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Quaestiones

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published at the Department of Entomology,
University of Alberta, Edmonton, Canada.

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Editorial – Profit without Honour

Could the widespread use of DDT be a disaster? This question was the title given by the late E. H. Strickland to a short paper which he wrote in 1945 (Ent. News 56: 85-88). He answered this rhetorical question with a qualified yes. His qualifications were two. Firstly, that DDT proved to approach in effectiveness the claims then made for it; secondly that it be employed on a widespread scale, over large connected areas. Both requirements have been met. For once, a commercial product had indeed met the claims made for it, at least as regards initial effectiveness. And DDT has certainly been used over large connected areas. Do we have a disaster on our hands? Or have we heeded this 25 year old prophesy in time?

When Strickland wrote, little was known of the persistence of DDT and less of its cumulative build-up in food chains. Yet he correctly foresaw the hazards of threatening the maintenance of populations of predators – at any level.

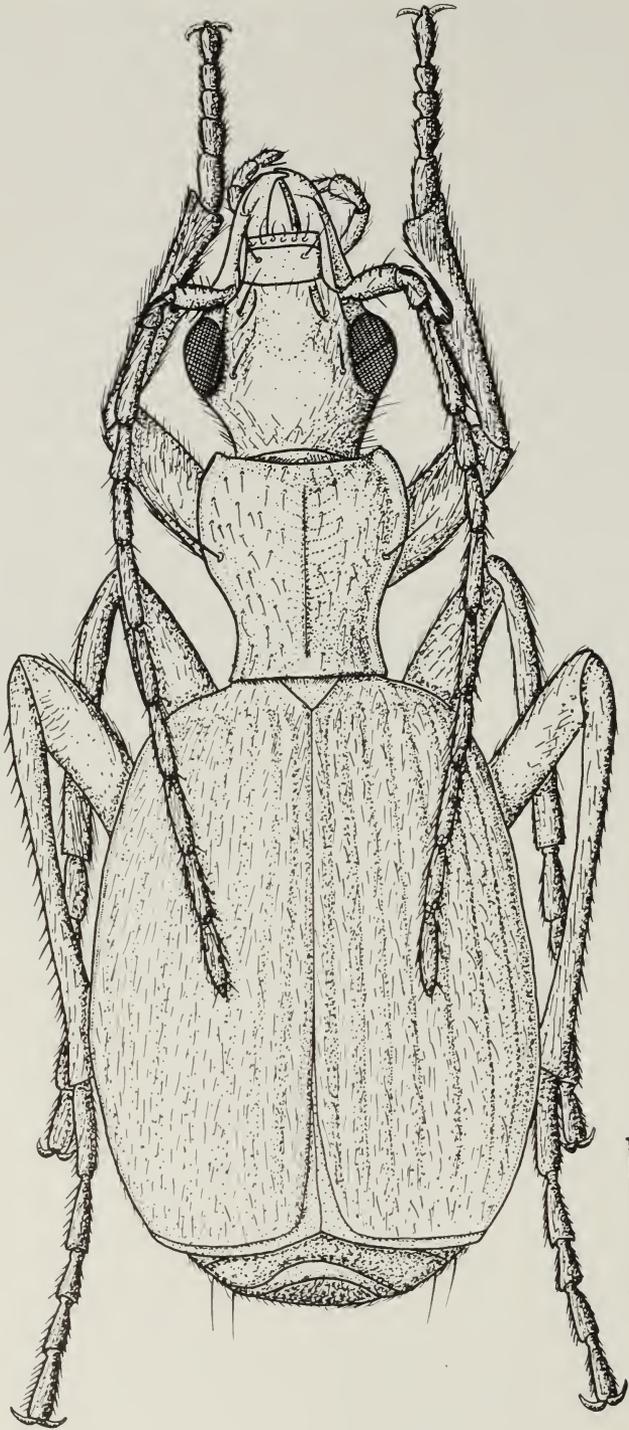
It can be estimated that about 4.5 million tons of DDT have been produced and most of this has been released into the biosphere. This would represent 0.25 lb. per acre of the 55½ million square miles of the land surface of the earth, or 2.4 lb. per arable acre. And for many years now DDT has not been alone; other chlorinated hydrocarbons with general toxicity and varying high persistence have joined it. Although it is now known that much of the DDT is in the atmosphere, much in the oceans (Frost, 1969, Environment 11(6): 14), and much in the top ends of food chains (Peterle, *loc. cit.* 34) and although its half-life in the soil may be rather less than 10 years, these figures have serious implications. Good control of mosquito larvae could be obtained in many areas with an application of 0.03 lb. of DDT per acre per annum. It seems inescapable that the insect fauna of the world must by now be so altered that we shall probably never know in any kind of detail what it was like before 1944. This, to an entomologist, is disaster; it will take decades, if not centuries, for a measure of normality to return; how long the first breakdown product, DDE, remains as a hazard in the environment is unknown. None can say how many species, potentially valuable, have gone for good. Let us hope we have at least learned the lesson that persistent broad-spectrum insecticides must be rigidly limited to narrow-spectrum applications.

Looking back, one wonders just how this came about. A chemical which can stop a typhus epidemic instantaneously and interrupt malaria transmission over large areas of the world, cannot be wholly bad. No other insecticide could have done these things so cheaply, nor with such negligible direct hazard to the sprayers – and the sprayed; 500 million people have lived for years in houses sprayed thrice yearly with DDT with virtually no records of sickness traceable to this. Factory workers making it, day in day out for 20 years, are no less healthy than other people (Laws, Curley, and Biros 1967, *Arch. environ. Health* 15: 766).

How much then, of the blame for the disaster rests with the users? How much with the manufacturers and their salesmen? Profits have been substantial from DDT (Bean, 1963, *Ag. Chem.* 18(1): 50-51, 118-119) and the profit motive has been evident in its abuse. The view that if one pound is good two pounds are twice as good is easily exploited. There is no honour in this. The marketing of insecticides should require the provision of details of procedures to detoxify them, in addition to the data on the hazards of their use. None can know for sure when this may be needed nor how urgently. If the environment must be done such damage, to keep the economy going, perhaps we have a sick economy and should cure this first. We are not yet so close to taking over a new planet that we can afford to ignore what we are doing to our present one.

There is indeed little honour to be gleaned in this situation; perhaps only for those who discovered the remarkable properties of this material, plus at best a handful of far-sighted entomologists who warned us early. Did we fail to listen because we have a generation gap at *both* ends?

Brian Hocking



Brachinus janthinipennis (Dejean), male, Cornwall, Connecticut.

A RECLASSIFICATION OF BOMBARDIER BEETLES
AND A TAXONOMIC REVISION OF THE NORTH AND MIDDLE AMERICAN
SPECIES (CARABIDAE: BRACHINIDA)

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Quaestiones entomologicae

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A taxonomic revision of the species of the North and middle American Brachinus Weber is presented. Sixty-two species are recognized as valid. Neobrachinus new subgenus, is erected to contain the New World species formerly included in Brachinus (sensu stricto). The following 14 taxa are described as new: Brachinus alexiguus, B. capnicus, B. chalchihuitlicue, B. chirriador, B. cibolensis, B. javalinopsis, B. imporcitis, B. oaxacensis, B. galactoderus, B. ichabodopsis, B. mobilis, B. explosus, B. aabaaba, B. sonorous. Twenty-five names are reduced to synonymy for the first time.

A key to the species is given. Each species and species group is described and synonymies are listed. The distribution of each species is presented by locality records and distribution maps. Structures used in identification are illustrated.

Two species of Pheropsophidius Hubenthal occur in Middle America and are included in the key to bombardier beetles of North and Middle America, one of these species is described. Structures of both species are illustrated.

A reclassification of the genera of the world bombardier beetles is presented. Seventeen genera are recognized as valid. These include 13 valid subgenera, one of which is new. Two tribes are included in the division Brachinida. One of these tribes includes four subtribes, two of which are new. Three generic names are reduced to synonymy for the first time. All taxa are described and keys for their identification are presented.

A discussion of the general morphology of members of the genera is presented. Structures discussed are illustrated.

A hypothetical phylogeny is presented for all genera of the division Brachinida and all species of Neobrachinus new subgenus. The geographical distribution of these taxa is also discussed. Figures and tables accompany the discussions.

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The bombardier beetles are a complex and taxonomically difficult group belonging to the family Carabidae. In 1862, LeConte stated: "I must also add that I consider the species of this genus very decidedly opinionative, and that I am only impelled to the publication of this note by the necessity of giving names to a certain number of recognized forms, and of placing as synonyms some which I formerly considered as distinct, but which increased collections have since shewn to be varieties." The situation had hardly changed 98 years later when Ball (1960: 164) wrote: "The taxonomy of the North American species of this group is very poorly understood and it is almost a waste of time at present to attempt to determine individuals to species."

Until now, a taxonomic revision of all North and Middle American species of *Brachinus* has not been undertaken, probably because of the great morphological similarity among the species, a lack of traditional characteristics for separating the species, and the unavailability of much of the "type" material. The first of these obstacles was surmounted after the discovery of external characteristics not used previously. The last problem was resolved with the help of G. E. Ball who compared my specimens with the type material of Dejean and Chaudoir in Paris. I was able to compare the LeConte and Blatchley types myself at the Museum of Comparative Zoology and Purdue University, respectively.

This paper is an extension of my 1965 publication and deals with the taxonomy and distribution of *Brachinus* and *Pheropsophidius* in North and Middle America. I also propose here a reclassification of bombardier beetles of the world, including subgeneric components; discuss phylogenetic and zoogeographic hypotheses; and present a preliminary study of the comparative morphology of bombardier beetles.

Bombardier beetles were first recognized formally when Linné described the species *Carabus crepitans* in 1758. Since that time, more than 600 trivial names have been proposed for members of the Brachinida. Dejean (1825, 1831), LeConte (1844, 1848, 1858, 1862), and Chaudoir (1868, 1876) have described most of the species in North and Middle America. Chaudoir's paper (1876) has been the only monographic treatment of the Brachinida as a whole. Basilewsky's 1959 revision of the Crepidogastrini must be considered monographic of that tribe. LeConte's 1862 paper and my revision of the California species (1965) contain the only new keys to North American species. (Blatchley's 1910 monumental "Coleoptera of Indiana" contains a key to the *Brachinus* species of Indiana, but it was based on LeConte's key.)

Many faunal studies have included partial taxonomic treatment of some of the taxa of the Brachinida. Notable are publications by Antoine (1962), Basilewsky (1962), Darlington (1968), Habu (1967), Jeannel (1942, 1949), Liebke (1934), Péringuey (1885, 1888, 1896, 1898), and Reitter (1919). No complete taxonomic classification has been proposed for the group as a whole. Most workers still seem to rely more heavily on the catalogue classification established by Csiki (1933) than on any other reference source.

MATERIALS AND METHODS

Materials

This study is the result of the examination of 28,633 specimens of North and Middle American *Brachinus*, and 2,172 specimens of other bombardier beetles. Most of these specimens have been loaned to me by museums and private collectors in Canada, Europe, Mexico, and the United States. The others were collected by my wife and me in the United States. Were it not for the intensive collecting of carabids in Mexico by G. E. Ball and D. R. Whitehead, this area would have been omitted from this study due to insufficient material.

Larval material was especially difficult to obtain. In addition to material from California (Erwin, 1967), I have seen one first instar larva of *Brachinus mexicanus* Dejean, and one unidentified last instar larva. This is still all that is known in North America, besides that which H. F. Wickham collected in the 1890's.

The following abbreviations indicate the various museums and private collections from which specimens were borrowed:

- AMNH American Museum of Natural History, New York, New York 10024, P. Vaurie, L. Herman Jr.
- ANSP Academy of Natural Sciences, Philadelphia, Pennsylvania 19103, H. R. Roberts.
- AUAA Auburn University, Auburn, Alabama 36830, K. L. Hays.
- BMNH British Museum (Natural History), London, England, R. D. Pope.
- CArm C. Armin, 191 West Palm Avenue, Reedley, California 93654.
- CAS California Academy of Sciences, San Francisco, California 94118, H. B. Leech.
- CBak C. Baker, Boise State College, 1907 Campus Drive, Boise, Idaho 83707.
- CCha C. Chantal, 425 Saint Olivier, Quebec 4, Quebec.
- CEWh C. E. White, 2441 East Northview Avenue, Indianapolis, Indiana 46220.
- CMPP Carnegie Museum, Pittsburgh, Pennsylvania 15213, G. E. Wallace.
- CNC Canadian National Collection of Insects, Entomology Research Institute, Ottawa, Ontario, E. C. Becker, W. J. Brown.
- CNHM Chicago Natural History Museum, Chicago, Illinois 60605, H. Dybas.
- CPBo C. Bolivar y Pieltain, Instituto Politecnico Nacional, Mexico D. F.
- CUNY Cornell University, Ithaca, New York, 14850, L. L. Pechuman.
- CVMA Coachella Valley Mosquito Abatement District Collection, Thermal, California 92274.
- DDLa D. J. Larson, University of Calgary, Calgary, Alberta.
- DHKA D. H. Kavanaugh, 1121 Garfield Street, Denver, Colorado 80206.
- DRWh D. R. Whitehead, University of Alberta, Edmonton 7, Alberta.
- DTRT Division of Tropical Research, Tela Railroad Company, La Lima, Honduras, Central America, W. G. C. Forsyth.
- FDAG Florida Department of Agriculture, Gainesville, Florida 32601, R. E. Woodruff.
- GRNo G. R. Noonan, University of California, Riverside, California 92502 (including collection of F. Andrews).
- HGou H. Goulet, University of Alberta, Edmonton 7, Alberta.
- HM^o Hope Museum, Oxford, England, E. Taylor.
- ISNH Illinois State Natural History Survey, Urbana, Illinois 61803, L. K. Gloyd.
- ISUA Iowa State University, Ames, Iowa 50010, J. Laffoon.
- JHen J. Hendrichs, Apartado Posta, 11-774, Mexico 11, D. F.
- JSch J. Schuh, 4039 Shasta Way, Klamath Falls, Oregon 97601.
- KMTB Koninklijk Museum Voor Midden-Afrika-Musée Royal del' Afrique Centrale, Tervuren, Belgium, P. Basilewsky.
- KSU Kansas State University, Manhattan, Kansas 66502, H. D. Blocker.
- LACM Los Angeles County Museum, Exposition Park, Los Angeles, California 90007, C. L. Hogue.
- LBSC Long Beach State College, Long Beach, California 90804, E. L. Sleeper.
- LRus L. Russell, Oregon State College, Corvallis, Oregon, 97331.
- LSUB Louisiana State University, Baton Rouge, Louisiana 70803, J. B. Chapin.
- MSUM Montana State University, Missoula, Montana, 59801, N. Anderson.
- McZ Museum of Comparative Zoology, Cambridge, Massachusetts 02138, P. J. Darlington, Jr.

- MHNP Museum National d'Histoire Naturelle, Paris, A. Bons.
- MMM Moscow Museum, Moscow, U.S.S.R.
- NSDA Nevada State Department of Agriculture, Reno, Nevada, 89504, R. C. Bechtel.
- OSUC Oregon State University, Corvallis, Oregon 97331, P. O. Ritcher.
- OSUS Oklahoma State University, Stillwater, Oklahoma 74075, W. A. Drew.
- OUCO Ohio State University, Columbus, Ohio 43210, C. A. Triplehorn.
- PSUU Pennsylvania State University, University Park, Pennsylvania 16802, W. W. Boyle, S. W. Frost.
- PUM Purdue University, Lafayette, Indiana 47907, R. H. Arnett.
- RCGr R. C. Graves, Bowling Green State University, Bowling Green, Ohio 43402 (including collection of W. Suter).
- RESt R. E. Stecker, San Jose State College, San Jose, California 95114.
- RFre R. Freitag, Lakehead University, Thunder Bay, Ontario.
- ROM The Royal Ontario Museum, University of Toronto, Toronto 5, Ontario, G. B. Wiggins.
- RTBe R. T. Bell, University of Vermont, Burlington, Vermont 05401.
- SDSNH San Diego Society of Natural History, San Diego, California 92112, C. F. Harbison.
- SDSU South Dakota State University, Brookings, South Dakota 57006, E. U. Balsbaugh, Jr.
- SJSC San Jose State College, San Jose, California 95114, J. G. Edwards.
- TAMU Texas A & M University, College Station, Texas 77840, H. R. Burke.
- TCBa T. C. Barr, Jr., University of Kentucky, Lexington, Kentucky 40506.
- TFHI T. F. Hlavac, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.
- TLEr T. L. Erwin, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.
- TMBH Termesztudományi Múzeum, Musée Hongrois d'Histoire Naturelle, Budapest, VIII., Baross-u. 13 (Hongrie), Z. Kaszab.
- UAFA University of Arkansas, Fayetteville, Arkansas 72701, R. T. Allen, E. P. Rouse.
- UASM University of Alberta, Strickland Museum, Edmonton 7, Alberta, G. E. Ball.
- UATA University of Arizona, Tucson, Arizona 85721, F. G. Werner.
- UBC University of British Columbia, Vancouver, British Columbia.
- UCD University of California, Davis, California 95616, R. O. Schuster.
- UCR University of California, Riverside, California 92502, S. Frommer.
- UIMI University of Idaho, Moscow, Idaho 83843, W. F. Barr.
- ULLK University of Louisville, Louisville, Kentucky 40208, C. V. Covell.
- UMAH University of Michigan, Ann Arbor, Michigan 48104, R. D. Alexander.
- UMCP University of Maryland, College Park, Maryland 20742, F. E. Wood.
- UMSP University of Minnesota, Saint Paul, Minnesota 55101, P. Clausen.
- UNCR University of North Carolina, Raleigh, North Carolina 27607, D. A. Young.
- UNLN University of Nebraska College of Agriculture, Lincoln, Nebraska 68508, W. T. Atyeo.
- UNSS University of Saskatchewan, Saskatoon, Saskatchewan, N. Church.
- UONO University of Oklahoma, Norman, Oklahoma 73069, C. E. Hopla.
- USNM Smithsonian Institution, Washington, D. C. 20560, O. L. Cartwright.
- USUL Utah State University, Logan, Utah 84321, W. J. Hanson.
- UWLW University of Wyoming, Laramie, Wyoming 82070, N. L. Marston.
- UWMW University of Wisconsin, Madison, Wisconsin 53706, R. D. Shenefelt.
- UWSW University of Washington, Seattle, Washington 98105, M. H. Hatch.

VMKi	V. M. Kirk, North Grain Insects Research Laboratories, Brookings, South Dakota 57006.
VVBa	V. V. Baicher, San Jose State College, San Jose, California 95114.
WHTy	W. H. Tyson, 823 Cashew Way, Fremont, California 94536.
WSUP	Washington State University, Pullman, Washington 99163, M. T. James.
ZMLS	Zoological Institute, University of Lund, Lund, Sweden, C. H. Lindroth.

Localities of specimens were determined from labels pinned with the specimens. These localities are given for each species alphabetically by country, state or province, and county. More exact localities are given alphabetically by towns or cities in parentheses behind the state or county. Behind the parentheses are listed the museums in which the particular specimens are located.

Methods

Dissecting techniques

Techniques described elsewhere (Erwin, 1965) were used. However, instead of the dissected male genitalia being stored in vials of 70% alcohol they were glued to cards, which were subsequently pinned beneath the specimens. For storing the female genitalia and various sclerites (described under comparative morphology) the same procedure was followed. The specimens that were completely disarticulated were stored in vials of 70% ethyl alcohol.

Measurements

Total length measurements were made of representatives of all species. The purpose of this measurement is to give a general impression of the size range of a species. The great variation in size of adults within any single species of these beetles is due to differences in amount of their larval food (Erwin, 1967). The lengths of adult specimens given below were all obtained in the following manner. From the material at hand, I visually selected both the largest and the smallest specimen, and measured the head from the anterior edge of the labrum to the center of the occipital ridge, the pronotum from the anterior margin to the posterior margin along the center line, and the left elytron from the apex of the scutellum to the elytral apex, along the suture. These three measurements were added together, providing a figure that is not affected by expansion and contraction of the membraneous parts in different killing agents, or by the swelling of the abdomen in gravid females and engorged beetles. A micrometer eyepiece in a Leitz stereoscopic microscope at a magnification of 50 diameters was used for these measurements. The scale interval represented 0.025 mm.

Illustrations

All drawings were prepared with the aid of a camera lucida on a stereoscopic microscope. After the outline was drawn with the camera lucida, the specimen was examined under higher magnification and finer details and shading were added to the drawings. Accompanying scale lines equal 1.0 mm.

Procedural methods

The 28,633 specimens of North and Middle American bombardier beetles were first categorized according to smaller geographic areas, for example, southern United States, northeastern United States, Mexico, Great Plains, etc. This reduced the amount of material to be concerned with at any one time. The specimens of each geographical area were divided into population samples on the basis of the label data. Each specimen from a given area was compared with every other specimen from that area, and comparable specimens were

grouped into "sets". Each set was then intensively studied, and dissections of the male genitalia were made. Those sets with identical genitalia, and at least one concordant external characteristic in common, were grouped together tentatively until all the material from the entire area had been analyzed. Only the male genitalia were arbitrarily weighed, all other characteristics that were studied were considered of equal value. When specimens were judged to be different, on the basis of their genitalia and at least one external characteristic, an attempt was made to associate females from the same population sample. No difficulty was encountered in determining probable male-female associations. Further details concerning the relationships between individuals from different species populations are discussed under Phylogeny.

Criteria for Species, Subspecies, and supra-specific Taxa

A species may be defined as "a naturally occurring population (or aggregate of populations) that is reproductively isolated and genetically distinctive" (J. Gordon Edwards, per. comm.). When the biology of a natural population is fairly well known and the criteria of this definition have been met, this definition may be applied with reasonable success in the recognition of species. In the present study, only genitalic and external morphology (including pubescence), color, distribution, and some life history data are used, because these are the only things known about most of the populations treated. When only museum specimens are utilized, different criteria are necessary, to supplant those given in the definition above, yet give approximately the same results in recognizing species. As working criteria for these cases, I use the following: A species is represented by the sum total of the specimens displaying a multidimensional continuum of characteristics, but ultimately delimited from other such species by gross morphological discontinuities. In this case the characteristics are external morphology (including pubescence), genitalic morphology, and color. The determination of the size and nature of the multidimensional discontinuity or "gap" (Mayr, Linsley, and Usinger, 1953) has traditionally been left to competent taxonomists with extensive experience in the group in question. In most cases, these taxonomists have failed to state what their criteria were when recognizing these gaps. My criteria for recognizing this "gap" are the following: two or more similar forms which are naturally sympatric or allopatric are considered separate species, if they differ in genitalic morphology and at least one external characteristic; allopatric forms are considered conspecific if their genitalic morphology is identical and they show intergradation of external characteristics in geographically proximal areas (or if no external morphological differences are apparent). Parapatric populations or aggregates of populations (that is, populations which meet only in a very restricted area, such as a single valley or single river system) are considered distinct species if there is no introgression of characteristics near the zones of contact. If there is introgression there, the forms are considered either to be conspecific or to be two hybridizing species, depending upon the nature of the introgression.

Naming of subspecies has been avoided, because I feel that more criteria than morphological characters of museum specimens is necessary for the recognition of limits of taxa below the species level. Subspecies are geographically or temporally delimited populations within a species that differ from other such populations (but which are capable of interbreeding with those other subspecies). Without extensive information on population dynamics, life histories, and genetic capabilities, subspecies would be ill-defined, and ambiguous trivial names might be introduced into the literature if such taxa were included in the present study.

Supra-specific taxa are groups which are established to include all the taxa of the next lowest rank that demonstrate monophyly. Hennig (1966) argues that all such supra-specific taxa which demonstrate sister relationships be given equal absolute rank, but the practicality

of this has been questioned (Ball and Erwin, 1969). Many supra-specific taxa presently in use are paraphyletic. In this paper I have realigned the taxa of the Brachinida in accord with Hennig's principles, but I have ranked taxa below the generic level with practicality in mind.

COMPARATIVE MORPHOLOGY

Introduction

Upon discovering the asymmetric anterior tarsal pads in male members of *Brachinus crepitans* (Linné), Antoine (1962) stated "il est incompréhensible qu'on ne l'ait pas encore signalé ...cet intéressant caractère saute aux yeux quand on examine les tarses par leur face inférieure." (It is incomprehensible that no one has yet seen this interesting character which is so obvious when one examines the ventral surface of the tarsi). This may be said for many other characteristics of the external morphology. These beetles have been studied by numerous European biologists for 200 years or more; even so the taxonomy of the group (and many other carabid groups) is still in a state of confusion. There can be only one reason. Those workers viewed the beetles from only the dorsal aspect, because their specimens were usually glued to cards in that position. I doubt that many of them ever examined the ventral side of a bombardier beetle. Numerous excellent characteristics have been overlooked by those using this method of mounting carabid beetles. Had Jeannel seen the aberrant characteristics of *Mastax* members, he surely would have placed this genus in a family of its own.

In this section I have attempted a beginning of a comprehensive comparative study of bombardier beetle morphology. The material I have seen that represents species of Old World genera is not extensive. I have not seen any members of species comprising three of the monotypic genera, but I believe that I have seen enough material to reach some valid conclusions. Based on these conclusions, I have proposed certain hypotheses which must be proved or disproved in subsequent studies. Some of these studies I hope to do myself, yet I also hope this presentation will provide a foundation for others who are interested in studying the evolution and biology of bombardier beetles.

By presenting my findings on the comparative morphology of bombardier beetles as Jeannel (1926) did for the Trechinae, I have established a foundation for phylogenetic considerations, using the principles proposed by Hennig (1966). In this section on "comparative morphology," I have tried to integrate the descriptive Taxonomy with my interpretations of the character states.

General characteristics

Size

The bombardier beetles range in size from the very small members of some *Mastax* and *Crepidogastrinus* species (2.0 and 3.0 mm overall length respectively), to the very large members of some *Aptinomorphus* species (30.0 mm).

The members of the genus *Mastax* are all very small, while beetles of the genus *Pheropsophus* are large to very large. The remaining genera usually have medium-sized members, but some kinds may vary from small to large (sometimes even intraspecifically). The *Crepidogastrini* range in size from 3.0 to 16.0 mm, according to Basilewsky (1959). I have seen specimens of *Pheropsophina* ranging from 10.0 to 30.0 mm; specimens of *Brachinina* ranging from 3.0 to 18.2 mm; specimens of *Aptinina* ranging from 4.5 to 15.0 mm; and specimens of *Mastacina* ranging from 2.0 to 3.5 mm.

There is considerable variation in size among the members of single species, particularly in the genera *Pheropsophus* and *Brachinus*. I believe that variation in size is due to the ectoparasitoid mode of life described for the larvae of these groups (Habu and Sandanaga, 1965;

Habu, 1967; Wickham, 1893, 1894; Erwin, 1967). I have shown (Erwin, 1967) that larvae of *Brachinus pallidus* in California are not host specific, but may attack pupae of at least two, and probably three, species of hydrophilid water beetles. Since one host is eaten by one parasitoid larva, the size of the host (larval food available) determines the size of the resultant adult *Brachinus pallidus*. Habu and Sadanaga (1965) and Habu (1967) have shown that the larva of *Pheropsophus jessoensis* Morawitz is an ectoparasitoid on the egg clutches of *Gryllotalpa africana* Palisot de Beauvois (Orthoptera, Gryllotalpidae). Those egg clutches vary in size (number of eggs), and since the larva attacks only one egg clutch the size of the clutch determines the size of the adult beetle. After the larva begins to undergo hypermetamorphosis, it cannot leave the chamber it invaded because of the decrease in its leg length and the increase in its body size (Erwin, 1967).

It has been repeatedly observed that the proportions of the individual adults remain constant, regardless of their total size.

General form

The bombardier beetles are a very homogeneous group. The narrow head and prothorax, together with the wide, truncate elytra and apically protruding abdomen, characterize all species of the Brachinida. Jeannel (1926) established names for four general body forms within the tribe Trechini. Three of these types are found in Brachinida, but they are slightly different from the forms described by Jeannel:

1. *Type ailé* (long-winged type) – pigmented, large eyes, small pronotum, square elytra with prominent humeri, and large metasternum (includes wing dimorphic species);
2. *Type aptère* (short-winged type) – pigmented, small or large eyes, enlarged pronotum, elytra short with narrow humeri, and short metasternum;
3. *Type anophthalme* (eyeless type) – depigmented, blind, enlarged pronotum, elytra short with narrow humeri, and short metasternum.

The members of Mastacina fit Jeannel's *type ailé*. In these beetles, the abdomen is not extended as in the crepidogastrines, but they do have the moniliform antennae of that group.

The members of Pherosophina, Aptinina, and Brachinina all have a similar habitus with filiform antennae, but in members of *Pheropsophidus*, *Pheropsophus*, and *Aptinus*, there is a tendency for the abdomen to extend far beyond the apex of the elytra. These subtribes have some members which correspond to Jeannel's *type ailé* and others that are *type aptère*.

The members of the Crepidogastrini are the most primitive of the division Brachinida, and are slightly different in habitus from other bombardier beetles. These beetles generally have very short elytra, exposing at least two full abdominal terga, even when the abdomen is not engorged or gravid. Most members belong to Jeannel's *type aptère*, but those of *Tyronia caeca* Basilewsky and *Brachynillus varendorffi* Reitter belong to *type anophthalme*. Also, the antennae of the crepidogastrines are moniliform rather than filiform.

Microsculpture

In general the microsculpture of bombardier beetles ranges from regularly to irregularly isodiametric. Slight variation occurs from this basic pattern.

Throughout the Brachinina, Mastacina, and Crepidogastrini, the isodiametric meshes may vary into a granulate condition, in which each individual mesh is a convex bump. In members of *Pheropsophus*, the meshes are extremely fine and barely impressed, and there is a tendency for them to be stretched and arranged into transverse rows. In *Aptinus*, the meshes are also barely impressed, but they are larger than in *Pheropsophus* and arranged in transverse rows particularly on the pronotum. *Aptinoderus* members have the meshes of the head almost effaced. Members of *Styphlomerus* have granulate isodiametric meshes arranged on the

elytra as in members of *Mastax*, and producing a “satin” appearance.

Pubescence

All bombardier beetles maintain at least some body pubescence in addition to the erect “depression setae” borne by the members of most species, on the elytra, and other variously located setae. The members of Crepidogastrini are totally pubescent, while other bombardier beetles may be totally pubescent or have extensive glabrous areas.

The Mastacina members have glabrous elytra, with the pronotum either glabrous or not. The elytra have erect setae in depressions 2, 4, 6, and 8. The epipleura are pubescent. The apical edges of the elytra are devoid of setae.

The members of Pheropsophina have the elytra almost glabrous, but with erect “depression setae” in all depressions, plus scattered pubescence near the scutellum and along depressions 1 and 8. However, the epipleura are glabrous. The apical edge of the elytra ranges from smooth in members of *Aptinomorphus* to densely pubescent in members of *Pheropsophus (sensu stricto)*. Some members of all the other Pheropsophina subgenera also have this apical fringe.

Among the Aptinina, the members of *Aptinus* have elytral pubescence arranged much like that of members of *Pheropsophus*, but it is usually more dense. Members of *Aptinus* also have the epipleura pubescent. In *Styphlomerus* and its allies, the elytra and epipleura are totally pubescent, with an additional apical fringe present (closely spaced setae along the apex of the elytra).

Among the members of Brachinina, all combinations of elytral pubescence exist, and the epipleura are always pubescent. These patterns of elytral pubescence are described in detail below (p.49). The apical fringe is absent from *Brachinus* subgenera *Metabrachinus* and *Aploa*, but is dense in members of *Brachinus viridipennis* Dejean, and has long widely spaced setae in members of *Brachinus crepitans* (Linné).

The amount of head and pronotum pubescence varies considerably among the species of Brachinida. The members of *Mastax* are densely pubescent to glabrous; those of *Pheropsophus*, *Pheropsophidius*, and *Aptinus* are sparsely setiferous; those of *Brachinus* are glabrous to densely pubescent; and *Styphlomerus* and its allies are densely pubescent.

The pubescence of the cephalic appendages is quite variable throughout the group. All members of the Crepidogastrini have dense pubescence on every appendage from base to the apex. The members of Aptinina, Brachinina, and Mastacina have dense pubescence on the outer articles of the appendages. This pubescence gradually increases in density from the base to the apex. The members of Pheropsophina are the least pubescent of the group, with only stiff spines or setae basally, and sparse pubescence distally. In these beetles and those of the preceding three subtribes, the antennal pubescence is fairly dense on article three, and very dense on articles four to eleven. The mandibular scrobes of the members of Crepidogastrini and Brachinina are plurisetose, while those of the other groups are unisetose. Besides the short pubescence, these two groups of beetles also have the single large seta in the scrobe.

The venter of the prothorax is densely pubescent medially in members of Crepidogastrini, and is less densely pubescent toward the proepipleura. In the other groups, the prosternum usually has numerous long and scattered setae, with the proepisterna, proepimera, and proepipleura variably setiferous. The venter of the mesothorax, metathorax, and abdomen are pubescent in all groups.

The legs of all groups, except the members of Pheropsophina, are pubescent. On these beetles the setae are scattered and spine-like, forming rows on members of some species.

Major setae occur in numerous places on bombardier beetles. Members of all groups have a single long seta in the mandibular scrobe, and a single pair of supraorbital setae. In *Mastax*,

however, a second "pseudosupraorbital" pair of setae is behind the eyes, one on either side of the vertex. With the exception of some crepidogastrines, all groups have one pair of lateral pronotal setae. The exceptions are members of *Tyronia*, *Crepidolomus*, and *Crepidogastrillus* which have a second pair of lateral setae in front of the hind angles. In *Crepidogastrius*, a series of spine-like setae occurs along the lateral margins of the pronotum from base to apex.

The major setae of the elytra are in the bottom of depressions between costae, in interval 8, and along depression 1 near the scutellum. Interval 8 and depression 1 have umbilicate punctures with setae of variable length, depending upon the species. The umbilicate series in depression 8 is continuous in all groups, except in members of *Crepidolomus extimus* (Jeannel). Basilewsky (1959) indicates this species has members with the umbilicate series divided into 8 setae anteriorly and 8 posteriorly.

The middle and hind coxae, hind trochanter, and the abdominal sterna 2-5 bear "ambulatory setae." The number and location of these long and widely spaced setae varies with the species. The setae of the tarsi are discussed in detail below (p. 22).

Head

Cranium

The general shape of the cranium is the same for all groups. In the few species with reduced eyes, and in the blind members of *Brachynillus*, the head is much narrower.

Eyes

Only one species, *Brachynillus varendorffi* Reitter, is known to have all members eyeless. Another species, *Tyronia caeca* Basilewsky, has all its members with highly reduced eyes with only a few facets, and according to Jeannel (1926), beetles with this type of eye are blind. The eyes of members of *Brachinulus viettei* Basilewsky and *Brachinus pygmaeus* Dejean are very small, and hardly protrude beyond the sides of the head. These species must be considered as somewhere between Jeannel's *type aptère* and *type anophthalme*, since they are "depigmented" in comparison to the normal bright colors of the other bombardier beetles. All other brachinines have fully functional eyes, although some *Brachinoaptinus* members have only a small number of facets.

Antennae

In general, the antennae of members of Brachinina are filiform, while those of Crepidogastrini are moniliform. Some groups of the Brachinina, however, have antennae with shortened articles, as the members of *Mastax*, *Styphlodromus*, *Styphlomerinus*, and *Styphlomerus*. In these groups, articles 5-11 are almost square, slightly longer than wide, or moniliform. All groups have a rather robust scape, a very short pedicel, and articles 3-11 are subequal. In members of *Neobrachinus*, *Aptinomorphus*, and some Asian and African Brachinina, the third article is elongate. The length of that third article may prove to be useful in the identification of *Brachinus* subgenera (defined on the basis of the internal sac of the male genitalia), when the Old World fauna is better known. Bell (1960) used this antennal character successfully in the genus *Chlaenius* to distinguish taxa.

Labrum

The labrum of all groups is essentially rectangular and slightly emarginate anteriorly. Six or eight setae occur along the anterior margin. There are six setae in members of Brachinina, Pheropsophina, and some Aptinina, and eight setae in *Mastax*, Crepidogastrini, and some *Aptinus*.

Mandibles

There is great divergence in the characteristics of the mandibles of the Brachinida members. One group, the Mastacina, has members with highly aberrant mandibles (fig. 6). These mandibles are no doubt adapted to some specialized feeding behavior, and are correlated with other modifications of the mouthparts (see below). The members of *Mastax* have flat, falciform mandibles, each with a large bifid retinaculum. The scrobe is absent, but the scrobal seta remains. The basal margin is densely setiferous, as is the ventral groove. This type of mandible looks very similar to larval mandibles in other bombardier beetles, and may represent a neotenous condition in these beetles. Jeannel (1926) has suggested neoteny for other characteristics in the Trechini.

All other groups have mandibles which are basally trigonal and apically subfalciform. All possess scrobes which are plurisetose in Brachinina (figs. 1, 8) and Crepidogastrini (fig. 7) members, and unisetose in Aptinina (figs. 2, 3) and Pheropsophina (figs. 4, 5) members. Members of all species possess a setiferous ventral groove, and in addition the members of Pheropsophina possess a brush of setae on the basal margin. There appears to be interspecific variation in the teeth of the cutting edge, but I have not studied this in detail. Intergeneric mandibular variation occurs as follows: Aptinina members have small rounded cusps, two terebral and one retinacular; *Styphlomerus* members have an elongate and ridge-like retinaculum; Crepidogastrini members have a single sharp terebral tooth and a retinacular ridge; Pheropsophina members have two types, the first is found in the primitive *Pheropsophidius*, and is a small square swelling on the terebrum, while the second is found in members of all other subgenera, and consists of a single terebral tooth and a bifid retinacular tooth; Brachinina members have the most complex pattern of mandibular teeth found in the bombardier beetles, consisting of several teeth on both the terebral and retinacular edge.

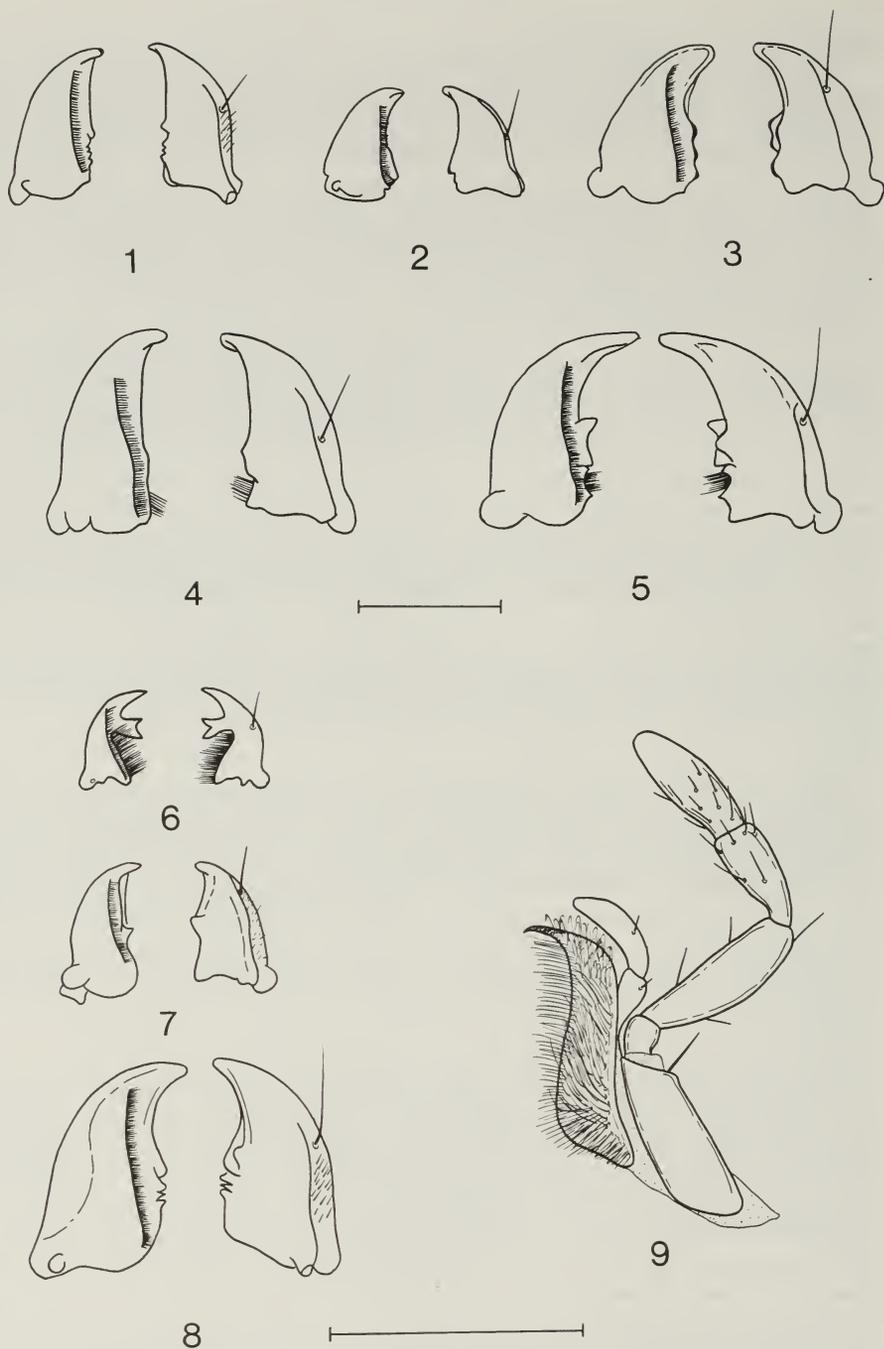
Maxillae

The maxilla (fig. 9) varies little throughout the bombardier beetles. The cardo is small. The stipes is about three times the length of the cardo. The galea is palpiform and two-articled, and the lacinia is falciform and sharply pointed at the apex. The dorsal surface of the lacinia is densely clothed with long setae. Only in members of *Mastax* is the acute apex of the lacinia slightly reduced. The palpus is composed of four articles, the last of which is subcylindrical, except in some members of the Old World Pheropsophina and *Brachinulus* (wedge-shaped), *Mastax* (globose-attenuate), and some Crepidogastrini (securiform, globose).

Labium

The characteristics of the labium are quite divergent throughout the bombardier beetles. The ligula probably represents the fused glossae and paraglossae. This is most evident in members of *Mastax* (fig. 10) in which the membranous setiferous lateral lobes (= paraglossae) are twice the size of the convex median sclerotized lobe (= fused glossae). In members of *Mastax* this median lobe generally has three or more long setae. The members of Crepidogastrini (fig. 11) possess a very small ligula which has a convex medial sclerotized area and small membranous lateral lobes, each with two or more setae. The members of Aptinina (figs. 16, 17) and Brachinina (figs. 13, 15) are generally the same, except the dorsal surfaces of the lateral lobes are setiferous. In the members of the Old World Pheropsophina (fig. 14), the venter of the ligula is carinate, but in New World Pheropsophina (fig. 12) this area is globose as in other bombardier beetles. In some cases, interspecific variation occurs in the disposition of ligular setae and in the shape of the central convexity. These characteristics can be used for reliable diagnosis of particular species.

In most members of Crepidogastrini (fig. 11), the last article of the palpus is securiform or



Figs. 1-8. Right mandible, ventral and dorsal aspect. 1. *Aploa nobilis* Dejean, Chad, Africa. 2. *Styphlomerus ?ciliatus* Liebke, Garamba, Congo, Africa. 3. *Aptinus bombarða* Illiger, Europe. 4. *Pheropsophidius rivieri* Demay, Ciudad Bolivar, Venezuela. 5. *Pheropsophus ?bimaculatus* (Linné), Mysore, India. 6. *Mastax ?hargreavesi* Liebke, Abalaliki, Nigeria. 7. *Crepidogaster caffra* Peringuey, Cape Point, South Africa. 8. *Brachinus phaeocerus* Chaudoir, Lake Roberts, New Mexico. Fig. 9. Right maxilla, dorsal aspect, *Aploa nobilis* Dejean, Chad, Africa. Accompanying scale lines equal 1.0 mm.

globose, or almost so. In members of most Old World Pheropsophina (fig. 14) and *Brachinulus*, is is narrowly wedge-shaped. In members of *Mastax* (fig. 10), it is globose-attenuate, otherwise it is subcylindrical.

The mentum is generally the same in all groups. It is toothed in members of Aptinina (figs. 16, 17) and *Mastax* (fig. 10), but in the latter it may be a result of the deep central pit surrounded by setae. The lateral lobes of the mentum are usually acute, but in members of *Mastax* they are broadly rounded. The deep pit in the center of the mentum is found in all members of *Mastax*, *Brachinus costipennis*, and *Brachinus longipalpis*. A shallower sulcus is found in some members of European *Brachinus* species and in *Brachinus (Neobrachinus) mobilis*. Two deep lateral pits are found in the mentum of members of *Brachinus sallei* (fig. 20) of Mexico and *Brachinus scotomedes* of Japan. Jeannel (1926) suggested that similar structures in some members of the Trechini might be acoustical organs and that the innervation should be traced. No one, however, has yet investigated these pits. The setae of the mentum provide many useful characteristics for species diagnosis. The submentum and its setae also provide useful characteristics.

The submentum is slightly variable among members of the Brachinida, particularly the sides that conceal the bases of the cardines (figs. 10-17). In members of *Mastax*, *Brachinus costipennis* (fig. 18), and *Brachinus longipalpis*, the submentum is very short. This shortening is concordant with the sulcate mentum.

The gular sutures are divergent in all groups except the crepidogastrines (fig. 11), in which they converge to the occipital groove, then diverge.

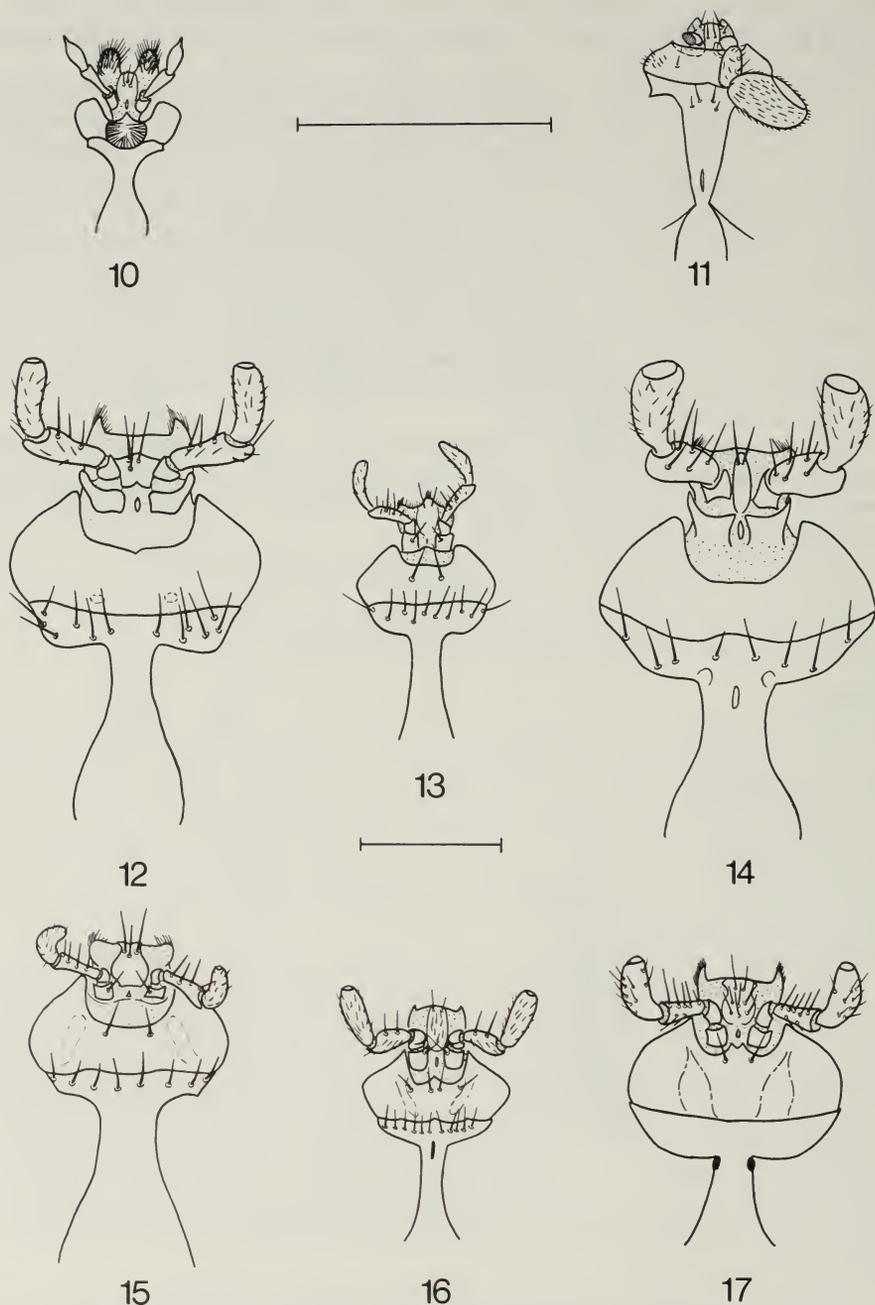
In summary, the characteristics of the head provide many useful criteria for phylogenetic considerations and taxonomic diagnoses at all categorical levels.

Prothorax

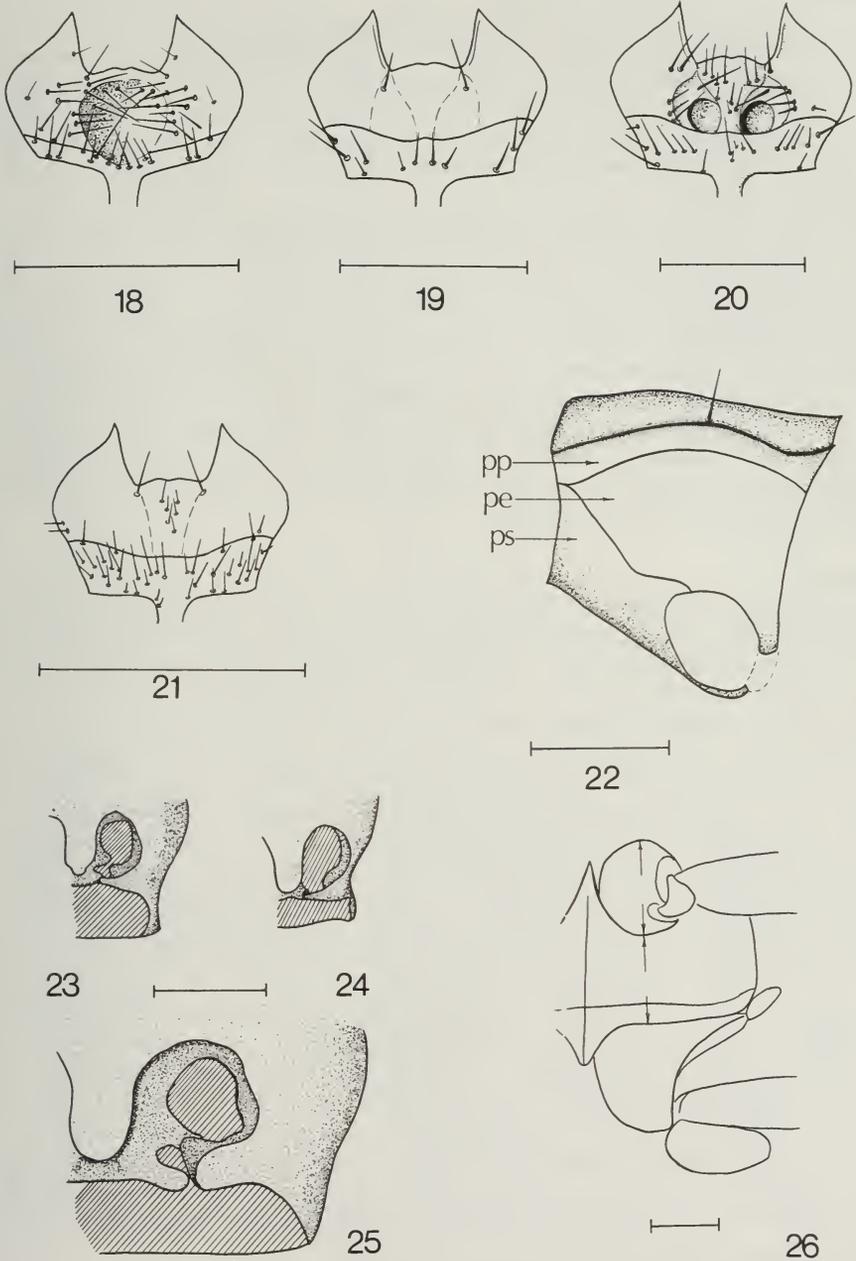
Externally the prothoraces of members of Brachinida are very similar (fig. 22). Internally, however, great divergence is exhibited in the structure of the coxal cavities. Both the uniperforate and biperforate conditions exist; that is, one or two holes enter the body cavity for the passage of muscles. Biperforate coxal cavities (fig. 25) occur in members of Crepidogastrini, Mastacina, and Pheropsophina, while the uniperforate condition (fig. 24) occurs in the Brachinina and Aptinina. The remnants of a bridge (fig. 23) are quite evident in members of *Brachinus (sensu stricto)*, *Brachynolomus*, and *Aptinina*, but are almost absent in other *Brachinus (Neobrachinus)*.

The proepimeron closes the procoxal cavity behind in all groups except in members of *Protopheropsophus* and *Stenaptinus*. In the members of the latter subgenus, the proepimeron barely reaches the prosternal process, and in some specimens there is a noticeable gap. This variation might not have phylogenetic significance if it were not for the members of *Protopheropsophus biplagiatus* Chaudoir, which have a wide and consistent gap behind the coxal cavity. When the coxal cavities are closed behind, it is usually due to the proepimeron overlapping the lateral process of the prosternum. However, in *Brachynolomus*, *Brachinoaptinus*, *Aploa*, and some *Cnecostolus* and *Neobrachinus* each lateral process of the prosternum forms a "socket" or "notch" into which the proepimeron inserts. Bell (1967) points this out as a generality for Brachinini, but he evidently examined members of *Neobrachinus* only.

The only other prothoracic character that shows intergeneric variation is the presence or absence of a propleural suture. Although the proepisternum and proepimeron are fused, a ridge runs the length of the fused sclerites in the area of juncture. This ridge occurs in the Crepidogastrini, Mastacina, and Old World Pheropsophina.



Figs. 10-17. Labium, mentum, and gula, ventral aspect. 10. *Mastax ?hargreavesi* Liebke, Abakaliki, Nigeria. 11. *Crepidogaster caffra* Peringuey, Cape Point, South Africa. 12. *Pheropsophidius rivieri* Demay, Ciudad Bolivar, Venezuela. 13. *Brachinus phaeocerus* Chaudoir, Lake Roberts, New Mexico. 14. *Pheropsophus ?bimaculatus* (Linne), Mysore, India. 15. *Aploa nobilis* Dejean, Chad, Africa. 16. *Styphlomerus ?ciliatus* Liebke, Garamba, Congo, Africa. 17. *Apтинus bombarda* Illiger, Europe. Accompanying scale lines equal 1.0 mm.



Figs. 18-21. Mentum and submentum, ventral aspect. 18. *Brachinus costipennis* Motschulsky, 12.2 miles south of El Banco, Durango, Mexico. 19. *Brachinus melanarthrus* Chaudoir, 5.0 miles northwest of Acayucan, Veracruz, Mexico. 20. *Brachinus sallei* Chaudoir, Cozumel Island, Quintana Roo, Mexico. 21. *Brachinus microamericanus* Erwin, Dundee, Mississippi. Fig. 22. Diagrammatic illustration of prothorax, left lateral aspect. Figs. 23-25. Procoxal cavities, ventral aspect. 23. *Brachinus crepitans* (Linné), Switzerland. 24. *Brachinus phaeocerus* Chaudoir, Lake Roberts, New Mexico. 25. *Pheropsophus ?bimaculatus* (Linné), Mysore, India. Fig. 26. Diagrammatic illustration of middle and hind coxae and metasternum, ventral aspect. Accompanying scale line equals 1.0 mm (pp = proepipleuron, pe = proepisternum, ps = prosternum).

Mesothorax

The mesothorax is usually unmodified externally throughout the members of Brachinida, with a few important exceptions. In members of the Crepidogastrini, the mesepimeron is lost or is very narrow, and is internal. The mesepisternum is in contact with the metepisternum. I discuss the importance of this character state under flightlessness. The coxal cavities are conjunct-separate in members of *Mastax*, *Pheropsophidius*, and *Pheropsophus*, and conjunct-confluent in the rest of the bombardier beetles. Bell (1967) defines coxal terminology.

The elytra exhibit considerable intergeneric variation. Generally, each elytron is rectangular (or hemi-ovate in some wingless species) with a moderately wide epipleuron. The truncate apex is either perpendicular to the suture or is angulate. In the latter case, the length along the suture is shorter than the epipleural length. The costae of the elytra are present in all groups, but differently modified in some. The members of the Old World Pheropsophina have carinate costae, separated by flat, macrosculptured depressions. The costae are narrow in *Aptinomorphus*, and wide in *Stenaptinus* and *Pheropsophus* (*sensu stricto*). The other bombardiers have rounded, low or moderately-high costae, alternating with the striae depressions. In members of some *Brachinus*, *Styphlomerus*, and Crepidogastrini, the costae are absent, but the erect "depression setae" mark the location of the striae commonly found in other carabid beetles.

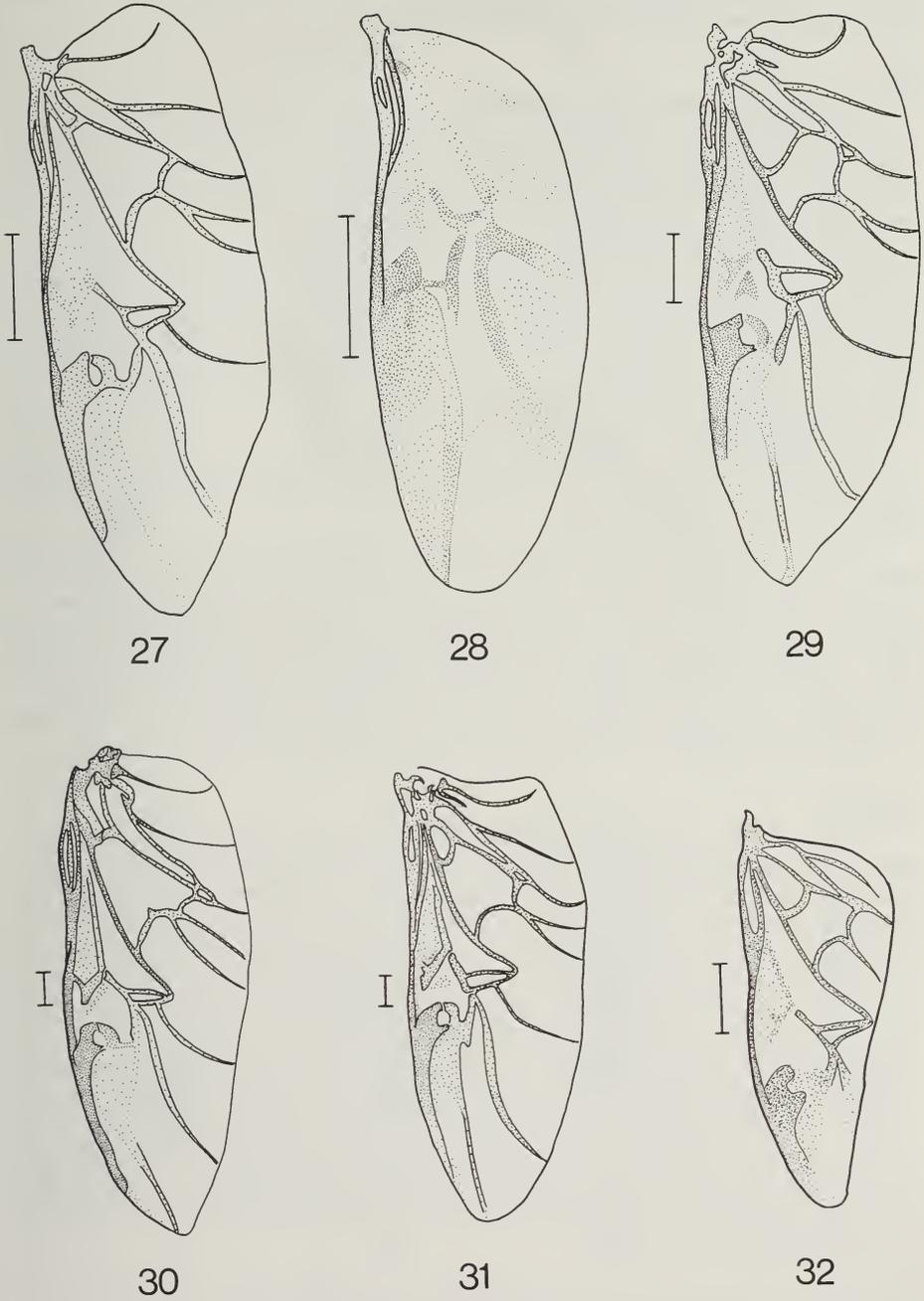
Metathorax

The metathorax is similar in all bombardiers, except in members of *Mastax*. This aberrant genus has members with the anterior metasternal process broadly rounded, rather than acute as in other bombardiers. Further, the members of this genus have the metacoxal cavities lobate-separate, rather than lobate-confluent as in other bombardiers.

In members of wingless Brachinida species, or those with reduced wing membranes (not wing dimorphic), there is a reduction in the length of the metasternum and metepisterna. In all cases where there has been wing reduction or loss of flight (even when not necessarily from reduction of wing membrane), the length of the metasternum behind the mesocoxa is subequal to or shorter than the diameter of the mesocoxa (fig. 26). The metepisternum has not become square as in some *Pterostichus* (Ball, 1960; Hacker, 1968), except in beetles with wings entirely absent as in members of *Aptinus* and Crepidogastrini. With the reduction in the length of these "flight components", the lobe of the metepimeron becomes larger, especially in *Aptinus*. In species which apparently have been flightless for a long time, such as the members of Crepidogastrini, the mesepimeron disappears, at least externally.

I believe that the relative ages of wingless species of bombardiers (and possibly other carabids) may be determined by comparisons of metathoracic structures. Hypothetically, the longer a species has been flightless, the shorter the metasternum, metepisterna, and wings, the more sloping the humeri, and the larger the lobe of the metepimeron. Ultimately, the elytra fuse along the suture, but this has not occurred in bombardier beetles. Of course the reduction probably begins with wing dimorphism as described by Lindroth (1945, 1963) and Darlington (1936, 1943), but after all members of the species have become flightless, then reduction in the mesothoracic and metathoracic flight components begins, and a building up of thoracic "ambulatory components" takes place.

Most groups of bombardier beetles have some wingless members, but I have not yet seen nor heard of any wingless members of *Mastax* nor of *Styphlomerus* and its allies. Among those bombardier beetles with wings (figs. 27-32), there is great similarity in the venation and wing-folding pattern. Both are clearly "caraboid" in nature (see Forbes, 1926), except in members of *Mastax*. This aberrant group has all the wing veins reduced to vague sclerotized fields on the membrane. The oblong cell has almost disappeared, and the wedge cell and



Figs. 27-32. Left wing, dorsal aspect. 27. *Styphlomerus ?ciliatus* Liebke, Garamba, Congo, Africa. 28. *Mastax ?hargreavesi* Liebke, Abakaliki, Nigeria. 29. *Brachinus phaeoceris* Chaudoir, Lake Roberts, New Mexico. 30. *Pheropsophus ?bimaculatus* (Linne), Mysore, India. 31. *Aploa nobilis* Dejean, Chad, Africa. 32. *Brachinus imporcitis* new species, Pinal Creek, Arizona. Accompanying scale lines equal 1.0 mm.

first and second anal complexes are absent. Further, the wing is rounded apically, rather than being acute as in the other bombardier groups.

Legs

The legs of bombardier beetles are quite similar throughout the various groups, but the pubescence and setae vary interspecifically. Only the anterior tibiae and anterior male tarsi offer obvious characters for taxonomic diagnoses and phylogenetic considerations. Possibly after enough study of additional representative material, the middle and hind legs may offer good characteristics in some groups (but not in *Neobrachinus*).

The anterior tibia has an antennal comb one third the distance from apex to base. The position of this comb, and the relative positions of its two associated spurs, have been used as the bases of some proposed classifications (Jeannel, 1941; Bell, 1967). In the bombardier beetles, the proximal spur (figs. 33-39) is located on the upper edge of the comb, either internally (Aptinina, Crepidogastrini), intermediately positioned (*Aploa*, *Brachinoaptinus*, *Pheropsophus*), or externally. It is absent from members of *Mastax* (fig. 40). The distal spur is located at the tibial apex, behind the tarsal insertion.

The vestiture of the male anterior tarsal articles is intergenerally quite diverse. The members of Crepidogastrini (fig. 50) have circular pads of setae, spongy in appearance, beneath either two or three basal tarsal articles.

An Indian species, *Tyronia humerata* (Chaudoir), has members with three articles with pads of vestiture, while the African *Tyronia kivuensis* Basilewsky has only two articles with vestiture. Members of *Mastax* have each of the two basal articles bearing two parallel rows of spatulate setae (fig. 49). The rows are symmetrically arranged on the underside of the articles. This same two-rowed pattern is seen in some Brachinina (fig. 42), and in all Pheropsopina (figs. 44, 45), except that in the latter two groups three articles have the vestiture. In members of the Aptinina (figs. 43, 47) and some Brachinina (fig. 41), the two parallel rows are diagonally placed on the three basal asymmetrical tarsal articles.

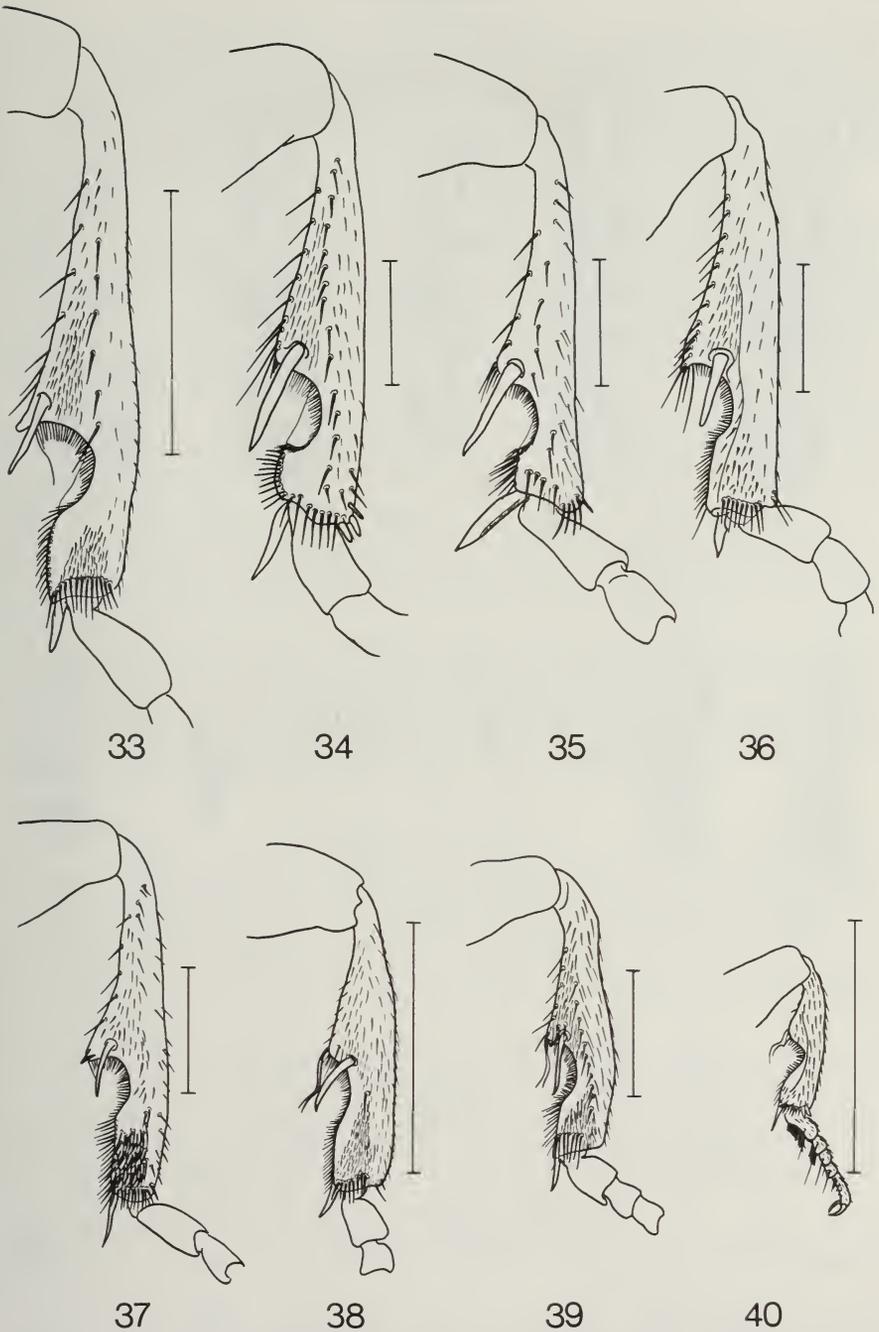
Abdomen

The abdomen of the bombardier beetles exhibits very little variation. The females have seven visible abdominal sterna, while the males have eight. In the male the eighth sternum is divided into two lateral halves, while in both sexes the ninth tergum is modified into twin "crepitation chambers", separated by a median keel. At the base of the keel, on either side, lies the outlet from the mixing chamber of the crepitating mechanism. When the mechanism is not being fired, the eighth tergum overlies the ninth. During crepitation the ninth tergum is telescoped caudally from under the eighth tergum, exposing the twin chambers. Each chamber consists of a smooth L-shaped trough bordered internally by the median keel, and bordered caudally by the up-turned apex of tergum nine. The foot of the L lies transversely at the base of the upturned apex of tergum nine. This construction allows the beetle to "aim" the chemical components of its irritant toward the predator. Eisner (1958) has studied the directional aspects of this defensive spray, and he shows it can be aimed. I have observed the aiming capabilities of these beetles while collecting them and while observing them in the laboratory. The extensible abdomen and truncate elytra allow free movement of the abdominal apex for aiming.

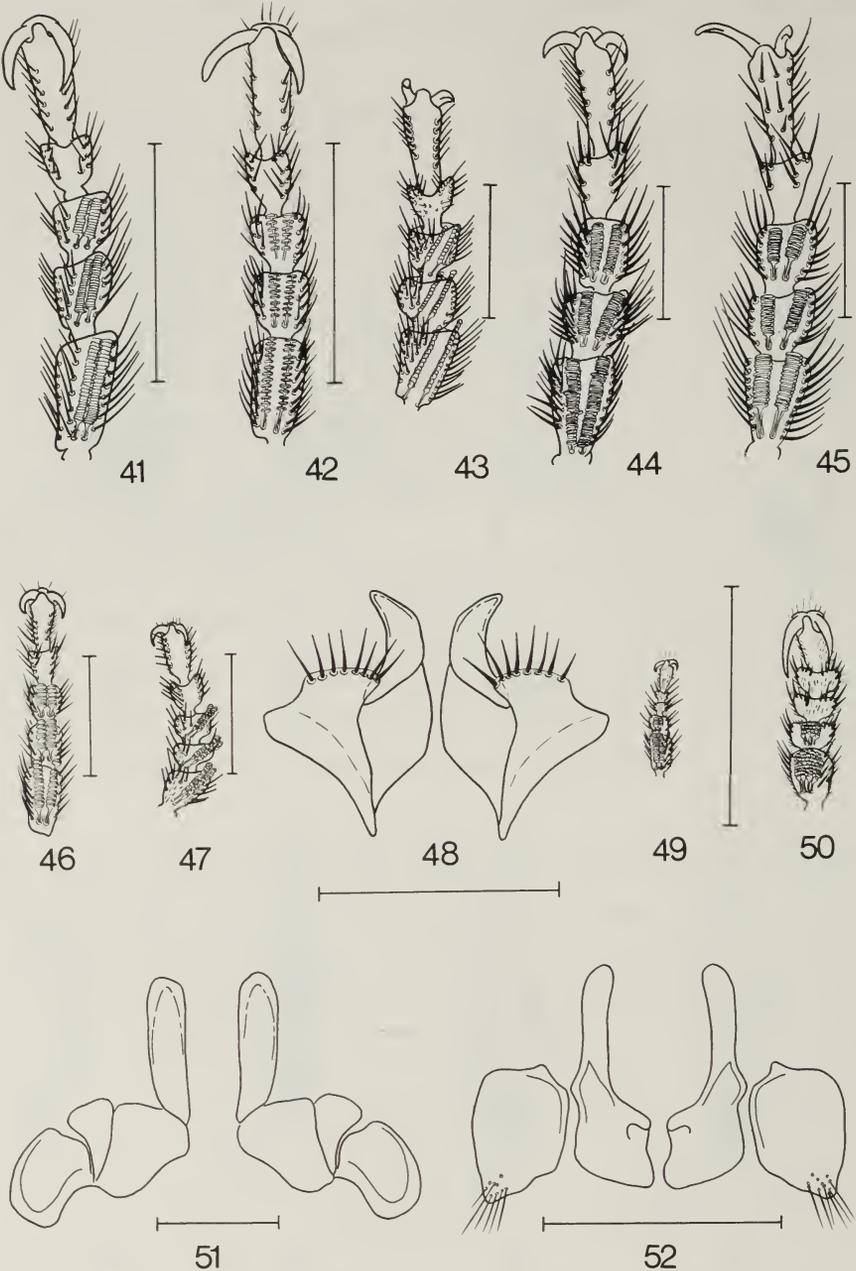
Genitalia

Female ovipositor and bursa copulatrix

Tanner (1927) discussed the family characteristics of carabid female genitalia. The bombardier beetles fit the basic description Tanner gives, with the exception of *Mastax* and



Figs. 33-40. Right front tibia of male, lateral aspect. 33. *Brachinus phaeocerus* Chaudoir, Lake Roberts, New Mexico. 34. *Pheropsophus ?bimaculatus* (Linné), Mysore, India. 35. *Pheropsophidius rivieri* Demay, Ciudad Bolivar, Venezuela. 36. *Aptinus bombarða* Illiger, Europe. 37. *Aploa nobilis* Dejean, Chad, Africa. 38. *Crepidogaster caffra* Peringuey, Cape Point, South Africa. 39. *Styphlomerus ?ciliatus* Liebke, Garamba, Congo, Africa. 40. *Mastax ?hargreavesi* Liebke, Abakaliki, Nigeria. Accompanying scale lines equal 1.0 mm.



Figs. 41-47, 49, 50. Right front tarsus of male, ventral aspect. 41. *Brachinus immaculicornis* Dejean, France. 42. *Brachinus phaeocerus* Chaudoir, Lake Roberts, New Mexico. 43. *Aptinus bombarða* Illiger, Europe. 44. *Pheropsophus ?bimaculatus* (Linné), Mysore, India. 45. *Pheropsophidius rivieri* Demay, Ciudad Bolivar, Venezuela. 46. *Aploa nobilis* Dejean, Chad, Africa. 47. *Styphlomerus ?ciliatus* Liebke, Garamba, Congo, Africa. 49. *Mastax ?hargreavesi* Liebke, Abakaliki, Nigeria. 50. *Crepidogaster caffra* Peringuey, Cape Point, South Africa. Figs. 48, 51, 52. Female ovipositor, ventral aspect. 48. *Styphlomerus ?ciliatus* Liebke, Garamba, Congo, Africa. 51. *Stenaptinus ?kolbei* Hubenthal, Cameroon, Africa. 52. *Crepidogaster caffra* Peringuey, Cape Point, South Africa. Accompanying scale lines equal 1.0 mm.

Crepidogaster. In members of *Mastax* (fig. 62) there are two lateral, elongate sclerites in the position Tanner illustrates for the ninth sternite. In the position Tanner illustrates for the tenth sternite behind the bursal opening, there are two small transverse rods. Further, members of *Mastax* have a single seta on the coxite that exceeds the length of the stylus. In members of *Crepidogaster* (fig. 52), the coxite and stylus are fused and articulated with the valvifer. Peculiarly, the base of the valvifer is plurisetose.

The members of Aptinina have the normal carabid three piece ovipositor. In *Aptinus* members (fig. 58), the apical-medial corner of the valvifer is plurisetose, while in members of *Styphlomerus*, *Styphlomerinus*, and *Styphlodromus* (fig. 48), the apical edge of the valvifer has several flattened spine-like setae. The styli of the Aptinina members are strongly curved blades, which are usually acute apically. The members of the remaining genera have variously modified styli, depending upon the species. In the members of Pheropsophina (fig. 51, 59, 61), the stylus blade is variously modified among the subgenera. *Pheropsophus* (*sensu stricto*) members have very elongate and narrow styli, some with microspinules along the inner edge (fig. 61). In *Stenaptinus* members, the styli are long and spatulate (fig. 51). In the members of *Pheropsophidius*, they are similar to those in members of *Brachinus*, but lack the setae (fig. 59).

The various members of *Brachinus* and *Aptinoderus* have the normal carabid three piece ovipositor. The stylus is flattened and triangular, but varies considerably between the species. The members of *Brachinus* have a single small seta on the ventral side near the apex of the spatulate stylus.

The female members of *Aptinus* (fig. 55) are the only Brachinida which possess bursal sclerites. The entire walls of the bursa are thinly sclerotized in a laminate fashion. A single large rod-like sclerite is dorsal to the entrance of the bursa. Laterad, near the base of this rod on the wall of the bursa, is a large and concave sclerite. At this point the entire bursa is transverse, with a large forked sclerite in a pouch near the concave sclerite.

Male genitalia

The male genitalia are interspecifically distinct, and they can be used to distinguish between species in at least *Neobrachinus*. They are composed of the following parts: median lobe, with the apex, shaft, ligule, basal bend, and basal portion; two parameres (the left one large and the right one small) attached to the ventral corner of the basal portion of the median lobe; and an endophallus, which is a membranous sac containing the gonopore, which in turn may or may not provide attachment for various apical or subapical sclerites and microtrichial fields.

The members of Crepidogastrini possess a very primitive type of male genitalia. The median lobe is tubular, straight or bent, sometimes with the shaft contorted. The parameres are not balteate, but are asymmetric. The left paramere is lobate, and is alongside the median lobe. The smaller right paramere is lobate and is held close to the shaft. The ligule of the shaft is absent. The endophallus is more than half the length of the median lobe, and in members of some *Crepidogaster*, the apex has microtrichial fields.

In members of Brachinini, the parameres are always balteate, the left is larger than the right, and both are wrapped around the basal portion of the median lobe and connected by a membrane.

The members of *Mastax* have the most aberrant median lobe and endophallus of all the Brachinida (fig. 53). The apex and shaft are similar to some *Bembidion*. The endophallus possesses a coiled ribbon-like sclerite, as well as one basal and one apical sclerotized plate. The parameres are smaller than in any other group, and they adhere tightly to the base of the basal portion of the median lobe.

The remaining groups have typical brachinine genitalia with balteate parameres, a more

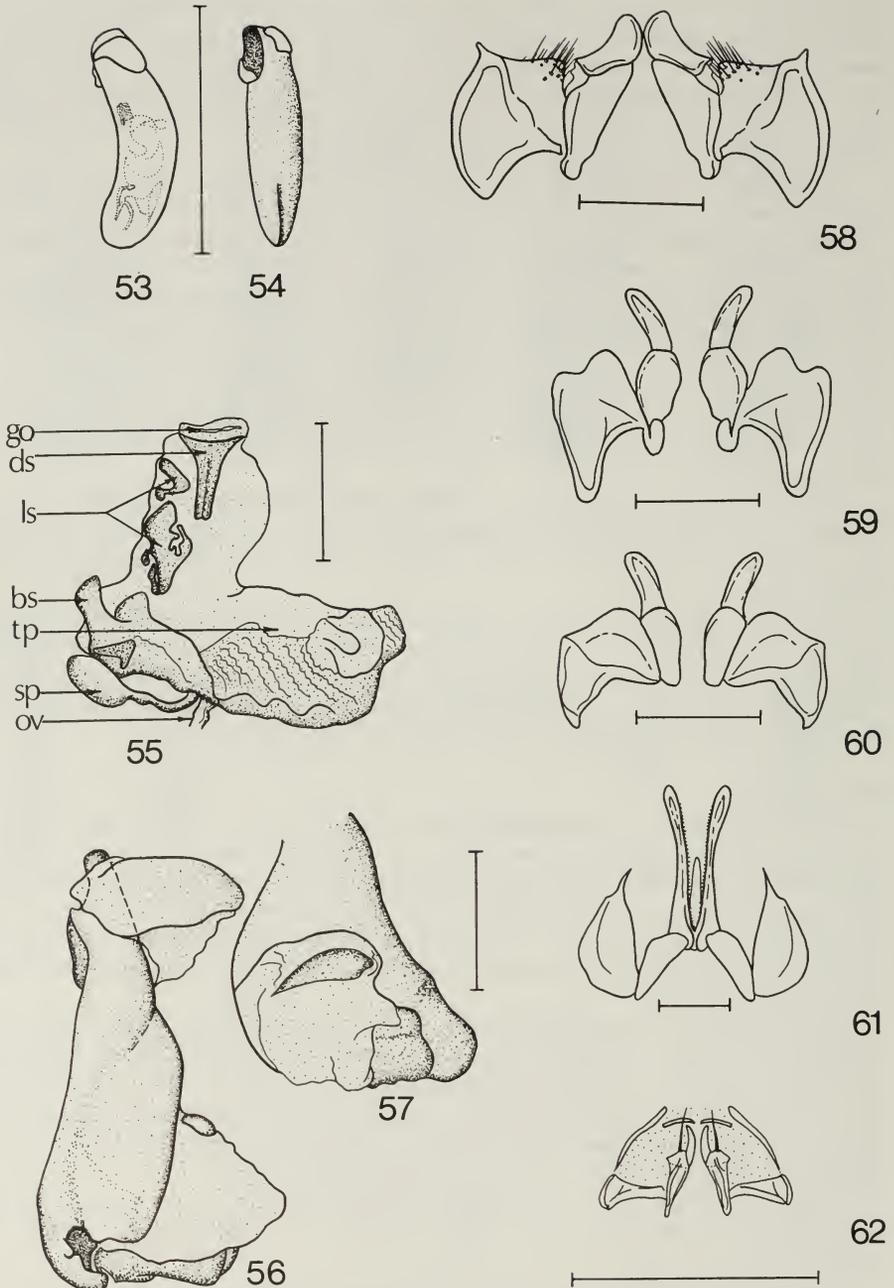


Fig. 53. Male genitalia of *Mastax ?hargreavesi* Liebke, Abakaliki, Nigeria, lateral aspect. Fig. 54. Ventral aspect of same. Fig. 55. Bursal sclerites of female *Aptinus bombardata* Illiger, Europe, dorsal aspect. Fig. 56. Male genitalia of *Aptinus bombardata* Illiger, Europe, lateral aspect. Fig. 57. Dorsal aspect of same. Figs. 58-62. Female ovipositor, ventral aspect. 58. *Aptinus bombardata* Illiger, Europe. 59. *Pheropsophidius rivieri* Demay, Ciudad Bolivar, Venezuela. 60. *Aploa nobilis* Dejean, Chad, Africa. 61. *Pheropsophus ?bimaculatus* (Linné), Mysore, India. 62. *Mastax ?hargreavesi* Liebke, Abakaliki, Nigeria. Accompanying scale lines equal 1.0 mm. (go = gonopore, ds = dorsal sclerite, ls = lateral sclerites, tp = transverse pouch, bs = basal sclerite, sp = spermatheca, ov = oviduct).

or less tubular median lobe, and generally a moderate-sized endophallus. Some of these groups have microtrichia or sclerites on the internal sac. The members of *Pheropsophus* (fig. 69) and *Pheropsophidius* (figs. 437-442) have fields of microtrichia on a very long endophallus. *Styphlomerus* members which I have seen have a shorter endophallus, but still with microtrichia (but I have seen very few examples). *Aptinus* members have very contorted median lobes with a very short endophallus. The endophallus has one basal and two apical sclerites. Although I have not studied *Aptinus* males and females *in copula*, I believe there is a definite correlation between the female bursal sclerites, and the male median lobe. A study of this relationship might prove fruitful.

Within the genus *Brachinus*, there have evolved many types of endophallic sclerites. The members of *Neobrachinus*, *Brachynolomus*, *Cnecostolus*, and some African lineages, have developed an apical sclerite surrounding the gonopore. Snodgrass (1935) has termed this sclerite the "virga". The members of *Brachinoaptinus*, *Brachinus (sensu stricto)*, *Metabrachinus*, other African lineages, and at least one Oriental lineage, do not have any sclerites on the endophallus. The members of one Oriental lineage have a long endophallus with a tube at the apex which bears microtrichia. The members of *Aploa*, and those of at least one west African lineage, have a subapical endophallic sclerite. The variation and homologies of these virgæ and sclerites are extremely important aids for persons attempting to understand the relationships and hence, the dispersal movements of the members of the genus *Brachinus*. Because of the extreme similarity in the external features of these beetles, the genitalic diversity often must be studied carefully to determine the species differences (see below under *Neobrachinus*).

The virgæ of all North and Middle American species of *Brachinus* with known males were studied in great detail. As a result of this study, certain patterns of evolution became apparent. From a simple sclerotized tip of the endophallus (as in extant *Brachinus dryas* Andrewes and members of the *americanus* group) more complex types evolved as indicated in fig. 461.

TAXONOMY

Division Brachinida Bonelli

Brachinii Bonelli, 1809: tab. syn.

Brachinida Ball, 1960: 164.

The following combination of characteristics is diagnostic of this division of higher Carabidae: anterior tibia anisochaetous middle coxae conjunct; lobe of metepimeron present; elytra truncate, costate, striae obscure; abdomen with seven or eight sterna normally exposed; outlets of the crepitating mechanism medial, in front of modified ninth tergum; ninth tergum modified into twin crepitating chambers in both males and females; male genitalia with an endophallus; parameres asymmetrical, the right minute, the left larger; cuticle of mature adult pliable.

This division includes the tribes Crepidogastrini and Brachinini.

Key to tribes and subtribes of the division Brachinida

- 1 Mesepimera absent or almost so; ventral vestiture of male anterior tarsal articles spongy and pad-like; terminal palpal articles swollen, usually securiform; gular sutures convergent behind Crepidogastrini
- 1' Mesepimera present, broad, clearly visible; vestiture beneath male anterior tarsal articles consisting of two parallel rows of modified setae; terminal palpal articles subcylindrical or wedge-shaped; gular sutures divergent behind Brachinini 2
- 2(1') Hind coxae contiguous; metasternal process acute; middle coxae not widely sep-

- arated; mandible with a scrobe; upper spur of anterior tibia present. 3
- 2' Hind coxae widely separated; metasternal process broadly rounded; middle coxae widely separated; mandible without a scrobe; upper spur absent Mastacina, new subtribe
- 3(2) Mandibular scrobe unisetose. 4
- 3' Mandibular scrobe plurisetose *Brachinina sensu stricto*
- 4(3) Vestiture of male anterior tarsal articles arranged diagonally on asymmetric articles; mentum with a tooth on anterior edge (absent in *Styphlodromus*); upper spur on anterior tibia internal (fig. 36). Aptinina, new subtribe
- 4' Vestiture of male anterior tarsal articles not diagonal, articles symmetric; mentum without a tooth; upper spur external or almost so (fig. 35). Pheropsophina, new subtribe

Tribe Crepidogastrini Jeannel

Crepidogastritae Jeannel, 1949: 1080.

Crepidogastrini Basilewsky, 1959: 233.

Type genus. — *Crepidogaster* Boheman, 1848: 68.

The following combination of characteristics is diagnostic of this tribe: labrum with eight setae; mandibular scrobe plurisetose; palpi with terminal articles swollen or securiform; gular sutures convergent behind; anterior coxal cavities biperforate, closed behind; propleural suture present; upper spur of anterior tibia internal; ventral vestiture of male anterior tarsal articles spongy and pad-like; middle coxal cavities conjunct-confluent; mesepimera absent or almost so; apical elytral membrane absent; hind coxal cavities confluent; metasternum and metepisterna greatly reduced; wings absent; male parameres not balteate; valvifers of female ovipositor setiferous anteriorly; coxite and stylus of female ovipositor fused.

This tribe contains the genera *Crepidogaster*, *Tyronia*, *Crepidogastrinus*, *Crepidonellus*, *Crepidogastrillus*, *Brachynillus*, and *Crepidolomus*.

Key to the genera of the tribe Crepidogastrini (translated and modified from Basilewsky, 1959)

- 1 Lateral edge of pronotum with many spine-like setae; lateral edge of elytron also with spine-like setae *Crepidogastrinus* Basilewsky
- 1' Lateral edge of pronotum with one or two pairs of setae; depression 8 of elytron with umbilicate setae only 2
- 2(1') Elytra short and wide, maximum width greater than length at suture 3
- 2' Elytra long and narrow, maximum width shorter than length at suture 4
- 3(2) Pronotum with one pair of lateral setae, near the middle; terminal article of labial palpus securiform. *Crepidonellus* Basilewsky
- 3' Pronotum with two pairs of lateral setae, one just before hind angles and one near the middle; last article of labial palpus globose. *Crepidogastrillus* Basilewsky
- 4(2) Pronotum with one pair of lateral setae, near the middle 5
- 4' Pronotum with two pairs of lateral setae, one just before hind angles and one near the middle 6
- 5(4) Terminal article of labial palpus strongly swollen or securiform; terminal article of maxillary palpus very swollen or securiform. *Crepidogaster* Boheman
- 5' Terminal article of labial palpus fusiform or subcylindrical; terminal article of the maxillary palpus globose, but not securiform; body slender and elongate. *Brachynillus* Reitter
- 6(4') Terminal article of labial palpus strongly swollen or securiform; terminal article of maxillary palpus very swollen or securiform. *Tyronia* Liebke

- 6' Terminal article of labial palpus fusiform or subcylindrical; terminal article of the maxillary palpus globose, but not securiform; body slender and elongate.
 *Crepidolomus* Basilewsky

Genus *Crepidogaster* Boheman
 (Figs. 7, 11, 38, 50, 52, 63, 64)

Crepidogaster Boheman 1848: 68. Type species. — *Crepidogaster bimaculatus* Boheman 1848: 68 (subsequent designation, Jeannel, 1949: 1081).

Crepidostoma Motschulsky 1862: 54. Type species. — *Crepidogaster rufescens* Motschulsky 1862: 54 (by monotypy).

Diagnostic combination. — Terminal article of labial palpus strongly swollen or securiform; terminal article of maxillary palpus very swollen or securiform; pronotum with one pair of setae, near the middle; elytra long and narrow, their combined maximum width shorter than their length along the suture.

Description. — Small to large-sized beetles, 4.0 to 16.0 mm (from Basilewsky, 1959).

Color. Generally ferruginous with brown or black elytra which are sometimes spotted.

Microsculpture. Isodiametric on head, pronotum, and elytra.

Macrosculpture. Entire dorsal surface covered by small setiferous punctulae.

Head. Labrum entire, with eight evenly spaced setae transversely arrayed on disc. Clypeus rectangular, with two large setae, one inside each anterior angle. Front punctate with numerous setae scattered throughout; furrows shallow; one supraorbital seta over each eye; bead over eye ending midway the length of eye. Eyes protruding, but not prominent. Antennae short, robust, pubescent throughout. Mandibles (fig. 7) each broad, triangular, curved at tip; cutting edge with one small retinacular tooth; ventral groove with short golden setae; scrobe plurisetose, but with one larger seta. Labial palpi (fig. 11) each with last article securiform; all articles with numerous small setae. Maxillary palpi each more or less filiform, last article swollen; all articles with numerous small setae. Ligula (fig. 11) membranous and square with anterior angles produced, and center ventrally produced into a plurisetose sclerotized convexity. Mentum (fig. 11) well developed without tooth. Gula (fig. 11) narrowed behind.

Prothorax. As described for the tribe Crepidogastrini, plus numerous punctulae on disc. Anterior tibiae (fig. 38) each with upper spur internal, at middle of comb emargination. Male anterior tarsal articles (fig. 50) symmetrical, vestiture beneath first and second consisting of apically widened setae forming pads. Female anterior tarsal articles without vestiture.

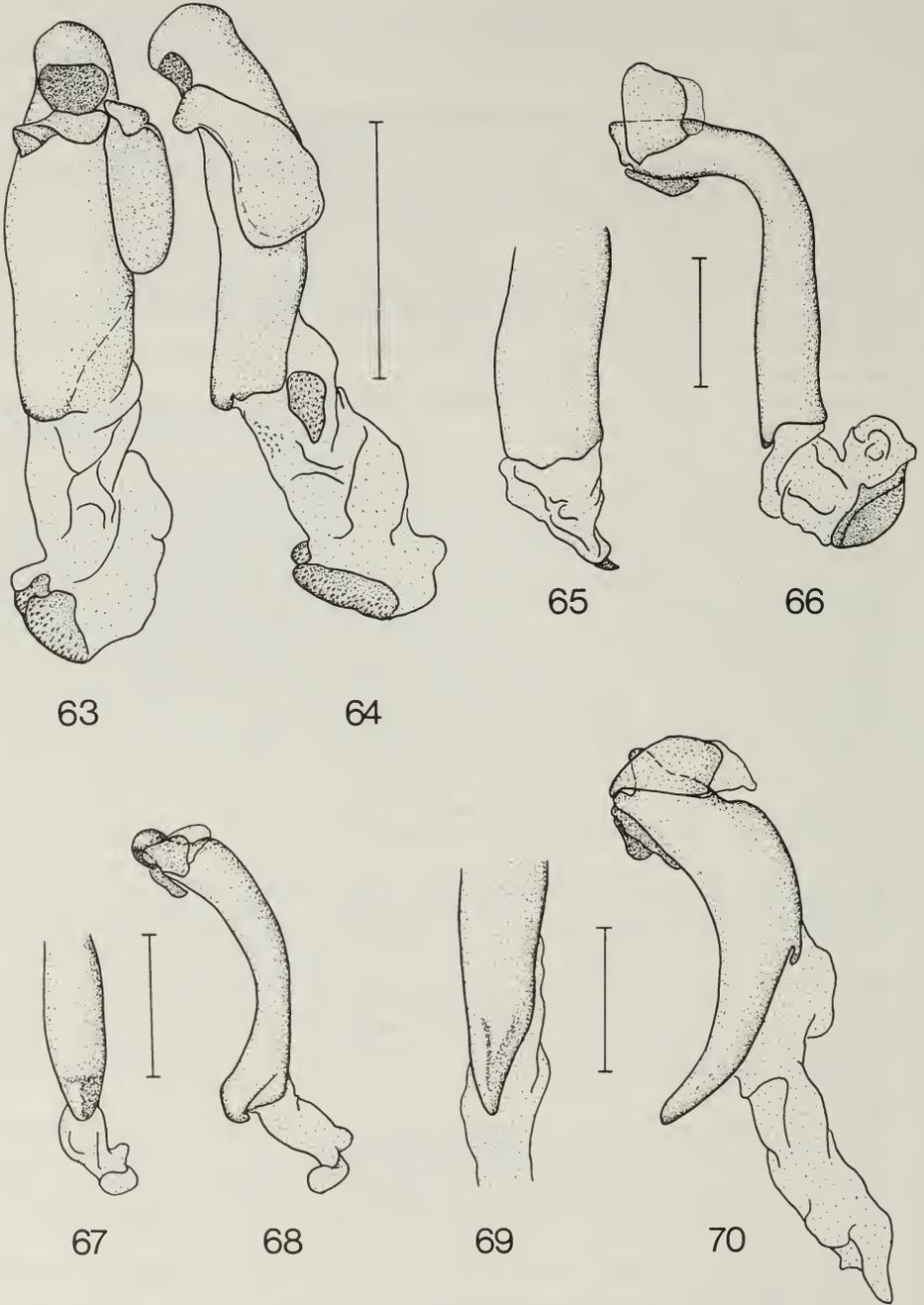
Pterothorax. Mesepimera absent, or almost so. Metathoracic process acute. Metepimeron lobe rounded apically. Elytral humeri sloping, lateral bead discontinuous before base of humerus. Depression setae present between well developed carinae or costae. Epipleura pubescent, wide anteriorly and medially, but narrowed toward apex. Wings absent.

Abdomen. As described for the tribe, plus a pair of ambulatory setae arising laterad, at apex of sterna 3-6.

Genitalia. Male (figs. 63, 64) with small parameres, not balteate, asymmetrical. Median lobe various, ligule absent. Endophallus of medium length, with two apical microtrichiate fields and one basal field; virga absent. Female (fig. 52) with elongate, narrow, spatulate, and unarmed styli; coxites small, continuous with stylus; valvifers setose anteriorly; bursa unarmed.

Etymology. — Latin, *crepo* = rattle; Greek, *gaster* = stomach; referring to the beetles' ability to crepitate.

Distribution. — The species of *Crepidogaster* occur south of the equator in Africa and Madagascar, with only two populations of one species known north of the equator in east Africa.



Figs. 63-70. Male genitalia. 63. *Crepidogaster caffra* Peringuey, Cape Point, South Africa, ventral aspect: 64. Lateral aspect of same. 65. *Aploa nobilis* Dejean, Chad, Africa, ventral aspect. 66. Lateral aspect of same. 67. *Styphlomerus ?ciliatus* Liebke, Garamba, Congo, Africa, ventral aspect. 68. Lateral aspect of same. 69. *Pheropsophus ?bimaculatus* (Linné), Mysore, India, ventral aspect. 70. Lateral aspect of same. Accompanying scale lines equal 1.0 mm.

Genus *Tyronia* Liebke

Tyronia Liebke, 1934: 18. Type species. — *Crepidogaster numeratus* Chaudoir, 1876: 96 (original designation).

Diagnostic combination. — As given in the key.

Description. — Small-sized beetles, 3.5 to 7.0 mm (from Basilewsky, 1959). For details see Basilewsky (1959).

Distribution. — The species of *Tyronia* occur in south and middle Africa on the eastern side of the continent. Two species occur in the Oriental Region, one in India, and one in Ceylon.

Genus *Brachynillus* Reitter

Brachynillus Reitter, 1904: 178. Type species. — *Brachynillus varendorffi* Reitter 1904 : 178 (by monotypy).

Diagnostic combination. — As given in the key.

Description. — Small-sized beetles, 5.0 to 5.5 mm (from Basilewsky, 1959). For details see Basilewsky (1959).

Distribution. — The type species is found as a troglobiont in the "Grottes de Kulumuzi" in Tanganyika. A second species placed in the genus by Basilewsky is known from one specimen labelled "Cape Town".

Genus *Crepidolomus* Basilewsky

Crepidolomus Basilewsky, 1959: 331. Type species. — *Brachynillus extimus* Jeannel, 1955 : 62 (original designation).

Diagnostic combination. — As given in the key.

Description. — Small-sized beetles, 5.5 mm (from Basilewsky, 1959). For details see Basilewsky (1959).

Distribution. — One female specimen is known from Andohahelo, on the southern tip of Madagascar.

Genus *Crepidonellus* Basilewsky

Crepidonellus Basilewsky, 1959: 334. Type species. — *Crepidogaster pusillus* Péringuey, 1888: 76 (original designation).

Diagnostic combination. — As given in the key.

Description. — Very small-sized beetles, 3.6 to 4.3 mm (from Basilewsky, 1959). For details see Basilewsky (1959).

Distribution. — The members of *Crepidonellus* are found in South West Africa and Cape Province.

Genus *Crepidogastrillus* Basilewsky

Crepidogastrillus Basilewsky, 1959: 337. Type species. — *Crepidogastrillus curtulus* Basilewsky, 1959: 338 (original designation).

Diagnostic combination. — As given in the key.

Description. — Very small-sized beetles, 3.4 to 3.6 mm (from Basilewsky, 1959). For details see Basilewsky (1959).

Distribution. — The range of this genus extends from Cape Province north into South West Africa, and east to northwest Rhodesia.

Genus *Crepidogastrinus* Basilewsky

Crepidogastrinus Basilewsky, 1957: 117. Type species. — *Crepidogastrinus kochi* Basilewsky, 1957: 118 (by original designation and monotypy).

Diagnostic combination. — As given in the key.

Description. — Very small-sized beetles, 3.0 mm (from Basilewsky, 1959). For details see Basilewsky (1957, 1959).

Distribution. — The range of this species is confined to southern Angola and south West Africa.

Tribe Brachinini Bonelli

Brachinii Bonelli, 1809: tab. syn.

Brachynidae Stephens, 1827: 5.

Brachynini Erichson, 1837: 25 (Brachinini, of authors).

Brachinida Heer, 1838: 4.

Brachinides Lacordaire, 1854: 97.

Brachinites Jacquelin du Val, 1857: 55.

Brachinina Thomson, 1859: 6 (Brachynina, of authors).

Brachyninae Kolbe, 1898: 60.

Brachynitae Alluaud, 1916: 50.

Brachinidae Jeannel, 1942: 1102.

The following combination of characteristics is diagnostic of this tribe: mandibular scrobe plurisetose or unisetose; labial palpus with terminal article wedge-shaped, subcylindrical, or globose-attenuate; gular sutures divergent behind; anterior coxal cavities uniperforate or biperforate; propleural suture present or absent; upper spur of anterior tibia present or absent, internal or external; ventral vestiture of male anterior tarsal articles composed of two parallel rows of modified setae; mesepimeron present, wide, but not reaching middle coxa; male parameres balteate.

This tribe contains the subtribes Mastacina new subtribe, Pheropsophina Jeannel, Aptinina new subtribe, and Brachinina Bonelli.

Subtribe Mastacina new subtribe

Type genus. — *Mastax* Fischer von Waldheim, here designated.

This subtribe contains a single genus. The diagnostic characteristics are given below.

Genus *Mastax* Fischer von Waldheim

(Figs. 6, 10, 28, 40, 49, 53, 54, 62)

Mastax Fischer von Waldheim, 1825-28: 111. Type species. — *Brachinus thermarum* Stevens, 1806: 166 (subsequent designation by Jedlička, 1963: 547).

Brachinus (of authors).

Diagnostic combination. — Mandibular scrobes reduced, unisetose; last article of palpi fusiform with subulate tip; mentum with single tooth and deep pit (fig. 10); mandibles each with large bifid terebral tooth; anterior coxal cavities biperforate-separate, closed behind; propleural sutures present; pronotum with two longitudinal ridges on disc; upper spur of anterior tibia absent; middle coxae conjunct-separate; metasternal process (between middle coxae) broadly rounded; hind coxae widely separated; wing (fig. 28); parameres of male genitalia extremely small, adherent to base of median lobe; ligule absent; coxite of female genitalia unisetose, stylus short.

Description. — Small-sized beetles, 2.5 to 4.0 mm.

Color. Head, prothorax, and legs generally ferruginous to brown. Abdomen, antennae, and "knees" infuscated. Elytra brown with white spots.

Microsculpture. Isodiametric on head and pronotum, except where obliterated by macrosculpture. Longitudinally-stretched meshes on elytra.

Macrosculpture. Longitudinal wrinkles on head and pronotum. Minute chevron-shaped wrinkles on costae of elytra, surface "satin-like" in appearance.

Head. Labrum emarginate, with eight evenly spaced setae transversely arranged on disc. Clypeus rectangular, with six evenly spaced setae transversely arranged on disc. Front longitudinally wrinkled with numerous scattered setae; furrows shallow, reflexed strongly at sides over antennal bases; one supraorbital seta over each eye, one pseudosupraorbital seta behind each eye; bead over eye carinate and prolonged on side of vertex behind pseudosupraorbital seta; shallowly depressed at middle. Eyes prominent. Antennae robust; articles 5-10 as wide as long, moniliform; article 11 fusiform and subulate at apex; all articles pubescent. Mandibles (fig. 6) arcuate each with a strong bifid terebral tooth; basal margin with dense brush of fine golden setae, also a row of fine setae in ventral groove; scrobes effaced, but unisetose. Palpi (fig. 10) each with terminal article fusiform, tip subulate; all articles pubescent. Ligula bilobed; lobes thin and densely setiferous; median portion slightly swollen with two large setae. Mentum (fig. 10) short, with single tooth medially on anterior edge; center of mentum excavated and surrounded by setae. Gula (fig. 10) widened behind.

Prothorax. As described for the subtribe Masticina, and disc with two longitudinal carinae on each side of midline. Anterior tibia (fig. 40) without upper spur. Male and female with first two tarsal articles expanded, the male (fig. 49) with modified vestiture beneath these two articles. Male with a curved nonarticulated spine (fig. 40) on right side of glabrous antennal comb-trough.

Pterothorax. Metathoracic process (between middle coxae) broadly rounded, middle coxae widely separated. Hind coxae widely separated. Metepimeron lobe small, but rounded caudally. Elytra quadrate, humeri prominent, lateral bead prolonged inside humerus to base of fifth stria. Setae present between weakly raised costae in striae 2, 4, 6, 8. Epipleura wide throughout; pubescent. Wings as in fig. 28.

Abdomen. As described for the division Brachinida, except with one pair of ambulatory setae at apex of sterna 2-5.

Genitalia. Male (fig. 53, 54) with extremely small parameres adherent to base. Median lobe various, but usually slightly arcuate and blunt at apex. Endophallus extremely complicated with (in repose) two sclerites apically and one sclerite basally; membrane reinforced with a thin, spiraled, sclerotized rod. Female (fig. 62) with short, narrow, arcuate and unarmed styli; valvifer transverse, narrow, and elongate; coxite unisetose; bursa unarmed; spermatheca present, sausage-shaped.

Etymology. — Greek, *mastokos* = jaw, mouth; referring to the huge retinacular tooth on the mandibles of these beetles.

Distribution. — (Fig. 457). Species of *Mastax* occur on both sides of the equator, but are not confined to the tropics. Species are known from south of the equator in South Africa and southern Sumatra. North of the equator some species occur in western, northern, and eastern Africa, the Congo, Saudia Arabia, Iraq (on both sides of the Caspian Sea), western India, Ceylon, southeast Asia, Hainan, and Formosa.

Subtribe Pheropsophina Jeannel

Pheropsophini Jeannel, 1948: 1084.

Type genus. — *Pheropsophus* Solier, 1833: 46.

The following combination of characteristics is diagnostic for this subtribe; mandibular scrobe unisetose; terminal palpal article wedge-shaped; anterior coxal cavities open or closed behind; propleural suture present or absent; upper spur of anterior tibia slightly internal; male anterior tarsal articles symmetrical or almost so; middle coxal cavities separate-conjunct; apical elytral membrane absent; at least some depressions of elytra microrugose; hind coxae contiguous-separate; lobe of metepimeron large; parameres of male genitalia small, balteate; dorsal surface of median lobe at basal bend notched; valvifer of female ovipositor glabrous.

This subtribe includes the genera *Pheropsophus* Solier and *Pheropsophidius* Hubenthal.

Key to the genera and subgenera of the subtribe Pheropsophina

- 1 Elytra costate, with costae low and rounded, evenly confluent with depressions; propleural suture absent *Pheropsophidius* 2
- 1' Elytra carinate, carinae sharp or rounded, well defined and abruptly confluent with depressions; propleural sutures present *Pheropsophus* 3
- 2(1) Anterior coxal cavities narrowly opened behind; depressions on disc of elytra without macrosculpture (except near scutellum); apex of elytra obliquely truncate, sutural length shorter than lateral length subgenus *Protopheropsophus* Hubenthal
- 2' Anterior coxal cavities closed behind; depressions on disc with macrosculpture; apex of elytron almost truncate; costae well defined subgenus *Pheropsophidius* Hubenthal
- 3(1') Apical border of elytron with numerous long setae subgenus *Pheropsophus* Solier
- 3' Apical border of elytron without long setae, with or without very small ones (barely visible at 50 X) 4
- 4(3') Carinae of elytra broader than the depressions, and rounded dorsally *Stenaptinus* Maindron
- 4' Carinae of elytra very narrow, sharp dorsally (Madagascar) *Aptinomorphus* Jeannel

Genus *Pheropsophus* Solier

(Figs. 5, 14, 25, 30, 34, 44, 51, 61, 69, 70)

Pheropsophus Solier, 1833: 463. Type species. — *Brachinus senegalensis* Dejean, 1825: 308 (subsequent designation by Jeannel, 1949: 1084).

Stenaptinus Maindron, 1906: 15. Type species. — *Stenaptinus krichna* Maindron, 1906: 15 (subsequent designation by Jeannel, 1949: 1084).

Parapheropsophus Hubenthal, 1914: 442. Type species. — *Brachinus verticalis* Dejean, 1825: 302 (subsequent designation by Jeannel, 1949: 1084; Darlington, 1968: 234).

Aptinomorphus Jeannel, 1949: 1091. Type species. — *Pheropsophus acute-costatus* Fairmaire, 1892: 168 (original designation).

Brachinus (of authors).

Diagnostic combination. — Elytral costae carinate, carinae sharp or rounded, well defined and more strongly contrasting with depressions; propleural sutures present.

This genus includes the subgenera *Pheropsophus* Solier, *Stenaptinus* Maindron, and *Aptinomorphus* Jeannel.

Subgenus *Pheropsophus* Solier

(Figs. 5, 14, 25, 30, 34, 44, 61, 69, 70)

Parapheropsophus Hubenthal, 1914: 442. Darlington, 1968: 234.

Diagnostic combination. — As given for genus *Pheropsophus*, plus apical border of elytra with fringe of long closely spaced setae.

Description. — Medium to large-sized beetles, 15.0 to 25.0 mm.

Color. Generally yellow or ferruginous, with black markings.

Microsculpture. Isodiametric on head, but slightly stretched transversely on pronotum and elytral carinae.

Macrosculpture. Depressions between elytral carinae with numerous longitudinal micro-irregularities.

Head. Labrum entire, with six evenly spaced setae transversely arranged near anterior margin. Clypeus rectangular, with two setae on each side near middle. Front smooth, glabrous; furrows very shallow; one supraorbital seta over each eye; bead over eye almost absent; eyes prominent. Antennae long, robust, first two articles setiferous, 3-11 pubescent. Mandibles (fig. 5) each broad, arcuate; cutting edge with two small terebral teeth and two retinacular teeth; ventral groove with short golden setae; basal margin with penicillus; scrobe unisetose. Labial palpi (fig. 14) each with terminal article narrowly wedge-shaped; terminal and penultimate articles with numerous stiff setae. Maxillary palpi each more or less filiform, terminal three articles with numerous stiff setae. Ligula (fig. 14) membranous and square, with anterior angles barely produced; center ventrally produced into a bisetose sclerotized carina. Mentum (fig. 14) well developed, without a tooth. Gula (fig. 14) widened behind.

Prothorax. As described under subtribe Pheropsophina. Anterior tibiae each with subterminal spur in intermediate position at top of comb emargination. Male anterior tarsal articles 1-3 slightly asymmetrical, vestiture beneath consisting of two parallel rows of spatulate setae. Female anterior tarsal articles symmetrical, vestiture absent. Anterior coxal cavities barely closed behind.

Pterothorax. Anterior metathoracic process acute. Middle coxal cavities contiguous-separate. Metepimeron lobe large, rounded apically. Elytral humeri square, lateral bead entire to base of humerus. Strial setae present between well developed carinae. Epipleura wide anteriorly and medially, but narrowing toward apex; not pubescent. Wings present (fig. 30).

Abdomen. As described under division Brachinida, except one pair of ambulatory setae at apices of sterna 3-6.

Genitalia. Male (fig. 69, 70) with small balteate, asymmetrical parameres; median lobe variable, but symmetrical, and notched near base; ligule double, narrow, and spatulate; endophallus short with various fields of microtrichia; virga absent. Female (fig. 61) with elongate, narrow, slightly curved styli, usually armed with small spines; coxites small, robust; valvifers glabrous; bursa unarmed, except an elongate sclerite at entrance of bursa.

Etymology. — Greek, *phero* = bearer; *psophos* = sound, or noise; hence "noise bearer" referring to the crepitating behavior of these beetles.

Distribution. — The range of this subgenus extends over much of Africa and Madagascar, with the exception of the desert region in the north of Africa, and eastward across Asia Minor, India, and eastern Asia, into the Malay Archipelago, New Guinea, New Britain, New Ireland, the Solomons, and Australia.

Subgenus *Stenaptinus* Maindron

(Fig. 51)

Diagnostic combination. — As in subgenus *Pheropsophus*, except wings absent, anterior coxal cavities slightly open behind; female styli shorter, more spatulate, unarmed.

Description. — Medium to large-sized beetles, about 10.0 to 15.0 mm.

Color. Ferruginous venter and legs, black above, sometimes head and pronotum also ferruginous.

Microsculpture. As in subgenus *Pheropsophus*.

Macrosculpture. As in subgenus *Pheropsophus*.

Head. As in subgenus *Pheropsophus*.

Prothorax. As in subgenus *Pheropsophus*, except coxal cavity slightly open behind.

Pterothorax. As in subgenus *Pheropsophus*, except metasternum very short, shorter than longitudinal diameter of middle coxa (fig. 26); metepisterna almost square; elytral humeri absent; wings absent.

Abdomen. As in subgenus *Pheropsophus*.

Genitalia. Male as in subgenus *Pheropsophus*. Female (fig. 51) styli unarmed, wider, and shorter than subgenus *Pheropsophus*, otherwise similar.

Etymology. — Greek, *stenos* = narrow; *Aptinus* = name of another brachinine genus; referring to the very narrow humeri of these beetles.

Distribution. — The range of this subgenus is the Old World Tropics, including tropical Africa, India, Ceylon, southeastern Asia, Celebes, Taiwan, Philippines, and possibly New Guinea.

Subgenus *Aptinomorphus* Jeannel

Diagnostic combination. — As in subgenus *Pheropsophus*, except for the following characters: wings absent; elytral carinae very narrow, ridge-like; apex of elytra without setae; female styli very short and broad.

Description. — Medium to large-sized beetles, 12.0 to 30.0 mm.

Color. Ferruginous venter and legs; head and pronotum ferruginous or brown; elytra black or brown.

Microsculpture. As in subgenus *Pheropsophus*.

Macrosculpture. As in subgenus *Pheropsophus*.

Head. As in subgenus *Pheropsophus*.

Prothorax. As in subgenus *Pheropsophus*.

Pterothorax. As in subgenus *Stenaptinus*.

Abdomen. As in subgenus *Pheropsophus*.

Genitalia. Male as in subgenus *Pheropsophus*. Female styli very short and broad, unarmed, otherwise as in subgenus *Pheropsophus*.

Etymology. — *Aptinus* = another brachinine genus; Greek, *morphe* = form or shape; referring to the narrow, wingless condition of these beetles, reminding one of members of *Aptinus*.

Distribution. — The species of this subgenus are confined to Madagascar.

Genus *Pheropsophidius* Hubenthal

(Figs. 4, 12, 35, 59, 423, 427, 437-442, 444, 445, 446)

Pheropsophidius Hubenthal, 1911: 547. Type species. — *Cicindela aequinoctialis* Linné, 1763:395 (subsequent designation by Jeannel, 1949: 1084).

Protopheropsophus Hubenthal, 1911: 548. Type species. — *Pheropsophus biplagiatus* Chaudoir, 1876: 18 (by monotypy).

Brachinus (of authors).

Diagnostic combination. — Elytra costate, costae low and rounded, evenly flared into depressions; propleural suture absent.

This genus includes the subgenera *Pheropsophidius* Hubenthal and *Protopheropsophus* Hubenthal.

Subgenus *Pheropsophidius* Hubenthal

(Figs. 4, 12, 35, 59, 423, 440, 441, 442, 445)

Diagnostic combination. — As in subgenus *Pheropsophus*, except costae of elytra not carinate, lower, rounded, and evenly confluent with depressions; propleural sutures absent; female styli short and broad.

Description. — Medium to large-sized beetles, about 12.0 to 20.0 mm.

Color. Yellow or ferruginous with black markings.

Microsculpture. As in subgenus *Pheropsophus*.

Macrosculpture. As in subgenus *Pheropsophus*, except discal depressions with fewer micro-

rugosities.

Head. As in subgenus *Pheropsophus*.

Prothorax. As in subgenus *Pheropsophus*, except propleural sutures absent.

Pterothorax. As in subgenus *Pheropsophus*, except elytral costae as described above.

Abdomen. As in subgenus *Pheropsophus*.

Genitalia. Male (figs. 440, 441, 442) as in subgenus *Pheropsophus*. Female (fig. 59) styli short and broad, otherwise as in subgenus *Pheropsophus*.

Etymology. — Greek, *phero* = bearer; *psophos* = sound; *idion* = little; referring to the smaller, but *Pheropsophus*-like members of this genus.

Distribution. — The range of this subgenus extends from southern Mexico to South America, as far south as 40° S in Argentina.

Subgenus *Protopheropsophus* Hubenthal

(Figs. 427, 437, 438, 439, 444, 446)

Diagnostic combination. — As in subgenus *Pheropsophidius*, except elytra scarcely costate on disc; anterior coxal cavities open behind; wings absent; humeri absent; apex of elytra obliquely truncate; microrugosities of elytral depressions absent from disc.

Description. — Small to large-sized beetles, 11.0 to 14.0 mm.

Color. Head, prothorax, venter around coxae, and legs ferruginous. Elytra and epipleura dull black, each with a large orange spot.

Microsculpture. As in subgenus *Pheropsophus*.

Macrosculpture. As in subgenus *Pheropsophus*, except microrugosities absent from disc.

Head. As in subgenus *Pheropsophus*.

Prothorax. As in subgenus *Pheropsophidius*, except anterior coxal cavities open behind.

Pterothorax. As in subgenus *Stenaptinus*, except elytra as described above.

Abdomen. As in subgenus *Pheropsophus*.

Genitalia. Male (figs. 437, 438, 439) as in subgenus *Pheropsophus*. Female styli (fig. 444) short and broad, otherwise as in subgenus *Pheropsophus*.

Etymology. — Greek, *proto* = first; *Pheropsophus*, another genus of brachinines; referring to Hubenthal's idea that this is the most primitive group of Pheropsophina.

Distribution. — (Fig. 446). The members of this monotypic subgenus are known only from the southern slopes of the Sierra Madre del Sur in Oaxaca, Mexico.

Subtribe Aptinina new subtribe

Type genus. — *Aptinus* Bonelli, here designated.

The following combination of characteristics is diagnostic of this subtribe: mandibular scrobe unisetose; mentum with tooth on anterior edge; anterior coxal cavities uniperforate; propleural suture absent; antennal comb spur internal; male anterior tarsi with articles 1-3 asymmetrical (figs. 43, 47); vestiture of male anterior tarsal articles diagonally arranged; middle coxal cavities confluent; apical elytral membrane absent; metacoxal cavities confluent; coxites of female ovipositor setiferous apically.

This subtribe includes the genera *Aptinus* Bonelli, *Styphlomerus* Chaudoir, *Styphlomerinus* Jeannel, and *Styphlodromus* Basilewsky.

Key to the genera of the subtribe Aptinina

- | | | |
|-------|---|------------------------|
| 1 | Integument black; dorsal pubescence sparse; wingless; humeri absent | |
| | | <i>Aptinus</i> Bonelli |
| 1' | Integument ferruginous or yellow, elytra with black areas; dorsal pubescence dense; winged; humeri square and prominent | 2 |
| 2(1') | Mentum with large tooth on anterior edge | 3 |

- 2' Mentum without large tooth on anterior edge *Styphlodromus* Basilewsky
 3(2) Dorsal surface with large punctures forming a very rugose surface; elytra concolorous *Styphlomerinus* Jeannel
 3' Dorsal surface finely and densely punctate; elytra bicolored *Styphlomerus* Chaudoir

Genus *Aptinus* Bonelli

(Figs. 3, 17, 36, 43, 55, 56, 57, 58)

Aptinus Bonelli, 1810: tab. syn. Type species. — *Brachinus bombarda* Illiger, 1800: 112 (subsequent designation by Jeannel, 1942: 1116).

Aptinidius Jeannel, 1942: 1116. Type species. — *Aptinus displosor* Dufour, 1811: 70 (original designation). NEW SYNONYMY. I do not believe this species is sufficiently different to warrant its placement in a separate monotypic subgenus.

Diagnostic combination. — Integument black (red prothorax in members of *Aptinus displosor* Dufour); dorsal pubescence sparse; humeri absent; wings absent; male genitalia variously contorted, endophallus with sclerite "complex"; female coxites plurisetose, setae unmodified, bursa with sclerite "complex".

Description. — Medium-sized beetles, 8.0 to 14.0 mm.

Color. Generally black, some species with rufous appendages and prothorax.

Microsculpture. Isodiametric on head, pronotum, and elytra, slightly transversely stretched on pronotum.

Macrosculpture. Pronotum usually with deep setiferous punctures.

Head. Labrum entire to slightly lobate, with six or eight evenly spaced setae transversely arranged near anterior margin. Clypeus rectangular, with numerous setiferous punctures scattered on disc. Front smooth, but with numerous setae; furrows very shallow, with deep groove separating them from antennal base cover and eye; one supraorbital seta over each eye; bead over eye ending at hind margin of eye. Eyes prominent. Antennae long, narrow, pubescent throughout. Mandibles (fig. 3) each broad, triangular, curved at tip; cutting edge with one small terebral tooth and three retinacular teeth; ventral groove with short golden setae; scrobe unisetose. Labial palpi (fig. 17) each with last article narrowly wedge-shaped; terminal and penultimate article bearing numerous stiff setae. Maxillary palpi more or less filiform; last three articles with numerous stiff setae. Ligula (fig. 17) membranous with anterior angles produced, and center ventrally produced into a plurisetose sclerotized convexity. Mentum (fig. 17) well developed with a single entire or emarginate tooth at anterior edge. Gula (fig. 17) widened behind.

Prothorax. As described under subtribe Aptinina, except that numerous, large, deep, setiferous, punctures occur on disc. Anterior tibiae (fig. 36) each with subterminal spur internal, at middle of comb emargination. Male anterior tarsal articles (fig. 43) 1-3 asymmetrical, with ventral vestiture consisting of two parallel rows of spatulate setae, diagonally arranged beneath each article. Female anterior tarsal articles symmetrical, vestiture absent.

Pterothorax. Anterior metathoracic process acute, mesocoxae contiguous-confluent. Hind coxae contiguous. Metepimeron lobe very large, rounded apically. Elytral humeri strongly sloping, lateral bead entire to base of humerus. Depression setae present between well developed costae. Epipleura wide medially and anteriorly, but narrowing toward apex; entirely pubescent. Wings absent.

Abdomen. As described under division Brachinida, except one pair of ambulatory setae at apices of sternites 2-5.

Genitalia. Male (figs. 56, 57) with small balteate, asymmetrical parameres; median lobe variable, but highly asymmetrical and contorted; ligule single, large, and spatulate; endophallus short, with two ventral microtuberculate plates and an apical sclerite. Female (fig.

58) with very short, broad, arcuate, and unarmed styli; valvifers robust and plurisetose; bursa with complicated arrangement of sclerites (fig. 55).

Etymology. — Greek, *apten* = unable to fly; referring to the winglessness of all known species of this genus.

Distribution. — The species of *Aptinus* occur in the southern parts of Europe from Spain to the Black Sea, mostly in the mountainous regions of the Alps and Pyrenees.

Genus *Styphlomerus* Chaudoir

(Figs. 2, 16, 27, 39, 47, 48, 67, 68)

Styphlomerus Chaudoir, 1875: in Rapport sur un memoire de M. le Baron de Chaudoir, by M. Putzeys. Type species. — *Brachinus quadrimaculatus* Dejean (subsequent designation by Andrewes, 1939: 138)

Styphromerus Chaudoir, 1876: 88. *Lapsus calami*.

Diagnostic combination. — Mandibular scrobe unisetose; labial palpus with terminal article cylindrical; mentum with a large median tooth; mandibles simple, each with one terebral tooth and one terebral ridge; propleural suture absent; anterior tibiae each with subterminal spur internal at middle of comb emargination; male anterior tarsal articles asymmetrical; middle coxae contiguous-confluent; elytra not costate; elytral epipleura wide or narrow; apical membrane of elytra absent; hind coxae confluent; metasternal process (between middle coxae) acute; wings present; parameres of male genitalia small, balteate; ligule double; valvifers of female genitalia plurisetose; styli short, narrow, and arcuate.

Description. — Medium-sized beetles, 4.5 to 12.0 mm.

Color. Generally testaceous to yellow, many species with blackish elytra with testaceous or yellow spots.

Microsculpture. Isodiametric on head, pronotum, and elytra.

Macrosculpture. Dorsal surface of head, pronotum, and elytra densely microrugose and punctate.

Head. Labrum entire, with six evenly spaced setae transversely arranged on disc. Clypeus rectangular with a single seta at each anterior corner and several small setae scattered over disc. Front microrugose, with numerous setiferous punctures; furrows very shallow; one supraorbital seta over each eye; bead over eye incomplete. Eyes prominent. Antennae long, robust, pubescent throughout. Mandible (fig. 2) broad, triangular, curved at tip; terebral margin with an elongate terebral ridge, and two retinacular teeth; ventral groove with short golden setae; scrobe unisetiferous. Labial palpi (fig. 16) each with terminal article slightly wedge-shaped; terminal and penultimate articles plurisetose, penultimate also bearing two large setae. Maxillary palpi each more or less filiform; last three articles plurisetose. Ligula (fig. 16) membranous and square with anterior angles produced, center ventrally produced into plurisetose sclerotized convexity. Mentum (fig. 16) well developed, with a single tooth at anterior edge. Gula (fig. 16) widened behind.

Prothorax. As described under subtribe Aptinina, except disc with microrugosities and scattered punctures. Anterior tibiae (fig. 39) with subapical spur internal at middle of comb emargination. Male anterior tarsal articles (fig. 47) 1-3 asymmetrical, vestiture beneath consisting of two parallel rows of spatulate setae. Female anterior tarsal articles symmetrical, vestiture absent.

Pterothorax. Anterior metathoracic process (between middle coxae) acute, prolonged, middle coxae contiguous-confluent. Hind coxae confluent. Metepimeron lobe small, parallel sided. Elytral humeri square, lateral bead entire to base of humerus. Depression setae present, erect. Epipleura pubescent; wide medially and anteriorly, but either narrowing toward apex or wide throughout. Wings present (fig. 27).

Abdomen. As described under division Brachinida, except one or more pairs of ambul-

atory setae at apices of sterna 2-5.

Genitalia. Male (figs. 67, 68) with small, balteate, asymmetrical parameres; median lobe various, but usually elongate, narrow, curved; apical sclerotization poorly defined, but present; ligule double; endophallus short with numerous microtrichia scattered over surface. Females with short, narrow, and arcuate, unarmed styli; coxites trapezoidal, thin; valvifers plurisetose; bursa without sclerites.

Etymology. — Greek. *stymphlos* = rough; *meros* = thigh; referring to the punctate femora of these beetles.

Distribution. — The range of this genus extends on both sides of the equator in southern and middle Africa.

Genus *Styphlomerinus* Jeannel

Styphlomerinus Jeannel, 1949: 1118. Type species. — *Styphlomerus fuscifrons* Fairmaire 1897: 367 (original designation).

Diagnostic combination. — As in *Styphlomerus*, except dorsum more strongly macropunctate; elytra without spots (in known species); ligule single.

Description. — Small to medium-sized beetles, about 5.0 to 8.5 mm (Jeannel, 1949).

Color. Head, prothorax, venter, and legs ferruginous; sometimes head and various sclerites infuscated. Elytra and epipleura dark grey or black.

Microsculpture. As in genus *Styphlomerus*.

Macrosculpture. Dorsal surface coarsely punctate and rugose.

Head. As in genus *Styphlomerus*.

Prothorax. As in genus *Styphlomerus*.

Pterothorax. As in genus *Styphlomerus*, except epipleura not wide throughout their length.

Abdomen. As in genus *Styphlomerus*.

Genitalia. Male as in genus *Styphlomerus*, except ligule single. Female as in genus *Styphlomerus*.

Etymology. — Greek, *stymphlos* = rough, *meros* = thigh, *inus* = having the nature of; referring to the similarity between members of this genus and *Styphlomerus*.

Distribution. — The range of this genus extends from India to Japan, and south in the Malayan Archipelago to Java, and on the islands of Madagascar, Hainan, and Taiwan. According to Jeannel (1949), no species inhabit continental Africa.

Genus *Styphlodromus* Basilewsky

Styphlodromus Basilewsky, 1959a: 240. Type species. — *Styphlodromus bicolor* Basilewsky, 1959a: 241 (original designation).

Diagnostic combination. — As in *Styphlomerus*, except mentum without tooth; dorsal surface macropunctate; ligule doubled or not (nature of doubling different than in *Styphlomerus*); elytra with stripes or spots.

Description. — Small to medium-sized beetles, 4.5 to 7.0 mm.

Color. Head, prothorax, venter, and legs ferruginous. Elytra and epipleura dark gray to black, variously spotted or striped.

Microsculpture. As in genus *Styphlomerus*.

Macrosculpture. As in genus *Styphlomerinus*.

Head. As in genus *Styphlomerus*.

Prothorax. As in genus *Styphlomerus*.

Pterothorax. As in genus *Styphlomerus*, except epipleuron not wide throughout its length.

Abdomen. As in genus *Styphlomerus*.

Genitalia. Male as in genus *Styphlomerus*, except ligule single or double, and endophallus

folding pattern more complex. Female as in genus *Styphlomerus*.

Etymology. — Greek, *styplos* = rough; *dromeus* = runner; referring to the rapidity with which these *Styphlomerus*-like beetles run.

Distribution. — The range of this genus extends from middle to southern Africa.

Remarks. — Although this genus is presently monotypic in the literature, I have seen specimens representing four more species. I have not described and named these, because it is possible they already have names and have been placed wrongly in the genus *Styphlomerus* or even *Brachinus*.

Subtribe Brachinina Bonelli

Type genus. — *Brachinus* Weber.

The following combination of characteristics is diagnostic of this subtribe: mandibular scrobes plurisetose; mentum without a tooth on anterior edge; anterior coxal cavities uniperforate, closed behind; propleural suture absent; anterior tibiae each with subterminal spur external or only slightly internal at top of comb emargination; male anterior tarsal articles either symmetrical or asymmetrical; vestiture beneath articles 1-3 longitudinally or diagonally arranged; middle coxal cavities confluent; apical elytral membrane present; hind coxal cavities confluent; coxites of female ovipositor glabrous apically.

This subtribe includes the genera *Brachinus* Weber, *Aptinoderus* Hubenthal, and *Brachinulus* Basilewsky.

Key to the genera of the subtribe Brachinina

- | | | |
|-------|--|-------------------------------|
| 1 | Apical membrane of elytron fully developed, wider than sutural flange near apex
..... | <i>Brachinus</i> Weber |
| 1' | Apical membrane of elytron narrow, narrower than sutural flange near apex . . . | 2 |
| 2(1') | Integument black, apical articles of labial and maxillary palpi cylindrical. | <i>Aptinoderus</i> Hubenthal |
| 2' | Integument brown to ferruginous, apical articles of labial and maxillary palpi
swollen proximally, acuminate and fusiform toward apex | <i>Brachinulus</i> Basilewsky |

Genus *Aptinoderus* Hubenthal

Aptinoderus Hubenthal, 1919: 332. Type species. — *Brachynus funebris* Péringuey, 1898: 320 (here designated).

Brachynomorphus Hubenthal, 1919: 335. Type species. — *Brachynus tibialis* Péringuey, 1898: 321 (here designated). NEW SYNONYMY. I do not believe this species is sufficiently different to warrant its placement in a separate genus.

Diagnostic combination. — Integument black; dorsum of head and pronotum with large, deeply impressed setiferous punctures; antennal article 3 subequal to articles 1 and 2 combined; anterior coxal cavities closed behind, proepimeron inserted into notch on prosternal process; male anterior tarsal articles asymmetrical, vestiture beneath diagonally arranged; subterminal spur of anterior tibia external on top of comb emargination; apterous; humeri strongly sloped; apical membrane of elytra narrower than sutural flange; endophallus without virga or sclerites.

Description. — Medium-sized beetles, about 10.0 to 11.0 mm (Hubenthal, 1919).

Color. Black, with legs and outer antennal articles ferruginous. Elytra black (except in *cyanipennis*, according to Hubenthal, 1919).

Microsculpture. Isodiametric, mostly effaced on head and pronotum, slightly beaded on elytra.

Macrosculpture. Dorsum of head and pronotum coarsely and densely punctate, each

puncture setiferous.

Head. As in subgenus *Brachinus*, except center of mentum convex.

Prothorax. As in subgenus *Brachinus*, except anterior coxal cavities closed behind, proepimeron inserted into notch of prosternal process.

Pterothorax. As in subgenus *Brachinus*, except metasternum short, shorter than longitudinal diameter of middle coxae; metepisternum short; apterous; humeri strongly sloped; apical fringe of elytra consisting of short, closely spaced setae.

Abdomen. As in subgenus *Brachinus*.

Genitalia. As in subgenus *Brachinus*, except both parameres small, more balteate. Female as in subgenus *Brachinus*.

Etymology. — *Aptinus* = another genus of bombardier beetles; Greek, *deros* = skin; referring to the black, *Aptinus*-like integument of these beetles.

Distribution. — The range of this genus is restricted to extreme southern Africa.

Genus *Brachinulus* Basilewsky

Brachinulus Basilewsky, 1958: 96. Type species. — *Brachinulus viettei* Basilewsky, 1958: 97 (original designation and by monotypy). For details see above and Basilewsky 1962a: 126.

Diagnostic combination. — Terminal palpal article swollen proximally, acuminate and fusiform toward apex; apical elytral membrane narrower than sutural flange, and with numerous small, and closely spaced apical setae.

Description. — Small-sized beetles, 5.0 mm. I have not seen specimens of this group, nor does Basilewsky provide information on the characteristics which I have utilized for other species.

Etymology. — *Brachinus* = another genus of bombardier beetles; Latin, *ulus* = small; referring to the small, but *Brachinus*-like form of these beetles.

Distribution. — These beetles are found only on Isla Principe, off the west coast of Africa.

Genus *Brachinus* Weber

Brachinus Weber, 1801: 22. Type species. — *Carabus crepitans* Linné, 1758: 414 (subsequent designation by Latreille, 1810: 426).

Brachynus (of authors). (Unjustified emendation by Ahrens, 1812: t. 9)

Aploa Hope, 1833: 91. Type species. — *Aploa pictus* Hope, 1833: 91 (by monotypy).

Pseudaptinus Porta, 1909: 90 (nec Castelnau). Type species. — *Brachinus italicus* Dejean, 1831: 409 (subsequent designation by Jeannel, 1942: 1105).

Cnecostolus Reitter, 1919: 133. Type species. — *Carabus exhalans* Rossi, 1792: 84 (subsequent designation by Jeannel, 1942: 1105).

Brachynolomus Reitter, 1919: 133. Type species. — *Brachinus immaculicornis* Dejean, 1826: 466 (subsequent designation by Jeannel, 1942: 1105).

Brachynidius Reitter, 1919: 133. Type species. — *Carabus scolopeta* Fabricius, 1792: 136 (subsequent designation by Jeannel, 1942: 1105).

Brachinoaptinus Lutshnik, 1926: 43. New name for *Pseudaptinus* Porta (nec Castelnau).

Aptinomimus Alluaud, 1935: 25. Type species. — *Pheropsophus microrrhodus* Alluaud, 1899: 381 (original designation).

Brachynaptinus Csiki, 1933: 1628 (unjustified emendation).

Metabrachin ♂ Jeannel, 1949: 1100. Type species. — *Brachinus connectus* Dejean, 1831: 417 (original designation).

Platybrachinus Jeannel, 1949: 1100. Type species. — *Pheropsophus fasciatocollis* Fairmaire, 1901: 129 (original designation and by monotypy).

Note. — Much confusion has resulted from the two different ways in which *Brachinus*

(= *Brachynus*) is spelled. The name is derived from the Greek *brachyus*, meaning short, and refers to the truncate elytra. A correct transliteration of the word results in the name *Brachynus*, however, Weber used *Brachinus* when he erected the genus (1801: 22). According to the International Rules of Zoological Nomenclature (Articles 31a, 32c, and 33a), the Law of Priority dictates that the name used must be as Weber first used it, that is *Brachinus*.

Diagnostic combination. — As given in the key.

This genus includes the subgenera *Brachinus* Weber, *Aploa* Hope, *Cnecostolus* Reitter, *Brachynolomus* Reitter, *Brachinoaptinus* Lutshnik, *Aptinomimus* Alluaud, *Metabrachinus* Jeannel, and *Neobrachinus* new subgenus.

Key to the subgenera of the genus *Brachinus*

Note. — At least four unnamed lineages are not included in this key, see Zoogeography for details.

- | | | |
|-------|---|----------------------------------|
| 1 | Apical edge of apical membrane of elytron with long widely spaced setae, the latter longer than width of membrane, and membrane with closely spaced fringe of shorter setae | <i>Brachinus (sensu stricto)</i> |
| 1' | Apical membrane without long, widely spaced setae; fringe of shorter setae present or not | 2 |
| 2(1') | Elytra with spotted or variegated color pattern | 3 |
| 2' | Elytra concolorous or with sutural stripe contrasting in color with disc | 5 |
| 3(2) | Antennal article 3 longer than articles 1 and 2 combined; anterior coxal cavities closed behind with prosternal process overlapped by proepimera | <i>Metabrachinus</i> Jeannel |
| 3' | Antennal article 3 subequal to articles 1 and 2 combined; anterior coxal cavities closed behind with proepimeron inserted into notch or socket of prosternal process | 4 |
| 4(3') | Upper spur of anterior tibia external | <i>Cnecostolus</i> Reitter |
| 4' | Upper spur slightly internal or in intermediate position | <i>Aploa</i> Hope |
| 5(2') | Antennal article 3 longer than articles 1 and 2 combined | 6 |
| 5' | Antennal article 3 subequal to articles 1 and 2 combined | 7 |
| 6(5) | Range limited to New World and Sikkim | <i>Neobrachinus</i> new subgenus |
| 6' | Range limited to Madagascar | <i>Aptinomimus</i> Alluaud |
| 7(5') | Upper spur of anterior tibia slightly internal; apical membrane of elytron without setae; humeri sloped; wingless | <i>Brachinoaptinus</i> Lutshnik |
| 7' | Upper spur of anterior tibia external; apical membrane of elytron with fringe of setae; humeri square, prominent; winged | <i>Brachynolomus</i> Reitter |

Subgenus *Brachinus* Weber (Fig. 23)

Diagnostic combination. — Antennal article 3 subequal to articles 1 and 2 combined; anterior coxal cavities closed behind, proepimeron overlapping prosternal process; male anterior tarsal articles 1-3 with vestiture beneath diagonally arranged; apical membranes of elytra with several widely spaced setae, each longer than the apical membrane; left paramere large and triangulate; internal sac without virga or other sclerites.

Description. — Small to medium-sized beetles, 4.6 to 9.0 mm.

Color. Ferruginous, with metallic blue elytra and epipleura. Various sclerites infuscated or not.

Microsculpture. Isodiametric on head, pronotum, and elytra.

Macrosculpture. Head at vertex, pronotum, and elytral depressions usually rugose and punctate.

Head. Labrum entire, with six setae transversely arranged on disc. Clypeus rectangular, with two setae, one each side near middle, and numerous smaller setae scattered over disc.

Front smooth, with a few scattered setae; furrows shallow; bead over eye continuous to behind eye; one supraorbital seta over each eye; eyes usually prominent. Antennae long, filiform, pubescent throughout, pubescence denser on articles 3-11 than on 1 and 2. Article 3 subequal to articles 1 and 2 combined. Mandibles (as in fig. 8) each broad, triangular, curved at tip, cutting edge with one terebral tooth, and four retinacular teeth; ventral groove with short golden setae; scrobes plurisetose. Labial palpi (as in fig. 13) each filiform; terminal article slightly swollen, with scattered pubescence; penultimate article plurisetose. Maxillary palpi (as in fig. 9) each filiform, all articles pubescent. Ligula (as in fig. 13) membranous and square, center ventrally produced into a setose sclerotized convexity. Mentum (as in fig. 13) well developed, without tooth; center slightly concave or convex. Gula (as in fig. 13) widened behind.

Prothorax. As described under subtribe Brachinina. Anterior tibia (as in fig. 33) with subterminal spur slightly internal. Male anterior tarsal articles (as in fig. 41) 1-3 asymmetrical, vestiture beneath consisting of two diagonal, but parallel rows of setae. Setae of vestiture spatulate, truncate, and rolled at apex. Female anterior tarsal articles symmetrical, vestiture absent.

Pterothorax. As described under subtribe Brachinina.

Abdomen. As described under division Brachinida.

Genitalia. Male with asymmetrical balteate parameres, the left large and triangulate, the right minute; median lobe various, but nearly symmetrical; ligule single, usually well defined; endophallus moderately long, without sclerites or virga. Female as in subgenus *Neobrachinus*.

Etymology. — Greek, *brachyus* = short; referring to the short truncate elytra of these beetles.

Distribution. — The range of this subgenus extends throughout Europe and North Africa.

Subgenus *Brachynolomus* Reitter

(Fig. 41)

Brachynidius Reitter, 1919: 133. NEW SYNONYMY. I do not consider the species placed in this subgenus by various workers sufficiently different to warrant a separate subgeneric taxon.

Diagnostic combination. — Antennal article 3 subequal to articles 1 and 2 combined; anterior coxal cavities closed behind, proepimeron overlapping prosternal process; apical membrane of elytra with numerous closely spaced setae, shorter than apical membrane; both parameres small, balteate; male anterior tarsal articles asymmetrical; vestiture beneath diagonally arranged; internal sac of median lobe with virga surrounding the gonopore.

Description. — Small to medium-sized beetles, about 4.5 to 10.0 mm (Jeannel, 1942).

Color. As in subgenus *Brachinus*, except some species with a ferruginous sutural stripe on elytra, and elytra usually vividly metallic.

Microsculpture. As in subgenus *Brachinus*.

Macrosculpture. As in subgenus *Brachinus*.

Head. As in subgenus *Brachinus*.

Prothorax. As in subgenus *Brachinus*.

Pterothorax. As in subgenus *Brachinus*.

Abdomen. As in subgenus *Brachinus*.

Genitalia. Male as in subgenus *Brachinus*, except both parameres small, more balteate; endophallus with an apical virga. Female as in subgenus *Neobrachinus*.

Etymology. — Greek, *brachyus* = short; *lomo* = fringe; referring to the fringe of setae on the apical membrane of the short elytra.

Distribution. — The range of this subgenus extends from northwestern Africa into south-

ern Europe, and east to Japan.

Subgenus *Metabrachinus* Jeannel

Platybrachinus Jeannel, 1949: 1100. NEW SYNONYMY. I do not believe the small forms placed in this subgenus are sufficiently different to warrant their separation from the larger *Metabrachinus*.

Diagnostic combination. — Antennal article 3 longer than 1 and 2 combined; anterior coxal cavities closed behind, proepimeron overlapping prosternal process; male anterior tarsal articles asymmetrical, but less so than in subgenus *Brachinus*; elytra spotted; apical membrane of elytron without setae; apical elytral membrane wide, wider than sutural flange; internal sac without virga or sclerites.

Description. — Medium to large-sized beetles, 7.0 to 20.0 mm (Jeannel, 1949).

Color. As in subgenus *Brachinus*, except elytra with spotted color pattern, epipleura usually yellow.

Microsculpture. As in subgenus *Brachinus*.

Macrosculpture. As in subgenus *Brachinus*.

Head. As in subgenus *Brachinus*, except mentum always convex at middle, and antennal article 3 as described above.

Prothorax. As in subgenus *Brachinus*.

Pterothorax. As in subgenus *Brachinus*, except costae of elytra sharper, more elevated.

Abdomen. As in subgenus *Brachinus*.

Genitalia. Male as in subgenus *Brachinus*, except left paramere small and more balteate. Female as in subgenus *Neobrachinus*.

Etymology. — Greek, *meta*, implying change; *Brachinus*, the common European genus; referring to Jeannel's idea that these beetles had diverged from the main *Brachinus* line of evolution.

Distribution. — The range of this subgenus extends throughout southern Africa and Madagascar.

Subgenus *Aploa* Hope

(Figs. 1, 9, 15, 31, 37, 46, 60, 65, 66)

Diagnostic combination. — Antennal article 3 subequal to articles 1 and 2 combined; anterior coxal cavities closed behind, proepimeron inserted into notch of prosternal process; subterminal spur of anterior tibia intermediately positioned on top of comb emargination; male anterior tarsal articles symmetrical; apical membrane of elytra without setae; parameres of male genitalia small, balteate; ligule single, small; endophallus with heavily sclerotized and pigmented subapical knife-shaped sclerite; valvifer of female genitalia glabrous; styli short, spatulate.

Description. — Medium-sized beetles, 12.0 to 14.0 mm.

Color. Generally yellow to testaceous, with black elytral markings.

Microsculpture. Isodiametric on head, pronotum, and elytra, almost effaced on head.

Macrosculpture. None.

Prothorax. As in subgenus *Brachinus*, except anterior tibiae (fig. 37) each with subterminal spur in intermediate position at top of comb emargination. Male anterior tarsal articles (fig. 46) 1-3 symmetrical, vestiture beneath consisting of two parallel rows of spatulate setae. Female anterior tarsal articles symmetrical, vestiture absent.

Pterothorax. As in subgenus *Brachinus*.

Abdomen. As described for division Brachinida.

Genitalia. Male (fig. 65, 66) with small balteate, asymmetrical, parameres; median lobe variable, but nearly symmetrical; ligule single, small, and narrow; endophallus short, with

one large sclerite near apex; virga absent. Female with short, narrow, spatulate, slightly curved, unarmed styli; coxites small, robust; valvifers glabrous; bursa unarmed.

Etymology. — Greek, *haploos* = single or simple; probably in reference to Hope's knowledge of only one species of this genus.

Distribution. — The range of this subgenus extends on both sides of the equator in the Old World. South of the equator the species are confined to southern Africa. In the north they occur around the periphery of the Sahara Desert, and in (parts of) the Middle East, southern Europe, India, and Ceylon.

Subgenus *Brachinoaptinus* Lutshnik

Pseudaptinus Porta, 1909: 90 (nec Castelnau). Primary homonym of *Pseudaptinus* Castelnau, 1834: 36, another genus of Carabidae.

Diagnostic combination. — Antennal article 3 subequal to articles 1 and 2 combined; anterior coxal cavities closed behind, proepimeron inserted into socket of prosternal process; subterminal spur of anterior tibia slightly internal on top of comb emargination; male anterior tarsal articles symmetrical; apical membrane of elytra without setae; apterous, humeri strongly sloping; both parameres of male genitalia small, balteate; endophallus without virga or sclerites.

Description. — Small to medium-sized beetles 4.5 to 11.0 mm.

Color. As in subgenus *Brachinus*. At least one species (*Brachinus pygmaeus* Dejean) has members which are partially depigmented, pale brown throughout.

Microsculpture. As in subgenus *Brachinus*.

Macrosculpture. As in subgenus *Brachinus*.

Head. As in subgenus *Brachinus*, except eyes smaller, not so convex; extremely reduced in *Brachinus pygmaeus* Dejean.

Prothorax. As in subgenus *Brachinus*, except as noted in diagnosis.

Pterothorax. As in subgenus *Brachinus*, except metasternum short, subequal to or shorter than longitudinal diameter of middle coxa; humeri sloping, wings absent or greatly reduced.

Abdomen. As in subgenus *Brachinus*.

Genitalia. Male as in subgenus *Brachinus*, except both parameres small, strongly balteate; endophallus without virga or sclerites. Female as in subgenus *Brachinus*.

Etymology. — Greek, *brachyus* = short; *apten*, unable to fly; referring to the *Brachinus* species that cannot fly.

Distribution. — The range of this subgenus extends around the Mediterranean Sea.

Subgenus *Aptinomimus* Alluaud

Diagnostic combination. — Antennal article 3 elongate, longer than 1 and 2 combined; anterior coxal cavities closed behind, proepimeron inserted into notch in prosternal process; subterminal spur of anterior tibia external on top of comb emargination; male anterior tarsal articles with ventral vestiture longitudinally arranged (according to Jeannel, 1949); endophallus not seen.

Description. — Medium to large-sized beetles, 9.5 to 22.0 mm (Jeannel, 1949).

Color. Brown, sometimes head and pronotum more ferruginous; legs ferruginous; elytra and epipleura brown.

Microsculpture. As in subgenus *Brachinus*.

Macrosculpture. As in subgenus *Brachinus*.

Head. As in *Brachinus* (*sensu stricto*), except terminal palpal article widened toward apex; antennal article 3 longer than articles 1 and 2 combined.

Prothorax. As in subgenus *Brachinus*, except anterior coxal cavities closed behind, proepimeron inserted into "notch" in prosternal process.

Pterothorax. As in *Brachinus* (*sensu stricto*), except metasternum short, subequal or shorter than longitudinal diameter of middle coxa; metepisternum short; humeri strongly sloping; wings absent; apical membrane with very short closely spaced setae.

Abdomen. As in subgenus *Brachinus*.

Genitalia. Male (see Jeannel, 1949: 1112, fig. 544 a-f) as in subgenus *Brachinus* except both parameres small. Female as in subgenus *Brachinus*.

Etymology. — Greek, *apten*, unable to fly; *mimos* = imitator, mimic; referring to the superficially similar appearance of these beetles to members of the genus *Aptinus*.

Distribution. — This subgenus is restricted to Madagascar.

Subgenus *Cnecostolus* Reitter

Diagnostic combination. — Antennal article 3 subequal to articles 1 and 2 combined; anterior coxal cavities closed behind; proepimeron inserted into notch of prosternal process; subterminal spur of anterior tibia external on top of comb emargination; male anterior tarsal articles with ventral vestiture longitudinally arranged; apical membrane of elytron without setae; both parameres of male genitalia small, balteate; internal sac with virga around gonopore.

Description. — Small to medium-sized beetles, about 4.0 to 12.0 mm (Jeannel, 1942; Reitter, 1919).

Color. As in subgenus *Brachinus*, except elytra with spotted color pattern, at least one species (*Brachinus cruciatus* Quensel) with brown head and pronotum.

Microsculpture. As in subgenus *Brachinus*.

Macrosculpture. As in subgenus *Brachinus*.

Head. As in subgenus *Brachinus*.

Prothorax. As in subgenus *Brachinus*, except anterior coxal cavities closed by notch insertion of proepimeron into prosternal process; male anterior tarsal articles with longitudinally arranged vestiture beneath.

Pterothorax. As in subgenus *Brachinus*, except apical membrane of elytra without fringe of setae.

Abdomen. As in subgenus *Brachinus*.

Genitalia. Male as in subgenus *Brachinus*, except both parameres small, more balteate; endophallus with apical virga around gonopore. Female as in subgenus *Brachinus*.

Etymology. — Greek, *knekos*, yellow; *stola*, folds; referring to the yellow spots of the costate elytra of these beetles.

Distribution. — The range of this subgenus extends from southern Europe (France), east to at least Mongolia, mostly in more northerly latitudes.

Subgenus *Neobrachinus* new subgenus

Type species. — *Carabus fumans* Fabricius, 1781: 307, here designated.

Diagnostic combination. — Antennal article 3 longer than articles 1 and 2 combined; anterior coxal cavities closed behind; proepimeron inserted into socket of prosternal process; male anterior tarsal articles with ventral vestiture longitudinally arranged; apical membrane of elytra with numerous, closely spaced, short setae; both parameres small, balteate, the left larger than the right; endophallus with a virga surrounding the gonopore.

Description. — Small to large-sized beetles, 4.8 to 18.5 mm.

Color. Variable, but usually head and prothorax ferruginous and elytra blue or brown.

Microsculpture. As in subgenus *Brachinus*.

Macrosculpture. As in subgenus *Brachinus*.

Head. As in subgenus *Brachinus*, except mentum of some species with one or two pits surrounded by setae; antennal article 3 longer than articles 1 and 2 combined.

Prothorax. As in subgenus *Brachinus*, except anterior coxal cavities closed behind, propimeron inserted into socket in prosternal process.

Pterothorax. As in subgenus *Brachinus*, except some species apterous as in members of subgenus *Brachinoaptinus*.

Abdomen. As in subgenus *Brachinus*.

Genitalia. As in subgenus *Brachinus*, except both parameres small, more balteate, and left larger than right; virga present at tip of endophallus. Female as in subgenus *Brachinus*.

Etymology. — Greek, *neo*, new or most recent; *brachyus*, short; referring to the probability that these beetles are the most recently derived of an Old World stock that invaded the New World.

Distribution. — The range of this subgenus extends throughout the New World from about 52°N to 40° S latitude. One relict species occurs in Sikkim, in the Himalaya Mountains.

Key to bombardier beetles of North and Middle America

Characteristics used in the keys

The more difficult to use characteristics in the key are further discussed here (see also comparative morphology).

Color differences are very useful in the identification of bombardier beetles, especially those of North and Middle America. For the most part, I have used the presence or absence of a color on various sclerites, rather than comparing shades of colors. Shades of color are used only for the elytra. In a very few species elytral color is so variable as to be useless for identification. Color combinations are usually constant. Very teneral adults do not have pigments deposited, but these are rarely collected.

In North and Middle America the head of *Brachinus* beetles is usually ferrugineous, but four Neotropical species have brown heads, and one eastern United States species has a black head. The mouth parts generally match the color of the head, but in four species with ferrugineous head color, the palpi are infuscated or black. The antennal articles 2 to 4 are quite variable, ranging from ferrugineous to black, with intermediate stages of infuscated apically and totally infuscated. The scape matches the head color. Antennal articles 5-11 are usually dusky in ferrugineous colored species, but specimens of some species have infuscated lateral stripes on each article, or each article is entirely infuscated.

The prothorax always matches the color of the head. The elytra are either blue, brown, black, green, or slate-colored. In some species the epipleura of some specimens are testaceous, but usually the epipleura match the elytral color. The sutural costa varies from ferrugineous to black. In two species in the study area, the ferrugineous color includes two costae and their adjacent depressions.

The venter is usually ferrugineous at the middle of the mesosterna and metasterna. The sides of the metasterna, mesepisterna, mesepimera, metepisterna, and the abdominal sterna and terga may be ferrugineous, infuscated, black, or (in two species) black with metallic blue luster. In species without the ferrugineous ground color, the various ventral sclerites are either infuscated or not. In species with black abdomens, the paramedial "dimples" are usually ferrugineous. The legs may be either ferrugineous, testaceous, brown, or black. Usually, testaceous colored legs have infuscated femoral apices ("knees"). This knee color also occurs in some ferrugineous-legged species. In some ferrugineous species, the tibiae and tarsi may be infuscated or black, and occasionally the femora also may be black.

Characteristics of pubescence and density of setae are very useful in species identification. The number of setae on the mentum and submentum of North and Middle American bombardier beetles is variable. Usually, the mentum has two long setae (fig. 19), and the submentum has about 8 to 12 setae transversely arranged (fig. 19). A second type of setal arrangement exists with the center of the mentum having a small patch of setae (fig. 21). One

3(1')	Elytron with ferrugineous sutural stripe, contrasting strongly with the otherwise darkly colored disc; elytral epipleura pale.	4
3'	Elytra concolorous, epipleura pale or dark	5
4(3)	Legs (at least tibiae) pale, with dark knees; palpi pale; elytra usually greenish	97
 <i>B. cinctipennis</i> Chevrolat, p.	
4'	Legs totally black; palpi infuscated to black; elytra usually bright blue	98
 <i>B. cibolensis</i> new species, p.	
5(3')	Head, prothorax, and elytra concolorous, either black or brown	6
5'	Head and prothorax testaceous or ferrugineous, strongly contrasting with darkly colored elytra	9
6(5)	Body completely black; elytra black with blue luster; wingless.	60
 <i>B. capnicus</i> new species, p.	
6'	Body brownish with testaceous legs and infuscated knees; winged.	7
7(6')	Mentum with two pits surrounded by numerous long setae (fig. 20)	69
 <i>B. sallei</i> Chaudoir, p.	
7'	Mentum flat to shallowly biconcave, with only two setae.	8
8(7')	Elytral pubescence confined to depression 8 (Mexico)	72
 <i>B. melanarthrus</i> Chaudoir, p.	
8'	Elytral pubescence not confined to depression 8 (Greater Antilles)	71
 <i>B. brunneus</i> Castelnau, p.	
9(5')	Mentum with a large deep median sulcus surrounded by a ring of setae (fig. 18)	10
9'	Mentum flat to shallowly biconcave OR with two shallow lateral pits (fig. 19)	11
10(9)	Elytra glabrous; venter ferrugineous.	85
 <i>B. costipennis</i> Motschulsky, p.	
10'	Elytra pubescent; venter mostly infuscated	159
 <i>B. mobilis</i> new species, p.	
11(9')	Wings rudimentary, each a narrow elongate pad; metasternum short between middle and hind coxae, no longer than diameter of middle coxa (fig. 26); humeri strongly sloped (fig. 72)	12
11'	Wing with at least reflexed apex; metasternum longer than diameter of middle coxa; humeri sloped, square (fig. 98) or protruding	14
12(11)	Abdomen, metepisterna, and sides of metasternum infuscated to black; abdominal sterna with ferrugineous paramedian dimples; mentum without central setal patch (fig. 19)	13
12'	Abdomen infuscated only at sides, rest of venter ferrugineous; paramedian dimples not of a contrasting color; mentum with central setal patch (fig. 21)	21
 <i>B. microamericanus</i> Erwin	
13(12)	Submentum densely setiferous (16 or more setae, fig. 21); larger, more robust beetles; antennae ferrugineous.	55
 <i>B. americanus</i> (LeConte), p.	
13'	Submentum sparsely setiferous (10 or less, fig. 19); smaller beetles; antennal articles 3 and 4 infuscated	57
 <i>B. alexiguus</i> new species, p.	
14(11')	Elytra brown; legs pale testaceous with dark knees	15
14'	Elytra blue, blue-black, greenish-blue, or slate colored; legs concolorous without darkly colored knees, or ferrugineous with darkly colored knees.	22
15(14)	Proepipleura and proepisterna pubescent throughout; venter pale; elytra not true brown	163
	(in part) <i>B. sonorus</i> new species, p.	
15'	Proepipleura glabrous; proepisterna with only a few scattered setae anteriorly and/or posteriorly, or glabrous.	16
16(15')	Elytral epipleuron at least at humerus pale testaceous, strongly contrasting with elytral color	17
16'	Elytral epipleura and disc of elytra concolorous	19

- 17(16) Metasternum at sides usually infuscated; elytral disc glabrous; median lobe as in figs. 156, 157, 158; stylus as in fig. 145; in United States, west of Rocky Mountains only *B. lateralis* Dejean, p. 73
- 17' Metasternum not infuscated at sides; elytral disc usually sparsely pubescent; in United States, east of Rocky Mountains only 18
- 18(17') Anterior third of proepisternum with a few setae; median lobe as in figs. 153, 154, 155; stylus as in fig. 142; range — United States, Mexico, Central America, and Cuba *B. adustipennis* Erwin, p. 81
- 18' Anterior third of proepisternum glabrous; median lobe as in figs. 147, 148, 149; stylus as in fig. 144; range — Mexico, South America . . . *B. aeger* Chaudoir, p. 77
- 19(16') Larger beetles, greater than 15.0 mm in length. *B. grandis* Brullé, p. 73
- 19' Smaller beetles, less than 12.0 mm in length. 20
- 20(19') Elytra prominently costate; median lobe as in figs. 159, 160, 161; stylus as in fig. 143 *B. chalchihuitlicue* new species, p. 79
- 20' Elytra almost smooth, costae barely elevated 21
- 21(20') Median lobe as in figs. 150, 151, 152; stylus as in fig. 146; elytral pubescence usually extensive, covering apical third of elytra . . . *B. arboreus* Chevrolat, p. 79
- 21' Median lobe as in figs. 162, 163, 164; stylus as in fig. 141; elytral pubescence usually discontinuous near middle of apical third of elytra *B. chirriador* new species, p. 80
- 22(14') Elytral pubescence in outer depressions 6, 7, 8, or just in 8; less dense pubescence usually across apical third of elytra and sometimes in vicinity of scutellum . . . 23
- 22' Elytral pubescence all along depressions between costae, usually costae pubescent. 28
- 23(22) Elytral pubescence confined to depression 8, behind humerus and at middle, although some setae scattered across apical sixth of elytron. 24
- 23' Elytral pubescence in depressions 6, 7, and 8, and across apical sixth of elytron 25
- 24(23) Venter mostly ferrugineous, except for infuscated metepisterna and (in some specimens) sides of abdomen; elytral costae prominent; microsculpture of pronotum isodiametric, surface rugose and shining *B. gebhardis* Erwin, p. 131
- 24' Venter infuscated; elytral costae barely elevated; microsculpture of pronotum granulate, surface rugose and dull, color milky ferrugineous *B. galactoderus* new species, p. 132
- 25(23') Tarsi, tibiae, and apices of femora infuscated to black (in part) *B. rhytiderus* Chaudoir, p. 63
- 25' Tarsi, tibiae, and femora ferrugineous 26
- 26(25') Venter and antennae ferrugineous *B. pallidus* Erwin, p. 95
- 26' Venter and usually antennal articles 3 and 4 infuscated to piceous 27
- 27(26') Elytra shiny black, very convex *B. explosus* new species, p. 161
- 27' Elytra blue, microsculpture coarse, surface dull *B. mexicanus* Dejean, p. 104
- 28(22') Median elevated portion of mentum with a dense patch of setae (fig. 21); submentum densely setiferous (more than 20 setae). 29
- 28' Median raised portion of mentum either glabrous or with one or two small setae (fig. 19); submentum various 33
- 29(28) Metasternum anterior to antecoxal piece, subequal in length to longitudinal diameter of middle coxa (fig. 26); antennal articles 3 and 4 infuscated at least apically; elytra usually greenish. *B. viridipennis* Dejean, p. 90
- 29' Metasternum longer than middle coxa; antennal articles 3 and 4 usually ferrugineous (except some populations of *B. alternans*); elytra bluish 30

30(29')	Proepipleura pubescent throughout their length; proepisterna completely pubescent	31
30'	Proepipleura and proepisterna pubescent only anteriorly and posteriorly, glabrous at middle	<i>B. perplexus</i> Dejean, p. 141
31(30)	Anterior tibia with anterior surface coarsely strigose; elytral costae barely elevated	32
31'	Anterior tibia with anterior surface punctate, rarely with punctures coalescing; elytral costae very pronounced, easily visible with unaided eye	<i>B. alternans</i> Dejean, p. 88
32(31)	Humeral angles square (fig. 98) prominent; elytra broad and quadrate with lateral margins behind humeri straight to at least middle.	<i>B. imperialensis</i> Erwin, p. 143
32'	Humeri rounded, not at all prominent; elytra narrow, with lateral margins behind humeri evenly arcuate entirely to apex.	<i>B. velutinus</i> Erwin, p. 142
33(28')	Abdominal sterna entirely ferruginous OR infuscated only marginally, with a pale center extending to apex OR mostly ferruginous except for infuscated lateral margins and sternum 6	32
33'	Abdominal sterna infuscated to piceous, rarely center of sterna 2 and 3 paler, but usually not equal in color to the hind coxae.	46
34(33)	Erect depression setae at least twice as long as elytral pubescence	<i>B. cyanipennis</i> Say, p. 127
34'	Erect setae subequal to or shorter than elytral pubescence	35
35(34')	Abdominal sterna completely ferruginous	36
35'	Abdominal sterna with infuscated margins	37
36(35)	Proepipleura glabrous; proepisterna with a few scattered setae; antennae ferruginous	<i>B. janthinipennis</i> (Dejean), p. 156
36'	Proepipleura pubescent; proepisterna pubescent; antennal articles 3 and 4 infuscated	(in part) <i>B. sonorous</i> new species, p. 163
37(35')	Pronotum without lateral setae at middle	38
37'	Pronotum with lateral setae present	40
38(37)	Proepipleura densely pubescent throughout their length	39
38'	Proepipleura with at most a few setae anteriorly	<i>B. kansanus</i> LeConte, p. 83
39(38)	Elytral depression 1 with erect depression setae at least twice as long as elytral pubescence; pronotum not densely pubescent.	<i>B. oaxacensis</i> new species, p. 117
39'	Elytral depression 1 with short depression setae; pronotum densely pubescent	<i>B. hirsutus</i> Bates, p. 93
40(37')	Elytra moderately to strongly costate	41
40'	Elytra barely costate, almost smooth	<i>B. ovipennis</i> LeConte, p. 121
41(40)	Pronotum completely pubescent	42
41'	Pronotum mostly glabrous, at most with a few scattered setae	(in part) <i>B. rhytiderus</i> Chaudoir, p. 63
42(41)	Proepipleura glabrous; proepisterna with scattered setae both anteriorly and posteriorly, glabrous medially	43
42'	Proepipleura with at least some setae posteriorly, proepisterna (except <i>fumans</i>) pubescent throughout	44
43(42)	Elytra bright blue, usually metallic	(in part) <i>B. elongatulus</i> Chaudoir, p. 65
43'	Elytra slate-grey with greenish luster.	(in part) <i>B. texanus</i> Chaudoir, p. 60
44(42')	Pronotum (fig. 336) densely covered with large pits, surface very rugose; mentum with numerous accessory setae scattered over surface	<i>B. favicollis</i> Erwin, p. 140

- 44' Pronotum (figs. 334-337) at most with fine punctures, not at all rugose; mentum without accessory setae (occasionally one or two small setae at middle) 45
- 45(44') Anterior tibia with anterior surface strigose; elytra with costae moderately elevated. *B. puberulus* Chaudoir, p. 140
- 45' Anterior tibia with anterior surface punctate, the punctulae sometimes coalescent, but not forming strigae; elytra with highly elevated costae
. *B. fumans* Fabricius, p. 134
- 46(33') Venter with metallic blue luster, tibiae and tarsi black; antennal articles 2-11 piceous to black; palpi black; elytra brilliant metallic blue
. *B. azureipennis* Chaudoir, p. 115
- 46' Venter without metallic blue luster, infuscated to blackish or not, otherwise combination of characteristics not as above 47
- 47(46') Proepipleura glabrous 48
- 47' Proepipleura with at least a few setae, either throughout their length or at both ends (observe both sides of beetle) 66
- 48(47) Metasternum infuscated at sides 49
- 48' Metasternum not infuscated at sides 61
- 49(48) Tibiae and tarsi infuscated, at least darker than femora 50
- 49' Tibiae and tarsi concolorous with femora. 51
- 50(49) Metasternal process (between middle coxae) usually infuscated; antennal article 3 shorter than diameter of eye; median lobe not ridged ventrally (fig. 257); stylus narrow (fig. 275) *B. phaocerus* Chaudoir, p. 111
- 50' Metasternal process ferrugineous; antennal article 3 longer than diameter of eye; median lobe ridged ventrally (fig. 240); stylus broad, spatulate (fig. 247)
. (in part) *B. quadripennis* Dejean, p. 99
- 51(49') Mesepisterna infuscated to black; elytra strongly costate
. *B. tenuicollis* LeConte, p. 123
- 51' Mesepisterna not darkly infuscated (if at all); elytra not or only moderately costate 52
- 52(51') Elytra with costae easily visible; elytral pubescence not dense 53
- 52' Elytra without costae; elytral pubescence very dense; elytral color dull slate-blue
. *B. sublaevis* Chaudoir, p. 149
- 53(52) Metasternum subequal in length to diameter of middle coxa; humeri sloped; lateral margin of elytron behind humerus arcuate to apex
. *B. patruelis* LeConte, p. 117
- 53' Metasternum longer than diameter of middle coxa; humeri square or prominent, margin behind humerus straight at least to middle of elytra 54
- 54(53') Anterior tibia with anterior surface punctate, punctulae small, rarely coalescing 55
- 54' Anterior tibia with anterior surface strigose 56
- 55(54) Median lobe with ventral ridge (fig. 237); stylus acute (fig. 250)
. *B. neglectus* LeConte, p. 110
- 55' Median lobe without ventral ridge (fig. 404); stylus rounded apically (fig. 410)
. *B. vulcanoides* Erwin, p. 155
- 56(54') Proepipleura and proepisterna glabrous (proepisterna rarely with one to three setae along anterior edge) (in part) *B. medius* Harris, p. 129
- 56' Proepipleura and proepisterna with pubescence both anteriorly and posteriorly, glabrous medially 57
- 57(56') Antennal article 3 infuscated throughout. 58
- 57' Antennal article 3 infuscated apically *B. cyanochroaticus* Erwin, p. 147
- 58(57) Median lobe with ventral depression (fig. 383) OR ridged ventrally (fig. 240);

- stylus very broad, spatulate (figs. 247, 386) 59
- 58' Median lobe without depression or ridge; stylus acute apically. 60
- 59(58) Median lobe with ventral depression (fig. 383); very long, narrow beetles with long legs and antennae; elytra elongate; pronotum (fig. 370)
. *B. ichabodopsis* new species, p. 150
- 59' Median lobe with ventral ridge (fig. 240); short broad beetles; elytra quadrate; pronotum (fig. 230) *B. quadripennis* Dejean, p. 99
- 60(58') Range — north of latitude 35° N from New England to Indiana; median lobe (figs. 407, 408, 409); stylus (fig. 411) *B. fulminatus* Erwin, p. 153
- 60' Range — south of latitude 35° N from Florida to Missouri; median lobe (figs. 398, 399, 400); stylus (fig. 412) *B. oxygenus* Chaudoir, p. 151
- 61(48') Elytra with major part of pubescence in rows between costae 62
- 61' Elytra with pubescence evenly scattered over surface, costae also pubescent . . 63
- 62(61) Elytra bright blue, usually metallic (in part) *B. elongatulus* Chaudoir, p. 65
- 62' Elytra slate-grey with greenish luster (in part) *B. texanus* Chaudoir, p. 60
- 63(61') Proepisterna glabrous, at most with 1-3 setae near anterior edge
. (in part) *B. medius* Harris, p. 129
- 63' Proepisterna pubescent, at least anteriorly and posteriorly 64
- 64(63') Antennal article 3 extensively infuscated (sometimes also article 2). 65
- 64' Antennal article 3 ferruginous (apex of 4 sometimes lightly infuscated).
. (in part) *B. cordicollis* Dejean, p. 144
- 65(64) Humeral angle square, elytral margin behind humerus straight, at least to middle; range — Florida. *B. conformis* Dejean, p. 119
- 65' Humeri sloped, margin behind humerus arcuate to apex; range — Arizona
. *B. inporcitis* new species, p. 114
- 66(47') Metasternum infuscated at sides 67
- 66' Metasternum not infuscated at sides. 69
- 67(66) Submentum densely setiferous (more than 20 setae); larger beetles, longer than 12.0 mm and wider than 5.0 mm across elytra at widest part
. *B. javalinopsis* new species, p. 109
- 67' Submentum sparsely setiferous (10 or less); smaller beetles, less than 11.5 mm in length and 4.9 mm in width 68
- 68(67') Knees infuscated; elytral pubescence evenly distributed over surface; pronotum narrow (fig. 421) *B. aabaaba* new species, p. 161
- 68' Knees not infuscated; elytral pubescence in rows between barely elevated costae; pronotum cordiform (fig. 226) *B. kavanaughi* Erwin, p. 108
- 69(66') Outer antennal articles and sutural costae of elytra black, strongly contrasting with color of elytra *B. consanguineus* Chaudoir, p. 116
- 69' Outer antennal articles ferruginous and sutural costae of elytra bluish, not contrasting with color of elytra 70
- 70(69') Proepisterna pubescent anteriorly and posteriorly, glabrous medially; ligule of median lobe broad, spatulate (fig. 182); stylus very narrow, elongate (fig. 192)
. *B. rugipennis* Chaudoir, p. 91
- 70' Proepisterna pubescent throughout; ligule of median lobe paralleliform (fig. 378); stylus wider, shorter (fig. 386) *B. cordicollis* Dejean, p. 144

The subgenus *Neobrachinus* new subgenus
in North and Middle America

The *americanus* group

The members of this group are characterized by the following: pouch-shaped virga, enlarged prothorax, and reduced wings together with the modifications of the metathorax.

Four species are included, in two subgroups.

The *americanus* subgroup

The three species included here, *B. americanus* (LeConte), *B. microamericanus* Erwin, and *B. alexiguus* new species differ from the species included in the following subgroup only in overall color, but this color difference is of major importance. The species included here are similar in color to the majority of North American brachinines, that is, head and pronotum ferrugineous, elytra blue, with various sclerites infuscated, depending upon the species.

Brachinus americanus (LeConte)

(Figs. 71, 79, 80, 81, 87, 88)

Aptinus americanus LeConte, 1844: 48. Lectotype, here selected a female, MCZ red type label number 5839, further labelled with a yellow disc and "72". *Type locality*. — Georgia, as originally given by LeConte.

Aptinus americanus Dejean, 1836: 13. NOMEN NUDUM.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Medium-sized beetles, 8.0 to 13.0 mm.

Color. Metepisterna, sometimes metasternum at sides, and abdominal sterna and terga infuscated, otherwise ferrugineous. Dorsal surface and epipleura of elytra blue.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows rugose and punctate. Surface of pronotum with numerous setiferous punctures, punctures moderately impressed.

Head. Frontal furrows moderately impressed. Antennal scape nearly cylindrical, widened a little apically. Ligula with sclerotized center area ellipsoid-convex with numerous setae scattered over its surface. Mentum and submentum without accessory setae.

Prothorax. Pronotum (fig. 71) slightly convex, flattened along center line, sides slightly reflexed. Proepipleura glabrous. Proepisterna with a few setae anteriorly and posteriorly, glabrous medially. Anterior tibia with anterior surface punctate.

Pterothorax. Elytra elongate, narrow, moderately costate. Humeri narrow, strongly sloped. Costae smooth, depressions pubescent. Hind wings reduced, elongate pads. Metasternum short, subequal to or shorter than diameter of middle coxa (fig. 26).

Abdomen. As described for genus.

Genitalia. Male (figs. 79, 80, 81). Median lobe with plane of shaft barely rotated from plane of basal bend. Basal bend moderately long. Shaft slightly swollen medially. Apex of shaft narrowed, rounded apically. Ligule short, narrow, rounded apically. Virga (figs. 79, 80). Female (fig. 87). Stylus short, narrow, narrowly rounded at apex.

Variation. — Besides the intrapopulational variation in the shape of the pronotum and total size, these beetles vary in the amount of reduction of the elytral humeri and in the amount of infuscation of the metasterna at the sides.

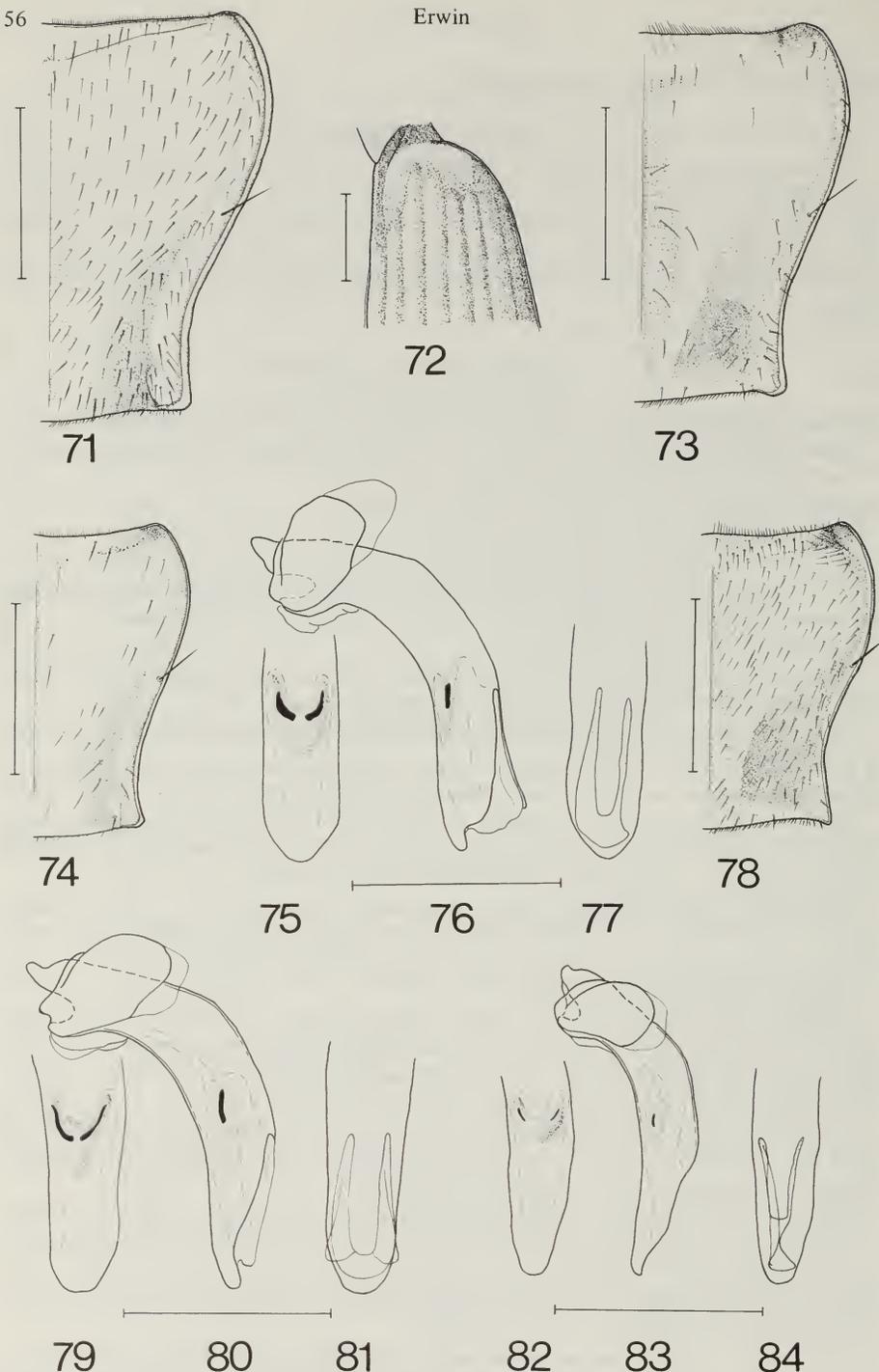
Flight. — The reduction of wing membrane makes these beetles incapable of flight.

Etymology. — The latinized form of America, the place where the types were collected.

Collecting notes. — W. Whitcomb (per. comm.) collected these beetles in Arkansas corn fields. There is no reason to believe that these beetles are restricted to areas near water (as are other species of *Brachinus* in North America).

Life history. — Members of this species have been collected from February to October. I have seen one teneral specimen collected in September from Hot Springs, Arkansas. Overwintering is probably as an adult as in *B. pallidus* Erwin (Erwin, 1967).

Distribution. — (Fig. 88). The range of this species extends from Texas north to Minnesota, east to New York, and south to Florida. I have seen 440 specimens from the follow-



Figs. 71, 73, 74, 78. Pronotum, right half, dorsal aspect. 71. *Brachinus americanus* (LeConte), Ludlow, Mississippi. 73. *Brachinus capnicus* new species, Smokemont, North Carolina. 74. *Brachinus alexigius* new species, College Station, Texas. 78. *Brachinus microamericanus* Erwin, Dundee, Mississippi. Fig. 72. Right elytron, dorsal aspect of humeral angle, *Brachinus capnicus* new species, Smokemont, North Carolina. Figs. 75-77, 79-84. Male genitalia. 75. *Brachinus alexigius* new species, College Station Texas, ventral aspect. 76. Lateral aspect of same. 77. Dorsal aspect of same. 79. *Brachinus americanus* (LeConte), Washington County, Arkansas, ventral aspect. 80. Lateral aspect of same. 81. Dorsal aspect of same. 82. *Brachinus microamericanus* Erwin, Dundee, Mississippi, ventral aspect. 83. Lateral aspect of same. 84. Dorsal aspect of same. Accompanying scale lines equal 1.0 mm.

ing localities:

UNITED STATES

ALABAMA: Blount County (Blount Springs) CMPP; Fayette County (Berry) UASM; Lee County (5.0 miles north of Auburn) AUA; Tuscaloosa County (Peterson) UASM. ARKANSAS: Benton County (Rogers) KSU; Garland County (Hot Springs) CAS, SJSC; (Hot Springs-Lake Hamilton) SJSC; Hempstead County (Hope) UMAH; Izard County UAFA; Lawrence County (Imboden) LACM, MCZ; Logan County (Mount Magazine) CNHM; Phillips County (West Helena) UMAH; Polas County (Ouachita Mountains) UASM; Sebastian County (Fort Chaffee) RCGr; Scott County UAFA; Washington County ISNH, UAFA; (Cove Creek Valley) RFre, UAFA; (Goshen) DRWh; (Mount Sequoyah) ISNH; County unknown (Knob Hill Ranch, Ozark Mountains) CAS. FLORIDA: (No locality given) WSUP. GEORGIA: (No locality given) MCZ. ILLINOIS: Alexander County (Olive Branch) CNHM; Champaign County (Urbana) ISNH; Cook County (Chicago area) CNHM, (La Grange) CAS, UMAH, USNM, (Palos Park) CAS, CNHM, UMAH, (Riverside) UMAH, (Summit) CNHM, ISNH, (Willow Springs) CAS, CNHM, UASM, UMAH, ZMLS; Hardin County (Junction Highway 34-146) RTBe; La Salle County RTBe; Putnam County ISNH; Richland County (Olney) ISNH; Will County (Beecher) CNHM; Counties unknown (Bowmanville) CAS, (Falling Spring) LACM. INDIANA: Crawford County CAS; Franklin County (Metamora) UMAH; Harrison County PUM; Jefferson County (Clifty Falls State Park) UASM; Knox County PUM; Lake County (Pine) USNM; Lawrence County (Bedford) PUM; Monroe County ISUA, (Bloomington) UMAH; Morgan County (Morgan-Monroe county line) CEWh; Posey County (Hovey Lake) PUM; Ripley County (Versailles) CEWh; Vigo County PUM. IOWA: Boone County (Ledges State Park) ISUA; Dickinson County (Lake Okoboji) ISUA; Johnson County (Iowa City) MCZ; Linn County (Palsades) USNM; County unknown (Foster) USNM. KANSAS: Douglas County (Lawrence) UMAH; Franklin County UMAH. KENTUCKY: Cumberland County (Franklin Branch) TCBA; Edmonson County (2.0 miles from Mammoth Cave) MCZ; Jessamine County UASM; Meade County (Fort Knox) UASM; Oldham County (Sleepy Hollow) ULLK; Wayne County (Wolf Creek Lake) ULLK; County unknown (Sanborn) MCZ. MICHIGAN: Monroe County (Monroe) PUM. MINNESOTA: Winona County UMSP. MISSISSIPPI: Leake County (near Ludlow) RCGr; Perry County (Richton) CUNY. MISSOURI: Boone County (Columbia) UNLN; Camden County (Camdenton) UMAH; (Ozark Lake) CAS; Jefferson County (Kimmswick) UMAH; Polk County (Aldrich) CUNY; Saint Charles County (Weldon Springs) UASM; Saint Francis County (Flat River) USNM; Saint Louis County JShu, UASM; (Rockwoods Reservoir) UASM; Teney County (Branson) CAS; Counties unknown (Mincy) ISUA, (Willard) UASM. NORTH CAROLINA: Orange County (Chapel Hill) CUNY; Wake County (Raleigh) UNCR. OHIO: Franklin County (Columbus) PUM; Mercer County (Mendon) UMAH; Ottawa County (near Marblehead) UMAH; Washington County (New Matamoras) OUCO; County unknown (Georgeville) OUCO. OKLAHOMA: Latimer County CAS, OSUS; Mayes County (Grand) OSUS; Payne County (Stillwater) OSUS; Pontotoc County OSUS; Tulsa County (Catoosa) CAS. PENNSYLVANIA: Allegheny County CUNY, (Pittsburgh) CMPP; Fayette County (Ohioyle) CMPP. TENNESSEE: Davidson County (Nashville) OUCO, USNM. TEXAS: Brazos County (College Station) MCZ, TAMU; Colorado County (Columbus) USNM; Cooke County (Gainesville) USNM; Dallas County (Dallas) MCZ; Kendall County (Comfort) CMPP; Lee County CMPP; McLennan County (Waco) MCZ; Newton County (Call) USNM. WISCONSIN: Green County (Albany) CEWh; La Crosse County (La Crosse) REST.

Brachinus alexiguus new species

(Figs. 74, 75, 76, 77, 89)

Type locality. — College Station, Texas.

Type specimens. — The holotype male and one paratype male are in the entomological museum at MCZ and CAS, respectively. The holotype was collected at the type locality on March 22, 1927. The paratype was collected in Latimer County, Oklahoma by R. D. Bird on April 25, 1931.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Small-sized beetles, 7.0 to 8.0 mm.

Color. Antennal articles 3 and 4, mesepisterna, metepisterna, metasternum at sides, and abdominal sterna and terga infuscated, otherwise ferrugineous. Dorsal surface and epipleura sterna and terga infuscated, otherwise ferrugineous. Dorsal surface and epipleura of elytra blue.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows and surface of pronotum punctate, punctures shallowly impressed.

Head. As in *americanus*.

Prothorax. As in *americanus*. Pronotum (fig. 74).

Pterothorax. As in *americanus*.

Abdomen. As described for genus.

Genitalia. Male (figs. 75, 76, 77). As in *americanus*, except median lobe slightly wider toward apex, and ligule more elongate and narrower. Virga (figs. 75, 76). Female unknown.



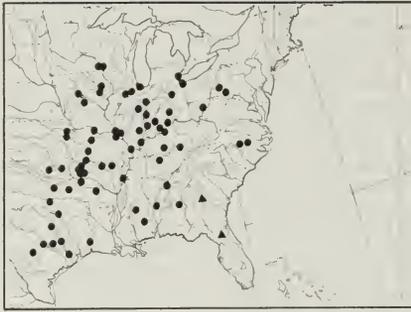
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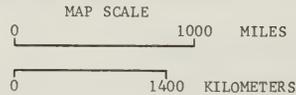
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91



LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION

Figs. 85-87. Right stylus of female ovipositor, ventral aspect. 85. *Brachinus capnicus* new species, Smokemont, North Carolina. 86. *Brachinus microamericanus* Erwin, Dundee, Mississippi. 97. *Brachinus americanus* (LeConte), Washington County, Arkansas. Accompanying scale lines equal 1.0 mm. Figs. 88-91. Geographical distribution maps. 88. *Brachinus americanus* (LeConte). 89. *Brachinus alexiguus* new species. 90. *Brachinus microamericanus* Erwin. 91. *Brachinus capnicus* new species. Map scale given here, used on all maps under Taxonomy; triangles (▲) indicate state locality only.

Variation. — Too few specimens are known to evaluate the geographic variation.

Flight. — The reduction of wing membrane makes these beetles incapable of flight.

Etymology. — Latin, *ala*, wing; *exiguus*, small, short or scanty; referring to the reduced wings of these beetles.

Life history. — The two specimens were collected in March and April, respectively, but neither were teneral.

Distribution. — (Fig. 89). I have seen two specimens from the following localities:

UNITED STATES

OKLAHOMA: Latimer County CAS. TEXAS: Brazos County (College Station) MCZ.

Brachinus microamericanus Erwin

(Figs. 78, 82, 83, 84, 86, 90)

Type locality. — Dundee, Mississippi.

Type specimens. — The holotype male and allotype female are in the entomological museum at UMAH, both were collected by T. H. Hubbell at the type locality on August 13, 1929. Two paratypes are in each of the following collections: CAS, MCZ, TLEr, UASM, UMAH.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Small-sized beetles, 6.0 to 8.7 mm.

Color. Metepisterna and sides of abdomen infuscated, otherwise ferruginous. Dorsal surface and epipleura of elytra blue.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows and surface of pronotum slightly rugose and punctate, punctures shallowly impressed.

Head. As in *americanus*, except antennal scape robust, widened apically, ligula with three setae in two rows on each side of center area, and mentum and submentum with accessory setae.

Prothorax. As in *americanus*, except proepipleura with a few setae anteriorly and posteriorly, glabrous medially. Pronotum (fig. 78). Anterior tibia with anterior edge strigose.

Pterothorax. As in *americanus*.

Abdomen. As described for genus.

Genitalia. Male (figs. 82, 83, 84). Median lobe with plane of shaft rotated about 45° from plane of basal bend. Basal bend short. Apex of shaft narrowed, narrowly rounded apically. Ligule short, narrow, truncate. Virga (figs. 82, 83). Female (fig. 86). Stylus short, angulate, widened apically.

Variation. — The series from Dundee is quite constant in all characteristics, except the accessory setae of the mentum and submentum which vary in number. However, the single specimen from Woodrow is considerably smaller and the shape of its pronotum is different. This specimen may not be conspecific with the others, but further material will have to be obtained before its relationship can be established.

Flight. — As in *americanus*.

Etymology. — Greek, *mikros*, small; *americanus*, nominate species of the group; referring to the resemblance, but smaller form of this species to the nominate species.

Life history. — The Dundee specimens were collected in August and the Woodrow specimen in May, and none were teneral.

Distribution. — (Fig. 90). I have seen 17 specimens from the following localities:

UNITED STATES

MICHIGAN: Huron County (Charity Island) UMAH. MISSISSIPPI: Tunica County (Dundee) UMAH. MISSOURI: County unknown (Woodrow) USNM.

The *capnicus* subgroup

The single species included here differs from the previous subgroup in its overall black color. This is the only known black *Neobrachinus*, although some species have black parts, and others are very dark brown.

Brachinus capnicus new species

(Figs. 72, 73, 85, 91)

Type locality. — Smokemont, Great Smoky Mountains National Park, North Carolina.

Type specimen. — The holotype female is in the entomological museum at CUNY. The single known specimen was collected by W. B. Jones *et al.* in 1938.

Diagnostic combination. — This is the only known species with all black members.

Description. — Medium-sized beetle, 10.0 mm.

Color. Black. Elytra black with metallic blue luster.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows rugose and punctate, disc of pronotum punctate, punctures moderately impressed.

Head. As in *americanus*, except submentum with accessory setae.

Prothorax. As in *americanus*, except center of pronotum concave along midline. Pronotum (fig. 73).

Pterothorax. As in *americanus*.

Abdomen. As described for genus.

Genitalia. Male unknown. Female (fig. 85). Stylus short, narrow, acute at apex.

Flight. — As in *americanus*.

Etymology. — Greek, *kapnikos*, smoky; referring to the darkly colored integument of these beetles, the place where the type was collected, and the ability of these beetles to crepitate, producing a cloud of "smoke".

Distribution. — (Fig. 91).

UNITED STATES

NORTH CAROLINA: Swain County (Smokemont) CUNY.

The *texanus* group

The members of this group are characterized as follows: virga of endophallus extensively pigmented and oriented horizontally on the internal sac; antennal articles robust; stylus of the female ovipositor very narrow and acute; elytral pubescence occurring in rows between costae. Three species, *B. texanus* Chaudoir, *B. rhytiderus* Chaudoir, and *B. elongatulus* Chaudoir, are included here, but certain South American species also belong to this group.

Brachinus texanus Chaudoir

(Figs. 93, 95, 96, 97, 107, 108)

Brachinus texanus Chaudoir, 1868: 299. Lectotype, here selected, a male, MHNP, labelled "Tejas" and "Ex Museo Chaudoir". *Type locality.* — Texas, as originally given by Chaudoir.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Medium-sized beetles, 7.3 to 9.9 mm.

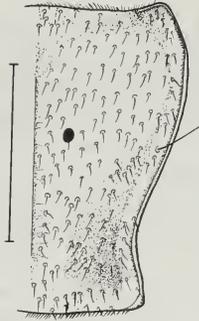
Color. Mesepisterna, metepisterna, usually metasternum at sides, sides of abdominal sternum, sternum 6, and abdominal terga infuscated, usually antennal articles 3 and 4 infuscated, otherwise ferruginous. Dorsal surface and epipleura of elytra slate-grey with greenish luster.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrow and surface of pronotum rugose and punctate, punctures moderately impressed.



92



93



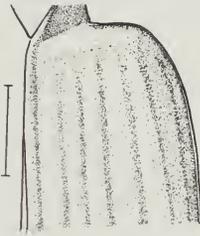
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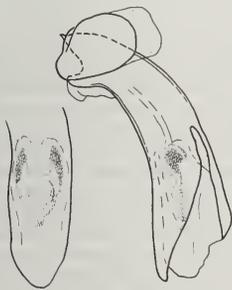


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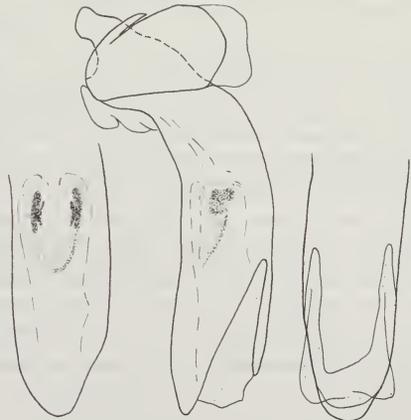
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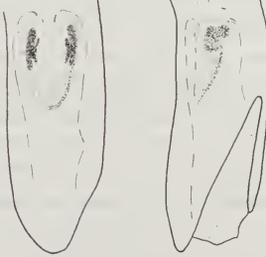
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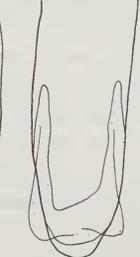
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104

Figs. 92-94. Pronotum right half, dorsal aspect. 92. *Brachinus rhytiderus* Chaudoir, Chuminopolis, Yucatan, Mexico. 93. *Brachinus texanus* Chaudoir, Mineral Wells, Texas. 94. *Brachinus elongatulus* Chaudoir, South West Research Station, Arizona. Figs. 95-97, 99-104. Male genitalia. 95. *Brachinus texanus* Chaudoir, Raymond, Mississippi, ventral aspect. 96. Lateral aspect of same. 97. Dorsal aspect of same. 99. *Brachinus rhytiderus* Chaudoir, 1.8 miles north of El Naranjo, San Luis Potosi, Mexico, ventral aspect. 100. Lateral aspect of same. 101. Dorsal aspect of same. 102. *Brachinus elongatulus* Chaudoir, Madera Canyon, Arizona, ventral aspect. 103. Lateral aspect of same. 104. Dorsal aspect of same. Fig. 98. Right elytron, dorsal aspect of humeral angle, *Brachinus elongatulus* Chaudoir, South West Research Station, Arizona. Accompanying scale lines equal 1.0 mm.

Head. Frontal furrows moderately impressed. Antennal scape robust, widest at middle. Ligula with sclerotized center area ellipsoid-convex with two paramedian setae and two apical setae. Mentum and submentum usually with accessory setae.

Prothorax. Pronotum (fig. 93), convex, flattened along center line, sides slightly reflexed. Proepipleura glabrous. Proepisterna with setae anteriorly and posteriorly, glabrous medially. Anterior tibia with anterior surface strigose.

Pterothorax. Elytra elongate, narrow, moderately costate. Humeral angles square. Costae smooth, glabrous, depressions pubescent. Hind wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 95, 96, 97). Median lobe with plane of shaft rotated slightly from plane of basal bend. Basal bend short. Shaft nearly straight, swollen slightly at middle, apex acute and narrow. Ligule broad, moderately long, truncate. Virga (figs. 95, 96). Female (fig. 107). Stylus narrow, long and acute at apex.

Variation. — Intrapopulational variation occurs in the following characteristics: shape of the pronotum; total length; extent of infuscation on the venter; and intensity of infuscation of the antennal articles 3 and 4. In all specimens the sides of the abdomen and the metepisterna are infuscated. Usually, sternum 6 is more darkly infuscated than the other abdominal sterna, but usually the latter are also quite dark, except at the very middle. In the very darkest specimens only the middle of sternum 2 between the hind coxae is ferruginous. Concordantly, the sides of the metasternum are also infuscated.

Flight. — These beetles have been repeatedly collected at lights in Texas.

Etymology. — The latinized form of Texas, the place where the types were collected.

Life history. — Members of this species have been collected from March to November. I have seen a teneral adult collected in July, at Austin, Texas. Overwintering probably takes place in the adult stage, as in *B. pallidus*.

Distribution. — (Fig. 108). The range of this species extends from New York to Alberta, Canada, south to southern Texas. The northern records from Massachusetts, Virginia, Michigan, Minnesota, and Alberta seem to be disjunctions from the main range. I have seen 1,549 specimens from the following localities:

CANADA

ALBERTA: Chin Coulee (Oldman River) UASM.

UNITED STATES

ALABAMA: Dallas County (Marion Junction) CNHM; Sumter County (Livingston) AMNH; Tuscaloosa County (Tuscaloosa) UASM; County unknown (Dilchamps) CAS. ARKANSAS: Chicot County (Lake Village) CUNY; Faulkner County (Conway) UAFA; Hempstead County UAFA, (Hope) CAS, MCZ, UMAH; Hot Springs County (Malvern) JSch; Pulaski County UAFA, (8.0 miles north of Camp Robinson) CNHM, (Little Rock) MCZ; Sebastian County (Fort Chaffee) RCGr; Washington County ISNH, (Cove Creek Valley) UAFA, (Fayetteville) UAFA. FLORIDA: Pinellas County (Dunedin) TAMU. KANSAS: Douglas County (Lawrence) PUM; Montgomery County (Independence) AUA; Rooks County KSU. LOUISIANA: Caddo-Bossier Parishes (Bossier City) CNC; De Soto Parish (Mansfield) USNM; East Baton Rouge Parish (Baton Rouge) UAFA; Franklin Parish (Chance) UAFA, (Chase) UAFA; Jefferson Davis Parish (Hathaway) UAFA; Madison Parish (Tallulah) MSUM; Natchitoches Parish (Vowells Mill) USNM; Ouachita Parish (Calhoun) UAFA; Vermilion Parish (Gueydan) USNM; Vernon Parish (Rosepine) UAFA; Parish unknown (Auston) UATA. MASSACHUSETTS: Plymouth County (Plymouth) CNHM. MICHIGAN: Allegan County (Allegan) CAS. MISSISSIPPI: Copiah County (Crystal Springs) MCZ; Hinds County (Jackson) TAMU, (Raymond) RCGr; Pike County (McComb) UWSW; County unknown (McCormick) UWSW. MISSOURI: Barry County (Monett) USNM; Pulaski County (Fort Leonard Wood) CAS; Saint Louis County (Saint Louis) CAS; Vernon County (Nevada) FDAG, UASM. NEBRASKA: Lancaster County (Lincoln) UNLN. OKLAHOMA: Canadian County (El Reno) CNHM; Choctaw County (Hugo) AMNH; Cleveland County (Norman) CAS, UONO; Custer County (Clinton) AMNH; Grandy County (Chickasha) OSUS; Grayson County (Juniper Point, Lake Texoma, 12.0 miles north of Whitesboro) RCGr; Latimer County OSUS; Lawton County (Fort Sill) ISUA; Logan County (Guthrie) CNHM; McClaine County UONO; Marshall County (Lake Texoma, Willis) RCGr, (Lake Texoma, 2.0 miles east of Willis) RCGr, UCD, (Madill) RCGr; Muskogee County (Muskogee) USUL; Nowata County (13.0 miles west of Vinita) RFr; Oklahoma County (Oklahoma City) CAS; Payne County (Stillwater) OSUS; Tulsa County (Tulsa) CAS, DHKa. TENNESSEE: Davidson County (Nashville) TCBA; Lincoln County (Fayetteville) GRNo; Madison County (Jackson) CNC; Putnam County (Cookville) TCBA. TEXAS: Baylor County (8.0 miles south Seymour) CNHM; Bell County (Temple) CNHM; Bexar County (San Antonio) CAS, CEWH, MCZ, OSUS, TAMU, TLer, UCR; Blanco County (Cypress Mill) USNM, (2.0 miles south of Round Mountain) UASM; Brazos County (College Station) CAS, TAMU, (Texas Experiment Station)

TAMU; Cameron County (Brownsville) USNM; Cass County (Linden) CNC; Cherokee County (Alto) JSch; Comal County (New Braunfels) TCBA, UASM, USNM; Cooke County (Gainesville) USNM; Dallas County (Dallas) CAS, CUNY, ISNH, MCZ, PSUU, UASM, UMAH, UMSP, USNM; Denton County CAS; Dimmit County (Texas Experiment Station) TAMU; Eastland County UMSP; El Paso County (El Paso) CMPP; Ennis County (Ennis) AMNH; Erath County (Dublin) ISUA; Grayson County (Sherman) AMNH; Hunt County (Wolfe City) CUNY; Jefferson County (Port Arthur) AMNH, (Sabine Pass) WSUP; Jones County (Stanford) AMNH; Karnes County (Gillett) CUNY; Kerr County (Kerrville) CNC; Kleberg County (Kingsville) CUNY, ISUA; Leon County CAS; Liberty County (Liberty) UWSW; McLennan County (China Spring) CNHM; Montague County (2.5 miles southwest of Forestburg) CNHM; Montgomery County (Willis) OSUC; Oldham County (Matador Ranch) UWSW; Palo Pinto County (Mineral Wells) TCBA; Panola County (Carthage) AMNH; Potter County (Amarillo) UWSW; Robertson County (Hearne) CAS; Scurry County (Snyder) TCBA; Stephens County (Breckenridge) TCBA; Tarrant County OSUS, UMAH, (Fort Worth) CUNY; Taylor County (Abilene) UATA; Travis County (Austin) CAS, FDAG, MCZ, OUCO, UASM, UWMW, WSUP, ZMLS; Val Verde County OUCO; Victoria County (Victoria) UASM, UMAH, USNM; Washington County (Brenham) USNM; Webb County (Laredo) UWSW; Williamson County (Elm Water Cave) TCBA; Zavalla County (Nueces) USNM; Counties unknown (Belgrave) MCZ, (Camp Barkely) OSUC, (Carancahua) USNM, (Fuller) USNM, (Virginia Point) USNM. VIRGINIA: (No locality given) ANSP. WISCONSIN: Iron County (Mercer) MCZ, UWMW.

Brachinus rhytiderus Chaudoir
(Figs. 92, 99, 100, 101, 105, 110)

Brachynus rhytiderus Chaudoir, 1876: 76. Lectotype, here selected, a male, MHNP, labelled "Mexique" and "Ex Museo Chaudoir", standing first in a series of seven specimens. *Type locality*. — Mexico, as originally given by Chaudoir, but herewith restricted to San Luis Potosi, Mexico.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Small to medium-sized beetles, 5.2 to 9.1 mm.

Color. Except for the constantly darkened terga, the infuscated areas of these beetles are ill-defined. Usually the antennal articles 3 and 4 darker than 1 and 2. Metepisterna and sides of abdomen usually quite dark, but center of abdominal sterna slightly infuscated, darker than color of pronotum. Tibiae infuscated, degree varied with specimens. Dorsal surface and epipleura of elytra slate-colored.

Microsculpture. As described for genus.

Macrosculpture. As in *texanus*.

Head. As in *texanus*, except mentum and submentum without accessory setae.

Prothorax. As in *texanus*. Pronotum (fig. 92).

Pterothorax. As in *texanus*, except pubescence usually very sparse in discal depressions.

Abdomen. As described for genus.

Genitalia. Male (figs. 99, 100, 101). Median lobe as in *texanus*, slightly more arcuate. Virga (figs. 99, 100). Female (fig. 105). Stylus elongate, narrow, apically acute, but not as sharp as in *texanus*.

Variation. — As in *elongatulus*. The intensity of infuscation seems to vary clinally with darker specimens on the Yucatan Peninsula, in the southern part of Mexico, and in Central America, while the paler individuals are in Texas.

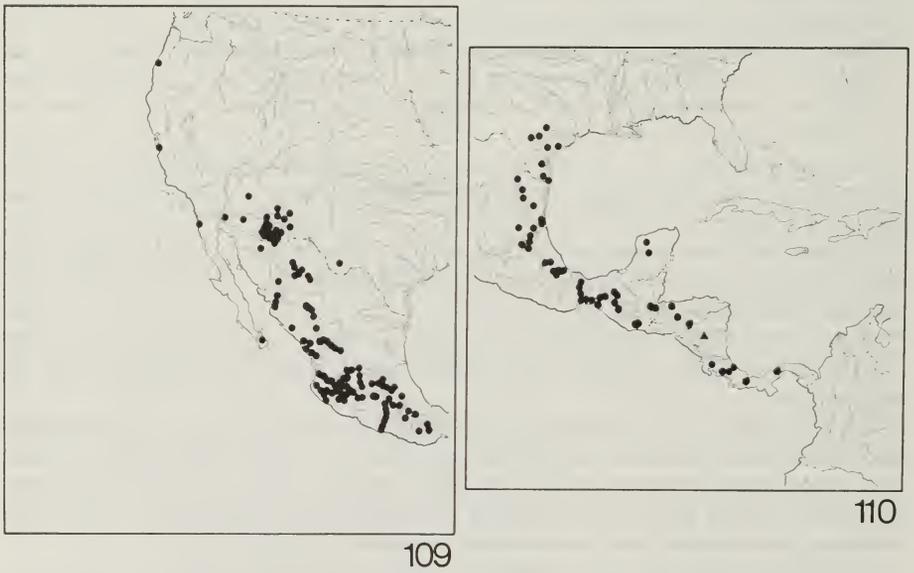
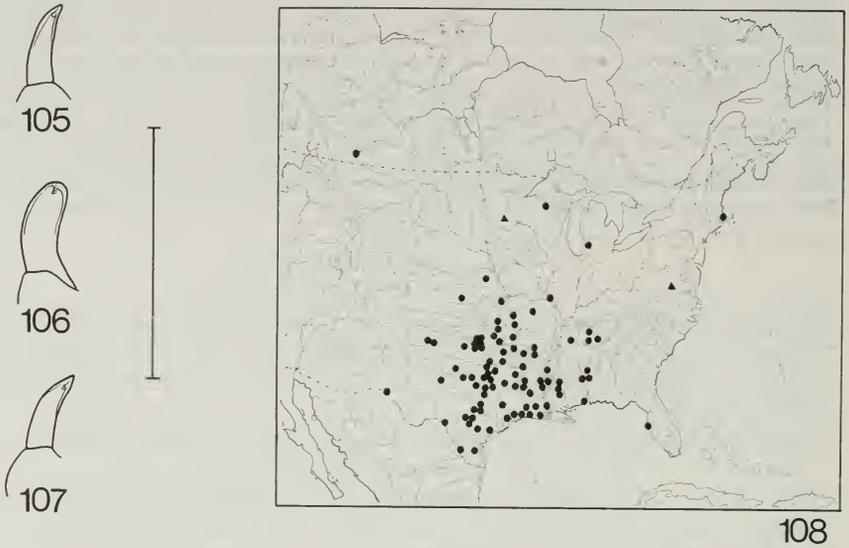
Flight. — The flight of these beetles has been recorded at lights repeatedly in Mexico.

Etymology. — Greek, *rhytido*, wrinkle, *deros*, skin; referring to the costate elytra of these beetles.

Collecting notes. — G. E. Ball and D. R. Whitehead have collected these beetles from under litter in palm forests at the edge of a large grassy swamp in San Luis Potosi; at the margin of the Rio Tula, in Hidalgo; and near the edge of a small stream (in litter) in Queretaro. They also collected specimens in roadside litter (vegetation) near Comitán, Chiapas. In Nicaragua, these beetles have been collected repeatedly in cotton fields.

Life history. — Members of this species have been collected in all months of the year, except January and February. I have seen a teneral adult collected in September in the state of Chiapas, Mexico. Overwintering or aestivation probably takes place in the adult stage.

Distribution. — (Fig. 110). The known range of this species extends from Texas south along the eastern side of Mexico to the Canal Zone, Panama. I have seen 625 specimens from



Figs. 105-107. Right stylus of female ovipositor, ventral aspect. 105. *Brachinus rhytiderus* Chaudoir, 1.8 miles north of El Naranjo, San Luis Potosi, Mexico. 106. *Brachinus elongatulus* Chaudoir, South West Research Station, Arizona. 107. *Brachinus texanus* Chaudoir, Raymond, Mississippi. Figs. 108-110. Geographical distribution maps. 108. *Brachinus texanus* Chaudoir. 109. *Brachinus elongatulus* Chaudoir. 110. *Brachinus rhytiderus* Chaudoir. Accompanying scale lines equal 1.0 mm.

the following localities:

CENTRAL AMERICA

CANAL ZONE: (Barro Colorado) MCZ. COSTA RICA: (5.0 kilometers north of Cañas) GRNo; (La Carpentera) USNM; (San Jose) MCZ, TCBA; (San Pedro) GRNo; (Tres Rios) MCZ; (Turrialba) CAS; (Zent, Limón) MCZ. GUATEMALA: (Agua Caliente) MCZ; (Antigua) AMNH, MCZ; (Los Amates) MCZ; (Palin) USNM; (Panzos) MCZ; (Tamahu) AMNH. NICARAGUA: (La Calera) USNM. HONDURAS: CUNY, (Copan) MCZ; (El Paraiso) UCD; (La Lima) DTRT; (Rancho Chiquito, Department of Comayagua) FDAG. PANAMA: (Rovira, Chiriqui) SJSC.

MEXICO

DURANGO: MCZ. CHIAPAS: (3.2 miles north of Arriaga) UASM; (15.6 miles west of Comitán) UASM; (32.5 miles east of Comitán) UASM; (El Rosario, northwest of Comitán) RTBe; (4.9 miles north of Frontera Comalapa) UASM; (7.7 miles north of Frontera Comalapa) UASM; (16.3 miles southwest of Las Cruces) UASM; (11.6 miles north of Ocozacoatlán) UASM; (Palenque ruins) UASM; (20.0 miles south of Tuxtla Gutiérrez) UCD. HIDALGO: (Jacala) CNC. MICHOACAN: (Sahuayo) WSUP. NUEVO LEON: (Huasteca Cañon, near Monterrey) CNC; (14.8 miles west of Linares) UASM; (Mesa de Chipinque, near Monterrey) AMNH; (Montemorelos) CAS; (Monterrey) CNC; (5.0 miles south of Monterrey) CNC; (6.0 miles south of Monterrey) CNC, FDAG; (Rio Elizondo, near Monterrey) MCZ; (Santa Rosa Cañon, 14.8 miles west of Linares) UASM. OAXACA: (La Ventosa) UCR; (50.0 miles north of La Ventosa) ISUA; (Oaxaca) BMNH; (Puente Zanatepec, near Zanatepec) UASM; (Rio Malatengo, 11.1 miles north of Matias Romero) UASM; (Rio Nilttepec, 18.4 miles west of Zanatepec) UASM; (Tapanatepec) UASM; (3.0 miles northwest of Tapanatepec) ISUA; (17.0 miles northwest of Zanatepec) ISUA. PUEBLA: (Villa Juarez) JHen. QUERETARO: (Landa de Matamoros) UASM. SAN LUIS POTOSI: (Ciudad de Valles) WSUP; (5.0 miles northeast of Ciudad del Maiz) CNC; (El Naranjo) OSUC; (1.8 miles north of El Naranjo) UASM; (3.6 miles west of El Naranjo) UASM; (El Salto Falls) FDAG; (2.7 miles west of Santa Catarina) UASM; (Tamazunchale) AMNH, DRWh, MCZ. TAMAULIPAS: (2.0 miles west of Antiguo Morelos) DRWh; (14.0 miles west of Antiguo Morelos) UASM; (Ciudad Mante) CNC; (47.0 kilometers south of Ciudad Victoria) MCZ; (Gomez Farias and vicinity) AMNH, CUNY; (73.1 miles north of Manuel) UASM; (101.1 miles north of Manuel) UASM; (20.0 miles south of Victoria) TCBA, UCD; (20.6 miles east of Villa de Casas) UASM; (23.1 miles east of Villa de Casas) UASM. VERACRUZ: (5.0 miles northwest of Acayucan) UCD; (30.0 miles south of Acayucan) UCD; (Cordoba) AMNH, CAS; (10.0 miles east of Cordoba) GRNo; (Cotaxtla Experiment Station) CAS; (Coyame, Lake Catemaco) DRWh; (Fortin de las Flores) CUNY, DRWh, UASM; (20.0 miles northwest of Huatusco) FDAG; (Jalapa) AMNH, ANSP, BMNH, CAS, MCZ; (3.0 miles northwest of Jalapa) GRNo; (Los Tuxtlas Range) TAMU; (Orizaba) MCZ; (2.5 miles west of Sontecomapan) UASM; (Tinajas) UCD; (Veracruz) UASM. YUCATAN: (Chuminopolis) AMNH; (Merida) AMNH; (Piste) SJSC; (Ruinas de Kabah) UASM.

UNITED STATES

TEXAS: Bee County (Beeville) USNM; Cameron County CAS, MCZ, USNM, UWMW, (Brownsville) USNM, WHTy; Comal County (New Braunfels) UASM, USNM; Kendall County (5-10.0 miles north of Boerne) UASM; Kleberg County (Kingsville) CUNY; Travis County (Austin) CAS, WSUP; Victoria County (Victoria) USNM; County unknown (Belfrage) USNM.

Brachinus elongatulus Chaudoir

(Figs. 94, 98, 102, 103, 104, 106, 109)

Brachynus elongatulus Chaudoir, 1876: 75. Lectotype, here selected, a female, MHNP, labelled "40" and "Ex Museo Chaudoir", standing first in a series of eleven specimens in front of label "B. elongatulus Chaudoir". *Type locality*. — Orizaba, Mexico, as originally given by Chaudoir.

Brachynus brevior Chaudoir, 1876: 75. Lectotype, here selected, a female, MHNP, labelled "Mexique" and "Ex Museo Chaudoir". *Type locality*. — Oaxaca, Mexico, as originally given by Chaudoir. Blackwelder, 1944: 71.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Small to medium-sized beetles, 4.8 to 10.6 mm.

Color. Antennal articles 3 and 4, metepisterna, and sides of abdominal sterna infuscated. Tibiae, and tarsi usually infuscated, otherwise beetles ferruginous. Dorsal surface and epipleura of elytra blue.

Microsculpture. As described for genus.

Macrosculpture. As in *texanus*, except punctures more deeply impressed.

Head. As in *texanus*.

Prothorax. As in *texanus*. Pronotum (fig. 94).

Pterothorax. As in *texanus*, except elytra more elongate and more strongly costate.

Abdomen. As described for genus.

Genitalia. Male (figs. 102, 103, 104). Median lobe with plane of shaft slightly rotated from plane of basal bend. Basal bend short. Shaft and apex as in *texanus*. Ligule short, broad,

truncate. Virga (figs. 102, 103). Female (fig. 106). Stylus narrow, moderately long, rounded apically.

Variation. — Intrapopulational variation occurs in the shape of the pronotum and in the total size, and the tibiae and tarsi may or may not be infuscated. Rarely the metepisterna are ferruginous.

Flight. — These beetles have been collected repeatedly at lights throughout the range of the species.

Etymology. — Latin, *elongatus*, prolonged; referring to the elongate elytra of these beetles.

Collecting notes. — My wife and I collected these beetles from beneath stones along streams in many localities. At Herb Martyr Dam near Portal, Arizona, these beetles were beneath stones piled on top of other stones which were embedded in loamy soil. The stones were covered with oak leaf litter and were next to flowing water.

Life history. — Members of this species have been collected during all months of the year. I have seen teneral adults collected in August from Arizona; in July from Michoacan; in November from Jalisco; and in October from Acapulco. Overwintering probably takes place in the adult stage.

Distribution. — (Fig. 109). The range of this species extends from Arizona south to Oaxaca and into Baja California. Two specimens have been recorded from the Pacific Coast, one from Oregon and one from California. I have seen 3,810 specimens from the following localities:

MEXICO

AGUASCALIENTES: (Aguascalientes) AMNH, JHen; (4.0 miles southwest of Aguascalientes) AMNH; (11.0 miles west of Aguascalientes) UASM; (Mal Paso, 7.0 miles east of Calvillo) AMNH; (15.0 miles west of Pabelon) UMAH. BAJA CALIFORNIA: (Big Cañon, Sierra Laguna) CAS; (La Laguna) GRNo; (Las Animas Cañon Ensenada) SDSNH; (Las Animas, Sierra Laguna) CAS; (12.0 miles northwest of San Bartolo) CAS. CHIHUAHUA: (Buena Vista) AMNH; (Carta Blanca, 16.0 miles west of Matachic) AMNH; (Catarinas) AMNH; (Chihuahua) CNC; (25.0 miles northwest of Chihuahua) CNC; (10.0 miles east of Cuaohemec) ISUA; (32.0 miles south of Hidalgo de Parral) CAS; (1.0 mile east of La Saucedá) AMNH; (8.0 miles west of Matachic) AMNH; (Mesa del Huracan, 108° 15' 30" 4') CNC; (23.0 miles south of Miñaca) UASM; (Ojo Laguna) AMNH; (Primavera) AMNH; (San Jose Babicora) AMNH; (San Rafael) AMNH; (Santa Barbara) AMNH; (Santa Clara Cañon, 5.0 miles west of Parrita) AMNH; (Santa Clara, Namiquipa District) AMNH; (Sombrerillo) CAS. DISTRITO FEDERAL: (Creek at Lomas de Chapultepec) MCZ; (Mexico City) JHen, MCZ, WSUP; (Mixcoac) JHen; (Peñon Viejo) MCZ; (Tacubaya) JHen; (Villa Guadalupe) JHen. DURANGO: (Arroyo El Sauz, 33.0 miles north of Durango) MCZ; (Durango City) AMNH, ANSP, CUNY, MCZ, WSUP; (5.0 miles west of Durango) CNC; (10.0 miles west of Durango) CNC, ISUA; (15.0 miles west of Durango) CNC; (20.0 miles west of Durango) CNC; (23.0 miles south of Durango) CNC; (25.0 miles west of Durango) CNC; (27.5 miles west of Durango) UASM; (18.0 miles east of El Salto) AMNH; (Las Puentes) AMNH; (Nombre de Dios) AMNH; (Rio Chico, 15.7 miles west of Durango) UASM; (Rio Florido, near Las Nieves) UASM. GUANAJUATO: (2.0 miles north of Irapuato) CNC; (Rio Guanajuato, 9.8 miles south Silao) UASM; (San Miguel Allende) AMNH. GUERRERO: (Acapulco) JHen, MCZ; (Apipilulco) MCZ; (Cacahuamilpa) JHen; (Chilpancingo) CNC; (8.4 miles west of Chilpancingo) UASM; (Rio Mezcala, 23.7 miles north of Zumpango) UASM; (Rio Papagayo, 41.0 miles north of Acapulco) UASM; (Xilitla) AMNH; (9.0 miles north of Zumpango) ISUA; (30.8 miles north of Zumpango del Rio) UASM. HIDALGO: (Guadalupe) MCZ; (Huichapan) LACM; (Rio Tula, near Tasquillo) UASM; (San Miguel) MCZ. JALISCO-NAYARIT: (No locality given) AMNH. JALISCO: (Ajijic) AMNH, JHen, UATA; (23.2 miles south of Autlan) UASM; (Atenquique) CAS; (3.0 miles north of Barra de Navidad, Bahía de Coahuacoma) UATA; (Barranquillas) UCR; (0.4 miles west of Cocula) UASM; (Cruzero de Malpaso, 17.7 miles northwest of Los Volcanes) UASM; (Guadalajara) AMNH, CUNY, MCZ, RTBe; (61.0 kilometers southwest of Guadalajara) UATA; (Huascato) USNM; (10.0 miles west of Jiquilpan) CAS; (15-20.0 miles west of Jiquilpan) CAS; (8.5 miles north of Juchitlan) UASM; (13.0 miles southeast of Lagos de Moreno) UASM; (17.9 miles west of Magdalena) UASM; (Mountains west of Tecalitlan) UATA; (Ocotlan) CAS; (Puente Caquixtle, 9.7 miles east of Encarnacion de Diaz) UASM; (Puente La Garita, near La Garita) UASM; (Puerto Vallarta) CNC; (Rio Grande de Santiago, 12.5 miles west of Ixtlahuacan del Rio) UASM; (4.0 miles south of Talpa de Allende) UASM; (6.5 miles south of Talpa de Allende) UASM; (21.0 miles northeast of Tepatitlan) CAS; (Tuxpan) MCZ; (Savula) USNM; (Valle de Guadalupe) CAS. MEXICO: (Lago Zumpango, near San Juan Zitlattepec) UASM; (Los Remedios) JHen; (Serros Guadalupe) JHen; (Temascaltepec, Tejuipilco) CAS. MICHOACAN: (Comanja) CAS; (1.3 miles east of Comanja) UASM; (5.0 kilometers west of Ciudad Hidalgo) MCZ; (11.0 miles west of Hidalgo) UCD; (Huajumbaro) UASM; (10.0 miles west of Jiquilpan) DRWh; (10.6 miles south of La Huerta) UASM; (Morelia) AMNH, UASM; (9.5 miles west of Morelia) UASM; (25.0 kilometers east of Morelia) RTBe; (3.0 miles west of Quiroga) AMNH; (6.0 kilometers east of Quiroga) UASM; (Tuxpan) CAS, RTBe; (near Tzintzuntzan) UASM; (8.1 miles east of Vallamar) UASM; (10.0 miles east of Zamora) GRNo; (14.0 miles northwest of Zitacuaro) UCD; (50.0 miles west of Zitacuaro) MCZ. MORELOS: (Cañon de Lobos, 9.1 miles east of Cuernavaca) UASM; (Cuautla) JHen; (Cuernavaca) CAS, CNC, CUNY, MCZ, RCGr, TMBH; (3.6 miles east of Cuernavaca) UASM; (5.4 miles east of Cuernavaca) UASM; (Progreso) CUNY; (Tejalpa) DRWh, FDAG; (Tepoztlan) RCGr; (Xochi-

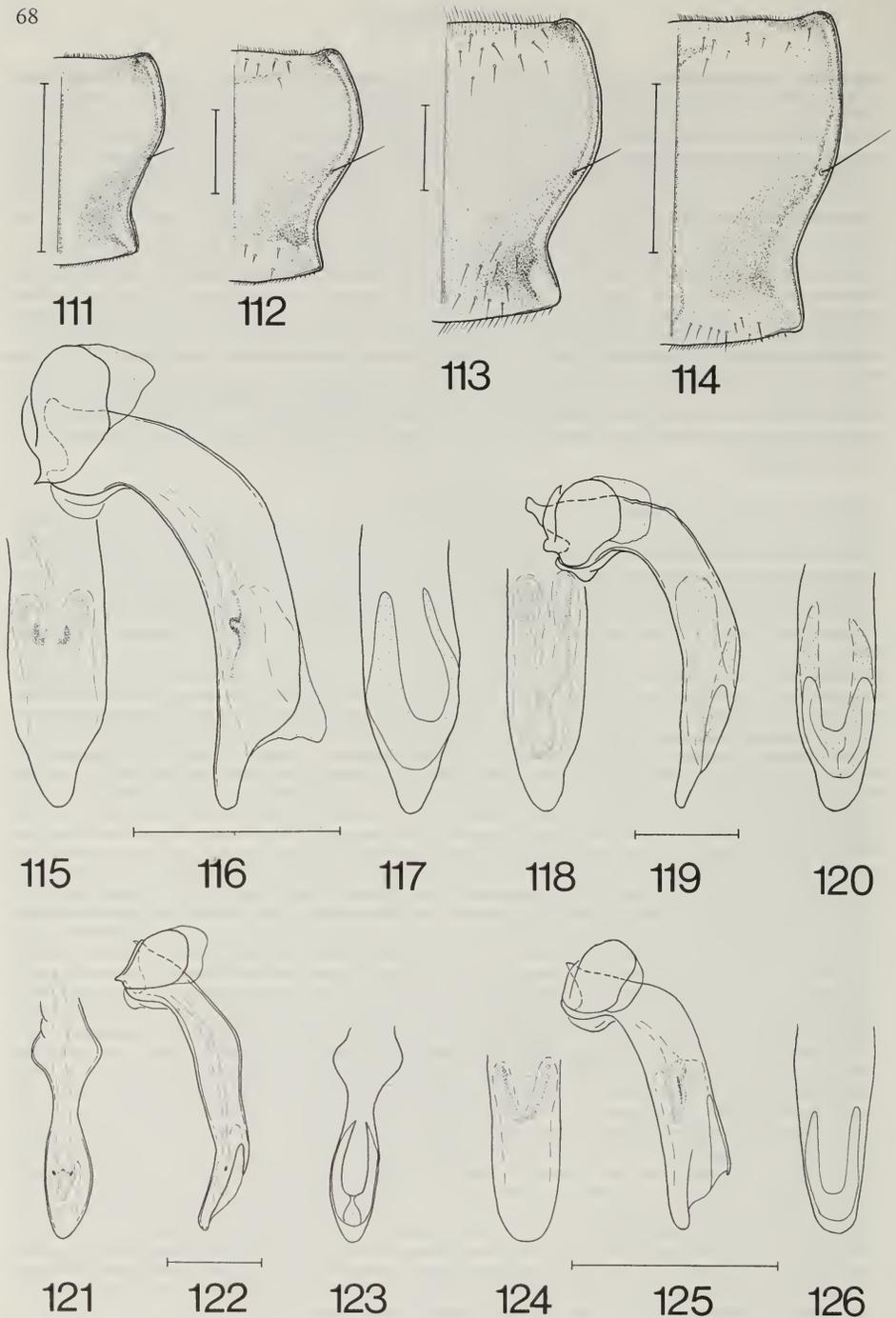
tepec) JHen; (Yautepec) UCD. NAYARIT: (5.1 miles north of Chapalilla) UASM; (20.3 miles west of Compostela) GRNo; (Ixtlan del Rio) CAS; (San Blas) UCD; (8.7 miles east of San Blas) GRNo; (13.8 miles east of San Blas) UASM; (Tepic) AMNH, UATA; (19.0 miles southeast of Tepic) CAS; (24.0 miles southeast of Tepic) CAS. OAXACA: (25.0 miles south of Mitla) ISUA; (Oaxaca) UMAH; (Rio Atoyac, near Juchatengo) UASM; (9.3 miles north of Sola de Vega) UASM; (72.5 miles south of Valle Nacional, Rio Grande) UASM. PUEBLA: (9.0 miles north of Amatitlan) CAS; (5.0 miles south of Izucar de Matamoros) UCD; (near Petlalcingo) UASM; (3.0 miles northwest of Petlalcingo) UCD; (Puente Tepexco, near Tepexco) UASM; (Tehuacan) CAS, JHen; (near Tehuiztingo) UASM; (near Tepexco) UASM. QUERETARO: (6.0 miles east of Celaya) UASM; (near Palmillas) UASM; (6.4 miles east of Pinal de Amoles) UASM; (Queretaro) UASM; (3.0 miles west of Queretaro) AMNH. SAN LUIS POTOSI: (25.0 kilometers east of Santa Domingo) MCZ. SINALOA: (Camino Real de Piaxtla) AMNH; (3.4 miles west, 5.0 miles south of Culiacan) GRNo; (3.0 miles east of Culiacancito) GRNo; (2.1 miles northeast of El Fuerte) GRNo; (Mazatlan) AMNH, MCZ, UCR; (5.0 miles north of Mazatlan) GRNo; (10.0 miles north of Mazatlan) GRNo; (Rio Baluarte, near Rosario) UASM; (Quiroroba, Alamosa) CAS; (Rio Panuco 11.2 miles northeast of Concordia) UASM; (Rio Piaxtla, 1.0 miles east of Route 15) UASM; (Rosario) CAS; (20.0 miles east of Villa Union) UCR; (21.0 miles east of Villa Union) CNC; (27.0 miles east of Villa Union) CNC; (33.0 miles east of Villa Union) CNC; (Venadillo) CAS; (Zenzontle, Culiacan) AMNH. SONORA: (65.0 miles southeast of Agua Prieta) ISUA; (Alamos) CAS; (4.0 miles west of Alamos) GRNo; (5.0 miles west of Alamos) UATA; (7.2 miles southeast of Alamos) GRNo; (Caramachi, Rio Mayo) CAS; (8.0 miles east of Imuris) CAS; (San Bernardo, Rio Mayo) CAS; (Yecora) CNC. TAMAULIPAS: (Ciudad Victoria) CNHM; (Sotano de La Joya de Salas) TCBA. TLAXCALA: (21.0 miles west of Apizaco) CNC. ZACATECAS: (29.0 miles northwest of Fresnillo) UASM; (Presa Choquen) JHen; (Rio Juchipila, 0.9 miles north of Jalpa) UASM; (1.3 miles southeast Sain Alto) UASM.

UNITED STATES

ARIZONA: Apache County (White Mountains) CAS; Cochise County (Benson) CAS, UWSW, (Bisbee) CAS, (Canelo) UATA, (Canelo, Pycatt's Ranch) CUNY, (Cave Creek) AMNH, (Cave Creek Canyon) CNHM, (Cave Creek, South Fork) GRNo, (Chiricahua Mountains) CAS, OUCO, UASM, USNM, (Chiricahua Mountains, Cave Creek Ranch) TCBA, UASM, (Chiricahua Mountains, 15.0 miles west of Portal) UCD, (Chiricahua Mountains, Redrock Canyon) CAS, (Chiricahua Mountains, Rustlers Park) CNC, (Chiricahua Mountains, Silver Creek wash, 3.3 miles west by northwest of Portal) CUNY, (Chiricahua Mountains, Texas Canyon) CAS, (Chiricahua National Monument) AMNH, CAS, (Cochise Stronghold) TLEr, UATA, (Douglas) CAS, CNHM, (10.0 miles west of Douglas) TLEr, (Guadalupe Canyon, 32.0 miles east of Douglas) CUNY, UCR, (Martyr Dam, South West Research Station) TLEr, (Huachuca Mountains) AMNH, CAS, TAMU, UATA; USNM, (Huachuca Mountains, Carr Canyon) AMNH, CAS, TLEr, (Huachuca Mountains, Fort Huachuca) LACM, (Huachuca Mountains, Garden Canyon) CAS, USNM, (Huachuca Mountains, Huachuca Canyon) LACM, (Huachuca Mountains, Miller Canyon) CAS, MCZ, OUCO, UCR, (Huachuca Mountains, Sunnyside Canyon) CAS, LACM, (Palmerlee) ANSP, CAS, UMAH, (Paradise) UASM, (Chiricahua Mountains, Pinery Creek) CNHM, (Portal) AMNH, RCGr, SJSC, TLEr, WHTY, WSUP, UCR, (Ramsey Canyon, Huachuca Mountains) CAS, SJSC, UATA, UMHN, USNM, (Chiricahua Mountains, Rucker Lake) UASM, (San Pedro near Palominas) UASM, (San Pedro River east of Sierra Vista) UATA, (South Fork Forest Camp, 4.5 miles west of Portal) CAS, (South West Research Station, Portal) AMNH, CNC, CUNY, FDAG, OSUC, SJSC, TLEr, UATA, UCD, UCR, UIMI, (Wood Canyon, Bisbee) UATA; Gila County (Globe) KSU, UCD, (base of Pinal Mountains) CAS, UCD, (Roosevelt Lake) CNC, (Winkelman) UATA; Graham County (Aravaipa) CAS, (Aravaipa Creek, between Klondyke and Aravaipa) DRWh, (Galiuro Mountains, Powers' Garden) UASM, (Galiuro Mountains, Reservoir, east slope) UASM, (Graham Mountains, Shennon Camp) GRNo; Navajo County (8-15.0 miles northeast of Whiteriver) AMNH; Pima County (Baboquivari Mountains) CAS, CUNY, LACM, (Baboquivari Mountains, Browns Canyon) AMNH, CAS, UATA, (Baboquivari Mountains, Schaffler Canyon) ANSP, (Baboquivari Mountains, Sabino Canyon Elkhorn Ranch) CAS, (East slope of Coyote Mountains, 0.5 miles north of Mendoza Canyon) UATA, (10.0 miles east of Continental) UATA, (4.0 miles south of Mountain View) CAS, (Sahuarita) MCZ, (Saint Xavier Mountains, Tucson) CAS, (Santa Catalina Mountains) CAS, UATA, USNM, (Santa Catalina Mountains, Mount Lemmon, Bear Canyon) CAS, CUNY, UATA, (Santa Catalina Mountains, Peppersauce Canyon) CAS, UASM, UATA, (Santa Catalina Mountains, Molino Basin) CUNY, TLEr, (Santa Rita Mountains) CAS, UATA, UMSP, USNM, (Santa Rita Mountains, Gardner Canyon) OSUC, (Tanque Verde) UATA, (Tucson) CAS, MCZ, UASM, UATA, UIMI, UMSP, USNM, (8.0 miles north of Vail) UATA; Pinal County (Oracle) USNM, (14.0 miles east of Oracle) CAS; Santa Cruz County OSUC, (Calabasas Canyon, east Tumacacori Mountains) UASM, (Canille) AMNH, UATA, (Luis Springs, San Pedro River) UASM, (Nogales) CAS, CNHM, LACM, MCZ, UCD, USNM, ZMLS, (3.0 miles north of Nogales) LACM, (10.0 miles west of Nogales) UCD, (15.0 miles northwest of Nogales) UCD, (Pajaritos Mountains, Yanks Spring, 4.0 miles southeast of Ruby) AMNH, CAS, (Patagonia) CAS, CMPP, CNHM, CUNY, UATA, UCD, (Peña Blanca) CNC, CUNY, UASM, UATA, (Santa Rita Mountains, Madera Canyon) AMNH, ANSP, CAS, CUNY, GRNo, LACM, SJSC, RCGr, UASM, UATA, UCD, UWSW, WHTY, (Sonoita) WHTY, (Sonoita River, Patagonia) AMNH, (4.0 miles west of Sombrero Butte, Cherry Creek) USNM, (Tumacacori Mountains, Sycamore Canyon) CUNY, (Tumacacori Mountains, Sycamore Canyon, near Ruby) CUNY, UATA, (2.0 miles west of Washington Camp) UATA; Maricopa County (Gillespie's Dam) CAS; Yavapai County (Mayer) GRNo, (Prescott) CAS; Yuma County (15.0 miles east of Yuma) CNHM; Counties unknown (Florida) UATA, (Reef) MCZ, (near San Fernando) USNM, (Santa Cruz River) UATA, (Tortolita Mountains) CAS, (Wake Field Mine) PUM. CALIFORNIA: CMPP, ISNH, TMBH; Santa Cruz County (Amado) UMSP. NEW MEXICO: Catron County (Mogollon Mountains, Big Dry Creek) CAS, (Mogollon Mountains, Willow Creek) TLEr; Grant County (Silver City) MCZ; Hidalgo County (Guadalupe Canyon) GRNo, (Rodeo) UCR, (12.0 miles southeast of Rodeo, Post Office Canyon) SJSC. OREGON: Lane County (Siltcoos Lake) CAS. TEXAS: Jeff Davis County (Limpia Canyon) TLEr.

The *sallei* group

The members of this group are characterized by their complete brown color, testaceous legs with infuscated knees, lateral pits of the mentum, and swollen median lobe. A single species, *B. sallei* Chaudoir is included here.



Figs. 111-114. Pronotum, right half, dorsal aspect. 111. *Brachinus melanarthrus* Chaudoir, Tamazunchale, San Luis Potosi, Mexico. 112. *Brachinus sallei* Chaudoir, Edzna, Campeche, Mexico. 113. *Brachinus grandis* Brullé, Macultepec, Tabasco, Mexico. 114. *Brachinus brunneus* Castelnau, Laguna Guanico, Puerto Rico. Figs. 115-126. Male genitalia. 115. *Brachinus melanarthrus* Chaudoir, Veracruz, Veracruz, Mexico, ventral aspect. 116. Lateral aspect of same. 117. Dorsal aspect of same. 118. *Brachinus grandis* Brullé, Macultepec, Tabasco, Mexico, ventral aspect. 119. Lateral aspect of same. 120. Dorsal aspect of same. 121. *Brachinus sallei* Chaudoir, Coyame, Lake Catemaco, Veracruz, Mexico, ventral aspect. 122. Lateral aspect of same. 123. Dorsal aspect of same. 124. *Brachinus brunneus* Castelnau, La Guanica, Puerto Rico, ventral aspect. 125. Lateral aspect of same. 126. Dorsal aspect of same. Accompanying scale line equals 1.0 mm.

Brachinus sallei Chaudoir

(Figs. 20, 112, 121, 122, 123, 128, 133)

Brachynus sallei Chaudoir, 1876: 85. G. E. Ball could not locate Chaudoir's specimens in MHNP. Chaudoir wrote (1876: 85) that other specimens were in Chevrolat's collection. E. Taylor informs me that these specimens are no longer in HMO. Therefore, I presume the type is lost.

Type locality. — Mexico, as originally given by Chaudoir, but herewith restricted to Tabasco, Mexico.

Notes. — Chaudoir compared *B. sallei* with Chevrolat's *B. spinipes*, in the original description of *B. sallei*. This name was never published by Chevrolat, and therefore not really in existence, but I add this note to stop possible confusion in the future.

Diagnostic combination. — See group characteristics and key.

Description. — Large-sized beetles, 12.1 to 15.1 mm.

Color. Dark brown, mouthparts and antennae somewhat paler. Legs testaceous with brown "knees" (femoral apices plus tibial bases). Dorsal surface of elytra dark brown, epipleura paler.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows rugose, sparsely punctate. Disc of pronotum finely rugose along center line, punctures barely impressed.

Head. Frontal furrows deeply impressed. Antennal scape quite robust, widest at middle. Ligula with sclerotized center area ellipsoid-convex with two apical setae. Mentum (fig. 20) with two lateral pits each surrounded by numerous setae. Submentum with numerous accessory setae.

Prothorax. Pronotum (fig. 112) convex, sides narrowly reflexed. Anterior and posterior margins with a few shallowly impressed setiferous punctures. Proepipleura glabrous. Propisterna with a few small setae both anteriorly and posteriorly, glabrous medially. Anterior tibia with anterior edge finely punctate.

Pterothorax. Elytra elongate, moderately costate. Humeral angle square. Pubescence confined to eighth depression, except near apex. Depressions punctate. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 121, 122, 123). Median lobe with plane of shaft slightly rotated from plane of basal bend. Basal bend short. Shaft swollen at basal third, flared and flattened at apical third. Ligule short, rounded apically. Virga (figs. 121, 122). Female (fig. 128). Stylus narrow, elongate, arcuate, acute at apex.

Variation. — Too few specimens are known for me to evaluate geographic variation, but the sixteen specimens I have seen are rather constant.

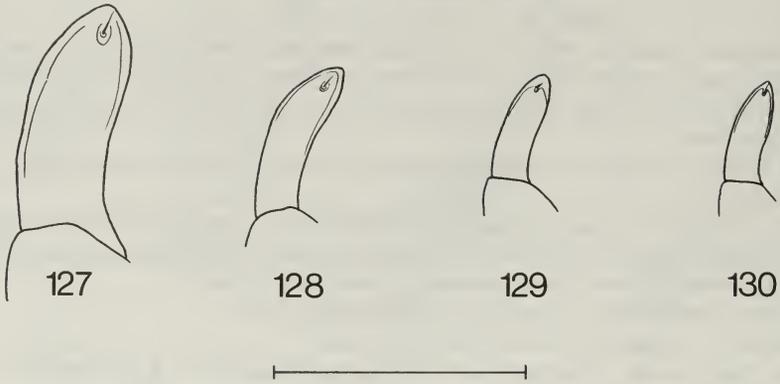
Flight. — J. G. Edwards collected a specimen at lights on Cozumel Island, Quintana Roo, Mexico.

Etymology. — Patronym for August Sallé, in whose collection Chaudoir first saw specimens of this species.

Collecting notes. — On the north shore of Lake Catemaco in Veracruz, Mexico, these beetles live in heavily shaded marshes about 10.0 meters from the lake edge. The predominant plant was a *Heliconia* species.

Life history. — Members of this species have been collected from December to April and August. One teneral adult was collected in January in the state of Campeche, Mexico.

Distribution. — (Fig. 133). The known range of this species extends from southern San Luis Potosi to southern Chiapas and the Yucatan peninsula. The species also occurs on Isla Cozumel, off the coast of Quintana Roo. I have seen 16 specimens from the following localities:



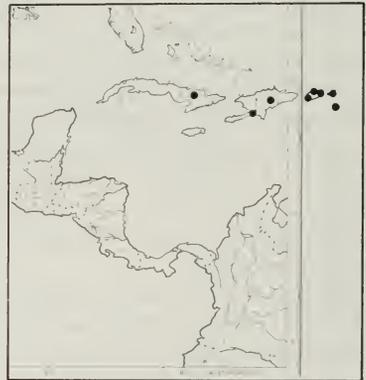
131



132



133



134

Figs. 127-130. Right stylus of female ovipositor, ventral aspect. 127. *Brachinus grandis* Brullé, Venedillo, Sinaloa, Mexico. 128. *Brachinus sallei* Chaudoir, Edzna, Campeche, Mexico. 129. *Brachinus melanarthrus*, Tela, Honduras. 130. *Brachinus brunneus* Castelnau, Humacao, Puerto Rico. Figs. 131-134. Geographical distribution maps. 131. *Brachinus grandis* Brullé. 132. *Brachinus melanarthrus* Chaudoir. 133. *Brachinus sallei* Chaudoir. 134. *Brachinus brunneus* Castelnau. Accompanying scale line equals 1.0 mm.

MEXICO

CAMPECHE: (Edzna) UASM. CHIAPAS: (San Quintin, Chiquita Miramar) UASM. QUINTANA ROO TERRITORY: (Cozumel Island) SJSC. SAN LUIS POTOSI: (Valles) CPBo. TABASCO: (Macultepec) JHen; (Tierra Colorado de Itzmate) JHen. VERACRUZ: (Coyame, Lake Catemaco) UASM; (San Andres Tuxtla) UCR.

The *brunneus* group

The members of this group are characterized by the form of the virga, brown color of the body, and testaceous legs and infuscated knees. These beetles lack the lateral mental pits found in *B. sallei*. I have seen specimens of South American species that belong to this group. It is possible that when the South American fauna is better known, this group will have to be redefined. Two species, *B. brunneus* Castelnau, and *B. melanarthrus* Chaudoir are included here.

Brachinus brunneus Castelnau

(Figs. 114, 124, 125, 126, 130, 134)

Brachinus brunneus Castelnau, 1834: 59. Lectotype, here selected, a male, MHNP, unlabelled, but standing third in a series of seven in front of box label "brunneus Castelnau Antilles Mus. Berl". Chaudoir (1876: 84) mentions that he received four specimens from Castelnau's type series. *Type locality*. — Cayenne, French Guiana as originally given by Castelnau.

Brachinus gilvipes Mannerheim, 1837: 41. Lectotype, here selected, a female, MHNP, labelled "St. Thomas, Mannerheim" and standing fifth in a series of seven specimens in front of box label "brunneus Castelnau Antilles Mus. Berl". *Type locality*. — St. Thomas Island, Antilles as given on Mannerheim's label, and indicated by Chaudoir (1876: 84). Chaudoir, 1876: 84.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Small to medium-sized beetles, 7.0 to 9.0 mm.

Color. As in *sallei*.

Microsculpture. As described for genus.

Macrosculpture. As in *sallei*.

Head. As in *sallei*, except antennal scape not as robust, mentum without pits or accessory setae, submentum without accessory setae.

Prothorax. As in *sallei*. Pronotum (fig. 114)

Pterothorax. As in *sallei*, except elytral pubescence extending along depressions 6, 7, and 8, and costae barely elevated.

Abdomen. As described for genus.

Genitalia. Male (figs. 124, 125, 126). Median lobe with plane of shaft rotated 45° from plane of basal bend. Basal bend short. Apex of shaft rounded. Ligule short, narrow, rounded apically. Virga (figs. 124, 125). Female (fig. 130). Stylus narrow, acute at apex.

Variation. — Besides the intrapopulation variation in the shape of the pronotum and the total size, these beetles exhibit color differences of the third and fourth antennal articles. The range is from testaceous with infuscated bases to completely infuscated, and occurs within single population samples.

Flight. — The flight of these beetles has not been recorded.

Etymology. — Medieval Latin, *brunneus*, brown; referring to the color of these beetles.

Life history. — Members of this species have been collected in October, January, March, and May. No teneral adults have been seen.

Distribution. — (Fig. 134). The known range of this species extends from French Guiana to Puerto Rico and Hispaniola (Haiti). I have seen 108 specimens from the following localities:

GREATER ANTILLES

CUBA: (Baragua) MCZ; (Colon) MCZ. DOMINICAN REPUBLIC: (Barahona) MCZ; (Monte Cristi) MCZ. HAITI: (Etang Lachaux southwest peninsula) MCZ. PUERTO RICO: (Ensenada) MCZ; (Humacao) CUNY, MCZ; (Laguna Guanićá) MCZ; (Mereidita Finca Ponce) MCZ; (Mayaguez) CUNY; (Toa-Baja) CUNY, MCZ.

VIRGIN ISLANDS

St. Croix Island, MCZ; St. Thomas Island, MHNP.

Brachinus melanarthrus Chaudoir

(Figs. 19, 111, 115, 116, 117, 129, 132)

Brachynus melanarthrus Chaudoir, 1876: 84. Lectotype, here selected, a male, MHNP, unlabelled, but standing first in front of box label "melanarthrus, Chaud. Caracas, Sallé".

Type locality. — Mexico, as originally given by Chaudoir, but herewith restricted to Veracruz, Mexico.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Small to medium-sized beetles, 6.6 to 11.2 mm.

Color. As in *sallei*.

Microsculpture. As described for genus.

Macrosculpture. As in *sallei*.

Head. As in *sallei*, except mentum (fig. 19) without deep lateral pits and accessory setae and submentum without accessory setae.

Prothorax. As in *sallei*. Pronotum (fig. 111).

Pterothorax. As in *sallei*.

Abdomen. As described for genus.

Genitalia. Male (figs. 115, 116, 117). Median lobe with plane of shaft slightly rotated from plane of basal bend. Basal bend long. Apex of shaft narrowed, elongate. Ligule short, broadened apically. Virga (figs. 115, 116). Female (fig. 129). Stylus narrow, parallel-sided, rounded apically.

Variation. — Too few specimens are known of this species to analyze the geographical variation. However, the size may vary clinally, the largest specimens in Mexico, the smallest specimens in Honduras. One female from Veracruz is darker in color and the surface of the pronotum is dull due to very sense rugosities.

Flight. — These beetles have been collected at lights in the state of San Luis Potosi, Mexico.

Etymology. — Greek, *melanos*, black; *arthron*, joint; referring to the infuscated knees of these beetles.

Life history. — Members of this species have been collected in May, July, and August, but no teneral adults were seen.

Distribution. — (Fig. 132). The known range of this species extends from southern San Luis Potosi, Mexico, to northern Honduras. I have seen seven specimens from the following localities:

CENTRAL AMERICA

HONDURAS: (La Lima) DTRT; (Tela) DTRT.

MEXICO

SAN LUIS POTOSI: (Tamazunchale) MCZ. VERACRUZ: (5.0 miles northwest of Acayucan) UCD; (Veracruz) CNC.

The *grandis* group

The members of this group are characterized by very large size and darkly pigmented and elongate virgae. One species, *B. grandis* Brullé, is included.

Brachinus grandis Brullé

(Figs. 113, 118, 119, 120, 127, 131)

Brachinus grandis Brullé, 1838: 19. Lectotype, here selected, a female, MHNP, unlabelled, but standing next to a pin with a point and the label "grandis Brullé". The point holds the labrum of the specimen. *Type locality*. — Bolivia, as originally given by Brullé. *Diagnostic combination*. — The diagnostic characteristics are given in the key.

Description. — Very large-sized beetles, 16.4 to 18.5 mm.

Color. Mesepisterna, metepisterna, metasternum at sides, abdominal sterna and terga, and knees infuscated, otherwise ferruginous. Dorsal surface and epipleura of elytra brown.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows rugose, sparsely punctate, punctures barely impressed.

Head. Frontal furrows moderately impressed. Antennal scape robust, widest apically. Ligula with sclerotized center area ellipsoid-convex with two apical setae. Mentum and submentum without accessory setae.

Prothorax. Pronotum (fig. 113), slightly flattened along center line, sides narrowly reflexed. Proepipleura glabrous, proepisterna with a few scattered setae both anteriorly and posteriorly. Anterior tibia with anterior surface sparsely punctate.

Pterothorax. Elytra elongate, broad, moderately costate. Humeral angle square. Pubescence confined to outer intervals, except in apical third. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 118, 119, 120). Median lobe with plane of shaft slightly rotated from plane of basal bend. Basal bend long. Apex of shaft narrowed to apex. Ligule poorly defined, short, truncate. Virga (figs. 118, 119). Female (fig. 127). Stylus very large, broad, narrowly rounded at apex.

Variation. — Too few specimens are known to evaluate geographic variation.

Flight. — The flight of these beetles has not been recorded.

Etymology. — Latin, *grandis*, large; referring to the very large size of these beetles compared to others in the genus.

Life history. — Members of this species have been collected in March, May, and June, but no teneral adults were seen.

Distribution. — (Fig. 131). The known range of this species extends from Sinaloa and San Luis Potosi in Mexico to Bolivia, South America, but this has been determined by only four localities. It is probable that this species has discontinuous and local populations. I have seen five specimens from the following localities:

MEXICO

SINALOA:(Venedillo),CAS. SAN LUIS POTOSI:(El Pujal) CPBo. TABASCO:(Macultepec) JHen.

The *lateralis* group

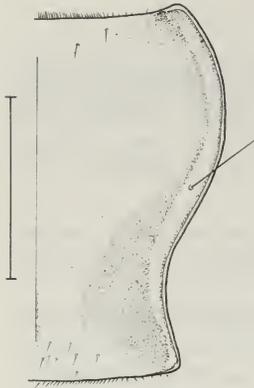
The members of this group are characterized by their brown elytra. It is a provisional group pending the outcome of a revision of the South American species many of which have brown elytra.

Brachinus lateralis Dejean

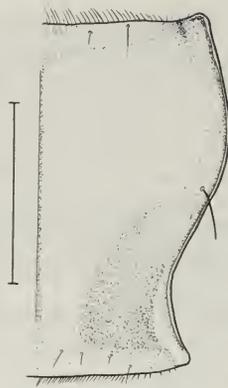
(Figs. 137, 145, 156, 157, 158, 169)

Brachinus lateralis Dejean, 1831: 424. Lectotype, here selected, a male, MHNP, labelled "male, lateralis m. in Amer. bor." on green paper, "Ex Museo Chaudoir" and "Type" on red paper. *Type locality*. — North America, as originally given by Dejean, but herewith restricted to Imperial County, California.

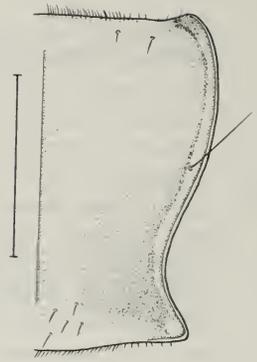
Brachinus leucoloma Chaudoir, 1868: 301. Lectotype, here selected, a male, MHNP, labelled "Californie, R. Gila, LeConte" and "Ex Museo Chaudoir." *Type locality*. — Gila



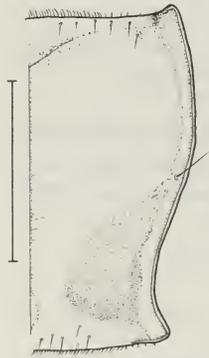
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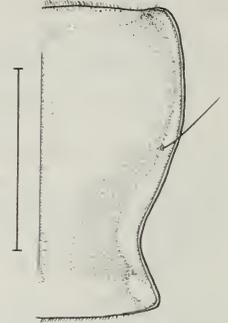
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Figs. 135-140. Pronotum, right half, dorsal aspect. 135. *Brachinus chalchihuitlicue* new species, San Blas, Nayarit, Mexico. 136. *Brachinus chirriador* new species, Puente La Garita, La Garita, Jalisco, Mexico. 137. *Brachinus lateralis* Dejean, 20.9 miles north of Arriaga, Chiapas, Mexico. 138. *Brachinus arboreus* Chevrolat, Mazatlan, Sinaloa, Mexico. 139. *Brachinus adustipennis* Erwin, 20.0 miles west of Rosario, Sinaloa, Mexico. 140. *Brachinus aeger* Chaudoir, Paso Antonio, Escuintla, Guatemala. Figs. 141-146. Right stylus of female ovipositor, ventral aspect. 141. *Brachinus chirriador* new species, Puente La Garita, La Garita, Jalisco, Mexico. 142. *Brachinus adustipennis* Erwin, 20.0 miles west of Rosario, Sinaloa, Mexico. 143. *Brachinus chalchihuitlicue* new species, Mazatlan, Sinaloa, Mexico. 144. *Brachinus aeger* Chaudoir, Paso Antonio, Escuintla, Guatemala. 145. *Brachinus lateralis* Dejean, Rio Niltepec, Oaxaca, Mexico. 146. *Brachinus arboreus* Chevrolat, Mazatlan, Sinaloa, Mexico. Accompanying scale lines equal 1.0 mm.

River, Imperial County, California, as originally given on Chaudoir's labelled specimen. Erwin, 1965: 7.

Diagnostic combination. — The brown elytra with pale epipleura and glabrous elytral disc separate members of this species from all others west of the continental divide in the United States. In Mexico and further south, only the genitalic characteristics provide reliable diagnostic characteristics (see key couplet 17).

Description. — Medium-sized beetles, 6.1 to 9.3 mm.

Color. Mesepisterna, metepisterna, abdomen at least at sides, and "knees" infuscated. Head and prothorax ferruginous. Usually mouth parts, antennal articles 1-4, legs, and middle of venter testaceous. Dorsal surface of elytra brown, epipleura testaceous.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows rugose, sparsely punctate. Surface of pronotum smooth with a few scattered shallowly impressed setiferous punctures.

Head. Frontal furrows shallowly impressed. Antennal scape robust, widest at middle. Ligula with sclerotized center area ellipsoid-convex with two apical setae, and a few small inconspicuous setae. Mentum and submentum without accessory setae.

Prothorax. Pronotum (fig. 137) convex, sides narrowly reflexed. Proepipleura glabrous. Proepisterna with a few setae anteriorly. Anterior tibia with anterior surface finely punctate.

Pterothorax. Elytra moderately long, barely costate. Humeral angle square. Pubescence usually confined to outer depressions and costae with some scattered patches occasionally on disc. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 156, 157, 158). Median lobe with plane of shaft slightly rotated from plane of basal bend. Basal bend moderately long. Apex of shaft flattened, ridged around edge and with a median ventral keel. Shaft swollen slightly at middle. Ligule short, truncate. Virga (figs. 156, 157). Female (fig. 145). Stylus long, narrow, apically rounded.

Variation. — Intrapopulational variation occurs in the following characteristics: the presence or absence of pubescence on the elytral disc, shade of brown color of the elytra, the height of the costae, the shape of the pronotum, and body size.

Flight. — The flight of these beetles has been recorded at lights throughout the range of the species.

Etymology. — Latin, *lateralis*, of the side; referring to the pale epipleura of the elytra on these beetles.

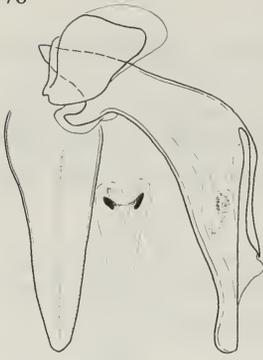
Collecting notes. — These beetles occur in a number of habitats. In California, they have been collected on the shores of the Salton Sea (saline) and Lake Elsinore (fresh water). In Arizona, they have been collected at the edges of lakes and in wet meadows. In Mexico, they have been collected in gravel beneath larger stones at the edges of streams.

Life history. — Members of this species have been collected in all months of the year. I have seen teneral adults collected in March in Puebla, in May and September in Sonora, and in August in California. These beetles probably overwinter (or aestivate) as adults.

Distribution. — (Fig. 169). The range of this species extends from northern Arizona south to Chiapas, Mexico, and populations occur in Baja California. I have seen 458 specimens from the following localities:

MEXICO

BAJA CALIFORNIA: (20.0 miles north of Comondú) CAS; (Estero, at mouth of Arroyo Rosario) CAS; (San Ignacio) CAS; (65.0 kilometers south of Tijuana) LACM. CHIAPAS: (20.9 miles north of Arriaga) UASM. DURANGO: (Durango City) AMNH, MCZ. GUANAJUATO: (Lago Yuriria, near Yuriria) UASM, GUERRERO: (Cacahuamilpa) JHen; (2.0 miles north of El Mogote) UASM; (Rio Mezcala, 23.7 miles north of Zumpango) UASM; (9.0 miles north of Zumpango) ISUA. JALISCO: (Ajijic) JHen, UATA; (Guadalajara) AMNH. MICHOACAN: (Morelia) AMNH, UASM; (near Tzintzuntzan) UASM. MORELOS: (Cañon de Lobos, 9.1 miles east of Cuernavaca) UASM; (Cuernavaca) ANSP, BMNH, MCZ, RTBe; (Progreso) CUNY, WSUP; (Xochitpec) JHen. NAYARIT: (San Blas) CAS; (Tepic) UATA; (19.0 miles southeast of



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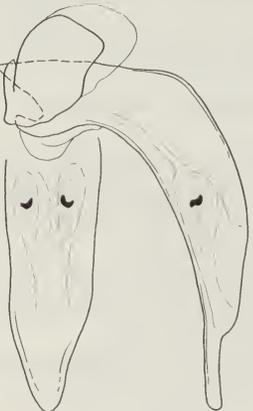
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Figs. 147-164. Male genitalia. 147. *Brachinus aeger* Chaudoir, Rio Teapa, Tabasco, Mexico, ventral aspect. 148. Lateral aspect of same. 149. Dorsal aspect of same. 150. *Brachinus arboreus* Chevrolat, 32.0 miles south of Acaponeta, Nayarit, Mexico, ventral aspect. 151. Lateral aspect of same. 152. Dorsal aspect of same. 153. *Brachinus adustipennis* Erwin, Manatee Springs State Park, Florida, ventral aspect. 154. Lateral aspect of same. 155. Dorsal aspect of same. 156. *Brachinus lateralis* Dejean, near Petlalcingo, Puebla, Mexico, ventral aspect. 157. Lateral aspect of same. 158. Dorsal aspect of same. 159. *Brachinus chalchihuitlicue* new species, San Blas, Nayarit, Mexico, ventral aspect. 160. Lateral aspect of same. 161. Dorsal aspect of same. 162. *Brachinus chirriador* new species, Puente La Garita, La Garita, Jalisco, Mexico, ventral aspect. 163. Lateral aspect of same. 164. Dorsal aspect of same. Accompanying scale lines equal 1.0 mm.

Tepic) CAS. OAXACA: (25.0 miles south of Mitla) ISUA; (Puente Zanatepec, near Zanatepec) UASM; (Rio Atoyac, near Juchatengo) UASM; (Rio Niltpec, 18.4 miles west of Zanatepec) UASM; (72.5 miles south of Valle Nacional) UASM. PUEBLA: (Puente Tepexco, near Tepexco) UASM; (near Petlalcingo) UASM; (near Tepexco) UASM. SINALOA: (13.0 miles north of Guamuchil) GRNo; (Los Mochis) CAS, GRNo; (Mazatlan) AMNH, CNC. SONORA: (10.0 miles west of Alamos) AMNH; (Ciudad Obregon) CNC; (16.0 miles northeast of Ciudad Obregon) CNC; (35.0 miles northeast of Ciudad Obregon) CNC; (14.0 miles southeast of Empalme) CAS; (Hermosillo) AMNH; (La Atascosa) UASM; (Navajoa) GRNo, JHen; (Pesqueria) CAS; (Rio Yagui 12.0 miles west of Ciudad Obregon) CNC; (Sonoyta) AMNH. VERACRUZ: (Jalapa) BMNH.

UNITED STATES

ARIZONA: Cochise County (Benson) CAS, (San Bernardino Ranch) KSU, LACM; Graham County (Thatcher) UCD; Maricopa County (Phoenix) MCZ, UATA, USNM; Mohave County (Littlefield) UCD; Pima County (Arivaca Creek at Arivaca) CAS, (Baboquivari Mountains, Browns Canyon) AMNH, (Santa Catalina Mountains) CAS, UATA, (Tucson) AMNH, ANSP, CAS, USNM; Pinal County (Picacho) CAS; Santa Cruz County (6.0 miles north of Nogales) UASM, (15.0 miles northwest of Nogales) UCD, (Pajarita Mountains) CAS, (Patagonia) CUNY, UATA, (Peña Blanca) UASM; Yuma County (Cibola) CAS, (Ehrenburg) UATA, (Fort Yuma) USNM, (Yuma) CAS, ISNH, MCZ, USNM; County unknown (Senator) AMNH. CALIFORNIA: Imperial County (Calpatria) CAS, (El Centro) CAS; Los Angeles County PSUU, USNM, ZMLS, (Cypress) LACM, (East Manhattan) LACM, (Lake Hodges) SDNHM, (Long Beach) CAS, (Los Angeles) CAS, (Pasadena) CAS, TLER; Orange County (Anaheim) SDNHM, (Laguna Canyon) UCD; Riverside County (Blythe) LACM, UIMI, (Corona) UCD, (Elsinore) CAS, (Lake Elsinore) CAS, CMPP, UIMI, UNLN, USNM, (Mecca) CVMA, (Riverside) CUNY, LACM, UMAH, USNM, (Salton Sea) VVBa, (Salton Sea, Mecca) CNC, USNM; San Bernardino County (Needles) CAS, (Ontario) CAS, (San Bernardino) MCZ, OUCO, (Saratoga Springs, Death Valley) UCD; San Diego County ANSP, CCha, CUNY, (Oceanside) CAS, (San Felipe Creek 14.0 miles east of Julian) UASM, (San Diego) SDNHM, (San Juan Capistrano) UIMI, (Sweetwater Valley) SDNHM. NEVADA: Clark County (Logandale) NSDA.

Brachinus aeger Chaudoir

(Figs. 140, 144, 147, 148, 149, 168)

Brachynus aeger Chaudoir, 1876: 82. Lectotype, here selected, a female, MHNP, labelled "Nouve Grenade," and standing first in a series of five specimens. *Type locality*. — Colombia, South America, as originally given by Chaudoir.

Diagnostic combination. — Only the genitalia provide reliable diagnosis, but see key couplet 18.

Description. — Small to medium-sized beetles, 5.8 to 8.9 mm.

Color. As in *lateralis*, except mesepisterna usually pale.

Microsculpture. As described for genus.

Macrosculpture. As in *lateralis*.

Head. As in *lateralis*, except ligula without inconspicuous setae.

Prothorax. As in *lateralis*, except costae weaker.

Pterothorax. As in *lateralis*, except costae weaker.

Abdomen. As described for genus.

Genitalia. Male (figs. 147, 148, 149). Median lobe with plane of shaft barely rotated from plane of basal bend. Basal bend long. Shaft bulbous at basal third; narrowed to acute boot-shaped apex; venter ridged medially. Ligule moderately long, broad, rounded apically. Virga (figs. 147, 148). Female (fig. 144). Stylus short, parallel-sided, narrowly rounded at apex.

Variation. — As in *lateralis*, except disc of elytra generally pubescent.

Flight. — The flight of these beetles has not been recorded.

Etymology. — Latin, *aeger*, sick, troubled; referring, I think, to the pale colors of these beetles compared to others in the genus.

Collecting notes. — G. E. Ball and D. R. Whitehead have collected these beetles on gravel banks of several rivers in Mexico.

Life history. — Members of this species have been collected from April to June and November to January, but no teneral adults were seen.

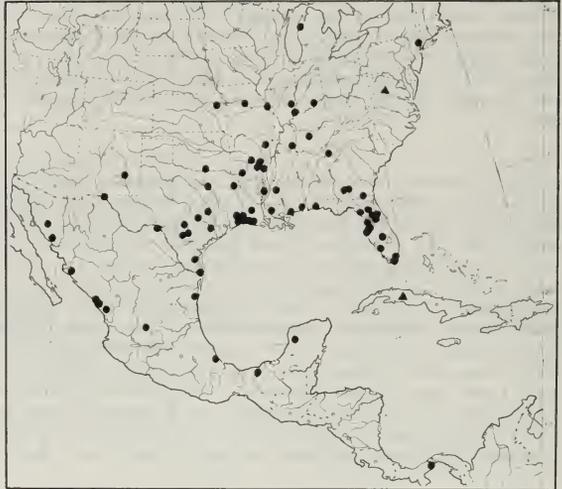
Distribution. — (Fig. 168). The range of this species extends from Sonora, Mexico, south to Colombia, South America. Most records are from the western coast of Mexico, but one specimen was collected in San Luis Potosi, Mexico. I have seen 15 specimens from the following localities:

CENTRAL AMERICA

GUATEMALA: (Paso Antonio, Escuintla) BMNH.



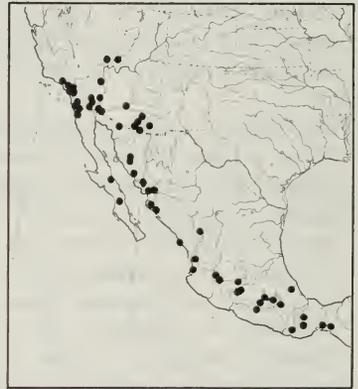
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Figs. 165-170. Geographical distribution maps. 165. *Brachinus chirriador* new species. 166. *Brachinus adustipennis* Erwin. 167. *Brachinus chalchihuitlicue* new species. 168. *Brachinus aeger* Chaudoir. 169. *Brachinus lateralis* Dejean. 170. *Brachinus aboreus* Chevrolat.

MEXICO

CHIAPAS: (Tuxtla Gutierrez) BMNH. GUERRERO: (Rio Mezcala, 23.7 miles north of Zumpango) UASM. NAYARIT: (Rio Acaponeta, 2.4 miles south of Acaponeta) UASM; (19.0 miles southeast of Tepic) CAS. OAXACA: (Oaxaca City) BMNH. SAN LUIS POTOSI: (El Pujal) CPBo. SINALOA: (Camino, Real de Piaxtla) AMNH. SONORA: (Ciudad Obregon) CNC; (Cocorit) UCR. TABASCO: (Rio Teapa, near Teapa) UASM. VERACRUZ: (San Andres Tuxtla) BMNH.

Brachinus chalchihuitlicue new species

(Figs. 135, 143, 159, 160, 161, 167)

Type locality. — San Blas, Nayarit, Mexico.

Type specimens. — The holotype male and allotype female are in the entomological collections at CAS; both were collected at the type locality by B. Malkin on September 17-21, 1953. Twenty paratypes collected at various localities and on various dates are in AMNH, CAS, MCZ, TLEr, UASM.

Diagnostic combination. — Although members of this species have their elytral costae elevated more than any other in the group, the only reliable diagnostic characters are the genitalia, but also see key couplet 20.

Description. — Medium-sized beetles, 8.7 to 11.0 mm.

Color. Antennal articles 3 and 4, mesepimera, metepisterna, abdominal sterna at least at sides, abdominal terga, and knees infuscated, otherwise ferruginous. Legs testaceous. Dorsal surface of elytra brown, epipleura slightly paler.

Microsculpture. As described for genus.

Macrosculpture. As in *lateralis*.

Head. As in *lateralis*, except ligula without minute setae.

Prothorax. As in *lateralis*. Pronotum (fig. 135).

Pterothorax. As in *lateralis*, except costae more highly elevated.

Abdomen. As described for genus.

Genitalia. Male (figs. 159, 160, 161). Median lobe with plane of shaft slightly rotated from plane of basal bend. Basal bend long. Apex of shaft very narrow, elongate. Ligule long and broad, rounded apically. Virga (figs. 159, 160). Female (fig. 143). Stylus broad, tapering to almost acute apex.

Variation. — Besides the intrapopulation variation in shape of the pronotum and in body size, these beetles vary locally in the height of their costae.

Flight. — The flight of these beetles has not been recorded.

Etymology. — Chalchihuitlicue, the goddess of runoff waters, streams, lakes, and the sea, in early Teotihuacan and Nahuatl-Toltec cultures of central Mexico. This goddess is also the wife of Tlaloc, the god of rain and thunder. The name refers to the habitat in which most *Brachinus* species are found.

Life history. — Members of this species have been collected from July to September. Teneral adults were collected in July in Sinaloa and in August in Guerrero.

Distribution. — (Fig. 167). The known range of this species extends from Sinaloa to Guerrero on the west coast of Mexico. I have seen 30 specimens from the following localities:

MEXICO

GUERRERO: (Acapulco) MCZ. NAYARIT: (San Blas) CAS; (Tepic) AMNH. SINALOA: (Mazatlan) AMNH, GRNo, UCR; (Venedio) CAS. STATE UNKNOWN: (Saltillo) MCZ.

Brachinus arboreus Chevrolat

(Figs. 138, 146, 150, 151, 152, 170)

Brachinus arboreus Chevrolat, 1834: 42. Lectotype, here selected, a male, HMO, Type number COL. 114 1/3, further labelled "Brachinus arboreus Chev. Col. Mex. 1 cent No. 2 Mexico Sallé." *Type locality.* — Orizaba, Mexico, as originally given by Chevrolat.

Diagnostic combination. — Only the genitalia provide reliable diagnosis, but see also key couplet 21.

Description. — Small to medium-sized beetles, 6.1 to 9.2 mm.

Color. Base of antennal articles 3 and 4, mesepisterna, metepisterna, abdominal sterna at least at sides, abdominal terga, and knees infuscated, otherwise ferruginous. Dorsal surface of elytra brown, epipleura seldom paler.

Microsculpture. As described for genus.

Macrosculpture. As in *lateralis*.

Head. As in *lateralis*, except ligula without inconspicuous setae.

Prothorax. As in *lateralis*. Pronotum (fig. 138).

Pterothorax. As in *lateralis*.

Abdomen. As described for genus.

Genitalia. Male (figs. 150, 151, 152). Median lobe with plane of shaft barely rotated from plane of basal bend. Basal bend short. Apex of shaft narrowed, acute, ridged ventrally at middle and at sides forming two small sulci. Ligule short, broad, truncate. Virga (figs. 150, 151). Female (fig. 146). Stylus narrow, parallel-sided, slightly curved, narrowly rounded apically.

Variation. — As in *lateralis*.

Flight. — The flight of these beetles has not been recorded.

Etymology. — Latin, *arboreus*, of the trees. The reason Chevrolat gave this name is unexplained in his description.

Collecting notes. — D. R. Whitehead has collected these beetles along a small stream in Jalisco.

Life history. — Members of this species have been collected in January, March, June, and November, but no teneral adults were seen.

Distribution. — (Fig. 170). The range of this species extends from Sinaloa south to Honduras. I have seen 57 specimens from the following localities:

CENTRAL AMERICA

HONDURAS: (Copan) MCZ; (La Lima) DTR.

MEXICO

JALISCO: (9.0 miles east of Guadalajara) AMNH, NAYARIT: (32.0 miles south of Acaponeta) CAS; (19.0 miles southeast of Tepic) CAS. MORELOS: (5.0 miles east of Cuernavaca) UCD. SINALOA: (Mazatlan) MCZ, TLER; (Rosario) CAS. VERACRUZ: (Cordoba) BMNH; (Jalapa) BMNH, MCZ.

Brachinus chirriador new species (Figs. 136, 141, 162, 163, 164, 165)

Type locality. — Six miles west of Cintalapa, Route 190, Chiapas, Mexico.

Type specimens. — The holotype male and allotype female are in the MCZ. The holotype was collected by G. E. Ball and D. R. Whitehead at the type locality on September 7, 1965. The allotype was collected at Jacala, Hidalgo by R. Haag on June 23, 1939. Eight paratypes collected on various dates at various localities are in CAS, CPBo, TLER, UASM.

Diagnostic combination. — The restriction of elytral pubescence to depressions 7 and 8 in the basal two-thirds of the elytra will usually separate these beetles from others with brown elytra in Mexico and Central America. Only the genitalia provide reliable diagnosis, however.

Description. — Medium-sized beetles, 7.2 to 10.0 mm.

Color. As in *lateralis*, except epipleura dark.

Microsculpture. As described for genus.

Macrosculpture. As in *lateralis*.

Head. As in *lateralis*.

Prothorax. As in *lateralis*, except anterior tibia with anterior surface finely strigose.

Pronotum (fig. 136).

Pterothorax. As in *lateralis*, except pubescence restricted to depressions 7 and 8. Abdomen. As described for genus.

Genitalia. Male (figs. 162, 163, 164). Median lobe with plane of shaft slightly rotated from plane of basal bend. Basal bend short. Apex of shaft narrow, slightly elongate. Ligule short, broad, truncate. Virga (figs. 162, 163). Female (fig. 141). Stylus very broad, tapering apically to narrowly rounded apex.

Variation. — Too few specimens are known to evaluate geographic variation.

Flight. — The flight of these beetles has not been recorded.

Etymology. — Mexican-Spanish, *chirriador*, the one who crepitates.

Collecting notes. — G. E. Ball and D. R. Whitehead collected these beetles at the edge of a pond at the type locality by treading coarse grass and emergent vegetation.

Life history. — Members of this species have been collected from April to June, and August to December, but no teneral adults were seen.

Distribution. — (Fig. 165). The known range of this species extends from northern Tamaulipas, Mexico, south along the east coast to Honduras and on the west coast of Mexico in Sinaloa and Nayarit. I have seen 11 specimens from the following localities:

CENTRAL AMERICA

HONDURAS: (La Lima) DTRT.

MEXICO

CHIAPAS: (6.0 miles west of Cintalapa) UASM. JALISCO: (Puente La Garita, near La Garita) UASM. NAYARIT: (San Blas) CAS. SAN LUIS POTOSI: (El Pujal) CPBo. TAMAULIPAS: (La Coma, Aldama) CPBo. VERACRUZ: (San Rafael, Jicaltepec) MCZ; (Veracruz) UCD.

Brachinus adustipennis Erwin

(Figs. 139, 142, 153, 154, 155, 166)

Type locality. — Myakka River, Myakka River State Park, Sarasota County, Florida.

Type specimens. — The holotype male and allotype female are in MCZ; both were collected at the type locality by T. L. and L. J. Erwin on May 29, 1968. Thirty paratypes collected at various localities and on various dates are in AMNH, CAS, DRWh, MCZ, TLER, and UASM.

Diagnostic combination. — The brown elytra and pale epipleura, and pubescent elytral disc separate members of this species from all others east of the continental divide in the United States. In Mexico and further south only the genitalic characters provide reliable separation, but see also key couplet 17.

Description. — Medium-sized beetles, 6.0 to 10.2 mm.

Color. Metepisterna, knees and sides of abdominal sterna infuscated. Antennal articles 3 and 4, usually terga slightly infuscated, otherwise body and limbs testaceous to ferruginous. Dorsal surface of elytra brown, epipleura usually paler.

Microsculpture. As described for genus.

Macrosulpture. As in *lateralis*.

Head. As in *lateralis*, except minute ligula setae apparently absent.

Prothorax. As in *lateralis*, except anterior tibia with anterior surface strigose. Pronotum (fig. 139).

Pterothorax. As in *lateralis*, except disc of elytra usually pubescent, and costae weaker.

Abdomen. As described for genus.

Genitalia. Male (figs. 153, 154, 155). Median lobe with plane of shaft barely rotated from plane of basal bend. Basal bend moderately long. Apex of shaft narrowed, rounded, and ridged ventrally; lateral ridges less prominent than in *lateralis*, ending before apex; apex slightly bent dorsally. Ligule short, narrowed toward rounded apex. Virga (figs. 153, 154).

Female (fig. 142). Stylus narrow, broadened slightly at apical third, rounded apically.

Variation. — As in *lateralis*, except disc of elytra usually pubescent.

Flight. — The flight of these beetles has been recorded at lights throughout the range of the species.

Etymology. — Latin, *adustus*, tanned, brown; *pennis*, wing; referring to the tan-colored elytra of these beetles.

Collecting notes. — My wife and I collected these beetles in a number of localities in the southern United States. Along the Myakka River, at the type locality, they occurred beneath boards and stones on the river's grassy banks. At Juniper Springs, Florida, and in the Okefenokee Swamp, we found them in the roots of grass clumps in *Scirpus-Typha* marshes. In Texas they occurred on the muddy banks of the San Jacinto River in grassy clumps.

Life history. — Members of this species have been collected from March to December. Teneral adults were collected in May in Florida, and in August in Tennessee. Overwintering (or aestivating) probably occurs in the adult state.

Distribution. — (Fig. 166). The range of this species extends from New York and Michigan, west to the west coast of Mexico, south to Panama. I have seen 552 specimens from the following localities:

CENTRAL AMERICA

PANAMA: (La Chorrera) CAS.

GREATER ANTILLES

CUBA: (No locality given) TMBH; (Camao, Havana) MCZ; (Soledad) MCZ.

MEXICO

AGUASCALIENTE: (15.0 miles west of Pabellon) UMAH. NAYARIT: (Acaponeta) AMNH; (32.0 miles south of Acaponeta) CAS. SINALOA: (Los Mochis) CAS; (Mazatlan) AMNH, CAS, UASM; (20.0 miles west of Rosario) UCR; (Venedillo) CAS. SONORA: (16.0 miles northeast of Ciudad Obregon) CNC; (Hermosillo) CNHM; (Rio Yagui, 12.0 miles west of Ciudad Obregon) CNC. TABASCO: (San Juan Bautista) BMNH; (Villa Hermosa) FDAG. TAMAULIPAS: (9.9 miles west of La Pesca) UASM. VERACRUZ: (Veracruz) UASM. YUCATAN: (Uxmal) TLER.

UNITED STATES

ALABAMA: Mobile County (Mobile) ANSP, USNM. ARKANSAS: Arkansas County (Almyra) USNM; Desha County (No locality given) UAFA; Hempstead County (Hope) CAS, MCZ; Poinsett County (No locality given) UAFA; Pulaski County (Little Rock) AMNH; Washington County (No locality given) UAFA. FLORIDA: Alachua County (Gainesville) FDAG, UMAH, (Payne's Prairie) UMAH; Brevard County (Indian River) USNM; Citrus County CAS, USNM, (Inverness) MCZ; Collier County (Naples) CUNY; Columbia County (Lake City) DRWH; Dade County (Florida City) UASM, (Miami) CMPP, (Royal Palm State Park) PUM; Escambia County (Pensacola) FDAG; Hernando County (Brooksville) CAS; Highlands County (Archbold Biology Station) CEWH, PSUU; Hillsborough County (Tampa) CAS, UMSP; Lake County USNM, (Fruitland Park) ANSP, UMAH, (Groveland) FDAG, (5.6 miles east of Juniper Springs) TLER; Lee County (Fort Myers) PUM; Levy County (Cedar Keys) USNM, (Manatee Springs State Park) RFre, UASM; Manatee County (Oneco) UASM; Marion County (No locality given) MCZ; Osceola County (Kissimmee) MCZ, PUM, UCD, USNM; Palm Beach County (Lake Worth) CAS; Pasco County (Dade City) FDAG; Pinellas County (Clearwater) CNHM, (Dunedin) AMNH, CAS, CUNY, UMAH, UWMW, (Tarpon Springs) AMNH, CNHM; Putnam County (Crescent City) USNM; Sarasota County (Myakka River State Park) TLER, UASM, (Sarasota) PUM; Seminole County (Lake Harney) USNM; Volusia County (Enterprise) CAS, ISNH, OUCO, UMSP, USNM; County unknown (Fort Capron) ISNH. GEORGIA: Baker County (Newton) CNC; Tift County (Tifton) OUCO; Ware County (8.0 miles northeast of Fargo) TLER. ILLINOIS: Richland and Lawrence Counties (Wabash) MCZ. INDIANA: Floyd County (New Albany) CEWH; Posey County (No locality given) PUM, KANSAS: Douglas County (Lawrence) PUM. LOUISIANA: USNM, Acadia Parish (Crowley) CAS; Allen Parish (Kinder) UASM; Calcasieu Parish (Lake Charles) USNM, (Sam Houston State Park) CUNY, TLER; East Baton Rouge Parish UAFA, (Baton Rouge) LSUB, UMAH; Evangeline Parish (Lake Chicot State Park) TLER; Franklin Parish (Chase) UAFA; Iberia Parish (Avery Island) ANSP; Jefferson Parish (Harahan) CNHM; Livingston Parish (Denham Springs) LSUB; Madison Parish (Tallulah) TAMU; Orleans Parish (New Orleans) ANSP, CAS, LACM, MCZ, USNM, UWMW, WSUP; Ouachita Parish (Calhoun) UAFA; Saint John the Baptist Parish (Garyville) LSUB; Saint Martin Parish (No locality given) UAFA; Vermilion Parish (Gueydan) USNM; Vernon Parish (Rosepine) UAFA; Parish unknown (Mound) FDAG. MICHIGAN: Benzie County (No locality given) PUM. MISSISSIPPI: Hinds County (Jackson) UCR; County unknown (McCormick) UWSW. MISSOURI: Boone County (Columbia) UCD; Saint Louis County (Saint Louis) UCR. NEW MEXICO: Chaves County (Roswell) UWSW. NEW YORK: Westchester County (Peekskill) MCZ. OKLAHOMA: Carter County (Ardmore) OSUS. TENNESSEE: Davidson County (Nashville) USNM; Madison County (Jackson) CNC. TEXAS: Atascosa County (Pleasanton) TAMU; Blanco County (Cypress Mills) USNM; Brazos County (College Station) TAMU; Cameron County (Brownsville) CAS, CNC, CUNY, OUCO, TLER, USNM; Colorado County (No locality given) UMSP; Dallas County (Dallas) MCZ; El Paso County (El Paso) CMPP; Fayette County (Engle) CAS; Frio County (5.0 miles north of Dilley) UASM; Hardin County (9.0 miles west of Beaumont) OSUC; Harris County USNM, (Highway 59 at San Jacinto River, near Houston) TLER; Harrison County (near Sabine River) TCBA; Hidalgo County (Mercedes) USNM, (Weslaco) TAMU;

Jefferson County (20.0 miles southwest of Sabine Pass) RCGr; Kerr County (Kerrville) CNC; Kleberg County (Kingsville) CUNY; Lee County (No locality given) UMAH; Smith County (Lake Palestine, 17.0 miles southwest of Tyler) DRWh; Travis County (Austin) CAS; Val Verde County (Del Rio) CNC.

The *kansanus* group

This group is characterized by its large shield-like virga, sharply costate elytra and lack of lateral pronotal setae. A single species, *B. kansanus* LeConte, is included.

Brachinus kansanus LeConte
(Figs. 175, 176, 177, 178, 195, 198)

Brachinus kansanus LeConte, 1862: 524. Lectotype, here selected, a male, MCZ red type label number 5851, further labelled with a green disc. *Type locality*. — Kansas, as originally given by LeConte.

Diagnostic combination. — This species is best characterized by its sharply costate elytra, lack of lateral pronotal setae, very narrowly reflexed sides of the pronotum, and almost glabrous proepipleura.

Description. — Medium-sized beetles, 8.7 to 11.5 mm.

Color. Ferruginous, sides of abdomen of some specimens slightly infuscated. Dorsal surface and epipleura of elytra blue.

Microsculpture. As described for genus.

Macrosculpture. Head behind eyes and frontal furrows rugose and shallowly punctate. Disc of pronotum with numerous shallowly impressed setiferous punctures.

Head. Frontal furrows moderately impressed. Antennal scape robust, widened apically. Ligula with sclerotized center area ellipsoid-convex with two apical setae. Mentum and submentum various, with or without accessory setae.

Prothorax. Pronotum (fig. 175) convex, flattened along center line, sides very narrowly reflexed. Proepipleura and proepisterna with a few scattered setae. Anterior tibia with anterior edge strigose.

Pterothorax. Elytra elongate, narrow, strongly costate. Humeral angle square. Costae smooth and glabrous, depressions between costae pubescent. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 176, 177, 178). Median lobe with plane of shaft rotated about 45° from plane of basal bend. Basal bend short. Median lobe nearly straight, slightly swollen at middle. Apex of shaft broadly rounded. Ligule short, very broad, truncate. Virga (figs. 176, 177). Female (fig. 195). Stylus elongate, narrow, parallel-sided, almost blunt apically.

Variation. — Besides the intrapopulation variation in body size and shape of the pronotum, these beetles vary in number of accessory setae of the mentum and submentum, the setal number of the ligula, and in the color of the elytra (blue to blue-green). The range of variation in all characteristics is seen in single population samples.

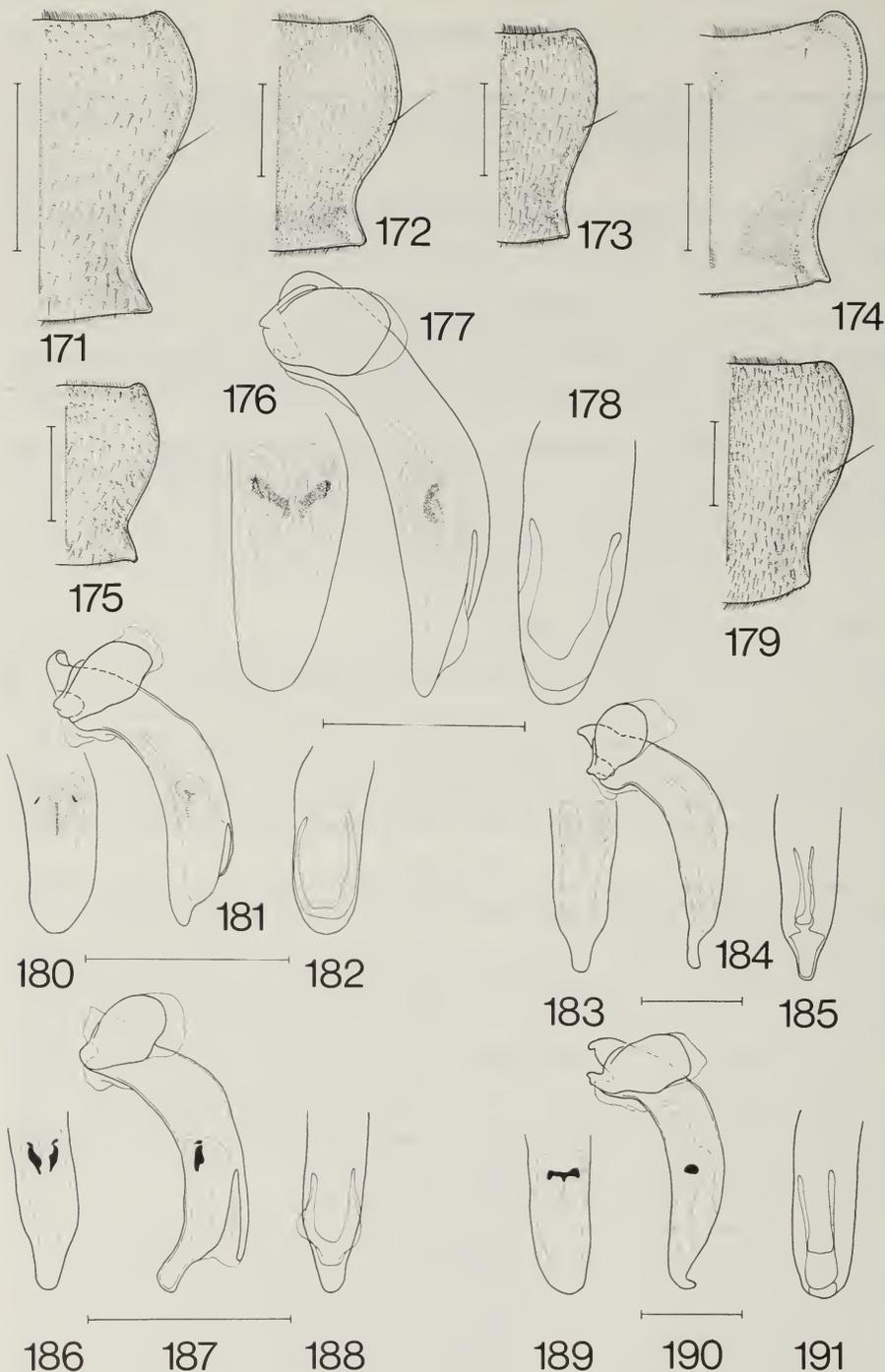
Flight. — The flight of these beetles has not been recorded.

Etymology. — The latinized form of Kansas, the place where the type was collected.

Collecting notes. — This species occurs along river and stream courses in very sandy areas beneath the broadleaf deciduous forest which follows these water courses into the Great Plains. K. L. Hays has also collected these beetles in the sand dunes near Manhattan, Kansas.

Life history. — Members of this species have been collected from June to October. One teneral adult was collected in July in Oklahoma. Overwintering is probably in the adult stage.

Distribution. — (Fig. 198). This is the only species restricted to the Great Plains area. It occurs along eastward flowing tributaries of the Mississippi and Missouri Rivers. I have seen 95 specimens from the following localities:



Figs. 171-175, 179. Pronotum, right half, dorsal aspect. 171. *Brachinus rugipennis* Chaudoir, Highlands County, Florida. 172. *Brachinus alternans* Dejean, Dallas County, Texas. 173. Same, Dallas County, Texas. 174. *Brachinus costipennis* Motschulsky, 12.2 miles south of El Banco, Durango, Mexico. 175. *Brachinus kansanus* LeConte, Scandia, Kansas. 179. *Brachinus viridipennis* Dejean, Mobile, Alabama. Figs. 176-178, 180-191. Male genitalia. 176. *Brachinus kansanus* LeConte, Scandia, Kansas, ventral aspect. 177. Lateral aspect of same. 178. Dorsal aspect of same. 180. *Brachinus rugipennis* Chaudoir, Archbold Research Station, Florida, ventral aspect. 181. Lateral aspect of same. 182. Dorsal aspect of same. 183. *Brachinus viridipennis* Dejean, Mobile, Alabama, ventral aspect. 184. Lateral aspect of same. 185. Dorsal aspect of same. 186. *Brachinus costipennis* Motschulsky, 12.2 miles south of El Banco, Durango, Mexico, ventral aspect. 187 & 188. Lateral & dorsal aspects of same. 189. *Brachinus alternans* Dejean, Okfenokee Swamp, Georgia, ventral aspect. 190 & 191. Lateral & dorsal aspects of same. Accompanying scale lines equal 1.0 mm.

UNITED STATES

ARKANSAS: Crawford County (No locality given) USNM. ? DAKOTA: (No locality given) MCZ. KANSAS: Atchison County (No locality given) CAS; Douglas County (No locality given) CMPP; Republic County (Republican River, Scandia) CAS; Riley County KSU, (Manhattan) USNM. ILLINOIS: Adams County (Quincy) CNHM; Calhoun County (Kampsville) MCZ. IOWA: Boone County (Ledges State Park) ISUA. MINNESOTA: (No locality given) UMSP. MISSOURI: (no locality given) ANSP, ISNH, MCZ, UMSP. NEBRASKA: Dodge County (Fremont) UNLN; Otoe County (Nebraska City) UNLN; Richardson County (Rulo) UNLN; Sioux County (Monroe Canyon) UNLN. OHIO: Preble County (No locality given) PUM. OKLAHOMA: Beckham County (No locality given) CAS; Cleveland County (No locality given) UONO; Grady County (Chickasha) USNM; Payne County (Stillwater) OSUS; Woodward County (Woodward) CNHM.

The *costipennis* group

This group is characterized by the form of the virga, form of the median lobe of the male genitalia, completely glabrous elytra, sulcate mentum surrounded by setae (shared with *B. mobilis* and some Old World species), and abbreviated submentum. One species, *B. costipennis* Motschulsky, is included.

Brachinus costipennis Motschulsky

(Figs. 18, 174, 186, 187, 188, 196, 197)

Brachinus costipennis Motschulsky, 1859: 138. Lectotype, here selected, a female, MCZ red type label number 8329. Further labelled with a green square and "37." As I pointed out (1965: 5), "this specimen is very likely a cotype from Motschulsky, with whom LeConte is known to have corresponded." *Type locality*. — California, as given originally by Motschulsky.

Brachinus carinulatus Motschulsky, 1859: 139. Lectotype, here selected, a male, MMM, labelled with a green square and "*Brachynus carinulatus* Motsch. California." *Type locality*. — California, as originally given by Motschulsky. Erwin 1965: 4.

Brachynus cognatus Chaudoir, 1876: 74. Lectotype, here selected, a female, MHNP, labelled "cognatus m. Mexico" and "Orizaba" on green paper and "Ex Museo Chaudoir" on white paper. *Type locality*. — Orizaba, Mexico, as given on Chaudoir's label. NEW SYNONYMY.

Brachinus cancellatus Bates, 1891: 269. Lectotype, here selected, a male, BMNH, labelled "Chihuahua City, Mexico," and "Höge." It is placed in the series labelled "B. cognatus Chaudoir." *Type locality*. — Chihuahua City, Mexico, as originally given by Bates. NEW SYNONYMY.

Diagnostic combination. — The lack of elytral pubescence immediately separates members of this species from all others of the genus.

Description. — Small-sized beetles, 5.0 to 8.0 mm.

Color. Ferrugineous, except antennal article 4 occasionally infuscated. Dorsal surface and epipleura of elytra blue.

Microsculpture. As described for genus.

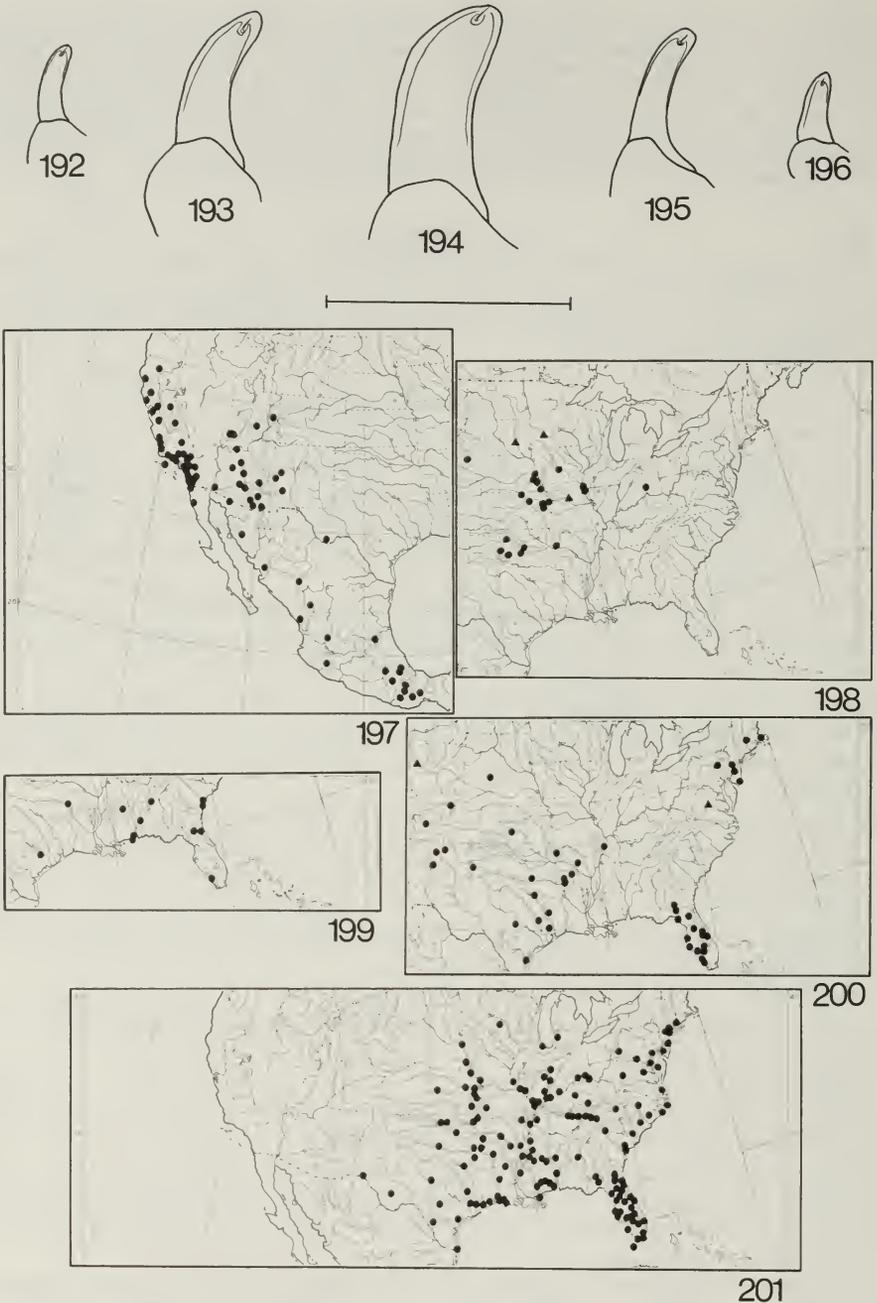
Macrosculpture. Frontal furrows rugose and punctate. Surface of pronotum microrugose, with an occasional setiferous puncture, but usually glabrous.

Head. Frontal furrows moderately impressed. Antennal scape cylindrical. Ligula with sclerotized center area ellipsoid-convex with two paramedian rows of three setae per row. Mentum (fig. 18) sulcate medially, sulcus surrounded by setae. Submentum (fig. 18) shortened and with accessory setae.

Prothorax. Pronotum (fig. 174) convex, flattened along center line, sides slightly reflexed. Proepipleura and proepisterna usually glabrous. Anterior tibia with anterior edge strigose.

Pterothorax. Elytra short and convex with quite arcuate sides. Humeral angles square, costae elevated and smooth, depressions between costae slightly rugose. Wings fully developed.

Abdomen. As described for genus.



Figs. 192-196. Right stylus of female ovipositor, ventral aspect. 192. *Brachinus rugipennis* Chaudoir, Hope, Arkansas. 193. *Brachinus viridipennis* Dejean, Mobile, Alabama. 194. *Brachinus alternans* Dejean, Seabrook, Texas. 195. *Brachinus kansanus* LeConte, Scandia, Kansas. 196. *Brachinus costipennis* Motschulsky, 26.1 miles north of Glenwood, New Mexico. Figs. 197-201. Geographical distribution maps. 197. *Brachinus costipennis* Motschulsky. 198. *Brachinus kansanus* LeConte. 199. *Brachinus viridipennis* Dejean. 200. *Brachinus rugipennis* Chaudoir. 201. *Brachinus alternans* Dejean. Accompanying scale line equals 1.0 mm.

Genitalia. Male (figs. 186, 187, 188). Median lobe with plane of shaft slightly rotated from plane of basal bend. Basal bend short. Median lobe slightly swollen medially, just before bend. Apex of shaft narrowed, blunt and deflected ventrally. Ligule short, broad, and truncate. Virga (figs. 186, 187). Female (fig. 196). Stylus short, narrow, tapering to acute apex.

Variation. — Besides the intrapopulational variation in body size and shape of the pronotum, these beetles are rather constant throughout the range of the species.

Flight. — These beetles have been recorded coming to lights in Mexico.

Etymology. — Latin, *costa*, rib; *pennis*, wing; referring to the raised costae of the elytra.

Collecting notes. — I collected these beetles along an intermittent stream on the eastern slope of the Mount Hamilton Range near San Jose, California. The sides of the stream were lined with specimens of *Salix* and *Quercus* species and an occasional specimen of *Platanus* species. The beetles were beneath small and large stones near the water.

Life history. — Members of this species have been collected in all months, except January. Teneral adults were collected in March in Oaxaca and in July in California.

Distribution. — (Fig. 197). The range of this species extends from Utah and northern California to Chiapas, Mexico, and east to the Big Bend area of Texas. The specimens labelled "Arkansas," "Kansas," and "Yukon," must be suspected of being mislabelled. I have seen 1,810 specimens from the following localities:

CANADA

YUKON: (No locality given) ISNH, WSUP.

CENTRAL AMERICA

GUATEMALA: (Agua Caliente) MCZ; (Los Amates) MCZ.

MEXICO

BAJA CALIFORNIA: (Hamilton Ranch) CAS; (San Vicente) CAS; (Tijuana) CNHM. DURANGO: (Durango City) MCZ; (12.2 miles south of El Banco) UASM. JALISCO: (Atenquique) CAS. OAXACA: (25.0 miles south of Mitla) ISUA; (Oaxaca City) CAS; (22.5 miles west of Oaxaca) UASM; (Paderon, Rio Tehuantepec) AMNH; (Rio Atoyac, near Juchatengo) UASM; (Rio Malatengo, 11.1 miles north of Matias Romero) UASM; (72.5 miles south of Valle Nacional) UASM. PUEBLA: (near Petlalcingo) UASM; (Puente Tepecco, near Tepecco) UASM. SAN LUIS POTOSI: (El Pujal) CPBo; (2.7 miles west of Santa Catarina) UASM; (Tamazunchale) AMNH, CAS, MCZ. SINALOA: (Roserio) CAS. SONORA: (7.2 miles southeast of Alamos) GRNo; (Hermosillo) CAS; (Sonoyta) AMNH. VERACRUZ: (Fortin de las Flores) UASM, CPBo; (Orizaba) UNLN. ZACATECAS: (Juchipila 0.9 miles north of Jalpa) UASM.

UNITED STATES

ARIZONA: Cochise County (Chiricahua Mountains) CAS, (17.0 miles east of Douglas) UCR, (Dragoon Mountains, Texas Pass) MCZ, (Portal) GRNo, RCGr, (San Pedro River, near Palominas) UASM, (San Pedro River, east of Sierra Vista) UATA, (Tombstone) SDNHM; Coconino County (Grand Canyon, mile 52.0) UATA, (Grand Canyon, Havasupai Indian Reservation) UMSP, (Oak Creek Canyon, near Flagstaff) CAS; Gila County (Carrizo Creek, near Carrizo) DRWh, (Gila Valley) CAS, (near Globe) UATA, (Payson) UATA, (Pinal Mountains) SDNHM, (San Carlos Lake) UATA, (Winkelman) UATA; Graham County (Aravaipa) CAS, (Aravaipa Creek, between Klondyke and Aravaipa) DRWh, (Geronimo) CAS, UATA; Maricopa County (Phoenix) CNC, MCZ, OUCO; Navajo County (8-15.0 miles northeast of Whiteriver) AMNH; Pima County (Saint Xavier Mountains) CAS, (Tucson) AMNH, CAS, MCZ, USNM; Pinal County (Aravaipa Canyon) CUNY, (Florence) ANSP, CMPP, (Sycamore Camp, 9.0 miles northwest of Payson) CAS; Santa Cruz County (Lewis Springs, San Pedro River) UASM, (Patagonia) CAS, CNHM, CUNY, UATA, UCD, UCR, (5.0 miles southwest of Patagonia) AMNH, (Pefia Blanca) UASM; Yavapai County (Bumble Bee) CAS, (Camp Verde) CAS, (Congress) UATA, (Prescott) AMNH, MCZ, (Verde River) USNM, (5.0 miles north of Wickenburg) UMAH; Yuma County (Fort Yuma) USNM, (Yuma) LACM, USNM; County unknown (Gila River) CNC. ARKANSAS: Hempstead County (Hope) MCZ. CALIFORNIA: Alameda County (Oakland Hills) CAS; Calaveras County (Mokelumne Hill) CAS; Fresno County (Camp Greeley) CAS, (Le Fevre Creek) CAS, (Sanger) CAS, (Trimmer) UMSP; Humboldt County (Garberville) CAS, LACM; Imperial County MCZ, (Carrizo) SDNHM, (Castiac) UIMI; Kern County AMNH, USNM, (Caliente) BMNH; Los Angeles County PSUU (Big Dalton Dam) UCD, (Big Tujunga) LACM, (Burbank) CNHM, ISNH, (Frenchman's Flats) GRNo, LACM, (Lake Arrowhead) CAS, (Los Angeles) CNHM, UATA, UNLN, USNM, (Los Angeles River) LACM, UCR, (Newhall) CUNY, USNM, (Pasadena) ANSP, CMPP, CNHM, CUNY, LACM, MCZ, (Rio Hondo) LACM, (Tujunga Pass) UCD, (San Francisquito Canyon) LACM, UCD, (San Gabriel Canyon) GRNo, TCBa, (San Gabriel Mountains, Camp Bonita) LACM, (Santa Monica) UMSP; Madera County (Coursegold) CAS, UIMI; Mendocino County (Navarro River, 2.0 miles northwest of Philo) CAS, (Ukiah) VVBa; Monterey County (Salinas) USNM, (Stone Canyon) CAS; Orange County (Costa Mesa) UCD, UCR, (Huntington Beach) USNM, (Olive) TAMU, (Santa Ana) CMPP, MCZ, TAMU; Placer County (No locality given) CAS; Riverside County (Corona) USNM, (Elsinore) CMPP, (Elsinore Lake) CAS, (Gilman Hot Springs) UCD, (Hemet) VVBa, (Palm Canyon) LACM, (Riverside) ANSP, CAS, CUNY, UMAH, USNM, (Simond's) LACM, (Temecula) CAS, (White Water Canyon) SJSC, UCR; Sacramento County (Folsom) USNM; San Bernardino County UUCO, (Afton Canyon) USNM, (San Bernardino) CAS, ISNH, (Cajon) CNHM, (Cajon Pass) UCD, (Cajon Wash) LACM, (Colton) CAS, CUNY, MCZ, UATA, UCR, UMAH, (Redlands) MCZ; San Diego

County CCha, UMAH, (Banner) SDNHM, (Dehesa) SDNHM, (Descanso) CAS, (El Monte Oaks) SDNHM, (Mission Dam) SDNHM, (Mission Valley) SDNHM, (Mountains of San Diego County) USNM, (Oceanside) CAS, (Pine Valley) CNC, MCZ, SDNHM, UMSP, (Poway) CAS, USNM, (Rincon) SDNHM, (San Diego) ANSP, CNHM, CUNY, MCZ, SDNHM, USNM, (San Pasqual) UCR, (Valley Center) SDNHM, (Warner's Hot Springs) PUM, (Warner's Ranch) SDNHM; San Francisco County (San Francisco) CMPP; San Luis Obispo County (Arroyo Grande) CAS; Santa Barbara County (Santa Barbara) MCZ, (Santa Cruz Island) CAS, (Santa Cruz Island, Christie Beach) TLEr, (Santa Cruz Island, Christie Ranch) UCR, (Shepherd's Inn) CAS; Santa Clara County (Adobe Creek) CAS; Sonoma County (Dry Creek, 9.0 miles northwest of Healdsburg) SJSC, (Duncan Mills) CAS, (2.0 miles east of Healdsburg) CAS, (Rio Nido) CAS; Stanislaus County (15.0 miles west of Patterson) TLEr; Tehama County (western hills of Tehama County) CAS; Tulare County (Sequoia National Park) VVBa; Ventura County (Santa Paula) ANSP, CAS; Yolo County (Davis) UCD; Counties unknown (Aliso Creek) UWSW, (Colorado Desert) MCZ, (Sylvania) MCZ. KANSAS: Douglas County (No locality given) CUNY. NEW MEXICO: Catron County (near Aragon) AMNH, (San Francisco Creek, 26.1 miles north of Glenwood) DRWh, UASM; Grant County (18.0 miles north of Mimbres, Roberts Lake) TLEr. TEXAS: Brewster County (Big Bend National Park, Hot Springs) CNC, (Rio Grande) CAS. UTAH: Garfield County (Boulder) ISUA; Grand County OUCO, (Moab) CAS, Washington County SDNHM, (3.0 miles south of Gunlock) GRNo, (Saint George) AMNH, KSU, MCZ, (Santa Clara Creek) UCD, (Zion National Park) CAS.

The *alternans* group

This small group of three species is characterized by the tripartite virga of the endophallus with elongate median apex, and plurisetose ligula. The group is divided into two subgroups.

The *alternans* subgroup

This subgroup is characterized by the accessory setae of the mentum and submentum, and the narrow ligule of the male median lobe. Two closely related species, *B. alternans* Dejean and *B. viridipennis* Dejean, are included

Brachinus alternans Dejean

(Figs. 172, 173, 189, 190, 191, 194, 201)

Brachinus alternans Dejean, 1825: 316. Lectotype, here selected, a female, MHNP, labelled "alternans m. in Amer. bor." on green paper, "Georgia" on green paper, "D. Escheri" on green paper, and "Ex Museo Chaudoir" on white paper. *Type locality*. — Georgia, as originally given by Dejean.

Brachinus liberator Dejean, 1831: 425. Lectotype, here selected, a male, MHNP, labelled "liberator m. in Amer. bor." and "LeConte." on green paper, and "Ex Museo Chaudoir" on white paper. *Type locality*. — North America, as originally given by Dejean. NEW SYNONYMY.

Brachinus deyrollei Laferté, 1841: 42. Lectotype, here selected, a male, MHNP, labelled "Missouri, Reiche" and "Ex Museo Chaudoir." *Type locality*. — Missouri, as given on the label. NEW SYNONYMY.

Brachinus strenuus LeConte, 1844: 48. Lectotype, here selected, a female, MCZ red type label number 5844. Further labelled with an orange disc and "76." *Type locality*. — Georgia, as originally given by LeConte. NEW SYNONYMY.

Brachinus tormentarius LeConte, 1848: 200. Lectotype, here selected, a female, MCZ red type label number 5845. Further labelled with a yellow disc and "77." *Type locality*. — Western States, as originally given by LeConte. NEW SYNONYMY.

Brachinus distinguendus Chaudoir, 1868: 287. Lectotype, here selected, a male, MHNP, labelled "fumans h. in Amer. bor." on green paper, and "Ex Museo Chaudoir" on white paper. *Type locality*. — United States, as originally given by Chaudoir. NEW SYNONYMY. *Diagnostic combination*. — The diagnostic characteristics are given in the key.

Description. — Large-sized beetles, 11.5 to 16.5 mm.

Color. Antennae and venter various. Elytra blue, rarely with greenish luster.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows, head behind eyes, and surface of pronotum moderately punctate, punctures moderately impressed.

Head. Frontal furrows moderately impressed. Antennal scape robust, widened apically.

Ligula with sclerotized center area ellipsoid-convex, plurisetose. Mentum and submentum with numerous accessory setae.

Prothorax. Pronotum (fig. 172) convex, flattened along center line, sides barely reflexed. Surface with punctures moderately impressed. Proepipleura and proepisterna pubescent. Anterior tibia with anterior margin weakly strigose.

Pterothorax. Elytra elongate, broad, moderately costate. Humeral angle square. Costae smooth, glabrous, depressions between costae pubescent. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 189, 190, 191). Median lobe with plane of shaft hardly rotated from plane of basal bend. Basal bend short. Median lobe arcuate, slightly swollen at middle, apex variable. Ligule short, narrow and truncate. Virga (figs. 189, 190). Female (fig. 194). Stylus broad, arcuate, and elongate, apex narrowly rounded.

Variation. — The members of this species are among the most variable of the genus in North America. Intrapopulation variation in the shape of the pronotum is illustrated in figures 172 and 173. Antennal articles 3 and 4 are or are not infuscated. The color of the ventor involves four combinations of ferruginous and infuscated areas, as follows: sides of abdomen infuscated, remainder ferruginous; the preceding, plus the mesepisterna and metepisterna, infuscated; both the preceding, plus the metasternum at sides, infuscated; and finally, the preceding, plus all the abdomen, infuscated (except ferruginous dimples). The pale condition is commonest in the midwest, and rare toward the south and east. However, one or more of these conditions is common to single populations. Variation occurs in the apex of the shaft of the male genitalia also. The bent or unbent condition is independent of the color cline described above, and (as color variation) is common to local populations.

Flight. — C. W. O'Brien has recorded these beetles flying to "blacklights" in Florida.

Etymology. — Latin, *alternus*, alternate; referring to the costate elytra.

Life history. — Members of this species have been collected during all months of the year. Teneral adults were collected in April in Illinois, in August in Tennessee, in September in Nebraska and Illinois, and in November in North Carolina. Overwintering probably takes place as an adult.

Distribution. — (Fig. 201). The range of this species extends from New Mexico north to Minnesota, east to Connecticut, and south to the Florida Keys. I have seen 1,141 specimens from the following localities:

UNITED STATES

ALABAMA: Clarke County (Salt Mountain, 6.0 miles south of Jackson) UMAH; Lee County (Auburn) AUA; Mobile County (Magazine Point) CAS, (Mobile) ANSP, CAS, MCZ, (Mount Vernon) AUA, OUCO; Tuscaloosa County (Tuscaloosa) UASM. ARKANSAS: (No locality given) AMNH; Conway County (No locality given) UAFA; Jefferson County (Pine Bluff) ISNH; Lawrence County (Imboden) CAS, USNM; Mississippi County UAF, (Osceola) UMAH. CONNECTICUT: New Haven County (Hamden) CAS. DISTRICT OF COLUMBIA: (Washington) UMSP. FLORIDA: Alachua County (Gainesville) FDAG, RFr, UMAH, (Grant's Cave) FDAG, (Poe Springs) UMAH; Baker County (Glen Saint Mary) FDAG; Brevard County (Indian River) ISNH, USNM; Broward County (Fort Lauderdale) UMAH; Charlotte County (Punta Gorda) CNC, CNHM; Citrus County (No locality given) CAS; Collier County (Everglades) OUCO, UMAH, USNM; Dade County UATA, (18.0 miles northwest of Hialeah) TLEr, (Homestead) AMNH, FDAG, TLEr, (Long Pine Key) MCZ, (Miami) UCD, (Paradise Key) AMNH, CNC, USNM, (Royal Palm State Park) AMNH, PUM, UCR, UMAH; Duval County (Arlington) AMNH, (Jacksonville) AMNH, ANSP, USNM; Glades County (Moore Haven) USNM, (Palmdale) AMNH; Hendry County (Clewiston) RCGr, (La Belle) PUM; Hernando County (Brooksville) CAS; Highlands County (Archbold Biology Station) CMPP, CUNY, PSUU, (Highlands Hammock State Park) TLEr, (4.5 miles west of Venus) TCBA; Hillsborough County (Plant City) UMAH, (Tampa) CAS; Jefferson County (Monticello) AMNH; Lake County UMAH, (Leesburg) CAS; Lee County (Fort Myers) PUM, (Sanibel Island) CAS; Leon County (Lake Jackson) UMAH; Levy County (No locality given) ANSP; Madison County (Greenville) FDAG; Manatee County (Oneco) UASM; Marion County (No locality given) MCZ; Orange County (Orlando) OUCO, (Winter Park) MCZ; Osceola County (Kissimmee) AMNH, ANSP, CUNY, PUM; Palm Beach County (Canal Point) CUNY, (Lake Worth) CMPP, (Stewart) UMAH; Pinellas County (Dunedin) CAS, PUM, UWMW, (Saint Petersburg) CAS, PUM; Putnam County (Crescent City) USNM, (Welaka) UMAH; Saint Johns County (Saint Augustine) AMNH, CAS; Sarasota County (Myakka State Park) CUNY, UASM, (Sarasota) PUM; Seminole County (Sanford) MCZ, PUM; Volusia County (Enterprise) ANSP, CAS, OUCO, USNM, (Ormond Beach) PUM; Counties unknown (Capron) USNM, (Cutler) USNM, (Detroit) USNM, (Hardkinville) MCZ, (Lake Apopka) AMNH, (Lake Okeechobee) PUM, (Lake Poinsett) USNM, (Port Sewall) AMNH, (Sand Point) USNM. GEORGIA: Charlton County (Okefenokee Swamp,

Billy Island) CUNY, USNM; Thomas County (Thomasville) AMNH, USNM. ILLINOIS: Alexander County (Olive Branch) CAS, CMPP, CNHM; Cook County (Chicago) CAS, (Palos Park) UMAH; Jackson County (Carbondale) ISNH, (Fountain Bluff) ISNH; Johnson County (South of Vienna) RTBe; Richland and Lawrence Counties (Wabash) MCZ; Saint Clair County (No locality given) CAS, UWMW; Union County (Alto Pass) CNHM; Counties unknown (Pike) ISNH. INDIANA: Knox County (No locality given) PUM; Perry County (No locality given) PUM; Posey County (Hovey Lake) CEWh, PUM, (Mount Vernon) CEWh; Spencer County (No locality given) CAS, PUM; Vigo County (No locality given) PUM. KANSAS: Coffey County (No locality given) ULLK; Douglas County (Baldwin) OSUC, (5.0 miles north of Baldwin City) RFre, (Lawrence) CAS, PUM, UCD, UMAH, USNM, (3.0 miles northwest of Lawrence) UNLN; Franklin County (No locality given) KSU; Montgomery County (Independence) CAS; Riley County (Manhattan) KSU; Shawnee County (Topeka) CMPP, KSU; County unknown (Fort Hays) MCZ. KENTUCKY: Bell County (Pineville) UAFA; Jefferson County (Louisville) UAFA; Jessamine County (Indian Falls) TCBA; Mercer County (Dix Dam) TCBA; Rockcastle County (Crooked Creek) TCBA. LOUISIANA: (No locality given) ISNH, UMSP; Cameron Parish USNM, (Grand Chenier) CNC; Iberia Parish (Avery Island) ANSP; Madison Parish (Tallulah) TAMU, UMAH; Natchitoches Parish (Natchitoches) UMAH; Orleans Parish (New Orleans) CAS, USNM, ZMLS; Ouachita Parish (Calhoun) UAFA; Plaquemines Parish (Nairn) MCZ; Vermilion Parish (Gueydan) USNM; Vernon Parish (Rosepine) UAFA. MARYLAND: Dorchester County (near Lloyds) USNM; Harford County (Edgewood) CUNY. MICHIGAN: Allegan County (Allegan) CAS. MINNESOTA: Olmsted County (No locality given) UMSP. MISSISSIPPI: Attala County (Cole Creek, Natchez Trace) RCGr; Carroll County (Avalon) UMAH; George County (Lucedale) CUNY; Greene County (Leakesville) CUNY; Hinds County (Jackson) UMAH; Lamar County (Lumberton) CUNY; Lauderdale County (Meridian) UMAH; LeFlore County (Greenwood) UMAH; Perry County (New Augusta) CUNY; Sharkey County (Rolling Fork) USNM; Tunica County (Dundee) UMAH; Washington County (Leroy Percy State Park) RCGr; County unknown (Moon) AMNH. MISSOURI: Buchanan County (Saint Joseph) USNM; Marion County (Hannibal) CAS; Saint Charles County (Saint Charles) MCZ; Vernon County (Nevada area) TLER; County unknown (Big Oak State Park) RTBe. NEBRASKA: Dakota County (South Sioux City) UNLN; Nemaha County (Peru) CNHM; Sarpy County (Bellevue, Childs' Point) CAS, UNLN. NEW JERSEY: Bergen County (Ramsey) USNM; Cape May County (Five Mile Beach) USNM; Gloucester County (Westville) MCZ; Ocean County (Lakehurst) AMNH; County unknown (Split Rock Lake) USNM. NEW YORK: New York County (New York City) MCZ; Westchester County (Peekskill) CAS, MCZ. NORTH CAROLINA: Catawba County (Newton) UCR; Darne County (Cape Hatteras) USNM; Duplin County (Wallace) UCR; Haywood County (Crestmont) UMAH; (Mount Sterling) CUNY; Robeson County (Boardman) USNM; Wake County (Raleigh) UCR, UNCR; County unknown (Beauford) MCZ. OHIO: Clinton County (No locality given) OUCO; Hamilton County (Cincinnati) UMAH; Scioto County (No locality given) OUCO. OKLAHOMA: Alfalfa County (No locality given) OSUS; Choctaw County (No locality given) OSUS, UONO; Cleveland County OUCO, UONO, (Norman) CAS; Dewey County (Seiling) OSUS; Le Flore County (Poteau) OSUS; McCurtain County RCGr, (Eagletown) OSUS, (Idabel) OSUS; Mizes County (No locality given) UONO; Nowata County (13.0 miles west of Vinita) RFre, UASM; Oklahoma County (Oklahoma) CEWh; Tillman County (No locality given) CAS; Tulsa County (Collinsville) CAS. PENNSYLVANIA: Allegheny County (Pittsburgh) CMPP. SOUTH CAROLINA: Florence County (Scranton) UMAH; Jasper County (Savannah River Refuge) UASM; Oconee County (Clemson) UASM; Sumter County (Poinsett State Park) VMKI. TENNESSEE: Knox County (Knoxville) MCZ; Morgan County (Sunbright) CMPP; Obion County (Reelfoot Lake) UMAH; Overton County (Cleeks Mill) TCBA; Putnam County (Cookeville) TCBA; Sevier County (Great Smoky Mountains National Park) CMPP; Smith County (Peyton Creek) TCBA. TEXAS: Brazos County (bottoms) ISNH, (College Station) MCZ, TAMU; Cameron County (Brownsville) OUCO, (Brownsville, Esperanza Ranch) USNM; Colorado County (Columbus) MCZ, UMSP; Dallas County CAS, ISNH, (Dallas) CMPP, MCZ; Dimmit County (Corrizo Springs) ISUA; El Paso County (El Paso) CMPP; Grayson County (Juniper Point, Lake Texoma, 12.0 miles north of Whitesboro) RCGr; Harris County (Houston) UCD, (Seabrook) CAS; Hunt County (Commerce) OUCO; Jeff Davis County (Davis Mountains) OUCO; Kendall County (Comfort) CMPP; Liberty County (Devers) UMAH; Rannels County (Ballinger) USNM; Travis County (S. F. Austin State Park) CNHM; Victoria County (Victoria) USNM; County unknown (Fuller) USNM. VIRGINIA: Alexandria County (No locality given) USNM; Fairfax County (Mount Vernon) USNM; Nansemond County (Cypress Chapel) ISUA; Norfolk County (Dismal Swamp) AMNH, CAS, USNM; Spotsylvania County (Fredericksburg) CAS. WEST VIRGINIA: Berkeley County (Leetown) RTBe; Greenbrier County (White Sulphur Springs) MCZ.

Brachinus viridipennis Dejean

(Figs. 179, 183, 184, 185, 193, 199)

Brachinus viridipennis Dejean, 1831: 426. Lectotype, here selected, a female, MHNP, labelled "v. viridipennis m. in Amer. bor.", "LeConte" on green paper, and "Ex Museo Chaudoir" on white paper. *Type locality*. — "l'Amerique septentrionale" as originally given by Dejean, but herewith restricted to Mobile, Alabama.

Brachinus viridis LeConte, 1844: 49. Lectotype, here selected, a male, MCZ red type label number 5840. Further labelled with a gold disc and "85." *Type locality*. — Georgia, as originally given by LeConte. LeConte 1862: 524.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Large-sized beetles, 8.9 to 15.0 mm.

Color. Antennal article 4, sides of mesosternum and metasternum, mesepisterna, metepisterna, and abdominal sterna and terga infuscated. Dorsal surface and epipleura of elytra greenish to bluish.

Microsculpture. As described for genus.

Macrosculpture. As in *alternans*.

Head. As in *alternans*.

Prothorax. As in *alternans*, except anterior tibia with anterior edge punctate, with punctures occasionally forming elongate grooves, but not strigae.

Pterothorax. Elytra elongate, narrow, weakly costate. Humeral angle sloped. Metasternum short, its length behind middle coxa less than diameter of middle coxa (fig. 26). Wings reduced outside stigma.

Abdomen. As described for genus.

Genitalia. Male (figs. 183, 184, 185). Median lobe with plane of shaft rotated slightly from plane of basal bend. Basal bend short. Median lobe straight, swollen medially, apex narrow, elongate. Ligule long, narrow, slightly widened at apex. Virga (figs. 183, 184). Female (fig. 193). Stylus long, narrow, arcuate, narrowly rounded apically.

Variation. — Besides the intrapopulational variation in body size and shape of the pronotum, these beetles may have greenish or bluish colored elytra. Those with bluish elytra are few and occur among the greenish populations.

Flight. — The flight of these beetles has never been recorded, and it is probable that they cannot fly.

Etymology. — Latin, *viridis*, green; *pennis*, wing; referring to the greenish elytra of these beetles.

Life history. — Members of this species have been collected in all months, except January, May, and August, but no general adults were seen.

Distribution. — (Fig. 199). The range of this species extends from eastern Texas to Florida. I have seen 81 specimens from the following localities:

UNITED STATES

ALABAMA: Clay County (Ashland) AUAA; Mobile County (Alabama Port) CAS, (Coden) AMNH, (Mobile) ANSP, CAS, CUNY, OUCO, UASM, UMAH, USNM. ARKANSAS: Hempstead County (Hope) MCZ. FLORIDA: Baker County (Glen Saint Mary) FDAG; Duval County (Jacksonville) MCZ, USNM. GEORGIA: Chatham County (Savannah) CAS; County unknown (Fort Stewart) TLEr. SOUTH CAROLINA: Beaufort County (Hardeeville) UMAH. TEXAS: Colorado County (Rock Island, Skull Creek) UMSP.

The *rugipennis* subgroup

This subgroup is characterized by the wide ligule of the male genitalia, absence of accessory setae, and narrow prothorax. One species, *B. rugipennis* Chaudoir, is included.

Brachinus rugipennis Chaudoir

(Figs. 171, 180, 181, 182, 192, 200)

Brachynus rugipennis Chaudoir, 1868: 297. Lectotype, here selected, a female, MHNP, labelled "Etas Unis Guex" in the box and "Ex Museo Chaudoir" on the specimen *Type locality*. — United States, as given originally by Chaudoir's label, but herewith restricted to Texas.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Small to medium-sized beetles, 7.1 to 9.4 mm.

Color. Antennal articles 3 and 4, abdominal terga, and sides of abdominal sterna infuscated, the latter two usually very dark. Remainder of abdominal sterna and usually some of metepisterna lightly infuscated, otherwise ferrugineous. Dorsal surface and epipleura of elytra blue.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows and surface of pronotum punctate, punctures shallowly impressed.

Head. Frontal furrows shallowly impressed. Antennal scape narrow, almost cylindrical. Ligula as in *alternans*. Mentum and submentum without accessory setae.

Prothorax. Pronotum (fig. 171) slightly convex, flattened along center line, sides narrowly

reflexed. Surface with punctures moderately impressed. Proepipleura and proepisterna pubescent anteriorly and posteriorly, glabrous medially. Anterior tibia with anterior surface strigose.

Pterothorax. Elytra elongate, narrow, weakly costate. Humeral angle slightly sloped. Costae rugose, as well as depressions between costae.

Abdomen. As described for genus.

Genitalia. Male (figs. 180, 181, 182). Median lobe with plane of shaft slightly rotated from plane of basal bend. Basal bend moderately long. Median lobe arcuate, broadened to apex, and with apex broadly rounded. Ligule short, widened apically, truncate. Virga (figs. 180, 181). Female (fig. 192). Stylus short, narrow, parallel-sided, narrowly rounded apically.

Variation. — This species is rather constant throughout its range, even in body size.

Flight. — These beetles have been collected repeatedly at lights throughout the range of the species.

Etymology. — Latin, *ruga*, wrinkle or fold; *pennis*, wing; referring to the rugose costae.

Collecting notes. — C. Armin collected these beetles along margins of lakes and irrigation ditches, and at the edges of small streams in Colorado.

Life history. — Members of this species have been collected from December to July, and in October. Teneral adults have been collected in March and December in Florida, and in October in Massachusetts.

Distribution. — (Fig. 200). The range of this species extends from western Colorado to Massachusetts, and south to Florida. There appears to be discontinuity between the New England populations and the Floridian one, and between these populations and those west of the Mississippi. I have seen 327 specimens from the following localities:

UNITED STATES

ARKANSAS: Garland County (Hot Springs National Park) SJSC; Hempstead County (Hope) CUNY, MCZ, UMAH; Pike County (Delight) CMPP; Washington County (No locality given) UAFA; White County (Searcy) UWSW. COLORADO: Boulder County (El Dorado Springs) CARM, (Teller Lake) CARM; Montrose County (Montrose) MCZ. FLORIDA: Alachua County (Gainesville) UMAH; Brevard County (Eau Gallie) MCZ, (Indian River) USNM; Charlotte County (Charlotte Harbor) AMNH, (Punta Gorda) AMNH, UMAH; Collier County (Collier Seminole State Park) TLER, (Naples) CUNY; Dade County (Royal Palm State Park) PUM; Hendry County (La Belle) OUCO; Highlands County (Archbold Biology Station) CUNY, PSUU, (Childs) RCGr, (Lake Placid) AMNH; Hillsborough County (Tampa) USNM; Lee County (Fort Myers) CNC; Lake County USNM, (Fruitland Park) UMAH; Manatee County (Bradenton) CAS, (Oneco) UASM; Marion County MCZ (Silver Springs) CAS; Orange County (Orlando) MCZ, (Pinecastle) FDAG, (Winter Park) MCZ; Osceola County (Kissimmee) AMNH; Pinellas County (Dunedin) CAS, PUM, TAMU, (Tarpon Springs) CNC; Sarasota County (Englewood) AMNH, (Sarasota) PUM; Taylor County (Steinhatchee) USNM; Volusia County (Enterprise) CAS, USNM; Counties unknown (Port Sewall) AMNH, (Suwannee River) CAS. GEORGIA: Lowndes County (Valdosta) UMAH. KANSAS: Stafford County (Salt Flats Area) UASM. MASSACHUSETTS: Hampden County (Chicopee) KSU, MCZ, (Wilbraham) MCZ; Plymouth County (Plymouth) AUA. OKLAHOMA: Marshall County (Lake Texoma, Willis) RCGr, (Madill) RCGr. NEBRASKA: Cherry County (Hackberry Lake) UNLN. NEW JERSEY: Cape May County (Seven Mile Beach) OUCO; Mercer County (Trenton) CAS; Warren County (Phillipsburg) CAS; County unknown (Anglesea) CAS. NEW MEXICO: Bernalillo County (Albuquerque) ANSP, CAS, MCZ, USNM; Sandoval County (Los Alamos) CNC; Taos County (Rio Grande River, near Taos) CAS. PENNSYLVANIA: Montgomery County (Arcola) ANSP; Montour County (Danville) CAS; Northampton County (Easton) CAS, (Watergap) AMNH, USNM. TENNESSEE: Lake County (Parnell Point) RTBe. TEXAS: Anderson County (Elkhart) TAMU; Blanco County (2.0 miles south of Round Mountain) UASM; Brazos County (College Station) MCZ, TAMU; Dallas County (Dallas) MCZ, UASM; Deaf Smith County (Hereford) TAMU; Montgomery County (Willis) USNM; Nueces County (Corpus Christi) MCZ; County unknown (Bathage) CAS. VIRGINIA: (No locality given) UMSP. WYOMING: (western Wyoming) USNM.

The *hirsutus* group

The members of this group are characterized by the form of the virga, compressed median lobe with a ventral sulcus, lack of lateral pronotal setae, and strongly costate elytra. Two species, *B. hirsutus* Bates and *B. pallidus* Erwin, are included.

Brachinus hirsutus Bates

(Figs. 205, 212, 213, 214, 220, 224)

Brachinus hirsutus Bates, 1884: 295. Lectotype, here selected, a male, BMNH, labelled "Pinos Altos, Chihuahua, Mexico, Buchan-Hepburn," "B. C. A. Col. I. l. *Brachinus hirsutus* Bates," "Type, H. T." and "*Brachinus hirsutus* Bates" (handwritten). *Type locality*. — Pinos Altos, Chihuahua, as originally given by Bates.

Brachinus puncticollis LeConte, 1858: 28. NOMEN NUDUM. Erwin, 1965: 13.

Notes. — In 1965 I wrongly placed *B. puncticollis* as a synonym of *B. tschernikhi* Mannerheim. After seeing LeConte's specimen, I now place the name here.

Diagnostic combination. — The densely pubescent cordiform pronotum, together with the strongly costate elytra, lack of lateral pronotal setae, and pale venter, separates members of this species from any others in the American Southwest and Mexico.

Description. — Medium-sized beetles, 7.6 to 10.3 mm.

Color. Ferruginous, sides of abdomen usually slightly infuscated. Dorsal surface and epipleura of elytra blue.

Microsculpture. As described for genus.

Macrosulpture. Frontal furrows, head behind eyes, and surface of pronotum densely punctate and rugose. Punctures moderately impressed.

Head. Frontal furrows moderately impressed. Antennal scape robust, widest at middle. Ligula with sclerotized center area ellipsoid-convex with two lateral rows of three setae per row. Mentum and submentum with accessory setae.

Prothorax. Pronotum (fig. 205) slightly convex, flattened along center line, sides moderately reflexed. Lateral setae absent. Proepipleura and proepisterna totally pubescent. Anterior tibia with anterior surface strigose.

Pterothorax. Elytra moderately long, narrow, strongly costate. Humeral angle square. Costae smooth, glabrous, depressions pubescent. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 212, 213, 214). Median lobe with plane of shaft rotated slightly from plane of basal bend. Basal bend long. Median lobe nearly straight, swollen just before compressed shaft. Apex of shaft narrow and acute, ventral surface sulcate. Ligule short, narrow, truncate. Virga (figs. 212, 213). Female (fig. 224). Stylus short, parallel-sided, rounded apically.

Variation. — The shape of the pronotum is much more constant in the members of this species than in other North and Middle American species. Intrapopulation variation occurs in the total size and in the color of the elytra (blue to bluish green).

Flight. — The flight of these beetles has been recorded by G. R. Noonan in Upper Sabino Canyon, Arizona.

Etymology. — Latin, *hirsutus*, hair; referring to the dense pubescence of the pronotum of these beetles.

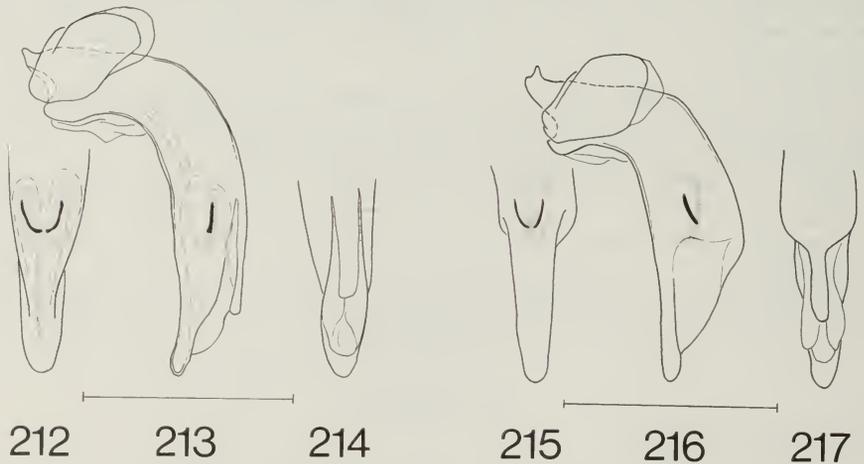
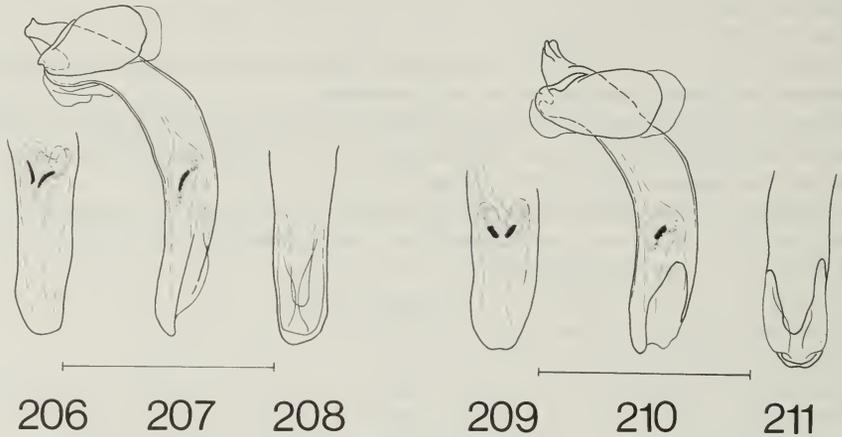
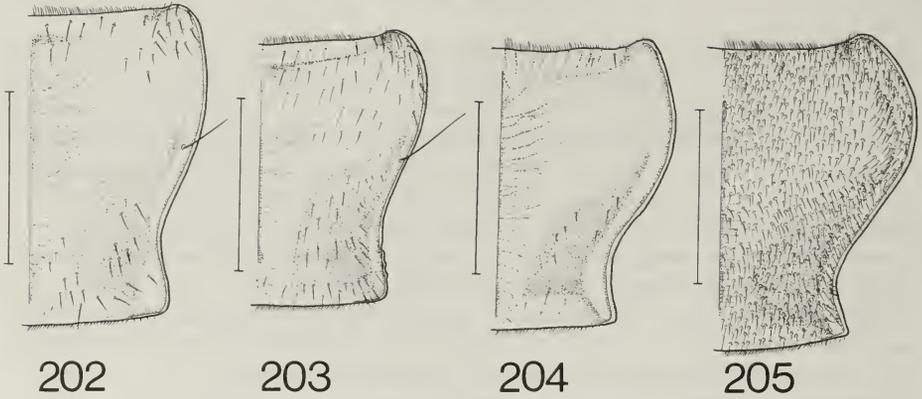
Collecting notes. — G. E. Ball and I collected these beetles in coarse gravel at the edges of an intermittent stream near El Banco, Durango, Mexico.

Life history. — Members of this species have been collected in all months of the year except February and November. Many teneral adults have been collected in June and July in Arizona, and in January in Jalisco, Mexico. The life cycle is probably much the same as in *B. pallidus* (Erwin, 1967).

Distribution. — (Fig. 220). The range of this species extends from southern Utah to the Mexican High Plateau. I have seen 456 specimens from the following localities:

MEXICO

DURANGO: (12.2 miles south of El Banco) UASM; (Nombre de Dios) AMNH; (Rio Chico, 15.7 miles west of Durango) UASM; (Rio Florido, near Las Nieves) UASM; (Rio Nazas, near Rodeo) UASM. HIDALGO: (Rio Tula, near Tasquillo) UASM. JALISCO (0.4 miles west of Coculo) UASM. SAN LUIS POTOSI: (Puente La Parada, 7.5 miles northwest of Mex-



Figs. 202-205. Pronotum, right half, dorsal aspect. 202. *Brachinus cibolensis* new species, near Paradise, Arizona. 203. *Brachinus cinctipennis* Chevrolat, 13.0 miles southeast of Lagos de Moreno, Jalisco, Mexico. 204. *Brachinus pallidus* Erwin, Kings Canyon, California. 205. *Brachinus hirsutus* Bates, Sonoyta, Sonora, Mexico. Figs. 206-217. Male genitalia. 206. *Brachinus cinctipennis* Chevrolat, 23.0 miles, southeast of Lagos de Moreno, Jalisco, Mexico, ventral aspect. 207 & 208. Lateral & dorsal aspects of same. 209. *Brachinus cibolensis* new species, Douglas, Arizona, ventral aspect. 210 & 211. Lateral & dorsal aspects of same. 212. *Brachinus hirsutus* Bates, Sonoyta, Sonora, Mexico, ventral aspect. 213 & 214. Lateral & dorsal aspects of same. 215. *Brachinus pallidus* Erwin, Kings Canyon, California, ventral aspect. 216 & 217. Lateral & dorsal aspects of same. Accompanying scale lines equal 1.0 mm.

quitic) UASM; (2.7 miles west of Santa Catarina) UASM. SONORA: (10.0 miles south of Alamos) UCD; (Sonoyta) AMNH. ZACATECAS: (Rio Juchipila, 0.9 miles north of Jalpa) UASM; (1.3 miles southeast of Sain Alto) UASM.

UNITED STATES

ARIZONA: Cochise County (Chiricahua Mountains) USNM, (14.0 miles northeast of Douglas) UCR, (Bear Creek, Montezuma Pass, Huachuca Mountains) CNC, (Portal) RCGr, (San Pedro River, east of Sierra Vista) UATA, (San Pedro River, 10.0 miles east of Sierra Vista) OSUC, (Tombstone) SDNHM; Coconino County (Bill Williams Fork) MCZ, (Grand Canyon, mile 116.5) UATA; Gila County (East Verde River, 6.0 miles north of Payson) LACM, (Globe) KSU, (Payson) UATA, (Sierra Ancha Mountains) UMAH; Graham County (Aravaipa Creek, between Klondyke and Aravaipa) DRWh, (San Carlos Reservoir) UATA; Maricopa County (Phoenix) CNHM, MCZ, OUCO, UATA, (Wickenburg) RCGr; Mohave County (Beaver Dam) LACM, (16.0 miles north of Wikieup) LACM; Pima County (Cienega Creek, Pantano) CUNY, (Organ Pipe Cactus National Monument, Quito Baquito) GRNo, (Redington) UATA, (Sabino Canyon) AMNH, (Upper Sabino Canyon) GRNo, (Saint Xavier Mountains) CAS, (Santa Catalina Mountains) CAS, USNM, (Santa Catalina Mountains, Bear Canyon) CAS, UATA, (Tucson) AMNH, CAS, CUNY, MCZ, UMAH, USNM; Pinal County (Aravaipa) CUNY, (Sycamore Camp, 9.0 miles northwest of Payson) CAS, (Near Sombrero Butte) USNM; Santa Cruz County (Bear Canyon Bridge, Lochiel-Bisbee Road) CAS, (Canelo Hills) UATA, (Nogales) CAS, USNM, (Patagonia) CNHM, CUNY, UATA, UCD, UCR, (Peña Blanca Lake, 16.0 miles northwest of Nogales) OSUC, (Santa Cruz River, near Nogales) CAS, (Yanks Spring, 4.0 miles southeast of Ruby) AMNH; Yavapai County AMNH (Bumble Bee) CAS, (Camp Verde) CAS, PSUU, (29.0 miles northwest of Congress) UATA, (Mayer) GRNo, (Prescott) CAS; Counties unknown (Hot Springs) CAS, (Palmerlee) CMPP, (Superstition Mountains) UATA. NEW MEXICO: Catron County (Glenwood) DRWh, (San Francisco Creek, 26.1 miles north of Glenwood) UASM; Grant County (near Gila) UASM. TEXAS: Jeff Davis County (Davis Mountains) CAS, UCD, USNM, (Fort Davis) AMNH, CNC, (6-10.0 miles west of Fort Davis) UASM, (Limpia Canyon) CNHM, DRWh, TLEr, SJSC, UASM; Reeves County (Balmorhea Lake) UASM; Presidio County (Presidio) TAMU. UTAH: Washington County (3.0 miles south of Gunlock) GRNo, (Saint George) USNM, (Santa Clara) UWSW.

Brachinus pallidus Erwin

(Figs. 204, 215, 216, 217, 218, 222)

Brachinus pallidus Erwin, 1965: 8. The holotype male and allotype female are in CAS.

Type locality. — Mad River, 5.0 miles east of Mad River Post Office, Trinity County, California.

Diagnostic combination — The diagnostic characteristics are given in the key.

Description. — Medium-sized beetles, 7.5 to 9.3 mm.

Color. As in *hirsutus*.

Microsculpture. As described for genus.

Macrosculpture. Head as in *hirsutus*, pronotum not as densely punctate.

Head. As in *hirsutus*, but ligula without constant setae.

Prothorax. As in *hirsutus*, but less densely setiferous. Pronotum (fig. 204).

Pterothorax. As in *hirsutus*, but only elytral depressions 6, 7, and 8 pubescent, except in apical third.

Abdomen. As described for genus.

Genitalia. Male (figs. 215, 216, 217). As in *hirsutus*, except more compressed and without ventral sulcus. Virga (figs. 215, 216). Female (fig. 222). Stylus straighter than in *hirsutus*, more acute apically.

Variation. — The members of this species vary within local populations in body size and the shape of the pronotum. Otherwise, they are quite constant throughout the range of the species.

Flight. — I have watched these beetles fly in captivity.

Etymology. — Latin, *pallidus*, pale; referring to the pale venter of these beetles.

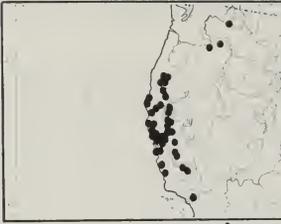
Collecting notes. — These beetles occur along intermittent streams and permanent rivers in coarse gravel.

Life history. — See p. 166 and Erwin 1967.

Distribution. — (Fig. 218). The range of this species extends from Los Angeles County in southern California north to eastern Washington. I have seen 835 specimens from the following localities:

UNITED STATES

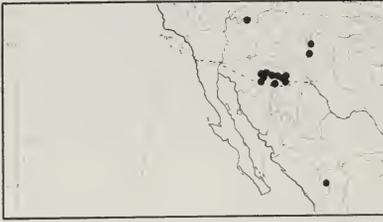
CALIFORNIA: Alameda County (Alameda Creek) CAS, (Arroyo Mocho) TLEr, (Berkeley) CUNY, (Livermore) CAS, (Los Moches Canyon, Livermore hills) CEWh, (Niles Canyon) ANSP, CAS, SDNHM, UASM, (Sunol) CAS; Amador County



218



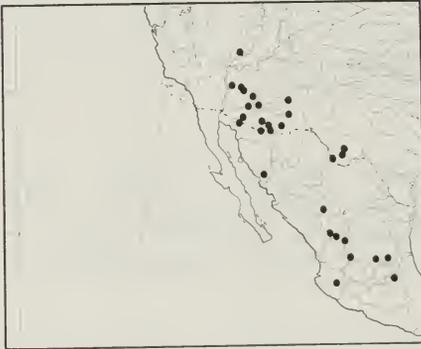
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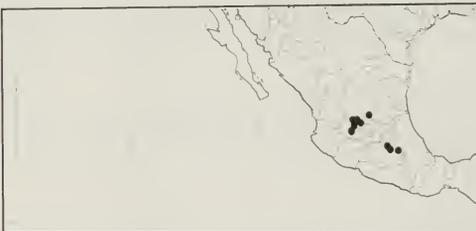
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224



221



225



Figs. 218-221. Geographical distribution maps. 218. *Brachinus pallidus* Erwin. 219. *Brachinus cibolensis* new species. 220. *Brachinus hirsutus* Bates. 221. *Brachinus cincitipennis* Chevrolat. Figs. 222-225. Right stylus of female ovipositor, ventral aspect. 222. *Brachinus pallidus* Erwin, Kings Canyon, California. 223. *Brachinus cibolensis* new species, near Paradise, Arizona. 224. *Brachinus hirsutus* Bates, Rio Chico, Durango, Mexico. 225. *Brachinus cincitipennis* Chevrolat, 13.0 miles southeast of Lagos de Moreno, Jalisco, Mexico. Accompanying scale line equals 1.0 mm.

(5.0 miles west of Sutter Creek on Horse Creek) TLER; Butte County (Oroville) CAS; Calaveras County (Mokelumne Hill) CAS, USNM; Contra Costa County (Marsh Creek) TLER; Fresno County (Camp Greeley) CAS, (Kings Canyon) CAS, (La Fevre Creek) ANSP, UASM; Glenn County (Elk Creek) CAS; Humboldt County AMNH, (6.0 miles east of Bridgeville) GRNo, (Eel River, Fernbridge) UASM, (Fort Seward) CAS, UIMI, (Garberville) CAS, UIMI, (5.0 miles south of Garberville) TLER, (Schively) UCD; Lake County (Lower Lake) CAS, (Middletown) CAS, JSch, UIMI, (North Fork Cache Creek, Highway 20) UCD, (Putah Creek) CAS; Los Angeles County USNM, (Los Angeles) CNHM; Madera County (Coursegold) CAS, UIMI; Marin County USNM, (Fairfax) CUNY, (Point Reyes) CAS, UCD; Mariposa County (Jolon) CAS, (3.0 miles southeast of Jolon) CAS; Mendocino County CNHM, (Eel River) CAS, (Long Valley Creek, 6.7 miles south of Laytonville) CAS, UWSW; Merced County (Merced Falls) UCD; Napa County CMPP, (Monticello) UCD, (Pope Valley) CAS, (Rutherford) TLER, (Saint Helena) AMNH, ROM, (Saint Helena Creek) CAS, (10.0 miles east of Shell Peak) CAS; Placer County (Auburn) UCD; Sacramento County (Folsom) JSch; San Joaquin County (No locality given) SJSC; San Luis Obispo County (Atascadero) CAS, (Nacimiento River, Camp Roberts) PSUU, (Paso Robles Creek) CAS; Santa Clara County CNHM, (Arroyo Bayo) SJSC, (Gilroy Hot Springs) TLER, (Hecker Pass) CAS, (Isabel Creek) TLER, (Los Gatos) CAS, (Morgan Hill) SJSC, (Mount Hamilton) CAS, JSch, (San Jose) CAS, (Santa Clara) CAS, (Uvas Creek) TLER; Santa Cruz County (Santa Cruz) USNM; Shasta County CNHM, (Anderson) CAS, (Redding) CAS, VVba; Siskiyou County (Klamath River) USNM, (10.0 miles west of Montague) JSch, (south of Shasta River) CAS, (Yreka) AMNH; Sonoma County UNHM, (Cloverdale) CUNY, (Del Puerto Creek) TLER, (Dry Creek, 9.0 miles northwest of Healdsburg) SJSC, (Guerneville) CAS, (2.0 miles east of Healdsburg) CAS, (Rio Nido) CAS, (Santa Rosa) CUNY, MCZ, OUCO; Tehama County (Red Bluff) CAS; Trinity County CMPP, (Mad River) TLER, (0.7 miles northwest of Ruth Dam) GRNo, (Weaverville) UWSW; Yolo County (Davis) CBak, UCD; Counties unknown (Aliso) UWSW, (Latrobe) CAS, (San Antonio Mission) CUNY, (Sylvania) CAS. OREGON: Douglas County (North Umqua River, near Winchester) JSch, (7.0 miles northwest of Roseburg) JSch, (Winchester) JSch; Jackson County (Eagle Point) CAS, (Medford) CAS, UCD, (8-14.0 miles south of Ruch) JSch, (10.0 miles south of Ruch) JSch, (Talent) UCD, (Trail) JSch, LRus; Josephine County (Applegate River) OSUC, (Illinois River) JSch, (Selma) JSch; Umatilla County (Umatilla) MCZ. WASHINGTON: Spokane County (Spokane Falls) MCZ; Walla Walla County (Walla Walla) OSUC.

The *fumans* group

This group is characterized by the virga, the sides of which are curled over ventrally from base to apex, forming a central trough. The diversity of this group warrants its division into twelve subgroups.

The *cinctipennis* subgroup

The members of this subgroup are characterized by an elytral ferruginous sutural stripe and a long narrow median lobe. Two species, *B. cinctipennis* Chevrolat and *B. cibolensis* new species, are included.

Brachinus cinctipennis Chevrolat

(Figs. 203, 206, 207, 208, 221, 225)

Brachinus cinctipennis Chevrolat, 1835: 163. Lectotype, here selected, a male, HMO, Type number Col. 113 1/3, further labelled "Brachinus cinctipennis Chev. Col de M. Z cent no 163 Mexico plaine de Mexico Aout sous des pierres Sallé 59." *Type locality*. — The high-plain of Mexico, as originally given by Chevrolat, but herewith restricted to the State of Mexico, Mexico.

Diagnostic combination. — The ferruginous sutural stripe on the elytra, together with the pale palpi, and extensively pale legs, separate these beetles from all others of the genus.

Description. — Medium-sized beetles, 6.6 to 9.4 mm.

Color. Antennal articles 3-11, apex of femur, mesepisterna, metepisterna, metasternum at sides, and abdominal sterna and terga infuscated, otherwise ferruginous. Dorsal surface of elytra greenish-blue with ferruginous sutural stripe, epipleura testaceous.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows and surface of pronotum slightly rugose and punctate, punctures barely impressed.

Head. Frontal furrows moderately impressed. Antennal scape cylindrical. Ligula with sclerotized center area ellipsoid-convex with two lateral rows of three setae per row.

Prothorax. Pronotum (fig. 203) convex, sides barely reflexed. Proepipleura glabrous. Proepisterna with a few scattered setae both anteriorly and posteriorly. Anterior tibia with anterior surface strigose.

Pterothorax. Elytra elongate, narrow, barely costate. Humeral angle square. Costae and depressions pubescent. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 206, 207, 208). Median lobe with plane of shaft rotated 45° from plane of basal bend. Basal bend long. Apex of shaft narrow, rounded. Ligule short, narrow, narrowly rounded apically. Virga (figs. 206, 207). Female (fig. 225). Stylus short, broad, narrowly rounded apically.

Variation. — Intrapopulational variation occurs in the following characteristics: presence or absence of accessory setae on the submentum; number of setae on the ligula; extent of infuscation on the tibia; width of the sutural stripe; and the color of the elytra.

Flight. — The flight of these beetles has not been recorded.

Etymology. — Latin, *cinctus*, belt; *pennis*, wing; referring to the broad, sutural stripe on the elytra of these beetles.

Collecting notes. — G. E. Ball and I collected these beetles from beneath stones at the edge of an artificial pond in Jalisco, Mexico.

Life history. — Members of this species have been collected in April, June to September, November, and December. Teneral adults were collected in April in Puebla, Mexico.

Distribution. — (Fig. 221). The range of this species extends from San Luis Potosi to Puebla. I have seen 105 specimens from the following localities:

MEXICO

AGUASCALIENTES: (Aguascalientes) AMNH; (El Rotono, 10.0 miles east of Aguascalientes) AMNH. DISTRITO FEDERAL: CPBo, (Mexico City) AMNH, BMNH, CUNY, TMBH. JALISCO: (Encarnacion de Diaz) UASM; (5.0 miles west of Lagos) UATA; (13.0 miles southeast of Lagos de Moreno) USNM; (12.0 miles west of Ojuelos) CAS. MEXICO: (Lago Zumpango, near San Juan Zitlaltepec) UASM. PUEBLA: (Lago Totolcingo, near Tlaxcala line) UASM. SAN LUIS POTOSI: (San Luis Potosi) AMNH. STATE UNKNOWN: (Presa de Angulo) JHen.

Brachinus cibolensis new species

(Figs. 202, 209, 210, 211, 219, 223)

Type locality. — Five miles west of Portal, Southwest Research Station, 5,400 feet, Cochise County, Arizona.

Type specimens. — The holotype male and allotype female are in the entomological museum at AMNH. The holotype was collected by E. Ordway, and the allotype was collected by M. Statham at the type locality on July 27, 1956 and May 8, 1958, respectively. Twenty-five paratypes collected in various localities on various dates are in AMNH, CAS, MCZ, TLEr, and UASM.

Diagnostic combination. — The ferruginous sutural stripe on the elytra, together with the entirely black legs and palpi, separate these beetles from all others in Mexico and United States.

Description. — Medium-sized beetles, 7.5 to 9.8 mm.

Color. Palpi, antennal articles 2-11, metepisterna, metasternum at sides, legs, and abdominal terga and sterna infuscated to black. Dorsal surface of elytra blue with ferruginous sutural stripe, epipleura testaceous.

Microsculpture. As described for genus.

Macrosculpture. As in *cinctipennis*.

Head. As in *cinctipennis*.

Prothorax. As in *cinctipennis*. Pronotum (fig. 202).

Pterothorax. As in *cinctipennis*.

Abdomen. As described for genus.

Genitalia. Male (figs. 209, 210, 211). Median lobe with plane of shaft rotated 45° from plane of basal bend. Basal bend long. Shaft long and narrow, apex rounded, slightly notched. Ligule short, tapering to narrowly rounded apex. Virga (figs. 209, 210). Female (fig. 223).

Stylus short, broad, tapering to narrowly rounded apex.

Variation. — Intrapopulational variation occurs in the shape of the pronotum, width of the sutural stripe on the elytra, and in the color of the elytra and antennal articles 2-11.

Flight. — These beetles have been collected at lights at Douglas, Arizona, Lordsburg, New Mexico, and Durango City, Mexico.

Etymology. — Cibola, from the legendary Seven Cities of Cibola that Coronado searched for in the American Southwest; Latin, *ensis*, denoting place, locality, or country.

Collecting notes. — G. E. Ball collected these beetles from under stones at the margin of a dirt water tank in the Chiricahua Mountains of Arizona.

Life history. — Members of this species have been collected from June to September, but no teneral adults were seen.

Distribution. — (Fig. 219). The range of this species extends from northern Arizona to Durango City, Mexico. I have seen 78 specimens from the following localities:

MEXICO

DURANGO: (Durango) AMNH, UASM; (15.0 miles west of Durango) CNC.

UNITED STATES

ARIZONA: Cochise County (Benson) UATA, (Douglas) CUNY, UASM, UCR, (near Paradise) UASM, (Portal) GRNo, (San Bernardino Ranch) ZMLS, (South West Research Station, 5.0 miles west of Portal) AMNH, UCD, (Tombstone) SDNHM, (Willcox) AMNH, UATA; Coconino County (Bill Williams Fork) AMNH; Santa Cruz County (Nogales) CAS, CNHM, UCR. NEW MEXICO: Bernalillo County (Albuquerque) CMPP, USNM; Hidalgo County (Animas) AMNH, (Lordsburg) CNC, UCR, (Rodeo) CUNY, UCD; Socorro County (Socorro) CAS.

The *quadripennis* subgroup

The members of this subgroup are characterized by the presence of a ridge on the ventral surface of the male genitalia. Five species, *B. quadripennis* Dejean, *B. mexicanus* Dejean, *B. neglectus* LeConte, *B. javalinopsis* new species, and *B. kavanaughi* Erwin, are included.

Brachinus quadripennis Dejean

(Figs. 230, 240, 241, 242, 247, 251)

Brachinus quadripennis Dejean, 1825: 316. Lectotype, here selected, a female, MHNP, labelled "quadripennis m. in Amer. bor." and "Lherminier" on green paper, and "Ex Museo Chaudoir" on white paper. *Type locality.* — North America, as originally given by Dejean, but herewith restricted to Florida.

Brachinus stygicornis Say, 1834: 415. Neotype designated by me, a male, in MCZ. *Type locality.* — South Bend, Nebraska. NEW SYNONYMY.

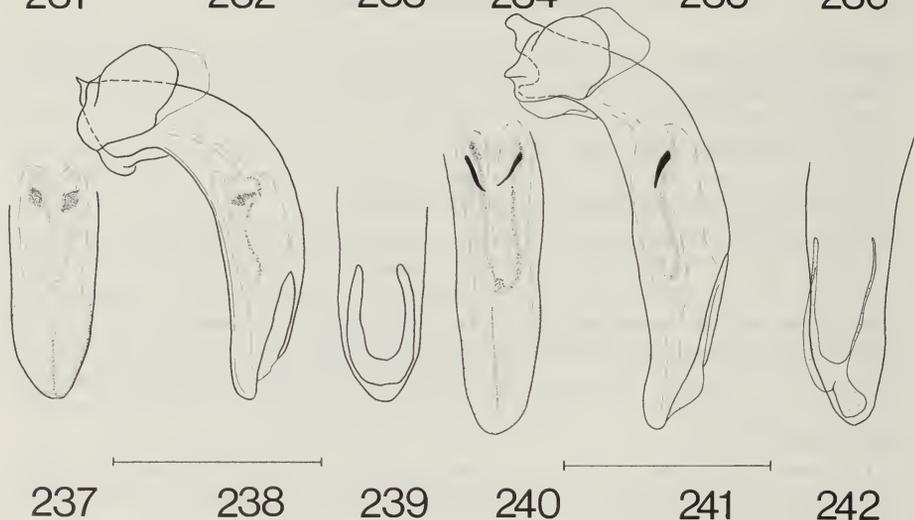
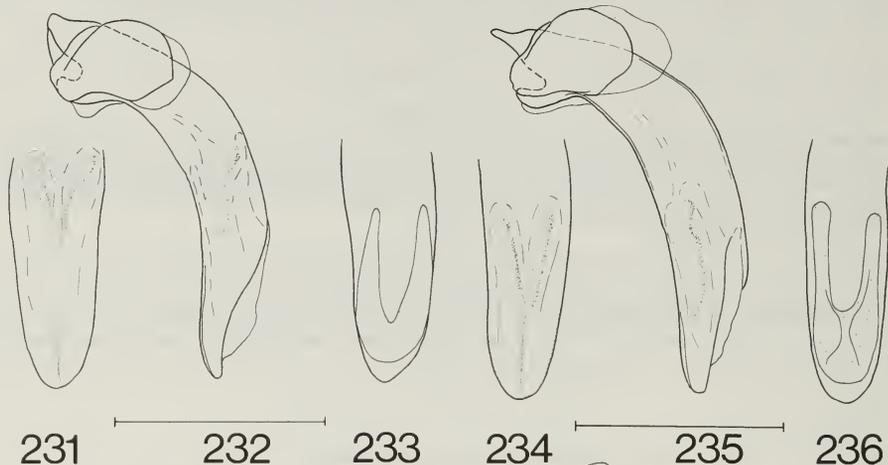
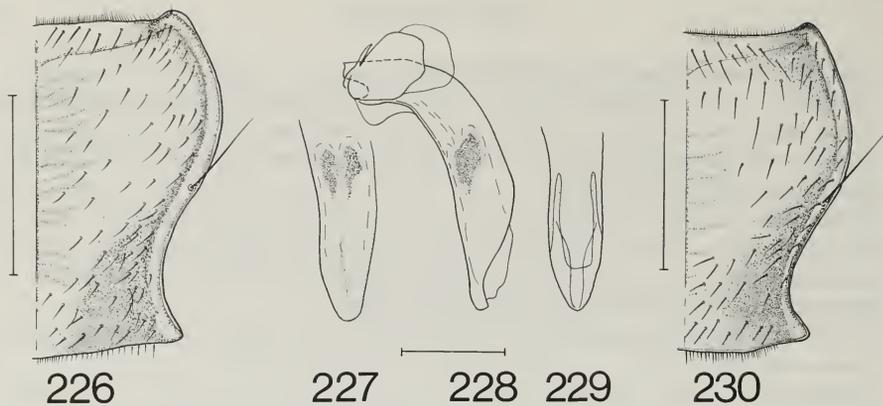
Brachinus tschernikhi Mannerheim, 1843: 184. Types presumed lost (see Erwin, 1965: 13).

Type locality. — California, as originally given by Mannerheim. NEW SYNONYMY.

Notes. — The neotype designated by Lindroth for *B. stygicornis* was selected by me from the Nebraska University material I had on loan, and sent to Lindroth. He subsequently deposited all Say's neotypes in MCZ. The specimen was labelled "South Bend, Neb." "5/8/09" and "R. W. Dawson Collection." This locality is the nearest to Say's original area from which we had specimens. The original area was "crevices of rocks ... Engineer Cantonment, near Council Bluff."

The name *B. sejungenius* Chaudoir is found on some of Chaudoir's specimens in MHNP. This name was never published, and is therefore not really in existence, but I add this note to prevent confusion in the future.

Diagnostic combination. — The diagnostic characters are given in the key, but in most cases the infuscated tarsi and tibiae will separate these beetles from all others of the genus in the United States, except individuals of *B. phaeocerus* and *B. azureipennis*. The members of *phaeocerus* are smaller and have bright blue elytra, while the members of *azureipennis* are



Figs. 226, 230. Pronotum, right half, dorsal aspect. 226. *Brachinus kavanaughi* Erwin, Superior, Colorado. 230. *Brachinus quadripennis* Dejean, Archbold Research Station, Florida. Figs. 227-229, 231-242. Male genitalia. 227. *Brachinus quadripennis* Dejean, Archbold Research Station, Florida. 228. Lateral aspect of same. 229. Dorsal aspect of same. 231. *Brachinus kavanaughi* Erwin, 6.9 miles north of Golden, Colorado, ventral aspect. 232. Lateral aspect of same. 233. Dorsal aspect of same. 234. *Brachinus mexicanus* Dejean, 0.9 miles northeast of Cedar Springs, California, ventral aspect. 235. Lateral aspect of same. 236. Dorsal aspect of same. 237. *Brachinus neglectus* LeConte, Guntown, Florida, ventral aspect. 238. Lateral aspect of same. 239. Dorsal aspect of same. 240. *Brachinus quadripennis* Dejean, Grand Coulee, Washington, ventral aspect. 241. Lateral aspect of same. 242. Dorsal aspect of same. Accompanying scale lines equal 1.0 mm.

larger, have black palpi and antennae, and have metallic blue luster on the infuscated abdomen.

Description. — Medium-sized beetles, 7.8 to 11.0 mm.

Color. Palpi, antennal articles 3 and 4, mesepimera, tibiae, and tarsi usually infuscated. Abdominal sterna, terga, metepisterna, and metasternum at sides infuscated to black, otherwise ferruginous. Dorsal surface and epipleura of elytra blue.

Microsculpture. As described for genus.

Macrosulpture. Frontal furrows, and sometimes disc of pronotum rugose, sparsely punctate, punctures barely impressed.

Head. Frontal furrows moderately impressed. Antennal scape cylindrical. Ligula with sclerotized center area ellipsoid-convex with two or three setae apically. Mentum and submentum without accessory setae.

Prothorax. Pronotum (fig. 230) slightly convex, flattened along center line, sides slightly reflexed. Proepipleura glabrous. Proepisterna with a few setae anteriorly and posteriorly, glabrous medially. Anterior tibia with anterior margin strigose.

Pterothorax. Elytra elongate, narrow, moderately costate. Humeral angle various, but usually prominent or at least square. Costae smooth on disc, depressions pubescent. Wings entire.

Abdomen. As described for genus.

Genitalia. Male (figs. 240, 241, 242). Median lobe with plane of shaft slightly rotated from plane of basal bend. Basal bend short. Apex of shaft narrowed, ridged ventrally. Ligule short, broad, narrowed apically. Virga (figs. 240, 241) elongated. Female (fig. 247). Stylus broad, parallel-sided, rounded apically.

Variation. — The color of the tibiae, tarsi, and palpi vary from almost black to ferruginous. The pale form occurs infrequently in the northwestern populations, but is common in the midwestern, eastern, and Floridian populations. Variation also occurs in the shape of the pronotum and humeral angle within single population samples.

Flight. — These beetles have been collected repeatedly at lights throughout the range of the species, especially Florida.

Etymology. — Latin, *quadratus*, square, *pennis*, wing; referring to the square shape of the elytra.

Collecting notes. — L. Russell collected these beetles on the floodplain of the Flathead River near Perma, Montana. They were beneath short grass, matted with algae, near an ephemeral pond formed by river floodwaters.

Life history. — Members of this species have been collected from January to September, and general adults have been collected in March in Florida, and in August in Washington and Michigan. These beetles probably overwinter as adults.

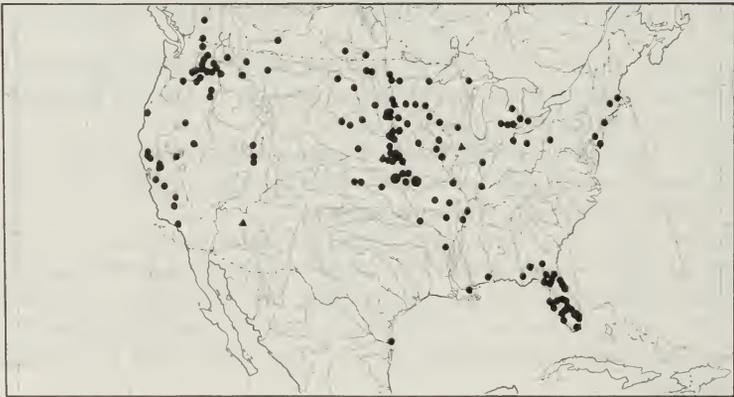
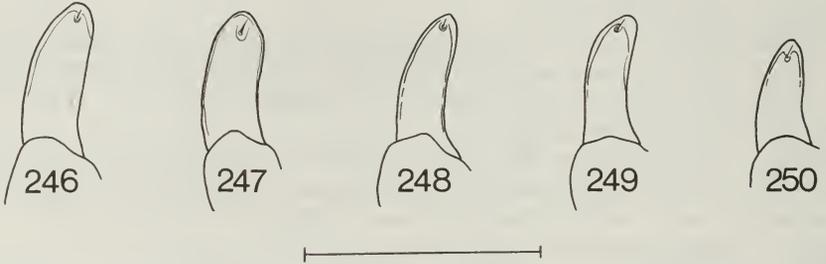
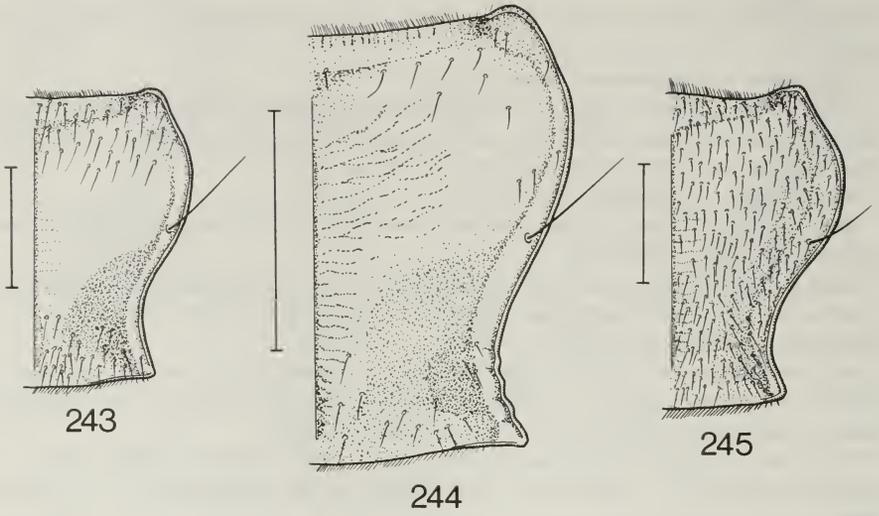
Distribution. — (Fig. 251). There are six areas from which these beetles have been commonly collected. These are the northwestern United States and adjacent Canada; the Great Salt Lake area; the areas drained by the Mississippi, and its northern tributaries east of longitude 105°, including the Great Lakes Region, New England, Florida and the eastern part of the Gulf Coast, and Brownsville, Texas. I have seen 2,405 specimens from the following localities:

CANADA

ALBERTA: (Medicine Hat) UASM. BRITISH COLUMBIA: (Kamloops) MCZ; (Oliver) CNC; (Osoyoos) CAS, UATA. MANITOBA: (Aweme) OUNO. ONTARIO: (Saint Williams, southwest of Simcoe) ZMLS. SASKATCHEWAN: (Kenosee) UNSS.

UNITED STATES

ALABAMA: Mobile County (Magazine Point) CAS. ARIZONA: (No locality given) USNM. ARKANSAS: Bradley County (8.0 miles south of Warren) JSch; Mississippi County (Osceola) UMAH; Washington County (No locality given) UAFA.



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Figs. 243-245. Pronotum, right half, dorsal aspect. 243. *Brachinus neglectus* LeConte, Southern Pines, North Carolina. 244. *Brachinus mexicanus* Dejean, Temecula, California. 245. *Brachinus javalinopsis* new species, Victoria, Texas. Figs. 246-250. Right stylus of female ovipositor, ventral aspect. 246. *Brachinus javalinopsis* new species, 15.0 miles north of Las Cruces, New Mexico. 247. *Brachinus quadripennis* Dejean, Smyrna, Washington. 248. *Brachinus mexicanus* Dejean, Temecula, California. 249. *Brachinus kavanaughii* Erwin, Superior, Colorado. 250. *Brachinus neglectus* LeConte, Jacksonville, Florida. Fig. 251. Geographical distribution map of *Brachinus quadripennis* Dejean. Accompanying scale lines equal 1.0 mm.

CALIFORNIA: Fresno County (Friant) CAS; Kings County (Hanford) USNM; Lake County (Cache Creek) UCR, (Clear Lake) CAS, (Lower Lake) CAS; Los Angeles County USNM, (Pasadena) CMPP; Merced County (Los Banos) CAS, TLE; Sacramento County (Sacramento) TLE, UCD, UIMI; Yolo County (Causeway) UCD, (Clarksburg) UCD, (Davis) CAS, TLE, UCD, UIMI. SOUTH DAKOTA: Beadle County (Huron) VMKi; Brookings County (Brookings) VMKi, (White) VMKi; Lawrence County (Spearfish) VMKi; Union County (Elk Point) VMKi; Yankton County (Yankton) VMKi. FLORIDA: Alachua County (Gainesville) CNC, FDAG, TLE, UMAH, USNM, (Newnans Lake, 5.0 miles east of Gainesville) RFre, UASM; Broward County (Fort Lauderdale) UMAH; Charlotte County (Punta Gorda) CNC, PSUU; Collier County (Everglades) USNM; Columbia County (O'Leno State Park) CUNY; Dade County FDAG, (3.0 miles south of Florida City) AMNH, (Homestead) CNC, TLE, (Long Pine Key) MCZ, (Miami) CAS, (Royal Palm State Park) PUM; De Soto County (Arcadia) CUNY; Duval County (Jacksonville) ISNH; Glades County (Palmdale) AMNH; Hendry County (Clewiston) OUCO; Highlands County (Archbold Biology Station) AMNH, CEWh, CMPP, CUNY, PSUU, RCGr, (Brighton) UASM, (Fish Eating Creek, 4.0 miles west of Venus) RCGr, (Highlands Hammock State Park) TLE; Hillsborough County (Tampa) USNM; Lee County (Fort Myers) AMNH, CUNY; Levy County FDAG, (Manatee Springs State Park) RFre, UASM, (Williston) UWSW; Liberty County (Camp Torreya) UMAH; Manatee County (Bradenton) FDAG, (Oneco) CNC, CUNY, UASM; Marion County (No locality given) MCZ; Okeechobee County (Lake Okeechobee, 6.0 miles south of Okeechobee) UASM; Orange County (Winterpark) MCZ; Palm Beach County (Belle Glade) CUNY, (North New River Canal) UASM; Pinellas County (Clearwater) CNHM, (Dunedin) CAS, CUNY, PUM, (Tarpon Springs) CNC, CNHM; Polk County (Lakeland) UMAH, (Lake Wales) FDAG, USNM, (Winter Haven) FDAG; Saint Johns County (Ponte Vedra Beach) AMNH, (Saint Augustine) AMNH; Sarasota County (Myakka River State Park) CUNY, UASM, (Sarasota) PUM; Seminole County (Sanford) CUNY, FDAG, JSch, PUM, USNM; Volusia County (Enterprise) CAS, USNM, (Ormond) AMNH; Counties unknown (Belleair) AMNH, (Fort Capron) ISNH, (Lake Harney) USNM, (Sand Point) USNM. GEORGIA: Lowndes County (No locality given) OUCO; Thomas County (Thomasville) CNHM, USNM. IDAHO: Bonner County (Sagle) UWSW; Latah County (Moscow) CMPP. ILLINOIS: (No locality given) ISNH. INDIANA: Vigo County (No locality given) PUM, UWMW; Posey County (Hovey Lake) PUM; County unknown (Mineral Springs) CMPP. IOWA: Boone County (Ledges State Park) ISUA; Dickinson County (Lake Okoboji) USNM, (Milford) USNM; Emmet County (No locality given) CAS; Henry County (Mount Pleasant) RTBe; Johnson County (Iowa City) MCZ, USNM; Palo Alto County (Ruthven) ISUA, (Silver Lake) USNM; Sioux County (Howarden) VMKi; Story County (Ame) ISUA, MSUM, OSUC, USNM, (Soper's Mill Dam, 3.0 miles east of Gilbert) ISUA; Woodbury County (Sioux City) UMSP. KANSAS: Atchison County (Atchison) CMPP; Douglas County CUNY, (Lawrence) UWMW; Pottawatomie County (Onaga) CAS; Riley County (Manhattan) KSU; Rooks County (No locality given) KSU; Saline County (Salina) CAS, CMPP, MCZ, PUM, ZMLS; Sheridan County (State Lake, near Sudley) RFre. LOUISIANA: Orleans Parish (New Orleans) ANSP. MASSACHUSETTS: Hampden County (Longmeadow) USNM; Hampshire County (Mount Tom) MCZ; Middlesex County (Arlington) MCZ, (Concord) MCZ, (Newton) MCZ, (Waltham) MCZ; Suffolk County (Dorchester) MCZ; County unknown (Forest Hills) MCZ. MICHIGAN: Huron County (Point aux Barques) UMAH; Ingham County (East Lansing) UATA; Macomb County (Mount Clemens) CNHM; Marquette County (Marquette) CAS; Oakland County (Milford) UMAH; County unknown (Aurelius) JSch. MINNESOTA: Big Stone County UMSP, (Ortonville) ISNH; Clearwater County (Lake Itasca) UMSP; Houston County (Mississippi Bluff, 1-2.0 miles north of State Line) UMSP; Jackson County (Jackson) USNM; Lincoln County (Lake Benton) VMKi; Lyon County (No locality given) UMSP; Norman County (No locality given) UMSP; Olmsted County (No locality given) UMSP; Polk County (Crookston) UMSP; Ramsey County (Saint Paul) UMSP; Saint Louis County (Duluth) ISNH; Stearns County (Koronis Lake, Paynesville) USNM; Washington County (No locality given) UMSP; Wright County (No locality given) UMSP. MISSOURI: Atchison County (Langdon) AMNH; Callaway County (Readsville) MCZ; Jackson County (Kansas City) KSU; Saint Louis County (Ranken) JSch; Wayne County (Williamsville) CNC; Wright County (Gull Creek, west of Mount Grove) TCBA. MONTANA: Cascade County (Great Falls) CAS; Flathead County (Kalispell) USNM; Sanders County (Perma) LRus. NEBRASKA: Cass County (South Bend) UNLN; Cuming County (West Point) UNLN; Dakota County (South Sioux) UNLN; Dodge County (Fremont) UNLN; Douglas County (Childs' Point, Omaha) CAS, UNLN; Lancaster County (Lincoln) UNLN, (Malcolm) USNM, (Roca) UNLN; Otoe County (Nebraska City) UNLN; Sarp County (Bellevue) UNLN; Saunders County (Ashland) SDSU, UNLN, (Cedar Bluffs) UNLN, USNM; Thomas County (Halsey) UMAH; York County (Bradshaw) UNLN, (York) UNLN. NEVADA: ANSP, USNM, MCZ, ISNH, Humboldt County (Golconda) CBak; Washoe County (Reno) RTBe. NEW JERSEY: Cape May County (Five Mile Beach) OUCO; Gloucester County (Woodbury) USNM. NEW YORK: Suffolk County (Montauk) CNHM. NORTH DAKOTA: Benson County (11.9 miles west of York) UASM; McKenzie County (North Roosevelt National Park) AMNH; Morton County (Heart River, 5.0 miles west of Mandan) UASM; Ramsey County (Devils Lake) MCZ, USNM, ZMLS. OHIO: Ashtabula County (Jefferson) USNM; Wood County (No locality given) PUM. OREGON: Baker County UMAH, (Wallowa Mountains) CAS; Curry County (8.0 miles east of Gold Beach) OSUC; Lake County (Hart Lake) JSch; Wasco County (The Dalles) MCZ, USNM; Umatilla County (Umatilla) MCZ; Union County (Alicel) REST, UIMI; County unknown (Stein Mountains) CAS. PENNSYLVANIA: Allegheny County (Pittsburgh) CMPP. SOUTH DAKOTA: Bon Homme County (Springfield) VMKi; Brookings County (Brookings) CMPP, SDSU, VMKi, (Volga) CAS, MCZ, USNM, VMKi, (White) VMKi; Brown County (Stratford) LACM; Brule County (Chamberlain) SDSU; Buffalo County (Fort Thompson) SDSU; Clay County (Vermillion) SDSU; Haakon County (Philip) SDSU; Hughes County (Pierre) VMKi; Jones County (Murdo) SDSU; Kingsburg County (Erwin) USNM; Turner County (Centerville) VMKi; Union County (Elk Point) SDSU, VMKi; Yankton County (Yankton) VMKi; County unknown (Darwood Lake) VMKi. TENNESSEE: Lake County (Gray's Landing) RTBe. TEXAS: Cameron County (Brownsville) CNC, CNHM, CUNY, OUCO, USNM. UTAH: Cache County (Logan) USUL, (Smithfield) USUL, (Wellsville) USUL; Salt Lake County (Salt Lake City) UIMI, USNM, UWSW; Utah County (Provo) MCZ, UASM, USNM, (Provo Canyon, 1.0 mile south of Springdale) UMSP, (Utah Lake, Provo) UASM, (Provo) UASM. WASHINGTON: Adams County (Lake McElroy) CAS, USNM, UWSW, (Othello) UWSW, (Ritzville) CAS, CMPP, MCZ, PUM, UMAH, USNM; Franklin County (Kahlotus) UWSW; Grant County (Coulee City) CAS, UWSW, (Crab Creek) UWSW, (Grand Coulee, Dry Falls) WSUP, UWSW, ZMLS, (Grand Coulee, Meadow Creek) WSUP, (Moses Lake) JSch, UWSW, (Smyrna) UWSW, (Soap Lake) UWSW, (Steamboat Rock) UWSW, (Stratford) CAS; Kittitas County (Vantage) UWSW; Lincoln County (Sprague) CAS, CMPP, PUM, UWSW, (Sprague Lake) CAS, (Wilbur) UASM; Okanogen County (5.0 miles south of Tonasket) CNHM; Spokane County (Cheney) JSch, UWSW, (Medical Lake) UWSW; Yakima County (Toppenish)

UWSW. WISCONSIN: Dane County (No locality given) UMMW.

Brachinus mexicanus Dejean

(Figs. 234, 235, 236, 244, 248, 252)

Brachinus mexicanus Dejean, 1831: 428. Lectotype, here selected, a male, MHNP, labelled "mexicanus m. in Mexico" "Hopfner" on green paper, and "Ex Museo Chaudoir" on white paper. *Type locality*. — Mexico, as originally given by Dejean, but herewith restricted to Baja California, Mexico.

Brachinus fidelis LeConte, 1862: 524. Lectotype, here selected, a female, MCZ red type label number 5852. Further labelled with a gold disc and "B. fidelis Kern. LeC." *Type locality*. — Kern County, California, here designated, based on LeConte's labels. NEW SYNONYMY.

Brachinus convexus Chaudoir, 1837: 7. Lectotype, here selected, a female, MHNP, labelled "convexus Mex. Chaud." and "Ex Museo Chaudoir." This specimen is pinned beneath a specimen of *B. mexicanus* Dejean, and placed in that series. *Type locality*. — Mexico, as given on Chaudoir's label. NEW SYNONYMY.

Brachinus lecontei Motschulsky, 1859: 139. Primary homonym of *B. lecontei* LeConte, 1844: 49 (see Erwin, 1965: 10).

Diagnostic combination. — The diagnostic characters are given in the key, but these beetles can be separated from all others in the study area by elytral pubescence restricted to depressions 6, 7, and 8, dark venter, blue elytra, and lack of accessory setae on the mentum.

Description. — Medium-sized beetles, 7.5 to 9.6 mm.

Color. See under Variation, below.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows and disc of pronotum rugose, sparsely punctate, punctures weakly impressed.

Head. Frontal furrows moderately impressed. Antennal scape robust, widest at middle. Ligula with sclerotized center area ellipsoid-convex with two lateral rows of three setae each. Mentum and submentum without accessory setae.

Prothorax. As in *quadripennis*, except proepipleura variable. Pronotum (fig. 244).

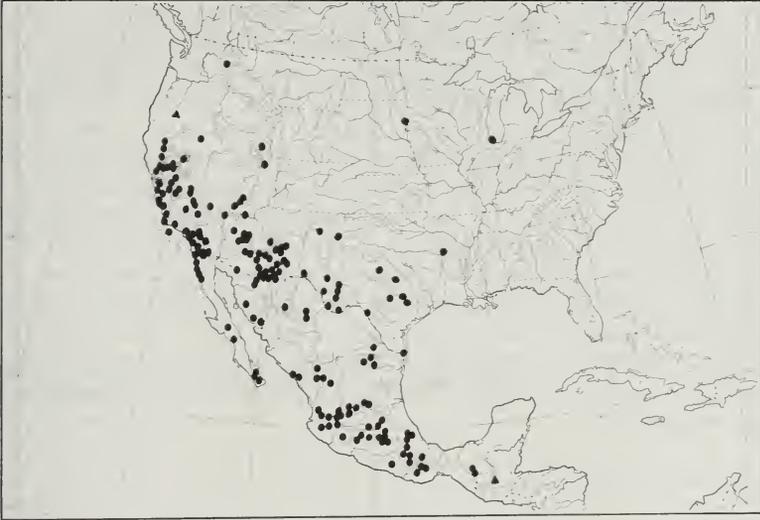
Pterothorax. Elytra as in *quadripennis*, except costae variable and pubescence confined to depressions 6, 7, 8, scutellar region, and across the apical sixth of the elytra. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 234, 235, 236). Median lobe with plane of shaft slightly rotated from plane of basal bend. Basal bend short. Apex of shaft various, ridged ventrally. Ligule short, broad, narrowed apically. Virga (figs. 234, 235). Female (fig. 248). Stylus broad, tapering to acute apex.

Variation. — The composition of this species seems to be more complex than most *Brachinus* species in the study area. Two forms are clearly recognizable in most of the range, except California. I refer to these forms as the "high-costae morph" and the "low-costae morph." In California, these two forms merge in all characteristics, with local populations having both the extreme and intermediate forms. In Mexico, the high-costae morph is known only in northern Baja California (Cataviña). Other populations are in Phoenix, Arizona, southern New Mexico, Hope, Arkansas, Chicago, Illinois, and Brookings, South Dakota. In Phoenix, there appears to be a mixed population, but the specimens seen were collected at different times. Except for the last three mentioned peripheral localities, the range of the low-costae morph overlaps that of the high-costae morph.

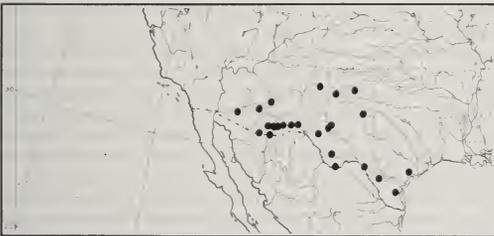
The high-costae morph generally has pale antennae, pale abdominal center, well developed costae, and a few setae on the proepipleura. The low-costae morph is quite dark be-



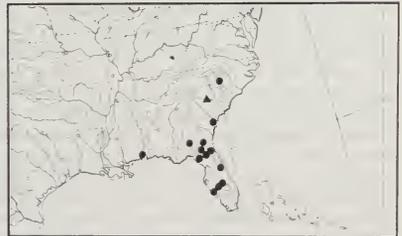
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253



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Figs. 252-255. Geographical distribution maps. 252. *Brachinus mexicanus* Dejean. 253. *Brachinus kavanaughii* Erwin. 254. *Brachinus javalinopsis* new species. 255. *Brachinus neglectus* LeConte.

neath, the abdominal center is infuscated, the third and fourth antennal articles are at least clouded, the outer articles are infuscated rather than being dusky, and finally the proepipleura are usually glabrous.

Further variation occurs in the male genitalia. In the low-costae morph the shaft is narrowed to apex, and the virga tapers evenly to the apex. The high-costae morph has the apex of the shaft almost truncate, and the virga is pinched medially. The flattened rim of the female stylus is more pronounced in the low-costae morph than in the high-costae morph, but the general shape is the same.

Flight. — These beetles have been collected repeatedly at lights throughout the species range.

Collecting notes. — I have collected these beetles on numerous occasions in California, New Mexico, and Mexico. They are always near water, either standing or flowing. At Rancho Nuevo, Chiapas they were beneath logs in grassy soil. In Santa Clara County, California they occur under stones in gravel covered with algae near stream margins.

Life history. — Members of this species have been collected in all months of the year. The life cycle is much the same as in *B. pallidus* (Erwin, 1967).

Distribution. — (Fig. 252). The range of this species extends from Washington south to at least Guatemala, and east to Arkansas and Illinois. I have seen 2,603 specimens from the following localities:

CENTRAL AMERICA

GUATEMALA: (No locality given) MCZ.

MEXICO

AGUASCALIENTES: (Aguascalientes) CNHM; (11.0 miles west of Aguascalientes) UASM; (15.0 miles west of Pabellon) UMAH. BAJA CALIFORNIA: (Arroyo de Purisima) CAS; (Arroyo del Rosario) CAS; (Cataviña) CAS; (south of El Sauzal) CAS; (1.3 miles northwest of El Truinfo) CAS; (Hamilton Ranch) CAS; (La Mision) GRNo; (12.4 miles east of La Paz) CAS; (Mira Flores) CAS; (Rancho Stacion Salsipuedes) UMSP; (San Ignacio) CAS; (3.0 miles east of San Isidro) CMPP; (San Vicente) CAS; (Tijuana) CNHM; (65.0 kilometers south of Tijuana) LACM; (Triunfo) CAS. CHIAPAS: (15.6 miles west of Comitán) UASM; (Rancho Nuevo, 8.6 miles east of San Cristobal) RTBe, UASM; (1.0 miles north of San Cristobal) RTBe; (8.6 miles east of San Cristobal) UASM. CHIHUAHUA: (Carta Blanca, 16.0 miles west of Matachic) AMNH; (Catarinas) AMNH; (Chihuahua City) AMNH; (25.0 miles northwest of Chihuahua City) CNC; (Primavera) AMNH; (San Jose Babicora) AMNH. COAHUILA: (Arroyo Palo Blanco, 15.0 miles north of Saltillo) DRWh; (Saltillo) AMNH, MCZ. DISTRITO FEDERAL: (Peñon Viejo) MCZ. DURANGO: (12.2 miles south of El Banco) UASM; (Encino) AMNH; (Nombre de Dios) AMNH; (Rio Chico, 15.7 miles west of Durango) UASM. GUANAJUATO: (Rio Guanajuato, 9.8 miles south of Sialo) UASM. GUERRERO: (13.9 miles west of Chilpancingo) UASM. HIDALGO: (Guadalupe) MCZ; (Huichapan) LACM; (Rio Tula, near Tasquillo) UASM; (Tula) JHen. JALISCO: (Ajijic) JHen, UATA; (4.0 miles west of Ajijic) AMNH; (21.4 miles south of Encarnacion de Diaz) UASM; (Cocula) USNM; (9.1 miles northwest of Cautla) UASM; (Guadalupe) AMNH, MCZ; (9.0 miles east of Guadalupe) AMNH; (13.0 miles southeast of Lagos de Moreno) UASM; (17.9 miles west of Magdalena) UASM; (12.0 miles west of Ojuelos de Jalisco) CAS; (Puente Caquixtle, 9.7 miles east of Encarnacion de Diaz) UASM; (Rio Grande de Santiago, 12.5 miles west of Ixtlahuacan del Rio) UASM; (21.0 miles northeast of Tepetitlan) CAS; (Valle de Guadalupe) CAS. MEXICO: (Lago Zumpango, near San Juan Zitlaltepec) UASM; (Temascaltepec) CAS; (7.0 miles north of Tenancingo) UASM; (Tonatico) JHen; (Valle de Bravo) JHen; (Villa Carbon) JHen. MICHOACAN: (7.0 miles south Arrio de Rosales) UASM; (10.0 miles west of Jiquilpan) DRWh; (Morelia) UASM; (Tuxpan) JHen; (50.0 miles west of Zitacuaro) MCZ. MORELOS: (Cuernavaca) ANSP; (Progreso) WSUP. NAYARIT: (5.1 miles north of Chapalilla) UASM; (Tepic) UATA; (19.0 miles southeast of Tepic) CAS; (19.3 miles southeast of Tepic) UASM. NUEVO LEON: (3.2 miles south of Galeana) UASM; (1.1 miles east of Iturbide) UASM; (1.3 miles east of Iturbide) UASM; (14.8 miles west of Linares) UASM; (Monterrey) AMNH; (6.0 miles south of Monterrey) FDAG; (Rio Linares, 20.0 miles west of Linares) CAS; (Rio Sabinas Hidalgo, 4.8 miles east of Sabinas Hidalgo) UASM; (Santa Rosa Cañon, 14.8 miles west of Linares) UASM. OAXACA: (Mitla) CPBo; (25.0 miles south of Mitla) ISUA; (Oaxaca) AMNH, CAS, MCZ; (Rio Atoyac, near Juchatengo) UASM; (1.4 miles west of Tamazulapan) UASM; (4.3 miles west of Tamazulapan) UASM; (72.5 miles south of Valle Nacional) UASM. PUEBLA: (9.0 miles north of Amatitlan) CAS; (near Petlalcingo) UASM; (Tehuacan) CAS; (near Tehuiztzingo) UASM; (1.3 miles south of Tlatlauiqui) UASM. QUERETARO: (33.0 kilometers north of Acambay) UASM; (near Palmillas) UASM. SAN LUIS POTOSI: (Puente de la Parada, 7.5 miles northwest of Mexquitic) UASM; (2.0 miles south of San Luis Potosi) CAS; (2.7 miles west of Santa Catarina) UASM. SINALOA: (Culiacan) AMNH; (Real de Piaxtla) AMNH. SONORA: BMNH; (7.2 miles southeast of Alamos) GRNo; (10.0 miles west of Alamos) AMNH; (Cocospera Cañon, 8.0 miles east of Imeris) AMNH; (16.0 miles northeast of Ciudad Obregon) CNC; (Pesqueria) CAS; (Rancho Atascosa, 42.0 kilometers south of Nogales) CNHM; (Rio Mayo, San Bernardo) CAS; (Sonoyta) AMNH. VERACRUZ: (Jalapa) ANSP; (Orizaba) ISUA, UNLN. ZACATECAS: (Rio Juchipila, 0.9 miles north of Jalpa) UASM; (1.3 miles southeast of Sain Alto) UASM. STATE UNKNOWN: (Tujipilco) CAS.

UNITED STATES

ARIZONA: Apache County (White Mountains) CAS, UATA; Cochise County (Benson) CAS, (Bisbee) CAS, (Cave Creek Canyon) PSUU, TCBA, (Cave Creek Ranch) UASM, (Chiricahua Mountains) CAS, OUCO, UASM, UATA, USNM, (Chiri-

cahua Mountains, Rucker Canyon) CAS, (Chiricahua Mountains, Rucker Lake) UASM, (Chiricahua Mountains, Rustler's Park) CNC, (Douglas) CMPP, (Guadalupe Canyon, 32.0 miles east of Douglas) CUNY, (15.0 miles southeast of Hookers Hot Springs) DRWh, (Huachuca Mountains) OUCO, USNM, (Portal) AMNH, CAS, SJSC, (San Bernardino Ranch) KSU, LACM, (San Pedro River, near Palominas) UASM, (San Pedro River, 10.0 miles east of Sierra Vista) OSUC, UATA, (South West Research Station, 5.0 miles west of Portal) AMNH, FDAG, GRNo, UCD, UCR, (Tombstone) SDNHM, (Willcox) AMNH; Cocconino County (Grand Canyon National Park) CAS, (Havasupai Indian Reservation, Supai Grand Canyon) UMSP; Gila County (Coolidge Dam) SJSC, (Globe) UASM, UATA, (14.0 miles south of Globe) UASM, (Payson) UATA, (Winkelman) UATA; Graham County (Aravaipa Canyon) CAS, (Aravaipa Creek, between Klondyke and Aravaipa) DRWh, (Galiuro Mountains) UASM, (Gila River, near Geronimo) UASM, (San Carlos Reservoir) SJSC, UATA; Maricopa County (Phoenix) MCZ, OUCO, UASM, USNM, (Salt River, Phoenix) MCZ, UATA; Mohave County (Beaver Dam) ISUA, (Hubbard Ranch) USNM, (Littlefield) UCD, (16.0 miles north of Wikieup) LACM; Navajo County (Show Low) LACM; Pima County (Baboquivari Mountains, Browns Canyon) AMNH, CAS, (Cienega Creek, Pantano) CUNY, (Coyote Mountain, 0.5 miles north of Mendoza Canyon) UATA, (Saint Xavier Mountains) CAS, (Santa Catalina Mountains) CAS, UATA, USNM, (Santa Catalina Mountains, Bear Canyon) CAS, (Santa Catalina Mountains, Sabino Canyon) CAS, TLER, UASM, UATA, (Santa Rita Mountains) CAS, (Tucson) CAS, CUNY, UASM, UATA, UIMI, UMAH, USNM; Pinal County (Aravaipa Canyon) CUNY, (Sycamore Camp, 9.0 miles northwest of Payson) CAS; Santa Cruz County (Canelo) UATA, CUNY, (Lewis Springs, San Pedro River) UASM, (Nogales) CAS, CNHM, UASM, UCD, USNM, (Pajarita Mountains) CAS, (Patagonia) CAS, CNHM, CUNY, UATA, (5.0 miles southwest of Patagonia) AMNH, (Peña Blanca) CUNY, OSUC, UASM, (Santa Rita Mountains, Madera Canyon) UASM, UCD, WHTY, (Tumacacori Mountains, Sycamore Canyon) CUNY, (Yanks Spring, 4.0 miles southeast of Ruby) AMNH; Yavapai County (Bumble Bee) CAS, (Camp Verde) PSUU, (Congress) UATA, (Cottonwood) UIMI, (Granite Mountain) CAS, (Prescott) CAS, UASM, USNM, (Wickenburg) ISUA, (5.0 miles north of Wickenburg) UMAH; Counties unknown (Atasco Mountains, Sycamore Canyon) UATA, (Cayetano Mountains) UMAH, (Kohl's Ranch) UATA, (Santa Cruz River) UATA, (Senator) AMNH, (Superstition Mountains) UATA, (Texas Pass) CUNY, (Tortolita Mountains) CAS. ARKANSAS: Garland County (Hot Springs) CAS; Hempstead County (Hope) MCZ. CALIFORNIA: Alameda County (Livermore) CAS, (Niles Canyon) UCD, (Oakland Hills) CAS, (San Leandro) UIMI; Amador County (5.0 miles west of Sutter Creek) TLER; Colusa County (Highway 20 and 16) UCD, (Rumsey Canyon) UCD; El Dorado County (No locality given) CAS; Fresno County (La Fevre Creek) CAS; Glenn County (Elk Creek) CAS; Imperial County (Calpatria) CAS; Inyo County (Big Pine) CAS, (Deep Springs Lake) CAS, (Diaz Lake) CAS, (Freeman) CAS, (Independence) CAS, (Little Lake) CAS, (Lone Pine) CAS, (Olancho) CAS, (Owens Lake) CAS, (Westgard Pass Plateau) CAS; Kern County (Caliente) ZMLS; Los Angeles County (Alhambra) CAS, (Arroyo Seco Canyon) VVBa, (Big Dalton Dam) UCR, (Frenchman Flats) CAS, (Los Angeles) CAS, (Pasadena) CAS, (San Dimas) CAS, (Tapica County Park) GRNo; Madera County (Coarsegold) CAS, (O'Neals) UCD; Mariposa County (Mariposa) CAS; Merced County (Merced) CAS; Monterey County (Carmel) UASM, (Jolon) CAS, (3.0 miles southeast of Jolon) CAS, (Stone Canyon) CAS; Napa County (Monticello) UCD; Orange County (Black Star Canyon) UCD, (Laguna Beach) CAS; Placer County (No locality given) CAS; Riverside County (Colton) CAS, (Hemet) VVBa, (Palm Canyon) CAS, (Palm Springs) CAS, (Riverside) CAS, (San Jacinto Mountains) CAS, (Temecula) CAS; San Benito County (Panoche Valley) CAS; San Bernardino County (Afton Canyon) USNM, (Cajon Pass) UCD, (0.9 miles northeast of Cedar Springs) GRNo; San Diego County (Carrizo) UIMI, (Chicken Creek) CAS, (3.0 miles south of Dehesa) TLER, (Guatay) UIMI, (Jacumba) CAS, (Knaus) CAS, (Mission Valley) UCD, (Mount Palomar) CAS, (9.0 miles east of Pine Valley) UCD, (Poway) CAS, (San Juan Capistrano) UIMI, (Sweetwater River) RES; San Joaquin County (Corral Hollow) TLER; San Luis Obispo County (Atascadero) CAS, (Cambria) CAS, (San Luis Obispo) CAS, (Santa Margarita) CAS; Santa Barbara County (Bluff Camp, San Rafael Mountains) UCD, (Cañada del Venadito) UCD, (Cuyama River) CAS, (Gaviota) CAS, (Santa Cruz Island) CAS, (Santa Ynez River, San Lucas) CAS; Santa Clara County (Alum Rock Park) CAS, (Arroyo Bayo) SJSC, (Gilroy Hot Springs) TLER, (Pacheco Pass) UIMI, (Uvas Creek) TLER; Santa Cruz County (Santa Cruz) CAS; Stanislaus County (Del Puerto Canyon) UIMI, (Del Puerto Creek) TLER; Tehama County (Hills west of Tehama County) CAS; Tulare County (Kaweah) CAS; Ventura County (Fillmore) CAS, (Foster Park) UCD, (Ojai) ZMLS, (Santa Paula) CAS, UCD, (Ventura) CAS, (Wheeler Hot Springs) CAS; Yolo County (Davis) UCD, (Putah Canyon) UCD, (Putah Creek) TLER. ILLINOIS: Cook County (Riverside) UMAH. NEW MEXICO: Catron County (near Argon) AMNH, (Cooney Canyon, 10.0 miles east of Alma) UASM, (2.0 miles west of Luna) CCha, (San Francisco Creek, 26.1 miles north of Glenwood) UASM; Dona Ana County (Mesquite) LACM; Grant County (Gila River, near Gila) UASM, (Sapillo Creek, 26.0 miles north of Silver City) TLER, (Silver City) USNM, (16.0 miles west of Silver City) CAS; Hidalgo County (Peloncillo Mountains) GRNo, (Post Office Canyon, 12.0 miles southeast of Rodeo) SJSC, (Rodeo) UCR; Quay County (Tucumcari) MCZ; San Miguel County (Sapello Canyon) USNM. NEVADA: Humboldt County (Soldier Meadows) NSDA; Kye County (Beatty) OSUC, UWSW; Washoe County (Reno) RTBe, UCD, USNM. OREGON: (No locality given) UMSP. SOUTH DAKOTA: Brookings County (Brookings) ANSP. TEXAS: Blanco County (2.0 miles south of Round Mountain) UASM; Brewster County (Alpine) CAS, CUNY, MCZ, (Big Bend National Park) CNC, MCZ, UASM, (Glenn Springs) UMAH, (Green Valley) CAS, (Saint Helena Canyon) CAS; Cameron County (Brownsville) CMPP, DHKa; Culberson County (2.5 miles east of Nickel Creek Station) CNHM; Fayette County (Flatonia) ANSP; Hudspeth County (9.0 miles west of Sierra Blanca) OUCO; Jeff Davis County (Barrel Springs Creek, 22.0 miles west of Fort Davis) DRWh, (Davis Mountains) CAS, OUCO, UCD, USNM, (Fort Davis) AMNH, CNC, MCZ, (6-10.0 miles west of Fort Davis) UASM, (Limpia Canyon, 2.0 miles northwest of Fort Davis) CNC, CNHM, DRWh, TLER, UASM; Presidio County (Presidio) TAMU; Reeves County (Balmorhea Lake) UASM, (Pecos) JSch; San Saba County (Camp San Saba) MCZ; Taylor County (25.0 miles southwest of Abilene) CMPP; Travis County (Austin) CAS; Val Verde County (9.0 miles southeast of Del Rio) DRWh. UTAH: Cache County (Logan) USUL; Utah County (Wasatch Mountains, Provo Canyon) CAS; Washington County (3.0 miles south of Gunlock) GRNo, (12.0 miles north of La Verkin) UMSP, (Santa Clara Creek) CAS, UCD, UWSW, (Saint George) AMNH, ISUA, MCZ, USNM, (Zion National Park) CAS. WASHINGTON: Spokane County (Spokane) CAS.

Brachinus kavanaughi Erwin
(Figs. 226, 231, 232, 233, 249, 253)

Type locality. — Superior, Boulder County, Colorado, along Coal Creek.

Type specimens. — The holotype male and allotype female are in CAS. Both were collected by D. H. Kavanaugh at the type locality, on June 4, 1968. Twenty-five paratypes collected on various dates and at various localities are in CAS, DHKa, MCZ, TLER, and UASM.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Medium-sized beetles, 8.0 to 12.0 mm.

Color. Antennal article 3 at apex and all of 4, metepisterna, metasternum at sides, abdominal sterna and terga infuscated to black, otherwise ferruginous. Dorsal surface and epipleura of elytra blue.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows and disc of pronotum rugose and punctate, punctures moderately impressed.

Head. As in *quadripennis*, except antennal scape robust, widest at middle.

Prothorax. As in *quadripennis*, except proepipleura with setae both anteriorly and posteriorly, glabrous medially. Pronotum (fig. 226).

Pterothorax. As in *quadripennis*.

Abdomen. As described for genus.

Genitalia. Male (figs. 231, 232, 233). Median lobe with plane of shaft as in *quadripennis*. Basal bend longer, more arcuate. Apex not so flattened. Ligule short, narrowed apically. Virga (figs. 231, 232). Female (fig. 249). Stylus broad, but narrowed toward apex.

Variation. — This is a fairly constant species throughout its range. The total size and the shape of the pronotum vary within populations.

Flight. — These beetles have been collected at lights in Del Rio, Texas.

Etymology. — The latinized form of Kavanaugh, named for D. H. Kavanaugh, an excellent collector of carabid beetles who collected the types.

Collecting notes. — Kavanaugh, my wife, and I collected these beetles near the type locality at an elevation of 5,400 feet. They were found beneath stones during the day along a clear cold stream whose edge was composed of stones embedded in clay and gravel, alternating with gravel bars. Beetles of this species also have been collected on the shores of lakes in Colorado by C. Armin.

Life history. — Members of this species have been collected from February to September. Teneral adults were collected in May in Texas and in September in Illinois. Overwintering probably takes place as an adult.

Distribution. — (Fig. 253). The range of this species extends from western New York through the Great Lakes region, south to Nuevo Leon, Mexico, and west to central Colorado and New Mexico. I have seen 508 specimens from the following localities:

MEXICO

NUEVO LEON: (Monterrey) AMNH; (Rio Blanquillo, 7.0 miles north of Montemorelos) UASM; (Rio Salinas at Cienaga de Flores) UASM. TAMAULIPAS: (20.0 miles north of Ciudad Victoria) MCZ.

UNITED STATES

COLORADO: Boulder County (Coal Creek, 6.9 miles north of Golden) DHKa, (Coal Creek, Marshall Lake Area) CArm, (Coal Creek, Superior) CArm, DHKa, (Four Mile Creek) CArm, (Hayden) CArm, (Left Hand Creek) CArm, (McCall Lake, Lyons) CArm, (North Saint Vrain, Lyons) CArm, (Red Gulch, Lyons) CArm, (Teller Lake) CArm; Yuma County (Wray) KSU; County unknown (Regnier) AMNH. KANSAS: Comanche County (No locality given) KSU; Montgomery County (Independence) CAS; Riley County (Manhattan) KSU; Sheridan County (State Lake, near Studley) RFre, UASM. ILLINOIS: Alexander County (Horseshow Lake) RTBe; Cook County (Chicago) CMPP; Knox County (Galesburg) MCZ; La Salle County (Ottawa) RTBe; Vermilion County (Kickapoo) RTBe, (Oakwood) ISNH; County unknown (30.0 miles south of Grape Creek) RTBe; MISSOURI: Gasconade County (Gasconade River) UWSW; Jefferson County (Kimmswick) UMAH; Saint Louis County (Saint Louis) CAS, SDNHM; Wright County (Gull Creek, west of Mount Grove) TCBA. NEW MEXICO: Bernalillo County (Cedro Canyon) AMNH;

Eddy County (Blue Spring, 10.0 miles east of Carlsbad) USNM; San Miguel County (Sapello Creek, Sapello) UASM. NEW YORK: Tompkins County (Ithaca) UASM. NEBRASKA: Banner County (Glen Rock Canyon) UNLN; Glen Sioux County (No locality given) AMNH. OHIO: Franklin County (Columbus) OUCO; Hamilton County (Cincinnati) UMAH; Ottawa County (Put-in-Bay, South Bass Island) UMAH. OKLAHOMA: Comanche County (Wichita National Forest) CAS, OSUS. SOUTH DAKOTA: Lawrence County (Spearfish) VMKi. TEXAS: Blanco County UMAH, USNM, (Round Mountain) OUCO, USNM, (2.0 miles south of Round Mountain) UASM; Brazos County (College Station) TAMU; Burnet County (Inks Lake State Park) UMSP; Cameron County (Brownsville) CNC, USNM; Comal County (New Braunfels) USNM; Corwell County (No locality given) MCZ; Culberson County (2.5 miles east of Nickel Creek Station) CNHM; Eastland County (No locality given) UMSP; Gillespie County (No locality given) OUCO; Gray County (McClellan) UMSP; Hays County (San Marcos) CAS; Kimble County (Roosevelt) CAS; Lampasas County (Lampasas River) CUNY; Lee County (Fedor) CMPP; McLennan County (Waco) MCZ, USNM, ZMLS; Pecos County (Sheffield) CAS; San Saba County (Camp San Saba) MCZ; Shelby County (Kerrville) CNC; Taylor County (25.0 miles southwest of Abilene) AMNH, CMPP, CNHM; Travis County UMAH, (Austin) AMNH, MCZ, WSUP; Val Verde County (Del Rio) CAS, CNC, (9.0 miles southeast of Del Rio) DRWh; Victoria County (Victoria) USNM; Counties unknown (Fuller) USNM, (Tiger Mills) USNM. WYOMING: Platte County (Glendo Reservoir, near Glendo) DRWh.

Brachinus javalinopsis new species
(Figs. 227, 228, 229, 245, 246, 254)

Type locality. — Willcox, Cochise County, Arizona.

Type specimens. — The holotype male and allotype female are in AMNH. Both were collected at the type locality by T. Cohn, P. Boone, and M. Cazier on September 7, 1950.

Fifteen paratypes collected on the same day at the same locality by the same collectors are in AMNH, CAS, MCZ, TLER, and UASM.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Large-sized beetles, 12.3 to 13.5 mm.

Color. As in *quadripennis*, except antennal articles 3 and 4 infuscated only apically, and tibiae, tarsi, and palpi ferrugineous.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows rugose and sparsely punctate, disc of pronotum densely rugose and punctate, punctures moderately impressed.

Head. Frontal furrows moderately to deeply impressed. Antennal scape robust, widest about middle. Ligula with center area ellipsoid-convex and plurisetose. Mentum and submentum with accessory setae.

Prothorax. Pronotum (fig. 245) convex, flattened along center line, sides widely reflexed. Proepipleura and proepisterna as in *quadripennis*. Anterior tibia with anterior margin punctate, punctures occasionally forming shallow strigae.

Pterothorax. As in *quadripennis*, except elytra broader, costae sharper, and pubescence denser and shorter. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 227, 228, 229). Median lobe with plane of shaft rotated about 45° from plane of basal bend. Basal bend short. Apex of shaft narrowed, ridged ventrally. Ligule short, broad, truncate apically. Virga (figs. 227, 228). Female (fig. 246). Stylus broad, narrowed apically, rounded at apex.

Variation. — Intrapopulation variation occurs in the shape of the pronotum, the color of the antennal articles, and in the total size. The color of antennal articles 3 and 4 is paler in some individuals.

Flight. — These beetles have been collected repeatedly at lights throughout the range of the species.

Etymology. — Spanish, *javili*, wild pig; Latin, *opsis*, likeness; referring to the very large, broad habitus of these beetles.

Collecting notes. — D. Larson and W. Sharp have collected these beetles at margins of ponds in Texas.

Life history. — Members of this species have been collected from May to September, and in January. Teneral adults were collected in July in New Mexico. Overwintering probably

takes place as an adult.

Distribution. — (Fig. 254). The range of this species extends over much of the American Southwest, from western Arizona to the Texas panhandle, and south to Brownsville. I have seen 118 specimens from the following localities:

UNITED STATES

ARIZONA: Cochise County (Douglas) UCD, UCR, (14.0 miles northeast of Douglas) UCR, (17.0 miles east of Douglas) UCR, (Guadalupe Canyon) CUNY, (3.0 miles east of Johnson) RCGr, (10.0 miles north of Paradise) TLER, (Portal) GRNo, UCD, (South West Research Station, 5.0 miles west of Portal) AMNH, UCD, (Willcox) AMNH, UATA; Gila County (Globe) UATA; Graham County (Thatcher) UCD; Maricopa County (Gila Bend) CAS. MISSOURI: (No locality given) ISNH. NEW MEXICO: Dona Ana County (Las Cruces) CNHM, (15.0 miles north of Las Cruces) RCGr, (State College) USNM; Eddy County AMNH, (Black River, near Whites City) UWSW, (Carlsbad) UWSW, (Whites City) UWSW; Hidalgo County (Lordsburg) CNC, (Post Office Canyon, Peloncillo Mountains) UCR, (Rodeo) GRNo, UCD, UCR, (13.0 miles north of Rodeo) AMNH; Luna County (Deming) AMNH; Quay County (Tucumcari) SDSU; San Miguel County (Las Vegas) UIMI. TEXAS: Brewster County (9.0 miles north of Alpine) OSUC, (Hot Spring, Big Bend National Park) CNC; Frio County (5.0 miles north of Dilley) UASM; Hudspeth County (9.0 miles southwest of Del City) AMNH; Kleburg County (Kingsburg) USNM; Presidio County (7.0 miles north of Marfa) RCGr; Randall County (Palo Duro State Park) UMSP; Scurry County (Snyder) TCBA; Val Verde County (Del Rio) UASM; Victoria County (Victoria) USNM.

Brachinus neglectus LeConte

(Figs. 237, 238, 239, 243, 250, 255)

Brachinus neglectus LeConte, 1844: 49. Lectotype, here selected, a male, MCZ red type label number 31,775. This specimen is unlabelled, but stands third in a series of four specimens behind label "B. quadripennis Dejean." *Type locality.* — Georgia, as given originally by LeConte.

Diagnostic combination. — The diagnostic characters are given in the key.

Description. — Medium-sized beetles, 8.4 to 12.3 mm.

Color. Metasternum at sides, metepisterna, and abdominal sterna and terga infuscated, otherwise ferruginous. Dorsal surface and epipleura of elytra blue.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows and sometimes disc of pronotum rugose and sparsely punctured, punctures moderately impressed.

Head. As in *quadripennis*, except antennal scape robust, widest at middle, mentum and submentum with accessory setae.

Prothorax. As in *quadripennis*, except anterior margin of anterior tibia punctate, punctures rarely forming strigae. Pronotum (fig. 243).

Pterothorax. As in *quadripennis*.

Abdomen. As described for genus.

Genitalia. Male (figs. 237, 238, 239). Median lobe with plane of shaft rotated slightly from plane of basal bend. Basal bend long. Apex of shaft narrowed, ridged ventrally. Ligule short, truncate. Virga (figs. 237, 238). Female (fig. 250). Stylus broad basally, narrowing to almost acute apex.

Variation. — The few specimens available representing this species exhibit the usual variation in the shape of the pronotum and its macrosculpture.

Flight. — These beetles have been collected repeatedly at lights in Georgia and Florida.

Etymology. — Latin, *neglectus*, forgotten.

Life history. — Members of this species have been collected from March to September. Teneral adults have been collected in May in Georgia. These beetles probably overwinter as adults.

Distribution. — (Fig. 255). The range of this species extends from North Carolina to southern Florida, and west to southern Alabama. I have seen 32 specimens from the following localities:

UNITED STATES

ALABAMA: Mobile County (Mobile) CAS, (Saraland) CAS. FLORIDA: Alachua County FDAG, (Gainesville) TLer, UMAH; Columbia County (O'Leno State Park) CUNY; Duval County (Jacksonville) CAS; Highlands County (Archbold Biology Station) PSUU; Levy County (Manatee Springs State Park) RFre; Orange County (Winter Park) MCZ; Pinellas County (Dunedin) CAS; Polk County (Lakeland) UMAH; County unknown (Guntown) ANSP. GEORGIA: Charlton County (Okefenokee Swamp, Billy's Island) CUNY; Chatham County (Savannah) CAS; Thomas County (Thomasville) ANSP, MCZ. NORTH CAROLINA: Moore County (Southern Pines) CAS. SOUTH CAROLINA: (No locality given) MCZ.

The *phaeocerus* subgroup

This subgroup is characterized as follows: median lobe with long narrow apex, elytra bright blue with a contrasting black suture, and outer antennal articles black. Four species, *B. phaeocerus* Chaudoir, *B. azureipennis* Chaudoir, *B. consanguineus* Chaudoir, and *B. imporcitis* new species, are included.

Brachinus phaeocerus Chaudoir

(Figs. 257, 258, 259, 265, 275, 279)

Brachinus phaeocerus Chaudoir, 1868: 300. Lectotype, here selected, a male, MHNP, labelled "Tejas" and "Ex Museo Chaudoir." *Type locality*. — Texas, as originally given by Chaudoir's label.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Small-sized beetles, 7.2 to 8.1 mm.

Color. Antennal articles 3 and 4, mesepimera, metepisterna, metasternum at sides, abdominal sterna and terga, tibiae and tarsi infuscated to black. Antennal articles 5-11, and metasternal process (between middle coxae), usually darkly infuscated. Female somites 7 and 8, and male somites 8 and 9, and remainder of beetle, ferruginous. Dorsal surface and epipleura of elytra bright blue with black sutural margins.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows and surface of pronotum densely rugose and punctate, punctures moderately deeply impressed.

Head. Frontal furrows moderately deeply impressed. Antennal scape robust, but nearly cylindrical. Ligula with sclerotized center area with two lateral rows of three setae per row. Mentum and submentum without accessory setae.

Prothorax. Pronotum (fig. 265) slightly convex, flattened along center line, sides slightly reflexed. Proepipleura glabrous. Proepisterna with a few setae both anteriorly and posteriorly, glabrous medially. Anterior tibia with anterior surface strigose.

Pterothorax. Elytra moderately long, narrow, moderately costate. Humeral angle square to prominent. Costae and depressions pubescent. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 257, 258, 259). Median lobe with plane of shaft rotated slightly from plane of basal bend. Basal bend moderately long. Apex of shaft narrowed to apex, elongate. Ligule short, narrow, truncate. Virga (figs. 257, 258). Female (fig. 275). Stylus narrow, tapering to acute apex.

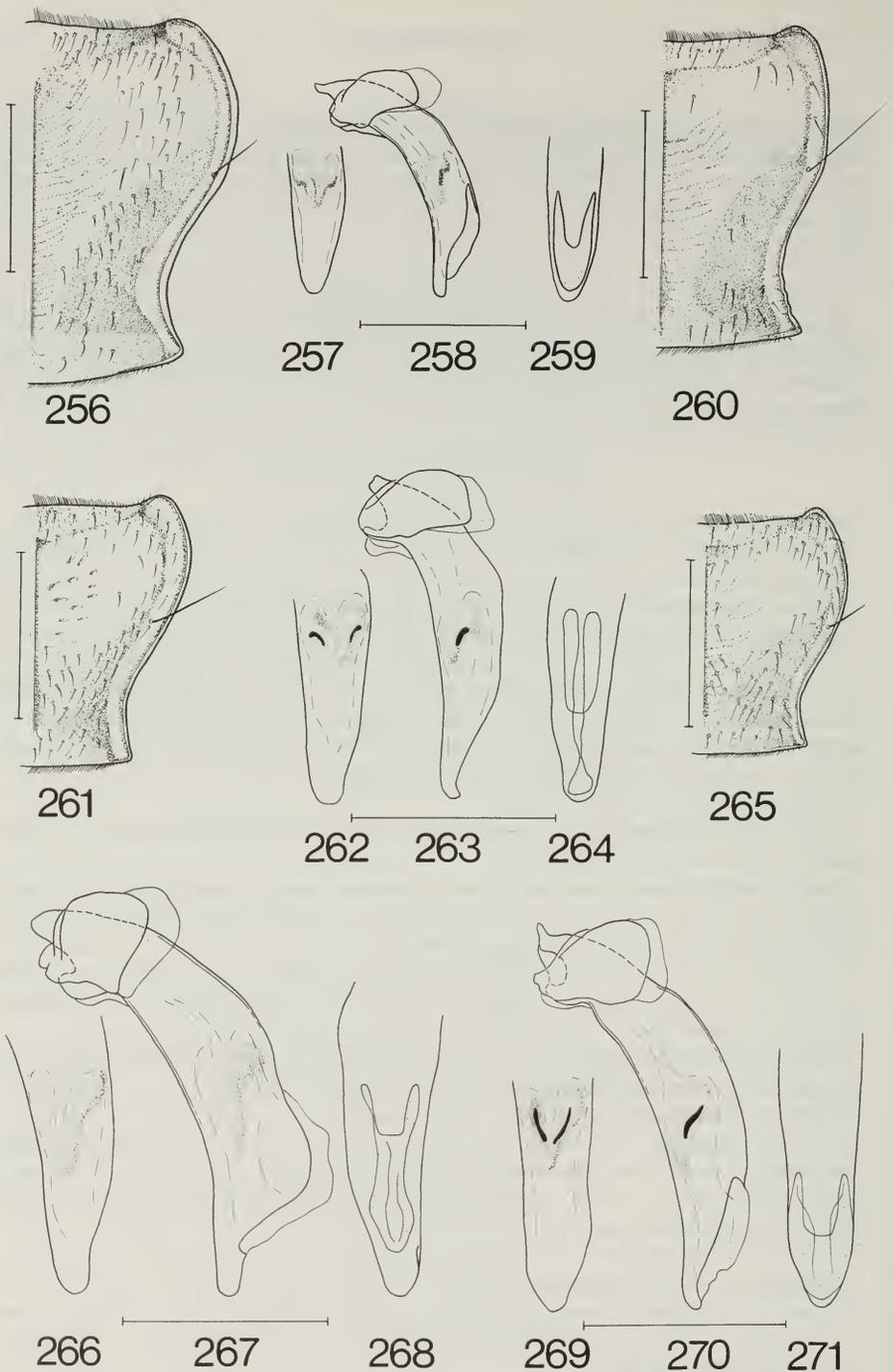
Variation. — Intrapopulational variation occurs in the shape of the pronotum, and degree of infuscation of the outer antennal articles.

Flight. — G. E. Ball collected these beetles at lights in Big Bend National Park, Texas.

Etymology. — Greek, *phaios*, dusky brown; *keros*, horn; referring to the infuscated antennae of these beetles.

Collecting notes. — G. E. Ball collected these beetles in *Carex* marshes at Colorado Springs; and my wife and I collected them with *B. kavanaughi* specimens along streams near Golden, Colorado.

Life history. — Members of this species have been collected from February to September.



Figs. 256, 260, 261, 265. Pronotum, right half, dorsal aspect. 256. *Brachinus consanguineus* Chaudoir, Rio Papagayo, Guerrero, Mexico. 260. *Brachinus azureipennis* Chaudoir, 20 miles north of El Mogote, Guerrero, Mexico. 261. *Brachinus imporcitis* new species, Globe, Arizona. 265. *Brachinus phaeocer* Chaudoir, 25.0 miles southwest of Abilene, Texas. Figs. 257-259, 262-264, 266-271. Male genitalia. 257. *Brachinus phaeocer* Chaudoir, 25.0 miles southwest of Abilene, Texas, ventral aspect. 258. Lateral aspect of same. 259. Dorsal aspect of same. 262. *Brachinus imporcitis* new species, Globe, Arizona, ventral aspect. 263. Lateral aspect of same. 264. Dorsal aspect of same. 266. *Brachinus consanguineus* Chaudoir, Rio Mayo, Sonora, Mexico, ventral aspect. 267. Lateral aspect of same. 268. Dorsal aspect of same. 269. *Brachinus azureipennis* Chaudoir, 2.0 miles north of El Mogote, Guerrero, Mexico, ventral aspect. 270. Lateral aspect of same. 271. Dorsal aspect of same. Accompanying scale lines equal 1.0 mm.



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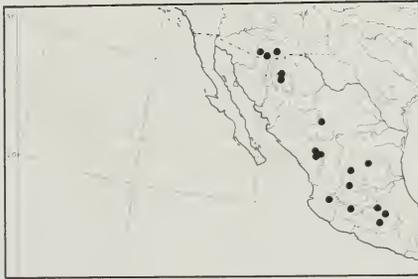
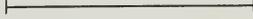
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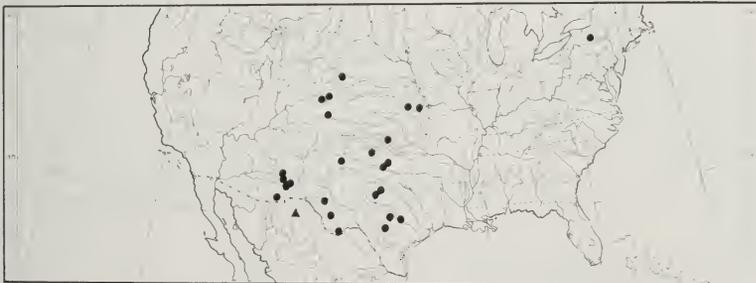
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Figs. 272-275. Right stylus of female ovipositor, ventral aspect. 272. *Brachinus consanguineus* Chaudoir, 41.4 miles north of Acapulco, Guerrero, Mexico. 273. *Brachinus azureipennis* Chaudoir, 2.0 miles north of El Mogote, Guerrero, Mexico. 274. *Brachinus imporcitis* new species, Pinal Creek, Arizona. 275. *Brachinus phaeocerus* Chaudoir, 25.0 miles south of Abilene, Texas. Figs. 276-279. Geographical distribution maps. 276. *Brachinus azureipennis* Chaudoir. 277. *Brachinus consanguineus* Chaudoir. 278. *Brachinus imporcitis* new species. 279. *Brachinus phaeocerus* Chaudoir. Accompanying scale line equals 1.0 mm.

Teneral adults were collected in May in Texas and in June in Oklahoma. Overwintering probably takes place as an adult.

Distribution. — (Fig. 279). The range of this species extends from Nebraska south to Chihuahua, Mexico. The distribution seems to be continuous to eastern Kansas, but a great discontinuity lies between Kansas and G. E. Ball's New York record. Ball recorded the capture of these specimens in his collecting notes, so there is no doubt that he took them alive near Ithaca, New York. To the west, these beetles extend to the east flank of the Chiricahua Mountains and the White Mountains of Arizona. They also range down the Gila River system into Arizona where they apparently hybridize with *B. imporcitis* new species. I have seen 213 specimens from the following localities:

MEXICO

CHIHUAHUA: (San Rafael) AMNH.

UNITED STATES

ARIZONA: Cochise County (Cave Creek Canyon, Portal) TCBA. COLORADO: Boulder County (Bear Creek Canyon) CARM, (Coal Creek, Marshall Lake Area) CARM, (Coal Creek, Plainview) CARM, (Coal Creek, east of Superior) CARM, (Four Mile Creek) CARM, (Left Hand Creek, Lyons) CARM, (Red Gulch, Lyons) CARM, (Rocky Flats Reservoir) CARM, (South Saint Vrain, east of Lyons) CARM; El Paso County (near Colorado Springs) UASM; Jefferson County (2.0 miles north of Golden) DHKa, TLEr; Weld County (Greeley) USNM. KANSAS: Douglas County (Lawrence) MCZ; Riley County (Manhattan) KSU. NEBRASKA: Banner County (Glen Rock Canyon) UNLN. NEW MEXICO: Catron County (Cooney Canyon, 10.0 miles east of Alma) UASM, (San Francisco Creek, 26.1 miles north of Glenwood) UASM; Grant County (18.0 miles north of Mimbres) TLEr, (Silver City) MCZ; Taos County (Rio Grande River, near Velarde) UASM. NEW YORK: Tompkins County (Ithaca) UASM. OKLAHOMA: Alfalfa County (No locality given) OSUS, Comanche County (Wichita National Forest) CAS; Jackson County (No locality given) CAS. TEXAS: Blanco County (Round Mountain) OUCO, (2.0 miles south of Round Mountain) UASM; Brewster County (Alpine) CAS, (Big Bend National Park) UASM; Culberson County (2.5 miles east of Nickel Creek Station) CNHM; Eastland County (No locality given) UMSP; Hemphill County (Canadian) USNM; Kerr County (10.0 miles north of Kerrville) UMSP; Taylor County (25.0 miles southwest of Abilene) CNHM; Travis County (Austin) WSUP.

Brachinus imporcitis new species

(Figs. 32, 261, 262, 263, 264, 274, 278)

Type locality. — Pinal Creek, Globe, Gila County, Arizona.

Type specimens. — The holotype male and allotype female are in CUNY. Both were collected at the type locality by A. and H. Dietrich on May 8, 1953 at an elevation of 5,500 feet. Fifteen paratypes collected at various localities on various dates are in AMNH, CAS, MCZ, TLEr, and UASM.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Small-sized beetles, 7.0 to 8.9 mm.

Color. Apex of antennal articles 3 and 4, metepisterna, and abdominal sterna and terga infuscated, otherwise ferruginous. Outer antennal articles usually dark. Dorsal surface and epipleura of elytra bright blue, with black sutural margins.

Microsculpture. As described for genus.

Macrosculpture. As in *phaeocerus*.

Head. As in *phaeocerus*, except antennal scape widest about middle.

Prothorax. As in *phaeocerus*, except proepisterna glabrous. Pronotum (fig. 261).

Pterothorax. As in *phaeocerus*, except humeri narrow, sloped and wings reduced outside stigma (fig. 32).

Abdomen. As described for genus.

Genitalia. Male (figs. 262, 263, 264). Median lobe with plane of shaft slightly rotated from plane of basal bend. Basal bend short. Apex of shaft narrowed to apex, slightly curved dorsally. Ligule short, broad, rounded apically. Virga (figs. 262, 263). Female (fig. 274). Stylus narrow, tapering to narrowly rounded apex.

Variation. — Intrapopulation variation occurs in the shape of the pronotum, and total size, otherwise the characters are constant.

Flight. — These beetles have never been recorded in flight and it is doubtful that they can fly.

Etymology. — Latin, *Imporcitis*, god of plowing; referring to the furrow-like costae of the elytra.

Life history. — Members of this species have been collected from May to September, and in January. Teneral adults have been collected in May at Bumble Bee, Arizona. Overwintering probably takes place as an adult.

Distribution. — (Fig. 278). The range of this species is confined to Arizona. In the San Simon Valley these beetles occur along the Gila River system where they apparently hybridize with *B. phaeocerus*. I have seen 81 specimens from the following localities:

UNITED STATES

ARIZONA: Cochise County (Chiricahua Mountains) UATA, USNM, (Chiricahua National Monument) CAS, (South West Research Station, 5.0 miles west of Portal) AMNH; Gila County (Globe) KSU, UMAH, (Middle Pioneer Camp, Pinal Mountains) UMNH, (Pinal Creek, Globe) CUNY, (base of Pinal Mountains) CAS, UATA, (Roosevelt Lake) UMAH; Greenlee County (Clifton) CAS; Pima County (Tucson) AMNH; Yavapai County AMNH, (Bumble Bee) CAS, (Crown King) CAS, (Monte Crypta Mine) CUNY, (Potter Creek, Prescott) CAS, (Prescott) CAS, MCZ, USNM; County unknown (Superstition Mountains) UATA.

Brachinus azureipennis Chaudoir

(Figs. 260, 269, 270, 271, 273, 276)

Brachynus azureipennis Chaudoir, 1876: 75. Lectotype, here selected, a male, MHNP, labelled "Matamoros," and "Ex Museo Chaudoir." *Type locality.* — Matamoros, Puebla, Mexico, as originally given by Chaudoir.

Diagnostic combination. — The black palpi, antennae, tibiae and tarsi, plus the metallic blue luster of the venter will separate these beetles from all others of the genus in North and Middle America.

Description. — Medium-sized beetles, 7.8 to 10.3 mm.

Color. Palpi, antennal articles 2-11, tibiae, tarsi, and elytra near suture, black. Metepisterna, metasternum at sides, and abdominal sterna and terga black with metallic blue luster, otherwise ferruginous. Dorsal surface and epipleura of elytra bright blue with black sutural margins.

Microsculpture. As described for genus.

Macrosculpture. As in *phaeocerus*.

Head. As in *phaeocerus*, except ligula with only two or three setae apically.

Prothorax. As in *phaeocerus*, except proepipleura and proepisterna completely pubescent.

Pterothorax. As in *phaeocerus*.

Abdomen. As described for genus.

Genitalia. Male (figs. 269, 270, 271). Median lobe with plane of shaft slightly rotated from plane of basal bend. Basal bend short. Apex of shaft narrow and elongate. Ligule moderately long, narrow, tapering to apex. Virga (figs. 269, 270). Female (fig. 273). Stylus broad at base, narrowed to acute apex.

Variation. — Intrapopulational variation occurs in the shape of the pronotum, body size and in the brightness of blue color of the elytra.

Flight. — The flight of these beetles has been recorded by F. G. Werner in Jalisco, Mexico.

Etymology. — French, *azur*, blue; Latin, *pennis*, wing; referring to the bright blue color of the elytra of these beetles.

Collecting notes. — G. E. Ball and D. R. Whitehead collected these beetles in a wet pasture beneath stones near El Mogote, Guerrero, Mexico. There was no water in the near vicinity.

Life history. — Members of this species have been collected in January and February, July and August, and October, but no teneral adults were seen.

Distribution. — (Fig. 276). The range of this species extends from southern Arizona south

to Guerrero, Mexico. I have seen 107 specimens from the following localities:

MEXICO

AGUASCALIENTES: (4.0 miles southwest of Aguascalientes) AMNH; (15.0 miles west of Pabellon) UMAH. CHIHUAHUA: (Madera) AMNH; (Primavera) AMNH; (Salaices) AMNH; (San Jose Babicora) AMNH. DISTRITO FEDERAL: (Temascaltepec) CAS. DURANGO: (Durango) AMNH; (15.0 miles west of Durango) CNC; (6.0 miles northeast of El Salto) AMNH; (Otinapa) AMNH. GUERRERO: (2.0 miles north of El Mogote) UASM. JALISCO: (Guadalajara) AMNH; (16.0 kilometers west of Jalostotitlan) MCZ. MEXICO: (4.3 miles north of Ixtapan de La Sal) UASM. MICHOACAN: (Tuxpan) RCGr. SAN LUIS POTOSI: (Puente La Parada, 7.5 miles northwest of Mexquitic) UASM. ZACATECAS: (Presa Choquen) JHen.

UNITED STATES

ARIZONA: Cochise County (San Pedro River, near Palominas) UASM, (South West Research Station, 5.0 miles west of Portal) AMNH; Santa Cruz County (Canelo) UATA.

Brachinus consanguineus Chaudoir
(Figs. 256, 266, 267, 268, 272, 277)

Brachynus consanguineus Chaudoir, 1876: 76. Lectotype, here selected, a male, MHNP, labelled "Ex Museo Chaudoir" and standing first of two specimens in front of box label "consanguineus Chaudoir, Mexique, Toluca Boucardi." *Type locality*. — Toluca, Mexico, as originally given by Chaudoir.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Medium-sized beetles, 10.2 mm.

Color. Antennal articles 3-11, metepisterna, and abdominal sterna and terga infuscated, otherwise ferruginous. Dorsal surface and epipleura of elytra bright blue with black sutural margins.

Microsculpture. As described for genus.

Macrosculpture. As in *phaeocerus*, except punctures finer.

Head. As in *phaeocerus*, except frontal furrow more deeply impressed, antennal scape widest apically, and ligula plurisetose.

Prothorax. As in *phaeocerus*, except sides widely reflexed, and proepipleura and proepisterna pubescent. Pronotum (fig. 256).

Pterothorax. As in *phaeocerus*.

Abdomen. As described for genus.

Genitalia. Male (figs. 266, 267, 268). Median lobe with plane of shaft rotated slightly from plane of basal bend. Basal bend short. Apex of shaft elongate, tubular. Ligule very short, truncate. Virga (figs. 266, 267). Female (fig. 272). Stylus narrow, longer than in *phaeocerus*, narrowed apically.

Variation. — Too few specimens are known to evaluate geographic variation.

Flight. — The flight of these beetles has not been recorded.

Etymology. — Latin, *consanguineus*, related by blood; probably referring to the similarity of these beetles to other members of the genus.

Life history. — Members of this species have been collected in August and December, but no teneral adults were seen.

Distribution. — (Fig. 277). The range of this species extends from Sonora to Guerrero along the western side of Mexico. I have seen four specimens from the following localities:

MEXICO

GUERRERO: (Rio Papagayo, 41.4 miles north of Acapulco) UASM. SINALOA: (28.0 miles east of Villa Union) CNC. SONORA: (Rio Mayo, Caramechi) CAS.

The *oaxacensis* subgroup

This subgroup is characterized as follows: virga elongate and strongly sclerotized, lateral pronotal setae lacking, and highly raised elytral costae. One species, *B. oaxacensis* new species, is included.

Brachinus oaxacensis new species
(Figs. 280, 290, 291, 292, 297, 300)

Type locality. — Twenty-five miles south of Mitla, Oaxaca, Mexico.

Type specimens. — The holotype male is in ISUA. The allotype female is in UASM. The male was collected at the type locality on January 4, 1956, by J. C. Schaffner. The female was collected by G. E. Ball and D. R. Whitehead on March 3, 1966 along the Rio Atoyac, near Juchatengo, Oaxaca. Three paratypes are in JHen, TLer, and UCD.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Medium-sized beetles, 10.2 to 10.6 mm.

Color. Sides of abdominal sterna slightly infuscated, otherwise ferruginous. Dorsal surface and epipleura of elytra bright bluish-green.

Macrosculpture. Frontal furrows and surface of pronotum finely rugose and punctate, punctures moderately impressed.

Head. Frontal furrows moderately impressed. Antennal scape cylindrical. Ligula with sclerotized center area ellipsoid-convex with two lateral rows of three setae per row. Mentum and submentum with accessory setae.

Prothorax. Pronotum (fig. 280) slightly convex, flattened along center line, sides slightly reflexed. Lateral setae absent. Proepipleura and proepisterna with numerous setae throughout their length. Anterior tibia with anterior surface strigose.

Pterothorax. Elytra elongate, broad, strongly costate. Humeral angle square. Depressions with numerous setae, costae smooth. Depression 1 with erect depression setae twice as long as elytral pubescence. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 290, 291, 292). Median lobe with plane of shaft rotated from plane of basal bend about 45°. Basal bend short. Apex of shaft broadly rounded. Ligule short, broad, rounded apically. Virga (figs. 290, 291). Female (fig. 297). Stylus narrow, parallel-sided, rounded apically.

Variation. — Too few specimens are known to evaluate geographic variation.

Flight. — The flight of these beetles has not been recorded.

Etymology. — Oaxaca, the place where the types are from; Latin, *ensis*, place, locality or county.

Collecting notes. — G. E. Ball and D. R. Whitehead collected one specimen of this species from under a rock at the edge of the Rio Atoyac, Oaxaca, Mexico.

Life history. — Members of this species have been collected in March, May, and December, but no teneral adults have been seen.

Distribution. — (Fig. 300). The range of this species extends from Sonora to Oaxaca. I have seen five specimens from the following localities:

MEXICO

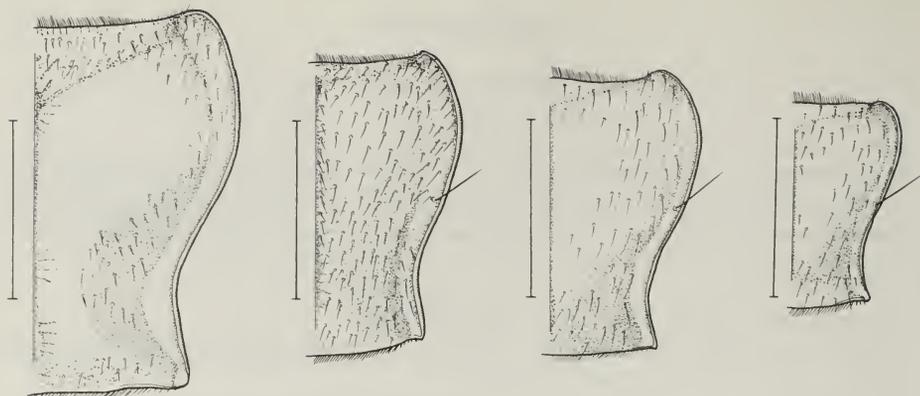
GUERRERO: (Cacahuamilpa) JHen. OAXACA: (Rio Atoyac, near Juchatengo) UASM; (25.0 miles south of Mitla) ISUA. SONORA: (10.0 miles southeast of Alamos) UCD.

The *patruelis* subgroup

The members of this subgroup are characterized by the short median lobe, with three ligules, and their narrow sloped humeri. One species, *B. patruelis* LeConte, is included.

Brachinus patruelis LeConte
(Figs. 282, 284, 285, 286, 296, 301)

Brachinus patruelis LeConte, 1844: 50. Lectotype, here selected, a female, MCZ red type label number 5842, further labelled with a pink disc and "B. conformis Dej. patruelis LeC." *Type locality.* — New York, as originally given by LeConte.

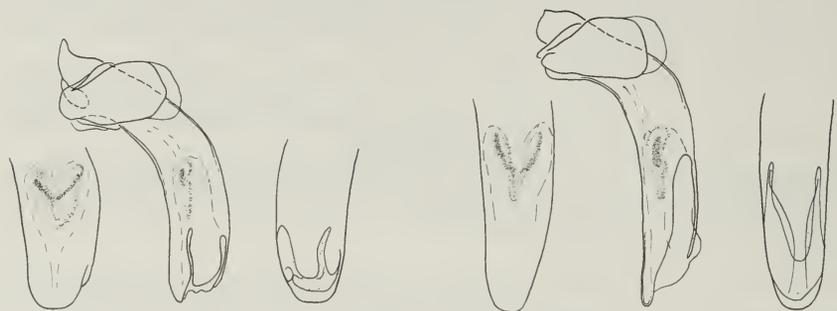


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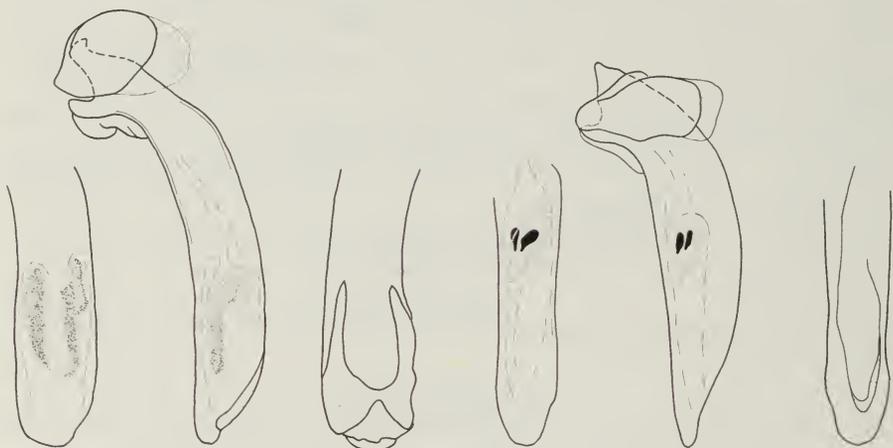
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Figs. 280-283. Pronotum, right half, dorsal aspect. 280. *Brachinus oaxacensis* new species, Rio Atoyac, Oacaca, Mexico. 281. *Brachinus ovipennis* LeConte, Charlotte, Vermont. 282. *Brachinus patruelis* LeConte, Towaco, New Jersey. 283. *Brachinus conformis* Dejean, Archbold Research Station, Florida. Figs. 284-295. Male genitalia. 284. *Brachinus patruelis* LeConte, Fall River, Massachusetts, ventral aspect. 285. Lateral aspect of same. 286. Dorsal aspect of same. 287. *Brachinus conformis* Dejean, Archbold Research Station, Florida, ventral aspect. 288. Lateral aspect of same. 289. Dorsal aspect of same. 290. *Brachinus oaxacensis* new species, Cacahuamilpa, Guerrero, Mexico, ventral aspect. 291. Lateral aspect of same. 292. Dorsal aspect of same. 293. *Brachinus ovipennis* LeConte, Prince Edward County, Ontario, Canada, ventral aspect. 294. Lateral aspect of same. 295. Dorsal aspect of same. Accompanying scale lines equal 1.0 mm.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Small-sized beetles, 5.7 to 8.3 mm.

Color. Antennal articles 3 and 4, mesepisterna, metepisterna, metasternum at sides, and abdominal sterna and terga infuscated, otherwise ferruginous. Dorsal surface and epipleura of elytra blue.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows rugose, sparsely punctate. Surface of pronotum sparsely punctate, punctures barely impressed.

Head. Frontal furrows moderately impressed. Antennal scape robust, widest at middle. Ligula with sclerotized center area ellipsoid-convex with two apical setae. Mentum and submentum without accessory setae.

Prothorax. Pronotum (fig. 282) convex, slightly flattened along center line, sides moderately reflexed. Proepipleura glabrous. Proepisterna with a few setae both anteriorly and posteriorly, glabrous medially. Anterior tibia with anterior surface strigose.

Pterothorax. Elytra short, weakly costate. Humeral angle narrow, sloped. Costae and depressions pubescent. Metasternum short, its length less than diameter of middle coxa. Wings reduced outside stigma, as in figure 32.

Abdomen. As described for genus.

Genitalia. Male (figs. 284, 285, 286). Median lobe with plane of shaft slightly rotated from plane of basal bend. Basal bend short. Median lobe very short and robust. Apex of shaft broadly rounded. Ligule short, broad, with two lateral accessory ligules. Virga (figs. 284, 285). Female (fig. 296). Stylus short, narrow, narrowly rounded apically.

Variation. — Intrapopulation variation occurs in the shape of the pronotum, body size, and in the prominence of the humeri.

Flight. — The flight of these beetles has not been recorded, and it is probable that they cannot fly.

Etymology. — Latin, *patruelis*, cousin, kin; referring probably to the similar habitus of these beetles to other *Brachinus* species.

Life history. — Members of this species have been collected from April to September. Teneral adults were collected in May in Massachusetts.

Distribution. — (Fig. 301). The range of this species extends from Massachusetts south to New Jersey. Western populations are in Michigan and Illinois. I have seen 61 specimens from the following localities:

UNITED STATES

CONNECTICUT: New London County (Old Lyme) CAS. ILLINOIS: (No locality given) ISNH. MASSACHUSETTS: Bristol County (Fall River) CAS; Middlesex County (Framingham) CAS, UNLN, (Newton) MCZ; Norfolk County (Brookline) MCZ; Plymouth County (Marion) MCZ; Suffolk County (Boston) CAS, (Dorchester) MCZ, UMAH; County unknown (Blue Hills) ISUA, USNM, (Forest Hills) USNM, (Freetown) CAS. MICHIGAN: Wayne County (Detroit) CAS. NEW JERSEY: Bergen County (Fort Lee) CAS; Burlington County (Atsion) CAS; Morris County (Towaco) USNM; Warren County (Great Piece Meadows) AMNH. NEW YORK: New York County (Staten Island) CAS, (Yonkers) CNHM; Suffolk County (Southold) CUNY; County unknown (Newtown, Long Island) CAS.

The *conformis* subgroup

This subgroup is characterized as follows: median lobe small, narrow, and chisel-shaped, and stylus of female ovipositor elongate and narrow. One species, *B. conformis* Dejean, is included.

Brachinus conformis Dejean (Figs. 283, 287, 288, 289, 298, 302)

Brachinus conformis Dejean, 1831: 427. Lectotype, here selected, a female, MHNP, labelled "conformis m. in Amer. bor." on green paper, "LeConte" and "Ex Museo Chaudoir" on white paper. *Type locality.* — North America, as originally given by Dejean, but herewith restricted to Florida.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Small-sized beetles, 5.0 to 8.0 mm.

Color. Terminal palpal articles, antennal articles 2, 3, and 4, metepisterna, and abdominal



300



301



302



303

Figs. 296-299. Right stylus of female ovipositor, ventral aspect. 296. *Brachinus patruelis* LeConte, Fall River, Massachusetts. 297. *Brachinus oaxacensis* new species, Rio Atoyac, Guerrero, Mexico. 298. *Brachinus conformis* Dejean, Archbold Research Station, Florida. 299. *Brachinus ovipennis* LeConte, Ithaca, New York. Figs. 300-303. Geographical distribution maps. 300. *Brachinus oaxacensis* new species. 301. *Brachinus patruelis* LeConte. 302. *Brachinus conformis* Dejean. 303. *Brachinus ovipennis* LeConte. Accompanying scale line equals 1.0 mm.

sterna and terga infuscated, otherwise ferrugineous. Dorsal surface and epipleura of elytra blue.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows and surface of pronotum punctate and microrugose, punctures barely impressed.

Head. Frontal furrows shallowly impressed. Antennal scape robust, widest at middle. Ligula with sclerotized center area ellipsoid-convex with two lateral rows of three setae per row. Mentum and submentum without accessory setae.

Prothorax. Pronotum (fig. 283) convex, slightly flattened along center line, sides barely reflexed. Proepipleura and proepisterna pubescent both anteriorly and posteriorly, glabrous medially. Anterior tibia with anterior surface strigose.

Pterothorax. Elytra elongate, narrow, moderately costate. Humeral angle square. Costae smooth, glabrous on disc, depressions between costae pubescent. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 287, 288, 289). Median lobe with plane of shaft barely rotated from plane of basal bend. Basal bend short. Shaft straight, narrow, flattened, apex narrowly rounded. Ligule short, narrowed apically, rounded at apex. Virga (figs. 287, 288). Female (fig. 298). Stylus elongate, narrow, rounded apically.

Variation. — Too few specimens are known to evaluate geographic variation.

Flight. — These beetles have been collected at lights repeatedly in Florida.

Etymology. — Latin, *conformis*, similar; referring to the similarity between these beetles and those of other species in the genus.

Life history. — Members of this species have been collected in May, June, and November, and no general adults have been seen.

Distribution. — (Fig. 302). The range of this species extends from middle Florida to northern Florida. I have seen 34 specimens from the following localities:

UNITED STATES

FLORIDA: Alachua County (Gainesville) USNM; Duval County (Jacksonville) OUCO; Highlands County (Archbold Biology Station) PSUU, (Highlands Hammock State Park) TLER; Osceola County (Kissimmee) USNM; Pinellas County (Dunedin) PUM; Putnam County (Welaka) CUNY.

The *ovipennis* subgroup

This subgroup is characterized by compressed and collapsed median lobe, the orientation of the virga in the median lobe, and the ovate elytra. One species, *B. ovipennis* LeConte, is included.

Brachinus ovipennis LeConte

(Figs. 281, 293, 294, 295, 299, 303)

Brachinus ovipennis LeConte, 1862: 525. Lectotype, here selected, a male, MCZ red type label number 31,774, further labelled with a pink disc, "89" and "B. cephalotes LeC, perplexus Dej, cephalotes LeC, ovipennis LeC." *Type locality.* — Middle states, as indicated by LeConte's pink disc, but herewith restricted to Vermont.

Brachinus cephalotes LeConte, 1862: 525. *Lapsus calami*.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Medium-sized beetles, 7.4 to 10.7 mm.

Color. Metepisterna and sides of abdomen infuscated, otherwise ferrugineous. Dorsal surface and epipleura of elytra blue.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows and surface of pronotum rugose and punctate, punctures barely impressed.

Head. Frontal furrows moderately impressed. Antennal articles robust, widest about middle. Ligula with sclerotized center area ellipsoid-convex with two lateral rows of three setae per row. Mentum with one to four accessory setae at middle. Submentum with accessory setae.

Prothorax. Pronotum (fig. 281) slightly convex, flattened along center line, sides slightly reflexed. Proepipleura and proepisterna pubescent both anteriorly and posteriorly, glabrous medially. Anterior tibia with anterior surface punctate, punctures in some specimens fused to form weak strigae.

Pterothorax. Elytra elongate, narrow, weakly costate. Humeral angle sloped. Costae and depressions pubescent. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 293, 294, 295). Median lobe with plane of shaft rotated 45° from plane of basal bend. Basal bend short. Apex of shaft narrowly rounded. Dorsal surface of median lobe usually collapsed, ligule ill-defined. Virga (figs. 293, 294), oriented sideways in median lobe. Female (fig. 299). Stylus short, narrow, narrowly rounded at apex.

Variation. — Intrapopulational variation occurs in body size, shape of the pronotum, shape of antennal scape, and amount of area infuscated on venter.

Flight. — The flight of these beetles has not been recorded.

Etymology. — Latin, *ovum*, egg; *pennis*, wing; referring to the ovoid-shaped elytra of these beetles.

Collecting notes. — R. T. Bell collected these beetles at the edge of ponds in Vermont, and V. M. Kirk collected them in pitfall traps in cornfields in South Dakota.

Life history. — Members of this species have been collected from March to October. Teneral adults were collected in April in New York, and in September in Indiana, Kansas, and New York. Overwintering probably takes place as an adult.

Distribution. — (Fig. 303). The range of this species extends from New England and Quebec, west to Kansas and South Dakota, south to Texas. I have seen 528 specimens from the following localities:

CANADA

ONTARIO: (Belleville) CNC; (Brimley) ZMLS; (Cedarvale) CAS; (De Cew Falls) CNC; (Erindale) CAS; (Forest Hill Village) CAS; (Point Pelee) ZMLS; (Prince Edward County) CAS, CUNY, MCZ; (Sarnia) UMAH; (Toronto) CAS, CNC, MCZ, ZMLS.

UNITED STATES

CONNECTICUT: Litchfield County (Cornwall) CAS; New Haven County (New Haven) CAS. ILLINOIS: Alexander County (Cairo) ISNH; Cook County (Chicago) CAS, (Evanston) UMAH, (Glencoe) UMAH, (La Grange) CAS, (Riverside) UMAH, (Schiller Park) CNHM; Lake County (Lake Zurich) RTBe, (Waukegan) USNM; Madison County (Mitchell) USNM; Mason County (Havana) ISNH; Rock Island County (Rock Island) UMAH. INDIANA: Knox County (No locality given) PUM; Posey County (Hovey) CEWh, PUM, (Mount Vernon) CEWh. IOWA: Dickenson County (Lake Okoboji) USNM; Johnson County (Iowa City) USNM. KANSAS: Douglas County (Lawrence) PUM, UMAH; Geary County (No locality given) KSU; Hamilton County (No locality given) CAS; McPherson County (McPherson) CMPP; Sedgwick County USNM, (Wichita) CAS; Seward County (No locality given) KSU. MASSACHUSETTS: Hampden County (Chicopee) MCZ, USNM. MICHIGAN: Huron County (Charity Island) UMAH; Kent County (Grand Rapids) UNLN; Macomb County (Mount Clemens) CNHM; Saint Clair County (Port Huron) USNM; Washtenaw County USNM, (Ann Arbor) JSch, UMAH, (Salem) UMAH; Wayne County (Detroit) USNM; County unknown (Pentwater) CNHM. MINNESOTA: Goodhue County (Lake Pepin, east of Frontenac) UMSP, Houston County (No locality given) UMSP; County unknown (Cook Creek) UMSP. MISSOURI: Saint Louis County (Webster Groves) USNM. NEBRASKA: Douglas County (Omaha) UNLN; Lancaster County (Lincoln) UNLN; Otoe County (Nebraska City) UNLN. NEW YORK: Cayuga County (Montezuma marsh) UASM; Chautauqua County (Dunkirk) CAS; Columbia County (Copake Falls) CNHM; Dutchess County (Red Hook) UMSP; Erie County (Buffalo) ANSP, CAS, CMPP, ISNH, USNM, (Hamburg) CAS; Genesee County (East Bethany) FDAG; Monroe County (Honeoye Falls) CUNY, (Rochester) LACM, MCZ; New York County (Bronx Park) CAS, (Staten Island) MCZ; Niagara County (Olcott) CUNY; Ontario County (Canandaigua) MCZ; Oswego County (Minetto, Oswego) CUNY; Tompkins County (Groton) UCD, (Ithaca) CAS, CUNY, GRNo, ISNH, KSU, MCZ, OUCO, PSUU, UASM, UCR, UNLN, (Six Mile Creek, Ithaca) TLER; Schuyler County (Watkins Glen) VMKi; Wyoming County (Gainesville) CUNY; County unknown (Atwaters) USNM, (Danby) UNLN. OHIO: Ashtabula County (Conneaut) PUM, (Rock Creek) PUM, (Saybrook) PUM; Cuyahoga County (Berea) USNM; Hamilton County (Cincinnati) UMAH; Lake County (Perry) PUM; Lucas County (No locality given) PUM; Ottawa County (Gypsum) OUCO; Sandusky County (Winous Point) SJSC. OKLAHOMA: Cleveland County (No locality given) UONO; Comanche County (Wichita National Forest) CAS. PENNSYLVANIA: Allegheny County (Pittsburgh) CMPP; Crawford County (Conneaut Lake) CMPP; Erie County (Fort Erie) CAS; Tioga County (Rut-

land) ANSP. RHODE ISLAND: Washington County (Watch Hill) USNM. SOUTH DAKOTA: Bennett County (Martin) VMKi; Brookings County (Brookings) SDSU, VMKi, (Volga) VMKi, (White) VMKi; Butte County (Belle Fourche) VMKi; Harding County (Buffalo) VMKi; Hutchinson County (Menno) VMKi; Jones County (Murdo) SDSU; Lawrence County (Spearfish) VMKi; Meade County (Bear Butte) VMKi. TEXAS: Dallas County (Dallas) MCZ. VERMONT: Addison County (Ferrisburg) UMAH; Chittenden County (Burlington) UATA, (Home Creek Delta, Charlotte) RTBe, (Shelburne) CAS, (Shelburne Pond, Shelburne) RTBe; Franklin County (La Moille River, East Georgia) RTBe; Grand Isle County (Alburg) ISNH. WISCONSIN: Dane County (Madison) UMMW; Green County (Brodhead) UMAH; Milwaukee County (No locality given) UMMW.

The *tenuicollis* subgroup

This subgroup is characterized as follows: median lobe elongate and narrow, elytra large, square, and strongly costate, and mesepisterna infuscated. One species, *B. tenuicollis* LeConte, is included.

Brachinus tenuicollis LeConte

(Figs. 307, 312, 313, 314, 324, 329)

Brachinus tenuicollis LeConte, 1844: 49. Lectotype, here selected, a female, MCZ red type label number 5849, further labelled with a pink disc and "v. *librator* Dej., *similis* LeC., 79 = *tenuicollis* - cat., *similis*." *Type locality*. — New York, as originally given by LeConte.

Brachinus ballistarius LeConte, 1848: 199. Lectotype, here selected, a male, MCZ red type label number 5846, further labelled with a pink disc. *Type locality*. — New York, as originally given by LeConte. NEW SYNONYMY.

Brachinus similis LeConte, 1848: 199. Lectotype, here selected, a female, MCZ red type label number 5849, further labelled as above. *Type locality*. — New York, as originally given by LeConte. NEW SYNONYMY.

Diagnostic combination. — The large size, strongly costate elytra, and infuscated mesepisterna separate these beetles from all others in North America.

Description. — Large-sized beetles, 11.9 to 14.5 mm.

Color. Mesepisterna, mesepimera, metepisterna, metasternum at sides, and abdominal sterna and terga infuscated to black. Antennal articles 3 and 4 infuscated at apex in some specimens, otherwise beetles ferruginous. Dorsal surface and epipleura of elytra blue.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows and disc of pronotum rugose and punctate, punctures barely impressed.

Head. Frontal furrows moderately impressed. Antennal scape cylindrical, or almost so. Ligula with sclerotized center area ellipsoid-convex with two lateral rows of three setae per row. Mentum and submentum without accessory setae.

Prothorax. Pronotum (fig. 307) slightly convex, flattened along center line, sides slightly reflexed. Proepipleura and proepisterna with or without setae. Anterior tibia with anterior surface punctate.

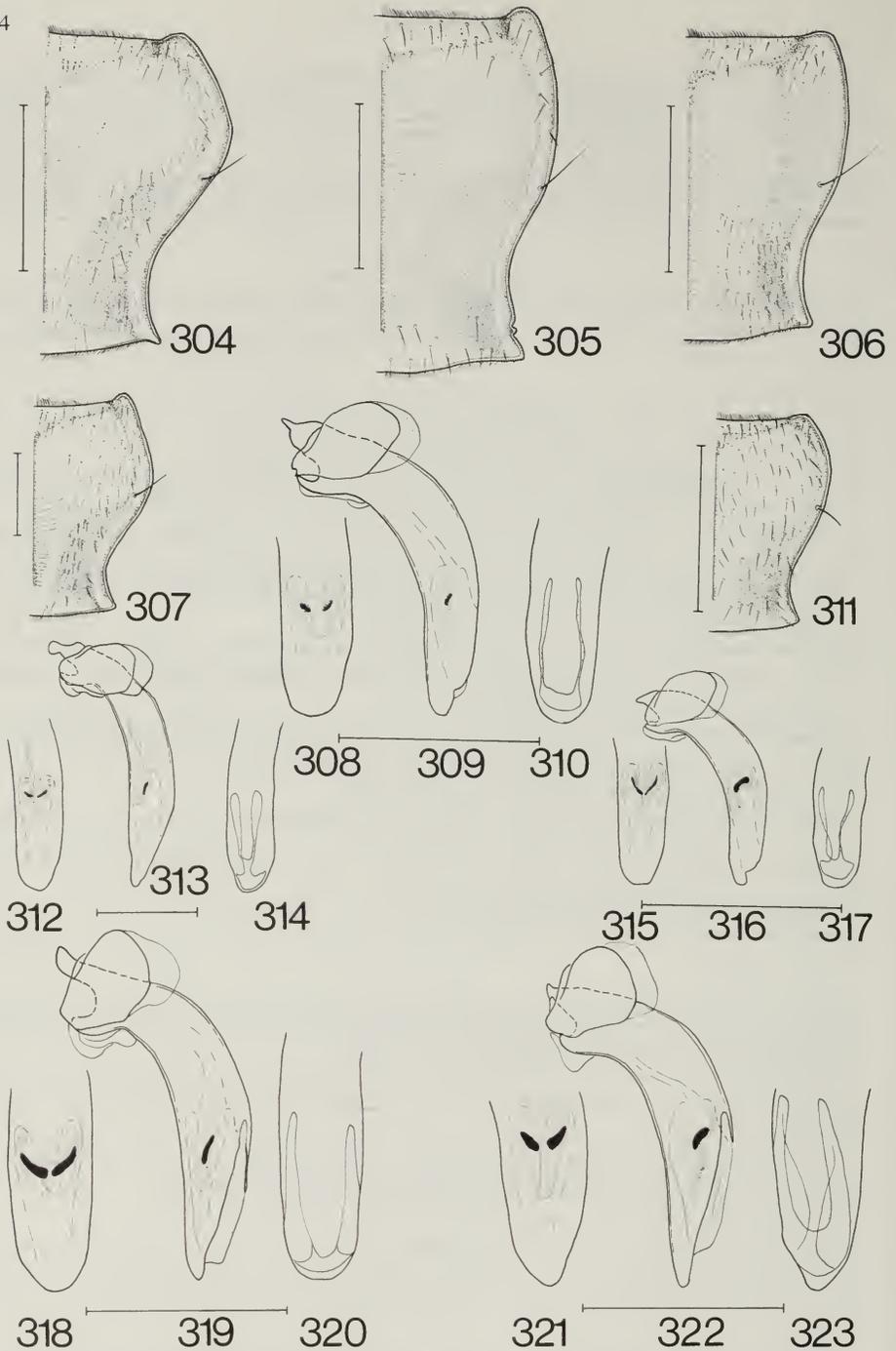
Pterothorax. Elytra elongate, broad, strongly costate. Humeral angle square. Depressions pubescent, costae at least on disc glabrous, smooth. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 312, 313, 314). Median lobe with plane of shaft slightly rotated from plane of basal bend. Basal bend short. Apex of shaft narrow, almost acute. Ligule short, narrow, truncate. Virga (figs. 312, 313). Female (fig. 324). Stylus broad, rounded apically.

Variation. — Intrapopulational variation occurs in the shape of the pronotum and in body size. The proepipleura and proepisterna are glabrous or setose, the setae either spread uniformly over the surface, or restricted anteriorly and posteriorly.

Flight. — These beetles have been collected repeatedly at lights throughout the range of the species.



Figs. 304-307, 311. Pronotum, right half, dorsal aspect. 304. *Brachinus cyanipennis* Say, Milton, Vermont. 305. *Brachinus galactoderus* new species, Rio Papagayo, Guerrero, Mexico. 306. *Brachinus gebhardis* Erwin, Horse Creek, California. 307. *Brachinus tenuicollis* LeConte, Olcott, New York. 311. *Brachinus medius* Harris, Ritzville, Washington. Figs. 308-310, 312-323. Male genitalia. 308. *Brachinus cyanipennis* Say, Milton, Vermont, ventral aspect. 309 & 310. Lateral & dorsal aspects of same. 312. *Brachinus tenuicollis* LeConte, Olcott, New York, ventral aspect. 313 & 314. Lateral & dorsal aspects of same. 315. *Brachinus medius* Harris, Atbara, British Columbia, Canada, ventral aspect. 316 & 317. Lateral & dorsal aspects of same. 318. *Brachinus galactoderus* new species, 12.0 miles south of Gusave, Sinaloa, Mexico, ventral aspect. 319 & 320. Lateral & dorsal aspects of same. 321. *Brachinus gebhardis* Erwin, Gilroy Hot Springs, California, ventral aspect. 322 & 323. Lateral & dorsal aspects of same. Accompanying scale lines equal 1.0 mm.

Etymology. — Latin, *tenuis*, thin; *collis*, neck; referring to the narrow pronotum of these beetles.

Life history. — C. H. Lindroth informs me that H. G. James (Belleville, Ontario) reared at least two specimens of this species from pupal cells of *Hydrophilus obtusus* Say (Chatterton, Ontario, 2.VIII.56). These beetles have been collected from March to September. It is probable that adults overwinter much the same as in *B. pallidus*.

Distribution. — (Fig. 329). The range of this species extends from Colorado and western Texas to the east coast from Massachusetts to Maryland and in Florida. The California record is doubtful. I have seen 649 specimens from the following localities:

CANADA

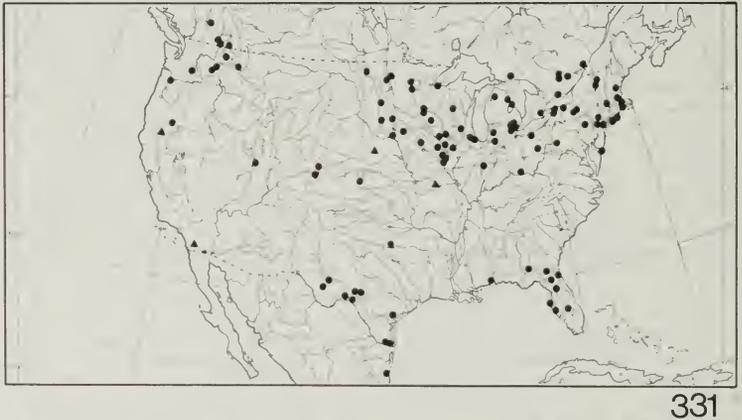
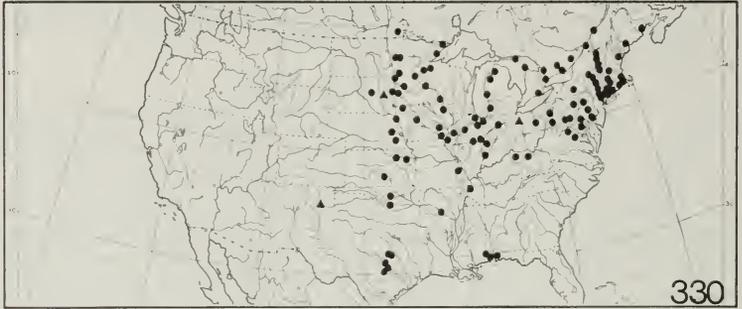
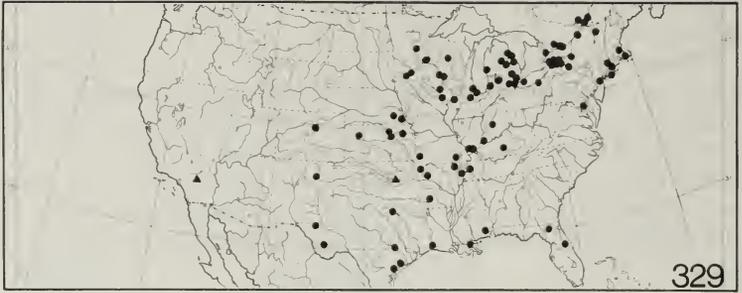
ONTARIO: (Belleville) RTBe; (Chatterton) ZMLS; (De Cew Falls) CNC; (Point Pelee) ROM; (Prince Edward County) CUNY, UATA, UCD; (Toronto) RTBe; (Trenton) CAS, CNC. QUEBEC: (Hull) USNM; (Montreal) CAS; (Outrem't) CAS; (Rigaud) CAS; (Saint Eustache) CAS; (Saint Rose) CAS.

UNITED STATES

ARKANSAS: Benton County (Rogers) KSU; Conway County (No locality given) UAFA; Hempstead County (Hope) MCZ; Lawrence County (Imboden) MCZ; Mississippi County (Osceola) JSch, UMAH; Washington County (No locality given) UAFA. CALIFORNIA: (No locality given) UMSP. COLORADO: Boulder County (Reservoir, Four Mile Mesa) CArm. CONNECTICUT: Hartford County (Windsor) MCZ; New London County (Old Lyme) CAS. FLORIDA: Columbia County (O'Leno State Park) CUNY; Seminole County (Sanford) PUM. ILLINOIS: Cook County (Chicago) UMAH, WSUP, (Elk Grove) CMPP, (La Grange) CAS, JSch, MCZ, UMAH, USNM, ZMLS, (Palos Park) RCGr, (Riverside) ANSP; Gallatin County (Shawneetown) ISNH; Lake County (Fort Sheridan) UMAH; La Salle County (No locality given) RTBe; Rock Island County (Moline) UMSP; Union County (Alto Pass) CNHM; Counties unknown (Falling Spring) UMAH, (Fountain Bluff) ISNH. INDIANA: Knox County (No locality given) PUM; Marion County (No locality given) PUM; Porter County (Dunes Beach) CEWh; Posey County (Hovey Lake) CEWh, PUM; Tippecanoe County (Lafayette) PUM; Vigo County (No locality given) PUM. IOWA: Buchanan County (Independence) MCZ; Johnson County (Iowa City) USNM. KANSAS: Ellis County (No locality given) KSU; Douglas County (No locality given) CAS; Riley County (No locality given) KSU; Shawnee County (Topeka) CMPP; County unknown (Williston) MCZ. KENTUCKY: Edmonson County (Mammoth Cave Nat Pk) TCBA. LOUISIANA: Calcasieu Parish (Sam Houston State Park) CUNY; East Baton Rouge Parish (Baton Rouge) LSUB. MARYLAND: Charles County (No locality given) MCZ. MASSACHUSETTS: Middlesex County (BillERICA) MCZ; (Boston) CAS, (Concord) MCZ, (Sudbury) MCZ, (Tyngsboro) CAS, (Waltham) MCZ, (Wayland) MCZ; Norfolk County (Dover) MCZ, (Newton) MCZ; Suffolk County (West Roxbury) MCZ; County unknown (Forest Hills) USNM. MICHIGAN: Allegan County (Allegan) CAS; Clinton County UMAH (Bath) JSch; Eaton County (Grand Ledge) USNM; Genesee County (Flint) RCGr; Gratiot County (No locality given) JSch, UMAH; Huron County (Charity Island) UMAH; Ingham County (Haslett) OSUS; Iosco County (No locality given) UMAH; Kent County (Grand Rapids) CNHM, OSUS; Lapeer County (Sawdel Lake) RCGr, UMAH; Livingston County (E. S. George Reserve) OSUS, UMAH; Macomb County (Mount Clemens) CNHM; Midland County (No locality given) JSch; Oakland County (No locality given) OSUS, UMAH; Saginaw County (No locality given) UMAH; Van Buren County (Paw Paw Lake) UMAH; Washtenaw County OSUS, (Ann Arbor) UMAH, (Whitmore Lake) CCha, JSch; Wayne County (Rockwood) UMAH; Wayne County (Detroit) MCZ, UMAH, USNM, (Eight Mile Road) UMAH; Counties unknown (Aurelius) OSUS, (Dun Scotus) PSUU. MINNESOTA: Dakota County (No locality given) UMSP; Hennepin County (No locality given) UMSP; Houston County (3.0 miles north of Hokah) UMSP; LeSeuer County (Lake Madison) UMSP; Nicollet County (Saint Peter) UMSP; Pine County (mouth of Snake River) UMSP, (4.0 miles east of Pine City) USNM; Ramsey County (Saint Paul) ISNH; Washington County (Saint Croix River) UMSP; Watonwan County (No locality given) UMSP. MISSISSIPPI: George County (Lucedale) CUNY. MISSOURI: Carter County (Van Buren) UMAH; Vernon County (Nevada Area) TLER. NEBRASKA: Lancaster County (Lincoln) UNLN; Nemaha County (Peru) UNLN. NEW JERSEY: Essex County (Cedar Grove) USNM; Morris County (Boonton) USNM, (Lincoln Park) CAS, CNHM, (Towaco) USNM. NEW MEXICO: San Miguel County (Las Vegas) CMPP. NEW YORK: Cayuga County (Montezuma Marsh) UASM; Erie County (Buffalo) ISNH, MCZ; Genesee County (Batavia) CUNY; Monroe County (Rochester) LACM, MCZ; New York County (Cypress Hills) AMNH; Niagara County (Olcott) CUNY; Ontario County (Canandaigua) MCZ; Oswego County (Oswego) ANSP, CUNY; Saint Lawrence County (Rоссie) JSch; Tompkins County (Ithaca) CAS, CUNY, MCZ; County unknown (Meadowdale) CUNY. OHIO: Ashtabula County (Rock Creek) PUM. OKLAHOMA: (No locality given) CCha. TENNESSEE: Lake County (Gray's Landing) RTBe. TEXAS: Brazos County (College Station) TAMU; Brewster County (Alpine) MCZ; Dallas County (Dallas) MCZ; Hudspeth County (9.0 miles southwest of Del City) AMNH; San Patricio County (Welder Wildlife Refuge, near Sinton) CNC; Victoria County (Victoria) USNM; County unknown (Fuller) USNM. VERMONT: Chittenden County (Burlington) RTBe, (Shelburne Pond, Shelburne) RTBe. WISCONSIN: Calumet County (No locality given) PUM; Crawford County (Wauzeka) UWMW; Dane County (No locality given) UWMW; Wood County (Griffith Street Nursery) UWMW, (Port Edwards) UWMW.

The *cyanipennis* subgroup

This subgroup is characterized by: median lobe with broad ligule, pronotum strongly cordate, and erect depression setae two to three times as long as the elytral pubescence. One species, *B. cyanipennis* Say, is included.



Figs. 324-328. Right stylus of female ovipositor, ventral aspect. 324. *Brachinus tenuicollis* LeConte, La Grange, Illinois. 325. *Brachinus galactoderus* new species, Lake Tehuantepec, Oaxaca, Mexico. 326. *Brachinus cyanipennis* Say, East Georgia, Vermont. 327. *Brachinus gebhardis* Erwin, Uvas Creek, California. 328. *Brachinus medius* Harris, McLeans Bogs, New York. Figs. 329-333. Geographical distribution maps. 329. *Brachinus tenuicollis* LeConte. 330. *Brachinus cyanipennis* Say. 331. *Brachinus medius* Harris. 332. *Brachinus gebhardis* Erwin. 333. *Brachinus galactoderus* new species. Accompanying scale line equals 1.0 mm.

Brachinus cyanipennis Say (Figs. 304, 308, 309, 310, 326, 330)

Brachinus cyanipennis Say, 1823: 143. Neotype designated by me, a male, in MCZ. The specimen was selected from University of Iowa material, and sent to Lindroth. He subsequently deposited all Say's neotypes in MCZ. *Type locality*. — Ames, Iowa. This locality is the nearest to Say's original area from which we had specimens. The original area was "fissures of the rocks . . . near Engineer Cantonment" near Council Bluffs, Iowa.

Brachinus cephalotes Dejean, 1825: 317. Lectotype, here selected, a male, MHNP, labelled "cephalotes mihi in Amer. Bor." "Latreille" and "Ex Museo Chaudoir" and standing first, in first of two rows below box label "cyanipennis Say." *Type locality*. — "Amerique septentrionale" as originally given by Dejean. NEW SYNONYMY.

Brachinus cordicollis LeConte, 1862: 525. *Lapsus calami*.

Brachinus rejectus LeConte, 1862: 525. Lectotype, here selected, a female, MCZ red type number 5843, further labelled with a pink disc and "B. cordicollis LeC. cyanipennis Say, cordicollis LeC., rejectus LeC." *Type locality*. — Kansas, as originally given by LeConte. NEW SYNONYMY.

Diagnostic combination. — The erect depression setae of the elytra standing 2 to 3 times higher than the elytral pubescence separate these beetles from all others in the United States.

Description. — Medium-sized beetles, 8.0 to 12.0 mm.

Color. Metepisterna usually infuscated, otherwise ferruginous. Dorsal surface and epipleura of elytra blue.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows and surface of pronotum rugose and punctate, punctures moderately impressed.

Head. Frontal furrows moderately impressed. Antennal scape robust, widened apically. Ligula with sclerotized center area ellipsoid-convex with two lateral rows of three setae per row. Mentum of some specimens with one or two small setae at center, submentum without accessory setae.

Prothorax. Pronotum (fig. 304) convex, strongly cordiform, sides moderately reflexed. Proepipleura and proepisterna with a few scattered setae both anteriorly and posteriorly, glabrous medially. Anterior tibia with anterior surface strigose.

Pterothorax. Elytra moderately long, narrow, moderately costate. Humeral angle square. Costae smooth on disc, otherwise pubescent, depressions pubescent. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 308, 309, 310). Median lobe with plane of shaft slightly rotated from plane of basal bend. Basal bend long. Apex of shaft blunt. Ligule short, widened apically, truncate. Virga (figs. 308, 309). Female (fig. 326). Stylus long, narrow, almost acute apically.

Variation. — Intrapopulation variation occurs in the following characteristics: the center of the mentum bears or lacks a few accessory setae; the antennal articles 3 and 4, metepisterna, and sides of the abdomen are or are not infuscated; the apex of the shaft is or is not notched; and the virga is narrowly or broadly rounded apically.

Flight. — These beetles have been recorded at lights in South Dakota.

Eymology. — Greek, *kyanos*, blue; Latin, *pennis*, wing; referring to the blue elytra of these beetles.

Collecting notes. — C. Chantal collected these beetles on river terraces above the Becancour River in Quebec. The beetles were beneath stones on sandy clay.

Life history. — Members of this species have been collected from March to October. Teneral adults were collected in May in Kansas. Overwintering probably takes place as an adult.

Distribution. — (Fig. 330). The range of this species extends from New Brunswick through New England, west to New Mexico, and south to Texas and Alabama. I have seen 2,095 specimens from the following localities:

CANADA

MANITOBA: (Lake Jessica, northeast of Winnipeg) UASM, NEW BRUNSWICK: (Saint John) USNM, ONTARIO: (Belleville) ZMLS; (Go Home Bay) CNC; (Kenora) ZMLS; (2.0 miles north of Little Current) UASM; (Marmora) CNC; (Oliphant, Bruce Peninsula Lake Huron) ZMLS; (Otter Lake, 9.0 miles south of Smith Falls) CCh; (Presque Isle) UASM; (Sever) CMPP; (Toronto) CAS, RTBe; (Walsingham, southwest of Simcoe) ZMLS, QUEBEC: (Beaucour) CCh, OSUC; (Como) CNC, CUNY, MCZ; (Montreal) MCZ; (Outrem't) CAS; (Rigaud) CAS, CCh; (Saint Ours) CCh; (Terre'ne) CAS.

UNITED STATES

ALABAMA: Baldwin County (No locality given) UASM; Mobile County (Calvert) ANSP, UASM, (Mobile) CAS. ARKANSAS: Pulaski County (Little Rock) AMNH. CONNECTICUT: Fairfield County (Canbury) AMNH; Hartford County (Burlington) ISUA; Litchfield County AMNH, (Cornwall) CAS, CUNY; New Haven County (Hamden) CAS, (New Haven) CAS, (South Meriden) CAS, MCZ; Tolland County (Union) ISUA; County unknown (Yoshen) AMNH. DISTRICT OF COLUMBIA: (Black Pond) USNM, (Rock Creek, Washington) USNM. ILLINOIS: Champaign County (Urbana) UMPP; Hancock County (Hamilton) ISUA; Knox County (Galesburg) MCZ; La Salle County (No locality given) RTBe; McHenry County (McHenry) WSUP; Vermilion County (Camp Robert Drake, Fairmount) RTBe. INDIANA: Fulton County (No locality given) PUM; Kosciusko County (Winona Lake) UMAH; Knox County (No locality given) PUM; Lake County (Miller) UMAH; Montgomery County (Shades) PUM, RTBe. IOWA: Boone County (Ledges State Park) ISUA; Clayton County (Guttenberg) ISUA, USNM; Dickinson County (Spirit Lake) USNM, UWMW; Johnson County (Iowa City) MCZ, USNM; Lee County (Fort Madison) ANSP, CMPP, MCZ, ZMLS; Palo Alto County (Ruthven) ISUA; Story County (Ames) ISUA; County unknown (Herrold) CAS. KANSAS: Douglas County (Lawrence) ANSP, CMPP, UWMW, (Lone Star) CNC; Reno County (Medora) MCZ; Riley County (Marlatt) KSU. KENTUCKY: Fayette County (Lexington) TCBA; Rowan County (Morehead) CNC. MAINE: Cumberland County (Sebago Lake, South Casco) AMNH; Oxford County (Norway) MCZ, (Paris) CUNY; Penobscot County (Orono) UATA, UMSP. MARYLAND: Baltimore County (Baltimore) CAS, MSUM; Montgomery County (No locality given) USNM; County unknown (Plummers Islands) USNM. MASSACHUSETTS: Barnstable County (Barnstable) MCZ, (Hyannis) ISUA, (Woods Hole) WSUP; Bristol County (Attleboro) ZMLS, (Fall River) CAS, (Swansea) MCZ; Franklin County (Northfield) MCZ; Hampden County (Chicopee) MCZ; Hampshire County (Amherst) CEWh, MCZ, (Mount Tom) CMPP, USNM; Middlesex County (Arlington) CAS, UASM, (Billerica) CAS, UASM, ZMLS, (Concord) MCZ, UASM, ZMLS, (Lincoln) MCZ, (Pepperill) UATA, (Sherborn) MCZ, (Sudbury) MCZ, (Tyngsboro) MCZ, (Wayland) MCZ, (Waltham) MCZ, (Woburn) MCZ; Nantucket County (Nantucket) ISNH, MCZ; Norfolk County (Brookline) MCZ, (Dedham) MCZ, (Dorchester) MCZ, (Dover) MCZ, (Sharon) CUNY, (Stoughton) USNM, (Wellesley) MCZ, (Westwood) MCZ; Worcester County (Ashburnham) CEWh; County unknown (Mount Toby) MCZ. MICHIGAN: Allegan County (Allegan) CAS; Charlevoix County (Beaver Island) UMAH; Eaton County (Grand Ledge) USNM; Grand Traverse County (Marion Island) UMAH; Huron County (SandPoint) UMAH; Kalamazoo County OUCO, (Gull Lake Biology Station) JSch; Kent County (Grand Rapids) UNLN; Lake County (Loon Lake) UMAH; Oakland County (No locality given) UMAH; Oceana County (Crystal Valley) CNHM; Otsego County (Lake Manuka) UMAH; Ottawa County (No locality given) KSU, PUM; Washtenaw County (Ann Arbor) UMAH, (Whitmore Lake) JSch. MINNESOTA: Benton County (No locality given) UMSP; Big Stone County (No locality given) UMSP; Clearwater County (Itasca State Park) UMSP, (Itasca State Park, BohallLake) UMSP, (Itasca State Park, De Soto Lake) UMSP; Crow Wing County (Mille Lacs Lake, near Garrison) UMSP; Dakota County (No locality given) UMSP; Douglas County (Alexandria) PSUU, UMSP; Hennepin County (Minneapolis) UMSP; Houston County (Mississippi Bluff, 1-2.0 miles north of State Line) UMSP; Lac qui Parle County (Madison) UMSP; Lake County (Basswood Lake) UMSP; Norman County (No locality given) UMSP; Otter Tail County (Battle Lake) UMSP; Pine County (Saint Croix River, 10.0 miles east of Pine City) UMSP, (Snake River, 6.0 miles east of Pine City) UMSP; Ramsey County UMSP, (Saint Paul) ISNH, WSUP; Traverse County (No locality given) UMSP; Washington County (Saint Croix River, 3.0 miles north of Stillwater) UMSP; County unknown (Cliff) UMSP. MISSISSIPPI: George County (Lucedale) CUNY. MISSOURI: Jefferson County (Kimmswick) USNM; Saint Louis County (No locality given) LACM. NEBRASKA: Dakota County (Hubbard) UNLN, (South Sioux City) UNLN; Lancaster County (Lincoln) UNLN; Saunders County (Cedar Bluffs) UNLN. NEW HAMPSHIRE: Cheshire County (Swanzy Pond) MCZ; County unknown (Three Mile Island) MCZ. NEW JERSEY: Bergen County (Bear Swamp, Ramsey) AMNH, (Emerson) CAS, (Oakland) CAS; Cumberland County (Bridgeton) CAS; Essex County (Cedar Grove) USNM; Hunterdon County (Hampton) AMNH; Morris County (Riverdale) MCZ; Passaic County (Great Notch) USNM; Somerset County (North Branch) DRWh; Union County (Berkeley Heights) AMNH; Warren County (Phillipsburg) CAS; County unknown (Chelcea) CMPP, (Split Rock Lake) CAS, USNM. NEW MEXICO: (No locality given) CMPP. NEW YORK: Clinton County (Plattsburg) CAS; Columbia County (Hudson) CAS; Cortland County (McLean Bogs) CUNY; Dutchess County (Red Hook) UMCP; Essex Cty (Fort Ticonderoga) PUM; New York Cty (Broad Channel) CAS, (Bronx Park) CAS, (Brooklyn) LACM, USNM, (New York City) CAS, MCZ, (Rockaway Beach) MCZ, (Staten Island) CAS, USNM, (Yonkers) CAS, CHNM, MCZ; Niagara County (Olcott) CUNY; Orange County (West Point) UMAH, USNM; Otsego County (Unadilla) MCZ; Putnam County (2.0 miles northwest of Brewster) PUM; Queens County (Cunningham Park) CAS; Rockland County (Bear Mountains) CNHM; Saint Lawrence County (Canton) OSUS; Suffolk County (Babylon) AMNH, (Montauk) CNHM, MCZ, (Southold) CUNY, (Wildwood State Park) CUNY; Tompkins County (Ithaca) CAS, CUNY, UASM, UIMI, (McLean) UMSP, (Tomkins Cove) AMNH, (Varna) UASM; Ulster County (Ashokan) AMNH, (Phoenicia) CAS; Washington County (Salem) CAS; Westchester County (Bedford) CAS, (Peekskill) MCZ; Wyoming County (Silver Lake) CAS; Counties unknown (Catskill Mountains) AMNH, (Hebron) AMNH, USNM, (Miller's Port) CUNY. OHIO: Coshocton County (Mohican River) PUM. OKLAHOMA: Cleveland County (No locality given) OUCO; Payne County (Stillwater) OSUS. PENNSYLVANIA: Allegheny County (Pittsburgh) CAS; Bradford County (Susquehanna River, Wyalusing) CAS, UASM; Burks County (No locality given) MCZ; Chester County (West Chester) UWMW; Cumberland County (New Cumberland) UASM, VMKi; Dauphin County (Harrisburg) CUNY, VMKi; Franklin County (Chambersburg) USNM; Monroe County (No locality given) USNM; Montgomery County (Arcola) OUCO; Northampton County (Easton) CAS, UASM, (Delaware Water Gap) AMNH; Pike County (Camp Colang) CNHM; Philadelphia County (Chestnut Hill) USNM; Venango County (French Lick Creek, south of Venango) PUM; Counties unknown (Belfast) CAS, (Bethlehem) CNHM, (Edge Hill) USNM, (Lehigh Water Gap) USNM,

(North Cumberland) CAS. RHODE ISLAND: Kent County (Quonset Point) CAS; Newport County (Newport) CNHM; Providence County (Providence) CMPP; County unknown (Moswansicut Lake) CMPP. SOUTH DAKOTA: Brookings County (Brookings) CMPP, SDSU, (Volga) VMKI; Hyde County (Highmore) SDSU. TENNESSEE: Lake County (No locality given) RTBe. TEXAS: Coryell County (No locality given) MCZ; Frio County (5.0 miles north of Dilley) UASM; Kerr County (Kerrville) CNC; McLennan County (Waco) MCZ; Travis County (Austin) WSUP. VERMONT: Addison County (Lewis Creek, North Ferrisburg) RTBe; Chittenden County (Burlington) RTBe, (Gilette Pond, Richmond) RTBe, (La Moille River, Milton) RTBe, (Sandbar State Park) RTBe, (Shelburne) CAS; Franklin County (LaMoille River, East Georgia) RTBe; Grand Isle County (Alburg) RTBe; Lamoille County (Ithiel Falls, Johnson) RTBe; Orange County (Wells River) MCZ; Rutland County (West Haven, Lake Champlain) RTBe; Windham County (Brattleboro) USNM, (West River, Brookline) RTBe, (West River, Newfane) RTBe, (West River, Townshend) RTBe. VIRGINIA: Fairfax County (Great Falls) ISUA, USNM; Loudoun County ANSP, (Harpers Ferry) USNM. WISCONSIN: Bayfield County (Lake Namekagon) UWMW; Dane County (No locality given) UWMW; Dodge County (Beaver Dam) UMAH; Milwaukee County (No locality given) CAS; Portage County (Stevens Point) UWMW; Sauk County (Prairie du Sac) CNHM, (Victory) USNM.

The *medius* subgroup

This subgroup is characterized as follows: size small, venter infuscated, female stylus small, arcuate, and median lobe small, generalized. One species, *B. medius* Harris, is included.

Brachinus medius Harris

(Figs. 311, 315, 316, 317, 328, 331)

Brachinus medius Harris, 1828: 117. Lectotype, here selected, a male MCZ red type label number 26411. *Type locality*. — Boston, Massachusetts. Here designated, because Harris neither labelled his specimens, nor gave a locality in his descriptions, but he collected in the Boston area.

Brachinus minutus Harris, 1828: 117. Lectotype, here selected, a male, MCZ red type label number 26412, further labelled "471 female, 104." Harris misidentified the sex of the beetle. *Type locality*. — Boston, Massachusetts (see above). NEW SYNONYMY.

Diagnostic combination. — The small size, glabrous proepisterna, and infuscated abdomen separate these beetles from all others in the study area.

Description. — Small-sized beetles, 5.2 to 7.3 mm.

Color. Antennal articles 3-11, metepisterna, and abdominal sterna and terga infuscated. Antennal articles 1 and 2, metepisternum at sides, apex of tibia, and tarsi infuscated in some specimens, in others these sclerites are ferruginous. Dorsal surface and epipleura of elytra blue, with greenish luster in some specimens.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows and surface of pronotum rugose and punctate, punctures barely impressed.

Head. Frontal furrows moderately impressed. Antennal scape robust, widened apically. Ligule with sclerotized center area ellipsoid-convex with two lateral rows of three setae per row. Mentum and submentum without accessory setae.

Prothorax. Pronotum (fig. 311) slightly convex, flattened along center line, sides slightly reflexed. Proepipleura, and usually proepisterna glabrous, the latter sometimes with 1-3 setae near anterior edge. Anterior tibia with anterior surface strigose.

Pterothorax. Elytra short, narrow, slightly costate. Humeral angle square. Depressions and costae pubescent. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 315, 316, 317). Median lobe with plane of shaft rotated 45° from plane of basal bend. Basal bend long. Apex of shaft blunt, slightly turned dorsally. Ligule short, narrowed toward apex. Virga (figs. 315, 316). Female (fig. 328). Stylus small, short, narrow, slightly arcuate, narrowly rounded apically.

Variation. — Intrapopulation variation occurs in the following characteristics: shape of pronotum; body size; proepipleura with or without setae; and color as indicated above. The elytra are greenish only in the Brownsville, Texas area.

Flight. — These beetles have been collected at lights in South Dakota, Minnesota, and

Texas.

Etymology. — Latin, *medius*, middle. Harris described this species in 1828, using two names because he had two very small specimens and two medium-sized specimens, in comparison with other New England *Brachinus* species. He called the small ones *minutus* and the others *medius*.

Collecting notes. — D. R. Whitehead collected these beetles from under stones along an intermittent stream in Texas. G. E. Ball collected them on the shores of a Texas lake. Other records indicate they also inhabit bogs, edges of reservoirs, and marshes.

Life history. — Members of this species have been collected in all months, except December. Teneral adults were collected in September in Michigan. Overwintering probably takes place as an adult.

Distribution. — (Fig. 331). The range of this species is disjunct. The general pattern is much the same as in *B. quadripennis*. I have seen 979 specimens from the following localities:

CANADA

BRITISH COLUMBIA: (Atbara, near Creston) UASM, ZMLS; (Osoyoos) CAS, ISNH, ISUA, ZMLS; (Salmon Arm) CNHM, CUNY, MCZ, UATA; (Shuswap Lake) ZMLS. ONTARIO: (Belleville) CNC; (Britannia) CNC; (Constance Bay) CNC; (Hamilton) CNHM; (Osgoode) CNC; (Toronto) CAS; (Trenton) MCZ. QUEBEC: (Becancour) CCha; (Choisypr Rigaud) ZMLS; (Fort Coulonge) CAS, CNC; (Montreal) CAS; (Rigaud) CAS; (Saint Eustache) CAS; (Saint Ours) CCha; (Saint Rose) CAS.

MEXICO

TAMAULIPAS: (9.9 miles west of Pesca) UASM.

UNITED STATES

ALABAMA: Mobile County (Mobile) ANSP, CAS, UMAH, USNM, (Orchard) CAS, KSU, (Spring Hill) USNM. CALIFORNIA: ANSP, UMSP, USNM, UWMW, San Diego County (San Diego) MCZ. COLORADO: Boulder County (Boulder Creek) CArm, (Crystal Lake) CArm, (Erie) CArm, (Longmont, Bellmire Reservoir) CArm, (Longmont, Divide Reservoir) CArm, (Rod and Gun Club Lake) CArm, (Teller Lake) CArm, (Viele Lake) CArm; Weld County (Greeley) USNM. CONNECTICUT: (No locality given) USNM. FLORIDA: Alachua County (Gainesville) FDA, (4.0 miles north of High Springs) CNC, (New nans Lake, 5.0 miles east of Gainesville) RFre; Duval County (Jacksonville) CAS, OUCO; Highlands County (Archbold Biology Station) PSUU; Hillsborough County (Tampa) USNM; Manatee County (Oneco) UASM; Marion County (3.0 miles southwest of Lake Marion) CNC; Osceola County (No locality given) FDA; Pinellas County (Dunedin) PUM, UMAH; Sarasota County (Myakka River State Park) CUNY, UASM. GEORGIA: Baker County (Newton) CNC; Charlton County (Okefenokee Swamp) TLEr. KANSAS: Sheridan County (State Lake, near Studley) RFre, UASM. IDAHO: Bonner County (Sagle) UWSW; County unknown (Sand Point) UWSW. ILLINOIS: Cook County (Chicago) UWSP; McHenry County (Algonquin) ISNH; Rock Island County (Moline) UMSP. INDIANA: Vigo County (No locality given) PUM. IOWA: Buchanan County (Independence) MCZ, USNM; Clayton County (Guttenberg) USNM; Des Moines County (Burlington) ANSP; Dickinson County (Lake Okoboji) USNM, (Spirit Lake) UWMW; Johnson County (Iowa City) MCZ, USNM; Lee County (Fort Madison) CAS, (Keokuk) USNM; Story County (Ames) ISUA. MARYLAND: (No locality given) UMSP. MASSACHUSETTS: Bristol County (Fall River) ISUA, MCZ; Hampshire County (Mount Tom) CMPP, USNM; Middlesex County (Acton) CNC, (Arlington) CNC, MCZ, (BillERICA) CNC, CUNY, (Boston) CAS, USNM, (Cambridge) ANSP, (Concord) MCZ, (Sudbury) CEWh, MCZ, (Waltham) MCZ, (Wayland) CNC, CNHM, MCZ, UASM; Norfolk County (Newton) MCZ, (Sharon) CUNY; Plymouth County (Marion) MCZ; Suffolk County (Dorchester) MCZ; Worcester County (Fitchburg) USNM; County unknown (Forest Hills) USNM. MICHIGAN: Alcona County UMSP; Charlevoix County (Beaver Island) UMAH; Cheboygan County (No locality given) CUNY; Huron County (Charity Island) UMAH; Kalamazoo County (Gull Lake Biology Station) TFHl; Lapeer County UMAH, (Lapeer State Game Area) RCGr; Livingston County (E. S. George Reserve) UMAH; Menominee County (Menominee) CEWh; Oakland County (No locality given) UMAH; Wayne County (Detroit) MCZ, UMAH; Washtenaw County (Ann Arbor) UMAH. MINNESOTA: Crow Wing County (Nisswa) UMSP; Hennepin County (Bloomington) ISNH; Olmsted County (No locality given) UMSP; Polk County (Crookston) UMSP; Ramsey County (Saint Paul) UMSP. MISSOURI: (No locality given) ANSP, USNM. MONTANA: Sanders County (Perma) LRus. NEBRASKA: (No locality given) ANSP, NEW HAMPSHIRE: Strafford County (Milton) MCZ. NEW JERSEY: Bergen County (Emerson) CAS; Cape May County (Cape May) CAS; Morris County (Boonton) USNM. NEW YORK: Cortland County (McLean Bogs) CAS, CUNY; Erie County (Buffalo) AMNH, ANSP; Essex County (Fort Ticonderoga) PUM; Monroe County (Rochester) LACM; Nassau County (Hewlett) USNM, (Roslyn) CAS; New York County (New York City) MCZ, (Yonkers) CAS, MCZ; Niagara County (Olcott) CUNY; Orange County (West Point) USNM; Queens County (Queens) CAS; Suffolk County (Brookhaven) UASM, VMKi, (Montauk Point) CNHM, CUNY, (Riverhead) VMKi; Tompkins County (Ithaca) CAS; Westchester County (Bedford) CAS, (Mount Vernon) CNHM; County unknown (Chicago Bog) UMSP. NORTH DAKOTA: Benson County (11.9 miles west of York) UASM; Grand Forks County (University) USNM. OKLAHOMA: Marshall County (Lake Texoma, Willis) RCGr. OHIO: Adams County (No locality given) OUCO; Cuyahoga County (Cleveland) MCZ; Lawrence County (Miller) UMAH; Tuscarawas County (No locality given) OUCO. OREGON: Clackamas County (Oregon City) CAS; Multnomah County (Portland) CAS, USNM; County unknown (Sauvie Island) JSch. PENNSYLVANIA: Lackawanna County (Scranton) UASM, USNM; Westmoreland County (Jeannette)

CMPP. SOUTH CAROLINA: Florence County (Florence) VMKi; Sumter County (Poinsett State Park) VMKi. SOUTH DAKOTA: Beadle County (Huron) VMKi; Brookings County (Brookings) SDSU, VMKi; Brown County (Hecla) SDSU; Clay County (Vermillion) SDSU; Lawrence County (Spearfish) VMKi; Yankton County (Yankton) VMKi. TEXAS: Blanco County (Cypress Mill) USNM; Cameron County (Brownsville) CAS, CNC, OUCO, SJSC, TLEr, USNM; Hidalgo County (Hidalgo) CMPP, (McAllen) UMAH, (Weslaco) TAMU; Reeves County (Balmorhea Lake) UASM, (Pecos) CNC; Sutton County (Sonora) TAMU; Terrell County (Chandler Ranch) UASM, (16.0 miles north of Dryden) UASM, (Lozier Canyon) MCZ; Val Verde County (9.0 miles southeast of Del Rio) DRWh; Victoria County (Victoria) USNM. UTAH: Salt Lake County (Salt Lake City) USNM; Utah County (Provo) MCZ, USNM. VERMONT: Addison County (Dead Creek, Addison) RTBe, (Lewis Creek, North Ferrisburg) RTBe; Chittenden County (Shelburne) CAS. WASHINGTON: Adams County (Ritzville) CAS, PUM, USNM, UWSW; Lincoln County (Sprague Lake) CAS; County unknown (Yakima River, Morgan's Ferry) MCZ. WISCONSIN: Bayfield County (No locality given) UWMW; Dane County (No locality given) ANSP; Wood County (Griffith Street Nursery) UWMW.

The *gebhardis* subgroup

This subgroup is characterized by elytra with pubescence restricted to depression 8, and by the form of the median lobe. The two species, *B. gebhardis* Erwin, and *B. galactoderus* new species, included here are very similar in their external form.

Brachinus gebhardis Erwin

(Figs. 306, 321, 322, 323, 327, 332)

Brachinus gebhardis Erwin, 1965: 6. Holotype male and allotype female are in CAS. *Type locality*. — Uvas Creek, 5.0 miles west of Morgan Hill, Santa Clara County, California.

Diagnostic combination. — The presence of pubescence in the eighth depression only, the pale center of the venter, and the accessory setae of the mentum separate these beetles from all others in North and Middle America.

Description. — Medium-sized beetles, 7.0 to 12.0 mm.

Color. Metepisterna and sides of abdomen infuscated, otherwise ferrugineous. Dorsal surface and epipleura of elytra blue.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows and surface of pronotum rugose and punctate, punctures moderately impressed.

Head. Frontal furrows moderately impressed. Antennal scape cylindrical. Ligula with sclerotized center area ellipsoid-convex with two lateral rows of three setae per row. Mentum and submentum with accessory setae.

Prothorax. Pronotum (fig. 306) slightly convex, flattened along center line, sides narrowly reflexed. Proepipleura and proepisterna with scattered setae both anteriorly and posteriorly, glabrous medially. Anterior tibia with anterior surface strigose.

Pterothorax. Elytra elongate, narrow, moderately costate. Humeral angle square. Depression 8 pubescent. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 321, 322, 323). Median lobe with plane of shaft moderately rotated from plane of basal bend. Basal bend short. Apex of shaft narrowed, almost acute. Ligule moderately long, broad, and rounded apically. Virga (figs. 321, 322). Female (fig. 327). Stylus narrow, arcuate, almost acute apically.

Variation. — Intrapopulation variation occurs in the following characteristics: width of the pronotal explanation at the anterior angles; presence or absence of the accessory setae on the mentum; sides of abdominal sterna infuscated or not; occasionally the metasternum is infuscated at sides. On the whole, the Arizona populations have larger members without mental accessory setae, but with wider pronotal explanations, and wider shafts of the median lobe.

Flight. — These beetles have been collected at lights by G. E. Ball in Arizona.

Etymology. — Greek, *geb*, born; Old French, *hardi*, shovel-shaped; referring to the dorsal outline of these beetles.

Collecting notes. — In Santa Clara County, California, these beetles occur along the margins of intermittent streams. The sides of the streams are generally rocky with underlying gravel, and very little vegetation near the actual stream, although emergent specimens of *Salix* species (at high water) are found in some areas.

Life history. — Members of this species have been collected in all months, except December. Teneral adults were collected in September in Santa Clara County, California. Overwintering probably takes place in the adult stage.

Distribution. — (Fig. 332). The range of this species extends from northern California, to the San Jacinto Mountains of southern California. Other aggregates of populations occur in southern Arizona, and in southern Baja California. I have seen 151 specimens from the following localities:

MEXICO

BAJA CALIFORNIA: (1.3 miles northwest of El Truinfo) CAS.

UNITED STATES

ARIZONA: Graham County (10.0 miles southwest of Safford) UCR; Santa Cruz County (Madera Canyon) UCD, CUNY, (Peña Blanca) UASM, (Yanks Spring, 4.0 miles southeast of Ruby) AMNH; Pima County (Box Canyon, Santa Rita Mountains) CNHM, (west side of Baboquivari Mountains) CAS, (Browns Canyon, Baboquivari Mountains) AMNH, (Santa Catalina Mountains) CAS, (Santa Catalina Mountains, Sabino Canyon) CAS, TCBa, UASM, (Santa Rita Mountains) CAS, (Tanque Verde) UATA, (Tucson) CAS. CALIFORNIA: Alameda County (Alameda Creek) CAS, (Arroyo Mocho) TLER, (Berkeley) USUL; Amador County (Horse Creek) TLER; Fresno County (Le Fevre) ANSP; Los Angeles County (2.7 miles south of Little Rock Ranger Station) GRNo, (Pasadena) CAS, MCZ, (San Francisquito Canyon) LACM, (San Gabriel Canyon) CAS, TCBa, (Soledad Canyon) LACM, (Tanbark Flat) UCR; Monterey County (Bryson) CAS; Orange County (Lower San Juan Campground) LACM; Riverside County (San Jacinto Mountains) CAS; San Diego County (Valley Center) SDNHM; San Luis Obispo County (Atascadero) CAS, (San Luis Obispo) CAS; Santa Barbara County (Buellton) CAS, (Cuyama River) CAS, (4.0 miles east of Los Prietos) UCD, (Oso Canyon) UCD, (Santa Barbara) MCZ, (Santa Cruz Island) CAS, (West Santa Ynez River) UCD; Santa Clara County CNHM, (Gilroy Hot Springs) TLER, (Mount Hamilton) JSch, (Pacheco Pass) UIMI, (Uvas Creek) TLER; Stanislaus County (Del Puerto Creek) TLER, (20.0 miles west of Patterson) TLER; Ventura County (Foster Park) UCD, (Ojai) MCZ, (Santa Clara River, Santa Paula) CUNY; County unknown (Cachuma Reservoir) CAS, (Shephards Inn) MCZ.

Brachinus galactoderus new species

(Figs. 305, 318, 319, 320, 325, 333)

Type locality. — Rio Papagayo, 41.4 miles north of Acapulco, Route 95, 700 feet, Guerrero, Mexico.

Type specimens. — The holotype male and allotype female are in MCZ. Both were collected at the type locality by G. E. Ball and D. R. Whitehead on December 20, 1965. Sixteen paratypes collected at various localities and on various dates are in CAS, MCZ, TLER, and UASM.

Diagnostic combination. — The milky appearance of the surface of the pronotum will separate these beetles from all others in Mexico.

Description. — Medium-sized beetles, 9.3 to 10.6 mm.

Color. Metepisterna, metasternum at sides, abdominal sterna and terga infuscated, otherwise ferrugineous. Dorsal surfaces and epipleura of elytra slate-black without blue luster.

Microsculpture. As described for genus, except surface of pronotum with isodiametric meshes raised into beads which apparently scatter the reflected light producing a milky appearance.

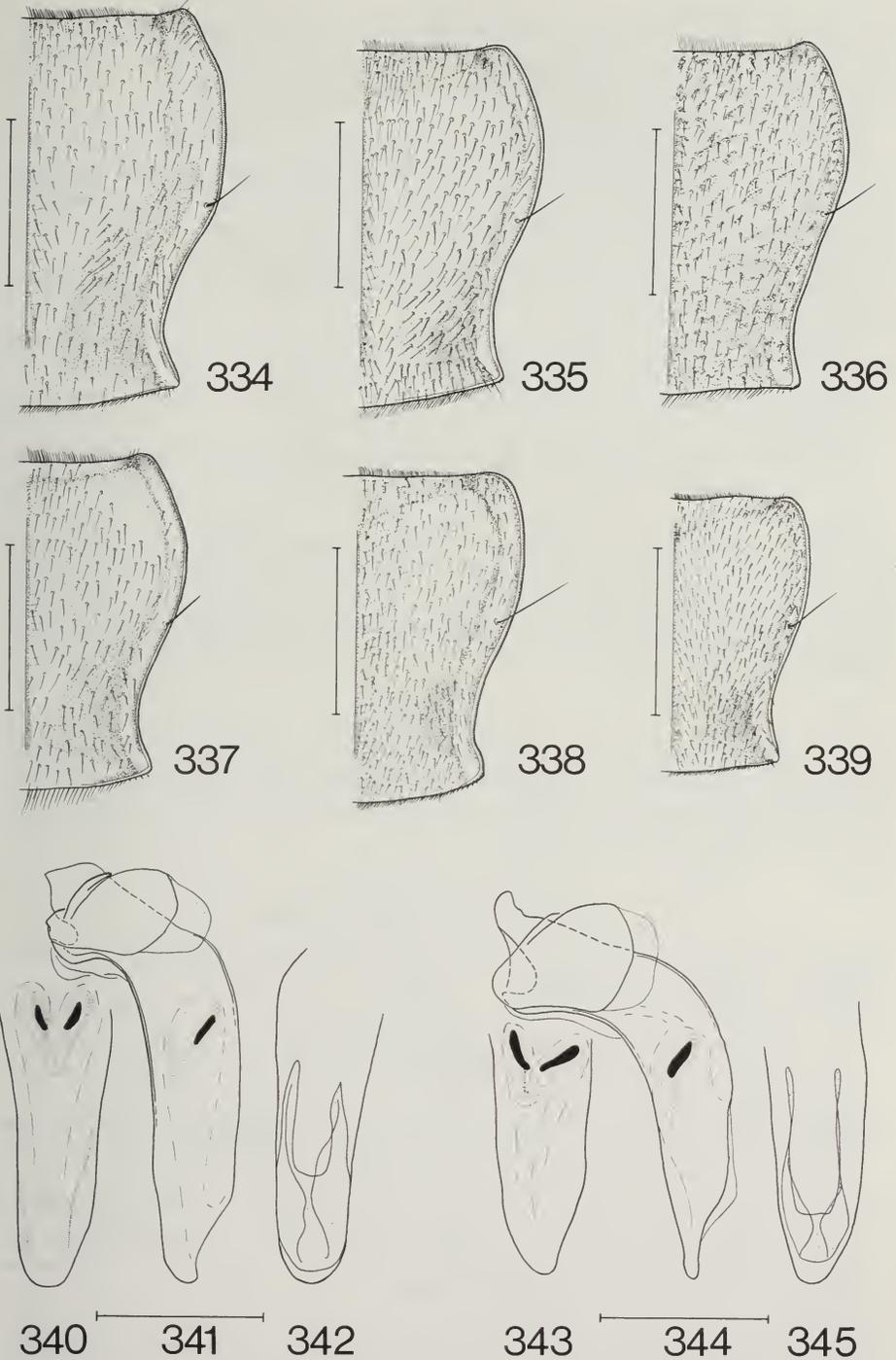
Macrosculpture. As in *gebhardis*.

Head. Frontal furrows moderately impressed. Antennal scape robust, widest about middle. Ligula with sclerotized center area ellipsoid-convex with two apical setae. Mentum and submentum without accessory setae.

Prothorax. As in *gebhardis*, except proepipleura glabrous.

Pterothorax. As in *gebhardis*.

Abdomen. As described for genus.



Figs. 334-339. Pronotum, right half, dorsal aspect. 334. *Brachinus fumans* Fabricius, Kahlotus, Washington. 335. *Brachinus perplexus* Dejean, Dundee, Mississippi. 336. *Brachinus favicollis* Erwin, Jamul, California. 337. *Brachinus puberulus* Chaudoir, Victoria, Texas. 338. *Brachinus imperialensis* Erwin, Douglas, Arizona. 339. *Brachinus velutinus* Erwin, Davis, California. Figs. 340-345. Male genitalia. 340. *Brachinus favicollis* Erwin, Jamul, California, ventral aspect. 341 & 342. Lateral & dorsal aspects of same. 343. *Brachinus perplexus* Dejean, Dundee, Mississippi, ventral aspect. 344 & 345. Lateral & dorsal aspects of same. Accompanying scale lines equal 1.0 mm.

Genitalia. Male (figs. 318, 319, 320). Median lobe with plane of shaft rotated about 30° from plane of basal bend. Basal bend short. Apex of shaft narrowed, almost acute. Ligule long, broad, tapering to narrow apex. Virga (figs. 318, 319). Female (fig. 325). Stylus short, broad, tapering to narrowly rounded apex.

Variation. — Intrapopulation variation occurs in the shape of the pronotum, and in total size. A cline may occur in the color of the knees. Those populations in the north have darkened knees, while those in Oaxaca and Guerrero have pale knees. No specimens are available from Jalisco and Michoacan to see where this trend develops.

Flight. — The flight of these beetles has not been recorded.

Etymology. — Greek, *galaktos*, milky; *derus*, neck; referring to the milky appearance of the pronotum of these beetles.

Collecting notes. — G. E. Ball and D. R. Whitehead collected these beetles from under rocks embedded in gravel at the margins of rivers in Mexico.

Life history. — Members of this species have been collected in all months, except February and October, but no teneral adults have been seen.

Distribution. — (Fig. 333). The range of this species extends from Sonora, south to Oaxaca on the west side of Mexico. I have seen 66 specimens from the following localities:

MEXICO

GUERRERO: (Rio Mezcala, 23.7 miles north of Zumpango) UASM; (Rio Papagayo, 41.4 miles north of Acapulco) UASM. NAYARIT: (Rio Acaponeta, 2.4 miles south of Acaponeta) UASM; (Rio de las Cañyas) CAS; (8.7 miles east of San Blas) GRNo; (19.0 miles southeast of Tepic) CAS. OAXACA: (Lago Tehuantepec, Benito Juarez Dam) UASM; (Rio Niltepec, 18.4 miles west of Zanatepec) UASM. SINALOA: (3.0 miles east of Culiacan) GRNo; (3.4 miles west, 5.0 miles south of Culiacan) GRNo; (12.0 miles south of Guasave) UASM; (Rio Panuco, 11.2 miles northeast of Concordia) UASM; (Venedillo) CAS. SONORA: (7.2 miles southeast of Alamos) GRNo; (10.0 miles southeast of Alamos) UCD; (Rio Mayo, San Bernardo) CAS.

The *fumans* subgroup

This subgroup is characterized by swollen median lobe, pale venter with infuscated sides, coarsely punctate pronotum, and generally similar habitus. Six species, *B. fumans* (Fabricius), *B. perplexus* Dejean, *B. puberulus* Chaudoir, *B. velutinus* Erwin, *B. favicollis* Erwin, and *B. imperialensis* Erwin, are included.

Brachinus fumans (Fabricius)

(Figs. 334, 346, 347, 348, 358, 369)

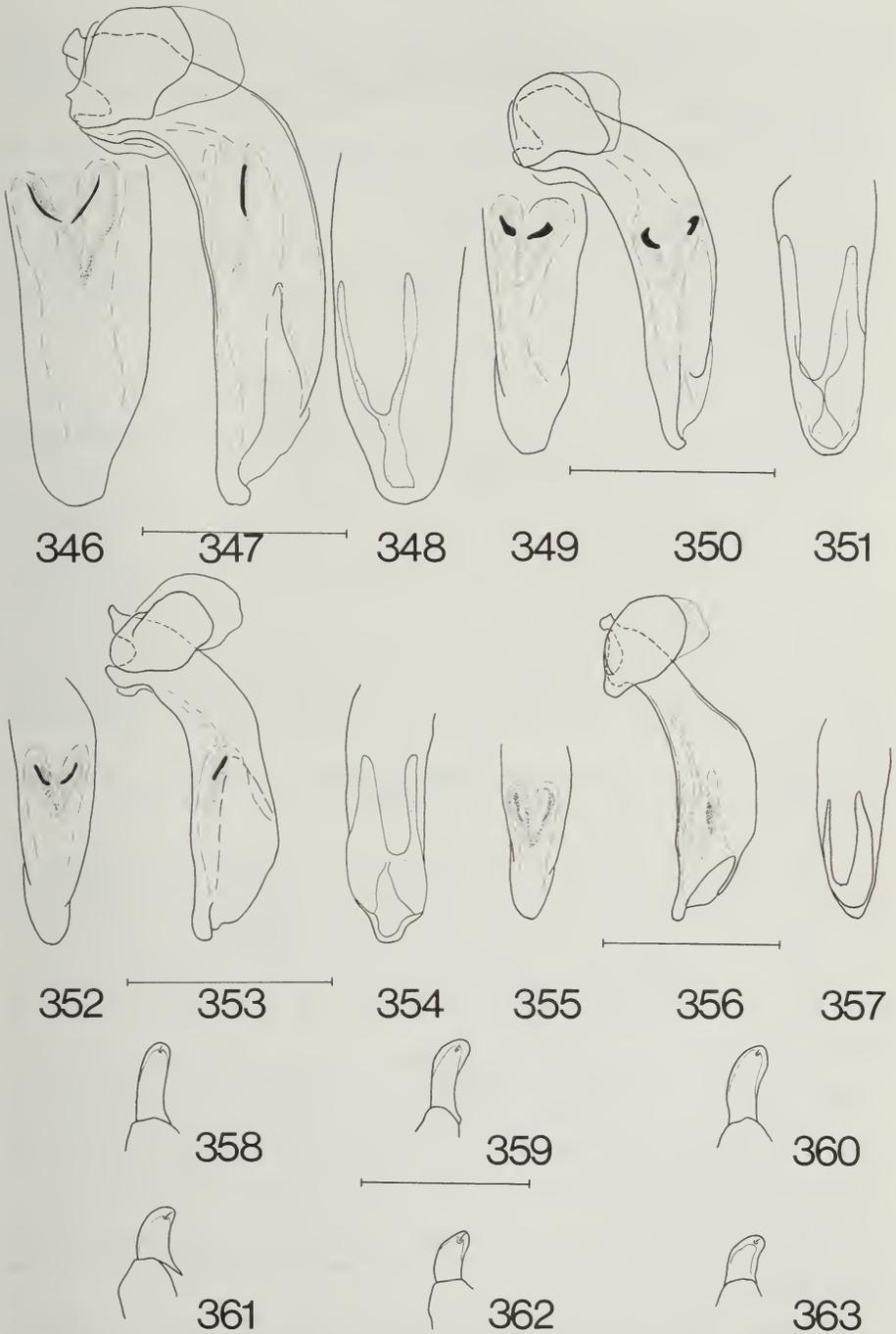
Carabus fumans Fabricius, 1781: 307. Lectotype, designated by Lindroth in Kiel Museum, labelled "in America, D. Blackburn."

Brachinus cyanopterus LeConte, 1844: 49. Lectotype, here selected, a female, MCZ red type label number 5847, further labelled with a pink disc and "B. fumans Fab., Dej., cyanopterus Say." *Type locality.* — New York, as originally given by LeConte. LeConte 1848: 203, LeConte 1862: 524.

Brachinus sufflans LeConte, 1848: 204. Lectotype, here selected, a female, MCZ red type label number 5648, further labelled with a pink disc and "86 v. sufflans LeC." *Type locality.* — New York, as originally given by LeConte. LeConte 1862: 524.

Brachinus affinis LeConte, 1848: 204. Lectotype, here selected, a male, MCZ red type label number 31881, further labelled with a yellow disc and "2747" and standing ninth in a series of 16 specimens behind box labelled "B. fumans Dej." *Type locality.* — Indiana, as originally given by LeConte. NEW SYNONYMY.

Brachinus perplexus LeConte, 1862: 524. This name must be considered a *lapsus calami* because LeConte (1848) correctly sites Dejean as author of this name. However, LeConte's concept of *perplexus* was different than that of Dejean, according to their labelled specimens.



Figs. 346-357. Male genitalia. 346. *Brachinus fumans* Fabricius, Vantage, Washington, ventral aspect. 347 & 348. Lateral & dorsal aspects of same. 349. *Brachinus imperialensis* Erwin, Douglas, Arizona, ventral aspect. 350 & 351. Lateral & dorsal aspects of same. 352. *Brachinus velutinus* Erwin, Davis, California, ventral aspect. 353 & 354. Lateral & dorsal aspects of same. 355. *Brachinus puberulus* Chaudoir, Hidalgo County, Texas, ventral aspect. 356 & 357. Lateral & dorsal aspects of same. Figs. 358-363. Right stylus of female ovipositor, ventral aspect. 358. *Brachinus fumans* Fabricius, Kahlotus, Washington. 359. *Brachinus favicollis* Erwin, El Sauzal, Baja California, Mexico. 360. *Brachinus puberulus* Chaudoir, Texas. 361. *Brachinus imperialensis* Erwin, Douglas, Arizona. 362. *Brachinus perplexus* Dejean, Dundee, Mississippi. 363. *Brachinus velutinus* Erwin, Davis, California. Accompanying scale lines equal 1.0 mm.

Brachinus tabasconus Bates, 1891: 268. Lectotype, here selected, a male, BMNH, labelled "San Juan Bautista, Tabasco" and "Höge" and standing first behind label "tabasconus Bates." *Type locality*. — San Juan Bautista, Tabasco, Mexico, as originally given by Bates. NEW SYNONYMY.

Brachinus amplipennis Bates, 1891: 268. Lectotype, here selected, a female, BMNH, labelled "Paso del Norte, Chihuahua, Höge" "Tr. Ent. S. L. 1891. Brachinus amplipennis Bates" "Syntype" and "1891-64." *Type locality*. — Villa Lerdo, Durango, Mexico, as originally given by Bates. NEW SYNONYMY.

Brachinus atbarae Stehr, 1950: 102. Holotype, male, at OUCO, labelled "Atbara, B. C. Canada, 24-IV-45, G. Stace Smith Coll." Allotype, a female, at OUCO, labelled as holotype, except 7-V-46. Thirteen paratypes in OUCO and UBC. *Type locality*. — Atbara, British Columbia, Canada. NEW SYNONYMY.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Medium-sized beetles, 9.0 to 14.0 mm.

Color. Metepisterna, sides of abdominal sterna, and terga infuscated, otherwise ferruginous. Dorsal surface and epipleura of elytra blue.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows, head behind eyes, and surface of pronotum rugose and punctate, punctures moderately impressed.

Head. Frontal furrows moderately impressed. Antennal scape robust, widened apically. Ligula with sclerotized center area ellipsoid-convex with two lateral rows of three setae per row. Mentum and submentum without accessory setae.

Prothorax. Pronotum (fig. 334) slightly convex, flattened along center line, sides slightly reflexed. Proepipleura and proepisterna with a few setae both anteriorly and posteriorly, glabrous medially. Anterior tibia with anterior surface punctate, punctures elongate, sometimes merged.

Pterothorax. Elytra elongate, narrow, moderately costate. Humeral angle square or projecting. Costae smooth on disc, depressions pubescent. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 346, 347, 348). Median lobe with plane of shaft rotated about 45° from plane of basal bend. Basal bend short. Shaft swollen medially, very robust, apex blunt and slightly turned dorsally. Ligule short, broad, narrowed toward apex. Virga (figs. 346, 347). Female (fig. 358). Stylus narrow, parallel-sided, rounded apically.

Variation. — Intrapopulational variation occurs in the following characteristics: body size; shape of the pronotum; height of costae; length to width ratio of elytra; and color of terga. No clines are apparent.

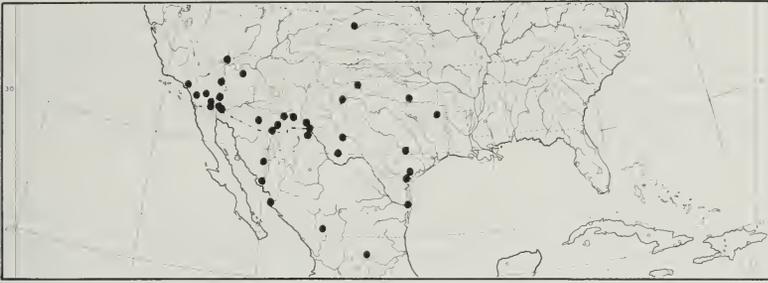
Flight. — These beetles have been repeatedly collected at lights in Arizona and Texas.

Etymology. — Latin, *fumans*, smoke; referring to the crepitating ability of these beetles.

Collecting notes. — D. R. Whitehead collected these beetles in gravel from under stones at the edges of an intermittent stream in Texas. In Colorado, C. Armin collected these beetles at lake and reservoir edges and along irrigation canals. In Arizona, these beetles were collected in wet meadows.

Life history. — Members of this species have been collected from March to October. Teneral adults were collected in British Columbia and Quebec in September. Overwintering probably takes place as an adult.

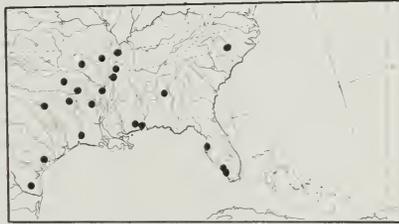
Distribution. — (Fig. 369). The range of this species extends from Maine to Washington, south to Tabasco, Mexico. It is the most widespread species in North America. I have seen 2,055 specimens from the following localities:



364



365



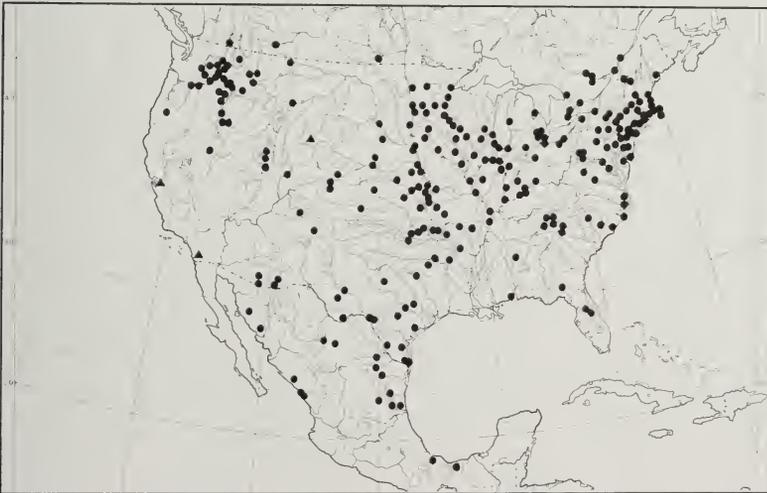
366



367



368



369

Figs. 364-369. Geographical distribution maps. 364. *Brachinus imperialensis* Erwin. 365. *Brachinus favicollis* Erwin. 366. *Brachinus perplexus* Dejean. 367. *Brachinus velutinus* Erwin. 368. *Brachinus puberulus* Chaudoir. 369. *Brachinus fumans* Fabricius.

CANADA

ALBERTA: (5.0 miles south of Etzikom) DRWh; (Lethbridge) UASM. BRITISH COLUMBIA: (Atbara, Creston) CUNY, UASM, ZMLS; (Rykerts, south of Creston) ZMLS. MANITOBA: (Aweme) UASM. ONTARIO: (Belleville) UASM; (Cedar-dale) CAS; (Grand Bend, Lake Huron) ZMLS; (Ottawa) CNC; (Peelee Island) CNC, CUNY, PUM; (Port Hope) CAS; (Prince Edward County) CAS; (South Cajuga, southwest of Dunnville, Lake Erie) ZMLS; (Toronto) CAS, CUNY, USNM, ZMLS. QUEBEC: (Becancour) CCh; (Fort Coulonge) CNC; (Hull) CAS, USNM; (Ile Saint Helene) UASM; (Lachine) CAS; (Montreal) CAS, UWMW; (Outrem't) CAS; (Rigaud) HGou, ZMLS; (Saint Eustache) CAS; (Saint Foy) CCh; (Saint Jean) CAS; (Saint Rose) CAS; (Vaudreuil) CAS.

MEXICO

CHIHUAHUA: (12.0 miles north of Escalon) CNC. COAHUILA: (Torreon) MCZ. NUEVO LEON: (Montemorelos) CAS; (Monterrey) AMNH; (5.0 miles south of Monterrey) CNC; (Rio Sabina's Hidalgo, 7.9 miles east of Sabinas Hidalgo) UASM. SAN LUIS POTOSI: (Presa de Guadalupe, 55.3 miles west of Ciudad del Maiz) UASM. SINALOA: (12.0 miles south of Guasave) UASM; (5.0 miles north of Mazatlan) GRNo; (Real de Piaxtla) AMNH; (Venedillo) CAS. SONORA: (Bahia San Francisquito) GRNo; (Hermosillo) CNHM; (Rio Mayo, San Bernardo) CAS. TAMAULIPAS: (Ciudad Mante) AMNH; (Ciudad Victoria) AMNH, CNHM; (Gomez Farias) UASM; (73.1 miles north of Manuel) UASM.

UNITED STATES

ALABAMA: Mobile County (Mobile) CAS; Tuscaloosa County (Tuscaloosa) UASM. ARIZONA: Cochise County (Cave Creek Ranch) UASM, (Douglas) UASM, (2.0 miles northeast of Douglas) OUCO, (South West Research Station, 5.0 miles west of Portal) CUNY, FDAG; Pima County (Tucson) AMNH, CAS, USNM; Pinal County (No locality given) JSch; Santa Cruz County (6.0 miles north of Nogales) UASM; County unknown (East Bridge) UMSP. ARKANSAS: Bradley County (No locality given) UAFA; Conway County (No locality given) UAFA; Garland County (Hot Springs) CAS; Greene County (No locality given) OSUC; Hempstead County (Hope) CUNY, MCZ, UMAH; Izard County (Franklin) ISUA; Lawrence County (Imboden) CAS, LACM, MCZ; Pulaski County (8.0 miles north of Camp Robinson) CNHM, (Little Rock) AMNH, MCZ; Pike County (Delight) CNHM; Washington County (No locality given) ISNH, UAFA. CALIFORNIA: San Diego County (No locality given) USNM; San Francisco County (San Francisco) CMPP. COLORADO: Boulder County (Arvada) CArm, (Baseline Lake) CArm, (Bellmare Reservoir, Longmont) CArm, (Boulder Creek, near Boulder) CArm, (Hillcrest Lake) CArm, (Hodgson-Harris Reservoir, Louisville) CArm, (Lyons) CArm, (McIntosh, Longmont) CArm, (Prince Lake, Erie) CArm, (Reservoir Four Mile Mesa) CArm, (Valmont) CArm; Denver County (Denver) CAS, USNM; La Plata County (Durango) MCZ; Otero County (Rocky Ford) USNM; Weld County (Greeley) USNM. CONNECTICUT: Fairfield County (Danbury) AMNH, (Redding) UCR, (Stamford) USNM; New London County (Norwich) MCZ, (Old Lyme) CAS, USNM; Windham County (Pomfret) CAS. DISTRICT OF COLUMBIA: (Black Pond) USNM, (Piney Branch) USNM, (Rock Creek) USNM, (Woodridge) USNM. FLORIDA: Lake County (No locality given) UMAH; Orange County (Orlando) LACM. GEORGIA: Thomas County (Boston) TAMU. IDAHO: Boise County (2.0 miles west of Boise) CNHM, (Boise River, Boise) CNHM, UMAH; Bonner County (Sagle) UWSW; Canyon County (Homedale) CNHM, (Parma) UIMI, UMAH; Idaho County (Clearwater) WSUP; Latah County (Kendrick) UIMI, (Moscow) UIMI; Nez Perce County (Lewiston) OUCO, UIMI, (Myrtle) UIMI, (Snake River, 4.0 miles south of Lewiston) UIMI, (Spalding) UIMI. ILLINOIS: Alexander County (Olive Branch) CAS; Bureau County (Bureau) MCZ; Champaign County (Urbana) CNHM; Clark County (No locality given) PUM; Cook County (Chicago) CNHM, MCZ, WSUP, (La Grange) CAS, (Willow Springs) CAS; Greene County (Hillview) UCD; Kendall County (Oswego) CNHM; Lake County (Fort Sheridan) UMAH, (Highland Park) UMAH; La Salle County (Ottawa) RTBe; McHenry County (McHenry) JSch, WSUP; McLean County (Hewytown) USNM; Monroe County (Bloomington) UMAH; Pike County (Florence) UCD; Putnam County (No locality given) ISNH; Richland and Lawrence Counties (Wabash) AMNH; Rock Island County (Moline) UMSP; Saint Clair County (No locality given) CAS; Sangamon County (Springfield) CNHM; Tazewell County (Tremont) CNHM; Vermilion County (Kickapoo State Park) RTBe, (Muncie) ISNH; Warren County (Pine) CMPP; Counties unknown (Falling Springs) LACM, (Saint Claire) LACM. INDIANA: Harrison County (No locality given) PUM; Lake County (Miller) CNHM, PUM; Porter County (Beverly Shores) CNHM; Posey County (Hovey Lake) CEWh, PUM, (Mount Vernon) CEWh; Steuben County (No locality given) PUM; Tippecanoe County (Lafayette) PUM. IOWA: Dickinson County (Lake Okoboji) USNM, (Spirit Lake) USNM; Guthrie County (8.0 miles southwest of Bayard) ISUA; Henry County (Mount Pleasant) CAS, ISUA, MCZ, RTBe, UASM, UMAH; Howard County (Elma) AMNH; Johnson County (Iowa City) CUNY, LACM, MCZ, USNM, (Solon) USNM; Iowa County (No locality given) MCZ; Palo Alto County (Ruthven) ISUA; Story County (Ames) CAS, GRNo, ISUA, MSUM, RTBe, USUL; Van Buren County (Lacey-Keosauqua State Park) ISUA; Woodbury County (Sioux City) UMSP; County unknown (Herrold) CAS. KANSAS: Atchison County (Atchison) CMPP; Clay County (No locality given) ANSP, USNM; Coffey County (No locality given) ULLK; Douglas County (Lawrence) UCD, UMAH, USNM, UWMW, (12.0 miles south of Lawrence) UCD; Ellis County (No locality given) KSU; Ellsworth County (Kanopolis Kam State Park) RCG; Franklin County (No locality given) KSU, UMAH; Hamilton County (No locality given) CAS; Leavenworth County (Tonganoxie) MCZ; Montgomery County (Independence) CAS; Pottawatomie County (Onaga) CAS, KSU, OSUC; Riley County UIMI, (Manhattan) KSU; Rooks County (No locality given) KSU; Saline County (Salina) CMPP, KSU, MCZ; Shawnee County (Topeka) CMPP; Wilson County (No locality given) LACM; Counties unknown (Fort Hays) MCZ, (Williston) MCZ. KENTUCKY: Jefferson County (Louisville) ULLK. MAINE: (No locality given) CNHM. MARYLAND: Montgomery County (Cabin John) USNM; Prince Georges County (College Park) UMCP; County unknown (Plummers Islands) USNM. MASSACHUSETTS: Barnstable County (Barnstable) MCZ, (Woods Hole) JSch, USNM; Bristol County (Fall River) CAS, (Somerset) CAS; Dukes County (Martha's Vineyard) USNM; Essex County (Manchester) MCZ, (Topsfield) UASM; Franklin County (Northfield) MCZ, ZMLS; Hampden County (Chicopee) MCZ, (Springfield) MCZ, ZMLS; Hampshire County (Mount Tom) CMPP; Middlesex County (Billerica) CAS, UATA, (Cambridge) CAS, MCZ, (Concord) MCZ, (Tyngsboro) CAS, MCZ; Nantucket County (Nantucket) ISNH; Norfolk County (Brookline) AMNH, (Newton) MCZ, (Wellesley) MCZ; Plymouth County (Duxbury) MCZ, (Marion) MCZ; Suffolk County (Dorchester) MCZ, ZMLS; County unknown (Forest Hills) USNM. MICHIGAN: Huron County (Charity Island) UMAH; Livingston County (E.S. George Reserve) UMAH; Oceania County (Pentwater) UMAH; Wayne County (Detroit) USNM; Washtenaw County (Ann Arbor) UMAH; (Sharon) UMAH. MISSOURI: Atchison County (Langdon) AMNH; Buchanan County (Saint Joseph) USNM; Greene County

(Willard) ANSP, UASM; Jackson County (Buckner) TAMU; New Madrid County (Big Oak State Park) RTBe; Pettis County (Sedalia) CNHM; Platte County (Parkville) ISUA; Saint Charles County (Saint Charles) MCZ; Saint Louis County (Saint Louis) CAS, (Valley Park) UMAH; Vernon County FDAG, (Nevada) TLer. MINNESOTA: Benton County (No locality given) UMSP; Big Stone County (No locality given) UMSP; Clearwater County (Bohall, Lake Itasca State Park) UMSP, (De Soto Lake, Itasca State Park) UMSP; Douglas County (Alexandria) PSUU; Goodhue County (Lake Pepin, east of Frontenac) UMSP; Hennepin County (Minneapolis) UMSP; Houston County (near Brownsville) UMSP; Olmstead County (No locality given) UMSP; Norman County UMSP, (Ada) USNM; Pine County USNM, (Snake River, 4.0 miles east of Pine City) USNM; Ramsey County (Saint Paul) ISNH, UMSP; Saint Louis County (Park Point, Duluth) AMNH; Stearns County (Lake Koronis, Paynesville) USNM; Traverse County (No locality given) UMSP; Washington County (3.0 miles south of Afton) UMSP, (Saint Croix River) UMSP; County unknown (Cliff) UMSP. MONTANA: Lake County (Polson) UWSW; Liberty County (Chester) MSUM; Mineral County (6.0 miles southeast of Saint Regis) LRus; Sanders County (Paradise) LRus; Stillwater County (Columbus) MSUM. NEBRASKA: Cass County (South Bend) UNLN, USNM; Dakota County (South Sioux City) UNLN; Lancaster County (Lincoln) CAS, UNLN, (Malcolm) CAS, USNM, (Roca) UNLN; Nemaha County (Peru) LSUB; Nuckolls County (Superior) OSUC; Otoe County (Nebraska City) UNLN; Saunders County (Ashland) SDSU, (Cedar Bluffs) UNLN; Thomas County (Halsey) UMAH, UNLN. NEVADA: Humboldt County (Golconda) Cbak. NEW HAMPSHIRE: Cheshire County (Jaffrey) MCZ; Grafton County (Hanover) USNM; Strafford County (Durham) ISNH. NEW JERSEY: Bergen County (Demarest) USNM, (Emerson) CAS, (Fort Lee) AMNH, (Palisade) MCZ, (Ramsey) AMNH; Camden County (Clementon) USNM; Cape May County (Seven Mile Beach) OUCO; Essex County (South Orange) CAS; Gloucester County (Glassboro) USNM, (Grenloch) USNM, (Malaga) ANSP; Morris County (Boonton) USNM, (Chester) AMNH; Middlesex County (South Amboy) AMNH; Passaic County (Clifton) USNM, (Oak Ridge) CNHM, (Passaic) AMNH, (Paterson) AMNH; Somerset County (No locality given) USNM; Sussex County (Hopatcong) AMNH; Warren County (Phillipsburg) CAS; Counties unknown (Estling Lake) USNM, (Gugnard) AMNH, (Midvale) USNM, (Snake Hill) USNM. NEW MEXICO: Sandoval County (Los Alamos) CNC. NEW YORK: Albany County (Altamont) CUNY; Columbia County (Copake Falls) CNHM; Cortland County (McLean Bogs) CAS, CUNY, ISNH, UMCP; Delaware County (Cooks Falls) CAS; Dutchess County (Poughkeepsie) UASM; Erie County (Buffalo) ISNH; Niagara County (Olcott) AUA; New York County (Bronx Park) AMNH, (Flatbush) AMNH, (Mosholu) AMNH, (Nepera Park) CAS, (New York City) CAS, MCZ, (Parkville) AMNH, (Rattlesnake Creek) CAS; Orange County (Huguenot) AMNH, (Pine Island) CUNY, (West Point) USNM; Richmond County (Staten Island) AMNH, CAS, USNM; Queens County (Jamaica) AMNH, MCZ; Rockland County (Suffern) USNM; Saint Lawrence County (Rossie) JSch; Tompkins County (Ithaca) CAS, CUNY, KSU, OUCO, PSUU, UASM, UMCP, UNLN, (McLean) UMSP; Ulster County (Ashokan) AMNH (Oliverea) USNM; Wayne County (Sodus) UASM; Westchester County (New Rochelle) CAS, (Peekskill) MCZ, (White Plains) CAS, USNM, (Yonkers) MCZ; County unknown (Catskill) CAS, (Danby) UNLN. NORTH CAROLINA: Beaufort County (Washington) MCZ; Haywood County (Mount Sterling) CAS; Moore County (Southern Pines) USNM; New Hanover County (Wilmington) CAS; Pasquotank County (Elizabeth City) MCZ; Polk County (Tryon) USNM; Robeson County (Lumberton) CNC; County unknown (Faison) CNC. OHIO: Ashtabula County (Chestnut Grove) PUM, (Jefferson) PUM, (Rock Creek) PUM, (Saybrook) PUM; Hamilton County (Cincinnati) UMAH; Ottawa County (Bass Island) PUM, (Put-in-Bay) UMAH; Putnam County (Sugar Creek) PUM; Summit County (Hudson) MCZ. OKLAHOMA: Cleveland County (Norman) OSUS, (Uono) CAS; Delaware County (Jay) OSUS; McCurtain County (Idabel) OSUS; Oklahoma County (No locality given) OSUS; Payne County (Stillwater) OSUS; Rogers County (Catoosa) CNHM; Tulsa County (Tulsa) CAS. OREGON: Baker County (Robinette) UWSW, (Snake River, Farewell Bend) UWSW; Douglas County (Roseburg) MCZ; Gilliam County (5.0 miles west of Arlington) JSch; Malheur County (Ontario) UWSW; Umatilla County (Camp Umatilla) MCZ; Union County (Alice) REST, UIMI; Wallaowa County (Wallaowa) OSUC; Wasco County (The Dalles) MCZ; County unknown (Olds Ferry) UIMI. PENNSYLVANIA: Allegheny County CAS, (Pittsburgh) CMPP; Bradford County (Susquehanna River, Wyalusing) UASM; Centre County (State College) PSUU; Chester County (Unionville) CMPP; Dauphin County (Harrisburg) UASM, (Hemmelstown) ANSP; Delaware County (Castlerock) USNM; Fayette County (No locality given) CMPP; Luzern County (Wyoming) USNM; Monroe County (Echo Lake) CAS; Northampton County (Easton) CAS, (Delaware Water Gap) AMNH, UASM; Philadelphia County (Olney) USNM, (Philadelphia) USNM; Pike County (Milford) CNHM; Tioga County UMAH, (Rutland) ANSP; Wayne County (White Mills) CAS; Westmoreland County (Jeannette) CMPP; Counties unknown (Conk Forest) PSUU, (Edge Hill) USNM, (Rockville) CAS, (The Rock) PSUU. RHODE ISLAND: Kent County (Quonset Point) CAS, (Warwick) UMAH; Newport County (Newport) USNM, (Portsmouth) CAS; Providence County (Providence) CMPP; Washington County (Watch Hill) USNM; County unknown (Touisset) UMAH. SOUTH CAROLINA: Oconee County (Clemson) WSUP. SOUTH DAKOTA: Brookings County (Brookings) CMPP, SDSU, VMK1, (Volga) CAS; Hughes County (Canning) SDSU, (Pierre) SDSU, VMK1; Tripp County (Winner) VMK1. TENNESSEE: Lake County (Gray's Landing) RTBe; Monroe County (Unaka Mountains) ANSD; Morgan County (Burrville) CNHM; Counties unknown (Lookout Mountain) MCZ, (Reelfoot Lake) CUNY, ISNH. TEXAS: Bexar County (San Antonio) CUNY, (10.0 miles northwest of San Antonio) CAS; Blanco County (Round Mountain) CAS; Brazos County ISNH, (College Station) TAMU; Brewster County (Castolon) TAMU, (Glenn Springs) UMAH; Cameron County (Brownsville) CAS, CUNY, DHKa, MCZ, USNM, (Esperanza Ranch, Brownsville) USNM; Comal County (New Braunfels) UASM; Dallas County (Dallas) MCZ, UASM; Dimmit County (No locality given) TAMU; Hidalgo County (Mission) UASM, (Weslaco) TAMU; Kleburg County (Kingsville) CUNY; Lamar County (Paris) USNM; Lee County (Fedor) CMPP; Reeves County (Balmorhea Lake) UASM, (Pecos) ISUA; Taylor County (Abilene) CAS; Terrell County (Lozier Canyon) MCZ; Travis County (Austin) UASM; Uvalde County (Uvalde) CAS; Val Verde County (Del Rio) UASM, (Devil's River, Del Rio) CNC, (9.0 miles southeast of Del Rio) DRWh; Victoria County (Victoria) USNM; Webb County (Laredo) CAS. UTAH: Cache County (Logan) USUL, (Wellsville) USUL; Salt Lake County (Fort Douglas) MCZ; Uinta County (No locality given) CMPP; Utah County (Provo) CAS; Weber County (Ogden) CNHM, USNM. VERMONT: Bennington County (No locality given) CAS, MCZ, USNM; Chittenden County (Burlington) RTBe; Franklin County (La Moille River, East Georgia) RTBe; Lamoille County (Stowe) AMNH; Windsor County (White River Junction) CAS. VIRGINIA: Fairfax County MCZ, (Alexandria) USNM, (Great Falls) USNM; Loudoun County (Bluemont) USNM, (Harpers Ferry) USNM; Montgomery County (No locality given) USNM; Nelson County (No locality given) USNM; Spotsylvania County (Fredericksburg) CAS. WASHINGTON: Adams County (Lake McElroy) CAS, PUM, USNM, (Lind) CAS, (Ritzville) USNM; Asotin County

(Grande Ronde River, Anatone) UWSW; Benton County (Hanford) UWSW; Franklin County (Kahlotus) CAS, UWSW, (Pasco) UWSW, WSUP; Grant County (Coulee City) CAS, UWSW, (Dry Falls, Grand Coulee) UWSW, WSUP, (Stratford) CAS, UIMI, USNM, UWSW; Kittitas County (Vantage) CAS, UWSW; Lincoln County (Sprague) USNM, (Sprague Lake) CAS; Pend Oreille County (Usk) USNM; Spokane County (Cheney) WSUP; Walla Walla County (Burbank) UWSW, (College Place) JSch; Whitman County (Almota) WSUP, (Wawawai) USNM, UWSW, WSUP; Counties unknown (Vila) UWSW, (Yakima River, Morgan's Ferry) MCZ. WEST VIRGINIA: USNM, Tucker County (No locality given) SJSC. WISCONSIN: Bayfield County (No locality given) UWMW; Dane County (No locality given) UWMW, UWSW; Dodge County (Beaver Dam) CAS, UMAH; Green County (Albany) CAS, (Brodhead) UMAH; Milwaukee County (Milwaukee) MCZ; Sauk County (Prairie du Sac) CNHM. WYOMING: (No locality given) CMPP.

Brachinus puberulus Chaudoir

(Figs. 337, 355, 356, 357, 360, 368)

Brachinus puberulus Chaudoir, 1868: 294. Lectotype, here selected, a male, MHNP, labelled "stylicornis sec. LeConte Say" and "Ex Museo Chaudoir." *Type locality*. — Texas, as originally given by Chaudoir.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Medium-sized beetles, 9.5 to 12.4 mm.

Color. As in *fumans*.

Microsculpture. As described for genus.

Macrosculpture. As in *fumans*, except punctures finer.

Head. As in *fumans*, except antennal scope widest at middle.

Prothorax. As in *fumans*, except anterior tibia with anterior surface strigose. Pronotum (fig. 337).

Pterothorax. As in *fumans*, except costae weaker.

Abdomen. As described for genus.

Genitalia. Male (figs. 355, 356, 357). Median lobe with plane of shaft barely rotated from plane of basal bend. Basal bend short. Median lobe swollen medially. Apex of shaft narrow, slightly turned dorsally. Ligule short, parallel-sided, rounded apically. Virga (figs. 355, 356). Female (fig. 360). Stylus long, narrow, rounded apically.

Variation. — Too few specimens are known to evaluate geographic variation.

Flight. — The flight of these beetles has not been recorded.

Etymology. — Latin, *pubis*, down or hair; *ulus*, diminutive; referring to the short pubescence covering these beetles.

Life history. — I have seen one adult collected in May, but it was not teneral.

Distribution. — (Fig. 368). This species is known only from Texas. I have seen six specimens from the following localities.

UNITED STATES

TEXAS:MCZ, MHNP, Cameron County (Brownsville) WHTy; Hidalgo County (No locality given) TAMU; Victoria County (Victoria) USNM.

Brachinus favicollis Erwin

(Figs. 336, 340, 341, 342, 359, 365)

Brachinus favicollis Erwin, 1965: 11. Holotype male and allotype female both in CAS.

Type locality. — Jamul, San Diego County, California.

Diagnostic combination. — The very deep punctures of the pronotum separate these beetles from others in the study area.

Description. — Medium-sized beetles, 9.5 to 10.5 mm.

Color. As in *fumans*, except terga ferruginous, and sterna more narrowly infuscated at side.

Microsculpture. As described for genus.

Macrosculpture. As in *fumans*, except pronotal punctures much deeper.

Head. As in *fumans*, except mentum and submentum with accessory setae.

Prothorax. Pronotum (fig. 336) similar to *fumans*. Proepipleura and proepisterna with

numerous scattered setae. Anterior tibia with anterior surface strigose.

Pterothorax. As in *fumans*, except costae more highly elevated.

Abdomen. As described for genus.

Genitalia. Male (figs. 340, 341, 342). Median lobe with plane of shaft rotated about 45° from plane of basal bend. Basal bend short. Shaft not as swollen as in *fumans*, apex more narrowed and slightly twisted. Ligule short, broad, truncate. Virga (figs. 340, 341). Female (fig. 359). Stylus narrow, widened apically and rounded.

Variation. — Intrapopulational variation occurs in the shape of the pronotum, the color of the elytra, and the degree to which the metepisterna are infuscated.

Flight. — These beetles have been collected at lights at Camp Verde, Arizona.

Etymology. — Latin, *favus*, honeycomb; *collis*, neck; referring to the strongly punctured pronotum of these beetles.

Collecting notes. — D. R. Whitehead collected these beetles at the edge of a permanent stream near Hooker's Hot Springs, Arizona. G. R. Noonan collected specimens from under stones in an intermittent stream bed in southern California at an elevation of 3,250 feet. The stream side was sandy and with small stones. The common trees in the bottom of the gully, through which the stream flowed, were specimens of *Platanus*, *Salix*, *Alnus*, *Populus*, and *Fraxinus* species.

Life history. — Members of this species have been collected from March to August, and in January and October. Teneral adults were collected in May in California and Arizona, and in July in Arizona. Overwintering probably takes place in the adult stage.

Distribution. — (Fig. 365). The range of this species extends from eastern Arizona into California, and south to Baja California. I have seen 152 specimens from the following localities:

MEXICO

BAJA CALIFORNIA: (Cataviña) CAS; (San Vicente) LACM; (South of El Sauzal) CAS.

UNITED STATES

ARIZONA: Cochise County (Bass Canyon, Tenney's Mule Shoe Ranch, near Hooker's Hot Springs) DRWh; Gila County (East Verde River, 6.0 miles north of Payson) LACM, (10.0 miles south of Globe) AMNH, (Base of Pinal Mountains) PUM, UATA; Graham County (Geronimo) UATA; Navajo County (8-15.0 miles northeast of Whiteriver) AMNH; Pima County (Santa Catalina Mountains) CAS, (Tucson) CAS, UATA; Pinal County (Aravaipa Creek) CUNY; Yavapai County (Camp Verde) CAS, (Cottonwood) UIMI; County unknown (Carrizo) UATA, (Kohl's Ranch) UATA. CALIFORNIA: Imperial County (Carrizo) UMAH; Los Angeles County CMPP, (Azusa) LACM, (Los Angeles) LACM, (Pasadena) CAS, (San Francisco Canyon) LACM, (San Gabriel Canyon) GRNo, (Tujunga Creek) LACM; Orange County (Black Star Canyon) UCD, (Trabuco) GRNo; Riverside County (Hemet) VVBa, (Palm Canyon) CNC, LACM, MCZ, (Palm Springs) UCD, (Temecula) CAS; San Bernardino County (Mojave River) CAS; San Diego County UCD, (Jumil) CAS, (Mission Valley) SDNHM, (Pamo Valley) LACM, (Poway Groove) GRNo; Santa Barbara County (4.0 miles east of Los Prietos) UCD; County unknown (San Juan) UWSW.

Brachinus perplexus Dejean

(Figs. 335, 343, 344, 345, 362, 366)

Brachinus perplexus Dejean, 1831: 426. Lectotype, here selected, a male, MHNP, labelled "perplexus ? var. in Amer. Bor." on green paper, and "Ex Museo Chaudoir" on white paper. This specimen stands first in second row of nine specimens. *Type locality.* — North America, as originally given by Dejean, but herewith restricted to Florida.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Medium-sized beetles, 7.9 to 11.0 mm.

Color. As in *fumans*, except terga usually ferruginous.

Microsculpture. As described for genus.

Macrosculpture. As in *fumans*.

Head. As in *fumans*, except antennal scape widest about middle, and mentum and submentum with accessory setae.

Prothorax. As in *fumans*, except anterior tibia with anterior surface strigose. Pronotum (fig. 335).

Pterothorax. As in *fumans*, except costae weaker and more densely punctate, and humeral angle not so prominent.

Abdomen. As described for genus.

Genitalia. Male (figs. 343, 344, 345). Median lobe with plane of shaft rotated 45° from plane of basal bend. Basal bend long. Apex of shaft narrow, slightly twisted. Ligule moderately long, broad, truncate. Virga (figs. 343, 344). Female (fig. 362). Stylus short, broad, slightly bent at apical third, narrowly rounded apically.

Variation. — Intrapopulational variation occurs in the body size and in the shape of the pronotum.

Flight. — These beetles have been collected at lights in Alabama and Louisiana.

Etymology. — Latin, *perplexus*, intricate, puzzling; referring to the similarity of these beetles to the other species in the genus.

Life history. — Members of this species have been collected in February, and May to August, but no teneral adults have been seen.

Distribution. — (Fig. 366). The range of this species extends from Florida to Texas, and north to southern Iowa. I have seen 71 specimens from the following localities:

UNITED STATES

ALABAMA: Mobile County (Mobile) CAS; Tallapoosa County (Smith Mountain Tower) AUA. ARKANSAS: Conway County (No locality given) UAFA; Desha County (No locality given) UAFA; Hempstead County (Hope) MCZ; Lawrence County (No locality given) CAS. FLORIDA: Dade County (Royal Palm State Park) PUM; Pinellas County (Tarpon Springs) CAS. LOUISIANA: Ouachita Parish (Calhoun) UAFA; Vernon Parish (Rosepine) UAFA. MISSISSIPPI: Carroll County (Avalon) UMAH; George County (Lucaledale) CUNY; Pike County (McComb) UWSW; Tunica County (Dundee) UMAH. NORTH CAROLINA: Moore County (Southern Pines) CNC. OKLAHOMA: Le Flore County (Summerfield) OSUS. TENNESSEE: Lake County (Gray's Landing) RTBe; Shelby County (Memphis) CAS. TEXAS: Dallas County (Dallas) MCZ; Kleberg County (Kingsville) CUNY; Morris County (Daingerfield State Park) UASM; Victoria County (Victoria) USNM; County unknown (Fuller) USNM.

Brachinus velutinus Erwin

(Figs. 339, 352, 353, 354, 363, 367)

Brachinus velutinus Erwin, 1965: 17. Holotype male and allotype female both in UCD.

Type locality. — Davis, Yolo County, California.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Small-sized beetles, 7.0 to 8.2 mm.

Color. As in *fumans*, except terga and metepisterna usually ferruginous.

Microsculpture. As described for genus.

Macrosculpture. As in *fumans*, except punctures very fine.

Head. As in *fumans*, except antennal scape almost cylindrical, and mentum with accessory setae.

Prothorax. As in *fumans*, except much narrower, proepipleura and proepisterna pubescent throughout, and anterior tibia with anterior edge strigose. Pronotum (fig. 339).

Pterothorax. Elytra narrower than in *fumans*, more sloped at humeri, costae hardly present, and with denser pubescence.

Abdomen. As described for genus.

Genitalia. Male (figs. 352, 353, 354). Median lobe with plane of shaft rotated about 45° from plane of basal bend. Basal bend short. Median lobe slightly swollen medially. Apex of shaft narrowed, slightly twisted, and slightly bent dorsally. Ligule short, narrow, and rounded apically. Virga (figs. 352, 353). Female (fig. 363). Stylus short, broad, arcuate, narrowly rounded apically.

Variation. — Too few specimens are known to evaluate geographic variation.

Flight. — The flight of these beetles has not been recorded.

Etymology. — Latin, *velutinus*, velvety; referring to the appearance of the elytral pubescence on these beetles.

Collecting notes. — W. H. Tyson collected members of this species in a *Typha-Scirpus* marsh near Los Banos when the water was near maximum height.

Life history. — Members of this species have been collected in April, May, and September, but no teneral adults were seen.

Distribution. — (Fig. 367). The range of this species extends along the Central Valley of California in the Sacramento and San Joaquin drainage systems. I have seen 19 specimens from the following localities:

UNITED STATES

CALIFORNIA: PUM, USNM, Contra Costa County (Brentwood) CAS; Stanislaus County (Newman) UCD; Tulare County (Visalia) UCD; Yolo County (Davis) CAS, UCD.

Brachinus imperialensis Erwin

(Figs. 338, 349, 350, 351, 361, 364)

Brachinus imperialensis Erwin, 1965: 17. Holotype and allotype both in CAS. *Type locality.* — Potholes, Imperial County, California.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Medium-sized beetles, 7.0 to 12.1 mm.

Color. Metepisterna and sides of abdominal sterna infuscated, otherwise ferruginous. Dorsal surface and epipleura of elytra blue.

Microsculpture. As described for genus.

Macrosculpture. As in *fumans*.

Head. As in *fumans*, except antennal scape widest at middle, and mentum and submentum with accessory setae.

Prothorax. As in *fumans*, except anterior tibia with anterior surface strigose.

Pterothorax. As in *fumans*, except costae weaker and elytra totally pubescent.

Abdomen. As described for genus.

Genitalia. Male (figs. 349, 350, 351). Median lobe with plane of shaft rotated about 45° from plane of basal bend. Basal bend short. Apex of shaft broad, slightly twisted. Ligule moderately long, broad, rounded apically. Virga (figs. 349, 350). Female (fig. 361). Stylus short, arcuate, rounded apically.

Variation. — Intrapopulational variation occurs in body size and in the shape of the pronotum.

Flight. — These beetles have been collected repeatedly at lights throughout the range of the species.

Etymology. — *Imperial*, English, from Imperial County, the place where the types were collected; *ensis*, place, locality, or county.

Life history. — Members of this species have been collected in March and April, June to September, and November, but teneral adults were not seen.

Distribution. — (Fig. 364). The range of this species extends from eastern Colorado, south to the Mexican Highplain, and from California east to Texas. I have seen 218 specimens from the following localities:

MEXICO

DURANGO: (Durango) AMNH; (Tlahualilo) USNM. SAN LUIS POTOSI: (San Luis Potosi) AMNH. SINALOA: (Los Mochis) CAS. SONORA: (Ciudad Obregon) AMNH; (Hermosillo) CAS.

UNITED STATES

ARIZONA: Cochise County (Cave Creek Ranch) SJSC, UASM; (Douglas) CNHM, CUNY, FDAG, UASM, UCD, UCR; (2.0 miles northeast of Douglas) OUCO; (5.0 miles west of Portal) UCD; (South West Research Station, 5.0 miles west of Portal) AMNH, CUNY; Coconino County (Cameron Trading Post) UASM; Graham County (Thatcher) UCD; Pima County (San Simon) LACM; (Tucson) MCZ, USNM; Yuma County (Fort Yuma) USNM, (Yuma) CAS, MCZ, TLER, TMBH, UATA, USNM; County unknown (East Bridge) ISUA, MCZ. CALIFORNIA: Imperial County (Brawley) CAS, CBak, (Calexico)

UCD, UWSW, (Calipatria) CAS, (El Centro) CAS, CNHM, TLEr, (Holtville) CAS, (Imperial Valley) UATA, (Needles) TLEr, (Palo Verde) UIMI, (Potholes) CAS; Los Angeles County (No locality given) CAS, UWSW; Riverside County (Blythe) CAS, (Colorado River, Blythe) TLEr, (Lake Elsinore) USNM, (Palm Springs) USNM. COLORADO: Yuma County (Wray) KSU. NEVADA: Clark County (Logandale) NSDA, (Overton) UASM, (Overton Boat Landing) JSch. NEW MEXICO: Curry County (Clovis) USNM; Hidalgo County (Animas) AMNH, (Rodeo) CUNY; Luna County (Deming) MCZ. TEXAS: Brewster County (Alpine) CAS, (Castolon) TAMU; Cameron County (Brownsville) CNC, CUNY, ISNH; El Paso County (El Paso) CMPP; Hidalgo County TAMU, (McAllen) UMAH; Jeff Davis County (Fort Davis) CNC; Kleberg County (Kingsville) CUNY; Randall County (Canyon) TAMU, (Palo Duro State Park) UMSP; Reeves County (Pecos) ISUA; San Patricio County (Welder Wildlife Refuge, near Sinton) CNC; Travis County (Austin) UASM; Victoria County (Victoria) UASM.

The *cordicollis* group

The single characteristic shared by the species of this group is the form of the virga of the endophallus. This structure is characteristically H-shaped with a dorsal fin on the midline or some modification of the basic H-shape. The more darkly pigmented areas extend from the median fin to the lateral lobes. The eight species belonging to this group are arrayed in four subgroups.

The *cordicollis* subgroup

The species of this subgroup are characterized by the robust median lobe, usually with a ventral depression on the shaft, and the true H-shaped virga. Four species, *B. cordicollis* Dejean, *B. sublaevis* Chaudoir, *B. cyanochroaticus* Erwin, and *B. ichabodopsis* new species, are included.

Brachinus cordicollis Dejean

(Figs. 376, 377, 378, 379, 387, 391)

Brachinus cordicollis Dejean, 1826: 466. Lectotype, here selected, a male, MHNP, labelled "cordicollis m. in Amer. Bor." and "D. LeConte." *Type locality*. — North America, as originally given by Dejean, but herewith restricted to Fairfax County, Virginia.

Brachinus velox LeConte, 1848: 206. Lectotype, here selected, a male, MCZ red type label number 5850, further labelled with a pink disc, "90" and "v. velox LeC." *Type locality*. — New York, as originally given by LeConte. LeConte, 1862: 524.

Brachinus leptocerus Chaudoir, 1868: 296. Lectotype, here selected, a female, MHNP, labelled "Ex Museo Chaudoir" and standing fifth in a series of six specimens behind box label "leptocerus Chaud. Etas Unis Guex." *Type locality*. — United States, as originally given by Chaudoir, but herewith restricted to New York. NEW SYNONYMY.

Brachynus gracilis Blatchley, 1910: 160. Lectotype, previously selected (Blatchley, 1930: 33), a male, PUM, labelled "Marshall Co., Ind. W. S. B. 10-14-03" "L-11/2-36" red type label, and a black bordered label "Holotype Brachynus gracilis Blatchley, 1910." *Type locality*. — Marshall County, Indiana, as originally given by Blatchley. NEW SYNONYMY.

Notes. — The specimen labelled *gracilis* holotype cannot be a holotype because Blatchley did not originally designate it so.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Medium-sized beetles, 7.0 to 10.2 mm.

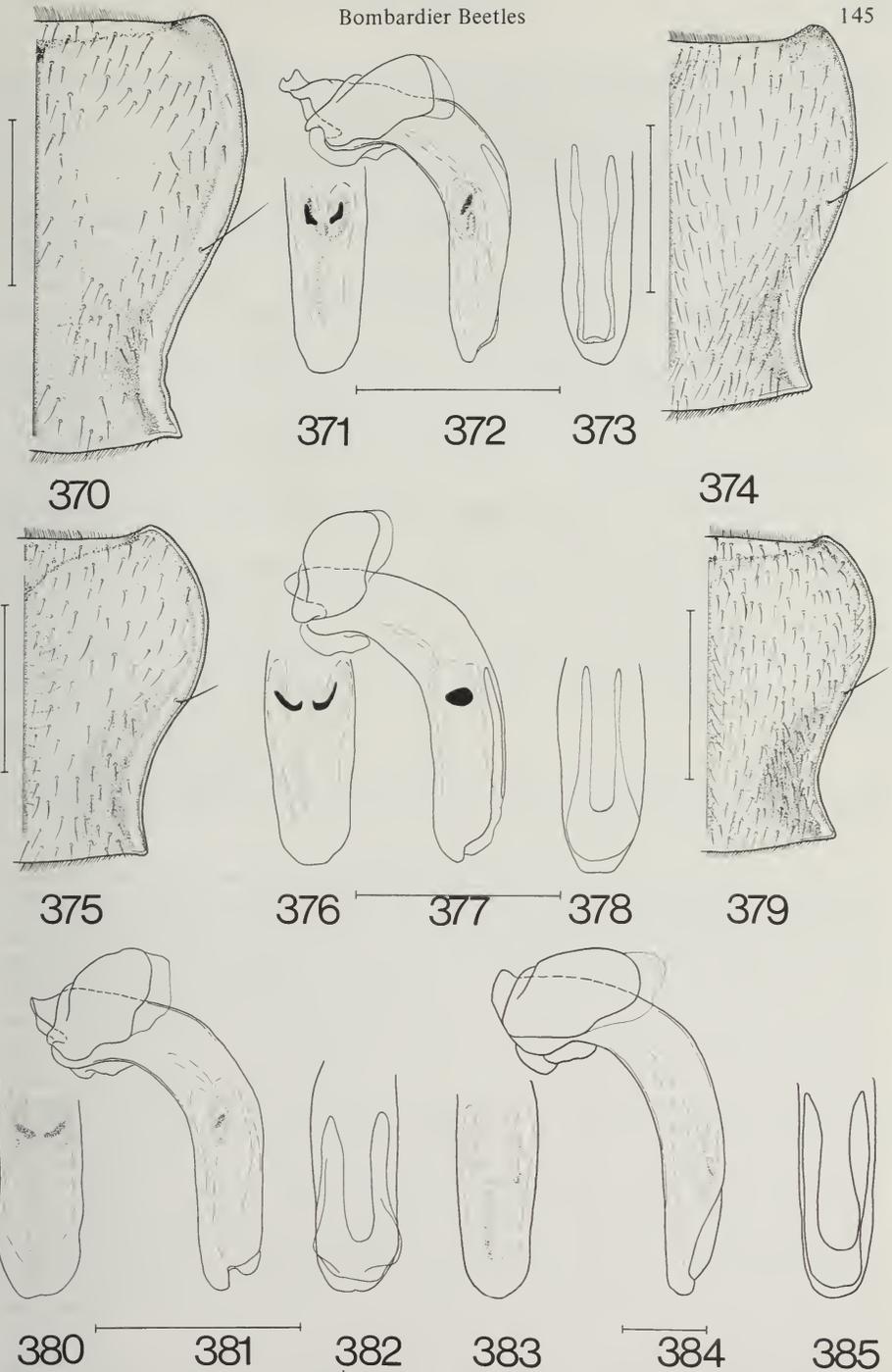
Color. Antennal articles 3 and 4 various. Metepisterna, and abdominal sterna and terga infuscated, otherwise ferruginous. Dorsal surface and epipleura of elytra blue.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows and disc of pronotum rugose and punctate, punctures moderately impressed.

Head. Frontal furrows moderately impressed. Antennal scape cylindrical or almost so. Ligula with center area ellipsoid-convex with two lateral rows of three setae per row. Mentum and submentum without accessory setae.

Prothorax. Pronotum (fig. 379) slightly convex, flattened along center line, sides narrowly



Figs. 370, 374, 375, 379. Pronotum, right half, dorsal aspect. 370. *Brachinus ichabodopsis* new species, Hardkingsville, Florida. 374. *Brachinus sublaevis* Chaudoir, Archbold Biology Station, Florida. 375. *Brachinus cyanochoaticus* Erwin, 11.9 miles west of York, North Dakota. 379. *Brachinus cordicollis* Dejean, Toronto, Canada. Figs. 371-373, 376-378, 380-385. Male genitalia. 371. *Brachinus sublaevis* Chaudoir, Archbold Biology Station, Florida, ventral aspect. 372 & 373. Lateral & dorsal aspects of same. 376. *Brachinus cordicollis* Dejean, Ithaca, New York, ventral aspect. 377 & 378. Lateral & dorsal aspects of same. 380. *Brachinus cyanochoaticus* Erwin, 11.9 miles west of York, Dakota, ventral aspect. 381 & 382. Lateral & dorsal aspects of same. 383. *Brachinus ichabodopsis* new species, Hardkingsville, Florida, ventral aspect. 384 & 385. Lateral & dorsal aspects of same. Accompanying scale lines equal 1.0 mm.

reflexed. Proepisterna pubescent throughout, proepipleura various. Anterior tibia with anterior surface strigose.

Pterothorax. Elytra elongate, narrow, costae weakly elevated. Humeral angle square. Costae and depressions pubescent. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 376, 377, 378). Median lobe with plane of shaft rotated 45° from basal bend. Basal bend long. Apex of shaft broad and blunt, with slight notch at middle. Venter of shaft with elongate longitudinal depression. Ligule elongate, narrow, rounded apically. Virga (figs. 376, 377). Female (fig. 387). Stylus narrow, parallel-sided, rounded apically.

Variation. — Besides the intrapopulational variation in the shape of the pronotum and the body size, setae of the proepipleura are present in some individuals, absent from others.

Flight. — The flight of these beetles has not been recorded.

Etymology. — Latin, *cordis*, heart; *collis*, neck; referring to the cordiform outline of the pronotum of these beetles.

Collecting notes. — C. Chantal collected these beetles from under stones on sandy clay terraces above the Becancour River in Quebec.

Life history. — Members of this species have been collected from April to October. Teneral adults were collected in April in New York, in May in Ontario, in July in Pennsylvania, and in September in Wisconsin. Overwintering is probably in the adult stage.

Distribution. — (Fig. 391). The range of this species extends from New Brunswick and Virginia west to Utah, Colorado, and New Mexico. I have seen 864 specimens from the following localities:

CANADA

NEW BRUNSWICK: (Saint John) UMMW. ONTARIO: (Belleville) UASM; (Erindale) CAS; (Lake Abitibi, Low Bush) CAS; (Rogue Hills) CAS; (Summerville) CAS; (Toronto) CAS; (Willowdale) CAS. QUEBEC: (Becancour) CCH; (Como) MCZ; (Perrot Isle) CMPP; (Vaudreuil) CAS.

UNITED STATES

ARKANSAS: Washington County (No locality given) UAFA. COLORADO: Boulder County (Viele Lake) CArm; Denver County (Denver) ISNH. ILLINOIS: Cook County (Chicago) WSUP, (Des Plaines) CNHM, (Willow Springs) UMAH; Kendall County (Oswego) CNHM; Lake County (Volo) RTBe; La Salle County (No locality given) RTBe; McHenry County (Algonquin) ISNH; Putnam County (No locality given) ISNH; INDIANA: CNHM, Lake County (Hessville) CMPP. IOWA: Buchanan County (Independence) MCZ; Henry County (Mount Pleasant) CAS; Howard County (Elma) AMNH; Johnson County (Iowa City) MCZ, USNM, (Solon) USNM; Story County (Ames) ISUA. KANSAS: Riley County (No locality given) KSU; Shawnee County (Topeka) KSU. MARYLAND: (No locality given) MCZ. MASSACHUSETTS: Hampden County (Chicopee) MCZ; Middlesex County (Cambridge) MCZ, (Concord) MCZ, (Sudbury) MCZ, (Wayland) MCZ. MICHIGAN: Barry County (Otis Lake) TFH; Charlevoix County (Garden Island) UMAH; Cheboygan County (No locality given) UMAH; Gratiot County (No locality given) UMAH; Kent County (Grand Rapids) UNLN; Saint Clair County (Port Huron) USNM; Washtenaw County (Ann Arbor) UMAH, (Whitmore Lake) JSch; Wayne County (Detroit) MCZ; County unknown (Aurelius) OSUS. MINNESOTA: Clearwater County (De Soto Lake, Itasca State Park) UMSP; Douglas County (Alexandria) PSUU; Hennepin County (No locality given) UMSP; Houston County (No locality given) UMSP; Mille Lacs County (Garrison) UMSP, (Mille Lacs Lake, near Garrison) UMSP; Olmstead County (No locality given) UMSP; Otter Tail County (Battle Lake) UMSP; Pine County (Snake River, 4.0 miles east of Pine City) UMSP; Ramsey County (No locality given) UMSP; Red Lake County (Plummer) UMSP; Washington County (No locality given) UMSP; County unknown (Vineland) UMSP. MISSOURI: (No locality given) ISNH. NEBRASKA: Dodge County (Fremont) UNLN; Lancaster County (Lincoln) UNLN; Saunders County (Ashland) UNLN. NEW JERSEY: Gloucester County (Woodbury) USNM; Hunterdon County (Hampton) AMNH; Middlesex County (New Brunswick) AMNH; Passaic County (Passaic) AMNH; Somerset County (No locality given) UMAH; Sussex County (Hopatcong) AMNH; Union County (Elizabeth) AMNH; County unknown (Snake Hill) AMNH. NEW MEXICO: Bernalillo County (Albuquerque) USNM. NEW YORK: Albany County (Altamont) CNHM, CUNY; Cayuga County (Cayuga) MCZ, (Fair Haven) LACM; Clinton County (Plattsburg) WSUP; Erie County (East Aurora) CUNY, (Hamburg) CAS; Greene County (Catskill) USNM; Jefferson County (Cape Vincent) CUNY; Monroe County (Rochester) LACM, MCZ; New York County (Bronx Park) CAS, (New York City) MCZ; Niagara County (Olcott) AUAA, CUNY; Ontario County (Fish Creek, near Victor) UASM, (Geneva) UMAH; Suffolk County (Babylon) AMNH; Schuyler County (Cayuta Lake) UASM, (Watkins Glen) AMNH, MCZ, VMK; Tompkins County (Buttermilk Falls) PUM, (Ithaca) AUAA, CAS, CUNY, ISNH, KSU, LACM, MCZ, OUCO, UASM, UCR, UIMI, UNLN, (Ludlowville) CUNY, (Varna) UASM; Westchester County (Peekskill) MCZ; Wayne County (No locality given) UASM; County unknown (Enfield Falls) CNC, (Taughannock Falls) CUNY. OHIO: Delaware County (No locality given) PUM; Franklin County (Columbus) OUCO, PUM; Pickaway County (No locality given) SJSC; Putnam County (Auglaize River) PUM; Ottawa County (Bass Island) PUM; Williams County (Saint Joseph River) PUM. PENNSYLVANIA: Allegheny County (Pittsburgh)

CMPP, OSUŠ; Bradford County (Susquehanna River, Wyalusing) GRNo; Crawford County (Conneaut Lake) CMPP; Cumberland County (Camp Hill) CUNY; Dauphin County (Harrisburg) VMK; Erie County CMPP, (Erie) CUNY; Franklin County (Chambersburg) USNM; Montgomery County (Arcola) ANSP, OUCO; Northampton County (Easton) CAS, (Delaware Water Gap) AMNH; Pike County (Milford) SDNHM; Westmoreland County (Jeanette) CMPP; County unknown (Edge Hill) USNM, (Lehigh Water Gap) USNM. UTAH: (No locality given) ISUA. VERMONT: Bennington County (No locality given) MCZ; Chittenden County (East Georgia) RTBe, (Grand Isle) MCZ. VIRGINIA: Fairfax County (Great Falls) USNM; Loudoun County (No locality given) ANSP, MCZ. WEST VIRGINIA: County unknown (Brush Creek) CUNY. WISCONSIN: Dane County (No locality given) UWMW; Green County (Brodhead) UMAH; Winnebago County (Oshkosh) CAS.

Brachinus cyanochromaticus Erwin

(Figs. 375, 380, 381, 382, 388, 392)

Brachinus cyanochromaticus Erwin, 1969: 283. The holotype male and allotype female are in MCZ. *Type locality*. — Eleven miles west of York, Benson County, North Dakota.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Medium-sized beetles, 7.0 to 11.3 mm.

Color. Antennal articles 3 and 4 apically, metepisterna, metasternum at sides, and abdominal sterna and terga infuscated, otherwise ferruginous. Dorsal surface and epipleura of elytra blue, usually with metallic luster.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows rugose and punctate. Disc of pronotum punctate, punctures barely impressed.

Head. Frontal furrows moderately impressed. Antennal scape robust, widest at middle, otherwise head as in *cordicollis*.

Prothorax. As in *cordicollis*, except sides of pronotum (fig. 375) more widely reflexed and proepipleura glabrous.

Pterothorax. As in *cordicollis*.

Abdomen. As described for genus.

Genitalia. Male (figs. 380, 381, 382). Median lobe with plane of shaft slightly rotated from plane of basal bend. Basal bend long. Shaft as in *cordicollis*. Entire median lobe more robust than in *cordicollis*. Virga (figs. 380, 381). Female (fig. 388).

Variation. — The members of this species vary considerably in the shape of the pronotum and in the color of the elytra. These are both local variations, but generally the color has a metallic luster in the north and western portions of the range, while in the south and eastern parts of the range, the color becomes dull blue.

Flight. — The flight of these beetles has not been recorded.

Etymology. — Greek, *kyanos*, blue; *chromaticus*, color of the skin; referring to the blue color of the elytra of these beetles.

Collecting notes. — H. Goulet collected these beetles near old beaver houses in the company of *Platypatrobis lacustris* Darlington, and G. E. Ball and R. T. Bell collected them at the edges of ponds.

Life history. — Members of this species have been collected from April to October. Ten general adults were collected in May in Quebec. At least some adults overwinter.

Distribution. — (Fig. 392). The range of this species extends from British Columbia and Idaho, east to Massachusetts, and south to Kansas. I have seen 342 specimens from the following localities:

CANADA

BRITISH COLUMBIA: (Salmon Arm) CAS. MANITOBA: (Boissevain, south of Brandon) ZMLS; (Whitewater Lake) UASM, ZMLS. ONTARIO: (Belleville) CUNY; (Britannia) CAS; (Craigleith, West Collingwood, Georgian Bay) ZMLS; (De Cew Falls) CNC; (Grand Bend, Lake Huron) ZMLS; (Gravenhurst) AMNH; (Hyde Park Corner) RTBe; (Lake of the Woods, Clearwater Bay) CNC; (Point Pelee) ZMLS; (Port Credit) ZMLS; (Prince Edward County) CUNY; (Toronto) CAS; (Turkey Point, Lake Erie) ZMLS. SASKATCHEWAN: (Regina) ZMLS. QUEBEC: (Dorval) CAS; (Gatineau, 1.0 mile southwest of Meach Lake) CNC; (Lachine) CAS; (Lac Saint Jean) CAS; (La Trappe) ZMLS; (Montreal) CAS; (Outrem't) CAS; (Rigaud) CAS, HGou; (Saint Eustache) CAS; (Saint Rose) CAS; (Venise) CCH.



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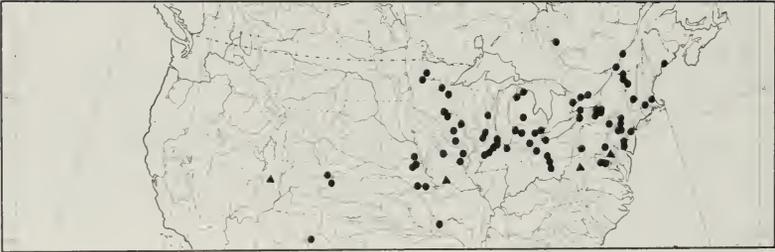
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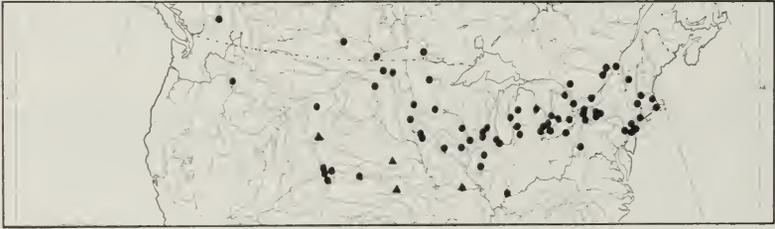
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Figs. 386-389. Right stylus of female ovipositor, ventral aspect. 386. *Brachinus ichabodopsis* new species, Florida. 387. *Brachinus cordicollis* Dejean, Toronto, Canada. 388. *Brachinus cyanochroaticus* Erwin, 11.9 miles west of York, North Dakota. 389. *Brachinus sublaevis* Chaudoir, Highlands Hammock State Park, Florida. Figs. 390-393. Geographical distribution maps. 390. *Brachinus ichabodopsis* new species. 391. *Brachinus cordicollis* Dejean. 392. *Brachinus cyanochroaticus* Erwin. 393. *Brachinus sublaevis* Chaudoir. Accompanying scale line equals 1.0 mm.

UNITED STATES

COLORADO: Boulder County (Bellmire Reservoir, Longmont) CARM, (McCall Lake, Lyons) CARM; Larimer County (Fort Collins) CAS; Weld County (Greeley) USNM; Yuma County (Wray) KSU. CONNECTICUT: New Haven County (New Haven) CAS. IDAHO: Nez Perce County (Lewiston) UIMI. ILLINOIS: Cook County (Chicago) WSUP; Putnam County (No locality given) ISNH. INDIANA: Posey County (Hovey Lake) PUM. IOWA: Clayton County (Guttenberg) ISUA; Dickinson County (Lake Okoboji) USNM; Johnson County (Iowa City) ANSP; Palo Alto County (Ruthven) UMAH; Story County (Ames) ISUA. KANSAS: (No locality given) USNM. MASSACHUSETTS: Bristol County (Dartmouth) ISUA; Hampshire County (Mount Tom) CMPP; Middlesex County (Waltham) MCZ, (Wayland) MCZ. MICHIGAN: Kalamazoo County (Gull Lake Biology Station) JSch; Eaton County (Grand Ledge) USNM; Huron County (Charity Island) UMAH; Kent County (Grand Rapids) CNHM, UNLN; Missaukee County (No locality given) UMAH; Oceania County (Crystal Valley) CNHM, (Silver Lake State Park) UMAH; Tuscola County (Fostoria) RCGr; Washtenaw County (Ann Arbor) ISUA, UMAH, (Whitmore Lake) JSch, UMAH; Wayne County (Detroit) CAS. MINNESOTA: Clearwater County (De Soto Lake, Itasca State Park) UMSP, (Itasca State Park) UMSP; Houston County UMSP, (Brownsville) USNM; Stearns County (Rice Lake, Paynesville) USNM; Traverse County (No locality given) UMSP. MISSOURI: Counties unknown (Cliff Caves) USNM, (Luxemburg) USNM. MONTANA: Big Horn County (Lodge Grass) MSUM. NEBRASKA: (No locality given) ISNH. NEW HAMPSHIRE: Cheshire County (Swanzy Pond) MCZ. NEW JERSEY: Essex County (Orange Mountains) USNM; Hudson County (Secaucus) CAS; Morris County (Towaco) USNM; Passaic County (Paterson) AMNH; Warren County (Phillipsburg) CAS; County unknown (Snake Hill) AMNH, CAS. NEW YORK: Cayuga County (Montezuma Marsh) UASM; Chautauqua County (Mayville) UASM; Cortland County (McLean Bogs) CUNY; Erie County (Buffalo) CAS, ISNH, (East Aurora) CUNY, (Lancaster) CAS; Genesee County UMAH, (Batavia) CUNY; Herkimer County (Warren) MCZ; Monroe County (Rochester) LACM; New York County (New York City) MCZ, (Staten Island) CNHM, USNM, (Yonkers) CAS; Niagara County (Olcott) CUNY; Orange County (West Point) USNM; Rockland County (Piermont) CAS, SDNHM, USNM; Tompkins County (Ithaca) CAS, CUNY, UASM; Wyoming County (Pike) AMNH, MCZ; County unknown (West Hebron) USNM. NORTH DAKOTA: Benson County (11.9 miles west of York) UASM; McLean County (Turtle Mountain) UMAH; Ramsey County (Devi's Lake) USNM. OHIO: Ashtabula County (Ashtabula, Chestnut Grove) PUM. PENNSYLVANIA: Allegheny County CMPP, USNM, (Pittsburgh) CMPP. SOUTH DAKOTA: Brookings County (Brookings) VMKi, (Volga) CAS. VERMONT: Chittenden County (Burlington) RTBe, (Gillette Pond, Richmond) RTBe, (Home Creek Delta, Charlotte) RTBe, (Shelburne) CAS, (Shelburne Pond, Shelburne) RTBe; Franklin County (La Moille River, East Georgia) RTBe. WISCONSIN: Dane County (Madison) UWMW; Dodge County (Beaver Dam) ROM, UMAH. WYOMING: Laramie County (Pine Bluffs) AMNH.

Brachinus sublaevis Chaudoir

(Figs. 371, 372, 373, 374, 388, 393)

Brachinus sublaevis Chaudoir, 1868: 293. Lectotype, here selected, a female, MHNP, labelled "ant maculat abdomn. gra" and "Ex Museo Chaudoir." *Type locality*. — Florida, here designated.

Brachynus pulchellus Blatchley, 1910: 161. Lectotype, a female, PUM, labelled "Posey Co. Ind. WSB" "4-18-07" "Purdue Blatchley Coll." and with a red type label. *Type locality*. — Posey County, Indiana, as originally given by Blatchley. NEW SYNONYMY.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Medium to large-sized beetles, 9.6 to 11.7 mm.

Color. Antennal articles 3 and 4, metepisterna, metasternum at sides, and abdominal sterna and terga infuscated, otherwise ferruginous. Dorsal surface and epipleura of elytra dull blue.

Microsculpture. As described for genus.

Macrosculpture. As in *cordicollis*.

Head. As in *cordicollis*, except ligula with only two apical setae.

Prothorax. As in *cordicollis*, except proepipleura glabrous and proepisterna pubescent both anteriorly and posteriorly, but glabrous medially.

Pterothorax. Elytra elongate, narrow, costae absent or almost so. Humeral angle square to projecting. Elytra densely pubescent. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 371, 372, 373). Median lobe with plane of shaft rotated slightly from plane of basal bend. Basal bend long. Apex of shaft blunt, venter of shaft concave at middle. Ligule long, narrow, truncate apically. Virga (figs. 371, 372). Female (fig. 388). Stylus short, narrow, rounded apically.

Variation. — The shape of the pronotum, body size and the height of the costae varies within population samples.

Flight. — These beetles have been collected at lights repeatedly throughout the range of the species.

Etymology. — Latin, *laevis*, smooth; *sub*, somewhat; referring to the barely-elevated costae of the elytra of these beetles.

Collecting notes. — My wife and I collected these beetles in *Scirpus-Typha* marshes in Florida and in the Okefenokee Swamp. The beetles were below water line in the rhizomes of grass clumps (along with members of 36 other species of Carabidae, in the Okefenokee).

Life history. — Members of this species have been collected from January to August, but no teneral adults were seen.

Distribution. — (Fig. 393). The range of this species extends from Florida north to Michigan, and west to western Texas. I have seen 234 specimens from the following localities:

UNITED STATES

ALABAMA: Mobile County (Magazine Point) CAS, (Mobile) CAS, USNM, (Saraland) CAS, (Whistler) ANSP; Tallapoosa County (Alexander City) AUA. ARKANSAS: Washington County (No locality given) UAFA. FLORIDA: Alachua County (Gainesville) FDAG, USNM; Collier County (Everglades) UONO; Dade County (Long Pine Key) CUNY, (Paradise Key) USNM; Duval County (Jacksonville) CAS; Hernando County (Brooksville) CNHM; Highlands County (Archbold Biology Station) CUNY, PSUU, (Avon Park) FDAG, (Highlands Hammock State Park) TLEr, UASM; Hillsborough County (Hillsborough River State Park) UMAH, (Plant City) UMAH, (Tampa) CUNY; Lake County (Fruitland Park) UMAH; Lee County (Fort Myers) CUNY; Levy County (Manatee Springs State Park) RFre; Manatee County (Oneco) UASM; Marion County MCZ, (Juniper Springs) TLEr; Pinellas County (Dunedin) CAS, PUM; Seminole County (Sanford) PUM; Charlotte County (Bermont) UASM; Taylor County (Salem) UCD. GEORGIA: Charlton County (Okefenokee Swamp) TLEr; Lowndes County (No locality given) OUCO. INDIANA: Posey County (Hovey Lake) CEWh, (Mount Vernon) CEWh. KENTUCKY: Edmonson County (Mammoth Cave National Park) TCba. LOUISIANA: Ouachita Parish (Calhoun) UAFA. MICHIGAN: Lapeer County (Lapeer State Game Area) RCGr. MISSISSIPPI: George County (Lucedale) CUNY; Harrison County (10.0 miles north of Biloxi) UCD. MISSOURI: Callaway County (Readsville) MCZ. OKLAHOMA: Rogers County (Catoosa) CAS. SOUTH CAROLINA: Horry County (Myrtle Beach) VMKi. TENNESSEE: Overton County (Cleeks Mill) TCba; Shelby County (Memphis) ANSP, CAS, UMAH. TEXAS: Hardin County (9.0 miles west of Beaumont) OSUC; Reeves County (Balmorhea Lake) UASM; Victoria County (Victoria) USNM.

Brachinus ichabodopsis new species

(Figs. 370, 383, 384, 385, 386, 390)

Type locality. — Saint John's River, Hardkinsville, Florida.

Type specimens. — The holotype male and allotype female are in MCZ. The holotype was collected at the type locality by G. A. Athen (No date of collection given on label). The allotype is labelled "Fla." and "F. C. Bowditch Coll."

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Large-sized beetles, 11.1 to 16.0 mm.

Color. Antennal articles 3 and 4, mesepisterna, mesepimera, metepisterna, metasternum at sides, and abdominal sterna and terga infuscated to black, otherwise ferruginous. Dorsal surface and epipleura of elytra dull blue-black.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows rugose and punctate. Disc of pronotum rugose along midline and punctate, punctures barely impressed.

Head. Frontal furrows moderately impressed. Antennal scape robust, widest apically, article 3 elongate, longer than diameter of eye. Ligula with center area ellipsoid-convex with two apical setae. Mentum and submentum without accessory setae.

Prothorax. Pronotum (fig. 370) slightly convex, elongate and narrow, concave along center line, sides slightly reflexed. Proepipleura glabrous. Proepisterna pubescent anteriorly and posteriorly, glabrous medially. Anterior tibia with anterior margin strigose.

Pterothorax. Elytra very elongate, narrow, weakly costate. Pubescence mostly confined to depressions on disc. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 383, 384, 385). Median lobe with plane of shaft slightly rotated from plane of basal bend. Basal bend long. Apex of shaft blunt and broad. Ligule long,

widened apically. Virga (figs. 383, 384). Female (fig. 386). Stylus very broad, parallel-sided, broadly rounded apically.

Variation. — Too few specimens are known to evaluate geographic variation.

Flight. — The flight of these beetles has not been recorded.

Etymology. — From English, Ichabod Crane, Washington Irving's long-legged character in the Legend of Sleepy Hollow; Latin, *opsis*, likeness; referring to the elongate, long-legged habitus of these beetles.

Distribution. — (Fig. 390). I have seen only two specimens designated as types. They are from the following locality:

UNITED STATES

FLORIDA: County unknown (Hardkinville, Saint John's River) MCZ.

The *oxygonus* subgroup

The species of this subgroup are similar in form of the median lobe and modification of the virga. Although the virga is not truly H-shaped, it has the dorsal fin and similar cross-brace structure. Also the beetles externally are characteristic in habitus with those of the *cordicollis* subgroup. Three species, *B. oxygonus* Chaudoir, *B. vulcanoides* Erwin, and *B. fulminatus* Erwin, are included here.

Brachinus oxygonus Chaudoir

(Figs. 395, 398, 399, 400, 412, 416)

Brachinus oxygonus Chaudoir, 1843: 714. Lectotype, here selected, a male, MHNP, labelled "oxygonus Chaud" and "Ex Museo Chaudoir." The specimen stands first in a series above the box label "stygicornis Say." *Type locality.* — North America, as originally given by Chaudoir, but herewith restricted to Highlands County, Florida.

Brachinus stenomus Chaudoir, 1868: 291. Lectotype, here selected, a male, MHNP, labelled "Guex" and "Ex Museo Chaudoir." *Type locality.* — North America, as originally given by Chaudoir, but herewith restricted to Highlands County, Florida. NEW SYNONYMY.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Medium-sized beetles, 7.4 to 10.0 mm.

Color. Antennal articles 3 and 4, metepisterna, metasternum at sides, and abdominal sterna and terga infuscated to black, otherwise ferruginous. Dorsal surface and epipleura of elytra blue.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows shallowly rugose. Surface of pronotum with scattered, shallowly impressed, setiferous punctures.

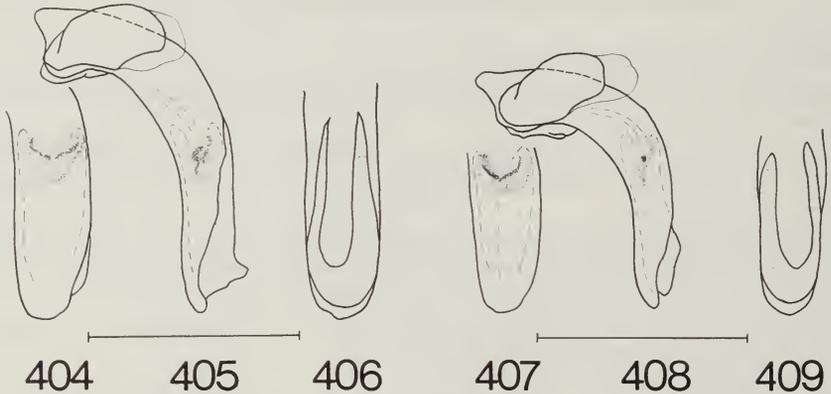
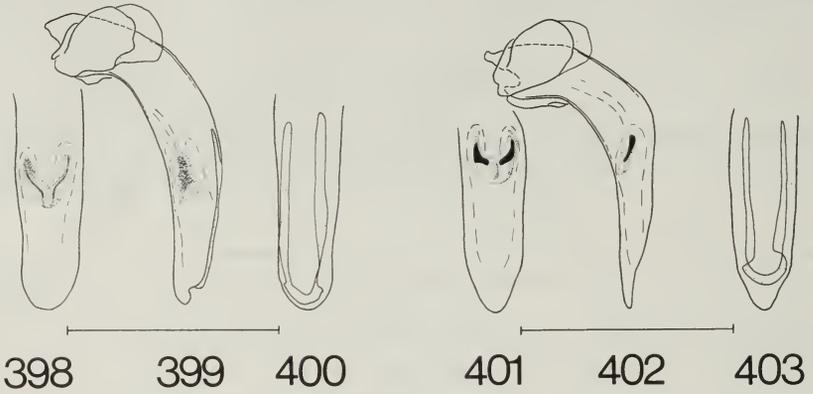
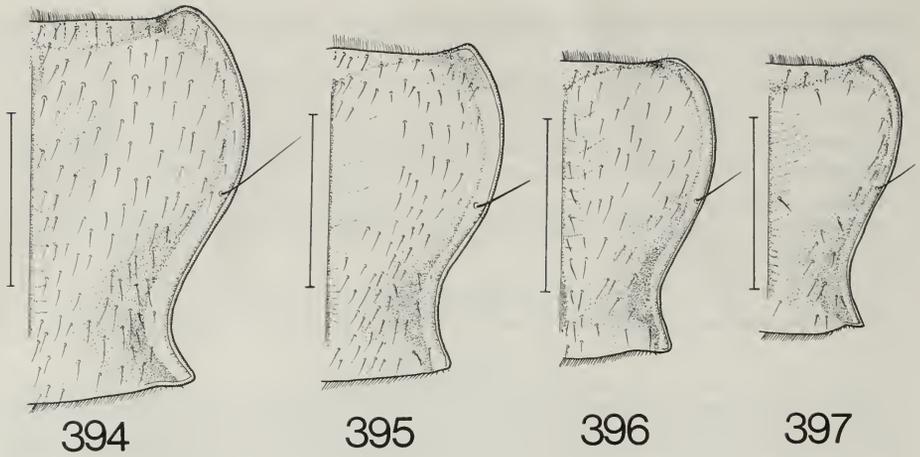
Head. Frontal furrows moderately impressed. Antennal scape cylindrical, or almost so. Ligula with center area ellipsoid-convex with two apical setae. Mentum and submentum without accessory setae.

Prothorax. Pronotum (fig. 395) slightly convex, flattened along center line, sides slightly reflexed. Proepipleura glabrous, proepisterna with a few setae both anteriorly and posteriorly, glabrous medially. Anterior tibia with anterior surface strongly strigose.

Pterothorax. Elytra elongate, narrow, weakly costate. Humeral angles square. Costae and depressions pubescent. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 398, 399, 400). Median lobe with plane of shaft rotated 45° from plane of basal bend. Basal bend long. Shaft narrow, not robust. Apex of shaft blunt, slightly notched at middle. Ligule elongate, paralleliform. Virga (figs. 398, 399). Female (fig. 412). Stylus broad basally, tapered gradually to broadly rounded apex.



Figs. 394-397. Pronotum, right half, dorsal aspect. 394. *Brachinus vulcanoides* Erwin, Milton, Massachusetts. 395. *Brachinus oxygonus* Chaudoir, Archbold Biology Station, Florida. 396. *Brachinus fulminatus* Erwin, Great Swamp, Rhode Island. 397. *Brachinus janthinipennis* (Dejean), Toronto, Canada. Figs. 398-409. Male genitalia. 398. *Brachinus oxygonus* Chaudoir, Archbold Biology Station, Florida, ventral aspect. 399 & 400. Lateral & dorsal aspects of same. 401. *Brachinus janthinipennis* (Dejean), Toronto, Canada, ventral aspect. 402 & 403. Lateral & dorsal aspects of same. 404. *Brachinus vulcanoides* Erwin, Milton, Massachusetts, ventral aspect. 405 & 406. Lateral & dorsal aspects of same. 407. *Brachinus fulminatus* Erwin, Edgewood, Maryland, ventral aspect. 408 & 409. Lateral & dorsal aspects of same. Accompanying scale lines equal 1.0 mm.

Variation. — Intrapopulational variation occurs in the amount of infuscation on antennal articles 3 and 4 and the metasternum, in the shape of the pronotum and body size, and in the number of setae on the proepisterna.

Flight. — These beetles have been collected repeatedly at lights in Florida.

Etymology. — Greek, *oxys*, sour, acid; *gonus*, product; referring to the chemical released by crepitation of these beetles.

Life history. — Members of this species have been collected from January to July, but no teneral adults were seen.

Distribution. — (Fig. 416). The range of this species extends from the Florida keys, north to Missouri, and North Carolina, and west to Texas. I have seen 137 specimens from the following localities:

UNITED STATES

ALABAMA: Mobile County (Magazine Point) CAS, (Mobile) ANSP, CAS, USNM; Tallapoosa County (Smith Mountain Tower) AUA. FLORIDA: Alachua County (Gainesville) CNC, FDAG, TLER, (Newnans Lake, 5.0 miles east of Gainesville) RFre, UASM; Brevard County (Cocoa) CNC, (Indian River) CAS; Collier County (Collier Seminole State Park) TLER; Columbia County (Lake City) DRWh; Dade County (Biscayne Bay) AMNH, MCZ, (Homestead) CNC, TLER, (Matheson Hammock) CNC, (Paradise Key) USNM, (Royal Palm State Park) PUM; Flagler County (Pellicer Creek, 13.0 miles north of Bunnell) CMPP; Hernando County (Brooksville) CNHM; Highlands County (Archbold Biology Station) CEWh, CUNY, PSUU, (Highlands Hammock State Park) TLER, (Lake Placid) CUNY; Lake County (5.6 miles east of Juniper Springs) TLER; Lee County (Fort Myers) AMNH; Marion County MCZ, (3.0 miles southwest of Lake Marion) CNC; Monroe County USNM, (Everglades National Park) FDAG; Orange County (Winter Park) FDAG, MCZ; Saint Lucie County (Fort Pierce) VMKi; Seminole County (Sanford) CAS; Volusia County (Enterprise) CAS; County unknown (Saint Nicholas) USNM. GEORGIA: Charlton County (Okefenokee Swamp) TLER, USNM; Lowndes County (No locality given) OUCO; Ware County (Waycross) UWSW. MISSOURI: Callaway County (Readsville) MCZ. NORTH CAROLINA: MCZ, Wake County (Raleigh) CNC. SOUTH CAROLINA: Florence County (Florence) VMKi.

Brachinus fulminatus Erwin

(Figs. 396, 407, 408, 409, 411, 414)

Type locality. — Wayland, Middlesex County, Massachusetts.

Type specimens. — The holotype male and allotype female are in MCZ. Both specimens were collected at the type locality by C. E. White on April 15, 1930. Twenty paratypes collected on various dates and at various localities are in AMNH, CAS, MCZ, TLER, and UASM.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Medium-sized beetles, 7.2 to 10.6 mm.

Color. As in *oxygonus*.

Microsculpture. As described for genus.

Macrosculpture. As in *oxygonus*.

Head. As in *oxygonus*, except antennal scape robust, widest at middle, and ligula with center area with two rows of three setae each on ellipsoid-convex area.

Prothorax. As in *oxygonus*. Pronotum (fig. 396).

Pterothorax. As in *oxygonus*.

Abdomen. As described for genus.

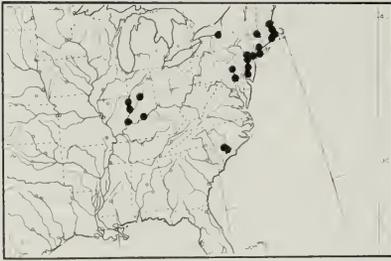
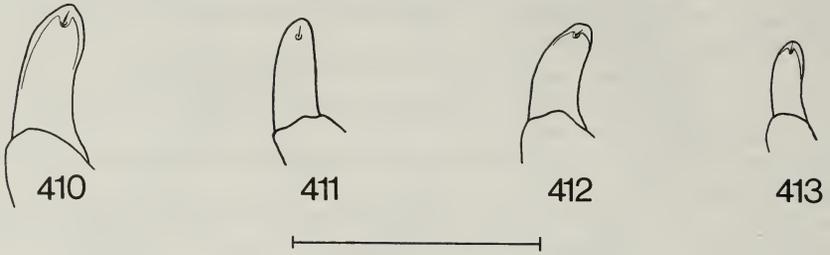
Genitalia. Male (figs. 407, 408, 409). Median lobe with plane of shaft slightly rotated from plane of basal bend. Basal bend long. Apex of shaft as in *cordicollis*. Virga (figs. 407, 408). Female (fig. 411). Stylus broad, tapered to acute apex.

Variation. — Besides the intrapopulational variation in total size and the shape of the pronotum, the North Carolina specimens have a more elongate and narrow pronotum.

Flight. — The flight of these beetles has not been recorded.

Etymology. — Latin, *fulminatus*, exploding with sudden violence; referring to the crepitating behavior of these beetles.

Collecting notes. — These beetles have been collected in the sphagnum bogs of the Great Swamp of Rhode Island.



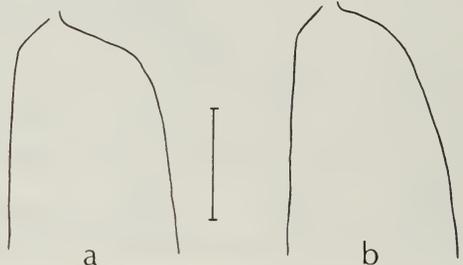
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415



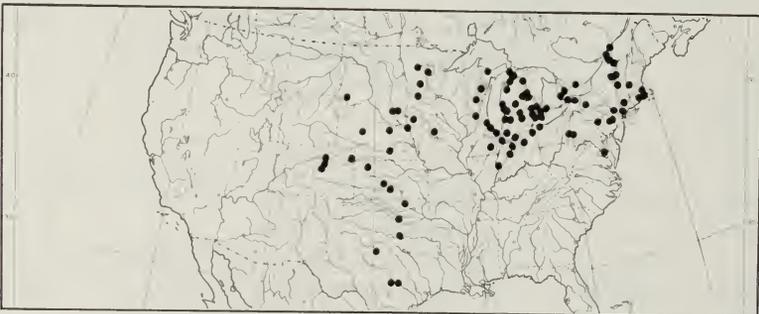
416



a

b

418



417

Figs. 410-413. Right stylus of female ovipositor. 410. *Brachinus vulcanoides* Erwin, Milton, Massachusetts. 411. *Brachinus fulminatus* Erwin, Edgewood, Maryland. 412. *Brachinus oxygonus* Chaudoir, Archbold Biology Station, Florida. 413. *Brachinus janthinipennis* (Dejean), Toronto, Canada. Figs. 414-417. Geographical distribution maps. 414. *Brachinus fulminatus* Erwin. 415. *Brachinus vulcanoides* Erwin. 416. *Brachinus oxygonus* Chaudoir. 417. *Brachinus janthinipennis* (Dejean). Accompanying scale line equals 1.0 mm. 418. Outline of right elytral humerus, dorsal aspect; a. *Brachinus janthinipennis* (Dejean), female, Brookline, Mass. b. Same, female, Sand Point, Michigan.

Life history. — Members of this species have been collected from April to November. One teneral adult was collected in April in Indiana.

Distribution. — (Fig. 414). The range of this species is discontinuous. The western most part is within the state of Indiana; the eastern most part extends from New York to Massachusetts, south to Maryland; and the southern part is within North Carolina. I have seen 139 specimens from the following localities:

UNITED STATES

CONNECTICUT: New Haven County (New Haven) CUNY. DELAWARE: Kent County (Bombay Hook) PSUU. INDIANA: Knox County (No locality given) CAS; Lake County (Miller) CAS; Marion County (No locality given) PUM; Posey County (No locality given) PUM; Spencer County (No locality given) PUM; Vigo County (No locality given) PUM. MARYLAND: Harford County (Edgewood) CUNY. MASSACHUSETTS: Bristol County (Swansea) CAS; Hampden County (Montgomery) MCZ; Middlesex County (Arlington) MCZ, (Concord) MCZ, (Newton) MCZ, (Tyngsboro) CAS, (Wayland) MCZ; Norfolk County (Brookline) MCZ; Suffolk County (Dorchester) MCZ; Counties unknown (Forest Hills) USNM. NEW JERSEY: Bergen County (Fort Lee) CAS, (Ramsey) AMNH; Burlington County (Atsion) CAS; Essex County (Caldwell) CNHM; Mercer County (Trenton) CAS; Morris County (Butler) USNM, (Towaco) USNM; Passaic County (Greenwood Lake) USNM. NEW YORK: Bronx County (Fleetwood) CAS; New York County (Brooklyn) USNM, (New York City) CAS, (Yonkers) CAS, CNHM; Suffolk County (Montauk) CNHM; Wayne County (Sodus Bay) UASM; Westchester County (Peekskill) MCZ; County unknown (Long Island) USNM. NORTH CAROLINA: Columbus County (Whiteville) UNCR; Robeson County (Boardman) USNM; County unknown (Beauford) MCZ. PENNSYLVANIA: Allegheny County (Pittsburgh) CMPP; Dauphin County (Harrisburg) CUNY. RHODE ISLAND: Kent County (Warwick) UMAH; Washington County (Great Swamp, South Kingston) RCGr, (Watch Hill) USNM.

Brachinus vulcanoides Erwin

(Figs. 394, 404, 405, 406, 410, 415)

Type locality. — Baychester, New York.

Type specimens. — The holotype male and allotype female are in MCZ. Both were collected by H. B. Leech on May 8, 1926. Twenty paratypes collected on various dates and at various localities have been deposited at AMNH, CAS, MCZ, TLER, and UASM.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Medium-sized beetles, 8.6 to 10.2 mm.

Color. As in *oxygonus*.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows and disc of pronotum rugose and punctate, punctures moderately impressed.

Head. As in *cordicollis*, except antennal scape robust, widest at middle.

Prothorax. As in *oxygonus*, except pronotum (fig. 394) with sides more widely reflexed and anterior tibia with anterior surface punctate, punctures small.

Pterothorax. As in *oxygonus*, except pubescence more confined to depressions.

Abdomen. As described for genus.

Genitalia. Male (figs. 404, 405, 406). Median lobe with plane of shaft rotated slightly from plane of basal bend. Basal bend long. Apex of shaft as in *cordicollis*. Virga (figs. 404, 405). Female (fig. 410). Stylus broad, parallel-sided, rounded at apex.

Variation. — Intrapopulational variation occurs in total size, shape of pronotum, and color of the antennal articles 3 and 4 which may be totally infuscated or only have the apical third infuscated.

Flight. — The flight of these beetles has not been recorded.

Etymology. — Latin, *Vulcanus*, God of Fire; *oides*, likeness; referring symbolically to the crepitating habit of these beetles.

Life history. — Members of this species were collected from March to November (excluding June), but no tenerals were seen.

Distribution. (Fig. 415). The range of this species extends from Massachusetts along the coast to New Jersey. One specimen (Crescent City, Florida) may be mislabelled. I have seen 110 specimens from the following localities:

UNITED STATES

FLORIDA: Putnam County (Crescent City) USNM. MASSACHUSETTS: Barnstable County (Barnstable) MCZ; Hampshire County (South Amherst) MCZ; Middlesex County (Arlington) ZMLS, (Concord) MCZ; Norfolk County (Dover) MCZ; (Milton) MCZ, (Quincy) MCZ; Plymouth County (Marion) MCZ, ZMLS. NEW JERSEY: Cape May County (Five Mile Beach) OUCO, (Ocean City) CAS; Ocean County (Surf City) USNM; Sussex County (Hopatcong) AMNH. NEW YORK: Nassau County (Jones Beach State Park) CAS, (Long Beach) CAS; New York County (Baychester) CAS, CNHM, MCZ, (Brooklyn) USNM, (New Lots) MCZ, (Pelham Bay Park) CNHM, (Rockaway Beach) CAS, ROM, USNM; Queens County (Flushing) AMNH; Suffolk County (Montauk) CNHM, (Quogue) CAS, (Wyandanch) USNM; Counties unknown (Aqueduct) ANSP, (Long Island) AMNH.

The *janthinipennis* subgroup

The species of this subgroup are characterized by their small, narrow, apically acute median lobe and modified H-shaped virga. The virga has a more apically extended cross-brace of the "H," thus the lower legs of the "H" appear to be missing. One species, *B. janthinipennis* (Dejean), is included.

Brachinus janthinipennis (Dejean)

(Frontispiece, Figs. 397, 401, 402, 403, 413, 417, 418)

Aptinus janthinipennis Dejean, 1831: 412. Lectotype, here selected, a female, MHNP, labelled "Aptinus" "janthinipennis m. in Amer. bor." "LeConte" and "Ex Museo Chaudoir." *Type locality*. — North America, as originally given by Dejean, but herewith restricted to New York.

Brachinus pumilio LeConte, 1848: 208. Lectotype, here selected, a male, MCZ red type label number 5841, further labelled with a pink disc and "94." *Type locality*. — Middle States, as given by LeConte's pink disc. NEW SYNONYMY.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Small-sized beetles, 5.7 to 8.9 mm.

Color. Ferruginous. Dorsal surface and epipleura of elytra blue.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows and disc of pronotum as in *cordicollis*.

Head. Frontal furrows moderately impressed. Antennal scape robust, widest at middle. Ligula with center area ellipsoid-convex with two apical setae. Mentum and submentum as in *cordicollis*.

Prothorax. Pronotum (fig. 397) more convex than in *cordicollis*, sides less reflexed. Propopleura glabrous. Proepisterna with a few setae both anteriorly and posteriorly, glabrous medially. Anterior tibia with anterior edge strigose.

Pterothorax. Elytra short, widest at apical third, humeral angle narrow, square or sloped. Costae weakly elevated. Elytra covered by pubescence.

Abdomen. As described for genus.

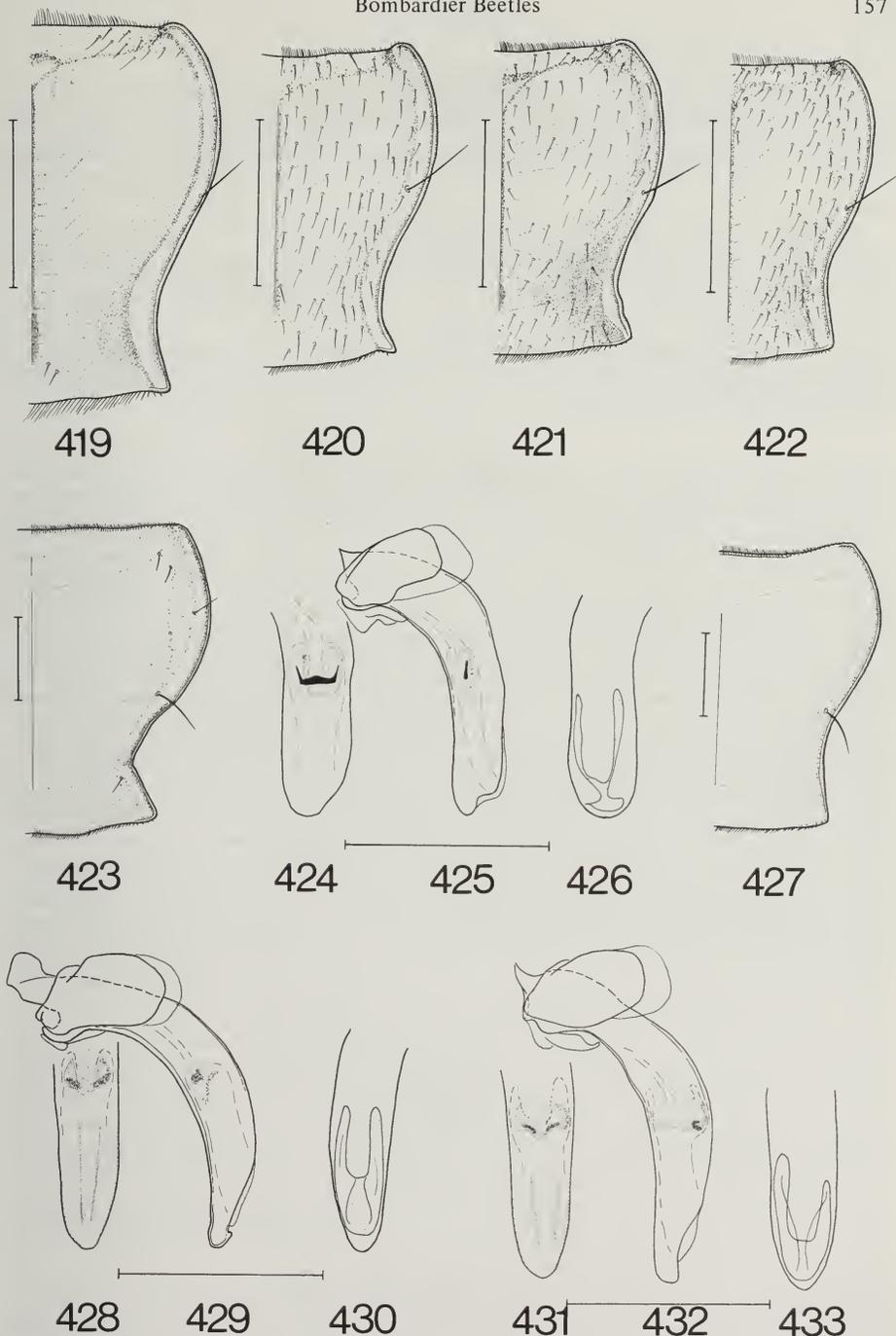
Genitalia. Male (figs. 401, 402, 403). Median lobe with plane of shaft slightly rotated from plane of basal bend. Basal bend short. Apex of shaft narrow, acute, and flattened dorso-ventrally. Ligule elongate, broad, rounded apically. Virga (figs. 401, 402). Female (fig. 413). Stylus narrow, parallel-sided, rounded apically.

Variation. — Intrapopulational variation was noted in the shape of the pronotum, body size, and the length of wings. All observed specimens have a reflexed apex, but the length outside the stigma varies locally.

Flight. — The flight of these beetles has not been recorded, and it is doubtful that they can fly.

Etymology. — Greek, *ianthinos*, violet-blue; Latin, *pennis*, wing; referring to the blue elytra of these beetles which may appear violet in certain lighting.

Collecting notes. — D. H. Kavanaugh and C. Armin collected these beetles from under stones at the edges of lakes and streams in Colorado, and T. Hlavac collected specimens on



Figs. 419-423, 427. Pronotum, right half, dorsal aspect. 419. *Brachinus explosus* new species, Tamazunchale, San Luis Potosi, Mexico. 420. *Brachinus mobilis* new species, Mobile, Alabama. 421. *Brachinus aabaaba* new species, Presa de Guadalupe, San Luis Potosi, Mexico. 422. *Brachinus sonoros* new species, 14.0 miles southeast of Empalme, Sonora, Mexico. 423. *Pheropsophidius aequinoctialis* Linné, Amazonas, Brazil. 427. *Pheropsophidius biplagiatus* Chaudoir, 22.4 miles north of Puerto Escondido, Oaxaca, Mexico. Figs. 424-426, 428-433. Male genitalia. 424. *Brachinus mobilis* new species, Mobile, Alabama, ventral aspect. 425 & 426. Lateral & dorsal aspects of same. 428. *Brachinus sonoros* new species, Mazatlan, Sinaloa, Mexico, ventral aspect. 429 & 430. Lateral & dorsal aspects of same. 431. *Brachinus aabaaba* new species, Presa de Guadalupe, San Luis Potosi, Mexico, ventral aspect. 432 & 433. Lateral & dorsal aspects of same. Accompanying scale lines equal 1.0 mm.

mud lake shores in Michigan.

Life history. — Members of this species have been collected from April to October. General adults were collected in May, July, August, and September in Michigan, in May and September in Toronto, in May in New York, in August in Massachusetts, in September in Connecticut, and in October in Colorado. Overwintering probably takes place in the adult stage.

Distribution. — (Fig. 417). The range of this species extends from Colorado to the New England coast, and from the Great Lakes region to Texas. The Edmonton, Alberta record is highly doubtful. I have seen 1,065 specimens from the following localities:

CANADA

ALBERTA: (Edmonton) CNHM. ONTARIO: (Belleville) CNC; (Cedarvale) RTBe; (De Cew Falls) CNC; (Fanshawe Lake, near London) UASM; (London) CNHM; (Long Point) HGou; (Point Pelee) CAS, CNC; (Stag Island) UMAH; (Toronto) CAS, CUNY, ROM, RTBe, UMAH, USNM, UWMW; (Trenton) CNC; (Willowdale) CAS, RTBe. QUEBEC: (Becancour) CCha; (Berthierville) ZMLS; (Saint Jean) CAS.

UNITED STATES

COLORADO: Boulder County (Baseline Lake) CArm, (Boulder) CArm, (El Dorado Springs) CArm, (Four Mile Creek) CArm, (Lyons) CArm, (McCall Lake) CArm, (Saint Vrain Creek) CArm, RCGr, (Teller Lake) CArm; Denver County (Denver) USNM; Jefferson County (Bear Creek, 2.0 miles east of Morrison) DHK; Yuma County (Wray) KSU. CONNECTICUT: Litchfield County (Cornwall) CAS, CUNY, MCZ, ZMLS. ILLINOIS: Champaign County (Urbana) CMPP; Cook County (No locality given) CNHM; Lake County (Waukegan) USNM; Union County (Wolf Lake) CNHM; County unknown (Powerton) ISNH. INDIANA: Elkhart County (Elkhart) MCZ; Fulton County (No locality given) PUM; Knox County (No locality given) CNHM; Kosciusko County CAS, PUM, (Winona Lake) UMAH; Lake County (No locality given) PUM; Marion County (Indianapolis) CEWh; Marshall County (No locality given) PUM; Starke County (No locality given) PUM; Whitley County (No locality given) PUM. IOWA: Dickinson County (Lake Okoboji) USNM; Story County (Ames) ISUA. KANSAS: Barton County (Arkansas River, Great Bend) RCGr; Reno County (No locality given) CAS; Sheridan County (State Lake, near Studley) RFre, UASM. MARYLAND: Calvert County (Port Republic) UWSW. MASSACHUSETTS: Bristol County (Fall River) CAS, MCZ; Essex County (Manchester) MCZ; Franklin County (Northfield) MCZ; Hampden County (Chicopee) MCZ, (Longmeadow) MCZ, (Wilbraham) MCZ; Hampshire County (Amherst) CEWh; Middlesex County (Woburn) MCZ; Norfolk County (Brookline) MCZ, (Wellesley) MCZ; County unknown (Egremont) MCZ. MICHIGAN: Allegan County (Douglas Lake) FDAG, KSU, OUCO, (Saugatuck) RCGr, TFHl; Alpena County UMAH, (Alpena) ISNH, USNM; Bay County (Bay City State Park) ISNH, (Pinconning) UWSW; Berry County (Otis Lake) TFHl, (Wall Lake) TFHl; Charlevoix County (Beaver Island) UMAH, (Garden Island) UMAH; Cheboygan County (No locality given) UMAH, UWMW; Clinton County (Park Lake) TFHl; Grand Traverse County (Interlochen) UMAH, (Lighthouse Beach) RCGr, (Marion Island) UMAH; Huron County (3.0 miles north of Bayport) MCZ, (Charity Island) JSch, UMAH, (Sand Point) MCZ, UMAH; Jackson County (Portage Lake) UMAH; Kent County (Grand Rapids) CNHM, UNLN; Lake County (Loon Lake) UMAH; Leelanau County (No locality given) UMAH; Mackinac County (Bois Blanc Island) UMAH, (Bois Blanc Island, Point aux Pins) UWSW, (Bois Blanc Island, Snake Islet) UWSW, (Horseshoe Bay) AMNH, (Naubinway) UASM, (Saint Martin Island) UMAH, (near Saint Ignace) CAS, UASM; Marquette County (Huron Mountains) UMAH; Oakland County UMAH, (Holly) PSUU; Oceana County (Crystal Valley) CNHM; Ottawa County (No locality given) KSU; Saint Clair County (Flats Canal) UMAH, (Port Huron) USNM; Washtenaw County (Ann Arbor) UMAH; Wayne County (Detroit) USNM; Counties unknown (Glen Haven) CAS, (Lake Huron shores) MCZ, (Newell's Camp) MCZ, (Pentwater) CNHM. MINNESOTA: Chisago County (No locality given) UMSP; Clearwater County (Bohall Lake, Itasca State Park) UMSP, (De Soto Lake, Itasca State Park) UMSP; Crow Wing County (Mille Lacs Lake, near Garrison) UMSP, (Pelican Lake, Nisswa) UNLN; Douglas County (Alexandria) UASM, (Lake Carlos) ISNH, PUM; Hennepin County (Minneapolis) UMSP; Kandiyohi County (Eagle Lake, Willmar) UMSP; Olmsted County (No locality given) UMSP; Traverse County (No locality given) UMSP; Wright County (No locality given) UMSP; County unknown (Vineland) UMSP. NEBRASKA: Cherry County (Hackberry Lake) UNLN, (Niobrara River, 3.5 miles northeast of Valentine) OSUC; Dakota County (South Sioux City) UNLN; Hall County (Junction U. S. 34 and Platte River, near Grand Island) UASM; Holt County (No locality given) UNLN. NEW HAMPSHIRE: Cheshire County (Swanzy Pond) MCZ. NEW JERSEY: Warren County (Phillipsburg) CAS; County unknown (Guymard) AMNH. NEW YORK: Erie County (Buffalo) ISNH; Orange County (Pine Island) CUNY; Tompkins County (Ithaca) CAS, CUNY, VMKl, UASM; Washington County (No locality given) MCZ; Westchester County (Golden's Bridge) CUNY; County unknown (Sandy Hill) CAS, (Varna) UASM. OHIO: Darke County (No locality given) UMSP; Erie County (Cedar Point) UMSP, (Sandusky) PUM; Wood County (Yellow Creek) PUM. OKLAHOMA: Cleveland County (Norman) CAS; Marshall County (Lake Texoma, Willis) RCGr; Payne County (Stillwater) OSUS. PENNSYLVANIA: Allegheny County (No locality given) CMPP; Montour County (Danville) CAS; Northampton County (Easton) CAS; Westmoreland County (Jeanette) CMPP. RHODE ISLAND: Providence County (Providence) CMPP, UWMW. SOUTH DAKOTA: Beadle County (Huron) VMKl; Harding County (Buffalo) VMKl; Kingsbury County (Erwin) USNM. TEXAS: Blanco County (2.0 miles south of Round Mountain) UASM; Taylor County (25.0 miles southwest of Abilene) CNHM; Travis County (Austin) WSUP; County unknown (Belfrage) USNM. VERMONT: Bennington County (Hoosick River, Pownal) RTBe; Chittenden County (La Moille River, Milton) RTBe; Franklin County (La Moille River, East Georgia) RTBe; Rutland County (Poultney River, Fair Haven) RTBe, (Poultney River, Poultney) RTBe. VIRGINIA: Fairfax County (Great Falls) MCZ. WISCONSIN: Dane County (No locality given) UWMW; Oconto County (Mountain) CNHM; Waupaca County (Waupaca) USNM, UWMW.

The *mobilis* subgroup

The species of this subgroup are characterized by the virga and sulcate mentum surrounded by setae. The virga has the cross-brace of the "H" displaced to the apex and the pigmented areas more extensive, crossing the midline to form a bar. One species, *B. mobilis* new species, is included.

Brachinus mobilis new species
(Figs. 420, 424, 425, 426, 435, 448)

Type locality. — Mobile, Alabama.

Type specimens. — The holotype male and allotype female are in CUNY. Both were collected at the type locality by H. Dietrich on March 19, 1932. Three paratypes collected at the same place are in CAS, MCZ, TLER.

Diagnostic combination. — The sulcate mentum and completely pubescent elytra separate these beetles from all others in North America.

Description. — Medium-sized beetles, 8.0 to 8.8 mm.

Color. Antennal articles 2-4, mesepimera, metepisterna, sides of metasternum, and abdominal sterna and terga infuscated, otherwise ferruginous. Dorsal surface and epipleura of elytra blue.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows rugose, surface of pronotum shallowly punctate.

Head. Frontal furrows moderately impressed. Antennal scape robust, widest at apex. Ligula with sclerotized center area ellipsoid-convex with two lateral rows of three setae per row. Mentum sulcate at middle, sulcus surrounded by setae. Submentum with numerous accessory setae, not shortened as in *costipennis*.

Prothorax. Pronotum (fig. 420) slightly convex, flattened along center line, sides narrowly reflexed. Proepipleura glabrous. Proepisterna with a few setae anteriorly and posteriorly, glabrous medially. Anterior tibia with anterior edge punctate.

Pterothorax. As in *cordicollis*, except costae weakly elevated.

Abdomen. As described for genus.

Genitalia. Male (figs. 424, 425, 426). Median lobe with plane of shaft rotated 45° from plane of basal bend. Basal bend moderately long. Median lobe arcuate, apex of shaft broadly rounded. Ligule short, broad, truncate. Virga (figs. 424, 425). Female (fig. 435). Stylus broad basally, tapered to acute apex.

Variation. — Too few specimens are known to evaluate geographic variation.

Flight. — The flight of these beetles has not been recorded.

Etymology. — Latin, *mobilis*, mobile; referring to the beetle's ability to run rapidly, and to Mobile, Alabama, the place the types were collected.

Life history. — The five known specimens were collected in March and none was teneral.

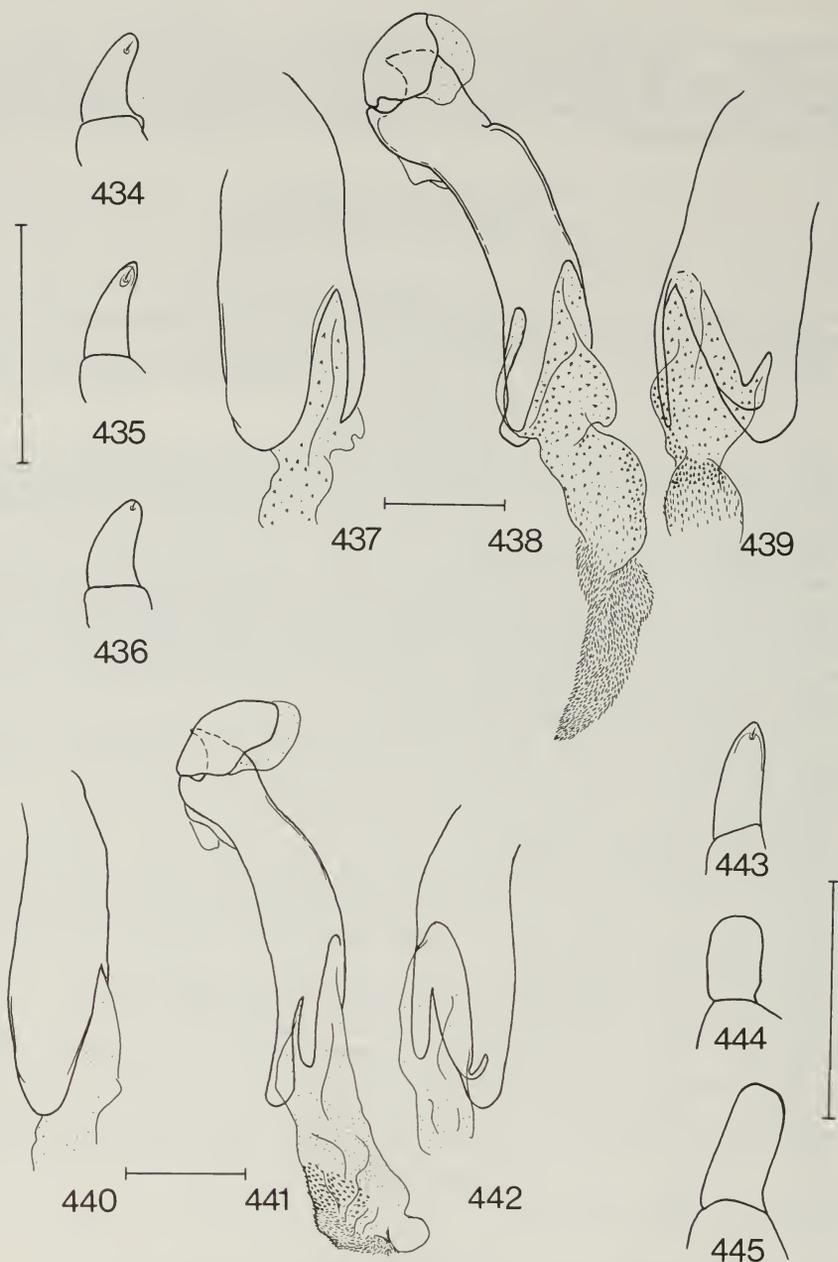
Distribution. — (Fig. 448). I have seen five specimens from the following locality:

UNITED STATES

ALABAMA: Mobile County (Mobile) CUNY.

The *explosus* group

This group is provisional until the male is known. The very shiny and almost black elytra plus the very convex shape of the elytra seem to indicate that the single species, *B. explosus* new species, forms a separate group.



Figs. 434-436, 443-445. Right stylus of female ovipositor, ventral aspect. 434. *Brachinus aabaaba* new species, Presa de Guadalupe, San Luis Potosi, Mexico. 435. *Brachinus mobilis* new species, Mobile, Alabama. 436. *Brachinus sonorensis* new species, 14.0 miles southeast of Empalme, Sonora, Mexico. 443. *Brachinus explosus* new species, Tamazunchale, San Luis Potosi, Mexico. 444. *Pheropsophidius biplagiatus* Chaudoir, 22.4 miles north of Puerto Escondido, Oaxaca, Mexico. 445. *Pheropsophidius aequinoctialis* (Linné), Amazonas, Brazil. Figs. 437-439, 440-442. Male genitalia. 437. *Pheropsophidius biplagiatus* Chaudoir, 22.4 miles north of Puerto Escondido, Oaxaca, Mexico, ventral aspect. 438. Lateral aspect of same. 439. Dorsal aspect of same. 440. *Pheropsophidius aequinoctialis* (Linné), Amazonas, Brazil, ventral aspect. 441. Lateral aspect of same. 442. Dorsal aspect of same. Accompanying scale lines equal 1.0 mm.

Brachinus explosus new species

(Figs. 419, 443, 448)

Type locality. — Tamazunchale, San Luis Potosi, Mexico.

Type specimens. — The holotype female is in MCZ. It and the single female paratype (MCZ) were collected at the type locality by W. Nutting and F. Werner on May 30, 1948.

Diagnostic combination. — The very shiny, almost black elytra with pubescence restricted to the outer intervals separate members of this species from all others.

Description. — Medium-sized beetles, 9.9 to 10.7 mm.

Color. Antennal articles 3 and 4, mesepisterna, mesepimera, metepisterna, metasternum, and abdominal sterna and terga infuscated, otherwise ferruginous. Dorsal surface and epipleura of elytra almost black, shiny.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows rugose and sparsely punctate. Disc of pronotum finely rugose. Punctures barely impressed.

Head. Frontal furrows moderately impressed. Antennal scape robust, widened toward apex. Ligula with sclerotized center area ellipsoid-convex with two apical setae. Mentum and submentum without accessory setae.

Prothorax. Pronotum (fig. 419) convex, slightly flattened along center line, sides narrowly reflexed. Proepipleura glabrous. Proepisterna with a few setae both anteriorly and posteriorly, glabrous medially. Anterior tibia with anterior surface punctate.

Pterothorax. Elytra long, narrow, very convex, costae moderately elevated. Humeral angle prominent or at least square. Depressions punctate. Pubescence confined to outer intervals, except in apical third. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male unknown. Female (fig. 443). Stylus short, broad, apically acute.

Variation. — Too few specimens are known to evaluate geographic variation.

Flight. — Both known specimens were collected at lights.

Etymology. — Latin, *explosus*, drive off, burst; referring to the crepitating ability of these beetles.

Collecting notes. — The two known specimens were collected at light in an open river bottom at 682 feet elevation.

Life history. — Both specimens were collected in May, and neither was teneral.

Distribution. — (Fig. 448). Known only from the following locality:

MEXICO

SAN LUIS POTOSI: (Tamazunchale) MCZ.

The *abaaba* group

The species of this group are characterized by the trilobed virga and its orientation on the endophallus, the sulcate ventral side of the median lobe and the slate-grey elytral color. Two species, *B. abaaba* new species and *B. sonorous* new species, are included.

Brachinus abaaba new species

(Figs. 421, 431, 432, 433, 434, 450)

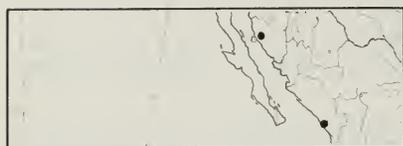
Type locality. — Presa de Guadalupe, 53.3 miles west of Ciudad del Maiz, San Luis Potosi, Mexico.

Type specimens. — The holotype male and allotype female are in MCZ. Both were collected at the type locality by G. E. Ball and D. R. Whitehead on October 14, 1965. Twenty paratypes are in AMNH, CAS, MCZ, TLER, and UASM.

Diagnostic combination. — The diagnostic characteristics are given in the key.



446



447



448



449



450

Figs. 446-450. Geographical distribution maps. 446. *Pheropsophidius biplagiatus* Chaudoir, 447. *Brachinus sonoroides* new species. 448. *Brachinus explosus* new species. 449. *Brachinus mobilis* new species. 450. *Brachinus aabaaba* new species.

Description. — Medium-sized beetles, 7.3 to 9.6 mm.

Color. Antennal articles 3 and 4, metepisterna, metasternum at sides, abdominal sterna and terga, and knees infuscated, otherwise ferrugineous. Dorsal surface and epipleura of elytra slate-grey.

Microsculpture. As described for genus.

Macrosculpture. Frontal furrows rugose and punctate. Surface of pronotum punctate, punctures barely impressed.

Head. Frontal furrows moderately impressed. Antennal scape slender, almost cylindrical. Ligula with sclerotized center area ellipsoid-convex with two lateral rows of three setae per row. Mentum and submentum without accessory setae.

Prothorax. Pronotum (fig. 421) slightly convex, flattened on disc, sides slightly reflexed. Surface with numerous setae. Proepipleura and proepisterna pubescent anteriorly and posteriorly, glabrous medially. Anterior tibia with anterior surface shallowly strigose.

Pterothorax. Elytra elongate, weakly costate. Humeral angle square. Costae and depressions pubescent. Wings fully developed.

Abdomen. As described for genus.

Genitalia. Male (figs. 431, 432, 433). Median lobe with plane of shaft rotated very little from plane of basal bend. Basal bend long. Median lobe arcuate, narrow throughout. Apex of shaft narrowly rounded, ventral side with two parallel ridges forming a central sulcus. Ligule short, truncate. Virga (figs. 431, 432). Female (fig. 434). Stylus short, broad basally, curving to narrowly rounded apex.

Variation. — Excepting the normal variation in body size and shape of the pronotum in local populations, this species is rather constant throughout its range.

Flight. — The flight of these beetles has been recorded repeatedly at lights in Texas.

Etymology. — *Aabaaba*, a barbaric combination of letters.

Life history. — These beetles were collected from April to October, but no teneral adults were seen.

Distribution. — (Fig. 450). The range of this species extends throughout Texas and eastern New Mexico, north to Kansas and south to San Luis Potosi, Mexico. I have seen 107 specimens from the following localities:

MEXICO

SAN LUIS POTOSI: (Presa de Guadalupe) UASM.

UNITED STATES

KANSAS: Atchison County (Atchison) CMPP; Seward County (No locality given) KSU. NEW MEXICO: Eddy County (Carlsbad) GRNo, (White's City) FDAG; Quay County (San Jon) CAS. TEXAS: Aransas County (Goose Island State Park, 9.0 miles north of Rockport) UASM; Bexar County (San Antonio) OSUS; Blanco County (Cypress Mill) USNM; Brazos County (College Station) VMK; Cameron County (Brownsville) CAS, CNC, JSch, TAMU, TLer, USNM, WHTy, (Esperanza Ranch, Brownsville) CAS; Colorado County (Columbus) USNM; Cottle County (Peducah) JSch; Dallas County (Dallas) USNM; Dimmit County (No locality given) UATA; Dawson County (Lamesa) TCBA; Hidalgo County (McAllen) UMAH, (Weslaco) TAMU; Hudspeth County (9.0 miles southwest of Dell City) AMNH; Kleburg County (Kingsville) CNC, CUNY, USNM; Nueces County (Corpus Christi) CUNY; Potter County (Amarillo) UWSW; Randall County (Palo Duro State Park) UMSP; Reeves County (Pecos) CNC; San Patricio County (Welder Wildlife Refuge, near Sinton) CNC; San Saba County (Camp San Saba) MCZ; Travis County (Austin) CUNY, UASM, USNM; Victoria County (Victoria) USNM.

Brachinus sonorous new species

(Figs. 422, 428, 429, 430, 436, 447)

Type locality. — Fourteen miles southwest of Empalme, Sonora, Mexico.

Type specimens. — The holotype male and allotype female are in CAS. Both were collected at the type locality by H. A. Hacker on May 1, 1962. Two paratypes are in AMNH and TLer.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Medium-sized beetles, 7.5 to 9.0 mm.

Color. Testaceous to ferruginous. Dorsal surface of elytra slate-grey, epipleura paler. Microsculpture. As described for genus.

Macrosculpture. As in *abaaba*.

Head. As in *abaaba*.

Prothorax. Pronotum (fig. 422) as in *abaaba*. Proepipleura and proepisterna pubescent throughout. Anterior tibia with anterior surface strigose.

Pterothorax. Elytra as in *abaaba*.

Abdomen. As described for genus.

Genitalia. Male (figs. 428, 429, 430). Median lobe with plane of shaft rotated slightly from plane of basal bend. Basal bend long. Median lobe arcuate, narrow throughout. Apex of shaft narrowly rounded, ventral side with central sulcus formed by two parallel ridges. Ligule short, narrow and truncate. Virga (figs. 428, 429). Female (fig. 436). Stylus short, broad at base, tapered to narrowly rounded apex.

Variation. — Too few specimens are known of this species to evaluate geographic variation.

Flight. — The flight of these beetles has not been recorded.

Etymology. — Latin, *sonorous*, sound; referring to the crepitating habit of these beetles and to the type locality in Sonora, Mexico.

Life history. — Members of this species have been collected in May and July, but no teneral adults were seen.

Distribution. — (Fig. 447). This species is known from only two localities on the west coast of Mexico. I have seen four specimens from the following localities:

MEXICO

SINALOA: (Mazatlan) AMNH. SONORA: (14.0 miles southeast of Empalme) CAS.

Fossil Material

Scudder (1900) described two *Brachinus* species, *B. repressus* and *B. newberryi*, from the Florissant beds of Colorado (Miocene). Through the kindness of F. M. Carpenter, I have examined Scudder's five specimens (MCZ). The four specimens assigned to *B. newberryi* consist of the following: Cotype number 1850, both elytra as a unit with scutellum plus middle and hind legs on left side in natural position; Cotype number 1851, meso and metasterna and abdominal sterna intact, plus remnants of right middle femur; Cotype number 1852, fragment of elytron; Cotype number 1853, fragment of elytron. The one specimen assigned to *B. repressus* consists of a fragment of an elytron and is labeled "Type. 1848."

None of these specimens can be correctly assigned to the genus *Brachinus* for the following reasons: Cotype 1850 does not have obliquely truncate elytra as in all *Brachinida* and in addition the fossil elytra appear to be striate rather than costate; Cotype 1851 has only six visible abdominal sterna while all *Brachinida* have seven in the male and eight in the female; Cotypes 1852 and 1853 have striae rather than costae; and "Type. 1848" has deeply punctate striae with coarse setae on the outer elytral intervals and in the scutellar region while no *Brachinida* have these characteristics.

The specimens assigned to *B. newberryi* should be placed in the genus *Lebia* (Carabidae: Lebiini). Cotype 1850 is remarkably similar in all respects to the extant *Lebia grandis* Hentz. The single specimen assigned to *B. repressus* is too fragmentary to make definitive comparisons, but is similar in some respects to members of *Cymindis* (Carabidae: Lebiini).

The genus *Pheropsophidius* in Middle America

Synonymy and characteristics on p. 36.

The subgenus *Protopheropsophus* Hubenthal

Synonymy and characteristics on p. 37.

Pheropsophidus biplagiatus (Chaudoir)

(Figs. 427, 437, 438, 439, 444, 446)

Pheropsophus biplagiatus Chaudoir, 1876: 18. Lectotype, here selected, a male, MHNP, labelled "Ex Museo Chaudoir" and standing first in a series of seven specimens. *Type locality*. — Oaxaca, Mexico, as given originally by Chaudoir.

Diagnostic combination. — The diagnostic characteristics are given in the key.

Description. — Large-sized beetles, 11.0 to 14.0 mm.

Color. Sides of abdomen at least and terga infuscated, otherwise ferrugineous. Dorsal surface of elytra dark brown, epipleura paler; disc of each elytron with ferrugineous spot.

Microsculpture. Head and pronotum with very fine irregular meshes approximating isodiametric meshes. Elytra with isodiametric meshes.

Macrosulpture. Elytral depression 1 in basal half, depressions 7 and 8 throughout with numerous microtubercles forming rugose surface.

Head. Frontal furrows barely impressed, smooth. Antennal scape robust, widest apically, shorter than eye diameter. Ligula carinate at middle with three setae at middle of carina and two apically. Mentum and submentum without accessory setae.

Prothorax. Pronotum (fig. 427), convex, sides beaded, not reflexed.

Pterothorax. Elytra short, weakly costate. Humeri narrow, sloped. Metathorax very short, shorter than diameter of middle coxa.

Abdomen. As described for genus.

Genitalia. Male (figs. 437, 438, 439). Median lobe almost straight, notched dorsally at basal third, broadly rounded apically. Ligule bifid, each lobe shifted to alternate sides. Endophallus (fig. 438) long, microtrichiated, apex acute, apical half pubescent. Female (fig. 444). Stylus short, broad, rounded apically.

Variation. — Within a sample I have seen from a single population, there is considerable difference in body size and in the diameter of the elytral spots.

Flight. — These beetles are incapable of flight.

Etymology. — Latin, *bi*, two; Greek, *plagio*, slope, oblique; Latin, *atus*, provided with; probably referring to the angular apex of the elytra.

Collecting notes. — G. E. Ball and D. R. Whitehead collected these beetles in leaf litter on the southern slopes of the Sierra Madre del Sur. The forest consisted of *Quercus* species.

Life history. — Members of this species were collected in July, and two of these were teneral.

Distribution. — (Fig. 446). The range of this species is confined to the southern slopes of the Sierra Madre del Sur in Oaxaca, Mexico. I have seen 15 specimens from the following locality:

MEXICO

OAXACA: (22.4 miles north of Puerto Escondido) UASM.

The subgenus *Pheropsophidius* Hubenthal

Synonymy and characteristics are presented on p. 36.

Pheropsophidius aequinoctialis (Linné)

(Figs. 423, 440, 441, 442, 445)

Bates (1883) records this species from the Yucatan Peninsula in Mexico. I have not seen specimens from anywhere in Middle America, and therefore, have only included "key characters." The species is quite divergent in South America, with many described "varieties."

LIFE HISTORIES AND IMMATURE STAGES

In 1967 I described the life history and behavior of *Brachinus pallidus* Erwin in California, and reviewed all available life history information concerning the bombardier beetles. Since then, I have reared a single first instar larva of *Brachinus mexicanus* Dejean from specimens G. E. Ball and I collected in Chiapas, and my wife and I collected a single last instar larva of either *Brachinus mexicanus*, *B. phaeocerus*, or *B. costipennis* in New Mexico.

I have chosen to delay the description of the first instar of *B. mexicanus* until more specimens are seen. The last instar specimen from New Mexico will also await description until comparative material of related species is available.

PHYLOGENY

Introduction

Ball (1966) wrote that "the study of evolution is the mainstream and unifying concept of biology, and the best way to join the study of *Cryobius* to this mainstream is to search for the evolutionary pathways of the extant species." Hennig (1956, 1966) provided principles that taxonomists may apply to their respective groups in order to show phylogenetic relationships. The first task, according to Hennig, is the recognition of a monophyletic group, then the search for its sister group. This process is repeated until the phylogeny is attained. At this point, Hennig writes that sister groups must have the same absolute rank in a phyletic system. I agree in principle, but I believe this to be practically impossible (see also, Ball and Erwin, 1969). With the addition of the numerous new categories and taxa created, any phylogeny would be so cluttered that relationships would be unclear. So long as named taxa are not polyphyletic (similarity due to convergence) or paraphyletic (similarity based on symplesiomorphy) and provided we can avoid a proliferation of names, we can eventually achieve a rational and usable classification that may reflect the phylogeny of the particular group of organisms under study. At least one phylogeneticist, Tuomikoski (1967), is willing to accept paraphyletic groups "sometimes" because of their "greater information content" and "better applicability to different branches of biology" outside pure phylogenetics. I have not recognized paraphyletic groups formally in the division Brachinida. Brundin (1966, 1968) has summarized the theory of phylogenetic systematics as advanced by Hennig.

I have applied Hennig's principles to the bombardier beetles, but only time and much additional study of these beetles might prove or disprove my hypotheses concerning the phylogeny of these taxa. Hennig's paleontological and parasitological methods are not applicable to bombardier beetles, because of the lack of fossils and the poor state of knowledge concerning ground beetle parasites. This leaves the holomorphological and chorological methods available, however, which I have used in arriving at my tentative phylogenetic arrangements.

The Division Brachinida

The bombardier beetles are a relatively recent derivative of the carabid line of evolution. The best evidence for this is the pattern of distribution which shows no large discontinuities (with the exception of Beringia), and few small discontinuities (see Zoogeography).

These beetles are "Anisochaeta : Lobopleuri" in Bell's scheme (1967), except that I have found that the members of Mastacina and Pheropsophina have the middle coxal cavities conjunct-separated. Bell reports this condition only in Metriini, Ozaenini, and Omophronini, all judged to be primitive on the basis of other characteristics. Further, the hind coxal cav-

ities of bombardier beetles are disjunct-lobate-confluent, with the exception of members of *Mastax* which have them disjunct-lobate-separated (and widely separated). This condition is reported by Bell as occurring only in Gehringiini and Rhysodini. Four other discrepancies arise when the bombardier beetles are placed among the higher Carabidae (Anisochaeta: Lobopleuri): the seta in the mandibular scrobe; the extra visible abdominal segments; the medially located outlets of the pygidial glands; and the very pliable cuticle of the body and elytra. A discussion of each discrepancy follows.

Most of the "lower" Carabidae possess a seta in the scrobe of the mandible. *Trachypachus* has a pore there, but lacks the seta. The paussines and ozaenines lack the seta, but *Metrius* (a paussine in all other respects) has one. Omophronines, gehringiines, opisthiines, notiophilines, elaphrines, trechines, bembidiines, nebriines, psydrines, patrobines, pogonines, and rhysodids also possess a seta in the scrobe. The "lower" carabids without the seta (promecognathines, loricerines, siagonines, and paussids) have highly modified mandibles without scrobes. As far as I know, the seta is not present in scaritines or any higher carabids. This character seems to place the bombardier beetles somewhere in this primitive group. I believe, however, that the adult scrobal seta is homologous with the mandibular seta of the carabid larvae (characteristic of all carabid groups). If so, the loss of this seta in "higher" adult carabids which maintain the seta in their larval stages does not mean the gene complex governing the appearance of the seta is absent, but simply that the seta has lost its usefulness in the adult stage. Therefore, the neotenous appearance of this scrobal seta might occur in any group of carabids primitive or advanced.

The large number of visible abdominal segments (seven in the female, eight in the male) is a direct result of the highly specialized crepitating mechanism, and must have evolved with that apparatus. Considered by themselves, these extra exposed segments would mean little when comparing bombardier beetles with other carabids.

The highly specialized crepitating mechanism, with its centrally located crepitating chambers and outlets, comprises the most outstanding difference between bombardier beetles and all other carabids. All other crepitating carabid beetles have lateral outlets and crepitating chambers. *Metriines* have very large reniform sclerotized "mixing" chambers laterad beneath tergum 9, with an outlet associated with tergum 8. Members of *Pachyteles*, an ozaenine, have smaller chambers than members of *Metrius*, but the location is the same. Members of *Helluomorphoides* have a spiral tubular chamber laterad under tergum 8, but no large mixing chambers. *Pseudomorpha* has a small tubular chamber laterad under tergum 8, and an outlet also in tergum 8. Members of *Galerita ruficollis* Dejean, a galeritine, have a small chamber laterad beneath tergum 8, behind the spiracle. The internal glands empty into this lateral chamber directly. There is no large mixing chamber.

In contrast, the bombardier beetles have two large heavily sclerotized reniform mixing chambers associated with tergum 8. The complete tergum 9 is modified into twin crepitating chambers with the outlets medially centered, one on each side of the median keel. This type is clearly derivable from any of the other crepitating mechanisms, including those of *Metrius* and *Pachyteles* (both very primitive types in all other respects), by the medial displacement of the outlets, and by the modification of tergum 9 into twin crepitating chambers. This modification also makes this body segment externally visible, whereas it is entirely concealed in other carabids.

The general plasticity and toughness of the body cuticle of bombardier beetles is found elsewhere only in the Galeritini. When squeezed, the sclerites of these beetles do not break, they merely bend. I believe this is an adaptation that parallels the warning coloration and crepitating mechanism, and is necessary for Müllerian mimics (synaposematics). Trimen (1869) was the first to point out that mimetic butterflies were unusually tough, and could withstand light attacks by predators without being crushed or torn apart. Subsequent auth-

ors have expanded this notion (for example, Carpenter and Ford, 1933). The elasticity of the body cuticle and extra visible abdominal segments can perhaps be ignored in the search for the sister group of the Brachinida.

The seta of the scrobe is probably neotenous, and therefore must be evaluated with caution. The crepitating mechanism is derivable from either primitive or advanced carabids and therefore contributes little of phylogenetic significance.

Another group of characters is seen in the anisochaete-lobopleurous condition of the bombardier beetles, which places them among the more advanced groups, as discussed by Bell (1967). There is no indication that this condition has evolved convergently in the carabids, and that possibility actually seems very unlikely.

Based on the above evidence, and other facts presented elsewhere in this paper, I consider the bombardier beetles to be a monophyletic group that has rather recently diverged from some extinct line of higher carabids. The identity of the extant sister group, if there be one, can only be determined by a careful study of those higher carabid groups, a feat possible only after the African and Oriental faunas are much better known. The relative geological age of the bombardier beetles is discussed under Zoogeography.

Using the foregoing data, in addition to that given under General Form, I believe that a hypothetical common ancestor to the Bombardier beetles might be characterized as in Table 1 in the plesiomorphous column.

Table 1. Plesiomorphous (primitive) and apomorphous (derived) conditions of some characters of bombardier beetles.

Character	Plesiomorphous	Apomorphous
Microsculpture:		
Head, pronotum, & elytra	Isodiametric meshes	Slightly stretched transversely
Head:		
Color	Brown-ferruginous	Black, yellow, or brown
Frontal furrows	Shallow	Deeply impressed
Antennal articles	Filiform	Flattened & quadrate or moniliform
Mandibles	Subfalciform	Like those of larvae
Scrobes	Unisetose	Plurisetose
Terminal palpal articles	Subcylindrical	Wedge-shaped or globose or securiform
Ligula	Bisetose	Plurisetose
Mentum	Entire	Toothed
Prothorax:		
Color	Brown-ferruginous	Black, yellow, or brown
Outline of pronotum	Cordate	Paralleliform
Propleural suture	Fused with remnant ridge	Fused & smooth
Anterior coxal cavities	Biperforate-separate-open	Uniperforate-separate-closed

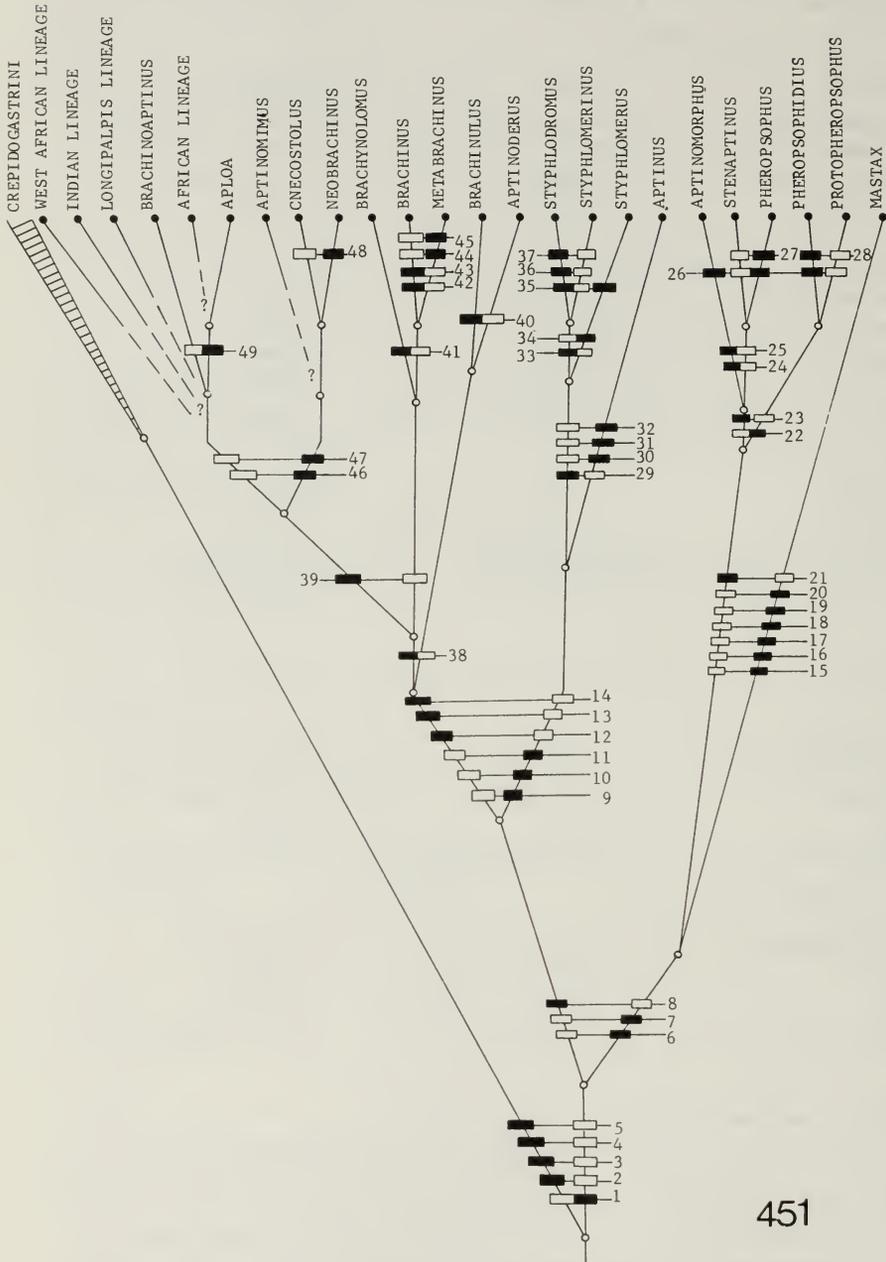
Mesothorax:		
Coxal cavities	Conjunct-confluent	Conjunct-separate
Mesepisterna	Present	Absent
Elytra:		
Pubescence	Present	Absent
Umbilicate setae	Uninterrupted	Two sets of eight setae
Erect setae	Short	Long
Intervals	Costate	Carinate or flat
Humeral angle	Square	Sloped
Metathorax:		
Metepisternum	Long	Short
Metepimera lobe	Small	Large
Metasternum	Long	Short
Coxal cavity	Conjunct-confluent	Conjunct-separate
Wings	Caraboid, veins present	Distinct veins absent
Anterior legs:		
Femoral vestiture	Scattered pubescence	Rows of short stiff setae
Subterminal spur	Internal on top of comb	External
Tarsal articles	Symmetrical	Asymmetrical
Male tarsal vestiture	Longitudinally arranged	Diagonally or circularly arranged
Abdomen:		
Segments	Seven or eight exposed	Unchanged
Male genitalia:		
Median lobe	Symmetrical	Twisted right or left
Parameres	Asymmetrical & not balteate	Asymmetrical balteate
Ligule	Absent	Present
Endophallus	Microtrichiated in part	Sclerotized in part
Female genitalia		
Bursa copulatrix	Membraneous	Sclerotized
Valvifer	Glabrous	Setiferous
Coxite	Glabrous	Setiferous
Stylus	Glabrous	Uni-setiferous

The Tribes, Genera, and Subgenera

As indicated in fig. 451, the ancestral species underwent differentiation, giving rise to the ancestor of the crepidogastrine stock and the mastacine-aptinine-pheropsophine-brachinine stock. The crepidogastrine stock gave rise to at least seven lineages, according to Basilewsky (1959). He ranks the seven extant groups (three of which are monotypic, and two others are represented by only two known species) as genera within the tribe Crepidogastrini. Tentatively, however, I would suggest, based on the picture I have presented for the other bombardier beetles, that Basilewsky's genera should be placed at the subgeneric rank.

The data available are not sufficient to apply Hennig's principles to these beetles.

The differentiation of the Crepidogastrini stock from the other Brachinini involved the



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Fig. 451. Hypothetical phylogeny for the major taxa of the division Brachinida based on the methods of detecting sister groups proposed by Hennig (1966). Note that open circles represent single ancestral species. Character states 1-49 are listed in Table 2. Black squares represent apomorphic character states; white squares represent plesiomorphic character states.

following derived characters which stand out as true synapomorphies in the Crepidogastrini: palpi securiform; gular sutures narrowed behind; male anterior tarsal vestiture spongy-pad type; mesepimeron shortened or absent. On the other hand, the apomorphous condition of the balteate parameres is a condition of the Brachinini male genitalia and never evolved in the crepidogastrine lineage.

Later the Brachinini underwent differentiation into the pheropsophine-mastacine lineage and the brachinine-aptinine lineage. The former line evolved the apomorphous condition of setae on the basal margin of the mandibles, and the separated middle coxal cavities, while the latter evolved the apomorphous condition characterized by uniperforate anterior coxal cavities.

Table 2. Plesiomorph and apomorph characters used in Fig. 451.

Number	Character	Character state	
		Plesiomorphous	Apomorphous
1	Male parameres *	Non-balteate	Balteate
2	Male anterior tarsal article vestiture†	Parallel rows	Spongy pads
3	Terminal palpal article *	Subcylindrical or wedge-shaped	Securiform
4	Mesepimeron *	Present	Absent
5	Gular sutures †	Diverging	Converging
6	Basal margin of mandible†	Glabrous	Setiferous
7	Middle coxal cavities †	Confluent	Separate
8	Anterior coxal cavities †	Biperforate	Uniperforate
9	Coxite of female ovipositor†	Glabrous	Plurisetose
10	Specialized setae of male anterior tarsi†	Scroll-like apically	Rounded
11	Mental tooth †	Absent	Present
12	Apical membrane of elytra†	Absent	Present
13	Mandibular scrobe†	Unisetose	Plurisetose
14	Upper spur of antennal comb*	Internal	External or almost so
15	Mandibular scrobe†	Present	Effaced
16	Basal margin of mandible†	Partially setiferous	Completely setiferous
17	Metasternal process*	Acute	Broadly rounded
18	Mandibular tooth†	Very small	Large
19	Hind coxal cavities*	Confluent	Separate
20	Dorsal notch at basal bend of male genitalia†	Absent	Present
21	Upper spur of antennal comb*	Present	Absent
22	Propleural suture†	Present	Absent
23	Elytral intervals†	Costate	Carinate
24	Elytral carinae†	Wide & rounded	Narrow & sharp
25	Apical elytra membrane†	Fringed	Glabrous

Table 2 (cont.)

Number	Character	Character State	
		Plesiomorphous	Apomorphous
26	Anterior coxal cavities*	Open	Closed
27	Female styli†	Short & spatulate	Elongate & narrow
28	Discal elytral depressions†	Microtuberculate	Smooth
29	Setae of coxite of female ovipositor†	Cylindrical	Flat
30	Male median lobe†	Tubular	Contorted
31	Bursal sclerites of female genitalia †	Absent	Present
32	Endophallus of male genitalia †	Long	Very short
33	Dorsal surface of body †	Micropunctate	Macropunctate
34	Ligule of male genitalia †	Single	Double
35	Color pattern of elytra †	Spotted	Concolorous
36	Mental tooth †	Strong	Reduced or absent
37	Folding pattern of endophallus †	Simple	Complete
38	Apical membrane of elytra †	Partially developed	Fully developed
39	Vestiture of male anterior tarsi †	Asymmetrical	Symmetrical
40	Terminal palpal article †	Fusiform	Wedge-shaped
41	Apical sclerite of endophallus †	Absent	Present
42	Apical elytral membrane †	Fringed	Widely spaced setae
43	Left paramere of male genitalia †	Small & balteate	Large & triangulate
44	Color pattern of elytra †	Concolorous	Spotted
45	Apical elytral membrane †	Fringed	Glabrous
46	Virga of endophallus †	Absent	Present
47	Upper spur of antennal comb †	Slightly internal	External
48	Antennal article three †	Short	Elongate
49	Subapical sclerite of endophallus †	Absent	Present

* = Objectively determined, that is the character state was determined to be apomorphous by its distribution throughout the Carabidae.

† = Subjectively determined, that is the character state was determined to be apomorphous by its distribution throughout the Brachinida or part thereof.

From the pheropsophine-mastacine lineage two stocks were derived, the aberrant *Mastax* and the more conservative Pheropsophina. The former evolved the following synapomorphies: well developed bifid retinacular mandibular teeth; extension of mandibular basal margin brush to the tooth; loss of a mandibular scrobe; rounded metasternal process between middle coxae; separated hind coxal cavities. The Pheropsophina stock evolved the apomorphic condition of a dorsal notch at the basal bend of the male median lobe. Within the Pheropsophina two lines arose, the second one replacing the first in all areas except the New World. The first, or more primitive, stock of the Pheropsophina, retained the costate elytral condition, but lost the propleural suture. This stock reached the New World, but subsequently, was not eliminated by a second wave of advanced Pheropsophina, which had carinate elytra. This second wave arrived in eastern Asia too late to cross into the New World.

Once in the New World, the primitive Pheropsophina remained in isolation (see Zoogeography) and underwent secondary radiation into two subgenera, *Protopheropsophus* and *Pheropsophidius*. *Protopheropsophus* retains the open anterior coxal cavities (a very primitive condition in carabid beetles), but it has lost the small rugosities in the depressions of the elytra, and has become wingless.

In the second radiation of Old World Pheropsophina, the ancestral stock of one group, *Aptinomorphus*, evolved the apomorphic condition of narrow, acute carinae, and lost the apical elytral fringe setae. Also from this second radiation came the subgenera *Stenaptinus* and *Pheropsophus (sensu stricto)*. *Pheropsophus* attained the apomorphic condition of elongate styli in the female, while *Stenaptinus* has retained the primitive spatulate styli and the nearly-open anterior coxal cavities.

The aptinine-brachinine lineage split very early into two ancestral stocks, the Aptinina and the Brachinina. The Aptinina stock attained the apomorphic condition of a toothed mentum, anterior male tarsal articles with apically disc-shaped setae in the ventral vestiture, and setiferous coxite. The Brachinina stock became apomorphic in the presence of the elytral membrane and the presence of pubescence in the scrobe of the mandible. At that point, it is possible that both stocks had asymmetrical anterior tarsal articles in the male, but in one lineage of Brachinina those articles later became symmetrical. A second alternative is that tarsal asymmetry developed convergently in Aptinina and part of Brachinina. It should be pointed out, however, that the modified setae of Aptinina members are disc-shaped at the apex (figs. 43, 47), whereas in all Brachinina members, including the ones with asymmetrical tarsal articles, the setae are expanded and rolled like a scroll at the apex (figs. 41, 42, 44, 45, 46, 49).

Subsequently, the Aptinina lineage evolved into the *Aptinus* stock and *Styphlomerus* stock. The *Aptinus* members became wingless mountain inhabitants of southern Europe, while the *Styphlomerus* stock converged in habitus and coloration with the Brachinina members, and subsequently spread as far as Japan. The *Aptinus* stock acquired the apomorphic conditions of bursal sclerites in the female, and a swollen and contorted median lobe in the male. Within this stock the apical opening of the shaft became contorted to the right in one group, while in the other (the extant *Aptinus displosor* Dufour) the opening contorted to the left. Both groups have a very short internal sac with several sclerites.

The *Styphlomerus* stock acquired the apomorphic condition of modified setae on the coxite, then subsequently divided into two lines. The first of these, represented by the members of *Styphlomerus*, acquired the apomorphic condition of a double ligule on the male median lobe, while the *Styphlodromus-Styphlomerinus* line acquired the apomorphic condition of macropunctate elytra. The members of *Styphlodromus* subsequently lost the mental tooth that was originally developed in the Aptinina stock. I have interpreted this character state as being apomorphic, and those beetles also became apomorphic in the com-

plex folding pattern of the endophallus.

Meanwhile, the Brachinina were undergoing a rather extensive radiation, resulting in at least 14 extant lineages. The brachinina are extremely difficult to sort out, because externally they exhibit very little diversity, due perhaps to the strong selective pressures of Müllerian mimicry (see Comparative Morphology). In order to determine the likely phylogenetic pathways, the internal sac and its associated sclerites, or microtrichated fields, should be carefully studied. In areas such as Africa and the Orient, the species are very poorly known and material is difficult to obtain. However, with the material available, I have applied Hennig's principles, and I believe that a reasonable picture emerges that can be used as a basis for further study.

After the split of the Brachinina from the aptinine-brachinine lineage, another split occurred as the apomorphous elytral membrane became more fully developed. A few extant species, *Aptinoderus* (= *Brachynomorphus*) and *Brachinulus* remain, however, with the poorly developed membrane. *Brachinulus* became apomorphous in the swollen-acuminate last palpal articles. *Aptinoderus* represents the most primitive group of species in the entire lineage. These species are wingless and highly endemic.

The lineage with the fully developed elytral membrane subsequently diverged into two lines of evolution. One of these lines acquired symmetrical male anterior tarsal articles, while the other line retained the previously acquired asymmetrical condition. I have discussed this character state above. It is difficult to say whether it is the result of convergence in the Aptinina and part of the Brachinina, or a gain of asymmetry in the aptinine-brachinine-lineage long ago and subsequent reversion to symmetry in part of the Brachinina. I favor the latter view because of the asymmetry in *Aptinoderus* males. These beetles are in the most plesiomorphic state of any Brachinina and therefore are morphologically the most similar to the Aptinina. Nevertheless, it does serve to unite two lines of evolution within the higher Brachinina, regardless of which line is apomorphic for the character state.

The "asymmetrical" lineage subsequently split (1) into an apomorphous line with a virga on the endophallus of the male genitalia, and (2) a plesiomorphic line. The former, the *Brachynolomus* stock, remained basically plesiomorphic in all character states except the virga, while the second line later subdivided into the more northern *Brachinus* (*sensu stricto*) and the southern *Metabrachinus*. The members of *Brachinus* (*sensu stricto*) acquired the apomorphous condition of long widely-spaced setae on the apical elytral membrane and the large triangular left paramere. The members of *Metabrachinus* became apomorphous by the loss of setae on the apical elytral membrane and by acquiring a spotted color pattern on the elytra, but remained plesiomorphic in the character states mentioned for *Brachinus* (*sensu stricto*).

The "symmetrical" lineage subsequently split into (1) an apomorphous line with a virga on the internal sac of the male genitalia and (2) a plesiomorphic line, just as did the "asymmetrical" lineage. In the line which acquired a virga, a further apomorphous condition arose when the spur of the antennal comb became external. The "virgate" line subsequently split into two groups, *Neobrachinus* and *Cnecostolus*, the common ancestor of which had split from the ancestor of *Aptinomimus*. Since I have not seen the male genitalia of *Aptinomimus*, I cannot place it exactly into the scheme. However, on the basis of the female characteristics, this group appears to be the southern vicar of this lineage (see Zoogeography).

The Old World *Cnecostolus* acquired the apomorphous conditions of a spotted color pattern of the elytra, and glabrous (or almost so) edge of the apical elytral membrane. Also, the virga of these beetles seems to be of a different nature than in *Neobrachinus*. The *Neobrachinus* lineage acquired the apomorphous condition of an elongate antennal article 3, which is longer than articles 1 and 2 combined, and the "socket-type" closing of the

anterior coxal cavities.

In the "non-irgare" plesiomorphic line of the symmetrical lineage, the upper spur of the anterior tibia has remained slightly internal, in an intermediate position. This line split, forming the ancestor of the extant *Aploa* and *Brachinoaptinus*. The former acquired the apomorphic condition of a subapical sclerite on the endophallus of the male genitalia, and a spotted elytral color pattern. The ancestral stock of *Brachinoaptinus* remained plesiomorphic in the character states discussed, and represents the ancestral stock of the "symmetrical" lineage.

I have seen specimens representing at least four other lineages not discussed above. Two of these are from India and the others are from Africa. Because of insufficient material, I cannot determine their affinities, but they belong to the "symmetrical" line, and probably have been derived from the *Aploa-Brachinoaptinus* ancestral stock.

The North and Middle American species of *Neobrachinus*

The methods used here are the same as I used in determining the phylogeny of the supra-specific taxa of Brachinida. It has been necessary to use the evolution of form of the virga in order to determine the primary branching points in figure 452. The underlying assumption in the study of the virgae is that change has proceeded from a simple to a more complex structure. The geographical distribution of members with the simple virga supports this assumption, that is one species existing as a relic in Asia, and three of the four other species occurring in endemic pockets in the American Midwest and Southeast.

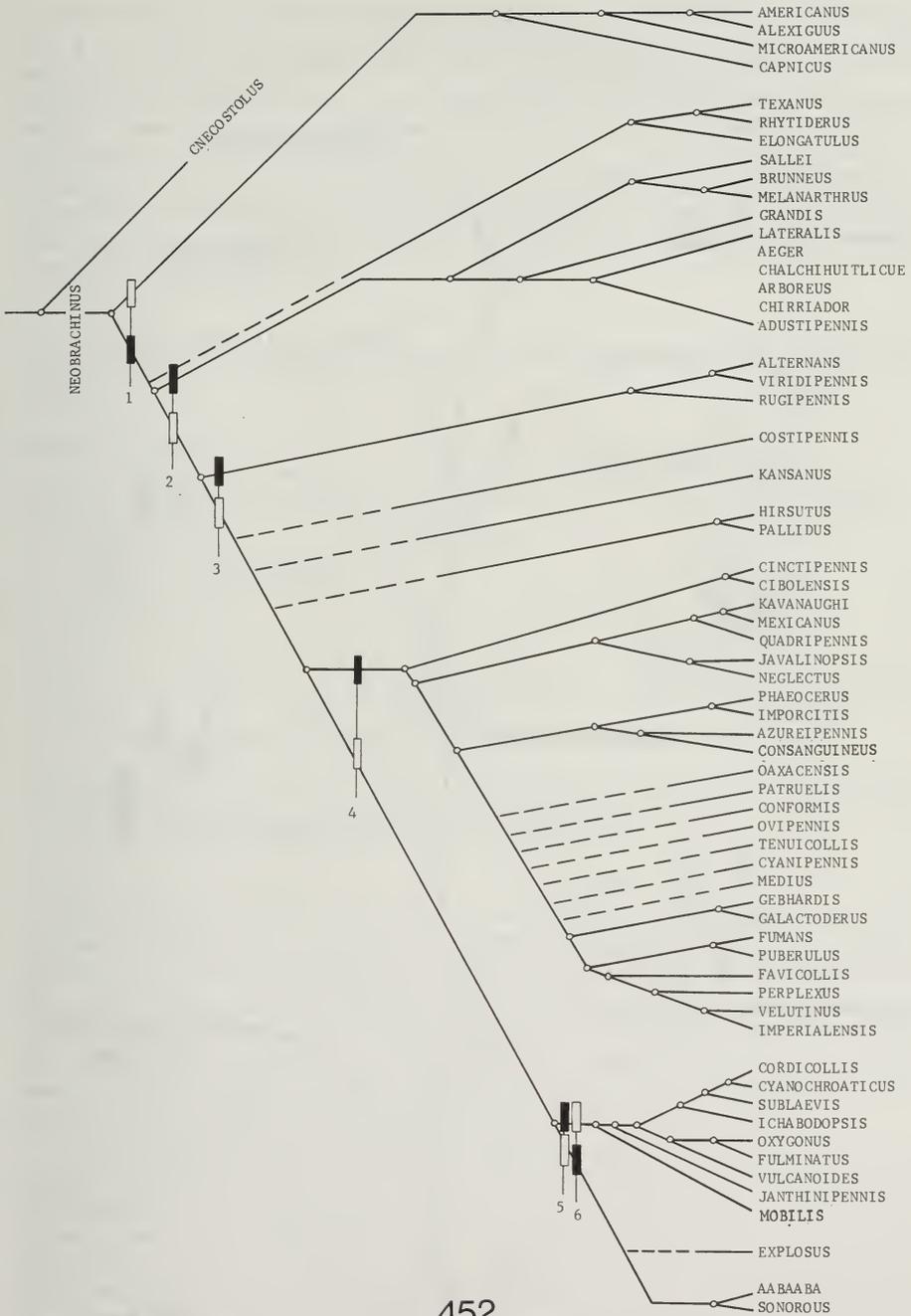
The comparison of the virga of *Neobrachinus* with that of Old World groups indicates that this subgenus is monophyletic. *Brachinus dryas* Andrewes (= *stenoderus* Andrewes) of the Himalayan region must be regarded as a member of subgenus *Neobrachinus*, and it is the only species from outside the New World that I know to have a *Neobrachinus*-type virga. All other characteristics of this species agree with the New World group; also for this reason, I regard *Brachinus dryas* as an Old World relic of the lineage that later crossed into North America (see also Zoogeography). Because of the homologous nature of the virgae of all the North and Middle American *Neobrachinus*, I believe that a single ancestral form crossed the Bering Land Bridge and subsequently radiated into the present pattern. The foregoing data, in addition to that given under Taxonomy, convinces me that the common ancestor of the species of *Neobrachinus* can be characterized in Table 3, plesiomorphous column.

Table 3. Plesiomorphous and apomorphic conditions of some characters of *Neobrachinus*.

Character	Plesiomorphous	Apomorphic
Color:		
Head & prothorax	Ferrugineous	Black or brown
Elytra	Blue	Black, brown, green, slate-grey, striped
Elytral epipleura	Blue	Testaceous
Mesepisterna	Ferrugineous	Brown or infuscated
Metepisterna	Infuscated	Ferrugineous or brown
Metasterna	Ferrugineous	Infuscated at sides
Abdomen	Infuscated	Ferrugineous, brown, or infuscated at sides only
Terga	Infuscated	Ferrugineous
Legs	Ferrugineous	Black or testaceous

Table 3 (cont.)

Character	Plesiomorphous	Apomorphous
Color:		
Knees	Ferruginous	Infuscated
Head:		
Frontal furrows	Shallow	Deep
Mentum	Flat to slightly convex at middle	Unisulcate or bisulcate
Submentum	Long	Short
Mental setae	Two	Plurisetose
Submental setae	Eight to ten	Sixteen to twenty or more
Pronotum:		
Outline of pronotum	Cordate	Narrow
Lateral setae	Present	Absent
Pronotal pubescence	Scattered	Dense or absent
Proepipleural pubescence	Absent	Scattered or confined anteriorly & posteriorly
Proepisternal pubescence	Scattered	Absent or confined anteriorly & posteriorly
Elytra:		
Costae	Moderately elevated	Highly elevated or absent
Humeral angle	Square	Sloped
Erect depression setae	Subequal to pubescence	Three or more times longer than pubescence
Pubescence	Evenly scattered	Restricted to intervals 6, 7, 8, or to 8, or absent
Metathorax:		
Metasternum, metepisternum	Long	Short
Legs:		
Anterior surface of anterior tibia	Strigose	Punctate
Male genitalia:		
Basal bend	Same plane as shaft	Rotated from plane of shaft
Virga	Simple	Complex



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Fig. 452. Hypothetical phylogeny for the species of North and Middle American genus *Brachinus* based on the methods of detecting sister species proposed by Hennig (1966). Primary branches numbered 1-6 described in Table 4. Unnumbered branches described in text, under Phylogeny. Note that open circles represent single ancestral species. Black squares represent apomorphous character states, white squares represent plesiomorphous character states.

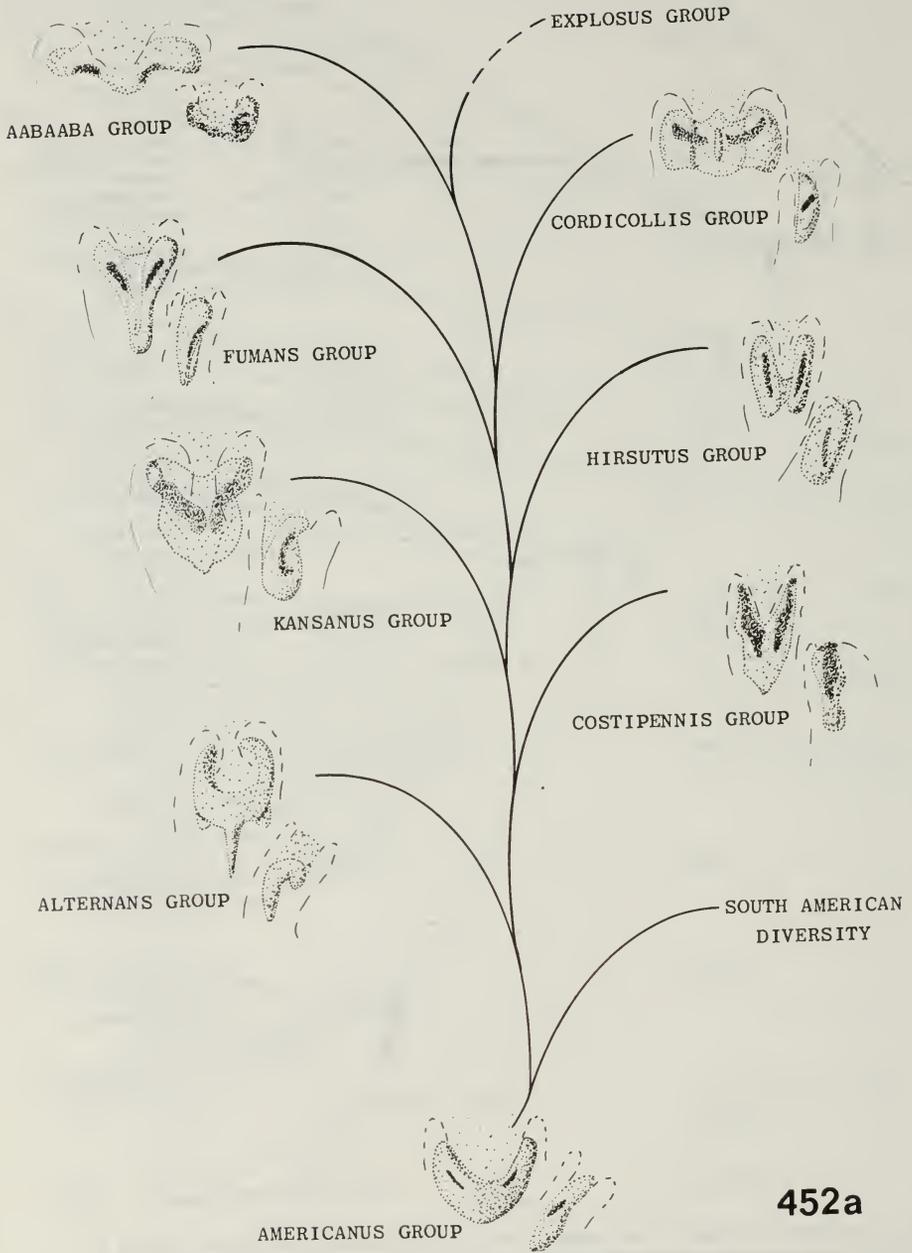


Fig. 452a. A pictorial "family tree" of the groups of *Neobrachinus* based on the structure of the virga.

Based upon these hypothetical features, I have tried to align the species of *Neobrachinus* into a developmental cline based upon the complexity of the virga. The starting point is the *americanus* group, the members of which have a virga almost identical to that of *B. dryas* of the Himalayan region. Further, the *americanus* group includes species that are wingless, which I believe shows some indication of ancient lineage. The following discussion is graphically illustrated in figure 452a.

The virga of members of the *americanus* group is simply the lightly sclerotized tip of the endophallus, and there are also two lightly pigmented areas, one on each side of the gonopore. This virga is the most plesiomorphic of the series, and is identical to that of members of *B. dryas* Andrewes in Sikkim.

Table 4. Plesiomorph and apomorph characters used in figure 452 for primary branching points.

Number	Character	Character State	
		Plesiomorphous	Apomorphous
1	Virga *	Pouch-shaped	Variouly modified
3	Virga *	Rounded apically	Acute apically, tripartite
4	Virga *	Unmodified	Ventral trough centrally
5	Virga *	Unmodified	"H" shaped
6	Virga *	Continuous with axis of endophallus	Perpendicular to axis of endophallus
2	Zoogeographic isolation in South America	Isolation in North America	

* = Subjectively determined, that is, the character state was determined to be apomorphous by its distribution throughout the Brachinida or part thereof.

The *americanus* group is subdivided into two subgroups. The *capnicus* subgroup has acquired the apomorphous condition of totally black integument, and must have differentiated long ago. The second subgroup next split and gave rise to *B. microamericanus* with the apomorphous condition of accessory setae on the mentum and with setae anteriorly and posteriorly on the proepipleura. The *B. americanus* - *B. alexiguus* lineage acquired the apomorphous male genitalia and the punctate anterior surface of the anterior tibia. This lineage divided to produce the very similar *B. americanus* and *B. alexiguus*. *B. alexiguus* acquired the apomorphous condition of infuscated antennal articles 3 and 4.

The next lineage must be considered here because it contains the modern members of an early group or groups isolated in South America throughout most of the Cenozoic Era (see Zoogeography). The members representing the ancestral stock that invaded South America from the north are represented by *B. nigricans* and *B. niger*, both now extant in South America. These species are probably of similar antiquity to those of the *americanus* group. During the Pliocene, species that had evolved in South American isolation invaded Mexico (via Central America) and North America. These various groups are considered below.

The *texanus* group includes many South American species not considered in this paper, therefore only tentative conclusions can be reached at this time. The stock moving out of South America split, giving rise to *B. elongatulus* and the ancestral stock of the *B. rhytiderus* - *B. texanus* lineage. The latter then split, giving rise to *B. rhytiderus* and *B. texanus*. The

determination of plesiomorphous-apomorphous conditions is difficult without studying more species of this group. It seems however, that the more rounded female stylus of *B. elongatulus* and its more elongate elytra may be apomorphous, while the loss of accessory setae of the mentum and the loss of discal elytral setae may be apomorphous in *B. rhytid-erus*. The slate-grey elytra and densely pubescent elytral depressions are certainly apomorphous in *B. texanus*.

The other groups that evolved in isolation in South America are those with the apomorphous condition of brown elytra. This lineage must have split long ago, giving rise to a stock with the apomorphous condition of brown head and prothorax, matching the color of the elytra. Two groups of this stock have invaded Middle America. The *sallei* group acquired the apomorphous condition of two paramedian pits in the mentum, while the *brunneus* group remained similar to forms in South America (such as *B. hyalea* Reichardt). The older lineage which gave rise to the *sallei* - *brunneus* stock, also gave rise to a complex and diverse group of beetles that I have tentatively placed in the *lateralis* group. Judging from the characteristics of the virgae and male median lobes, this group is far from being understood. A complete study of the South American *Neobrachinus* with brown elytra will have to be undertaken before the taxonomy of this complex group is understood.

Both the *kansanus* group and the *costipennis* group contain only single, rather aberrant species, neither showing any relationship to other extant *Brachinus*. Members of *B. kansanus* have acquired the apomorphous condition of the lack of lateral pronotal setae, highly elevated (almost carinate) costae, and narrowly reflexed side margins of the pronotum. The virga is only slightly modified from the *americanus* type, in that only the dorsal apex has become sclerotized, but the pigmented areas near the gonopore are extensive.

The members of *B. costipennis* are probably the most aberrant of the subgenus *Neobrachinus*. The mentum is deeply sulcate, with the single pit surrounded by setae. This character state is surely apomorphous. Other apomorphous conditions are the glabrous elytra, the almost carinate costae, the shape of the apex of the median lobe and the shortened submentum. The virga is unlike any others, but could easily have been derived from the *americanus* type.

The virga of the *alternans* group is highly aberrant and its derivation cannot be easily hypothesized. This stock probably split from the main line of evolution long ago, as indicated by the flightless condition in one of its species. The lineage split, giving rise to *B. rugipennis*, which acquired the apomorphous condition of a wide ligule of the male median lobe, and to a stock containing the forebears of *B. alternans* and *B. viridipennis*. Ultimately, *B. alternans* acquired the apomorphous condition of a broad stylus in the female ovipositor, while *B. viridipennis* developed the apomorphous green elytra, punctate anterior surface of the anterior tibiae, and elongate apex of the median lobe.

The next group, the *hirsutus* group, consists of two closely related sister species that show no close relationship to other groups in the structure of the virga. The ancestral stock acquired the apomorphous condition of a compressed median lobe, strongly costate elytra, and the loss of lateral pronotal setae. This stock diverged, giving rise to *B. hirsutus* and *B. pallidus*. The former acquired the apomorphous conditions of a depression on the venter of the shaft of the male genitalia, and a densely pubescent pronotum. The latter developed a more compressed shaft of the male median lobe. The virga of this group was clearly derivable from the *americanus* type by a reduction in dorsal and ventral sclerotization, leaving two lateral lobes connected in the area of the gonopore.

The members of the *fumans* group have similarly constructed virgae, but exhibit great diversity among the members. The virga is essentially like that of the *americanus* group, but the ventral surface has lost its sclerotization and the sides have curled over, ventrally, leaving a central trough. Once this type of virga had arisen, the lineage split, forming the *cincti-*

pennis subgroup and the ancestral stock of the other *fumans* subgroups. The *cinctipennis* subgroup acquired the apomorphic condition of a ferruginous sutural stripe on the elytra. The other ancestral stock subsequently divided, giving rise to the ancestors of the *quadripennis* and other subgroups.

The *quadripennis* subgroup developed the apomorphic condition of a ridge on the venter of the shaft of the male median lobe, and has diverged into two sister stocks, one with the apomorphic smooth anterior tibiae with only punctures on the anterior surface, and accessory setae on the submentum. This line subsequently split to form *B. neglectus*, with its apomorphic acute styli, and *B. javalinopsis* with its apomorphic plurisetose ligula. The other sister stock also divided, giving rise to *B. quadripennis* with its apomorphic spatulate and broad stylus of the female ovipositor, and infuscated palpi and tibiae, and to the ancestral stock of *B. mexicanus* - *B. kavanaughi*. This stock subsequently divided giving rise to the species mentioned. *B. mexicanus* acquired the apomorphic condition of reduced elytral pubescence and *B. kavanaughi* has remained the most plesiomorphic of the lineages, probably being representative of the ancestral stock.

The sister stock of the *quadripennis* subgroup subsequently divided, giving rise to the *phaeocerus* subgroup, with its apomorphic conditions of a long narrow apex on the shaft of the male median lobe, the bright blue elytra with contrasting black suture, and the black outer antennal articles. This ancestral stock diverged giving rise to two sister stocks. One of these acquired the apomorphic condition of completely pubescent proepisterna and propiopleura. This line subsequently split giving rise to *B. azureipennis*, with its apomorphic black tibiae and tarsi, and *B. consanquineus*. The other line subsequently split, giving rise to *B. phaeocerus*, with its apomorphic bent apex of the shaft of the male median lobe, and its infuscated tibiae and tarsi, and *B. imporcitis* with its apomorphic glabrous proepisterna. none of which left morphological characteristics that can be interpreted using Hennig's principles. That is none of these numerous species have present sister relationships with other species or groups. *B. oaxacensis* acquired the apomorphic conditions of a lack of lateral pronotal setae, an elongate and strongly sclerotized virga, and highly raised and ridge-like costae. *B. patruelis* acquired the apomorphic condition of two accessory ligules on the shaft of the male genitalia. *B. conformis* acquired the apomorphic condition of a narrow and chisel-shaped shaft of the male genitalia, and an elongate and narrow stylus of the female ovipositor. *B. ovipennis* acquired the apomorphic condition of a compressed and collapsed shaft of the male median lobe, and slight rotation in the orientation of the virga within the shaft. *B. tenuicollis* acquired the apomorphic condition of an elongate and very narrow shaft of the male median lobe, highly elevated costae of the elytra, and the broad styli of the female ovipositor. *B. cyanipennis* acquired the apomorphic condition of a broad ligule of the shaft of the male median lobe, and elongate erect depression setae. *B. medius* acquired the apomorphic condition of small wide styli of the female ovipositor.

After these groups diverged from the *fumans* lineage, the main ancestral stock split, giving rise to the *gebhardis* subgroup and the *fumans* subgroup. The former acquired the apomorphic condition of elytral pubescence restricted to the eighth interval, and then divided into *B. gebhardis* with its apomorphic accessory setae on the mentum, and *B. galactoderus* with its apomorphic slate-grey color of the elytra and milky color of the pronotum.

The ancestral stock of the remaining *fumans* subgroup acquired the apomorphic conditions of a swollen shaft of the male median lobe, and infuscated sides of the venter.

This lineage divided into two sister stocks, the first of which had the apomorphic condition of accessory setae on the mentum and submentum. This stock subsequently split, forming *B. favicollis*, with its apomorphic large punctures of the pronotum, and an ances-

tral stock which subsequently split into *B. perplexus* with its apomorphic non-twisted median lobe, and another ancestral stock. This latter stock subsequently divided, giving rise to *B. velutinus* with its apomorphic dense pubescence, and *B. imperialensis*. The second ancestral stock without accessory setae on the mentum also split forming two sister species, *B. fumans* with its apomorphic punctate anterior surface of the anterior tibia, and its median lobe with the basal bend rotated about 45 degrees from the plane of the shaft, and *B. puberulus*. *B. puberulus* is the most plesiomorphic of the lineage, and is probably representative of the ancestral stock.

From the ancestral type of virga, there also arose the virga characteristic of the *cordicollis* group. This type virga is slightly more complex than that of the *fumans* group in that the apex has become somewhat truncated and a dorsal fin has developed distal to the gonopore. The ancestral *cordicollis* lineage split giving rise to *B. mobilis*, with its apomorphic sulcate mentum, and another ancestral stock. This latter ancestral stock subsequently split again giving rise to *B. janthinipennis* with its apomorphic narrow and acute male median lobe, and to still another ancestral stock, which subsequently split into two lineages. The first of these, the ancestor of the *cordicollis* subgroup acquired the apomorphic condition of a longitudinal depression on the ventral surface of the shaft of the male median lobe. This ancestral lineage subsequently split giving rise to *B. ichabodopsis*, with its apomorphic broad stylus of the female ovipositor and the very elongate third antennal article, and to still another stock. This latter stock subsequently divided giving rise to *B. sublaevis*, with its apomorphic narrow stylus of the female ovipositor and its lack of elytral costae, and still another stock. This stock split giving rise to *B. cyanochromaticus*, with its apomorphic bright metallic blue elytra, and *B. cordicollis*. *B. cordicollis* is the most plesiomorphic of the lineage, and is probably representative of the ancestral stock.

The second *cordicollis* lineage gave rise to the *oxygenus* subgroup with its apomorphic broadly rounded virgal apex. This lineage subsequently split giving rise to *B. vulcanoides*, with its apomorphic broad stylus of the female ovipositor and punctate anterior surface of the anterior tibia, and an ancestral stock. This ancestral stock subsequently split giving rise to *B. oxygenus*, with its apomorphic elongate ligule of the shaft of the male genitalia and cylindrical antennal scape, and *B. fulminatus*. *B. fulminatus* is the most plesiomorphic of the lineage, and is probably representative of the ancestral stock.

The male (and therefore the virga) of the *explosus* group is unknown. This makes placing *B. explosus* into the scheme difficult, but because of the synapomorphies in relation to those of all other *Neobrachinus* species, I believe *B. explosus* is a rather recent lineage. The group has acquired the following apomorphic conditions: elytra strongly convex, shiny black; outer intervals only with pubescence; acute styli of the female ovipositor.

The last and probably most recently derived lineage of *Neobrachinus* in North America is the *aabaaba* group. The virga has become oriented transversely on the endophallus and very shortened. It has also become trilobate. The ancestral stock split giving rise to two sister species, *B. aabaaba* and *B. sonorous*. *B. aabaaba* acquired the apomorphic condition of an arcuate, narrow styli of the female ovipositor, while *B. sonorous* acquired the apomorphic condition of pale colored elytral epipleura, and completely pubescent proepipleura.

As can be seen from the data presented above, and under Taxonomy, many characteristics of the external morphology of *Neobrachinus* have arisen several times. If convergence in external characteristics was ruled out either by hypothesis or fact, and a phylogenetic arrangement was made utilizing only these external characteristics, then the virgae and male median lobes would show convergence. In the hypothesis set forth in fig. 452, the characteristics listed in Table 5 have arisen more than once, in *Neobrachinus* of North and Middle America.

Table 5. Convergent characters of the species of North and Middle American *Neobrachinus* derived from figure 452.

Character and Character State	Number of Times Arisen
Infuscated palpi	2
Testaceous antennal article 2	2
Infuscated outer antennal articles.	2
Testaceous antennal articles.	2
Testaceous leg color	2
Single median mental pit	2
Elongate erect depression setae.	2
Slate-colored elytra	3
Infuscated knees	3
Loss of lateral pronotal setae	3
Glabrous proepisterna	3
Elytral pubescence restricted to eighth interval	3
Elytral epipleura pale-colored	4
Reduction of wings	4
Infuscated antennal article 2.	5
Infuscated legs in part (other than knees).	5
Mesepisternum infuscated at sides	5
Abdominal sterna ferrugineous.	5
Elytral pubescence restricted to intervals 6, 7, 8	6
Antennal articles 3 and 4 partially infuscated	7
Metepisternum ferrugineous.	8
Proepipleura completely pubescent	8
Proepisterna completely pubescent	8
Sloped humeri	8
Highly elevated costae	9
Abdominal sterna infuscated at sides	12
Proepipleura pubescent both anteriorly and posteriorly	12
Elytral costae barely elevated	12
Median lobe with basal bend rotated 45° from plane of shaft	12
Metasternum infuscated at sides	13
Terga infuscated	13
Anterior tibia with anterior surface punctate	13
Accessory setae on mentum	15
Accessory setae on submentum	15
Antennal articles 3 and 4 completely infuscated	17

ZOOGEOGRAPHY

Introduction

In order to assess the movements of animals, we must use various clues to geographical histories of the animals we are discussing. Darlington (1957) discussed these clues and their shortcomings as part of his "working principles." Briefly, these clues are as follows:

1. Number clues, or information provided by counts of genera or species. — The highest concentration indicates the place of origin of the taxa in question. Recession and extinction of animals and differential latitudinal diversity sometimes mask the help number clues give us in this regard, but used critically this type of clue is very good.
2. Degree of differentiation. — Greater diversity and more endemism should occur where a taxon has been for a long time, rather than where it has just arrived. The masking effects of recession, extinction, and latitudinal diversity also apply here.
3. Extent of area. — The area occupied by a group of organisms increases directly with the group's age. The assumption here is that groups are continuously spreading. Of course, recession and extinction make this clue worthless by itself, but viewed in conjunction with other clues, it has some value.
4. Continuity of area. — Whether or not a group is relict.
5. Vicariance. — The distribution of sister groups.
6. Fossil clues. — The distribution of fossil remains of ancestors of the group under study.

With the exception of fossil clues (there are none), I have looked for places to apply these clues in considering the general patterns of bombardier beetle movements. In the more detailed study of North and Middle American *Brachinus* species, I have used numerical clues more extensively, especially methods proposed by Ball and Freitag (*in* Freitag, 1969). Because of the slightly different treatment resulting from more detailed knowledge of North and Middle American *Brachinus* species, I have dealt separately with this after considering the general patterns of bombardier beetle distribution and past dispersal.

General Patterns of Distribution

The division Brachinida is represented in all major faunal regions of the world, with the exception of Oceania. Table 6 gives the distribution of the genera and subgenera in terms of the major faunal regions, and the island of Madagascar. Madagascar is generally treated as part of the Ethiopian Region, but because of the interesting diversity and great amount of endemism, I provide figures and separate considerations for that island. For consistency it is also included as part of the Ethiopian Region, except when the two are directly compared.

Table 6. Distribution of the genera and subgenera of the division Brachinida in terms of the major faunal regions.

	Nearctic	Neo-tropical	Pale-arctic	Ethiopian	Oriental	Australian	Madagascar
<i>Crepidogaster</i>				X			X
<i>Tyronia</i>				X	X		
<i>Brachynillus</i>				X			
<i>Crepidolomus</i>				-			X
<i>Crepidonellus</i>				X			
<i>Crepidogastrillus</i>				X			
<i>Crepidogastrinus</i>				X			
<i>Mastax</i>			X	X	X		
<i>Pheropsophus</i>			X	X	X	X	X

Table 6 (cont.)

	Nearctic	Neo-tropical	Pale-arctic	Ethiopian	Oriental	Australian	Madagascar
<i>Stenaptinus</i>				X	X		
<i>Aptinomorphus</i>				-			X
<i>Pheropsophidius</i>		X					
<i>Protopheropsophus</i>		X					
<i>Aptinus</i>			X				
<i>Styphlomerus</i>				X			
<i>Styphlomerinus</i>			X	-	X		X
<i>Styphlodromus</i>				X			
<i>Brachinus</i>			X				
<i>Metabrachinus</i>				X			X
<i>Aploa</i>				X	X		
<i>Brachinoaptinus</i>			X				
<i>Aptinominus</i>				-			X
<i>Cnecostolus</i>			X				
<i>Neobrachinus</i>	X	X			X		
<i>Aptinoderus</i>				X			
<i>Brachinulus</i>				X			
<i>Brachynolomus</i>			X		X	X	
Total:	1	3	8	19	8	2	7
Total endemic groups	0	2	4	14	0	0	3
Percentage endemic	0	7.4	14.8	51.8	0	0	11.1

The genera and subgenera are considered equally, and for this analysis both are referred to as "groups." The greatest diversity in numbers of groups occurs in the Ethiopian Region south of the Sahara Desert with nineteen groups represented. The Palearctic and Oriental Regions have eight groups each. Madagascar alone has seven groups. The Neotropical Region has three groups, the Australian Region has two, and the Nearctic has only one.

Of the eight Palearctic groups, three are shared with the Ethiopian Region. Of the eight Oriental groups, six are shared with the Ethiopian Region. Both of the Australian groups are shared with the Oriental Region, and one with the Ethiopian Region. Of the three Neotropical groups, one is shared with the Nearctic. This same shared group has a single known relict species extant in the Himalayan mountains. The Palearctic and Oriental Regions share four groups. Of the seven Madagascan groups, three are shared with Africa and one is shared with the Oriental Region. A summary of comparisons between major faunal regions is presented in Table 6, and an index of dissimilarity for each region is presented in Tables 7 and 8. This index is discussed below. Table 6 indicates the percentage of the entire group that is endemic to each major faunal region.

Table 7. Dissimilarity values among faunal regions of the groups of the division Brachnida.

Faunal Regions	Statistics	Neo-tropical	Pale-arctic	Ethiopian	Oriental	Australian	Madagascar
Nearctic	t*	4	9	20	9	2	8
	c**	1	0	0	1	0	0
	t - c	3	9	20	8	2	8
	t-c/t x 100	75	100	100	88.8	100	100
Neotropical	t		12	22	12	4	10
	c		0	0	1	0	0
	t - c		12	22	11	4	10
	t - c/t x 100		100	100	91.6	100	100
Palearctic	t			27	16	9	15
	c			3	4	1	2
	t - c			24	12	8	13
	t-c/t x 100			88.8	75	88.8	80
Ethiopian	t				27	20	26
	c				6	1	3
	t - c				21	19	23
	t-c/t x 100				77.7	95	88.4
Oriental	t					9	15
	c					2	2
	t - c					7	13
	t-c/t x 100					76.6	80
Australian	t						8
	c						1
	t - c						7
	t-c/t x 100						87.5

* = Total number of groups in each pair of faunal regions.

** = Number of groups in common between each pair of faunal regions.

Table 8. Indices of dissimilarity determined from Table 7.

Area	Index of dissimilarity
Nearctic Faunal Region	564
Neotropical Faunal Region	567
Palearctic Faunal Region	533
Ethiopian Faunal Region	555
Oriental Faunal Region	491
Australian Faunal Region	549
Madagascar	534

Table 9 presents the distribution of allopatric sister groups of the division Brachinida. Three relationships seem evident: east - west vicariance, north - south vicariance, and mainland - island vicariance. The movements in terms of probable direction and general distance covered are indicated on maps (figs. 454-458). Figure 453 indicates possible centers of diversification.

Table 9. Distribution patterns of allopatric sister groups of the division Brachinida.

East - West Relationships			
Western Vicar		Eastern Vicar	
Name	Center	Name	Center
<i>Styphlodromus</i>	Ethiopian	<i>Styphlomerinus</i>	Oriental-Madagascan
<i>Cnecostolus</i>	Transcaspian	<i>Neobrachinus</i>	New World

North - South Relationships			
Northern Vicar		Southern Vicar	
Name	Center	Name	Center
<i>Protopheropsophus</i>	Mexico	<i>Pheropsophidius</i>	South America
<i>Aptinus</i>	Europe	<i>Styphlomerus</i> & allies	Ethiopia-Oriental
<i>Brachinus</i>	Europe	<i>Metabrachinus</i>	Ethiopian
<i>Brachinoaptinus</i>	Europe	<i>Aploa</i>	Ethiopian
<i>Cnecostolus-Neobrachinus</i>	Palaearctic	<i>Aptinomimus</i>	Ethiopian

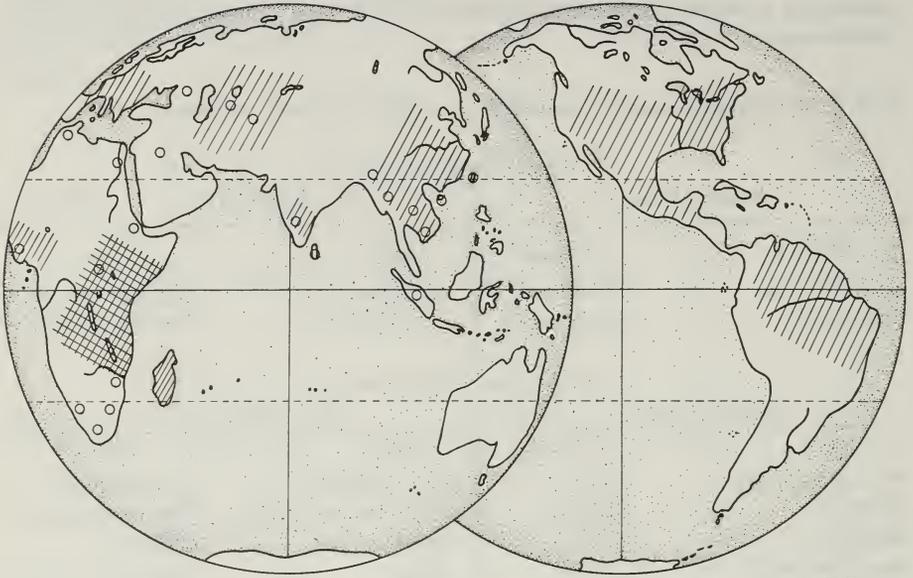
Mainland - Island Relationships			
Mainland Vicar		Island Vicar	
Name	Center	Name	Center
<i>Stenaptinus-Pheropsophus</i> (<i>sensu stricto</i>)	Ethiopian	<i>Aptinomorphus</i>	Madagascan
<i>Aptinoderus</i>	Africa	<i>Brachinulus</i>	Isla Principe

Historical zoogeography

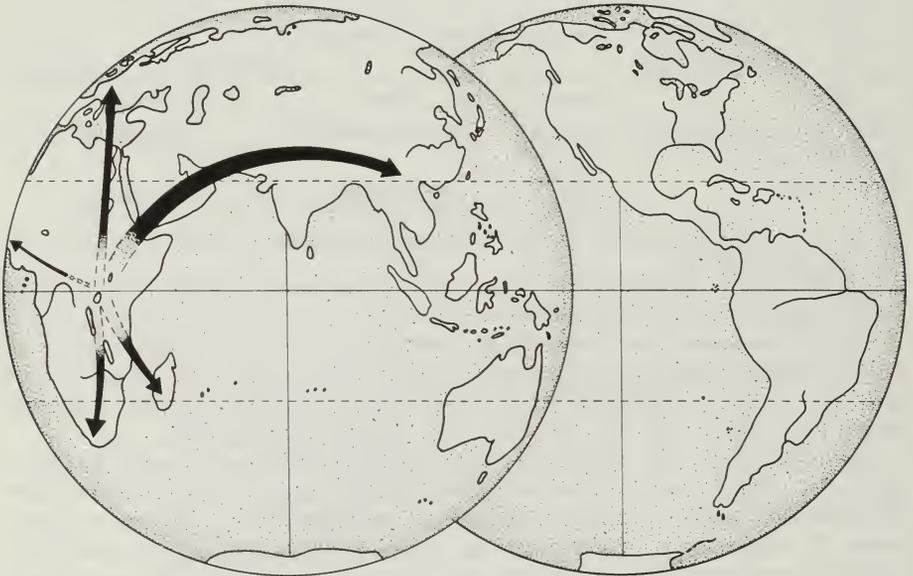
This section and the following present a series of hypotheses to explain the distribution pattern described in the preceding section.

I think the evidence clearly indicates that the bombardier beetles originated on the African continent, probably near the equator, or slightly further south. The separation of the primitive ancestor of bombardier beetles from its sister group probably took place in the middle to late Cretaceous, and after Africa and South America separated.

The timing of the initial bombardier beetle migration is based on two events. The first is the necessity that ancestral *Brachinus* and *Pheropsophidius* members arrived in South America before that continent became isolated in the early Eocene. This is discussed more fully below. The second event is the timing of the break-up of Gondwanaland. Most studies describe this event as occurring before the middle Cretaceous. If primary bombardier beetle radiation had occurred before the continents separated, probably more groups would be present in South America, but there is a general paucity of bombardier beetle genera in South America and Australia. Further, the South American forms are not closely related to any African groups. Since the middle Cretaceous, Africa has remained an unsubmerged and rather stable piece of land (Moreau, 1952, 1966), and it was here that bombardier beetles



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Fig. 453. Hypothetical primary (cross hatch) and secondary (single hatch) centers of radiation of the taxa of division Brachinida, and distribution of extant species of the genus *Mastax* (open circles); orthographic projection modified from Darlington (1957). Fig. 454. Hypothetical directions and routes of dispersal of the major taxa of the division Brachinida.

began their dispersal.

The primitive ancestor probably inhabited tropical savannahs as the crepidogastrines do today (Basilewsky, 1962a). From this center, radiation took place in at least five directions in the latter part of the Cretaceous. It was during this period that the ancestral lineage split into five stocks. However, these five stocks are not equal with the five major directions of dispersal. It was also during the late Cretaceous and early Paleocene that subtropical elements extended to at least 60° N (Axelrod, 1959). At this time these beetles were not restricted from northward migration by climatic conditions.

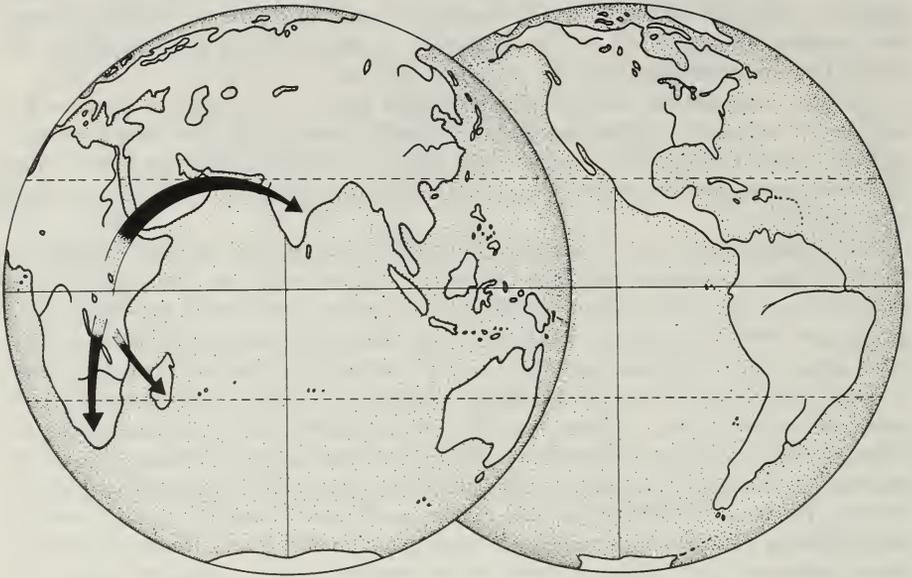
The five directions in which bombardier beetles made their prehistoric movements is indicated in figure 454. Various groups have evidently spread in the same directions but at different times. The pathways were probably diverse, but the directions were similar. Those directions and possible pathways are discussed in conjunction with each of the five radiating stocks, below.

The crepidogastrines were at one time more widespread (fig. 454), but they have become extinct except in southern India, and Ceylon (one species each). The crepidogastrines are the most primitive of the division Brachinida. All members are wingless and evidently the groups have been that way for a considerable time. No other group has undergone so extensive a reduction in flight components, therefore, I believe these beetles are similar in other respects to the ancestral bombardier beetles, although they have become apomorphous in numerous characteristics. I believe Jeannel (1949) is incorrect in his contention that the Indian-Madagascar-African distribution exhibited by these beetles indicates origin on the hypothetical landmass of southern India, Madagascar, and southern Africa called Lemuria. *Tyronia*, the genus represented in India, is the group that extends the furthest north in eastern Africa. Further, this group is not represented on Madagascar. There has probably been a withdrawal into Africa and India, with extinction in Arabia, during the development of intense desert conditions late in the Tertiary (Moreau, 1952). This would explain why *Tyronia* species are very similar in India and Africa.

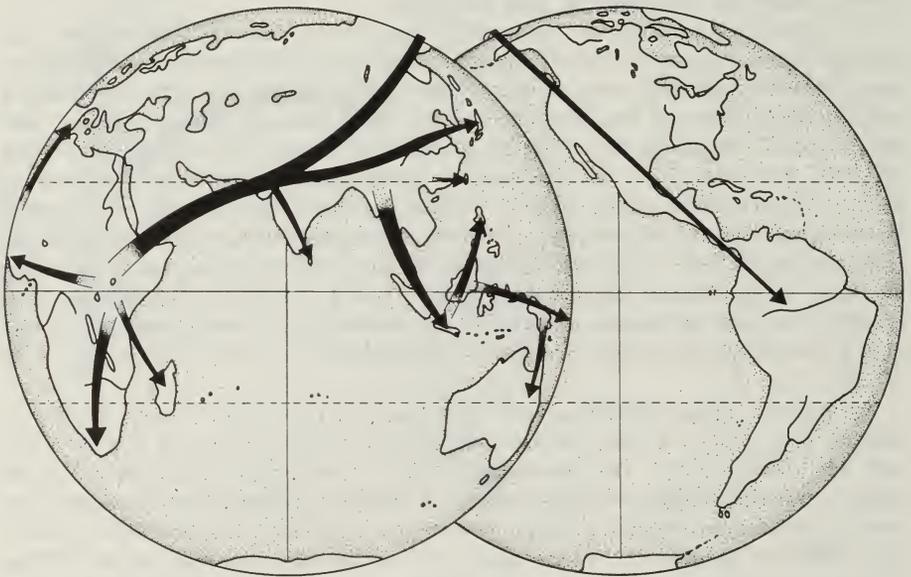
Two genera of Crepidogastrini occur on Madagascar. One of these, *Crepidolomus*, may represent the most primitive type of bombardier beetle species still in existence. Its members have a divided umbilicate series of setae in the eighth interval. This genus is endemic in southern Madagascar and may have been on the island before it became separated from Africa (near the beginning of the Tertiary according to Moreau, 1952; but see also Darlington, 1957: 519). The other genus occurring now on Madagascar is *Crepidogaster*, represented by three species. These species probably reached the island more recently, across water. However, Basilewsky (1959) does not state their relationships and I have not seen specimens.

Briefly, the history of the crepidogastrines has been one of early expansion at least to the edges of the Oriental Region, followed by a period of differential extinction. More recently, the group has become restricted to the southern and eastern parts of Africa, with only a few phylogenetic relicts occurring on Madagascar (four species) and in India (two species).

The ancestral lineage of *Mastacina* must have separated from its sister group, the Pheropsophina, very early. The many aberrant characteristics of this small group indicate a long and independent history. The distribution pattern of the extant species (fig. 453) also indicates isolation long ago. The pattern can be described as widespread, but consisting of at least 12 disconnected endemic pockets. Because of this pattern, it is very difficult to determine where the group arose. Its sister group, the Pheropsophina, probably arose in Africa, but the masticine-pheropsophine ancestral lineage may have been widespread. *Mastax* has as many species in Asia as in Africa. In order to judge where *Masticina* arose and how it dispersed, a thorough study of relationships of the species of *Mastax* must be undertaken. Faunal studies presently available should expedite this task, for example see Andrewes



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Fig. 455. Hypothetical directions and routes of dispersal of the taxa of the tribe Crepidogastrini. Fig. 456. Same of subtribe Pheropsophina.

(1924, 1930), Bates (1892), Jedlička (1963), Liebke (1934), Péringuey (1885, 1896), and Schmidt-Goebel (1846).

The subtribe Masticina is widespread, but the discontinuous pattern does not provide clues to past movements.

The species of Pheropsophina display a very complex distribution pattern (fig. 456). The most pleisomorphic species are now found only in southern Mexico and South America, but the group must have originated in Africa. Probably an original radiation of an ancestral *Pheropsophidius* group (with costate elytra like all other bombardier beetles) occurred in late Cretaceous or very early Tertiary times. This group was widespread and occurred in the eastern part of Asia. One species invaded the New World via the Bering Land Bridge. This probably occurred in the Paleocene when tropical conditions extended north nearly to 60° N. This species continued to spread southward and crossed into South America. The withdrawal of tropical conditions, and the closing of the Central American Land Bridge to South America isolated this primitive stock on both the north and south side of the bridge (but see also Hershkovitz, 1966). In the vast South American tropics it underwent secondary radiation, resulting in the extant species of *Pheropsophidius (sensu stricto)*. In Middle America, they withdrew to the southern slopes of the Sierra Madre del Sur, finally evolving into the wingless species of *Protopheropsophus*.

Meanwhile, in Africa, another more successful lineage arose with carinate costae on the elytra. An early member of this lineage invaded Madagascar and radiated there in isolation (*Aptinomorphus*). The rest of the lineage radiated and ultimately displaced the ancient *Pheropsophidius* lineage in Africa and Asia. By the time this wave reached the eastern part of Asia, the tropics had receded from the Beringian region, thus there was no chance for an invasion of the New World (even if the Bering Bridge was still in existence). Members of this second lineage (*Stenaptinus*) still exist as far east as Formosa, the Philippines, and New Guinea. These beetles subsequently became wingless and now show an endemic pattern (except in Africa, where they are widespread in the tropics). Finally, a third wave, the *Pheropsophus (sensu stricto)* lineage, overtook this second wave. It shows a continuous pattern of distribution throughout the tropics from west Africa to the Solomon Islands in the Pacific. Most members are winged and presumably highly vagile. These forms have moved into many continental islands and have occupied Madagascar. Species now living on the Comoro Islands indicate that those islands may have been the route by which bombardier beetles have invaded Madagascar (see also Darlington, 1957 : 520). The movement onto Madagascar, the Japanese Archipelago, Formosa, the Philippines, and other islands may have occurred more than once, since some of the islandic species are endemic, yet others are widespread on the Asian mainland. This is also true of the Indonesian fauna and the species of New Guinea. There has been at least one recent movement down the Malay Archipelago, engulfing most of the islands, and continuing to Australia. This movement probably took place in the Pleistocene when the seas were lower and the gaps between islands were narrower. The fact that one species reached Australia but has thus far diverged into only "varieties" indicates that this movement was rather recent.

Briefly, the history of Subtribe Pheropsophina has been one of wave after wave of more apomorphic groups, arising in Africa and spreading eastward into the Oriental Region. The first wave invaded the New World and is now confined to the Neotropical Region. The two successive waves have been successful island-hoppers, at least when water gaps were not too great. The *Stenaptinus* lineage has withdrawn into geographically isolated pockets, and the members have become flightless. The third wave is still dispersing, or was dispersing as recently as the Pleistocene epoch.

I suspect that these beetles also may be susceptible to dispersal by human agencies. The larvae of at least one species are ectoparasitoids on mole cricket egg clutches and occur in

paddy fields and other agricultural lands (Habu, 1967). Plants transported with soil may possibly carry these larvae or adults and their hosts into new areas.

The members of Aptinina probably had a very early dispersal into southern Europe from Africa (fig. 457). This early lineage subsequently became isolated and underwent changes common to mountain isolates (Darlington, 1943), as the *Aptinus* stock became fragmented in the changing mountain systems of southern Europe (Povolný, 1966). They became wingless and most became very darkly colored overall. One species, which still occupies the lowlands has members with a red prothorax, and the males have the median lobe contorted to the left.

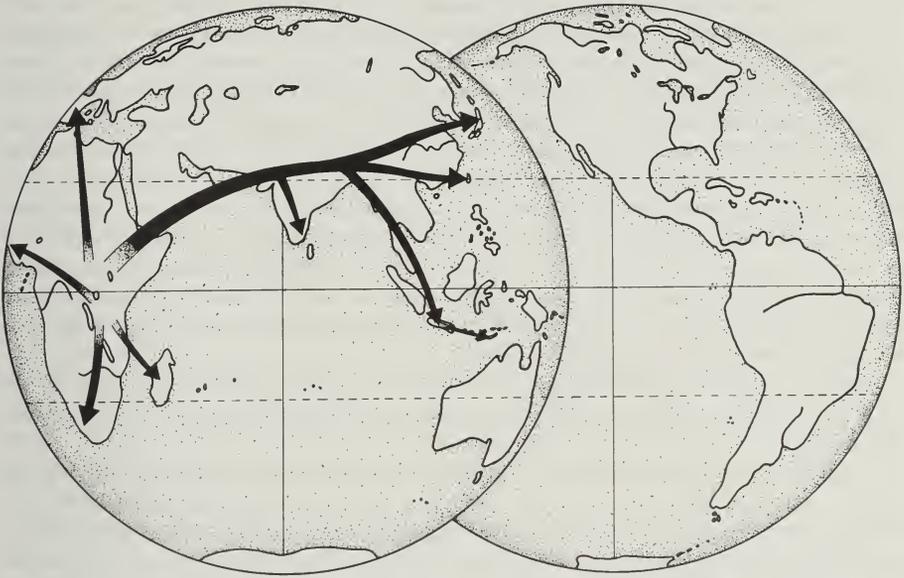
Concurrently, the vicariant sister group underwent considerable change and converged with the members of *Brachinus* in Africa. Since the original exchange, no dispersal of *Aptinus*, or *Styphlomerus* and its allies has occurred across the Mediterranean area. *Styphlomerus*, the most primitive of this African lineage, has either remained in Africa, or has withdrawn into Africa as the more advanced *Styphlomerinus* dispersed. This derived group (*Styphlomerinus*) has spread from Africa in two directions (fig. 457), extending south to Madagascar and east to Japan and the Malay Archipelago. Still another group emerged in Africa, probably from a *Styphlomerinus*-like ancestor, and subsequently displaced *Styphlomerinus* in Africa. This group, the *Styphlodromus*, are now still within the primary center of bombardier beetle radiation.

Briefly, the history of the Aptinina has been one of early dispersal into Europe, subsequent isolation of both groups, and secondary dispersal of the African lineage. During this secondary dispersal, some species have island-hopped at least onto continental islands.

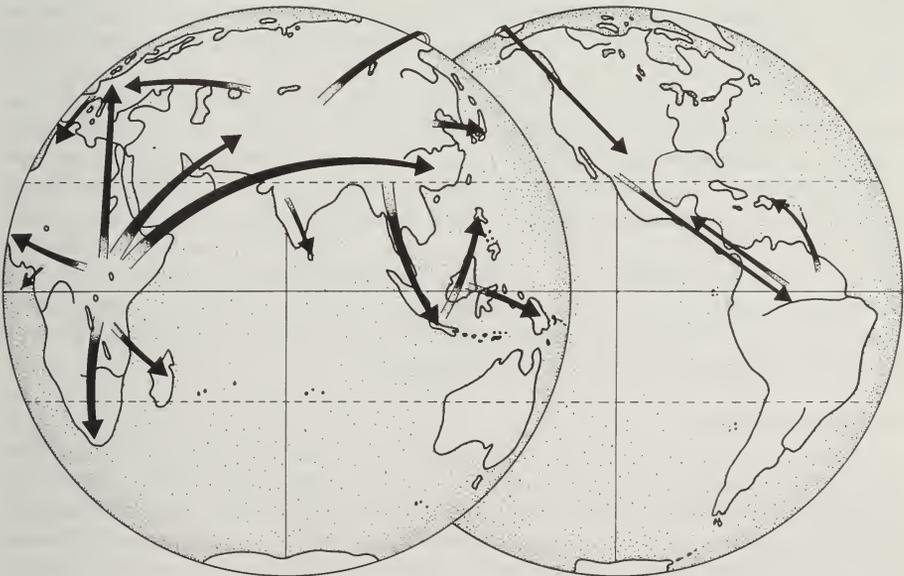
The members of Brachinina differentiated sufficiently long ago for one stock to have entered the New World via the Bering Land Bridge, when it was still tropical or warm temperate. This probably occurred about the same time that the *Pheropsophidius* ancestral lineage invaded the New World. The primary radiation from Africa must therefore have occurred sometime in the late Cretaceous or early Tertiary. Remnants of this early group (*Aptinoderus* and *Brachinulus*) are presently found in southern-most Africa and on the west African island of Principe, respectively.

These two groups represent the earliest radiation of Brachinina, and have probably been isolated and pushed to the periphery (fig. 457) of the original range by successive groups. The first of these successive groups was probably the "asymmetrical" lineage, which gave rise to *Brachinus (sensu stricto)*, *Brachynolomus*, and *Metabrachinus*. All three arose in middle Africa and radiated north, north and east, and south, respectively. *Brachynolomus* is widespread from Europe to New Guinea, while the range of *Brachinus (sensu stricto)* is narrow and confined to Europe. Both groups have subsequently invaded northwestern Africa, probably during the Pleistocene, since the species there are the same as in Europe. Both groups were replaced in Africa by the southern vicar, *Metabrachinus*. This group has invaded Madagascar at least once. The members of *Brachynolomus* that reached the Malay Archipelago probably reached New Guinea recently, because *B. papua* Darlington is hardly (if at all) different from *B. bigutticeps* Chaudoir of Java (Darlington, 1968). This may not be true of the Philippine species, as I have not seen mainland representatives of *Brachinus luzonicus* Chaudoir.

Concurrently with the origin and dispersal of the "asymmetrical" ancestral stock the second group referred to as the "symmetrical" lineage, arose in the primary center. An early offshoot of this lineage spread north into the area adjacent to the Caspian Sea, while another invaded Madagascar. Yet a third group of this symmetrical lineage radiated into many regions. One of these latter forms *Brachinoaptinus*, moved north into Europe, and subsequently invaded northwest Africa from there. It probably did so before *Brachinus (sensu stricto)* and *Brachynolomus*, since there are many differentiated species found only in this area, and all members of this lineage are wingless and highly endemic. Another symmetrical form,



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Fig. 457. Hypothetical directions and routes of dispersal of taxa of the subtribe Aptinina. Fig. 458. Same of subtribe Brachinina.

Aploa, moved to the periphery of the African continent, and east at least to India. These species appear to be adapted to desert conditions and probably have dispersed since the desert areas expanded during the late Tertiary. Various other lineages probably arose from this stock, but the relationships are still unclear (see Phylogeny). The early offshoot that spread into the region adjacent to the Caspian Sea underwent secondary radiation into *Cnecostolus* and *Neobrachinus*, and subsequently spread eastward and westward, respectively. At least one species of *Cnecostolus* spread to Europe, while another, the ancestral *Neobrachinus*, invaded the New World via the Bering Land Bridge. Once in the New World, extensive radiation occurred with at least one species (probably more) reaching South America. Subsequently, the Bering Land Bridge became broken or the climate changed, and no further exchange took place. Without more study of the Asian species of *Brachinus*, it is impossible to state whether *B. dryas* of Sikkim is a phylogenetic relict or a part of subgenus *Neobrachinus* that moved back across Beringia, after differentiating in the New World. Also the route to South America became broken and two brachinine stocks were isolated (*Brachinus* and *Pheropsophidius*), and became adapted to Neotropical conditions. In the North, members of these groups also existed, becoming temperate and desert types. The details of these patterns are discussed below.

Briefly, the history of the Brachinina has been very complex, and definite conclusions cannot be reached until these unnamed and unstudied African and Indian lineages are more fully studied.

In summary, the bombardier beetles have radiated from middle Africa in five directions. To the west each group sent a few species along the tropical west coast. One definitely endemic genus is found on the island of Principe in the Gulf of Guinea. At least one unnamed *Brachinus* lineage occurs in this area. Further south, primitive groups survived and became isolated. Madagascar has received members of seven groups, and is a center of secondary radiation on a small scale. One group spread to Europe from the region of the Caspian Sea, and four groups spread northward, including three lineages of *Brachinus* and the ancestral *Aptinus*. The three *Brachinus* lineages subsequently invaded the northwest coast of Africa.

The region of the Caspian Sea acted as a staging area preceding movements into the New World for *Neobrachinus*, and movement into Europe for *Cnecostolus*.

In general, all groups have spread at one time or another to the east. Very early the Crepidogastrini spread from Africa as far east as India and then withdrew, isolating some species in southern India. All other groups have spread eastward, three of these to Japan, and all four to the Malay Archipelago, two as far east as New Guinea, and one on to Australia. Two groups invaded the New World via the Bering Land Bridge sometime before the Eocene. Both groups spread to South America and became isolated on both sides of the Middle American Seaway until the Pliocene. At that time, southern groups began spreading northward, and northern groups possibly spread southward.

Evidence of barriers

Movement of animals can be restricted or halted by at least three kinds of barriers. The first kind of barrier is a physical obstruction, such as large bodies of water or mountain ranges. The second kind of barrier is one of unsuitable climate. The third type might be called an ecological barrier (including biological factors such as competition, etc.). The patterns of movements displayed by bombardier beetles have been greatly influenced by barriers. In this section, I analyze those movements in terms of the barriers indicated by studies of present and past geological and climatic conditions. I have consulted the following references: Andrewes (1929), Axelrod (1959), Ball (1959), Basilewsky (1962a), Cohn (1965), Darlington (1957, 1965), Espenshade (1964), Halffter (1964), Moreau (1952, 1966),

HersHKovitz (1966), Paulian (1961), Povolný (1966), Romer (1966), Savage (1967), Simpson (1947), and Woodford (1965).

Eighteen groups have dispersed from Africa during the history of the bombardier beetles. Movement to the north has been relatively slight, only four groups having spread into Europe from Africa. To me this indicates that an intensive and long-lasting barrier has been present. The two possible barriers are the Tethys Sea, early in the Tertiary, and the climatic conditions during the late Tertiary and Quaternary Epochs. Three of the four European groups are now confined to temperate conditions, while the fourth is wide-ranging both in temperate and tropical regions. These groups were probably able to cross the Tethys via temporary land connections early in the Tertiary and became adapted to temperate conditions later. The relatively small number of species and the general lack of diversity in the European fauna suggests that bombardier beetles have not been as successful in Europe as elsewhere. This may be a direct result of climate, aided by the slowness with which tropical groups adapt themselves to temperate climates.

Movement to the east has been more extensive, for nine groups have spread in this direction. This indicates some interruption of spread, but not nearly as severe as that which limited spread toward the north. Physical barriers have probably been more important between the Ethiopian Region and the Oriental Region than have climatic barriers. Geological evidence does not admit connections between Asia and Africa until the late Miocene, but birds, plants, and bombardier beetles indicate that some exchange must have occurred. Temporary and partial connections would explain why so few bombardier beetles have spread eastward early in the Tertiary.

The lineages that spread to the Oriental Region have all dispersed continuously over landmasses, with no barriers to stop them. However, the water gaps between the mainland and the Oriental islands have acted as partial barriers. No group has crossed extensive water barriers. The movement down the Malay Archipelago occurred at least twice, but both invasions probably occurred when sea level was lower and the water gaps narrower. This is substantiated by the pattern of distribution.

Movement to the New World occurred only after the climatic barrier in Beringia ameliorated during the early Tertiary as described below.

Minor barriers between species of *Neobrachinus* are discussed below. However, within the New World, the major barrier has been the water gap which existed in the past, between Central and South America. The patterns of distribution of both *Neobrachinus* and *Pheropsophidius* indicate that this barrier was in existence throughout a major part of the Tertiary (but see also HersHKovitz, 1966).

Movement to Madagascar from Africa seems to have occurred throughout the history of the bombardier beetles and therefore has occurred over water, at least in part. Madagascar has seven endemic groups, but it also has species of African groups that are hardly differentiated. One species of *Pheropsophus (sensu stricto)* occurs on Madagascar and some of the Comoro Islands. This may have been the route by which bombardier beetles have crossed into Madagascar. Movement of ancient ancestral lineages to Madagascar may have been direct, however, if that island was ever actually connected with Africa.

Movement into southern Africa has been uninterrupted, with fourteen out of eighteen groups moving in this direction from their Central African origin. The southern flow of bombardier beetles probably has been affected only by shifting climatic zones and surface relief changes.

Movement into western Africa has been very slight, with only six out of eighteen groups moving in this direction. This indicates that efficient barriers have always existed in the center of the African continent. Evidence indicates that the East African mountain systems and the arid belt west of those mountains have barred movements between lowland forests of

the east and west (Moreau, 1952). Several authors indicate this must have existed at least since mid-Pleistocene, and possibly much longer. The patterns of distribution of bombardier beetles indicate that there have been extensive mid-African barriers, at least since the early Tertiary.

The major limiting factor in the dispersal of bombardier beetles has evidently been climatic. Only six of twenty-seven groups have become adapted to temperate conditions in the north. Four of these are restricted to the temperate zone, while the other two still have tropical representatives. Physical barriers have also played an important role in the dispersal of these beetles, particularly between continents.

Distribution patterns of North and Middle American *Brachinus*

Introduction

The genus *Brachinus* is represented in all parts of North and Middle America south of 52° N. The present pattern of distribution is the result of climatic and physiographic changes throughout most of the Tertiary and Quaternary, roughly 60 to 70 million years. In the more northern latitudes of this area, the Pleistocene glaciations have probably affected these distribution patterns. In the southern latitudes, Pleistocene glaciations have probably indirectly affected the patterns in at least three ways: by changing drainage systems; by changing climatic patterns; and by pushing northern groups south into the habitats of the southern groups, and therefore into at least partial competition with these southern groups.

Much has been written about climatic and physiographic changes, and these changes in relation to animal distributions in North and Middle America. The following references have been consulted: Axelrod (1948, 1950, 1958, 1959); Ball (1956, 1959); Cohn (1965); Espenshade (1964); Graham (1964); Halffter (1964); King (1958, 1959); MacGinitie (1958); Martin (1958); Martin and Mehringer (1965); Ross (1965); and Whitehead (1965). Ball and Freitag (*in* Freitag, 1969), and Larson (1969) have briefly summarized the climatic and physiographic changes in relation to ground beetle movements.

Methods and general patterns

This section quantifies the data on the zoogeography of recent bombardier beetles in North and Middle America. The numbers of species in different parts of the area present various patterns and it is my object to discover possible factors influencing these patterns. I have attempted to parallel this section with the zoogeographical analysis of *Evarthrus* by Ball and Freitag (*in* Freitag, 1969) in order to test their methods in a comparison with highly vagile bombardier beetles (*Evarthrus* are all flightless). I think this comparison is a valid one because both *Brachinus* and *Evarthrus* are ground beetles and general omnivores, and are taxa of more or less equal rank.

The descriptions of species in *Neobrachinus* are accompanied by dot maps. Overlaying these dot maps with a grid map (fig. 459) provided a means of obtaining total numbers of species in each grid quadrant. The grid map of North and Middle America is divided into 5° intervals, both longitudinally and latitudinally. The number in each grid represents the total number of species recorded from that area, as determined by the dot maps. Based on methods proposed by Ball and Freitag (*in* Freitag, 1969), I have determined the "total interval values" (TIV) for each 5° interval of longitude and latitude (fig. 459 and table 10). Because of the greater extent of coastline involved in the distribution of subgenus *Neobrachinus* compared with that of *Evarthrus* studied by Ball and Freitag, I have used an "average landmass 5° interval value" (ALIV), rather than just an "average 5° interval value." The "average landmass value" was determined by dividing the "total interval value" (number of species in each 5° interval, both horizontally and vertically) by the number of intervals. The number of "landmass intervals" was adjusted at the coasts by approximating the amount of

land in the 5° x 5° interval to the nearest 25%.

The primary information derived from this grid map indicates that the number of species is maximum in southern Texas, slightly less in the American Southwest and Northern Mexico, and from those areas, it decreases in all directions, but subsequently increases slightly in Florida and the Great Lakes Region. The great reduction in numbers of species known from Central America is probably due to inadequate collecting in the area. The paucity of species from the Great Basin and Rocky Mountain region is less easily explained.

The alkali sinks of the Basin and Range Province of the Great Basin provide the aquatic habitats. Since most (if not all) *Brachinus* in North and Middle America are confined to water-side habitats, the high percentage of soil alkali may be restrictive. The fact that the few species occurring in the Great Basin are the most widespread in North America, indicates that these beetles are probably more tolerant to various conditions, and may be able to tolerate alkalinity. *Brachinus* populations in North and Middle America do not live at higher elevations in mountains. The few species within 5,000 to 7,000 feet elevation in New Mexico, Arizona, and Mexico are living in subdesert conditions on high plateaus. The Rocky Mountains provide a partial barrier, probably because they lack suitable conditions in which these beetles can live. This is apparently true of the southern Appalachian Mountains also, since only two species occur in these old mountains, both of which may not be restricted to waterside habitats.

The general reduction of species toward the north is perhaps due to Pleistocene glaciation and its effects on climate (Howden, 1969), however it should be noted that nowhere in the world do bombardier beetles extend very far beyond warm temperate conditions.

The general east - west pattern is one of reduction in both directions from the American Southwest. The east - west lateral asymmetry, with average species densities higher in the west, that Simpson (1964) shows for mammals is reversed in bombardier beetles. Numbers of breeding land birds is also much higher in the west (Robbins, et al. 1966, from MacArthur and Wilson, 1967). High numbers in the west for both birds and mammals can certainly be correlated with diverse topographic relief (as Simpson, 1964, states for mammals), but it is just this relief that eliminates lowland bombardier beetles from existing in these areas.

Secondary information derived from the grid map is used in determining the overall range of *Neobrachinus* species, the centers of concentration, and an analysis of vicariance.

It is interesting to compare the data given by Ball and Freitag (*in* Freitag, 1969) for the "flightless" members of the genus *Evarthrus* with that given below for the "highly vagile" members of most *Neobrachinus* species.

Table 10. Total number of species, "Average Landmass 5° Interval Values" (ALIV), and "Total Interval Values" (TIV) values derived from figure 459.

°N	#spp.	ALIV	TIV
A	0	0	0
a	0	0	0
B	9	6.6	20
b	3	1.2	5
C	13	5.8	26
c	16	4.5	50
D	19	6.5	35
d	26	10.8	114

Table 10 (cont.)

°N	#spp.	ALIV	TIV
E	32	11.6	61
e	39	13.5	129
F	32	9.8	72
f	39	15.3	115
G	45	21.2	106
g	38	20.5	72
H	33	15.3	73
h	28	26	52
I	29	11.2	57
i	20	16.7	39
J	24	19	56
j	2	4	3
K	21	10.8	38
k	2	4	3
L	17	11.5	33
M	4	5	5
N	0	0	0

Table 11 expresses the index of range extent, determined by a linear measurement between the two furthest localities on the dot maps. The four species known from only one locality (*B. capnicus*, *B. explosus*, *B. ichabodopsis*, and *B. mobilis*) were omitted from this analysis. If the species are divided into three general categories, 35 per cent of the species have ranges less than 1,000 miles in extent, 39 per cent have ranges between 1,001 and 2,000 miles and 19 per cent have ranges of more than 2,000 miles in extent. *Evarthrus*, on the contrary has nearly 50 per cent of its species ranges extending less than 500 miles, and only 11 per cent of the *Brachinus* species have ranges covering less than 500 lineal miles.

The restricted ranges of *Evarthrus* species suggested to Ball and Freitag that either (1) barriers to dispersal existed, or (2) that many of the ranges of the *Evarthrus* species are less extensive than they used to be, and the species are surviving as relics. In *Brachinus* only 11 per cent of the species fit into these categories. The extensive ranges of 89 per cent of *Brachinus* species in North and Middle America are probably less restricted by physical barriers than they are by broad climatic zones. The relationships between centers of concentration (in fig. 460) and broad climatic zones are discussed below.

Table 11. Frequency distribution of maximum linear extent of geographical range in miles of the species of *Brachinus* of North and Middle America.

Class	Number	Percentage
2,501 - 2,750	5	
2,251 - 2,500	5	19%
2,001 - 2,250	2	
1,751 - 2,000	9	
1,501 - 1,750	2	
1,251 - 1,500	8	39%
1,001 - 1,250	5	
751 - 1,000	11	
501 - 750	4	
251 - 500	3	35%
1 - 250	4	
1 locality only	4	6%

In order to locate centers of concentration, a second grid map was made by plotting only species with ranges of less than 1,000 miles. The ranges were examined for concordance, and centers of concentration were discovered. Each interval containing one or more species was lettered. Subsequently, these lettered squares were combined to provide the centers of concentration (fig. 460), and described in Table 12. The distribution of all species was compared with these centers as indicated in Table 13.

Table 12. Centers of concentration of the species of *Brachinus*.

Center Number	Limits
1	Pacific coast states, in California west of Sierra Nevada crest, north of Tehachapi crest.
2	Southwestern deserts (including southern California south of the Tehachapi), Arizona, New Mexico, western Texas west of 100° W, and northwestern Mexico including Baja California del Norte and the Mexican Highplain.
3	Great Plains between 90° W and 105° W, 45° N, and 35° N.
4	Central and Southern Texas
5	Southern Mexico around the Bahia de Compeche and eastern Yucatan.
6	Northeastern United States and southern Great Lakes Region.
7	Southeastern United States east of the Mississippi River, south of 35° N.
8	Greater Antilles

Table 13 (cont.).

Name of Species	Center Number							
	1	2	3	4	5	6	7	8
<i>puberulus</i>				X				
<i>favicollis</i>		X						
<i>perplexus</i>			X	X			X	
<i>velutinus</i>	X							
<i>imperialensis</i>		X	X	X				
<i>cordicollis</i>		X	X			X		
<i>cyanochroaticus</i>	X		X			X		
<i>sublaevis</i>		X	X	X		X	X	
<i>ichabodopsis</i>								X
<i>oxygonus</i>			X	X				X
<i>fulminatus</i>						X		
<i>vulcanoides</i>						X	X	
<i>janthinipennis</i>			X	X		X		
<i>mobilis</i>								X
<i>explosus</i>		X						
<i>aabaaba</i>		X	X	X				
<i>sonorous</i>		X						
Totals:	10	34	25	25	12	21	20	2

These centers were then compared with each other by means of an index of difference (Ball and Freitag, *in* Freitag, 1969; Greenslade, 1968). Of 28 comparisons, only one scored 100, that is, a pair of centers shared no species in common. Five scored between 95 and 99, or between 90 and 94, respectively. By adding the sums in Table 14 (the indices of difference) for each center, an overall "index of dissimilarity" was obtained (Table 15). Centers 1, 5, 8 are the most distinct, probably because of their peripheral positions. Centers 3 and 4 have the lowest indices of difference (59) and indices of dissimilarity. This is probably due to their central position.

Center 8 is actually an artifact of these comparative methods because it includes two species, one of which also occurs in northern South America. The other species is represented by one very old specimen labelled "Cuba." This species is common throughout Florida and the southern United States and may have been collected in Cuba, aboard ship, or may be mislabelled. This "Center" will probably become important when the distribution of the South American fauna is studied.

Centers 3 and 6 share many species (Index 61), but between these centers the species of Center 6 display a pattern of subtraction westward through Center 3, and those of Center 3 display a pattern of subtraction eastward through Center 6. This pattern probably is the result of the separation of these centers by Pleistocene glaciation (Ross, 1965). Center 3 corresponds roughly to "Kansan" and "Illinoian" mammal provinces of Hagmeier and Stults (1964), while Center 6 corresponds to their "Canadian" mammal province.

Table 14. Dissimilarity values among centers of concentration of the genus *Brachinus*.

Center Number	Statistics	Center Number						
		2	3	4	5	6	7	8
1	t*	44	35	34	22	31	29	12
	c**	6	5	4	3	5	3	0
	t - c	38	30	30	19	26	26	12
	t-c/t x 100	86	86	88	86	84	90	100
2	t		59	58	46	55	53	36
	c		13	13	9	11	7	1
	t - c		46	45	37	44	46	35
	t-c/t x 100		78	78	80	80	87	97
3	t			49	37	46	44	27
	c			20	3	18	12	1
	t - c			29	34	28	32	26
	t-c/t x 100			59	92	61	73	96
4	t				36	45	43	26
	c				4	15	13	1
	t - c				32	30	30	25
	t-c/t x 100				89	67	70	96
5	t					33	31	14
	c					3	2	1
	t - c					30	29	13
	t-c/t x 100					91	94	93
6	t						40	23
	c						11	1
	t - c						29	22
	t-c/t x 100						73	96
7	t							21
	c							1
	t - c							20
	t-c/t x 100							95

* = total number of species in each pair of centers.

** = number of species in common between each pair of centers.

Table 15. Index of dissimilarity among centers of concentration of the genus *Brachinus* in North and Middle America determined from Table 14.

1.*	Center 8	673
2.	Center 5	625
3.	Center 1	620
4.	Center 2	586
5.	Center 7	582
6.	Center 6	552
7.	Center 4	546
8.	Center 3	545

* = arranged in order from most dissimilar to least dissimilar center.

Centers 4 and 7 also share many species (Index 70), but not as many as would be expected in view of the fact these Centers occur within the same climatic zone. Between these Centers is the Mississippi River, but it is highly doubtful that this relatively narrow body of water is a barrier to these highly vagile beetles. However, the long-standing Mississippi Embayment probably was a barrier, and only recently has an exchange of species apparently occurred between the centers. As in Centers 3 and 6, a pattern of mutual subtraction exists for the species of Centers 4 and 7. Center 7 corresponds to the "Australoriparian" mammal province of Hagmeier and Stults (1964) while Center 4 corresponds to their "Texan" province.

A striking correlation exists between the centers and broad climatic zones within North and Middle America. Center 1 (roughly the "Californian" and "Oregonian" of Hagmeier and Stultz) has a dry summer subtropical or Mediterranean climate, broadly referred to as a humid mesothermal climate. The northern portions of Center 1 are Marine West Coast climates with cool summers. Center 2 (a complex of many mammal provinces) has dry climates referred to as steppes and deserts. The southern portions are subtropical steppes and deserts. Center 3 has a humid continental climate with warm summers and with rainfall throughout the year. This is broadly referred to as a humid microthermal climate. Center 4 has a humid subtropical climate with warm summers and with rainfall throughout the year. This is part of the humid mesothermal climate. Center 5 (the "gulf arc component" of Martin, 1958) has a tropical rainy climate and is composed of both tropical rain forest and tropical savannahs. Center 6 has a humid continental climate with cool summers and with rainfall throughout the year. This is part of the humid microthermal climate. Center 7 has the same type of climate as Center 4. Center 8 has the same type as Center 5. The limits of these centers correspond very well with the limits of the broad climatic zones as defined by Espenshade (1964).

In summary, bombardier beetle movements are hardly influenced by physical barriers. Their high vagility allows them to pass over or around most barriers present now, and in the past, in North and Middle America. One notable exception may have been the Mississippi Embayment, in the past. The eight centers of concentration illustrated in figure 460 have apparent boundaries that are climatic in nature. It is interesting to note that in the same area (North and Middle America) mammals have at least 48 provinces defined by various authors, while bombardier beetles have eight. Also, *Evarthrus* has eight, but just in eastern North America. *Evarthrus* "Centers" 1, 5, 7, and 8, and part of 3 and 4 correspond to *Brachinus* Centers 7, 4, 3, and part of 6, respectively.

Historical Zoogeography

The lack of fossil evidence of members of *Brachinus* in North and Middle America dictates that the history of this group must be interpreted by indirect means. Using the data given above, and that in Phylogeny, a hypothetical reconstruction of the history of the group can be made. The time of entrance into the New World was discussed above. The subsequent history of the New World species may be deduced from their present distribution, seeming dependence upon broad climatic zones, and vicariant sister groups.

The ancestral lineage probably entered North America in the early Tertiary when conditions of climate and relief were much different than they are now. Subtropical conditions extended to 60° N and the great inland Cretaceous Sea extended almost to the present Canadian border (Axelrod, 1958). North of that sea, as well as further east, Arcto-Tertiary Geoflora elements predominated, while in the west the Neotropical-Tertiary Geoflora predominated. The Cretaceous Sea was rapidly retreating from its epicontinental position. In the area now called the American Southwest, the Madro-Tertiary Geoflora was arising.

Rapid spreading of the ancestral *Brachinus* lineage must have taken place in a southerly direction in order for at least one species to have invaded the South American Continent before it became separated from Middle America in the Eocene by a water gap. As a result of this water gap there was only a very little amount of faunal exchange (if any) between Middle and South America for a long period of time. This has resulted in the distinctive South American fauna of today, and in the pattern of subtraction displayed by some of these South American forms (*texanus* group, *lateralis* group, *sallei* group, *brunneus* group and *grandis* group), as they have recently spread northward into Mexico and rarely into the southern United States.

During the Eocene and early Oligocene, supplemental angiosperm flora was added to the flora already existing in the southeastern United States (Graham, 1964). The nature of this flora was tropical, and with it probably came elements of the tropical fauna existing in the southwestern United States, including the ancestral stock of the *alternans* group. It is probably from these areas in the southwestern and southeastern United States that subsequent radiation spread species into the Arcto-Tertiary habitats of the north and east (*cordicollis* group, *fumans* group in part), into the newly forming Madro-Tertiary habitats of the west (*costipennis* group, *hirsutus* group, *fumans* group in part, *explosus* group, and *aabaaba* group), and the subsequently formed grasslands and savannahs (*kansanus* group, *fumans* group in part). From those centers, the geographical history of the North and Middle American bombardier beetles is untraceable because of the lack of fossil clues, the predominantly sympatric distribution of a majority of extant species, and the lack of habitat data which might be used to trace histories of stenoecious species. However, the distribution of extant sister species may provide evidence of locations of former or present barriers, if the sister species are parapatric or allopatric. Only 12 pairs of *Neobrachinus* species have these types of distribution, but they provide information which might suggest how diversity has been generated in the North and Middle American *Brachinus*.

Among the extant sister species of North and Middle American *Brachinus*, two types of vicariant relationships exist. These are east - west and north - south relationships and are listed in Table 16. These taxa are discussed below in phylogenetic sequence. The widespread distributions of the other species of *Brachinus* in North and Middle America does not even allow speculation concerning their geographic origins. The acquisition of additional habitat data may alter this situation in the future. For example, if species are restricted to marshes or to river drainage systems, then the histories of these habitats may provide clues to the history of the beetles.

Table 16. Distribution patterns of allopatric sister species of the genus *Brachinus* in North and Middle America.

East - West Relationships			
Western Vicar		Eastern Vicar	
Name	Center	Name	Center
<i>mexicanus</i>	1, 2, 3, 4, 5, 6	<i>kavanaughi</i>	2, 3, 4, 6
<i>javalinopsis</i>	2, 4	<i>neglectus</i>	7
<i>imporcitis</i>	2	<i>phaeocerus</i>	2, 3, 4, 6
<i>sonorus</i>	2	<i>aabaaba</i>	2, 3, 4
<i>melanarthrus</i>	5	<i>brunneus</i>	8

North - South Relationships			
Northern Vicar		Southern Vicar	
Name	Center	Name	Center
<i>gebhardis</i>	1, 2	<i>galactoderus</i>	2, 5
<i>cibolensis</i>	2	<i>cinctipennis</i>	2
<i>pallidus</i>	1	<i>hirsutus</i>	2
<i>cordicollis</i>	2, 3, 6	<i>sublaevis</i>	2, 3, 4, 6, 7
<i>fulminatus</i>	6	<i>oxygonus</i>	3, 4, 7
<i>texanus</i>	3, 4, 6	<i>rhytiderus</i>	4, 5
<i>velutinus</i>	1	<i>imperialensis</i>	2, 3, 4

The species *B. texanus* and *B. rhytiderus* of the *texanus* species group are derivatives of a South American complex which began spreading northward, probably in the Pliocene. *B. rhytiderus* (fig. 110) is essentially a species of the humid tropics, but in the north it has spread into thorn scrub. *B. texanus* (fig. 108) is essentially a species of woodlands, grasslands, and temperate humid forests, but in the south it enters thorn scrub. This area of thorn scrub was probably vast grassland during late Pliocene times (Cohn, 1965). It is possible that the ancestral stock was separated by grassland conditions into a northern and southern component and subsequent development of thorn scrub on both sides of the Rio Grande River may have allowed these groups to become parapatric in southern Texas. The limited movement into thorn scrub areas by both groups was probably secondary. Further study may show that the present occurrence in the thorn scrub is along river courses with more luxuriant vegetation rather than the surrounding thorn scrub.

Speciation of the *brunneus* group probably occurred in South America but there is no evidence of exactly where this took place. One sister species, *B. brunneus* (fig. 134) has spread northward along the Lesser Antilles to at least Haiti in the Greater Antilles, while the other sister species, *B. melanarthrus* (fig. 132) spread northward into Mexico and presently occupies the "Gulf Arc."

The species of the *hirsutus* group (*B. pallidus* and *B. hirsutus*) have been only recently separated and have diverged little in their morphological characteristics. The members of *B. pallidus* (fig. 218) are distributed in the Mediterranean climatic zone of California, north

of the Tehachapi Mountain range, while the members of *B. hirsutus* (fig. 220) are distributed on the High Plateau of Mexico and in the American Southwest. The development of intense desert conditions in the Pleistocene in the area of southeastern California and western Arizona probably separated this lineage, and speciation occurred. The northern group became adapted to humid coastal conditions and the southern group became adapted to subdesert conditions in the Mojave and Chihuahuas Deserts.

The species of the *cinctipennis* subgroup are presently distributed on the Mexican High Plateau, in southern Arizona, and in New Mexico. The two sister species are closely related, and any factor that separated them must have developed rather recently. Martin (1958) suggested that a continuous woodland corridor connected the Sierra Madre Oriental and Occidental. Cohn (1965) supported Martin's findings. This corridor probably existed across northern Durango and Southern Coahuila in the Pliocene and early Pleistocene. Such a condition may have separated populations of the ancestral *cinctipennis-cibolensis* stock long enough for speciation to occur. *B. cinctipennis* (fig. 221) may have become a centrant (see below) species during that time, for it has not spread northward. But *B. cibolensis* (fig. 219) did spread southward, extending as far as Durango City. (The actual ranges of the two species do not overlap, however).

Two species of the *quadripennis* subgroup exhibit sister relationships and are parapatric, however, the extent of overlap is such that definite statements cannot be made. It appears that the Rocky Mountains and southern deserts may be partial barriers to the eastern or western movements of *B. mexicanus* (fig. 252), and full barriers to the westward movements of *B. kavanaughi* (fig. 253).

Two other species of the *quadripennis* subgroup exhibit east - west vicariance and are presently separated by the Mississippi Embayment region. Inundation of the Mississippi River Valley in the Pleistocene (Ross, 1965) may have separated a once widespread southern species long enough so that speciation occurred. This also may explain why Centers 4 and 7 are relatively distinct (Index 70), but still occur within the same broad climatic zone. The species confined to Florida became "centrants" (Ball and Freitag, *in* Freitag, 1969) by loss of variability, due in turn to reduction in population size in a small confined area. On the other hand, the species west of the Embayment had a large area over which to spread, and became "radiants." The species *B. neglectus* (fig. 255) of the southeast, and *B. javalinopsis* (fig. 254) of the southwest display this type of distribution.

Two sister species of the *phaeocerus* subgroup exhibit east - west vicariance. They are presently separated by the Chiricahua Mountains, Peloncillo Mountains, and San Francisco Mountains of eastern Arizona and western New Mexico. *B. imporcitis* (fig. 278) occurs in the west and *B. phaeocerus* (fig. 279) in the east, and the two species meet and apparently hybridize in the narrow Gila River system between the Peloncillo and Chiricahua Mountain ranges. Separation of these two species must have occurred long ago, because the western group (*imporcitis*) has reduced wings, and is also quite different in several morphological and color characteristics. Further north in Colorado, *B. phaeocerus* does not cross the Rocky Mountains. The orogeny of the Arizona mountain systems mentioned above in the Late Pliocene-Pleistocene (Cohn, 1965) may have separated the ancestral stock, and more recently *B. phaeocerus* has extended its range into the Gila system. The more northern Rockies have probably always been a barrier to *B. phaeocerus*.

The species of the *gebhardis* subgroup (figs. 332, 333) display the pattern described for *hirsutus* group, presumably for the same reasons given in that discussion. The same is true for *B. velutinus* (fig. 367) and *B. imperialensis* (fig. 364) of the *fumans* subgroup.

Two species pairs of the *cordicollis* group (figs. 391, 392, 414, 416) display north - south vicariance in the eastern half of the United States. It is difficult to discuss any prehistoric physical barriers that might have brought about separation in these cases, but there are

presently possible climatic barriers. It also is possible that speciation was brought about during glacial stages when species now widespread were restricted to more southern pockets.

The present distributions of the species of *Brachinus* in North and Middle America are influenced by broad climatic zones. Development of the present distribution patterns has been mainly under the influence of climatic changes, and to a lesser extent physical barriers.

The climatic changes that have had much influence are those which developed in the American Southwest and on the Mexican High Plateau. Physical factors that have had much influence are the orogeny of the various western mountain ranges, the inundation of the Mississippi River Valley, and the separation of the Great Plains from eastern North America by glacier lobes.

The major center (fig. 460) of North and Middle American *Neobrachinus* dispersal has been the American Southwest and northern parts of the Mexican High Plateau. Minor centers (fig. 460) include the southeastern United States, probably in peninsular Florida, and in the northeastern United States. From these centers dispersal has occurred as follows. Centers 1, 3, 4, and 6, and possibly 7, have received species from Center 2. Center 1 has received species mainly from Center 2, but also from Centers 3 and 6. Center 6 has received species from Centers 2, 3, and 7. Centers 5, and 8 have received species from South America.

Thus each center has received species from other centers (addition); each center has lost species to other centers (subtraction); and species of each center have differentiated within that center (multiplication). Within these centers, differentiation has taken place resulting from climatic shifts which, in turn, shift the centers of concentration, and hence, at least part of the fauna. These shifts result in isolation of older "pocket" groups (centrants) in the former range and new terrain in the acquired range. During these climatic fluctuations, isolation results in speciation. To a lesser extent in bombardier beetles, geological changes have resulted in isolation which in turn has led to speciation.

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Book Review

KARLSTROM, THOR N. V. & BALL, GEORGE B. (editors). 1969. The Kodiak Refugium: Its Geology, Flora, Fauna, and History. Ryerson Press, Toronto, for The Boreal Institute, University of Alberta, xvi + 262 p., 1 plate, 28 figs. \$10.00.

One of the authors contributing to this small book notes that it is not often that refugia are first proposed on geological grounds alone; yet this is the case with the small area of southwest Kodiak Island which was ice free during the last two glaciations of the island. The book shows that the ice free area served as a biotic refugium.

Carl Lindroth, discusses in one of the early chapters the different types of Pleistocene refugia and the history of the concept of refugia. Later he contributes chapters on the carabid beetles of the Kodiak refugium and a summary of the conclusions of all of the contributing authors. Another paper by George Ball discusses in detail the probability of survival and evolution of a subgenus *Cryobius* of carabid beetles in the Kodiak refugium. Eric Hultén deals with the implications of the distributions of higher vascular plants, but his chapter also includes much information on the flora of all of Kodiak Island. Other papers contribute less information concerning the Pleistocene biota of the refugium, but like Hultén's paper are of value because they document the present biota. H. Persson's chapter on the Kodiak bryophytes and D. K. Hilliard's chapter on the Chrysophyceae are of this sort. In another chapter, Ball and Lindroth using the taxonomic determinations of numerous specialists, provide a list of the invertebrates collected in the refugium and detailed information on collecting localities. Vertebrates of Kodiak Island are discussed by J. D. McPhail, dealing with fishes, and R. L. Rausch, dealing with mammals. A lengthy chapter by Thor Karlstrom outlines the geological basis for the Kodiak refugium.

Because their distribution and ecology are relatively well known, carabid beetles and the higher plants provide the best evidence for the survival of a terrestrial biota in the Pleistocene Kodiak refugium. Ball and Lindroth show that the fauna of the refugium includes flightless carabid beetles adapted to alpine (arctic) environments. Presently these insects are restricted to the alpine areas of the refugium, but during the glaciation of Kodiak Island, they probably occupied lowland sites. Hultén's data for plants is of a similar nature.

Karlstrom suggests that faunal exchange between Kodiak and the mainland could have occurred either in the Sangamon interglacial or during a mid-Wisconsin "interglacial." The alpine (arctic) adapted beetles which survived glaciation of the island in the refugium are thought by Ball to have immigrated during the Sangamon interglacial. But world-wide evidence shows that interglacial climates were as mild or milder than the present. Lowland habitats of Kodiak Island and the adjacent mainland would have been similar to those of today or perhaps even forested. I find it difficult to believe that flightless alpine (arctic) carabid beetles could have moved through such habitats to Kodiak Island. The waters separating Kodiak Island from the mainland would have posed another formidable barrier for certain elements of the present fauna. Ball assumes that there must have been an interglacial land connection, but higher sea levels concomitant with an interglacial would enlarge rather than diminish the sea barrier.

None of the authors have dealt explicitly with this dilemma, even though the explanation is rather obvious. The alpine beetles now found in the Kodiak refugium could have invaded

the island during a glacial advance from an ice marginal refugium on the now submerged continental shelf. Lowered sea levels during major glaciations and submerged linear features on the continental shelf near Kodiak (interpreted as moraines by Karlstrom) make this suggestion highly probable. An ice marginal area would by definition possess a periglacial climate suitable for occupation by arctic and alpine adapted species of beetles. At some time during the advance of glaciers on Kodiak Island and the nearby Alaska Peninsula or perhaps during an interstadial, the continental shelf refugium could have extended from the inner Aleutian Islands to southwest Kodiak Island. This seems to be the logical explanation for the strong Aleutian affinities of the Kodiak refugium fauna as noted by Lindroth. Further glacial advances isolated the Kodiak refugium and probably obliterated large areas of the shelf refugium.

In as much as sea levels were 60 feet lower than at present as late as 8000 years ago, the continental shelf areas may have also been important for the postglacial colonization of the island.

It is unfortunate that Karlstrom did not explore some of these possibilities. Bathymetric maps of the areas near Kodiak, and the Alaska and Kenai Peninsulas, or diagrams indicating the probable extent of unglaciated, emerged continental shelf under various hypothetical combinations of glaciation and sea level would have been much more pertinent to the theme of this book than world wide correlation charts (p. 37) or the table listing data for a Potassium Argon analysis of the granitic intrusives of the island (p. 28).

The ages of the last two glaciations of the island are critical since it was during these events that the refugium was large enough to support a terrestrial biota. It is unfortunate that Karlstrom has no C^{14} dates to substantiate his claim that both are of Wisconsin age. His correlation of a marine unit separating the drifts of the last two glaciations on the island with the mid-Wisconsin Woronzofian sediments in the Cook Inlet may be incorrect since the Woronzofian sediments have reached their present position as a result of tectonism, a process that Karlstrom feels was not important near the refugium. Correlation of the interval between the Ikpik and Olga Bay advances of the last (Akalura) glaciation on Kodiak Island with the Two Creeks oscillation of Northern Europe (p. 34) is unjustified. I feel that such correlations must be based on C^{14} dated sedimentary sequences. As noted above, the Kodiak sequence is totally lacking in C^{14} dates.

Finally I object to Karlstrom's use of the term interglacial for the climatic oscillation represented by the Woronzofian transgression. Most geologists consider this world wide event to be an interstadial. Moreover, foraminifera from the Woronzofian sediments in the Cook Inlet area show that water temperatures were colder than at present, a conclusion consistent with interstadial rather than interglacial conditions.

My only technical complaint about this book is that the map showing the distributions of moraines surrounding the refugium is practically illegible. Otherwise I think it very fortunate that all of these papers could be printed in one volume. But I hope that the book is not considered to be the final statement on the Kodiak refugium. Hultén rightly suggests the need for pollen analytical studies. In addition a comparison of soil development and weathering in the refugium and other glaciated areas of the island would be interesting. I have already stated the need for more detailed geological investigations.

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Quaestiones

entomologicae

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

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Book Review

CHAPMAN, R. F. 1969. *The Insects — Structure and Function*. American Elsevier Publishing Company, Inc., New York. Library of Congress Catalog No. 71-75216. xii + 819 pp., 509 text fig., c. 1000 refs., \$15.00.

This book is a welcome addition to the literature on insect structure and function.

Chapman has considered these two topics under six major sections: the head, ingestion and utilization of food; the thorax and movement; the abdomen, reproduction and development; the cuticle, respiration and excretion; the nervous and sensory systems; and the blood, hormones and pheromones. Each section is further subdivided. For example Section E, "The Nervous and Sensory Systems" has the following chapters; the nervous system, the eyes and vision, sound production, mechanoreception, chemoreception, and temperature and humidity. Further subdivision occurs within each chapter, each beginning with a general discussion in which significant literature and review articles are cited.

A book of this type, with such a wide scope, will no doubt be disappointing to some specialists but it is aimed at the post-graduate not the specialist. The layout and arrangement of the material in this book makes it an excellent reference text. However, the documentation in parts of the text is not adequate and this leaves the origin of some statements in doubt.

There are also some surprising deficiencies in places. For instance in the generally adequate chapter on the head and its appendages, the sucking mouthparts are dispensed with in two paragraphs and one figure, with only scant mention being made of the Hemiptera and Diptera. Again, the chapter on reproduction is generally very good but is weak on spermatogenesis and oogenesis.

Chapman's style of writing is telegraphic and he inserts specialized terms in the text with little or no explanation. This results, at times, in the text being difficult to follow. However, in a reference book of this type such a style is acceptable. The line diagrams, taken from many different sources, are clear and very well labelled. However, the scraperboard technique used in some instances, particularly for cellular detail, does not do justice to the original figures.

Despite these criticisms this book is, in overlapping areas, as good as Wigglesworth's "The Principles of Insect Physiology". Many of the comparable chapters by Chapman are more extensive and up-to-date than those by Wigglesworth, for instance those on the integument and mechanoreception. For these reasons Chapman's text will, for some uses, supplant that of Wigglesworth.

This well-produced book should be on the shelf of everyone who teaches entomology or who considers himself a serious entomologist. Chapman's book is not only a particularly good, up-to-date reference book but is relatively good value.

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SOLITARY WASPS FROM SUBARCTIC NORTH AMERICA —
I. POMPILIDAE FROM THE NORTHWEST TERRITORIES AND YUKON, CANADA

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Questiones entomologicae
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Spider wasps (Pompilidae) of 19 species were collected in the Northwest Territories during part of the summer in 1967 and 1968 and in Yukon, during part of the summer in 1968. Previous locality records of 6 species in the literature have been added to the list. A list of sample localities is given and discussed in relation to general and local geographical, physiographic, geological, and ecological features of the study areas and adjacent regions. Distribution and composition of this fauna are analyzed in the light of known zoogeography of spider wasps. Holarctic elements and elements with circumpolar distribution are well represented. The range of distribution of some transcontinental elements is surprisingly broad, including regions as far south as California, Arizona, New Mexico, Texas and Mexico. Some northern extensions reach the Arctic Coast area (on the Mackenzie Delta), at least within its subarctic portion in Northwest America, and along the favorable axis of dispersion of the Mackenzie River System.

Fossorial wasps thrive particularly in tropical, subtropical, and warm temperate climates, wherever soil, moisture, and vegetation are adequate. Northern and even Subarctic regions, however, are by no means devoid of hunting wasps; moreover, some species or groups are seen predominantly or exclusively in these areas. Some bees range to the Arctic and High Arctic, in North America to Ellesmere Island for instance (Hocking and Sharplin, 1964, 1965).

Therefore it seemed interesting to obtain some information — limited as it may be — on the northern distribution and composition of wasp faunas, Pompilidae in particular, and on some associated physiographic, geological and ecological features. All sampling localities visited by me are situated south of the Arctic Circle (see Fig. 1).

GENERAL PHYSIOGRAPHIC, GEOLOGICAL, AND ECOLOGICAL PROFILES

The boundaries of the Subarctic Region (see Fig. 1) are not always clear cut, especially the southern one. To the north, the tree-line is generally considered the approximate boundary with the Arctic Region. The interpenetration of trees and tundra, however, complicates the pattern.

Fossorial wasps were collected in two areas: the Great Slave Lake area (Northwest Territories) (Figs. 1:2 and 2) and the Southern Yukon Territory area (Figs. 1:3 and 3). The former only is generally included in the Subarctic Region, the latter being considered part of the Cordilleran Region and Intermontane Belt. At first view, the characteristic features of the regions considered and in particular the Subarctic Region do not look very favorable for solitary wasps.

Most of the area lies on the forest-tundra transition or is covered with the boreal forest and the taiga, characterized by the dominance of coniferous trees (mainly spruce and jack pine) in its climax communities. Often the conifers grow so close together that there is very little understory and the soil, covered with mossy vegetation, is not directly accessible to fossorial wasps. The muskeg and the general post glacial topography, characterized by many lakes, bogs, and poorly drained surfaces, does not seem to provide a very good habitat for fossorial wasps either. The situation seems more favorable for fossorial wasps in clear-

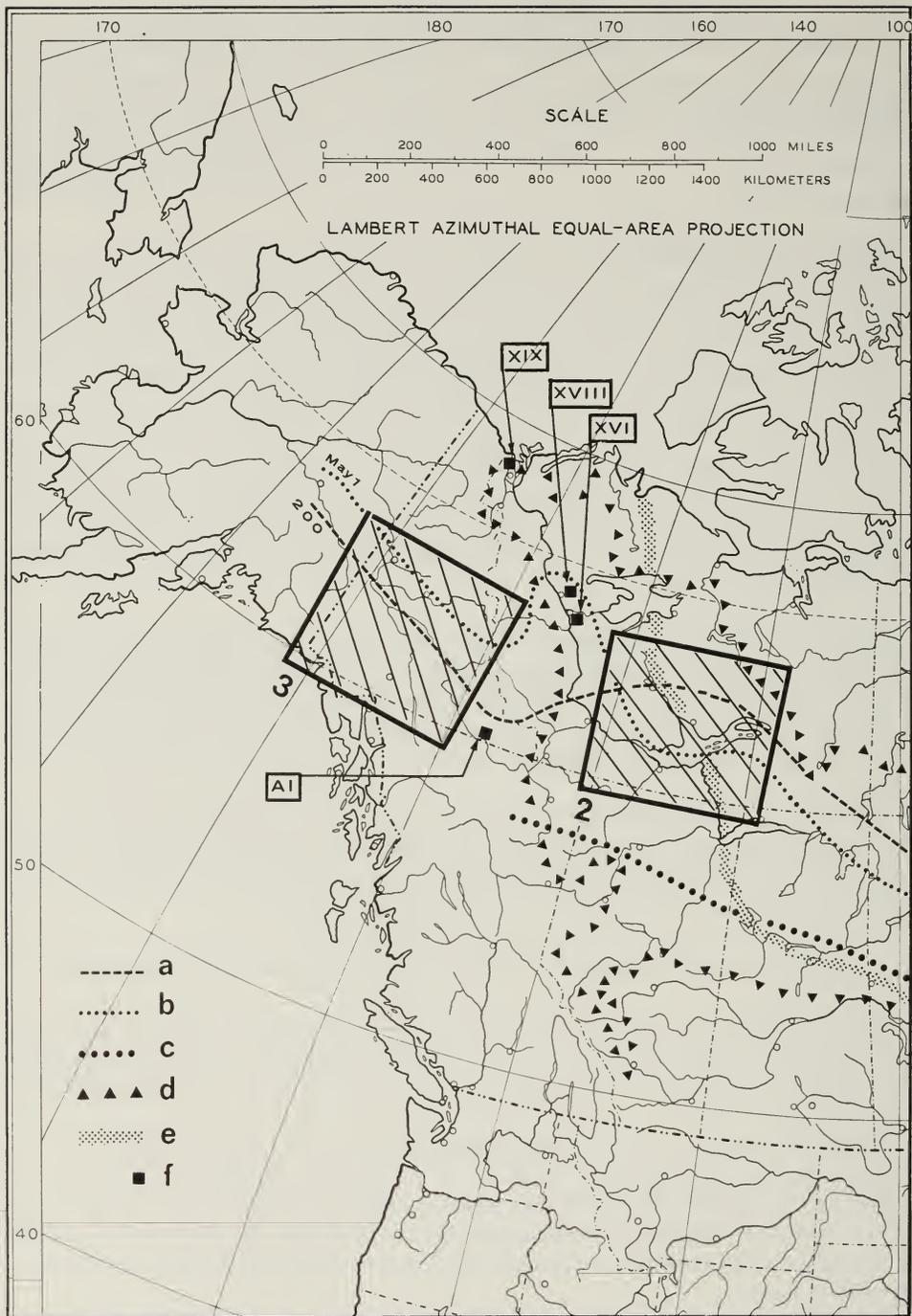


Fig. 1 Northwest America: Great Slave Lake (Fig. 2) and Yukon (Fig. 3) study areas hatched. *a.* mean annual number of days with snow cover one inch or more (adapted from Laycock, in Warkentin, 1968); *b.* average day on which mean daily temperature rises to 32°F (adapted from Laycock, in Warkentin, 1968); *c.* approximate southern limit of discontinuous permafrost (after Brown, in Wonders, 1968); *d.* approximate delimitation of "Subarctic Region" (adapted from Wonders, in Warkentin, 1968); *e.* approximate delimitation of western margin of the Canadian Shield (adapted from Wonders, in Warkentin, 1968); *f.* sample localities in previous literature (Evans, 1950-1951) and situated outside study areas 2 and 3; Northwest Territories: XVI = Fort Norman; XVII = Cameron Bay of Great Bear Lake (not represented); XVIII = Norman Wells; XIX = Reindeer Depot. Yukon Territory: A1 = Watson Lake.

ings, sand, gravel pits, along ridges, hillocks, roadsides, river banks, lake shores, fixed sand dunes, some old dugouts, and forest edges. The forest cover is locally interrupted or eliminated altogether in disturbed areas where early successional stages are found. Most of the wasps collected were found in such natural or man-made disturbed areas.

The climate, at first view, does not seem to provide a better picture than physiography: the long and severe winter in Subarctic Regions (at least in the northwest) is generally as cold as in the Arctic with even lower extreme temperatures. Discontinuous permafrost underlies much of the Subarctic (Warkentin *et al.*, 1968); the first study area (Great Slave Lake) lies entirely north of the southern limit of discontinuous permafrost. The growing season is short, varying from approximately 60 to 150 days, through the continental taiga. The summer, however, is often very hot, with long daylight hours, favorable to rapid development of plant and animal life. Insects, in general, are abundant. Favorable microclimates for solitary wasps are provided by river banks, lake shores, and sandy areas.

The mean daily temperature for the various months or mean daily minimum or maximum temperatures are often used to express the amount of energy in the environment available for the conversion of minerals and moisture into plant tissue. The length of the growing season is especially important for plant and animal life. A detailed study of climate and meteorological conditions is beyond the scope of this paper (see current literature). Some limited meteorological information is condensed in Figs. 1, 2 and 3. Exploitation of favorable microclimates (Hocking and Sharplin, 1965), the short favorable summer, and an efficient resting stage for overwintering, probably allow the wasps to cope with these severe conditions (see also Fuller, 1969).

Geological and soil conditions seem far from optimal. In the Subarctic Regions, much of the surface was totally stripped of regolith and soil by glaciation, leaving pockets of morainic debris, ponds, muskegs, and poorly drained soil. The last is typically a grey thin podzol usually cold (at least on the shield portion of the area). However one also finds in this region lighter, sandier soils of kame or lacustrine origin (Warkentin *et al.*, 1968) which probably are a more favorable habitat for fossorial wasps, particularly in the form of sand ridges, cleared areas, lake shores and river banks. The Great Slave Lake area lies partly on the podzol zone, in the east on the Canadian Shield, and partly on the grey wooded soil zone, which also is from a podzol type, west of the Shield. The soil conditions in the Yukon study area are more complex with considerable variety of slope, altitude, and cover.

THE GREAT SLAVE LAKE STUDY AREA (FIGS. 1:2 AND 2)

This area is subdivided geologically and physiographically into two distinct parts: the Canadian Shield and the circum-Shield plains and plateaus. Most of the sample localities are in the latter part, but localities XII, XIII, XV, (Fig. 2) are on the Shield.

The Canadian Shield, a vast expanse of Precambrian gneisses and granites has undergone a complex geomorphic evolution. In the shield region of the study area, north and northeast of Great Slave Lake, the Shield is included in the Kenoran orogenic region, whereas the eastern part (east of the Slave River) and a limited part of the north belong to the Hudsonian orogenic region. In this part of the study area, predominantly rocky, the soil cover is particularly restricted, both in depth and expanse. However, some "islands" of favorable soil, particularly around lake shores (localities XII and XIII, Fig. 2) have been found. Reduction of forest cover in many areas may also influence favorably colonisation by fossorial wasps. The vegetation in the Shield region of this study area is classified as "forest and barren", forest section 27 (Northwestern Transition Section, a subdivision of the Boreal Forest Region) (Rowe, 1959). "It is a zone of open subarctic woodland where unfavorable

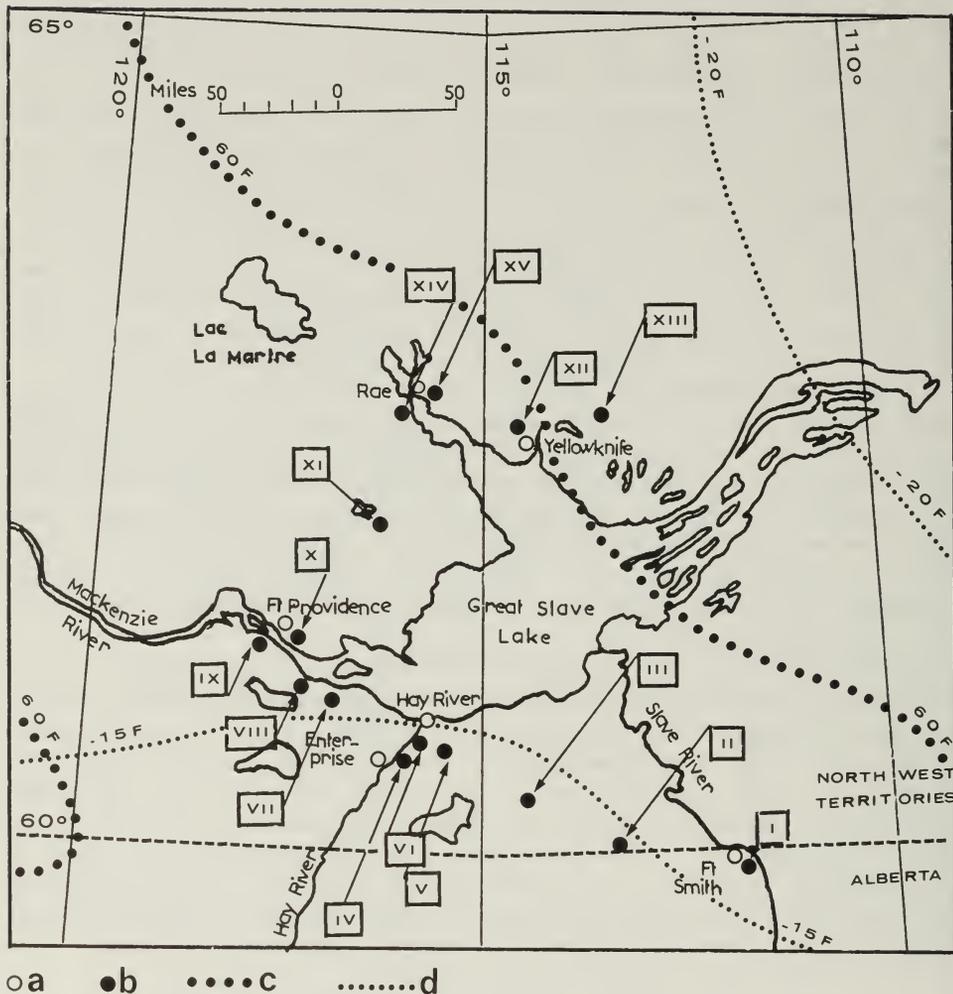


Fig. 2. Great Slave Lake study area. a. towns; b. sample localities visited; c. mean daily temperature for July; d. mean daily temperature for January (c and d adapted from "Yukon today", 1968; source: Meteorological Branch, Department of Transport). I = Fort Smith; II = Sass River; III = Wood Buffalo Park northern boundary; IV = Enterprise; V = Buffalo River; VI = Banks of the Hay River; VII = Heart Lake Biological Station; VIII = Kakisa River banks; IX = Fort Providence, South; X = Fort Providence, North; XI = Birch Lake; XII = Yellowknife; XIII = Yellowknife-Prelude Lake; XIV = Frank Channel; XV = Rae.

climatic conditions, thin soil, and frequent fires have combined to reduce distribution, abundance, and size of tree species; . . . open stands of dwarfed trees, with local patches of sheltered, deep, frost-free soil where density and high growth of forest patches can be surprisingly good;" . . . most abundant tree: black spruce (*Picea mariana* (Mill.) B. S. P.), sometimes white spruce (*P. glauca* (Moench) Voss) tamarack (*Larix laricina* (DuRoi) K. Koch) jack pine (*Pinus Banksiana* Lamb.); . . . southern parts: stunted aspen (*Populus tremuloides* Michx.) balsam poplar (*Populus balsamifera* L.). All in all (except for some species and locally), the Shield part seemed the less favorable.

The circum-Shield plains (western interior basin) part of the study area belongs to a sedimentary basin which fringes the Shield, on the west. The sedimentary cover varies in thickness, age, and landforms; Devonian reef structures can be found for instance on the southwest part of the Great Slave Lake area. More detailed information is provided in the list of sample localities. The banks of the Mackenzie River, near Fort Providence, seemed to offer particularly good soil, climate, (microclimate?), and vegetation cover. Therefore, these banks were searched intensively and successfully for fossorial wasps (sample localities IX and X). In the sedimentary part of the study area, the vegetation is classified as "Upper Mackenzie Section of the Boreal Forest" (Rowe, 1959, 23a): white spruce and balsam poplar form the main cover types on alluvial flats bordering rivers; large areas of sandy soils are occupied by pines (*Pinus Banksiana*, *P. contorta* Dougl. var. *latifolia* Engelm.), aspen, and in moist to wet positions, black spruce and tamarack. Alluvial flats are bordered by low benchlands and terraces giving way to undulating or rolling uplands with isolated ridges and low hills; there are large areas of swamp and peat.

In the following list, the localities sampled are arranged in a series of increasing latitude, to facilitate detection of possible impoverishment in number of species with latitude. Each locality is preceded by its identification numeral on the maps. The plus sign indicates localities not prospected by me, but found in previous literature. Species collected are represented by their identification number in list of species (the same applies to the list of localities from the Yukon study area, given later). Sources of geological information used are Brown, 1958, Geological Survey of Canada, 1955 and Jolliffe, 1942.

Characteristics of sample localities and conditions of sampling

I. *Fort Smith* (Mountain Portage-Slave River banks, 59° 58' N, 111° 45' W, 700-750' elevation).

Description. — Sandy banks, terraces, cutbanks, pits; many natural and man-made disturbed areas, with early successional stages.

Geology. — On sand, silt or drift covered area, probably contact between: west, Palaeozoic-Silurian (mainly sedimentary rocks: dolomite, limestone, etc.) and east, Archaean (Cambrian?): granodiorite, granite, etc.; mainly acid rocks.

Conditions of sampling. — 15 August 1967; clouded over, some sun, some rain. Sampling probably not very significant (weather, short duration).

Species collected. — 1 (numbers refer to species list below).

II. *Sass River (Wood Buffalo Park)* (road to Fort Smith, 60° 10' N, 113° 30' W, approx. 900-950' elevation).

Description. — Sandy roadside, early successional stages (man-made disturbed area); represents clearing in forest cover.

Geology. — On Palaeozoic — Middle Devonian (limestone, bituminous limestone, dolomite).

Conditions of sampling. — 14 August 1967; warm, sunny weather, wind moderate. Sampling probably not very significant (short duration).

Species collected. — 3.

III. *Wood Buffalo Park northern boundary* (road to Fort Smith, 60° 28' N, 114° 35' W, approx. 900-950' elevation).

Description. — Same as II.

Geology. — Situated approximately on limit between geological areas described in II and IV.

Conditions of sampling. — 14 August 1967; warm, sunny, wind moderate.

Species collected. — None.

IV. *Enterprise* (about 20 miles north of Enterprise, on highway to Hay River, 60° 40' N, 116° W, approx. 850-900' elevation).

Description. — Clearing (man-made?) in wooded banks of the Hay River (aspen predominant); early successional stage, soil apparently favorable, soft, sandy, gravelly.

Geology. — On Palaeozoic — Upper Devonian (Simpson Formation, shale).

Conditions of sampling. — 28 July 1967; stormy weather threatened, but sunny at times — 11 August 1967; warm, cloudy, sunny at times, very strong wind. Sampling probably not very significant (weather, short duration, time of day).

Species collected. — 1.

V. *Buffalo River* (road to Pine Point, from Hay River, 60° 45' N, 115° 05' W, approx. 800-850' elevation).

Description. — Sandy clearing (man-made?) in wooded road sides; early successional stage.

Geology. — Same as IV.

Conditions of sampling. — 14 August 1967; warm, sunny, wind moderate. Sampling probably not very significant (short duration).

Species collected. — 15, 17.

VI. *Banks of the Hay River* (near Hay River, Pine Point road junction, 60° 45' N, 115° 50' W, approx. 500-550' elevation).

Description. — Sandy spots, banks; loose flat earth and compact cutbanks; variety of vegetation covers, ranging from densely forested (spruce, aspen, etc.) to sparsely covered with vegetation in early successional stages.

Geology. — Same as IV.

Conditions of sampling. — 29 July 1967; weather average — 12 August 1967; clouding over rapidly and becoming completely overcast; wind increasingly strong. Probably not very good sampling conditions.

Species collected. — 1, 12.

VII. *Heart Lake Biological Station area* (Hart Creek, road to Fort Providence, 60° 50' N, 116° 35' W, approx. 800-850' elevation).

Description. — Apparently favorable soft sandy earth, in open wooded banks of the creek; trees with important understory, shrub, herbaceous.

Geology. — Same as IV.

Conditions of sampling. — 10 August 1967; very hot, sunny, windy.

Species collected. — 5, 15, 22.

VIII. *Kakisa River Banks* (Mackenzie Highway, 61° N, 117° 15' W, approx. 650-700' elevation).

Description. — River banks, apparently not very favorable compact earth, although sparse vegetation (early successional stage) seems adequate.

Geology. — Same as IV.

Conditions of sampling (probably very unfavorable). — 10 August 1967; very hot, sunny, windy.

Species collected. — None.

IX. *Fort Providence* (South bank of Mackenzie River, 61° 17' N, 117° 36' W, approx. 500' elevation).

Description. — Rather compact earth, variety of vegetation cover conditions ranging from open forested areas (aspen mainly) to shrub and sparse herbaceous vegetation.

Geology. — Same as IV (but alluvial deposits).

Conditions of sampling (probably not very significant). — 1 August 1967; very good weather, hot, sunny, slight wind.

Species collected. — 7, 21, 24.

X. *Fort Providence* (North bank of Mackenzie River, 61° 17' N, 117° 30' W, approx. 500' elevation).

Description. — Apparently very favorable area, with a great variety of vegetation conditions; soil of various types and conformations: sandy spots, hillocks, small ridges, flats, etc.

Geology. — See IV and IX.

Conditions of sampling. — Probably the most complete sample of the study, with samplings taken frequently, on various days ("season") and at various times, weather conditions, etc. 21 July 1967 — 22 July 1967; overcast day, wind from W. — 25 July 1967 — 26 July 1967 — 31 July 1967; amelioration of weather, previously rather bad for one to two days — 9 August 1967; sunny, hot day — 11 July 1968; sunny, windy, very hot, a few clouds, hazy, intense activity of Hymenoptera recorded — 17 July 1968; excellent weather, sunny, warm, no wind.

Species collected. — 1, 4, 5, 7, 9, 12, 15, 17, 20, 25.

XI. *Birch Lake area* (roadside, Mackenzie Highway, about half way between Fort Providence and Rae, 62° N, 116° 17' W, 650-700' elevation).

Description. — Rather small gravel, sand pit (with some slated rocks), along the highway, in forested area (jack pine mainly?): sparse vegetation, herbaceous, shrubs.

Geology. — On Palaeozoic — Middle Devonian (limestone or dolomite).

Conditions of sampling (probably not very good). — 2 August 1967; very hot, sunny, moderate wind, some light clouds at high altitude, rain storm on nearby Great Slave Lake in the evening — 8 August 1967; clouding over rapidly but increasingly warm.

Species collected. — 5.

XII. *Yellowknife* (mostly shores of Long Lake, 62° 27' N, 114° 23' W, approx. 650. elevation).

Description. — Apparently one of the restricted favorable localities found on the Shield section of the study area, with spots of sandy soil covered with low, sparse vegetation (herbaceous and shrub, dwarfed trees); however flowers very scarce (in contrast to Mackenzie River localities: IX and X).

Geology. — Archaean (granodiorite, granite, etc.; also sand and silt, or drift covered areas).

Conditions of sampling. — Average to good, but perhaps affected by generally cold weather and strong wind. 4 August 1967; cool, windy, but sunny (cold, cloudy and windy the day before with short sunny periods) — 5 August 1967 — 7 August 1967; cold, strong wind, sunny — 29 July 1968; sunny, very hot, hazy, wind rather strong.

Species collected. — 7, 12, 16, 18, 23, 25.

XIII. *Yellowknife area* (shores of Prelude Lake, 62° 32' N, 113° 48' W, approx. 600-650' elevation).

Description. — One of the best spots found on the Shield section: local conditions apparently very favorable, as far as soil conditions (soft earth, sandy spots) and vegetation cover are concerned; the latter ranges from open woodland (jack pine predominant?) to sparse shrub and herbaceous vegetation; flats, hillocks, and sand pits provide a good variety of topographical microclimates.

Geology. — Archaean (Yellowknife group, mainly sedimentary and derived metamorphic rocks).

Conditions of sampling (apparently average to good). — 6 August 1967; sunny, cloudy periods, strong rather cold wind — 7 August 1967; weather better than previous day, mostly sunny, moderate wind.

Species collected. — 1, 6, 8, 12, 15, 16, 21, 22.

XIV. *Frank Channel* (shores of Great Slave Lake: northwestern arm, near Rae, 62° 43' N, 116° 03' W, approx. 600' elevation).

Description. — Sandy spots on shores of lake; apparently favorable area, flowers and vegetation varied; clearings, pits, etc.

Geology. — Palaeozoic — Ordovician (dolomite, red arenaceous limestone, sandstone, etc.).

Conditions of sampling (average to good). — 8 August 1967; weather good but increasing cloudiness — 26 July 1968; sunny, warm, clouding over.

Species collected. — 1, 3, 12, 15, 25.

XV. *Rae* (about 10 miles East, on the road to Yellowknife, 62° 46' N, 115° 50' W, approx. 500-550' elevation).

Description. — The northernmost sampling locality in the Great Slave Lake study area; transition between Shield and sedimentary sections; rather restricted pit, with flat sections, cutbanks, in rather compact and not sandy soil; man-made disturbed area, early successional stages; apparently not very favorable.

Geology. — Archaean.

Conditions of sampling. — 8 August 1967; sunny, windy.

Species collected. — 5, 22, 23.

The following localities have been found in previous literature: (Evans, 1950-1951); being not included in the study area (Fig. 2), they have been represented on the general map, Fig. 1. Species identification numbers preceded by + represent species which have not been found by me.

XVI. + *Fort Norman* (Mackenzie River, approx. 65° N, 125° 30' W).

Geology. — Cenozoic — Tertiary (shale, conglomerate, sandstone, limestone, coal).

Dates. — 6, 9, 15 August.

Species collected. — +10, +13, +14, 23, +26.

XVII. + *Cameron Bay* (Great Bear Lake? not represented on map).

Dates. — 1 July.

Species collected. — +10.

XVIII. + *Norman Wells* (Mackenzie River, approx. 65° 30' N?, 127° W).

Geology. — Palaeozoic — Upper Devonian (Imperial-Bosworth-formation; sandstone and shale).

Dates. — 12 July — 3 August; 20-28 July; 20-29 July 1949; 12-23 August.

Species collected. — 6, 9, +11, 15, +19.

XIX. + *Reindeer Depot* (Mackenzie Delta, approx. 67° 20' N?, 134° 20' W).

Geology. — Cenozoic — Pleistocene and recent (alluvium, glacial drift).

Dates. — 8 July 1948; 11 July; 12 July — 13 August.

Species collected. — 1, 12, 15, 17.

THE YUKON STUDY AREA (FIGS. 1:3 AND 3)

The climatic, geological, and ecological features of the Yukon study area are much more complex and varied than the preceding one. On the other hand, the sampling in this area has been limited and is probably less significant.

Most of the sampling localities are situated in one "geological province", characterized by intrusives, plateaus, rocks ranging in age from Precambrian to Recent (Anon., 1968). This area, of low to moderate altitude is part of the physiographic "Intermontane Belt" region of the Cordilleran Continental Façade. This belt is underlain largely by folded Jurassic strata and Tertiary volcanics and composed of low mountains, rolling hills, tablelands dissected by rivers, and flat glacial lake plains. No samples have been taken from the mountain regions, south, north and east in the Yukon Territory. The sampling area is situated mostly on the basin-like area known as the Yukon Plateau in the interior of the Territory. The average elevation is 2,000 to 3,000 feet. There is a certain lack of precipitation in this interior basin.

The climate is characterized by wide variations in temperature from year to year. One reason is the proximity of both the relatively warm Pacific and the cold Arctic Ocean. The climate thus depends on the frequency and duration of air mass invasions. The same applies to summer temperatures. These characteristics may affect the populations of fossorial wasps and may produce important year to year population fluctuations. On the average the last spring frost occurs in mid-June and the first autumn frost in mid-August. Annual precipitation is low in the Yukon, which is in the "rain shadow" of the mountains bordering the Pacific.

Forest types found in the study area are classified (Rowe, 1959) as Dawson, Central Yukon, Eastern Yukon, and Kluane sections of the Boreal Forest Region. Sample localities A, C, D (Fig. 3) are situated in the Central Yukon section (26b), where white spruce grows on the lower slopes of protected lowlands. On the uplands, it associates with alpine fir (*Abies lasiocarpa* (Hook.) Nutt.). On the mountain slopes are islands of park-like white spruce, willow and aspen interspersed with patches of grassland. In the valleys, on water modified tills and coarse terrace materials lodgepole pine (*Pinus contorta* var. *latifolia*) and white spruce are the dominant species, frequently associated with aspen. Black spruce occupies areas of high water table. Sample localities E, G, (Fig. 3) are included in the Eastern Yukon Forest section (26c) where forestless barrens are more common, and north and east slopes frequently non-forested. Flood plains are generally narrow in the sharply cut valleys with low representation of balsam poplar. Peaty soils are extensively developed. Sampling stations I, J (Fig. 3) belong to the Dawson Forest section (26a) comparable to the Central Yukon section but lodgepole pine has only a scattered distribution. Surface deposits are mainly residual, derived from breakdown of the underlying Precambrian and Tertiary rock. Sample localities A3, B, B2 (Fig. 3) are in the Kluane Forest section (26d) characterized by a dry cold climate, with park-like appearance vegetation. White spruce and poplar are abundant. There is no lodgepole pine and relatively little black spruce.

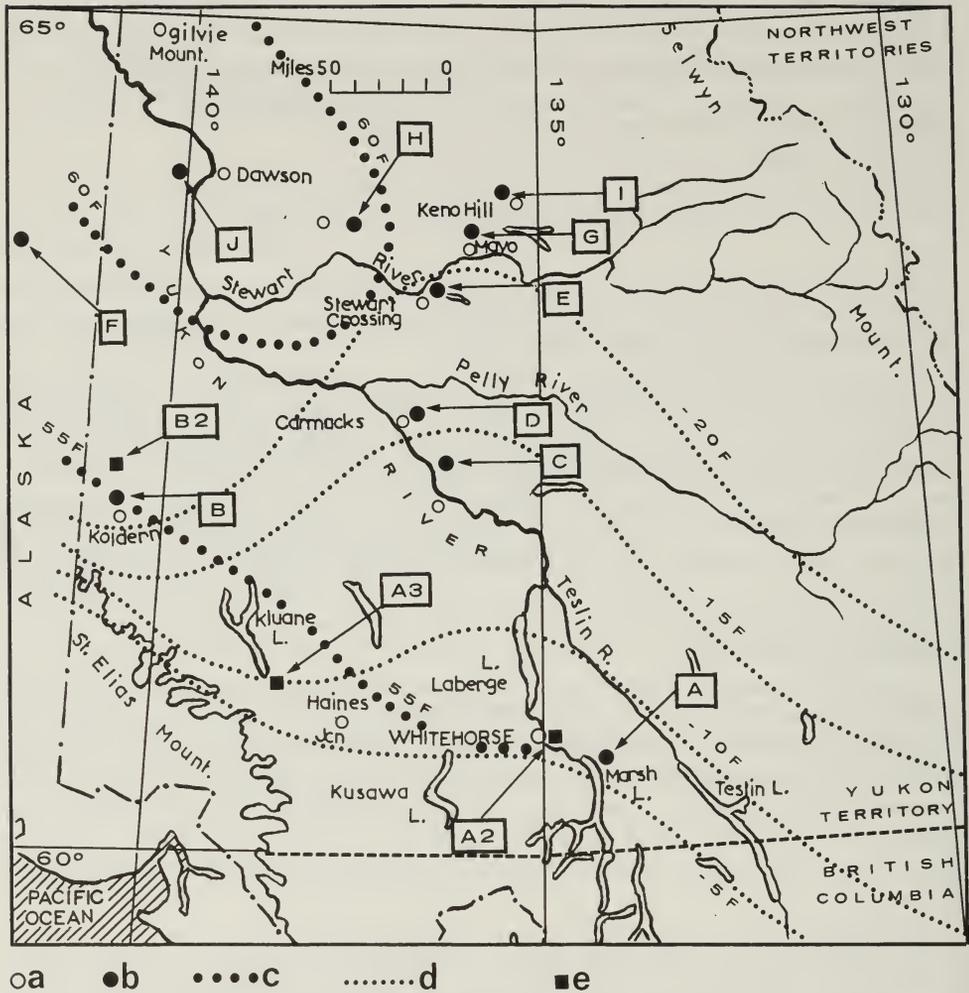


Fig. 3. Yukon study area. *a.* towns; *b.* sample localities visited; *c.* mean daily temperature for July; *d.* mean daily temperature for January (*c* and *d* adapted from "Yukon today", 1968; source: Meteorological Branch, Department of Transport); *e.* sample localities found in previous literature (Evans, 1950-1951). A = Marsh Lake; A2 = Whitehorse; A3 = Kluane; B = Pickhandle Lake; C = Tatchun Lake; B2 = Snag; D = Minto; E = Stewart River valley; F = Taylor Creek; G = Mayo; H = Gravel Lake; I = Keno Hill; J = Dawson City.

As in the Great Slave Lake study area, the spots which were the most favorable for fossorial wasps were clearings, roadsides, old sandpits, river banks, lake shores, ridges, cut-banks, and in general disturbed areas and early successional stages.

Characteristics of sample localities and conditions of sampling

Localities preceded by + in the following list, are those which have been found in previous literature (Evans, 1950-1951) and species numbers preceded by + correspond to species not found by me.

A1. + *Watson Lake* (see Fig. 1, 60° 04' N, 128° 49' W, 2,500-3,000' elevation).

Dates. — 17-24 June; 20-25 June; 25 June.

Species collected (not by me). — 6, 12, 15, +19, 23.

A. *Marsh Lake* (Mile 880, Alaska Highway, east of Whitehorse, 60° 30' N, 134° 18' W, approx. 2,300' elevation).

Description. — Old sand-gravel pit, rather compact soil, sparse low vegetation, apparently not very favorable.

Conditions of sampling (not very good). — 5 August 1968; cloudy, sunny at times, windy.

Species collected. — +10, 23.

A2. + *Whitehorse* (60° 43' N, 135° 03' W, approx. 2,500-3,000' elevation).

Dates. — June-July; 1 July; 3-4 July; 3 July — 1 August; 4-5 July; 9-11 July; 25 July 1948; July-August.

Species collected (not by me). — 1, 2, 3, 9, 15, 18, 21, 23, 24.

A3. + *Kluane* (South tip of Kluane Lake, 61° 02' N, 138° 23' W, approx. 2,500-3,000' elevation).

Dates. — 28 July.

Species collected (not by me). — 8.

B. *Pickhandle Lake* (near Koidern: Alaska Highway, near U. S. border, 61° 57' N, 140° 20' W, 2,500' elevation).

Description. — Narrow strip of earth in rock pit, with sparse low vegetation; apparently not very favorable (but some Sphecidae found, no Pompilidae).

Conditions of sampling (not very significant). — 15 August 1968; weather excellent, very hot.

Species collected. — None.

C. *Tatchun Lake area* (near Carmacks, Mile 122, Highway from Whitehorse to Dawson, 62° 20' N, 136° 17' W, approx. 1,700' elevation).

Description. — Series of pits and flats, with small hillocks and ridges; shrub and herbaceous vegetation, numerous flowers, some trees (aspen); soil rather compact.

Conditions of sampling (average to good). — 9 August 1968; sunny, windy — 10 August 1968; weather excellent, sunny, warm, slight wind.

Species collected. — 2, 12 23.

B2. + *Snag* (north of locality B, 62° 25' N, 140° 23' W, approx. 2,500-3,000' elevation).

Dates. — 24 July.

Species collected (not by me). — 1, 8, 9, +19.

D. *Minto* (Mile 147, Highway from Whitehorse to Dawson, 62° 37' N, 136° 52' W, approx. 1,700' elevation).

Description. — Fairly restricted sandy area, probably a very old small sand pit; small sand ridges.

Sampling conditions (not very significant). — 10 August 1968; good weather but windy.

Species collected. — None.

E. *Stewart River Valley* (Mile 223, Whitehorse to Mayo highway, 63° 26' N, 136° 27' W,

approx. 1,700' elevation).

Description. — Flats, terraces in the river valley and sand gravel pits, various soil and vegetation conditions, probably good variety of microclimates.

Conditions of sampling (too restricted although area probably favorable). — 10 August 1968; very hot.

Species collected. — 3, 15.

F. *Taylor Creek area* (Alaska, Mile 52, North of Tetlin Jctn., approx. 63° 30' N, 142° 25' W, 4,000? elevation).

Description. — Pit and ridge of rather compact soil, bordering boggy area (black spruce); vegetation sparse, herbaceous, flowers numerous.

Conditions of sampling (fairly restricted). — 14 August 1968; hot, hazy.

Species collected. — 3.

G. *Mayo* (some Miles North of town, Mile 248, direction Keno Hill, 63° 38' N, 135° 53' W, approx. 1,700' elevation).

Description. — The area is described in tourist guides as “the hottest and coldest spot in the Yukon”; potential good areas (pits, clearings, etc.) appeared rather limited; several man-made disturbed areas (sand pits) were visited; soil rather compact, flowers scarce, (already outgrown).

Conditions of sampling. — 12 August 1968; very good weather, very hot, some clouds.

Species collected. — 3.

H. *Gravel Lake* (near McQuesten, Mile 52, Highway 3 to Dawson City, 63° 47' N, 137° 45' W, approx. 2,200' elevation).

Description. — Rather small sand/gravel pit, with many flowers.

Conditions of sampling (not very conclusive). — 12 August 1968; very good weather, very hot.

Species collected. — 1.

I. *Keno Hill* (63° 54' N, 135° 18' W, approx. 3,200' elevation).

Description. — Small areas of potentially good soil, in a generally rocky area; apparently not very favorable in general.

Conditions of sampling. — 11 August 1968; very hot, sunny, no wind.

Species collected. — None.

J. *Dawson City* (Mile 15, west of Dawson, 64° 10' N, 139° 40' W, approx. 3,500? elevation).

Description. — The northernmost sample locality of this study; potentially good areas for fossorial wasps apparently fairly limited, at least as seen from the highway; some narrow strips of soil on the roadside and pits were visited; flowers relatively abundant (many bumblebees).

Conditions of sampling (probably not very significant). — 13 August 1968.

Species collected. — None.

DISTRIBUTION OF SAMPLES IN TIME (SEASONAL AND DAILY)

The total sampling time was about 54 hours for the Great Slave Lake study area and only 10 for the Yukon study area. Although these figures are very low, the sampling was

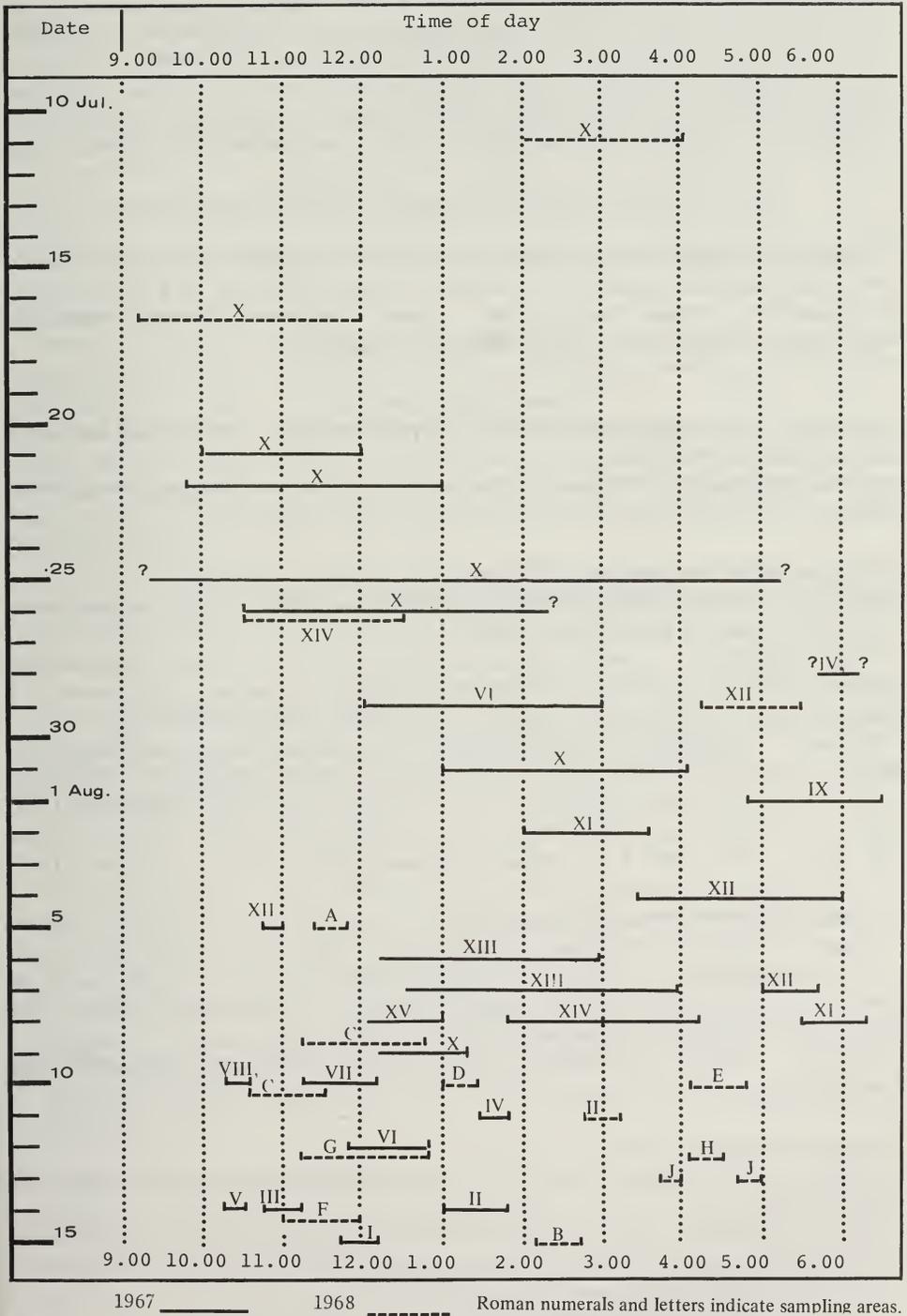


Fig. 4. Seasonal and daily distribution of samples of subarctic Pompilidae

distributed as efficiently as possible both in space – only the potentially “good spots” have been visited – and in time – only the best season (July, August) and best part of the day (between 9:00 a.m. and 6:00 p.m.) were used. Figure 4 represents diagrammatically the distribution of the samples in time (season and time of day) and shows that the samples cover a reasonable cross section. In the light of this limited sampling, conclusions must be drawn with prudence, particularly as to negative evidence concerning certain species and localities and the problem of possible impoverishment with increasing latitude. This is confirmed by the previous literature, which mentions many species not found in this study.

LIST OF SPECIES COLLECTED AND PREVIOUS INFORMATION

Species and sample localities found in the literature are preceded by the sign +. Species and localities have been given identification numbers, used on the maps. N.W.T. = Northwest Territories; Y.T. = Yukon Territory; C.N.C. = Canadian National Collections, Ottawa, Ontario; C.A.S. = California Academy of Sciences, San Francisco.

Genus *Evagetes* Lepeletier

Biology. – All social parasites of other Pompilini, destroying the host egg and laying their own (Evans, 1950-1951).

Known distribution. – Palaearctic, Nearctic, and Neotropical Regions (Evans, 1950-1951).

1. *Evagetes crassicornis crassicornis* Shuckard.

Biology. – In Europe, social parasite of several Pompilini. Inhabits sandy or gravelly areas, often in the vicinity of woods (Evans, 1950-1951).

Known distribution. – Widely distributed holarctic species. In Europe, throughout the northern part of the continent; in North America across the continent in Hudsonian and Canadian Zones, and to a limited extent the Transition Zone (Evans, 1950-1951).

Records. – NORTHWEST TERRITORIES. – I, ♀ 15 August 1967. IV, ♀ 28 July 1967. VI, ♀ 29 July 1967. X, ♀ 11 July 1968, ♀ 17 July 1968, ♀ 22 July 1967, 3 ♀♀ 26 July 1967, ♀, ♂ 31 July 1967, ♀ 9 August 1967. XIII, ♀ 6 August 1967. XIV, 2 ♀♀ 26 July 1968. +XIX, ♂, ♀ 13 August (Evans, 1950: CNC). YUKON TERRITORY. – A2, ♂, 3 ♀♀ 3-4 July (Evans, 1950: CNC). B2, 2 ♀♀ 24 July (Evans, 1950: CNC). H, ♀ 12 August 1968.

2. *Evagetes crassicornis consimilis* Banks.

Biology. – Collected on sand and on flowers (Evans, 1950).

Known distribution. – Canadian and Transition faunas of western U. S. and Canada. In general occurs south of the range of typical *crassicornis*, but considerable overlap in range (found also in New Mexico, California, etc.) (Evans, 1950).

Records. – YUKON TERRITORY. – +A2, 2 ♀♀ 4-5 July (Evans, 1950: CNC). C, ♀ 9 August 1968.

3. *Evagetes subangulatus* Banks.

Biology. – Either in open country or in clearings in woodlands, is partial to sandy soil (Evans, 1950).

Known distribution. – Occurs transcontinentally from the Hudsonian to the Transition Zones, from Labrador and Yukon to Georgia in the Appalachians and to New Mexico, Arizona, etc. Not mentioned from N.W.T. (Evans, 1950).

Records. – NORTHWEST TERRITORIES. – II, ♀ 14 August 1967. XIV, ♀ 26 July

1968, ♀ 8 August 1967. YUKON TERRITORY. — +A2, 2 ♀♀ June, July (Evans, 1950: CNC, CAS). E, ♀ 10 August 1968. F, ♀ 14 August 1968. G, ♀ 12 August 1968.

4. *Evagetes bradleyi* Banks.

Records. — NORTHWEST TERRITORIES. — X, ♀ 11 July 1968.

5. *Evagetes hyacinthinus* Cresson (all individuals collected by me are of the very hairy form called "scudderi" by Banks: Evans, *personal communication*).

Known distribution. — Transcontinental, primarily in the Transition Zone. Not mentioned from N.W.T. in list of localities (Evans, 1950).

Records. — NORTHWEST TERRITORIES. — VII, 2 ♀♀ 11 August 1967. X, ♀ 25 July 1967, 4 ♀♀ 26 July 1967, 5 ♀♀ 31 July 1967. XI, ♀ 8 August 1967. XV, ♀ 8 August 1967.

6. *Evagetes parvus* Cresson.

Biology. — Frequents sand pits, waste places, gardens, occasionally clearings in woodlands. Occurs throughout the summer months, and may have several generations during this time (Evans, 1950).

Known distribution. — Transcontinental in Canadian, Transition, and Upper Austral Zones, but less common southward and westward. One of the commonest Pompilini in the northeastern and north central U. S. and eastern Canada; there are but few records from west of the Rocky Mountains (Evans, 1950). This species is also reported from Arizona, New Mexico, etc.

Records. — NORTHWEST TERRITORIES. — XIII, ♀ 6 August 1967. +XVIII, 6 ♂♂, 5 ♀♀ 20-28 July 1949 (Mason, *in* Evans, 1951). YUKON TERRITORY. — +A1, ♂, ♀ 25 June (Evans, 1950: CNC).

Genus *Priocnemis*

7. *Priocnemis notha alaskensis* Townes.

Reported from Alaska, Northwest Territories (Krombein *et al.*, 1958).

Records. — NORTHWEST TERRITORIES. — IX, ♀ 1 August 1967. X, ♀ 25 July 1967. XII, ♀ 5 August 1967.

Genus *Anoplius* Dufour

Known distribution. — Some species rather restricted ecologically and others very wide-ranging throughout the World (except Australia?). Well represented in the Nearctic and Neotropical regions (Evans, 1951).

Subgenus *Anoplius* Dufour

Biology. — Various in habits, none seems to be a strict psammophile. Some in restricted ecological niches, others: more wide-ranging (Evans, 1951).

Known distribution. — Species seen from Nearctic, Neotropical, Palaeartic, and Oriental regions (Evans, 1951).

8. *Anoplius (Anoplius) ithaca* Banks.

Biology. — Confined to stony stream sides. Appears to have several (perhaps 3) generations a year throughout its range (Evans, 1951).

Known distribution. — Transcontinental in Transitional and Upper Austral Zones (Muesebeck *et al.*, 1951). Exceedingly wide distribution, although rather local: Texas . . . , etc. north to Yukon, Manitoba . . . , etc. Not mentioned from N.W.T. (Evans, 1951).

Records. — NORTHWEST TERRITORIES. — XIII, ♀ 7 August 1967. YUKON TERRITORY. — +A3, 2 ♀♀ 28 July (Evans, 1951: CNC). +B2, 2 ♀♀ 24 July (Evans, 1951: CNC).

9. *Anoplius (Anoplius) imbellis* Banks.

Biology. — Taken along streams (cf *ithaca*); does not appear to be restricted to this habitat (Evans, 1951).

Known distribution. — Transcontinental, from the Hudsonian to the Upper Austral Zones, but appears to be most common in the Transition Zone (more common in the Pacific States?) (Evans, 1951).

Records. — NORTHWEST TERRITORIES. — X, ♀ 26 July 1967. XVIII, 22 ♂♂, 11 ♀♀ 12 July — 3 August (Evans, 1951: CNC). YUKON TERRITORY. — +A2, 3 ♂♂ 9-11 July (Evans, 1951: CNC). +B2, 2 ♂♂, ♀ 24 July (Evans, 1951: CNC).

Species not found by me but reported from previous literature in N.W.T. or Y.T. or both:

+10. *Anoplius (Anoplius) nigerrimus* (Scopoli) (in Evans, 1951).

Known distribution. — Holarctic species known from almost the whole of Europe; in North America it occurs transcontinentally in the Hudsonian and Canadian Zones, entering the Transition Zone sparingly (Evans, 1951).

Records. — NORTHWEST TERRITORIES. — +XVI, ♀ 9 August (Evans, 1951: CNC). +XVIII, ♀ 1 July (Evans, 1951: CNC). YUKON TERRITORY. — A, ♂ 10 July (Evans, 1951: CNC).

+11. *Anoplius (Anoplius) tenuicornis* Tournier (*basalis* Dreisbach, in Evans, 1951).

Known distribution. — Holarctic. Apparently uncommon species, transcontinental distribution in the Canadian Zone, south to New Brunswick, Vermont, Manitoba, and at high altitudes to New Mexico and California (Evans, 1951, 1956, 1966).

Records. — NORTHWEST TERRITORIES. — +XVIII, ♂, ♀ 20-29 July 1949 (Mason, in Evans, 1951 CNC).

Subgenus *Pompilinus* Ashmead

Predominantly inhabitants of sandy areas; remarkable unselectivity in prey selection (Evans, 1951).

12. *Anoplius (Pompilinus) tenebrosus* Cresson.

Biology. — Sandy places, especially vicinity of woods (Evans, 1951).

Known distribution. — Common across the continent from upper extremities of Upper Austral Zone far into the Hudsonian Zone; Canadian and Transition Zones (Evans, 1951).

Records. — NORTHWEST TERRITORIES. — VI, 2 ♂♂ 29 July 1967. X, ♀ 11 July 1968. XII, ♂ 5 August 1967. XIII, 6 ♂♂, ♀ 6 August 1967, 2 ♂♂ 7 August 1967. XIV, ♀ 26 July 1968, ♂ 8 August 1967. +XIX, ♀ 11 July (Evans, 1951: CNC). YUKON TERRITORY. — +A1, 12 ♀♀ 20-25 June (Evans, 1951: CNC). C, ♂ 9 August 1968.

Species not found by me but reported from previous literature in N.W.T. or Y.T. or both:

+13. *Anoplius (Pompilinus) cylindricus* (Cresson).

Known distribution. — Widely distributed species, Florida . . . , Texas, etc., Ontario, N.W.T.

Records. — NORTHWEST TERRITORIES. — +XVI, ♂ 6 August (Evans, 1951: CNC).

+14. *Anoplius (Pompilinus) marginatus* (Say).

Known distribution. — Temperate North America, east of the Rockies, from Florida, Texas . . . , etc. to Quebec, N.W.T. . . , etc.

Records. — NORTHWEST TERRITORIES. — +XVI, ♀ 15 August (Evans, 1951: CNC).

Genus *Pompilus* Fabricius

Known distribution. — Cosmopolitan (Evans, 1951).

Subgenus *Ammosphex* Wilcke

Biology. — Variety of habitats, but seems particularly characteristic of wooded places (close to the ground, sunny spots) (Evans, 1951).

Known distribution. — Holarctic Region; eight species known in the Nearctic Region; (also in Europe), (Evans, 1951).

15. *Pompilus (Ammosphex) luctuosus* Cresson.

Known distribution. — Transcontinental in Hudsonian and Canadian Zones, sparingly entering the Transition Zone in western states; . . . Quebec . . . New Mexico, California . . . N.W.T., Y.T., etc. True *luctuosus* is apparently a common species only in the far north (Evans, 1951).

Records. — NORTHWEST TERRITORIES. — V, ♂ 14 August 1967. VII, ♀ 11 August 1967. X, 2 ♀♀ 25, 31 July 1967. XIII, ♀ 6 August 1967 (dragging paralyzed spider prey: *Tarentula* sp., immature; Fam. Lycosidae), ♀ 7 August 1967. XIV, ♀ 8 August 1967. +XVIII, ♂, ♀ 12-23 August (Evans, 1950-1951: CNC). +XIX, ♂, 8 ♀♀ 12 July — 13 August (Evans, 1951: CNC). YUKON TERRITORY. — +A1, ♂, ♀ 17-24 June (Evans, 1951: CNC). +A2, ♂, 4 ♀♀ 3 July — 1 August (Evans, 1951: CNC). E, ♀ 10 August 1968.

16. *Pompilus (Ammosphex) occidentalis* Dreisbach.

Known distribution. — Mountain forests of the west, apparently chiefly in the Transition Zone, ranging from Alberta and British Columbia south at high altitude to New Mexico, Arizona and California; not uncommon, western U. S., Canada. Not mentioned from N.W.T. and Y.T. (Evans, 1951). Mexico (Puebla, Mexico) (Krombein *et al.*, 1958).

Records. — NORTHWEST TERRITORIES. — XII, ♀ 29 July 1968. XIII, ♀ 6 August 1967.

17. *Pompilus (Ammosphex) imbecillus ojobwae* Evans.

Known distribution. — Across the continent, chiefly in Canadian Zone (north of the range of the nominate subspecies); also Hudsonian Zone, . . . north to N.W.T. (Evans, 1951).

Records. — NORTHWEST TERRITORIES. — V, ♀ 14 August 1967. X, 2 ♀♀ 21, 25 July 1967, ♂ 31 July 1967. +XIX, ♀ 8 July 1948 (Evans, 1951: CNC).

18. *Pompilus (Ammosphex) angularis* Banks.

Biology. — In sheltered sandy areas and open woodlands, where the soil is light (Evans, 1951).

Known distribution. — Transcontinental in Transition and Upper Austral Zones; occasional record from Canadian and Lower Austral Zones; . . . Yukon . . . California (San Diego, etc.) (Evans, 1951).

Records. — NORTHWEST TERRITORIES. — XII, 2 ♀♀ 4 August 1967, ♀ 5 August 1967. YUKON TERRITORY. — +A2, ♂ 3 July (Evans, 1951: CNC).

Species not found by me but reported from previous literature in N.W.T. or Y.T. or both:

+19. *Pompilus (Ammosphex) michiganensis michiganensis* Dreisbach.

Known distribution. — Hudsonian, Canadian, and Transition Zones, N.W.T. . New York . . . and at high elevations to Colorado and Georgia (Evans, 1951).

Records. — NORTHWEST TERRITORIES. — +XVIII, ♂ 20 July (Evans, 1951: CNC). YUKON TERRITORY. — +A1, 3 ♂♂, 2 ♀♀ 20-25 June (Evans, 1951: CNC). +B2 : 2 ♂♂ 24 July (Evans, 1951: CNC).

Subgenus *Anoplochares* Banks

Known distribution. — Holarctic (Europe) (Evans, 1951).

20. *Pompilus (Anoplochares) apicatus* Provancher.

Biology. — Not uncommon; chiefly in sheltered places, particularly sunny spots in woodlands; also open prairie country (Great Plains) (Evans, 1951).

Known distribution. — Very wide; most abundant in Transition Zone, where transcontinental in distribution; from the Great Plains eastward occurs also in Canadian, Upper and Lower Austral Zones, as far north as Labrador and far south as Alabama, Texas; not mentioned from N.W.T. and Y.T. (Evans, 1951).

Records. — NORTHWEST TERRITORIES. — X, ♂, ♀ 25 July 1967.

Subgenus *Arachnospila* Kincaid

Biology. — The three species found in the Nearctic Region are fairly common (Evans, 1951).

Known distribution. — Holarctic (Evans, 1951).

21. *Pompilus (Arachnospila) fumipennis fumipennis* Zetterstedt.

Known distribution. — Holarctic; the most boreal of our Pompilidae; circumpolar in distribution: northern Eurasia (. . Finland . .); in North America ranges transcontinentally in the Hudsonian and Canadian Zones, except British Columbia and Alberta southward in the Rockies and Coastal Ranges, where replaced by the subspecies *eureka* Banks; . . Labrador . . N.W.T., Y.T. . . Alaska . . (Evans, 1951).

Records. — NORTHWEST TERRITORIES. — IX, ♂, ♀ 1 August 1967. XIII, ♂ 7 August 1967, ♀ 10 August (Evans, 1951: CNC). YUKON TERRITORY. — +A2, ♂ 1 July (Evans, 1951: CNC).

22. *Pompilus (Arachnospila) scelestus* Cresson.

Biology. — The best known and possibly the most common species of *Pompilus* in our fauna; variety of habitats, including sand dunes, fields, gardens, open woodlands (Evans, 1951).

Known distribution. — Transcontinental in Upper Austral and Transition Zones, entering the Canadian Zone to a limited extent, especially in the West; peripheral localities: . . Quebec, Manitoba, Alberta, British Columbia California, Arizona, New Mexico . . Not mentioned from N.W.T. and Y.T. (Evans, 1951).

Records. — NORTHWEST TERRITORIES. — VII, ♀ 11 August 1967. XIII, ♀ 7 August 1967. XV, ♀ 8 August 1967 (dragging paralyzed spider prey: *Phidippus* sp., immature; Fam. Salticidae).

23. *Pompilus (Arachnospila) arctus* Cresson.

Biology. — One of the more common species of *Pompilus* within its range; most often encountered on or near the ground in open wooded areas or in parks; nests in soft earth; (Evans, 1951).

Known distribution. — Transcontinental in the Hudsonian, Canadian and Transition Zones; some peripheral localities: . . . Labrador . . . California, New Mexico . . . (Evans, 1951).

Records. — NORTHWEST TERRITORIES. — XII, ♀ 5 August 1967. XV, ♀ 8 August 1967. +XVI, ♀ 6 August (Evans, 1951: CNC). YUKON TERRITORY. — A, ♀ 5 August 1968. +A1, 2 ♂♂ 24 June (Evans, 1951: CNC). +A2, 3 ♂♂ July, August (Evans, 1951: CNC). C, ♀ 9 August 1968.

Genus *Episyron* Schiødt

Biology. — Usually in sandy or gravelly areas, where the nest is in the earth (Evans, 1951).

Known distribution. — All the zoogeographic regions of the world, except apparently Australian; twelve species recorded in the Nearctic Region (Evans, 1951).

24. *Episyron oregon* Evans.

Known distribution. — Western U. S. and Canada, from Yukon and Alberta to Wyoming and California; principally a Transition Zone species; not mentioned from N.W.T. (Evans, 1951).

Records. — NORTHWEST TERRITORIES. — IX, ♀ 1 August 1967. YUKON TERRITORY. — +A2, ♀ 2 July 1948 (Mason, in Evans, 1950: CNC).

25. *Episyron quinquenotatus quinquenotatus* Say.

Known distribution. — Throughout the Canadian Alleghanian and Carolinian faunas of eastern U. S. and Canada; more common northward; ranges westward sparingly to Texas, Colorado, Montana, British Columbia. Not mentioned from N.W.T. or Y.T. (Evans, 1950).

Records. — NORTHWEST TERRITORIES. — X, 3 ♂♂, 2 ♀♀ 11 July 1968 (one ♀ digging in sandy soil), 3 ♂♂, 4 ♀♀ 25 July 1967 (one ♀ digging burrow in sandy hillock; another ♀ dragging paralyzed spider prey: *Araneus cornutus* Clerck; Fam. Araneidae), ♂, 3 ♀♀ 31 July 1967 (one ♀ dragging paralyzed spider prey: *Araneus*, immature; Fam. Araneidae), ♀ 9 August 1967 (dragging paralyzed spider prey: *Araneus patagiatus* Clerck; Fam. Araneidae). XII, 2 ♀♀ 29 July 1968. XIV, 2 ♀♀ 26 July 1968 (one on flowers, the other digging burrow in sandy, flat, soil).

Species not found by me but reported from previous literature in N.W.T. or Y.T. or both:

+26. *Episyron biguttatus biguttatus* (Fabricius).

Known distribution. — Occurs throughout North America east of the Rockies, from Texas and Florida to N.W.T. and Labrador; west of the eastern slopes of the Rockies, and also in the Black Hills of South Dakota . . . , etc. (Evans, 1950).

Records. — NORTHWEST TERRITORIES. — +XVI, ♀ 6 August (Evans, 1950: CNC).

GENERAL ZOOGEOGRAPHY AND DISTRIBUTION OF POMPILINI (Evans, 1951)

Species, subgenera, and genera collected in N.W.T. or Y.T. or both are marked * in the following text.

Many species have remarkably broad ranges. The range of approximately 46 per cent of the species found in the Nearctic Region is "transcontinental".

Three major distribution patterns have been proposed: — a predominantly northern group

extending further south in mountains, with strong affinities with the Eurasian fauna — a possible indication of Holarctic distribution. The affinities of the following genera or subgenera are considered predominantly holarctic: * *Evagetes*, *Agenioideus* (s. str.), * *Episyron*, *Lophopompilus*, * *Pompilinus*, * *Anoplius* (s. str.), * *Ammosphex*, * *Arachnospila* and * *Anoplochares*. As can be seen, this group is heavily represented in the sample taken from the Northwest Territories and Yukon. According to Evans, this northern group represents approximately 59 per cent of the total number of species found in the Nearctic Region and is also well represented in Eurasia; a few of them are also found in the Neotropical Region. This strongly suggests a migration pattern — probably intermittent — through the Siberia-Alaska regions and the Bering land bridge. Present day patterns of distribution and the importance of morphological differences between Eurasian and North American relatives have been interpreted in terms of possible successive migration waves at different ages. * *Evagetes crassicornis crassicornis*, * *Anoplius (Anoplius) tenuicornis* and * *Anoplius (Anoplius) nigerrimus*, for instance, are found both in Eurasia and northern North America, which suggests a possible recent (postglacial?) migration. According to Evans the following, somewhat less boreal forms, differ only slightly — in color, size, pilosity, for instance — from their nearest Eurasian relatives: * *Evagetes crassicornis consimilis*, *Pompilus (Arachnospila) fumipennis eureka*, and * *Pompilus (Ammosphex) luctuosus*; this is perhaps indicative of a more ancient (last interglacial?) migration wave. More important differences are recorded in: * *Evagetes parvus*, *Anoplius (Anoplius) virginensis* and * *Pompilus (Arachnospila) arctus*, which occur in general slightly farther south. * *Evagetes hyacinthinus*, *Anoplius (Anoplius) ventralis*, *Pompilus (Ammosphex) solonus* are considered predominantly Austral in distribution. *Anoplius (Anoplius) fulgidus*, although of Holarctic origin is now predominantly tropical in distribution.

A second group is predominantly a southern one, with some northern extension along coastal areas, and big river systems. Tropical affinities predominate in this group which represents 25 per cent of the species found in the Nearctic Region; some are found in the tropics of the whole World, others only in the Neotropics with some northern extension in the southern parts of North America; some reach even to Canada: *Anoplius (Arachnophroctonus) relativus* and *Aporinellus taeniatus*, for instance.

Affinities of a third "Sonoran group" are still debated; the group (an "endemic" group?) is characteristic of arid regions of the southwest of the U. S.

CONCLUSION

Considering the limited sample involved, no sweeping generalization is attempted. In order to assess the possible effect of latitude, altitude, geology, general and local climates, microclimates, soil and vegetation cover and man, a more complete and systematic sample, both in space and time seems required.

It is clear, however, that Pompilidae are able to cope with the severe conditions of subarctic regions; some of them even extend as far north as the Arctic Coast, on the Mackenzie River Delta (Reindeer Depot), which, however, is still included in the Subarctic Region. To what extent such a northern extension is possible only along a big river system such as the Mackenzie, is not known; undoubtedly this huge river system provides, at least locally if not all along its course, favorable habitats for fossorial wasps, probably in terms of soils, microclimates as well as vegetation cover. It would be interesting to see how far north this fauna extends on the Shield section of the Subarctic Region — where distribution of potentially favorable areas appears to be much more patchy — and whether or not it reaches the Arctic Region, as some bees do (and even the High Arctic: Hocking and Sharplin, 1964-1965).

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THE FUNCTIONAL MORPHOLOGY OF THE MOUTHPARTS
OF BLACKFLY LARVAE (DIPTERA: SIMULIIDAE)

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Blackfly larvae select their food on the basis of size. Diameters of particles ingested by four filter-feeding species; Cnephia dacotensis Dyar and Shannon, Simulium decorum Walker, Simulium venustum Say, and Simulium vittatum Zetterstedt, range from less than 1 micron to about 350 microns. Most commonly ingested particles ranged from 10-100 microns in diameter. The size distribution of ingested particles varied between species. Larvae of Twinnia biclavata Shewell, a non-filter feeding species, ingests particles of a similar size by grazing. Differences in feeding among filtering species are not attributed to morphological differences. The mouthparts of filtering and grazing species are well adapted for their respective modes of feeding.

Chemical control programs have been aimed at blackfly larvae for over 20 years. Among the most effective formulations is DDT adsorbed on particles which blackfly larvae ingest along with their particulate food (Fredeen, Arnason and Berck, 1953; Fredeen, Arnason, Berck and Rempel, 1953; Noel-Buxton, 1956; Kershaw et al., 1965).

The primary aim of this study was to determine the size of particles which blackfly larvae ingest. This information would be helpful in developing a particulate larvicide which is specific for blackfly larvae and less harmful to other aquatic fauna. The size range of the particles ingested was determined by feeding the larvae variously sized beads. Species variability in feeding was examined in a detailed morphological study of the mouthparts of the species involved.

The most comprehensive morphological studies on head capsules of blackfly larvae are those of Puri (1925), Fortner (1937) and Grenier (1949). More recently Davies (1960), Dumbleton (1962a, b) and Rubtsov (1964) produced detailed works on the larval head capsule and its appendages. Other morphological studies on larval blackflies include those of Debot (1932), Sommerman (1953), and Wood (1963).

Naumann (1924) and Fortner (1937) also studied filter-feeding by blackfly larvae. The most recent review of filter-feeding is that of Jørgensen (1966), who was concerned mainly with marine invertebrates but also included most of the work done on insects. Pucat (1965) studied filtering by mosquito larvae. Burt (1940) and Walshe (1947, 1951) studied filtering by midge larvae.

Among the most important studies on the biology of larval blackflies are those of Wu (1931), Grenier (1949), Peterson (1956), Zahar (1957), Davies and Syme (1958), Anderson and Dicke (1960), Carlsson (1962, 1967), Phelps and DeFoliart (1964), Rubtsov (1964) and Maitland and Penny (1967). Feeding habits are also discussed by Smart (1944), Badcock (1949), Jones (1949a, b, 1950, 1951, 1958), Fredeen (1960, 1964), Williams et al. (1961) and Abdelnur (1968). I have reviewed (*Quaest. ent.*, in press) control programs aimed at blackfly larvae.

MATERIALS AND METHODS

Larvae of *Cnephia dacotensis* Dyar and Shannon, *Simulium decorum* Walker, *Simulium venustum* Say or *Simulium verecundum* Stone and Jamnback, and *Simulium vittatum* Zett., were reared in the laboratory. It was not practical to separate larvae of *S. venustum* and *S. verecundum* and these are treated here as *S. venustum*. Larvae of *Prosimulium* species, mainly *P. travisi* Stone, and larvae of *Twinnia biclavata* Shewell were also collected.

Three methods were used to rear larvae in the laboratory; all of them were closed systems. Two were stream methods and were not as successful as the third, a jar method similar to that used by Puri (1925) and Davies and Smith (1958). Several battery jars were filled with 4 to 8 litres of a mixture of tapwater and deionized water. Air breaker stones in each jar produced the necessary water movement and aeration. The air was taken from a laboratory air supply of gauge pressure of 1.7 to 2.0 atm. and passed through an oil trap and charcoal filter. At the bottom of each jar there was a layer of charcoal 4 to 6 cm deep. The temperature of the water varied with the room temperature from 22 to 27 C. Larvae were fed on bakers' yeast. Organic material which was gathered during collections and which accumulated in the jars was also available to the larvae. Blackflies were reared from egg to adult by this method.

Live larvae were observed through a stereomicroscope through the wall of a containing vessel. Larvae were also observed while attached to a thin plastic or glass plate inverted over a container of water.

Specimens were preserved in 90% ethanol or 1:3 glacial acetic acid and 90% ethanol. Whole mounts of head capsules in Canada Balsam were also examined. Most of the head structures could be studied without any special preparation, especially in recently moulted specimens. For detailed study, specimens were treated with a solution of 4% potassium hydroxide at room temperature for 24 hours. Borax carmine was used to stain muscles. Mallory's triple stain (Pantin, 1960; modification by Sharplin, *personal communication*) was used for studying cuticular structures. Serial sections of heads stained in Ehrlich's haematoxylin and eosin were also studied.

To determine the size range of particles ingested, blackfly larvae were exposed to four types of 'Sephadex' beads (Pharmacia Fine Chemicals Inc.): 'G-25 superfine', 'G-25 fine', 'G-100' and 'G-200'. Diameters of beads after swelling ranged from 10 to 445 microns. The beads were swollen according to their individual requirements ('Sephadex' booklet No. 2, Theory and Experimental Technique).

The samples of 'Sephadex' to which the larvae were exposed were made up of equal volumes (17.5 ml) of the four types of 'Sephadex'. After varying lengths of time (10 min to 2 hr), larvae were removed from the jars and their guts examined. To determine the frequency distribution of sizes of beads available to the larvae, 500 randomly selected beads from each of five exposure samples (also made up of equal parts of the four 'Sephadex' types) were measured.

Larvae were classified into three age groups: small, medium and large, using a technique similar to that of Phelps and DeFoliart (1964). The categories are defined on the basis of the length of the cephalic apotome, the width of the head capsule at its widest part, and the degree of development of the pupal histoblast. Consideration of the histoblast was subjective. Small larvae have no readily visible histoblasts. Large larvae have coloured or large white histoblasts in which the respiratory filaments are well differentiated. Medium larvae have histoblasts of intermediate development. The lengths and widths of the head capsules of the four filtering species of blackfly larvae are tabulated below (Table 1).

Table 1. Size in microns of head capsules of small, medium and large larvae of four species of blackflies.

No small larvae of *S. decorum* or *S. venustum* were available for measurement.

Species	Small		Medium		Large	
	length	width	length	width	length	width
<i>C. dacotensis</i>	140-519	120-319	520-759	320-539	760-1159	540-779
<i>S. decorum</i>	-599	-399	600-719	400-519	720- 919	480-559
<i>S. venustum</i>	-699	-519	700-799	520-599	800- 899	640-719
<i>S. vittatum</i>	140-499	80-379	500-819	380-659	820-1039	660-799

MORPHOLOGY OF THE MOUTHPARTS AND RELATED STRUCTURES

Filter-feeding species

The head capsule of blackfly larvae is subcylindrical, and tapers towards the cervical region (Fig. 1). It is prognathous. The cephalic cleavage lines (c. c. l.) are roughly parallel in well-developed larvae but converge at the midline of the posterodorsal margin of the head in first instars.

The ventral wall of the head capsule has recently been considered part of the head capsule and is referred to as the hypostomium (hypo., Fig. 2, 3) (Grenier, 1949; Crosskey, 1960; Wood, 1963; Dumbleton, 1964; Davies, 1965). Since the terminology used in this study follows closely that of Crosskey (1960), this term is adopted here. However, Matsuda (1965) describes the tendency for the submentum of insects to become sclerotized and to fuse with the gular region of the prognathous head. The posterior margin of the submentum is then recognized by the origins of the submento-mental muscles which lie on the line connecting the posterior tentorial pits. This being so, the ventral wall of the blackfly larval head is submental. Craig's (1969) embryological study supports this relationship.

The head spots (hd. spot, Fig. 1) mark the origins of the cephalic muscles. The antennae (ant., Fig. 1, 3) are at the anterolateral corners of the cephalic apotome. In late instar larvae they have four articles and bear two sensory papillae on the apex of the second article. In early instar larvae the antennae have two or three articles.

The origin of the pair of food collecting organs, the cephalic fans (c. fan, Fig. 1 to 3), is still controversial. On the basis of conflicting theories they have been considered messorial (Cook, 1949), from the Latin term *messor*, meaning reaper, first applied to structures of the head capsule of mosquito larvae (Cook, 1944). This concept has been rejected by most as being erroneous (Snodgrass, 1959; Chaudonneret, 1962, 1963). Puri (1925) and others (Fortner, 1937; Grenier, 1949; Craig, 1969) considered the cephalic fans premandibular, and Crosskey (1960) and others (Wood, 1963; Davies, 1965) considered them labral. They have been termed mouth-brushes (Smart, 1944; Dumbleton, 1962b) and cephalic fans (Puri, 1925; Crosskey, 1960; Dumbleton, 1962a). Since 'fan' is a more accurate description and since they are not members of the typical insect mouthparts, I prefer to call them cephalic fans.

Cephalic fans. — The cephalic fans (Fig. 1 to 3) are paired structures arising from the anterolateral corners of the cephalic apotome adjacent to a pair of unpigmented knobs (Fig. 1, 3). This is the first time these knobs have been reported. The dorsal surface of the cephalic fan stem is sclerotized and consists of two large sclerites which Puri (1925) considered segments. The larger sclerite, called P1 (= *large plaque*, after Grenier 1949, Fig. 4, 54) forms most of the dorsal surface and articulates with the head capsule. The upper third

of the sclerite bears three to six sensory hairs; one large hair is present close to the tip of the stem. The second sclerite, Pb (= *plaque basal*, after Grenier 1949) is spindle-shaped and horizontally arranged. It lies basal to Pl, lateral of the stem.

The ventral wall of the stem is concave and membranous. It supports three well-developed fans (Fig. 4). The primary fan (p. f.) arises from the apex of the stem; the secondary fan (s. f.), elsewhere called the accessory fan (Grenier, 1949), and the basal fan (Rubtsov, 1964), lies laterobasal to the primary fan; the medial fan (m. f.), elsewhere called the marginal fan (Fortner, 1937; Grenier, 1949) and the small fan (Rubtsov, 1964), lies on the medial side of the stem.

The distal half of the ventral wall is reinforced by a strongly sclerotized rod, Sc₁ (after Grenier, 1949) (Fig. 5). Some workers consider this rod to represent part of the torma (Wood, 1963; Wood et al., 1963). It consists of two parts: a ventral, rectangular piece and a dorsal bar. When viewed from the side (Fig. 54) it resembles a 'T', the medial, rectangular part forming the stem. When viewed from the ventral surface, it appears to be highly ridged as described by Grenier. The dorsal bar lies inside the stem and articulates basally with another rod, Sc_b (after Grenier, 1949). The apex of Sc₁ extends beyond the base of the secondary fan and spreads out laterally to form a fulcrum (ext. Sc₁, Fig. 5) for the rotation of the primary fan rays. Wood (1963) called this extension the connective sclerite in larvae of *Cnephia strenua* MacKerras and MacKerras, and *Simulium pictipes* Hagen. In the species studied here it neither connects directly with the rays and has neither a well-defined border nor division from Sc₁. I consider it an extension of Sc₁. The second rod Sc_b (Fig. 5) is at right angles to Sc₁, passing from articulation with Sc₁ to the ventrolateral wall between the two dorsal sclerites. It forms the ventrobasal wall of the stem. A third, thinner rod Sc_m (Fig. 5) (after Grenier, 1949) supports the medial lobe.

The retractor muscle of the cephalic fan inserts on the base of Sc₁ and is composed of three bundles. Two originate on the posterior region of the cephalic apotome, the precise spot being marked externally by the posterolateral head spots. These two bundles interdigitate with those from the other side before passing anteriorly. The third and smallest bundle originates on the midline of the cephalic apotome at the posteriomedial head spot, close to the posterior margin of the head capsule.

The rays of the primary fan are arranged in semicircle around the apex of the stem. When fully expanded, the rays cover an angle of between 200 and 250 degrees. The individual rays are sickle-shaped and hollow. Their bases are expanded into vanes of flexible, membranous cuticle. The shape of the basal expansion varies with the position of the ray in the fan (Fig. 8 to 10). The rays of the lateral side of the fan have slender, narrow expansions; the medial rays have acute, wide, basal expansions.

The numbers of rays of each fan vary with instar and with species. The numbers of rays in each of the three fans of the four filtering species studied are listed in Table 2.

The primary rays have microtrichia on their inner curved surface. The pattern of trichiation varies within the fan and with species. The more lateral rays have fewer microtrichia than the medial ones and the microtrichia are more numerous midway along rays. The larvae of both *C. dacotensis* and *S. vittatum* have no pattern of trichiation (Fig. 11, 15); however, among *C. dacotensis* larvae the microtrichia occur irregularly in two rows along the concave surface of the ray. The primary rays of *S. decorum* larvae have no pattern of trichiation but the arrangement of one long, two short, one long is sporadically repeated (Fig. 16). The trichiation of *S. venustum* larvae is arranged in a pattern similar to that of *Prosimulium* species studied (Fig. 17).

The bases of the secondary fan rays lie in a curved line (Fig. 7). This base line connects with that of the primary rays along a row of approximately 10 blades (Fig. 4, 5, not all

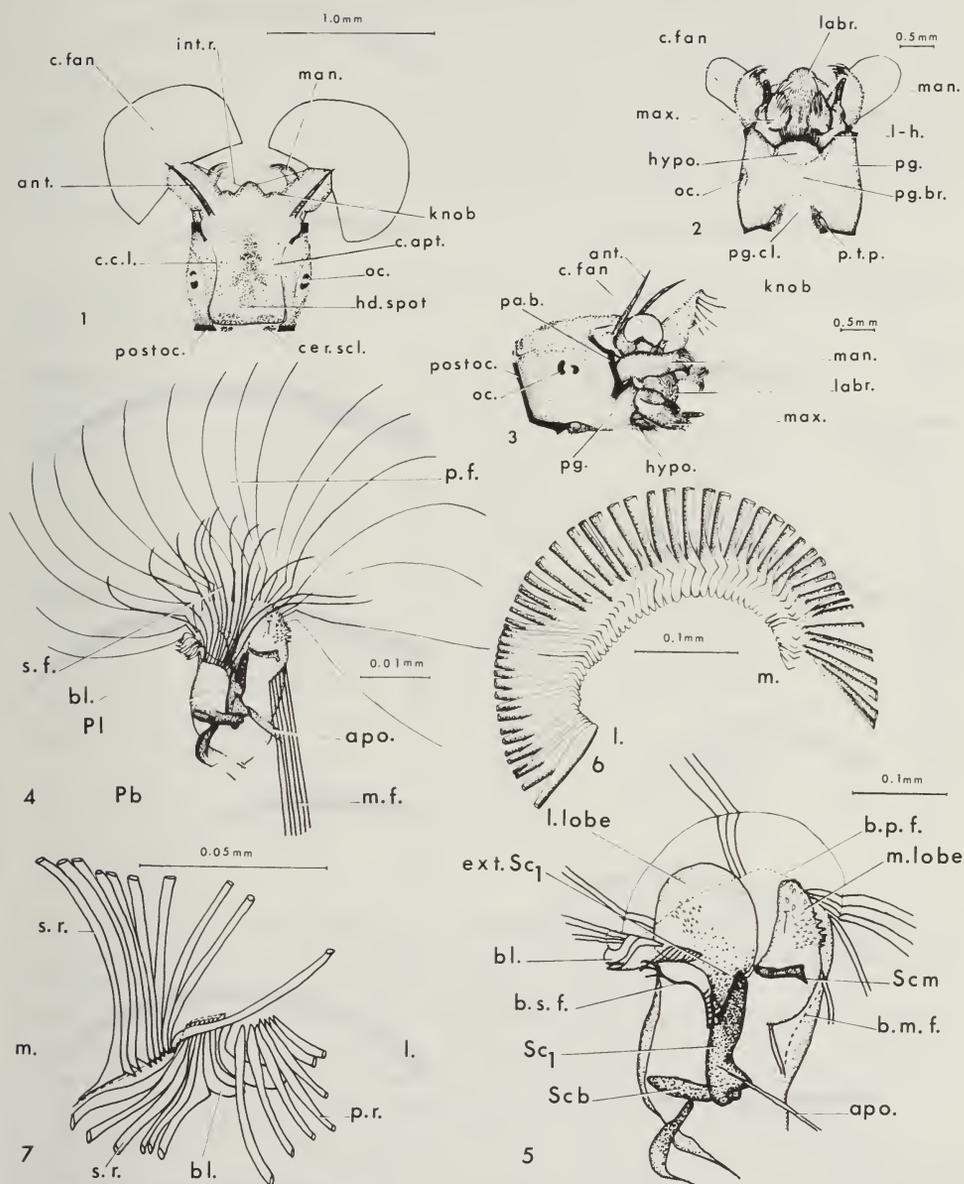


Fig. 1-7. Fig. 1-3: Head capsule of *S. vittatum* larva. 1, dorsal view; 2, ventral view; 3, lateral view. Fig. 4-7: Cephalic fan of *S. vittatum* larva. 4, ventral view; 5, ventral view of stem; 6, primary fan base; 7, secondary fan base. ant. = antenna, apo. = apodeme, bl. = blades, b. m. f. = base of medial fan, b. p. f. = base of primary fan, b. s. f. = base of secondary fan, c. apt. = cephalic apotome, c. c. l. = cephalic cleavage lines, cer. scl. = cervical sclerite, c. fan = cephalic fan, ext. Sc₁ = extension of Sc₁, hd. spot = head spot, hypo. = hypostomium, int. r. = intermediate ray, l. = lateral, labr. = labrum, l-h. = labio-hypopharyngeal complex, l. lobe = lateral lobe, m. = medial, man. = mandible, max. = maxilla, m. f. = medial fan, m. lobe = medial lobe, oc. = ocelli, pa. b. = postantennal buttress, Pb = dorsal sclerite of fan stem, p. f. = primary fan, pg. = postgena, pg. br. = postgenal bridge, pg. cl. = postgenal cleft, Pl = dorsal sclerite of cephalic fan stem, postoc. = postociput, p. r. = primary ray, p. t. p. = posterior tentorial pits, Sc₁ = sclerite of fan stem, s. f. = secondary fan, s. r. = secondary ray.

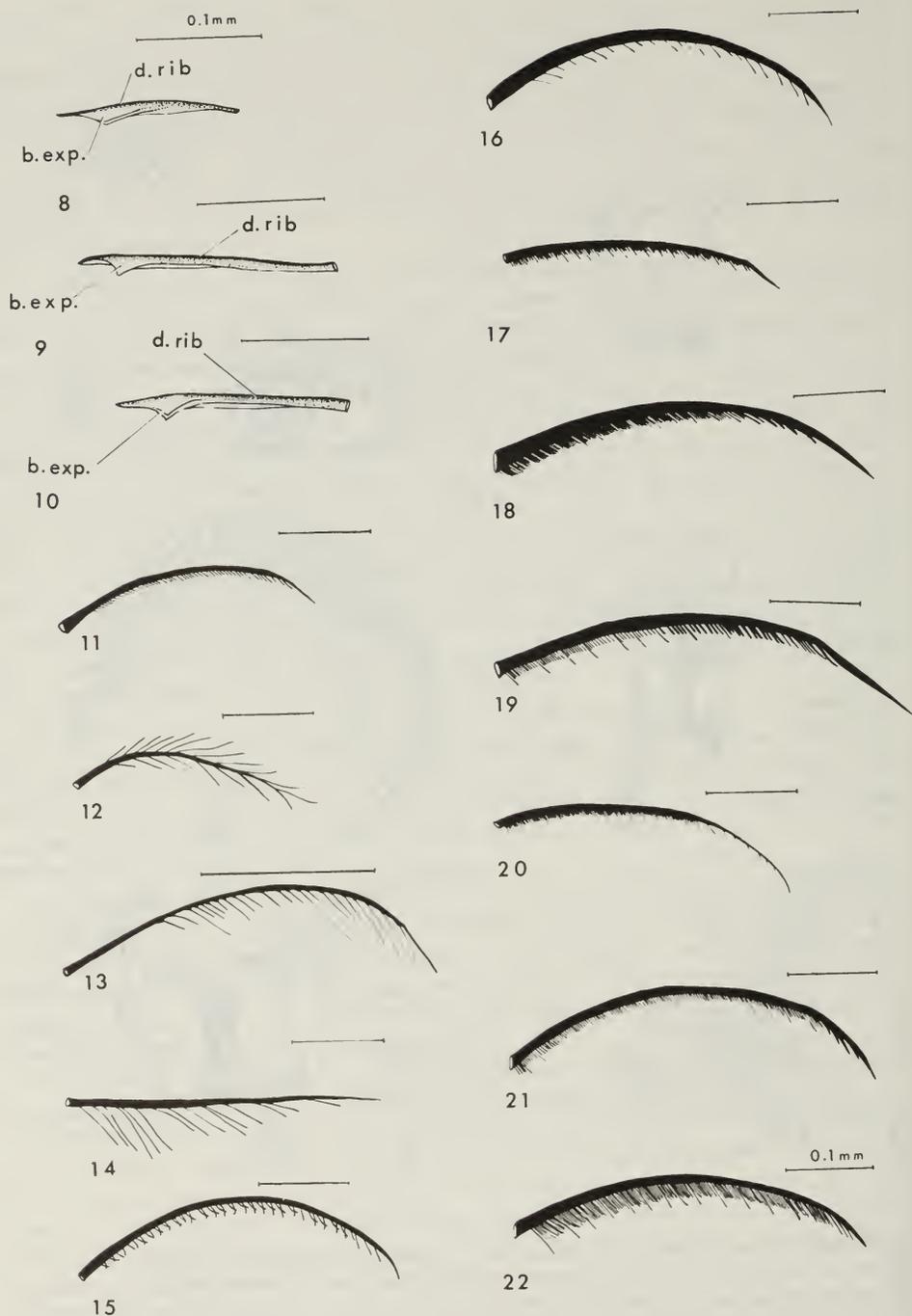


Fig. 8-22. Fig. 8-10: Bases of primary rays of *S. vittatum* larva. 8, lateral ray; 9, mid-fan ray; 10, medial ray. 11, primary ray of *S. vittatum*; 12, secondary ray of *S. vittatum*; 13, intermediate ray of *S. vittatum*. 14, medial ray of *C. dacotensis*. Fig. 15-22: primary rays. 15, *C. dacotensis*; 16, *S. decorum*; 17, *S. venustum*; 18, *P. fontanantum*; 19, *P. frohnei*; 20, *P. fuscum*; 21, *P. multidentatum*; 22, *P. travisi*. b. exp. = basal expansion, d. rib = dorsal rib.

blades are represented in Fig. 7). These decrease in size towards the secondary fan. These blades probably represent degenerate rays. The curve of the base line of the secondary rays contributes to the whirling of the rays during opening and closing of the secondary fan. When the fan is fully expanded, the rays cover an angle of about 270 degrees. They overlie the basal quarter of the medial primary rays. Lacking a dorsal rib, the secondary rays are weaker than the primary rays. The bases of the individual rays are triangular, similar to those of the primary rays, but there is less variation in the basal expansions. Unlike the bases of the primary rays, the bases of the secondary rays are flexible. The secondary ray itself is rigid.

Table 2. Numbers of rays in the three fans of larvae of four species of blackflies at three stages of development.

Size of larvae	Species	Primary	Secondary	Medial
Large	<i>C. dacotensis</i>	47-56	23-35	10-15
	<i>S. decorum</i>	54-64	29-39	9-15
	<i>S. venustum</i>	34-45	12-28	8-12
	<i>S. vittatum</i>	42-54	20-30	9-14
Medium	<i>C. dacotensis</i>	39-50	22-32	7-12
	<i>S. decorum</i>	44-54	16-35	6-12
	<i>S. venustum</i>	41-54	20-29	9-13
	<i>S. vittatum</i>	42-54	11-29	6-11
Small	<i>C. dacotensis</i>	19-32	6-14	2- 8
	<i>S. decorum</i>	44-46	16-22	6-10
	<i>S. venustum</i>	18-36	10-25	5- 9
	<i>S. vittatum</i>	27-46	9-16	4- 7

The trichiation of the secondary fan is similar in all species, however, the secondary rays of *S. decorum* larvae are crescent-shaped. Secondary rays bear microtrichia on their ventral and lateral surfaces (Fig. 12). The microtrichia are longer and denser than those of the primary rays and they form an acute angle with the ray, giving it a plumose appearance.

The medial rays differ from the rays of the other fans in that they lie in a straight line, are not curved, and have bulbous bases. The rays lie parallel to each other and do not spread out when the fan is opened. The rays are flexible and the bases are membranous.

The medial rays of *C. dacotensis* (Fig. 14) and *S. vittatum* bear microtrichia. These are sparse and arise from small notches on one side of the ray. Larvae of *S. decorum* and *S. venustum* do not have microtrichia on the medial rays. This situation is found among other species (Fortner, 1937; Rubtsov, 1964).

The single intermediate ray is present in all age groups of larvae of all species studied. It is located between the primary and medial fans, adjacent to the most lateral primary ray. It resembles the medial rays of *C. dacotensis* and *S. vittatum* in trichiation and is straight and colourless (Fig. 13).

In the first instars of *C. dacotensis* and *S. vittatum* the cephalic fan is functional but only the primary fan is present. The primary rays have the same basal expansion found in later instars but have no microtrichia. Neither the medial nor the lateral lobe is present. The

rod Sc_1 is present and has the expanded distal tip. It bears the apodeme of the cephalic fan muscle. The structure of the cephalic fan of *S. pictipes* first instar, described by Wood (1963), is very similar to that of these two species.

The cephalic fan of the second instar of both *C. dacotensis* and *S. vittatum* is fully formed.

The dimensions of the primary fans vary between species and between larvae of different ages. The midfan widths of the open fan are tabulated below for the four species studied (Table 3). The frontal area (F. A.) of the fan was calculated from the modified equation for the area of an ellipse: $F. A. = \frac{ab\pi}{4}$ where, a = width of the fan, b = depth of the fan.

Table 3. Dimension in microns of the expanded primary fan of four species of blackfly larvae at three stages of development.

Size of larvae	Species	Width	Depth	Frontal Area (mm ²)
Large	<i>C. dacotensis</i>	1020-1200	420-540	0.34-0.51
	<i>S. decorum</i>	800-1060	240-340	0.15-0.26
	<i>S. venustum</i>	800- 880	260-420	0.16-0.29
	<i>S. vittatum</i>	890-1120	380-540	0.17-0.48
Medium	<i>C. dacotensis</i>	380- 700	140-380	0.04-0.21
	<i>S. decorum</i>	-	-	-
	<i>S. venustum</i>	460- 720	200-320	0.07-0.18
	<i>S. vittatum</i>	780- 850	360-460	0.22-0.31
Small	<i>C. dacotensis</i>	260- 340	80-160	0.02-0.04
	<i>S. decorum</i>	-	-	-
	<i>S. venustum</i>	200- 400	80-200	0.01-0.06
	<i>S. vittatum</i>	460- 560	200-260	0.08-0.12

The cephalic fans of the *Prosimulium* species examined differ from those already described in several probably functionally insignificant ways. Because of its diagnostic value, the arrangement of the rays of the secondary fan is important. When the fan expands, the apices of the ray lie in a straight line. This feature differentiates *Prosimulium* species, as well as some *Gigantodax* and *Cnephia* species (Wood, 1963), from other genera of blackflies (Sommermann, 1953). The arrangement of the bases of the secondary rays, in addition to the length of the rays, contributes to this distinction. Wood (1963) stated that the number of rays and the length of the base line of the secondary fan is a fundamental difference between the secondary fan of *Prosimulium* species and that of other species of blackflies.

The secondary fan of *Prosimulium* larvae is separated from the primary one by about six blades. These are of equal size. The separation between medial and primary fans is obscured by four to six large rays all of which resemble the intermediate ray. Wood (1963) represented only one such ray for *Prosimulium fontanatum* Syme and Davies larvae. The medial rays lack microtrichia.

In general, the trichiation of *P. fontanatum*, *Prosimulium frohnei* Sommermann, *Prosimulium fuscum* Syme and Davies, *Prosimulium multidentatum* Twinn and *Prosimulium travisi* Stone resembles that of *S. venustum*, but the pattern of trichiation of the primary rays is more pronounced (Fig. 18 to 22). Differences of pattern of trichiation are specific.

Labrum. — The labrum in all species studied was very similar. It is a beak-shaped structure overhanging the cibarium (cib., Fig. 56), and is joined to the cephalic apotome by a membranous area. This area (mem. ar., Fig. 23, 24) lacks bristles but is provided with numerous sensory hairs. In *S. vittatum* larvae the margin of the cephalic apotome immediately dorsal to the membrane has three patterns of pigmentation (Fig. 25): a straight border, a border with a small indentation in the midline, or a border with a protruding central lobe.

The posterior margin of the labrum is marked by a single line of well-developed simple bristles with bulbous bases (Fig. 23). Behind this line there is a medial pair of sensory hairs. The posterior margin of the main bristled area of the labrum is marked by another straight line of bristles; these have triangular bases. The main bristled area of the labrum is covered by shorter bristles which occur in groups of two to four. In the midline towards the apex of the labrum there is a spindle-shaped patch of stout, blunt, conical spines (c. sp. br., Fig. 23) which are located on an elevated base. In *P. fontanatum* and *P. multidentatum*, they are poorly developed; in *P. frohnei*, they are dorsally located. In other simuliids these spines have been described as labral hooks similar to those of the thoracic proleg and the posterior disc (Hora, 1930), and as pectinate hairs (Grenier, 1949).

The labrum is strengthened by a spade-shaped sclerite (labr. scl., Fig. 24, 26). Some authors have considered this sclerite to consist of three sclerites (Puri, 1925; Wood, 1963; Rubtsov, 1964 and others). Rubtsov stated that each sclerite bears a brush; this was not found among the species studied. Other workers consider the sclerite as a unit (Davies, 1964). The latter interpretation is accepted here as no sutures are evident. However, in the following description the sclerite is considered in three sections; the apex (ax.), the connecting rod (conn. r.) and the basal piece (b. p., Fig. 26). The basal piece is at right angles to the connecting rod on the same plane. The apex of the sclerite forms the tip of the ventral wall. The anterior margin of the apex is dentate (Fig. 26). The teeth are peg-shaped, usually of equal length and of varying widths. However, the lateral teeth of the labral sclerite of *P. travisi* larvae are curved and longer than their fellows. In the larva of an unidentified species of blackfly, four of these teeth, two medial and two lateral, have neural connections (D. A. Craig, *personal communication*), showing that the teeth are sensory. The lateral borders of the sclerite are composed of three to five sclerotized blades (l. bl.) each of which bears several bristles arranged in a row (Fig. 26). The basal piece of the sclerite passes inwards and supports the epipharynx (epi., Fig. 56). Ventrally the connecting rod supports a lobe (v. lobe) bearing a dense brush of long, thick, compound bristles (Fig. 24). Grenier (1949) considered this lobe to be the epipharynx.

The cuticle of the labrum is flexible. The bristles are stiff although the shorter, central ones of the main bristled area are more flexible than the others. The apex of the labral sclerite is of more rigid cuticle.

The labrum has only one pair of muscles, the labral retractors (labr. r., Fig. 24). All but one pair of labral retractors have been lost in other nematocerous larvae as well (Hinton, 1958a; Chaudonneret, 1963). In simuliids the retractors insert on the ventral surface of the labral sclerite where the apex joins the connecting rod. They originate at the anteromedian head spot in the midline of the cephalic apotome. Contraction of the labral retractors moves the labrum ventrally and orally. Chaudonneret (1963) stated that the elasticity of the cuticle and the pressure of the internal environment play an antagonistic role to that of the labral muscles. The cavity of the labrum is filled by a pair of dorsal glands (d. gl., Fig. 56) which open directly into the cibarium.

Midway between the labrum and the stem of the cephalic fan there is a patch of compound bristles (Fig. 24). The number, from 15 to 50, and colour vary with species.

Mandibles. — The mandibles are broadly rectangular and flattened laterally (Fig. 27, 28). They are curved medially and bear brushes on their concave surface. The mandibular articulations have changed position from those of the primitive insect, a trend found among other

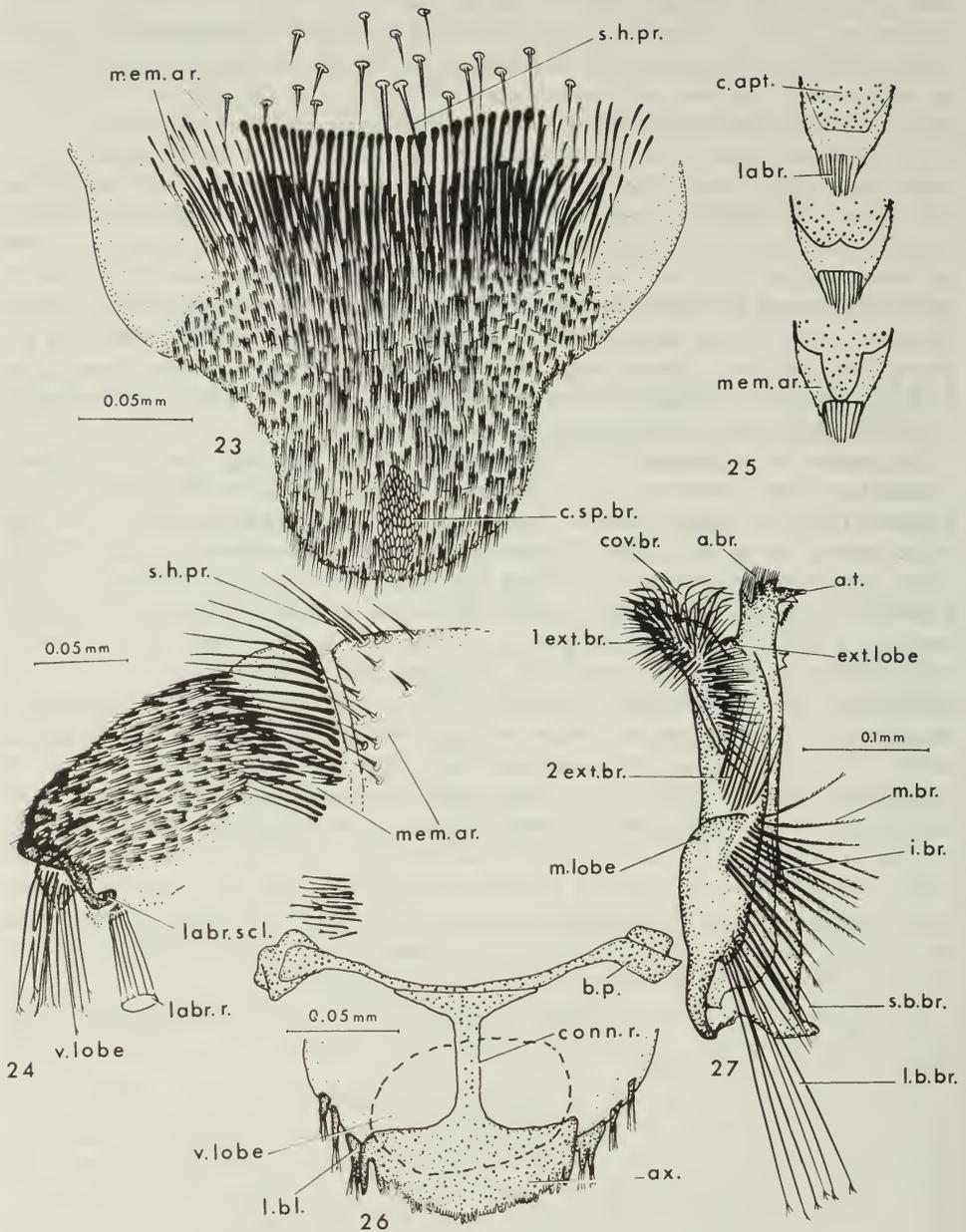


Fig. 23-27. Fig. 23-26, Labrum of *S. vittatum*. 23, dorsal view; 24, lateral view; 25, pigmentation of the anterior of cephalic apotome, not to scale; 26, labral sclerite. 27, mandible of *S. vittatum*, inner view. a. br. = apical brush, a. t. = apical teeth, ax. = apex of labral sclerite, b. p. = basal piece, c. apt. = cephalic apotome, conn. r. = connecting rod, cov. br. = covering brush, c. sp. br. = conical spine-like bristles, 1 ext. br. = first external brush, 2 ext. br. = second external brush, ext. lobe = external lobe, i. br. = inner brush, labr. = labrum, labr. r. = labral retractor muscle, labr. scl. = labral sclerite, l. b. br. = large basal brush, l. bl. = lateral blade, m. br. = middle brush, mem. ar. = membranous area, m. lobe = middle lobe, s. b. br. = small basal brush, s. h. pr. = pair of sensory hairs, v. lobe = ventral lobe.

Nematocera (Cook, 1949). The mandibles of blackfly larvae articulate in sockets formed by strong, heavily sclerotized X-shaped structures, the postantennal buttresses (pa. b., Fig. 3). Two ventrally-directed arms of each buttress provide a pivot for the base of the lateral sides of the mandible. The anterior dorsal arm of the buttress supports the base of the wall of the cephalic fan; the fourth arm passes ventral to the antenna. With its points of articulation midway along the ventral arm of the buttress, the mandible moves in a plane forming an angle of 30 to 40 degrees with the vertical plane through the longitudinal axis of the body. This angle is subsequently called the angle of articulation.

The base of the mandible is strengthened by a thick, strongly sclerotized ridge which follows a longitudinal cleft in the medioventral surface of the mandible. The apodeme of the retractor muscle inserts at the apex of this cleft. The extensor muscle inserts directly opposite at the base of the adoral surface. Both muscles originate at the posterior margin of the postgenae. The extensor consists of five bundles; the retractor consists of three bundles.

The mandible bears three sets of teeth (Fig. 29, 30). There are usually four large, black, heavily sclerotized apical teeth (a. t.), of which three are orientated in different directions with the fourth immediately above these three. *P. frohnei* and *P. travisi* larvae have a fifth tooth which lies adjacent to the fourth. The small, pale inner teeth (i. t.) vary in number between instar and species (Fig. 29, 30). The number and orientation of the marginal teeth (m. t.) vary with species. In *S. vittatum* larvae there are two apically directed teeth; the basal one is the smaller one. *S. venustum* larvae have two to three marginal teeth at right angles to the edge of the mandible. The two marginal teeth of *C. dacotensis* larvae may point either apically or basally. *Prosimulium* larvae have 8 to 14 marginal teeth (Fig. 30). Some of the marginal teeth of *P. frohnei* and *P. travisi* have compound apices.

The mandible bears eight brushes (Fig. 27, 28). The apical brush (a. br.) is made up of rows of short, fine bristles of equal length. They are arranged on small lobes and curve towards the apical teeth. The first external brush (1 ext. br.) stretches from the apex of the mandible to the middle lobe (m. lobe), midway along the concave surface. It consists of numerous, fine bristles with relatively rigid bases. The second external brush (2 ext. br.) arises from the base of the middle lobe. Its few long bristles are directed apically. The middle brush (m. br.) is fan-shaped and its bristles bear microtrichia. Basal to the middle brush there is a small basal brush (s. b. br.) consisting of fine bristles. The inner brush (i. br.), consisting of three to five thick bristles, arises from the apex of the mandibular cleft and is apically directed.

The covering brush (cov. br.) arises distal and medial to the external lobe (ext. lobe) (Fig. 27) located at the apex of the mandible (Fig. 29). The bristles are compound and arise from individual lobes. In contrast to other compound bristles, these branch close to their bases. Both covering brush and the first external brush deflect away from the mandible and so describe a 'V' with the apical teeth (Fig. 27, 52). This deflection and the curve of the bristles permit the two apical brushes to curve over the retracted primary cephalic fan.

The large basal brush (l. b. br.) is the second brush composed of compound bristles. Rubtsov (1964) divided this brush into two parts: large basal bristles and small basal bristles. However, here the 10 to 15 bristles are all long and straight.

The mandible bears small, sensory hairs scattered over both oral and adoral surfaces. There is a pair of large sensory hairs on the apical surface immediately behind the first external brush (Fig. 28). Small spines are present on the dorsobasal corner and on the apical lobe. The basal spines of *S. decorum* larvae are arranged in rows. A large apical spine is present on the ventral surface just behind the inner teeth. In *C. dacotensis* and *S. venustum* larvae this spine is oddly twisted. *Prosimulium* species lack the spine.

To compare the size of the mandible of the three age groups of the four species, three

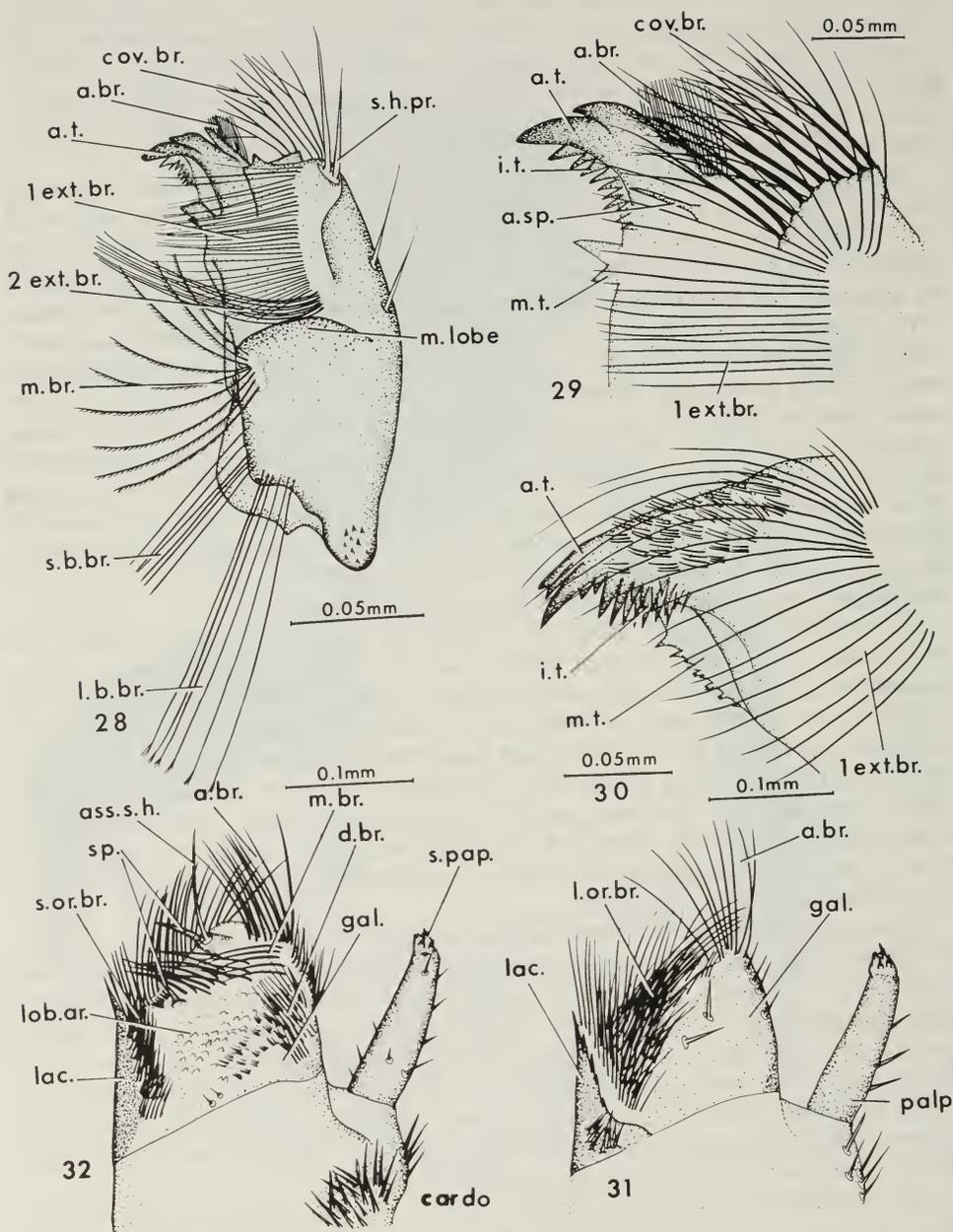


Fig. 28-32. 28, Mandible of *S. vittatum*, lateral view; 29, apex of mandible of *S. vittatum*; 30, apex of mandible of *P. travisi* larva; 31, right maxilla of *S. vittatum*, dorsal view; 32, left maxilla of *S. vittatum*, ventral view. a. br. = apical brush, a. sp. = apical spine, ass. s. h. = associated sensory hair, a. t. = apical teeth, cov. br. = covering brush, d. br. = diffuse brush, 1 ext. br. = first external brush, 2 ext. br. = second external brush, gal. = galea, i. t. = inner teeth, lac. = lacinia, lob. ar. = lobulate area, l. b. br. = large basal brush, m. br. = middle brush, m. lobe = middle lobe, m. t. = marginal teeth, s. b. br. = small basal brush, s. h. pr. = pair of sensory hairs, s. or. br. = small oral brush, sp. = spine, s. pap. = sensory papillae.

parameters were measured: (1) the distance between the apex of the covering brush and the base of the second external brush, (2) the distance between the apex of the covering brush and the base of the middle brush, (3) the distance between the apex of the covering brush and the base of the large basal brush (Table 4). Measurements were made on five larvae in each category of each species.

Table 4. Distance in microns between the covering brush 'c', and the base of the second external brush 'e', the middle brush 'm', and the large basal brush 'lb' of the mandibles of four species of blackfly larvae at three stages of development.

Size of larvae	Species	c-e	c-m	c-lb
Large	<i>C. dacotensis</i>	140-180	180-200	220-310
	<i>S. decorum</i>	150-180	160-190	220-280
	<i>S. venustum</i>	130-150	130-180	220-280
	<i>S. vittatum</i>	140-150	160-180	140-290
Medium	<i>C. dacotensis</i>	50-100	50-120	80-180
	<i>S. decorum</i>	-	-	-
	<i>S. venustum</i>	70-120	90-140	140-220
	<i>S. vittatum</i>	100-120	120-140	180-220
Small	<i>C. dacotensis</i>	40- 50	50- 60	80-110
	<i>S. decorum</i>	-	-	-
	<i>S. venustum</i>	40- 60	50- 80	90-130
	<i>S. vittatum</i>	70- 80	80-100	120-150

The mandibles of the first instar of *S. vittatum* have an almost complete set of teeth and brushes. However, there are no marginal teeth and the large basal brush is represented by only one bristle. The only other anatomical difference is the position of the pair of sensory hairs on the apex. In first instars it arises in front of the first external brush rather than behind as in later instars. The mandible of the second instar has a similar smaller number of component parts but the pair of sensory hairs is behind the first external brush.

On some *S. vittatum* larvae the bristles of the large basal brush have a globular structure which has not been described elsewhere (Fig. 55). These bulbs are always found on the bristles at the region where they branch. Usually two or three bristles in one brush each have a bulb. On later instars the bulbs are darkly coloured; on younger larvae they are pale. The bulbs turn pink and subsequently become colourless when treated with a 4% solution of potassium hydroxide but they do not dissolve. The colour returns when the larvae are returned to alcohol. I have observed the bulbs preserved in 90% ethanol, 70% ethanol after Bouin's fixative, and in a mixture of glacial acetic acid and 70% ethanol. I have also observed them on specimens mounted in Canada balsam after exposure to alcohols and xylene. Larvae bearing these bulbs have been found in one population from Ontario (railway yards, Belleville) and two populations in Alberta (Johnson Lake inlet, Banff National Park; Whitemud Creek, Edmonton). The proportion of larvae of the Ontario population is tabulated below (Table 5). A few larvae, about 5%, of the Johnson Lake collections had bulbs. One specimen of *P. travisi* collected in Alberta had a bulbous structure resembling those on the mandible of *S. vittatum* larvae. It was on a large basal bristle. Two specimens of *S. vittatum* had similar bulbs on simple labral bristles.

Table 5. Proportion of *S. vittatum* larvae from an Ontario population bearing bulbs on large basal bristles of the mandibles.

Size of larvae	On both mandibles		On one mandible		No bulbs		Total	
	no.	%	no.	%	no.	%	no.	%
Large	16	45.7	4	11.4	15	42.9	35	100.0
Medium	10	28.6	4	11.4	21	60.0	35	100.0
Small	3	8.6	2	5.7	25	71.4	30	100.0
No. exam.	29	29.0	10	10.0	61	61.0	100	100.0

These bulbs are not a fungus (H. T. Brodie, Department of Botany, University of Alberta, *personal communication*) neither are they a particle impaled by the bristles. They may be a swelling of the apices of the bristles or some type of sensory organ.

Maxillae. — The maxilla of blackfly larvae is mitten-shaped, the maxillary palp representing the thumb (Fig. 31, 32). The structure of the maxillae is consistent among all the species studied. The maxillae lie ventral to the mandibles and dorsolateral to the labio-hypopharyngeal complex. The palp is aboral.

The maxilla is sclerotized in three areas which Rubtsov (1964) considered as the cardo, lacinia and galea. According to Cook (1949), the maxilla is reduced and consists of the stipes which is partly sclerotized and partly membranous. The sclerotized areas are of relatively inflexible cuticle; the other areas, except the pigmented area of the palp, are of flexible cuticle.

The maxillary lobe bears five brushes. The ventral adoral surface bears a diffuse brush (d. br.) composed of fine, randomly-arranged bristles. Medial to this brush, on the apical half of the lobe, the middle brush (m. br.) is similarly composed of fine, simple bristles. A large oral brush (l. or. br.) lies adjacent to the middle brush. This brush is composed of 10 to 15 rows each containing 12 to 15 long, thick and darkly-pigmented bristles. Laterobasal to the large oral brush lies a small oral brush (s. or. br.) similarly composed of bristles arranged in rows. The apical brush (a. br.) consists of six to ten simple bristles which are long and thick and have expanded bases.

On its distal border, the lacinia bears a row of teeth which increase in size towards the apex of the lacinia. The most distal tooth is spine-like, long and curved at its apex. The lacinia has one small patch of bristles on the corner adjacent to the small oral brush. The galea bears a large, central sensory hair and five to eight small apical hairs.

Basal to the middle brush there is a bare area with a lobulate surface (lob. ar.). These lobes are present on all specimens and have been described elsewhere (Rubtsov, 1964).

The maxillary lobe bears two large sensory spines (sp.) (D. A. Craig, *personal communication*). The largest is curved, stout, and often blunt, and shares a raised base with another large sensory hair (ass. s. h.). The second spine is more basal and lies adjacent to a patch of several very short, densely-arranged bristles.

The palp of the maxilla is one-segmented (Fig. 31, 32). The length of the palp in relation to the maxillary lobes varies among species. The palp bears six to ten sensory hairs over its pigmented surface and four to six sensory papillae (s. pap.) on its apex. There is a patch of five to ten sensory hairs at the base of the palp. These numbers of sensory hairs and papillae vary with species. On the ventral surface of the cardo there is a patch of 20 to 25 fine, unpigmented bristles. *S. venustum* larvae have an additional patch of fine bristles basal to the maxillary lobe.

The maxilla has two muscles. The retractor, consisting of three bundles, inserts on the

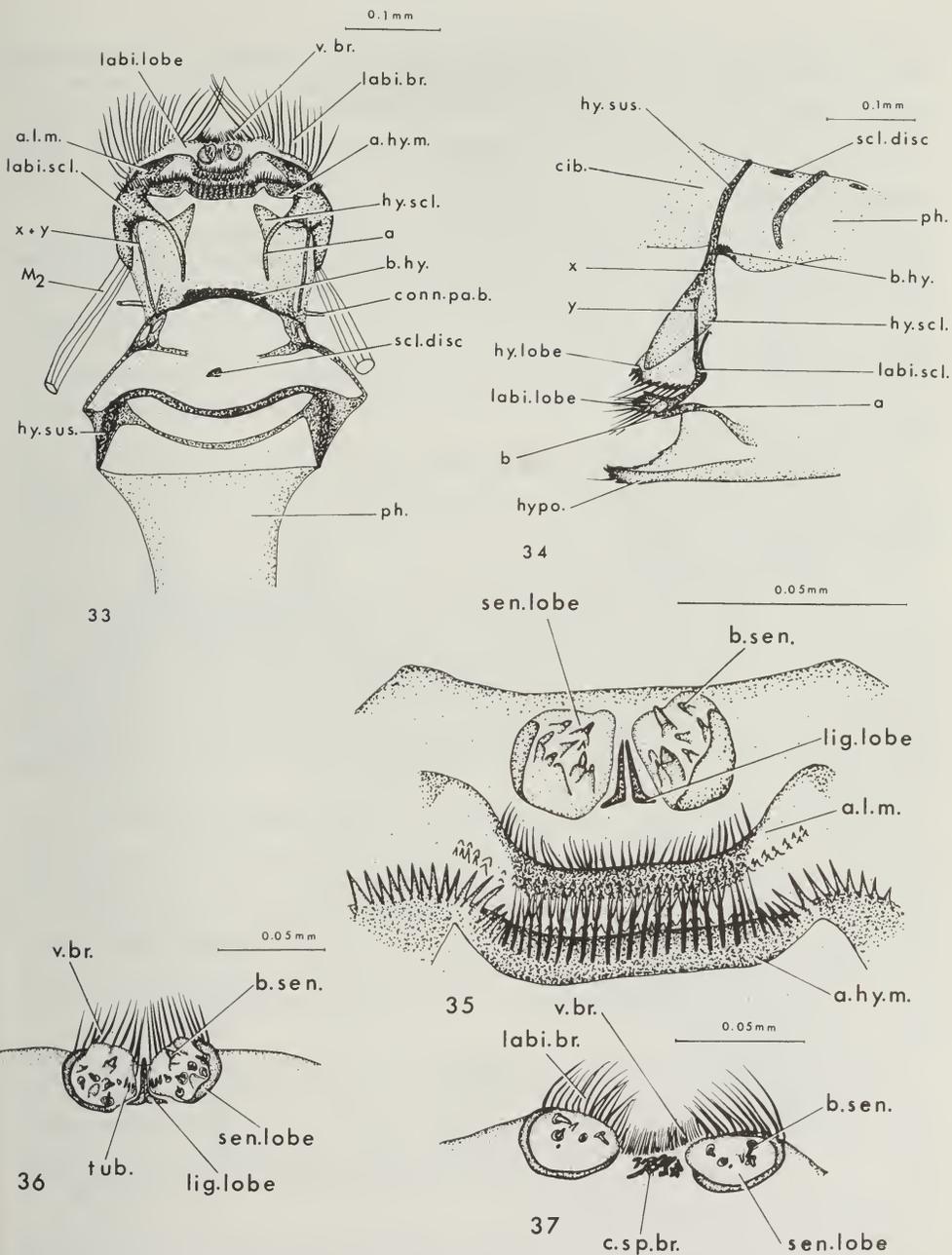


Fig. 33-37. Fig. 33-34: Labio-hypopharyngeal complex of *S. vittatum*. 33, dorsal view; 34, lateral view. Fig. 35-37: apex of labial lobe. 35. *S. vittatum*; 36, *C. dacotensis*; 37, *P. travisi*. a = bar 'a', a. hy. m. = anterior margin of the hypopharyngeal lobe, a. l. m. = anterior margin of the labial lobe, b = bar 'b', b. hy. = base of hypopharynx, b. sen. = basiconic sensilla, cib. = cibarium, conn. pa. b. = connection to postantennal buttress, c. sp. br. = conical spine-like bristles, hypo. = hypopharynx, hy. lobe = hypopharyngeal lobe, hy. scl. = hypopharyngeal sclerite, hy. sus. = hypopharyngeal suspensorium, labi. br. = labial brush, labi. lobe = labial lobe, labi. scl. = labial sclerite, lig. lobe = lobes of the ligula, M₂ = labial retractor muscle, ph. = pharynx, scl. disc = sclerotized disc, sen. lobe = sensory lobe, tub. = tubercles, v. br. = ventral brush, x = bar 'x', y = bar 'y'.

middle of the oral surface level with the base of the palp. It originates near the posterior border of the postgena, and moves the maxilla dorsomedially towards the cibarium. The extensor inserts basal to the retractor at the medioventral corner of the postgena, ventral to the retractor. It moves the maxilla ventromedially. The palp has no muscles (Craig, 1968).

The maxilla of the first instar of *S. vittatum* is fully developed. The bristles are smaller and fewer; the palp has two or three sensory hairs.

Labio-hypopharyngeal complex. — The labium and the hypopharynx are considered together because they form a complex unit and because the homologies of the labium are under dispute (Crosskey, 1960; Craig, 1969). The labio-hypopharyngeal complex (l-h., Fig. 33, 34) fills the ventromedial part of the mouth area. The complex is broadly semicircular and is in two main parts. The dorsal part, called here the hypopharyngeal lobe (hy. lobe), lies directly over the ventral labial lobe (labi. lobe). Both lobes are weakly sclerotized but are strengthened by a complicated set of relatively strong sclerites. They are covered ventrally by the hypostomium.

The dorsal surface of the base of the hypopharynx is strongly sclerotized (b. hy.) and marks the anterior of the cibarium. It is contoured to fit the labrum. At the lateral margin of this ridge the suspensorium is connected to the ventroposterior arm of the postantennal buttress by membranous cuticle (conn. pa. b.).

The anterior margin of the hypopharyngeal lobe has two rows of bristles (Fig. 35). The medial bristles of the posterior row are compound. The labial margin bears one row of short bristles and one row of blunt, paired teeth. In *C. dacotensis* and *S. venustum* larvae, the medial bristles are compound; in other species studied, they are simple. Grenier (1949) numbered the rows of hypopharyngeal and labial bristles; rows one to three are hypopharyngeal and row four is labial. His third row of the hypopharynx is probably the medial bristles of the anterior row which are longer than their fellows and point dorsally rather than anteriorly.

The labial lobe lies ventral to the labial margin and bears a brush on its ventroapical surface (labi. br.). The dorsoapical surface bears two prominent spherical sensory lobes (sen. lobe, Fig. 35 to 37). These bear a number of basiconic sensilla (b. sen.). *C. dacotensis* larvae have six on each lobe. *Simulium* species have six to eight and *Prosimulium* species have five. Some species have a trio of small tubercles (tub., Fig. 36) on the medial part of the sensory lobes. Rubtsov (1964) referred to them as *Höcker* (= tubercle). In *C. dacotensis* and *S. decorum* larvae they are crescent-shaped; in *S. venustum*, circular. *Prosimulium* and *S. vittatum* larvae lack them.

The lobes of the ligula (lig. lobes) are present medial to the sensory lobes (Fig. 35, 36). These are paired, slender, L-shaped, and strongly sclerotized. Ventral to the lobes of the ligula there is a small brush of short bristles (v. br., Fig. 36, 37). The *Prosimulium* species studied have a group of stout, spine-like bristles similar to those of the dorsum of the labrum (Fig. 37) in place of paired ligular lobes. These are immediately dorsal to the ventral brush and medial to the sensory lobes.

The silk (salivary) canal (sk. can.) is formed dorsally by the hypopharyngeal lobe and ventrally by the labial lobe. The paired salivary ducts pass anteriorly from the salivary glands along the midline of the head capsule and fuse to form the silk canal in the medioventral part of the head. The silk canal continues forward and expands laterally at the level of the first hypopharyngeal bar to join the corners of the labio-hypopharyngeal complex. The wall of the silk canal is reinforced by annular thickenings in its cuticular intima. The fusion of the salivary ducts begins ventrally, and the dorsal surface of the canal has a dorso-medial projection formed from the dorsal walls of the ducts for some distance anteriorly (Fig. 57). The silk thread emitted from the silk canal is dorsoventrally flattened and grooved

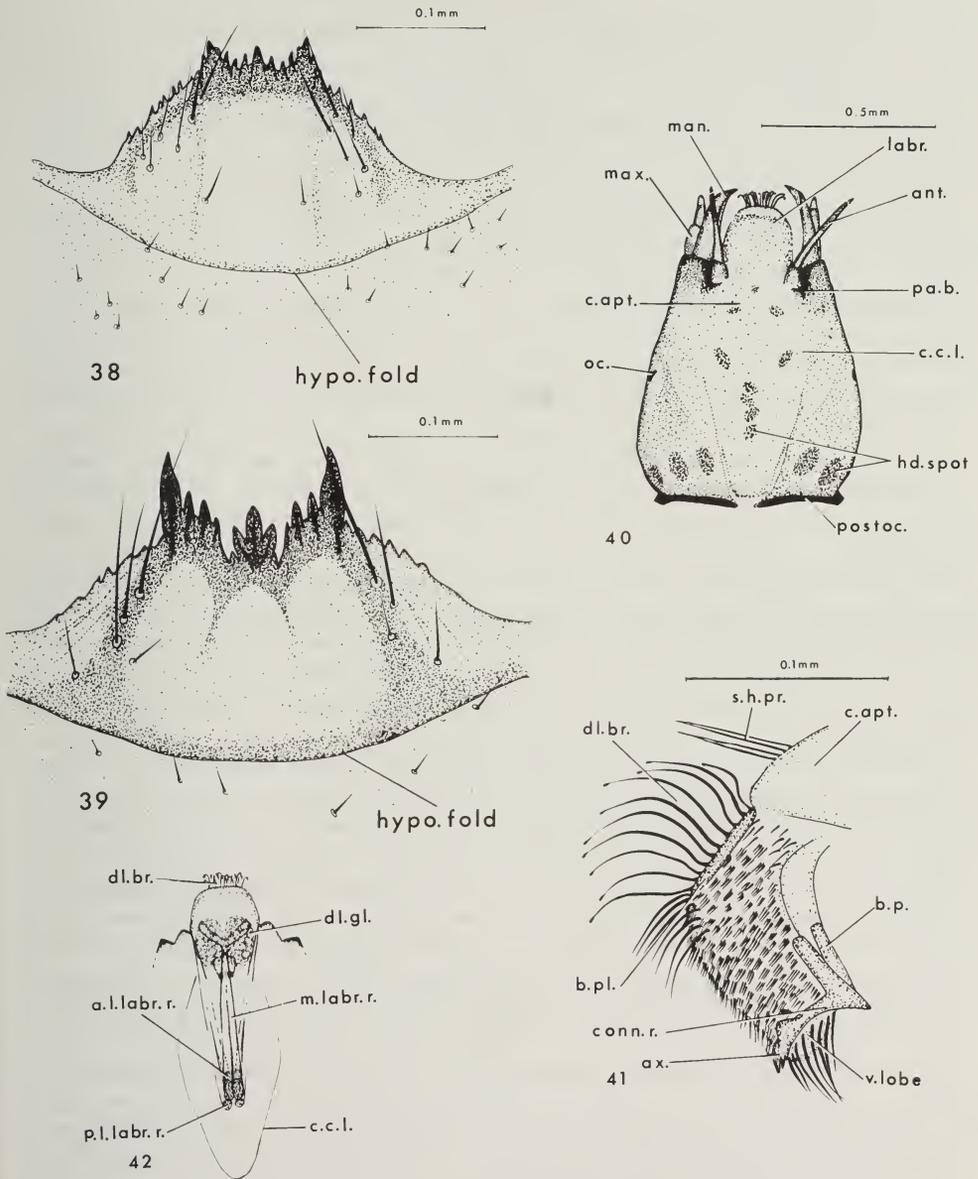


Fig. 38-42. 38, Hypostomium of *S. vittatum*. 39, hypostomium of *P. trivisi*. 40, head capsule of *T. biclavata*. 41, labrum of *T. biclavata*, lateral view. 42, sketch of labral musculature of *T. biclavata*, not to scale. a. hy. m. = anterior margin of hypopharyngeal lobe, a. l. labr. r. = anterior lateral labral retractor muscle, a. l. m. = anterior margin of the labial lobe, ant. = antenna, ax. = apex of labral sclerite, b. p. = basal piece, b. pl. = basal plate, b. sen. = basiconic sensilla, c. apt. = cephalic apotome, c. c. l. = cephalic cleavage lines, conn. r. = connecting rod, c. sp. br. = conical spine-like bristles, d. gl. = dorsal gland, dl. br. = dorsal brush, hd. spot = head spot, hypo. fold = hypostomial fold, labr. = labrum, labi. br. = labial brush, lig. lobe = lobes of the ligula, sen. lobe = sensory lobe, man. = mandible, max. = maxilla, m. labr. r. = medial labral retractor muscle, oc. = ocellus, pa. b. = postantennal buttress, p. l. labr. r. = posterior labral retractor muscle, postoc. = postocciput, s. h. pr. = pair of sensory hairs, tub. = tubercles, v. br. = ventral brush.

along the mid-dorsal line, either because of the dorsomedial projection of the canal or the paired salivary ducts.

The labio-hypopharyngeal complex has two pairs of muscles. The paired muscle of the 'press' of the silk canal, M_3 (after Grenier, 1949) stretches from the dorsolateral surface of the hypopharynx to the roof of the silk canal (Fig. 57). The second muscle, M_2 (after Grenier, 1949), inserts on the posterior tip of the labial sclerite (Fig. 33) and originates at the posterior margin of the postgenae adjacent to the postgenal cleft. It pulls the labial lobe posteriorly.

There is a pair of ventral glands (v. gl., Fig. 57), histologically resembling the dorsal glands, at the corners of the labio-hypopharyngeal complex adjacent to the labial sclerite. The glands have no apparent opening.

Hypostomium. — The hypostomium is a double-walled triangular plate of strong cuticle. The margin of the inner wall is distinguished by the hypostomial fold (hypo. fold, Fig. 38, 39) (Wood, 1963). The hypostomium is concave, forming a sheath for the labio-hypopharyngeal complex. The midline is invaginated dorsally near the apex and forms a ridge between the two sensory lobes of the labium.

The anterior margin of the hypostomium is strongly sclerotized and bears numerous teeth which have patterns of specific diagnostic value (Fig. 38, 39). The taxonomically important characters are the number of teeth, their relative sizes, and their simple or compound nature.

The hypostomium bears two rows of sensory hairs, one parallel to each of the lateral, dentate margins. The apical hairs are longer than the basal ones. The numbers of hairs vary with larval instar and with species: *C. dacotensis* larvae have one to five; *S. decorum* larvae, two to five; *S. venustum* larvae, two to six; *S. vittatum* larvae, two to nine; *Prosimulium* larvae, three to four. The number increases with instar. Ventral to the hypostomial fold there is a number of randomly-arranged sensory hairs.

Cibarium. — The anterior margin of the cibarium (cib., Fig. 34) is marked by the sclerotized base of the hypopharynx. Anterior to this lies the epipharynx dorsally and the hypopharynx ventrally (Fig. 56). The walls of the cibarium are reinforced by the hypopharyngeal suspensorium (hy. sus., Fig. 33, 34). Midway along its length, the cibarial wall thickens and becomes corrugated. There is a depression in the ventral surface. This region of the cibarium is provided with fine bristles which are continuous with groups of small bristles present on the epipharynx. The bristles on the wall of the ventral depression are longer than those of the dorsal surface. In the midline the bristles are stout, blunt, and conical, resembling those of the spindle-shaped patch on the labrum. Both epipharyngeal and cibarial bristles are directed posteriorly.

The cibarium has two pairs of muscles. Both are dilators. The anterior pair inserts medially on a sclerotized disc on the dorsal wall of the cibarium in between the two rings of the hypopharyngeal suspensorium (disc, Fig. 33, 34). It originates on the dorsal part of the cephalic apotome lateral to the labral retractor, at the anterolateral head spots. The second smaller pair of muscles inserts on a smaller sclerotized disc in the midline of the dorsal wall of the cibarium, posterior to that of the anterior muscles. This originates on the cephalic apotome just posterior and adjacent to the anterior pair of muscles.

Comparison with a non-filtering species

The head capsule of the larva of *Twinnia biclavata* Shewell is more tapered anteriorly (Fig. 40) than that of the other species of blackflies studied. The cephalic cleavage lines converge both anteriorly and posteriorly and the ends of the postoccipt meet dorsally in the midline. The ventral wall of the head capsule is almost complete. The postgenal cleft

is very shallow and the postgenal bridge is complete. The antennae have four articles. There are two sensory papillae distally on the second article.

Labrum. — The labrum of larvae of *Twinnia biclavata* is joined to the cephalic apotome by a membranous area (mem. ar.). The anterior margin of the cephalic apotome is straight rather than curved as in filtering species. The arrangement of the labral bristles differs greatly from that of filtering species studied. There is a well-developed dorsal brush (dl. br.) of simple bristles which are dark, blunt, and curved at their apices (Fig. 41, 43). They differ from those of the larvae of *Twinnia tibblesi* Stone and Jamnback which are pectinate (Davies, 1965). The base of the brush is reinforced by a sclerotized plate, termed the basal plate (b. pl.) by Davies (1965). Immediately ventral to this brush there is a group of thinner, simple bristles. These are shorter than those of the dorsal brush but longer than the rest of labral bristles. They curve ventrally. The lateral and apical areas of the labrum are covered with smaller simple bristles in groups of two to five. All of them are directed medially. The ventral lobe (v. lobe) of the labrum is supported by the connecting rod (conn. r.) of the labral sclerite (labr. scl.). It bears simple bristles which are not so well developed as the compound bristles of the filtering species studied.

The labral sclerite is similar to those of the larvae of the other species studied. The apex (ax.) has 10 to 12 teeth along the anterior margin (Fig. 43). These are longer than the labral teeth of the filtering species studied. The basal piece of the labral sclerite is orientated at right angles to the connecting rod (Fig. 41). It supports the ventral surface of the labrum and epipharynx. The medial pair of sensory hairs on the dorsum of the labrum is well developed. These are immediately posterior to the dorsal brush and not on the cephalic apotome as in other species. There is a scattering of small sensory hairs on the cephalic apotome. The dorsal gland fills the cavity of the labrum. Histologically it is the same as that found in other species but it is composed of fewer cells.

The labrum of *T. biclavata* has two pairs of labral retractor muscles (Fig. 42). The medial pair is homologous with the medial retractor muscle of filtering species. It originates on the midline of the posterior half of the cephalic apotome and inserts on the ventral surface of the labrum immediately posterior to the connecting rod of the labral sclerite. The lateral pair is smaller and each muscle consists of two bundles. These originate respectively anterior and posterior to the medial retractor muscles. The origins of the lateral retractors are marked externally by the median head spots. These lateral muscles pass between the two lobes of the dorsal gland and insert dorsal to the medial retractors at the lateroposterior margins of the labrum. The lateral retractors differ from those described by Davies (1965) in *Twinnia tibblesi* larvae in that they do not insert on the curved rod (c. r.) which articulates with the basal plate of the dorsal brush (see below). Furthermore, the lateral retractors of *T. tibblesi* larvae consist only of one bundle each and this originates posterior to the medial retractors. The insertion of the lateral muscle on the curved rods in *T. tibblesi* indicates that this muscle is homologous to the cephalic fan retractors (Davies, 1965). This suggests here that the two bundles of the lateral muscles and their individual origins in *T. biclavata* possibly foreshadow the complex origin of the three-bundled cephalic fan retractors.

The pair of curved rods present in *T. tibblesi* larvae and *Gymnopsis* sp. larvae (Davies, 1965) is present in *T. biclavata* larvae. The rods lie lateral to the basal plate and appear to articulate with it. They do not form an X-shaped complex as illustrated by Davies for *T. tibblesi* (his Fig. 47, 1965). The curved rods (c. r., Fig. 43, 44) are immediately anterior to the bare knobs found in filtering species adjacent to the cephalic fan stem (Fig. 1, 3). They are in the same relative position as the cephalic fan stem sclerites in filtering species. Davies points out that the orientation of the rods is nearly at right angles to the cephalic fan

stem sclerites. He rejects the theory that the rods or the cephalic fans are tormal, and suggests that the rods are homologous with the cephalic fan sclerites. Wood (1963) considered the curved rods, the sclerites of *Gymnopsis* larvae, and the cephalic fan sclerites all tormal.

Mandible. — The mandible of *T. biclavata* is shorter and stouter than that of filtering species (Fig. 45). The angle of articulation is more parallel to the plane of the longitudinal axis of the body than it is in other species. Therefore, according to Cook's theory (Cook, 1949), *T. biclavata* larvae are more advanced in this respect than filtering forms. The mandible articulates with the postantennal buttress. This is less well developed than it is in the other species studied, having only three arms, one passing on each side of the antennal base and one forming the dorsal mandibular articulation. The fourth arm is represented only by a pocket of rigid cuticle formed by the invagination and thickening of the margin of the head capsule. A projection of the medial side of the mandible articulates with this pocket.

The retractor muscle of the mandible is very well developed. It is composed of four large bundles inserting on a large, sclerotized apodeme located on the oral surface of the mandible. The bundles originate laterally on the posterolateral parts of the postgenae, ventral to the extensor muscle. The ventral bundles originate adjacent to the postgenal cleft; the dorsal, immediately lateral to the labral muscles. The extensor muscle consists of four smaller bundles which insert on a shorter, non-sclerotized apodeme on the adoral side. They originate lateral and dorsal to the retractor muscle. Both these muscles are larger than those of filtering species.

The arrangement of teeth on the mandible differs from that of the other species studied (Fig. 46). There are 10 to 12 teeth arranged in a curved line along the apex. The dorsalmost teeth are largest with the size decreasing towards the base of the mandible. There is an extra basal tooth between the fourth and fifth, or fifth and sixth teeth from the apex. The apices of the teeth are occasionally broken off, presumably during feeding. There are two minute, apically-directed marginal teeth. Three apical spines are present behind some small spines near the base of the marginal teeth.

The brushes of the mandibles are less well developed than those of filtering species (Fig. 45). There are no covering, apical or second external brushes and the first external brush is shorter and composed of small bristles. In filtering species, these four brushes comb the fans. The external lobe which separates the two apical brushes from the mandibular teeth is lacking, as is the inner brush. The bristles of the middle, small basal, and large basal brushes are fewer and finer than those of the filtering species. Only some of the bristles of the large basal brush are compound. The middle lobe is present.

The mandibles have fewer sensory hairs. There is one large sensory hair at the base of the mid-dorsal line and a second about half way up the mid-dorsal line. Some more sensory hairs are present on the oral and adoral surfaces. The pair of sensory hairs with a common base is immediately behind the base of the first external brush and both are smaller than those found in other species.

Maxilla. — The maxilla of *T. biclavata* larvae is similar in shape to that of other species but the maxillary lobe is more tapered at the apex (Fig. 47, 48). The arrangement of brushes is different. There is only one oral brush (or. br.) which has bristles arranged in rows. This is adjacent to the lacinia. The lacinia has numerous patches of very small bristles arranged in groups of two to five, however, it does not have the bristles on its distal border. Apical to the oral brush, the middle brush (m. br.) has long, orally-directed bristles. The apical brush (a. br.), found on both oral and adoral surfaces, has large bristles directed apically. Another large brush, the second apical brush (2 a. br.), lies ventral to the apical brush on the adoral side; this brush is not found in the filtering species. The bristles of the two apical brushes are thick and curved at their apices. The rest of the dorsal surface is bare.

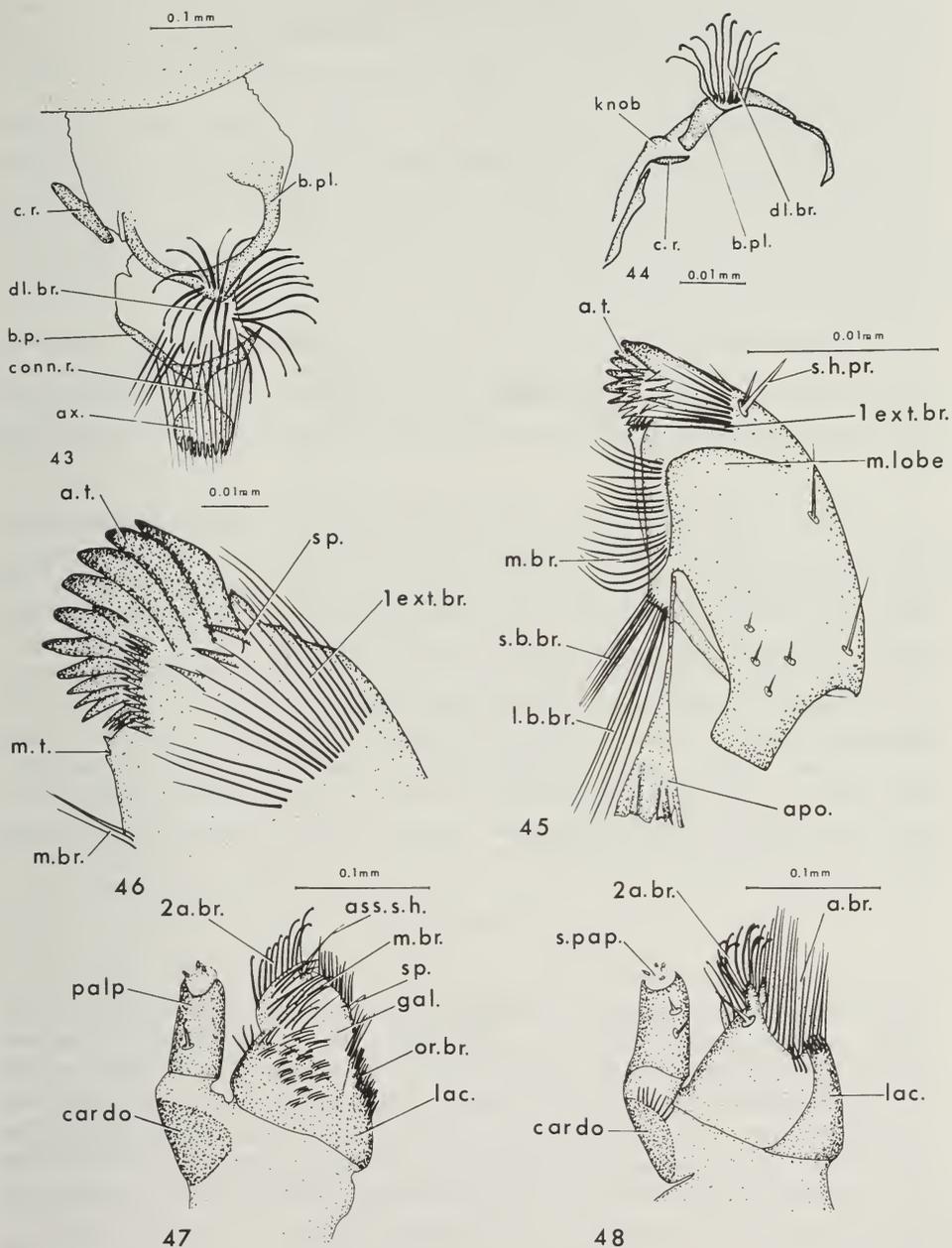


Fig. 43-48. *T. biclavata*. 43, labrum, dorsal view; 44, curved rods; 45, mandible, lateral view; 46, detail of apex of mandible; 47, right maxilla, ventral view; 48, left maxilla, dorsal view. a. br. = apical brush, 2 a. br. = second apical brush, apo. = apodeme, ass. s. h. = associated sensory hair, a. t. = apical teeth, ax. = apex of labral sclerite, b. pl. = basal plate, c. r. = curved rod, conn. r. = connecting rod, dl. br. = dorsal brush, 1 ext. br. = first external brush, gal. = galea, l. b. br. = large basal brush, lac. = lacinia, m. br. = middle brush, m. lobe = middle lobe, m. t. = marginal teeth, or. br. = oral brush, s. b. br. = small basal brush, s. h. pr. = pair of sensory hairs, sp = spine, s. pap. = sensory papillae.

There is no lobulate area.

The maxillary lobe has two spines (sp.). These are much shorter than those of the other species studied. Neither spine has a raised base; the apical spine, however, does have an associated sensory hair (ass. s. h.). On the bare adoral surface there are two sensory hairs, one apical and one basal.

Both muscles of the maxilla originate anterolateral to the mandibular muscles and have two bundles. The smaller bundle of the retractor originates just below the ocelli and dorsal to the larger bundle. The extensor muscle originates on the posterior region of the postgena.

The maxillary palp is the same length as the maxillary lobe. It has three to four small sensory hairs scattered over the pigmented surface and three to four sensory papillae in the centre of the apex. There are two sensory hairs on the adoral side of the palp base. As in other species, a patch of the large bristles is present at the base of the palp.

Labio-hypopharyngeal complex. — The labio-hypopharyngeal complex of *T. biclavata* is similar to that of the other species studied, but the sclerotized framework is less well developed. The connection between the hypopharyngeal sclerite and the hypopharyngeal suspensorium is membranous. Only one ring of the hypopharyngeal suspensorium surrounds the gut.

The hypopharyngeal lobe has two anterior rows of bristles and spines. The dorsal one consists of short spines rather than bristles. The labial margin is not so well developed as that of the other species studied. The ventral brush has uniform bristles of equal length. They are distinct from those of the labial brush but not separated from them (Fig. 49).

The two sensory lobes each bear three sensory papillae but no trio of tubercles. The lobes of the ligulae are paired but they curve laterally at the apex.

The musculature of the labio-hypopharyngeal complex, the ventral glands and the salivary ducts are all similar to those found in the filtering species.

Hypostomium and cibarium. — The hypostomium of *T. biclavata* larvae (Fig. 50) has compound teeth. There are three sensory hairs per row and there is one mediobasal pair.

The cibarium of *T. biclavata* larvae does not differ from that of the other species. Two pairs of dorsal cibarial muscles are present but these are smaller than those of filtering species and do not insert on sclerotized discs.

FEEDING

Feeding behaviour

Blackfly larvae attach themselves to a silken pad on the substratum, usually within 8 to 10 centimeters of the surface of the water, with their posterior circler of hooks. They attach dorsal side down and rotate their body some 90 to 180 degrees to the left or right between the fourth and fifth segments. They are orientated with respect to the current so that the head is downstream from the abdomen and is held so that the fans face the current. The angle between the substratum and the body is not actively maintained but varies with the current. Hocking and Pickering (1954) described the pattern of larval attachments in streams. Fortner (1937) described the feeding stance in detail.

Both primary and secondary fans catch particles. The particles held in the centre of the primary fans may be retained there through three or four flicks (retractions and extensions) of the fans, or they may be swept out of the fan before it closes. Loss of particles either from the fans or the mouthparts is frequent. Larvae may not flick their fans immediately on catching a particle. They may flick them without having caught any particles.

The frequency of flicking is irregular. A larva extends its fans for several seconds and then flicks them continually for several seconds. The fans are generally flicked alternately, one of

the pair retracting and extending, and then the other. The duration of periods of flicking and non-flicking varies greatly. The frequency of flicking does not vary either between late instars and young larvae or between larvae with full guts and larvae with empty guts.

Larvae retain food in the cibarium until a bolus is formed and swallowed. Some selection of the particles with respect to size occurs during the transfer of particles from fans to mandibles. Larvae will retract fans which have trapped particles of 800 microns in diameter, larger than the mouth orifice. These are passed to the mandibles and maxillae but are not ingested. Occasionally, however, large sephadex particles with diameters slightly larger than that of the intima were found in the gut, compressed into a cylindrical shape by the walls of the gut. These particles progressed through the gut and did not appear to harm the larvae.

The first instar larvae of *S. vittatum* filter with their cephalic fans. They are able to feed while suspended from the surface film of still water. They are very active. Some had only yolk in their guts; others had small pieces of charcoal, sephadex, and organic matter.

No cannibalism was observed among laboratory populations. However, three fights were observed. In all fights a larger larva attacked a smaller one. Larvae were never injured. One fight ended when the smaller larva moved out of reach of the larger one whereupon both larvae resumed feeding.

Movements of mouthparts of filtering larvae

Food collection. — A blackfly larva gathers food both by filtering particulate matter from the water with its cephalic fans, and by scraping organic material off the substratum. The first mechanism is the commoner. Particles caught in the cephalic fans are transferred to the cibarium when the fans are retracted and cleaned. The fans are believed to open by an increase in pressure of the body fluids in the fan stem (Grenier, 1949; Wood, 1963). This is probably the same mechanism as that described by Chaudonneret (1963) for the labrum. The opening of the fans of living or preserved larvae can be achieved by squeezing the thorax or cervical region of the larvae (Wood, 1963).

The primary fans open with the ventral movement of the apex of Sc_1 and the lateral movement of the ventral lobes of the cephalic fan stem (Fig. 53, 54). Infrequently, when the fan expands the primary rays are hooked over each other. When this occurs the larva immediately flicks the fan and the rays become unhooked. Fortner (1937) stated incorrectly that the closing mechanism of the cephalic fans prevented the rays from becoming entangled with each other. The secondary fan unfolds in a spiral movement. The medial fan moves laterally (with respect to the fan stem) with the movement of the medial lobe.

The fans are closed by the contraction of the cephalic fan retractor muscle. The fan stem sclerite Sc_1 moves posterobasally and its apex moves dorsally. This movement is combined with the dorsal and medial (with respect to the fan stem) movement of Sc_m (Fig. 53, 54). The apices of the ventral lobes of the stem move together (Fig. 53). The primary fan closes in response to the downward movement of Sc_1 as well as to the increased curvature of the primary fan base due to the movement of the ventral lobes. The rays move together one after another like the struts of a venetian blind being raised. The inner rays move first. As the expanded bases of the rays act as buffers (Fig. 6), the closing of the fan is smooth and regular. The secondary fan closes in a similar way.

The rays of the medial fan do not diverge from one another at any time. This fan closes when the medial lobe moves medially prior to the closing of the primary fan. Both secondary and medial fans lie underneath the primary fan when the latter is retracted (Fig. 54).

The stem of the cephalic fan moves medially and orally when the fan is retracted. The sclerites Sc_b and P_b act as fulcrums. The cephalic fans have two positions of retraction. The more frequently occurring is the retraction for cleaning. If the larvae are disturbed, the fans

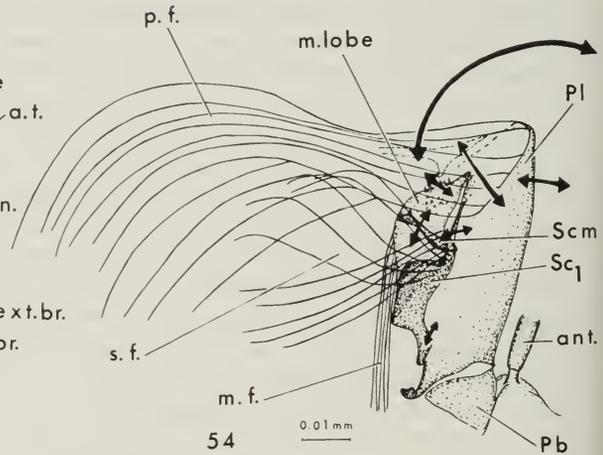
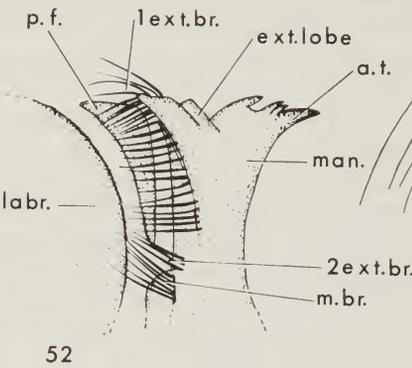
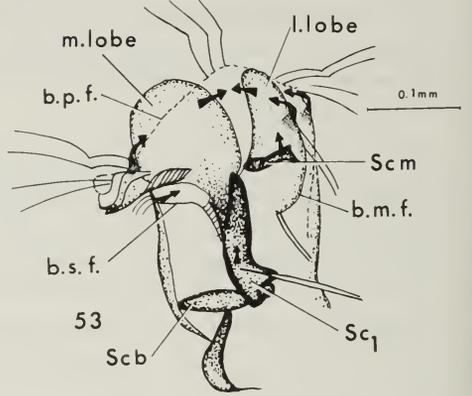
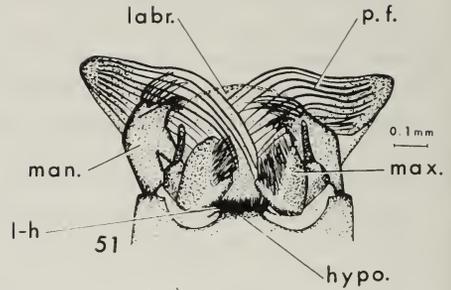
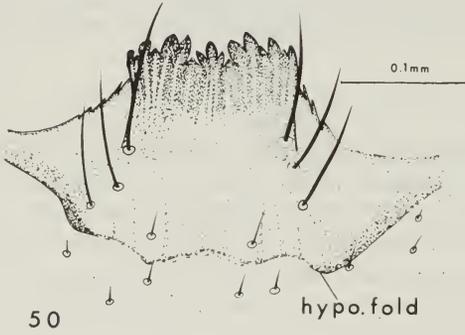
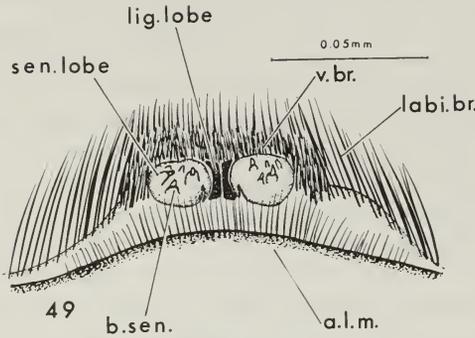


Fig. 49-54. Fig. 49-50: *T. biclavata*. 49, apex of labial lobe; 50, hypostomium. Fig. 51-54: *S. vittatum*. 51, position of retracted fans; 52, sketch of retracted fans when rays are combed, not to scale; 53-54, movements of elements of fan stem; 53, ventral view; 54, lateral view. a. l. m. = anterior margin of the labial lobe, ant. = antenna, a. t. = apical teeth, b. m. f. = base of medial fan, b. p. f. = base of primary fan, b. sen. = basiconic sensilla, b. s. f. = base of secondary fan, 1 ext. br. = first external brush, 2 ext. br. = second external brush, ext. lobe = external lobe, hypo. = hypostomium, hypo. fold = hypostomial fold, labr. = labrum, labi. br. = labial brush, lig. lobe = lobe of the ligula, l-h. = labio-hypopharyngeal complex, l. lobe = lateral lobe, man. = mandible, max. = maxilla, m. f. = medial fan, m. lobe = middle lobe, p. f. = primary fan, sen. lobe = sensory lobe, s. f. = secondary fan, v. br. = ventral brush.

are retracted further into the mouth orifice. In the latter case the mandibles and maxillae are also retracted.

The labrum, mandible, and maxilla have a simple movement of retraction and extension. All three appendages may twitch rapidly, a motion best described as 'shivering'. The mandibles usually move simultaneously. Although they can move independently they do so rarely. They are extended when the cephalic fans are retracted and they then retract to clean the closed fan. During periods of intensive feeding, the mandibles move in conjunction with the labrum and maxillae, being extended and retracted at the same time. Infrequently the labrum and maxillae are retracted while the mandibles are extended.

On several occasions larvae in the laboratory caught asymmetrical particles. These were transferred to the cibarium by the mandibles and maxillae and ingested. Although no special manipulatory movements were seen, the particles entered the cibarium with their longitudinal axes parallel to that of the body. The shape of the cibarium coupled with the movements of the mouthparts and the folding of the fans appear to orientate particles.

The second form of feeding is that of scraping material off the substratum. The head is held more or less at right angles to the substratum. The whole body is used, at times twisting in a complete circle to wrench material free. The labrum, mandibles and maxillae sometimes 'shiver' while the larvae feed off the substratum.

The mandibular teeth scrape the surface. The orientation of the apical teeth is suited for this function. The external lobe of the mandible prevents the apical brushes from scraping although these brushes may collect superficial material scraped free by the mandibular teeth. The bristles of the labrum, especially those of the ventral lobe, also collect material. The labral teeth are too well covered by bristles to be useful in substratum feeding. The position of the hypostomial teeth, slightly more dorsal than the rest of the hypostomium, and their covering of sensory hairs suggests that the hypostomium is not used in scraping.

Combing. — The transfer of particles from the fans to the cibarium occurs when the fans retract. The fans are combed by the mandibles and labrum (Fig. 51). The inner surface of the mandible is contoured to fit the curve of the folded fan and the labrum similarly fits the curve of the labral surface of the fan (Fig. 52). The folded fan passes underneath the covering and first external brushes of the mandible and above the middle lobe of the mandible. These brushes comb the convex surface of the folded fan. The second external brush passes beneath the fan. The mandibles do not clean the labral surface of the fans as described by Fortner (1937). The mandibles are very active during feeding and comb the fans several times during one retraction of the fans. Both mandibles and labrum retract while the fans are extended, combing each other free of particles. When the fans are held extended for long periods, the mandibles are also extended.

The fans are well adapted for filtering; the mandibles are well adapted for combing the fans. The development of the labral bristles and mandibular brushes, the shape of the labrum and mandibles as well as the development of the complex fan are major adaptations for filtering. Furthermore both labrum and mandible are also capable of scraping the substratum. However, these are not as efficient scraping appendages as those of the non-filtering species. The bristles of the labrum and the plane of movement, teeth, and musculature of the mandibles of *T. biclavata* larvae are better adapted for scraping. The mandibles of *T. biclavata* larvae are not adapted for combing fans.

The maxillae are continually active during feeding. Their role is less well defined than that of the other mouthparts. The arrangement of brushes differs between filtering species and non-filtering species yet both types of larvae have maxillae well provided with brushes. This suggests that the maxillae do not assist in filtering or combing but have a similar function in all species.

The frequent retractions of the labrum, mandibles and maxillae may contribute to the ingestion of food by pushing particles into the mouth. The ventral compound bristles of the labrum and the basal brushes of the mandible enter the pharynx. When the primary rays of the cephalic fan enter the pharynx, these bristles may comb the apices of the rays; they are not in a position to comb the rays outside of the cibarium. However, the large basal and middle brushes may act as guides for the rays or food particles; they may keep the epipharynx and the bases of the fan stem, mandibles, and maxillae free of particulate matter. The inner brush of the mandibles protects the mandibular cleft; it has no role in combing.

During feeding the proleg is held close to the body with its apex just below the hypostomial teeth. This position contributes to the streamlining of the body. The proleg is often brought close to the mouthparts and cleaned of debris or silk.

Silk secretion. — Blackfly larvae secrete silk very rapidly. Within a few seconds a larva can select a new site of attachment, produce a silk strand, apply it to the substratum and hook into it with its posterior circlet of hooks. Throughout the process the fans are extended, and held out of the way of the sticky secretion. The mandibles, maxillae and labio-hypopharyngeal complex are in constant and rapid motion. The labio-hypopharyngeal complex moves anteroposteriorly. The mechanism by which the silk is brought anteriorly and out of the canal is not clear. The M_3 muscle of the labio-hypopharyngeal complex dilates the silk canal and silk may be sucked forward by the increase in diameter of the canal. The simultaneous action of the retractors of the labio-hypopharyngeal complex may help this movement. The labio-hypopharyngeal complex acts as a press, and the activity of the M_2 and M_3 muscles may contribute to the dorsoventral flattening of the silk strand. The constant motion of the mouthparts and the body may also aid in the anterior movement of silk. The head is repeatedly extended and retracted; it arches upwards and stretches forwards. The proleg hooks onto the silk strand and draws it down from the silk canal. The mouthparts are then applied to the substratum and the silk, which is very sticky, adheres readily. Either the proleg or the posterior circlet of hooks then hooks into the pad. The hypostomial teeth sever the strand (Wood, 1963). Since the teeth do not move, the strand must be drawn across them by the movement of the labio-hypopharyngeal complex. The larva may maintain its position by using the unsevered strand until it hooks on with its proleg or posterior circlet of hooks.

The silk thread is very strong. Large larvae can be lifted out of water on the end of a six inch strand. The strand is used as a safety line by which floating larvae catch onto projections of the substratum. Larvae climb up their strands using their prolegs and mouthparts. Hora (1930) suggested that larvae use the stout bristles of the labrum to climb along the silk strand, however, the labral bristles of the species studied are not structurally suited for this task. It is probable that the mandibles and maxillae are used. Feeding larvae have no anchor line and rely on the posterior circlets of hooks for attaching onto the substratum.

The pupal case is made of silk. Peterson (1956), Hinton (1958b), Burton (1966) and others have described the spinning of the cocoon. The fans are retracted and the mandibles rarely move during cocoon formation. A pharate pupa spins the cocoon which is constructed of a leathery, coloured silk probably of a different composition from that of larval silk.

Mouthpart movements of a non-filtering larva

Larvae of *Twinnia biclavata* were observed feeding in still and flowing water. The larvae graze the substratum. Attached by their prolegs, the larvae feed off the substratum in front and to the side. The mouthparts are very active; the labrum and maxillae retract while the mandibles extend. The labrum moves so that its dorsal brush scrapes the substratum. The

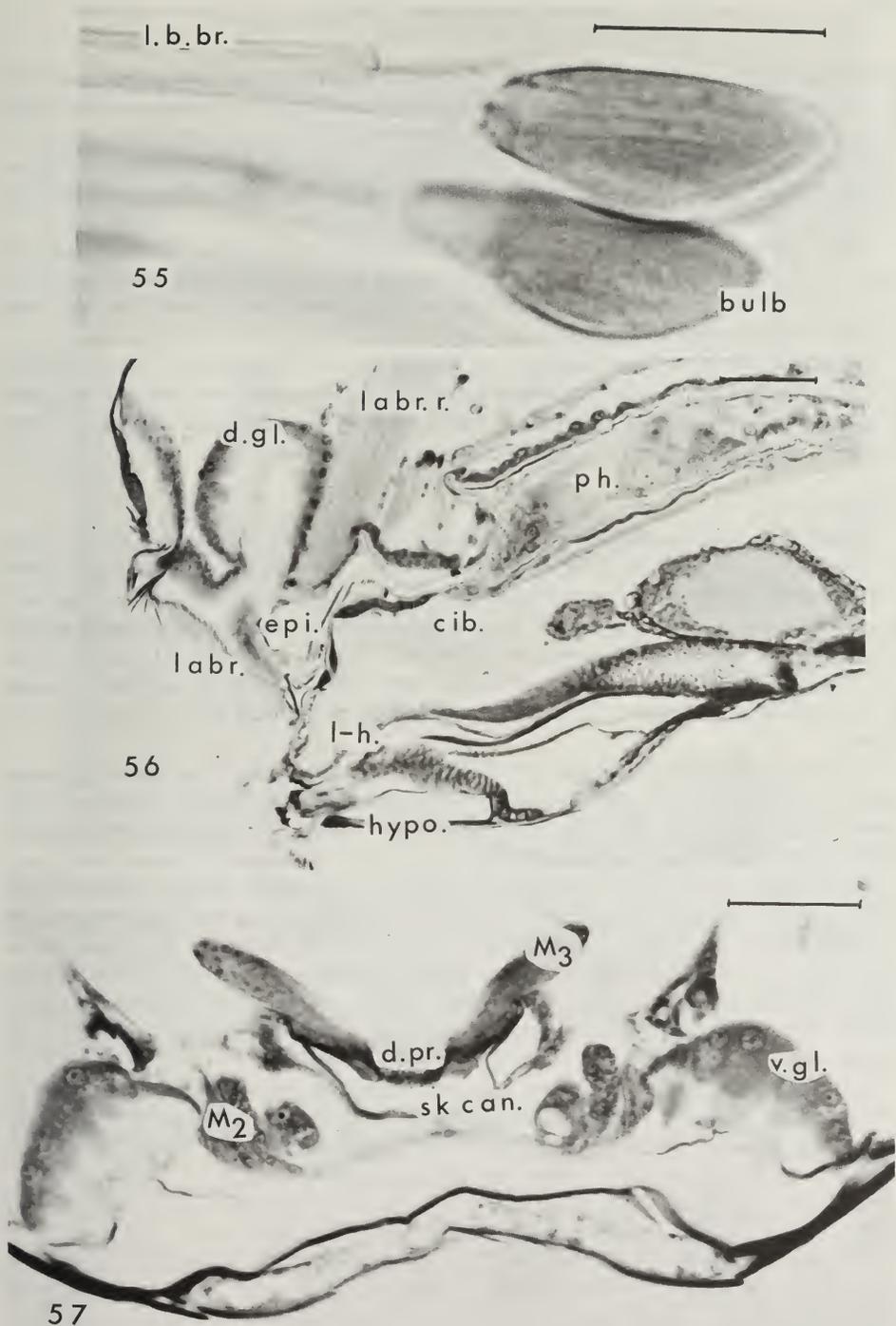


Fig. 55-57. 55, Photomicrograph of bulbs found on the large basal bristles of the mandibles of *S. vittatum*; 56, photomicrograph of a sagittal section of the head capsule of a blackfly larva; 57, photomicrograph of a transverse section of the ventral half of the head capsule of a blackfly larva. Scale for Fig. 55-57 is 5 microns. cib. = cibarium, d. gl. = dorsal gland, d. pr. = dorsal projection, epi. = epipharynx, hypo. = hypopharynx, labr. = labrum, labr. r. = labral retractor muscle, l. b. br. = large basal bristle, l-h. = labio-hypopharyngeal complex, M₂ = labial retractor muscle, M₃ = muscle of the press, ph. = pharynx, sk can. = silk canal, v. gl. = ventral gland.

mandibles move nearly parallel to the labrum, their teeth scraping the substratum. The brushes of the maxillae are retracted and move dorsomedially with respect to the larval body. The mouthparts 'shiver' as do those of the filtering species. Periodically the larvae cease feeding and clean their mouthparts. Cleaning is achieved in the same manner as by filtering larvae, i.e., brushing the mouthparts against each other so that the mandibles clean the labrum and the maxillae and are in turn cleaned themselves.

Larvae were observed eating filaments of algae by progressively ingesting from one end along the filament. Larvae were also observed grazing the surface of strands of algae. They pick at the algae by grasping filaments between their mandibles and slowly moving their mouthparts along them.

Silk is secreted in the same manner as in filtering species. Having cleaned the substratum around themselves of food, larvae progress forwards or sideways to a new site. Larvae appear to search for a new site by raising their heads up from the substratum and waving them around.

Ingestion

Blackfly larvae are unselective with respect to the composition of their food. Gut contents of larvae collected from the field consist of leaf litter, spores, pollen, algae, pieces of plant stems and unrecognizable organic debris. Fragments of insect cuticle are the only recognizable animal matter present. These include pieces of blackfly larvae, pupal respiratory filaments, head capsule parts, and mandibles. The gut contents of larvae reared in the laboratory also had a large proportion of charcoal and, after the addition of yeast to the rearing jars, clumps of yeast. Silt and sand form the bulk of the inorganic components.

The organic contents of the gut are not always digested. There is no visible difference between contents in the foregut and rectum. Naumann (1924) stated that utilization of the ingested algae was slight. Maciolek and Tunzi (1968) stated that blackfly larvae digested diatoms but hardly affected organic detritus.

Measurements were made of 200 particles ingested by blackfly larvae collected in the field. These particles were among the largest the larvae ingested. The two largest dimensions of the particles were measured. Sizes ranged from 0.5 to 300 microns in length and 0.5 to 120 microns in width. Most particles were 20 to 100 microns long and 10 to 60 microns wide. Fragments of insect cuticle, which were flexible and may have been folded during feeding, were the largest particles ingested. The biggest of these were 500 x 160 x 120 microns, 440 x 120 x 40 microns, and 320 x 120 x 60 microns.

The smallest gut particles measured were 0.5 microns in diameter but smaller particles were abundant. Due to the nature of the organic debris which adheres to the microtrichia of the primary rays and which is transferred to the gut when the fan is cleaned, it was not possible to get accurate measurements of the smaller particles.

Diameters of particles ingested by first instars ranged from 0.5 to 4 microns. Second instars ingested particles with a maximum diameter of 8.5 microns.

The frequency distributions, expressed as percentages of sephadex beads ingested by larvae in the laboratory are tabulated below (Table 6a and b). The difference between the size distribution of beads available to the larvae and those ingested by the larvae was tested for significance using the Chi-square test. The level of significance was set at $P = 0.05$ with P being the probability. Frequencies of categories less than five within a species size were lumped and Yates' correction was applied. The mass median diameter (MMD) for the frequency distributions of ingested beads was determined both by calculation (MMD_c) and graphically (MMD_g).

Table 6a. Percentage frequency distributions of sephadex beads ingested by larvae of three species of blackflies, Summer 1966.

Diameter (microns)	% of beads available	% frequency distribution <i>C. dacotensis</i>			<i>S. venustum</i>	<i>S. vittatum</i>
		small	medium	large	medium	medium
25	0.0	0	0.0	0.0	0.0	0
45	0.0	4	0.0	0.14	2.1	0
65	3.0	0	1.9	1.15	3.1	0
85	4.0	8	19.1	12.1	7.3	0
105	1.5	13	9.3	6.05	2.1	0
125	16.7	25	32.1	28.39	22.9	0
145	11.6	29	15.4	13.11	6.3	0
165	18.2	17	13.0	17.72	14.6	0
185	15.2	4	2.3	4.03	14.6	40
205	2.0		7.0	14.12	11.5	20
225	4.0			0.43	5.2	20
245	12.1			2.16	8.3	20
265	3.5			0.14	0.0	
285	2.0			0.43	2.1	
305	0.5					
325	2.0					
345	0.0					
365	2.0					
385	0.5					
405	0.5					
425	0.0					
445	0.5					
Total nos. of beads ingested		24	215	649	96	10
MMD _c *	204	136	128	146	162	187
MMD _g **	134	134	142	162	170	188
Nos. of larvae		5	19	11	10	2

Range of mean no. of beads per millilitre = 17 to 32.

* mass median diameter, calculated

** mass median diameter, determined graphically

Most of the *C. dacotensis* larvae and the medium larvae of *S. venustum* and *S. vittatum* were exposed only to sephadex G-200 (Table 6a) as that was the only type then available. No small larvae of *S. decorum* and *S. venustum* were collected live from the field or reared.

Without exception the frequency distribution of sizes of ingested beads differed significantly from that available to the larvae in each species in each age group. Large *C. dacotensis* larvae ingested a frequency distribution size different from that of medium *C. dacotensis* larvae. All interspecific comparisons show statistically significant differences in the size distribution of particles ingested. No other comparisons show differences significant at the 5% level.

Table 6b. Percentage frequency distributions of sephadex beads ingested by larvae of four species of blackflies, Summer 1967.

Diameter (microns)	% of beads available	% frequency distribution ingested							
		<i>C. dacotensis</i>		<i>S. decorum</i>		<i>S. venustum</i>		<i>S. vittatum</i>	
		large	medium	large	medium	large	small	medium	large
25	27.76	42.6	76.2	63.30	54.8	41.6	85.9	56.58	47.04
45	22.96	42.9	16.2	18.75	16.4	18.6	10.9	26.40	25.99
65	11.3	8.8	4.3	4.15	11.3	11.5	2.2	5.32	8.12
85	6.81	2.1	1.0	2.56	9.6	12.9	0.0	3.78	4.27
105	4.29	1.8	1.3	2.10	4.5	9.3	1.1	2.24	4.36
125	3.81	0.6	0.3	2.16	0.6	3.9		1.57	2.99
145	4.05	0.3	0.3	0.08	2.3	1.4		1.67	2.96
165	3.89	0.6	0.0	1.25	0.0	0.4		1.09	1.70
185	3.49	0.0	0.0	0.91	0.0	0.4		0.45	0.96
205	3.25	0.3	0.3	1.59	0.0			0.54	0.84
225	2.32			1.02	0.6			0.10	0.45
245	1.76			0.68				0.19	0.09
265	1.32			0.40				0.00	0.06
285	0.68			0.11				0.03	0.06
305	0.64			0.17				0.03	0.09
325	0.64			0.00					0.03
345	0.48			0.06					
365	0.28								
385	0.20								
405	0.08								
Total nos. of beads ingested		329	303	1760	177	279	92	3121	3348
MMD _c * 177		276	74	146	93	57	45	97	109
MMD _g ** 195		245	85	155	107	81	51	115	118
Nos. of larvae		2	5	5	1	2	9	20	14

Range of mean no. of beads per millilitre = 17 to 32.

* mass median diameter, calculated

** mass median diameter, determined graphically

The individual Chi-square values indicate that the large larvae, especially *S. decorum* and *S. vittatum* larvae, tended to select particles of a diameter of 25 microns.

The maximum size of sephadex particle ingested by each group of larvae is tabulated below (Table 7).

The minimum size which could be ingested was not determined because the smallest sephadex bead was still large enough to be trapped by the fans. Measurements of gut contents of larvae collected in the field included sizes of about 0.5 microns, 50 times smaller than the smallest size of sephadex bead.

The gut contents of field collected *Twinnia biclavata* larvae consisted mostly of diatoms with filamentous algae, spores, plant fragments and unidentifiable debris comprising the remainder of the organic material. A mixture of silt and sand, the second most common material, was the only inorganic material present.

Table 7. Maximum diameters (in microns) ingested by four species of blackfly larvae at three stages of development.

Species	small	medium	large
<i>C. dacotensis</i>	105	305	325
<i>S. decorum</i>	—	205	345
<i>S. venustum</i>	—	285	185
<i>S. vittatum</i>	185	205	285

Largest particles found in the guts of preserved (in 90% ethanol) *T. biclavata* larvae were plant fragments which ranged in size from 150 to 210 microns in length and 4 to 20 microns in width. Largest diatoms ranged from 124 to 170 microns long and 28 to 110 microns wide. Most particles ranged from 20 to 40 microns long and two to four microns wide.

Based on the concentration of beads available, 17 to 32 beads/ml, and the number of beads ingested per minute, the rate of filtration of six medium and six large larvae of *S. vittatum* were calculated to be 0.4 to 1.7 ml/min and 0.2 to 1.3 ml/min respectively. Because so little is known about the feeding behaviour of blackfly larvae, and because conditions in the rearing jars varied, these values should only be considered approximations of filtration rates.

DISCUSSION

Morphology

Head capsule. — The larval head capsules of the four filtering species studied are structurally very similar. There are no anatomical differences to which variations in particle size selection can be attributed. The only major morphological differences were seen between filtering larvae and *Twinnia biclavata* larvae, which do not filter feed.

Measurement of the head capsules, cephalic fans and mandibles of *C. dacotensis* and the *Simulium* species show that the head capsules of all four species are approximately the same size. The size of the head capsule and appendages increases with the growth of the larvae. Slight differences are shown by *C. dacotensis* and *S. vittatum* larvae. The head capsules of the larvae of these two species are larger than those of *S. decorum* and *S. venustum* (Table 1). The fans of both large *C. dacotensis* and *S. vittatum* larvae are bigger than those of the larger larvae of the other species, however, medium and small larvae of *S. vittatum* have larger fans than larvae of the same groups of the other species. The mandibles of large larvae of all filtering species are the same size; medium and small larvae of *S. vittatum* have larger mandibles than larvae of the same age of other species.

The three patterns of pigmentation of the anterior margin of the cephalic apotome of *S. vittatum* larvae are a variation within the species. This is one of several intraspecific anatomical variations found among *S. vittatum* larvae.

Cephalic fans. — Because *Prosimulium* is considered to be a primitive genus of blackflies, the occurrence of four to six intermediate rays in the cephalic fan and the presence of fewer blades suggests that the cephalic fans once consisted of a single big fan which has evolved into three differentiated fans. The central, largest fan is the principal filtering organ. However, the role of the secondary fan has given rise to speculation. Some authors consider the secondary fan to increase the filtering area of the primary fan since the secondary rays extend lateroventrally to the primary fan. Others maintain that it prevents particles from

falling among the bases of the primary rays or into the ventral wall thereby hindering the closing of the fan. It does both. Particles are caught by the secondary fan and those observed were not caught to the side of the primary fan. Further, the secondary rays extend distal to the bases of the primary rays; the dense trichiation prevents particles from falling among the primary fan bases.

Fortner (1937) suggested that the medial fan probably stabilizes the cephalic fan stem. Others have suggested that it guides particles into the primary fan. However, as it is located ventral and basal to the primary fan, I think that this is unlikely.

Fortner's description of the opening of the cephalic fan, which proceeds as a result of an increase in pressure exerted by the body fluids being forced into the head capsule, is correct. However, I found no evidence of either a basal membrane interconnecting the ventral surfaces of the primary rays or the rotation of Sc_1 , as she described. Fortner illustrated the two lobes of the ventral stem wall but did not describe their movement.

Fortner maintained that the initial extension of the fan is maximal and is subsequently adjusted by an equilibrium between the elastic cuticle of the stem and the force of the current. This equilibrium is controlled by the muscles of the cephalic fan and the muscles of the body. According to her, these muscles are very sensitive to the force of the current and it is through this sensitivity that the larvae detect current variations.

Grenier (1949) and Carlson (1962) found evidence that anatomical differences in the cephalic fans are correlated with feeding differences. However, the difference in the numbers of rays of the three fans in the species studied here is not reflected in feeding habits. Larvae of *S. decorum* have the most rays in each of the three cephalic fans; *C. dacotensis* larvae have the least. The primary fan of *S. decorum* larvae has a small area; the rays are shorter and closer together. The fan thus has a finer 'grid' than that of the other species. In comparison, *C. dacotensis* larvae have fewer rays, a larger fan and a larger 'grid'. Further, the medium larvae of *S. venustum* have more rays than do the large larvae. This apparent discrepancy may be a result either of the measurement of large medium larvae or possibly because medium larvae are adapted to feed more than large larvae. Phelps and DeFoliart (1964) identified two periods of intensive feeding of *S. vittatum* larvae; the first by medium larvae and the second by final instars.

Grenier (1949) described some ecologically important differences in the shape and strength of primary rays of 20 species of blackflies found in France. He concluded that species living in strongly flowing water have shorter, more curved rays composed of stronger cuticle than do species living in moderate currents. He lists *S. venustum* as an intermediate species. As he considered the strength of the cuticle without any special techniques, his conclusions are subjective. Lewis (1953) observed that larvae of species breeding in large breeding sites (larger streams and rivers) tend to have stronger, more flexible primary rays with smaller and thicker basal expansions than larvae of species breeding in small breeding sites. The rays of the various species studied here are structurally similar. However, since preservatives influence the cuticle, interspecific comparisons of cuticle strength were not possible.

The microtrichia of the primary fan rays have attracted much interest. Strickland (1911) claimed that the microtrichia of each primary ray extended to the adjacent ray so that a complete sieve was formed when the primary rays were extended. Fortner (1937) suggested that the microtrichia of the secondary rays have a similar function. Both workers were mistaken. The microtrichia are rarely longer than 1 micron and the rays are about 50 microns apart at their apices. Further, the microtrichia are on the inner curved surface of the ray and not on the side. The microtrichia of any one ray may extend to the adjacent ray but only along the basal quarter of the ray.

Specific differences in the trichiation of the primary rays apparently have no effect on feeding in the species studied here. Rubtsov (1964) claimed that the microtrichia on the primary rays of bloodsucking species are sparse, being 10 to 20 microns apart, and that the microtrichia on the primary rays of non-bloodsucking species are dense, being about 1 micron apart. Yet the three *Simulium* species and *P. fuscum*, *P. fontanatum* and probably *P. multidentatum* are bloodsucking species and these have microtrichia spaced about 1 micron apart or less. *C. dacotensis* is autogenous; the microtrichia are less than 1 micron apart. Thus these species do not support Rubtsov's claim.

Carlsson (1962) reported another ecologically important feature of the structure of the cephalic fans. Larvae of *P. ursinum* Edwards have 24 to 26 large rays and "relatively long 'finer' rays". They are unable to catch bacteria whereas the larvae of *Wilhemia equina* L. have about 46 large rays and "relatively smaller 'finer' rays", which are probably fine enough to catch bacteria. *W. equina* is found in bacteria-rich streams; *P. ursinum* is found in bacteria-poor streams. It is not clear whether Carlsson referred to primary microtrichia or secondary rays as 'finer' rays. The lack of such interspecific differences in the structure of the cephalic fans of the species studied here is probably due to the similarity of their ecological requirements; the three *Simulium* species are all found in the same microhabitat.

The microtrichia of the medial rays of *C. dacotensis* larvae are unique among the species studied. It is doubtful that the medial fan acts as a filter; certainly the sparse microtrichia would be of little help if it did. Although the microtrichia on the primary and secondary rays collect fine particulate debris, the trichiation of the medial ray is probably of little functional importance.

Labrum. — The labrum of *Twinnia biclavata* larvae differs from that of filtering species in that the differentiated labral bristles and their arrangement are adapted for a grazing habit. The dorsal brush of *T. biclavata* larvae may be represented in filtering species by the spindle-shaped patch of spines; in *P. frohnei* larvae this is located posteriorly on the surface of the labrum. The presence of the well-developed, ventral lobe of the labrum in both grazing and filtering species is evidence that the ventral lobe bristles are used for scraping in both types of larvae.

The labral sclerite of *T. biclavata* larvae differs from that of filtering species in orientation of the basal section. The apex of the labral sclerite lacks the lateral blades found in filtering species; this may be a result of the grazing habit. The labral teeth in *T. biclavata* larvae are used in scraping; unlike the labral sclerite of filter-feeding species, the apex of the sclerite projects out from the surface of the labrum (Fig. 41). The sensory labral teeth of filtering species may be lost in *T. biclavata* larvae, or they may be represented by the four medial teeth.

Mandibles. — The mandibles of filtering larvae and of *T. biclavata* larvae represent two forms which are adapted to two modes of feeding. Blackfly larvae which are not typical filterers or grazers, as *Simulium oviceps* Edwards and *Crozetia crozetensis* (Wormersley) larvae, have mandibles intermediate between the two forms. In *T. biclavata* the arrangement of the apical teeth and the stronger development of the flexor muscle are both requirements for scraping. The postantennal buttress of *T. biclavata* larvae, however, is weaker than that of filtering species.

The variation of the arrangement of the mandibular teeth of filtering species has little functional significance. The larger number of teeth of *Prosimulium* larvae may be a primitive feature. The 10 to 12 teeth of *T. biclavata* larvae probably represent undifferentiated apical and inner teeth although their position on the apex of the mandible differs slightly from that of filtering species.

In *T. biclavata*, the brushes which comb the retracted fans of filtering larvae are either lacking or are very poorly developed. Other species without fully developed cephalic fans

have similar reduced complements of brushes. Dumbleton's (1962a) illustrations of the mandible of the larvae of *S. oviceps* and *C. crozetensis* show that they also lack apical brushes and have only poorly developed middle brushes. Davies' (1960) illustrations of the mandible of the first instar of a *Prosimulium* species show a lack of apical brushes. The teeth of the first instar of *Prosimulium* sp. are arranged like those of *T. biclavata* larvae. The basal brushes in all species are the best developed of the mandibular brushes, supporting the suggestion that they aid in the passage of food into the cibarium.

Maxillae. — The shape and arrangement of the brushes of the maxillary lobe of *T. biclavata* larvae are suited for scraping. The apical bristles of the maxillary lobe of *T. biclavata* larvae closely resemble those of the dorsal brush of the labrum which also scrapes the substratum. The palp of *T. biclavata* larvae is similar to that of filtering larvae; the maxillary lobe and the palp of filtering species are all similar.

The role of the curved maxillary spines is unknown. Fortner (1937) suggested that they guide the silk thread. However, this role would be as important in *T. biclavata* larvae as in larvae of filtering species and *T. biclavata* larvae have only very short spines. Further, they are not in suitable position to act as guides for the retracted fans. Work in progress indicates that the apical spine in *Simulium* sp. larvae is sensory (D. A. Craig, *personal communication*).

Labio-hypopharyngeal complex. — The labio-hypopharyngeal complex shows no particular modifications for filtering or grazing. The labial brush probably keeps the silk thread clean and protects the sensory lobes. The role of the lobes of the ligulae is unknown. It is doubtful that they help in the secretion of silk because the *Prosimulium* species examined do not have paired ligular lobes but a group of conical, spine-like bristles and the *Prosimulium* secrete silk as do other species.

Cibarium. — The thickening of the cibarial wall midway along its length probably aids the formation of a bolus prior to swallowing. Fortner (1937) described the movement of food through the pharynx resulting from the contraction of the pharynx. Contraction of circular muscles of the pharynx may contribute to the passage of food in conjunction with the action of the anterior pharyngeal dilators, the cibarial dilators and the labral and mandibular bristles.

Glands. — The function of the dorsal and ventral glands is unknown. Neither Puri (1925) nor Grenier (1949) were able to identify any secretion in the lumen of the glands. Strickland (1911) claimed that the dorsal gland secreted a sticky substance which adhered to the epipharyngeal microtrichia and aided in cleaning the cephalic fan rays. Grenier (1949) suggested that the dorsal gland aided in digestion. He further suggested that the ventral gland is the site of formation of a specialized elastic cuticle required for the movement of the labial lobe within the sheath of the hypostomium. He supported his argument mentioning the occurrence of two similar glandular formations, one at the posterior discs of simuliids and the other at the posterior suckers of blepharocerids. More work is required before the function of the glands is clarified.

Food. — Filter-feeding blackfly larvae ingest any particulate matter of suitable size. The quality and quantity of the gut contents, both nutritive and non-nutritive material found here, are similar to reports in the literature (Chance, 1969). Any differences in food ingested are related to differences in collection localities (Puri, 1925; Grenier, 1949; Jones, 1949a, b, 1950, 1951, 1958; Peterson, 1956). The quantity and quality of food, the quantity of inorganic matter present as well as other environmental factors all influence colonization of water courses by various species of blackflies. However, as long as there is plenty of food available, several species of blackflies may be present in the same stream community (Carlson, 1962). The maximum dimension of measured particulate matter ingested by simuliid larvae ranges from 0.3 to 10,000 microns. The largest particle size is far greater than the

dimension of the cibarium, therefore, the larvae must be capable of ingesting long filaments of food by drawing food through the mouth continuously. The maximum size of globular natural food ingested is approximately 300 microns in diameter. The largest sephadex bead ingested in this study was 345 microns in diameter; the largest size available was 445 microns in diameter. The majority of particles measured, both natural and sephadex, were from 10 to 100 microns in diameter. This size and type of food corresponds closely to those already recorded.

T. biclavata larvae ingest smaller particles; this is probably due to the food available rather than to the limitations of their mouthparts.

The sephadex ingestion experiment shows that the filtering larvae select sephadex only with respect to size. Chemical and physical features other than size have no bearing on the potential of particulate matter for ingestion. This character of simuliid feeding is due to the passive nature of blackfly filtering. Although certain age groups of some species, large *S. decorum* and large and medium *S. vittatum* larvae, ingested a large number of small beads, no trend towards ingestion of any particular size is apparent. Differences in ingestion between age groups within each species is due to the increase in size of the larvae with age. Differences in frequency distribution or mass median diameter of beads ingested by the filtering species studied here cannot be explained by the structural features considered here. More work is required before the effect of the morphology and behaviour on filter feeding of blackfly larvae can be fully described.

The largest diameter of sephadex bead ingested by large *S. venustum* larvae is 185 microns; by medium *S. venustum* larvae, 285 microns. This discrepancy between the size of ingested bead and the size of the larvae may be a result of feeding habits varying with age (Phelps and DeFoliart, 1964). Medium *S. venustum* larvae have more primary rays than do large larvae. However, *S. vittatum* larvae have no structural evidence for differences in feeding with age.

Filter-feeding mosquito larvae ingest particulate matter varying from 7.5 to 165.0 microns. Sizes of particles ingested most commonly by *Aedes fitchii* (F and Y.) and *Culiseta inornata* (Will.) ranged from 15 to 22 microns (Pucat, 1965). *Anopheles messae* Falleroni larvae ingest particles ranging from 22.8 to 34.2 microns in the first instar to 68 to 165 microns in the fourth instar. The diameter of ingested particles is 20% of the width of the head of the first instar and this percentage increases to 31.2% for the fourth instar (Shipitina, 1935, in Bates, 1949). *Culex* sp. ingest particles varying from less than 1 micron to 50 microns in length (Naumann, 1924).

Work done on chironomid larvae indicates that they also ingest smaller particles. *Chironomus plumosus* L. traps all particles above 17 microns and most above 12 microns in its net (Walshe, 1947). The mesh of the net of *Glyptotendipes glaucus* Mg. ranges from 5 to 40 microns (Burt, 1940). Other measurements available for filtering insect larvae are those for trichopterans. Meshes of nets range from 3 by 19 microns in *Macronema* (Stattler and Kracht, 1963) to 50 to 100 microns in diameter for *Hydropsyche* (Kaiser, 1962).

Jørgensen suggests that *Simulium* larvae ingest smaller particles; his assumption is based on the fact that blackfly larvae can be reared on diets consisting only of bacteria (Fredeen, 1960). This diet is not typical for most blackfly larvae.

Mode of feeding

In the earliest reports of larval blackfly feeding, the cephalic fans were described as a current creating apparatus which functioned in a manner similar to that of the mouth brushes of mosquito larvae (Riley, 1870; Osborn, 1896). Strickland (1911) was the first to describe the filtering activity of the fans although there are earlier reports of the mandible cleaning the fans (Osten Sacken, 1870; Miall, 1895). Naumann (1924) and Puri (1925)

gave a more detailed description of feeding and Fortner (1937) gave a comprehensive account of the activity of the fans as well as the transfer of food from the rays to the labrum and mandibles. The filtering mechanism has also been described by Smart (1944), Grenier (1949), Peterson (1956), Anderson and Dicke (1960) and Maitland and Penny (1967) among others.

Filtering is the principal way of feeding for simuliid species having cephalic fans. Although filter-feeding larvae were observed scraping the substratum, they did so only in areas surrounding their posterior discs. When there is sufficient particulate food present in the water, scraping apparently only serves to keep the substratum adjacent to the larvae and the silk pad on which they attach free of debris. Filter feeders do not scrape as rapidly or methodically as *T. biclavata* larvae.

Rubtsov (1964) stated that *Twinnia* larvae filter with their mandibular brushes as well as graze. However, *T. biclavata* larvae were only observed to graze off mats of algae and large clumps of debris as well as the substratum. Yet filter-feeding larvae with the rays of the cephalic fan removed continue normal feeding movements of the mouthparts and particles caught on the labral bristles are transferred to the mouth (Fortner, 1937). *S. oviceps* and *C. crozetensis* larvae filter with abnormal fans as well as graze (Dumbleton, 1962a). These two species probably ingest a size distribution of particles different from typical filtering species.

Reports of cannibalism in the literature are conflicting. Smart (1944) stated that large blackfly larvae eat smaller ones. Badcock (1949) and Maitland and Penny (1967) stated that blackfly larvae occasionally eat members of their own species. Jones (1949b) reported seeing no attacks of cannibalism. However, Peterson and Davies (1960) give a detailed description of a large larva in the laboratory eating first instars, grasping them with its mandibles and forcing them into its oral cavity. Wu (1931) stated that larvae in stagnant water eat dead larvae.

The simuliid cuticle frequently found in the gut is most likely the remains of dead insects or exuvia filtered from the water and cannot be considered evidence of cannibalism. It is possible that late instar larvae may catch and ingest floating first instars, however, there have been no observations or reports to confirm this. Fighting between larvae is not predatory but competition for sites of attachment. A blackfly larva is capable of escaping from a fellow larva before it suffers any lethal wounds.

Filter feeding

Jørgensen (1966) lists three factors on which filter feeding depends: (1) concentration of food available, (2) water flow through the filters whether this is passive as for stream fauna or created by the animal itself, and (3) the efficiency of the filter. Size of particles is a fourth critical factor. Blackfly larvae are typical filterers. This is shown by the influence of current on their feeding, the efficiency (incomplete) of their cephalic fans as filters and their selection of particles by size. Concentration of suspended food may determine whether or not the larvae scrape the substratum to supplement their filtering. There is a minimum concentration of food below which the larvae cannot survive. This level is lower than that required for growth (Carlsson, 1962).

Blackfly larvae at times ingest more than they require. Gut contents apparently may undergo little change as they progress through the alimentary canal. In many cases this is probably due to a high inorganic content of ingested material. Larvae living in streams with large amounts of inorganic material, for example glacial silt in mountain streams, may starve with their guts full of silt. This superfluous feeding reflects the automaticity of filter feeding. In addition, the fact that blackfly larvae catch particles far larger than their mouth orifice is a consequence of automatic feeding.

CONCLUSION

Species of filter-feeding blackfly larvae ingest different distributions of particle sizes. These distributions overlap. None of the structural variation discussed here can explain the differences in ingestion habits. All species ingest particles within a suitable size range whether they may be food or not. Interspecific differences in feeding may be due to differences in behaviour. More work is required before the feeding habits of blackflies can be fully understood.

Feeding differences between filterers and grazers are paralleled by structural variations. The labrum, mandibles, and maxillae of *Twinnia biclavata* larvae are anatomically adapted for grazing; however, the movements of these mouthparts are almost the same as those of the mouthparts of filtering species. The cephalic fans, labrum and mandibles of filtering species are suited for catching and ingesting particles carried by the current.

Blackfly larvae ingest larger particles than other filtering insect larvae. Since filters of insect larvae tend to have a large pore size, especially when compared to those of marine invertebrates (Jørgensen, 1966), blackfly larvae can ingest larger particles than most filter-feeding invertebrates.

The automatic nature of filter feeding by blackfly larvae is a useful tool to increase the selectivity of control against blackflies. Particulate larvicides such as an insecticide adsorbed onto solids which form a suspension when added to streams are the most specific insecticides against blackflies. Grazing species are not pests, and would probably not be affected by such an insecticide since they do not filter feed, but ingest smaller particles than do filter-feeding species.

An insecticide with a particulate formulation in the larger half of the ingested size distribution, 100 to 250 microns for example, would be more readily ingested by blackfly larvae than by other species in the stream fauna. This size range is probably suitable for most species of blackflies, although only later instars would be affected. Because there is not enough information on the feeding habits of other members of the stream fauna, repeated applications may be preferable to a larvicide composed of smaller particles.

Due to the nature of the larval habitat, the exposure time of the larvae to the insecticide can only be a matter of hours. Because of this and because feeding by blackfly larvae is influenced by the concentration of food and current and because larvae tend to prefer particles smaller than 100 microns, enough particulate matter would be required to 'force' the larvae to ingest it by its abundance. The physical character of such an insecticide and its behaviour in streams will have to be carefully investigated before it can be used.

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

QUAESTIONES ENTOMOLOGICAE

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Editorial — The Patience of Job

Employment opportunities for entomologists are . . . no; let me start again. Jobs for bugmen are harder to find today than they have been for sometime. In some other fields it is worse. Thereby hangs a tale.

Vanessa Cole was born with an interest in insects. At school, in the dirty thirties, she embarrassed her teachers — otherwise good teachers and good biologists — with specimens she picked up on her way there, for she was a country girl. She learned all she could from these same teachers, and they learned something from her. Thence to university, where she learned some of it again and how to avoid doing this, and much else besides. Eventually, to another university where they taught her how to find out things for herself — which she had been doing most of her life — in a manner acceptable to the current crop of scientists, and how to say that she had done so, verbally and in writing. She worked at a field station — as a post-hole digger — to earn her keep. She passed courses, learned another language, read some of the literature, gave a seminar, wrote a thesis and defended it, and she took the first job that offered — digging post-holes on a farm, with a vial in each pocket. Her job did not, of itself, require much thought so she thought about the insects she unearthed from her post-holes and accumulated in her vials. She wrote a paper entitled: “Insects of the top 50 cm of grey-wooded soils”.

In another part of the country Tom Tegula was at school in the dirty thirties too; he took aptitude tests, received counsel from counsellors, and learned that he was best fitted for making money. He became handsome and, after on the job training, did pretty well in the forties and fifties selling insecticides to farmers for wireworm control. One day in spring, after completing an important sale to a farmer, he felt so good that he decided to walk across the fields back to his car. His roving eye lighted on a down-to-earth girl across the pasture wielding a post-hole auger so he walked across to her and said: “Que faites-vous?” Having passed her language requirement she replied: “Je cherche de l’or”. He said that augured well for her future as he had gold enough for two and, since her education was as — er — broad as her nature was flexible, she took him at his word and married him.

The most profitable product of the company Tom worked for turned out to have long term side-effects on the chromosomes of wheat, resulting in monstrosities which rendered the product unsaleable. The salesmen were sacked; Tom, with all the stubbornness of the

Tegulae could adapt to nothing new. Meanwhile, three tiny Tegulae had been growing and would soon need to be sent to University, so Vanessa went back to work, studying wireworms for Tom's company which had suddenly become interested in these animals. Tom puttered around the home, trying to make himself useful, but becoming more desperate as week succeeded week. One day he came across Vanessa's old post-hole auger in the basement which started him on a train of thought leading to a new job with his old company; taking soil samples for Vanessa's work on wireworms.

By the time the tiny Tegulae got to university it was the empty seventies. After talking things over with mother they all decided to study what they wanted to study.

If this tale has a moral it is that times change; that it is best to seek an education in a subject that interests you rather than in one which the market, when you start out, seems to suggest; to be guided by auger rather than augur. Whichever way you choose, and whatever the current state of the market, there can hardly have been a time in human history when the world had a greater need than now for education in biology and especially in population biology. And there is no more suitable group of animals as a basis for such education than the insects. Training may be wasted, education never.

Brian Hocking

A REVIEW OF CHEMICAL CONTROL METHODS FOR BLACKFLY LARVAE (DIPTERA: SIMULIIDAE)

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Chemical methods of controlling blackflies are reviewed. DDT has been the most satisfactory material in terms of selectivity and economy. Methods of application of DDT, its effect on blackflies and other aquatic invertebrates, and research on safer alternative compounds to DDT including methoxychlor and Abate® are discussed.

Methods of control of blackfly larvae have been mainly chemical. Many chemicals have been tested for effectiveness as simuliid larvicides (Cope et al., 1949; Kindler and Regan, 1949; Gjullin, Cope, Quisenberry and DuChanois, 1949; Hocking et al., 1949; Wanson et al., 1949; Wanson et al., 1950; Hocking, 1950, 1953; Travis et al., 1951; Lea and Dalmat, 1954, 1955a, 1955b; Taufflieb, 1955; Noel-Buxton, 1956; Muirhead-Thompson, 1957; Davies et al., 1962; Fredeen, 1962; Jamnback and Eabry, 1962; Travis and Wilton, 1965; Guttman et al., 1966; Frempong-Boadu, 1966; Jamnback and Frempong-Boadu, 1966; Travis and Guttman, 1966; Kuzoe and Hagan, 1967; Raybould, 1967; Swabey et al., 1967; Burdick et al., 1968; Jamnback and Means, 1968; Travis and Schuchman, 1968).

Until recently DDT (2,2-bis[*p*-chlorophenyl]-1,1,1-trichloroethane) was considered the most satisfactory because of its specificity, cost and ease of application and it has been used almost exclusively since the earliest control programs. The first control program with DDT was by Fairchild and Barreda (1945) in South America. Garnham and McMahon (1947) eradicated *Simulium neavei* Roubaud in Kenya where it was the vector for onchocerciasis. Wanson et al. (1949) applied it aerielly to combat *Simulium damnosum* Theobald at Leopoldville in the Congo. These and other control programs in Africa have been reviewed by McMahon et al. (1958), Brown (1962), and J. B. Davies et al. (1962) who reviewed control programs in Africa as well as South America. Jamnback and Collins (1955) comprehensively reviewed control programs, in particular those carried out in New York State, U. S. A.

CONTROL WITH DDT

Research on control has been concerned mainly with formulation of DDT, and its mode and time of application. DDT has been applied in oil solutions (Hoffmann and Merkel, 1948; Hocking et al., 1949; Barnley, 1958; Crosskey, 1959; Davies et al., 1962; Fredeen, 1962), as emulsions, emulsifiable concentrates (= solutions in xylene or toluene and Triton X-100), and wettable powders (Tiller and Cory, 1947; Hocking et al., 1949; Fredeen, Arnason and Berck, 1953; Fredeen, Arnason, Berck and Rempel, 1953; Lea and Dalmat, 1955b; Noel-Buxton, 1956; Brown, 1962; Travis and Wilton, 1965; Kershaw et al., 1968), in suspension (Travis and Wilton, 1965), as miscible liquids (McMahon et al., 1958; Davies et al., 1962), as solutions in acetone (Cope et al., 1949; Gjullin, Cope, Quisenberry and DuChanois, 1949; Prevost, 1949), in cakes of plaster-impregnated sawdust bags, impregnated plaster blocks, and impregnated muslin sand bags (Fairchild and Barreda, 1945; Prevost, 1949; Jamnback, 1952; Hocking and Richards, 1952; Hocking, 1953; Jamnback and Collins, 1955). The emulsified form is preferred over other formulations, being one of the most effective formulations in the field, and one of the easiest to apply by hand (Brown, 1962; Jamnback and Frempong-Boadu, 1966). Spectacular results have been achieved using DDT adsorbed onto solids which form a suspension when put into streams (Fredeen, Arnason and

Berck, 1953; Fredeen, Arnason, Berck and Rempel, 1953; Noel-Buxton, 1956).

Fredeen (1962) has shown that formulations including oil are more effective when added to turbid waters than when added to clear waters. The DDT probably adsorbs onto the suspended solids and is ingested by the blackfly larvae.

In large scale programs where the terrain is rugged, aerial application has been very successful, not only against larvae but also, at higher dosages, against the adults. Aerially applied formulations are more concentrated but the exposure time is shorter (Hocking, 1953; Jamnback and Collins, 1955). Oil solutions are best (Hocking, 1950; Hocking and Richards, 1952) and are generally applied at a rate of 0.1 lb.—0.3 lb. DDT/swath-acre (Gjullin, Sleeper and Husman, 1949; Travis et al., 1951; Brown, 1952), although as much as 1 lb./swath-acre has been applied (Goulding and Deonier, 1950). Application of larvicides should be made immediately after hatching and before the beginning of pupation. Water level and rate of flow influence the dosage required (Jamnback, 1952; Jamnback and Collins, 1955; Noel-Buxton, 1956; McMahon et al., 1958; Crosskey, 1959; Davies et al., 1962; Kuzoe and Hagan, 1967).

The popularity of DDT as a blackfly larvicide is due to its greater toxicity to blackflies than to some other members of the stream fauna, and to its greater safety for mammals. Larvae are killed at very low concentrations, 0.025–0.05 ppm. Under Canadian conditions a dosage of 0.1 ppm for 15 minutes is sufficient applied direct to the water; dosages as high as 0.5 ppm for 60 minutes are applied in other parts of the world.

Effects on other aquatic animals

Despite the selectivity of DDT for blackfly larvae, other members of the stream fauna are affected. Many of these animals are also susceptible to other candidate larvicides. The variation in amount of DDT applied in the studies referred to here is partially responsible for the differences in results. After application of DDT, up to 80% reductions have been recorded in populations of mayflies, stoneflies, and caddisflies (Arnason et al., 1949; Corbet, 1958; Hynes, 1960; Hynes and Williams, 1962). Garnham and McMahon (1947) reported that many invertebrates and fish were destroyed. Hoffmann and Merkel (1948) reported reductions of 61% and 90% of the stream fauna for five miles downstream from application. Hoffmann and Drooz (1953) found 70% and 90% reductions in fish foods. Hoffmann and Surber (1948) reported reductions of 74% in insects, including caddisflies, mayflies, beetles, and flies. Some species of stoneflies, beetles, dobsonflies, alderflies, water mites, dragonflies, crustaceans, molluscs and worms were not affected. Gjullin, Cope, Quisenberry and DuChanois (1949) found 90% to 100% mortality of caddisflies. Hocking et al. (1949) recorded deaths in 37 families of stream-inhabiting organisms. McMahon et al. (1958) reported losses of large numbers of insects. However, certain species of mayflies, midges, and leeches appeared to be resistant. Hynes and Williams (1962) reported the elimination of species of ostracods, mayflies, beetles, and three families of flies. Jamnback and Eabry (1962) reported a reduction of mayflies and flies.

Populations of blackflies and mayflies reappeared in treated streams within a year (Garnham and McMahon, 1947; Hoffmann and Merkel, 1948; Hoffmann and Drooz, 1953; Brown, 1962; Davies et al., 1962) and were the most numerous members of the stream fauna after repopulation (Hoffmann and Merkel, 1948; Hynes and Williams, 1962). This increase in their numbers is attributed to the absence of predators and shows that applications of DDT can lead to outbreaks of blackflies (Davies, 1950).

In comparison, in a 10-year program carried out in New York State, DDT had little effect on some arthropods (Collins and Jamnback, 1958; Jamnback and Eabry, 1962). After years of use of DDT in the streams, the populations of mayflies and flies differed signifi-

cantly between treated and untreated streams; but populations of beetles, dragonflies, stoneflies, dobsonflies, caddisflies, and crustaceans were the same. Overall productivity was also the same.

Although Garnham and McMahon (1947) reported deaths among fish, other workers found fish unharmed immediately after applications of DDT in the recommended dosages (Cope et al., 1949; Gjullin, Cope, Quisenberry and DuChanois, 1949; Hocking et al., 1949; Travis et al., 1951; Collins et al., 1952; Hoffmann and Drooz, 1953; Jamnback, 1955; Noel-Buxton, 1956; Corbet, 1958; Hoffmann, 1959; Brown, 1962). Fish kill occurs but only in atypical conditions (Browne, 1960; Brown, 1962; Kershaw et al., 1968) or when the flow of insecticide is impeded (Crosskey, 1959; Kuzoe and Hagan, 1967). Post and Garms (1966) report that small and young fish are more susceptible than large and full-grown fish. They suggest that fish mortality is due to the differential distribution of insecticide in the water. The species of fish they studied are more susceptible to long exposure of low concentration of DDT than to short exposure of high concentration of DDT. Hocking (1950), and Hocking and Hocking (1962) suggested that the long term effects on fish may be profound.

Mortality of aquatic invertebrates other than blackflies is greatly reduced when DDT adsorbed onto solids is used (Fredeen, Arnason, Berck and Rempel, 1953; Noel-Buxton, 1956; Kershaw et al., 1965; Kershaw et al., 1968). Cope et al. (1949) suggested that a solution of DDT in acetone provided a safety margin between blackflies and fish, mayflies, and caddisflies.

ALTERNATIVE COMPOUNDS TO DDT

With the discovery of its long term stability in nature and its accumulation through a food chain, DDT has become less popular in control programs. Furthermore there is evidence that the larvae of a species of blackfly are resistant to DDT (Suzuki et al., 1963). In the last few years investigations have centered on discovering a biodegradable substitute for DDT. However, few of the more promising candidate compounds are either as safe to handle or as economical as DDT.

Both Lindane (δ -1,2,3,4,5,6-hexachlorocyclohexane) and crude benzene hexachloride (BHC) had also been used in Africa (Wanson et al., 1949; Wanson et al., 1950; Taufflieb, 1955) but were far from successful, killing other fauna including fish and giving poor control of blackflies. BHC and chlorten (chlorinated α -pinene) have also been used to control blackflies with limited success in Russia (Petrishcheva and Saf'yanova, 1959).

Screening tests of many compounds have been carried out under the sponsorship of the World Health Organization (Jamnback and Frempong-Boadu, 1966) and other organizations. The most promising compounds so far discovered include Abate® (*O,O,O',O'*-tetramethyl *O,O'*-thio-*p*-phenylene phosphorothioate) (Travis and Guttman, 1966; Swabey et al., 1967; Jamnback and Means, 1968), carbaryl (*N*-methyl-1-naphthyl carbamate) (Frempong-Boadu, 1966), diazinon (*O,O*-diethyl *O*-[2-isopropyl-4-methyl-6-pyrimidinyl] phosphorothioate) (Jamnback, 1962; Travis and Guttman, 1966; Swabey et al., 1967), Dursban® (*O,O*-diethyl *O*-[3,5,6-trichloro-2-pyridal] phosphorothioate) (Travis and Schuchman, 1968), fenthion (*O,O*-dimethyl *O*-4-[methylmercapto]-3-methylphenyl phosphorothioate) (Jamnback, 1962; Frempong-Boadu, 1966; Raybould, 1967; Swabey et al., 1967), heptachlor (1,4,5,6,7,8,8-heptachloro-3a,4,7,7a-tetrahydro-4,7-endomethanoindene) (Fredeen, 1962), Korlan® (24% ronnel) and ronnel (*O,O*-dimethyl *O*-2,4,5-trichlorophenyl phosphorothioate) (Travis and Schuchman, 1968) and methoxychlor (2,2-bis[*p*-methoxyphenyl]-1,1,1-trichloroethane) (Frempong-Boadu, 1966; Travis and Guttman, 1966; Burdick et al., 1968; Jamnback and Means, 1968). Methoxychlor is safer than DDT and is an acceptable substitute as a blackfly

larvicide (Burdick et al., 1968; Travis and Schuchman, 1968). More work is required before the efficiency and safety of the other compounds as larvicides are fully known.

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SEASONAL OCCURRENCE AND RELATIVE ABUNDANCE OF TABANIDAE (DIPTERA) IN THREE LOCALITIES IN ALBERTA

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A total of 4,010 female and 48 male tabanids was collected from three localities, each in a different ecological zone, in Alberta during the spring and summer of 1968 and 1969. Ten species were collected in the Canadian zone, north of Edmonton; 23 species in the Northern Central Rocky Mountain zone, at Nordegg; and 27 species in the Southern Foothills of the Rocky Mountains, southwest of Calgary. Twenty-nine species in six genera were collected: *Atylotus* 2 species, *Chrysops* 6 sp., *Glaucops* 1 sp., *Haematopota* 1 sp., *Hybomitra* 18 sp., *Tabanus* 1 sp. Flies were rarely active at temperatures below 65 F.

Little has been published on the tabanids of Alberta since Strickland (1938, 1946) reported on the regional and seasonal distributions of 35 species or subspecies. McAlpine (1961) reported on the distribution of three species and Shamsuddin (1966) listed four localities where the larvae of three species were collected. Philip (1965) records 51 species or subspecies for Alberta. However, Pechuman (*in litt*) suggests that only 46 species are found in the province.

The regional and seasonal distributions of tabanids in Alberta are still imperfectly known. This paper describes the seasonal distribution of tabanids in two localities and lists the species collected during an eleven-day period in another.

LOCALITIES AND METHODS

In 1968 two localities were sampled, one at George Lake (53° 57' N, 114° 06' W; 2,000 feet) 50 miles northwest of Edmonton and one at Nordegg (52° 28' N, 116° 04' W; 4,500 feet) 60 miles west of Rocky Mountain House.

In 1969, areas in the vicinity of the R. B. Miller Biological Station (50° 38' N, 114° 39' W; 5,000 feet) in the Bow River Forest Reserve 50 miles southwest of Calgary were sampled.

The George Lake locality has been described by Graham (1969). Four habitats in this locality were sampled from early June until late July when tabanids became scarce. Two Manitoba fly traps (Thorsteinson, Bracken and Hanec, 1965) were placed in a *Carex* meadow bordered on the west by a forest of *Populus tremuloides* Michx. and *Populus balsamifera* L. and on the east by a floating *Typha* mat adjacent to a lake. One Manitoba fly trap and a Malaise trap (Townes, 1962) were in an open *Carex* and *Typha* habitat alongside a stream flowing out of the lake. Another Manitoba fly trap was alongside this stream, but in the forest. Two Manitoba fly traps were in a bog consisting of *Sphagnum* moss covered with a dense growth of *Ledum groenlandicum* Oeder. This bog was surrounded by a forest of *Populus* and *Picea glauca* (Maench).

The Nordegg locality was sampled from July 31 until August 10. One Manitoba fly trap was erected in an open area alongside Shunda Creek. The ground cover was composed of mosses and *Carex* and the surrounding forest was spruce (*Picea* sp.). Collections were also made by netting females attracted to horses in a nearby meadow.

The Bow River Forest Reserve was sampled from June 9 until August 21. One Manitoba fly trap was erected in an open area in a white spruce forest (*Picea glauca* (Moench)) alongside Macabee Creek at 4,500 feet. Two Manitoba fly traps were in a partially flooded meadow at the edge of a beaver pond at 5,000 feet. One Manitoba fly trap was in a

Sphagnum bog at 5,200 feet, and two others were in a muskeg and *Carex* marsh at 5,200 feet. One Manitoba fly trap was in a meadow adjacent to a horse corral at 5,000 feet. Also, all flies entering the buildings of the research station were collected.

Except for the period July 30 – August 3, 1969, when the traps were not working, all traps in each locality were emptied daily.

RESULTS

A total of 4,010 females and 48 males representing six genera and 29 species was collected.

The distribution of the 10 species collected at George Lake is shown in Table 1. *Hybomitra illota* (Osten Sacken) was the dominant species, accounting for 83% of the females. The total daily number of females collected is shown in Fig. 1. Daily maximum temperatures are plotted in the same figure to show the influence of temperature upon activity. Except for June 14 when the maximum was 58 F and two flies were collected, no flies were collected on any days when the daily maximum temperature was less than 64 F.

Table 1. Number of female and male (in parentheses) tabanids collected at George Lake, Alberta in 1968; with first and last dates of capture.

	Man & Vehicles	<i>Carex</i> Meadow	<i>Carex</i> & <i>Typha</i> Marsh		Forest	<i>Sphagnum</i> Bog
			A	B		
<i>Hybomitra affinis</i> (Kirby) 19.VI – 3.VII	1	1	2			1
<i>Hybomitra epistates</i> (Osten Sacken) 26.VI – 12.VII		9	1		2	11
<i>Hybomitra frontalis</i> (Walker) 25.VI – 26.VII	6	31	3	4	1	14
<i>Hybomitra illota</i> (Osten Sacken) 7.VI – 26.VII	23	160	157 (3)	63 (10)	87	374 (10)
<i>Hybomitra lasiophthalma</i> (Macquart) 14.VI – 11.VII	4	8	7		2	12
<i>Hybomitra nuda</i> (McDunnough) 7.VI – 3.VII	5 (1)	1		3 (2)		1 (1)
<i>Chrysops frigidus</i> Osten Sacken 23.VII – 26.VII				2		1
<i>Chrysops furcatus</i> Walker 18.VI – 26.VII	4			11 (2)		3
<i>Chrysops nubiapex</i> Philip 5.VII	1					
<i>Haematopota americana</i> (Osten Sacken) 22.VI – 25.VII	1		2 (1)	22 (4)		2 (1)

A = Manitoba fly trap

B = Malaise trap.

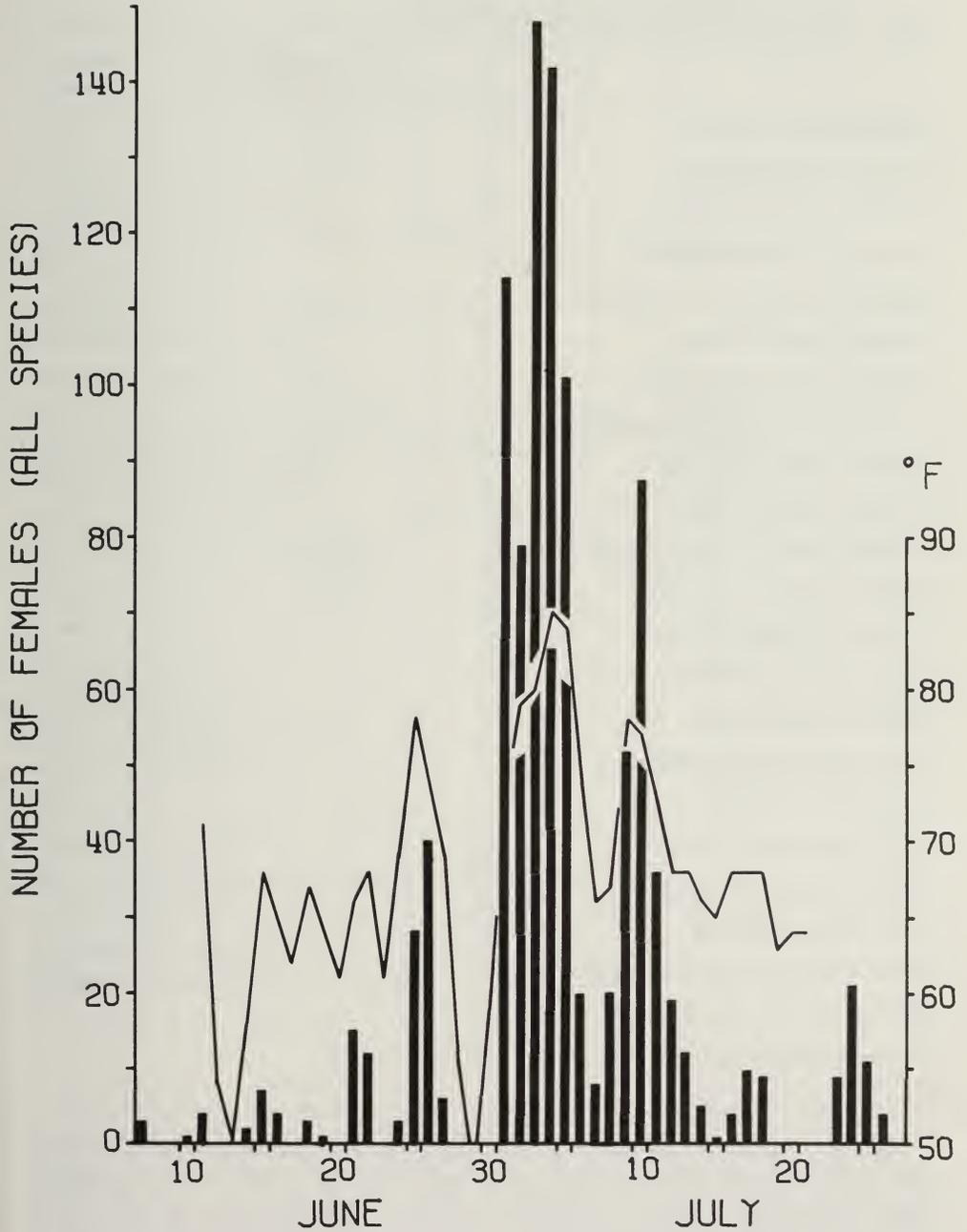


Fig. 1. Total daily catches of tabanid females (bars) and daily maximum temperatures (line) at George Lake, Alberta, 1968.

The distribution of the 23 species collected at Nordegg is shown in Table 2. *Hybomitra frontalis* (Walker) and *Hybomitra typhus* (Whitney) were the dominant species, accounting for 62% of the catch.

Table 2. Female tabanids collected at Nordegg, Alberta, July 31 – August 10, 1968.

	Stream edge (Manitoba fly trap)	Meadow (Horses)
<i>Hybomitra affinis</i> (Kirby)	10	47
<i>Hybomitra arpadii</i> (Szilády)	3	4
<i>Hybomitra frontalis</i> (Walker)	38	275
<i>Hybomitra illota</i> (Osten Sacken)	1	2
<i>Hybomitra lasiophthalma</i> (Macquart)	6	61
<i>Hybomitra liorhina</i> (Philip)		1
<i>Hybomitra melanorhina</i> (Bigot)		5
<i>Hybomitra metabola</i> (McDunnough)	3	
<i>Hybomitra opaca</i> (Coquillett)		2
<i>Hybomitra osburni</i> (Hine)		15
<i>Hybomitra rupestris</i> (McDunnough)	8	7
<i>Hybomitra tetrica hirtula</i> (Bigot)	1	1
<i>Hybomitra typhus</i> (Whitney)	37	195
<i>Hybomitra zonalis</i> (Kirby)		3
<i>Chrysops excitans</i> Walker	10	2
<i>Chrysops frigidus</i> Osten Sacken	3	3
<i>Chrysops furcatus</i> Walker	25	50
<i>Chrysops nitis</i> Osten Sacken	6	2
<i>Chrysops nigripes</i> Zetterstedt	1	
<i>Chrysops nubiapex</i> Philip	2	
<i>Haematopota americana</i> Osten Sacken	5	30
<i>Atylotus incisuralis</i> (Macquart)	1	1
<i>Tabanus marginalis</i> Fabricius	1	

The habitat distribution of the 27 species collected in the Bow River Forest is shown in Table 3, and the seasonal distribution (of 26 species) in Fig. 2 and 3; *Hybomitra astuta* (Osten Sacken) was collected on August 9, 10 and 11. The total daily catches and the maximum temperatures are shown in Fig. 4. Except for July 5 when the maximum was 54 F and one fly was collected, no flies were collected on any days when the daily maximum temperature was less than 62 F.

Table 3. Habitat distribution of female and male (in parentheses) tabanids collected in the Bow River Forest Reserve, Alberta, June – August, 1969.

	White Spruce Forest	Beaver Pond	<i>Sphagnum</i> Bog	Muskeg & <i>Carex</i> Marsh	Meadow	Buildings
<i>Hybomitra affinis</i> (Kirby)	2	51 (1)	60	33	58 (1)	26 (1)
<i>Hybomitra arpadí</i> (Szilády)	66 (2)	4	9	1	1	4
<i>Hybomitra astuta</i> (Osten Sacken)		3				1
<i>Hybomitra epistates</i> (Osten Sacken)	5			1	1	
<i>Hybomitra frontalis</i> (Walker)	2	12	6	51	13	58
<i>Hybomitra illota</i> (Osten Sacken)	22 (1)	4	6	2	1	
<i>Hybomitra itasca</i> (Philip)		1		49		
<i>Hybomitra lasiophthalma</i> (Macquart)	52 (1)	46 (2)	21 (1)	9	19	13 (1)
<i>Hybomitra liorhina</i> (Philip)		10	10	136	2	11
<i>Hybomitra melanorhina</i> (Bigot)			1		1	1
<i>Hybomitra metabola</i> (McDunnough)	3	20	41	20	2	
<i>Hybomitra nuda</i> (McDunnough)	18 (1)	24	24	4	1	2
<i>Hybomitra opaca</i> (Coquillett)						2
<i>Hybomitra osburni</i> (Hine)	59	23	3	73	483	135
<i>Hybomitra rupestris</i> (McDunnough)		29		32	3	45
<i>Hybomitra tetrica hirtula</i> (Bigot)	6			2	10	1
<i>Hybomitra typhus</i> (Whitney)	3	15	4	10	12	1
<i>Hybomitra zonalis</i> (Kirby)	3			2	4	
<i>Chrysops excitans</i> Walker	1					
<i>Chrysops frigidus</i> Osten Sacken	2	1		7		
<i>Chrysops furcatus</i> Walker	2		5	18 (1)		1
<i>Chrysops mitis</i> Osten Sacken	1	2				
<i>Chrysops nubiapex</i> Philip	5					
<i>Haematopota americana</i> Osten Sacken		2			1	2
<i>Atylotus incisuralis</i> (Macquart)	1	9		20		8
<i>Atylotus duplex</i> (Walker)				1		
<i>Glaucopterus fratellus</i> Williston		4		3		

DISCUSSION

The George Lake locality is included in Strickland's (1938) ecological zone 10 from which he listed 13 species of tabanids. The few species at George Lake is probably a consequence of the limited larval habitats in the area. The Nordegg area is in zone 20 from which Strickland (1938) listed nine species. Considering the limited period I spent there, this locality seems especially rich in tabanids. The Bow River Forest is in Strickland's (1938) ecological zone 17; the 27 species collected form 59% of the Albertan fauna.

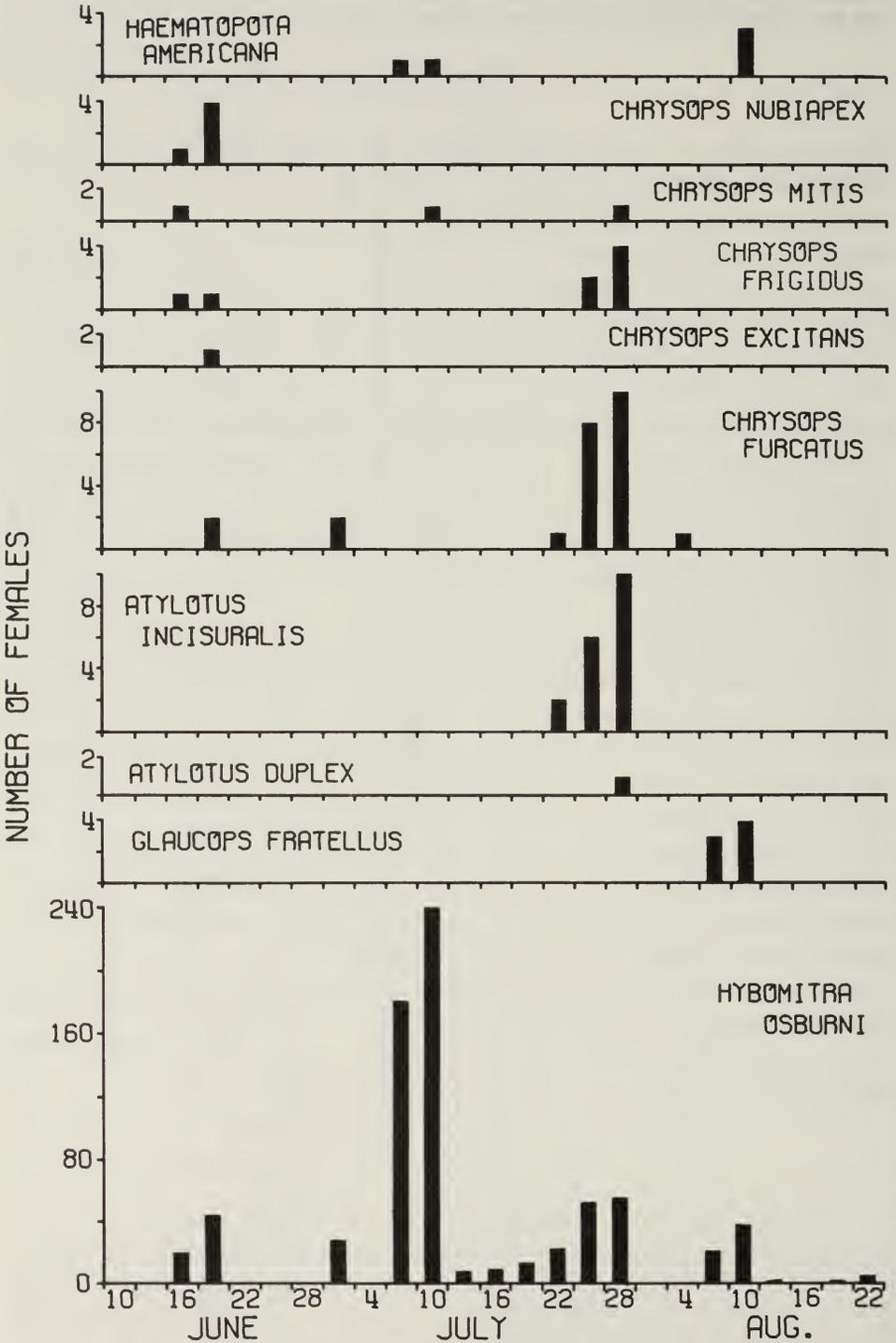


Fig. 2. Three day totals of catches by species of tabanid females in the Bow River Forest Reserve, Alberta, 1969.

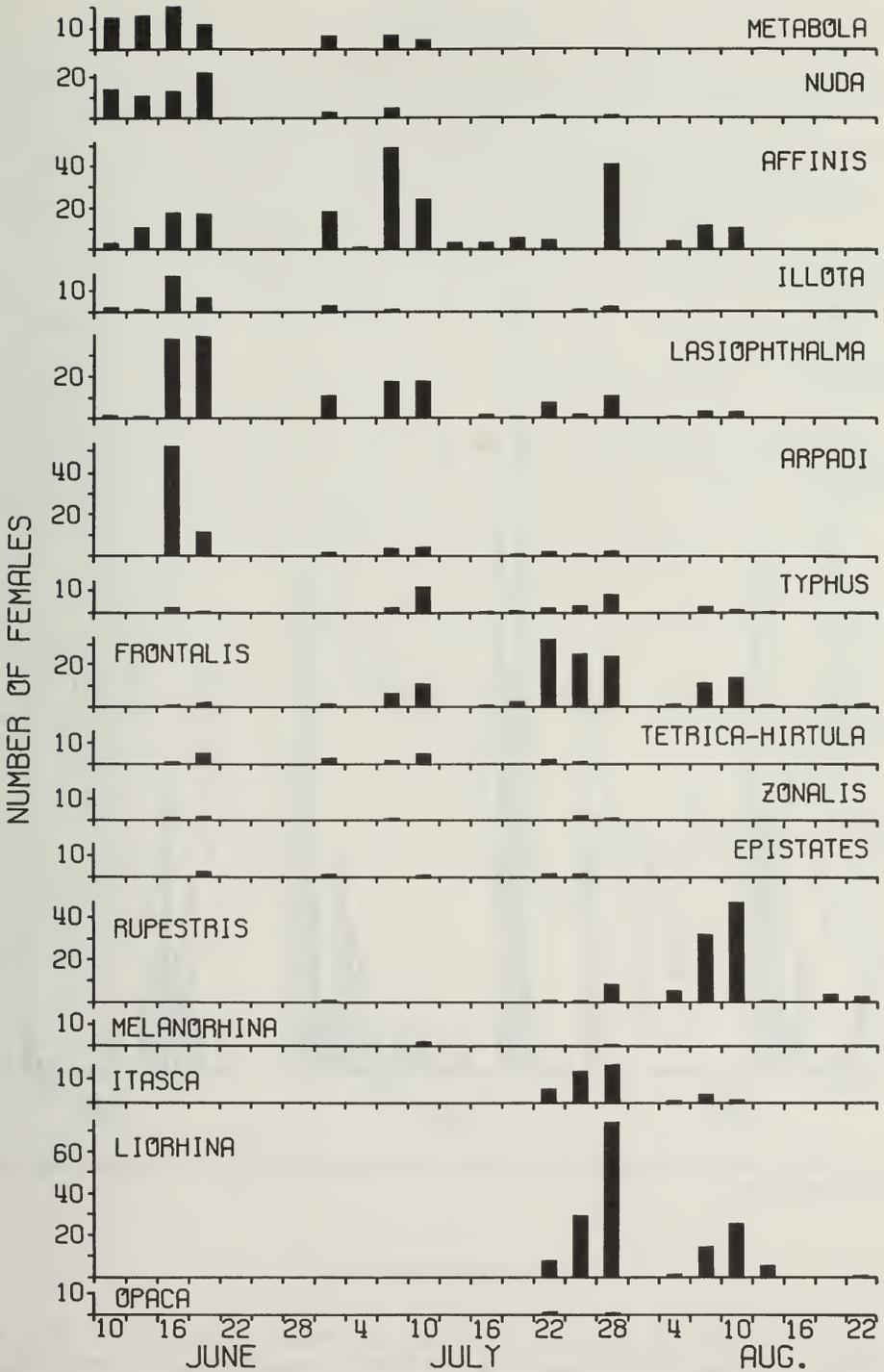


Fig. 3. Three day totals of catches by species of female *Hybomitra* species collected in the Bow River Forest Reserve, Alberta, 1969.

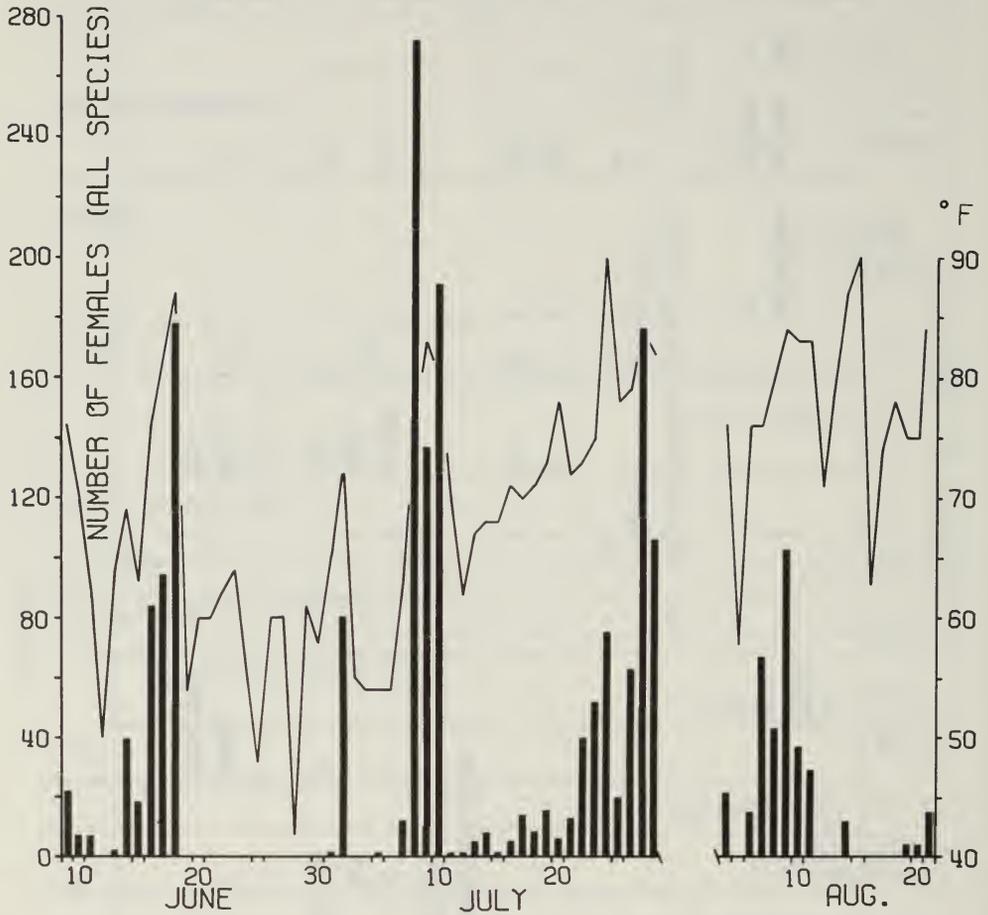


Fig. 4. Total daily catches of tabanid females (bars) and daily maximum temperatures (line) in the Bow River Forest Reserve, Alberta, 1969.

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I wish to thank W. G. Evans and B. Hocking for financial assistance, D. A. Boag for allowing me the use of the facilities at the R. B. Miller Biological Station (Bow River Forest Reserve), and L. L. Pechuman who assisted with the identification of specimens. The labels on the figures were drawn by a model 770/663 CalComp Plotter with a program developed by C. R. Ellis, to whom I am grateful.

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Book Review

JOHNSON, C. G. 1969. Migration and dispersal of insects by flight. Methuen and Co. Ltd., London. xxii + 763 pp., 217 text fig., c. 1300 refs., £7/10/-.

In his massive tome (there are 62 pages of references; as well as six pages of Addenda containing an additional 27 references, some of them dated 1969) Johnson has gathered together an enormous amount of information dealing with practically all aspects of insect flight. But, as he maintains several times throughout the book, his aim is to stress mechanisms rather than the outcome of migratory, dispersal, or other kinds of flights made by insects, and this he has done admirably. The concise manner in which ideas are logically presented, interpreted and discussed is characteristic of the book; and it is the interpretation and conclusions, which are clearly Johnson's, that make this book so valuable, as well as enjoyable to read. Johnson, after all, is an expert on the flight of insects in relation to their ecology and he has expertly integrated a topic that previously consisted of an immense scattered literature on insect flight (since the vast majority of insects fly, there is bound to be reference to flight in most works dealing with the habits and life cycles of insects) as well as a few landmark works on insect migration into a cohesive form that emphasizes the importance of flight as a dominant aspect of insect ecology. For this reason the book is highly recommended as a text for a course in insect ecology.

There are six main parts in the book, with the first three (General Aspects; Individual Aspects; Collective Aspects) dealing essentially with the physiology and ecology of insect flight, while the last three (Selected Examples of Short-range and Medium-range Displacement, especially in Relation to the Life-histories of the Insects; Long-range Displacement in Relation to Large-scale Weather Systems; Migration and Habitats) give detailed discussions of items such as swarm displacement of the desert locust and the ecological significance of migration and of flightlessness.

There is very little to criticize in this book. The title includes the terms "migration" and "dispersal" yet because migration is synonymous with "adaptive dispersal" one wonders whether "dispersal" refers to "accidental or inadvertent dispersal between breeding habitats" as Johnson states on page 8 or to "the scattering of insect populations over wider areas than those occupied during development" which he terms, on page 3, "dispersal" or "dissemination". Nevertheless, the emphasis throughout the book is on migration, the "transfer of populations from place to place by mass flights" and "dispersal" does not rate a single entry in the index. Also, if migration and adaptive dispersal are synonymous, why are both terms given as though they were separate entities, such as on page 20? And I wonder about the use of the term "hibernation" in reference to the overwintering of the Monarch butterfly which, in Pacific Grove, California, at least, I have seen flying and feeding throughout the day on introduced ornamental flowers during the whole of the sunny winter. But this is quibbling; Johnson has written a book that brings into focus what he states as "the quantitative contribution of flight to the collective life of species", and in doing so he has produced a work that will remain for many years the main reference on insect flight. It is recommended to all who have an interest in this topic.

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The following acknowledgement was inadvertently omitted from the paper "A reclassification of bombardier beetles and a taxonomic revision of the North and Middle American species (Carabidae: Brachinida)" *Quaest. ent.*, 1970, 6(1): 4-215. Field and museum work was supported by grants to George E. Ball from the National Research Council of Canada (NRC A-1399) and National Science Foundation (GB-3312). Publication was financed by the National Research Council grant.

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CORRIGENDA:

Quaest. ent. 6(2) 1970:

P. 223, line 4 after the Abstract: "Some bees (i.e. bumblebees) range to the Arctic and High Arctic, in North America to Ellesmere Island for instance (Hocking and Sharplin, 1964)."

P. 225, line 19 (from top): "Exploitation of favorable microclimates, the short favorable summer, and an efficient resting stage for overwintering, probably allow the wasps to cope with these severe conditions (see also Fuller, 1969; Hocking and Sharplin, 1965)."

P. 242, last line: ". . . as some bees (i.e. bumblebees) do (and even the High Arctic: Hocking and Sharplin, 1964)."

E. D. - Q974

Quaestiones

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Editorial – How Many is Too Much?

Are we producing too many Ph.Ds? This has become a much asked question; for those of us who believe in education there can be only one answer. Of course, we may be producing too many Ph.Ds for the jobs we are prepared to pay them to do; rather, we may be producing too few jobs or more correctly too few salaries. There can be no question that the jobs are there and need doing – a great many of them, and the need is too often desperate. We are also, of course, producing too many Ph.Ds in the same sense that we are producing too many people; many of our Ph.Ds could be contributing to a solution to this urgent problem, some indeed are; unpaid. But the need to reduce our population carries with it not only the opportunity but the obligation to do so selectively; by keeping the cream and discarding the skimmed milk and learning to tell the difference. And if this is not a task that calls for the highest level of education then there is none such.

The reduction of human population will take time and time is running out, for some small part of our excessive population, which regards itself as cream, is excessively producing and excessively consuming and excessively polluting its environment and will too soon (or too late, depending on your viewpoint) poison itself off and thus effect a pathetically small reduction in our total population. The remainder of the human population meanwhile is excessively reproducing, and may achieve the same end in a similarly short time and effect a bigger reduction in our total population. If the haves and the have-nots achieve these ends at the same time, global chaos must surely follow, and perhaps man's departure from this earthly scene will be more spectacular than his arrival was. It is interesting to speculate on the course of events should either group eliminate itself well ahead of the other. The economic problems of production and consumption, the biochemical and ecological problems of pollution and environmental quality, the biological, sociological, and psychological problems of population control, are all complex. They are basic and long term problems and their solution will call for the cooperation of many men and women with the highest level of education in many fields for many years to come.

When our current problems are solved and our reduced population can sustain itself on a maximum of technology and a minimum of effort, there will be, we are told, the problem of how to use our leisure. Education, it may be predicted, will lead us out of this one too.

It seems unarguable that nobody should be denied the opportunity to develop whatever intellectual potential he was born with to the highest level possible. If this be so, the number of Ph.Ds we produce is determined by our population and its genetical make-up. Of course by changing the nature of the Ph.D. degree we could produce more or less people with it, and standards are difficult of definition and far from absolute. We might – and perhaps should – raise our standards and produce fewer Ph.Ds. We might lower them, by requiring no imagination or original thought, insisting on nothing but technological production and training for a specific occupation or activity, and produce many more “Ph.Ds”. To some small extent, doubtless, supply and demand will occasion some fluctuation in standards: to be resisted. So perhaps some who enquire whether we are producing too many Ph.Ds should be asking instead whether we are lowering our standards.

This question is often asked in a rather local frame of reference, and relates to local availability of positions for which a salary which Ph.Ds have learned to expect is offered. But a Ph.D. is neither a local nor an economic degree; as an international document it is far more versatile and valuable than most national currencies and passports, but as a money maker it ranks below degrees in medicine and engineering – fields in which Ph.D. degrees are relatively rare – not to mention, of course, fraudulent activities in many fields, which depend on congenital cunning rather than education of any kind. Regardless of the mood of the moment, those who embark on a Ph.D. program have always committed themselves to thinking in international terms. Neither intellect nor education have ever been necessarily the handmaidens of wealth.

We may admit that in these special circumstances our initial question could be answered in the affirmative, and admit, too, that persons involved in the production of Ph.Ds may be biased. But when a person with every appearance of intellectual potential which could be developed to a level justifying the award of a Ph.D. degree of impeccable standard presents himself, has anybody a right to deny him an opportunity to try? We can no more produce too many Ph.Ds than we can have too much education, least of all, perhaps, in the life sciences.

Brian Hocking

**OBSERVATIONS ON MOSQUITOES DURING 1969
CONTROL OPERATIONS AT EDMONTON, ALBERTA**

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Quaestiones entomologicae

6 : 307-310 1970

Numbers of mosquito larvae and pupae in various types of ponds at sites in and near the City of Edmonton's mosquito control area were recorded. The type of pond influenced both the proportion of ponds with larvae and the numbers at the beginning of the season. Data on temporal and spatial distribution of larvae and pupae of 12 species of Aedes are given.

During 1969 field trials of Abate and Dursban (Tawfik and Gooding, 1970) for control of mosquito larvae, we made some observations on the ecology of mosquitoes which may be of use to mosquito control programs and in further research on mosquito problems.

Figure 1 shows the area covered by the City's mosquito control program during 1969, the areas treated with Abate, Dursban, and DDT, and the location of the six areas from which the information reported here was obtained. Two square miles were selected in the Dursban-treated area, 2.5 sq miles in the Abate-treated area, and two 0.5 sq mile sites in the untreated area. An effort was made to locate and mark all ponds at each site, which for purposes of analyzing the data, were classified as: Roadside pond (R): any accumulation of water near the edge of a road. Field pond (F): any pond situated away from a road and not in wooded land. Wooded pond (W): any pond situated away from a road and surrounded by or containing trees and/or shrubs. Ponds at the edge of a road but confluent with a field pond were classed as R-F, those confluent with a wooded pond as R-W.

Ponds of types F and W were treated by aerial application with insecticides adsorbed to granular clays, and R ponds were treated with emulsions applied by ground crews. Ponds of types R-F and R-W may have been treated by both methods. All applications were made for the City of Edmonton under the direction of Mr. J. D'Aoust.

Numbers of larvae and pupae taken in 10 dips were recorded for each pond at least once a week using an 800 ml dipper. Some of the larvae collected were isolated as 4th instars and reared to maturity so that identifications could be based on both the larval skin (using Carpenter and LaCasse, 1955) and the corresponding adult (using Graham, 1969). The number of females of each species reared from larvae collected during the period April 29 to June 5 are reported in table 1. Table 2 summarizes the information on each of the pond types in the six study areas.

Since the primary concern of our field activities was insecticide testing, our observations were co-ordinated with the City's spray program. As a result, data are not available for different areas on the same day. The data on the numbers of larvae plus pupae (table 2) are for just prior to the spray operations: R and R-F data were collected on April 22 for sites 1 and 2 and on April 23 for sites 3 and 4; F and W data were collected on May 2 for sites 1 to 4; all data for sites 5 and 6 were collected on April 28.

Influence of pond type on presence or absence of larvae

Some ponds of each type, roadside most commonly, were without larvae or pupae (table 2). In sites 1 to 4 only 27% of roadside ponds had larvae or pupae at the beginning of the season; all but one roadside pond dried up by June 12. Similarly we observed few, if any, larvae in ponds in cultivated fields. This was probably because eggs laid during the previous season would be buried during cultivation, the point needs to be confirmed since no data were recorded.

Table 2. Relationship between pond type and mosquito incidence and population. Edmonton, Alberta, 1969.

	Roadside	Field	Wooded	R-F	R-W
Area 1 – Dursban treated					
No. positive/no. of ponds	8/18	12/16	0/0	2/2	0/0
No. dried* positive/no. positive	8/8	7/12		1/2	
No. dried negative/no. negative	9/10	4/4		0/0	
Larvae + pupae in 10 dips - mean	1.7	74.9		35.0	
Larvae + pupae in 10 dips - range	(0-14)	(0-500)		(30-40)	
Area 2 – Dursban treated					
No. positive/no. of ponds	4/11	8/16	4/5	8/10	0/0
No. dried* positive/no. positive	4/4	7/8	1/4	8/8	
No. dried negative/no. negative	7/7	2/8	1/1	2/2	
Larvae + pupae in 10 dips - mean	1.6	29.9	5.8	6.5	
Larvae + pupae in 10 dips - range	(0-8)	(0-130)	(0-14)	(0-30)	
Area 3 – Abate treated					
No. positive/no. of ponds	0/7	14/20	5/7	4/6	0/0
No. dried* positive/no. positive	0/0	10/14	3/5	4/4	
No. dried negative/no. negative	7/7	5/6	2/2	2/2	
Larvae + pupae in 10 dips - mean	0	23.2	88.1	24.2	
Larvae + pupae in 10 dips - range	—	(0-200)	(0-240)	(0-81)	
Area 4 – Abate treated					
No. positive/no. of ponds	2/16	5/6	2/2	5*/7	0/0
No. dried* positive/no. positive	2/2	5/5	2/2	5/5	
No. dried negative/no. negative	14/14	1/1	0/0	2/2	
Larvae + pupae in 10 dips - mean	0.3	24.2	19.0	6.9	
Larvae + pupae in 10 dips - range	(0-4)	(0-79)	(2-36)	(0-32)	
Area 5 – Untreated					
No. positive/no. of ponds	0/1	5/5	1/1	7/7	3/4
No. dried* positive/no. positive	0/0	2/5	1/1	4/7	3/3
No. dried negative/no. negative	1/1	0/0	0/0	0/0	1/1
Larvae + pupae in 10 dips - mean	0	67.6	175.0	46.9	20.0
Larvae + pupae in 10 dips - range	—	(26-79)	—	(16-106)	(0-56)
Area 6 – Untreated					
No. positive/no. of ponds	3/3	2/3	4/5	1/1	2†/2
No. dried* positive/no. positive	3/3	2/2	2/4	1/1	2/2
No. dried negative/no. negative	0/0	1/1	1/1	0/0	0/0
Larvae + pupae in 10 dips - mean	120.7	15.0	41.2	12	200.0
Larvae + pupae in 10 dips - range	(91-160)	(0-44)	(0-106)	—	(0-400)

* by June 12

**two ponds negative the first day but positive later

† one pond negative the first day but positive later

If sites 1 to 4 are representative of the remainder of the mosquito control area and if the presence or absence of mosquito larvae is independent of the size of the pools studied, it appears that treating all ponds in an area results in a waste of about 20% of the material, time, and effort in the treatment of wooded ponds and as much as 75% in the treatment of roadside ponds.

Influence of pond type upon numbers of larvae and pupae

All study areas had ponds classified as R, F, and R-F. In areas 1, 2, 4 and 5 these ponds may be ranked R, R-F, and F in order of increasing numbers of larvae plus pupae. In area 3 the R-F ponds had slightly more larvae plus pupae than F ponds and in area 6 R ponds had the greatest number. All areas except 1 have wooded ponds and the numbers of larvae plus pupae in these ponds varies from the second least (area 2) to the most abundant (areas 3 and 5). Only two areas had ponds classed as R-W; in area 6 this was the pond type with the greatest number of larvae plus pupae and in area 5 it had the second least. At sites within the City's mosquito control area (1-4) the numbers of larvae plus pupae in R ponds is so low that they should not be treated with insecticides.

COMPARISON OF SITES INSIDE AND OUTSIDE THE MOSQUITO CONTROL AREA

Of the 12 species of *Aedes* found during this study five occurred both inside and outside the City's mosquito control area; two were found only within the control area; five were found only outside the control area. The numbers of larvae plus pupae found in each pond type outside the control area were greater than those found inside the control area. The ponds outside the control area were examined several days after those inside the control area and this no doubt accounts for some of the differences observed.

CONCLUSION

The information summarized above indicates a need for research in mosquito ecology in the Edmonton area. Information arising from such a study could reduce both the costs of the City's mosquito control program and the amount of environmental pollution.

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COLLEMBOLA AS POLLEN FEEDERS AND FLOWER VISITORS
WITH OBSERVATIONS FROM THE HIGH ARCTIC¹

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The literature is reviewed and observations are presented on the association between Entomobrya comparata Folsom (Entomobryiidae) and Lesquerella arctica (Wormskjöld) S. Watson (Cruciferae) in northern Ellesmere Island. Collembola can feed directly on pollen from flower anthers. Collembola which visit flowers may be associated with those upon which they are inconspicuous because of their colour. E. comparata appears in the corollas of L. arctica flowers during a short "sensitive period" in its life history. It seems that the ameliorated thermal regime of the flowers may hold E. comparata and, combined with a rich source of nutrients, permit more rapid metabolism and greater activity than in hostile ambient arctic (or alpine) conditions. L. arctica is not dependent on arthropods for cross-pollination, so that E. comparata plays no significant role in the fertilization of the one plant with whose flowers it is known to be associated.

Some Collembola species are certainly catholic in their choice of food, whereas others are much less so, although satisfactory evidence regarding the food preferences of any species is virtually lacking (Christiansen, 1964). Bödvarsson (1970) has recently given a comparative account of the gut contents of a few soil-inhabiting species, but there is no evidence of specific food preference. Pollen is one of the materials ingested by Collembola, and there are numerous references to this in the literature, although most of them are second-hand. Original observations are few and there is little published evidence that Collembola obtain pollen directly from the anthers of flowers, although this has been implied by Handschin (1919, 1924, 1926): "Von Pollen dürften sich . . . die Anthophilen ernähren"; "Blütenbewohner sind Pollenfresser"; and ". . . auf den Antheren der offenen Blüten [alpiner Ranunculaceen] . . .". There are a few published records of known pollinivorous species found in flowers (Carl, 1901; Handschin, 1919, 1924, 1926; Folsom in Brittain, 1924; Macnamara, 1924; Strebel, 1932, Folsom, 1933, 1934), but this does not necessarily mean that the Collembola feed directly on pollen from the anthers, although, in some instances, this appears to be so. Most records of pollen feeding, if they indicate the source of pollen found in gut examinations, suggest or imply that the pollen is wind-borne. Agrell (1941:56) makes a point of stating that, although *Bourletiella (Deuterosminthurus) repanda* (Ågren) [as *D. bicinctus* (Koch) f. *repanda*] clearly feeds on the pollen of *Trollius europaeus* Linnaeus (Ranunculaceae) in Swedish Lapland, he found the species only under leaves. *B. repanda* was not common, but found its optimum conditions in *Trollius* meadows.

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Agrell (1941: 127) also observes that, although *Entomobrya nivalis* (Linnaeus) and *Lepidocyrtus lanuginosus* (Gmelin) are both known to feed on pollen, when living in a macrophytic habitat they seldom had pollen in their intestines; these usually contained plant epidermis and parenchyma cells. This confirms his statement (p. 126) that a given species may feed mostly on one thing (e.g., fungus) in one locality, and chiefly on another (e.g., litter) in a different place. There seems to be no evidence that any species of Collembola so far observed is solely dependent upon pollen for its nutrition (see also Gisin, 1948), nor that any pollen-feeding species is dependent for its food supply upon the visiting of flowers, although Handschin (1924) suggests that this may be so for *Bourletiella lutea* (Lubbock).

LITERATURE REVIEW

The early works on pollination by Müller (1873) and Knuth (1898-1905, 1906) – like later works, such as those of Vogel (1954) and Faegri and Pijl (1966) – make no mention of Collembola. Neither does the classic work of Lubbock (1873) on Collembola mention pollen feeding by these animals. And although Linnaniemi (1907, 1912) in his monumental study of the Finnish Collembola mentions a number of species associated with vascular plants, he does not indicate that any of them visit flowers or consume pollen.

One of the earliest records of Collembola visiting flowers is that of Carl (1901), who records *Sminthurus luteus* [= *Bourletiella lutea*], in numbers of 10 to 25 together, from the involucre of woolly, high Alpine Compositae in Switzerland. He refers particularly to *Leontodon taraxaci* (Allioni) Loiseleur-Deslongchamps [= *L. montanus* Lamarck] and believed that the Collembola sought refuge from the cold. He also suggested that the glandular hairs might serve as food, but no mention is made of the inflorescence proper, or of pollen. Doflein (1914: 92, 244), in discussing the food of snow and ice fauna, indicates that the 'snow-flea', *Degeeria* [= *Entomobrya*] *nivalis*, and the 'glacier-flea', *Desoria glacialis* Nicolet [= *Isotoma saltans* (Nicolet)], feed on debris, mainly pollen, especially, it seems, of conifers, but gives no direct evidence for this. Schött (1917) provides one of the earliest positive references when he mentions that, in South Australia, the intestines of many specimens of the 'Lucerne flea', *Sminthurus viridis* (Linnaeus) var. *medicaginis* Schött, contained pollen grains of dicotyledonous plants, although the principal gut contents were hyphal remains and spores of ascomycetes.

Handschin (1919) mentions that Collembola are found, among other places, on the flowering parts of plants, and states that 'anthophiles' must feed on pollen, instancing *Bourletiella lutea* and *B. pruinosa* (Tullberg) [? = *B. signata* (Nicolet)]. Both species are found in numbers up to 50 together in flowers of the European (Alpine) *Ranunculus glacialis*. The association between these Collembola and the flowers was so constant that he could predict the presence of the animals from that of the flowers. In a footnote, Handschin notes that, in glasshouses, *Entomobrya spectabilis* Reuter lives in orchid blooms and that it is found almost exclusively at flowering time. Handschin (1924) notes that *Bourletiella lutea* is always found in the blossoms of *Ranunculus glacialis*, so constantly in fact, that an interrelationship between plant and animal might be postulated. Apparently this collembolan seems to Handschin to be specialized to alpine and snowfield macrophytes and to seek out flowers of all suitable low plants, which differ according to locality. He states that there is but one conclusion to be drawn: that this animal finds its source of nourishment in the reproductive organs of higher plants and seeks out suitable localities to this end. The question of whether the Collembola play a part in pollination is left open. In addition to the two species previously recorded in *Ranunculus glacialis* flowers, Handschin (1924) also lists *Bourletiella* (*Deuterosminthurus*) *repanda* [as *D. bicinctus repandus*],

B. (D.) pallipes (Bourlet) [as *D. bicinctus pallipes*] and *Lepidocyrtus lanuginosus* [as *L. l. albicans* Reuter]. From the flowers of *Anthyllis vulneraria* Linnaeus (Leguminosae) he records *B. lutea* and *Entomobrya nivalis* [ab.] *immaculata* Schäffer; and from *Campanula barbata* Linnaeus (Campanulaceae), *B. pruinosa* [?] = *B. signata*. With reference to the Alpine 'glacier-flea', *Isotoma saltans*, he indicates that coniferous pollen filled the intestines of this species, all of the pollen grains being intact.

Macnamara (1924) states that *Sminthurus hortensis* Fitch [?] = *Bourletiella signata*] occurs in dandelion [*Taraxacum*, Compositae] heads in Canada [Ontario], but he does not indicate that it feeds on the pollen from this plant. Folsom (*in* Brittain, 1924) makes the same observation for the United States of America. Although Macnamara says that some pollen-feeding species go directly to flowers (his examples being the ones already cited), he also mentions that *Isotomurus* [as *Isotoma*] *palustris* (Müller) and *Sminthurides* [as *Sminthuris* (*sic*)] *aquaticus* (Bourlet) are species that occur on the surface of pools and streams (where they often pick up diatoms and desmids) and which, in spring, feed largely upon wind-borne pollen of conifers.

Handschin (1926) reviews what was known of the feeding habits of Collembola up to that time. He makes several references to Collembola inhabiting flowers and mentions that the species he reported to occur on the anthers of open blossoms of Alpine Ranunculaceae are now and again found, fortuitously, in *Campanula* bells and in Compositae. The same author (Handschin, 1929) mentions that *Deuterosminthurus bicinctus* [presumably referring to *Bourletiella (D.) repanda*] lives largely in flowers and on plants, and reiterates his earlier statements.

Steinböck (1931) repeats earlier statements and quotes Keller (1911) as saying that the 'Gletscherfloh' [*Isotoma saltans*] utilizes tiny fragments of animals and plants for food when conditions are adverse, although no specific mention is made of pollen. Steinböck agrees that *I. saltans* feeds on conifer pollen and wind-blown plant detritus particles, but showed that it would not feed upon the dried remains of spiders or on other animal debris deposited in the icy heights by storm winds; nor did he believe that pollen grains play an essential, or even always an important role in the diet. *I. saltans* apparently has a distinct liking for chocolate on such rare occasions as this may be preferred! Steinböck (1939) emphasizes his earlier observations that *I. saltans* is not dependent upon conifer pollen for food, although it will feed on this, but largely consumes other materials, particularly algae in the form of "Kryokonit", or "Gletscherschlamm", and not small wind-blown insects and other small creatures as indicated by earlier authors (he cites [*Taschenberg in*] A.E. Brehm's 4th Edition of [*Illustriertes Tierleben*, which we have not consulted).

Strebel (1932) also refers to pollen feeding by Collembola and mentions that *Bourletiella* (including *Deuterosminthurus*) and *Sminthurus* species are pollen feeders. His material of *B. (D.) repanda*, collected off grasses, contained large quantities of unbroken pollen grains, but he observes that it still remains to be determined whether the species feeds exclusively on pollen. His observations thus agree with those of Agrell (1941) already referred to. Strebel (1932) also mentions pollen in field-collected *Sminthurus viridis* (quantities of grains, mostly whole, some broken) and *Lepidocyrtus cyaneus* Tullberg (unbroken grains). He notes that *Folsomia fimetaria* (Linnaeus) occurred in the flowers of the house plant *Aspidistra elatior* Blume (Liliaceae) and that the intestines were filled with broken pollen grains. Pollen also adhered to the bodies of the animals so that Collembola could conceivably play a role in the pollination of *Aspidistra*. It may be noted that *F. fimetaria* is a soil-dweller, but the flowers of the plant are unusual in that they occur on the surface of the ground.

Folsom (1933, 1934) repeats his earlier statement (*in* Brittain, 1924) that, in North

America, *Bourletiella hortensis* [? = *B. signata*] is common on the flowers of dandelion [*Taraxacum* (Compositae)]. He adds (Folsom, 1934) that it devours pollen there. Ritchie (1935) observed that, under conditions of scanty and irregular rainfall, an undescribed species of *Drepanocyrtus* [probably nr. *D. flavovirens* (Börner)] may damage the blossoms (and kill minute fruits) of coffee [*Coffea* sp., ? *C. arabica* Linnaeus (Rubiaceae)] in Tanganyika.

Agrell (1941) mentions that Lapland sminthurids which normally live in macrophytic vegetation may have gut contents consisting almost exclusively of unbroken pollen grains. He refers, it seems, mainly to *Bourletiella* (*Deuterosminthurus*) *repanda* (see above); *Entomobrya nivalis* and *Lepidocyrtus lanuginosus* are the other pollen feeders mentioned. Kos (1944) reported similar findings in respect of the Balkan 'glacier-flea' ["triglavler schwarzen Isotomen"], referred to *Isotoma nigra* Kos and subsequently identified (Paclt, 1956) as *I. kosi* Paclt = *I. kosiana* Bagnall] to those of Steinböck (1931) for *I. saltans*. Gut contents included mechanically undamaged pollen grains, probably of *Pinus mughus* Scopoli, together with other plant and fungous material.

Gisin (1947) mentions that the gut contents of Collembola may include pollen grains, and illustrates part of the intestine of a sminthurid – by implication, *Sminthurides pumilis* (Krausbauer) – containing collapsed pollen grains, spores and mineral matter. The same author (Gisin, 1948) remarks that the principal source of food for what he terms epigeic Collembola, is pollen, and that lactic-acid microscope preparations reveal in the gut the presence of various kinds of pollen grains, which are sometimes entire, sometimes fragmented or shrivelled, but that monophagy is unknown in Collembola.

Works by Denis (1949), Kühnelt (1950, 1957, 1961), Maynard (1951), Sedlag (1953), and Bellinger (1954), add nothing new. A brief general discussion of pollen feeding by Collembola is given by Paclt (1956). He lists *Bourletiella*, *Sminthurus*, *Katianna* and *Parakatianna* as plant dwellers and indicates that species belonging to most of these genera are known also as pollen feeders, although, so far, we have been unable to find any published reference to the habit in the last two genera. Species of *Folsomia* and *Lepidocyrtus* are also said to be known to consume pollen (cf. Strebel, 1932). Handschin's (1926) observations (above) are referred to, and it is considered unproven that any Collembola, including *Isotoma saltans*, can obtain all their food requirements from pollen grains (or the spores of higher fungi). Paclt observes, however, that if they cannot do so, one must enquire how they obtain their nutriment if the gut is filled only with pollen (or spore masses). He concludes that the possibility has been suggested that 'glacier-fleas' (*Isotoma saltans* and *I. kosi* [= *I. kosiana*]) may sometimes feed on animal matter, but that Steinböck (1931) and Kos (1944), referred to above, have shown them to be vegetarian, and that pollen does not necessarily always play a significant role in their diet.

Bödvarsson (1957) only repeats that, in Europe, *Bourletiella pruinosa* [= *B. signata*] lives to a great extent on the pollen of various plants; Poole's (1959) studies on the food of Collembola in a British Douglas fir plantation make passing reference to the fact that *Sminthurides aquaticus*, as reported by Macnamara (1924), will feed on conifer pollen, and that *Sminthurus viridis* will also ingest pollen [of unstated origin – he wrongly attributes the record for the latter species also to Macnamara instead of to Schött (1917) or Strebel (1932)]. Strebel and Altner (1961) indicate that the gut contents of a specimen of *Sminthurinus* [as *Sminthurus*] *aureus* (Lubbock) consisted mainly of broken-down pollen grains, that the intestine of *Heterosminthurus cornutus* Stach [= *Bourletiella bilineata* (Bourlet)] contained pollen, and that that of *Sminthurus viridis* included isolated dark brown pollen grains.

Schaller's (1962) success in culturing the 'glacier-flea' *Isotoma saltans* may have been partial because he was unable to provide the right food (? pollen). Mani (1962: 156) says that, in the Himalaya, in nearly every snow community, some species of Collembola are at the base of the pyramid of numbers and that this pyramid base includes mostly pollen and spore feeding species etc. at the snow edge. Genera mentioned are *Isotoma* Bourlet, *Proisotoma* Börner and *Hypogastrura* Bourlet (although the last is probably not a pollen feeder). The same author (p. 110) also states that wind-blown pollen grains (and spores) constitute the food of "numerous species of Collembola. . . . Vast numbers . . . come here [to the snow at elevations of 4000 m] for feeding on the wind-blown derelicts . . . including truly immense quantities of pollen grains, spores. . . . Many species of Collembola feed on the pollen grains of juniper [*Juniperus* (Coniferae, Cupressaceae)] and other plants scattered on the snow surface". Sharma and Kevan (1963) refer again very briefly to the known pollen-feeding habits of the 'glacier-fleas', *Isotoma saltans* and *I. kosiana*.

Results of an investigation of the digestion of conifer pollen grains by a collembolan, *Onychiurus pseudofimetarius* Folsom, are reported from Florida by Scott and Stojanovitch (1963). Pollen of *Juniperus pachyphloea* Torrey (Cupressaceae) was found in the gut of this species, but it is not stated whether the animal fed directly on juniper flowers; we assume not. It was concluded, either that the exines of the pollen grains were penetrated by the digestive enzymes, or that the exine of each grain was burst by the intestine in response to moisture. This occurred at or just before the cardiac valve. The intines were attacked at the mid gut, the inner ones approximately at the position of abdominal segments II and III, and the outer ones about on a level with the middle of segment III. Exines were broken up just before the pyloric valve. This investigation thus confirms that one species of collembolan, at least, can digest as well as ingest pollen, although there are indeed several previous reports of broken pollen grains in collembolan intestines (see above).

In his review of the bionomics of Collembola, Christiansen (1964) states that spores and pollen grains make up a large portion of the diet of surface-dwelling species (*cf.* Gisin, 1948). He ranks the various items of diet in several groups in a tentative order of frequency of occurrence. "Pollen grains, unicellular algae and spores" (most pigmented Entomobryinae) are listed second after "fungal hyphae, bacteria, dead and decaying plants and grass"; "pollen grains, spores and live plant material" (most sminthurids) are ranked third [our italics]. Sharma (1964, 1967) notes that pollen grains probably do not constitute a large part of the diet of *Tomocerus vulgaris* Tullberg, but coniferous pollen was frequently found in field-collected specimens (Sharma, 1964).

Brauns (1968) notes briefly again that the 'glacier-flea', *Isotoma saltans*, feeds on detritus particles and, above all, on conifer pollen deposited on ice and snow; the same is implied for the 'snow-flea', *Hypogastrura socialis* Uzel, although this may merely be an assumption. Mani (1968: 69, 70, 91) merely repeats his earlier remarks already quoted (Mani, 1962) on pollen feeding by high altitude Collembola. Walters (1968) notes that *Sminthurus viridis* will feed readily on the pollen of macrophytes. In the Canadian High Arctic, Hocking (1968) recorded in 1963, a species of collembolan "hidden in" the flowers of *Cerastium arcticum* Lange (Caryophyllaceae) at Hazen Camp, northern Ellesmere Island (see below), and *Isotoma viridis* (Bourlet) associated with those of *Saxifraga hirculus* Linnaeus (Saxifragaceae) at Resolute Bay, Cornwallis Island.

De Bernardi and Parisi (1969) mention that *Orchesella bifasciata* Nicolet includes small quantities of pollen in its diet and give a table showing quantitative estimates of the rather small proportion of the gut contents that are made up of pollen grains in that species and in *O. quinquefasciata* Bourlet, *O. villosa* (Geoffroy), *Tomocerus minor* Lub-

bock and *T. flavescens* Tullberg; *O. quinquefasciata* contained most, and *T. minor* least. They also discuss the topic briefly and suggest that *O. quinquefasciata* contained more pollen grains (and blue-green algae) than other species of *Orchesella* because this species, in the adult stage, is less restricted to soil; pollen grains are more important in the diet of epigeic Collembola than in that of hemiedaphic species (cf. Gisin, 1948). Bödvarsson (1970) has indicated that, of seven soil-inhabiting species studied, pollen grains were found very infrequently in the guts — in 3.5 per cent of *Lepidocyrtus lanuginosus* (a surface dweller), and in 1.3 per cent of *Megalothorax* [= *Neelus*] *minimum* Willem (a subterranean species).

In concluding this review of pollen feeding by Collembola, some recent unpublished observations may also be mentioned. One of us (D.K.K.) recently observed *Sminthurus viridis* [? var. *medicaginia*] on the flowers of yellow medic (*Medicago* sp., Leguminosae) in a pasture in S.E. South Australia in late winter (August), 1968, but without direct evidence of pollen feeding, although the species is reported to consume pollen. Stainer (1969), from gut examinations, found that, in spring, *Entomobryoides purpurascens* (Packard), living in wood piles in south-western Quebec, fed extensively on drifted pollen of various [deciduous] trees [mostly *Betula* spp. (Betulaceae)]. In summer they also ingested pollen, probably of ragweed [*Ambrosia trifida* Linnaeus (Compositae)] or golden-rod [*Solidago* spp. (Compositae)]. He indicated that the highest proportion of his field-collection individuals that contained pollen was 14 per cent (7 out of 50 in one sample); many samples contained none. Specimens of the same species collected by K. P. Butler under dead bark in a Red pine plantation, Kirkwood Township, Algoma District, Ontario, 6.VI.1965, also showed a few, mostly unbroken, unidentified pollen grains in the gut. Specimens of the following species collected (in pitfall traps unless stated otherwise) near Ste. Anne de Bellevue, Quebec, during May and June, 1966, by members of the McGill University Department of Entomology, also contained varying quantities of mostly unbroken, unidentified pollen: *Lepidocyrtus* sp. (immature, in *Tsuga* litter, abundant pollen), *Entomobrya clitellaria* Guthrie (under bark), *Sminthurus viridis* Linnaeus (on vegetation), *S. facialis* Banks, *Sminthurinus aureus* (Lubbock) (few grains), *S. elegans* (Fitch) (few grains) and *S. radiculis* Maynard.

Dr. J. T. Salmon (*in litt.*, 1969) writes that, in New Zealand, *Parakatianna albirubrafrons* Salmon and *P. diversitata* Salmon and their "varieties" are most common when tauhinu [*Pomaderris phylacaeifolia* Loddige (Rhamnaceae)] is in flower, and, as flowers are copiously supplied with pollen, they could be pollen feeders, but he has no conclusive evidence of this; also *Polykatianna flammea* Salmon and *Pseudokatianna lutea* Salmon are taken off native New Zealand "broom" trees [presumably *Carmichaelia* spp. (Leguminosae), although *Notospartium* and *Chordospartium* spp. are also "brooms"], particularly when they are in flower, so these might also be pollen feeders. Dr. H. G. Scott (*in litt.*, 1969) has kindly supplied us with a list of species swept off vegetation, particularly conifers and grasses, in New Mexico, and it is quite likely that some of these may feed on pollen, although there is no direct evidence for this. The following were involved: *Isotoma notabilis* Schäffer, *Entomobrya assuta* Folsom, *Sinella binoculata* (Schött), *Isotobryoides ochracius* Maynard, *Lepidocyrtinus domesticus* (Nicolet), *Orchesella hexafasciata* Harvey, *O. zebra* Guthrie, *Bourletiella aquatica* Maynard, *B. arvalis* (Fitch), *B. batroches* (Wray), *B. fallonae* Maynard, *B. hortensis* (Fitch) [? = *B. signata*], *B. russata* Maynard, *B. spinata* Macgillivray and two new species of the same genus, as well as *Sminthurus obscurus* Mills, *S. fitchi* Folsom and *S. dorsalis* (Banks).

Table 1 lists alphabetically the species of Collembola recorded as visiting flowers or as ingesting pollen or both, or suspected of so doing.

Table 1. Species of Collembola recorded ingesting pollen†, visiting flowers*, or both†*, or unmarked, suspected of so doing (see text). A question mark indicates a literature record as feeding on pollen, evidence not given; (†*) indicates ingesting pollen while visiting flowers.

<i>Bourletiella</i> spp.†	<i>Lepidocyrtus</i> spp.†
<i>B. aquatica</i> Maynard	<i>L. cyaneus</i> Tullberg†
<i>B. arvalis</i> (Fitch)	<i>L. lanuginosus</i> (Gmelin)†*
<i>B. batroches</i> (Wray)	
<i>B. bilineata</i> (Bourlet)†	<i>Megalothorax minimum</i> Willem†
<i>B. fallonae</i> Maynard	
<i>B. lutea</i> (Lubbock)(†*)	<i>Onychiurus pseudofimetarius</i> Folsom†
<i>B. pallipes</i> (Bourlet)†*	
<i>B. repanda</i> (Ågren)†*	<i>Orchesella bifasciata</i> Nicolet†
<i>B. russata</i> Maynard	<i>O. hexafasciata</i> Harvey
<i>B. signata</i> (Nicolet)(†*) [incl. <i>B. pruinosa</i>	<i>O. quinquefasciata</i> Bourlet†
(Tullbert) and <i>B. hortensis</i> (Fitch)]	<i>O. villosa</i> (Geoffroy)†
<i>B. spinata</i> Macgillivray	<i>O. zebra</i> Guthrie
<i>B. n. spp.</i> (2)	
	<i>Parakatianna</i> spp. (?)†
<i>Drepanocyrtus</i> sp. nr. <i>flavovirens</i> (Börner)*	<i>P. albirubrafrons</i> Salmon
	<i>P. diversitata</i> Salmon
<i>Entomobrya assuta</i> Folsom†	
<i>E. clitellaria</i> Guthrie	<i>Polykatianna flammea</i> Salmon
<i>E. comparata</i> Folsom(†*)	
<i>E. nivalis</i> (Linnaeus)†* [incl. var.	<i>Proisotoma</i> spp. (?)†
<i>immaculata</i> Schäffer]	
<i>E. spectabilis</i> Reuter*	<i>Pseudokatianna lutea</i> Salmon
<i>Entomobryoides purpurescens</i> (Packard)†	<i>Sinella binocolata</i> (Schött)
<i>Folsomia</i> spp.†	<i>Sminthurides aquaticus</i> (Bourlet)†
<i>Folsomia fimetaria</i> (Linnaeus)(†*)	<i>S. pumilis</i> (Krausbauer) [inference only]
<i>Hypogastrura</i> spp. (?)†	<i>Sminthurinus aureus</i> (Lubbock)†
<i>Hypogastrura socialis</i> Uzel (?)†	<i>S. elegans</i> (Fitch)†
	<i>S. radicleus</i> Maynard†
<i>Isotobryoides ochracius</i> Maynard	
	<i>Sminthurus</i> spp.†
<i>Isotoma</i> spp.†	<i>S. dorsalis</i> (Banks)†
<i>I. kosiana</i> Bagnall† [incl. <i>I. nigra</i> Kos	<i>S. facialis</i> Banks†
and <i>I. kosi</i> Paclt]	<i>S. fitchi</i> Maynard
<i>I. notabilis</i> Schäffer	<i>S. obscurus</i> Mills
<i>I. saltans</i> (Nicolet)†	<i>S. viridis</i> (Linnaeus)†* [incl. var.
<i>I. viridis</i> (Bourlet)*	<i>medicaginis</i> Schött]
<i>Isotomurus palustris</i> (Miller)†	<i>Tomocerus vulgaris</i> Tullberg†
	<i>T. flavescens</i> Tullberg†
<i>Katianna</i> spp. (?)†	<i>T. minor</i> Lubbock†
<i>Lepidocirtinus domesticus</i> (Nicolet)	Undetermined (2 spp.)*

Pollen as food

Faegri and Pijl (1966: 50) state that there is good reason to consider pollen as the original attractant for insects to flowers. Pollen is eaten by some beetles, bees, and flies as well as by Collembola. The chemical composition of pollen has been studied particularly in reference to the nutrition of honey-bees (Haydak, 1970). Lunden (1954) and Lubliner-Mianowska (1956) have reviewed the literature on aspects of pollen chemistry, the former author including works on allergens.

Protein content of pollens varies from 8.67 to 45.37 per cent (Lubliner-Mianowska, 1956) and averages over 25 per cent (Lunden, 1954). Conifer pollen, a well documented collembolan food, is low in protein content at about 16 per cent. The essential amino-acids in pollen show less variation (*cf.* Auclair and Jamieson, 1948; Weaver and Kuiken, 1951; Lunden, 1954). Todd and Bretherick (1942) found that carbohydrates (sugars and starches) make up about 25 per cent of pollen extracts. Lipids and other ether-extractable materials are in very variable amounts, ranging from 1 to 20 per cent (Hügel, 1962), with a mean of about 5 per cent. Interestingly, pollens of Cruciferae (*Brassica* spp.) – see below – and Compositae (*Taraxacum* sp.) are rich in lipids (Todd and Bretherick, 1942). The vitamins in pollen are diverse and in different concentrations (Lunden, 1954). Other pollen constituents reported by the above authors are pigments, enzymes, co-enzymes, and minerals, as well as undetermined materials or ash. Clearly pollen is a highly valuable food, not only for its protein content, but for all the basic nutrients for any animal able to use it.

OBSERVATIONS ON COLLEMBOLA AND FLOWERS IN THE CANADIAN HIGH ARCTIC

Although there are several records of Collembola from the arctic regions of Canada, only one (Hocking, 1968), already mentioned, has relevance in their association with flowers or pollen.

During the summers of 1967 and 1968 Collembola were collected (by P. G. K.) from the corollas of two species of flowers mostly near Hazen Camp (81° 49' N., 71° 18' W.), Ellesmere Island, District of Franklin, North West Territories. The general ecology of this area has been described by Savile (1964), who divided it by a grid used here to give precise localities within the area.

On 16 June, 1969, a single specimen of an unidentified dark species was taken from within the corolla of a flower of *Saxifraga oppositifolia* Linnaeus (Saxifragaceae). More interesting are the 20 observations and collections of *Entomobrya comparata* Folsom, within the yellow corollas of *Lesquerella arctica* (Wormskjöld) S. Watson (Cruciferae). *E. comparata* is a widespread arctic and alpine species showing much geographic polymorphism. The form here referred to is virtually restricted to arctic tundra zones (Dr. K. Christiansen, *in litt.*, 1970).

On 3 July, 1967, five specimens were collected. They were all deep in the corollas, at the base of the gynoeceium and near the nectaries at the bases of the petals. This collection was made along the shore of Lake Hazen, in square L13 (Savile, 1964) (about 1 km from Hazen Camp). On the same day one other specimen was collected in square C14 (along the west bank of Blister Creek some 3.5 km from camp) in exactly the same circumstances. No further collection or observation was made, despite searching, until 16 July when two specimens were collected, again from deep within the same species of flower growing along the lake shore to the west of Gilman Camp (*ca.* 81° 54' N., 69° 30' W.), some 40 km east of Hazen Camp. On both occasions in 1967 the weather was heavily overcast.

On 3 July, 1968, at 10:30 hours Eastern Standard Time, at Hazen Camp itself (N11), two specimens of this collembolan were observed and photographed on a single plant of the same species, but within different flowers. They were watched through a 20X hand-lens as they appeared to feed directly from the dehisced anthers of the flowers. Each was observed within the same flower for more than 15 minutes, during which time they moved about on the anthers. One moved from one anther to another, crawling down the filament of one, and up on to the anther of the adjacent stamen. Whilst on the anthers, the postures of the animals did not change. Fig. 1 shows, left, how they held on with all six feet, their abdomens loosely curled over the surface of the anther but not appressed to it; and right, a specimen using the style for support; this posture was seen only once. The collembolans continually waved their antennae, again curved over the surface of the anther which they frequently touched. Their mouthparts were seen to be applied to the surface of the anther, but it was impossible to determine for certain that they were ingesting pollen grains. The assumption that they were doing so has been verified by subsequent examinations of the gut contents of the specimens observed. On this same sunny day, one further specimen was collected from another *Lesquerella* flower in the same area. On the next day, 4 July, one specimen was observed in a flower 2.5 km northeast of camp (T3). On 5 July, six specimens were collected, two more closely observed on anthers as in Fig. 1, and others seen in various parts of the Hazen Camp area. Of the six taken, three were collected from the same flowering stalk, two from within the same flower.

Fifteen specimens were sent to the Lyman Entomological Museum, Macdonald Campus, McGill University, for identification. Microscopic examination of all gut contents revealed spherical pollen grains, agreeing exactly with photomicrographs of *Lesquerella arctica* pollen. The pollen grains had been swallowed whole (a feat akin to our swallowing tennis balls!), as is reported by several authors for other pollen-feeding Collembola. Presumably these Collembola digest the nutrient-rich protoplast by diffusion through the thin micropylar membranes, as do bee larvae (Whitcomb and Wilson, 1929; Faegri, 1962), Syrphidae (Müller, 1873: 35-36; Kevan, 1970) and *Pogonomyioides segnis* (Hucket *nec* Holmgren) (Muscidae) (Kevan, 1970).

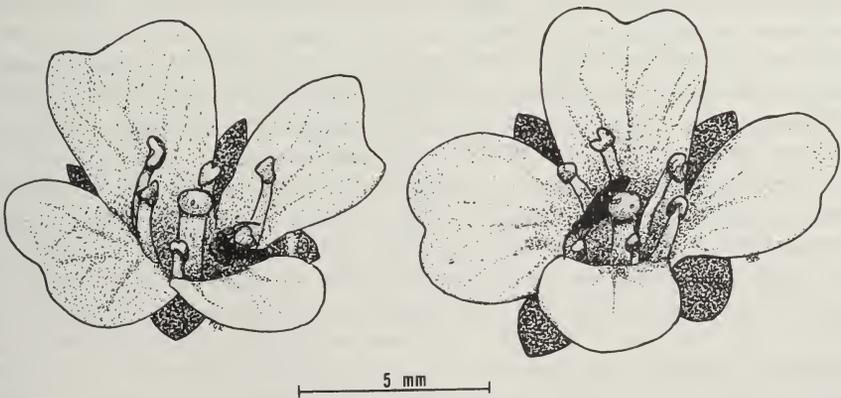


Figure 1. *Entomobrya comparata* feeding on pollen from the anthers of *Lesquerella arctica*. Left, usual position curled around an anther. Right, using style for support. Redrawn from photographs: contrast enhanced.

Entomobrya comparata has not been found, so far, in any other species than *Lesquerella arctica*, and there only around Lake Hazen; neither was it observed at any time on the ground in the vicinity of the plants, nor on their green parts. The activity occurred over a very limited period of time: for one day only in 1967, and over a three-day period in 1968. At Gilman Camp, the single record is for July 16, 1967. This short spell, the small size, and the colour match reduce the chances of observing this activity. Such an activity can be regarded as occurring within a "sensitive period" of their life cycles (Shelford, 1963: 8-9). In Shelford's words, "Sensitive periods sometimes last only a few days and may be difficult to detect. However, the identification of these sensitive periods in the life cycles of both plants and animals and the factors that affect them is very important for understanding their distribution, seasonal occurrence, and abundance". He also writes: "The activity or vital process which takes place within the narrowest environmental limits is usually the most important ecological feature of a life cycle".

Thus, the activity of these collembolans within the flowers of *L. arctica* may be extremely important to their life history. Pollen feeding may be important for nutrition, particularly for the maturation of eggs. Possibly some of the specimens were also feeding on nectar, the sugars of which could provide fuel for prolonged activity. Although Collembola have never been reported to feed on nectar, such a possibility is not precluded for, in the present case, they were found near the nectaries.

DISCUSSION

Attraction of Collembola to Flowers

Carl's (1901) suggestion, that *Bourletiella lutea* seeks refuge from the cold by inhabiting the woolly involucre of high alpine Compositae, particularly *Leodonton taraxaci*, may have some validity, for Tikhomirov *et al.* (1960) have demonstrated that elevated temperatures occur within the involucre of *Novosieversia glacialis* (Adams) F. Bolle (Rosaceae) in the Yakutsk A.S.R. in the Soviet Arctic. Similarly, the densely pubescent catkins of *Salix* spp. (Salicaceae) become considerably warmed in sunshine (Krog, 1955; Büdel, 1957; Kevan, 1970). Büdel (1956, 1959a, b) considers the microclimate within a variety of flowers with particular reference to nectar secretion (review in Hodgson, 1961), and Hocking and Sharp-*lin* (1961) consider elevated temperatures in Arctic flowers as important to insects basking within the corollas.

With regard to flowers known to be visited by Collembola, Knuth (1906, 1: 101-103) considered that some flowers offer shelter to insects during rain and at night, and among these flowers he mentions both *Campanula* and *Taraxacum*. Büdel (1959a, b) and Shamurin (1966) investigated *Taraxacum* spp. and found them to be considerably warmer under sunny conditions than under overcast conditions, and colder than the ambient air at night — by 3 C (Büdel, 1959b) — when the inflorescence had closed; yet it was this very closing which Knuth postulated would trap heat. Kevan (1970) measured temperatures within the corollas of *Lesquerella arctica* in sunshine and found that the mean temperature elevations above ambient air at the same level were 1.7 C and 1.5 C for 20 and 25 flowers at ambient air temperatures of 7.9 and 18.4 C respectively. *Cerastium alpinum* L. also has elevated temperatures within the corollas during sunshine, but this is lost under heavily overcast skies (Hocking, 1968; Kevan, 1970). The same is true of *Lesquerella arctica*, which shows a slight epinastic closing response in dim light. Kevan also made measurements and found elevated temperatures within the bowl-shaped corollas of several other species of arctic flowers. No doubt an investigation of the European *Ranunculus glacialis*, which is known to harbour Collembola would produce similar results. Among zygomorphic flowers, the legume, *Anthyllis vulneraria*, another European species in which Collembola have been found, probably also

develops a considerably warmer environment with its corollas in sunshine as a result of a "greenhouse" effect such as occurs in *Pedicularis* spp. (Scrophulariaceae) (Kevan, 1970).

Of interest, also, in the association between Collembola and flowers, is the possible cryptic nature of the coloration of most flower-visiting Collembola. Table 2 shows the colours of Collembola and of flowers known to be visited by them. Information on ultra-violet reflection within the insect visual spectrum is inferred from, or given by, Kevan (1970). Data on ultra-violet reflections from a few Lepidoptera and spiders (Thomisidae) (cf. Lutz, 1924, 1933; Eisner *et al.*, 1969) are available, but there is nothing, unfortunately, on Collembola.

Of the 14 species of Collembola reported to occur in association with flowers, 10 are known to be light (white to yellow-green) and only three, including those from high altitudes and high latitudes, to be dark in colour. Rapoport (1969), however, indicates that Collembola from such localities are, in general, darker than those from warmer habitats. Of the 10 light-coloured species, only one, the soil-inhabiting *Folsomia fimetaria*, was reported in dark flowers, and then only in the ground-level flowers of *Aspidistra elatior*, where no colour correlation should be inferred. Eight of the remaining nine light species were recorded from white or yellow (with or without ultra-violet) flowers growing in the open; the ninth was recorded from greenhouses, probably on light-coloured flowers.

There is thus a strong suggestion that light-coloured Collembola visiting exposed flowers prefer those in which they are least conspicuous. Objections to this suggestion could, however, be raised because the relative abundance of dark and light Collembola and flowers within the range of cohabitation of each is not known (see also Rapoport, 1969).

The three dark species visiting flowers show little or no comparable association with dark flowers; only one (unidentified) species was collected from the dark (purple) flowers of *Saxifraga oppositifolia*, which had a colour saturation of only about 50 per cent within the insect visual spectrum (Kevan, 1970). The others are recorded from white and/or yellow (\pm ultra-violet) flowers, although, interestingly enough, one of them, *Bourletiella signata*, occurred also in the light blue (probably without ultra-violet) flowers of *Campanula barbata*.

Brief résumés on sensory perception in Collembola are given by Denis (1949) and Paclt (1956), but the greater part of what is known is due to Strebel (1932), who made experimental observations on the reactions of various species of Collembola to light, temperature, smell, taste, and touch. If the suggestion that Collembola select flowers in which they are inconspicuous is valid, colour vision might be expected, but there is no direct evidence for this in the literature.

Most of the flowers listed as being visited by Collembola are relatively conspicuous, but they also produce scent and nectar as well as pollen. Those of *Lesquerella arctica* are no exception. Although not large (*ca.* 1 cm in diameter), they, too, are brightly coloured (yellow without ultra-violet), and produce scent, nectar, and pollen. A sense of smell was indicated for Collembola by Handschin (1926) and Ripper (1930), on account of their retreat from repellent volatile substances. Strebel (1932) observed, in several species, reactions towards or away from odours, the main sensory region (in *Tomocerus minor*) being on the antennae. He concluded, however, that the sense of smell does not play a significant role in the location of food. There is no evidence that scent attracts Collembola to flowers. Taste is apparently well developed in Collembola according to Strebel but, from his observations, sweet substances neither attract nor repel them. Thus there is again no evidence that nectar attracts Collembola to flowers.

Strebel's (1932) experiments on temperature reactions were confined to *Hypogastrura purpurascens* Lubbock, in which he indicated sensitivity to both warmth and cold. The sensory regions were found to be located mainly on the antennae and the posterior part of the abdomen. Strebel also indicates that warmth overcame negative phototaxis. The

Table 2. Colour correlation between species of Collembola and flowers visited by them.

Species of Collembola	Colour	Flowers of —	Colour
<i>Bourletella lutea</i>	Yellow, white below	<i>Anthyllis vulneraria</i> <i>Leontodon taraxaci</i> [= <i>L. montanus</i>] (involucres only)	Rosy white — yellow Yellow (involucres grey-green)
<i>B. pallipes</i>	Black-violet, yellow face, appendages and maculae	<i>Ranunculus glacialis</i>	White, yellow centre and androecium
<i>B. repanda</i>	Yellow	<i>Ranunculus glacialis</i>	White, yellow centre and androecium
<i>B. signata</i> [incl.]	Variable, black- to green-violet, head partly yellowish	<i>Ranunculus glacialis</i> <i>Taraxacum</i> sp.	White, yellow centre and androecium Yellow (probably UV distally on rays)
<i>B. hortensis</i> and <i>B. pruinosa</i>	? Yellow-green	<i>Campanula barbata</i> <i>Coffea</i> sp.	Pale blue White, yellow androecium
<i>Drepanocyrtus</i> sp. [nr. <i>D. flavovirens</i>]	Pale yellow	<i>Anthyllis vulneraria</i>	Rosy white — yellow
<i>Entomobrya nivalis</i> ab. <i>immaculata</i>	Yellow, variegated	Orchidaceae	? (some yellow?)
<i>E. spectabilis</i>	Yellow	<i>Lesquerella arctica</i>	Yellow (no UV)
<i>E. comparata</i>	White*	<i>Aspidistra elatior</i> *	Purplish and greenish*
<i>Folsomia fimetaria</i> *	Variable. Yellowish, usually dull yellow-green, sometimes grey-green, reddish or bluish	<i>Saxifraga hirculus</i>	Yellow (UV distally)
<i>Isotoma viridis</i>	Yellow-white to brown-red	<i>Ranunculus glacialis</i>	White, yellow centre and androecium
<i>Lepidocyrtus lanuginosus</i>	Yellow-green	<i>Medicago</i> sp.	Yellow
<i>Sminthurus viridis</i> [? var. <i>medicaginis</i>]	Unknown	<i>Cerastium arcticum</i>	White, pale yellow androecium (no UV)
Unidentified	Blackish	<i>Saxifraga oppositifolia</i>	Purple (no UV)

*Flowers hidden at soil level; visiting species soil inhabiting; presumably no colour correlation involved.

ameliorated microclimate within the flowers of *Lesquerella arctica* may or may not serve to hold *Entomobrya comparata* (which is not a negatively phototactic species), for it was found in the corollas on both overcast and sunny days. However, Collembola in an ameliorated thermal regime, such as that provided by flower corollas, would metabolize more rapidly and be more active, and this would surely be advantageous in arctic and alpine regions of low heat budget.

Lesquerella arctica grows in dry sandy places around Lake Hazen. The plant is decumbent, its flowers held upright about 1 cm above the ground. Thus a combination of attractants, cryptic protection, accessibility, and perhaps cohabitation, make for the relationship in the High Arctic between this plant and *Entomobrya comparata*. This collembolan was not found in flowers of any other species growing in the vicinity of *L. arctica*, nor, for that matter, anywhere else.

Collembola as Pollinators

Handschin (1924) believed there was a relationship between *Bourletiella lutea* and *Ranunculus glacialis*. He concluded that the Collembola seek out the flowers in order to obtain nourishment from their reproductive organs. From the observations on *Entomobrya comparata* in the flowers of *Lesquerella arctica*, a similar relationship is postulated in respect of the "sensitive period" in the life of this collembolan. Handschin left open the question of pollination by *Bourletiella lutea*, but Strebel (1932) suggested that *Folsomia fimetaria* might be a pollinator of *Aspidistra elatior*. Kevan (1970), however, found that *L. arctica* is independent of arthropods for pollination, although some cross-pollination by arthropods may occur.

The behaviour and probably the size of *E. comparata* precludes these collembolans from being effective pollinators, even within a single flower, although pollen grains do adhere to their hairy bodies. Arthropods as small as Collembola would have no cause to visit more than one flower within the period of viability of any pollen they might carry on their bodies, so that, even if they did occasionally effect cross-pollination, this would be fortuitous.

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THE TAXONOMY OF THE NEARCTIC SPECIES OF THE GENUS
BYRRHUS LINNAEUS (COLEOPTERA: BYRRHIDAE)

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On the basis of a study of external characteristics and male genitalia, the taxonomy of the Nearctic species of Byrrhus is reviewed. Seven species, named as follows, are recognized: americanus LeConte; cyclophorus Kirby; geminatus LeConte; fasciatus Forster; eximius LeConte; kirbyi LeConte; and concolor Kirby. Twenty three species-group names are placed in synonymy. Relationships of the species are briefly considered.

The present study is the first of a series dealing with a taxonomic revision of the genera and species of Nearctic Byrrhidae. This study started many years ago at the Department of Entomology, University of Alberta, and was suggested by George E. Ball. The type specimens available in North America were studied in the summer of 1959, on a trip financed by a National Research Council of Canada grant (A-1399) held by Ball. A tentative classification and a key to the genera of this family was published by me in 1961.

MATERIALS AND METHODS

The material examined consisted of 1100 specimens borrowed from the major entomological collections in the United States and Canada. Type specimens examined are in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ), in the Smithsonian Institution, Washington, D. C. (USNM), and in the British Museum, Natural History (BMNH).

My interpretation of the Kirby, Horn, and Forster names is based on study of the original descriptions and on specimens identified by LeConte. Ball examined the Kirby types. He informed me (*in litt.*) that they were badly rubbed females, and thus could not be positively identified.

All of the specimens available were examined for details of vestiture, body markings, and structure of various sclerites, especially the male genitalia. To relax specimens for dissection, they were placed for several hours in an atmosphere of ammonium hydroxide. The male genitalia were removed and cleared in a 10 per cent solution of potassium hydroxide.

To make drawings, the dissected parts were photographed through a Russian stereo binocular microscope, model MBS-2. The outlines were traced with ink on the photographic prints, and the latter were reproduced as one-tone pictures. Magnifications of the drawings were obtained by means of stage and ocular micrometers.

Genus *Byrrhus* Linnaeus, 1767

Type species. — *Byrrhus pilula* Linnaeus, 1758

Description. — Body form oval, convex. Length 6.0 - 12.0 mm, width 3.5 - 6.0 mm. Color black or dark brown; elytra with dark or dirty gray stripes or pale grayish spots, more or less characteristic of each species. Integument covered with simple hairs. Antennae (Fig. 1) clavate, from dorsal view exposed in resting position; each antenna of 11 articles, article 3 narrow, elongate, following articles widened. Eyes partly hidden with head in resting position. Mouthparts, except labrum, hidden. Labrum (Fig. 2) heavily sclerotized. semi-circular or triangular in shape. Mandibles (Fig. 3) multidentate at extremities each with internal notch toward middle, and with ciliated leathery lamella. Maxillae (Fig. 4) each with

galea densely setose at extremity, lacinia narrower, shorter, densely setose at extremity and on inner margin. Maxillary palpus with first article narrow, small; second and third articles subequal; terminal article noticeably long, gradually dilated toward apex. Mentum (Fig. 5) short, transverse, notched-sinuate anteriorly. Ligula large, divided by incision in middle, each lobe subcircular apically and densely setose. Labial palpus with first article narrow, second setose, terminal article large and dilated apically.

Legs (Fig. 6, 7 and 8) each with tibia enlarged toward apex; middle tibia strongly arched and dentate on dorsal side. Tarsi in resting position, each received in depression on internal face of tibia; each article with setae ventrally; first article much longer than articles 2 - 4; article 5 very long. Male with claws of anterior tarsus large and strongly curved.

Elytra with intervals flat, striae shallowly impressed. Vestiture dense, patterned, with paler scales in form of central transverse mark, extended each side from suture to beyond mid line of each elytron; and four rows of longitudinally arranged tufts (vittae) of more prominent scales in intervals 2, 4, 6 and 8, extended from base to apical three fourths of each elytron.

Wings normally fully developed, venation as in Fig. 9, brachyptery rare.

Abdomen (Fig. 10) with crural depressions (grooves in first sternum for reception of hind femora) large, occupying more than half sternum 1.

Remarks. — The Leng catalogue (1920) lists the names of 30 species-group taxa under the generic name *Byrrhus*. However, because of synonymies proposed below, only seven species should now be recorded from North America.

Key to the Nearctic species of the genus *Byrrhus* Linnaeus

1. Margins of elytra, hind coxae and abdominal sterna with stout, blunt bristles; median lobe and parameres almost twice length of basal piece (Fig. 11), median lobe broad, tapered toward apex, parameres markedly narrowed at distal one fourth of length *americanus* LeConte, p. 329.
- Margins of elytra, hind coxae and abdominal sterna without blunt bristles; male genitalia various 2.
2. (1). Central transverse mark of elytra with cinereous spot near center; antennae and legs stout; median lobe of male genitalia narrowed at middle, enlarged near apex and pointed; parameres broad at base, strongly narrowed toward apices (Fig. 15) *eximius* LeConte, p. 331.
- Central transverse mark without cinereous spot at center 3.
3. (2). Elytron in apical one fourth with large black spot extended from near lateral margin to near mid line; median lobe tapered toward apex; parameres each with apex slightly curved laterally (Fig. 16) *kirbyi* LeConte, p. 331.
- Markings of dorsal surface otherwise 4.
4. (3). Central transverse mark of elytra represented by two lines, posterior one strongly concave anteriorly; median lobe narrow, parameres narrowed gradually from bases, each acuminate apically (Fig. 13) *geminatus* LeConte, p. 330.
- Markings of dorsal surface otherwise 5.
5. (4). Parameres of male genitalia with apices rounded, median lobe with apex bluntly pointed (Fig. 12) *cyclophorus* Kirby, p. 329;
- Parameres with apices acuminate, apex of median lobe various 6.
6. (5). Median lobe with apex broadly rounded; parameres tapered more gradually (Fig. 14) *fasciatus* Forster, p. 330.
- Median lobe with apex bluntly pointed; parameres abruptly narrowed close to apices (Fig. 17) *concolor* Kirby, p. 332.

1. *Byrrhus americanus* LeConte

(Fig. 11 and 18)

Byrrhus americanus LeConte, 1850: 224. LECTOTYPE a female (here selected), collected at Lake Superior; first specimen of eight; paralectotypes three males and four females [MCZ].

Byrrhus brunnescens Casey, 1912: 21. HOLOTYPE female, collected at White Point; Casey bequest 1925; Type USNM 48332 [USNM]. NEW SYNONYMY.

Byrrhus imperitus Casey, 1912: 22. HOLOTYPE female, collected at West St. Modest, Labrador; Casey bequest 1925; Type USNM 48335 [USNM]. NEW SYNONYMY.

Byrrhus angustulus Casey, 1912: 22. HOLOTYPE female, collected at Aweme, Manitoba by Norman Criddle; Casey bequest 1925; Type USNM 48336 [USNM]. NEW SYNONYMY.

Byrrhus angustulus neglectus Casey, 1912: 22. LECTOTYPE (here selected) first of two specimens, collected in New Hampshire; Casey bequest 1925; Type USNM 48333 [USNM]; one paratype, sex not determined. NEW SYNONYMY.

Byrrhus angustulus manitobae Casey, 1912: 22. HOLOTYPE male, collected at Aweme, Manitoba by N. Criddle; Casey bequest 1925; Type USNM 48334 [USNM]. NEW SYNONYMY.

Byrrhus criddlei Casey, 1912: 24. LECTOTYPE (here selected), male, collected at Aweme, Manitoba, May 26, 1910; Casey bequest 1925; labelled as Type USNM 48339 [USNM]; one paratype, sex not determined [USNM] NEW SYNONYMY.

Description. — Total length 8.0 - 12.0 mm, width 5.0 - 6.0 mm. Labrum triangular. Vittae of elytral intervals 4, 6, and 8 in apical one fourth with patch of cinereous scales. Median lobe and parameres almost twice length of basal piece (Fig. 11). Median lobe broad, tapered toward apex; parameres markedly narrowed in distal one fourth of their length.

Relationships. — The marked similarity in form of the male genitalia shared by members of this species and *B. cyclophorus* suggests that these two species are closely related.

Geographical distribution. — This species is northern and transcontinental in distribution. It ranges from Labrador (West St. Modest) to interior Alaska (Eagle Summit) and the Pacific coast (Cannon Beach, Oregon). To the south, representatives of *americanus* have been collected in Pennsylvania, Colorado (Cumbres Pass), and in Oregon. See Fig. 18.

Material examined. — 494 specimens.

2. *Byrrhus cyclophorus* Kirby

(Fig. 12 and 19)

Byrrhus cyclophorus Kirby, 1837: 117. HOLOTYPE female, labelled as follows: Type [circular label, bordered in red]; N. Amer. [top], 5828 a [bottom, circular label, handwritten]; *Byrrhus cyclophorus* Kirby, N. Amer., 5828, Rev. Wm. Kirby [handwritten]. [BMNH].

Byrrhus canterius Casey, 1912: 27. LECTOTYPE (here selected) male, collected at Leadville, Colorado, 11,000', July 14, 1896, by Wickham; Casey bequest 1925; Type USNM 48348 [USNM]. One paratype. NEW SYNONYMY.

Byrrhus fulvovestitus Casey, 1912: 27. LECTOTYPE (here selected) female, collected in Oregon; Casey bequest 1925; Type USNM 48344 [USNM]. One paratype. NEW SYNONYMY.

Description. — Total length 6.5 - 8.0 mm, width 3.5 - 4.0 mm. Labrum triangular. Markings on elytra as in *B. americanus* specimens, but less transverse and outer black vitta represented by two or three obscure small spots. Male genitalia with median lobe and para-

meres twice as long as basal piece (Fig. 12). Median lobe constricted near middle, enlarged gradually toward apex, narrowed at extreme tip. Parameres each tapered gradually from base to apex and slightly curved toward median lobe.

Relationships. — Probably the specimens of this species are closely related to those of *B. americanus*, on the basis of overall similarity, including form of the male genitalia.

Geographical distribution. — This species is confined to the west, ranging from Oregon to eastern Alberta (Medicine Hat), north to northern Alberta (Beaverlodge) and south in the Rocky Mountains to central Colorado. See Fig. 19.

Material examined. — 22 specimens.

3. *Byrrhus geminatus* LeConte

(Fig. 13 and 20)

Byrrhus geminatus LeConte, 1854: 114. LECTOTYPE (here selected) female, collected at Lake Superior; Casey bequest 1925; Type 2297 [MCZ] and four paratypes [MCZ].

Byrrhus pettiti Horn, 1870: 76 (type material not seen). NEW SYNONYMY.

Byrrhus concolor pacificus Casey, 1912: 23. HOLOTYPE male, collected in "Washington Territory"; Casey bequest, 1925; Type USNM 48337 [USNM].

Description. — Total length 8.0 - 10.0 mm, width 5.0 - 6.0 mm. Central transverse mark of elytra represented by two lines of cinereous scales: posterior line strongly concave anteriorly. Male genitalia with median lobe and parameres about 1.5 times length of basal piece (Fig. 13). Median lobe very narrow. Parameres each narrowed gradually from base toward acuminate apex.

Relationships. — The form of the median lobe suggests that this species does not have any close relatives, at least in North America.

Geographical distribution. — This species is represented in eastern and western North America, but not in the northern mid-continental areas. In the east, specimens of this species are found from Minnesota eastward to New York (Mt. Marcy), and from western Quebec (Duparquet) southward to North Carolina (Mt. Mitchell). The western part of the range extends from the Rocky Mountains to the Pacific Coast (Cannon Beach, Oregon), northward to central Alaska (Mt. McKinley) and southward to southern Wyoming (Laramie). See Fig. 20.

Material examined. — 80 specimens.

4. *Byrrhus fasciatus* Forster

(Fig. 1 - 10, 14 and 21)

Byrrhus fasciatus Forster, 1771: 12. Type not seen.

Byrrhus torpidus Casey, 1912: 25. HOLOTYPE male, collected at Nain, Labrador; Casey bequest 1925; Type USNM 48340 [USNM]. NEW SYNONYMY.

Byrrhus stolidus Casey, 1912: 28. HOLOTYPE male, collected at Palouse, Washington; Casey bequest 1925; Type USNM 48345 [USNM]. NEW SYNONYMY.

Byrrhus difficilis Casey, 1912: 29. LECTOTYPE (here selected) male, collected on Mt. Washington, New Hampshire, 5000 - 6000'; Casey bequest 1925; Type USNM 48347 [USNM]. Two paratypes [USNM]. NEW SYNONYMY.

Description. — Total length 7.0 - 9.0 mm, width 4.0 - 5.0 mm. Body noticeably broadened posteriorly. Color black, brown or golden brown, with grayish-yellow or silvery-white hairs. Labrum triangular (Fig. 2). Male genitalia with median lobe and parameres about 1.5 times length of basal piece (Fig. 14). Median lobe lancet-shaped, evenly curved ventrally, apical

portion broad, apex broadly rounded. Parameres each gradually narrowed toward apex.

Relationships. — Similarities in the form of the median lobe and parameres shared by specimens of this species and those of *B. eximius* suggest a close relationship.

Geographical distribution. — The pattern of this Holarctic species in North America seems to be bi-centric, with specimens known from eastern and western North America, but not from mid-continental areas. The eastern segment of the range extends from Wisconsin (Bayfield) eastward to Labrador (Nain) and southward to the White Mountains of New Hampshire. The western segment of the range extends from the Rocky Mountains to the Pacific coast (Olympia, Washington), and from Nome, Alaska in the north to Loveland Pass in southern Colorado. See Fig. 21.

Material examined. — 70 specimens.

5. *Byrrhus eximius* LeConte

(Fig. 15 and 22)

Byrrhus eximius LeConte, 1850: 224. HOLOTYPE female, collected at "Lake Superior"; LeConte Collection, Type 2298 [MCZ].

Byrrhus callidus Casey, 1912: 25. HOLOTYPE male, collected in Oregon; Casey bequest 1925; Type USNM 48341. [USNM]. NEW SYNONYMY.

Byrrhus centralis Casey, 1912: 27. HOLOTYPE female, collected in Idaho; Casey bequest 1925; Type USNM 48349 [USNM]. NEW SYNONYMY.

Byrrhus explicatus Casey, 1912: 27. HOLOTYPE female, collected in Leavenworth Valley, Colorado, 10,000 - 11,000'; Casey bequest 1925; Type USNM 48350 [USNM]. NEW SYNONYMY.

Description. — Total length 6.0 - 7.0 mm, width 3.5 - 4.0 mm. Central transverse mark of elytra with striking cinereous spot near center. Sterna covered with fine, decumbent hairs. Antennae and legs noticeably stout. Male genitalia with median lobe and parameres about 1.5 times length of basal piece (Fig. 15). Median lobe narrowed at middle, enlarged at apex. Parameres each broad at base, strongly narrowed toward apex.

Relationships. — The closest relative seems to be *B. fasciatus* Forster.

Geographical distribution. — Except for the type locality ("Lake Superior"), this species is known only from the west: eastern Alberta (Medicine Hat) to the Pacific coast (Prince Rupert, British Columbia and Port Angeles, Washington), and from Dawson City, Yukon Territory in the north to Mt. Lyell, California, and Loveland Pass, Colorado in the south. See Fig. 22.

Material examined. — 93 specimens.

6. *Byrrhus kirbyi* LeConte

(Fig. 16 and 23)

Byrrhus picipes Kirby, 1837: 116 (not Duftschmid, 1825). HOLOTYPE female, labelled as follows: Type [circular label, bordered in red]; N. Amer. [top], 5826 a [bottom, circular label, handwritten]; *Byrrhus picipes* Kirby, N. Amer., 5826, Rev. W. Kirby (handwritten). [BMNH]. According to original description, collected at "Lat. 54".

Byrrhus kirbyi LeConte, 1854: 111.

Byrrhus perditus Casey, 1912: 24. LECTOTYPE female (here selected), collected in Oregon; Casey bequest 1925; Type USNM 48338 and four paratypes [USNM]. NEW SYNONYMY.

Byrrhus egenus Casey, 1912: 29. HOLOTYPE female, collected at Donald, British Columbia, by A. G. Smith; Casey bequest 1925; Type USNM 48346 [USNM]. NEW SYNONYMY.

Byrrhus vafer Casey, 1912: 30. HOLOTYPE male, collected at Leadville, Colorado 10,000 - 11,000', July 7 - 14, 1890, by H. F. Wickham; Casey bequest 1925; Type USNM 48351 [USNM]. NEW SYNONYMY.

Byrrhus wickhami Casey, 1912: 31. LECTOTYPE (here selected), male, collected in Idaho; Casey bequest 1925; Type USNM 48352 and three paratypes [USNM]. NEW SYNONYMY.

Byrrhus consuetus Casey, 1912: 31. HOLOTYPE female, collected at Aldermere, British Columbia; Casey bequest 1925; Type USNM 48353 [USNM].

Description. — Total length 7.0 - 8.5 mm, width 4.0 - 5.0 mm. Each elytron laterad of its mid line in apical one fourth with black spot formed by scales of vittae and additional ones on intervals between vittae. Labrum semicircular. Elytra broad, obtuse posteriorly. Male genitalia with median lobe and parameres about 1.5 times length of basal piece (Fig. 16). Median lobe broad, tapered toward bluntly pointed apex. Parameres each broad at base, tapered to apex, latter slightly curved laterad.

Relationships. — The similarities in form and proportions of the median lobe and parameres shared by members of this species and *B. concolor* suggest a close relationship.

Geographical distribution. — This species is transcontinental in the north, ranging from Labrador (West St. Modest) to the Commander and Pribilof Islands, north to northern Alaska (New Rampart House), south to central California, Colorado at high elevations, and southern New York (Rockaway Beach). See Fig. 23.

Material examined. — 280 specimens.

7. *Byrrhus concolor* Kirby

(Fig. 17 and 24)

Byrrhus concolor Kirby, 1837. LECTOTYPE female (here selected), labelled as follows:

Type [circular piece of paper, bordered in red]; N. Amer [top], 5827 a [bottom of circular label, handwritten]; *Byrrhus concolor* Kirby, N. Amer 5827, Rev. W. Kirby [handwritten]. [BMNH]. According to original description, collected at "lat. 54".

Byrrhus laramiensis Casey, 1912: 26. LECTOTYPE (here selected), female, collected at Laramie, Wyoming by C. J. Wigwander; Casey bequest 1925; Type USNM 48342, and one male paratype [USNM]. NEW SYNONYMY.

Byrrhus rigens Casey, 1912: 26. LECTOTYPE (here selected), male, collected at Bayfield, Wisconsin, by H. F. Wickham; Casey bequest 1925; Type USNM 48343 and one paratype [USNM]. NEW SYNONYMY.

Description. — Total length 6.0 - 7.0 mm, width 3.5 - 4.0 mm. Markings of dorsal surface as in *B. americanus*. Labrum triangular. Male genitalia with median lobe and parameres about 1.5 times length of basal piece (Fig. 17). Median lobe constricted before apex, latter bluntly pointed. Parameres each broad basally, tapered gradually toward apex, latter obliquely subtruncate.

Relationships. — The members of this species are probably most closely related to those of *B. kirbyi*.

Geographical distribution. — This species is transcontinental in the north ranging from Nova Scotia (Kentville) and Ungava Bay, Quebec to southern Alaska (Matanuska). Southward, the range of this species extends to the Rocky Mountains of Colorado, and Pennsylvania (Pocono Lake). See Fig. 24.

Material examined. — 59 specimens.

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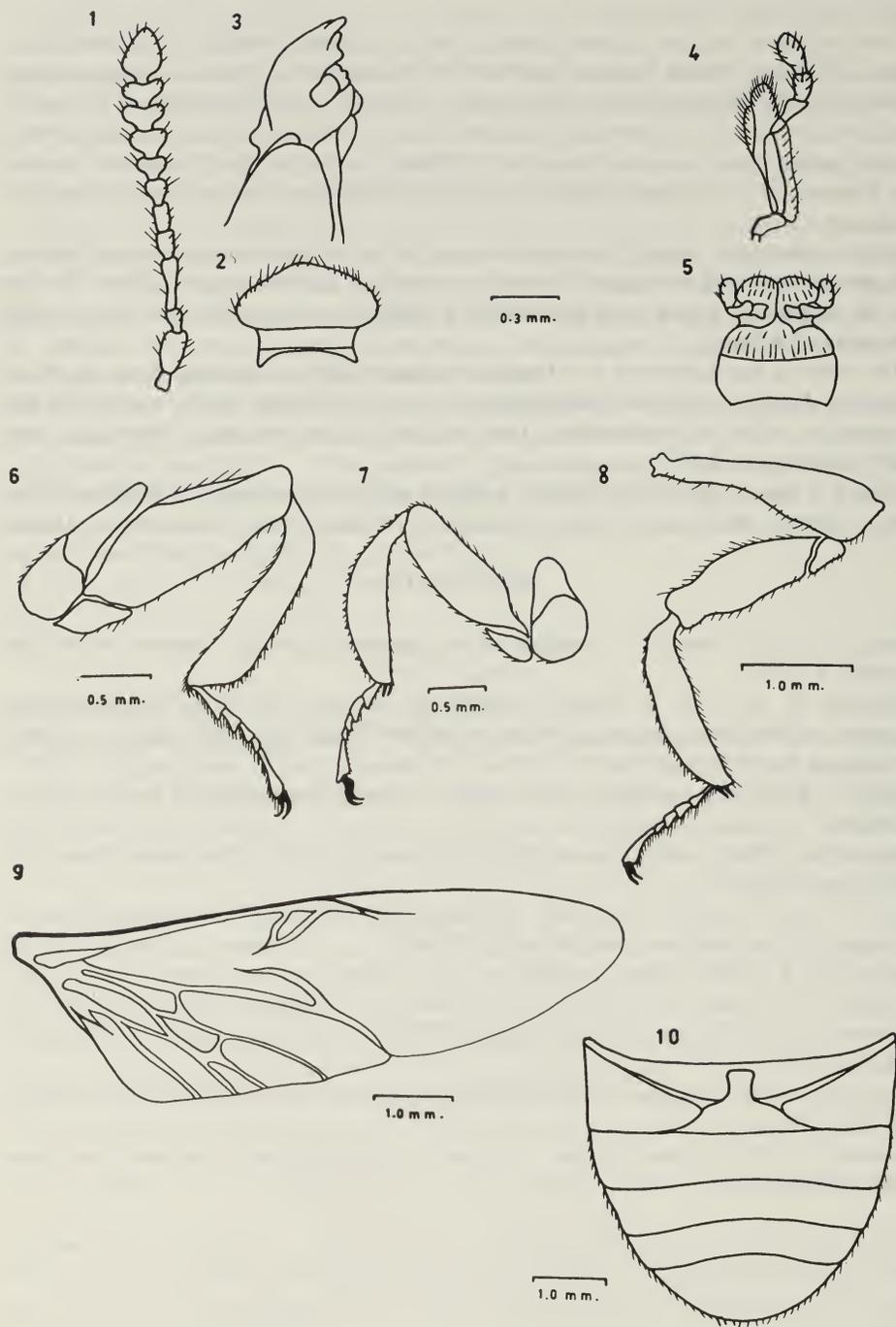


Fig. 1-10. *Byrrhus fasciatus*. 1. Antenna. 2. Labrum. 3. Mandible. 4. Maxilla. 5. Labium. 6. Fore-leg. 7. Mid-leg. 8. Hind-leg. 9. Wing venation. 10. Abdominal sterna.

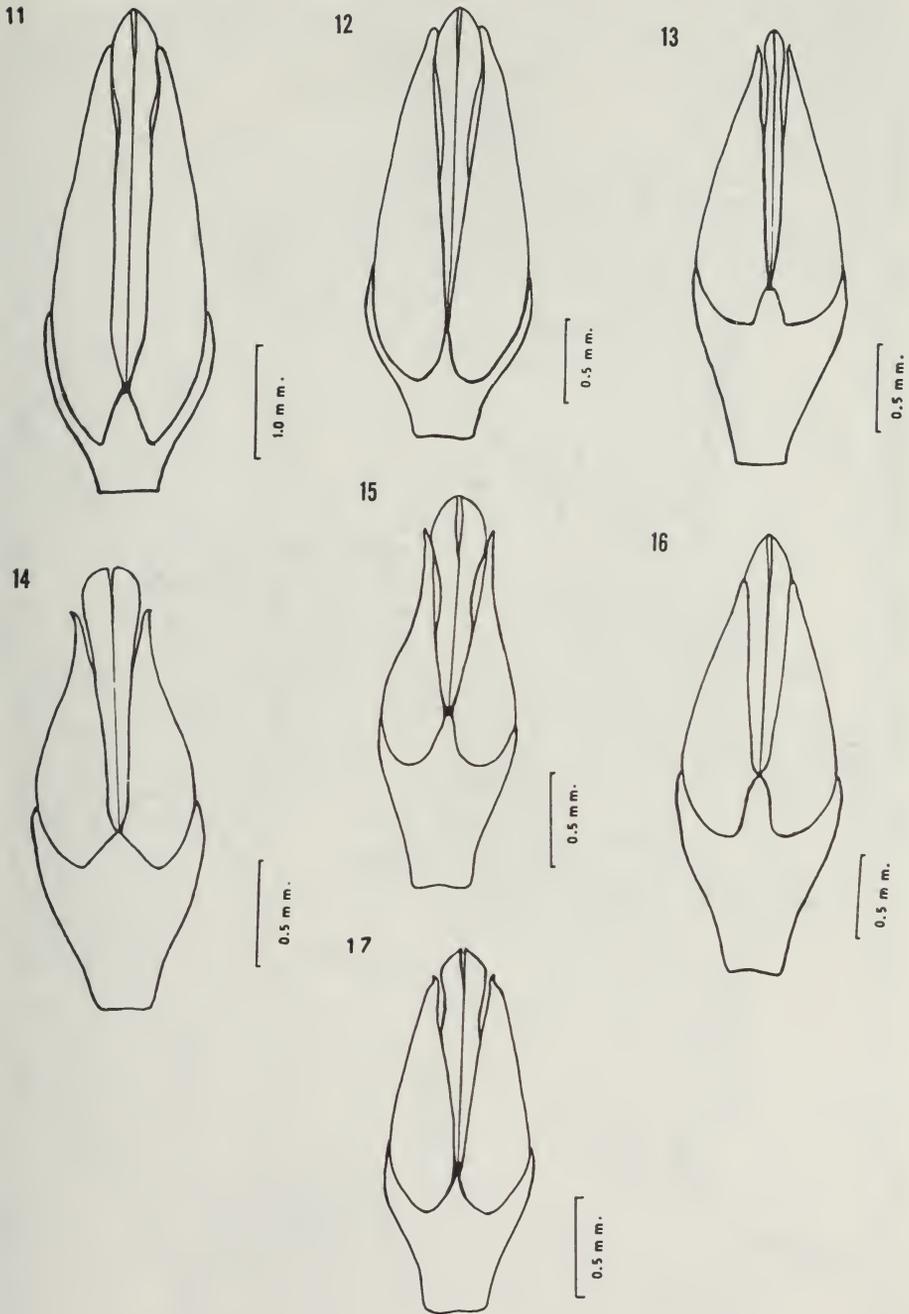


Fig. 11–17. Male genitalia. 11. *Byrrhus americanus*. 12. *B. cyclophorus*. 13. *B. geminatus*. 14. *B. fasciatus*. 15. *B. eximius*. 16. *B. kirbyi*. 17. *B. concolor*.

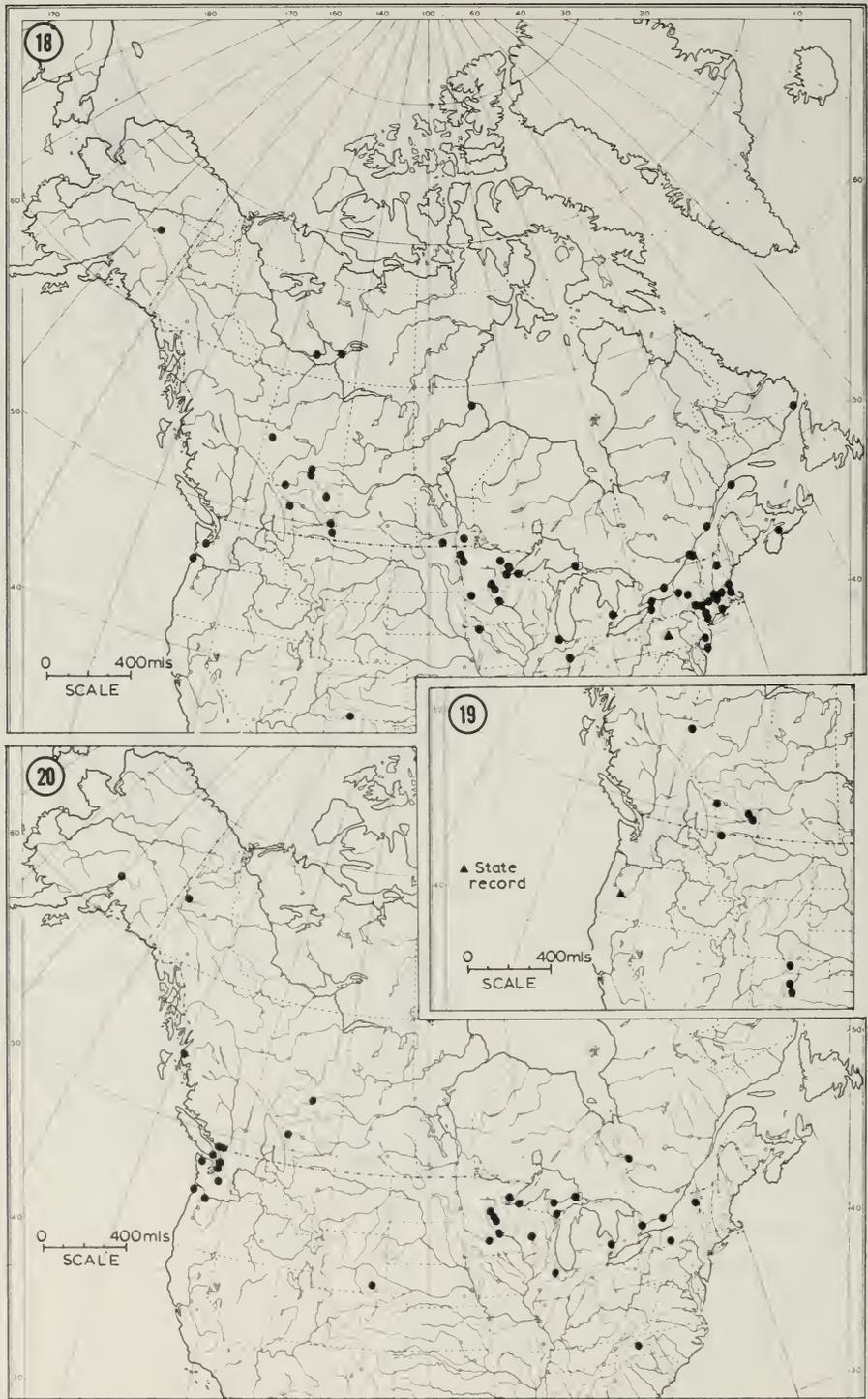


Fig. 18–20. Maps of northern and western North America, illustrating the geographical distribution of *Byrrhus americanus* (18), *Byrrhus cyclophorus* (19), and *Byrrhus geminatus* (20). Filled-in circles – localities; triangles – state records.

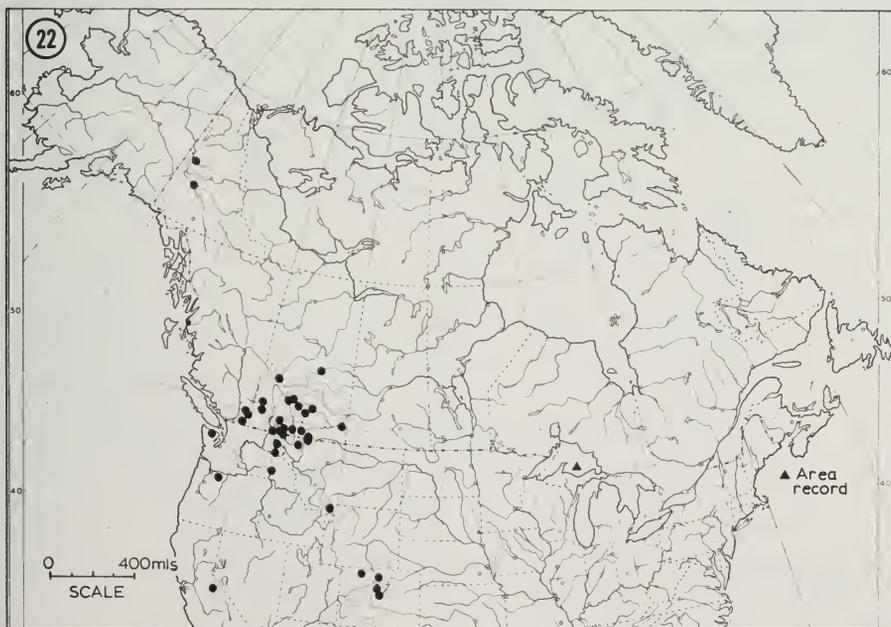
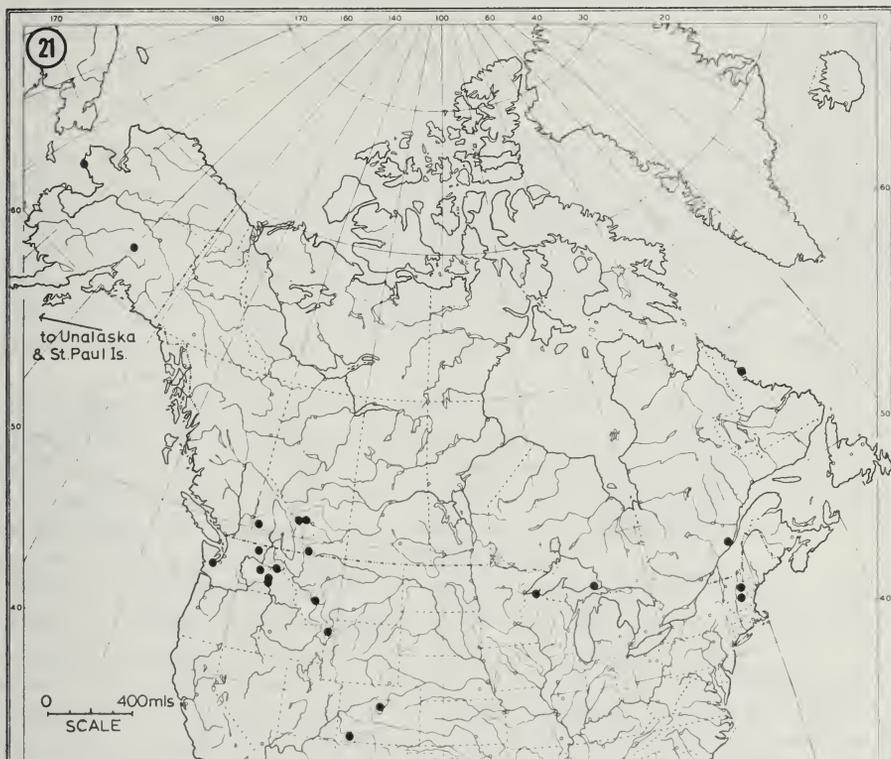


Fig. 21–22. Maps of northern North America, illustrating the geographical distribution of *Byrrhus fasciatus* (21) and *Byrrhus eximius* (22). Filled-in circles – localities; triangle – area record.

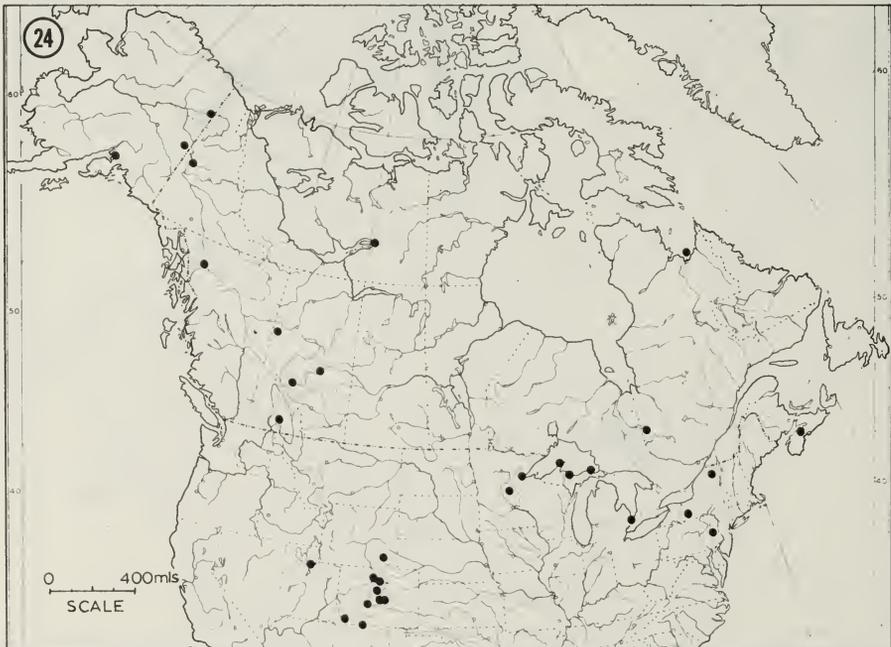
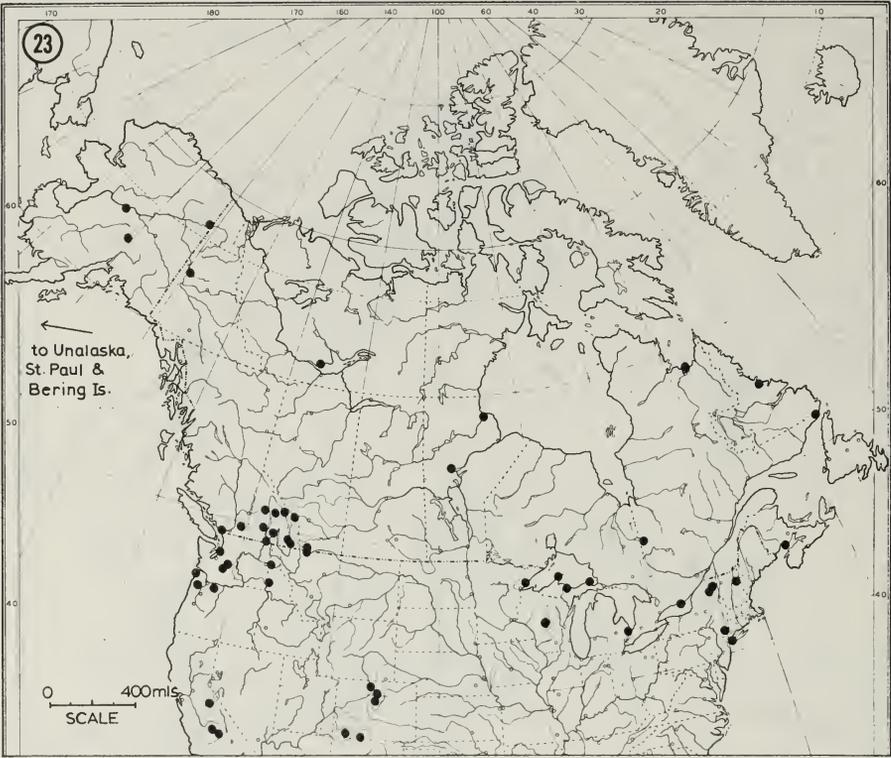


Fig. 23–24. Maps of northern North America, illustrating the geographical distribution of *Byrrhus kirbyi* (23) and *Byrrhus concolor* (24).

THE MODE OF ACTION OF INSECT REPELLENTS I: CHOICE CHAMBER
EXPERIMENTS WITH THE GERMAN COCKROACH *BLATTELLA GERMANICA* (L.)

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*Apparatus was designed to separate the effects of liquid and vapour phases of insect repellents. It was used to study the sites of action of these two phases on the German cockroach *Blattella germanica* (L.). The antennae contain the main sites of repellent receptors with the legs of secondary and the palps of little or no importance. Both the legs and antennae carry receptors for both liquid and vapour repellent phases. The vapour phase appears more effective than the liquid phase, but the combined effect of the two phases is greater than the sum of their individual effects.*

The purpose of this study was to determine the sites of action on insects of insect repellents and to clarify the nature of the senses involved, with particular reference to the common chemical sense. The common chemical sense has been defined by Roys (1954) as a fundamental sensitivity of all nerve tissue to irritant chemical stimuli. This paper is concerned with true repellency or the production of an avoiding response, not with the interference with normal behaviour by repellent chemicals.

There are many empirical methods of evaluating insect repellents (Shepard, 1960). Most of these are designed to test the repellents under the conditions in which they will be used. For example, mosquito repellents are often tested for protection time and degree of protection whilst applied to the human skin under field conditions. In many such tests the repellent is being tested in the presence of attractive factors, and as a preventive against both normal and specialized behaviour, such as blood feeding. Such methods cannot be comparably applied to all insects, nor can they differentiate between compounds which interfere with some behavioural pattern and those compounds which induce active repellency. Since I wished to consider simple repellency, to determine the sites of action on insects and the part played by the liquid and vapour phases of repellents, I chose a method of repellent evaluation that would allow the repellent effect to be tested in the absence of all other known attractive or repellent stimuli.

The simple binary choice test chamber is a commonly used method of testing insect behaviour. Originally, the chamber was used to determine the humidity preferences of insects (Gunn and Cosway, 1938) and has been repeatedly used for that purpose since (Willis and Roth, 1950; Bar-Zeev, 1960). The use of this type of chamber to screen repellents was suggested by Bar-Zeev (1962). The long neglect of the simple choice chamber for testing repellents is not an oversight on the part of repellent workers, but merely because for practical purposes more severe and demanding tests are usually desired for repellent evaluation. The binary-choice chamber is divided into two parts, identical in all ways except for the experimentally introduced variable. Other factors such as temperature and illumination must be the same on both sides of the chamber, so that any deviation from an expected distribution of the insects placed in the chamber can be attributed to the introduced factor.

I designed a variation of this type of chamber to test repellents separately in their two phases, liquid and vapour. By this method, I hoped to separate the repellent effect into contact and olfactory repellency. By using, in this test chamber, insects with some of their appendages painted with nail varnish to block the sense organs, it was hoped to discover which groups of sense organs mediated the response to each of the two phases of the repellent, and to what extent.

EXPERIMENTAL METHODS

Associated with a layer of liquid is a layer of vapour above it, emanating from the liquid. If a liquid repellent is applied to a porous material, sufficient flow of air down through the material will effectively remove this vapour layer. A circular binary-choice test chamber 12 cm in diameter was constructed in the inlet port of a 1.5 kw centrifugal blower (Fig. 1). The outlet port of the blower was vented to the outside of the building. The wire mesh floor of the test chamber was covered with glass fibre cloth, two unconnected halves joined with cellophane tape. One half was treated with repellent by soaking in acetone with a known concentration of repellent in solution, the other half was untreated, soaked merely in pure acetone. Glass fibre cloth has a loose porous construction as well as being insoluble in most organic solvents (most repellents are plasticizers and soften rayon and acetate fibres). The vapour layer associated with the treated cloth could be sucked down by turning the blower on, which maintained a flow through the cloth's surface of about 60 cm/sec. Test insects were prevented from leaving the floor of the chamber by treating the smooth glass walls with polytetrafluorethylene which had a surface too smooth for the insects to climb.

Four arrangements of the test cage were possible: (1) a single layer of cloth in the cage, half treated half untreated, suction off; test conditions for total repellency. (2) a single cloth layer as (1), but the suction fan on; test conditions for contact repellency with a liquid phase only. (3) two layers of cloth; the lower half treated and half untreated, the upper layer entirely untreated, and separated from the lower layer by a 1 mm thick non-absorbent monofilament mesh, of the type used in insect window screens, made of glass fibre 12 x 12 mesh; test conditions for vapour repellency only, since the test insects were kept from contact with the liquid but still exposed to the vapour layer. (4) two cloth layers as (3) but with suction on; test conditions for the total efficiency of the setup. If the apparatus works properly, the insects are not in contact with either liquid or vapour and there should be no repellency.

Readings were taken by camera (Fig. 1) to avoid any bias from visual observations. The camera was triggered to take a single frame at the end of 3 minutes by means of a switch on a slow moving kymograph.

Preliminary experiments indicated that the repellent would remain effective at the same level for up to 70 hours with no air flow through the test chamber, and up to 50 hours with air flow. Subsequent experiments were run over shorter periods of time than this (Fig. 2).

Tests were designed to use German cockroaches (*Blattella germanica* (L.)) and the cockroach repellent MGK R-874 (2-hydroxyethyl-n-octyl sulphide), since this is an extremely efficient repellent to cockroaches (Goodhue, 1960). The logic behind the preference for a repellent known to be almost entirely effective is that such a material may be supposed to possess all the characteristics of a 'total' repellent; any less efficient material may be deficient in some aspect of repellency. Only adult male German cockroaches were used, avoiding the possibility of introducing sex attractants into the chamber from female insects; the insects were reared at 23 C in a culture room and the tests conducted in a drakened room at 23 C and relative humidity of 30%-40%; all insects used were first anaesthetized with carbon dioxide, transferred to individual vials and allowed to recover in the test room for 2 hours, whether they had been treated with nail varnish to block their sense receptors or not; the insects were adults between 3 and 10 days old, and were not used more than once. Since cockroaches have a tendency to congregate or clump, readings were taken with only one cockroach in the chamber at a time. For each reading, a roach was dropped on the centre line of the test chamber, allowed to settle for exactly 3 minutes, and a photograph taken of its position. The cockroach was removed and dropped again for a second reading, and so on through

the 10 readings. The cockroach was then discarded. Thus after each reading the insect was thoroughly disturbed, and to this extent the readings may be said to be independent.

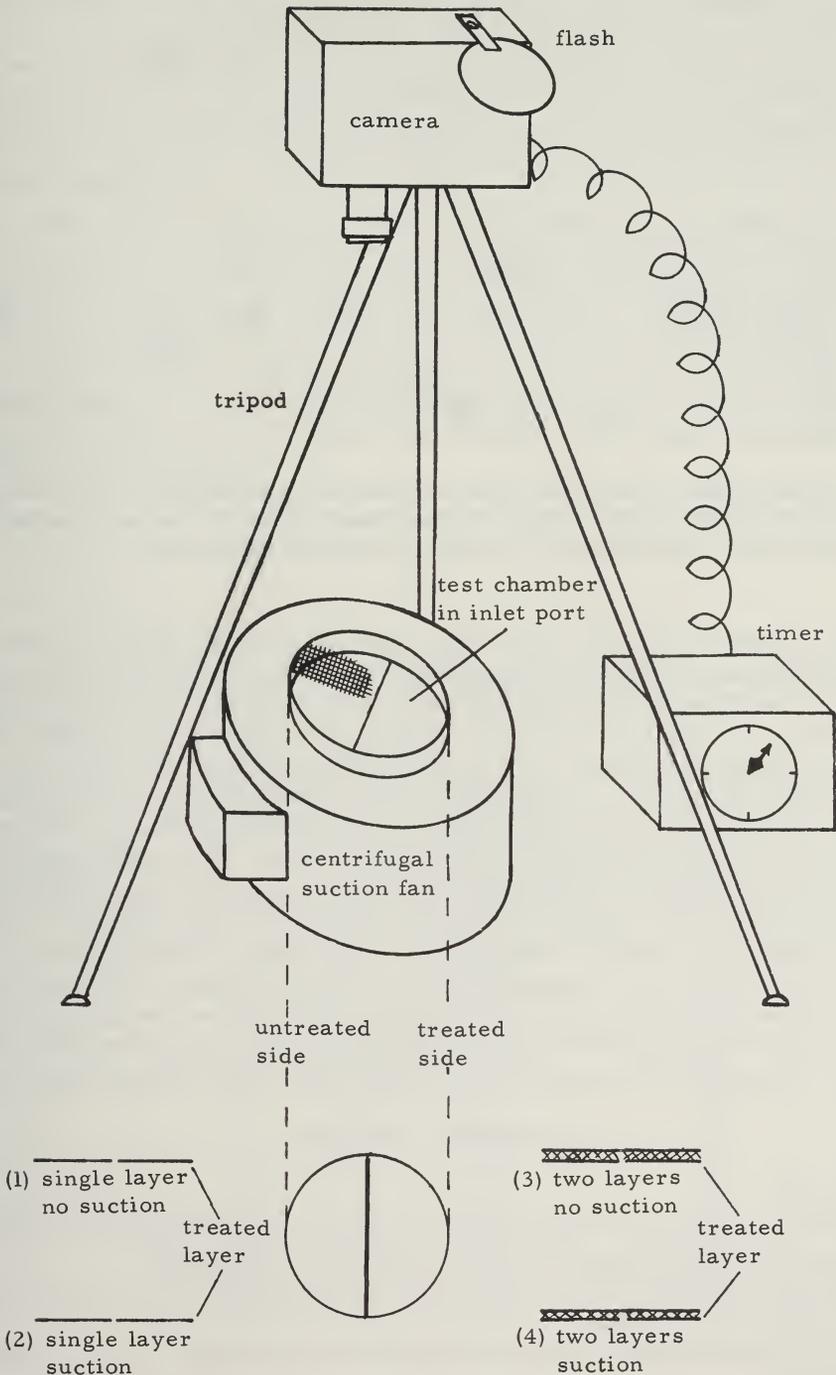


Figure 1. Sketch of the choice-chamber apparatus, and chamber floor arrangements for separating the repellent phases: (1) liquid and vapour present, (2) liquid only present, (3) vapour only present, (4) neither phase present (control).



Figure 2. *Blattella germanica*, untreated insects. Above, both phases of the repellent MGK R-874 present. Below, liquid MGK R-874 only present (suction fan on). Indices of repellency averaged at intervals of 10 readings, showing that there is no consistent decrease in the repellent effect over the period of time that the tests were run.

There is another reason why single insects were used rather than batches of insects. If several readings are taken of the distribution of a single insect in the test chamber, the data produced must follow a binomial pattern since the insect can only be counted as on the treated side of the chamber or not. The resulting ratio of readings on the treated side versus readings on the untreated side will give an estimate of the probability of the insect being on the untreated side, which is a measure of the degree of repellency for that insect alone. If the experiment is repeated using different insects, a measure can be obtained of the variability of this degree of repellency within the insect population. This variation may not be binomial; indeed, it is more likely to follow a normal pattern, since it is the variation shown by a natural population in response to a repellent substance. If a batch of insects is used, say 10 at a time, and an average of three counted on the repellent treated side, unless each insect is marked and counted separately we have no way of knowing whether each insect spent three-tenths of its time on the treated side, or whether three insects spent all their time on the treated side and seven insects spent all their time on the untreated side. Thus we have no measure of the variability of the repellent effect within the insect population.

EXPERIMENTAL RESULTS

Experiment I

To show that there is no difference between the behaviour of untreated male German cockroaches when they are placed in a binary-choice test chamber with:

1. no repellent present and no air flow down through the chamber, both halves of the chamber being untreated cloth;
2. no repellent present, identical untreated halves to the chamber floor, but with the suction fan on;
3. two layers of cloth separated by glass fibre mesh, half the lower layer treated with

repellent (MGK R-874), suction fan on; these are the conditions for testing the efficiency of the apparatus (see Fig. 1).

For each test, 10 separate readings were taken on each of 20 cockroaches. For every reading, a cockroach was placed on the centre line of the chamber, allowed to settle in the dark, and a photograph taken of the insect's position. The results of each test were tabulated (tables 1, 2 and 3) and tested statistically against the following null hypothesis: there is no difference between the observed distribution of the experimental data and an expected binomial distribution, with a proposed probability of 0.5 that an insect will be on either side of the chamber.

The results are given in tables 1, 2 and 3. In none of these tests is χ^2 significant at the 0.05 probability level, and therefore in no case can the null hypothesis be rejected. In the absence of the experimentally introduced repellent stimulus, the test insects chose their side of the test chamber at random, with the expected probability of 0.5 (table 1). This distribution was binomial (tables 1 and 2), and was not affected by air flow down through the chamber (table 2). With the apparatus set to remove both the liquid and vapour phases of a repellent present in one side of the test chamber, the test insects showed no significant preference for either side of the chamber, indicating that the two repellent phases had been effectively removed (table 3).

Table 1. Binomial distribution fit for 20 *Blattella germanica* adult males, no repellent, no treatment, no airflow in the test chamber. For the binomial fit calculations see Steel and Torrie (1960).

N = number of times each insect recorded on the right hand side	O = observed insect frequency	Expected probability $p^N(1-p)^{10-N}$ times the binomial coefficients	E = expected frequency = expected probability times 20	$\frac{(O-E)^2}{E}$
10	0	0.00098	0.02	0.02
9	0	0.0098	0.20	0.20
8	1	0.0439	0.88	0.16
7	1	0.1172	2.34	0.77
6	6	0.2051	4.10	0.88
5	6	0.2500	5.00	0.20
4	4	0.2051	4.10	0.00
3	0	0.1172	2.34	2.34
2	2	0.0439	0.88	1.42
1	0	0.0098	0.20	0.20
0	0	0.00098	0.02	0.02
	20	1.000		$\chi^2 = 6.21$

$p = 0.5, 1 - p = 0.5$

10 degrees of freedom (only one degree of freedom is lost, since p was not estimated)

Table 2. Binomial distribution fit for 20 *Blattella germanica* adult males, no repellent, no treatment, but with the suction fan on; i.e., airflow down through the chamber.

N = number of times each insect recorded on the right hand side	O = observed insect frequency	Expected probability $p^N(1-p)^{10-N}$ times the binomial coefficients	E = expected frequency = expected probability times 20	$\frac{(O-E)^2}{E}$
10	0	0.00098	0.02	0.02
9	0	0.0098	0.20	0.20
8	2	0.0439	0.88	0.16
7	2	0.1172	2.34	0.05
6	4	0.2051	4.10	0.00
5	5	0.2500	5.00	0.00
4	4	0.2051	4.10	0.00
3	1	0.1172	2.34	0.77
2	2	0.0439	0.88	1.42
1	0	0.0098	0.20	0.20
0	0	0.00098	0.02	0.02
	20			$\chi^2 = 2.84$

$p = 0.5, 1 - p = 0.5$

10 degrees of freedom (only one degree of freedom is lost, since p was not estimated).

Table 3. Binomial distribution fit for 20 *Blattella germanica* adult males, repellent MGK R-874 present in the lower left layer of the choice chamber floor. Suction fan on, and the insects separated from the repellent by a layer of fibre mesh and a second layer of cloth. Control conditions for the removal of both the liquid and vapour phases of repellent.

N = number of times each insect recorded on the untreated side	O = observed insect frequency	Expected probability $p^N(1-p)^{10-N}$ times the binomial coefficients	E = expected frequency = expected probability times 20	$\frac{(O-E)^2}{E}$
10	0	0.00098	0.02	0.02
9	0	0.0098	0.20	3.20
8	1	0.0439	0.88	0.16
7	1	0.1172	2.34	0.77
6	2	0.2051	4.10	0.88
5	6	0.2500	5.00	0.20
4	4	0.2051	4.10	0.00
3	4	0.1172	2.34	0.05
2	1	0.0439	0.88	0.16
1	0	0.0098	0.20	0.20
0	0	0.00098	0.02	0.02
	20	1.000		$\chi^2 = 5.86$

$p = 0.5, 1 - p = 0.5$

10 degrees of freedom (only one degree of freedom is lost, since p was not estimated).

Experiment II

This experiment was designed to test the response of treated and untreated German cockroaches to various phases of the repellent MGK R-874 (purity 96.4%). It was hoped to answer the following questions. Can the repellent effect be partitioned into a vapour effect and a liquid effect? Which receptor sites on the insect respond to repellent, and to what extent? Is there an association between the receptor sites and the repellent phases; i.e., do the legs mostly respond to liquid and the antennae to vapour?

Ten readings were taken for each of the 20 separate insects used in each treatment combination. The experiment was designed as a 3 x 4 factorial, and the results analysed by standard analysis of variance procedures. The controls for the experimental design were not included in the main analysis, but treated separately (experiment I) because the analysis of variance presumes a common error variance. In the experimental readings there were two sources of error variation, the binomial variation present in the test chamber readings on each insect (sampling error), and the variation in the response of different insects from the population to the repellent stimulus. An assumption of the analysis is that all measured variables are normally independently distributed. Since the basic readings were binomial, they were transformed by the arcsin \sqrt{X} transformation (Steel and Torrie, 1960), giving data which is approximately normal.

A randomization procedure was carried out on the treatment combinations to minimize error, and the design was as follows.

A: repellent phase treatments. $a = 3$.

A_1 liquid repellent only

A_2 vapour repellent only

A_3 liquid plus vapour repellent.

B: insect treatments. $b = 4$.

B_1 palps exposed (legs and antennae blocked)

B_2 legs exposed (palps and antennae blocked)

B_3 antennae exposed (legs and palps blocked)

B_4 untreated, all sensory areas exposed.

R: 20 male cockroaches used per treatment. $r = 20$.

10 readings taken on each insect, $y = \sin^{-1} \sqrt{X}$ where

X = recordings of each insect on untreated side as a proportion.

The gross data and results are summarized in table 4. Since interaction was statistically significant when compared with the error term, the main effects were compared with the interaction, showing that overall only factor A repellent phase was significant. The interaction means that in this experiment the two factors, repellent phase and insect treatment did not act independently of each other; and that for meaningful interpretation of the data, the effect of each treatment must be examined separately; such effects are known as simple effects.

Before going on to the simple effects, the nature of the interaction was examined to see if its meaning could be understood in terms of the experiment. An interaction can be expressed as a function of the regression characteristics of the treatment means. Tukey (1949) has dealt with this type of problem and devised an approach, even though the levels of each factor are not orthogonal. If the treatment means for each level of a factor are averaged over all levels of the other factor, factor level means are obtained, (\bar{A} and \bar{B} in table 5). These are estimates of proportions, and for ease of calculation were transferred into deviations from the overall treatment mean, giving the x_A and x_B values in table 5. The experimental treatment means are denoted as \bar{y} values. Using the x values as the basis for linear regression equations, theoretical sums of squares can be calculated for the linear

regression of A on B, B on A, and for the A-linear B-linear interaction, which is a measure of the extent to which the two regressions are not additive but multiplicative. The A-linear B-linear sum of squares comes to 2853.8, which is significant. A multiple regression equation based on the linear additive and linear multiplicative sums of squares was estimated as: $\hat{y} = x_A + x_B + 0.1x_Ax_B + 56.48$ (all figures in the transformed range). The \hat{y} 's are estimates of the treatment means \bar{y} (see table 6). Table 6 also shows the residues ($\bar{y} - \hat{y}$) of the treatment means not attributable to linear additive and multiplicative regression. These residues would include any effect due a particular association between two specific levels of the main factors, such as between the vapour phase of repellent and the antennae. These residues are all non-significant, both individually and collectively. This indicates that there is no significant correlation between any particular group of sense organs and any particular phase of repellent.

Table 4. Analysis of variance table for experiment II, and a summary of the results. Values shown are based on transformed data.

	A ₁ liquid repellent	A ₂ vapour repellent	A ₃ liquid and vapour repellent
B ₁ palps only exposed	$\Sigma y =$ 929.0 $\Sigma y =$ 46494.64	968.4 51035.12	993.6 55583.24
B ₂ legs only exposed	980.0 53073.04	1090.0 63864.88	1172.0 72020.24
B ₃ antennae only exposed	1067.0 60857.56	1243.6 80918.32	1395.8 99569.96
B ₄ legs, palps and antennae exposed (untreated)	1036.0 56448.20	1098.6 61180.56	1581.2 127078.16

Source	degrees of freedom	sums of squares	mean square	F
Treatments	(ab-1) = 11	(20591.5)		
A	a-1 = 2	8246.8	4123.4	5.63*
B	b-1 = 3	7949.3	2650.0	3.62
AB	(a-1)(b-1) = 6	4395.4	732.6	3.99*
Error	ab(r-1) = 228	41909.2	183.8	
Total	rab-1 = 239	62500.7		

*significant at 0.05 probability level.

Table 5. Transformed treatment means (denoted as \bar{y}) for three levels of repellent factor, A₁ liquid, A₂ vapour, A₃ liquid plus vapour; and four levels of sense organ treatment, B₁ palps only, B₂ legs only, B₃ antennae only, B₄ all sense organs exposed. Average effects of a factor at each level of the other factor are shown under \bar{A} and \bar{B} , x_A and x_B are the deviations of \bar{A} and \bar{B} from the overall mean 56.48. Untransformed values for these means, i.e., percent of insects on the untreated side, are given in brackets.

	A ₁	A ₂	A ₃	\bar{B}	x_B
B ₁	46.46 (52.55)	48.42 (55.95)	49.68 (58.13)	48.19 (55.56)	-8.29
B ₂	49.00 (56.96)	54.50 (66.28)	58.60 (72.86)	54.03 (65.50)	-2.45
B ₃	53.35 (64.36)	62.18 (78.21)	69.79 (88.06)	61.77 (77.63)	5.29
B ₄	51.80 (61.75)	54.93 (66.98)	79.06 (96.40)	61.93 (77.86)	5.45
\bar{A}	50.15 (58.94)	55.01 (67.12)	64.28 (81.17)	56.48 (69.50) overall mean	
x_A	-6.33	-1.47	7.80		

Table 6. Estimates (\hat{y}) of the transformed experimental means (\bar{y} , see table 5), based on the multiple regression equation $\hat{y} = x_A + x_B + 0.1x_Ax_B + 56.48$. This equation was estimated from the experimental sums of squares. The non-significant residues ($\bar{y}-\hat{y}$) include the contributions due to any particular association between a repellent phase A, and an insect treatment B. The term $0.1x_Ax_B$ accounts for most of the significant interaction noted in the main analysis (table 4). The increase in the repellent effect due to insect treatment is greater if accompanied by an increase in the repellent effect due to repellent phase.

		A ₁ liquid repellent	A ₂ vapour repellent	A ₃ liquid and vapour repellent	x_B
B ₁ palps only exposed	\hat{y}	47.11	47.94	50.01	-8.29
	$\bar{y}-\hat{y}$	-0.65	0.48	-0.33	
B ₂ legs only exposed	\hat{y}	49.16	52.92	59.92	-2.45
	$\bar{y}-\hat{y}$	-0.16	1.58	-1.32	
B ₃ antennae only exposed	\hat{y}	52.09	59.52	73.70	5.29
	$\bar{y}-\hat{y}$	1.26	2.66	-3.91	
B ₄ untreated	\hat{y}	52.15	59.66	73.98	5.45
	$\bar{y}-\hat{y}$	-0.35	-4.73	5.08	
	x_A	-6.33	-1.47	7.80	

The simple effects are a measure of the effect of each level of each factor examined separately over all levels of the other factor. Table 7 shows these effects. Factor A, repellent phase had a significant effect when the test insects were untreated or had their antennae exposed. The repellent phase was not significant when the insects used had only the legs or palps exposed. Factor B, insect treatment, had a significant effect when the insects were exposed to the vapour phase of repellent or to both phases together. The insect treatment was not significant when the insects were exposed to liquid alone. In table 8, the treatment means are arranged in order of magnitude and classified according to levels of significance, based on Duncan's multiple range test.

In addition to the main analysis, the simple effects of repellent phase were analysed separately, including the control from table 1, (table 9). Duncan's multiple range test was also applied to these treatment means.

The significant differences between the treatment means for a factor at fixed levels of the other factor, based on Duncan's test, are summarized in table 10. This completes the analysis. The conclusions are as follows.

Table 7. Simple treatment effects. Figures in the transformed range. The effect of differing repellent phases A is significant for B_3 (insects with the antennae exposed) and B_4 (untreated insects). The effect of the differing insect treatments B is significant for A_2 (exposure to repellent vapour) and A_3 (liquid plus vapour together).

Source	degrees of freedom	sums of squares	mean square	F
A in B_1	2	105.3	52.7	0.29
A in B_2	2	928.2	464.1	2.53
A in B_3	2	2707.8	1353.9	7.37*
A in B_4	2	8901.1	4450.5	24.21*
A + AB	8	12642.4		
B in A_1	3	558.1	186.0	1.01
B in A_2	3	1902.1	634.0	3.45*
B in A_3	3	9883.9	3294.6	17.92*
B + AB	9	12344.1		
Error			183.8	

*significant at 0.05 level

Table 8. Significance levels for the 12 treatment means. Treatments which are not significantly different from each other have the same number opposite.

Treatment	average % insects on untreated side	transformed treatment means	significance levels
A ₃ B ₄	96.40	79.06	(1)
A ₃ B ₃	88.06	69.79	(2)
A ₂ B ₃	78.21	62.18	(2) (3)
A ₃ B ₂	72.86	58.60	(3) (4)
A ₂ B ₄	66.98	54.93	(3) (4) (5)
A ₂ B ₂	66.28	54.50	(3) (4) (5)
A ₁ B ₃	64.36	53.35	(3) (4) (5)
A ₁ B ₄	61.75	51.80	(4) (5)
A ₃ B ₁	58.13	49.68	(4) (5)
A ₁ B ₂	56.96	49.00	(5)
A ₂ B ₁	55.95	48.42	(5)
A ₁ B ₁	52.55	46.46	(5)

A₁ liquid repellentB₁ palps exposedA₂ vapour repellentB₂ legs exposedA₃ liquid and vapour repellentB₃ antennae exposedB₄ untreated insects

The effect of different repellent phases

With untreated insects, the shown repellent effect was greatest for both phases of repellent together. There was no significant difference between the effect produced by liquid repellent alone and vapour repellent alone, but all repellent treatments caused a significantly greater effect than the control without repellent.

For insects with only the antennae exposed and the legs and palps covered, the effect of both repellent phases together was significantly greater than for liquid alone, but not than for vapour alone. There was no significant difference between the effect of the liquid and vapour phases of repellent.

For insects with either the legs only exposed or palps only exposed, differences in repellent phase treatment had no significant effect.

The effect of insect treatment (blocking groups of sense organs with nail varnish)

With both phases of repellent present together, all four insect treatments were significantly different from each other. In order of descending repellent effect, they were: untreated insects; antennae exposed; legs exposed; palps exposed.

Table 9. Analysis of variance for untreated insects. Repellent phase treatments are the same as in the main analysis in experiment II, but include also the no repellent control.

	mean % of insects on untreated side	\bar{y} transformed treatment means	Σy	Σy^2
A ₀ no repellent	49.48	44.70	894.0	41489.12
A ₁ liquid repellent	61.75	51.80	1036.0	56448.20
A ₂ vapour repellent	66.98	54.93	1098.6	61180.56
A ₃ liquid and vapour repellent	96.40	79.06	1581.2	127078.16
Source	degrees of freedom	sums of squares	mean square	F
repellent phase treatments	3	13354.2	4451.4	46.9*
error	76	7210.6	94.9	
	79	20564.8		

*significant at 0.05 probability

With repellent vapour only present, insects with the palps only exposed were significantly less repelled than insects with legs, antennae, or all sense organs exposed. There was no significant difference between these last three treatments.

With repellent liquid only present, there was no significant difference shown due to insect treatment. Some answers may be made to the questions posed on page 345. The removal by the experimental apparatus of either the liquid or vapour phase of repellent did reduce the repellent effect, but still left it greater than the control. The vapour phase seemed more effective than the liquid, but in no case could this be declared significant. The legs and antennae were both shown to be capable of responding to repellent, but the palps were not. The response produced by the antennae was greater than that shown by the legs, although this was only significant with both phases of repellent present. No qualitative differences could be shown between the responses of the various groups of sense organs to the two phases of repellent. All observed differences could be explained in quantitative terms; i.e., as the repellent effect connected with repellent phase increased from liquid to vapour to both phases, the importance of the sensitivity of the sense organ groups was increased geometrically as well as arithmetically. This fits well with the simple morphological observation that there are more sense organs on the antennae of German cockroaches than on the legs, and more on the legs than on the palps. It also indicates that there is little qualitative difference between these groups of receptors. If there are separate receptors involved in the perception of repellent vapours and repellent liquids, they do not seem to be confined to separate areas.

As far as the repellent response is concerned, no distinctions could be made between olfaction, gustation or the common chemical sense.

Table 10. Duncan's multiple range significance levels for all significant simple effects from the main analysis (table 7) and the separate analysis with control (table 9). Treatments which are not significantly different from each other share the same number opposite.

Treatment	average % insects on untreated	transformed treatment means	significance levels
A ₃ B ₄	96.40	79.40	(1)
A ₂ B ₄	66.98	54.93	(2)
A ₁ B ₄	61.75	51.80	(2)
A ₀ B ₄	49.48	44.70	(3)

4 repellent phase treatments, untreated insects

A ₃ B ₃	88.06	69.79	(1)
A ₂ B ₃	78.21	62.18	(1) (2)
A ₁ B ₃	64.36	53.35	(2)

3 repellent phase treatments, insects with antennae exposed

A ₃ B ₄	96.40	79.06	(1)
A ₃ B ₃	88.06	69.79	(2)
A ₃ B ₂	72.86	58.60	(3)
A ₃ B ₁	58.13	49.68	(4)

4 insect treatments, liquid and vapour repellent present

A ₂ B ₃	78.21	62.18	(1)
A ₂ B ₄	66.98	54.93	(1)
A ₂ B ₂	66.28	54.50	(1)
A ₂ B ₁	55.95	48.42	(2)

4 insect treatments, vapour repellent only present

factor A, repellent phases	factor B, insect treatment
A ₀ no repellent	B ₁ palps active
A ₁ liquid	B ₂ legs active
A ₂ vapour	B ₃ antennae active
A ₃ liquid and vapour	B ₄ all groups active

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THE MODE OF ACTION OF INSECT REPELLENTS II: ELECTROPHYSIOLOGICAL STUDIES

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Apparatus was designed to record sensory nerve impulses coming from the cerci, antennae, and legs of American cockroaches. Recordings were made after stimulation of these sensory zones with an attractant, repellents, and other irritant chemicals. The cercal receptors could not be shown to respond to any chemical stimulation. The leg receptors responded to repellents and irritant chemicals but not to the attractant. The antennal receptors responded to repellents and irritant chemicals plus the attractant. The type of response from both leg and antennal sensory nerves was similar for both repellents and irritant chemicals, when applied either as a liquid or as a vapour. The response of the antennal receptors to attractant vapour was characteristically different.

Recordings were also made of receptor responses from the German cockroach to the repellent MGK R-874. The cercal receptors did not respond. A response to both liquid and vapour was obtained from the leg and antennal receptors. A weak response to repellent liquid only was obtained from the palp receptors.

Possible mechanisms of repellent action are discussed.

Although behavioural studies remain the most important methods in evaluating insect repellents, such experiments are subject to the physiological state and individual variation of the insects used. Statistical comparisons between the presence or absence of a single given stimulus can be made when batches of insects are tested under identical background conditions. In practice however, it is not possible to exclude all other stimuli. This can result in complicated interactions, since any behavioural response other than the simple reflex arc is the outcome of a complex processing in the brain. The study of electrophysiological recordings taken from the sensory nerves is more objective. By comparing nerve responses after chemical stimulation of the sense organs to the resting discharge rate obtained in the absence of known stimuli one is observing sensory inputs on the way to the brain. Any obvious and consistent differences observed in these nerve responses can be interpreted to give direct evidence of the location of the receptors involved with insect repellents. By comparing the nerve responses to other stimuli, such as mechanical ones, with the responses to a combination of repellent and mechanical stimulation, one can also show whether repellents interfere with the reception of other stimuli at the receptor sites or whether they act independently at these sites. Should the various stimuli act independently at the receptor sites, any effect by the repellent on the normal responses to other stimuli is the result of interaction in the brain.

No satisfactory method has been devised for recording the electrical responses of single sense organs being stimulated by vapours. Some success was achieved by Morita and Yamashita (1961) but the method used is inconsistent in results when compared with Hodgson's (1957) method for recording the electrical responses from labial chemosensory hairs of the blowfly to water soluble chemical stimuli. Antennal preparations have been used by a great number of authors to characterize odour responses (Roys, 1954; Smith and Roys, 1955; Boistel, Lecompte and Coraboeuf, 1956; Schneider, 1957a; Roessler, 1961; Schneider and Boeckh, 1962; Boeckh, 1962; Schneider, Lacher and Kaissling, 1964; Lacher, 1964; Schneider, Block, Boeckh and Priesner, 1967). Large probes placed in the antennae of insects to record the activity from the antennal nerve do not record potential spikes of the frequency

that would be expected from a single nerve fibre, but record overall potential changes resulting from the stimulation of a large number of sensory neurons. Such a slow overall change in electrical potential has been called an electroantennogram (Schneider, 1957a). In the present investigation this preparation has been used to compare the antennal response of cockroaches to various attractants and repellents, in the vapour phase and in the liquid phase. A similar preparation has been used to study the effect of these chemicals on the cockroach leg receptors and the effects compared with those obtained from the antennae.

MATERIALS AND METHODS

Electrodes. — The electrodes used in most experiments were tungsten wire. The wire was sharpened to a point by dipping in molten sodium nitrite and then polished electrolytically after a method described by Hubel (1957). The tungsten needles were insulated to the tip by dipping in Insulex, a vinyl lacquer (Donaldson, 1958). The impedance of tungsten electrodes is quite high, depending on the size of the uninsulated tip, but decreases as the frequency of an applied varying potential increases (Donaldson, 1958). This impedance variation in tungsten and other polarizable electrodes makes them unsuitable for the measurement of static potentials such as the cell membrane resting potential, but they are quite suitable for comparative studies of nerve action potentials, providing two identical electrodes are used. They have the advantage of being mechanically robust compared with the fragile glass micro-pipettes of the non-polarizable silver-silver chloride electrodes. Such standard silver-silver chloride electrodes (Donaldson, 1958) were also used in a few preparations to check the results obtained with the tungsten electrodes. These were quite comparable; both tungsten and glass electrodes had an impedance of one to two megohms.

The preamplifier. — Shielded leads from the electrodes were connected to the input (push-pull) stage of a battery operated Grass p-8 d-c preamplifier. The intrinsic noise level of this model is rated at 20 microvolts at the maximum amplification of 2000, and is a little greater than this in practice. This means that any detectable spike must be greater than 30 microvolts. High sensitivity of this order is necessary for a number of reasons. Although the action potential across the membrane of a single nerve fibre is of the order of 100 millivolts (Hodgkin, 1951), the full potential can only be detected by electrodes placed directly on the membrane, and the recorded potential drops rapidly as the electrode distance from the nerve fibre increases. This drop in potential is most often the case with recordings from whole nerves or bundles of fibres, as in these experiments. Types of response are identified by frequency not by amplitude.

The oscilloscope. — The output leads from the preamplifier were connected to the d-c difference input terminals of a Tektronix dual-beam oscilloscope. With these connections, the oscilloscope records only the difference in absolute potential between the two input leads and potential fluctuations affecting both probes are not registered.

Permanent recordings were made with a Polaroid Land camera fixed on the bezel mount flange of the screen. High contrast positive transparency film was used. The single shot nature of the camera limited the number of recordings that could be made. Most of the results are based on written notes taken during visual observations of the screen.

Methods of stimulation

Bursts of electrical activity in the ventral nerve cord of a cockroach are produced when the cerci are stimulated mechanically with a puff of clean air from an eye dropper. A similar eye dropper could be filled with a repellent or attractant vapour and any of the preparations could be subjected to a puff or treated air.

Vapour stimulation without the accompanying puff was achieved by merely holding a glass rod which had been dipped in the liquid repellent or attractant, close to the preparation.

Repellents were applied in liquid form with a squirrel hair paint brush.

The most common method of delivering a vapour stimulus to electrophysiological preparations is by adding the chemical stimulus to a continuous stream of vapour blown over the preparation. This tends to produce mechanical vibrations of the preparation which are transduced into electrical pulses (Schneider, 1957b). A more gentle method of delivering a vapour stimulus was devised. The leg or antennal preparation was set up on a cork stopper in a glass vial so that the leg or antenna protruded through a hole in the stopper into the lumen of the vial. Two pieces of glass tubing were welded into the bottom of the vial and rubber hose attached to these. A slow water flow was maintained through these tubes across the bottom of the vial. A hypodermic syringe could be filled with saturated chemical vapour, and a bubble of known volume injected into the rubber tubing. The bubble would travel slowly along the tubing and pop up into the vial, exposing the preparation to whatever vapour the bubble contained without causing any violent mechanical artifacts. This preparation was only good for vapours insoluble in water, and for single stimulations or combined effects, since there was no way of removing the vapour once it had been delivered.

Repellents used were MGK R-874 (2-hydroxyethyl-n-octyl sulphide), dimethyl phthalate and diethyl toluamide; other chemicals used included benzene, toluene, and ether; the attractant used was banana vapour. Ripe bananas produced a vapour extremely attractive to cockroaches, although the active ingredients have not been determined (Dethier, 1947).

More sophisticated apparatus was available for the *Blattella* work than that used with *Periplaneta*, but the methods and techniques were basically the same. Silver-silver chloride electrodes were used, the reference electrode being placed generally in the body of the cockroach and the recording electrode placed by micromanipulator on the desired nerve via a fluid-filled microcapillary. The signals went through a Medistor A-35 electrometer amplifier (single-sided input) and a Tektronix Type 122 amplifier to a Tektronix 502 oscilloscope. Permanent records were taken with a Grass C4 camera, which inverts the traces (positive is down in Fig. 9-15). The apparatus was capable of making continuous recordings of greater sensitivity than the apparatus described in the previous section. The nerve activity recorded ranged from 8–1000 Hz, in contrast to the slow d-c shifts recorded with *Periplaneta*.

RESULTS

American cockroaches *Periplaneta americana* (L.) were mainly used for this work because their size made them convenient for operation. They were readily available from laboratory cultures, and their nervous anatomy is well known.

Probes were placed with the aid of two Leitz micromanipulator units mounted on a cast steel base. The operation was observed through a Zeiss binocular stereomicroscope. Four basic insect preparations were used:

Cercal preparation (American cockroach). — Decapitated cockroaches were dissected from the dorsal side, revealing the ventral nerve cord. Probes were placed under the ventral nerve cord about 1 mm apart and the cord lifted slightly off the underlying tissue. The abdominal cavity was then filled with mineral oil, which prevented desiccation as well as stimulation of the cord itself due to the presence of repellent vapour (Roys, 1954).

Mechanical stimulation of cockroach cerci either by a puff of air or by touching with a needle produces easily recorded electrical activity in the ventral nerve cord. Spikes of various amplitudes may be present and in general it can be said that spikes of different amplitudes represent recordings from different nerve fibres. Since the action potential of

all nerve tissue is about 100 millivolts (Hodgkin, 1951) two main factors are responsible for different amplitudes being recorded. These are: the distance of the probes from the various nerve fibres, since recorded potential drops rapidly as the distance of the probe from the neuron membrane increases; the size of the neuron in question, since although the action potential of all neurons is similar the current is not, and a large current from a large fibre records as a higher potential than a small current from a small fibre. The frequency of the recorded spikes from the cercal preparation depends on the intensity of the stimulation, the greater the stimulation the greater the frequency (Roeder, 1953). Action potentials recorded from the abdominal cord in a cercal preparation to a burst of stimulation such as a puff of air are bursts of high frequency spikes which adapt slowly approaching the normal resting activity of the nerve. No difference in the spike amplitude or frequency of the recordings was observed between a cercal preparation stimulated with clean air and the same preparation stimulated by a puff of air containing any chemical whatsoever, repellent or attractant. Furthermore, the mechanical response was not affected by painting the cerci with liquid repellent. It should be noted here again that the ventral nerve cord was covered with mineral oil to prevent it being directly affected by chemical vapours. Refined mineral oil itself does not appear to affect the preparation in any way other than to increase its longevity by preventing desiccation.

Complete antennal preparation (American cockroach). — The head of the cockroach was removed from the body and dissected in the eye region to reveal the antennal nerve. Two probes were placed on the nerve and the exposed preparation was covered with mineral oil. Since, in this preparation, the brain was still intact and connected to the antennal nerve, the recordings were complicated by signals going from the brain through the motor neurons.

Detached antennal preparation (American cockroach). — A cockroach antenna was cut off near the base and a reference electrode inserted well into the antenna lumen. Fluid soon congealed in the space between the electrode and the antennal walls, preventing desiccation of the interior of the antenna. A very fine recording electrode was inserted at a joint in the antenna, usually between segments 5 and 6 (Roys, 1954). Beyond the first antennal segments, there are no muscles in a cockroach antenna, and any signals received from this type of preparation are of sensory origin.

Antennal preparations where the antennal nerve was still attached to the brain produced spikes which could be associated with the antennal muscles (Fig. 1). These spikes were of a frequency range normally associated with nerve — muscle preparations, about 100 spikes per second. These unwanted signals disappeared in preparations where the antenna was removed from the head, and the only action potentials recorded from such preparations in still clean air, were from weak mechanical vibrations (Fig. 2). These mechanovibrations just showed above the 20 microvolt limit of amplification of the apparatus. Neither the muscle spikes nor the response to mechano-vibrations could be confused with the 40 times slower frequency changes of the electroantennograms. Slow potential changes of the electroantennogram are thought to be the summed potentials coming from the many receptors on the antenna. The cockroach antenna responded quite violently to stimulation by banana vapour (Fig. 3). The response to repellent vapours was much less marked (Fig. 4 right) and closely resembled in amplitude the continuous stimulation produced when the antenna was painted with liquid repellent (Fig. 5). Breaks appeared in the response to continuous repellent application (Fig. 5). Such breaks were also noted by Roys (1954). After stimulation with repellent vapour the response of the antenna to stimulation by attractant vapour was considerably reduced for several minutes (Fig. 4). Full recovery was effected after about 20 to 30 minutes. Benzene, toluene, and ether vapours acted very similarly to the vapours of repellents such as MGK R-874, diethyl toluamide, and dimethyl phthalate (Fig. 6).

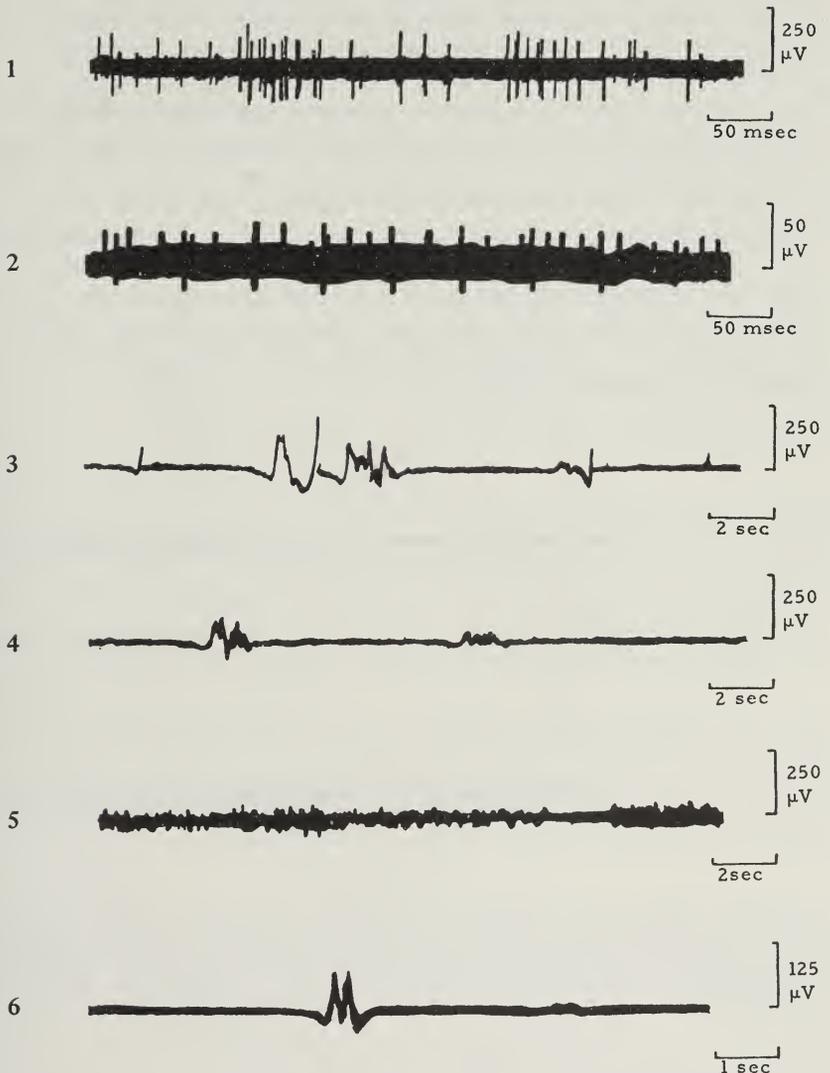


Fig. 1-6. *Periplaneta americana*. 1. Complete antennal preparation. Nerve-muscle potentials whose presence makes this type of preparation unsuitable for investigations into chemosensory responses. Note the frequency of the responses from the time base. 2-6. Detached antennal preparations. 2. Action potentials recorded from an isolated antenna in still clean air. These weak potentials were the only noted steady state responses from the preparation. The baseline of about $20\mu\text{V}$ shows the limit of amplification of the recording apparatus. 3. Electroantennogram from an antenna stimulated with an attractant, banana vapour. Stimulus applied by holding a glass rod which had been dipped in crushed banana, near the preparation. Note the time base; this is a very slow-changing potential. 4. Responses to stimulation with banana vapour (left) and repellent vapour (right), 5 minutes after exposing the preparation to repellent vapour for 1 minute. The repellent was MGK R-874, and the stimuli were applied with glass rods. The decreased amplitude of the attractant response (cf. Fig. 3) shows the very slow recovery of the preparation from the effects of repellents. 5. Response to liquid repellent MGK R-874 painted on the antenna. The amplitude of the response is similar to that obtained from repellent vapour (Fig. 4). The breaks seen in the response to continuous stimulation were noted by Roys (1954). 6. Response to benzene vapour delivered by the bubble apparatus. Allowing for the greater scale of this recording compared with that of Fig. 3, 4, and 5, this response is similar to that produced by insect repellents.

Leg preparation (American cockroach). — The decapitated cockroach was dissected in the coxal region of the foreleg. The main nerve leading from the leg (ganglionic nerve No. 5) was severed from the ganglion and probes placed on it. The exposed region was covered with mineral oil to prevent desiccation.

The cockroach leg did not respond to the attractant vapour at all. The leg did respond to repellent vapours in very much the same way as the antenna (Fig. 7). Repellent liquids painted on the leg produced the same sort of response as vapours except that the duration of response was much greater. I could detect no difference in the response of the legs to stimulation by liquid repellents from the response of the antennae (Fig. 8). The presence of repellent liquid on the leg caused stimulation for a great length of time, breaks in the stimulation gradually becoming longer and longer. However, activity was still noted even after an hour and a half (Fig. 8). Benzene, toluene, and ether all acted similarly to repellents when applied to the leg in either liquid or vapour form although the response, particularly to ether, was slightly more pronounced.

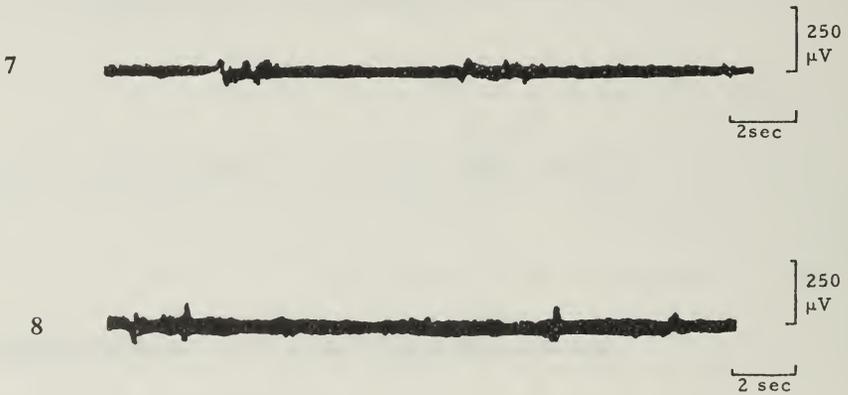


Fig. 7–8. *Periplaneta americana*, leg preparations. 7. Response to repellent vapour, dimethyl phthalate. Two separate stimulations from a treated glass rod. The leg is not as sensitive as the antenna, but the form of the response is very similar. 8. Recording taken 90 minutes after painting the leg with liquid DMP. The breaks between the bursts of activity are much longer than they were just after the onset of stimulation, cf. antennal preparation, Fig. 5.

Although most of the experiments were done with the American cockroach, some tests were carried out with the German cockroach *Blattella germanica* (L.) so that the results could be compared with previous behavioural findings (Reddy, 1970). Adult male German cockroaches were used for all the following experiments. The insects were between 3 and 10 days old and had been reared at 23 C. Each specimen was anaesthetized with carbon dioxide, attached to a wax coated slide and allowed to recover for 30 minutes. The probes were placed in the cockroach and the recordings made in the dark. The repellent stimuli, both vapour and liquid were applied by means of a fine glass rod which had been dipped in MGK R-874. A flashlight was used during stimulus application, since the bench light caused 60 cycle interference. The light itself did not appear to affect the preparation.

Cercal preparation (German cockroach). — The recording electrode was placed on one of the two cercal nerves posterior to the last abdominal ganglion, and the exposed preparation covered in mineral oil. Although this preparation responded well to mechanical stimuli, no response was obtained when a glass rod dipped in MGK R-874 was held near the cercus. When liquid MGK R-874 was applied to the cercus with a glass rod there was a short initial response to the mechanical stimulation, but no further response to the repellent itself (Fig. 9).

Antennal preparation (German cockroach). — The recording electrode was placed in the antenna in the region of the sixth antennal segment. When a glass rod dipped in MGK R-874 was held near the antenna, a sharp burst of electrical activity lasting about 1 second was recorded (Fig. 10). When the antenna was painted with liquid MGK R-874, activity of similar amplitude and duration was noted (Fig. 11). This was followed by a resting period of about 2 seconds, another burst of activity, a resting period of 3 seconds, more activity and so on, with the periods of inactivity getting longer. Similar patterns of activity were observed when the preparation was subjected to continuous stimulation by MGK R-874 vapour. This pattern was also noted by Roys (1954). The antennal responses to MGK R-874 were obtained in 9 out of 10 attempts.

Leg preparation (German cockroach). — With the recording electrode placed in the tibial region of an isolated cockroach foreleg, responses could only be obtained in 5 out of 10 attempts, probably due to the greater difficulty in placing the probe on the nerve. The response of the leg to MGK R-874 vapour was similar to that of the antennae, but of shorter duration (about $\frac{1}{2}$ second, Fig. 12). The response of the leg to MGK R-874 liquid was $\frac{1}{2}$ second bursts of activity with intermittent resting periods similar to those noted for the antennae (Fig. 13).

Palp preparation (German cockroach). — The recording electrode was placed in the first segment of a labial palp, and the rest of the mouthparts sealed with wax to prevent undue mechanical activity. No response to MGK R-874 vapour could be obtained (Fig. 14). In four out of six attempts the palps responded to MGK R-874 liquid with irregular bursts of activity and resting periods (Fig. 15). The resting periods were shorter than those observed in the legs and antennae.

The electrophysiological experiments with *Blattella* confirmed the general conclusions reached with *Periplaneta*. Both the legs and antennae can respond to both the vapour and liquid phases of repellent. The type of nervous response was similar for both liquid and vapour with the legs and antennae of *Blattella*. The bursts of activity produced by the legs were of shorter duration than those produced by the antennae. The situation with the palps is not clear; I could detect a response to liquid MGK R-874 but not to vapour. It is possible that the small number of chemosensory organs present on the palps are contact chemoreceptors in the sense that they respond only to very high concentrations of chemical stimuli.

DISCUSSION

My experiments with the American cockroach indicate that insects respond similarly to both repellents and irritant chemicals such as benzene, toluene, and ether. This is not surprising; benzene for instance, is a known insect repellent, but it has no commercial application since it is so volatile.

Roys (1954) noted that the exposed ventral nerve cord of insects can be stimulated by irritant chemicals. Even if the response to an irritant chemical stimulus is a fundamental

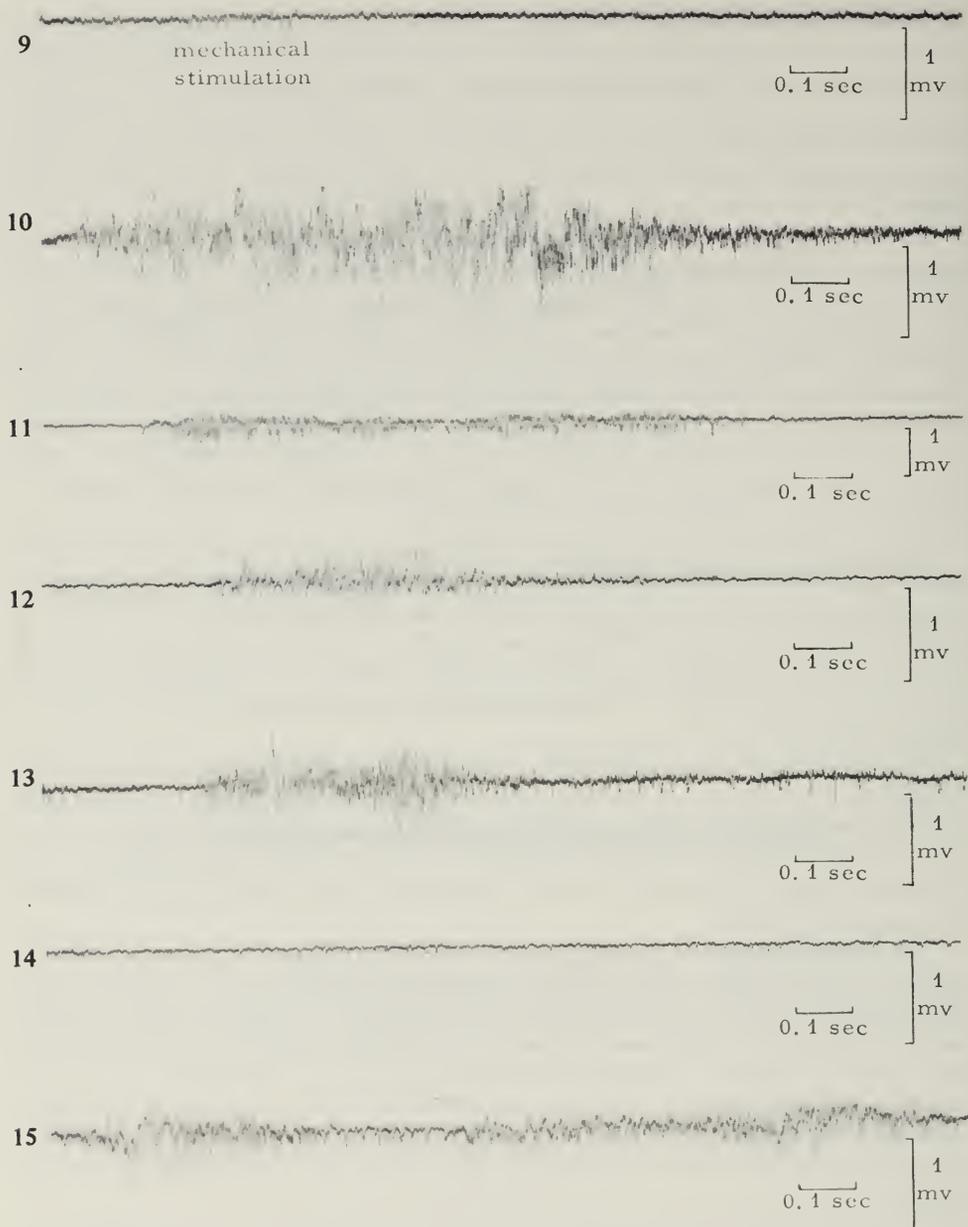


Fig. 9-15. *Blattella germanica*. 9. Recording from the left cercal nerve. After the slight initial response to mechanical stimulation, no activity was produced by MGK R-874 liquid. 10. Response of the right antennal nerve to stimulation by MGK R-874 vapour. 11. Response of the right antennal nerve to stimulation with MGK R-874 liquid. The vertical recording scale is one half that of Fig. 10, which makes both these responses of the same order of amplitude. This response was followed by alternating resting periods and further activity. 12. Response from the right foreleg after stimulation with MGK R-874 vapour. 13. Response from the right foreleg after stimulation with MGK R-874 liquid. This response was followed by alternating resting periods and further activity. 14. Recording from the left labial palp. Lack of response to stimulation by MGK R-874 vapour. 15. Recording from the left labial palp. Response to MGK R-874 liquid. This response was followed by irregular resting periods and activity.

property of all nervous tissue, that tissue must be exposed to the chemical for any response to be noted. The sensory nerves of insect mechanoreceptors are not exposed to the surface, but are protected by the insect cuticle which is a good barrier to most chemicals (Ebeling, 1964). This may explain why I could demonstrate no effect by repellents on mechanoreception in the American cockroach. For chemoreception to be possible, chemicals must have access to sensory tissue, and insect chemoreceptors have pores or openings which make this possible, (Dethier, 1955; Slifer and Sekhon, 1962). Indeed, the chemoreceptors and possibly the hygroreceptors seem to be the only locations on insects where nervous tissue is exposed to stimulation by chemicals, and for this reason are the areas where insect repellents act.

In a previous paper (Reddy, 1970) behavioural evidence was given for locating the main sensory areas on the German cockroach to the repellent MGK R-874 on the antennae, with sensory areas of secondary importance on the legs. The vapour phase of the repellent was more effective than the liquid phase. Combining this behavioural evidence with the electrophysiological evidence in this paper, I interpret the emerging pattern as follows. The principal sites of action of insect repellents are on the legs and antennae, and to a lesser extent on the labial palps. These areas possess thin walled chemoreceptors which are the only parts of insects where chemicals have access through the cuticle to the sensory tissue. The chemoreceptors on both the antennae and legs can respond to both vapours and liquids, and do so in a similar electrophysiological way. In practice insect antennae are rarely in contact with the substrate and therefore play little part in the behavioural response to contact repellency. In practice the vapour phase of repellents is more important than the liquid phase because both the antennae and legs are exposed to vapours and the antennae have more chemoreceptors than do the legs. The antennal receptors of American cockroaches respond to attractant vapour but the leg receptors do not, therefore either there are two types of receptor neuron on the antennae (one for attractants and one for repellents) or the antennal receptor neurons differ from those of the legs in being able to respond to both attractants and repellents. The latter theory would require that there are different biochemical mechanisms involved in the reception of attractants as compared with repellents and irritant chemicals. Now the response of the American cockroach antenna to banana vapour was considerably reduced after the preparation had been exposed to repellents. If the olfactory receptors for attractants are capable of responding to repellents by a separate mechanism, then this reduction in attractant response must be due to adaptation along the nerve axon and not to competition at the site of action. On the other hand, if the neurons responsible for the reception of repellents are separate from those responsible for the perception of attractants, they cannot act independently or repellents would not cause a reduction in the attractant response.

Repellent treated mosquitoes do not display their normal response to humidity and carbon dioxide (Wright, 1962). The receptors for both humidity and carbon dioxide are found on the antennae of insects and closely resemble other chemoreceptors in structure, many of them having pores opening to the surface. Some of these receptors are also sensitive to heat (Lacher, 1964).

If repellents can stimulate olfactory, gustatory, hygro- and carbon dioxide receptors in insects, and fail to stimulate the mechanoreceptors only because the concerned neurons are not exposed, then the confused behaviour of repellent treated insects noted by Khan (1965) is not surprising. I do not think that the sensory mechanisms of insects are so inelegant in function as to allow total disruption of their powers of discrimination by repellents, especially since the standard insect response to high concentration of repellent is oriented repulsion.

There is convincing electrophysiological evidence for the presence of distinct neurons which respond to general or irritant chemical stimuli (Hodgson, 1957; Boeckh, Kaissling and Schneider, 1965). These 'generalist' neurons are commonly associated in the receptor end organs with 'specialist' neurons which respond to a more restricted class of chemicals such as sugar (Hodgson, 1957), or attractants (Schneider, 1962). Even hygroreceptors contain at least two neurons and carbon dioxide sensory are similar in structure to other chemoreceptors (Lacher, 1964). The 'specialist' neurons of chemosensory organs respond to attractants or stimulants such as sugar, and the 'generalist' neurons respond to a wider range of chemical stimuli. Inhibition of the 'specialist' impulse potentials by 'generalist' receptor potentials could account for the observations that repellents reduce the response to attractants and disrupt the behavioural response to humidity and carbon dioxide. Inhibition, however, does not account for the general sensitivity of nerve tissue to irritant chemicals (Roys, 1954).

The known facts of repellency are best accounted for by combining a two neuron system with an overall sensitivity to irritant chemicals and repellents, as follows.

All chemoreceptors in insects (including hygroreceptors and carbon dioxide receptors) contain at least two types of sensory neurons, the 'generalists' which respond to a wide spectrum of chemical stimuli, and the 'specialists' which respond selectively to a narrow range of chemical stimuli at a much greater sensitivity.

Both types of receptor can respond to general irritant chemicals such as repellents, through the common chemical sense. At very low concentrations of repellent stimulus, only the 'specialist' receptors would respond, resulting in attraction.

At higher concentrations of repellent, the 'specialist' receptors for all types of attractant stimuli including water, carbon dioxide and heat are stimulated and some of the 'generalist' neurons are stimulated, causing slight decrease in activity of the 'specialist' impulse potentials. The result is confusion, disorientation and various types of abnormal behaviour. At a very high concentration of repellents, total stimulation of the 'generalist' neurons produces total decrease in activity of the 'specialist' impulse potential resulting in active repellency.

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Corrigenda:

Quaest. ent. 6(3): 298 (July 1970)

Fig. 2, under *Chrysops frigidus* add one fly Aug. 7 and one fly Aug. 10; under *Chrysops furcatus* add two flies Aug. 7; under *Atylotus incisuralis* add six flies Aug. 7, 11 flies Aug. 10, and one fly each Aug. 13, 19, and 22.

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