes, disc of pronotum, and intervals of elytra with microsculpture composed of highly sinuous entwined lines.

Head slightly glossy; frontal grooves deep, distinct, with middle bend, posterior halves directed laterally. Penultimate article of labial palpus with five setae.

Pronotum dull, shape quadrate in outline as in fig. 36, disc somewhat flattened in middle; sides slightly produced, slightly constricted anteriorly and posteriorly, sinuate in front of posterior angles; posterior angles small and slightly produced, clearly obtuse; anterior transverse impression complete and deeply impressed; basal lateral fovea with sides continuous or not posteriorly; lateral bead slightly broadened posteriorly. Prosternal process with longitudinal groove moderately or deeply impressed. Middle femur with five to seven setae on anterior face.

Elytra very dull, matte; obsoletely sinuate apically; intervals flat or slightly convex; striae not deep, distinctly punctate anteriorly, indistinctly punctate or impunctate posteriorly.

Male genitalia (fig. 109) with median lobe moderately arcuate, angle clearly obtuse, evenly rounded; apical blade broad, apex broadly rounded almost truncate, lateral edges deflected dorsally; right paramere very narrow apically extended to approximately halfway point of median lobe; internal sac with serrulate field apically; apical sclerite light amorphic plate with dark oval basal portion. The genitalia of five males were examined.

Stylus of female ovipositor slightly tapered apically.

Notes on synonymy. – The type specimen of *enormis* Casey is an average specimen of *nonnitens* in all respects.

Geographical distribution (fig. 132). – This species is known from southern Arkansas and the Gulf Coastal Plain in Mississippi, Louisiana and eastern Texas. I have seen 33 specimens collected in the following localities.

United States – ARKANSAS: Bradley County: (UA); Crimson Clover (UA); Pine Oak Woods (UA). Clarke County: (UA). Hempstead County: Hope (MCZ, UASM, UMMZ). LOUISIANA: Grant County: Grant Point, Dryprong (CNHM). Lincoln County: five miles east of Ruston (AMNH); Ruston (MCZ). County not determined: Red River (MCZ). MISSISSIPPI: Adams County: Natchez (CAS). TEXAS: Harris County: Houston (USNM). San Jacinto County: two miles east of Oakhurst (AMNH).

The *hypherpiformis* Group

Characteristics. – Penultimate article of labial palpus with five setae. Pronotum quadrate in outline; anterior transverse impression complete, shallow medially. Prosternal process without setae on apex. Three to five setae on third interval of elytron. Median lobe of male genitalia with medial ventral bump; apex of apical blade flat and sharp, deflected ventrally. Right paramere short and markedly tapered apically. This group is represented by one species, *hypherpiformis*. It occurs in the northern Coastal Plain area of Alabama and Mississippi.

Evarthrus hypherpiformis new species

Figures 37, 110, 132

Recognition. – The combination of body size, three to five setae on the third interval of the elytron, flattened pronotum, and form of the male genitalia is diagnostic for this species. Specimens of *hypherpiformis* resemble those of *nonnitens* but without setae on the apex of the prosternal process.

Description. – HOLOTYPE, male, labelled as follows: "Marengo Co., ALABAMA Prairies s. Demopolis June, 1935 A. F. Archer; loan from UMMZ; HOLOTYPE Evarthrus hypherpiformis R. Freitag (red label)." UMMZ.

Body length 18.0 mm, width 7.4 mm. Form somewhat flat, with parallel sides.

Microsculpture of head between eyes composed of isodiametric and amorphic meshes; disc of pronotum with amorphic meshes; intervals of elytra with isodiametric bead-like meshes. Integument of dorsum slightly glossy.

Head length 2.0 mm, width 4.1 mm; frontal groove deep and broadly impressed, posterior halves slightly directed laterally. Penultimate article of labial palpus with five setae.

Pronotum length 5.3 mm, width 5.6 mm; form quadrate in outline as in fig. 37; disc distinctly flattened in centre; sides not prominent, constricted moderately anteriorly slightly posteriorly, slightly sinuate in front of posterior angles; posterior angles not prominent, slightly obtuse, somewhat sharp; anterior transverse impression complete; basal lateral fovea with sides not continuous posterio-medially, central depressed portion flattened and somewhat rugose, extension from inner side to middle longitudinal line represented by a small roughly sculptured area; lateral bead same width throughout length. Apex of prosternal process extended far beyond middle coxae, longitudinal groove obsolete. Anterior faces of middle femora with five setae on one, six setae on the other.

Elytra length 10.7 mm, width 7.4 mm; sides parallel, obsoletely sinuate apically; intervals distinctly convex; striae with small but distinct punctures anteriorly, obsoletely punctate posteriorly. Third interval of each elytron with three setae.

Male genitalia (fig. 110): median lobe moderately arcuate, with ventral medial bump; apical blade with apex deflected dorsally at a sharp right angle; right paramere very short, markedly tapered apically; internal sac serrulate apically, apical sclerite elongate, pale colored plate.

Derivation of specific name. – The habitus of specimens of *hypherpiformis* is vaguely like that of individuals of some species of the subgenus *Hypherpes* of the genus *Pterostichus.*

Variation among paratypes (four males, Alabama, Mississippi). – Body length 17.7 – 18.5 mm. The number of setae in the third interval of the elytron ranges from three to five. The genitalia of one male was examined. It resembled that of the holotype in all respects.

Disposition of type material. – The holotype and one paratype are in the collections of the UMMZ, and the three other paratypes are in the collections of AMNH, CU, and UASM.

Geographical distribution (fig. 132). – This species is found in Alabama and Mississippi only. I have seen five specimens from the following localities.

United States – ALABAMA: Dallas County: Hazen (AMNH). Marengo County: south of Demopolis (UASM, UMMZ). MISSISSIPPI: Oktibbeha County: Agriculture College (CU).

The *sodalis* Group

Characteristics. – Penultimate article of labial palpus with five to seven setae. Pronotum subcordiform, sides moderately or strongly constricted posteriorly; anterior transverse impression complete or incomplete. Prosternal process with shallow or obsolete longitudinal groove, without setae at apex. Middle femur with 5 – 11 setae on anterior face. Male genitalia with median lobe slightly or moderately arcuate; internal sac with apical sclerite light amorphic plate usually with darker basal tooth, tooth sometimes unsclerotized. The species *sodalis, parasodalis, furtivus, alternans* and *iowensis* are included in this group. They occur across northeastern United States from New Jersey west to South Dakota, Nebraska, and Kansas, and south to northern Alabama and Arkansas.

Evarthrus sodalis LeConte, 1848

Frontispiece and Figures 38–48, 64, 111, 133

Feronia (Molops) sodalis LeConte, 1848:349. LECTOTYPE (here selected) a male, labelled as follows: "yellow disc; Type 5659; E. sodalis Lec. orbatus Lec." MCZ. TYPE LOCALITY, Illinois. – LeConte, 1852:229 (*Evarthrus*). – LeConte, 1870:5. – LeConte, 1873: 318. – Schaupp, 1880:49. – Blatchley, 1910:101. – Casey, 1918:356 (*Eumolops*). – Casey, 1920:197 (*Evarthrinus*). – Leng, 1920:57 (*Eumolops*). – Leonard, 1926:222. – Csiki, 1930:672 (*Pterostichus*).

Feronia (Molops) colossus LeConte, 1848:343. LECTOTYPE (here selected) a male, labelled as follows: "yellow disc; colossus 4." MCZ. TYPE LOCALITY, Missouri. NEW COMBINATION. – LeConte, 1852:233 (*Evarthrus*). – LeConte, 1863a:8. – LeConte, 1873: 318. – Schaupp, 1880:49. – Casey, 1918:356 (*Eumolops*). – Leng, 1920:57. – Csiki, 1930:672 (*Pterostichus*).

Feronia (Molops) corax LeConte, 1848:347. LECTOTYPE (here selected) a male, labelled as follows: "green disc; Type 5661; E. corax Lec." MCZ. TYPE LOCALITY, near Long's Peak. – LeConte, 1852:229 (*Evarthrus*). – Motschulsky, 1865:261. – LeConte, 1873: 318. – Schaupp, 1880:49. – Casey, 1918:357. – Leng, 1920:57. – Csiki, 1930:672 (*Eumolops*).

Feronia (Pterostichus) vagans LeConte, 1848:349. LECTOTYPE (here selected) a male, labelled as follows: "yellow disc; Type 5664; E. vagans Lec." MCZ. TYPE LOCALITY, Ohio. NEW SYNONYMY. – LeConte, 1852:229 (*Evarthrus*). – LeConte, 1863a:8. – LeConte, 1873:320. – Leng, 1920:57.

Evarthrus fatuus LeConte, 1852:233. LECTOTYPE (here selected) a male, labelled as follows: "yellow disc; Type 5060; E. fatuus LeC." MCZ. TYPE LOCALITY, Iowa. – LeConte, 1873:318 (*Evarthrus*). – Schaupp, 1880:49. – Casey, 1918:356 (*Eumolops*). – Casey, 1920:197 (*Evarthrinus*). – Leng, 1920:57 (*Eumolops*). – Csiki, 1930:672 (*Pterostichus*). – Lindroth, 1966:474.

Evarthrus furtivus; Blatchley, 1910:101 (not LeConte).

Evarthrinus (Evarthrops) retractus Casey, 1920:197. HOLOTYPE, female, labelled as follows: "L. CASEY bequest 1925; TYPE USNM 47132; retractus Csy." USNM. TYPE LOCALITY, "probably Indiana." NEW SYNONYMY. – Leng and Mutchler 1927:10 (*Evarthrinus*). – Csiki, 1930:673 (*Pterostichus*).

Evarthrinus inflatipennis Casey, 1924:78. HOLOTYPE, female, labelled as follows: "Ill.; CASEY bequest 1925; TYPE USNM 47133; inflatipennis Csy." USNM. TYPE LOCALITY, near Chicago, Illinois. NEW SYNONYMY. – Leng and Mutchler 1927:10 (*Evarthrinus*). – Csiki, 1930:673 (*Pterostichus*).

Eumolops sulcata Casey, 1918:355. HOLOTYPE, male, labelled as follows: "Fla; CASEY bequest 1925; TYPE USNM 47134; sulcata Casy." USNM. TYPE LOCALITY. FLORIDA (this locality is probably incorrect). NEW SYNONYMY. – Casey, 1920:196 (*Evarthrinus*). – Leng, 1920:57 (*Eumolops*). – Csiki, 1930:672 (*Pterostichus*).

Evarthrus lodingi Van Dyke, 1926:118. HOLOTYPE, male, labelled as follows: "Monte Sano, Ala. Madison Co. 6.9.11." H. P. Löding; Van Dyke Collection. CAS. TYPE LOCALITY, Monte Sano, Alabama. NEW COMBINATION. – Csiki, 1930:673 (*Pterostichus*). – Leng and Mutchler, 1933:13 (*Evarthrus*).

Recognition. – The species *alternans, furtivus, iowensis* and *parasodalis* are remarkably similar to *sodalis* in their external non-genitalic structures. Although some specimens of *sodalis* can be distinguished from individuals of the first four species by external features, the male genitalia are the only reliable diagnostic character of *sodalis*. The apical blade of the median lobe is elongate and narrow in *sodalis* while it is shorter and broader in the other species (fig. 111 cf. figs. 112, 113, 114, 115).

Description. – Body length 12.4 – 20 mm. Form robust.

Microsculpture: head between eyes with flattened amorphic meshes, disc of pronotum with highly sinuous entwined lines, or transversely directed lines, or meshes transversely stretched; intervals of elytra with isodiametric bead-like or flattened meshes, or highly sinuous lines.

Head moderately glossy; frontal grooves of average depth, not sharply defined, straight or with slight bend in middle, convexity directed medially. Penultimate article of labial palpus with five to seven setae.

Pronotum moderately glossy; shape subcordiform in outline as in figs. 38 – 48; disc of average convexity; sides moderately or strongly produced, constricted moderately anteriorly strongly posteriorly, sinuation in front of posterior angles well marked, moderate, slight, or absent; posterior angles produced or not, broadly obtuse or slightly acute; anterior transverse impression complete or incomplete; basal lateral fovea with sides usually but not always, continuous posteriorly; lateral bead same width throughout. Prosternal process with shallow, broadly excavated or obsolete longitudinal groove. Middle femur with five to eight setae on anterior face.

Elytra of males moderately glossy or iridescent, females dull; apical sinuation slight, obsolete, or absent; intervals flat, moderately convex, or highly convex; striae of average depth, punctate anteriorly, impunctate or obsoletely punctate posteriorly.

Male genitalia (fig. 111) with median lobe slightly arcuate, angle broadly obtuse; apical blade elongate, right side and apex deflected dorsally; right paramere of average length extending to halfway point of median lobe, rather broad, slightly tapered apically, apex broadly rounded; internal sac with serrulate apical field, apical sclerite light apically with darker basal tooth, or tooth not sclerotized. The genitalia of 21 males were examined in detail.

Stylus of female ovipositor elongate, slightly tapered apically.

Geographical variation and subspecies. – There are three populations which are more or less distinct in several structural features.

In Kansas and proximal areas specimens referred to the nominal species *colossus* are distinguished from typical *sodalis* by larger body size, more prominent posterior angles of the pronotum, and the absence of an apical sclerite of the internal sac of the median lobe of the male. Between these populations there are populations which have intermediate characteristics and therefore all of these groups appear to be the same species. Because of the differences I recognize a subspecies *s. colossus* west of the Mississippi River, and mainly south of the Missouri River, and an eastern subspecies mainly east of the Mississippi River and north of Alabama and Tennessee.

The third distinct form, formerly the species *lodingi*, occurs in Tennessee, and northern Alabama. It is distinguished from *s. sodalis* and *s. colossus* by highly convex and iridescent elytral intervals of the males. This iridescence is because of the microsculpture which is composed of numerous highly sinuous lines, placed very close to one another. Both *s. sodalis* and *s. colossus* have isodiametric meshes forming the microsculpture on the elytral intervals of the male. Furthermore, specimens from Alabama and Tennessee are generally larger than *s. sodalis* specimens. They also differ from *s. colossus* individuals by having an apical sclerite in the internal sac of the median lobe of the male. The few *sodalis* specimens which I have seen from Kentucky appear intermediate in structural features between those of Tennessee and Alabama, and Indiana, Illinois and Ohio. I believe the Alabama and Tennessee specimens form a third subspecies, *s. lodingi*.

Notes on synonymy. – The lectotype of *colossus* LeConte is a *sodalis* specimen larger than the average size and of the form which inhabits Kansas and Missouri.

The lectotype of *corax* LeConte, is an average *sodalis* specimen that inhabits western areas of this species range; and it is characterized by the small prominent basal angles of the pronotum.

The lectotype of *vagans* LeConte, is a *sodalis* specimen with very broadly rounded basal angles of the pronotum, which is the common condition of specimens in northern Ohio.

The lectotype of *fatuus* LeConte is a *sodalis* specimen with rectangular hind angles of the pronotum as in fig. 43. This form is common in eastern Iowa.

The type specimen of *inflatipennis* Casey is a *sodalis* specimen that is average for the form found in Illinois but slightly smaller in body size.

The type specimen of *sulcata* Casey is a *sodalis* specimen that is of the common form and size found in Illinois.

The type specimen of *lodingi* Van Dyke is a *sodalis* specimen of the common form inhabiting northern Alabama.

Collecting notes. – Specimens of *s. sodalis* and *s. colossus* are found in open grassy places under cover. G. E. Ball collected specimens of *s. sodalis* beside railroad tracks under ties near Ithaca, New York. I have taken *s. colossus* from under boards in pasture and abandoned farmyards in Kansas. The subspecies *s. lodingi* is forest adapted and occurs in leaf litter.

The gut of a female *s. colossus* specimen, which I examined, was full of the remains of ants.

Geographical distribution (fig. 133). – This species is widespread in northeastern United States ranging from Pennsylvania west to Kansas and Nebraska, south to northern Mississippi and Alabama, and north to Duluth, Minnesota.

E. s. sodalis LeConte

I have seen 664 specimens from the following localities.

Canada – ONTARIO: Point Pelee (Lindroth 1966).

United States – ILLINOIS: Adams County: five miles east of LaPrairie (CNHM). Bureau County: Princeton (UMMZ). Champaign County: Champaign (CNC, INHS, RTB, UASM); Seymour (MCZ); Urbana (CNHM, INHS, RTB, RU, UMMZ, UW). Cook County: Carle Woods (CNHM); Chicago (CAS, CNHM, CU, UASM, UMMZ, USNM, UW); Evanston (ASNP, CAS, UMMZ); Glencoe (CNHM, UMMZ); Palos Park (CAS, CNHM, UMMZ); River Forest (CNHM); River Grove (USNM); Summit (CNHM, INHS); West Northfield (MCZ); Willow Springs (CAS, CNHM, CNC, UMMZ). DuPage County: Glen Ellyn (CNHM). Lake County: Fort Sheridan (UMMZ); Lake Zurich (RTB); Ravinia (UMMZ). LaSalle County: Ottawa (RTB). McHenry County: Algonquin (INHS). McLean County: Bloomington (CNHM, CU, USNM); Normal (INHS). Mason County: Havanna (INHS). Ogle County: Oregon (UMMZ). Peoria County: Peoria (INHS). Putnam County: (INHS). Richland and Lawrence County: Wabash Valley (CM, MCZ, USNM). Rock Island County: Rock Island (UMMZ). Sangamon County: Springfield (CNHM). Vermilion County: Danville (INHS); Kickapoo State Park (RTB); Oakwood (INHS). Washington County: Dubois (INHS). Will County: Joliet (CNHM), Winnebago County: Rockford (CAS). Counties not determined: Edgebrook (UMMZ); Somerset (INHS). INDIANA: Cass County: (MCZ). Gibson County: (UMMZ); Princeton (USNM). Jefferson County: Clifty Falls State Park (GEB); Hanover (UMMZ). Knox County: Vincennes (USNM); Wheatland (UMMZ). Kosciusko County: Winona Lake (UMMZ). Lagrange County: Lagrange (UMMZ). Marion County: (MCZ, UP). Monroe County: Bloomington (UMMZ). Posey County: (CNHM); Mount Vernon (CNHM). Wells County: LaFayette (UMMZ). Warren County: Pine (CNHM). Wells County: Blufton (UMMZ). County not determined: Indiana Dunes State Park: (RTB). IOWA: Benton County: (UMMZ). Clayton County: McGregor (UMMZ). Des Moines County: Burlington (MCZ). Hamilton County: Randall (CNC). Johnson County: Iowa City (CAS, MCZ, UMMZ, USNM); Solon (USNM). Linn County: Cedar Rapids (UMMZ). Tama County: Traer (ISU). KENTUCKY: Edmonson County: Bee Spring (MCZ); Mammoth Cave National Park (TCB). Fayette County: Lexington (TCB). Franklin County: Stony Creek, north of Frankfort (UMMZ). Hardin County: Summit (CNHM). Harlan County: Cumberland Gap (MCZ). Henderson County (CNC). MICHIGAN: Jackson County: Jackson (TH). Kalamazoo County: Climax (UMMZ); Gull Lake Biology Station (TH). Lenawee County: Adrian (TH). Munroe County: (UMMZ). Oakland County: (UMMZ). Wayne County: Detroit (USNM). MINNESOTA: Houston County: Caledonia (UMMZ). St. Louis County: Duluth (MCZ). MISSISSIPPI: Tishomingo County: Cook's lodge near Iuka (UMMZ); six miles east of Iuka (FDPI). MISSOURI: Buchanan County: St. Joseph (USNM). NEW JERSEY: Morris County: Lincoln Park (CNHM). NEW YORK: Chautauqua County: Findley Lake (GEB); Mayville (GEB); Pendergast Creek, near Lake Chautauqua (GEB). Erie County: Buffalo (GEB); Hamburg (CAS). Tompkins County: Ithaca (GEB, FDPI, UA); Turner Hill

(GEB). Yates County: Dresden (UMMZ). Counties not determined: Van Cort'dt Park (CU); Windom (CU). OHIO: Allen County: Lima (UMMZ, USNM). Columbiana County: Salineville (CAS, CU). Cuyahoga County: Cleveland (MCZ). Darke County: (CAS); Beamville (UMMZ). Fairfield County: Millersport (CM). Franklin County: Columbus (CAS, MCZ, RU). Hamilton County: (CNHM); Cincinnati (ANSP, CAS, UMMZ). Licking County: Alexandria (RTB). Mercer County: Mendon (UMMZ). Ottawa County: Lakeside (UMMZ); Put-in-Bay, South Bass Island (UMMZ). Preble County: Eaton (UMMZ). PENNSYLVANIA: Allegheny County: (CM, CU); Pittsburgh (CM, RU). Erie County: (CM). Forest County: Cook's Forest (CM). Warren County: (UMMZ). Westmoreland County: Jeanette (CM). TENNESSEE: Knox County: Knoxville (CNC); 30 miles west of Knoxville (AMNH). WISCONSIN: Bayfield County: (MCZ). Dane County: (UW); Madison (UASM, UW). Dodge County: Beaver Dam (CAS, MCZ, TE, USNM). Green County: Albany (CAS, CNHM); Brodhead (UMMZ). Jefferson County: Fort Atkinson (GEB). Milwaukee County: (UW); Milwaukee (CAS). Racine County: Burlington (CNHM). Walworth County: Walworth (CNHM). County not determined: Rautubug (MCZ).

E. s. colossus LeConte

I have seen 151 specimens from the following localities.

United States – ARKANSAS: (UASM). IOWA: O'Brien County: four miles east of Sanborn (ISU). Woodbury County: Sioux City (UMMZ). KANSAS: Chase County: (UK). Doniphan County: Wathena (UASM, USNM). Douglas County: (UK); five miles north of Baldwin City (DL, RF); Lawrence (CAS, MCZ, UK, UMMZ). Franklin County: (UMMZ). Johnson County: Mission (UK). Lawrence County: (UMMZ). Leavenworth County: Leavenworth (CAS, CNHM); Tonganoxie (MCZ). Linn County: (UK). Pottawatomie County: Onaga (UK). Reno County: (ANSP). Riley County: (USNM); Manhattan (KSU, USNM). Shawnee County: Topeka (USNM). Wilson County: Benedict (CAS). Woodson County: two miles east of Yates Centre (DL, RF). MISSOURI: Boone County: Columbia (CNHM). Buchanan County: St. Joseph (USNM). Clinton County: Cameron (CAS); Lathrop (CNC). Jackson County: Kansas City (UK). Pettis County: Sedalia (CNHM). St. Louis (CAS, CNHM, USNM). County not determined: Pickle Springs (UMMZ). NEBRASKA: Cedar County: Randolph (MCZ). Knox County: Creighton (CAS).

E. s. lodingi Van Dyke

I have seen 53 specimens collected in the following localities.

United States – ALABAMA: Jackson County: Point Rock (UMMZ). Madison County: Monte Sano (CAS, MCZ, UASM, UK, UMMZ, USNM); Monte Sano State Park (CNHM). TENNESSEE: Cumberland County: Grassy Cove (CAS, UMMZ). Davidson County: Madison (CU); Nashville (AMNH, USNM). Maury County: Columbia (ANSP). County not determined: Cedar Glade (USNM).

Evarthrus parasodalis new species

Figures 49, 112, 133

Recognition. – The following combination of structures characterizes this species: pronotum with sides not sinuate or obsoletely sinuate in front of posterior angles, posterior angles not prominent and broadly obtuse; apex of median lobe of male genitalia short and broad, right paramere rather narrow apically; range, Arkansas. These features distinguish *parasodalis* from the similar *sodalis lodingi* which has the following corresponding features: pronotum with more produced sides, distinctly sinuate in front of posterior angles; apex of median lobe elongate and narrow, right paramere broader apically; known from northern Alabama and Tennessee.

Description. – HOLOTYPE, male, labelled as follows: "Washington Co., Ark. 1962 Trap A 29–VI; HOLOTYPE Evarthrus parasodalis R. Freitag (red label)." MCZ.

Body length 16.9 mm, width 7.1 mm. Form typical of *sodalis* group.

Microsculpture: head between eyes and disc of pronotum with isodiametric and amorphic meshes; intervals of elytra with transversely stretched meshes. Integument of dorsum moderately glossy.

Head length 1.9 mm, width 3.7 mm; frontal groove deep, broadly impressed, middle bend with convexity directed medially. Penultimate article of labial palpus with three medial and three apical setae.

Pronotum length 4.8 mm, width 5.9 mm; form subcordate in outline as in fig. 49; disc of average convexity; sides not prominent, constricted slightly anteriorly, moderately posteriorly, not sinuate in front of posterior angles; posterior angles not prominent, broadly obtuse; anterior transverse impression complete, obsoletely impressed medially; basal lateral foveae with sides not continuous posterio-medially, amorphic depression medially beside inner side; lateral bead gradually broadened posteriorly. Prosternal process with obsolete longitudinal groove. Anterior faces of middle femora with eight setae on one and 11 setae on the other.

Elytra length 10.2 mm, width 7.1 mm; sides slightly produced, obsoletely sinuate apically; intervals raised with flattened centres; striae deep with rather small indistinct punctures throughout.

Male genitalia (fig. 112): median lobe moderately arcuate; apical blade short, broad, apex evenly rounded; right paramere elongate, extended to apical half of median lobe, strongly tapered apically; internal sac with serrulate field apically, apical sclerite light amorphic plate with dark basal tooth.

ALLOTYPE, female, labelled as follows: "Washington Co. Ark. VII–16–1960; Forest leaf litter; Otis and Maxine Hite; ALLOTYPE Evarthrus parasodalis R. Freitag (green label)." MCZ.

Body length 16.8 mm, width 7.1 mm. Form same as in holotype except pronotum with sides more strongly constricted posteriorly.

Microsculpture on head between eyes and disc of pronotum same as in holotype; intervals of elytra with raised bead-like isodiametric meshes.

Pronotum moderately glossy; length 4.5 mm, width 5.6 mm.

Elytra dull; length 10.5 mm, width 7.1 mm.

Stylus of ovipositor elongate and quite tapered apically.

Derivation of specific name. – This species is closely related to *sodalis* which is what the name *parasodalis* connotes.

Variation among paratypes (41 males, 40 females, Arkansas). – Total length 15.6 – 19.3 mm. The genitalia of three males were examined in detail and in all respects resemble those of the holotype. One female specimen collected at Hot Springs has produced and rather sharp posterior angles of the pronotum.

Disposition of type material. – The holotype and allotype are in the collections of the MCZ. The paratypes are in the collections of the following: CU, INHS, RF, RTB, UASM and UA.

Collecting notes. – I collected a specimen of *parasodalis* in deciduous forest leaf litter on a hillside near Fayetteville, Arkansas.

Geographical distribution (fig. 133). – This species is known from Arkansas, only. I have seen 83 specimens from the following localities.

United States – ARKANSAS: Conway County: (UA). Franklin County: (UA). Garland County: Hot Springs (UMMZ). Montgomery County: north of Mount Ida (RTB). Washington County: (UA, UASM, CU); Cove Creek, 27 miles northwest of Fayetteville (RF); Cove Creek Valley (CU).

Evarthrus furtivus LeConte, 1852

Figures 50–51, 113, 133

Evarthrus furtivus LeConte, 1852:234. LECTOTYPE (here selected) a male, labelled as follows: "white disc: Type 5662; E. furtivus Lec." MCZ. TYPE LOCALITY, here restricted to Virginia. – LeConte, 1863a:8 (*Evarthrus*). – LeConte, 1873:319. – Schaupp, 1880:49. – Casey, 1918:355 (*Eumolops*). – Casey, 1920:195 (*Evarthrinus*). – Leng, 1920:57 (*Eumolops*). – Csiki, 1930:672 (*Pterostichus*).

Recognition. – Specimens of *furtivus* are extremely difficult to distinguish from individuals of *s. sodalis* by their external nongenitalic structures. The posterior angles of the pronotum of *furtivus* are less broadly rounded than those of *s. sodalis* in southwestern Pennsylvania where their geographical ranges overlap. For a certain identification however, it is necessary to examine the male genitalia.

Description. – Body length 13.0 – 17.0 mm. Form typical of the *sodalis* group with sides of pronotum and elytra somewhat convex.

Microsculpture: head between eyes and disc of pronotum with highly sinuous entwined lines, often almost effaced; intervals of elytra with bead-like or more flattened isodiametric meshes. Integument of dorsum moderately glossy; elytra slightly glossy in some specimens.

Head: frontal grooves not deep, not sharply defined, fairly straight, slightly oblique toward one another. Penultimate article of labial palpus with five setae.

Pronotum subcordiform in outline as in figs. 50 – 51; disc of average convexity; sides slightly or strongly produced, constricted moderately anteriorly, moderately or strongly posteriorly, obsoletely or distinctly sinuate in front of posterior angles; posterior angles produced or not produced, broadly obtuse; anterior transverse impression incomplete; basal lateral fovea with sides usually continuous posteriorly; lateral bead not broadened posteriorly. Prosternal process with shallow or obsolete longitudinal groove. Middle femur with five or six setae on anterior face.

Elytra with apical sinuation obsolete; intervals slightly convex or flat; striae distinct, not deep, indistinctly punctate anteriorly, obsoletely or impunctate posteriorly.

Male genitalia (fig. 113): median lobe slightly arcuate, angle broadly obtuse, apical blade short, broad with apex evenly rounded; right paramere extended to halfway point of median lobe, markedly tapered apically; internal sac with apical serrulate field, apical sclerite light, broad, somewhat triangular with apical end graded into serrulate field around genital opening. The genitalia of 11 males were examined.

Stylus of female ovipositor elongate, moderately tapered apically.

Geographical variation. – Specimens possessing pronota with somewhat sharp posterior angles are common in southwestern Pennsylvania, but decrease in number southward where specimens with more broadly rounded posterior angles are more numerous.

Geographical distribution (fig. 133). – This species ranges from southern Pennsylvania south to Virginia. I have seen 113 specimens collected in the following localities.

United States – DISTRICT OF COLUMBIA: Washington (USNM). MARYLAND: Montgomery County: (USNM). NEW JERSEY: Gloucester County: Malage (USNM). PENNSYLVANIA: Allegheny County: (CM); Pittsburg (CM). Cumberland County: New Cumberland (CAS, CU, MCZ); Shippensburg (UMMZ). Dauphin County: Harrisburg (CU, MCZ). Fayette County: Ohiopyle (CM). Philadelphia County: Germantown (ANSP); Philadelphia (CAS, MCZ). Westmoreland County: Jeanette (CM). Counties not determined: Inglenook (CAS); Rockville (ANSP, CAS, MCZ). VIRGINIA: Arlington County: Rosslyn (MCZ). Fairfax County: Mount Vernon (USNM). Henrico County: Richmond (AMNH). Nelson County: (USNM). Spotsylvania County: Fredricksburg (MCZ). Counties not determined: Blackpond (MCZ, USNM); Edsall (USNM); Glencarlyn (USNM); Merdon (USNM). WEST VIRGINIA: Pocahontas County: Swamp Creek (TCB).

Evarthrus alternans Casey, 1920

Figures 52, 114, 134

Evarthrinus (Evarthrops) alternans Casey, 1920:196. HOLOTYPE, male, labelled as follows: "Ia; CASEY bequest 1925; TYPE USNM 47131; alternans Csy." USNM. TYPE LOCALITY, Keokuk, Iowa. PARATYPE, female, labelled as follows: "Iowa, CASEY bequest 1925; alternans –2 PARATYPE 47131." USNM. – Leng and Mutchler 1927:10 (*Evarthrinus*). – Csiki, 1930:673 (*Pterostichus*).

Recognition. – The similar *sodalis colossus* is distinguished from *alternans* by structural details of the male genitalia and by the more laterally produced posterior angles of the pronotum (figs. 45–47 cf. fig. 52). These species are largely allopatric.

Description. – Body length 13.4 – 18.4 mm. Form robust notably constricted at base of pronotum.

Microsculpture: head between eyes with highly sinuous entwined lines, occasionally amorphic meshes formed; disc of pronotum with highly sinuous lines or transversely stretched meshes, often partially effaced; intervals of elytra with isodiametric meshes, bead-like in females, flatter in males.

Head moderately glossy; frontal grooves of average depth, somewhat broad, generally straight, slightly oblique toward one another. Penultimate article of labial palpus with six setae.

Pronotum moderately glossy; shape somewhat cordiform in outline as in fig. 52; disc of average convexity; sides markedly produced, moderately constricted anteriorly, strongly and sharply constricted posteriorly, markedly sinuate in front of posterior angles; posterior angles produced, almost right or slightly obtuse; anterior transverse impression incomplete; basal lateral fovea with sides usually continuous posteriorly, medial side with anterior end directed laterally; lateral bead not broad posteriorly. Prosternal process with shallow or obsolete longitudinal groove. Middle femur with six to nine setae on anterior face.

Elytra of males slightly glossy, females dull; apical sinuation obsolete or absent; intervals slightly convex, almost flat; striae of average depth, with small distinct punctures anteriorly, obsoletely punctate or impunctate posteriorly.

Male genitalia (fig. 114): median lobe moderately arcuate, broadly obtuse; apical blade short, broad, with apex very broadly rounded, almost truncate slightly deflected dorsally; right paramere extended to apical half of median lobe, slightly tapered apically; internal sac with serrulate field apically, preapical sclerite light near genital opening with darker basal tooth. The genitalia of 20 males were examined.

Stylus of female ovipositor elongate, slightly tapered apically.

Collecting notes. – Members of this species are found under cover in open grassy places.

Geographical distribution (fig. 134). – Members of this species are common in a relatively restricted range in Iowa and margins of peripheral states. I have seen 830 specimens from the following localities.

United States – ILLINOIS: Adams County: five miles northeast of La Prairie (CNHM). Hancock County: Pilot Knob State Park (ISU). Macoupin County: Chesterfield (RTB). Pike County: Rockport (CAS). IOWA: Appanoose County: Moulton (UMMZ). Boone County: Boone (ISU); Ledges State Park (ISU). Crawford County: (MCZ); Denison (AMNH). Dallas County: Perry (ISU). Davis County: (CAS). De Moines County: Burlington (MCZ). Dickenson County: Cayler Prairie (ISU); Lakeside Laboratory (ISU). Hamilton County: Blairsburg (ISU); five miles south of Stanhope (ISU); Randall

(ISU). Hardin County: Iowa Falls (CNHM). Henry County: Mount Pleasant (CAS, UASM, UMMZ). Johnson County: Iowa City (ANSP, MCZ, UASM, USNM). Lee County: Fort Madison (MCZ). Linn County: Cedar Rapids (UMMZ); Palisades (USNM). Lucas County: Chariton (USNM). Marshall County: State Centre (CU); ten miles west of Marshall Town (ANSP). Montgomery County: Red Oak (ISU). O'Brien County: four miles east of Sanborn (ISU). Page County: Shenandoah (ISU). Palo Alto County: Ruthuen (UMMZ). Plymouth County: Le Mars (ISU). Pochahontas County: Kaslow (ISU). Polk County: Des Moines (ISU). Pottawattamie County: Council Bluffs (ISU). Sioux County: Hawarden (VMK). Story County: Ames (AU, CAS, CU, ISU, MCZ, MSU, UMMZ, USNM, UW); four miles east of Gilbert (ISU); Maxwell (ISU); Nevada (UASM); Soper's Mill Dam near Gilbert (ISU). Tama County: Traer (ISU, USNM). Van Buren County: (ISU). Wayne County: Lineville (ISU). Webster County: three miles west of Dayton (ISU). Winnebago County: Forest City (UMMZ). Thompson (ISU). Counties not determined: Boonsboro (MCZ); Harold (CU); Lake Okoboji (USNM). MINNESOTA: Lincoln County: Lake Benton (VMK). MISSOURI: Livingston County: six miles north of Chilloeothe (ISU). St. Louis County: (CU); Overland (CAS); St. Louis (USNM). County not determined: Onandaga Cave (UMMZ). SOUTH DAKOTA: Brookings County: Brookings (VMK); White (VMK). Deuel County: Gary (VMK). WISCONSIN: Bayfield County: (MCZ).

Evarthrus iowensis new species

Figures 53, 115, 134

Recognition. – The following combination of characteristics is diagnostic for the species *iowensis*: small size; pronotum usually with complete anterior transverse impression; elytra with first two umbilicate punctures of umbilicate series with normally raised areas around them, and third puncture as large as either first or third; and form of male genitalia. Specimens of *alternans* generally resemble individuals of *iowensis* but are distinguished by the larger body size, sides of pronotum more strongly constricted posteriorly, incomplete anterior transverse impression of pronotum, and relatively longer right paramere of male genitalia.

The species *substriatus* and *constrictus* also strikingly resemble *iowensis*. In *substriatus* and *constrictus* however the first and second anterior umbilicate punctures have areas between them which are flatter than the normal condition, and the third puncture is distinctly larger than the first two. In addition the male genitalia are different (fig. 115 cf. figs. 116, 117 and 118).

Description. – HOLOTYPE, male, labelled as follows: "Iowa City, Iowa 5–15 Buchanan; Loan from USNM: HOLOTYPE Evarthrus iowensis R. Freitag (red label)." USNM.

Body length 11.7 mm, width 5.0 mm. Form less robust than other species of *sodalis* group.

Microsculpture of head between eyes, disc of pronotum, and intervals of elytra with highly sinuous somewhat sparsely distributed lines, partially effaced. Integument of dorsum glossy.

Head length 1.4 mm, width 2.8 mm; frontal grooves shallow and broad, slightly curved with middle bend directed medially. Penultimate article of labial palpus with two medial and three apical setae.

Pronotum length 3.2 mm, width 4.1 mm; form subcordate in outline as in fig. 53; disc of average convexity; sides prominent, constricted moderately anteriorly and strongly posteriorly, distinctly sinuate in front of posterior angles; posterior angles prominent, sharp, slightly obtuse; anterior transverse impression complete, distinctly impressed throughout; basal lateral fovea with sides continuous posteriorly; lateral bead not broad posteriorly. Prosternal process with longitudinal groove obsolete. Middle femur with five setae on anterior face.

Elytra length 7.1 mm, width 5.0 mm; sides slightly produced, not sinuate apically; intervals almost flat; striae of average depth, indistinctly punctate throughout. Third interval of each elytron with two setae.

Male genitalia (fig. 115): median lobe moderately arcuate; apical blade short, broad, apex evenly rounded, almost truncate; right paramere not extended to apical half of median lobe, strongly tapered apically; internal sac with apical serrulate field, apical sclerite light with darker basal tooth.

ALLOTYPE, female, labelled as follows: "Iowa City, Iowa IV.14 Wickham; Wickham Collection 1933; loan from USNM; ALLOTYPE Evarthrus iowensis R. Freitag (green label)." USNM

Body length 11.5 mm, width 4.9 mm. Form same as in holotype.

Microsculpture on head between eyes and disc of pronotum same as in holotype; intervals of elytra with raised, bead-like isodiametric meshes.

Pronotum glossy; length 3.0 mm, width 3.1 mm.

Elytra slightly glossy; length 7.1 mm, width 4.9 mm.

Stylus of ovipositor slightly tapered apically, apex broadly rounded.

Derivation of specific name. – This species is named *iowensis* because much of its range is in Iowa.

Variation among paratypes (16 males, 15 females, Iowa, Minnesota, South Dakota). – Total length 11.2 – 13.9 mm. The genitalia of five males were examined and varied little or not at all from that of the holotype. The elytra of females are duller than those of the males. The number of setae in the third interval of an elytron varies from one to three.

Disposition of type material. – The holotype and allotype are in the collections of the USNM. The paratypes are in the following collections: CAS, CU, ISU, KLE, MCZ, UASM, UMMZ, USNM, and VMK.

Collecting notes. – V. M. Kirk has collected specimens of *iowensis* in corn fields in southeastern South Dakota.

Geographical distribution (fig. 134). – This species is confined to Iowa, Minnesota and South Dakota. I have seen 33 specimens from the following localities.

United States – IOWA: Dickinson County: Cayler Prairie (ISU, UASM). Howard County: Elma (USNM). Johnson County: Iowa City (USNM). Story County: Ames (ISU). Woodbury County: Sioux City (UMMZ). MINNESOTA: Olmsted County: Rochester (CU). SOUTH DAKOTA: Brookings County: Brookings (VMK). Hutchinson County: Menno (VMK). Yankton County: Yankton (VMK)

The *substriatus* Group

Characteristics. – Penultimate article of labial palpus with four or five setae. Pronotum with sides strongly constricted posteriorly; anterior transverse impression complete or not complete. Prosternal process with shallow or obsolete longitudinal groove without setae apically. Middle femur with four to seven setae on anterior face. First two anterior punctures of umbilicate series of elytra without normally raised ridges around them, third umbilicate puncture distinctly larger than first two. Median lobe of male genitalia strongly arcuate; internal sac with elongate narrow amorphic plate.

This group includes *substriatus* and *constrictus* whose aggregate geographical range includes the grasslands of central United States and northwestern Mexico.

Evarthrus substriatus LeConte, 1848

Figures 54, 77–78, 116–117, 134

Feronia (Molops) substriata LeConte, 1848:344. LECTOTYPE (here selected) a female, labelled as follows: "green disc; Type 5616; E. substriatus Lec." MCZ. TYPE LOCALITY, near the Rocky Mountains. – LeConte, 1852:233 (*Evarthrus*). – LeConte, 1858:28. – LeConte, 1863a:8. – LeConte, 1873:319. – LeConte, 1876:519. – Schaupp, 1880:49. – Casey 1918:343 (*Anaferonia*). – Leng, 1920:56. – Csiki, 1930:671 (*Pterostichus*).

Evarthrus latebrosus LeConte, 1852:233. LECTOTYPE (here selected) a male, labelled as follows: "green disc; Type 5617; E. latebrosus Lec." MCZ. TYPE LOCALITY, Missouri Territory. – LeConte, 1863a:8 (*Evarthrus*). – LeConte, 1873:319. – Schaupp, 1880:49. – Leng, 1920:56 (*Anaferonia*). – Csiki, 1930:671 (*Pterostichus*).

Anaferonia evanescens Casey, 1918:343. HOLOTYPE, female, labelled as follows: "Mex; CASEY bequest 1925; TYPE USNM 47100; evanescens Csy." USNM. TYPE LOCALITY, Colonia Garcia, Sierra Madre Mts., Chihuahua, Mexico. NEW SYNONYMY. – Csiki, 1930:671 (*Pterostichus*). – Leng and Mutchler, 1933:12.

Anaferonia pantex Casey, 1918:344. HOLOTYPE, female, labelled as follows: "Tex; CASEY bequest 1925; TYPE USNM 47099; Anaferonia pantex Csy." PARATYPES, two males and three females, labelled as follows: "Tex; CASEY bequest 1925; pantex –2 to pantex –6; PARATYPE USNM 47099." USNM. NEW SYNONYMY. – Csiki, 1930:671 (*Pterostichus*). – Leng, 1920:56 (*Anaferonia*).

Recognition. – The species *substriatus* can be separated from the structurally similar *constrictus* by the following characters: elytra with marked apical sinuation, plica large; last external abdominal sternum with prominent dorsal lateral knob that articulates with plica (more distinct in females); elytral striae almost effaced in some specimens; apex of apical blade of median lobe of male evenly rounded. In contrast with these the structures of *constrictus* are as follows: elytra with slight apical sinuation; plica average for subgenus; last external abdominal sternum with slightly raised mound that fits onto plica; elytral striae always distinctly impressed; apex of apical blade of median lobe more truncate.

Specimens of *iowensis* also can be mistaken for those of *substriatus*. The structures that distinguish them are recorded in the recognition section of *iowensis*.

Description. – Body length 9.5 – 14.5 mm. Form short with broad pronotum.

Microsculpture: head between eyes and disc of pronotum with sparsely distributed sinuous lines and/or amorphic meshes, largely effaced; intervals of elytra with isodiametric meshes.

Head slightly or moderately glossy; frontal grooves of average depth, bent medially with convexity directed medially. Penultimate article of labial palpus with four or five setae.

Pronotum moderately or slightly glossy; shape in outline as in figs. 54–55; disc of average convexity; sides markedly produced, moderately constricted anteriorly, strongly constricted posteriorly, strongly sinuate in front of posterior angles; posterior angles prominent, approximately right; anterior transverse impression complete or not complete; basal lateral fovea with sides continuous posteriorly, shape as in fig. 54. Prosternal process with shallow or obsolete longitudinal groove. Middle femur with four to six setae on anterior face.

Elytra slightly glossy; apical sinuation sharply defined (fig. 78); intervals slightly convex or completely flat; one to three setae on the third interval of elytron; striae very shallow with impunctate obsolete dashes, or of average depth and indistinctly punctate; plica large and prominent (fig. 77).

Last external abdominal segment with prominent dorsolateral knob which fits onto plica.

Male genitalia (fig. 116 – 117): median lobe strongly arcuate, angle approximately right; apical blade elongate, apex evenly rounded, right paramere extended to halfway point of median lobe or shorter, apically slightly curved or straight, tapered apically; internal sac with apical serrulate field, apical sclerite light, elongate. The genitalia of 23 males were studied.

Stylus of female ovipositor of average size, slightly tapered apically.

Geographical variation. – The pronotum is not markedly constricted posteriorly in specimens from the southern end of the species range. In specimens from the state of Durango, Mexico, for example, the sides of the pronotum are generally less prominent than those of fig. 54. Further north in the state of Chihuahua, Mexico, specimens have a pronotum with produced sides (fig. 54). The shape of the pronotum gradually changes northward until the common condition is a pronotum with strongly produced sides and a marked posterior constriction, which is like that of *constrictus* shown in fig. 55.

There is also a south-north cline in the depth of the striae of the elytra. In Mexico the striae are obsolete and impunctate. These become gradually deeper and more distinctly punctate northward.

The intervals of the elytra correspondingly change clinally from a completely flat condition in Mexico to distinctly convex in Kansas and Nebraska.

The male genitalia of Durango specimens differ from those of individuals from the rest of the species range (fig. 117 cf. fig. 116). In Durango, the median lobe is usually strongly arcuate, and the right paramere is slightly curved. Further north the median lobe is more broadly rounded and the right paramere is straighter.

Notes on synonymy. – The lectotype of *latebrosus* LeConte is a *substriatus* specimen with impressed elytral striae.

The type specimen of *evanescens* Casey represents an average *substriatus* specimen that is found in northern Mexico. The type specimen of *pantex* Casey is a *substriatus* specimen of the average kind found in Texas.

Collecting notes. – G. E. Ball collected specimens of this species in dry pine forest in Mexico, and under tumbleweed in desert areas of New Mexico. Specimens are also found under cover in open places such as pastures and corn fields.

Geographical distribution (fig. 134). – This species ranges from Durango, Mexico, north to southern Wyoming and Minnesota, and from eastern Arizona east to the eastern regions of Nebraska, Kansas, Oklahoma and Texas. I have seen 525 specimens from the following localities.

Mexico – CHIHUAHUA: Guerrero (USNM); Miñaca (GEB); 31.9 miles south of Miñaca (GEB). DURANGO: Arroyo Hondo near LaFlor (DRW, GEB); Ciudad (AMNH); 18 miles east of El Salto (AMNH); J. Manuel 9300', El Salto (CAS); Otinapa (DRW, GEB); two miles east of La Ciudad (CNC).

United States – ARIZONA: Cochise County: Huachuca Mountains (GEB). Pima County: Madera Canyon, St. Rita Mountains (GEB). COLORADO: Fremont County: Canon City (UASM). Huerfano County: Walsenburg (UMMZ). Las Animas County: Trinidad (USNM). Logan County: Sterling (AMNH, USNM). Prowers County: Granada (CAS, MCZ).

County not determined: Regnier (AMNH). KANSAS: Chase County: Elmdale (KSU). Clark County: (CNC, UK). Dickinson County: (CNHM). Douglas County: (UK). Ford County: (UMMZ); Dodge City (UK). Geary County: Fort Riley (CAS); Junction City (UMMZ). Gove County: (UK). Hamilton County: (CNHM, UK). Harvey County: Sedgewick (CAS, USNM). Kearny County: Lakin (MCZ). Kiowa County: Belvidere (UK). Meade County: (USNM). Ness County: Ness City (UK). Pottawatomie County: Onaga (CAS). Reno County: (UMMZ, USNM). Riley County: (USNM); Manhattan (FDPI, KSU, USNM). Scott County: Scott City (USNM). Sedgwick County: Mount Hope (USNM). Shawnee County: Topeka (CNHM, USNM). Sheridan County: State Lake, near Studley (RF, UK). Sherman County: five miles west of Goodland (RF); Goodland (CAS). Thomas County: Colby (RF). Wallace County: (CAS, UK, USNM); Sharon Springs (CNHM). Wilson County: Benedict (UK). MINNESOTA: Hennepin County: Bloomington (AMNH). NEBRASKA: Furnas County: Cambridge (MCZ). Lancaster County: Lincoln (CAS). Red Willow County: Indianola (MCZ). NEW MEXICO: Colfax County: Raton (CAS). Lincoln County: Ruidoso (CAS). McKinley County: Coolidge (AMNH, MCZ, USNM); near Ramah (GEB). Otero County: Cloudcroft (ANSP, CAS, CNHM, CNC, GEB, MCZ, UASM, UK, USNM); Mescalero Reservation (MCZ); Sacramento (MCZ); Sacramento Mountains (CAS); 16 Springs Canyon, Sacramento Mountains (GEB). Quay County: Tucumcari (MCZ, USNM). San Miguel County: Las Vegas (CAS); Las Vegas near Hot Springs (UK); Porvenir (CAS). Santa Fe County: Sante Fe (ANSP, CAS). Torrance County: Tajique (UK). County not determined: Tajano Experimental Station (CAS). OKLAHOMA: Beckham County: (CAS). Cleveland County: Norman (CAS). Comanche County: Fort Sill Military Reservation (UMMZ); Wichita National Forest (CAS, UMMZ). Custer County (CAS). Garfield County: Enid (AMNH). Harmon County: seven miles southwest of Hollis (UMMZ). Oklahoma County: Oklahoma City (CAS). Woods County: (CAS). SOUTH DAKOTA: Yankton County: Yankton (VMK). TEXAS: Baylor County: eight miles south of Seymour (CNHM). Bastrop County: Bastrop State Park (CNC). Bexar County: Somerset (CAS). Blanco County: (UMMZ); Round Mountain (AMNH, CAS, CNHM, RU). Brazos County: College Station (RU). Brewster County: Alpine (USNM); two miles south of Alpine (CAS). Brown County: Brownwood (RU). Comal County: New Braunfels (USNM). Coryell County: Gatesville (AMNH). Crockett County: Ozona (AMNH). Dallam County: Rita Blanca Lake, Dalhart (AMNH). Dallas County: Dallas (MCZ). DeWitt County: Cuero (AMNH). Edwards County: eight miles northeast of Rocksprings (TCB). Gillespie County: Fredricksburg (RU). Hays County: San Marcos (CNHM). Howard County: Big Spring (CAS, USNM). Jeff Davis County: Davis Mountains (CAS); Davis Mountains, six – ten miles west of Fort Davis (GEB); Davis Mountains, 10 miles north of Fort Davis (DL); Fort Davis (CNC, MCZ); Limpia Canyon (DRW, GEB). Kerr County: Kerrville (CNC); nine miles southwest of Kerrville (GEB); 20 miles southeast of Kerrville (CNC). Kleberg County: Riviera (DRW). Llano County: Llano (AMNH). Pecos County: Blackstone Ranch, 16 miles south of Sheffield (GEB); Fort Stockton (UMMZ). Runnels County: Ballinger (RU). San Patricio County: Lake Corpus Christi (UMMZ). Taylor County: Abiline (AMNH, CAS); 25 miles southwest of Abiline (CNHM). Terrell County: Chandler Ranch (GEB); 16 miles north of Dryden (GEB). Tom Green County: Christoval (AMNH, TAM); San Angelo (RU). Travis County: (UMMZ); Austin (CAS, MCZ, USNM). Uvalde County: one mile south of Montell (TCB); Uvalde (CNHM). Wichita County: Wichita Falls (CAS). Williamson County: Georgetown (TCB); Leander (TCB). County not determined: Camp Bullis (DRW). WYOMING: Laramie County: Cheyenne (UMMZ).

Evarthrus constrictus Say, 1823

Figures 55, 79–80, 118, 134

Feronia constricta Say, 1823b:147. Type lost. TYPE LOCALITY, Arkansas River near the Rocky Mountains. – LeConte, 1848:344 (*Feronia*). – LeConte, 1852:233 (*Evarthrus*). – LeConte, 1863a:8. – LeConte, 1873:319. – Schaupp, 1880:49. – Casey, 1918:345 (*Anaferonia*). – Leng, 1920:56. – Csiki, 1930:671 (*Pterostichus*). – Van Dyke, 1943:27 (*Anaferonia*). – Blackwelder and Blackwelder, 1948:2 (*Evarthrus*).

Feronia (Molops) ovipennis LeConte, 1848:345. LECTOTYPE (here selected) a female, labelled as follows: "green disc; Type 5619; E. ovipennis Lec." MCZ. TYPE LOCALITY, near the Rocky Mountains. – LeConte, 1852:232 (*Evarthrus*). – LeConte, 1863a:8. – LeConte, 1873:319. – Schaupp, 1880:49. – Casey, 1918:343 (*Anaferonia*). – Leng, 1920:56. – Csiki, 1930:671 (*Pterostichus*). – Van Dyke, 1943:26 (*Evarthrus*). – Blackwelder and Blackwelder, 1948:2.

Anaferonia vernicata Casey, 1918:344. HOLOTYPE, male, labelled as follows: "N. M. CASEY bequest 1925; TYPE USNM 47105; vernicata Csy." USNM. TYPE LOCALITY, Alamogordo, New Mexico. NEW SYNONYMY. – Leng, 1920:56 (*Anaferonia*). – Csiki, 1930:671 (*Pterostichus*).

Anaferonia pimalis Casey, 1918:345. HOLOTYPE, female, labelled as follows: "Ari; CASEY bequest 1925; TYPE USNM 47106; pimalis Csy." USNM. TYPE LOCALITY, Southern Arizona. NEW SYNONYMY. – Leng, 1920:56 (*Anaferonia*). – Csiki, 1930:671 (*Pterostichus*).

Anaferonia latebrosus; Casey, 1918:346 (not LeConte).

Anaferonia pudica Casey, 1918:346. HOLOTYPE, female, labelled as follows: "Tex; CASEY bequest 1925; TYPE USNM 47101; pudica Csy." USNM. TYPE LOCALITY, Texas. NEW SYNONYMY. – Leng, 1920:56 (*Anaferonia*). – Csiki, 1930:671 (*Pterostichus*).

Anaferonia papago Casey, 1918:346. HOLOTYPE, female, labelled as follows: "Ari; CASEY bequest 1925; TYPE USNM 47102; papago Csy." USNM. TYPE LOCALITY, Arizona. NEW SYNONYMY. – Leng, 1920:56 (*Anaferonia*). – Csiki, 1930:671 (*Pterostichus*).

Anaferonia lixa; Leng, 1920:56 (not LeConte).

Pterostichus (Pterostichus) (Sect *Anaferonia) lixa*; Csiki, 1930:671 (not LeConte).

Recognition. – Specimens of *constrictus, substriatus* and *iowensis* are structurally similar. Their distinguishing features are described in the recognition sections of the two preceeding species.

Description. – Body length 9.5 – 12.8 mm. Form relatively less robust than other species of the subgenus *Evarthrus.*

Microsculpture: head between eyes, disc of pronotum with lines partially or completely effaced; sparsely distributed sinuous lines; intervals of elytra with largely effaced to distinct isodiametric meshes.

Head glossy; frontal grooves of average depth, curved with convexity directed medially. Penultimate article of labial palpus with two median and four apical setae.

Pronotum glossy; shape as in fig. 55; disc strongly convex; sides markedly produced, strongly constricted posteriorly with marked sinuation in front of posterior angles; posterior angles produced, acute or nearly so; anterior transverse impression complete; basal lateral fovea with sides continuous posteriorly. Prosternal process with shallow or obsoletely impressed longitudinal groove. Middle femur with six or seven setae on anterior face.

Elytra of males moderately glossy; females slightly duller; apical sinuation not sharply defined (fig. 80); intervals of average convexity or slightly flatter; striae distinctly impressed with small punctures anteriorly; impunctate posteriorly; plica not prominent (fig. 79).

Last external abdominal segment with low dorsal convexity articulating with plica.

Male genitalia (fig. 118) with median lobe strongly arcuate, angle almost right, ventral median hump present or absent; apical blade elongate, apex almost truncate, apical lateral edges strongly deflected dorsally; right paramere extended to halfway point of median lobe, slender apically; internal sac with serrulate field apically, apical sclerite dark, elongate. The genitalia of 11 males were examined.

Stylus of female ovipositor of average size, slightly tapered apically.

Notes on synonymy. – The original description of *constrictus* Say was used to identify this species. The lectotype of *ovipennis* LeConte is an average specimen of *constrictus*. The type specimens of *vernicata* Casey, *pimalis* Casey, *pudica* Casey, and *papago* Casey are all average *constrictus* specimens.

Collecting notes. – This species has been collected in corn fields, and open pasture under rocks.

Geographical distribution (fig. 134). – The range of this species extends as a relatively narrow band from Arizona east to Kansas and Nebraska. I have seen 218 specimens from the following localities.

United States – ARIZONA: Apache County: eight – 15 miles northeast of White River (AMNH); McKay's Peak, White Mts. (AMNH); White Mts. (AMNH, CAS, MCZ); Springville (UMMZ); White Mountain Reservation, east of McNary (AMNH). Coconino County: five miles northwest of Flagstaff (AMNH); eight miles south of Flagstaff (GEB); Flagstaff (CAS); 23 miles southwest of Heber (UMMZ); Williams (CAS, USNM). Gila County: Globe (MCZ). Navajo County: Heber (UMMZ); Show Low (CAS). COLORADO: Denver County: Denver (CAS). El Paso County: Colorado Springs (AMNH, CAS, MCZ, USNM). Huerfano County: Gardner (AMNH); LaVeta (CAS). Otero County: LaJunta (MCZ). Prowers County: Granada (CAS, MCZ). Pueblo County: (MCZ). County not determined: Clayton (CNHM). IOWA: Woodbury County: Sioux City (USNM). Clark County: (CAS, CNHM, MCZ, UASM, UK). Douglas County: (UK). Ford County: Dodge City (UK). Grove County: (UK). Greeley County: (UK). Hamilton County: (UK). Harvey County: Sedgewick (CAS). Reno County: (UMMZ, USNM); Hutchinson (CAS); Medora (UK). Scott County: Scott City (USNM). Wallace County: (UK); Sharon Springs (CNHM); Wallace (USNM). County not determined: Fort Hayes (MCZ). NEBRASKA: Lancaster County: Lincoln (CAS). NEW MEXICO: Catron County: Luna (UMMZ); seven miles south of Luna (AMNH). Colfax County: Koehler (USNM); Prairie, near Koehler (CAS, USNM). Quay County: Tucumcari (USNM). San Doval County: Jemez Mountains (CAS). San Miguel County: Beulah (ANSP, CAS); Las Vegas (INHS); Porvenir (CAS). Counties not determined: Pinedale (GEB); Tres Ritos (CAS); Water Canon (UK). SOUTH DAKOTA: Hutchinson County: Menno (VMK). Yankton County: Yankton (VMK). County not determined: Cedar Pass (USNM). TEXAS: Bell County: Belton Dam (CU). Bexar County: 20 miles north of San Antonio (CAS). Hemphill County: Canadian (CAS). McLennan County: China Springs (CNHM). Tarrant County: Fort Worth (MCZ). Travis County: Austin (MCZ).

The *torvus* Group

Characteristics. – Penultimate article of labial palpus with five to seven setae. Pronotum more or less quadrate, not markedly constricted posteriorly, disc usually rugose, sides not very prominent, distinctly sinuate in front of posterior angles; anterior transverse impression complete. Prosternal process with shallow or obsolete longitudinal groove, without setae. Middle femur with six – ten setae on anterior face. Male genitalia with apical blade of median lobe relatively short and evenly rounded.

The species *torvus* and *gravidus* are included in this group. Both occur west of the Mississippi River and occupy the Great Plains from Texas north to South Dakota.

Evarthrus torvus LeConte, 1863

Figures 56–57, 119–120, 135

Evarthrus torvus LeConte, 1863b:9. LECTOTYPE (here selected) a male, labelled as follows: "Col; Type 5657; E. torvus Lec." MCZ. TYPE LOCALITY, Colorado. – LeConte, 1863a:8 (*Evarthrus*). – Schaupp, 1880:49. – Casey, 1918:356 (*Eumolops*). – Leng, 1920:57. – Csiki, 1930:672 (*Pterostichus*).

Feronia (Evarthrus) acuminata Chaudoir, 1868:52. LECTOTYPE, male, one of two unlabelled specimens of both sexes, beside which is a box label: "Tejas." MHNP. NEW SYNONYMY.

Eumolops prominens Casey, 1918:353. HOLOTYPE, female, labelled as follows: "Fla; CASEY bequest 1925; TYPE USNM 47128; prominens Csy." USNM. TYPE LOCALITY, Florida (this locality is probably incorrect). NEW SYNONYMY. – Leng, 1920:57 (*Eumolops*). – Csiki, 1930:672 (*Pterostichus*).

Eumolops sexualis Casey, 1918:354. HOLOTYPE, male, labelled as follows: "N. M.; CASEY bequest 1925; TYPE USNM 47124; Eumolops sexualis, Csy." USNM. TYPE LOCALITY, New Mexico. PARATYPE, one male and one female, labelled as follows: "N. M.; CASEY bequest 1925; *sexualis* –2 and *sexualis* –3; PARATYPE USNM 47124." NEW SYNONYMY. – Leng, 1920:57 (*Eumolops*). – Csiki, 1930:672 (*Pterostichus*).

Eumolops inflatula Casey, 1918:354. HOLOTYPE, female, labelled as follows: "Col; CASEY bequest 1925; TYPE USNM 47127; inflatula Csy." USNM. TYPE LOCALITY, Akron, Colorado. NEW SYNONYMY. – Leng, 1920:57 (*Eumolops*). – Csiki, 1930:672 (*Pterostichus*).

Eumolops (Evarthrinus) decepta Casey, 1918:357. HOLOTYPE, female, labelled as follows: "Ind; CASEY bequest 1925; TYPE USNM 47356; Evarthrinus deceptus Csy." USNM. TYPE LOCALITY, Indiana (this locality is incorrect). NEW COMBINATION. – Casey 1920:194 (*Evarthrinus*). – Leng, 1920:57 (*Eumolops*). – Csiki, 1930:672 (*Pterostichus*).

Eumolops (Evarthrinus) impolita Casey, 1918:358. HOLOTYPE, male, labelled as follows: "Tex; CASEY bequest 1925; TYPE USNM 47130; impolita Csy." USNM. TYPE LOCALITY, Texas. PARATYPE, female, labelled as follows: "Tex; CASEY bequest 1925; impolita –2 PARATYPE USNM 47130." USNM. NEW SYNONYMY. – Casey, 1920:195 (*Evarthrinus*). – Leng, 1920:57 (*Eumolops*). – Csiki, 1930:673 (*Pterostichus*).

Evarthrinus (Evarthrinus) minax Casey, 1920:194. HOLOTYPE, male, labelled as follows: "L; CASEY bequest 1925; TYPE USNM 47124; minax Csy." USNM. TYPE LOCALITY, Indiana (this locality is probably incorrect). PARATYPE, female, labelled as follows: "Ind; CASEY bequest 1925; minax –2 PARATYPE USNM 47129." USNM. NEW SYNONYMY. – Leng and Mutchler 1927:10 (*Evarthrinus*). – Csiki, 1930:673 (*Pterostichus*).

Recognition. – The following characteristics are diagnostic for *torvus*: pronotum moderately constricted anteriorly and posteriorly, subcordiform, almost quadrate, sides not strongly produced (figs. 56–57), disc and basal fovea rugose north and west of Oklahoma; male genitalia (figs. 119–120).

Specimens of the similar species *gravidus* are generally broader than are those of *torvus*. In addition the pronotum of *gravidus* is more quadrate with distinctly crenulated sides in front of the basal angles, and the sides of the basal foveae are not continuous posteriorly (fig. 58). Further these two species can be separated by their different genitalic structures, (figs. 119–120 cf. fig. 121).

Specimens of *iowensis* are also similar to southern *torvus* individuals. The species are allopatric and are also distinguished by their genitalia (fig. 115 cf. figs. 119–120).

Description. – Body length 12.7 – 19.5 mm. Form robust or slender and elongate. Microsculpture: head between eyes and disc of pronotum with sinuous lines distinctly defined or effaced; intervals of elytra with isodiametric meshes occasionally slightly stretched longitudinally.

Head moderately glossy; frontal grooves of average depth, somewhat broad, curved with convexity directed medially. Penultimate article of labial palpus with five or six setae.

Pronotum slightly or moderately glossy, more or less rugose or smooth; shape as in figs. 56–57; disc of average convexity; sides not strongly produced, slightly or moderately constricted anteriorly, moderately constricted posteriorly, distinctly sinuate in front of posterior angles; posterior angles prominent, approximately right; anterior transverse impression complete; basal lateral fovea markedly rugose or not, sides almost always continuous posteriorly. Prosternal process with longitudinal groove slightly impressed or obsolete. Middle femur with six to nine setae on anterior face.

Elytra glossy to dull; apical sinuations slight or obsolete; intervals distinctly convex to flat; one to three setae on third interval; striae of average depth, with small distinct punctures in anterior half, impunctate posteriorly.

Male genitalia (figs. 119–120) with median lobe moderately arcuate, angle broadly obtuse; apical blade of average length or shorter, apex evenly rounded; right paramere extended to apical half of median lobe or shorter, strongly tapered apically; internal sac with apical serrulate field, apical sclerite light, elongate, basal and curled in or not. The genitalia of 11 males were examined.

Stylus of female ovipositor of average size, slightly tapered apically.

Geographical variation and subspecies. – This species can be divided into two geographically separate groups of populations, one south and east of Oklahoma, the other north and west of Oklahoma. In Oklahoma there are intermediate forms. Specimens of western and northern populations are characterized by the following structures: body form robust; pronotum with disc and basal lateral foveae deeply rugose; elytra of male glossy, female slightly glossy, usually one seta in third interval; scutellar striae present; median lobe of male with apical blade of average length; internal sac of median lobe with light apical sclerite recurved basally. The corresponding structures of southern specimens differ as follows: body more slender and elongate; pronotum with disc and basal lateral foveae with normal sculpturing; elytra of males slightly glossy, females matte, two or three setae normally in third interval; scutellar striae absent; apical blade of median lobe short; internal sac with light apical sclerite not recurved basally.

I regard these populations as subspecies, *torvus torvus* north and west of Oklahoma, and *torvus deceptus* further south and east.

Notes on synonymy. – The lectotype of *torvus* is similar to the common form that inhabits Colorado. The type specimens of *prominens* Casey, *sexualis* Casey, and *inflatula* Casey all look like the lectotype of *torvus* LeConte. The type specimens of *decepta* Casey, *impolita* Casey, and *minax* Casey are the average specimens from southern portions of this species range that have dull elytra and three punctures in the third interval of the elytron.

Collecting notes. – D. J. Larson and I collected *t. torvus* specimens under logs in a dried out stream bed near Castle Rock, Colorado and under boards in a farmyard near Colby, Kansas. G. E. Ball collected some specimens under rocks near the river, Cache la Poudre, Colorado. Specimens have also been taken in corn fields.

Geographical distribution (fig. 135). – This species inhabits the Great Plains from southern Texas north to South Dakota.

E. torvus torvus

I have seen 307 specimens from the following localities.

United States – ARKANSAS: Hempstead County: Hope (UMMZ). COLORADO: Adams County: Bennett (CAS). Boulder County: Boulder (CNC). Clear Creek County: Empire (CAS). Denver County: Denver (CAS, CNHM, CU, GEB, USNM). Douglas County: ten miles north of Castle Rock (DL, RF). Jefferson County: Golden (CAS). Larimer County: Fort Collins (CAS, KSU, RTB); Loveland (CAS); Poudre Canyon (GEB). Weld County: Greeley (CAS). Counties not determined: Genessee Mountain Park (CAS); Lookout Mountain (CAS). IOWA: Louisa County: Oakville (ISU). O'Brien County: four miles east of Sanborn (ISU). KANSAS: Chase County: Elmdale (KSU). Cheyenne County: (KSU). Clay County: (ANSP, CAS, UMMZ, USNM). Doniphan County: Wathena (USNM). Douglas County: (CU, KSU, MCZ); five miles north of Baldwin City (DL). Geary County: Junction City (UMMZ). Harper County: Harper (USNM). Kiowa County: Belvidere (KSU). Marion County: Marion (CAS). Pottawatomie County: Onaga (CAS, MCZ, USNM, UW). Riley County: (CNHM, USNM); Manhattan (KSU, USNM). Sedgwick County: Mount Hope (ANSP, UMMZ, USNM). Sherman County: Goodland (CAS, CNHM). Sumner County: Wellington (USNM). Thomas County: Colby (RF). Wabaunsee County: (KSU). Wallace County: Sharon Springs (CNHM); Wallace (KSU). Wilson County: (CNHM); Benedict (CAS). Wyandotte County: Argentine (AMNH, MCZ). MISSOURI: Carter County: Van Buren (UMMZ). Greene County: Willard (ANSP). St. Charles County: St. Charles (MCZ). Vernon County: (GEB). NEBRASKA: Cedar County: Randolph (MCZ). Furnas County: Cambridge (MCZ). Hall County: Jct. U. S. 34 and Platte River near Grand Island (GEB). Lancaster County: Lincoln (CAS, CNHM, USNM). Phelps County: Holdredge (CAS). Platte County: near Platte (CAS). Red Willow County: McCook (USNM). NEW MEXICO: Dona Ana County: near Rincon (MCZ). Otero County: Bent (CU); Cloudcroft (CAS, GEB, MCZ, USNM); Mescalero Reservation (CU). San Miguel County: Gallinas Cañon (MCZ); Las Vegas (CAS, INHS, KSU); Sapello Creek (GEB). OKLAHOMA: Canadian County: Yukon (CAS). Cleveland County: (CAS). Kingfisher County: Kingfisher (ANSP). Murray County: (CAS). Tulsa County: Tulsa (CAS, CNHM). County not determined: Wichita National Forest (CAS). SOUTH DAKOTA: Custer County: (VMK). Fall River County: five miles south of Hot Springs (AMNH). Lawrence County: Spearfish (VMK). TEXAS: Hidalgo County: Edinburg (UMMZ), (probably incorrectly labelled).

E. torvus deceptus

I have seen 28 specimens collected in the following localities.

United States – TEXAS: Dallas County: Dallas (MCZ, RTB). DeWitt County: Cuero (AMNH). El Paso County: El Paso (CM). Grayson County: Sherman (MCZ). Grimes County: Roans Prairie (AMNH). Lee County: Fedor (CM). Montague County: Forestburg (UMMZ). Tom Green County: Cristoval (AMNH).

Evarthrus gravidus Haldeman, 1853

Figures 58, 121, 135

Evarthrus gravidus Haldeman, 1853:361. Type lost. TYPE LOCALITY, Texas (here selected). – LeConte, 1858:28 (*Evarthrus*). – LeConte, 1863a:8. – LeConte, 1873:318. – Schaupp, 1880:49. – Casey, 1918:354 (*Eumolops*). – Leng, 1920:57. – Csiki, 1930:672 (*Pterostichus*).

Eumolops ampla Casey, 1918:353. HOLOTYPE, female, labelled as follows: "Tex.; CASEY bequest 1925; TYPE USNM 47126; ampla Csy." USNM. TYPE LOCALITY, Texas. NEW SYNONYMY. – Leng, 1920:57 (*Eumolops*). – Csiki, 1930:672 (*Pterostichus*).

Recognition. – The robustness of the body, crenulate sides near the basal angles of the pronotum, and lateral basal foveae of pronotum broad with sides not continuous posteriorly, combined, distinguish members of *gravidus* from specimens of all other species of *Evarthrus*.

The pronotum of specimens of *torvus* is more constricted posteriorly than that of specimens of *gravidus*. Also the sides of the basal lateral foveae of the pronotum are continuous posteriorly in *torvus* but not in *gravidus*.

Description. – Body length 15.5 – 21.7 mm. Form robust.

Microsculpture: head between eyes and disc of pronotum with sinuous lines and amorphic meshes, sometimes partially effaced; intervals of elytra with isodiametric meshes. Integument of dorsum moderately glossy.

Head: frontal grooves of average depth, bent with convexity directed medially. Penultimate article of labial palpus with six or seven setae.

Pronotum with surface more or less rugose; shape somewhat quadrate as in fig. 58; disc of average convexity; sides not strongly produced, moderately constricted anteriorly, slightly constricted posteriorly, slightly sinuate in front of posterior angles, crenulated posteriorly; posterior angles sharp, approximately right; anterior transverse impression complete; basal lateral fovea with sides usually not continuous posterio-medially. Prosternal process with longitudinal groove shallow or obsolete. Middle femur with eight to ten setae on anterior face.

Elytra slightly or obsoletely sinuate apically; intervals of normal convexity or completely flat; one to three setae on third interval; striae of average depth or more shallow, apical two thirds with small punctures, impunctate posteriorly.

Male genitalia (fig. 121): median lobe strongly arcuate, angle slightly acute; apical blade short with apex evenly rounded; right paramere large, extended to apical third of median lobe, moderately tapered apically; internal sac with apical serrulate field, apical sclerite light, elongate, with basal tooth. The genitalia of four males were examined.

Stylus of female ovipositor slightly tapered apically with apex broadly rounded.

Notes on synonymy. – I selected Texas as the type locality because *gravidus* is known from Texas only. The type specimen of *ampla* Casey is an average *gravidus* specimen.

Geographical distribution (fig. 135). – This species is confined to Texas. I have seen 137 specimens from the following localities.

United States – TEXAS: Collin County: Plano (USNM). Comal County: New Braunfels (CU, USNM). Dallas County: Dallas (USNM). El Paso County: El Paso (CAS). Kerr County: Kerrville (CNC). Lee County: Fedor (CAS, CM). McLennan County: China Springs (CNHM); Waco (MCZ). Montague County: Forestburg (UMMZ). Travis County: Austin (MCZ, USNM). Victoria County: Victoria (USNM). County not determined: Therman (MCZ).

The *gigas* Group

Characteristics. – Body size large. Penultimate article of labial palpus with five or six setae. Pronotum strongly constricted posteriorly, posterior angles prominent, anterior transverse impression complete, prosternal process with obsolete longitudinal groove. Middle femur with 7 – 11 setae on anterior face. Male genitalia with short, stub-like, right paramere and apical blade of median lobe twisted 45° from horizontal plane, or right paramere long and apical blade with left side deflected dorsally.

The species *gigas, heros* and *sallei* form this group. All three are known from eastern Texas, southern Oklahoma, and Arkansas.

Evarthrus sallei LeConte, 1873

Figures 59, 122, 136

Evarthrus sallei LeConte, 1873:319. LECTOTYPE (here selected) a male, labelled as follows: "9; red disc; Type 5663; E. sallei Lec." MCZ. TYPE LOCALITY, Texas. – Schaupp, 1880:49 (*Evarthrus*). – Casey, 1918:356 (*Eumolops*). – Leng, 1920:57. – Csiki, 1930: 672 (*Pterostichus*).

Recognition. – The following combination of characteristics is diagnostic of this species: basal lateral fovea of pronotum with sides continuous posteriorly forming straight base; elytra with marked apical sinuation, intervals of males with transversely stretched meshes comprising microsculpture; male genitalia with reduced stub-like paramere, apical blade of median lobe twisted 45° from horizontal plane.

The subspecies *sodalis colossus* is similar to *sallei* in general appearance, but the basal lateral fovea is U-shaped at the base. In addition these species are allopatric.

Description. – Body length 18 – 21 mm. Form robust, body with relatively parallel sides.

Microsculpture: head between eyes and disc of pronotum with sparsely distributed sinuous lines often effaced or nearly so; intervals of males with transversely stretched meshes, females with isodiametric meshes.

Head moderately to markedly glossy; frontal grooves of average depth, bent medially with convexity directed medially. Penultimate article of labial palpus with five setae.

Pronotum moderately or slightly glossy; shape as in fig. 59; disc of average convexity; sides strongly produced, moderately constricted anteriorly, strongly constricted posteriorly, sharply sinuate in front of posterior angles; posterior angles very prominent, acute; anterior transverse impression complete; basal lateral fovea with sides continuous posteriorly forming straight base. Middle femur with seven or eight setae on anterior face.

Elytra of males moderately glossy iridescent in a few specimens, females less glossy; apical sinuation sharply defined; intervals distinctly convex in males, slightly convex in females. Striae of average depth, distinctly punctate anteriorly, apical parts indistinctly punctate.

Male genitalia (fig. 122) median lobe strongly arcuate, angle slightly obtuse, often with low ventral medial bump; apical blade short with apex evenly rounded, twisted more than 45° from horizontal plane; right paramere very small, stub-like; internal sac with serrulate field apically, apical sclerite dark elongate tooth. The genitalia of four males were examined.

Stylus of female ovipositor slightly tapered apically with broadly rounded apex.

Geographical distribution (fig. 136). – This species is known from Texas, only. I have seen 48 specimens from the following localities.

United States – TEXAS: Comal County: New Braunfels (USNM). Dallas County: (CAS, INHS, UMMZ); Dallas (CAS, INHS, KSU, MCZ, USNM). Jackson County: (USNM); Baroncuhua (USNM). Victoria County: Victoria (USNM).

Evarthrus gigas Casey, 1918

Figures 60, 123, 136

Megasteropus gigas Casey, 1918:350. HOLOTYPE, female, labelled as follows: "Tex; CASEY bequest 1925; TYPE USNM 47123; Megasteropus gigas Csy." USNM. TYPE LOCALITY, Texas. PARATYPE, female, labelled as follows: "Tex; CASEY bequest 1925; gigas –2 PARATYPE USNM 47123." USNM. – Leng, 1920:57 (*Megasteropus*). – Csiki, 1930:672 (*Pterostichus*).

Recognition. – The combination of large body size, elytra with flat intervals and very shallow impunctate striae, and male genitalia (fig. 123), distinguishes *gigas* from all other species of *Evarthrus*. Specimens of *heros* superficially resemble individuals of *gigas* but are distinguished by their distinctly punctate elytral striae.

Description. – Body length 19.4 – 23.8 mm. Form robust.

Microsculpture: head between eyes and disc of pronotum with sinuous lines, almost effaced in males, very dense in females; intervals of elytra with isodiametric, flat meshes in males, markedly amorphic meshes in females.

Head markedly glossy in males, slightly so in females; frontal grooves short, of average depth, sometimes bent with convexity directed medially. Penultimate article of labial palpus with five setae.

Pronotum markedly glossy in males, slightly glossy in females; shape as in fig. 60; disc of average convexity; sides strongly produced, moderately constricted anteriorly, strongly constricted posteriorly, sharply sinuate in front of posterior angles; posterior angles acute and very prominent; anterior transverse impression complete; basal lateral fovea with sides not continuous posteriomedially. Middle femur with seven to ten setae on anterior face.

Elytra of males markedly glossy, those of females slightly glossy; distinctly sinuate apically; intervals completely flat. Striae very shallowly impressed almost effaced, impunctate, series of dashes rather than continuous lines in some specimens.

Male genitalia (fig. 123) with median lobe strongly arcuate, angle slightly obtuse, large lobe-like evagination ventromedially; apical blade twisted more than 45° from horizontal plane; right paramere very small, stub-like; internal sac with apical serrulate field, apical sclerite dark elongate tooth. The genitalia of three males were examined.

Stylus of female ovipositor slightly tapered apically with broadly rounded apex.

Geographical distribution (fig. 136). – This species inhabits southeastern Texas. I have seen 22 specimens from the following localities.

United States – TEXAS: Kleberg County: Kingsville (CU). Victoria County: Victoria (USNM).

Evarthrus heros Say, 1823

Figures 61, 65, 76, 124, 136

Feronia heros Say, 1823b:145. Type lost. TYPE LOCALITY, "The Arkansa." MCZ. – LeConte, 1848:350 (*Feronia*). – LeConte, 1852:233 (*Evarthrus*). – Haldeman, 1853: 361. – LeConte, 1858:28. – LeConte, 1863a:8. – LeConte, 1873:318. – Schaupp, 1880:49. – Casey, 1918:352. – Leng, 1920:57. – Csiki, 1930:672 (*Pterostichus*). – Van Dyke, 1943:27 (*Eumolops*). – Blackwelder and Blackwelder, 1948:2 (*Evarthrus*).

Feronia (Pterostichus) americana; LeConte, 1848:350 (not Dejean).

Megasteropus gigas; Van Dyke, 1943:27 (not Casey).

Recognition. – The following combination of characteristics is diagnostic of *heros*: large body size; scutellar stria of elytron long, separate from second stria; base of second stria beginning near basal seta; intervals of elytra very shallow, usually indicated by rows of distinctly impressed punctures; apex of median lobe of male with left side deflected dorsally.

Specimens of the similar species *gigas* are distinguished from *heros* by possession of very shallow impunctate elytral striae.

Description. – Body length 18.7 – 27.1 mm. Form robust.

Microsculpture: head between eyes and disc of pronotum with sinuous lines, sometimes almost effaced; intervals of elytra with isodiametric meshes.

Head glossy; frontal grooves of average depth, usually bent posteriorly with convexity directed laterally. Penultimate article of labial palpus with five or six setae.

Pronotum glossy; shape as in fig. 61; disc of average convexity; sides strongly produced, moderately constricted anteriorly, strongly constricted posteriorly, sharply sinuate in front of posterior angles; posterior angles produced and acute; anterior transverse impression complete; basal lateral foveae with sides not continuous posteriomedially. Middle femur with 9 – 11 setae on anterior face (fig. 76).

Elytra of males markedly glossy, those of females moderately glossy, slightly sinuate apically; intervals completely flat; striae very shallowly impressed, usually only rows of punctures; scutellar stria long and separated from second stria which begins near basal seta (fig. 65).

Male genitalia (fig. 124) with median lobe moderately arcuate, angle broadly obtuse; apical blade with left side of apex deflected dorsally; right paramere extended to apical half of median lobe; internal sac with apical serrulate field, apical sclerite elongate light plate. The genitalia of five males were examined.

Stylus of female ovipositor slightly tapered apically with broadly rounded apex.

Collecting notes. – The original description of *E. heros* was used to identify this species. Specimens of this species have been collected in cotton fields.

Geographical distribution (fig. 136). – This species is found in Arkansas, Oklahoma, and eastern Texas. I have seen 69 specimens from the following localities.

United States – ARKANSAS: County not determined: Arkansa (MCZ). OKLAHOMA: McCurtain County: Millerton (USNM). TEXAS: Collin County: Plano (USNM). Comal County: New Braunfels (CNHM, USNM). Cooke County: Gainesville (USNM). Dallas County: Dallas (ANSP, CNHM, MCZ, UMMZ, USNM). Delta County: Cooper (USNM). Ellis County: Waxahachic (USNM). Fannin County: Ladonia (USNM). Lee County: (UMMZ). McLennan County: Waco (CAS). Montague County: Forestburg (UMMZ).

The *gravesi* Group

Characteristics. – Body size average. Penultimate article of labial palpus with three setae. Pronotum constricted posteriorly, posterior angles prominent, sides of basal fovea not continuous posteriorly, anterior transverse impression complete; posterior lateral setae on bead. Middle femur with four setae on anterior face. Plica of elytron absent. Only one species, *gravesi*, is included in this group.

Evarthrus gravesi new species

Figures 62, 136

Recognition. – The combination of the glossy dorsum, form of the pronotum, and complete anterior transverse impression, absence of the plica of the elytron, and four setae on the anterior face of the middle femur, distinguishes *E. gravesi* from all the other species of *Evarthrus*. The general habitus of *gravesi* resembles that of *substriatus* or *constrictus*.

Description. – HOLOTYPE, female, labelled as follows: "Pearl (Jackson) Rankin Co. Miss. 23–III–1959 R. C. & A. Graves; HOLOTYPE Evarthrus gravesi R. Freitag." MCZ.

Body length 12.8 mm., width 5.5 mm. Form robust.

Microsculpture on head between eyes effaced; sparsely distributed, almost effaced, sinuous lines on disc of pronotum; isodiametric meshes on intervals of elytra. Dorsum glossy.

Head length 1.5 mm., width 3.0 mm.; frontal grooves of average depth, sharply defined, straight, oblique. Penultimate article of labial palpus with three setae: two medial and one apical.

Pronotum length 3.5 mm., width 4.5 mm.; form cordiform in outline as in fig. 62; disc moderately convex; sides produced, constricted slightly anteriorly, strongly posteriorly, distinctly sinuate in front of posterior angles; posterior angles produced, obtuse; anterior transverse impression complete and deeply impressed. Middle femur with four setae on anterior face; lateroventral margins of last article of tarsus with setae.

Elytra length 7.8 mm., width 5.6 mm.; not sinuate apically; plica absent; intervals moderately convex; intervals deeply impressed and indistinctly punctate.

Stylus of ovipositor broad, slightly tapered apically.

This is the only specimen of this species seen by me. The position of the type locality is indicated on fig. 136.

Derivation of specific name. – The type specimen was collected by Dr. Robert C. Graves, Department of Biology, Bowling Green State University, Ohio. This species is named in honour of the collector.

FOSSIL MATERIAL

Of the nominal fossil species *Evarthrus tenebricus* Scudder, only the head is preserved. Scudder (1900) placed it in the genus *Evarthrus* "on account of the brevity of the last joint of the labial palpus." This structure is not diagnostic for the genus *Evarthrus*. Furthermore the other characteristics given by Scudder in his description are common to many carabid genera. I have not seen the specimen. It may or may not be a member of the genus *Evarthrus*.

PHYLOGENY AND ZOOGEOGRAPHY OF THE SPECIES OF *EVARTHRUS* LECONTE

Phylogeny

My views concerning the phylogeny of *Evarthrus* are based on structural similarities and differences of extant species, because a fossil record is not available. Fig. 137 is a time divergence dendrogram of the history of *Evarthrus*. It is based on the principle that similar organisms are related. Species that have many similar structures are closely related, while those which are dissimilar are more remotely related. Since rate of divergence is unknown the slopes of the branches of the dendrogram are not significant.

To determine the relationships of the genus *Evarthrus*, I compared its characteristics with those of a representative selection of Nearctic and Palaearctic genus-group taxa of the tribe Pterostichini. I believe *Evarthrus* is most closely related to the *Molops* group (tribe Molopini Jeannel, 1942 and 1948) of Europe and Africa. Among other structures the three that *Evarthrus* and the *Molops* group share, and which I regard as patristic affinities are: pleura and thoracic and abdominal sterna impunctate; basal portion of interval 7 of the elytron raised and not deflected downward like other intervals; and antennae of larva with five articles each (Van Emden, 1942).

Because the genera *Evarthrus* and *Pterostichus* have many structural similarities a word about their relationships is necessary. A remarkably stable characteristic of *Pterostichus* is the presence of punctures on the ventral sclerites, particularly in the groove of the mesepisternum. Rarely the punctures are feebly developed but they usually can be found on the mesepisternum. Also the known larvae of species of *Pterostichus* have antennae of four articles each. Because adults of *Evarthrus* and of the *Molops* group have impunctate ventral sclerites and the larvae have antennae of five articles, and are similar to *Pterostichus* in most other features, I believe *Pterostichus* is a distant relative of these genera.

The progenitor of the genus *Evarthrus* probably had characteristics which are present in extant species of the *Molops* group and *Evarthrus*, and some which are widespread in other pterostichine genera. The hypothetical ancestor of *Evarthrus* probably possessed in combination the primitive states of characters presented in Table 1. Advanced conditions of these characters are also listed in Table 1, and illustrate the extent of evolutionary change. The determination of the trends of change in these characters or morpho-clines (Maslin 1952) provide a basis for establishing a phylogeny of *Evarthrus*.

One trend that is apparent is the increase of body size in all three subgenera and it is most evident in the subgenus *Evarthrus*. The largest species of this subgenus are specialized, and there is no doubt that large size is the specialized condition.

Another evolutionary trend is in the increase in the number of setae of the penultimate article of the labial palpus. Most of the species in *Fortax* and *Cyclotrachelus* have two setae, several species have three, or four, while *E. unicolor* has four, five, or six setae. In the subgenus *Evarthrus* most species possess five or six setae.

Two setae on the penultimate article of the labial palpus is the primitive condition because it is common in pterostichine genera which are related to *Evarthrus*. Similarly the setae on the anterior face of the middle femur tend to increase in number. Four setae is the common condition in *Fortax, Cyclotrachelus*, and in the less specialized species of the subgenus *Evarthrus*. This is probably the primitive condition. The setae range in number from seven to eleven in specialized species of the subgenus *Evarthrus*.

There are two distinct trends in the direction of the eversion of the internal sac of the median lobe. The internal sac everts dorsoapically in all species of *Cyclotrachelus*. In the subgenus *Fortax*, the internal sac tends to evert to the left while in the subgenus *Evarthrus* the eversion is to the right. The intermediate dorsoapical eversion is probably the primitive state.

TABLE I. Primitive and Specialized conditions of some characters of *Evarthrus*.

CHARACTER	PRIMITIVE	ADVANCED
BODY:		
Size	Small	Large
Colour	Black	Unchanged
Surface	Glossy	Dull
Venter	Impunctate	Unchanged
MICROSCULPTURE:		
Head, pronotum and elytra	Almost effaced, sinuous, sparsely distributed lines	Amorphic meshes or isodiametric meshes
HEAD:		
Frontal grooves	Deep, straight, parallel	Shallow, crescent-shaped, oblique
Gula	Without knobs on each side	Flanked by raised knobs
Penultimate article of labial palpus	With two medial setae	With more than two medial setae
PRONOTUM:		
Outline, dorsal aspect	Quadrate	Cordate
Basal angles	Not prominent	Prominent
Anterior transverse impression	Complete with medial portion feebly present	Medial portion absent or medial portion clearly impressed
Basal lateral fovea	Monostriate	Bistriate or punctiform
Basal seta	Near basal angle beside lateral bead	In front of basal angle on lateral bead
PROSTERNAL PROCESS:		
Basal and preapical portion	With obsoletely impressed longitudinal groove	With deep longitudinal groove
Apex	Not marginate, glabrous	Marginate with setae
METEPISTERNUM:	Short	Unchanged
ELYTRA:		
Intervals	Low convexity	High convexity
Interval 3	With one puncture	With two or more punctures
Interval 7	Raised at base	Unchanged
Striae	Shallow, finely punctate	Deeply impressed or coarsely punctate
Umbilicate series	Distinct ridges separating first three anterior punctures	Without distinct ridges between first three anterior punctures
Plica	Small	Large or absent
LEGS:		
Colour	Rufopiceous	Red
Middle femur	With four setae on anterior face	With more than four setae on anterior face
Basal article of middle and hind tarsus	With lateral groove	Without lateral groove
Last tarsal article	With ventral lateral setae	Without ventral lateral setae
ABDOMEN:		
Last external sternum of female	With two setae	Unchanged
MALE GENITALIA:		
Median lobe	Moderately arcuate	Strongly arcuate or slightly arcuate
Right paramere	Extended to halfway point of median lobe	Very long or very short and stub-like
Eversion of internal sac	Dorsoapical	Right or left
Apex of internal sac	With light apical serrulate field	With serrulate field and sclerite
FEMALE GENITALIA:		
Stylus	Slightly tapered apically	Broadly rounded apically or strongly tapered apically

The progenitor of *Evarthrus* probably differentiated into the "ancestors" of the subgenus *Fortax* and the *Cyclotrachelus-Evarthrus* lineage. The *Fortax* ancestor acquired a cordiform pronotum and the basal foveae became deeper posteriorly and shorter. Most of the structures of the ancestor of the *Cyclotrachelus-Evarthrus* group underwent slight modifications. The *Fortax* stock diverged into the *morio* group and *obsoletus* group lineages. The basic stock of the *morio* group lost the ventral lateral setae of the last tarsal articles. It differentiated and first gave rise to *laevipennis* which acquired sharp and somewhat produced basal angles of the pronotum, but retained a relatively primitive eversion of the internal sac. A later stock in which a left eversion of the internal sac developed, diverged into *morio* and *hernandensis*. The primitive stock of the *obsoletus* group acquired a cordiform pronotum with punctiform basal lateral foveae and basal setae which were developed anteriorly a short distance in front of the basal angles. It evolved into the extant species *obsoletus* in which developed a modified median lobe of the male, and the progenitor of *iuvenis* and *approximatus*. The latter two species inherited a more primitive median lobe, but *iuvenis* acquired a derived eversion of the internal sac, to the left and when everted curled around the left ventral side of the median lobe. This type of eversion is convergent with that of *hernandensis* and *morio* because *iuvenis* is not closely related to them.

The basic stock of *Cyclotrachelus* acquired a modified pronotum with constricted posterior sides and basal setae which became situated in the head. It retained the.primitive monostriate basal lateral foveae of the pronotum, and dorsoapical eversion of the internal sac of the median lobe.

The complementary stock which gave rise to the subgenus *Evarthrus* gained more setae on the penultimate article of the labial palpus. It also acquired modified bistriate basal lateral foveae of the pronotum and an internal sac that everted to the right.

The ancestral stock of the subgenus *Cyclotrachelus* differentiated into two stocks. One gave rise to the *spoliatus* group. It retained the primitive internal sac with an apical sclerite. The other evolved into the *ovulum-faber* complex, and it acquired a light-colored sclerite in the internal sac. The species *brevoorti* is the earliest derivative of the *spoliatus* group because the other members of the group are more closely related to one another than to *brevoorti*. It evolved a modified truncate apex of the median lobe and lost the apical serrulate field of the internal sac. The stock complementary to *brevoorti* gave rise to *unicolor* and the ancestor of *fucatus* and *spoliatus*. It retained the primitive apex of the median lobe and light serrulate apical field in the internal sac. The species *unicolor* gained a few extra setae on the penultimate article of the labial palpus, and evolved a modified internal sac. The progenitor of *fucatus* and *spoliatus* perhaps closely resembled the latter. The acquisition of an extra seta on the penultimate article of the labial palpus of some *fucatus* individuals is probably a recent modification.

The species *vinctus* evolved early in the history of the *ovulum-faber* complex for it is not closely related to any of the other members of the group. It inherited the primitive sclerite of the internal sac, and evolved produced, sharp, basal angles of the pronotum. The sister stock of *vinctus* acquired a cleft apical sclerite characteristic of the *ovulum* group and the *faber* group. The one which differentiated into *alabamensis* and the ancestor which gave rise to *texensis*, *macrovulum* and *ovulum* evolved sharp, produced basal angles of the pronotum.

The early derivative *alabamensis* acquired a deep longitudinal groove in the prosternal process, and lost the glossiness of the elytra, while its diverging sister stock developed crescent-shaped frontal grooves on the head before evolving into the ancestor of *macrovulum* and *texensis* and *ovulum*. The species *ovulum* developed a deep longitudinal groove in the prosternal process, but the ancestral stock, *macrovulum-texensis* retained the primitive condition of that structure. Recently, *macrovulum* evolved a short paramere, while the paramere of *texensis* has not changed from the primitive condition. The three members of the *faber* group possess a deep groove in the prosternal process which was probably a feature inherited from the ancestral stock of this group. It first gave rise to *parafaber*, a somewhat distant relative of *faber* and *levifaber*, which retained the cleft apical sclerite of the internal sac. Later the sister stock of *parafaber* acquired a modified C-shaped sclerite of the internal sac and then differentiated into *faber* and *levifaber*.

Returning to the ancestor of the subgenus *Evarthrus*, this stock differentiated into two stocks. One stock retained four setae on the anterior face of the middle femur, and then it evolved the ancestor of the *incisus* group and the progenitor of the *blatchleyi* and *sigillatus* groups. The other stock gained an extra seta on the anterior face of the middle femur, and it gave rise to the *seximpressus* group ancestor and the forerunner of the rest of the lineages in the subgenus *Evarthrus*.

The posterior constriction of the pronotum, short right paramere and median dorsal hump on the median lobe of the male, and the dark elongate apical sclerite of the internal sac, which are characteristic of *incisus* and *whitcombi*, were modifications acquired by their common ancestor.

A change in the shape of the basal lateral foveae of the pronotum and formation of a deep medial longitudinal groove in the prosternal process were modifications which occurred in the stock that gave rise to the ancestors of the *blatchleyi* and *sigillatus* groups. Both characteristics are present in all of the extant species of the two groups.

The ancestor of *blatchleyi* and *floridensis* probably evolved a slightly arcuate median lobe and narrow apical blade; both extant species probably resemble their common ancestor in most features.

The primitive stock that differentiated into *sigillatus* and the ancestor of *sinus* and *convivus* acquired a light-colored apical sclerite in the internal sac but retained the primitive type of median lobe and parameres of the male. Because the male genitalia of *sigillatus* are unlike that of *convivus* and *sinus*, I believe *sigillatus* is an earlier derivative of this lineage. The species *sigillatus* probably evolved as the sister stock of the ancestor of *convivus* and *sinus*. Geographical variation in non-genitalic structures of *sigillatus* such as the shape of the pronotum and elytra is probably evidence of recent differentiation. The ancestor of *convivus* and *sinus* acquired modified genitalia which were inherited by both species.

One of the extraordinary structural modifications in the history of *Evarthrus* was the acquisition of apical setae on the prosternal process by the basic stock of the *seximpressus* group. This ancestor gave rise to two stocks: one which differentiated into *alabamae* and *seximpressus*, gained rounded basal angles of the pronotum; and one that gave rise to *engelmanni* and *nonnitens* acquired distinct produced basal angles of the pronotum.

The relationships of *hypherpiformis* are not clear because besides having its own distinct appearance it shares structures with two distinctly related groups. Specimens of this species have the general external habitus of the members of the *seximpressus* group, but lack the setae of the prosternal process. They have 3 – 5 punctures on the third interval of the elytron and the stump-like right paramere of the male genitalia which resembles that of sallei and *gigas* of the *gigas* group. I have placed *hypherpiformis* close to the *seximpressus* group on the dendrogram. This position requires that similar male genitalia were evolved in unrelated lineages.

The sister stock of the one which gave rise to the *seximpressus* group acquired a pronotum with a posterior constriction and small basal angles. It gave rise to the ancestors of two stocks. One of them retained the primitive pronotal form, and differentiated into the basal stocks of the *sodalis* group. Its sister group gained prominent angles of the pronotum and diverged into the primitive stocks of the *substriatus* group, and the *torvus* and *gigas* groups.

The extant species *furtivus*, *parasodalis* and *sodalis* are descendants of a common form which inherited and maintained a primitive pronotum with small basal angles. The prominent angles of the pronotum of *sodalis colossus* are probably a recent modification. Also the narrow apical blade of *sodalis* has probably evolved recently. The species *alternans* and *iowensis* evolved from an ancestor that acquired prominent basal angles of the pronotum. The three punctures on the disc of the elytron of some specimens of *iowensis* is probably a recent change.

The species *constrictus* and *substriatus* are characterized by the absence of normal ridges between the first three anterior punctures of the umbilicate series. This feature was probably acquired by their common ancestor. Some specimens of *substriatus* have three punctures on the third interval of the elytron which is probably a recent modification.

Only insignificant structural changes developed in the stock which gave rise to the ancestors of the *torvus* and *gigas* groups. The derivative stock which evolved the *torvus* group retained the primitive pronotal shape. The presence of three punctures in the third interval of the elytron in some *gravidus*, *torvus* and *deceptus* individuals is probably a recent modification.

A more pronounced posterior constriction of the pronotum was acquired by the ancestor of the *gigas* group. It first gave rise to *heros* which inherited the primitive type of right paramere of the male genitalia. The sister stock of *heros* evolved a stump-like right paramere and differentiated into the extant species *sallei* and *gigas*.

The *gravesi* group is not closely related to any other *Evarthrus* group. Its members have lost the plica and resemble the species of *Cyclotrachelus* in some detail, but generally look like western species of the subgenus *Evarthrus*.

According to this phyletic scheme, the following characteristics have evolved more than once in the *Evarthrus* lineage: pronotum with posterior constriction, four times; posterior setae on lateral bead, twice; deep, sharply defined medial longitudinal groove of the prosternal process, four times; three or more setae on the third interval of the elytron, five times; short stump-like parameres, three times; and sclerite of the internal sac, at least four times.

Zoogeography [1]

Introduction. – The chief objective of historical zoogeography is to interpret the geographical relationships of extant organisms in terms of past climate and physiography. These events often provide evidence of former barriers, or alternatively, opportunities for dispersal now no longer available. When a measure of concordance is found between such evidence and present distributions of extant species, it may be assumed that these distribution patterns are explained by changes which occurred in the past. In turn, geographical relationships of species judged to be closely related phylogenetically can provide evidence about past changes. The distribution of the species of *Evarthrus* is considered from both aspects. In the sections which follow, we provide an account of the historical background, a description of the distribution pattern of the extant species, and an analysis of the distribution pattern in historical terms.

The hypotheses we propose below are weakened by two defects in our data: we cannot relate in detail the distribution of the species to different vegetation types, although the patterns suggest such a relationship; and many of the species are rarely encountered so that their ranges may be incompletely known. The following essay must, therefore be regarded as only a first approximation to a description of the geographical distribution of *Evarthrus.* Our analysis is thus preliminary, but we hope not too premature.

Historical background. – The history and dispersal of the genus *Evarthrus* must be related to that of the biota of eastern North America, and to the geological history of that area. Much has been written about this topic, and the following references have been consulted: Auffenberg and Milstead, 1965; Ball, 1956, 1959; Berry, 1922, 1926; Blair, 1965; Braun, 1950; Carlston, 1950; Clarke, 1896; Coleman, 1946; Davis, 1965; Flint, 1965; Graham, 1964; Hibbard *et al*, 1965; Howden, 1963, 1969; King, 1959; Muller, 1965; Richards and Judson, 1965; Ross, 1965; Schafer and Hartshorn, 1965; Selander, 1965; Stebbins, 1951; and Whitehead, 1965. The most important events are: the history of the distribution of the Arcto-Tertiary Geoflora; and Pleistocene events which relate to changes in water level, and climate.

Briefly, the Arcto-Tertiary Geoflora in the early Tertiary was Holarctic in distribution, occurring at higher latitudes than now. At present, its elements are concentrated in more southern temperate regions, especially eastern Asia and eastern North America. Concerning the Pleistocene, it is fairly well established that the glacial periods had two important effects: there was a lowering of temperatures, resulting in a certain amount of faunal and floral shifting; and second, sea level was lowered, resulting in the appearance of additional land in coastal areas. During interglacial stages, the reverse changes occurred, and the Mississippi River became greatly enlarged, as a result of glacial meltwater. Thus, this river probably became a highly effective barrier to movement of flightless terrestrial animals.

The cyclical nature of these events during the Pleistocene should have led to alternation of range contraction and expansion of organisms, with consequent geographical isolation resulting from fragmentation of once-continuous ranges during unfavorable time, with the reverse taking place during favorable times. Evolution occurred as a result of both sets of circumstances.

The distribution pattern, in general. – This is simply illustrated by means of a grid (Table 2), oriented like a map, with columns representing longitude and rows representing

---

[1] This section was written jointly by G. E. Ball and me.

TABLE 2

THE NUMBER OF SPECIES OF *Evarthrus* PLOTTED IN 5° INTERVALS OF LONGITUDE AND LATITUDE*

Degrees N. Latitude	Degrees W. Longitude									Total Interval Value	Avg. Interval Value	No. Species
	110-114	105-109	100-104	95-99	90-94	85-89	80-84	75-79	70-74			
45 – 49					2					2	2.00	2
40 – 44			2	7	7	5	6	5	2	34	4.86	13
35 – 39	1	3	4	7	8	6	9	7	–	45	5.65	19
30 – 34	2	4	3	11	10	17	12	3	–	62	7.75	35
25 – 29		1		9	1	–	6	–	–	17	4.25	13
20 – 24		1			–	–	1	–	–	2	1.00	2
Total Interval Value	3	9	9	34	28	28	34	15	2			
Avg. Interval Value	1.50	2.25	3.00	8.55	5.60	9.35	6.80	5.00	2.00			
No. Species	2	4	4	15	15	18	21	9	2			

* Intervals entirely or partly occupied by sea contain a dash.

latitude. Each square represents 5° longitude and 5° latitude, as in figs. 125–136. The number in each square represents the total number of species recorded from within that space in figs. 125–136. The numbers are totalled horizontally and vertically to obtain a "total interval value" for each 5° interval of longitude and latitude, and the "average 5° interval value" is obtained by dividing the total interval value by the number of squares relevant to the total interval value. In addition, the total number of species found in each 5° interval is recorded. The absence of continental land is indicated by short horizontal lines in the appropriate squares.

In general, the number of species is maximum in the southeast (30° – 34°N., east of 90°W.), and decreases in all directions. In part, the decrease is the result of restriction of land area (for the squares 30 – 34; 79 – 75; and 20 – 24; 80 – 84, occupied mainly by ocean, and the square 25 – 29; 80 – 84, including peninsular Florida). However, other factors must be considered to explain the northern, western, and southern decreases.

The simplest explanation probably involves historical factors. The genus *Evarthrus* was probably warm temperate and forest adapted, and has probably undergone most of its evolution under these conditions. All three subgenera are represented in warm temperate forest. With one exception, spread into peripheral areas has been accomplished by the most highly evolved subgenus, *Evarthrus s. str.* The exception is *E. (Cyclotrachelus) faber*, which is represented in the Florida keys, at the southeastern extremity of the range of the genus.

Howden (1969) suggests that the principal factor accounting for reduction of species toward the north is Pleistocene glaciation and its associated drastic climatic and other effects on species living in or near glaciated areas. We agree that these factors probably influenced the diversity of *Evarthrus* toward the north, but we also believe that even if glaciation had not taken place the genus would still have exhibited maximum diversity in the southeast.

The Floridian *Evarthrus* fauna seems to be especially poor. Could this be the result of climate encountered on the peninsula? Rohwer and Woolfenden (1969) provide historical evidence that peninsular climate is one of the major factors accounting for Florida's depauperate breeding bird fauna, and reasoning by analogy we suggest that the impoverishment of the *Evarthrus* fauna can be accounted for in similar fashion.

Simply expressed, the distribution pattern of *Evarthrus* is one of subtraction from a fauna of maximum diversity on the eastern Gulf Coast. However, in detail, the distribution pattern is much more complex, and the complexities must be described before it is possible to present a more detailed account of historical zoogeography. For purposes of this analysis, taxa of subspecific and specific rank are treated as equivalent. This more detailed analysis is considered under four headings: extent of range, centers of concentration, effects of the Pleistocene, and species pairs.

Extent of range. – One of the striking features of the distribution pattern is the relatively small range of many of the species. This is illustrated by the data presented in Table 3. We used as an index of range extent the linear distance between the most widely separated localities because it was simply obtained and was sufficiently accurate for our purposes. Because *gravesi* and *parafaber* are known from single localities only, they were excluded from this analysis. Note that almost one-half of the taxa have ranges less than 500 miles long, and that 80% of the taxa have ranges of 1000 miles or less.

TABLE 3

FREQUENCY DISTRIBUTION OF MAXIMUM LINEAR EXTENT OF GEOGRAPHICAL RANGE IN MILES OF THE SPECIES OF *Evarthrus*.

CLASS	N
2001 - 2250	2
1751 - 2000	1
1501 - 1750	3
1251 - 1500	1
1001 - 1250	2
751 - 1000	8
501 - 750	5
251 - 500	10
0 - 250	12

Restricted ranges seem to suggest the existence of barriers to dispersal, or alternatively, that the present ranges of many of the species are less extensive than they once were, and that the surviving populations are relics of a once more extensive group of populations. This second alternative is discussed below.

A simple test for the existence of barriers would be to compare the present known ranges of species with physical features of the landscape suspected of being effective barriers to flightless, lowland terrestrial animals. In the east are two obvious candidates: the Mississippi River and the Appalachian Mountains. Data on distribution of species and subspecies with reference to the Mississippi River are presented in Table 4.

TABLE 4

COMPARISON OF DISTRIBUTION OF THE SPECIES OF *Evarthrus* IN RELATION TO THE MISSISSIPPI RIVER

	WEST ONLY	%	BOTH SIDES	%	EAST ONLY	%	TOTAL
ALL SPECIES	13	28	6	13	27	59	46
ONLY SPECIES NEAR RIVER	9	33	6	22	12	12	27

Two groups are compared: the total *Evarthrus* fauna and that segment of the fauna whose taxa are either known to reach the banks of the Mississippi or can reasonably be expected to be there. Both sets of data show that less than one-third of the total number of species are represented on both sides of the river. Additional details are provided in the following section.

The effectiveness of the Appalachian system as a barrier was measured in terms of the distribution patterns of 11 taxa whose ranges flank the mountains (Table 5). Less than one-third of these taxa occur on both sides. Of this group, two species are mainly to the east and one is mainly to the west of the mountains.

TABLE 5

COMPARISON OF DISTRIBUTION OF THE SPECIES OF *Evarthrus* IN RELATION TO THE APPALACHIAN MOUNTAINS

	WEST ONLY	BOTH SIDES	EAST ONLY	TOTAL
ONLY SPECIES NEAR MOUNTAINS	5	3	3	11

These data appear to support the view that topographical features are important in restricting the ranges of the species of *Evarthrus*.

Centers of concentration. – Although the distribution patterns of the extant taxa of *Evarthrus* appear to have been influenced by obvious barriers, these are not the limiting factors for all of the species. This can be seen most clearly by a comparison of the patterns of the species with more or less restricted ranges.

The object of this comparison was to attempt to locate centers of concentration, to be used in conjunction with a consideration of historical zoogeography of the species of *Evarthrus*. Excluded from the analysis initially were the wide-ranging species, and those represented on both sides of the major barriers. The ranges of the remaining species were examined for concordance, and centers of concentration were discovered. Subsequently, the species with restricted ranges but occurring in two or more centers of concentration were excluded. The species included in the analysis are called "centrant" species; those excluded are "radiant" species (terminology after Hultén, 1937).

The distribution patterns of the centrant species are indicated in Table 6. The vertical lines represent lines of longitude, the horizontal lines represent lines of latitude. Each resulting square containing one or more species was lettered. The squares which contained a number of species in common were combined to provide the centers of concentration, as in Table 7.

TABLE 6

THE DISTRIBUTION OF THE SPECIES OF *Evarthrus* WITH RESTRICTED RANGES

DEGREES N. LATITUDE	DEGREES WEST LONGITUDE 95-99	90-94	85-89	80-84	75-79	70-74
45 – 49		alternans A				
40 – 44	iowensis alternans B	iowensis alternans C				furtivus I
35 – 39		whitcombi parasodalis alternans D		iuvenis approximatus vinctus furtivus K	iuvenis approximatus spoliatus levifaber furtivus J	
30 – 34	nonnitens engelmanni heros sallei G	whitcombi nonnitens parasodalis gravesi texensis E	laevi. paraf. brev. sinus unicol. hypherp. alabam. M	laevi. ovul. brev. vinctus unicol. spol. levif. blatch. L		
25 – 29	engelmanni gigas heros sallei H	texensis F		ovulum blatchleyi floridensis hernandensis N		

TABLE 7

CENTERS OF CONCENTRATION OF THE SPECIES OF *Evarthrus*.

CENTER NUMBER	INTERVALS INCLUDED [1]	LIMITS
1	N	Peninsular Fla., s. of 30°N.
2	L, M [2]	Coastal plain north to Fall Line, e. to South Carolina, w. to Mississippi River.
3	I, J	East of Appalachian Mts., between 35° and 40°N.
4	K	West of Appalachian Mts., to Mississippi River, N. of 35°N.
5	F, G, H [3]	Texas east of 100°W., and south of 35°N.
6	D, E	West Arkansas, South Missouri.
7		North of 35°N., West of 95°W., South of Missouri River, and Texas West of 100°W.
8	A, B, C	West of Mississippi River, North of Missouri River.

1. Letters are designations for intervals in Table 6.
2. species *gravesi* is included, from E.
3. species *nonnitens* is included, from E.

The locations of the centers are illustrated in Fig. 138. We are doubtful about the reality of Center 6. It is based on the presence of two species there, known from nowhere else.

Center 7 contains no endemic species, but it seems central for a number of wide-ranging western species.

These Centers of Concentration, several of which are at least partly independent of the Appalachian-Mississippi barriers, suggest the existence of additional barrier systems. The restricted ranges may be simply by-products of biotype impoverishment, discussed below.

The distribution of all species, in terms of these centers of concentration, is indicated in Table 8.

TABLE 8

DISTRIBUTION OF THE SPECIES OF *Evarthrus* IN RELATION TO THE CENTERS OF CONCENTRATION

NAME OF SPECIES	CENTER NUMBER 1	2	3	4	5	6	7	8
morio	x	x						
hernandensis	x							
laevipennis		x						
iuvenis			x					
approximatus			x					
obsoletus		x		x				
brevoorti		x						
spoliatus		x	x					
fucatus				x				
unicolor		x						
vinctus		x	x					
alabamensis		x						
macrovulum		x						
texensis					x			
ovulum	x	x						
parafaber		x						
levifaber		x						
faber	x	x						
incisus				x	x		x	x
whitcombi						x		
blatchleyi	x	x						
floridensis	x							
sigillatus		x	x	x				
sinus		x						
convivus		x		x				
seximpressus				x	x	x	x	x
alabamae		x			x			
engelmanni					x			
nonnitens		x			x			
hypherpiformis		x						
s. sodalis			x	x				x
s. colossus						x	x	
s. lodingi				x				
parasodalis						x		
furtivus			x	x				
alternans								x
iowensis				x				x
substriatus					x		x	x
constrictus					x		x	x
t. torvus					x	x	x	x
t. deceptus					x		x	
gravidus					x		x	
sallei					x			
gigas					x			
heros					x			
gravesi		x						
TOTALS	6	21	7	10	14	5	8	8

Degree of difference among these centers is indicated in Table 9, by means of an index of difference (Greenslade, 1968). Of 28 comparisons, 12 were scored as 100, i.e., pairs of centers shared no species in common. Five scored between 91 and 94.

TABLE 9

DISSIMILARITY VALUES AMONG CENTERS OF CONCENTRATION OF THE GENUS *Evarthrus.*

CENTER NUMBER	STATISTICS	CENTER NUMBER						
		2	3	4	5	6	7	8
1	t[1.]	23	13	16	20	11	14	14
	c[2.]	4	0	0	0	0	0	0
	t - c	19	13	16	20	11	14	14
	$\frac{t-c}{t}$ x 100	**83**	**100**	**100**	**100**	**100**	**100**	**100**
2	t[1.]		23	24	33	26	29	29
	c[2.]		3	3	2	0	0	0
	t - c		20	21	31	26	29	29
	$\frac{t-c}{t}$ x 100		**87**	**87**	**94**	**100**	**100**	**100**
3	t[1.]			14	21	12	15	14
	c[2.]			3	0	0	0	1
	t - c			11	21	12	15	13
	$\frac{t-c}{t}$ x 100			**78**	**100**	**100**	**100**	**93**
4	t[1.]				22	14	16	14
	c[2.]				2	1	2	4
	t - c				20	13	14	10
	$\frac{t-c}{t}$ x 100				**91**	**93**	**88**	**71**
5	t[1.]					17	15	17
	c[2.]					2	7	5
	t - c					15	8	12
	$\frac{t-c}{t}$ x 100					**88**	**53**	**71**
6	t[1.]						10	12
	c[2.]						3	1
	t - c						7	11
	$\frac{t-c}{t}$ x 100						**70**	**92**
7	t[1.]							11
	c[2.]							4
	t - c							7
	$\frac{t-c}{t}$ x 100							**64**

1. Total number of species in each pair of centers.
2. Number of species in common between each pair of centers.

In general, the peripheral centers differ strongly from one another. Center 7, for example, shares no species with Centers 1, 2 and 3, and Center 8 shares a single species with Centers 2 and 3. Centers 4 and 8 are each connected with six other Centers, and, consequently, are the least distinctive.

Because of its central position, one would expect Center 4 to be minimally distinctive. Center 8, on the other hand, is peripheral, and for this reason, might be expected to hold a more distinctive fauna. The expectation is not realized, probably because the area, although suitable for a variety of species, has few endemics.

In striking contrast to Centers 4 and 8 is Center 1. It shares species with only one other Center, and consequently, has the most distinctive fauna of any Center.

A more interesting comparison involves the Centers of about the same latitude, but on different sides of the Mississippi River. Centers 2 (southeastern) and 5 (southwestern), have a combined fauna of 35 species, of which only two are shared (Index 94). Centers 4 (northeastern) and 8 (northwestern) have a combined fauna of 13 species of which three are shared (Index 77). In each case, few species occur on both sides of the river. The difference in Index values is the result mainly of the much more diverse southern fauna. However, this fact is of less interest than is the thought that the effectiveness of the river as a barrier is less in the north than in the south. This may be the result of one of two factors: the river, being narrower, is easier to cross, and consequently a greater proportion of the northern fauna has done so; or, the species occurring in the north are more adept at crossing water barriers. Probably both factors are involved.

The barriers marking off other centers are not clear. Probably they are complexes of direct climatic factors, and indirect ones, transmitted through conditions of soil and vegetation. Barriers of this type may have been as consequential in the development of diversity in *Evarthrus* as have been the more obvious barriers. How did these barriers develop? We suggest it was through loss of variability brought about as a by-product of the glacial stages.

Effects of the Pleistocene epoch. – The fact that Centers of Concentration of species with limited ranges can be identified suggests the operation of some powerful factor. We suggest that this factor was climatic fluctuation during the Pleistocene, which is known to have caused range expansion and contraction of many species. Especially during glacial stages, one might expect the ranges of more or less warm adapted species to have become more or less restricted, with a consequent reduction in population size and number. During interglacials and post-glacial time, the ranges of more broadly adapted species, the radiants, might be expected to expand, whereas species which lost too much variability as a result of reduction in population size and number would not be able to spread. This is essentially Hultén's Theory of Equiformal Progressive Areas (1937).

The position of the Centers of Concentration probably do not coincide precisely with the former distribution of the centrant species during the Pleistocene epoch. The northern species must have been south of their present ranges during the glacial stages, and the coastal species must have been north of their present ranges during the interglacial periods. However, at a more general level, a correlation is apparent. The centrant species on each side of the Mississippi River and Appalachian Mountains were probably in the same longitudinal zones in the past as they are now, and it seems unlikely that the ranges of centrant species from different centers overlapped. Can this be taken as evidence that the southeastern biota was not radically displaced by the cold glacial periods (Braun, 1950)? We think it can be.

Thus the significance of the Centers is that they indicate in part positions of refugia during the glacial stages. One can also infer from the locations that different species have different ecological tolerances of rather narrow range, and that the evolution of diversity in *Evarthrus* has involved development of these limited tolerances. Although evolution in general seems to have led to the development of species of limited tolerances, especially in the east, more broadly adapted species have evolved in the west. Some of the latter may be of relatively recent origin, an inference based on their postulated phylogeny.

Species-pairs. – The analysis of the distribution of pairs of closely related species (sister species) seems to be the most fruitful approach to historical zoogeography at the local level. Their distributions are likely to provide the clearest evidence of location of former barriers and of patterns of phylogeny. Of course, this is true only if the two sister species are largely allopatric.

The two members of some species pairs are largely or completely sympatric, and consequently, their present distribution gives no indication about their past geographical relationships. These are: *morio – hernandensis; iuvensis – approximatus; alternans – iowensis; substriatus – constrictus;* and *torvus – gravidus.* These are excluded from the following discussion. Also excluded are *gravesi* and *hypherpiformis*, both representing monotypic groups and lacking close living relatives.

The distribution patterns are of several types: east – west; Floridian – Gulf Coast; and north – south (Table 10). The last category is common among the western species of the subgenus *Evarthrus.*

The range disjunctions of most of the east-west pairs of vicariant species are correlated with the Mississippi River or with the Appalachian Mountains. In these cases, speciation has taken place between present Centers of Concentration, and it is easy to imagine how the isolation and consequent differentiation came about. There are also several instances of vicariant distributions within Centers 2 and 5. These involve species with coastal ranges, and one can imagine the requisite range disjunctions arising as a result of changes in coast line with fluctuation in sea level and sizes of rivers during the waxing and waning of the glacial stages. The same explanation is relevant for vicariant distributions within Florida, and between Florida and the mainland.

The north-south disjunctions are more difficult to explain, because, for the most part, obvious barriers do not occur between the northern and southern members of the pairs. However, during glacial stages, one can imagine that range restriction occurred, as described above, with isolates of once more wide-ranging species surviving and differentiating.

Vicariance relationships of these same kinds are evident within sister species-groups, and are presumably the result of the same causes having been effective at an earlier time in the phylogeny of the genus.

These distribution patterns suggest to us a model of how diversity has been generated in the genus *Evarthrus.* Beginning with a species of relatively restricted range and tolerance (Stage A), range expansion takes place as tolerances are expanded (Stage B). If a wide

TABLE 10

DISTRIBUTION PATTERNS OF ALLOPATRIC SISTER SPECIES OF THE GENUS *Evarthrus*

A. EAST – WEST RELATIONSHIPS

WESTERN VICAR		EASTERN VICAR	
NAME	CENTER	NAME	CENTER
fucatus	4	spoliatus	2, 3
macrovulum	2	texensis	5
blatchleyi	1	floridensis	1
engelmanni	5	nonnitens	2, 5
sodalis	3, 4, 6, 7, 8	furtivus	3
s. colossus	6, 7	s. sodalis	3, 4, 8
gigas	5	sallei	5

B. FLORIDA – COASTAL PLAIN RELATIONSHIPS

COASTAL PLAIN VICAR	FLORIDIAN VICAR
faber	levifaber

C. NORTH – SOUTH RELATIONSHIPS

NORTHERN VICAR		SOUTHERN VICAR	
NAME	CENTER	NAME	CENTER
incisus	4, 5, 7, 8	whitcombi	6
convivus	2, 4	sinus	2
seximpressus	4, 5, 6, 7, 8	alabamae	2, 5
sodalis	3, 4, 6, 7, 8	parasodalis	6
s. sodalis	3, 4, 8	s. lodingi	4
t. torvus	5, 6, 7, 8	t. deceptus	5, 7

temperature tolerance evolves, the species may spread longitudinally into climatic zones different from the ancestral one. If not, the species spreads latitudinally. Major physical barriers may be crossed, or barriers may appear and become effective subsequently, breaking the range of Stage B species. Differentiation of the resulting segregates takes place, leading initially to divergence to the subspecies level (Stage C), and later to the species level (Stage D). At this stage, two allopatric species are present in place of the original ancestral species. Next, the ranges of these sister species may expand. The sister species may meet one another, and eventually, the two sister species become sympatric (Stage E). Examples of all of these stages are found among the extant species of *Evarthrus*. Stage A, Stage D and some Stage E species form the nuclei of the Centers of Concentration – the centrants. Stage B and Stage E species usually are widespread in more than one center – the radiant species.

It is suggested that the barriers are provided by permanent physiographical features, such as mountains, rivers and the sea, or by temporary interruptions of ranges as a result of Pleistocene climatic change.

Historical zoogeography. – In this section, an attempt is made to reconstruct the geographical history of the genus *Evarthrus*, based to a large extent on the considerations presented above. The primitive ancestry of this genus became separated from its Palaearctic sister stock (the ancestor of the Palaearctic molopine genera) sometime in the early Tertiary, when the Bering Land Bridge was covered by the sea. This New World group inhabited the Arcto-Tertiary forests in warm temperate regions during the middle Tertiary, possibly ranging across the north from the west coast to the east. As this biota withdrew from the west, so did *Evarthrus*, ultimately becoming restricted to the east. Probably representatives of the genus arrived too late on the Gulf Coast to be able to enter eastern Mexico. This suggests that they arrived in the area in post-Miocene time. Martin and Harrell (1957) suggest that grasslands formed in this area in the Miocene. Had the early members of *Evarthrus* been present before the grasslands formed they might be expected to be found today in Mexico.

Because of the present extensive overlap in ranges of the extant subgenera, it is impossible to guess the geographical relationships of these groups at the time of their origin. And, for the same reason, it is impossible to reconstruct much of the subsequent history of the genus. However, it is possible to suggest events which led to the development of many of the extant species pairs.

The general assumption is that much of the evolution of markedly similar allopatric species took place in the Pleistocene, a time span of several million years. Zoogeographers, such as Blair (1958), Hubbell (1954) and Howden (1963), have suggested that such species have arisen during the Pleistocene, because of the coincidence of the ranges of such species with barriers that could have arisen during this time, only. However, on the basis of fossil evidence, Shotton (1965) and Lindroth (1963) have denied that any stock diverged to species level. The difference may be that in general, the more widespread species have been collected as fossils, and they may be older, less rapidly evolving. In any event, it is clear that a number of vertebrates have undergone evolution to the species level during the Pleistocene, and we fail to see that insects should not have done the same. The taxa are discussed below, in phylogenetic sequence.

The *morio* and *obsoletus* groups of the subgenus *Fortax* are largely allopatric (Fig. 125, cf. Fig. 126). The *morio* group occupies the Gulf Coastal Plain, while the *obsoletus* group has a more northern distribution. Possibly the ancestral stock of these groups became divided during early Pleistocene or late Pliocene time into a northern and southern stock.

Speciation of *hernandensis* and *morio* of the *morio* species group undoubtedly took place in Floridian refuges, possibly during an interglacial period, when Florida was isolated by water barriers from the mainland. Both species are presently almost completely confined to Florida (Fig. 125). Because these are sympatric their geographical history is difficult to determine. The species *laevipennis* and the ancestor of *morio* and *hernandensis* were probably separated during an early interglacial. *E. laevipennis* evolved on the mainland coast just west of Florida, and has moved northward in recent times.

The Appalachian Mountains are an effective barrier between the species *obsoletus* and the other two members of the *obsoletus* group (Fig. 126). The *obsoletus* group ancestor probably became disjunct and gave rise to *obsoletus* west of the mountains while its sister stock which ultimately give rise to *approximatus* and *iuvenis* speciated east of the mountains. Since *approximatus* and *iuvenis* are very closely related and sympatric, little can be said about the history of their geographical distribution.

Widespread sympatry among the species groups of the subgenus *Cyclotrachelus* masks most of their distributional history. Within the species groups, however, the distribution pattern among some species merits comment.

In the *spoliatus* group the more remotely related species *brevoorti* and *unicolor* are sympatric on the Gulf Coastal Plain (Fig. 127). Little can be said about their geographical history. The sister species *fucatus* and *spoliatus* flank the Appalachians. Since both extant species are cool tolerant the separation of the ancestral population could have occurred as follows: the ancestral population was distributed somewhere at the southern end of the Appalachian System during a glacial period; with the coming of an interglacial the biota began to shift northward and along with it went the ancestral population; as it moved north it became divided at the base of the mountains; the northward shift continued and the two populations, now completely separated, moved north one on either side of the mountains, then differentiated into *fucatus* and *spoliatus*.

Each species of the *ovulum* group has a highly restricted geographical distribution (Fig. 128). The species *vinctus* is confined to high elevations of the southern Appalachians. It may have become disjunct in the mountains during early stages of the Pleistocene. The remaining species, *alabamensis* and the closely related *ovulum, macrovulum,* and *texensis* are southern Gulf Coastal forms. The ancestor which gave rise to *alabamensis* and the basic stock of *ovulum, macrovulum* and *texensis* was probably distributed along the coast from southern Alabama down into Florida. During an early interglacial the Florida stock of the species probably became isolated in a Florida refuge where it evolved, while the mainland population evolved into *alabamensis*. With the advent of another glacial period and consequent lowering of sea level, Florida was again united with the mainland. The ancestor of *ovulum*, *macrovulum*, and *texensis* then moved north and became distributed from Florida along the coast to Mobile, Alabama where it became sympatric with *alabamensis*. In the following interglacial period this stock, just as its ancestor, became divided into a mainland population and one separated on a Floridian island. The mainland form differentiated into the ancestor of *macrovulum* and *texensis*, and the other into *ovulum*. The *macrovulum-texensis* stock crossed the Mississippi River, and differentiated into two species.

The zoogeography of the *faber* group probably parallels that of the *ovulum* group (Fig. 129). The ancestor of *faber* and *levifaber*, and *parafaber* probably ranged along the Gulf Coast from Mobile, Alabama to peninsular Florida. During an interglacial it became divided into a mainland population which speciated into *parafaber* and a Floridian isolate which also speciated. During the following glacial period the Florida population radiated. When the next interglacial occurred this population was separated. One portion became isolated in a Florida refuge, while another part remained on the mainland northeast of Florida. Both populations differentiated giving rise to *faber* in Florida and to *levifaber* on the mainland.

The subgenus *Evarthrus* is the only subgenus with extensive representation west of the Mississippi River, although it is rich in species to the east of the river, as well. Clearly the subgenus has been on both sides of the Mississippi for an extended period of time.

The two species of the *incisus* group are exclusively or largely west of the Mississippi River (Fig. 130), and of these *whitcombi* is confined to Center 6, south of the Arkansas River. To the north occurs the radiant species *incisus*. Possibly the Arkansas River constituted a partial barrier to dispersal, and the *incisus* stock differentiated to the north and south of that barrier.

Figure 131 illustrates the distribution of the taxa of the *blatchleyi* and *sigillatus* groups. The barrier effect of the Mississippi River and the Appalachian System is shown in remarkable clarity. In addition Florida contains two more essentially endemic species. The ancestral stock of the *blatchleyi* group undoubtedly had a southern distribution perhaps near northeastern Florida, while its sister stock which gave rise to the *sigillatus* group was isolated further north. Possibly during an interglacial, the species *floridensis* evolved in a Floridian refuge while *blatchleyi* evolved on the mainland near Florida; then during the following glacial period *blatchleyi* moved south into Florida. Alternatively, the two could have evolved from a discontinuously distributed Floridian stock.

Because of Pleistocene north-south biotic shifts, the ancestral stock of the *sigillatus* group was divided into two populations one on either side of the Appalachians. That on the east evolved into *sigillatus*. The western population then became disjunct. The species *sinus* must have evolved on the Gulf Coast, while *convivus* evolved further north.

Extant species of the *seximpressus* group are mainly Gulf Coastal Plain species where they are largely sympatric (Fig. 132). Only *seximpressus* ranges northward to Minnesota and Wisconsin. Two species *alabamae* and *nonnitens*, have managed to cross the Mississippi River. The ancestral stocks of the present species probably evolved on or near the Gulf Coastal Plain. The species *seximpressus* probably evolved further north as a cool adapted form, while the other three species arose on the Gulf Coastal Plain.

Because the relationships of the *hypherpiformis* group are not clearly understood there is nothing to write concerning the zoogeography of it (Fig. 132).

All of the extant species of the *sodalis* group are relatively northern forms and as a group cross the northern headwaters of the Mississippi River (Fig. 133). There is no doubt that the primitive ancestors of this species group also had northern ranges and were cool adapted.

Geographical variation in the species *sodalis* is probably recently acquired because at present some distinct populations are partially isolated west of the Missouri River and some in northern Alabama. The species *parasodalis* is confined to central and western Arkansas while its sister species *sodalis* occurs further north, where it probably evolved.

The species *furtivus* may have been pinched off to the east of the Appalachians from its immediate ancestral population during a general southward biotic glacial shift (Fig. 133).

The closely related species *alternans* and *iowensis* are sympatric (Fig. 134). They may have evolved in the general region where they are now found, near the upper reaches of the Mississippi River, but they could not have survived the glacial stages in this area. Therefore, their present distribution is post-glacial.

The sympatric species *substriatus* and *constrictus*, which make up the *substriatus* group, are two of the most widespread forms in the genus *Evarthrus* (Fig. 134). Together they occupy the Great Plains from Durango, Mexico north to Minnesota and from central Arizona east to the margin of the Mississippi River valley. They evolved in the Great Plains. They, along with the species *torvus* and possibly *gravidus* are the only extant species of *Evarthrus* which occur mainly on dry prairie.

E. gravidus occurs mainly in southeastern Texas but it has been collected as far west as El Paso, Texas (Fig. 135). It is not as widespread in the Great Plains as its sister species *torvus*. The subspecies of *torvus* occur north and south of one another in the Great Plains. This suggests that southeastern Texas and the northern Great Plains could be centers of speciation in which population became disjunct during the south-north Pleistocene biotic shifts. *E. gravidus* could have speciated in isolation in southeastern Texas after a northward interglacial shift while *torvus* speciated in the northern Great Plains. A southern shift during the next glacial stage (Wisconsin?) brought *torvus* south into *gravidus* territory. During the next interglacial (Recent?) again *torvus* moved north and southern and northern populations which were partially separated subspeciated.

Because the members of the *gigas* group are largely sympatric the historical zoogeography of the *gigas* group is almost impossible to reconstruct (Fig. 136). Speciation must have occurred in the southeastern Great Plains area.

Phylogenetic relationships between the species *gravesi* and other *Evarthrus* species is uncertain. We cannot comment on the geographical history of this species.

The present distributions of the species of *Evarthrus* indicate that Pleistocene events profoundly affected the genus as a whole. At the present time forest species which live in warm temperate regions have distinctly restricted distributions. Conversely, cold tolerant and/or dry tolerant species are clearly more widespread and some may be undergoing further divergence at the present time. Those species which were specifically suited for warm temperate forest conditions, i.e. species on the Gulf Coastal Plain, probably moved southward along with their biotic neighbourhood as a northern ice mass developed. Species which could not tolerate even a slight depression in the temperature probably perished along the Gulf Coastal Plain. Some moved into peninsular Florida. Other slightly more broadly adapted forest species probably moved southward or eastward on the Gulf Coastal Plain as sea level dropped and land emerged. At the height of the glacial periods, the ranges of these species may have been greatly reduced, and their ranges have remained restricted to the present time.

On the other hand broadly adapted species made adaptive shifts during the Pleistocene. Some became successful cold tolerant forms and others invaded dry regions west of the Mississippi River. These species are dominant at the present time.

Because the species of *Evarthrus* are wingless it is not surprising that water is an effective barrier to these species. The Mississippi drainage system and ocean around Floridian islands were undoubtedly the two most important water barriers in the history of this genus. In addition. another great obstacle was, and remains the Appalachian Mountains. These barriers in conjunction with Pleistocene climatic changes forged the geographical patterns of the present species of *Evarthrus*.

ACKNOWLEDGEMENTS

I am indebted to G. E. Ball for his guidance, aid, suggestions, encouragement and constant interest throughout this study, and for reading and editing the manuscript.

I thank Dr. B. Hocking for reading the manuscript and offering suggestions concerning this problem. I also thank C. H. Lindroth, W. G. Evans, and H. F. Clifford for reading and criticizing the thesis on which this paper is based.

I thank the following institutions and persons for the loan of specimens: Norman Anderson, Montana State University; T. C. Barr, Jr., University of Kentucky; R. T. Bell, University of Vermont; H. D. Blocker, Kansas State University; H. R. Burke, Texas A & M University; G. W. Byers, University of Kansas; L. Chandler, Purdue University; C. V. Covell, Jr., University of Louisville; P. J. Darlington, Jr., Museum of Comparative Zoology at Harvard University; T. L. Erwin, University of Alberta; K. L. Esau, Iowa State University; Leonora K. Gloyd, State Natural History Survey Division, Urbana, Illinois; R. C. Graves, Bowling Green State University; Kirby L. Hays, Auburn University; T. Hlavac, Michigan State University; T. H. Hubbell, University of Michigan; V. M. Kirk, United States Department of Agriculture; J. L. Laffoon, Iowa State University; D. J. Larson, University of Calgary; Hugh B. Leech, California Academy of Sciences; J. E. H. Martin, Canada Department of Agriculture: L. L. Pechuman, Cornell University; H. Radcliffe Roberts, Academy of Natural Sciences, Philadelphia; P. Rouse, University of Arkansas; J. B. Schmitt, Rutgers University; R. D. Shenefelt, University of Wisconsin; P. J. Spangler, Smithsonian Institution, United States National Museum; P. Vaurie, American Museum of Natural History; G. E. Wallace, Carnegie Museum; R. L. Wenzel, Chicago Natural History Museum; D. R. White head, University of Alberta; R. Woodruff, State Plant Board of Florida; D. A. Young, North Carolina State University.

I thank P. J. Darlington, Jr., (Museum of Comparative Zoology) and P. J. Spangler, (United States National Museum) for permitting me to examine type specimens in their institutions, and for their kind hospitality.

R. B. Madge (British Museum of Natural History, London), and Jacques Nègre, (Museum Nationale d'Histoire Naturelle, Paris) compared material with type specimens. I am grateful to both gentlemen.

I would like to thank my wife Gayla for typing and reading the manuscript.

I thank L. L. Kennedy of the University of Alberta, who kindly identified fungus zygotes which were found in the gut of an *Evarthrus* specimen.

Thanks are also due to: D. R. Whitehead for criticizing the key and reading the manuscript; David Larson for accompanying me on a collecting trip to southeastern United States and for his criticisms of the key; J. Barron, T. Erwin, and R. E. Leech for criticizing the key and for suggestions on other aspects of this problem; J. Scott for photographing specimens of *Evarthrus*, and assisting with the preparation of distribution maps.

REFERENCES

Auffenberg, W., and W. W. Milstead. 1965. Reptiles in the Quaternary of North America, pp. 557-568. *In* H. E. Wright, Jr., and D. G. Frey (ed.). The Quaternary of the United States. Princeton University Press, Princeton.

Ball, G. E. 1956. A revision of the North American species of the genus *Helluomorphoides* Ball, 1951 (Coleoptera, Carabidae, Helluonini). Proc. ent. Soc., Washington, 58(2) : 67-91.

Ball, G. E. 1959. A taxonomic study of the North American Licinini with notes on the Old World species of the genus *Diplocheila* Brullé (Coleoptera). Mem. Amer. ent. Soc., 16, 258 p.

Ball, G. E. 1960. Carabidae (Latreille, 1810), 55-181 pp. *In* Ross H. Arnett, Jr., The Beetles of the United States. The Catholic University of America Press, Washington.

Ball, G. E. 1966. A revision of the North American species of the subgenus *Cryobius* Chaudoir (*Pterostichus*, Carabidae, Coleoptera). Opusc. ent. Supp. 28, 166 pp.

Ball, G. E. 1967. Book review (of Lindroth, C. H. 1966. Part 4, Ground beetles of Canada and Alaska). Coleopterists Bulletin, 21(2) : 40, 56, 58, 63, and 64.

Basford, N. L., J. E. Butler, C. A. Leone and F. J. Rohlf. 1968. Immunologic comparisons of selected Coleoptera with analyses of relationships using numerical taxonomic methods. Syst. Zool., 17(4) : 388-406.

Bates, H. W. 1882. Biologia Centrali-Americana, Insecta. Coleoptera, Carabidae. 1(1) : 40-152.

Berry, E. W. 1922. Additions to the flora of the Wilcox group. U. S. Geol. Sur. Prof. Paper. 13 : 1-121.

Berry, E. W. 1926. Pleistocene plants from North Carolina. U. S. Geol. Sur. Prof. Paper. 140 : 97-119.

Blackwelder, R. R., and R. M. Blackwelder. 1948. Fifth supplement 1939-1947 (inclusive) to the Leng catalogue of Coleoptera of America, north of Mexico. Mount Vernon, New York. 87 p.

Blair, W. F. 1958. Distributional patterns of vertebrates in the southern United States in relation to past and present environments. *In* Hubbs, Carl. L. (editor). Zoogeography. Publication No. 51 of the American Association for the Advancement of Science, Washington, D. C. pp. 433–468, 11 figs.

Blair, W. F. 1965. Amphibian speciation, 543-556 pp. *In* H. E. Wright, Jr., and D. G. Frey, (ed.). The Quaternary of the United States. Princeton University Press, Princeton.

Blatchley, W. S. 1910. The Coleoptera or beetles of Indiana. Bulletin of the Indiana Department of Geology and Natural Resources. No. 1. 1386 p.

Böving, A. G. and F. C. Craighead. 1930. An illustrated synopsis of the principal larval forms of the order Coleoptera. Ent. amer. 11 : 1-351.

Braun, E. L. 1950. Deciduous forests of eastern North America. Blakiston Company, Philadelphia, 596 p.

Brimley, C. S. 1938. The insects of North Carolina. North Carolina Department of Agriculture. Division of Entomology. 560 p.

Carlston, C. W. 1950. Pleistocene history of coastal Alabama. Geol. Soc. Amer. Bull. 61 : 1119-1130.

Casey, T. L. 1918. Amarinae and Pterostichinae. Memoirs on the Coleoptera. Lancaster Press Inc., Lancaster, Pa. 8, 427 p.

Casey, T. L. 1920. Random studies among the American Caraboidea. Memoirs on the Coleoptera. Lancaster Press Inc., Lancaster Pa. 9, 529 p.

Casey, T. L. 1924. Additions to the known Coleoptera of North America. Memoirs on the Coleoptera. Lancaster Press Inc., Lancaster Pa. 11, 347 p.

Chaudoir, M. de. 1838. Tableau d'une nouvelle subdivision du genre *Feronia* Dejean suivi d'une characteristique de trois nouveau genres de carabiques. Bull. Soc. Nat. Moscou, 11 : 3-32.

Chaudoir, M. de. 1868. Observations synonymiques sur les carabiques de l'Amerique septentrionale et descriptions d'espèces nouvelles de ce pays. Extrait de la Revue et Magasin de Zoologie. p. 1-64.

Clark, W. B. 1896. The Eocene deposits of the Middle Atlantic Slope in Delaware, Maryland, and Virginia. U. S. Geol. Sur. Bull. 141, 167 p.

Coleman, A. P. 1946. The last million years. The University of Toronto Press, Toronto. 216 p.

Csiki, E. 1930. Pars 112. Carabidae:Harpalinae, 4(2) : 529-737. *In* W. Junk, and S. Schenkling, (ed.). Coleopterorum catalogus auspiciis et auxilio. Berlin and 's-Gravenhage.

Davis, M. B. 1965. Phytogeography and palynology of northeastern United States, p. 377-402. *In* H. E. Wright, Jr., and D. G. Frey (ed.). The Quaternary of the United States. Princeton University Press, Princeton.

Dejean, P. F. M. A. 1828. Species général des coléoptères de la collection de M. le compte Dejean, Paris. 3, 556 p.

Flint, R. F. 1965. Introduction: Historical Perspectives, p. 3-11. *In* H. E. Wright, Jr., and D. G. Frey. (ed.). The Quaternary of the United States. Princeton University Press, Princeton.

Germar, E. F. 1824. Insectorum species novae aut minus cognitae, descriptionibus illustratae. Halae. 624 p.

Graham, A. 1964. Origin and evolution of the biota of southeastern North America: evidence from the fossil plant record. Evolution 18(4) : 571-585.

Greenslade, P. J. M. 1968. Island patterns in the Solomon Islands bird fauna. Evolution, 22(4) : 751-761.

Haldeman, S. S. 1853. Descriptions of some new species of insects, with observations on described species. Proc. Acad. nat. Sci. Philad. 6 : 361-365.

Hibbard, C. W., D. E. Ray, D. E. Savage, D. W. Taylor, and J. E. Guilday. 1965. Quaternary mammals of North America. *In* H. E. Wright, Jr., and D. G. Frey, (ed.). The Quaternary of the United States. Princeton University Press, Princeton.

Horn G. H. 1875. Synonymical notes and descriptions of new species of North American Coleoptera. Trans. Amer. ent. Soc. 5 : 126-156.

Horn, G. H. 1881. On the genera of Carabidae with special reference to the fauna of Boreal America. Trans. Amer. ent. Soc. 9 : 91-196.

Horn, G. H. 1886. Notes on the Biologia Centrali-Americana. Trans. Amer. ent. Soc. 13 : 1-16 (Proc.).

Howden, H. F. 1963. Speculations on some beetles, barriers and climates during the Pleistocene and pre-Pleistocene periods in some non-glaciated portions of North America. Syst. Zool. 12 : 178-201.

Howden, H. F. 1969. Effects of the Pleistocene on North American insects. Ann. Rev. Ent., 14 : 39-56.

Hubbell, T. H. 1932. A revision of the *Puer* Group of the North American Genus *Melanoplus* (Orthoptera, Acrididae). Misc. Publ. Univ. Mich. Mus. Zool. 23 : 1-64.

Hubbell, T. H. 1952. Distribution of the *Furcatus* Group of *Melanoplus*, map and discussion, 385 p. *In* Rodgers, Hubbell, and Byers, Man in the Biological World. McGraw-Hill, New York.

Hultén, E. 1937. Outline of the history of arctic and boreal biota during the Quarternary Period. Bokforlags Akteibolaget Thule, Stockholm. 168 pp., 42 plates.

Jeannel, R. 1942. Coléoptères Carabiques, 2me partie. Faune de France. Paris. 40 : 573-1173.

Jeannel, R. 1948. Coléoptères Carabiques de la Region Malgache, 2me partie. Faune de l'Empire Francais. 10 : 373-765.

King, D. B. 1959. The evolution of North America. Princeton University Press, Princeton. 189 p.

Lacordaire, J. T. 1854. Histoire naturelle des insectes. Genera des Coléoptères ou expose methodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes. Paris. 1, 486 p.

LeConte, J. L. 1848. A descriptive catalogue of the geodaphagous Coleoptera inhabiting the United States east of the Rocky Mountains. Annals of the Lyceum of Natural History of New York, 4 : 173-474.

LeConte, J. L. 1852. Synopsis of the species of *Pterostichus* Bon and allied genera inhabiting temperate North America. J. Acad. nat. Sci. Phil. 2 : 225-256.

LeConte, J. L. 1858. Catalogue of Coleoptera of the regions adjacent to the boundary line between the United States and Mexico. Acad. Nat. Sci. Phil. 4 : 9-42.

LeConte, J. L. 1863a. List of the Coleoptera of North America. Prepared for the Smithsonian Institution. Smithson. Misc. Coll., No. 140, 78 p.

LeConte, J. L. 1863b. New species of North American Coleoptera. Prepared for the Smithsonian Institution. Smithson. Misc. Coll., No. 167, 92 p.

LeConte, J. L. 1870. Types of Mr. Newman (British Museum). Ann. Mag. nat. Hist. 4 : 5.

LeConte, J. L. 1873. The Pterostichi of the United States. Proc. Acad. nat. Sci. Phil. 302-320 pp.

LeConte, J. L. 1876. II. Coleoptera of southern Colorado and northern New Mexico, collected in 1875, by Lieut. W. L. Carpenter, Ninth Infantry, 519-520 p. Report upon new species of Coleoptera collected by expeditions for geographical surveys west of the 100 meridian, Lieut. G. M. Wheeler, Corps of Engineers, U. S. Army, in charge.

LeConte, J. L. and G. H. Horn. 1883. Classification of the Coleoptera of North America. Smithson. Misc. Coll. No. 507, 567 p.

Leng, C. W. 1915. List of the Carabidae of Florida. Bull. American Mus. Nat. Hist., 34 : 555-601.

Leng, C. W. 1920. Catalogue of the Coleoptera of America, north of Mexico. Mount Vernon, New York, 470 p.

Leng, C. W. and A. J. Mutchler. 1927. Supplement 1919-1924 (inclusive) to catalogue of the Coleoptera of America, north of Mexico. Mount Vernon, New York, 78 p.

Leng, C. W. and A. J. Mutchler. 1933. Second and third supplements 1925-1932 (inclusive) to catalogue of the Coleoptera of America, north of Mexico. Mount Vernon, New York, 112 p.

Leonard, M. D. 1926. A list of the insects of New York with a list of the spiders and certain other allied groups. Cornell University agr. Expt. Sta. Mem. 101 : 1121 p.

Lindroth, C. H. 1955. Dejean's types of North American Carabidae (Col.). Opusc. ent. 20 : 10-34.

Lindroth, C. H. 1963. The problem of late land connections in the North Atlantic area. *In* Löve, A. and D. Löve. North Atlantic biota and their history. The MacMillan Company, New York, pp. 73-85, 6 figs.

Lindroth, C. H. 1966. The ground-beetles of Canada and Alaska. Part 4. Opusc. ent. 29 : 409-648.

Löding, P. H. 1945. Monograph II. Catalogue of the beetles of Alabama. Geological Survey of Alabama. University of Alabama. Wetumpka Printing Co., Wetumpka, Alabama, 172 p.

Martin, P. S. and B. E. Harrell. 1957. The Pleistocene history of temperate biotas in Mexico and eastern United States. Ecology 38 : 468-480.

Maslin, T. P. 1952. Morphological criteria of phyletic relationships. Syst. Zool., 1 : 49-70.

Motschulsky, V. 1865. Enumeration des nouvelles espèces de coléoptères rapportes de ses voyages. Bull. Soc. Imp. Nat. Moscou, 38(4) : 227-313.

Muller, E. H. 1965. Quaternary Geology of New York, 99-112 p. *In* H. E. Wright, Jr., and D. G. Frey, (ed.). The Quaternary of the United States. Princeton University Press, Princeton.

Newman, E. 1838. Entomological notes. Ent. Mag. 5 : 372-402.

Olson, A. L., T. H. Hubbell, and H. F. Howden. 1954. The burrowing beetles of the genus *Mycotrupes* (Coleoptera:Scarabaeidae : Geotrupinae). Univ. Mich. Mus. Zool. Misc. Publ. 84, 59 p.

Richards, H. G. and S. Judson. 1965. The Atlantic Coastal Plain and the Appalachian Highlands in the Quaternary. *In* H. W. Wright, Jr., and D. G. Frey, (ed.). The Quaternary of the United States. Princeton University Press, Princeton.

Rohwer, S. A. and G. E. Woolfenden. 1969. Breeding birds of two Florida woodlands: comparisons with areas north of Florida. Condor, 171(1) : 38-48.

Ross, H. H. 1965. Pleistocene events and insects. *In* H. E. Wright, Jr., and D. G. Frey, (ed.). The Quaternary of the United States. Princeton University Press, Princeton.

Ross, H. H., G. L. Rotramel, J. E. H. Martin, and J. F. McAlpine, 1967. Postglacial colonization of Canada by its subboreal winter stoneflies of the genus *Allocapnia*. Can. Ent. 99(7) : 703-712.

Say, T. 1823a. Descriptions of insects of the families of Carabiei and Hydrocanthari of Latreille, inhabiting North America. Trans. Amer. phil. Soc. 2 : 1-109.

Say, T. 1823b. Descriptions of coleopterous insects collected in the late expedition to the Rocky Mountains, performed by order of Mr. Calhoun, Secretary of War, under the command of Major Long. J. Acad. nat. Sci. Phil. 3 : 139-216.

Say, T. 1834. Descriptions of new North American insects and observations on some already described. Trans. Amer. phil. Soc. 4 : 409-470.

Schafer, J. P., and J. H. Hartshorn. 1965. The Quaternary of New England, p. 113-128. *In* H. E. Wright, Jr., and D. G. Frey, (ed.). The Quaternary of the United States. Princeton University Press, Princeton.

Schaupp, F. G. 1880. Synoptic tables of Coleoptera. *Evarthrus* LeConte. Bull. Brooklyn ent. Soc. 3 : 49.

Schuler, L. 1962. La Spermatheque des *Chlaenius* de France (Callistomorphi Jeannel). L'Entomologiste. 18(4) : 77-86.

Schuler, L. 1963a. La spermatheque chez les Harpalidae et les Pterostichitae de France. Rev. franc. Ent. 30(2) : 81-103.

Schuler, L. 1963b. Les organes genitaux femelles chez les Pterostichidae de France. Les tribus Anchomenini et Sphodrini (suite). Le Cas des Patrobidae (Col. Carabiques). Bull. Soc. ent. Fr. 68 : 13-26.

Scudder, S. H. 1900. Adephagous and clavicorn Coleoptera from the Tertiary deposits at Florissant, Colorado with descriptions of a few other forms and a systematic list of the non-rhynchophorous Tertiary Coleoptera of North America. Mon. U. S. Geol. Sur. 40, 148 p.

Selander, R. K. 1965. Avian speciation in the Quaternary, p. 527-542. *In* H. E. Wright, Jr., and D. G. Frey, (ed.). The Quaternary of the United States. Princeton University Press, Princeton.

Shotton, F. W. 1965. Movements of insect populations in the British Pleistocene. Geol. Soc. Amer., Special Paper 84, pp. 17-33.

Simpson, G. G. 1961. Principles of animal taxonomy. Columbia University Press, New York. 247 p.

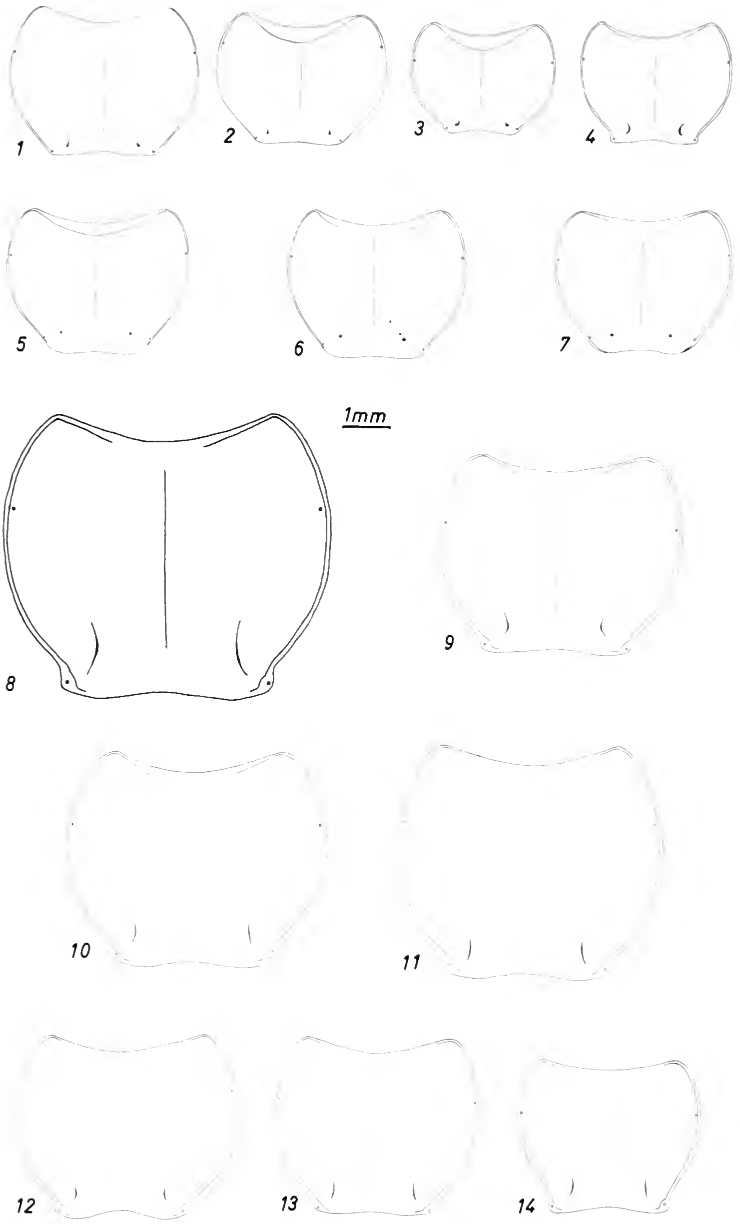
Stebbins, G. L., Jr., 1951. Variation and evolution in plants. Columbia University Press, New York. 643 p.

Van Dyke, E. C. 1926. New species of Carabidae in the subfamily Harpalinae chiefly from western North America. Pan-Pacific ent. 2 : 113-126.

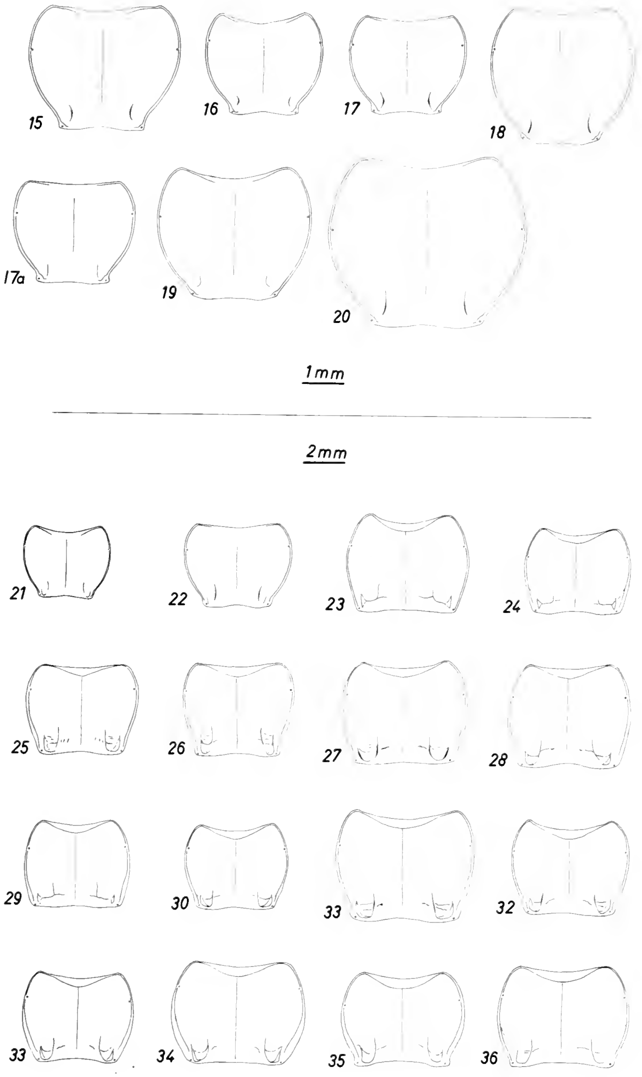
Van Dyke, E. C. 1943. New species and subspecies of North American Carabidae. Pan-Pacific ent. 19 : 17-30.

Van Emden, F. I. 1942. A key to the genera of larval Carabidae (Col.). Trans. R. ent. Soc., Lond. 92 : 1-99.

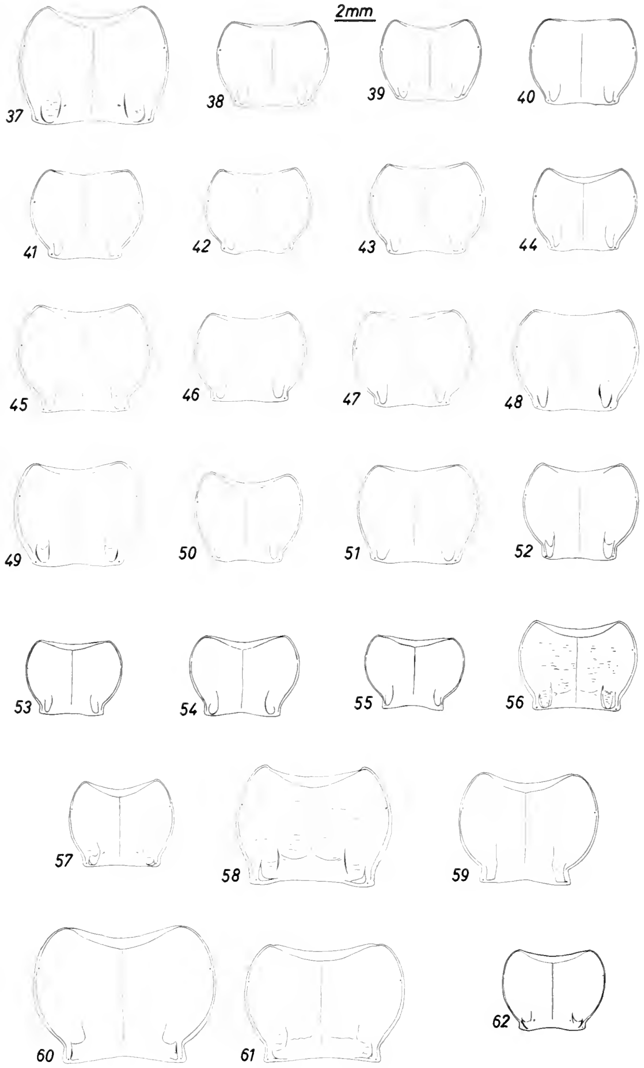
Whitehead, D. R. 1965. Palynology and Pleistocene phytogeography of unglaciated eastern North America. *In* H. E. Wright, Jr., and D. G. Frey, (ed.). The Quaternary of the United States. Princeton University Press, Princeton.



Figs. 1-14. Pronotum, dorsal aspect. 1. *E. hernandensis* (Citrus County, Florida). 2. *E. morio* (Alma, Georgia). 3. *E. laevipennis* (Mobile, Alabama). 4. *E. laevipennis* (near Spartensburg, South Carolina). 5. *E. approximatus* (Rosslyn, Virginia). 6. *E. iuvenis* (near Roanoak, Virginia). 7. *E. obsoletus* (near Tuscaloosa, Alabama). 8. *E. unicolor* (Umadilla, Georgia). 9. *E. fucatus* (Leesburg, Alabama). 10. *E. spoliatus* (Rock Creek, Washington, D. C.). 11-13. *E. brevoorti* (11. Mobile, Alabama; 12. Calvert, Alabama; 13. Clemson, South Carolina). 14. *E. vinctus* (Clayton, Georgia).



Figs. 15-36. Pronotum, dorsal aspect. 15. *E. alabamensis* (Mobile, Alabama). 16. *E. ovulum* (Tallahassee, Florida). 17. *E. macrovulum* (Mobile, Alabama). 17a. *E. texensis* (Kirbyville, Texas). 18. *E. parafaber* (Mobile, Alabama). 19. *E. levifaber* (Georgia). 20. *E. faber* (Punta Gorda, Florida). 21. *E. incisus* (near Morrilton, Arkansas). 22. *E. whitcombi* (Hot Springs, Arkansas). 23. *E. blatchleyi* (Jacksonville, Florida). 24. *E. floridensis* (Winter Park, Florida). 25-28. *E. sigillatus* (25. Easton, Pennsylvania; 26. Black Mountains, North Carolina; 27. Climax, North Carolina; 28. Auburn, Alabama). 29. *E. sinus* (Alabama Port, Alabama). 30-32. *E. convivus* (30. Beamsville, Ohio; 31. Talladega, Alabama; 32. near Toomsuba, Mississippi). 33. *E. seximpressus* (Le Flore County, Oklahoma). 34. *E. alabamae* (Gulfport, Mississippi). 35. *E. engelmanni* (Cuero, Texas). 36. *E. nonnitens* (Bradley County, Arkansas).



Figs. 37-62. Pronotum dorsal aspect. 37. *E. hypherpiformis* (near Demopolis, Alabama). 38-44. *E. sodalis sodalis* (38. near Lake Chautauqua, New York; 39. Cleveland, Ohio; 40. Albany, Wisconsin; 41. near Frankfort, Kentucky; 42. Chicago, Illinois; 43. Dubois, Illinois; 44. near Luka, Mississippi). 45-47. *E. sodalis colossus* (45. near Yates Centre, Kansas; 46. St. Joseph, Missouri; 47. St. Louis, Missouri). 48. *E. s. lodingi* (Monte Sano State Park, Alabama). 49. *E. parasodalis* (Washington County, Arkansas). 50-51. *E. furtivus* (50. N. Cumberland, Pennsylvania; 51. Rosslyn, Virginia). 52. *E. alternans* (Ames, Iowa). 53. *E. iowensis* (Iowa City, Iowa). 54. *E. substriatus* (Cloudcroft, New Mexico). 55. *E. constrictus* (Hamilton County, Kansas). 56. *E. torvus torvus* (near Grand Island, Nebraska). 57. *E. torvus deceptus* (Cuero, Texas). 58. *E. gravidus* (Austin, Texas). 59. *E. sallei* (Victoria, Texas). 60. *E. gigas* (Victoria, Texas). 61. *E. heros* (Dallas, Texas). 62. *E. gravesi* (Pearl, Mississippi).

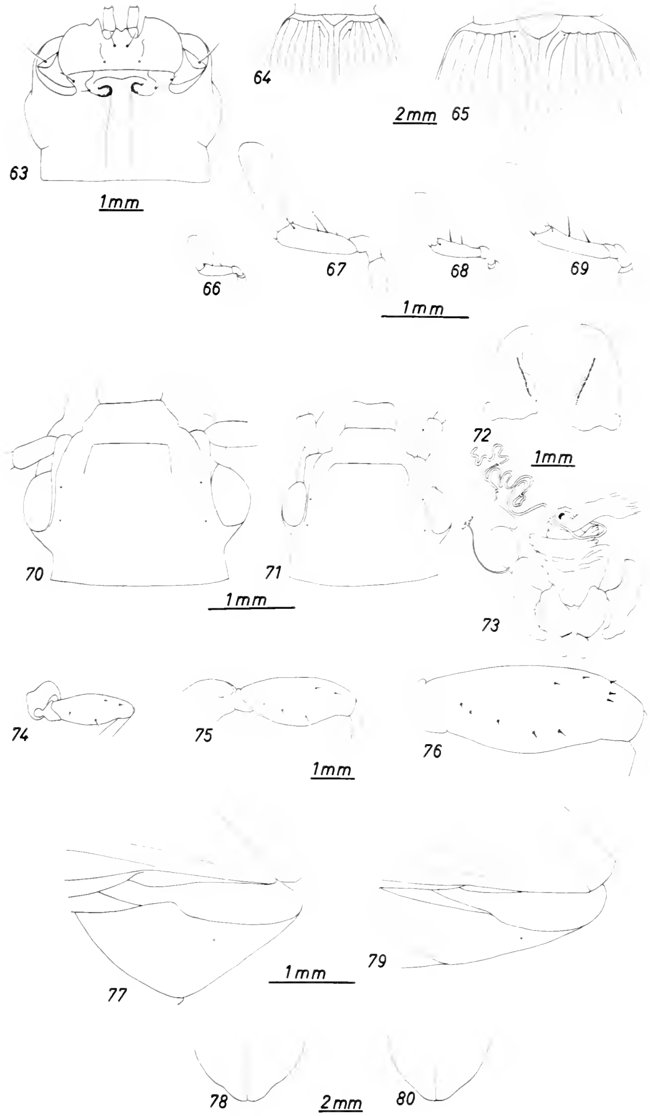
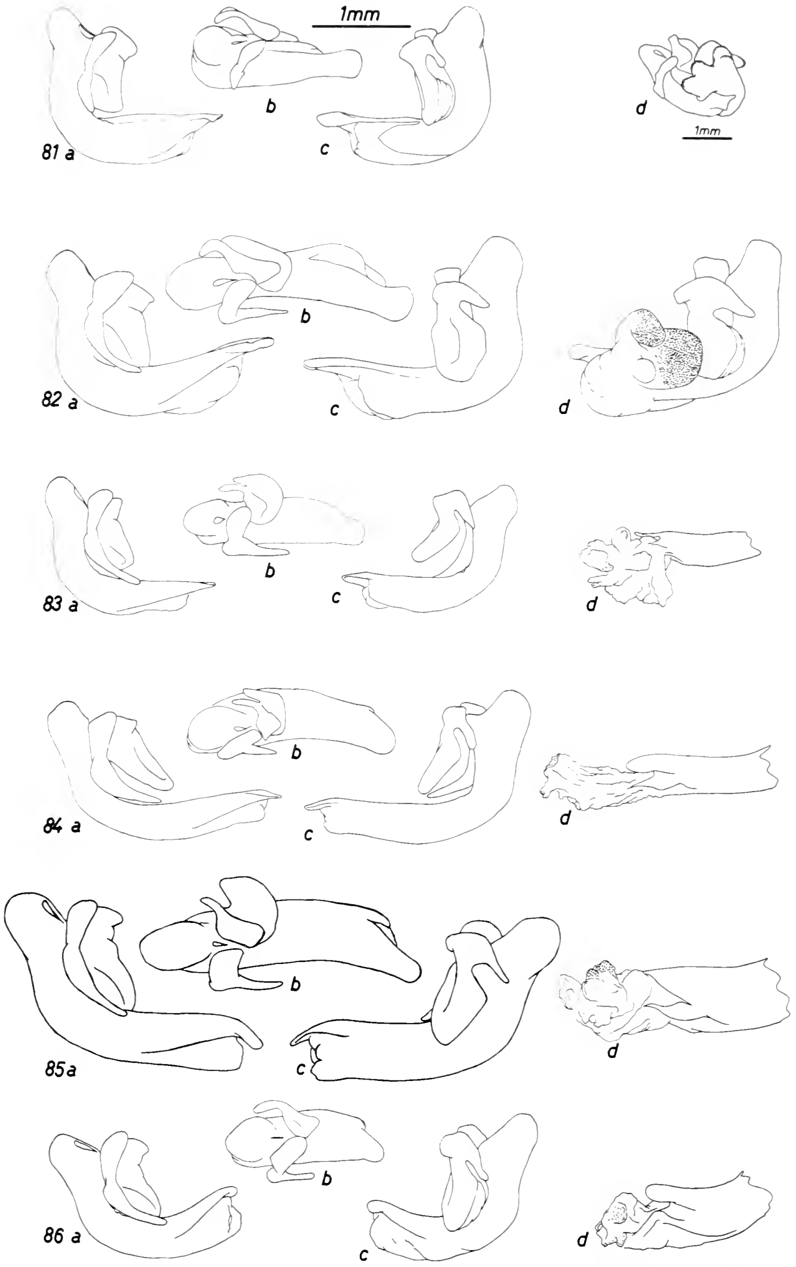
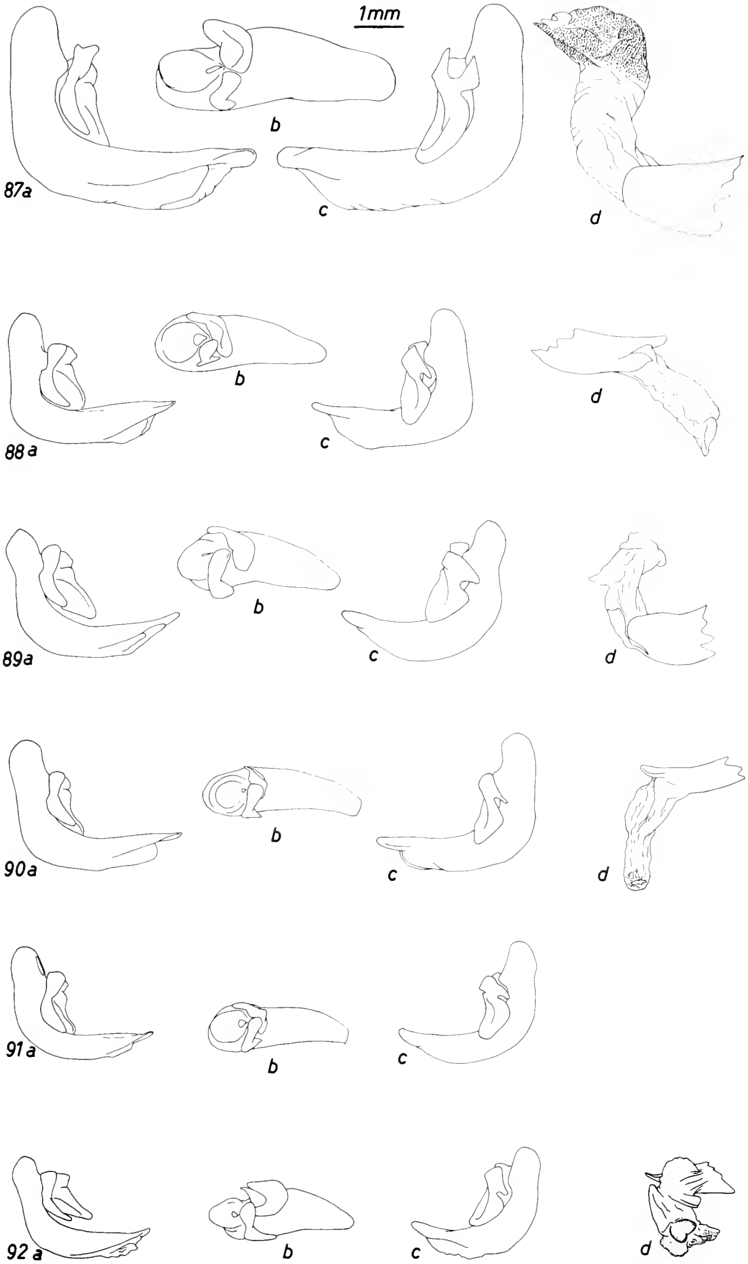


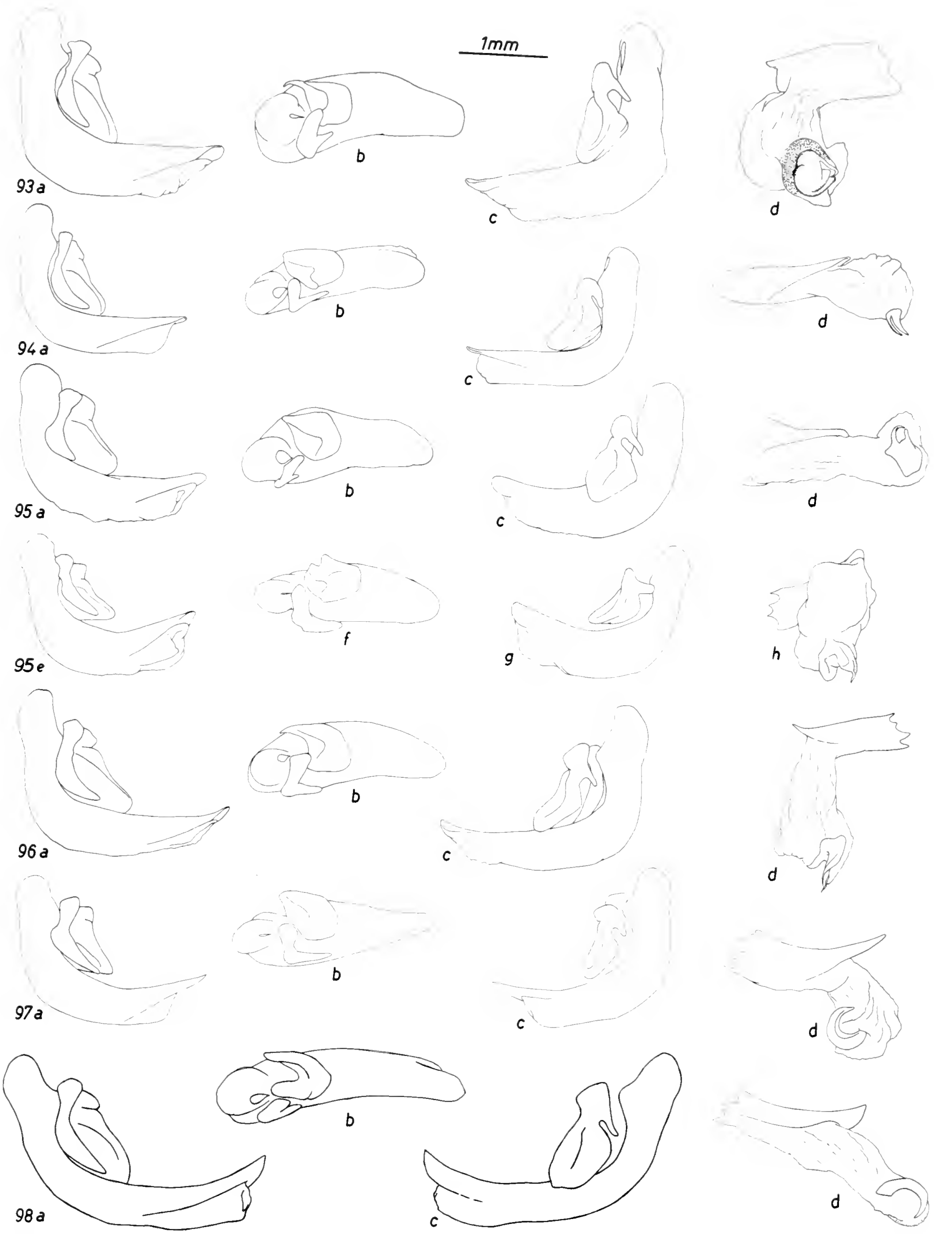
Fig. 63. Ventral aspect of head of *E. unicolor*. Figs. 64-65. Elytra, basal portion. 64. *E. sodalis colossus* (St. Joseph, Missouri). 65. *E. heros* (Dallas, Texas). Figs. 66-69. Palpus of labium. 66. *E. hernandensis*. 67. *E. unicolor*. 68. *E. faber*. 69. *E. blatchleyi*. Figs. 70-71. Head, dorsal aspect. 70. *E. alabamensis*. 71. *E. ovulum*. Fig. 72. Ventral aspect of mandibles of *E. sigillatus*. Fig. 73. Genitalia of female *E. sigillatus*. Figs. 74-76. Middle femur, anterior face. 74. *E. hernandensis*. 75. *E. seximpressus*. 76. *E. heros*. Fig. 77. Plica of elytron and dorsal hump of abdomen of *E. substriatus* (Kerrville, Texas). Fig. 78. Dorsal aspect of posterior portion of elytra of *E. substriatus* (near Ft. Davis, Texas). Fig. 79. Plica of elytron and dorsal hump of abdomen of *E. constrictus* (Denver, Colorado). Fig. 80. Dorsal aspect of posterior portion of elytra of *E. constrictus* (Clark County, Kansas).



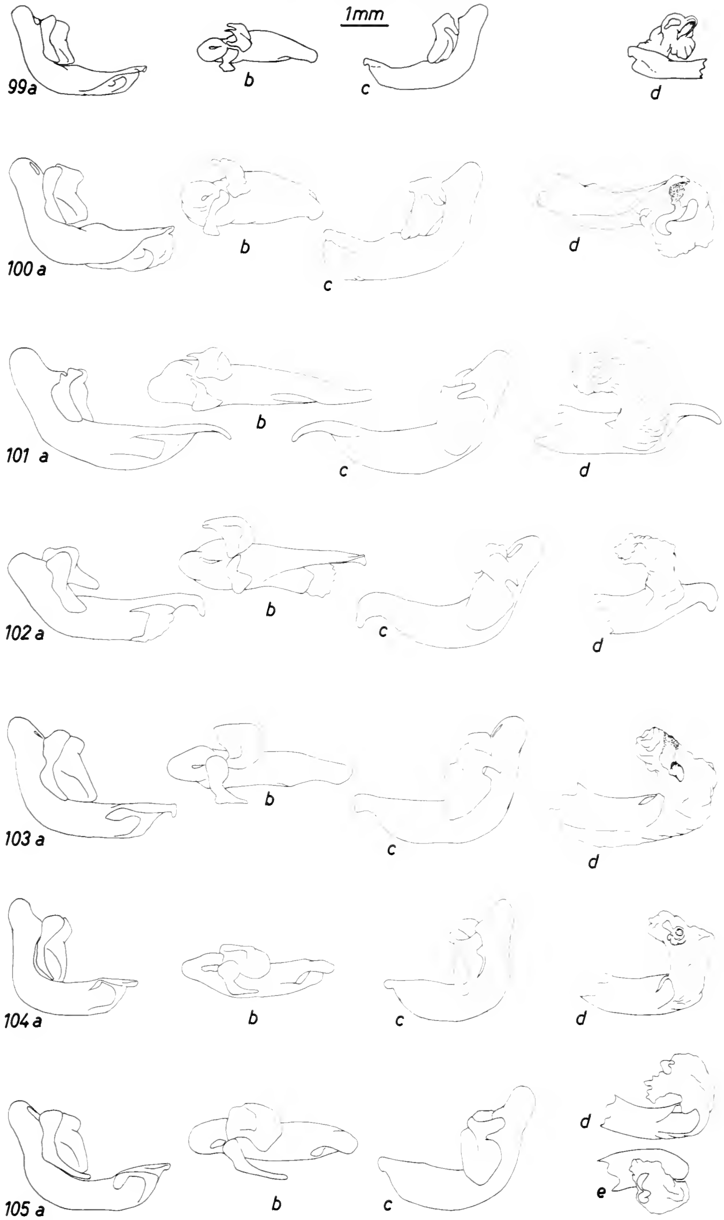
Figs. 81-86. Male genitalia, median lobe and parameres: a, right lateral aspect; b, ventral aspect; c, left lateral aspect; d, median lobe with internal sac everted. 81. *E. hernandensis* (Juniper Springs, Florida), d, right apical aspect. 82. *E. morio* (Wellborn, Florida), d, left lateral aspect. 83. *E. laevipennis* (Mobile, Alabama), d, left lateral aspect. 84. *E. approximatus* (Fairfax County, Virginia), d, left lateral aspect. 85. *E. iuvenis* (near Roanoke, Virginia), d, left lateral aspect. 86. *E. obsoletus* (Talladega, Alabama), d, left lateral aspect.



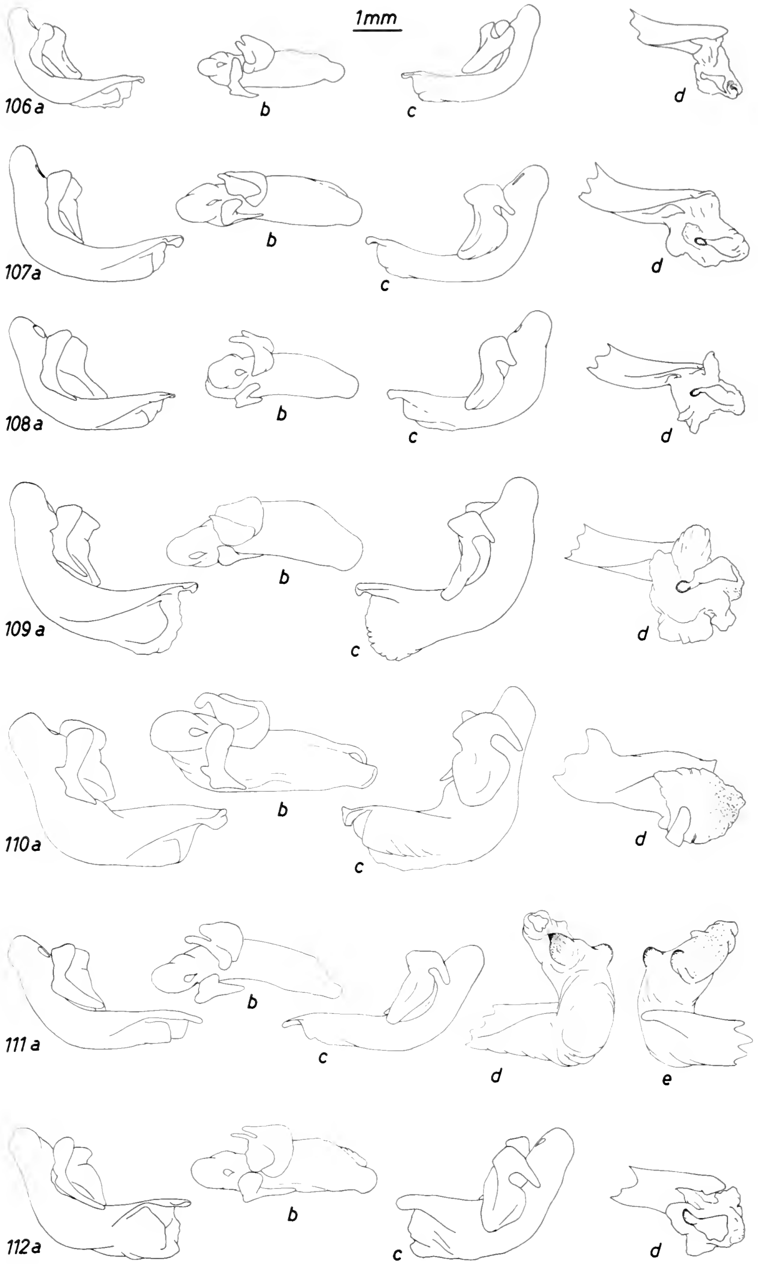
Figs. 87-92. Male genitalia, median lobe and parameres: a, right lateral aspect; b, ventral aspect; c, left lateral aspect; d, median lobe with internal sac everted. 87. *E. unicolor* (Leesburg, Alabama), d, ventral aspect. 88. *E. fucatus* (Leesburg, Alabama), d, right lateral aspect. 89. *E. spoliatus* (Rock Creek, Washington, D. C.), d, ventral aspect. 90. *E. brevoorti* (Mobile, Alabama), d, left lateral aspect. 91. *E. brevoorti* (Lucedale, Mississippi). 92. *E. vinctus* (Rabun County, Georgia), d, left lateral aspect.



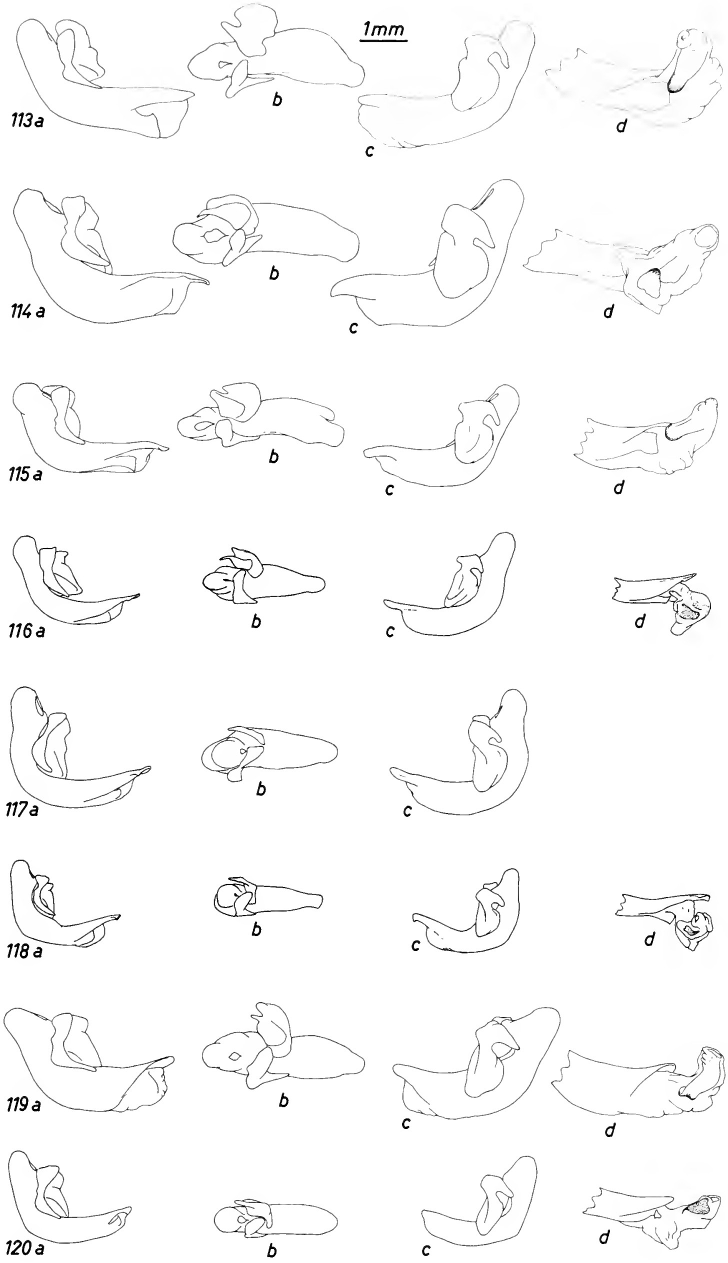
Figs. 93-98. Male genitalia, median lobe and parameres: a, right lateral aspect; b, ventral aspect; c, left lateral aspect; d, median lobe with internal sac everted, similarily e-h. 93. *E. alabamensis* (Mobile, Alabama), d, left lateral aspect. 94. *E. ovulum* (Toombs County, Georgia), d, right lateral aspect. 95a-d. *E. macrovulum* (Mobile, Alabama), d, right dorso-lateral aspect. 95e-h. *E. texensis* (Tyler Co., Texas). 96. *E. parafaber* (Mobile, Alabama), d, left lateral aspect. 97. *E. levifaber* (Georgia), d, right lateral aspect. 98. *E. faber* (Punta Gorda, Florida), d, right lateral aspect.



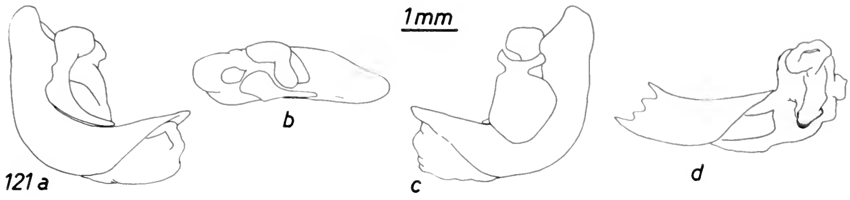
Figs. 99-105. Male genitalia, median lobe and parameres: a, right lateral aspect; b, ventral aspect; c, left lateral aspect; d, median lobe with internal sac everted. 99. *E. incisus* (Washington County, Arkansas), d, ventral aspect. 100. *E. whitcombi* (Hot Springs, Arkansas), d, right lateral aspect. 101. *E. blatchleyi* (Gainesville, Florida), d, right lateral aspect. 102. *E. floridensis* (Winter Park, Florida), d, right lateral aspect. 103. *E. sigillatus* (Easton, Pennsylvania), d, right lateral aspect. 104. *E. sinus* (Alabama Port, Alabama), d, right lateral aspect. 105. *E. convivus* (near Toomsuba, Mississippi), d, right lateral aspect; e, median lobe with internal sac everted, ventral aspect.

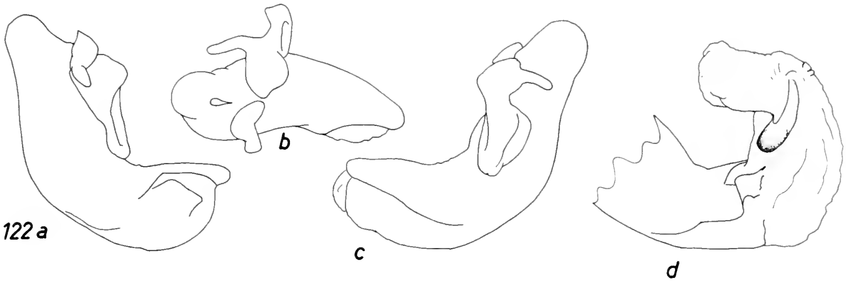


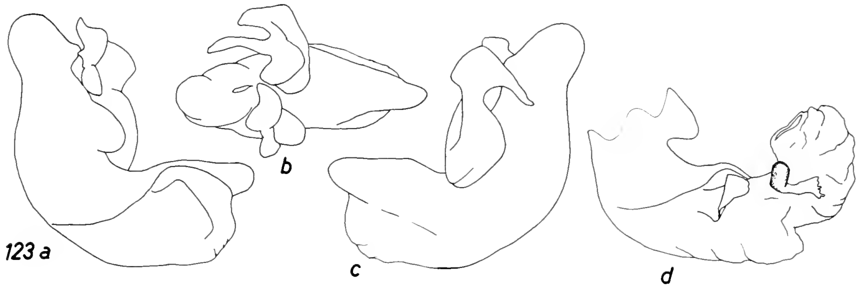
Figs. 106-112. Male genitalia, median lobe and parameres: a, right lateral aspect; b, ventral aspect; c, left lateral aspect; d, median lobe with internal sac everted, right lateral aspect. 106. *E. seximpressus* (Washington County, Arkansas). 107. *E. alabamae* (Mobile, Alabama). 108. *E. engelmanni* (College Station, Texas). 109. *E. nonnitens* (Bradley County, Arkansas). 110. *E. hypherpiformis* (Manego County, Alabama). 111. *E. sodalis* (Mayville, N. Y.). 112. *E. parasodalis* (Washington County, Arkansas).

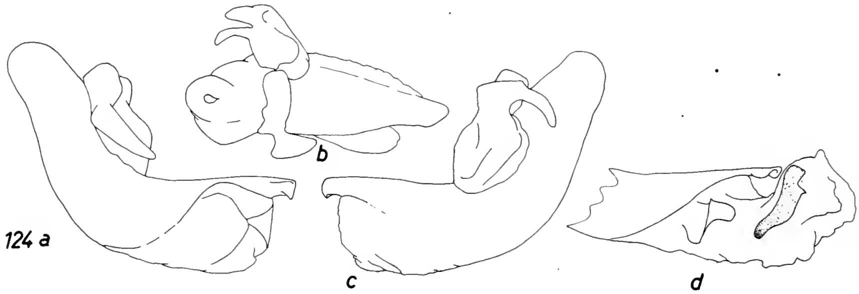


Figs. 113-120. Male genitalia, median lobe and parameres: a, right lateral aspect; b, ventral aspect; c, left lateral aspect; d, median lobe with internal sac everted, right lateral aspect. 113. *E. furtivus* (Mt. Vernon, Virginia). 114. *E. alternans* (Adams County, Illinois). 115. *E. iowensis* (Iowa City, Iowa). 116. *E. substriatus* (Minaca, Chihuahua, Mexico). 117. *E. substriatus* (Durango, Mexico). 118. *E. constrictus* (Austin, Texas). 119. *E. torvus torvus* (near Castle Rock, Colorado). 120. *E. torvus deceptus* (Texas).

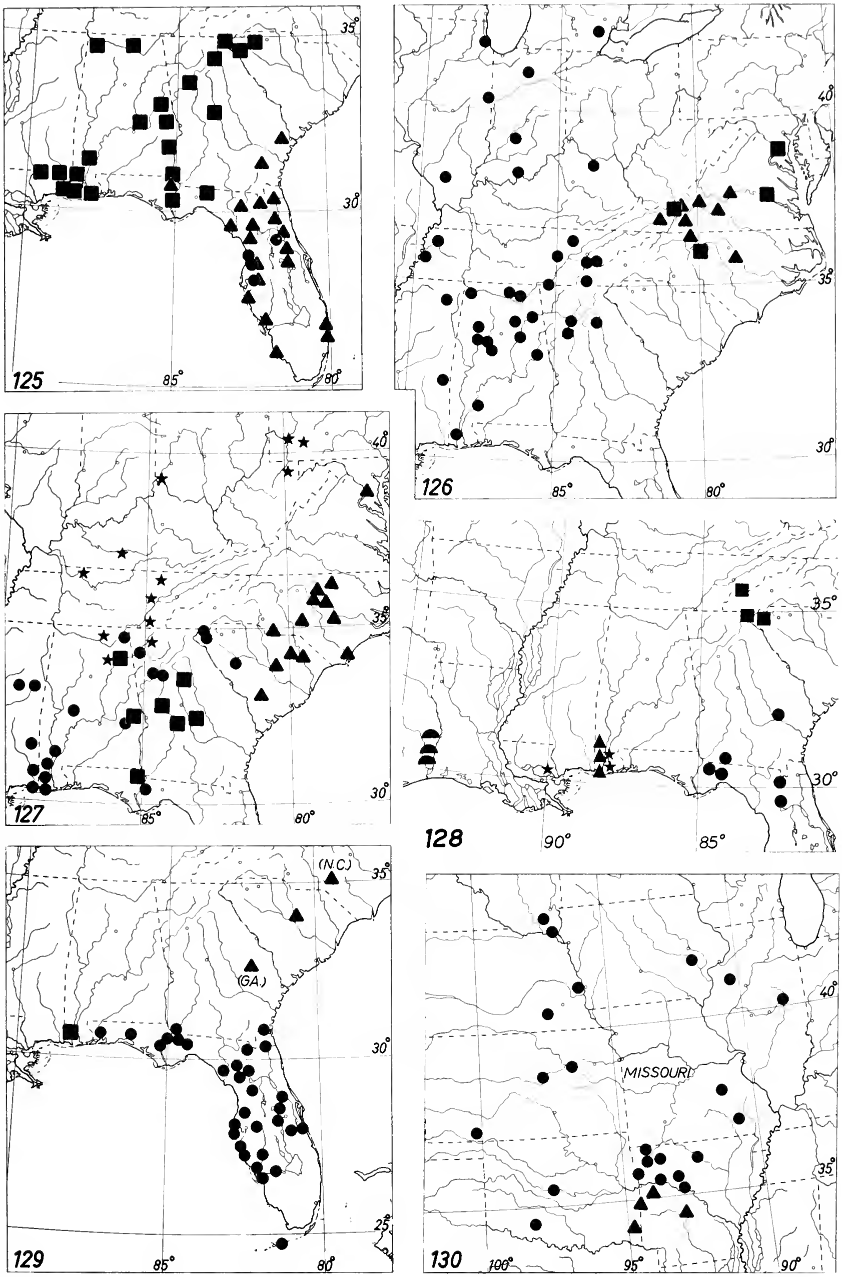




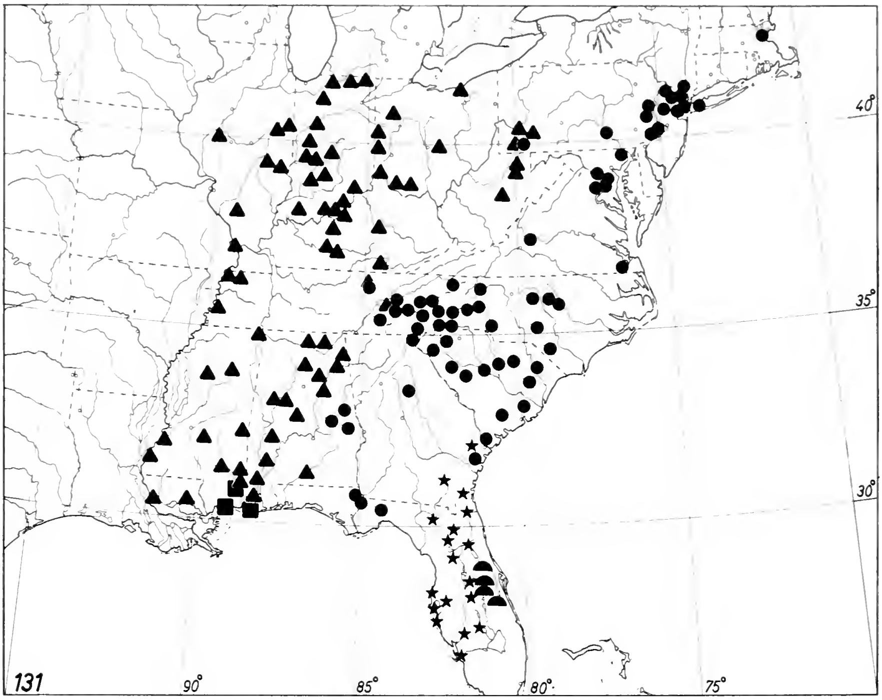


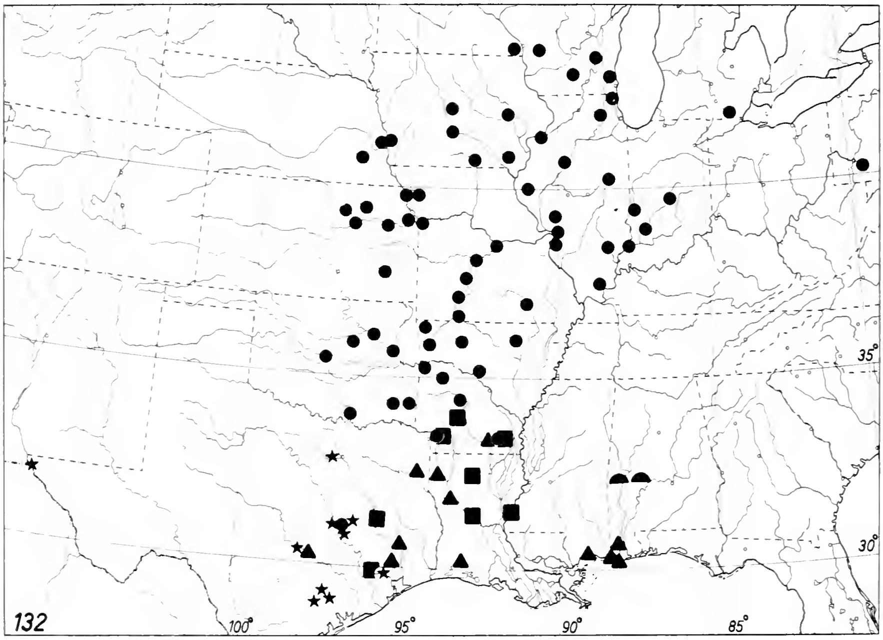


Figs. 121-124. Male genitalia, median lobe and parameres: a, right lateral aspect; b, ventral aspect; c, left lateral aspect; d, median lobe with internal sac everted, right lateral aspect. 121. *E. gravidus* (Forestburg, Texas). 122. *E. sallei* (Victoria, Texas). 123. *E. gigas* (Kingsville, Texas). 124. *E. heros* (Gainesville, Texas).

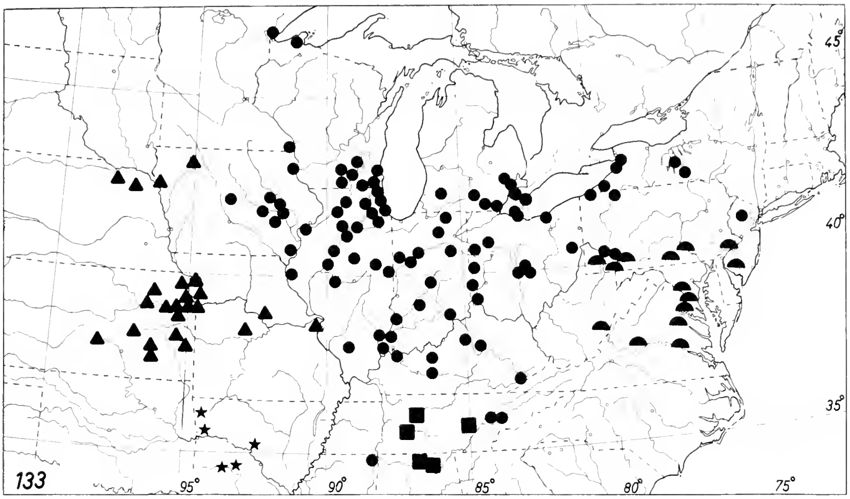


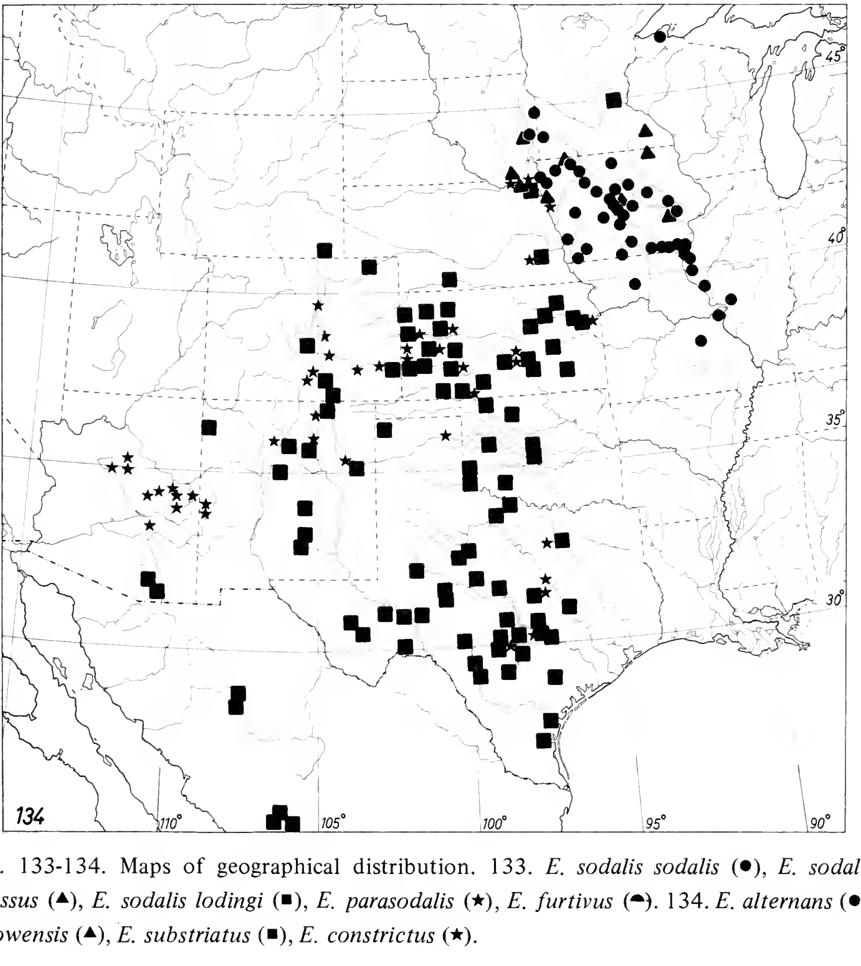
Figs. 125-130. Maps of geographical distribution. 125. *E. hernandensis* (●), *E. morio* (▲), *E. laevipennis* (■). 126. *E. approximatus* (■), *E. iuvenis* (▲), *E. obsoletus* (●). 127. *E. unicolor* (■), *E. fucatus* (★), *E. spoliatus* (▲), *E. brevoorti* (●). 128. *E. vinctus* (■), *E. alabamensis* (▲), *E. ovulum* (●), *E. macrovulum* (★), *E. texensis* (▼). 129. *E. parafaber* (■), *E. levifaber* (▲), *E. faber* (●). 130. *E. incisus* (●), *E. whitcombi* (▲).



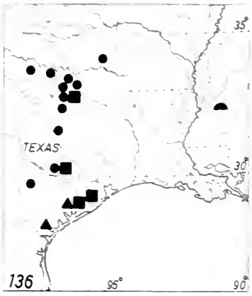


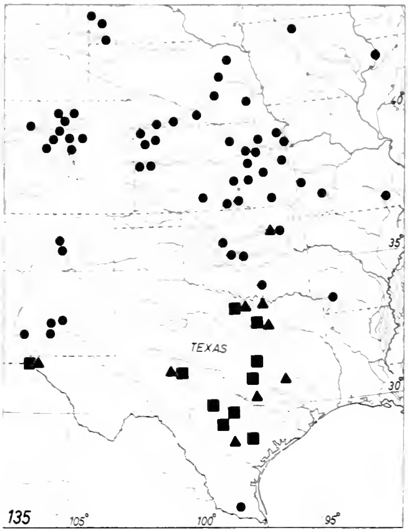
Figs. 131-132. Maps of geographical distribution. 131. *E. blatchleyi* (★), *E. floridensis* (⏶), *E. sigillatus* (●), *E. sinus* (■), *E. convivus* (▲). 132. *E. seximpressus* (●), *E. alabamae* (▲), *E. engelmanni* (★), *E. nonnitens* (■), *E. hypherpiformis* (⏶).

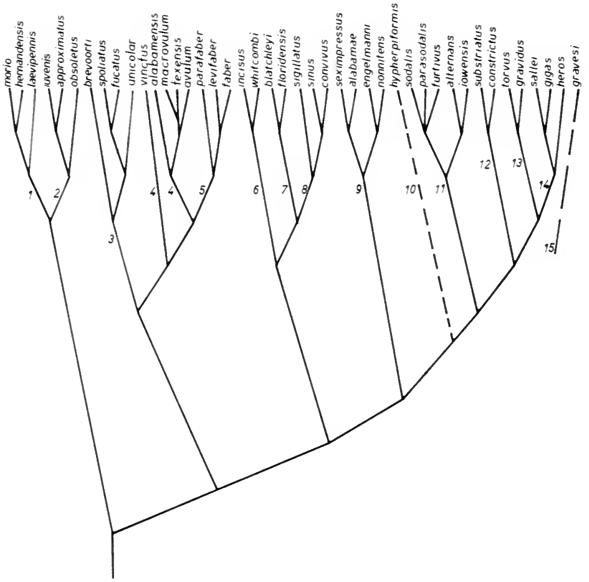




Figs. 133-134. Maps of geographical distribution. 133. *E. sodalis sodalis* (●), *E. sodalis colossus* (▲), *E. sodalis lodingi* (■), *E. parasodalis* (★), *E. furtivus* (◓). 134. *E. alternans* (●), *E. iowensis* (▲), *E. substriatus* (■), *E. constrictus* (★).







137

Figs. 135-136. Maps of geographical distribution. 135. *E. torvus torvus* (●), *E. torvus deceptus* (▲), *E. gravidus* (■). 136. *E. sallei* (■), *E. gigas* (▲), *E. heros* (●), *E. gravesi* (◓). Fig. 137. Hypothetical phylogeny of the species of the genus *Evarthrus*. Species groups are numbered as follows: 1 - the *morio* group, 2 - the *obsoletus* group, 3 - the *spoliatus* group, 4 - the *ovulum* group, 5 - the *faber* group, 6 - the *incisus* group, 7 - the *blatchleyi* group, 8 - the *sigillatus* group, 9 - the *seximpressus* group, 10 - the *hypherpiformis* group, 11 - the *sodalis* group, 12 - the *substriatus* group, 13 - the *torvus* group, 14 - the *gigas* group, 15 - the *gravesi* group.

138

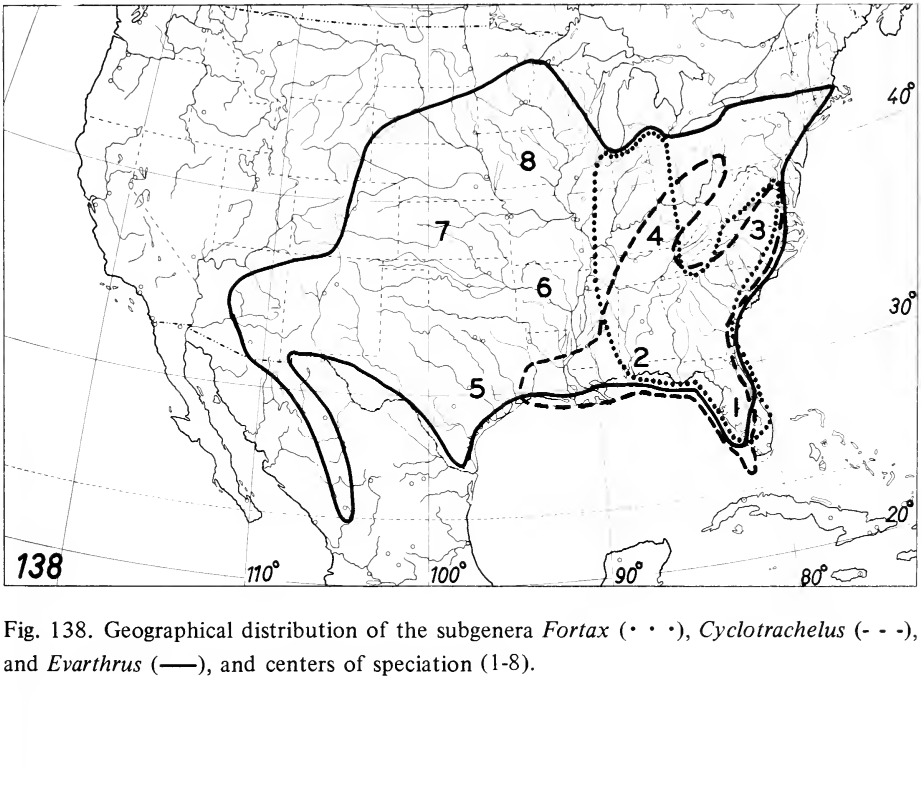


Fig. 138. Geographical distribution of the subgenera *Fortax* (• • •), *Cyclotrachelus* (- - -), and *Evarthrus* (——), and centers of speciation (1-8).

ERRATA – Quaest. ent. 1969: 5(1):

"New distributional records for Canadian soldier flies (Diptera:Stratiomyidae. Part I. Beridinae and Sarginae". By Max W. McFadden.

page 5. The species *Allognosta brevicornis* Johnson is known from Quebec, not Quebic.
page 7. The title of the paper by James (1951) is "The Stratiomyidae of Alaska", not Alberta.

. . . .

"A revision of the genera *Philophuga* Motschoulsky and *Tecnophilus* Chaudoir with notes on the North American Callidina (Coleoptera:Carabidae)". By David J. Larson.

page 29. Page references in key:
. . . . *Tecnophilus* Chaudoir, p. 44, not page 38.
. . . . *Philophuga* Motschoulsky, page 29, not page 24.
. . . . *Infernophilus* new genus, page 43, not page 37.
page 67 - Table 17. The unnamed branch arising from the *Philophuga* stem was accidentally inserted by the Temporary Editor, and should be deleted.

. . . .

For all of these errors the Temporary Editor (G. E. Ball) apologizes to the authors and to the readers of *Quaestiones entomologicae*.

Quaestiones entomologicae

A periodical record of entomological investigations, published at the Department of Entomology, University of Alberta, Edmonton, Canada.

VOLUME V NUMBER 3 JULY 1969

QUAESTIONES ENTOMOLOGICAE

A periodical record of entomological investigation published at the Department of Entomology, University of Alberta, Edmonton, Alberta.

Volume 5 Number 3 July 1969

CONTENTS

BOOK REVIEW

SMITH, DAVID, S. 1968. Insect Cells. Their Structure and Function. Oliver and Boyd Ltd., Edinburgh, Scotland. xvii + 372 pp., cxviii plates. Cloth bound. $16.00 U. S. A.

With the publication of this volume Smith has done for Entomology what D. W. Fawcett in his *An Atlas of Fine Structure, The Cell* (1966) did for Vertebrate Zoology. He has produced a concise and beautifully illustrated summary of our current knowledge of the fine structure and function of insect cells.

Each tissue and tissue product of the insect body is illustrated by one or more carefully chosen transmission or scanning electron micrographs, many of which originated in Smith's laboratory. The cells and cell products treated are: integument, muscle, neuromuscular junctions, nervous system, corpus cardiacum, corpus allatum, compound eye, tracheal system, dorsal vessel, haemocytes, pericardial cells, oenocytes, fat body, mycetocytes, salivary glands, silk glands, fore-gut, mid-gut, hind-gut, peritrophic membrane, rectal papillae, Malpighian tubules, anal papillae, testis, vas deferens, accessory glands, ovary and spermatheca. Although 24 species of insect are represented in the book, the majority of the plates contain micrographs prepared from only five: *Oncopeltus fasciatus, Ephestia kühniella, Carausius morosus, Calliphora erythrocephala,* and *Periplaneta americana*. In all the plates abbreviations are minimal.

The text of the book includes up-to-date background summaries of the basic morphology and physiology of each of the tissues illustrated. In each summary the reader is referred, for further information, to the relevant chapter in the sixth edition of V. B. Wigglesworth's *The Principles of Insect Physiology* (1965). Reference to each of the micrographs is made in the text and the main features contained in these illustrations are mentioned in the captions. Each summary is supplied with a list of references covering the principal contributions made in that area. Throughout the text reference is made to ultrastructural studies of comparable tissues in vertebrate animals, a consistency which will undoubtedly enhance the value of the book for general biologists as well as broadening the perspective of entomologists. A selected list of references to papers published after the submission of the manuscript (June 1967) is added as an appendix. Throughout the text Smith is careful also to mention avenues worthy of further investigation.

No experience is required, on the part of the reader, in the interpretation of electron micrographs. The necessary background is provided in the introduction in the form of a foldout illustration. On this is centered a diagram of the "generalized cell" and its organelles. Each organelle is also illustrated by a small electron micrograph prepared from insect material. Each of these micrographs is numbered and, in a key on either side of the diagram, its role in cell physiology is summarized.

Although the manufacture of the book is good, the book is very heavy (2.75 lbs.) for its linear dimensions and it is possible that the strength of the binding will prove insufficient to support the weight of the pages over a long period of time.

The editing of the book is excellent. I list here the few typographical errors noticed. On page 220, mention is made in the last line of the caption to a plate which is not included. On page 232 it is the *outer* not the inner surface of the crop that bears a lattice work of visceral muscle fibres. On page 256 the magnification of the plate and the insert are reversed. Exception is taken also to the statement on page 183 that insects possess no sex hormones. Beginning in 1963 Jacqueline Naisse published a series of papers proving convincingly that androgens are produced by the developing testes of the lampyrid beetle *Lampyris noctiluca L.*

The addition of a conventional photomicrograph of the tissue under discussion in each section would have eased the reader's difficulty in positioning the electron micrographs that follow in their relative positions in the tissue.

These are minor criticisms of a text that will probably become a classic. This book should be present in the personal collection of every insect morphologist and physiologist. The reason is that most of the papers cited on insect ultrastructure have been published in journals few of which are generally perused by entomologists – an enlightening observation on the origin of most contributions in this field.

B. S. Heming
Department of Entomology
University of Alberta.

A COMPARISON OF SAMPLING METHODS FOR ADULT MOSQUITO POPULATIONS IN CENTRAL ALBERTA, CANADA

PETER GRAHAM
Department of Biology
Lindenwood College
St. Charles, Missouri 63301
U. S. A.

Quaestiones entomologicae
5 : 217-261 1969

Nine sampling methods for adult mosquitoes were compared: Malaise traps, Malaise traps baited with carbon dioxide, light traps, visual attraction trap, rotary sweep net, animal bait, human bait and captures of resting mosquitoes in a trailer. The position of the trap as well as its type was found to affect both the size and composition of the catch. Rotary sweep nets were found to have a definite attraction for mosquitoes and this may be selective for some species. Light traps caught a relatively larger proportion of parous mosquitoes than other methods, but other physiological stages showed no differences between methods.

In recent years a vast literature on sampling methods for mosquito populations has accumulated but this deals mainly with size and species composition of the catches.

In any study of trapping methods for insects it must be realized that the catch depends on three sets of factors: those in the trap, those in the environment and those in the insect.

The catch depends on the population density of the insect, its "availability" and its activity. Corbet (1961) considered that light traps in Uganda sampled only those mosquitoes engaged in non-specific activities and did not catch those engaged in feeding, swarming, or oviposition. Biddlingmayer (1967) has published a study of the effects of environment and species composition on different trap types but has not considered the effects of the physiological state of the mosquito.

Apart from Corbet (1961) I know of only one study relating the physiological state of an insect of medical importance to survey methods, the work of Bursell (1961). Barr (1958) mentions that the age and physiological state of mosquitoes affects the captures in light traps, but the citation he gives for this, Nielsen and Nielsen (1953), is incorrect, as this paper makes no mention of factors affecting light trap captures. Russian workers have paid considerable attention to the physiological age of mosquitoes, have elucidated many factors in the biology of the insects and have provided methods for determining age (Detinova, 1962) but have not related age to sampling procedure. I have attempted to fill part of this need in relation to woodland mosquitoes in central Alberta.

THE STUDY AREA

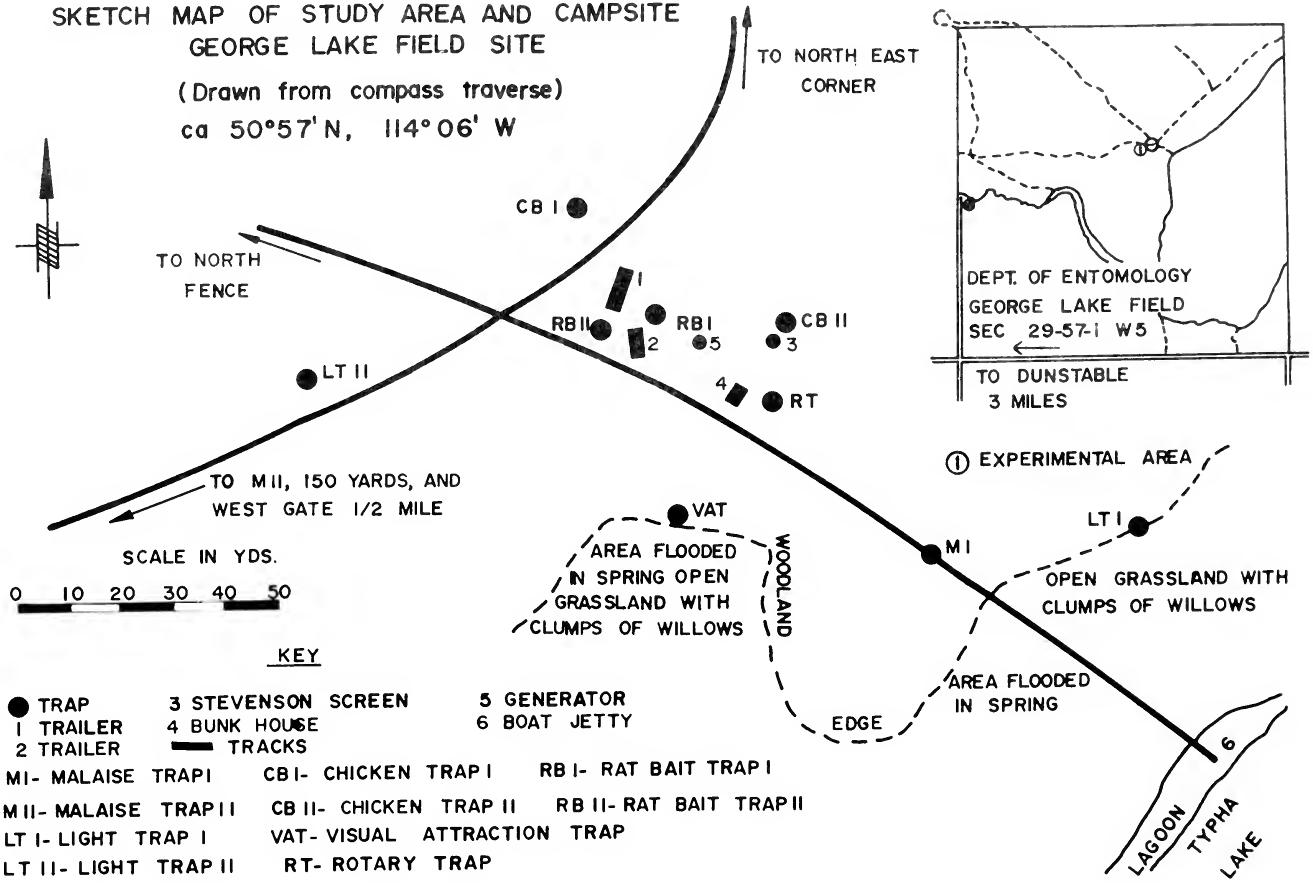
The study area is on the west shore of George Lake, 53°57'N and 114°06'W, about 40 miles northwest of Edmonton, Alberta. The area lies at the southern margin of the boreal mixed forest subzone (LaRoi, 1968). All traps were within 300 yards of the campsite, more or less in the centre of a square mile field site operated by the Department of Entomology, University of Alberta, (Fig. 1).

FIGURE I

SKETCH MAP OF STUDY AREA AND CAMPSITE GEORGE LAKE FIELD SITE

(Drawn from compass traverse)

ca 50°57'N, 114°06' W



Away from the lake shore the vegetation of the field site consists of almost untouched mature poplar forest, with small areas of spruce on the northern and western boundaries. Prior to 1930 some trees were removed by neighbouring farmers, but otherwise the forest has not been disturbed. The principal trees are *Populus tremuloides* Michx. and *P. balsamifera* L.. Other trees are *Picea glauca* (Moench.), *Betula papyrifera* Marsh., *Alnus tenuifolia* Nutt. and *Salix* species. *Larix laricina* Koch. is common in neighbouring wetlands but rare on the field site. The understory is more diverse, consisting of a large number of shrub and herb species: *Amelanchier alnifolia* Nutt., *Viburnum edule* (Michx.), *Rosa acicularis* Lindl., *Cornus stolonifera* Michx. and *Ribes lacustre* (Pers.) are common shrubs. *Cornus canadensis* L., *Solidago* species, *Epilobium angustifolium* L., and *Aster* species are common herbs. *Ledum groenlandicum* Oeder. forms more or less oval bogs in a few places, usually on clumps of sphagnum moss. On the northern boundary there is an area of sedge (*Carex* species) meadow which contains a number of permanent water holes. A stream flows out of the lake just south of the campsite and is blocked by several beaver dams. There is a fringe of *Carex* bordering the lake and a floating mat of *Typha* species round the lake edge.

About half the surrounding country is cleared for cultivation and grazing, mainly on the east, south and northwest, resulting in a patchwork of woodland, pasture and cultivation which allows a rich mosquito fauna (Graham in prep.).

In the winter of 1964-1965 above normal snow falls were recorded and melt water remained well into summer. Also nearly six inches of rain fell in the last two weeks of June 1965. Thus the majority of spring larvae were able to complete their development and second broods of many species developed. In the winter of 1965-1966, below normal snow falls occurred and most melt water had dried up by late spring, so many larvae did not complete development. Heavy rains did not fall till late July and August and the resulting pools soon dried up, so second broods were not prominent. Heavy snow fell in the winter of 1966-1967, but did not melt till the end of April. In 1966, snow had almost disappeared by 21 April, but in 1967 it was still deep on this date. Break up of ice on the lake had occurred on 21 April 1966 but did not take place till the end of the first week of May in 1967. According to Mr. E. Donald, a neighbouring farmer, the 1967 spring was ten days to two weeks behind the long term average at George Lake. Table 1 presents names of the major species of mosquitoes taken and their abundance in 1966.

An example of the difference in mosquito populations in the 1965 and 1966 seasons is given by the captures in a light trap operated at the Victoria Golf Course in the City of Edmonton. In 1965 this trap was run from 9 July to 30 August and caught 2826 mosquitoes, an average of 75 per night. In 1966 the same trap was run from early May to the end of August and caught six mosquitoes. Control measures in the urban area were the same in both years. In the spring of 1967 traps at George Lake caught approximately four times as many mosquitoes as in the spring of 1966, though I had the impression that the mosquito nuisance in the field site was worse in 1966.

METHODS

Sampling

Nine methods of sampling adult mosquitoes – Malaise traps, New Jersey light traps, a

Table 1 Numbers of mosquito species identified at George Lake in the spring and in summer of 1966.

Species	Number Identified	% of total Identified
Anopheles earlei	41	1.8
Culiseta inornata	187	8.4
Other *Culiseta*	63	2.8
Culex territans	43	1.9
Mansonia perturbans	36	1.6
Aedes cinereus	62	2.8
A. communis	75	3.3
A. excrucians	518	23.3
A. fitchii	199	8.9
A. implicatus	47	2.1
A. punctor	188	8.4
A. riparius	80	3.6
A. vexans	517	23.3
Other *Aedes*	186	8.4
Total *Aedes*	1871	83.5
Total caught	2459	
Number of species	28	

visual attraction trap, a rotary sweep net, chicken bait, rat bait, human bait, carbon dioxide bait, and collections of resting mosquitoes inside a trailer – were tested in this study. The localities of these traps are shown in Fig. 1. Traps used in different years were operated in the same places.

All meteorological data were obtained from a recording thermohygrograph in a Stevenson screen at the campsite.

Malaise traps. – This type of trap was first described by Malaise (1937), but its importance in ecological studies has only recently become apparent. I chose the modification of Townes (1962) as it is operational from all four directions. Breeland and Pickard (1965) and Smith *et al.* (1965) have recently demonstrated the value of this type in mosquito studies.

One trap was used in 1965 and two in 1966 and 1967. These had four entrances four feet high and six feet wide and the catching head was eight feet above the ground. The traps were erected over old tracks, MI near the lake shore and MII on the top of a low rise about 300 yards into the forest. Calcium cyanide, in the form of Cyanogas G, was used as a killing agent. Three teaspoonfuls in a manila envelope remained lethal for five days. The traps are shown in Plates 1, 2 and 3.

Light traps. – Two battery-operated standard New Jersey light traps (Lt) were used. This type was chosen as it is perhaps the trap most frequently used by mosquito workers. I decided not to use ultra violet light since the standard model is more often used and some studies (Zhogolev 1959; Downey 1962) have indicated that while U. V. greatly increases the catch

Plate 1 Malaise trap I as seen from the bunk house.

Plate 2 Malaise trap II in April 1967.

of some biting flies it might be less attractive to some mosquito species. It was not possible to compare U. V. with the standard model.

One of the two, Lt I, was situated at the forest edge on the lake shore and the other, Lt II, a short distance into the forest. A six volt car battery operated one of these traps for three nights. Air flowed at 121.5 cubic feet per minute through Lt I and at 120 cubic feet per minute through Lt II. These figures were determined with a Biram's anemometer. The light traps are shown in Plates 4, 5 and 6.

Visual attraction trap. – A visual attraction trap of the type described by Haufe and Burgess (1960) was used, with a net, instead of the hourly timing device described, for collecting the catch (Plate 7). Unfortunately, only one trap was available and the power supply permitted only restricted hours of operation.

The cylinder made one complete revolution every two seconds and the air flowed through the trap at 741 cubic feet per minute. Complete engineering blue prints of this trap are obtainable from the Canada Department of Agriculture, Medical and Veterinary Entomology Branch, Lethbridge, Alberta.

This type of trap was originally developed for use in the north, where short summer nights make light traps inefficient.

Rotary sweep net. – A group of four electrically driven rotary sweep nets was used. Two nets were at 45.5 inches and two at 58 inches above the ground. At each level, the base of one was 23 inches and the other was 34 inches from the shaft, so that no two nets swept the same volume of air. The nets were 12.5 inches in diameter and the trap made one complete revolution per second, thus the trap swept 1167 cubic feet of air per minute (Plate 8). The insects caught were removed with an aspirator. Operation of this trap was restricted by the power supply.

Rotary traps have been used by several workers (Chamberlin and Lawson, 1945; Stage and Chamberlin, 1945; Stage *et al.*, 1952; Love and Smith, 1957) who assumed the traps have no attraction for insects and take unbiased random samples.

Chicken baited traps. – Two small traps were constructed in 1965; each held one chicken. These were not very successful.

Two large traps each capable of holding several birds were used in 1966. They were six feet long, by four feet wide, 12 inches high at the corners and 22 inches high at the centre. One end was closed in with a roosting box 17 inches by four feet in dimension. The floor was one inch mesh wire cloth. Four egress traps protruded from the roosting box, two on each side. The rest of the sides were made of 14 x 18 inch mesh galvanized wire gauze. Ingress traps were tried but the birds sat on them and broke them. The mosquitoes entered by the wire cloth floor and were caught in the egress traps as they left. The traps did not catch many mosquitoes, possibly because the birds ate them.

The two traps were designated CBI and CBII (Plates 9 and 10). CBI was baited with white leghorns and CBII with bantams. The latter often escaped so that the number in the trap varied from two to five. These traps were only operated in 1966.

Rat baited traps. – The two traps used with chickens in 1965 were modified and used with rats in 1966. Each was of a different design. They were designated RBI and RBII. RBI was a modified Magoon (1935) trap 19 inches long and 17 inches wide and 12 inches high. The animal chamber was closed in by 14 x 18 inch mesh galvanized wire gauze so that

Plate 3 Catching head of Malaise trap I.

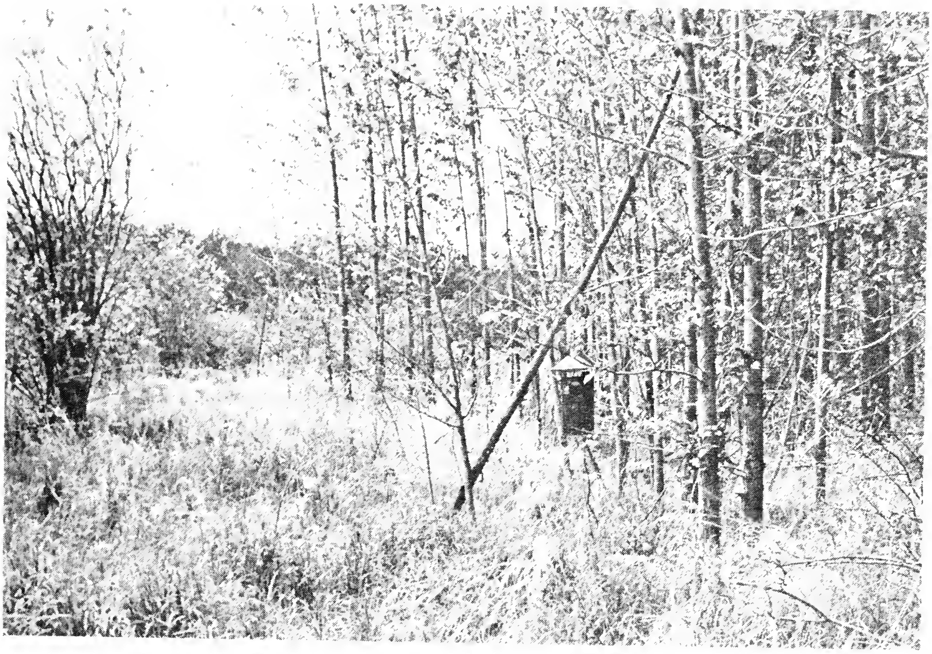


Plate 4 Light trap I as seen from the Lake shore.

Plate 5 Light trap I showing proximity to the Lake.

Plate 6 Light trap II showing position in the forest.

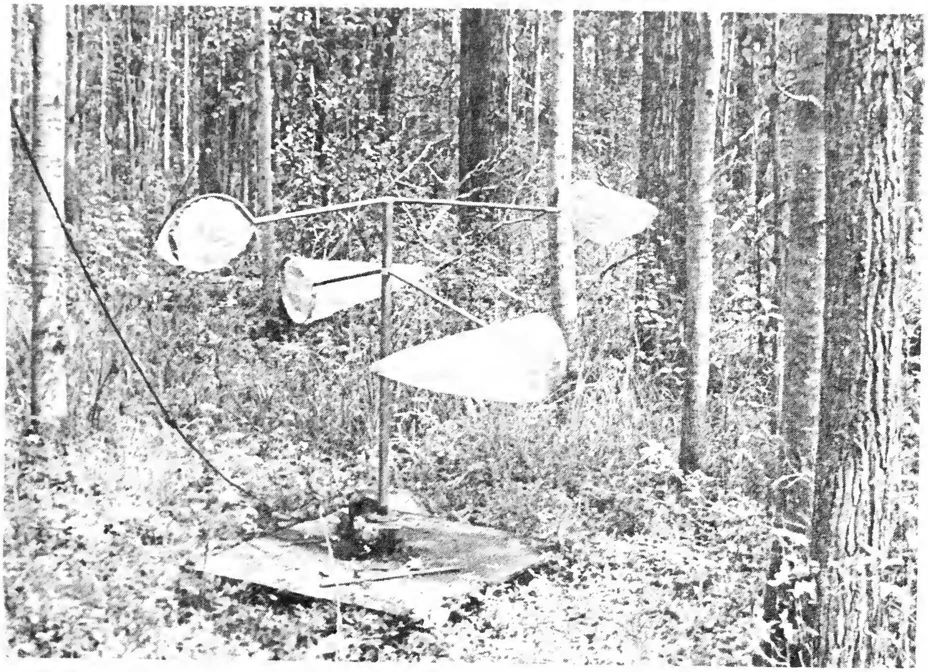


Plate 7 The visual attraction trap.

Plate 8 The Rotary trap.

Plate 9 Chicken baited trap I.

Plate 10 The catching cages of chicken baited trap II.

the mosquitoes could not reach the bait. The mosquitoes entered a collecting cage 19 inches long, six inches high and six inches wide by means of a no-return baffle and were removed with an aspirator. RBII was a circular trap, 15 inches in diameter with the bait cage coming to a cone 12 inches high. This cone projected through a hole three inches in diameter in the top plate into a cone three inches high in the bottom collecting cage, the two forming a no-return baffle. The catching cage was a removable cylinder nine inches high and 10 inches in diameter. Flanges six inches wide in RBI and 4½ inches wide in RBII were added in 1966 to direct the mosquitoes into the trap. These traps are shown in Plates 11 and 12.

Originally three rats were used in each cage, but births often modified this. These two traps were run close to each other in the middle of the campsite. RBI was operated in June, July and August 1966 and May and June 1967; RBII was only operated in July and August of 1966.

Many designs have been suggested for animal bait traps using large animals, the so-called stable traps of Magoon (1935), Bates (1944), Roberts (1965), but relatively little attention has been given to the use of small animals as mosquito bait (Southwood, 1966). These would appear to offer certain advantages because of their smaller size and the fact that they need less attention than cattle or horses.

Human bait. – On one day in most weeks from late May to the end of August, 1966, I sat quietly with trouser legs rolled up and caught any mosquitoes which alighted in a fifteen minute period. In May these collections were made in the afternoon and after that at 1800 hours.

Carbon dioxide baited traps. – Several authors (Brown, 1951; Bellamy and Reeves, 1952; Newhouse *et al.*, 1966 and others) have shown that carbon dioxide used alone or in conjunction with another attractant is good bait for mosquitoes. I decided to try the release of carbon dioxide from a cylinder in Malaise traps. The gas was released at from one to six litres per minute with an average rate of five litres per minute (approximately equivalent to the amount of carbon dioxide expired by 20 men at rest). It proved difficult to control the flow accurately in the field with changing conditions of temperature and barometric pressure. The gas was released through a flowmeter and led up into the catching head by means of a plastic tube (Plate 13). On the night of 12/13 July, 1966 releasing the gas direct from the cylinder without a flowmeter was tried. Both 25 lb. and 50 lb. cylinders of carbon dioxide were tried; the former proved better as they were more portable. One 25 lb. cylinder lasted approximately 16 hours. The traps were run from 1700 hours to 0900 hours the following morning.

Carbon dioxide was used on alternate nights, the other Malaise trap being used as a control. Carbon dioxide traps were operated in July and August 1966 and May and June 1967.

Collections of resting mosquitoes and miscellaneous collections. – Also on one day per week in June, July and August, 1966 and from 16 May to 15 June 1967, all mosquitoes found resting in one of the trailers at the camp were collected early in the afternoon. In June 1966 this trailer was used as a kitchen and dining room, thereafter as a store. In 1966 a carton of dry ice was kept in it and rats were kept there over weekends in a screened cage. In 1967 rats were kept in the trailer in a unscreened cage.

Plate 11 Rat baited trap I.

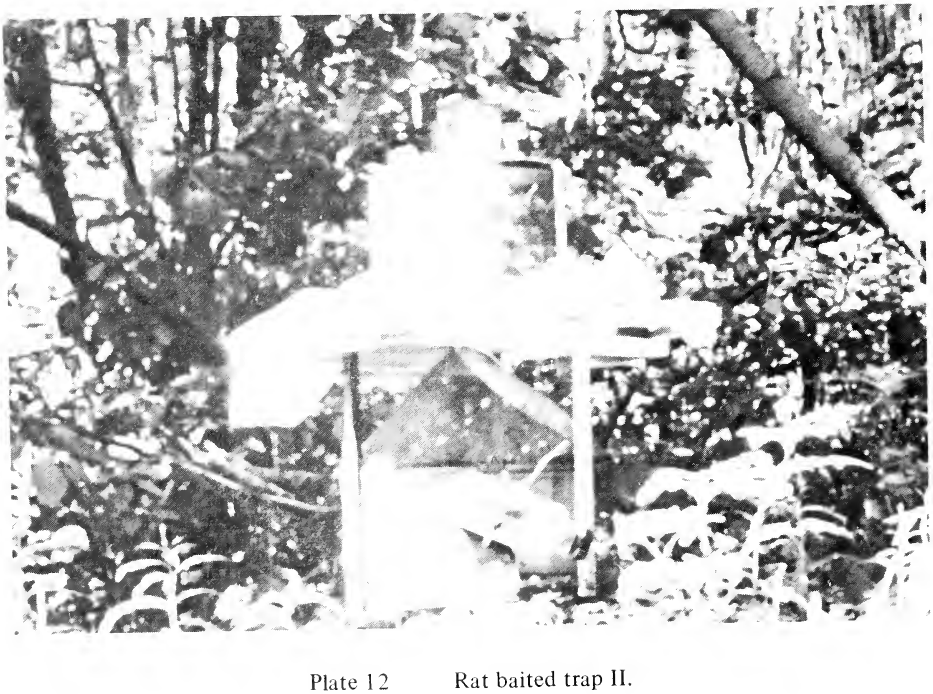


Plate 12 Rat baited trap II.

Plate 13 Malaise trap I with CO_2 cylinder in place.

At various times during the summer of 1966, mosquitoes were caught with a sweep net, when biting at times other than when human bait captures were in progress and in a C. D. C. (Communicable Diseases Center) miniature light trap. These collections have been included only in total catch figures.

Handling and Dissection

Weekend catches of Malaise traps, human bait, and miscellaneous collections were identified and counted. All other collections were frozen and taken to the laboratory. There they were identified, counted and dissected or, if numerous, subsampled and dissected. In 1967 the very large collections in carbon dioxide traps were subsampled for dissection and subsampled again for identification. The number of specimens in each sample was estimated from these two subsamples. This estimated number was used to obtain the proportion of each species in the total carbon dioxide trap catch. The number identified varied from 100% to 20% of the total, being proportionately smaller in the larger samples. This is probably an accurate estimate of the numbers of the more numerous species but not of the rarer ones.

Specimens for dissection were first assigned to a stage of Sella (Detinova, 1962) and to one of five arbitrary categories of external wear. They were dissected in distilled water under X12 of a Wild M5 stereomicroscope. The contents of the ventral oesophageal diverticulum and the mid gut were noted. The ovaries were then examined under X50 for the stage of Christophers (Clement, 1963).

The ovaries were removed to a drop of water on a microscope slide, allowed to dry and stored till they could be examined for parity or nulliparity by Detinova's method of ovarian tracheation (Detinova, 1962). The ovaries were then examined in a drop of distilled water under X100 of a Propper compound microscope.

All dissections were done within one week of capture and the specimens were kept frozen in dry ice until dissected. Corbet (1961) showed that mosquitoes were suitable for dissection after being kept frozen for three months. I found that it was possible to use Detinova's method on ovaries which had been stored dry on a slide for a year.

Males were counted and identified to genus only.

Except for Malaise trap captures all mosquitoes were killed by freezing with dry ice.

RESULTS AND DISCUSSION

Malaise traps, light traps, visual attraction trap, rotary trap, rat bait, chicken bait and Malaise and carbon dioxide were compared both quantitatively and qualitatively. Two methods – human bait and collections in the trailer – were not standardized enough for quantitative comparison.

Note on statistics used

The statistical analysis of the data obtained in this study presented certain difficulties, since the nature of the study did not allow the randomization of catches. All traps had to be operated in the same place and technical difficulties as well as the nature of some of the traps prevented simultaneous operation. Therefore the statistical tests applied are not all strictly applicable to the data obtained, though I believe they assist in the interpretation of the results.

Quantitative comparison of the trap types was obtained by converting the catch into catch per 100 trap hours to standardize and to allow for the fact that the different traps were run for different lengths of time. This test is not strictly applicable but does help to confirm conclusions reached by other methods. An index of trap "effectiveness" was obtained by dividing the catch per 100 trap hours in the trap or trap type under consideration by the catch per 100 trap hours in the combined Malaise traps over the same period. The Malaise traps were chosen as standards as they appear to be passive and to have no attraction for mosquitoes. The combined Malaise traps were used in an attempt to minimize the effects of trap position. This "index of effectiveness" permits a ranking of traps and trap types in order of effectiveness.

A modified geometric mean, the Williams mean (Haddow, 1960), was used for studying the effects of the addition of carbon dioxide to Malaise traps. It is obtained by the expression $M_W = \text{antilog} \left[\frac{(\Sigma \log(x+1))}{N} \right] -1$ where x is the value of each sample and N is the number of samples. The addition of one to each sample value allows the inclusion of zero catches which cannot be included in a normal geometric mean. Williams has shown that where there is a large variation in the size of samples or one sample is very different from the others, this mean gives a better measure of central tendency than the arithmetic mean.

The χ^2 test was used in the qualitative comparison of the trap types. Simpson *et al.* (1960) was the principal reference used for statistical methods.

Relative effectiveness – catch per unit time

Table 2 shows the relative effectiveness of the traps in 1966 and 1967 and Table 3, the effectiveness in June of 1966 and 1967. Table 4 shows the catch per 1000 trap hours of the five most abundant species and *Culex territans* which is believed to feed on cold blooded vertebrates and so differs from the other species caught which are believed to feed mainly on warm blooded vertebrates.

The results in May and June 1967 are similar to those in 1966 except that light traps caught less than either the visual attraction or the rotary traps and the catch per 100 trap hours in all traps averaged four times larger than in 1966.

Perhaps the most interesting result was the high catch in the rotary trap which is generally believed to have no attractive influence and to take a random sample of flying insects (Stage and Chamberlin, 1945; Love and Smith, 1957; Juillet, 1963; Southwood, 1966). This trap had an index of effectiveness of 5.1 in 1966 and 9.7 in 1967 and was well within the range of traps with an attractive influence, namely light, bait, and visual attraction traps. This indicates that the rotary trap does in fact exert some attractive influence on mosquitoes. It was impossible to observe the approach of mosquitoes to a trap of this size so that the nature of this influence could not be elucidated. It is well known that many biting Diptera including mosquitoes (Clement, 1963) are attracted to moving objects. Tabanids and tsetse flies (*Glossina* sp.) are attracted to moving motor vehicles (Duke, 1955; Glascow, 1963). The stimulus of a rotary trap may be similar to that of a moving vehicle.

Though the light traps caught nearly three times as many mosquitoes in June 1967 as in June 1966, their relative effectiveness was nearly halved. This is probably due to the absence of *Culiseta inornata* in 1967 as this species formed a large proportion of the 1966 catch.

Table 2 The numbers of adult female mosquitoes taken per 100 trap hours in different traps at George Lake 1966 and 1967.

Trap	No. Caught	No. trap hours	No. mosq/ 100 hours	Index of *** Effectiveness
		1966 (June July August)		
Malaise I	146	2099.5	7.0	0.8
Malaise II	214	2048	10.7	1.2
Total Malaise	365	4147	8.8	1.0
Mal I+CO$_2$*	589	104.5	559.4	67.6
Mal II+CO$_2$*	264	98	269.9	30.7
Total Mal+CO$_2$*	853	207.5	411.1	51.1 ** (35.1)*
Light I	141	266.5	52.9	6.0
Light II	48	267	18.0	2.0
Total Light	184	533.5	35.4	4.0
Vis. attr.	93	261.2	35.6	4.0
Rotary	116	260	44.6	5.1
Rat baited I	154	711.5	21.6	2.5
Rat baited II*	19	191	9.9	1.1
Total rat baited	172	902.5	19.1	2.2
Chick. baited I*	42	744	5.6	0.6
		1967 (May June)		
Malaise I	124	977	12.7	0.53
Malaise II	344	977	35.3	1.47
Total Malaise	468	1954	24.0	1.0
Mal I+CO$_2$	1080	112	964.2	40.26
Mal II+CO$_2$	5640	112	5035.7	210.2
Total Mal+CO$_2$	6720	224	3000.0	125.3 ** (97.4)*
Light I	93	120	77.5	3.4
Light II	37	120	30.8	1.3
Total Light	130	240	54.2	2.3
Vis. attr.	56	49	114.3	4.8
Rotary	114	49	232.6	9.7
Rat baited I	129	262	49.2	2.1
Rat baited II	–	–	–	–
Chick. baited I	–	–	–	–

* August only.

** Adjusted using Malaise trap figures per equivalent nights.

*** The 'Index of Effectiveness' is the no. of mosquitoes per 100 trap hours taken in trap, divided by the no. of mosquitoes per 100 trap hours in the combined Malaise traps.

Table 3 Comparison of mosquito captures per 100 trap hours in June 1966 and June 1967 at George Lake.

Trap	1966	1967	Index of Effectiveness 1966	Index of Effectiveness 1967	Comparative Increase in catch 1966/67
Malaise I	5.14 (37)	16.8 (108)	0.76	0.49	3.26
Malaise II	9.45 (59)	51.3 (329)	1.32	1.50	5.43
Total Malaise	7.13 (96)	34.1 (437)	1.0	1.0	4.78
Light I	45.83 (44)	135.9 (87)	6.40	3.98	2.96
Light II	15.0 (12)	51.6 (33)	2.10	1.51	3.44
Total Light	35.0 (56)	93.8 (120)	4.91	2.75	2.68
Vis. attr.	41.30 (46)	137.5 (55)	5.79	4.03	3.32
Rotary	31.40 (36)	285.0 (114)	4.40	8.36	9.08
Rat baited I	25.4 (97)	79.2 (122)	3.56	2.32	3.12

Fig. in brackets = no. mosquito caught. Av. increase 4.30

Apart from the rotary and light traps the "indices of effectiveness" for the two years are very similar. This indicates that the relative effectiveness of a trap does not change much with population size; but it may be changed considerably if the species composition changes.

The number of mosquitoes per unit volume of air filtered in June 1967 was calculated for the rotary, visual attraction, and light traps. Only the volume of air flowing through the trap was used; no estimate of "area of influence" was made. This gives an estimate of the actual efficiency of these traps. The rotary trap captured 2.4 mosquitoes, the visual attraction trap 0.3 and the light traps 1.3 mosquitoes per 10,000 cubic feet of air. If it is assumed that rotary traps have no attraction to mosquitoes but capture only those which come within range, then the efficiency of rotary and Malaise traps should be approximately the same. I calculated the air flow needed to give a catch of 34.1 mosquitoes per 100 trap hours (the figure in Malaise traps) if the efficiency in Malaise traps is the same as that of the rotary trap. This was 23.5 cubic feet per minute, which means that the average wind speed through these traps would have been 0.9 feet per minute. That is, these traps would have to have been standing in virtually still air during June 1967; since this was not so, I infer that the efficiency of the Malaise traps was below that of the rotary trap.

The high actual efficiency of the rotary trap, above both light and visual attraction traps, is additional evidence that this type of trap does provide an attractive stimulus for mosquitoes.

Proportion of males

Comparatively few males were taken and relatively little attention was paid to them as they formed only about 1% of the total catch in 1966 and 1967. Table 5 shows the proportion of males taken in 1966 and 1967.

Table 4 Numbers of adult females of selected species of mosquito caught per 1000 trap hours and actual numbers caught in different trap types at George Lake from 1 June to 1 September 1966.

Trap	*Culiseta inornata*	*Culex territans*	*Aedes excrucians*	*A. fitchii*	*A. punctor*	*A. vexans*
Malaise I	20 (72)	6 (20)	10 (37)	1 (3)	3 (11)	7 (23)
Malaise II	6 (18)	2 (6)	27 (89)	10 (32)	3 (11)	4 (14)
Total Malaise	13 (90)	4 (26)	19 (126)	5 (35)	3 (22)	6 (37)
Malaise I+CO_2	100 (11)	9 (1)	632 (69)	289 (36)	421 (46)	3352 (336)
Malaise II+CO_2	10 (1)	10 (1)	1165 (114)	405 (40)	112 (11)	785 (77)
Total Malaise +CO_2	58 (12)	10 (2)	1002 (183)	365 (76)	275 (57)	2135 (413)
Light I	264 (70)	8 (2)	30 (8)	49 (13)	8 (2)	23 (6)
Light II	4 (9)	0 (0)	38 (10)	8 (2)	8 (2)	22 (6)
Total Light	148 (79)	4 (2)	34 (18)	28 (15)	8 (4)	22 (12)
Visual attraction	0 (0)	38 (10)	70 (18)	27 (7)	54 (14)	8 (2)
Rotary	12 (3)	15 (4)	39 (10)	31 (8)	50 (13)	31 (8)
Rat baited I	1 (1)	0 (0)	59 (42)	21 (15)	31 (22)	7 (5)

Table 5 Proportions of male mosquitoes in traps at George Lake, 1966 and 1967.

Trap	1966 (1st June – 1st Sept.)			1967 (15 May – 30 June)		
	No. ♂♂	Total catch	♂ : ♂ + ♀	No. ♂♂	Total catch	♂ :♂ + ♀
Malaise I	12	158	0.076	9	133	0.068
Malaise II	8	228	0.035	21	365	0.058
Total Malaise	20	386	0.052	30	498	0.060
Mal I+CO_2	2	512	0.0039*	5	1085	0.00461
Mal II+CO_2	0	130	0.00*	5	5645	0.000886
Total Mal+CO_2	2	642	0.0031*	10	6730	0.00148
Light I	10	149	0.067	6	99	0.061
Light II	35	78	0.45	5	42	0.12
Total Light	45	227	0.20	11	141	0.078
Vis. attr.	13	106	0.123	2	58	0.034
Rotary	4	120	0.033	1	114	0.0088
Total	83	1480	0.00561	52	75.36	0.00069

χ^2_2 1966 – 33.033 $P = 0.005$ (Light against rest)

χ^2_2 1967 – 1.457 $P = 0.5$ (Light against rest)

* August only

In both years light traps took the largest proportion of males, but the statistical significance of this is doubtful. The position of the trap was important; Lt II took a much greater proportion in both years than Lt I. Light traps are known to take a larger proportion of the males of some insects than are in the population (Southwood, 1966) and to take large numbers of male mosquitoes (Barr, 1958). Belton and Galloway (1965) found 50% of light trap captures of nearly 6000 mosquitoes were males at Belleville in Ontario. Breeland and Pickard (1965), however, found 22% in Malaise trap captures were males but only 12% in light traps.

Species composition

Diversity. – The index of diversity α was introduced by Fisher *et al.* (1943) as a measure of the diversity of a population. It is obtained from the expression $S = \alpha \log_e(1+N/\alpha)$ where S is the number of species and N the number of individuals. An approximation, adequate for most needs, can be obtained from nomograms in Williams (1964) and Southwood (1966). This index is dependent on the size of the sample as well as its diversity but is useful for comparing traps operated the same period and has been successfully used to compare methods of catching Heteroptera by Southwood (1960).

The indices of diversity for the trap types in 1966 are shown in Table 6. There were no significant differences between trap types, which indicates that the smaller catches were due to lower effectiveness rather than to the unavailability of certain species.

Table 6 Comparison of the percentages of the more numerous mosquito species in the traps 1st June to 1st September 1966 at George Lake.

Species	Total Malaise	Total Light	Visual Attr.	Rotary	Rat baited I	Chicken Baited	Human Bait	Trailer
Anopheles earlei	1.4	9.9	8	6	–	–	–	0.9
Culiseta inornata	11.1	43.4	–	4	0.8	–	0.8	0.9
Other *Culiseta*	4.7	1.6	–	–	–	–	0.8	–
Culex territans	1.7	1.1	13	5	–	–	–	–
Mansonia perturbans	0.6	2.8	–	1	3.9	–	1.7	–
Aedes cinereus	3.0	2.2	3	1	0.8	–	14.2	–
A. communis	2.8	0.6	3	7	9.4	12	5.0	8.9
A. excrucians	34.1	9.9	24	12	33.1	42	29.2	17.8
A. fitchii	9.7	8.2	9	10	7.9	–	18.3	7.1
A. implicatus	3.9	1.1	4	6	3.2	4	4.2	2.7
A. punctor	5.8	2.2	19	16	17.3	8	5.8	29.6
A. riparius	5.8	3.8	3	6	6.3	4	4.2	0.9
A. vexans	9.2	6.6	3	10	3.9	4	5.0	1.8
Other *Aedes*	6.4	6.7	12	17	13.4	25	10.8	29.4
Total *Aedes*	82.9	40.7	79	84	94.6	100	96.7	98.3
Total no. identified	361	182	75	83	127	24	120	111
No. Species taken	24	22	15	18	18	7	17	16
Index of Diversity *a*	6±0.6	0.6±0.9	5±1.0	6±1.0	5±0.8	3±1.5	6±1.2	5±1.0

χ^2_{13} Mal vs. Lt. = 75.664 $P = < 0.001$

χ^2_{9} Mal. vs. Human bait = 108.127 $P = < 0.001$

χ^2_{9} Mal. vs. rotary 44.99 $P = < 0.001$

χ^2_{5} Mal. vs. Rat baited = 22.964 $P = < 0.001$

χ^2_{8} Mal. vs. Vis. attr. = 38.204 $P = < 0.001$

χ^2_{6} Mal. vs. Trailer = 95.857 $P = < 0.001$

χ^2 Human bait vs. Rat baited = 14.283 $P = < 0.05$

Proportions of different species. – The proportions of the major species in the catches of the different trap types are shown in Table 6. Table 7 shows the proportions in paired traps.

Table 7 Comparison of the proportions of mosquito species taken in paired traps 1st June – 1st September 1966 at George Lake.

Species	Mal		$Mal+CO_2$*		Light	
	I	II	I	II	I	II
Anopheles earlei	1.4	1.4	0.012	0	9.4	12
Culiseta inornata	26.7	0.5	1.7	0.4	50.3	21
Other *Culiseta*	8.2	2.3	0.5	0	2.2	–
Culex territans	1.4	1.9	0.2	0.4	1.4	–
Mansonia perturbans	0.7	0.5	2.5	0.7	2.2	5
Aedes cinereus	1.4	4.2	2.0	0.4	0.7	7
Aedes communis	0.7	4.2	0.6	0	0.7	–
A. excrucians	23.3	41.5	14.8	43.2	5.6	23
A. fitchii	2.1	14.9	5.6	15.1	4.4	5
A. implicatus	5.5	2.8	0.2	0	0.7	2
A. punctor	6.9	5.1	7.6	4.2	1.4	5
A. riparius	3.4	7.4	3.6	2.6	5.1	–
A. vexans	13.0	6.5	57.6	29.2	4.3	4
Other *Aedes*	5.5	7.0	4.7	3.8	6.5	7
Total *Aedes*	61.5	96.0	97.4	98.6	33.8	63
Total ident.	146	215	636	264	139	43
No. species taken	21	19	19	13	21	11

* July and August only

χ^2_{12} Malaise 170.65 $P = < 0.001$

χ^2_{6} $Mal+CO_2$ 15.11 $P = < 0.01$

χ^2_{6} Light 26.23 $P = < 0.005$

The low catch of *Culiseta inornata* in the rotary trap and the absence of this species from the visual attraction trap in 1966 is hard to explain since this species formed 27% of the catch in the nearby Malaise I.

The animal bait traps showed great similarity. The rat and chicken bait traps did not differ significantly while the human bait and rat bait traps differed only at the 5% level. *Aedes canadensis* formed over 20% of the catches in chicken bait traps but was scarce in other traps and *A. cinereus* was most abundant in human bait catches.

Discussion. – The results of Breeland and Pickard (1965) are of interest. They found 52% of Malaise trap captures were *Aedes* compared to 54% in light traps and 50% in biting catches. Forty seven percent of the *Aedes* in their Malaise traps and 52% in their light traps were *A. vexans*, which indicates that the preponderance of this species in light traps is often more due to its preponderance in the population rather than to any specific attraction to light, though this species is often stated to be greatly attracted to light (Huffacker and Bach, 1943; Love and Smith, 1957). Although Love and Smith found a high "index of attractivity" to light for this species, the proportion of *A. vexans* was actually higher in their sweep nets than in their light traps (53% and 50% respectively). Breeland and Pickard found light traps gave a significantly lower diversity, 3±0.3, than the Malaise traps, 5±0.5 (my calculations). At George Lake only *Culiseta inornata* and *Anopheles earlei* were above the numbers expected in light traps if there was no difference between trap type.

Haufe and Burgess (1960) compared a visual attraction trap to a suction trap, which like a Malaise trap presumably takes a random sample of the flying insect population. They found that though a visual attraction trap caught ten times as many mosquitoes as a suction trap, there was no significant difference between the proportion of band-legged and black-legged *Aedes* between the two traps. At George Lake the main difference between Malaise I and the visual attraction trap was the low number of *Culiseta inornata* and the high number of *Culex territans* in the visual attraction trap and there were no significant differences in the proportions of *Aedes* species, which indicates that this trap takes a random sample of the mosquitoes which approach it. Haufe and Burgess (1960) found this trap caught all mosquitoes approaching to within about 30 inches of it and observations at George Lake support this.

The rotary trap catch was significantly different from the Malaise trap catch but this applies mainly to the catch of *Culiseta inornata* which was lower than expected and that of *Aedes punctor* which was higher than expected. In 1967 this species formed 58% of the catch. The evidence shows that this trap exerts an attractive stimulus to mosquitoes and this may be selective for some species, possibly *A. punctor.*

The animal bait traps differ from the others in that their attraction depends on the feeding habits of the adult female mosquitoes. Captures on chickens, rats and humans differed very little. Differences between human bait and the others were probably due to position.

Effects of carbon dioxide on the catch in Malaise traps

Rudolfs (1922) suggested that mosquitoes were attracted to carbon dioxide and since then some controversy has arisen over whether this is merely an activating agent (Willis, 1947; Laarman, 1955) or whether it also has an orienting effect (Reeves, 1953), but Clement (1963) states the importance of carbon dioxide as an aid in host finding by mosquitoes has yet to be determined.

Several workers have found that the addition of dry ice (solid carbon dioxide) to light traps greatly increases the catch (Reeves and Hammon, 1942; Huffacker, 1942; Huffacker and Bach, 1943 and Newhouse *et al.*, 1966). Carestia and Savage (1967) found that the catch in a C. D. C. miniature light trap was greatly increased by the addition of carbon dioxide from a cylinder and that the catch increased as the rate of flow was increased. Reeves (1953) used carbon dioxide as bait in a stable trap and caught large numbers of *Culex tarsalis* at 26 ml. CO_2 per minute (equivalent to one chicken) and the catch increased as the rate of flow increased. Bellamy and Reeves (1952) designed a portable trap, from a twenty pound lard can, which used dry ice as bait.

Hayes *et al.* (1958) and Dow (1959) have compared carbon dioxide bait with other mosquito attractants and find it compares very favorably as an attractant for adult females and Brown (1951) and Brown *et al.* (1951) have found carbon dioxide an effective attractant in the field.

Table 8 shows the catch of mosquitoes in Malaise + CO_2 traps and in Malaise traps over a period of six nights in 1966 and seven in 1967. The traps were run from 1700 hours to 0900 hours the following morning.

Table 8 Numbers of mosquitoes caught in Malaise and Malaise + CO_2 traps on equivalent nights at George Lake in July, August 1966 and May and June 1967.

Date	MI CO_2	MII	Date	MII CO_2	MI
1966					
27/28 July	79	4	28/29 July	134	2
2/ 3 August	253	0	3/ 4 August	24	4
4/ 5 August	152	1	9/10 August	48	8
10/11 August	30	1	17/18 August	27	1
18/19 August	39	2	23/24 August	27	0
24/25 August	36	2	31/ 1 September	4	1
Total	589	10	Total	264	16
Mw	48.2	1.3		28.5	1.8
Grand Total M+CO_2	853	Mw* 37.0			
Malaise	26	Mw 1.6			
1967					
16/17 May	13	3	17/18 May	14	0
24/25 May	1	1	23/24 May	17	0
30/31 May	2	0	31/ 1 June	457	5
7/ 8 June	452	7	8/ 9 June	1103	2
13/14 June	165	14	14/15 June	1590	5
21/22 June	240	4	22/23 June	536	6
29/30 June	207	13	28/29 June	1923	9
Total	1080	42	Total	5640	27
Mw	42.9	3.9		300.1	2.6
Grand Total M+CO_2	6702	Malaise 69			
Mw	114.1	3.0			

* Mw = Williams mean = $\text{antilog}\left[\frac{\Sigma \log (x+1)}{N}\right] -1$

x = Number per sample

N = Number of samples

Table 9 shows the proportions of species in the Malaise and the Malaise + CO_2 traps. The complete Malaise trap captures are used, rather than only those on equivalent nights for these latter were too low for accurate analysis. These figures show that the addition of carbon dioxide to a Malaise trap greatly increases its catch and the numbers of nearly all species caught are increased. The increase for some species is greater than for others, *Aedes* species appearing to be more attracted to carbon dioxide than non-*Aedes* species. Three *Aedes* species showed significantly higher proportion in Malaise + CO_2 traps; these were

Table 9 Proportion of female mosquito species in Malaise and Malaise + CO_2 traps at George Lake.

Species	1966 (August)		1967 (May–June)	
	Malaise	Mal+CO_2	Malaise	Mal+CO_2*
Anopheles earlei	1.1 (1)	0.1 (1)	0.8 (4)	0.3 (22)
Culiseta alaskaensis	–	–	2.2 (10)	1.7 (115)
C. inornata	25.8 (24)	0.8 (8)	1.2 (6)	0.1 (7)
Other *Culiseta*	7.5 (7)	0.1 (1)	2.8 (13)	0.3 (21)
Culex territans	–	0.1 (1)	6.5 (39)	0.02 (2)
Mansonia perturbans	–	1.7 (1)	–	–
Total non-*Aedes*	34.4 (32)	2.8 (23)†	13.5 (63)	2.4 (160)†
Aedes cataphylla	–	–	1.8 (8)	0.9 (60)
A. cinereus	–	1.7 (11)	–	0.02 (3)
A. communis	–	0.5 (3)	4.4 (21)	3.0 (200)
A. excrucians	25.8 (24)	16.2 (102)	14.8 (69)	15.7 (1055)
A. fitchii	5.4 (5)	4.4 (27)	6.9 (22)	5.6 (375)
A. implicatus	–	0.1 (1)	19.8 (93)	21.3 (1430)
A. intrudens	–	–	6.3 (29)	16.4 (1120)**
A. punctor	6.5 (7)	5.7 (36)	14.8 (69)	23.0 (1540)**
A. riparius	3.2 (3)	3.5 (22)	13.2 (62)	6.3 (420)
A. vexans	23.7 (22)	61.4 (386)**	–	–
Other *Aedes*	1.1 (1)	3.6 (23)	4.6 (22)	5.4 (360)
Total *Aedes*	65.6 (61)	97.1 (611)	86.5 (405)	97.6 (6560)
Total	93	633	468	6720
No. species taken	9	15	16	25
a	3 ± 0.6	4 ± 0.5	3 ± 0.4	3 ± 0.3
	$\chi^2_7 = 184.484$	$P = < 0.001$	$\chi^2_7 = 235.787$	$P = < 0.001$

* Estimated total

** above expected in CO_2 trap

† below expected in CO_2 trap

Fig. in brackets = no. caught

A. vexans in 1966 and *A. intrudens* and *A. punctor* in 1967. *A. punctor* showed no significant difference in 1966 and in fact the proportion was slightly higher in the Malaise traps, possibly because this species is relatively less abundant in August than in the spring. The greatly increased proportion of *A. vexans* in carbon dioxide traps is interesting as Huffacker and Bach (1943) took a lower proportion of this species in light traps with carbon dioxide than in light alone, but Carestia and Savage (1967) and Newhouse *et al.* (1966) took slightly higher proportions of *A. vexans* in light traps with carbon dioxide than with light alone. Both Carestia and Savage and Newhouse *et al.* found the proportions of *Culex* species were greatly increased when carbon dioxide was added to light traps. This did not occur at George Lake as the only common *Culex* was *C. territans* which feeds mainly on amphibians.

Table 10 shows the Williams mean catch per trap night in Malaise, Malaise + CO_2 and light traps. To obtain some idea on how carbon dioxide attracts mosquitoes I watched both traps on several evenings in May and June in 1967. The traps had to be observed through binoculars from at least twenty yards distance; otherwise the mosquitoes left the trap for the observer. About half an hour after the traps were started, a swarm of mosquitoes formed over the catching head of Malaise I + CO_2, which was on low ground. At Malaise II + CO_2, which was on the top of a low ridge, no swarm formed but large numbers of mosquitoes settled on the baffles of the trap. I saw very few settling on these in Malaise I + CO_2. Many of the settled mosquitoes crawled or flew upwards and were caught.

In both traps many mosquitoes remained settled very close to the carbon dioxide outlet for periods of up to fifteen minutes.

The formation of a swarm over the carbon dioxide outlet and the very large numbers caught show that carbon dioxide probably exerts a considerable orienting stimulus to adult female mosquitoes; but it is easily overridden by the approach of a host animal such as man.

Table 10 Comparison of mosquito captures per night in Malaise, Malaise + CO_2 and Light traps at George Lake, July and August 1966 and May and June 1967.

	Malaise	Malaise+CO_2	Light
1966			
No. caught	26	589	69
No. of trap nights	12	12	26
Mw*/trap night	1.6	37.0	1.7
Range	0-8	4-253	0-14
1967			
No. caught	69	6720	130
No. of trap nights	14	14	30
Mw/trap night	3.0	114.1	1.4
Range	0-14	1-1923	0-59

* Mw = Williams mean

Physiological state

The contents of the ventral diverticulum. – Trembley (1952) and Hocking (1953) have shown that sugar solutions and nectar normally pass into the ventral oesophageal diverticulum and not into the stomach. Hocking (1953) has shown the importance of nectar as an energy source for mosquitoes. Thus, the contents of the ventral diverticulum are a partial measure of the energy resources available to the mosquito. The amounts of liquid in the ventral diverticulum in female mosquitoes caught in different trap types are shown in Table 11. In most mosquitoes the ventral diverticula were either empty or only partially filled; in only 30 out of 650 mosquitoes were they full.

There were no significant differences between trap types.

Table 11 Comparison of the contents of the ventral diverticulum of mosquitoes caught in the trap types at George Lake in 1966.

	Contents of Ventral Diverticulum				
Trap type	0	1	2	Mean	Total examined
Malaise	64	60	6	0.6	130
Mal+CO_2	78	38	4	0.4	120
Light	51	46	3	0.5	100
Vis. attr.	21	26	3	0.6	50
Rotary	25	39	4	0.7	68
Rat baited	45	49	3	0.6	97
Chicken baited	13	6	2	0.5	21
Coll. in trailer	22	37	5	0.7	64
Total catch	319	301	30	0.6	650

0 = empty
1 = partially full
2 = full

Ovarian development and stage in gonotrophic cycle. – Tables 12 and 13 show the stages of Sella and Tables 14 and 15 show the stages of Christophers. Table 16 shows the occurrence of gravid females in the traps. In 1966 light traps caught a significantly higher proportion of the higher stages than the other traps but this was not so in 1967. A striking difference between the two years was the large number of resting mosquitoes which had ovaries in stages III–V of Christophers in 1967, which has been discussed above.

Three gravid females were taken in animal bait traps and seven in carbon dioxide traps, but it is unlikely they were attracted to the bait.

Corbet (1961) found that in *Mansonia fuscopennata* (Theobald), in Uganda, light traps sampled only those specimens engaged in "non-specific activity" i.e., those not engaged in

Table 12 Comparison of the stages of Sella of mosquitoes caught in the different trap types at George Lake over the periods 1st June to 1st September 1966 and 16th May to 30th June 1967.

1966

Trap type	Stage of Sella 1	2	3	4	5	6	7	Mean	Total examined
Malaise	152	3	1	–	–	–	28	1.9	184
Mal+CO_2*	178	1	–	2	1	–	6	1.3	188
Light	95	1	1	1	1	3	75	3.7**	177
Vis. attr.	59	1	2	–	1	1	2	1.3	65
Rotary	77	1	2	2	–	1	4	1.5	87
Rat baited	124	6	–	–	–	–	–	1.0	130
Chicken baited	27	3	–	–	–	–	–	1.1	30
Trailer	76	2	–	–	1	–	–	1.1	79

* operated from 27th July to 1st September only

** $\chi^2_4 = 186.220$ $P = < 0.001$

1967

Trap type	Stage of Sella 1	2	3	4	5	6	7	Mean	Total examined
Total Malaise	129	–	1	–	–	2	2	1.2	134
Total Mal+CO_2	319	1	7	1	–	–	–	1.1	328
Total Light	108	2	–	–	–	–	–	1.0	110
Vis. attr.	48	1	–	1	–	–	–	1.1	50
Rotary	70	–	1	–	–	–	–	1.0	71
Rat baited	85	1	3	–	–	–	–	1.1	89
Trailer	43	7	10	10	5	4	6	2.6	85

swarming, biting, or ovipositing. Standfast (1965) confirmed this for *Culex annulirostris* Skuse but he believed this indicated activity in the intermediate stages of the gonotrophic cycle, that is females in stages III and IV of Christophers or III to VI of Sella. Corbet (1961), on the other hand, found 90% of *M. fuscopennata* in light traps were in stages I and II of Christophers and none were gravid. George Lake results do not support this since a number of gravid females and individuals in intermediate stages of the gonotrophic cycle were taken in light traps. Both Corbet and Standfast based their conclusions on the fact that peak light trap captures did not coincide with peaks of biting, swarming or oviposition activity. Captures were not recorded at hourly intervals at George Lake, but mosquitoes were often found biting round light traps in the evenings and in the mornings of nights when none were caught. Corbet and Standfast worked on tropical mosquitoes, which may explain some of the differences.

Table 13 Comparison of the stages of Sella of *Aedes* species in the different trap types at George Lake 1st June to 1st September 1966 and 16th May to 30th June 1967.

1966

Trap type	1	2	3	4	5	6	7	Mean	Total examined
	Stage of Sella								
Malaise	146	1	1	–	–	–	5	1.2	153
Mal+CO_2*	167	1	–	2	–	–	3	1.1	173
Light	63	–	–	–	–	–	6	1.5	69
Vis. attr.	46	–	2	–	1	–	1	1.3	50
Rotary	65	–	2	2	1	1	2	1.4	73
Rat baited	120	6	–	–	–	–	–	1.0	126
Chicken baited	27	3	–	–	–	–	–	1.1	30
Trailer	74	2	–	–	–	–	–	1.1	76

* only operated 27th July to 1st September

No siginificant difference

1967

Trap type	1	2	3	4	5	6	7	Mean	Total examined
	Stage of Sella								
Total Malaise	122	–	1	–	–	1	1	1.0	125
Mal+CO_2	276	1	6	–	–	–	–	1.0	283
Total Light	95	1	–	–	–	–	–	1.0	96
Vis. attr.	43	–	–	1	–	–	–	1.1	44
Rotary	69	–	1	–	–	–	–	1.0	70
Rat baited	84	1	3	–	–	–	–	1.1	88
Trailer	28	6	8	4	1	–	1	1.9	48

Physiological age of adult females as shown by the proportion of parous females. – In three years of study 1683 pairs of ovaries were examined for parity. The proportions of pars in the traps are shown in Tables 17–21. Except in August 1966, light traps caught a higher proportion of pars than other traps. In August 1966 the greater part of the light trap catch was *Culiseta inornata* and *Anopheles earlei*, most of which were probably about to overwinter and these species appear to overwinter as nullipars. All the *Aedes* taken in light traps in August 1966 were parous. The statistical significance of the higher proportion of pars in light traps is doubtful. In 1965 and 1966 the proportion of pars in light traps was significantly higher at the 5% level when tested against the rest combined but not significant when the traps were tested individually. In the spring of 1967, however, the proportion of pars in light traps was significantly higher at the 1% level when the traps were tested individually. In all cases the parity rate in light traps was higher for *Aedes* species than for the total catch.

Table 14 Comparison of the stage of Christophers of mosquitoes in different trap types at George Lake from 1st June to 1st September 1966 and 15th May to 30th June 1967.

1966

	Stage of Christophers						
Trap type	I	II	III	IV	V	Mean	Total examined
Malaise	57	80	8	5	23	2.2	173
Mal+CO_2*	77	94	2	1	6	1.7	180
Light	30	51	7	6	71	3.2**	165
Vis. attr.	27	28	3	1	2	1.7	61
Rotary	29	45	3	2	4	1.9	83
Rat baited	43	78	–	–	–	1.6	121
Chicken baited	5	21	–	–	–	1.8	26
Trailer	32	41	4	–	–	1.6	77

* only operated 27th July to 1st September

** significant at 1% level $\chi^2_4 = 198.005$ $P = < 0.001$

1967

	Stage of Christophers						
Trap type	I	II	III	IV	V	Mean	Total examined
Malaise	32	97	1	2	2	1.8	134
Mal+CO_2	100	216	9	–	2	1.7	327
Light	19	87	1	–	–	1.8	107
Vis. attr.	11	37	2	–	–	1.8	50
Rotary	13	54	3	–	–	1.8	70
Rat baited	14	71	2	–	–	1.9	87
Trailer	7	50	16	6	6	2.4	85

Table 21 shows the parity rate in five species taken in different trap types. With the exception of *Anopheles earlei* the parity rate in light traps was higher than in other traps.

It is clear that light traps have a slightly higher attraction for older female mosquitoes than the other trap types tested.

Damage to mosquitoes by different collection methods

I noticed that the condition of specimens caught in different traps varied considerably. I investigated this using six arbitrary damage categories. The results are shown in Table 22. The specimens taken in Malaise traps both with and without carbon dioxide are in much better condition then those taken in other traps, probably because the insects were dead before falling into the collecting bottle and there were no moving parts in the traps. These traps also involved a minimum of handling both during and after capture. The rotary trap

Table 15 Comparison of the stage of Christophers of *Aedes* species in different trap types at George Lake, 1st June to 1st September 1966 and 16th May to 30th June 1967.

1966

	Stage of Christophers						
Trap type	I	II	III	IV	V	Mean	Total examined
Malaise	55	77	8	1	5	1.8	146
Mal+CO_2*	75	92	2	–	4	1.7	173
Light	12	45	4	–	6	2.2**	67
Vis. attr.	21	22	2	1	1	1.7	47
Rotary	23	39	3	2	1	1.8	68
Rat baited	43	72	–	–	–	1.6	115
Chicken baited	5	21	–	–	–	1.8	26
Trailer	31	40	4	–	–	1.6	75

* only operated 27th July to 1st September

** significant at 1% level. $\chi^2_3 = 19.27$ $P = < 0.001$

1967

	Stage of Christophers						
Trap type	I	II	III	IV	V	Mean	Total examined
Total Malaise	32	89	1	1	1	1.8	124
Mal+CO_2	100	171	7	–	2	1.7	280
Total Light	17	76	1	–	–	1.8	94
Vis. attr.	10	32	2	–	–	1.8	44
Rotary	13	53	3	–	–	1.8	69
Rat baited	14	70	2	–	–	2.0	86
Trailer	7	33	10	1	1	2.2	52

damaged specimens more than any other and the mean shown is possibly too low as the catch of this trap included a high proportion of unidentified specimens which were not assigned to any damage category.

General discussion

Southwood (1966) has reviewed methods of sampling insects, including mosquito populations. Though a great deal of ingenuity has been expended on the design of methods for sampling adult mosquito populations and on the refinement of these methods, they are mainly aimed at the largest possible catch. A few methods have been designed for special purposes such as window traps (Muirhead-Thompson, 1951) which are designed to catch mosquitoes entering or leaving buildings, a trap to catch mosquitoes emerging from cesspits (Saliternik, 1960) and several traps designed to catch resting mosquitoes (Russell and San-

Table 16 Occurrence of gravid female mosquitoes in the different traps at George Lake in 1965, 1966 and 1967.

Species	Mal I	Mal II	Mal I + CO_2	Light I	Light II	Visual Attr.	Rotary	Animal baited	Trailer	Total
Anopheles earlei	–	–	1	2	–	–	1	–	4	8
Culiseta alaskaensis	2	–	–	–	–	–	–	–	–	2
C. inornata	31	–	–	93	6	–	–	2	–	132
Culex territans	1	1	–	–	–	1	1	–	1	5
Aedes communis	1	–	–	–	–	–	–	–	–	1
A. excrucians	1	–	1	–	1	1	2	–	–	6
A. implicatus	1	1	–	–	–	–	–	–	1	3
A. intrudens	–	–	1	–	–	–	–	–	–	1
A. pionips	–	–	–	1	–	1	–	–	–	2
A. vexans	4	–	1	2	3		1	–	–	11
Unidentified	–	–	–	–	–	–	–	1	–	1
Totals	41	2	4	98	10	3	5	3	6	172

Table 17 Proportion of parous mosquitoes in trap types at George Lake 1st June to 1st September 1966.

Trap type	Parous	Nulliparous	P:N+P
Malaise	57	87	0.40
Light	49	41	0.49**
Vis. attr.	19	36	0.34
Rotary	32	43	0.42
Rat baited*	42	50	0.46
Coll. in trailer	30	43	0.41
Total	229	300	0.43

* Operated 27th July to 1st September only

** significant at 5% level for those traps run for the whole period.

$\chi^2_2 = 5.447$ (Light vers. rest) $P = < 0.05$

Table 18 Comparison of like proportion of parous mosquitoes in trap types operated in August 1965 and August 1966 at George Lake.

Trap type	1965			1966		
	Par	Null	P:N+P	Par	Null	P:N+P
Malaise	12	10	0.54	19	11	0.64
Mal+CO$_2$	Not done	–	–	82	30	0.73
Light	30	13	0.70	15	10	0.60*
Vis. attr.	5	7	0.42	7	2	0.78
Rotary	1	3	0.25	11	1	0.92
Animal baited	24	15	0.62	40	11	0.78
Trailer	Not done			8	3	0.73
Total	72	48	0.60	182	68	0.73
		not significant			not significant	

* all 13 *Aedes* species caught were parous.

Table 19 Comparison of the proportion of parous mosquitoes taken in various trap types at George Lake in June 1966 and 1967.

Trap type	June 1966			May, June 1967		
	P	N	P:P+N	P	N	P:P+N
Malaise	17	43	0.28	17	115	0.13
Mal+CO_2	–	–	–	51	278	0.16
Light	13	18	0.42	37	112	0.25
Vis. attr.	8	24	0.25	3	44	0.06
Rotary	8	27	0.22	14	57	0.20
Rat baited	17	31	0.35	9	78	0.10
Total	63	143	0.31	131	684	0.11

no significant difference between traps at 0.05 level $\chi^2_5 = 15.75$ $P = < 0.005$

Table 20 Comparison of the proportion of parous *Aedes* females at George Lake in trap types operated for the whole period, 1st June to 1st September 1966, and May and June of 1967.

1966

Trap type	Par	Null	P:N+P
Malaise	52	85	0.38
Light	35	25	0.58
Vis. attr.	14	28	0.33
Rotary	25	27	0.48
Rat baited I	38	48	0.44
Coll. in trailer	29	42	0.41
Total	193	265	0.42

$\chi^2_2 = 7.967$ $P = < 0.01$ (light vers. rest)

1967

Trap type	Par	Null	P:N+P
Malaise	17	109	0.15
Malaise CO_2	32	243	0.12
Light	26	68	0.28
Vis. attr.	3	38	0.07
Rotary	14	56	0.20
Rat baited I	8	77	0.09
Total	100	591	0.14

$\chi^2_5 = 20.14$ $P = < 0.001$

Table 21 Comparison of the proportion of parous females of selected mosquito species in trap types at George Lake (Results for 1965, 1966 and 1967 combined).

Trap	Species *Anopheles earlei*	*Culiseta inornata*	*Aedes excrucians*	*A. punctor*	*A. vexans*
Malaise	0.50 (4)	0.60 (15)	0.30 (79)	0.16 (37)	0.66 (21)
Light	0.54 (28)	0.63 (19)	0.56 (55)	0.35 (31)	0.70 (20)
Vis. attr.	0.42 (12)	0.14 (7)	0.25 (20)	0.25 (24)	0.50 (4)
Rotary	0.67 (6)	0.00 (3)	0.33 (9)	0.27 (45)	0.17 (6)
Bait	–	0.5 (4)	0.38 (57)	0.14 (49)	0.36 (14)

Figure in brackets = no. examined

Table 22 Comparison of the damage done to mosquito specimens by different trap types.

	Damage Category*							
Trap type	0	1	2	3	4	5	Mean	Total examined
Malaise	40	38	73	12	16	3	1.6	182
Mal+CO_2	44	48	65	21	5	2	1.5	185
Light	8	16	31	23	43	31	3.1	152
Vis. attr.	8	6	23	6	19	10	2.7	72
Rotary	0	4	13	16	36	25	3.9	84
Rat baited	5	7	40	23	54	21	3.2	150
Chicken baited	2	4	11	9	7	8	2.9	41
Coll. in trailer	7	10	45	35	13	16	2.9	126

* Key

0. Pristine, unrubbed, very fresh appearance.
1. Very good, unrubbed, but not so fresh.
2. Good, some mesonotal scales missing but pattern clearly discernible.
3. Fair, mesonotum rubbed, but species still identifiable by scale pattern.
4. Rubbed, mesonotum with most scales missing, species not identifiable by scale pattern.
5. Bald, almost all scales missing, black legged *Aedes* sp. rarely identifiable.

tiago, 1934; Smith, 1942; Snow, 1949; and Muirhead-Thompson, 1958). These methods are usually biased towards a few species. Many resting-site methods have been designed to catch anopheline vectors of malaria. Methods designed for general survey work should catch as wide a spectrum of species as possible and should not be selective for any species or physiological state.

A large number of factors affect the efficiency of sampling methods. One of these is geographical location. The pit shelter (Muirhead-Thompson, 1958), was designed and worked well in Rhodesia and in Java (D. A. Muir, *pers. comm.*), two areas very different in climate and with very different mosquito species but failed when tried in Sarawak, an area similar in climate and with many mosquito species in common with Java. The methods I tested were all designed to be of use in general survey work. The findings may apply only to central Alberta but should also apply to much of the southern part of the boreal forest in which similar conditions and species occur. The mosquito fauna of this area is peculiar for the great preponderance both in the numbers and in the number of species of *Aedes* and the relative unimportance of all other genera except *Culiseta*. At George Lake five genera were found but *Aedes* comprised 72% of the species and 85% of the individuals. This can be compared to Kentucky, where eight genera were found and *Aedes* comprised 31% of the species and 52% of the individuals (Breeland and Pickard, 1965). It is thus improbable that findings in one area will apply *in toto* to the other.

The importance of the physiological state of the mosquitoes has been ignored in most studies on sampling adult mosquito populations. Bursell (1961) showed that the physiological state of tsetse flies (*Glossina swynnertoni* Austen) varies according to the sampling method used and this greatly affected interpretation of the results. Differences in the physiological age of mosquitoes taken by different sampling methods could affect the results in disease transmission studies as mosquitoes only become infected with disease-causing microorganisms after they have fed on an infected host. Thus a trap which takes a higher proportion of physiologically older females than occur in the population will give an exaggerated infection rate and if the method is selective for a few species may cause the vectorial importance of some species to be overrated. Though such a method may be useful where infected females are rare or a pool of mosquitoes is used and an exact infection rate is not required.

The low activity of the adult females in stages III and IV of Christophers is important and must be taken into account in population studies using sampling methods which catch active mosquitoes, as this means that a significant proportion of the population is inactive and so unavailable for sampling. Most studies, including this one, which show population peaks of mosquitoes are actually showing peaks of activity rather than actual population peaks and though the activity and population peaks are probably similar, this is by no means certain. Methods of capturing resting adult female mosquitoes are inaccurate, biased towards a few species and almost impossible to correlate with methods of taking active mosquitoes. If the length of the gonotrophic cycle at different temperatures and the average number of gonotrophic cycles passed through by the females in a population were known, an estimate of the proportion in the stages III and IV of Christophers could be obtained. Polovodova's method enables the number of gonotrophic cycles passed through by a female mosquito to be accurately determined and work on this in North America has been started both on

Culex tarsalis (Nelson, 1964; Burdick and Kardos, 1963) and on univoltine *Aedes* species (Carpenter and Nielsen, 1965), but almost nothing appears to be known of the length of the gonotrophic cycle in most North American species of mosquito. This is a fruitful field for future research. The use of Polovodova's method in determining the life history, vectorial importance and population dynamics of *Anopheles maculipennis* Meigen is shown by Detinova (1962).

The contents of the ventral diverticulum provide a partial measure of the energy reserves available to the mosquito. Theoretically it should be possible to distinguish the proportion of mosquitoes which have recently migrated into an area; these should have empty or nearly empty ventral diverticula, having used up most of their energy resources on the flight and the resident population should have full or nearly full diverticula. However, it would be necessary to conduct a thorough investigation of the nectar resources available and of the plants frequented by mosquitoes before the contents of the ventral diverticulum could be used to distinguish migrants from resident mosquitoes. At George Lake the majority of mosquitoes had empty or only partially filled ventral diverticula in 1966. Since flowers were abundant during the whole of the investigation, it is possible that many of the mosquitoes caught had migrated in from outside the field site; this is supported by the very few larvae found near the study area and the few males caught. Males are believed to be more sedentary than females, seldom moving more than a few miles from breeding sites, while adult female *Aedes* in temperate regions may undertake long distance migrations (Clement, 1963).

Since male mosquitoes do not take blood meals, relatively little attention has been paid to them in the past, as is shown by the few references to males in Bates (1949) and Clement (1963). I paid little attention to male mosquitoes in this study. In the last few years the development of sterile male methods of insect control has resulted in considerable interest in male mosquitoes. Males probably give a better idea of the population breeding in the vicinity of the study because they are more sedentary than the females and the adult males of many species provide more reliable characters for specific determination than do the adult females. It is unlikely that any one method will be equally effective for sampling both adult females and adult males because their biologies differ considerably. The swarming habits of the males of many species of mosquito will make the siting of traps even more critical for males than females and this, coupled with the fact that females appear to be longer lived than males and as they only mate once, it is unlikely that any one sampling method will give a true sex ratio. The important sex ratio, the number of males to unmated females, can probably be best estimated from rearing experiments.

Methods believed to take a random sample of the active population. – Malaise traps exert no recognizable attraction to mosquitoes and so I believe they take a random sample of the active mosquitoes and that this is unbiased both towards species and towards physiological state. There is one possible area of bias, that is, against blood meal seeking mosquitoes. If the generally accepted theory of host finding in mosquitoes, which is, that the biting cycle represents the frequency with which a population in random flight comes within the range of attraction of a host (Mattingly, 1949), is correct then there is no bias. However, Corbet (1961) has shown that there may be a definite urge to bite and it is possible that some mosquitoes with this urge may rest on the vegetation until activated by the presence of a possible host as do tsetse flies (*Glossina* species) (Glascow, 1963). If this is so then not many hungry mosquitoes will be caught in Malaise traps which would introduce an element of physiological bias.

At George Lake the proportion of the rarer species in Malaise traps was less than in traps which used an attractive element. This indicates that these traps are unlikely to catch large samples of these species, though they took a larger number of species than any other trap type probably because of the longer operating time. The four species not taken in Malaise traps were all rare, no more than two specimens of each being taken by all methods in 1966. No species were taken by Malaise traps alone. Breeland and Pickard (1965) found that Malaise traps caught a higher proportion of rare species and several species they recorded were only taken in Malaise traps.

The Malaise trap has certain advantages over other traps; it has no moving parts; it can work with a minimum of servicing, and needs to be emptied only once or twice a week, which allows it to be operated in remote places; it operates twenty-four hours a day and the catch is preserved in good condition. A few disadvantages are important; if left for any length of time spiders spin webs across the entrances; it is very vulnerable to vandalism; low efficiency and large size make it necessary to operate this trap for a prolonged period in a single site and the position of the trap is more critical than for other trap types; many mosquitoes which enter the base of the trap get attracted out before they are caught, so that the number seen round the traps is no indication of the catch; and it is very difficult to obtain a meaningful estimate of the volume of air filtered and so obtain an absolute density figure. These disadvantages may preclude the use of Malaise traps for some studies.

Smith *et al.* (1965) found Malaise traps alone were capable of predicting outbreaks of biting flies in Kentucky. The advantages listed above make this trap superior to most other presumably unbiased methods of collection where absolute density figures are not required.

Suction traps (Southwood, 1966) require a motor or permanent electric supply and require regular servicing. The position of these traps is critical as in Malaise traps. The volume of air filtered can be easily obtained so this trap can give an absolute density figure for flying mosquitoes.

A fairly recent innovation is a net attached to a car. These have been used by Stage and Chamberlin (1945), Biddlingmayer (1964, and 1967) and Sommerman and Simmet (1965). Provided the car is driven fast enough to eliminate attraction to moving bodies these nets probably give a random sample of active insects. The period of operation is limited but this method can cover a wide area. Sommerman and Simmet (1965) have provided a design that enables the catching container to be changed at distance or time intervals, which makes the results easier to interpret. If driven along the same route at the same time of day at regular intervals this method should produce useful results, but a series of Malaise traps at strategic intervals would probably provide as useful if not more useful information at less cost.

The rotary trap is generally considered to take a random sample of flying insects and the volume of air filtered can be easily determined, so if this trap had no attraction for mosquitoes an absolute density figure would be given. But the randomness of the sample taken in these traps is open to doubt as the traps almost certainly exert some attractive stimuli to mosquitoes and these may be selective for some species. Also, Maw (1964) has shown that the nets can become charged with static electricity and repel some small flying insects. This trap is bulky, requires considerable attention and damages the catch. I do not believe rotary traps can supply data that cannot be obtained equally well by Malaise traps.

Much the same is true of the visual attraction trap, though this trap probably does take a random sample of active mosquitoes.

If a random sample of active mosquitoes over a prolonged period is required and absolute density figures are not necessary, Malaise traps can obtain this with less trouble than any type of mechanically operated trap and are just as capable of detecting variations in population level. Where a large sample is required or only a limited time is available some other method such as visual attraction or car trap will possibly be better.

Methods known to take biased samples of the population. – Methods which use light, a bait or which capture mosquitoes in resting places are considered here.

A large number of designs of light traps for insects have been described (Southwood, 1966), but relatively few are suitable for mosquitoes. Many small insects including mosquitoes are repelled by strong light (Verheijen, 1960; Barr *et al.*, 1963) and so traps designed to catch these usually include a suction fan, like the New Jersey trap. Loomis (1959) considered that the air flow through a New Jersey trap must be standardized if two traps are being compared. At George Lake in 1966 the number of mosquitoes per 10,000 cubic feet of air filtered was 0.73 in Lt. I and 0.25 in Lt. II which are in the same ratio as the catches per 100 trap hours are (2.9). This shows that the difference between the catches in the two traps was not due to difference in air flow through them.

The species composition of light trap captures is usually considerably different from that in the natural population. This has been shown by Southwood (1960) for Heteroptera and it has also been found in mosquitoes. The attraction to light may vary within a single species over its geographical range and under different environmental conditions. *Anopheles earlei* was one of the species in which a high proportion of the catch was taken in light traps at George Lake, but McLintock *et al.* (1966) found a much lower proportion of this species was taken by light traps than in collections by other methods in Saskatchewan.

Light traps can only provide data on relative changes in mosquito populations and are probably of little use in life-table studies or in studies in which the true species composition of the mosquito fauna is required. In spite of many drawbacks, light traps are useful survey tools for mosquitoes and, if the attraction for older (parous) mosquitoes is found to be widespread, will prove especially useful in some disease transmission studies. Light traps are easily standardized and if run in the same place over a long period give an indication of population changes. Clark and Wray (1967) used light traps in studies which enabled accurate prediction of *Aedes vexans* invasions of Illinois cities. Few modern workers would go as far as Mulhern (1953), who stated that since light traps were mechanized they gave better results than methods involving collection by hand, such as human biting rate collections, since these have a human element in them.

Light traps are particularly efficient for male mosquitoes (Belton and Galloway, 1965; Southwood, 1966) and they are probably the most efficient method of sampling males. Light traps were not very effective at George Lake because it is near the northern limit at which light traps are useful.

Animal bait traps are often used and collections of mosquitoes settling on man have frequently been used to obtain density figures for mosquitoes. Human baited traps are described by Gater (1935) and Klock and Biddlingmayer (1953), and traps baited with large animals by Magoon (1935), Shannon (1939), Bates (1944) and Roberts (1965). Wharton *et al.* (1963) modified a Malayan trap (Gater, 1935) for use with monkeys as bait. In recent years interest has arisen in mosquitoes which attack birds, in connection with studies on arbor viruses, and several traps baited with chickens or other birds have been described (Flemings, 1954 and Rainey *et al.*, 1962). Lumsden (1958) and Worth and Jonkers (1962) have designed traps which use small vertebrates as bait. The Lumsden trap uses a fan and can give timed captures; portable versions of it are described by Snow *et al.* (1960) and Minter (1961).

The advantages of small mammal traps seem to be great. At George Lake captures in rat baited traps were very similar in composition to human bait captures, so white rats appear to have great value as bait in mosquito surveys. They are hardy, can survive outdoors if given shelter and can be left unattended for several days. As they give an approximation of the human biting rate they will give an idea of the nuisance value of the mosquito species present. Human bait captures while very useful can only be done for limited periods and are more expensive. Birds require more attention and large traps and, while essential in some virus transmission studies, they may give a false impression of the species composition, in studies where nuisance to man is important.

The only animal-substitute bait tested was carbon dioxide. When added to a Malaise trap this greatly increased both the catch and the number of species per unit time, but it appears to be especially attractive to some species, destroying the random nature of Malaise trap captures. For most purposes this is probably not too great a disadvantage and the increased catch will offset this, as the species attracted will probably be pest species.

The erratic behaviour of the dry ice trap of Bellamy and Reeves (1952) was possibly due to the small entrance area since the orienting stimulus of carbon dioxide appears to be weak. The main disadvantage of the addition of carbon dioxide from a cylinder to Malaise traps is that it is expensive and cannot be operated in remote places. However, dry ice is reasonably cheap and when in large enough blocks and suitably packed can last for several days while emitting large quantities of carbon dioxide. I believe that a useful mosquito trap for general survey purposes in places which cannot be visited every day would be a Malaise type trap modified to use dry ice as a bait. In central Alberta 25 pounds of dry ice lasts two to three days, which would make it possible to service this trap at bi-weekly intervals. Alone or combined with small mammal bait traps these traps could be operated in places several miles from a city, close to major mosquito breeding areas, and provide accurate data for forecasting the need for control measures in the city.

Olkowski *et al.* (1967) found Malaise traps baited with dry ice caught significantly more tabanids (Diptera; Tabanidae) than did unbaited traps in California. At George Lake tabanids were too scarce and erratic in occurrence for any conclusions to be drawn. Anderson *et al.* (1967) found the same proportion of the population of *Symphoromyia* (Diptera; Leptidae) were taken in Malaise traps baited with dry ice as were attracted to their natural hosts. They considered that these traps could give equivalent information on factors influencing attack rates at a lower cost, as could direct observation and collection of the flies from the hosts.

Collections in resting sites are useful for a few limited purposes, especially for obtaining blood fed females for host determination (World Health Organization, Division of Malaria Eradication and Lister Institute of Preventive Medicine, 1960) or for obtaining detailed information on the resting habits of mosquitoes for control with residual insecticides (Muirhead-Thompson, 1951). These methods have proved very valuable in studies on anophelines but less successful for northern *Aedes*.

Results from central Alberta (Graham in Prep. and Happold, 1965) indicate that no local *Aedes* species exhibit any special tendency to enter buildings, but *Anopheles earlei, Culiseta inornata* and *Culex tarsalis* are known to hibernate in basements. Shemanchuk (1965) has shown that the principal hibernation sites of these species are in animal burrows. Further studies on the resting habits of Alberta mosquitoes are required.

Conclusions

The principal conclusions drawn from this study are that the position as well as the trap type greatly affects the size and composition of the catch. Malaise traps both with and without carbon dioxide are probably the most useful types of traps for general mosquito survey work as they can be operated away from sources of power and need relatively little attention. Light traps will continue to be very useful in mosquito surveys, especially inside urban areas, as long as their limitations are clearly understood. Animal bait and resting-site captures are useful for specific purposes. Human bait captures are particularly useful for assessing mosquito nuisance and should always be used by urban mosquito control organizations in conjunction with other sampling methods but are of little value alone for forecasting the need for adult control measures in cities.

Although not tested in this study, car trap captures will probably be very useful in areas where vandalism or other factors prevent the use of Malaise or animal bait traps outside the city limits, but they should not be used instead of these.

ACKNOWLEDGEMENTS

I wish to express my thanks to B. Hocking, G. E. Ball, D. A. Boag, W. G. Evans, K. Smillie and J. A. Downes for reading and criticizing the manuscript; to N. Wood for assistance in the field and to W. Proctor for help with equipment. I also wish to thank the City of Edmonton and the University of Alberta for the provision of grants and the Canada Department of Agriculture, Lethbridge, Alberta, for the loan of traps.

REFERENCES

Anderson J.R., W. Olkowski and J.B. Hoy. 1967. Relationship between host attack rate and CO_2 baited Malaise trap catches in certain *Symphoromyia* species. Proc. 35th Conf. Calif. Mosquito Control Assoc.: 77.

Barr A.R. 1958. The mosquitoes of Minnesota. Univ. Minn. Agric. exp. Sta. Tech. Bull. 228. 154 pp.

Barr A.R., T.A. Smith, M. Boreham and K.E. White. 1963. Evaluation of some factors affecting the efficiency of light traps in collecting mosquitoes. J. econ. Ent. 56: 123-127.

Bates M. 1944. Notes on the construction and use of stable traps for mosquito studies. J. nat. Mal. Soc. 3: 135-145.

Bates M. 1949. The natural history of mosquitoes. New York, Harper and Row, 1965 reprint: x + 378 pp.

Bellamy R.E. and W.C. Reeves. 1952. A portable mosquito bait trap. Mosquito News 12: 256-258.

Belton P. and M. Galloway. 1965. Light trap collections of mosquitoes near Belleville, Ontario. Proc. ent. Soc. Ont. 96: 90-96.

Biddlingmayer W.L. 1964. The effect of moonlight on the flight activity of mosquitoes. Ecology 45: 87-94.

Biddlingmayer W.L. 1967. A comparison of trapping methods for adult mosquitoes: Species response and environmental influence. J. Med. Ent. 4: 200-220.

Breeland S.G. and E. Pickard. 1965. The Malaise trap – an efficient and unbiased mosquito collecting device. Mosquito News 25: 87-94.

Brown A.W.A. 1951. Studies on the responses of the female *Aedes* mosquito; Part IV; field experiments on Canadian species. Bull. ent. Res. 42: 575-582.

Brown A.W.A., D.S. Sarkaria and R.P. Thompson. 1951. Studies on the responses of the female *Aedes* mosquito; Part I; the search for attractant vapours. Bull. ent. Res. 42: 105-114.

Burdick D.J. and E.H. Kardos. 1963. The age structure of fall, winter and spring populations of *Culex tarsalis* in Kern County, California. Ann. ent. Soc. Amer. 56: 527-535.

Bursell E. 1961. The behavior of tsetse flies (*Glossina swynnertoni*) in relation to problems of sampling. Proc. R. ent. Soc. Lond. A. 36: 69-74.

Carestia R.R. and L.B. Savage. 1967. Effectiveness of carbon dioxide as a mosquito attractant in the C.D.C. miniature light trap. Mosquito News 27: 90-92.

Carpenter M.J. and L.T. Nielsen. 1965. Ovarian cycles and longevity in some univoltine *Aedes* species in the Rocky Mountains of the western United States. Mosquito News 25: 128-135.

Chamberlin J.C. and F.R. Lawson. 1945. A mechanical trap for the sampling of aerial mosquito populations. Mosquito News 5: 4-7.

Clark J.C. and F.C. Wray. 1967. Predicting influxes of *Aedes vexans* into urban areas. Mosquito News 27: 156-163

Clement A.N. 1963. The physiology of mosquitoes. Oxford, Pergamon Press. ix + 393 pp.

Corbet P.S. 1961. Entomological studies from a high tower in Mpandga forest, Uganda, VI: Nocturnal flight activity of Culicidae and Tabanidae as indicated by light traps. Trans. R. ent. Soc. Lond. 113: 301-314.

Detinova T.S. 1962. Age grouping methods in Diptera of medical importance, with special reference to some vectors of malaria. Monogr. Wld. Hlth. Org. No. 47: 216 pp.

Dow R.P. 1959. A method of testing insect traps and attractants and its application to studies of *Hippelates pusio* and *Culex tarsalis*. J. econ. Ent. 52: 496-502.

Downey J.E. 1962. Mosquito catches in New Jersey mosquito traps and ultra violet light traps. Bull. Brooklyn ent. Soc. 57: 61-63.

Duke B.O.L. 1955. Studies on the biting habits of *Chrysops*, III. Ann. trop. Med. Parasit. (Liverpool). 49: 362-367.

Fisher R.A., A.S. Corbet and C.B. Williams. 1943. The relation between the number of individuals and the number of species on a random sample of an animal population. J. anim. Ecol. 12: 42-58.

Flemings M.P. 1954. An altitude biting study of *Culex tritaeniorhyncus* and associated mosquitoes in Japan. J. econ. ent. 52: 275-285.

Gater B.A.R. 1935. Aids to the identification of Anopheline imagines in Malaya. Govt. S.S. and Mal. Adv. Board. F.M.S. 242 pp.

Glascow J.P. 1963. The distribution and abundance of tsetse. Oxford, Pergamon Press. xi + 241 pp.

Graham P. in prep. Observations on the biology of adult female mosquitoes at George Lake, Alberta.

Haddow A.J. 1960. Studies on the biting habits and medical importance of East African mosquitoes in the genus *Aedes*. Bull. ent. Res. 50: 759-779.

Happold D.C.B. 1965. Mosquito ecology in central Alberta. II. Adult populations and activities. Can. J. Zool. 43: 821-846.

Haufe W.O. and L. Burgess. 1960. Design and efficiency of mosquito traps based on visual response to patterns. Can. Ent. 92: 124-140.

Hayes R.O., R.E. Bellamy, W.C. Reeves and M.J. Willis. 1958. Comparison of four sampling methods for measurement of *Culex tarsalis* adult populations. Mosquito News 18: 218-227.

Hocking B. 1953. The intrinsic range and speed of flight of insects. Trans. R. ent. Soc. Lond. 104: 223-345.

Huffacker C.B. 1942. Tests with carbon dioxide and light as an attractant for mosquitoes with especial emphasis on the malaria mosquito, *Anopheles quadrimaculatus*. Mosquito News 2: 561-569.

Huffacker C.B. and R.C. Bach. 1943. A study of methods of sampling mosquito populations. J. econ. Ent. 36: 561-569.

Juillet J.A. 1963. A comparison of four traps used for capturing flying insects. Can. J. Zool. 41: 219-223.

Klock J.W. and W.L. Biddlingmayer. 1953. An adult mosquito sampler. Mosquito News 13: 157-159.

Laarman J.J. 1955. Host seeking behavior of the malaria mosquito *Anopheles maculipennis atroparvus*. Acta Leidensia 25: 1-144.

LaRoi G. 1968. Taiga. *In* W.G. Hardy, Editor. Alberta, a natural history. Edmonton, M.G. Hurtig.

Loomis E.C. 1959. A method for the more accurate determination of air volume displacement in light traps. J. econ. Ent. 52: 342-345.

Love G.J. and W.W. Smith. 1957. Preliminary observations on the relation of light traps to mechanical sweep net collections in sampling mosquito populations. Mosquito News 17: 9-14.

Lumsden W.H.R. 1958. A trap for insects biting small vertebrates. Nature, Lond. 181: 819-820.

Magoon E.H. 1935. A portable stable trap for capturing mosquitoes. Bull. ent. Res. 26: 363-372.

Malaise R.A. 1937. A new insect trap. Ent. Tidskr. 58: 148-164.

Mattingly P.F. 1949. Studies on West African forest mosquitoes. Part II. The less common species. Bull. ent. Res. 40: 387-402.

Maw M.G. 1964. An effect of static electricity on captures in insect traps. Can. Ent. 96: 1482.

McLintock J., A.N. Burton, H. Dillenberg and J.G. Rempel. 1966. Ecological factors in the 1963 outbreak of western equine encephalitis in Saskatchewan. Can. J. Publ. Hlth. 57: 561-575.

Minter D.M. 1961. A modified Lumsden suction trap for biting insects. Bull. ent. Res. 52: 233-238.

Muirhead-Thompson R.C. 1951. Mosquito behavior in relation to malaria transmission in the tropics. London, Arnold viii + 219 pp.

Muirhead-Thompson R.C. 1958. A pit shelter for sampling outdoor mosquito populations. Bull. Wld. Hlth. Org. 19: 1116-1118.

Mulhern T.D. 1953. Better results with mosquito light traps through standardizing mechanical performance. Mosquito News 13: 130-133.

Nelson R. 1964. Parity in winter populations of *Culex tarsalis* Coquillet in Kern County, California. Amer. J. Hyg. 80: 242-253.

Newhouse V.F., R.W. Chamberlain, J.G. Johnson and W.D. Sudia. 1966. Use of dry ice to increase mosquito catch in the C.D.C. miniature light trap. Mosquito News 26: 30-35.

Nielsen L.T. and A.T. Nielsen. 1953. Field observations on the habits of *Aedes taeniorhynchus*. Ecology 34: 141-156.

Olkowski W., J.R. Anderson and J.B. Hoy. 1967. Relationship between host attack rates and CO_2 baited Malaise trap catches of certain Tabanid species. Proc. 35th Conf. Calif. Mosquito control Assoc.

Rainey M.B., G.V. Warren, A.D. Hess and J.S. Blackmore. 1962. A sentinel chicken shed and mosquito trap for use in encephalitis field studies. Mosquito News 22: 337-342.

Reeves W.C. 1953. Quantitative field studies of a carbon dioxide chemotropism of mosquitoes. Amer. J. trop. Med. Hyg. 2: 233-246.

Reeves W.C. and McD. Hammon. 1942. Mosquitoes and encephalitis in Yakima Valley, Washington. IV. A trap for collecting live mosquitoes. J. inf. Dis. 70: 275-277.

Roberts R.H. 1965. A steer baited trap for sampling insects affecting cattle. Mosquito News 25: 281-285.

Rudolfs W. 1922. Chemotropisms of mosquitoes. New Jersey Agr. Exp. Sta. Bull. 367. 22 pp.

Russel P.F. and D. Santiago. 1934. An earth-lined trap for anopheline mosquitoes. Proc. ent. Soc. Wash. 35: 1-21.

Saliternik Z. 1960. A mosquito light trap for use on cesspits. Mosquito News 20: 295-296.

Shannon R.G. 1939. A method for collecting and feeding mosquitoes in jungle yellow fever studies. Amer. J. trop. Med. 19: 131-138.

Shemanchuk J.A. 1965. On the hibernation of *Culex tarsalis* Coquillet, *Culiseta inornata* (Williston) and *Anopheles earlei* Vargas (Diptera: Culicidae) in Alberta. Mosquito News 25: 456-462.

Simpson G.G., A. Roe and R.C. Lewontin. 1960. Quantitative Zoology, 2nd edition. New York, Harcourt-Brace. vii + 440 pp.

Smith G.E. 1942. The keg shelter as a diurnal resting place for *Anopheles quadrimaculatus.* Amer. J. trop. Med. 22: 257-269.

Smith G.E., S.G. Breeland and E. Pickard. 1965. The Malaise trap, a survey tool in medical entomology. Mosquito News 25: 389-400.

Snow W.E. 1949. Studies on portable resting stations for *Anopheles quadrimaculatus* in the Tennessee Valley. J. nat. Mal. Soc. 8: 336-343.

Snow W.E., E. Pickard and R.E. Sparkman. 1960. A fan trap for collecting biting insects attacking avian hosts. Mosquito News 20: 315-316.

Sommerman K.M. and R.P. Simmet. 1965. Car top trap with terminal cage in auto. Mosquito News 25: 172-182.

Southwood T.R.E. 1960. The flight activity of Heteroptera. Trans. R. ent. Soc. Lond. 112: 173-220.

Southwood T.R.E. 1966. Ecological methods. London, Methuen. xviii + 291 pp.

Stage H.H. and J.C. Chamberlin. 1945. Abundance and flight activity of certain Alaskan mosquitoes as determined by means of a rotary trap. Mosquito News 5: 8-16.

Stage H.H., C.M. Gjullin and W.W. Yates. 1952. Mosquitoes of the north-western states. U.S.D.A. Handbook No. 45. 95 pp.

Standfast H.A. 1965. A miniature light trap which automatically segregates the catch into hourly samples. Mosquito News 25: 48-53.

Townes H. 1962. Design for a Malaise trap. Proc. ent. Soc. Wash. 64: 253-264.

Trembley H.L. 1952. The distribution of certain liquids in the oesophageal diverticulae and stomach of mosquitoes. Amer. J. trop. Hyg. 1: 693-710.

Verheijen F.J. 1960. The mechanism of the trapping effect of artificial light sources upon animals. Arch. Neerland. Zool 13: 1-107.

Wharton D.H., D.E. Eyles and M.C.W. Warren. 1963. The development of methods for trapping vectors of monkey malaria. Ann. trop. Med. Parasit. Liverpool. 57: 32-46.

Williams C.B. 1964. Patterns in the balance of nature. London, Academic Press. vii + 324 pp.

Willis E.R. 1947. The olfactory responses of female mosquitoes. J. econ. Ent. 40: 769-778.

World Health Organization, Division of Malaria Eradication and Lister Institute of Preventive Medicine. 1960. A study of the blood feeding patterns of anopheline mosquitoes through precipitin tests. Bull. Wld. Hlth. Org. 22: 685-720.

Worth C.B. and A.H. Jonkers, 1962. Two traps for mosquitoes attracted to small vertebrates. Mosquito News 22: 15-21.

Zhogolev D.T. 1959. (Light traps as a method for collecting and studying vectors of disease organisms.) Ent. Obozr. 38: 766-773. (In Russian).

SOME PHARMACOLOGICAL PROPERTIES OF THE NERVE CORD OF THE COCKROACH; *PERIPLANETA AMERICANA* (L.)

PETER K. CHIANG
Department of Entomology
University of Alberta
Edmonton, Alberta

Quaestiones entomologicae
5 : 263-306 1969

Fluctuations in the endogenous activity and synaptic transmission were observed in intact, in situ *nerve cords of* Periplaneta americana *(L.). The endogenous activity and synaptic transmission were inhibited by hemicholinium; choline reversed this inhibition. Carbachol inhibited electrical activity entirely. Nicotine stimulated immediately upon application, followed by block. Neither dimethylphenyl piperazinium nor methacholine produced any observable effect. Pilocarpine depressed endogenous activity and synaptic transmission. Acetylcholine at* 10^{-3} *M produced no observable effect, but at* 10^{-2} *M caused a progressive blocking without apparent stimulation. Choline blocked synaptic transmission in some preparations. Eserine caused synaptic facilitation, followed by block; tetraethylpyrophosphate produced similar effects. Pyridine-2-aldoxime methiodide reactivated synaptic transmission and endogenous activity in TEPP-treated nerve cords. Choline apparently did not reactivate the electrical activity of TEPP-treated nerve cords. Phenoxybenzamine and tranylcypromine blocked both the endogenous activity and synaptic transmission. Spectrofluorometric assay did not reveal the presence of noradrenaline in the nerve cords. The acetylcholinesterase activity of individual 6th abdominal ganglion varied considerably.*

In *Periplaneta americana* (L.), a system of neurons has been described which is called the giant fiber system (Hess, 1958; Roeder, 1948a, 1953, 1962). Afferent fibers from mechanoreceptors on the caudal segments converge on the last abdominal (6th) ganglion and synapse with a small number of giant fibers. The giant axons ascend the nerve cord through the abdominal ganglia, and there appears to be no synapse at any point in the giant fibers of the abdominal nerve cord (Hess, 1958; Roeder, 1948a). Some of the giant fibers apparently ascend to the brain without interruption, and others synapse in the thoracic ganglia with motor neurons supplying the leg muscles (Hess, 1958). The giant fiber system mediates evasive response of the insects (Roeder, 1948a, 1962, 1963). In the intact roach, puffs of air applied to the sensilla on the cerci induce an alarm reaction causing evasive response (Roeder, 1948a, 1962).

In vertebrates, acetylcholine plays a vital role in preganglionic transmission in the autonomic nervous system, skeletal neuromuscular junctions, and the central nervous system (Koelle, 1963, 1965; and others). Acetylcholine may also have a role in adrenergic transmission (Burn and Rand, 1965; Koelle, 1963). Acetylcholine (ACh) and the enzymes, choline acetylase (ChA) and acetylcholinesterase (AChE) which facilitate ACh synthesis and hydrolysis respectively, have been demonstrated in the insect tissues including nervous tissue, yet the physiological role of ACh in insects remains to be demonstrated (Colhoun, 1963b; Smith, 1965).

Acetylcholine has been suggested as a transmitter substance in the cockroach nervous system (Smith and Treherne, 1965; Treherne, 1966; Yamasaki and Narahashi, 1960). An increase of ACh content was demonstrated in nerve cords of *P. americana* treated with eserine (Colhoun, 1958b; Mikalonis and Brown, 1941). Colhoun (1963b) summarized the amounts of ACh content in various species of insects. ACh content in the 6th abdominal ganglion was 63 μ gm./gm. (Colhoun, 1958a), and is located in "structural compartments." Cholinacetylase, the enzyme for the synthesis of ACh, was demonstrated in blowfly heads (Smallman, 1956). True acetylcholinesterases have been demonstrated in or isolated from the central nervous system (CNS) of various species of insects (Treherne, 1966).

Investigating synaptic and axonic transmission in *P. americana*, Roeder (1948b) first concluded that there was no evidence showing that ACh was a synaptic transmitter of nerve activity, although anticholinesterases disrupted synaptic transmission in the 6th abdominal ganglion. The conclusion was also based on the failure of high external concentrations of ACh, other choline esters, and cholinergic blocking agents to interfere with synaptic conduction.

Later, Roeder and Kennedy (1955) proposed that organophosphates could, besides inhibiting AChE, block ACh receptors at high concentrations. To circumvent the ineffectiveness of externally applied ACh, Twarog and Roeder (1956, 1957) desheathed the last abdominal ganglion, and observed that ACh, between 10^{-2} M and 10^{-3} M exerted a rapid and pronounced effect on the synaptic transmission of the ganglion. In two of a series of seventeen experiments, only a moderate decrease in synaptic response was noted. In all others, within one to five minutes, bursts of synchronous action potentials were followed by synaptic depression and block. Desheathing also reduced the concentrations at which other pharmacological agents affected synaptic transmission. This led to the postulation of an ion barrier theory, which held that the connective tissue sheath investing the roach nervous system retards the passage of ions from the bathing medium to the interior of ganglion and connectives (Twarog and Roeder, 1956, 1957). But the authors also pointed out the possibility of well protected synapses in insect ganglia (Twarog and Roeder, 1957).

Based on his observations on the electrical activity of *Locusta migratoria* (L.), Hoyle (1952, 1953) also suggested that the sheath surrounding peripheral nerves and ganglia of insects may act as a selectively permeable barrier, separating the molecules and ions of the haemolymph from those of the nervous system. O'Brien (1957, 1959a, b) reported that ionized pharmacological compounds had low toxicity to insects. Histological studies demonstrated that methylthiocholine was completely prevented from penetrating the intact nerve sheath (Winton, Metcalf, and Fukuto, 1958).

Treherne (1961a, b, c; 1962a, b), and Treherne and Smith (1965a, b) demonstrated that inorganic ions and ACh do penetrate the nerve tissue of insects. The influx of ^{14}C-labelled ACh into the extracellular system of the roach nerve cord occurred extremely rapidly, with a half-time of approximately 50 seconds (Treherne and Smith, 1965a). The insect nervous system is not virtually isolated beneath an impermeable nerve sheath, but is in a dynamic equilibrium with some smaller ions and molecules in the haemolymph (Treherne, 1965b).

Intense AChE activity was demonstrated in the neuropile, sheaths encapulating the neuron perikarya, and the perineurium of the nerve sheath of the insect CNS (Iyatomi and

Kanehisa, 1958; Wigglesworth, 1958). Electron microscopy has revealed the following distribution of eserine-specific esterase activity in the 6th abdominal ganglion of the roach, *P. americana* (Smith and Treherne, 1965): (1) in the glial sheaths of the axons in the connective and cercal nerves; (2) in the glial folds encapsulating the neuron perikarya in the ganglion: (3) in localized areas along the membrane of axon branches with the neuropile, frequently in association with local clusters of synaptic vesicles.

Bisset *et al.* (1960) found *β*, *β*-dimethyl acrylcholine in the prothoracic gland of the garden tiger moth *Arctia caja*. But Chang and Kearns (1961), and Colhoun and Spencer (1959) failed to demonstrate the presence of any free choline esters, other than ACh in the nervous system of the cockroach. Colhoun (1963b) pointed out the difficulty in accepting ACh as a synaptic transmitter first because of the failure to prove that ACh accumulated in nervous tissue as a free ester following stimulation in the presence of anticholinesterases, and second, the lack of evidence for antidromic stimulation or the blocking effects of some pharmacological agents, such as curare and atropine.

The role that biogenic amines may play in synaptic transmission in insects is largely uncertain, though catecholamine-like substances have been extracted from insects. Frontali (1968) demonstrated the presence of catecholamines in the roach brain by means of a fluorescence histochemical method.

EXPERIMENTAL METHODS

Pumphrey and Rawdon-Smith (1937), and Roeder (1948a) have shown that stimulation of the cercal sensilla of *P. americana* elicits a volley of impulses from the cercal sensory fibers which pass to the 6th abdominal ganglion, and the impulses subsequently pass to the nerve cord. Colhoun (1958b, 1960) studied synaptic transmission in the 6th abdominal ganglion *in situ* when the cerci were exposed to air puffs. Adaptation to air puffs was not shown in the 6th abdominal ganglion (Colhoun, 1960). There was an increase in total ACh content in eserinized, isolated nerve cords, which were stimulated by air puffs (Colhoun, 1960). But there was no detectable change in total ACh content in the *in situ* nerve cords or the 6th abdominal ganglia, treated the same way (Colhoun, 1960).

Since each step involved in neurohumoral transmission represents a potential point of drug attack, Koelle (1965) proposed the following four possible approaches for identifying a cholinergic synapse by considering the prototype drugs that affect processes concerned in each step:

(1) Interference with the release of the transmitter:

Hemicholinium (HC-3) can block synaptic transmission by blocking the transport system by which choline accumulates in the terminals of cholinergic fibers, and thus it limits the synthesis of ACh.

(2) Promotion of the transmitter release:

Carbachol is supposed to act by releasing ACh at the synapse. It also probably acts directly at postsynaptic cholinergic receptors.

(3) Combination with postsynaptic receptor sites:

When a drug combines with a receptor, two effects may be observed: the same effect as that of ACh (i.e., cholinomimetic); or no apparent direct effect but, by occupying the receptor site, the drug prevents the action of endogenous ACh (i.e., cholinergic blockade).

(4) Interference with the destruction or dissipation of the transmitter:

The primary action of anticholinesterases, such as organophosphates and carbamates, is the inhibition of AChE, with the consequent accumulation and action of endogenous ACh at sites of cholinergic transmission. All drugs in this class probably have in addition, direct actions at cholinoreceptive sites, and elsewhere.

Electrophysiological Studies

Materials

The chemicals were obtained as follows: acetylcholine chloride, nicotine, and pyridine-2-aldoxime methiodide (2-PAM) from City Chemical Corporation; acetyl-beta-methyl choline chloride, and eserine sulfate from Nutritional Biochemical Corporation; choline chloride from Eastman Kodak Company; hemicolinium-3(HC-3) from Aldrich Co.; carbachol (carbamylcholine) and pilocarpine from British Drug House; phenoxybenzamine hydroxide (dibenzyline), and tranylcypromine from Smith Kline and French. Tetraethylpyrophosphate (TEPP) was donated by California Chemical Company, and 1, 1-dimethyl-4-phenyl piperazinium (DMPP) was donated by Dr. Graham Chen of Parke, Davis & Company.

Methods

Rearing of P. americana. – The roaches were reared in glass battery jars in the culture room at 30°C and 50 to 60% R.H. The insects were supplied with water and rabbit pellets as food. The roaches were kept in the laboratory first for at least 12 hours before an experiment. Only male, adult roaches were used for the electrophysiology experiments.

In situ *nerve cord preparation.* – A male cockroach was lightly anaesthetized with carbon dioxide. After the wings, antennae, and legs were cut off, the roach was pinned on a wax block, slit dorsally and eviscerated. The nerve cord was cleared of connectives on both sides from the last abdominal ganglion up to the thorax, and moistened with insect saline: NaCl 9.0 gm., KCl 0.2 gm., $CaCl_2$ 0.2 gm. per liter of distilled water, pH 7.0 (Pringle, 1938). A fresh wax block was used for each roach. Mounted on a micro-manipulator, a pair of fine-tapered platinum electrodes was hooked under the nerve cord between the 5th and 6th abdominal ganglia. A period of 15 minutes was allowed for the nerve cord to achieve its steady state (Weiant, 1958). Stimulation of the anal cerci by air puff was accomplished by pressing a rubber bulb connected to a 16 cm. long Pasteur pipette, the tip of which was 0.5 cm. from, but directed toward, the left cercus. Modified after Colhoun (1958b, 1960), this method eliminated the possible production of neuroactive agents by electrical stimulation reported by Sternburg, Chang and Kearns (1959). Potentials evoked by drugs or by preganglionic stimulation could be detected conveniently. The analysis of synaptic response was according to that of Prosser (1940).

Before recording the electrical activity of a nerve cord, the bathing solution was carefully withdrawn with a Pasteur pipette, leaving the nerve cord resting on the electrodes. Wires from the two platinum electrodes were connected push-pull to a Tektronix Type 122 preamplifier, from which single-ended output was connected to a Tektronix Type 502 dual-beam oscilloscope. The upper beam was used to display the electrical activity.

A flexible copper plate was placed above, and a second one was placed below the rubber bulb which did the air puffing. These plates were held in place by a piece of lucite. One piece of wire was soldered to each of the copper plates; one led directly to a terminal of a six volt radio battery and the other led to an input of the lower beam of the oscilloscope. From the other terminal of the battery, a wire was connected to the grounding input of the lower beam. Whenever the bulb was pressed, a current occurred between the two copper plates, resulting in a short visible trace on the oscilloscope screen. This indicated the beginning of the effect of air puffing the cerci of roaches, not the duration of the air puff. Recording of the electrical activity was made with a Grass C-4 oscilloscope camera, using Kodak Kind-1732 photographic paper.

The spikes were counted under a pair of binocular microscopes by the use of a tabulator. Each set of records was counted twice, and the average was used. Since the synaptic response varied in duration, the activity is expressed as spikes/air puff, whereas the endogenous activity in spikes/sec.

Eserine was first dissolved in acetone, and then diluted to the desired concentrations in insect saline with no more than 1% acetone in the final solutions. Up to 8% acetone produced no detectable effect on the AChE activity (Dauterman, Talens, and van Asperen, 1962). Each solution was applied gently by a Pasteur pipette to the 6th abdominal ganglion. After the initial observation was made, the entire nerve cord was bathed in the solution. Since the solution gradually leaked out of the roach abdomen, additional solution was applied as required.

Determination of AChE Activity

The AChE was assayed by a modification of van Asperen's method (1962) which was based on Gomori's technique (1953). This sensitive method is primarily a colorimetric determination of naphthol produced by the enzymatic hydrolysis of naphthylacetate.

Materials

Naphthol was obtained from Fisher Scientific Company, α-naphthylacetate from Eastman Kodak Company, and diazoblue-B from Edward Gurr, Limited.

Methods

Enzyme Preparation. – The 6th abdominal ganglion was dissected from an adult roach, male or female, and rinsed in insect saline solution. The ganglion was then homogenized in ice-cold 0.01 M phosphate buffer pH 7 in a Potter and Elvehjem homogenizer. The homogenate was centrifuged at 30,000 x g for 20 minutes and the supernatant diluted to one-half ganglion per ml.

Substrate Solutions. – Substrate solution was prepared by diluting a stock solution of α-naphthylacetate (0.03 M) in acetone with 0.01 M phosphate buffer pH 7 to give a final substrate concentration of 3×10^{-4} M.

Diazoblue-B, Sodium Laurylsulfate Solution. – This solution, used for the quantitative determination of the amount of naphthol produced, consists of 3 parts of a 1% diazoblue-B solution and 7.5 parts of a 5% sodium laurylsulfate solution. The α-naphthol reacts with diazoblue-B to give a strong blue color. Sodium laurylsulfate immediately stops all esterase activity, and solubilizes the naphthol-diazoblue complex (van Asperen, 1962).

Assay of AChE. – Cockroach nervous system contains AChE, ali-esterase (AliE), and aryl-esterase (ArE) (Chadwick, 1963). Eserine is believed to inhibit the AChE activity completely, but not the other two esterases (Chadwick, 1963).

The assay was started by pipetting 0.5 ml. of enzyme solution (¼ ganglion) into 5 ml. of the substrate solution. The reaction was stopped by the addition of 1 ml. of diazoblue laurylsulfate solution (DBLS). In each assay, enzymatic hydrolysis was permitted in 1 tube for 0 minutes and a second tube for 10 minutes at 40°C. The resulting color was read in a Beckman DU-2 spectrophotometer at 600 m μ 5 minutes after addition of DBLS. The total esterase activity (EΔO.D.) was equal to O.D. of material incubated 10 minutes – O.D. of material incubated 0 minutes. To determine the nonspecific esterase activity, the same procedure was followed, except that the substrate solution contained eserine at a particular concentration. This gave an O.D. after AChE inhibition (IΔO.D.). The AChE activity (N O.D.) which was calculated as N O.D. = EΔO.D. – I O.D.

The same procedure was followed to assay the AChE inhibited by TEPP when electrical activity of the roaches ceased, except that the ganglia were homogenized with a phosphate buffer (pH 7) containing 0.3% acetylcholine chloride (Colhoun, 1959a).

Spectrofluoremetric Determination of Noradrenaline

Modified after that of Shore and Olin (1958), this procedure has been successful in assaying catecholamines of mammalian hearts (C. W. Nash, personal communication). The catecholamines are first oxidized to red indole derivatives which then become strongly fluorescent hydroxyindoles in the alkali.

Materials

The distilled water used throughout this experiment was demineralized twice.

(1) Salt-saturated butanol: 49 g. of sodium chloride, and 2 ml. of HCl were added to 946 ml. of reagent grade n-butanol.

(2) 4% versene (pH 6.3-6.5): 8 g. of EDTA were dissolved in 200 ml. of distilled water, and the pH adjusted to 6.3-6.5 using sodium hydroxide

(3) 0.1 M Iodine: 0.75 g. of iodine and 14.40 g. of potassium iodide were dissolved in 300 ml. of distilled water.

(4) Alkaline sulfite solution: 0.63 g. of anhydrous sodium sulfite were dissolved in 5 ml. of distilled water; to this 20 ml. of 5 N NaOH were added.

(5) Standard noradrenaline was obtained from New England Nuclear Corportation.

Method

The abdominal nerve cords were dissected from adult roaches, and transferred to ice-cold saline. The nerve cords were then frozen in lots of 10, and stored overnight in a deep freeze. Before the extraction procedure began, the nerve cords were thawed, taken out of the vials and frozen again by liquid nitrogen. The total weight of the nerve cords was 0.493 g. The nerve cords were homogenized in Potter and Elvehjem homogenizer with 4 ml. of cold, acid, salt-saturated butanol for 5 minutes. The homogenate was transferred to a 15 ml. screw-cap centrifuge tube, shaken for 5 minutes and centrifuged for 10 minutes at 540 x g. The supernatant was transferred to another 15 ml. screw-cap centrifuge tube, and mixed with 6 ml. of heptane and 1.5 ml. of 0.01 N HCl. The mixture was shaken and centrifuged at 540 x g for 5 minutes. The organic layer was discarded.

The acid layer was then pipetted in 0.5 ml. aliquots into three test tubes containing 1 ml. of 4% versene each, and 0.2 ml. of 0.1 M iodine was added to two of these tubes. After 2 minutes, 0.5 ml. of alkaline sulfite solution was added. The third tube was used as a tissue blank, which had its order of oxidation reversed, i.e., alkaline sulfite preceding iodine. After another 2 minutes, 0.6 ml. of 5 N acetic acid was added. The contents of the tubes were heated in a boiling water bath for 5 minutes, and cooled rapidly in cold water to room temperature. The fluorescence for noradrenaline was read in an Aminco Bowman spectrofluorometer with activation and fluorescence wavelength at 385 m μ and 485 m μ respectively.

Two noradrenaline standards, and two reagent blanks were run together with the sample. The noradrenaline standards would give a reading sensitive to about 0.5 μ g./g. of roach nerve tissue, comparable to those of vertebrate concentrations in the CNS (Udenfriend, 1964).

RESULTS

The Normal Endogenous Activity

Four roach nerve cords were treated with saline alone, and the endogenous activity was observed during an 8-hour period (Fig. 1). The synaptic transmission was generally good even at the 8th hour. The endogenous activity and synaptic transmission varied from hour to hour. The patterns of endogenous activity and synaptic transmission were almost identical although the peaks did not always coincide. The endogenous activity showed a tendency to decrease during the first hour. This might be due to the decomposition of arginine phosphate during dissection, attendant stimulation and injury of the nerve cord (Engel and Gerard, 1935).

Tobias *et al.* (1946) demonstrated that roach nerve cords could synthesize ACh. Though excised, nerves of lobster leg were able to synthesize ACh (Dettbarn and Rosenberg, 1966).

The Effect of Hemicholinium (HC-3)

Hemicholinium (10^{-3} M) blocked synaptic transmission of two roaches (Fig. 2C, D), and incompletely blocked the synaptic activity of two other roaches (Fig. 2A, B). Both the endogenous activity and synaptic transmission showed steady decline. Starting after an hour or two, the amplitudes of the endogenous activity and synaptic response decreased (Fig. 3). In order to facilitate the depletion of endogenous ACh, the cerci were exposed to puffs for a period of ten minutes each hour. The endogenous activity of the nerve cord of four roaches was completely abolished after one to five hours.

Three other roaches were treated first with hemicholinium (10^{-3} M), and then choline chloride (10^{-3} M) was applied when both the endogenous activity and synaptic transmission appeared to reach the lowest level (Figs. 4, 5). Again, the activity pattern showed a decline in the presence of HC-3 alone. After the choline was applied, the endogenous activity was increased, and the synaptic transmission was greatly improved.

No previous work has been done on the effect of HC-3 on the electrical activity of insect nervous system. HC-3 is reported to interfere with the synthesis of ACh by preventing the

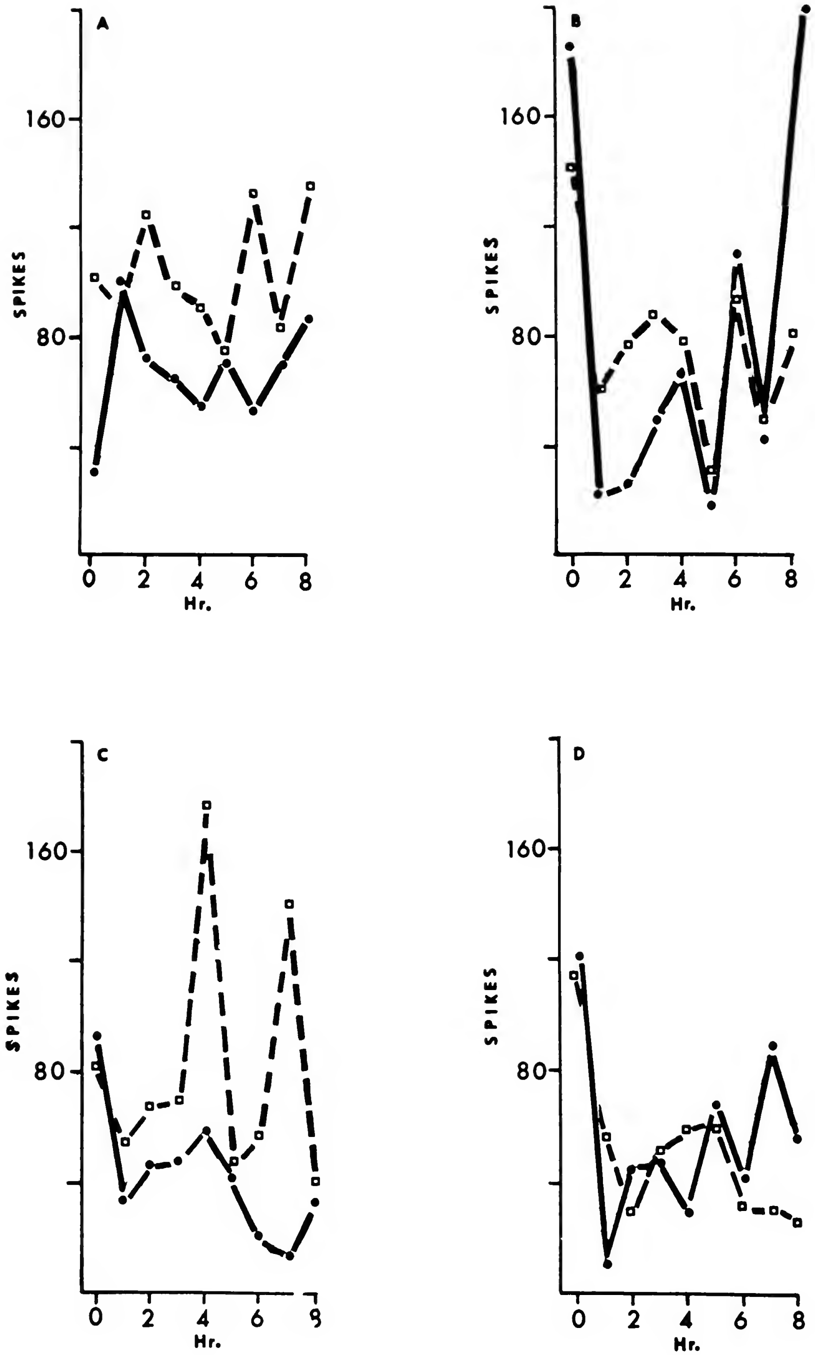


Fig. 1. Electrical activity in the ventral nerve cord of *P. americana* treated with insect saline. Each graph represents the data from a different roach; ● spikes/sec., □ spikes/air puff.

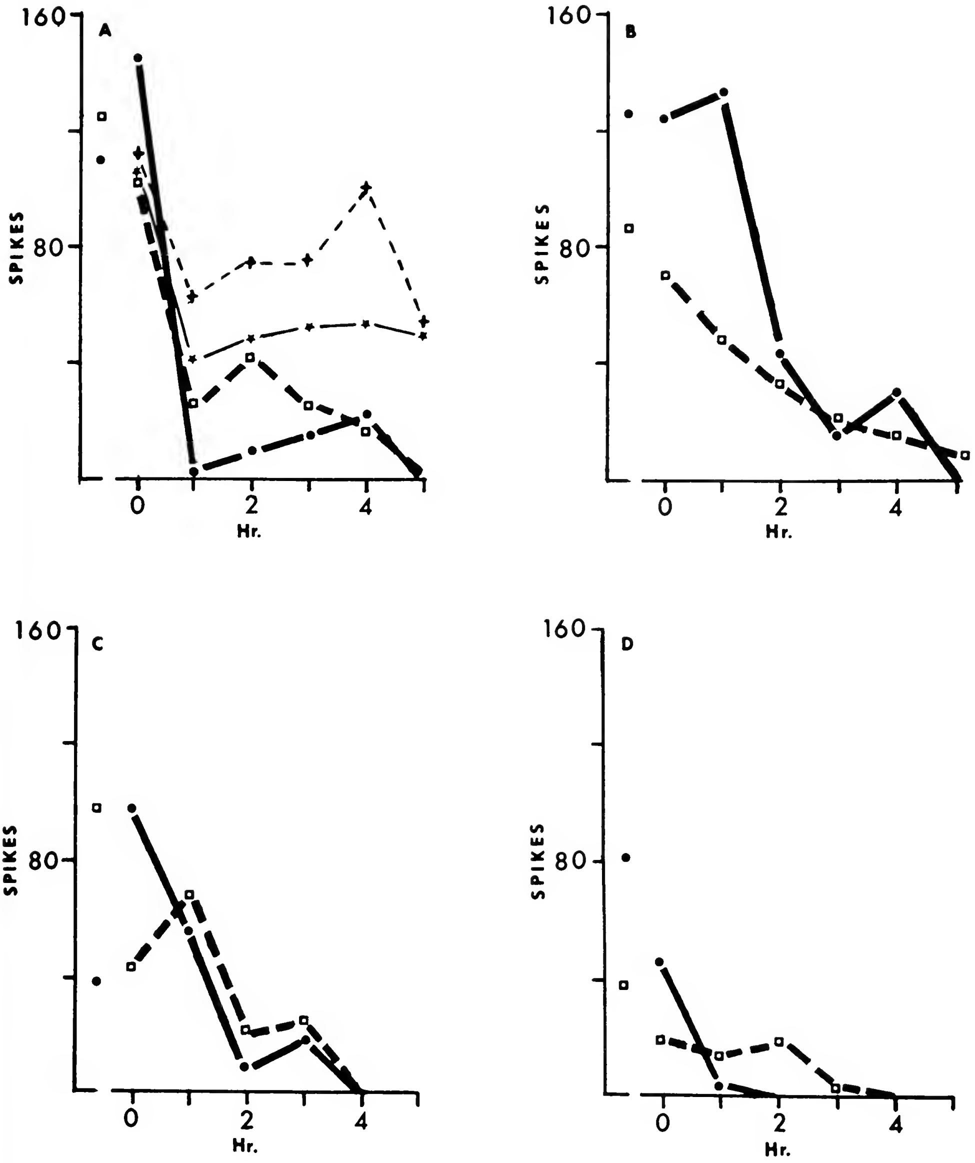


Fig. 2. Electrical activity in the ventral nerve cord of *P. americana* treated with 10^{-3} M HC-3. Each graph represents the data from a different roach; ● spikes/sec., □ spikes/air puff. In Fig. 2A, the data from 4 controls treated with saline are also presented; * average spikes/sec., + average spikes/air puff.

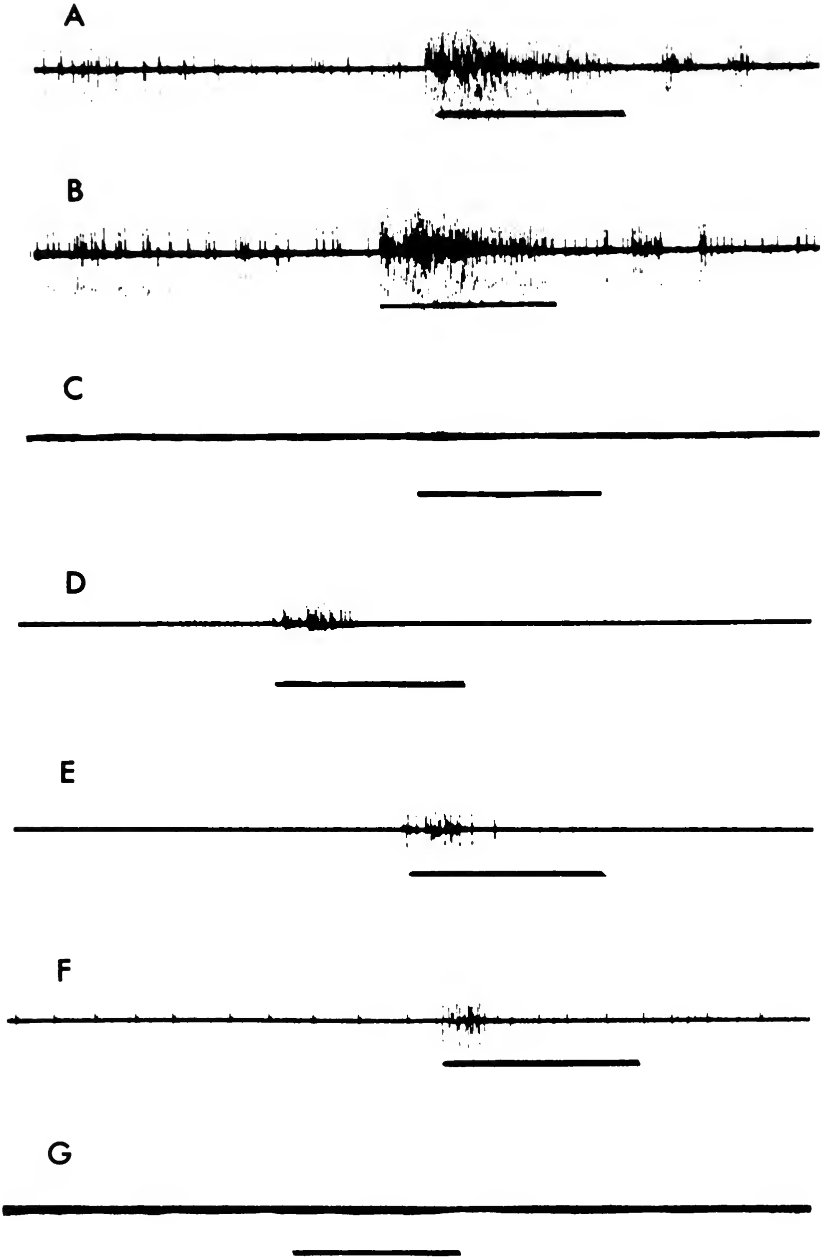


Fig. 3. Electrical activity in the ventral nerve cord of *P. americana* treated with 10^{-3} M hemicholinium. (A) before treatment; (B) 0 hour; (C) 1 hour; (D) 2 hours; (E) 3 hours; (F) 4 hours; (G) 5 hours. Solid line air puff applied. Film speed 10 cm/sec.

access of choline to choline acetylase (Gardiner, 1961), or by blocking the transport system by which choline accumulates in the terminals of cholinergic fibers (MacIntosh, 1961). HC-3 inhibited the ACh synthesis in mammalian sympathetic ganglia (Birks and MacIntosh, 1961; MacIntosh, Birks and Sastry, 1956). HC-3 also inhibited the synthesis of ACh in minced mouse brain (Gardiner, 1961). Postganglionic sympathetic transmission was blocked by HC-3 (Burn and Rand, 1960). The block of ACh synthesis by HC-3 could be reversed by large doses of choline (Birks and MacIntosh, 1961; Gardiner, 1961).

The degree of inhibition of ACh synthesis by HC-3 depended upon the concentration of choline present (Gardiner, 1961). The variation in the inhibitory effect on the electrical activity in the present study could probably be explained on such basis.

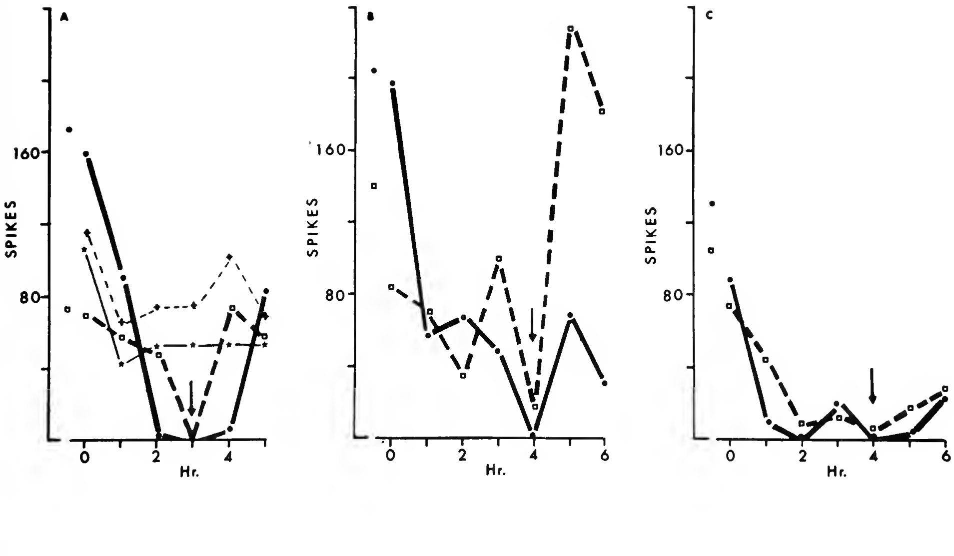


Fig. 4. Reactivation of electrical activity by 10 $^{-3}$ M choline in the ventral nerve cord of *P. americana* treated with 10^{-3} M HC-3. Each graph represents the data from a different roach; ● spikes/sec., □ spikes/air puff, ↓ choline added. In Fig. 3A the data from 4 controls treated with saline are also presented; * average spikes/sec., + average spikes/air puff.

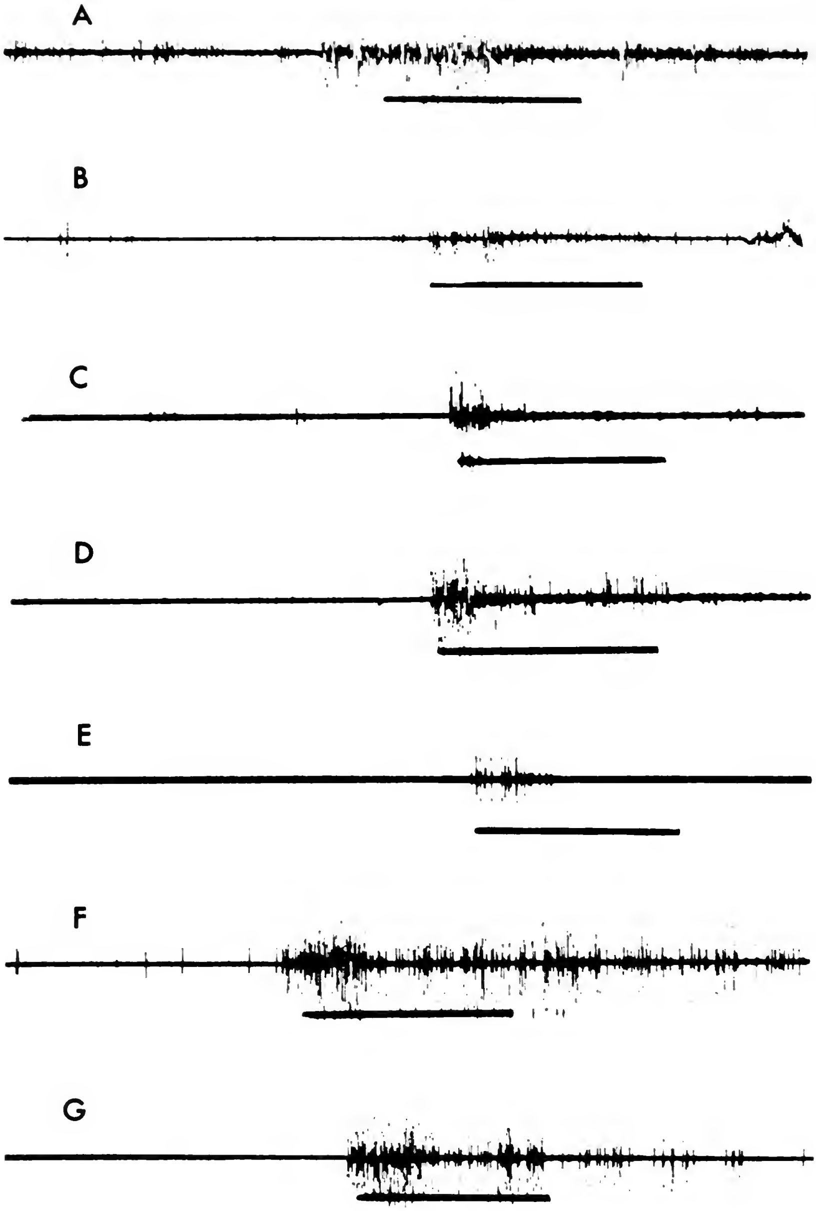


Fig. 5. Reactivation of electrical activity by choline in the ventral nerve cord of *P. americana* treated with 10^{-3} M hemicholinium (HC-3). (A) before treatment; (B) 0 hour; (C) 1 hour; (D) 2 hours; (E) 3 hours; (F) 4 hours; (G) 6 hours. Solid line air puff applied. Film speed 10 cm/sec.

The Effect of Carbachol (Carbamylcholine)

Carbachol at 10^{-3} M had no observable effect on the endogenous activity or the synaptic transmission of three roaches (Fig. 6A, B, C). But at 10^{-2} M, carbachol blocked both the endogenous activity and synaptic transmission in three nerve cords after approximately two hours (Fig. 6D, E, F). Half an hour after the application of carbachol, the endogenous activity decreased almost to zero in one nerve cord (Fig. 6E). The spikes of synaptic transmission were barely visible. In the other two nerve cords, there was some indication that some nerve cells were acted upon. The spikes of these cells were of low amplitudes.

The results were contrary to Roeder's finding (1948b): carbachol at 10^{-2} M had no effect on synaptic transmission in the roach's 6th abdominal ganglion. Perhaps his period of observation was different.

Ginsborg and Guerrero (1964) reported that carbachol depolarized the sympathetic ganglion cells of the frog, and the amplitude of the spontaneous synaptic potential was depressed five minutes after addition of carbachol. It was concluded that the depolarization was apparently a direct result of the drug acting on the receptor, and not due to a "drug induced" release of transmitter from the presynaptic fibers (Ginsborg and Guerrero, 1964). Carbachol can release ACh only for brief periods before desensitization ensues (McKinstry and Koelle, 1967). Carbachol itself is hydrolyzed much more slowly than ACh, and is completely unaffected by AChE (Barlow, 1964; Koelle, 1965).

The Effect of Nicotine

Since nicotine can mimic ACh in cholinergic synapses and junctions (Albert, 1965), it was used so that the stimulatory and blocking effect of other drugs of the same category could be compared. As reported by others (Roeder and Roeder, 1939; Welsh and Gordon, 1947), nicotine (10^{-3} M) caused an immediate stimulation upon application, and then blocked synaptic and endogenous activity irreversibly. Since the effect was immediate, a graph is not presented.

The Effect of Dimethylphenylpiperazinium (DMPP)

DMPP produced no observable effect even at 10^{-2} M (Fig. 7). The electrical activity pattern was similar to that of the saline controls.

No previous work has been done on the effect of DMPP on the electrical activity of insects. DMPP is a selective stimulant of autonomic ganglion cells in vertebrates, although its blocking effect is less potent than nicotine (Chen and Portman, 1954; Chen, Portman, and Wickel, 1951; Leach, 1957).

The Effect of Methacholine (Acetyl-β-methylcholine)

Methacholine at 10^{-2} M did not produce any observable effect on the electrical activity of the roach nerve cords within a period of five hours (Fig. 8). Methacholine is equiactive as ACh in vertebrates at the postganglionic parasympathetic nerves (Albert, 1965; Bebbington and Brimblecombe, 1965). Geber and Volle (1965) observed that methacholine was even more potent than ACh as a depolarizing agent in the sympathetic (superior cervical) ganglion of the cat. Methacholine may also produce ganglionic hyperpolarization by a direct action on the sympathetic ganglion cells (Volle, 1965).

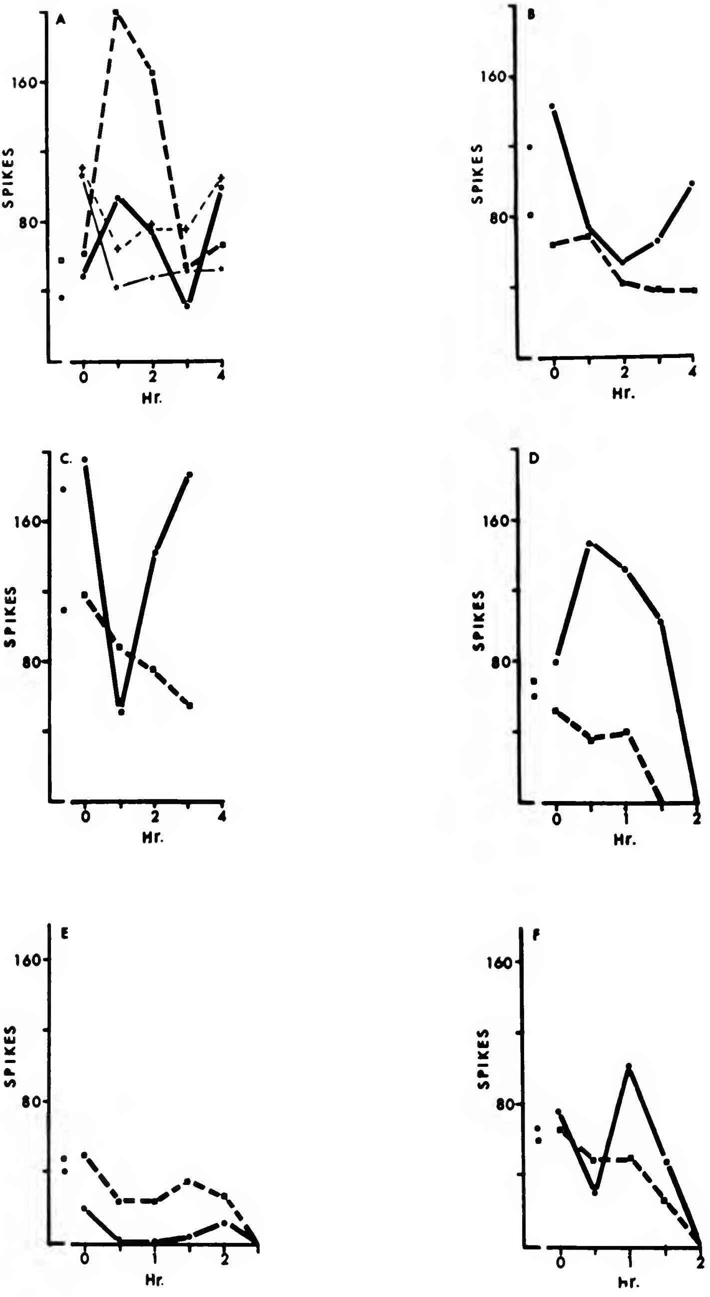


Fig. 6. Electrical activity in the ventral nerve cord of *P. americana* treated with carbachol; A, B, & C 10^{-3} M; D, E, & F 10^{-2} M. Each graph represents the data from a different roach; ● spikes/sec., □ spikes/air puff. In Fig. 6A, the data from 4 controls treated with saline are also presented; * average spikes/sec., + average spikes/air puff.

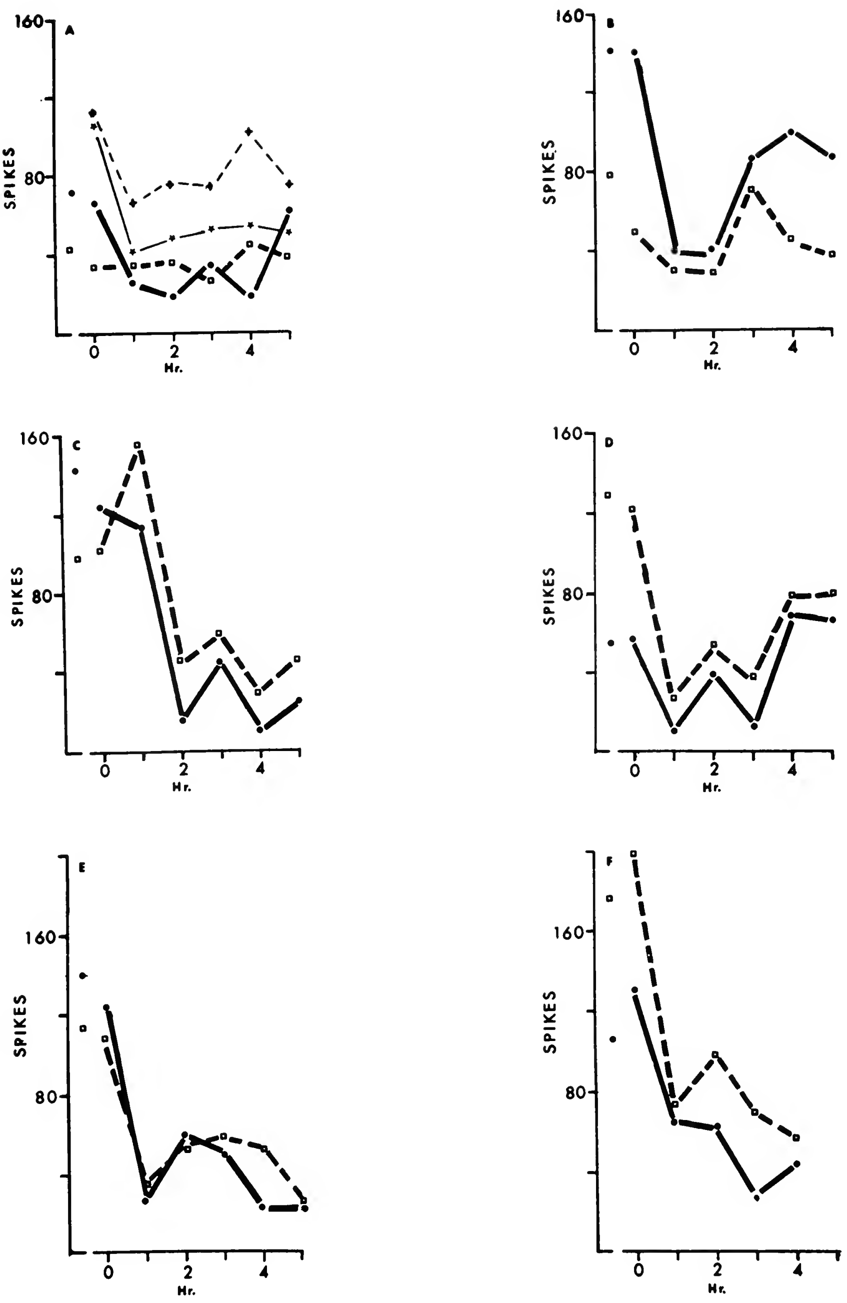


Fig. 7. Electrical activity in the ventral nerve cord of *P. americana* treated with 10^{-2} M dimethylphenyl piperazinium (DMPP). Each graph represents the data from a different roach; ● spikes/sec., □ spikes/air puff. In Fig. 7A, the data from 4 controls treated with saline are also presented; * average spikes/sec., + average spikes/air puff.

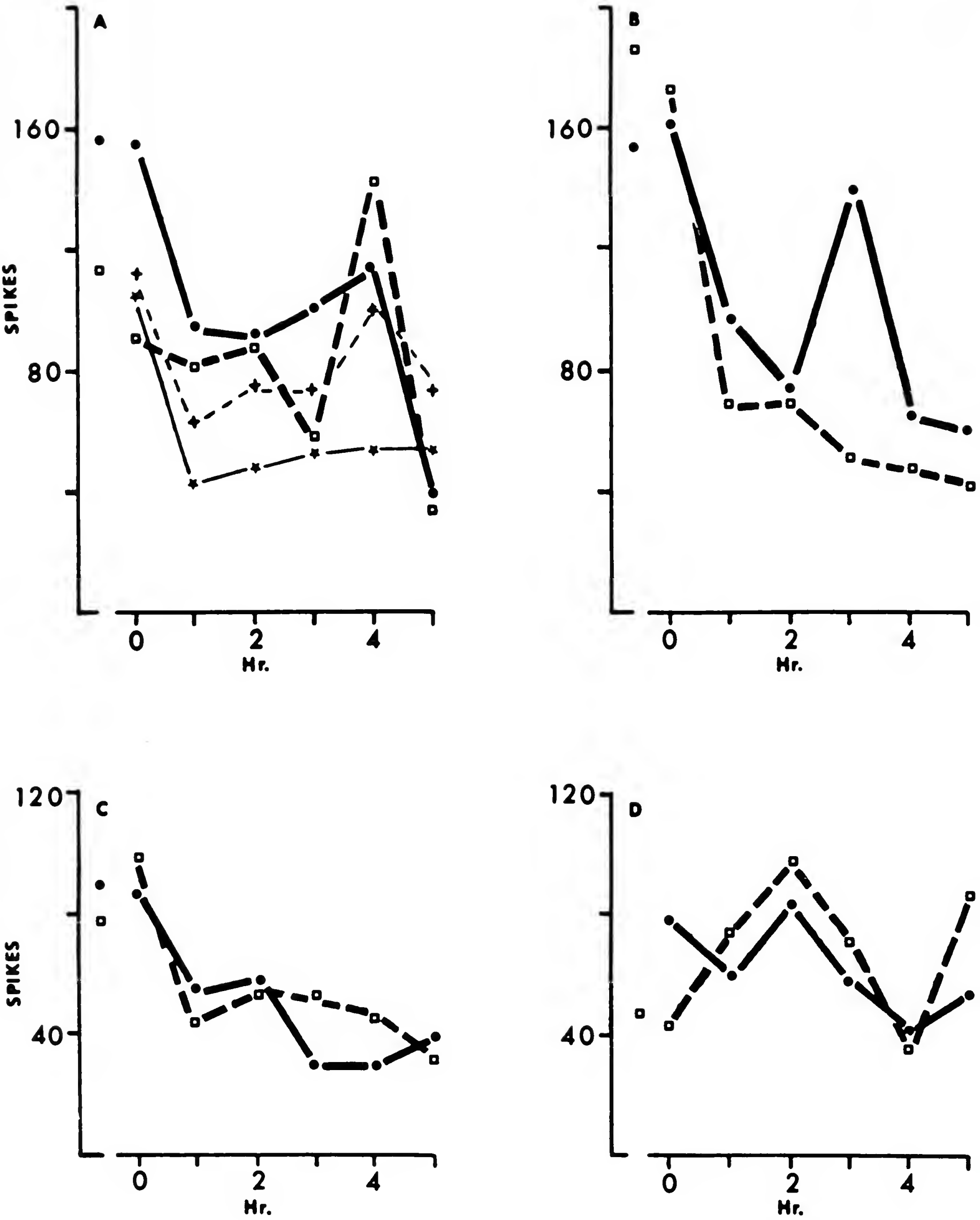


Fig. 8. Electrical activity in the ventral nerve cord of *P. americana* treated with 10^{-2} M methacholine. Each graph represents the data from a different roach; ● spikes/sec., □ spikes/air puff. In Fig. 8A, the data from 4 controls treated with saline are also presented; * average spikes/sec., + average spikes/air puff.

Since methacholine is less readily hydrolyzed than ACh (Grollman, 1960), the failure of methacholine to affect synaptic transmission is probably not due to its destruction by hydrolysis. Roeder (1948b) also showed that methacholine was ineffective in stimulating or blocking synaptic transmission in the roach.

The Effect of Pilocarpine

Pilocarpine at 10^{-3} M showed a definite depressing effect on both the endogenous activity and synaptic transmission (Fig. 9). The amplitudes of the spikes decreased with time. The endogenous activity and synaptic transmission were both blocked in one preparation (Fig. 9D). Some low amplitude spikes appeared after one hour, indicating some cells were acted upon. These low amplitude spikes resembled those induced by carbachol. Twarog and Roeder (1957) also observed such effects from nerve cords, the ganglia of which were desheathed.

Although pilocarpine is chiefly a powerful parasympathomimetic agent, stimulating the organs innervated by postganglionic fibers, it can also exert ganglionic stimulation (Koelle, 1965; Grollman, 1960).

Pilocarpine is a weak competitive inhibitor of fly-head AChE *in vitro*, and does not exert any progressive inhibition (Chadwick, 1964). The results of the present investigation support the conclusion of Chadwick (1964) that inhibition of AChE is not involved in the poisoning of roaches by pilocarpine.

Pilocarpine injected into the heads of praying mantis produced a state of great excitation. But when injected into the roaches, it produced immobility and apparent paralysis (Roeder and Roeder, 1939).

The Effect of Acetylcholine

ACh (10^{-3} M) produced no observable effect within a period of five hours. But at 10^{-2} M ACh blocked both the endogenous activity and synaptic transmission in five out of six intact preparations (Fig. 10). The stimulatory effect of ACh observed in mammalian ganglia (Geber and Volle, 1965; Takeshige and Volle, 1962, 1963; Volle, 1965) was not observed in the roaches. ACh exhibited a progressive depressing effect (Fig. 11). Three eserinized nerve cords (eserine 10^{-5} M) were washed with saline when synaptic after-discharge occurred, and then 10^{-4} M, 10^{-3} M, 10^{-2} M ACh was applied to them immediately. No apparent stimulation was observed. The endogenous activity and synaptic transmission approached normal within a period of 30 minutes.

Roeder and Roeder (1939) reported that 10^{-3} M ACh produced a definite increase in the level of endogenous activity in isolated nerve cords. But when the nerve cords were *in situ*, ACh 10^{-2} M had no effect (Twarog and Roeder, 1957). If the ganglia were desheathed and eserinized, 10^{-3} M ACh caused a partial synaptic block, and in concentrations between 3×10^{-3} M and 5×10^{-3} M, most preparations showed brief after-discharge followed by block; some preparations were incompletely blocked (Twarog and Roeder, 1957). Yamasaki and Narahashi (1960) claimed that 10^{-2} M ACh was effective in depolarizing isolated roach ganglia. They also found that if the ganglia were desheathed and eserinized, ACh was effective at concentrations as low as 10^{-4} M; but 10^{-5} M had little effect. However, Takeshige and Volle (1964) observed that when small doses of ACh were applied to eserinized cat's

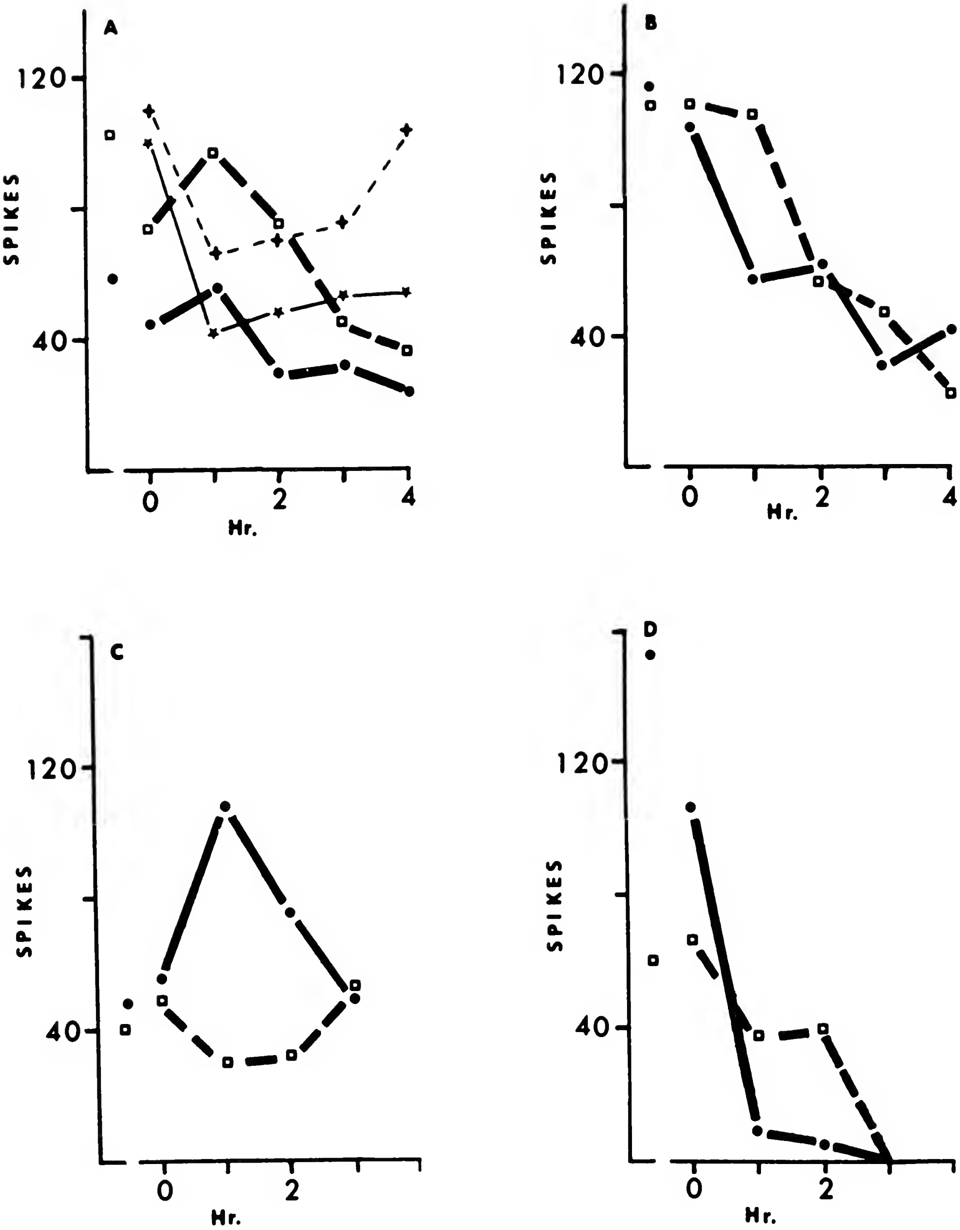


Fig. 9. Electrical activity in the ventral nerve cord of *P. americana* treated with 10^{-3} M pilocarpine. Each graph represents the data from a different roach; ● spikes/sec., □ spikes/air puff. In Fig. 9A, the data from 4 controls treated with saline are also presented; * average spikes/sec., + average spikes/air puff.

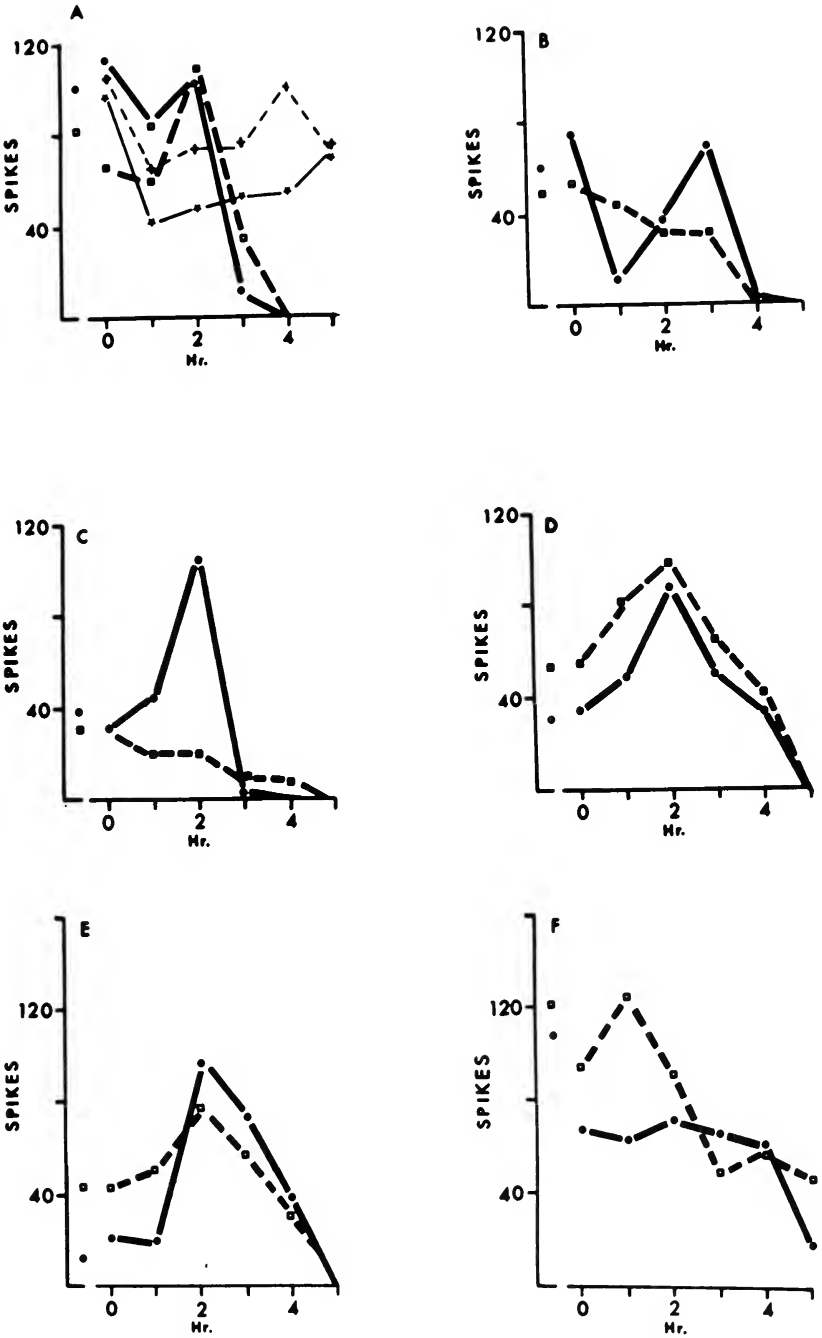


Fig. 10. Electrical activity in the ventral nerve cord of *P. americana* treated with 10^{-2} M acetylcholine. Each graph represents the data from a different roach; ● spikes/sec., □ spikes/air puff. In Fig. 10A, the data from 4 controls treated with saline are also presented; * average spikes/sec., + average spikes/air puff.

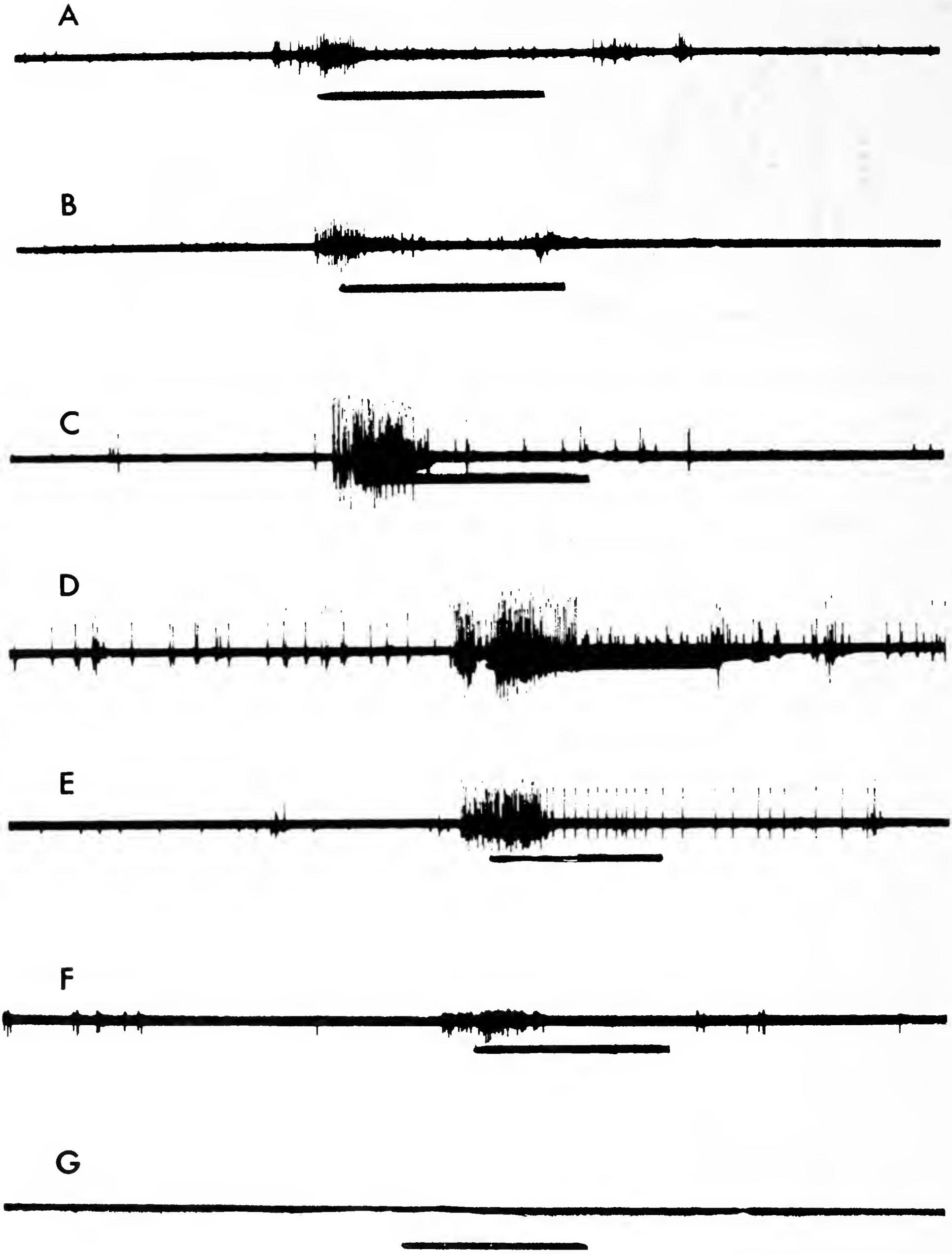


Fig. 11. Electrical activity in the ventral nerve cord of *P. americana* treated with 10^{-3} M ACh. (A) before treatment; (B) 0 hour; (C) 1 hour; (D) 2 hours; (E) 3 hours; (F) 4 hours; (G) 5 hours. Solid line air puff applied. Film speed 10 cm/sec.

sympathetic ganglia, hyperpolarization occurred also, in addition to depolarization caused by a larger dose of ACh (Takeshige and Volle, 1962).

The Effect of Choline

Choline (10^{-2} M) blocked synaptic transmission in four out of six preparations (Fig. 12). Both the endogenous activity and synaptic transmission of one preparation were blocked. The endogenous activity of the other five preparations was unimpaired. In some preparations, regular medium-high and low amplitude spikes occurred. In doses three to four times greater than ACh, choline caused a low amplitude, but sustained, depolarization of the cat's sympathetic ganglia (Geber and Volle, 1965). Choline accelerated the rate of failure of postganglionic firing in cat's sympathetic ganglion (Volle and Koelle, 1961).

The Effect of Eserine

Eserine at 10^{-7} M produced no observable effect. But anticholinesterase effects were observed with 10^{-5} M eserine about one hour after treatment; these effects consisted of periodic bursts of low amplitude spikes and synaptic after-discharge in response to a single puff, i.e., facilitation. Washing the preparation with saline abolished these effects. These observations are in agreement with those of Roeder (1948b), and Yamasaki and Narahashi (1960). The low amplitude spikes increased in frequency and magnitude with time. A synaptic block sometimes developed after the onset of after-discharge caused by a single puff. Since the effect of eserine is well established, a graph is not presented.

When the *in situ* ganglion was desheathed, Twarog and Roeder (1957) found that eserine at 10^{-5} M was effective within five minutes, compared with 10 to 40 minutes in intact but isolated nerve cords (Yamasaki and Narahashi, 1960).

The Effect of Tetraethylpyrophosphate (TEPP)

TEPP (10^{-4} M) exerted a rapid and pronounced effect on the nerve cords. Within a minute of application, repetitive discharge occurred. The duration of the discharge varied from 22 to 60 seconds. A synaptic block and an electrical quiescent period followed the initial discharge. Four out of six nerve cords did not show any recovery from the completely inactive state when washed with saline. The "endogenous" activity of one preparation reappeared for four hours after an initial quiescent period, but air puffs could not elicit a synaptic response (Fig. 13A). However, in one preparation, both the "endogenous" activity and the synaptic transmission persisted, despite the alternation of electrical quiescence and synaptic block (Fig. 13B).

TEPP was reported to block synaptic transmission in nerve cords that were *in situ* (Colhoun, 1960; Roeder, 1948b), and in nerve cords with desheathed ganglia (Yamasaki and Narahashi, 1960). Sternburg *et al.* (1959) proposed that TEPP caused a neuroactive substance to be released as a result of synaptic facilitation, and this rather than TEPP was responsible for blocking the electrical activity. They also suggested that the same substance participates in neurotransmission within the central nervous system of roaches. The number of replicable observations was not indicated.

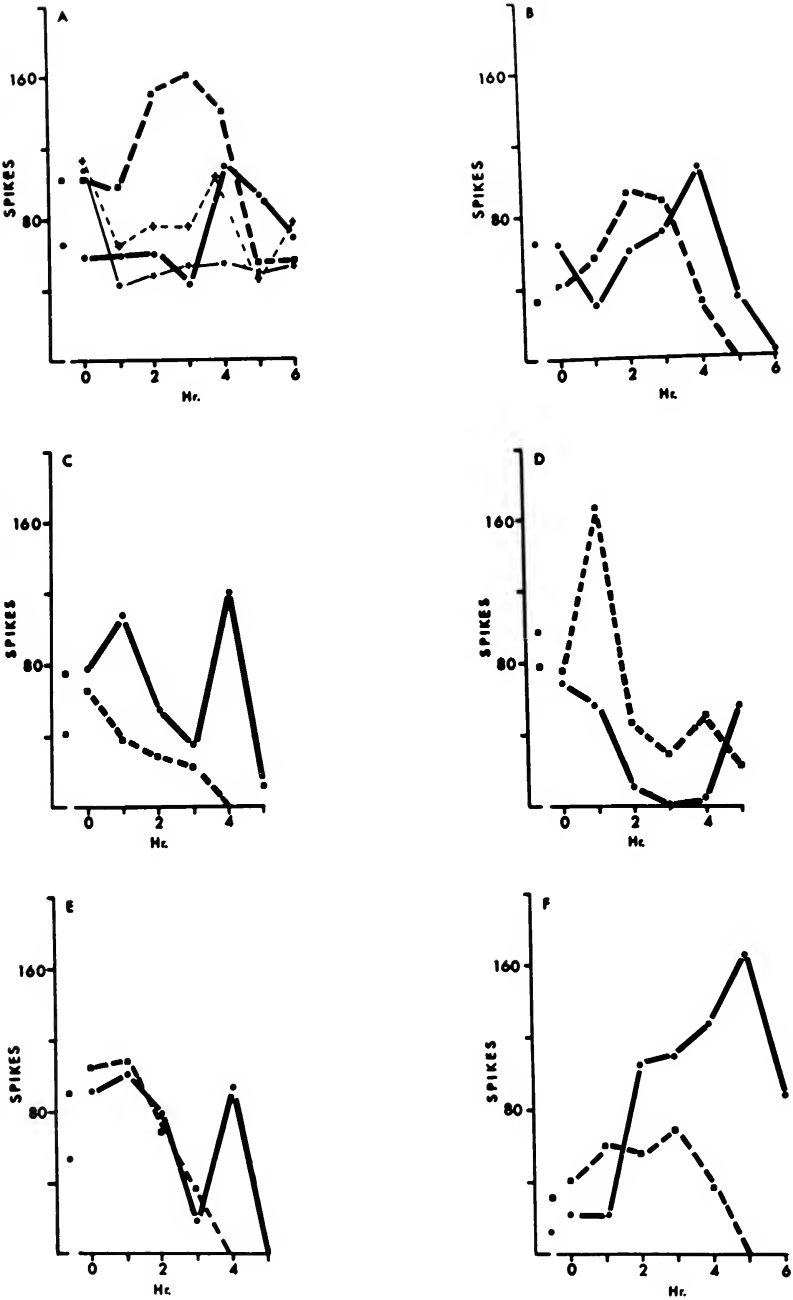


Fig. 12. Electrical activity in the ventral nerve cord of *P. americana* treated with 10^{-2} M choline. Each graph represents the data from a different roach; ● spikes/sec., □ spikes/air puff. In Fig. 12A, the data from 4 controls treated with saline are also presented; * average spikes/sec., + average spikes/air puff.

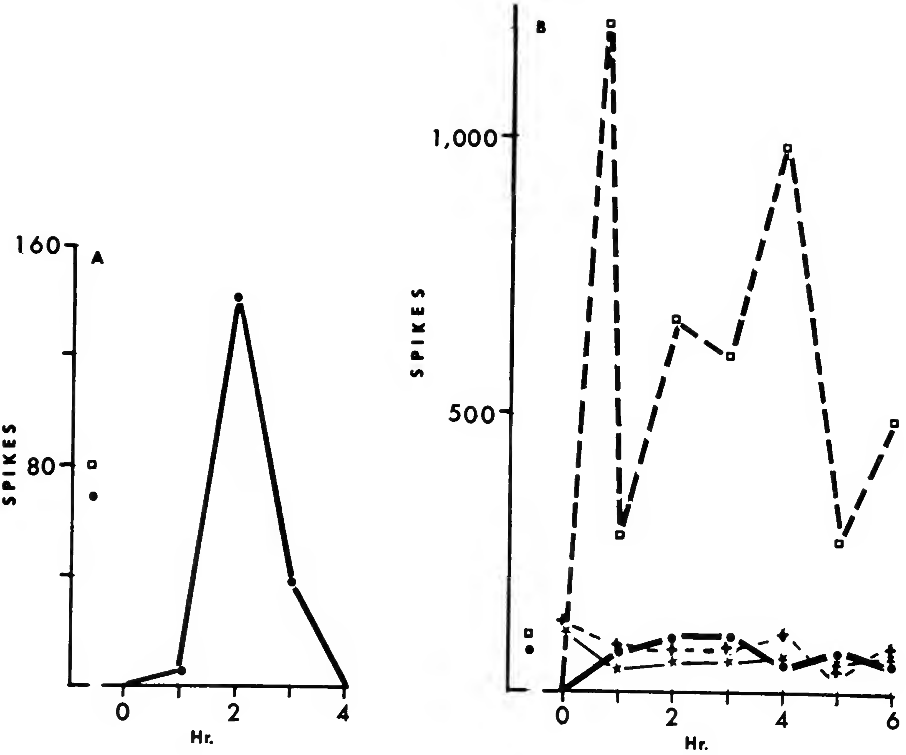


Fig. 13. Electrical activity in the ventral nerve cord of *P. americana* treated with 10^{-4} M TEPP. Each graph represents the data from a different roach; ● spikes/sec., □ spikes/air puff. In Fig. 13B, the data from 4 controls treated with saline are also presented; * average spikes/sec., + average spikes/air puff.

The Effect of Pyridine-2-aldoxime Methiodid (2-PAM) upon TEPP-Treated Nerve Cords

When complete electrical blockade was observed in four nerve cords, two treated with 10^{-4} M TEPP, two with 10^{-3} M TEPP, 2-PAM (10^{-3} M) was applied to them (Figs. 14, 15). Both the endogenous activity and synaptic transmission reappeared at the first hour, with the occurrence of facilitation and quiescence. With the exception of one preparation, synaptic after-discharge and electrical quiescence stopped at the third hour. The electrical activity of all four appeared normal at the fourth hour.

When applied alone, 10^{-3} M 2-PAM had no apparent effect on the electrical activity of the nerve cords (Fig. 16). In mammals, 2-PAM is a potent neuromuscular blocking agent (Holmes and Robins, 1955).

Phosphorylated AChE can be reactivated by 2-PAM effectively (Hobbiger, 1963). The reactivation of phosphorylated AChE by 2-PAM involves the bonding of 2-PAM's quarternary ammonium group to the anionic site of the phosphorylated AChE, thus allowing the hydrolysis of the phosphorylated-oxime-enzyme complex to occur, giving AChE and phosphorylated-oxime (Loomis, 1956; Wilson, 1960; Wilson and Ginsburg, 1958).

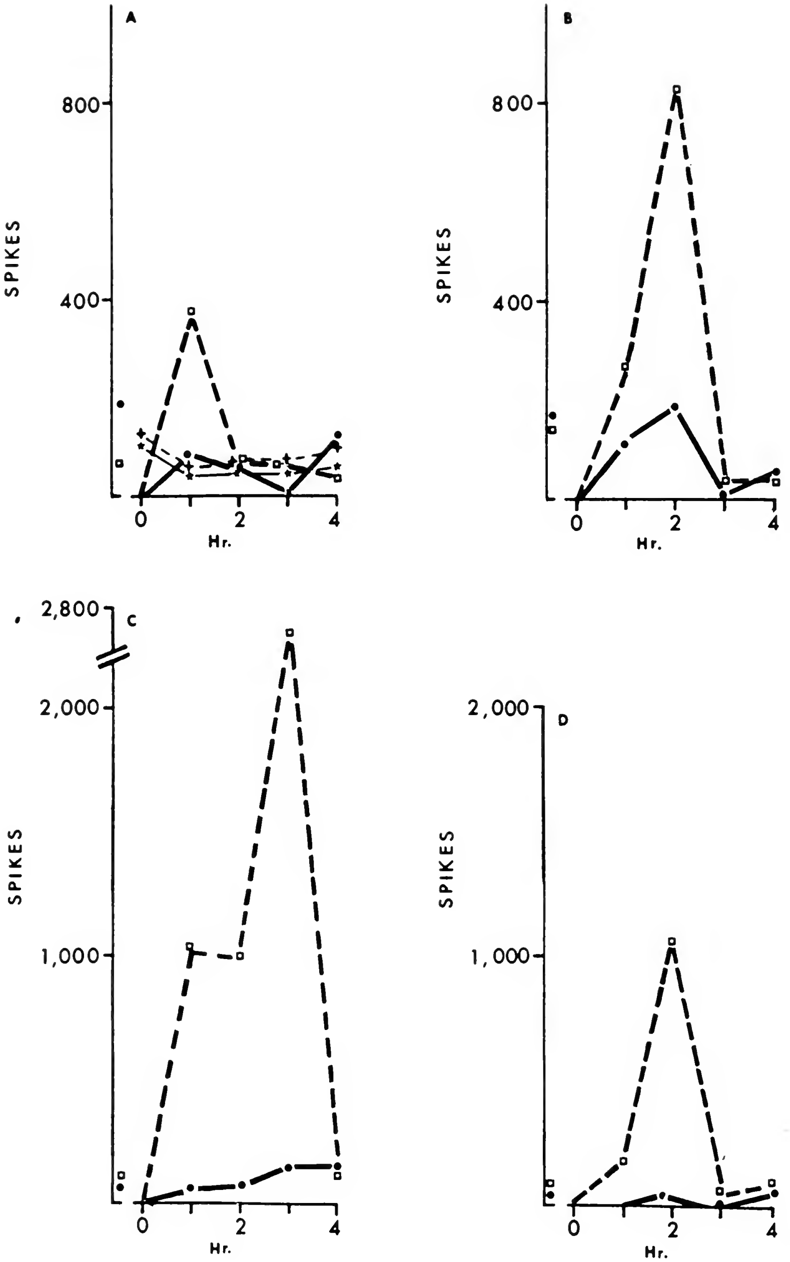


Fig. 14. Reactivation of electrical activity by 2-PAM in the ventral nerve cord of *P. americana* treated with TEPP; A & B 10^{-3} M TEPP, C & D 10^{-4} M TEPP; 10^{-3} M. 2-PAM was added at 0 hour when complete block was observed; ● spikes/sec., □ spikes/air puff. In Fig. 14A, the data from 4 controls treated with saline are also presented; * average spikes/sec., + average spikes/air puff.

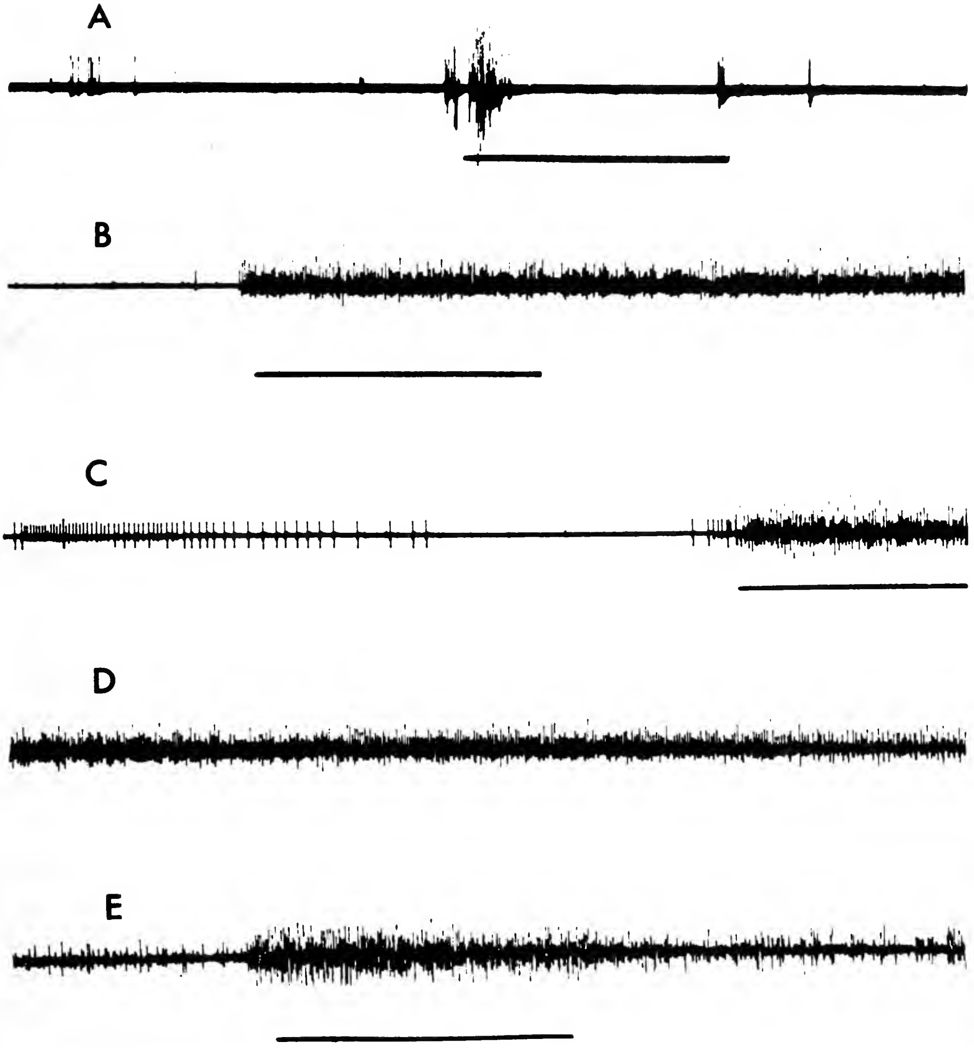


Fig. 15. Reactivation of electrical activity by 2-PAM in the ventral nerve cord of *P. americana* treated with 10^{-4} M TEPP. (A) before the nerve cord was treated with TEPP. Electrical activity ceased at 0 hour. (B) 1 hour after 10^{-3} M 2-PAM added; (C) & (D) 2 hours; (E) 4 hours. Solid line air puff applied. Film speed 10 cm/sec.

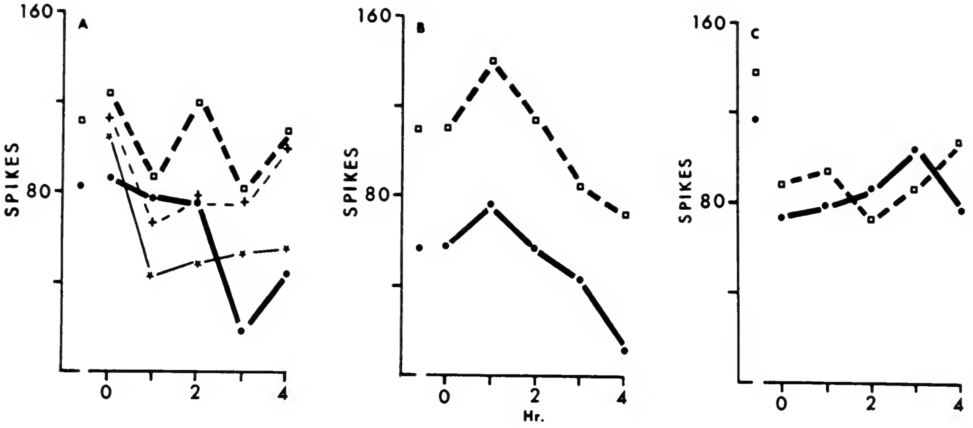


Fig. 16. Electrical activity in the ventral nerve cord of *P. americana* treated with 10^{-3} M 2-PAM. Each graph represents the data from a different roach; ● spikes/sec., □ spikes/air puff. In Fig. 16A, the data from 4 controls treated with saline are also presented; * average spikes/sec., + average spikes/air puff.

Phosphorylated roach AChE was reactivated by 2-PAM *in vitro* (Colhoun, 1959b; Brady and Sternburg, 1966). The dose of 2-PAM necessary to reverse neuromuscular block in the rat nerve-diaphragm was close to the toxic dose for TEPP (Holmes and Robins, 1955), and the time taken for the reversal of block by 2-PAM was the same whether the anticholinesterase had been in contact with the preparation for a few minutes or for many hours.

The Effect of Choline upon TEPP-Treated Nerve Cords

After immersion in 10^{-3} M TEPP for 30 minutes, three nerve cords were then treated with 10^{-3} M choline (Fig. 17). One preparation remained completely blocked. The endogenous activity of another preparation appeared at the first hour, but became blocked again at the fourth hour. Both the endogenous activity and synaptic transmission of a third preparation resumed at the third hour, with typical signs of AChE inhibition. But the endogenous activity stopped again an hour later, with synaptic block to follow two hours later. Choline is a weak reactivating agent of phosphorylated AChE (Hobbiger, 1963).

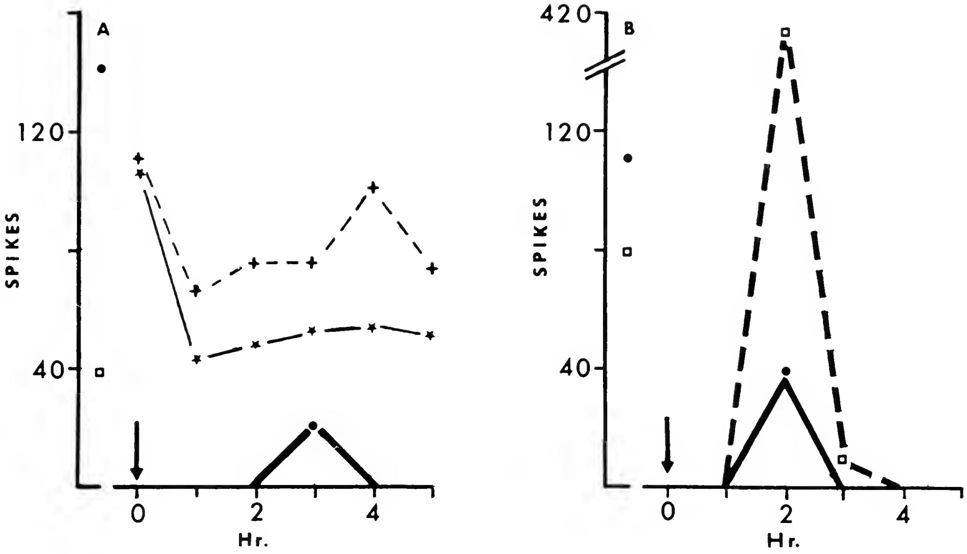


Fig. 17. Effect of 10^{-3} M choline on the electrical activity of the ventral nerve cord of *P. americana* treated with 10^{-3} M TEPP. Each graph represents the data from a different roach; ● spikes/sec., □ spikes/air puff; ↓ choline added. In Fig. 17A, the data from 4 controls treated with saline are also presented; * average spikes/sec., + average spikes/air puff.

Determination of AChE Activity

Fig. 18 shows the effect of eserine concentration upon the rate of α-naphthylacetate hydrolysis by the esterases in the roach 6th abdominal ganglion. About 50% of the total activity was readily inhibited by 10^{-8} M eserine. The addition of 10^{-5} M eserine apparently blocked the AChE completely after 10 minutes of incubation. This is in agreement with the results of van Asperen (1962) when fly-head AChE was used. Using manometric technique, Chadwick and Hill (1957) reported that 96% of the roach nerve cord AChE was inhibited by 10^{-5} M eserine.

The activity of the individual ganglia varied from 1.520 μ M naphthol to 2.96 μ M naphthol produced per minute, with a mean of 1.947 μ M naphthol per minute (Table 1). The mean activity of three pooled homogenates was 2.111 μ M naphthol produced per minute. But the difference between the two means is not statistically significant ($P < 0.05$) by Student-t test. Yamasaki and Narahashi (1960) observed considerable variation of AChE activity in roach nerve cords.

After an electrical block became apparent in three roach nerve cords treated with 10^{-4} M TEPP, the AChE activity was assayed immediately (Table 2). The mean AChE activity was 11.16% of that of the control. Inactivation of AChE ran parallel with the synaptic afterdischarge (Yamasaki and Narahashi, 1960).

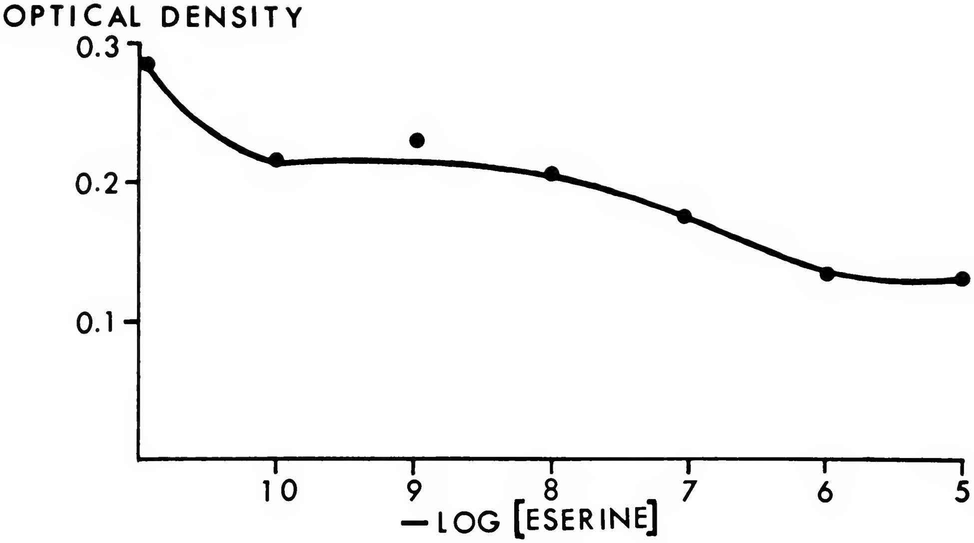


Fig. 18. Inhibition of roach ganglion AChE activity by eserine. Temperature 40°C. Substrate 3×10^{-4} M α-naphtyl acetate. Homogenate concentration ¼ ganglion per tube. Incubation time 10 minutes.

The Effect of Adrenergic Drugs

Phenoxybenzamine (dibenzyline) blocks the α-receptors of the adrenergic nerves effectively and persistently (Nickerson, 1965). When phenoxybenzamine (10^{-3} M) was applied to the nerve cords of roaches, a blocking effect was observed (Fig. 19A, B, C). Washing with saline did not eliminate the blocking effect. Being a β-haloalkylamine that can cause tissue damage as nitrogen mustard (Nickerson, 1949), phenoxybenzamine may not be specific in its action. Phenoxybenzamine increased the spontaneous efflux of H^3-noradrenaline by 50% in cat's colon (Costa *et al.*, 1966).

Monoamine oxidase (MAO) is the enzyme chiefly responsible for the physiological inactivation of 5-hydroxytryptamine (5-HT), and endogenous catecholamines (Kopine, 1964; Page, 1958; Shore *et al.*, 1957). Tranylcypromine, a MAO inhibitor, blocked the endogenous activity and the synaptic transmission of the nerve cords of roaches at 10^{-3} M (Fig. 19E, F, G). MAO inhibitors can produce an irreversible inactivation of MAO by forming stable complexes with the enzyme, causing an elevation of biogenic amines (Javik, 1965; Pletscher, 1966). But MAO inhibitors can also inhibit other enzymes as well (Javik, 1965).

Table 1: AChE activity in 6th abdominal ganglion of *P. americana*.

	$E\Delta O.D._{600}/0.25$ ganglion less eserine	$I\Delta O.D._{600}/0.25$ ganglion with eserine ($10^{-5}M$)	AChE Activity*		
			$N\Delta O.D._{600}/0.25$ ganglion	Unit[1] /ganglion	
Individual ganglion in 2 ml. phosphate buffer (pH 7.0)	0.415	0.296	0.119	1.587	Mean unit/ganglion 1.947**
	0.320	0.193	0.127	1.693	
	0.445	0.297	0.148	1.973	
	0.488	0.266	0.222	2.960	
	0.268	0.154	0.114	1.520	
5 ganglia in 10 ml. phosphate buffer	0.293	0.120	0.173	2.307	Mean unit/ganglion 2.111**
	0.293	0.158	0.135	1.800	
	0.278	0.111	0.167	2.227	

* AChE activity = $E\Delta O.D._{600}$ less eserine - $I\Delta O.D._{600}$ with eserine

[1] One unit activity = 1 μM. of naphthol produced/min.

$O.D._{600}$ 0.03 = 1 μM.

** $p<0.05$

Table 2: AChE activity in 6th Abdominal ganglion of *P. americana* treated with 10^{-4} M TEPP.

Individual ganglion in 2 ml. phosphate buffer (pH 7) containing 0.3% ACh	$E\Delta O.D._{600}/0.25$ ganglion less eserine	$I\Delta O.D._{600}/0.25$ ganglion with eserine (10^{-5} M)	AChE Activity*		
			$N\Delta O.D._{600}/0.25$ ganglion	Unit [1]/ganglion	% control[+]
	0.037	0.016	0.021	0.280	14.380
	0.021	0.001	0.020	0.266	13.662
	0.018	0.010	0.008	0.106	5.444

* AChE activity = $E\Delta O.D._{600}$ less eserine - $I\Delta O.D._{600}$ with eserine

[1] One unit activity = 1 μM of naphthol produced/min.

$O.D._{600}$ 0.03 = 1 μM

Mean unit activity = 11.16% of control

[+] Control = Mean AChE activity of individual ganglia in Table 1

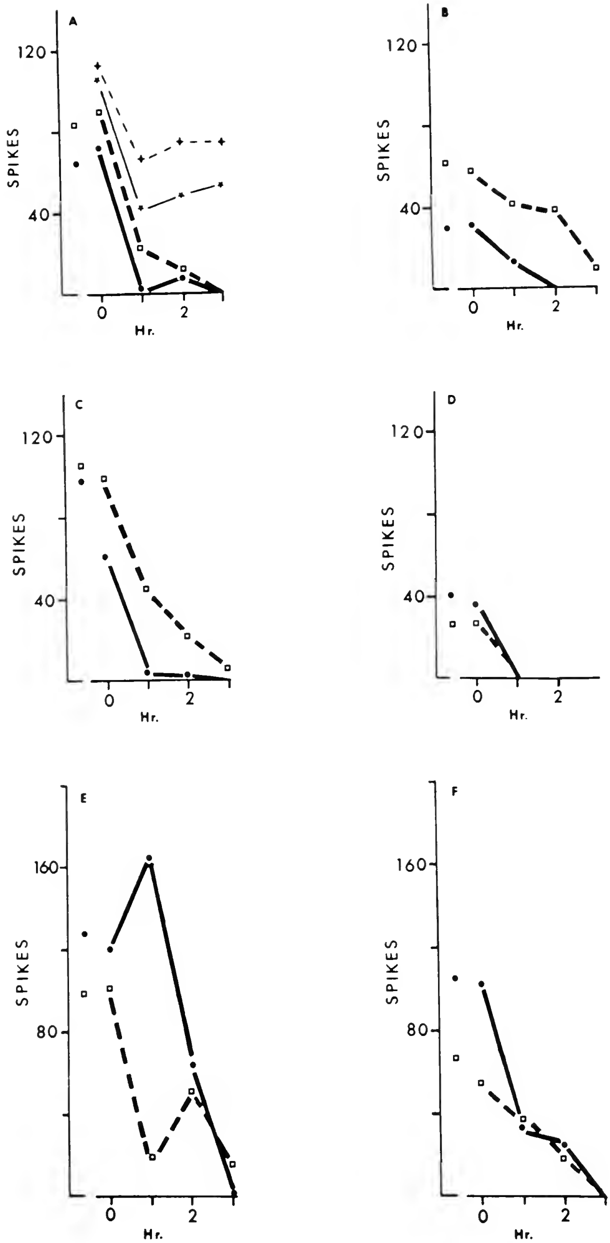


Fig. 19. Electrical activity in the ventral nerve cord of *P. americana* treated with 10^{-3} M phenoxybenzamine (A, B, C), and 10^{-3} M tranylcypromine (D, E, F). Each graph represents the data from a different roach; ● spikes/sec., □ spikes/air puff. In Fig. 18A, the data from 4 controls treated with saline are also presented; * average spikes/sec., + average spikes/air puff.

Spectrofluorometric Determination of Noradrenaline

There was no indication of the presence of noradrenaline in the sample (Fig. 20). Owing to the large number of roaches required to yield sufficient amount of nerve cords, the experiment was run only once. Unger (1957) believed that adrenaline, noradrenaline, and histamine are not among a number of cardiac accelerators obtained from the abdominal nerve cords, corpora allata, corpora cardiaca and haemolymph.

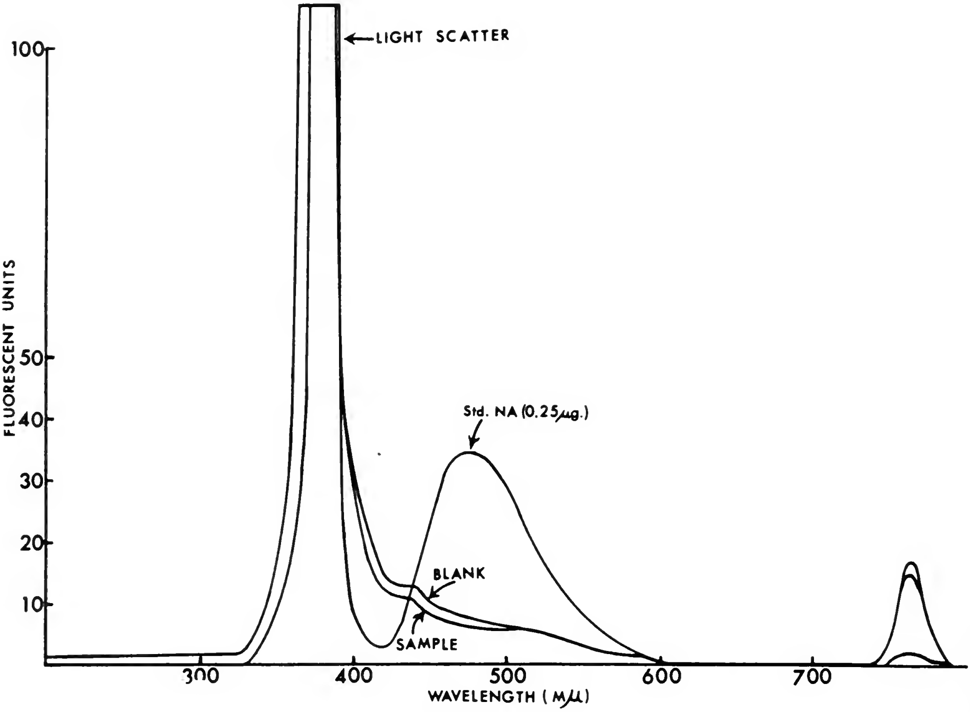


Fig. 20. Fluorescence spectra and light scatter of 0.25 μ g of standard noradrenaline, a sample of extraction of roach abdominal nerve cords, and a reagent blank assayed by the iodine method. Excitation was at 385 m μ.

DISCUSSION

The physiological role of ACh in nerve tissues has been reviewed extensively by Koelle (1963). In the synaptic and neuroeffector sites, there are three possible roles that can be attributed to ACh. (1) On arrival of an impulse in an axon terminal, ACh is liberated and diffuses across the synaptic cleft to combine with a receptor to bring about a localized depolarization, the postsynaptic potential (PSP). The latter in turn initiates electronically a nerve action potention (AP) in the second neuron. (2) ACh acts first at an axon terminal from which it is liberated to cause the release of additional quanta of ACh, which produce the

PSP. (3) In non-cholinergic neurons, AP liberates ACh from presynaptic terminals, which acts at the same terminals to effect release of another synaptic transmitter. The latter produces PSP, which initiates AP.

The demonstration that hemicholinium blocked both the endogenous activity and the synaptic transmission either entirely or partially (Fig. 4), and the restoration of activity by choline, indicates that the neural activity of the roach nerve cord is dependent upon ACh.

Drugs that act at cholinergic sites are generally divided into two categories: nicotinic and muscarinic (Albert, 1965; Goth, 1966). The muscarinic drugs act mainly on the peripheral autonomic nervous system, stimulating the post-ganglionic parasympathetic receptors of organs such as smooth muscles, cardiac muscle, endocrine glands, etc., without having an effect upon ganglionic transmission or skeletal muscles (Goth, 1966). The muscarinic receptors are atropine sensitive (Goth, 1966). The nicotinic drugs can stimulate autonomic ganglion and end-plates of skeletal muscles (Goth, 1966). The nicotinic receptors are divided into the ganglionic receptors which are hexamethonium sensitive, and the skeletal muscle receptors which are sensitive to curare (Goth, 1966). Nicotine has effects on both the ganglionic and neuromuscular transmission (Albert, 1965; Goth, 1966). However, these are only working hypotheses for the mammalian peripheral nervous system. The terms "nicotinic" and "muscarinic" are not applicable to the central nervous system (Curtis, Ryall and Watkins, 1965; Feldberg, 1950).

Khromov-Borisov and Michelson (1966) pointed out that the invertebrate muscles are mainly nicotinic. This invites the speculation that the roach cercal synapse does not have a muscarinic receptor. The failure of atropine and methacholine to produce any blocking or killing effect (Roeder, 1948b; Tobias *et al.*, 1946) supports such a hypothesis.

Ambache (1955) pointed out the limitations of using atropine as a pharmacological criterion for cholinergic nerves: (1) atropine might be destroyed by an esterase; (2) true atropine resistance in cholinergic systems might be due to "proximity", (3) secondary formation of atropine-resistant pharmacological agents.

The failure of DMPP, a nicotinic drug, to produce any observable effects points to the uniqueness of the roach cercal ganglion.

It is of interest to compare the *in vivo* effects of injecting carbachol, ACh, and methacholine into roaches with the results of the present investigation. The toxic dose of carbachol for the roaches was 0.5 to 0.1 g./kg., and 7 to 10 g./kg. for the ACh; methacholine even at 20 g./kg. produced no killing effect (Tobias *et al.*, 1946).

Treherne (1966) postulated a "biochemical barrier" theory, which is partly based on the histochemical evidence that AChE is situated "strategically" on the glial membranes bordering extracellular channels. Despite the rapid influx of ACh, the concentration of ACh within the roach ganglion was reduced to 8.1×10^{-5} M when the nerve cord was bathed with a solution of 10^{-2} M ACh (Treherne and Smith, 1965b). The relative inability of externally applied ACh to affect insect nerves would thus seem to result from the presence of this "biochemical barrier" rather than to the "ion barrier" (Treherne, 1966).

Although choline could block synaptic transmission, the overall effect of the ACh in the present investigation could not be explained entirely by the hydrolysis of ACh to choline and acetate. In addition to its depolarizing property, it is possible that ACh also hyperpolarizes the nerve cells in the roach cercal ganglion. When the nerve cords were isolated, or desheathed, ACh was allowed to reach a cholinoreceptive site to cause depolarization. This would be completely in accord with the finding that there are multiple cholinoreceptive sites within the mammalian ganglia, and that ACh can be excitatory or inhibitory depending on the receptor (Eccles and Libet, 1961; Geber and Volle, 1965; Koelle, 1965; Takeshige and Volle, 1963, 1964). Since the ganglionic potentials represent an algebraic summation of simultaneous processes, it is conceivable that the temporally related hyperpolarization and postganglionic firing resulted from monitoring certain populations of cells and fibers (Takeshige and Volle, 1964). Thus, while the ganglion as a whole appeared to be in a hyperpolarized state, the postganglionic fibers monitored might have been partially depolarized (Takeshige and Volle, 1964). Unfortunately, this possibility could not be tested with the present experimental technique. The results of carbachol and pilocarpine could also be explained by this postulation. It is also possible that ganglionic hyperpolarization caused by ACh was mediated by means of an inhibitory transmitter liberated within a ganglion (Volle, 1965). Simultaneous presynaptic inhibition could also occur (McLennan, 1963).

It was recently found that ACh acts both as an excitatory and inhibitory transmitter in the same abdominal ganglion of two species of marine mollusc of the genus *Aplysia* (Kandel and Frazier, 1967; Tauc and Gershenfeld, 1962). Two types of ganglion cells have been demonstrated by the actions of ACh. The response of one group of cells to ACh was characterized by depolarization and acceleration of the rate of firing. Conversely, ACh produced hyperpolarization and the blockade in the second group.

The possible role ACh may play in the sodium pump mechanism (Hokin, Hokin and Shelp, 1960) should not be overlooked. A given drug, such as ACh itself, may produce either cholinomimetic or cholinergic blocking action at certain sites, depending upon the dose, rate of combination with the receptors, and other factors (Koelle, 1962; Paton, 1961). Also of equal importance is the role the inhibitory system may play when the insect CNS is either intact or semi-intact (Milburn, Weiant, and Roeder, 1960; Roeder, 1962).

Koelle (1963) surmised that the earliest function of ACh and its associated enzymes in primitive organisms was probably the modification of the passage of various substances across the cell membranes. With the subsequent development of different types of structural complexity of cellular membranes in accordance with their various functions, the ACh-AChE system itself has been achieved in nervous tissues, where its components and function are concentrated predominantly at synapses and junctional sites. At such regions, the ACh may serve both as the transmitter and as the agent for the liberation of other chemical mediators.

Catecholamines have been demonstrated by fluorescence microscopy in the autonomic ganglia of mammals (Jacobowitz and Koelle, 1963; Hamberger, Norberg and Sjöqvist, 1965; Hamberger, Norberg and Unguestedt, 1965; Norberg and Sjöqvist, 1966; Owen and Falck, 1965). Adrenergic sensory neurons were demonstrated in two genera of molluscs (Dahl *et al.*, 1963). Noradrenaline and adrenaline have both inhibitory and facilitatory actions on sympathetic ganglia of the cat (De Groat and Volle, 1966a, b). Eccles and Libet (1961) proposed that ACh can release an adrenergic substance through a chromaffin cell to produce an action potential. It was postulated that ACh released from sympathetic fibers could liberate noradrenaline from a peripheral store, in the same way as injected ACh (Burn, 1966; Burn and Rand, 1965; Chang and Rand, 1960).

The possibility that catecholamines may participate in roach synaptic transmission was suggested by Twarog and Roeder (1957), who recorded asynchronous bursts of low voltage spikes following application of adrenaline and noradrenaline to desheathed roach ganglion. After-discharge and synaptic blocking were observed at concentrations between 10^{-3} M and 10^{-2} M. But when applied to intact ganglion, noradrenaline and adrenaline failed to show any stimulatory or blocking effect (Colhoun, 1959a). Application of 5×10^{-5} M dopamine to the roach cercal ganglion induced bursts of activity which propagated along the nerve cord; however, this substance did not have any effect on the synaptic transmission (Gahery and Boistel, 1965). Since not all the regions in the roach cercal ganglion, as shown by electron micrograph, are associated with membrane-bound cholinesterase activity (Smith and Treherne, 1965), such non-cholinergic synapses could be regarded as possible candidates for transmission mechanisms involving catecholamines (Treherne, 1966).

Injection of adrenaline into roaches paralyzed them temporarily, but injection of noradrenaline produced no recognizable response (Barton Brown *et al.*, 1961). All adrenergic neuron blocking agents examined in detail show a variety of actions at cholinergic sites (Boura and Green, 1965).

Colhoun (1963a) showed the presence of 5-HT in the nerve cords of roaches, though the amount is extremely low in comparison with ACh. Grollman (1960) believed that 5-HT is a primitive synaptic transmitter. It is a chemical transmitter in some invertebrates and vertebrates (Brodie and Shore, 1957; Owen and Falck, 1965; Welsh, 1957), and can potentiate and buffer ganglionic transmission (Page, 1958). If some of the noncholinergic regions are occupied by 5-HT, then the data for the adrenergic drugs in the present investigation become interpretable. But alpha adrenergic blocking agents can also react with receptors for histamine, 5-HT and ACh (Nickerson, 1965).

Catecholamines and adrenaline-like substances have been extracted from insects (Cameron, 1953; Gregerman and Wald, 1952; Östlunde, 1954; von Euler, 1961). The neurosecretion from corpus cardiacum of *P. americana* and *Rhodinus sp.* is related to adrenaline (Barton Browne *et al.*, 1961; Wigglesworth, 1954). The present investigation conforms to the belief of Unger (1957) that noradrenaline is not present in the nerve cord of roaches. The exact nature of the catecholamines present in the roach brain (Frontali, 1968) has yet to be determined chemically.

Four possible functions have been proposed for the AChE in cholinergic nervous systems (Koelle, 1963; Volle and Koelle, 1961): (1) temporal or spatial limitation of the transmitter action of ACh at the postsynaptic site; (2) rapid hydrolysis of ACh to provide an immediate source of choline for uptake by the presynaptic terminals and synthesis to ACh; (3) protection of the presynaptic terminals against reactivation by self-liberated ACh; (4) prevention of accumulation of activating concentrations of ACh during the resting stage.

Confirmation of the first and fourth proposal can be obtained by the results of anticholinesterases (Figs. 13, 14; Tables 1, 2), only on the ground that ACh is a transmitter that diffuses across the synaptic cleft to act on a postsynaptic receptor site in the roach cercal ganglion. The synaptic after-discharge, facilitation and electrical quiescence were probably due to the accumulation of endogenous ACh on the postsynaptic sites. It is also possible that ACh caused another transmitter substance to be released and act on the postsynaptic sites, and since the ACh was unable to be hydrolyzed, it blocked all the sites that would release the stimulatory transmitter.

No evidence was obtained to support the second proposal. When choline was applied to the nerve cords with or without AChE-inactivation by TEPP, it either could not restore the electrical activity to its normal state or it only accelerated the rate of failure of postganglionic firing. Nothing can be said about the third proposal until more is known about the synapses in insects.

The present investigation brought out the effectiveness of the "biochemical barrier". Indeed, such a barrier may be highly advantageous for the insects, because of their open circulatory system. Ginetsinskii (1947) concluded that in the course of evolution, reduction occurs in the cholinoreceptive zone, and in the number of drugs to which the cholinoreceptive zone is sensitive, i.e., an increase in the precision and specificity of cholinoreception. Such may be the case for the insects. The "biochemical barrier" and the cholinoreceptive specificity may explain the well protected synapses in insect ganglion.

The experiments with 2-PAM (Fig. 15) point to the significance of AChE in synaptic transmission, although 2-PAM was also shown to reactivate axonal transmission (Dettbarn, Rosenberg and Nachmansohn, 1964). The concentration of AChE in a given neuron reflects the extent of the participation of ACh in the synaptic transmission (Koelle, 1962). Ehrenpreis (1967) pointed out the possible function of AChE as part of the receptor for ACh and other cholinergic compounds.

The slow *in vivo* inhibition of AChE by carbamates indicates the effective concentrations of ACh at the active sites of enzymes are normally very low (Winteringham, 1966). Stimulated central activity may, accordingly, result in relatively large increases in effective substrate concentrations at the enzyme sites, but this would not be reflected in detectable changes in total ACh content of the central nervous system, and may only involve a small fraction of the total ACh (Winteringham, 1966).

Colhoun (1959a), and Smallman and Fisher (1958) observed an increase of ACh content in roach nerve cords treated with TEPP. Treating the roach with DDT also resulted in a marked accumulation of ACh although the AChE was not inhibited (Colhoun, 1959a, b; Tobias *et al.*, 1946). But the elevation of ACh content in the nerve cords treated with TEPP could be resolved into 2 peaks, an initial peak occurring at the first half hour, and a second peak at 24 hours (Colhoun, 1959a). The initial peak was absent in the DDT-treated nerve cords. It was postulated that the ACh increases in late TEPP and DDT poisoning were the result of ACh synthesis in a form not available to AChE (Colhoun, 1959a), and that DDT might accelerate the rate of ACh synthesis (Lewis, 1953).

A neuroactive substance was released into the blood of the roach during the course of DDT poisoning (Colhoun, 1959b; Sternburg *et al.*, 1959). It was suggested that the source of the toxicant was apparently the CNS itself during periods of great nervous activity, whether initiated by electrical stimulation or by constant bombardment of sensory-central synapses due to excessive afferent impulses generated in the sensory nerves by direct action of DDT (Sternburg *et al.*, 1959). It seems possible that ACh itself could act as a releaser of the neuroactive substance.

Spontaneous recovery of AChE activity in organophosphate-treated insects has been demonstrated, but the recovery was a result of AChE synthesis rather than a reversal of inhibited AChE activity (Brady and Sternburg, 1966).

The considerable variations of AChE concentration in the roach ganglion (Table 1) may explain the occasional ineffectiveness of ACh and some other related drugs at the same dosage. But that the electrical activity of one roach nerve cord could continue in the presence of high concentration of TEPP was perplexing, unless there is an enzyme in the nerve cord that can hydrolyze TEPP. It was demonstrated that diisopropyl fluorophosphate (DEP) was hydrolyzed readily by a phosphatase to diisopropyl phosphoric acid inside a squid axon (Hoskin, Rosenberg and Brazin, 1966).

Since the whole field of insect neuropharmacology is "conditioned" by rather well documented experiments with mammals (E. H. Colhoun, personal communication), there are limitations in interpreting these data.

ACKNOWLEDGMENTS

I am greatly indebted to R. H. Gooding for advice and supervision, and to B. Hocking for his encouragement and suggestions. I am grateful to F. R. Calaresu, and C. Heath, Department of Physiology; and to W. G. Evans, Department of Entomology, for their advice. I sincerely thank C. W. Nash, Department of Pharmacology, for his advice and facilities for the spectrofluorometric work; and R. J. Reiffenstein, Department of Pharmacology, for his advice and gift of some drugs. Thanks are also due to E. H. Colhoun, Department of Pharmacology, University of Western Ontario, for his helpful criticism of the manuscript, G. Chen, Parke, Davis & Company, for the gift of DMPP, and Cyanamid of Canada for partial support of the research.

REFERENCES

Albert, A. 1965. Selective toxicity. Methuen, London. 394 p.

Ambache, N. 1955. The use and limitation of atropine for pharmacological studies on autonomic effectors. Pharmacol. Rev. 7: 467-500.

Barlow, R. B. 1964. Introduction to chemical pharmacology. Methuen, London. 455 p.

Barton Brown, L., L. F. Dobson, E. S. Hodgson and J. K. Kiraly. 1961. Adrenergic properties of the cockroach corpus cardiacum. Gen. comp. *Endocrinol.* 1: 232-236.

Bebbington, A. and R. W. Brimblecombe. 1965. Muscarinic receptors in the peripheral and central nervous systems, p. 143-172. *In* N. J. Harper and A. B. Simmonds (eds.). Advances in drug research, vol. 2. Academic Press, New York.

Birks, R. and F. C. MacIntosh. 1961. Acetylcholine metabolism of a sympathetic ganglion. Can. J. Biochem. Physiol. 39: 787-827.

Bisset, G. W., J. F. D. Frazer, M. Rothschild, and M. Schachter. 1960. A pharmacologically active choline ester and other substances in the garden tiger moth, *Arctia caja* (L.). Proc. R. Soc., B. 152: 255-262.

Boura, A. L. A. and A. F. Green. 1965. Adrenergic neurone blocking agent. Ann. Rev. Pharmacol. 5: 183-212.

Brady, U. E. and J. Sternburg. 1966. Recovery of the cholinesterase activity in organophosphate treated insects. J. Ins. Physiol. 12: 1171-1185.

Brodie, B. B. and P. A. Shore. 1957. A concept for a role of serotonin and norepinephrine as chemical mediators in the brain. Ann. N. Y. Acad. Sci. 66: 631-642.

Burn, J. H. 1966. Adrenergic transmission. Pharmacol. Rev. 18: 459-470.

Burn, J. H. and M. J. Rand. 1960. Transmission failure in sympathetic nerves produced by hemicholinium. Brit. J. Pharmacol. 15: 588-600.

Burn, J. H. and M. J. Rand. 1965. Acetylcholine in adrenergic transmission. Ann. Rev. Pharmacol. 5: 163-182.

Cameron, M. C. 1953. Secretion of an orthodiphenol in the corpus cardiacum of the insect. Nature, Lond. 172: 349-350.

Chadwick, L. E. 1963. Actions on insects and other invertebrates, p. 741-748. *In* G. B. Koelle (ed.). Cholinesterases and anticholinesterases. Springer-Verlag, Berlin.

Chadwick. L. E. 1964. Inhibition of fly-head cholinesterase *in vitro* by pilocarpine and atropine. J. ins. Physiol. 10: 573-585.

Chadwick, L. E. and D. L. Hill. 1957. Inhibition of cholinesterase by di-isopropyl fluorophosphate, physostigmine and hexamethyl tetraphosphate in the roach. J. Neurophysiol. 10: 235-246.

Chang, S. C. and C. W. Kearns. 1961. The occurrence of acetylcholine in the nervous tissue of American cockroaches. Ann. ent. Soc. Amer. 54: 711-715.

Chang, V. and M. J. Rand. 1960. Sympathetic postganglionic cholinergic fibers. Brit. J. Pharmacol. 15: 56-66.

Chen, G., and R. Portman. 1954. Effect of 1, 1-dimethyl-4-phenyl piperazinium iodide on peristaltic reflexes of isolated guinea pig ileum. Proc. soc. exp. Biol. N. Y. 85: 245-248.

Chen, G., R. Portman and A. Wickel. 1951. Pharmacology of 1, 1-dimethyl-4-phenyl piperazinium iodide, a ganglionic stimulating agent. J. Pharmacol. 103: 330-336.

Colhoun, E. H. 1958a. Physical release of acetylcholine from the thoracic nerve cord of *Periplaneta americana* L. Nature, Lond. 181: 490.

Colhoun, E. H. 1958b. Acetylcholine in *Periplaneta americana* L. II. Acetylcholine and nervous activity. J. Ins. Physiol. 2: 117-127.

Colhoun, E. H. 1959a. Acetylcholine in *Periplaneta americana* L. III. Acetylcholine in roaches treated with tetraethyl pyrophosphate and 2, 2-bis(p-chlorophenyl)-1, 1-trichloroethane. Can. J. Biochem. 37: 160-272.

Colhoun, E. H. 1959b. Physiological events in organophosphorus poisoning. Can. J. Biochem. 37: 1127-1134.

Colhoun, E. H. 1960. Acetylcholine in *Periplaneta americana* L. IV. The significance of esterase inhibition in intoxication, acetylcholine levels, and nervous condition. Can. J. Biochem. 38: 1363-1367.

Colhoun, E. H. 1963a. Synthesis of 5-hydroxytryptamine in the American cockroach. Experientia 19: 9-10

Colhoun, E. H. 1963b. The physiological significance of acetylcholine in insects and observations upon other pharmacological substances, p. 1-46. *In* J. W. L. Beament, J. E. Treherne, and V. B. Wigglesworth (eds.). Advances in insect physiology, vol. 1. Academic Press, New York.

Colhoun, E. H. and E. Y. Spencer. 1959. Acetylcholine effects of gamma-carbomethoxypropyltrimethyl-ammonium bromide. Science 130: 504-505.

Costa, E., D. J. Boullin, W. Hammer, W. Vogel, and W. B. Brodie. 1966. Interactions of drugs with adrenergic neurons. J. Pharmacol. 18: 577-597.

Curtis, D. R., R. W. Ryall and J. C. Watkins. 1955. Cholinergic transmission in the mammalian central nervous system, p. 137-145. *In* G. B. Koelle, W. W. Douglas, A. Carlsson and V. Trcka (eds.). Pharmacology of cholinergic and adrenergic transmission. Macmillan, New York.

Dahl, E., B. Falck, C. von Mecklanburg, and H. Myhrberg. 1963. Adrenergic sensory neurons in invertebrates. Gen. comp. Endocrinol. 3: 693.

Dauterman, W. C., A. Talens and K. van Asperen. 1962. Partial purification and properties of fly-head cholinesterase. J. Ins. Physiol. 8: 1-14.

De Groat, W. C. and R. L. Volle. 1966a. The actions of the catecholamines on transmission in the superior cervical ganglion of the rat. J. Pharmacol. 154: 1-13.

De Groat, W. C. and R. L. Volle. 1966b. Interactions between the catecholamines and ganglionic stimulating agents in sympathetic ganglia. J. Pharmacol. 154: 200-215.

Dettbarn, W. and P. Rosenberg. 1966. Effect of ions on the efflux of acetylcholine from peripheral nerve. J. gen. Physiol. 50: 447-460.

Dettbarn, W., P. Rosenberg and D. Nachmansohn. 1964. Restoration by a specific chemical reaction of "irreversibly" blocked axonal electrical activity. Life Sci. 3: 55-60.

Eccles, R. M. and B. Libet, 1961. Origin and blockade of synaptic responses of curarized sympathetic ganglia. J. Physiol. 157: 487-503.

Engel, L. G. and R. W. Gerard. 1935. The phosphorus metabolism of invertebrate nerve. J. biol. Chem. 112: 370-392.

Ehrenpreis, S. 1967. Molecular aspects of cholinergic mechanisms, p. 1-78. *In* A. Burger (ed.). Drugs affecting the peripheral nervous system. Marcel Dekker, New York.

Euler, U. S. von. 1961. Occurrence of catecholamines in Acrania and invertebrates. Nature, Lond. 190: 170.

Feldberg, W. 1950. The role of acetylcholine in the central nervous system. Brit. med. Bull. 6: 312-321.

Frontali, N. 1968. Histochemical localization of catecholamines in the brain of normal and drug-treated cockroaches. J. Ins. Physiol. 14: 881-886

Gahery, Y. and J. Boistel. 1965. Study of some pharmacological substances which modify the electrical activity of the sixth abdominal ganglion of the cockroach, *Periplaneta americana*, p. 73-78. *In* J. E. Treherne and J. W. L. Beament (eds.). Insect central nervous system. Academic Press, New York.

Gardiner, J. E. 1961. The inhibition of acetylcholine synthesis in brain by a hemicholinium. Biochem. J. 81: 297-303.

Geber, G. L. and R. L. Volle, 1965. Ganglionic stimulating properties of aliphatic esters of choline and thiocholine. J. Pharmacol. 150: 67-74.

Ginetsinskii, A. G. 1947. Quoted by Magazanik *et al.* (1965).

Ginsborg, B. L. and S. Guerrero. 1964. On the action of depolarizing drugs on sympathetic ganglion cells of the frog. J. Physiol. 172: 189-206.

Gomori, G. 1953. Human esterases. J. Lab. clin. Med. 42: 445-453.

Goth, A. 1966. Medical pharmacology: principles and concepts. Mosby, Saint Louis. 668 p.

Gregerman, R. I. and G. Wald. 1952. The alleged occurrence of adrenaline in the mealworm. J. gen. Physiol. 35: 489-493.

Grollman, A. 1960. Pharmacology and therapeutics. Lea and Febiger, Philadelphia. 1079 p.

Hamberger, B., K.-A. Norberg and F. Sjöqvist. 1965. Correlated studies of monoamines and acetylcholinesterase in sympathetic ganglia, illustrating the distribution of adrenergic and cholinergic neurons, p. 41-54. *In* G. B. Koelle, W. W. Douglas, A. Carlsson, and V. Trcka (eds.). Pharmacology of cholinergic and adrenergic transmission. Macmillan, New York.

Hamberger, B., K.-A. Norberg and U. Ungestedt. 1965. Adrenergic synaptic terminals in autonomic ganglia. Acta Physiol. Scand. 64: 285-286.

Hess, A. 1958. Experimental anatomical studies of pathways in the severed central nerve cord of the cockroach. J. Morph. 103: 479-507.

Hobbiger, F. 1963. Reactivation of phosphorylated acetylcholinesterase, p. 921-988. *In* G. B. Koelle (ed.). Cholinesterases and anticholinesterase agents. Springer-Verlag, Berlin.

Hokin, M. R., L. E. Hokin and W. D. Shelp. 1960. The effects of acetylcholine on the turnover of phosphatidic acid and phosphoinositide in sympathetic ganglia and in various parts of the central nervous system *in vitro*. J. Gen. Physiol. 44: 217-226.

Holmes, R. and E. L. Robins. 1955. The reversal by oximes of neuromuscular block produced by anticholinesterase. Brit. J. Pharmacol. 10: 490-495.

Hoskin, F. C. G., P. Rosenberg and M. Brazin. 1966. Re-examination of the effect of DFP on electrical and cholinesterase activity of squid giant axon. Proc. Nat. Acad. Sci. Wash. 55: 1231-1235.

Hoyle, G. 1952. High blood potassium in insects in relation to nerve conduction. Nature, Lond. 169: 281-282.

Hoyle, G. 1953. Potassium ions and insect nerve muscle. J. exp. Biol. 30: 121-135.

Iyatomi, K. and K. Kanehisa. 1958. Localization of cholinesterase in the American cockroach. Jap. J. appl. Ent. 2: 1-10.

Jacobowitz, D. and G. B. Koelle. 1963. Demonstration of both acetylcholinesterase (AChE) and catecholamines in same nerve trunk. The Pharmacologist 5: 270.

Javik, M. E. 1965. Drugs used in the treatment of psychiatric disorders, p. 159-214. *In* L. Goodman and A. Gilman (eds.). The pharmacological basis of therapeutics. Macmillan, New York.

Kandel, E. R. and W. T. Frazier. 1967. Opposite synaptic actions mediated by different branches of an identifiable interneuron in *Aplysia*. Science 155: 346-349.

Khromov-Borisov, N. V. and M. J. Michelson. 1966. The mutual dispositions of locomotor muscles and the changes in their disposition in the course of evolution. Pharmacol. Rev. 18: 1051-1090.

Koelle, G. B. 1962. A new general concept of the neurohumoral functions of ACh and AChE. J. Pharm. Pharmacol. 14: 65-90.

Koelle, G. B. 1963. Cytological distribution and physiological functions of cholinesterases, p. 187-298. *In* G. B. Koelle (ed.). Cholinesterase and anticholinesterases. Springer-Verlag, Berlin.

Koelle, G. B. 1965. Neurohumoral transmission and the autonomic nervous system; anticholinesterase agents; parasympathomimetic agents, p. 399-476. *In* L. Goodman and A. Gilman (eds.). The pharmacological basis of therapeutics. Macmillan, New York.

Kopin, I. J. 1964. Storage and metabolism of catecholamines: the role of monoamine oxidase. Pharmacol. Rev. 16: 179-191.

Leach, G. D. H. 1957. Ganglionic blocking action of dimethylphenyl piperazinium (DMPP). J. Pharm. Pharmacol. 9: 747-751.

Lewis, S. E. 1953. Acetylcholine in blowflies. Nature, Lond. 172: 1004-1005.

Loomis, J. 1956. The effect of an aldoxime on acute serin poisoning. J. Pharmacol. 18: 123-128.

MacIntosh, F. C. 1961. Effect of HC-3 on acetylcholine turnover. Fed. Proc. 20: 562-568.

MacIntosh, F. C., R. I. Birks and P. B. Sastry. 1956. Pharmacological inhibition of acetylcholine synthesis. Nature, Lond. 178: 1181.

Magazanik, L. G., N. R. Fruentov, E. K. Roshkova, R. S. Rybolovlev and M. Ya. Mikhel'son. 1965. On the evolution of cholinoreceptive sites of locomotor muscle, p. 113-127. *In* G. B. Koelle, W. W. Douglas, A. Carlsson and V. Trcka (eds.). Pharmacology of cholinergic and adrenergic transmission. Macmillan, New York.

McKinstry, D. N. and G. B. Koelle. 1967. Acetylcholine release from the cat superior cervical ganglion by carbachol. J. Pharmacol. 157: 319-327.

McLennan, H. 1963. Synaptic transmission. W. B. Saunders, Philadelphia. 134 p.

Mikalonis, S. J. and R. H. Brown. 1941. Acetylcholine and cholinesterase in the insect central nervous system. J. cell.comp. Physiol. 18: 401-402.

Milburn, N., E. A. Weiant, and K. D. Roeder. 1960. The release of efferent activity in the roach, *Perplaneta americana*, by extracts of the corpus cardiacum. Biol. Bull. 118: 111-119.

Nickerson, M. 1949. The pharmacology of adrenergic blockade. Pharmacol. Rev. 1: 27-101.

Nickerson, M. 1965. Adrenergic receptor mechanism, p. 303-315. *In* G. B. Koelle, W. W. Douglas, A. Carlsson and V. Trcka (eds.). Pharmacology of cholinergic and adrenergic transmission. Macmillan, New York.

Norberg, K.-A. and F. Sjöqvist. 1966. New possibilities for adrenergic modulation of ganglionic transmission. Pharmacol. Rev. 18: 743-751.

O'Brien, R. D. 1957. Esterases in the semi-intact cockroach. Ann. ent. Soc. Amer. 50: 223-229.

O'Brien, R. D. 1959a. Comparative toxicology of some organophosphorus compounds in insects and mammals. Can. J. Biochem. Physiol. 37: 1113-1122.

O'Brien, R. D. 1959b. Effect of ionization upon penetration of organophosphates to the nerve cord of the cockroach. J. econ. Ent. 52: 812-816.

Östlunde, E. 1954. The distribution of catecholamines in lower animals and their effects on the heart. Acta physiol. Scand. 31: suppl. 112: 1-65.

Owen, C. and B. Falck. 1965. Localization of neuronal monoamines at the cellular level, p. 165-183. *In* G. B. Koelle, W. W. Douglas, A. Carlsson and V. Trcka (eds.). Pharmacology of cholinergic and adrenergic transmission. Macmillan, New York.

Page, I. H. 1958. Serotonin (5-hydroxytryptamine), the last four years. Physiol. Rev. 58: 277-335.

Paton, W. D. M. 1962. A theory of drug action based on the rate of drug-receptor combination. Proc. roy. Soc., B. 154: 21-69.

Pletscher, A. 1966. Monoamine oxidase inhibitors, Pharmacol. Rev. 18: 121-129.

Pringle, J. W. S. 1938. Proprioception in insects. I. A new type of mechanical receptor from the palps of the cockroach. J. exp. Biol. 15: 101-113.

Prosser, C. L. 1940. Action potentials in the nervous system of the crayfish. Effects of drugs and salts upon synaptic transmission. J. cell. comp. Physiol. 16: 25-38.

Pumphrey, R. J. and A. F. Rawdon-Smith. 1937. Synaptic transmission of nerve impulses through the last abdominal ganglion of the cockroach. Proc. R. Soc., B. 122: 106-118.

Roeder, K. D. 1948a. Organization of the ascending giant fiber system in the cockroach (*Periplaneta americana*). J. exp. Zool. 108: 243-261.

Roeder, K. D. 1948b. The effect of anticholinesterases and related substances on nervous activity in the roach. Johns Hopk. Hosp. Bull. 83: 587-603.

Roeder, K. D. 1953. Electric activity in nerves and ganglia, p. 423-462. *In* K. D. Roeder (ed.). Insect physiology. John Wiley and Sons, Inc., New York.

Roeder, K. D. 1962. Neural mechanisms of animal behavior. Am. Zoologist 2: 105-115.

Roeder, K. D. 1963. Nerve cells and insect behavior. Harvard University Press, Massachusetts. 189 p.

Roeder, K. D. and N. K. Kennedy. 1955. The effect of certain trisubstituted phosphine oxides on synaptic conduction in the roach. J. Pharmacol. 114: 211-230.

Roeder, K. D. and S. Roeder. 1939. Electrical activity, nerve cord, roach. J. cell. comp. Physiol. 14: 1-12.

Shore, P. A. and J. Olin, 1958. Identification and chemical assay of norepinephrine in brain and other tissues. J. Pharmacol. 122: 295-300.

Shore, P. A., J. A. R. Mead, R. G. Kuntzman, S. Spector and B. B. Brodie. 1957. On the physiological significance of monoamine oxidase in brain. Science 126: 1063-1064.

Smallman, B. N. 1956. Mechanisms of acetylcholine synthesis in the blowfly. J. Physiol. 132: 343-357.

Smallman, B. N. and R. W. Fisher. 1958. Effect of anticholinesterases on acetylcholine levels in insects. Can. J. Biochem. Physiol. 36: 575-594.

Smith, D. S. 1965. Synapses in the insect nervous system, p. 39-57. *In* J. E. Treherne and J. W. L. Beament (eds.). Insect central nervous system. Academic Press, New York.

Smith, D. S. and J. E. Treherne. 1965. The electron microscopic localization of cholinesterase activity in the central nervous system of an insect, *Periplaneta americana* L. J. cell. Biol. 26: 445-465.

Sternburg, J., S. C. Chang and C. W. Kearns. 1959. The release of a neuroactive agent by the American cockroach after exposure to DDT or electrical stimulation. J. econ. Ent. 52: 1070-1076.

Takeshige, C. and R. L. Volle. 1962. Bimodal response of sympathetic ganglia to acetylcholine following eserine or repetitive preganglionic stimulation. J. Pharmacol. 138: 66-73.

Takeshige, C. and R. L. Volle. 1963. Cholinoreceptive sites in denervated sympathetic ganglia. J. Pharmacol. 141: 206-213.

Takeshige, C. and R. L. Volle. 1964. A comparison of the ganglion potentials and block produced by acetylcholine and tetramethylammonium. Brit. J. Pharmacol. 23: 80-89.

Tauc, L. and H. M. Gershenfeld. 1962. A cholinergic mechanism of inhibitory synaptic transmission in a molluscan nervous system. J. Neurophysiol. 25: 236-262.

Tobias, J. M., J. J. Kollros and J. Savit. 1946. Acetylcholine and related substances in cockroach, fly and crayfish and the effect of DDT. J. cell. comp. Physiol. 28: 159-182.

Treherne, J. E. 1961a. Sodium and potassium fluxes in the abdominal nerve cord of the cockroach, *P. americana* L. J. exp. Biol. 38: 315-322.

Treherne, J. E. 1961b. The movement of sodium ions in the isolated abdominal nerve cord of the cockroach, *Periplaneta americana*. J. exp. Biol. 38: 629-636.

Treherne, J. E. 1961c. The efflux of sodium ions from the last abdominal ganglion of cockroach, *P. americana* L. J. exp. Biol. 38: 729-736.

Treherne, J. E. 1962a. Transfer of substances between the blood and central nervous system in vertebrate and invertebrate animals. Nature, Lond. 196: 1181-1183.

Treherne, J. E. 1962b. The distribution and exchange of some ions and molecules in the central nervous system of *Periplaneta americana*. J. exp. Biol. 39: 193-217.

Treherne, J. E. 1965b. The chemical environment of the insect central nervous system, p. 21-30. *In* J. E. Treherne and J. W. L. Beament (eds.). Insect central nervous system. Academic Press.

Treherne, J. E. 1966. The neurochemistry of arthropods. Cambridge University Press, Cambridge. 149 p.

Treherne, J. E. and D. S. Smith. 1965a. The penetration of acetylcholine into the central nervous system of an instect (*Periplaneta americana* L.). J. exp. Biol. 43: 13-22.

Treherne, J. E. and D. S. Smith. 1965b. The metabolism of acetylcholine in the intact central nervous system of an insect (*Periplaneta americana* L.). J. exp. Biol. 43:441-454.

Twarog, B. M. and K. D. Roeder. 1956. Properties of the connective tissue sheath of the cockroach abdominal nerve cord. Biol. Bull. 111: 278-286.

Twarog, B. M. and K. D. Roeder. 1957. Pharmacological observations on the desheathed last abdominal ganglion of the cockroach. Ann. ent. Soc. Amer. 50: 231-237.

Udenfriend, S. 1964. Fluorescence assay in biology and medicine. Academic Press, New York. 517 p.

Unger, H. 1957. Untersuchunger zur neurohormonalen Steuerung der Herzatigkeit bei Schaben. Biol. Zbl. 76: 204-225.

Van Asperen, K. 1962. A study of housefly esterase by means of a sensitive colorimetric method. J. Ins. Physiol. 8: 401-416.

Volle, R. L. 1965. Interactions of cholinomimetic and cholinergic blocking drugs at sympathetic ganglia, p. 85-94. *In* G. B. Koelle, W. W. Douglas, A. Carlsson and V. Trcka (eds.). Pharmacology of cholinergic and adrenergic transmission. Macmillan, New York.

Volle, R. L. and G. B. Koelle. 1961. The physiological role of acetylcholinesterase (AChE) in sympathetic ganglia. J. Pharmacol. 133: 223-240.

Weiant, E. A. 1958. Control of spontaneous activity in certain efferent nerve fibers from the metathoracic ganglion of the cockroach *Periplaneta americana*. Proc. 10*th* Int. Cong. Ent. 2: 81-82.

Welsh, J. H. 1957. Serotonin as a possible neurohumoral agent: evidence obtained in lower animals. Ann. N. Y. Acad. Sci. 66: 618-630.

Welsh, J. H. and H. T. Gordon. 1947. The mode of action of certain insecticides on arthropod axon. J. cell. comp. Physiol. 30: 147-172.

Wigglesworth, V. B. 1954. Neurosecretion and the corpus cardiacum of insects. Pub. Staz. Zool. Napoli 24: 41-45.

Wigglesworth, V. B. 1958. The distribution of esterase in the nervous system and other tissues of the insect *Rhodnius prolixus.* Quart. J. micro. Sci. 99: 441-450.

Wilson, I. B. 1960. Acetylcholinesterase, p. 501-517. *In* P. Boyer, H. Lardy and K. Myrback (eds.). The enzymes, vol. 4. Academic Press, New York.

Wilson, I. B. and S. Ginsburg. 1958. Reactivation of alkylphosphate inhibited acetylcholinesterase by bis quaternary derivatives of 2-PAM and 4-PAM. Biochem. Pharmacol. 1: 200-206.

Winteringham, F. P. W. 1966. Metabolism and significance of acetylcholine in the brain of the adult housefly, *Musca domestica* L. J. Ins. Physiol. 12: 909-924.

Winton, M. Y., R. L. Metcalf and T. R. Fukuto. 1958. The use of acetylthiocholine in the histochemical study of action of organophosphorus insecticides. Ann. ent. Soc. Amer. 51: 436-448.

Yamasaki, T. and T. Narahashi. 1960. Synaptic transmission in the last abdominal ganglion of the cockroach. J. Ins. Physiol. 4: 1-13.

ERRATA – *Quaestiones entomologicae*. 1969: 5(2)

"A revision of the species of the genus *Evarthrus* Le Conte (Coleoptera: Carabidae)" by Richard Freitag.

Page 96. Key, couplet 10. The species *Evarthrus vinctus* Le Conte is known from Tennessee, Georgia, North and South Carolina, not from Mississippi.

Page 207. Locality records for *Evarthrus texensis* Freitag are indicated on Fig. 128 by filled half-circles, not by inverted triangles.

Page 211. On Fig. 138, the numbers 1 – 8 represent centers of concentration, not centers of speciation.

Quaestiones entomologicae

A periodical record of entomological investigations,
published at the Department of Entomology,
University of Alberta, Edmonton, Canada.

VOLUME V NUMBER 4 OCTOBER 1969

QUAESTIONES ENTOMOLOGICAE

A periodical record of entomological investigation published at the Department of Entomology, University of Alberta, Edmonton, Alberta.

Volume 5 Number 4 27 October 1969

CONTENTS

OBSERVATIONS ON THE BIOLOGY OF THE ADULT FEMALE MOSQUITOES (DIPTERA:CULICIDAE) AT GEORGE LAKE, ALBERTA, CANADA

PETER GRAHAM
Department of Biology
Thomas More College
Covington, Kentucky 41017
U.S.A.

Quaestiones entomologicae
5: 309-339 1969

The seasonal distribution of the more important mosquito species is discussed. No species was found to be particularly abundant inside buildings and mosquitoes did not appear to enter buildings to digest their blood meals, but appear to digest these near the feeding site. A significant difference was found between the occurrence of certain species at the lake shore and in the forest. Mosquitoes were found to be relatively inactive when in stages II-IV of Christophers and 3-5 of Sella of the gonotrophic cycle. Retention of eggs by parous females was found to be widespread and to occur in 7% of the parous females.

A key to the adult female mosquitoes of central Alberta is given.

During studies comparing the effectiveness of different mosquito sampling methods at the George Lake field site, in 1965, 1966 and 1967, a number of observations on the biology of the adult female mosquitoes was made. As these observations were incidental to the main study, they are somewhat superficial, but I believe they are worth recording as relatively little is known about the biology of mosquitoes in this area.

The methods of collection and the study area are described elsewhere (Graham, 1969).

NOTES ON THE IDENTIFICATION OF AND KEY TO THE ADULT FEMALES OF CENTRAL ALBERTA SPECIES OF MOSQUITOES

No key to mosquitoes was found to be completely satisfactory for the identification of the adult female mosquitoes taken at George Lake. I, therefore, constructed a key, based largely on the works of Barr (1958), Carpenter and LaCasse (1955), Rempel (1953) and

Vockeroth (1954b), which includes all species of mosquito recorded from Edmonton, George Lake and Flatbush. It includes most if not all species of mosquito likely to be found in the parkland and boreal forest regions of the province. Fig. 1 illustrates characteristics used in the key. This key may prove useful until such time as a complete taxonomic study of Alberta species of mosquitoes is carried out. Such a study is required before a full understanding of this mosquito fauna can be achieved.

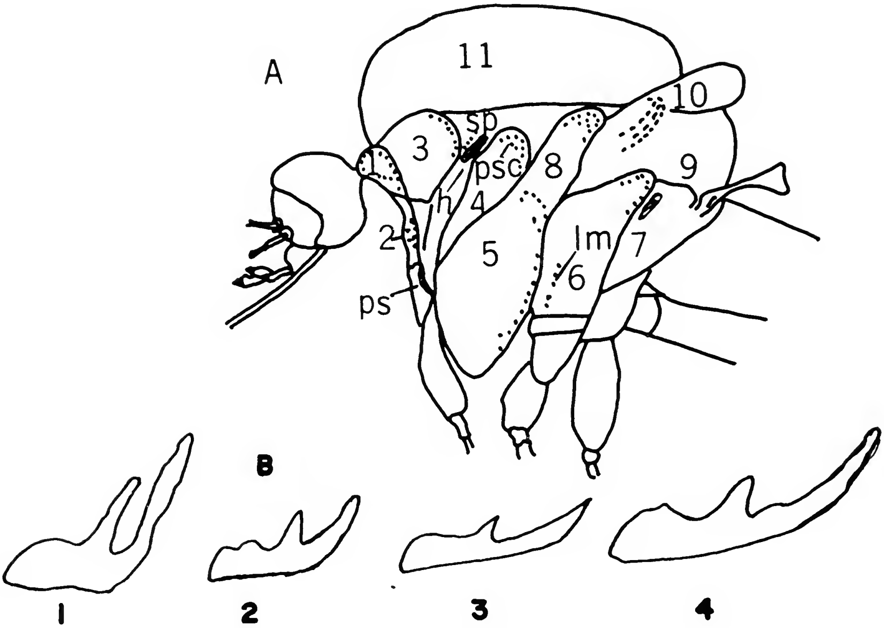


FIG. 1. A. Lateral view of a generalized mosquito thorax. (After Steward and McWade, 1961).
B. Claw characters of *Aedes* species (from Vockeroth, 1954b).

KEY A.			
1.	Pronotum	7.	Metepisternum
2.	Proepisternum	8.	Prealar area
3.	Post pronotum	9.	Postnotum
4.	Mesanepisternum	10.	Scutellum
5.	Sternopleuron	11.	Mesonotum
6.	Mesepimeron		
h.	Hypostigial scale patch	lm.	Lower mesepimeral bristles
ps.	Post coxal scale patch	psc.	Post spiracular bristles
sp.	Spiracular bristles		

KEY B.
1. *Aedes excrucians*
2. *A. fitchii*
3. *A. riparius*
4. *A. flavescens*

Keys to the adult female mosquitoes of central Alberta

Key to Genera. –

1. Palps almost as long as proboscis; scutellum rounded . . . *Anopheles earlei,* p. 316
– Palps short, less than 1/3 length of proboscis; scutellum trilobed 2
2. (1) Spiracular bristles present . . . . *Culiseta,* p. 316
– Spiracular bristles absent 3
3. (2) Post spiracular bristles present; tip of abdomen pointed . . . . *Aedes,* p. 322
– Post spiracular bristles absent; tip of abdomen rounded 4
4. (3) Wings with many pale scales, wing scales broad . . . .
. . . . *Coquillettidia perturbans,* p. 322
– Wing scales all dark and narrow . . . . *Culex,* p. 322

Key to Culex species (from Rempel, 1953)

1. Tarsal segments ringed with white . . . . *tarsalis,* p. 322
– Tarsal segments not ringed with white 2
2. (1) White bands on apices of abdominal terga . . . . *territans,* p. 322
– White bands on bases of abdominal terga . . . . *restuans,* p. 322

Key to Culiseta species

1. Hind tarsal segments ringed with white 2
– Hind tarsal segments not ringed with white 5
2. (1) Wing scales forming conspicuous spots 3
– Wings without conspicuous spots 4
3. (2) Tarsal white rings broad; very large species . . . . *alaskaensis,* p. 316
– Tarsal white rings narrow . . . . *incidens,* p. 320
4. (2) Abdominal pale bands on bases of terga only, white in color . . . .
. . . . *C. morsitans dyari,* p. 321
– Abdominal pale bands on both apices and bases of terga, usually pale yellow brown in color . . . . *C. sylvestris minnesotae,* p. 321
5. (1) Costa of wing with mixed pale and dark scales . . . . *inornata,* p. 320
– Costa with dark scales only . . . . *impatiens,* p. 320

Key to Aedes species (based on Vockeroth, 1954b)

1. Hind tarsal segments ringed with white 2
– Hind tarsal segments not ringed with white 11
2. (1) Tarsal white rings on both apices and bases of tarsal segments 3
– Tarsal white rings on bases of tarsal segments only 5
3. (2) Wings with both dark and light scales on most veins 4
– Wing scales entirely dark . . . . *canadensis,* p. 325
4. (3) Dark and light scales equally distributed on veins . . . . *campestris,* p. 324
– Third vein (R4+5) with more dark scales than 2nd (R2+3) or 4th(M). . . . .
. . . . *dorsalis,* p. 325
5. (2) Tarsal white rings very narrow, ¼ or less than length of segment . . . .
. . . . *vexans,* p. 324

– Tarsal white rings broader, at least 1/3 of length of segment 6

6. (5) Large yellow species; abdominal terga almost completely yellow scaled; tarsal claw as in Fig. 1B 4 .... *flavescens,* p.326

– Not as above, abdominal terga with abundant dark scales 7

7. (6) Tarsal claw large, main claw almost parallel to accessory tooth and slightly sinuate, Fig. 1B 1 .... *excrucians,* p.325

– Tarsal claw smaller, not sharply bent beyond tooth 8

8. (7) Mesonotum with some contrasting markings; tarsal claw with long accessory tooth, Fig. 1B 2 9

– Mesonotum almost uniform yellow brown; tarsal claw with short accessory tooth, Fig. 1B 3 .... *riparius,* p.327

9. (8) Palps and torus with some white scales; lower mesepimeral bristle 1, 2 or absent .... *fitchii*,* p.325

– Palps and torus usually without white scales; lower mesepimeral bristles 3 or more 10

10. (9) Palps lacking hairs on basal half of apical segment at inner edge .... *increpitus*,* p.326

– Palps with hairs on basal half of apical segment at inner ventral edge .... *stimulans*,* p.327

11. (1) Fore coxa with a patch of brown scales on anterior surface; small species .... *cinereus,* p.324

– Fore coxa with patch of white scales on anterior surface 12

12. (11) Wing scales distinctly bicoloured 13

– Wing scales all dark or with pale scales restricted to base of costa 14

13. (12) Wings with pale and dark scales intermixed, dark predominating; lower mesepimeral bristles usually present .... *niphadopsis*

– Wing veins alternating black and white scaled; lower mesepimeral bristles absent .... *spenceri,* p.327

14. (13) Post-coxal scale patch present 15

– Post-coxal scale patch absent 21

15. (14) Hairy species, postpronotum with setae scattered over posterior half .... *impiger*

– Less hairy species, postpronotal setae restricted to a single or irregular double row along posterior margin 16

16. (15) Sides of mesonotum silvery grey; base of costa with numerous white scales in a conspicuous patch 17

– Sides of mesonotum yellow or dark; base of costa with only a few or no white scales 19

17. (16) White scales on costa covering basal 1/7 .... *cataphylla,* p.325

– White scales on costa restricted to extreme base 18

18. (17) Sternopleuron with scales extended to anterior angle; mesonotum with numerous white scales giving a "frosted" appearance, medium strip indistinct .... *trichurus,* p.327

– Sternopleuron with scales extending half way to anterior angle; mesonotum with distinct median brown stripe .... *implicatus,* p.326

---

*Adult females of these species cannot be distinguished with certainty.

19. (16) Bristles of scutellum and mesonotum black; postmetasternal membrane with 15 or more scales . . . . *pionips*, p. 326
— Bristles of scutellum and mesonotum yellow or bronze; postmetasternal membrane bare or with less than 12 scales 20
20. (19) Base of costa with distinct patch of white scales . . . . *hexodontus*, p. 326
— Base of costa with no or few scattered white scales at most . . . . . *punctor*, p. 327
21. (14) Hypostigial scale patch present . . . . *pullatus*, p. 327
— Hypostigial scale patch absent 22
22. (21) Scales on sternopleuron extended to anterior angle; mesepimeron scaled to near lower margin; mesonotum with contrasting dark lines 23
— Scales of sternopleuron extended half way to anterior angle; lower 1/3 of mesepimeron bare; mesonotum usually uniform yellow brown . . . . . *intrudens*, p. 326
23. (22) Bristles of scutellum and mesonotum bright yellow; abdominal white bands indistinct or absent . . . . *diantaeus*, p. 325
— Bristles of scutellum and mesonotum black or bronze; abdominal white bands distinct 24
24. (23) Lower mesepimeral bristles present . . . . *communis*, p. 325
— Lower mesepimeral bristles absent . . . . *sticticus*, p. 327

Notes on identifications of adult females. – The characters given in the key should enable most specimens of adult female mosquitoes from central Alberta to be identified, provided they are not badly rubbed, but some qualifications and explanations are necessary.

Central Albertan species of *Anopheles, Culex,* and *Coquillettidia* present no problems and even badly rubbed specimens of these genera can usually be determined. The only confusion likely in *Culiseta* is that rubbed specimens of *C. sylvestris minnesotae* Barr may be mistaken for *C. morsitans dyari* (Coquillett). However, a close examination will usually reveal a few pale scales on the apices of the terga.

The genus *Aedes* presents most of the identification problems and all specimens unidentified in this study were in this genus. *Aedes cinereus* Meigen is best distinguished by the brown patch of scales on the fore coxa. A character often given in keys, the absence of white bands on the abdominal terga is unreliable in central Alberta; Carpenter and LaCasse (1955: 266) state that the abdomen of this species is as follows: "First tergite with a median patch of brown scales, a few pale scales intermixed; remaining tergites brown without pale bands or with narrow partial or complete bands"; the specimen they figure has complete bands. Forty four specimens of *A. cinereus* collected at George Lake in 1965 and 1966 were examined. Of these 14 had complete bands, 14 had no bands, and 16 had incomplete bands. Specimens of *A. cinereus* are likely to be confused with small specimens of *Aedes intrudens* (Dyar) which have white fore coxal scale patches, and specimens of *Aedes vexans* (Meigen) which have pale bands on the tarsi.

In the subgenus *Ochlerotatus* the species with pale bands on both apices and bases of the tarsal segments are no problem. The "*stimulans*" group, those with bands only on the bases of the tarsal segments, are difficult to separate. Claw characters distinguish *A. excrucians* (Walker) and *A. riparius* Dyar and Knab from the others. *A. flavescens* (Muller) can only be confused with *A. riparius* and then only when rubbed. Specimens of *A. fitchii* (Felt and Young), *A. stimulans* (Walker) and *A. increpitus* Dyar are easily separated from other band-legged species by claw characters, but are impossible to distinguish from each other with any certainty. The characters in the key are all unreliable. In this study all doubtful specimens were referred to *A. fitchii* since larval surveys and other work (Happold, 1965a and 1965b; Wada, 1965) have shown this to be by far the most abundant species of the three in central Alberta and the larvae of *A. fitchii* only have been found at George Lake.

Black legged *Ochlerotatus* are a difficult group. *A. punctor* (Kirby) and *A. hexodontus* Dyar occur in two forms: "tundra" type with uniform yellow brown mesonota and "*punctor*" type which have contrasting lines on their mesonota. Wada (1965) considered the best way to distinguish these two species was the presence of a white spot on the base of the costa of *A. hexodontus*, but Jenkins and Knight (1950) state that *A. punctor* "tundra" type may also have a few white scales on the costal base. The criterion I used was – a conspicuous white spot on the base of the costa – *A. hexodontus;* none or only a few scattered white scales on the base of the costa – *A. punctor.*

Vockeroth (1952, 1954b) has discussed the separation of *A. pionips* Dyar from *A. communis* (De Geer). The presence of a postcoxal scale patch in *A. pionips* appears to be the best character. I could find no completely satisfactory way of distinguishing *A. pionips* from *A. punctor* or *A. hexodontus*. The black mesonotal bristles are usually adequate but some specimens of *A. punctor* and *A. hexodontus* have dark bronze bristles. These may be separated with difficulty by the characters given by Beckel (1954).

Specimens of *A. intrudens*, *A. communis*, and *A. sticticus* (Meigen) present some problems of differentiation. *A. intrudens* is the only species whose members lack postcoxal scale patches which normally lack contrasting lines on the mesonotum, but a few individuals have indistinct lines on the mesonotum and closely resemble *A. communis*, and a few of these may lack lower mesepimeral bristles and resemble *A. sticticus.* The scale patch on the sternopleuron which only reaches half way to the interior angle in *A. intrudens* will distinguish these. The presence of lower mesepimeral bristles distinguishes specimens of *A. communis* from those of *A. sticticus* and the bright yellow mesonotal bristles and incomplete abdominal bands distinguish specimens of *A. diantaeus* Howard, Dyar and Knab from other species without a postcoxal scale patch.

DIVERSITY

Twenty nine species of mosquitoes have been recorded from the George Lake field site. Nineteen species were taken in 1965, 27 in 1966 and 25 in 1967. The species found and their relative abundance are shown in Table 1. Pucat (1965) records 38 species of Culicinae from Alberta.

Seven species made up 80% of the 1966 collections. These were: *Culiseta inornata* (Williston), *Aedes excrucians, A. fitchii, A. communis, A. punctor, A. riparius* and *A. vexans*. This preponderance of a few species was expected from the work of Williams (1964) and has been recorded in northern mosquitoes by Happold (1965a, 1965b) in Alberta, and by Skiersca (1965) in Poland, as well as by other authors elsewhere.

Table 1. Mosquito species collected at George Lake in 1965, 1966 and 1967, with their relative abundance.

Genus *Anopheles* Meigen, 1818
A. earlei Vargas, 1943 c
Genus *Culiseta* Felt, 1904
Subgenus *Culiseta* Felt, 1904
C. alaskaensis (Ludlow), 1906 fc
C. inornata (Williston), 1893 a
Subgenus *Culicella* Felt, 1904
C. sylvestris minnesotae Barr, 1957 fc
C. morsitans dyari (Coquillett). 1901 p
Genus *Culex* Linnaeus, 1758
Subgenus *Culex* Linnaeus, 1758
C. tarsalis Coquillett, 1896 p
Subgenus *Neoculex* Dyar, 1905
C. territans Walker, 1856 c
Genus *Coquillettidia* Dyar, 1905
C. perturbans (Walker), 1856 c
Genus *Aedes* Meigen, 1818
Subgenus *Aedes* Meigen, 1818
A. cinereus Meigen, 1818 c
Subgenus *Aedimorphus* Theobald, 1903
A. vexans (Meigen), 1830 Va
Subgenus *Ochlerotatus* Lynch Arribalzaga, 1891
A. canadensis (Theobald), 1901 r
A. cataphylla Dyar, 1916 p
A. communis (De Geer), 1776 c
A. diantaeus Howard, Dyar & Knab, 1913 p
A. dorsalis (Meigen), 1830 p
A. excrucians (Walker), 1856 Va
A. fitchii (Felt & Young), 1904 a
A. flavescens (Muller), 1764 fc
A. hexodontus Dyar, 1916 r
A. implicatus Vockeroth, 1954 c
A. intrudens Dyar, 1919 fc
A. pionips Dyar, 1919 fc
A. pullatus (Coquillett), 1904 r
A. punctor (Kirby), 1837 a
A. riparius Dyar & Knab, 1907 c
A. spencerii (Theobald), 1901 p
A. sticticus (Meigen), 1838 fc
A. stimulans (Walker), 1848 p
A. trichurus (Dyar), 1904 p

Key
Va – Very abundant
a – Abundant
c – Common
fc – Fairly common
r – Rare
p – Present

The coefficient of diversity (Fisher *et al.*, 1943) was 5 ± 0.04 in 1966 and 3 ± 0.02 in 1967, even though the number of species found was almost the same. It appears that this coefficient is a function of sample size as well as population size in a population with a large number of individuals, but a limited number of species. The coefficient of diversity is of use in comparing different areas or traps sampled at the time, as has been shown by Williams (1964) for mosquitoes taken in light traps in several cities in Iowa. It is also useful for comparing captures in the same trap in different years, provided the samples are similar in size or the number of possible species is very large, as in the Lepidoptera studied by Williams (1964).

Genus Anopheles Meigen, 1818

Anopheles earlei Vargas, 1943. – One species of *Anopheles* is recorded from Alberta. This is a member of the widespread "*Anopheles maculipennis*" complex and until recently was confused with a Pacific Coast species, *A. occidentalis* Dyar and Knab. It is distributed over much of the northern U. S. A. and Canada north to Labrador and Alaska. Probably all records of *A. occidentalis* from east of the mountains refer to this species. It is fairly common at George Lake.

There is believed to be only one generation per year in Alberta (Happold, 1965a). Overwintering appears to be by nulliparous females, which hibernate in basements and animal burrows (Shemanchuk, 1965). They leave their hibernation sites in early spring and oviposit soon after. At George Lake adults emerged in late July in 1966 but in late June in 1967. The adult females are long lived and overwintered females could still be found in late July 1966. Dissections for parity rate confirmed the presence of only one generation in 1966 (Fig. 2) but the situation in 1967 was not clear as nullipars predominated in late June. Fig. 3 shows the parity rate in 1967 compared with *Culiseta alaskaensis* (Ludlow) which has only one generation. No hibernation sites were found at George Lake but a series of females taken at animal burrows by Shemanchuk at Rimbey, Alberta in October, 1966, were all nulliparous.

Larvae of this species were found in a sedge meadow along with those of *Aedes vexans* in August 1966 at George Lake.

Genus Culiseta Felt, 1904

This genus is often referred to as *Theobaldia* Neveu-Lemaire, 1902, but this name was not available for this group of insects.

Culiseta alaskaensis (Ludlow), 1906. – This circumboreal species is a typical mosquito of the boreal forest. It overwinters as an adult female and is one of the earliest species to leave hibernation, becoming active as soon as the snow thaws. Though Happold (1965a) states "It is common in Alaska . . . but rare in Alberta and Saskatchewan" it is far from rare at George Lake, and was numerous enough to be a nuisance in May of both 1966 and 1967. In 1966 the emerging generation was seldom encountered, only two adults being taken in July and August. The overwintered generation had disappeared by late June. The females which leave hibernation are voracious biters, but there is no information on whether the newly emerged females bit or not.

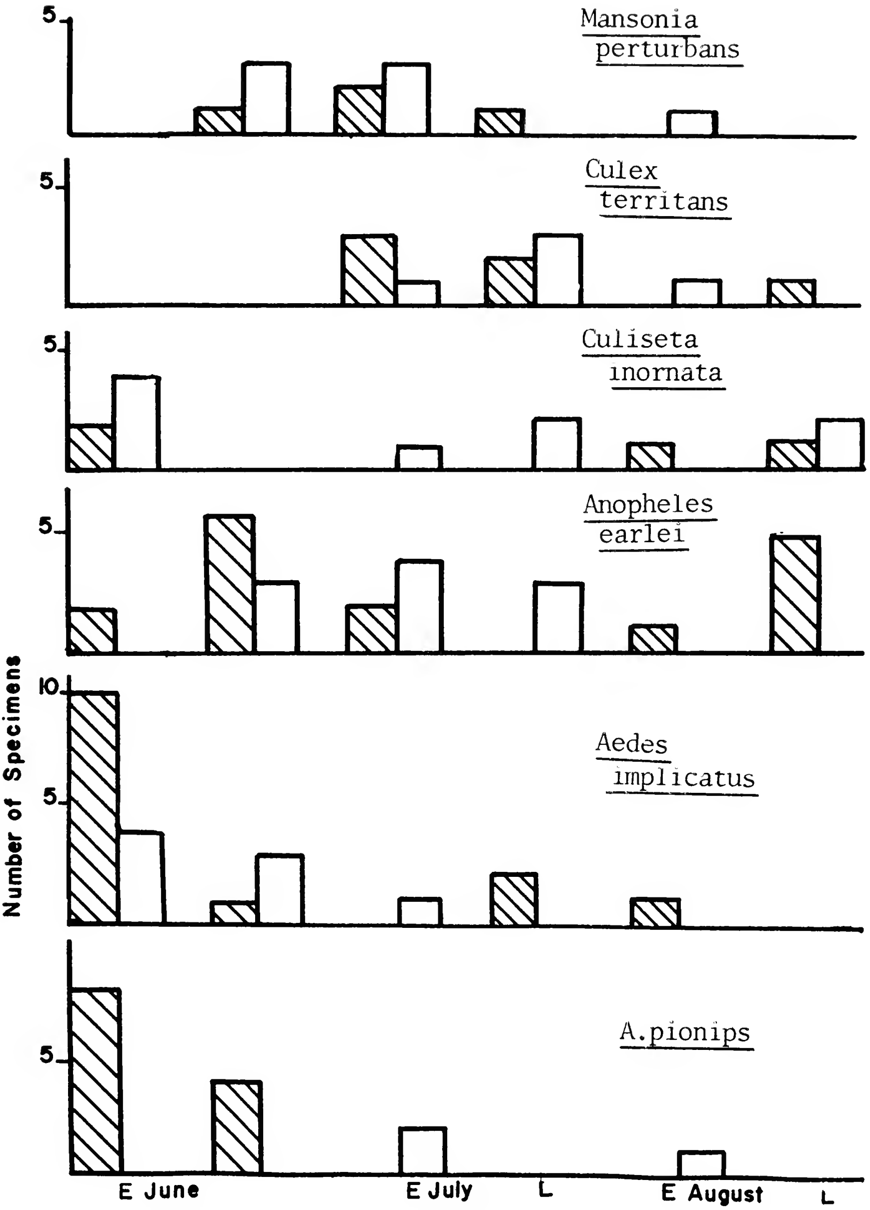


Fig. 2. Seasonal changes in the numbers of parous and nulliparous female mosquitoes at George Lake. June to August 1966.

Shaded area = no. nulliparous E = early; L = late

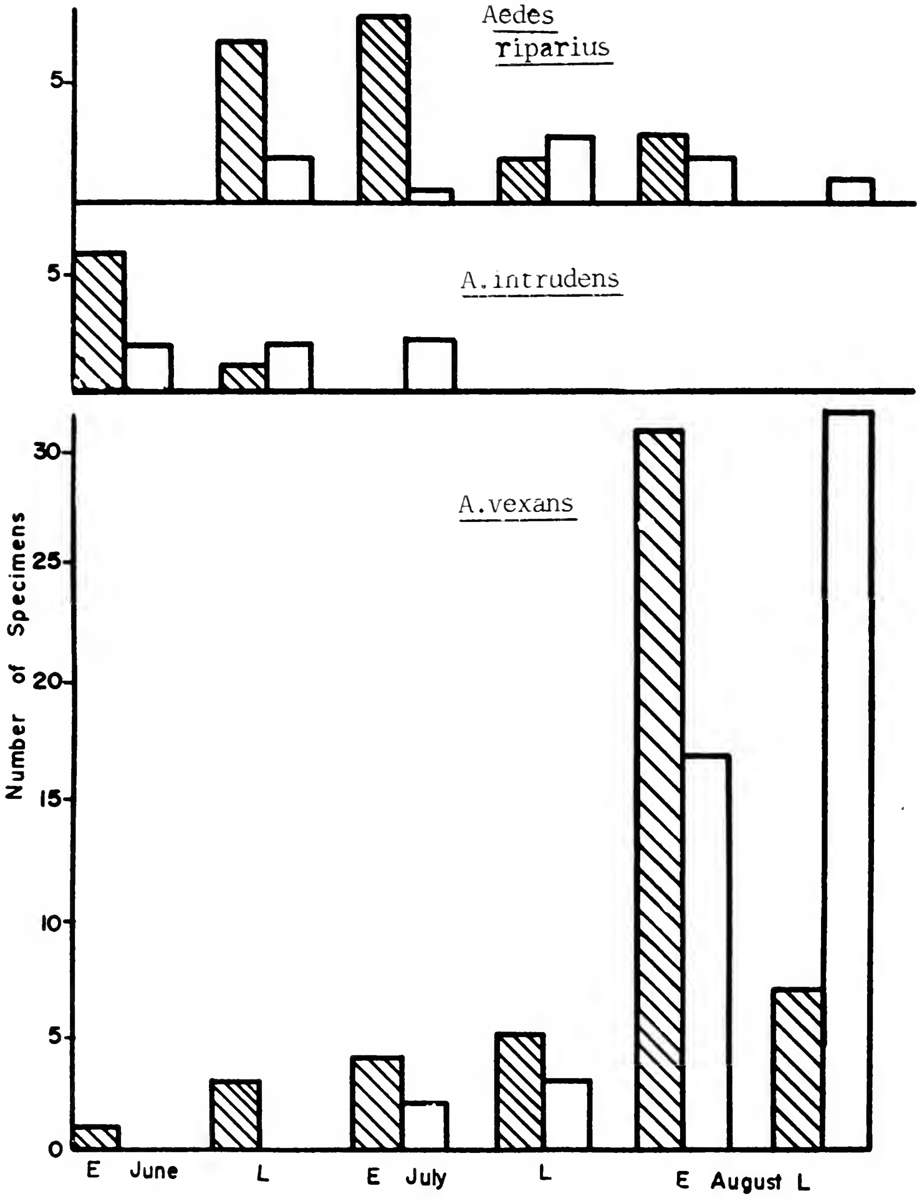


Fig. 2. Continued

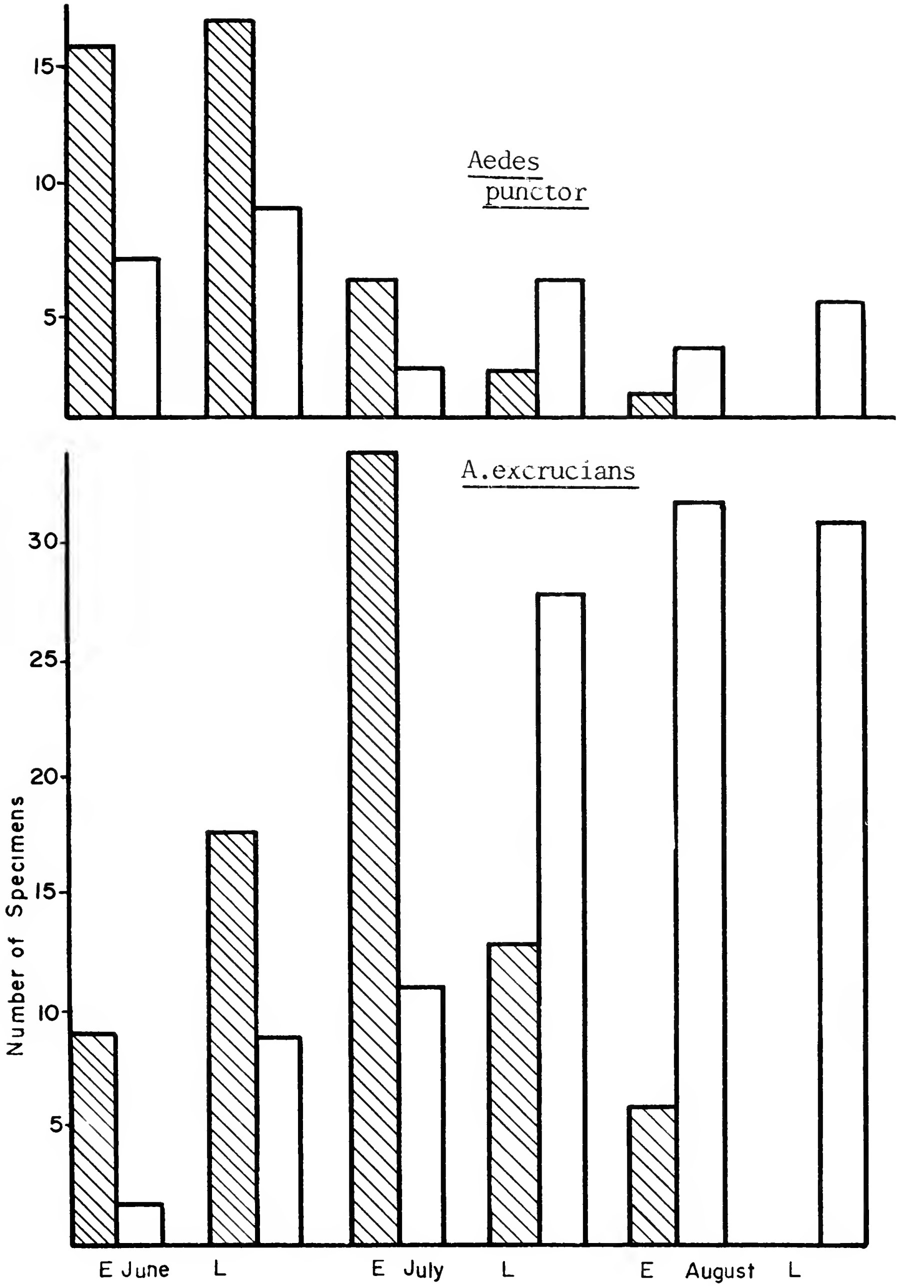


Fig. 2. Continued

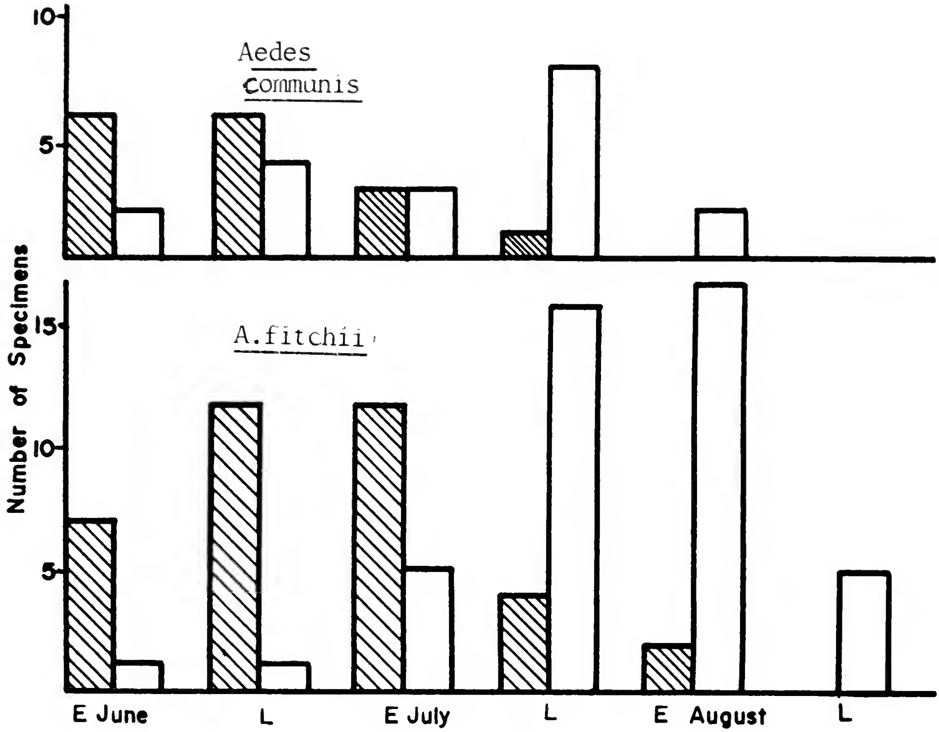


Fig. 2. Continued

Culiseta impatiens (Walker), 1848. – This species has not been found at George Lake, though it occurs at Flatbush (Happold, 1965a).

Culiseta incidens (Thompson), 1869. – This is a western North American species. It has not been found at George Lake but occurs at Flatbush.

Culiseta inornata (Williston), 1893. – Unlike the other Central Albertan species of *Culiseta* this species, which is confined to North America, appears to be a southern rather than a northern or mountain form. It occurs in both forest and open country and has successfully adapted to urban conditions, forming a large proportion of the mosquitoes breeding in Edmonton. It was common at George Lake in 1966, when it was most abundant near the lake shore, but was not taken after the second week in May in 1967. Happold found it to be rare at Flatbush; he found no larvae and very few adult females.

This species overwinters as an adult female, but has several generations in a summer. Wada (1965) found that oviposition in Edmonton continued into mid August. Unfortunately most of the females taken at George Lake were gravid so no confirmation of generation number was possible. Malaise trap captures in 1966 show three peaks, which suggests two generations: one peak in early May, when overwintered females leave hibernation sites, one peak in early August, when the adults resulting from eggs laid by the overwintered females emerge and one in September, which may represent a second generation. Larvae have been found in woodland pools in Edmonton but none have been found at George Lake.

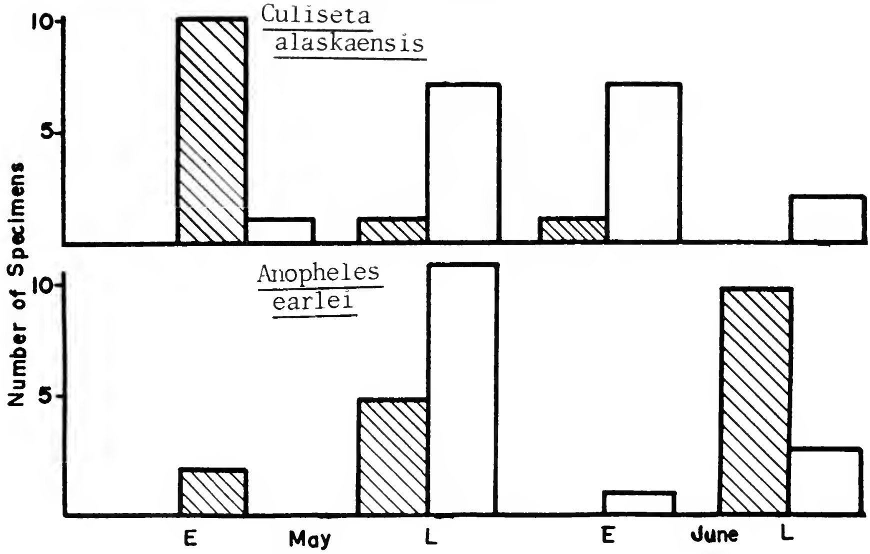


Fig. 3. Changes in the number of parous and nulliparous females of *Culiseta alaskaensis* and *Anopheles earlei* during the spring and early summer of 1967 at George Lake.

Shaded area = no. nulliparous E = early; L = late

Culiseta sylvestris minnesotae Barr, 1957. – Specimens of this species are often confused with specimens of *C. morsitans dyari* (Coquillett). I did not distinguish between the two species in 1965. All 1966 specimens which I preserved were *C. sylvestris minnesotae* but it is possible that a few *C. morsitans dyari* (Coquillett) may have been taken.

C. sylvestris minnesotae hibernates as an adult female, which leaves winter quarters early in the spring, being recorded in the first week of May 1967, before *C. alaskaensis*. The distribution of this species is not yet well known. Stone (1965) records it from Minnesota, Utah, Ontario, New Jersey and Massachusetts. Curtis (1967) states it has been recorded from the borders of British Columbia but not yet in that province. Probably many records of *C. morsitans dyari* (Coquillett) will prove to be *C. sylvestris minnesotae*. Barr (1958) states that females of *C. sylvestris minnesotae* do not appear to take human blood.

Culiseta morsitans dyari (Coquillett), 1901. – This is a holarctic species with a more or less northern distribution. It is not common at George Lake, where only five specimens have been definitely identified. Elsewhere in Alberta I have seen specimens of this species from the Cypress Hills, Edmonton, and Flatbush.

Very little is recorded of the biology of this species in North America. In Europe, Marshall (1938) and Wesenberg-Lund (1921) found that it overwinters as a larva, and unlike other *Culiseta* species it oviposits on wet mud, laying eggs singly instead of in rafts. Howard *et al.* (1915) considered it hibernated as an egg in North America but this does not seem to be so, and there is no study of its life history. Stone *et al.* (1959) suggest that the North American form may be different from the palearctic one. At George Lake in 1967 females appeared in late June, and one dissected was nulliparous.

Genus Culex Linnaeus, 1758

Culex restuans Theobald, 1901. – This species has not been found at George Lake but was taken by Klassen (1959) in Edmonton.

Culex tarsalis Coquillett, 1896. – Two specimens of this common prairie species were taken in 1966. They had probably migrated into the field site from surrounding open lands. This species may be extending its range north in Alberta. Hocking (pers. comm.) informs me that it has increased in abundance in Edmonton in the last ten years.

Culex territans Walker, 1856. – This is a holarctic species which until 1949 was confused with *C. apicalis* Adams in North America. It is probable that all records of *C. apicalis* east of the mountains and north of Utah refer to *C. territans*. Possibly because it rarely bites man, it is recorded as rare in most regional mosquito records (Happold, 1965a, 1965b; Curtis, 1967; Steward and McWade 1961). It is believed to feed mainly on cold blooded vertebrates but Means (1965) has recorded it feeding on man. It was fairly common at George Lake in 1966 and 1967, and was one of the first mosquitoes to leave winter quarters. In 1967 *C. territans* was the first mosquito taken, one specimen being taken in a Malaise trap in April before the snow had completely melted.

From seasonal distribution data it appears that there were two generations in 1966 (Fig. 4), but dissections were too few to confirm, though they do support this.

Genus Coquillettidia Dyar, 1905

This is a mainly tropical genus; two species penetrate into northern regions, one in Eurasia and one in North America.

Coquillettidia perturbans (Walker), 1856. – This widespread North American species was first taken in Alberta at Flatbush by Happold in 1961, (Happold, 1965a) and this is still the only published locality (Pucat, 1964, 1965). I have seen specimens from Edson, and P. Shera (unpublished report) recorded it from Elk Island National Park. At George Lake it was not found in 1965, but was fairly common in 1966 and had just appeared in 1967 when work was stopped. It is probably common and widespread over the forested parts of Alberta. There appears to be only one generation per year and this is the only Canadian mosquito definitely known to overwinter as a larva (Happold, 1965a). As yet no larvae have been found in Alberta.

Adult females of this species are reputed to be fierce biters, but were not numerous enough to be a nuisance at George Lake. Happold (1965a) at Flatbush and Burgess and Haufe (1960) in Ontario found this species abundant in the forest canopy.

Genus Aedes Meigen, 1818

This is the predominant mosquito genus in Alberta and in most northern regions. It includes 70% of the species and 80% of the specimens caught at George Lake. The genus is distributed from the equator to the limit of land in the north and is found on many oceanic islands.

Three subgenera, *Aedes* Meigen, *Aedimorphus* Theobald, and *Ochlerotatus* Lynch Arribalzaga, are found in Alberta.

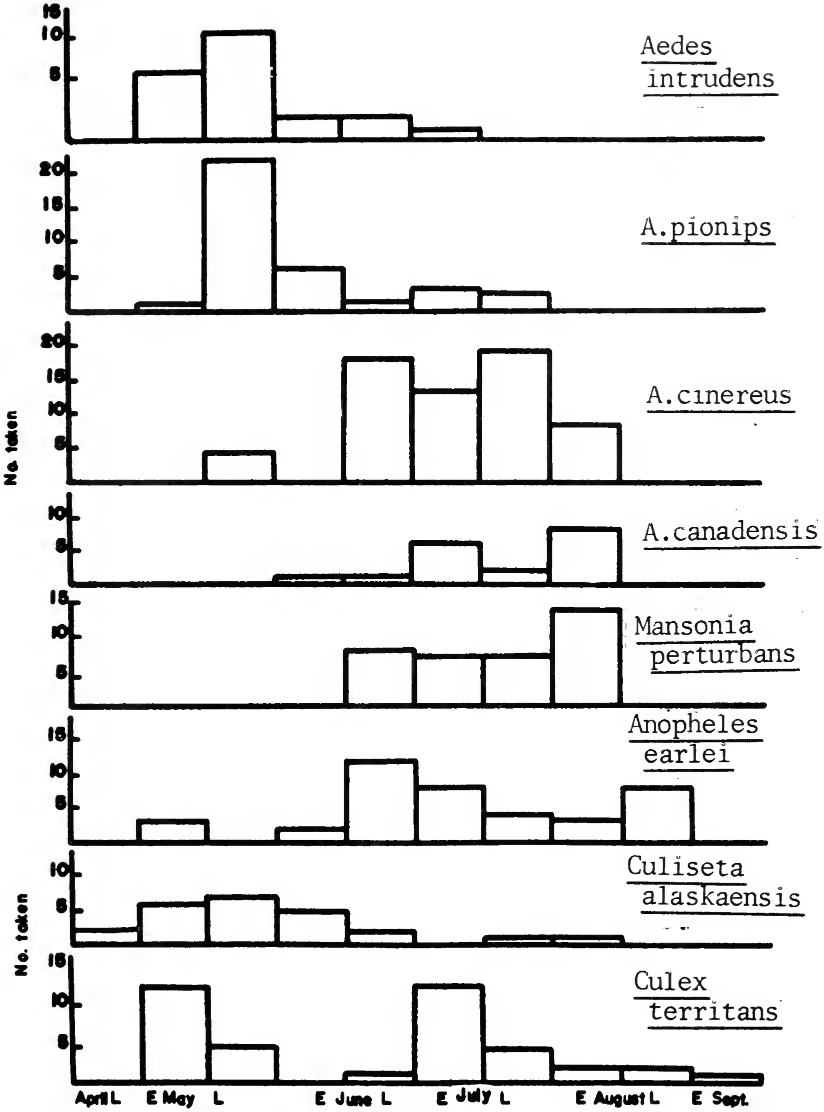


Fig. 4. Seasonal changes in the numbers of some of the less common mosquito species taken by all methods at George Lake. 21 April to 29 September 1966.

E = early L = late

All Alberta *Aedes* species overwinter as eggs and with the possible exceptions of *A. vexans* and *A. dorsalis*, there is only one generation per year. Brust (pers. comm.) informs me that diapause is not obligatory in the eggs of *A. sticticus*, so this species may also be multivoltine if the season permits.

Aedes (Aedes) cinereus Meigen, 1818. – This small holarctic species is common in central Alberta. It is a woodland species which is also common in Poland (Skiersca, 1965). It is common at George Lake, where it is a late-appearing species reaching an adult population peak in July and early August in 1966. I noticed that it is a low flier and bites mainly below the knee and around the ankles.

Aedes (Aedimorphus) vexans (Meigen), 1830. – This appropriately-named species has one of the widest and most unusual ranges of any mosquito, being found in the Palearctic, Nearctic, and Oriental regions and also in the Transvaal, Fiji, Samoa and New Caledonia (Stone *et al.*, 1959). It was very common at George Lake in 1965 and 1966 but was not found there in 1967, though it may have appeared after work stopped. It was taken in June 1966.

Rempel (1953) suggested there were two forms of *A. vexans* in Saskatchewan, a large form in the prairies and a smaller one in the parklands and forest.

A. vexans is a migratory species, capable of flying long distances. Horsfall (1955) records many instances of migration in temperate regions and de Meillon and Khan (1965) have recorded a large migration in Burma. A result of this migratory tendency is that this species is often a major pest species in cities like Edmonton with efficient control programs, as it migrates in from breeding sites which may be several miles from the city. Clark and Wray (1967) have studied the influx of *A. vexans* into Des Plaines, Illinois, and provided a method of predicting invasions.

A. vexans is a late emerging species with a 1966 population peak in late summer. The adult females continued well into September 1966 and larvae were taken in late August. Stage *et al.* (1938) recovered a marked female 55 days after release.

In the southern part of its range the species is multivoltine, but the number of generations in northern parts is not clear, as the eggs do not hatch simultaneously. Some may require several floodings before hatching (Horsfall, 1955), giving rise to broods. Gjullin *et al.* (1950) found that eggs remained viable for three to four years if kept moist.

Nullipars were found from June to the end of August 1966 and predominated up to late August, indicating that emergence took place in June, July, and early August, but there was no evidence of more than one brood.

Subgenus Ochlerotatus Lynch Arribalzaga, 1891

This is the dominant subgenus in northern regions, but also occurs in the tropics. In North America this subgenus extends further north than any other culicid. Two species, *A. nigripes*, and *A. impiger*, occur within 500 miles of the pole. Nineteen species have been recorded at George Lake, and Pucat (1965) records 25 from Alberta.

Aedes campestris Dyar and Knab, 1907. – This species has been recorded at Edmonton (Klassen, 1959; Wada, 1965), but not yet at George Lake.

A. canadensis (Theobald), 1901. – This species is widespread in the forested parts of North America. It is not common at George Lake. Rempel (1950) found it to be fairly common in the aspen grove parkland of Saskatchewan. It is a late emerger. At George Lake it appeared at the end of June in both 1966 and 1967.

Aedes cataphylla Dyar, 1916. – This holarctic species is confined to western Northern America in the Nearctic Region (Stone, 1965). It is not common at George Lake, but is often a major pest species in Edmonton (Klassen, 1959; Klassen and Hocking, 1963). It is one of the first species to emerge and Klassen found emergence completed by 19 May, 1958, at Edmonton.

Aedes communis (De Geer), 1776. – This is an important woodland species with a circumboreal distribution and is a well known pest species in Europe and North America. Chapman and Barr (1964) have described a subspecies *A. communis nevadensis*, from the western U. S. A. and two larval forms of the typical subspecies. All larvae examined from Alberta belonged to the eastern form. Hocking (1954) described an autogenous form from Churchill on Hudson Bay in which autolysis of the flight muscles takes place. The species is common at George Lake.

It is a fairly early emerging species; in 1966 a population peak of adult females occurred in early June. Nullipars predominated to late June, indicating that some emergence took place up to then.

Aedes diantaeus Howard, Dyar and Knab, 1917. – This species has a wide distribution in the boreal forests of the old and new worlds, but it is seldom abundant (Vockeroth, 1954b). In Alberta it has only been recorded from Flatbush (Happold, 1965a; Pucat, 1964). A single specimen was found at George Lake in 1966.

Aedes dorsalis (Meigen), 1830. – This species occurs in the grasslands of the Palearctic and Nearctic regions. It is abundant in southern Alberta but uncommon north of Edmonton. One specimen was taken at George Lake in 1965.

Khelevin (1958) has shown that diapause in the egg of this species is facultative and it can have several generations per year. Like *A. vexans* it is a migratory species (Horsfall, 1955).

Aedes excrucians (Walker), 1856. – This is a holarctic woodland species with a somewhat more southerly distribution than *A. communis.* Together with *A. vexans*, it was one of the two most abundant species at George Lake in 1965 and 1966. It was also abundant in 1967, but work stopped before it reached population peak. It is a fairly early emerger, first appearing in the last week in May 1966 but not till the second week in June 1967. The emergence period appears to be prolonged as nullipars predominated until mid July and could still be found in early August 1966. The adult females were found up to the end of August but none were taken in September 1966. Matheson (1944) records a single instance of larvae being found in September in New York. It is a persistent biter, and is a major pest species in central Alberta.

Aedes fitchii (Felt and Young), 1904. – This species is confined to North America, where it has the same range as *A. excrucians*. It is common in central Alberta. At George Lake it appeared in early June 1966. Nullipars predominated until mid July and were found till mid August, indicating a prolonged emergence period. Adult females were taken up to the end of August but were not taken in September either in 1965 or in 1966.

It is an important pest species in central Alberta.

Larvae were found in a pool in a spruce grove on the western fence of the George Lake field site along with those of *A. implicatus* in May 1966.

Aedes flavescens (Muller), 1764. – This species occurs in grassland areas of Eurasia and North America. It is common in central Alberta and fairly common at George Lake. Specimens taken on the field site had probably migrated in as it is an open country species. Hearle (1929) considered it to be the most numerous mosquito on the Canadian prairies. Happold (1965a) did not find it in the forest at Flatbush but found it common in an alfalfa field.

Adult females were taken from early June to mid August 1966 at George Lake. Nullipars were found till early July. A single male was taken in June 1967, when females were more abundant than in 1966.

Aedes hexodontus Dyar, 1916. – This tundra and open country species was first recorded from Alberta by Wada in 1964 at Edmonton (Wada, 1965). It was not common at George Lake. It is an early species and was not found after June in either year.

Aedes implicatus Vockeroth, 1954. – This is a boreal forest species, confined to North America, and occurs north almost to the tree line. It is locally common in central Alberta, being common at George Lake but rare at Flatbush. In late May and early June 1967 this species was the most abundant *Aedes* at George Lake.

It is an early emerger, the adult females reaching a population peak in mid June in both 1966 and 1967. There was some indication that a second brood occurred in late July 1966, as pars predominated in late June and early July, but the three specimens dissected in late July and early August were nulliparous. In 1967 only nullipars were taken in May but pars predominated in late June and the numbers taken began to decline in mid June. Nielsen and Rees (1961) believed this to be a short lived species; if so, then second broods are needed to account for nullipars occurring in late summer.

In early May 1966 larvae were found in pools in ruts in the road near the campsite and in a pool on the western boundary along with those of *A. fitchii*.

Aedes increpitus Dyar, 1916. – This species has been taken at Edmonton by Klassen and Wada, but has not yet been found at George Lake.

Aedes intrudens Dyar, 1919. – Another species with a circumboreal distribution, it was common at Flatbush and relatively rare at George Lake in 1966, but common there in 1967.

It is an early species, with a population peak in late spring and only pars were taken in July 1966. Happold recorded it as the most important *Aedes* species in buildings at Flatbush. At George Lake only one specimen was taken in the trailer in 1966 but it was prominent indoors in spring 1967. Matheson (1944) writes of *A. intrudens*: "Dyar states that this species readily invades houses, but I have never taken them in houses though I have found them abundantly in wooded areas throughout the season."

Aedes pionips Dyar, 1919. – This Nearctic species is found in Canada and the western U. S. A. It is rare at George Lake.

It is generally considered to be a late emerger (Carpenter and LaCasse, 1955) but at George Lake in 1966 the population peak appeared to be in early summer, adult females continued into August, nullipars were found in late July.

Aedes pullatus (Coquillett), 1904. – This species is confined to the western mountains and to the Ungava peninsula and South Baffin Island in North America. It also occurs in Europe, where it is not a mountain species. In Alberta it is common in the Rocky Mountains. Klassen and Wada did not find it at Edmonton but in some years it is common there (Hocking, pers. comm.). It was rare at George Lake, and only found there in late May and early June.

Jenkins and Knight (1950) found it to be one of the most abundant species at Great Whale River on the east coast of Hudson Bay and Vockeroth (1954b) states that the eastern forms may be different from the western, though no morphological differences could be found.

Aedes punctor (Kirby), 1837. – This is an important woodland species with a holarctic distribution. It is a major pest species in both North America and northern Eurasia. It is common in central Alberta, being the major black-legged *Aedes* species at both George Lake, Edmonton and Flatbush.

In 1966 adult females were taken from late May into September, the population peak being in early June. In 1967 this species reached its peak somewhat later than *A. implicatus,* becoming the most abundant species in the third week in June. In 1966 there was a second peak in August, which may have signified a second brood, but the few dissections done at this time did not confirm this, the individuals examined being mainly parous. Nullipars predominated until early July and were found until mid August; probably some emergence took place in each summer month in 1966.

Aedes riparius Dyar and Knab, 1907. – This species occurs in western North America and northern Eurasia. It is mainly an open country species but also occurs in woodlands. It is common in central Alberta.

In 1966 it was not found until late June when it occurred in fairly large numbers, which possibly indicates it did not breed in the area. Nullipars predominated in June and July and some were found in August. In 1967 this species was taken in late May and was the most abundant band-legged *Ochlerotatus* species till the end of June when *A. excrucians* began to reach peak emergence.

Aedes spencerii (Theobald), 1901. – This is a prairie species, confined to western North America; it is among the most numerous species in southern Alberta but rare north of Edmonton. One specimen was taken at George Lake in August 1966 and several in late May 1967.

A. sticticus (Meigen), 1838. – This is a holarctic species which extends its range south to the Gulf of Mexico in North America. It is locally common in central Alberta being fairly common at George Lake and rare at Flatbush.

Adult females were taken from late May to the end of July and nullipars to mid July in 1966.

Aedes stimulans (Walker), 1848. – This species has much the same range as *A. fitchii.* It is common over much of the forest country of Canada, but appears to be rare in central Alberta. Only four specimens have been definitely identified at George Lake and Happold did not find it at Flatbush.

Aedes trichurus (Dyar), 1904. – This is a woodland species found in the northern U. S. A. and southern Canada. In Alberta it occurs as far north as Beaverlodge (Rempel, 1950). It was rare at George Lake.

SEASONAL DISTRIBUTION

Happold (1965b) discussed the seasonal distribution of mosquitoes at Flatbush, where most of the important species found at George Lake occur, and the George Lake findings are in agreement with his.

Fig. 5 shows the 1966 distribution of the commoner species in Malaise trap catches corrected to 100 hours running time.

The mosquito population showed three peaks in 1966: the first in early May when the overwintering females left hibernation; one in early July, representing the peak population of *Aedes* species; and the third in early August formed by the emergence of those females which enter hibernation and second broods of *Aedes*. This peak was probably much more pronounced in 1965, when weather conditions favoured second broods.

In 1965, adults of *Anopheles intrudens* and pars of *Anopheles earlei* were taken in August. This was almost certainly the result of weather conditions in 1965. Happold (1965a) noted that in 1961 adults of *Anopheles earlei* survived for a longer period than in 1962. During 1961 the weather conditions were like those in 1965. The adults of other species may exhibit increased longevity as a result of favorable climatic conditions.

In all three years *Aedes* mosquitoes became abundant each spring approximately at the same time as the poplars flushed.

MOVEMENT INTO BUILDINGS

Unlike tropical areas where disease transmission inside human dwellings is important, there is relatively little information from North America on the movement of mosquitoes into buildings. Matheson (1944) mentions a few species as persistent house enterers and Happold (1964b) has recorded the species he collected indoors at Flatbush.

During June, July, and August 1966 and in May and June 1967 special captures were carried out in a partially screened trailer at George Lake. In 1966, 112 specimens of 16 species and in 1967, 96 specimens of 12 species were taken in this trailer (Table 2).

In 1966 70% of the indoor catch was composed of *A. punctor, A. excrucians, A. pionips* and *A. communis*, while in 1967 *Anopheles earlei, Aedes punctor* and *A. intrudens* made up the body of the catch. *A. hexodontus* and *A. sticticus* were also prominent in both years.

Happold (1965b) found *A. earlei* and *A. intrudens* made up 80% of the indoor catch at Flatbush. In 1967 all *A. earlei* found indoors at George Lake were taken in May. This may indicate that the overwintered females enter buildings to feed but that the trailer did not provide a good hibernation site. Elsewhere individuals of this species are known to hibernate in buildings, especially basements. The most striking difference between the George Lake and Flatbush results was the absence of *A. punctor* from indoor captures at Flatbush, although it was one of the most abundant local species. It formed over 30% of the indoor catch at George Lake.

In central Alberta, the entry of mosquitoes into buildings depends more on the environment rather than on specific innate tendency to enter buildings as has been recorded in the tropics, where exophilous and endophilous genera and species are recognized (Holstein, 1954; Muirhead-Thompson, 1951).

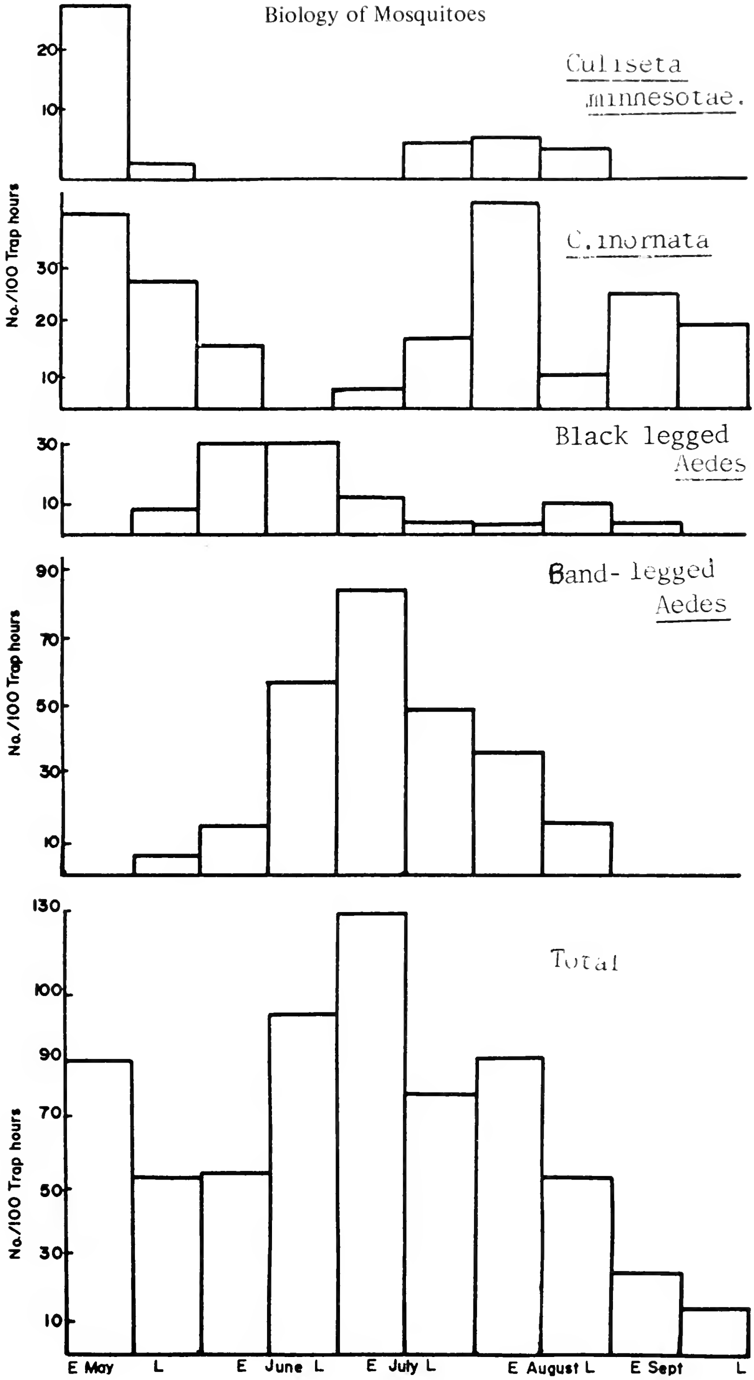


Fig. 5. Seasonal changes in the numbers of mosquitoes caught per 100 trap hours, in Malaise traps, at George Lake. May to September 1966.

E = early L = late

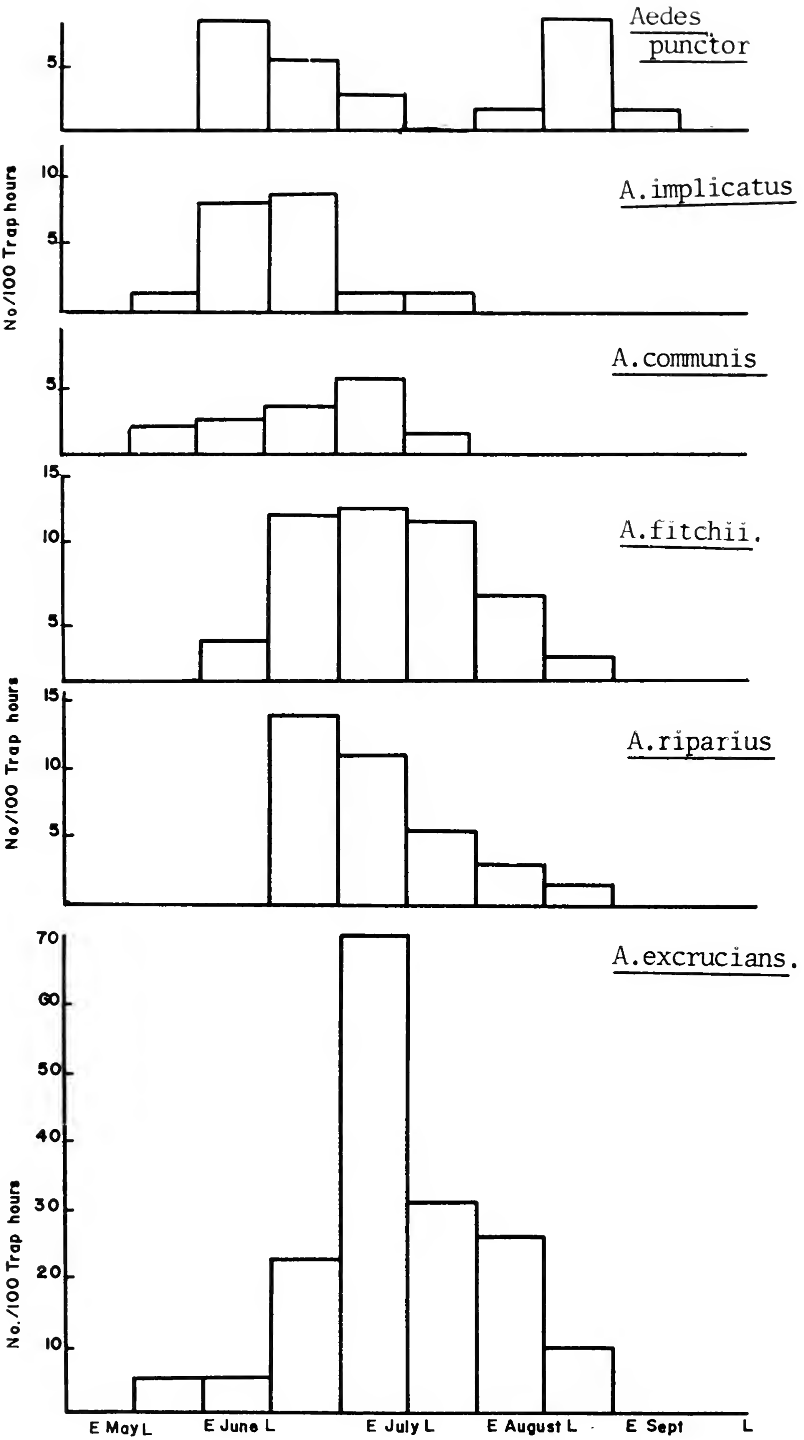


Fig. 5. Continued

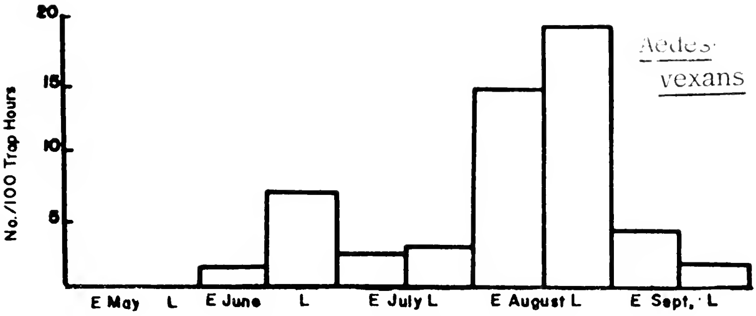


Fig. 5. Continued

Table 2. Mosquito species taken indoors at George Lake in 1966 and in 1967 and numbers taken.

Species	Number Caught			
	1st June – 1st September 1966		16th May – 15th June 1967	
	No.	%	No.	%
Anopheles earlei	1	0.9	25	26.0
Culiseta alaskaensis	0	0	5	5.2
C. inornata	1	0.9	0	0
Culex territans	0	0	3	3.1
Aedes cataphylla	1	0.9	0	0
A. communis	10	8.9	5	5.2
A. diantaeus	1	0.9	0	0
A. excrucians	19	17.0	0	0
A. fitchii	8	7.1	0	0
A. hexodontus	5	4.5	3	3.1
A. implicatus	3	2.7	5	5.2
A. intrudens	1	0.9	9	9.4
A. pionips	14	12.6	2	2.1
A. pullatus	0	0	2	2.1
A. punctor	34	30.4	33	34.4
A. riparius	1	0.9	1	1.0
A. sticticus	9	8.0	3	3.1
A. trichurus	1	0.9	0	0
A. vexans	2	1.8	0	0
Unidentified	1	0.9	0	0
Total	112		96	

DISTRIBUTION WITHIN THE STUDY AREA

Fig. 6 shows the relative abundance of the major species at the lake shore and in the forest in 1966. *Culiseta inornata* and *Aedes vexans* were more abundant in the lake shore traps and *A. excrucians* and *A. fitchii* in the forest traps. The other species were more or less evenly distributed. In 1967 *A. implicatus* was far more abundant in the forest traps.

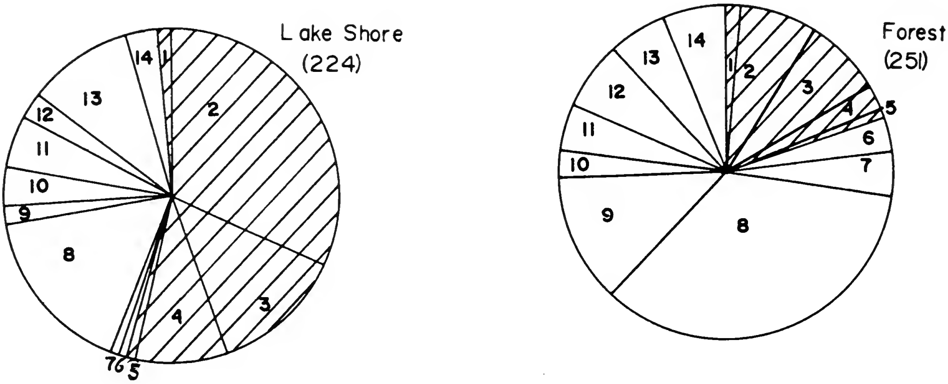


Fig. 6. Relative abundance of mosquito species taken in Malaise traps at the lake shore and in the forest at George Lake in 1966. Shaded – genera other than *Aedes*

1 = *Anopheles earlei*
2 = *Culiseta inornata*
3 = other *Culiseta*
4 = *Culex territans*
5 = *Coquillettidia perturbans*
6 = *Aedes cinereus*
7 = *A. communis*
8 = *A. excrucians*
9 = *A. fitchii*
10 = *A. implicatus*
11 = *A. punctor*
12 = *A. riparius*
13 = *A. vexans*
14 = other *Aedes*

PROPORTION PAROUS

Fig. 2 shows the seasonal distribution of pars and nullipars* in the species taken more abundantly in 1966 and Fig. 3 shows the parity rate for *Culiseta alaskaensis* and *Anopheles earlei*, in the spring of 1967. The distributions in *Aedes excrucians* and *A. fitchii* exactly fit those expected for a univoltine species which overwinters as eggs, i.e. there are two overlapping curves, one in early summer with nullipars predominant and one in late summer with pars predominant. The curve for *Anopheles earlei* in 1966 fits the expected for a univoltine species which overwinters as an adult female, though the number dissected was small. The 1967 curve, however, indicates that considerable emergence took place in late

---

*Nullipars = those individuals which have not yet laid eggs.
Pars = those individuals which have laid at least one batch of eggs.

June and as this appears rather early for females to enter hibernation it is possible that there was a second generation. The 1967 curve for *Culiseta alaskaensis* is as expected for a species which overwinters as an adult nulliparous female. The picture for the other species is not so clear.

Shelenova (1959) found that in Russia, members of *Aedes* were generally shorter lived than were members of *Anopheles* in the same area, few *Aedes* individuals having passed four gonotrophic cycles, while anophelines often had passed 12 to 29. Carpenter and Nielsen (1965) also found few individuals of *Aedes* with more than four dilations in the ovarian ducts in Utah.

Corbet (1961) and Hamon *et al.* (1964) have studied differences in activity between pars and nullipars, especially with regard to biting activity. Neither found any significant differences, though Hamon *et al.* found a modification of the biting cycle after spraying with insecticide had removed the older portion of the population. They concluded that extrinsic factors, such as light intensity and temperature are more important in controlling activity of adult female mosquitoes than the age of the insect.

OVARIAN DEVELOPMENT AND ACTIVITY

Table 3 shows the stages of Sella and of Christophers in the total catch, in total *Aedes* species and in the commoner species of mosquitoes. By far the greater proportion of all

Table 3. Distribution of the stages in the gonotrophic cycle (stages of Sella and of Christophers) in the more important species of mosquito taken at George Lake in 1966.

	Stage of Sella							
Species	1	2	3	4	5	6	7	% gravid
Anopheles earlei	26	–	–	–	–	–	3	10
Culex territans	12	1	–	1	–	–	3	17
Culiseta inornata	15	1	–	1	2	3	90	80
Coquillettidia perturbans	12	–	–	–	–	–	–	0
Aedes communis	38	–	–	–	–	–	1	2
Aedes excrucians	198	2	3	–	1	1	5	2
Aedes fitchii	95	1	1	–	–	–	–	0
Aedes punctor	83	–	–	1	1	–	–	0
Aedes riparius	36	–	–	–	–	–	–	0
Aedes vexans	120	1	1	1	–	–	7	5
Total *Aedes*	707	13	5	4	3	1	17	2
Total catch	786	18	6	5	4	4	115	12

Table 3. continued.

	Stage of Christophers				
Species	I	II	III	IV	V
Anopheles earlei	16	10	–	1	2
Culex territans	5	7	1	–	3
Culiseta inornata	13	3	–	9	81
Coquillettidia perturbans	–	10	2	–	–
Aedes communis	14	13	–	–	1
Aedes excrucians	51	132	6	1	5
Aedes fitchii	23	57	3	–	–
Aedes punctor	39	33	3	1	–
Aedes riparius	9	22	4	–	–
Aedes vexans	58	53	1	1	7
Total *Aedes*	265	403	22	4	17
Total catch	300	438	27	15	106

females caught were in stages 1 and 7 of Sella and I, II or V of Christophers. Thus they were either unfed or gravid, with few in the intermediate stages. Christophers (1911) and Clement (1963) have shown that the eggs normally develop to stage II of Christophers and then development stops until a blood meal is taken. This agrees with the findings of Carpenter and Nielsen (1965) in Utah, where 89% of the active females examined were in stages I and II of Christophers.

A surprising part of the 1966 findings at George Lake was that very few of the resting older females caught in the trailer were gravid or in intermediate stages. In 1967 rats were kept in unscreened cages in the trailer and many specimens of *Anopheles earlei* as well as *Aedes* species were found in the intermediate stages of Sella and Christophers. This indicates that these mosquitoes enter houses in search of food and if they find it remain to digest their blood meals, but otherwise leave fairly soon. It also indicates their digestion of blood meals is done very close to the feeding site. Carpenter and Nielson (1965) found about half the resting females taken in their study were gravid but found very few intermediates.

These findings indicate that there is very little flight activity during intermediate stages of the gonotrophic cycle. This is most probably because the blood fed or gravid female mosquito is a relatively inefficient flying machine as the weight of the blood meal may exceed the weight of the insect. This little flight activity may apply mainly to woodland species as individuals resting in grassland or tundra are more likely to be disturbed by passing animals. Corbet (1961) found that most individuals engaging in "non-specific activity" were in the early stages of Christophers but Standfast (1965) believed that light trap captures in Australia showed that a considerable part of the population was engaging in "non-specific activity" during the night, interpreted this to mean that there was considerable activity in the intermediate stages of the gonotrophic cycle, but did not record any dissections to support this.

Carpenter and Nielson (1965) report that a fair number of biting mosquitoes had ovaries in stage II of Christophers and were nulliparous. They suggest that this is an indication of autogeny and mention that some of the species in which this occurred have been shown to be capable of autogeny by Chapman (1962).

At George Lake in 1966 and 1967 records were kept of specimens in stage I of Sella and stage III of Christophers. Twenty three were found of which seven were nulliparous, forming 0.007% of all nullipars. These seven consisted of five species: *A. communis, A. fitchii, A. intrudens, A. punctor*, and *A. riparius*. Two of these, *A. communis* and *A. punctor* were included in those found by Carpenter and Nielson (1965) and are mentioned as capable of autogeny by Chapman (1962) but the phenomenon appears to be rarer at George Lake than in Utah where 4% of the biting females had ovaries in stage III of Christophers.

Eighty percent of the females of *Culiseta inornata* taken at George Lake in 1965 and in 1966 were gravid. The reason for this is not known but it could indicate some degree of autogeny. No indication of autogeny in this species had been found in the laboratory.

RETENTION OF EGGS BY PAROUS FEMALE MOSQUITOES AND OTHER OVARIAN ABNORMALITIES

During dissections for parity rate I noticed that several parous females with ovaries of otherwise normal appearance (i.e., they did not have the sac-like appearance of those in females which have just oviposited) had retained eggs in one ovary. The number of eggs retained was usually one but six were found in one *Aedes excrucians*.

Table 4 shows the species and the number in each with retained eggs. This appears to be a widespread phenomenon as it was recorded in ten species of three genera. It is also interesting to note that the percentage of pars with retained eggs in each year was approximately 7%. The slightly higher proportion in August over June, may be due to older multiparous females having a greater tendency to retain eggs over younger pauciparous females; but this will need further study.

In one parous *Aedes punctor* taken in a Malaise trap in late June 1967 there was differential development in the ovaries, one being in stage II and one in stage IV of Christophers.

Table 4. Parous female mosquitoes at George Lake with eggs retained in one ovary.

Species	1965 (August)	1966 (June–August)	1967 (May–June)	Total
Anopheles earlei		1	2	3
Culiseta inornata	2	2		4
C. alaskaensis			1	1
Aedes excrucians		11		11
A. fitchii		1		1
A. flavescens		1		1
A. intrudens	1		1	2
A. punctor		2	3	5
A. riparius		1	2	3
A. vexans	2	5		7
Total	5	24	9	38
Total No. Pars.	67	337	139	543
% Pars. retaining eggs	7.5	7.1	6.5	7.0

ACKNOWLEDGEMENTS

I wish to express my thanks to B. Hocking, G. E. Ball, W. G. Evans, D. A. Boag, K. Smillie and J. A. Downes for reading and criticizing the manuscript and to N. Wood for much help in the field.

I should also like to thank the City of Edmonton and the University of Alberta for the provision of grants to enable this work to be carried out.

REFERENCES

Barr, A. R. 1958. The mosquitoes of Minnesota. Univ. Minn. Agric. exp. Sta. Tech. Bull. 228. 154 pp.

Beckel, W. E. 1954. The identification of adult female *Aedes* mosquitoes (Diptera:Culicidae) of the blacklegged group, taken in the field at Churchill, Manitoba. Can. J. Zool. 32: 324–358.

Burgess, L. and W. O. Haufe. 1960. Stratification of some prairie and forest mosquitoes in the lower air. Mosquito News 20: 341–346.

Carpenter, S. J. and W. J. LaCasse. 1955. The mosquitoes of North America (north of Mexico). University of California Press, Berkeley. 360 pp; 127 pl.

Carpenter, S. J. and L. T. Nielsen. 1965. Ovarian cycles and longevity in some univoltine *Aedes* species in the Rocky Mountains of the western United States. Mosquito News 25: 128-135.

Chapman, H. C. 1962. A survey for autogeny in some Nevada mosquitoes. Mosquito News 22: 134-136.

Chapman, H. C. and A. R. Barr. 1964. *Aedes communis nevadensis*, a new subspecies of mosquito from western North America. Mosquito News 24: 440-447.

Christophers, S. R. 1911. The development of egg follicles in *Anopheles*. Paludism 2: 73-88.

Clark, J. C. and F. C. Wray. 1967. Predicting influxes of *Aedes vexans* into urban areas. Mosquito News 27: 156-163.

Clement, A. N. 1963. The physiology of mosquitoes. Pergamon Press, Oxford. 393 pp.

Corbet, P. S. 1961. Entomological studies from a high tower in Mpanga forest, Uganda, VIII: The age composition of biting mosquito populations, according to time and level. Trans. R. ent. Soc. Lond. 113: 336-345.

Curtis, L. C. 1967. The mosquitoes of British Columbia. Occasional papers, British Columbia Provincial Museum No. 15. 90 pp.

de Meillon, B. and Z. H. Khan. 1965. Examples of the use of simple age grading in the assessment of *Culex fatigans* populations. W.H.O./V.C./Sem./W.P./25.64.(mimeographed).

Fisher, R. A., A. S. Corbet and C. B. Williams. 1943. The relation between the number of individuals and the number of species on a random sample of an animal population. J. anim. Ecol. 12: 42-58.

Gjullin, L. M., W. W. Yates and H. H. Stage. 1950. Studies on *Aedes vexans* (Meig.) and *Aedes sticticus* (Meig.), flood water mosquitoes in the lower Columbia River valley. Ann. ent. Soc. Am. 43: 262-275.

Graham, P. 1969. A comparison of sampling methods for adult mosquito populations in central Alberta, Canada. Quaest. ent. 5: 217-261.

Hamon, J., S. Sales, J. P. Adam and P. Grenier. 1964. Age physiologique et cycles d'agresservite chez *Anopheles gambiae* et *A. funestus* dans la region de Bobo-Dioulasso (Haute Volta). Bull. Soc. ent. Fr. 69: 110-121.

Happold, D. C. B. 1965a. Mosquito ecology in central Alberta. I. The environment, the species and studies of the larvae. Can. J. Zool. 43: 795-819.

Happold, D. C. B. 1965b. Mosquito ecology in central Alberta. II. Adult populations and activities. Can. J. Zool. 43: 821-846.

Hearle, E. 1929. The life history of *Aedes flavescens* (Muller). Trans. Roy. Soc. Can. Sect. V. Ser. 3. 23: 85-101.

Hocking, B. 1954. Flight muscle autolysis in *Aedes communis* (de Geer). Mosquito News 14: 121-123.

Holstein, M.H. 1954. Biology of *Anopheles gambiae*. Monogr. Wld. Hlth. Org. No. 9: 172 pp.

Horsfall, W. R. 1955. Mosquitoes; their bionomics and relation to disease. Ronald, New York. 723 pp.

Howard, L. O., H. G. Dyar and F. Knab. 1915. The mosquitoes of North and Central America, Vol. III. Carnegie Institute, Washington, Publ. No. 159. 523 pp.

Jenkins, D. W. and K. L. Knight. 1950. Ecological survey of the mosquitoes of Great Whale

River, Quebec. Proc. ent. Soc. Wash. 52: 209-223.

Khelevin, N. W. 1958. The effects of environmental factors on the embryonic diapause and on the number of generations in a season of *Aedes caspius dorsalis* Mg. (Diptera: Culicidae). Effect of temperature on embryonic diapause in *Aedes caspius dorsalis* Mg. Ent. Rev. 37: 19-35.

Klassen, W. 1959. The influence of the North Saskatchewan river on the dispersion of *Aedes.* Thesis. University of Alberta, Edmonton. 120 pp.

Klassen, W. and B. Hocking. 1963. Control of the dispersion of *Aedes* along a deep river valley. Mosquito News 23: 23-26.

Marshall, J. F. 1938. The British mosquitoes. British Museum (Nat. Hist.) London. 341 pp.

Matheson, R. 1944. Handbook of the mosquitoes of North America. Comstock Publishing Co., Ithaca, N. Y. 314 pp.

Means, R. G. 1965. *Culex territans* Walker biting man in nature. Mosquito News 25: 489.

Muirhead-Thompson, R. C. 1951. Mosquito behavior in relation to malaria transmission in the tropics. Arnold, London. 219 pp.

Nielsen, E. T. and D. M. Rees. 1961. An identification guide to the mosquitoes of Utah. University of Utah, Biological Series 12(3), 63 pp.

Pucat, A. 1964. Seven new records of mosquitoes from Alberta. Mosquito News 24: 419–421.

Pucat, A. 1965. List of mosquitoes from Alberta. Mosquito News 25: 300-302.

Rempel, J. G. 1950. A guide to the mosquito larvae of western Canada. Can. J. Res. D. 28: 207-248.

Rempel, J. G. 1953. The mosquitoes of Saskatchewan. Can. J. Zool. 31: 433-509.

Shelenova, M. F. 1959. The biology of the principal series of *Aedes* in the forest zone of the European part of the U. S. S. R. Med. Parazit. (Mosk.) 28 : 456-462. (In Russian, English summary).

Shemanchuk, J. A. 1965. On the hibernation of *Culex tarsalis* Coquillett, *Culiseta inornata* (Williston) and *Anopheles earlei* Vargas (Diptera:Culicidae) in Alberta. Mosquito News 25: 456-462.

Skiersca, B. 1965. Ecological studies on the occurrence and distribution of the Culicine fauna in the coastal forest belt. Ekologia Polska A. 3: 527-573.

Stage, H. H., C. M. Gjullin and W. W. Yates. 1938. Flight range and longevity of flood water mosquitoes in the lower Columbia River valley. J. econ. Ent. 30: 940-945.

Standfast, H. A. 1965. A miniature light trap which automatically segregates the catch into hourly samples. Mosquito News 25: 48-53.

Steward, C. C. and J. W. McWade. 1961. The mosquitoes of Ontario (Diptera:Culicidae), with keys to species and notes on distribution. Proc. ent. Soc. Ont. 91: 121-188.

Stone, A. 1965. Family Culicidae, pp. 105-120. *In* A. Stone, C. W. Sabrosky, W. W. Wirth, R. H. Foote, and J. R. Coulson (Editors). Agriculture Handbook No. 276. 1696 pp.

Stone, A., K. L. Knight and H. Starke. 1959. A synoptic catalogue of the mosquitoes of the world. Thos. Say Foundation. 358 pp.

Vockeroth, J. R. 1952. The specific status of *Aedes pionips* Dyar (Diptera: Culicidae). Can. Ent. 84: 243-247.

Vockeroth, J. R. 1954. Notes on the identification and distributions of *Aedes* species of northern Canada, with a key to the adult females (Diptera:Culicidae). Can. Ent. 86: 241-245.

Wada, Y. 1965. Population studies of Edmonton mosquitoes. Quaest. ent. 1: 187-222.

Wesenberg-Lund, C. 1921. Contributions to the biology of Danish Culicidae. Mem. Acad. Roy. Sci. et Lettres, Copenhagen, Sec. Sci. 8th ser. No. 1. 210 pp.

Williams, C. B. 1964. Patterns in the balance of nature. Academic Press, London. 324 pp.

OUTBREAKS OF THE BLACK FLY *SIMULIUM ARCTICUM* MALLOCH IN ALBERTA*

F. J. H. FREDEEN
Entomologist
Canada Agriculture Research Station
University Campus
Saskatoon, Saskatchewan

Quaestiones Entomologicae
5: 341-372 1969

The subgenus Gnus *Rubzov is represented in Alberta by at least four species. One of these,* Simulium arcticum *Mall., is the only species of black fly known to kill large farm animals in the province. It is widely distributed, the immature stages occurring in most or all streams and rivers originating on the slopes of the Rocky Mountains and other elevated areas such as the Swan Hills. Outbreaks that have killed animals are known from only two areas. Near Minburn, east of Edmonton, a few cattle were killed and people suffered serious effects from bites in June of 1956 and in late May of 1961. Near Athabasca, north of Edmonton, outbreaks occur throughout a period of several weeks every summer, disrupting grazing and breeding activities and reducing production of milk and beef. A few cattle were killed there in 1955 or 1956, and in June of 1963 and 1964.*

Although bulls are most affected, no farm animals are exempt from attack. Initial attacks are usually so sudden and violent that animals are damaged before they can be taken indoors. Humans are relatively immune to attack but when bitten sometimes require medical attention or even hospitalization.

Other species of the subgenus Gnus *known to occur in Alberta are* S. corbis *Twinn and* S. malyshevi *D. R. and V. in west-central and northern areas and* S. defoliarti *S. and P. in the extreme south-west.* S. nigricoxum *S. is not known outside of the Northwest Territories and Alaska. Damaging outbreaks of* S. defoliarti *occur in south-central British Columbia but not in Alberta.*

DISTRIBUTION OF *S. ARCTICUM* IN ALBERTA

Simulium arcticum Malloch is widely distributed in Alberta (Table 1 and Fig. 1). In addition to the records in Table 1, Hearle (1932) reported that *S. arcticum* was abundant in the Athabasca River at Jasper (no date), Strickland (1938) listed it as occurring on July 19 in the Jasper area (possibly Hearle's collection) and Abdelnur (1968) reported on some aspects of its life history and habits in the Pembina and Athabasca Rivers at Flatbush.

Although larvae and pupae were encountered throughout the entire collecting season (mid-May to early September) the period of greatest abundance on the plains was June 5 to 15, and in the mountains, early July. Future surveys in greater detail will undoubtedly prove that these periods of peak abundance vary from year to year. In Saskatchewan the immature stages have been collected in almost every month of the year although the species normally overwinters as eggs (Fredeen *et al.*, 1951) and larvae and pupae attain greatest abundance between mid-May and mid-June each year.

---

*Contribution No. 349, C. D. A. Research Station, Saskatoon.

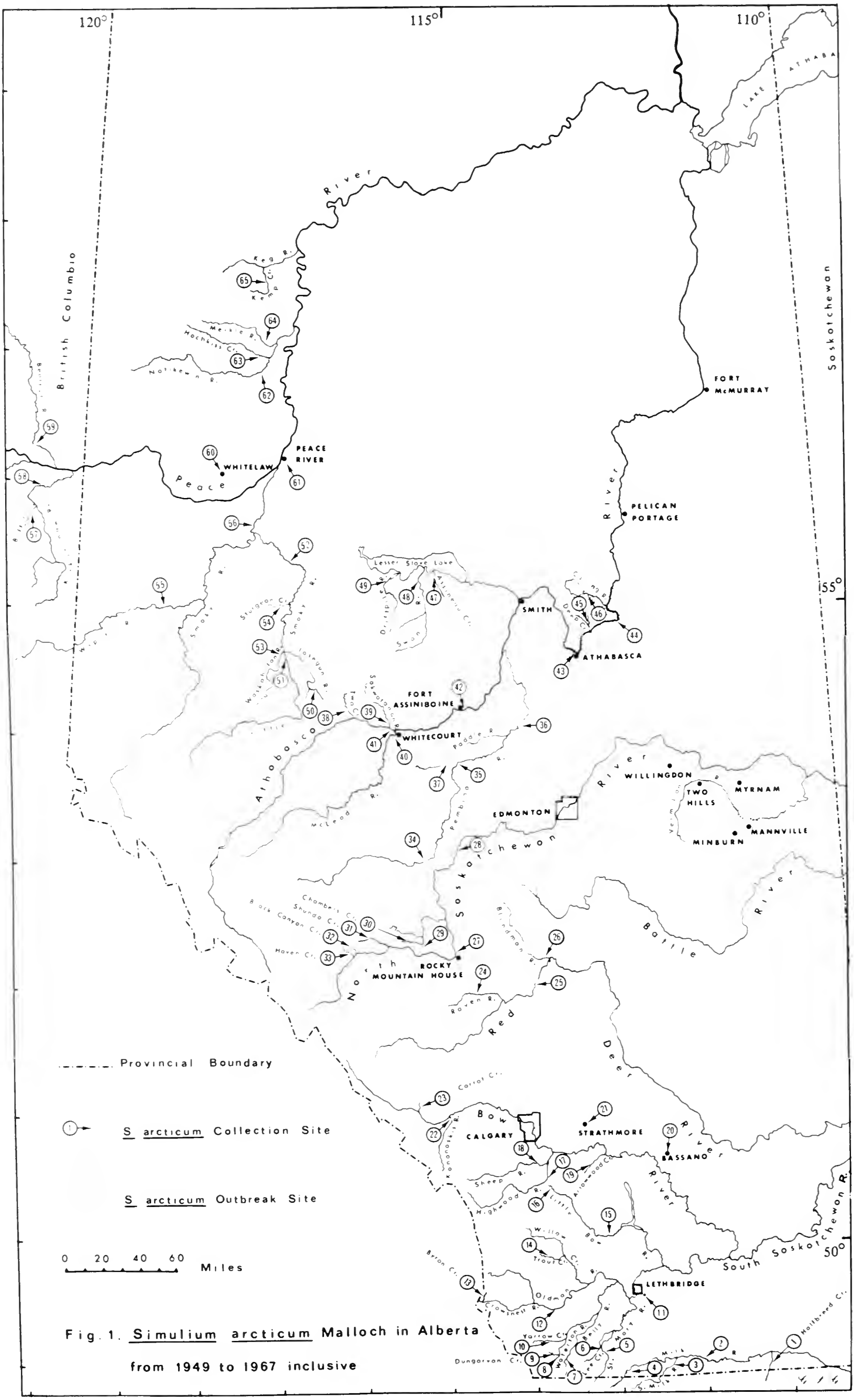


Fig. 1. *Simulium arcticum* Malloch in Alberta from 1949 to 1967 inclusive

TABLE 1. Streams and rivers in Alberta and the Peace River District in British Columbia, from which the immature stages of *Simulium arcticum* Mall. were collected.

Site*	Location	Date	Abundance	Stages of Development**
1	Half Breed Creek, Aden	August 9, 1953	Scarce	L, P.
2	Milk River, Milk River	August 27, 1952	Scarce	L, P.
3	South Milk River, Del Bonita	August 27, 1952	Scarce	L, P.
4	North Milk River, Whiskey Gap	August 27, 1952	Scarce	L, P.
5	St. Mary River, Cardston	August 28, 1952	Scarce	L, P.
		August 10, 1953		
		July 12, 1958		
		September 4, 1958		
6	Lee Creek	August 10, 1953	Scarce	L, P.
7	Belly River, Mountain View	August 28, 1952	Moderate	L, P.
		August 10, 1953		
8	Waterton River, Waterton	August 28, 1952	Moderate	L, P.
9	Dungarvan Creek, Twin Butte	August 10, 1953	Moderate	L, P.
		May 16, 1961		
10	Yarrow Creek, Twin Butte	August 28, 1952	Moderate	L, P.
		August 10, 1953		
11	Irrigation canal, Lethbridge	August 11, 1954	Scarce	L, P.
12	Oldman River, Brocket	August 28, 1952	Scarce	L, P.
13	Byron Creek, Crowsnest	August 8, 1954	Scarce	L, P.
14	Trout Creek, Claresholm	May 15, 1961	Scarce	L, P.

TABLE 1 (continued)

Site*	Location	Date		Abundance	Stages of development**
15	Little Bow River, Carmangay	May	17, 1961	Moderate	L, P. (30% emerged)
16	Little Bow River, High River	August	29, 1952	Scarce	L, P.
17	Highwood River, High River	August	8, 1954	Scarce	L, P.
18	Sheep River, Okotoks	August	29, 1952	Scarce	L, P.
19	Arrowwood Creek, Mossleigh	May	17, 1961	Scarce	L, P. (emergence not begun)
20	Irrigation Canal, Bassano	August	7, 1954	Scarce	L, P.
21	Irrigation Canal, Strathmore	June	18, 1958	Scarce	L, P.
22	Kananaskis River, Seebe	September	8, 1947	Moderate	L, P.
23	Carrot Creek, Duthill	August	31, 1951	Scarce	L, P.
24	Raven River, Caroline	May	28, 1950	Moderate	L, P.
25	Red Deer River, Penhold	June	11, 1949	Scarce	L, P. (emergence beginning)
25	Red Deer River, Penhold	August	30, 1952	Scarce	L, P.
26	Blindman River, Burbank	June	1, 1950	Moderate	L, P. (emergence beginning)
27	N. Saskatchewan R., Rocky Mt. House	June	12, 1949	Abundant	L, P. (2% emerged)
27	N. Saskatchewan R., Rocky Mt. House	September	3, 1952	Scarce	L, P.
28	N. Saskatchewan R., Drayton Valley	July	18, 1961	Scarce	L.
29	Small rill, Horburg	June	10, 1963	Scarce	L, P.
30	Chambers Creek, Horburg	June	10, 1963	Abundant	L, P. (Emergence beginning)
31	Shunda Creek, Nordegg	June	10, 1963	Abundant	L, P.
31	Shunda Creek, Nordegg	July	4, 1963	Scarce	L, P.
32	Black Canyon Creek, Nordegg	June	10, 1963	Scarce	L, P.
		July	4, 1963		

TABLE 1 (continued)

Site*	Location	Date	Abundance	Stages of development**
33	Haven Creek, Nordegg	July 4, 1963	Abundant	L, P. (emergence beginning)
34	Pembina River, Lodgepole	July 11, 1961	Absent	Other species abundant
35	Pembina River, Sangudo	July 11, 1961	Absent	Other species abundant
36	Pembina River, Westlock	July 14, 1961	Scarce	Other species abundant
37	Paddle River, Rochfort	July 11, 1961	Scarce	L, P.
		June 5, 1963		
38	Two Creeks, Windfall	June 5, 1963	Scarce	L, P. (emergence beginning)
38	Two Creeks, Windfall	June 10, 1963	Scarce	L, P. (90% emerged)
39	Sakwatamau River, Whitecourt	June 5, 1963	Abundant	L, P. (emergence beginning)
40	McLeod River, Whitecourt	July 12, 1961	Absent	
40	McLeod River, Whitecourt	June 5, 1963	Abundant	L, P. (about 50% emerged)
40	McLeod River, Whitecourt	July 14, 1964	Scarce	L, P.
41	Athabasca River, Whitecourt	July 14, 1964	Scarce	L.
41	Athabasca River, Whitecourt	July 14, 1964	Moderate	L, P.
42	Athabasca River, Fort Assiniboine	July 14, 1964	Moderate	L, P. (18% emerged)
43	Athabasca River, Athabasca	June 9, 1963	Scarce	P. (empty)
44	Athabasca River, Athabasca	August 3, 1967	Scarce	Adults floating on river surface
45	Deep Creek, Athabasca	June 17, 1966	Scarce	P.
45	Deep Creek, Athabasca	May 30, 1967	Moderate	L.
46	Calling River, Athabasca	August 4, 1967	Scarce	L.
47	Assineau Creek, Wagner	June 9, 1963	Scarce	L, P. (emergence beginning)

TABLE 1 (continued)

Site*	Location	Date	Abundance	Stages of development**
48	Swan River, Kinuso	June 9, 1963	Scarce	L, P. (emergence beginning)
49	Driftpile River, Joussard	June 9, 1963	Scarce	L, P.
50	Iosegun River, Fox Creek	June 10, 1963	Abundant	L, P.
51	Little Smoky River, Fox Creek	June 5, 1963	Abundant	L, P. (emergence beginning)
52	Little Smoky River, Donnelly	June 10, 1963	Moderate	P.
53	Waskahigan River, Little Smoky	June 5, 1963 June 10, 1963	Abundant	L, P. (about 50% emerged)
54	Sturgeon Creek, Valleyview	June 5, 1961	Scarce	P. (all empty)
55	Wapiti River, Grande Prairie	June 9, 1961	Scarce	L, P.
56	Smoky River, Watino	June 21, 1961	Moderate	L.
57	Buffalo Creek, Dawson Creek, B. C.	June 6, 1963	Scarce	L, P. (emergence beginning)
58	Kiskatinaw River, Dawson Creek, B. C.	June 15, 1961	Abundant	L, P. (5% emerged)
59	Beaton River, Cecil Lake, B. C.	June 16, 1961	Scarce	P.
60	Whitelaw, Alberta	July 21, 1964	Scarce	Adults only
61	Peace River, Alberta	July 21, 1964	Scarce	Adults only
62	Notikewin River, Manning	June 7, 1963	Scarce	P. (all empty)
63	Hotchkiss River, Manning	June 7, 1963	Scarce	L, P. (emergence beginning)
64	Meikle River, Manning	June 7, 1963	Scarce	P. (emergence beginning)
65	Kemp Creek, Keg River	June 11, 1963	Scarce	L, P.

* See Figure 1

**L = larvae, P = pupae

The subgenus *Gnus* (Rubzov, 1940) to which *S. arcticum* belongs is holarctic. *S. arcticum*, however, is restricted to western North America, occurring throughout the mountainous regions from Alaska south to California. Specimens have been collected as far east as Churchill, Manitoba (Twinn *et al.*, 1948). In Saskatchewan, farm animals have been killed in numerous outbreaks originating in the Saskatchewan River system (Cameron, 1922; Rempel and Arnason, 1947; Fredeen, 1958). The most destructive series of outbreaks in Saskatchewan occurred 1944 to 1947 inclusive when more than 1100 animals were killed. Some aspects of the life cycle of this black fly other than these outbreaks are described by Fredeen (1958, 1963), Fredeen *et al.* (1951) and Abdelnur (1968). In Alberta, livestock has been killed in at least five outbreaks (Table 2).

The immature stages of three other species of the subgenus *Gnus* were also collected in Alberta and northern British Columbia but these species have never been implicated in damaging outbreaks in Alberta. Specimens of *S. corbis* Twinn were obtained from a few streams and rivers in northern areas and the west-central foothills as follows:

Assineau Creek at Canyon Creek (July 3, 1950, May 31 and June 23, 1961); Fawcett River, Smith (May 31, 1961); Sucker Creek, High Prairie (May 31, 1961); Sweeney Creek, 10 miles S.W. of Clear Prairie (June 16, 1961); Clear Creek, Clear Prairie (June 16, 1961); Wagner Creek, Widewater (June 23, 1961); Sakwatamau River, Whitecourt (June 5, 1963); Ksituan River, Gordondale (June 7, 1963); Chambers Creek and Shunda Creek, Horburg (June 7, 1963); Haven Creek, Nordegg (July 4, 1963); Kiskatinaw River, Dawson Creek, B. C. (June 15, 1961); Buffalo Creek, Progress, B. C. (June 6, 1963).

S. defoliarti was collected only in the foothills in the S. W. corner of the province:

Belly River, W. of Mountain View (August 28, 1962; August 10, 1953); Highwood River, W. of Longview (August 8, 1954); Castle River, W. of Pincher Creek (May 7, 1955); Crowsnest River, N. of Lundbreck (May 7, 1955).

In the Shuswap River in south-central British Columbia this species breeds in such large numbers that chemical control of the larvae is occasionally required. Severe outbreaks in 1951 affected gains in beef animals, causing losses in excess of 24,000 dollars (Curtis, 1954). However, in Alberta it is not known to occur in nuisance numbers. *S. malyshevi* D. R. and V. was collected as follows:

Clearwater River, Waterways (June 18, 1948); E. Prairie River, Enilda (June 3, 1961); Goose Creek, Calais (June 6, 1961); Beaton River, Cecil Lake, B. C. (June 16, 1961).

A fifth species of the subgenus *Gnus*, *S. nigricoxum* S. may also occur in the north end of the province as it is widely distributed in the Northwest Territories and Alaska.

Samples of the immature stages of these black fly species were obtained by wading into the margins of rapids to pick up rocks and tree branches by hand. Equipment has not yet been devised that will allow the river bed to be quantitatively sampled in deep, fast-flowing rapids. Since the levels of mountain-fed rivers are relatively unstable, even at distances of 1000 miles or more from their sources, and since the margins of these rivers advance and retreat irregularly according to rates of snow melt and precipitation in the watersheds, our marginal samples served only to indicate the presence or absence of *S. arcticum*. Seldom were water levels low enough to allow examination of infestations of larvae and pupae in the relatively permanent mid-river sites. However, on June 5, 1963, low levels on the McLeod River at Whitecourt and the Waskahigan and Little Smoky Rivers at Little Smoky, exposed dense infestations of larvae and pupae, approximately similar to those sometimes seen in both branches of the Saskatchewan River in Saskatchewan prior to damaging outbreaks. Moderately dense infestations were discovered in several other large rivers including the

TABLE 2. Damaging black fly outbreaks in Alberta attributed to *Simulium arcticum* Mall.

Source	Area affected		Dates of outbreaks	Damage
	Location	Approximate size (sq miles)		
N. Saskatchewan River	Minburn, etc.	900	1956, second week of June	A few cattle killed, milk production reduced, many people injured, two requiring hospital treatment
N. Saskatchewan River	Minburn, etc.	900	1951, last week of May	A few cattle killed, milk and beef production reduced, some people injured
N. Saskatchewan River	Minburn, etc.	900	1962, May 22 to 25	A mild outbreak, milk cows bothered for a few days
Athabasca River	Grassland, Boyle, etc.	1000	1955 or 1956	A few cattle killed, general productivity of livestock reduced
Athabasca River	Grassland, Boyle, etc.	1000	1963, mid-June to mid-July	Several animals killed including two bulls and four calves, several bulls became sterile, others improved after treatment, production of milk and beef declined noticeably, people and livestock occasionally forced indoors
Athabasca River	Grassland, Boyle, etc.	1000	1964, May 30 to Sept. (worst on June 10-16)	At least one bull killed and two others sterilized; production of milk and beef declined; people, cattle, sheep and horses occasionally forced indoors
Athabasca River	Grassland, Boyle, etc.	1000	1965, June 7 to 24	Livestock severely bothered on June 24
Athabasca River	Grassland, Boyle, etc.	1000	1966, June 24 to Aug. 27 (worst on July 2 to 21 and Aug. 26, 27)	No fatalities but grazing and breeding of livestock affected, beef and milk production noticeably declined, men and cattle were occasionally driven indoors, a few people required medical attention
Athabasca River	Grassland, Boyle, etc.	1000	1967, June 5 to Sept. 28 (worst on June 19 to July 25 and on Sept. 17)	Effects similar to those observed in 1966

North Saskatchewan River at Rocky Mountain House on June 12, 1949 and the Athabasca at Fort Assiniboine on July 14, 1964. Eight per cent of the *S. arcticum* larvae in the Athabasca River in mid-July of 1964 were parasitized with mermithid nematodes, but nowhere else were these parasites observed.

SOME CHARACTERISTICS OF THE NORTH SASKATCHEWAN AND ATHABASCA RIVERS

These two rivers and their major tributaries flow in vegetation-free beds consisting mainly of boulders, gravel and clean sand. The growth of vegetation is effectively prevented by the eroding effect of the ice during the spring breakup and by frequent flood crests during the summer.

In the upper reaches, gradients are relatively steep and boulders and gravel predominate; on the plains the gradient is flatter, often averaging only about one foot per mile, and here the river bed consists mainly of sand. In some regions of the plains, however, the gradients are much steeper than this and the rivers flow in series of rapids over gravel and boulders. These boulders provide favoured attachment sites for enormous numbers of *S. arcticum* larvae and pupae. An outstanding example is a rock-filled weir across the North Saskatchewan River at Prince Albert, Saskatchewan which on June 9 and 10, 1947 was estimated to contain more than 7 x 10^9 pupae (Fredeen, 1958).

On the North Saskatchewan River in Alberta there are rapids north of Willingdon and Myrnam, north to north-west of the outbreak area near Minburn (Fig. 1). On the Athabasca River there are numerous rapids between Whitecourt and Smith, a few scattered rapids from Smith down to about the Pelican Portage Settlement and very numerous rapids and falls downriver from there to Fort McMurray. This latter section of the river has an average gradient of about 5.4 feet per mile and, although it was not sampled during these investigations, was considered likely to be a major breeding site for *S. arcticum*. It is 65 miles and more, directly north of the center of the annual outbreak area in the county of Athabasca.

The average ice-free period in these two rivers lasts from 6.5 to 7.0 months (Table 3). Ice breakup in the spring generally begins when the river level rises sharply as a result of melting snow on the plains and foothills. Following this crest the level generally subsides irregularly until a new major crest occurs in late June or early July as a result of rapid thawing and precipitation in the mountains. Maximum volume discharges ranging up to about 200,000 cu feet/sec have been recorded on both rivers and minimum discharges of less than 2000 cu feet/sec generally occur in the winter.

Water temperatures during the summer in these two rivers are likely to be a few degrees lower than those on the North Saskatchewan at Prince Albert in Saskatchewan where maxima of 70 to 75°F are attained in July and August. There the larvae and pupae of *S. arcticum* attain greatest abundance in May and June when water temperatures range from 45 to 65°F.

Water turbidity increases with increases in the water level. Values greater than 3000 ppm have been measured on the South Saskatchewan River. This turbidity has been used to advantage during black-fly larviciding (Fredeen *et al.*, 1953).

TABLE 3. Some characteristics of the North Saskatchewan River at Edmonton, Alberta. and the Athabasca River at Athabasca, Alberta. (Canada Department of Energy, Mines and Resources, 1967).

	North Saskatchewan River	Athabasca River
Drainage area (sq. miles)	10,500	29,600
Average annual discharge (ft^3/sec)	7,660 (54 years)	15,100 (30 years)
Maximum discharge (ft^3/sec)	204,500 (June 28, 1915)	199,600 (June 10, 1954)
Minimum discharge (ft^3/sec)	220 (Jan. 1, 1940)	1,610 (December 14, 1956)
Average ice-free period (months)	7.0 (April 13 to Nov. 10)	6.5 (April 21 to November 8)

SOME FACTORS INVOLVED IN THE DEVELOPMENT OF DAMAGING OUTBREAKS

Rempel and Arnason (1947) suggested that the appearance of a massive swarm of *S. arcticum* was due simply to mass emergence plus fortuitous winds. Additionally there is recent evidence that the first ovarian cycle may be completed autogenously; in some instances at least, the females do not attack animals for blood until after the eggs from the first ovarian cycle have been laid (Fredeen, 1963). This means that emerging females can accumulate, perhaps throughout a period of several days, awaiting weather conditions suitable for oviposition. This could result in the release of enormous numbers of blood-thirsty black flies within a period of a very few hours. Perhaps both factors have been responsible in the development of damaging outbreaks.

Winds play a very important part in the distribution of adult black flies. Variable-direction winds will scatter them over a wide sector, thinly enough that they will obtain their blood meals unnoticed. However, livestock owners should be wary when the wind blows steadily from proven breeding grounds for even a few hours. In one Saskatchewan outbreak, livestock was killed 140 miles downwind from such a breeding site. In a few other instances an abrupt shift in the wind direction has been known to transfer black flies from one area into another, with resultant fatalities in both (Rempel and Arnason, 1947).

The appearance of large numbers of black flies in a district is generally sudden and furthermore often occurs in the early morning or late evening so that a severe attack can begin before livestock owners are aware of their presence. Also, reactions to massive injections of the toxin are swift, and the animals can become fatally ill within a few hours after the black flies commence their attack.

The nature of the toxin is poorly known. Hutcheon and Chivers-Wilson (1953) showed that the salivary extract contained an anticoagulant and a substance that gave reactions similar to those from histamine. A detailed account of symptoms in cattle is given by Millar and Rempel (1944) who investigated an outbreak of *S. arcticum* in the Macdowall area in Saskatchewan. They reported that residents in the district noticed the appearance of black flies in the district on the evening of May 30 but did not consider them to be unusually abundant until the following morning. Animals subjected to heavy attack throughout May 31 developed fluid-filled swellings along the underlines. Some additionally developed a heavy, jerky breathing accompanied by a strong trembling of the muscles. Animals with such symptoms either died within 15 minutes to two hours, or made a complete recovery within 48 hours. Deaths were attributed to acute toxemia but anaphylactic shock was not ruled out.

TYPES OF LOSSES TO BE EXPECTED DURING OUTBREAKS OF *S. ARCTICUM*

Fatalities

The numbers of fatalities in livestock that have occurred in Alberta as a result of black fly outbreaks are small when compared with losses during the large outbreaks in Saskatchewan in the 1940s. However, about half of the losses were those of herd sires (generally the most expensive animals in the herds). Mature bulls are often more attractive to blood-sucking flies than are cows or calves. Furthermore, imported bulls show less resistance to attack and damage than do native bulls, especially those allowed to spend most of their time out-of-doors. However, whether imported or native, at the first signs of an outbreak the herd sires require special attention and should be stabled or at least kept under close observation.

Some veterinarians were reluctant to agree that these livestock fatalities in Alberta resulted from black fly attacks. Although I did not personally observe any of the fatalities, I agree with the conclusions reached by the owners, none of whom were preconditioned in their thinking by being aware of similar occurrences in Saskatchewan.

Suspension of breeding activities

During black fly outbreaks, breeding activities are interrupted when the cattle become involved in protective activities, i.e. seeking shelter in buildings, dense brush and sloughs. This suspension of breeding activities results in an irregular and delayed calf crop the following year, thus decreasing net returns from the enterprise. Also, individuals of *S. arcticum* normally attack along the underline of an animal and the bull's sheath thus becomes inflamed and may develop secondary infections requiring treatment by a veterinarian. Some bulls remain permanently sterile despite treatment.

Declines in the production of milk and beef

These phenomena are frequently observed by livestock owners but losses are difficult to measure. These losses naturally occur when normal pasture grazing is interrupted and physical activities are increased. Additionally, however, a milking cow's udder is a favourite target for black flies and this makes extraction of milk a more difficult process, either for the nursing calf or for man. Reports from owners such as "black flies drove cattle out of the pasture", "black flies kept cattle in shed all day", "cows' udders red with blood", "cows difficult to milk because of black flies", "milk production down something terrible", are commonplace during outbreaks.

General losses resulting from repeated threats of outbreaks

A loss that is seldom recognized in an area subjected to frequent, severe black fly outbreaks is the general shift from livestock to alternate farm enterprises. In the Athabasca region of Alberta livestock enterprises should predominate to ensure the healthiest economic development of the region because of the relatively short frost-free season, the rough terrain with much marginal land suitable only for pasture and forage crops, and soils that require crop rotations for best productivity. However, some residents have either reduced or eliminated their livestock enterprises and certain highly skilled breeders have even emigrated to other districts where they will not be threatened by black flies. These shifts do not seem to be warranted in terms of measurable losses that have occurred but rather can be attributed to the general suspense created by unpredictable and uncontrolled outbreaks.

The moderate numbers of black flies that occur almost daily during the summer can be tolerated by men and animals without too much discomfort. However, increases in the numbers of black flies can generally be expected whenever the wind blows steadily for a few hours from breeding grounds in the river and occasional outbreaks have also occurred when the wind has blown from some direction other than the river (Fig. 2). Since winds often shift during the night, and black fly flight activity is generally greatest in early morning and late evening hours, many severe outbreaks have begun with surprising suddenness. Sometimes the first indication of an outbreak has been the stampede of cattle from pasture to barn. Less fortunate operators have their livestock scatter into the brush where they are less likely to be protected. Thus a strong element of suspense prevails throughout the outbreak season.

Effects on man

Although people can generally protect themselves with repellents, there are occasional days in the County of Athabasca when people are driven indoors along with their cattle to escape savage attacks. Normally individuals of *S. arcticum* do not attack man but when attacks occur, medical attention may be required to alleviate severe swelling and itching of the affected limbs.

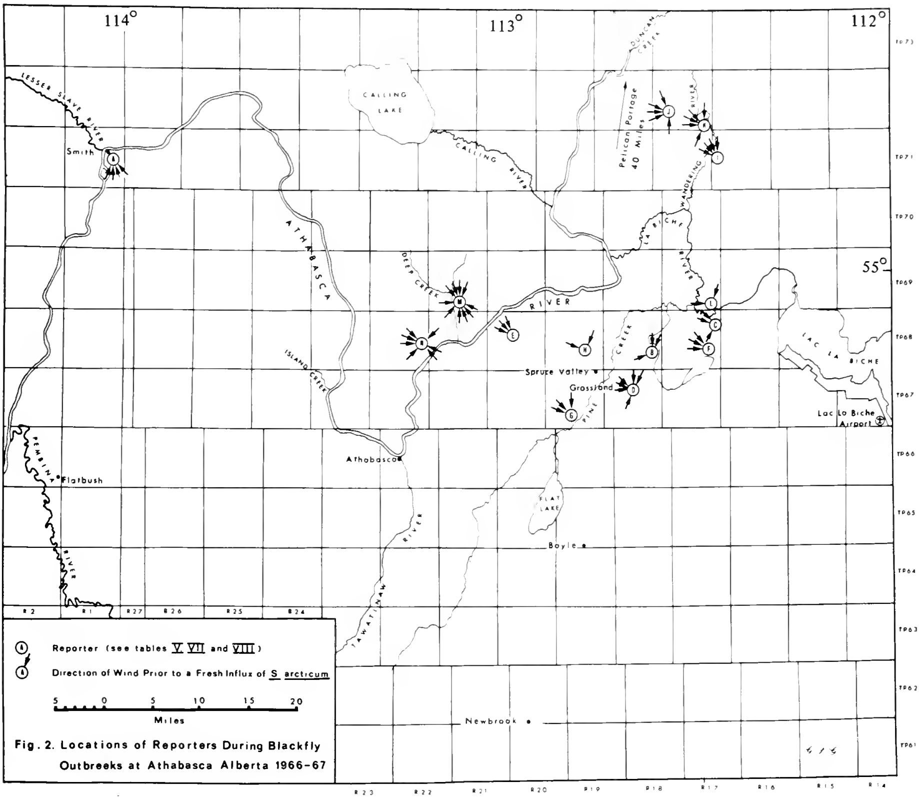


Fig. 2. Locations of Reporters During Blackfly Outbreaks at Athabasca Alberta 1966-67

DESCRIPTIONS OF OUTBREAKS OF *S. ARCTICUM* IN ALBERTA

Outbreaks adjacent to the North Saskatchewan River

A black fly outbreak in the Municipal District of Minburn No. 72 was investigated on July 9 and 10, 1961 at the request of Mr. J. B. Gurba, Supervisor of Crop Protection and Pest Control for the Alberta Department of Agriculture. The outbreak had actually occurred during the third week in May but was of such short duration that by the time the black flies had been identified as *S. arcticum* conditions had already returned to normal. Thus the purpose of my visit in July was to determine the extent and severity of the outbreak by interviewing livestock owners. The following were interviewed at a Municipal Council meeting and others on their farms: Mr. C. Gamble, a local livestock feeder and Field Supervisor for the Municipal District, Mr. Ed. McLaughlin, farming about 6 miles N. W. of Mannville, Mr. A. W. Roland, about 5 miles S. of Minburn and Mr. G. Grabos, ½ mile S. of Innisfree. They stated that black flies were pests of mammals, especially milking cows, every year for a few days around the third week in May. Outbreaks were reported to have been especially severe in dry years, the worst outbreaks having occurred in 1956 and 1961 when an area of about 900 square miles centering on Mannville was affected (Fig. 1). During each of these two outbreaks a few cattle were reported to have been killed and the udders of milk cows were red with blood. Among others, Mr. McMillan farming east of Mannville lost cattle during the 1956 outbreak.

Perhaps the most serious aspect of these two outbreaks was the requirement by many people for medical attention as a result of complications following black fly bites. This has also been a common feature of *S. arcticum* outbreaks in Saskatchewan. Dr. Hasinoff of the Municipal Hospital at Minburn informed me that he had treated many people for black fly bites in 1956. They had come from an area 30 to 40 miles in diameter surrounding Mannville and Minburn. Black flies collected while attacking people were all *S. arcticum.*

Two men in particular had had such severe reactions in 1956 that they required long medical attention and one of these, a Mr. S., was still unwell in 1961. The following symptoms, and the results of clinical tests in Edmonton, led Dr. Hasinoff to believe that Mr. S. exhibited a distinct case of Arthus' syndrome (Brown *et al.*, 1938) or localized anaphylactic reactions following sensitization by injections of black fly toxins. Dr. Hasinoff stated that Mr. S. reported to him on June 10, 1956 in respiratory distress, itchy and with evidence of black fly bites. Later he developed ulcers down to the bone on limbs that had not been bitten. These were not due to infection but could only be ascribed to allergic reactions to the black fly toxins. Mr. S. spent 5 months in the hospital before the ulcers finally healed. Gudgel and Grauer (1954) and others have described severe reactions in humans that necessitated medical treatment at the actual locations of black fly bites, but this may be the first case where reactions have been observed in areas of the body remote from locations where the bites occurred.

In 1962, May 22 to 25, another outbreak of *S. arcticum* occurred in the Mannville area but this was of moderate intensity. By the time we received word of it and visited the area on May 26 to 30 the outbreak had ended. However, specimens collected from barn windows were all *S. arcticum.* On May 26, only a few adults could be collected around cattle and these were a mixture of *S. arcticum* and *S. venustum* Say. The weather became cool and wet about this time and individuals of these two species disappeared. Near Two Hills and Myrnam a few specimens of *Cnephia saskatchewana* S. and F. were collected flying around cattle but none were actually seen on the cattle.

Since 1962 no further reports of black fly outbreaks have been received from this district. On May 22, 1963 only a few *S. venustum* and *S. vittatum* Zett. were found around cattle.

These outbreaks of *S. arcticum* all occurred following northerly winds and thus the extensive rapids on the North Saskatchewan River at several sites north of Willingdon and Myrnam may have been the sources (Fig. 1). I have never examined these rapids for larvae or pupae because of high water levels at the times I was in the area. However, on several occasions I found abundant *S. arcticum* larvae in the North Saskatchewan River or its tributaries above Edmonton (Table 1) and also at several sites in the province of Saskatchewan. Individuals of this species have never been collected from the Vermilion or Battle Rivers despite several thorough searches. On the other hand species such as *S. venustum* breed in these smaller rivers but not in the Saskatchewan River. Experience has shown that individuals of *S. venustum* can be annoying to animals and man living within a half mile of their breeding places but not far beyond that distance. Individuals of *S. arcticum* are known to have a much longer flight range and thus when animals have been killed or damaged several miles from the nearest potential breeding site, *S. arcticum* rather than *S. venustum* has always been the culprit.

The possibility should not be overlooked that the Athabasca River rather than the Saskatchewan may have been the source of the black flies in the outbreaks in the Minburn area. This would have required flights of about 150 miles, but in one outbreak of *S. arcticum* in Saskatchewan, livestock were killed by black flies that had been carried by the wind more than 140 miles from their point of origin (Fredeen, 1958). Two separate sources however are suggested by the differences in the seasons of the outbreaks, those at Minburn occurring between late May and early June, and those at Athabasca between late May and July and occasionally August or September.

In the North Saskatchewan above Edmonton, *S. arcticum* larvae and pupae are sometimes abundant but severe outbreaks have never been reported from that area. A farmer near Rocky Mountain House reported in 1949 that black flies were common and troublesome throughout June, July and August every year. He had also observed swellings under the jaws of horses during the black fly seasons and reported that a disease locally called "swamp fever" used to kill many horses. Horses newly brought into the area were said to have been particularly susceptible to swamp fever. The symptoms included swellings under the belly, bleeding from the mouth and nostrils and rapid mortalities. These symptoms suggest black fly damage but for the fact that fatalities in cattle did not occur according to the reporter.

Outbreaks adjacent to the Athabasca River

Residents in the County of Athabasca report that since the earliest years of settlement, annual outbreaks of "sand flies" or black flies have occurred. They were believed to originate in the large swampy areas near the Athabasca and La Biche Rivers. Although they make their first appearance during northerly winds in late May or in June and often persist into September, the swarms doing the greatest damage are always expected in late June or early July.

Livestock has been killed apparently only in three years, 1955 (or 1956), 1963 and 1964. However, every year livestock productivity is affected to some degree. These outbreaks were regarded as uncontrollable events until 1963, following establishment of a County Agricultural Service Board. When an unusually severe outbreak occurred in 1963, the County Agricultural Fieldman, Mr. H. Armfelt, recognized the problem as one that required immediate attention. He obtained the assistance of Mr. J. B. Gurba and on July 12 they surveyed the outbreak area and obtained the following information (Gurba, 1963). The "sand flies" had appeared suddenly that year after the first warm period in June. Arriving on northerly winds they caused greatest damage in an area measuring about 20 miles north and south by 5 miles east and west, centered on Grassland and Spruce Valley. Scattered instances of attack occurred as far south as Boyle and Newbrook. Two bulls and four calves were killed by the black flies about June 15 and many other animals became ill, some requiring a veterinarian's attention. Livestock and people new to the area were most severely affected. Insecticide sprays and smudges gave some relief to milking cows but in general milk and beef production declined noticeably during June and July. Black flies collected from cattle on July 12 were all *S. arcticum*. As a result of this outbreak I was asked to help locate breeding areas and recommend control measures.

In July of 1964 a careful examination of the Athabasca River between Whitecourt and Smith proved the existence of numerous rapids well populated with *S. arcticum* larvae and pupae. Unfortunately a sudden rise in the water level prevented examination of rapids below Smith at that time.

Also in July of 1964, a number of livestock owners in the eastern half of the County of Athabasca were interviewed and their reports showed that another extensive outbreak had occurred. Black flies had been first seen around cattle on May 30 after an all-day wind from the north. However, June 10 was the first day that the cattle were noticeably irritated by the black flies. On June 16 a new influx of black flies on a north wind forced man and livestock alike to remain indoors and killed at least one bull. This appearance of the first damaging swarms of the year during the first warm weather in mid-June was said to be typical. For about three weeks in 1964 these attacks continued to affect normal grazing and breeding activities, milk production and weight gains.

Black flies collected alive from cattle and horses in many localities in the County on July 18 and 19, 1964 were 92% *S. arcticum*, 6% *S. venustum* and 2% *S. vittatum*. Although these black flies were moderately abundant around cattle, the latter were grazing normally in the pastures. Collections of dead flies from the windows of a barn six miles northwest of Grassland, presumably trapped during the spring outbreak of 1964, contained 99% *S. arcticum* and 1% *S. venustum*. Thus although *S. arcticum* seemed to be the main species involved in the outbreaks of 1964, precise information as to the relative importance of it and other local species throughout all spring and summer outbreaks was still lacking. This information was obtained in two ways: by a widespread survey for the immature stages in streams and rivers in and near the County in 1964, 1966 and 1967, and by collecting adults from widespread attacking swarms throughout the entire outbreak seasons of 1966 and 1967.

The area in and around the County of Athabasca is traversed by many small streams, a few small rivers such as the La Biche and Wandering Rivers, and one large river, the Athabasca (Fig. 2). Early in these investigations it was thought that *S. venustum*, especially from the La Biche and Wandering Rivers, might have been at least partly responsible for the severe outbreaks in nearby farmlands almost directly south of these rivers. The survey of rivers and streams showed that *S. venustum* was actually widespread, but abundant in only two streams, Pine Creek (May 31, 1967) and Wandering River (May 18 and June 7, 1966, and May 31, 1967) (Table 4). Other species whose immature stages were also widespread included *S. verecundum* S. and J. (a close relative of *S. venustum* although apparently nonbiting (Stone and Jamnback, 1955)), *S. vittatum* and *S. tuberosum* (Lund.). Individuals of *S. vittatum* are large and grey, commonly seen in the ears of livestock, but are not usually considered to be serious pests. They were occasionally abundant in the La Biche River, Calling River and Pine Creek. *S. tuberosum*, although widespread, was never abundant. *S. arcticum* was abundant only in the Athabasca River. Insignificant numbers were found breeding in Calling River and Deep Creek but these sources were too small to have contributed significantly to the outbreaks.

TABLE 4. Species of black fly larvae and pupae found in rivers and streams in Athabasca County and its environs, 1964 to 1967 inclusive

Species	Collection data
Prosimulium gibsoni (Twinn)	Duncan Creek, May 17, 1966
Simulium arcticum Mall.	Athabasca River (Whitecourt to Smith) (moderate numbers) July 14, 1964; Deep Creek, rare, June 17, 1966 and May 30, 1967; Calling River, rare, August 4, 1967
S. aureum Fries	La Biche River, July 19, 1964
S. croxtoni N. and M.	Island Creek, June 15, 1966
S. decorum Walker	Tawatinaw River, July 16, 1964; Flat Creek, June 20, 1967; Pine Creek, June 14, 1967; Babiak Creek, June 20, 1967
S. furculatum (Shewell)	Deep Creek, June 15, 1966
S. latipes (Meigen)	Pine Creek, June 14, 1966; Creek S. E. 27-68-20, June 16, 1966; Wandering River, June 7, 1966
S. luggeri N. and M.	Pembina River, July 15, 1964
S. meridionale Riley	Pembina River, July 15, 1964; Lesser Slave River, July 20, 1964
S. rugglesi N. and M.	Pembina River, July 15, 1964
S. tuberosum (Lund.)	Widespread but scarce, May to July inclusive
S. venustum Say	Widespread, May to August inclusive; abundant in Pine Creek, May 31, 1967; Wandering River, May 18 and June 7, 1966, May 31, 1967
S. verecundum S. and J.	Widespread, June and July; abundant in Bear Creek and Deer Creek, June 16, 1966
S. vittatum Zett.	Widespread, May to October inclusive; abundant in La Biche River, July 19, 1964 and May 17, 1966, Calling River, July 18, 1964 and Pine Creek, July 21, 1966

Altogether the immature stages of 14 species were discovered. Of these, *S. arcticum*, because of the immensity of its breeding site, was considered to have the greatest potential for developing large, damaging swarms.

Despite these extensive collections of the immature stages, decisive evidence as to the actual species involved in the outbreaks was obtained only with the co-operation of 14 residents, situated in and near the County (Table 5, Fig. 2) who netted more than 46,000 black flies from swarms attacking their livestock in 1966 and 1967 (Table 6). At some of the sites black flies were netted every three days or so (oftener during outbreaks), throughout much of the spring and summer flight periods; at other sites, collections were taken only during prominent outbreaks.

In 1966, *S. arcticum* represented 92.2% of all black flies netted and in 1967, 89.6%. *S. venustum* appeared in moderate abundance on only one occasion, May 31, 1967, (site no. 14, Fig. 2) and *S. vittatum* on one occasion, September 17, 1967 (site no. 9, Fig. 2). At all

TABLE 5. Collectors and observers of black fly activity in and near the County of Athabasca in 1966 and 1967.

Reference symbol (See map, Fig. 2)	Years of observations		Name	Direction of winds required to bring black flies from major breeding sites on the Athabasca River
	1966	1967		
A		x	Earl, J.	S. and E.
B	x		Davidiuk, J.	N. and N. W.
C		x	Fischer, Mrs. J.	N. and N. W.
D	x	x	Guy, M.	N. and N. W.
E	x	x	Kamelchuk, J.	N. and N. W.
F	x	x	Semashkewich, J.	N. and N. W.
G	x	x	Whitney, J.	N. and N. W.
H	x	x	Zelinski, N.	N. and N. W.
I *	x	x	Coonan, B. and L.	N., N. W. and W.
J *		x	Mitchell, M.	N., N. W. and W.
K *	x	x	Rabkavich, P.	N., N. W. and W.
L *	x		Steed, L.	N., N. W. and W.
M	x	x	Klak, W.	N., E. and S. E.
N	x	x	Shalapay, D.	N., E. and S. E.

*These sites are north of the La Biche River but, except for L, are located near the Wandering River.

TABLE 6. Species of black flies collected from swarms near farm animals, in and near the County of Athabasca*, Alberta, 1966 and 1967

	1966		1967		
Total no. collected	12,764 % of total	No. of times collected	33,603 % of total	No. of times collected	Sources of collections**
S. arcticum Mall.	92.2	70	89.6	92	Cattle, hogs, horses, sheep
S. decorum Walk.	0.1	6	0.9	18	Cattle, horses
S. furculatum (S.)	< 0.1	1	0.0	0	Farmyard
S. latipes (M.)	0.0	0	> 0.1	1	Cattle
S. meridionale Riley	< 0.1	2	0.0	0	Cattle
S. pugetense (D. & S.)	< 0.1	2	0.0	0	Farmyard
S. tuberosum (L.)	< 0.1	3	0.5	20	Cattle, hogs
S. venustum Say and *S. verecundum* S. & J.	4.5	33	2.3	58	Cattle, hogs, horses, sheep
S. vittatum Zett.	3.1	52	6.7	63	Cattle, hogs, horses, sheep

* See Fig. 2 for locations of the collection sites.

**Some of the *S. arcticum* were collected from barn windows after detaching from livestock that had carried them into the buildings.

other times only relatively small numbers representing species other than *S. arcticum* were collected (Table 6). Thus it seems certain that the several severe and sometimes damaging outbreaks in 1966 and 1967 were caused by individuals of *S. arcticum*, only.

Although the immense numbers of *S. arcticum* observed could only have had their origin in a large river, i.e. the Athabasca, additional evidence as to the sources of these outbreaks was obtained by relating the times of the outbreaks as reported by the co-operators, to hourly wind data obtained from the Canada Department of Transport Meteorological Station at the Lac La Biche Airport located 29 miles east and four south of Grassland P. O. These data are listed in Tables 7 and 8. Almost invariably, each fresh invasion of black flies, as indicated by a distinct increase in the severity of attack, was found to have been preceded by winds blowing from some section of the Athabasca River (Fig. 2). On a few occasions, however, the wind had been blowing from some other direction, or had been virtually calm. Perhaps some of these anomalies were due to the fact that the wind and black fly data came from sites separated by 30 miles or more. However, individuals of *S. arcticum* have been observed to move upwind for short distances during outbreaks in Saskatchewan. In one instance they seemingly moved 1.5 miles against a wind strong enough to raise dust from the

TABLE 7. Wind conditions prior to outbreaks of *S. arcticum* Mall. in and near the County of Athabasca, Alberta, in 1966

Time of report and/or collection		Data from observers			Number of hours that the wind** had been blowing from the Athabasca River immediately prior to the observations	Net wind vector**	
Day	Hour	Observer*	Report	No. of *S. arcticum* collected		Direction	Total miles
June 24	1900 (est)	H	From cattle	1	8	NW	28
June 25	1900 (est)	D & F	From cattle	2	8	W	82
June 26	1900 (est)	F	From cattle	8	0	(winds light, ESE)	
June 28	1900 (est)	F	From cattle	6	0	(winds SE)	
June 30	1900 (est)	B	From cattle	22	2	WSW	13
July 1	1900 (est)	F	From cattle	19	13	WNW	46
July 2	0930	B	Extremely bad in morning	340	0 The black flies	(calm in AM,	
July 2	1120	D	Air black with flies	473	0 apparently	then light, easterly)	
July 2	0830	F	Solid cloud around cattle	1470	0 entered the		
July 2	1000	G	First big outbreak	30	0 area on the		
July 2	0600	H	First big outbreak; came early in AM	91	0 westerly winds		
July 2	1100	I	From cattle and barn window	206	0 of July 1		
July 3	1900 (est)	M	From cattle	330	39	ESE	296
July 3	1900 (est)	N	From cattle	21	39	ESE	296
July 4	1920	F	Many around cattle	84	4	WNW	10
July 5	1975	F	Many around cattle; girl bitten	269	7	NW	45
July 5	1500	G	Flies quite bad	0	2	N	19

TABLE 7. (continued)

Time of report and/or collection		Data from observers			Number of hours that the wind** had been blowing from the Athabasca River immediately prior to the observations	Net wind vector**	
Day	Hour	Observer*	Report	No. of *S. arcticum* collected		Direction	Total miles
July 6	1900 (est)	B	From cattle	6	5	W	47
July 7	1600	M	From cattle	103	13	SW	59
July 7	1600	N	From cattle	11	13	SW	59
July 8	0830	E	Many around cattle, making them nervous	9	1	SW	8
July 9	1900	F	From cattle	622	8	W	67
July 9	1900 (est)	L	From cattle	6	8	W	67
July 10	1830	B	Very bad today	47	3	N	4
July 10	1900 (est)	N	From cattle	1	11	W	19
July 11	0815	D	Lots of flies	243	15	WNW	87
July 11	0930	E	Many around cattle	43	17	WNW	105
July 11	1900 (est)	M	From cattle	232	0	(NW wind)	
July 12	0830	F	From cattle	128	36	NW	216
July 12	1900 (est)	K	From cattle	19	0	(wind light, SE)	
July 13	1900 (est)	M	From cattle	55	39	SE	103
July 14	1900 (est)	E	From cattle	49	0	(wind light, E)	
July 14	1900 (est)	G	From cattle	1	0	(wind light, E)	
July 15	1900	B	From cattle	112	0	(wind light, SE, NE)	

TABLE 7. (continued)

Time of report and/or collection		Data from observers			Number of hours that the wind** had been blowing from the Athabasca River immediately prior to the observations	Net wind vector**	
Day	Hour	Observer*	Report	No. of *S. arcticum* collected		Direction	Total miles
July 15	1900	H	Many in evenings of July 15 and 16	247	0	(wind light, SE, NE)	
July 16	1930	D	Flies pretty thick	256	4	NNE	14
July 16	1900 (est)	K	From cattle	23	3	NE	11
July 16	1900 (est)	M	From cattle	411	9	ESE	16
July 17	1900 (est)	E	From cattle	49	28	WNW	125
July 17	2030	F	From cattle in barn	480	29	WNW	125
July 17	1900 (est)	N	From cattle	1	0	(wind light, NW)	
July 18	1800	F	Collected near barn	53	0	(calm)	
July 20	1900 (est)	B	From cattle	17	22	WNW	122
July 20	0700	E	Lots of flies in morning	63	11	NNW	40
July 21	2030	D	Bad attack on cattle today	314	47	WNW	428
July 21	1915	F	Collected from cattle near barn	58	46	WNW	428
July 23	1900 (est)	E	From cattle	54	7	W	70
July 23	1900	F	From cattle near barn	74	7	W	70
July 24	1900	H	Many, although none earlier today	158	19	NNE	75
July 24	1900 (est)	H	From cattle	1	19	NNE	75
July 26	1900 (est)	E	From cattle	28	19	NW	37

TABLE 7. (continued)

Time of report and/or collection		Data from observers			Number of hours that the wind** had been blowing from the Athabasca River immediately prior to the observations	Net wind vector**	
Day	Hour	Observer*	Report	No. of *S. arcticum* collected		Direction	Total miles
July 26	1900 (est)	F	From cattle	9	19	NW	37
July 28	1500	F	From cattle	10	14	W	89
July 29	1900	E	From cattle	27	13	W	146
July 30	1700	B	From cattle	10	4	W	13
Aug. 1	0800	E	Many around cattle	86	0	(7 hour calm in AM)	
Aug. 1	1900 (est)	F		1	0	(7 hour calm in AM)	
Aug. 4	1200	E	From cattle	15	11	WNW	26
Aug. 8	1900 (est)	E	From cattle	30	0	(winds SSE)	
Aug. 12	1900 (est)	E	From cattle	32	19	WNW	123
Aug. 26	1900 (est)	B	From cattle	216	18	NNE	45
Aug. 26	0800	I	From cattle	2648	24	WNW	33
Aug. 27	0800	I	From cattle	922	48	N	127

* See map (Fig. 2) for locations of observers.

**Wind data were obtained from the Canada Department of Transport, Meteorological Branch Station at Lac La Biche Airport, Alberta.

TABLE 8. Wind conditions prior to outbreaks of *S. arcticum* Mall. in and near the County of Athabasca, Alberta, in 1967

Time of report and/or collection		Data from observers			Number of hours that the wind** had been blowing from the Athabasca River immediately prior to the observations	Net wind vector**	
Day	Hour	Observer*	Report	No. of *S. arcticum* collected		Direction	Total miles
June 5	1730	I	A few flying, others on cattle	1	17	NNW	93
June 15	1800	K		2	0	(calm)	
June 19	1930	C	Black cloud around animals	527	42	WNW	225
June 19	1600	D	Black flies came all at once	164	38	WNW	231
June 19	0930	J	Not too many up until now	13	32	WNW	88
June 20	1800	D	Very bad around sheep	268	65	WNW	325
June 20	0900	E	First appearance of large numbers	47	56	WNW	252
June 20	1000	G	Flies worst yet; not really bad though	1	57	WNW	259
June 20	1900	K		39	66	NW	341
June 20	2100	M	Flies chased cows out of pasture	47	5	N	38
June 20	1100	N	From milk cows	70	58	WNW	269
June 21	0900	M	Cows would not stay in pasture	63	17	NNE	77
June 22	2100	C	Flies very bad since June 18	1888	115	NW	518
June 22	0730	D	Yard was full of black flies	385	102	NW	435
June 22	1600	D	Flies came by the millions	262	110	NW	496
June 23	1200	E	Many flies, mostly around noon	42	130	NW	514

TABLE 8. (continued)

Time of report and/or collection		Data from observers			Number of hours that the wind** had been blowing from the Athabasca River immediately prior to the observations	Net wind vector**	
Day	Hour	Observer*	Report	No. of *S. arcticum* collected		Direction	Total miles
June 23	1830	G	Flies moderately bad	2	137	NW	504
June 23	2030	I	Flies thicker in late afternoon	632	139	NW	504
June 23	0900	J	From cattle in yard	29	127	NW	510
June 23	0900	M	Hordes of flies in barnyard	48	127	NW	510
June 23	1100	N	Bad on cows' udders	42	129	NW	510
June 24	1830	F	From cattle in yard	1	0	(virtually calm)	
June 24	0900	M	From barn window	93	26	W	30
June 25	1830	A	Today is the heaviest infestation	46	15	SSW	38
June 25	2010	C	Milk production down something terrible	137	0	(light S. winds)	
June 25	1800	D	Flies on cattle in pasture	34	0	(light S. winds)	
June 25	1000	G	Flies not bad; cattle resting easily	8	0	(light S. winds)	
June 25	1830	K	Flies very bad	37	10	SSW	32
June 26	2000	D	Black flies everywhere	300	13	NW	41
June 26	1100	E	Lots feeding on hogs and cattle	116	4	W	20
June 26	1000	J	On cattle	190	5	WSW	17
June 27	0800	F	By cattle	55	25	WNW	45

TABLE 8. (continued)

Time of report and/or collection		Data from observers			Number of hours that the wind** had been blowing from the Athabasca River immediately prior to the observations	Net wind vector**	
Day	Hour	Observer*	Report	No. of *S. arcticum* collected		Direction	Total miles
June 27	0930	G	Worst yet but not bad	4	27	WNW	58
June 29	2015	C	Feeding only; not as many as on 26, 27, 28	875	19	W	259
June 29	1700	E	Not many sandflies	15	16	W	232
June 29	1530	J	Infestation less heavy than normal	750	15	W	222
June 30	1930	D	Black flies kept cattle in shed today	890	24	W	299
July 1	1900	D	Air black with flies; they kept sheep in shed	571	11	N	64
July 1	0930	G	Not many flies	20	38	WNW	375
July 1	1700	I	Flies very thick; many feeding	2048	9	NNW	67
July 1	1830	K	Flies very bad	1495	11	N	65
July 1	0900	M	From barn window	71	6	WNW	48
July 1	2000	N	Flies around cattle	22	7	NE	44
July 2	0630	A	Heaviest infestation; flies mainly feeding	46	8	NNW	37
July 2	2030	C	Worst yet; flies in clouds	1160	14	SSW	36
July 2	2000	D	Millions; cows stayed in barn all day	393	13	SSW	36
July 2	1730	E	Flying around hogs	114	11	NNW	42
July 3	0745	J	Around cows in yard	248	25	S	52

TABLE 8. (continued)

Time of report and/or collection		Data from observers			Number of hours that the wind** had been blowing from the Athabasca River immediately prior to the observations	Net wind vector**	
Day	Hour	Observer*	Report	No. of *S. arcticum* collected		Direction	Total miles
July 3	2100	M	On barn windows	75	56	SSE	175
July 6	0730	E	Lot of sand flies around cattle	404	0	(light S. winds)	
July 6	1630	G	Flies pretty bad around horse	3	2	NW	9
July 6	1500	I	Very many flies; mostly feeding	932	0	(light SE winds)	
July 6	1100	J	From cows in yard	387	0	(light SE winds)	
July 8	0630	A	Not too thick but bothering cattle some	65	7	S	8
July 8	0900	F	Quite mean to cattle this morning	662	4	WNW	4
July 8	1130	N	From cows in yard	840	3	NE	10
July 9	2000	D	From cows in yard	826	25	WNW	195
July 9	1800	F	From cows in yard	473	23	WNW	184
July 10	2030	C	Clouds of black flies; most this year	1520	50	WNW	478
July 10	2000	H	From barn window	163	49	WNW	469
July 10	1400	J	From cow in yard	1635	43	WNW	419
July 11	0700	A	From cattle in yard	62	0	(calm)	
July 11	0730	E	Lots of sand flies around cattle	404	61	WNW	440
July 11	1030	M	From barn window	50	5	ENE	11

TABLE 8. (continued)

Time of report and/or collection		Data from observers			Number of hours that the wind** had been blowing from the Athabasca River immediately prior to the observations	Net wind vector**	
Day	Hour	Observer*	Report	No. of *S. arcticum* collected		Direction	Total miles
July 11	1000	N	From cattle in yard	268	5	NE	7
July 13	0630	A	Quite a few on cattle	95	7	SE	70
July 13	0930	F	Around cattle in yard	198	0	(from SE)	
July 13	0800	N	Around cattle in yard	509	52	SE	382
July 14	0800	F	Around cattle in yard	6	16	W	113
July 14	1930	F	Very many; seem to be meaner than usual	497	28	W	287
July 14	1330	J	Around cattle in yard	765	22	W	202
July 15	1830	K	Flies very bad	264	51	W	226
July 15	1000	N	Around cattle in yard	349	10	W	28
July 16	0900	E	Very many all day	249	0	(winds light from SE)	
July 17	0600	A	Flies worst when air is calm	71	7	SE	42
July 17	0830	N	Around cattle in yard	374	57	SE	164
July 18	0830	F	Flies have been quite bad last few days	844	9	NW	27
July 18	0900	M	Flies from barn window	59	0	(light N winds)	
July 19	1815	A	From cattle in yard	80	1	SSE	5
July 19	0800	E	Many flying and feeding	192	6	N	5

TABLE 8. (continued)

Time of report and/or collection			Data from observers			Number of hours that the wind** had been blowing from the Athabasca River immediately prior to the observations	Net wind vector**	
Day		Hour	Observer*	Report	No. of *S. arcticum* collected		Direction	Total miles
July	19	1700	J	Around cattle in yard	83	3	WNW	6
July	19	0900	N	Around cattle in yard	543	1	ESE	5
July	23	2015	C	Flies quite bad	434	39	W	208
July	23	0900	E	Many sandflies; cattle kicking	370	28	WNW	168
July	23	0900	F	From cattle in yard	76	28	WNW	168
July	25	1700	D	Air black with black flies	338	4	W	37
July	27	1430	J	From cattle in yard	187	4	NNW	25
Aug.	13	1830	J	From cattle in yard	308	40	W	266
Aug.	16	1700	D	Not many black flies	73	0	(from NE)	
Sept.	17	1000	I	Around cattle in yard	184	22	SSW	31
Sept.	18	0900	M	From barn window	34	19	S	22
Sept.	28	1800	K		14	12	WNW	133

* See map (Fig. 2) for locations of observers

**Wind data were obtained from the Canada Department of Transport, Meteorological Branch Station at Lac La Biche Airport, Alberta.

fields. The livestock they attacked was pastured near the edge of a wooded valley connected to the Saskatchewan River Valley and the black flies presumably made most of their upwind approach in the shelter of the valley walls and trees.

The annual outbreaks in the County of Athabasca are of unusual duration. Outbreaks at Minburn and in the Province of Saskatchewan last for only a few days whereas at Athabasca they often last for three or four weeks. For instance, in 1966 an outbreak began with typical violent suddenness on July 2 and continued with slowly declining severity until August 1. Remissions occurred mainly on those days when the wind was blowing towards the river rather than from it. An apparent second outbreak in 1966, lasting only two days, occurred in late August (Table 7). (Similar autumn outbreaks have occurred in Saskatchewan).

In 1967 the annual outbreak began suddenly on June 19 and continued with only a few brief remissions until at least July 25. Again there was a distinctly separate autumn outbreak, this time on September 17 and 18, but the outbreak was sufficiently mild that it was observed at only two sites.

Abdelnur (1968) recorded four apparent cycles of *S. arcticum* larval abundance in the Athabasca River in 1965, with peaks in late May, early July, early August and mid-September. However, his data, based on direct counts of larvae, presumably obtained by wading into shallow marginal areas of the river bed, would have been indirectly affected by daily changes in the water level. For example, samples obtained from marginal waters when the river level was stationary or falling could be expected to contain relatively large numbers of larvae from permanent colonies whereas samples obtained from newly colonized areas during periods of rising levels would contain relatively few larvae.

DISCUSSION, CONCLUSIONS AND FUTURE OUTLOOK

S. arcticum is widespread in Alberta and individuals typically breed in mountain-fed rivers and streams. Although individuals of a few other species of black fly also breed occasionally in these rivers, only those of *S. arcticum* are believed capable of developing in such large numbers that damaging outbreaks can occur. The precise factors affecting abundance and the subsequent development of outbreaks are not known.

Outbreaks in the Minburn area, presumably arising from the North Saskatchewan River downriver from Edmonton are rare. Only two brief damaging outbreaks have been recorded, one having occurred in late May of 1956 and the other in late May of 1961. Perhaps records of additional outbreaks of earlier years may eventually be discovered.

Outbreaks in the Athabasca area, arising from the Athabasca River, occur annually and generally last for several weeks at a time. Beginning as early as mid-June, they have lasted until about mid-September.

An abatement programme is presently being developed for the Athabasca area. Biological abatement does not seem feasible with our current state of knowledge of the species; thus chemical larviciding will be attempted. The development of a programme suitable for the Athabasca River requires a large number of field trials. Quantitative assessments of the effects on black fly larvae and other aquatic organisms are difficult in this river because of the irregular and often large fluctuations in the water depth. The study should also include the accumulation of information on the durability, distribution and effects of not only the insecticide used but also of its break-down products. The major sources of black flies in the river should be accurately determined to allow best use of chemical larvicides, especially any with a short life. Possibly the entire river contributes to these outbreaks but in view of the lengthy flight range known for this species in Saskatchewan (Fredeen, 1958), the major sources may well be the extensive rapids downriver from Pelican Portage.

Another profitable area of research is the documentation of events associated with the development of outbreaks, eventually to permit, if possible, prediction of the time and severity of each impending outbreak. Such information would not only remove the elements of suspense that occur annually in this area but would also be useful in planning livestock management procedures and in planning the most economic utilization of larvicides.

ACKNOWLEDGMENTS

I am very much indebted to J. B. Gurba and L. K. Peterson of the Alberta Department of Agriculture, Edmonton, and the many co-operators at Athabasca, for collecting thousands of specimens during the 1966 and 1967 outbreaks at Athabasca, and for reporting many of the details of these outbreaks. I also wish to thank co-operators in the Minburn area and particularly Dr. Hasinoff for information about the Minburn outbreaks. I am very much indebted to Gordon Glen of the Canada Agriculture Research Station, Saskatoon for his assistance in sorting the specimens collected in 1966 and 1967 and for careful preparation of the two maps illustrating this paper. I am also indebted to M. E. Taylor and L. Burgess of the Canada Agriculture Research Station, Saskatoon, K. R. Depner of the Research Station, Lethbridge, and L. K. Peterson for editing the manuscript.

REFERENCES

Abdelnur, O. M. 1968. The biology of some black flies (Diptera: Simuliidae) of Alberta. Quaest. ent. 4: 113-174.

Brown, A., T. H. D. Griffitts, S. Erwin and L. Y. Dyrenforth. 1938. Arthus's phenomenon from mosquito bites. Southern Med. J. 31: 6, 590-596.

Cameron, A. E. 1922. The morphology and biology of a Canadian cattle-infesting black fly, *Simulium simile* Mall. Canada Dept. Agr. Tech. Bull. 5, n.s.

Canada Department of Energy, Mines and Resources. 1967. Surface water data, Alberta, 1965. Queen's Printer, Ottawa (i-xii) 241 pp.

Curtis, L. C. 1954. Observations on a black fly pest of cattle in British Columbia (Diptera: Simuliidae). Proc. ent. Soc. British Columbia 51: 3-6.

Fredeen, F. J. H. 1958. Black flies (Diptera: Simuliidae) of the agricultural areas of Manitoba, Saskatchewan and Alberta. Proc. 10th Int. Congr. Ent. Montreal, 1956: 3, 819-823.

Fredeen, F. J. H. 1963. Oviposition in relation to the accumulation of bloodthirsty black flies (*Simulium (Gnus) arcticum* Mall. (Diptera)) prior to a damaging outbreak. Nature (London) 200: 4910, 1024.

Fredeen, F. J. H., J. G. Rempel and A. P. Arnason. 1951. Egg-laying habits, overwintering stages, and life cycle of *Simulium arcticum* Mall. (Diptera: Simuliidae). Can. Ent. 83: 3, 73-76.

Fredeen, F. J. H., A. P. Arnason and B. Berck. 1953. Adsorption of DDT on suspended solids in river water and its role in black-fly control. Nature (London) 171:700.

Gudgel, E. F. and F. H. Grauer. 1954. Acute and chronic reactions to black fly bites (*Simulium* fly). A. M. A. Arch Derm. Syph. 70, 609-615.

Gurba, J. B. 1963. Personal communication.

Hearle, E. 1932. The black flies of British Columbia. Proc. ent. Soc. British Columbia. 29: 5-19.

Hutcheon, D. E. and V. S. Chivers-Wilson. 1953. The histaminic and anti-coagulant activity of extracts of the black fly. Rev. Can. Biol. 12: 1, 77-85.

Millar, J. L. and J. G. Rempel. 1944. Livestock losses in Saskatchewan due to black flies. Can. J. Comp. Med. Vet. Sci. 8: 334-337.

Rempel, J. G. and A. P. Arnason. 1947. An account of three successive outbreaks of the black fly, *Simulium arcticum,* a serious livestock pest in Saskatchewan. Sci. Agr. 27: 9, 428-445.

Rubzov, I. A. 1940. Fauna of the U. S. S. R. Diptera, Simuliidae. Acad. Sci. U. S. S. R. Moscow 6: 6, 1-532.

Stone, A. and H. A. Jamnback. 1955. The black flies of New York State (Diptera: Simuliidae). N. Y. St. Mus. Bull. 349, 1-144.

Strickland, E. H. 1938. An annotated list of the Diptera (Flies) of Alberta. Can. J. Res., D, 16: 175-219.

Twinn, C. R., B. Hocking, W. C. McDuffie and H. F. Cross. 1948. A preliminary account of the biting flies at Churchill, Manitoba. Can. J. Research (D) 26: 334-357.