QUAESTIONES ENTOMOLOGICAE ISSN 0033-5037

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

Volume 26 1990

CONTENTS

Quaestiones Entomologicae

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

VOLUME 26 NUMBER 1 WINTER 1990

Publication of *Quaestiones Entomologicae* was started in 1965 as part of a memorial project for Professor E.H. Strickland, the founder of the Department of Entomology at the University of Alberta in 1922.

It is intended to provide prompt relatively low cost publication for comprehensive accounts of entomological research of greater than average length. However, shorter papers about insects in the Prairie Provinces of Canada are acceptable. Page charges are normally levied, the rate determined by printer's charges. For information about current page charges, consult the Editor.

Copy for all types of papers should conform to the Style Manual for Biological Journals, published by the American Institute of Biological Sciences, Second Edition, 1964, except that title of periodicals should be given in full. For style of taxonomic papers, the Editor should be consulted. Two copies of a manuscript are requested. All manuscripts will be reviewed by referees.

Abstracts are required, one in English and one in another language, preferably French.

Copy for illustrations must accompany the manuscript, and be of such character as to give satisfactory reproduction at page size (less 1/2 inch, or 1.2 cm on plates of full page size [7 X 4 1/4 inches or 17.8 X 10.7 cm]). Reprints must be ordered when proofs are returned, and will be supplied at cost.

Subscription rates are the same for institutions, libraries and individuals, $20.00* per volume of four issues, normally appearing at quarterly intervals; single issues $5.00**. Back volumes and issues are available at the same cost. These prices supersede those previously indicated, and are subject to change as required by inflationary pressure on the value of money.

Communications regarding subscriptions should be addressed to the Subscription Manager, and regarding manuscripts to the Editor.

* Same rate in US$ for non-Canadian subscriptions.

** Single issues of more than 100 pages: $10.00; exception: volume 21(4) - $20.00.

Published quarterly by:

Department of Entomology
University of Alberta
Edmonton, Alberta, CANADA
T6G 2E3

Second Class Mail Registration Number 5222

Return Undeliverable mail to the address above. Return Postage Guaranteed

Issued March 1990

QUAESTIONES ENTOMOLOGICAE ISSN 0033-5037

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

Volume 26 Number 1 1990

CONTENTS

RECONSTRUCTION OF A SPECIFIC EXAMPLE OF INSECT INVASION WAVES: THE CLADISTIC ANALYSIS OF *CANTHON* (COLEOPTERA: SCARABAEIDAE) AND RELATED GENERA IN NORTH AMERICA[1]

Bert Kohlmann
Gonzalo Halffter

Instituto de Ecología, A.C.
Apartado Postal no 63
Xalapa, Veracruz, 91000
MEXICO

Quaestiones Entomologicae
26: 1—20

ABSTRACT

The historical biogeography of insects of the Mexican Transition Zone is extremely complex. Holarctic, Nearctic and Neotropical lines seem to have invaded and speciated in the area at different times. The neotropical lines in particular are thought to have invaded the Mexican Transition Zone from South America on two occasions, one during the Miocene, the other during Plio-Pleistocene. The subgenus *Canthon* and its closely related taxa, the subgenus *Boreocanthon* and the genus *Melanocanthon*, as well as the subgenus *Glaphyrocanthon,* have been proposed as an example for the analysis of this process.

The implications from such an event allow predictions regarding the phylogenesis and ecological evolution of these three taxa, as follows. First, the proposed Miocene invasion lineage(s) shared a common history and diversified in the biomes that evolved in North America during the Miocene and Pliocene. Second, those species which diversified from a common ancestor form a phylogenetically related group that reflects the history of the group in accordance with the history of the area and biomes which they occupy. Third, the species stemming from the proposed South American Plio-Pleistocene invasion evolved under a different set of ecological and biogeographic conditions, and as such are distantly related in phylogenetic terms to the members of the first invasions wave. Fourth, consequently, in a cladogram including species of both invasion waves, the Plio-Pleistocene elements branch at the base of the tree. Fifth, moreover, the branching sequence of the cladogram is not in concordance with the estimated age of appearance of the different biomes which the species occupy. These five predictions were supported in the present study, by the species cladogram. The

---

[1] This paper is a contribution from the "Ecology and Animal Behaviour" project with the support of the "Studies on the fauna of Coleoptera Lamellicornia from Sierra Madre del Sur" (P220CCOR - 880061) project, contribution number 21, sponsored by the Dirección Adjunta de Desarrollo Científico of the Consejo Nacional de Ciencia y Technología (Conacyt), Mexico.

results of this analysis therefore lend support to the hypothesis of two waves of invasions of the Mexican Transition Zone by Neotropical elements from South America.

RESUMEN

La zona de Transición Mexicana es un área de gran complejidad ecológica, geológica y biogeográfica. En relacion a su dinámica zoogeográfica, Halffter (1962, 1964, 1972, 1974, 1976, 1978 y 1987) ha propuesto una serie de hipótesis basadas en las relaciones taxonómicas, riqueza específica, historia geológica y patrones de distribución de diferentes grupos de insectos, en las que señala que diferentes linajes de origen holártico, neártico y neotropical invadieron esta zona en diferentes épocas. En el caso específico de los linajes neotropicales, considera dos invasiones mayores, una durante el Mioceno, la segunda del Plio-Pleistoceno al actual. El subgénero *Canthon* y otros dos taxa muy emparentados, el subgénero *Boreocanthon* y el género *Melanocanthon*, al igual que el subgénero *Glaphyrocanthon*, son buena evidencia de estas dos invasiones. Los invasores miocénicos se encuentran en biomas que comenzaron a originarse en este período, como es el caso de formaciones áridas, pastizales, bosques de encino-piñón y bosques templados decíduos; o en épocas más recientes, pliocénicas, como bosques de pino y pino-encino (Axelrod, 1975, 1979). Las líneas propuestas como invasoras plio-pleistocénicas o posteriores se encuentran distribuídas principalmente en biomas de penetración reciente, como las selvas tropicales, sobre todo la selva alta perennifolia (Germeraad *et al.*, 1968; Graham, 1973, 1981; Toledo, 1976, 1982; Gentry, 1982; Prance, 1982). En base a estudios biogeográficos y taxonómicos anteriores (Halffter, 1958, 1961, 1962, 1972, 1974, 1976; Halffter y Martínez, 1966, 1967, 1968, 1977) se propone que las siguientes especies del subgénero *Canthon*: *humectus, pilularius, imitator, vigilans, chalcites* y *obliquus* así como el subgénero *Boreocanthon* y el género *Melanocanthon* han derivado de la invasión miocénica. Las especies *indigaceus, cyanellus* y *morsei* del subgénero *Canthon* y el subgénero *Glaphyrocanthon* se consideran parte de la invasión plio-pleistocénica.

El objetivo de este estudio es aportar una nueva evidencia que apoye la existencia de los dos procesos invasores por elementos neotropicales a la Zona de Transición Mexicana, a partir de un unálisis cladístico del subgénero *Canthon* y taxa cercanos. El análisis cladístico puede apoyar o no las predicciones que emanen de las hipótesis biogeográficas.

Con respecto a las invasiones neotropicales pueden establecerse dos hipótesis complementarias. La primera consideraría la posibilidad de que a partir de la línea miocénica ocurriera una diversificación congruente con la aparición de zonas adaptativas disponibles (Simpson, 1953), creadas por el surgimiento de nuevos biomas. La diversificación de especies originada a partir de un ancestro común resultaría en un grupo filogenéticamente emparentado (Hennig, 1966; Wiley, 1981), cuyo cladograma reflejaría la historia evolutiva del mismo y presentaría un major o menor grado de concordancia con la historia del área y de los biomas que ocupan las especies. La segunda hipótesis supondría que los invasores plio-pleistocénicos, al tener una historia ecológica y evolutiva diferente a la de los miocénicos, presentaría relaciones filogenéticas distintas y una distribución geográfica y ecológica también diferente. Por ello, al construirse el cladograma, los invasores plio-pleistocénicos se encontrarán en la base la ramifacación del árbol y no existirá congruencia directa entre la secuencia de ramificación del cladograma y la secuencia de aparición de los diferentes biomas en Norteamérica.

El análisis cladístico (Fig. 2) se basa en 29 especies y 29 caracteres (Cuadro I) y emplea el paquete de análisis filogenético PAUP. Los caracteres no fueron codificados en forma ordenada, ya que estamos de acuerdo con Meacham (1984) en que la polarización de caracteres no se puede definir con certitud. La base del cladograma fue determinada utilizando el subgénero *Glaphyrocanthon* como grupo externo. La decisión de elegir a este subgénero como grupo externo se encuentra fundamentada por los resultados de la estimación del grado de similitud de todos los géneros y subgéneros de los componentes americanos de la tribu *Canthon*ina indicado en la Fig. 1. Cincuenta cladogramas igualmente parsimoniosos fueron obtenidos. Posteriormente se utilizó el programa CONTREE para establecer un cladograma de consenso "estricto" (Rohlf, 1982) (Fig. 2). También se obtuvo un cladograma siguiendo el método de consenso de Adams (1972), pero no fué incluído en este estudio por ser muy semejante al primero.

El cladograma de consenso obtenido fue correlacionado con los diferentes biomas (Fig. 2) en donde se encuentran distribuídas las especies (Mapas 1-7) y su análisis concuerda con las predicciones de la existencia de dos líneas invasoras neotropicales en Norteamérica.

TABLE OF CONTENTS

INTRODUCTION

The dynamics of insect biogeography in the Mexican Transition Zone (hereafter referred to as MTZ; Halffter, 1976), which includes the southwestern United States, all of México and a large part of Central America extending to the Nicaraguan lowlands, are of great complexity. The MTZ is species-rich because of the great variety of environments and ecological refuges available and presents a complex and varied overlap of the Neotropical and Nearctic faunas. The area is also an important part of the north-south dispersal corridor for faunas and floras of diverse origin that have dispersed during different geological eras between North and South America (Stehli and Webb, 1985).

Halffter (1962, 1964, 1972, 1974, 1976, 1978, 1987) has developed a set of hypotheses to explain comprehensively the distribution of insects in the MTZ. His inferences, based on taxonomic relationships, species richness, geological history and distribution patterns derived for several insect groups, support the notion that the present insect fauna of the MTZ has originated from multiple invasions and *in situ* speciation at different times from Nearctic, Holarctic and Neotropical lines, conferring on this region a mixed transitional character in insect composition. The Neotropical lines which invaded North America from South America are thought to be represented by a Miocene and by a Plio-Pleistocene component (Halffter, 1972, 1974, 1976). These components show distinctive geographic patterns, the distribution cores of which are centered on areas defined by actual ecological conditions.

Geological support for the possibility of migration between the American land-masses has been summarized recently. Donnelly (1988) presents a scenario constructed from the concordant features of the diverse and conflicting analyses made for the Caribbean and Central American Bridge and concludes that faunal movements requiring short (tens of kilometers) overwater dispersal conditions might have occurred during brief intervals during the late Cretaceous through a proto-Antillean arc and during the middle Cenozoic through Central America. Overland dispersal became possible when the Central American Land Bridge was finally consolidated at the beginning of the Pliocene, about 5.7 m.y. B.P. (Kaneps, 1979), or late Pliocene, 3 m.y. B.P. (Webb, 1977, 1978; Keigwin, 1978; Marshall *et al.*, 1982). Biological evidence presented by Savage (1982) suggests a connection between North and South America early in the Cenozoic, based on inferred concordant dispersal to Central America of South American organisms such as angiosperms, fishes, amphibians and reptiles. Mammals, however, did not exhibit the same patterns. Nevertheless, some evidence indicates that mammals had a limited dispersal between North and South America in the late Cretaceous and again in the Oligocene, that increased during the late Miocene, and culminated in an extensive faunal interchange in the Pliocene (Stehli and Webb, 1985).

One of the examples given by Halffter (*op. cit.*) of a Neotropical invasion into North America in two waves, one during Miocene, the other during Plio-Pleistocene, is the genus *Canthon*. This taxon belongs to the subtribe Canthonina, which, together with three other subtribes, is grouped into the tribe Scarabaeini. It is characteristic of adults of the tribe Scarabaeini to have fine, long and bowed metatibiae, used by most species to roll food balls made from droppings (mostly mammalian) or small carcasses, the latter being more common in the Neotropical Region. Members of this group do not show marked sexual dimorphism, a fact that contrasts strikingly with the situation characteristic of other tribes. Most of these species form balls at the food source. Subsequently, this ball is rolled and buried at a shallow depth. This same process is followed by many of the species for nesting; ball-rolling is then carried out by a bisexual pair.

The subtribe Canthonina has a Gondwanian distribution. More than half of all the species of Canthonina are Neotropical, as well as 27 of 28 American genera (Halffter and Edmonds, 1982). The subtribe is also richly represented in Australia, South Africa and Madagascar. The other Ethiopian and Oriental faunas are less rich, a consequence of strong competition or perhaps ecological replacement from other tribes of ball-rolling beetles.

ASSUMPTIONS

The biogeographic analyses of the MTZ by Halffter (*op. cit.*) and the taxonomic study of the American Canthonina by Halffter (1958, 1961) and Halffter and Martínez (1966, 1967, 1968, 1977), suggests that some North American species of the subgenus *Canthon* (*C. humectus, obliquus, chalcites, imitator, pilularius, and vigilans*), all species of the closely related subgenus *Boreocanthon,* and those of the genus *Melanocanthon* originate from an ancestral Miocene invasion from South America, and that the species *C. indigaceus, C. cyanellus* and *C. morsei*, of subgenus *Canthon*, as well as the subgenus *Glaphyrocanthon,* represent recent Plio-Pleistocene invaders into North America. We accept these suggestions.

PREDICTIONS

The MTZ biogeographic scenario as proposed by Halffter (*op. cit.*) allows predictions for *Canthon*, *Boreocanthon* and *Melanocanthon*, concerning phylogenesis and ecological evolution in North America. These predictions can be tested by Methods outlined below.

Prediction 1.

Beginning with the proposed migration wave from South into North America by an ancestral *Canthon* component in Miocene time along a discontinuous corridor formed by islands (Briggs, 1987; Donnelly, 1988), this area would have varied in its ability to allow the passage of some elements into North America, and thus would have isolated these elements from their ancestral lineages in South America. Therefore, this Miocene component would have been subjected to the same macroecological pressures for a prolonged period of time, would have lived under the same physiographic conditions and would have had a common biogeographic history in North America.

Prediction 2.

Several biomes originated in North America during Miocene times, such as arid zones, grasslands, piñon-oak woodland and hardwood forest (Axelrod, 1975, 1979). Other biomes started evolving in North America in the Pliocene, such as pine and pine-oak forests (Axelrod, 1975, 1979). These emerging biomes would represent newly-available habitats and one could expect species diversification to occur in the invading line(s) (Simpson, 1953). If this species diversification originated from one common Miocene ancestor, one can consider also on the basis of phylogenetic tenets (Hennig, 1966; Wiley, 1981) that the derived species form groupings which are phylogenetically related to each other and reflect the historical course of speciation.

Prediction 3.
Those species that are thought to be derived from this Miocene invasion and that have diversified in the new adaptive zones, exhibit relationships that reflect some degree of congruence with the historical sequence of biome appearance in which the species now live, as has been postulated for area cladograms (Rosen, 1978, 1979).

Prediction 4.
Species *C. cyanellus, C. indigaceus* and *C. morsei,* of subgenus *Canthon*, are considered to be derived from a Plio-Pleistocene invasion from South America (Halffter, 1961, 1962, 1964, 1972, 1974, 1976; Halffter and Martínez, 1977) associated with several types of tropical forest, and in particular with rainforest. The association with the tropical forest suggests that those three *Canthon* species are South American taxa which have enjoyed range expansions during and after the closing of the Isthmus of Panamá (Liebherr, 1988). These tropical species should be distantly related in phylogenetic terms to the members of the Miocene invasion waves, because they evolved under a different set of ecological and biogeographic conditions. This permits that these species branch at the base of the species-tree and cause the cladogram branching sequence to be in disorder in relation to the age of appearance of the different biomes in which the species now live and therefore be incongruent with the biogeographic history of the area, since they may represent different phyletic lines. This prediction and those put forward for the Miocene lineage of invasion can be compared with the results of the concordance between the cladogram and the biome evolution sequence as a test of the MTZ insect biogeographical hypothesis.

MATERIAL AND METHODS

Material

This study is the result of the examination of several thousands of specimens of American Canthonina. All North American species of the subgenera *Canthon* and *Boreocanthon*, the majority of *Glaphyrocanthon,* as well as the totality of the *Melanocanthon*, were studied for the cladistic analysis Many representative species of American genera and subgenera of Canthonina were studied for the phenetic analysis.

All this material comes from the G. Halffter collection, Xalapa, México, which is one of the best collections for this group.

Terminal Taxa..— We accept the diagnoses given by Halffter and Martínez (1977) for the genus *Canthon* and the subgenera *Canthon*, *Boreocanthon* and *Glaphyrocanthon* as well as the genus *Melanocanthon*. With the exception of some mentioned later on, the species included in these genera and subgenera in North America are those assigned in the earlier papers of Halffter and Martínez (1977) and Halffter (1958, 1961).

Terminal taxa so defined are listed in Table II. Halffter and Martínez (1977) consider *Canthon* (*Boreocanthon*) *bisignatus* Balthasar as a doubtful member of the subgenus *Boreocanthon*. This species is not included in the analysis as only a scanty description of it is available and we have been unable to obtain additional material. A second species of subgenus *Boreocanthon* that has been excluded is *B. nyctelius* Bates, since Howden (1966) considers it to be conspecific with *C. puncticollis* Le Conte. Lastly *C. forreri* Bates is almost identical to *C. integricollis* Schaeffer, and for this reason it is not included in our analysis.

We consider *Glaphyrocanthon* as a convenient external group to root the cladogram. This subgenus is composed mainly of species of South American origin with a limited penetration into North America. A phenetic analysis (Fig. 1 and Appendix) shows that *Glaphyrocanthon* has rather distant relationships with the other genera and subgenera considered in this analysis and can be considered safely as an outgroup.

Cladistic Methods.

The cladistic analysis based on the data presented in Tables I and II was carried out using the PAUP (Phylogenetic Analysis Using Parsimony) computer program, version 2.4.0 (1985), distributed by Dr. L. Swofford (Illinois Natural History Survey, 607 East Peabody Drive, Champaign, Illinois 61820), and run on a VAX 8700 computer employing the following options: NOTU=29; NCHAR=29; ROOT=OUTGROUP; GO/SWAP=GLOBAL; MULPARS; CONFILE; MAXTREE=50; ALL CHARACTERS UNORDERED. Subsequently Swofford's CONTREE program (Version 1/3/86, distributed with PAUP) was used to calculate Adams and strict consensus trees from the multiple trees that resulted from the PAUP analysis.

Characters.— Of the twenty-nine characters employed, twenty-three were binary and six multistate. Unordered multistate characters represent no problem for a cladistic analysis using PAUP. The majority of characters are derived from Halffter (1958, 1961) but, some of them derive from personal (B.K.) observations.

For the present analysis all characters were coded as unordered, since sister groups in and outside Canthonina are not yet defined, thus rendering the character transformation series unknown. Character polarities can be determined subsequently by rooting the tree with an outgroup using the parsimony criterion (Swofford, 1985). However, Meacham (1984) has argued that character polarities are not known with certainty. We consider that an analysis of character polarity under such circumstances would not be very informative, since we are analyzing only a few species and the results could be misleading. For this reason we have not attempted to determine character polarities.

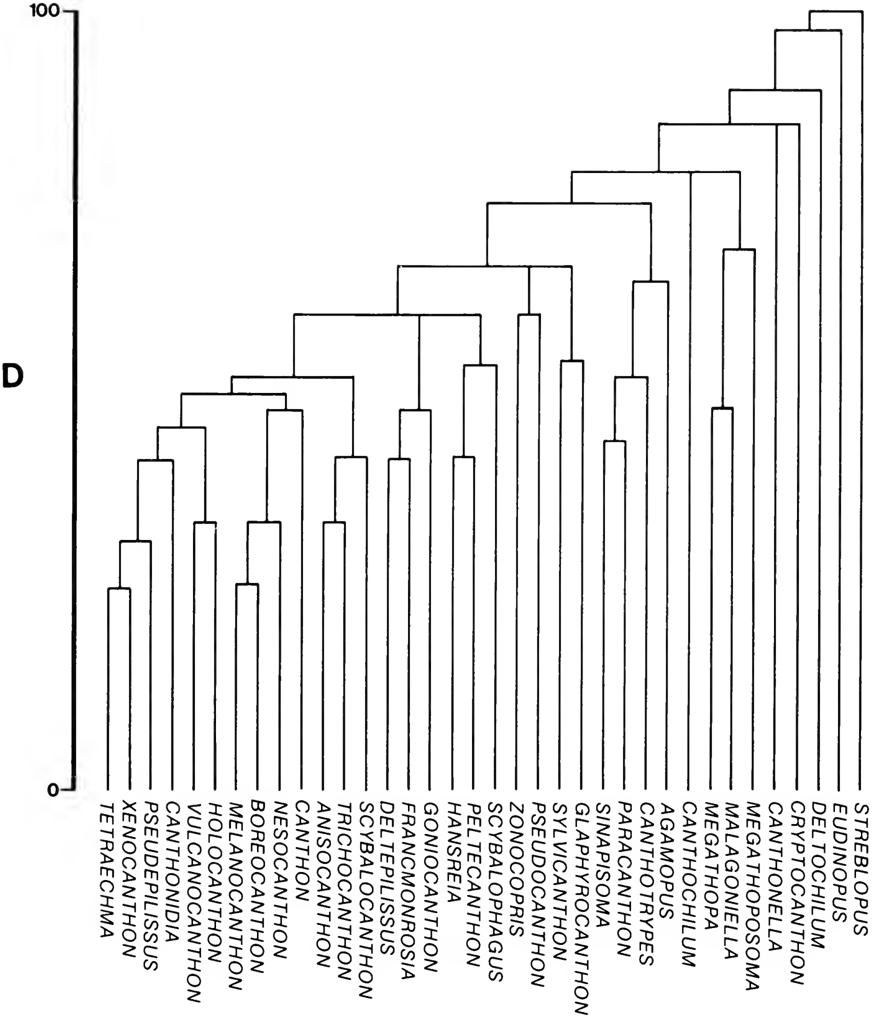


Fig. 1. Phenogram of the genera and subgenera of the American Canthonina. The scale measures the dissimilarity (D) between taxa based on the Manhattan metric. The phenogram has been constructed according to the UPGMA clustering procedure.

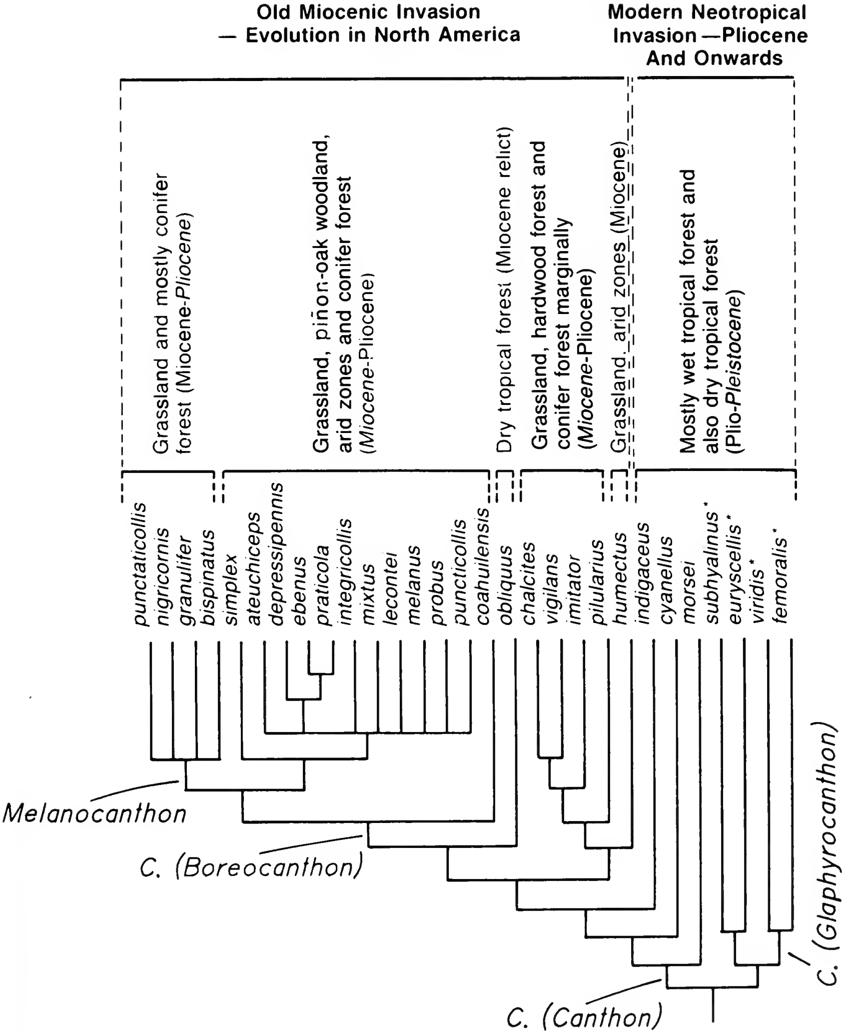


Fig. 2. Strict consensus cladogram of the North American species of the subgenus *Canthon* and related taxa of the subgenus *Boreocanthon* and the genus *Melanocanthon*. The distribution of the taxa in different biomes is indicated as well as the inferred age of appearance of the biome in North America. The age of appearance of biomes correlated with the greatest number of associated species is in italics. The proposed invasion time of the different lines into North America are also indicated. Species marked with a star represent outgroups used for rooting the cladogram. The length of the cladogram branches have no meaning.

Zoogeographic Methods.

The subject of this paper is to examine further evidence regarding the interpretation of two different dispersal waves in the speciation process of the subgenus *Canthon* and its closely related taxa *Boreocanthon* and *Melanocanthon* in relation to the biogeographical history of the MTZ as put forward by Halffter. Broadly, the biogeographic history of the dung-rollers under study in North America is inferred from a cladistic analysis and related to the sequence of the age of appearance of the different biomes where they are distributed now. More particularly, the cladogram of all species pertaining to a taxon (including or not other related taxa) which is distributed in defined study areas is constructed. Then we relate the cladogram with the sequence of events suggested by the age of appearance of the different biomes where the dung-rollers live now and compare it with the predictions stemming from the MTZ hypotheses, in order to gain some insight into vicariant and dispersal events that have taken place in the area.

Two other approaches for reconstructing the biogeographic and ecological history of taxa using a phylogenetic-tree analysis have been proposed (Brooks, 1985, Legendre, 1986). Brooks' method treats species as characters of the areas in which they occur and lineages of species are thus considered transformation series linking different areas in an historical pattern. Legendre (1986) reconstructs the dispersal of a community into adjacent territories by using data of species presence/absence, obtaining tree-like structures of dispersal from a single trunk. Connor (1988) analyzes and gives a summary of the bases for inferring the historical dynamics of biogeographic distributions using phylogenetic methods. For vicariance biogeography (Nelson, 1973, 1975, 1978) incongruent patterns between the area cladograms of two or more groups may be interpreted as dispersal, but different modes of speciation may also be invoked as an explanation (Wiley, 1981; Wiley and Mayden, 1985).

RESULTS

Cladogram Construction.

A maximum limit was set of 50 equally parsimonious trees to be retained for analysis. The analysis resulted in 50 such trees with length=57. Consensus trees using the strict method (Rohlf, 1982) and the method of Adams (1972) were obtained. The result of the strict consensus tree is depicted in Fig. 2. It has a consensus fork index (Colless, 1980) of CF=0.704. The consensus tree of Adams is not shown, because it is very similar to the first one. The only difference is in species *C. lecontei* and *C. melanus* forming a trichotomy with the rest of the *Boreocanthon* species group, instead of being part of it, after having branched from *C. simplex*.

Correlation with Biomes

Maps of the different taxa recognized by Halffter (1958, 1961) and Halffter and Martínez (1977) have been elaborated based on personal collections and publications (Halffter, 1958, 1961; Halffter, and Martínez, 1977; Howden, 1966, Woodruff, 1973). The biomes where the different taxa are distributed generally have been indicated in the cladogram as well as the probable age of biome appearance (Fig. 2).

TESTS OF ZOOGEOGRAPHIC PREDICTIONS

Taxonomic Congruence

The results of the consensus cladogram have been compared with the accepted classification of the North American groups (Halffter 1958, 1961). These original groups were not based solely on phylogenetic considerations, but represent a classification combining phylogenetic information, morphological distinctiveness and ease of identification. Therefore, it is not surprising that the cladogram does not recover the exact grouping. However, the species sequence of the cladogram agrees in terms of grouping. The cladogram reveals that *Canthon* (*C.*) *obliquus* and *Canthon* (*B.*) *coahuilensis* have a somewhat isolated position regarding the old invasion line of American Canthonina. This situation will be considered in taxonomic terms in a subsequent systematic treatment of the group.

Historical Congruence.

The consensus cladogram (Fig. 2) shows two distinct groups, one composed by the species of the subgenus *Glaphyrocanthon,* which have been used as outgroups for rooting the cladogram and secondly, the ingroup, formed by the subgenus *Canthon* and related taxa, the subgenus *Boreocanthon* and the genus *Melancanthon*. We will start our discussion with the ingroup.

We observe, as expected from our predictions based on the biogeographic hypotheses of the MTZ, that species *C. morsei, C. cyanellus,* and *C. indigaceus* branch out at the base of our ingroup and that they are distributed in tropical biomes of Plio-Pleistocene invasion into North America (Fig. 2, Map 1). Their branching order is therefore incongruent with the rest of the ingroup sequence of events if these three species had derived from the same Miocene ancestor that invaded North America from South America and had diversified in biomes that had originated (not invaded) in North America. This lack of congruence supports the assumption that these three species represent separate invaders into North America (Halffter, *op. cit.*). As can be seen from the consensus cladogram (Fig. 2), none of the three taxa are grouped within a clade but form isolated lines in the study area. They represent actually, northern ends of groups whose species richness is centered in South America. *Canthon morsei* (Map 1) is a member of the *juvencus* line (Halffter and Martínez, 1977), all other species of which are South American; *Canthon cyanellus* (Map 1) stems from Colombia, Peru and Venezuela (Halffter, 1961) and its line has a major diversification in South America. These two taxa more probably invaded North America in conjunction with rainforest dispersal into the area and from there *C. cyanellus* expanded its range into other types of tropical forests. *Canthon indigaceus* (Map 2) stems from a diversification process in tropical México (Halffter, 1961). Its three subspecies are limited to tropical conditions, in accordance with the pattern that Halffter (*op. cit.*) has designated typical Neotropical and which is essentially modern in the biogeographic history of the MTZ. All these species are isolated from the Mexican and North American Canthonina (Fig. 2) and are only distantly related to them.

The outgroup, subgenus *Glaphyrocanthon* (Map 3), shows the same type of distribution and biome association as the three above-mentioned invading species. The species *C.* (*G.*) *subhyalinus* is distributed from northern Amazonia to southern tropical México and together with *C.* (*G.*) *euryscelis,* which is distributed in Central American rainforests, they belong to a line with greatest species diversity in the northern part of Amazonia (Martínez, Halffter and Kohlmann, unpubl.). *Canthon* (*G.*) *femoralis* stems from Colombia (Martínez and Halffter, 1972), and *C. viridis* belongs to a species group whose greatest richness is South American (Martínez, Halffter and Halffter, 1964). The northern presence of *Glaphyrocanthon* suggests a concordant expansion with the rainforest, sometimes associated with subspecies formation and penetration into eastern North America (*C. viridis*; Martínez, Halffter and Halffter, 1964). Several other genera of Canthonina, such as *Deltochilum, Cryptocanthon, Pseudocanthon, Malagoniella,* and *Megathoposoma* (Halffter and Martínez, 1966, 1967, 1968, 1977; Howden, 1973) follow a pattern of association with tropical biomes, particularly rainforest, reinforcing the Plio-Pleistocene insect invasion hypotheses into the MTZ from South America (Halffter, *op. cit.*).

The consensus cladogram (Fig. 2) shows a recognizable group formed by two main branches, one with *Canthon* species and the other with mostly *Boreocanthon* and *Melanocanthon* species. This group encompasses all those species with an origin stemming from a postulated Miocene invasion into North America. The group conforms also with our prediction that most of the species diversification coincides with the sequence of biome appearances in North America, Miocene events at the root of the group and subsequently a trend toward species association with Pliocene biomes.

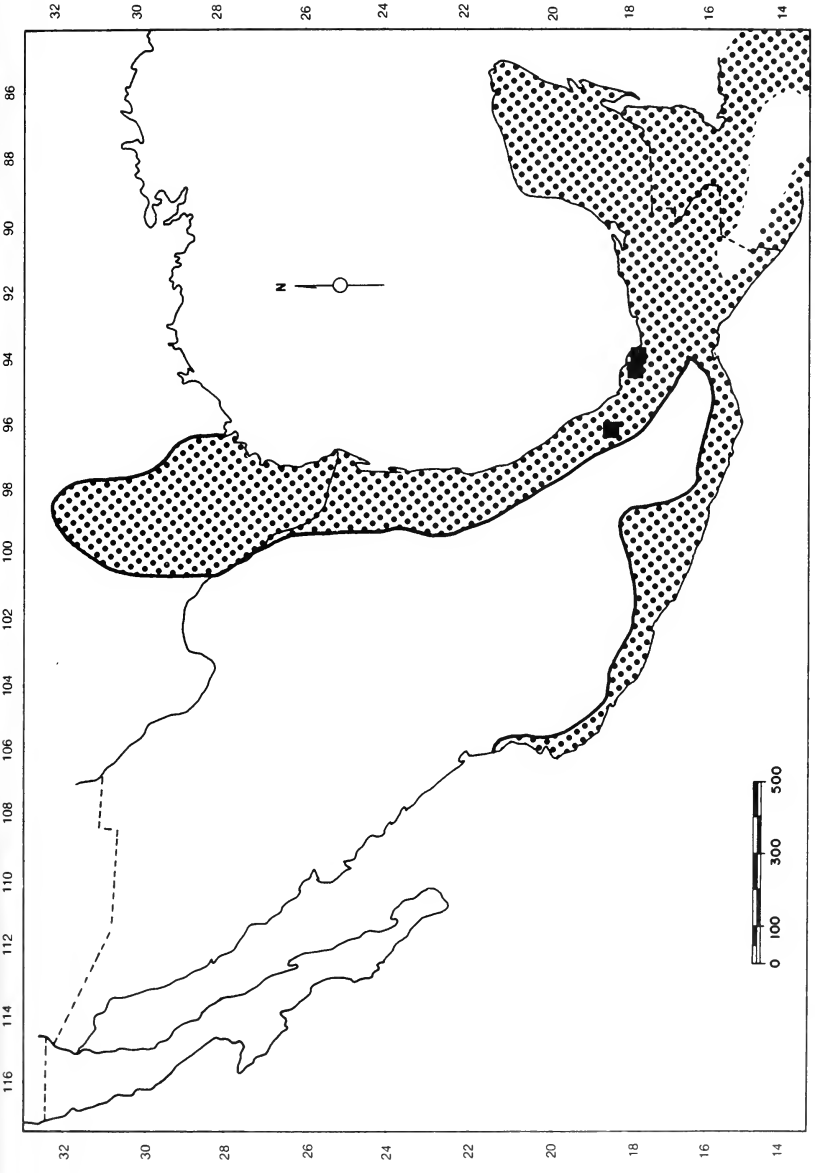
The *Canthon* branch includes the "*humectus*" and "*pilularius*" lines of Halffter (1961) and relates them mainly to Miocene events. *Canthon humectus* is distributed in the Mexican Highland in grasslands and arid areas with the exception of the most arid zones, and the highlands of Oaxaca, Chiapas and Guatemala (Map 4). As Halffter (*op. cit.*) indicates, Neotropical species of recent migration have not invaded the highlands; those that do, arrived at the area before its actual rising, a phenomenon that started during the Miocene. The later disruption of their area is attributed by Halffter (*op. cit.*) to the aridity process, which is more recent (Heine, 1973). The *pilularius* line must have colonized the east of the USA during Miocene or somewhat later, but not in recent times. Its actual distribution covers the grasslands of the Great Plains and the forests of the east and south of the country; its distribution nucleus is centered on deciduous hardwood forests (Map 5). Axelrod (1979) indicates that during Middle Oligocene cold winters had eliminated the majority of evergreen dicotyledons in eastern USA, leaving only a deciduous hardwood forest. It was not until the Plio-Pleistocene that prairies and pine forests started to spread (Axelrod, 1979). It is possible therefore, that the *pilularius* line invaded this sort of habitat from the deciduous hardwood forest, explaining the correspondence with the present-day distribution of all four species.

The other branch of the proposed Miocene invasion group includes *Canthon obliquus*, the subgenus *Boreocanthon* and the genus *Melanocanthon*. *Canthon obliquus* is unique (Map 6). It is confined to a relict, deciduous tropical forest (Rzedowski, 1978; Arriaga and Ortega, 1988) at the Sierra de la Laguna in Baja California, having become isolated by the drift process of the Baja California Peninsula. The rift started by late Miocene (Karig and Jensky, 1972) and by early Pliocene separation was very advanced. This species is a relict, since the tropical deciduous forest in which it now lives, was well established in south-central USA during Miocene (Axelrod, 1979) and from that moment it started retreating towards México, its area being steadily reduced. *Canthon obliquus* thence would have become isolated in a remaining island of deciduous tropical forest. Later on, all of the peninsula, with the exception of the southernmost mountains, suffered from desertification and invasions of biota adapted to these conditions, as for *C.* (*B.*) *puncticollis*. A similar scheme is known for the *Bursera* (Burseraceae) species from Baja California (Kohlmann and Sánchez-Colón, 1984).

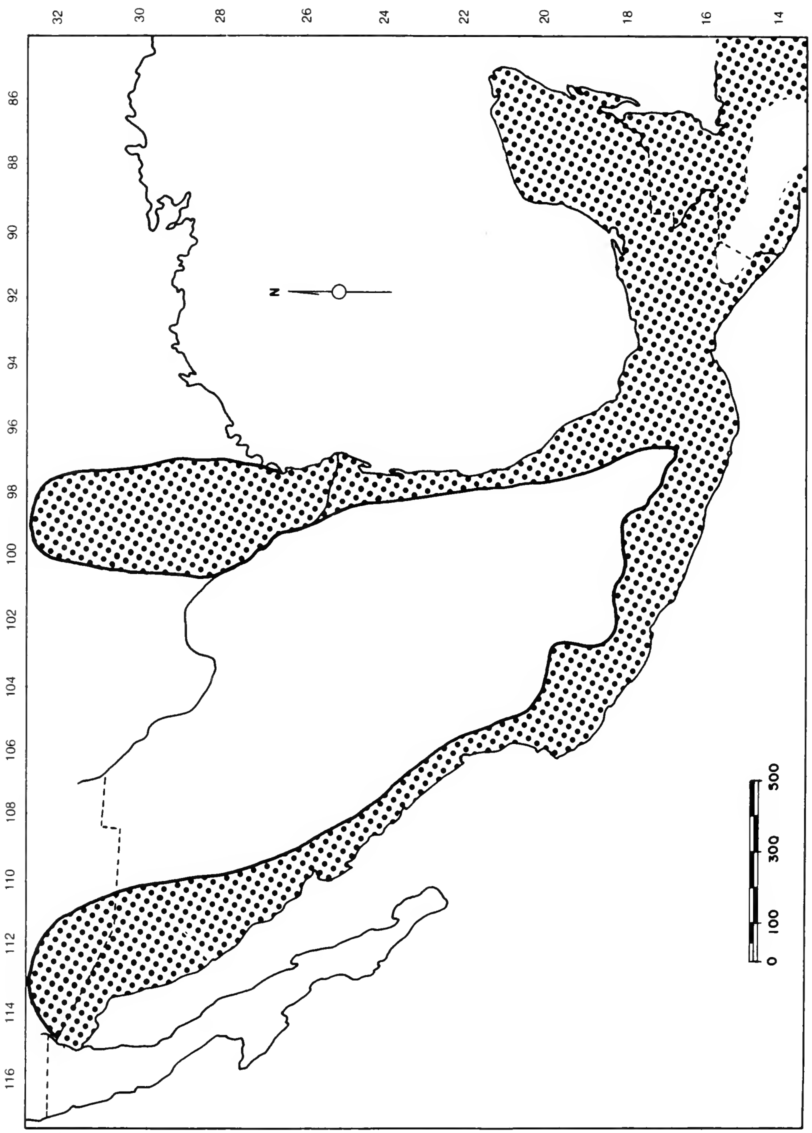
The ancestor of *Melanocanthon-Boreocanthon* would have been distributed originally in northern México and south-central USA, while the area was covered by tropical deciduous forest. By the end of Miocene the forest started to be replaced by grasslands and piñon-oak woodland, a process that was advanced in the Pliocene by the spread of pine forest and very recently the appearance of deserts. Most *Boreocanthon* species (Map 6) live in this area, which leads us to think that this was the main evolutionary arena for this group. Nowadays, many of the species live in grasslands of the Great Plains (*C. simplex, C. lecontei, C. integricollis, C. mixtus, C. praticola,* and *C. ebenus*) or in arid zones (*C. puncticollis* and *C. ateuchiceps*). This last species seems to be a recent invader of the arid zones of Puebla, Morelos and Oaxaca following the scheme proposed by Axelrod (1979), where endemic species of the southern arid zones of México are recent relicts, which have been pushed into these areas by climatic events of the late Cenozoic (Heine, 1973). One species, *C. melanus*, apparently is confined largely to the Arizona mountains in piñon-oak woodland,, although there is one record from Guaymas, Sonora, for the coastal desert. Two species, *C. probus* and *C. depressipennis,* follow a similar pattern to *Melanocanthon*; in addition to being present in the Great Plains, both penetrate into eastern USA through the conifer forest corridor. This distribution could represent an invasion from the grasslands into the conifer forest corridor. With the exception of these two species, all the rest of *Boreocanthon* is associated with biomes that originated in the Miocene.

The last group, *Melanocanthon* (Map 7) is associated mostly with Pliocene biomes. The only species associated exclusively with a Miocene biome is *M. nigricornis*, which is distributed in the grasslands of the Great Plains. The remainder occur in the conifer forest corridor in the south and east of the USA (*M.*

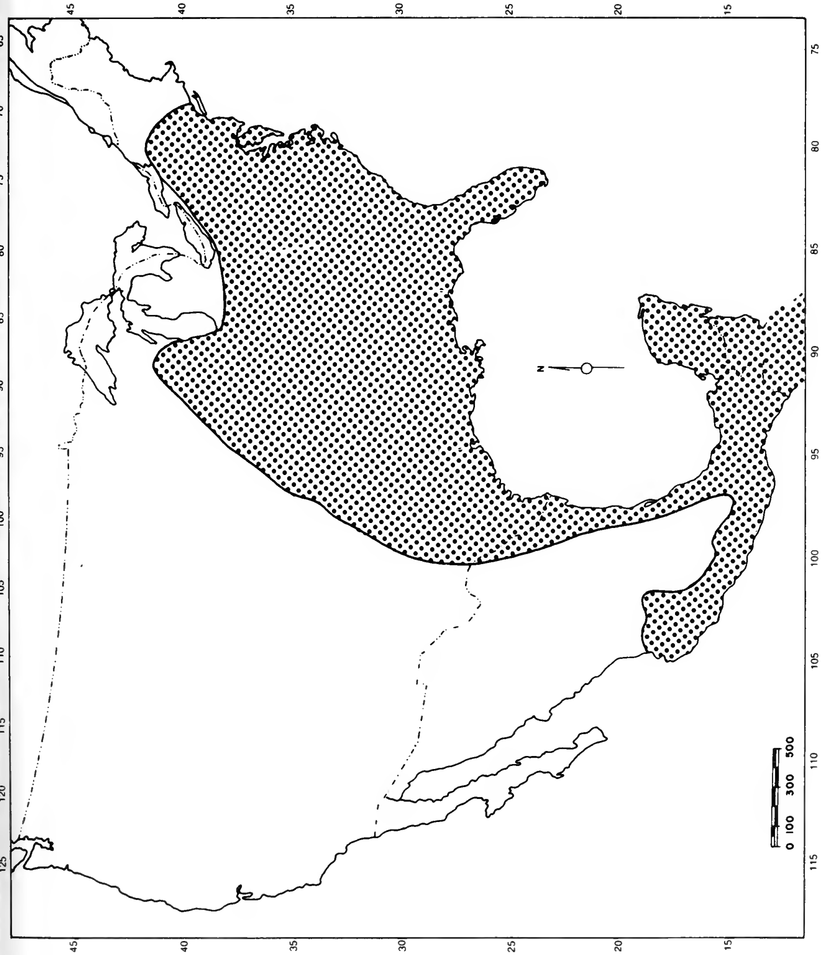
bispinatus); in the grasslands and conifer forests of Texas and northern Florida (*M. granulifer*); or else in northern Florida (*M. punctaticollis*). The invasion and speciation process seems to have shifted to the east in this group, relative to the other south-central diversification areas and follows the pine and pine-oak forest corridors that established themselves around the deciduous forests. It seems to be the only member of the Miocene group whose speciation events are recent (Pliocene), whereas in *Canthon* and *Boreocanthon* some species seem to have invaded but not speciated in Pliocene biomes. The invasion and speciation pattern in *Melanocanthon* is somewhat similar to that of *Ateuchus* (Coleoptera: Scarabaeidae), since it is proposed that the latter genus invaded and diversified in an approximately similar zone in Plio-Pleistocene time (Kohlmann and Halffter, 1988).



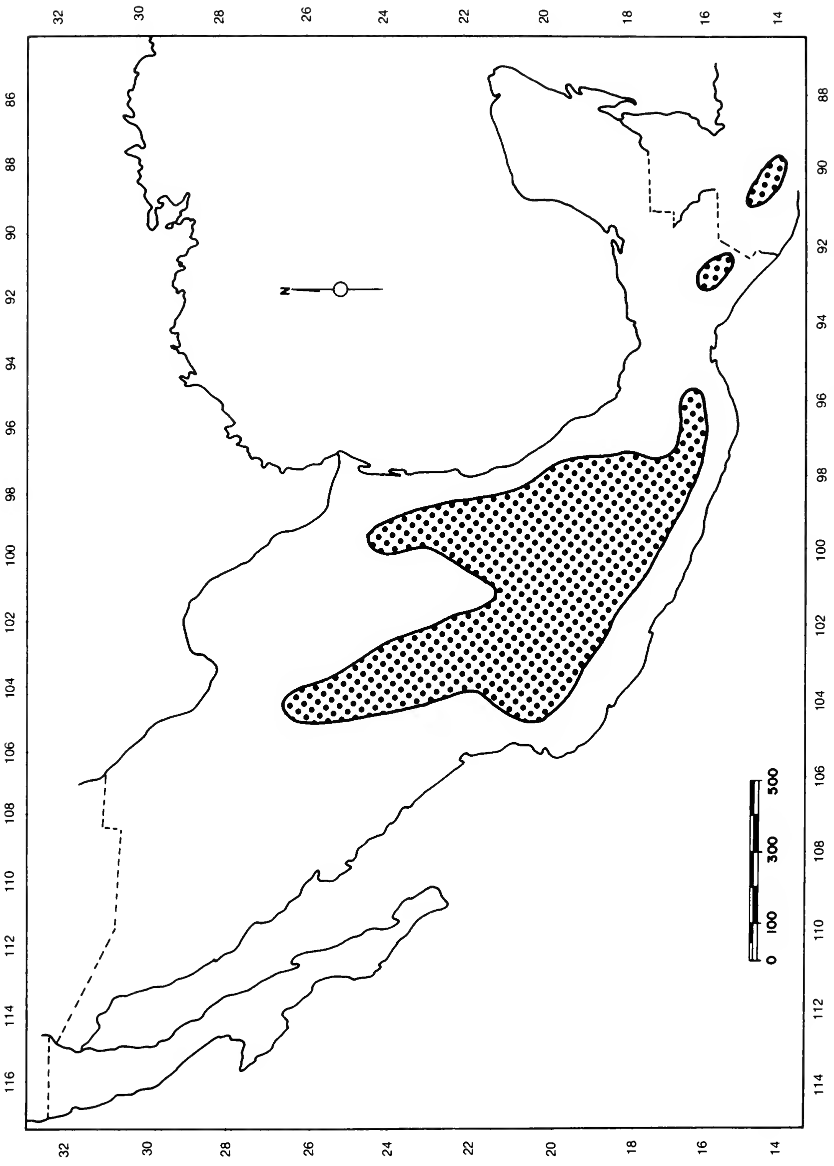
Map 1. Geographical distribution of the *C.* (*Canthon*) *cyanellus* line in northern Middle America and in southern United States of America. Black squares represent the known localities for *Canthon morsei*.



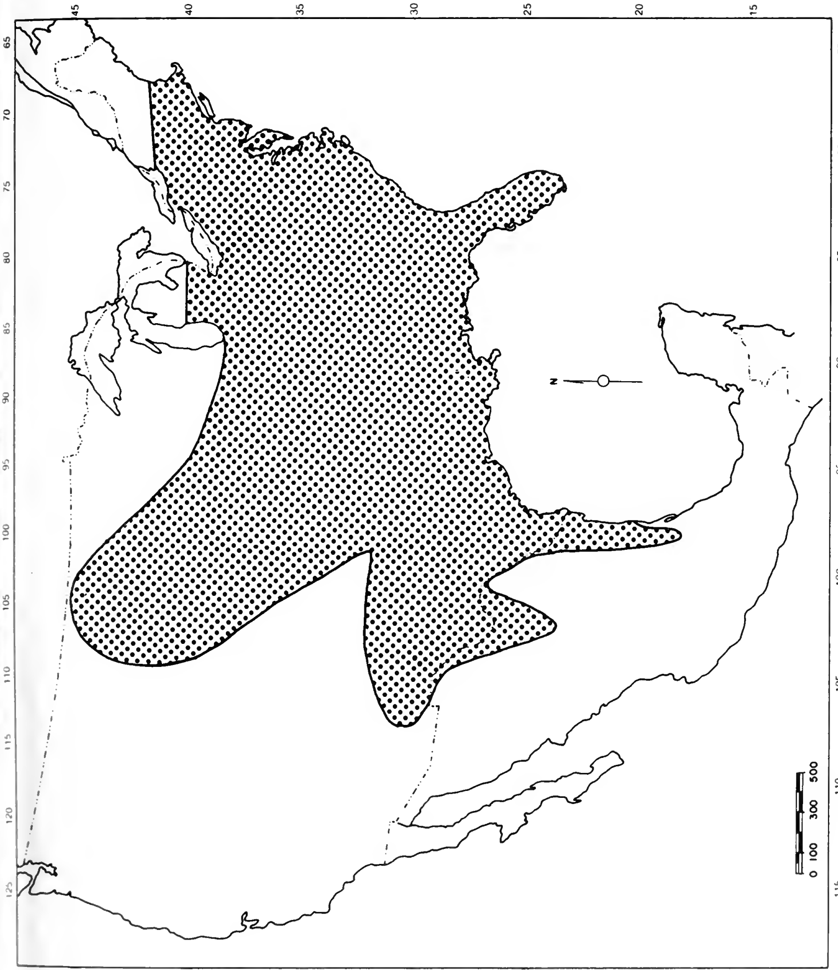
Map 2. Geographical distribution of the *C.* (*Canthon*) *indigaceus* line, in northern Middle America and in southern United States of America.



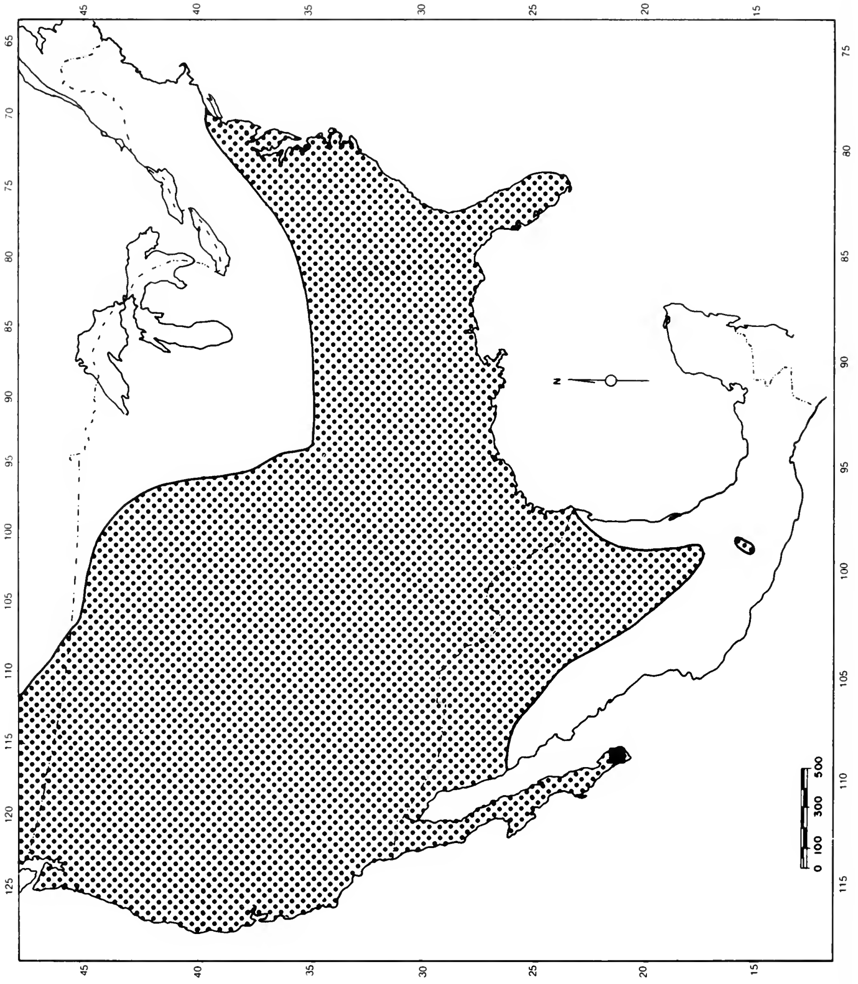
Map 3. Geographical distribution of *C.* (*Glaphyrocanthon*) in northern Middle America and in southern United States of America.



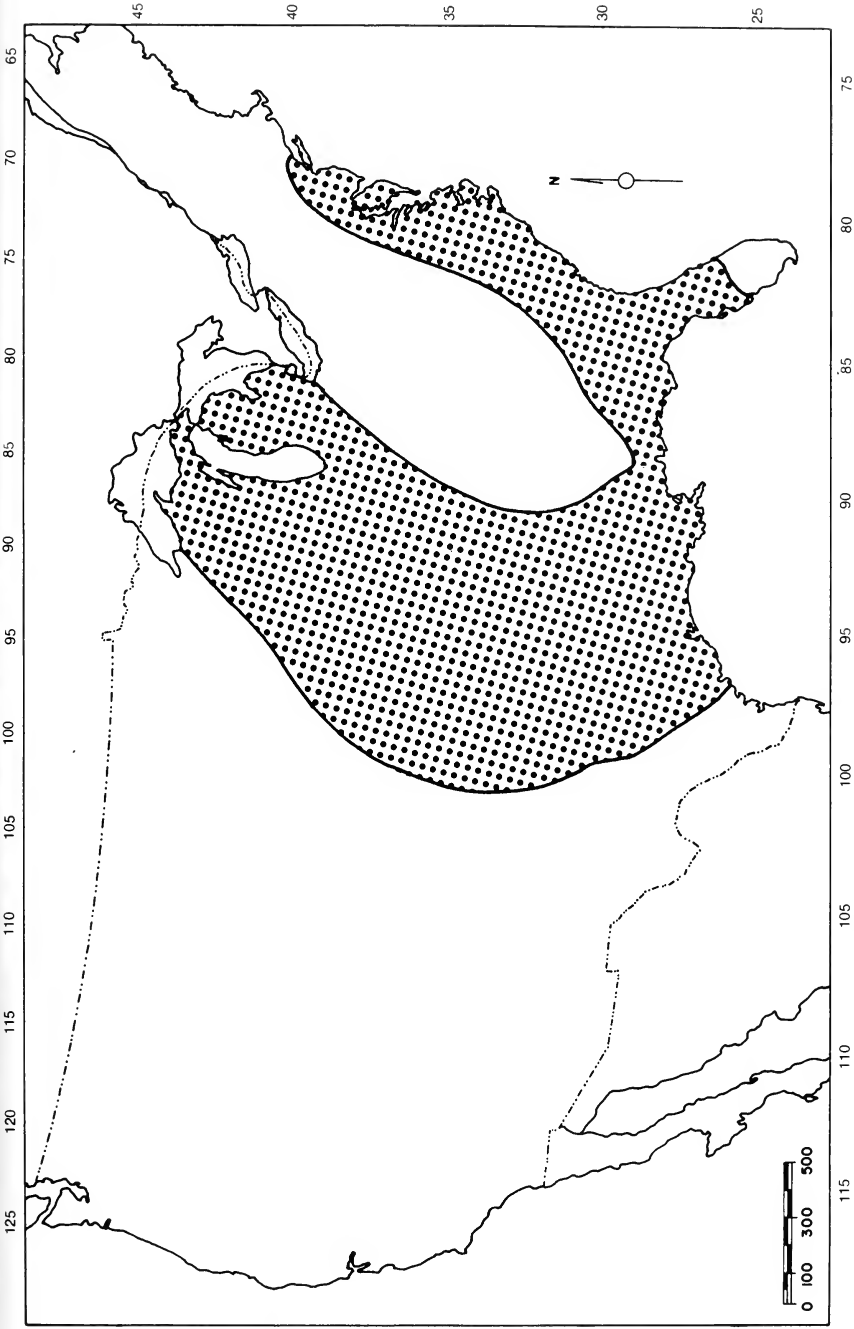
Map 4. Geographical distribution of the *C.* (*Canthon*) *humectus* line in Mexico and Guatemala.



Map 5. Geographical distribution of the *C.* (*Canthon*) *pilularius* line in Mexico and in the United States of America.



Map 6. Geographical distribution of *C. (Boreocanthon*) in Mexico and in the United States of America. The square at the bottom end of the peninsula of Baja California represents the distribution of *C. (Canthon) obliquus.*



Map 7. Geographical distribution of *Melanocanthon* in eastern United States of America.

CONCLUDING STATEMENT

We observe from the previous analysis that the concordance of the consensus cladogram with the age of appearance of the different biomes is congruent with our predictions based on the biogeographical hypotheses of the MTZ. Therefore this fact may be considered supportive of the supposition of two different insect invasion waves from South into North America. Moreover, the analysis points to a strong correlation between a great diversification of the Miocene invasion lineage with biomes that started to originate in the Miocene. Far fewer species are associated with Pliocene biomes, and in several of such seem to represent secondary invasions. Finally, no species stemming from the proposed Miocene invasion have been found in Pleistocene biomes (tropical rainforest). This would suggest that ball-rollers of the Miocene invasion have not had enough time to diversify in this new environment, or that most probably ecological replacement stemming from the many South-American-derived species living in tropical forests in North America have precluded species diversification effectively.

This analysis may be corroborated by other studies. However, not many insect examples with a suspected similar history are known. The scarabaeid genus *Phanaeus* seems to follow a related pattern (Halffter, 1962; Edmonds, 1972). This genus is being revised by Edmonds (pers. coms.), and a similar analysis may be very illuminating. Savage (1982) already has presented evidence for a late Cretaceous and a Plio-Pleistocene dispersal of South American fishes, amphibians and reptiles into Central America. For floras, Gentry (1982) also proposes two migrations of Neotropical floristic elements from South to North America. Gentry (1982) considers that the two main waves occurred at the end of the Cretaceous and then again in Pliocene. The history of the dung-rollers seems to be more similar to the one postulated for mammals (Stehli and Webb, 1985), where an increasing frequency of connection started in Miocene and culminated in Plio-Pleistocene. At any rate the existence of two different invasion processes is supported by the present analysis for the dung-rollers, although the exact timing of the first wave may be debatable still. In conclusion we would consider that the approach presented here may be of help in other situations where several invasion or dispersal waves in different taxa are suspected.

ACKNOWLEDGEMENTS

We thank Professor B. John who read an early draft of the manuscript and D. Colgan for reviewing and commenting on this paper. Special thanks go to D. Colless for his detailed reading of the manuscript, for providing much help during the cladistic analysis and introducing one of us (B.K.) to the use of PAUP. Constructive criticism of two anonymous reviewers is also thankfully acknowledged.

REFERENCES CITED

Adams, E.N. 1972. Consensus techniques and the comparison of phylogenetic trees. Systematic Zoology. 21: 390-397.

Arriaga, L. and A. Ortega (eds.) 1988. La Sierra de la Laguna de Baja California Sur. Centro de Investigaciones Biológicas de Baja California Sur, La Paz, Baja California Sur, México. 203 p.

Axelrod, D.I. 1975. Evolution and biogeography of Madrean-Tethyan sclerophyll vegetation. Evolution 62: 280-334.

Axelrod, D.I. 1979. Age and origin of Sonoran Desert vegetation. Occasional Papers of the California Academy of Sciences. 132: 1-74

Briggs, J.C. 1987. Biogeography and Plate Tectonics. Developments in Paleontology and Stratigraphy, 10. Elsevier, Amsterdam. 204 p.

Brooks, D.R. 1985. Historial ecology: A new approach to studying the evolution of ecological associations. Annals of the Missouri Botanical Garden. 72: 660-680.

Colless, D.H. 1980. Congruence between morphometric and allozyme data for *Menidia* species: A Reappraisal. Systematic Zoology. 29: 288-289.

Connor, E.F. 1988. Fossils, phenetics, and phylogenetics: Inferring the historial dynamics of biogeographic distributions, p. 254-269. In: Zoogeography of Caribbean Insects, J. K. Liebherr (ed.). Cornell Univ. Press, Ithaca, N.Y. 285 p.

Donnelly, T.W. 1988. Geologic constraints on Caribbean biogeography p. 15-37. In: Zoogeography of Caribbean Insects, J.K. Liebherr (ed.). Cornell Univ. Press, Ithaca, N.Y. 285 p.

Edmonds, W.D. 1972. Comparative skeletal morphology, systematics and evolution of the Phanaeinae dung beetles (Coleoptera: Scarabaeidae). University of Kansas Science Bulletin. 49: 731-874.

Gentry, A.H. 1982. Neotropical floristic diversity: Phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny. Annals of the Missouri Botanical Garden. 69: 557-593.

Germeraad, J.H., C.A. Kopping and J. Muller, 1968. Palynology of Tertiary sediments from tropical areas. Reviews of Paleobotany and Palynology. 6: 189-348.

Graham, A. 1973. History of the arborescent temperate element in the Latin American biota. p. 301-314. In: Vegetation and Vegetational History of Northern Latin America, A. Graham (ed.). Elsevier, Amsterdam. 393 p.

Graham, A. 1981. Diversification beyond the Amazon Basin. p. 78-90. In: Biological Diversification in the Tropics, G. Prance (ed.). Plenum Press, N.Y. 714 p.

Halffter, G. 1958. Dos neuvos géneros de Canthonini (Coleoptera: Scarabaeidea). Ciencia (Méx.). 17: 207-212.

Halffter, G. 1961. Monografía de las especies norteamericanas del género Canthon Hoffsg. (Coleoptera: Scarabaeidae). Ciencia (Méx.). 20: 225-320.

Hallfter, G. 1962. Explicación preliminar de la distribución geográfica de los Scarabaeidae mexicanos. Acta Zoológica Mexicana. 5: 1-17.

Halffter, G. 1964. La entomofauna americana, ideas acerca de su origen y distribucíon. Folia Entomológica Mexicana. 6: 1-108.

Halffter, G. 1972. Eléments anciens de l'entomofaune néotropicale. Ses implications biogéographiques. In: Biogéographie et liaisons intercontinentales un cours du Mésozoïque. XVII éme Congrés International de Zoologie, Monte Carlo. 40 p.

Halffter, G. 1974. Eléments anciens de l'entomofaune néotropicale. Ses implications biogéographiques. Quaestiones entomologicae. 10: 223-262.

Halffter, G. 1976. Distribución de los insectos en la Zona de Transición Mexicana. Folio Entomológica Mexicana. 35: 1-64.

Halffter, G. 1978. Un nuevo patrón de dispersión en la Zona de Transición Mexicana: El Mesoamericano de Montaña. Folia Entomológica Mexicana. 39-40: 210-222.

Halffter, G. 1987. Biogeography of the montane entomofauna of Mexico and Central America. Annual Review of Entomology. 32: 95-114.

Halffter, G. and W.D. Edmonds. 1982. The Nesting Behaviour of Dung Beetles (Scarabaeidae). An Ecological and Evolutive Approach. Publs. Instituto de Ecología 10, México, D.F. 176p.

Hallffter, G. and A. Martínez. 1966 Revisión monográfica de los Canthonina americanos (1a. Parte). Revista de la Sociedad Mexicana de Historia Natural. 27: 89-171

Halffter, G. and A. Martínez. 1967. Revisión monográfica de los Canthonina americanos. (2a. Parte). Revista de la Sodiedad Mexicana de Historia Natural. 28: 79-116.

Halffter, G. and A. Martínez. 1968. Revisión monográfica de los Canthonina americanos (3a. Parte). Revista de la Sociedad Mexicana de Historia Natural. 29: 209-290.

Halffter, G. and A. Martínez. 1977. Revisión monográfica de los Canthonina americanos (4a. Parte). Folia Entomológica Mexicana. 39: 29-108.

Heine, K. 1973. Variaciones más importantes del clima durante los últimos 40,000 años. Communicaciones Proyecto Puebla-Tlaxcala (Fundación Alemana para la Investigacíon Científica). 7: 51-58.

Hennig, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana. 263 p.

Howden, H.F. 1966. Notes on Canthonini of the "Biologia Centrali-Americana" and descriptions of new species (Coleoptera: Scarabaeidae). Canadian Entomologist. 98: 725-741.

Howden, H.F. 1973. Revision of the New World genus *Cryptocanthon* Balthasar (Coleoptera: Scarabaeidae). Canadian Journal of Zoology. 60: 2713-2724.

Kaneps, A.C. 1979. Gulf Stream: Velocity fluctuations during Late Cenezoic. Science. 204: 297-301.

Karig, D.E. and W. Jensky, 1972. The proto-Gulf of California. Earth and Planetary Science Letters. 17: 169-174.

Keigwin, L.D. 1978. Pliocene closing of the Isthmus of Panama, based on biostratigraphic evidence from nearby Pacific Ocean and Caribbean sea cores. Geology. 6: 630-634.

Kohlmann, B. and G. Halffter. 1988. Cladistic and biogeographical analysis of *Ateuchus* (Coleoptera: Scarabaeidae) of Mexico and the United States. Folia Entomológica Mexicana. 74: 109-130.

Kohlmann, B. and S. Sánchez-Colón. 1984. Estudio areográfico del género Bursera Jacq. ex L. (Burseraceae) en México: Una síntesis de métodos. p. 41-120. In: Métodos Cuantitativos en la Biogeografía, E. Ezcurra and B. Kohlmann (eds.). Publs. Instituto de Ecología 12, México, D.F. 125 p.

Legendre, P. 1986. Reconstructing biogeographical history using phylogenetic-tree analysis of community structure. Systematic Zoology. 35: 68-80.

Liebherr, J.K. 1988. The Caribbean: Fertile ground for zoogeography, p. 1-14. In: Zoogeography of Caribbean Insects, J.K. Liebherr (ed.). Cornell Univ. Press, Ithaca, N.Y. 285 p.

Marshall, L.G., S.D. Webb, J.J. Sepkoski and D.M. Raup. 1982. Mammalian evolution and the great American interchange. Science. 215: 1351-1357

Martínez, A. and G. Halffter. 1972. New taxa of American Canthonina (Coleoptera: Scarabaeidae). Entomologische Arbeiten des Museums Georg Frey. 23: 33-66.

Martínez, A., G. Halffter and V. Halffter. 1964. Notas sobre el género Glaphyrocanthon (Coleoptera: Scarabaeidae) Acta Zoológica Mexicana. 7: 1-42

Meacham, C.A. 1984. The role of hypothesized direction of characters in the estimation of evolutionary history. Taxon 33: 26-38.

Nelson, G.J. 1973. Comments on Leon Croizat's biogeography. Systematic Zoology. 22: 312-320.

Nelson, G.J. 1975. Historical biogeography: An alternative formulation. Systematic Zoology. 23: 555-558.

Nelson, G.J. 1978. From Candolle to Croizat: Comments on the history of biogeography. Journal of Historical Biology. 11: 293-329.

Prance, G.T. 1982. A review of the phytogeographic evidences for Pleistocene climate changes in the neotropics. Annals of the Missouri Botanical Garden. 69: 594-624.

Rohlf, F.J. 1982. Consensus indices for comparing classifications. Mathematical Biosciences. 59: 131-144.

Rosen, D.E. 1978. Vicariant patterns and historical explanation in biogeography. Systematic Zoology. 27: 159-188.

Rosen, D.E. 1979. Fishes from the uplands and intermontane basins of Guatemala: Revisionary studies and comparative geography. Bulletin of the American Museum of Natural History. 162: 267-376.

Rzedowski, J. 1978. Vegetación de México. Editorial Limusa, México, D.F. 432 p.

Savage, J.M. 1982. The enigma of the Central American herpetofauna: Dispersals or vicariance? Annals of the Missouri Botanical Garden. 69: 464-547.

Simpson, G.G. 1953. The Major Features of Evolution. Columbia Univ. Press. N.Y. 434 p.

Stehli, F.G. and S.D. Webb, eds. 1985. The Great American Biotic Interchange. Plenum Press, N.Y. 532 p.

Swofford, D.L. 1985. PAUP phylogenetic analysis using parsimony. Version 2.4.0. Illinois Natural History Survey, Champaign, Illinois.

Toledo, V.M. 1976. Los cambios climáticos del Pleistoceno y sus efectos sobre la vegetación natural cálida y húmeda de México. M.Sc. Thesis, Faculty of Sciences, UNAM México. 74 p.

Toledo, V.M. 1982. Pleistocene changes of vegetation in tropical Mexico. p. 92-111. In: Biological diversification in the Tropics, G.T. Prance (ed.). Columbia Univ. Press, N.Y. 714 p.

Webb, S.D. 1977. A history of savanna vertebrates in the New World. Part I: North America. Annual Review of Ecology and Systematics. 8: 355-380.

Webb, S.D. 1978. A history of savanna vertebrates in the New World. Part II South America and the great interchange. Annual Review of Ecology and Systematics. 9: 393-426.

Wiley, E.O. 1981. Phylogenetics. The Theory and Practice of Phylogenetic Systematics. Wiley-Interscience, N.Y. 439 p.

Wiley, E.O. and R.L. Mayden. 1985. Species and speciation in phylogenetic systematics, with examples from the North American fish fauna. Annals of the Missouri Botanical Garden. 72: 596-635.

Woodruff, R.E. 1973. The scarab beetles of Florida. Florida Department of Agriculture and Consumer Services. Division of Plant Industry, Gainesville, Florida. 220 p.

APPENDIX

The phenetic analysis of the American canthonine genera and subgenera of *Canthon* (Fig. 1) is based on the work of Halffter and Martínez (1966, 1967, 1968 and 1977). Seventy-one characters of external and internal structures have been taken into consideration; thirty-two of them are binary and thirty-nine are multistate. The distribution of these characters and their description are available from the authors.

Some problems exist in the analysis. The male of *Canthotrypes* is not known. The aedeagus of *Zonocopris* and *Deltepilissus* could not be examined.

The phenogram (Fig. 1) was elaborated using the UPGMA method. As a distance measure the Manhattan coefficient was used. This coefficient implies the existence of orthogonal axes. The character correlation matrix (not reproduced) has low correlation values, therefore this metric is acceptable.

The analysis of the phenogram indicates various groups:

Tetraechma-Xenocanthon-Pseudepilissus-Canthonidia; Vulcanocanthon-Holocanthon; Melanocanthon-Boreocanthon -Nesocanthon-Canthon; *Anisocanthon-Trichocanthon-Scybalocanthon; Deltepilissus-Francmonrosia-Goniocanthon; Hansreia-Peltecanthon-Scybalophagus; Zonocopris-Pseudocanthon; Sylvicanthon-Glaphyrocanthon; Sinapisoma-Paracanthon-Canthonotrypes-Agamopus; Megathopa-Megathoposoma;* and the following isolated lines - *Canthochilum, Canthonella, Cryptocanthon, Deltochilum, Eudinopus* and the most removed one, *Streblopus*. It should be mentioned here that *Deltochilum* is a very heterogeneous entity.

The ladder structure in the phenogram suggests that the relationships between taxa is a very gradual one, implying that the group is very homogeneous in its morphological characteristics. The low morphological character correlation seems to indicate that there has not been any tendency to form groups of associated characters.

Until a detailed cladistic analysis is performed, the present study should be considered as preliminary.

TABLE 1

Morphological Characters Used in the Study of North American Canthonina

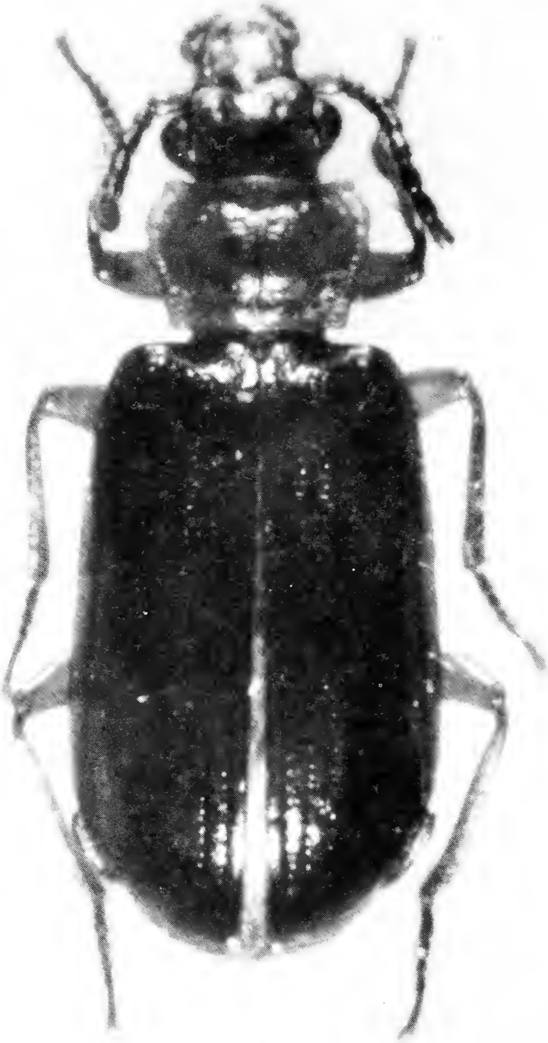
1.- Number of elytral striae. Usually eight: a; usually nine: b.
2.- First article of the metatarsi. Usually bigger than the second: a; usually shorter than the second: b; equal: c.
3.- Anterior margin of the metafemur. Without margin: a; with margin: b.
4.- Elytra. Translucent: a; opaque: b.
5.- Clypeo-genal suture. With broad external notch: a; with narrow external notch: b.
6.- Subhumeral stria. Usually not keeled: a; usually keeled: b; usually slightly keeled: c.
7.- Number of clypeal teeth. No teeth: a; bidentate: b; quadridentate: c.
8.- Clypeal teeth separation. Narrowly separated: a; widely separated: b.
9.- Separation between proepisternum and proepimeron. Without a keel: a; keeled: b; slightly keeled: c.
10.-Proepisternum. Shallowly excavated: a; excavated: b.
11.-Prescutellar impression. Usually not marked: a; usually marked: b.
12.-Dorsal surface. Usually not granulated: a; usually granulated: b.
13.-Granules. Simple: a; like shining spots: b; flattened: c; elongated: d.
14.-Pronotum. Without punctuation: a; with punctuation: b.
15.-Protibia straightly truncate: a; obliquely truncate: b.
16.-Eyes. Narrow: a; wide: b.
17.-Metatibia. With one spine: a; with two spines: b.
18.-Separation between gula and submentum. Narrow "V": a; wide "V": b; arched: c.
19.-Elytral external striae. As deep as the internal ones: a; deeper than the internal ones: b
20.-Dorsal eye margin. With border: a; without a border: b.
21.-Dorsal eye margin. Bordered by a wide flat band: a; bordered by a raised fold: b.
22.-Ventral clypeal structure. With a tooth: a; without a tooth: b.
23.-Protibia. Not widened along its internal margin: a; widened along its internal margin: b.
24.-Mesosternum. Short: a; very wide; b.
25.-External margin of the clypeo-genal suture. Straight or slightly pointed: a; with an evident tooth: b.
26.-Lateral pronotal margin. Usually not serrated: a; usually serrated: b.
27.-Posterior angle. Pointed: a; blunt: b.
28.-Elytral margins. Slightly curved upwards behind the humeral angle: a; strongly curved upwards behind the humeral angle: b.
29.-Elytral colour. Orange: a; not orange: b.

?= Character not applicable.

TABLE 2

Character distribution in the North American Canthonina species

Melanocanthon punctaticollis (Schaeffer)	BAABAACBAAABBBAABAAABABAAABAB
Melanocanthon nigricornis (Say)	BAABAACBAAABCBAABAAABABAAABAB
Melanocanthon granulifer (Schmidt)	BAABAACBAAABABAABAAABABAAABAB
Melanocanthon bispinatus (Robinson)	BAABAACBAAABDBAABAAABABAAABAB
C. (Boreocanthon) simplex LeConte	BAABAACBAAABBBAAAAAAABBBABABAB
C. (Boreocanthon) ateuchiceps Bates	BAABBBCBAAAA?BAAAAAAAABBABABAB
C. (Boreocanthon) depressipennis LeConte	BAABBACBAAABAAAAAAAAABBBABBBAB
C. (Boreocanthon) ebenus (Say)	BAABBACBAAABAAAAAABABBBABBBAB
C. (Boreocanthon) praticola LeConte	BAABBBCBAAABAAAAAABABBBABBBAB
C. (Boreocanthon) integricollis Schaeffer	BAABBBCBAAABBBAAAAAAABBBABABAB
C. (Boreocanthon) mixtus Robinson	BAABBBCBAAABBBAAAAAAABBBABABBB
C. (Boreocanthon) lecontei Harold	BAABABCBAAABBAAAAAAAABBBABABAB
C. (Boreocanthon) melanus Robinson	BAABABCBAAABBBAAAAAAABBBABABAB
C. (Boreocanthon) probus Germar	BAABBCCBAAABBBAAAAAAABBBABABAB
C. (Boreocanthon) puncticollis LeConte	BAABBBCBAABBBBAAAAAAABBBABABAB
C. (Boreocanthon) coahuilensis Howden	BAABAACBAAAA?BAAAAAABBBAAABAB
C. (Canthon) obliquus Horn	BABBAAA?AABA?BAAAAAAAABBAABAB
C. (Canthon) chalcites (Haldeman)	BABBAABBAAABAAAAABAAABBAAABAB
C. (Canthon) vigilans LeConte	BABBAABBAAABAAABABAAABBAAABAB
C. (Canthon) imitator Brown	BABBAABAAAABBAAAABAAABBAAABAB
C. (Canthon) pilularius (Linnaeus)	BABBAABBAAABBAAAABAAABBAAABAB
C. (Canthon) humectus (Say)	BABBAABBBBABABAAACAAABBAAABAB
C. (Canthon) indigaceus Harold	BABBAABAAAAA?BAAACAAABBAAABAB
C. (Canthon) cyanellus LeConte	BABBABCACABA?BBAACAAABBAAABAB
C. (Canthon) morsei Howden	BBBBAABACAAA?BBAACAAABAAAABAB
C. (Glaphyrocanthon) subhyalinus Harold	BBAAAABABBAA?BBAACAAABAAAAAAA
C. (Glaphyrocanthon) euryscelis Bates	BBAAAABABBAA?BBAACAAABAAAAAAB
C. (Glaphyrocanthon) viridis (de Beauvois)	BBABAABABBAA?BAAACAAABBAAAAAB
C. (Glaphyrocanthon) femoralis (Chevrolat)	ABABAACABBAA?AAAACAAABAAAAAAB



Frontispiece. Photograph of habitus of *Entomoantyx cyanipennis* (Chaudoir), dorsal aspect. Mexico, Veracruz, NE Catemaco, Los Tuxtlas Biological Station (CNCI). Standardized Body Length = 4.4 mm.

THE MIDDLE AMERICAN GENERA OF THE TRIBE OZAENINI WITH NOTES ABOUT THE SPECIES IN SOUTHWESTERN UNITED STATES AND SELECTED SPECIES FROM MEXICO

George E. Ball
Department of Entomology
University of Alberta
Edmonton, Alberta
Canada T6G 2E3
and
Scott McCleve
2210 13th Street
Douglas, Arizona
85607 U.S.A.

Quaestiones Entomologicae
26: 30—116

ABSTRACT

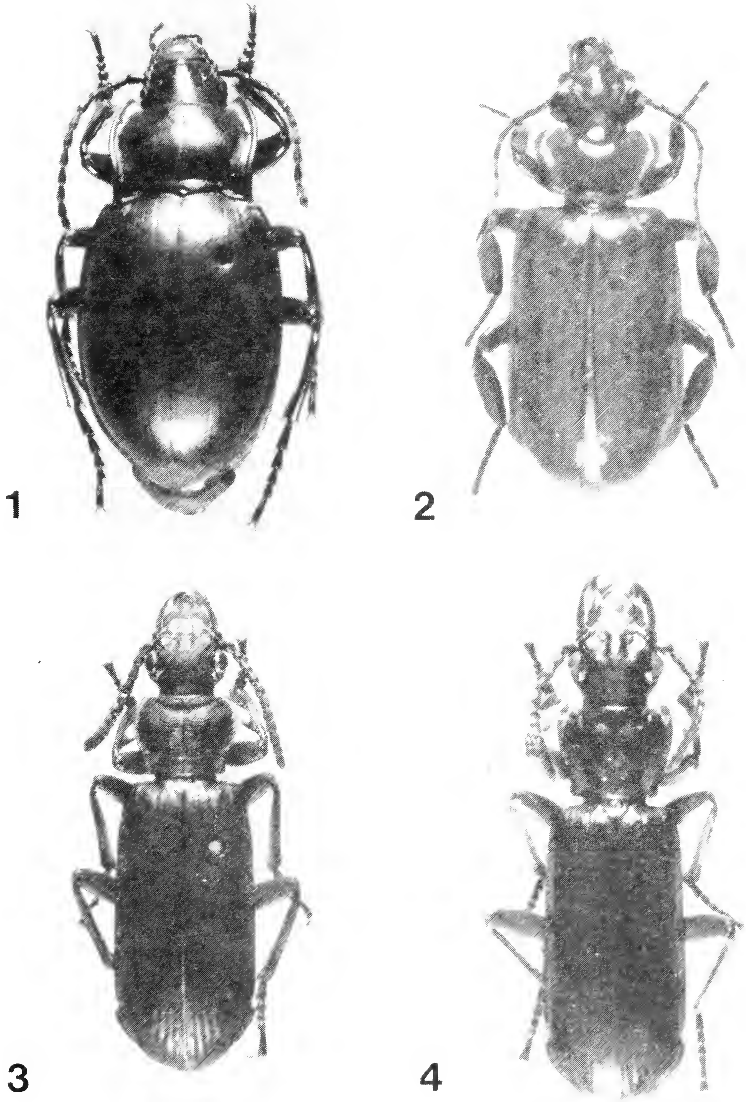
Based on structural features of adults, the following new taxa are described: Entomoantyx, *new genus (type species—* Ozaena cyanipennis *Chaudoir, 1852); and* Pachyteles *(*sensu stricto*)* enischnus, *new species (type locality— México, Jalisco, near Ixtapa). Combined in a single genus, but ranked as subgenera are:* Pachyteles *(*s. str.*) Perty, 1830 (type species—* P. striola *Perty, 1830);* Goniotropis *Gray, 1832 (type species—* G. braziliensis *Gray, 1832), with its junior synonym,* Scythropasus *Chaudoir, 1852 (type species—* S. elongata *Chaudoir, 1852); and* Tropopsis *Solier, 1849 (type species—* T. marginicollis *Solier, 1849). The following species-level synonymy is proposed, with the senior synonym and thus valid name listed first for each combination:* Pachyteles *(*Goniotropis*)* parca *LeConte, 1884 (type area— U.S.A., Arizona)* = P. beyeri *Notman, 1919 (type locality— México, Baja California Norte, San Felipe);* Pachyteles *(*s. str.*)* gyllenhali *(Dejean, 1825) (type area— Cuba)* = P. verticalis *(Chaudoir, 1848) (type area— Colombia)* = P. testaceus *Horn, 1868 (type locality— Fort Grant,Arizona U.S.A.); and* Ozaena lemoulti *Bänninger, 1931 (type locality— French Guiana, St. Jean du Maroni)* = O. halffteri *Ogueta, 1965b (type locality—México, Veracruz, Tlapacoyan). The genera are characterized in terms of adults, using defensive secretions and structural features, including chaetotaxy, antennae, mouthparts (labrum, mandibles, maxillae, and labium), antenna cleaner of the fore tibia, male genitalia, ovipositor, and internal genitalia of females. To facilitate future phylogenetic analysis, transformation series were postulated for each character, using the Metriini (genus* Metrius *Eschscholtz) as out-group. This provided a linear series for the genera, from most like to least like* Metrius*:* Entomoantyx*;* Pachyteles *(*s. lat.*);* Physea*;* Ozaena*; and* Platycerozaena. Ozaena *and* Platycerozaena *are postulated to be sister groups, but relationships to one another of the remaining genera have not been postulated. The following species are characterized, in terms of adult features and geographical distribution:* Entomoantyx cyanipennis *(Chaudoir);* Physea hirta *LeConte, 1853 and* P. latipes *Schaum, 1864;* Pachyteles *(*Goniotropis*)* parca *LeConte,* P. kuntzeni *Bänninger, and* P. elongatus *(Chaudoir);* Pachyteles *(*s. str.*)* gyllenhali *Dejean,* P. enischnus, *new species, and* P. mexicanus *(Chaudoir, 1848); and* Ozaena lemoulti *Bänninger. A key is provided to these species and to the Middle American genera. Based on general zoogeographic theory for Middle America, the following hypothesis is developed to explain the distribution patterns of the Middle American genera and the species* *whose ranges either enter the United States or are near the U.S.-Mexican border: Middle America was entered at various times during the Tertiary by the ancestor of* Entomoantyx *and members of each of the genera; i.e., the only genus to evolve as such in Middle America was* Entomoantyx. *Most of the extant species differentiated in Late Tertiary time as east-west vicariants, as a result of the influence of climatic change and mountain building on the ranges of the ancestral populations. Two species, P* gyllenhali *and* O. lemoulti, *arrived in the northern areas comparatively recently, each becoming widespread during Pleistocene time.*

TABLE OF CONTENTS

INTRODUCTION

The roots of this study extend back in time to the early 1950's, when the first author found in the collections of the U. S. National Museum of Natural History a specimen of *Ozaena* collected in a Plant Quarantine Station at Nogales, Arizona. As far as was known then, this record represented a substantial range extension for the genus, and it seemed not unlikely that the specimen was an accidental import from the American tropics, to the south. Max Bänninger, at that time the foremost authority on Ozaenini, was consulted, and he reported the identity of the specimen as *Ozaena elevata* (*cf.* Bänninger, 1956: 400), a species otherwise known only from South America. The specimen was labelled by him as *Ozaena elevata* var.

In 1978, the second author collected a specimen of *Ozaena* at Peña Blanca, Pajarito Mountains, southern Arizona— a locality near Nogales, but far enough away to suggest that the species represented was indeed native to the area. Comparison of this specimen with the one taken at Nogales showed that the two were sufficiently similar to be regarded as conspecific. But, what species did they represent? Having entered into discussion about ozaenines in the United States, we



Figs. 1—4. Photographs of habitus, dorsal aspect, of: 1, *Metrius contractus* Eschscholtz; U.S.A. California, Siskiyou County, Pickewish Campground (UASM); Standardized Body Length = 10.9 mm. 2, *Physea latipes* Schaum; México, Venedio (CASC); SBL = 11.1 mm. 3, *Pachyteles (Goniotropis) parca* LeConte; U.S.A., Arizona, Santa Cruz County, Santa Rita Mts., Madera Canyon; SBL = 10.9 mm. 4, *P.* (*Goniotropis*) *kuntzeni* (Bänninger); U.S.A. Arizona, Santa Cruz County, Peña Blanca (UASM); SBL = 15.2 mm.

5

6

7

8

Figs. 5—8. Photographs of habitus, dorsal aspect, of: 5, *P*. (*sensu stricto*) *gyllenhali* (Dejean); U.S.A., Arizona, Graham County, Aravaipa Canyon, 17.7 km. N. Klondyke (UASM); SBL = 4.4 mm. 6, *P*. (*sensu stricto*) *enischnus*, new species; Mexico, Jalisco, nr. Ixtapa, gallery forest SBL = 7.0 mm. 7, *Ozaena lemoulti* Bänninger; U.S.A., Arizona, Pajarito Mts., Peña Blanca; SBL = 18.0 mm. (SMCC); 8, *Platycerozaena brevicornis* (Bates); French Guiana Monte de Kaw, Piste de Kaw, Km. 3 (UASM); SBL = 11.4 mm.

asked this question of one another some seven years ago. Encouraged by Terry L. Erwin, we decided to answer it, and at the same time to put into a more general context the ozaenines inhabiting the southwestern United States.

In the course of our preliminary investigation, we found striking differences among the genus-level taxa represented in the United States, and these discoveries led us into an investigation of the Middle American ozaenine genera. Gradually, the emphasis of the study changed from a species-level faunal study to a generic treatment, with data about these species appended.

This paper is intended to achieve two goals: first, to establish the basis for a phylogenetic analysis of the ozaenine genera of the world; and second, to summarize the information that can be gleaned from knowledge of ozaenine species at the northern limits of the Tribe in the New World. The only questions we attempt to answer are two: first, proximity of relationships of ozaenines and the genus *Metrius* Eschscholtz, made necessary by the potential out-group status of the latter; and two, the original question about the identity of the specimens of *Ozaena* that led to this study. Darlington's (1950) demonstration of close relationships between ozaenines and paussines is so well established as to be unchallengeable. The principal matter here is to establish at the generic or genus-group level the propinquity of ancestry of the two tribe-level groups.

MATERIAL AND METHODS

Material

We studied about 400 specimens of Metriini and Ozaenini, and representatives of several paussine genera. The material is in the collections noted below. Each collection is designated in the text by a coden; these are listed below, in alphabetical order, in association with the names and addresses of the institutions represented. Names of curators are indicated in parentheses.

AMNH- Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York, 10024, U.S.A. (L. H. Herman).
ASUT- Department of Zoology, Life Sciences Center, Arizona State University, Tempe, Arizona 85281, U.S.A. (F. Hasbrouck).
BMNH- Department of Entomology, British Museum (Natural History), Cromwell Road, London, SW7 5BD, United Kingdom. (N.E. Stork).
CASC- Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A. (D.H. Kavanaugh)..
CISC- California Insect Survey, Division of Entomology, University of California, Berkeley, California, 94720, U.S.A. (J. Chemsak)..
CNCI- Canadian National Collection of Insects, Biosystematics Research Centre, Agriculture Canada, Ottawa, Ontario, K1A 0C6. (J. M. Campbell).
CUIC- Department of Entomology, Comstock Hall, Cornell University, Ithaca, New York, 14850, U.S.A. (J.K. Liebherr).
EGRC- Edward G. Riley Collection, Department of Entomology, Texas A & M University, College Station, Texas 77843, U. S. A.
ETHZ- Entomologische Institut, Eidgenossische Technische Hochschule-Zentrum, Universitätstrasse 2, CH-8006, Zürich, Switzerland (W. Sauter).
FSCA- Florida State Collection of Arthropods, Division of Plant Industry, 1911 34th Street, S.W., P.O. Box 1269, Gainesville, Florida, 32602, U.S.A. (R.E. Woodruff).

MCZC- Department of Entomology, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, 02138, U.S.A. (S.R. Shaw; D.R. Maddison).
MCZC Fall- H.C. Fall Collection, MCZC, address as above..
MNHP- Entomologie, Museum National d'Histoire Naturelle, Paris 75005, France. (H. Perrin)..
OSUC- Ohio State University Collection of Insects and Spiders, 1735 Neil Avenue, Columbus, Ohio, 43210, U.S.A. (C.A. Triplehorn).
SMCC- Scott McCleve, 2210 13th Street, Douglas, Arizona, 85607, U.S.A.
TAIU- Department of Biology Collections, Texas A&I University, Kingsville, Texas, 78363, U.S.A. (James A. Gillaspy).
TAMU- Department of Entomology, Texas A&M University, College Station, Texas, 77843, U.S.A. (Horace R. Burke).
UASM- Strickland Entomological Museum, Department of Entomology, University of Alberta, Edmonton, Alberta, Canada, T6G 2E3.
USNM- United States National Entomological Collection, Department of Entomology, United States National Museum of Natural History, Washington, D.C., 20560, U.S.A. (T.L. Erwin).
ZMHB- Museum für Naturkunde der Humboldt Universität zu Berlin, Bereich Zoologisches Museum, Invalidenstrasse 43, DDR-1040 Berlin (F. Hieke).

Methods.

Methods were standard, involving visual comparison of structural features, using magnifying equipment from an 8X hand lens to stereobinocular microscopes to a Cambridge Scanning Electron Microscope. Data were recorded in print, as line drawings, and as photographs.

Measurements.— These were made with a Wild stereobinocular microscope Model M-5, at 25X magnification. They were taken to determine size and proportions.

Length is expressed as Standardized Body Length, determined as the sum of length of: head (from mandibular condyle to posterior margin of compound eye); pronotum (along mid-line); and elytra (along the suture, from apex of scutellum to apex of elytra). Width is maximum transverse width of elytra. Measurements presented in the species descriptions are of the smallest and largest males and females, as determined by visual inspection of the material at hand. The values obtained are thus rough approximations of total range in body size.

Ranking.— Used are subfamily, tribe, genus, subgenus and species. For the higher ranks, we accepted those proposed by Bänninger (1927), Kryzhanovskij (1976), and Erwin (1979a). For genus and subgenus, we sought major gaps in continuity of variation of structural features. The resulting taxonomic treatment is thus conservative.

Relationships.— Statements about this topic are based on inferred relative propinquity of descent, as determined by shared derived features. As out-group, we used the monobasic tribe Metriini. Because of our deliberately limited data base, we did not attempt a formal phylogenetic analysis of the taxa.

Species are regarded as evolving units reproductively isolated from other such units, the gaps being judged by discontinuity in structural features.

HISTORICAL ASPECTS

Tribal-level Synonymy

Tribe OZAENINI

"La cinquieme division" (in part) Latreille, 1817: 189.

Bipartis (in part) Latreille and Dejean, 1822: 79.—Latreille, 1829: 386.

Scaritides (in part) Dejean, 1825: 356.— Dejean and Boisduval, 1829: 230.

Brachinides (in part) Audouin and Brullé, 1834: 240.— Chenu, 1851: 87.

Ozenides Lacordaire, 1854: 154, 155.— Chaudoir, 1868: 43.

Ozaenidae Hope, 1838: 107.— LeConte, 1861: 5, 14.— Jeannel, 1941: 89.— 1946: 46 .— Regenfuss, 1975: 283.

Ozaeninae Bates, 1881: 24.— Winkler, 1924: 83.— Crowson, 1955: 6.— Basilewsky, 1962: 291.— Nagel, 1979a: 9, 10, 11.— 1979b: 15.— Crowson, 1981: 502, 504.

Ozaenini Schaum, 1860: 773.— LeConte, 1861: 14.— Horn, 1881: 124, 128.— LeConte and Horn, 1883: 23.— Sloane, 1920: 118.— Leng, 1920: 49.— Sloane, 1923: 242.— Csiki, 1927: 425.— Bänninger, 1927: 177.— Andrewes, 1929: 162.— van Emden, 1942: 24.— Blackwelder, 1944: 23.—Darlington, 1950: 49.— Ball, 1960: 94.— Bell, 1967: 105.— Lindroth, 1969: XXII.— Hlavac, 1971: 57.— Kryzhanovskij, 1976: 82, 87.— Eisner *et al.*, 1977: 1385.—Reichardt, 1977: 377.— Ball, 1979: 91, 95, 100.— Ward, 1979: 185, 186, 188, 190.— Moore, 1979: 198.— Goulet, 1979: 205.— Thompson, 1979: 212, 226, 231, 232.— Erwin, 1979b: 481, 557, 583, 591.- Erwin and Sims, 1984: 374.— Ball, 1985: 24.— Erwin, 1985: 451, 467.— Stork, 1985: 1113.

Ozaenina Iakobson, 1906: 316.— Bousquet, 1986: 378.

Mystropomini Horn, 1881: 116-117.— Sloane, 1923: 246.

Mystropominae Dupuis, 1911: 2.

Mystropomitae Jeannel, 1946: 47.

Paussidae (in part) Crowson, 1955: 6.— Deuve, 1988: 176.

Paussitae (in part) Erwin and Sims, 1984: 374.— Erwin, 1985: 467.

Paussinae (in part) Moore, in Moore *et al.*, 1987: 26.

Classification and Relationships

Tribal level.— Latreille (1817: 189) included *Ozaena* in his fifth division of the Carabiques, which included also "Les Morions", "Les Aristes", "Les Harpales", "Les Feroniens"," Les Licinines", "Les Badistes", and "Les Panagees". Latreille and Dejean (1822), Dejean (1825), and Dejean and Boisduval (1829) included *Ozaena* in the Bipartis, along with the scaritines and genus *Morio*n Latreille. Dejean (1825: 355) stated implicitly, however, that *Ozaena* was an aberrant element, and later authors (Audouin and Brullé, 1834, and Chenu, 1851) included the ozaenines with the brachinines and various lebiomorphs. In part, this association was based on the crepitating behavior of adults ozaenines and brachinines, though the diagnostic feature given was habital— adults with rather thick bodies.

Hope (1838) first recognized ozaenines as a distinct assemblage, though he included with them *Nomius* Castelnau, *Melisodera* Westwood, and *Catapiesi*s Brullé. Hope neglected to give reasons for erecting the Ozaenidae. Lacordaire (1854) followed suit, including in the group eight ozaenine genera and *Nomius*, characterized in part on a reduced mesosternum so that the mid-coxae are in contact with one another. He noted also the posterolateral elytral flanges, and that they did not occur in *Nomius*.

Schaum (1860) did not treat the Ozaenini in detail, though he (*l.c.*, p. 773) located the group (as defined by Lacordaire) in the carabine assemblage (*i.e.*, adults with mid-coxal cavities open) and in a sub-group including Omophronini, Elaphrini, Carabini, Loricerini, Promecognathini, and Mormolycini. He did not place them in the sub-group that followed that included the Scaritini, Siagonini, and Hiletini, nor with the brachinines and other truncatipennian groups. This was indeed a radical departure in classification at that time, and quite appropriate.

Chaudoir (1868) provided a synopsis of the Ozaenini, bringing together information about all of the taxa previously described, and describing new genera and species. For the group diagnosis, he gave special emphasis to the reduced mesosternum that Lacordaire had recorded, and noted as well, following Schaum (1860) that the mesothoracic suture extended to the mid-coxae. He stated also his belief that the ozaenines should be placed between the brachinines and helluonines, where they had been placed by previous authors. Perhaps Chaudoir's most important contribution in this work was to identify the distinctiveness of *Ozaena dentipes* Olivier (type species of *Ozaena*), separating it from the other species that had been described in the genus, and transferring the latter to other taxa—principally to *Pachyteles* Perty.

Bates (1881: 24) placed the ozaenines about as Schaum had done, between loricerines and scaritines, in their own subfamily. In the same year, Horn arrayed the ozaenines in two tribes: Mystropomini and Ozaenini. The basis for this division was an error: Horn, while correctly recording that the middle coxal cavities were open in *Mystropomus*, . mistakenly stated that they were closed in the remaining genera of ozaenines. He placed the Ozaenini (minus *Mystropomus*) in the subfamily Harpalinae, near the Panagaeini. *Mystropomus* was left in the Carabinae, or first major division of the Carabidae. Although Bates (*l.c.*) had pointed out the error (Horn sent him his MS before it was published), he did so in such a gentlemanly manner that the point seemed to have been lost. Thus, LeConte and Horn (1883) and Leng (1920) followed Horn's arrangement. Dupuis (1911) also recognized the mystropomines as a group separate from the Ozaenini, at least implicitly. Because he treated the Metriinae in the same publication, evidently he accepted Horn's opinion about a close relationship between the latter and the mystropomines.

Sloane (1923: 246) noted Horn's mistaken interpretation of the thoracic structure of the Ozaenini (*sensu* Horn), and re-combined the latter with *Mystropomus*. He placed the re-constituted Ozaenini in his "Carabidae Clausae", along with Metriini, Migadopini, Scaritini, Siagonini, Enceladini, Promecognathini, Elaphrini, Loricerini, and Omophronini. Csiki (1927) and Andrewes (1929) followed Sloane's sequencing.

Bänninger (1927) revised the Ozaenini, providing a much more comprehensive treatment than Chaudoir's. He gave a clear tribal diagnosis and detailed description, based on adult external features of the known genera. He confirmed that the affinities of the Ozaenini were with the carabines (broad sense), and particularly with the Cicindisini, Nototylini, and Metriini. Among diagnostic features for the Ozaenini that he emphasized were the elytral flanges.

Kolbe (1927) hypothesized that ozaenines and paussids were closely related.

Van Emden (1942) characterized the larvae of the Ozaenini, emphasizing the unusual modifications of the urogomphi and posterior abdominal segments.

Jeannel (1941) included in his new taxon Isochaeta (based on the apical position of both fore tibial spurs): trachypachines, gehringiines, metriines, ozaenines, and paussines. However, he did not pursue the matter of relationships of any of these groups to one another. Nonetheless, one can see from the sequence of taxa that probably he considered the last three to be related to one another.

Darlington (1950: 48) re-asserted the basis for hypothesizing close relationship between paussids and ozaenines, noting that Kolbe was the first so to insist. Nonetheless, he retained the ozaenines as a separate tribe, and in effect treated the paussids as an informal taxon to include the Protopaussini and Paussini. Darlington did not comment about classification of the ozaenine genera, but he developed a detailed classification for the paussine genera.

Basilewsky (1962: 291) transferred the Protopaussini from the subfamily Paussinae to the Ozaeninae, on the basis of the plesiotypic unreduced antennal pedicel. He did not take into account the apotypic features shared by protopaussines and paussines.

Transformation series in a variety of character systems support adequately the hypothesis of monophyly of paussines and ozaenines. Crowson (1955) accepted this, but rather than treating this complex as a group within the family Carabidae, he chose to recognize the paussine complex as a separate family, including therein the Ozaenini.

While there is little doubt that the ozaenine-paussine complex is monophyletic, there is some doubt that the Ozaenini are monophyletic relative to the paussines, *i.e.*, some extant ozaenine genus might be the sister group of the Protopaussini + Paussini. So, the more distal part of the reconstructed phylogeny of this complex is not resolved at the tribal level. What about the more basal part: is there an extant sister group for the ozaenine-paussine complex?

Luna de Carvalho (1959) pointed out the marked similarity between the genitalia of metriines and ozaenine-paussine males. Bell (1967) united in his new taxon Septisternia the tribes Metriini, Ozaenini and Paussini (implicitly Protopaussini + Paussini), implying thereby that *Metrius* was the sister group of the ozaenine-paussine complex. This hypothesis was accepted by Regenfuss (1975) and by various subsequent authors.

On the basis of superficial examination of larval features, Goulet (1979: 205) suggested that "metriines are simply ozaenines", and this opinion of striking similarity was borne out by Bousquet's (1986) detailed study of the larval characteristics of *Metrius*.

Similarity between adults of *Metrius* and those of the ozaenine-paussine complex in complex defensive secretions and their delivery systems provide more evidence of close relationships of these taxa (Eisner and Aneshansley, 1981).

Thus, metriines and the ozaenine-paussine complex can be treated as a monophyletic assemblage. Without going into detail here, we assert that the Metriini is the sister group of the hypothetical ancestor of the ozaenine-paussine complex.

Erwin and Sims (1984) and Erwin (1985) hypothesized a close relationship among the supertribes Metriitae (including Metriini, only), Paussitae (including Ozaenini + Paussini and four other tribes) and Brachinitae. These supertribes were included in the subfamily Paussinae. As indicated above, metriites belong with the paussite assemblage. Thus only two main lineages are represented in the Paussinae: Paussitae and Brachinitae. Are these two really sister groups? In addition to Erwin and Sims (*l.c.*), Eisner *et al.* (1977), Bousquet (1986) and Deuve (1988) have stated so. Others (Forsyth, 1972; Crowson, 1981, p. 503, Bell, 1983, p. 595, and Moore *et al.*, 1987, p. 26 and 48) indicate either implicitly or explicitly their belief that the similarity between brachinites and paussites, in complex defensive secretions and complex delivery systems— the best evidence available for close relationship— are the result of convergence. We favor the latter opinion.

Similarities between brachinites and Psydriformes (*sensu* Erwin, 1985) are in apotypic features of several systems that seem to be functionally independent (thoracic structure, organization of the antennal cleaner of the fore tibia, structure of the male genitalia and ovipositor). It seems to us that the best explanation for this array of similarities is inheritance from a common ancestry. Thus, we hypothesize that the brachinites are either members of the Psydriformes, or at least are the sister group of this group of carabids that, overall, is more highly derived than is the ozaenine-paussine complex.

Incredible as it seems, then, the elaborate defensive system of brachinites and paussites must have evolved independently if the similarities between brachinites and psydriforms are indicative of close relationship— as we hypothesize. Thus, there is a clear conflict of evidence. This conflict must be resolved, in terms of additional evidence yet to be found that will tip the balance one way or the other. Forbes (1926: 59) in his monumental publication about wing folding, pointed out the similarity between *Brachinus* and *Passus* adults in their distinctive folding pattern of the hind wings. He believed that this similarity did, in fact, indicate relationship (personal communication). It remains to be determined, however, if other brachinines and paussines have this same form of wing folding, and it remains to be determined, as well, if the pattern is plesiotypic or apotypic in the Carabidae. This lead is worth pursuing.

The question of ranking of the metriine + ozaenine + paussine complex remains to be answered. Erwin and Sims (*l.c.*) and Erwin (*l.c.*) recognize two supertribes, as noted above. Bousquet (1986: 378) proposes recognition of one tribe, the Paussini, to include two subtribes— Ozaenina and Paussina (Metriini + Protopaussini + Paussini of authors). We favor treating this complex as a subfamily, with three tribes, only: Metriini, Ozaenini, and Paussini. (We exclude thereby Nototylini, and Cicindisini that were included by previous authors). If we did not use the rank of subfamily in the Carabidae, we would follow Bousquet in his system of ranking.

The history of classification of the Ozaenini has been one of surprising discoveries and recurrent themes. The most surprising discovery is that of close relationship between metriines and ozaenines+paussines. It was presaged by Horn (1881: 117), when he pointed out the similarities in structural features between *Mystropomus* . and *Metrius*. However, this lead was not followed for many years. The recurrent theme is the relationship between ozaenines and scaritines on the one hand, and between paussines (present sense) and brachinines, on the other. The linear arrangement by Erwin (1985: 467) is very similar in part to that presented in the past, with ozaenines either in (Dejean, 1825) or near (Schaum, 1860) a complex including the scaritines, and either in (Audouin and Brullé, 1834) or near (Chaudoir, 1868) the brachinines. We conclude that our predecessors of the last century did rather well, though they had simpler equipment and lacked the knowledge of carabid diversity that we have now.

Generic level.— The only explicit attempt to classify the genera of Ozaenini was by Jeannel (1946: 46-48). Treating this assemblage as a family, he recognized three subfamilies: the monogeneric Australian Mystropomitae and Neotropical Physeitae, and the Neotropical-Afrotropical-Oriental Ozaenitae to include all of the remaining genera. For the Ozaenitae, he recognized three tribes: the Oriental Eustrini, including *Eustra* Schmidt-Goebel and *Dhanya* Andrewes; the monogeneric Neotropical Pachytelini for the genus *Pachyteles* Perty; and the Neotropical-Afrotropical-Oriental Ozaenini for the remaining genera.

For the Afrotropical-Madagascan fauna, Jeannel erected the subgenus *Afrozaena*, and included it, *Sphaerostylus* Chaudoir, and *Pseudozaena* Castelnau as subgenera of the genus *Pseudozaena*. Basilewsky (1962: 291-293) accepted implicitly Jeannel's classification, but added the Protopaussini to the Ozaenidae (treated by Basilewsky as a subfamily). However, he disagreed with Jeannel's treatment of *Pseudozaena*, ranking each of the three subgenera as a genus, and reranking *Itamus* Schmidt-Goebel as a genus separate from *Pseudozaena* (*sensu stricto*).

For the classification of genera, we agree that *Mystropomus* should be placed in a higher taxon of its own (as a subtribe), at the base of the tribe. The evidence that we have seen suggests that *Ozaena* and its close relative, *Platycerozaena* Bänninger, are not closely related to any of the other ozaenine genera, and we think that *Pachyteles* may be a plesiotypic sister group to at least some of the Old World genera. *Physea* and its close relative *Physeomorpha* Ogueta,are abundantly distinctive in features of adults, some of which indicate marked primitiveness. Overall though, we think that this group is not far removed from the pachyteline assemblage.

In the light of these observations, we cannot offer much support for Jeannel's classification of the ozaenine genera, though we have nothing to put in its place. See also Stork (1985: 1120). We think it best to avoid a formal classification of these genera at this time, though we realize that preparation of such a classification must be a high priority for future workers on this tribe.

COMPARATIVE MORPHOLOGY

Structural and Biochemical Features

In this section, we describe and compare in an evolutionary context, microsculpture, various setal patterns, structures, and defensive secretions useful in characterizing the genera of ozaenine carabids.The major purpose of this section is to explain the details of character complexes which either have not been used extensively in classifying ozaenines, or have been used only superficially. As a working hypothesis, we accept the tribe Metriini (genus *Metrius* Eschscholtz) as out-group for the tribes Ozaenini and Paussini (*sensu lato*, including Protopaussini and Paussini *sensu* Darlington, 1950, or Paussidae Jeannel, 1946), which we believe are sister groups.

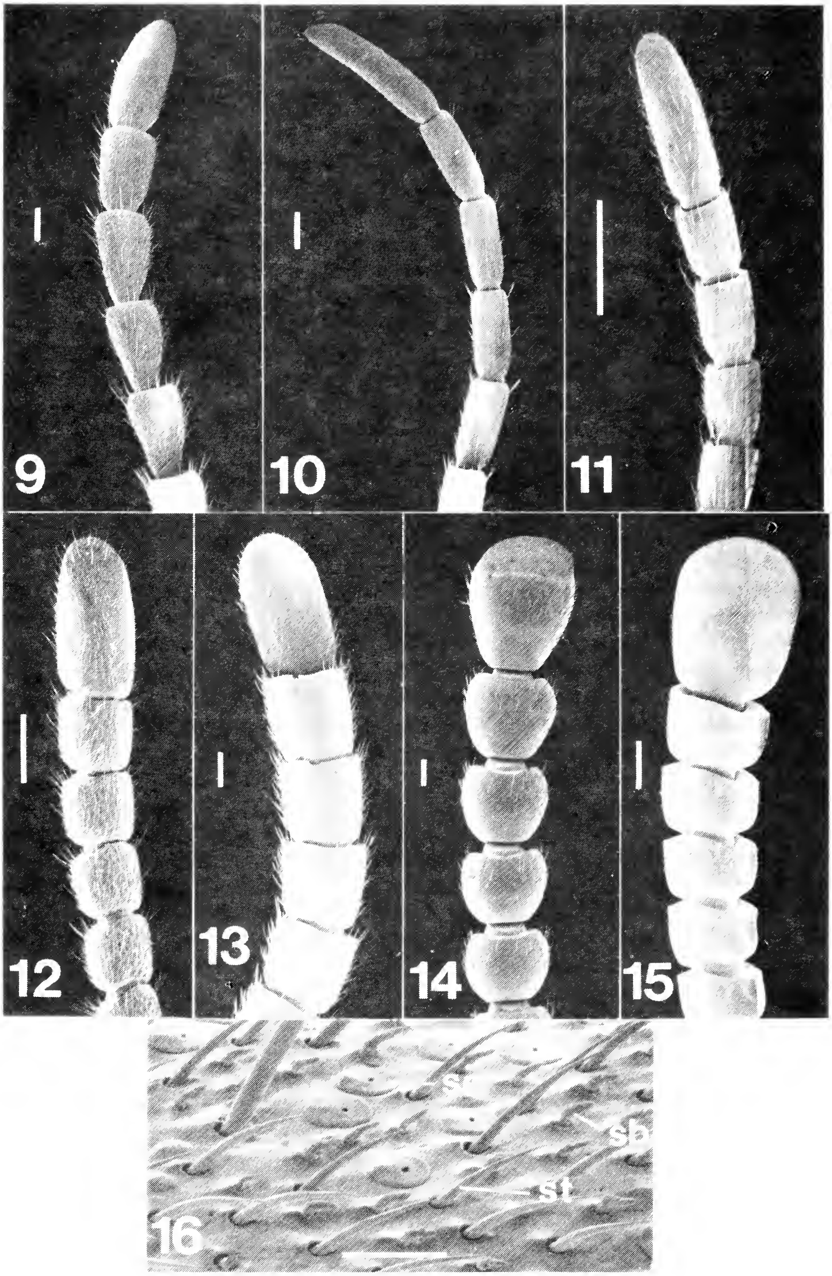
Microsculpture.— Adults of *Metrius* exhibit an isodiametric mesh pattern over almost the entire body surface. For the ozaenines, dorsal sculpture is isodiametric, with microlines either distinct or reduced and hard to see, or lost (Figs. 107A-C). For the ventral surface, mesh pattern varies from isodiametric to transverse, with most sclerites exhibiting a transverse pattern. No marked or taxonomically very useful trends were identified.

Setae on dorsal surfaces of head and pronotum.— *Metrius* adults have a generalized pattern of setal number: clypeus and vertex, one pair each; pronotum, two pairs of marginal setae. Ozaenines are more setose generally, or have fewer setae. Entomoantyx .i.Entomoantyx, new genus; adults have a pair of clypeal setae, a pair of supraorbitals, and several in a transverse row across the vertex. The lateral margins of the pronotum have three to five pairs of setae. Physea .i.Physea Brullé; and Pachyteles .i.Pachyteles Perty;adults have about 12 clypeal setae, one pair of supraorbitals, and several pairs of setae posterad the compound eyes. The lateral pronotal setae are several pairs, as in Entomoantyx.

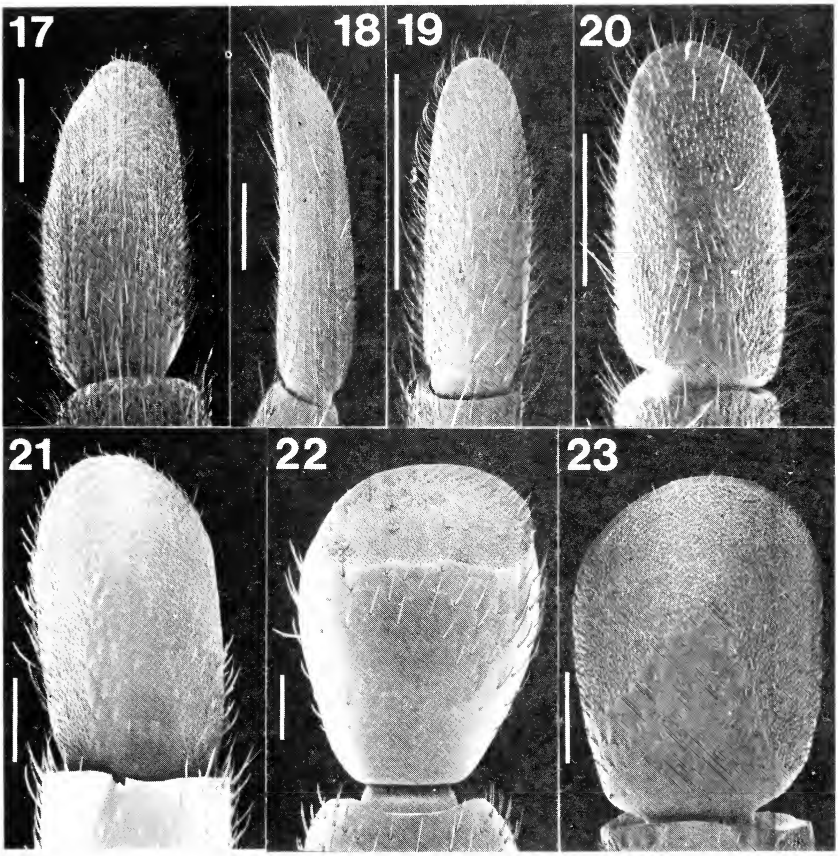
In contrast, adults of *Ozaena* and *Platycerozaena* lack clypeal, supraorbital and lateral pronotal setae.

The transformation series would seem to be:

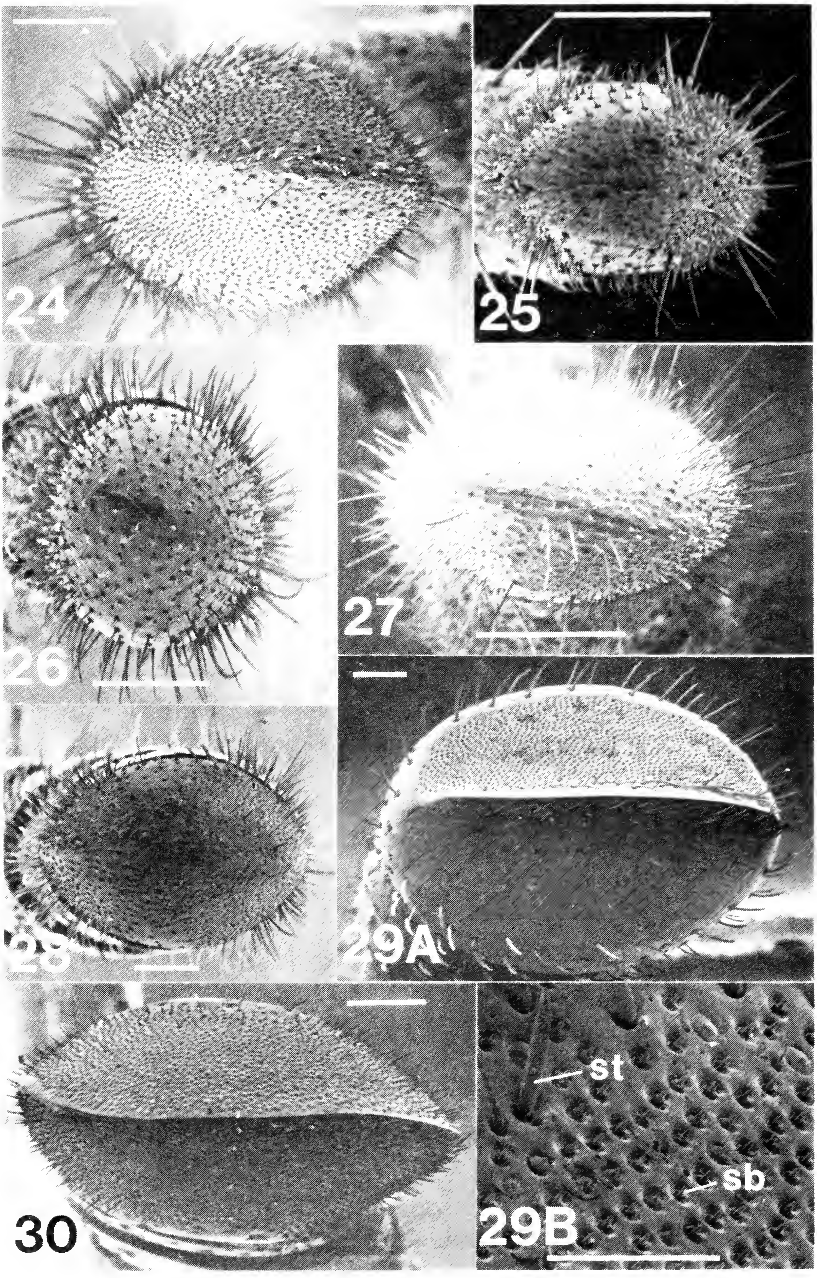
Ozaena ←——*Metrius* ——→*Entomoantyx*
Platycerozaena *Physea*
Pachyteles



Figs. 9—16. 9—15, Left antennomeres, 7—11, of: 9, *Metrius contractus* Esch.; 10, *Physea hirta* LeC.; 11, *Entomoantyx cyanipennis* (Chd.); 12, *Pachyteles* nr. *striola* Perty; 13, *Pachyteles kuntzeni* (Bänn.); 14, *Ozaena lemoulti* Bänn.; 15, *Platycerozaena panamensis* (Bates).16, Left antennomere 11, sense organs, of *Metrius contractus* Esch. Scale bars = 200 μm, Figs. 9-15; 20 μm, Fig. 16. Legend: sb- *sensillum basiconicum*; sc- *sensillum coeloconicum*; and st- *sensillum trichodeum*.



Figs. 17—23. Left antennomere 11, of: 17, *Metrius contractus* Esch.; 18, *Physea hirta* LeC.; 19, *Entomoantyx cyanipennis* (Chd.); 20, *Pachyteles* nr. *striola* Perty; 21, *Pachyteles kuntzeni* (Bänn.); 22, *Ozaena lemoulti* Bänn.; 23, *Platycerozaena panamensis* (Bates). Scale bars = 200 µm,



Figs. 24—30. Left antennomere 11, apical aspect, of: 24, *Metrius contractus* Esch.; 25, *Physea hirta* LeC.; 26, *Entomoantyx cyanipennis* (Chd.); 27, *Pachyteles* nr. *striola* Perty; 28, *Pachyteles kuntzeni* (Bänn.); 29, *Ozaena lemoulti* Bänn. .—A, lower mag.; B, higher mag., showing sense organs; 30, *Platycerozaena panamensis* (Bates). Scale bars = 100 µm, Figs. 24—29A, and 30; 50µm, Fig. 29B. Legend: sb- *sensillum basiconicum*; st- *sensillum trichodeum*.

Antennae.— Variation occurs in overall length, form of antennomeres, and distribution and frequency of types of sensilla. Overall length can be appreciated from examination of Figs. 1 to 8. These and Figs. 9 to 30 illustrate also differences in form and proportions of antennomeres. Note particularly the moniliform articles of Ozaena adults (Figs. 14 and 22), quadrate form of antennomeres 4-10 characteristic of *Pachyteles* (Figs. 12, 13, 20, and 21), and transverse antennomeres 4-10 characteristic of *Platycerozaena* (Fig. 15).

Antennomere 11 among Ozaenini differs from the more basal antennomeres in being longer (Figs. 10 and 11), and either as broad as (Figs. 12 and 13) or broader than (Figs. 14 and 22) the latter. Of special note are: slender curved antennomere 11 of *Physea* (Fig. 18), the basally constricted antennomere 11 of *Ozaena* (Fig. 22) and the very broad antennomere 11 of *Platycerozaena* (Figs. 15 and 23). Compared to Metrius (Fig. 17), antennomere 11 is narrow in *Physea* and *Entomoantyx*, slightly wider in *Pachyteles* (Fig. 20), and markedly wider in *Ozaena* and *Platycerozaena*.

Antennomere 11 exhibits differences in cross section also, which are best appreciated from an apical aspect (Figs. 24-30). For *Metrius* (Fig. 24), antennomere 11 is terete, without a sharply delimited apical ridge. For *Physea* and *Entomoantyx* (Figs. 25 and 26), antennomere 11 is nearly circular, and without a sharply differentiated apical ridge. For *Pachyteles* (Figs. 27 and 28) antennomere 11 is terete, but with a moderately sharply defined apical ridge. For *Ozaena* and *Platycerozaena* (Figs. 29A and 30), antennomere 11 is terete, with apical ridge sharply delimited as a carina: straight in *Ozaena* Fig. 29A), and sinuate in *Platycerozaena* (Fig. 30). The orientation of this carina is dorso-ventral.

Sensillar types of ozaenine antennomeres were identified through the publication of Zacharuck (1985: 25-26). Three types were recognized: trichodea (relatively long setiform hairs, st in Fig. 16); basiconica (relatively short and thick setiform hairs, sb in Fig. 16); and coeloconica (cones set in the floor of shallow depressions or pits in the cuticle, open to the outside through a small round hole, sc in Fig. 16). Only sensilla trichodea and basiconica are considered here.

Antennomeres 1 (scape) to 4 have few sensilla trichodea, and the intervening surfaces are relatively smooth. These antennomeres are not considered further. For antennomeres 5- 11, the surfaces bearing sensilla are more or less shagreened, the roughened appearance being the result of the raised cuticular rims around the bases of the sensilla.

Four types of distribution and frequency of sensilla are recognized.

Type a: sensilla trichodea numerous on antennomeres 5-11, each article with anterior and posterior faces with reduced setation at the middle, and in the triangle at the base of antennomere (Figs.9, 10, 12 and 13); sensilla basiconica numerous and rather long, ca. one-fifth length of sensilla trichodea, and confined to dorsal and ventral areas of antennomeres (*cf* Fig. 16). Taxa whose adults exhibit type a antennomeres are: *Metrius, Physea*, and *Pachyteles*.

Type b: for antennomeres 5-10, as in type a, above; for antennomere 11, toward apex, sensilla basiconica few and ordered in more or less parallel rows (Fig. 26); exhibited by *Entomoantyx* adults.

Type c (Fig. 29A-B): for antennomeres 5-10, sensilla trichodea and basiconica relatively few, basiconica very short, glabrous or nearly glabrous areas extensive; ventrally, or ventro-laterally, with small groups of sensilla basiconica; for antennomere 11, sensilla trichodea sparse dorso-ventrally, preapically, and a row each side of apical carina; about one-third of apex occupied by a dense concentration of sensilla basiconica. Type **c** is exhibited by *Ozaena* adults.

Type d (Fig. 23): for antennomeres 5-10, sensilla trichodea sparse and only about half length of those of types a-c; sensilla basiconica ventrally in dense groups, each side of a carina; antennomere 11 with relatively sparse, short sensilla trichodea apically, dorsally and ventrally, around triangular central area; sensilla basiconica very dense apically and along dorsal and ventral surfaces. Adults of *Platycerozaena* exhibit this sensillar type.

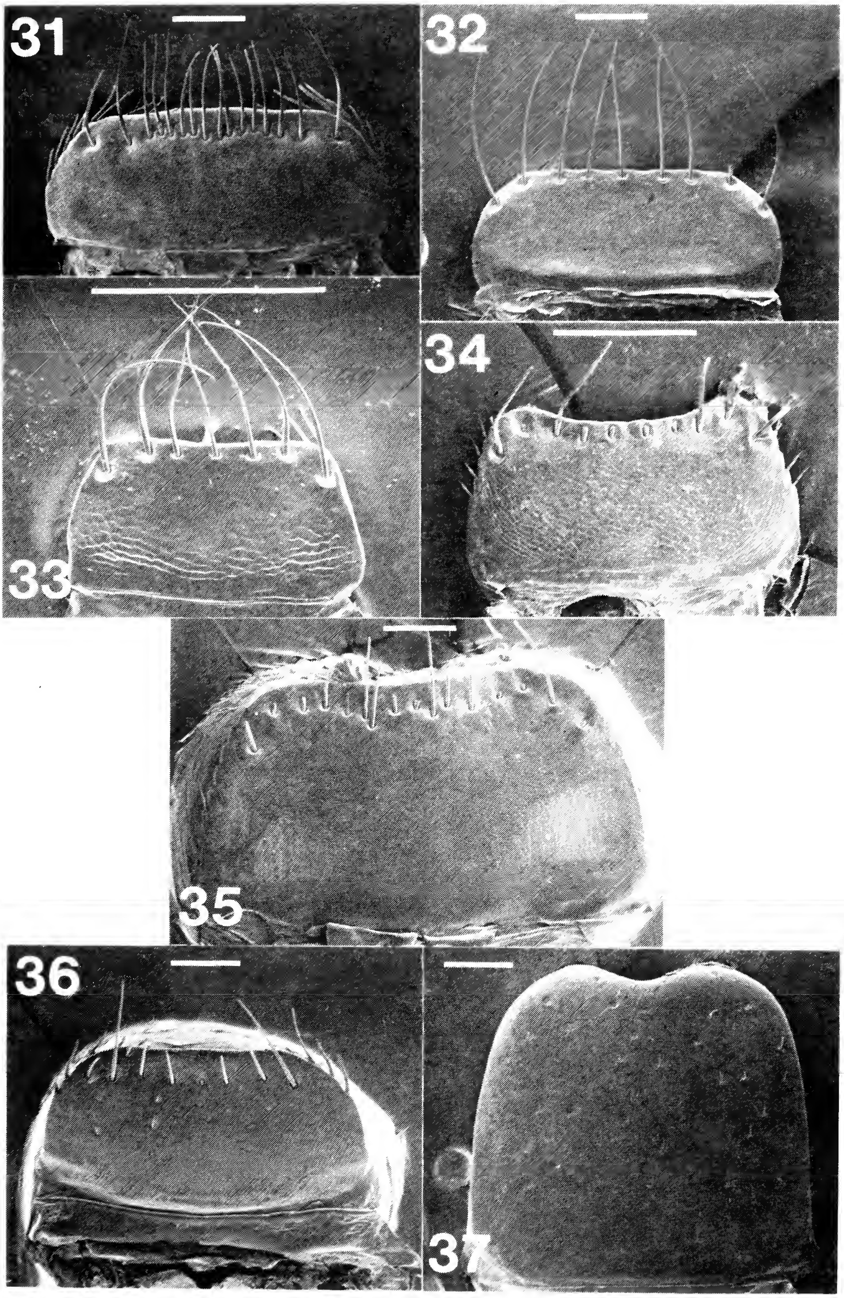
Based on extent of departure from the antennae of *Metrius*, these data suggest the following linear transformation series:

Metrius ———→*Physea*———→*Pachyteles*———→*Ozaena*
Entomoantyx *Platycerozaena*

Labrum.— This sclerite varies in form and setation. In form, it is transverse, i.e., wider than long, with the anterior margin truncate or nearly so (Figs. 31-33, 35 and 36), or broadly concave (Fig. 34), or elongate, with anterior margin notched (Fig. 37). Number of long preapical setae varies from 0 (*Platycerozaena*, Fig. 37) to 12 to 16 (*Metrius*, Fig. 31), with 7 to 12 intermediate (*Physea*, Fig. 32; *Entomoantyx*, Fig. 33; *Pachyteles*, Fig. 34; and *Ozaena*, Fig. 36). The highest number group is postulated as plesiotypic, since it is characteristic of the outgroup. Short setae (sensilla basiconica) are also evident on the dorsal surfaces of the labra of *Ozaena* and *Platycerozaena*. The data suggest the following branched transformation series:

Physea
Entomoantyx
↑
Metrius———→*Pachyteles*———→*Ozaena*———→*Platyceroz.*

Mandibles.— These are illustrated in Figs. 38 to 43, and characterized for each genus in Table 1. Mandibles of Carabidae have been described in several publications (*cf.* Shpeley and Ball, 1978; Forsythe, 1982; and Evans and Forsythe, 1985), and a detailed and more or less consistent nomenclature developed. The anterior incisor area, of varied width, terminates in the apical incisor tooth. The occlusal margin of the incisor is the terebral ridge or margin (**tm**, Figs. 38A-B). A terebral tooth (**tt**) is near the posterior part of the terebral margin. Below the tooth is the retinaculum (**r**, Fig. 38C), more or less prominent, with an anterior (**art**) and posterior (**prt**) retinacular tooth, joined by a retinacular ridge (Figs. 42A-B, 43E-F). The retinaculum is terminated by a groove, the premolar incision. Posterior to this incision is the molar area, divided or not by a molar incision: if divided, the anterior part of the molar area is the premolar (Figs. 38A-B, **pm**), the posterior part, the molar (Figs. 38A-B, **m**). Ventrally, various ridges occur in different taxa. In metriines and ozaenines, a ventral retinacular ridge (Fig. 39C, **vrr**) and a premolar ridge (Fig. 38C, **pr**) are recognized. A ventral groove (Fig. 38D, **vg**) of varied length bears a row of setae, the latter of varied length and density. The thicker lateral surface of each mandible contains a triangular depression, the scrobe. In *Metrius*, the scrobe bears a single long seta (Fig. 38A, **ss**); in ozaenines, it bears a single long seta (Fig. 40A) or a varied number of shorter setae (Figs. 39A and 41A). The dorsal surface is variously sparsely covered with setae shorter than those in the scrobe.



Figs. 31—37. Labrum, dorsal aspect, of: 31, *Metrius contractus* Esch.; 32, *Physea hirta* LeC.; 33, *Entomoantyx cyanipennis* (Chd.); 34, *Pachyteles* nr. *striola* Perty; 35, *Pachyteles kuntzeni* (Bänn.); 36, *Ozaena lemoulti* Bänn.; 37, *Platycerozaena panamensis* (Bates). Scale bars = 200 µm.

In all their features, the mandibles of *Metrius* adults are much like those of the still more primitive genus *Trachypachus*. Thus, we accept these features as plesiotypic. Mandibles of ozaenines are apotypic in the following features: terebral ridge short (not extended on to retinaculum); retinaculum reduced; and molar area not divided by an incision. The mandibles characteristic of all the genera examined, except *Platycerozaena*, exhibit additionally the following apotypic features: posterior retinacular tooth moderate to large, extended posteriorly; and ventral groove long. Considering the generally derived features of *Platycerozaena* and its close relationship to *Ozaena*, we believe that the seemingly plesiotypic conditions of the former genus (small posterior retinacular tooth and short ventral groove) are secondary losses, and are thus apotypic.

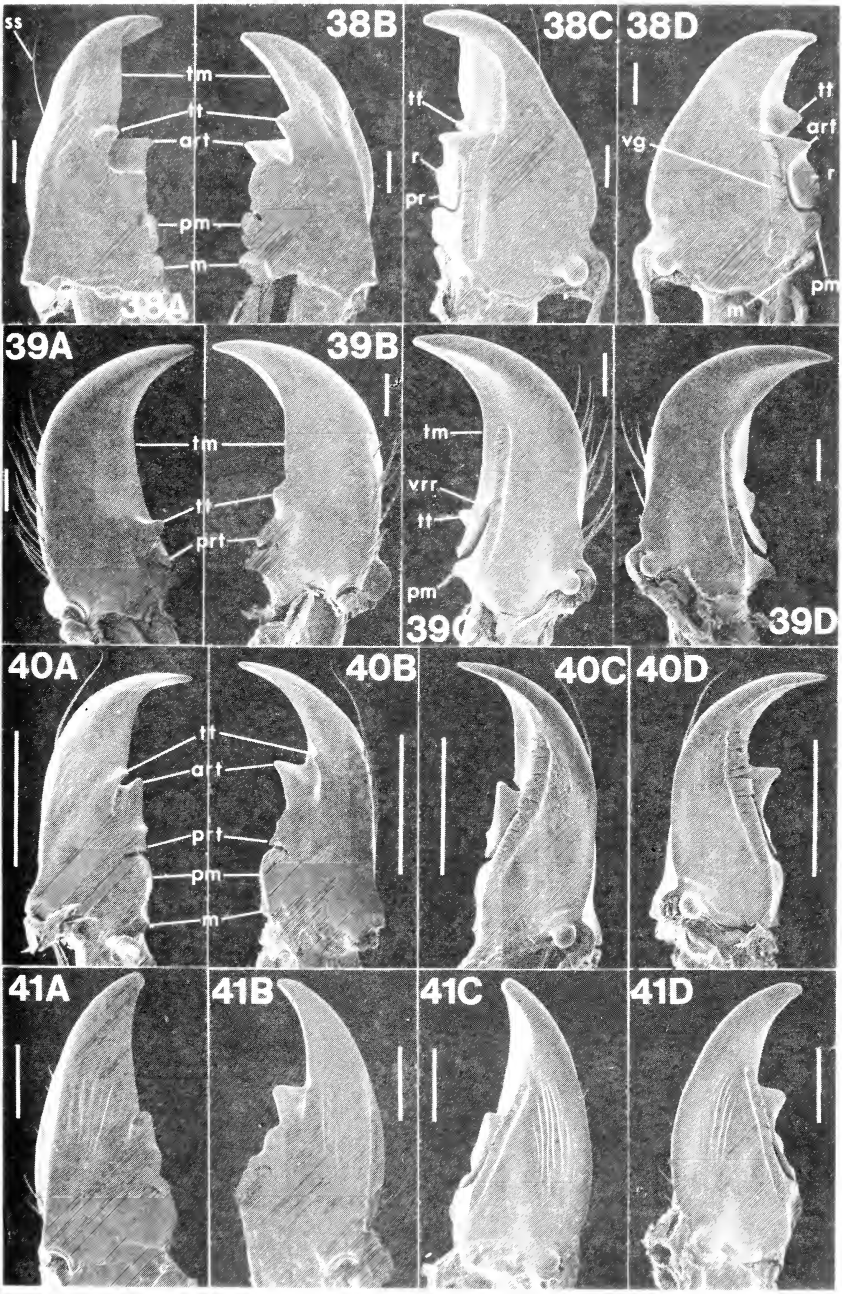
Within the Central American Ozaenini, we regard as most plesiotypic the mandibles of *Entomoantyx*: scrobe with single long seta, surface otherwise glabrous; and anterior retinacular tooth of the left mandible prominent. Most derived are the mandibles of *Physea*: falcate in form, and with the retinacular ridge reduced by loss of the anterior retinacular tooth. The mandibles of *Platycerozaena* also seem markedly apotypic, with broad, partially punctate dorsal surfaces, and somewhat reduced system of teeth and short ventral grooves. The mandibles of *Ozaena*, much like those of *Pachyteles*, are more derived in that the dorsal surfaces are punctate, as in *Platycerozaena*. We believe that the data presented are best summarized by the following branched transformation series:

Physea
↑
Metrius———→*Entomo.*———→*Pachytel.*———→*Ozaena*———→*Platycer.*

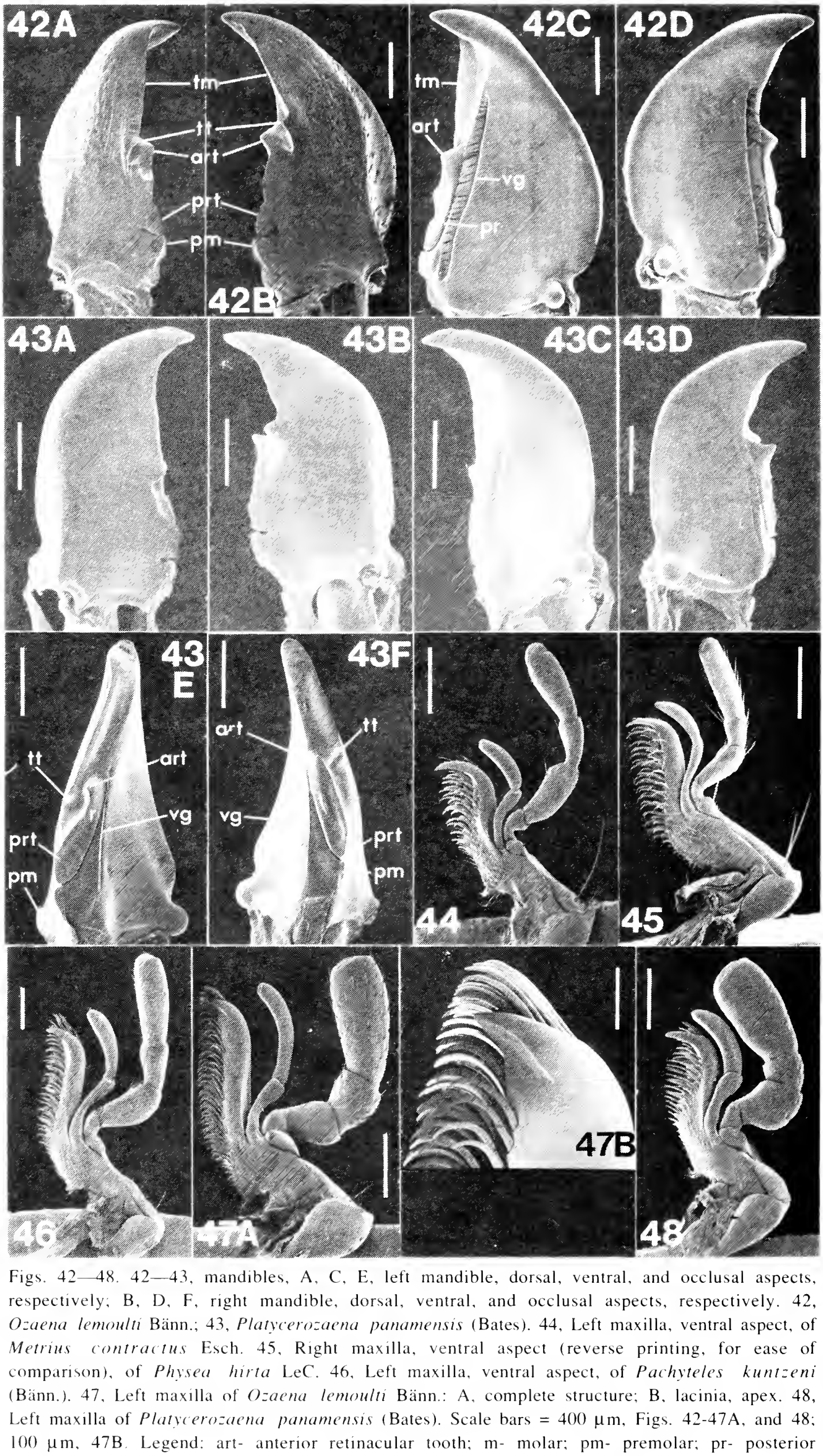
Nothing is known about feeding habits of adult *Metrius* and ozaenines, though the structural features of the mandibles and maxillae (see below) suggest that these beetles are "mixed feeders, ingesting food as fluid, semi-fluid, mush and fragments, or a mixture of all of them" (Evans and Forsythe, 1985: 122).

Maxillae.— Among ozaenines, these structures exhibit limited variation except in form of terminal palpomeres. For the Central American ozaenines, however, the more interesting variation is in details of the lacinia. Most taxa have a moderately long, sharp, slightly curved apical tooth and a moderately dense brush of marginal setae. Characteristic of *Physea* (Fig. 45) is a lacinia like that of *Metrius* (Fig. 44), with a long markedly curved apical tooth. The lacinia characteristic of *Ozaena* (Figs. 47 and 48) has a short, chisel-like, apical tooth, and a very dense brush of setae. Laciniae with fewer setae and longer teeth are more likely to be used as rakes to draw food particles into the mouth, whereas laciniae with more setae are more likely to be involved in a system of pre-oral digestion, with the dense setae serving to hold the digestive fluid used to liquefy partially the prey before ingesting it (Evans and Forsythe, 1985: 123). Certainly the most derived maxillae are those of *Ozaena*. The data seem to indicate the following linear transformation series:

Entomoantyx
Metrius———→*Physea*————→*Pachyteles*———→*Ozaena*
Platycerozaena



Figs. 38—41. Mandibles, A, C, left mandible, dorsal and ventral aspects, respectively; B, D, right mandible, dorsal and ventral aspects, respectively: 38, *Metrius contractus* Esch; 39, *Physea hirta* LeC.; 40, *Entomoantyx cyanipennis* (Chd.); 41, *Pachyteles* nr. *striola* Perty. Scale bars = 200 µm. Legend: art- anterior retinacular tooth; m- molar; pm- premolar; pr- premolar ridge; prt- posterior retinacular tooth; r- retinaculum; tt- terebral tooth; vg- ventral groove; vrr- ventral retinacular ridge.



Figs. 42—48. 42—43, mandibles, A, C, E, left mandible, dorsal, ventral, and occlusal aspects, respectively; B, D, F, right mandible, dorsal, ventral, and occlusal aspects, respectively. 42, *Ozaena lemoulti* Bänn.; 43, *Platycerozaena panamensis* (Bates). 44, Left maxilla, ventral aspect, of *Metrius contractus* Esch. 45, Right maxilla, ventral aspect (reverse printing, for ease of comparison), of *Physea hirta* LeC. 46, Left maxilla, ventral aspect, of *Pachyteles kuntzeni* (Bänn.). 47, Left maxilla of *Ozaena lemoulti* Bänn.: A, complete structure; B, lacinia, apex. 48, Left maxilla of *Platycerozaena panamensis* (Bates). Scale bars = 400 µm, Figs. 42-47A, and 48; 100 µm, 47B. Legend: art- anterior retinacular tooth; m- molar; pm- premolar; pr- posterior retinacular ridge; prt- posterior retinacular tooth; r- retinaculum; tt- terebral tooth; vg- ventral groove.

TABLE 1. Characteristics of Mandibles of *Metrius* Eschscholtz, and of Ozaenine Genera of North and Middle America

NAME OF GENUS	Scrobe	Dorsal Surface	Setation Dorsal Surface	Width Terebral Tooth	Terebral Margin	Retinacul. Thickness	Retinaculum Teeth		Molar Area	Ventral Groove
							Ant.	Post.		
Metrius	1 seta	–	moderate	moderate	slight curvature extended on to Retinacul.	marked	large	small	divided	short
Entomoantyx	1 seta	–	moderate	small	slight curvature not extended on to Retinacul.	thin	large	moderate	not divided	long
Physea	many setae	–	moderate	moderate	marked curvature not extended on to Retinacul.	thin	absent	large	not divided	long
Pachyteles	many setae	–	moderate	small	slightly curved extended on to Retinacul.	thin	large	large	not divided	long
Ozaena	many setae	+	moderate	small	slightly curved extende on to Retinacul.	thin	moderate	large	not divided	long
Platycerozaena	many setae	+	wide	moderate	slightly curved not extended on to Retinacul.	thin	moderate	small	not divided	short

We believe that this structural transformation series parallels a functional transformation series, involving a shift from ingestion of particulate to ingestion of more liquid food.

Labium.— Features of note involve the mentum, and terminal labial palpomeres (Figs. 49-55). On the menta of *Metrius*, *Entomoantyx*, and *P.* (*Goniotropis*) (Figs. 49, 51 and 53), one or two pairs of long tactile setae are located paramedially posterad the tooth. Such setae are absent from the menta of *Physea*, *Ozaena*, and *Platycerozaena* (Figs. 50, 54 and 55).

Lateral lobes of the mentum are moderately long in *Metrius*, *Physea*, *Entomoantyx*, and *Pachyteles*, and markedly long in *Ozaena* and *Platycerozaena*. In addition, in the last-named genus, the lateral lobes are markedly narrowed and pointed apically.

Epilobes (Fig. 49, **el**) are broader medially in *Metrius*, *Physea*, and *Pachyteles*. They are broader apically in *Entomoantyx*, and in *Ozaena* and *Platycerozaena* they are narrow.

The mental tooth is moderately long in *Metrius*, *Entomoantyx*, *Physea*, and *Pachyteles*; somewhat reduced in *Ozaena*, and markedly reduced in *Platycerozaena*. The apex of the tooth is notched in *Metrius contractus* Esch., and not notched in an undescribed species of *Metrius* (Y. Bousquet, personal communication) or in the New World ozaenine genera— though it is notched in the Australian genus *Mystropomus*. .

The glossal sclerites (Fig. 49, **gs**) are bisetose in members of *Metrius*, *Entomoantyx*, *Physea*, and *Pachyteles*. These setae are lacking from the glossal sclerites of *Ozaena* and *Platycerozaena*, evidently a reflection of the general reduction in setae characteristic of these genera.

Terminal palpomeres vary somewhat within the New World ozaenine genera. In most, they are like those of *Pachyteles* (Fig. 52), thus broader than those of *Metrius* (Fig. 49). The terminal palpomeres of *Physea*, however, are parallel-sided and more elongate (Fig. 50).

We believe that the following branched transformation series summarizes adequately the pattern of the various forms and details of the labium:

$$\begin{tikzcd}
 & \textit{Entomoantyx} & & \\
\textit{Metrius} & \textit{Pachyteles} \arrow[l] \arrow[u] \arrow[r] \arrow[d] & \textit{Ozaena} \arrow[r] & \textit{Platycerozaena} \\
 & \textit{Physea} & &
\end{tikzcd}$$

Thoracic structures.— *Metrius* adults exhibit an hypertrophied intercoxal process of the prosternum, which is so large that it covers the mesosternum. The mesosternal and metasternal intercoxal processes are firmly articulated to one another, as in most carabids. Ozaenines seem to be rather more loosely articulated than are adults of most carabid groups. The intercoxal process of the prosternum is of normal size. The intercoxal processes of the meso- and metasterna are rather loosely articulated in adults of *Entomoantyx*, *P.* (*Goniotropis*), *Ozaena*, and *Platycerozaena*. Among adults of *Physea* and *P.* (*Pachyteles*), the processes are reduced so that the middle coxae are in contact with one another medially.

The following linear transformation series summarizes this system:

Entomoantyx
Metrius ⟶ *P*. (*Goniotropis*) ⟶ *P*. (*Pachyteles*)
Ozaena *Physea*
Platycerozaena

Stork (1985: 1115 and Fig. 12) reports in adults of *Dhanya* prothoracic pits, one on each side, laterad the fore coxal cavities. He notes also the presence of such structures in adults of *Mystropomus,* but that they are positioned differently, and thus probably not homologues of the pits in *Dhanya.* He notes a possible involvement of these pits in a possible association with ants.

The metathorax of *Metrius* adults is small, the result of loss of the flight function and ultimately of the metathoracic wings and associated muscles. This group of losses and reductions is apotypic for *Metrius.*

Metathoracic wings.— The Middle American genera are characterized by wings with the wedge cell lacking, but otherwise with complete venation, and with the oblongum cell large, and quadrangular (*cf.* Ward, 1979: 183, Figs. 1-3 and 7). In contrast, members of the Oriental genus *Dhanya* exhibit markedly reduced venation, including a triangular, stalked oblongum cell (Stork, 1985: 1129, Fig. 43). In this latter feature, members of this genus resemble those of the Paussina (Darlington, 1950).

Legs.— Features of particular note include projections of the fore femora, antennal cleaner of the fore tibiae, and sexual dimorphism of the fore tarsomeres.

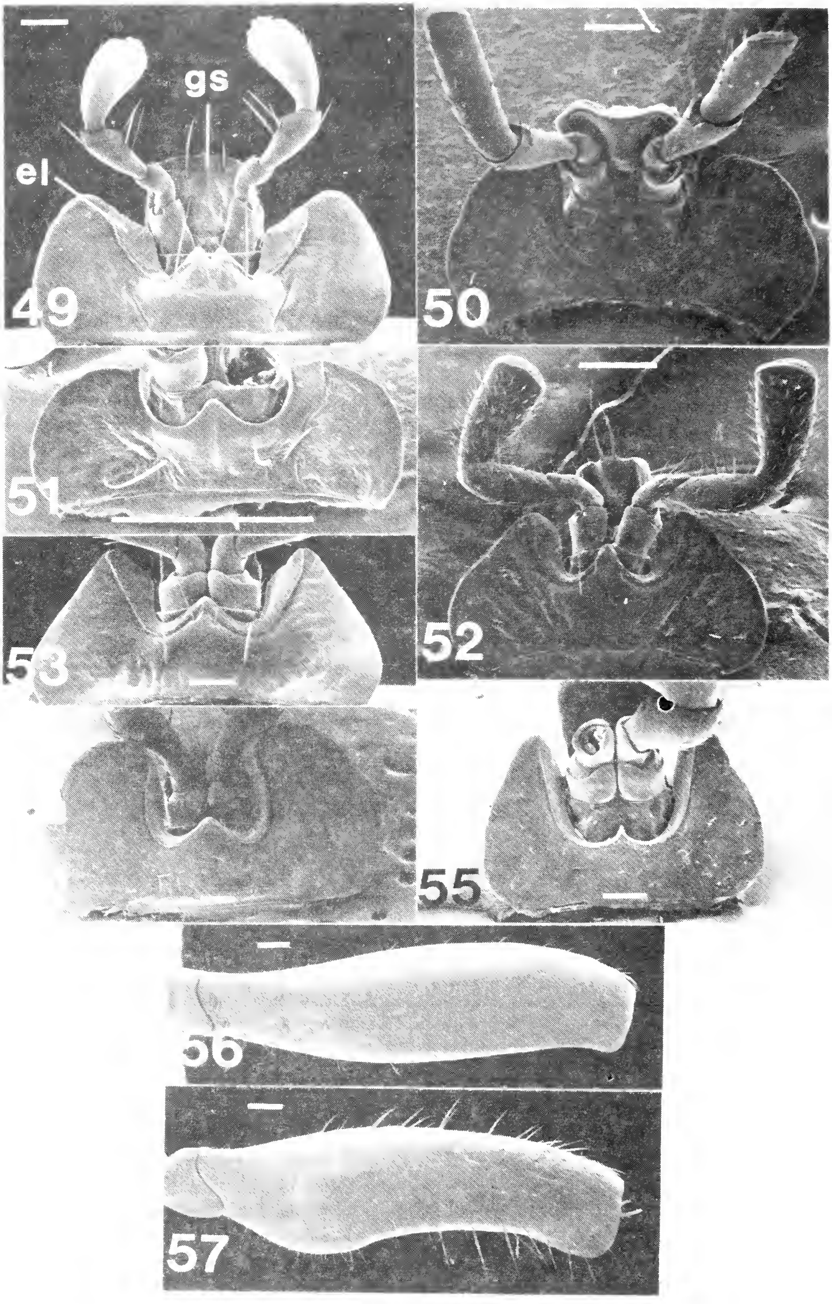
The fore femora without projections are those of adults of *Metrius* (Fig. 56), *Entomoantyx* (Fig. 58), and some South American species of *Pachyteles* (subgenus *Tropopsis*). Adults of *Physea* (Fig. 57) and of *Platycerozaena* (Fig. 62) exhibit a prominent broad swelling ventrally. Adults of *Pachyteles* (Figs. 59 and 60) have prominent narrow projections, whereas those of *Ozaena* (Figs. 61A-B) have shorter, setose projections.

The transformation series indicated by these data is the following:

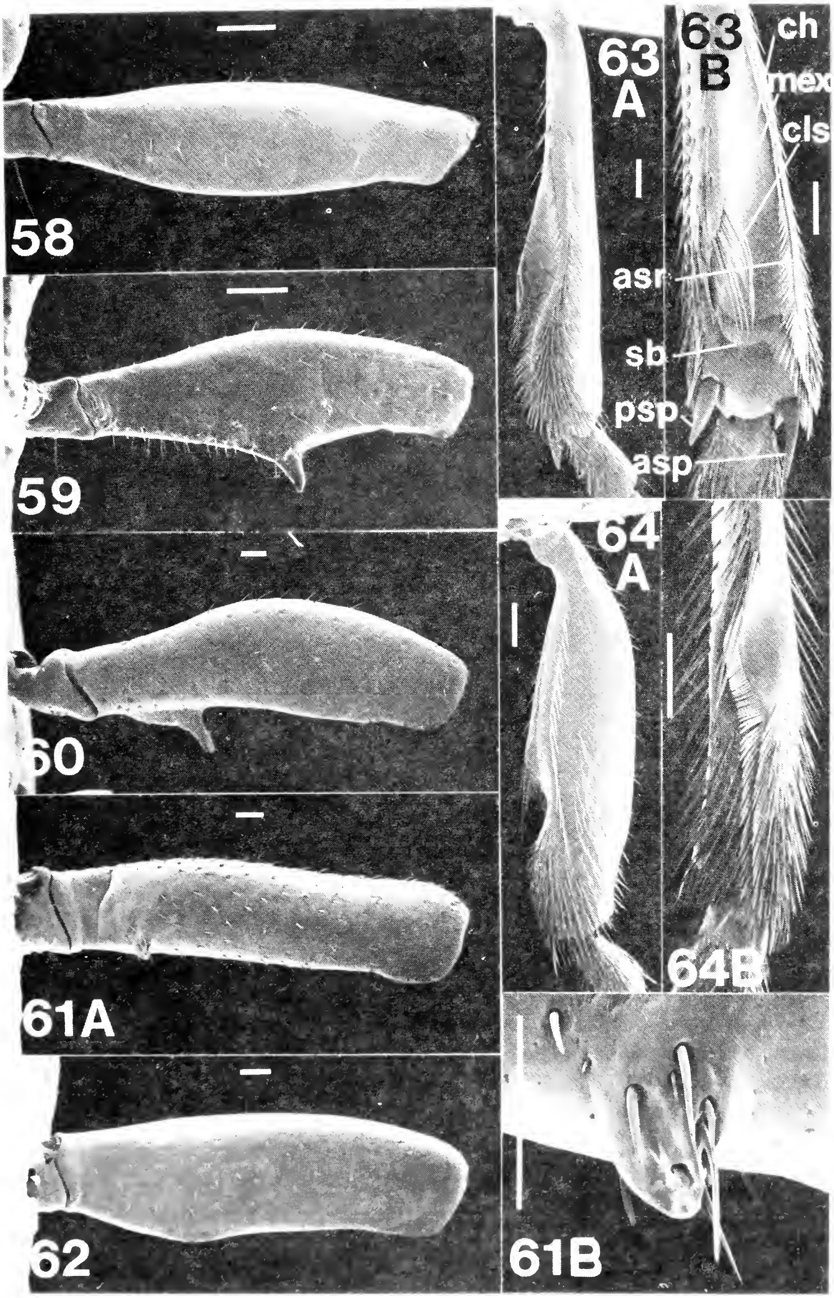
Physea ⟵ *Metrius* ⟶ *Pachyteles*
Platyceroz. *Entomoantyx* *Ozaena*

Antennal cleaner.— This complex comb organ (Darlington, 1950: 60), includes some form of groove or notch on the front tibia, and associated setae and spines, projections, and/or spurs. Hlavac (1971) provides a detailed analysis for the Carabidae. Figures 63 to 69 illustrate antennal cleaners for *Metrius* and the ozaenines. Table 2 provides details for the taxa of interest.

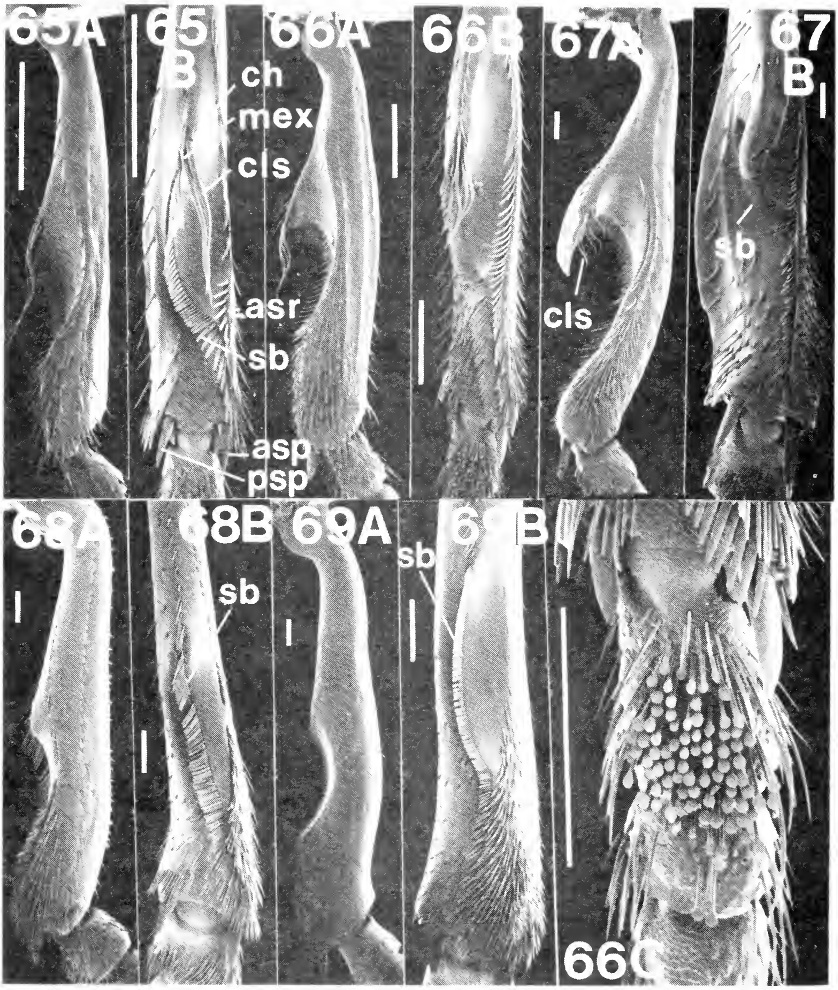
Structures are as follows: a more or less extensive groove in the mesal surface of the fore tibia, the cleaning channel (**ch**); a more or less expanded portion of the tibia adjacent to the channel (**mex**); a setal band (**sb**) extended across the channel and parallel to the posterior edge of the channel; several large sinuate clip setae (**cls**), origin posteriorly at the medial expansion; and anterior row of setae (**asr**) along the anterior edge of the channel; a zone of confluence distally, where the setal band and anterior setal row almost meet, and in some taxa seem to disappear in a dense patch of other setae (Fig. 69B).



Figs. 49—57. 49—55, Labium, ventral aspect, of: 49, *Metrius contractus* Esch; 50, *Physea hirta* LeC.; 51, *Entomoantyx cyanipennis* (Chd.); 52, *Pachyteles* nr. *striola* Perty; 53, *Pachyteles parca* LeC.; 54, *Ozaena lemoulti* Bänn.; 55, *Platycerozaena panamensis* (Bates). 56-57, left fore femur, anterior aspect, of: 56, *Metrius contractus* Esch; 57, *Physea hirta* LeC. Scale bars = 200 µm, Legend: el- epilobe of mentum; gs- glossal sclerite of mentum.



Figs. 58–64. 58–62, Left fore femur, 58, and 60-62, anterior aspect, 59, posterior aspect, of 58, *Entomoantyx cyanipennis* (Chd.); 59, *Pachyteles* nr. *striola* Perty; 60, *Pachyteles kuntzeni* (Bann.); 61, *Ozaena lemoulti* Bann., A- entire sclerite, B- spine; 62, *Platycerozaena panamensis* (Bates). 63-64, Left fore tibia, A- anterior aspect, B- inner aspect, of 63, *Metrius contractus* Esch; 64, *Physea hirta* LeC. Scale bars = 200 µm. Legend: asp- anterior tibial spur; asr- anterior setal row; ch- channel; cls- clip setae; mex- median expansion; psp- posterior tibial spur; sb- setal band.



Figs. 65—69. 65—66A-B, and 67—69, front tibiae, 65—66 and 68-69, left; 67, right (printed in reverse, for ease of comparison); A, anterior aspect, B, inner aspect, of: 65, *Entomoantyx cyanipennis* (Chd.); 66, *Pachyteles* nr. *striola* Perty; 67, *Pachyteles kuntzeni* (Bänn.); 68, *Ozaena lemoulti* Bänn.; 69, *Platycerozaena panamensis* (Bates). 66C, Left fore tarsomeres 1-3, ventral aspect of male *Pachyteles* nr. *striola* Perty. Scale bars = 200 μm, Legend: asp- anterior tibial spur; asr- anterior setal row; ch- channel; cls- clip setae; mex- median expansion; psp- posterior tibial spur; sb- setal band.

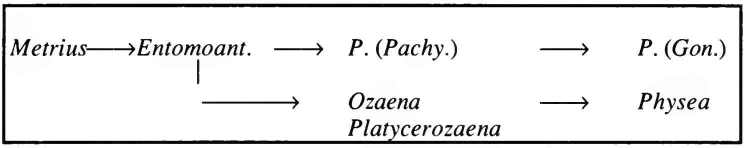
TABLE 2. Characteristics of Antennal Cleaning Organ of *Metrius* Eschscholtz, and of Ozaenine Genera of North and Middle America

NAME OF GENUS	Grade	Channel	Median Expansion	No. Clip Setae	Anterior Setal Row	Setal Band
Metrius	B	large, ext. basad MEx	moderage	5+	setae large	short, sharply sinuate
Entomoantyx	C	large, ext. basad MEx	moderate	5-	setae large	long, sinuation moderate
Physea	C	small, term. at MEx	slight	0	not evident	long, sinuation slight
Pachyteles (*s. str.*)	C	large, ext. basad MEx	marked	5-	setae large	long, sinuation moderate
Pachyteles (*Goniotropis*)	C	large, ext. basad MEx	marked, w/ claw-like projection	5+	setae large	long, sinuation moderate
Ozaena	C	small, term. at MEx	slight	0	setae large	long, sinuation slight
Platycerozaena	C	small, term. at MEx	slight	0	setae small sparse	long, sinuation slight

Hlavac (1971: 56) places *Metrius* and the Australian ozaenine genus *Mystropomus* . in grade B, characterized as follows: tibial spurs not part of cleaning mechanism; setal band long, with distinct vertical section and confluent zone, length of setal band/length of tibia 26-58 per cent, in most taxa less than 40 per cent; confluent zone short, 15 to 35 per cent length of band; median expansion evident, in most taxa not shifted far anterad; channel shallow, developed far basad of clip setae or not; fore tibia not compressed antero-posteriorly. *Metrius* and *Mystropomus* are classified as "advanced Grade B", presumably because of the extended channels that they exhibit. However, this condition would seem to be plesiotypic among ozaenines.

The remaining ozaenines are classified by Hlavac as members of Grade C: setal band long (length of setal band/length of tibia 33-69 per cent), divided into a large distal region or confluent zone, and a proximal cleaning arc; distal region from 33 to 69 per cent length of setal band; median expansion markedly developed anteriorly; channel deep, short, not extended above clip setae; anterior and posterior setal rows, if present, not in from of cleaning aggregations.

The various forms of cleaning organs seem to form the following branched transformation series:



Following development of the more complex cleaner (C from B), further development occurs with hypertrophy of the median expansion (Figs. 66A-B, and 67A-B). In contrast, the cleaning organ is reduced in the line *Ozaena* + *Platycerozaena- Physea* (Figs. 68A-B, 69A-B, and 64A-B), with decrease in size of channel, loss of clip setae and loss or reduction of the anterior setal row. This reduction probably coincides with modification of other parts of the fore tibiae (markedly broadened in *Physea*), or in modifications of the antennae (reduction in setae in *Ozaena* and *Platycerozaena*; thickening of the antennomeres in *Ozaena*, shortening of the antennae in *Platycerozaena*). In any event, it seems unlikely that the reduced organs can function as antennal cleaners. Darlington (1950: 65) claims that such reduction is a precursor to total loss of the antennal cleaner exhibited by paussine adults, many of which have markedly expanded tibiae, and markedly expanded antennomeres that lack standard tactile and chemosensory setae. We can appreciate that the antennal modifications of *Ozaena* and *Platycerozaena* render the cleaning organ superfluous, but the antennomeres of *Physea* seem to have a normal complement of sense organs. If other carabids with normal antennae need to groom them, how do *Physea* adults manage? Do they have some other mechanism, or is their grooming behavior so modified that they can use effectively the remnants of their cleaning organs?

Genital segments of males.— These are abdominal segments VIII and IX/X. The latter segment is either composite, or one of either IX or X (*cf* Bils, 1976). Although Bils' paper treats females, we assume that the tergum that bears the explosion chambers of the defensive system is the same in both sexes, and Bils labels this "T IX/X" (*l.c.*, Figs. 9 and 11, *EK*).

Tergum VIII is of about the same form in all taxa examined. We do not comment further about it. Sternum VIII and the "ring sclerite" (sclerites of segment IX/X) do exhibit some interesting variation.

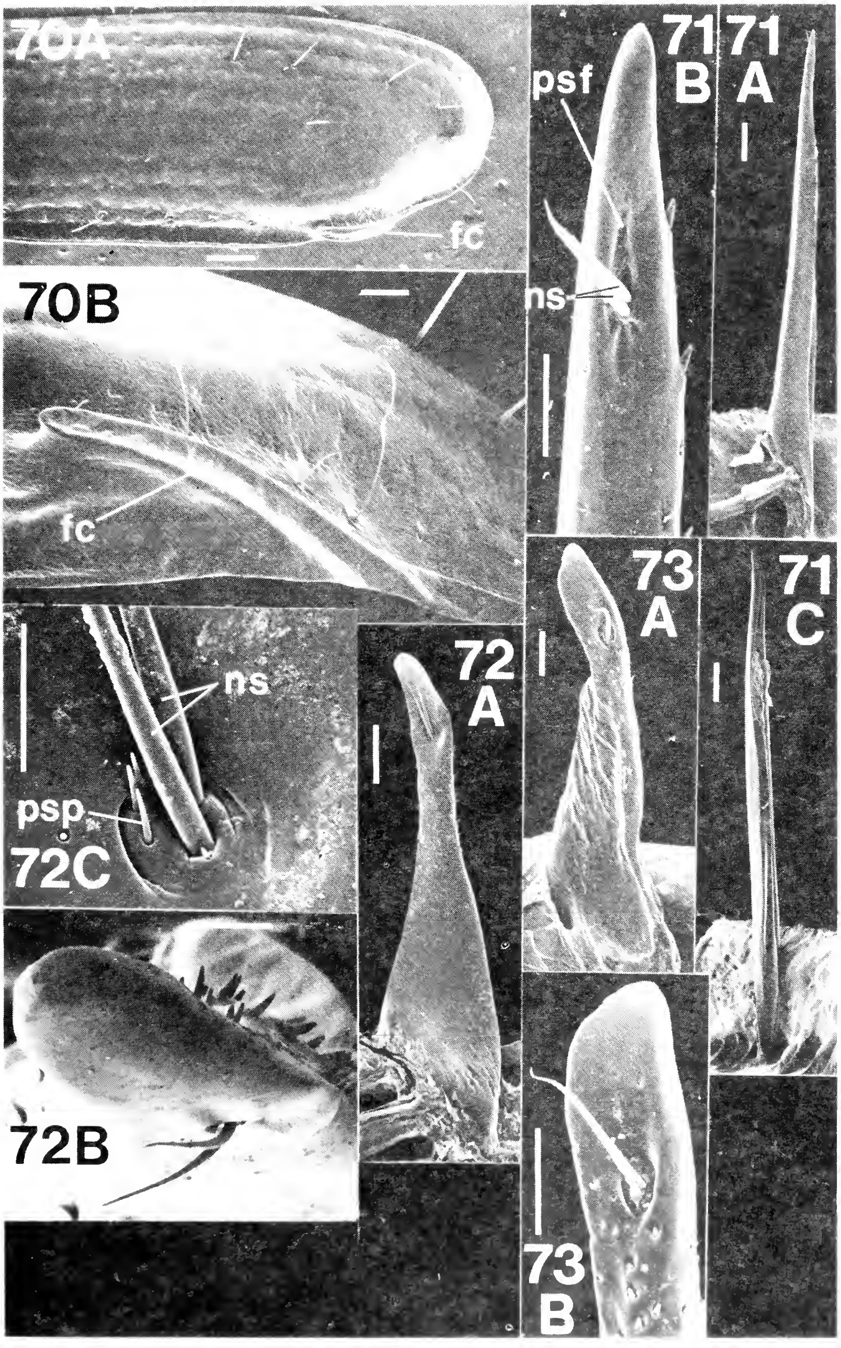
TABLE 3. Characteristics of Male Genitalia of Metrius Eschscholtz, and of the Ozaenine Genera of North and Middle America

NAME OF GENUS	Median Lobe		Sc. Rod	Internal Sac			Parameres	
	Shaft	Apex	Length	Basal Area (1)	Collar Area (2)	Apical Area (3)	Left	Right
Metrius	curvature preapically marked	prominent narrow, pointed posteriorly	*ca.* .25 L. median lobe	micro-trichia extensive microspines	semi-circle, right of	membranous lobe	few preapical	digitate; apical/preap. fringe of long setae
Entomoantyx	curvature moderate	broad, not prominent pointed ventrally	*ca.* .75 L. median lobe	sagittate microtrich. field	complete collar of micro-trichia	sclerot. terminal sclerite	asetose	digitate; longer than left; apical/preap. fringe of shorter setae.
Physea	curvature moderate	as for *Entomoant.*	*ca.* .50 L. median lobe	without micro-trichia	as for *Entomoant.*	membr. lobe on left; w/o terminal sclerite	few preapical setae	spatulate asetose; shorter than left.
Pachyteles (*sensu stricto*)	curvature moderate to marked	as for *Entomoant.*	subequal to length median lobe	micro-trichia few	as for *Entomoant.*	w/o term. sclerite; lightly scl. tube	asetose	spatulate to blade-like; setation various.

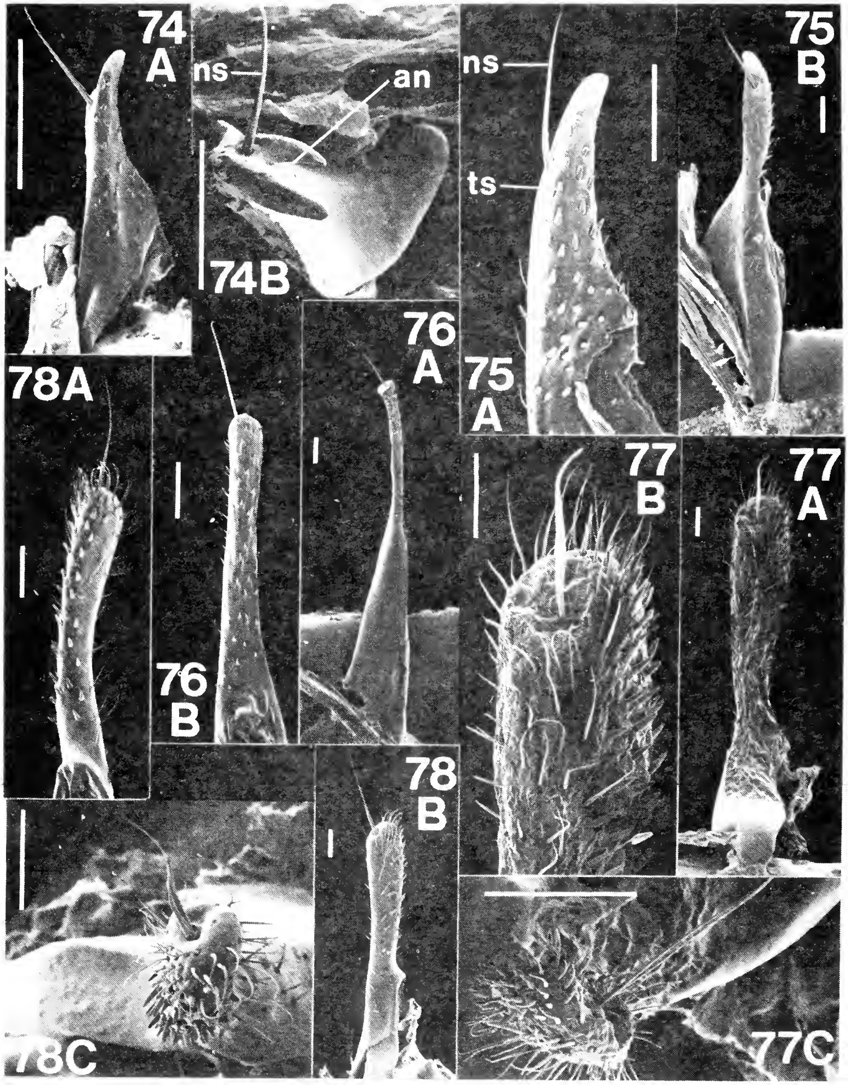
(continued on next page)

TABLE 3 (continued)

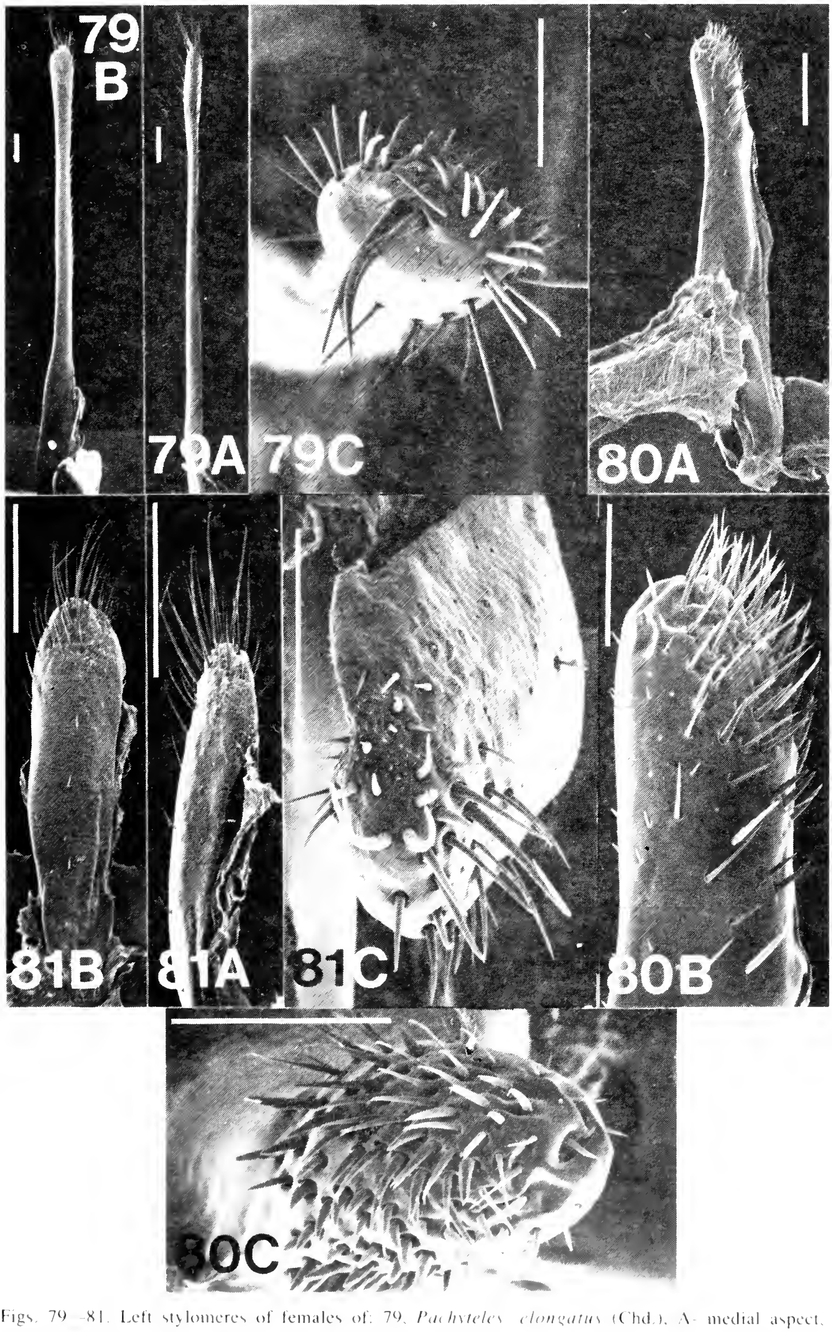
NAME OF GENUS	Median Lobe		Sc. Rod	Internal Sac			Parameres	
	Shaft	Apex	Length	Basal Area (1)	Collar Area (2)	Apical Area (3)	Left	Right
Pachyteles (*Goniotropis*)	curvature marked	prominent, broad, obl. truncate or broadly rounded	*ca.* .60 L. median lobe	microtrichia few	extensive collar of microtrichia	apical brush; terminal sclerite	few preapical setae	falcate setose on much of medial margin; longer than left
Ozaena	curvature very slight	not projected ventrally obsolete	*ca.* .90 L. median lobe	without microtrichia	extensive mainly on left	term scl. broad, w/ broad vent. dir. lobe	few preapical setae	falcate; setose on much of medial margin; longer than left.
Platycerozaena	curvature very slight	slightly projected ventrally	*ca.* .90 L. median lobe	without microtrichia	as in *Ozaena*	as in *Ozaena*	as in *Ozaena*	spatulate; setose on much of medial margin; longer than left.



Figs. 70–73. 70, left elytron of *Entomoantyx cyanipennis* (Chd.): A, apical half, dorsal aspect; B, flange of Coanda, lateral aspect. 71-73, left stylomeres of females of: 71, *Physea hirta* LeC., A- ventral aspect, B- ventral aspect, apical portion, C- medial aspect; 72, *Metrius contractus* Esch., A, ventral aspect, B- caudo-ventral aspect, C- apical portion, ventral aspect; 73, *Entomoantyx cyanipennis* (Chd.), A- ventral aspect, B- apical portion, ventral aspect. Scale bars = 200µm, Figs. 70A, 71A,C, 72A; 40mm, 70B, 71B, 72B,C, 73A,B. Legend: fc- flange of Coanda; ns- nematiform setae; psf- preapical sensory furrow; psp- preapical sensory pegs.

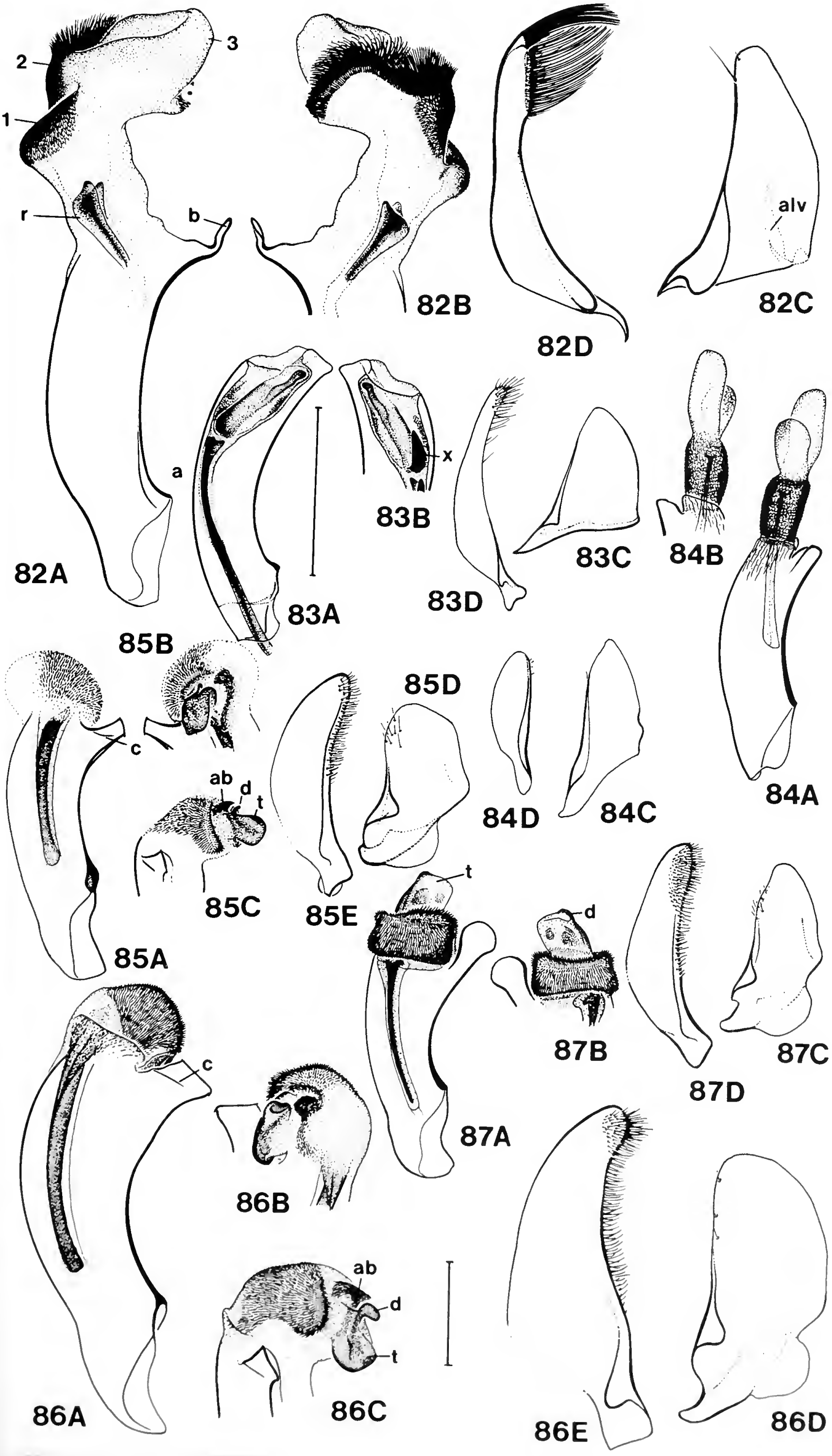


Figs. 74—78. Left stylomeres of females of 74, *Pachyteles gyllenhali* (Dej.), A- medial aspect, B- caudal aspect; 75, *Pachyteles enischnus*, new species, A- medial aspect, B- ventral aspect; 76, *Pachyteles mexicanus* Chd., A- medial aspect, B- ventral aspect; 77, *Pachyteles kuntzeni* (Bänn.), A- ventral aspect, B- apical portion, ventral aspect, C- caudal aspect; 78, *Pachyteles parca* LeC., A- medial aspect, B-ventral aspect, C- caudal aspect. Scale bars = 100 µm, Legend: an- apical notch; ns- nematiform seta; ts, trichoid seta.

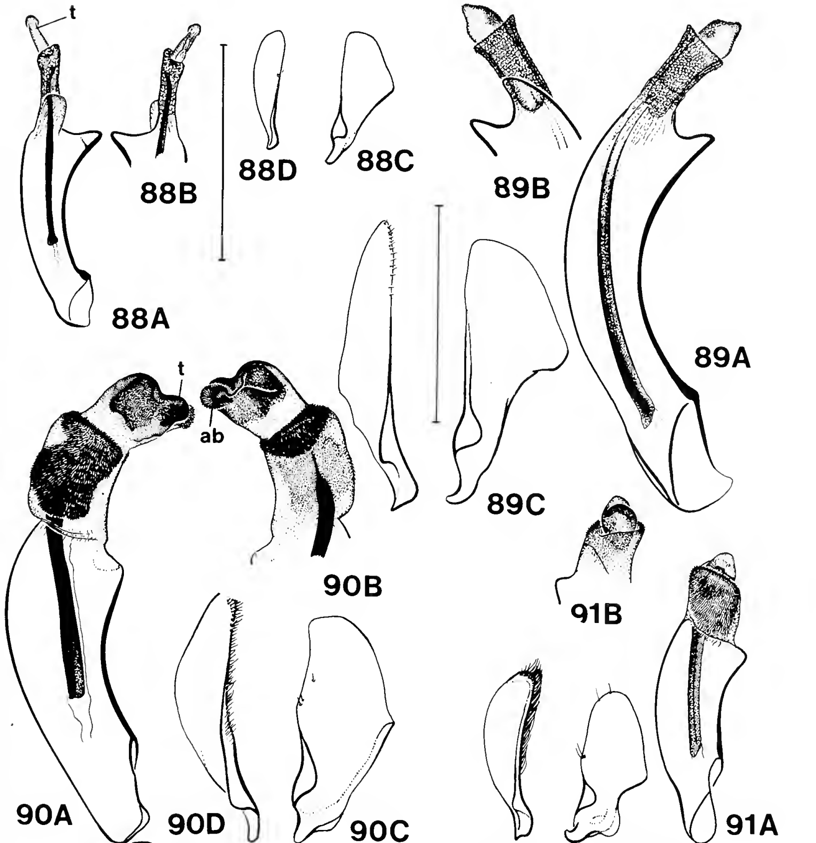


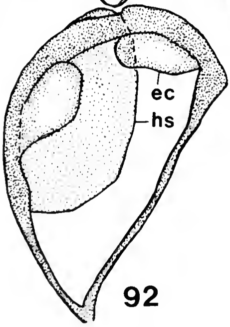
Figs. 79–81. Left stylomeres of females of: 79, *Pachyteles elongatus* (Chd.), A- medial aspect, B- ventral aspect, C- caudal aspect; 80, *Ozaena lemoulti* Bann., A- ventral aspect, B-apical portion, ventral aspect, C- caudal aspect; 81, *Platycerozaena panamensis* (Bates), A- medial aspect, B- apical portion, medial aspect, C- caudal aspect. Scale bars = 200 mm, 79A-B, 80A-B, and 81A, 100 mm, 79C, 80C, and 81B-C.

Figs. 82—87. Male genitalia of: 82, *Metrius contractus* Esch., A- median lobe, left lateral aspect, internal sac everted, B- same, right lateral aspect, apical portion, C-D, left and right parameres, respectively, dorsal aspect; 83, *Entomoantyx cyanipennis* (Chd.), A- median lobe, left lateral aspect, internal sac inverted, B- same, right lateral aspect, C-D, left and right parameres, respectively, dorsal aspect; 84, *Physea hirta* LeC., A- median lobe, left lateral aspect, internal sac everted, B- same, apical portion, right lateral aspect, C-D, left and right parameres, respectively, dorsal aspect; 85, *Pachyteles parca* LeC., A- median lobe, left lateral aspect, internal sac everted, B- same, apical portion, right lateral aspect, C- same, apical portion, ventral aspect, D-E, left and right parameres respectively, dorsal aspect; 86, *Pachyteles kuntzeni* (Bänn.), A- median lobe, left lateral aspect, internal sac everted, B- same. apical portion, right lateral aspect, C- same, apical portion, ventral aspect; D-E, left and right parameres, respectively, dorsal aspect; 87, *Pachyteles elongatus* (Chd)., A- median lobe, left lateral aspect, internal sac everted, B- same, right lateral aspect; C-D, left and right parameres, respectively, dorsal aspect. Scale bars = 0.5 µm, Legend: 1-3, major regions of internal sac; a- median lobe, basal articulation point for parameres; ab, apical brush of internal sac; b- apical portion of median lobe; c- carinula of apical portion of median lobe; d- digital projection of terminal sclerite of internal sac; r- rod of apical portion of ejaculatory duct; t- terminal sclerite of internal sac.

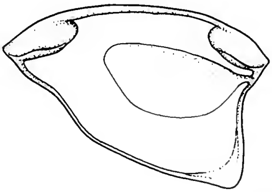

2
3
1
r
b
82B
82C
82D
alv
a
82A
83B
x
83A
83C
83D
84B
84A
85B
c
85D
ab
d
t
85C
85E
85A
84D
84C
t
d
87B
87C
87D
87A
c
86B
ab
d
t
86C
86A
86E
86D

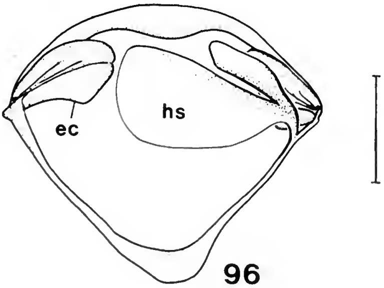
Figs. 88—96. 88—91, Male genitalia of: 88, *Pachyteles gyllenhali* (Dej.), A- median lobe, left lateral aspect, internal sac everted, B, same, apical portion, right lateral aspect, C-D, left and right parameres, respectively, dorsal aspect; 89, *Pachyteles mexicanus* Chd., A-median lobe, left lateral aspect, internal sac everted, B- same, apical portion, right lateral aspect; C-D, left and right parameres respectively, dorsal aspect; 90, *Ozaena lemoulti* Bänn., A- median lobe, left lateral aspect, internal sac everted; B, same, apical portion, right lateral aspect, C-D, left and right parameres, respectively, dorsal aspect; 91, *Platycerozaena panamensis* (Bates), A- median lobe, left lateral aspect, internal sac everted; B, same, apical portion; C and D, left and right parameres, respectively, dorsal aspect. 92-96, Ring sclerites of segments IX/X of: 92, *Metrius contractus* Esch., dorsal aspect; 93, *Entomoantyx cyanipennis* (Chd.), dorsal aspect; 94, *Physea hirta* LeC., ventral aspect; 95, *Pachyteles marginicollis* (Solier), dorsal aspect; 96, *Platycerozaena magna* (Bates). Scale bars = 0.5 µm, Legend: ab- apical brush of internal sac; ec- explosion chamber of pygidial gland system; hs- hemisternite of segment IX/X; t- terminal sclerite of internal sac.

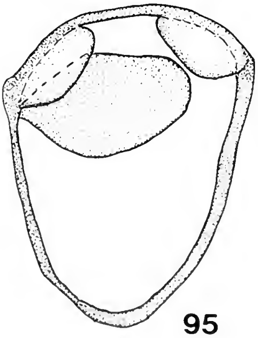

t
88B
88D
88C
89B
88A
89A
t
ab
89C
90B
91B
90A
90D
90C
91A
91D
91C

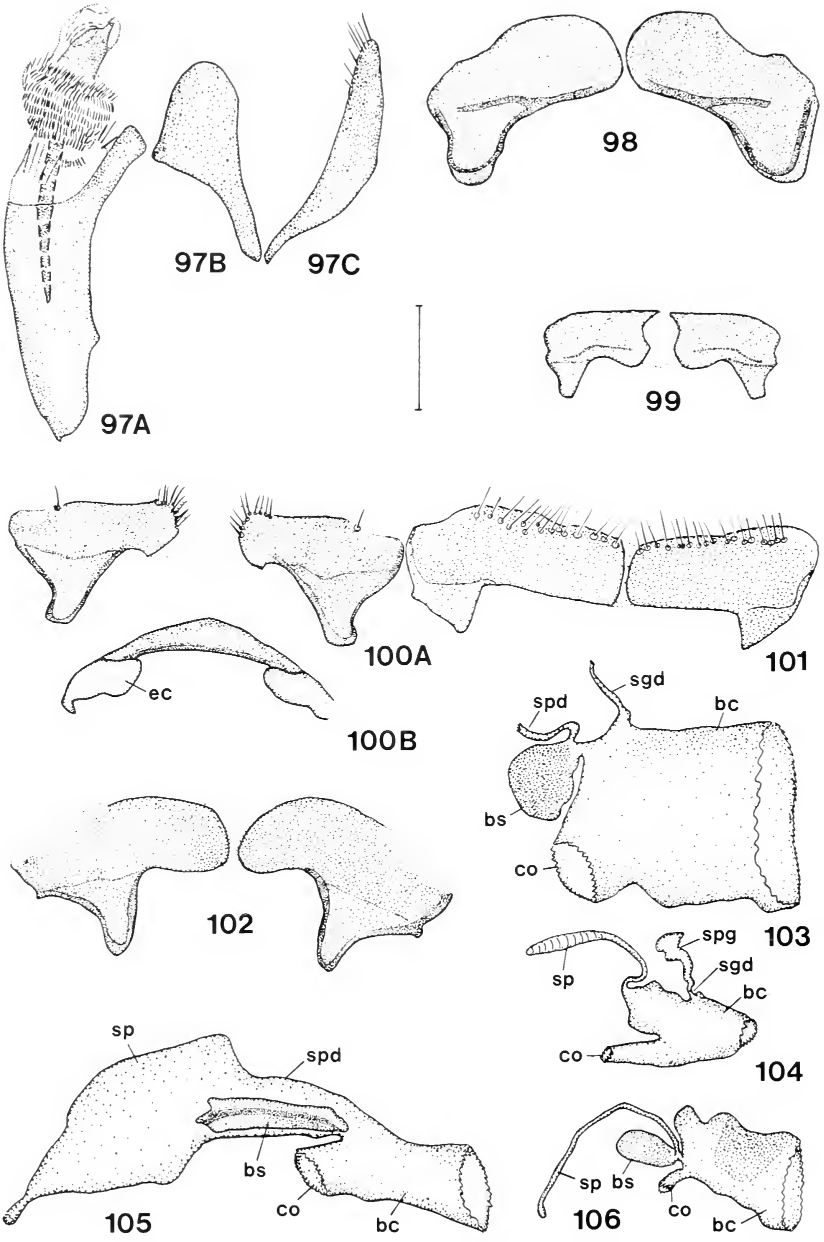

ec
hs
92


93


94


hs
ec
96


95



Figs. 97—106. 97, Male genitalia of *Pachyteles enischnus*, new species: A, median lobe, left lateral aspect, with internal sac everted; B-C, left and right parameres, respectively, ventral aspect. 98-100A and 101—102, Sternum VIII, ventral aspect, of: 98, *Metrius contractus* Esch.; 99, *Entomoantyx cyanipennis* (Chd.); 100A, *Physea latipes* Schaum; 101, *Pachyteles parca* LeC.; 102, *Pachyteles mexicanus* Chd. 100B, Tergum IX/X, dorsal aspect, of *Physea latipes* Schaum. 103-106, female reproductive tracts, lateral aspects, of: 103, *Metrius contractus* Esch; 104, *Entomoantyx cyanipennis* (Chd.); 105, *Physea latipes* Schaum; 106, *Pachyteles parca* LeC. Scale bars = 0.5 µm, Legend: bc- bursa copulatrix; bs- bursal sclerite; co- common oviduct; ec- explosion chamber; sgd- spermathecal gland duct; sp- spermatheca; spd- spermathecal duct.

In *Metrius* males, the posterior margin of sternum VIII is broadly notched. The two anterior projections join at their apices to form a ring. We interpret these projections as apodemes. Among males of the Ozaenini, sternum VIII consists of a pair of small lateral sclerites connected to one another by membrane, and without apodemes.

The ring sclerite (Figs. 92-96) surrounds the genitalia which, during copulation, protrude between tergum and sternum. The tergum is narrow, and laterally on each side bears the explosion chambers (Fig. 92, *ec*). The sternum comprises a pair of apodemes joined anteriorly to form the ring; to the right one is connected a hemisternite (Fig. 92, *hs*), which is more or less extensive. This hemisternite is larger in *Metrius* males, being smaller among the ozaenines.

The sternal apodemes of *Metrius* males, at their junction, form a narrow angle. This angle is greater among the ozaenines, the junction being broadly rounded in *Entomoantyx* males (Fig. 93). The ring is markedly asymmetrical in *Metrius* and *Physea* males (Fig. 94), slightly to the right in *Ozaena* and *Platycerozaena* (Fig. 96), and about symmetrical in *Entomoantyx* and *Pachyteles* males. These data suggest the following linear transformation series:

Metrius———→*Physea*———→*Ozaena*———→*Pachyteles*———→*Entomo.*
Platycerozaena

Although the ring sclerite of *Physea* is in form much like that of *Metrius*, in fact the former ring is a good deal shorter than the latter, and is thus more derived than is apparent at first.

Male genitalia.— This system comprises the sclerotized median lobe which has enfolded in it the actual organ of intromission, the internal sac or endophallus, and attached externally to the base is a pair of plate-like or digit-like parameres. Stork (1985: 1120 and Figs. 32-37) provides excellent data about the male genitalia of the species of *Dhanya.*

Among *Metrius* and ozaenine males, the median lobe is a compressed tube, with an open base, *i.e.*, without a distinct basal bulb (*cf.* Figs. 82A-91A and 97A).

In lateral aspect, the articulation point for the parameres (Fig. 82A, *a*) marks the ventral base of the shaft. The shaft is curved ventrad, more abruptly so apically in *Metrius* males, and narrowed in males of the ozaenine genera. The apical portion (Fig. 82A, *b)* located ventrad, is marked in *Metrius* males by a sharp constriction in the median lobe, and comprises a thin lobe with apex directed posterad, and bent sharply away from the ventral curve. Among ozaenine males, the apical portion varies from non-existent (Figs. 90A-B) to prominent and subtruncate (Figs. 86A-B), or round and spatulate (Figs. 87A-B). See Table 3 for details.

The internal sac is complicated in form and more so in its armature of microtrichial fields and microspines derived from microtrichia. An additional piece of armature associated with the internal sac is the rod (Fig. 82A, **r**) of the ejaculatory duct— a trough-like structure on the dorsal surface of the duct, and which is varied in length. It is designated posterior rod by Stork (1985: 1120), and is very long in males of *Dhanya* (*l.c.*, Figs. 32-37).

Details of armature are best appreciated with the internal sac everted and, if possible, fully inflated (Figs. 82A-B, 84A-B, *etc.*). (for ozaenines, it is difficult to extend fully the sac; for the few males of *Entomoantyx* that we had available, it proved to be impossible). Three areas or fields are recognized: a dorso-basal lobe of microtrichia (1); a median band or collar of microtrichia or microspines (2); and an apical lobe that bears the ostium or gonopore and various sclerites and microtrichial fields (3). Details for the genera are provided in Table 3. Stork (*l.c.*, Figs. 32-37) figures similar structures for the species of *Dhanya.*

The parameres are varied in form, setation, and relative size. Illustrations (Figs. 82-91 and 97) were made from the dorsal aspect. Details are in Table 3. Compared to the genitalia of *Metrius* males, those of the Ozaenini exhibit median lobes with less differentiated apices, longer sclerotized rods of the internal sac, internal sacs with the apical parts more elaborate, and right parameres of most taxa broader, and either asetose or with shorter setae. A possible transformation series is the following:

$$\begin{tikzcd}
 & & \textit{Physea} & \\
\textit{Metrius} \arrow[r] & \textit{Entomoant.} \arrow[r] & \textit{P. (Pachytel.)} \arrow[r] \arrow[u] \arrow[d] & \textit{P. (Gonio.)} \\
 & & \textit{Ozaena, Platycerozaena} &
\end{tikzcd}$$

This series emphasizes the close association of *Entomoantyx* with *Metrius* in form and setation of the right paramere, and internal sac with a concentration of microtrichia on the dorso-basal area. Farthest from *Metrius* is subgenus *Goniotropis*, with its elaborate apical part of the internal sac. Males of subgenus *Pachyteles* seem to occupy a central point in the Ozaenini, with a structural plan of genitalia sufficiently complex to be ancestral to the other types. Although elaboration seems to be the main thrust of evolution of the genitalia, reduction seems to characterize *Physea*: shorter rod, reduced parameres, and a rather simple internal sac with the only projection being a large apical lobe. Also, the microtrichial field in the basal area seems to have been reduced in *Physea*, *Pachyteles*, *Ozaena*, and *Platycerozaena.*

Genital segments of females.— Abdominal terga VIII and IX/X (Fig. 100B) are essentially the same in *Metrius* and the ozaenines and are not noted further. Sternum VIII consists of a pair of hemisternites, each of which in *Metrius* females has an asetose broad median part and a broad, anteriorly directed apodeme. Among ozaenines, there is appreciable intergeneric variation. The median posterior parts are less extensive in most taxa than in *Metrius* (Fig. 98), and the apodemes are narrower. *Physea* females have the median parts shorter, with more membrane between (Fig. 100A), and *Physea* and *P.* (*Goniotropis*) females (Fig. 101) have setae variously distributed. Females of *Entomoantyx* have reduced hemisternites with the median margins markedly sinuate (Fig. 99). No transformation series is offered because the complexity of these structures cannot be summarized so simply.

Ovipositor sclerites.— These consist of a pair of slender valvifers articulated with tergum IX/X , and articulated to each valvifer a single-articled stylomere (Figs. 71-81), of varied length and setation, but each with a preapical sensory pit with one or more nematiform setae. The stylomeres are articulated in such a way that they are exserted straight posterad, without first being partially rotated from a flattened position in the body cavity. Presumably, this is a primitive feature of the paussine stock.

Stylomeres of *Metrius* females (Figs. 72A-B) are moderately long, broad at base, and broadly rounded at the apex; the surface, especially dorsally, has numerous basiconic sensilla; and the sensory furrow is preapical, with a pair of long nematiform setae and several basiconic sensilla (Fig. 72C) that are longer than usual for Carabidae. The stylomeres of *Entomoantyx* females (Figs. 73A-B) are similar to those of *Metrius*.

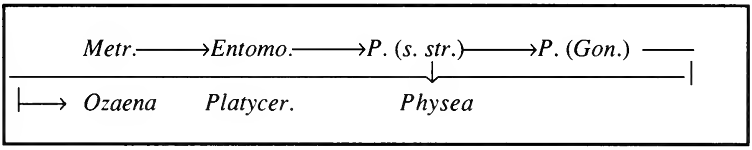
The stylomeres of *Physea* females (Figs. 71A-B) are much more elongate and slender, the surface with few sensilla, but including two preapical nematiform setae.

The stylomeres of *Pachyteles* females are various in form and proportions. Those of *P. enischnus* n. sp. (Figs. 75A-B) are most like the stylomeres of *Metrius*: mandible-like, falcate, with broad base and rounded apex, the nematiform setae preapical; however, the surface is covered with thick, short trichoid setae. The stylomeres of *P. gyllenhali* differ from those of *P. enischnus* n. sp. by the bifid apices (Fig. 74B). The stylomeres of *P. mexicanus* (Fig. 76A-B) are much more slender, digitiform, cylindrical (at least preapically), the surface with numerous slender trichoid setae in addition to those that are short and thick, and the sensory furrow and nematiform setae are apical rather than preapical.

The stylomeres of *P. parca* (Figs. 78A-C) and *P. kuntzeni* (Figs. 77A-C) are markedly similar to one another, and are much like those of *P. mexicanus*: cylindrical, with nematiform setae nearly apical; but they are shorter (palpiform) and with a much denser vestiture of setae. In contrast, the stylomeres of *Pachyteles elongatus* are long and very slender (Figs. 79A-C), like those of *Physea*, except that the nematiform setae are apical and the surface is moderately densely setose.

The stylomeres of *Ozaena* (Figs. 80A-C) are short, palpiform, cylindrical, with the nematiform setae apical, and with numerous trichoid setae apically and preapically. Those of *Platycerozaena* (Figs. 81A-C) are similar to the stylomeres of *Ozaena*, but the form is terete rather than cylindrical, and the apical and preapical setae are longer.

The following linear transformation series summarizes these data:



Along the main horizontal axis, there is an overall decrease in stylomere length, a shift of the sensory furrow toward the apex, and an increase in setation. *Physea* females are exceptional, with their long glabrous stylomeres, and *Pachyteles elongatus* varies in a similar way.

Bursal sclerite and spermatheca.— At the posterior end of the bursa copulatrix (**bc**) of female *Metrius* (Fig.103), a posterior chamber is extended dorsad the common oviduct (**co**), connected to the dorsal wall of the bursa is a spermatheca (not shown, but like **sp** in Fig. 104) with a short sinuous duct (**spd**), and an extensive spermathecal gland (not shown) connected by a short spermathecal gland duct (**sgd**). Table 4 provides details for the ozaenine genera studied. Based on absence or presence of the bursal sclerite and on form of the latter, the following branched transformation series is postulated:

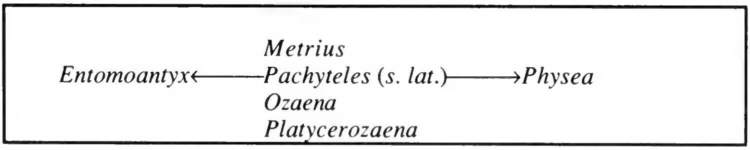


TABLE 4. Characteristics of the Reproductive Tract of Females of *Metrius* and of Ozaenine Genera of North and Middle America

NAME OF GENUS	Posterior Chamber	Bursal Sclerite	Spermatheca Insertion	Spermatheca Duct	Spermatheca Chamber
Metrius	large	moderate	dorsal wall of bursa	short	long
Entomoantyx	moderate	absent	apex of post. chamber	moderate	short, digitate annulate
Physea	large	elongate	apex of post. chamber	wide, annulate	long, slender
Pachyteles (*Goniotropis*)	very small	moderate	dorsal wall of bursa	narrow, short	digitate, small
Pachyteles (*sensu stricto*)	very small	small	dorsal wall of bursa	narrow, very long	short
Ozaena	very small	large of bursa	dorsal wall short	narrow,	short
Platycerozaena	very small	large of bursa	dorsal wall short	narrow,	short

TABLE 5. Defensive Secretions Recovered from Adult *Metrius* and Adults of Three Genera of Ozaenini. From Eisner, *et al.*, 1977; and Roach, *et. al.*, 1979.

NAME OF GENUS	1-4 benzo-quinone	2-Methyl-1,4-benzo-quinone	2-3 Dimethyl-1,4-benzo-quinone	2-Ethyl-1,4-benzo-quinone	n-penta-decane	Total Compounds
Metrius[1].	X				X	2
Physea[2].	X	X	X			3
Pachyteles (*sensu lato*)3.	X	X	X		X	4
*Platycerozaena*4.	X	X	X	X	X	5

[1]., *Metrius contractus* Esch.; [2]., *Physea hirta* LeC.; [3]., *P.* (*Pachyteles*) nr. *striola* Perty, *P.* (*P.*) *longicornis* Bates, and *P.* (*Goniotropis*) sp?; [4]., *Platycerozaena panamensis* Bates.

Defensive secretions and their delivery.— Eisner *et al.* (1977), Roach *et al.* (1979), and Eisner and Aneshansley (1981) analyze in some detail the defensive secretions and their delivery for ozaenines. Forsyth (1972) describes the structure of the pygidial glands that produce the secretions, and Deuve (1988: 167, Fig. 10) contributes an analysis of the position of the openings of the pygidial glands.

The secretions are various benzoquinones and the hydrocarbon n-pentadecane. Table 5 shows the names of secretions that have been recovered from adults of *Metrius* and representatives of three ozaenine genera considered here. The limited data show a graded series with numbers of compounds increasing from two (in *Metrius*) to three and five in ozaenines. Lack of n-pentadecane from the armory of *Physea* would seem to be a loss.

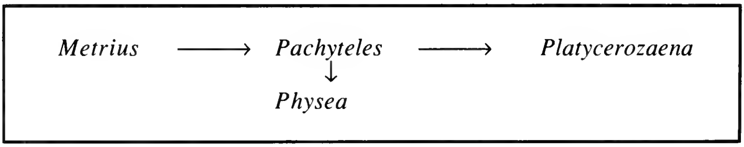
The mixtures are hot and are delivered with explosive force, in a cloud of corrosive vapor. Details of the process are explained by Eisner and Aneshansley (*loc. cit.*), though it was known for 150 years that these beetles were "bombardiers".

Ozaenines and paussines are able to direct the defensive jets forward by means of the flanges of Coanda on the elytra (Stork, 1985: 1115), as explained by Eisner and Aneshansley (*loc. cit.*).

Another part of the delivery system includes umbilical setae that are expanded (Figs. 107C-D), and to which droplets of the defensive secretions adhere when they are fired forward. Also, the beetles brush the secretions over the body, using the legs (Eisner and Aneshansley, *l.c.*). Characteristic of *Ozaena* and *Platycerozaena* adults are modified setae (basiconic Type 2; *cf.* Nagel, 1979b: 27). These are illustrated in Figs. 107A-B. They are on the lateral margins of the pronotum, as well as on the elytra. Their flattened, ridged surfaces would seem to be ideal for increasing the evaporative surface area for the defensive secretions, and thus enhancing the effectiveness of the latter. Unfortunately, Eisner and his co-workers did not mention these setae.

Forsyth, and Eisner and Aneshansley report that the pygidial glands of adult *Metrius* and the ozaenines are similar in structure, *i.e.*, two chambered. We have not studied them in detail, though we have seen the explosion chambers located laterally on Tergum IX/X (*cf.* Figs. 92-96 and 100B). This, combined with the numerous other similarities in structural features, is strong evidence for linking these taxa phylogenetically.

In summary, the defensive system shows remarkable complexity both in structure and function between *Metrius* and the Ozaenini + Paussini, linking these taxa in a single higher-level taxon. The ancestor of the group evidently evolved a system for development and release of simple hot benzoquinones. The delivery system was improved by evolution of the flanges of Coanda, and the chemical system became more complex with development of additional corrosive components. With data for only four of the six genera, the following branched transformation series is incomplete:



Sexual dimorphism: adhesive setae of fore tarsomeres.— Males of *Metrius* have fore tarsomeres 1 and 2 or 1, 2 and 3 (Y. Bousquet, personal communication)

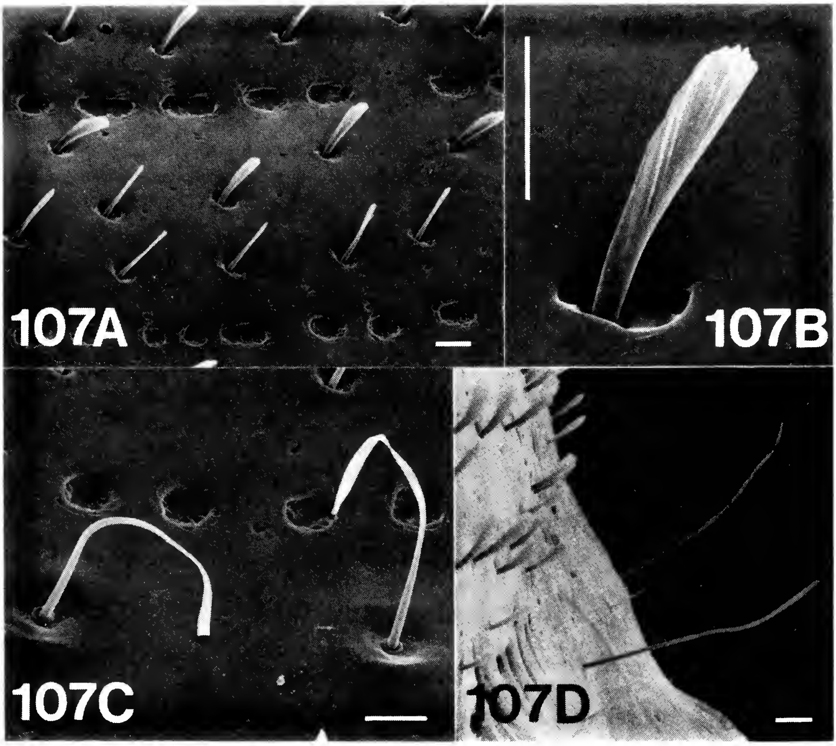


Fig. 107. Specialized setae on the elytron of *Ozaena lemoulti* Bänn.: A-B, sensilla basiconica, type 2; C, umbilical setae; D- sensilla basiconica, type 2. Scale bars = 50 µm,

markedly expanded, and on the ventral surface of each is a pad of adhesive articulo-setae (Stork, 1980: 287; *cf.* his Figs. 15B-E; referred to as "spongy pubescence" by previous authors). Among ozaenines, the vestiture-bearing tarsomeres are less expanded. Males of *Physea*, almost all of *Pachyteles* (*s. str.*) (Fig. 66C) and some of subgenus *Goniotropis* have adhesive setae on only fore tarsomeres 1 and 2. Males of some species of *Goniotropis*, and of *Entomoantyx* have vestiture on tarsomeres 1-3. Males of *Pachyteles gyllenhali*,. *Ozaena* and *Platycerozaena* (and some species of *Dhanya*— see Stork, 1985: 1115) lack adhesive vestiture and none of the fore tarsomeres are expanded. The data are summarized in the following branched transformation series:

P. (P) gyll. *Ozaena* *Platyceroz.*	⟵	*Metrius* *P. (Pachytel.)* *P. (Goniotr.)* *Physea*	⟶	*Entomoantyx* *P. (Goniotr.)*

Trends are in two directions: increase in number of tarsomeres with vestiture; and complete loss of adhesive vestiture.

Summary

In the absence of evidence that the New World ozaenine genera are monophyletic relative to their Old World counterparts, only a limited evolutionary analysis seems practical. This analysis consists of statements about phylogenetic distance from the putative out-group, *Metrius*, and about striking features of evolutionary divergence in particular character systems.

In terms of overall divergence, as measured by a summation of the relative distance from *Metrius* in each of the postulated transformation series, the sequence of genera is as follows, from most like to least like: *Entomoantyx—Pachyteles—Physea—Ozaena-Platycerozaena*. Probably this sequence does not represent a system of sister-group relationships, though *Ozaena* and *Platycerozaena* must be sister groups. *Physea* is strikingly aberrant in details of mandibles, male and female genitalia and ovipositor, as well as body form. The few defensive secretions lend credence to the proposition that this genus, though aberrant, is from a basically primitive stock.

A reviewer of a previous draft of the manuscript on which this paper is based, conducted a numerical cladistic analysis of the data, using the program HENNIG 86, and reported that a single most parsimonious cladogram resulted, expressed linearly as a series of inclusions: *Metrius* + (*Entomoantyx* + (*Pachyteles* + (*Physea* + (*Ozaena* + *Platycerozaena*)))). The consistency index is 0.81 or 26/32, indicating that there are only six extra steps in the cladogram of the six genera.

The sequence of genera is exactly the same as in the linear arrangement presented above. Nonetheless, as explained above, we do not believe that evolutionary significance should be accorded to the branching pattern, *i.e.*, that *Physea* is really sister-group of *Ozaena* + *Platycerozaena*.

We note two striking developments in the New World Ozaenini. Both may involve close association with ants. One of these developments is an escape from the constraints of life under bark, and is represented by the genus *Physea*. Body form is markedly modified (*i.e.*, broadened, as in Fig. 2; *cf.* Figs. 3 and 4). Other divergent features of *Physea* are noted above. We do not know their functional significance in relation to life in an environment with fewer physical constraints, or if some of these modifications evolved in response to life with ants. An explanate body plus flattened appendages may have to do with provision of a dorsal shield under which the appendages can be concealed as a safeguard against attacks by ants. The elongate antennae, which we believe are secondarily elongated, are anomalous, especially considering the reduced antennal cleaner. One would think that short antennae would be more easily protected from the ravages of ants.

A second striking development involves the genera *Ozaena* and *Platycerozaena*. The more evolved chemical defensive system includes possibly setae that are specialized for enhanced effectiveness in dispersion of the defensive secretions, which in turn are more numerous than in other New World ozaenines (demonstrated for *Platycerozaena*; inferred for *Ozaena*). This more complex system suggests evolution to cope with more efficient enemies— as for *Physea*, possibly ants. Loss of the normal tactile setae from the dorsal surface of head, pronotum and elytra also suggests association with ants— by analogy with lack of setae in paussines. Other striking modifications of these two ozaenine genera involve: antennae, with general reduction in sensilla trichodea, modification in form, and antennomere 11 with its concentration of sensilla basiconica; various modifications of labrum, maxillae, and labium, suggesting changes in food or feeding mechanisms; and the peculiarly modified palpiform stylomeres of the females, which suggest a sensory function rather than one of simple deposition of eggs.

We believe that the reduced antennal cleaner of the fore tibia has developed twice: once in the ancestral stock of *Physea* + *Physeomorpha*, and once in the ancestral stock of *Ozaena* + *Platycerozaena*. This feature, plus loss of tactile setae from the *Ozaena-Platycerozaena* lineage, presages similar losses from the paussine lineage, as pointed out by Darlington (1950) for *Physea*. He noted, as well, the myrmecophilous habits of *Physea* and the paussines. Another similarity to the paussine lineage is the peculiar sensilla basiconica of adults of *Ozaena* and *Platycerozaena*. Conceivably, either the *Physea* or *Ozaena* lineage could be the sister group of the paussines, though the similarities might reflect simply parallel developments, based on an underlying general similarity.

The general ecologically-based scenario that we think the data reflect is one of: evolution in the tropics of form, structure and habits for life under bark (*Entomoantyx* and *Pachyteles*); differentiation in the sub-cortical habitat (*Pachyteles*); secondary loss or modification of these features, associated with development of a myrmecophilic existence (*Physea* and *Physeomorpha*). We do not have information about habitat for the *Ozaena-Platycerozaena* lineage, but we judge from body form of adults that they are sub-cortical, and we believe that they are adapted for life with ants, too.

A different scenario, based on lack of association of *Physea* adults with sub-cortical habits, places its lineage at the base of the Ozaenini.

Finally, we believe that *Metrius* is a relict genus, surviving in the temperate zone, living in an ancestral-type habitat of leaf litter, beyond the periphery of the range of its more evolved ozaenine relatives. In many body features, adults are primitive, but not in body form, absence of wings, or in development of the large intercoxal process of the prosternum. Thus, this basically primitive group has evolved its own special features.

TAXONOMIC TREATMENT

Provided in this section are: description of the Tribe Ozaenini based on features of adults of New World taxa; descriptions of the genera known from Middle America; and descriptions of selected species. These species are either known from the United States, or their northern limit of geographical range is near the U. S.-Mexican border, or their structural features indicate aspects that we found instructive in appreciating the divergence of the New World Ozaenini.

For the species, we report limited quantitative data: range of body size (Standardized Body Length and maximum width). The only generally useful ratio that we found and report here is width of elytra/ Standardized Body Length (W/SBL). Two groups are recognized in the material that we examined: species with low values (0.31-0.35), whose adults have long slender bodies; and species with higher values (0.37-0.46), whose adults have broader, stouter bodies.

Tribe OZAENINI

Description.— Adults small to average for Carabidae (SBL *ca.* 3-18 mm.). Body form sub-cylindrical to terete and explanate.

Color. Body uniform black to testaceous, or various combinations of these somber colors, or aeneous-green; elytra somber-colored, or aeneous, like rest of body, or bright metallic blue-green.

Microsculpture. Most members with mesh pattern of dorsal sclerites (including elytra) isodiametric, mesh pattern of lateral and ventral sclerites predominantly transverse, though surface not grated (Allen and Ball, 1980: 487); some members with mesh pattern of body sclerites and elytra uniformly isodiametric; microlines distinctly developed, or partially effaced and thus difficult to see at magnification of 50X or less, or absent (Fig. 107A).

Luster. Dorsum (including elytra) dull (most members) or glossy, venter more glossy, or dull as dorsum.

Vestiture. Surfaces of body and elytra either with or without pile of short trichoid (hair-like) setae, pilosity dense or sparse; members of most taxa with ventral and lateral sclerites sparsely pilose. Articles of legs sparsely or densely pilose. Members of some taxa with setae on head and prothorax, and/or serially arranged setae on various intervals of elytra. Wider, flat, costate setae (Fig. 107A and B) on dorsal surfaces of pronotum and elytra of members of some taxa. Fore tarsomeres 1-3 of males (Fig. 66C) with or without adhesive vestiture. Mandibles, cardines, submentum and mentum with or without pilosity.

Fixed (or standard) setae (*i.e.*, those characteristic of most carabid taxa) and spines. Clypeus with one to three pairs of setae laterally, or asetose. Head with one pair of supraorbital setae (members of some taxa with supraorbital setae indistinguishable from other long trichoid setae of head), or asetose. Antennae: trichoid setae as follows— antennomere 1 with one to several; antennomeres 2 and 3 with ring of few near apex, antennomere 4 with one or several rings of few, preapically; antennomeres 5-11 with many to few, variously arranged, or antennomere 11 without; other setae— shorter, thicker basiconic sensilla on antennomeres 5-11, associated with rugose matt areas variously, from numerous and widely distributed on lateral surfaces to very few concentrated in small oval areas on ventro-lateral surfaces, or toward apex of antennomere 11 (Figs. 29A&B, 30). Labrum pre-apically with seven to 12 forward-directed setae, or asetose (*Platycerozaena* members). Mandibles each with or without single long seta in scrobe (Fig. 40A) (members of *Physea* with numerous long setae, one of which may be the normal seta of the scrobe). Maxillary setae: cardo asetose or with one to three; stipes, two; palpomere, several. Labial setae: submentum, two to five or six; mentum, two to five or six; glossal sclerite, two to four; palpomeres 2 and 3 plurisetose (Figs. 44-47); palpomere 1 glabrous or with few setae. Pronotum with more than two pairs of lateral marginal setae, or without marginal setae. Prosternum with apex glabrous or sparsely setae. Elytra with umbilical setae (each elytron with about 30), without parascutellar setae, with or without (members of few taxa) discal setae. Tibiae each with several rows of spines. Tarsomeres 1-5 ventro-laterally with one or two rows of setae on each margin, ventral surfaces of tarsomeres 1-4 with patches of longer setae. Standard setae of abdominal sterna not distinguishable from vestiture.

Head. Form approximately quadrate. Clypeus transverse, surface plane, anterior margin slightly concave. Frons and vertex uniformly slightly vaulted, or frons with pair of indistinctly delimited impressions near fronto-clypeal suture. Supra-antennal areas ridged laterally, flat or reflexed. Occipital area broad, not constricted, or with shallow groove dorsally. Temporal areas either small or swollen laterally, each as narrow lobe extended on posterior surface of eye. Antennal fossae close to anterior margin of eye, sub-antennal area either plane or depressed. Gula average. Eyes elliptical, with long axis either parallel or perpendicular to long axis of head.

Antennae. Varied in relative length, from shorter than combined length of head and pronotum, to about one third of body length; filiform to sub-clavate; antennomere 1 (scape) large; antennomere 2 (pedicel) shorter than scape, small; antennomeres 3 and 4 elongate or short and moniliform; antennomeres 5-10 sub-cylindrical, longer than wide (Fig. 10); or more or less compressed, extended ventro-laterally, broad surfaces anterior and posterior with antenna extended at right angles to longitudinal body axis, either longer than wide (Fig. 11), quadrate (Fig. 13), or wider than long (Fig. 15); or moniliform, short, thick and cylindrical (Fig. 14); antennomere 11 (Figs. 25-30) more or less enlarged, either longer or wider than antennomeres 5-10, shape various— pre-apically sub-cylindrical (Fig. 25) or more or less transverse (Figs. 29A-30), apex blunt or narrowly keeled, keel straight (Fig. 29A) or sinuate (Fig. 30).

Mouthparts. Labrum transverse, narrow (Fig. 32), or broader (Figs. 33, 35, and 36), or almost as long as wide (Fig. 37); anterior margin straight or broadly concave, or narrowly notched (Fig. 37). Mandibles: trigonal, with broad bases, symmetrical in general outline, scrobes broad, distinctly marked, retinaculum very large (Figs. 40A-D) or small (Figs. 39A-D); terebral margins prominent, posteriorly extended or not on dorsal surface of retinaculum (Fig. 42A); terebral tooth evident on both left and right mandibles (Figs. 39A,B- 43A,B); retinaculum prominent or not, posterior tooth more or less evident, directed posterad, anterior tooth prominent or not; molar area variously toothed; ventral groove more (Fig. 40C-D) or less (Fig. 39C-D) extensively densely setose. Maxillae: average for Carabidae; lacinia with apical tooth normal (long and slender, Fig. 46), or shorter and broader, chisel-like (Fig. 47B); galeomeres 1 and 2 of various proportions; palpomeres various, 4 relatively slender (Fig. 45) to broad (Figs. 47A and 48). Labium: submentum narrow, transverse; mentum transverse, lateral lobes of various lengths, more or less tapered apically; epilobes prominent; mental tooth large or small, apically not notched (in New World taxa); ligula uniformly sclerotized, paraglossae adnate to glossal sclerite, latter with blunt apex. Palpomeres 2 and 3 subequal, longer than 1; palpomere 3 slender or broad, apical margin broad, subtruncate.

Prothorax. Pronotum transverse or longer than wide, short compared to length of elytra; base and apex similar in width, but base distinctly narrower than apex; disc slightly convex, median longitudinal and anterior transverse impressions shallow, posterior transverse impression shallow to deep; lateral grooves distinct, postero-lateral impressions shallow to deep; sides plane or reflexed, lateral margins broad or narrow, evenly curved throughout length or more or less sinuate posteriorly; antero-lateral and postero-lateral angles various, from broadly obtuse to narrowly acute. Proepipleura broad, either sharply extended laterally and horizontal to pleuronotal margin, or extended dorsad in same plane as pleuron. Pleural sclerites average for Carabidae. Prosternum with intercoxal process broad or slender, with apex near posterior margins of coxae.

Pterothorax. Mesepisternum and mesosternum separated by suture. Mesepimeron extended to margin of mid-coxa, broad, posterior margin sinuate, medially overlapping metepisternum. Mesosternum narrow, intercoxal process in contact or not with process of metasternum. Metathorax of average proportions, or distinctly shortened. Metepisternum long and slender, with lateral margin much longer than width of basal margin; or short and broad, with lateral and basal margins subequal. Metepimeron distinct, wide in relation to apical width of metepisternum. Metasternum average for Carabidae.

. Elytra. Elongate, parallel-sided, or expanded and inflated, with widest point near middle, and tapered both anteriorly and posteriorly. Disc flattened or somewhat inflated, tapered gradually apically. Basal ridge short, extended no farther than plane of base of interneur 4, and anterad discal plane. Humeri each denticulate or rounded. Apical margin oblique. Flange of Coanda (Fig. 70B) preapico-lateral. Intervals moderately convex to flat, interneurs shallow, punctate or not, obsolescent or absent. Epipleura average for Carabidae.

Metathoracic wings. Fully developed in adults of most taxa, variously reduced in few. Oblongum cell large, quadrangular; wedge cell absent.

Legs. Coxae, trochanters, middle and posterior femora and tibiae average for carabids, or tibiae markedly compressed (Figs. 64A-B). Anterior and posterior coxae separated from one another by intercoxal processes; middle coxae separated or not by intercoxal processes. Front femur more or less cylindrical or flattened, with or without antero-ventral projections (Figs. 58-61A,B) or swellings (Fig. 57). Front tibia isochaete (both spurs terminal), expanded apically or flattened and generally explanate. Antennal cleaner with channel large (Figs. 66A-B) or smaller; medial expansion prominent (Figs. 67A-B) or not (Figs. 68A-B); clip setae (Fig. 65) present or absent; anterior setal row with setae large (Figs. 67A-B) or small (Figs. 64A-B); setal band not sinuate (Fig. 68B) to markedly so (Figs. 67A-B). Tarsomeres thickened, with dorsal surfaces slightly depressed, 5 longer than any of 1-4, tarsal claws smooth, not denticulate.

Abdomen. Sterna II-VII and tergum VIII average for carabids, without distinctive features. Males with sternum VIII with pair of small hemisternites, without apodemes, joined medially by membrane. Ring sclerite (Segment IX-X, Figs. 92-96) of males with tergum narrow, laterally each side with sclerotized explosion chambers (*ec*) of pygidial gland system; sternal apodemes joined in form of symmetrical or markedly asymmetrical ring; right hemisternite various in form, bilobed or not. Females with sternum VIII (Figs. 98-102) with pair of more or less reduced hemisternites, joined medially by membrane; hemisternites setose or asetose, each with short apodeme projected anteriorly. Tergum IX/X narrow.

Male genitalia. Median lobe compressed, basal opening wide; apical portion various, from simple short point to more or less elaborate ventrally-directed projection (Fig. 87A) or cleft (Fig. 89B); apical orifice dorsal. Ejaculatory duct in median lobe surrounded by long, rod-like sclerite (rod, **r**, Figs. 83A-91A, and 97A). Internal sac short, infolded but only partially inverted, with three areas: basal asetose membranous area; medial collar, with microtrichia; and apical portion variously lobed and with or without sclerites (Figs. 83-91, and 97). Parameres extensive, left broad basally but tapered apically, apex with or without few setae. Right paramere long, apex extended nearly to apex of median lobe, medial margin fringed with setae, more or less extensively (Figs. 83-91, and 97).

Ovipositor. Ventral surface ventrally directed in repose. Valvifer slender, moderately long. Stylomere single sclerite, slender, of various length, variously setose and spinose, apex pointed (Fig. 71A), more broadly rounded (Fig. 81A), subtruncate (Fig. 73A), or cleft (Fig. 74B). Sensory furrow preapical (Figs. 71, 74A-B) or apical (Figs. 76A-B) with long nematoid setae and furrow peg setae, margins without ensiform setae.

Way of life.— Little is known about this topic (Ball, 1960: 94). Adults of various species of *Pachyteles* (*sensu lato*) have been collected from under bark of fallen tree trunks in lowland wet tropical forests and from under bark of fallen cottonwood poplars along waterways in semi-desert areas. Adults of *Pachyteles kuntzeni* have been collected at night, on dead oak trees and stumps. Adults of *Physea hirta* LeConte have been collected in association with leaf-cutter ants of the genus *Castelnau*. Most ozaenine adults, however, have been collected at ultra-violet light at night, showing that they are active nocturnally.

Adults and larvae of the non-myrmecophilous species probably are general predators under bark, an inference based on their general structural features. Forsythe (1982 and 1987) recognizes three types of feeding in carabids: fluid feeding; fragmentary feeding; and mixed feeding. Mixed feeders are of two types: either predominantly zoophagous or predominantly phytophagous. Each of these types has characteristic mandibles and maxillae. Details of mandibular and maxillary structure of adult ozaenines indicates that they are mixed feeders, predominantly zoophagous. This means that individuals take particulate animal matter, but secrete digestive juices extra-orally, on the prey. Thus, presumably, a certain amount of digestion is extra-oral.

Geographical distribution.— In the New World, the range of the Ozaenini extends from southern South America (Argentina in the east and Chile in the west) northward through Central America to southwestern United States (southern Texas in the east, and southern Arizona in the west).

Included taxa.—Six New World genera are included in the Ozaenini: *Entomoantyx*, new genus; *Physea* Brullé; *Physeomorpha* Ogueta; *Pachyteles* Perty; *Ozaena* Olivier; and *Platycerozaena* Bänninger. Of these, *Physeomorpha* is confined to South America, and *Entomoantyx* to Middle America. The remaining genera are in both South and Middle America, and *Physea*, *Pachyteles* and *Ozaena* reach their northern limits in southern-most southwestern United States.

Key to Genera of Metriini and Ozaenini of Middle and North America, and Species of Southwestern United States and Northern Mexico

1 Fore tibia with both spurs terminal (Fig. 65B). Fore coxal cavities closed by medial extension of proepimera. Pterothorax with middle coxal cavities disjunct (mesepimeron extended to middle coxa)..2

1' Combination of character states otherwise. ....other tribes of Carabidae.

2 (1) Elytron without flange of Coanda (*cf.* Fig. 70A). Mentum with tooth notched apically (Fig. 49) or not. Metathorax with metepisternum short, length of lateral margin subequal to width at basal margin. Mandible with single seta in scrobe....................

.........Tribe Metriini, *Metrius* Eschscholtz. (not treated further).

2' Elytron with flange of Coanda (Fig. 70A), body form various. Tooth of mentum not notched apically (Figs. 50-55). Mandibles with one or many setae in scrobe ....
..........................Tribe Ozaenini. 3

3 (2') Mandible with single long seta in scrobe (Fig. 40A). Antennae filiform, antennomeres 5-11 densely setose, 1-4 sparsely so. Elytra metallic blue-green, sharply contrasted with rufous head and prothorax..............*Entomoantyx cyanipennis* (Chaud.), p. 84

3' Mandible with several (five or more) setae in scrobe (Figs. 39A, 41A). Antennae various in form. Dorsal surface more or less uniform in color, black, piceous, or testaceous.............................4

4 (3') Tibiae markedly compressed and broad (Fig. 64A). Fore femur with prominent broad swelling near base (Fig. 57). Head with broad depression (antennal fossa) beneath anterior margin of eye ....*Physea* Brullé 5

4' Tibiae sub-cylindrical, not compressed and broad. Fore femur with broad swelling or spine (Figs. 58-62). Head without antennal fossa 6

5 (4) Elytra with uniform vestiture of short setae, in addition to long tactile setae...*Physea hirta* LeConte, p. 87

5' Elytra without vestiture of short setae, only several rows of long, tactile setae.............................*Physea latipes* Schaum, p. 87

6 (4') Anterior tibia with prominent clip setae associated with antennal cleaning channel (Fig. 65B), latter extended beyond median expansion. Head, pronotum and elytra with normal long setae, with or without more or less dense vestiture of short trichoid setae. Mandibles with dorsal surfaces impunctate.........
....*Pachyteles* Perty.. 7

6' Fore tibia without clip setae, channel of antennal cleaner terminated at plane of median expansion (Fig. 68A). Head, pronotum and elytra without normal long setae, glabrous, or with vestiture of short, thickened setae (Fig. 107A). Mandibles with dorsal surfaces more or less densely punctate (Figs. 42A, B-43A, B) 12

7 (6) Middle coxae in contact with one another, not separated by intercoxal extensions of meso- and metasterna...................................8

7' Middle coxae separated by extensions of meso- and metasterna...10

8 (7) Pronotum and dorsal surface of elytra with vestiture of short setae.. ....*Pachyteles gyllenhali* (Dejean), p. 94

8' Pronotum and elytra with sparse, longer setae, those of elytra in rows on intervals...9.

9 (8') Pronotum with anterior and posterior lateral angles acute............
....*Pachyteles mexicanus* Chaudoir, p. 97

9' Pronotum with anterior angles rounded, posterior angles about rectangular....................*Pachyteles enischnus*, new species, p. 96

10 (7') Pronotum narrow, only slightly wider than, or about as wide as, head..................................*Pachyteles elongatus* (Chaudoir), p. 93

10' Pronotum broader, distinctly wider than head 11
11 (10') Smaller (SBL 9-12 mm.), pronotum narrower (Fig. 3). .... *Pachyteles parca* LeConte, p. 90
11' Larger (SBL 15-18 mm.), pronotum broader (Fig. 4) .... *Pachyteles kuntzeni* (Bänninger), p. 92
12 (6') Antennae long, about one third length of body; antennomere 11 with shagreened area confined to apical third (Fig. 22), apical ridge straight (Fig. 29A)........*Ozaena lemoulti* Bänninger, p. 100
12' Antennae short, claviform, antennomeres 5-11 markedly broad and flat; antennomere 11 with shagreened area apical and extended along dorsal and ventral margins (Fig. 23); apical ridge sinuate (Fig. 30) ....*Platycerozaena* Bänninger, p. 101

Entomoantyx, new genus

Frontispiece, and Figs. 11, 19, 26, 33, 40A-D, 51, 58, 65A-B, 70A-B, 73A-B, 83A-D, 93, 99, and 104.

TYPE SPECIES: *Ozaena cyanipennis* Chaudoir, 1852: 40. Here designated.
Ozaena; Chaudoir, 1852: 40.—1854: 307.
Pachyteles; Chaudoir, 1868: 66.— Bates, 1881: 27.— Csiki, 1927: 427.
Tropopsis; Bänninger, 1927: 207.— Blackwelder, 1944: 23.— Reichardt, 1977: 377.— Erwin, 1979B: 557.

Notes about synonymy.— The type species of *Entomoantyx* was removed from *Pachyteles* and included in *Tropopsis* Solier by Bänninger on the basis of plesiotypic features (middle coxae separated; fore femur without ventral spine; antennal cleaner of fore tibia less modified). But, in apotypic features of antennal form and development of the antennal cleaner, *T. marginipennis* Solier (type species of *Tropopsis*) is more like *Pachyteles* than like *E. cyanipennis*. Furthermore, *E. cyanipennis* is characterized by a unique derived feature (form of mental epilobes), reduced number of labral setae (seven or eight), and more plesiotypic features than *Pachyteles* or *Tropopsis* in retaining a scrobal seta, a hardly modified antennal cleaner, and probably structure of the male genitalia (presence of a dense dorso-basal patch of microtrichia, and styliform right paramere). We believe, thus, that *E. cyanipennis* is not closely related to either *Tropopsis* or *Pachyteles*. For these reasons, we remove *E. cyanipennis* from *Tropopsis*. Because *E. cyanipennis* does not have a named genus for assignment, we have proposed a new one. Because the differences between *Tropopsis* and *Pachyteles* are slight, we combine these taxa, with the former name being a junior synonym. See below for details.

Derivation of generic name.— From the Greek *entomon*, cut, and *antyx*, margin, a name that alludes to the scalloped lateral margins of the pronotum of adult *E. cyanipennis*.

Recognition.— Adults are recognized easily among Middle American ozaenines by the bright bluish-green elytra that contrast strikingly with the rufous head and pronotum. The lateral margins of the pronotum (Frontispiece) are scalloped. Body size is small. The antennae, though rather short, have antennomeres 5-11 longer than wide (Fig. 11). Males have fore tarsomeres 1-3 with adhesive setae ventrally, median lobe of genitalia with a broad truncate apex (Figs. 83A-B), and internal sac with a sagittate dense patch of microtrichia dorso-basally (**x**,Fig. 83B), and left paramere digitate and densely setose apically. Females are characterized by rather short, broad stylomeres (Figs. 73A-B), with subtruncate apex and sensory groove markedly preapical.

Description.— Habitus as in Frontispiece. Size small, SBL ca. 3.5-4.5 mm., width 1.5-2 mm.

Color. See "Recognition" section, above.

Microsculpture and luster. Pterothoracic pleura and sterna with mesh pattern transverse; otherwise, as described for tribe. Surface generally slightly shining.

Vestiture. Tarsomeres with dorsal surfaces sparsely setose; fore tarsomeres 1-3 of males ventrally with adhesive vestiture. Thoracic and abdominal sterna with sparse covering of rather long setae. Otherwise, as described for tribe.

Chaetotaxy. Clypeus with two pairs of setae. Vertex of head with one pair of supraorbital, one pair of paramedial, and one pair of paralateral setae, latter two groups in row across vertex. Antennae: antennomere 1 with several setae; antennomeres 2-4 with apical row of long setae; antennomeres 5-11 with dense covering of setae, except nearly glabrous areas on anterior and posterior faces. Mouthparts: labrum with seven to eight long setae near anterior margin; mandibles each with one long seta in scrobe (Figs. 40A-B); maxillary stipites each with two lateral setae; submentum, mentum, and glossal sclerite each with one pair of setae. Pronotum with three pairs of lateral setae: one pair anteriorly, one pair near middle, and one pair anterior to postero-lateral angles; one pair of paramedial setae near anterior margin. Each elytron with about five setae in intervals 3 and 5, umbilical setae *ca.* 15. Legs, number of setae (fore, middle and hind): coxae, 0-numerous-numerous; trochanters, 1-1-1; femora, numerous, numerous, numerous.

Head. Frons without impressions. Eyes moderately prominent (Frontispiece); temporal area each side small, not swollen. Supraantennal area each side with sharp ridge.

Antennae (Figs. 11, 19 and 26). Filiform, antennomeres 5-10 slightly longer than wide, antennomere 11 distinctly so (Fig. 11). Antennomere 11 (Fig. 19) with apex about symmetrical, moderately broadly rounded; circular in cross section, apical margin without distinct keel (Fig. 26).

Mouthparts. Labrum (Fig. 33) transverse. Mandibles (Figs. 40A-D): see Table 1 for details. Maxillae: average for Ozaenini, as in Figs. 45 and 46. Labium (Fig. 51): mentum with prominent tooth, lateral lobes broadly rounded apically, epilobes each with sharp tooth near apex; palpomere 3 triangular, with apex subtruncate.

Prothorax. Pronotum (Frontispiece) transverse; lateral grooves moderately broad; disc convex; linear impressions (anterior transverse and median longitudinal) clearly impressed; lateral margins scalloped; postero-lateral impressions deep. Propleura and prosternum as described for tribe.

Pterothorax. As described for tribe, and middle coxal cavities separate, with meso- and meta- intercoxal processes in contact with one another. Metepisternum not overlapped by extension of mesepimeron.

Elytra. Intervals broad, indistinctly elevated, interneurs shallow, indistinct. Basal ridge extended to about base of interneur 5.

Legs. In most features, as described for Ozaenini. Fore femur terete in cross section, without ventral projections. Antennal cleaner of fore tibia (Figs. 65A and B): grade C (see under "Structural and Biochemical Features"); details in Table 2.

Abdomen. Segments II-VII with tergum and sternum unmodified. or description of segments VIII and IX/X, see under "Structural and biochemical features, genital segments".

Male genitalia (Figs. 83A-D) and ovipositor Figs. 73A-B). See these items under "Structural and biochemical features", and Table 3 for details of male genitalia.

Ovipositor (Figs. 72A-C). Stylomeres of moderate length, broad at base. For details, see this topic under "Structural and biochemical features".

Bursa copulatrix and spermatheca. See Fig. 104 and for details, Table 4.

Way of life.— Members of this genus live in lowland tropical forests. Adults have been collected under bark of fallen tree trunks, and at U-V light, at night. The distinctive color pattern of red and blue suggests aposomaty, and this may be indicative of a way of life that differs from other New World ozaenines— for example, more time spent by adults in situations where they are exposed to predators that hunt using visual stimuli.

Geographical distribution.— This genus is known only from the Gulf-Caribbean Versant of Middle America: from Nicaragua northward to the state of Veracruz, México.

Relationships.— This genus is either a very primitive member of the *Pachyteles* assemblage of Ozaenini, or possibly even the sister group of the other assemblages of ozaenine genera, excluding the Australian *Mystropomus* Chaudoir and Oriental *Anentmetus* Andrewes.

Included species.— *Entomoantyx* includes only the species *E. cyanipennis* (Chaudoir).

Entomoantyx cyanipennis (Chaudoir)

Ozaena cyanipennis Chaudoir, 1852: 40. TYPE MATERIAL: three males, each labelled "Ex Musaeo Chaudoir [red print] in front of following box label: "*cyanipennis* Chaud. Mexique 57 Salle"; Chaudoir-Oberthür Coll., Box 132 bis (MNHP). LECTOTYPE (here selected), first specimen in series.— Species synonymy same as for genus, above.

Ozaena cyanoptera Thomson, 1856: 330. TYPE MATERIAL: HOLOTYPE female, labelled "Ex Musaeo Chaudoir" [red print], in front of following box label: "cyanipennis Chaud Bul Mus 1852 p. 40 cyanoptera Thomson Ann Soc Ent 1856 p. 330 Toxpam".

Pachyteles cyanipennis Chaudoir, 1868: 66.— Bates, 1881: 27.— Csiki, 1927: 428.

Tropopsis cyanipennis; Bänninger, 1927: 207.— Blackwelder, 1944: 23.— Reichardt, 1977: 377.

Pachyteles cyanoptera; Chaudoir, 1868: 66.

Notes about synonymy.— Chaudoir (1868: 66) recognized the taxonomic identity of the types of *Ozaena cyanipennis* and *O. cyanoptera*, and established the synonymy, accordingly.

Recognition.— Among New World ozaenines, adults of *E. cyanipennis* are unique in color pattern: rufous head and prothorax, and metallic blue elytra. Adults are small in size.

Habitus as in frontispiece. Standardized Body Length (male) 4.4 mm; females 3.8-4.1 mm. Width, male 1.92 mm., females 1.6-1.7 mm; W/SBL male 0.44, females 0.42-0.43. Other features as noted for genus *Entomoantyx*, above.

Way of life and geographical distribution.— As above, under *Entomoantyx.*

Material examined.— In addition to the types, we have seen 14 specimens from México, as follows.

Chiapas. 27 km. SW Simojovel, VII.17.1962; J.M. Campbell (CNCI). **Veracruz**. Cordova, VI.29.1966; J.S. Buckett, M.R.& R.C. Gordon (CISC). 33 km. NE Catemaco, Los Tuxtlas Biological Station, 160 m, VII.1983; S.& J. Peck (UASM). Coyame, at Lake Catemaco, VII.1-15.1963; D.R. Whitehead (UASM). Lake Catemaco, V.24-25.1969; H.F. Howden (UASM). Dos Amates, VI.16-17.1969; D. Bright & J.M. Campbell (CNCI). Sontecomapan, VI.10.1969; H.F. Howden (UASM).

Physea Brullé, 1834

Physea 1834: 473. TYPE SPECIES: *Trachelizus rufa* Brullé [= *Ozaena testudinea* Klug, 1834: 80]; by monotypy.— Chaudoir, 1854: 289, 310.— 1868: 72.— Lacordaire, 1854: 160.— Bates, 1881: 27.— Csiki, 1927: 431.— Bänninger, 1927: 212.— Van Emden, 1942: 25.— Blackwelder, 1944: 23.— Jeannel, 1946: 47.— Darlington, 1950: 50, 51, 65.— Ball, 1960: 94.— Reichardt, 1977: 376.—Thompson, 1979: 214.— Erwin, 1979: 557.

Trachelizus Brullé, 1834: 258. TYPE SPECIES: *T. rufa* Brullé, 1834: 259; by monotypy.— Solier, 1836: 598.— Chevrolat, in d'Orbigny, 1848: 626.— Chaudoir, 1854: 310.

Trachelyzus Chenu, 1851: 89.

Notes about synonymy.— The generic name *Trachelizus* appeared first in the Dejean catalogue (1834: 243), credited to Chevrolat, for a genus of brentids. Brullé (in Audouin and Brullé, 1834: 258) used this name, credited to Solier, for a genus of ozaenine carabids, with *T. rufus* Solier as the only included species, and thus type of this genus. Subsequently, in an addendum to the same volume (1834: 473), *Physea* Brullé was proposed as a replacement name for *Trachelizus*, on the basis that the latter name was, in effect, a junior homonym of *Trachelizus* Dejean. Also implied in the text was that *Ozaena testudinea* Klug, 1834 was a senior synonym of *T. rufus* Brullé. In any event, the name of the type species of *Physea* must be *Trachelizus rufus,* though the correct name of the *species* is *P. testudinea* Klug.

Derivation of generic name.— From Greek, meaning ampoule or bulb-shaped lamp; a vial for holy oil; evidently in allusion to the body form of an adult, which resembles a rather broad bottle constricted toward the top. with a narrow opening, corked by the head. The word *Trachelizus* is from Greek, meaning to wring or twist, presumably in allusion to the seemingly marked constriction between head and pronotum.

Recognition.— Adults are rufous or rufo-brunneous in color, with partially darkened appendages. The elytra are inflated and broad in relation to length (Fig. 2). Antennomeres 5-10 (Fig. 10) are filiform, distinctly longer than wide. The legs are flattened, especially the tibiae (Figs. 64A and B), and the tarsomeres are relatively slender. These features render *Physea* the most easily recognized genus in the Ozaenini.

Description.— Habitus as in Fig. 2. Size moderate, SBL ca. 10-12 mm., maximum width 4.9-5.2 mm.

Color. Body uniform rufous or rufo-brunneous; appendages same color, or mandibles, antennomeres and tibiae darkened.

Microsculpture and luster. As for Ozaenini, with mesh pattern transverse on mesepimera, isodiametric on mesepisterna, and isodiametric to slightly transverse on metepisterna. Dorsal surface matte, ventral surface matte or pterothoracic and abdominal sterna slightly iridescent.

Vestiture. Dorsal surface setose or glabrous, mandibles with scrobes setose basally. Ventral surface generally setose, or at least abdominal sternum IV with paramedial patches of setae, and row of setae near posterior margin of each of sterna IV to VII. Male fore tarsomeres 1 and 2 with adhesive vestiture ventrally.

Chaetotaxy. Clypeus with about 12 setae. Vertex with one pair of supraorbital setae and transverse row of about four shorter setae. Antennae: antennomere 1 (scape) with several setae; 2 and 3 each with preapical ring of setae; antennomere 4 with scattered setae; antennomeres 5-11 generally setose except anterior and posterior glabrous areas. Mouthparts: labrum (Fig. 32) with row of about 10 setae near anterior margin; mandibles without fixed setae; maxillary stipes laterally with two setae; submentum, mentum, and glossal sclerite each with single pair of setae; mentum without paramedial setae; labial palpomere 2 trisetose. Pronotum with marginal setae numerous anteriorly and posteriorly, asetose medially. Each elytron with several rows of long setae on disc. Legs (number of setae, fore, middle, and hind): coxae, 0-numerous-numerous; trochanters, several-several-one or two; femora, numerous-numerous-numerous.

Head. Frontal impressions not indicated. Eyes in lobate setose clefts, large. Supraantennal area reflexed strikingly anteriorly, in form of broad plate each side (Fig. 2).

Antennae (Figs. 10, 18 and 25). Antennomeres 5-11 (Fig. 10) filiform, distinctly longer than wide. Antennomere 11 (Fig. 18) with apical margin markedly asymmetrical, apex narrowly rounded, without distinct ridge (Fig. 25).

Mouthparts. Labrum transverse (Fig. 32). Mandibles (Figs. 39A-D) falcate, most of occlusal margin smooth. or details, see Table 1. Maxillae average for Ozaenini, lacinia (*cf.* Fig. 46) terminated in long sharp tooth; palpomeres slender, elongate, apex of maxillary palpomere 4 subtruncate. Labium (Fig. 50): mentum with broadly rounded lateral lobes, each epilobe widened preapically; tooth prominent; labial palpomere 3 elongate, slender, apex truncate.

Prothorax. Pronotum (Fig. 2) markedly transverse, sides markedly reflexed, lateral margins smooth; lateral grooves broad; impressions shallow. Prosternum with intercoxal process narrow.

Pterothorax. As described for Ozaenini, and intercoxal processes of meso- and metasternum reduced, middle coxal cavities and middle coxae in contact medially. Metepisternum overlapped by lobe of mesepimeron.

Elytra. Markedly expanded, convex. Surface smooth, flat, no indication of intervals and interneurs. Basal ridge extended only to about base of interneur 6.

Legs. Middle coxae globose, more so than usual. Femora (Fig. 57) and tibiae (Figs. 64A and B) markedly compressed, especially tibiae. Femora with ventral surfaces grooved, fore femur (Fig. 57) with swelling ventrally, near base. Antennal cleaner of fore tibia (Figs. 64A and B) small. For details, see Table 2.

Abdomen. Sclerites of segments II-VII unmodified. or description of sclerites of segments VIII and IX-X, see under "Structural and biochemical features, genital segments". See also Figs. 94 and 100A and B.

Male genitalia (Figs. 84A-D). For details, see this topic under "Structural and biochemical features" and Table 3.

Ovipositor (Figs. 71A-C). Ştylomeres long and slender, blade-like. or details, see this topic under "Structural and biochemical features".

Bursa copulatrix and spermatheca (Fig. 105). For details, see this topic under "Structural and biochemical features", and Table 4.

Defensive secretions.— Three compounds, only. See Table 5 for details.

Way of life.— Members of this genus seem to be associated with leaf-cutter ants of the genus *Atta*. See under species treatments, below, for additional details.

Geographical distribution.— This genus is confined to the New World, ranging on the mainland from Argentina to southwestern United States.

Relationships.— In body and leg form and structure of the antennal cleaner, adults of *Physea* are much like those of the monobasic genus (1965a: 113). They differ in form of antennomeres, however, those of *Physeomorpha* being very short and transverse. In spite of this difference, we believe that these genera are closely related, and may be congeneric.

Jeannel (1946: 47) placed *Physea* in a monobasic subfamily, because of its obvious distinctiveness within the Ozaenini. Enhancing the distinctiveness of body form and leg form are the distinctive mandibles, male genitalia, elongate stylomeres of the ovipositor, bursa copulatrix, and bursal sclerite, and myrmecophilous way of life. In other derived features (pterothoracic structure, absence of the scrobal seta from the mandibles, trisetose labial palpomeres and a complex set of defensive chemicals), adults of *Physea* are like other New World ozaenines.

The filiform antennae seem to be a remarkably plesiotypic feature, for they are more slender than the antennae of adult *Metrius*, the primitive sister-group of the Ozaenini. This feature should not be over-emphasized, for two reasons. First, the putative sister-genus of *Physea* exhibits more typical ozaenine antennae. Second, the antennal cleaner is suggestive of a taxon whose members once had antennal articles that were too extensive to be cleaned effectively by such a structure, and accordingly the latter was reduced. Subsequently, then, the antennomeres became slender, once more. Thus, their seeming primitiveness is secondary, and therefore, these structures are apotypic.

At this time, we are not in position to offer an hypothesis that provides a sister group for the lineage *Physea* + *Physeomorpha*.

Included species.— Six species are members of this genus, including two, *P. hirta* LeConte and *P. latipes* Schaum, that live in México (with the former also occurring in Texas), and that are treated below.

Physea hirta LeConte

Figs. 10, 18, 25, 32, 39A-D, 45, 50, 57, 64A-B, 71A-C, 84A-D, 94, and Map 1.

Physea hirta LeConte, 1853: 393. TYPE MATERIAL: HOLOTYPE male, labelled "Type 5488" [red paper]; "*Physea* hirta Lec" [handwritten]; (MCZ). TYPE LOCALITY (from original description): México, near U.S. border (Haldeman).— Chaudoir, 1854: 312.— 1868: 72.— Bates, 1881: 27.— Csiki, 1927: 431.— Bänninger, 1927: 212.— Blackwelder, 1944: 23.— Leng, 1920: 49.— Johnson, 1978: 67.

Recognition.— In habitus (Fig. 2), adults are similar only to those of *P. latipes* Schaum Fig. 2). The two species are distinguished by setation (see key) and pronotal form: elevated lateral portions much broader in *P. hirta*, and anterior margin sharply concave.

Habitus as in Fig. 2. Characteristics of *Physea*. Standardized Body Length, males 10.7-11.1 mm., females 10.5-11.7 mm; W/SBL males 0.44-0.45, females 0.44.

Way of life.— Adults were collected in Chiapas and Veracruz in and around the midden heaps of *Atta* nests, in daylight hours. Van Emden (1936), in a description of the larva of *P. setosa* Chaudoir, notes that both larvae and adults of this species live in *Atta* nests. Specimens have been collected at night, also. The late Jorge Hendrichs, of México City, advised the senior author that he had collected specimens of what was probably this species at night, in the vicinity of columns of *Atta* workers.

Geographical distribution.— This species is known from the Gulf and Pacific Versants of Middle America, from Guatemala to southeastern Texas.

Material examined.— From México and the United States, we have seen 20 specimens from the following localities.

UNITED STATES OF AMERICA. **Texas**. **Comal Co.** (USNM). **Kennedy Co.** 27°10'N, 97°40'W, VIII.28.1976; J.E. Gillaspy (TAIU).

MÉXICO. **Chiapas**. E. slope, Sierra de la Colmena, 16° 24'18"N, 91 24'16"W, Arroyo Santa Maria, 213 m., nr. *Atta* nest, VI.5-10.1972; G.E. & K.E. Ball, P.A. Meyer (UASM). Same, VI.1-10.1972 (UASM). 27 km. SE Teopisca, Rte. 24, VI.3-4.1969; H.. Howden (UASM). **Oaxaca**. Rte. 131, 82 km. S. Juchatengo, oak forest VII.16-17.1972; P.A. Meyer, G.E. Ball (UASM). Hwy. 125, 13 km. N. Hwy. 200, nr. Pinotepa Nacional, U-V light, 195 m., VII.19.1986; S. McCleve, P. Jump (UASM).**San Luis Potosi**. El Salto, VIII.8-9.1968; J.W. McReynolds (CASC). Same, U-V light, VII.7.1966; R.E. Woodruff (UASM). Tamazunchale, VII.13.1956; D.H. Janzen (CISC).**Veracruz**. Fortin de las Flores, 1010 m., VIII.1.1964; H.V. Daly (CISC). Same, U-V light, VII.7-12.1974; J.A. Chemsak, J. Powell (CISC). Rio Metlac Cn., NW. Fortin de las Flores, U-V light, VII.10.1974; J.A. Chemsak, E.& J. Linsley, & J. Powell (CISC). Canyon, SW. Rio Metlac. nr. Fortin, 975-1036 m., *ex* refuse deposit *Atta mexicana,* VIII.13-18, 1971, A. Newton (MCZC).

Physea latipes Schaum

Figs. 2, 100A-B, 105, and Map 1

Physea latipes Schaum, 1864: 117. TYPE MATERIAL: not seen. TYPE AREA: "Mexico" (from original description). Chaudoir, 1868: 74 .— Bates, 1881: 27 (as junior synonym of *P. hirta* LeC.).— Csiki, 1927: 431 (as junior synonym of *P. hirta* LeC).— Bänninger, 1927: 212.— Blackwelder, 1944: 23.

Recognition.— See key and treatment of this topic for *P. hirta.*

Habitus as in Fig. 2. Standardized Body Length, males 10.3-11.4 mm., females 11.0-11.4 mm; W/SBL, males 0.44-0.46, females 0.45-0.46.

Female sternum VIII and tergum IX-X as in Figs. 100A and B, respectively. Bursa copulatrix as in Fig. 105.

Geographical distribution.— We have seen material from the Pacific Versant of México, only. However, we expect that *Physea latipes* ranges into southern Arizona, as do many other carabids that occur in the vicinity of Mazatlan, Sinaloa. This prediction is supported by occurrence in southern Arizona of the host of other *Physea* species, *Atta mexicana* (Smith, 1951). .

Material examined.— We have seen 34 adults from the following localities.

MÉXICO. **Colima**. Manzanillo, VII.18.1953; C.& P. Vaurie (AMNH).**Guerrero.** Iguala, IX; Barrett (CASC). **Jalisco**. Ajijic, U-V light, VII.25.1964; W. L. Nutting (UASM). Estacion Biologia Chamela, VII.8-16.1985; J. Chemsak *et al.* (CISC). 61 km. SW Guadalajara, 1310 m., VII.24.1952; F.W. & F.G. Werner (UASM). Hwy. 200, 33.5 km. S. Puerto Vallarta, 724 m., U-V light, VII.21.1986; S. McCleve, P. Jump (UASM). **Sinaloa**. Mazatlan, IX.15.1918 (CASC). "Venedio" [=Venedillo], VII.10- VIII.27.1918 (CASC).

Pachyteles Perty

Pachyteles Perty, 1830: 3. TYPE SPECIES: *Pachyteles striola* Perty, 1830: 4; fixed by Hope, 1838: 99; subsequent designation.— Chevrolat, in d'Orbigny, 1847: 392.— Lacordaire, 1854: 157.— Chaudoir, 1868: 51.— Bates, 1881: 26. — Horn, 1881: 129.— LeConte and Horn, 1883: 24.— Leng, 1920: 49.—Csiki, 1927: 427.— Bänninger, 1927: 208.— van Emden, 1942: 25.— Blackwelder, 1944: 23.— Ball, 1960: 94.— Erwin *et al.*, 1977: 4.3.— Reichardt, 1977: 376.— Eisner *et al.*, 1977: 385.— Ward, 1979: 185.— Thompson, 1979: 232.— Erwin, 1979a: 359. 1979b: 557.- Erwin and Sims, 1984: 374, 427.

Goniotropis Gray, 1832: 274. TYPE SPECIES: *Goniotropis braziliensis* Gray, 1832: 274; by monotypy.— Duponchel, in d'Orbigny, 1845: 274.—Lacordaire, 1854: 157.— Chaudoir, 1868: 51.— Bates, 1881: 25 .— Csiki, 1927: 427 (as junior synonym of *Pachyteles*).— Bänninger, 1927: 202.— Blackwelder, 1944: 23.— Ball, 1960: 94.— Erwin *et al.*, 1977: 4.3.— Reichardt, 1977: 377.— Moore, 1979: 194.— Erwin, 1979: 557.— Eisner and Aneshansley, 1981: 83.

Tropopsis Solier, 1849: 179. TYPE SPECIES: *Tropopsis marginicollis* Solier, 1849: 181 (here designated, the first of two species named by Solier).— Lacordaire, 1854: 159.— Chaudoir, 1868: 67 (as a section of *Pachyteles*).— Csiki, 1927: 427.— Bänninger, 1927: 207.— Blackwelder, 1944: 23.— Erwin, *et al.*, 1977: 4.3.— Reichardt, 1977: 377.

Scythropasus Chaudoir, 1852: 289. TYPE SPECIES: *Scythropasus elongatus* Chaudoir, 1852: 289 (by monotypy).— 1868: 48.— Bates, 1881: 24.— Csiki, 1927: 427.— Bänninger, 1927: 207.— Erwin, *et al.*, 1977: 4.3.

Notes about synonymy.— *Pachyteles*, *Goniotropis* and *Tropopsis* are treated as congeneric because the differences among them seem rather slight, compared to differences among other New World genera. Certainly, the group as a whole is markedly divergent, especially in features of the male genitalia and ovipositor. However, such differences do not seem to be correlated with other features. The name *Scythropasus* Chaudoir was synonymized with *Goniotropis* by Bänninger. The basis for selecting *Pachyteles* as the name for the genus is priority.

Derivation of generic name.— According to its author (Perty,1830: 4), the word *Pachyteles* is derived from incrassate antennomere 11, and means thick spear (Greek, *pachy* + *telum*).

Recognition.— Among Middle American ozaenines, adults of *Pachyteles* are recognized by a combination of: antennomeres 5-10 short, each about as wide as long; fore femur with ventral spines (Figs. 59 and 60); antennal cleaner of fore tibia with median expansion prominent; and base of mental tooth of labium with a pair of setae. Adults of the South American subgenus *Tropopsis* lack the femoral spine, and one undescribed species has long and slender antennal articles.

Description.— Habitus as in Figs. 3-6, body slender, elongate. Size varied, Standardized Body Length *ca.* 3.5-17.5 mm, maximum width 1.3-5.9 mm.

Color. Various somber shades: flavo-rufous to dark piceous, but not black; appendages of most specimens rather paler than body color.

Microsculpture and luster. As for Ozaenini, and pterothoracic pleura and sterna with mesh pattern isodiametric or transverse.

Vestiture. Dorsal surface various, from almost glabrous to densely setose, especially elytra. Fore tarsomeres 1 and 2 or 1-3 of males with adhesive vestiture ventrally, or fore tarsomeres glabrous.

Chaetotaxy. Clypeus with three pairs of setae. Vertex of head with several pairs of supraorbital setae and several behind eyes, also. Antennae, number of setae: antennomere 1, one to several; 2-3, apical ring; antennomere 4, *ca.* apical half setose; antennomeres 5-11 densely setose, except anterior and posterior glabrous triangular areas. Mouthparts: labrum (Figs. 34 and 35) with 10 or more (*ca.* 16) setae near anterior margin; maxillary stipes with two or three setae; submentum and mentum with one or more pairs of setae, each; glossal sclerite apically with one pair setae; labial palpomere 2 with numerous setae, but three preapical setae longer than rest; palpomere 3 also setose. Pronotum with marginal setae numerous (*ca.* 10). Each elytron with several rows of discal setae of about 10 in each of intervals 1, 3, 5, and 7; umbilical setae *ca.* 25. Legs (number of setae, fore, middle, hind): coxae, 0-numerous-numerous; trochanters, several-several-several, each with one long seta, others short; femora, numerous-numerous-numerous.

Head. Frontal impressions shallow, broad, but recognizable. Eyes (Figs. 3-6) subtruncate posteriorly, moderately prominent; temporal lobes small. Supraantennal area not reflexed, though ridges generally sharp.

Antennae (Figs. 12, 13, 20, 21, 27 and 28). Antennomeres 5-10 almost quadrate, 11 clearly longer than wide (Figs. 12 and 13),flattened antero-posteriorly, terete in cross section (*cf.*Figs. 27 and 28). Antennomere 11 (Figs. 20 and 21) with apex broadly rounded, terminated in straight keel (Figs. 27 and 28).

Mouthparts. Labrum transverse (Figs. 34 and 35). Mandibles (Figs. 41A-D) falcate, occlusal margins with prominent teeth. For details, see Table 1. Maxillae average for Ozaenini, as in Fig. 46. Labium (Figs. 52 and 53): mentum with lateral lobes more or less pointed apically, each epilobe widened preapically; tooth prominent; labial palpomere 3 narrowly securiform, apex subtruncate.

Prothorax. Pronotum (Figs. 3-6) transverse, distinctly wider than long, to distinctly longitudinal, slender and slightly longer than wide. Lateral grooves moderately wide. Lateral margins smooth to crenulate, sides posteriorly sinuate or not; antero- and posterolateral angles projected or not. Disc moderately convex, impressions distinct but shallow.

Pterothorax. As described for Ozaenini and anterior margin of metepisternum near coxa overlapped by posterior lobe of mesepimeron.

Elytra. Surface various: distinctly striate, indistinctly so, or smooth; intervals, if evident, moderately to slightly convex, but broad and not carinulate. Basal ridge extended to about plane of base of intervals 4 or 5.

Legs. In most features, as described for Ozaenini, no parts remarkably compressed. Fore femur (Figs. 59 and 60) with dentiform projection ventrally near base (subgenera *Pachyteles* and *Goniotropis*), or without such projection (subgenus *Tropopsis*). Antennal cleaner of fore tibia various. See Figs. 66A and B, and 67A and B. See Table 2 for details.

Abdomen. Sclerites of segments II-VII unmodified. or sclerites of segments VIII and IX/X, see Figs. 95, 101, and 102. or details, see under "Structural and biochemical features, genital segments".

Male genitalia (Figs. 85-89, and 97). For details, see Table 3.

Ovipositor (Figs. 74-79). Stylomeres various, from long and slender with narrow apex to short, rather broad, and with apex bifurcate.

Bursa copulatrix and spermatheca (Fig. 106). For details, see Table 4 .

Defensive secretions.— Four compounds. See Table 5 for details.

Way of life.— Adults of *Pachyteles* are probably insect predators, most of them living under bark of fallen tree trunks, and probably flying at night. At the northwestern periphery of the range, a few individuals have been collected in agricultural fields, but it is not clear from the labels whether they were collected at light, at night, or if they were found on the ground during the day. Adults of other species have been collected at night, in association with dead oaks.

Geographical distribution.— The range of this genus extends through the forested parts of the Neotropical Region from southern Chile to México, and into southwestern United States, in the Nearctic Region.

Relationships.— In external features, adults of *Pachyteles* resemble most closely those of the Afrotropical genus *Afrozaena* Jeannel. This apparent similarity, however, is not borne out by detailed study of structural features. *Pachyteles* is without close extant relatives in the New World, also..

Included taxa.— We recognize three subgenera, two of which [*Goniotropis* and *Pachyteles* (*sensu stricto*)] occur in southwestern United States, and are treated further below. Included in subgenus *Goniotropis* is *Pachyteles elongatus* (Chaudoir), the type species of *Scythropasus* Chaudoir. The subgenus *Tropopsis* is confined to South America, and is not considered further.

Subgenus *Goniotropis* Gray

Derivation of subgeneric name.— In the original description of the type species, *G. braziliensis* Gray, the author notes (1832: 274) that the anterior femora and tibiae are strongly toothed and that each elytron terminates in an apical hook. The name is derived from Greek *gonio*, meaning angle, and *tropis*, meaning keel. We believe the word refers to the flanges of Coanda, which are keel-like, and are located posteriorly on the outer angles on each elytron.

Recognition.— Adults of *Goniotropis* have the middle coxal cavities closed medially, with the intercoxal process of meso- and metasterna in contact, and the antennal cleaner of the fore tibia (Figs. 67A and B) with a prominent projection extended from the medial expansion. A more detailed characterization is not required here.

Way of life.— Adults of a few species of *Goniotropis* have been collected under the bark of fallen tree trunks, and one was found in a bromeliad growing on the trunk of a standing pine tree, about 5 meters above the ground. Most specimens have been taken at U-V light, at night.

Geographical distribution.— The range of *Goniotropis* includes the northern half of South America, all of Middle America, and southern Arizona in southwestern United States.

Relationships.— We hypothesize *Goniotropis* to be sister group of subgenus *Pachyteles*, with their common ancestor being the sister group of subgenus *Tropopsis*. This hypothesis is based on transformation series for the intercoxal processes, armature of the fore tibia and structure of the antennal cleaner.

Included species.— Bänninger (1927: 203-204) included 14 species in this group. Two species occur in Arizona, in southwestern United States. We describe these because they are in the study area, and as well, the tropical Mexican *P. elongatus* (Chaudoir) because it is the type species of *Scythropasus*, a junior synonym of *Goniotropis*.

Pachyteles parca LeConte
Figs. 3, 53, 78A-C, 85A-E, 101, 106, and Map 1

Pachyteles parca LeConte, 1884: 2. HOLOTYPE female, in LeConte-Horn Collection, labelled: "Ari."; "Type 5487" [red paper]; "*Pachyteles* parca LeC" [handwritten] (MCZC). TYPE AREA: Arizona, U.S.A.— Horn, 1894: 308.— Leng, 1920: 49.— Csiki, 1927: 430.

Goniotropis parca; Bänninger, 1927: 204.— Ball, 1960: 94.— Erwin, *et al.*, 1977: 4.3.

Pachyteles beyeri Notman, 1919: 225. HOLOTYPE male, labelled: "San Felipe Low Cal"; "*Pachyteles beyeri* TYPE" [handwritten, on blue paper] (Staten Island Museum, New York). NEW SYNONYMY.— Csiki, 1927: 204.

Goniotropis beyeri Bänninger, 1927: 204.— Ball, 1960: 94.— Erwin, *et alii.*, 1977: 4.3.

Notes about synonymy.— In form of median lobe and details of the internal sac, the male genitalia of the type of *P. beyeri* match those of males of *P. parca*, collected in Madera Canyon, Santa Rita Mountains, Arizona. In other features, specimens of the two nominal species are identical, also. We have no doubt that they are conspecific.

Recognition.— Adults of this species are slender, with transverse pronotum with sinuate lateral margins (Fig. 3), and of moderate size (Standardized Body Length less than 12 mm). In general form, they look like small specimens of *P. kuntzeni* (Bänninger):males differ from those of the latter species in form of the apical portion of the median lobe (Figs. 85A-B; *cf* Figs. 86A-B; also, *cf* Figs. 87A-B).

Description.— Habitus as in Fig. 3, with character states of *Goniotropis* and: SBL males, 9.9-11.4 mm., females 8.8-11.2 mm.; W/SBL males 0.31-0.32, females 0.33.

Male genitalia (Figs. 85A-D). Median lobe in lateral aspect with apical portion with carinula (**c**) on left side, apex nearly truncate; internal sac with small apical brush (**ab**) and digitus (**d**), terminal lobe small. Left paramere (Fig. 85D) with patch of setae preapically; right paramere (Fig. 85E) with about half medial margin setose.

Ovipositor. Stylomeres each as in *P. kuntzeni* (*cf.* Figs. 77A-C), cylindrical, straight, apex broad and circular, not tapered to point, sensory furrow nearly apical; surface with irregular rows of thick basiconic and slender trichoid sensilla, dense cluster of these near apex.

Bursa copulatrix. As in Fig. 106.

Way of life.— All known specimens have been collected at night, at light, principally at ultra-violet light, in the vicinity of oak-pine forests. Months of collection are from June to September.

Relationships.— Based on marked similarity in structural features and on evidently parapatric distribution pattern we hypothesize that this species and *P. kuntzeni* are sister taxa.

Geographical distribution (Map 1).— This species is known from northwestern México (Baja California and northern Sonora) western Durango, and southern Arizona, in southwestern United States. The Durango specimen, a male, was determined by Bänninger, in 1926, as "Goniotropis sp?"

Material examined.— In addition to the types, we have seen 29 specimens from the following localities.

UNITED STATES OF AMERICA. **Arizona.** *Cochise County.*— Chiricahua Mts., Portal, VII.15.1968; D.J. & J.N. Knull (OSUC). Guadalupe Canyon, at light, VII.1.1975; S. McCleve, M. Topham (SMCC). Same, at light, VII.31.1975; S. McCleve (SMCC). Huachuca Mts., VIII.18.1936; J.N. Knull (OSUC). Same, Miller Canyon, 1524 m., VIII.17.1974; E. R. Hoebeke (CUIC). Peloncillo Mts., 53 km. E. Douglas, at light, VII.17.1973; S. McCleve (SMCC). *Graham County.*— Galiuro Mts., Aravaipa Canyon, 17.7 km. N. Klondyke, U-V light, VII.24.1976; G.E. Ball, J.M. Campbell, P.M. Hammond (UASM). Same, on Turkey Creek, VI.22.1976; S. McCleve (SMCC). *Pima County.*— Santa Catalina Mts., Molino Basin, VII.31.1974; D.M. Bright (CNCI). Same, VIII.8.1969 (FSCA). *Santa Cruz County.*— Pajarito Mts., Peña Blanca Canyon, 1191 m., U-V light, VII.2.1980; S. McCleve (SMCC). Same, VII,13,1968 (FSCA). Same, VII.16.1964; R.H. Arnett, Jr. & E. R. Van Tassell (SCA). Same, VII.13.1970; K. Stephan (SCA). Same, VIII.7.1959; R.H. Arnett, Jr. (FSCA). Same, U-V light, VIII.11.1968; G.E. Ball family & R.B. Madge (UASM). Same, U-V light, VII.28.1978; S. McCleve (SMCC). 4.3km. above Peña Blanca, VIII.12.1983; E. Riley (EGRC). Santa Rita Mts., Madera Canyon, VIII.8.1977; .T. Hovore (SCA). Same, 1490 m., VIII.23.1959; J.G. Franclemont (CUIC). Same, VII.20.1959 (CUIC).Same, VIII.11-24.1963; G.E. and K.E. Ball (UASM).

MÉXICO. **Baja California Sur**. 3 km. E. La Burrera, 515 m., IX.2.1977 (CASC). San Jose del Cabo [Horn, 1894: 308. Sierra El Chinche [Horn, 1894: 308]. **Durango**. Canelas; J. Flohr [ZMHB]. **Sonora**. 55 km. SW Moctezuma, 1066 m., VI.10.1982; S. McCleve (SMCC). Rte. 16, 32.3 km. E. Rio Yaqui, U-V light, VII.26-27.1987; S. McCleve (UASM). Sierra Alamos, 2.7 km. S. 1.9 km. W. Alamos, U-V light; S. McCleve (UASM).

Pachyteles kuntzeni (Bänninger) NEW COMBINATION
Figs. 4, 13, 21, 28, 35, 46, 60, 67A-B, 77A-C, 86A-E, and Map 1

Goniotropis kuntzeni Bänninger, 1927: 204. HOLOTYPE female, labelled: Canelas, Durango Mexico Flohr (Bänninger Coll., ETHZ) TYPE LOCALITY: México, Durango, Canelas.— Blackwelder, 1944: 23.— Erwin, *et al.*, 1977: 4.3.— Erwin and Halpern, 1978: 360.

Notes about type material.— We have not seen the holotype, but we have seen a male paratype in ZMHB from the type locality, and our material (from Sonora and southern Arizona) matches the features, including those of the male genitalia, of that specimen. Accordingly, we are confident that our identification is correct.

Recognition.— Adults of this species are large (SBL 16.0- 17.6 mm), the largest known of *Pachyteles*, with transverse pronotum with sinuate lateral margins (Fig. 4). They are much like large specimens of *P. parca*. Males of the two species are similar in details of the genitalia, but in males of *P. kuntzeni*, the apex of the median lobe (Fig. 86A) is obliquely truncate. or additional details, see the description, below. In shape of the stylomeres of the ovipositor, females of *P. kuntzeni* and *P. parca* are similar, but those of *P. kuntzeni* have more setae (Figs. 77A-C; *cf* Figs. 78A-C).

Description.— Habitus as in Fig. 4. With character states of subgenus *Goniotropis* and Standardized Body Length males 16.0-16.9 mm., females 15.7-17.2 mm; W/SBL males 0.33-0.35, females 0.32-0.33.

Male genitalia (Figs. 86A-E). Median lobe in left lateral aspect (Fig. 86A) with apical portion prominent, rather broad, carinulate on left side, apex obliquely truncate. Internal sac with large apical brush (**ab**), pendent terminal lobe (**t**) with large digitus (**d**). Left paramere (Fig. 86D) with few setae preapically along medial margin. Right paramere (Fig. 86E) with extensive brush of setae for most of length of medial margin.

Ovipositor (Figs. 77A-C). Stylomeres of moderate length, cylindrical, with broad circular apex, not tapered to point, and sensory groove preapical. Vestiture moderately dense, of longer sensilla trichodea and thicker sensilla basiconica.

Bursa copulatrix. About same as that of *P. parca* (above; *cf* Fig. 106).

Way of life.— Specimens have been collected in association with dead oak trees, at night.

Geographical distribution (Map 1).— This species is known only from northwestern México (Durango and Sonora) and southernmost United States (Arizona).

Relationships.— This species is postulated to be the sister taxon of *P. parca*.

Material examined.— In addition to the male paratype, we have seen 13 specimens, from the following localities.

UNITED STATES OF AMERICA. . **Arizona**. *Cochise County*.—Huachuca Mts., Ash Canyon, 1548m., VIII.2.1979; N. McFarland (SMCC). *Maricopa County*.— Tempe, XI.28.1966; T. Paca (ASUT). Santa Cruz County.— Atascosa Mts., Sycamore Canyon, on oak stump at night, VII.12.1977; S. McCleve (SMCC). Pajarito Mts., Walker Canyon, 1191 m., on dead oak, at night, VII.28.1978. S. McCleve (SMCC). Pajarito Mts., Peña Blanca, 1219 m., U-V light; G.E.&K.E. Ball, & R.B. Madge (UASM). *County not known*.— S. Graham Mts., 1524 m., VIII.20.1974; K. Stephan (FSCA).

MÉXICO. **Sonora**. 16.1 km. E. Cananea, VIII.16.1949; G.M. Bradt (AMNH).

Pachyteles elongatus (Chaudoir)
Figs. 79A-C, 87A-D

Scythropasus elongatus Chaudoir, 1854: 295. TYPE MATERIAL: HOLOTYPE male, in Chaudoir-Oberthür Collection Box 132, labelled "Mexique"; "Ex Musaeo Mniszech"; "Elongatus Chaud." [handwritten, not in Chaudoir's hand] (MNHP).—1868: 48.— Bates, 1881: 24.— Csiki, 1927: 427.

Goniotropis elongatus; Bänninger, 1927: 203.— Blackwelder, 1944: 23.— Erwin, *et al.*, 1977: 4.3.

Notes about type material.— The specimen indicated above as holotype is in a series with a female labelled "Temax, N. Yucatan Gaumer" (Bates Coll) and a male labelled "Yucatan (Bates Coll)", and is not labelled as type. However, Chaudoir (1868: 48) recorded that the single specimen on which the name was based was collected in México and was in the Mniszech collection. The specimen labelled as holotype fits these conditions.

Recognition.— The slender body and pronotum as long as or slightly longer than wide distinguishes adults of this species from other Mexican members of *Pachyteles* (*sensu lato*). Males have adhesive vestiture on fore tarsomeres 1-3, rather than on 1-2 only, as in most other species of *Pachyteles*, and the apical portion of the median lobe (Fig. 87A) is distinctive (*cf* Figs. 85A and 86A). The long slender stylomeres of the ovipositor (Figs. 79A-C) are distinctive for females.

Description.— With character states of subgenus *Goniotropis* and form slender, pronotum as long or longer than wide. Standardized Body Length males 10.6-11.0 mm., females 9.6-11.6 mm.; W/SBL males 0.30-0.32, females 0.32-0.33.

Male genitalia (Figs. 87A-D). Median lobe in lateral aspect (Fig. 87A) with apical portion broadly rounded, prominent. Internal sac (Figs. 87A-B) with collar area covered with slender microtrichia; without apical brush; terminal sclerite truncate, not lobed. Parameres (Figs. 87C-D): left paramere with narrowed apex, with few setae preapically on medial margin; right paramere elongate, medial margin extensively setose, most densely so preapically.

Ovipositor (Figs. 79A-C). Stylomeres long and slender, each with two or more nematiform setae (Fig. 79C), surfaces with few trichoid setae in median area, more densely setose preapically and apically.

Bursa copulatrix. Not studied.

Way of life.— Specimens known to us were collected at ultra-violet light, at night, in or in the vicinity of lowland tropical forest.

Geographical distribution.— This species is in the northern part of the Neotropical region, ranging in Central America from Nicaragua to Tamaulipas on the Gulf Versant, and to Nayarit on the Pacific Versant.

Relationships.— The distinctive body form, form of apex of median lobe, armature of the internal sac, and slender stylomeres of the ovipositor indicate that this species is not very close to *P. parca* and *P. kuntzeni*, the only other known species of *Goniotropis* in México.

Material examined.— In addition to the type and Yucatan specimens in the Chaudoir-Oberthür collection noted above, we have seen 10 specimens from localities in México.

Chiapas.. Palenque ruins, 122 m., U-V light, VI.8.1966; G.E. Ball & D.R. Whitehead (UASM). **Jalisco**. 24 km. S. Tomatlan, lowland 2nd growth forest and pasture, 110 m., at U-V light, VII.11.1984; S. McCleve & P. Jump (UASM). **Nayarit**.. 58 km. SW Las Piedras lowland forest 118 m, at U-V light, VII.7-8.1984; S. McCleve & P. Jump (UASM). **San Luis Potosi**.. Palitla, VIII.5.1966; O.S. lint (USNM). **Tamaulipas**.. *ca*. 40 km. N. Ciudad Monte Nacimiento, at light, VII.31.1970; C.W. O'Brien (UASM). **Veracruz**. Lake Catemaco, U-V light, VII.10-18.1963; D.R. Whitehead (UASM). Same, VI.9-25.1969; H. F. Howden (UASM). Same, Coyame, U-V light, VII.5.1967; R.E. Woodruff (UASM). Los Tuxtlas Biological Station, *ca*. 30 km. E. Catemaco, *ca*. 30 m., VI.29-30.1983; R.S. Anderson (UASM).

Subgenus *Pachyteles* (*sensu stricto*)

Recognition.— See this topic above, for subgenus *Goniotropis*. Habitus is illustrated by Figs. 5 and 6. These forms are rather similar to one another, and though other members of the subgenus look like them generally, some have strikingly different pronota, and differ as well in punctation of the dorsal surface and striation pattern of the elytra.

Way of life.— See the general statement under the genus, and details in the following species treatments.

Geographical distribution.— The range of *Pachyteles* (*sensu stricto*) is coextensive with the range of the genus.

Relationships.— See this topic under *Goniotropis* and *Pachyteles* (*s. lat.*).

Included species.— According to Bänninger (1927: 210-212), 48 species are included in *Pachyteles* (*s. str.*), arranged in several groups. We treat only three here, including one that is new.

Pachyteles gyllenhali (Dejean)
Figs. 5, 74A-B, and 88A-D

Ozaena gyllenhali Dejean, 1825: 436. TYPE MATERIAL: in Chaudoir-Oberthür Collection, Box 132, in front of the following box label— "Gyllenhali Dej. Antilles? C. Dejean." HOLOTYPE female, labelled: "Gyllenhali m. in Amer. inf." [green paper]; "Gyllenhali" [green paper]; "Ex Musaeo Chaudoir" [red print on white paper].— Chaudoir, 1854: 301.

Pachyteles gyllenhali; Chaudoir, 1868: 55.—Csiki, 1927: 428.— Bänninger, 1927: 211.— Blackwelder, 1944: 23.— Erwin, *et alii.*, 1977: 4.3.— Erwin and Sims, 1984: 427.

Ozaena verticalis Chaudoir, 1848: 104. TYPE MATERIAL: two females— first labelled "Ex Musaeo Chaudoir" [red print on white paper]; second, "Goudet" [green paper], "Ex Musaeo Chaudoir" [red print on white paper]— in Chaudoir-Oberthür Collection, Box 132, in front of the following box label: "verticalis Chaud. Colombie Duport". LECTOTYPE (here selected) first female in series (MNHP).—1854: 301. NEW SYNONYMY.

Pachyteles verticalis; Chaudoir, 1868: 56.— Bates, 1881: 25.— Csiki, 1927: 428.— Bänninger, 1927: 210.— Blackwelder, 1944: 23.

Pachyteles testaceus Horn, 1868: 129. LECTOTYPE female, in LeConte-Horn Coll., labelled: "Ariz"; TYPE NO. 1029.1 [red paper]; "*Pachyteles* testaceus Horn" (MCZC). NEW SYNONYMY. TYPE LOCALITY: Fort Grant, Arizona.—Horn, 1881: 128.— LeConte and Horn, 1883: 24.— Horn, 1894: 308.— Leng, 1920: 49.— Blackwelder, 1944: 23.— Ball, 1960: 94.— Erwin, *et al.*, 1977: 4.3.

Notes about synonymy.— The type specimens of the three nominal taxa noted above are very similar in size and external features. Horn (1868: 130) noted the marked similarity among them, but based on the limited material at his disposal he concluded that three species were represented. With the more extensive material available to us, especially of the nominal mainland taxa, we are unable to distinguish among them.

Recognition.— A combination of small body size (Standardized Body Length *ca.* 3.5- 6 mm.), densely setose dorsal surface, and pale (rufo-flavous) integument distinguishes adults of this species from other North-Middle American species of *Pachyteles*. Males lack adhesive setae of the fore tarsomeres, and the apical portion of the median lobe (Fig. 88A) is small, narrow and pointed. Females have the stylomere of the ovipositor with a bifurcate apex (Fig. 74B).

Description.— Habitus of adults as in Fig. 5, with features of subgenus *Pachyteles*.SBL males 4.0-5.4 mm., females 3.6-4.6 mm; W/SBL males 0.40, females 0.37-0.39.

Color. Integument pale, especially specimens from Arizona and northwestern México, but many from elsewhere with irregular fuscous cloud medially on elytra.

Microsculpture. Average for genus.

Vestiture. Dorsal surface of head, pronotum and elytra densely setose. Males without adhesive vestiture on fore tarsomeres.

Head. Average for Ozaenini.

Pronotum (Fig. 5). Subrotund, transverse; lateral margins sinuate posteriorly. Anterior angles acute; posterior angles rectangular.

Elytra. Moderately densely punctate, interneurs very shallow to obsolescent, intervals nearly flat.

Legs. Average for subgenus.

Male genitalia (Figs. 88A-D). Median lobe (Figs. 88A-B) with apical portion small, apex pointed. Internal sac with basal rod (**r**; *cf.* Fig. 82A) long, terminal lobe (**t**) penis-like, without preapical lobe, dorsal lobe, or microspines. Left paramere asetose (Fig. 88C); right paramere with single seta on medial margin.

Ovipositor (Figs. 74A-B). Stylomeres triangular in outline, each with base broad , cupped medially (Fig. 74A), somewhat flattened, apex bifurcate (Fig. 74B); sensory groove at base of furcation, preapical in position. Setation rather sparse, principally of sensilla basiconica.

Way of life.— Adults of this species have been collected on dead tree trunks, under bark, and in saguaro cactus. Many specimens have been collected at night, at light, and particularly ultra violet light. The wide range of this species, including islandic localities in both the Caribbean Sea and Pacific ocean, indicates that adults disperse readily.

Geographical distribution.— The range of this species is extensive, including the Greater Antillean island of Cuba, the Tres Marias Islands off the Pacific Coast of México, and on the mainland, from Brazil in South America (Blackwelder, 1944: 23), throughout Middle America to southern Arizona.

Material examined.— We have seen 193 specimens of this species, from the following localities in Cuba, the United States, and México.

UNITED STATES OF AMERICA. **Arizona.** *Cochise County.*— Guadalupe Canyon, U-V light, VII.31.1975; S. McCleve (SMCC). Same, VIII.2.1977 (SMCC). *Gila County.*— Globe, VII.1927; D.K. Duncan (MCZC). Wheatfield, near Globe, II.25.1932; . Parker, D.K. Duncan (MCZC). Same (CASC). *Graham County.*— Galiuro Mts., Aravaipa Canyon, east end, U-V light, VII.24-25.1974; S. McCleve (SMCC). Same (AMNH). Aravaipa Canyon, U-V light, VIII.12.1975; S. McCleve (SMCC). Same, Turkey Creek, 1.6 km. S. Aravaipa Creek, U-V light, VIII.11.1975; S. McCleve (SMCC). Same, ca. 16 km. NW Klondyke, 900 m., U-V light, VII.30-31.1975; G. E. Ball, H.E. Frania (UASM). Same, U-V light, VII.24.1976; G.E. Ball, J.M. Campbell, P.M. Hammond (UASM). Same, U-V light, VIII.24.1977; G.E. & K.E. Ball (UASM). Arivaipa, VIII.29.1933; Bryant (CASC). Safford, under bark of cottonwood, beside creek, I.10.1938; O. Bryant (CASC). *Maricopa County.*— Phoenix, XI.27.1919; E. Schiffel (MCZC). *Pima County.*— Ajo Mts., Alamo Canyon, in rotting saguaro cactus, VII.24; H.B. Leech (CASC). Same, VII.25; H.B. Leech, J.W. Green (CASC). Arivaca, XI.30.1969; K. Stephan (FSCA). Same, Arivaca Creek, VII.31.1952; H.B. Leech, J.W. Green (CASC). Baboquivari Mts., W. side, Baboquivari Canyon, VII.25-27.1952; H.B. Leech, J.W. Green (CASC). Redington, XII.7.1969; K. Stephan (FSCA). Tucson, VII.21.1917 (CUIC). Same, San Xavier Mission, VII.29.1924; E.P. Van Duzee (CASC). *Pinal County.*— Florence (Fall, MCZ). *Santa Cruz County.*— Cobabi Mts., Santa Cruz Village, X.12.1916 (USNM). Pajarito Mts., Peña Blanca Canyon, Lot 511, VII.26.1961; R.H. Arnett, E. Van Tassell (FSCA). Patagonia, VII.36; E.S. Ross (CASC). Same, VIII.9.1940; E.S. Ross (CASC). Same, VII.18.1948; C. & P. Vaurie (AMNH). Same, IX.28.1968 (SCA). *County not known.*— Galiuro Mts.; Hubbard and Schwarz (FSCA, USNM). Arizona, Charles Palm (AMNH).

CUBA. Cayamas, I.14; E.A. Schwarz (MCZC).

MÉXICO. **Baja California**. Pelican Island, VII.5.1921; J.C. Chamberlin (CASC). **Baja California Norte**. 14.5 km. SE Rancho Laguna, VII.1.1973; Fisher, Westcott (CASC). **Baja California Sur**. El Sargento, VII.29.1971; H.G. Real, R.E. Main (CASC). Miraflores, VIII.7.1971; H.G. Real, R.E. Main (CASC). 8 km. S. Miraflores, VII.10.1938; Michelbacher, Ross (CASC). 24 km. E. San Jorge, VII.24.1971; H.G. Real, R.E. Main (CASC). San Jose Island, V.28.1921; E.P. Van Duzee (CASC). Santa Rosa (Fall, MCZC). [Sierra] El Chinche, 609 m., under stones (CASC).**Chiapas**. Cerro Baul, ridge SE of, 21 km. W Rizo del Oro, 1615 m., cloud forest, IX.6-8.1970; C. Mullinex, D.E. Breedlove (CASC). 48 km. NW Ocosingo, VI.30.1977; E.M. Fisher (CASC). Sierra de la Colmena, e. slope, nr. La Caverna, Arroyo Santa Maria, 16°24'18"N, 91°24'16"W, 213 m., on ground, VI.1-10.1972; G.E.& K.E. Ball, P.A. Meyer (UASM). Sierra de la Colmena, San Cristobal trail, 701-853 m., VI.8.1972; P.A. Meyer, G.E.& K.E. Ball (UASM). 19 km. S. Solosuchiapa, Rte. 195, 640 m., IV.25.1966; G.E. Ball, D.R. Whitehead (UASM). **Colima**. 11.3 km. NE Colima, XII.3.1948; E.S. Ross (CASC). Mt. Colima, SE slope, XII.2.1948; H.B. Leech (CASC). **Jalisco**. nr. Ixtapa, ca. 30 m., gallery forest, dead tree; XII.22.1970; G.E.& K.E. Ball (UASM). 15 km. S. Mazamitla, 1676 m., VII.29-31.1952; F.W. & F.G. Werner (UASM). 20 km. S Tecalitlan, 1615 m., VIII.3.1967; Ball, T.L. Erwin, R.E. Leech (UASM). **Nayarit**. Jesus Maria, VII.6.1955; B. Malkin (CASC). San Blas, VI.15.1955; B. Malkin (CASC). Islas Tres Marias, Madre Maria Island, Arroyo Hondo, V.17.1925; H.H. Keifer (CASC). **Sinaloa**. 8 km. N. Mazatlan, U-V light; J.A. Chemsak (CISC). **Sonora**. 8 km. E. Alamos, VIII.11.1973; K. Stephan (FSCA). 21 km. SE. Alamos, X.30.1972; K. Stephan (FSCA). Bahia Kino, X.25.1980; P. Jump (SMCC). Sierra San Luis, Varela Ranch, Cañon Bonita, U-V light, and under bark of cottonwood logs; G.E. Ball & D.R. Maddison (UASM).**Tabasco**. 96 km. SE. Villahermosa, U-V light, VI.6-7.1972; P.A. Meyer, G.E.& K.E. Ball (UASM). **Veracruz**. Atoyac, VI.24.1982; M.A. Ivie (OSUC). Cordoba; D.A. Fenyes (CASC). Fortin de las Flores, VI.20-30.1963; D.R. Whitehead (UASM). park cañon, 3.2 km. W. Fortin de las Flores, Rte. 150, VIII.3-6.1965; Cornell Univ. Mexico Field Party, 1965 (CUIC). 56 km. SE. Jalapa, XII.26.1963; C.A.& M.J. Tauber (CUIC). Sierra de las Tuxtlas, Lake Catemaco, Coyame, under bark, VII.1-15.1963; D.R. Whitehead (UASM). Same, under bark, VII.10-18.1963; D.R. Whitehead (UASM). 0.5 km. W. Sontecomapan, 305 m., IX.20&26.1965; G.E. Ball, D.R. Whitehead (UASM). Same, IX.18-26.1965 (UASM). 4 km. W. Sontecomapan, IV.3&10.1966; G.E. Ball, D.R. Whitehead (UASM). Same, on log, VI.1-5 & 20.1966 (UASM). Same, U-V light (UASM).

Pachyteles enischnus, new species

Figs. 6, 75A-B, 97A-D, and Map 1

Type material.— HOLOTYPE male, labelled: "MEX. Jalisco nr. Ixtapa gallery forest dead tree ca. 100' [elevation above sea level] XII.22.70"; "Puerto Vallarta MEX trip 1970 G.E.&K.E. Ball collectors" (USNM). ALLOTYPE female, "15 km.S. Mazamitla Jal. MEX. 5500' pine-oak forest July 30, 1952 FE & FG Werner" (USNM). Two male PARATYPES (USNM) labelled same as holotype, and one male PARATYPE (UASM) labelled same as allotype. Eleven additional PARATYPES, labelled as follows. Male and female, "MEXICO Jalisco 33.8 km. S. Puerto Vallarta pine-oak forest 750 m., at U-V light 9,10.VII.1984 S. McCleve, P. Jump" (UASM). our males, three females, "MEXICO Nayarit 57.9 km. s.w. Las Piedras lowland forest 118 m., at U-V light 7-8.VII.1984 S. McCleve, P. Jump" (UASM). Male, "Sin. Mex. 200 ft. 5-3-49"; "GM Bradt Collector" (AMNH). Female, "5 mi. E. Alamos SONORA MEX VIII.11.1973 K. Stephan & D.S. Chandler" (OSUC).

Derivation of specific epithet.— This is based on the Greek adjective *enischnos*, meaning thin, in allusion to the slender adult body form (Fig. 6).

Recognition.— Body size, reduced setation of the dorsal surface, and pronotum with markedly sinuate lateral margins distinguish this species from other members of the genus that range into northern México and southwestern United States.

Description.— Habitus as in Fig. 6. Standardized Body Length of males 7.2-7.6 mm., females 7.0-7.7 mm.; W/SBL males 0.34-0.35, females 0.33-0.35.

Color. Body rufous to rufo-piceous, legs, antennae and palpi slightly paler than body.

Microsculpture and luster. Head dorsum with mesh pattern isodiametric, microlines fine, nearly effaced on center of vertex. Pronotum with mesh pattern transverse, partly effaced on disc. Elytra with mesh pattern isodiametric in lateral channels, transverse and partly effaced on disc. Dorsal surface generally shiny.

Vestiture. Dorsal surface of head and pronotum sparsely setose. Elytra with discal intervals serially, sparsely setose. Thoracic and abdominal sterna moderately densely setose.

Head (Fig. 6). Eyes average in size and convexity. Frontal impressions broad, irregular in outline, irregularly punctate. Vertex coarsely, sparsely punctate.

Pronotum (Fig. 6). Transverse, surface sparsely, irregularly punctate. Anterior and posterior margins nearly straight. Lateral margins markedly sinuate posteriorly. Postero-lateral angles about rectangular. Disc slightly convex. Lateral grooves broad anteriorly and posteriorly, narrow medially, margins not beaded. Postero-lateral impressions broad and irregular, continuous anteriorly with lateral grooves.

Elytra. In form, average for *Pachyteles*, humeri broadly rounded, slightly prominent. Interneurs shallow, rather broad, intervals only slightly convex. Intervals sparsely punctate.

Metathoracic wings. Macropterous, fully developed.

Legs. Average for subgenus *Pachyteles*.

Male genitalia (Figs. 97A-C). Median lobe (Fig. 97A) with apical portion distinct, extended ventrad, apex broadly rounded, nearly subtruncate. Internal sac with collar area with dense covering of slender seta-like microtrichia; apical portion with broad sclerite on left side, terminated in obtusely pointed lobe; basal part of sac with distinct longitudinally oriented ridges and several setae near apex of median lobe. Left paramere (Fig. 97B) shorter than right paramere (Fig. 97C), glabrous. Right paramere digitate, sparsely setose apically and on apical part of medial margin.

Ovipositor (Figs. 75A-B). Stylomeres falcate, each with apex broadly pointed, not bifurcate. Sensory groove ventral, remote from apex. Lateral and ventral surfaces with numerous thick sensilla basiconica (Fig. 75A).

Way of life.— Adults were collected from under bark of dead trees in gallery forest bordering deciduous tropical forest, near sea level, to pine-oak forest at *ca.* 1500 m. Most specimens, however, were taken at light, at night, indicating nocturnal flight activity during the rainy season in northwestern México.

Geographical distribution.— This species is known only from western México, from Jalisco to Sonora.

Relationships.— Adults of this species are like those of *P. filiformis* Chaudoir, in size and body form. The latter species occurs in the east, and farther southward in México. General similarity plus allopatric ranges suggest that these two species might be closely related to one another.

Pachyteles mexicanus (Chaudoir)
Figs. 76A-B, 89A-D, and 102.

Ozaena mexicana Chaudoir, 1848: 106. TYPE MATERIAL: two males, two females, in Chaudoir-Oberthür Collection, Box 132, each labelled "Ex Musaeo Chaudoir [red print], in front of the following box label: "mexicana Chaud Mexique". LECTOTYPE (here selected): a male, first specimen in series (MNHP).— 1854: 306.

Pachyteles mexicanus; Chaudoir, 1868: 65.— Bates, 1881: 27.— Csiki, 1927: 429.— Blackwelder, 1944: 23.— Erwin, *et al.*, 1977: 4.3.

Recognition.— Adults are broad-bodied, with pronotum with anterior angles acute and projected laterally, and smooth or nearly smooth elytra.

Description.— With features of *Pachyteles* (*s. str.*) and body broad and sturdy. Standardized Body length of males 5.9-7.2 mm., females 6.6-7.6 mm; W/SBL males 0.39-0.43, females 0.42-0.46.

Metathoracic wings. Relatively small, with apical portion reduced.

Male genitalia (Figs. 89A-D). Median lobe in right lateral aspect (Fig. 89B) with apex broadly bifid. Internal sac (Figs. 89A-B) narrow, with slender collar with dense covering of seta-like microtrichia; apical part (only partly everted) with broadly pointed apex. Left paramere (Fig. 89C) with apex broadly pointed, asetose. Right paramere (Fig. 89D) slender, elongate, preapical part of medial margin sparsely setose, setae short.

Ovipositor (Figs. 76A-B). Stylomeres moderately elongate, apex blunt, obliquely truncate; nematiform setae terminal; surface with long slender trichoid sensilla and short broad basiconic sensilla.

Way of life.— Specimens have been collected under bark of fallen trees in lowland tropical rain forest, at about 720 m. elevation, and in cloud forest at

1400m., in a pile of leaf litter and oak branches. Specimens were collected at night, on the surface, also. The reduced wings of adults indicate that flight is not possible, and this indication is supported by absence of specimens from catches by light traps.

Geographical distribution.— The range of this species extends from Nicaragua northward to San Luis Potosi on the Gulf Versant of México.

Relationships.— The distinctive male genitalia and ovipositor, and smooth glabrous elytra place this species clearly apart from the others treated in this paper.

Material examined.— In addition to the types, we have seen 57 specimens of this species, from the following localities in México.

Chiapas. 11 km. S. Jitotol, Rte. 195, pine-sweetgum, *ca*. 1650 m., V.5.1977; Mexican Exp. 1977, J.S. Ashe, H.E. Frania, D. Shpeley (UASM). Sierra de la Colmena, San Cristobal trail, 701-853 m. [Lacandon forest], June 8, 1972; P.A. Meyer, G.E.& K.E. Ball (UASM). Yerba Buena Hospital, 2.4 km. N. Pueblo Nuevo, 1554-1829 m., June 21-22, 1972; P.A. Meyer, G.E. Ball (UASM). **Oaxaca**. 21 km. S. Valle Nacional, 1128 m., VIII.71; A. Newton (MCZC). 9.7 km. S. Valle Nacional, 650 m., V.18-20.1971; H.. Howden (UASM). Same, VII.20-31.1971; 299CS (UASM). 17.3 km. S. Valle Nacional, Rte. 175, montane trop. for., *ca*. 1000 m., IV.26.1977; Mexican Exp. 1977, J.S. Ashe, H.E. Frania, D. Shpeley (UASM). **Puebla**. 2.4 km. N. Tlaxcalantonga, VII.3-8.1971; 273 DH (UASM). **San Luis Potosi**. 29 km. S. Tamazunchale, XI.22.1946; E.S. Ross (CASC). **Veracruz**. 3.9 km. N. Coscomatepec, 1400 m., VIII.12.1987; Mexico Field Party, 1987: J. K. Liebherr, D.K. Millman (CUIC). 6.4 km. N. Huatusco, 1280 m., VII.2.1973; A. Newton (MCZC). 7.1 km. N. Huatusco, 1300 m., on clay bank, at night, VIII.15.1987; Mexican Field Party, 1987: J.K. Liebherr, D.K. Millman (CUIC). 7 km. S. Huatusco, cloud forest, *ca*. 2164 m., VII.24.1977; Mexican Exp., 1977, J.S. Ashe, H.E. Frania, D. Shpeley (UASM). Jalapa; M. Trujillo (AMNH). Jalapa, May (CASC).

Ozaena Olivier

Ozaena Olivier, 1812: 617. TYPE SPECIES: *Ozaena dentipes* Olivier, 1812: 620; by monotypy.— Dejean, 1825: 356, 433.— Dejean and Boisduval, 1829: 186, 231.— Dejean, 1831: 471.— Brullé, in Audouin and Brullé, 1834: 258.— Castelnau-Laporte, 1834: 144.— Blanchard, in Cuvier, 1842: 127.— Chevrolat, in d'Orbigny, 1847: 376.— Lacordaire, 1854: 156.— Chaudoir, 1854: 289, 297.— 1868: 49.— Csiki, 1927: 427 .— Bänninger, 1927: 193.— 1931: 184.— Blackwelder, 1944: 22.— Bänninger, 1949: 132.— Ball, 1960: 95.— Ogueta, 1965: 75.— Reichardt, 1977: 377.— Erwin, *et al*, 1977: 4.3.

Ictinus Castelnau-Laporte, 1834: 53. TYPE SPECIES: *Ictinus tenebrioides* Castelnau-Laporte,1834: 53; by monotypy; = *O. dentipes* Olivier.— 1835: 144.— Hope, 1838: 99.— Duponchel, E., in d'Orbigny, 1846: 16.

Ozena Chenu, 1851: 87 (misspelling).

Nomenclatural note.— Hope (1838: 99) fixed "*Ic. Rogerii* Dejean" as type species of *Ictinus*, but this name was not among those originally associated with that generic name.

Derivation of generic name.— From Greek, meaning to smell, in allusion to the odorous defensive secretions of the adults. Here is a fine but simple example of the fact that even the museum taxonomists of the early 19th Century were cognizant of features of living organisms, and were prepared to use such features. The bizarre notion that museum taxonomists were interested in structural features only should be put to rest.

Recognition.— Mature adults have black integuments. The antennae are relatively long for ozaenines (Fig. 14). The labium (Fig. 54) has long lateral lobes of the mentum, broadly rounded apically. The elytra and lateral margins of the pronotum have short broad setae with ridged surfaces (Fig. 107A-B).

Description.— Habitus as in Fig. 7, size large, Standardized Body Length *ca*. 14-20 mm, maximum width 5.1-6.1 mm.

Color. Body and appendages black, or very dark piceous.

Microsculpture and luster. As in Tribe Ozaenini, and on mesopleura mesh pattern transverse, on metapleura isodiametric to transverse. Surface shining in most species, dull in some.

Vestiture. Scrobes of mandibles with normal setae. Dorsal surface of elytra and lateral margins of pronotum with short broad setae, surface ridged and flattened, and apex cleft (Fig. 107B). Males without adhesive vestiture on fore tarsomeres. Ventral surface generally setose, with normal trichoid setae, abdominal sterna densely setose.

Chaetotaxy. Clypeus and vertex of head asetose, temporal areas each side with several setae. Antennae (Figs. 7, 14, and 29A-B): with antennomeres sparsely setose, setae generally short; antennomere 11 with dense concentration of sensilla basiconica in apical third to half. Mouthparts: apical margin of labrum with about 12 setae; mandibular scrobes without setae; maxillary stipes with two setae laterally; labial submentum and mentum with several setae each; glossal sclerite apically without setae; labial palpomere 2 without long setae. Pronotum: without fixed trichoid setae. Disc of elytra: without fixed trichoid setae. But note sensilla basiconica, Figs. 107A-C. Legs (fore, middle hind): coxae, 0-numerous-numerous; trochanters, generally setose; femora, asetose.

Head. Frontal impressions elongate, shallow, irregular. Eyes (Fig. 7) prominent, posteriorly with moderately large temporal lobes. Supraantennal areas not reflexed, but extended laterally each side as obtuse point.

Antennae. Long, extended posteriorly clearly past elytral humeri (Fig. 7); antennomeres 1-4 cylindrical, 5-11 (Fig. 14) moniliform, with 11 (Figs. 29A-B) distinctly swollen and apically with distinct straight sharp keel.

Mouthparts. Labrum (Fig. 36) transverse. Mandibles (Figs. 42A-D) short, thick, occlusal margin toothed. For details, see Table 1. Maxillae average in most respects, but lacinia (Figs. 47A,B) with thick brush of curved setae and terminated in short chisel-like tooth. Palpomere 4 thick, apex obliquely truncate. Labium (Fig. 54) with lateral lobes of mentum large, broadly rounded apically; tooth short; epilobes narrow, not extended to apex; palpomere 3 thick, short in *O. lemoulti* adults, apex truncate.

Prothorax. Pronotum (Fig. 7) short, distinctly wider than long. Sides explanate, elevated or flat (*O. lemoulti*). Disc convex. Impressions distinct. Prosternum with intercoxal process broad, short.

Pterothorax. As for Tribe Ozaenini, and mid-coxal cavities closed medially by junction of intercoxal processes of meso-and metasternum. Metepisternum overlapped by posterior lobe of mesepimeron.

Elytra. Intervals broad, slightly elevated. Interneurs shallow, punctate, punctures large. Basal ridge very short, hardly evident. Humeri denticulate.

Metathoracic wings. Fully developed.

Legs. As described for Ozaenini, and fore femora (Fig. 61A) about cylindrical, thickened apically, each ventrally toward base with small setose denticulate process (Fig. 61B). Fore tibia with antennal cleaner (Figs. 68A-B) reduced. or details, see Table 2. Tarsi average for Ozaenini.

Abdomen. Sclerites of segments II-VII unmodified. or details of sclerites of segments VIII and IX/X, see under "Structural and biochemical features- genital segments".

Male genitalia (Figs. 90A-D). or details, see under Structural and biochemical features", and Table 3.

Ovipositor (Figs. 80A-C). Stylomeres short, moderately densely setose apically, sensory furrow apical, with single nematiform seta.

Bursa copulatrix and spermatheca. See Table 4 for details.

Way of life.— Evidently, most known specimens of this genus preserved in museums have been collected at light, in lowland (principally tropical) forest. Nothing else is known about habitat or activity.

Geographical distribution.— The range of *Ozaena* extends from Argentina in South America to southern Arizona in North America. Only one species, *O. lemoulti* Bänninger, is known to occur in Middle and southern North America.

Relationships.— The sister group of *Ozaena* seems to be *Platycerozaena*, based on similarities in setal reduction, type of setae, reduction of antennal cleaner, distribution of setation on the antennae, and form of the stylomeres, bursa copulatrix, and spermatheca. We have considered seriously the proposition that these two groups are congeneric. The relationships of the lineage represented by these two genera is not evident at this time.

Included species.— *Ozaena* includes ten species, eight of which have been described.

Ozaena lemoulti Bänninger

Figs. 7, 14, 22, 29A-B, 36, 42A-D, 47A-B, 54, 61A-B, 68A-B, 80A-C, 90A-D, and 107A-D.

Ozaena lemoulti Bänninger, 1932: 185. TYPE MATERIAL: HOLOTYPE male, labelled "GUYANE FRANCSE St Jean du Maroni Collection LeMoult"; "*Ozaena lemoulti* Bänninger" [handwritten] (Bänninger Collection, Zurich). TYPE LOCALITY: as indicated on locality label of holotype.— Blackwelder, 1944: 23.— Bänninger, 1949: 133.— Ogueta, 1965b: 87.— Erwin *et al,* 1977: 4.3. Bänninger, 1956: 400.

Ozaena elevata Ball, 1960: 95 (not Bänninger, 1956).

Ozaena halffteri Ogueta, 1965b: 83. HOLOTYPE female, labelled "México, estado de Veracruz, Tlapacoyan, 5.IX.1953, leg. Ticul Alvarez y Gonzalo Halffter" (Ogueta Collection). NEW SYNONYMY.— Erwin, *et al.*, 1977: 4.3.

Notes about synonymy.— We have not seen the holotype of *O. halffteri*, but we have seen specimens from Arizona and from localities extending collectively through the whole of Middle America and northern South America. A detailed study shows that the supposed diagnostic features given by Ogueta in his key to species (*l.c.*, 76-77) exhibit too much variation to support the hypothesis that two species are represented in the material noted above. Thus, we regard the names *O. lemoulti* and *O. halffteri* as synonyms of one another.

The name *Ozaena elevata* was published for a specimen of *O. lemoulti*, collected at Nogales, Arizona (Ball, 1960: 95), based on Bänninger's determination as *Ozaena elevata* var? However, that determination was made before the material was available to indicate the limits of *O. lemoulti* and *O elevata*. We are satisfied that the present identification of the Nogales specimen is correct. Nonetheless, we are a bit doubtful if *O. lemoulti* and *O elevata* Bänninger are specifically distinct. The material available is not sufficient to permit this second synonymy. See Bänninger, 1956: 400.

Recognition.— The only species of *Ozaena* in Middle and North America, adults of this species might be confused only with those of *Pachyteles kuntzeni*, which are also large and uniformly dark in color. Form of the antennae (Figs. 14, 22, and 29A-B) distinguishes readily members of these taxa. The pronotum (Fig. 7) of adult *O. lemoulti* is shorter, broader, and with lateral margins evenly curved, not sinuate posteriorly. The elytra of adult *O. lemoulti* bear dorsally distinctive ribbed, apically branched setae (Fig. 107A-B), not exhibited by adults of *P. kuntzeni.*

Description.— Habitus as in Fig. 7. Standardized Body length males 16.8-18.4 mm., females 16.4-18.2 mm.; W/SBL males 0.31, females 0.31-0.33. Other features as described above, for genus.

Geographical distribution.— The range of this species extends from Ecuador and Cayenne in northern South America through Middle America to southern Arizona.

Relationships.— Based on details of body form, of distribution of antennal sensilla, and of mandibular structure, and allopatric geographical distribution, we postulate that *O. lemoulti* and *O. elevata*, if distinct, are sister species.

Material examined.— From México and the United States, we have seen 11 specimens from the following localities. We have seen also 22 additional specimens from localities in Brazil (Para), Cayenne, and Venezuela, in northern

South America; and from Belize, Costa Rica, Guatemala, and Panama, in Middle America .

UNITED STATES OF AMERICA. **Arizona.** *Santa Cruz County*.— Nogales, VI.19.1945, in house (USNM). Peña Blanca Canyon, Pajarito Mts., 1191 m., VII.27.1978; S. McCleve (SMCC).

MÉXICO . **Chiapas**. Palenque ruins, 100 m., U-V light, May 20, 1972; P. Meyer, G.E.&K.E. Ball (UASM). **Coahuila**. Saltillo; E. Palmer (MCZC). **Morelos**. Cuernavaca; V. Barrett (CASC). **San Luis Potosi.** El Salto, VIII.8.1966; O. S. Flint (USNM). Palitla, at light, VII.21.1970; Schafffner, Murray, Phelps, Hart (TAMU). Tamazunchale, V.20.1952; M. Cazier, W. Gertsch, R. Schrammel (AMNH). **Tamaulipas**. El Salto Falls, 42 km. W. Antiguo Morelos, 610 m., VII.11-14.1963; Duckworth & Davis (USNM). **Veracruz.** Fortin de las Flores, 1010 m., at light, VII.7-12.1974; J.A. Chemsak, E.& J. Linsley, and J. Powell (CISC).

Platycerozaena Bänninger
Figs. 8, 15, 23, 30, 37, 43A-F, 48, 55, 62, 69A-B, 81A-C, 91A-D, and 96.

Ozaena (in part); Bates, 1874: 23.— 1881: 25.— Csiki, 1927: 427.

Platycerozaena Bänninger, 1927: 197. TYPE SPECIES: *Ozaena brevicornis* Bates, 1874: 24; by monotypy.— Blackwelder, 1944: 23.— Ogueta, 1965c: 361.— Reichardt, 1977: 377.— Erwin, 1979: 557.— Roach, *et al.*, 1979: 18.

Ozaena (*Platycerozaena*) Bänninger, 1949: 133.

Nomenclatural note.— Ogueta (1965c: 361) indicated *O magna* as type species of *Platycerozaena*. However, this name was not associated with this generic name when the latter was proposed.

Derivation of generic name.— From Greek, *platyceros*, meaning flat horn, to be interpreted as antenna, combined with *Ozaena*; literally, the *Ozaena* with flat antennae.

Ranking.— Bänninger (1949), without explanation, included *Platycerozaena* as a subgenus of *Ozaena*. We agree with Ogueta (1965c: 361) that the two groups, though no doubt closely related, are each monophyletic and abundantly distinct from each other. Accordingly, we choose to rank *Platycerozaena* as a distinct genus.

Recognition.— Adults of this genus are readily distinguished by black color, elongate labrum (Fig. 37), short antennae with markedly transverse antennomeres 5-10 (Fig. 15), mentum with very small tooth (Fig. 55), and small antenna cleaner (Figs. 69A-B).

Description.— Habitus as in Fig. 8, moderate in size, Standardized Body length *ca*. 6.0-8.0 mm., maximum width 1.8-2.5 mm, slender in form.

Color. Body and appendages of mature adults black.

Microsculpture and luster. As for Tribe Ozaenini, and pterothoracic pleura and sterna with transverse mesh pattern. Elytra with microlines fine, mesh pattern transverse. Surface shining to subiridescent.

Vestiture. Dorsum with sparse covering of short setae, these flattened, expanded, ribbed and branched on pronotum and elytra (*cf.* Fig. 107A-B). Ventral surface sparsely setose.

Chaetotaxy. Labrum (Fig. 37), clypeus, vertex and temporal areas of head, lateral margins of pronotum and elytra without long tactile ("fixed") setae. Antennae: antennomeres 1-10 with short trichoid setae; 5-10 each with patch of sensilla basiconica on ventral anterior and posterior surfaces; antennomere 11 with sensilla basiconica extensive laterally and preapically; central triangular area more or less glabrous (Figs. 23 and 30). Mouthparts: without fixed setae (as in *Ozaena*). Legs (fore-middle-hind): coxae, numerous-numerous-numerous; trochanters, numerous-numerous-sparse. Basal fore tarsomeres of males without adhesive setae.

Head. Frontal impressions broad, shallow. Eyes (Fig. 8) prominent, posteriorly with small temporal lobe each side. Supraantennal area each side not reflexed, ridged, extended laterally as obtuse point.

Antennae. Short, not extended posteriorly beyond basal margin of pronotum. Antennomeres 1-4 more or less cylindrical, rather short; antennomeres 5-11 (Fig. 15) slender, markedly compressed; antennomere 11 (Figs. 23 and 30) more elongate, broad, apical margin broadly rounded in lateral aspect, apex narrowly keeled, keel sinuate (Fig. 30).

Mouthparts. Labrum (Fig. 37) elongate. Mandibles (Figs. 43A-F) with occlusal margins toothed, short, broad (see Table 1 for details). Maxillae (Fig. 48) average for Ozaenini, palpomere 4 markedly broad, apical margin obliquely truncate. Labium (Fig. 55): mentum with long slender lateral lobes, each pointed apically; epilobes slender, terminated just short of apex; palpomere 3 broad, apex truncate.

Prothorax. Pronotum transverse, lateral margins narrow, beaded, sinuate posteriorly or evenly rounded; impressions distinct. Prosternum with intercoxal process short, rather slender.

Pterothorax. As for Ozaenini, and base of metepisternum narrowly overlapped by base of mesepimeron.

Elytra. Intervals broad, slightly elevated. Interneurs narrow, punctate. Basal ridge very short, hardly evident. Humeri denticulate.

Legs. In most features, as described for Ozaenini. Fore femora each clavate, with ventral margin protruded as broad projection (Fig. 62). Antennal cleaner of fore tibia (Figs. 69A-B) reduced (see Table 2 for details).

Abdomen. Sclerites of segments II-VII unmodified. or description of sclerites of segments VIII and IX/X, see under "Structural and biochemical features, genital segments". See also Fig. 96.

Male genitalia. See under "Structural and biochemical features" and Table 3. See also Figs. 91A-D.

Ovipositor (Figs. 81A-C). Stylomeres short, moderately densely setose toward apex, rather broad in ventral aspect, sensory furrow and nematiform setae not identified.

Bursa copulatrix and spermatheca. See Table 4 for details.

Defensive secretions.— Five compounds. See Table 5 for details.

Way of life.— Nothing has been reported about this topic for *Platycerozaena*. The reduced setation suggests some unusual mode of living, in which tactile sensation is not a premium. Paussines also exhibit reduction in sensilla, and they live with ants. Perhaps, then, members of *Platycerozaena* are myrmecophilous, too.

Geographical distribution.— This genus is known only from central Brazil northward to Nicaragua, in Lower Middle America.

Relationships.— This genus seems to be the sister group of *Ozaena* Olivier. For details, see under the latter genus.

Included species.— According to Ogueta (1965c: 362-363), *Platycerozaena* includes four species.

ZOOGEOGRAPHY

Because the boundaries of this study are artificial both phylogenetically and geographically, it lacks the unity required to develop a coherent generalizing evolutionary hypothesis. Accordingly, we attempt only to relate to general patterns the taxonomic bits and pieces that we have treated.

The Tribes

Metriines are confined to dry temperate forests of the west coast of United States, beyond the periphery of the range of the Ozaenini. The latter group is pantropical, and in the New World ranges from the margins of the Sonoran desert in southwestern United States to the Chilean rain forests in South America. The group is centered in the lowland tropics, with numbers of species declining with increasing altitude and latitude.

Two historical interpretations seem possible. First, the ancestral stock of the Metriini and Ozaenini occupied the whole of Pangaea before its breakup, toward the end of the Palaeozoic. With breakup, the northern vicar evolved into the

Metriini, and the southern one produced the Ozaenini (Erwin, 1979b: 577). Second, the ancestral stock of the Metriini + Ozaenini was Gondwanian, appearing after breakup of Pangaea. An initial split produced a less progressive line, the Metriini, which was replaced gradually in the tropics by the more progressive sister group, the Ozaenini. Metriines were replaced eventually, throughout the tropics, and survive today only in a small area of the north temperate zone, beyond the range of their ozaenine sister group. Either of these interpretations recognizes *Metrius* as a relict group.

A more specific hypothesis accounts for the occurrence of *Metrius* (and other relict taxa) in coastal areas in western United States. According to some geologists, various small Pacific terranes have drifted eastward, eventually encountering and becoming part of the west coast of North America. Perhaps these tectonic plates carried with them the remnants of old taxa that populated the coastal areas (Downes and Kavanaugh, 1988: 8). We give little credence to this possibility.

The Genera

Patterns.— Four of the Middle American genera (*Physea*, *Pachyteles*, *Ozaena* and *Platycerozaena*) occur in both the South and North American continents. *Entomoantyx* is confined to the Middle American part of the North American continent. In terms of northward limits, *Physea*, *Pachyteles*, and *Ozaena* reach southwestern United States. The range of *Entomoantyx* extends north of the Isthmus of Tehuantepec in northeastern México, and *Platycerozaena* reaches only Nicaragua, at the southern edge of Nuclear Middle America. *Pachyteles* is the only ozaenine genus known from the West Indies, where it is represented in the Greater Antilles by two species. In South America, *Physea*, *Pachyteles*, and *Ozaena* reach Argentina, whereas *Platycerozaena* reaches only central Brazil.

In terms of diversity, all of the bi-continental genera are more speciose on the South American than the North American continent, though for *Physea* and *Platycerozaena* the difference is slight.

Historical interpretation.— Accepting a Gondwanian origin of the Ozaenini, we believe that occurrence of the tribe in Middle America and southwestern United States on the North American continent, must have been accomplished by dispersal— in part over sea and in part over land, in Tertiary time. There could have been an over land movement, if in fact there was an early Tertiary inter-continental connection, as has been postulated by some authors (for a discussion, see Donnelly, 1988, and Savage, 1982).

Based on phylogenetic position, diversity pattern and extent of northward penetration, we believe the genera arrived in the following sequence: first, the ancestral stock of *Entomoantyx*, a genus which we take to be a relict; second, *Pachyteles* and *Physea*; third, *Platycerozaena* (few Middle American species, limited penetration); and fourth, *Ozaena* (only one species, which occurs in northern South America, as well).

Number of incursions postulated varies. For the bi-continental genera, we indicate: one each, for *Physea* and *Ozaena*; for *Platycerozaena*, two (one endemic species in Middle America, and one shared between the northern and southern continents); for *Pachyteles*, several incursions, with several each for the nominotypical subgenus and for *Goniotropis*.

For time of arrival, we postulate Late Cretaceous to Early Tertiary for *Entomoantyx*; Middle Tertiary for *Physea*; Pliocene and Pleistocene for *Platycerozaena*; and Pleistocene for *Ozaena*. Because *Pachyteles* is represented by several of the same species on both continents, as well as by an array of endemic species in Middle America, we postulate a range of times from Early Tertiary to Pleistocene and possibly even Recent.

The Greater Antilles were invaded probably at two different times by *Pachyteles* : once early, possibly in mid-Tertiary (this invasion represented by an endemic flightless species, living in the Jamaican highlands, undescribed, and possibly now extinct); and once recently (Pleistocene or Recent), and represented by *P. gyllenhali*, on the island of Cuba. The Lesser Antilles were probably invaded comparatively recently by one or two species of *Pachyteles.*

Mid-Tertiary arrival of the ancestral stock of the species of *Pachyteles* on Jamaica could have been facilitated by a land bridge, now foundered, but represented by the Nicaraguan Rise (Donnelly, 1988), or possibly by a mobile Jamaica that was closer to the mainland than it is now (Rosen, 1985, and references therein). We are inclined to doubt the latter possibility.

In conclusion, then, we postulate that the Middle-North American fauna has developed partly by incursions of taxa from South America, and partly by *in situ* differentiation of invading stocks. This is a common biogeographic pattern, described by many biogeographers.

Ozaenine Species of Southwestern United States and Vicinity

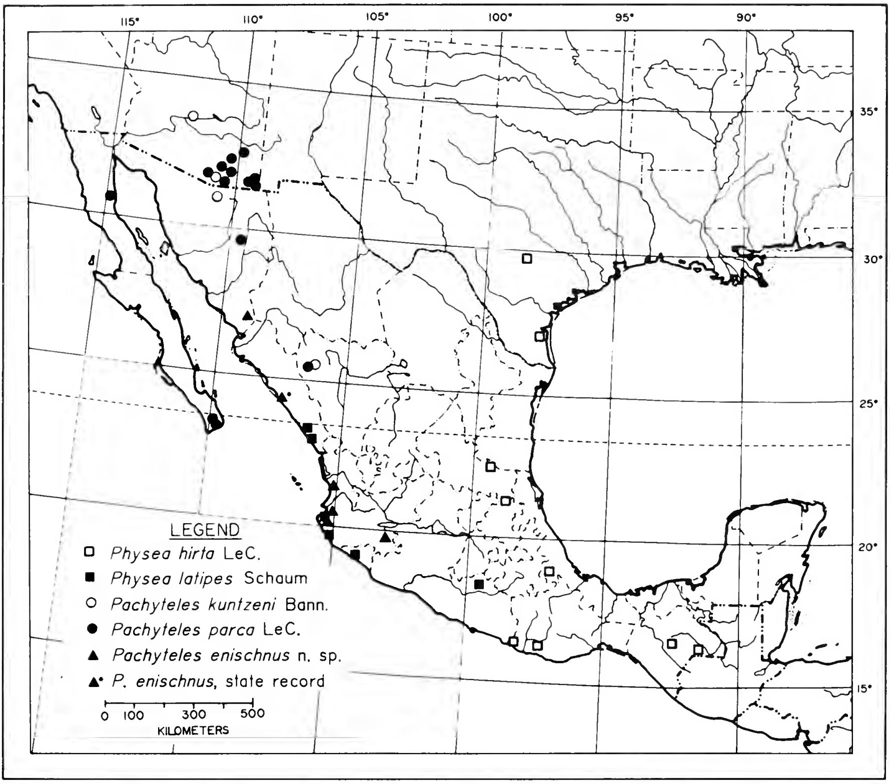
The pattern.— This is described partly in terms of extent of range and habitats. The latter are numbered below, according to the classification of Brown and Lowe (1980) and Brown, *et al.* (1980). Of the ozaenine species that are in or near southwestern United States, one (*Physea hirta*) reaches its northern limits in southern Texas, on the Gulf Versant. The remaining six are in the west, entering United States in Arizona, with the range of *Pachyteles gyllenhali* extended northward to approximately 33°30'N.

The northwestern species comprise two groups in terms of extent of range: those confined to the west (*Physea latipes*, *Pachyteles parca*, *P. kuntzeni*, and *P. enischnus*; Map 1), and those with ranges extended southward for various distances (*P. gyllenhali* and *Ozaena lemoulti*). *Physea hirta* belongs to this latter group, also.

In terms of habitat, the species confined to the west occupy dry habitats primarily, including tropical Sinaloan thorn scrub (134.3), Sinaloan deciduous forest (124.6), Madrean evergreen woodland (123.3), Sonoran desert scrub (154.11), Chihuahuan desert scrub (153.2), and interior chaparral (132.2). However, it is important to realize that desert areas are probably marginal for ozaenines, because no extensive diversification of the group has taken place in such areas, and no species are confined to desert habitats. The wide-ranging western species occupy some of these habitats, and as well Riparian cottonwood-willow series (224.53), and southward, evergreen tropical and cloud forest.

Another aspect of the pattern is distribution of putative sister species. *Physea hirta* and *P. latipes* are probably sister species, and their range overlap is only partial (Map 1). *Pachyteles parca* and *P. kuntzeni* seem to be sister species, whose ranges are in contact, probably narrowly, in southern Arizona and in northern México. *P. enischnus* has a probable sister species (*P. filiformis* Chaudoir) *filiformis* Chaudoir, *Pachyteles;*in eastern México. The sister species of *P. gyllenhali* as not been postulated, though we suspect it will be South American. That of *Ozaena lemoulti* is probably the more southern Brazilian *O. elevata* Bänninger, with the area of disjunction being the Amazon Basin.

The fact that most of the northern ozaenine species have vicariant or parapatric sister species suggests relatively recent differentiation of each of the stocks to which these species belong. From the standpoint of interpretation, it is



Map 1. Geographical positions of known localities in México and southwestern United States for five species of Ozaenini.

particularly interesting that each of the three species endemic on the Pacific Versant (*Physea latipes*, *Pachyteles parca*, and *P. enischnus*) have putative eastern counterparts.

In summary, the species at the northern end of the range of the Ozaenini occupy there principally dry forests and marginally, desert habitats. Most of the endemic Middle American-U.S. taxa are confined to such habitats. The two taxa whose ranges extend into South America plus *Physea hirta* occur in wet tropical forests, as well. The endemic Middle American-U.S. taxa exhibit east-west disjunction or near-disjunction, of closely related species.

Geographical history.— The general pattern described above is like the distribution patterns of many other taxa that occur in the same area (see Liebherr, 1986: 161-172, for details of the *Agonum extensicolle* group, and associated references to other authors and taxa. See also Ball and Nimmo, 1983, and Ball and Maddison, 1987).

The explanation seems rather simple. Each ancestral stock of the Recent endemic Middle American elements was divided and thus isolated, to the east and west of the north-south trending Sierra Madre Occidental, as a result of drying of the climate in the later part of the Tertiary Period. In isolation, the now vicariant elements differentiated from one another, becoming specifically distinct. Also, the western species probably became adapted to some extent to desert conditions, and succeeded in establishing in habitats marginal to their ancestral dry forests.

In Holocene time, and possibly earlier during the wetter glacials, the erstwhile vicariants *P. parca* and *P. kuntzeni* came into contact with one another, their ranges overlapping.During the wetter glacials of the Pleistocene, probably, the ranges of *Pachyteles gyllenhali* and *Ozaena lemoulti* expanded, (the former species reaching Cuba in the Caribbean Ocean, and the Tres Marias Islands in the Pacific), and these taxa reached the northern limits of the tribe Ozaenini in the New World, and came to overlap the ranges of the more northern endemics. Possibly the range of *Physea hirta* expanded similarly, with this predominantly eastern species spreading through the Isthmus of Tehuantepec to the lowlands on the Pacific Versant of México.

More generally, we believe that these northern ozaenine stocks provide some perception about how the dry adapted fauna of western México evolved. Certain species, ranging northward from the wet tropics, are able to enter drier habitats. In the course of changing circumstances, the expanded ranges of these species become disjunct. In the fullness of time, and under the influence of natural selection, the dry forest stocks become adapted to such conditions to the extent that they either become confined to them, or are able to enter still drier habitats. So far, ozaenines have not penetrated the extreme habitats encountered in the Sonoran and Chihuahuan deserts. Such penetration remains as a future evolutionary possibility.

Corollaries.— If this zoogeographic scenario is correct, the following should be found to be true.

1. Future work will not refute the hypothesized sister-group relationships.
2. *Pachyteles parca*, most collections of which have been made in Arizona, will be found further south along the Pacific coast, in Sinaloan deciduous forest.
3. The range of *Pachyteles kuntzeni* is in fact limited in northwestern México, to the eastern slopes of the Sierra Madre Occidental, as is suggested by present limited data. It will be found, farther south, in tropical forest, as well.

CONCLUDING STATEMENT

Nearly 30 years ago, when Ross H. Arnett, Jr., published his treatment of the beetle genera of North America north of México, knowledge of the included Ozaenini was hardly more than what was known in the previous century, when most of the species of the group resident in southwestern United States were described. In this work, we add a few points about relationships and distribution of these species, but much more must be done, both ecologically and systematically, to bring this small but markedly divergent faunule (seven species, only, in three genera) to that stage of understanding at which ecologists can make use of the species as elements in ecosystems, *et cetera.*

At a more general level, we have added to understanding of the ozaenine genera of Middle America by detailed comparisons of a number of systems of structural features, and by entering into the structural characterizations the important data that have been generated by others concerning the defensive secretions of the pygidial glands. For the first time, we have used in detail the features of *Metrius* in out-group comparison to polarize in an evolutionary context the features of the ozaenine genera. Still to be done is to work out relationships of these genera on a worldwide basis, and to relate the reconstructed phylogenetic patterns to the movement of continents as described by plate tectonic theory.

In our investigations of structural features, we have uncovered a wealth of detail that could be analyzed profitably by functional morphologists: mouthparts and ovipositors are two such systems.

We hope we have provided an adequate basis for the next stage of systematic analysis of the New World Ozaenini, which must be treatment of the species, particularly of *Pachyteles* (*sensu lato*). We hope that those who use this publication find in the wealth of implied questions about ozaenines adequate recompense for the lack of answers that we have been able to provide.

ACKNOWLEDGEMENTS

We thank the entomologists whose names appear in the list of codens and addresses of collections from which we received the material on which this study is based. The senior author adds a special note of appreciation to those who made possible his visits to study their collections, and who extended warm hospitality to him during those visits: M. E. Bacchus, P. M. Hammond, R. D. Pope, and N. E. Stork (BMNH); D. H. Kavanaugh (CASC); S. R. Shaw and D. R. Maddison (MCZC); and L. Sims and T. L. Erwin (USNM). Lee H. Herman (AMNH) made special efforts to arrange for the loan of the type of *Pachyteles beyeri* Notman.

Most of the line drawings of the male genitalia were prepared by D. R. Maddison, while he was a graduate student at the University of Alberta. D. Shpeley and G. D. Braybrook worked together in preparing the material and photographs of structural features, using the Department of Entomology's scanning electron microscope. J. S. Scott prepared the photographs of habitus and the plates of illustrations.

At our request, a draft of the manuscript was reviewed by Yves Bousquet (Biosystematics Research Centre, Agriculture Canada, Ottawa, Ontario) and by Donald R. Whitehead (Systematic Entomology Laboratory, United States Department of Agriculture, Washington, D. C.). Although we were not able to take advantage of all of their proposals for improvement, we adopted many of them and made corrections, as required.

We hope that our colleagues and associates who contributed so generously to this study find adequate recompense for their efforts in the resulting publication.

Financial support for field and museum work was received through grants to the senior author: A-1399, Natural Sciences and Engineering Research Council of Canada; and GB-3312, National Science Foundation, U.S.A. Publication costs were met with funds from NSERCC Grant A-1399. We are grateful for this important assistance.

REFERENCES CITED

Allen, R. T. and G. E. Ball, 1980. Synopsis of Mexican taxa of the *Loxandrus* series. (Coleoptera: Carabidae: Pterostichini). Transactions of the American Entomological Society, 105: 481-576.

Andrewes, H. E. 1929. Coleoptera Carabidae. Vol. 1.- Carabinae. *In*, The Fauna of British India, including Ceylon and Burma (J. Stephenson, Editor). Taylor and Francis, London. xviii + 431 pp., 5 plates.

Audouin, J. V. and A. Brullé. 1834. Histoire naturelle des Insectes, traitant de leur organization et de leurs moeurs en general, et comprenant leur classification et la description des espèces. Volume 4, Coléoptères I. . D. Pillot, Paris. 479 pp.

Bänninger, M. 1927. Die Ozaenini. Deutsche Entomologische Zeitschrift for 1927, 177-216.

Bänninger, M. 1932. Uber Carabinae, Erganzungen und Berichtigungen. (Col.) 17 Beitrag. Deutsche Entomologische Zeitschrift, (1931): 177-212.

Bänninger, M. 1949. Ueber Carabinae (Col.) Erganzungen und Berichtgungen III, mit Bemerkungen zu R. Jeannel's neuer Einteilung der Carabiden. Mitteilungen der Müncher Entomologischen Gesellschaft e. V., 35-39, 1945-1949, pp. 127-157.

Bänninger, M. 1956. Uber Carabinae, Erganzungen und Berichtigungen (IV). Entomologischen Arbeiten aus dem Museum G. Frey, Tutzing, 7 (1): 398-411.

Ball, G. E. 1960. Carabidae, Fascicle 4, pp. 55-210. *In*, The beetles of the United States (A manual for identification) (R. H. Arnett, Editor). The Catholic University of America Press, Washington, D. C. XI + 1112 pp.

Ball, G. E. 1979. 2.21. Conspectus of carabid classification: history, holomorphology and higher taxa, pp. 63-111. *In*, Carabid beetles, their evolution, natural history and classification, *etc*. (T. L. Erwin, G. E. Ball, D. R. Whitehead and A. L. Halpern, Editors). Dr. W. Junk bv Publishers. The Hague, The Netherlands. X + 644 pp.

Ball, G. E. 1985. The contributions of Philip J. Darlington, Jr. to the study of carabid beetles in the Americas, and a bibliography of his publications, pp. 17-30. *In*, Taxonomy, phylogeny and zoogeography of beetles and ants: a volume dedicated to the memory of Philip Jackson Darlington, Jr. (1904-1983). (G. E. Ball, Editor). Dr. W. Junk Publishers, Dordrecht, Boston, Lancaster. XIV + 514 pp.

Ball, G. E. and D. R. Maddison. 1987. Classification and evolutionary aspects of the species of the New World genus *Amblygnathus* Dejean, with description of *Platymetopsis* new genus, and notes about selected species of *Selenophorus* Dejean (Coleoptera: Carabidae: Harpalini). Transactions of the American Entomological Society, 113: 189-307.

Ball, G. E. and A. P. Nimmo. 1983. Synopsis of the species of subgenus *Progaleritina* Jeannel, including reconstructed phylogeny and geographical history (Coleoptera: Carabidae: *Galerita* Fabricius). Transactions of the American Entomological Society, 109: 295-356.

Basilewsky, P. 1962. Les Ozaeninae d'Afrique et de Madagascar. Revue de Zoologie et Botanique Africaine, 66 (3-4): 291-314.

Bates, H. W. 1874. Notes on Cicindelidae and Carabidae and descriptions of new species (No. 17). Entomologists Monthly Magazine, 11: 22-28.

Bates, H. W. 1881. Insecta, Coleoptera, Carabidae, Volume 1, part 1, pp. 1-40, plates i-ii. *In*, Biologia Centrali-Americana, 1879-1911, Coleoptera, 7 volumes in 17 parts (F. D. Godman and O. Salvin, Editors). London.

Bell, R. T. 1967. Coxal cavities and the classification of the Adephaga (Coleoptera). Annals of the Entomological Society of America, 60 (1): 101-107.

Bell, R. T. 1983. What is *Trachypachus*? (Coleoptera: Trachypachidae), pp. 590-596. *In*, The Baron Maximilien de Chaudoir (1816-1881): a symposium to honor the memory of a great coleopterist during the centennial of his death (D. R. Whitehead, Editor). The Coleopterists Bulletin, 36 (3&4): 459-609.

Bils, W. 1976. Das Abdomenende weiblicher, terrestrich lebender Adephaga (Coleoptera) und seine Bedeutung fur die Phylogenie. Zoomorphologie, 84 (2): 113-193.

Blackwelder, R. E. 1944. Checklist of the coleopterous insects of Mexico, the West Indies and South America. Part 1. Bulletin of the United States National Museum, No. 185, pp. 1-188.

Blanchard, E. See below, under Cuvier.

Bousquet, Y. 1986. Description of first instar larva of *Metrius contractus* Eschscholtz (Coleoptera: Carabidae) with remarks about phylogenetic relationships and ranking of the genus *Metrius* Eschscholtz. The Canadian Entomologist, 118: 373-388.

Brown, D. E. and C. A. Lowe. 1980. [Map of} Biotic communities of the southwest. General Technical Report RM 78. Rocky Mountain Forest and Range Experiment Station Forest Service, U.S.D.A. U. S. Government Printing Office, 1980. 679.042.

Brown, D. E., C. A. Lowe, and C. P. Pase. 1980. A digitized systematic classification for ecosystems with an illustrated summary of the natural vegetation of North America. U.S.D.A. Forest Service General Technical Report RM-73, 93 pp. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Brullé, A. 1834. See Audouin and Brullé, above.

Castelnau, F. L. Laporte, de. 1834. Etudes entomologiques ou description des insectes nouveaux; et observations sur leur synonymie. Paris. viii + pp. 1—94.

Castelnau, F. L. Laporte, de. 1835. Etudes entomologiques ou description d' insectes nouveaux; et observations sur leur synonymie, part 1. Paris. pp. 95-195. 4 colored plates.

Chaudoir, M. de. 1848. Memoire sur la famille des carabiques. Bulletin de la Société Imperiale des Naturalistes de Moscou, 21 (1): 3-134.

Chaudoir, M. de. 1852. Memoire sur la famille des Carabiques, Part 3. Bulletin de la Société Imperiale des Naturalistes de Moscou, 25 (1): 3-104.

Chaudoir, M. de. 1854. Memoire sur la famille des carabiques. Bulletin de la Société Imperiale des Naturalistes de Moscou, 27: 112-144, 279-352.

Chaudoir, M. de. 1868. Revision du groupe des ozenides. Annales de la Société Entomologique Belgique, 11: 43-74.

Chenu, J. C. 1851. Encyclopedie d'histoire naturelle ou Traite complet de cette Science d'apres les travaux des naturalistes les plus éminents de tous les pay et de toutes les epoques. Coléoptères Cicindeletes, carabiques, *etc*. Volume 1. Paris. 312 pp., 12 + 28 plates.

Chevrolat, L. A. A. See below, under d'Orbigny.

Crowson, R. A. 1955. The natural classification of the families of Coleoptera. Nathaniel Lloyd and Co., Ltd. 187 pp., 213 figs.

Crowson, R. A. 1981. The biology of the Coleoptera. Academic Press, London and New York. xi + 802 pp.

Csiki, E. 1927. Coleopterorum Catalogus, pars. 92, Carabidae: Carabinae II, pp. 315-622 (Vol. 1).(S. Schenkling, Editor). W. Junk, Berlin W 15.

[Cuvier, G.]. 1842. Le regne animal distribue d apres son organisation, pour servir de base a l'histoire naturelle des animaux, pp. 121-128. Volume 1, Disciples' Edition, 1838-1845. Paris. 557 pp.

Darlington, P. J., Jr. 1950. Paussid beetles. Transactions of the American Entomological Society, 76: 47-142.

Dejean, P. F. M. A. 1825. Species general des Coléoptères de la collection de M. le Comte Dejean. Volume 1. Mequignon-Marvis, Paris. xxx + 463 pp.

Dejean, P. F. M. A. 1831. Species general des Coléoptères de la collection de M. le Comte Dejean. Mequignon-Marvis, Paris. viii + 883 pp.

Dejean, P. F. M. A. 1834. Catalogue des Coléoptères de la collection de M. le Comte Dejean, Deuxieme edition, livr. 3, pp. 177-256. Paris.

Dejean, P. F. M. A. 1837. *Ibid*., Troisieme edition, revue, corigeé et augmenteé, livr. 1-4, pp. 1-468. Paris.

Dejean, P. F. M. A. and J. B. A. Boisduval. 1829. Iconographie et histoire naturelle des coléoptères d'Europe. Tome 1. Mequignon-Marvis, Paris. XIV + 400 pp, 60 plates.

Deuve, T. 1988. Etude phylogenetique des Coléoptères Adephaga: redefinition de la famille Harpalidae, *sensu novo*, et position systematique des Pseudomorphinae et Brachinidae. Bulletin de la Société Entomologique de France, 92 (5-6): 161-182.

Donnelly, T. W. 1988. 2. Geologic constraints on Caribbean biogeography, pp. 15-37. *In*, Zoogeography of Caribbean insects (J. K. Liebherr, Editor). Comstock Publishing Associates, Cornell University Press, Ithaca and London. xi + 285 pp.

Downes, J. A. and D. H. Kavanaugh. 1988. Origins of the North American insect fauna: introduction and commentary, pp. 1-12. *In*, Origins of the North American insect fauna (J. A. Downes and D. H. Kavanaugh, Editors). Entomological Society of Canada, Memoirs, No. 144: 168 pp.

Duponchel, E. See d'Orbigny, C. D., 1845, below.

Dupuis, P. 1911. Coleoptera Adephaga Carabidae Subfam. Metriinae and Mystropominae, asc. 116, 3 pp., 2 plates. *In*, Genera Insectorum (P. Wytsman, Editor). Verteneuil et Desmet, Bruxelles.

Eisner, T., T. H. Jones, D. J. Aneshansley, W. R. Tschinkel, R. E. Silberglied, and J. Meinwald. 1977. Chemistry of defensive secretions of bombardier beetles (Brachinini, Metriini, Ozaenini, Paussini). Journal of Insect Physiology, 23: 1383-1386.

Eisner, T. and D. J. Aneshansley. 1981. Spray aiming in bombardier beetles: jet deflection by the Coanda effect. Science, 215: 83-85.

Emden, F. I. van. 1936. Eine interessante zwischen Carabidae und Paussidae vermittelnde Käferlarve. Arbeiten uber physiologische und angewandte Entomologie aus Berlin-Dahlem, 3: 250-256.

Emden, F. I. van. 1942. A key to the genera of larval Carabidae. Transactions of the Royal Entomological Society of London, 92: 1-99, 100 figs.

Erwin, T. L. 1979a. The American connection, past and present, as a model blending dispersal and vicariance in the study of biogeography,pp. 355-367. *In*, Carabid beetles: their evolution, natural history and classification (T. L. Erwin, G. E. Ball, D. R. Whitehead and A. L. Halpern, Editors). W. Junk, b.v., Publishers, The Hague. X + 644 pp.

Erwin, T. L. 1979b. Thoughts on the evolutionary history of ground beetles: hypotheses generated from comparative faunal analyses of lowland forest sites in temperate and tropical regions (Coleoptera: Carabidae), pp. 539-592. *Ibid.*

Erwin, T. L. 1985. The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles, pp. 437-493. *In*, Taxonomy, phylogeny and zoogeography of beetles and ants. A volume dedicated to the memory of Philip Jackson Darlington, Jr. (1904-1983). (G. E. Ball, Editor). Dr. W. Junk Publishers, Dordrecht, Boston, Lancaster. XIII + 514 pp.

Erwin, T. L. and A. L. Halpern. 1978. Max Bänninger: his collection and publications (Coleoptera: Carabidae). The Coleopterists Bulletin, 32: 357-366.

Erwin, T. L. and L. L. Sims. 1984. Carabid beetles of the West Indies (Insecta: Coleoptera): a synopsis of the genera and checklist of tribes of Caraboidea, and of the West Indian species. *Quaestiones Entomologicae,* 20 (4): 350-466.

Erwin, T. L., D. R. Whitehead, and G. E. Ball. 1977. Family 4. Carabidae. The ground beetles, pp. 4.1-4.68. *In*, Checklist of the beetles of Canada, United States, Mexico, Central America, and the West Indies (R. E. Blackwelder and

R. H. Arnett, Jr., Editors). World Digest Publications, Oxycopis Pond, Wallace Road, Kinderhook, New York, 12106.

Evans, M. E. G. 1986. Carabid locomotor habits and adaptations, pp. 59-77. In, Carabid beetles, their adaptations and dynamics. XVIIth International Congress of Entomology, Hamburg, 1984 (P. J. den Boer, M. L. Luff, D. Mossakowski and F. Weber, Editors). Gustav Fischer, Stuttgart- New York. Contents + 351 pp.

Evans, M. E. G. and T. G. Forsythe. 1985. Feeding mechanisms and their variation in form, of some adult ground beetles (Coleoptera: Caraboidea). Journal of Zoology, London (A), 206: 113-143.

Forbes, W. T. M. 1926. The wing folding patterns of the Coleoptera. Journal of the New York Entomological Society, 34: 42-139.

Forsyth, D. J. 1972. The structure of the pygidial glands of the Carabidae. Proceedings of the Zoological Society of London, 32 (4): 253-309.

Forsythe, T. G. 1982. Feeding mechanisms of certain ground beetles (Coleoptera: Carabidae). The Coleopterists Bulletin, 36 (1): 26-73.

Forsythe, T. G. 1987. Ground beetles: form and function. Antenna, 11 (2): 57-61.

Goulet, H. 1979. 2.25. Contributions of characters of larvae to systematics of Carabidae, pp. 205-208. *In*, Carabid beetles: their evolution, natural history and classification (T. L. Erwin, *et al.*, Editors). Dr. W. Junk bv Publishers. The Hague, The Netherlands. X + 644 pp.

Gray, G. R. 1832. Notices of new genera and species. *In,* The Animal Kingdom arranged in conformity with its organization by the Baron Cuvier, vol. 14 (Insecta, vol. 1), (Griffith and Pidgeon, Editors). London. 570 pp.

Hlavac, T. . 1971. Differentiation of the carabid antenna cleaner. Psyche, 78: 51-66.

Hope, F. W. 1838. The Coleopterists Manual, Part the Second, containing the predaceous land and water beetles of Linnaeus and Fabricius. H. G. Bohn, London. xvi + 168 pp., 3 colored plates.

Horn, G. H. 1868. New species of Coleoptera from the Pacific District of the United States. Transactions of the American Entomological Society, 2: 129-178.

Horn, G. H. 1881. On the genera of Carabidae with special reference to the fauna of Boreal America. Transactions of the American Entomological Society, 9: 91-196, plates 1-10.

Horn, G. H. 1894. The Coleoptera of Baja California. Proceedings of the California Academy of Sciences, (2), 4: 302-449.

Iakobson, G. G. 1906. Zhuki Rossii i Zapadnoi rukovdstvo k opredieleniiv Zhukov. Lief. 4, pp. 241-320. A. F. Devrient, St. Petersburg.

Jeannel, R. 1941. Coléoptères carabiques, premiere partie. Faune de France, 39: 1-571, 213 Figs. Paris.

Jeannel, R. 1946. Coléoptères carabiques de la region malgache (premiere partie). Faune de l'Empire francaise, 6: 1-372.

Johnson, J. W. 1978. A preliminary list of South Texas Carabidae. Cordulia, 4 (2): 66-69.

Klug, J. C. F. 1834. Jahrbücher der Insektenkunde, mit besonderer Rucksicht auf die Sammlung im Königl. Museum in Berlin herausgegeben. Volume 1. Enslin, Berlin. 96 pp., 2 plates.

Kolbe, H. 1927. Die Einstammigkeit der Paussiden und die primitiven Gattungen dieser myrmekophilen Coleopteren familie. Zoologische Anzeiger, 72: 205-218.

Kryzhanovskij, O. L. 1976. Revised classification of the family Carabidae. Entomological Reviews 1: 80-91 (translated from Russian).

Lacordaire, T. 1854. Histoire naturelle des insectes, genera des coléoptères ou exposé methodique et critique de tous les genres proposees jusqu'ici dans cet ordre d'insectes. Volume 1. Cicindeletes-Palpicornes. Libraire encyclopedique de Roret, Paris. x + 486 pp.

Latreille, P. A. 1817 [Insectes]. *In*, Le regne animal (G. C. L. D. Cuvier), Vol. 3. Paris. 653 pp.

Latreille, P. A. 1829. Les crustaces, les arachnides et les insectes, distribues en familles naturelles, ouvrage formant les tomes 4 et 5 de celui de M. le Baron Cuvier sur le regne animal (deuxieme edition). Vol. 1. Paris. 584 pp.

Latreille, P. A. and P. F. M. A. Dejean. 1822. Histoire naturelle et iconographie des insectes coléoptères d'Europe. Livr. 1. Crevot, Paris. 89 pp., plates 1-5.

LeConte, J. L. 1853. Notes on the classification of the Carabidae of the United States. Transactions of the American Philosophical Society (2), 10: 363-403.

LeConte, J. L. 1861. Classification of the Coleoptera of North America. Prepared for the Smithsonian Institution. Smithsonian Miscellaneous Collections, III (No. 136): 1-286. Part 1.

LeConte, J. L. 1884. Short studies of North American Coleoptera (No. 2). Transactions of the American Entomological Society, 12: 1-32.

LeConte, J. L. and G. H. Horn. 1883. Classification of the Coleoptera of North America. Prepared for the Smithsonian Institution. Smithsonian Miscellaneous Collections, 26, part 4 (No. 507), pp. i-xxxvii, 1-567.

Leng, C. W. 1920. Catalogue of the Coleoptera of America north of Mexico. Sherman, Mt. Vernon, New York. X + 470 pp.

Liebherr, J. K. 1986. Cladistic analysis of North American Platynini and revision of the *Agonum extensicolle* group (Coleoptera: Carabidae). University of California Publications in Entomology, 106: x + 198 pp.

Lindroth, C. H. 1969. The ground-beetles (Carabidae excl. Cicindelinae) of Canada and Alaska, Part 1, pp. I-XLVIII. *Opuscula Entomologica, Supplementum* 35.

Luna de Carvalho, E. 1959. Notas sobre Paussideos (Col. Carab. Isochaeta). Publicacoes culturais da Companhia de Diamantes de Angola, 48: 47-90.

Moore, B. P. 1979. 2.24. Chemical defense and its bearing on phylogeny, pp. 193-203. *In*, Carabid beetles: their evolution, natural history and classification...(T. L. Erwin, G. E. Ball, D. R. Whitehead, and A. L. Halpern, Editors). W. Junk, b.v., Publishers. The Hague. X + 635 pp.

Moore, B. P., T. A. Weir, and J. E. Pyke. 1987. Rhysodidae and Carabidae, pp. 20-320. *In*, Volume 4, Coleoptera: Archostemata, Myxophaga and Adephaga, viii + 444 pp. *In*, Zoological catalogue of Australia (D. W. Walton, Executive Editor). Australian Government Publishing Service, Canberra.

Nagel, B. P. 1979a. The classification of Carabidae, pp. 7-14. *In*, On the evolution of behaviour in carabid beetles. (P. J. den Boer, H.-U. Thiele, and . Weber, Editors). Miscellaneous Papers 18 (1979). Agricultural University, Wageningen, The Netherlands. A. Veenman and Zonen B.V.- Wageningen, The Netherlands. Contents + 222 pp.

Nagel, B. P. 1979b. Aspects of the evolution of myrmecophilous adaptations in Paussinae (Coleoptera, Carabidae), pp. 15-34. *Ibid.*

Notman, H. 1919. Records and new species of Carabidae. Journal of the New York Entomological Society, 27 (2-3): 225-237.

Ogueta, E. 1965a. Descripciones, redescripciones y comentarios sobre Ozaenini I. (Coleop. Carabidae). Revista de la Sociedad Entomologica Argentina, 26: 111-118.

Ogueta, E. 1965b. Descripciones, redescripciones y comentarios sobre Ozaenini II. El genero *Ozaena* Olivier (Coleoptera: Carabidae). Physis, 25 (68): 73-88.

Ogueta, E. 1965c. Descripciones, redescripciones y comentarios sobre Ozaenini III. El genero *Platycerozaena* Bänninger (Coleoptera: Carabidae). Physis, 25 (70): 361-368.

Olivier, A. G. 1812. Encyclopedie methodique. Histoire naturelle. Insectes, vol. 8 (pt. 2), pp. 361-722.

d'Orbigny, C. D. 1845. Dictionnaire universel d'histoire naturelle. Volume 6. MM Renard, Martinet et cie. Paris. 792 pp.

d'Orbigny, C. D. 1846. *Ibid.* Volume 7. *Ibid.* 808 pp.

d'Orbigny, C. D. 1847. *Ibid.* Volume 9. *Ibid.* 776 pp.

d'Orbigny, C. D. 1848. *Ibid.* Volume 12. *Ibid.* 816 pp.

Perty, J. A. M. 1830. Insecta Brasiliensia. *In*, Delectus animalium articulatorum, quae in itinere per Brasiliam annis MDCCCXVII-MDCCCXX jussu et auspiciis Maximiliani Josephi I. Bavariae regis augistissimi peracto...(fasc. 1) pp. 1-60, illustrated.

Regenfuss, H. 1975. Die Antennen-Putzeinrichtung der Adephaga (Coleoptera), parallele evolutive Verwollkammung einer komplexer Struktur. Zeitschrift fur zoologische Systematik und Evolutions-forschung, 13: 278-299.

Reichardt, H. 1977. A synopsis of the genera of Neotropical Carabidae. *Quaestiones Entomologicae,* 13 (4): 347-485.

Roach, B., K. R. Dodge, D. J. Aneshansley, D. Wiemer, J. Meinwald and T. Eisner. 1979. Chemistry of defensive secretions of ozaenine and paussine bombardier beetles (Coleoptera: Carabidae). The Coleopterists Bulletin, 33 (1): 17-19.

Rosen, D. E. 1985. Geological hierarchies and biogeographic congruence in the Caribbean. Annals of the Missouri Botanical Garden, 72: 636-659.

Savage, J. M. 1982. The enigma of the Central American herpetofauna: dispersal or vicariance? *Ibid,* 69: 464-547.

Schaum, H. R. 1856-1860. Erste Abtheilung Coleoptera Erster Band, 791 pp. *In*, Naturgeschichte der Insecten Deustchlands (W. F. Erichson). Nicolaische Verlagsbuchandlung (G. Pathey), Berlin.

Schaum, H. R. 1864. Beitrage zur Kenntniss der Carabicinen. Berliner Entomologische Zeitschrift, 8: 114-126.

Shpeley, D. and G. E. Ball. 1978. *Anisocnemus*, a Neotropical genus: classification and geographical distribution (Coleoptera: Carabidae: Harpalini). The Coleopterists Bulletin, 32 (2): 77-92.

Sloane, T. G. 1920. The Carabidae of Tasmania. Proceedings of the Linnaean Society of New South Wales, 45: 113-178.

Sloane, T. G. 1923. The classification of the family Carabidae. Transactions of the Royal Society of London, 1923, pp. 234-250.

Smith, M. R. 1951. Family Formicidae, pp. 778-875. *In*, Hymenoptera of America north of Mexico (C. F. W. Musebeck, K. V. Krombein and H. K. Townes, Editors). United States Department of Agriculture, Monograph No. 2. Washington, D. C. 1420 pp.

Solier, A. J. J. 1836. Memoire sur quatre genres de la famille des carnassier-terrestres. Annales de la Société Entomologique de France, 5: 589-602.

Solier, A. J. J. 1849. Orden III. Coleopteros. *In*, Gay, Historia fisica y politica de Chile. Vol. 4, pp. 105-380, 414-511.

Stork, N. E. 1980. A scanning electron microscope study of tarsal adhesive setae in the Coleoptera. Zoological Journal of the Linnean Society, 68: 173-306.

Stork, N. E. 1985. *Dhanya*, a South-east Asian genus of ozaenine ground beetles. Journal of Natural History, 19: 1113-1138.

Thompson, R. G. 1979. Larvae of North American Carabidae with a key to the tribes, pp. 209-291. *In*, Carabid beetles: their evolution, natural history and classification...(T. L. Erwin, G. E. Ball, D. R. Whitehead, and A. L. Halpern, Editors). W. Junk b.v., Publishers, The Hague. X + 635 pp.

Thomson, J. 1856. Description de quelques Coléoptères nouveaux ou peu connus. Annales de la Société entomologique de France (3) 4: 317-335, 2 colored plates.

Ward, R. D. 1979. Metathoracic wing structures as phylogenetic indicators in the Adephaga, pp. 181-191. *In*, Carabid beetles, *etc*. For complete citation, see Thompson, R. B., above.

Winkler, A. *Catalogus Coleopterorum regionis palaearcticae, Pars* 1, pp. 1-112. Albert Winkler, Wien. 1924-1932. viii + 1698 pp.

Zacharuck, R. Y. 1985. Antennae and sensilla,pp. 1-69. *In*, Comprehensive insect physiology, biochemistry and pharmacology. Volume 6. (G. A. Kerkut and L. I. Gilbert, Editors). Pergamon Press, Oxford. xvi + 710 pp.

INDEX TO NAMES OF TAXA

(Junior synonyms in italics)

SPECIES AND SUBSPECIES

BOOK REVIEW

MANUAL OF NEARCTIC DIPTERA. Volume 3. J. F. McAlpine and D.M. Wood (editors). 1989. Minister of Supply and Services Canada. vi + pp. 1333-1581. $75.95 (Canada), US $91.15 (outside Canada).

This third (and last) volume of the Manual of Nearctic Diptera contains chapters 114-116 on the phylogeny and classification of subgroups of the Diptera, together with two pages of corrections to volumes 1 and 2 and a very long composite index of the taxonomic names of Diptera and morphological terms used in all three volumes. This third volume is mainly illustrated by phylogeny diagrams (the reader being referred to the previous volumes for morphological illustrations), but a few important new illustrations of larval head structure illustrate chapter 114.

Until publication of this work the most comprehensive modern reviews of the phylogeny of the Diptera were contained in various works of B. B. Rohdendorf and W. Hennig, both of whom died in the seventies. The work of both authors has certain defects. Rohdendorf's system contained much that was arbitrary and not in accordance with cladistic methodology (which he rejected). Hennig pioneered cladistic methods, but in his later years wrote too quickly without sufficient morphological studies; as a result his later works contain much that is superficial or erroneous. The authors of Manual 3 take Hennig's work as the main starting point of their studies, but find much that is in need of revision. I agree that extensive revision of Hennig's system is needed, and welcome the publication of this work which will hopefully stimulate renewed interest in this field of fundamental importance to the whole of dipterology.

Of course this is not to say that I agree with everything proposed, and the authors themselves recognize that there are many areas of the system where only tentative proposals can be offered. In this review I will comment on the validity of new proposals to the extent that this is possible on the basis of existing literature and my previous studies in this field. But there are too many new observations for me to try and check them against insects in the context of writing a review. Evaluation of some new proposals will require a period of years, as the literature develops.

Before discussing each chapter, there are two points of a formal nomenclatural nature and one of a methodological nature which need comment.

Some of the superfamily names used in this work, especially within the Schizophora, are contrary to longstanding usage, e.g. Sciaroidea (for Mycetophiloidea), Ephydroidea (for Drosophiloidea), Carnoidea (for Chloropoidea), Nerioidea (for Micropezoidea) and Oestroidea (for Tachinoidea). It is explained that this is an application of Article 36(a) of the 1985 International Code of Zoological Nomenclature, in which it is stated that "a name established for a taxon at any rank in the family group is deemed to be simultaneously established with the same author and date ... at other ranks in the family group". Thus, the oldest family-group name is used, even if this was previously used only as a family, not as a superfamily, name. It remains to be seen whether other dipterists will accept these changes, or whether reference will be made to the Commission to conserve long-accepted superfamily names. The question of priority of superfamily names was given scant consideration in previous literature, since the dates of first proposal were not known for many of the older family-group names. This situation has changed as a result of bibliographic studies by C. W. Sabrosky, who gave advice to the authors on this matter. If we are to strictly apply the priority principle to superfamily names in the future, it is essential that Sabrosky's work be published.

A second formal question concerns the formation of names for higher taxa (above the family group). Such names are not regulated by the Code. The authors of the Manual have made wide use of the suffix -morpha attached to the root of generic names (following the precedent of Rohdendorf), even in cases where other names are well established and have priority (e.g. Muscomorpha instead of Cyclorrhapha). In my opinion this extension of the principle upon which family-group names are formed to higher levels is misguided, and will cause instability because changes in suffices have to be made whenever new research causes the relative ranking of groups to be revised. Therefore I intend to continue to use names formed upon other principles when these have priority, and to apply names formed by adding suffices to generic roots in their original senses irrespective of ranking changes. In this connection it should be noted that names formed with the suffix -formia have priority over many of those formed with the suffix -morpha.

I have found one difficulty regarding the phylogeny diagrams in this volume. All diagrams are of the type in which characters assumed to be autapomorphies are ascribed to each branch of a dendrogram. This type of illustration is of course widely used and valid. However, there is a difficulty when many of the characters used are subject to homoplasy and the interpretation of their distribution is debatable. In such cases it is necessary to know the complete distribution of the characters in order to be able to judge the validity of proposed groupings. This is especially a problem in the treatment of "Acalyptratae", in which many groupings are based solely on characters known to be subject to homoplasy. I recommend that in future treatments diagrams with bars across showing the total distribution of characters should also be included, so that readers can retrieve this information directly from the illustration without the need to search the text and other literature for information on the wider distribution of characters.

Chapter 114. Phylogeny and Classification of the Nematocera (by D. M. Wood and A. Borkent)

This chapter includes discussion of the origin of the Diptera, as well as the relationships between the groups traditionally included in the "Nematocera" (probably a paraphyletic grouping). A system of seven infraorders is proposed (Tipulomorpha, Blephariceromorpha, Axymyiomorpha, Bibionomorpha, Psychodomorpha, Ptychopteromorpha and Culicomorpha). The major innovation of this system in comparison with Hennig's (1973) treatment is the new concept of Psychodomorpha, containing the Trichoceridae (removed from Tipulomorpha) and four families removed from Bibionomorpha, the Perissommatidae, Anisopodidae, Scatopsidae and Synneuridae (the last should be called Canthyloscelididae on grounds of priority). Groups included in Psychodomorpha by Hennig (1973) but removed by Wood & Borkent are the Blephariceridae, Deuterophlebiidae and Nymphomyiidae (grouped as infraorder Blephariceromorpha) and the Ptychopteridae and Tanyderidae (grouped as infraorder Ptychopteromorpha). The enigmatic family Axymyiidae (formerly in Bibionomorpha) is also segregated as the new infraorder Axymyiomorpha.

In the discussion of the origin of the Diptera, Wood and Borkent advance the hypothesis that the Nannochoristidae are the sister-group of the Diptera + Siphonaptera despite certain contrary evidence. I do not find the evidence they offer for regarding the Siphonaptera as the sister-group of the Diptera (larval thoracic legs absent, pupal mandibles immovable) convincing, as these characters are subject to homoplasy. There is a series of characters which suggests that the

Siphonaptera are more closely related to the Mecoptera, especially the structure of the spermatozoa (see Christensen 1975, 1981). The question of the relationships of the Nannochoristidae is addressed in greater detail in a new work by Willmann (1989), which also redescribes and reinterprets Mesozoic fossils relevant to the origin of the Diptera. Willmann's outstanding work will obviously provide the main starting point for future investigations of the origin and relationships of the Diptera as well as Mecoptera. Willmann treats the Nannochoristidae as the sister-group of all other Mecoptera in the recent fauna, while leaving open the question of the position of the Siphonaptera within the Antliophora (= Diptera + Mecoptera + Siphonaptera).

Although Wood & Borkent's opinion that the Nannochoristidae should be removed from the Mecoptera because they are more closely related to the Siphonaptera + Diptera seems unlikely, it should be noted that use of the Nannochoristidae as an outgroup for assessing character polarity in the Diptera is not in contention. The Nannochoristidae are recognized by Willmann and other mecopterists as the relatively plesiomorphous subgroup of the Mecoptera in most respects. They remain an important basis of outgroup comparison in studies of relationships within the Diptera and Siphonaptera, irrespective of what view is taken of their position within the Antliophora.

The changes in the content of the infraorders of "Nematocera" proposed by Wood & Borkent in my opinion represent a considerable advance over the systems proposed by Hennig and Rohdendorf. Their work should provide one of the main starting points for further investigations in this field. My main criticism is that the changes do not go far enough.

The new concept of Psychodomorpha is justified by Wood & Borkent on the basis of a complex of characters (nos. 38-42) of the larval head (labrum with posteriorly pointed hairs, "premandibles" dentate or pectinate, torma articulating with dorsal labral sclerite, mandible moving in nearly vertical plane and striking hypostoma, mandible chela-shaped). I support the view that this character complex is apomorphous and characterizes the groundplan of a major subgroup of the Diptera. However, I think that the group to whose groundplan these characters belong may be more extensive than Wood & Borkent's Psychodomorpha. There are grounds for suggesting that the larval head structures of the groups called Tipulomorpha, Ptychopteromorpha and Culicomorpha by Wood & Borkent represent further modifications of the same groundplan condition.

Wood & Borkent show the Tipulomorpha (Tipulidae *s.l.*) as the sister-group of all other "Nematocera" on their phylogeny diagram, the grouping of all other Nematocera being supported by the apomorphous state of character 1 (prostheca arising directly from median surface of larval mandible). The opposing state (mandible with prostheca on articulated lobe) is assumed to belong to the groundplan of the Tipulomorpha (and of the Diptera as a whole) on the basis of outgroup comparison with Nannochoristidae. I am sceptical whether the presence of an articulated prosthecal lobe in *Tipula* is a genuinely plesiomorphous character. The larval head capsule of *Tipula* is of a highly modified type with the posterior margins of the capsule strongly indented. The interpretation that an articulated prosthecal lobe belongs to the groundplan of the Tipulomorpha will only be convincing, if it is also shown to be present in other groups of Tipulomorpha with less modified head capsule. I favour a quite different interpretation of the relationships of the Tipulidae *s.l.*

It appears to me that the apparent synapomorphies between Tipulidae (*s.l.*) and Trichoceridae (especially reduction of the male cerci, development of gonopods from posterolateral zones of proliferation, female cerci with single article, only 3 branches of radial sector reaching wing margin, forwards displacement of distal section of m_{1+2}) cannot be dismissed as due to homoplasy. The view that the Trichoceridae and Tipulidae *s.l.* are sister-groups is reconcilable with Wood & Borkent's justified emphasis on the synapomorphies between the larval head structure of Trichoceridae and that of other Psychodomorpha, if we assume that the considerable diversity of head structure shown by the larvae of Tipulidae *s.l.* represents a transformation series from a groundplan structure similar to that of *Trichocera*. On this interpretation the horizontal plane of movement of the mandibles of some Tipulidae *s.l.* is assumed to be secondary. Final resolution of how the polarity of characters of the larval head structure in Tipulidae *s.l.* should be interpreted must obviously await more detailed comparative morphological studies than we presently have available. Meanwhile, readers should note that Wood & Borkent's interpretation of the position of the Tipulidae *s.l.* as the sister-group of all other "Nematocera" is poorly supported, and other interpretations are possible. I would place the Tipulidae *s.l.* within their Psychodomorpha as the sister-group of the Trichoceridae.

The grouping of Ptychopteridae and Tanyderidae (as Ptychopteromorpha) following Hennig (1973) is supported only by character 52 (male tarsal claws folding against basal swelling on tarsomere 4), a character found in the Tanyderidae and *Ptychoptera* (but not in other Ptychopteridae). Whether this feature belongs to the groundplan of the Ptychopteridae is doubtful, since it has not been found in any of the Mesozoic Ptychopteroidea (information from N. S. Kalugina). In my opinion the relationships of the Ptychopteroidea (Ptychopteridae and related fossil groups) and Tanyderidae should be considered separately. Both groups are archaic, represented in the earliest Mesozoic fossil assemblages. In their discussion Wood & Borkent present new evidence that the Ptychopteridae alone may be the sister-group of the Culicomorpha based on the structure of the larval labrum and mandibles. This seems to me more convincing evidence of the relationships of the Ptychopteridae than the dubious tarsal character. At the same time we must not lose sight of the fact that the larval head structures of the Tanyderidae, Ptychopteridae and Culicomorpha may be derived from the same groundplan structure as that postulated for the groundplan of the Psychodomorpha. Wood & Borkent do in fact unite these groups at a higher level on their phylogeny diagram, but do not name the more inclusive group.

The inclusion of the Scatopsoidea (Scatopsidae + Canthyloscelididae) in the Psychodomorpha on the basis of larval head structure seems to me fully justified. Wood & Borkent place this group as the sister-group of the Anisopodidae. However, I am aware of one unique character which suggests that they may be the sister-group of the Psychodidae. This is that the 8th pair of abdominal (the larval hind) spiracles lacking in most adult Diptera persist in the adult male but are displaced to a dorsal position within the 9th tergite (epandrium). Further investigation of the position of the Scatopsoidea within the Psychodomorpha is needed. The transference of the Perissommatidae to the Psychodomorpha based on new observations of the larval head structure also appears fully justified. Krivosheina (1988) has also recently examined the larvae of Perissommatidae, and concludes that they "have characters relating them variously with the Scatopsidae, Trichoceridae, and to a considerable degree with the Psychodidae" (*i.e.* with families included by Wood & Borkent in the Psychodomorpha). It seems that there was no contact between Krivosheina and Wood & Borkent, but both reached similar conclusions independently.

Wood & Borkent expand the concept of Blephariceromorpha (Blephariceridae + Deuterophlebiidae) to include also the Nymphomyiidae. This is controversial, and rests on interpreting the abdominal prolegs of larval Deuterophlebiidae and Nymphomyiidae as of common origin and belonging to the groundplan of the Blephariceromorpha. Unfortunately, the development of prolegs is subject to much homoplasy in Diptera, so I do not have confidence in this character in isolation. In Rohdendorf's (1964) system the Nymphomyiidae (as Archidiptera) were considered the sister-group of all other recent Diptera, a view which is best justified by the primitive structure of the adult nervous system (retaining 8 separate ganglia, as in larvae). Wood & Borkent argue that this character may be neotenous, a possibility which certainly cannot be excluded. The position of the Nymphomyiidae remains in doubt. The two interpretations currently held are both essentially based on the distribution of single characters. Further morphological studies are needed, so that additional evidence can be brought to bear on the problem.

The treatment of the Bibionomorpha is a weak part of Wood & Borkent's work, and no constitutive (autapomorphous) characters of this group are suggested. After removal of the heterogenous elements included by previous authors, the Bibionomorpha in Wood & Borkent's sense consists of two certainly monophyletic groups: the Pachyneuroidea + Bibionoidea (which I would amalgamate) and the Sciaroidea. These groups have been closely associated in all recent systems and may well be monophyletic, but a critical assessment is still impeded by lack of sufficiently detailed studies of primitive Sciaroidea (especially Ditomyiidae). The monophyly of the Pachyneuroidea + Bibionoidea is demonstrated by the synapomorphous structure of the larval labium and hypopharynx, which Wood & Borkent do not discuss.

The recognition of Axymyiidae as a group of high rank (Axymyiomorpha) is probably the best treatment on present information, since there are no convincing grounds for including the group within any other infraorder. Krivosheina (1989), who has made special studies of this group, has also accepted the concept of Axymyiomorpha.

The strongest part of Wood & Borkent's work is no doubt the treatment of the Culicomorpha, a group on which both authors have worked for many years. I agree with them that the content of this group is no longer contentious. Their discussion is authoritative and will provide a sound basis for future studies.

Chapter 115. Phylogeny and classification of the "Orthorrhaphous" Brachycera (By N.E. Woodley)

This chapter treats all Brachycera except the Cyclorrhapha (= Muscoidea in the sense of this chapter, Muscomorpha in the sense of chapter 116). Four infraorders are recognized, the Xylophagomorpha, Stratiomyomorpha, Tabanomorpha and Muscomorpha (in a new wide sense, different from the usage in chapter 116). The different usages of the same names in the two chapters is confusing, and well illustrates how the use of suffices to denote relative ranking causes instability.

Woodley's discussion is generally sound, and I do not find much to disagree with. But I think that his Xylophagomorpha and Tabanomorpha can be combined at infraordinal level, thus reducing the number of infraorders to three. I base this suggestion on the structure of the male genitalia in the Coenomyiinae (Xylophagidae), which agrees substantially with that of Rhagionidae (Tabanomorpha). I infer from the work of Nagatomi (1984) that there is a major subgroup of the Brachycera corresponding to the Xylophagomorpha + Tabanomorpha *sensu* Woodley characterized by fusion of the ejaculatory apodeme with the base of the aedeagus and sheathing of the aedeagus and gonites ("tines") by a dorsal and pair of lateral/ventral processes.

The Stratiomyomorpha should probably also include the Pantophthalmidae, listed by Woodley as *incertae sedis*. The distal parts of the powerful mouthhooks of pantophthalmid larvae bear palpi, indicating that they are of maxillary origin as in the Stratiomyidae and Xylomyidae. Also the structure of the male genitalia described by Nagatomi (1984) is incompatible with inclusion of this family in the Xylophagomorpha + Tabanomorpha.

Regarding the genera *Exeretoneura* and *Heterostomus*, also listed as *incertae sedis* by Woodley, Nagatomi's descriptions of the male genitalia suggest that both belong somewhere in the Xylophagomorpha + Tabanomorpha. Woodley's placement in the vicinity of Xylophagidae seems appropriate pending further studies.

More enigmatic is the position of the Vermileonidae, listed by Woodley as a family *incertae sedis* within the Tabanomorpha. I agree with Woodley that this family cannot belong in the Asiloidea, where it was placed by Teskey in Volume 1 of this Manual. If Kovalev (unpublished MSS) is correct in referring the lower Jurassic *Protobrachyceron* (the earliest described fossil brachyceron) to this family, then it is possible that it merits higher rank in the system. Woodley's proposal to place the Vermileonidae provisionally in the Tabanomorpha seems reasonable pending further studies.

The infraorder Muscomorpha is proposed by Woodley in a new sense, inclusive of the Nemestrinoidea, Asiloidea, Empidoidea and Muscoidea. The concept seems to me well justified, but not the nomenclature. The numerous different senses in which the name Muscomorpha has been used cause confusion. A new name would have been preferable. The superfamilies Asiloidea, Empidoidea and Muscoidea are ranked more highly by most other authors (including McAlpine in chapter 116), who hence use other suffices if they believe in forming names of higher taxa in this way. I recommend forgetting about rank and suffices and using the earliest appropriate names (Pleroneura, Orthogenya and Cyclorrhapha). These names can remain applied to the same groups, irrespective of different relative ranking by different authors.

Woodley (correctly in my opinion) restricts the concept of Nemestrinoidea to the Nemestrinidae + Acroceridae, referring the Bombyliidae to the Pleroneura ("Asiloidea"). Some previous authors, including Hennig (1973), placed the latter family in the Nemestrinoidea on account of the hypermetamorphic larval development, but subsequent morphological studies leave no doubt that it belongs to the Pleroneura. Woodley considers that all Muscomorpha except Nemestrinoidea form a monophyletic group characterized by a setiform empodium. I agree with this view, and suggest that we follow the precedent of Lameere (1906) in applying the name Heterodactyla to this group.

In his phylogeny diagram Woodley shows a trichotomous subdivision of the Heterodactyla into Asiloidea (Pleroneura), Empidoidea (Orthogenya) and Muscoidea (Cyclorrhapha). This fence-sitting on the issue of the validity of the concept Eremoneura (Orthogenya + Cyclorrhapha) presumably reflects the fact that he has not worked personally on these groups and does not wish to involve himself in controversy. At the end of the chapter he quotes verbatim the characterization of the Eremoneura which I gave in 1984, with the disclaimer that "I cannot personally evaluate these characters and their distributions within the Brachycera". I suggest that these characters and their distributions have already been evaluated, and that the grounds for grouping the Orthogenya with the Cyclorrhapha are in fact overwhelming. This grouping is indicated by numerous autapomorphies involving the structure of the male and female terminalia, the wing venation and the chaetotaxy, probably also by the larval head structure (but interpretation of the character sequence in larvae remains problematical due to inadequate information on the larvae of Orthogenya). Woodley offers two characters in support of the traditional grouping of the Orthogenya with the Pleroneura; presence of three antennal flagellomeres, and presence of acanthophorites (spinous halves of 10th tergite) in the female. In my opinion neither of these characters provides reliable evidence for such a relationship. Presence of three (as in most Orthogenya) or four (as in most Cyclorrhapha) flagellomeres does not indicate that the aristate antennae in these groups originated independently. Several cases are now known in which the change from a 3- to 4-articled flagellum or vice versa must have occurred. Within the Orthogenya, 4-articled flagella are certainly known in *Dryodromia* and *Meghyperus*; within the Cyclorrhapha 3-articled flagella are known in *Opetia* (the probable sister-group of all other Cyclorrhapha) and in one subgroup of Diopsidae. Thus there is no fundamental difference between the aristate antennae of Orthogenya and Cyclorrhapha. Development of spines on the female 10th tergite is also a character prone to homoplasy. For instance, my studies indicate that such spines have evolved several times within the family Anthomyiidae alone. So even if more complete information causes us to revise the prevailing opinion that acanthophorites do not belong to the groundplan of the Orthogenya, I fail to see how this could cast doubt on the validity of the concept of Eremoneura. In this connection I draw attention to the recent thesis by Wiegmann (1989), who sees the problem not as determining whether the Eremoneura are monophyletic but whether the Orthogenya are monophyletic or paraphyletic with respect to the Cyclorrhapha.

Chapter 116. Phylogeny and Classification of the Muscomorpha

(by J. F. McAlpine)

The Muscomorpha in the sense of this chapter is the group normally called Cyclorrhapha, here ranked as an infraorder (both naming and ranking being inconsistent with the previous chapter). In order to avoid confusion I shall refer to this group as the Cyclorrhapha. This chapter is the longest of the three, and sets out J. F. McAlpine's views on the origins of the Cyclorrhapha and the relationships between included families in far more detail than previously available. I welcome its publication as a major contribution to this field, although I do not accept the author's views regarding the origin of the Cyclorrhapha and homologization of the male genitalia and proctiger. McAlpine's system of superfamilies and families contains a variety of differences from previous treatments by me (Griffiths [1972]) and by Hennig (1973, with modifications in subsequent papers). Some of the changes are clearly justified, a few seem to me retrograde.

I included extensive comments on McAlpine's interpretation of the homologies of the male genitalia and proctiger in my review of Volume 1 of this Manual (Griffiths 1981). His views seem little changed, so the criticisms remain. But it does not seem necessary to occupy space in this review by repeating them. Readers who want a summary of my views may refer to that review and also to my characterization of the Eremoneura (Griffiths [1984]) quoted at the end of Chapter 115. Of course the description of some of the characters used by McAlpine to characterize the groundplan of the Cyclorrhapha is affected by how homologies are interpreted, and I would describe some of the genitalia characters quite differently. Despite disagreements over the interpretation of certain characters, I recognize McAlpine's long and detailed review of the groundplan characters of the Cyclorrhapha as an important contribution and certainly justifying his conclusion that the monophyly of this group is "one of the best substantiated and most universally accepted assumptions in the phylogeny of the Diptera".

McAlpine goes on to present an interesting argument that the Cyclorrhapha are more closely related to Stratiomyoidea (= Stratiomyomorpha in the sense of chapter 115) than to the Orthogenya or Pleroneura. In my opinion this cannot be correct in view of the overwhelming evidence for the monophyly of the Eremoneura (Orthogenya + Cyclorrhapha). I offer the following comments on the list of 12 suggested synapomorphies: The first five characters involve alleged synapomorphies in the larval head structure and feeding mechanism. However, Schremmer (1951) established that the mouthparts of larval Stratiomyoidea are of a fundamentally different type from those of all other Brachycera (including Cyclorrhapha) with the palpus-bearing part of the maxilla involved in the formation of the mouthhooks. Characters 8 and 9 can be dismissed also. The presence of a cone-shaped condyle inserted into the base of the first flagellomere is not a groundplan character of the Cyclorrhapha. Nor is the first flagellomere of Cyclorrhapha of composite origin as in some Stratiomyoidea. Characters 7, 10 and 11 are inconclusive, since not confined to the Stratiomyoidea and Cyclorrhapha. There remain only two characters (6 and 12): formation of a puparium, and male with ejaculatory apodeme free from aedeagus and body wall. The first feature is found only in Stratiomyidae among the Stratiomyoidea, where it is normally assumed to have evolved independently of the Cyclorrhapha. The ejaculatory apodeme character requires clarification. The ejaculatory apodeme is primitively a separate sclerite in Diptera, but connected by muscles to some part of the outer body wall around the base of the aedeagus. The apomorphous modification in Cyclorrhapha is that the muscles on this apodeme connect only to the walls of the ejaculatory bulb, which has allowed the apodeme to become withdrawn from the base of the aedeagus. A similar modification is reported to have occurred in Stratiomyidae, but no detailed morphological description is available. Nor is it known whether a free ejaculatory apodeme belongs to the groundplan of the Stratiomyoidea. Even if the condition in Stratiomyidae proves to be the same as in Cyclorrhapha, I think that homoplastic modification will have to be assumed in view of the extensive evidence for the monophyly of the Eremoneura. A free ejaculatory apodeme also has evolved independently in some Scatopsidae.

McAlpine accepts the traditional division between Aschiza and Schizophora as the primary subdivision of the Cyclorrhapha. The recent suggestion that *Opetia* (Opetiidae) may be the sister-group of all other Cyclorrhapha unfortunately is not discussed. Although the larvae of *Opetia* are unknown, Wiegmann (1989) points out that the lack of pupal muscle plaques on the adult abdomen indicates that the pupa is contained within a puparium. Thus there seems no possibility that *Opetia* is misplaced in the Cyclorrhapha. Either it is the sister-group of all other Cyclorrhapha, or its lack of hypopygial rotation is secondary. Presumably McAlpine holds the latter opinion, since he lists Opetiidae as a synonym of Platypezidae.

If we accept that *Opetia* is probably the sister-group of all other Cyclorrhapha, the question arises whether the Aschiza exclusive of *Opetia* form a monophyletic group. The evidence in favour of this interpretation according to McAlpine's extensive tabulation of the "character states in ground plans of Aschiza and Schizophora" is fusion of the larval hypopharyngeal and tentopharyngeal sclerites and enlargement of the pupal respiratory horns. On the other hand it may be pointed out that the immature stages of some families of Aschiza (especially Platypezidae) are poorly studied, so the existence of these synapomorphies needs confirmation. An equally plausible hypothesis is that the Platypezidae are the sister-group of all other Cyclorrhapha (exclusive of *Opetia*), since only in platypezids is hypopygial rotation partly reversible. Pending further studies I think we should keep an open mind.

It is interesting that McAlpine regards the Lonchopteridae as the sister-group of the group usually called Hypocera or Phoridea (Ironomyiidae + Sciadoceridae/Phoridae). Formerly (Griffiths 1972) I followed the opinion that the Lonchopteridae (= Acroptera, Anatriata) are the sister-group of all other Cyclorrhapha (Atriata), but now regard this as improbable. The sole apomorphous character upon which McAlpine bases his grouping of the Lonchopteridae with the Phoridea is the dichoptic condition in males. However, the apparently synapomorphous structure of the male postabdomen (loss of 7th tergite, 7th sternite and inverted 8th tergite) also supports this grouping. These sclerites are present in the groundplan of all other subgroups of Cyclorrhapha except *Opetia* . The position of the cleavage lines on the puparium may also represent a synapomorphy of the Lonchopteridae and Phoridea. McAlpine interprets the pattern in Lonchopteridae as closest to the groundplan of the Cyclorrhapha, but it is more parsimonious in terms of his phylogeny diagram to interpret is as apomorphous. In all other Cyclorrhapha the operculum which is broken off when the adult emerges includes the dorsal half of the thoracic segments of the puparium. McAlpine places the Platypezidae as the sister-group of the Lonchopteridae + Phoridea (forming the superfamily Platypezoidea), but I regard this with scepticism. He justifies this concept of Platypezoidea mainly on the basis of chaetotaxy. However, the chaetotactic characters may not be apomorphous, since the reduced chaetotaxy of the Syrphoidea is surely secondary. Some of the setae in question (such as ocellar setae) belong to the groundplan of the Cyclorrhapha, if not of the Eremoneura as a whole. The relationships between the Platypezidae and other Cyclorrhapha remain controversial and in need of further study.

The treatment of the families of Schizophora is long and detailed. McAlpine follows the traditional subdivision of this group into the Acalyptratae and Calyptratae, rejecting my criticism of the former as a residual paraphyletic group (Griffiths 1972). I have checked the apomorphous character states listed in the extensive table of "character states in ground plans of Acalyptratae and Calyptratae" and do not find the suggested apomorphies of the former convincing. There is no groundplan difference in the development of the pupal respiratory horn, which pierces the wall of the puparium in Heleomyzidae as well as in many Calyptratae. Since there are several groups with holoptic male eyes also in the Acalyptratae, it cannot be assumed that dichopticism belongs to the groundplan of this group; and in any case the change from a holoptic to dichoptic condition is very prone to homoplasy. Presutural dorsocentral and postsutural acrostichal setae are both present in some Acalyptratae (e.g. Agromyzidae), so I am sceptical whether the absence of these setae can be ascribed to the groundplan. Some other chaetotactic characters suggested (lower surface of scutellum bare, latepimeron bare, meron bare, laterotergite bare) seem to me trivial, and I cannot accept them as significant without more information on their distribution. The relative size of the lower calypter is prone to variation both in Acalyptratae and Calyptratae, and I know of no basis in terms of outgroup comparison for inferring that possession of a relatively large lower calypter is the groundplan condition of the Schizophora. Only the two characters of the female reproductive system listed at the end of McAlpine's table represent major structural differences. But I doubt that their distribution validates the concept of Acalyptratae. Possession of a common duct by 2 of the 3 spermathecae is in my opinion an autapomorphy of the Cyclorrhapha exclusive of *Opetia*, not of the Acalyptratae alone, and certainly belongs to the groundplan of the Calyptratae also (possession of 3 spermathecae with 3 separate ducts in part of the Oestroidea being secondary). Information on the arrangement of spermathecae in the families of "Aschiza" is meagre, but at least in some Phoridae there are 3 spermathecae of which 2 share a common duct (information from B. V. Brown). The question of the ventral receptacle requires further study. Such a structure is certainly widespread in the "Acalyptratae", but the information on non-sclerotized parts of the female reproductive system in other Cyclorrhapha seems to me too meagre for us to determine whether or not homologous structures occur.

The basic subdivision of the Schizophora remains controversial. In my 1972 book I subdivided this group into 5 superfamilies (Lonchaeoidea, Lauxanioidea, Drosophiloidea, Nothyboidea and Muscoidea) mainly on the basis of the structure of the male postabdomen. Subsequently the description of *Morgea* (McAlpine 1981) has satisfied me that the Lonchaeoidea belong within what I called the "Tephritidae family-group" (Tephritoidea in McAlpine's sense) within the Muscoidea in my sense. McAlpine's remarks on the Lauxanioidea and the families I included in the Nothyboidea indicate that he believes that the male postabdominal structure of these groups too is derived from the muscoid type. I have not seen some of the insects upon which his remarks are based, so refrain from agreeing or disagreeing with him at this time. However, if it is confirmed that what I called the muscoid type of postabdominal structure (with asymmetrically reduced 7th tergite) is also basic to the Lauxanioidea and Nothyboidea, this would leave the Ephydroidea (Drosophiloidea) as the sister-group of all other Schizophora. For further discussion of the fundamental differences between the male postabdominal structure and development in the Ephydroidea and Muscoidea (in my sense) see pages 81-83 of that book (Griffiths 1972).

I have the following comments on the treatment of particular superfamilies of "Acalyptratae". They have to be brief in order to contain the length of this review.

The treatment of the first superfamily, Nerioidea (= Micropezoidea) has my support. This grouping has been accepted by all recent authors.

The "Diopsoidea" appear to me to be an assemblage of heterogenous long-bodied forms. For the Diopsidae and its close relatives Syringogastridae and Centrioncidae, the new work of Feijen (1989) gives a more detailed and up-to-date treatment. Feijen treats these families as monophyletic (grouped as the prefamily Diopsioinea). The Megamerinidae are a possible sister-group of the Diopsioinea, but the family is too poorly studied for a firm opinion to be given. Whether the further relationships of the Megamerinidae and Diopsioinea are with the Nothybidae, as McAlpine suggests, or with the Sciomyzoidea (as suggested in my 1972 book) should be addressed in future studies. Two other families included by McAlpine in the "Diopsoidea", the Tanypezidae (including Strongylophthalmyiidae) and Psilidae, have elongate ovipositors with partially fused cerci and may belong to or be closely related to the Tephritoidea (see below).

McAlpine recognizes the Conopoidea (Conopidae *s.l.*) as closely related to the Tephritoidea, in agreement with my opinion (Griffiths 1972).

The concept of Tephritoidea proposed by McAlpine is equivalent to the Tephritidae family-group of my 1972 book with the addition of the Lonchaeidae. This inclusion is justified, but I think that the Cryptochetidae should also be included. McAlpine places the Cryptochetidae as the sister-group of the Chloropidae, *i.e.* within the group Milichiidae + Chloropidae characterized by reduced spermathecae with long fine ducts. This is wrong, because the female reproductive system in Cryptochetidae is not of that type. On present information I continue to regard the Cryptochetidae as probably derived from a lonchaeid-like ancestor and would include them in Tephritoidea. But I agree with the exclusion of *Librella* from the Cryptochetidae for the reasons given by McAlpine.

In connection with the Cryptochetidae, I was astonished to read on page 1406 that I mistook the female for the male terminalia of *Cryptochetum nipponense* Tokunaga in my 1972 book. Evidently this is a reference to the unfounded claim by D. K. McAlpine (1976) that both I and Okada (1956) had mistaken the sexes of this species. For the record, the mistake was D. K. McAlpine's, as anyone can confirm by reviewing other literature on this group. For instance, Hennig's (1937) figures of the male terminalia of *C. buccatum* Hendel are quite similar to my figures of *C. nipponense* Tokunaga.

While McAlpine's concept of Tephritoidea is clearly an advance, I suggest that there may be additional families which belong in this group: for instance, the Carnidae. The structure of *Neomeoneurites* Hennig (1972) casts doubt on the traditional grouping of this family with the Milichiidae + Chloropidae. The structure of both the male and female terminalia in *Neomeoneurites* (long coiled aedeagus, extremely long ovipositor bearing fused cerci) indicate that the Carnidae belong to the Tephritoidea. Other groups which should be reviewed for possible inclusion in the Tephritoidea on the basis of the structure of the male and female terminalia are the Tanypezidae (including Strongylophthalmyiidae) and the Psilidae.

McAlpine accepts the concept of Lauxanioidea introduced by Hennig (1958) and followed by me (Griffiths 1972). His interpretation differs from mine at that time in that he regards the male postabdominal structure of this group as derived from what I called the muscoid type. This allows him to consider *Cremifania* (a genus of typical muscoid structure which I removed to the Sciomyzoinea as family Cremifaniidae) as a primitive chamaemyiid. He also claims to have evidence that the postabdominal structure of Lauxaniidae is similarly derived.

As far as *Cremifania* is concerned, its position remains disputed. Tanasiychuk (1986) did not accept it as a chamaemyiid. The undoubted chamaemyiids with somewhat asymmetrical postabdomen (*Acrometopia* and *Parochthiphila*) do not show the typical muscoid pattern of sclerites (asymmetrical reduction of 7th tergite not demonstrable). I am not aware of any lauxaniid with an asymmetrical postabdominal structure. If such exist, it would be helpful if the species were stated so that McAlpine's arguments can be checked.

McAlpine's concept of Sciomyzoidea is close to that in other recent treatments by Hennig and me. All recent authors include here the families included by McAlpine. There is disagreement only regarding whether additional families, such as Cremifaniidae and Megamerinidae, should also be included. As noted above, if the Megamerinidae belong to the Sciomyzoidea, probably the Diopsioinea should also be included here as a subordinate group. Since the Megamerinidae are poorly studied, I note this possibility as one to be considered in future studies, not as a firm opinion.

The concept of Opomyzoidea is new and unsatisfactory. That should not be taken as a criticism, since the relationships of most of the included families have been poorly studied and any superfamily arrangement at this time must be arbitrary and tentative. The apomorphous characters given for the groundplan of the Opomyzoidea all have wider distributions and may be subject to homoplasy. Regarding the subgroups (suprafamilies sensu McAlpine) of Opomyzoidea, it appears to me that the Opomyzoinea and Asteioinea are defensible groupings which will serve as a good basis for further studies. But his Clusioinea and Agromyzoinea seem to me most improbable groupings. The structure of the male genitalia suggests that the Acartophthalmidae and Odiniidae belong in the vicinity of the Tethinidae and other families included by McAlpine in the "Carnoidea", as they were treated in my 1972 book. I find McAlpine's argument that the characters of the fossil *Acartophthalmites* demonstrate a relationship between Acartophthalmidae and Clusiidae unconvincing, since the only synapomorphies suggested between these families are in characters subject to homoplasy.

In connection with the comments on Agromyzidae, it should be noted that the old report of sclerotized strips on the left side of the male abdomen was checked many years ago and found to be erroneous. I am not aware of any members of this family with any asymmetry in the structure of the male postabdomen. If McAlpine has observed anything different, he should state what species he examined so that specialists can check the observation.

McAlpine's concept of "Carnoidea" mainly includes families treated in my 1972 book as belonging to the Tephritoinea but not to the Tephritidae family-group, that is families in which the aedeagus is long and flexible (or assumed to be derived from such a type) and in which a retractile ovipositor is developed but not showing the full suite of apomorphies (such as fused cerci) shown by females of the Tephritidae family-group (Tephritoidea in McAlpine's sense). This concept of relationship remains valid, but there remain problems regarding which families belong in the Tephritoinea *sensu lato.* McAlpine's proposal to recognize a separate superfamily for the Tephritoidea exclusive of the Tephritidae family-group seems reasonable pending further investigations. But the superfamily cannot be called Carnoidea, because (as noted above) the Carnidae belong to the Tephritidae family-group (Tephritoidea sensu McAlpine). I think the name Chloropoidea is the appropriate one.

There are some other misplacements in McAlpine's treatment of the "Carnoidea". The Cryptochetidae do not belong in the subgroup Milichiidae + Chloropidae, as discussed above. More probably they are close to the Lonchaeidae (Tephritoidea). The Risidae belong to the Ephydroidea (see Chandler 1987), and in my opinion represent an aberrant subgroup of the Ephydridae not a separate family. On the other hand, two families placed in Opomyzoidea by McAlpine, Acartophthalmidae and Odiniidae, should be included here according to the structure of their male and female terminalia.

The relationships of the two families separated by McAlpine at the base of the "Carnoidea", Australimyzidae and Braulidae, are unclarified. The case for including them here (or in any other superfamily of "Acalyptratae") is quite weak, since based only on characters subject to homoplasy. The Australimyzidae show some highly plesiomorphous features, and may represent a group of higher rank (as treated in my 1972 book).

The superfamily Sphaeroceroidea is proposed by McAlpine for part of the Anthomyzoinea in the sense of my 1972 book. The concept is reasonable pending further investigations. While most of the Heleomyzidae of the Northern Hemisphere probably represent a monophyletic group, the same cannot be said for the Southern Hemisphere forms. D. K. McAlpine (1985), the lone current worker on these southern groups, was unable to justify his suprageneric concepts in terms of cladistic analysis, so we may well be dealing with an assemblage of diverse origins. It is obvious that progress in clarifying the limits of and relationships within the Sphaeroceroidea will be slow, so long as additional dipterists do not take up the study of the "Heleomyzidae" of the Southern Hemisphere.

McAlpine's treatment of the Ephydroidea (= Drosophiloidea) generally has my support, except that he tries to reverse the separation of the Campichoetidae from *Diastata* proposed in my 1972 book. This seems to me retrograde. That these groups are not monophyletic is confirmed in the important paper by Chandler

(1987), which contains a review of the relationships between the families of Ephydroidea (in which Risidae must also be included, as noted above). Presumably McAlpine's manuscript was finalized before Chandler's work was received, since he does not mention it. Future studies should take account of Chandler's, as well as McAlpine's, treatment.

The treatment of the Calyptratae contains much less that is controversial than the treatment of the "Acalyptratae". Numerous autapomorphies justify the concept of Calyptratae, as shown in McAlpine's table of "character states in groundplans of Acalyptratae and Calyptratae". Three subgroups are recognized (ranked as superfamilies), the Hippoboscoidea, Muscoidea and Oestroidea. The first and last are groups recognized (under a diversity of names) in all recent treatments. But whether the Muscoidea (sensu McAlpine) is a monophyletic group requires further study. The three characters of this group shown on his phylogeny diagram in my opinion all belong to the groundplan of more inclusive groups.

CONCLUSION

The publication of this volume represents an important advance in our understanding of the phylogeny of the Diptera. In writing this critical review I have tried to distinguish what seems to me well established from what is controversial or in certain cases demonstrably erroneous. I hope my remarks will assist future workers in this most interesting field. J. Frank McAlpine is to be congratulated for his persistence and hard work over many years in bringing the Manual project to completion. This phylogeny volume will prove seminal, but should not be regarded as the source of all truth on this subject. We are still at a stage where considerably divergent opinions can reasonably be held concerning many areas of the system, and many changes may be expected as a result of future research.

REFERENCES CITED

Chandler, P. J. 1987. The families Diastatidae and Campichoetidae (Diptera, Drosophiloidea) with a revision of Palaearctic and Nepalese species of *Diastata* Meigen. Entomologica Scandinavica 18: 1-50.

Feijen, H. R. 1989. Diopsidae. Flies of the Nearctic Region 9 (12). 122 pp.

Griffiths, G. C. D. 1972. The phylogenetic classification of Diptera Cyclorrhapha, with special reference to the structure of the male postabdomen. Series Entomologica no. 8. 340 pp. Dr. W. Junk N. V., The Hague.

Griffiths, G. C. D. 1981. Review of: McAlpine, J. F. et al. (eds.). Manual of Nearctic Diptera. Volume 1. Entomological Society of Canada Bulletin 13: 49-55.

Griffiths, G. C. D. 1984. Note on characterization of Eremoneura, Orthogenya and Cyclorrhapha. 1 p. Distributed at XVII International Congress of Entomology, Hamburg.

Hennig, W. 1937. Milichiidae et Carnidae. Die Fliegen der Paläarktischen Region 5 (52). 39 pp.

Hennig, W. 1958. Die Familien der Diptera Schizophora und ihre phylogenetischen Verwandtschaftsbeziehungen. Beiträge zur Entomologie 8: 505-688.

Hennig, W. 1972. Beiträge zur Kenntnis der rezenten und fossilen Carnidae, mit besonderer Berücksichtigung einer neuen Gattung aus Chile (Diptera: Cyclorrhapha). Stuttgarter Beiträge zur Naturkunde, no. 240. 20 pp.

Hennig, W. 1973. Ordnung Diptera (Zweiflügler). Handbuch der Zoologie 4(2): 2/31 (Lieferung 20). 337 pp.

Kristensen, N. P. 1975. The phylogeny of hexapod "orders". A critical review of recent accounts. Zeitschrift für Zoologische Systematik und Evolutionsforschung 13: 1-44.

Kristensen, N. P. 1981. Phylogeny of insect orders. Annual Review of Entomology 26: 135-157.

Krivosheina, N. P. 1988. Approaches to solutions of questions of classification of the Diptera. Entomologicheskoye Obozreniye 67: 378-390 (in Russian). Also in English translation in Entomological Review 68 (1989): 111-124.

Krivosheina, N. P. 1989. Ontogeny and evolutionary ecology of the Diptera. Itogi Nauki i Techniki, Seriya Entomologiya, no. 9. 164 pp. (in Russian).

Lameere, A. 1906. Notes pour la classification des Diptères. Mémoires de la Société Entomologique de Belgique 12: 105-140.

McAlpine, D. K. 1976. A new genus of flies possibly referable to Cryptochetidae (Diptera, Schizophora). Australian Entomological Magazine 3: 45-56.

McAlpine, D. K. 1985. The Australian genera of Heleomyzidae (Diptera: Schizophora) and a reclassification of the family into tribes. Records of the Australian Museum 36: 203-251.

McAlpine, J. F. 1981. *Morgea freidbergi* new species, a living sister-species of the fossil species *M. mcalpinei*, and a key to world genera of Pallopteridae (Diptera). Canadian Entomologist 113: 81-91.

Nagatomi, A. 1984. Male genitalia of the lower Brachycera (Diptera). Beiträge zur Entomologie 34: 99-157.

Okada, T. 1956. Systematic study of Drosophilidae and allied families of Japan. 183 pp. Gihodo, Tokyo.

Rohdendorf, B. B. 1964. The historical development of Diptera. Trudy Paleontologicheskovo Instituta no. 100. 311 pp. (in Russian). Also in English translation (1974), xv + 360 pp. University of Alberta Press, Edmonton.

Schremmer, F. 1951. Die Mundteile der Brachycerenlarven und der Kopfbau der Larve von *Stratiomys chamaeleon* L. Oesterreichische Zoologische Zeitschrift 3: 326-397.

Tanasiychuk, V. N. 1986. Silver flies (Chamaemyiidae). Fauna U.S.S.R., Diptera 14(7). 335 pp. (in Russian).

Wiegmann, B. M. 1989. A phylogenetic revision of the family Atelestidae (Diptera: Empidoidea) and its implications for the origin of the cyclorrhaphous Diptera. viii + 205 pp. University of Maryland, M.Sc. thesis.

Willman, R. 1989. Evolution und Phylogenetisches System der Mecoptera (Insecta: Holometabola). Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, no. 544. 153 pp.

G. C. D. Griffiths
Department of Entomology
University of Alberta

BOOK REVIEW

TRAUTNER, J. and K. GEIGENMÜLLER. 1987. Carabid beetles, tiger beetles. Illustrated key to the Cicindelidae and Carabidae of Europe / Sandlaufkäfer, Laufkäfer. Illustrierter Schlüssel zu den Cicindeliden und Carabiden Europas. Verlag Joseph Margraf, Aichtel, FRG. 210 x 150 mm. Soft cover. 487 pp. 1200 text figures + 11 colour photographs. Price unknown.

Recently, through the generosity of a colleague in West Germany, I received a collection of European carabids, as well as the above book to facilitate their identification. Because of its wide geographical coverage and treatment of a large and widespread group of beetles, this book would be quite valuable to many systematists, ecologists and amateur beetle collectors.

The volume has several sections, beginning with an introduction, including a very brief history of the classification of Carabidae, ecology, and natural history. To increase its potential usage, the authors have divided the text into German and English, on alternate pages or columns on single pages. Following this preliminary material, the classification used in the book is given. The authors adopted the system of Kryzhanovskiy except that his subfamilies are regarded as families (*i.e.* Omophronidae, Brachinidae), and his supertribes are elevated to subfamily rank. No reasons are provided for these changes in rank. A key to families of European terrestrial Adephaga is provided, followed by a key to subfamilies/tribes of Carabidae (*sensu stricto*). The third key is the generic key, in which a total of 138 genera are actually keyed out, while 30 genera of blind, cave-inhabiting Bembidiini and Trechinae are keyed into two groups and mentioned by name only. Thankfully and also commendably, the page number of the treatment of each genus is given, thus preventing more page flipping. What follows is the bulk of the book: 377 pages of keys to species of the various genera. For most genera, each species is keyed out, but for several of the larger genera (including *Trechus* Clairville, *Duvalius* Delarouzée, *Bembidion* Latreille, *Pterostichus* Bonelli, *Agonum* Bonelli, *Amara* Bonelli, *Harpalus* Latreille, and .i.*Brachinus* Weber;) reduced coverage is given. For these and other genera (total of 27), completeness of treatment varies from only references to more detailed taxonomic works, to only a key to subgenus, to keys to species of a more restricted geographical area.

For each genus, the following data are provided: author and date of publication of generic name, suprageneric classification, brief description including mainly colour and size, brief habitat characterization, and pertinent literature. The keys to species are for the most part clear, concise, and profusely illustrated with line drawings. The authors use unambiguous characters and most are effectively illustrated. Characters of the male genitalia are used only when necessary. A habitus drawing accompanies the treatment of all but very few genera. Distribution maps are provided for some genera but each species' couplet mentions the species' geographical distribution.

The book treats species whose distributions are within Europe except: Turkey, the western part of U.S.S.R., and the eastern parts of Bulgaria and Romania. As mentioned above, some genera are treated on a smaller scale, and this is mentioned with or without an accompanying map showing the smaller geographical area covered in the key.

There are also some noticeable problems, most of which are minor. The English translation of the original German is adequate, although in certain places it is difficult to understand. The page numbers for several genera in the index are not actually the pages on which these taxa are treated in the text. Several of the references to taxonomic papers cited in the text are not listed in the references. A number of typographical errors are also evident, perhaps at least partly due to the translation. Two of the most commonly cited authors in the text are C. Jeanne and R. Jeannel, and in a few instances, these names are inadvertently switched. One glaring and inexcusable error is the consistent placement of all authors' names in parentheses. One would expect that the proper use of parentheses in dealing with authors and dates of published taxonomic names would be common knowledge to the authors of such a work. Hopefully this was just an oversight on their part.

This volume is intermediate between a field guide and taxonomic monograph. Therefore, its readership will have a wide range of interests. The book's main selling points are its good illustrations and easily followed keys. In fact, almost the entire text is occupied by keys and figures, and the fact that both have been prepared with care and accuracy ensures the value of this book. Not being an expert on Carabidae, I was still able to determine easily the lot of beetles that I received with the book. Although there are no actual descriptions with which one could be certain of a determination, the couplets in the keys are such that descriptions are unwarranted. Literature in which descriptions and/or more complete taxonomic treatment may be found is always given, in any case.

In conclusion, I have found this book's many merits outweigh considerably the few flaws. It is certainly not an easy task to prepare both brief and unambiguous taxonomic keys, especially when dealing with such a large number of genera in comparatively few pages. The authors have seemingly done a fine job of this, and the resulting work is highly recommended for those with even a cursory interest in this large and interesting group of beetles.

Darren A. Pollock
Department of Entomology,
University of Alberta

BOOK NOTICES

FAUNA OF NEW ZEALAND. C. T. Duval, Series Editor. Science Information Publishing Centre, DSIR, P.O. Box 9741, Wellington, New Zealand.

The year 1988 was the twenty fifth anniversary of the Systematics Group, Department of Scientific and Industrial Research, of the Government of New Zealand. It was marked, among other events, by the appearance of Numbers 13 and 14 of the Fauna of New Zealand. Number 15 was published, as well. In 1989, Numbers 16-18 were published. These issues are of the same high quality and with the same desirable features as reported for previously published numbers (see Ball, 1983, *Quaestiones Entomologicae*, 19 (3-4): 487-488). Below, a citation is given to each number published in 1988 and 1989, with a few notes that draw attention to generalizing or other interesting statements in the text. Such statements by the authors extend coverage of these publications beyond that of identification manuals.

Each publication contains keys to the taxa treated, and each is illustrated extensively, principally with line drawings of high quality that are interpreted easily. In only two publications, however, are scales provided (Numbers 15 and 16), so that one can judge size of the parts illustrated.

It is gratifying to note that five of these publications treat relatively obscure groups (microlepidoptera and microhymenoptera). It is high time that such taxa receive the attention that is their due, for each has its own distinctive brand of biological importance.

These, and previous Numbers, may be ordered through: The Bookshop, DSIR Publishing, PO Box 9741, Wellington, New Zealand.

NOYES, J. S. 1988. Encyrtidae (Insecta: Hymenoptera). FNZ, Number 13, 187 pp. Price, US $44.95.

Encyrtid adults are small (0.3-3.0 mm. in length) chalcidoid wasps. Most of the species as larvae are endoparasitoids or hyperparasitoids of coccoid bugs or arachnids. Most of the New Zealand species for which life history data are available are parasitoids of coccoids.

Thirty five genera and 70 species of Encyrtidae are recorded from New Zealand and the adjacent subantarctic islands. In this publication, four genera and 32 species are described as new.

Although a classification to subtribe is provided, the taxonomic treatments are alphabetical in sequence, based on generic names, and within each genus, on specific epithets. That is, the classification is not used in a meaningful way.

The author accounts for the marked intraspecific variation exhibited by the encyrtids of New Zealand by suggesting recent occupation of many ecological niches that have become available as a result of post-glacial speciation of the coccoid hosts.

Nearly half of the known encyrtid species of New Zealand probably are man-introduced, mostly from Europe and Australia. Of the 39 native taxa, eight occur in Australia also, and are postulated to be recent overseas arrivals in New Zealand.

The detailed treatment of taxa is useful not only for identification of New Zealand encyrtids, but also as a basis for comparison with the encyrtid fauna of other parts of the world. Another generally useful feature is the description of collecting methods, with its emphasis on yellow pan traps and Malaise traps.

Book Review

DUGDALE, J. S. 1988. Lepidoptera-- annotated catalogue, and keys to family-group taxa. FNZ, Number 14, 262 pp. Price, US $49.95.

Appropriately, this publication begins with a dedication to "the memory of three amateur lepidopterists" whose combined efforts contributed so much to knowledge of the lepidopteran fauna of New Zealand: "George Vernon Hudson, 1867-1946, whose life work this publication attempts to keep evergreen"; "Alfred Philpott, 1871-1933, whose pioneering studies in Lepidoptera morphology are now assuming their true significance"; and "Kenneth John Fox, FRCOG, 1936-1986, who died before this catalogue reached full term but whose enthusiasm and insistence ensured its completion". A quotation from John Tyndall's `Fragments of Science', published in 1876, reminds readers of the empirical basis of science: "I would advise you to get a knowledge of the facts from actual observation. Facts looked at directly are vital; when they pass into words half the sap is taken out of them". To that comment, I note that one living in the present age of published pap and propaganda must be concerned not only about the sap that is taken out when "facts" are published, but also about the polluted sap that may be interjected as facts by authors who are more concerned with self-aggrandizement than with honest exposition and appraisal.

This volume is a valuable historical account of knowledge of basic taxonomic aspects of the Lepidoptera of New Zealand. The 1761 species (1582 endemic) from New Zealand are assigned to family and the families are grouped into superfamilies. For genera, type species are indicated. For species, type specimens are indicated by label data, sex, and institution where housed. An appendix provides a list of the taxa of Lepidoptera recorded from the Kermadec Islands.

The excellent illustrations include habitus figures of representative specimens placed at the beginning of the text for each family.

An incisive discussion of the taxa of Lepidoptera above the level of superfamily outlines major classificatory problems, and provides an entrance to the literature about this subject. The author points out that "most species belong to "one division (Ditrysia) of relatively uniform structural organization", whereas "the remaining 1 -2% show a great variety of structural and genital organization,and often profound differences between groups". The evolution of Lepidoptera is characterized by the Hennigian term "additive typogenesis", implying a gradual acquisition of group characters, from the primitive micropterygoids onward, culminating in the endoporian ditrysian suite of characters.

A discussion of the composition of the lepidopteran fauna of New Zealand emphasizes the marked endemicity of the fauna and the good representation of the non-ditrysian groups which comprise at the species level 5 percent of the total fauna. However, a number of non-ditrysian families are absent, even though their food plants are present. More generally, the faunal relationships of the New Zealand taxa are varied, but such relationships have been determined for few groups. Much zoogeographical work remains to be done.

This scholarly work will serve well the development of study of the lepidopteran fauna of New Zealand. The discussion of relationships of the higher taxa will be of interest to systematic entomologists, generally. Those to whose memory this volume is dedicated are indeed honored.

NAUMANN, I. D. 1989. Ambositrinae (Insecta: Hymenoptera: Diapriidae). FNZ, Number 15, 165 pp. Price, US $39.95.

The Ambositrinae are one of the major hymenopterous components of the forest fauna of New Zealand. Probably, as larvae, all are parasitoids of the immature stages of nematocerous Diptera (Mycetophilidae and Keroplatidae, for example), the members of which are also abundant in the litter and low vegetation of New Zealand forests. Wing reduction, a phenomenon that is common among islandic taxa, is marked in the Ambositrinae, with 89 percent of the New Zealand species being brachypterous or apterous.

The New Zealand component of this proctotrupoid subfamily comprises seven genera (three described as new) and 46 species. Thirty four species are described as new, and 11, known only from inadequate material, are not named formally.

Although keys are provided to the subfamilies of Diapriidae in New Zealand, to the genera of Ambositrinae and to the species of each genus, no information is offered about how one distinguishes the Diapriidae from other proctotrupoid families.

A reconstructed phylogeny, based on analysis of 45 characters, is provided for 13 groups of Ambositrinae (12 genera and the *Dissoxylabis* genus-group of seven genera). Within this assemblage, the genera of the New Zealand fauna range from the most archaic to the most highly derived. As the author indicates, this reconstruction must be viewed with considerable caution, because many of the branches are based on symplesiotypy, only.

The present-day austral disjunct distribution of Ambositrinae reflects a Gondwana radiation no later than the Cretaceous, and the marked structural divergence in the subfamily is evidence of a long evolutionary history.

The most appealing feature of this admirable study is the author's attempt to go beyond provision of a clear report about a group of very small and taxonomically difficult creatures. The reconstructed phylogeny and general observations about the geographical history of the Ambositrinae will serve well future workers in their endeavors to understand relationships and classification of this taxon.

DONNER, H. and C. WILKINSON. 1989. Nepticulidae (Insecta: Lepidoptera). FNZ, Number 16, 88 pp. Price, US $22.95.

Nepticulid larvae are leaf miners. The species in New Zealand (28 in total, 14 described as new in this publication) are variously recorded from plants of eight families, with the majority of species mining leaves of the family Asteraceae.

All of the New Zealand species are assigned to the genus *Stigmella* Schrank. One species, *S. microtheriella* (Stainton) was introduced from western Europe. The remaining 27 species are endemic.

The illustrations of genitalia are especially well done, and are laid out in such a way that comparisons are made easily.

Unfortunately, no attempt is made to treat the New Zealand fauna by means of an evolutionary analysis. Comparisons, made in the text to ease the task of identifying these small moths (wing span 2-9 mm.), could have served as well as the basis for a reconstructed phylogeny.

NOYES, J. S. and E. W. VALENTINE. 1989. Mymaridae (Insecta: Hymenoptera)-- introduction and review of genera. FNZ, Number 17, 95 pp. Price, US $24.95.

The family Mymaridae is represented in New Zealand by 160 species distributed among 42 genera. Known as "fairy flies", adult mymarids range in body size from less than 0.4 to about 4.0 mm. They are so small that effectively they swim through the air rather than fly. They can be carried for great distances as part of the aerial plankton.

Most mymarids as larvae are egg parasitoids. Most mymarid species develop from eggs of sternorrhynchous Homoptera, but various species have been reared from the eggs of other Hemiptera, Coleoptera and Psocoptera.

The proportion of flightless species is high: at least 17 genera have species with flightless adults. The largest number of flightless species lives in leaf litter.

Of the 42 genera treated, 20 are known from New Zealand, only; four are shared with Australia, only; one is shared with South America, only; one is distributed through Australasia and ranges to South America; three reach the Indian sub-continent; and 13 are cosmopolitan.

NOYES, J. S. and E. W. VALENTINE. 1989. Chalcidoidea (Insecta: Hymenoptera)-- introduction and review of genera in smaller families. FNZ, Number 18, 91 pp. Price, $22.95.

Treated taxonomically are the New Zealand genera of 15 families of Chalcidoidea. Also included is the Mymarommatidae (two genera, one in New Zealand), which is the putative sister group of the Chalcidoidea. A table provides data about hosts for this important group of wasps. Most chalcidoid parasitoids seek hosts among members of the suborder Homoptera. However, there are phytophagous taxa, such as members of the family Agaonidae. Also, phytophagous species appear in genera in five additional families.

The number of taxa is instructive. Described are 93 species in 75 genera. However, represented in collections in New Zealand are a total of 636 species in 202 genera. These latter figures represent a 2.7 fold increase for genera, and a 6-fold increase for species. One can conclude that much remains to be done, before the chalcidoid fauna of New Zealand is even tolerably well known. This publication is an important step toward attaining a more complete knowledge of New Zealand chalcidoids.

In conclusion, I am pleased to report that the Editors and authors continue to serve admirably, with their contributions to this outstanding series of publications, the entomological community not only of New Zealand but of the world. The individual volumes provide full value at their asking prices.

George E. Ball
Department of Entomology
University of Alberta

Quaestiones Entomologicae

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

VOLUME 26 NUMBER 2 SPRING 1990

Publication of *Quaestiones Entomologicae* was started in 1965 as part of a memorial project for Professor E.H. Strickland, the founder of the Department of Entomology at the University of Alberta in 1922.

It is intended to provide prompt relatively low cost publication for comprehensive accounts of entomological research of greater than average length. However, shorter papers about insects in the Prairie Provinces of Canada are acceptable. Page charges are normally levied, the rate determined by printer's charges. For information about current page charges, consult the Editor.

Copy for all types of papers should conform to the Style Manual for Biological Journals, published by the American Institute of Biological Sciences, Second Edition, 1964, except that title of periodicals should be given in full. For style of taxonomic papers, the Editor should be consulted. Two copies of a manuscript are requested. All manuscripts will be reviewed by referees.

Abstracts are required, one in English and one in another language, preferably French.

Copy for illustrations must accompany the manuscript, and be of such character as to give satisfactory reproduction at page size (less 1/2 inch, or 1.2 cm on plates of full page size [7 X 4 1/4 inches or 17.8 X 10.7 cm]). Reprints must be ordered when proofs are returned, and will be supplied at cost.

Subscription rates are the same for institutions, libraries and individuals, $20.00* per volume of four issues, normally appearing at quarterly intervals; single issues $5.00**. Back volumes and issues are available at the same cost. These prices supersede those previously indicated, and are subject to change as required by inflationary pressure on the value of money.

Communications regarding subscriptions should be addressed to the Subscription Manager, and regarding manuscripts to the Editor.

* Same rate in US$ for non-Canadian subscriptions.

** Single issues of more than 100 pages: $10.00; exception: volume 21(4) - $20.00.

Published quarterly by:

Department of Entomology
University of Alberta
Edmonton, Alberta, CANADA
T6G 2E3

Second Class Mail Registration Number 5222

Return Undeliverable mail to the address above Return Postage Guaranteed

Issued July 1990

THIRD INTERNATIONAL CONFERENCE ON CLASSIFICATION, PHYLOGENY, AND NATURAL HISTORY OF HYDRADEPHAGA (COLEOPTERA)

Proceedings

Organized and Edited by

R. E. Roughley and R.B. Aiken

Convened at the XVIIIth International Congress of Entomology

Vancouver, British Columbia, Canada
3 - 9 July 1988

QUAESTIONES ENTOMOLOGICAE ISSN 0033-5037

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

Volume 26 Number 2 1990

CONTENTS

NATURAL HISTORY OF HYDRADEPHAGA

SYSTEMATICS OF HYDRADEPHAGA

INTRODUCTION

In 1982, Rob Roughley and Bill Wolfe organized the First International Conference on the Classification, Phylogeny and Natural History of the Hydradephaga in Toronto. The proceedings of the meetings were published in the Proceedings of the Academy of Natural Sciences of Philadelphia, 137(1) in 1985. The second conference was organized by Michel Brancucci and Konrad Dettner and was convened at the XVII International Congress of Entomology in Hamburg in 1984. The results of this symposium were published in Entomologica Basiliensia, 11 in 1986. The next two issues of *Quaestiones Entomologicae* (Volume 26, Numbers 2 and 3) mark the culmination of the third such conference held in conjunction with the XVIII International Congress of Entomology in Vancouver in 1988.

The rationale for these International Conferences has been and continues to be to stimulate international collaboration. This is the preferred method for advancing science in general and the study of Hydradephaga in particular. Nevertheless, science is a human endeavour: its advancement depends on the enthusiasm and ideas of the participants. We hope that the latest proceedings will lead to even greater collaboration and further advance the study of Hydradephaga. From this viewpoint, it is encouraging to note that, in the present proceedings, European authors discuss Nearctic taxa and North American authors discuss Palearctic taxa.

As with the other conferences, the majority of the papers in this volume deal with hydradephagan systematics. As such, they represent significant contributions rarely found in one proceeding. Several of these papers treat the systematics of families (Beutel - Gyrinidae; Burmeister - Amphizoidae) and genera (Wolfe and Roughley - *Laccornis;* Roughley -*Dytiscus*). These studies lay a solid foundation for phylogenetic and evolutionary analyses of this important group of aquatic insects.

The five families which comprise the Hydradephaga include 5,000 - 6,000 species in the world fauna and encompass a wide range of structural diversity. An analysis of the literature on Hydradephaga over the last five years suggests that about 200 papers per year are being published by about 200 authors. This literature is primarily systematic-taxonomic-faunistic, suggesting that much more work is needed in these areas. Nevertheless, there are encouraging signs that other studies about natural history, behaviour and ecology of Hydradephaga are becoming more common. This melding of a variety of research efforts holds great promise for both the interpretation of relationships within the Hydradephaga and an understanding of evolutionary changes occasioned by invasions of fresh water.

Several colleagues helped in the preparation of this volume by reviewing mansucripts for us. We offer our sincere thanks to Anders Nilsson, Yves Bousquet, Gary Gibson, Rolf Beutel, Phil Perkins, Dave Larson, Ales Smetana, Valerie Behan-Pelletier, Olof Biström, Sule Oygur, F. Merv Atton, Bill Wolfe, Richard Garcia, Ingolf Askevold and Terry Galloway. We also extend a vote of thanks to George Ball, Editor, *Quaestiones Entomologicae* and Mrs. Suseela Subbarao for their efforts in getting these proceedings into print.

R. E. Roughley, Winnipeg, Manitoba
R. B. Aiken, Sackville, New Brunswick

Publication of *Quaestiones Entomologicae* was started in 1965 as part of a memorial project for Professor E.H. Strickland, the founder of the Department of Entomology at the University of Alberta in 1922.

It is intended to provide prompt relatively low cost publication for comprehensive accounts of entomological research of greater than average length. However, shorter papers about insects in the Prairie Provinces of Canada are acceptable. Page charges are normally levied, the rate determined by printer's charges. For information about current page charges, consult the Editor.

Copy for all types of papers should conform to the Style Manual for Biological Journals, published by the American Institute of Biological Sciences, Second Edition, 1964, except that title of periodicals should be given in full. For style of taxonomic papers, the Editor should be consulted. Two copies of a manuscript are requested. All manuscripts will be reviewed by referees.

Abstracts are required, one in English and one in another language, preferably French.

Copy for illustrations must accompany the manuscript, and be of such character as to give satisfactory reproduction at page size (less 1/2 inch, or 1.2 cm on plates of full page size [7 X 4 1/4 inches or 17.8 X 10.7 cm]). Reprints must be ordered when proofs are returned, and will be supplied at cost.

Subscription rates are the same for institutions, libraries and individuals, $20.00* per volume of four issues, normally appearing at quarterly intervals; single issues $5.00**. Back volumes and issues are available at the same cost. These prices supersede those previously indicated, and are subject to change as required by inflationary pressure on the value of money.

Communications regarding subscriptions should be addressed to the Subscription Manager, and regarding manuscripts to the Editor.

* Same rate in US$ for non-Canadian subscriptions.

** Single issues of more than 100 pages: $10.00; exception: volume 21(4) - $20.00.

Published quarterly by:

Department of Entomology
University of Alberta
Edmonton, Alberta, CANADA
T6G 2E3

Second Class Mail Registration Number 5222

Return Undeliverable mail to the address above. Return Postage Guaranteed

Issued July 1990

THIRD INTERNATIONAL CONFERENCE ON CLASSIFICATION, PHYLOGENY, AND NATURAL HISTORY OF HYDRADEPHAGA (COLEOPTERA)

Proceedings

Organized and Edited by

R. E. Roughley and R.B. Aiken

Convened at the XVIIIth International Congress of Entomology

Vancouver, British Columbia, Canada
3 - 9 July 1988

QUAESTIONES ENTOMOLOGICAE ISSN 0033-5037

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

Volume 26 Number 2 1990

CONTENTS

NATURAL HISTORY OF HYDRADEPHAGA

SYSTEMATICS OF HYDRADEPHAGA

INTRODUCTION

In 1982, Rob Roughley and Bill Wolfe organized the First International Conference on the Classification, Phylogeny and Natural History of the Hydradephaga in Toronto. The proceedings of the meetings were published in the Proceedings of the Academy of Natural Sciences of Philadelphia, 137(1) in 1985. The second conference was organized by Michel Brancucci and Konrad Dettner and was convened at the XVII International Congress of Entomology in Hamburg in 1984. The results of this symposium were published in Entomologica Basiliensia, 11 in 1986. The next two issues of *Quaestiones Entomologicae* (Volume 26, Numbers 2 and 3) mark the culmination of the third such conference held in conjunction with the XVIII International Congress of Entomology in Vancouver in 1988.

The rationale for these International Conferences has been and continues to be to stimulate international collaboration. This is the preferred method for advancing science in general and the study of Hydradephaga in particular. Nevertheless, science is a human endeavour: its advancement depends on the enthusiasm and ideas of the participants. We hope that the latest proceedings will lead to even greater collaboration and further advance the study of Hydradephaga. From this viewpoint, it is encouraging to note that, in the present proceedings, European authors discuss Nearctic taxa and North American authors discuss Palearctic taxa.

As with the other conferences, the majority of the papers in this volume deal with hydradephagan systematics. As such, they represent significant contributions rarely found in one proceeding. Several of these papers treat the systematics of families (Beutel - Gyrinidae; Burmeister - Amphizoidae) and genera (Wolfe and Roughley - *Laccornis;* Roughley -*Dytiscus*). These studies lay a solid foundation for phylogenetic and evolutionary analyses of this important group of aquatic insects.

The five families which comprise the Hydradephaga include 5,000 - 6,000 species in the world fauna and encompass a wide range of structural diversity. An analysis of the literature on Hydradephaga over the last five years suggests that about 200 papers per year are being published by about 200 authors. This literature is primarily systematic-taxonomic-faunistic, suggesting that much more work is needed in these areas. Nevertheless, there are encouraging signs that other studies about natural history, behaviour and ecology of Hydradephaga are becoming more common. This melding of a variety of research efforts holds great promise for both the interpretation of relationships within the Hydradephaga and an understanding of evolutionary changes occasioned by invasions of fresh water.

Several colleagues helped in the preparation of this volume by reviewing mansucripts for us. We offer our sincere thanks to Anders Nilsson, Yves Bousquet, Gary Gibson, Rolf Beutel, Phil Perkins, Dave Larson, Ales Smetana, Valerie Behan-Pelletier, Olof Biström, Sule Oygur, F. Merv Atton, Bill Wolfe, Richard Garcia, Ingolf Askevold and Terry Galloway. We also extend a vote of thanks to George Ball, Editor, *Quaestiones Entomologicae* and Mrs. Suseela Subbarao for their efforts in getting these proceedings into print.

R. E. Roughley, Winnipeg, Manitoba
R. B. Aiken, Sackville, New Brunswick

LIFE HISTORY, TERMINATION OF SUMMER DIAPAUSE, AND OTHER SEASONAL ADAPTATIONS OF *AGABUS DISINTEGRATUS* (CROTCH) (COLEOPTERA: DYTISCIDAE) IN THE CENTRAL VALLEY OF CALIFORNIA

R. Garcia
K.S. Hagen
W.G. Voigt

Division of Biological Control
University of California
Berkeley, CA 94720
U.S.A.

Quaestiones Entomologicae
26: 139–149 1990

ABSTRACT

The predaceous diving beetle, Agabus disintegratus, *breeds in temporary water sources, and adults pass the summer dry period in a state of diapause. Diapausing beetles bury themselves at the base of wetland plants until the pond is reflooded. Diapause is terminated in the laboratory by a short photoperiod, and weight changes and reproductive activity of field collected adults indicate that termination of diapause begins in the early fall before the ponds refill with water. Laboratory experiments indicate that microhabitats must maintain 100% relative humidity for long term survial of aestivating adults. Beetles could not be induced to fly during diapause. Flight activity corresponds to the most optimal period for finding natural water sources in California's Mediterranean climate.*

INTRODUCTION

Adults of the predaceous diving beetle, *Agabus disintegratus* (Crotch), pass the dry summer months in diapause (Garcia and Hagen 1985, Garcia and Hagen 1987). *A. disintegratus* is a univoltine species. Larval development takes place through the winter, and in early March teneral adults emerge, feed, and synthesize fat reserves through the spring prior to summer aestivation. As the water source dries, adults bury into the root layer and debris of plants in the basin of the pond, where they pass the summer. Although Young (1960) reported that *A. disintegratus* flew from drying ponds in Indiana, Garcia and Hagen (1987) could find no evidence for flight in adult *A. disintegratus* collected in the summer, even though the wings appeared to be normal.

The conditions and habitats in which *A. disintegratus* aestivates were described in Garcia and Hagen (1987). However, little is known about the adaptations of this beetle to the absence of water, its dispersal ability, or about conditions which regulate the termination of diapause. This report investigates these aspects of the biology of this aquatic beetle.

MATERIALS AND METHODS

Study Site.— Field observations and collections of *A. disintegratus* were made at approximately one month intervals from June 1986 through August 1988. All experimental materials were collected from pond #78 at the Gray Lodge

Wildlife Area, Butte County, California, which has been described in detail by Garcia and Hagen (1987). The basin of this pond is now almost completely covered with bermudagrass (*Cynodon dactylon* L.), in contrast to only partial coverage in 1986. Pond #78 was filled with water during the first week of October 1986, and remained full until the pond was drained in mid-May 1987. The pond was flood-irrigated for 3-6 days in June and again in July, 1987. In 1987, pond #78 was filled in early October and remained so until it dried in mid-April 1988. There were no summer irrigations in 1988.

Immatures.— Immature beetles were collected with a fine-mesh aquatic sweep net. Mature larvae, pupae and post-eclosion adults of *A. disintegratus* were collected from the soil on the north-western embankment above the water line of pond #78. A 5 cm diameter soil corer was used to sample the first 6 cm of soil, which was later sorted in the laboratory. These samples were taken at approximately 2 week intervals from March 2, 1988 through May 5, 1988, at which time no pupae or adults remained. Fifteen mature larvae were removed from their pupal cells, weighed and transferred to 2 cc vials with moist cotton on the bottom. The resulting pupae were reweighed within 1 day of pupation. Larval instar determinations were based on body length and head capsule width.

Adults.— Adult beetles were collected either from aquatic sweep net samples when standing water was present (October through April), or from the sod beneath the bermudagrass (late April through late September) (see Garcia and Hagen 1987). Beetles collected in the summer were sieved from bermudagrass sod collected with a shovel as described in Garcia and Hagen (1987). Other adults were reared in the laboratory from larvae and pupae collected from soil samples taken along the exposed banks of the pond.

Adult *A. disintegratus* collected from each field visit were weighed to ± 0.1 mg on an analytical balance and 5-10 specimens were dissected to determine reproductive activity and fat development as described by Garcia and Hagen (1987). Adults collected from water were blotted lightly with dry tissue paper before weighing. Beetles were weighed within 24 hrs after field collection or laboratory emergence. Teneral adult weights were determined by weighing 33 individuals within 1 day of eclosion. Beetles were held alive for up to one week until they could be dissected.

Weight Gain.— The rate of weight increase of adults was determined in the laboratory using newly emerged *A. disintegratus* adults. One to three-day old adults were placed individually in a 250 cc jars of water with a small piece of *Elodea* sp. for a resting substrate. The beetles were fed 20 late instar *Culex pipiens* L. larvae every other day and weighed at 7-10 day intervals until their weights stabilized.

Weight Loss.— Adult *A. disintegratus* in diapause were subjected to various levels of water moisture to estimate their ability to withstand desiccation. Eighteen adults were collected from sod samples on July 29, 1988, and weighed the following day. All beetles were held overnight (18 hrs) in 200 cc of water to equalize hydration levels and then reweighed . Half of the beetles (5 females, 4 males) were placed in 250 cc jars with moistened sand (100 g sand with 20 cc water), while the other group (5 females, 4 males) was placed in sand which had previously been dried to constant weight. Both groups were held at room temperature (20 ± 5°C). Beetles were weighed at 1–2 day intervals until no survivors remained in the dry sand group.

Weight loss of adult beetles at various relative humidities was measured as follows: relative humidities estimated at 100%, 90%, 69%, and 50% were attained by mixing 0, 10, 37.5, and 62.5 g of potassium hydroxide, respectively with 100 cc water in 0.94 l jars (Peterson 1959). Beetles were placed in refugia made from tubes of black cotton fabric (15 x 6 mm diameter) and closed at one end. The refugia provided a dark, constricted resting place which most beetles voluntarily entered. Two beetles (1 male & 1 female) in separate refugia were placed in a plastic cup (3 cm diameter), which was supported above the solution by a 2.8 cm diameter PVC pipe which had several holes drilled in it to facilitate equilibration of water vapor. A lid with 1.2 mm mesh screen was placed on the cups to prevent beetles from escaping. All jars were covered with a lid and placed in a sealed box to exclude light, and the box was then placed in a constant temperature cabinet at 21.5 ± 1°C. The beetles were weighed at 4-6 day intervals for 25 days. Body weights were transformed to proportion of original body weight at day 0. Regression lines based on these values over time were tested for parallelism, and *post hoc* comparisons of the slopes of the regression lines were made using Scheffé's multiple comparison (Marascuilo & Levin 1983).

Flight activity.— To determine time of year when *A. disintegratus* individuals could be induced to fly, field collected adult beetles were tested for flight within 2-3 days after collection and laboratory reared animals within 3 days of emergence. A 250 cc jar with a mouth opening of 6 cm in diameter was filled with 5 cm of sand and 150 cc of water. A round wooden stick about 10 cm in length and 0.3 cm in diameter was inserted vertically in the sand so that its apex extended about 1 cm above and in the center of the mouth of the jar. Ten jars were then placed in a water bath.

An individual beetle was placed into each jar and allowed to acclimate for at least 15 minutes before observations were started. Flight tests were usually conducted in full sun at mid-day, and run until water temperatures exceeded 30°C unless otherwise noted. Flight was determined from direct observations or from the presence of beetles in the surrounding water bath. The beetles were unable to escape the jar without flight; therefore any beetles which were missing or found in the water bath were assumed to have flown.

A single flight test was conducted on an overcast day (March 31, 1987) in which two randomly selected groups of 12 adults each (6 males, 6 females) were placed in water artificially heated from 23 to 36°C or in water kept at ambient temperatures (23 to 25°C).

Occasionally, adults were placed directly on loose dry soil exposed to full sun, and gross behavioral reactions recorded. Beetles observed to fly from any of the above conditions were recaptured when possible and dissected to determine reproductive condition and fat reserve.

Termination of diapause.— Adults used in this experiment (three groups of 5 pairs each) were collected from sod samples in May and June 1987. On June 29, each male/female pair was held in moistened sand (100 g sand and 15 cc water) in a 250 cc jar. A lid was placed on each jar to reduce evaporation. A 2 mm hole in the lid allowed for gas exchange. Each group of 5 jars was placed in one of three environmental chambers under the following conditions: "short light" (12L:12D hr) at 13°C and 18°C and "long light" (16L:8D) at 15°C. All temperatures were controlled to within ± 1°C. On September 9, 1987, the 14 surviving pairs from the three groups were placed in jars with 200 cc of tap water and one or two pieces of *Elodea* as an oviposition substrate under 16L:8D, 15°C conditions. Ten to 20 *Culex pipiens* L. larvae (3rd-4th instar) were given to the beetles every one or two days, and the plants were inspected daily for eggs from September 10 to September 18, 1987, at which time the beetles were dissected and examined for reproductive condition.

Another group of adults collected from sod on June 22, 1987 was paired by sex and placed directly in jars with 250 cc of water and one or two pieces of *Elodea* on June 25, 1987, and given 10 late instar *Cx. pipiens* larvae every three to five days. Three groups of five male/female pairs were placed under the same light regimes as the groups placed in moist sand. The *Elodea* was examined each week for eggs until the beetles were dissected September 2-4, 1987.

RESULTS

Immatures.— First instar *A. disintegratus* larvae were observed from October 26 through April 16, indicating continuous egg laying through the winter and early spring. Second instars were observed from November 23 through April 16, and third instars were observed from January 14 through April 16.

Mature larvae were observed leaving the pond to pupate from January 23 through April 12, 1988. Larvae crawled up the slope (a 1.5 m levee) to a vertical height of about 1 m above the water line and buried about 1-2 cm deep into the moist soil of the slope. Once under the soil, the larva shaped a spherical mud pupation cell about 6 mm in diameter. Several mature larvae but no pupae were observed inside their cells on February 17, 1988. Pupae were first observed on the following visit (March 2), and the first adults were recovered from pupal cells on March 15. In 1986 and 1987, teneral adults were first observed in the water on March 19, and March 26, respectively, but in 1988, they were not seen until April 12.

Mature larvae collected from the field inside their pupal cells weighed 23.1 ± 2.0 mg S.D. and the resulting pupae weighed 28.8 ± 1.8 mg (N = 15). The apparent increase in weight must have resulted from absorption of water, as they were held in a 100% humidity chamber on moist cotton.

Adults.— Figure 1 shows seasonal changes in adult body weight and fat reserves from eclosion to termination of diapause in the fall. A sharp increase in body weight and fat reserves was noted in the spring. Body weight and fat reserves remained relatively constant until mid-August when a decline was noted in both categories. After the pond was filled in the fall, body weights increased, but fat reserves declined.

No evidence of reproductive activity was noted in dissected adults collected from sod samples in the summer. Reproductive activity was observed in beetles collected from water in early October 1987, only five days after the field had been filled with water. Of five females dissected, all contained sperm in their spermathecae and 10-19 large developing eggs. Evidence of reproductive activity (*i.e.*, mature eggs in the ovarioles, sperm in the spermathecae, *etc.*) was observed from October through April.

In March and April of 1986 and 1987, both teneral and older generation adults were found together in the pond. In 1988, however, no older generation adults were seen in the pond after mid February. On February 15, 1987 more than a hundred adults (approx. 30 were collected within 30 m^2) were observed under plant debris along the levee of the pond. These were all reproductively active, older generation adults, as determined by dissection. On March 2, adults were not found on the bank, and could not be found in the pond by sweeping with an aquatic net. Only a small percent of the mature larvae in the soil samples had pupated by March 2, and teneral adults were not observed in pupal chambers until March 15. All adults had emerged from pupal cells and returned to the water by the end of April.

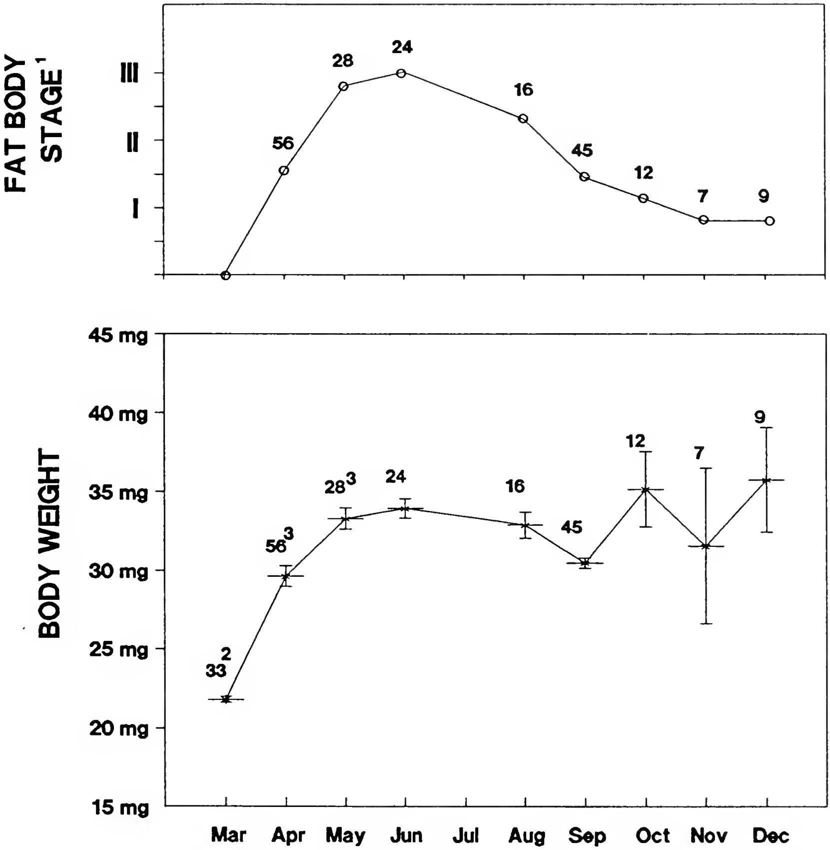


Fig. 1. Seasonal changes in average body weights and fat body reserves of field collected *Agabus disintegratus* Crotch from 1986-1988[1]. Midline horizontal line indicates mean. Vertical bars of weights indicate ± 2 standard error of the mean. The numbers indicate the number of beetles measured.

[1] Fatbody stages: I, layer of fat bound to integument; II, free fat bodies; III, "filled" with free fat bodies.

[2] Values for March represent weights from teneral adults reared from field collected pupae. Adults were weighed within 2 days of eclosion.

[3] Only non-reproductive adults were included in the April and May averages, since they represented the current generation.

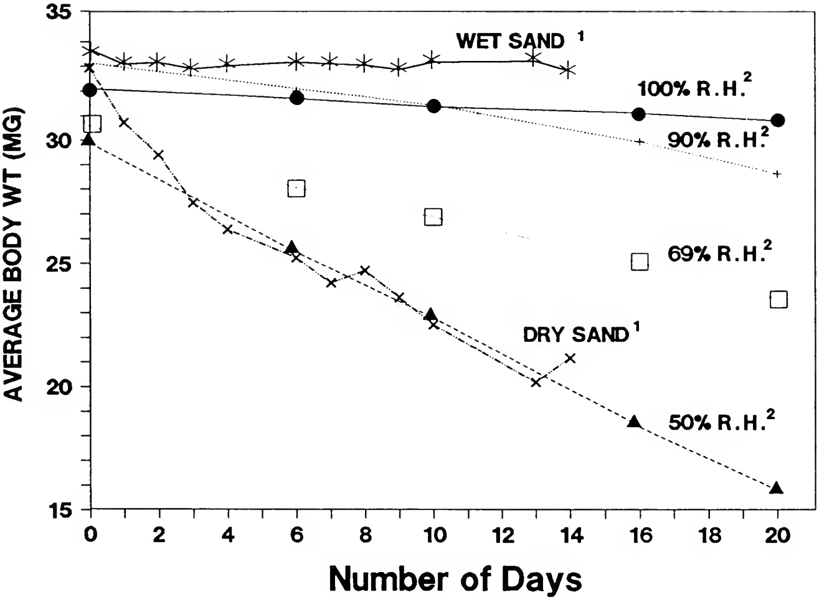


Fig. 2. Body weights of aestivating *Agabus disintegratus* Crotch under various conditions and relative humidities. The groups at various relative humidities were held in the dark in a 21 ± 1°C chamber.

[1] Held under room conditions (15-25°C).

[2] Held in dark at 21±1°C.

Table 1. *Post hoc* comparisons of slopes of weight loss vs. time for adult *A. disintegratus* under various conditions. Body weights were transformed to proportions of original body weights. Comparisons were of the slopes of regression lines using Scheffé's multiple comparison at P = 0.05.

	Test Conditions					
	Wet Sand	100%	90%	69%	50%	Dry Sand
Wet Sand	—	ns	sig	sig	sig	sig
100%		—	sig	sig	sig	sig
90%			—	sig	sig	sig
69%				—	sig	sig
50%					—	ns

Table 2. Tests for flight behavior and reproductive activity of *Agabus disintegratus*.

	Tested		Flew		Reproductive Activity[1]		
Date	Male	Female	Male	Female	Male	Female	Temperature Range (°C)
Jan-88	5	5	1	1	1A	1A	24–29
Feb-88	6	5	2	0	2A	—	30–35
Mar-87[2]	6	6	2	2	—	—	22–36
Mar-87[3]	6	6	0	0	—	—	22–25
Mar-88[4]	5	5	0	0	—	—	22–25
Mar-88[5]	2	2	2	0	2I	—	DRY SOIL[5]
Apr-87	32	32	13	11	8I 2A	4I 3A	22–36
May-87	10	10	0	0	—	—	29–32
Jun-87	10	10	0	0	—	—	27–34
Aug-87	5	5	0	0-	—	—	25–30
Oct-87	6	6	0	0	—	—	—
Oct-87	3	3	3	1	3A	1A	DRY SOIL[5]
Nov-87	5	5	2	2	2A	2A	21–26

[1] I = Reproductively inactive, A = Reproductively active. From beetles which were recovered after flight.

[2] In artificially heated water bath under overcast skies.

[3] Unheated water bath under overcast skies. Conducted concurrently with heated group.

[4] Reared from mature larvae collected February 2, 1988.

[5] Tested in shallow soil exposed to bright sun.

Table 3. Effects of photoperiod and substrate on reproductive conditions of field collected female *Agabus disintegratus*.

Substrate	Photoperiod (Light:Dark)	Temp. (°C)	N	Number Oocytes[1]	Number Mated[2]
Soil[3]	12L:12D	13.0	4	4	0
	12L:12D	18.0	2	2	2
	16L:8D	15.5	4	0	0
Water[4]	12L:12D	13.0	4	3	0
	12L:12D	18.0	2	2	1
	16L:8D	15.5	4	0	0

[1] Oocytes conspicuous in ovarioles at 10X

[2] Sperm present in spermathecae

[3] Held in soil from 29 Jun through 4 Sept, 1987, then placed in water and fed on mosquito larvae under 16L:8D photoperiod until dissected on 18 Sept.

[4] Held in water with mosquito larvae from 25 Jun until dissected on 2-4 September.

Weight Gain.— Teneral females averaged 21.3 ± 2.8 mg (N=20) and males averaged 22.4 ± 3.0 mg (N=13). Newly emerged adults fed 10 late instar mosquito larvae/day gained an average of 48% of their body weight in the first 10 days of observation.

Weight Loss.— Beetles placed in dry sand were found consistently on the surface, whereas those under moist sand remained buried. Results of the weight loss experiments are summarized in Figure 2. Body weights of the 100% R.H. and moist sand groups remained constant, while the beetles exposed to dry sand or lower humidities lost weight. The 50% R.H. group lost weight at about the same rate as the dry sand group, and rate of weight loss was inversely proportional to relative humidity. Regardless of the conditions of the experiment, all beetles that died had an average body weight of 19.8 ± 2.4 mg. There were no significant differences between the 100% R.H. and wet sand groups, nor between the dry sand and 50% R.H. groups. Otherwise, all other groups had significantly different slopes (Table 1).

Flight activity.— Flight from the test containers was observed in the laboratory during the fall, winter, and spring (Table 2). Beetles which flew during the flight tests typically climbed to the tip of the vertical stick, oriented with its back to the sun for up to 15 minutes, and then initiated flight. Some of the newly emerged, laboratory reared beetles were observed to attempt flight in indoor containers covered with clear plastic. This occurred in early March, after several days under dry but cool conditions (20–24°C). Beetles exposed to the sun on bare soil (March & October) attempted to fly sooner (*i.e.* in less than 15 min.) than beetles in water filled jars. In October 1987, 4 out of 6 beetles flew from soil, and 2 out of 4 beetles flew from soil in March 1988. No beetles were observed to fly from the surface of the water in any of the flight tests.

In the March 1987 test under overcast skies, four beetles flew from the heated water bath (at >31°C), while none of the beetles in the unheated water (maximum

22°C) attempted flight although three were observed to move up the stick and out of the water. All the beetles in the heated group moved up and down the stick or swam about their container as the water temperatures rose above 28°C. After water temperatures exceeded 32°C, the beetles spent the majority of time above the water on the stick. The unheated group usually remained below the surface grasping the stick near the sand except for occasional surfacing to breathe, but seldom climbed on the stick.

In April 1987, both reproductive (2 males, 3 females) and teneral adults (8 males, 4 females) flew. None of the beetles collected from summer sod samples were observed to fly, in spite of being exposed to high water temperatures.

Termination of Diapause.— Females collected in June and held with a male in either soil or water under a photoperiod of 12L:12D for 10 weeks exhibited reproductive activity upon dissection as indicated by conspicuous oocyte development and the presence of sperm in the spermathecae (Table 3). No eggs were observed on the *Elodea* in the holding containers under any of the conditions tested. Beetles under 12L:12D at both 13 and 18°C consumed 33.0 ± 4.2 S.D. and 33.2 ± 5.6 mosquito larvae, respectively, while those held at 16L:8D (15°C) consumed 28.6 ± 6.4 larvae. Differences in number of larvae consumed were not significant (Student's t-test, $P > 0.05$).

DISCUSSION

In the Central Valley of California, *A. disintegratus* is adapted to breeding and developing during the fall and winter months. Artificial inundation of pond 78 has occurred near the first week of October for the last two years, and adults have been observed mating by mid-October. In addition, dissection of adult females a few days after flooding in early October revealed developing oocytes and sperm in the spermathecae. Thus, reproductive activity begins in the early fall in these artificially flooded ponds. Under natural conditions, however, standing water, such as temporary ponds and vernal pools formed from precipitation and runoff, usually does not accumulate in the Central Valley until late November or December. Thus artificial flooding at the refuge allows for earlier development for *A. disintegratus*. Whether this is advantageous or not is unclear at this time, because despite observations of early reproductive development and the appearance of 1st instar larvae in late October, third instar larvae have not been seen until January. Since water temperatures are relatively mild through the fall, the occurrence of 3rd instar larvae should be expected much earlier in the season. We have no evidence at this time whether mortality or some physiological factor in larval development accounts for the lack of later instars.

The artificially manipulated water systems in waterfowl management areas may be an advantage for this species by providing more optimal conditions for adults during summer diapause, particularly in bermudagrass. Body weights of beetles collected through the dry summer remained relatively constant, which is apparently related to high humidities in the sod microhabitat. Maintenance of body weight through the summer may be partly influenced by the summer irrigations of the field. Summer irrigations not only provide standing water for a short period but more importantly, remoisten the rhizome debris layer where the beetles reside. In addition, growth and transpiration by the plants moderate the high temperature extremes that are common during the summer months in this part of California. Total rainfall for Colusa (15 km SW from the study site) during June, July, August and September, averaged 3.1, 1.0, 1.3, and 3.8 cm, (U.S. Weather Bureau summaries, 1980-1985). During 1987, however, no precipitation was recorded for the entire summer. Such small amounts of summer precipitation are normally insufficient to moisten the soil, especially under a thick canopy of bermudagrass. Consequently, moisture levels where these beetles reside would be dependent mostly on water retained in the soil from the spring or from water added by summer irrigations.

In the laboratory, adults placed in moist conditions maintained a constant body weight, but under totally dry conditions lost weight rather quickly and died within 15 days. This indicates that the microhabitat where the beetles reside cannot become completely dry even for relatively short periods during aestivation.

Natural habitats with wetland macrophytes such as cattails (*Typha* spp.) and bulrushes (*Scirpus* spp.), from which *A. disintegratus* has been recovered (Garcia and Hagen 1987), may provide a more suitable microhabitat than artificial habitats with bermudagrass. The soil around these more robust plants more readily forms cracks at the base of the stems which would allow beetles access into the deeper zones of the soil-root interface.

Beetles were able to fly throughout the fall, winter and spring, which corresponds to periods when standing water is likely to be available. During the summer, beetles did not fly, even after exposure to harsh conditions. The increased activity of beetles subjected to dehydration indicates that although beetles are unable to fly from drying conditions, they probably do crawl about in the field seeking more favorable microhabitats. This is highly adaptive in that other natural water sources are likely to be unavailable, and flight dispersal at that time would deplete fat and water reserves with little possibility of achieving success. By seeking out relatively insulated refugia for diapause, *A. disintegratus* avoids the extreme heat and dryness of the Central Valley in summer.

Female *A. disintegratus* dissected after being held in the laboratory with males in either soil or water under a photoperiod of 12L:12D were reproductively active, whereas the females held at 16L:8D were not, suggesting that diapause is terminated by a short-day photoperiod. Termination of summer diapause by short photoperiod has been demonstrated in several other insect species, including four different orders (see reviews in Tauber *et al*, 1986; Brown and Hodek, 1980). The decline in average body weight and fat reserves in late summer prior to inundation of the fields further suggests that termination of diapause begins while beetles are still in the dry state.

Several species of dytiscids exploit more permanent water sources, and through aestivation, *A. disintegratus* avoids competing with these species. In turn, *A. disintegratus* is able to exploit immediately temporary aquatic habitats as soon as they become available, without having to expend energy to seek them out through dispersal. Seasonal flight activity allows dispersal of reproductive and teneral adults during periods when natural water sources are more likely to occur.

ACKNOWLEDGEMENTS

We thank Kim Des Rochers and Aaron Goldberg for laboratory assistance for some of the experiments. R.B. Reno and Lee Ashford of the California Department of Fish and Game at the Gray Lodge Waterfowl Area provided logistical assistance. This study was supported in part by special funds for mosquito research in California.

REFERENCES CITED

Brown, V.K., and I. Hodek (eds.) 1983. Diapause and life cycle strategies in insects. Dr W. Junk Publishers. The Hague, Boston, London.

Garcia, R. and K.S. Hagen 1985. The occurrence of adult dytiscids in dry waterfowl refuge ponds in California (Coleoptera:Dytiscidae). Coleopterists Bulletin, 39: 391-392.

Garcia, R. and K.S. Hagen 1987. Summer dormancy in adult *Agabus disintegratus* (Crotch)(Coleoptera:Dytiscidae) in dried ponds in California. Annals of the Entomological Society of America, 80: 267-271.

Marasuilo, L.A., and J.R. Levin 1983. Multivariate statistics in the social sciences. Brooks/Cole Publ., Monterey.

Peterson, A. 1959. Entomological techniques. How to work with insects. Edwards Brothers, Inc., Ann Arbor.

Tauber, M.J., C.A. Tauber, and S. Masaki 1986. Seasonal adaptations of insects. Oxford University Press, New York and Oxford.

Young, F.N. 1960. The water beetles of a temporary pond in southern Indiana. Proceedings of the Indiana Academy of Sciences, 169: 154-169.

ODONATE PREDATION AS A FACTOR INFLUENCING DYTISCID BEETLE DISTRIBUTION AND COMMUNITY STRUCTURE

David J. Larson
Dept. of Biology,
Memorial University of Newfoundland
St. John's, Nfld.
A1B 3X9
CANADA

Quaestiones Entomologicae
26: 151–162 1990

ABSTRACT

Dragonfly larvae and predacious water beetles (Dytiscidae) are abundant predators in many shallow lentic habitats. The distributions of members of these two groups differ somewhat with odonates dominating in more open and permanent sites while dytiscids are more abundant in habitats of less stability and denser vegetation. It is postulated that predation of odonate larvae on dytiscids, especially the larval stages, is at least a contributory factor to this partitioning. Evidence in support of this hypothesis is drawn from general considerations of the biology and behaviour of the two groups, literature records, collecting experiences and a study that measured odonate density and the prevalence of dytiscids as food items in their guts. In certain Newfoundland bog pools, the density of odonate larvae is adequate to eliminate vulnerable dytiscids in a matter of days. Mechanisms by which dytiscids can avoid odonate predation are discussed.

INTRODUCTION

What governs the nature of natural communities? This question has generated much interest among biologists. The major conclusion to come out of the considerable research conducted on the question seems to be that there is no simple answer. Historical factors determine the suite of species present in a fauna that can interact potentially in communities. Abiotic tolerances determine which set of species can occur in a given physical arena. Within this arena, biotic interactions such as predation and competition further affect species densities and dispersion. Add to this niche and trophic specialization and temporal and behavioral similarities or differences among species, and the complexities of community organization are readily apparent.

Water beetle workers have recognized characteristic associations of water beetles species, at least within regional faunas. There is a long history of these associations being described and related to habitat characteristics. Recently, several authors (e.g. Larson 1985, Ranta 1985, Flechtner 1986, and Cuppen 1986) have used numerical techniques to define communities and relate species distributions to habitat parameters. Most studies of water beetle communities have emphasized the importance of physical, chemical and vegetal features of habitats as determiners of beetle distribution, although some authors have considered also predation and competition effects (Nilsson 1986, 1988).

There are two aspects to the problem of whether predation pressures have had a role in shaping dytiscid communities. First, past predation pressures may have been responsible for shaping aspects of the ecology, behaviour and morphology of dytiscids, for example the development of defensive glands that produce a complex array of defensive substances (Dettner 1985), or the evolution of protective coloration by species in certain types of habitat (Young 1960). However, if these traits have become fixed because of this pressure, no direct evidence is left with which to demonstrate the relationship so that selection pressures for the evolution of the feature must be inferred based on concepts of its function. The second aspect involves current and continuing interactions where predation effects and outcomes are not stabilized and vary depending upon the conditions under which they occur. These sorts of interactions are amenable to observation and this aspect of predation interaction is considered here.

It is necessary, first, to establish if predators in aquatic systems are capable of exerting enough pressure on prey populations to modify the prey species mix, population structure, and/or their morphological traits. There is abundant evidence to indicate that many littoral habitats are predator dominated systems. When present, fish generally have a major impact on invertebrate communities, occupying the role of top predator by virtue of their large size and activity (Gilinsky 1984). Fish predation on invertebrates may result in elimination of species from a system, change the population densities, or change the morphology and behaviour of prey (Stenson 1978, Nilsson 1981, Morin 1984). Wilson (1923) was concerned about the impact of water beetle predation on fish in fish-culture ponds. However, he came to the conclusion that beetle larvae and adults are eaten freely by many fish, and that all beetle larvae and adults of smaller species constitute a very important item of fish food. Wilson reviewed and supported the observation made by many authors that dytiscids tend to be much less abundant and diverse in large ponds and lakes than in smaller bodies of water. With qualification, this observation is still generally valid (Larson 1985, Ranta 1985). It is probable that fish predation in larger bodies of water has a bearing on this distribution.

While fish are undisputably important predators, certain factors limit their distribution, *e.g.*, drying of habitat, oxygen depletion, freezing, and dense debris or plant structure in the habitat. Fish are absent from many northern lentic habitats. In such habitats, can other groups of predators exert the same type of impact on invertebrate communities on which they prey? If so, which groups of predators are likely to do this? Within the Insecta, Odonata, Hemiptera (which will not be considered here) and Coleoptera are especially diverse and abundant predators in lentic habitats. The relative abundance and success of each group varies from site to site. The purpose of this paper is to evaluate the evidence for predation by odonate larvae as a factor affecting the distribution of dytiscid beetles.

ODONATES AS SIGNIFICANT PREDATORS OF DYTISCIDS?

Evidence from literature and observation

Wissinger (1988) found large odonates increased in numbers to become top predators in the absence of fish. Benke (1976) recorded dragonfly larvae in very high densities in a South Carolina pond, where he concluded they were capable of rapidly annihilating their prey (most animals of suitable size [Pritchard 1964]) which survived only because they found refuges. The high density of odonate larvae observed by Benke is not unusual: for example Ball and Hayne (1952), Beatty and Hooper (1958) and Macan (1964) reported high densities of odonate larvae in shallow lentic habitats. In fact, the standing crop of odonates commonly may exceed that of their prey (Benke 1976). Thorp and Cothran (1984) showed that dragonfly predation can influence significantly a benthic community, primarily by changing prey density rather than community diversity. Density dependent

Table 1. Comparison of predation strategies of odonate and dytiscid larvae

	ODONATA	DYTISCIDAE
a	ambush and searchers hidden or not exposed deriving protection from predators	hunters, searchers exposed and mobile, at risk to predators
b	high assimilation rate of ingested food efficient predators	? probably less efficient predators
c	variable growth rate population taking wide range of prey sizes at any one time	less variation, population in synchrony in growth
d	ultimate size of larvae larger on average, growth slower	smaller larvae but growth faster

effects may be major factors controlling odonate communities (*e.g.*, Johnson *et. al.*, 1985) and may result in both inter- and intraspecific asynchrony in growth so that odonates of a range of sizes are present to crop prey of a range of sizes.

Larson and Colbo (1983) suggested that odonates are significant predators of dytiscids. This idea derives from consideration of population densities, feeding methods and life history patterns of both groups. The most important interactions are probably between the larval stages because this is the only active stage of odonates to be in the water. Adult beetles appear to be fairly well protected from predation by size, hard cuticle and perhaps defensive secretions; larvae are apparently more vulnerable (Pritchard 1964, Griffiths 1973). Table 1 summarizes major differences in the predation strategies of odonate and dytiscid larvae.

Several lines of observation lend support to the idea that odonates negatively affect dytiscids. A few examples will illustrate this.

A. Numerous authors made the general observation that dytiscids are scarce in large lakes and are most numerous with the greatest diversity in seasonal habitats, newly formed ponds and the flooded margins or zone of dense emergent vegetation of larger ponds (Galewski 1971, Nilsson 1984, Larson 1985). Stability does not seem to favour many species. On the other hand, dragonfly larvae are generally not numerous or diverse in highly variable habitats, possibly due to their inability to cope with habitat drying (Fischer 1961) or freezing. In other words, there is somewhat of a habitat segregation between odonates and dytiscids. Historical and physical characteristics may limit the range of habitats occupied by odonates, but why are dytiscids not more successful in the habitat types occupied by odonates?

B. In 1986, John Carr and I sampled a series of small moraine ponds on the western slope of the Nahanni Mountains, Yukon Territories, along the Cantung

Table 2. Frequencies of co-occurrence of major taxa in habitats from which dytiscid beetles have been collected (after Flechtner 1986, Fig. 5).

Taxon	Frequency of co-occurrence (%)
Pisces	31
Odonata	39
Amphibia and Reptilia	40
Megaloptera (larvae)	40
Haliplidae	42
Heteroptera	44
Ephemeroptera and Plecoptera	51
Hydraenidae	52
Hydrophilidae	63
Trichoptera (larvae)	64
Diptera (larvae)	94

Road. The ponds ranged in elevation from the coniferous forest zone, through birch-lichen habitat to alpine habitats. Ponds within and near the coniferous forest zone had abundant odonates but few beetles which were largely confined to emergent vegetation at the very edges. Higher elevation ponds were superficially similar to those of lower elevations but odonate density was dramatically less while beetles were much more numerous. These ponds reflect a common faunal pattern for in general, with increasing elevation or latitude (at the highest latitudes), and deteriorating climates, beetles tend to be found more widely distributed in lentic habitats and occupy more open waters. For example, in barren alpine or arctic pools agabines and hydroporines occupy a wider range of depths and habitat types than is generally observed for lower elevation or lower latitude populations. Odonates are usually absent or in very low densities in such pools.

C. Some types of dytiscids occur regularly in habitats with dense populations of odonate larvae. These include: species of *Dytiscus* and *Cybister* which, because of their very large size, probably enjoy a switch in predator advantage; thermonectines, the larvae of which are pelagic and occupy a different zone than the dragonfly larvae; and very small species of dytiscids (*e.g.*, bidessines) which generally occur among very dense detritus, in moss or algal mats, or in very shallow water right at the water's edge - zones in which odonate populations are low. Larson (1985) pointed out that the size distribution profile within the dytiscid faunas of Alberta and Florida differed, with very small species comprising a proportionally much larger element in the Florida fauna. A partial explanation could be that the rich odonate (as well as fish) fauna of Florida selects for dytiscid forms that escape predation through adaptation to microhabitats which provide refuge from predators.

D. Flechtner (1986) challenged the suggestion of Larson and Colbo (1983) of a negative correlation between dytiscids and odonates. However, the data of Flechtner's Fig. 5 (reproduced in Table 2) which give percentage occurrence of various major taxa in collections with dytiscids, provide support for Larson and Colbo. It is significant that fish have the lowest co-occurrence (ca 30%) with dytiscids, followed by odonates (ca 38%). These data do not indicate how many samples contained either fish or odonates but not dytiscids, which would even further lower the co-occurrence rates.

Dytiscid beetles and larvae are subject to different predation pressures, with the larvae more vulnerable to predators. Life history theory predicts that selection acts to reduce the duration of the stage with the higher mortality rate (Wilbur 1980). This appears applicable to dytiscids, for in general, the larval stage is relatively short compared with the life span of adults. For example, even for the many species the life histories of which are not known, adults can be collected throughout much of the year while larvae appear to occur for a shorter and more specific period. This pattern of life history probably has more to do with habitat seasonality than predation (Larson 1985), but also could be reinforced by predation pressures.

A QUANTITATIVE ESTIMATE OF PREDATION

Diverse groups of insects, such as dytiscids and odonates, can be expected to interact in a variety of ways depending upon the taxa and habitats involved. A recent study on insect communities in a series of ombrotrophic bog pools (Larson and House 1990) provided an opportunity for a quantitative assessment of odonate predation on dytiscids in this habitat. The primary objective of the study was to determine abundance and distribution patterns of macroscopic animals within the pool system, and to interpret these in relation to habitat features and interaction patterns between taxa. For the purposes of this discussion, only the patterns observed for odonates and dytiscids will be discussed. Full details of the habitat and arthropod community structure are published elsewhere (Larson & House 1990).

The study was carried out on an ombrotrophic, domed bog located on the Avalon Peninsula 20 km south of St. John's, Newfoundland. The bog was treeless with the principal vegetation being sphagnum mosses, ericaceous shrubs, rushes and sedges. The bog contained in excess of 200 pools ranging in surface area from less than one to greater than 500 m^2. The pools were divided into four size classes based on their surface area, namely: Class A - > 100 m^2; B - 10 to 100 m^2: C - 1 to 10 m^2; and D < 1 m^2). In spite of the size differences, the pools were similar in water quality and form. Pool depth was positively correlated with surface area. Water level fluctuation was similar across all pools which meant that some of the smaller, shallower pools lost visible water during dry periods.

Pools were sampled by collecting all insects within a quadrat of 1 m^2. The entire area of pools less than 1 m^2 was sampled and the resulting counts transformed to numbers per m^2. Regardless of pool size, one edge of the quadrat was always formed by the pool bank so that edge effects were standardized across

Table 3. List of taxa collected and their density (number m^{-2}), (standard error) and prevalence (%) in pools of the four size classes. The numbers for Dytiscidae include pooled larvae and adults. * - mean density less than 0.1 m^{-2}.

	POOL SIZE CLASS			
	D	C	B	A
surface area, m^2	< 1	1 - 10	10 - 100	> 100
# samples	14	28	54	13
ODONATA				
Coenagrionidae				
Enallagma	*	*	24.3 (5.6)	86.1 (25.0)
cyathigerum (Ch.)	7	4	89	100
Lestidae				
Lestes	0	*	1.3 (0.5)	1.0 (0.6)
disjunctus Selys	0	4	29	23
Aeshnidae				
Aeshna	0	0	5.0 (1.1)	1.7 (0.5)
eremita Scudder	0	0	77	69
A. juncea L.	0	*	*	0
	0	4	2	0
A. sitchensis	2.9 (1.2)	2.1 (0.5)	*	*
Hagen	57	56	4	8
A. subarctica	0	0.2 (0.1)	1.9 (0.5)	2.3 (1.0)
Walker	0	15	68	77
A. umbrosa	0	*	*	0
Walker	0	4	4	0
Corduliidae				
Cordulia	0	0.2 (0.1)	11.2 (2.0)	11.4 (3.9)
shurtleffi Scudder	0	11	84	84
Somatochlora	0	0	0.2 (0.1)	0.2 (0.1)
cingulata (Selys)	0	0	14	15
S. forcipata	0	*	0	0
Scudder	0	4	0	0
S. septentrionalis	0.1 (0.1)	0.5 (0.2)	8.8 (2.0)	4.8 (1.8)
Hagen	7	26	77	77
Libellulidae				
Leucorrhinia	1.9 (1.4)	8.9 (3.0)	38.9 (7.3)	13.6 (4.2)
hudsonica Selys	29	37	100	92
Libellula	6.6 (4.4)	7.0 (1.7)	0.5 (0.2)	0.5 (0.4)
quadrimaculata L	43	63	25	15
Total Odonata	11.5 (6.1)	19.2 (3.8)	92.2 (11.6)	121.7 (30.2)

(continued on next page)

Table 3 (continued)

	POOL SIZE CLASS			
	D	C	B	A
COLEOPTERA				
Dytiscidae				
Acilius	0	*	*	0
semisulcatus Aube	0	4	2	0
Agabus	0	0.1 (0.1)	0.1 (0.1)	0
anthracinus Mann	0	4	5	0
A. confinis	0.2 (0.1)	0	0	0
Gyllenhal	15	0	0	0
A. inscriptus	1.6 (0.7)	0.8 (0.4)	0	0
Crotch	46	7	0	0
A. leptapsis	0.7 (0.4)	0	0	0
LeConte	14	0	0	0
Dytiscus	0	0	*	0.2 (0.2)
alaskanus B.-B.	0	0	2	15
Graphoderus	0	0	0	*
liberus Say	0	0	0	8
G. perplexus	0	0	0.2 (0.1)	0.6 (0.5)
Sharp	0	0	13	23
Hydroporus	1.0 (0.6)	5.2 (4.0)	0.1 (0.1)	0.1 (0.1)
badiellus Fall	31	25	7	8
H. brevicornis	4.4 (2.3)	2.1 (0.9)	0	0
Fall	50	33	0	0
H. morio	1.2 (0.6)	0	0	0
Aubé	21	0	0	0
H. notabilis	0.1 (0.1)	0	0	0
LeConte	7	0	0	0
H. obscurus	8.2 (2.1)	4.3 (1.5)	0.4 (0.2)	0.1 (0.1)
Schaum	79	52	21	15
H. paugus	1.8 (0.6)	0.3 (0.1)	0	0
Fall	57	22	0	0
H. rectus	0.1 (0.1)	0	0	0
Fall	7	0	0	0
H. signatus	3.5 (2.2)	2.6 (1.2)	0	0
Mannerheim	21	33	0	0
H. tristis	0.5 (0.3)	1.5 (0.6)	0	0
Paykull	14	37	0	0
Ilybius discedens	1.7 (0.5)	1.1 (0.4)	*	0.1 (0.1)
Sharp	57	37	4	15
I. pleuriticus	0	0	3.7 (0.6)	0.5 (0.3)
LeConte	0	0	64	23
Rhantus	0.1 (0.1)	0	0	0
binotatus Say	7	0	0	0
R. wallisi	0.1 (0.1)	0.4 (0.1)	0.2 (0.1)	0.9 (0.5)
Hatch	7	33	13	46
Total Dytiscidae	25.2 (4.6)	18.4 (5.9)	4.7 (0.6)	2.5 (0.9)

Table 4. Odonate density and predation rates on dytiscids in bog pools

	POOL SIZE, M^2			
	<1	1 - 10	10-100	> 100
A. Odonate population density	11.5	19.2	92.2	121.7
B. Odonate predation rate (density (A) X prevalence of dytiscids in gut) dytiscids consumed/day/m^2	0.59	0.54	1.99	4.11
C. Beetle density	32.8	23.8	5.1	3.3
D. Prey clearance rate (days) C/B	55.5	44.1	2.5	0.8

samples. Sampling was conducted by repeatedly sweeping the quadrat with an aquatic net of 1 mm mesh, then visually picking insects from the sweepings. A quadrat was repeatedly swept until no further specimens were found.

A list of the species of Odonata and Dytiscidae and the density of each in pools of the four size classes is presented in Table 3. Beetle and odonate densities (logten (number $m^{-2}+1$)) were inversely correlated ($r = -0.39$, $p < .01$). Beetle populations were densest in the smallest pools and decreased rapidly with increasing pool size, while odonate populations were more than ten times as dense in the A pools as in the D pools.

Size of adult beetles was positively correlated to pool size ($r = 0.56$, $p < .01$). The correlation was calculated between mean adult size of each species represented in each pool and pool surface area. Thus, the occurrence of a species in a pool was treated as a single observation. If the size of each individual and the pool size in which it was found were correlated, the relationship would be even stronger. Generally, small species occurred in small pools: however, *Hydroporus badiellus* Fall and *H. obscurus* Schaum also occurred in low frequencies in the A and B pools. This was a result of including a length of bank in each sample, because these species occur in the moss at the water's edge. If the samples were taken farther from the bank so as to exclude these peripheral species, the pool size - beetle size correlation would strengthen.

To determine if the odonates actually were preying upon dytiscids, gut contents of 500 odonate larvae, representing the five most abundant species collected from pools of all sizes from May through October, were examined. Some specimens of all species were found with dytiscid larvae in their guts and the *Aeshna* species also contained hydrophilid and hydroporine adults. Prevalence of dytiscid remains in the gut contents of these species ranged from 0.7 % in *Leucorrhinia hudsonica* Selys to 15% in *Aeshna sitchensis* Hagen. If prevalence of dytiscid remains in the gut of each species of dragonfly is multiplied by the density of the respective species in pools of each size class and these values then summed, an estimate of the predation rate of dragonflies on dytiscids can be obtained (Table 4). If it is assumed that residence time of material in a dragonfly gut is one day (indicated by Pritchard 1964) then this figure represents the daily predation rate of dragonflies on dytiscids averaged over the ice-free season - the period over which odonate larvae were collected for gut content analysis. Dividing the mean density of dytiscids by this predation rate gives an estimate of the length of time it would take for odonates to eliminate the dytiscid population from each habitat type (Prey clearance rate, Table 4). This is highly simplified with many possible sources of error such as the fact that "dytiscids" includes both adults and larvae and that adults may not in fact be at risk to predation. Nevertheless, the figures still indicate that odonates exert a powerful predation pressure on dytiscids and that in the presence of a dense odonate population, low dytiscid numbers may be explained by predation.

In this study, the most abundant dytiscid in the larger pools was *Ilybius pleuriticus* LeConte (Table 3). This is the largest North American *Ilybius* (Larson 1987), and occurs in deeper and more open water habitats than other members of the genus. Its larvae crawl around on the substrates, generally in habitats with dense odonate populations. Why are they not annihilated by dragonflies? *I. pleuriticus* larvae are distinctive among known North American *Ilybius* larvae (unpublished data) in that they have a very bold pattern of longitudinal stripes extended the length of the dorsal surface of the body. Perhaps this striped pattern makes the larvae more difficult for an odonate larva to hit with a visually aimed labial strike. By itself, this explanation is not compelling. However, within the same habitat are two species of *Aeshna, A. eremita* Scudder and *A. subarctica* Walker. *Aeshna* larvae probably behave more like dytiscid larvae than do other dragonfly larvae, *i.e.* they are rather active and move around considerably. As cannibalism occurs amongst odonate larvae, the small Aeshna larvae should be at risk to odonate predators due to their movement. Larvae of both *Aeshna* species are very boldly coloured: *A. eremita* larvae are black with the middle third of the body pale yellow; *A. subarctica* larvae are longitudinally striped, similar to that of larval *I. pleuriticus*. The color pattern of both *Aeshna* species is very disruptive to the human eye. These markings are strongest on the smallest larvae, tending to obliterate in larvae of 10 to 15 mm length, with the larger specimens more uniformly dark.

The most probable function of color pattern is to provide protection from visually hunting predators. If the predators were vertebrates, it would seem most likely that the predation pressure would become more intense as larvae became larger thus large larvae should possess protective coloration. But it is the small larvae that have the disruptive color pattern and this pattern disappears at about the size that larvae become large enough to escape odonate predation. Thus it is probable that strikingly disruptive color patterns are a defense against odonate predation.

EXPERIMENTS AND CAVEATS

If dragonflies are important predators on dytiscids, removal of odonates from a habitat should result in an increase in beetle density and also perhaps in a broadening of range of habitat occupied by at least the larvae. Such an experiment has not been conducted specifically to test the impact of odonates on beetles. However, Benke (1978) did a removal experiment in which odonate populations were reduced within pond enclosures and he noted an increase in prey abundance and survivorship of remaining odonates.

Laboratory rearing confirms the finding from gut content analysis: odonates prey on smaller dytiscid larvae and strike at adults although they may have difficulty in handling them (Pritchard 1964, Griffiths 1973). However, laboratory studies should be done to determine patterns of interaction occurring across a range of sizes of dytiscids and odonate larvae. Is there a size of dytiscid adult or larvae which is too large or active for particular odonate species to capture or handle? Are the tables turned by large dytiscids? Large larvae of species of *Dytiscus* and *Cybister* can prey upon large odonate larvae. For example, third instar larvae of *D. alaskanus* Balfour-Browne successfully attacked *Aeshna* larvae that had been thrown back into a pond after being collected in a dip net (B.C., Cassiar Road km 723, July 18, 1987). R. Trottier (pers. comm., 1987), studying the large odonatid, *Anax junius* Drury, in southern Ontario thought that *Dytiscus* larvae were preying upon the dragonfly larvae. Compared to dytiscids, odonates hatch at a small size and grow slowly through a large number of instars. Probably these small odonates are suitable prey for many dytiscids.

The extent of dytiscid larval predation on odonates will be difficult to determine. Because dytiscid larvae feed on prey fluids, predation could be determined only through direct observation or by serological analysis of gut contents. In any event, high predation rates on odonate larvae may not have a major effect on trophic patterns. There is evidence that many habitats are overstocked with dragonfly larvae such that cannibalism and competition are severe and limiting. In such situations, mutual predation between dytiscids and odonates probably would favour the odonates for the lower starting populations of dytiscids put them at a disadvantage. Based on consideration of predation characteristics (Table 1), it is predicted that under conditions of low prey density odonates will out-compete dytiscids. This could be tested in the lab.

Although it has not been proven that odonate larvae have a major impact on dytiscid distribution and abundance, there is much evidence to suggest this is so. Odonate predation must be less important than physical suitability and trophic opportunities as factors structuring lentic dytiscid communities. However, predation and competition pressures within shallow lentic habitats are significant factors shaping resident communities and dytiscids can not be immune to these forces. Many of their behaviours and adaptations are likely to be responses to such biotic pressures.

ACKNOWLEDGEMENTS

I thank Peter Genge, Nancy House and Marie McCarthy for their assistance in field sampling and odonate gut content analysis, and Margaret Larson and Dr. J. Pickavance for reviewing the manuscript. This study was supported by an operating grant from the Natural Sciences and Engineering Research Council of Canada and by the Canadian Forestry Service.

REFERENCES CITED

Ball, R. C. and D. W. Hayne. 1952. Effects of the removal of the fish population on the fish-food organisms of a lake. Ecology, 33: 41 - 48.

Beatty, L. D. and F. F. Hooper. 1958. Benthic associations of Sugarloaf Lake. Papers of the Michigan Academy of Sciences, 43: 23 - 106.

Benke, A. C. 1976. Dragonfly production and prey turnover. Ecology, 57: 915 - 927.

Benke, A. C. 1978. Interactions among coexisting predators - a field experiment with dragonfly larvae. Journal of Animal Ecology, 47: 335 - 350.

Cuppen, J. G. M. 1986. The influence of acidity and chlorinity on the distribution of *Hydroporus* species (Coleoptera, Dytiscidae) in the Netherlands. Entomologica Basiliensia 11: 327 - 336.

Dettner, K. 1985. Ecological and phylogenetic significance of defensive compounds from pygidial glands of Hydradephaga (Coleoptera). Proceedings of the Academy of Natural Sciences of Philadelphia, 137: 156 - 171.

Fischer, Z. 1961. Some data on the Odonata larvae of small pools. Internationale Revue des Gesamten Hydrobiologie und Hydrographie, 46: 269 - 275.

Flechtner, G. 1986. Association analysis of water beetle communities (Coleoptera: Dytiscidae et Haliplidae). Entomologica Basiliensia 11: 297 - 308.

Galewski, K. 1971. A study on the morphobiotic adaptations of European species of the Dytiscidae (Coleoptera). Polskie Pismo Entomologiczne, 41: 488 - 702.

Gilinsky, E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. Ecology 65: 455 - 468.

Griffiths, D. 1973. The food of animals in an acid moorland pond. Journal of Animal Ecology, 42: 285 - 293.

Johnson, D. M., P. H. Crowley, R. E. Bohanan, C. N. Watson, and T. H. Martin. 1985. Competition among larval dragonflies: a field experiment. Ecology, 66: 119 - 128.

Larson, D. J. 1985. Structure in temperate predacious diving beetle communities (Coleoptera: Dytiscidae). Holarctic Ecology 8: 18 - 32.

Larson, D. J. 1987. Revision of North American species of *Ilybius* Erichson (Coleoptera: Dytiscidae). with systematic notes on Palaearctic species. Journal of the New York Entomological Society, 95: 341 - 413.

Larson, D. J. and M. Colbo. 1983. The aquatic insects: biogeographic considerations. pp. 593 - 677 in South, G. R. (Ed.), Biogeography and Ecology of the Island of Newfoundland. Monographiae Biologicae 48. Junk, The Hague.

Larson, D. J. and N. House. 1990. Insect communities of Newfoundland bog pools with special reference to Odonata. Canadian Entomologist (in press).

Macan, T. T. 1964. The Odonata of a moorland fishpond. Internationale Revue der gesamten Hydrobiologie und Hydrographie, 49: 325 - 360.

Morin, P. J. 1984. The impact of fish exclusion on the abundance and species composition of larval odonates: results of a short-term experiment in a North Carolina farm pond. Ecology, 65: 53 - 60.

Nilsson, A. 1984. Species richness and succession of aquatic beetles in some kettlehole ponds in northern Sweden. Holarctic Ecology, 7: 149 - 156.

Nilsson, A. 1986. Community structure in the Dytiscidae (Coleoptera) of a northern Swedish seasonal pond. Annales Zoologica Fennici, 23: 39 - 47.

Nilsson, A. 1988. Larval consumption rates, interspecific predation, and local guild composition of egg-overwintering *Agabus* (Coleoptera, Dytiscidae) species in vernal ponds. Oecologia, 76: 131 - 137.

Nilsson, B.-I. 1981. Susceptibility of some Odonata larvae to fish predation. Verhandeln Internationale Verein Limnology, 21: 1612 - 1615.

Pritchard, G. 1964. The prey of dragonfly larvae (Odonata; Anisoptera) in ponds in northern Alberta. Canadian Journal of Zoology, 42: 785 - 800.

Ranta, E. 1985. Communities of water-beetles in different kinds of waters in Finland. Transactions of the Philadelphia Academy of Science, 137: 33 - 45.

Stenson, J. A. E. 1978. Differential predation by fish in two species of *Chaoborus* (Diptera, Chaoboridae). Oikos, 31: 98 - 101.

Thorp, J. H. and M. L. Cothran, 1984. Regulation of freshwater community structure at multiple intensities of dragonfly predation. Ecology, 65: 1546 - 1555.

Wilbur, H. M. 1980. Complex life cycles. Annual Review of Ecology and Systematics, 11: 67 - 93.

Wilson, C. B. 1923. Water beetles in relation to pondfish culture, with life histories of those found in fishponds at Fairport, Iowa. Bulletin of the United States Bureau of Fisheries, Washington, 39: 231 - 345.

Wissinger, S. A. 1988. Life history and size structure of larval dragonfly populations. Journal of the North American Benthological Society 7: 13 - 28.

Young, F. N. 1960. The colors of desert water beetles - environmental effect or protective coloration? Annals of the Entomological Society of America, 53: 422 - 425.

PHYLOGENETIC ANALYSIS OF THE FAMILY GYRINIDAE (COLEOPTERA) BASED ON MESO- AND METATHORACIC CHARACTERS

ROLF G. BEUTEL
Institut für Biologie II (Zool.)
RWTH Aachen
D-5100 Aachen
West Germany

Quaestiones Entomologicae
26: 163–191 1990

ABSTRACT

Thirty six characters of the meso- and metathorax of adults of Spanglerogyrus albiventris *Folkerts and other members of Gyrinidae were examined and analyzed phylogenetically. The acquired data suggest that Spanglerogyrinae are the sister-group to the remainder of Gyrinidae; oar-like tibial processes, feather-like swimming hairs, and the presence of one tibial spur only are autapomorphies of* Spanglerogyrus. *Members of Gyrininae are characterized by a large number of synapomorphic character states. Some of these are: anepisternal-elytral opening, excavations for the prolegs in repose, paddle-like middle- and hind legs, swimming lamellae, metanotum extended laterally, metapostnotum inflected below the scutellum, metasternal transverse-ridge completely reduced, metafurca arising from the fused medial metacoxal walls, lateral metafurcal projections reduced, medial metacoxal walls fused, loss of several flight muscles, loss of Mm. furca-coxalis anterior and lateralis (M 81 and M 82), presence of M. noto-trochanteralis (M 84). The absence of M. sterno-episternalis (M 72) is considered as a possible synapomorphy of* Gyrinus *and* Aulonogyrus *(+* Metagyrinus, Heterogyrus *?). Orectochilini and the enhydrine genera seem to form a well-founded monophyletic unit. The following characters are interpreted as synapomorphies of this assemblage: anterior and posterior walls of tibiae and proximal tarsomeres connected by cuticular columnae, markedly developed elytral glossula, median metanotal area only half as broad as lateral parts, metanotum without membranous area. The modified shape and position of metatarsomeres 4 + 5 is considered as a synapomorphy of the genera* Dineutus, Porrorhynchus, Macrogyrus, Andogyrus *and Orectochilini. Consequently, Enhydrini are not monophyletic. The concealed mesoscutellar lobe in members of* Dineutus *and* Porrorhynchus *is a possible synapomorphy of both genera. The modified shape and position of mesotarsomeres 4 + 5 is considered as a synapomorphy of a monophyletic group comprising* Macrogyrus, Andogyrus *and Orectochilini. The attachment of the anterior metacoxal wall to the hind margin of the ventral sclerite of the metathorax is another apomorphic character state that suggests a close relationship between Orectochilini and* Andogyrus *(+* Macrogyrus *?). Orectochilini are characterized by distinctive synapomorphies, some of which are: opening between elytra and mesothoracic anepisternum narrow, anterior median ridge of the mesothoracic preepisternum present, lateral internal process of the mesocoxae trilobed, tendons of M. noto-coxalis (M 40) and M. coxa-subalaris (M 43) arise from the lateral internal process of the mesocoxa, basalar disc absent, loss of further flight muscles. A sister group relationship between* Orectogyrus *and* Orectochilus *is indicated by two apomorphic character states: anterior walls of mesocoxae* *attached to the ventral sclerite of the mesothorax, lateral internal process of the mesocoxae fused with the anepisternum. Whether* Heterogyrus *is more closely related to the genera* Gyrinus, Metagyrinus *and* Aulonogyrus, *or to the enhydrine-orectochiline lineage remains open to question.*

Zusammenfassung

Sechs und dreizig Merkmale des Meso- und Metathorax von adulten Vertretern der Gyrinidae, insbesondere von Spanglerogyrus albiventris *Folkerts wurden untersucht und phylogenetisch ausgewertet. Die vorliegenden Daten legen den Schluß nahe, daß die Spanglerogyrinae den übrigen Gyrinidae als Schwestergruppe gegenüberstehen. Ruderartige Tibialfortsätze, gefiederte Schwimmhaare, und das Vorhandensein von nur einem Tibialsporn sind autapomorphe Merkmale von* Spanglerogyrus. *Die Gyrininae sind durch eine größere Anzahl von Synapomorphien gekennzeichnet. Einige dieser Merkmale werden im Folgenden aufgeführt: Öffnung zwischen dem mesothorakalen Anepisternum und der Elytrenbasis, Vertiefungen zum Anlegen der Vorderbeine in Ruhestellung, paddelartige Mittel- und Hinterbeine, Schwimmblättchen, Metanotum lateral verbreitert, Metapostnotum unter das Scutellum eingeschlagen, metasternale Transversalleiste völlig reduziert, Ursprung der Metafurca von den verwachsenen medialen Hinterhüftswänden, seitliche Metafurcalarme reduziert, mediale Hinterhüftswände verwachsen, Reduktion einiger Flugmuskeln, Mm. furca-coxalis anterior und lateralis (M 81 und 82) fehlen, M. furca-trochanteralis (M 84) ist vorhanden. Das Fehlen von M. sterno-episternalis (M 72) wird als mögliche Synapomorphie der Gattungen* Gyrinus *und* Aulonogyrus *(+* Metagyrinus, Heterogyrus*?) angesehen. Die Orectochilini scheinen zusammen mit den Gattungen der Enhydrini eine wohlbegründete monophyletischeEinheit zu bilden. Folgende Merkmale werden als Synapomorphien dieser Gruppierung interpretiert: die vorderen und hinteren Wände der Tibiae und der proximalen Tarsomeren sind durch kutikuläre Verstrebungen fest miteinander verbunden, die Glossula der Elytren ist stark ausgeprägt, das Metanotum ist median nur etwa halb so breit wie lateral, die mediane membranöse Zone fehlt. Die abgewandelte Form und Stellung der Metatarsomeren 4 + 5 wird als Synapomorphie der Gattungen* Dineutus, Porrorhynchus, Macrogyrus, Andogyrus *und der Orectochilini gedeutet. Daraus folgt, daß die Enhydrini nicht monophyletisch sind. Das verdeckte Schildchen des Mesoscutellum ist eine mögliche Synapomorphie der Gattungen* Dineutus *und* Porrorhynchus. *Die abgewandelte Form und Position der Mesotarsomeren 4 + 5 wird als Synapomorphie einer monophyletischen Gruppe gewertet, die die Gattungen* Macrogyrus, Andogyrus, *sowie die Orectochilini umfaßt. Die Verwachsung der vorderen Wand der Metacoxae mit dem Hinterrand des ventralen Sklerit des Metathorax ist ein weiteres apomorphes Merkmal, das eine nähere Verwandtschaft zwischen* Andogyrus *(+* Macrogyrus *?) und den Orectochilini nahelegt. Die Orectochilini sind durch aussagekräftige Synapomorphien gekennzeichnet: die öffnung zwischen dem mesothorakalen Anepisternum und der Elytrenbasis ist verengt, das Praeepisternum des Mesothorax ist mit einer anteromedianen Leiste versehen, der laterale, innere Fortsatz der Mittelhüfte ist in drei Sektionen aufgefächert, die Sehnen von M. noto-coxalis (M 40) und M. coxa-subalaris (M 43) entspringen am lateralen Fortsatz der Mittelhüfte, die Basalarscheibe fehlt, weitere Flugmuskeln sind reduziert. Ein Schwestergruppenverhältnis zwischen* Orectochilus *und* Orectogyrus *wird durch zwei apomorphe Merkmale nahegelegt: die vordere Mittelhüftwände sind mit dem ventralen Sklerit des Mesothorax verwachsen, der lateralen Fortsatzes der Mittelhüfte ist mit dem Anepisternum verwachsen. Ob* Heterogyrus *näher mit den Gattungen* Gyrinus, Aulonogyrus *und* Metagyrinus, *oder näher mit den Gattungen der Enhydrini und Orectochilini verwandt ist bleibt ungeklärt.*

TABLE OF CONTENTS

INTRODUCTION

The purpose of this paper is to reconstruct the evolution of gyrinid meso- and metathoracic structures, and to use the acquired data to analyse the phylogenetic relationships within the family. Special emphasize is placed upon the study of *Spanglerogyrus albiventris* Folkerts, which was described by Folkerts in 1979, and placed in a newly erected subfamily Spanglerogyrinae Folkerts.

An outstanding and comprehensive study of the locomotor organs of Gyrinidae was made by Larsén (1966), and it should be emphasized that Larsén's work was an indispensable prerequisite for this study. However, *Spanglerogyrus*, which is substantially different from other gyrinids in many features (Folkerts, 1979; Steiner & Anderson, 1981; Beutel, in press, in prep.), was not known at that time. Moreover, Larsén's purpose was a comparative study of structure and function, and he did not subject his data to rigorous phylogenetic analysis. Larsén (1966) did not use cladistic methods (Hennig, 1966), and many of his phylogenetic statements remain vague.

Despite the great interest in Gyrinidae over a long period, and many brilliant taxonomic studies (*e.g.*, by Georg Ochs and Per Brinck), a stringent, cladistic analysis of Gyrinidae is lacking. This study proposes to reconstruct the evolutionary history of Gyrinidae through examination and phylogenetic interpretation of meso- and metathoracic characters of adult gyrinids. Emphasis is placed upon determination of the polarity of character states and on functional considerations.

MATERIAL AND METHODS

All specimens of *Spanglerogyrus albiventris* used for this study were collected by R. E. Roughley and R. G. Beutel at a shaded stream near Evergreen (Conecuh County, Alabama). The specimens were fixed in Kahle's fluid and preserved in alcohol. Araldite was used as an embedding medium for microtome sections. The sections were cut with a glass knife at 2-5 μm and stained in methylene blue. Drawings were made with an ocular reticule (stereo microscope) and with the help of SEM micrographs (Cambridge Stereoscan 250 Mk 2).

Representatives of the genera *Gyrinus* L., *Aulonogyrus* Motschulsky, *Orectochilus* Lac., *Orectogyrus* Rég., *Gyretes* Brullé, *Andogyrus* Ochs, *Dineutus* Macleay, *Enhydrus* Laporte were examined for external skeletal structures. Specimens of *Dineutus assimilis* Kirby, *Andogyrus colombicus* Rég., *Gyretes iricolor* Young, *Orectochilus villosus* Müll., *Aulonogyrus coccinus* Klug, and *Gyrinus marginellus* Fall were examined for both external and internal structures. Furthermore representatives of all the remaining adephagan groups, and specimens of *Priacma serrata* LeConte and *Tetraphalerus* (undescribed species) (Cupedidae) were examined.

Out-group comparison is used for the determination of the polarity of character states whenever possible. A flexible and comprehensive out-group, comprising terrestrial and aquatic families of Adephaga, and Cupedidae, was chosen, as recommended by Beutel (in press). The In-group or character-correlation criterion is used for structures of adults of Gyrinidae that either are not present or are radically different in the remaining Adephaga. As strong evidence is given for the monophyly of Gyrininae (*sensu* Folkerts) and a sistergroup relationship

Table I : Distribution of character states among genera of Gyrinidae. See text for explanations of character states.

Genera	Character and Character States[†]																	
	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.
Spanglerogyrus	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
Gyrinus	0	1	1	0	0	0	0	1	0	2*	0	0	1	1	1	1	1	1
Aulonogyrus	0	1	1	0	0	0	0	1	0	2*	0	0	1	1	1	1	1	1
Metagyrinus	0	?	1	?	?	?	?	1	0	2*	0	0	1	?	?	?	?	?
Heterogyrus	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Enhydrus	0	?	1	?	?	?	?	1	0	2*	0	1	1	?	?	?	2	1
Dineutes	1	1	1	0	0	0	1	1	0	2*	0	1	1	2	1	1	2	1
Porrorhynchus	1	?	1	?	?	?	?	1	0	2*	0	1	1	?	?	?	2	1
Macrogyrus	0	?	1	?	?	?	?	1	0	2*	0	1	2	?	?	?	?	?
Andogyrus	0	1	1	0	0	2	0	1	0	2*	0	1	2	2	1	1	2	1
Orectochilus	0	2	1	1	1	3b	1	1	0	2*	0	1	2	2	2	1	2	1
Orectogyrus	0	2	1	1	1	3b	1	1	0	2*	0	1	2	2	2	1	2	1
Gyretes	1*	2	1	1	0	3a	1	1	0	2*	0	1	2	2	2	1	2	1

[†] 0 = plesiomorphic;
1 = apomorphic, step 1;
2 , 3 = apomorphic, steps 2, 3;
3a, 3b = substates of apomorphic character state 3;
1*, 2* = apomorphic character states which have evolved independently from 0 or 1.

(continued on next page)

Table I (continued)

Genera	Character and Character States[†]																	
	19.	20.	21.	22.	23.	24.	25.	26.	27.	28.	29.	30.	31.	32.	33.	34.	35.	36.
Spanglerogyrus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gyrinus	1	0	1	2	1	1	1	2	1	0	1	1	1	1	1	1	0	1
Aulonogyrus	1	0	1	2	1	1	1	2	1	0	1	1	1	1	1	1	0	1
Metagyrinus	?	?	?	2	1	?	?	2	?	?	1	?	?	?	?	?	?	?
Heterogyrus	?	?	?	1	?	?	?	1	?	?	?	?	?	?	?	?	?	?
Enhydrus	1	?	?	1	1	?	?	1	?	?	1	1	?	?	?	?	?	?
Dineutes	1	0	1	1	1	1	1	1	2	0	2	1	1	0	1	1	0	1
Porrorhynchus	1	?	?	1	1	?	?	1	?	0	2	1	?	?	?	?	?	?
Macrogyrus	?	?	?	1	1	?	?	1	?	?	2	1	?	?	?	?	?	?
Andogyrus	1	0	1	1	1	1	1	1	2	1	2	1	1	0	1	1	0	1
Prectochilus	1	1	1	2*	1	1	1	2*	2	2	2	2	2	0	1	1	1	1
Prectogyrus	1	1	1	2*	1	1	1	2*	2	2	2	2	2	0	1	1	1	1
Gyretes	1	1	1	2*	1	1	1	2*	2	2	2	2	2	0	1	1	1	1

[†] 0 = plesiomorphic;
1 = apomorphic, step 1;
2 , 3 = apomorphic, steps 2, 3;
3a, 3b = substates of apomorphic character state 3;
1*, 2* = apomorphic character states which have evolved independently from 0 or 1.

between Gyrininae and *Spanglerogyrus* (Beutel, in press, in prep.), character states that are shared by *Spanglerogyrus* and some members of Gyrininae are most likely primitive, whereas the corresponding character state is derived. *Spanglerogyrus* is used as an out-group for character evaluation within Gyrininae. Missing data for some characters resulted because no specimens of *Heterogyrus*, and no internal structures of members of the genera *Metagyrinus*, *Enhydrus*, *Porrorhynchus*, and *Macrogyrus* were examined. My analysis of these latter taxa is based on examination of dried specimens on loan from the British Museum (Natural History).

Some character states which are hypothesized as synapomorphies of Orectochilini in this study, may be found to be synapomorphies of a monophyletic group comprising Orectochilini and a part of the enhydrine set of genera. There is, however, little chance that future reevaluation of characters based on studies of internal structures of members of the genera listed above will affect the positions of the genera in the cladogram (Fig. 16).

Larsén's (1966) nomenclature is used for the muscles throughout the paper. The characters below are discussed from anterior to posterior on the body. The distribution of characters by taxon are shown in Table 1 and a cladogram of the relationships of the genera is given in Fig. 16.

Plesiomorphic character states are indicated as 0, apomorphic character states as 1, 2, 3 (transformation series). An asterisk designates an hypothesis of an independently derived apomorphic character state.

CHARACTERS

Mesoscutellar lobe of mesothorax (Character 1)

Character state O.— The mesoscutellar lobe is triangular and visible externally. In members of *Spanglerogyrus* (Fig. 1, 2), *Heterogyrus* (Brinck, 1955), *Enhydrus*, *Andogyrus*, *Macrogyrus*, *Orectochilus*, *Orectogyrus*, *Metagyrinus*, *Gyrinus* and *Aulonogyrus* (Hatch, 1926).

Character state 1.— The mesoscutellar lobe is covered by the elytra at rest. In members of *Gyretes* and the enhydrine genera *Porrorhynchus* and *Dineutus* (Hatch, 1926).

Polarity rationale.— An exposed mesoscutellar lobe is characteristic of most adephagan adults and those of Cupedidae. The mesoscutellar lobe is concealed in members of Hydroporinae (Dytiscidae), Noteridae excl. *Phreatodytes* (Uéno, 1957), and Haliplidae.

Analysis.— It appears most plausible to interpret character state 1 as a possible synapomorphy of *Dineutus* and *Porrorhynchus* (char. 1. 1), and as independently derived in members of *Gyretes* (char. 1. 1*). As an exposed mesoscutellar lobe is present in members of *Orectochilus* and *Orectogyrus*, this condition has to be assigned to the groundplan of *Orectochilini*. The monophyly of Orectochilini is demonstrated by various synapomorphous character states in the following. This character should not be overvalued, as a concealed mesoscutellar lobe has evolved several times independently within Adephaga (see polarity rationale).

Opening between anepisternum and elytron of mesothorax (Character 2)

Character state O.— No opening between basal elytral margin and anepisternum. In adults of *Spanglerogyrus* (Fig. 5).

Character state 1.— A conspicuous, fairly wide and triangular opening between basal margin of elytron and anepisternum (Larsén, 1966; Fig. 7). In members of *Gyrinus*, *Aulonogyrus*, *Dineutus* (Larsén, 1966), and *Andogyrus*.

Character state 2.— Opening between basal margin of elytron and anepisternum, narrowed by bulged dorsal parts of anepisternum (Larsén, 1966, Fig. 25). In members of Orectochilini (Larsén, 1966).

Polarity rationale.— Character state 0 is plesiomorphic, as an opening described above is found neither in members of Cupedidae, nor in members of any other adephagan group. Conspicuously bulged dorsal parts of the anepisternum are not found in *Spanglerogyrus*, and are not described for members of any other adephagan group. Therefore it appears plausible to consider character state 2 as derived from character state 1.

Analysis.— The opening between the basal elytral margin and the anepisternum allows compression of air into the subelytral space, as described by Larsén (1966). This uncommon feature is probably correlated with the highly efficient meso- and metathoracic locomotor system. Character state 1 is a derived groundplan feature of Gyrininae (char. 2.1). Character state 2 is a synapomorphy of Orectochilini (char. 2.2).

Excavations for reception of the prolegs in repose (Character 3)

Character state 0.— No excavations for reception of the forelegs in repose. In members of *Spanglerogyrus* (Fig. 5).

Character state 1.— A distinct concavity extended from hind margin of prothorax over lateral part of mesothoracic preepisternum, mesepimeron, metathoracic anepisternum, and elytral epipleuron. In members of *Gyrinus*, *Aulonogyrus*, *Metagyrinus*, in members of the enhydrine genera, and in members of Orectochilini (Hatch, 1927; Larsén, 1966; personal observation).

Polarity rationale.— A concavity for reception of the prolegs in repose as described above is not found in members of Cupedidae or members of other adephagan groups, and is thus plesiomorphic. Thus character state 1 is apomorphic.

Analysis.— These excavations improve the streamlining of the ventral body surface when the prolegs are drawn up against the body. Character state 1 is the result of a complex modification of the ventral body surface and a synapomorphy of Gyrininae (char. 3.1).

Anteromedian ridge of the mesothoracic preepisternum (Character 4)

Character state 0.— No internal median ridge in anterior region of preepisternum. In members of *Spanglerogyrus*, *Gyrinus*, *Aulonogyrus*, *Dineutus*, and *Andogyrus*.

Character state 1.— A high internal ridge, not marked by external suture, in anterior region of the preepisternum. In members of *Orectogyrus* (Larsén, 1966), *Orectochilus*, and *Gyretes* (pers. obs.).

Polarity rationale.— An internal ridge of anterior region of mesothoracic preepisternum is absent from members of Cupedidae (*Priacma serrata*; Baehr, 1975), and from members of other adephagan families. Thus character state 1 is apomorphic.

Analysis.— By means of this ridge the area of attachment of M. sternotrochanteralis (M 51) is considerably enlarged. The ridge is a synapomorphy of Orectochilini (char. 4.1).

Flexibility of the mesocoxae (Character 5)

Character state 0.— Mesocoxal motility restricted to abduction and adduction. In members of *Spanglerogyrus*, *Gyrinus*, *Aulonogyrus*, *Dineutus*, *Andogyrus*, and *Gyretes*.

Character state 1.— Anterior walls of mesocoxae are solidly attached to hind margin of ventral sclerite of mesothorax. In members of *Orectochilus* and *Orectogyrus* (Larsén, 1966).

Polarity rationale.— Immobilized mesocoxae are not known from members of Cupedidae or members of any other adephagan group. Thus character state 1 is apomorphic.

Analysis.— Character state 1 is a synapomorphy of *Orectochilus* and *Orectogyrus* (char. 5.1).

Lateral process of the mesocoxae (Character 6)

Character state 0.— Internal, lateral process as attachment area of lateralmost part of M. coxo-trochanteralis (M 54). The process is slender in its basal section, and is extended distally. In members of *Spanglerogyrus* (Fig. 6), *Gyrinus*, and *Aulonogyrus*.

Character state 1.— The lateral process is short, fairly broad in the basal part and extended distally. In members of *Dineutus*.

Character state 2.— Lateral process of mesocoxae extensive, broad in the basal section, and extended distally. In members of *Andogyrus*.

Character state 3.— Lateral process trilobed, and strongly enlarged. In members of *Orectogyrus* (Larsén, 1966), *Orectochilus*, and *Gyretes* (Fig. 11).

Substate 3 a.—Anterolateral lobe of process not fused with the anepisternum. In members of *Gyretes*.

Substate 3 b.— Anterolateral lobe fused with anepisterum. In members of *Orectogyrus* and *Orectochilus* (Larsén, 1966)

Polarity rationale.— Following the in-group criterion, character state 0 has to be considered as plesiomorphic within Gyrinidae. Character states 1 and 2 represent similar conditions, although the difference in relative size of the process is distinct. It is quite likely that character states 1 and 2 are intermediate stages between character state 0 and character state 3. The latter character state is undoubtedly highly derived. Nothing comparable is known from any member of other adephagan groups. Substate 3 b is derived from 3 a in correlation with the immobilization of the mesocoxae (5.1).

Analysis.— The complex trilobed internal process of the mesocoxae is a synapomorphy of Orectochilini (6.3). Substate 3 b is a possible synapomorphy of *Orectochilus* and *Orectogyrus* (6.3 b). For a phylogenetic interpretation of character states 1 and 2, study of specimens of *Heterogyrus*, *Enhydrus*, *Porrorhynchus*, and *Macrogyrus* is needed.

Tendons of M. noto-coxalis (M 40) and M. coxa-subalaris (M 43) (Character 7)

Character state 0.— Tendons of both muscles arise from lateral region of posterior wall of mesocoxae. In members of *Spanglerogyrus* (Fig. 6), *Gyrinus*, *Aulonogyrus*, *Dineutus* (Larsén, 1966), and *Andogyrus*.

Character state 1.— Tendons of M 40 and M 43 (if this muscle present) arise from median lobe of internal, mesocoxal process. In members of Orectochilini (Fig. 11) (Larsén, 1966; pers. obs.).

Polarity rationale.— A condition similar to character state 1 is not described for any member of other adephagan groups or members of Cupedidae. Consequently, character state 1 is apomorphic.

Analysis.— Character state 1 is interpreted as a synapomorphy of Orectochilini (7.1).

Shape of femur and tibia (Character 8)

Character state 0.— Femora and tibiae not shortened, broadened, and only very slightly flattened. In adults of *Spanglerogyrus* (Fig. 12, 13).

Character state 1.— Femora and tibiae markedly shortened, broadened, and flattened. In members of Gyrininae examined (Bott, 1928; Larsén, 1966; Nachtigall, 1961; pers. obs.).

Polarity rationale.— Nothing similar to the highly specialized, paddle-like legs is found in any other group of Coleoptera. Character state 1 is thus apomorphic.

Analysis.— Character state 1 is a synapomorphy of Gyrininae (8.1).

Insertion of the tarsus (Character 9)

Character state 0.— Mesotarsus inserted at distal end of tibia. In members of Gyrininae.

Character state 1.— Mesotarsus inserted close to base of tibia. Oar-like tibial projection extended almost parallel to tarsus. In adults of *Spanglerogyrus* (Fig. 12, 13).

Polarity rationale.— Character state 1 is apomorphic as a similar condition is not described for members of any other adephagan group or for members of Cupedidae.

Analysis.— Character state 1 is autapomorphic for *Spanglerogyrus* (9.1).

Swimming hairs (Character 10)

Character state 0.— Mesotibiae and mesotarsi with simple, unmodified swimming hairs. Not found among extant members of Gyrinidae.

Character state 1.— Mesotibiae and mesotarsi with ctenoid or feather like swimming-hairs, of stem with two rows of side branches. In members of *Spanglerogyrus* (Fig. 15).

Character state 2.— Mesotibiae and mesotarsi with swimming blades or lamellae. In members of Gyrininae (Bott, 1928; Nachtigall, 1962; Larsén, 1966; pers. observation).

Polarity rationale.— Character states 1 and 2 are apomorphic as nothing similar is known from members of any other adephagan group or from members of Cupedidae. It is very unlikely that one of both character states is derived from the other. Both structures are distinctly different in terms of structure and function. There is good reason to assume that they have evolved independently from simple, unmodified swimming hairs (character state 0).

Analysis.— The swimming blades or lamellae are an important part of the extremely efficient locomotor apparatus of members of Gyrininae, as pointed out by Nachtigall (1961). At the same time character state 2 is a significant synapomorphy of this group. Character state 1 is an autapomorphy of *Spanglerogyrus*.

Tibial spurs (Character 11)

Character state 0.— Two mesotibial spurs. In members of Gyrininae examined.

Character state 1.— Single large mesotibial spur with unusual fir-cone-like surface structure. In members of *Spanglerogyrus* (Fig. 13).

Polarity rationale.— Two mesotibial spurs are present in members of other adephagan families and members of Cupedidae. Consequently, character state 1 is apomorphic.

Analysis.— Character state 1 is autapomorphy of *Spanglerogyrus.*

Anterior and posterior wall of the tibiae and first tarsal segments connected by cuticular columnae (Character 12)

Character state 0.— Anterior and posterior walls of tibiae and first tarsal segments of middle (and hind) legs not connected by cuticular columnae. In members of *Gyrinus*, *Aulonogyrus* (Larsén, 1966), *Metagyrinus*, and *Spanglerogyrus.*

Character state 1.—Anterior and posterior walls of mesotibiae and first mesotarsomeres firmly connected by cuticular columnae. In members of Orectochilini, *Dineutus*, (Larsén, 1966), and remaining enhydrine genera (pers. obs.).

Polarity rationale.— Character state 1 is apomorphic because it is not described for any other member of Adephaga.

Analysis.— The firm connection of the anterior and posterior walls increases the rigidity of tibiae and proximal tarsomeres. Character state 1 is a synapomorphy of a monophyletic unit comprising Orectochilini and the enhydrine genera.

Arrangement and shape of mesotarsomeres (Character 13)

Character state 0.— Mesotarsomeres only very slightly flattened, and arranged in usual manner. In members of *Spanglerogyrus* (Fig. 13).

Character state 1.— Mesotarsomeres extremely flattened. Tarsomeres 1–4 together form a fan shaped structure; tarsomere 1 triangular; tarsomeres 2 and 3 very short, with long lobes; tarsomere 4 long whereas tarsomere 5 very short.; tarsomeres 4 + 5 semilunar in shape (Larsén, 1966); all tarsomeres connected in one plane. In members of *Gyrinus*, *Aulonogyrus*, *Dineutus* (Larsén, 1966), *Enhydrus*, and *Porrhorhynchus* (pers. obs.).

Character state 2.— Mesotarsomeres 1-3 arranged and shaped as above (character state 1); dorsal margin of tarsomeres 4 + 5 turned posteriorly, thus in form of shovel together with proximal tarsomeres; tarsomeres 4 + 5 nearly parallel sided. In members of *Andogyrus*, *Macrogyrus* (pers. obs.), and Orectochilini (Larsén, 1966).

Polarity rationale.— Character state 0 is plesiomorphic because the same condition characterizes members of all remaining adephagan families and those of Cupedidae. Character state 2 is probably derived from 1. This interpretation would be in agreement with other derived features which indicate a closer relationship between the enhydrine genera and Orectochilini. The modified shape and position of tarsomeres 4 + 5 (character state 2) improves the backstroke of the leg according to Larsén (1966). It is quite likely that a more efficient structure has evolved from a less efficient preceding stage (character state 1).

Analysis.— Character state 1 is a derived groundplan feature and a synapomorphy of Gyrininae (13.1). Character state 2 is a synapomorphy of a monophyletic unit comprising *Andogyrus*, *Macrogyrus*, and Orectochilini (13.2). This implies that Enhydrini are not monophyletic.

Elytral glossula (Character 14)

Character state 0.— No elytral glossula. In members of *Spanglerogyrus* (Fig. 8).

Character state 1.— Elytral glossula slightly developed. In members of *Gyrinus*, and *Aulonogyrus* (Larsén, 1966).

Character state 2.— Elytral glossula markedly developed. In members of Orectochilini, *Dineutus* (Larsén, 1966), and *Andogyrus*.

Polarity rationale.— Based on in-group comparison, character state 0 has to be considered as plesiomorphic. From this follows that character state 2 is derived from character state 1.

Analysis.— An elytral glossula, which acts as a locking device, is considered as a derived groundplan feature and synapomorphy of Gyrininae (14.1). The enlarged glossula (character state 2) represents a possible synapomorphy of Orectochilini and the enhydrine genera (14.2).

M. sterno-trochanteralis (M 51) (Character 15)

Character state 0.— M. sterno-trochanteralis (M 51) absent. In members of *Spanglerogyrus* (Fig. 6).

Character state 1.— M. sterno-trochanteralis present and originates from anterior margin of preepisternum. In members of *Gyrinus*, *Aulonogyrus*, *Dineutus* (Larsén, 1966), and *Macrogyrus*.

Character state 2.— M. sterno-trochanteralis present; originates from anterior wall of preepisternum, and from newly acquired median ridge in anterior region of ventral sclerite of mesothorax (see char. 4). In members of Orectochilini (Larsén, 1966; pers. obs.)

Polarity rationale.— M. sterno-trochanteralis (M 51) absent from members of *Priacma serrata* LeConte (Baehr, 1975) and from all members of Coleoptera examined by Larsén (1966) except for Gyrinidae. Therefore its presence is considered as an apomorphic character state. Anteromedian ridge is a derived feature (see char. 4). Consequently, the origin of M 51 from this structure is apomorphic.

Analysis.— M. sterno-trochanteralis has probably evolved by expansion of the origin of M. episterno-trochanteralis (M 48). Both muscles are inserted on the same trochanteral tendon. The efficiency of the hindstroke of the middle-leg is considerably improved by the action of M. sterno-trochanteralis. The newly developed muscle is a derived groundplan feature and a synapomorphy of Gyrininae (15.1). The expansion of the origin of M 51 (character state 2) is a possible synapomorphy of Orectochilini (15.2).

M. furca-coxalis anterior (M 44) (Character 16)

Character state 0.— M. furca-coxalis anterior (M 44) present. In members of *Spanglerogyrus* (Fig. 6).

Character state 1.— M. furca-coxalis anterior absent. In all members of Gyrininae examined by Larsén (1966), and those of *Andogyrus*.

Polarity rationale.— Character state 0 is plesiomorphic, as the muscle is present in all members of Coleoptera examined by Larsén (1966) except for Gyrininae.

Analysis.— The absence of M 44 is a possible synapomorphy of Gyrininae (16.1).

Shape of the metanotum, median membranous area (Character 17)

Character state 0.— Metanotum of normal adephagan shape and construction; medially about as long as laterally, with membranous area in front of alacristae; transverse suture separating attachment area of M. metanoti secundus (M 61) and M. noto-coxalis anterior (M 75) (Larsén, 1966) distinct, and extended to lateral margin of scutum. In members of *Spanglerogyrus* (Fig. 3).

Character state 1.— Metanotum distinctly broader laterally than in median region; membranous area present; transverse suture indistinct and totally obliterated in lateral scutal area. In members of *Gyrinus* and *Aulonogyrus.*

Character state 2.— Metanotum about twice as broad laterally as medially; median membranous area absent; transverse suture indistinct and totally obliterated in lateral scutal area. In members of Orectochilini, *Dineutus* (Larsén, 1966), *Porrorhynchus* (Hatch, 1926; Brinck, 1980), *Enhydrus*, and *Andogyrus* (pers. obs.).

Polarity rationale.— Character state 0 plesiomorphic, as a metanotum of this type is generally found in members of other adephagan groups. Character state 2 is derived from character state 1.

Analysis.— Modifications of metanotum that lead from character 0 to 1, and from character state 1 to 2 are correlated with the profound changes in the flight musculature in members of Gyrininae. Character state 1 is a derived groundplan character state and synapomorphy of Gyrininae (17.1). Character state 2 is a synapomorphy of a monophyletic unit comprising Orectochilini and the enhydrine genera (17.2).

Metapostnotum (Character 18)

Character state 0.— Metapostnotum of normal adephagan size and shape (Larsén, 1966; Beutel, 1986, 1988; Belkaceme, 1986), and visible from above. In members of *Spanglerogyrus* (Fig. 3).

Character state 1.— Median postnotal area inflected below scutellum; actual posterior margin fused to the V-shaped ridge. In the members of Gyrininae examined (Hatch, 1926; Larsén, 1966; pers. obs.).

Polarity rationale.— Character state 1 is apomorphic, as nothing similar is found in members of other adephagan families or members of Cupedidae.

Analysis.— Character state 1 is a synapomorphy of Gyrininae (18.1).

Anterior notal process (Character 19)

Character state 0.— Anterior notal process of normal size and position; clearly visible from above as in other members of Adephaga (Larsén, 1966; Beutel, 1986, 1988; Belkaceme, 1986). In members of *Spanglerogyrus* (Fig. 3).

Character state 1.— Anterior notal process distinctly smaller and hardly visible from above. In all members of Gyrininae examined (Hatch, 1926; Larsén, 1966; pers. obs.).

Polarity rationale.— Character state 0 is plesiomorphic because such a condition is found in most members of other adephagan groups, and in members of Cupedidae.

Analysis.— Character state 1 is a synapomorphy of Gyrininae (19.1).

Basalar disc (Character 20)

Character state 0.— Basalar disc present. In members of *Spanglerogyrus* (Fig. 7), in members of *Gyrinus*, *Aulonogyrus* (considerably smaller; Larsén, 1966), *Dineutus* (Larsén, 1966), and *Andogyrus.*

Character state 1.— Basalar disc absent.; basalare solidly attached to anepisternum and pleural wing process. In members of Orectochilini (Larsén, 1966).

Polarity rationale.— Character state 0 is plesiomorphic because a well developed basalar disc is found in members of most adephagan groups (Larsén, 1966).

Analysis.— Character state 1 is a synapomorphy of Orectochilini, and correlated with loss of coxo-basalar muscle (M 42).

Subalare (Character 21)

Character state 0.— Subalare well developed. In members of *Spanglerogyrus* (Fig. 4).

Character state 1.— Subalare minute. In members of Gyrininae examined (Larsén, 1966; pers. obs.).

Polarity rationale.— Character state 0 is plesiomorphic, because a well developed subalare is found in most members of other adephagan families with developed flight organs (Larsén, 1966; Beutel, 1986, 1988; Belkaceme, 1986).

Analysis.—Reduction in size of subalare is correlated with loss of M. coxa-subalaris (M 79) in members of Gyrininae (Larsén, 1966). Character state 1 is a synapomorphy of Gyrininae (21.1).

Size of the ventral sclerite of the metathorax (Character 22)

Character state 0.— Ventral sclerite of metathorax, largely represented by preepisternum (Matsuda, 1970), only slightly constricted between posteromedial margin of mesocoxae and anterior metacoxal margin; broad in lateral parts. In members of *Spanglerogyrus* (Fig. 5, 12).

Character state 1.— The ventral sclerite is reduced to a narrow strip between the posteromedial margin of mesocoxa and anterior margin of metacoxa, but fairly broad and triangular in lateral parts. In members of *Heterogyrus* (Brinck, 1955), and in members of enhydrine genera (Hatch, 1926; pers. obs.).

Character state 2.— Ventral sclerite reduced to narrow strip except small central area between medial walls of mesocoxae and anterior walls of metacoxae. In members of Orectochilini, *Gyrinus*, *Aulonogyrus*, and *Metagyrinus*.

Polarity rationale.— Character state 0 is closest to characteristic of terrestrial members of Adephaga excl. Trachypachidae, and in members of Cupedidae. Therefore this character state is plesiomorphic, and a groundplan feature of Gyrinidae. Character state 1 is an intermediate stage, and is closer to groundplan than character state 2.

Analysis.— As a gradual modification, the reduction of the ventral sclerite should not be overvalued. Character state 1 is probably a derived groundplan feature and a synapomorphy of Gyrininae (22.1). As a working hypothesis, character state 2 is interpreted as a synapomorphy of Orectochilini (22.2*) on one hand, and as a synapomorphy of a monophyletic unit comprising *Metagyrinus*, *Gyrinus*, and *Aulonogyrus* on the other (22.2). This interpretation is suggested by several characters which indicate a closer relationship between Orectochilini and the enhydrine genera.

Metasternal transverse ridge (Character 23)

Character state 0.— Complete transverse ridge, dividing metathoracic preepisternum from katepisternum (Matsuda, 1970). In members of *Spanglerogyrus* (Fig. 5).

Character state 1.— Transverse ridge completely reduced. In members of Gyrininae examined (Hatch, 1926; Larsén, 1966; pers. obs.).

Polarity rationale.— Character state 0 is plesiomorphic because a complete metasternal transverse ridge is present in members of Cupedidae (Baehr, 1975, pers. obs.), Haliplidae (Belkaceme, 1986), and in the vast majority of terrestrial members of Adephaga.

Analysis.— Character state 1 is a possible synapomorphy of Gyrininae (23.1). This character should not be overvalued, as the metasternal transverse ridge is also reduced in members of Noteridae and Dytiscidae.

Metafurcal origin (Character 24)

Character state 0.— Metafurca origin from katepisternum and attached to medial metacoxal walls by posteriorly directed process. In members of *Spanglerogyrus* (Beutel & Roughley, 1988).

Character state 1.— Metafurca origin from fused medial metacoxal walls. In members of Gyrininae examined (Larsén, 1966; pers. obs.).

Polarity rationale.— Metafurca arises from the katepisternum in terrestrial members of Adephaga, in members of Haliplidae (Beutel & Belkaceme, 1986), and in adults of *P. serrata* (Baehr, 1975). Therefore character state 0 is considered plesiomorphic.

Analysis.— The origin of the metafurca from the fused medial metacoxal walls is considered as a synapomorphy of Gyrininae (24.1). A similar condition is found in members of Noteridae, Amphizoidae, Hygrobiidae, and Dytiscidae (Beutel & Roughley, 1986). This is certainly a result of parallel evolution, and interpreted as a synapomorphy of these adephagan families by Beutel & Roughley (1988).

Lateral projections of the metafurca (Character 25)

Character state 0.— Metafurca with extensive lateral projections. In members of *Spanglerogyrus* (Fig. 7).

Character state 1.— Lateral metafurcal projections absent. In members of Gyrininae examined (Hatch, 1926; Larsén, 1966; pers. obs.).

Polarity rationale.— Well developed lateral metafurcal projections are generally characteristic of members of other adephagan families (Crowson, 1938; 1942). These projections are markedly reduced in members of *Rhysodes* (Crowson, 1938) and *Omoglymmius* (pers. obs.), but well developed in members of *Clinidium* (pers. obs.). The lateral metafurcal projections of members of Cupedidae are hardly developed (Crowson, 1938; Baehr, 1975). It appears more plausible to interpret absence of lateral projections as a secondary condition for Gyrininae, rather than as plesiomorphic. There are significant differences between the gyrinine and the cupedid metafurca in terms of shape and muscle attachment (Larsén, 1966; Baehr, 1975).

Analysis.— As a working hypothesis, character state 1 is considered a synapomorphy of Gyrininae (25.1).

Shape of metacoxae (Character 26)

Character state 0.— Metacoxae triangular, elongate in medial parts, and markedly tapered laterally. In members of *Spanglerogyrus* (Fig. 5, 12, 14).

Character state 1.— Metacoxae trapezoidal; fairly broad laterally, but not expanded anterolaterally. In members of *Heterogyrus* (Brinck, 1955) and the enhydrine genera.

Character state 2.— Metacoxae parallelogram-shaped, and markedly expanded anterolaterally. In members of *Gyrinus*, *Aulonogyrus*, *Metagyrinus*, and Orectochilini.

Polarity rationale.— Out-group comparison suggests that character state 0 is plesiomorphic; metacoxae of a similar type are found in members of Cupedidae (Baehr, 1975; pers. obs.) and in terrestrial members of Adephaga excluding Trachypachidae (Beutel & Belkaceme, 1986). Character state 1 is an intermediate stage between character states 0 and 2.

Analysis.— It is apparent that this character is closely correlated with reduction of ventral sclerite of metathorax (char. 22), and with fusion of metacoxae. Enlargement of metacoxae results in an expansion of attachment areas of coxo-trochanteral muscles. Character state 1 is an apomorphic groundplan feature of Gyrininae (26.1). Character state 2 is a possible synapomorphy of Orectochilini (26.2*) on one hand, and a possible synapomorphy of a monophyletic unit comprising *Gyrinus*, *Aulonogyrus*, and *Metagyrinus* on the other (26.2; see char. 22). Distinctly expanded metacoxae are found also in members of Noteridae, Amphizoidae, Hygrobiidae, and Dytiscidae. Metacoxae of members of Trachypachidae are slightly expanded.

Medial metacoxal walls (Character 27)

Character state 0.— Medial metacoxal walls not fused to each other but only attached to posterior process of metafurca on either side. In members of *Spanglerogyrus* (Beutel & Roughley, 1988).

Character state 1.— Medial metacoxal walls fused along their anterior margin. In members of *Gyrinus* and *Aulonogyrus* (Larsén, 1966).

Character state 2.— Medial metacoxal walls completely fused. In members of Orectochilini, *Dineutus* (Larsén, 1966), and *Macrogyrus* (pers. obs.).

Polarity rationale.— Medial metacoxal walls not fused in members of Cupedidae (Baehr, 1975; pers. obs.), Haliplidae (Beutel & Belkaceme, 1986), and in terrestrial members of Adephaga excluding Trachypachidae. Character state 0 is thus plesiomorphic. Character state 1 is an intermediate stage between character states 0 and 2.

Analysis.— Character state 1 is a derived groundplan feature and a synapomorphy of Gyrininae (27.1). Character state 2 is a possible synapomorphy of Orectochilini and the enhydrine genera (27.2).

Anterior metacoxal wall (Character 28)

Character state 0.— Anterior metacoxal wall and ventral sclerite linked by a membrane. In adults of *Spanglerogyrus*, *Gyrinus*, *Aulonogyrus*, and *Dineutus* (Larsén, 1966; pers. obs.).

Character state 1.— Medial parts of anterior metacoxal walls fused with ventral sclerite. In adults of *Andogyrus*.

Character state 2.— Medial parts of anterior metacoxal walls fused with ventral sclerite. Anterolateral metacoxal wall in form of high ridge, expanded over triangular part of ventral sclerite, and fused to margin of preepisternal pouch (Larsén, 1966). In members of Orectochilini (Larsén, 1966).

Polarity rationale.— Anterior metacoxal wall is not fused to ventral sclerite in members of Cupedidae (Baehr, 1975; pers. obs.), and terrestrial members of Adephaga excluding Trachypachidae. Therefore character state 0 is plesiomorphic. Character state 1 is probably an intermediate stage between character states 0 and 2.

Analysis.— Character state 1 is an apomorphic feature which suggests a closer relationship between *Andogyrus* (*Macrogyrus*?) and Orectochilini. Character state 2 is a synapomorphy of Orectochilini. This character should not be overvalued as fusions of the anterior metacoxal wall and the ventral sclerite are characteristic of members of Trachypachidae, Haliplidae, Noteridae, Amphizoidae, Hygrobiidae, and Dytiscidae.

Position of metatarsomeres 4 + 5 (Character 29)

Character state 0.— Metatarsomeres slightly flattened, arranged in usual manner (see char. 13., mesotarsomeres). In members of *Spanglerogyrus* (Fig. 14).

Character state 1.— Metatarsomeres modified in same manner as mesotarsomeres (character state 13.1). Tarsomeres 4 + 5 of semilunar shape.; all tarsomeres connected in one plane. In adults of *Gyrinus*, *Aulonogyrus*, *Metagyrinus*, and *Enhydrus*.

Character state 2.— Tarsomeres 4 + 5 almost parallel-sided and turned posteriorly, in form of kind of shovel together with proximal tarsomeres. In members of Orectochilini, *Dineutus* (Larsén, 1966), *Porrorhynchus*, *Macrogyrus*, and *Andogyrus*.

Polarity rationale.— see character 13.

Analysis.— Character state 1 is a derived groundplan feature, and a synapomorphy of Gyrininae (29.1). Character state 2 is a possible synapomorphy of a monophyletic unit comprising Orectochilini and the enhydrine genera excluding *Enhydrus* (29.2).

Further characters of the hind-legs are not treated here, as the characters of the middle-legs described above also apply to the hind-legs.

Cubital angle of the hind wing (Character 30)

Character state 0.— No cubital angle. In members of *Spanglerogyrus* (Figs. 9, 10).

Character state 1.— Slightly expressed cubital angle. In members of *Gyrinus*, *Aulonogyrus*, *Enhydrus*, *Porrorhynchus*, *Andogyrus* (Hatch, 1926), and in adults of *Dineutus melhyi* Rég. (Ward, 1979).

Character state 2.— Cubital angle is markedly pronounced. In members of Orectochilini (Hatch, 1926).

Polarity rationale.— No cubital angle is present in members of *Hygrobia*, *Amphizoa*, Dytiscidae, and most members of Carabidae examined by Ward (1979). Therefore character state 0 is plesiomorphic. Character state 1 is an intermediate stage between character states 0 and 2.

Analysis.— Character state 1 is a derived groundplan feature and a possible synapomorphy of Gyrininae (30.1). Character state 2 is a synapomorphy of Orectochilini (30.2).

Flight muscles (Character 31)

Character state 0.— Full complement of flight muscles. Flight muscles were reduced in all specimens of *Spanglerogyrus* examined for this study (Fig. 7). However, flight is reported by Steiner & Anderson (1981), and skeletal structures clearly suggest that a full complement of flight muscles is present in a certain percentage of populations of *Spanglerogyrus*, especially during early imaginal life.

Character state 1.— M. metanoti primus and secundus (M 60 and 61), M. dorsoventralis primus and secundus (M 64 and 65), M. sterno-basalaris (M 73), M. noto-coxalis anterior (M 75), and M. coxa-subalaris (M 79) absent. In members of *Gyrinus*, *Aulonogyrus*, *Dineutus* (Larsén, 1966), and *Andogyrus*.

Character state 2.— M 60, M 61, M 64, M 65, M 73, M 75, M 79, M. noto-basalaris (M 69), and M. coxa-basalaris (M 78) absent. In members of Orectochilini (Larsén, 1966).

Polarity rationale.— Full set of flight muscles is a groundplan feature of Coleoptera and Adephaga (Larsén, 1966; Baehr, 1975). Character state 1 is an intermediate stage between character states 0 and 2.

Analysis.— Loss of flight muscles in members of Gyrininae is not correlated with loss of flying capabilities. Reduced muscles are functionally replaced by M. noto-trochanteralis (M 84). Character state 1 is a derived groundplan feature and synapomorphy of Gyrininae (31.1). Character state 2 is a synapomorphy of Orectochilini (31.2).

M. sterno-episternalis (M 72) (Character 32)

Character state 0.— M. sterno-episternalis (M 72) present. In members of Orectochilini, *Dineutus* (Larsén, 1966), *Andogyrus*, and *Spanglerogyrus*.

Character state 1.— M 72 absent. In members of *Gyrinus* and *Aulonogyrus* (Larsén, 1966).

Polarity rationale.— The presence of M 72 is plesiomorphic. This muscle is found in *Priacma serrata* (Baehr, 1975), and in most members of Coleoptera examined by Larsén (1966).

Analysis.— Character state 1 is a common derived feature of *Gyrinus* and *Aulonogyrus* (32.1). Whether M 72 is also absent from members of *Heterogyrus* and *Metagyrinus* is not known at present. As a muscle reduction which has certainly occurred several times independently within Adephaga (Larsén, 1966), this character should not be overvalued.

M. furca-coxalis anterior (M 81) (Character 33)

Character state 0.— M. furca-coxalis present. In members of *Spanglerogyrus* (Fig. 7).

Character state 1.— M 81 absent. In members of Gyrininae examined (Larsén, 1966; pers. obs.).

Polarity rationale.— Character state 0 is plesiomorphic, as M 81 is present in *Priacma serrata* (Baehr, 1975), and in most members of Coleoptera examined by Larsén (1966).

Analysis.— Loss of M 81 is probably correlated with the origin of the metafurca from the fused medial metacoxal walls. Character state 1 is a synapomorphy of Gyrininae (33.1). The muscle is reduced also in members of Noteridae, Amphizoidae, Hygrobiidae, and Dytiscidae (Beutel & Roughley, 1988). Absence of the muscle in members of these families is interpreted as a result of parallel evolution.

M. furca-coxalis lateralis (M 82) (Character 34)

Character state 0.— M. furca-coxalis lateralis (M 82) present. In adults of *Spanglerogyrus* (Fig. 7).

Character state 1.— M 82 absent. In the members of Gyrininae examined (Larsén, 1966; pers. obs.)

Polarity rationale.— M 82 is present in members of *Priacma serrata* (Baehr, 1975), and most members of Coleoptera examined by Larsén (1966). Character state 1 is apomorphic.

Analysis.— Absence of M 82 from members of Gyrininae is probably correlated with loss of lateral metafurcal projections, and presence of M. noto-trochanteralis (M 84). Character state 1 is a synapomorphy of Gyrininae (34.1). Reduction of M 82 in members of Noteridae (*Notomicrus*, *Phreatodytes* ?) is correlated with fusion of lateral metafurcal projections with posterior metacoxal wall.

M. furca-coxalis posterior (M 83) (Character 35)

Character state 0.— M. furca-coxalis posterior (M 83) present. In members of *Gyrinus*, *Aulonogyrus*, *Dineutus* (Larsén, 1966), *Andogyrus*, and *Spanglerogyrus* (pers. obs.).

Character state 1.— M 83 absent. In members of Orectochilini.

Polarity rationale.— M 83 is present in adults of *Priacma serrata* (Baehr, 1975), and in most members of Coleoptera examined by Larsén (1966). Character state 0 is plesiomorphic.

Analysis.— Character state 1 is a synapomorphy of Orectochilini (35.1). Parallel loss of M 83 has occurred in members of Noteridae, Amphizoidae, Hygrobiidae, and Dytiscidae according to Beutel & Roughley (1988).

M. noto-trochanteralis (Character 36)

Character state 0.— M. noto-trochanteralis (M 84) absent. The muscle is absent from members of *Spanglerogyrus*. A modestly sized M 84 in specimens with well developed flight muscles cannot be fully excluded, but is unlikely, as suggested by skeletal features, such as shape of the metanotum (char. 17), and presence of extensive lateral metafurcal projections (char. 25).

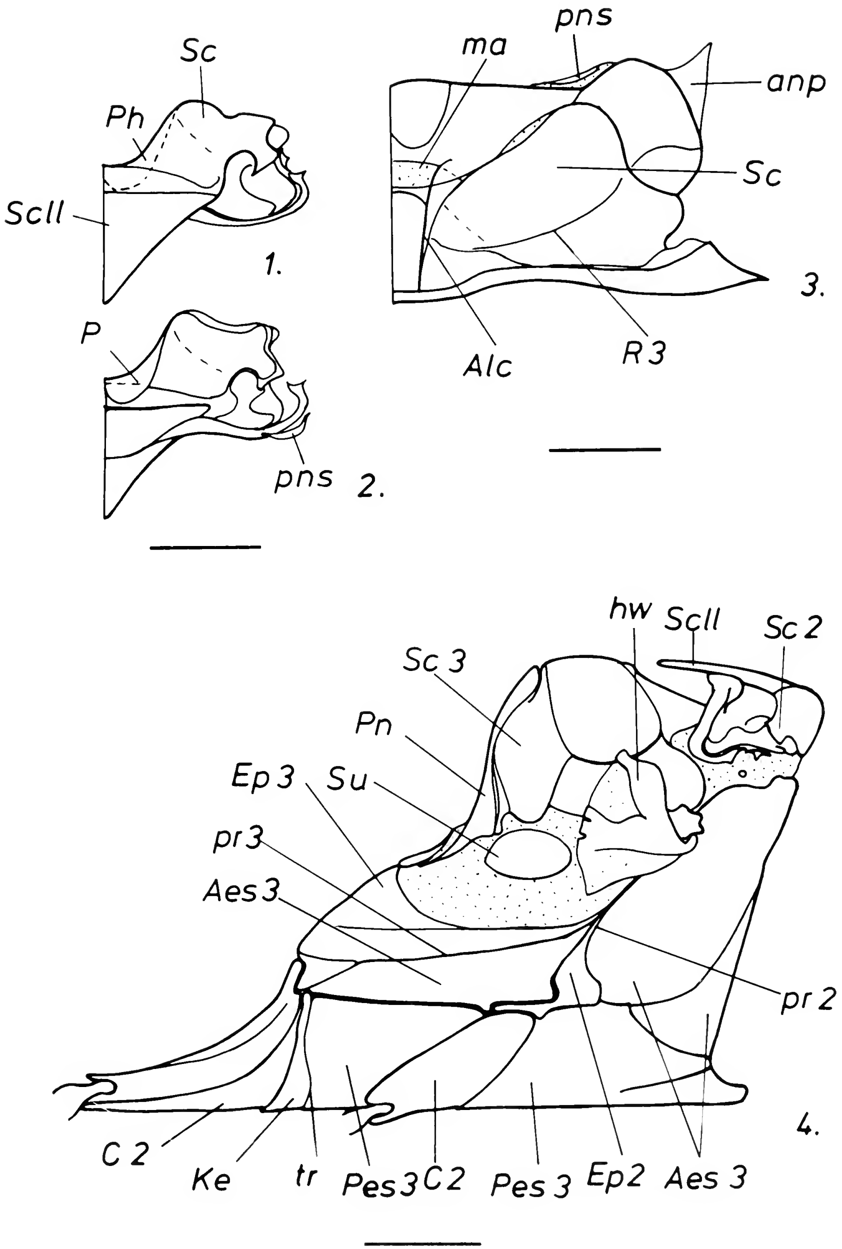
Character state 1.— M 84 is markedly developed. In members of Gyrininae examined.

Polarity rationale.— M 84 is present in adults of *Priacma serrata* (Baehr, 1975), but absent from all members of Coleoptera examined by Larsén (1966) except *Sphaeridium scarabaeoides* L.. The muscle is also absent from members of *Amphizoa lecontei* (Beutel, 1988) and *Noterus laevis* Sturm (Belkaceme, pers. comm.). Determination of the polarity is difficult in this case, if Gyrinidae are considered as the sistergroup of the remaining Adephaga, as suggested by Beutel & Roughley (1988). Skeletal structures, which are obviously correlated with presence of M 84, such as shape of metanotum (char. 17), and complete absence of lateral metafurcal projections (char. 25) are almost certainly apomorphic. Therefore it appears more plausible to interpret presence of M 84 as a secondary condition in case of Gyrininae.

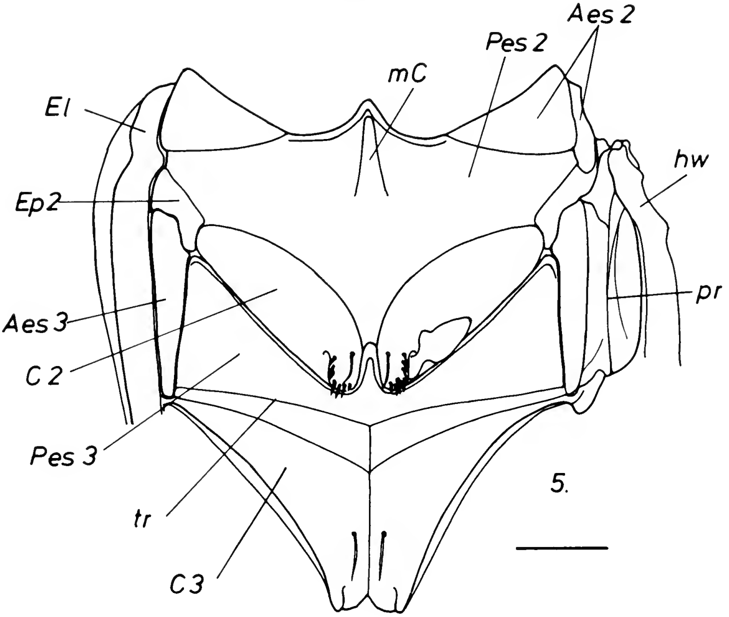
Analysis.— M 84 is the dominant flight muscle in members of Gyrininae. The muscle has replaced functionally several flight muscles which are reduced (char. 31), and is the main depressor muscle of the hind leg when the beetles swim. M 84 is probably derived from lateral parts of M. furca-trochanteralis (M 85) which is extremely weak in members of Gyrininae (Larsén, 1966), but powerful in adults of *Spanglerogyrus* and members of other adephagan families (Larsén, 1966; Beutel, 1986, 1988; Belkaceme 1986). As a working hypothesis, character state 1 is considered as a synapomorphy of Gyrininae (36.1).

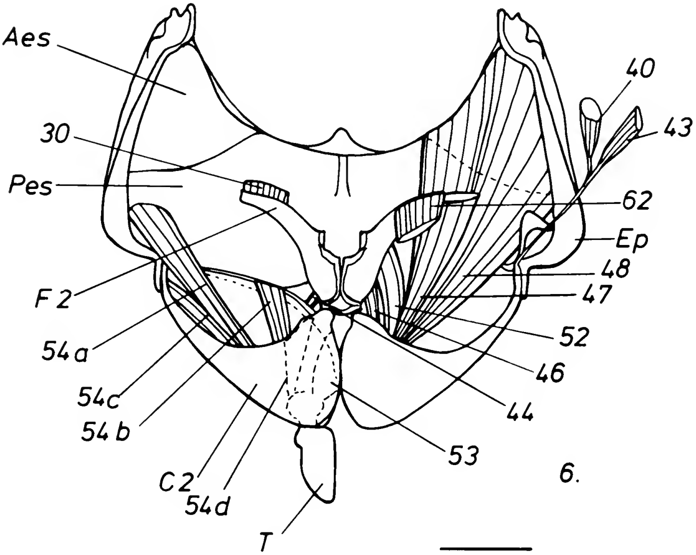
NOTES ABOUT THE EVOLUTIONARY HISTORY OF GYRINIDAE AND PHYLOGENETIC CONCLUSIONS (Table 1, Fig. 16)

The crucial step in evolution of Gyrinidae, after having acquired surface swimming habits with various adaptive characters, *e.g.*, highly specialized antennae, divided eyes, and others, was the splitting event, resulting in the two extant subfamilies Spanglerogyrinae and Gyrininae (Folkerts, 1979). In addition to the many newly acquired characters of the head and prothorax of Gyrininae, such as widely separated eyes, and the loss of the ventral procoxal joint (Beutel, in press, in prep.), dramatic changes in the skeleto-muscular system of the meso- and metathorax must have taken place.

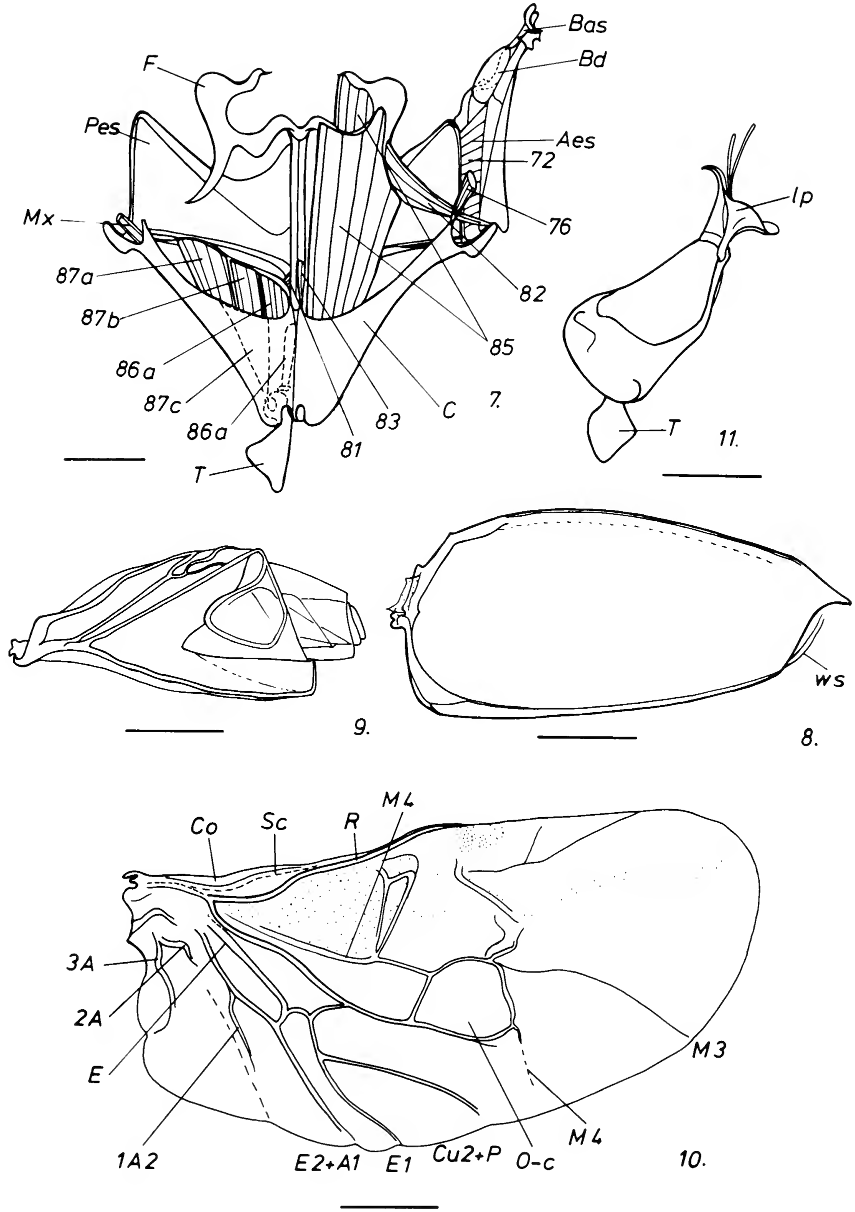


Figs. 1–4. *Spanglerogyrus albiventris* Folkerts. 1, Mesonotum, dorsal view. 2, Mesonotum, ventral view. 3, Metanotum, dorsal view. 4, Meso- and metathorax, lateral view. Legend: Aes, anepisternum; Alc, alacrista; anp, anterior notal process; C, coxa; Ep, epimeron; hw, hind wing; Ke, katepisternum; ma, membranous area; Pes, preepisternum; Ph, phragma; Pn, postnotum; pns, prenotal sclerite; pr, pleural ridge; R 3, posterior scutal ridge; Sc, scutum Scll, scutellar lobe; Su, subalare; tr, transverse ridge. Scale bars = 0.25 mm.

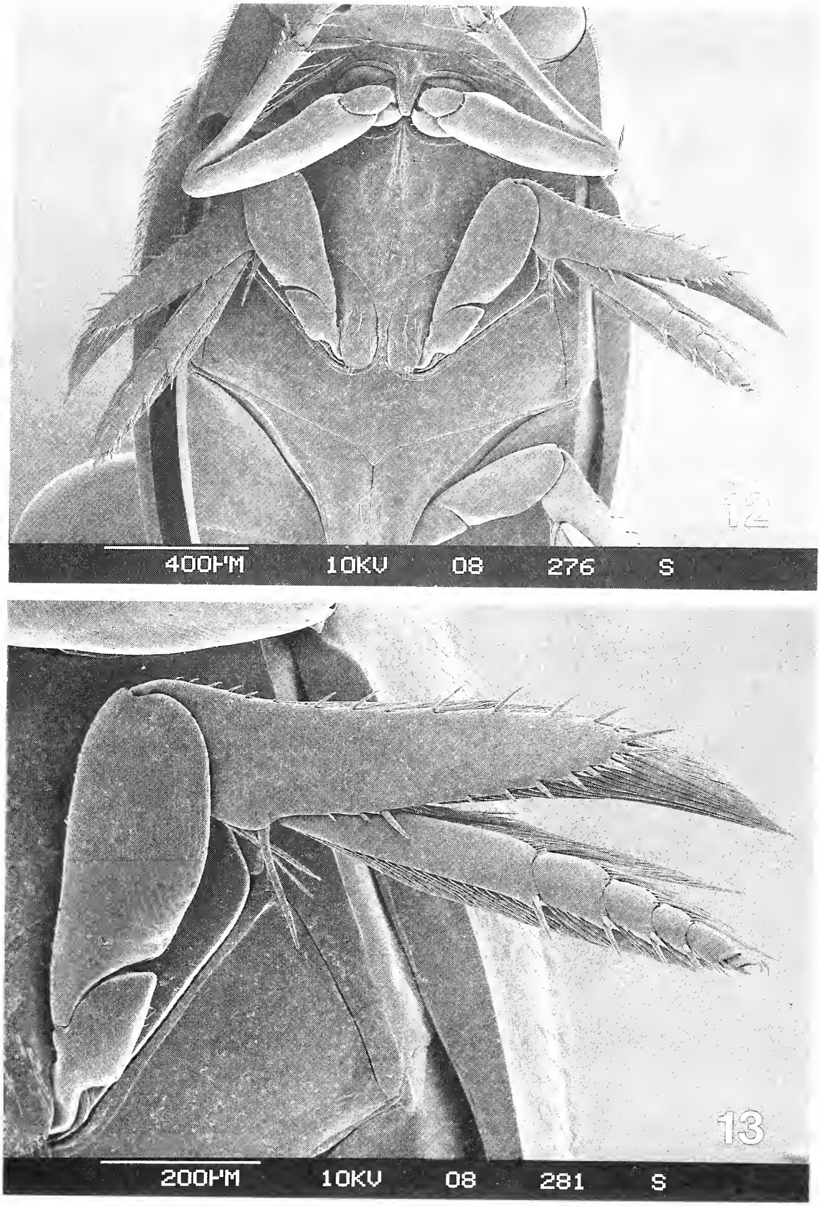




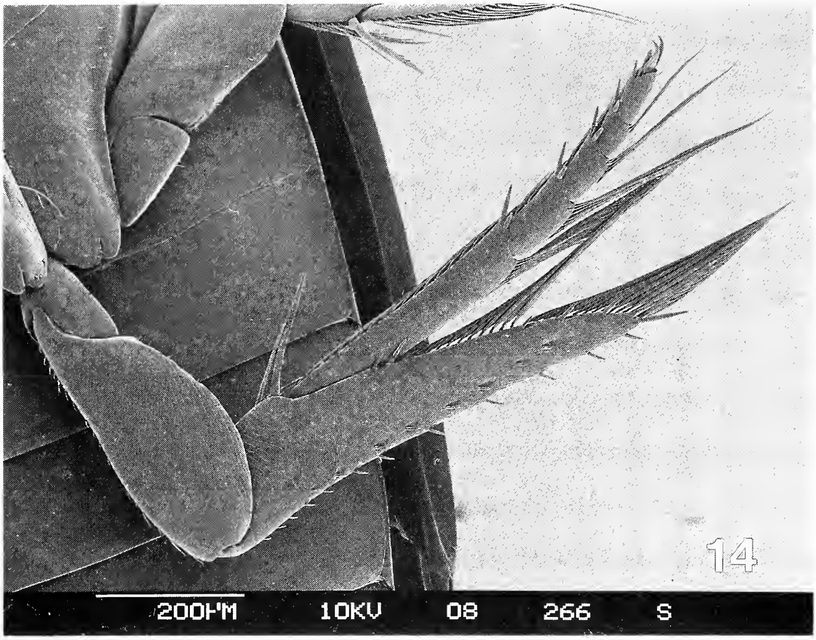
Figs. 5–6. *Spanglerogyrus albiventris* Folkerts. 5, Meso- and metathorax, ventral view, right elytron removed. 6, Mesothorax, dorsal view, notum removed. Legend: Aes, anepisternum; Bas, basalare; Bd, basalar disc; C, coxa; El. elytra; Ep, epimeron; F. furca; hw, hind wing; lp, lateral process of mesocoxa; mC, median carina; Pes, preepisternum; pr, pleural ridge; T, trochanter; tr, transverse ridge. Mesothoracic muscles: 30, M. mesosterni primus; 43, M. coxa-subalaris; 44, M. furca-coxalis anterior; 46, M. furca-coxalis posterior; 47, M. noto-trochanteralis; 48, M. episterno-trochanteralis; 52, M. furca-trochanteralis; 53, M. coxa-trochanteralis medialis; 54, M. coxa-trochanteralis lateralis. Scale bars = 0.25 mm.

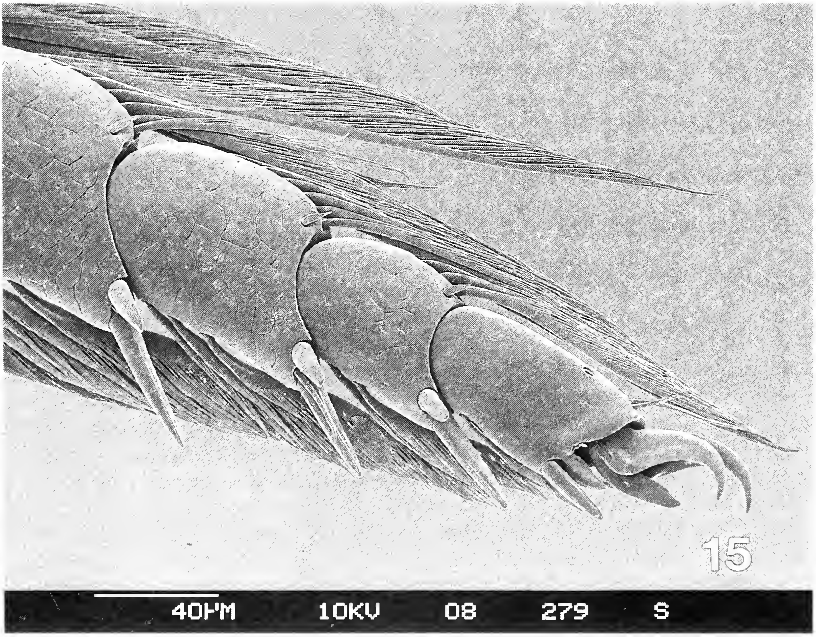


Figs. 7–11. Figs. 7–10. *Spanglerogyrus albiventris* Folkerts. 7, Metathorax, dorsal view, notum removed. 8, Elytron, ventral view. 9, Hind wing, completely folded. 10, Hind wing, unfolded. 11, *Gyretes iricolor* Young, mesocoxa, dorsal view. Legend: A, anal vein; aes, anepisternum; C, coxa; Co, costa; Cu, cubitus; E, empusal vein; Ep, epimeron; F, furca; lp, lateral process of mesocoxa; M, media; O-c, oblongum cell; P, plical vein; Pes, preepisternum; T, trochanter; ws, whip-like setae. Metathoracic muscles: 72, M. sterno-episternalis; 76, M. noto-coxalis posterior; 81, M. furca-coxalis anterior; 82, M. furca-coxalis lateralis; 83, M. furca-coxalis posterior; 85, M. furca-trochanteralis; 86, M. coxa-trochanteralis medialis; 87, M. coxa-trochanteralis lateralis. Scale bars = 0.50 mm.



Figs. 12–13. *Spanglerogyrus albiventris* Folkerts. 12, Meso- and metathorax, ventral view. 13, Middle leg.





Figs. 14-15. *Spanglerogyrus albiventris* Folkerts. 14. Hind leg. 15. Distal mesotarsomeres, swimming hairs.

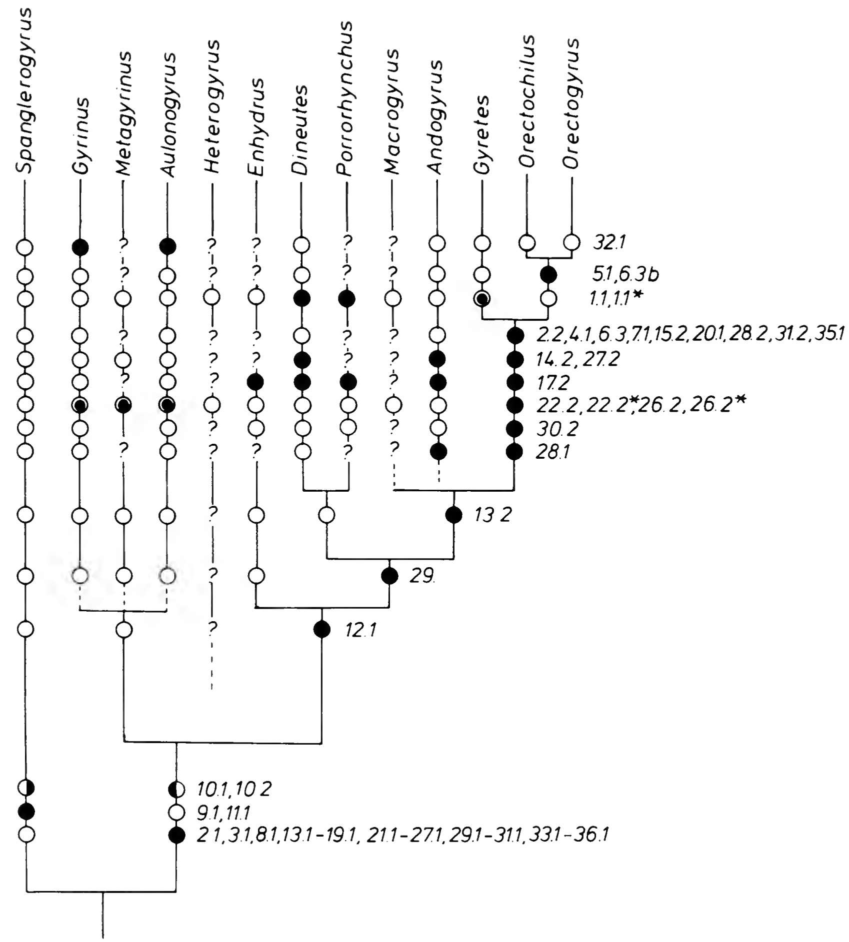


Fig. 16. Reconstructed phylogeny of gyrinid genera. Apomorphic character states are indicated by full circles (char. state 1) or spots within circles (independently acquired; 1*).

The locomotor organs of Gyrininae are the most efficient rowing apparatus of the animal kingdom according to Nachtigall (1961). Frequencies of 50-60 strokes per second result in a maximum speed of 100 cm/s. The total efficiency factor exceeds that of comparable technical machines (Nachtigall, 1961). As described above, the middle and hind legs of members of Gyrininae are broadened, shortened, and markedly flattened. The tarsomeres are arranged in a fan-like manner and are able to rotate posteriorly and to be partly withdrawn into an excavation of the distal end of the tibia. The swimming lamellae contribute 52% of the whole propulsion force, but result in a minimum of counterthrust, when they reflex toward the rigid parts of the legs during the upward stroke (Nachtigall, 1961). The counterthrust during the upward stroke is only about 1/40 of the thrust resulting from the backward stroke (Nachtigall, 1961). The decrease of propulsion force as a result of the comparatively short axis of rotation is certainly overcompensated by the high frequency of strokes, which is correlated with the decrease in length of the middle- and hind-legs.

The middle- and hind-legs of *Spanglerogyrus*, which are almost identical in size and shape (Figs. 13, 14), may be very efficient during the backward stroke due to the arrangement of the tibia and tarsus described above (9.1), and the feather-like swimming hairs (10.1), which increase the area creating the propulsion force even more than in members of Gyrininae. However, the minimization of the counterthrust during the upward stroke is not as efficient as it is in members of Gyrininae. The tarsus as a whole is rigidly constructed, the segments of the legs are only slightly flattened, and the swimming hairs may cause considerable counterdrive when the leg is drawn forward.

The disadvantages of the swimming apparatus of *Spanglerogyrus* may be largely compensated for by the small size of the beetle. This view is supported by investigations of Nachtigall (1960) on the locomotion of dytiscids of different sizes. It is probably not by accident that the only extant representative of Spanglerogyrinae is distinctly smaller than any other member of Gyrinidae. The specialized niche occupied by *Spanglerogyrus*, which is certainly correlated with small size, may exclude direct competition by larger members of the gyrinine genera *Gyrinus*, *Dineutus* and *Gyretes*, which occur in the same habitat.

The muscular system of members of Gyrininae is adapted to the perfect locomotor system of the middle and hind-legs. The newly evolved mesothoracic M. sterno-trochanteralis results in a considerable improvement of the propulsion forces of the middle leg. The most important change however, is the acquisition of the metathoracic M. noto-trochanteralis, which is probably derived from lateral parts of M. furca-trochanteralis. M. furca-trochanteralis is a feeble muscle in members of Gyrininae, but powerful in *Spanglerogyrus* and members of other adephagan groups, especially in the aquatic families (Larsén, 1966; Beutel, 1986; Belkaceme, 1986). Lateral parts of the metafurca (and M. furca-trochanteralis lateralis) are reduced in Gyrininae, but well developed in *Spanglerogyrus*, and in members of other adephagan families (Larsén, 1966; Beutel, 1986, 1988; Belkaceme, 1986). It appears plausible, that lateral parts of M. furca-trochanteralis have shifted their area of attachment from the metafurca to the metanotum. M. noto-trochanteralis acts as a dominant flight muscle and as a powerful swimming muscle, which is able to perform high-frequency movements as do other indirect flight muscles. The hind legs are interlocked by antagonistic muscles during flight. Most of the regular flight muscles are absent from Gyrininae (see 31.1), and functionally are replaced by M. noto-trochanteralis. These changes of metathoracic structures are not known from any other group of Coleoptera, and represent a masterpiece of economy and efficiency. The double function of M. noto-trochanteralis results in superb swimming abilities with high frequency movements, and capacity of flight, which is not affected by the loss of several flight muscles, and decrease in size of the metafurca and M. furca-trochanteralis.

Structural changes of the metanotum in members of Gyrininae (17.1, 2) are doubtlessly a result of the muscular changes described above. Flight muscles were reduced in all specimens of *Spanglerogyrus* dissected for this study, but well developed aleae are present. Attempts at flight are reported by Steiner & Anderson (1981), and the metanotal structures suggest, that the arrangement of flight muscles in specimens with the abilities to fly is the same as in members of other adephagan families. It appears plausible that flight muscles are reduced in a high percentage of specimens of *Spanglerogyrus* during early imaginal life. A similar phenomenon is known from members of *Noterus* (Jackson, 1956), *Platambus* (Larsén, 1966), and *Amphizoa* (Beutel, 1988). This is probably a matter of economy, especially when flight as a matter of dispersal appears risky, as the chance of finding a new suitable habitat is low. Specialized running water habitats are characteristic for *Spanglerogyrus*, *Amphizoa* and *Platambus*. The limited geographic range of *Spanglerogyrus* may be correlated with the loss of flying abilities in a high percentage of specimens.

The opening between the elytral base and the mesothoracic anepisternum of members of Gyrininae allows to press air into the subelytral space, and is certainly correlated with the highly efficient locomotor apparatus. The excavations for reception of the prolegs in repose improve the streamlining of the ventral body surface, thus resulting in a further improvement of swimming abilities of members of Gyrininae.

A much less dramatic step in the evolutionary history of Gyrinidae than the separation of the spanglerogyrine and the gyrinine lineage, was the splitting event, separating the *Gyrinus-Aulonogyrus-Metagyrinus* lineage from the orectochiline-enhydrine lineage. The apomorphic characters acquired by members of *Gyrinus* and *Aulonogyrus*, *e.g.*, anterolateral expansion of metacoxae, and loss of M. sterno-episternalis, are of a relatively minor, functional importance.

Some more important adaptive changes mark the start of the orectochiline-enhydrine lineage. As described above, the metanotum is highly derived (17.2), the elytral glossula is markedly developed (14.2), the medial metacoxal walls are fused to each other over their whole length (27.2), and the anterior and posterior walls of the tibia and proximal tarsomeres of the middle and hind-legs are connected by cuticular columnae and provided with air sacs (12.1). The latter two features may increase the capacity of the locomotor apparatus by stabilization of the metacoxae, which are not involved in movement of the hind legs, and an increase of the rigidity of the distal segments of the legs.

The loss of the dorsal pubescence, increase in size and a broadly oval, flat appearance are characteristic for most members of the enhydrine lineage, and are considered as groundplan conditions of the orectochiline-enhydrine lineage.

The hypothesized sister-group relationship between *Enhydrus* and the remaining orectochiline-enhydrine lineage is based on one derived character. Tarsomeres 4 + 5 of the hind legs are nearly parallel-sided, and are turned posteriorly, thus forming a kind of shovel with respect to the proximal tarsomeres in members of Orectochilini, *Dineutus*, *Porrorhynchus*, *Macrogyrus* and *Andogyrus*. This arrangement results certainly in a considerable increase of swimming abilities. Reversal of this character state in the stream-dwelling *Enhydrus* is quite unlikely.

The monophyly of *Dineutus* + *Porrorhynchus* is supported by the concealed mesoscutellar lobe, a character state which is quite common among Adephaga, and of little adaptive significance. The monophyly of *Dineutus* is doubtful, as no synapomorphic characters are available at present. *Porrorhynchus* seems to be more closely related to certain members of *Dineutus*, and is considered as a subgenus of *Dineutus* by Ochs (1926).

The modification of both the middle and hind tarsi in the manner described above (13.2, 29.2), causing a further improvement of swimming abilities, may indicate that the genera *Macrogyrus* and *Andogyrus* form a monophyletic unit together with Orectochilini. As pointed out by Brinck (1977), no reliable characters for generic separation of species of *Andogyrus* and *Macrogyrus* are available at present. A close relationship between both taxa is quite likely, even though no common derived feature is presented within this study. The body shape of *Macrogyrus* and *Andogyrus*, which is more parallel-sided and more convex than in other members of enhydrine genera, may be supportive of the hypothesized closer relationship between these genera and Orectochilini.

A substantial advance in the evolutionary history of Gyrinidae was appearance of the orectochiline lineage. The comparatively young age of this group is indicated by its absence from Australia. Orectochilini represent a very well characterized monophyletic group of fairly small, stream-dwelling forms, with markedly convex body and lateral pubescence. A median row of setae on the abdominal sternites VII and VIII (strongly prolonged) (Hatch, 1925) acts as a steering organ.

Members of Orectochilini show the highest degree of efficiency of the locomotor organs within Gyrinidae. This is achieved by enlargement of the attachment area of M. sterno-trochanteralis (M 51, 4.1, 15.2), and conspicuous modifications of middle and hind coxae which are described above (6.3, 6.3 b, 7.1, 26.2, 28.2). Another feature of Orectochilini is the tendency toward reduction of flying organs. The basalar disc and several flight muscles, which are present in other gyrinids (20.1, 31.2), are absent from all members of Orectochilini.

A sister group relationship of the genera *Orectochilus* and *Orectogyrus* is suggested by rigid fusion of mesocoxae with the preepisternum (5.1), and fusion of the anterolateral metacoxal process with the preepisternal pouch (6.3 b). This is in agreement with biogeographic data. The distribution of *Orectochilus* is mainly Oriental, with one species in Europe and North Africa, and one species in Central Africa (Ochs, 1969). *Orectogyrus* is confined to the Ethiopian region (Ochs, 1969). *Gyretes* represents the orectochiline lineage in America, ranging from Patagonia to California, Texas and Alabama (Hatch, 1925; Ochs, 1969; personal observation).

It appears as a kind of ironic fate of evolution that Orectochilini as the most highly developed members of Gyrinidae, and *Spanglerogyrus* as the most primitive representative are very similar in their appearance. The comparatively small body size, markedly convex dorsal surface, and lateral pubescence are characters shared by the first and the latest offshoot of the gyrinid lineage. However, despite Oscar Wilde's statement, that "it is only shallow people who do not judge by appearances", it is a well known fact that superficial similarities are misleading in phylogenetic analysis. This view is confirmed by the results of this study.

ACKNOWLEDGEMENTS

I am greatly indebted to R. E. Roughley, Department of Entomology, University of Manitoba for carefully reviewing the manuscript. Collecting of specimens of *Spanglerogyrus albiventris*, *Dineutus assimilis* and *Gyretes iricolor* in Alabama was made possible by an NSERC grant in aid of research No. A0428 to RER. I also thank N. E. Stork (British Museum, Natural History) for providing facilities for study of specimens at the British Museum, and for loan of specimens.

Hearty thanks are conveyed to I. Askevold, Dept of Entomology, University of Manitoba for generous gift of well preserved specimens of *Andogyrus colombicus*. It is gratefully acknowledged, that SEM facilities were provided by the Lehrstuhl für spez. Zoologie, Inst. für Biologie III, Universität Tübingen.

REFERENCES CITED

Baehr, M. 1975. Skelett und Muskulatur des Thorax von *Priacma serrata* LeConte (Coleoptera, Cupedidae). Zeitschrift für Morphologie der Tiere, 81: 55-101.

Belkaceme, T. 1986. Skelet und Muskulatur der Hinterhüfte von *Haliplus lineatocollis* Mrsh. (Haliplidae, Coleoptera). Stuttgarter Beiträge zur Naturkunde (A), 393: 1-12.

Beutel, R. G. 1986. Skelet und Muskulatur des Kopfes und Thorax von *Hygrobia tarda* (Herbst). Ein Beitrag zur Klärung der phylogenetischen Beziehungen der Hydradephaga (Insecta: Coleoptera). Stuttgarter Beiträge zur Naturkunde (A), 388: 1-54.

Beutel, R. G. 1988. Studies on the metathorax of the trout-stream beetle, *Amphizoa lecontei* Matthews (Coleoptera: Amphizoidae): Contribution towards clarification of the systematic position of Amphizoidae. International Journal for Insect Morphology and Embryology, 17 : 63-81.

Beutel, R. G. (in press). The head of *Spanglerogyrus albiventris* Folkerts (Coleoptera: Gyrinidae). Contribution towards clarification of the phylogeny of Gyrinidae and Adephaga. Zoologische Jahrbücher für Anatomie.

Beutel, R. G. (in preparation). The prothorax of *Spanglerogyrus albiventris* Folkerts (Coleoptera: Gyrinidae). Contribution towards clarification of the phylogeny of Gyrinidae and Adephaga.

Beutel, R. G. & T. Belkaceme 1986. Comparative studies on the metathorax of Hydradephaga and Trachypachidae (Coleoptera). Entomologica Basiliensia, 11: 221-229.

Beutel, R. G. & R. E. Roughley 1988. On the systematic position of the family Gyrinidae (Coleoptera: Adephaga). Zeitschrift für systematische Zoologie und Evolutionsforschung, 26: 380-400.

Bott, R. H. 1928. Beiträge zur Kenntnis von *Gyrinus natator substriatus* Steph. Zeitschrift für Morphologie und Ökologie der Tiere, 10: 207-306.

Brinck, P. 1955. A revision of the Gyrinidae (Coleoptera) of the Ethiopian region. I. Lunds Universitets Årsskrift N.F. 2, 51: 1-141.

Brinck, P. 1977. Evolution and taxonomy of *Andogyrus* Ochs (Coleoptera: Gyrinidae). Entomologica Scandinavica, 8: 241-269.

Brinck, P. 1978. Derivation, taxonomy and history of distribution of the whirligig beetle genus *Enhydrus* (Coleoptera: Gyrinidae). Entomologica Germanica, 4: 317-326.

Brinck, P. 1980. *Porrorhynchus indicans* Walker (Coleoptera: Gyrinidae). A representative of the relict montane forest ecosystem in Sri Lanka. P. E. P. Deraniyala Commemoration Volume, (Sri Lanka 1980): 103-108.

Crowson, R. A. 1938. The metendosternite of Coleoptera: a comparative study. Transactions of the Royal Entomological Society of London, 87: 397-416.

Crowson, R. A. 1942. Further studies on the metendosternite in Coleoptera. Transactions of the Royal Entomological Society of London, 94: 273-310.

Folkerts, G. W. 1979. *Spanglerogyrus albiventris*, a primitive new genus and species of Gyrinidae (Coleoptera) from Alabama. Coleopterists' Bulletin, 33: 1-7.

Hatch, M. H. 1925. The phylogeny and phylogenetic tendencies of Gyrinidae. Papers of the Michigan Academy of Science, Arts and Letters, 5: 429-467.

Hatch, M. H. 1926. The morphology of Gyrinidae. Papers of the Michigan Academy Science, Arts and Letters, 7: 311-350.

Hennig, W. 1966. Phylogenetic systematics. Urbana, University of Illinois Press. 263 pp.

Jackson, D. J. 1956. Observation on flying and flightless water beetles. The Journal of the Linnean Society of London, 43: 18-42.

Larsén, O. 1966. On the morphology and function of the locomotor organs of the Gyrinidae and other Coleoptera. Opuscula Entomologica Supplementum, 30: 1-242.

Matsuda, R. 1970. Morphology and evolution of the insect thorax. Memoirs of the Entomological Society of Canada, 76: 1-431.

Nachtigall, W. 1960. Über Kinematik, Dynamik und Energetik des Schwimmens einheimischer Dytisciden. Zugleich ein Beitrag zur Anwendung von Kurzzeitphotographie und Hochfrequenzkinematographie auf biologische Probleme. Zeitschrift für vergleichende Physiologie, 43: 48-118.

Nachtigall, W. 1961. Funktionelle Morphologie, Kinematik und Hydromechanik des Ruderapparates von *Gyrinus*. Zeitschrift für vergleichende Physiologie, 45: 193-226.

Ochs, G. 1926. Die Dineutini. 2. Tribus der Unterfam. Enhydrinae, Fam. Gyrinidae (Col.). A. Allgemeiner Teil. Entomologische Zeitschrift Frankfurt am Main, 40: 61-74, 112-126, 129-140, 190-197.

Steiner, W. E., Jr. & J. J. Anderson 1981. Notes on the natural history of *Spanglerogyrus albiventris* Folkerts, with a new distribution record (Coleoptera: Gyrinidae). Pan-Pacific Entomologist, 57: 124-132.

Uéno, S.-I. 1957. Blind aquatic beetles of Japan, with some accounts of the fauna of Japanese subterranean waters. Archiv für Hydrobiologie, 53: 250-296.

Ward, R. D. 1979. Metathoracic wing structures as phylogenetic indicators in the Adephaga (Coleoptera). pp. 181-191. *In* Carabid beetles: their evolution, natural history, and classification. T. L. Erwin, G. E. Ball, D. R. Whitehead and A. L. Halpern (Editors). 635 pp. The Hague (Dr. W. Junk).

USE OF GONOCOXAE AND THE STERNAL APEX TO IDENTIFY ADULT FEMALES OF NORTH AMERICAN *GYRINUS* GEOFFROY (COLEOPTERA: GYRINIDAE)[1]

William L. Hilsenhoff
Department of Entomology
University of Wisconsin
Madison, WI 53706
U.S.A.

Quaestiones Entomologicae
26: 193–197 1990

ABSTRACT

A taxonomic study of species of Gyrinidae occurring in Wisconsin revealed that the large, sclerotized gonocoxae of adult females of Gyrinus *differ substantially among species. By using their shape and the shape of the apex of the last visible abdominal sternum, along with the microsculpture on the elytra and characters also found on males, positive identification of females of* Gyrinus *can be achieved.*

INTRODUCTION

Taxonomic studies of North American Gyrinidae have relied heavily on structures of the male genitalia for identification of specimens of the various species. As a result, adult females are often difficult or impossible to identify with published keys and descriptions. In his revision of *Gyrinus* H. C. Fall (1922: 272-273) noticed the female genitalia with their large, paddle-shaped gonocoxae, but remarked that "they seem to be substantially alike in all species". He stated that while specimens of most species could be identified by characters in his key, one should always check the male genitalia and that "in fact there are a few species which I am disposed to believe can never certainly be recognized in any other way". He further concluded that "Females are often very difficult to place except through association with males". Since individuals of several species often occur in the same aggregation, identification of females by association with males is risky.

More recently, Ferkinhoff and Gundersen (1983: 7) also concluded that the male genitalia were the only dependable character for identifying adults of some species and that "Females in such cases can only be tentatively identified by matching them with males taken from the same location on the same date.". Like Fall, they too stated that "The genitalia of female *Gyrinus* are very similar in all species and are of little-or-no diagnostic value.". In her 1988 revision or *Gyrinus*, Oygur also relied primarily on male genitalia for separating specimens; her key to female adults (1988: 60-71) did not use the genitalia and did not offer means to identify females of 12 species. However, F. E. Wood (1968: 3) did use

---

[1] Research supported by the College of Agricultural and Life Sciences, University of Wisconsin-Madison.

gonocoxae of females in synonymizing *Dineutus analis* Régimbart with *D. serrulatus* LeConte, and in Europe, Franciscolo (1979: 171-175) and Holmen (1987: 36-45) used gonocoxae to aid in identification of females. The gonocoxae, which are derived from the ninth sternum and are part of the genital segments (Burmeister 1976: 229-231), were called "coxites" by Tanner (1927: 21) and"hemisternites" by Lindroth (1957: 250-251).

MATERIAL AND METHODS

To develop reliable species keys for both male and female adults of Gyrinidae, I studied more than 25,000 specimens from Wisconsin. Seventy-eight percent of them were distributed among 20 species of *Gyrinus*; the remainder included 4 species of *Dineutus*. I studied the gonocoxae, the shape of the last visible abdominal sternum, and the elytral microsculpture of females of all Wisconsin species. I also studied adults of a few additional species known to occur in the western Great Lakes region, but was unable to borrow specimens of many other North American species because they were being used in a revisionary study.

RESULTS AND DISCUSSION

The results of this study illustrate the value of gonocoxae, and to a lesser extent the sternal apex, for identifying females of *Gyrinus*. In females of *Dineutus* the gonocoxae (Fig. 1), which differ substantially from those of females of *Gyrinus* (Figs. 2-14) by being widened near the mid-length, are not substantially different in the four species that were studied (*D. assimilis* Aubé, *D. discolor* Aubé, *D. hornii* Roberts, *D. nigrior* Roberts), and no difference was noticed in the broadly rounded sternal apex (Fig. 15). The gonocoxae of females of females of *Gyrinus*, however, vary greatly, ranging from elongate in the very large specimens of *Gyrinus impressicollis* Kirby (Fig. 2) to short and round in specimens of *Gyrinus* sp. nr. *minutus* (Fig. 3), a species that is very similar to *G. minutus* Fabricius and is being described by F. M. Atton, Saskatoon, Sask. Also, the shape of the apex of the last visible abdominal sternum differs between females of several species of *Gyrinus* in which specimens are otherwise similar.

In *Gyrinus*, the gonocoxae of specimens often differ so greatly that they are a valuable aid in sorting females in collections of individuals of similar size, color, and elytral structure. For example, females of *Gyrinus marginellus* Fall have narrow, divergent gonocoxae (Fig. 4) that readily distinguish them from females of *Gyrinus aeneolus* LeConte, which have broader, more rounded, parallel gonocoxae (Fig. 5). Similarly, females of *Gyrinus analis* Say have elongate, parallel-sided, and apically truncate gonocoxae (Fig. 6) that differ markedly from the divergent gonocoxae of females of *Gyrinus frosti* Fall (Fig. 7), *Gyrinus sayi* Aubé (Fig. 8), and other species with black venters.

The following examples illustrate the use of gonocoxae and the shape of the last visible abdominal sternum to separate females of species that otherwise are very similar. The stout and rounded gonocoxae of females of *G. frosti* (Fig. 7) can be used to separate them from females of *G. sayi*, which have narrower gonocoxae that are concave on the inner margin (Fig. 8); also, the last abdominal sternum of females of *G. frosti* (Fig. 16) is broadly concave apically and distinctly sinuate laterally, while in females of *G. sayi* (Fig.17) it is narrowly truncate apically and not sinuate laterally. The truncate gonocoxae of females of *Gyrinus ventralis* Kirby (Fig. 9) differ greatly from those of females of the structurally similar *Gyrinus gehringi* Chamberlain (Fig. 10) and females of other Wisconsin species with pale venters. Females of *Gyrinus lecontei* Fall, which are also similar in many respects to those of *G. gehringi*, can be separated from that species by their narrower, infuscate gonocoxae (Fig. 11), which are not convex laterally as they are in females of *G. gehringi*. The gonocoxae of females of *G. lecontei* can be used to tell them apart from the almost identical females of *Gyrinus aquiris* LeConte, which have gonocoxae (Fig. 12) that are shorter, concave on the inner margin, and never infuscate. Furthermore, the sternal apex in females of *G. lecontei* is rounded (Fig. 18), while it is narrowly truncate in females of *G. aquiris* (Fig. 19). Females of *Gyrinus bifarius* Fall and *Gyrinus confinis* LeConte also have been difficult to separate, but the narrow and distinctly concave sternal apex of females of *G. bifarius* (Fig. 20), differs markedly from the rounded to truncate sternal apex of females of *G. confinis* (Fig. 21), and the gonocoxae are much shorter and broader in females of *G. bifarius* (Fig. 13) than in those of *G. confinis* (Fig. 14).

Revisions of families or genera of insects frequently rely on differences in male genitalia, and this often has been the situation in Hydradephaga. The large, sclerotized gonocoxae in females of *Gyrinus* differ substantially among closely related species and should be used to identify specimens in future studies of North American Gyrinidae. I also have noticed distinct differences in the gonocoxae of females of species of Dytiscidae that otherwise are structurally very similar. In future revisions of Hydradephaga, more attention should be paid to differences in the female genitalia to enable positive identification of females as well as males.

REFERENCES CITED

Burmeister, E. G. 1976. Der Ovipositor der Hydradephaga (Coleoptera) und seine phylogenetische Bedeutung unter besonderer Berücksichtigung der Dytiscidae. Zoomorphologie, 85: 165-257.

Ferkinhoff, W. D. and R. W. Gundersen. 1983. A key to the whirligig beetles of Minnesota and adjacent states and Canadian provinces. (Coleoptera: Gyrinidae). Scientific Publications of the Science Museum of Minnesota, New Series, Vol. 5, No. 3. 53 pp.

Fall, H. C. 1922. The North American species of *Gyrinus* (Coleoptera). Transactions of the American Entomological Society, 47: 260-307.

Franciscolo, M. E. 1979. Coleoptera: Haliplidae, Hygrobiidae, Gyrinidae, Dytiscidae. Fauna d'Italia Vol. 14. vi + 804 pp. Edizioni Calderini, Bologna.

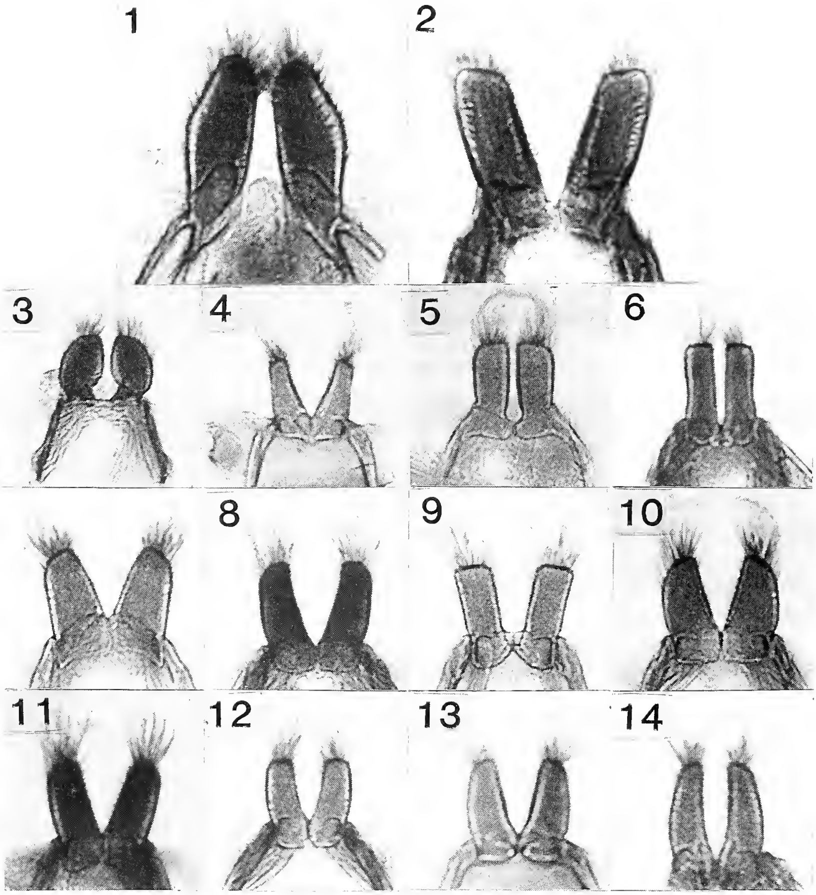
Holmen, M. 1987. The aquatic Adephaga (Coleoptera) of Fennoscandia and Denmark. I. Gyrinidae, Haliplidae, Hygrobiidae, and Noteridae. Fauna Entomologica Scandinavica Vol. 20. 168 pp. E. J. Brill/Scandinavian Science Press Ltd., Leiden, Copenhagen.

Lindroth, C. H. 1957. The principal terms used for male and female genitalia in Coleoptera. Opuscula Entomologica, 22: 241-256.

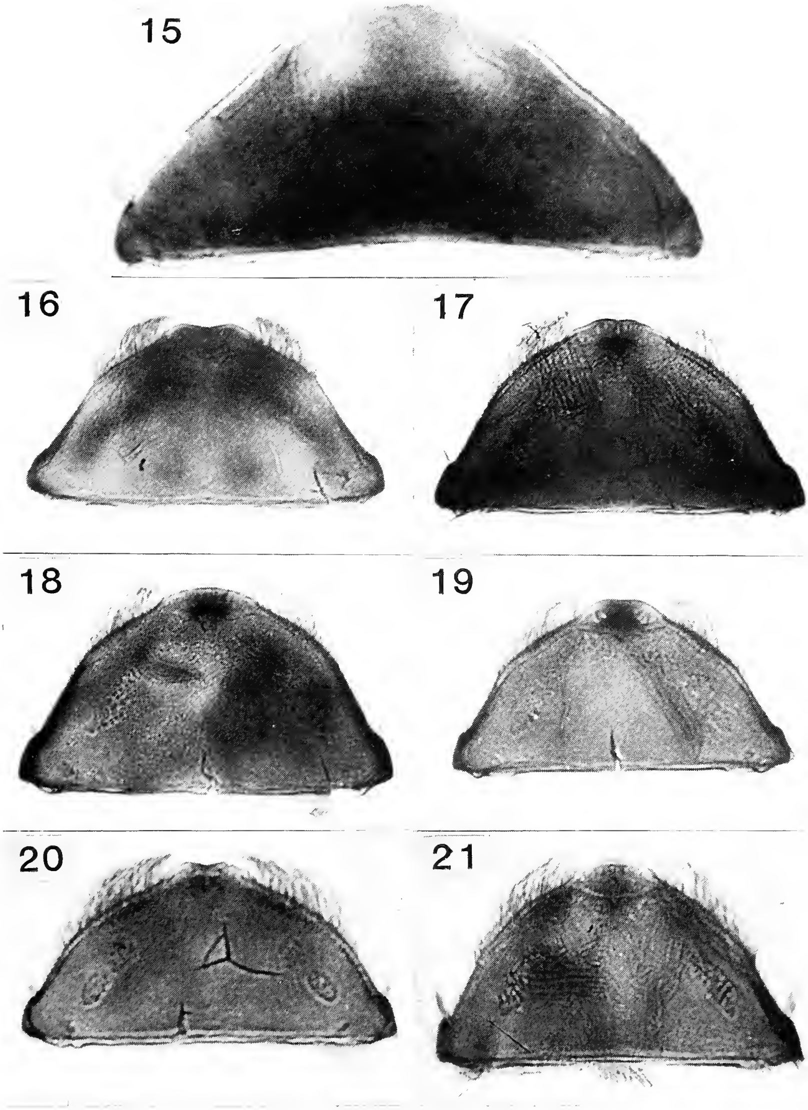
Oygur, S. 1988. Taxonomy, distribution, and phylogeny of North American (north of Mexico) *Gyrinus* Geoffroy (Coleoptera: Gyrinidae). Ph.D. Dissertation, Rutgers University, New Brunswick, New Jersey. xv + 296 pp.

Tanner, V. M. 1927. A preliminary study of the genitalia of female Coleoptera. Transactions of the American Entomological Society, 53: 5-50.

Wood, F. E. 1968. The taxonomic status of *Dineutus serrulatus* and *Dineutus analis* in North America (Gyrinidae: Coleoptera). Proceedings of the United States National Museum, 124 (3646): 1-9



Figs. 1–14. Gonocoxae of adult females: 1, *Dineutus nigrior* Roberts; 2, *Gyrinus impressicollis* Kirby; 3, *G.* sp. nr. *minutus* Fabricius; 4, *G. aeneolus* LeConte; 5, *G. marginellus* Fall; 6, *G. analis* Say; 7, *G. frosti* Fall; 8, *G. sayi* Aubé; 9, *G. ventralis* Kirby; 10, *G. gehringi* Chamberlain; 11, *G. lecontei* Fall; 12, *G. aquiris* LeConte; 13, *G. bifarius* Fall; 14, *G. confinis* LeConte.



Figs. 15–21. Last abdominal sternum of adult females: 15, *Dineutus nigrior* Roberts; 16, *Gyrinus frosti* Fall; 17, *G. sayi* Aubé, 18, *G. lecontei* Fall; 19, *G. aquiris* LeConte; 20, *G. bifarius* Fall; 21, *G. confinis* LeConte.

PRIMARY SETAE AND PORES ON LEGS OF LARVAE OF NEARCTIC HYDROPORINAE (COLEOPTERA: DYTISCIDAE)

Y. Alarie
P.P. Harper

Département de Sciences biologiques
Université de Montréal
Montréal, Québec
H3C 3J7

A. Maire
Département de Chimie-Biologie
Université du Québec à Trois-Rivières
Trois-Rivières, Québec
G9A 5H7

Quaestiones Entomologicae
26: 199–210 1990

ABSTRACT

The first instar larvae of 22 North American species of Hydroporinae (Coleoptera: Adephaga: Dytiscidae) and one species each of Amphizoidae and Hygrobiidae were analyzed. The ancestral system of primary setae and pores on the legs of hydroporine larvae was deduced and differences between genera are discussed in a phylogenetic perspective. This system is similar to that described by Nilsson mainly from Palaearctic species except for the addition of one pore dorso-posteriorly on femur of most larval Hydroporinae (pore FEa). This addition is suggested since this pore seems homologous to the pore found in larval Carabidae, Amphizoidae, and Hygrobiidae. Such an hypothesis led to suppose that the pore FEa was independently lost within the family Noteridae, as well as within the hydroporine genera Laccornis, Liodessus, *and* Desmopachria. *In the light of this work,* Potamonectes griseostriatus *stands out as the species deviating least from the ancestral system proposed for the Hydroporinae.*

RESUME

Les premiers stades larvaires de 22 espèces nord-américaines d'Hydroporinae (Coleoptera: Adephaga: Dytiscidae) ainsi que d'une espèce d'Amphizoidae et d'Hygrobiidae sont étudiés. Le système ancestral des soies et des pores primaires observé sur les pattes des larves d'Hydroporinae est proposé et les différences génériques observées sont discutées d'un point de vue phylogénétique. Le système proposé est semblable à celui développé par Nilsson principalement à partir d'espèces paléartiques à l'exception de l'addition d'un pore localisé dorsopostérieurement sur le fémur de plusieurs larves d'Hydroporinae (pore FEa). Ce pore y est inclus parce qu'il est homologue au pore retrouvé chez les larves de Carabidae, d'Amphizoidae et d'Hygrobiidae. Pareille hypothèse suggère que le pore FEa soit disparu indépendamment dans la famille des Noteridae ainsi que chez Laccornis, Liodessus *et* Desmopachria, *trois genres d'Hydroporinae. Sur la base de ce travail,* Potamonectes griseostriatus *appara^it l'espèce la plus proche du système ancestral proposé pour les larves d'Hydroporinae.*

INTRODUCTION

Data about immature stages, particularly in holometabolous insects, are likely to improve adult classifications, since larvae may be considered as different expressions of the same genotype (Bousquet and Goulet, 1984). Each instar thus represents an ontogenetic stage with its own characters, each being important in determining taxa, reconstructing phylogenies, and building classifications.

Bousquet and Goulet (1984) have indicated that the least studied and potentially the most significant set of characters on beetle larvae is that of setae and pores in the first instar and their homologous structures in subsequent instars. They have shown the great stability of these primary setae and pores in carabid larvae.

Few authors have undertaken an analysis of the chaetotaxy of dytiscid larvae. The first real effort to code and name series of sensilla is that of De Marzo (1973) on the mature larva of *Agabus bipustulatus* (L.). Recently, Wolfe and Roughley (1985) have proposed a system for naming sensilla on mouthparts, legs, and urogomphi of the mature larvae of *Matus ovatus ovatus* Leech. This system was modified slightly by Nilsson (1986, 1987a, 1987b) who stressed the highly diagnostic value of secondary leg chaetotaxy in Palaearctic Hydroporinae (including some Holarctic species) and suggested an ancestral pattern of primary setae and pores on the legs of dytiscid larvae (Nilsson, 1988).

The subfamily Hydroporinae is the most diverse subfamily of Dytiscidae with six tribes (eight if the genera *Siettitia* Abeille de Périn and *Pachydrus* Sharp are separated into their own separate tribes), and containing some 75 genera. Adult members of the subfamily are characterized by a number of unique features such as the form of the pro- and mesotarsi which presumably indicate that this subfamily is a monophyletic unit. In addition, one feature is the small size of the individuals. Certain features of the larvae also indicate that the subfamily is monophyletic, the synapomorphy judged the most important being the development of the frontoclypeus into a nasale (Wolfe, 1985).

In contrast to European species, only a small number of Nearctic hydroporine larvae are described. Of the approximately 320 known species, only 41 have larvae and adults associated, and only 10 first instar larvae are actually known. This lack of knowledge may be due both to the difficulty of collecting small larvae and to the problems associated with rearing (Matta and Peterson, 1981).

In a phylogenetic perspective it is useful to study additional taxa and search for new characters in order to increase knowledge about the group in revision and to improve the hypotheses. Given the small number of first instar larvae described, this paper represents the first extensive effort to record and number the primary sensilla of several Nearctic Hydroporinae (including some Holarctic species). The aims of this paper are: (1), to examine the chaetotaxy on the legs of the first instar larvae of Nearctic Hydroporinae, with a special emphasis on Hydroporini, and to propose the ancestral pattern of primary setae and pores for the subfamily; and (2), to classify the generic differences observed into apomorphies and plesiomorphies.

MATERIAL AND METHODS

The notation of primary setae and pores proposed is based on the study of the first instar larvae of 22 species of Hydroporinae belonging to three tribes (six genera) and two species of other families of Hydradephaga, Amphizoidae and Hygrobiidae (Table 1). All the species were reared *ex ovo* except for the out-group families loaned from the Canadian National Collection of Insects (Biosystematic

Table 1. List of the species studied (* = Holarctic species)

Tribe	Species
Hydroporinae	
Bidessini	*Liodessus affinis* (Say)
Hyphydrini	*Desmopachria convexa* (Aubé)
Hydroporini	*Hydroporus (oblitus) paugus* Fall
	Hydroporus (*s. str.*) *badiellus* Fall
	Hydroporus (*s. str.*) *columbianus* Fall
	**Hydroporus* (*s. str.*) *fuscipennis* Schaum
	**Hydroporus* (*s. str.*) *morio* Aubé
	Hydroporus (*s. str.*) *niger* Say
	**Hydroporus* (*s. str.*) *puberulus* LeConte
	Hydroporus (*s. str.*) *signatus* Mannerheim
	**Hydroporus* (*s. str.*) *striola* (Gyllenhal)
	Hydroporus (*s. str.*) *tenebrosus* LeConte
	**Hydroporus* (*s. str.*) *tristis* (Paykull)
	Hydroporus (Neoporus) undulatus Say
	Hygrotus hudsonicus (Fall)
	**Hygrotus impressopunctatus* (Schaller)
	Hygrotus laccophilinus (LeConte)
	Hygrotus patruelis (LeConte)
	Hygrotus picatus (Kirby)
	Hygrotus sayi Balfour-Browne
	Laccornis latens (Fall)
	Potamonectes griseostriatus (De Geer)
Hygrobiidae	*Hygrobia tarda* Herbst
Amphizoidae	*Amphizoa* sp.

Research Centre). Field collected adults were brought into the laboratory for identification, and placed in breeding containers. Except for some rare species, no food was given to the adults. Hatchlings were isolated and fed with mosquito larvae of an appropriate size.

Legs from both sides were removed and mounted in Hoyer's solution (Barbosa 1974). The structures were examined under a compound microscope.

TERMS

For a better understanding, some of the terms used in the text need to be defined. Most of them have already been discussed by authors studying larval chaetotaxy of insects, but it seems useful to repeat them here.

Sensillum - refers collectively to all socketed chaetotaxal surface structures (Wolfe and Roughley, 1985).

Pore (*placoid sensillum*) - a minute, generally circular, hole-like (under a compound microscope) sensillum on the cuticule (Bousquet and Goulet, 1984).

Seta - corresponds to a contact receptor (Nilsson, 1988). It is a structure within which the energy of a stimulus arising outside or within the insect is transferred into transmittable information, usually in the form of a nervous impulse (McIver, 1982). This common type of sensillum is elongate, slender, and evenly tapering. Depending on its form, a seta is spiniform or setiform (hair-like), simple (unifid) or compound (bifid, trifid, *etc.*). Spiniform structures refer to short (approximately equal to or less than two times the maximal width of the tarsal claw) and moderately long seta with the base distictly enlarged (*e.g.*, the ventral series of the femur (Fig. 1)) as compared to very long setiform seta the base of which is narrower (*e.g.*, setae TR4 and TR7, (Fig. 1)).

Spinula - a non-socketed cuticular structure (Nilsson, 1988) [flat bundles of small setae of Jeppesen (1986)] that occurs on the surface of all segments of the legs. They are usually stronger on the inferior margin of the tibia and the tarsus.

Primary seta and pore - a seta and a pore in the first instar larva and their homologous structure on subsequent instars. As emphasized by Bousquet and Goulet (1984), these are further divided into ancestral (recognized and homologized in most or all the taxa examined) and additional (secondarily evolved).

NOTATION OF SETAE AND PORES

The system used for coding and naming the sensilla is inspired both by Bousquet and Goulet (1984) and Wolfe and Roughley (1985). Setae are coded by two capital letters corresponding to the first two letters of the name of the structure on which the designated seta is located (AB, last abdominal segment; CO, coxa; FE, femur; PT, pretarsus; TA, tarsus; TI, tibia; TR, trochanter) and a number. Pores are coded in the same manner except that the number is replaced by a lower case letter. The position of the sensilla is described by adding the following abbreviation: A, anterior; D, dorsal; Di, distal; P, posterior; Pr, proximal; V, ventral.

The ancestral system of setae and pores was constructed both by out-group and in-group comparisons. All homologous setae and pores present on the larvae of at least one species of hydroporine studied and on larvae of at least one out-group species (Amphizoidae, Hygrobiidae) was considered as part of the ancestral system. Furthermore, setae and pores on larvae of most species of hydroporine studied were also considered as part of the ancestral system. Homologization has followed the code used by Bousquet and Goulet (1984) for carabid larvae.

RESULTS

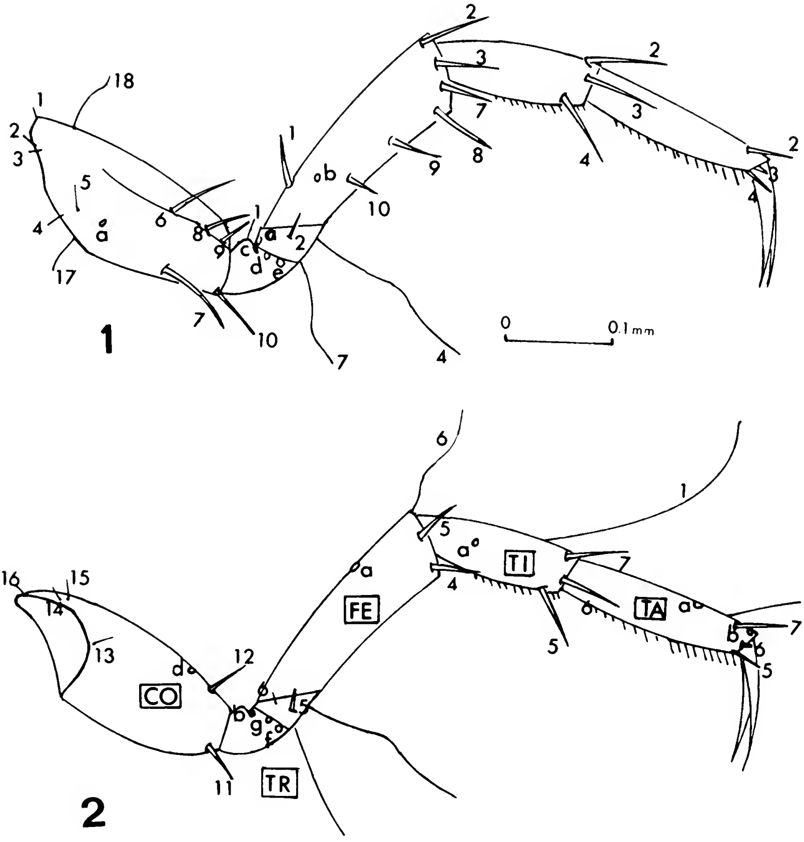
The description of the ancestral systems of primary setae and pores for larval hydroporines refers to a reconstructed species bearing all and only the ancestral setae and pores (Fig. 1-4). Peculiarities of individual species are noted in the text. Except for some few details, the pattern is remarkably constant among all legs and species. Sixty-six sensilla (48 setae and 18 pores) are coded. The position and name of each seta and pore of the ancestral system of legs are listed in Table 2.

Coxa

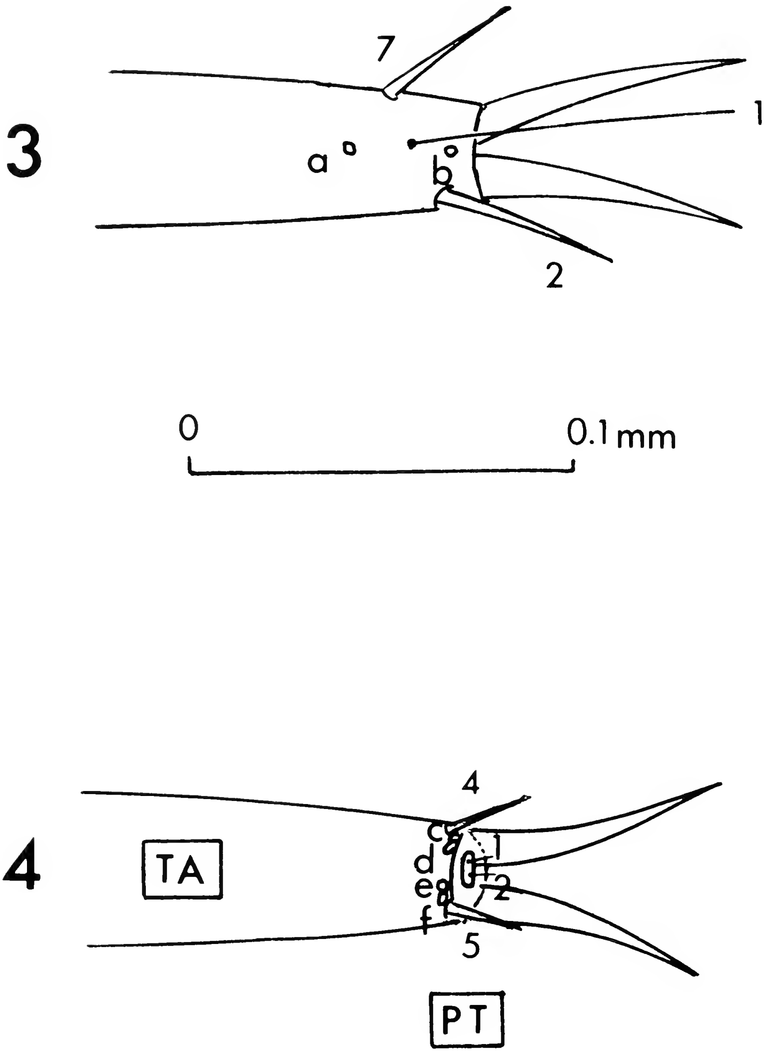
Twenty sensilla are on each coxa. Eleven small setae and one pore appear on the proximal portion of the segment and seven setae and one pore on the distal portion. The setae are spiniform, except CO18, and, in *Desmopachria convexa*, CO12, which are setiform. Seta CO7 is more proximal on the procoxa than on the meso- and metacoxae.

Trochanter

Six setae and seven pores compose the basal number of primary sensilla. These are invariable, with two setiform setae on the ventral margin (TR4, TR7)



Figs. 1–2. Distribution of ancestral setae and pores on hind leg of a generalized first instar larva of Hydroporinae (Coleoptera: Dytiscidae). 1, Anterior face. 2, Posterior face.



Figs. 3–4. Distribution of ancestral setae and pores on hind leg of a generalized first instar larva of Hydroporinae (Coleoptera: Dytiscidae). 3, Dorsal face of tarsus. 4, Ventral face of tarsus (with pretarsus).

and four short spiniform setae. Seta TR5 is more robust consistently than any other seta of the trochanter. All spiniform setae are simple except in first instar larvae of *Desmopachria convexa*, *Hydroporus* (*Neoporus*) *undulatus*, *Hydroporus* (*s. str.*) *tenebrosus*, *H.* (*s. str.*) *striola*, *Hygrotus sayi*, and *H. patruelis*, where TR5 is a compound spine on the posterior surface. Seta TR2 is absent consistently from first instar larvae of *Desmopachria convexa*, *Liodessus affinis*, *Hydroporus (Neoporus) undulatus*, and all species of *Hygrotus* examined. Seta TR2 is facultative in *Laccornis latens* being either present, partially present or absent. Observations of third instar larvae of this species have shown that this seta is constant, and therefore is incorporated into the ancestral system.

Femur

Ten setae and two pores characterize this segment. All setae are spiniform except the setiform FE7 on the distal portion of the superior margin. Most of the spiniform setae are compound in first instar larvae of *Desmopachria convexa*, *Liodessus affinis*, and all *Hygrotus* and *Hydroporus* species. Pore FEa is absent from those of *Laccornis latens*, *Desmopachria convexa*, and *Liodessus affinis*. Setae FE7 is slightly more ventral in position on the profemur than on the meso- and metafemora. Two additional setae, ADi (*H. puberulus*, *H. columbianus*, and *H. tenebrosus*) and AVPr (*L. affinis*), were sporadically noted in some specimens.

Tibia

Seven setae (six spiniform and one setiform) and one pore are on the tibia. First instar larva of *Desmopachria convexa* is characterized by a setiform seta TI7. The inferior margin of the segment is usually marked by a pronounced thickening of the spinulae on the inferior margin. This spinular row is lighter in *Desmopachria convexa*, *Liodessus affinis*, and *Hydroporus paugus*. Compound spines are observed among the same species as above (see femur).

Tarsus

Seven setae (six spiniform and one setiform) and six pores are on the tarsus (Fig. 1-4). Setae TA3 and TA6 are short and robust. The individual pores of the pairs TAc/TAd and TAe/TAf are very difficult to distinguish in some taxa because they are positioned close together (Fig. 4). The spinular row is markedly developed in larvae of most species except those of *Desmopachria convexa*.

Pretarsus.

Two short spiniform setae are located distally on the ventral surface of the pretarsus (Fig. 4). These may be overlooked easily and incorporated into the row of spinulae of the tarsus.

COMPARISONS AND TAXONOMIC IMPLICATIONS

Except for a few details, the ancestral system of the larval leg of Nearctic Hydroporinae is similar to that described by Nilsson (1988). Differences in the nomenclature of the sensilla (marked by an asterisk in Table 2) are a matter of interpretation rather than of taxonomic difference except for the pore FEb that corresponds apparently to the pore FEa of Nilsson. By comparison with the ancestral pattern of Carabidae, Nilsson's description of pore FEa (APr, antero-proximal) seems much more like pore FEb (LAB, lateral-anterior-basal) than FEa (DB, dorsal-basal).

Table 2. Position of ancestral setae and pores on legs of first instar larvae of Hydroporinae; A - anterior, CO - coxa, D - dorsal, Di - distal, FE - femur, P - posterior, PT - pretarsus, Pr - proximal, TA - tarsus, TI - tibia, TR - trochanter, V - ventral. [* different from Nilsson's (1988) codes].

Setae or pores	Position	Setae or pores	Position
CO1	DPr	TI1	DDi
CO2	ADPr	TI2	ADDi
CO3	ADPr	TI3	ADi
CO4	APr	TI4	AV
CO5	APr	TI5	PV
CO6	A	TI6	PDi
CO7	AV	TI7	PDDi
CO8	ADi	TIa	P
CO9	ADi		
CO10	AVDi	TA1	DDi
CO11	PVDi	TA2	ADDi
CO12	DDI	TA3	ADi
CO13	PPr	TA4	AV
CO14	PDPr	TA5	PV
CO15	PDPr	TA6	PDi
CO16	DPr	TA7	PVDi
CO17	VPr	TAa	D
CO18	ADP	TAb	DDi
COa	*APr	TAc	AVDi
COb	DDi	TAd	AVDI
		TAe	PVDi
TR1	D	TAf	PVDi
TR2	ADi		
TR4	VDi	PT1	AVDi
TR5	PDi	PT2	AVDi
TR6	PDi		
TR7	V		
TRa	*ADDi		
TRb	*D		
TRc	AD		
TRd	A		
TRe	A		
TRf	P		
TRg	P		
FE1	DPr		
FE2	ADDi		
FE3	ADi		
FE4	PVDi		
FE5	PDi		
FE6	DDi		
FE7	AVDi		
FE8	AV		

(continued on next page)

Table 2. (continued)

Setae or pores	Position	Setae or pores	Position
FE9	AV		
FE10	AVPr		
FEa	*P		
FEb	*APr		

Table 3. Differences in the character states of primary setae and pores on larval legs of selected genera of Nearctic Hydroporinae; (0) plesiotypic state, (1) apotypic state, (a) *Laccornis*, (b) *Desmopachria*, (c) *Liodessus*, (d) *Hydroporus s. str.*, (e) *Hydroporus* (*oblitus* group), (f) *Hydroporus* (*Neoporus*), (g) *Hygrotus*, (h) *Potamonectes*.

Character states		a	b	c	d	e	f	g	h
1-	CO12 spiniform	0		0	0	0	0	0	0
	CO12 setiform		1						
2-	TI7 spiniform	0		0	0	0	0	0	0
	TI7 setiform		1						
3	TR2 present	0			0	0	0		
	TR2 absent	1	1		1	1			
4-	FEa present				0	0	0	0	0
	FEa absent	1	1	1					
5	setae simple	0							0
	setae compound	1	1	1	1	1	1		

Table 3 summarizes the differences in the character states for the primary chaetotaxal pattern among genera of the Hydroporinae studied. Character states are presented here as plesiomorphic and apomorphic to underline apparent evolutionary tendencies, but these should be considered first order hypotheses. Because of the large number of genera in this subfamily, a comprehensive treatment should incorporate a larger number of species of a variety of genera and a larger number of characters.

The presence or absence of seta TR2 represents an interesting diagnostic character. Nilsson (1988) noticed that this seta is absent from the legs of Bidessini(*Bidessus* Sharp, *Yola* Des Gozis), *Hydrovatus* Motschulsky, *Hyphydrus* Illiger, and *Hygrotus* Stephens. If the absence of this seta from the legs of species of Nearctic representatives of *Hygrotus* is consistent with Nilsson's data, it is interesting to include in the group of hydroporine genera without TR2 some strictly Nearctic lineages such as *Desmopachria* and *Liodessus*, and the subgenus *Neoporus* (*Hydroporus*). The absence of TR2 from the trochanter of third instar larvae of *Hydroporus (Neoporus) carolinus* (unpublish. data) reinforces the hypothesis that this seta is absent from all the species of *Neoporus*. Considering that until now a generic distinction among Nearctic *Hygrotus* and *Hydroporus* based on larval characters was not possible (Watts, 1970; Matta, 1983), it is noteworthy that, except for the subgenus *Neoporus*, the first instar larva of all the *Hydroporus* species studied can be discriminated from the first instar larva of the species of *Hygrotus* by the presence of this seta.

Larvae of *Desmopachria convexa* deviate farthest from the ancestral pattern. The setiform aspect of seta TI7 associated with the absence of seta TR2 and pore FEa is similar to that described for larvae of *Hyphydrus* species studied by De Marzo (1977) and Nilsson (1988). The similarities in the basal pattern of both genera are interesting given that Young (1980) and Biström (1982) have suggested that *Desmopachria* and its relatives should be removed from Hyphydrini and placed in a distinct tribe.

The only fundamental difference between the basal pattern proposed herein and that of Nilsson (1988) is incorporation of pore FEa (as defined in this paper) into the ancestral system of larvae of Hydroporinae. Two different hypotheses may be examined with respect to this pore. Hypothesis 1 is that the pore is part of the ancestral system of larvae of Dytiscidae and also of Hydroporinae since it seems homologous to the pore found in most larvae of Hydroporinae as well as in larval Carabidae (Bousquet and Goulet, 1984), Amphizoidae, and Hygrobiidae. There are certainly various interpretations of Adephagan phylogeny but if we accept the idea that Dytiscidae have evolved from a terrestrial carabid ancestor (Hammond, 1979; Ward, 1979; Nichols, 1985), and, even if this is more contested, that Trachypachidae, Dytiscidae, Amphizoidae, Hygrobiidae, and Noteridae could represent a monophyletic unit (Beutel and Roughley, 1988), it seems reasonable to accept pore FEa of the Hydroporinae as ancestral. Based on immature characters, the work of Ruhnau (1986) reinforces this hypothesis since he has shown that Amphizoidae, Hygrobiidae, and Dytiscidae share numerous striking synapomorphies. As a result, hypothesis 1 suggests that pore FEa was independently lost from Noteridae, as well as from *Laccornis*, *Liodessus*, and *Desmopachria*.

Hypothesis 2 is that pore FEa is not part of the ancestral pattern of either Hydroporinae or Dytiscidae. This appears to be the premise of Nilsson (1988) which is supported by the absence of this primary pore in first instar larvae of Haliplidae, Noteridae, and Gyrinidae and by the phylogenetic hypothesis that Noteridae are the sister-group of Dytiscidae (Kavanaugh, 1986). Such a viewpoint suggests thus that the presence of this pore in exactly the same position by larvae of independent families of Adephaga [as well as in most Dytiscidae (Nilsson, 1988)] could result from independent gains.

From both hypotheses, hypothesis 1 appears more acceptable since it seems more logical that pore FEa was lost independently rather than gained independently. In the light of this hypothesis, *Potamonectes griseostriatus* stands out as the species deviating least from the ancestral system proposed for the Hydroporinae. Nilsson (1988) has emphasized that the Holarctic *Laccornis oblongus* Stephens should present the most plesiomorphic condition within Hydroporinae and this is in accord with the previous conclusion of Wolfe (1985). The pattern of primary setae and pores of *Laccornis latens* could also be used as an argument to consider that FEa is an additional rather than an ancestral pore. In order to solve this apparent contradiction, additional larval characters are needed. A study of the primary setae and pores of other structures such as those of the last abdominal segment and the urogomphi may assist in resolving this controversy.

ACKNOWLEDGEMENTS

We are deeply grateful to Dr. Anders Nilsson, University of Umeå, Sweden, for allowing us access to his unpublished manuscript and to Dr. Yves Bousquet, Biosystematics Research Centre, Ottawa, Canada, for the loan of larvae of Amphizoidae and Hygrobiidae. Financial support was provided by the Natural Sciences and Engineering Research Council of Canada in the form of research grants and a Postgraduate Scholarship.

REFERENCES CITED

Barbosa, P. 1974. Manual of basic techniques in insect histology. Palmer Journal Register, Library of Congress, 245 pp.

Beutel, R.G. and R.E. Roughley. 1988. On the systematic position of the family Gyrinidae (Coleoptera: Adephaga). Zeitschrift für zoologische Systematik und Evolutionsforschung, 26: 380-400.

Bistrom, O. 1982. A revision of the genus *Hyphydrus* Illiger (Coleoptera, Dytiscidae). Acta Zoologica Fennica, 165: 1-121.

Bousquet, Y., and H. Goulet. 1984. Notation of primary setae and pores on larvae of Carabidae (Coleoptera: Adephaga). Canadian Journal of Zoology, 62: 573-588.

De Marzo, L. 1973. Studi sulle larve dei colleoteri ditiscidi. I. Note morfologiche sulle larve mature de sei specie del genere *Agabus* Leach. Entomologica, Bari, 9: 47-83.

De Marzo, L. 1977. Studi sulle larve dei coleotteri ditiscidi. VIII. Morfologia dei tre stadi larvali di *Oreodytes rivalis* Gyll. e *Hyphydrus aubei* Ganglb. e considerazioni sul comportamento di alcuni caratteri esoscheletrici nelle larve della subf. Hydroporinae. Entomologica, Bari, 13: 85-119.

Hammond, P.M. 1979. Wing-folding mechanisms of beetles, with special reference to investigation of adephagan phylogeny (Coleoptera). pp.113-180. *In* Carabid beetles: their evolution, natural history and classification. T.L. Erwin, G.E. Ball, D.R. Whitehead, and A.N. Halpern (Editors). Dr. W. Junk bv Publishers, The Hague, x+635 pp.

Jeppesen, P.C. 1986. Dytiscid beetles in Greenland, with description of the three larval stages of *Hydroporus melanocephalus* (Marsham, 1802). Entomologica Basiliensia, 11: 67-79.

Kavanaugh, D.H. 1986. A systematic review of amphizoid beetles (Amphizoidae: Coleoptera) and their phylogenetic relationships to other Adephaga. Proceedings of the California Academy of Sciences, 44: 67-109.

Matta, J.F. 1983. Description of the larva of *Uvarus granarius* Aubé with a key to the Nearctic Hydroporinae larvae. Coleopterists Bulletin, 37: 203-207.

Matta, J.F. and D.E. Peterson. 1985. The larvae of six Nearctic *Hydroporus* of the subgenus *Neoporus* (Coleoptera: Dytiscidae). Proceedings of the Academy of Natural Sciences of Philadelphia, 137: 53-60.

McIver, S.B. 1982. Sensilla of mosquitoes (Diptera: Culicidae). Journal of Medical Entomology, 19: 489-535.

Nichols, S.W. 1985. *Omophron* and the origin of Hydradephaga (Insecta: Coleoptera: Adephaga). Proceedings of the Academy of Natural Sciences of Philadelphia, 137: 182-201.

Nilsson, A.N. 1986. Larval morphology and phenology of four Fennoscandian species of *Hydroporus* Clairville (Coleoptera: Dytiscidae). Aquatic Insects, 7: 165-172.

Nilsson, A.N. 1987a. The 3rd-instar larvae of 8 Fennoscandian species of *Hydroporus* Clairville (Coleoptera: Dytiscidae), with notes on subgeneric classification. Entomologica Scandinavica, 17: 491-502.

Nilsson, A.N. 1987b. Larval morphology of Fennoscandian *Oreodytes* Seidlitz (Coleoptera: Dytiscidae), with notes on hydroporine leg chaetotaxy and taxonomy. Entomologisk Tidskrift, 108: 99-108.

Nilsson, A.N. 1988. A review of primary setae and pores on legs of larval Dytiscidae (Coleoptera). Canadian Journal of Zoology, 66: 2283-2294.

Ruhnau, S. 1986. Phylogenetic relations within the Hydradephaga (Coleoptera) using larval and pupal characters. Entomologica Basiliensia, 11: 231-271.

Ward, R.D. 1979. Metathoracic wing structures as phylogenetic indicators in the Adephaga (Coleoptera). pp. 181-192. *In* Carabid beetles: their evolution, natural history and classification. T.L. Erwin, G.E. Ball, D.R. Whitehead (Editors). Dr. W. Junk bv Publishers, The Hague, x+635 pp.

Watts, C.H.S. 1970. The larvae of some Dytiscidae (Coleoptera) from Delta, Manitoba. Canadian Entomologist, 102: 716-728.

Wolfe, G.W. 1985. A phylogenetic analysis of plesiotypic hydroporine lineages with an emphasis on *Laccornis* Des Gozis (Coleoptera: Dytiscidae). Proceedings of the Academy of Natural Sciences of Philadelphia, 137: 132-155

Wolfe, G.W. and R.E. Roughley. 1985. Description of the pupa and mature larva of *Matus ovatus ovatus* (Coleoptera: Dytiscidae) with a chaetotaxal analysis emphasizing mouthparts, legs and urogomphus. Proceedings of the Academy of Natural Sciences of Philadelphia, 137: 61-79.

Young, F.N. 1980. Predaceous water beetles of the genus *Desmopachria* Babington: the subgenera with descriptions of new taxa (Coleoptera: Dytiscidae). Revista de Biologia Tropical, 28: 305-321.

REVISION OF THE GENUS *QUEDA* SHARP (COLEOPTERA: DYTISCIDAE)[1]

Olof Biström
Finnish Museum of Natural History
Entomology Division
Norra Järnvägsgatan 13, SF-00100
Helsingfors, Finland.

Quaaestiones Entomologicae
26: 211–220 1990

ABSTRACT

This revision of the genus Queda *Sharp, 1882 (occurring in Central and South America) is based on examination of adult specimens. The systematic position of the genus is briefly reviewed. Structural features of adults are described and figured.* Q. youngi *n.sp. is described from Panama, Venezuela and Brazil. A lectotype is designated for* Q. compressa *Sharp and* Q. hydrovatoides *Zimmermann.*

INTRODUCTION

This revision is a part of a larger taxonomic study of members of the dytiscid tribe Hydrovatini of the subfamily Hydroporinae. Examination of material of the genus *Queda* revealed an undescribed species and additionally it was discovered that no lectotype designations were made for the two previously recognized species. Thus an evaluation of the present taxonomy of *Queda* Sharp is justified.

Few authors have discussed the systematics of the genus *Queda*. The genus was introduced by Sharp (1882), with only one species, *Q. compressa* Sharp. The genus *Queda* was assigned to Hydrovatini, a tribe which includes only two genera: *Queda* and *Hydrovatus* Motschulsky. According to Sharp (1882) adult members of this tribe are distinguished from other hydroporines by having the posterior coxal cavities widely separated, each with an elongate coxal excision, and extra rimal lobe. Since Sharp, few studies have been published, that deal with classification of *Queda*. Zimmermann (1921) introduced a second species. A phylogenetic investigation of some plesiomorphic hydroporines by Wolfe (1988) considered also the position of Hydrovatini and the two genera attributed to it. He concluded that *Hydrovatus* and the tribe Methlini could form a monophyletic unit, and that assignment of *Queda* to Hydrovatini may be uncertain (*cf.* also Wolfe 1985). With present state of knowledge, *Queda* could still be monophyletic, exhibiting characteristics not found in other Hydrovatini. I am, however, not able to decide if these character states are apomorphies or plesiomorphies - only that these characteristics distinguish *Queda* from the genus *Hydrovatus*.

---

[1] Contribution to the study of Dytiscidae 51.

MATERIAL AND METHODS

The material (in all 27 specimens) for the present study came from a number of collections abbreviated in the text as follows:

BMNH	British Museum (Natural History), Cromwell Road, London, England (dr. Martin Brendell)
CY	Coll. Young, Indiana Univ., Dept. Biology, Bloomington, Indiana, USA (Prof. Frank N. Young)
MNHN	Museum National d'Histoire Naturelle, Rue de Buffon 45, Paris, France (Mlle Hélène Perrin)
MZH	Zoological Museum, University of Helsinki, N. Järnvägsg. 13, Helsingfors, Finland
ZSM	Zoologische Staatssammlung, Münchhausenstr. 21, München, FRG (dr. Gerhard Scherer)

The methods for examination of material and presentation of literature follow the same format as Biström (1982). Illustrations of genitalia are made with the technique explained in Biström (1988).

TAXONOMY

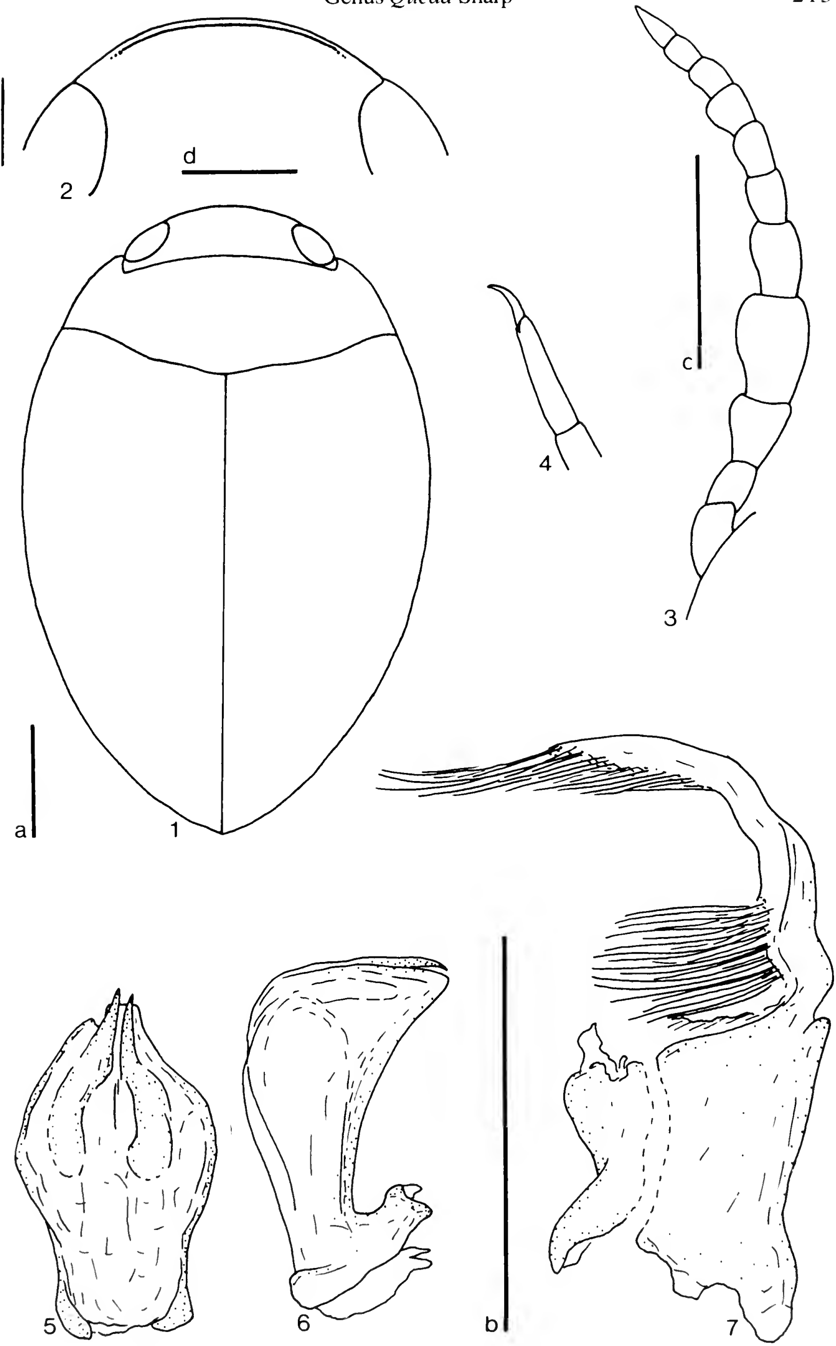
Queda Sharp

Queda Sharp 1882:320, 336, 849; Zimmermann 1919:126; 1920:36; Blackwelder 1944:75; Omer-Cooper 1965:93; Wolfe 1988:327-344. Type species: *Queda compressa* Sharp, 1882 by monotypy.

Diagnosis of Hydrovatini and Queda..— Hydroporines with base of trochanter partially concealed by apicolateral portion of metacoxal process, pronotum without longitudinal, lateral impressed lines, metatarsal claws, equal, prosternal process with apex broad, subtriangular or spatulate, mesocoxae widely separated, metacoxal process with posterior margin incised are assigned to Hydrovatini. Adult specimens of *Queda* are distinguished from these of *Hydrovatus* by form of the metacoxal excision, which in members of *Queda* are shorter in the longitudinal than in the transverse direction (Fig. 13, 21). Additionally, only the fringes of labrum are visible (in *Hydrovatus* labrum visibly exserted), and the body apically is not acuminate, as are most *Hydrovatus* species, and finally members of *Queda* always lack a stridulatory apparatus on ventral side of body (in males of some *Hydrovatus* species a distinct stridulatory apparatus visible on ventral side of body).

Queda is restricted geographically to Central and South America.

The natural history of *Queda* is unknown.



Figs. 1–7. *Queda compressa* Sharp. 1, habitus; 2, head; 3, male antenna; 4, apex of male metatarsus; 5, penis, dorsal view; 6, penis, lateral view; 7, paramere. Scale bars: Figs. 1 (a), 5–7 (b) = 1.0 mm; Figs. 2 (d), 3, 4 (c) = 0.5 mm.

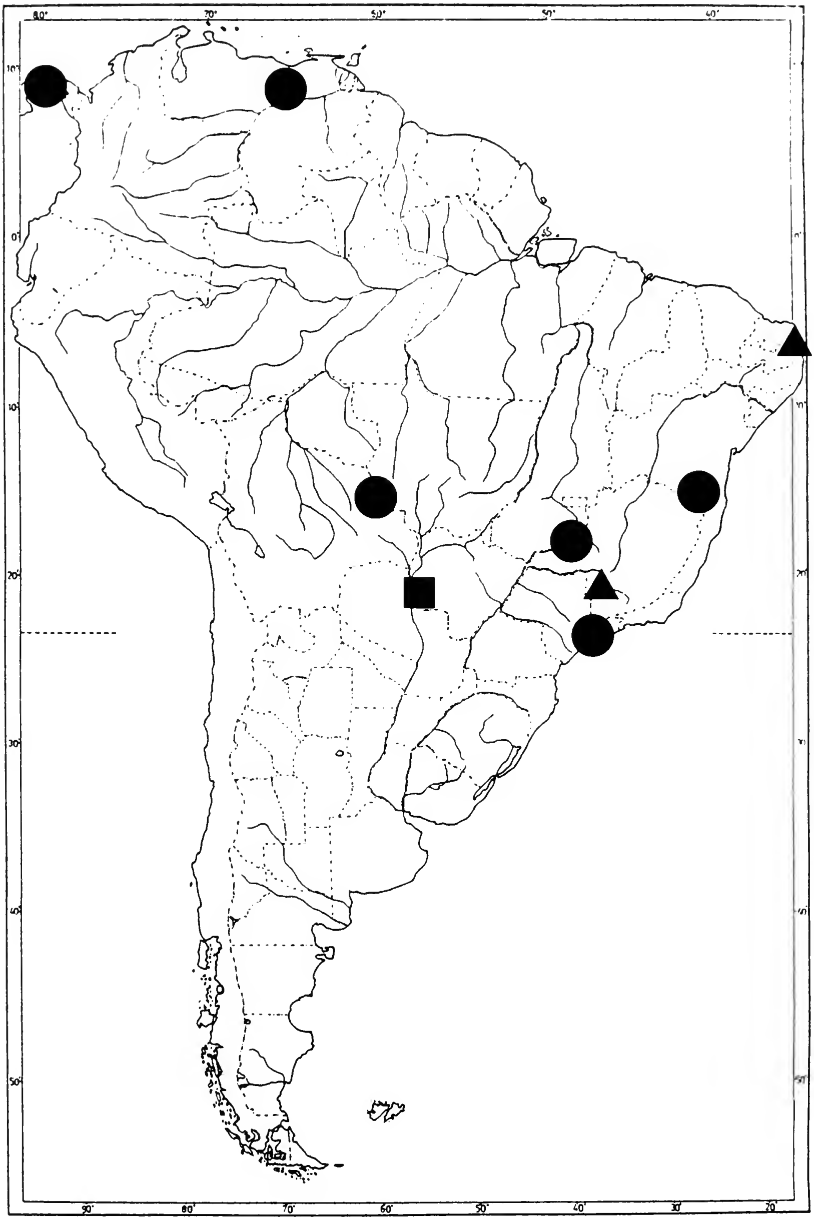
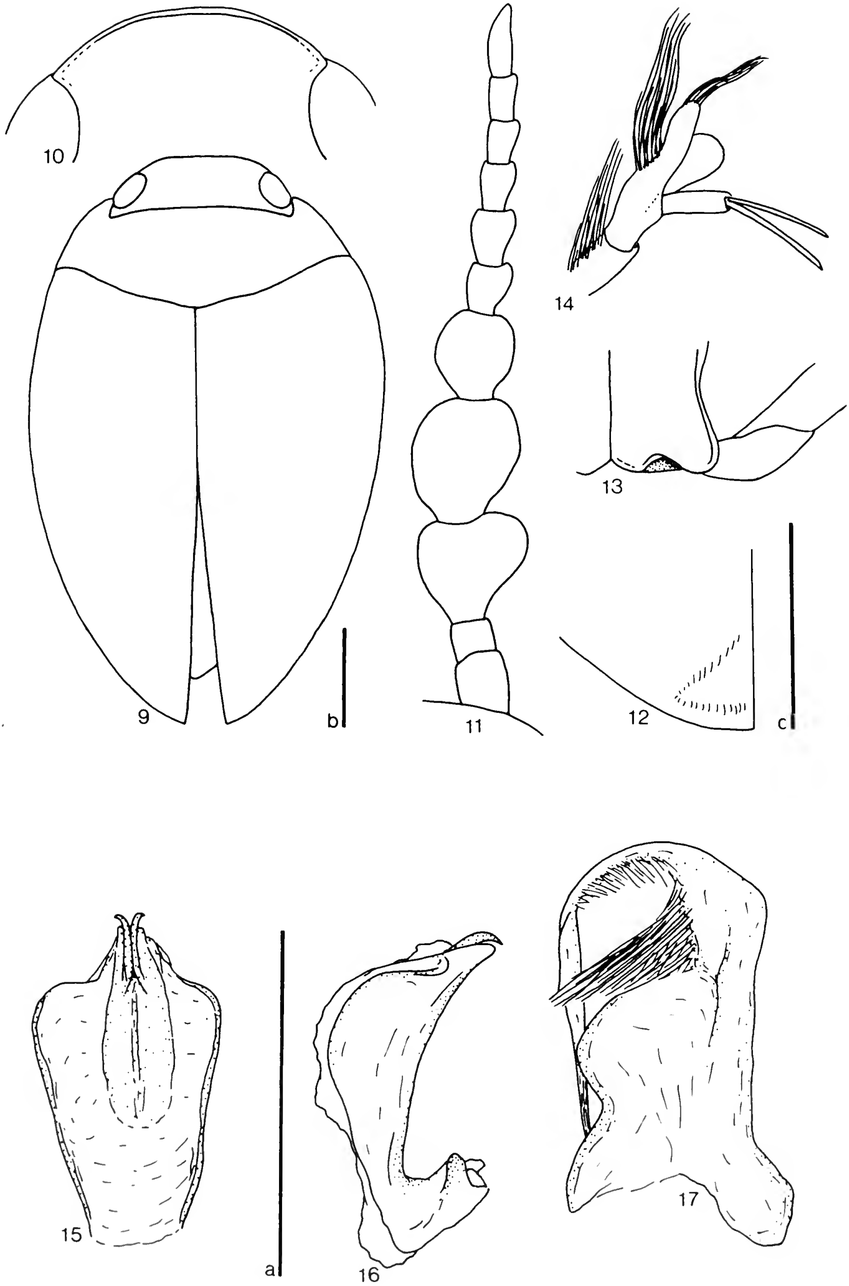


Fig. 8. Known distribution of *Queda* species. Symbols: triangle, *Q. compressa* Sharp; dot, *Q. youngi* n. sp.; square, *Q. hydrovatoides* Zimmermann.



Figs. 9–17. *Queda youngi* n.sp. 9, habitus; 10, head; 11, male antenna; 12, apex of elytron; 13, male metacoxal region.; 14, apex of male metatarsus; 15, penis, dorsal view; 16, penis, lateral view; 17, paramere. Scale bars: Figs. 11, 14–17 (a), 9 (b), 10, 12, 13 (c) = 1.0 mm.

Key to species

1 Smaller specimens (length of body 2.50-2.76 mm).. ....*Q. hydrovatoides* Zimmermann. p. 219

1' Larger specimens (length of body 5.00-6.20 mm)..2

2 Male metarsomere 4 modified, bilobed (Fig. 14); male antennomeres 3 to 5 broader, antennomere 3 wider than long (Fig. 11)................................ ....*Q. youngi* n.sp., p. 216

2' Male metarsomere 4 not modified, similar in shape to metarsomere 3 (Fig. 4); male antennomeres 3 to 5 narrower, antennomere 3 longer than wide (Fig. 3)..*Q. compressa* Sharp, p. 216

Queda. compressa Sharp

Figs. 1–7

Queda compressa Sharp 1882:336; Zimmermann 1920:36; 1921:206; Blackwelder 1944:75; Wolfe 1985:132-155; 1988:329.

Queda conspersa; Zimmermann 1921:191 (lapsus).

Type locality.— Santa Rita, Brazil.

Type material— Lectotype, ♂, by present designation: *Queda compressa* ♂ Type Santa Rita 1850 D.S./Type/Type 25/S. America Brazil/Sharp Coll. 1905-313/*Queda compressa* Brazil (BMNH). - Paralectotypes. *Queda compressa* Ind. typ. D.S./Cotype/S. America Brazil/Sharp Coll. 1905-313 (1 BMNH); Cotype/S. America Brazil/*Queda compressa* Sharp co-type (1 BMNH).

Additional material studied. Brazil: Minas Gerais/F. Sahlb./*Q._compressa* Sharp det. A. Zimmermann (1 MZH).

Diagnosis.— See below under diagnosis of *Q. youngi* n.sp.

Only features which differ from those given for *Q. youngi* are listed below.

Description.— Length of body 5.20-5.48 mm, breadth 3.44-3.52 mm. Habitus (Fig. 1).

Head. Frontal margin at eyes not visible from above (Fig. 2). Antennal segments 3 to 5 moderately flattened (Fig. 3).

Legs. Metatarsus simple, not modified (Fig. 4).

Male genitalia: Fig. 5-7. Only minor differences from male genitalia of *Q. youngi* recognized. Their diagnostic value is unclear. Paramere with a dense hairtuft above basal part (cf. *Q. hydrovatoides*).

Female. Antennae slender, without flattened segments.

Distribution.— Brazil (Fig. 8).

Queda. youngi n.sp.

Figs. 9–17

Type locality.— Encruzilhada, Brazil.

Type material.— Holotype, ♂. Brazil Bahia Encruzilhada XI.7. 72 960 m M. Alvarenga (CY). - Paratypes. Panama Tocumen IX.7-11. 70 D Navas BLT/*Queda compressa* Zimm. Det. F.N. Young (1 MZH). Panama Tocumen vi. 1-5. 70 BLT Diego Navas (2 CY, 1 MZH). Venezuela: S. Maria de Ipire (Edo. Guarino) m. 200/Bordon leg. 21-10-1961 (1 CY). Brazil: Sao Paulo Piracicaba 10 Jan. 1966 Blacklight A. Triplehorn (1 CY). Minas Gerais Aguas Vermelhas xii. 1983 BLT M. Alvarenga (1 CY). Matto Grosso Caceres xii. 1955 M. Alvarenga leg. (1 CY).

Derivation of specific epithet.— The new species is named after Professor Frank N. Young (Indiana), who on several occasions kindly has loaned material for my studies on Dytiscidae.

Diagnosis.— Specimens are very similar to those of *Q. compressa*, but male specimens at least are very easily distinguished by comparison of form of metatarsus (markedly modified in *Q. youngi*) and by the more flattened, broader third to fifth antennomeres in *Q. youngi*. Females of the two species are difficult to distinguish. Those of *Q. youngi* are almost totally black to blackish ferrugineous in dorsal colour while those of *Q. compressa* have a ferrugineous head and dark ferrugineous to ferrugineous pronotum. Additionally, the pronotal punctation is generally coarser in *Q. youngi* than in *Q. compressa*. Possibly *Q. youngi* is identical to the undescribed species mentioned by Sharp (1882:336).

Description.— Length of body 5.00-6.20 mm, breadth 3.20-3.96 mm. Habitus (Fig. 9).

Head. Blackish ferrugineous to dark ferrugineous. Punctation rather fine, distinct, fairly dense, head posteriorly almost impunctate. Shiny, not microsculptured, except posterior to eyes where fine reticulation discernible. Head frontally rounded, finely margined, but margin slightly developed close to eyes (Fig. 10). Surface of head posterior to frontal margin and between eyes somewhat uneven. Antenna pale brown, segments 3 to 5 broadly flattened (Fig. 11).

Pronotum. Blackish to dark ferrugineous. Punctation rather fine, fairly dense, somewhat irregularly distributed. Shiny, not microsculptured. Sides of pronotum rounded.

Elytra. Black to dark ferrugineous, palest laterally, but without colour pattern. Punctation rather fine, dense, slightly irregularly distributed. Without distinct rows of punctures. Shiny, not microsculptured. Apically elytral surface depressed (Fig. 12). Epipleuron dark ferrugineous, punctation rather fine and dense, surface shiny, not microsculptured.

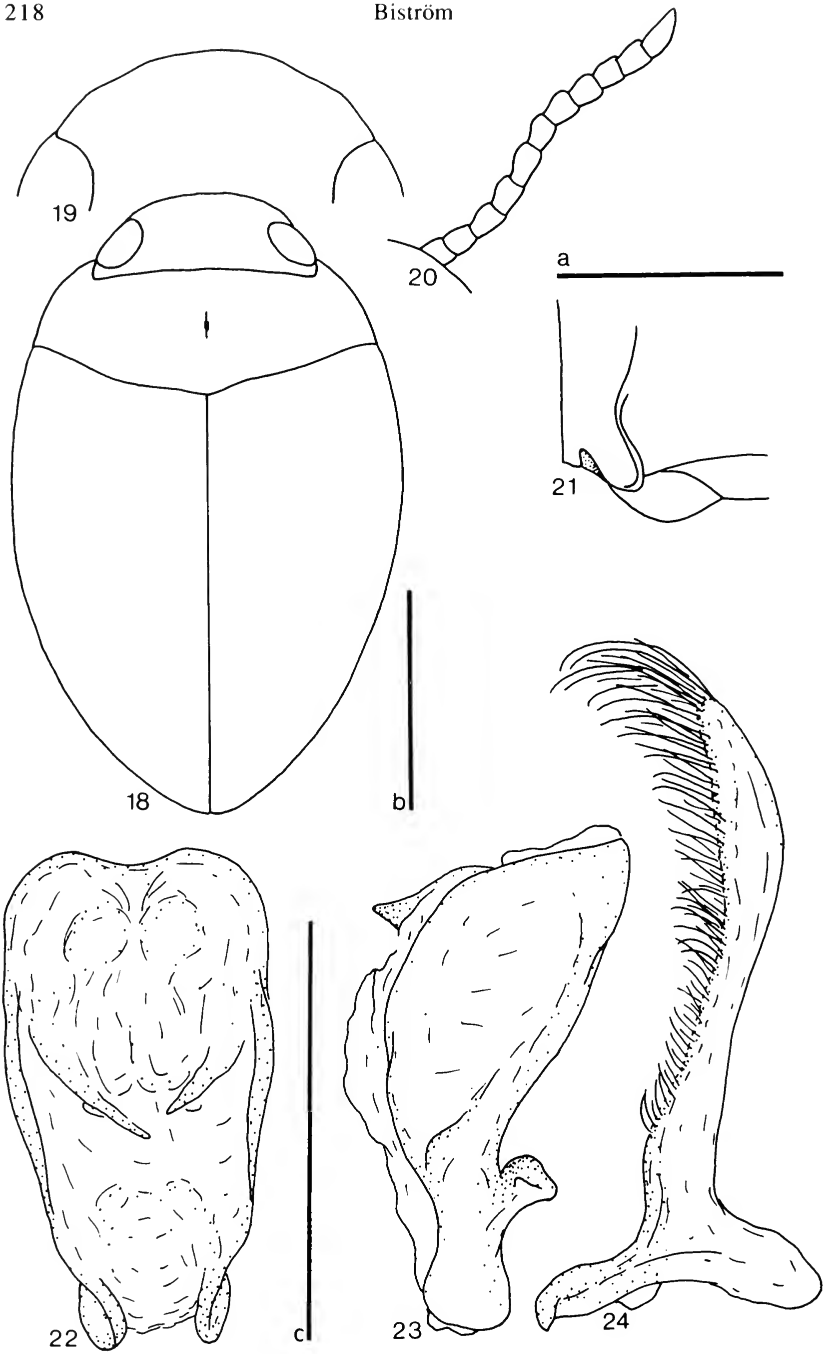
Ventral surface. Black to dark ferrugineous. Punctation fairly coarse to rather fine, fairly dense but somewhat irregularly distributed. Shiny, not microsculptured. Prosternal process laterally margined, medial area slightly uneven, densely punctate.

Legs. Dark ferrugineous to pale brown. Pro- and mesotarsus fairly broad. Metatarsus strongly modified (Fig. 14).

Male genitalia. Fig. 15-17. See also under *Q. compressa*.

Female. Antenna slender, without flattened segments. Metatarsi simple, not modified.

Distribution.— Panama, Venezuela, Brazil (Fig. 8).



Figs. 18-24. *Queda hydrovatoides* Zimmermann. 18, habitus; 19, head; 20, male antenna; 21, metacoxal region; 22, penis, dorsal view; 23, penis, lateral view; 24, paramere. Scale bars: Figs. 19–21 (a) = 0.5 mm; Fig. 18 (b) = 1.0 mm; Figs. 22–24 (c) = 0.4 mm.

Queda. hydrovatoides Zimmermann
Figs 18–24

Queda hydrovatoides Zimmermann 1921:191, 206; Blackwelder 1944:75.

Type locality.— Corumba, Brazil.

Type material — Lectotype, ♂, by present designation: Brasilien/Matto-Grosso Corumba/Type/Samml. A. Zimmermann (ZSM). - Paralectotypes. Principally with same data as lectotype (10 ZSM, 3 MNHN).

Diagnosis.— Specimens of Q. hydrovatoides are easily separated from those of the two other Queda species by the distinctly smaller body length.

Description.— Length of body 2.50-2.76 mm, breadth 1.64-1.78 mm. Habitus (Fig. 18).

Head. Dark ferrugineous to ferrugineous. Punctation fine to very fine, rather sparse, head posteriorly with punctures hardly visible. Rather shiny, finely microsculptured (meshes very weakly developed, partly indistinct). Head frontally rounded and posterior to sharp outline widely and quite distinctly depressed. Head not margined frontally (Fig. 19). Antenna pale ferrugineous to ferrugineous, apically darkest, rather slender (Fig. 20).

Pronotum. Dark ferrugineous to ferrugineous. Punctation on a single specimen, rather fine to fine, sparse to fairly dense (densest and coarsest laterally). Finer and coarser punctures intermixed. In central part with a minute but quite sharp longitudinal impression. Rather shiny, very finely microsculptured (meshes partly indistinct). Sides of pronotum rounded.

Elytra. Dark ferrugineous to ferrugineous, without distinct colour pattern. Punctation double, consisting of mixed, very fine (sometimes partly indistinct punctures) and quite coarse punctures. Both kinds of punctures quite evenly distributed, except coarser punctures almost absent laterally. Rather shiny, microsculptured (meshes discernible but slightly developed). Epipleuron ferrugineous to dark ferrugineous, quite densely punctate, rather shiny, with indistinct reticulation.

Ventral surface. Dark ferrugineous to ferrugineous. Punctation fairly coarse to rather fine, fairly dense. Punctation coarsest on metacoxal plates and finest on apical sternite. Rather shiny, very finely microsculptured. Meshes very slightly developed but generally discernible. Prosternal process laterally narrowly but distinctly margined, medial area slightly convex, surface uneven, with indistinct punctation and minute ridges.

Legs. Ferrugineous to dark ferrugineous. Pro- and mesotarsi fairly broad.

Male genitalia. Fig. 22-24. Details in outline of penis different from the two other Queda species. Paramere without dense hairtuft above basal part.

Female. Externally as male.

Distribution.— Brazil (Fig. 8).

ACKNOWLEDGEMENTS

I express my sincere thanks to curators of different collections and private persons for kind loan arrangements of material for this study. I am also grateful to Dr. Maria del Carmen Coscaron (La Plata) and to an anonymous referee for valuable comments on the manuscript.

REFERENCES CITED

Biström, O. 1982. A revision of the genus *Hyphydrus* Illiger (Coleoptera, Dytiscidae). Acta Zoologica Fennica,165: 1–121.

Biström, O. 1988. Generic review of the Bidessini (Coleoptera, Dytiscidae). Acta Zoologica Fennica, 184: 1–41.

Blackwelder, R.E. 1944. Checklist of the coleopterous insects of Mexico, Central America, The West Indies, and South America. 1. Bulletin of the United States National Museum, 185: 1–188.

Omer-Cooper, J. 1965. Coleoptera: Dytiscidae. South African Animal Life, 11: 59–214.

Sharp, D. 1882. On aquatic carnivorous Coleoptera or Dytiscidae. Scientific Transactions Royal Dublin Society, 2: 179–974.

Wolfe, G.W. 1985: A phylogenetic analysis of plesiotypic Hydroporinae lineages with an emphasis on *Laccornis* Des Gozis (Coleoptera: Dytiscidae). Proceedings of the Academy of Natural Sciences of Philadelphia, 137: 132–155.

Wolfe, G.W. 1988: A phylogenetic investigation of *Hydrovatus*, Methlini and other plesiotypic hydroporines (Coleoptera: Dytiscidae). Psyche, 95: 327–344.

Zimmermann, A. 1919. Die Schwimmkäfer des Deutschen Entomologischen Museums in Berlin-Dahlem. Archiv für Naturgeschichte, (A) 83: 68-249.

Zimmermann, A. 1920. Dytiscidae. Coleopterorum Catalogus 4(71), 296 pp.

Zimmermann, A. 1921. Beiträge zur Kenntniss der südamerikanischen Schwimmkäferfauna nebst 41 Neubeschreibungen. Archiv für Naturgeschichte, (A) 87: 181–206.

THE SYSTEMATIC POSITION OF THE GENUS *AGABETES* CROTCH WITHIN DYTISCIDAE (COLEOPTERA, ADEPHAGA)

Ernst-Gerhard Burmeister
Zoologische Staatssamlung
Münchhausenstrasse 21
D-8000 München 60
Federal Republic of Germany

Quaestiones Entomologicae
26: 221–238 1990

ABSTRACT

Structural features of the ovipositor, its musculature and associated structures are described and used to assess the phylogenetic position of Agabetes *Crotch. Assignment to the subfamily Colymbetinae is not tenable because it is based on plesiomorphic character states. Rather it should be assigned to the subfamily Agabetinae which is the sister group to Laccophilinae based on six synapomorphies: (1), ventral teeth on genital appendages VIII; (2), genital appendages divided proximally into three separate arms; and (3), with the ventromedial arm articulated with gonocoxosterna; (4), presence of muscle 26, and unique origins; (5), of muscle 28 which is the retractor muscle of genital appendages VIII; and (6), of muscle 37 on lateral arms of genital appendages VIII.*

ZUSAMMENFASSUNG

Die Anatomie des Ovipositors mit seiner Muskulatur und Anhangsorganen von Agabetes acuductus *Harris wird beschrieben. Die Merkmale werden zur Klärung des systematischen Stellung der Gattung* Agabetes *Crotch innerhalb der Dytiscidae heranzgezogen. Die bisherige Zuordnung zur Unterfamilie Columbetinae beruht auf plesiomorphen Merkmalen. Auf Grund folgender sechs Synapomorphien ist die Unterfamilie Agabetinae als Schwestergruppe der Laccophilinae aufzufassen: (1) Genitalanhänge VIII mit ventralen Zahnreihen; (2) Genitalanhänge VIII cranial in drei Teile aufgespalten, der (3) ventromediane unpaare Fortsatz besitzt jederseits ein Gelenk mit den lateralen Gonocoxosterna; (4) Vorhandensein des Depressors der Genitalanhänge VIII (M 26) und der Ursprung (5) des Retractors (M 28) zusammen mit der Protractor der Genitalanhänge (M 37) an den Lateralfortsatzen (6). Die Bedeutung anderer Merkmale für die Phylogenie dieser Unterfamilien der Dytiscidae wird diskutiert.*

INTRODUCTION

Crotch (1873) proposed the genus *Agabetes* to receive the single Nearctic species, *Colymbetes acuductus* Harris. Zimmermann (1920) assigned *A. acuductus* to the tribe Copelatini of the subfamily Colymbetinae. However, at an earlier date, Van den Branden (1885) had provided the family-group name Agabetini for this genus. Presumably, Van den Branden did this because Sharp (1882) had noted that *Agabetes* did not show much affinity to other groups of colymbetines. Many North American authors (*e.g.*, Arnett 1968, Dillon and Dillon 1972) have used the tribal rank of Agabetini and placed it within the subfamily Colymbetinae. Thus for many years, *Agabetes* was assigned to various groups of Colymbetinae.

Burmeister (1976) first demonstrated a relationship among *Agabetes* and *Laccophilus* Leach (Laccophilinae), based on apomorphic structural features of female genitalia. Subsequently, Nilsson (1989) described a second species of *Agabetes*, *A. svetlanae*, from Iran. He discussed certain features of adults and larvae of *Agabetes* and placed it within the tribe Agabetini Van den Branden as the sister group to Laccophilini Bedel, both within the subfamily Laccophilinae Bedel. Nilsson (1989) noted that I had studied members of only one genus (*Laccophilus*) of 11 genera presently assigned to Laccophilinae (Brancucci 1983).

I did not examine any specimens of *A. svetlanae* which, according to Nilsson (1989), is very similar to *A. acuductus*. Therefore, structural features of adults of *A. acuductus* are very likely generic features.

The purposes of this paper are: (1), to present a description of the ovipositor and related structures of *Agabetes acuductus* Harris; (2), to provide further information about these structures among other genera of Laccophilinae; and (3), to examine the phylogenetic position of *Agabetes* and Laccophilinae. This represents an extension of my earlier research (Burmeister 1976) on this topic.

MATERIALS AND METHODS

Materials and methods used are described in Burmeister (1976). The terms and definitions used herein are explained in my previous paper. To facilitate comparison among illustrations, in this paper the structures and muscles are labelled in the same manner as in Burmeister (1976).

In addition to the taxa listed in Burmeister (1976), specimens of the following species were examined for this study.

Dytiscidae:Laccophilinae — *Neptosternus sumatrensis* Régimbart, *N. ornatus* Régimbart, *N. cosmani* Peschet, *N. jacobsoni* Zimmermann, *Laccodytes americanus* Peschet, *Laccophilus obliquatus* Régimbart, *L. maculosus maculosus* Germar, *L. maculosusus decipiens* LeConte, and *L. pictus* Castelnau; Colymbetinae — *Copelatus pulchellus* Klug, *C. erichsoni* Guer., *C. aethiopicus* Régimbart, *C. substriatus* Kirsch, *Lacconectes oceanicus* Régimbart, *L. laccophiloides* Zimmermann, *Matus bicarinatus* Say, and *Agaporomorphus knischi* Zimmermann; Amphizoidae — *Amphizoa lecontei* Matthews, and *A. insolens* LeConte.

OVIPOSITOR OF *AGABETES ACUDUCTUS* (HARRIS)

The general structure of the ovipositor of *A. acuductus* is shown in Fig. 6. In many aspects it is similar to other types of tactile ovipositor. The elongate gonocoxae are equipped with ventro-apical, small setae and in this character they are similar to those of females of Copelatini (Burmeister 1976). The elongate, narrow portions of tergum IX appear clasper-like and are connected with the gonocoxae by a ventral articulation. Tergum IX has a broad dorsal apodeme in the middle where the depressor (M32, Fig. 6) and levator muscles (M33, Fig. 6) have their origins. The origin of the depressor is on the inner side of tergum IX ventral to that of the levator. Both muscles are situated close together and are stretched out in a horizontal plane at rest. On the outer side of the process of tergum IX is the strong muscle (M15, Fig. 6) which acts as protractor of tergum IX.

The entire ovipositor is inserted into the gonocoxosternum (coxosternum). The gonocoxosterna (CS) are rectangular in shape (Figs. 6, 7a, 7c) with a ventroproximal appendix (A, Figs. 6, 7a-c). The ventromedial and distal borders of the gonocoxosterna are fringed with rows of short setae (Fig. 6a). At rest, the goncoxosterna are flat on top of sternum VIII. The small ventromedial appendix (A) of the gonocoxosternum is in contact with the unpaired, medial portion of genital appendages VIII (GH VIII, Figs. 6, 7). This is the same kind of articulation of gonocoxosternum with genital appendages VIII found in laccophilines (Fig. 4) (Burmeister 1976).

Genital appendages VIII are elongate and extend posteriorly nearly to the ventral papilla of the gonocoxae which have distal tactile setae (Fig. 7a). Genital appendages VIII are complex. They are fused into a single structure apically (Fig. 7b) but proximally there are three portions (Figs. 7a, b). The ventral portion is single and its distal end is differentiated by a small, membranous slit from the pair of lateral sclerites. The proximal tip of the ventral portion is articulated with the lateral appendages of the gonocoxosterna (Figs. 7, 8, 9). The more dorsal portion of this structure is paired proximally into lateral clasps. These clasps are elongated proximally past the point of articulation of the ventral portion (Figs. 7a, b). Distally, the fused portion of genital appendages VIII, is equipped with two, ventrolateral rows of small teeth extending to the tip. The dilator and depressor muscle (M28, Fig. 6) has its origin at the dorsoproximal margin of the gonocoxosternum.

The bursa copulatrix (bc, Fig. 7b) which receives the spermatophore during copulation, is elongated anteriorly with a well-developed system of musculature surrounding it. The receptaculum seminis is on the left side and is connected to the bursa by the ventral ductus receptaculi. The ductus seminalis originates at the receptaculum and extends posteriorly to the dorsal area of the divided vagina (va, Figs. 7b, d). At rest, the vagina ends distally between the three portions of genital appendages VIII.

PHYLOGENETIC CONSIDERATIONS

Plesiomorphic features of *Agabetes*.

The theory of cladistic analysis (Hennig 1950, 1981) specifies that primitive characteristics of any taxonomic unit can not be used to demonstrate its relationship with another group. Only derived or apomorphic features are used to document phylogenetic affinity. Nevertheless, the plesiomorphic characters of a group are important in the formulation of a ground-plan of structural features within a taxon.

The traditional placement of *Agabetes* within the subfamily Colymbetinae is based on the common presence of plesiomorphic character states. Among these are the following: (a) Size of specimens as indicated by total length which ranges from about 6.3 to 7.5 mm. (b) In specimens of *Agabetes*, the scutellum is visible externally (Fig. 1g). The scutellum is very small and anteriorly it is depressed to the level of the mesothoracic tergum and it is connected to the prothorax. (c) The metatarsomeres are not lobed posterolaterally. (d) Male specimens have pro- and mesotarsomeres I to III narrowly widened and supplied with numerous adhesive setae used to grasp the female during copulation. Character states (a) and (d) are widespread among members of Laccophilinae and Colymbetinae; character states (b) and (c) are widespread among members of Colymbetinae and Dytiscinae. Therefore these features are plesiomorphic based on out-group analysis.

Presumptive synapomorphies of *Agabetes* and Colymbetinae

Certain other character states of *Agabetes* could be interpreted as synapomorphies of *Agabetes* and Colymbetinae. One aspect of my study was to determine whether these are shared derived features or independently derived in both (or more) groups. These characters are eye shape and form of metepisternum.

Eye shape.— Two states: (1) inner margin rounded (Fig. 2a), (2) inner margin emarginate (Figs. 2b-f).

In many keys to subfamily and diagnoses of Colymbetinae (*e.g.*, Watts 1978) the emarginate eye of colymbetines is used as a diagnostic feature. The emargination is formed by a protrusion of the frons dorsally and distally from the antennal insertion (Figs. 3b-f). Common presence of emarginate eyes could be interpreted, incorrectly, as a synapomorphy of *Agabetes* + Colymbetinae.

Specimens of *Agabetes* have emarginate eyes but the feature is not prominent (Fig. 2b), whereas in most colymbetines (*e.g.*, Fig. 2c, Franciscolo 1979), this feature is more pronounced. More revealing, however, is the presence of an emarginate eye in specimens of Noteridae (*e.g.*, Fig. 2e), Laccophilinae (*e.g.*, Fig. 2f) and *Copelatus* Erichson (Fig. 2d). Among laccophilines, members of *Laccophilus* and *Neptosternus* Sharp have a prominent ocular emargination.

In summary, the presence of an emarginate eye is not a synapomorphy of *Agabetes* and Colymbetinae. The polarity of this character was not determined during this study. Study of further outgroup taxa would be needed for this.

Relative length of metepisternum.— Two states: (1) metepisternum extended to mesocoxal cavity and forming part of the lateral wall of mesocoxal wall (Figs. 3a, c-h); (2) metepisternum not attaining the mesocoxal cavity (Figs. 3b,i).

Sharp (1882:222-228, 967-972) used this character extensively in his classification of Dytiscidae. It is clear from Sharp's discussion of this character that he considered state 2 as plesiomorphic. Kavanaugh (1986: 84, 92, 94, 95) also discussed this character but assessed state 2 as apomorphic. Kavanaugh's polarity of this character is most likely correct.

Among Adephaga, Kavanaugh (1986) reported state 1 for one species of gyrinid (*Spanglerogyrus albiventris* Folkerts; Spanglerogyrinae), some dytiscids, fossils of Liadytidae, Triaplidae and *Necronectulus* Ponomarenko, amphizoids as well as eodromeine and protorabine carabids. In all other Adephaga examined by Kavanaugh, state 2 is present. Examination of the distribution of this character on his cladogram (Kavanaugh 1986, Fig. 22) suggests that his derived state is found in many, otherwise unrelated groups of Adephaga.

Among dytiscids, members of Vatellini (Hydroporinae) and Laccophilinae exhibit state 2 whereas all other dytiscids possess the first state. Therefore, *Agabetes* (Fig. 3a) and Laccophilinae (Figs. 3b, i) have opposite states and, if Kavanaugh is correct, laccophilines possess the apomorphic state and *Agabetes* is grouped with colymbetines based on a plesiomorphic state. Even if it could be demonstrated that Sharp's polarity is correct, the amount of homoplasy found in the distribution of character states would suggest that this is a weak, phylogenetic character.

Autapomorphic features of Laccophilinae

The 11 genera of Laccophilinae form a homogeneous group. The subfamily exhibits six synapomorphies, numbered below as they appear on Fig. 10.

1. Scutellum hidden in dorsal view. This feature may be convergent in members of Hydroporinae.
2. Metatarsus with single claw.
3. Metatarsomeres with posterolateral lobe.
4. Male specimens with parameres very short.
5. Female specimens with tactile portion of gonocoxae without setae and oriented dorsodistally (Fig. 4). The distal portion of the gonocoxosternum tactile.
6. Female specimens with ovipositor with large teeth on apicoventral margin (Fig. 4).

Relationship of *Agabetes* and Laccophilinae

Burmeister (1976) briefly discussed possible synapomorphies of *Agabetes* and Laccophilinae. These features are discussed in further detail below. They are numbered as they appear on Fig. 10.

7. Genital appendages VIII with fused, distal portion with two rows of ventral teeth and appearing saw-like (Figs. 4, 6, 7, 8). In specimens of *Agabetes* (Fig. 6) these teeth are not prominent. In other groups of dytiscids, serrate gonocoxae are known only from female specimens of *Ilybius* Erichson (Agabini, Colymbetinae) and *Hydrovatus* Motschulsky (Hydrovatini, Hydroporinae). However, in other features the female genitalia of *Ilybius* and *Hydrovatus* are markedly different from each other and from either *Agabetes* and Laccophilinae (see Burmeister 1976).

8. Genital appendages VIII composed of three elements proximally which are fused distally. Details of this structure differ among *Agabetes* (Fig. 7a) and Laccophilinae (Figs. 7c, 9b). However, in all other dytiscids studied to date, there is no separation of the genital appendages VIII proximally (Burmeister 1976).

9. Genital appendages VIII articulated with a ventroproximal appendix of gonocoxosternum. No other dytiscids have this type of articulation (Burmeister 1976).

Female specimens of *Agabetes* have this articulation at the distal margin of the ventral portion of genital appendages VIII (A, Fig. 6). In those of *Laccophilus*, in which the two lateral and the ventral appendages are fused for much of their length, the articulation is at the bases of the lateral arms (Figs. 4, 8). The condition found in *Laccophilus* may be more derived relative to that of females of other genera of laccophilines examined, for instance, those of *Neptosternus* and *Laccodytes* Régimbart [and possibly *Napodytes* Steiner also, see Steiner (1981)]. In representatives of these genera the fusion of the lateral and ventral arms is less than that expressed by *Laccophilus*. The articulation with the gonocoxosterna is near the proximal end of the ventromedial process (Fig. 8).

10. Tergum IX with a divided, median, dorsally elongate appendage Figs. 4, 6). This structure is the site of origin of the tergogonocoxal muscles and in no other groups of Dytiscidae are there divided areas of tergum IX which are similar.

11. Distal depressor muscle (M26) of genital appendages VIII (Figs. 4, 6). This muscle has its origin on the distal, ventromedial edge of the gonocoxa and inserts ventrally on the ventromedial process of genital appendages VIII. These muscles do not exist in other Dytiscidae (Burmeister 1976).

12. Origin of vaginal protractor muscle (M37) on lateral arms of genital appendages VIII (Fig. 6). Among other dytiscids, in particular *Copelatus*, this muscle acts to dilate the vagina and vaginal papilla. In *Agabetes* and Laccophilinae the vagina is between the unfused arms of genital appendages VIII. Therefore in these taxa (but not in *Laccophilus*) dilation of the vagina is brought about as muscles 37 pull outward on the lateral arms. This functional complex may be important for manoeuvering the saw-like ovipositor during endophytic, egg deposition.

Muscle 40 which is also a flexor of genital appendages VIII is known only from the genus *Laccophilus* and does not occur in other genera of laccophilines examined . Earlier, I suggested that M40 could be derived from M36 (Burmeister 1976: 209). In *Laccophilus*, muscle 36 inserts on genital appendages VIII near where all three arms are fused, whereas muscle 40 is more distal and it connects with the short, unfused portions of the lateral and ventromedial arms (Burmeister 1976, Fig. 27). Therefore muscle 40 may have been derived as a result of greater fusion of genital appendages VIII in *Laccophilus* relative to that of other laccophilines.

13. Origin of retractor muscle (M28) of genital appendages VIII. In most dytiscids, muscle 28 originates on the ventral edge of the gonocoxosternum posterior to the ventral apodeme and inserts on the posterior end of genital appendages VIII which are fused distally. In Laccophilinae and *Agabetes,* M28 extends from the dorsoventral edge of the gonocoxosternum and the posterior ends of the lateral arms of genital appendages VIII which are separated distally. In part, the different origin of M28 is due to the very elongate genital appendages. Nevertheless, this muscle has a dual function in *Agabetes* and Laccophilinae. It acts as a retractor muscle when the genital appendages are pulled posteriorly toward the resting position; toward the end of the retraction process, M28 acts to dilate the lateral arms and depress the genital appendages into the final resting position.

Autapomorphies of *Agabetes*

Many autapomorphies of *Agabetes* could be suggested [see Nilsson (1989) for discussion of some of these]. Other possible autapomorphies are (a) absence of lateral pronotal bead, (b) elongate protarsal claws of males, (c) presence of deep impressions laterally on sternum VIII (which is the apical, visible sternal sclerite). In addition, the median lobe of the male genitalia is elongate and has two dorsal appendages. However, this last character state may well be plesiomorphic.

RELATIONSHIPS AND CLASSIFICATION OF *AGABETES*

The function of the ovipositor of *Agabetes* is undoubtedly similar to that of Laccophilinae even though I have not observed oviposition of *Agabetes.* In both taxa, the genital appendages are differentiated into elongate sclerites with ventral serrations. These are adapted for cutting into aquatic plants during oviposition. In *Agabetes,* the gonocoxae appear to have retained a sensory function as indicated by presence of ventro-apical setae; the gonocoxae are used to assess the nature of the substrate prior to oviposition. In contrast, the gonocoxae of laccophilines lack sensory setae and are in the form of a knife-like cutting apparatus.

The reconstructed phylogeny of *Agabetes* and Laccophilinae is shown in Fig. 10. It is clear that these taxa are sister groups. The remaining problem is relative ranking of these two taxa. Nilsson (1989) chose to arrange these taxa into two tribes (Agabetini and Laccophilini) of a single subfamily (Laccophilinae).

An alternate arrangement would be to have both taxa at the rank of subfamily and I prefer this arrangement. In part, this is because of the number of apomorphic character states which isolate both taxa as a monophyletic unit and the number of synapomorphies expressed by each taxon individually. An important element of this is comparison of the number of apomorphies and synapomorphies shown by other tribes and subfamilies. For instance, comparison of Fig. 48 of my previous analysis (Burmeister 1976) and the present Fig. 10 suggests that each of these taxa (*Agabetes* and Laccophilinae) is as distinctive as are the other subfamilies of Dytiscidae (Hydroporinae, Colymbetinae and Dytiscinae). An important consideration is that all of these apomorphic states are based on a single functional complex of characters (female ovipositor, associated muscular and apical abdominal segment). However, this relationship remains a preliminary hypothesis and is in need of further study. Examination of other functional complexes of characters may necessitate modifications of the relative rank of these taxa.

ACKNOWLEDGEMENTS

I express my gratitude to my colleague, Dr. G. Scherer, for the loan of specimens of Dytiscidae and to my wife, Hedwig Burmeister, for her helpful comments and for proof-reading this manuscript together with Dipl. biol. F. Foeckler. Also, Dr. R. E. Roughley, of Winnipeg, assisted in editing the manuscript.

REFERENCES CITED

Arnett, R.H. 1968. The Beetles of the United States (A manual for identification). Catholic University of America Press, Washington, D.C. xii + 1112 pp.

Brancucci, M. 1983. A new genus of the subfamily Laccophilinae (Coleoptera, Dytiscidae). Aquatic Insects, 5:251-254.

Balfour-Browne, F. 1940. British Water Beetles. Volume 1. The Ray Society, London. xix + 375 pp + 5 plates.

Burmeister, E.G. 1976. Der Ovipositor der Hydradephaga Coleoptera und seine phylogenetische Bedeutung unter besonderer Berrücksichtigung der Dytiscidae. Zoomorphologie, 85: 165-257.

Crotch, G.R. 1873. Revision of the Dytiscidae of the UnitedStates. Transactions of the American Entomological Society, 4: 383-424.

Dillon, E.S., and L. S. Dillon. 1961. A Manual of Common Beetles of Eastern North America. Row, Peterson and Co., Evanston, Ill. viii + 884 pp + 4 plates.

Franciscolo, M.E. 1979. Coleoptera. Haliplidae, Hygrobiidae, Gyrinidae, Dytiscidae. Fauna d'Italia XIV. Calderini, Bologna. vi + 804 pp.

Guignot, F. 1959-1961. Revision des Hydrocanthares d'Afrique (Coleoptera Dytiscoidea). Annales du Musée royal du Congo Belge, Tervuren, 70, 78, 90: 1-995.

Hennig, W. 1950. Grundzüge einer Theorie der phylogenetischen Systematik. Deutscher Zentralverlag, Berlin. 370 pp.

Hennig, W. 1981. Insect phylogeny. (Translated and edited by A.C. Pont, revisionary notes by D. Schlee et al.). John Wiley & Sons, Chichester, New York, Brisbane, Toronto. xxii + 514 pp.

Kavanaugh, D.H. 1986. A systematic review of amphizoid beetles(Amphizoidae: Coleoptera) and their phylogenetic relationships to other Adephaga. Proceedings of the California Academy of Sciences, 44: 67-109.

Nilsson, A.N. 1989. On the genus Agabetes Crotch (Coleoptera,Dytiscidae, with a new species from Iran. Annales entomologici Fennici, 55: 35-40.

Sharp, D. 1882. On aquatic carnivorous Coleoptera or Dytiscidae.Scientific Transactions of the Royal Dublin Society, 2 : 179-1003 + plates I-XVIII.

Steiner, W.E. 1981. A new genus and a new species of Laccophiline water beetle from Ecuador (Coleoptera:Dytiscidae). Pan-Pacific Entomologist, 57: 251-259.

Van den Branden, C. 1885. Catalogue des Coléoptères carnassiers aquatiques (Haliplidae, Amphizoidae, Pelobiidae et Dytiscidae). Annales de la Société entomologique de Belgique, 29: 5-114.

Watts, C.H.S. 1978. A revision of the Australian Dytiscidae (Coleoptera). Australian Journal of Zoology, Supplement Series, 57: 1-166 pp.

Zimmermann, A. 1920. Dytiscidae, Haliplidae, Hygrobiidae, Amphizoidae. Coleopterororum Catalogus, 71: 1-325. W. Junk, Berlin.

Zimmermann, A. 1933. Monographie der palärktischen Dytisciden. IV. Hydroporinae (4. Teil). Koleopterologische Rundschau, 19: 153-193. [Reprinted in Reitter, Edm. Bestimmungs-Tabellen der europischen Coleopteren. 111 Heft. Edm. Reitter Verlag, Troppau. 41 pp.]

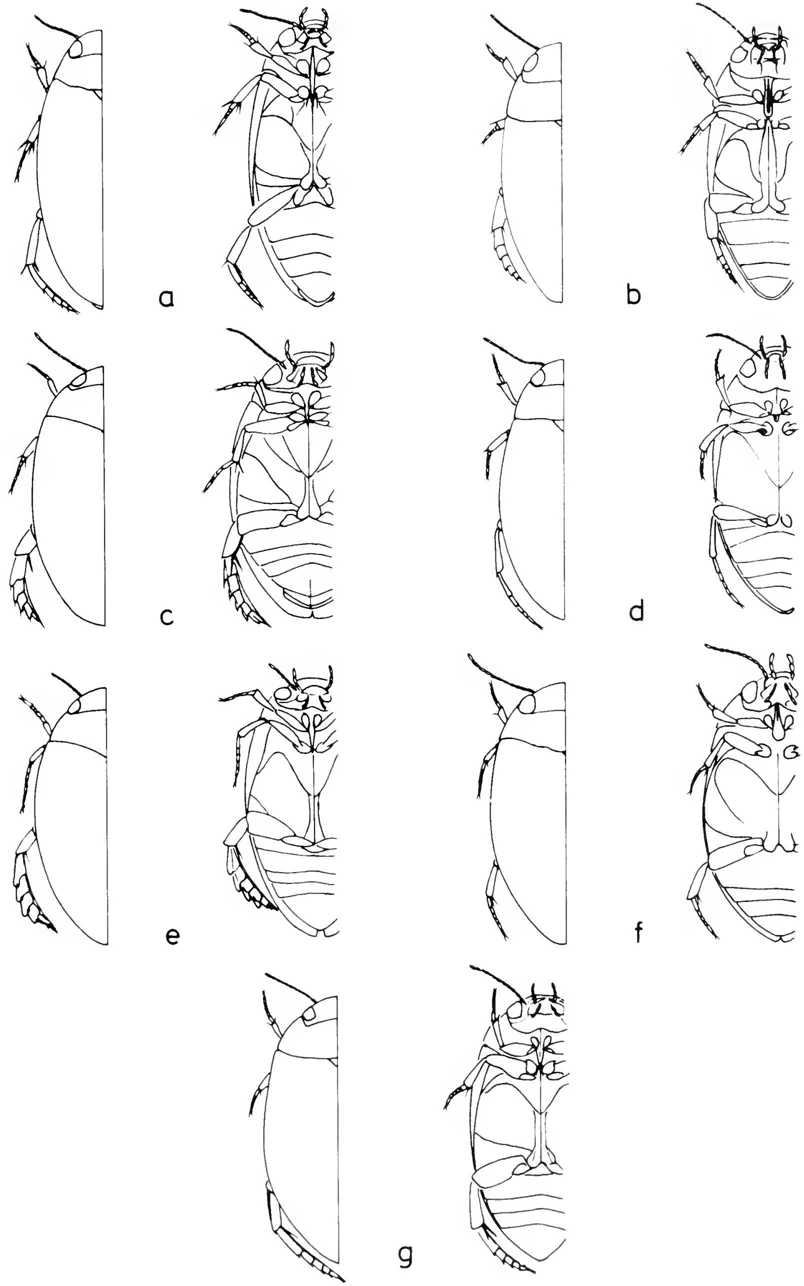


Fig. 1. Dorsal (left) and ventral (right) view of various females of Dytiscidae. (a), *Lancetes lanceolatus* Clark; (b), *Matus bicarinatus* Say; (c), *Laccophilus decipiens* LeC.; (d), *Agaporomorphus knischi* Zimmermann; (e), *Laccophilus maculosus* Germ.; (f), *Lacconectes laccophiloides* Zimm.; (g), *Agabetes acuductus* (Harris).

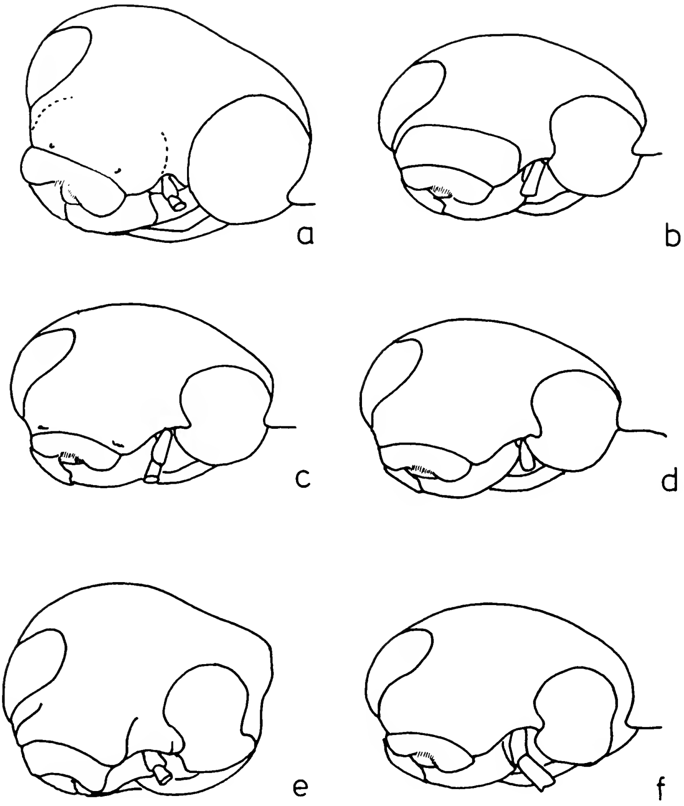


Fig. 2. Anterolateral view of head of various species of Hydradephaga. (a), *Cybister tripunctatus* Oliv. (redrawn from Franciscolo 1979); (b), *Agabetes acuductus* (Harris); (c), *Meladema coriaceum* Cast. (redrawn from Franciscolo 1979); (d), *Copelatus haemorrhoidalis* (F.); (e), *Noterus clavicornis* (Deg.); (f), *Laccophilus hyalinus* (Deg.).

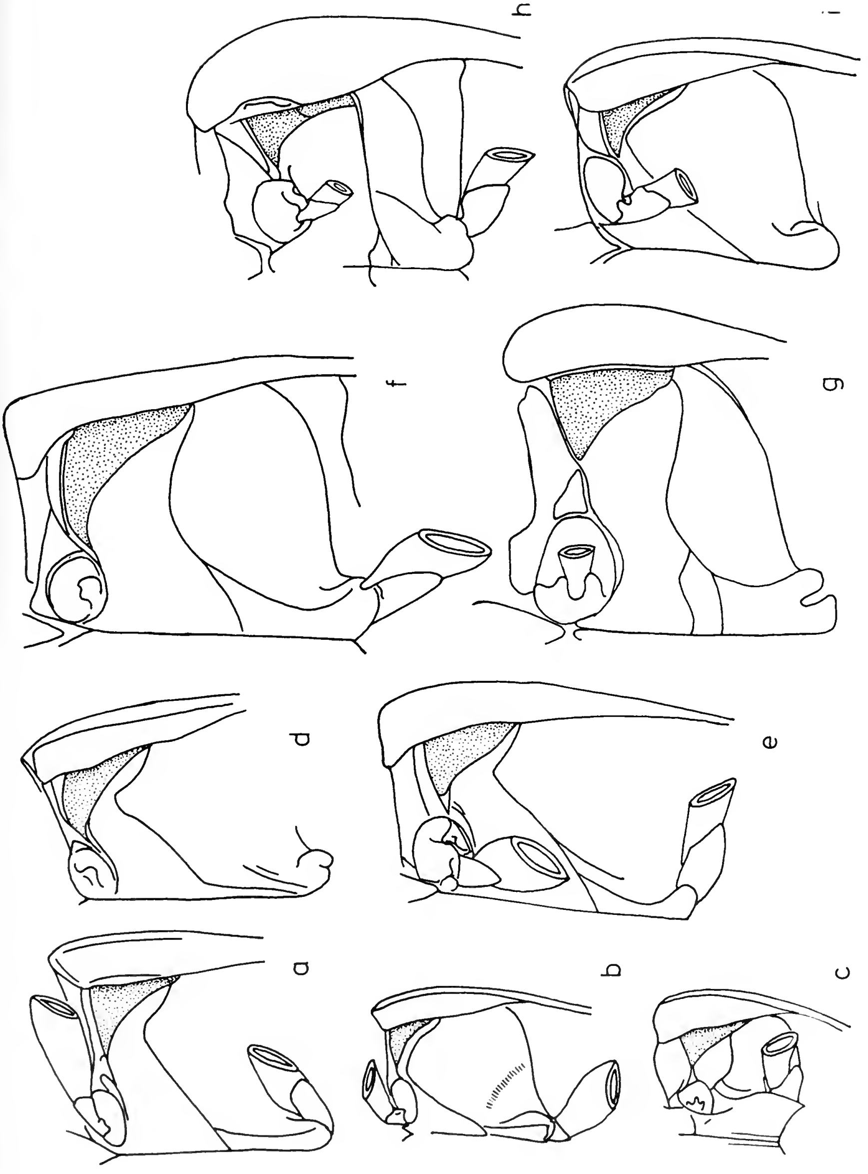


Fig. 3. Ventral view of meso- and metasternal area of various species of Hydradephaga. Metathoracic episternum stippled. (a), *Agabetes acuductus* (Harris); (b), *Laccophilus hyalinus* (Deg.); (c), *Noterus clavicornis* (Deg.); (d), *Copelatus haemorrhoidalis* (F.); (e), *Scarodytes halensis* (F.); (f), *Agabus bipustulatus* (L.); (g), *Hygrobia tarda* Herbst; (h), *Amphizoa lecontei* Matthews; (i), *Laccodytes americanus* Pesch.

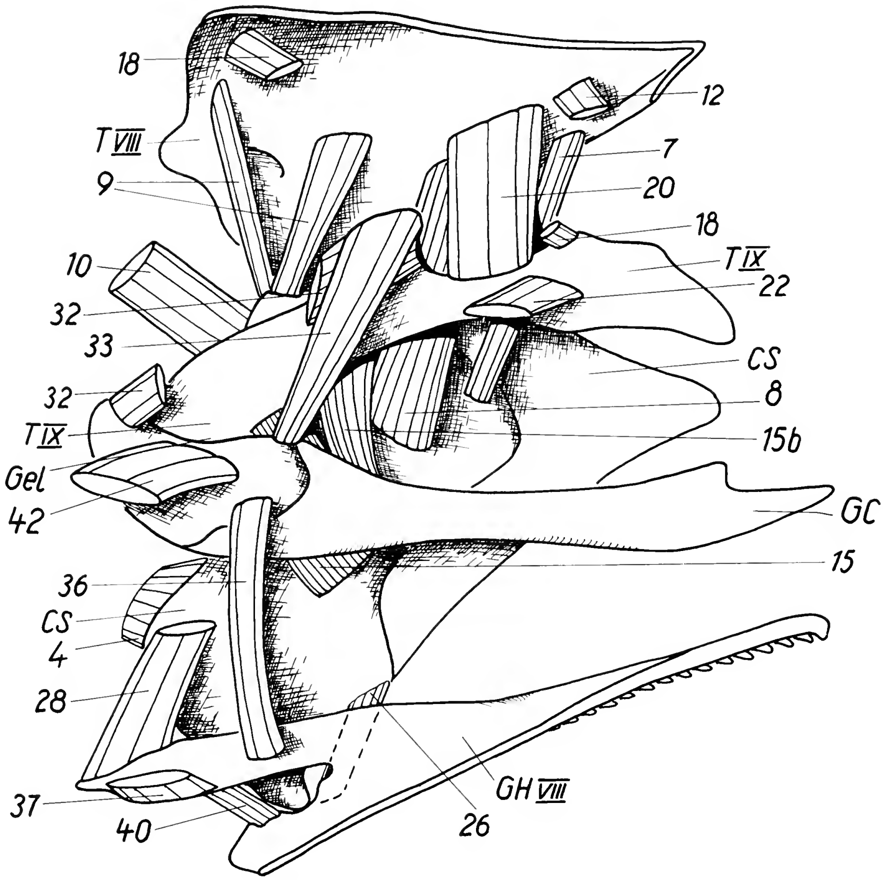


Fig. 4. Schematic view of female genitalia (last abdominal segment) of *Laccophilus hyalinus* (Deg.) with muscular system (modified from Burmeister 1976). Legend: CS- gonocoxosternum; GC- gonocoxa; Gel - articulation of tergum IX with gonocoxae; GH VIII- genital appendages of segment VIII; T VIII- tergum of segment VIII; T IX- tergum of segment IX which is divided into two lateral clasps together with gonangulum. Arabic numerals refer to muscles as follows: 4-10+32+33, gonocoxosternal muscles: 4 - retractor, 7-9 - levators, 10 - retractor, 32 - depressor, 33 - levator. 12 - retractor of membrane between terga VIII and IX. 15-26, muscles of tergum IX: 15-15b, depressors and protractors, 18 - retractor, 20 - levator, 22+26 - levators of membrane between lateral halves. 28+36+40, muscles of genital appendages VIII: 28 - depressor, 36 - extensor and levator, 40 - flexor. 37 - protractor and dilator of bursa copulatrix.

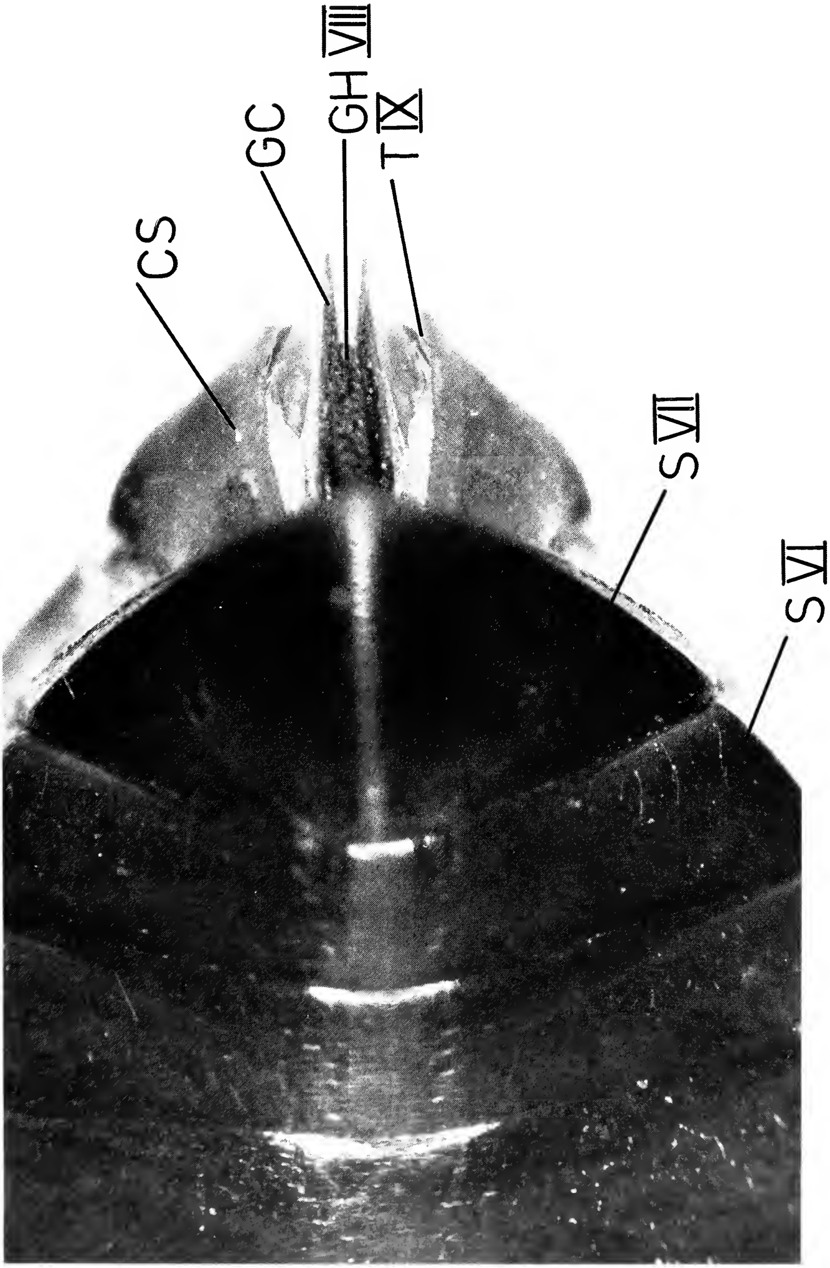


Fig. 5. Ventral view of the tip of abdomen of female *Agabetes acuductus* (Harris). The ovipositor is evaginated distally.

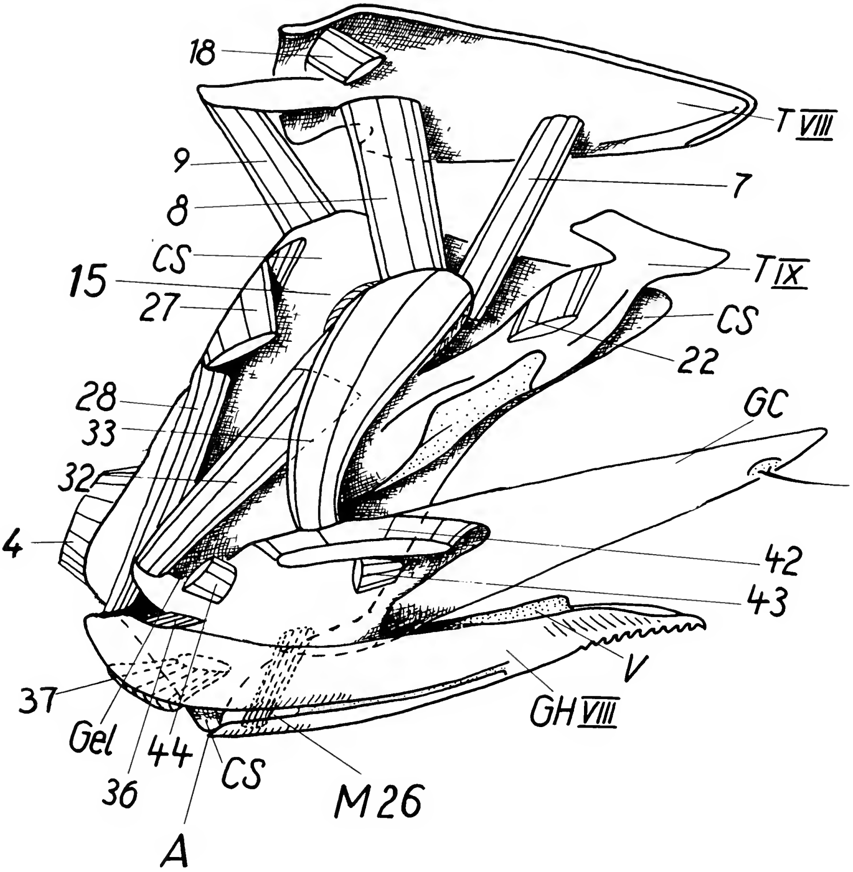


Fig. 6. Schematic view of female genitalia and last abdominal segment of *Agabetes acuductus* (Harris) with muscular system (modified from Burmeister 1976). Legend: A- articulation of gonocoxosternum with genital appendages VIII; CS- gonocoxo-sternum; GC- gonocoxa; Gel - articulation of tergum IX with gonocoxae; GH VIII- genital appendages of segment VIII; T VIII- tergum of segment VIII; T IX- tergum of segment IX which is divided into two lateral clasps together with gonangulum; V- papilla at vaginal opening. Arabic numerals refer to muscles as follows. 4-9, gonocoxosternal muscles: 4 - retractor, 7-9 - levators. 15-26, muscles of tergum IX: 15 - depressor and protractor, 18 - retractor, 20 - levator, 22+26 - levators of membrane between lateral halves. 27+32+33+42 - muscles of gonocoxa: 27+32 - depressors, 33 - levator, 42 - adductor. 28+36, muscles of genital appendages VIII: 28 - depressor, 36 - extensor and levator. 37 - protractor and dilator of bursa copulatrix. 43+44, vaginal muscles: 43 - protractor, 44 - dilator.

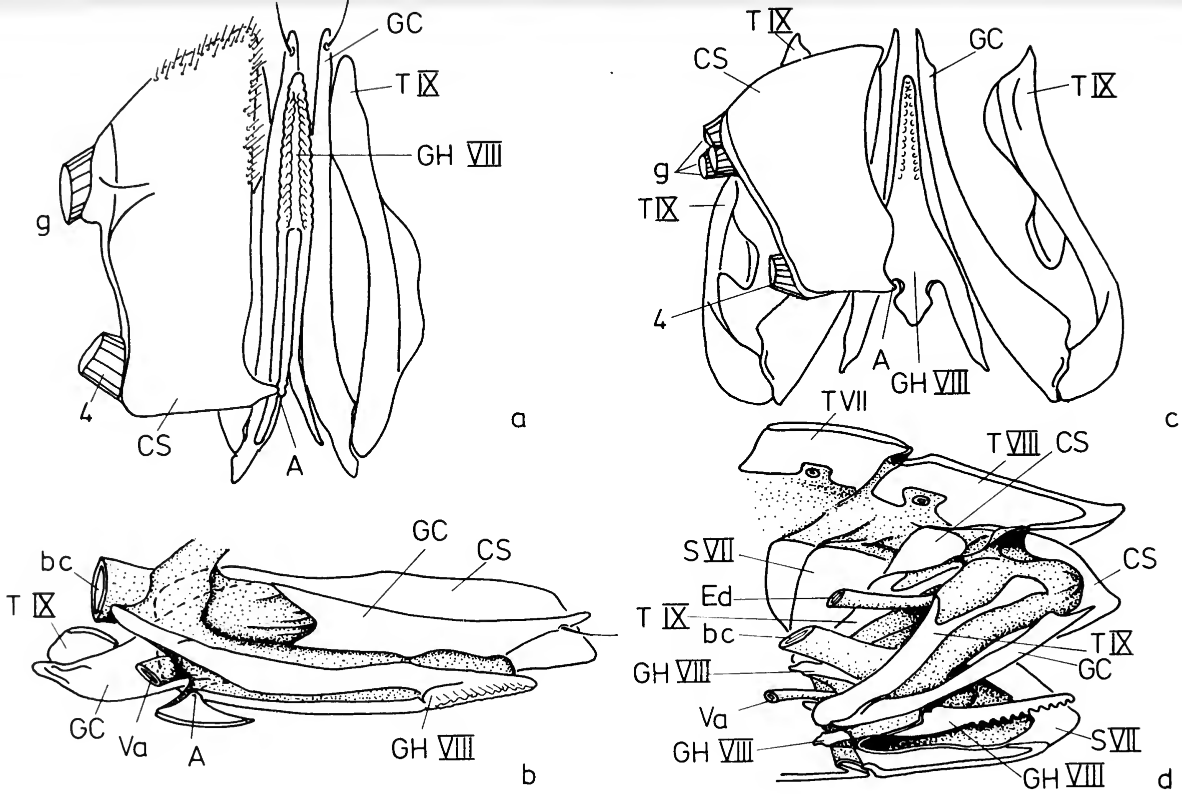


Fig. 7. Female genitalia of *Agabetes acuductus* (Harris) (a, b) and *Laccophilus* Leach (c, d). Ventral view (a, c) of sclerites and lateral view (b, d) of the sclerites and genital ducts in resting position. Legend: A - articulation of gonocoxosternum and genital appendages VIII; bc - bursa copulatrix; CS- gonocoxosternum; Ed - end of gut; g - levator of gonocoxosternum; GC- gonocoxa; GH VIII- genital appendages of segment VIII; S VII- sternum of segment VII; T VII-IX- terga of segments VII-IX; Va- vagina. 4 - retractor muscle of gonocoxosternum.

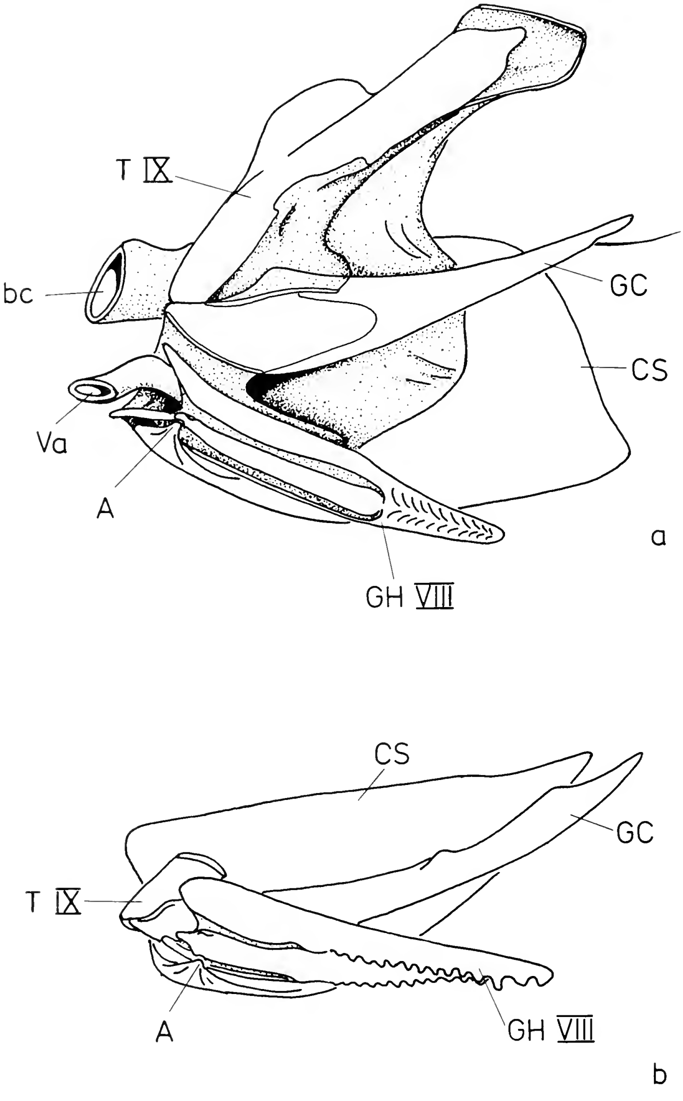


Fig. 8. Ventrolateral view of the appendages of female genitalia of (a) Agabetes acuductus (Harris) and (b) *Neptosternus sumatrensis* Rég. Legend: A- articulation of gonocoxosternum and genital appendages VIII; bc- bursa copulatrix; CS- gonocoxo-sternum; GC- gonocoxa. GH VIII- genital appendages of segment VIII; T IX- tergum of segment IX which is divided into two lateral clasps together with gonangulum; Va- vagina.

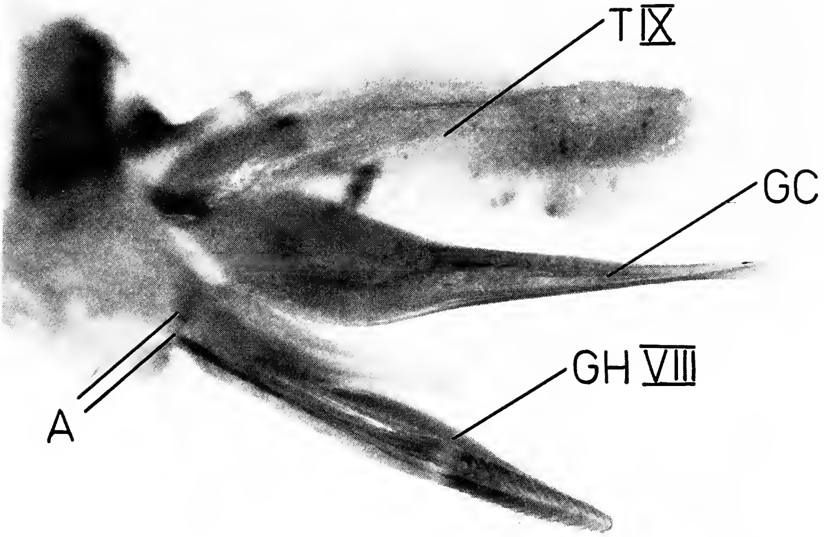


Fig. 9. Ventrolateral view of ovipositor of *Agabetes acuductus* (Harris). Legend: A- articulation of gonocoxosternum and genital appendages VIII; GC- gonocoxosternum.; GH VIII- genital appendages of segment VIII; T IX tergum of segment IX which is divided into two lateral clasps together with gonangulum.

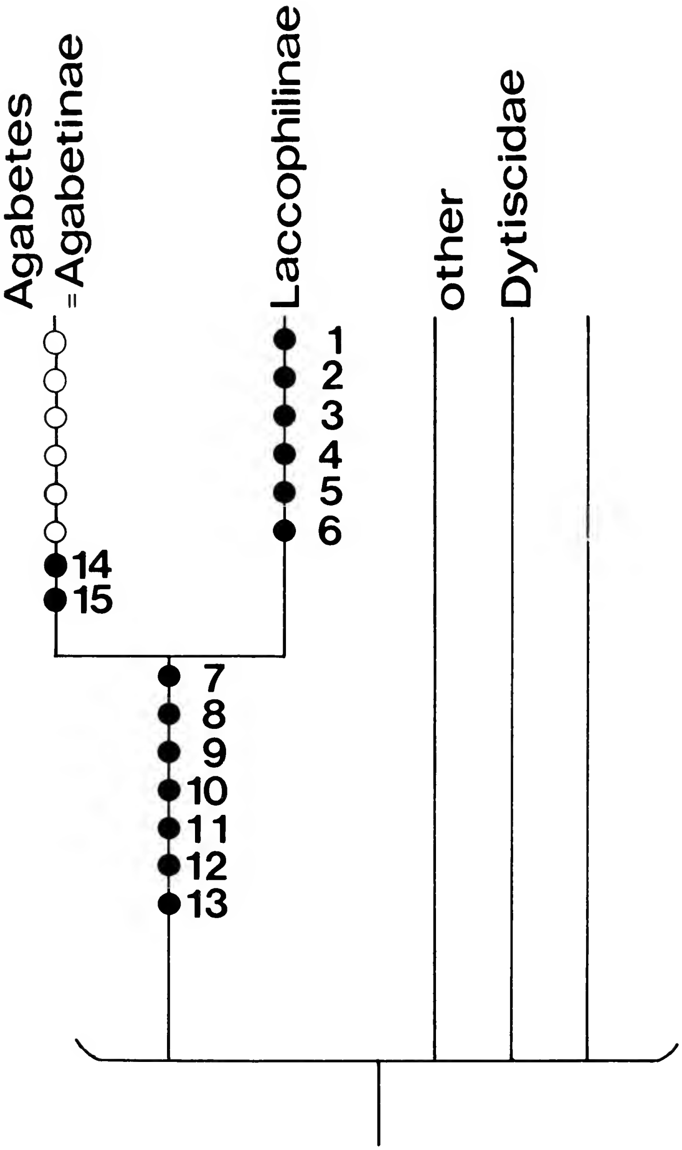


Fig. 10. Sister-group relationship of *Agabetes* Crotch and Laccophilinae shown by apomorphies (7 - 13), autapomorphies of Laccophilinae (1 - 6) and autapomorphies of *Agabetes* (14 - 15). Only characters of female genitalia are shown; for discussion of characters see text.

A NEW SPECIES OF *PLATAMBUS*, SUBGENUS *AGRAPHIS*, FROM NEPAL AND NOTES ON *P. GUTTULUS* (RÉGIMBART) (COLEOPTERA, DYTISCIDAE).

Michel Brancucci
Entomology Department
Natural History Museum
Augustinergasse 2
CH-4001 Basel
Switzerland

Quaestiones Entomologicae
26: 239–243 1990

ABSTRACT

A new species of Platambus, P. khukri, *from the Himalaya of Nepal (type locality Nepal, Bagmati, Sindhupalchok, Dapkakharka, 1800 m) is the fourth known species of the subgenus* Agraphis. *A revised key to the species of* Agraphis *is included.*

The subgeneric name Neoplatynectes *Vazirani is a synonym of* Platambus *Thomson and somes additional notes about the type-series of* Platambus (s.str.) guttulus *(Régimbart) are given.*

RÉSUMÉ

L'auteur décrit P. khukri *n.sp., un nouveau* Platambus *(sous-genre* Agraphis*) récolté au Népal (Népal, Bagmati, Sindhupalchok, Dapkakahrka, 1800 m). Il s'agit de la quatrième espèce attribuée au sous-genre* Agraphis. *Une clé de détermination révisée est proposée.*

Le sous-genre Neoplatynectes *Vazirani est considéré comme synonyme du genre* Platambus *et quelques notes complémentaires sur la série typique de* P. guttulus *(Rég.) sont données.*

INTRODUCTION

During the latest expedition (1989) of the Natural History Museum of Basel to the Himalaya of Nepal, several species of the colymbetine genus *Platambus* Thomson were collected. One of these proved to be new to science and is described here as *Platambus khukri*. The new species belongs to the subgenus *Agraphis* Guignot and is the fourth species to be assigned to this subgenus which otherwise includes *P.* (*A.*) *sawadai* (Kamiya) from Japan, *P.* (*A.*) *punctatipennis* Brancucci from China and *P.* (*A.*) *kempi* Vazirani from Darjeeling Distr., India and Sikkim (Brancucci, 1988).

Further, several type-specimens of *P. guttulus* (Rég.) have been found in the Paris Museum. This allows me to make some additional comments about this species.

Platambus Thomson

Platambus Thomson, 1859:14.

Platynectes subg. *Paraplatynectes* Vazirani, 1970:342 (type species: *Platynectes guttula*). - Vazirani, 1977:68. NEW SYNONYMY

Vazirani erected the subgenus *Paraplatynectes* for *Platynectes guttula* Rég. As this species has been recognized as a *Platambus* (Brancucci, 1988), the subgenus *Paraplatynectes* should be treated as consubgeneric with *Platambus*.

Platambus (*sensu stricto*) *guttulus* (Régimbart)

Platynectes guttula Régimbart, 1899:283.

Platynectes (*Paraplatynectes*) *guttula*; Vazirani, 1970:342. -Vazirani, 1977:68.

Platambus guttulus; Brancucci, 1988:205.

Since my revision (Brancucci, 1988), I have found four more specimens in the collection of the Paris Museum which are part of the type series. At the time, I was not aware of Vazirani's lectotype designation (Vazirani, 1970, 1 ♂ from Hochan) and I referred to the single specimen available to me as the holotype. The earlier designation by Vazirani should be followed. Besides the male from Chang-Hai mentioned in my revision, the lectotype and the four paralectotypes are from the following localities: Hochan (1 ♂ and 1 ♀), Shanghai (2 ♀).

Females.— The female is similar to male, except for lacking the broadened tarsal articles.

Platambus (*Agraphis*) *khukri* n.sp.

Figs 1-8.

Description.— Body broadly oval, completely black except labrum, anterior part of clypeus and two small postmedian rounded patches ferrugineous-brown (Fig 1).

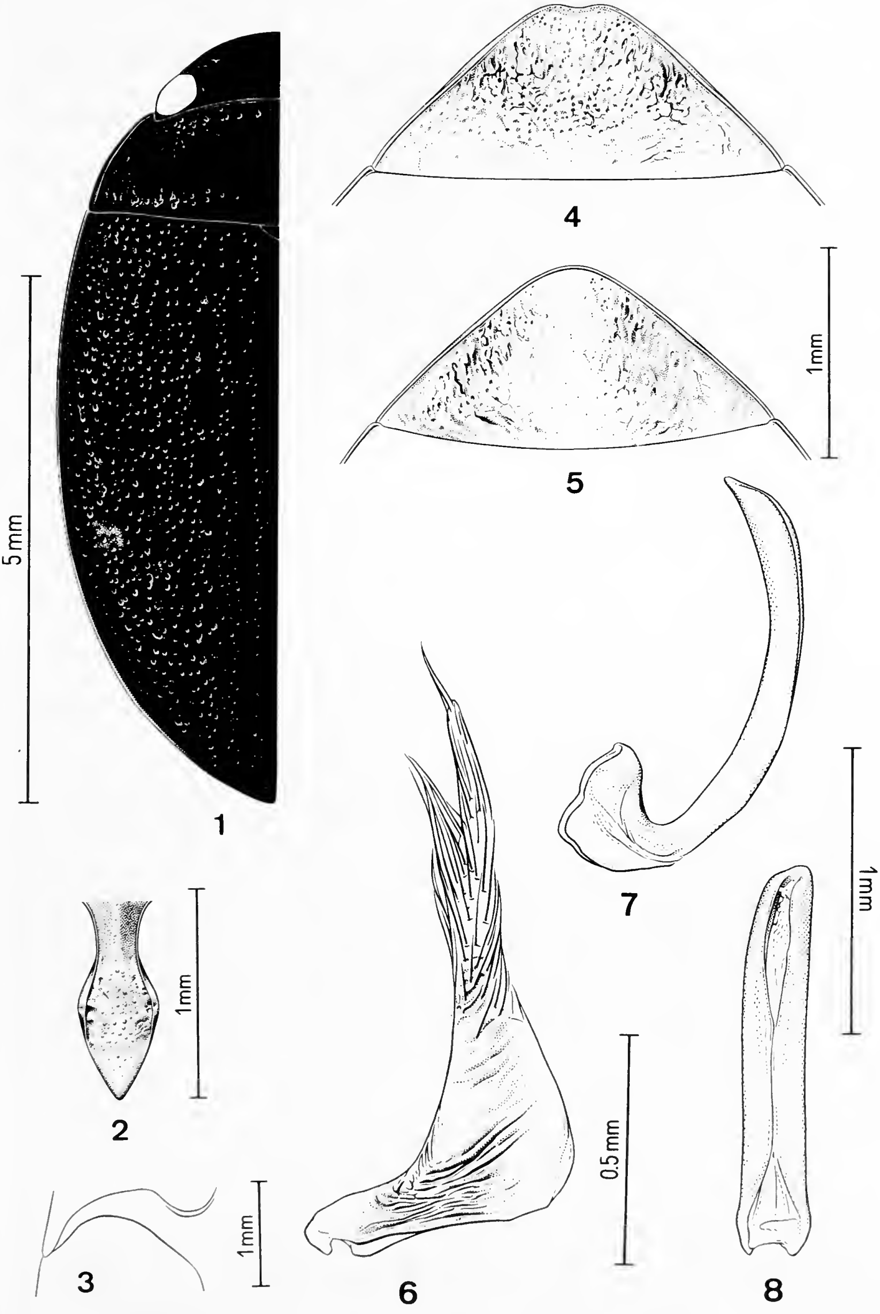
Head black, indistinctly ferrugineous-brown on labrum and on anterior part of clypeus. Antennae and palpi ferrugineous-brown. Reticulation of polygonal meshes with numerous minute punctures on inner surfaces and densely covered by larger punctures, latter particularly large and dense on disc. Row of punctures alongside eyes and two close-set punctures beside eyes deeply impressed (frontal grooves). Fronto-clypeal grooves deep, formed by confluence of several punctures.

Pronotum completely black, except lateral margins very narrowly ferrugineous-brown. Reticulation slightly-impressed; meshes with minute punctures on their inner surfaces and with numerous larger punctures at intersection of meshes, particularly large and numerous laterally. Anterior, transverse row of punctures not interrupted at middle; punctures very large, irregularly distributed, absent at level of anterior angles. Posterior, transverse row of punctures broadly interrupted at middle, limited to mediolateral portion of each side; punctures large and confluent. Lateral margin distinctly margined.

Elytron black with postmedian rounded ferrugineous-brown spot (Fig. 1). Epipleuron dark brown to black. Elytral reticulation slightly impressed, of small polygonal meshes with one to five very minute punctures on inner surfaces and with larger and sparser punctures at intersections. Entire surface irregularly covered with very large and deep punctures (Fig. 1); on disc, punctures slightly grouped along normal, serial row of punctures. Sutural row of punctures complete; punctures of medium size, placed close together and in straight line, except on anterior fifth more sparse, well separated and irregularly distributed.

Underside ferrugineous-brown to dark brown. Prosternal process flat, transversely depressed on posterior half, distinctly bordered on basal part and covered with coarse punctures, particularly large and confluent at sides (Fig. 2). Metasternal wings narrow (Fig. 3). Metacoxa markedly rugose. Metatrochanter transverse. Metafemur with several short setae distally near posterior angle. Ventral surface of metatibia with about 10 large punctures on outer half.

Males.— Pro- and mesotarsus slightly dilated, with small pads on tarsomeres 1–3. Anal sternite very coarsely sculptured, markedly wrinkled longitudinally and with indistinct longitudinal depression, particularly distinct on posterior half. Posterior margin very slightly excavated at middle (Fig 4), margined only at sides.



Figs 1-8: *Platambus* (*Agraphis*) *khukri* n.sp.: 1, Habitus and color pattern. 2, Prosternal process. 3, Metasternal wings. 4, Anal sternite of the ♂ 5, Anal sternite of the ♀. 6, Right paramere. 7, Aedeagus in lateral view. 8, Aedeagus in dorsal view.

Parameres with basal portion slightly transverse and apical portion elongate (Fig. 6). Aedeagus, in lateral view, slightly curved, widest at subapical portion, flattened at apex and ended in short point; in dorsal view, parallel-sided almost to apex and rounded at apex (Figs 7-8).

Females.— Similar to males except anal sternite distinctly reticulate and covered with small punctures; posterior margin rounded apically, not excavated medially, and finely margined (Fig. 5).

Total length.— 7-7.3 mm; width: 4-4.2 mm.

Types.— Holotype ♂ (coll. Brancucci, NHM-Basel) and 7 paratypes (3 ♂ and 4 ♀; coll. Brancucci, NHM-Basel). Locality: Nepal, Bagmati, Sindhupalchok, Dapkakharka, 1800 m, 11.VI.1989, M. Brancucci.

Derivation of specific epithet.— The species name is derived from the Sanskrit word 'खुक्रि'(Khukri). A khukri is a long knife commonly used in Nepal. *P. khukri* n.sp. was found in a region well known for its manufacture of a particularly strong kind of khukri.

Collecting notes.— Specimens were collected in small pools on large stone slabs which are continuously fed with fresh water alongside the actual river bed.

Affinities.— Because of its size and rounded form, this species is similar to *P.* (*A.*) *kempi* Vazirani but specimens are distinguished easily by the form of the basal portion of the parameres which is only slightly transverse (Fig. 6) and by form of aedeagus which is not markedly tapered distally in dorsal view (Fig. 8). Furthermore, the coarse punctation of the elytra is more dense and more evenly distributed (Fig. 1), the last abdominal sternite of the male is less markedly excavated (Fig. 4) and the prosternal process is distinctly more depressed (Fig. 2).

Key to the species of the subgenus *Agraphis*

In the key to species of *Agraphis* presented in my earlier revision (Brancucci, 1988), the measurements of *P.* (*A.*) *sawadai* Kamiya and *P.* (*A.*) *kempi* Vazirani unfortunately were transposed. Consequently I think it would be more useful to publish a complete, revised key instead of simply listing the additions and corrections.

1 Larger specimens (6.9–8.2) mm). Punctures on elytra varied in size, unevenly distributed, partly arranged in rows 2

1' Smaller specimens (6.4 mm). Punctures on the elytra very dense, uniform in size and evenly distributed, not arranged in rows. China (Fukien) .... 2. *P.* (*A.*) *punctatipennis* Brancucci

2 (1) Smaller specimens (6.9-7.5 mm). Elytra black with postmedian, ferrugineous-brown spot. Male with aedeagus, in lateral view, broadened apically; in dorsal view, symmetrical or asymmetrical 3

2' Larger specimens (7.9-8.2) mm. Elytra completely black. Male with aedeagus, in lateral view, tapered apically; in dorsal view asymmetrical. Japan .... 1. *P.* (*A.*) *sawadai* (Kamiya)

3 (2) Males. Paramere markedly transverse basally. Aedeagus, in dorsal view, markedly tapered in apical third, symmetrical. India (Darjeeling Distr., Sikkim) .... 3. *P.* (*A.*) *kempi* Vazirani

3' Males. Paramere slightly transverse basally (Fig. 6). Aedeagus, in dorsal view, not markedly tapered in apical third, parallel-sided almost to apex, asymmetrical (Fig. 8). Nepal (Bagmati). .... 4. *P.* (*A.*) *khukri* n.sp.

ACKNOWLEDGEMENTS

I thank my friend Carolus Holzschuh (Vienna) for his help in collecting many insects during this joint expedition to the Himalayas. I am also greatly indebted to Adrian Pont (Goring, U.K.) and Robert E. Roughley (Winnipeg, Canada) for reading and correcting the English of my manuscript.

Armin Coray, Scientific Illustrator, made the illustrations. This was possible through a grant from the Swiss National Foundation for Scientific Investigation (application no. 31-9089-87).

REFERENCES CITED

Brancucci, M. 1988. A revision of the genus *Platambus* Thomson (Coleoptera, Dytiscidae). Entomologica Basiliensia, 12: 165-239.

Régimbart, M. 1899. Revision des Dytiscidae de la région Indo-Sino-Malaise. Annales de la Société entomologique de France, 68: 186-367.

Thomson, C.G. 1859. Skandinaviens Coleoptera, synoptisk bearbetade. Tomus I. Gleerups, Lun. (4) + 290 pp.

Vazirani, T.G. 1970. Contributions to the study of aquatic beetles (Coleoptera). VII. A Revision of Indian Colymbetinae (Dytiscidae). Oriental Insects, 4: 303-362.

Vazirani, T.G. 1977. Catalogue of Oriental Dytiscidae. Records of the Zoological Survey of India, Occasional Paper, 6: 1-111.

Quaestiones Entomologicae

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

VOLUME 26 NUMBER 3 SUMMER 1990

Publication of *Quaestiones Entomologicae* was started in 1965 as part of a memorial project for Professor E.H. Strickland, the founder of the Department of Entomology at the University of Alberta in 1922.

It is intended to provide prompt relatively low cost publication for comprehensive accounts of entomological research of greater than average length. However, shorter papers about insects in the Prairie Provinces of Canada are acceptable. Page charges are normally levied, the rate determined by printer's charges. For information about current page charges, consult the Editor.

Copy for all types of papers should conform to the Style Manual for Biological Journals, published by the American Institute of Biological Sciences, Second Edition, 1964, except that title of periodicals should be given in full. For style of taxonomic papers, the Editor should be consulted. Two copies of manuscript are requested. All manuscripts will be reviewed by referees.

Abstracts are required, one in English and one in another language, preferably French.

Copy for illustrations must accompany the manuscript, and be of such character as to give satisfactory reproduction at page size (less 1/2 inch, or 1.2 cm on plates of full page size [7 X 4 1/4 inches or 17.8 X 10.7 cm]). Reprints must be ordered when proofs are returned, and will be supplied at cost.

Subscription rates are the same for institutions, libraries and individuals, $20.00* per volume of four issues, normally appearing at quarterly intervals; single issues $5.00*+. Back volumes and issues are available at the same cost. These prices supersede those previously indicated, and are subject to change as required by inflationary pressure on the value of money.

Communications regarding subscriptions should be addressed to the Subscription Manager, and regarding manuscripts to the Editor.

Same rate in U.S.$ for non-Canadian subscriptions

Single issues of more than 100 pages: $10.00, exception: volume 21(4) - $20.00.

Published quarterly by:

Department of Entomology
University of Alberta
Edmonton, Alberta, CANADA
T6G 2E3

Second Class Mail Registration Number 5222

Return Undeliverable mail to the address above. Return Postage Guaranteed

Issued November 1990

QUAESTIONES ENTOMOLOGICAE .... ISSN 0033-5037

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

Volume 26 Number 3 1990

CONTENTS

ON THE SYSTEMATIC POSITION OF AMPHIZOIDAE, EMPHASIZING FEATURES OF THE FEMALE GENITAL ORGANS (INSECTA: COLEOPTERA: ADEPHAGA)

Ernst-Gerhard Burmeister
Zoologische Staatsammlung
Münchhausenstraße 21
D-8000 München 60
Germany

Quaestiones Entomologicae
26: 245– 272 1990

ABSTRACT

Amphizoidae have been considered a group of adephagan beetles phylogenetically situated between the Ge- and Hydradephaga. Study of structure of larvae, metathorax of adults and female genitalia, particularly the ovipositor, demonstrates that this family belongs within the Hydradephaga. Monophyly of the group comprising Amphizoidae, Hygrobiidae and Dytiscidae, is compared with results of other phylogenetic investigations. Autapomorphies of members of Amphizoa *and especially of the female genitalia of* Amphizoa lecontei *are compared with those of other members of Hydradephaga.*

ZUSAMMENFASSUNG

Die artenarme Familie der Amphizoidae wurde bisher systematisch zwischen die Ge- und Hydradephaga eingereiht. Untersuchungen zur Morphologie der Larven, des Metathorax der Imagines und des weiblichen Genitalapparates insbesondere des Ovipositors ziegen, daß diese Familie phylogenetisch zu den Hydradephaga gehört. Nach diesen vergleichenden Untersuchungen sind Amphizoidae, Hygrobiidae und Dytiscidae monophyletisch und die Amphizoidae stehen den beiden anderen Familien als Schwestergruppe gegenüber. Ergebnisse anderer systematischer und phylogenetischer Untersuchungen werden mit dieser These in Beziehung gezetzt und verglichen. Die Autapomorphien der Arten der Gattung Amphizoa *im Besonderen die weiblichen Genitalorgane und Anhänge von* Amphizoa lecontei *werden mit denen anderer Vertreter der Hydradephaga verglichen.*

INTRODUCTION

Aspects of phylogenetic relationships of the six families of Hydradephaga (Amphizoidae, Dytiscidae, Gyrinidae, Haliplidae, Hygrobiidae and Gyrinidae), the relationship of Hydradephaga to Geadephaga, and the relationship of Trachypachidae to both subdivisions of Adephaga have been examined by Bell (1966, 1982), Forsyth (1968, 1970), Crowson (1975, 1981), Burmeister (1976, 1980), Dettner (1979), Roughley (1981), Evans (1985), Baehr (1979), Hammond (1979), Ward (1979), Ruhnau and Brancucci (1984), Kavanaugh (1986), Ruhnau (1986), Beutel and Belkaceme (1986) and Beutel and Roughley (1988).

A common result of most of these studies is that Hygrobiidae, Dytiscidae and possibly Amphizoidae belong to a monophyletic unit (*e.g.*, Burmeister 1976, 1980). The relationship of the remaining families to this group and to each other is more controversial.

These studies may be characterized collectively by study of a wide variety of structural, chemical and histological features of adults (as well as some features of larvae and pupae), and all discuss the systematic position of Amphizoidae at least in part. The purpose of the present study is to examine the systematic position of Amphizoidae by synthesizing all of the available information and using the character states in a cladistic analysis.

The ovipositor of Hydradephaga possesses a number of functional character systems useful for phylogenetic reconstruction. These character systems were studied for most Hydradephaga by Burmeister (1976, 1980) although a detailed study of Amphizoidae was not presented there. Therefore, in the present study a more detailed description of the female organs includes muscular features and functional considerations. This is used for placement of Amphizoidae within Hydradephaga and supplementary characters are taken from the literature to ascertain whether or not they support this hypothesis.

MATERIALS AND METHODS

List of species examined (adults)

Amphizoidae — *Amphizoa insolens* LeConte, *A. lecontei* Matthews.
Hygrobiidae — *Hygrobia tarda* (Herbst), *H. nigra* (Clark), *H. australasiae* (Clark).
(Dytiscidae: Copelatinae) — *Copelatus atriceps* Sharp, *C. haemorrhoidalis* (Fabricius).
Dytiscidae: Colymbetinae: Agabini — *Hydronebrius cordaticollis* (Reitter), *Agabus bipustulatus* (Linnaeus), *Platambus maculatus* (Linnaeus).
Dytiscidae: Colymbetinae: Colymbetini — *Rhantus pulverosus* (Stephens).
Noteridae — *Noterus clavicornis* (DeGeer).
Haliplidae — *Haliplus lineaticollis* Marsham.
Gyrinidae — *Gyrinus substriatus* Stephens.

Only dried specimens of *Hydronebrius* were available. All other specimens were preserved in FAE or in 80% ethanol prior to dissection. Drawings show internal skeletal structures, internal genital organs and the musculature systems, but other internal organs are omitted.

The names of sclerites, internal organs and muscles are based on the ground plan of female genitalia of Adephaga developed by Bils (1976) and Burmeister (1976, 1980).

Apomorphies of the ovipositor of amphizoids and their relatives can be used to refine the reconstructed phylogeny of Hydradephaga proposed by Burmeister (1976). For families such as Amphizoidae and Hygrobiidae analysis is easier because each contains only a single genus.

Among Hydradephaga, members of Dytiscidae are the most difficult to characterize in terms of a ground plan, This is in part because Dytiscidae is the most diverse family of Adephaga and because the form and function of various structures of the female genitalia, in particular, has been altered during the development of various mechanisms of oviposition and copulation (Burmeister 1980).

The current classification of Dytiscidae suggests seven subfamilies: Copelatinae, Colymbetinae, Hydrporinae, Laccophilinae, Agabetinae, Dytiscinae and Aubehydrinae. Not all authors would agree with the limits and composition of these subfamilies and Aubehydrinae are exluded from this discussion because I have not dissected specimens of the single included species.

Burmeister (1976) suggested that *Copelatus* Erichson (Copelatinae) is the sister group to the remaining Dytiscidae. This phylogenetic position for copelatines is suggested also by studies of larval and pupal structure (Ruhnau and Bruncucci 1984, Brancucci and Ruhnau 1985, Ruhnau 1986). Among the remaining subfamilies of Dytiscidae, phylogenetic relationships are more problematic. For instance, Colymbetinae is a stage group and is not monophyletic (Burmeister 1976). However, among "colymbetines", members of Agabini and Colymbetini form a monophyletic group and are probably the sister group of the remaining groups (Burmeister 1976) although representatives of some tribes and many genera were not examined. This phylogenetic position is also suggested by study of larval and pupal characters (see above). Members of Hydroporinae, Dytiscinae and Laccophilinae + Agabetinae form well defined monophyletic groups but their relationships to each other are difficult to assess (Burmeister 1976, in press). In part, this latter is due to reductions and specializations due to mode of oviposition, body size, *etc.*

The method for deducing synapomorphies of Dytiscidae was to develop a ground plan of dytiscid structure based on features of Copelatinae which were compared to those found in Agabini + Colymbetini. Derived features of these groups were taken as synapomorphies of Dytiscidae. This method was used extensively with features of the female ovipositor but also with other character states from other character systems.

In general, for phylogenetic analysis I reject apomorphic characters expressed only as character reductions or losses. Such characters provide supplementary information only if supported by a wealth of character gains. All characters are polarized as primitive (plesiomorphic) or derived (apomorphic) according to the methods of phylogenetic systematics of Hennig (1950, 1963, 1965, 1981).

STRUCTURE OF THE OVIPOSITOR

Internal skeletal structures

For *Amphizoa lencontei* Matthews, the structure of the terminal segments of the female abdomen, including the ovipositor, was first described by Edwards (1951). I use the terms and abbreviations of Burmeister (1976, 1980); however, to facilitate comparison a list of equivalent terms to those used by Edwards (1951) is as follows:

Sternum 8 = gonocoxasterna (CS), anal orifice = end of gut (Ed), coxite with terminal tuft of bristles = gonacoxa (GC), sternum 10 = genital appendages of segment VIII (GH VIII), genital pore = vaginal opening (m Va), valvifer, dorsal part - paraproct = lateral clasp of tergum IX (T IX). In addition, the proctiger of Edwards (1951) may be equivalent to my opening of the bursa copulatrix (Mbc); However, homology of these is not certain.

The amphizoid ovipositor belongs to the sensitive, touching type: gonocoxae (gonocoxites) are elongated and possess some apical bristles (Fig. 2). Edwards (1951, plate 3) illustrated the last segments in a hyperextended position. While these figures show general structures, they suggest that lateral tergites IX (valvifers) have lost contact with tergite VIII. This is not so because of the function of these segments. During oviposition, the dorsal portion of tergum IX is shifted proximally and the ventral portion is shifted distally which pushes tergite VIII which in turn is articulated with the gonocoxae. This functional complex operates in a similar manner among all Hydradephaga (Burmeister 1980).

The gonocoxosternites (coxosternites VIII) are not in contact ventrally. They are positioned laterally and are heavily sclerotized. When extended (Figs. 3,4), the posterior extensions of tergum IX are shifted laterally whereas when the ovipositor is retracted they are shifted medially. The ventral view provided by Edwards (1951) shows a sclerite (which he called sternite X) which is situated dorsal to the gonocoxae and which is fused medially. Comparison with the ovipositor of other members of Adephaga and with the hypothetical ground plan of the ovipositor, shows that this sclerite which surrounds the orifice of the vagina (genital pore) is homologous with the genital appendages of Burmeister (1976).

Distally, sclerotized plates enclose ventrally a small slit. In this slit is the papilla of the vagina, which can be fully extended distally. Different species of *Amphizoa* show some differences in form of gonocoxae. Genital appendages VIII cannot be shifted into a distal position as in other groups of Hydradephaga and females can deflex the apex only a little bit to extend the vaginal papilla.

Internal genital organs of *A. lecontei*

Burmeister (1976) suspected that female members of Amphizoidae, like those of Hygrobiidae and Dytiscidae, have a double genital pore (secondarily reduced to a single pore among females of the subfamily Dytiscinae), because the female genitalia of Amphizoidae, as demonstrated by Edwards (1951), shows affinities to those of *Hygrobia* Latreille and to the ground plan of Dytiscidae. The present study verifies presence of two separate genital openings: vagina and bursa copulatrix. The vagina (Va, Figs. 2, 4c, 5a) is ventral to the bursa copulatrix and is distinctly separate from it. Among noterids and primitive carabids there is a single external opening of the vagina and bursa copulatrix (Fig. 16 of Burmeister 1976). The bursa copulatrix opens into a membranous sac with its external aperture between the basal parts of the gonocoxae (bc, Figs. 2, 5a). After copulation, this reservoir is filled by the spermatophore and is expanded. The ductus receptaculi originates in the ventral area of the proximal part of the bursa. This tube-like ductus is thickened and surrounded by glandular epithelium (apomorphic character?), in contrast to that of all other Hydradephaga. The ductus receptaculi has a process which projects from the distal curve of the vagina (Figs. 4c, 5a); this tube contacts the mouth of the long receptaculum seminis, which is the reservoir for sperm. This reservoir is situated beneath the distal part of the bursa. The ductus seminalis, the tube for sperm transport into the vagina, is very short. A circular muscle can close the median oviduct, anterior to the opening of the ductus seminalis into the vagina (autapomorphic state of Amphizoidae?). The expansion of the receptaculum depends on the physiological condition of the female after or before copulation or oviposition.

A small, rounded, clasp-like sclerite is present on either side of the bursa copulatrix in *A. lecontei* (SK, Fig. 5a). Two small sclerites are present in the lateral wall surrounding the opening of the bursa copulatrix. These sclerites are different from sclerotizations of the bursal wall that are found among Carabidae and some Dytiscidae; most members of these groups possess sclerotized areas (bursal sclerites, Burmeister 1980) in the ventral or proximal areas of the bursa which are contacted by the aedeagus and spermatophore during copulation. In most members of Agabini (Dytiscidae) there is a ventral sclerite with insertion of muscle between bursa and vagina; in female specimens of *Hydronebrius* Jakowlew (Fig. 5, 6) (Agabini), a sclerotized area is not evident, but the bursa and vagina are connected by surrounding musculature (Fig. 5d).

Arrangement of ductus receptaculi and ductus seminalis

The ductus receptaculi and dutcus seminalis are tubes for transport of sperm to and from the receptaculum seminis and to and from the vagina. The ductus seminalis (Ds) extends from the receptaculum seminis (rs) and opens into the vagina (Va) posterior to the median oviduct (Od). The ductus receptaculi (Dr) extends from the bursa copulatrix (bc) to the receptaculum seminis (Fig. 5). The differing arrangements of these ducts suggests that they have phylogenetic value. Among females of Carabidae, Dytiscidae and Hygrobiidae the ductus receptaculi opens ventrally into the bursa copulatrix (Fig. 5b,c,d) and therefore the origin of the ductus receptaculi is distinctly posterior of the proximal end of the bursa copulatrix (Fig. 5a) and this is a feature unique to Amphizoidae among all Adephaga which have been studied.

The relative lengths and positions of these ducts and associated organs is important also. Females of *Amphizoa* LeConte (Fig. 5a) have the receptaculum seminis located beneath the bursa copulatrix and therefore the ductus receptaculi is moderately short whereas the ductus seminalis is very short. In addition both ducts are distinctly separated from each other throughout most of their lengths.

Females of *Hygrobia tarda* (Hygrobiidae, Fig. 5b) have the receptaculum seminis isolated from the bursa copulatrix, the ductus receptaculi and ductus seminalis are elongated and they are connected throughout much of their length. A unique feature of *Hygrobia* is the presence of an accessory gland located at the proximal end of the bursa copulatrix (Figs. 5b, 9). This character was observed in specimens of both *H. nigra* and *H. tarda.*

The arrangement among members of Dytiscidae is less straightforward. Among Dytiscidae, the ductus receptaculi are much thinner than the ductus seminalis which is the inverse of the size ratio of ducts in *Hygrobia* (Figs. 5b to 5c,d). In females of most taxa the ductus receptaculi and ductus seminalis are elongate, separated ducts (Fig. 5b) leading to and from an isolated receptaculum seminis. This ground plan for the family Dytiscidae is exemplified by *Copelatus* (Fig. 5c)[1]

Among females of Agabini of Colymbetinae and Dytiscinae, however, the ductus seminalis and ductus receptaculum are connected throughout most of their length (*e.g., Hydronebrius* Agabini, Fig. 5d). Therefore this state in these otherwise derived and phylogenetically separate taxa (Agabini, and Dytiscinae) is probably due to convergence.

Selected muscular features of *Amphizoa* in comparison with conditions in other Adephaga

Most muscles of the female genitalia of *Amphizoa* can be homologized with those of the ground plan of Hydradephaga (Burmeister 1976, 1980). This is more straightforward for muscles of the genital appendages. For other muscles it is easiest to establish homology to the muscles of Hygrobiidae and Dytiscidae first and then by extension to the ground plan. This is because other hydradephagan groups show differing alterations of musculature associated with specialization in copulation and oviposition. Analysis of the ground plan of Hydradephaga allows comparison to Geadephaga and extrapolation to the ground plan of all Adephaga (Burmeister 1976, 1980).

---

[1] Ordish (1966, 1985) has figured females of the austral species *Copelatus australis* (Clark) with a very large vagina and very small bursa copulatrix. This is the opposite situation to that which I have found from study of European species, *C. atriceps* and *C. haemorroidalis.* I suspect that the specimen figured by Ordish is a subadult.

Most of the muscles of the last segments and the female genitalia, and especially those of the genital appendages (gonocoxae and genital appendages VIII, see Figs. 2, 3, 7, 8, 9) are described by Burmeister (1976, 1980) and are not redescribed here. Study of further specimens and of better preserved specimens of *Amphizoa* has allowed a more detailed study of these muscles and a few of these are reported below. The muscle numbers follow Burmeister (1976).

In *Amphizoa* two retractors (M4, M5, Figs. 2-4) of the coxosternum (=coxosternite) originate from the proximal portion of sternum VII, as in many members of Dytiscidae and Carabidae. The protractor muscle (M15, Figs, 2-4) is divided into two components, as in *Hygrobia* (Fig. 9). Among Dytiscidae (but excluding Copelatini and Agabetini) another muscle (M14) also acts as a depressor of tergum IX (Figs 7, 8). As in carabids, gyrinids and hygrobiids, amphizoids have two dorsal retractors (M18, M19) originating at the proximal edge of tergum VIII and inserting distally at the dorsal part of tergum IX and at the dorsodistal membranous area (Figs. 2, 3).

The depressor of the gonocoxae (M27) originates from the coxosternum. It is divided into two bundles dorsoproximally (Fig. 3). The other gonocoxal depressor (M32) is also divided into two components and originates from below the levator (M33) in the ventral area of the lateral portions of tergum IX (Fig. 3). The origin of M32 below M33 is unique among all Hydradephaga studied so far. The two portions of M32 share a single insertion on the gonocoxa. As a result of the arrangement of gonocoxal muscles, the genital appendages can not be extended very markedly nor can they move very far distally.

The parameres and median lobe (= penis) of the adeagus of males of *Amphizoa* are elongate to accomodate contact with gonocoxae and the inner part of the bursa copulatrix during copulation. The dorsal membranous area above the opening of the bursa is lifted by the strong elevator muscle (M22, Figs. 3, 4). Among carabids, hygrobiids (Fig. 9) and amphizoids (Fig. 4) there is a muscle (M 24) extending between the distal and proximal parts of tergum IX dorsally. Among carabids this muscle is larger and extends between the relatively separated portions (dorsal and lateral) of tergum IX. Among dytiscids this muscle occurs only in females of *Copelatus* (*e.g.*, compare Figs. 8 and 9). Earlier (Burmeister 1976), I had represented this incorrectly. Therefore the trend among these four families is toward reduction and eventual loss of this muscle as the movement of the ovipositor changes.

Females of *Amphizoa* have a unique muscle among all Hydradephaga examined. This muscle (M55, Fig. 3) originates from the inner part of the gonocoxa near the articulation with the ventrolateral area of tergum IX and inserts onto the lateral wall of the vagina. The function of this muscle is probably to retain the relative positions of genital appendages VIII and the vagina.

PYGIDIAL DEFENSE GLANDS

The pygidial glands were used as indicators of phylogenetic relationship among hydradephagan groups by Forsyth (1968, 1970); Dettner (1985) considered the systematic value of the chemical substances produced by these glands. Pygidial glands in females of *Hygrobia* and *Amphizoa* are divided into two, separated, and opposing areas. This character could be considered a synapomorphy for these two families. Beutel (1986) considered the non-doubled character state in Dytiscidae as a reduction, and stated that this state is convergent with that found in other Hydradephaga because there are doubled glands in some dytiscid genera (*e.g.*, *Colymbetes* Clairville, *cf.* Dettner 1985).

Females of *Hydronebrius* (Colymbetinae: Agabini) have accessory glands with a longitudinal extension of the duct of the gland to the reservoir. This reservoir is surrounded by many small muscles. In females of *Amphizoa* the glandular parts of this defensive system (dg, Fig. 4b) are in the form of two lobes which open by means of a single tube (= collecting channel of Dettner 1985) into the glandular reservoir (gr, Fig. 4b). This tube, in specimens I have examined, is not surrounded by a well-developed epithelial structure as illustrated by Forsyth (1968). A unique feature of Amphizoidae is an elongate muscle (Mg, Fig. 4b) which extends longitudinally from the proximal end of the glandular reservoir to the edge of tergite IX near the opening of the glandular reservoir. Therefore in *Amphizoa*, Mg pulls longitudinally and compresses the glandular reservoir distally. In other Hydradephaga, Mg is a short muscle (*e.g.*, Fig. 8a, *Copelatus*) which pulls transversely.

THE SYSTEMATIC POSITION OF AMPHIZOIDAE

Below are listed the synapomorphies of Amphizoidae + Hygrobiidae + Dytiscidae, autapomorphies of Amphizoidae, synapomorphies of Hygrobiidae + Dytscidae, autapomorphies of Hygrobiidae and autapomorphies of Dytiscidae. Characters of the ovipositor, associated internal organs and musculature are denoted by Arabic numerals. Other characters which are from publications are derived from other structural systems and they are listed as letters. For all characters the apmorphic state is given and characters are listed in the order that they appear on Fig. 13.

Synapomorphies of Amphizoidae, Hygrobiidae, Dytiscidae

The connection among these three families is demonstrated by Burmeister (1976), and subsequent studies by Ruhnau (1986) and Beutel and Roughley (1988) agree with this phylogenetic interpretation.

1. Bursa copulatrix and vagina separated; two genital openings between the genital appendages of females (Burmeister, 1976).
2. Genital appendages of segment VIII fused ventrally and, in the resting position, forming a cavity that contains the vaginal papilla.
3. Muscles of genital appendages of segments VIII and IX divided into those that contact the sclerites, and those that are separated by bursal and vaginal muscles.
4. Levator and extensor muscles of genital appendages VIII, which originate at the inner part of the gonocoxa and insert at the anterodorsal edge of the appendages (M 36). These muscles are absent from members of Carabidae examined by Bils (1976).
5. Separation of ductus receptaculi and ductus seminalis.

The arrangement of the gonocoxal depressor (M27) (which originates from the anterodorsal edge of the gonocoxosternum, and inserts at the anterior gonocoxal apodeme near the insertion of M32, the depressor of tergum IX) is similar to that found in most members of Carabidae.

- a. Specialization of pygidial defense glands, which are divided into two sections (Forsyth 1968, 1970; Dettner 1985).
- b. Tergoapodemal ring (Hieke 1966) of segment IX (tergal region) in male genitalia interrupted (Beutel 1986).

c. Ruhnau (1986) listed larval and pupal synapomorphies of Amphizoidae + Hygrobiidae + Dytiscidae. These are not repeated here.

Autapomorphies of Amphizoidae

Conclusions presented here are based on study of a limited number of species. Specimens of *Amphizoa davidi* Lucas, *A. carinata* Edwards and *A. striata* Van Dyke have not been studied. Nevertheless from the specimens examined the following synapomorphies seem appropriate.

6. Origin of protractor of bursa copulatrix (M43) inside the gonocoxa near the articulation with the lateral part of tergum IX and at the anterodorsal edge.
7. Origin of dilator of bursa copulatrix (M44) directly under the articulation of tergum IX and gonocoxa and inside the gonocoxa. This character state is related to structure of the bursa, which is fixed between the gonocoxae, and its opening can be moved distally during copulation.
8. A small, newly acquired muscle, the elevator of the vagina (M55), present between M43 and M44. It is undetermined from which muscle system this is derived; possible sources are from those of the gonocoxa, or from either of the independent systems of the bursa or vagina.
9. Presence of a separate depressor of the gonocoxa (M 27b), with origin at the anterior edge of the coxosternum, between M27a and M28.
10. Origin of the depressor of the gonocoxa (M 32) at the inner part of the ventrolateral area of tergum IX, displaced from the anterodorsal edge of the tergite. The origin is double whereas in other taxa the insertion is double (*e.g., Agabus* Leach, Burmeister 1976).
11. Ductus receptaculi with origin at the proximal end of bursa copulatrix (Fig. 5).
12. Bursa copulatrix with two lateral sclerites in the area of the opening (Fig. 5).
13. Position of receptaculum seminis shifted from the anterior area of the bursa copulatrix to near the opening of the median oviduct into the muscular vagina. The ductus seminalis is therefore very short.

d. Clypeus very large (Beutel 1986).

e. Galea one-segmented (reduction) (Beutel 1986). This derived character state occurs within Gyrinidae also, with the exception of Enhydrinae: Dineutini, where the galea is absent (Hatch 1927, Franciscolo 1979, Horn 1867, 1881). However, in *Spanglerogyrus* Folkerts, the most primitive known gyrinid, the galea is two-segemented (Beutel 1986).

f. Metafurca markedly reduced in size (Beutel 1986).

g. Gular region very large, prementum not separated and therefore fused with mentum.

h. Lacinia with two extremely differentiated, functional areas on the inner edges.

i. Cavity formed by anterolateral area of elytra and epipleura very deep, such that epipleura in this basal area expanded. In some Carabidae and Noteridae there is also a triangular cavity, but in these taxa the epipleurites are surrounded by a border and separated from the dorsal part of elytra; this latter state is therefore not homologous to that found in amphizoids.

j. Elongate form of Mg (Fig. 4b) of the pygidial defense gland.

k. The form of wing-folding exhibited by adult Amphizoidae is considered a provisional autapomorphy of this family. Wing-folding in amphizoids encloses the distal one-fifth of the total wing length (Fig.

10). This contrasts with that known for all other Adephaga except those with secondarily reduced wing-length and Rhysodidae (Hammond (1979). This common character state of rhysodids and amphizoids would be due to convergence.

l. Kavanaugh (1986) characterized amphizoids as semiaquatic passive drifters in terms of life history. It seems that this could be a secondarily derived condition from a state of fully aquatic habits. This is another provisional autapomorphy of amphizoids.

Synapomorphies of Hygrobiidae and Dytiscidae

The movement of the ovipositor and its functional consequences among groups of Adephaga is discussed by Burmeister (1980). In ground beetles and amphizoids the ovipositor moves primarily in an anterior to posterior direction with little movement in the dorsal-ventral plane. The vaginal opening is shifted ventrally during oviposition, however.

Among the remaining Hydradephaga the amount of dorsal-ventral movement is increased but in different ways. Among noterids + haliplids + gyrinids, the elongated appendages of the ovipositor are more moveable due to reduction of the dorsal part of tergum IX (see Fig. 30 of Burmeister 1980). Among hygrobiids + dytiscids tergum IX remains large and the increased mobility is brought about by a shift in position of tergum IX and articulation with the gonocoxae. Thereby tergum IX and the gonocoxae act together as a jacknife to accomodate the greatly elongated gonocoxae (see Figs. 7, 29 and 30 of Burmeister 1980 and Fig. 40 of Burmeister 1976). Members of Hydroporinae are an exception among dytiscids because in this group tergum IX is reduced in size but this is almost certainly a secondary occurrence.

Rearrangement of these sclerites among hygrobiids and dytiscids suggests a change in functional criteria which are interrelated. The following synapomorphies are apparent.

14. Capability for extreme protraction of coxosterna and tergum IX and the genital appendages; protractor muscles very strong; dorsal retractors of the distal part of tergum IX strong and expansible. Articulation of lateral parts of tergum IX and the gonocoxae act as a fulcrum for evagination of ovipositor.
15. Gonocoxosterna ventrally close together in resting position, with genital appendages VIII positioned medially near the anterior edge; depressor of these appendages short and strong (M28) (lost in members of subfamily Dytiscinae). The depressor M28 of Burmeister (1976, 1980) is not homologous with M13 of Bils (1976) in Carabidae.

Beutel (1986:44-46) listed 10 synapomorphies of Hygrobiidae and Dytiscidae. Of these, five are reductions and two are difficult to polarize because similar states occur in a variety of members of Adephaga. Therefore I prefer to use only the synapomorphies which represent character state gains and which are confidently polarized.

m. Presence of thoracic defensive gland (Forsyth 1968, 1970, Beutel 1986).

n. Scapus elongated (Beutel 1986).

o. Contact of prosternal process with metasternum (Baehr 1979, Beutel 1986).

p. Ruhnau (1986) listed four larval and pupal synapomorphies shared by Hygrobiidae and Dytiscidae.

Autapomorphies of Hygrobiidae

16. Presence of an accessory gland at the anterior end of the bursa copulatrix (ag, Fig. 9).
17. Ductus seminalis and ductus receptaculi lie close together; the ductus seminalis proximal to the opening in the vagina is attached at the ventral part of the bursa copulatrix, surrounded by a strong system of muscles (Fig. 5).
18. Only one retractor of the coxosternum (M 5); it is enlarged and fanlike at its origin.
19. Retractor of tergum IX (M 18) with two insertions on the dorsal ridge of this sclerite.
    - q. Beutel (1986:43-44) listed 12 apomorphies of *Hygrobia*, which are not repeated here.
    - r. Adult hygrobiids show a uniqe set of of features associated with stridulation (Beutel (1986:44). On the underside of the elytra is a row of teeth (Fig. 11). This file is in the basal 1/5 of the elytra near the suture. It rubs against the sharp edge of sternum VII. No other Hydradephaga are known to use elytra to stridulate.

The wing folding mechanism and contact of the subcubital binding patches (Hammond 1979) or setal patches (Ward 1979) with the inner elytral surface has been discussed as a phylogenetic character (*e.g.*, Kavanaugh 1986). Its absence from hygrobiids is probably a loss associated with stridulation, because stridulation in this group involves the elytral apex. The function of the binding patches among hygrobiids has been assumed by a broad area of the subcosta and radius (Fig. 12) which contacts the prominent, ventral ridge of the elytron.

- s. Chemical components produced by the pygidial defensive glands are quite isolated when compared to those of other Hydradephaga (Dettner 1985:167). Some of these compounds are not known to be produced by any other insects.
- t. Although not discussed specifically by Ruhnau (1986), it is clear that the larvae of *Hygrobia* exhibit a variety of unique character states.

Autapomorphies of Dytiscidae

20. The muscle M42 in other Hydradephaga, that is extended between the two gonocoxae (contraction), is the dilator of the distal membranous sac, for prolongation of the bursa copulatrix with insertion at the dorsal area of this membranous area.
21. Existence of a depressor of the gonocoxa, originating from the inner part of the halves of tergum IX and inserting at the dorsal part of the sclerotized appendages of segment VIII (M35).

Other apomorphic characteristics of Dytiscidae presented by Beutel (1986) are reductions or are also found in other hydradephagan groups, and are therefore of less significance as evidence for monophyly of Dytiscidae.

- u. Basal constriction of scapus with S-like curvature (Beutel 1986).
- v. Condylus of ventral procoxal jiont reduced (Baeher 1979).
- w. Abdominal sternites with median groups (rows) of bristles (Beutel 1986).
- x. Two types of cells in the pygidial defensive glands (Forsyth 1968).
- y. Nine larval and pupal characters, interpreted as synapomorphic for Dytiscidae, were listed by Ruhnau (1986).

RELATIONSHIPS OF THE FAMILIES OF HYDRADEPHAGA

The ovipositor of *Amphizoa* is rather primitive, compared with that of Hygrobiidae and some Dytiscidae. The sclerites and appendages of segments VIII and IX are more constrained in *Amphizoa* than in other Hydradephaga allowing less movement of parts of genital segments for oviposition and copulation. The most important derived characters of Amphizoidae, Hygrobiidae and Dytiscidae are in the internal genital tubes of females. In these families, there are double genital openings for the bursa copulatrix (between the base of the gonocoxae) and the vagina (opening between the genital appendages VIII); among these families these genital openings are differentiated according to various functions in copulation and oviposition. These derived character states demonstrate the monophyly of a group comprising Amphizoidae + (Hygrobiidae + Dytiscidae).

The fixed appendages between the lateral sclerites of segment VIII (coxosterna) and segment IX (lateral areas of tergum IX) may be a plesiomorphic character state in *Amphizoa*, as in Geadephaga. The fixed position of the genital appendages between the gonocoxae is very important for oviposition in aquatic habitats and has been lost altogether with the sclerotization of the appendages from most carabids and cicindelids (Bils 1976, Burmeister 1976). These appendages close the female genital tube during burrowing movement of the gonocoxae. In the course of evolution within Hydradephaga these appendages function in testing substrate before egg-laying; during probing, the ovipositor moves from a lateral to a distal position and therefore the gonocoxae are markedly sclerotized and elongate. This tendency is seen in members of *Trachypachus* Motschulsky and *Amphizoa*. This adaptation is more fully expressed among Hygrobiidae and Dytiscidae, in which the dorsally separated lateral sclerites of tergum IX are very strong, especially in its articulation with the gonocoxa, which is its center of rotation.

Among Hydradephaga the relationships of other families is less clear. The monophyletic unit of Amphizoidae + (Hygrobiidae + Dytiscidae) is quite convincing [but see Kavanaugh (1986) for a quite diferent viewpoint]. These three families I will refer to as Dytiscoidea *s.str.* However, the relative position of Trachypachidae, Noteridae, Haliplidae and Gyrinidae is more difficult. Questions about the positions of these families are important for establishing the sister group of Dytiscoidea *s.str.*

Most authors writing about the phylogenetic position of trachypachids (see references above in Introduction) have considered this group as integral to Hydradephaga except for Kavanaugh (1986) who placed them among carabids. Similarly, gyrinids have been placed among the Hydradephaga by most authors but Beutel and Roughley (1988) placed them as the sister group of all other Adephaga. Also for haliplids there are a variety of opinions [*e.g.*, compare Burmeister (1976), Kavanaugh (1986) and Beutel and Roughley (1988)] about phylogenetic position.

This would appear to leave noterids as the sister group of Dytiscoidea *s.str.* Three examples of differing placement of noterids demonstrate that such can not be done confidently yet. Kavanaugh (1986) placed noterids as the sister group of dytiscids only. This was based on the derived state of two characters (12, 16 — Kavanaugh 1986:92-95). Of these, one (Char. 12) is a loss which occurs broadly among other higher taxa of Adephaga. The other (Char. 16) represents an elongation of the metacoxa. This may represent a useful character; on the other hand, the three states are subjectively divided and it would be more convincing to have other characters to support this hypothesis.

Beutel and Roughley (1988) listed six characters (13-19, 27 — Beutel and Roughley 1988:388-390, 393-395) which support a phylogenetic grouping of Noteridae + Dytiscoidea *s.str.* From the evidence presented above about the monophyly of Dytiscoidea *s.str.* this would suggest that noterids are the sister group of Dytiscoidea *s.str.* However, the evidence for this is not compelling. Of the five characteres, three (Chars. 16, 17 and 27) are reductions. Furthermore, two characters (Chars. 15, 19) are weak characters by the authors' own admission. This leaves only one reliable synapomorphy (Char. 13) of the origin of the metafurca from the intercoxal wall.

Ruhnau (1986) placed Noteridae as the sister group of Haliplidae based on seven characters (Chars. 16-22 -- Ruhnau 1986:242-247, 260-261). Of these, four (Chars. 17, 18, 20, 21) are reductions. Therefore three characters suggest a sister group relationship between noterid and haliplids. Unfortunately, Ruhnau (1986) did not list the genera of noterids larvae which were examined. In the text he mentioned only relatively derived taxa and emphasis was placed on *Noterus* Clairville. Beutel and Roughley (1987:1904) pointed out the problems of working with a phylogenetically derived genus and of using that taxon as representative of a family.

In conclusion, there are at least three radically different hypotheses about the phylogenetic position of Noteridae as well as about the relationships and constituents of Hydradephaga. There is no basis for accepting any of these yet as well documented. Comparison among these three hypotheses suggests that much further research is required and I suspect that the final outcome, if a consensus can be reached, may be different from any of the above hypotheses.

ACKNOWLEDGEMENTS

I am greatly indebted to and thank R. E. Roughley, (University of Manitoba) who has corrected the manuscript based on presentation at the Third International Conference on Classification, Phylogeny and Natural History of Hydradephaga in Vancouver (Canada), July 1988. His time spent in making additions and correcting English is much appreciated.

REFERENCES CITED

Baehr, M. 1979. Vergleichende Untersuchungen am Skelett und an der Coxalmusculatur des Prothorax der Coleoptera. Ein Beitrag zur Klärung der phylogenetischen Beziehungen der Adephaga (Coleoptera: Insecta). Zoologica, 44: 1-76.

Bell, R.T. 1966. *Trachypachus* and the origin of the Hydradephaga (Coleoptera). The Coleopterists' Bulletin, 20: 107-112.

Bell, R.T. 1982. What is *Trachypachus?* (Coleoptera: Trachypachidae). The Coleopterists' Bulletin, 36: 590-596.

Beutel, R. 1986. Skelett und Musculatur des Kopfes und Thorax von *Hygrobia tarda* (Herbst). Ein Beitrag zur Klärung der phylogenetischen Beziehungen der Hydradephaga (Insecta: Coleoptera). Stuttgarter Beiträge für Naturkunde, Serie A (Biologie), 388: 1-54.

Beutel, R. 1988. Studies on the metathorax of the trout-stream beetle, *Amphizoa lecontei* Matthews (Coleoptera: Amphizoidae): Contribution towards clarification of the systematic position of Amphizoidae. International Journal of Insect Morphology and Embryology, 17: 63-81.

Beutel, R. 1989. The head of *Spanglerogyrus albiventris* Folkerts (Coleoptera: Gyrinidae). Contribution towards clarification of the phylogeny of Gyrinidae and Adephaga. Zoologische Jahrbücher (Anatomie), 118: 431-461.

Beutel, R. and T. Belkaceme. 1986. Comparative studies on the metathorax of Hydradephaga and Trachypachidae. Entomologia basiliensia, 11: 221-229.

Beutel, R. and R.E. Roughley. 1988. On the systematic position of the family Gyrinidae (Coleoptera: Adephaga). Zeitschrift für zoologische Systematik und Evolutionsforschung, 26: 380-400.

Bils, W. 1976. Das Abdomenende weiblicher, terrestrisch lebender Adephaga (Coleoptera) und seine Bedeutung für die Phylogenie. Zoomorphologie, 84: 113-193.

Burmeister, E.G. 1976. Der Ovipositor der Hydradephaga (Coleoptera) und seine phylogenetische Bedeutung unter besonderer Berücksichtigung der Dytiscidae. Zoomorphologie, 85: 165-257.

Burmeister, E.G. 1980. Funktionsmorphologie und Evolution des Ovipositor der Adephaga (Coleoptera). Verhandlungen des naturwissenschaftlichen Vereines für Hamburg, 24(1): 89-184.

Burmeister, E.G. 1990. The systematic position of the genus *Agabetes* Crotch within Dytiscidae (Coleoptera, Adephaga). *Quaestiones entomologicae*, 26: 221-238.

Crowson, R.A. 1975. The evolutionary history of Coleoptera, as documented by fossil and comparative evidence. Atti del X Congress nazionale Italiono di Entomologia, (Sassari 1974): 47-90.

Crowson, R.A. 1981. The Biology of Coleoptera. Academic Press, London. 802 pp.

Dettner, K. 1979. Chemotaxonomy of water-beetles based on their pygidial gland constituents. Biochemical Systematics and Ecology, 7: 129-140.

Dettner, K. 1985. Ecological and phylogenetic significance of defensive compounds from pygidial glands of Hydradephaga (Coleoptera). Proceedings of the Academy of Natural Sciences of Philadelphia, 137: 156-171.

Edwards, J.G. 1951. Amphizoidae of the world. Wasmann Journal of Biology, 8(1950): 303-332.

Evans, M.E.G. 1985. Hydradephagan comparative morphology and evolution: some locomotor features and their possible phylogenetic implications. Proceedings of the Academy of Natural Sciences of Philadelphia, 137: 172-181.

Forsyth, D.J. 1968. The structure of the defence glands in the Dytiscidae, Noteridae, Haliplidae and Gyrinidae (Coleoptera). Transactions of the Royal Entomological Society of London, 120: 159-182.

Forsyth, D.J. 1970. The structure of defence glands of the Cicindelidae, Amphizoidae and Hygrobiidae (Coleoptera). Journal of Zoology (London), 160: 51-69.

Franciscolo, M.E. 1979. Fauna d'Italia XIV. Coleoptera. Haliplidae, Hygrobiidae, Gyrinidae, Dytiscidae. Calderini, Bologna. 604 pp.

Hammond, P.M. 1979. Wing folding mechanisms of beetles, with special reference to Adephagan phylogeny. Pp 113-180 *In* T.L. Erwin, G.E. Ball, D.R. Whitehead and A.L. Halpern (*Editors*). Carabid beetles, their evolution, natural history and classification. W. Junk, The Hague, x+635 pp.

Hatch, M.H. 1927. The morphology of Gyrinidae. Papers of the Michigan Academy of Science, Arts and Letters, 7: 311-350.

Hieke, F. 1966. Vergleichende funktionelle Anatomie der Abdominalmuskulatur einiger männlicher Coleopteren unter besonderer Berücksichligung des Genitalkomplexes. Deutsche Entomologische Zeitschrift, 13: 1-168.

Hennig, W. 1950. Grundzüge einer Theorie der phylogenetischen Systematik. Deutscher Zentralverlag, Berlin. 370 pp.

Hennig, W. 1953. Kritische Bemerkungen zum phylogenetischen System der Insekten. Beitrage Entomologie 3, (Sonderheft): 1-85.

Hennig, W. 1965. Phylogenetic systematics. Annual Review of Entomology, 10: 97-116.

Hennig, W. 1981. Insect phylogeny. (translated and edited by A.C. Pont; revisonary notes by D. Schlee *et al.*). John Wiley & Sons, Chichester, New York, Brisbane, Toronto. xxii + 514 pp.

Horn, W. 1867. On *Amphizoa insolen*s LeConte. Transactions of the American Entomological Society, 1867: 154–158.

Horn, W 1881. On the genera of Carabidae with special reference to the fauna of Boreal America. Tansactions of the American Entomological Society, 9: 91-196.

Kavanaugh, D.H. 1986. A systematic review of the amphizoid beetles (Amphizoidae: Coleoptera) and their phylogenetic relationships to other Adephaga. Proceedings of the California Academy of Sciences, 44: 67-109.

Ordish, R.G. 1966. A systematic revision of the New Zealand water beetles (Coleoptera: Dytiscidae). Records of the Dominion Museum (Wellington), 5: 217-264.

Ordish, R.G. 1985. A review of spermathecal structure in New Zealand dytiscids. Proceedings of the Academy of Natural Sciences of Philadelphia, 137: 128-131.

Roughley, R.E. 1981. Trachypachids and Hydradephaga (Coleoptera): a monophyletic unit? The Pan-Pacific Entomologist, 57: 273-285.

Ruhnau, S. 1986. Phylogenetic relations within the Hydradephaga (Coleoptera) using larval and pupal characters. Entomologica Basiliensia, 11 :231-271.

Ruhnau, S. and M. Brancucci. 1984. Studies on the genus *Lancetes*. 2. Analysis of its phylogenetic position using preimaginal characters (Coleoptera: Dytiscidae). Entomologica Basiliensia, 9: 80-107.

Ward, R.D. 1979. Metathoracic wing structures as phylogenetic indicators in the Adephaga (Coleoptera). pp 181-191. *In* T.L. Erwin, G.E. Ball, D.R. Whitehead and A.L. Halpern (*Editors*). Carabid beetles, their evolution, natural history and classification. W. Junk, The Hague. 635 pp.

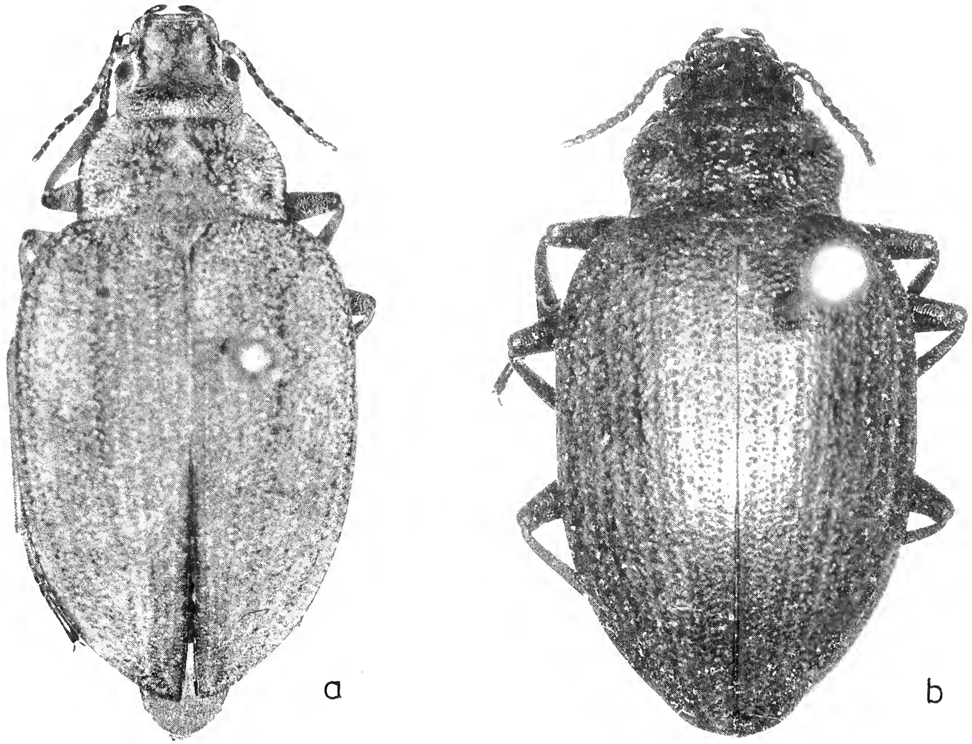


Fig. 1. Dorsal view of Amphizoidae. a. *Amphizoa lecontei* Matthews. b. *Amphizoa insolens* LeConte.

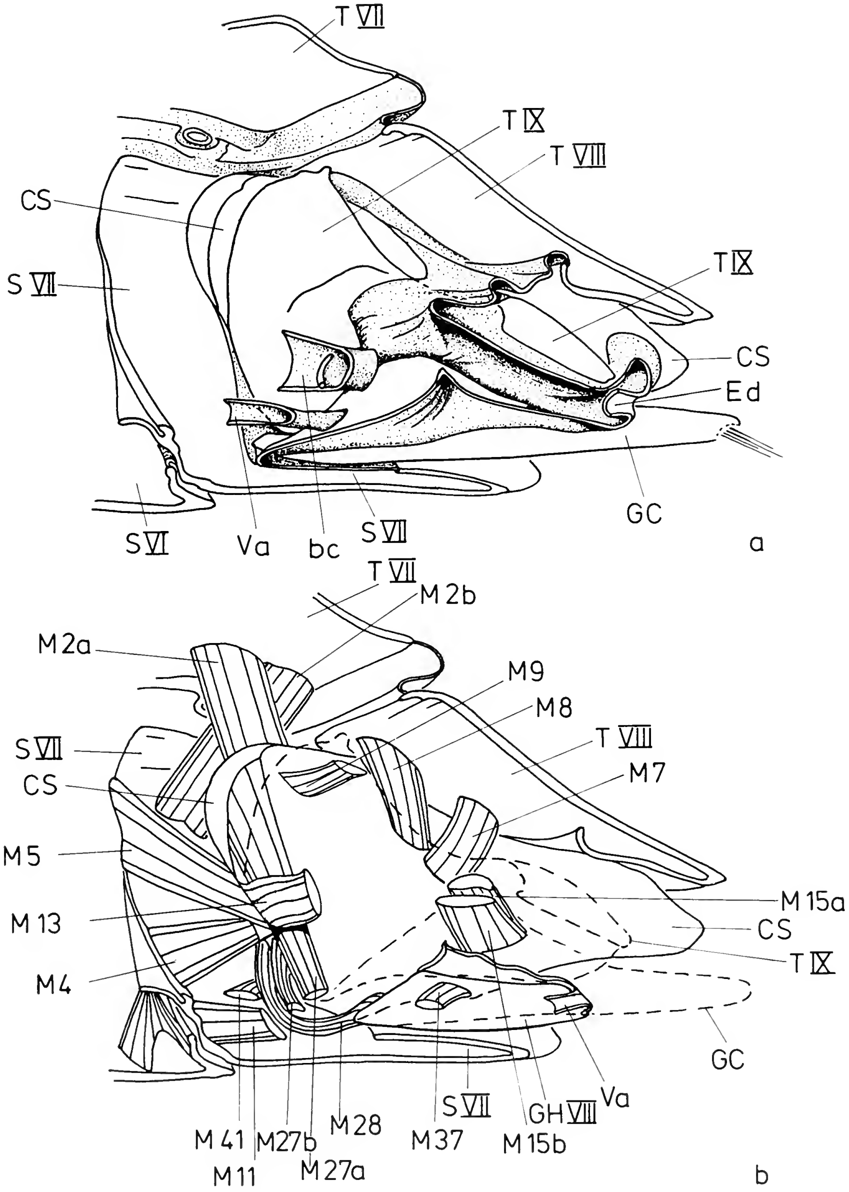


Fig. 2. *Amphizoa lecontei* Matthews, end of abdomen and female genitalia. a. inner view of right side of sclerites and genital ducts, genital appendages VIII removed. b. muscular system of segment VIII, tergum IX and gonocoxa as interrupted lines. Legend: bc - bursa copulatrix; CS - gonocoxosternum; Ed - end of gut; GC - gonocoxa; GH VIII - genital appendages of segment VIII (1. gonapophysis); M - muscular system - muscles - of the abdominal segments and female genitalia; S VI, S VII - sternites of segment VI and VII; T VII, T VIII - tergites of segment VII and VIII; T IX - tergum IX divided in two lateral clasps; Va - vagina.

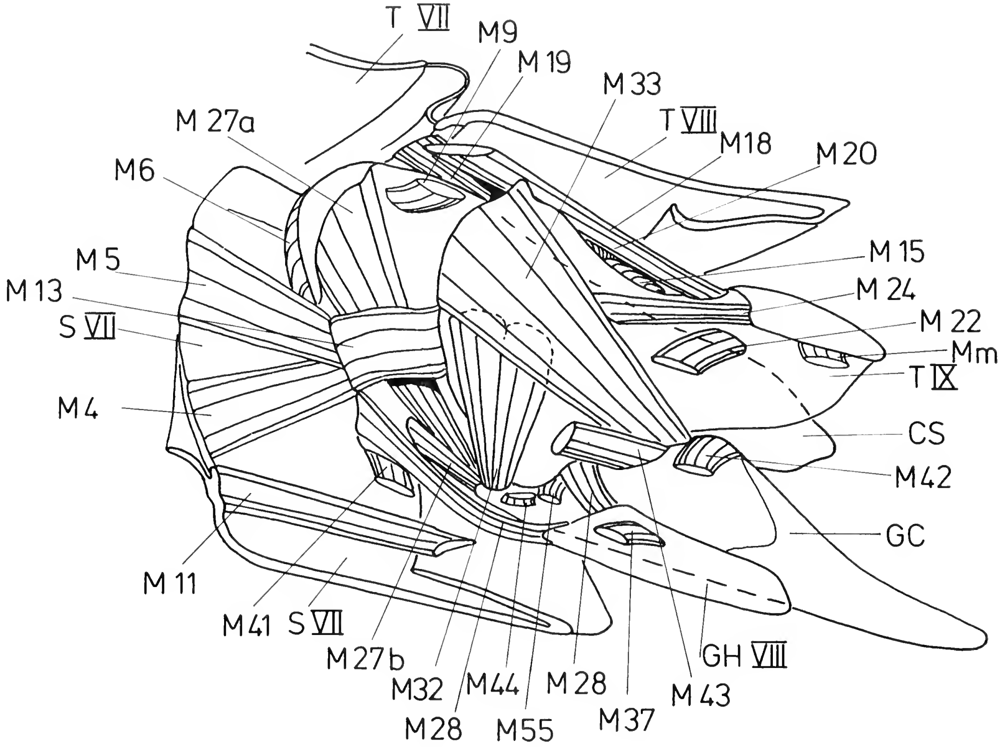


Fig. 3. *Amphizoa lecontei* Matthews, right side of female genitalia, sclerites and muscles. Legend: CS - gonocoxosternum; GC - gonocoxa; GH VIII - genital appendages of segment VIII (1. gonapophysis); M - muscular system - muscles - of the abdominal segments and female genitalia (see text); Mm - muscle of membrane between the halves of tergum IX; S VII - sternum of segment VII; T VII, T VIII - tergites of segment VII and VIII; T IX - tergum IX divided in two lateral clasps.

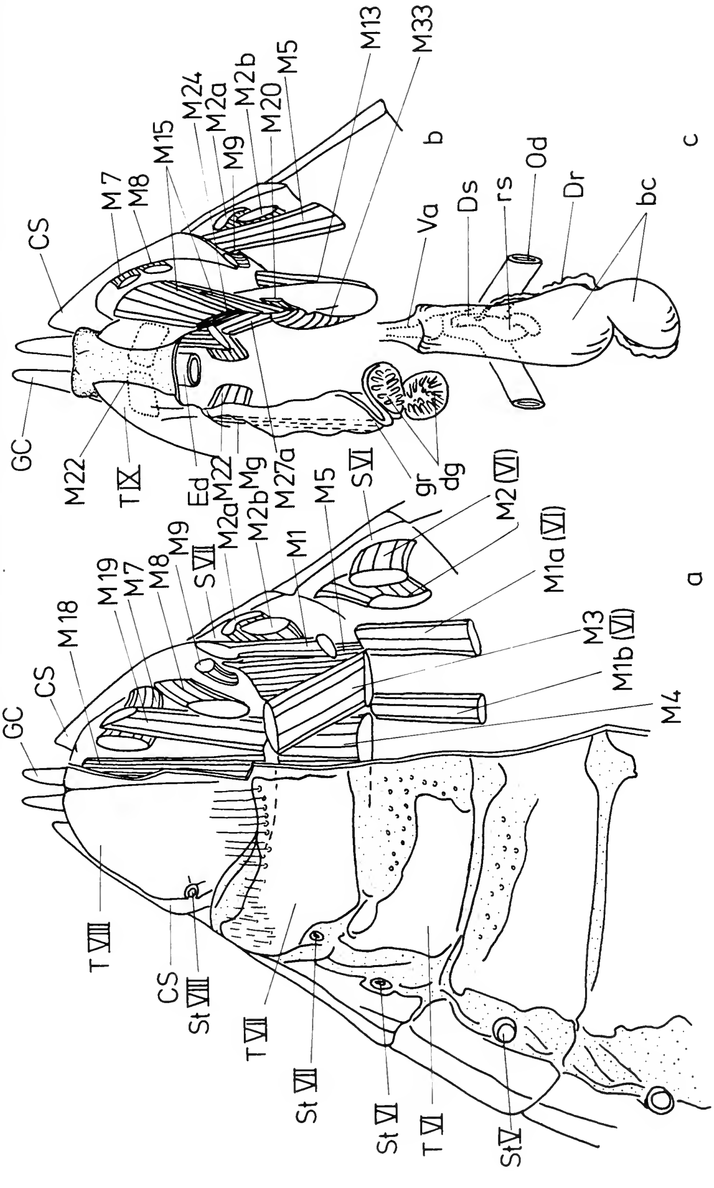


Fig. 4. *Amphizoa insolens* LeConte, dorsal view of female genitalia. a. dorsal view of the tip of abdomen and the dorsal muscular system. b. muscular system of the genital appendages and the defense gland. c. inner genital organs. Legend: bc - bursa copulatrix; Cs - gonocoxosterna; dg - defense gland; Dr - ductus receptaculi; Ds - ductus seminalis; Ed - end of gut; GC - gonocoxa; gr - resErvoir of defense gland; M - muscular system - muscles - of the abdominal segments and female genitalia; M 1–3 (VI) - segmental muscles of segment VI, same position as muscles M 1–3 in segment VII; Mg - protractor of defense gland; Od - oviduct; S VI, S VII - sternites of segment VI and VII; St V - VIII - stigmata of the segments V to VIII; T VI–T VIII - tergites of segment VI to VIII; T IX - tergum IX divided in two lateral clasps; Va - vagina.

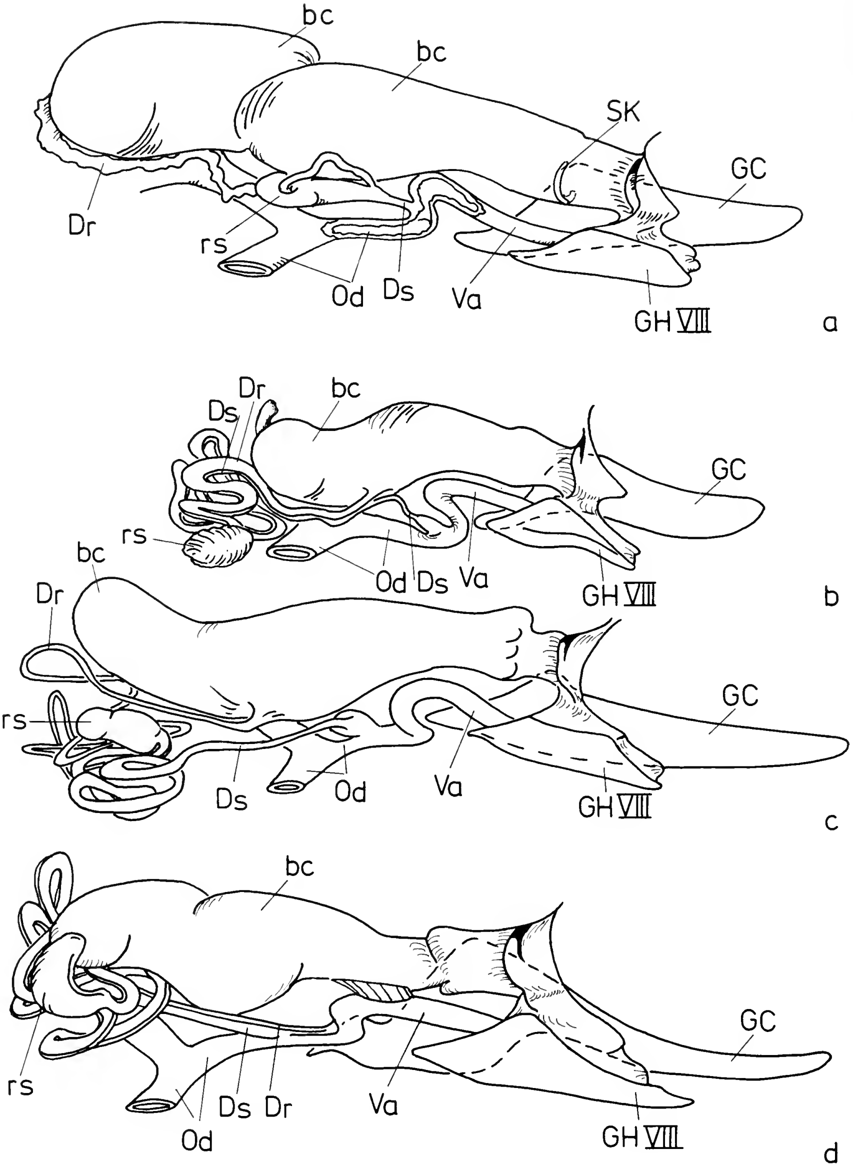


Fig. 5. Inner female genital organs of different species of Hydradephaga. a. *Amphizoa lecontei* Matthews (Amphizoidae). b. *Hygrobia tarda* (Herbst) (Hygrobiidae). c. *Copelatus haemorrhoidalis* (F.) (Dytiscidae, Colymbetinae). d. *Hydronebrius cordaticollis* (Reitter) (Dytiscidae, Colymbetinae). Legend: bc - bursa copulatrix; Dr - ductus receptaculi; Ds - ductus seminalis; GC - gonocoxa; GH VIII - genital appendages of segment VIII (1. gonapophysis); Od - oviduct; rs - receptaculum seminis; Sk - sclerites in the wall of bursa copulatrix; Va - vagina;

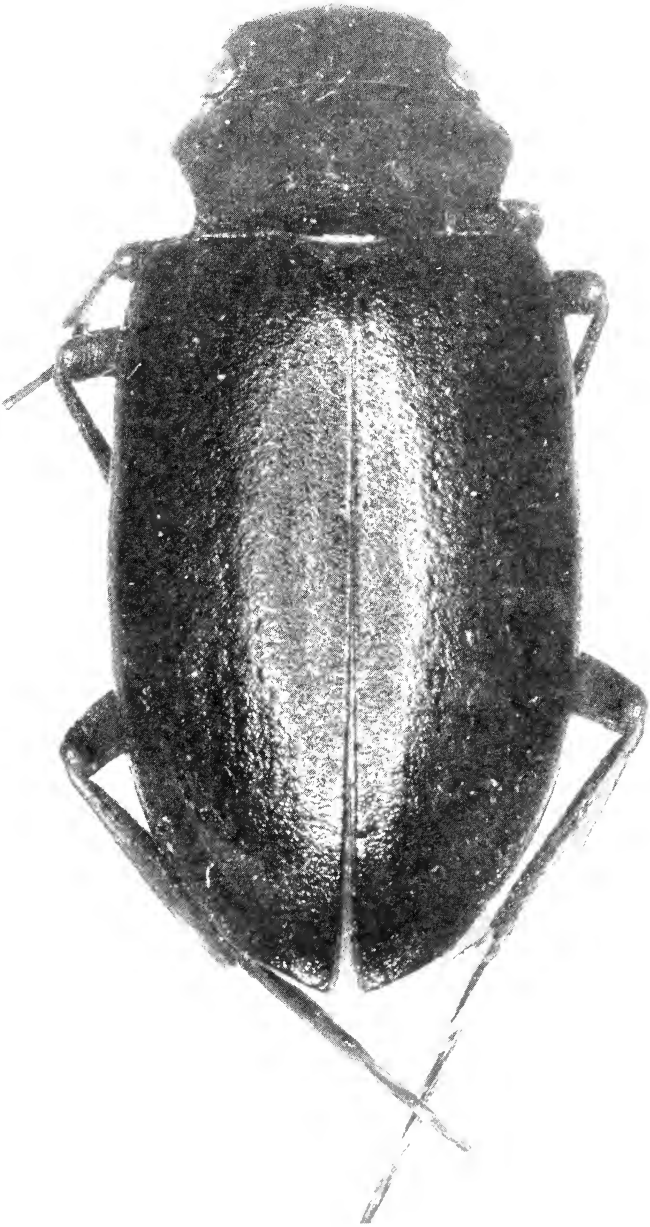


Fig. 6. *Hydronebrius cordaticollis* (Reitter), dorsal view.

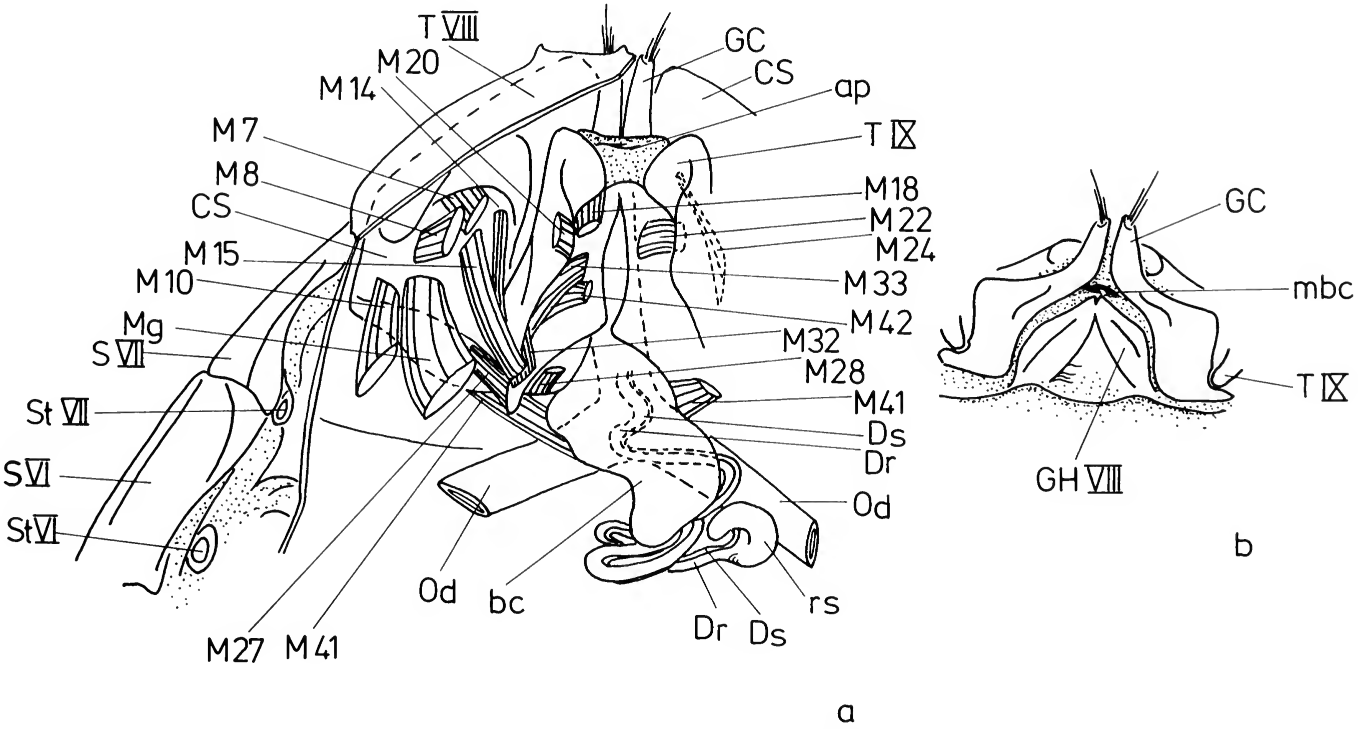


Fig. 7. *Hydronebrius cordaticollis* (Reitter), female genitalia. a. dorsal view of abdomen and muscular system of the genital area and inner genital organs. b. view of the genital appendages. Legend: ap - anal papilla; bc - bursa copulatrix; CS - gonocoxosterna; Dr - ductus receptaculi; Ds - ductus seminalis; GC - gonocoxa; GH VIII - genital appendages of segment VIII (1. gonapophysis); M - muscular system - muscles - of the abdominal segments and female genitalia; mbc - mouth of bursa copulatrix; Od - oviduct; rs - receptaculum seminis; S VI, S VII - sternites of segment VI and VII; T VIII - tergum VIII; T IX - tergum IX divided in two lateral clasps.

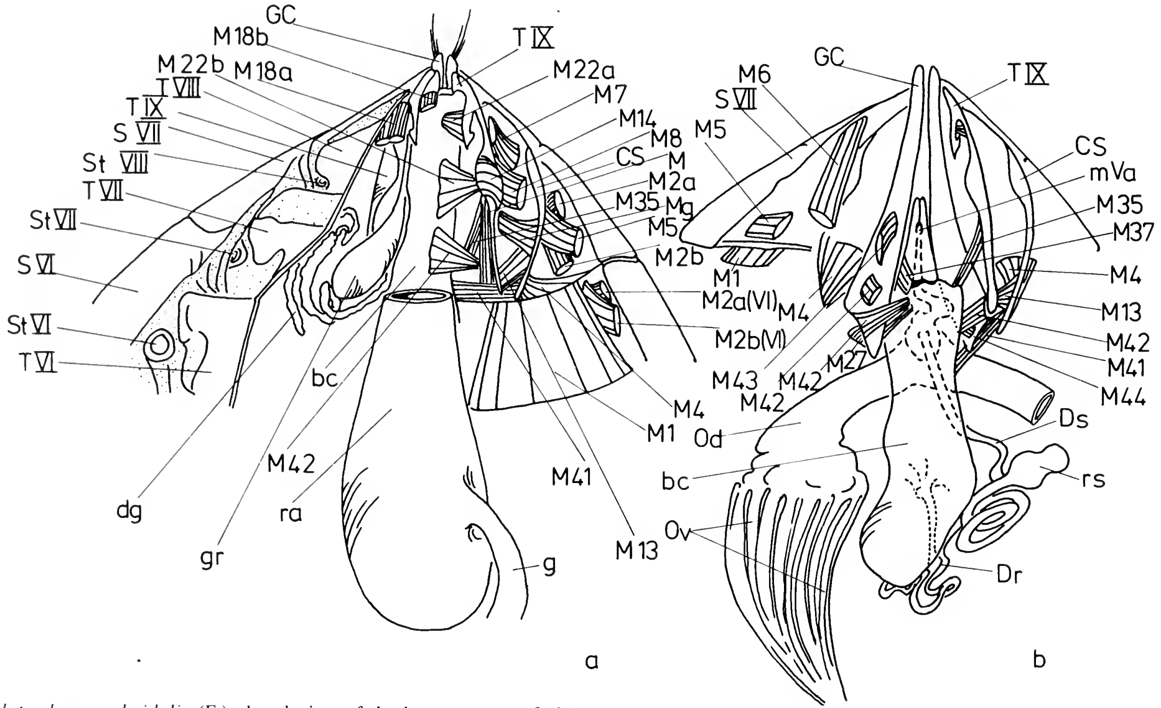


Fig. 8. *Copelatus haemorrhoidalis* (F.), dorsal view of the last segments of abdomen and female genitalia. a. sclerites, muscular system and defense gland, end of rectal ampulla removed. b. muscles of genital appendages and inner genital organs. Legend: bc - bursa copulatrix; CS - gonocoxosterna; dg - defense gland; Dr - ductus receptaculi; Ds - ductus seminalis; g - gut; GC - gonocoxa; GH VIII - genital appendages of segment VIII (1. gonapophysis); gr - reservoire of defense gland; M - muscular system - muscles - of the abdominal segments and female genitalia; mVa - mouth of vagina; Od - oviduct; Ov - ovarium; ra - rectal ampulla; rs - receptaculum seminis; S VI, S VII - sternites of segment VI and VII; St VI - VIII - stigmata of segment VI to VIII; T VI - T VIII - tergites of segment VI to VIII; T IX - tergum IX divided in two lateral clasps. (correction M g = M 9).

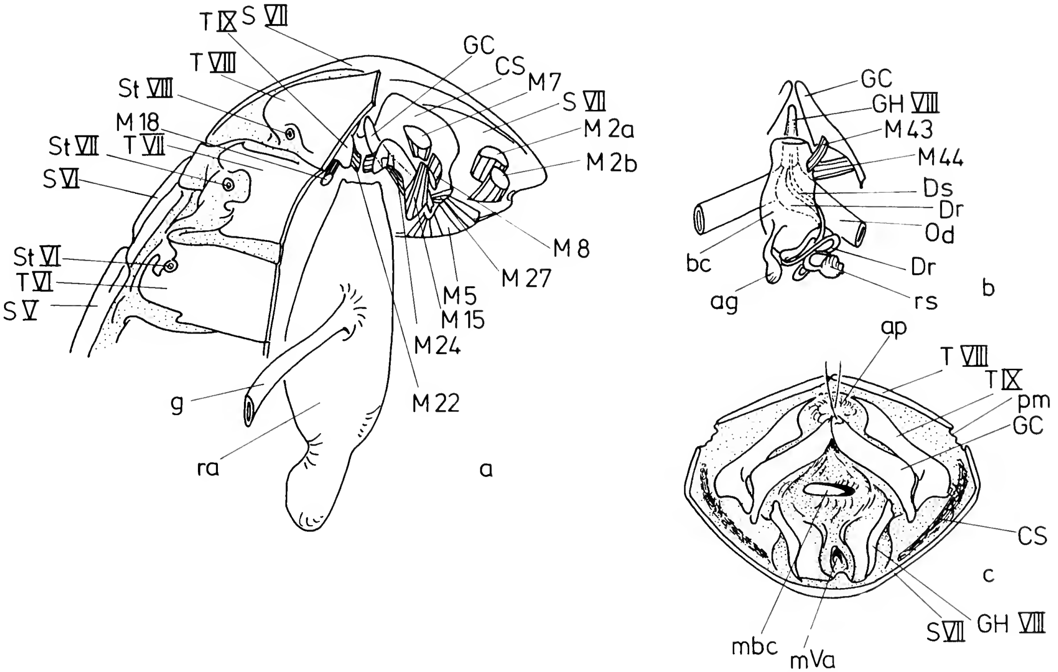


Fig. 9. *Hygrobia tarda* (Herbst), female genitalia. a. dorsal view of the tip of female abdomen and the muscular system of female genitalia and appendages. b. dorsal view of inner genital organs. c. view of the tip of abdomen, from posterior aspect, showing the genital appendages and the two openings of the genital ducts in a position before copulation - the gonocoxites are covered by membranes. Legend: ag - accessory gland; ap - anal papilla; bc - bursa copulatrix; CS - gonocoxosterna; Dr - ductus receptaculi; Ds - ductus seminalis; g - gut; GC - gonocoxa; GH VIII - genital appendages of segment VIII (1. gonapophysis); M - muscular system - muscles - of the abdominal segments and female genitalia; mbc - mouth of bursa copulatrix; mVa - mouth of vagina; Od - oviduct; pm - membrane of pleural area; ra - rectal ampulla; rs - receptaculum seminis; S V - S VII - sternites of segment V to VII; St VI -VIII - stigmata of segments VI to VIII; T VI - T VIII - tergites of segment VI to VIII; T IX - tergum IX divided in two lateral clasps.

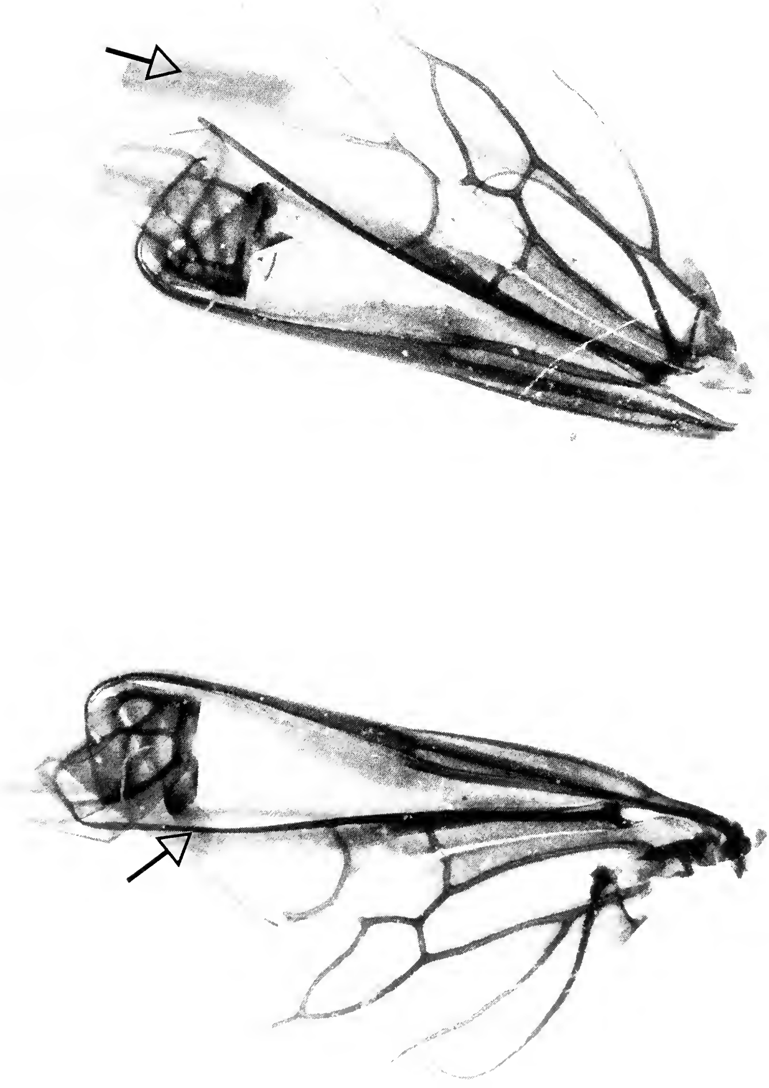


Fig. 10. Folded wings of a. *Amphizoa lecontei* Matthews, Amphizoidae. b. the arrow indicates the area of setal patches or sub-cubital binding patches.

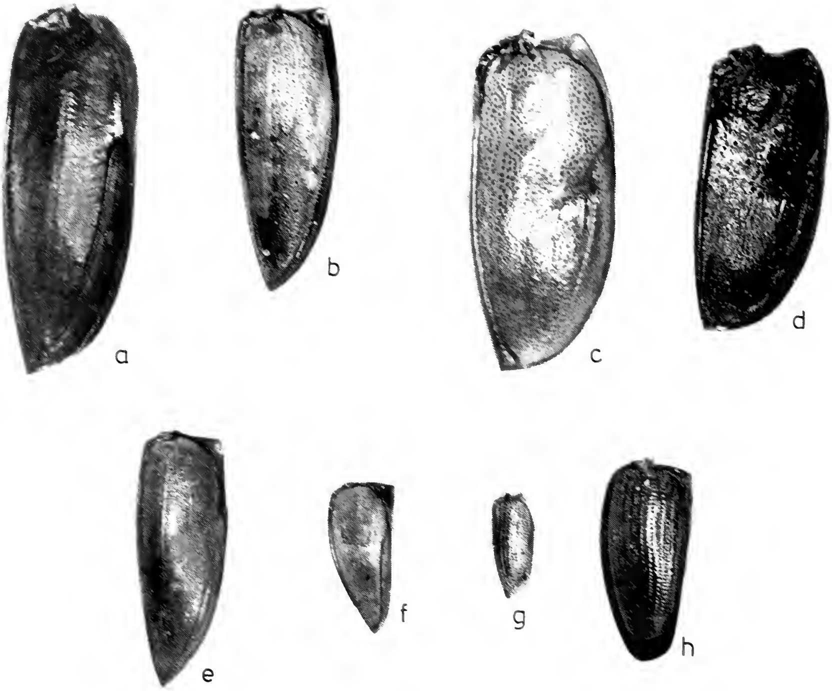


Fig. 11. Inner view of left elytron in different species of Hydradephaga. a. *Amphizoa lecontei* Matthews, Amphizoidae. b. *Agabus bipustulatus* (L.), Dytiscidae. c. *Hygrobia tarda* (Herbst), Hygrobiidae. d. *Hygrobia nigra* (Clark), Hygrobiidae. e. *Copelatus haemorrhoidalis* (F.), Dytiscidae. f. *Noterus clavicornis* (DeGeer), Noteridae. g. *Haliplus lineatocollis* Marsham, Haliplidae. h. *Gyrinus substriatus* Stephens, Gyrinidae.

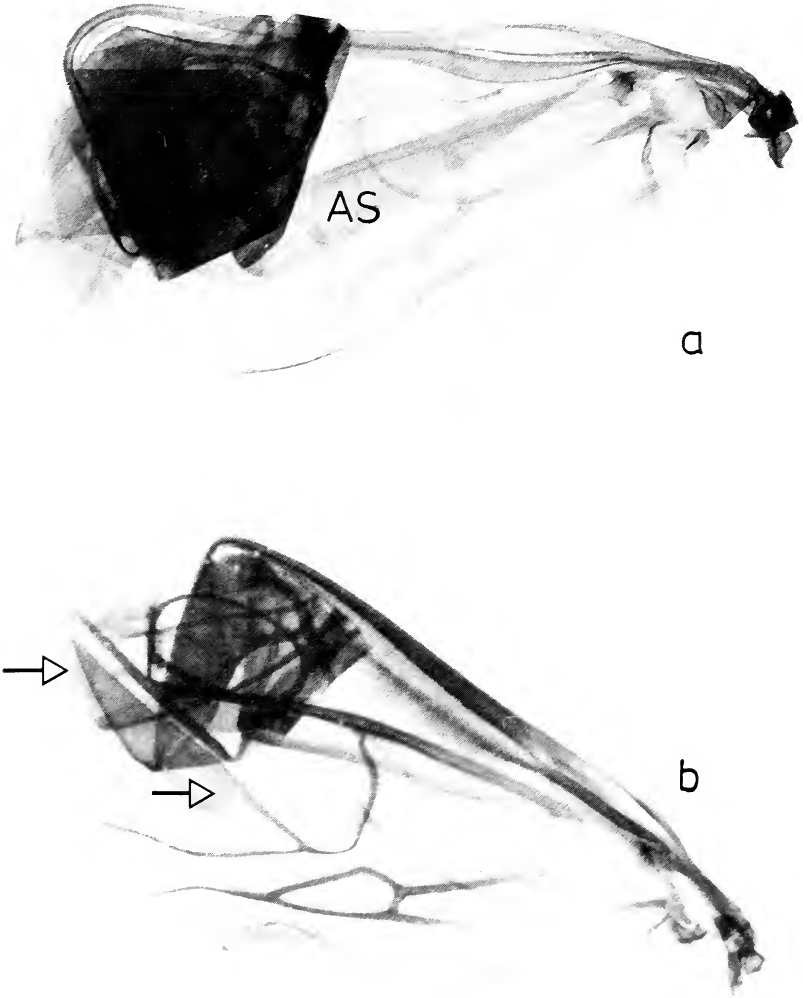


Fig. 12. Folded left wings of a. *Hygrobia tarda* (Herbst), and b. *Agabus bipustulatus* (L.). The arrow indicates the area of setal patches or subcubital binding patches (see Fig. 10). In the genus *Hygrobia* this area is lost and an other area with setae is expanded in the basal area, the wing (AS).

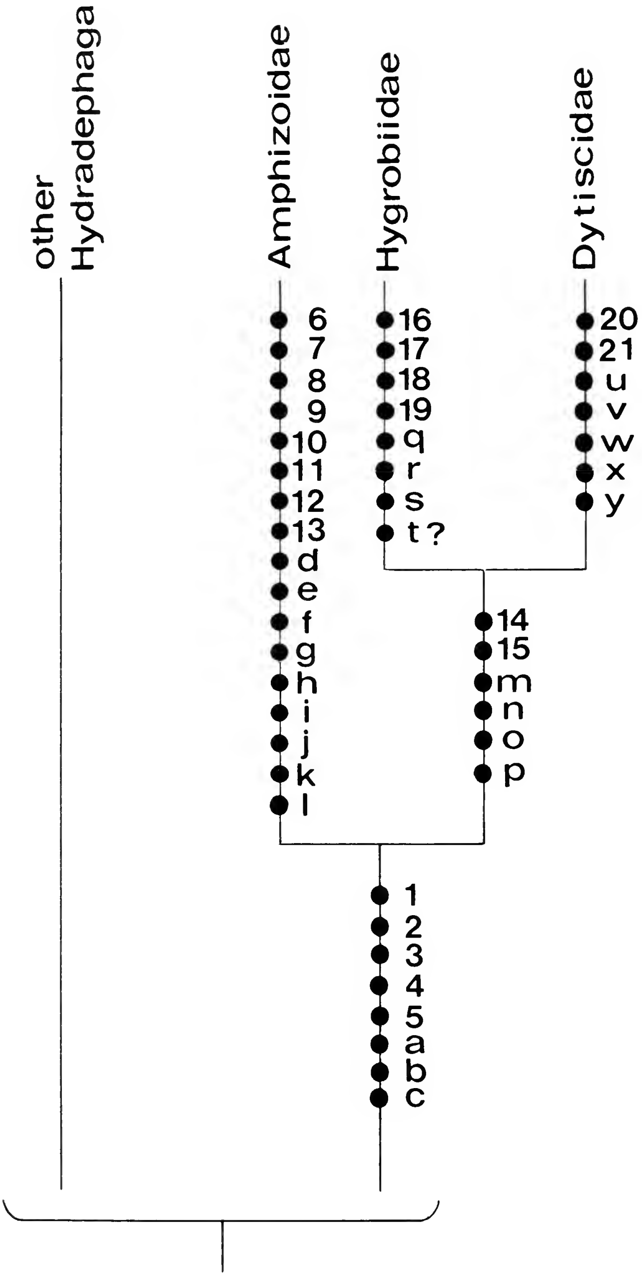


Fig. 13. Proposed phylogeny of Amphizoidae, Hygrobiidae and Dytiscidae. (For discussion of apomorphies 1-21 and a-y, of female genitalia, see text).

A TAXONOMIC, PHYLOGENETIC, AND ZOOGEOGRAPHIC ANALYSIS OF *LACCORNIS* GOZIS (COLEOPTERA: DYTISCIDAE) WITH THE DESCRIPTION OF LACCORNINI, A NEW TRIBE OF HYDROPORINAE

G. William Wolfe[1]
Department of Entomology and Economic Zoology
Cook College, P.O. Box 231
New Jersey Agricultural Experiment Station
Rutgers University
New Brunswick, NJ 08903
U. S. A.

and

R.E. Roughley
Department of Entomology
University of Manitoba, Winnipeg, Manitoba
R3T 2N2
Canada

Quaestiones Entomologicae
26: 273– 354 1990

ABSTRACT

All members of the genus Laccornis *Gozis 1914 are keyed, described and illustrated; the genus* Laccornis *is redefined and the new, monobasic tribe Laccornini is erected for* Laccornis. *Phylogenetic and zoogeographic analyses demonstrate that members of Laccornini are restricted to the Northern Hemisphere and form the most plesiotypic tribe of Hydroporinae. Ten species are assigned to* Laccornis. Laccornis nemorosus, *new species, is described from Reelfoot Lake, Tennessee, USA and a lectotype male is designated for* L. deltoides *(Fall 1923) from Beaver Creek, Illinois. The species are assigned to three species-groups. Species-group I is monobasic and contains only the southern European species,* L. kocai *(Ganglbauer). It represents the sister clade to the remainder of* Laccornis *and was probably isolated in the early to mid-Cretaceous. Species-group II has three species; the most plesiotypic is the Holarctic species,* L. oblongus *(Stephens), and the more derived, Nearctic species pair of* L. conoideus *(LeConte) and* L. pacificus *Leech. This species-complex was isolated in Asiamerica by the late Cretaceous - early Cenozoic intercontinental seaway. The ancestral stock of* L. oblongus *was isolated in the Oligocene by the origin of the Bering Sea. Its modern occurrence in northwestern North America is probably the result of secondary and late Pleistocene events. Uplift of the Rocky Mountain chain in the late Miocene divided the common ancestor of* L. conoideus *(east of Rockies) and* L. pacificus *(west of Rockies).*

Species-group III is the sister group to species-group II and contains L. deltoides *(Fall),* L. nemorosus *n.sp,* L. latens *(Fall),* L. difformis *(LeConte),* L. schusteri *Wolfe and Spangler and* L. etnieri *Wolfe and Spangler. The ancestor of*

---

[1] Present address: Division of Mathematics and Science, Dobbs Hall, Reinhardt College, Waleska, Georgia 30183, U. S. A.

this species-group was isolated in Euramerica in the late Cretaceous; its members are now distributed in eastern North America and are most diverse in the southeastern United States. No distinct, vicariant events are invoked to explain their present distribution.

TABLE OF CONTENTS

INTRODUCTION

This project originated over ten years ago with what at the time seemed a relatively uncomplicated problem; *Laccornis difformis* (LeConte) of Fall (1923) was actually a complex of three species. However, what began as a restricted taxonomic investigation of the *L. difformis*-complex grew into a larger systematic investigation of not only this species-complex, but also of the genus *Laccornis* and eventually to a survey of basal lineages of Hydroporinae.

The scope of the problem was extended because a casual attempt to define the genus and later an intensive search for generic synapotypies failed to provide insight into what was and what was not "*Laccornis*". The problem became all the more difficult when we realized that *Laccornis* was a very primitive hydroporine, perhaps representing the sister group to all other hydroporines; this complicated the choice of an outgroup and attempts to polarize characters.

Recent studies have shed considerable light on most of the original problems (Wewalka 1969, 1981, Wolfe and Spangler 1985, Wolfe 1985, 1989, Roughley and Wolfe 1987). However, this publication advances previous analyses by: i) describing another new species, ii) taxonomically revising all known species and providing keys for their identification, iii) documenting distributions and habitats, iv) redescribing the genus, v) describing a new tribe to include *Laccornis*, vi) reconstructing a phylogeny, and vii) developing a zoogeographic hypothesis for the species included within *Laccornis*.

MATERIALS AND METHODS

Materials

Source of specimens.— Specimens used in this study were borrowed from the collections or institutions listed below, indicated in the text by the associated two-, three-, or four-letter codens.

ANSP	Academy of Natural Sciences of Philadelphia, 19th and the Parkway, Philadelphia, Pennsylvania 19103, USA (D. Azuma).
AMNH	American Museum of Natural history, Central Park West at 79th Street, New York, New York, USA 10024 (L.H. Herman).

AU	Auburn University, Department of Zoology-Entomology, Funchess Hall, Auburn, Alabama 36849 (G. Folkerts).
BMNH	British Museum (Natural history), Department of Entomology, Cromwell Road, London, SW7 5BD, England (N. Stork, M.E. Bacchus).
CARR	J.L. and B.F. Carr, 24 Dalrymple Green NW, Calgary, Alberta, Canada T3A 1Y2.
CAS	California Academy of Science, Department of Entomology, Golden Gate Park, San Francisco, California, 94118 USA (D.H. Kavanaugh).
CNC	Canadian National Collections, Biosystematic Research Centre, Research Branch, Ottawa, Ontario, Canada, K1A OC6 (A. Smetana).
CUIC	Cornell University Insect Collection, Department of Entomology, Cornell University, Ithaca, New York 14853 USA (Q. Wheeler).
FM	Field Museum of Natural history, Chicago, Illinois, 60605 USA (J. Ashe, L. Watrous).
INHS	Illinois Natural history Survey, Natural Resources Building, Urbana, llinois, 61801 USA (W.U. Brigham).
IU	Indiana University, Department of Biology, Jordan Hall 138, Bloomington, Indiana, 47405 USA (F.N. Young).
JBWM	J.B. Wallis Museum, Department of Entomology, University of Manitoba, Winnipeg, Manitoba, Canada R3T 2N2 (R.E. Roughley).
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, 02148 USA (A. Newton).
NMNH	Smithsonian Institution, National Museum of Natural history, Department of Entomology, Washington, D.C., 20560 USA (P.J. Spangler).
NMW	Naturhistorisches Museum Wien, Zoologische Abteilung (Insekten), Postfach 417, Burging 7, A-1014 Wien, Austria (F. Janczyk).
ODU	Old Dominion University, Department of Biology, Norfolk, Virginia, 23508 USA (J.F. Matta).
OSU	Oregon State University, OSU Systematic Entomology Laboratory, Department of Entomology, Oregon State University, Corvallis, Oregon, 97331 USA (G.L. Peters).
PM	Peabody Museum of Natural history, Yale University, 170 Whitney Avenue, P.O. Box 6666, New Haven, Connecticut, 06511 USA (C.L. Remington, D.G. Furth).
RU	Rutgers University, Department of Entomology and Economic Zoology, Cook College, P.O. Box 231, New Brunswick, New Jersey, 08903 USA (M. May).
SMK	Snow Entomological Museum, University of Kansas, Lawrence, Kansas, USA (P. Ashlock).
SCSU	St. Cloud State University, Department of Biological Sciences, St. Cloud, Minnesota, 56301 USA (R. Gundersen).
SBSK	State Biological Survey of Kansas, the University of Kansas, 66044 USA (B. Coler).
UASM	Strickland Museum, University of Alberta, Department of Entomology, Edmonton, Alberta, Canada T6G 2E3 (G.E. Ball, D. Shpeley).
UC	University of Connecticut, Department of Biology, Storrs, Connecticut, 06268 USA (P.W. Severance).
UMMZ	University of Michigan, Museum of Zoology, Division of Insects, Ann Arbor, Michigan, 48109 USA (B. O'Connor).
UW	University of Wisconsin, Department of Entomology, Madison, Wisconsin, 53706 USA (W. Hilsenhoff).

ZIH	Zoologiska Institutionen Helsingfors Universitetet, N. Jänvägsgatan 13, F-00100 Helsingfors 10, Finland (O. Biström).
ZM	Zoology Museum, Department of Zoology, Helgonavägen 3, S-223 62 Lund, Sweden (R. Danielsson).
ZSM	Zoologische Staatssammlung München, Münchhausenstraße 21, D-8000 München 60, West Germany (G. Scherer).

Methods

Dissection, measurements and illustrations.— Standardized techniques were used and these are described in Wolfe (1984, 1985) and Roughley and Pengelly (1982). Representatives of all specimens, except the rare *L. deltoides* (Fall), were completely disarticulated prior to detailed systematic study (see Wolfe 1985:133).

Species concept.— We use the evolutionary species concept as explained in Wiley (1981). We favor this concept because it is broadly applicable; it does not require evidence regarding reproductive isolation and all species are part of a phylogeny. All species concepts (biological, evolutionary or phenetic) initially require discernment of character discontinuities (Rosen 1978). In the process of partitioning specimens initially we used Erwin's (1970) criteria for species recognition: an array of specimens displaying a multidimensional continuum of characters which is separable from other sets of specimens by a distinct gap. For us, a sufficient gap could be a single character, provided there was substantial evidence for absence of intergradation.

The method of analysis and progressive grouping of specimens in this revision generally follows Roughley and Pengelly (1982). Specimens of *Laccornis* were segregated first on differences in aedeagal and/or anterior protarsal claw structure of males. Subsequently a search was made for correlation of these characters with other characters (antennal form, punctation, elongate femoral setae, *etc.*). Thus the taxa were distinguished by means of phenetic methods. Subsequently these taxa were assessed using phylogenetic criteria. The evolutionary species concept could be considered as equivalent to the phenetic species concept since phenetic methods are used to delimit species. However, an important distinction is that, with the evolutionary species concept, a species almost always is distinguished by a synapotypy. Therefore species and all higher taxa are justified ultimately by synapotypic similarity.

Even though reproductive isolation is not a required element for the evolutionary species concept, evidence for intergradation versus isolation is useful and should be used if available. In revisionary research, absence of intergradation in areas of sympatry or parapatry almost always is the test for isolation. For allopatric populations, species status is considered justified if the gap among populations in question is equivalent to the disparity among species which occur sympatrically and in the absence of clinal trends of important characters. For sympatric populations, this test is maximally significant only if it involves sister species or at least closely related taxa. Within *Laccornis*, we did not find any sister species to be broadly sympatric. Therefore while we used the criterion of sympatry to invalidate certain characters (*e.g.*, color characters), the taxa which we established cannot be evaluated by the sympatry criterion.

In consequence, the validity of the taxa that we propose rests on documentation of the distinctness or separateness of the lineages. For us, this is not just a matter of designating a gap, but, when possible, recognizing uniquely derived character states (autapomorphies) that suggest that distinct lineages have evolved. Conceivably, species could be found that lack autapomorphies (*e.g.*, if an ancestral species does not become extinct at the time of speciation event). In this latter situation, synapomorphies before and after (on the cladogram, above and below) the dichotomization in question are used to justify the species as a lineage.

In summary, evaluation of species status, even under the premises of the evolutionary species concept, requires a holistic approach and their recognition and evaluation requires phenetic, phylogenetic and chorological data. However, our species concept and analysis of relationships emphasizes a phylogenetic approach and we believe that this is less arbitrary than a study based completely on phenetics and/or presumed reproductive isolation.

Descriptions.— Distinction among tribal, genus, and species level characters is somewhat arbitrary. However, we divide characteristics among the three levels of classification based on the phylogenetic level at which character diversification first occurred, traditional use of characters in keying out tribes, genera, and species, and our own experience with the usefulness of the characters. Tribal and generic descriptions are presented traditionally. However, our species descriptions are in the form of a character matrix. This technique is modified from that of Erwin (1982). This character matrix format is not better in every way from traditional descriptions. For example, it is more difficult to describe subtle differences among characters when assigning them to a matrix. We compensate for this by providing figures of the alternative as well as the subtly differing character states. We prefer this method because, in addition to the advantages listed by Erwin (1982), it forces consistent treatment of virtually every character for each species under consideration; it makes comparison of characters conspicuous and it allows for easy addition of new characters. We use ten character systems with 55 characters with a total of 160 character states to describe the ten known species of *Laccornis.*

Locality information.— The known distribution of each species is shown in Figs. 21A-D. Exact locality data for specimens examined is on file at JBWM.

Phylogenetic methods.— The phylogenetic procedures used in this study are essentially Hennigian. The best general references for this approach are Wiley (1981) and Nelson and Platnick (1981); other useful references are Kavanaugh (1972, 1978), Whitehead (1972), and Ross (1974) and references cited therein.

Character states were polarized from a generalized, outgroup concept based on our studies of other groups of Dytiscidae. A general treatment of many of these is presented in Wolfe (1985, 1989) for members of Hydroporinae. In particular we examined the character states known from members of the tribe Methlini (especially *Celina hubbelli* Young) because methlines are a relatively plesiotypic group of hydroporines closely related to *Laccornis* (Wolfe 1985, 1989). When characterizing the plesiotypic state from methlines we also considered the state found in members of *Laccornellus* Roughley and Wolfe which is also a plesiotypic member of Hydroporini (Roughley and Wolfe 1987).

When characters existed in only two states (binary characters) polarization was a rather straight forward, unambiguous procedure for the characters examined in members of *Laccornis.* In most examples this was because the outgroup did not have the inferred apotypic state found within *Laccornis.* These binary characters therefore contribute to an initial framework of the cladogram. Multistate characters can be more difficult to resolve. This is because what may appear as a linear array of character states may be a number of more or less separate series of character transformations. In assessing such multistate characters we have found useful the computer program PAUP (Swofford 1985).

Multistate characters, when used in the process of tree construction with PAUP, can be considered as ordered or unordered and the ramifications of this designation are important. If a specific transformation series is stipulated for a character (*i.e.*, that character is ordered) then, when the tree is constructed using PAUP, this sequence may bring about homoplasy in a few to many other characters. For example, if a character sequence is specified initially as transforming from character state 0 to state 1 to state 2 then additional homoplasy will result in other characters if the sequence should have been 0 to 2 to 1. By analyzing the contribution of each character separately it was possible to discover which characters were contributing to homoplasy. Therefore our first task on discovering such characters was to very carefully re-analyze these characters to make sure that the evolution of the character states was as we had coded it. This was particularly helpful, for instance, in assessing the features of the male antennomeres of *Laccornis* which was much more complex than we had thought initially.

After reanalyzing each character which was contributing to homoplasy certain multistate characters remained difficult to polarize and to arrange into a sequence. The only way to choose among the array of possibilities available was by means of parsimony. Using this method the character states are unordered and the sequence of transformation which requires the fewest number of changes is accepted as correct.

While total reliance on ordered characters can artificially increase the amount of homoplasy within a cladogram similarly total reliance on unordered characters can overly minimize the amount of homoplasy that actually exists. Therefore we tried to balance our phylogenetic analysis by using both ordered and unordered formats to check the robustness of our phylogenetic hypotheses, to understand the contributions that each character was making to the cladogram and to test the validity of suspected evolutionary changes (see Phylogeny for details).

The value of synapomorphies that supported hypotheses of monophyly were evaluated with a consistency index (CI). This index is a measure of the amount of homoplasy within a character series and is calculated by dividing the range of a character (*i.e.*, the minimum number of character state changes possible) by the actual length that the character contributes to the cladogram. CI values close to zero indicate high degrees of homoplasy and a CI value of one indicate a perfectly consistent character with no homoplasy. For example, a binary character has a range or minimum possible length of one and if a binary character changes from 0 to 1 only once on a cladogram the CI value would be one. However, if a binary character undergoes one reversal (0 to 1 to 0) the actual length contributed would be two and the CI value (1 divided by 2) would be 0.5. The CI value for each character is given in Table 3.

STRUCTURAL FEATURES

Notes about taxonomic and phylogenetic characters

The characters below are discussed from anterior to posterior as they occur on the body of the insect and they are arranged sequentially in Table 1. Most character states will be easily understood from use of Table 1 and the figures. In the treatment below some character states found in the descriptions of species are discussed as well as our reasoning for the phylogenetic value of those characters used in the reconstructed phylogeny (Fig. 19).

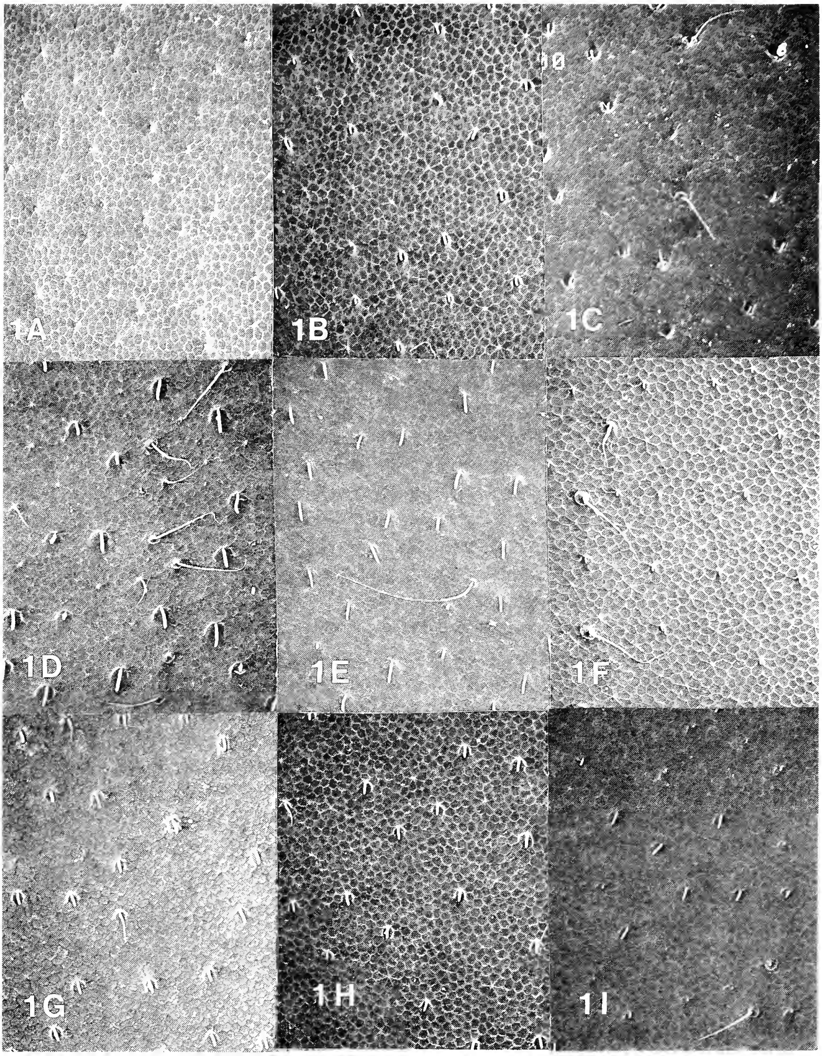
Antennal structure.— Divergence in antennomere shape is remarkable among males of *Laccornis* (Figs. 3A-H). Males of all species except *L. kocai* have some or all of antennomeres 3-7 modified. We at first suspected that the various antennal forms were part of a single morphocline. However, detailed studies of structural differences indicates that the spectrum of differences should be partitioned into two independent morphotypes - I and II.

In morphotype I, antennomeres 3-5 are characterized as a unit and in morphotype II antennomeres 3-7 are characterized as a separate unit. In morphotype I, the least derived antenna is that of males of *L. latens* (Fig. 3A), and involves only antennomere 4; progressively greater change involves primarily modification of antennomere 4 (compare that of males of *L. latens* , Fig. 3A, to that of *L. difformis*, Fig. 3F, and to *L. nemorosus*, Fig. 3C, D, F) and to a lesser extent antennomeres 3 and 5. In morphotype II, the least modified antenna is that of males of *L. oblongus*. In male specimens of that species antennomeres 3-7 are modified, but barely so and predominantly on the ventral surface; successive modifications in other taxa (*e.g., L. conoideus*, Figs. 3E, H) involve only those antennomeres. Therefore, in both morphotypes, modification simultaneously affects either antennomeres 3-5 or 3-7, and antennomeres appear to change as a unit, in morphotypes I and II respectively.

Although there is increased size of antennomeres in morphotypes I and II, we are confident that morphotype I and II represent two independent character systems because numerous other comparisons of structure reveal substantial differences. For example, within morphotype I, the ventral surface of antennomere 4 becomes progressively more concave, the reticulation more effaced, and the posterior and/or anterior edge setose (compare Figs. 3F, G). Changes in morphotype II involve none of those modifications; the ventral surface becomes convex/sinuate on some antennomeres, reticulation becomes rugose and no setal development is evident (Fig. 3H). Antennomere shape within morphotypes I and II also is fundamentally different. In morphotype I, antennomere 4 appears to become progressively enlarged (compare Figs. 3A-C) but there is relatively little distortion of shape, even in the most derived state which is found on males of *L. deltoides* and *L. nemorosus*. In morphotype II, the posteroapical corner of antennomeres 3 and 4 is produced giving a distinctly asymmetric shape (Figs. 3E, H). Within each morphotype, changes appear correlated and we coded several associated changes as one integrated complex; coding of each morphotype for phylogenetic analysis is summarized in Table 3.

The completely unmodified antenna of males of *L. kocai* occurs also in the outgroup and that state is considered plesiotypic (Tables 3-5). For morphotype I, the second state of development (state 1) involves the barely perceptible enlargement of antennomere 4 (Fig. 3A); in state 2, antennomere 3 is slightly enlarged and antennomere 4 even more so, the ventral surface of antennomere 4 is a little more concave basally and setae occur along the posterior edge (Figs. 3B, F); in state 3, the fourth antennomere reaches maximum size, the ventral surface is distinctly concave, and setae are present on the anterior and posterior edge (Fig. 3C, G, 4I). For morphotype II, state 1 involves no antennomere enlargement, however, the ventral surface of antennomeres 3-7 are a little flattened with reticulate sculpticels elongaged longitudinally and scarcely rugose. In state 2, antennomeres 3, 4, and 5 are distinctly enlarged asymetrical, and the ventral surfaces are a little more convex/sinuate and distinctly rugose (Figs. 3E, H).

Mouthparts and proventriculus.— Mouthpart structure among Hydradephaga in general and Dytiscidae in particular is reviewed by Wolfe (1984, 1985). Mouthpart and proventricular structure are described in the tribal description and



Figures 1A-I. Elytral microsculpture (200X). A) *Laccornis kocai*, B) *L. oblongus*, C) *L. conoideus*, D) *L. pacificus*, E) *L. latens*, F) *L. nemorosus*, G) *L. difformis*, H) *L. schusteri*, I) *L. etnieri*.

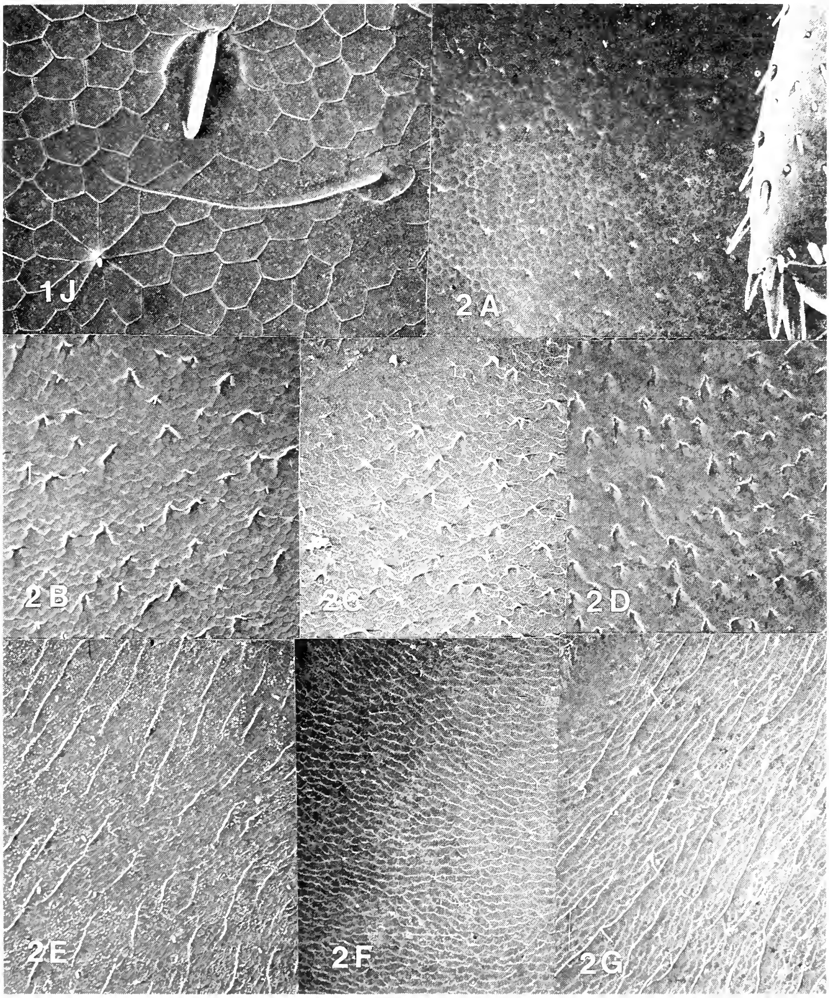
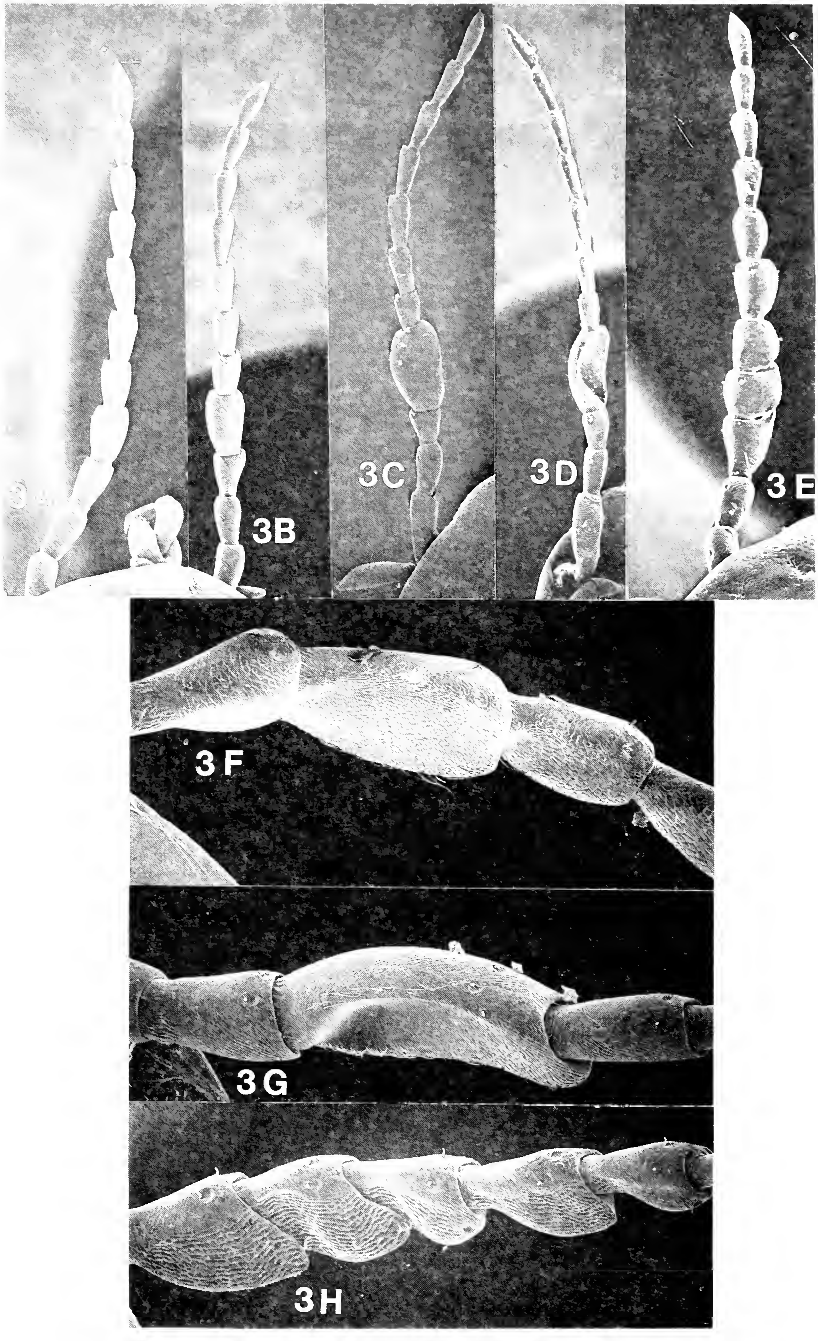
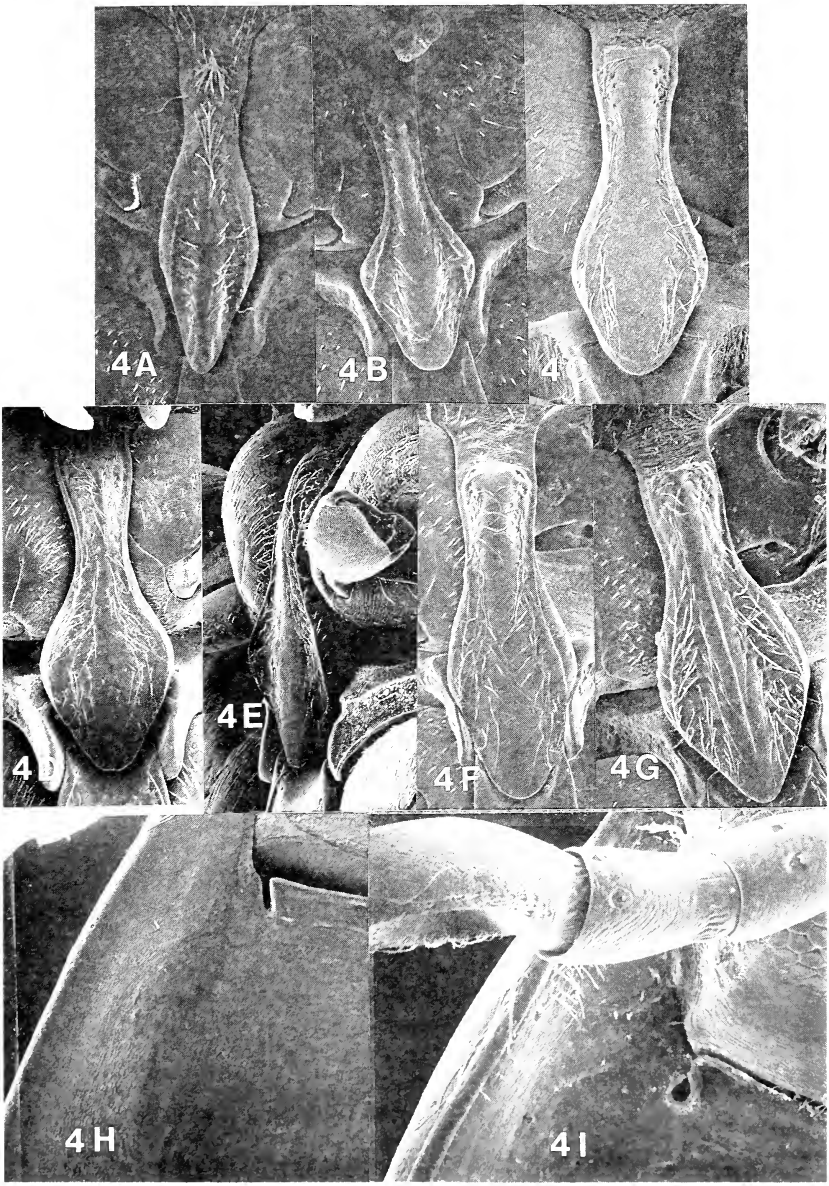


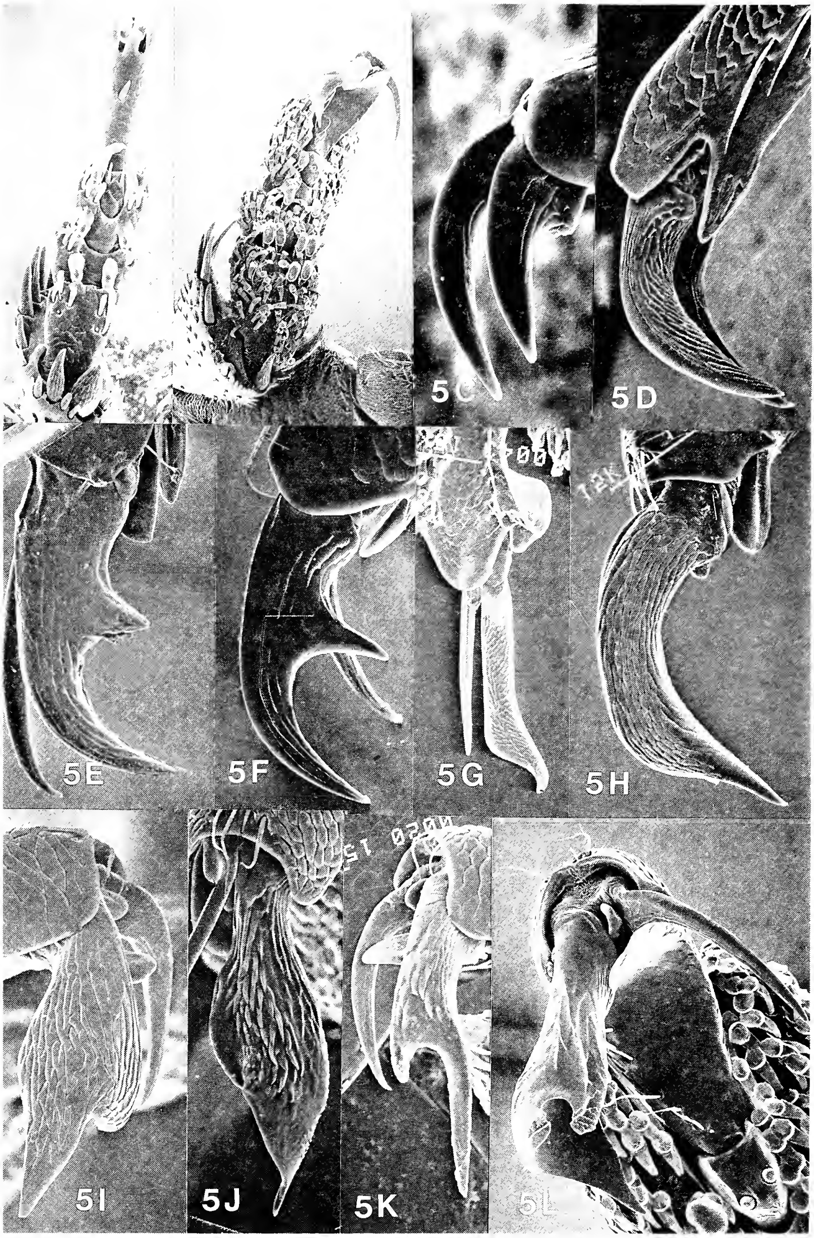
Figure 1J and 2A-G. Fig. 1J. Elytral microsculpture, *Laccornis pacificus* (1000x) showing reticulate pattern and from left to right, simple puncture, compound eccentric puncture and compound concentric puncture (with thickened sides). Figs. 2A-G. Metacoxal microsculpture. A) *Laccornis kocai* (200x), B) *L. oblongus* (200x), C) *L. conoideus* (200x), D) *L. pacificus* (200x), E) *L. latens* (150x), F) *L. nemorosus* (150x), G) *L. schusteri* (150x).



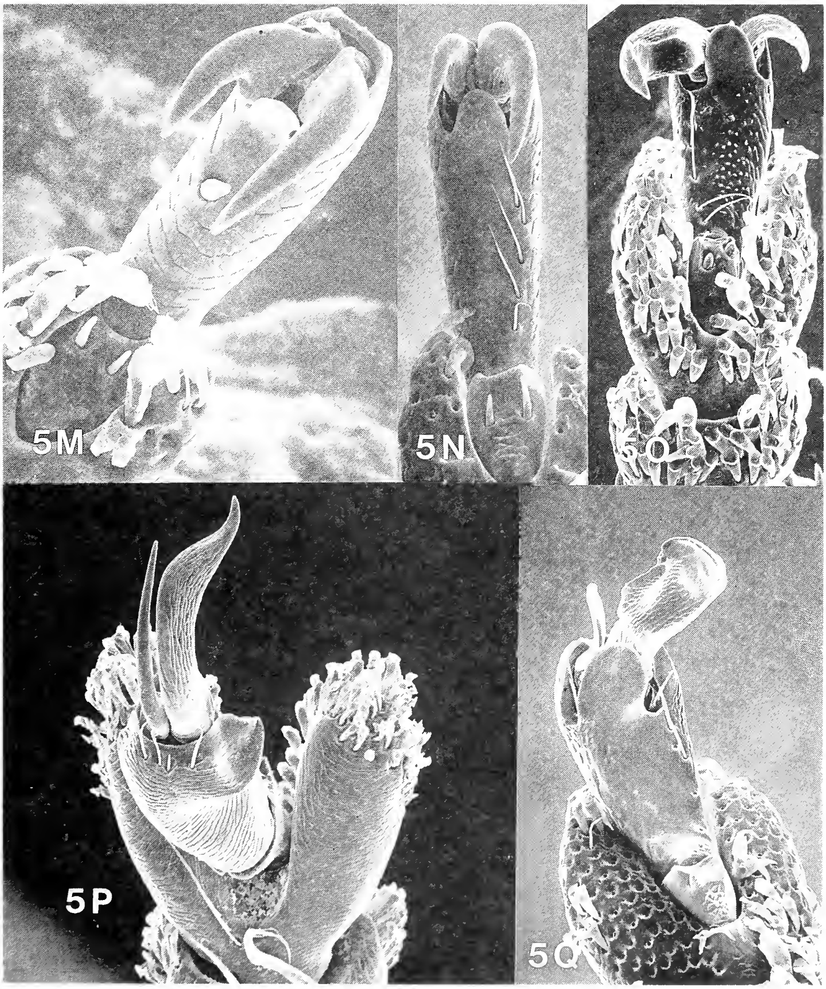
Figures 3A-H. Antennal structure. A) *Laccornis latens*, dorsal view, antennomeres 1-11 (50x), B) *L. schusteri*, dorsal view, antennomeres 1-11 (40x), C) *L. nemorosus*, dorsal view, antennomeres 1-11 (40x), D) *L. nemorosus*, anteroventral view, antennomeres 1-11 (40x), E) *L. conoideus*, dorsal view, antennomeres 1-11 (60x), F) *L. difformis*, anteroventral view , antennomeres 3-6 (150x), G) *L. nemorosus*, anteroventral view, antennomeres 3-5 (150x), H) *L. conoideus*, anteroventral, antennomeres 3-7, (150x).



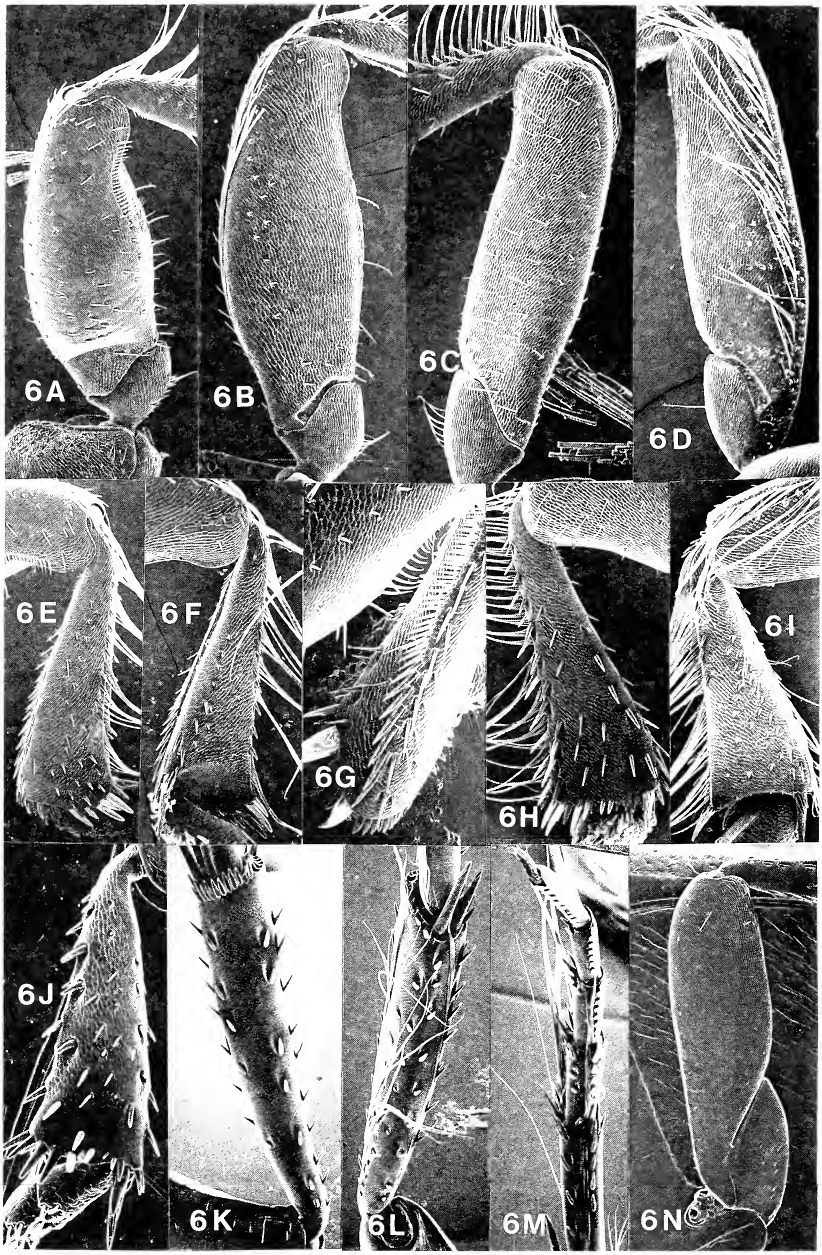
Figures 4A-I. Prosternal structure. Figs. A-G. Prosternal process, ventral view unless otherwise indicated. A) *Laccornellus lugubris* (150x). B) *Laccornis kocai* (150x). C) *L. oblongus* (150x). D) *L. nemorosus* (80x). E) *L. nemorosus*, ventrolateral view showing depressed medial area (80x). F) *L. latens* (100x). G) *L. schusteri* (100x). Figs. 4H-I. Ventral anterolateral corner of prosternum. H) *L. oblongus*, cleft present (250x). I) *L. nemorosus*, pore present (200x).



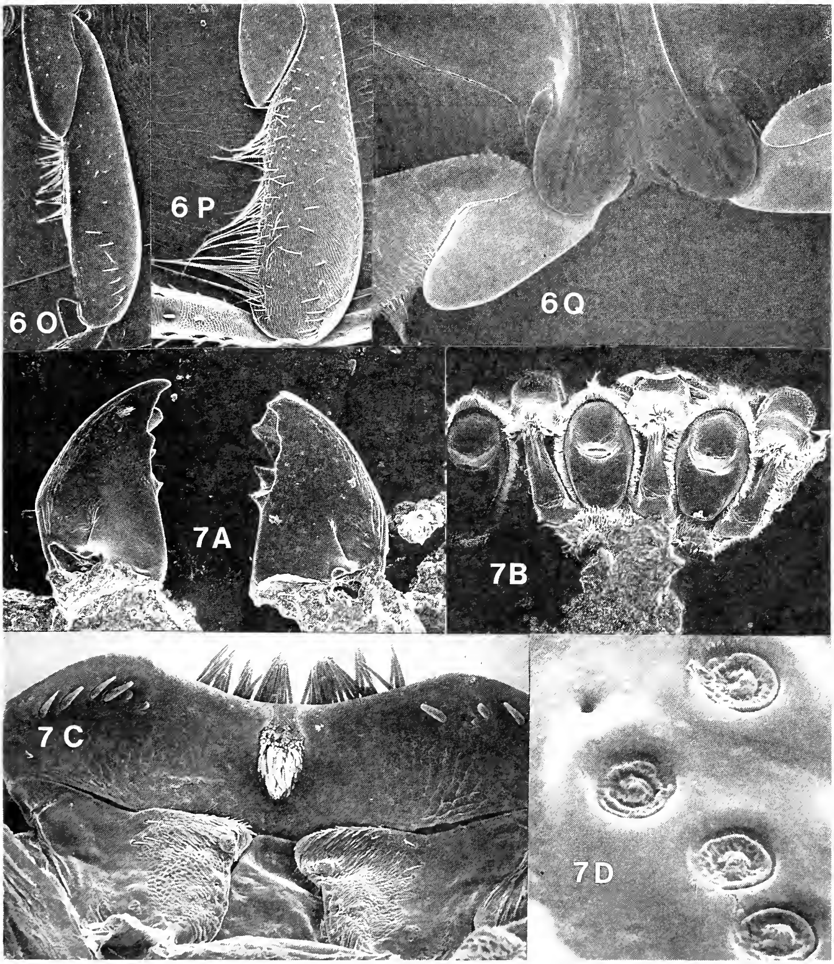
Figures 5A-L. Figs. 5A-B. Protarsus, ventral view. A) *Laccornis kocai*, two modified palettes on tarsomeres 1-3, B) *L. etnieri*, four modified palettes on tarsomeres 1-2. Figs. 5C-L. Protarsal claw structure. C) *L. kocai* (800x), D) *L. oblongus* (600x), E) *L. conoideus* (600x), F) *L. pacificus* (600x), G) *L. nemorosus*, note distinct asymmetry of protarsomere 5, ventral view (200x), H) *L. nemorosus*, lateral view (300x), I) *L. latens* (400x), J) *L. difformis* (300x), K) *L. schusteri* (300x), L) *L. etnieri*, note somewhat asymmetrical shape of fifth protarsomere, (300x).



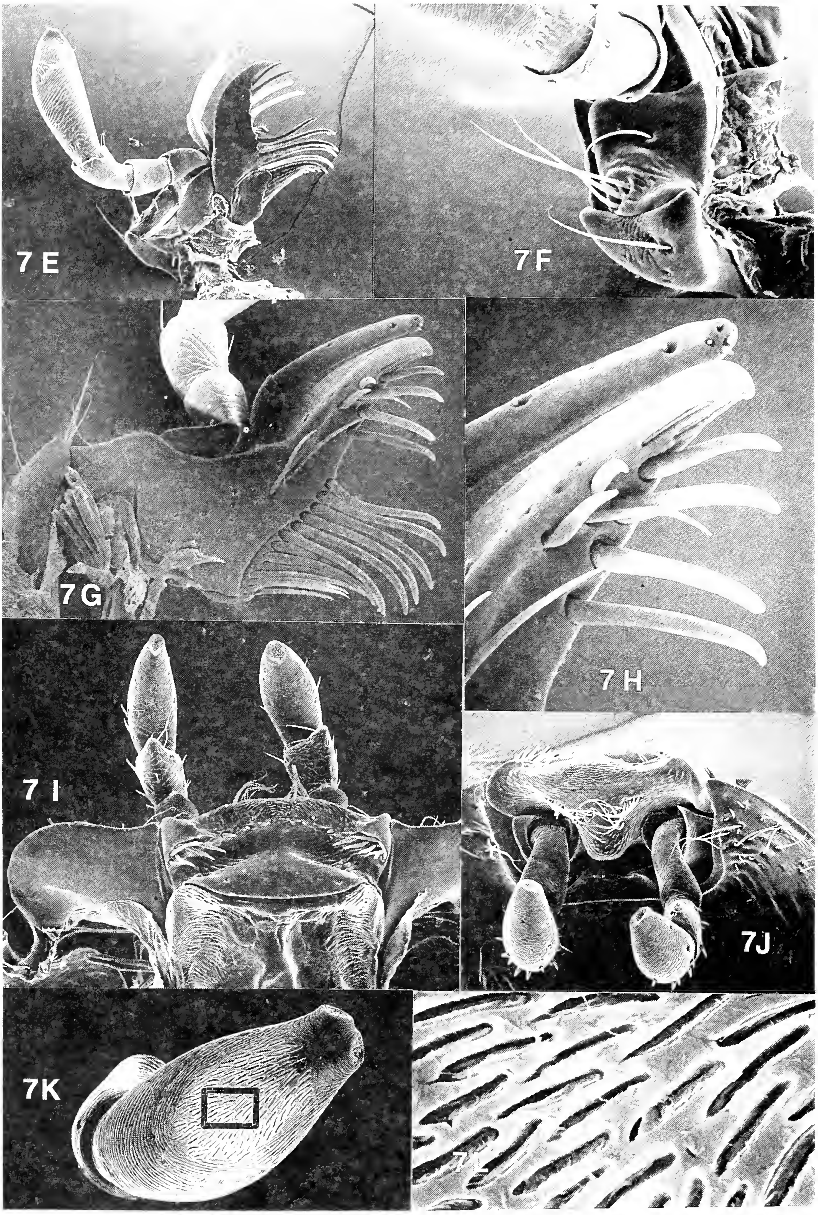
Figures 5M-Q. Protarsomeres 4 and 5. M) *Laccornis kocai*, ventral view (300X), N) *L. oblongus*, ventral view (300X), O) *L. latens*, ventral view (200X), P) *L. nemorosus*, dorsoapical view (200X), Q) *L. difformis*, ventral view (200X).



Figures 6A-N. Leg chaetotaxy. Figs. 6A-I, *Laccornis difformis*, J, *L. latens*, K-M, *L. kocai*, N, *L. latens*. A) Profemur, anterior view (80x), B) Profemur, posterior view (80x), C) Mesofemur, anterior view (80x), D) Mesofemur, posterior view (80x), E) Protibia, anterior view (80x), F) Protibia, posterior view (80x), G) Protibia, ventral edge (150x), H) Mesotibia, anterior view (80x), I) Mesotibia, posterior view (80x), J) Mesotibia, anterior view (100x), K) Metatibia, anterior view (80x), L) Metatibia, posterior view (80x), M) Metatarsus, ventral view (80X), N) Metafemur, anterior view (80x).



Figures 6 O-Q and 7A-D. Figs. 6O-P. Metafemur, ventral view. O) *Laccornis pacificus* (60x), P) *L. etnieri* (60x), Q) Metacoxal processes, base of each femur contacting process, (40x). Figs. 7A-D. Mouthpart and proventricular structure. A) Mandibles, *L. latens*, ventral view (80x), B) Proventriculus, *L. difformis*, (80x), C) Labrum and epipharynx, *L. difformis* (200X), D) Peculiarly modified epipharyngeal sensilla (6000x).



Figures 7E-L. Mouthparts. Figs. 7E-H, *Laccornis difformis*, I-L, *L. latens*. E) Maxilla, ventral view, arrow indicates basal sclerite, F) Cardo and stipes, showing setal pattern (300x), G) Maxilla, dorsal view (200x), apex further magnified in 7H, H) Lacinial tip, medial view, showing digitiform sensilla (500x), I) Labium, dorsal view (150x), J) Labium, ventral view, (150x), K) Apical labial palpomere, anterolateral view, box indicates area enlarged in 7L, L) Apical labial palpomere , enlargement of area indicated in 7K.

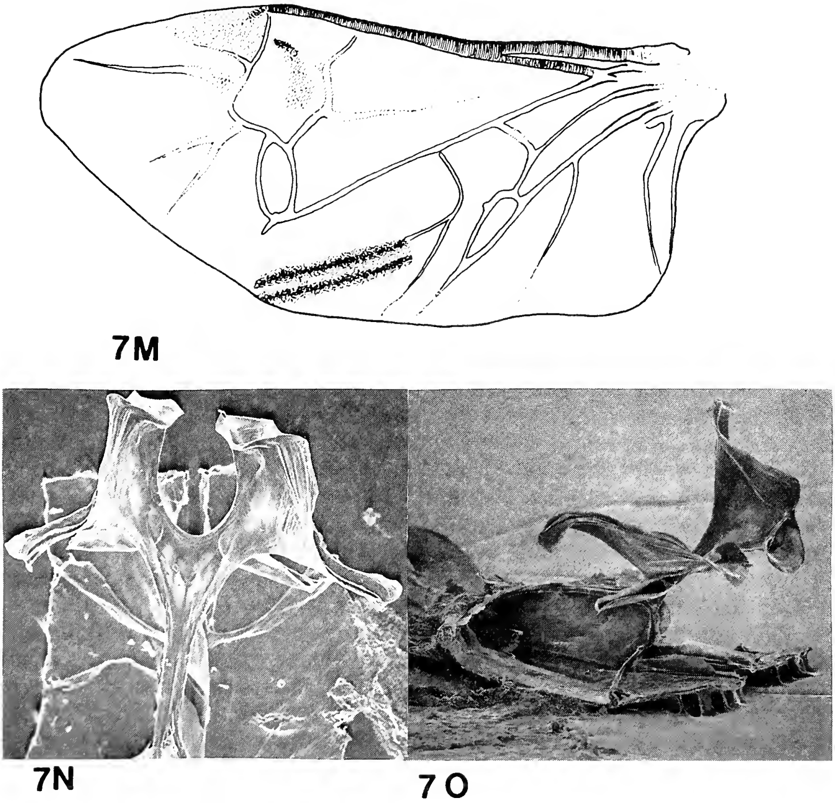


Figure 7M-O. Thoracic structure. *Laccornis difformis*. M) Flight wing, N) Metafurca, dorsal view (30X), O) Metafurca, anterolateral view (30X).

they are illustrated in Figs. 7A-L but no characters were found that are useful in taxonomic or phylogenetic analyses within the genus.

Prosternal process.— Two important characters are associated with the prosternal process: general shape and longitudinal, medial convexity. The shape of the prosternal process varies gradually among members of *Laccornis*, however, the process is relatively broad in all species. The shape is narrow and elongate in specimens of the methline outgroup taxon, *C. hubbelli*. To polarize these character states an additional outgroup was necessary and *Laccornellus lugubris* (Aubé) was used for this (see Roughley and Wolfe 1987); the process in specimens of the latter species is long and slender (Fig. 4A) and that state is considered plesiotypic. Therefore, the broadened shape of members of *Laccornis* is a generic synapotypy.

The prosternal process is longitudinally and medially convex in most species. In specimens of *L. deltoides* (Fall) and *L. nemorosus*, n. sp., the convexity is scarcely developed and the middle of the prosternal process appears almost concave (Fig. 4D, E). Since the medial portion of the prosternal process of specimens of *C. hubbelli* is more distinctly elevated and convex that state is considered plesiotypic.

Prosternal pore.— The explanation of this state and the basis for its polarity is given in Wolfe (1985). The plesiotypic state is that of a V-shaped notch located at the anterolateral corner of the prosternum (Fig. 4H). The derived state (Fig. 4I) is a pore-like opening in the same position. In clean specimens the different states can be discerned at about 50x magnification.

General leg chaetotaxy.—.We describe and illustrate by scanning electron microscope (SEM), in the tribal description, major setal and spine characteristics of legs. Leg chaetotaxy is very inadequately known and this review serves primarily as a starting point for future comparisons [but see information in Balfour-Browne (1940) and Wolfe (1985)]. In our overall survey we found five chaetotaxal characteristics (see below) useful for phylogenetic and/or taxonomic purposes.

Femoral setae.— On males of various species of *Laccornis*, elongate, femoral setae are present on the distal margin. These setae are distinct from the standard series of natatory setae (*e.g.*, Fig. 6D). The elongate, femoral setae are present on mesofemora (only) of members of *L. conoideus* and *L. pacificus*, on metafemora (only) of members of *L. difformis*, *L. schusteri*, and *L. etnieri* (Fig. 6P), and on both meso- and metafemora (Fig. 6O) of members of *L. pacificus* and *L. conoideus*. Elongate femoral setae are absent from specimens in the outgroup (*e.g.*, Fig. 6N) and therefore occurrence among some members of *Laccornis* is apotypic. We hypothesize that derivation of these setae on mesofemora occurred independently of development on metafemora. These elongate setae of the mesofemora and metafemora are easy to see at low magnifications and are useful for identification of male specimens.

Mesotibial spines.— Wolfe (1985) discusses the form of the mesotibial row of spines (compare Figs. 30-34 of Wolfe 1985). Among members of *Laccornis* there is a sublateral row of spines on the anterior surface of each mesotibia and proximity (denseness/sparseness) of spines in this sublateral row varies. Variation is somewhat gradual but we have partitioned variation in number of spines into two groups: eight or fewer (Fig. 6J), and nine or more spines (Fig. 6H). The continuous nature of variation in this character diminishes its reliability in phylogenetic reconstruction; however, members of *L. kocai* are clearly at the low end of spine number and that is the condition found in members of *C. hubbelli*. Therefore, while we think this character is evidence for the primitiveness of *L. kocai*, it is not used directly in further phylogenetic resolution of the species, except by character correlation.

Protarsal palettes.— In male specimens of *L. kocai*, there are two enlarged palettes on each of protarsomeres 1-3 (Fig. 5A); there are four palettes on at least each of the first two protarsomeres of males of all other species (Fig. 5B). Two palettes per tarsomere occur in most groups of hydroporines and on specimens of *C. hubbelli*; therefore the higher number of modified palettes is considered apotypic.

Spines of protarsomere 4.— Protarsomere 4 of all hydroporines is very short and it is usually concealed between lobes of protarsomere 3. Two spines are located on protarsomere 4. In members of some species of *Laccornis*, these spines are longer and more slender (Fig. 5A, M, N); in members of other species, the spines are short and cone-shaped (Fig. 50). Spines on the protarsomere 4 of *C. hubbelli* are long and slender and this state is considered plesiotypic.

Sensilla of protarsomere 5.— Protarsomere 5 of most hydroporines is elongate and extends well beyond the lobes of protarsomere 3. In specimens of *L. kocai*, sensilla on the ventral surface of protarsomere 5 are short and spine-like (Figs. 5A, M); in all other members of *Laccornis* seta-like sensilla are present (Figs. 5N, O, Q). The spine-like condition is evident in member of *C. hubbelli* and is considered plesiotypic.

Ridge of protarsomere 5.— Male specimens of *L. deltoides* and *L. nemorosus* have a ridge evident on the anteroapical edge of protarsomere 5 (Fig. 5P). The ridge is absent in members of all other species and the outgroup; therefore, presence of the ridge is considered apotypic.

Lobe of protarsomere 5.— The ventroapical lobe of protarsomere 5 tilts anteriorly so that its overall shape is asymmetical in males of *L. difformis* (Fig. 5Q) and *L. etnieri*. This condition is not as pronounced in any other members of *Laccornis* (Figs. 5N, O) or the outgroup and thus asymmetry is considered apotypic.

Claw structure.— Anterior, protarsal claw characters of males are important in reconstructing the phylogeny as well as for identification of males of *Laccornis*. Modifications within the genus are remarkably divergent. Males of *L. oblongus* have the least modified claw wherein the anterior claw is slightly thickened (Fig. 5D). Males of *L. kocai* have a small basal lobe on the anterior, protarsal claw (Fig. 5C). Males of *L. pacificus* (Fig. 5F) and *L. conoideus* (Fig. 5E) possess a distinct medial tooth on the anterior, protarsal claw. Claw structure in males of *L. deltoides*, *L. nemorosus*, *L. latens*, *L. difformis*, *L. etnieri*, and *L. schusteri* is extremely complicated. The anterior, protarsal claw of male specimens of *L. deltoides* and *L. nemorosus* (Figs. 5G, H) is contorted and slightly expanded while in those of *L. latens* and *L. difformis* it is distinctly contorted and foliate (Figs. 5I, J). Males of *L. schusteri* and *L. etnieri* also have foliate, contorted claws, however, the end of the claw is truncate and the apex is displaced laterally (Figs. 5K, L). An indistinct lateral notch occurs in males of *L. difformis*, whereas a distinct lateral notch is evident in those of *L. etnieri*.

The anterior, protarsal claw of members of the outgroup is scarcely modified. Based on this, we interpret three independent changes in claw structure among lineages within *Laccornis*: 1) development of the basal lobe, 2) development of medial tooth, and 3) tendency towards the progressively more foliate/contorted condition described above. The lateral notch is considered separately and presence of the notch is apotypic.

Elytral punctation.— For terms for surface punctures/sensilla see Balfour-Browne (1940a) and Wolfe and Zimmerman (1984). On *Laccornis* specimens, there are three kinds of punctures: 1) simple, 2) compound concentric with thickened walls, and 3) compound eccentric (see Fig. 1J). Simple punctures are present uniformly on elytral surfaces in all members of *Laccornis* but are extremely difficult to see except with the high magnification of SEM. Compound concentric, thick-walled punctures form the sparsely punctured, elytral striae (Fig. 1F). Compound, eccentric punctures are the most taxonomically important kind of puncture; eccentric punctation varies from almost invisible in members of *L. deltoides* and *L. nemorosus* (Fig. 1F) to relatively coarse and double-sized in members of *L. pacificus* (Fig. 1D)

Metacoxal sculpture.— As with elytral punctation, metacoxal punctation varies from almost effaced (Fig. 2F) to distinctly evident (Figs. 2B-D). However, the metacoxae of some specimens have short, impressed lines or strigae. This characteristic is dichotomous (present or absent), relatively easily visible and it is not sexually dimorphic. Therefore we have used it as a good taxonomic as well as a useful phylogenetic character. These strigae are present only in members of *L. latens*, *L. difformis*, *L. etnieri* and *L. schusteri* (Figs. 2E, G). Other species of *Laccornis* (Figs. 2A-D, F) lack metacoxal strigae as do members of the outgroup. Therefore its presence in the four species of *Laccornis* listed above is considered synapotypic.

Apex of aedeagus.— The apex of the aedeagus of males of most species is bent downward and/or reflexed to varying degrees. In members of *L. kocai* (Fig. 9), the distal portion is sinuate and bent upward at the tip. In male specimens of *L. etnieri* (Fig. 16), the tip of the aedeagus is deflected ventrally only slightly. Males of *L. difformis* (Fig. 17) and *L. schusteri* (Fig. 18) have the tip of the aedeagus more distinctly bent downward. In male specimens of *L. latens* , *L. deltoides*, and *L. nemorosus* (Figs. 13-15), the tip of the aedeagus is reflexed 180° such that the tip is oriented toward the base of the aedeagus. Males of *L. oblongus*, *L. pacificus*, and *L. conoideus* (Fig. 8, 11, 12) also have aedeagal apices that are relexed 180°and in addition the reflexed portion is ligulate. Since the aedeagal apex of the outgroup is not ventrally bent or reflexed, the latter condition is considered plesiotypic. Progressively more bent/reflexed and ligulate apices are considered increasingly apotypic (see Table 3).

Base of aedeagus.— The base of the aedeagus is enlarged and expanded in members of *L. difformis*, *L. schusteri*, and *L. etnieri* (Figs. 16-18). That condition is absent in other members of *Laccornis* and the outgroup and the enlarged base is considered apotypic.

Setae of aedeagus.— In males of *L. oblongus* (Fig. 8), *L. conoideus* (Fig. 12) and *L. pacificus* (Fig. 11) long setae are present along each dorsolateral edge of the aedeagus; this condition is least developed in members of *L. conoideus*. Such setae are not present in any other members of *Laccornis* or the outgroup; presence is apotypic.

Shape of aedeagus.— In males of *L. difformis* (Fig. 17), *L. etnieri* (Fig. 16) and *L. schusteri* (Fig. 18) the aedeagus is expanded medially into a plate-like structure; this condition is unique to these three species and it is considered apotypic.

Lateral projections of aedeagus.— Males of *L. pacificus* and *L. conoideus* (Figs. 11, 12) have subapical anterolateral projections of the aedeagus (more distinctive in males of *L. conoideus*). Projections are absent in all other members of *Laccornis* and the outgroup and are considered to be apotypic.

Shape and orientation of hinge of paramere.— The hinge by which the paramere articulates with the aedeagus is enlarged and oriented horizontally in males of *L. oblongus*, *L. pacificus* and *L. conoideus* (Figs. 8, 11, 12). Associated with this is a change in overall paramere shape such that the apical two thirds of the paramere is abruptly tapered. Among other species of *Laccornis* the hinge of the paramere is longitudinal (Figs. 9, 16) and the paramere is tapered gradually. These modifications (hinge enlargement, vertical orientation and shape change) are absent in other members of *Laccornis* and in the outgroup and therefore are considered apotypic.

Setation of parameres.— In males of *L. oblongus*, *L. conoideus*, and *L. pacificus* (Figs. 8, 11, 12), setae on parameres are arranged in two series: a vertically oriented, basal series and a dorsal, medial series. In all other species of *Laccornis* (Figs. 9, 13-18) and the outgroup there is only a single series on the ventral edge; this latter state is plesiotypic.

Membrane of parameres.— In males of *L. etnieri*, *L. difformis*, and *L. schusteri* a large membranous lobe is evident (Figs. 16-18) on the inner, subapical portion of the paramere. Since the lobe is not present in other taxa (Figs. 8, 9, 11-15), including the outgroup, its presence is judged apotypic.

Coloration.— Coloration is not very useful taxonomically. The dark (piceous) colour of the pronotum in contrast to lighter colour of the head and elytra of specimens of *L. latens* has been cited as diagnostic of that species. However, this condition also is closely approached in specimens of *L. difformis*, *L. etnieri*, and *L. schusteri*.

Specimens of many species (*L. pacificus*, *L. conoideus*, *L. latens* , *L. difformis*, *L. etnieri*, and *L. schusteri*) occasionally have a distinctly lighter, transverse band across the base of the elytra. As striking as that characteristic can be in some specimens it is virtually absent in others. We have not used colour as a phylogenetic character. However, when sorting specimens, it is useful to know that specimens of *L. deltoides* and *L. nemorosus* are more uniformly, lightly coloured than are those of any other species of *Laccornis*.

Total length.— Total length (and greatest width) was measured as described in Roughley and Pengelly (1982). These measurements are given for each taxon in Table 2. Because most of our samples are composed only of few specimens from separate localities and dates, we have not calculated a mean for any of these taxa but instead have concentrated on the range of this statistic. As such it falls into four non-overlapping categories which are useful taxonomically. These categories are 3.30 to 3.50 mm (*L. kocai* only), 4.32 to 4.92 mm (*L. oblongus*, *L. pacificus* and *L. conoideus*), 5.23 to 6.60 mm (most species of *Laccornis*) and 7.00 to 7.23 mm (*L. nemorosus*). By setting limits between the observed measurements we have used these measurements in the key below. These groupings of total length correlate fairly well with the phylogenetic groupings proposed on other characters but we have not used them in the phylogenetic reconstruction.

Body shape.— Among members of *Laccornis*, the outline of the body in dorsal view varies from rather oval to parallel-sided to posteriorly tapered. A rough measure of body shape can be achieved by total length/greatest width (Table 2). Differences among specimens of different species are subtle and therefore this character is of limited taxonomic value. However for some few species, body shape is somewhat distinctive: *L. kocai* is more oval than any of its congeners, *L. oblongus* is more parallel-sided, and *L. deltoides* and *L. nemorosus* are distinctly tapered posteriorly.

Table 1.

Matrix of structural characters used for description of species of *Laccornis*; see text for description of character states. kc- *Laccornis kocai*, ob-*L. oblongus*, pc-*L. pacificus*, cn-*L. conoideus*, lt-*L. latens*, dl-*L. deltoides*, nm-*L. nemorosus*, df-*L. difformis*, et-*L. etnieri*, sc-*L. schusteri;* 1=yes or character state present, 0=no or character state absent, S=sometimes, character state present or not. For consistency and clarity, antennal character states which form part of a morphocline and are recorded on successive antennomeres are characterized uniformly for all species.

		kc	ob	pc	cn	lt	dl	nm	df	et	sc
1)ANTENNA											
1.1)	*Antennomere 7*										
1.1.1)	Enlargement										
1.1.1.1)	normal size (3 A-D)	1	1	0	0	1	1	1	1	1	1
1.1.1.2)	slightly enlarged (3 E, H)	0	0	1	1	0	0	0	0	0	0
1.1.1.3)	distinctly enlarged	0	0	0	0	0	0	0	0	0	0
1.1.1.4)	greatly enlarged	0	0	0	0	0	0	0	0	0	0
1.1.2)	Ventral sculpture										
1.1.2.1)	reticulate (3 F)	1	1	0	0	1	1	1	1	1	1
1.1.2.2)	scarcely rugose	0	0	1	1	0	0	0	0	0	0
1.1.2.2)	rugose (3 H)	0	0	0	0	0	0	0	0	0	0
1.1.3)	Ventral shape										
1.1.3.1)	normal	1	1	0	0	1	1	1	1	1	1
1.1.3.2)	slightly flattened	0	0	0	0	0	0	0	1	1	1
1.1.3.3)	slightly concave	0	0	0	0	0	0	0	0	0	0
1.1.3.4)	distincly concave	0	0	0	0	0	0	0	0	0	0
1.1.3.5)	sinuate/convex (3 H)	0	0	1	1	0	0	0	0	0	0
1.2)	*Antennomere 6*										
1.2.1)	Enlargement										
1.2.1.1)	normal size (3 A-D)	1	1	0	0	1	1	1	1	1	1
1.2.1.2)	slightly enlarged	0	0	0	0	0	0	0	0	0	0
1.2.1.3)	distinctly enlarged (3 E, H)	0	0	1	1	0	0	0	0	0	0
1.2.1.4)	greatly enlarged	0	0	0	0	0	0	0	0	0	0

(continued on next page)

Table 1 (continued)

		kc	ob	pc	cn	lt	dl	nm	df	et	sc
1.2.2)	Ventral sculpture										
1.2.2.1)	reticulate (3 F)	1	1	0	0	1	1	1	1	1	1
1.2.2.2)	scarcely rugose	0	0	0	0	0	0	0	0	0	0
1.2.2.3)	rugose (3 H)	0	0	1	1	0	0	0	0	0	0
1.2.3)	Ventral shape										
1.2.3.1)	normal	1	1	0	0	1	1	1	0	0	0
1.2.3.2)	slightly flattened (3 F)	0	0	0	0	0	0	0	1	1	1
1.2.3.3)	slightly concave	0	0	0	0	0	0	0	0	0	0
1.2.3.4)	distincly concave	0	0	0	0	0	0	0	0	0	0
1.2.3.5)	sinuate/convex 3 E, H)	0	0	1	1	0	0	0	0	0	0
1.3	*Antennomere 5*										
1.3.1)	Enlargement										
1.3.1.1)	normal size (3 A-D)	1	1	0	0	1	1	1	1	1	1
1.3.1.2)	slightly enlarged	0	0	0	0	0	0	0	0	0	0
1.3.1.3)	distinctly enlarged	0	0	0	0	0	0	0	0	0	0
1.3.1.4)	greatly enlarged (3 E, H)	0	0	1	1	0	0	0	0	0	0
1.3.2)	Ventral sculpture										
1.3.2.1)	reticulate (3 F)	1	1	0	0	1	1	1	1	1	1
1.3.2.2)	scarcely rugose	0	0	0	0	0	0	0	0	0	0
1.3.2.3)	rugose (3 H)	0	0	1	1	0	0	0	0	0	0
1.3.3)	Ventral shape										
1.3.3.1)	normal (3 A, D)	1	1	0	0	1	1	1	1	1	1
1.3.3.2)	slightly flattened	0	1	0	0	0	0	0	0	0	0
1.3.3.3)	slightly concave	0	0	0	0	0	0	0	0	0	0
1.3.3.4)	distincly concave	0	0	0	0	0	0	0	0	0	0
1.3.3.5)	sinuate/convex (3 H)	0	0	1	1	0	0	0	0	0	0
1.3.4)	Symmetry (dorsal outline)										
1.3.4.1)	rather symmetrical (3 A-D)		1	0	0	1	1	1	1	1	1
1.3.4.2)	distinctly asymmetrical (3 E, H	0	0	1	1	0	0	0	0	0	0

(continued on next page)

Table 1 (continued)

		kc	ob	pc	cn	lt	dl	nm	df	et	sc
1.4	*Antennomere 4*										
1.4.1)	Enlargement										
1.4.1.1)	normal size	1	0	0	0	0	0	0	0	0	0
1.4.1.2)	slightly enlarged (3 A)	0	1	0	0	1	0	0	0	0	0
1.4.1.3)	distinctly enlarged (3 B, F)	0	0	0	0	0	0	0	1	1	1
1.4.1.4)	greatly enlarged (3 C-E, G, H, 4I)	0	0	1	1	0	1	1	0	0	0
1.4.2)	Ventral sculpture										
1.4.2.1)	reticulate (3 F)	1	0	0	0	1	1	1	1	1	1
1.4.2.2)	scarcely rugose	0	1	0	0	0	0	0	0	0	0
1.4.2.3)	rugose (3 H)	0	0	1	1	0	0	0	0	0	0
1.4.3)	Ventral shape										
1.4.3.1)	normal	1	0	0	0	0	0	0	0	0	0
1.4.3.2)	slightly flattened	0	1	0	0	1	0	0	0	0	0
1.4.3.3)	slightly concave (3 F)	0	0	0	0	0	0	0	1	1	1
1.4.3.4)	distincly concave (3 G)	0	0	0	0	0	1	1	0	0	0
1.4.3.5)	sinuate/convex (3 H)	0	0	1	1	0	0	0	0	0	0
1.4.4)	Symmetry (dorsal outline)										
1.4.4.1)	rather symmetrical (3 A-D)	1	1	0	0	1	1	1	1	1	1
1.4.4.2)	distinctly asymmetrical (3 E, H)	0	0	1	1	0	0	0	0	0	0
1.5	*Antennomere 3*										
1.5.1)	Enlargement										
1.5.1.1)	normal size (3 A)	1	1	0	0	1	0	0	0	0	0
1.5.1.2)	slightly enlarged (3 C, D)	0	0	0	0	0	1	1	1	1	1
1.5.1.3)	distinct enlarged	0	0	0	0	0	0	0	0	0	0
1.5.1.4)	greatly enlarged (3 E, H)	0	0	1	1	0	0	0	0	0	0

(continued on next page)

Table 1 (continued)

		kc	ob	pc	cn	lt	dl	nm	df	et	sc
1.5.2)	Ventral sculpture										
1.5.2.1)	reticulate	1	0	0	0	0	0	0	0	0	0
1.5.2.2)	scarcely rugose	0	1	0	0	0	0	0	0	0	0
1.5.2.3)	rugose (3 H)	0	0	1	1	0	0	0	0	0	0
1.5.3)	Ventral shape										
1.5.3.1)	normal	1	1	0	0	1	0	0	0	0	0
1.5.3.2)	slightly flattened (3 F)	0	0	0	0	0	1	1	1	1	1
1.5.3.3)	slightly concave	0	0	0	0	0	0	0	0	0	0
1.5.3.4)	distinctly concave	0	0	0	0	0	0	0	0	0	0
1.5.3.5)	sinuate/convex (3 H)	0	0	1	1	0	0	0	0	0	0
1.5.4)	Symmetry (dorsal outline)										
1.5.4.1)	rather symmetrical (3 A-D)	1	1	0	0	1	1	1	1	1	1
1.5.4.2)	distinctly asymmetrical (3 E)	0	0	1	1	0	0	0	0	0	0
2) PROSTERNUM											
2.1)	*Prosternal process*										
2.1.1)	Width										
2.1.1.1)	moderately broad (4 F)	0	0	0	0	1	0	0	0	0	0
2.1.1.2)	distinctly broad 4 B-E, G)	1	1	1	1	0	1	1	1	1	1
2.1.2)	Longitudinal convexity										
2.1.2.1)	moderately distinct (4 B, C, F, G)	1	1	1	1	1	0	0	1	1	1
2.1.2.2)	less evident	0	0	0	0	0	1	0	1	1	1
2.1.2.3)	scarcely evident (4 D, E)	0	0	0	0	0	0	1	0	0	0
2.2)	*Prosternal pore*										
2.2.1)	absent (slit present) (4 H)	1	1	1	1	0	0	0	0	0	0
2.2.2)	present (4 I)	0	0	0	0	1	1	1	1	1	1

(continued on next page)

Table 1 (continued)

		kc	ob	pc	cn	lt	dl	nm	df	et	sc
3) **LEGS**											
3.1)	*Sublateral mesotibial spines*										
3.1.1)	6 or fewer (6 J)	1	0	0	0	0	0	0	0	0	0
3.1.2)	7 or more (6 H)	0	1	1	1	1	1	1	1	1	1
3.2)	*Mesofemoral elongate setae*										
3.2.1)	absent	1	1	0	0	1	1	1	1	1	1
3.2.2)	present	0	0	1	1	0	0	0	0	0	0
3.3)	*Metafemoral elongate setae*										
3.3.1)	absent (6 N)	1	1	0	0	1	1	1	0	0	0
3.3.2)	moderately evident (6 O)	0	0	1	1	0	0	0	0	0	0
3.3.3)	distinctly evident (6 P)	0	0	0	0	0	0	0	1	1	1
3.4)	*Protarsal enlarged palettes*										
3.4.1)	maximum of 2/row (5 A)	1	0	0	0	0	0	0	0	0	0
3.4.2)	maximum of 4/row (5 B)	0	1	1	1	1	1	1	1	1	1
3.5)	*Ridge of protarsomere 5*										
3.5.1)	absent (5 M,N)	1	1	1	1	1	0	0	1	1	1
3.5.2)	present (5 P)	0	0	0	0	0	1	1	0	0	0
3.6)	*Shape of protarsomere 5*										
3.6.1)	symmetrical (5 N,O)	1	1	1	1	1	1	1	0	0	1
3.6.2)	asymmetrical (5 Q)	0	0	0	0	0	0	0	1	1	0
3.7)	*Ventral sensilla of protarsomere 4*										
3.7.1)	spine-like (5 M)	1	0	0	0	0	0	0	0	0	0
3.7.2)	hairlike (5 N, O, Q)	0	1	1	1	1	1	1	1	1	1
3.8)	*Ventral spines of protarsomere 5*										
3.8.1)	elongate (5 N)	1	1	1	1	0	1	1	0	0	0
3.8.2)	cone shaped (5 O)	0	0	0	0	1	0	0	1	1	1

(continued on next page)

Table 1 (continued)

		kc	ob	pc	cn	lt	dl	nm	df	et	sc
3.9)	*Anterior protarsal claw*										
3.9.1)	scarcely modified (5 D)	0	1	0	0	0	0	0	0	0	0
3.9.2)	with basal lobe (5 C)	1	0	0	0	0	0	0	0	0	0
3.9.3)	with larger medial tooth (5 F)	0	0	1	0	0	0	0	0	0	0
3.9.4)	with smaller medial tooth (5 E)	0	0	0	1	0	0	0	0	0	0
3.9.5)	slightly contorted (5 G, H)	0	0	0	0	0	1	1	0	0	0
3.9.6)	distinctly contorted (5 I-L)	0	0	0	0	1	0	0	1	1	1
3.9.7)	apex laterally displaced (5 K, L)	0	0	0	0	0	0	0	0	1	1
3.9.8)	apex rather medial (5 I, J)	0	0	0	0	1	0	0	1	0	0
3.9.9)	with slight notch (5 J)	0	0	0	0	0	0	0	1	0	0
3.9.10)	with distinct notch (5 L)	0	0	0	0	0	0	0	0	1	0
4) **ELYTRA**											
4.1)	*Punctation*										
4.1.1)	coarse (1 D)	0	0	1	0	0	0	0	0	0	0
4.1.2)	moderately coarse (1 C)	0	0	0	1	0	0	0	0	0	0
4.1.3)	less coarse (1 A, B, E, G-I)	1	1	0	0	1	0	0	1	1	1
4.1.4)	fine (1 F)	0	0	0	0	0	1	1	0	0	0
4.2)	*Internal ridge*										
4.2.1)	absent	1	0	0	0	0	0	0	0	0	0
4.2.2)	scarcely evident	0	1	1	1	0	0	0	0	0	0
4.2.3)	indistinct	0	0	0	0	0	0	0	1	1	1
4.2.4)	evident	0	0	0	0	1	1	1	0	0	0

(continued on next page)

Table 1 (continued)

		kc	ob	pc	cn	lt	dl	nm	df	et	sc
5) **METACOXA**											
5.1)	*Sculpture*										
5.1.1)	punctation fine (2 A, F)	1	0	0	0	1	1	1	1	1	1
5.1.2)	punctation coarse (2 B-D)	0	1	1	1	0	0	0	0	0	0
5.1.3)	strigae present (2 E, G)	0	0	0	0	1	0	0	1	1	1
6) **AEDEAGUS**											
6.1)	*Shape of base*										
6.1.1)	base enlarged (16-18)	0	0	0	0	0	0	0	1	1	1
6.2)	*Aedeagal setae*										
6.2.1)	not evident	1	0	0	0	1	1	1	1	1	1
6.2.2)	somewhat evident (8)	0	1	0	0	0	0	0	0	0	0
6.2.3)	distinctly evident (11, 12)	0	0	1	1	0	0	0	0	0	0
6.3)	*Anterolateral projections*										
6.3.1)	less distinct (11)	0	0	1	0	0	0	0	0	0	0
6.3.2)	less distinct (12)	0	0	0	1	0	0	0	0	0	0
6.4)	*Ventrally reflexed apex*										
6.4.1)	not ventrally reflexed (9)	1	0	0	0	0	0	0	0	0	0
6.4.2)	slightly vent. bent (17)	0	0	0	0	0	0	0	1	0	0
6.4.3)	distinctly vent. bent (16, 18)	0	0	0	0	0	0	0	0	1	1
6.4.4)	reflexed (8, 11, 12)	0	0	0	0	1	1	1	0	0	0
6.4.5)	reflexed and ligulate	0	1	1	1	0	0	0	0	0	0
6.5)	*Shape (dorsal view)*										
6.5.1)	not expanded apically or medially	1	1	1	1	1	0	0	0	0	0
6.5.1)	apex slightly expanded (14)	0	0	0	0	0	1	0	0	0	0
6.5.2)	apex distinctly expanded (15)	0	0	0	0	0	0	1	0	0	0

(continued on next page)

Table 1 (continued)

		kc	ob	pc	cn	lt	dl	nm	df	et	sc
6.5.3)	aedeagus expanded medially (16-18)	0	0	0	0	0	0	0	1	1	1
7) **PARAMERES**											
7.1)	*Setal series*										
7.1.1)	ventrally only (9, 13-18)	1	0	0	0	1	1	1	1	1	1
7.1.2)	ventrally and dorsally (8, 11, 12)	0	1	1	1	0	0	0	0	0	0
7.2)	*Apex*										
7.2.1)	not expanded	1	1	0	0	1	1	1	1	1	1
7.2.2)	expanded (11,12)	0	0	1	1	0	0	0	0	0	0
7.2.3)	with small ventral tip (11, 12)	0	0	1	1	0	0	0	0	0	0
7.3)	*Hinge orientation*										
7.3.1)	longitudinal (9, 16)	0	0	0	1	1	1	1	1	1	
7.3.2)	horizontal (11, 12)	0	1	1	1	0	0	0	0	0	0
7.4)	*Size of hinge*										
7.4.1)	rather enlarged (8)	0	1	0	0	0	0	0	0	0	0
7.4.2)	distinctly enlarged										
(11,12)	0	0	1	1	0	0	0	0	0	0	
7.5)	*Apical membranous lobe*										
7.5.1)	absent (8, 9, 11-15)	1	1	1	1	1	1	1	0	0	0
7.5.2)	present (16-18)	0	0	0	0	0	0	0	1	1	1
8) **BODY**	**SHAPE\COLOR**										
8.1)	*Shape*										
8.1.1)	rather oval	1	0	S	0	S	0	0	S	S	S
8.1.2)	more parallel sided	0	1	S	S	S	0	0	S	S	S
8.1.3)	tapering posteriorly	0	0	0	S	S	1	1	S	S	S
8.2)	*Color*										
8.2.1)	darker	1	1	1	1	1	0	0	1	1	1
8.2.2)	lighter	0	0	0	0	0	1	1	1	1	1
8.2.3)	with tranverse band	S	0	S	S	S	S	S	S	S	S

Table 2.
Range of measurements (mm) for total length (TL), greatest width (GW) and ratio of total length to greatest width (TL/GW) for specimens of each species of *Laccornis*.

	Total length Min/Max	Greatest width Min/Max	TL/GW
L. kocai	3.30–3.35	1.69–1.84	1.82–1.95
L. oblongus	4.30–4.69	2.00–2.15	2.15–2.18
L. pacificus	4.69–4.92	2.23–2.38	2.07–2.10
L. conoideus	4.23–4.58	2.15–2.46	1.86–1.97
L. latens	5.23–5.62	2.46–2.62	2.13–2.14
L. deltoides	6.26–6.60	3.23–3.46	1.91–1.94
L. nemorosus	7.00–7.23	3.54–3.69	1.96–1.98
L. difformis	5.60–6.15	2.69–3.08	2.00–2.08
L. etnieri	5.23–6.00	2.62–2.92	2.00–2.01
L. schusteri	5.35–6.10	2.63–3.00	2.00–2.03

CLASSIFICATION

Laccornini, New Tribe

Type genus.— *Laccornis* Gozis, 1914.

Diagnosis.— Members of Laccornini are diagnosed among Hydroporinae by common presence of the following character states of adults: mandibles without a ventral, medial row of setae (Fig. 7A), base of metafemur extending distally and contacting metacoxal lobes (Fig. 6Q), and the metathoracic episternum contacting the mesocoxal cavity.

Most previous workers assigned members of *Laccornis* to the tribe Hydroporini of the subfamily Hydroporinae [except Arnett (1960) who placed *Laccornis* in Agabini of Colymbetinae]. However, Hydroporini with *Laccornis* is polyphyletic (Wolfe 1985, 1989). Creation of Laccornini therefore assists in creating a more natural classification of Hydroporinae.

Description.— The rationale for division of characters amoung tribal, generic and species level is given above under Materials and Methods.

Head. Clypeus not thickened. Labrum (Fig. 7C) with transverse, dense row of setae along medial 1/3 of anterior edge. A dense, somewhat elliptical patch of thick setae located on ventral, anteromedial portion of labrum, these setae not more spine-like in anterior portion of elliptical patch. A transverse row of 4-7 spines located ventrally on each side in anterolateral region of labrum, spines approximately 4 times longer than wide and separated by 1 to 3 times their width. Ephipharynx (Fig. 7C) with a distinct but small, lobe-like structure on each side of middle in anterior region; lobes with sparse, peg-like sensilla. Surrounding each lobe are dense microtrichia that extend posteriorly on each side of middle; intermixed with microtrichia and only just posterior to the lobes are sparsely placed, short sensilla each with an expanded base. Three, long, seta-like sensilla located on each side of epipharynx in anterolateral region and a group of placiform-like sensilla (Fig. 7D) located on each side in posterolateral, epipharyngial region. Labium (Fig. 7J) with long setae located anteromedially on ventral surface, distinctly denser laterally so that two patches of dense setae are evident. Dorsally, mentum (Fig. 7I) with an anterior, transverse row of spines, more laterally placed spines distinctly longer than medial ones, lateral spines in some specimens appearing as a double row; anterior to the transverse row is a group of about 5, short, peg-like spines; mentum with dorsal surface distinctly elevated posteriorly, elevated area with a sparse group of very short sensilla. Labial palp (Figs. 7I-L) 4-segmented; palpomere 2 not cleft anteriorly; palpomere 3 anteroapically produced, apex with a group of about 5 to 6 sensilla, 1 or 2 long and hair-like, at least one short spine, the others peg-like; palpomere 4 not apically emarginate and with only one dense patch of sensilla (Figs. 7K, L); palpomeres 3 and 4 otherwise with short, stout irregularly placed spines. Maxilla (Figs. 7E-H) concealed in repose. Maxillary cardo (Fig. 7F) with two long setae apicolaterally and a group of irregularly placed, very short spines just posterior to long setae. Stipes (Fig. 7F) with a posteromedial group of 3 to 4, closely placed setae and one long seta in anteromedial region. Lacinia basolaterally somewhat furrowed, galea 2-segmented (Figs. 7E, G) and articulated within furrow; maxillary palp placed just behind galea. Galeomere 2 with short coniform, irregularly placed sensilla along entire length, apex with a cluster of about 5-7 sensilla, two of these larger and broader than others. Lacinia curved, tapering to blunt point, scythe-like in shape; basomedial, oval sclerite evident (Figs. 7E, G); dorsomedial row of at least 4 spines, posterior ones longer and thinner than anterior ones; posterior to dorsal medial row is an elongate patch of very short, stout spines. Medial lacinial edge with a row of about 15 long, curved, stout spines (Figs. 7G, H); these medial spines separated into an apical (4 spines) and basal (16 spines) group by a medial gap; on basal sclerite there are 8 spines on dorsal medial edge and 4 spines on alternate side; sub-apex of lacinia with one, medially placed, more slender, seta-like spine; apex of lacinia (Fig. 7H) with elongate digitiform sensilla; one short spine on ventromedial surface. Maxillary palp (Fig. 7E) 4-segmented, maxillomere 1 not distinctly cleft medially, maxillomere 4 with 2 dense patches of sensilla at apex; apicolaterally with oval series of digitiform sensilla. Mandibles (Fig. 7A) without dorsolateral groove; apex truncate, with 2-3 retinacular teeth, retinacular teeth of left mandible smaller than those of right mandible. No ventromedial, mandibular setae evident; apical patch of setae present or not.

Prothorax. Prosternum and prosternal process in different plane.

Pterothorax. Metasternal process interlocked onto mesosternum. Metafurca (Figs. 7N, O) expanded into a triangularly shaped, broad, flat plate on each side; anteromedial portion with two pairs of distinct concave depressions for muscle insertion; another pair of less distinct depressions in anterolateral region, one on each side; anterodorsal edge of basal portion of metafurca cleft (in dorsal view) but cleft portion not projecting anteriorly between anterolateral extensions of metafurca. Flight wing (Fig. 7M) with M4 vein not connected to oblongum cell; subcubital binding patch very distinct. Elytral apex evenly rounded, not acute. Proventriculus (Fig. 7B) of typical hydroporine type; each oval crushing lobe with transverse medial tooth, each valve-like inner lobe with anterior ciliate flap.

Legs. Natatory setae observed on each (Figs. 6A-P) of: dorsal edge of profemur (Fig. 6B) and mesofemur (Fig. 6D); dorsal and ventral edge of protibia (Figs. 6E-G), mesotibia (Figs. 6H-J), and metatibia (Fig. 6L); natotory setae sparse on ventral edge of protibia; dorsal surface of protarsus and mesotarsus and dorsal and ventral surface of metatarsus. Some species additionally with elongate setae on meso- and metafemora (Figs. 6O, P) of males, otherwise no sexual differences in placement of elongate setae. Profemur with a shallow ventroapical sinuation which has a row of closely placed, short spines (Fig. 6A); anterior, dorsal edge with a longitudinal row of spines and another row just below this; irregularly placed spines on lower 1/2 of anterior profemoral surface, longer and more dense posteriorly and ventrally. Ventral edge with fewer (but longer) spines than dorsal edge. Posterior, profemoral surface (Fig. 6B) with fewer spines than anterior surface; an irregular, longitudinal row of short spines about 1/4 of length from dorsal edge; a more or less transversely arranged group of small spines at medial and distal end. Protibia (Figs. 6E-G) with a row of spines along dorsal edge on each side of elongate setae but extending only 3/4 of length; ventral edge with a dense row of very closely placed spines extending almost to apex, just beside this is another, more irregularly arranged, more sparse row; anterior face with scattered, short spines becoming stouter and more numerous apically; ventral surface with fewer spines than anterior surface, arranged primarily longitudinally in ventral 1/3; apical edge of protibia with a row of very stout spines, 4 to 6 of these prolonged at dorsoapical and ventroapical edge. Chaetotaxal characteristics of midlegs (Figs. 6C, D, H, I, J) generally as for anterior legs but spines larger and stouter; anterior apical sinuation absent; an extra, sublateral row of 7 to 15 widely spaced spines evident. Metafemur (Figs. 6N-P) with sparse, randomly arranged, short setae, some specimens with a discernable, short row of setae evident in apical 1/3. Metatibia (Figs. 6K, L) with sparse row of distinct, short and stout spines. Ventral surface with two rows of short spines, one in anterior 1/3 and the other in posterior 1/3; dorsal surface with short spines more randomly placed than on ventral side; apex of metatibia ringed with a row of short, proximately placed spines, spines at anteroapical and posteroapical edge longer, ventroapical spines longest. Each metatarsomere (Fig. 6M) with 2 distinct longitudinal rows of short spines along anterior and posterior margins of ventral edge, one row on each side of ventral, elongate setae; posteroventral row progressively more abbreviated on tarsomeres 2-5; posterodorsal, apical edge of tarsomeres 1-4 with transverse row of closely placed spines; metatibial claws equal in length.

Genus *Laccornis* Gozis

Laccornis Gozis 1914a:111 [Erected as subgenus of *Hydroporus* Clairville.Type species, *Hydroporus oblongus* Stephens 1835:437, fixed by subsequent monotypy of Gozis 1914b:146]; Zimmermann 1930:94; Guignot 1932:283, 419; Zimmermann 1933:190, Balfour-Browne 1934:225; Houlbert 1934:43, 71; Zaitzev 1953:125, 177; Leech and Chandler 1956:309; Leech and Sanderson 1959:992; Arnett 1960:195, 198; Wewalka 1969:49; Schaeflein 1971:20, 46; Malcolm 1971:16, 22; Larson 1975:257, 325; Brigham 1982:10.53, 10.57; White *et al.* 1984:385.

Agaporus Zimmermann 1919:147, 160, 194. [Type species, *Hydroporus oblongus* Stephens 1835:437, fixed by subsequent designation in Zoological Record for 1923, volume 60 (11):132, published in 1925]; Zimmermann 1920:134; Fall 1923:6, 121.

Taxonomic history.— Sharp (1882) in his key to species-groups of *Hydroporus*, diagnosed members of his species-group 9 on the form of the metacoxal processes. To this species-group he assigned one Palearctic species, *H. oblongus* Stephens, one Nearctic species, *H. difformis* LeConte, two Neotropical species, *H. lugubris* Aubé and *H. copelatoides* Sharp, and an African species, *H. advena* Sharp.

Gozis (1914a, b) described *Laccornis* as a subgenus of *Hydroporus* and assigned to it only *H. oblongus*. Apparently unaware of this Zimmermann (1919: 147, 160, 194) provided the name *Agaporus* for most of Sharp's group 9 except that he transferred *H. advena* to his new genus *Canthyporus* Zimmermann. As with most of Zimmermann's new genera he did not designate a type species for *Agaporus*.

Fall (1923) discussed the characteristics of *Agaporus* in his revision of Nearctic species and described one new species, *A. deltoides*. Later Fall (1937) described another North American species, *A. latens*. Zimmermann (1930) first noted synonymy of *Agaporus* and *Laccornis* and elevated *Laccornis* to generic level. Generic status was maintained by Guignot (1932) and Balfour-Browne (1934, 1938 and 1940a, b). The latter reviewed many of the structural features which distinguish the majority of the members of *Laccornis*, although he limited his discussion to *L. oblongus*.

In 1935, Gschwendtner described a species from Austria which he named *Hydroporus breviusculus*. This species was later transferred to *Laccornis* by Gschwendtner (1939) and subsequently found (Wewalka 1969) to be a junior, subjective synonym of *L. kocai* (Ganglbauer) which had been assigned variously to *Hydroporus* Clairville or *Graptodytes* Seidlitz.

As listed above, the first designation of the type species that we can find for *Agaporus* is in the Zoological Record 6 (11):132 (1925) for 1923. This appears to be an inadvertent error. However, according to Article 69 (iv) of ICZN (1985), this type designation is valid and therefore *Agaporus* is a junior, objective synonym of *Laccornis* Gozis. Subsequently, Balfour-Browne (1940b:205) writes of *Agaporus* "...type, sole species cited = *oblongus* Steph." As noted above, Zimmermann (1919:160) clearly included more taxa within his concept of *Agaporus* and Zimmermann did not indicate a type species although he does formally describe only *A. oblongus* (Zimmermann 1919:192). Also in 1940, Leech described another North American species, *L. pacificus*.

Guignot (1955) described an African species which he assigned to *Laccornis*, *L. sigillatus*, however, this species was transferred to *Canthyporus* by Wewalka (1981). Wolfe and Spangler (1985) described two additional species, *L. etnieri* and *L. schusteri*, from the eastern United States. Wolfe (1985, 1989) presented a phylogenetic analysis of plesiotypic members of Hydroporinae and provides much of the rationale for recognizing *Laccornis* as belonging to a distinct tribe. Roughley and Wolfe (1987) have erected a new genus, *Laccornellus*, to receive the two Neotropical species previously placed in *Laccornis*.

Diagnosis.— Members of *Laccornis* are characterized by the short rather broad prosternal process (Figs. 4B-G), presence of enlarged setae on ventral surface of protarsomere 3 (Fig. 5B) and the presence of valvifer in adult females (Fig. 10).

Description .—

Size and shape. Total length of body from 3.30 to 7.3 mm. Greatest width from 1.69 to 3.69 mm. Shape of outline of body short and broad, to parallel, to elongate (Total length/greatest width = 1.87 - 2.18). Head, pronotum and elytron in continuous outline; posterolateral corner of pronotum not distinctly angulate.

Head. Without cervical carina behind eye.

Microsculpture. Microreticulation of most specimens hexagonal-pentagonal (Figs. 1A-J). Three types of punctures: compound, eccentric punctures; compound, concentric punctures with thickened walls; and simple punctures, in which about nine, reticulate lines radiate out from each puncture so that arrangement of sculpticels around it has a rosette-like appearance (Fig. 1J).

Prothorax. Lateral, pronotal bead distinct, maximum width about 1/2 width of terminal antennomere. Prosternal process broad, length to width ratio at least 2.5; laterally margined; declivity not distinctly protuberant; apex broadly rounded (Figs. 4B-G). Prosternal process reaching metasternal process and interlocking with apical, metasternal notch. Pronotum without plicae.

Pterothorax. Elytron with lateral edge almost straight in lateral view, not ascending anteriorly, without humeral carina; ventral, elytral ridge evident but not distinctly elevated or ligulate posteriorly. Metacoxal process medially incised (in ventral view, Fig. 6Q) but not recessed (in posterolateral view).

Coloration. Primarily brownish to blackish dorsally and ventrally, some specimens with a lighter transverse band across elytral base.

Protarsus. Protarsus with 2 to 4 modified palettes on each of tarsomeres 1-3 (Figs. 5A-B). Protarsomere 4 with 2 short spines.

Female genitalia. Valvifer present (Fig. 10). Genital valve with short apodeme; lateral edge, apicomedial edge and apex with dense setae of variable length. Vulval sclerite with a row of setae along posterior edge.

Sexual dimorphism.— Males of most taxa have modified antennae and protarsi. Additionally, males of some species have elongate setae on the meso- and/or metafemora.

Geographic distribution and habitat.— The genus as now constituted is restricted to the Holarctic region. Except for the enigmatic *L. kocai* (see below), most specimens of *Laccornis* are collected in woodland pools. Many of these pools are temporary in nature and exist only in spring and into early summer.

Key to Adults of Species of *Laccornis*

A key to most of the North American species of *Laccornis* is given in Wolfe and Spangler (1985). That key extensively uses sexual characteristics of male specimens. However specimens of many species of *Laccornis* exhibit a large degree of sexual dimorphism and this makes a key which is effective for both sexes, simultaneously, difficult to construct. Therefore in the following key the sexes are separated beyond couplet 3. Confident determination of specimens is best accomplished with male specimens. Identification of female specimens in much less confidently accomplished in the key below because of use of fewer and less reliable characters such as colour, size and distribution. Therefore female specimens are best identified by association with males; the key may be helpful in corroborating the identification of some female specimens.

1 Palearctic specimens 2

1' Nearctic specimens 3

2 (1) Shorter specimens, TL=3.30-3.50 mm; body shape oval, TL/GW=1.82- 1.95; distribution more southern (Fig. 20C).... .... *L. kocai* (Ganglbauer), p. 308

2' Longer specimens, TL=4.30-4.69 mm; body shape more elongate, TL/GW= 2.15-2.18; distribution more northern (Fig. 20C) .... *L. oblongus* (Stephens), p. 309

3 (1') Protarsomeres 1 to 3 ventrally each with four, enlarged palettes (Fig. 5B); antennomere 4, at least, of most species enlarged and/or of different shape from subapical antennomeres (Figs. 3A- H); anterior protarsal claw modified and of different shape from posterior claw. Male specimens....... 4

3' Protarsomeres 1 to 3 ventrally with all setae of about same size; antennomere 4 not modified, similar in shape to subapical antennomeres; anterior protarsal claw not modified, similar in shape to posterior claw. Female specimens 12

4 (3) Metacoxa with punctation coarse (Figs. 2B-D), appearing subrugose; shorter specimens, TL less than 5.1 mm (TL=4.23-5.00 mm) 5

4' Metacoxal punctation fine (Figs. 2A, E-G); longer specimens, TL. more than 5.1 mm (TL=5.23-7.23 mm)............ 7

5 (4) Anterior protarsal claw without medial tooth (Fig. 5D); meso- and metafemur (Fig. 6N) without elongate setae on posterior margin........................... *L. oblongus* (Stephens), p. 309

5' Anterior, protarsal claw with medial tooth (Figs. 5E-F); meso- and metafemur (Fig. 6O) with elongate setae on posterior margin 6

6 (5') Shorter specimens, TL less than 4.60 mm (TL=4.23-4.58 mm); anterior, protarsal claw with medial tooth shorter (Fig. 5E); distribution transcontinental but predominantly east of Rocky Mtns. (Fig. 20C) .....*L. conoideus* (LeConte), p. 312

6' Longer specimens, TL more than 4.6 mm (TL=4.69-4.92 mm); anterior, protarsal claw with medial tooth longer (Fig. 5F); distribution western, predominantly west of Rocky Mtns. (Fig. 20C) ....*L. pacificus* Leech, p. 313

7 (4') Metacoxa without evident strigations (Fig. 2F); longer specimens, TL more than 6.2 mm (TL=6.28-7.23 mm); protarsomere 5 with apex with anterolateral ridge (Fig. 5P); elytral punctation fine (Figs. 1A, F) 8

7' Metacoxa with evident strigations (Figs. 2E-G); shorter specimens, TL less than 6.2 mm (TL=5.23-6.15 mm); protarsomere 5 with apex symmetrical (Fig. 5P); elytral punctation coarse (Fig. 1B, G-I) 9

8 (7) Longer specimens, TL more than 6.8 mm (TL=7.0-7.23 mm); aedeagus more expanded apically (Fig. 15C); distribution more southern (Fig. 20B)..........*L. nemorosus*, ***n.sp.***, p. 317

8' Shorter specimens, TL less than 6.8 mm (TL=6.26-6.60 mm); aedeagus less expanded apically (Fig. 14C); distribution more northern (Fig. 20B)...................*L. deltoides* (Fall), p. 316

9 (7') Metafemur without elongate setae (Fig. 6N) on posterior margin; antennomere 4 scarcely enlarged (Fig. 3A); aedeagus parallel-sided medially, apex reflexed (Fig. 13 A-C) ....*L. latens* (Fall), p. 315

9' Metafemur with elongate setae (Fig. 6P) on posterior margin; antennomere 4 evidently enlarged (Fig. 3B); aedeagus broadly expanded medially, apex bent but not reflexed (Figs. 16A-C - 18A-C 10

10 (9') Anterior protarsal claw with apex placed medially (Fig. 5J).. ....*L. difformis* (LeConte), p. 319

10' Anterior protarsal claw with apex placed laterally (Figs. 5K, L)..11

11 (10') Anterior protarsal claw with long, anterolateral process, notch absent (Fig. 5K).. ....*L. schusteri* Wolfe & Spangler, p. 320

11' Anterior protarsal claw with short, anterolateral process, notch present (Fig. 5L).. ....*L. etnieri* Wolfe & Spangler, p. 316

12 (3') Metacoxa with evident strigations (Figs. 2E-G)....................17

12' Metacoxa without evident strigations (Fig. 2F)....................13

13 (12') Metacoxa with punctation coarse (Figs. 2B-D), appearing subrugose; TL less than 5.0 mm (TL=4.23-4.92 mm); body in dorsal aspect relatively rounded posteriorly..........................14

13' Metacoxa with punctation fine (Figs. 2A, F); TL more than than 6.0 mm (TL=6.26-7.23 mm); body in dorsal aspect relatively attenuate posteriorly.......................................16

14 (13) TL/GW >2.13 (TL/GW=2.15-2.18); most specimens with elytra not distinctly paler basally; known from northwestern North America (Fig. 20C) ....*L. oblongus* (Stephens)

14' TL/GW<2.13 (TL/GW=1.86-2.10); most specimens with elytra distinctly paler basally; distribution transcontinental including northwestern North America (Fig. 20C) 15

15 (14') TL less than 4.63 mm (TL=4.23-4.58); distribution transcontinental with most records from east of Continental Divide (Fig.20C)..............*L. conoideus* (LeConte), p. 312

15' TL more than 4.63 mm (TL=4.69-4.92 mm); distribution western with most records from west of Continental Divide (Fig. 20C) ....*L. pacificus* Leech, p. 313

16 (13') Longer specimens, TL more than 6.8 mm (TL=7.0-7.23 mm); distribution more southern (Fig. 20B)............................ ....*L. nemorosus*, n.sp., 317

16' Shorter specimens, TL less than 6.8 mm (TL=6.26-6.60 mm); distribution more northern (Fig. 20B)............................ ....*L. deltoides* (Fall), p. 316

17 (12) Prosternal process narrower (Fig. 4F)............................ ....*L. latens* (Fall), p. 315

17' Prosternal process broader (Fig. 4G).................................18

18 (17') Distributed primarily on the Atlantic coastal plain (Fig. 20A) ....*L. difformis* (LeConte), p. 319

18' Distributed primarily to the west of the Atlantic coastal plain (Fig. 20A) 19

19 (18') *Distribution* more eastern and/or more northern (Fig. 20A) ... .*L. etnieri* Wolfe & Spangler, p. 320

19' *Distribution* more western and/or more southern (Fig. 20A) ... .*L. schusteri* Wolfe & Spangler, p. 320

Laccornis kocai (Ganglbauer)

(Figs. 1A, 4B, 5A, 5C, 6J, 9A-D, 10, Map, Fig. 20D)

Hydroporus kocae Ganglbauer 1906:352 [Type locality-- Vinkovci, eastern Croatia, Yugoslavia. Type repository-- NMW], Zimmermann 1920:88.

Graptodytes kocae; Zimmermann 1932:70; Csiki 1946:623.

Laccornis breviusculus Gschwendtner 1935:2 [Type locality-- Zurndorf, Burgenland, Austria. Information about type specimens in Wewalka (1969). Types not re-examined. Type repository-- Oberösterreichischen Landesmuseum in Linz, Austria], Gschwendtner 1939:17; Csiki 1946:627; Zaitzev 1953:178.

Laccornis kocae Wewalka 1969:46. *Laccornis kocai*; Schaeflein 1970:89 [Justified emendation], 1971:47.

Type information and taxonomic notes.— The type was examined by GWW and it is a female. It is deposited in NMW and bears the following label information: Vinkovci, Slav 74900 G. kocai/Hydroporus kocae Gangl. Typ/TYPUS/Coll Mus. Vin. dob./Laccornis kocae Gangl. det Wewalka 68. Although we did not re-examine the type of *L. breviusculus*, we accept Wewalka's (1969) conclusion that *L. breviusculus* is a junior, subjective synonym of *L. kocai*.

Diagnostic combination.— The short body length (TL=3.30-3.50mm) and southern European range (Fig. 20D) should easily separate specimens of both sexes from all other species of *Laccornis*. In addition, male specimens have the aedeagus bisinuate in lateral view and the tip deflexed in the opposite direction (Fig. 9) to that of all other extant *Laccornis*.

Description.— Taxonomically important characters are given in Table 1; measurements in Table 2. Prosternal process illustrated in Fig. 4B; elytral punctation, Fig. 1A; metacoxal punctation, Fig. 2A; male protarsus, Fig. 5A; male protarsal claws, Fig. 5C; male genitalia, Fig. 9; female genitalia, Fig. 10.

Sexual dimorphism.— Males have unmodified antennomeres. The male protarsus is scarcely broader than that of the female and there are only two, enlarged palettes on each of protarsomeres 1 to 3 of males (Fig. 5A). The male, anterior, protarsal claw is slightly shorter than the posterior and has a distinctive, basal lobe (Fig. 5C). Wewalka (1969) mentioned also that abdominal sterna 2 and 3 are more distinctly strigate in males than in females.

Natural history.— There is little biological information published on this species. Adults were collected in a cold, spring-fed pond at Moosbrunn, 40 km south of Vienna (Wewalka 1969), and one specimen was collected in the margin of rushes of the Neusiedler See, Austria (Schaeflein 1979). Up to 1970 only 22 specimens were known from six localities in Austria, Hungary and Yugoslavia (Geiser 1978). Subsequently however more than 100 specimens were taken in a flooded meadow at St. Margarethen, Burgenland, Austria (Geiser 1978, Schaeflein 1983). This meadow is frequently dry by late summer but specimens were collected from the larger ditches in association with other tyrphophilic or tyrphobiontic species (Geiser 1978).

Distribution.— (Fig. 20D). This species is known from only one or a few localities in each of Austria, Hungary and Yugoslavia. The map of its known distribution was compiled from locality information provided by Wewalka (1969) and Schaeflein (1979, 1983). The known range is completely allopatric to all other species of *Laccornis*.

Phylogenetic relationships.— *Laccornis kocai* represents the sister lineage to all other members of *Laccornis* (Fig. 19).

Laccornis oblongus (Stephens)
(Figs. 1B, 2B, 4C, 4H, 5D, 8A-E; Maps, Figs, 20C-D)

Hydroporus oblongus Stephens1835:437 [Type locality-- Cambridge, England. Type not examined. Type repositoty-- BMNH. **Note**--a complete catalogue of *H. oblongus*, *H. nitidus* and *H. bohemani* is given in Zimmermann (1920:134) and is not repeated here].

Hydroporus nitidus Sturm 1835:38, plate 207 [Type locality-- Lappland. Type not examined. Type repository-- ZSM].

Hydroporus bohemani Thomson 1856:198 [Type locality-- Lappland. Type not examined. Type repository-- ZM].

Laccornis oblongus; Gozis 1914b:146, Guignot 1932: 420, Zimmermann 1933:190, Balfour-Browne 1934:225, Houlbert 1934:71, Balfour-Browne 1938:36, 1940a:361, Leech 1940:127, Csiki 1946:626, Guignot 1947:125, Balfour-Browne 1953:19, Zaitzev 1953:177, Schaeflein 1971:46, Wolfe and Spangler 1985:71.

Agaporus oblongus Zimmermann 1919:192, 1920:134; Fall 1923:121.

Type information and taxonomic notes.— We have not examined the type of this well-known species and have followed European taxonomists in recognizing *H. nitidus* and *H. bohemani* as junior, subjective synonyms of *L. oblongus*. Confusion between this species and *L. conoideus* is discussed more fully in the treatment of latter.

Diagnostic combination.— Palearctic specimens are easily determined because they are longer (TL=4.30-4.69 mm), the body shape is more elongate

(TL/GW=2.15-2.18 and the distribution is more northern and/or more eastern (Figs. 20C-D) compared to that of the only other Palearctic species, *L. kocai*. In the Nearctic region, the size of specimens and phylogenetic characters group *L. oblongus* with *L. conoideus* and *L. pacificus*. Males of the latter two species, however, have the anterior, protarsal claw toothed medially and antennomere 4 is distinctly widened. Females of *L. oblongus*, *L. pacificus*, and *L. conoideus* are difficult to separate; however, most female specimens of *L. oblongus* are not as long as those of *L. pacificus* and have a distinctly narrower more parallel sided shape than those of *L. conoideus*.

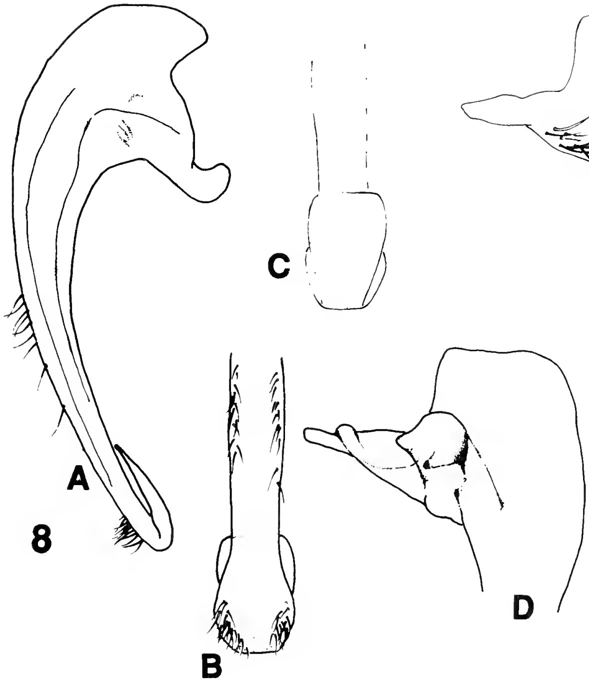
Description.— Taxonomically important characters are given in Table 1; measurements in Table 2. Prosternal process illustrated in Fig. 4C; elytral punctation, Fig. 1B; metacoxal punctation, Fig. 2B; male protarsal claws, Fig. 5D; male genitalia, Fig. 8.

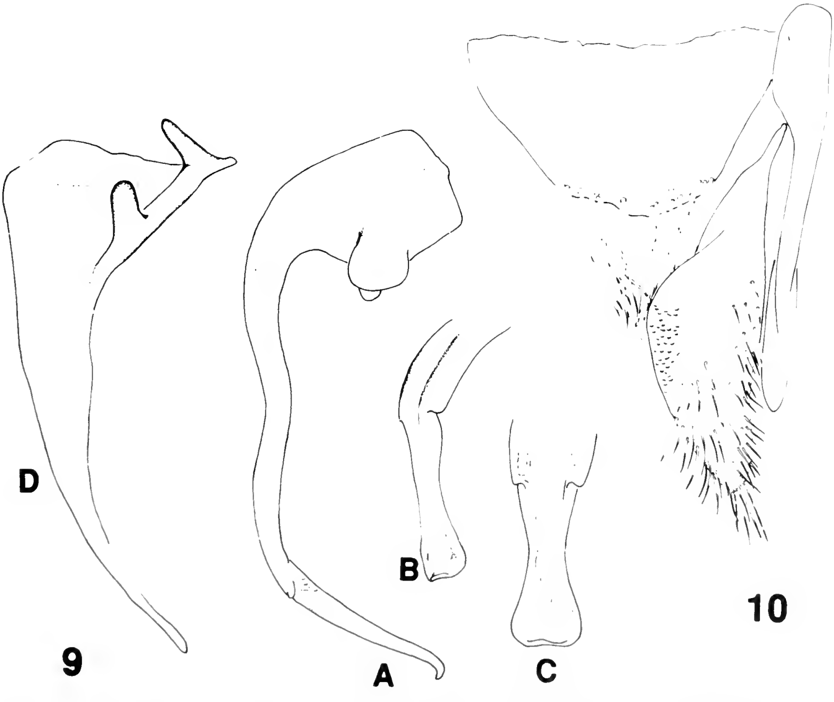
Sexual dimorphism.— Male specimens of *L. oblongus* have antennomere 4 only slightly widened/modified and antennomere 4 has the reticulation of the ventral surface little modified. The anterior, protarsal claw of males is scarcely thicker than the posterior claw (Fig. 5D) and the claws are almost equal in length. Except for *L. kocai*, *L. oblongus* is the least sexually dimorphic species of *Laccornis*.

Natural history.— In the British Isles this species is known to overwinter, as an adult, in ponds under ice and its "...normal habitat is mossy, peaty or rushy pools and swamps of clear water, but it also occurred...less frequently in muddy and swampy dykes in which the water was thick with ordinary fresh-water vegetation..." (Balfour-Browne 1940a:364). From his experience in northern France, Guignot (1947) adds an affinity for pools with decomposing leaves. In a survey of water beetle habitats in south-central Finland, Koskinen (1960) collected adult *L. oblongus* only from field pools formed by snow melt or rain. It is described as tyrophophilous species and it occurrs among coarse organic debris of aquatic vascular plants (Schaeflein 1971, Cuppen and Dettner 1987). The specimens from Siberia, which we examined were collected from small ponds on the taiga, overgrown with *Hypnum* (Poppius 1905). The life history and larval instars are described by Cuppen and Dettner (1987).

Distribution.— (Figs. 20C-D). This is the only Holarctic species of *Laccornis*. It occurs across northern Europe, Siberia and into northwestern North America. In Fig. 20C, which illustrates only the European distribution, filled circles indicate localities from which we examined specimens and the approximate limits of the range (solid line) are generalized from Borchert (1938), Lindroth *et al* (1960), Balfour-Browne (1960) and Nilsson (1983). Extralimital to this map we saw specimens from Shigansk, (=Zigansk, 66°45'N 123°20'E) and Ust Aldan, in Siberia, USSR. The single North American specimen is from Tununuk, NWT (Wolfe and Spangler 1985) and this locality is indicated in Fig. 20D. However, this species is probably more widespread in the Nearctic portion of Beringea, as Hamilton (1894a) records *L. oblongus* from Unalaska, Alaska although Hamilton may have been examining specimens of *L. conoideus* which he considered to be a synonym of *L. oblongus*.

Phylogenetic relationships.— *Laccornis oblongus* is the sister species to *L. conoideus* + *L. pacificus* (Fig.19). This relationship is established by synapotypic character states of male antennomeres and genitalia.





Figures 8A-E, 9A-D, 10. Fig. 8. *Laccornis oblongus*, male genitalia. A-C. Aedeagus (150x). A) Lateral view, B) Dorsoapical view, C) Ventroapical view. D-E. Paramere (150x). D) Posteromedial view, showing enlarged, modified hinge, E) Lateral view. Fig. 9. *L. kocai*, male and female genitalia. A-C. aedeagus (200X). A) lateral view, B) apicodorsal, lateral view, C) dorsoapical view, D) paramere, medial view. Fig. 10. *L. kocai* (200x). Female genitalia, vulval sclerite, ovipositor, and valvifer.

Laccornis conoideus (LeConte)
(Figs. 1C, 2C, 3E, 3H, 5E, 12A-F; Map, Fig. 20C)

Hydroporus conoideus; LeConte 1850:216 [Type locality-- Eagle Harbor, Lake Superior. Type repository-- MCZ], LeConte 1855:292, Crotch 1873:396. *Hydroporus oblongus*; Sharp 1882:485, *ex parte* Hamilton 1894a:13, 1894b:357, *ex parte* Wickham 1895:76, *ex parte*, Hamilton 1889:100, *ex parte* (*nec* Stephens 1835).

Agaporus conoideus; Zimmermann 1919:192, 1920:134, Fall 1923:122. *Laccornis conoideus*, Leech 1940:126, Hatch 1953:215, Wewalka 1969:49, Wallis and Larson 1973:106, Larson 1975:326, Wolfe and Spangler 1985:70.

Type information and taxonomic notes.— The holotype is a male with the following label information: [light greenish, circular tag]/3405/type 6037 [red label, black type]/*H. conoideus* Lec. [hand written]. The type locality, although not recorded on labels, is known to be Eagle Harbor, Michigan (see LeConte 1850).

Sharp (1882) was the first author to consider *L. conoideus* as a junior synonym of *L. oblongus*. Most European authors, thereafter, have recorded *L. oblongus* as occurring in North America. Fall (1923) re-established the current usage of these two names.

Diagnostic combination.— Except for those of *L. pacificus*, males of *L. conoideus* are recognized easily by the unique modifications of antennomeres 3-7 (Figs. 3E, H), medially toothed, anterior, protarsal claw (Fig. 5E), and elongate setae on meso- and metafemora. Males of *L. conoideus* are separated from those of *L. pacificus* by the less distinctly toothed, anterior, protarsal claw. Males and females both can be separated from those of *L. pacificus* by presence of slightly denser and finer elytral punctation (compare Figs. 1C, D), shorter total length of the body (Table 2), and the more northern and eastern distribution (Fig. 20C).

Description.— Taxonomically important character states are presented in Table 1; measurements in Table 2. Prosternal process as illustrated for *L. oblongus* in Fig. 2C; elytral punctation, Fig. 1C; metacoxal punctation as in Fig. 4C; male antenna, Figs. 3E, H; male protarsal claws, Fig. 5E; male metafemur with elongate setae as in *L. pacificus*, Fig. 60, and mesofemur with elongate setae; male genitalia, Fig. 12.

Sexual dimorphism.— The distinctive modifications of male antennae, protarsal claws, and presence of elongate setae on meso- and metafemora establish this species and *L. pacificus* as the most sexally dimorphic species among *Laccornis*.

Natural history.— The majority of our records of *L. conoideus* are from the boreal biome where it is collected predominantly from quite cold, shallow pools or ponds dominated by *Carex* or by *Carex* and *Sphagnum* (Larson 1975:327, pers. obs.). Therefore this is probably the most typical habitat of *L. conoideus*. However, specimens also occur in snowmelt ponds in parkland regions and in non- to low salinity ponds in grassland areas (Larson 1975:326). These relatively temporary ponds provide an additional biotype for *L. conoideus* and apparently exist just long enough for them to complete larval development.

We collected specimens from shaded portions of a drying streambed and a calcareous bog in southern Ontario, from shaded margins of a large *Carex* marsh, small depressions in the *Sphagnum* mat of a cedar and black spruce bog, and dense moss in a non-acidic bog surrounded by larch in Manitoba, as well as from a richly vegetated, permanent pond north of Old Crow, Y.T. In the sandhills region of Nebraska, three specimens were collected in a small, possibly semipermanent pond which was partially shaded by saplings. Specimens from Colorado were taken at 9,000 ft. elevation.

The larva of this species was described by Watts (1970) and Alarie (1989). Teneral adult specimens were examined from (arranged approximately south to north): 20/v/1937 (Wisconsin), 10/vi/1969 (Minnesota), 18/vi/1933, 21/vi/1978 and 2/vii/1978 (Ontario), 21/viii/1935 (Quebec), and 10/viii/1920 (Manitoba). Larson (1975) recorded teneral specimens from July to late August in Alberta.

Distribution (Fig. 20C).— As noted above under *L. oblongus*, Hamilton's (1894a) record of *L. oblongus* from Unalaska, Alaska may represent either *L. oblongus* or *L. conoideus*. It is difficult to assign this record to either species without re-examining his specimens which we were unable to find. Even without this record, *L. conoideus* has a large range. It extends from the northern Yukon Territory east to Newfoundland and the most southern records are from northern Colorado and Nebraska in the midwestern United States. In North America, *L. conoideus* is probably allopatric to *L. oblongus*, however, they may be sympatric within Beringea. The distribution of *L. conoideus* is parapatric to that of *L. pacificus* (Larson 1975). In the northeastern United States, *L. conoideus* is sympatric with *L. latens* and *L. deltoides* although some range overlap with *L. difformis* is possible, (compare Figs. 20A and Fig. 20C).

Phylogenetic relationships.— *Laccornis conoideus* is the sister species to *L. pacificus* (Fig. 19).

Laccornis pacificus Leech
(Figs. 1D, 2D, 5F, 60, 11A-E; Map, Fig. 20C)

Hydroporus oblongus; Sharp 1882:485, *ex parte* (*nec* Stephens 1835).

Agaporus conoideus; Fall 1923:122, *ex parte* (*nec* LeConte 1850).

Laccornis pacificus Leech 1940:123 [Type locality-- Salmon Arm, British Columbia. Type repository-- CNC], Hatch 1953:215, Wewalka 1969:49, Larson 1975:327, Wolfe and Spangler 1985:70.

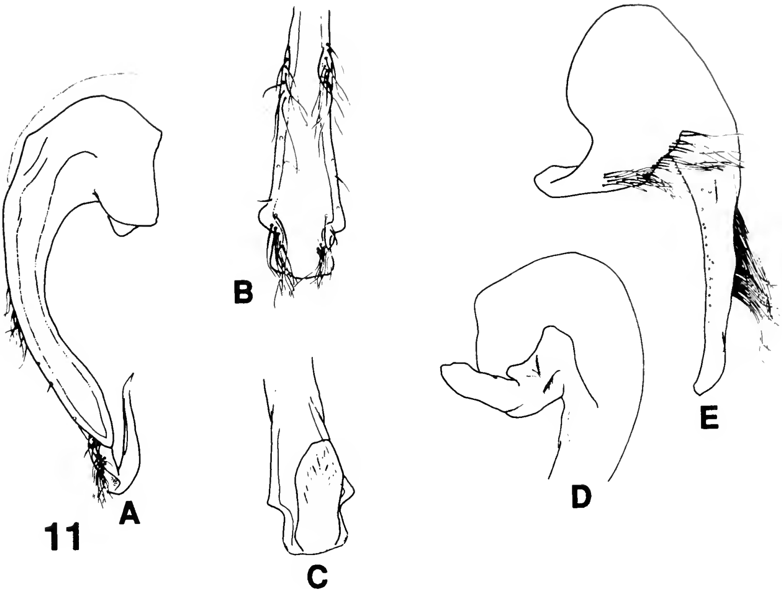
Type information and taxonomic notes.— Full data about types is presented in Leech (1940) and the label data of the holotype male is given in Ruette (1970:42). We examined the holotype as well as numerous paratypes from various collections. Prior to 1940, specimens of *L. pacificus* were confused with *L. conoideus* or *L. oblongus*.

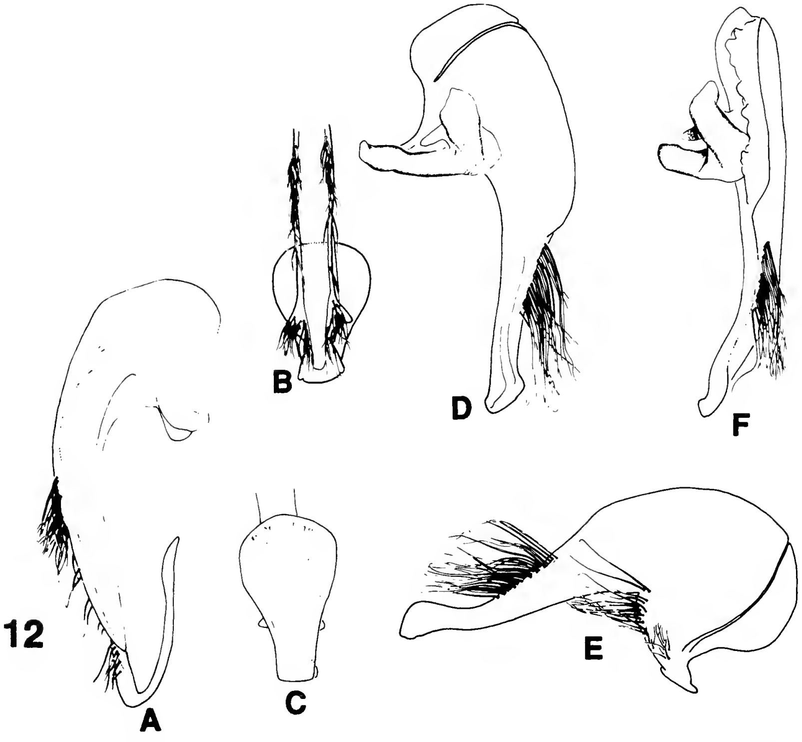
Diagnostic combination.— This species is most similar to *L. conoideus* and is discussed under the above species treatment.

Description.— Taxonomically important character states are presented in Table 1; measurements in Table 2. Prosternal process as illustrated for *L. oblongus* in Fig. 4C; elytral punctation, Fig. 1D; metacoxal puntation, Fig. 2D; male antenna as in *L. conoideus*, Figs. 3E, H; male protarsal claws, Fig. 2D; male antenna as in *L. conoideus*, Fig. 3H; male protarsal claws, Fig. 5F; male metafemur with elongate setae, Fig. 60, and mesofemur with elongate setae; male genitalia, Fig. 11.

Sexual dimorphism.— The distinctive modifications of male antennae, protarsal claws, and presence of elongate setae on meso- and metafemora establish this species and *L. conoideus* as the most sexually dimorphic species among *Laccornis*.

Natural history.— As with *L. conoideus*, this species is found in a wide variety of habitats. Leech (1940) commonly collected specimens from a small, temporary pond in an open meadow and mentioned that as pools dried, specimens were found in damp soil under a log. He records, also, specimens from





Figures 11 A-E, 12 A-F. Male genitalia (150X). Fig. 11. *Laccornis pacificus.* A-C. Aedeagus. A) Lateral view, B) Dorsoapical view, C) Ventroapical view. D-E. Paramere. D) Posteromedial view, E) Lateral view. Fig. 12. *Laccornis conoideus.* A-C. Aedeagus. A) Lateral view, B) Dorsoapical view, C) Ventroapical view. D-F. Paramere. D) Medial view, E) Lateral view, F) Dorsal view. D and F show enlarged modified hinge of paramere.

a cold spring, from a small stream at 1170 ft. elevation and from elvations up to 4,300 ft. (Copper Mountain, B.C.). We examined only one teneral specimen which is from British Columbia and it is dated 24/v/1939.

Distribution (Fig. 20C).— This is the only species occurring west of the Rocky Mountains. It is allopatric to all other species of *Laccornis* but its distribution is proximate to that of *L. conoideus* in southeastern Alberta (Larson, 1975).

Phylogenetic relationships.— *Laccornis pacificus* is the sister species to *L. conoideus* (Fig. 19).

Laccornis latens (Fall)

(Figs. 1E, 2E, 3A, 4F, 5I, 5O, 7A, 7J, 7N, 13A-D; Map, Fig. 20B)

Agaporus latens Fall 1937:10 [Type locality-- Sherborn, Massachusetts. Type repository--MCZ].
Laccornis latens ; Leech 1940:126, Wolfe and Spangler 1985:70.

Type information and taxonomic notes.— Fall (1937) reported that six specimens were used to compile the original description. Only two specimens are in the MCZ type collection. The male holotype has the following label data: Sherborn, Mass. 1934 VI-18 CA Frost/N.B. XIII p. 94/*latens* /*Type* M.C.Z. 23695 [black type on red label]HC. Fall Collection/. Prior to Fall`s (1937) description of *L. latens* , specimens were confused with those of *L. difformis*.

Diagnostic combination.— Both sexes of *L. latens* are longer than those of *L. kocai*, *L. oblongus*, *L. conoideus* and *L. pacificus* and shorter than those of *L. deltoides* and *L. nemorosus*. Male and female *L. latens* have strigate metacoxae which are absent from the above taxa. These characters place *L. latens* in a complex which includes also *L. difformis*, *L. schusteri* and *L. etnieri*. Within this complex females can be identified conclusively only by association with males; however specimens of *L. latens* do have a narrower prosternal process (compare Figs. 4F to 4G). Males of *L. latens* are recognized by scarely modified antennomere 4 (Fig. 3A) and absence of meso- and metafemoral elongate setae. The anterior, protarsal claw of male specimens of *L. latens* (Fig.5I) is distinctive; it is similar to that of *L. difformis* (Fig. 5J) but lacks any indication of a lateral notch.

Description.— Taxonomically important character states are given in Table 1; measurements in Table 2. Prosternal process as illustrated in Fig.4F; elytral punctation, Fig. 1E; metacoxal punctation, Fig. 2E; male antenna, Fig. 3A; male protarsal claws, Fig. 5I; male genitalia, Fig. 13.

Sexual dimorphism.— This species is relatively more sexually dimorphic than *L. kocai* or *L. oblongus*, however, the sexual dimorphism is less developed than in any of the other species of *Laccornis*. Although the male, anterior, protarsal claw is dramatically contorted and broadened, males lack elongate, femoral setae and distinctly enlarged antennomeres.

Natural history.— We collected specimens in southern Ontario from a small pond almost completely shaded by maple trees and from a small depression in a *Sphagnum* mat. The general area around these habitats was dominated by a more boreal flora, typical of the Canadian Shield. Specimens were collected in central New Jersey in small, completely shaded pools that were drying remnants of a seasonally, more extensively flooded, deciduous forest. At all of the above sites, vascular aquatic plants were scarce to absent and the bottom substrate was composed primarily of decaying leaves. These habitats are in marked contrast to specimens collected at Douglas Lake, Michigan, where specimens were taken from exposed beach pools with a sand substrate and dense growths of *Chara* and *Carex.*

Distribution. (Fig. 20B).— Specimens of *L. latens* are known from the Great Lakes region, northeastern United States (New York, Massachusetts, Connecticut and New Jersey) and eastern Canada (Ontario to New Brunswick). It is sympatric with more species of *Laccornis* than is any other single species in the genus.

Phylogenetic relationships.— *Laccornis latens* is the sister species to *L. difformis* + *L. etnieri* + *L. schusteri* (Fig. 19).

Laccornis deltoides (Fall)
(Figs. 14 A-D; Map, Fig. 20C)

Agaporus deltoides Fall 1923:123 [Type locality--Beaver Creek, Ilinois. Type repository--MCZ].

Laccornis deltoides; Leech 1940:127, Wolfe and Spangler 1985:70.

Type information and taxonomic notes.— Fall (1923) stated that his description was based on four specimens from the University of Illinois Collection and that all were labelled with the number 1331. According to Fall, accession records indicated that this number refers to material taken in 1883 by HA. Peters at Beaver, Illinois. Malloch (in Fall 1923) stated that the locality should be interpreted as Beaver Creek, Illinois. Fall (1923) indicated that "The type is a male in my own collection; paratypes in the University of Illinois Collection". There are two specimens (one male and one female) deposited in MCZ. The holotype male was examined and it has the following label information: Beaver (Creek)? Ill H.A. Peters 1883/TYPE *deltoides*/M.C.Z. Type 23964/HC. Fall Collection. The references to *L. deltoides* in Folkerts and Donavan (1974) and Folkerts (1978) from Alabama are referred to *L. nemorosus* below.

Diagnostic combination.— Except for specimens of *L. nemorosus*, all specimens of *L. deltoides* can be separated easily from those of all other species of *Laccornis* by their substantially greater length of 6.28 to 6.60 mm. The outline of the body is distinctly tapering posteriorly and specimens are light brown in colour. Members of *L. deltoides* are a little shorter than those of *L. nemorosus* (7.00 to 7.23 mm) and the prosternal process is slightly more convex medially. Nevertheless genitalic characteristics of males should be used for conclusive identification. The apex of the aedeagus of males of *L. deltoides* is less expanded than is that of *L. nemorosus.*

Description.— Taxonomically important characters are given in Table 1; measurements in Table 2. This is the rarest species of *Laccornis* and no specimens were used for SEM. However, below, we indicate characteristics that are very similar. Prosternal process a little more convex medially than in Figs. 4D, E; elytral punctation as in Fig. 1F; metacoxal punctation as in Fig. 2F; male antenna modified as in Figs. 3C, D, G; male protarsal claws as in Fig. 5I; male genitalia, Fig. 14.

Sexual dimorphism.— Among members of species-group III, males of *L. deltoides* have the most modified antennae but the least modified, anterior, protarsal claws and are without elongate, femoral setae.

Natural history.— The label information about the type locality may indicate that members of *L. deltoides* occur in stream or steam-associated habitats.

Distribution (Fig. 20B).— *Laccornis deltoides* is sympatric with *L. latens* but the distribution of the former is centered a little further south. This species is known from about 10 specimens and more specimens and/or more knowledge of the preferred habitat are needed to document its range more fully.

Phylogenetic considerations.— *Laccornis deltoides* is the sister species to *L. nemorosus*. These two species together form the sister clade to *L. latens* + *L. difformis* + *L. schusteri* + *L. etnieri*.

Laccornis nemorosus NEW SPECIES

(Figs. 1F, 2F, 3C, 3D, 3G, 4D, 4E, 4I, 4P, 5G, 5H, 15A-D; Map, Fig. 20C)

Type information and taxonomic notes.— The holotype, allotype, and paratypes are all from the same locality. The holotype is a male and has the following label information: *L. cf. deltoides* 4 May 76 Reelfoot Lk. Lake Co. Tn GWW 70/*Laccornis nemorosus* Holotype. The holotype is desposited in NMNH

Specimens of *L. nemorosus* previously were confused with those of *L. deltoides*. We examined one of the specimens from Alabama, referred to as *L. deltoides* by Folkerts and Donavan (1974) and Folkerts (1978), and consider it to be *L. nemorosus*.

Etymology.— The name of this species is derived from a Latin word for a "wooded" or "shady" place. This name is used in reference to the habitat characteristics of the type locality.

Diagnostic combination.— This is the longest species of *Laccornis*. Members of *L. nemorosus* can be confused only with those of *L. deltoides*. Characteristics distinguishing among these two taxa are discussed in treatment of the latter.

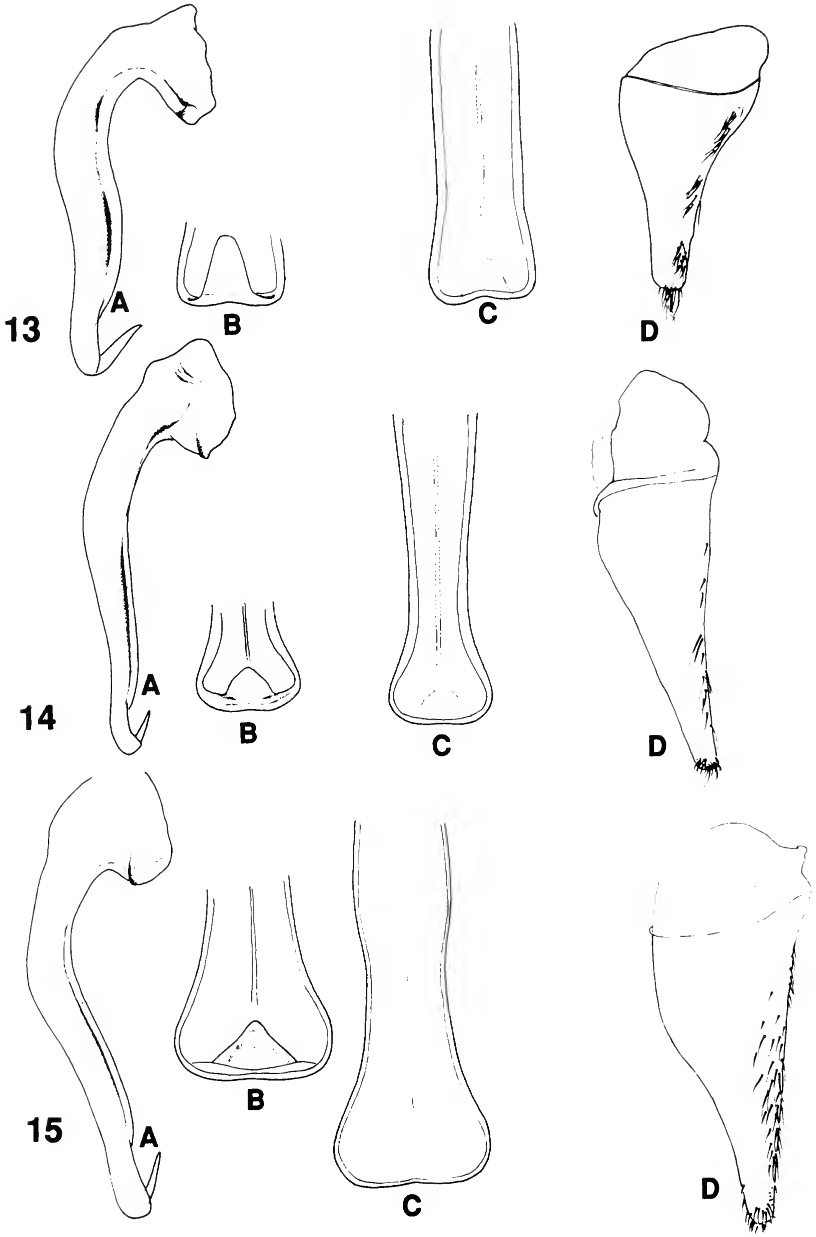
Description.— Taxonomically important character states are given in Table 1; measurements in Table 2. Prosternal process as illustrated in Figs. 4D, E; elytral punctation, Fig. 1F; metacoxal punctation, Fig. 2F; male antenna, Figs. 3C, D; male protarsal claws, Fig. 5G, H; male genitalia, Fig. 15.

Sexual dimorphism.— Males of *L. nemorosus* have the antennae extremely modified. The anterior protarsal claws are not as modified as among other members of species-group III and elongate, femoral setae are absent.

Natural history.— Folkerts and Donavan (1974) reported collecting a specimens from root masses along the margins of a small, gravel-bottom steam. At the type locality, GWW collected approximately 30 specimens, some of which are teneral, in small woodland pools that appeared to be the remnants of a formerly, more extensively flooded area. There was little vascular vegetation and decaying leaves were the predominant substrate.

Distribution (Fig. 20B).— *Laccornis nemorosus* is known only from one locality in each of Tennessee and Alabama. We predict that its distribution is more widespread, that it is centered in the southeastern U.S. and allopatric to that of *L. deltoides*. Folkerts and Donavan (1974) report *L. deltoides* from Alabama and Florida. The Bullock Co., Alabama specimen is a teneral male that we have tentatively assigned to *L. nemorosus*; we did not examine the specimen recorded from Calhoun Co., Florida.

Phylogenetic relationships.— *Laccornis nemorosus* is the sister species to *L. deltoides*. These two species together are the sister clade to *L. latens* + *L. difformis* + *L. schusteri* + *L. etnieri* (Fig. 19).



Figures 13A-D, 14A-D, 15A-D. Male genitalia (150X). A-C. Aedeagus. A) Dorsal view, B) Ventroapical view, C) Dorsoapical view, D) Lateral view of paramere. Fig. 13. *Laccornis latens*. Fig. 14. *L. deltoides*. Fig. 15. *L. nemorosus*.

Laccornis difformis (LeConte)
(Figs. 1G, 3F, 5J, 5Q, 6A-I, 7B-I, 7M-O, 17A-C; Map, Fig. 20A)

Hydroporus difformis LeConte 1855:292, 298 [Type locality-- Georgia. Type repository-- MCZ], Crotch 1873:396, Sharp 1882:484, Wickham 1895:76.

Agaporus difformis; Zimmermann 1920:134, Fall 1923:124 *ex parte*.

Laccornis difformis; Leech 1940:126, Malcolm 1971:22, Brigham 1982:10.57, Wolfe and Spangler 1985:61.

Type information and taxonomic notes.— LeConte (1855) specifically mentioned that only one specimen was available at the time he described *L. difformis*; that specimen is therefore the holotype. The only locality information provided is "Georgia". The holotype male in MCZ was examined and it is labelled as follows: [orange circle]/3412/Type 6036 [black type on red label]/*H difformis* LeC./ The type is teneral and very fragile; the protarsus was removed and placed in a microvial on the pin.

Diagnostic combination.— Males of *L. difformis* are recognized by the enlarged antennomere 4 (Fig. 3F and as in *L. schusteri*, Fig. 3B), apex of anterior, protarsal claw located medially and with a minute lateral notch (Fig. 5J), and the presence of elongate, metafemoral setae (as in *L. etnieri*, Fig. 6P). Female specimens of *L. difformis* cannot be reliably separated from those of *L. schusteri* and *L. etnieri*; however, most females of *L. difformis* are longer and the prosternal process is a little broader than in those of *L. latens* .

Description.— Taxonomically important character states are given in Table 1; measurements in Table 2. Prosternal process as illustrated for *L. schusteri*, Fig. 4G; elytral punctation, Fig. 1G; metacoxal punctation as in *L. schusteri*, 2G; male antenna, Fig. 3F; male elongate, metafemoral setae as in *L. etnieri*, Fig. 6P; male protarsal claws, Fig. 5J; male protarsomere 5, Fig. 5Q, male genitalia, Fig. 17.

Sexual dimorphism.— Specimens of *L. difformis* are more sexually dimorphic than members of either the *L. latens* or *L. deltoides*-complexes because of presence of elongate, metafemoral setae. However, the anterior, protarsal claw of male *L. difformis* is not as modified as that of either *L. etnieri* or *L. schusteri.*

Natural history.— This species apparently is restricted to woodland habitats, especially temporary pools. We collected specimens in New Jersey and North Carolina. At both sites specimens were in small pools that were remnants of a seasonally, more extensively flooded area. Some moss was present, there was scarcely any vascular vegetation, and the substrate was dominated by leaves. Leech (1941) reported that many specimens were taken by placing leaf debris from the shoreline of pools onto a sheet and then waiting for specimens to become active as this material dried.

Distribution (Fig. 20A).— Laccornis difformis is restricted primarily to the Atlantic coastal plain. The most southern record is that of the holotype and is not exactly known other than that it is in Georgia. To the north, *L. difformis* extends off of the coastal plain but still proximate to the coast into northeastern USA; the exact northern limits are uncertain. Fall (1923) mentions specimens from Marquette, Michigan; however, he later (Fall 1937) described them as *L. latens*. Malcolm (1971) mentions specimens from Maine but we were unable to locate them. Two female specimens from Rhode Island are probably this species. The range of *L. difformis* is proximate to that of *L. etnieri* in Maryland.

Phylogenetic relationships.— *Laccornis difformis* is placed as the sister species to *L. etnieri* in Fig. 19; however, the relationship aamong *L. difformis*, *L. etnieri*, and *L. schusteri* requires further study (see Reconstructed Phylogeny).

Laccornis etnieri Wolfe and Spangler
(Figs. 1I, 5L, 6P, 16A-F; Map, Fig. 20A)

Laccornis etnieri Wolfe and Spangler 1985:67 [Type locality -- Jefferson Co., Tennessee. Type repository -- NMNH].

Type information and taxonomic notes.— Full label data for the types is given in Wolfe and Spangler (1985). Members of this species were probably confused with *L. difformis* formerly.

Diagnostic combination.— Males of *L. etnieri* are recognized by presence of enlarged antennomere 4 (as in *L. schusteri*, Fig. 3B), apex of anterior, protarsal claw located laterally and with a minute lateral notch (Fig. 5L), and the presence of elongate, metafemoral setae (Fig. 6P). Female specimens of *L. etnieri* cannot be separated from those of *L. difformis* and *L. schusteri* based on structural characters. Most female specimens of *L. etnieri* are longer and the prosternal process is a little broader than in *L. latens* .

Description.— Taxonomically important character states are given in Table 1; measurements in Table 2. Prosternal process as illustrated for *L. schusteri*, Fig. 4G; elytral punctation, Fig. 1I; metacoxal punctation as in *L. schusteri*, Fig. 2G; male antenna as in *L. schusteri*, Fig. 3B; male with elongate, metafemoral setae, Fig. 6P; male protarsal claws, Fig. 5L; male genitalia, Fig. 16.

Sexual dimorphism.— This species is the most sexually dimorphic in species-group III based on the quite derived condition of the male anterior protarsal claw.

Natural history.— We have collected this species on several occasions in Tennessee. At one locality, there was a temporary pond (about 6m x 6m) in an open field that was partially shaded by trees at the margin and there was abundant vascular vegetation. At several other sites the habitat was peripheral pools at the margins of extensively flooded forest (*e.g.*, Goose Pond, Tennessee) where it appeared that flooding was seasonal

According to Wolfe and Spangler (1985), the larva described as *L. difformis* by Spangler and Gordon (1973) is actually that of *L. etnieri*. We have examined teneral specimens captured on 11/xi/1921 (Maryland) and 12/iv/1976 (Tennessee).

Distribution (Fig. 20A).— The distribution of *L. etnieri* approaches that of *L. schusteri* at the northern end of its range; the distribution of *L. etnieri* is proximate to that of *L. difformis*.

Phylogenetic relationships.— *Laccornis etnieri* is probably the sister species to *L. difformis* (Fig. 19); however, *L. schusteri* is closely related to both of the above species and the relationships among all three species requires further study (see Reconstructed Phylogeny).

Laccornis schusteri Wolfe and Spangler
(Figs. 1H, 2G, 3B, 4G, 5K, 18A-C; Map, Fig. 20A)

Laccornis schusteri Wolfe and Spangler 1985:68 [Type locality-- Cotrell Pond, Stewart Co., Tennessee. Type repository-- NMNH].

Type information and taxonomic notes.— Full information about types is given in Wolfe and Spangler (1985). Members of this species were probably confused with *L. difformis* formerly.

Diagnostic combination.— Males of *L. schusteri* are recognized by enlarged, antennomere 4 (Fig. 3B), anterior protarsal claw of male with apex placed laterally but without a minute lateral notch (Fig. 5K), and presence of elongate, metafemoral setae (as in *L. etnieri*, Fig. 6P). Females of *L. schusteri* are difficult to distinguish from females of *L. difformis* and *L. etnieri* based on structural characters. Most female specimens of *L. etnieri* are longer and the prosternal process is a little broader than in those of *L. latens* .

Description.— Taxonomically important characters are given in Table 1; measurements in Table 2. Prosternal process as illustrated for *L. schusteri*, Fig. 4G; elytral punctation, Fig. 1H; metacoxal punctation, 2G; male antennae as in *L. schusteri*, Fig. 3B; male with elongate, metafemoral setae as in *L. etnieri*, Fig. 6P; male anterior protarsal claws, Fig. 5K; male genitalia, Fig. 18.

Sexual dimorphism.— Except for specimens of *L. etnieri*, this is the most sexually dimorphic in species-group III.

Natural history.— This species has been collected only twice. At the type locality the habitat was a rather large, semipermanent pond surrounded by trees at the edge of a pasture. Specimens of *L. schusteri* were distinctly more abundant in the more shaded portions of the pond with little or no aquatic vegetation. The other locality was on the flood plain of the Obion River, Tennessee. At this latter site, there were numerous small pools in dense forest (completely shaded); the pools were unvegetated but with an abundance of decaying leaves. Teneral specimens were captured on 12/vi/1977.

In June 1979, an attempt was made to find pupal cells at Cotrell Pond. No pupae were found but third instar larvae were discovered about two meters above the water line, most abundantly at the base of a rotten log. Several larvae were trapped in spider webs at this spot. Attempts were made to rear larvae; unfortunately only one female successfully emerged.

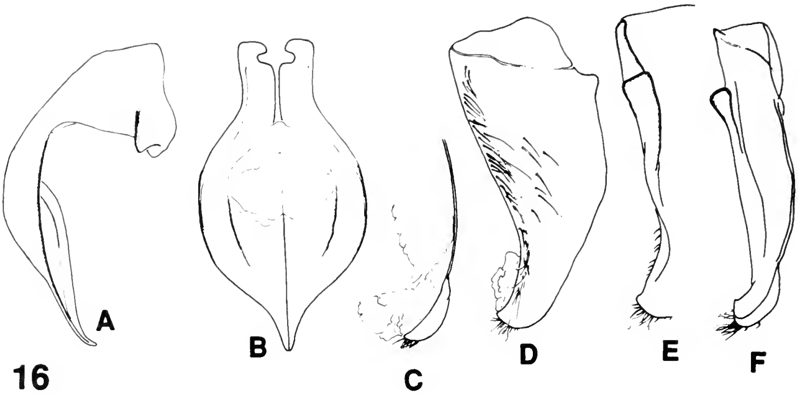
Distribution (Fig. 20A).— We have captured *L. schusteri* on the Gulf Coastal plain and Highland Rim in Tennessee. However, the Highland Rim locality was literally "within a stone's throw" of the coastal plain faunal region which extends up the Mississippi River to southern Illinois and includes western Tennessee. We predict therefore that the distribution of this species is centered on the Gulf Coast.

Phylogenetic relationships.— This species is very closely related to *L. etnieri* and *L. difformis*. Our analysis suggests that *L. etnieri* and *L. difformis* are sister species (Fig. 19); however, relationships among these three species requires further study (see Reconstructed Phylogeny).

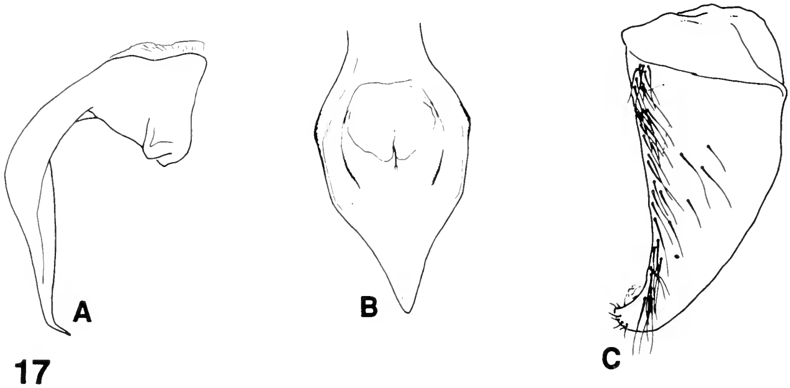
RECONSTRUCTED PHYLOGENY

Our approach to reconstructing the phylogeny of members of *Laccornis* was to incorporate every noticeable difference of external structure that could be coded reliably and for which a moderate level of polarity could be demonstrated. This follows from our studies of structure in which representative specimens of each species, except the very rare *L. deltoides*, were disarticulated and for which all sclerites were examined.

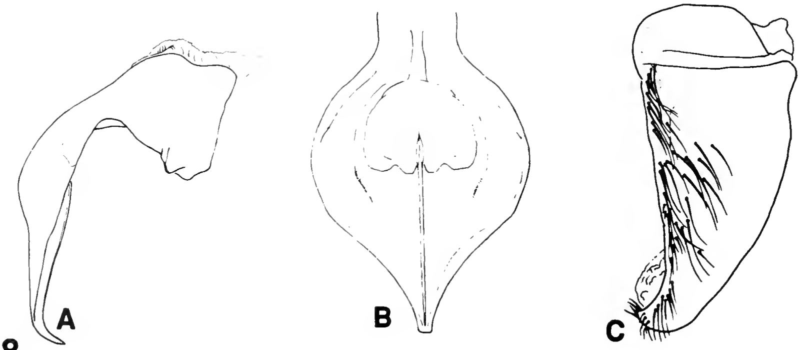
Phylogenetic character state changes and polarities are shown in Table 3; the array of phylogenetic character states by taxon are shown in the matrix in Table 4. Table 5 shows phylogenetic character state changes by character and associated consistency index value; homoplasy and structural divergence are summarized in Table 6; change by lineage is shown in Fig. 19. If all characters are ordered, only one most parsimonious phylogeny can be constructed (Fig. 19).



16



17



18

Figures 16A-F, 17A-C, 18 A-C. Male genitalia, (150X). Fig. 16. *Laccornis etnieri*. A-B. Aedeagus. C-F. Paramere. A) Lateral view, B) Dorsal view, C) Dorsoapical view clearly illustrating membranous lobe, D) Lateral view, E) Ventromedial view, F) Dorsal view. E and F show hinge structure. Fig. 17. *L. difformis*. A) Aedeagus, lateral view, B) Aedeagus dorsal view, C) Paramere, lateral view. Fig. 18. *L. schusteri*. A) Aedeagus, lateral view, B) Aedeagus dorsal view, C) Paramere, lateral view.

The character state changes and justifications associated with our reconstructed phylogeny are described below. Also, overall patterns of structural divergence are discussed.

Laccornis as a monophyletic unit

Previous authors have defined *Laccornis* primarily by the fact that the metafemora contact metacoxal lobes (Fig. 7A) (e.g., Fall 1923 and Leech 1940). However, Wolfe (1985) and Roughley and Wolfe (1987) pointed out that that characteristic was shared with other hydroporines (Methlini, *Hydrovatus* Motschulsky, *Canthyporus* Zimmermann and *Laccornellus* Roughley and Wolfe) and that it is plesiotypic.

Information in Burmeister (1976) and Wolfe (1985) indicates that female members of *Laccornis* are unique among all hydroporines in their possession of a valvifer (=Tergum IX of Burmeister, 1976). Wolfe (1985) demonstrated that presence of a valvifer is plesiotypic and absence is derived among members of Hydroporinae.

There is only one demonstrable synapotypy for all members of *Laccornis*, if *L. kocai* is included; the prosternal process is broadened apically (see Figs. 4A vs 4B-G). This character is coded as PSTSHP in Tables 3-5 and on Fig. 19. We are not absolutely confident in the reliability of prosternal process shape. Several other hydroporine groups also possess a broadened prosternal process (notably, at least some members of *Canthyporus*). However, since all other known hydroporines have lost the valvifer and the most common prosternal shape among hydroporines is elongate and tapered, we retain *L. kocai* in *Laccornis* and we accept PSTSHP as a generic synapotypy.

Not used in the phylogenetic analysis is the presence of enlarged palettes on protarsomere 3 (Figs. 5A, B) which may be a synapotypy of *Laccornis*. Most hydroporines have these enlarged setae restricted to protarsomeres 1 and 2. This character state was not used because we have not examined a sufficient number of outgroup taxa to develop a firm hypothesis about the polarity of this character. The enlarged palettes are easily abraided and are difficult to see on most museum specimens (*cf.* Larson 1975).

Species-group relationships

Three species-groups are recognized within *Laccornis* for 10 species; each species-group is subdivided, where appropriate, into species-complexes as follows: i) species-group I monobasic, with *L. kocai*; ii) species-group II - two species-complexes, a) *L. conoideus*-complex with *L. conoideus* and *L. pacificus* and b) *L. oblongus*-complex - monobasic; iii) species-group III - three complexes; a) *L. deltoides*-complex with *L. deltoides* and *L. nemorosus*, b) *L. latens* -complex, monobasic, and c) *L. difformis*-complex with *L. difformis*, *L. etnieri* and *L. schusteri*.

Species-group I.— *Laccornis kocai* is the most plesiotypic member of *Laccornis*. Our analysis of characters suggests that it is a very unspecialized species. It is because of this that other species of *Laccornis* demonstrate a relatively high number of steps of change from *L. kocai* (Table 6) which we refer to as structural divergence.

In only two character states--form of anterior protarsal claw of males (3.9, Table 1) with basal lobe, and elytral punctation (4.1, Table 1) less coarse do members of *L. kocai* differ from a generalized ancestor of *Laccornis*. However these two character states are very difficult to polarize because a broad array of states is shown by a variety of hydroporines and they may be plesiotypic.

Species-groups II + III.— Four synapotypies suggest common ancestry of all members *Laccornis*, exclusive of *L. kocai*: 1) aedeagus distinctly reflexed (AEDREFL), 2) increased number of mesotibial spines in the anterior lateral row (MSTSPIN), 3) increased number of protarsal palettes (PROPALE), and 4) form of ventral sensilla of protarsomere 4 (PROVSEN).

Of these four characters, the least reliable is probably the number of mesotibial spines in the anterolateral row (MSTSPIN). This character is partitioned into two states but distinction among these two states is not well defined. However, specimens of *L. kocai* are clearly at the low end of MSTSPIN number and despite variation in this character a low number of spines almost surely is plesiotypic (Wolfe 1985).

We are not certain about the phylogenetic value of the number of enlarged palettes; among hydroporines in general the most common state is two per row, however, in many species of a variety of genera there is an increase in number of palettes per row (*cf.* Larson 1975). We judge such increases as probably secondary development. Our recognition of increased number of enlarged palettes as apotypic within *Laccornis* is justified based on the comparison to the state present among members of Methlini, or *Laccornellus* (outgroup representatives).

The presence of hair-like setae on protarsomere 5 (PROVSEN) is interesting because the difference between the state in *L. kocai* and all other members of *Laccornis* is marked and the condition of *L. kocai* clearly is present in the outgroup. Because this character is distinctly dichotomous and easily interpreted by outgroup comparison we give it considerable weight.

Of the four synapotypies uniting species-groups II and III, the aedeagal reflexed character (AEDREFL) is the only one that is not perfectly consistent [CI (consistency index) = .667]. However, aedeagal structure is probably the most well studied character among members of Hydroporinae and the reflexed aedeagal condition is very rare (as far as we know, otherwise only known in some males of *Canthyporus* and *Hydrovatus*). The decreased CI value results from secondary loss among the members of the *L. difformis*-complex of species-group III.

In order to search for biases with this character (AEDREFL) system in our analysis, phylogenies were constructed under several premises: 1) all character states unordered, 2) all character states associated with aedeagal reflex unordered, 3) all characters ordered. When characters were considered fully ordered, generally we hypothesized that they changed from less developed to more developed (*i.e.*, aedeagal apex not reflexed, *e.g.*, *L. kocai*, to maximally reflexed and ligulate, *e.g.*, *L. conoideus*). If characters were considered unordered no sequence is specified *a priori*. If either all characters, or only the states associated with AEDREFL, were unordered the character state change preceding divergence of species-groups II and III was from state 0 to state 4, with successive subsequent loss in species-group III. By ordering all characters, the analysis obviously is biased in favor of generating phylogenies with taxa with the less reflexed aedeagal condition in more basal (plesiotypic) positions. However, even under this latter premise the character state change preceding divergence of species-groups II and III was 0 to 3 with successive loss only in the *L. difformis*-complex (Fig.19). Therefore, under any of the above premises, a change took place in AEDREFL early in the evolution of this group with subsequent loss of the reflexed condition only in members of species-group III.

With ordered characters, only one most parsimonius tree was obtained (Fig. 19) and in that hypothesis five other characters clearly establish the monophyly of both the *L. difformis*-complex and specis-group II. Therefore, we are confident that the reflexed aedeagal condition (state 0 or 3) is a reliable synapotypy for species-groups II + III.

Evolution has independently tended towards increased sexual dimorphism in species-groups II and III, primarily in modifications to antennae, protarsal claws, and elongate setae of meso- and metafemora of males. Modifications within species-group II involve enlargement, change in shape, and ventral reticulation of antennomeres 3-7, development of a medial tooth on the anterior protarsal claw, and presence of meso- and metafemoral elongate setae. These modifications all are maximally evident in the *L. conoideus*-complex. Within species-group III, elongate femoral setae occur only on metafemora; anterior protarsal claws are without a medial tooth, rather the claws are progressively contorted and foliately expanded. Only antennomeres 3-5 are modified, and of these only antennomere 4 is distinctly developed. Parallel trends toward sexual dimorphism therefore occur within species-groups II and III, but by different and independently derived modifications of the same structures (antennae and anterior protarsal claws).

Species-group II.— Six synapotypies suggest monophyly of species-group II. Four are genitalic: 1) aedeagal reflexed condition (AEDREFL) maximally developed, 2) dorsolateral aedeagal setae present (AEDSETA), 3) paramere setation altered into a unique configuration (PARASET), and 4) paramere shape altered (PARASHP). Additionally among males, antennomeres 3-7 are modified (ANTTYP2) and metafemoral setae are present (METASET). Within species-group II, *L. conoideus* and *L. pacificus* are clearly sister species based on more extensive modification of genitalic (AEDSETA) and antennal (ANTTYP2) characters. Additionally, the anterior lateral processes (AEDALPR) are developed at the apex of the aedeagus, mesofemoral setae (MESOSET) are present, and anterior protarsal claws are medially toothed (CLTOOTH). The anterior lateral aedeagal process is maximally distinct in *L. conoideus* and the medial tooth of anterior protarsal claw is most developed in males of *L. pacificus*.

The modifications associated with the aedeagus, parameres, mesofemoral setae and protarsal claws are unique within *Laccornis*; antennal modifications are also unique as long as our hypothesis concerning its independent origin in species-groups II and III is correct. Presence of metafemoral setae occurred independently in the *L. difformis*-complex. The aedeagal reflex is not homoplastic within species-group II; however, this character is secondarily lost in members of the *L. difformis*-complex of species-group III.

Overall species-group II is very distinctive and exhibits a high degree of structural divergence (Table 6) and we are very confident about the species relationships within it, especially concerning the sister species status of *L. conoideus* and *L. pacificus*.

Species-group III.— Monophyly of species-group III is based on claw shape (CLSHAPE), antennal structure (ANTTYP1), and presence of a prosternal pore (PSTPORE). Presence of a prosternal pore (Fig. 4I) in this clade is interesting. The notched condition (Fig. 4H) of all other members of *Laccornis* exists in the more plesiotypic hydroporines so far examined, such as members of *Canthyporus*, Methlini and Hydrovatini (Wolfe 1985, 1989). The pore is present in more apotypic hydroporines both in the northern and southern hemisphere (Wolfe 1985). Antennal and claw structural modifications each form a morphocline. Successively more apotypic stages of development are synapotypies for lineages in this species-group as shown in Fig. 19.

The *L. deltoides*-complex is the sister-group to all other members of species-group III. *Laccornis deltoides* and *L. nemorosus* are extremely similar in size, shape, and coloration. They are grouped together based on maximal development of antennomere 4 (ANTTYP1), protarsal structure (PRORIDG), and more distinctly concave condition of the prosternal process (PSTPRCV).

Monophyly of the *L. latens* - and *L. difformis*-complexes is based on derived shape of spines on protarsomere 4 (PRO4SPI), presence of coxal strigae (CXSTRIG) and more foliate anterior protarsal claws (CLSHAPE). However, there is a loss in degree of antennomere development in the *L. latens* -complex and this is the direct cause for decreased CI of this character (.750) in species-group III.

The *L. difformis*-complex is the most structurally divergent in the genus (Table 6). Six synapotypies suggest monophyly of this group. One of the six is a character loss (AEDREFL). The aedeagus becomes non-reflexed although the apex still is distinctly deflected ventrally in two of the three species (Figs. 16-18). Other synapomorphies are associated with the aedeagus (AEDBASE, AEDSHAPE), presence of membranous lobe of apex of paramere (PARAMEM) and presence of distinctly evident metafemoral setae (METASET). The CI for the aedeagal reflex and claw shape is decreased because of partial character loss in males of *L. difformis* and *L. etnieri* respectively. The CI for metafemoral setae is .750 because it arose twice in the genus (species-group II and *L. difformis*-complex) as discussed above.

Relationships within the *L. difformis*-group are a little ambiguous. If all characters are ordered, *L. difformis* and *L. etnieri* are sister species based on presence of asymmetrical ventral lobe of protarsomere 5 (PROLOBE), and presence of at least a subtle notch on the anterior claw (CLNOTCH). If all characters are unordered, it is equally parsimonius that *L. etnieri* could be considered the sister species to *L. schusteri*. Unordering of all phylogenetic characters is perhaps too unrealistic; however, it is interesting to note that even under this condition only relationships within the *L. difformis*-group are altered.

We have considered the possibility that *L. latens* is the sister species to all other members of species-group III based on the less evidently modified antenna of members of that species (Figs. 3A vs 3B). That hypothesis was rejected for three reasons. First, while reversing the positions of the *L. deltoides*- and *L. latens* -complexes eliminates inconsistency in antennal structure, a new reversal would be introduced with respect to anterior protarsal claw structure. Although the anterior protarsal claw of both members of the *L. deltoides*-complex is contorted, it is distinctly less foliately expanded than it is in males of *L. latens* ; thus if *L. latens* diverged first there would have to be partial character loss accepted with respect to claw structure. Second, additional homoplasy involving metacoxal striga and shape of sensilla of protarsomere 4 is introduced if the position of *L. latens* and the *L. deltoides*-complex are switched. Third, we think it ill advised to weigh the antennal structural changes more than anterior protarsal claw changes because antennal modifications similar to those of members of *Laccornis* are known in numerous other hydroporine taxa. There is a noticeable tendency for this character to be homoplastic among hydroporines and indeed among various groups of Dytiscidae in general (*cf.* Larson 1975). On the other hand, the type of protarsal claw modification (contorted and foliate) present in members of species-group III is unique and unknown in any other dytiscid group. Therefore, if we were to weight any character in our analysis of species-group III members, it would be claw structure (which already in part is contributing strongly to the more parsiomonius resolution).

Table 3.

Phylogenetic characters, their abbreviations, character states, character state changes, polarities, and consistency index used for phylogenetic analysis of species of *Laccornis*. See Fig. 19 for arrangement of characters by lineage. 0 - plesiotypic state, higher numbers indicate progressively more apotypic conditions. Numbers in parentheses refer to figure numbers.

	Changed			
CHARACTER	from	to	Along branch	CI
Leg characters.				
1) Claw tooth (CLTOOTH)				
not toothed (5 G-L)....................0	0	1	12–11	
toothed (5E)............................1	1	2	11–*pacificus*	1.000
distinctly toothed (5F)...............2				
2) Claw shape (CLSHAPE)				
not foliate (5C-F)......................0	0	1	18–17	
contorted (5G,H)........................1	1	2	17–15	
foliate (5I-L)............................2	2	3	15–14	
foliate and apically				
truncate (5K-L) 3	3	2	13–*difformis*	0.750
3) Claw notch (CLNOTCH)				
absent (5K)..............................0	0	1	13–12	
slightly evident (5J) 1	1	2	12–*etnieri*	1.000
distinctly evident (5L)................2				
4) Protarsal palettes (PROPALE)				
maximum of two enlarged (5A)......0	0	1	19–18	1.000
four enlarged (5B).....................1				
5) Shape of apicolateral lobe of protarsomere 5 (PROLOBE)				
symmetrical (5M, N)..................0	0	1	14–13	1.000
not symmetrical (5Q) 1				
6) Sensilla of protarsomere 5 (PROVSEN)				
sensilla spine-like (5M).............0	0	1	19–18	1.000
sensilla seta-like (5N, O, P) 1				
7) Spines of protarsomere 4 (PRO4SPI)				
long, slender (5M).....................0	0	1	17–15	1.000
short, cone-like (5O)..................1				

.... (continued on next page)

Table 3 (continued)

		Changed			
	CHARACTER	from	to	Along branch	CI
8)	Ridge of protarsomere 5(PRORIDG)				
	ridge absent (5M, N) 0	0	1	17–16	1.000
	ridge present (5P) 1				
9)	Mesotibial spines (MSTSPIN)				
	anterior lateral row with less				
	than eight spines (6O)................0	0	1	19–18	1.000
	anterior lateral row with				
	nine or more spines (6H).............1				
10)	Mesofemoral elongate setae (MESOSET)				
	absent..................................0	0	1	18–12	1.000
	present.................................1				
11)	Metafemoral elongate setae (METASET)				
	absent (6N).............................0	0	2	15–12	
	present (6O)............................1	0	1	12–11	0.667
	distinctly present (6P)................2				
Genitalic characters.					
12)	Aedeagal ventrally bent/reflexed (AEDREFL)				
	not vent. bent/reflexed (9)...........0	0	3	19–18	
	slightly bent (16).....................1	3	2	15–14	
	distinctly bent (17-18) 2	3	4	18–12	
	reflexed (13-15)........................3	2	1	13–*etnieri*	0.667
	reflexed and ligulate (8, 11, 12).....4				
13)	Aedeagal base (AEDBASE)				
	not enlarged (8, 9, 11-15............0	0	1	15–14	1.000
	enlarged (16-18) 1				
14)	Aedeagal setae (AEDSETA)				
	absent (9, 13-18) 0	0	1	18–12	
	present, not long	1	2	12–11	1.000
	and dense (8) 1				
	present, long dense (11-12) 2				

.... (continued on next page)

Table 3 (continued)

CHARACTER	Changed from	to	Along branch	CI
15) Aedeagal shape (AEDSHAP)				
not distinctly expanded (8-15)......0	0	1	15–14	1.000
broadly expanded (16-18)............1				
16) Aedeagal lateral projections (AEDALPR)				
absent.................................0	0	1	12–11	
present (11)...........................1	1	2	11–*conoideus*	1.000
distinctly present (12)...............2				
17) Paramere shape/hinge (PARASHP)				
gradually tapering; hinge				
horizontally oriented (16).....0	0	1	18–12	
abruptly narrowed apically;..........1	2	2	12–11	1.000
hinge enlarged and vertically				
oriented (8).......................1				
as in state 1 but hinge with ventral				
apodeme and apex w/slightly				
expanded tip (11, 12)..........2				
18) Paramere setation (PARASET)				
one ventral setal series...............0	0	1	18–12	1.000
ventral and dorsal series.............1				
19) Paramere membrane (PARAMEM)				
not enlarged apically				
(8-9, 11-15)......................0	0	1	14–13	1.000
enlarged (16-18)......................1				
Antennal characters.				
20) Antenna - morphotype 1 (ANTTYP1)				
no modification.......................0	0	2	18–17	
4th slightly enlarged,................	2	3	17–16	
slightly concave (3 A)..........1	2	1	15–*latens*	0.750
4th evidently enlarged, 3rd and 5th				
slightly; 4th slightly oncave;				
post edge with setae (3 B, F)...2				

....(continued on next page)

Table 3 (continued)

CHARACTER	Changed from	to	Along branch	CI
4th distinctly enlarged, 3rd and 5th scarcely; 4th distinctly concave; ant. and post. edge w/setae, vent. reticulation effaced (3 C-E, G, H, 4I)........3				
21) Antenna - morphotype 2 (ANTTYP2)				
no modification.......................0	0	1	18–12	
3-7 scarcely modified, vent.......... surface slightly rugose..........1	1	2	12–11	1.000
3-5 distinctly enlarged, 6 and 7 slightly; 3-5 asymmetrically shaped, ventral surface convex sinuate and distinctly rugose.............................2				
Prosternal characters.				
22) Prosternal pore (PSTPORE)				
absent, cleft/notch present (4H)....0	0	1	18–17	1.000
pore present (4I).......................1				
23) Prosternal process shape (PSTSHP)				
elongate (4A)...........................0	0	1	generic	
broad (4B-G)............................1			synapotypy	
24) Prosternal convexity (PSTPRCV)				
evident (4B, C, F, G)..................0	0	1	15–14	1.000
reduced (4D, E).........................1				
Metacoxal characters.				
26) Metacoxal strigae (CXSTRIG)				
absent (2A-D, F).......................0	0	1	17–15	1.000
present (2E, G).........................1				

Table 4

Matrix of phylogenetic character states used for reconstruction of phylogeny of species of *Laccornis* (Fig. 19). Character abbreviations (*i.e.* column designations) are listed and explained in Table 5.

Charac. Species	CLTOOTH	CLSHAPE	CLNOTCH	PROPALE	PROLOBE	PROVSEN	PRO4SPI	PRORIDG	MSTSPIN	AEDREFL	AEDBASE	AEDSETA	AEDSHAP	AEDALPR	PARASET	PARASHP	PARAMEM	ANTTYP1	ANTTYP2	PSTPORE	PSTSHP	PSPRCV	CXSTRIG	MESOSET	METASET
L. kocai	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
L. conoideus	1	0	0	1	0	1	0	0	1	4	0	2	0	2	1	2	0	0	2	0	1	0	0	1	1
L. pacificus	2	0	0	1	0	1	0	0	1	4	0	2	0	1	1	2	0	0	2	0	1	0	0	1	1
L. oblongus	0	0	0	1	0	1	0	0	1	4	0	1	0	0	1	1	0	0	1	0	1	0	0	1	0
L. latens	0	2	0	1	0	1	1	0	1	3	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0
L. difformis	0	2	1	1	1	1	1	0	1	2	1	0	1	0	0	0	1	2	0	1	1	1	1	0	2
L. etnieri	0	3	2	1	1	1	1	0	1	1	1	0	1	0	0	0	1	2	0	1	1	1	1	0	2
L. schusteri	0	3	0	1	0	1	1	0	1	2	1	0	1	0	0	0	1	2	0	1	1	1	1	0	2
L.deltoides	0	1	0	1	0	1	0	1	1	3	0	0	0	0	0	0	0	3	0	1	1	0	0	0	0
L.nemorosus	0	1	0	1	0	1	0	1	1	3	0	0	0	0	0	0	0	3	0	1	1	0	0	0	0
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 5.

Observed character state changes (alphabetically arranged by character abreviation) and consistency index (CI) for each character used in reconstructed phylogeny of species of *Laccornis* (Fig.19). See Table 3 for hypothesized transformation series; see Fig. 19 for arrangement of character states by lineage.

CHARACTER	Changed from	to	Along branch	CI
AEDALPR - Development of anterolateral process of aedeagus.	0	1	12 – 11	
	1	2	11 – *conoideus*	1.000
AEDBASE - Enlargement of aedeagal base.	0	1	14 – 13	1.000
AEDREFL - Aedeagus more reflexed.	0	3	19 – 18	
	3	2	15 – 14	
	3	4	18 – 12	
	2	1	13 – *etnieri*	0.667
AEDSETA - Increased distinctiveness of aedeagal setae	0	1	18 – 12	
	1	2	12 – 11	1.000
AEDSHAP - Aedeagus medially expanded.	0	1	15 – 14	
ANTTYP1 - Progressive development antennal morphotype 1.	0	2	18 – 17	
	2	3	17 – 16	
	2	1	15 – *latens*	0.750
ANTTYP2 - Progressive development antennal morphotype 2.	0	1	18 – 12	
	1	2	12 – 11	1.000
CLNOTCH - Distinctiveness of claw notch.	0	1	13 – 12	
		2	12 – *etnieri*	1.000
CLSHAPE - Claw shape modification.	0	1	18 – 17	
	1	2	17 – 15	
	2	3	15 – 14	
	3	2	13 – *difformis*	0.750

(continued on next page)

Table 5 (continued)

CHARACTER	Changed from	to	Along branch	CI
CLTOOTH - Progressive development of claw tooth.	0	1	12 – 11	
	1	2	11 – *pacificus*	1.000
CXSTRIG - Coxal strigae present.	0	1	17 – 15	1.000
MESOSET - Mesofemoral elongate setae.	0	1	18 – 12	1.000
METASET - Metafemoral elongate setae present.	0	2	15 – 14	
	0	1	12 – 11	0.667
MSTSPIN - Density of anterior lateral row of mesotibial spines.	0	1	19 – 18	1.000
PARAMEM - Development of paramere membrane.	0	1	14 – 13	1.000
PARASET - Pattern of setation of paramere altered.	0	1	18 – 12	1.000
PARASHP - Progressively more tapered shape of paramere.	0	1	18 – 12	
	1	2	12 – 11	1.000
PROLOBE - Protarsal lobe asymmetrical.	0	1	14 – 13	1.000
PROPALE - Increased number of protarsal palettes.	0	1	19 – 18	1.000
PRORIDG - Anterodistal ridge of protarsomere 5.	0	1	17 – 16	1.000
PRO4SPI - Spines of protarsomere 4 more cone-shaped.	0	1	17 – 15	1.000
PROVSEN - Protarsal ventral sensilla more hairlike.	0	1	19 – 18	1.000

(continued on next page)

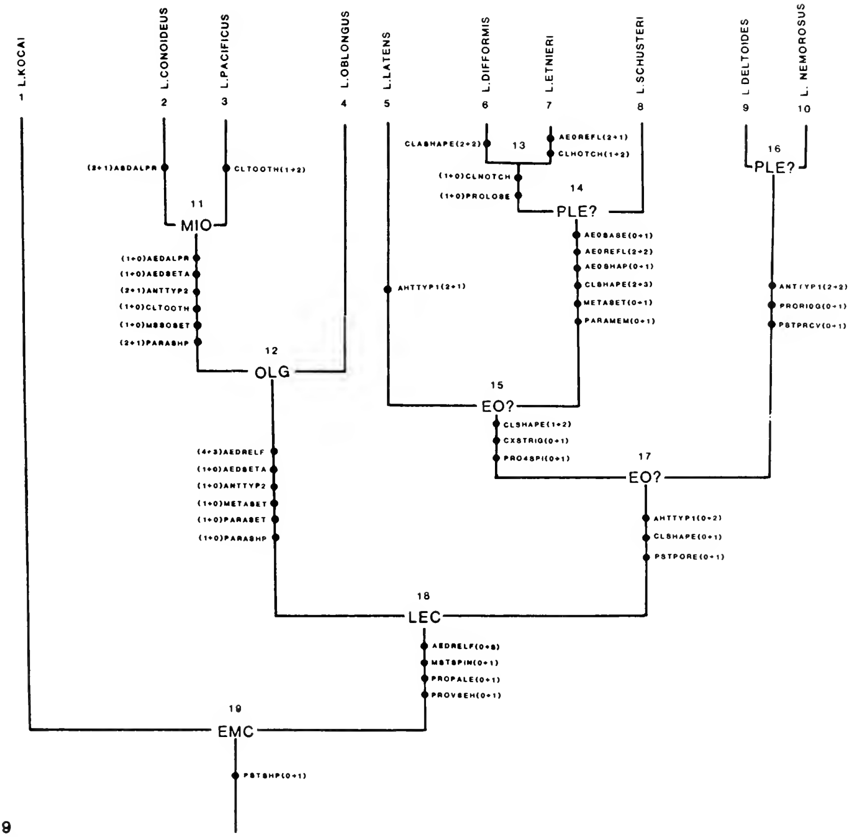
Table 5 (continued)

CHARACTER	Changed from	to	Along branch	CI
PSTPORE - Prosternal pore present.	0	1	18 – 17	1.000
PSTPRCV - Prosternal process more concave.	0	1	15 – 14	1.000
PSTSHP - Prosternal process shape broader.	0	1	Generic Synapotypy	1.000

Table 6.

Summarization of phylogenetic character change, homoplasy, and structural divergence in reconstructed phylogeny of species of *Laccornis* (Fig. 19); see text for explanation.

	Steps changed from *L. kocai*	Number of homoplasies	Divergence from *L. kocai* (First column minus second column)
1) *L. conoideus*	19	0	19
2) *L. pacificus*	19	0	19
3) *L. oblongus*	12	0	12
4) *L. latens*	14	2	12
5) *L. difformis*	24	4	20
6) *L. etnieri*	25	4	20
7) *L. schusteri*	21	2	19
8) *L. deltoides*	12	0	12
9) *L. nemorosus*	12	0	12



19

Figure 19. Proposed phylogeny of species of *Laccornis*. EMC-early to middle Cretaceous, LEC-late Cretaceous to early Cenozoic, OLG-Oligocene, MIO-Miocene, PLE-Pleistocene, EO-Eocene.

Homoplasy.— Within *Laccornis* only one character has independently arisen twice and that is elongate metafemoral setae. Three character losses are recognized (see Table 6): i) antennal development in *L. latens* reverts to state 1 from state 2, ii) claw shape changes back to state 2 from state 3 in *L. difformis*, and iii) the aedeagus becomes progressively less reflexed in the *L. difformis*-complex. All losses occur in species-group III and mostly they occur within the *L. difformis*-complex.

Conclusion.— Parallel trends in modification of secondary Sexual characteristics could be interpreted as homoplasy but by careful re-evaluation of character states this potential problem was resolved. Nine of 10 species of *Laccornis* are remarkably divergent in terms of structural characters from their nearest relative (Table 6). Examination of Fig. 19 suggests that there were irregular episodes of structural divergence, followed by diversification of closely related and similar taxa within the *L. conoideus-*, *L. difformis-* and *L. deltoides*-complexes.

ZOOGEOGRAPHY

Introduction.

The distribution of species of *Laccornis* is interpreted by means of vicariance biogeography. The elements of vicariance biogeography are disussed in Nelson and Platnick (1981), Platnick (1976), Rosen (1978) and Humphries and Parenti (1987). Excellent reviews of land configuration, global climates and timing of vicariant events in the Northern Hemisphere are provided by Matthews (1979), Allen (1983), and Noonan (1986, 1988) and we have relied on these references extensively when developing our biogeographic hypotheses.

Several investigators (Coope 1979, Matthews 1977) have demonstrated that many (most?) extant species of beetles existed prior to Pleistocene glacial episodes. Matthews (1977) specifically indicated that the earliest fossil deposits with substantial numbers of extinct species are of late Miocene age. Thus based on fossil evidence (albeit none of which include *Laccornis*), it does not seem tenable to explain speciation within *Laccornis* exclusively in terms of Pleistocene events. Primarily because of this and the inferred age of origin of *Laccornis*, we assume that older geological events were important in the zoogeographic *history* of the taxa included within this genus.

However, we do invoke Pleistocene divergence of extremely similar species which all occur allopatrically within the southeastern United States. We are more tentative about this assumption compared to the ages postulated for earlier vicariant events.

We rely exclusively on a vicariant model of allopatric speciation. As pointed out by Kavanaugh (1979), this model depends on the assumption that structural divergence among taxa is positively correlated with: 1) genetic differentiation, 2) degree of reproductive isolation, and 3) length of period of geographical isolation. Although these assumptions are not without exception, the phylogenetic position of Laccornini within Hydroporinae combined with extensive amount of structural divergence of certain clades represented in Fig. 19 supports our view that *Laccornis* constitutes an ancient lineage among hydroporine dytiscids.

Kavanaugh (1979) suggested that slow rates of speciation would be more apparent in beetle taxa of lowland habitats as compared to higher rates of speciation for taxa occurring in montane habitats. Members of *Laccornis* are predominantly lowland and the moderate diversity of species (10), we think, adds credibility to our assumption of antiquity of origin.

Distributional patterns.— Distributional ranges are illustrated in Figs. 20 A-D and these are generalized into patterns in Figs. 21A-D.

At the species level, generalized patterns of distribution tend to be allopatric, especially when closely related taxa are compared. No known species is sympatric with its sister species [compare ranges of *L. conoideus* - *L. pacificus* (2, 3 in Fig. 21A), *L. deltoides* - *L. nemorosus* (9, 10 in Fig. 21A) and *L. difformis* - *L. etnieri* (6, 7 in Fig. 21A). However, the distributions of members of some species pairs are virtually proximate (*L. difformis* - *L. etnieri* and *L. conoideus* - *L. pacificus*). Collections from areas of maximum proximity in Maryland/eastern Virginia and southern British Columbia/Alberta of the respective species pairs have failed to demonstrate any evidence of parapatry and/or hybridization. *Laccornis latens* is the sister lineage to the *L. difformis*-complex and these two lineages are largely allopatric (compare 5 to 6+7+8 in Fig. 21A); as is that of *L. oblongus* and the *L. conoideus*-complex (compare 4 to 2+3 in Fig. 21A).

Often distributions are irregularly shaped and they are often imperfectly known. One way to factor out such vagaries is to use the center of endemism approach of Kavanaugh (1980). To conduct such an analysis we drew circles, approximately scaled to the size of the long-axis length of the distribution of each species. The circle representing each species was located on the map so that its center approximated the center of the "real" distribution (Fig. 21B). It is obvious immediately that there is no center of endemism based on concentric overlap of circles. As a matter of fact with this approach, "allopatry" is even more evident in the genus. Only circles of *L. difformis* and *L. etnieri* (6, 7 in Fig. 21B) narrowly overlap and only circles of *L. nemorosus* and *L. schusteri* (8, 10 in Fig. 21B) overlap completely.

Species-complexes show more distributional overlap than do species-groups (Figure 21C). The distribution of the *L. latens* -complex is completely contained in that of the *L. conoideus*-complex. The *L. difformis*- and *L. deltoides*-complexes each are narrowly sympatric at their independent northern limits with the *L. latens* - and *L. conoideus*-complexes. The *L. deltoides*- and the *L. difformis*-complexes are allopatric towards the north with respect to each other but are largely sympatric in the south on the Gulf Coast based on the speculation that *L. schusteri* extends onto the Gulf Coastal Plain, as discussed above.

A somewhat generalized composite picture of species-group distributions (except *L. kocai*, endemic to southeastern Europe) is shown in Fig. 21D. Generalizations about these patterns are as follows. 1) Species-group I (*L. kocai* has the most restricted range (Fig. 20D). As discussed above, the limited distribution of *L. schusteri* and *L. nemorosus* is probably artificial and both almost surely occur throughout the Gulf Coastal Plain. 2) Species-group II (Fig. 21D) occurs in both the northern Nearctic and Palearctic areas; it is circumboreal 3) Species-group III is restricted to eastern North America, primarily south of the Great Lakes Region. Therefore, species-group distributions are allopatric, except for narrow overlap between species- groups II and III in eastern North America.

Based on these distribution patterns we feel that our assumption of allopatric speciation is justified and that this group is amenable to interpretation by vicarant zoogeography. Similarly because these distributions are allopatric and because we are confident in the time of origin of *Laccornis* we added the timing of vicariant events to the cladogram (Fig. 19).

Age of origin of the genus Laccornis.— Wolfe (1985), based on a phylogenetic analysis of primitive lineages of the subfamily Hydroporinae, suggested that the genus *Laccornis* represented either the sister group to all other Hydroporinae, or, at least, the sister group to hydroprine genera with centres of diversity in the Northern Hemisphere. It was proposed that the initial break-up of Pangea in mid-Jurassic [about 170 million years before present (mybp)] separated the faunas of the Northern and Southern Hemispheres and that the northern isolate included the common ancestor of *Laccornis* as well as that of the hydroporine genera which are most diverse there today. There is no reason to challenge this conclusion at the present time.

Historical analysis.— After origin of the genus *Laccornis* on Laurasia (Wolfe 1985), the first vicariant event was the dichotomization of the common ancestors of species-group I (*L. kocai*) and species-groups II + III (all other species of *Laccornis*). The first major vicariant event within Laurasia was division into Euramerica and Asiamerica by the development of the Turgai Straits which existed from mid-Jurassic up to Oligocene times (Hallam 1981). This broad saltwater barrier would have been an effective isolating mechanism. The ancestral species to species-group I could have been isolated within western Asiamerica. If so it probably dispersed southeastward to its present range some time after regression of the Turgai Striats. Alternatively it may have remained in Euramerica but was disjunct from the common ancestor of species-groups II + III. Maps of continental land mass configuration of Jurassic and Late Cretaceous times provided by Noonan (1988:42) suggest that small isolated areas existed within the Turgai Straits and such areas may have provided a refuge for the ancestor of *L. kocai*. This vicariant event occurred in Early to Middle Cretaceous or prior to 100 million years before present.

An important element of this scenario is the phylogenetic position of *L. kocai* which is the sole member of species-group I. We interpret it as being a member of *Laccornis* and therefore of having diverged early in the history of *Laccornis*. If *L. kocai* represents an undescribed genus which is the sister group to *Laccornis* our scenario will remain accurate. However, if *L. kocai* is misplaced and it is not a close relative to *Laccornis* then our scenario would be misconstrued by virtue of polyphyly. It should be emphasized that there is only one relatively weak synapotypy linking *L. kocai* with the remainder of *Laccornis* and that the amount of structural divergence among it and members of species-groups II+III is considerable. However, until evidence from other sources (*e.g.*, immature stages) is presented to the contrary, *L. kocai* should be considered correctly assigned.

The common ancestor of species-groups II + III was probably a widespread species occurring at least in Euramerica but more likely it was distributed among eastern Asiamerica and Euramerica if these land masses were indeed continuous at high latitudes. The formation of the Mid-Continental Seaway through central North America led to the divergence of species-groups II + III. Species-group II was thus isolated in Asiamerica.

Our historical, zoogeographic hypothesis requires a vicariant zone across Beringia which isolated Eurasian populations (*L. oblongus*-complex) from the North American populations (*L. conoideus*-complex). Considering the amount of divergence between the members of these two complexes, we suspect that the vicariant event involved is relatively old.

Asiamerica was broadly connected by a Beringian land bridge from Cretaceous through Pliocene times (Matthews 1979). Several climatically induced filters to disperal across Beringia have been proposed that could have impeded faunal interchange; however, the evidence supporting their existence is equivocal (Matthews 1979). Matthews (1979) indicated that Beringia was maximally eroded in the early Oligocene and this may have provided a barrier to dispersal. However, it is certain that sometime between the late Miocene and early Pleistocene times, Beringia was breached and Siberia and Alaska were separated until the late Pliocene-Pleistocene.

We propose that the vicariant event which vicariated the two complexes of species-group II pre-dates the late Miocene-Pliocene inundations of Beringia and that it probably corresponds to the maximal reduction of the land bridge in the Oligocene which may have provided enough of a filter effect to allow divergence of Eurasian and North American populations. Kavanaugh (1986) proposed a similar (also somewhat vague by his own admission) vicariant event at Beringia at approximately the same time for members of *Amphizoa* LeConte (Coloptera: Amphizoidae).

Beginning in the late Miocene, mountain building and orogenic activity in northwestern North America was sufficient to cause divergence of floras on the eastern and western sides of the developing continental divide (J.A. Wolfe 1969). Kavanaugh (1986) and Perkins (1980) each have proposed this region as a vicariant zone for amphizoids and hydraenid water beetles respectively. We think that this uplift was the event that divided the range of the ancestor of the *L. conoideus*-complex and led to the divergence of *L. pacificus* and *L. conoideus*.

The distribution of the members of the eastern North American species-group III do not suggest distinct geographic areas or paleogeological events with vicariant attributes/effects. Species-group III is composed of three sets of species: *L. latens* -, *L. deltoides*- and *L. difformis*-complexes. Within the latter two complexes the taxa are quite similar. However, there has been significant structural divergence of the common ancestor of the *L. difformis*-complex from that of *L. latens*. Similarly the ancestor of this *L. deltoides*-complex is moderately distinct from that of the *L. latens* - + *L. difformis*-complexes.

The amount of structural divergence among the complexes of species-group III suggests an early divergence which is at least pre-Pleistocene. It has been demonstrated that divergence of eastern North American and European floras and faunas was accentuated during the Eocene. Perhaps the factors influencing the North American flora/fauna in general at that time affected the ancestors of the species-complexes of species-group III.

Perkins (1980) suggests a vicariant zone in eastern North America for hydraenids (his vicariance zone 6) that very approximately coincides with the distributions of the *L. latens* - and *L. difformis*-complexes. Perkins (1980) was unable to associate this vicariant zone with a paleogeological event; however, he did support its existence with distributional evidence of three synvicariads. He interpretted this vicariant event as occurring within the Pleistocene. We propose, as an alternative explanation, that if these-groups occupied a common area and were divided by a common event that it was pre-Pleistocene in age and probably Eocene as discussed above.

The members of the *L. difformis*- and *L. deltoides*-complexes are quite similar in structure. This suggests that divergence and speciation within these complexes were induced by Pleistocene glacial episodes.

Rate of speciation within Laccornis.— Askevold (1988) provided a cogent discussion of rates of speciation in certain groups of Chrysomelidae

(Coleoptera) based on phylogeny and zoogeography. This provides an intertesting analogy to the rate of speciation within *Laccornis*.

Overall, and assuming that *Laccornis* originated 100+ mybp and that it includes 10 extant species then the average rate of speciation for the genus is one extant species/10 my. This is within the range of 0.01 to 0.06 species/my of the groups examined by Askevold (1988). However, as pointed out by Whitehead (1972) and Askevold (1988) speciation rates so derived are not meant to be taken as constants, but rather as averages to allow comparisons of speciation rates among clades of equal age and of similar macrohabitats (*e.g.*, temperate lowlands).

Our zoogeographic/phylogenetic analysis indicates that rates of speciation within *Laccornis* is unequal (Fig. 19). For instance, our hypothesis suggests that the division of species-group I (one species) and species-groups II + III (nine species) occurred 70 mybp. Therefore, it is safe to assume that within this overall pattern of slow rates of speciation there have been times of relatively rapid diversification.

Evolution with respect to habitat.— Members of *Laccornis* have been collected from a variety of habitats in North America. In this section we use this information to generalize the preferred habitat of members of the genus *Laccornis* from a phylogenetic perspective.

In total, the habitat valence is quite broad. Specimens were collected from extensive sedge marshes (Alberta and Manitoba), extensive marshes and swamps (Ontario and Tennessee), small or medium sized temporary woodland pools (Ontario and Tennessee), permanent ponds with little shade (Yukon), and temporary ponds that are partially shaded in open fields (New Jersey and Tennessee). Also there are some few records of *Laccornis* from lotic habitats (*e.g.*, *L. conoideus* and *L. nemorosus*).

Despite this array of habitats, we believe that the members of *Laccornis* occur most often and most abundantly in temporary, vernal pools that are heavily shaded by forests. See Wiggins *et al* (1980) for a discussion of the features of this habitat. Within this broad category specimens of *Laccornis* are known from cooler pools with less daily temperature variation. Below we refer to temporary, vernal pools as the preferred habitat. Our conclusions on the preferred habitat are based on three lines of evidence: 1) most specimens were collected in this habitat, 2) collecting at more extensive habitats (*e.g.*, marshes, swamps and fens) has yielded more specimens from shaded, marginal areas that are isolated from the main body of water, and 3) within a single partially shaded pond, specimens are most abundant in areas with shade for the majority of the day. The occurrence of specimens in such habitats as streams probably indicates accidental occurrence; however in many low gradient streams subject to high water in the spring time, conditions in marginal pools could be appropriate. There are other features of this preferred habitat which may be important. One of these is that these habitats normally have very little vegetation. There is very little to no wave action within these pools and this may be important in that adults and larvae tend to crawl on the pool substrate rather than swimming actively.

These pools exist until mid-summer. The shallow and temporary or seasonally flooded habitats contain water for only a short time and food resources may be abundant for only a restricted period of time corresponding to larval development. Adults of *Laccornis* presumably aestivate in the substrate of the dry pond (*cf.* Leech 1940, Cuppen and Dettner 1987). Another aspect of these pools may be a reduction of predators such as fish (Wolfe 1985) and/or odonates.

When examining this analysis with respect to the reconstructed phylogeny (Fig. 19) two distinct trends are evident. Members of species-groups I + II + *L. latens* -complex, in general, are moss-associated species (tyrphophilic/ tyrphobiontic, Hebauer 1974) whereas the remaining members of species-group III are woodland pool specialists (acidophilic, Hebauer 1974). Tyrphophilic and tyrphobiontic species very often uses mosses such as *Sphagnum* or *Drepanocladus* as a substrate within which to crawl. Many other species of dytiscids also use this habitat type and therefore the number of co-occurring species may be quite high (*cf.* Larson 1987).

The members of species-group II use a wider variety of habitats and present the greatest known divergence from the narrow definition of preferred habitat given above (see Natural history for *L. oblongus*, *L. conoideus* and *L. pacificus*). The distribution of those three species generally is more northern than is that of other members of *Laccornis*. Interestingly, members of these species appear to occupy fewer kinds of habitats in the southern portion compared to those used in the more northern portions of their ranges.

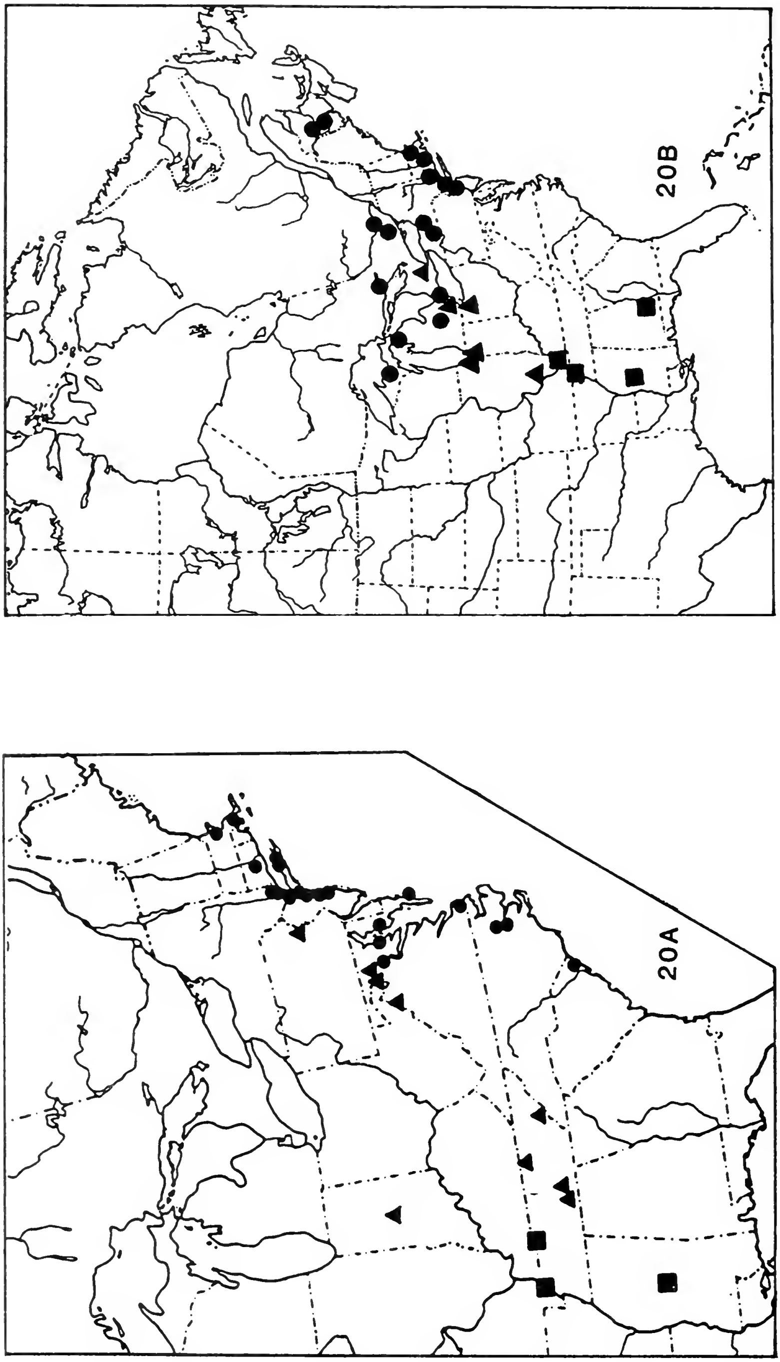
Members of the *L. difformis*- and *L. deltoides*-complexes of species-group III tend to prefer temporary woodland pools in which the substrate is composed of dead leaves from surrounding trees. Within the spectrum of this habitat type the members of these complexes occur at the more austere end of the range, based on our own field collections throughout eastern North America and in particular the southeastern United States. Such pools are without the diversity of niches and food resources associated with other habitat types. Diversity of species, including other groups of dytiscids, is very low. This may explain, in part, why so few specimens are known of many of the species within these complexes; the number of invertebrates collected per unit of effort is extremely low but such low return is often an indicator that it is a good pool for collecting specimens of *Laccornis*.

In summary, the three species-groups each prefer temporary pools and they are adapted to aquatic sites in which the water has cooler temperatures. An important question is whether or not the habitat and temperature preferences are positively correlated and follow the historical development of the genus. We believe that the preferred habitat referred to above has always represented the preferred habitat of members of *Laccornis* since the origin of the genus. The habit has existed continuously through time and there is no evidence to suggest that any other habitat was used by ancestral members of *Laccornis*.

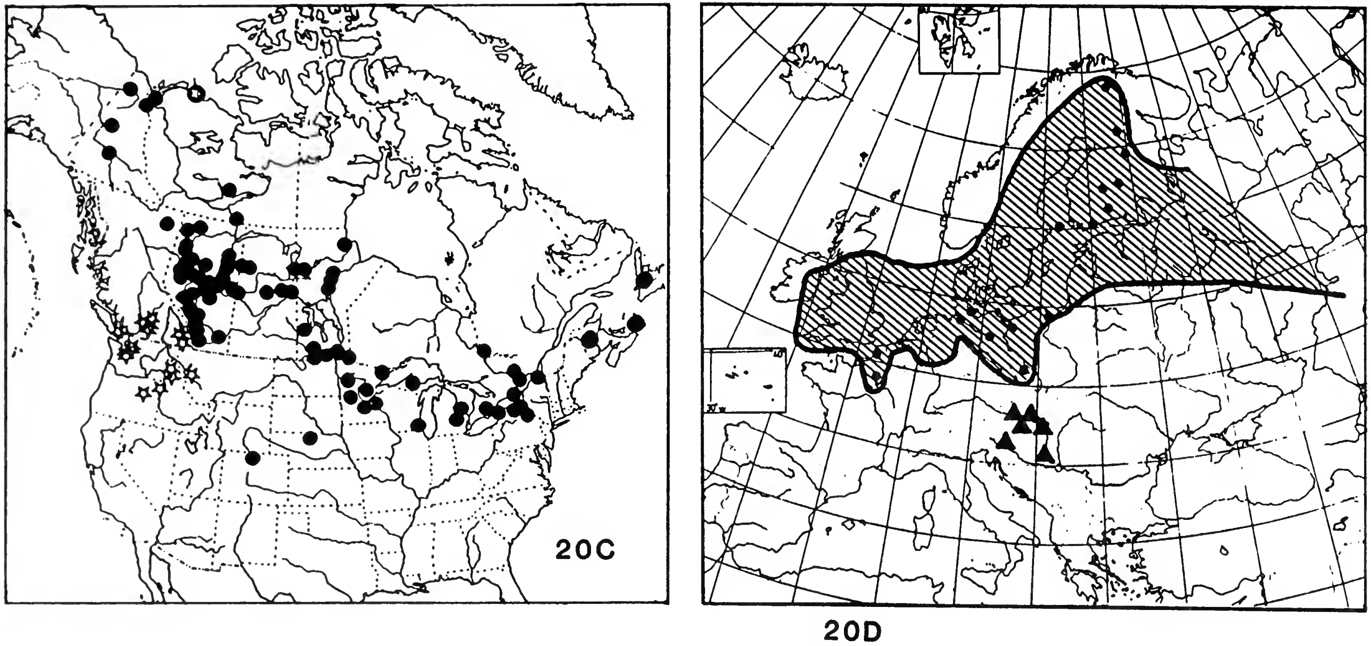
Adaptations to cooler temperatures are more difficult to analyze. There are two equally viable hypotheses. As we are unable to choose among these they are both presented below.

Hypothesis 1.— Adaptations to cooler temperatures occurred independently in each of the ancestors of species-groups I, II and III. Above we postulated that the genus *Laccornis* arose at least by the start of the Cretaceous.

This becomes important when we overlay global climate onto the cladogram. Warm temperate climates (analagous to modern climates) existed in the Northern Hemisphere since early Cretaceous which includes the time of origin of *Laccornis*. However, during the Eocene when the common ancestors of species-groups I to III were present there was a distinct, upward pulse of temperature; even climates at very high latitudes at this period were nearly tropical in nature (J.A. Wolfe 1969); however, small areas of cooler temperate habitats may have co-existed with the more warm termperate and subtropical biota and then become more widespread during Eocene/Oligocene cooling (Noonan 1986, 1988). Nevertheless, if the three lineages of *Laccornis* were



Figures 20A-B. Distribution maps of species of *Laccornis*. A) circles-*Laccornis difformis*, triangles- *L. etnieri*, squares-*L. schusteri*, B) circles-*L. latens*, triangles-*L. deltoides*, squares-*L. nemorosus*.



Figures 20C-D. Distribution maps of species of *Laccornis*. C) circles-*L. conoideus*, stars-*L. pacificus*, star in circles-*L. oblongus*, D) triangles-*L. kocai*, circles and cross-hatched area-*L. oblongus*.

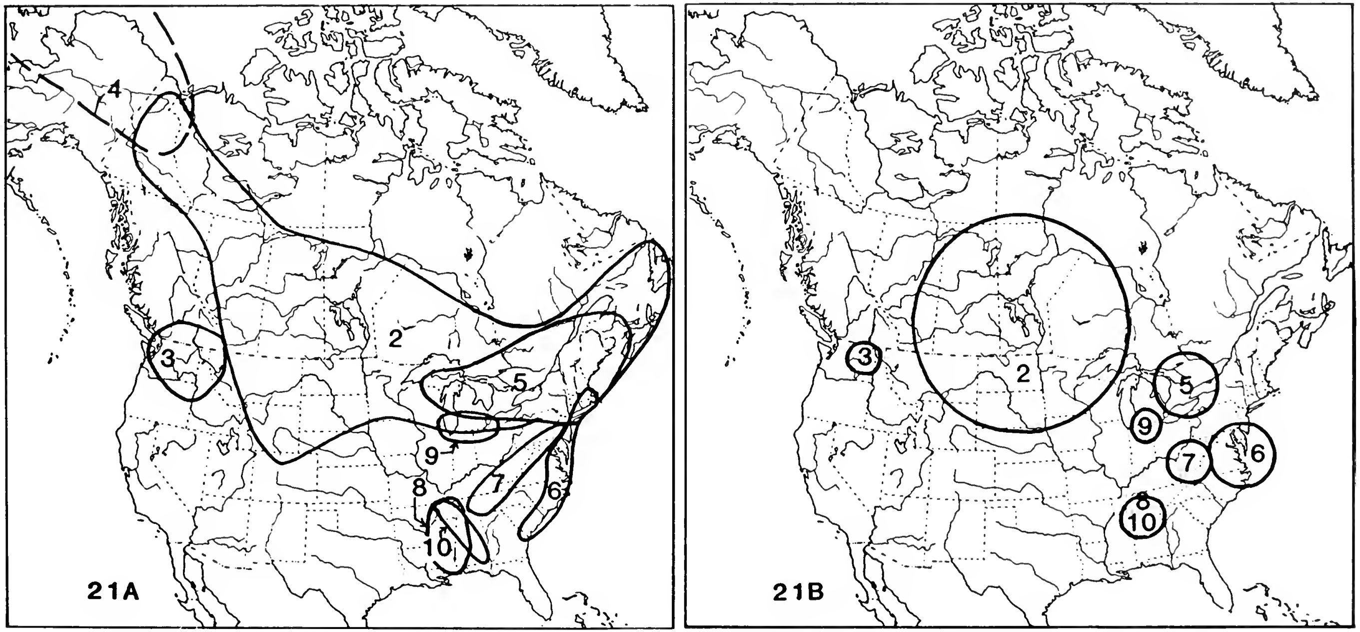
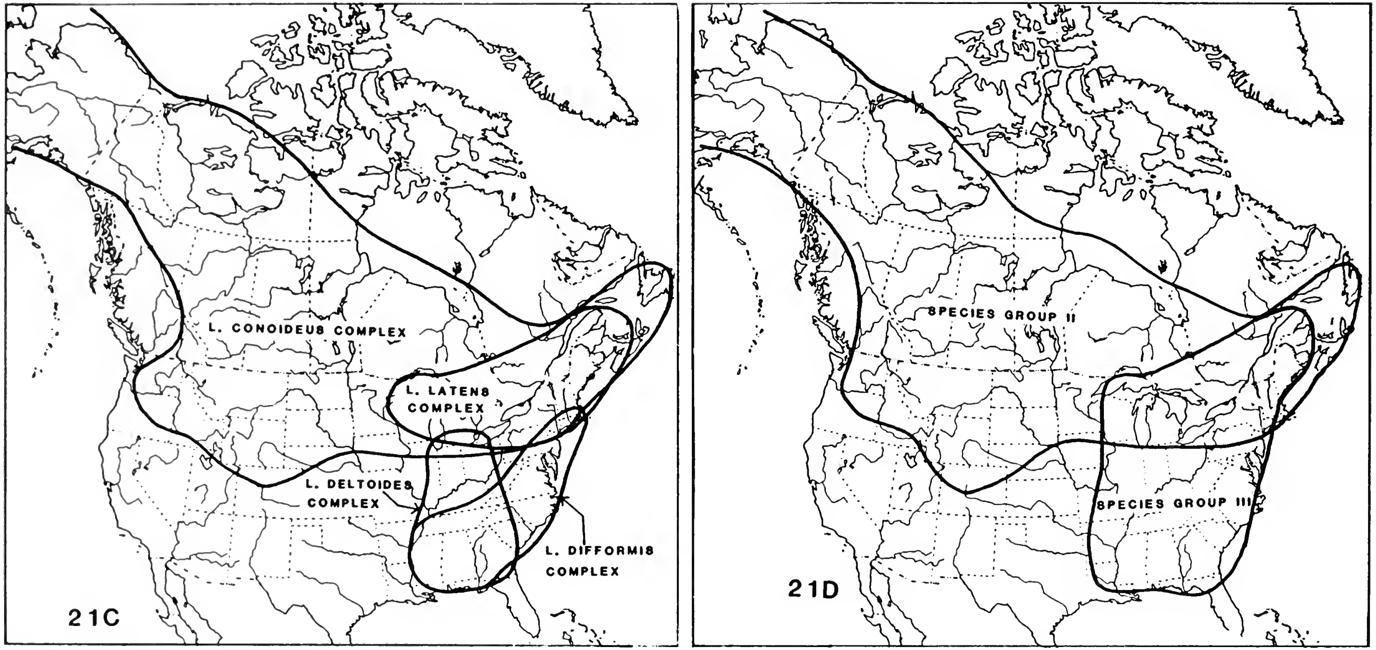


Figure 21A-B. Generalized distributional patterns. A) Generalized Nearctic distributions. Numbers coincide with species numbers within reconstructed phylogeny (Fig. 19); 2=*Laccornis conoideus*, 3=*L. pacificus*, 4=*L. oblongus*, 5=*L. latens*, 6=*L. difformis*, 7=*L. etnieri*, 8=*L. schusteri*, 9=*L. deltoides*, 10=*L. nemorosus*. B) Species ranges scaled down to demonstrate centers of endemism.



Figures 21C-D. Generalized distributional patterns. C) Generalized distribution of species-complex eswithin *Laccornis*, D) Generalized distribution of species-groups within *Laccornis*.

adapted to cooler habitats since the early Cretaceous it is difficult to explain how such a grographically widespread group could have survived. In this hypothesis, then the cool temperature adaptations would have occurred after climates returned to a more temperate regime.

Hypothesis 2.— Adaptations to cooler temperatures are a ground plan feature of *Laccornis*. This hypothesis is similar to the above except that it assumes that preference for cooler water habitats has always been a feature of *Laccornis* since the origin of the genus. This requires that the lineages became widespread during the Cretaceous in part because they were well adapted to the temperate environment. The diversification which occurred in the Cenozoic could be a direct result of the warming that occurred during the Eocene. The geographical ranges of the formerly widespread ancestral lineages would have been disrupted by the warming trend. During this period, isolated populations of the ancestors could have survived (and diverged) within isolated refugia in which cooler temperatures prevailed.

A clear choice between these two hypotheses cannot be made on available evidence. Nevertheless, it is interesting to note that speciation in *Laccornis*, in the phylogeny that we propose (Fig. 19), increased markedly after the post-Eocene cooling trend which resulted once again in more widespread temperate conditions.

ACKNOWLEDGEMENTS

G. W. Wolfe's participation in this research and/or publication was supported by the University of Tennessee, Smithsonian Institute (National Museum of Natural History), Rutgers University (Experiment Station Project 08412), and Reinhardt College. R. E. Roughley's participation was supported by NSERC, Canada Grant #A0428. We are grateful to Ms. D. Ducceschi and Ms. C. Bevere (Rutgers) and Ms. G. Léger (U. of Manitoba) for the endless hours they spent helping to prepare this manuscript. Mr. D. Holder of the Dept. of Entomology, Univ. of Manitoba helped prepare the final plates for this publication. D. Pollock (Edmonton) carefully read a previous version of this manuscript and assisted with compilation of the references cited. Their assistance was greatly appreciated. We thank Drs. P. Perkins (Boston), A. Smetana (Ottawa), D. Larson (St. John's), A. Nilsson (Umeå), R.G.Beutel (Aachen) and G. Wewalka (Vienna) for insightful comments and other kindnesses which substantially improved this publication. Any errors, omissions or misinterpretations of their advice are the responsibility of the authors.

REFERENCES CITED

Alarie, Y. 1989. The larvae of *Laccornis* Des Gozis 1914 (Coleoptera: Adephaga: Dytiscidae) with description of *L. latens* (Fall 1937) and redescription of *L. conoideus* (LeConte 1850). The Coleopterists Bulletin, 43: 365-378.

Allen, R.T. 1983. Distributional pattern among arthropods of the North Temperate deciduous forest biota. Annals of the Missouri Botanical Garden, 70: 616-628.

Arnett, R.H., Jr. 1960-1962. The beetles of the United States. (A manual for identification). Catholic University of America Press, Washington, D.C. xi + 1112 pp. [Pp. xii + 1-120 (1960), pp. 369-1112 (1962)].

Askevold, I.S. 1988. The genus *Neohaemonia* Székessy in North America (Coleoptera: Chrysomelidae: Donaciinae): Systematics, reconstructed phylogeny, and geographic history. Transactions of the American Entomological Society, 113: 360-430.

Balfour-Browne, F. 1934. Systematic notes upon British aquatic Coleoptera. Part V. *Hydroporus (Suphrodytes, Scarodytes* and *Hydroporus* s.str.) and *Laccornis*. The Entomologist's Monthly Magazine, 70: 224-230.

Balfour-Browne, F. 1938. Systematic notes upon British aquatic Coleoptera, being a corrected and revised edition of a series of papers which appeared in the "Entomologists' Monthly Magazine" from 1934 to 1936. Volume 1. Hydradephaga. Nathaniel Lloyd and Co., Ltd., London. 95 pp.

Balfour-Browne, F. 1940a. British Water Beetles. Volume I. The Ray Society, London, 375 pp.

Balfour-Browne, F. 1940b. Part 7. The generic names of the British Hydradephaga, with a check list of the British species, pp. 195-209. *In*, The generic names of British insects, prepared by the Committee on generic nomenclature of the Royal Entomological Society of London with the assistance of the Department of Entomology of the British Museum (Natural History). Royal Entomological Society of London, London.

Balfour-Browne, F. 1953. Volume IV (3). Coleoptera:Hydradephaga. Handbooks for the identification of British insects. Royal Entomological Society of London. 33 pp.

Balfour-Browne, F. 1960. The aquatic Coleoptera of Scotland and their routes of arrival. The Entomolgist's Gazette, 11: 69-106.

Borchert, W. 1938. Die Verbreitung der Käfer Deutschlands. Tatsachen und Folgerungen. Privately printed by author. 137 + 9 pp. + 94 maps.

Brigham, W.U. 1982. Aquatic Coleoptera, pp. 10.1-10.136. *In*, Brigham, A.R., W.U. Brigham and A. Gnilka, Editors. Aquatic insects and oligochaetes of North and South Carolina. Midwest Aquatic Enterprises, Mahomet, Illinois. 837 pp.

Burmeister, E.-G. 1976. Der Ovipositor der Hydradephaga (Coleoptera) und seine phylogenetische Bedeutung unter besonderer Berückischtigung der Dytiscidae. Zoomorphologie, 85: 165-257.

Coope, G.R. 1979. Late Cenozoic fossil Coleoptera, evolution, biogeography and ecology. Annual Review of Ecology and Systematics, 10: 247-267.

Crotch, G.R. 1873. Revision of the Dytiscidae of the United States. Transactions of the American Entomological Society, 4: 383-424.

Csiki, E. 1946. Die Käferfauna des Karpaten-Beckens. I. Band. Allgemeiner Teil und Caraboidea. Naturwissenschaftliche Monographien IV. Tasnádi Kubacska Andras, Budapest. 798 pp.

Cuppen, J.G.M. and K. Dettner. 1987. The larvae of the predaceous water beetle *Laccornis oblongus* (Stephens) (Coleoptera: Dytiscidae), with notes on ecology and distribution. Aquatic Insects, 9: 211-220.

Erwin, T.L. 1970. A reclassification of Bombardier beetles and a taxonomic revision of the North and Middle American species (Carabidae: Brachinida). *Quaestiones Entomologicae*, 6: 4-215.

Erwin, T.L. 1982. *Agra*, arboreal beetles of Neotropical forests: *erythropus* group systematics (Carabidae). Systematic Entomology, 7: 39-71.

Fall, H.C. 1923. A revision of the North American species of *Hydroporous* and *Agaporous*. J.D. Sherman, Jr., Mt. Vernon, N.Y. 129 pp.

Fall, H.C. 1937. A new *Agaporus* (Dytiscidae - Coleoptera). Entomological News, 48: 10-12.

Folkerts, G.W. 1978. A preliminary checklist of the Hydradephaga (Coleoptera) of Alabama. The Coleopterists Bulletin, 32: 345-347.

Folkerts, G.W. and L.A. Donavan. 1974. Notes on the ranges and habitats of some little-known aquatic beetles of the southeastern U.S. (Coleoptera:Gyrinidae, Dytiscidae). The Coleopterists Bulletin, 28: 203-208.

Ganglbauer, C.L. 1906. Neue Arten aus den Gattungen *Tregus* (*Anophthalmus*), *Hydroporus* und *Riolus*. Münchener Koleopterologische Zeitschrift, 2: 350-354.

Geiser, R. 1978. Der erste Massenfund von *Laccornis kocai* (Gglb.). Nachrichtenblatt der Bayerischen Entomologen, 27: 126-129.

Gozis, M. des. 1914a. Tableaux de détermination des Dytiscides, Notérides, Hyphydrides, Hygrobiides, et Haliplides de la faune Franco-rhénane. Miscellanea entomologica, 21 (1913): 97-112.

Gozis, M. des. 1914b. *Ibid.* Miscellanea entomologica, 22: 113-208.

Gschwendtner, L. 1935. Zwei neue europäische Schwimmkäfer. Entomologische Anzeiger, 15: 205-207.

Gschwendtner, L. 1939. Monographie der paläarktischen Dytisciden. X. Ergänzungen und Register. Koleopterologische Rundschau 25: 23-69. [Also reprinted in Reitter, Edm. Editor. Bestimmungs-Tabellen der europäischen Coleopteren. Heft 122. 47 pp. Verlag Edm. Reitter. Troppau].

Guignot, F. 1931-1933. Les Hydrocanthares de France. Hygrobiidae, Haliplidae, Dytiscidae et Gyrinidae de la France contientale avec notes sur les especes de la Corse et de l'Afrigue du Nord francaise. Douladoure, Toulouse. xv + 1057 pp. + planches I-VII. [pp. 1-188 (1931), pp. 189-786 (1932), pp. 787-1057 (1933)].

Guignot, F. 1947. Coléoptères Hydrocanthares. Faune de France 48: 1-287. Lechevalier, Paris.

Guignot, F. 1955. Nouveaux Dytiscides et Gyrinides du Congo Belge et de Madagascar. Revue de Zoologie et de Botanique Africaines, 51: 190-196.

Hallam, A. 1981. Relative importance of plate movements, eustasy, and climate in controlling major biogeographical changes since the early Mesozoic, pp. 303-330. *In,* Nelson G. and D. E. Rosen. Editors. Vicariance Biogeography: a critique. Columbia University Press, New York. xvi + 593 pp.

Hamilton, J. 1894a. Catalogue of the Coleoptera of Alaska, with the synonymy and distribution. Transactions of the American Entomological Society, 21: 1-38.

Hamilton, J. 1894b. Catalogue of the Coleoptera common to North America, northern Asia and Europe, with distribution and bibliography. Second edition. Transactions of the American Entomological Society, 21: 345-416.

Hamilton, J. 1889. Catalogue of the Coleoptera common to North America, northern Asia and Europe, with the distribution and bibliography. Transactions of the American Entomological Society, 16: 88-162.

Hatch, M.H. 1953. The beetles of the Pacific Northwest. Part 1. Introduction and Adephaga. University of Washington Publications in Biology 16: fp + 1-340.

Hebauer, F. 1974. Über die ökologische Nomenklatur wasserbewohnender Käferarten (Coleoptera). Nachrichtenblatt der Bayerischen Entomologen, 23: 87-92.

Houlbert, C. 1934. Faune entomologique Armoricaine. Coléoptères, Hydrocarabiques (Hydaticidormes). Bulletin de la Société scientifique de Bretagne, 11: 1-147.

Humphries, C.J. and L.R. Parenti. 1987. Cladistic Biogeography. Oxford Monographs on Biogeography 2: xii + 1-98. Clarendon Press, London.

ICZN. 1985. International Code of Zoological Nomenclature. Third Edition. British Museum (Natural History), London. xx + 338 pp.

Kavanaugh, D.H. 1972. Hennig's principles and methods of phylogenetic systematics. The Biologist, 54: 115-127.

Kavanaugh, D.H. 1978. Hennigian phylogenetics in contemporary systematics: principles, methods and uses, pp. 139-150. *In,* Beltsville symposia in agricultural research, 2. Biosystematics in Agriculture. Romberger, J. A., R. H. Foote, L. Knutson and P. L. Lentz. Editors. Allenheld, Osmun and Company, Montclair, New Jersey. xii + 340 pp.

Kavanaugh, D.H. 1979. Rates of taxonomically significant differentiation in relation to geographical isolation and habitat: examples from a study of the Nearctic *Nebria* fauna, pp. 35-57. *In,* Erwin, T.L., G. E. Ball, D. R. Whitehead and A.L. Halpern. Editors. Carabid beetles: their evolution, natural history and classification. W. Junk b.v. Publishers, The Hague. x + 635 pp.

Kavanaugh, D. H. 1980. Insects of western Canada, with special reference to certain Carabidae (Coleoptera): present distribution patterns and their origin. The Canadian Entomologist, 112: 1129-1144.

Kavanaugh, D. H. 1986. A systematic review of amphizoid beetles (Amphizoidae: Coleoptera) and their phylogenetic relationships to other Adephaga. Proceedings of the California Academy of Science, 44: 67-109.

Koskinen, A. 1960. Faunistische-ökologische studien uber die Wasserk fer von Saarijärvi (PH), Mittelfinnland. Annales entomologici Fennici, 26: 173-191.

Larson, D.J. 1975. The predaceous water beetles (Coleoptera: Dytiscidae) of Alberta: systematics, natural history and distribution. *Quaestiones Entomologicae*, 11: 245-498.

Larson, D.J. 1987. Aquatic Coleoptera of peatlands and marshes in Canada. Memoirs of the Entomological Society of Canada, 140: 99-132.

LeConte, J.L. 1850. General remarks upon the Coleoptera of Lake Superior, pp. 201-242. *In,* Agassiz, J.L.R. Lake Superior: Its physical character, vegetation and animals compared with those of other and similar regions, with a narrative of the tour by J. Elliot Cabot, and contributions by other scientific gentlemen. Gould, Kendall and Lincoln, Boston x + 248 pp. + plates 1-8 + 8 unnumbered landscapes.

LeConte, J.L. 1855. Analytical table of the species of *Hydroporus* found in the United States, with descriptions of new species. Proceedings of the Academy of Natural Sciences of Philadelphia, 7: 290-299.

Leech, H.B. 1940. Description of a new species of *Laccornis* with a key to the Nearctic species (Coleoptera, Dytiscidae). The Canadian Entomologist, 72: 122-128.

Leech, H.B. 1941. Collecting of the rare water beetle *Laccornis difformis* (Lec.) by the late Ch. Roberts. The Canadian Entomologist, 73: 96.

Leech, H.B., and H.P. Chandler. 1956. Aquatic Coleoptera, pp. 293-371. *In,* Usinger, R.L. Editor. Aquatic insects of California with keys to North American genera and California species. University of California Press. Berkeley and Los Angeles. ix + 508 pp.

Leech, H.B. and M.W. Sanderson. 1959. Coleoptera, pp. 98-1023. *In*, Edmondson, W.T. Editor. Fresh-water Biology. Second Edition. John Wiley & Sons, New York and London. xx + 1248 pp.

Lindroth, C.H., V. Hansen, E. Klefbeck, O. Sjöberg, G. Stenius and A. Strand. 1960. Catalogus Coleopterorum Fennoscandiae et Daniae. Entomologiska Sällskapet, Lund. 478 pp. + map.

Malcolm, S.E. 1971. The water beetles of Maine: including the families Gyrinidae, Haliplidae, Dytiscidae, Noteridae, and Hydrophilidae. University of Maine, Technical Bulletin, 48: 1-49.

Matthews, J. V. 1977. Tertiary Coleoptera fossils from North American Arctic. The Coleopterists Bulletin, 31: 297-308.

Matthews, J. V. 1979. Tertiary and Quaternary environments: historical background for an analysis of the Canadian insect fauna. Memoirs of the Entomological Society of Canada, 108: 31-86.

Nelson, G. and N. Platnick. 1981. Systematics and Biogeography. Cladistics and Vicariance. Columbia University Press, New York. xi + 567 pp.

Nilsson, A.N. 1983. A mapping of the diving, predaceous water beetles (Coleoptera: Noteridae & Dytiscidae) of northern Sweden. Fauna Norrlandica, 5: 1-43.

Noonan, G.R. 1986. Distribution of insects in the Northern Hemisphere: Continental drift and epicontinental seas. Bulletin of the Entomological Society of America, 32: 80-84.

Noonan, G.R. 1988. Faunal relationships between eastern North America and Europe, as shown by insects. Memoirs of the Entomological Society of Canada, 144: 39-53.

Pennak, R.W. 1953. Fresh-water invertebrates of the United States. Ronald Press, New York. ix + 769 pp.

Perkins, P. D. 1980. Aquatic beetles of the family Hydraenidae in the western hemisphere: classification, biogeography, and inferred phylogeny (Insect: Coleoptera). *Quaestiones Entomologicae*, 16: 3-554.

Platnick, N. I. 1976. Drifting spiders or continents? Vicariance biogeography of the spider subfamily Laroniinae (Araneae: Gnaphosidae). Systematic Zoology, 25: 101-109.

Poppius, B. 1905. Beiträge zur Kenntniss der Coleopteren-Fauna des Lena-Thales in Ost-Sibirien. I. Haliplidae und Dytiscidae. Finska Vetenskaps-Societetens Förhandlingar, 47 (#16): 1-24.

Rosen, D.E. 1978. Vicariant patterns and historical explanatin in biogeography. Systematic Zoology, 27: 159-188.

Ross, H.H. 1974. Biological Systematics. Addison-Wesley, Reading, Massachusetts. [5] + 346 pp.

Roughley, R.E. and D.H. Pengelly. 1982. Classification, phylogeny and zoogeography of *Hydaticus* Leach (Coleoptera:Dytiscidae) of North America. *Quaestiones Entomologicae*, 17 (1981): 249-309.

Roughley, R.E. and G.W. Wolfe. 1987. *Laccornellus* (Coleoptera:Dytiscidae), a new hydroporine genus from austral South America. Canadian Journal of Zoology, 65: 1346-1353.

Ruette, R. de. 1970. A catalogue of types of Coleoptera in the Canadian National Collection of Insects. Memoirs of the Entomological Society of Canada, 72: 1-134.

Schaeflein, H. 1969. Nach mehr als 30 Jahren wiedergefunden: (*Laccornis breviusculus* Gschwendtner). Entomologische Blätter für Biologie und Systematik der Käfer, 65:118.

Schaeflein, H. 1970. *Laccornis breviusculus* Gschw. identisch mit *Graptodytes kocae* Gglb. Nachrichtenblatt der Bayerischen Entomologen, 19: 89.

Schaeflein, H. 1971. Familie: Dytiscidae, echte Schwimmkäfer, pp. 16-89 + table. *In,* Freude, H., W. Harde, and G.A. Lohse. Editors. Die Käfer Mitteleuropas. Band 3. Goecke & Evers Verlag, Krefeld. 365 pp + table.

Schaeflein, H. 1979. Beitrag zur Dytisciden fauna Mitteleuropas (Gol.), nebst einigen ökologischen Miszellen. Stuttgarter Beiträge zur Naturkunde, Serie A (Biologie), 325: 1-20.

Schaeflein, H. 1983. Zweiter Beitrag zur Dytiscidenfauna Mitteleuropas (Coleoptera) mit faunistisch-ökologischen Betrachtungen. Stuttgarter Beiträge zur Naturkunde, Serie A (Biologie), 361: 1-41.

Sharp, D. 1882. On aquatic carnivorous Coleoptera or Dytiscidae. The Scientific Transactions of Royal Dublin Society 2 (New Series) Part II: 179-1003 + plates vii-xviii.

Spangler, P.J. and R.D. Gordon. 1973. Description of the larvae of some predaceous water beetles (Coleoptera:Dytiscidae). Proceedings of the biological Society of Washington, 86: 261-278.

Stephens, J.F. 1828-1829. Illustrations of British Entomology; or, a synopsis of indigenous insects; containing their generic and specific distinctions; with an account of their metamorphoses, times of appearance, localities, food, and economy, as far as practicable. Mandibulata. Volume II. 200 pp. + plates I-XV. Baldwin and Craddock, London. [Pp. 1-112 + plates X-XIV (1828), pp. 113-200 + plates I-IX, XV (1929)].

Stephens, J.F. 1832-1835, *Ibid.* Volume V. 447 pp. + plates XXIV-XXVII. [Pp. 1-240 + plates XXIV-XXVI (1832), pp. 241-304 + plate XXVII (1834), pp. 369-447 (1835).

Sturm, J. 1835. Deutschlands Fauna in Abbildungen nach der Natur mit Beschreibungen. Abtheilung V. Die Insecten. Band 9. Vorwort und Nachtrag zu Band 8. xxii + 1-120 incl. Register + Tafeln 203-216.

Swofford, D.L. PAUP. Phylogenetic Analysis Using Parsimony. Version 2.4. Privately produced computer program.

Thomson, C.G. 1856. Ofversigt of de arter inom Dytisci, som blifvit anträffade på Skandinaviska halfön. Kongliga Svenska Vetenskaps-Akademien Förhandlinger, 1854: 177-237.

Wallis, J.B. and D.J. Larson. 1973. An annotated list of the Hydroadephaga (Coleoptera: Insecta) of Manitoba and Minnesota. Quaestiones entomologicae 9: 99-114.

Watts, C.H.S. 1970. The larvae of some Dytiscidae (Coleoptera) from Delta, Manitoba. The Canadian Entomologist, 102: 716-728.

Wewalka, G. 1969. Beitrag zur Kenntnis der Dytiscidae (Col.): *Laccornis breviusculus* Gschwendtner 1935 synonym mit *Laccornis kocae* Ganglbauer 1906. Zeitschrift der Arbeitsgememeinschaft österreichischer Entomologen, 21: 46-50.

Wewalka, G. 1981. Die Arten der Gattung *Canthyporus* Zimmermann aus Zentral-Afrika mit beschreibung einer neuen Art (Dytiscidae, Col.). Koleopterologische Rundschau, 55: 57-64.

White, D.S., W.U. Brigham and J.T. Doyen. 1984. Chapter 19. Aquatic Coleoptera, pp. 361-437. *In,* Merritt, R.W. and K.W. Cummins. Editors. An introduction to the aquatic insects of North America. Second Edition. Kendall/Hunt, Dubuque, Iowa. xiii + 722 pp.

Whitehead, D.R. 1972. Classification, phylogeny, and zoogeography of *Schizogenius* Putzeys (Colelptera: Carabidae:Scaritini:). *Quaestiones Entomologicae*, 8: 131-348.

Wickham, H.F. 1895. The Coleoptera of Canada. Part VIII. The Haliplidae and Dytiscidae of Ontario and Quebec. The Canadian Entomologist, 27: 69-76.

Wiggins, G.B., R.J. Mackay and I.M. Smith. 1980. Evolutionary and ecological strategies of animals in annual temporary pools. Archiv für Hydrobiologie, Supplementum 58: 97-206.

Wiley, E.O. 1981. Phylogenetics. The theory and practice of phylogenetic systematics. John Wiley & Sons, New York. xv + 439 pp.

Wolfe, G. W. 1984. A revision of the *vittatipennis* species group of *Hydroporus* Clairville, subgenus *Neoporus* Guignot (Coleoptera: Dytiscidae). Transactions of the American entomological Society, 110: 389-433.

Wolfe, G. W. 1985. A phylogenetic analysis of plesiotypic hydroporine lineages with an emphasis on *Laccornis* Des Gozis (Coleoptera: Dytiscidae). Proceedings of the Academy of natural Sciences of Philadelphia, 137: 132-155.

Wolfe, G.W. 1989. A phylogenetic investigation of *Hydrovatus*, Methlini and other plesiotypic hydroporines (Coleoptera: Dytiscidae). Psyche, 95 (1988): 327-426.

Wolfe, G. W. and P.J. Spangler. 1985. A synopsis of the *Laccornis difformis* species group with a revised key to North American species of *Laccornis* Des Gozis (Coleoptera: Dytiscidae). Proceedings of the Biological Society of Washington, 98: 61-71.

Wolfe, G.W. and J.R. Zimmerman. 1984. Sensilla, punctation, reticulation, and body shape in the Hydroporinae (Coleoptera:Dytiscidae). International Journal of Insect Morphology and Embryology, 13: 373-387.

Wolfe, J. A. 1969. Neogene floristic and vegetational history of the Pacific Northwest. Madroño, 20: 83-110.

Zaitsev, F.A. 1953. Fauna of the U.S.S.R. Coleoptera, Volume IV. Amphizoidae, Hygrobiidae, Haliplidae, Dytiscidae, Gyrinidae. **xxx** pp. English Translation by Israel Program for Scientific Translation, Jerusalem (1972).

Zimmermann, A. 1919. Die Schwimmkäfer des Deutschen entomologischen Museums in Berlin-Dahlem. Archiv für Naturgeschichte, (1917) 83: 68-249 + Tafeln I-II.

Zimmermann, A. 1920. Pars 71: Dytiscidae, Haliplidae, Hygrobiidae, Amphizoidae. 326 pp. *In*, Junk, W. and S. Schenkling. Editors. Coleopterorum Catalogus. Volumen IV. W. Junk, Berlin and s'Gravenhage.

Zimmermann, A. 1930. Monographie der paläarktischen Dytisciden. I. Noterinae, Laccophilinae, Hydroporinae (1. Teil). Koleopterologische Rundschau, 16: 35-118. [Reprinted in Reitter, Edm. Editor. Bestimmungs-Tabellen der europäischen Coleopteren. Edm. Reitter Verlag, Troppau. Heft 99. 86 pp. (1930).

Zimmermann, A. 1932. Monographie der paläarktischen Dytisciden. III. Hydroporinae (3. Teil). Koleopterologische Rundschau, 18:69-111. [Reprinted in Reitter, Edm. Bestimmungs-Tabellen der europäschen Coleopteren. Edm. Reitter Verlag, Troppau. Heft 103. 43 pp.].

Zimmermann, A. 1933. Monographie der paläarktischen Dytisciden IV. Hydroporinae (4. Teil). Koleopterologische Rundschau 19: 153-193.

[Reprinted in Reitter, Edm. Bestimmungs-tabellen der europäischer Coleopteren. Heft 111. 41 pp. Edm. Reitter Verlag, Troppau.]

INDEX TO NAMES OF TAXA
(Junior synonyms in italics)

A REVIEW OF CLASSIFICATION OF THE WATER BEETLES OF THE NEW WORLD GENUS *BIDESSONOTUS* RÉGIMBART (COLEOPTERA: DYTISCIDAE: HYDROPORINAE: BIDESSINI)

F.N. Young
Department of Biology
Indiana University
Bloomington, Indiana
USA 47405

Quaestiones Entomologicae
26: 355–381 1990

ABSTRACT

Classification of species of water beetles of the New World genus Bidessonotus *Régimbart (Coleoptera: Dytiscidae) is reviewed with illustrations to aid in their determination. New species are described from the following localities:* B. dubius *(Cayenne, Brasil, Suriname, Venezuela)*, B. inigmaticus *(Mexico)*, B. pollostus *(Honduras)*, B. otrerus *(Colombia, Venezuela)*, B. paludicolus *(Costa Rica, Mexico, Venezuela)*, B. pictus *(Costa Rica)*, B. ploterus *(Brasil)*, B. rhampherens *(Mexico)*, B. rubellus *(Panama-Canal Zone, Panama, Venezuela)*.

INTRODUCTION

The genus *Bidessonotus* Régimbart is composed of a number of small water beetles (Coleoptera: Dytiscidae) whose composite range is from Paraguay to Canada. Total length of adult specimens if from about 1.3 to 2.6 mm; maximum width is from about 0.64 to 1.1 mm near middle of elytra. Members of *Bidessonotus* are recognized readily by the common presence of a transverse cervical stria just behind the eyes, impressed pronotal and elytral plicae, thickened but unmargined clypeus, clearly 5-segmented anterior tarsi although protarsomere 4 is short, and by strong dimorphism of males and females. The females are often rather stoutly oval with the elytra showing a purple iridescence; males have the metasternum and inner coxal laminae curved and the middle tibiae curved to varying degrees, evidently as adaptations for grasping the female during copulation.

STRUCTURAL FEATURES

Most of the species of *Bidessonotus* resemble each other closely in size, shape, and vestiture, but the males show great variation in the structure of the external genitalia. The aedeagus (median lobe) resembles a leg with heeled shoe in lateral profile. The parameres are also complex and usually differ on either side. In distinction among species most reliance is placed on the differences in the male external genitalia especially in the lateral outline of the aedeagus. Females may be unidentifiable if not associated with males.

Other characters which differ among species but may be hard to assess are as follows: *Head* with *transverse fronto-clypeal sulcus or impressions* which extend inward from either side and may meet at the middle with various forms of punctation and microsculpture. *Frontal impressions* on either side above the insertions of the antennae may differ in depth or coarseness of the rows of punctures in them. *Microsculpture* present but usually not conspicuous except in females in which the elytra may appear purplish iridescent. *Pronotum* with punctation various on the disk and especially between the basal pronotal plicae. *Basal plicae on pronotum* are usually about 1/2 the length of pronotum at midline and may be curved or nearly straight. *Pronotal microsculpture* is usually inconspicuous as on the head. *Elytra* vary in degree of punctation of disk and degree of impression of the microsculpture. On female specimens *microsculpture* is always more evident, and on some specimens it results in a distinctly purplish iridescent lustre. The *basal elytral plicae* of most specimens are detectably longer, rarely shorter, than the pronotal plicae and on most specimens they are nearly straight and slanting inward on the disk or parallel with suture. A *preapical elytral tooth* is present in females of several species. On some female specimens it is conspicuous, but the development of the tooth seems too variable to be a reliable taxonomic character. The *venter* may be more darkly colored in some species than in others, but the metacoxal laminae of the majority of specimens are distinctly and very coarsely setate-punctate at middle and with roughened areas approximately where the middle and hind femora may overlap. It is possible that these are stridulatory devices. *Prosternal process* of most specimens is lanceolate toward the tip or process and with a longitudinal sulcus down the middle; members of certrain species lack a medial longitudinal sulcus or it is indistinct. *Last visible sternite* transversely or otherwise impressed and that of most specimens with coarser setate punctures and rough sculpture toward apex. *Mesofemur* of some males modified. *Mesotibia* of most males is curved to some degree.

The structure of the anterior and middle tarsi with the 4th segment reduced but not hidden in the lobes of the 3rd, suggests that *Bidessonotus* is primitive in relation to remainder of Bidessini. However, the structure of the male external genitalia with jointed or segmented parameres (lateral lobes), and the presence of pronotal and basal elytral plicae are feature typical of Bidessini (Biström 1988, Young 1967). I consider *Bidessonotus* to be an ancient and specialized group possibly related to some of the Australian bidessines which would suggest a Gondwanian origin (Young, 1967).

NATURAL HISTORY

The species of *Bidessonotus* are found in a wide variety of natural habitats, but their preferred conditions are usually associated with heavy organic debris in the water. In the southeastern United States, the three species (*B. pulicarius*, *B. longovalis*, and *B. inconspicuus*) are usually found in small pools or the edges of slow streams with considerable vegetation and debris in the water. In South America the species are most abundant in the Hylaen Forest of the Amazon-Orinoco Basin and extend southward into Paraguay and the Argentina. All the species come readily to ultra-violet light, but less abundantly to ordinary white light traps.

MATERIAL

The specimens examined were borrowed from the following museums.

BMNH	British Museum (Natural History), London, United Kingdom.
CASC	California Academy of Sciences, San Francisco, California, USA.
CNC	Canadian National Collection, Ottawa, Ontario, Canada.
FSCA	Florida State Collection of Arthropods, Gainesville, Florida, U.S.A.

MCZ	Museum of Comparative Zoology, Cambridge, Mass., U.S.A.
NMNH	United States National Museum of Natural History, Washington, D.C., U.S.A.
MNHN	Musée National d'Histoire Naturelle, Paris, France.
UMMZ	University of Michigan Museum of Zoology, Ann Arbor, Michigan, U.S.A.

CLASSIFICATION

Bidessonotus tibialis Régimbart

Bidessonotus tibialis Régimbart 1985: 337 (Brasil: Mato Grosso, P. Germain, 1886).

Diagnosis.— Specimens are similar to those of *B. pulicarius* but average smaller in size and they possess distinctive external male genitalia (Fig. 1). Fronto-clypeal sulcus narrowly interrupted at middle. Apex of prosternal process lanceolate and narrowly sulcate. Most females with elytra not purplish iridescent. Color pattern seldom evident, usually eliminated by melanization of elytra; if detectible composed of usual lateral dark spots and lighter areas, and two irregular elongate spots or an irregular stripe on disk. Antennae longer and more slender in male than in female, about as in specimens of *B. pulicarius*.

Male.— *Head* finely, sparsely punctate more coarsely so basally. Microsculpture not evident, surface shining between punctures. Fronto-clypeal sulcus distinct, somewhat more broadly interrupted at middle than in specimens of *B. pulicarius*. *Pronotum* punctate about as coarsely and closely as on disk of head; coarsely and irregularly punctate between the basal plicae with punctures in part confluent, but less coarsely and irregularly punctate than on specimens of *B. pulicarius*. Basal plicae about 1/2 as long as pronotum at midline, slanting inward from base and slightly curved basally and recurved apically as in specimens of *B. pulicarius*. *Elytron* with setate punctures about as coarse but closer than those on disk of pronotum. *Microsculpture* between punctures less apparent than on specimens of *B. pulicarius* especially in females which are only feebly iridescent purple on the elytra. *Basal plicae* feebly curved at base and then nearly straight slanting inward (toward suture) on disk and detectably longer than basal pronotal plicae, somewhat longer proportionately than in specimens of *B. pulicarius*. *Venter* very similar to that of specimens of *B. pulicarius* except in sulcation of prosternal process. Metacoxal plates and first and 2nd abdominal sternites with coarse setate punctures, coarser punctures on posterior part of metacoxal lamina as in specimens of *B. pulicarius*.

Female.— Similar to male except for secondary sexual characters.

Color.— Head light yellow to reddish brown; darker behind the transverse cervical suture. Pronotum light yellow, darker along base between plicae as usual. Dark color of base of head visible through translucent front margin of pronotum. Elytra brown, the color pattern usually indistinct in fully hardened adults. Teneral specimens with lighter marginal spots connected to a complex discal stripe or spots. The darker areas on the margins are distinct in teneral specimens, but sometimes obliterated by melanization in mature adults. Venter light brown without much pattern if any. Appendages light yellow brown or brownish yellow.

Distribution.— I have seen this species in numbers from Brazil, Bolivia, and Peru, and suspect that specimens identified as *B. sobrinus* from Colombia, Panama, Suriname, and Venezuela may also represent this species.

Bidessonotus sobrinus J. Balfour-Browne

Bidessonotus sobrinus J. Balfour-Browne 1947: 445, Fig. 10 (Panama).

Diagnosis.— Specimens are very similar to those of *B. tibialis* and probably this is at most a subspecies confined to northwestern South America into Panama. Balfour-Browne (1947: 446) cites the species as being "perfectly distinct by the deeper transverse fronto-clypeal sulcus, the different form of the 'blade' of the aedeagus, the apparently narrower and more elongate form of the female compared to *tibialis*." All of these characteristics vary, and the form of the male external genitalia (Fig. 2) does not clearly distinguish specimens of *B. sobrinus*. Total length 1.4 to about 1.6 mm.

Bidessonotus morosus J. Balfour-Browne

Bidessonotus morosus J. Balfour-Browne 1947: 446, Fig. 11 (Mazatlan, Sinaloa, Mexico).

Diagnosis.— Specimens are similar to those of *B. tibialis*, but they are more lightly pigmented, and exhibit differences in structure of the male aedeagus of the external genitalia (Fig. 3). Male specimens are distinct from those of other species found with it in form of the rounded tip of the blade of the aedeagus. Apex of prosternal process medially sulcate as in specimens of *B. tibialis*. This species is apparently confined to northwestern Mexico (Sinaloa, Jalisco) and does not overlap with the range of *B. tibialis*. Total length: 1.5-1.9 mm.

Male.— *Head* finely and rather sparsely punctate anteriorly, more coarsely and distinctly punctate toward the base much as in specimens of *B. tibialis*. Fronto-clypeal sulcus distinct, rather deeply impressed at sides, narrowly interrupted at middle. Antennae just perceptibly longer than those of female. *Pronotum* with setate punctation on disk finer than on base of head, but much coarser in two rather regular rows in elongate, transverse impressions on either side between the basal plicae. Basal plicae a little more than 1/2 length of pronotum at midline, distinctly impressed and curved inward onto disk; microsculpture evident, but not giving an iridescent cast to surface. *Elytra* with setate punctation on disk about as at sides of pronotum, coarser along base and between the basal plicae; basal plicae curved inward at base and then nearly straight on disk of elytron and nearly parallel to suture; about 1/4 longer than pronotal plica. *Venter* with apex of prosternal process lanceolate and distinctly sulcate, the apex acute. Posterior part of metacoxal laminae and basal sternites of abdomen coarsely setate punctate and sculptured. Last visible abdominal sternite roughly sculptured and punctate, but not distinctly impressed. Middle tibiae curved about as in specimens of *B. tibialis*.

Female.— Similar to male but usually somewhat smaller and with the microsculpture of the elytra more evident. Antennae just perceptibly shorter than those of male. Elytra sometimes iridescent, but not usually with a purplish cast.

Color.— Head testaceous (light yellow) darker yellow brown behind the transverse cervical suture. Pronotum usually light yellow anteriorly but darker between the basal plicae. Elytra dark brown usually without any discal markings except in very teneral individuals; pattern of lighter and darker areas along margin indistinct; the darker areas not as distinct as on specimens of *B. tibialis* but pattern otherwise similar. Venter brown with darker areas along sutures on the coxal laminae, etc. Male and female patterns of elytra usually similar, but females may appear darker because of the microsculpture. Legs brownish yellow.

Distribution.— Besides the types from northwestern Mexico, I have seen this species from other localities in Sinaloa and Jalisco (3.5 mi. N. of LaHuerta, 22 March 1971, J.R. Zimmerman (CASC). Nayarit, San Blas, 5 July 1972, K. Stephen (FSCA). The genus was not recorded from Baja, California by Leech (1948).

Bidessonotus pulicarius (Aubé)

Hydroporus pulicarius Aubé 1838: 494 (United States).

Diagnosis.— A small species about 1.7 to 2.0 mm in length, the females usually smaller than males. Fronto-clypeal sulcus interrupted at middle in both sexes. Venter usually lightly pigmented, the coxal laminae and basal abdominal sternites with large setate punctures in irregular rows. Basal elytral plica slightly longer than pronotal plica. Prosternal process with apex lanceolate, roughly setate punctate, vaguely sulcate. Males usually with brown elytra, but otherwise rather lightly pigmented. Females of two types, one small and stout with microsculpture of most specimens giving elytra a purplish iridescent sheen, the other more slender, male-like, but with straight middle tibiae. Male external genitalia, especially the lateral outline of the middle lobe or aedeagus, diagnostic (Fig. 4); and should separate male specimens of *B. pulicarius* from all species of the genus except those of *B. caraibus*. Female with small but distinct marginal tooth on elytral margin.

Male.— *Head* rather finely and sparsely punctate anteriorly with coarser, closer punctures in the region of the fronto-clypeal sulcus and toward base in front of transverse cervical suture behind the eyes; impunctate behind the transverse cervical suture. *Microsculpture* not very distinct. Disk of pronotum more coarsely and closely punctate than disk of head, about as coarsely and closely punctate as base of head in front of the transverse cervical suture. Base of pronotum between the basal plicae with larger setate punctures in rough rows and with some irregular sculpture. Basal plicae curved at base and curving out onto disk, less than 1/2 as long as pronotum at midline. Setate punctures on lateral parts of pronotum coarser than those on disk. Margin distinct, but irregular. Microsculpture detectible, but surface between punctures shining. *Elytra* with setate punctation on disk somewhat finer than at base of pronotum, but coarser along inner edges of plicae at base. Elytral basal plica curved at base and then nearly straight slanting inward toward the suture; detectibly longer than pronotal plicae. Surface of elytra with evident microsculpture, but surface shining between the microstrigae and not purplish iridescent. Middle tibia feebly but distinctly curved. Outer lamina of metacoxa with rough sculpture and coarse setate punctures in irregular rows in the posterior part. First and second visible sternites with distinct transverse rows of coarse setate punctures. Last visible sternite roughly sculptured and setate punctate, but not distinctly impressed.

Female.— Apparently represented by two different kinds of individuals as given under the diagnosis--many specimens short, stocky, with the elytra distinctly purplish iridescent from the microsculpture or some few specimens male-like with elytra dark or light brown or iridescent, and middle tibiae straight. Balfour-Browne (1947) considered these male-like females which he had not seen to be the females of *B. longovalis*, but they are too small to be that species.

Color.— Head light yellowish brown, darker basally. Pronotum yellowish brown, darker between the basal plicae. Elytra light brown to dark brown in males and some females or dark purplish in the female. Elytral pattern not distinct in most specimens, but dark subhumeral, postmedian, and preapical spots usually detectible accompanied by lighter subhumeral, postmedian and apical spots. A few teneral individuals examined show marginal spots and irregular discal light spots or stripes. The lateral elytral pattern of dark and light spots seems to be essentially the same as the pattern of the South American species, *B. obtusatus* (Fig. 9a), but less distinct.

Distribution.— I have seen this species from many localities in Florida, southern Georgia, Alabama, Mississippi, and Louisiana, but not farther north in the U.S.A. I believe that older records for Indiana apply to *B. inconspicuus*, but some coastal species extend into southwestern Indiana.

This species may be very widely distributed in the Antilles and Central America. I have seen specimens with identical genitalia from Belize and from Cuba which I have referred to *B. caraibus*.

Bidessonotus caraibus (Chevrolat)

Hydroporus caraibus Chevrolat 1863: 199 (Cuba).

Bidessonotus caraibus; Balfour-Browne 1947: 435 (Redescribed on basis of specimens from Cuba and description of Régimbart 1895: 335 and Sharp 1882: 364).

I am uncertain as to the identity of this species. I believe it is at most a subspecies of *B. pulicarius* which it closely resembles. The outline of the lateral aspect of the male aedeagus of the external genitalia is almost identical (see Fig. 4).

I have examined material I believe represents *B. caraibus* from the following localities (all in NMNH). CUBA: Matanzas, Zapata Swamp northwest of Buenaventura, 1 May 1983, P.J. Spangler and Iliana Fernandez C.; 4 km. northeast of Palpite, Zapata Swamp, 1 May 1983, P.J. Spangler and Iliana Fernandez C.; Zapata Swamp 2 km. northeast of Palpite, 2 May 1983, P.J. Spangler and Iliana Fernandez C.; Cienega Zapata at Playa Larga, 10-11 Feb. 1981, D. Davis and P.J. Spangler; 1 km. east of Playa Larga, Zapata Swamp, 2 May 1983, P.J. Spangler and Iliana Fernandez C. Santa Clara, Cayamas, various dates, E.A. Schwarz. BELIZE: Corazal Town, 30 Aug. 1967 and 1 Sept. 1967, G. and R. Lacy.

Bidessonotus inigmaticus sp. nov.

Diagnosis.— A small species similar to *B. pulicarius* and *B. morosus*, but with distinctive male external genitalia (Fig. 5). Apex of prosternal process broader than in *B. morosus* but medially sulcate. Marginal lightly pigmented areas of elytra more conspicuous than in specimens of *B. morosus*. Basal elytral plicae just perceptibly longer than basal pronotal plicae. Total length 1.3 to 1.76 mm.

Holotype Male.— Total length 1.76 mm, greatest width near middle of elytra 0.8 mm; width of pronotum at base 0.72 mm; width of pronotum at apex 0.72 mm; length of pronotum at midline 0.32 mm. *Head* finely and sparsely punctate anteriorly, the punctures separated by two or more times their diameter. More coarsely and closely punctate posteriorly, but impunctate behind the transverse cervical suture. Fronto-clypeal impression not greatly interrupted at the middle, less so than in specimens of *B. morosus*. *Pronotum* with disk less coarsely and closely punctate than in specimens of *B. morosus*; discal punctures separated by more than 2 times the diameter of each. Punctures between the basal plicae finer than in specimens of *B. morosus*. Basal plicae curving onto disk, about 1/2 as long as pronotum at midline. *Elytra* with punctures coarser and thus closer than on elytra of specimens of *B. morosus*. Basal plicae curved at base then nearly straight on elytron parallel to the suture and just perceptibly longer than basal pronotal plicae in contrast to being distinctly longer in specimens of *B. morosus*. Microsculpture present but not giving an iridescent sheen to surface. *Venter* coarsely punctate on coxal plates and basal abdominal segments much as in specimens of *B. morosus*. Last visible abdominal sternite with setate punctures, but not impressed, similar to that of *B. morosus* but less coarsely punctate.

Allotype Female (= paratype female).— Very similar to male but slightly smaller and with an iridescent sheen to the elytra due to microsculpture. Prosternal process similar to that of male. Middle tibiae straight. Last visible abdominal sternite similar to that of male. Total length 1.70 mm; greatest width near middle of elytra 0.72 mm; width of pronotum at base 0.56 mm; pronotum at apex 0.40 mm; length pronotum at midline 0.28 mm.

Color.— Both male and female specimens similar to those of *B. morosus* with dark brown elytra and venter except for the pale brownish yellow legs, antennae, and palpi. Color pattern mostly obscured by melanization in mature adults, only areas along the margins and at the apices of each elytron lighter, the usual accompanying dark spots reduced in intensity.

Distribution.— Holotype, allotype, and 4 paratypes from MEXICO: Colima, N. of Manzanillo, 19 Jan. 1961, C.O. Morris (California Academy of Science). Nayarit, San Blas, 24-25 April 1961, Howden & Martin, 1 male, 1 female paratype (CNC).

Bidessonotus inconspicuus (LeConte)

Hydroporus inconspicuus LeConte 1855: 290 (Louisiana).

Diagnosis.— A medium sized species for the genus measuring about 1.76 to 2.2+ mm in length, most female specimens slightly smaller than males. Frontoclypeal sulcus uninterrupted, narrowly interrupted at middle, or with the interruption shallow. Venter usually dark brown, especially on the coxal laminae. Apex of prosternal process in both sexes sulcate but roughly setate punctate. Female specimens with microsculpture more distinct than in males, often purplish iridescent on elytra. Marginal tooth of elytron near outer angle of truncation in female obsolete or reduced, difficult to see. Male external genitalia, especially the lateral outline of middle lobe diagnostic (Fig. 6).

Male.— *Head* punctate much as in specimens of *B. pulicarius* but frontoclypeal sulcus complete across front or only narrowly or shallowly interrupted. Pronotal punctation much as in specimens of *B. pulicarius* allowing for the slightly larger size; basal pronotal plica much as in specimens of *B. pulicarius*. *Elytra* with setate punctures on disk coarser than on specimens of *B. pulicarius*; basal plica curved at base then nearly straight on disk slightly angled toward suture, and detectibly longer than pronotal plica. Microsculpture of elytron less conspicuous than on specimens of *B. pulicarius*. Venter darker in color than on specimens of *B. pulicarius* or *B. longovalis*, but similarly punctate on coxae and basal abdominal sternites. Mesotibiae slightly curved. Fore tarsi not as broadly dilated as in specimens of *B. pulicarius*. Prosternal process with apex sulcate but roughly setate punctate as indicated in diagnosis. Last visible sternite setate punctate and vaguely impressed in a roughly circular area toward apex.

Female.— Similar to male specimens but with elytra often darker and sometimes purplish iridescent as in specimens of *B. pulicarius.*

Color.— Both male and female specimens are similar to those of *B. pulicarius* in color but darker; venter usually dark brown at least in part. The marginal dark and light elytral spots usually indistinct about as in specimens of *B. pulicarius.* Disk of elytra without lighter areas except in very teneral individuals.

Distribution.— I have seen this species in large numbers from northern Florida, Georgia, Alabama, Mississippi, and Louisiana and more rarely from Arkansas, Tennessee, Kentucky, Maryland, Michigan, Illinois, Massachusetts, South Carolina, North Carolina, New York, New Jersey, Indiana, and eastern Texas. It probably occurs in most of the eastern United States and southern Canadian provinces. I have not encountered it in southern Florida although it is recorded from Dunedin and Royal Palm State Park (W.S. Blatchley coll.) by Balfour-Browne (1947).

The size, darker color, and distinctive outline of the aedeagus of the male external genitalia (Fig. 6) should distinguish this species. The lateral outline of the aedeagus suggests that of specimens of *B. championi* (Fig. 7), but the two species occur in different regions and are distinct in a number of characteristics of size, color, and structure.

Bidessonotus championi Balfour-Browne

Bidessonotus championi Balfour-Browne 1947: 436, Fig. 6 (Guatemala).
Bidessus adumbratus; Sharp 1882: 25, in part.

Diagnosis.— A medium sized species about 1.8 to 2.0 mm in length. The outline of the aedeagus of the male external genitalia (Fig. 7) is similar to that of *B. inconspicuus* (LeConte) but is diagnostic. Head finely punctate with the fronto-clypeal sulcus almost complete across front. Pronotum moderately coarsely punctate, less so than in some species, with some irregular and coarser sculpture along the inner margins of the plicae. Basal pronotal plicae curved at base then almost straight slanting inward on disk but less than 1/2 length of pronotum at middle. Elytra coarsely and densely setate-punctate with microsculpture between the sculptures in both sexes but not giving a purplish sheen to the surface. Basal elytral plicae curved at base, as if continuing curves of pronotal plicae, then straightening on the disk and slanting toward suture, about 1/4 or less longer than pronotal plicae. Apex of prosternal process narrowly lanceolate, sulcate in both sexes. Outer coxal laminae coarsely setate-punctate, but punctures not very deep. Impressions on either side of basal abdominal sternites more conspicuous in female than in male. Last visible sternite in male with coarse elongate sculpture toward apex and with tiny rounded impressions on either side of base.

Female.— Head and pronotal punctation and pronotal and elytral plicae similar, but with elytral punctation less impressed and microsculpture giving a purplish iridescence to surface.

Color.— Head yellowish brown to dark brown on base and front and along either side adjacent to the eyes; base of head of most specimens very dark brown, visible through the anterior margin of pronotum; pronotum yellowish brown with dark area between the plicae along the base; elytra dark brown with usual indications of lighter and darker areas along edges; venter yellowish brown to dark brown with appendages and epipleura of elytra brownish yellow; abdomen appears to be darkly banded transversely in some specimens.

Distribution.— Besides the type from Paso Antonio, GUATEMALA, 400 feet (Champion) in the Biologia Americana material (BMNH) typical males of this species were seen from HONDURAS: 5 mi. E. of Choluteca, 28 July 1965, P.J. Spangler (NMNH). COSTA RICA, 12 mi. S.W. of Liberia, 25 July 1965, P.J. Spangler (NMNH). NICARAGUA, 2 mi. W. Nadaime, 13 July 1974, L.B. O'Brien, BLT (NMNH), 13 mi. S. San Benito, 11 July 1965, P.J. Spangler (NMNH).

Bidessonotus longovalis (Blatchley)

Bidessus longovalis Blatchley 1919: 310 (Florida: Dunedin, LaBelle, Kissimmee.)

Diagnosis.— Most specimens are distinguishable from species with which it occurs by the larger size (length 1.75-2.4 mm) and the long basal elytral plicae which are distinctly longer than the basal pronotal plicae. Apex of prosternal process setate punctate not sulcate. Female specimens are similar to males but smaller. The punctation of the dorsum is coarse and punctures are sometimes confluent giving the appearance of rugae. The male external genitalia, especially the lateral aspects of the middle lobe or aedeagus, is diagnostic (Fig. 8).

Male.— Disk of head more coarsely punctate than in specimens of *B. pulicarius* or *B. inconspicuus* with coarser punctures toward base as usual. Fronto-clypeal sulcus shallowly interrupted at middle. *Pronotum* with disk more coarsely punctate than in species with which it may occur; more coarsely punctate and with confluent punctures forming elongate grooves between the basal plicae. Plicae about 1/2 length of pronotum at midline, curved at base and nearly straight angling inward onto disk. *Elytra* coarsely setate punctate, more coarsely so than in specimens of *B. pulicarius* or *B. inconspicuus*. Microsculpture not very evident, surface shining between the punctures. Basal plicae curved at base, nearly straight but slanting inward on disk toward the suture; distinctly longer than pronotal plicae. Tips of elytra feebly truncate. Prosternal process with setate punctures, but not sulcate or canaliculate. Coxal and basal abdominal punctation similar to specimens of *B. pulicarius*. Last visible sternite setate punctate and irregularly depressed before apex. Middle tibiae slightly curved. Fore tarsi not as strongly expanded comparatively as in specimens of *B. pulicarius*.

Female.— Similar to male with a small tooth on the outer margin of elytron near outer end of truncation (difficult to see but usually distinct). Female elytra without strong iridescence produced by microsculpture.

Color.— Head and pronotum about as in specimens of *B. pulicarius* and *B. inconspicuus*. Elytra dark brown with the marginal dark spots and light areas inconspicuous or lacking. Epipleurae yellowish brown, narrower than in specimens of *B. pulicarius*. Venter yellow brown with darker areas along sutures and in other areas.

Distribution.— This species is known only from Florida, Alabama (Washington County), and Georgia (Terrell County). In Florida it occurs abundantly in the peninsular counties.

Bidessonotus obtusatus Régimbart

Bidessonotus obtusatus Régimbart 1895: 336 (Brazil, Paraguay). Type species of *Bidessonotus*, designated by Balfour-Browne, 1947:427.)

Diagnosis.— A medium sized species about 1.6 to 2.2 mm in length with distinctive male external genitalia (Fig. 9). Fronto-clypeal sulcus impressed at sides but obsolete in middle with the impression of two tiny tubercles. Pronotum with coarse punctures and sculpture along base between plicae; basal plicae distinctly impressed, curved inward at base then feebly recurved toward outer margin on disk, about 1/2 length of pronotum at midline. Elytra moderately coarsely and closely not deeply setate punctate, basal elytral plicae sligthtly curved at base then nearly straight, about 1 1/4 times as long as pronotal plicae. Apex of prosternal process narrow, not sulcate, but with setate punctures. Middle tibiae curved. Last visible sternite roughly punctate toward apex, impressed on either side of base.

Color.— Specimens of this species are generally yellow or yellowish brown with elytra dark to very dark brown; teneral pattern of the elytra distinctive (Fig. 9a). Many specimens have a characteristic light spot on the disk of each elytron covering the tip of the elytral plica.

Distribution.— This species is widespread in the Hylaen Forest in Brazil, Bolivia, Cayenne, Colombia, Ecuador, Peru, Suriname, and Venezuela south to Paraguay and Argentina. I have seen several hundred specimens of this species which is abundant in ultraviolet light trap collections from most of the countries listed above.

Comments.— The closest relatives of *B. obtusatus*, to judge from the configuration of the male external genitalia, are *B. pollostus, B. rubellus, B. dubius*, and B. *ploterus*.

Bidessonotus nepotinus J. Balfour-Browne

Bidessonotus nepotinus Balfour-Browne 1947: 443 (Trinidad).

Described from a female and not recognized in the material examined. According to the original description the insect appears to be very close to *B. obtusatus*.

Bidessonotus nepotinus is described as being 2.152 to 2.165 mm in length by 1.050 to 1.085 wide at widest point of elytra. Fronto-clypeal impression or sulcus shallow, widely obsolete (broadly interrupted) at middle. Transverse cervical stria very fine, rather obsolete and indistinct. Pronotum with basal plicae distinctly curved, slightly oblique, quite strongly and widely impressed, about 1/2 length of pronotum from the base. Basal plicae of elytra slightly oblique, weakly sinuate, rather shallow but distinctly impressed about 1 and 1/4 times the length of the pronotal plicae. Apex of prosternal process lanceolate but not or very feebly sulcate. Last visible sternite densely, finely, obsoletely punctate.

Color.— The color pattern is described as being represented on the elytra by three transverse bands, one at the base widest in the middle and tapering toward each side, one in the middle not quite attaining the margins, and one post medially both anteriorly and posteriorly sinuate. None of the bands very distinct or sharply limited. The head, antennae, legs, and venter yellowish brown.

Distribution.— Known so far only from Trinidad (MCZ).

Bidessonotus dubius sp. nov.

Diagnosis.— Specimens are similar to those of *B. obtusatus* Régimbart, but averaging larger in size and with similar but distinctive male external genitalia

(Fig. 10). Teneral color pattern similar to that of specimens of *B. obtusatus*. Elongate spot on elytra at apex of elytral plica occasionally present. Punctation of head and structure of transverse fronto-clypeal sulcus interrupted at middle much as in specimens of *B. obtusatus*. Pronotal and elytral punctation also similar to that of adults of *B. obtusatus*, but elytra of many specimens uniformly dark, purplish. Elytral plicae about 1 1/4 times as long as pronotal plicae, slightly longer and more curved than in specimens of *B. obtusatus*. Apex prosternal process not sulcate. Mesotibiae and mesofemora similar to those of *B. obtusatus*. Last visible sternites similar to those of *B. obtusatus*, the tiny circular impressions on either side of base somewhat more conspicuous. Total length about 1.7 to 1.9 mm.

Holotype Male.— Oblong, irregularly oval, the greatest width near middle of elytra. Moderately convex above and almost flat below but mesosternum and coxal plates slightly concave along midline. Total length 1.8 mm; greatest width near middle of elytra 0.88 mm; width of pronotum at apex 0.48 mm; width of pronotum at base 0.72 mm; length of pronotum along midline 0.24 mm. *Head* finely sparsely punctate anteriorly somewhat more coarsely but shallowly punctate on front between eyes, impunctate behind transverse cervical suture; punctation finer and less impressed than on specimens of *B. inconspicuus*, about as in those of *B. obtusatus*; microsculpture inconspicuous. *Pronotum* with punctation of anterior part and most of disk fine, sparse, similar to that on front; base of pronotum between basal plicae irregularly sculptured near the curved plicae, but not conspicuously coarsely setate punctate; pronotal plicae curved inward, deeply impressed, a little more than 1/2 length of pronotum at midline; microsculpture detectible throughout but most of surface appearing smooth, shining. *Elytra* with setate punctation coarser and denser than on pronotal disk, but much finer and shallower than on specimens of *B. inconspicuus*; microsculpture evident throughout, the minute areas between the mostly transverse strigae appearing smooth and shining; basal elytral plicae slightly curved inward (toward elytral suture) at base, then almost straight on disk parallel with suture and detectibly longer than basal pronotal plicae, deeply impressed. *Venter* with punctation of hind coxae and abdominal sternites shallow, not conspicuous; prosternal process narrow, and with apex covered with closely set, yellow setae not detectibly sulcate. Mesotibiae thickened, curved, somewhat heavier than in *obtusatus*. Mesofemora without teeth. Last visible sternite more coarsely setate punctate toward apex but not distinctly impressed, with tiny rounded impressions on each outer corner of the base. Aedeagus of male external genitalia less extended than on males of *B. obtusatus* (Fig. 9).

Allotype Female (= paratype female).— Similar to male except for the secondary sexual characters and distinct discal light spots on elytra. Rounded impressions on base of last sternite reduced in comparison to male. Elytral plicae just detectibly longer than pronotal. Total length 1.76 mm; greatest width near middle of elytra, 0.88 mm; width of pronotum at apex 0.48 mm; width of pronotum at base 0.72 mm; length of pronotum on midline 0.24 mm.

Color.— Male and female specimens are similar. *Head* and pronotum brownish yellow, darker brown along base of head and base of pronotum. *Elytra* dark, purplish brown. Lighter color pattern not conspicuous, lighter spots along outer margin consist of subhumeral, postmedian and preapical spots with a distinct lighter spot near apex of each elytral plica as in some few specimens of *B. obtusatus*.

Distribution.— Holotype male, allotype, plus 1 male and 4 female paratypes from VENEZUELA: Mirando, Panaquire, 18-22 Feb. 1982, at Black

Light Trap (Ultraviolet light), J.H. Frank (FSCA). Other paratypes from the following localities: VENEZUELA: Guarico, 32 kms. S.W. of Calabozo, 11 Feb. 1969, Paul and Phyllis Spangler (84, in NMNH); 44 kmns. S. of Calabozo, 11 Nov. 1969, Paul and Phyllis Spangler 153, NMNH); 44 kms. S. of Calabozo, Mata Masagural, 5 Mar. 1986, P.J. Spangler (737, NMNH); 12 kms. S. of Calabozo, 6-12 Feb. 1969, Paul and Phyllis Spangler (1, NMNH); Guarico, San Fernando, 12 Feb. 1969, Paul and Phyllis Spangler (167, NMNH). Bolivar, Medio Orinoca, Isla Cuba o Playa del Medio, Selva humeda, 12 Feb. 1962, Carlos Bordon (4, FSCA). BRASIL: Mato Grosso, Jacare, Parque Nacional Xingu, Nov. 1963, Moacir Alvarenga and W.C.A. Bokermann (17, FSCA); Mato Grosso, S 12° 31' W 55° 37', Oct. 1974, (1 male, 1 female, CNC). CAYENNE: Marispassula, Lawa River, 3 Dec. 1953, Borys Malkin, in waterfilled canoe (11, in FSCA). SURINAME: 25 km n. S. Paramaribo, 12 July 1969, Paul and Phyllis Spangler (1 ♀ NMNH).

Comments.— This species is closely related to *B. obtusatus*. However, they are largely sympatric, *B. obtusatus* occurring from Panama and Venezuela to Paraguay and Argentina, throughout Brazil and in eastern Bolivia. *B. dubius* occurs abundantly in Venezuela, but seems to be rare in Brasil.

Bidessonotus rubellus sp. nov.

Diagnosis.— A medium-sized species about 1.6 to 1.9 mm in total length. Male external genitalia similar to those of *obtusatus* but distinctive (Fig. 11). Fronto-clypeal sulcus impressed without interruption at middle. Elytral plicae about 1/2 again as long as pronotal plicae. Apex of prosternal process lanceolate, but not conspicuously widened and not sulcate. Metacoxal laminae and basal abdominal sternites coarsely punctate with serial punctures impressed.

Holotype Male.— Elongate, irregularly oval, convex above and flattened ventrally with usual concavity of metasternum and metacoxal laminae in lateral aspect. Total length 1.84 mm; greatest width near middle of elytra 0.96 mm; width pronotum at base 0.78; width pronotum at apex 0.48; length of pronotum at midline about 0.28 mm. *Head* with clypeus very finely and very sparsely punctate; front finely and sparsely punctate, more coarsely and densely punctate between eyes in front of transverse cervical stria; fronto-clypeal impressions distinct, not interrupted in middle with dense fine irregular punctures at either side and extending in rows onto disk. *Pronotum* with setate punctures coarser and denser than on disk of front; basal plicae curved inward, distinctly impressed, about 1/2 length of pronotum at midline; coarser punctures and rugose sculpture along base, less conspicuous than in several other species. *Elytra* moderately coarsely setate punctate, but punctures not deeply impressed; microsculpture evident throughout with surface not strongly shining, not strongly iridescent; basal plicae curved at base then nearly straight on disk, well impressed and about 1/2 again as long as pronotal plicae. *Venter* with apex of prosternal process lanceolate, but not conspicuously widened and not sulcate; middle tibiae curved. Metacoxal laminae and basal abdominal sternites with rows of large impressed punctures. Area on hind margins of coxal laminae with sculpture somewhat coarser than microsculpture possibly forming a stridulatory organ. Last visible sternite with setate punctures over whole surface, but punctures not very conspicuous; rougher rugose sculpture toward apex; impressions at either side of base not conspicuous.

Allotype Female (= paratype female).— Very similar to male except for secondary sexual characters. Size almost the same as male. Fronto-clypeal impressions similar, complete across front. Some paratypes with fronto-clypeal impressions interrupted at middle.

Color.— Adult specimens are generally brownish yellow with base of pronotum narrowly darker, elytra darker brown with a vaguely reddish cast, not very purplish, and venter yellowish brown with areas of darker brown. *Head* brownish yellow, darker brown behind transverse cervical suture. *Elytra* with pattern vaguely indicated, similar to that of specimens of *B. obtusatus* with lateral spots and very vague discal spots on elytra.

Distribution.— Holotype male, allotype female (= paratype female), and 3 paratypes from PANAMA. C.Z. Albrook Forest Site, Ultraviolet trap at ground level, 8-9 June 1967, R.S. Hutton; (NMNH). Same data except 10-11 Aug. 1967, 21-22 Dec. 1967, 5 (NMNH). PANAMA, Tocumen, Ultraviolet light trap, 1-5 June 1970; 20-24 July 1940, 31 Aug.-4 Sept. 1970, 31 Aug. 1970 Diego Navas, 6 (FSCA). ECUADOR: Los Rios, Babahoya, Blacklight trap, 21 June 1975, Cohen, Langley, and Monnig, 2 (NMNH). COLOMBIA: Amazonas, Leticia, 19-25 Feb. 1972, Henry and Ann Howden, 700; 2 males (Canadian National Collection). VENEZUELA: Guarico, 32 kms. W. of Calabozo, 11 Feb. 1969, Paul and Phyllis Spangler, 1 (NMNH). PARAGUAY: Central, Aragua, 26-27 Apr. 1980, Paul J. Spangler, 1 male (NMNH). Paraguari, 25 kms. S.E. of Ybycui in Ybycui National Park, 12-24 Apr. 1980, Paul J. Spangler, 1 male (NMNH).

Bidessonotus ploterus sp. nov.

Diagnosis.— A small species resembling *B. obtusatus* but with the clypeus finely and densely punctate, the prosternal process with lanceolate apex sulcate, and distinctive male external genitalia (Fig. 12). Generally brownish in color throughout without very much lightening of the margins or venter and no apparent color pattern in mature specimens. Total length about 1.3 to 1.8 mm, greatest width near middle of elytra about 0.64 to 0.72 mm.

Holotype Male.— Elongate, roughly oval, convex above and flattened below with usual concavity of meso- and metasterna and coxal laminae. Total length 1.6 mm; greatest width near middle of elytra 0.72 mm; width of pronotum at base 0.56 mm; width of pronotum at apex 0.36 mm; length of pronotum at midline 0.24 mm. *Head* with clypeus finely and rather densely punctate and front back to between the eyes about as coarsely but less densely punctate than on clypeus. Fronto-clypeal sulcus not strongly impressed, but evident on either side and interrupted in middle. Front with small tubercles at either side above the ends of the fronto-clypeal impression. *Pronotum* finely punctate on disk and anterior part, about as coarsely and densely punctate as front of head; coarsely, irregularly punctate along base between the plicae with rugose sculpture and roughly punctate and sculptured also outside the plicae along the base; plicae curving inward, about 1/2 length of pronotum at midline, deeply impressed with especially rough sculpture immediately next to the inner edges. *Elytra* with rather fine, shallowly impressed setate punctures often confused with the microsculpture; microsculpture evident, surface not strongly shining, but only feebly purplish; plicae slightly curved at base but nearly straight on disk, about same length as pronotal plicae. *Venter* with prosternal process lanceolate, distinctly sulcate along most of its length. Mid-tibiae moderately curved. Hind coxal laminae not coarsely or deeply punctate, but setate punctures in transverse rows as usual intermixed with microsculpture and some rough sculpturing; posterior margin of hind coxal laminae with fine sculpture suggesting a stridulatory organ; first and 2nd abdominal sternites not coarsely punctate, but setate punctures in rows as usual; last visible sternite not very coarsely punctate but with rugose sculpture toward the apex; lateral basal impressions not conspicuous.

Allotype Female (= paratype female).— Very similar to male except for secondary sexual characters. Tubercles on head reduced. *Color.* very similar, elytra darker somewhat purple iridescent. A few paratype females show traces of pattern especially along edges of elytra.

Color.— Specimens are somewhat more uniformly brown than most species. (Possibly discolored, but other species from same collection do not appear particularly darker than usual.) Head, pronotum, and elytra yellow brown, somewhat lighter along clypeus and anterior and lateral parts of the pronotum, darker along bases as usual. Edges of elytra, legs, mouthparts, and abdominal sternites somewhat lighter yellow brown. *Venter* with metacoxal laminae darker brown.

Distribution.— Holotype, allotype and 15 male and female paratypes from BRASIL: Mato Grosso, Parque Nacional Xingu, at light, Nov. 1965, Moacir Alvarenga, and W.C.A. Bokermann (FSCA). One female paratype Mato Grosso, Tapirape, at light, 26 July 1963, Boris Malkin (FSCA).

Bidessonotus otrerus sp. nov.

Diagnosis.— A small species about 1.5 to 1.8 mm in total length. Male external genitalia (Fig. 13) diagnostic. Apex of prosternal process narrow and feebly sulcate. Front of head and part of venter dark brown. *Pronotum* brownish yellow except narrowly along the base and lateral margins which are dark brown. *Elytra* lighter brown than head, moderately coarsely and regularly punctate, not purple iridescent.

Holotype Male.— Elongate, irregularly oval, convex above, flattened below except for usual metasternal-coxal lamina concavity. Total length 1.7 mm; greatest width near middle of elytra about 0.8 mm; width of pronotum at base 0.64 mm; width of pronotum at apex 0.44 mm; length of pronotum at midline 0.28 mm. *Head* with clypeus finely and sparsely punctate; front between the eyes about as finely but more closely and irregularly punctate; rest of front about as finely punctate but more sparsely and more in rows; punctation coarser and closer on either side near the fronto-clypeal sulcus; fronto-clypeal sulcus distinct at sides obsolete at middle. *Pronotum* setate punctate about as finely but more regularly than on anterior part of front; punctation and sculpture between the plicae relatively fine, without rugose areas; microsculpture transverse, evident over entire dorsum; pronotal plicae deeply impressed at bases, curved inward, less than 1/2 length of pronotum at midline. *Elytra* moderately coarsely and regularly setate punctate; microsculpture evident throughout, surface not strongly shining; basal plicae fairly straight, impressed, slightly longer than pronotal plicae. *Venter* with metacoxal laminae moderately punctate in rows; posterior border of coxal laminae with apparent stridulatory area; abdominal sternites 1 and 2 also with moderately large punctures in transverse rows at sides; all sternites with setate punctures but setae more evident than punctures. Prosternal process with apex somewhat widened and feebly sulcate. Last sternite with coarse rugose sculpture toward apex, but lateral impressions on either side of base not conspicuous. Middle tibiae curved.

Allotype Female (= paratype female).— Similar to male except for secondary sexual characters.

Color.— Head with clypeus brownish yellow, rest of front and clypeus dark brown; pronotum mostly brownish yellow on disk and at sides narrowly dark brown along the base and lateral margins; elytra lighter brown than head, with vague brownish yellow spots along sides roughly conforming to a subhumeral, postmedian, and apical light spots (in some specimens with darker spots between the light spots as in specimens of *B. obtusatus*; epipleurae lighter brownish yellow; venter with lower aspect of head, mouthparts, antennae, mesosternum, and lateral parts of prosternum, and legs brownish yellow, but metasternum, metacoxal laminae, and abdominal sternites dark brown, about same color as front of head.

Distribution.— Holotype, allotype, and 68 paratypes from: COLOMBIA, Magdelena, 8 km E. of Baranquilla, 19 March 1969, Paul and Phyllis Spangler (NMNH); 1 paratype same data except 18 March 1969, (NMNH). VENEZUELA: Mirando, Panaquire, 1-13 Aug. 1983, ultraviolet light trap, J.H. Frank, 1 male paratype (FSCA).

Bidessonotus pollostus sp. nov.

Diagnosis.— A small dark species about 1.3 to 1.6 mm long, the female smaller than male. Aedeagus of male external genitalia (Fig. 14) somewhat similar to that of *B. obtusatus*, but with blade longer. Fronto-clypeal sulcus nearly complete across front. Setate punctation of dorsum less impressed than in many species, the surface shining between the punctures. Microsculpture evident, but not giving a distinct purple iridescence to elytra in either male or female. Pronotal plicae somewhat longer and more deeply impressed than in most species. Elytral plicae longer than pronotal. Prosternal process in male rounded at apex and rather broadly sulcate; female similar. Last visible sternite in male with rather fine setate punctures but with irregular oval impressions on either side. *Female* without distinct tooth at outer end of apical truncation of elytra. *Color.* almost uniformly dark brown on dorsum and venter.

Holotype Male.— Oblong oval, not very much arched in lateral profile. Total length 1.60 mm, greatest width near middle of elytra about 0.72 mm; width of pronotum at base 0.56 mm; width of pronotum at apex about 0.48 mm; length of pronotum at midline about 0.28 mm. *Head* finely and sparsely punctate on clypeus and front somewhat more coarsely on disk. *Pronotum* finely and shallowly punctate on disk, somewhat more coarsely setate punctate at the sides, but relatively finely and sparsely between the basal plicae; rough sculpture between plicae reduced; plicae a little more than 1/2 length of pronotum at midline, deeply incised, slightly curved inward onto disk. *Elytra* rather finely, sparsely, and shallowly setate punctate; basal plicae longer than pronotal plicae, nearly straight, slanting inward. *Venter* with prosternal process and last visible sternite as described under diagnosis above. Basal abdominal sternites and metacoxal laminae with coarse series of punctures as usual.

Allotype Female (= paratype female).— Similar to male, but smaller. Total length 1.36 mm, greatest width near middle of elytra 0.64 mm, width of pronotum at base about 0.56 mm, width of pronotum at apex about 0.48; length of pronotum at midline about 0.28 mm. *Color.* very similar to the male, darker than any other species of *Bidessonotus* seen except for some *B. melanocephalus.*

Color.— Predominantly dark with front of pronotum, legs, antennae, and palpi lighter yellowish brown.

Distribution.— I have seen this species only from the type locality: BELIZE: Coraxol Town, 30 Aug. 1967, G. and R. Lacey (NMNH). Holotype and allotype only.

Bidessonotus vicinus J. Balfour-Browne

Bidessonotus vicinus Balfour-Browne 1947: 428 (British Honduras, Punta Gorda).

This species was described from the female, but I have no doubt that the species treated here as *B. vicinus* is the same. The male genitalia (Fig. 15) are diagnostic. In mature individuals the head is distinctly brown. The melanization of the elytral is reduced so that they sometimes appear lightly striped with brown and usually have much darker spots associated with the usual light spots along the sides of the elytra above the epipleura. Fronto-clypeal sulcus nearly complete across front. Prosternal process narrowly lanceolate, sulcate. Elytral plicae slightly longer than pronotal plicae. The total length is only about 1.5 to 1.7 mm.

Distribution.— Besides the type females, I have seen material from the following localities. PANAMA: C.Z. Albrook Forest Site, ultraviolet light trap at ground level, 14-15 July; 21-30 July, and 14-18 Dec. 1967, R.S. Hutton (NMNH). BRITISH HONDURAS: Cayo District, Mile 66 on Western Highway, ultraviolet light trap, 30 June, 1969, W. and D. Hasse (FSCA); Cayo District, 14 km S. San Ignacio, 23 V. 1986, P.J. Spangler and Robin A. Faitoute. VENEZUELA: Miranda, Panaquire, ultraviolet light trap, 22 Feb. 1984, J.H. Frank (FSCA).

Bidessonotus mexicanus Régimbart

Bidessonotus mexicanus Régimbart 1895: 333, plate 8, Figs. 10, 11. (Mexico on tobacco.)

Diagnosis.— A medium sized species about 1.6 to 2.1+ mm in total length. Outline of the aedeagus of the male external genitalia diagnostic, blade with a distinctive upper and lower tooth or point (Fig. 16). Fronto-clypeal sulcus nearly or quite complete across front. Discal elytral plicae about 1 1/2 times as long as those on the pronotal base. Apex of prosternal process not very wide but distinctly sulcate. Elytral pattern in teneral specimens with humeral, median, and preapical dark spots at margin, and part of disk irregularly brown (Fig. 16a). Most specimens have only a vague indication of elytral pattern. Base of head, base of pronotum between the plicae, and the elytra usually brown to dark brown.

I have not seen the male specimens cited by Régimbart in the original description. Régimbart gives the range of total length of his specimens as from 1 7/8 (=1.8mm+) to 2 1/8 (= 2.1 mm+). J. Balfour-Browne says that his female from which he redescribed *mexicanus* measured 2.034 mm. I have not seen specimens over 1.8+ mm.

Distribution.— Mexico, San Luis Potosi, stream near Palmira, 20 July 1969, F.N. Young (FSCA). Vera Cruz, Lake Catemaco ("Coyame"), ultraviolet light trap, 5 July 1963, R.E. Woodruff (FSCA); 15 mi. S. Tantoyuca, 28 August 1965, P.J. Spangler (NMNH). Tamaulipas, Rio Frio at Limon, 11 June 1960, F.N. Young (FSCA); Rio Guayalejo near Magiscatzin, 11 June 1960, F.N. Young (FSCA); ditch N. of Mante, 12 June 1960, F.N. Young (FSCA). Tabasco, Villahermosa, 25 July 1965, P.J. Spangler (NMNH). Jalisco, 1 mi. N.W. Mazimitla, 8 February 1953, I.J. Cantrall (UMMZ). Nayarit, San Blas, 24-26

April 1961, Howden & Martin (Cal. Acad.) BELIZE, Cayo District, Mile 66 Western Highway, 30 June, 3 July, 7 July 1969, W. and D. Hasse (FSCA). U.S.A.: TEXAS: Trinity County, Pond on Hwy. 96 near Vair, Oct. 4, 1980, G. Challet (FSCA), new U.S. record.

Bidessonotus pictus sp. nov.

Diagnosis.— Similar to *B. mexicanus* Régimbart, but lacking the dorsal tooth on the male aedeagus (Fig. 17), the elytral plicae shorter than the pronotal plicae, and the microsculpture reduced especially on the elytra which under low magnification appear smooth and shining. Color. pattern distinct in all specimens seen, but all are somewhat teneral so that pattern may be inapparent in fully mature specimens. *Head* and pronotal punctation similar to that of *mexicanus,* but elytral setate punctures deeply impressed and the microsculpture between them greatly reduced. Fronto-clypeal sulcus distinct at sides but broadly interrupted at middle. Last visible sternite more finely punctate than in *mexicanus,* the impression on base at either side deep, conspicuous in proper light. Total length of males about 1.68 to 1.76 mm; greatest width near middle or elytra about 0.80 to 0.88 mm. Females total length about 1.60 to 1.68 mm; greatest width near middle of elytra about 0.80 mm.

Holotype Male.— Oblong, irregularly oval, the greatest width near middle of elytra; not very convex above and almost flat ventrally but with mesosternum and coxal plates slightly concave along midline. Total length 1.68 mm; greatest width near middle of elytra 0.80 mm; width of pronotum at apex 0.48 mm; width of pronotum at base about 0.64 mm; length of pronotum at midline about .024 mm. *Head* finely sparsely punctate anteriorly and on front. Fronto-clypeal impressions distinct at sides but rather broadly interrupted at middle. *Pronotum* with sides regularly curved wider across middle than elytral bases. Punctation of pronotum in anterior part and most of disk moderately fine and sparse. Base of pronotum between the basal plicae more coarsely irregularly punctate especially near the incurving plicae. Pronotal plicae incurved, distinct, slightly longer than 1/2 length of pronotum at midline. Head and pronotum with very fine microsculpture giving touches of iridescence in certain lights. *Elytra* with setate punctures deeply, regularly, and rather densely distributed, the punctures coarser than in *B. mexicanus* and about as in *B. inconspicuus.* Microsculpture not deeply impressed, inapparent in part, not imparting a purplish iridescence to elytra as in *B. pulicarius* and several other species. Basal elytral plicae lightly curved toward margin and distinctly shorter than pronotal plicae. *Venter* with outer laminae of coxal plate coarsely but rather shallowly punctate in part. Mesosternum and inner laminae of hind coxal plates appearing impunctate except for some setate punctures along margins. Abdominal sternites with coarse punctures on basal sternites. Last visible sternite less coarsely setate punctate than in *B. mexicanus*, but the oval impressions on either side of base deep, regular, and conspicuous in proper light. Prosternal process with apex broadly lanceolate, shallowly sulcate on apex, but not sulcate nor densely setate in front of fore coxae. Mesotibiae thickened, gently curved.

Allotype Female (= paratype female).— Very similar to male except for secondary sexual characters. Apex of prosternal process broadly lanceolate but not distinctly sulcate. Size almost identical to male. *Elytra* with more evident microsculpture, but not as purple as in some species.

Color.— Holotype, allotype, and paratype females with very similar color patterns on elytra (Fig. 17a). Head and thorax yellow with darker brown along pronotal base between the plicae. *Venter* mostly yellowish with darker brown areas along sutures, at joints, and other hardened areas as usual.

Distribution.— Holotype, allotype, 2 males, and 1 female paratype from: COSTA RICA, Puentarenas, 22 July 1955, P.J. Spangler (NMNH).

As indicated this species is close to *B. mexicanus*, but seems distinct in several characters. The prettily spotted elytral pattern of the type specimens may be illusory and fully hardened adults are probably more uniformly colored.

Bidessonotus paludicolus sp. nov.

Diagnosis.— A small species about 1.5 to 1.7 mm in length and about 0.8 mm wide near middle of elytra. Similar to *B. mexicanus* Régimbart, but with distinctive male external genitalia (Fig. 18). Head with fronto-clypeal sulcus less impressed at middle but not distinctly interrupted. Apex of prosternal process sulcate (shortened and bent in holotype, but similar to that of *B. mexicanus* in paratypes). Pronotal plicae impressed, curved at base but nearly straight slanting inward on disk. Elytral plicae impressed, curved at base but nearly straight slanting inward on disk, a little longer than pronotal plicae. Color pattern usually not evident in mature individuals. Elytra not conspicuously iridescent in either sex. Teneral pattern of paratypes shows vague stripes on disk of elytra and a subhumeral, postmedian, and preapical dark spot along elytral margins with lighter areas between them and at apex.

Holotype Male.— Elongate, irregularly oval, convex above and flattened below as usual except for usual concavity of the metasterna and metacoxal laminae. Total length 1.68 mm; greatest width near middle of elytra 0.8 mm; width of pronotum at base 0.68 mm; width of pronotum at apex 0.40 mm; length of pronotum at midline about 0.28 mm. *Head* with fronto-clypeal sulcus only vaguely less evident at middle, not distinctly interrupted. Frontal impressions not conspicuous. Clypeus with a few fine, scattered punctures. Anterior part of front finely and sparsely punctate except for some denser punctures behind the fronto-clypeal impression and the usual converging lines of punctures in the frontal impressions. Punctures not much denser or coarser between the eyes along the distinct transverse cervical suture just behind the eyes. *Pronotum* with setate punctures on the anterior part not much coarser than those on front but more regularly distributed over surface. Punctures coarser and some rugose sculpture along pronotal base between the plicae. Pronotal plicae about 1/2 length of pronotum at midline, impressed and curved at base but nearly straight slanting inward on disk. *Elytra* with moderately coarse setate punctures, but the punctures not deeply impressed. Transverse microsculpture distinct between setate punctures, but surface shining, not iridescent. Elytral plicae slightly longer than pronotal plicae, curved at base and then nearly straight slanting onto disk. *Venter* with apex of prosternal process slightly widened, sulcate, but shortened (in holotype only). Metacoxal laminae with coarse punctures in middle, and roughened areas along fore and back margins which may represent stridulatory organs. Middle tibiae curved. Basal abdominal sternites with transverse rows of large, deep setate punctures as usual. Last visible sternite with coarser setate punctures and some rough sculpture toward apex, but not conspicuously impressed, lateral basal impressions not conspicuous.

Allotype Female (= paratype female).— very similar to male except for shortened more obovate form and secondary sexual characters. *Elytra* with dense microsculpture but not strongly iridescent. Apex of prosternal process widened at base and then elongated as usual with a distinct longitudinal sulcus. Fronto-clypeal impression almost complete across head, only slightly interrupted at middle.

Color.— Specimens are of much the same color as those of *B. mexicanus* when mature. Clypeus and fore part of front yellow or brownish yellow, rest of head back of transverse cervical suture brown. Pronotum largely yellow or brownish yellow, narrowly dark brown along hind margin and between the basal plicae. Elytra dark brown, not iridescent, and with only vague indications of darker and lighter areas toward margins. Venter mostly yellow or brownish yellow, darker in places along sutures and at joints as usual. Appendages mostly yellow.

Variation in the few specimens seen is largely confined to differences in coloration which may be attributed to the degree of hardening of the cuticle. Males from Mexico and Venezuela, with male genitalia apparently identical with those of the holotype, show the teneral pattern with distinct lighter stripes on the elytra and distinct dark humeral, postmedian, and preapical spots alongside associated with lighter areas between the dark spots and at the apex.

Distribution.— Holotype, allotype (= female paratype), and one female paratype from COSTA RICA, Turrialba, 1-19 July 1965, P.J. Spangler (NMNH). One male, one female paratype from MEXICO, Vera Cruz, Cuitlahuac, 10-12 August 1964, P.J. Spangler (FSCA). One male paratype from VENEZUELA, Guarico, 12 mi. S. Calabozo, Est. Biologica Los Llanos, 6-12 February 1969, ultraviolet light trap, Paul and Phyllis Spangler (NMNH).

Bidessonotus fallax J. Balfour-Browne

Bidessonotus fallax Balfour-Browne 1947: 429, Fig. 2 (Cuba).

Diagnosis.— A small dark species about 1.4 to 1.6 mm in total length. Related to *B. mobilis* and *B. rhampherus* by the shape of the aedeagus of the male external genitalia (Fig. 19). Fronto-clypeal sulcus completely across front. Elytral plicae about same length as pronotal plicae or slightly shorter. Prosternal process lanceolate with apex broadly but shallowly hollowed out or sulcate. Metacoxal laminae and basal abdominal sternites with coarse punctures about as in specimens of *B. pulicarius*. Last visible sternite in male with shallow large punctures and rugose sculpture on either side, but not conspicuously impressed; tiny rounded impressions on either side of base. Middle tibiae of male curved. Females with a minute tooth at the outer angle of the apical truncation of elytra (very difficult to see or absent in some specimens). *Color*. in mature specimens distinctly bicolorous, the light anterior part of pronotum contrasting with the dark brown head and very dark brown elytra and base of pronotum. *Venter* dark brown with appendages and underside of head light yellowish brown.

Distribution. I have seen specimens of *B. fallax* only from Cuba where it appears to come to light readily. I originally mistook it for *B. caraibus* so the name commemorates my youthful error. Specimens from the following localities have been examined: CUBA: Mantanzas, 1 km N. Playa Larga, Zapata Swamp, 2 May 1983, P.J. Spangler and Iliana Fernandez C.; Vienega Zapata at Playa Larga, Zapata Swamp, 10-11 Feb. 1981, D. Davis and P.J. Spangler. Pinar del Rio, San Vicente, 7 Feb. 1981, P.J. Spangler and A. Vega. Habana, Cayamas, various dates, E.A. Schwarz, all in NMNH.

Bidessonotus mobilis J. Balfour-Browne

Bidessonotus mobilis Balfour-Browne 1947: 427, Fig. 1 (Mexico, Tabasco, San Juan Bautista.)

Diagnosis.— A moderately large species, about 1.6 to 2.2 mm in total length, and about 0.76 to 1.0 mm in greatest width near middle of elytra. Fronto-clypeal sulcus interrupted at middle. Prosternal process broadly lanceolate, not sulcate. Elytral plicae a little longer than pronotal. Easily distinguished from all other species, except *B. fallax* and *B. rhampherens*, by the curious recurved aedeagus of the male. It is distinguishable from specimens of *B. fallax* by its larger size as well as the different aspect of the male aedeagus (Fig. 20), and from those of *B. rhampherens* by the different structure of the aedeagus which comes to an acute end in males of *B. mobilis* (Fig. 20) but in males of *B. rhampherens* the aedeagus is widened and flattened toward the apex (Fig. 21). In other characters the latter two species are similar to one another but they apparently are not allopatric; *B. mobilis* occurs in eastern Mexico and Central America while the other inhabits the western Cordillera of Mexico.

Male.— In the male of *B. mobilis* the head is much like that of *B. rampherens* except that the frontal impressions along the inside of the eyes are inconspicuous and indicated mainly by the rows of slightly coarser punctures. *Elytra* somewhat more coarsely punctate than on specimens of *B. rampherens*, the setigerous punctures more strongly impressed. The microsculpture of the elytra is evident, but does not give an iridescent cast to the surface. Roughened areas beneath the middle and hind femora are reduced, but with strigate sculpture. Last visible sternite impressed on either side toward the apex and the sculpture somewhat coarser toward apex. Female not seen.

Color.— Most of head, base of pronotum, and elytra dark brown; elytra with usual dark and light areas along outer margins; pronotal disk and side margins, clypeus, and appendages yellow or brownish yellow; meso- and metasterna ventrally dark brown; abdominal sternites yellowish brown or brownish yellow with darker transverse bands across middle. Holotype with suggestion of dark transverse bands of darker color across elytra. Fully mature individuals do not show any suggestion of dark banding except along the outer margins of elytra.

Distribution.— Besides the types from Mexico, I have seen this species from the following localities: MEXICO: San Luis Potosi, Clear stream at Palitla, Dec. 22, 1948, H.B. Leech (CAS). GUATEMALA: North of Morales on Atlantic Highway at milestone 239, 16-18 July 1965, P.J. Spangler (NMNH). BELIZE: Corazal Town, 1 Sept. 1967, G. and R. Lacy (NMNH): Cayo District, 14 km S. San Ignacio, 23 May 1986, at blacklight trap, P.J. Spangler and Robin A. Faitoute (NMNH).

Bidessonotus rhampherens sp. nov.

Diagnosis.— A moderately large species and specimens are similar to those of *B. mobilis*, about 1.8 to 2.0 mm in total length by about 0.8 to 1.04 mm in width at about the middle of the elytra. Body form in males elongate with the outline constricted between pronotum and elytra; somewhat more broadly ovate in females. Males may be separated from those of *B. mobilis* by reference to the shape of the aedeagus and parameres (Fig. 21). Prosternal process with apex narrow, sulcate.

Holotype Male.— Total length about 1.92 mm; greatest width near middle of elytra about 0.96 mm; width of pronotum at base about 0.76 mm; width of pronotum at apex about 0.48 mm; length of pronotum at midline about 0.36 mm.

Elongate oval, somewhat constricted at base of pronotum as in specimens of *B. inconspicuus*. *Head* finely punctate, the clypeal margin almost impunctate, less coarsely punctate on disk than on specimens of *B. inconpicuus*. Fronto-clypeal impression interrupted at middle. Discal impressions along inner margins of eyes distinct with rows of punctures slightly coarser than those on disk. *Pronotum* moderately coarsely punctate on disk, less coarsely than on specimens of *B. inconspicuus*. Punctures between basal plicae coarser than on disk, but not as coarse as on specimens of *B. inconspicuus* and less coarse and confluent just inside the basal plicae on either side. Basal pronotal plicae each about 1/2 length of pronotum at midline, each curved at base then almost straight slanting inward onto disk. *Elytra* with setigerous punctures less impressed than on pronotum. Elytral plicae distinctly impressed, nearly straight slightly longer than pronotal plicae. Microsculpture of head, pronotum, elytra, and venter reduced, most of surfaces smooth and shining. *Venter* with coarse punctures on middle of outer laminae of hind coxae and roughened places beneath middle and hind coxae which may be stridulation devices. Basal abdominal sternites with usual transverse rows of coarse setigerous punctures. Last sternite not transversely impressed and with setigerous punctures fine and more or less regularly distributed over sternite except for a tiny patch where the punctures are more closely spaced just before the apex. Prosternal process narrow, roughened, longitudinally sulcate. Mesotibiae rather feebly curved.

Color.— Head with clypeus brownish yellow and front and base dark brown; color particularly dark along base behind the transverse cervical stria, visible through translucent front margin of pronotum; pronotum dark brown between the basal plicae and with irregular extensions at middle toward the margins; most of disk and front margin of pronotum brownish yellow; elytra dark brown except along margins which are light brownish yellow; venter with legs, antennae, and mouthparts brownish yellow and most of under surface dark brown except along mid-line ventrally which is lighter yellowish brown.

Allotype Female (= paratype female).— Total length about 2.0 mm; greatest width near middle of elytra about 1.04 mm; width of pronotum at base 0.80 mm; width of pronotum at apex about 0.50 mm; length of pronotum at midline about 0.32 mm. Body outline as viewed from above somewhat more regularly oval than in male. Prosternal process medially sulcate. Elytral punctation fine, the microsculpture giving a violet iridescence to surface. Elytra not toothed at margin apically.

Distribution.— Holotype, allotype, and 3 paratypes from MEXICO: Michoacan, Patzcuaro, 7 July 1964, Paul J. Spangler (NMNH). Two paratypes, Jalisco, 25 mi. S. of Guadalajara, 6 July 1964, Paul J. Spangler (NMNH).

Bidessonotus melanocephalus Régimbart

Bidessonotus melanocephalus Régimbart 1895: 332 (Brasil, in tobacco).

Diagnosis.— A dark species similar to *B. inconspicuus* but with very distinctive male external genitalia (Fig. 22). The darkened base of the head and venter should be diagnostic in mature specimens of either sex. The microsculpture is less impressed on the surface of pronotum and elytra than in some species, and the surface is often shining with a reddish cast. Head and pronotum less coarsely punctate but elytra more coarsely punctate than on specimens of *B. inconspicuus*. Fronto-clypeal sulcus nearly complete across front only shallowly interrupted at middle. Elytral plicae about 1 1/4 to 1 1/2 times as long as pronotal plicae. Prosternal process lanceolate but not culcate in either sex, covered with long yellow setae. Last visible sternite not transversely impressed or otherwise modified except for coarser setate punctures and some rugose sculpture toward the apex. The male external genitalia diagnostic; aedeagus more heavily sclerotized than in most species; lateral lobes or parameres relatively simple. Length about 1.7 to 2.25 mm; greatest width near middle of elytra about 0.8 to 1.0 mm.

Females are similar to the males except in the secondary sexual characters, and purplish iridescence is lacking on the elytra. Some individuals of both sexes show indications of a teneral color pattern with dark subhumeral, post-median, and preapical dark spots with lighter areas between and at the apex.

Distribution.— I have seen specimens which I take to be *B. melanocephalus* from the following localities: BRASIL, Bahia, Encruzilhada, 960 meters, ultraviolet light trap, 7 Nov. 1972, M. Alvarenga (FSCA); Bahia, 5 km west of Ilheus, 4 July 1969, Paul and Phyllis Spangler (NMNH). PERU, Huanuco, Tingo Maria, April 19-24, 1969, Paul and Phyllis Spangler (NMNH).

Bidessonotus truncatus J. Balfour-Browne

Diagnosis.— A medium sized to small species about 1.6 to 2.1 mm long with unique male external genitalia, the aedeagus with a recurved subterminal horn (Fig. 23). Fronto-clypeal sulcus nearly or quite complete across front. Apex of prosternal process lanceolate, but not sulcate; narrow and nearly parallel sided in female, not sulcate, but densely covered with setate punctures. Apices of elytra in females more distinctly truncate than in most species. Color.similar to that of specimens of *B. mexicanus* with darkened base of head, narrowly darkened pronotal base between the plicae, and brown eldytral which have a purplish cast in females due to the microsculpture.

Distribution.— I have examined specimens with similar male external genitalia from the following localities. BOLIVIA, Santa Cruz, 11-12 May 1969, Paul and Phyllis Spangler (NMNH). BRASIL: Mato Grosso, Jacaré, Parque Nacional Xingu, Nov. 1965, Moacir Alvarenga and W.C.A. Bokermann (FSCA). GUYANA: Mazaruni-Potaro, District, Takutu Mountains, 6°15'N, 59°5'W, 17 Dec. 1983, Earthwatch Research Expedition, W.E. Steiner and P.J. Spangler (NMNH). PARAGUAY: Central, 15 km N.E. Asuncion, 21 June 1969, Paul and Phyllis Spangler. San Bernardino, 22 June 1969, Paul and Phyllis Spangler (NMNH). PERU: Madre de Dios, Rio Tambopata Res., 30 km S.W. Pto. Maldanado, (subtropical moist forest), 16-20 Nov. 1969, J.B. Heppner (NMNH). SURINAME: Kraaka-Phedra Road, Dist. 25, 25 Oct. 1967 (tiny forest pool with much fallen foliage), Borys Malkin (FSCA). TRINIDAD: Cumoto, 1929, P.J. Darlington, Jr. (MCZ).

Bidessonotus browneanus J. Balfour-Browne

Bidessonotus browneanus Balfour-Browne 1947: 441, Fig. 8 (Jamaica).

Diagnosis.— A medium size to small species ranging in total length from about 1.6 to nearly 2 mm, and in width near middle of elytra from about 0.8 to 0.96 mm. Male external genitalia very distinctive (Fig. 24), and although there may be slight differences in populations from Jamaica, the Dominican Republic, and Puerto Rico, most variation seems to be due to differential changes in drying of the parameres.

Male.— The large axe-like aedeagus varies only slightly from island to island. *Head* finely punctate in front, a little more coarsely punctate on disk but very finely punctate compared with that of specimens of *B. inconspicuus*. Frontal impressions along margins of eyes with slightly coarser punctures in rows. Fronto-clypeal impression distinct or indistinct, sometimes interrupted at middle, sometimes imperceptibly so. *Pronotum* with discal punctures coarser than in specimens of *B. inconspicuus*, but those between the basal plicae finer and less often united than in specimens of *B. inconspicuus*. Basal plicae curved at base and then recurved onto disk of pronotum, about 1/2 length of pronotum at midline. Elytral setigerous punctures not strongly impressed about the same as the pronotal punctures. Elytral plicae each about 1 1/2 length of a pronotal plicae, well impressed. Microsculpture of head, pronotum, and elytral not strongly impressed, surfaces shining. Outer lamina of hind coxae with coarser setigerous punctures medially and rugose areas beneath middle and hind femora which may be stridulating devices. Last visible sternite transversely impressed with setigerous punctures, but not with coarse, elongate strigae as in some species sometimes with distinct patch of setae in a tiny patch toward apex. First and second abdominal sternites with rows of coarse punctures as usual in genus. Middle tibiae of male curved. Prosternal process narrowly lanceolate, sulcate in both sexes. *Female* similar to male except for secondary sexual characters.

Color.— Head brownish yellow, darker along base; pronotum about same color as head, darker between the basal plicae; elytra dark brown with vague indications of lineate markings on disk and a subhumeral, postmedian, and preapical dark spot separated by lighter areas along outer margins. *Venter* mostly brown shining; legs and antennae lighter yellowish brown.

Distribution.— Besides the types of *B. browneanus* from JAMAICA, I have seen this species or its choromorphs from JAMAICA, St. Catherine Parish, Bushy Park, Worth Park and Spanish Town (Institute of Jamaica and FSCA) and Porus, 28 Feb. 1937, flying at dusk, R.E. Blackwelder (NMNH), and Good Hope, 11 August 1966, H.F. Howden (FSCA). DOMINICAN REPUBLIC, Altagarcia, Nisibon, 3 May 1978, R.E. Woodruff and G.B. Fairchild (FSCA) in large numbers at ultraviolet light trap; El Siebo, 17 km S.E. Rio Chavon, 9 June 1976, ultraviolet light trap, R.E. Woodruff (FSCA); PUERTO RICO, Mayaguez, 30 June 1940, ultraviolet light trap, R.E. Woodruff (1 male, FSCA). CUBA: Several localities particularly the Zapata Swamp. I believe the island forms may eventually be shown to be subspecies.

Bidessonotus peregrinus J. Balfour-Browne

Bidessus adumbratus Sharp 1887: 754, *nec* Clark.
Bidessonotus peregrinus Balfour-Browne 1947: 444. Fig. 9 (Panama, Pearl Islands).

Diagnosis.— A small species measuring about 1.3 to 1.8 mm in total length and about 0.72 to 0.9 mm in width near middle of elytra. The lateral outline of the male aedeagus is diagnostic (Fig. 25). Elytral plicae about 1 1/2 times as long as pronotal. Fronto-clypeal impression nearly complete across front. Female usually with distinct purplish iridescence on elytra from the dense microsculpture. Prosternal process narrow, sulcate. Male sometimes with lighter areas at elytral margin extended onto disk.

Male.— *Head* finely punctate on clypeus and on disk with even the rows of punctures in the frontal impressions reduced as well as those in the fronto-clypeal impression which is nearly complete across the front. *Pronotum* with discal punctures fine, but those along base of pronotum between the plicae coarser and especially coarse and partly confluent punctures adjacent to the basal plicae within and extending outward nearly to the margin. Basal plicae deep, curved onto disk, about 1/2 length of pronotum at midline. *Elytra* moderately coarsely punctate, the setigerous punctures on disk about as coarse as those on base of pronotum. Elytral basal plicae deeply impressed, curved at base and nearly straight extending onto disk, about 1 1/2 times as long as pronotal plicae. Microsculpture reduced, most body surfaces smooth and shining. *Venter* with outer laminae of hind coxae with very coarse setigerous punctures over much of surface. Roughened areas beneath middle and hind femora reduced, but finely strigate. Basal sternites with usual transverse rows of coarse punctures. Last visible sternite not greatly modified, setate punctures distributed over surface with coarser punctures near hind margins. Prosternal process narrow in both sexes longitudinally sulcate. Middle tibiae feebly curved in male.

Female.— Similar to males except for secondary sexual characters and color.

Color.— Head and pronotum brownish yellow. Elytra dark brown with microsculpture giving an iridescent purple sheen in females. Venter with legs, antennae, and mouthparts brownish yellow and most body surfaces dark brown. Elytra sometimes with lighter areas extending inward on elytra, but humeral, postmedian, and preapical dark spots only vaguely indicated.

Distribution.— Besides the unique male type, I have seen this species from Panama, C.Z. Albrook Forest site, various dates at ultraviolet light trap, R.S. Hutton (FSCA, NMNH).

Bidessonotus regimbarti J. Balfour-Browne

Bidessonotus adumbratus (Clark) Régimbart 1895:336 336, pl. 8, fig. 12, 12a, *nec* Clark, *nec* Sharp (Mexico in tobacco).

Bidessonotus regimbarti Balfour-Browne 1947: 430 (*nom. nov.* for *Bidessonotus adumbratus* Régimbart *nec* Clark, *nec* Sharp (Mexico).

This name may be clarified when specimens in the Régimbart collection in the Paris Museum (MNHN) are examined. I have not recognized it among my material. The species which I have described as *B. otrerus* from Colombia and Venezuela fits the description and is about the right size (total length 1.75-2.0 mm), but the prosternal process is definitely not triangular and sulcate in the form of a small trench. The description of the darker and lighter spots along the elytral margins fit most species of the genus before the full adult coloration develops. *Bidessonotus vicinus* may be this species, but the prosternal process although feebly sulcate can scarcely be described as having a nearly triangular process. The average size of specimens of *B. vicinus* (total length 1.5-1.7 mm) is also too small. Specimens of *B. vicinus* occurs abundantly in Belize, Venezuela, and the Canal Zone, but I have not seen any from Mexico.

Bidessonotus bicolor Guignot

Bidessonotus bicolor Guignot 1957: 36, Fig. 3 (Brasil, Para, Cachimbo).

The type of this species was not located in the Paris museum (MNHN), nor was it recognized among the material examined. The species may be based on a teneral specimen of *B. melanocephalus* which has not yet developed the very dark head and venter. The prosternal process is described as subrectangular, but no mention is made of a longitudinal sulcus. Guignot's figure of the male external genitalia (Fig. 26) shows a distinct tooth near the outer apex of the aedeagal "blade" and a distinctly pointed basal angle to the "blade" both of which are unlike specimens of *B. melanocephalus* that I have seen. The parameres are described as dilated after the base, a little narrowed then again dilated at the summit which is rounded and bears a few short hairs. The length is given as 2.1 mm which would place the species among the larger species of the genus.

REFERENCES CITED

Aubé, C. 1838. Tome sixième. Spécies général des Hydrocanthares et Gyriniens. *In*, Dejean, P.F.M.A. Spécies général des Coléoptères de la collection de M. le Comte Dejean. Méquignon, Paris. xvi + 804 pp.

Balfour-Browne, J. 1947. A revision of the genus *Bidessonotus* Régimbart (Coleoptera: Dytiscidae). Transactions of the Royal Entomological Society of London, 98: 425-448.

Blatchley, W.S. 1919. Insects of Florida. Va. Supplementary notes on the water beetles. Bulletin of the American Museum of Natural History, 41: 305-322.

Biström, O. 1988. Generic review of the Bidessini (Coleoptera, Dytiscidae). Acta Zoologica Fennica, 184: 1-41.

Chevrolat, A. 1863. Coléoptères de l'Ile de Cuba. (Suite) (1). Notes, synonymies et descriptions d'espèces nouvelles. Familles des Cicindélètes, Carabiques, Dytiscides, Gyrinides et Palpicornes. Annales de la Société Entomologique de France (Série 4), 3: 183-210.

Guignot, F. 1957. Contribution à la connaissance des Dytiscides sud-américains (Coleopt.). Revue française d'Entomologie, 24: 33-45.

LeConte, J.L. 1855. Analytical table of the species of *Hydroporus* found in the United States, with descriptions of new species. Proceedings of the Academy of Natural Sciences of Philadelphia, 7: 290-299.

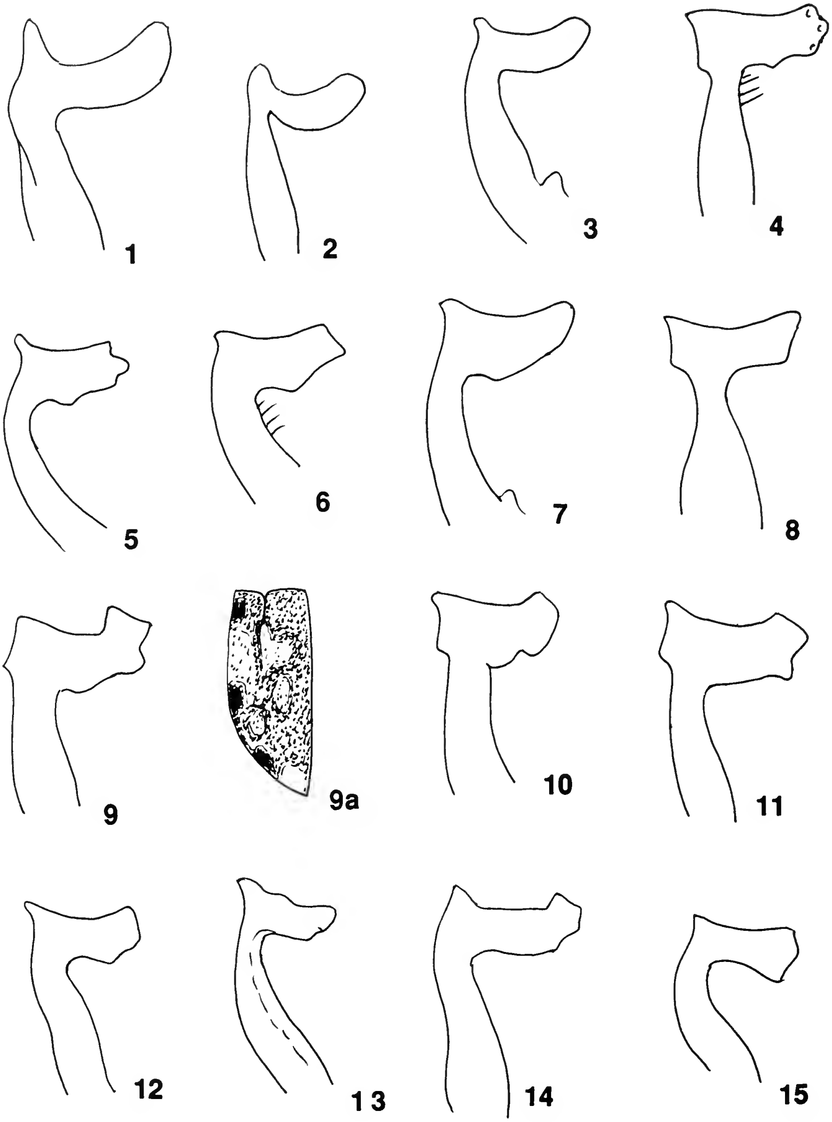
Leech, H.B. 1948. Contributions toward a knowledge of the insect fauna of Lower California. No. 11. Coleoptera: Haliplidae, Dytiscidae, Gyrinidae, Hydrophilidae, Limnebiidae. Proceedings of the California Academy of Sciences, (Series 4) 14: 375- 484 + plates 20 and 21.

Régimbart, M.A. 1895. Dytiscides trouvés dans les tabacs par les soins de M. Antoine Grouvelle. Annales de la Société entomologique de France, 64: 321-348.

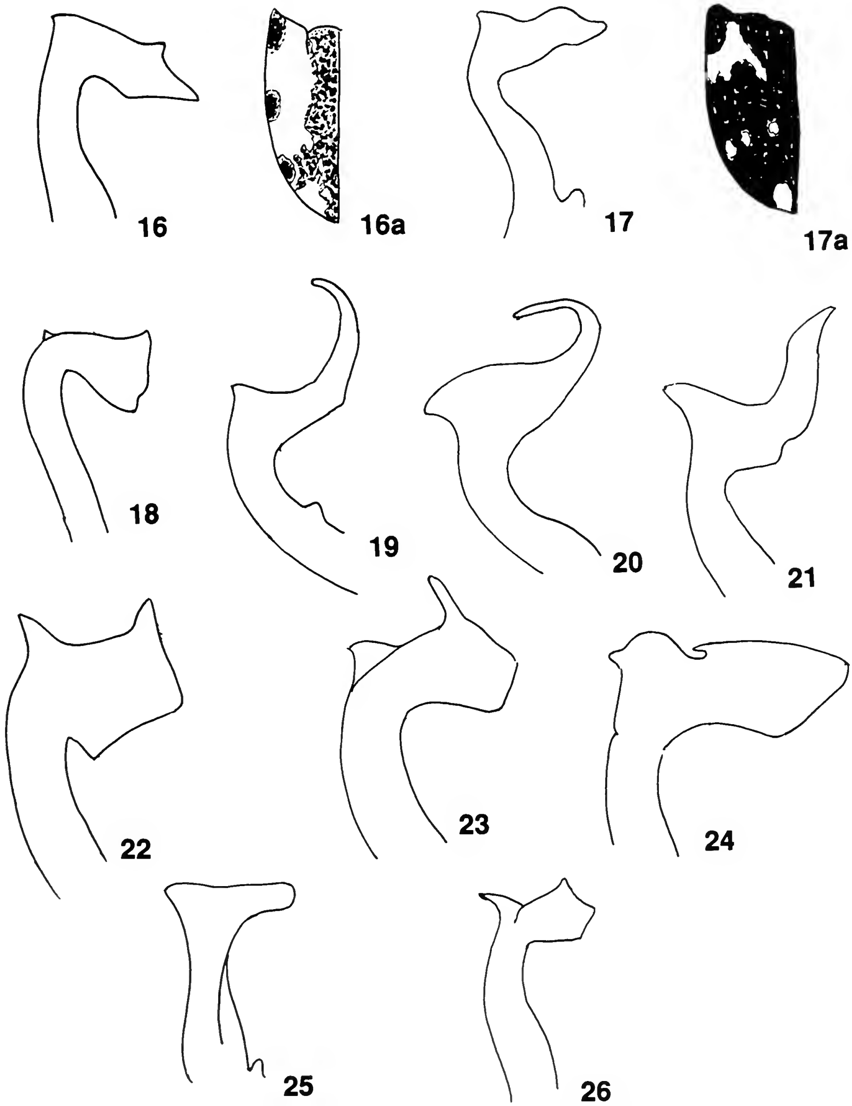
Sharp, D. 1882. Tribe Adephaga (continued). Families Haliplidae, Dytiscidae, Gyrinidae, Hydrophilidae, Heteroceridae, Parnidae, Georissidae, Cyathoceridae. *In* Godman, F.C. and O. Salvin. Editors. Biologia Centrali-Americana; or, contributions to the knowledge of the fauna and flora of Mexico and Central America. Zoology, Botany and Archaeology. R.H. Porter, London. Zoologia 15. Insecta, Coleoptera. Volume 1, part 2: 1-144 + plates 1-4.

Sharp, D. 1887. Staphylinidae; Supplement. *Ibid.* Volume 1, part 2: 673-802.

Young, F.N. 1967. A key to the genera of American bidessine water beetles with descriptions of three new genera (Coleoptera: Dytiscidae, Hydroporinae). The Coleopterists' Bulletin, 21: 75-84.



Figures 1-15. Left lateral aspect of tip of aedeagus in copulatory position of males of various species of *Bidessonotus* Régimbart. Fig. 9a. Diagrammatic representation of teneral color pattern of elytron of *B. obtusatus*. 1) *B. tibialis* Régimbart, 2) *B. sobrinus* J. Balfour-Browne, 3) *B. morosus* J. Balfour-Browne, 4) *B. pulicarius* (Aubé), 5) *B. inigmaticus sp. nov.*, 6) *B. inconspicuus* (LeConte), 7) *B. championi* J. Balfour-Browne, 8) *B. longovalis* (Blatchley), 9, 9a) *B. obtusatus* Régimbart, 10) *B. dubius* sp. nov.,11) *B. rubellus sp. nov.*, 12) *B. ploterus* sp. nov., 13) *B. otrerus sp. nov.*, 14) *B. polostus sp. nov.*, 15) *B. vicinus* J. Balfour-Browne.



Figures 16-26. Left lateral aspect of tip of aedeagus in copulatory position of males of various species of *Bidessonotus* Régimbart. Fig. 16a. Diagrammatic representation of color pattern of elytra of *B. mexicanus* Régimbart. Fig. 17a. Same of *B. pictus sp. nov.* 16, 16a) *B. mexicanus* Régimbart, 17, 17a) *B. pictus sp. nov.*, 18) *B. paludicolus sp. nov.*, 19) *B. fallax* J. Balfour-Browne, 20) *B. mobilis* J. Balfour-Browne, 21) *B. rhampherens sp. nov.*, 22) *B. melanocephalus* Régimbart, 23) *B. truncatus* J. Balfour-Browne, 24) *B. browneanus* J. Balfour-Browne, 25) *B. peregrinus* J. Balfour-Browne, 26) *B. bicolor* Guignot (after Guignot, 1957).

A SYSTEMATIC REVISION OF SPECIES OF *DYTISCUS* LINNAEUS (COLEOPTERA: DYTISCIDAE). PART 1. CLASSIFICATION BASED ON ADULT STAGE.

R.E. Roughley,
Department of Entomology,
University of Manitoba,
Winnipeg, Manitoba,
CANADA R3T 2N2

Quaestiones Entomologicae
26: 383–557 1990

ABSTRACT

Each of the 26 species of the world fauna of Dytiscus *Linnaeus is keyed, defined, characterized and illustrated. Arrangement of* Dytiscus *into subgenera is unwarranted based on the phylogenetic analysis presented. Taxonomic changes include recognition of* D. carolinus *Aubé 1838, formerly confused with* D. fasciventris *Say 1824;* D. validus *Régimbart 1899 is placed as a junior subjective synonym of* D. sharpi *Wehncke 1875; use of* D. czerskii *Zaitsev 1953 at subspecific rank for eastern Palearctic specimens of* D. marginalis *Linnaeus 1758 (western Palearctic specimens);* D. marginalis *is not found in the Nearctic region; arrangement of* D. lapponicus *Gyllenhal 1808 into two subspecies, the nominate, widespread Palearctic form, and* D. lapponicus disjunctus *Camerano 1880 from the Italian Alps; and placement of* D. piceatus *Sharp 1882 as a junior subjective synonym of* D. latro *Sharp 1882 (page priority);* D. mutinensis *var.* striatus *Leblanc 1982 is placed as a junior subjective synonym of* D. dimidiatus *Bergsträsser 1778. The name* D. albionicus *Motschulsky 1859 is transferred from a junior synonym of* D. circumcinctus *Ahrens 1811 to a junior synonym of* D. marginicollis *LeConte 1845. Lectotype designations are provided for the following:* D. sharpi *Wehncke 1875 (male in MNHN, labelled: Japonia);* D. validus *Régimbart 1899 (male in MNHN, labeled: Nagahama);* D. pisanus *Castelnau 1835 (male in BMNH, labelled: Italia);* D. submarginalis *Stephens 1828 (=*D. marginalis *L.) (male in BMNH, without locality data);* D. angustatus *Stephens 1826 (=* D. circumcinctus *Ahrens 1811) (male in BMNH, without locality data);* D. parvulus *Motschulsky 1852 (=*D. alaskanus *J. Balfour-Browne 1944) (male in UMHF, labelled: Kadjak); and* D. dauricus *Gebler 1832 (male in MNHN, labelled Sib.or. 62). Holotypes were studied of* D. marginicollis *LeConte 1851 (MCZC),* D. hatchi *Wallis 1950 (CNIC),* D. sublimbatus *LeConte 1857 (=*D. cordieri *Aubé 1838) (MCZC),* D. pisanus *var.* nonsulcatus *Zimmermann 1919 (ZSBS),* D. persicus *Wehncke 1876 (MNHN),* D. latro *Sharp 1882 (BMNH),* D. piceatus *Sharp 1882 (=*D. latro *Sharp 1882) (BMNH),* D. stadleri *Gschwendtner 1938 (=*D. latro *Sharp 1882) (ZSBS),* D. sinensis *Feng 1935 (USNM) and* D. thianshanicus *Gschwendtner 1923 (OLML). In addition the name* Dytiscus distantus *Feng 1937 (Type locality - Manchuria) is* incertae sedis.

Treatment of each taxon includes, when appropriate: synonymic list with information about type locality and label information from types examined, derivation of epithet; notes about type material; diagnostic combination; description in tabular form; taxonomic notes; discussion of variation; brief discussion of natural history; general description of distribution as well as map *of localities; chorological and phylogenetic relationships. In addition line drawings are provided of: dorsal aspects of adults; color pattern of pterothoracic and abdominal sterna; metacoxal processes; and trochanters. Views of dorsal, ventral and lateral aspect of the median lobe of genitalia of adult males are represented by scanning electron micrographs.*

A preliminary reconstructed phylogeny shows that the sister group of Holarctic Dytiscus *is the Australian genus* Hyderodes *Hope; these two genera comprise the tribe Dytiscini. The most plesiomorphic species of* Dytiscus *is the Nearctic species,* D. verticalis *Say, 1823, and it is assigned to its own species-group; the next species-group to diverge is represented by a clade of four Nearctic species; female specimens of these two clades have non-sulcate elytra. The remaining 21 species are arranged in four species-groups. Three of these species-groups occur in both Nearctic and Palearctic regions; the majority of females in these species-groups have sulcate elytra.*

CONTENTS

INTRODUCTION

The genus *Dytiscus* is one of the 25 genera originally recognized as comprising the Coleoptera by Linnaeus (1758:342). The Linnaean definition of *Dytiscus* was based primarily on natatory setae on the posterior legs, and as such it contained beetles now assigned to Hydrophiloidea and Dryopoidea as well as Dytiscoidea. Of the fifteen taxa assigned to *Dytiscus* by Linnaeus, only two (*D. latissimus* and *D. marginalis*) are accepted within the present definition of the genus, established by Erichson (1832).

The correct spelling and meaning of the generic name has engendered controversy. According to Blunck (1913:8) and J. Balfour-Browne (1960), Geoffroy (1762:185) was probably the first author to note that *Dytiscus* was an incorrect transliteration of the Greek word for 'diver'. Many authors subsequently used the emended "*Dyticus*" or "*Diticus*", although Schmiedlin (1786:239) suggested that Linnaeus' spelling may be derived from the word 'disci' referring to the form of the male protarsus of specimens of *Dytiscus*

(Blunck 1913:9). This would appear unlikely given the composition of the genus by Linnaeus. The present spelling of the generic name was established as valid in 1961 by Opinion 619, Bulletin of Zoological Nomenclature 18.

One hundred years have passed since the world fauna of *Dytiscus* was last treated taxonomically (Sharp 1882). Previous to this, the only comprehensive analysis of the burgeoning knowledge of the world fauna was by Aubé (1838). Both monographs included much new knowledge about adult Hydradephaga in general, and about members of *Dytiscus* in particular. Many of the characters used in the present classification of these groups were presented first in these works. These books, in my opinion, represent two of the most outstanding studies of classification of Hydradephaga. Quality and importance of such works is dependent upon two factors: ability of the author and quality and diversity of specimens available. The high degree of ability of both these workers is evident from, and has been tested by, the continuing importance of these publications. Almost as important are the collections with which these men worked. Aubé and Sharp had the advantage of extensive, worldwide collections accumulated within Europe during the 18th and 19th centuries.

Blunck (1913:2-30) discussed the early, including pre-Linnean, taxonomic history of *Dytiscus*. Blunck's treatment is exceptionally thorough and is invaluable as a source for, and interpretation of, the early treatises which include various species of *Dytiscus*, but perhaps more importantly, he has allowed entrance into philosophical and interpretive aspects of the work of these early systematists. This is particularly useful because of the nomenclatural problems such as those created by the treatment of dimorphic adult females (elytron either sulcate or non-sulcate). Perhaps no other feature of *Dytiscus* has led to the proliferation of names, long and sometimes heated discussions of nomenclature in the literature, as well as loss of time from more important taxonomic endeavours, as has that created by the occurrence of two states of female elytra. The two forms of any given European species were provided consistently with separate specific level epithets. Subsequent demonstration of the dimorphic nature of this variation has led to retention and demotion of these names to the level of variety and aberration. Use of such names in one taxon has precipitated creation of corresponding names in other taxa, which has in turn brought about debate of proper assignment of varietal names, concluding in further confusion and nomenclatural difficulties.

The Zoological Institute of Marburg, Germany must have been an exciting place for study of dytiscids during the late 19th and early 20th centuries. Professor E. Korschelt was in charge of a battery of students whose general project was intensive and careful investigations of all aspects of classification, natural history, structure, function, *etc.* of *Dytiscus*. This group concentrated on one of the larger, most commonly available species, *Dytiscus marginalis* L. Their collective efforts culminated in a magnificent two volume work of more than 1800 pages edited by Korschelt (1923, 1924). Some, but not all, chapters of this work were published elsewhere by the contributing authors. This work and subsequent contributions by both these and other workers must make *D. marginalis* at least one of the most studied members of Adephaga and possibly one of the most studied beetles.

Since Sharp's (1882) monograph, additional names and synonyms have been proposed, and many new distribution records acquired. Because of the amount of information available concerning various members of *Dytiscus*, even knowledgeable coleopterists have assumed that this genus was well understood taxonomically. However, those who have attempted to identify specimens of

Dytiscus to species (from areas outside Europe) discovered that this was difficult to accomplish. Reference to such recent works as Wallis (1950), Zaitsev (1953:341-354), Pederzani (1971) and Larson (1975:394-405) demonstrated that there was no lack of distinctive character states in external features and male genitalia, yet showed that type material of some species was inadequately understood and generally made it apparent that much still remained to be discovered about classification of the species of this genus. More specifically, they revealed that an adequate revision would have to be based on a world-wide study.

Achievement of the means to identify easily and accurately specimens of species is only the first step in gaining understanding of a genus. Additional steps which taxonomists ought to take are analyses of any further information that they have available concerning the members of the genus (i.e. holomorphological, chorological, paleontological and parasitological - Hennig 1966) and integration of this into an appreciation of evolutionary aspects of the taxon under study. Amount of the latter two types of information is severely limited for *Dytiscus*.

Part 1 of this revision offers means of identification of adults, information about type specimens, description of adult stage, a brief characterization of natural history and geographic distribution of species of *Dytiscus*. Subsequent parts of the revision will deal with immature stages and then these data will provide the basis for phylogenetic and zoogeographic analyses.

MATERIAL AND METHODS

Material

This revision is based on study of about 20,000 adult specimens of *Dytiscus*, either borrowed from museums or personally collected. The following alphabetically arranged codens represent collections from which specimens were borrowed or at which specimens were examined. Names of respective curators are also presented. In this list, private collections have the person's name placed first, after the coden. For institutional collections, the curator's name is placed last. My collection is included in the material denoted JBWM.

AMNH	American Museum of Natural History, Central Park W. at 79th St., New York, New York 10024; L.H. Herman, Jr.
ANIC	Australian National Insect Collection, C.S.I.R.O., Division of Entomology, P.O. Box 1700, Canberra City, A.C.T. 2601, Australia; J.F. Lawrence.
ANSP	Academy of Natural Sciences, 19th and the Parkway, Philadelphia, Pennsylvania 19103; S.S. Roback.
ANSU	A.N. Nilsson, Department of Biology, Section of Ecological Zoology, University of Umeå, S-901 87 Umeå, Sweden.
BMNH	Department of Entomology, British Museum (Natural History), Cromwell Road, London, England SW7 5BD; M.E. Bacchus and P.M. Hammond.
BYUC	Department of Zoology and Entomology, Brigham Young University, Provo, Utah 84601; S.L. Wood.
CARR	Mr. and Mrs. J.F. Carr, #24 Dalrymple Green NW, Calgary, Alberta T3A 1Y2.
CASC	Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118; D.H. Kavanaugh.

CISC	Division of Entomology and Parasitology, Agricultural Experiment Station, College of Agricultural Sciences, University of California-Berkeley, Berkeley, California 94720; J.A. Chemsak.
CNIC	Coleoptera Section, Biosystematics Research Centre, Agriculture Canada, Ottawa, Ontario K1A OC6; A. Smetana.
CUCC	Department of Entomology and Economic Zoology, Clemson University, Clemson, South Carolina 29631; S.B. Hays.
CUIC	Department of Entomology, Comstock Hall, Cornell University, Ithaca, New York 14853; L.L. Pechuman.
DEFW	Department of Entomology, Fisheries and Wildlife, University of Minnesota, St. Paul, Minnesota 55101; P.J. Clausen.
EMUS	Entomological Museum, Department of Biology, Utah State University, Logan, Utah 84322; W.J. Hanson.
ENMV	Entomologie, Naturhistorisches Museum, Burgring 7, A–1014 Vienna, Austria; F. Janczyk.
FMNH	Division of Insects, Field Museum of Natural History, Roosevelt Road at Lakeshore Drive, Chicago, Illinois 60605; E.H. Smith.
FNYC	Department of Zoology, Indiana University, Bloomington, Indiana 47401; F.N. Young.
GWSC	G. Swenson, Department of Biology, Ithaca College, Ithaca, New York 14850.
GWVA	G. Wewalka, Kandlgasse 19-21, 1070 Vienna, Austria.
GWWC	G.W. Wolfe, Department of Entomology and Economic Zoology, Rutgers University, New Brunswick, New Jersey 08903.
HBLC	H.B. Leech, 1435 Howell Mountain Road North, Angwin, California 94508.
HNHM	Hungarian Natural History Museum, Baross utca 13, H-1088 Budapest, Hungary; Z. Kaszab.
ICCM	Section of Insects and Spiders, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213; G.E. Wallace.
INHS	Natural Resources Building, Illinois Natural History Survey, Urbana, Illinois 61801; W.U. Brigham.
ITZA	Afd. Entomologie, Instituut voor Taxonomische Zoölogie (Zoölogische Museum), Universiteit van Amsterdam, Plantage Middenlaan 53, Amsterdam 1004, Netherlands.
JBWM	J.B. Wallis Museum, Department of Entomology, University of Manitoba, Winnipeg, Manitoba R3T 2N2; R.E. Roughley.
LACM	Department of Entomology, Los Angeles County Museum of Natural History , 900 Exposition Boulevard, Los Angeles, California 90007; C.L. Hogue.
MCZC	Department of Entomology, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138; M. Thayer.
MNHN	Entomologie, Muséum Nationale d'Histoire Naturelle, 45 bis, Rue de Buffon, Paris 75005, France; H. Perrin and J.J. Menier.
MSUC	Department of Entomology, Michigan State University, East Lansing, Michigan 48824; R. L. Fisher.
MUIC	Department of Biology, Memorial University, Saint John's, Newfoundland AlB 3X9; D.J. Larson.
NDSU	Department of Entomology, North Dakota State University, Fargo, North Dakota 58102; E.U. Balsbaugh, Jr.
NMSU	Department of Biology, New Mexico State University, Las Cruces, New Mexico 88001; J.R. Zimmerman.

ODUC	Department of Biological Sciences, Old Dominion University, Norfolk, Virginia 23508; J.F. Matta.
OLML	Entomologie, Oberösterreichisches Landesmuseum, Museumstrasse 14, A-4010 Linz, Austria; F. Gusenleitner.
OSUC	Department of Entomology and Zoology, Collection of Spiders and Insects, Ohio State University, Columbus, Ohio 43210; C.A. Triplehorn.
OSUO	Department of Entomology, Oregon State University, Corvallis, Oregon 97331; J. D. Lattin.
PMNH	Peabody Museum of Natural History, Yale University, New Haven, Connecticut 06520; C.L. Remington.
RHTC	R.H. Turnbow, Jr., Department of Entomology, University of Georgia, Athens, Georgia 30602.
ROMC	Department of Entomology and Invertebrate Zoology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario M5S 2C6; G.B. Wiggins.
SCSU	Department of Biological Sciences, St. Cloud State University, St. Cloud, Minnesota 56301; R.D. Gundersen.
SDMC	Entomology Department, San Diego Natural History Museum, P.O. Box 1390, San Diego, California 92112; K. Faulkner.
SDSU	Entomology-Zoology Department, South Dakota State University, Brookings, South Dakota 57006; B. McDaniel.
SMFM	Forschungsinstitut Senckenberg, Senckenberganlage 25, 6000 Frankfurt 1, West Germany; R. zur Strassen.
SMNS	Entomologie, Staatliches Museum für Naturkunde Stuttgart, 7140 Ludwigsburg, Arsenalplatz 3, West Germany; K.W. Harde.
SPMC	Saskatchewan Museum of Natural History Wascana Park, Regina, Saskatchewan S4P 3V7; R.R. Hooper.
TAMU	Department of Entomology, College of Agriculture, Texas A & M University, College Station, Texas 77843; H.R. Burke and S.J. Merritt.
UAIC	Department of Entomology, University of Arizona, Tucson, Arizona 85721; F.G. Werner.
UANH	Department of Zoology-Entomology, Auburn University, Auburn, Alabama 36830; G.W. Folkerts.
UASM	Department of Entomology, University of Alberta, Edmonton, Alberta T6G 2E3; G.E. Ball.
UBCZ	Spencer Entomological Museum, Department of Zoology, University of British Columbia, 2075 Wesbrook Place, Vancouver, British Columbia V6T 1W5; G.G.E. Scudder.
UCEC	University of Colorado Museum, Department of Entomology, University of Colorado, Boulder, Colorado 80309; U.N. Lanham.
UCIC	Department of Biology, University of Calgary, Calgary, Alberta T2N 1N4; G. W. Pritchard.
UCRC	UCR Entomological Collection, Department of Entomology, University of California-Riverside, Riverside, California 92502; S.I. Frommer.
UCSE	Biological Sciences Group, Museum of Natural History, University of Connecticut, Storrs, Connecticut 06268; P.W. Severance and C.S. Henry.
UGIC	Department of Environmental Biology, University of Guelph, Guelph, Ontario N1G 2W1; D.H. Pengelly and S.A. Marshall.

UMBS	University of Michigan Biological Station, Pellston, Michigan 49769; E.M. Barrows.
UMHF	Division of Entomology, Zoology Museum, University of Helsinki, N. Järnvägsgatan 13, SF-00100 Helsinki 10, Finland; H. Silfverberg and O. Biström.
UMMZ	Division of Insects, Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48104; R.D. Alexander.
UMRM	Entomology Research Museum, 1-87 Agriculture Building, University of Missouri, Columbia, Missouri 65201; W.R. Enns.
UNHC	Department of Entomology, University of New hampshire, Nesmith Hall, Durham, New Hampshire 03824; D.S. Chandler.
USNM	Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560; P.J. Spangler.
UVCC	Marsh Life Science Building, Department of Zoology, University of Vermont, Burlington, Vermont 05401; R.T. Bell.
UWEM	Department of Entomology, University of Wisconsin, Madison, Wisconsin 53706; W.E. Hilsenhoff.
WEHC	W.E. Hilsenhoff, Department of Entomology, University of Wisconsin, Madison, Wisconsin 53706.
WUBC	W.U. Brigham, Natural Resources Building, Illinois Natural History Survey, Urbana, Illinois 61801.
ZILR	Division of Entomology, Zoological Institute, USSR Academy of Sciences, Unversitetskaya naberezhnaya 1, Leningrad, V-34, USSR; B.A. Korotyaev.
ZMLS	Zoological Institute, University of Lund, S-223 62 Lund, Sweden; P. Brinck and S. Arlebo.
ZMUM	Division of Entomology, Zoological Museum, Moscow State University, Moscow, USSR; N.B. Nikitsky.
ZSBS	Entomologie, Zoologisches Staatssammlung, Münchhausenstrass 21, D-8000 München 60 Germany; G. Scherer.

Methods and Techniques

Cleaning and dissection of specimens.— Many specimens of *Dytiscus* are greasy and dirty, and, as such, they are not useful for detailed examination of structural features. Specimens were cleaned by placing them in a beaker of warm water to which was added a small amount of ammonia-enriched detergent. The beaker was placed on a hot plate adjusted to low heat for about 12 hours. After removal, specimens were rinsed with clean water and appendages positioned to avoid possibility of breakage.

Dissection of genitalia preceded the clean-water rinse. A number of techniques for extracting the sclerotized terminalia of adult *Dytiscus* were tried. The most effective method for male specimens is to grasp the relaxed beetle in one hand and to deflex the abdomen. An incision made between the third and fourth terga allows the base of the median lobe and parameres to be grasped with a pair of fine forceps. By pushing anteriorly and then pulling upward and posteriorly, the median lobe and parameres of most specimens can be extracted without damage and the remainder of the aedoeagus left in place. Removal of the male genitalic capsule by grasping the apex of the median lobe, parameres or associated structures is to be avoided because of the probability of damage. The median lobe is best separated from the parameres by placing two pairs of forceps into the basal space provided by the curvature of the median lobe and then gently pulling the forceps in opposite directions. This technique pulls the base of the median lobe away from the bases of the parameres and allows for clean preparation with a minimum of damage.

Terminalia of adult female specimens were dissected in a different manner. Musculature around an ovipositor was cut with a lancet inserted through the abdominal apex and then the capsule pulled out with forceps. Because stylomere I, at rest, is flexed anteriorly over the top of the remainder of the capsule there is little possibility of damage using this technique. Preliminary analysis of shape of the apex of stylomere I (*e.g.* Pederzani [1971:221], Régil and Salgado [1984]) indicates that this feature may be taxonomically useful. However, the distinction among taxa is difficult to characterize and was not used in this study.

Portions of both male and female genitalic capsules removed from specimens were glued to cards placed on the pin of the specimens from which they were removed. Teneral or unsclerotized genitalia were placed in small, glycerine-filled vials and mounted on the specimen pin.

Measurements.— Adult specimens of *Dytiscus* were measured for total length (TL) and greatest width (GW) of the body. A ratio of these values (TL/GW) gives an index of body shape. Measurements were taken by means of a moveable stage Vernier scale to which a specimen holder was attached. By aligning a set of cross-hairs in the microscope eyepiece with an end of the beetle and then turning the knob on the stage micrometer until the other end of the specimen was lined up with the cross-hairs, the numerical value could be read from the scale on the stage micrometer.

An investigation of absolute size measurements of specimens of *Dytiscus* and its taxonomic value was initiated after noting discrepancies in overall size of specimens. For instance, Larson (1975:397) commented on the smaller mean TL of adult specimens of *D. harrisii* from Alberta and the Northwest Territories compared to specimens from Ontario and Wisconsin. I found a similar but less striking difference: average TL for 10 specimens from Alaska, Alberta, Northwest and Yukon Territories was 34.9 mm, compared to 36.8 mm for 10 specimens from Ontario. Three adult male specimens of *D. harrisii* which I collected by bottle traps near Old Crow, Yukon Territory, however, had an average TL of 36.6 mm. In addition, a single male collected as a prepupa from Kneehills Creek near Acme, Alberta is 39 mm long. This suggests a sampling bias, although there was no significant difference, possibly because the eastern sample contained more males (male specimens are commonly slightly larger than females).

Another taxon, *D. dauricus*, which is more common in Alberta, was investigated more intensively for average specimen size with respect to method of capture. The results are presented in Table 1. Similar trends were found in most species for which I have sufficient numbers of bottle-trapped specimens.

Adults of larger species of dytiscids are very quick and agile swimmers and are more difficult to collect with a dip net whereas smaller species are more commonly and easily collected with this method. For instance, at George Lake near Busby, Alberta, hours of dip net collecting yields only a few specimens of *Dytiscus* but hundreds of specimens of smaller species, whereas bottle traps have yielded in excess of 80 specimens of *Dytiscus* per trapping period (Aiken and Roughley 1985). This same phenomenon could be true for specimens of a single species of *Dytiscus* - *i.e.*, smaller specimens have a greater chance of being caught by dip netting. Differences in TL for adult *Dytiscus* noted above are probably correlated with the method of capture.

Because of this sampling bias, I have excluded body measurements of population samples of species of *Dytiscus* from the descriptions of the species.

Table 1. Comparison of total length, greatest width, and ratio of total length - greatest width (TL/GW) of bottle trapped specimens of *Dytiscus dauricus* Gebler (Coleoptera: Dytiscidae) from George Lake, Alberta, and values reported by Larson (1975:403) for specimens captured by unspecified methods.Values are mean q standard deviation, with ranges in parentheses. Sample size is 28 for both samples. Lengths in mm.

Collecting method	Total Length	Greatest Width	TL/GW
Bottle trap	34.3 ± 0.8 (33.2-36.2)	18.2± 0.5 (17.5-19.1)	1.91± 0.04 (1.8801.98)
Various methods (Larson, 1975:403)	32.9±1.3 (30.0-35.0)	16.5±0.7 (15.5-18.5)	1.93±0.04 (1.86-2.03)
Probability of a larger value for *t*-statistic	$p < 0.005$	$p < 0.005$	0.05-0.10

I present only the extremes of measurements of TL, GW and TL/GW for each taxon, and only as an indication of size range (Table 2). These measurements are based on specimens examined.

Taxonomic Procedure.— Physically large museum specimens do not travel well by mail, and cause problems if large numbers of them are assembled in one institution by borrowing— the normal practice by taxonomists. Instead of borrowing, I identified and obtained data from most specimens within the museums possessing them. Therefore, I had to learn the characteristics and limits of species before leaving for museum travel by intensive study of representatives of each species and reference to important faunistic treatments such as Larson (1975) for Nearctic species, and F. Balfour-Browne (1950), Zaitsev (1953) and Schaeflein (1971) for Palearctic taxa. In addition, other publications of more restricted scope were used to allow interpolation of other taxa treated in these references.

A problem with such on-site study is that assignment of specimens to a particular name is done comparatively quickly, with little opportunity for re-examination. Therefore, there is a pronounced possibility of misdetermination of specimens. To reduce such errors, specimens difficult to identify were borrowed from museums and studied in a manner similar to that described by Erwin (1970:9-10) and Whitehead (1972:140-141).

Descriptive Format.— The treatment of each taxon begins with reference to the original description of each valid name or synonym of that taxon. This is followed by information about type locality and information about label data from, and repository of, type material, if known. Most species of *Dytiscus* have a long taxonomic history. Instead of citing all references, the above information is followed by reference to Zimmermann's (1920) thorough catalogue, which provides reference to most, if not all, pre-1920 literature of importance. Any citations of a name after 1920 follow the Zimmermann reference in chronological order, but citations of other catalogue or faunal lists are omitted.

For the valid name of each taxon, I have provided an explanation of the meaning of the name. If further explanation is needed for the status or location of type specimens, this follows the etymological section. A diagnostic combination provides a list of characteristics useful for identification of adult specimens.

Descriptions of species are provided by reference to Table 3. A tabular method of description is of great value because of reduced length and increased ease of comparison. Construction of this table follows the general format presented by Erwin (1982) except that the characters are arranged in phylogenetic sequence - *i.e.*, the first character state of each character discussed is plesiotypic while the second is apotypic. For explanation of the rationale of character state assignment see characters used in phylogenetic analysis. The description also contains reference to figures of structural features provided for each taxon.

Treatment of variation in structural features is confined to taxonomically important characters, regional differences in number of females with grooved elytra, and geographically related trends of other features. In the section on natural history, I provide information about the habitat or habitats of occurrence and some life history features for adults of *Dytiscus*. These sections are generally more extensive for Nearctic species for which I have field and laboratory observations. For most Palearctic species, I present little information; in general, information about these species is discussed in the papers which were used to compile the distribution ranges (see below) or in various papers in Korschelt (1923, 1924), Balduf (1935), Blunck (1913-1924) or Wesenberg-Lund (1912, 1943) and is not summarized here.

Distribution is shown on maps (see Distribution Maps section below for explanation of procedures used to make up the maps) and this information is generalized into a description of the range. A section entitled chorological relationships provides information about geographic co-occurrence with other species of the genus.

Many Nearctic species of *Dytiscus* have their closest relatives in the Palearctic region, while other species of either realm are members of a small clade restricted to that realm. The relative phylogenetic position of each taxon is presented in a discussion of phylogenetic relationships. A total of the number of specimens examined as well as the number of each sex is the final entry of each species treatment.

Illustrations other than distribution maps.— Line drawings were made with the aid of a camera lucida mounted on a Leitz steroscopic microscope. Illustrations of median lobes of males of various taxa of *Dytiscus* were made by mounting these structures on stubs, onto which was placed two-sided tape, coating with gold and photographing with the aid of a scanning electron microscope, Cambridge Stereoscan 5150. Subsequently median lobes were removed from the stubs and placed back on the genitalia card of the specimen from which they originated.

Distribution maps: mapping of specimen localities.— Standard techniques were used for mapping specimen localities and consisted of finding a locality, usually in an atlas (but see below), and placing a symbol on the approximate locality on an outline map and within the region indicated (e.g. province, state, départemente, kraj, *etc*.). Within the Nearctic region, this process was straightforward and did not present many problems. All Nearctic locality records are based on specimens seen during this study or by Larson (1975). All Nearctic locality records and all Palearctic records for which specimens were examined are indicated by filled symbols (*e.g.* •).

Because of logistic problems explained elsewhere, I have accepted some published records that I could not verify for some Palearctic species of *Dytiscus*, because it was determined that the historical assignment of most Palearctic taxa was in agreement with, or could be assigned to, my concepts of these taxa. Also, examination of collections within selected European museums convinced me that the degree of accuracy of assignment of most Palearctic taxa was quite high. Principally because of consistency, literature records were accepted as useful and accurate additions to knowledge of distribution of these taxa. I believe that amount of error introduced is insignificant compared to amount of information that would be lost by exclusion of literature records. Literature records for localities are also indicated by filled symbols (*e.g.* •).

For the most part, published records for political areas in which a specific locality is not mentioned were ignored. An exception to this is locality information for the USSR from which I saw very few specimens. In this instance, published records for political areas were accepted and are represented by open symbols which are placed over the former capital city of that political area. Most of these records were obtained from Jakobson (1905) and represent political divisions which no longer exist or are presently known by different names.

Interpretation of presumptive locality names.— Within the Palearctic region, assignment of locality names to particular places is more difficult and complicated than for the Nearctic region. This is because of my lack of familiarity with Palearctic localities, lack of a country or regional name on many Palearctic specimens, differences in language and transliteration, as well as problems associated with interpretation of enigmatic or cryptic label data. Procedures used when confronted with these problems include the following. 1, Inference based on the collector (I have assumed that most collectors have collected within the vicinity of their geographic home or homeland). 2, Commonly used historical interpretations of locality names were generally accepted (*e.g.* "Königsberg" interpreted as "Kaliningrad, Russian S.F.S.R." 3, When a name refers to both a region and a populated place (*e.g.* Astrachan is both the name of a city and an oblast in Russian S.F.S.R., U.S.S.R.) I have used consistently the place name for purposes of mapping. 4, Transliteration is a particular problem with certain locality names (*e.g.*, the Siberian city, Čita, is rendered 'Tschita' in German, 'Chita' in English, *etc.*). In this revision, I have followed the practice of recent international atlases, and used the official transliteration schemes adopted by the country in which localities are presently located (thus 'Čita', rather than 'Chita'; 'Astrachan' instead of 'Astrakhan'). 5, Maximum concordance among all label data is important. For example, a label in Cyrillic script was transliterated as "Jakovskoje, Spas. u., Ussuri kr." and this was interpreted as "Jakovskoje, near Spassk Dal'niy in the former Ussuri Kraj of Russian S.F.S.R., U.S.S.R." even though modern atlases list many places with the name Jakovskoje, but none in the Ussuri region. Similarly, date of collection of specimens was used as an aid in choice of locality names. The presumptive locality must have been known by that name during a time span that includes the date of collection. For instance, the specimen referred to above was collected in 1926 and the Ussuri Kraj existed as an official entity only from 1926 until 1938 (Seltzer 1962). 6, Concordance of presumptive locality with known range of a species was used in examples where a choice among probable localities was necessary. If presented with a choice of presumptive localities, some of which were outside, and only one of which was inside the known range of a species, then the latter was accepted as correct. The known range was decided on the basis of other, unambiguous locality information. 7, When the above methods failed, an appeal was made to colleagues or other workers who have specialized knowledge of various geographic areas. Finally, if all or some of these procedures were insufficient to determine where a presumptive locality might be, then the locality name is listed under the heading "Locality not determined". In the list of specimens examined (deposited in JBWM), my interpretation of problematic localities is given, for any locality "A", as "A [=A']" for locality interpretations which I think are probably correct, and as "A [?=A']" for less certain interpretations.

Sources of information about geographical localities.— Many sources were used for tracing locality names. Most extensively used sources for place names were Bartholomew (1955, 1956, 1957, 1958, and 1959) and Seltzer (1962). The latter was particularly useful because of the historical treatment given various place or regional names. Most Nearctic localities were found by means of state and provincial maps. Many Canadian localities were found in Energy, Mines and Resources Canada (1980) atlas. Modern German and French language world atlases were essential. Other sources, used mainly for older names in the Palearctic region were Chisholm (1899) and Blackie (1887) which were especially useful for many 19th Century place names. Room (1979) was an invaluable source for following the changes of many place names from 1900 to 1978. Many European cities have been known by Latin names, and for interpretation of these, the work of Deschamps (1870) served admirably.

An appeal for more complete labelling of specimens.— Many specimens from European as well as North American collections do not include country names on the labels. Thus, an inordinate amount of time and effort is required to compile correct locality information. Two examples demonstrate the amount of time and effort wasted by taxonomists because of this oversight of collectors (previously including me).

In the course of this study, a specimen received was labelled "S. Georgia" with no further information supplied (*i.e.*, collector, date, or country). This locality information could be variously interpreted as: 1) southern Georgia, U.S.S.R., 2) southern Georgia, U.S.A., 3) south of Georgia, Vermont, U.S.A., 4) Strait of Georgia, British Columbia, Canada, or 5) South Georgia, an island in the South Atlantic Ocean. Application of procedure 6 noted above meant that the U.S.S.R. locality was most likely the correct one.

The second example concerns various abbreviations used for States and Provinces. For instance, the current abbreviation used by the U.S. Post Office for the Province of Alberta is "AB" while the abbreviation most commonly used by Canadians is "Alta". Both of these abbreviations have been and are being used by collectors without any indication of country of origin.

During a recent trip to Europe, a colleague talked to a European lepidopterist who had traded specimens with workers in Alberta. This colleague was asked about the incredible diversity of butterflies occurring at "Alta, Colorado". Not realizing that "Alta" was an abbreviation for the name of a province in Canada, the collector had made a choice among the four "Alta" localities which he could find in his sources of information about North American geography: Alta, Colorado; Alta, California; Alta, Iowa; and Alta, Utah, all of which are in the wrong country.

Problems associated with interpretation of label data and locality information probably account for a good deal of reluctance of some entomologists to study the fauna of other regions. This situation runs counter to the developing trend in insect systematics to consider the total fauna of groups so that more information is available for phylogenetic and zoogeographic analysis. Much is lost and confusion and conflicts occur when a common fauna (in this example, Holarctic) is studied by vicariant systematists working in isolation from one another. Part of the problem can be solved so easily by proper labelling of specimens.

Ranking: subgenera.— Subgenera are taxonomically useful and provide the basis for organization of species within large, divergent genera or within smaller genera which encompass a large amount of divergence (Ball and Roughley 1982). This utility is enhanced if different subgenera occupy different adaptive zones. Each subgenus however, must represent a natural evolutionary unit, *i.e.*, it must be monophyletic.

I have recognized no subgenera within *Dytiscus*. Subgenera recognized previously are nomenclaturally invalid and/or do not represent phylogenetically distinct clades. As well, I can discern no new adaptive zones of member taxa, nor does any group of species diverge sufficiently from the basic structural pattern enough to warrant subgeneric assignment.

Ranking: species groups.— Use of species-groups provides increased information and convenience without the demands and increased complexity of formal nomenclature. They represent an abbreviated notation for a group of species which are defined in a more complex manner. For instance, the group of species of *Dytiscus* which possess acuminate metacoxal processes are referred to herein as the D. *dauricus*-group. See Lindroth (1969:xxiii-xxiv) for further discussion of use of species-groups.

I have used species-groups for small monophyletic clades because of communicative value and ease with which these smaller groups are discussed in treatments of classification; however, these species-groups are not characterized formally. I have not used any uniform manner in selecting the nominate taxon of species-groups. Instead, I have used the name of that taxon which represents a mental image of the species-group to me (Fig. 52).

Ranking: species.— Most animal taxonomists subscribe, at least nominally, to some form of Mayr's (1942) "biological" species definition. This, however, represents a theoretical ideal of how animals should behave, and is most difficult to test or even infer consistently or uniformly from the patchy samples characteristic of most analyses of taxa. After comparing and contrasting various species concepts used by botanists and zoologists and their uses and values in practice, Cronquist (1978:3) suggested that: "Species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means." Cronquist further details problems with strict use of a narrow or even a single species definition. Similarly, Hammond (1981a and b) has suggested that concepts of species and speciation built from experience with large, mobile vertebrates with low reproductive rates do not apply well to many insect groups.

The more important goals of the brief discussion above are to point out the need for a re-evaluation of species concepts by practicing animal taxonomists. Of paramount importance is the need for every taxonomist to state clearly the criteria for species recognition which they have used.

My study of taxonomic status of population samples of species of *Dytiscus* was hampered by low numbers of most samples, and samples from widely separated areas. Such disparate samples probably come about because of lack of collecting attempts in certain areas, shortage of museum storage space, difficulty of collecting large fast-swimming beetles, seasonal occurrence of adults, relatively low levels of abundance, and bias of certain collecting techniques (see Measurements). While it is true that most species of *Dytiscus* so far encountered in the field are common to very abundant in the correct habitat at the correct time of year, it is also true that they are always at a relatively low density [*e.g.* see James (1970) for *D. fasciventris* and discussion of natural history in my treatment of *D. cordieri*]. Low density is almost certainly a result of the status of these beetles as major predators within most pond ecosystems.

I required a practical and useful means of delimiting species which could circumvent such problems. The most useful criteria I have found for delimitation of species of *Dytiscus* is form of apex of median lobe and sympatry. Characteristics of the median lobe are distinctive, so that even closely related species are differentiated consistently, and median lobes of male specimens of the same species from widely separated parts of the species range are similar. For instance, the median lobes illustrated in Figs. 18D and 19A are close to the extremes of variation found within a single putative species (in this example *D. circumcinctus*), yet the respective specimens are from Edmonton, Alberta, Canada and Berlin, Germany. Females were associated on the basis of co-occurrence with males and by general similarity in body shape and colour pattern. Although not used in my study, Régil and Salgado (1984) have shown useful taxonomic characters in the form of the female genitalia. Sympatry of divergent forms was used as a corroborative test of species status. However, in examples for which no sympatry is known (*e.g. D. habilis* - *D. marginicollis*; *D. semisulcatus* - *D. sharpi*) difference in form of median lobe is considered sufficient for assignment to species status.

Ranking: subspecies.— Mayr (1963, 1969) and Simpson (1961) provide thorough analyses of theoretical and genetic aspects of subspecies and subspeciation. Kavanaugh (1979:92-94) and Lafontaine (1982:9-10) presented balanced and valuable discussions of use of subspecific rank, and more importantly have expressed their practical criteria for recognition of subspecific status. I have accepted, amalgamated, and used the criteria of the latter two authors. Subspecific names are used for sets of population samples which are: 1, independent or isolated evolutionary units; 2, presently differentiated from other conspecific units but excluding differences thought to be ecophenotypic; 3, sufficiently phenotypically distinct that, except for similarity of aedoeagus of male specimens, they approach the amount of phenotypic divergence found among any two closely related species; and 4, of significance in analysis of historical zoogeography. Such populations are inferred to be isolated at present only by geographical gaps in range. If this barrier to gene flow is maintained for a sufficient period of time, then it is predicted that these populations will diverge sufficiently to preclude future mixing of genetic information. In short, subspecies status is used for inferred incipient species status.

The amount of meristic variation observed in most species of *Dytiscus* is quite low. I believe this is due in large part to various aspects of life history of these species, such as dispersal, which lead to panmixis. Because of the normally uniform nature of most species, phenotypically distinct populations are quite apparent, *i.e.*, they stand out. Therefore, my procedure for assignment of rank is recognition of subspecific allopatric populations of consistently distinct phenotype, but of which male specimens have sufficiently similar forms of the apex of the median lobe of the aedoeagus to be included in the same species.

Infraspecific categories other than subspecies.— Literature concerned with taxonomy of European species of *Dytiscus* is replete with names for such infraspecific categories as variety, form and aberration. As such, and provided that they are truly intended as something other than subspecific levels, they are outside the jurisdiction of the *International Code of Zoological Nomenclature* and each taxonomist is free to deal with them as seems appropriate. Within species of *Dytiscus* these names are used predominantly to express differences in sulcation of the elytra of female specimens. For instance, female specimens of *D. marginalis marginalis* vary in degree of elytral sulcation, from those with distinct elytral sulci to those with no trace of sulci, with every conceivable intermediate. However, the latter category is decidedly less numerically common in collections. These respective forms are generally named *forma typica*, var. *conformis* Kunze (even though Kunze described *conformis* as a distinct species), and var. *semicostatus* Reineck.

I believe that use of such names, some of which have no obvious descriptive value, to be retrogressive and needless. If Nearctic and other Palearctic species were all treated in a similar manner, then proliferation of names would be extensive, but our understanding of this intriguing phenomenon would, I think, be diminished and obscured. In an attempt to increase the descriptive and therefore communicative value of variation in degree of elytral sulcation I have not recognized any names below the rank of subspecies and instead I have discussed it as occurring in two states: sulcate and non-sulcate. The former state includes all specimens with any trace of sulcation visible on an elytron. Use of these two states allows clear and unambiguous expression of any geographical pattern in elytral sulcation without detailed knowledge of the taxonomic history of a species.

STRUCTURAL FEATURES

Sexual dimorphism

Adults of *Dytiscus* exhibit a number of characters which are sexually dimorphic. Excluding male and female genitalia, the most obvious of these are the following: 1, male specimens are broader and longer on average; 2, pronota of male specimens are wider at the base and less narrowed anteriorly; 3, profemora of males are bowed along their length and are more robust and more deeply emarginate ventrally; 4, male specimens have two tufts of long setae at the base of each profemur compared to one tuft on female specimens; 5, male protibiae are more robust and widened basally; 6, three basal protarsomeres of male specimens are laterally expanded and form a large subcircular acetabulum, with tarsomere I bearing two very large and numerous small suckers and tarsomeres II and III each with only numerous smaller suckers; 7, male mesotibiae are slightly longer and very slightly more robust; 8, male specimens with three basal mesotarsomeres elongated and widened to form an acetabulum, these tarsomeres bearing numerous small suckers; 9, some adult females of some species have 10 longitudinal narrow grooves or sulci on each elytron; and 10, male specimens possess natatory setae on both the anterior and posterior faces of both the metatibiae and basal metatarsomeres, while female specimens bear natatory setae on the anterior faces of the metatibiae and on the posterior faces of basal metatarsomeres, only.

Body size and shape.— Despite the limitations of measurements of body length (see Measurements), I have made limited use of total length (TL) in distinguishing among members of certain pairs of species, especially where there is no overlap among the adults in size. However, TL is used also in examples where the majority of specimens of a species tend to be larger or smaller than the majority of specimens of another species treated in the other rubric of a couplet in the key. Ranges of lengths of specimens examined are shown in Table 2 for each species of *Dytiscus*. In general, the most common length of specimens is toward the upper end of the range, but there are exceptions (*e.g.* compare information in Tables 1 and 2 for Nearctic specimens of *D. dauricus*). Body shape (TL/GW) is relatively uniform among species of *Dytiscus* (Table 2, except *D. latissimus*). Differences in body shape are used in certain species pairs where there is no overlap of range in this ratio.

Head.— Five taxonomic characters of the head are used. The anterior margin of the clypeus of specimens of most species is linearly transverse or slightly concave, whereas in specimens of *D. harrisii a*nd *D. latissimus* it is distinctly bisinuate. The posterior margin of the clypeus is normally on the same plane as the frons. In female specimens of *D. dauricus*, however, it is distinctly and abruptly raised above the level of the anterior margin of the frons, and is quite useful for recognizing female specimens of this species.

All members of *Dytiscus* have a more or less distinct chevron-shaped pale mark on the frons between the eyes. Typically the lateral arms of the chevron are not extended antero-laterally to the antennal bases, but in some species where this occurs in most specimens, this character state is taxonomically useful. In some specimens, yellow coloration associated with increased chevron size extends posteriorly from the antennal bases along the inner margins of the eyes and thus forms an inverted M-like mark on the frons. However, members of only one species, *D. circumcinctus*, were observed to have the entire eye ringed with yellow on the dorsal surface.

Members of all species of *Dytiscus* have lateral yellow bands on the pronotum. Anterior and posterior bands are or are not present. Specimens of any given species vary in colour and, generally, lighter specimens of a taxon which would normally show no trace of, for instance, an anterior pronotal band, have a very narrow yellowish or reddish band. Characterization of relative width of anterior or posterior bands is quite important. For instance, in couplet 3 of the key to Nearctic species, the alternatives are anterior band less than 0.4 versus more than 0.5 width of lateral band. I have not recorded a specimen of either category which is very close to these measurements. For instance, most specimens following the first alternative are in the range of 0.3 or less and those following the second alternative are in the range of 0.6 or more. Therefore, the values used in the key were chosen to allow for more variation than recorded and to avoid a strictly comparative character such as anterior pronotal band wider versus narrower. Even if exceptional specimens are encountered, subsequent comparison to the diagnostic combination of each species should allow discovery of misidentification.

The pronotum of most specimens of *Dytiscus* has a longitudinal, shallow channel near the lateral margin. When this character state is present the pronotum is described as explanate. Reduction or lack of an explanate pronotum is characteristic of the members of the *D. hybridus*-group and of male (but not female) specimens of *D. cordieri*.

Legs.— Length of the apical pro- or mesotarsal segment is used commonly in the keys as an aid for determination, but in the form of a comparative rather than as an absolute numerical value. Pro- and/or mesotarsal claws are longer or shorter than pro- or mesotarsomere V, or the values are converted to a proportional value. Proportional length of protarsomere V to width of protibia, measured at the widest point, allows establishment of two species-specific categories for males of some species. Relative number of punctures on the anterior surface of protarsomere V is also used.

Male specimens of *D. hybridus* and *D. marginicollis* are distinctive in that mesotarsomeres II and III lack suckers from a small longitudinal area. Male specimens of all other species of *Dytiscus* have suckers evenly distributed over mesotarsal acetabula.

Coloration of metacoxal plates follows that of pterothoracic sterna discussed below.

Form of the metacoxal process varies considerably among sets of species but relatively little within species and therefore is of great taxonomic value for establishing major sections in the key. The inner margin of a metacoxal process is convex (*e.g.* Fig. 21A), or concave (*e.g.* Fig. 22K). Apically the metacoxal process is more or less rounded (*e.g.* Fig. 21A), or the lateral margins form an acute angle (*e.g.* Fig. 22A), or the apex is drawn out into an elongate acuminate process of varied length (*e.g.* Fig. 22K).

Shape of the apex of the metatrochanter varies extensively within some taxa, is sexually dimorphic in some, and is characteristic in still others. When used as a taxonomic character, it occurs in two states: apex broadly rounded, or drawn out into a fine point apically (acuminate).

Elytra.— Colour of elytra of most specimens is piceous to black with lateral yellow stripes. Many specimens have the lateral stripe abruptly curved inward pre-apically to form a more or less obscure subapical fascia, but in specimens of *D. verticalis* this fascia is quite distinctive because it is uninterrupted, broad, and highly contrasted with elytral ground colour. Elytra of some specimens of *D. lapponicus* have a yellow ground colour with infuscation reduced to linear rows of small dots.

The elytral epipleuron is exceptionally expanded laterally in specimens of *D. latissimus* and accounts for much of the unique width and body shape characteristic of this species (Table 2). Specimens of *D. harrisii* have the epipleuron slightly widened but not nearly as greatly as in the former species. No other species shows expansion of the elytral epipleuron.

Elytra of some female specimens are sulcate. Sulci are narrow longitudinal depressions of the surface cuticle and each sulcus is separated from its neighbour by an inter-sulcal ridge. No female specimens of the Nearctic *D. verticalis*- or *D. hybridus*-groups that I have seen were sulcate. Among other species groups the proportion of sulcate and non-sulcate females varies greatly. Only in *D. carolinus* and *D. latissimus* were all female specimens observed sulcate. No sulcate females were seen of some Palearctic species (*e.g. D. delictus*), but this is probably because of the low numbers of specimens available for study. Relative length of elytral sulci is not used as a taxonomic character, but there is a phylogenetic trend toward increasing sulcal length. Members of certain taxa with very long sulci have distinctive patterns. For instance, sulcate female specimens of *D. dauricus* have inter-sulcal ridges VII and IX (numbered from suture) curved toward each other and in contact, thus V-shaped, apically . The shorter intermediate ridges VIII and IX do not meet apically. Sulcate females of *D. alaskanus* have the respective members of each pair of ridges curved toward and apically in contact such that each pair forms its own exaggerated V-shape.

Pterothoracic and abdominal sterna.— Colour pattern of abdominal and pterothoracic sterna is diagnostic given an understanding of infraspecific variation, which is relatively low among species of *Dytiscus*. Extremes in pattern are shown in Figs. 7 to 13. The median lobe of male specimens at the end points of colour variation were examined carefully to determine that they did indeed belong to a given taxon. In these figures, infuscation is shown as black, yellow as white, and red as various densities of stippling. The darker the red coloration, the more dense the stippling. These figures are mostly composite, *i.e.*, they represent the lightest or darkest sterna respectively of series of species studied intensively. As such they should represent close to the extremes of specimens which will be encountered. This is somewhat dependent on the total number of specimens that I have examined. For instance, I have greater confidence that the limits of variation are approached in the representation of *D. marginicollis* (972 specimens examined), than in that of *D. persicus* (16 specimens examined). Important character states are presence or absence of red coloration, whether or not the abdominal and pterothoracic sterna are unicolorous piceous or black or yellow versus yellow with infuscated areas and, if the latter, then the relative amounts and positions of the infuscations.

Median lobe of aedoeagus.— Exceptionally diagnostic and uniform characteristics are in shape of the apex of the male median lobe (Figs. 14-20). Of specimens examined, variation within species is insignificant. I have not used length of the median lobe as a taxonomic character because this is probably correlated with variation in total body length of specimens (see Measurements). Important character states of median lobe shape are: 1, comparative deflection of apex from line formed by basal portion of median lobe; 2, rounded versus irregular apex; 3, presence or absence of apical knob; 4, presence or absence of subapical, lateral notches; 5, width of apical knob relative to preapical width of shaft; 6, relative position (dorsal/ventral) position of lateral bead or ridge; and 7, overall similarity to that shown in the scanning electron micrographs.

Distribution.— Perhaps the most desirable and easiest couplets to use are those which separate eastern and western species (*e.g. D. sharpi* and *D. semisulcatus*). The degree of confidence in the use of such couplets is related to amount of gap between ranges and degree to which the range of a species is known or at least the degree to which it can be predicted. When this confidence is fairly high, I have not hesitated to use range as a character of equal value to structural features. In the keys the geographic range of a species or subspecies is not used as the only character state because of numerous specimens with no or only cryptic label information.

CLASSIFICATION

Genus *Dytiscus* Linnaeus

Dytiscus Linnaeus 1758:411. Type species - *Dytiscus marginalis* Linnaeus 1758:411, designated by Latreille 1810:426, attributing the species to Fabricius 1775:230. Curtis (1826:99), Westwood (1838:9), Crotch (1873:406), Guignot (1946:118), Leech (1948:413), J. Balfour-Browne (1960:252), Guignot (1961:856) and Nilsson *et al.* (1989:294) cite *D. marginalis* as type species. Hope (1839:131, 137), Duponchel (1845:154), Jacquelin du Val and Migneaux (1857:77), and Thomson (1859:12) all have designated independently *Dytiscus latissimus* Linnaeus 1758:411 as type species.

Dyticus Müller 1776:69. Incorrect emendation; rejected and invalid generic name (Opinion 619, 1961).

Macrodytes Thomson 1859:12, 1860:41. Type species - *Dytiscus marginalis* Linnaeus 1758:411, by original designation. Therefore *Macrodytes* Thomson is a junior, objective synonym of *Dytiscus* L. Guignot (1961:857, "...désigné ici.") subsequently and therefore invalidly designated *D. marginalis* L. as type species of subgenus *Macrodytes*.

Leionotus Kirby 1837:76. Type species - *Dytiscus conformis* Kunze 1818:58 (junior synonym of *D. marginalis* L.), designated by Hope (1839:131), who attributed the species name to Stephens (1828:87). Therefore *Leionotus* Kirby is a junior, subjective synonym of *Dytiscus* L.

Dyticopsis Houlbert 1934:134. Type species -not designated. This name is not available because the original description was not accompanied by type fixation (ICZN 1985, Art. 13b).

Description (Adults)

Size large, TL 22.0 to 44.0 mm, body form ovate (TL/GW 1.76 to 2.10 except *D. latissimus* 1.55 to 1.62), outline continuous, widest just behind middle. Colour dark brown to piceous, many specimens with greenish cast, with yellow or reddish markings.

Surfaces shining, with singular isodiametric sculpture, microlines very fine and difficult to see except at very high magnifications; surface of some specimens dulled by dense accumulation of coarse pores at apex and/or base of elytra, laterally on pronotum, or on sulci of sulcate females. (Detailed studies of adult structure of *D. marginalis* are provided by Buhlmann [1923:16-79] and F. Balfour-Browne [1932:29-51]).

Head.— Large, prognathous, inserted firmly into thorax, without raised carinae. Labrum excised on anterior margin (except nearly truncate in *D. latissimus*), yellow to red, with brush of fine short hairs in emargination. Labro-clypeal suture distinct, evenly curved (except bisinuate in *D. harrisii*). Clypeus distinct, yellow to red, clypeo-frontal suture present. Frons of most specimens dark brown to piceous or black, most specimens with yellow to red chevron and yellow to red markings over antennal bases and, on many specimens, on inner margins of eyes. Chevron of few specimens extended to antennal bases. Vertex short, dark brown to piceous or black. Occiput normally inserted into thorax. Eyes large, anterior margin not emarginate. Palpi and antennae yellowish to reddish-brown, articles of many specimens infuscated apically. Antennomeres elongate, glabrous, otherwise unmodified. Mandible with retinacular and two terebral teeth, and with row of stiff, short setae ventrally. Maxilla with palpomeres elongate, glabrous, otherwise unmodified. Lacinia with apex acute and abruptly bent, setose on inner margin only. Galea with apex bluntly pointed and abruptly bent. Labium with palpomeres elongate, glabrous, otherwise unmodified. Mentum distinct, deeply emarginate at middle, with two low lobes in emargination, without setae. Submentum slightly wider than mentum, without setae. Gula narrowest just posterior to contact with submentum, wider apically, at narrowest 0.25 to 0.33 width of prementum, without setae. (Further structural information about head in Sharp [1882:203-215], Buhlmann [1923:17-33], F. Balfour-Browne [1932:29-30], and Guignot [1931b:13-19]).

Thorax.— **Pronotum** transverse, without carinae, with lateral margins acute but not margined, wider at base than at head, with lateral outline rounded, antero-lateral margins produced anteriorly as rounded lobes on either side of head. Dorsally glabrous, with base continuous with and overlapping bases of elytra, posterior margin more or less bisinuate on each side, majority of specimens explanate with linear depression laterally extended from anterior lobes to base, disc dark brown to black with lateral yellowish bands, some specimens with anterior and/or posterior yellowish to reddish bands. Ventrally with prosternum markedly compressed by enlarged procoxae, procoxae confluent, open-bridged (Bell 1967, Evans 1977, Baehr 1979). Prosternal process with ventral surface convex basally to flat apically, apex broadly rounded, marginal bead complete except apically. (Further details of prothoracic structure in Sharp [1882:215-222], Evans [1977, 1985] and Baehr [1979]). **Mesosternum** with mesocoxa of complex-type of Bell (1967), metepisternum in contact with mesocoxal cavity (Dytisci complicati of Sharp 1882:964). (Further details of structure of mesosternum in Sharp [1882:222-228] and Evans [1977]. **Metasternum** with short broad notch for reception of prosternal process, metasternal wing with antero-lateral margin not straight, metasternum wide, most specimens with shortest distance from mesocoxa to metasternum greater than width of metacoxa measured along same line; metasternal wing not extended to epipleuron. Metacoxae of incomplete-type of Bell (1965), metacoxal plates transverse, length approximately 0.5 width. Metafurca (metendosternite) with space between anterior rami narrow and short, base wide and transverse, with arm at each end (Crowson 1938, 1944, F. Balfour-Browne 1944, 1961, 1967, Říha 1955:391-393). (Further details on thoracic structure in F. Balfour-Browne [1932:30-36, 1965, 1967]).

Proventriculus.— Bowl- or calyx-shaped, outer (main) lobes triangular, ciliate, and without teeth, inner (intermediate) lobes triangular (F. Balfour-Browne 1934, 1944).

Legs.— Short, broad, sexually dimorphic in setation. Anterior and middle legs quite short, with marked sexual dimorphism of form, in repose retracted into prosternal-mesosternal cavity. Relative length (longest to shortest): femur, tarsi, tibia. Hind legs longer, without sexual dimorphism of form, strikingly modified for aquatic life. Relative length: tarsi, femur, tibia. (Further details of structure of legs in Sharp [1882:234-239, 146-257], Buhlmann [1923:48-64], Guignot [1931b:34-44], and F. Balfour-Browne [1950:259-263]).

Elytra.— Continuous with outer margin of pronotum at base, widest just behind middle, apices rounded. Dorsal surface shining or dulled by dense, coarse punctation basally, apically and/or laterally, long fine setae on postero-lateral margin. Dark brown to black, many specimens with greenish cast, with lateral yellow margins, some specimens with sublateral transverse fascia. Lower surface without sublateral carina and ligula; subapical binding-patch of modified setae present (Hammond 1979).

Males with upper surface without sulci, female with or without sulci. Sulci sub-basal, in form of narrow shallow longitudinal trenches, ending from 0.5 to about 0.85 of elytral length. (Further details of structure of elytron in Sharp [1882:241-243], Buhlman [1923:68-70], Guignot [1931b:28-31] and Hammond [1979]).

Metathoracic wings.— Normally developed, no specimens observed to be brachypterous. Wedge cell normally developed. Oblongum cell in shape of parallelogram, with M-vein attached anterior to middle. Distinct area of modified dense setae along posterior margin of cubitus vein near wing margin. (Further details of structure of flight wing in Sharp [1882:243-246], Forbes [1922, 1926], Buhlman [1923:64-67], Guignot [1931b:32-33], Goodliffe [1939], F. Balfour-Browne [1944], Hammond [1979] and Ward [1979]).

Abdomen.— Dorsally with basal pleuron transversely grooved. Apical two pleura with stigmata markedly enlarged and transversely elliptical, these pleura densely covered with long setae. Sterna glabrous except some specimens with long fine scattered setae on last visible sternum. Various in colour, unicolorous black or yellow or marked with black, yellow, or red. Proportional length of visible sterna (longer to shorter): last, second, third, fourth, fifth and first subequal at epipleuron. (Further details of structure of abdomen in Sharp [1882:239-241], Buhlmann [1923:72-77], F. Balfour-Browne [1932:50-51] and Guignot [1931b:44-49]).

Aedoeagus.— Similar to that of *Hydaticus* (Roughley and Pengelly 1982:256-257, 295, Figs. 4 and 5), except as follows: 8th sternum with deep narrow emargination, 9th pleuron with small longitudinal sclerite on membrane, median lobe without lateral flanges, paramere without flange and with setae on antero-dorsal margin, preputial covering not complete to apex, incised, and epipenite absent. (Further details of structure of aedoeagus are in Demandt [1924:209-275], Guignot [1931b:49-58] and F. Balfour-Browne [1932:40-45; 1950:255-256]).

Ovipositor.— Apical sternum with deep narrow emargination extended to base, central portions membranous. Paraproct triangular with posterior margin membranous centrally. Valvifer articulated with stylomere I apically, of two lateral elongate struts joined by membrane. Vulval sclerite lamellate, without setae, inserted into stylomere I ventrally. Stylomere I elongate, sclerotized, acute apically, without setae and cultriform in shape. (Further details of structure of ovipositor in Demandt [1924:151-209], F. Balfour-Browne [1932:46-50], Guignot [1931b: 58-67] Burmeister [1976, 1980] and Régil and Salgado [1984]).

Geographical distribution.— The genus *Dytiscus* is Holarctic, ranging from Arctic habitats in the north to the northern slopes of the Himalaya and North Africa, in the Old World; and to the edge of the Tropics, in Guatemala in the New World.

Chorological and phylogenetic relationships.— The sister genus of *Dytiscus* is the Australian genus *Hyderodes* Hope. The two genera are thus distributed vicariously.

Species groups.— The 26 species of *Dytiscus* are arranged in six groups, as indicated in the following list. The species-groups which I recognize are based on the reconstructed phylogeny (Fig. 52). These are:

D. verticalis-group:	*D. verticalis* Say
D. hybridus-group:	*D. harrisii* Kirby

	D. hybridus Aubé
	D. marginicollis LeConte
	D. habilis Say
D. semisulcatus-group:	*D. semisulcatus* Müller
	D. sharpi Wehncke
	D. carolinus Aubé
	D. fasciventris Say
	D. hatchi Wallis
D. dimidiatus-group:	*D. cordieri* Aubé
	D. dimidiatus Bergsträsser
	D. mutinensis Pederzani
	D. pisanus C. de Castelnau
D. marginalis-group:	*D. marginalis* Linnaeus
	D. persicus Wehncke
	D. delictus (Zaitzev)
D. dauricus-group:	*D. latissimus* Linnaeus
	D. circumcinctus Ahrens
	D. alaskanus J. Balfour-Browne
	D. dauricus Gebler
	D. lapponicus Gyllenhal
	D. circumflexus Fabricius
	D. thianshanicus Gschwendtner
	D. latro Sharp
	D. sinensis Feng

Key to Adults of Nearctic Species of *Dytiscus* Linnaeus

1 (0) Metacoxal process with inner margin convex, apex rounded to obtusely angulate, but not acuminate (Figs. 21A-E, H-K) 2

1' Metacoxal process with inner margin concave, apex acutely angulate, more or less acuminate (Figs. 22F-H) 12

2 (1) Clypeus with anterior margin shallowly but distinctly bisinuate (Fig. 23A); pterothoracic sterna predominantly piceous to black, metacoxa and abdominal sternum I marked with yellow, sterna II to V or II to VI with reddish markings (Fig. 7B)..*D. harrisii* Kirby, p. 433

2' Clypeus with anterior margin straight or slightly concave; ventral markings various...3

3 (2') Pronotum with anterior yellow band less than 0.4 width of lateral bands (Figs. 1A, D, 2C-E).....................................4

3' Pronotum with anterior yellow band of most specimens more than 0.5 width of lateral bands (Figs. 1B, C)........................9

4 (3) Pterothoracic and abdominal sterna piceous to black...............5

4' Pterothoracic and/or abdominal sterna with yellow or reddish markings...7

5 (4) Pronotum with lateral margins not explanate; males with mesotarsomeres II and III with median glabrous area ventrally; females not sulcate...*D. hybridus* Aubé, p. 434

5' Pronotum with lateral margins explanate; males with mesotarsomeres II and III with uniform distribution of ventral suckers; females sulcate or not 6

6 (5') Size larger, TL from 29.6 to 36.0 mm; elytron of most specimens with yellow subapical transverse fascia (Fig. 1A); females not sulcate.....................*D. verticalis* Say, p. 431

6' Size smaller, TL from 22.0 to 26.1 mm; elytron without yellow subapical transverse fascia (Fig. 2C); females sulcate ....*D. carolinus* Aubé (in part), p. 446

7 (4') Metepisternum, metasternal wings and metacoxae predominantly piceous to black, abdominal sterna black with reddish to piceous markings (Fig. 8D); distribution more southern, Atlantic Coast (Connecticut, south to Georgia), Gulf Coast, and northward along Mississippi River (Fig. 31) ....*D. carolinus* Aubé (in part), p. 446

7' Metepisternum, and metacoxae predominantly testaceous, abdominal sterna testaceous with black markings (Figs. 9A, B); distribution more northern and western..........................8

8 (7') Males with protarsal claws of most specimens longer than protarsomere V (Fig. 23C); females with mesotarsal claw longer than mesotarsomere V (Fig. 23E); pronotum more broadly margined with yellow (Fig. 2E); distribution west of Rocky Mountains from central California to northern British Columbia (Fig. 33) ....*D. hatchi* Wallis, p. 449

8' Males with protarsal claws of most specimens shorter than protarsomere V (Fig. 23D); females with mesotarsal claws shorter than mesotarsomere V (Fig. 23F); pronotum more narrowly margined with yellow (Fig. 2D); transcontinental in northern North America (Fig. 32)..*D. fasciventris* Say, p. 447

9 (3') Pronotum distinctly explanate; protarsal claws subequal to protarsomere V; abdominal sterna yellow with basolateral infuscations (Fig. 9A, B)...8

9' Pronotum not or indistinctly explanate; protarsal claws much shorter than protarsomere V; abdominal sterna predominantly yellow (Fig. 9C) or predominantly black with various coloured markings (Fig.7D, 8A).......................................10

10 (9') Pterothoracic and abdominal sterna testaceous to pale rufous (Fig. 9C); frons of most specimens with chevron extended to antennal bases (Fig. 23B); females with pronotum shallowly explanate, some specimens with elytron sulcate ....*D. cordieri* Aubé, p. 456

10' Pterothoracic and abdominal sterna with extensive infuscation (Figs. 7D, 8A); frons with chevron not extended to antennal bases (*e.g.* Fig. 23A); females with pronotum not explanate, elytron not sulcate...11

11 (10') Pronotum with discal infuscation narrower than lateral yellow band (Fig. 1C); male with mesotarsomeres II and II with uniform distribution of suckers ventrally; distribution as in Fig. 28 ....*D. habilis* Say, p. 437

11' Pronotum with discal infuscation wider than lateral yellow band; male with mesotarsomeres II and III with median glabrous area ventrally; distribution as in Fig. 27 ....*D. marginicollis* LeConte, p. 435

12 (1') Eye enclosed dorsally by narrow yellow band, or, some specimens with band narrowly broken near inner posterior margin of eye; pterothoracic and abdominal sterna I to III very narrowly infuscate in some specimens (Fig. 11D) ....*D. circumcinctus* Ahrens, p. 477

12' Eye not enclosed dorsally by narrow yellow band, some specimens with inner margin margined with yellow or red; pterothoracic sterna with at least metasternum medially infuscate (Figs. 12A, B), abdominal sterna various in colour pattern..13

13 (12') Male with apical portion of median lobe sinuate laterally and apical knob distinct in dorsal view (Fig. 19C); females with postero-median margin of clypeus distinctly raised above level of frons along clypeal suture; sulcate females with ridges of sulci VII and X fused apically, and those of VII and IX not fused apically; size larger, TL from 29.7 to 40.0 mm...*D. dauricus* Gebler, p. 483

13' Male with apical portion of median lobe evenly curved laterally and apical knob indistinct in dorsal view (Fig. 19B); females with postero-median margin of clypeus on same level as frons along clypeal suture; sulcate females with ridges of sulci VII and X, and of VIII and IX fused apically forming a a 'V-V' pattern (Fig. 5A); size smaller, TL from 22.6 to 30.2mm.................*D. alaskanus* J. Balfour-Browne, p. 481

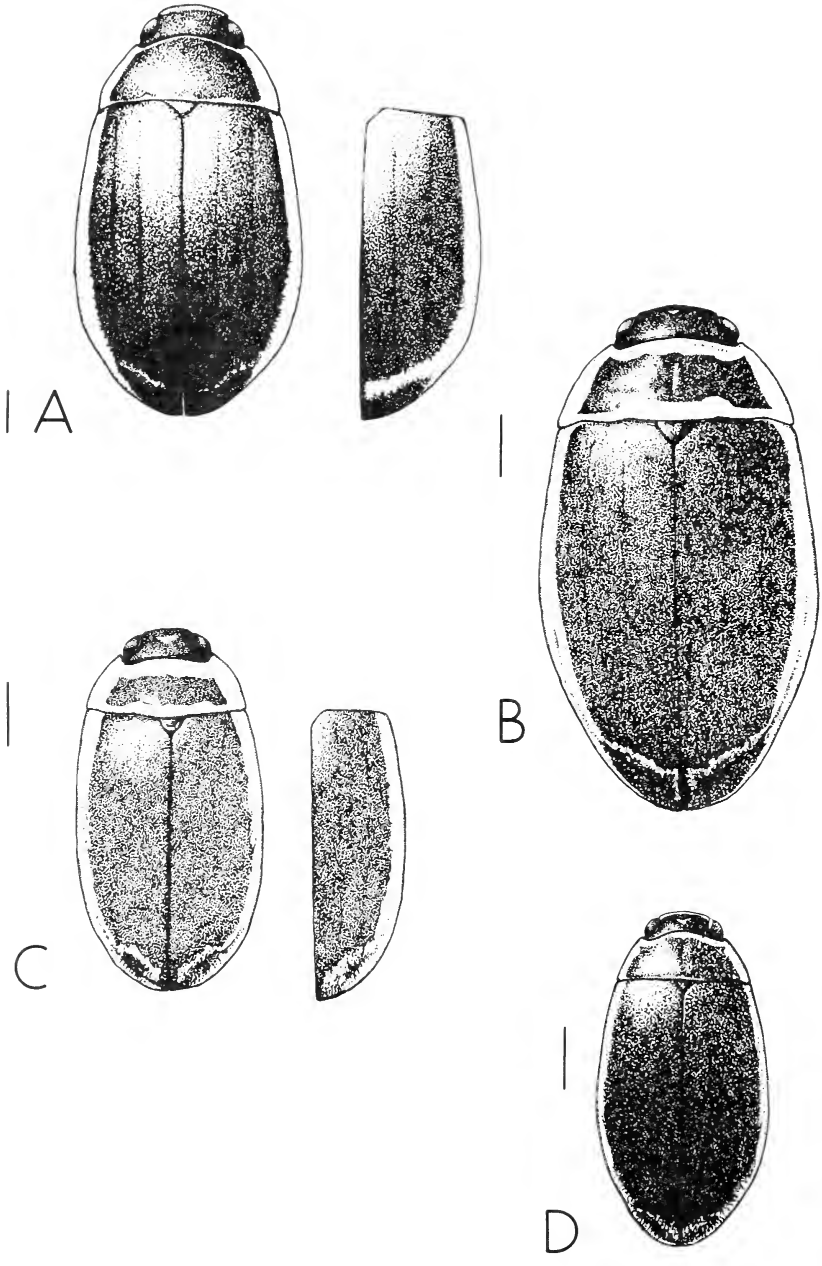


Fig. 1. Dorsal view of body of species of *Dytiscus* Linnaeus. A, *D. verticalis* Say; B, *D. harrisii* Kirby; C, *D. habilis* Say; D, *D. hybridus* Aubé.

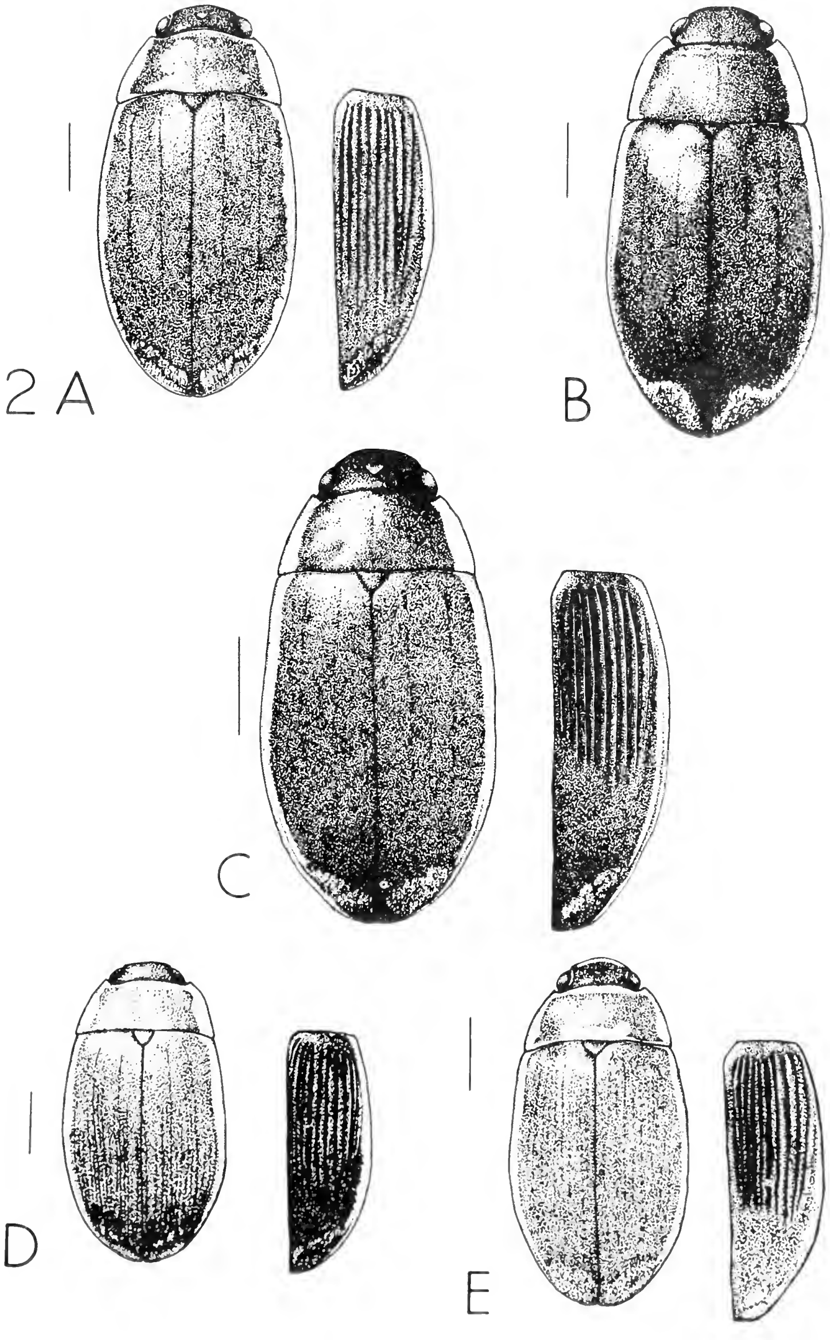


Fig. 2. Dorsal view of body of species of *Dytiscus* Linnaeus. A, *D. semisulcatus* Müller; B, *D. sharpi* Wehncke; C, *D. carolinus* Aubé; D, *D. fasciventris* Say; E, *D. hatchi* Wallis.

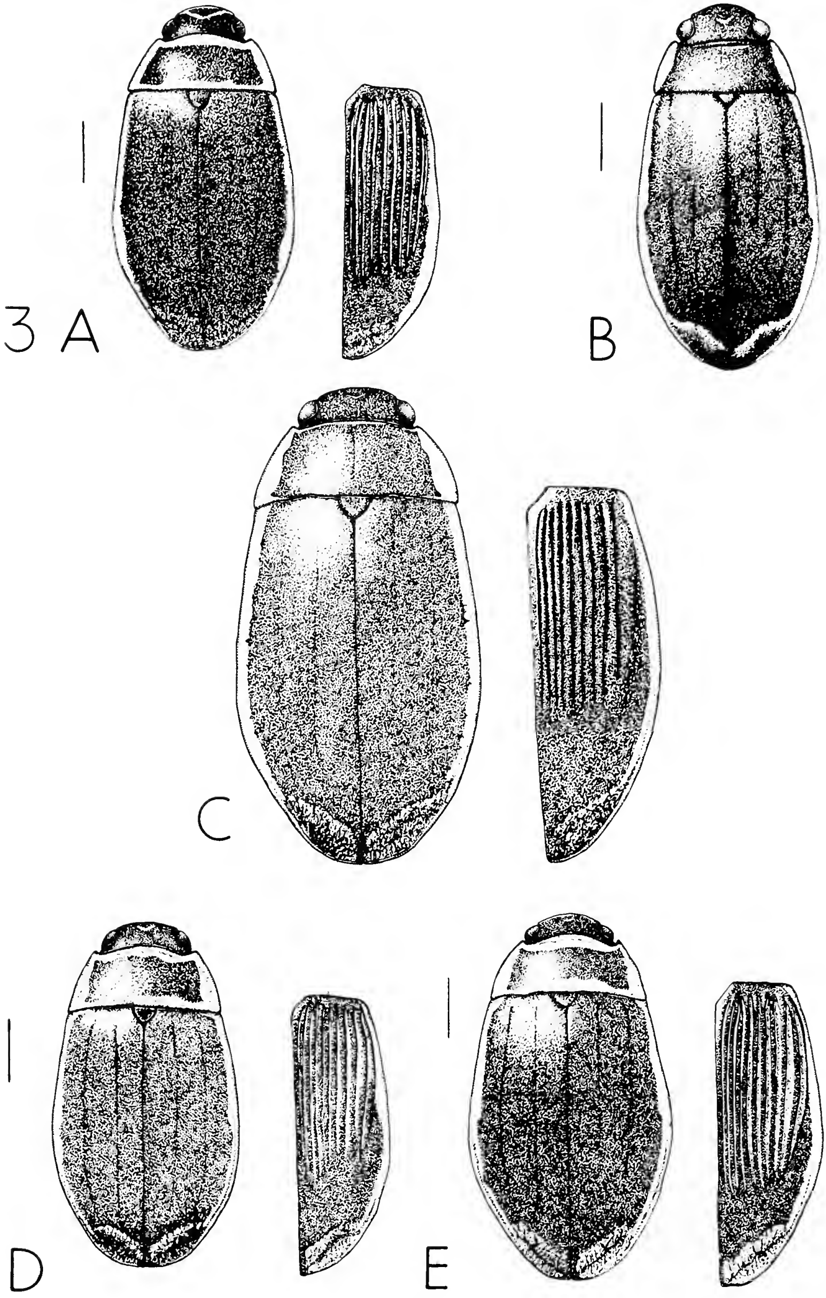


Fig. 3. Dorsal view of body of species and subspecies of *Dytiscus* Linnaeus..A, *D. cordieri* Aubé; B, *D. mutinensis* Pederzani; C, *D. dimidiatus* Bergsträsser; D, *D. pisanus* Castelnau; E, *D. marginalis marginalis* Linnaeus.

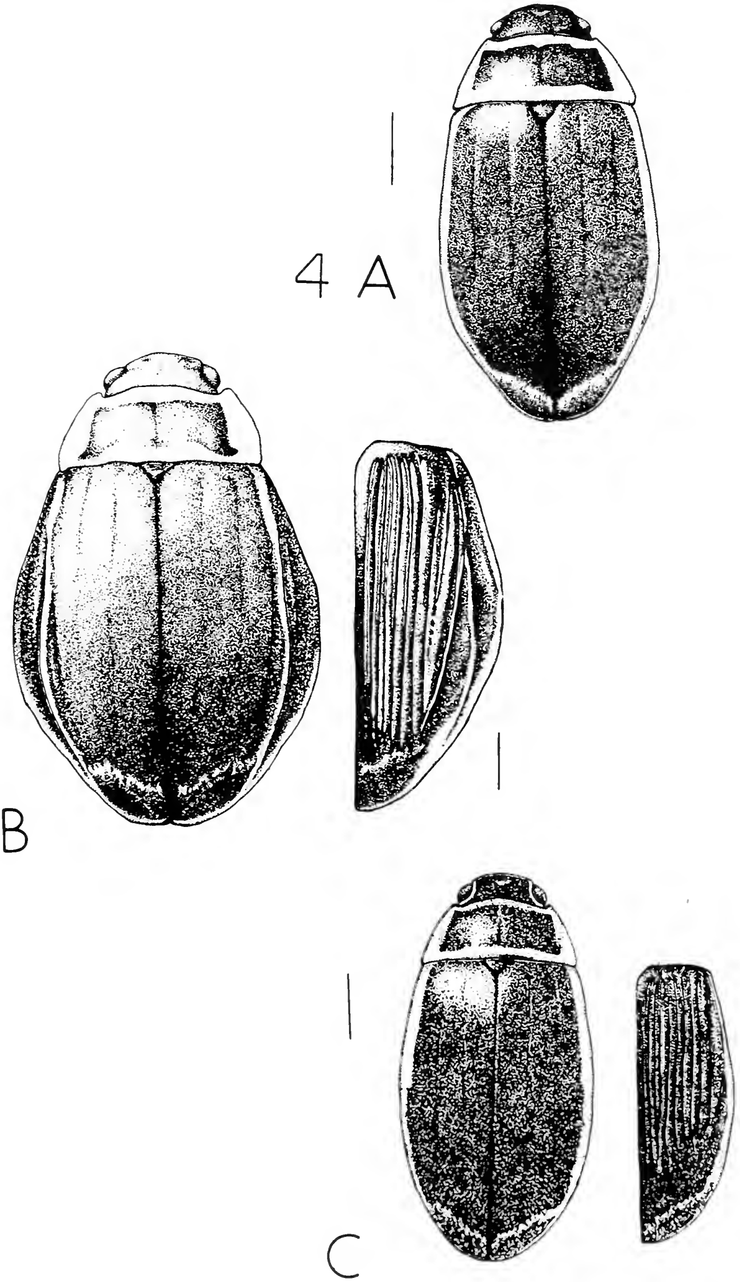


Fig. 4. Dorsal view of body of species of *Dytiscus* Linnaeus. A, *D. delictus* (Zaitzev); B, *D. latissimus* Linnaeus; C, *D. circumcinctus* Ahrens.

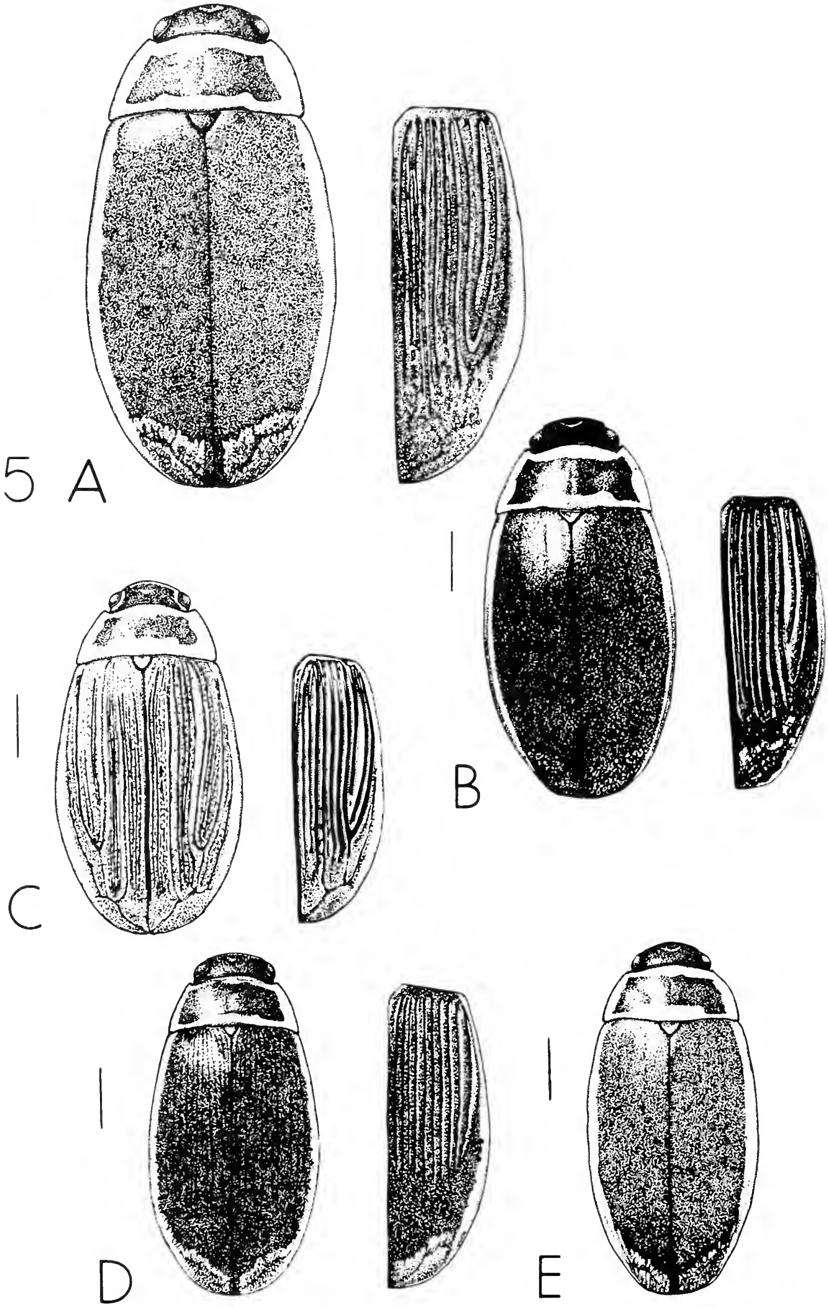


Fig. 5. Dorsal view of body of species and subspecies of *Dytiscus* Linnaeus. A, *D. alaskanus* J. Balfour-Browne; B, *D. dauricus* Gebler; C, *D. lapponicus lapponicus* Gyllenhal; D, *D. circumflexus* Fabricius; E, D. thianshanicus Gschwendtner.

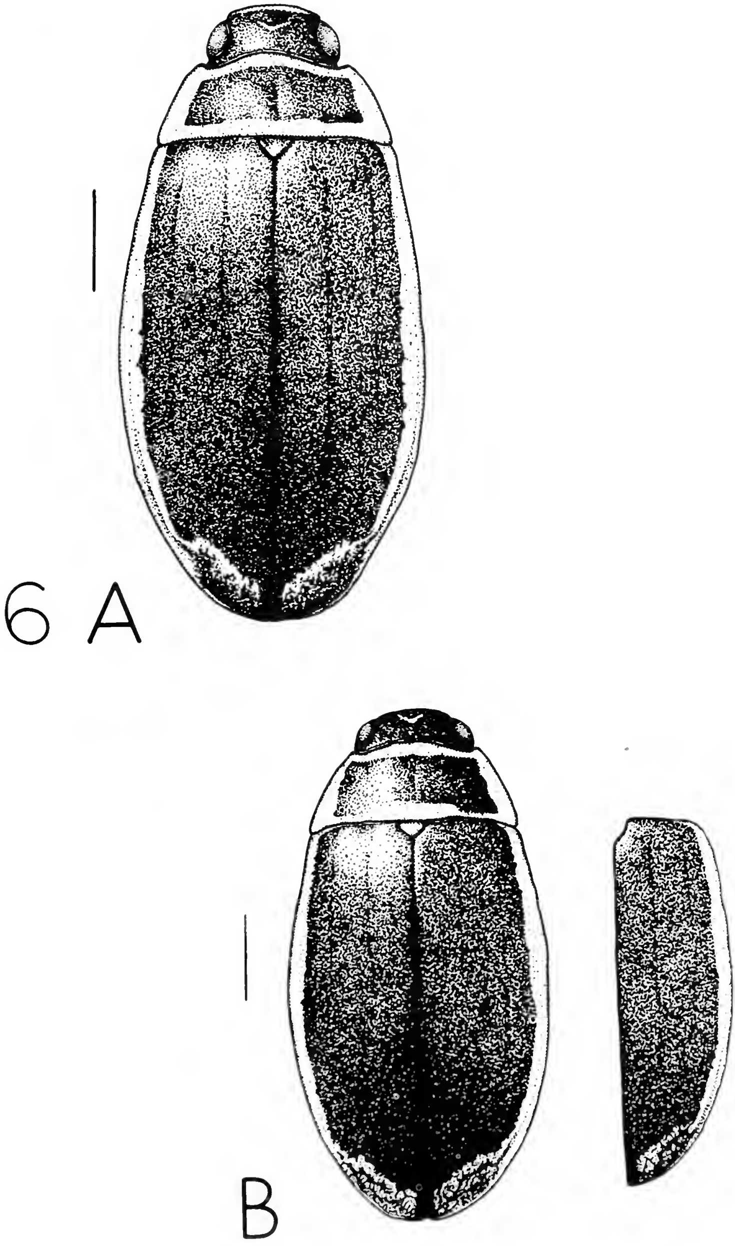


Fig. 6. Dorsal view of body of species of *Dytiscus* Linnaeus. A, *D. latro* Sharp; B, *D. sinensis* Feng.

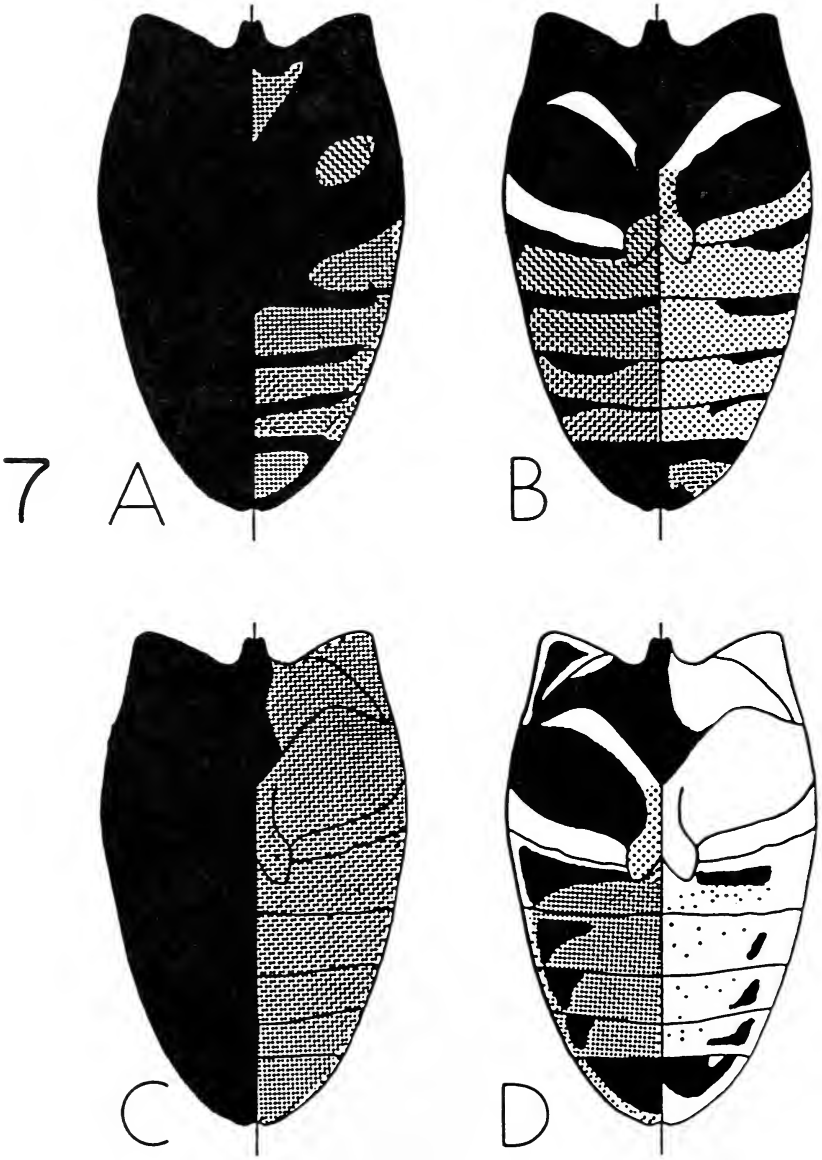


Fig. 7. Schematic representation of colour pattern of pterothoracic and abdominal sterna of species of *Dytiscus* Linnaeus. A, *D. verticalis* Say; B, *D. harrisii* Kirby; C, *D. hybridus* Aubé; D, *D. marginicollis* LeConte.

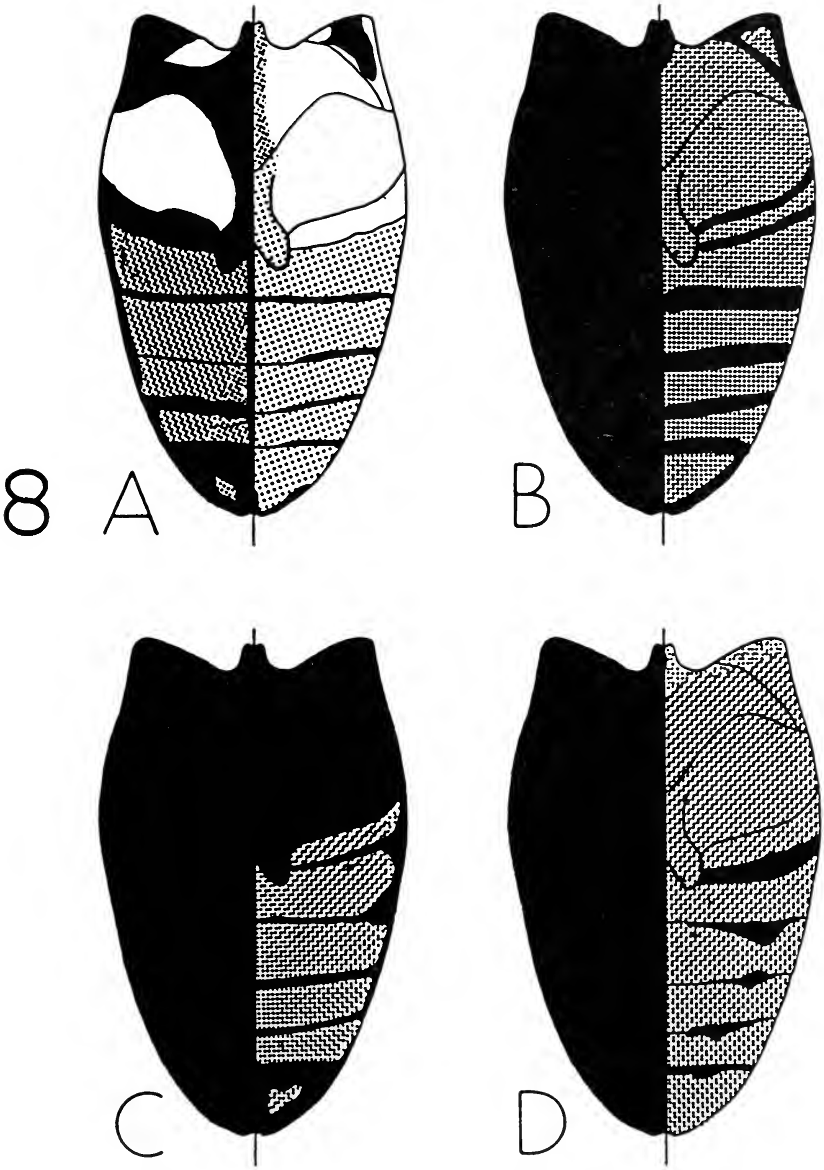


Fig. 8. Schematic representation of colour pattern of pterothoracic and abdominal sterna of species of *Dytiscus* Linnaeus. A, *D. habilis* Say; B, *D. semisulcatus* Müller; C, *D. sharpi* Wehncke; D, *D. carolinus* Aubé.

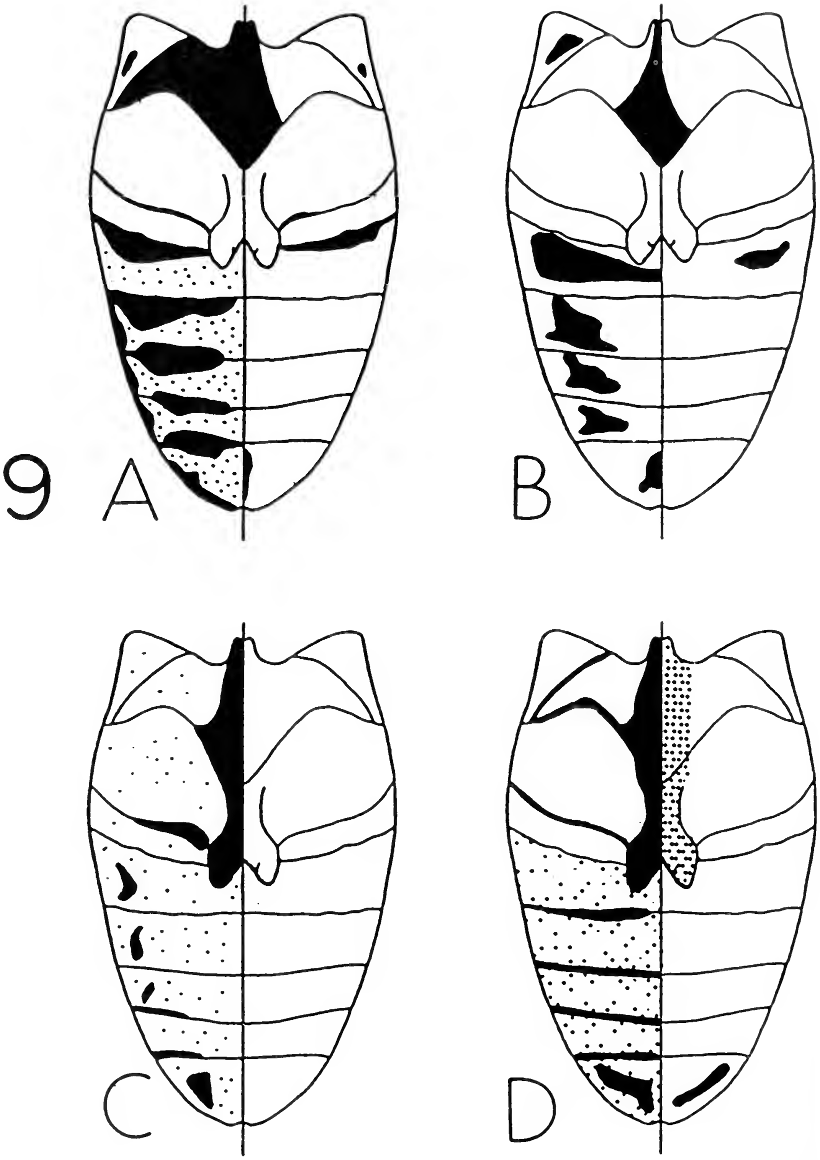


Fig. 9. Schematic representation of colour pattern of pterothoracic and abdominal sterna of species of *Dytiscus* Linnaeus. A, *D. fasciventris* Say; B, *D. hatchi* Wallis; C, *D. cordieri* Aubé; D, *D. mutinensis* Pederzani.

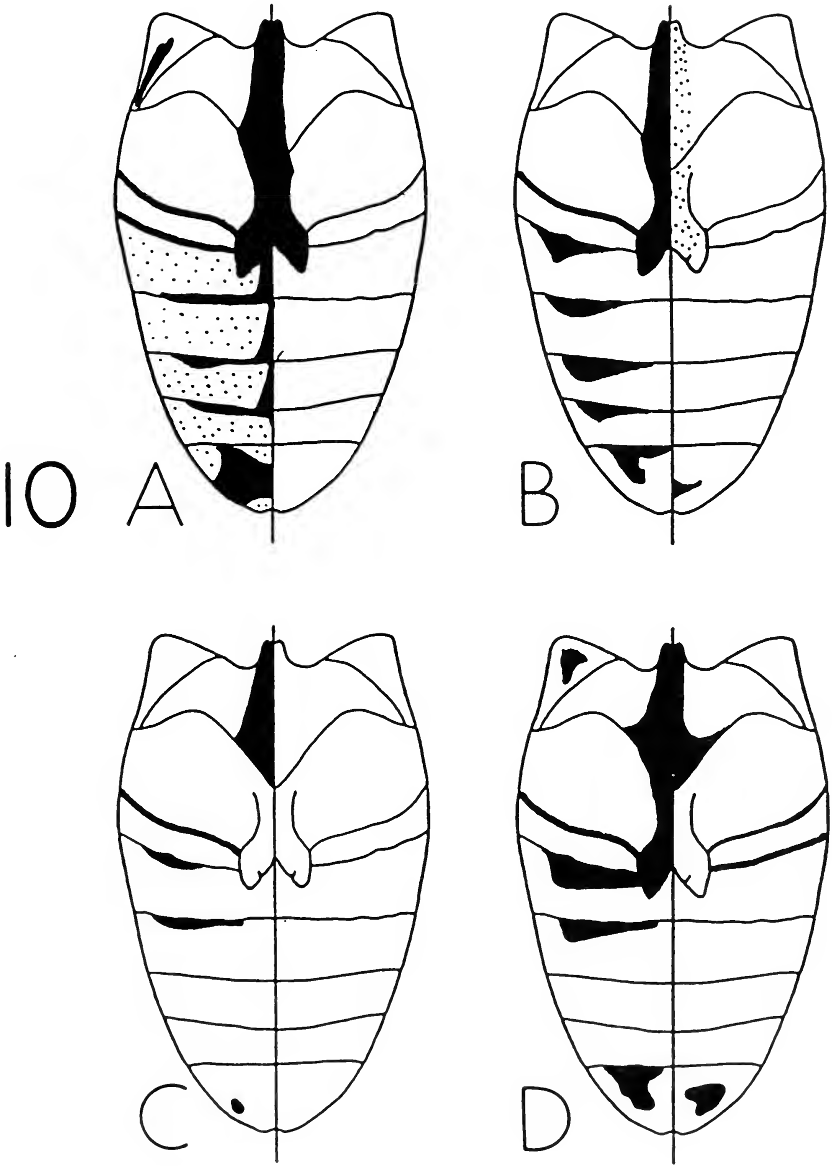


Fig. 10. Schematic representation of colour pattern of pterothoracic and abdominal sterna of species and subspecies of *Dytiscus* Linnaeus. A, *D. dimidiatus* Bergsträsser; B, *D. pisanus* Castelnau; C, *D. marginalis marginalis* Linnaeus; D, *D. marginalis czerskii* Zaitzev.

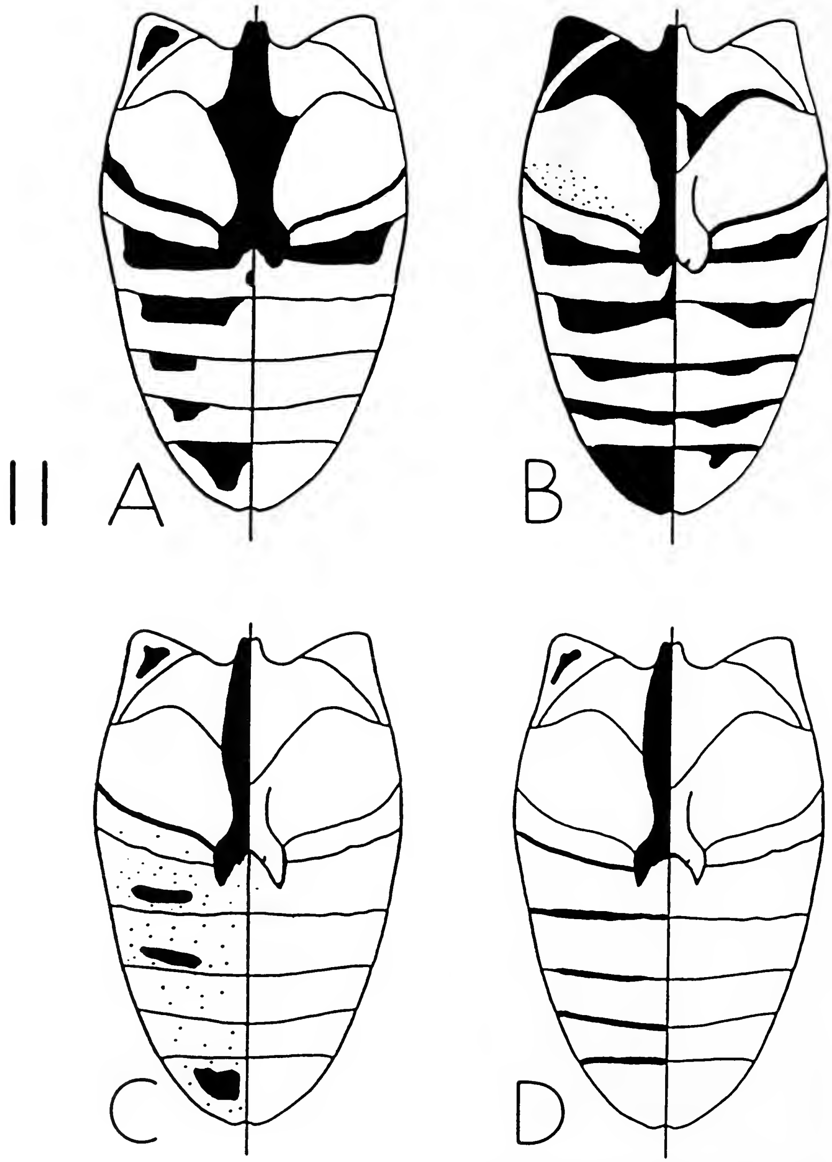


Fig. 11. Schematic representation of colour pattern of pterothoracic and abdominal sterna of species of *Dytiscus* Linnaeus. A, *D. persicus* Wechncke; B, *D. delictus* (Zaitzev); C, *D. latissimus* Linnaeus; D, *D. circumcinctus* Ahrens.

12

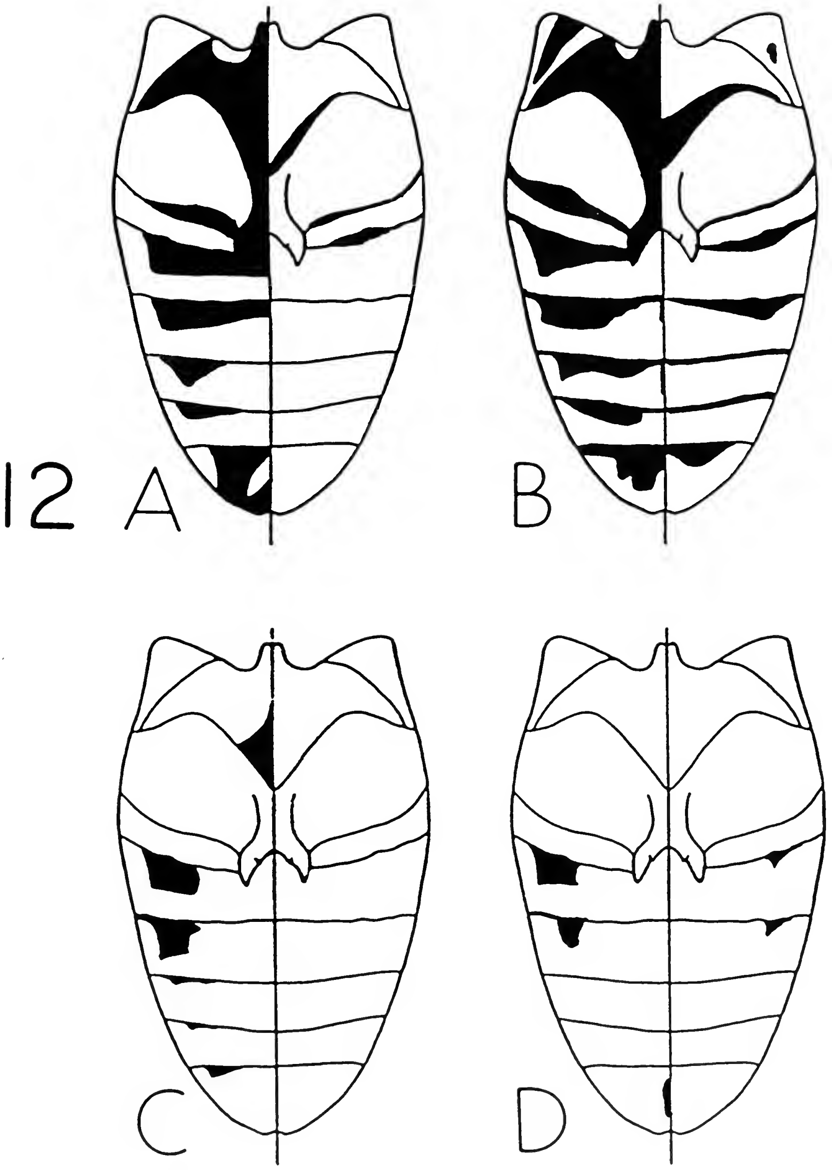


Fig. 12. Schematic representation of colour pattern of pterothoracic and abdominal sterna of species and subspecies of *Dytiscus* Linnaeus. A, *D. alaskanus* J. Balfour-Browne; B, *D. dauricus* Gebler; C, *D. lapponicus lapponicus* Gyllenhal; D, *D. lapponicus disjunctus* Camerano.

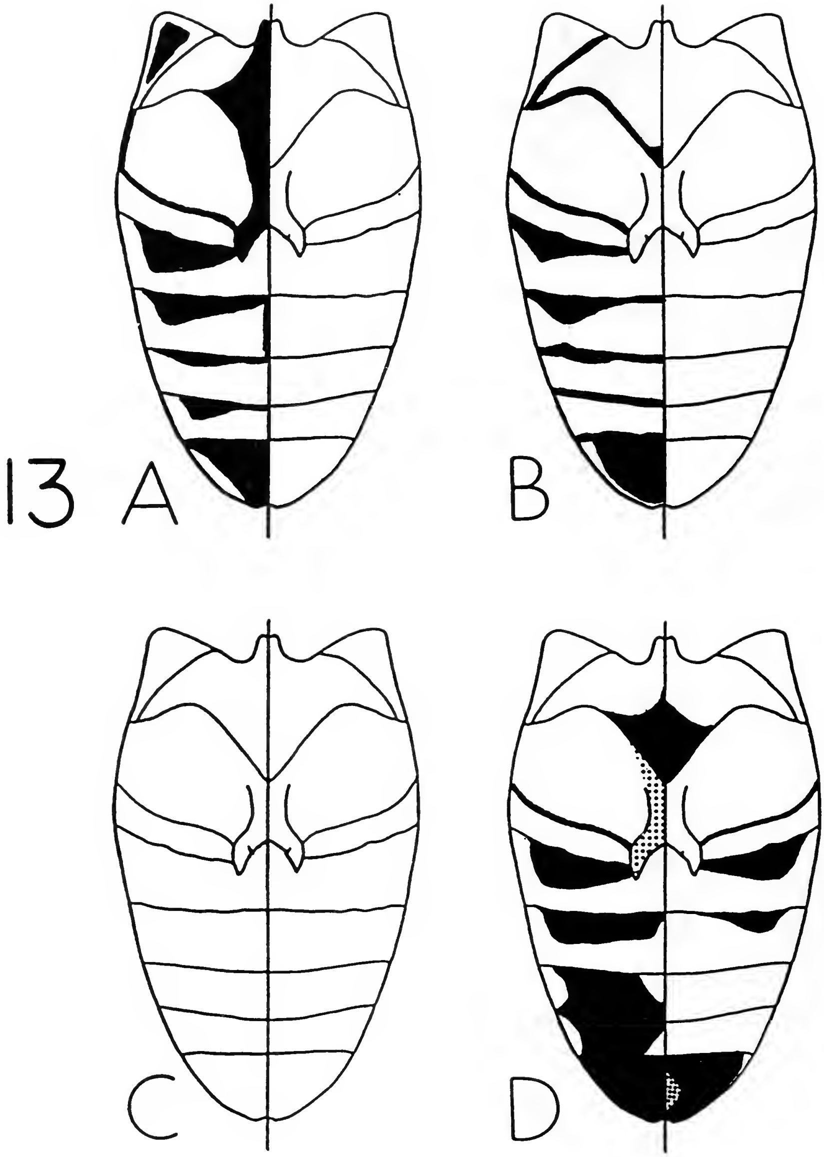


Fig. 13. Schematic representation of colour pattern of pterothoracic and abdominal sterna of species of *Dytiscus* Linnaeus. A, *D. circumflexus* Fabricius; B, *D. thianshanicus* Gschwendtner; C, *D. latro* Sharp; D, *D. sinensis* Feng.

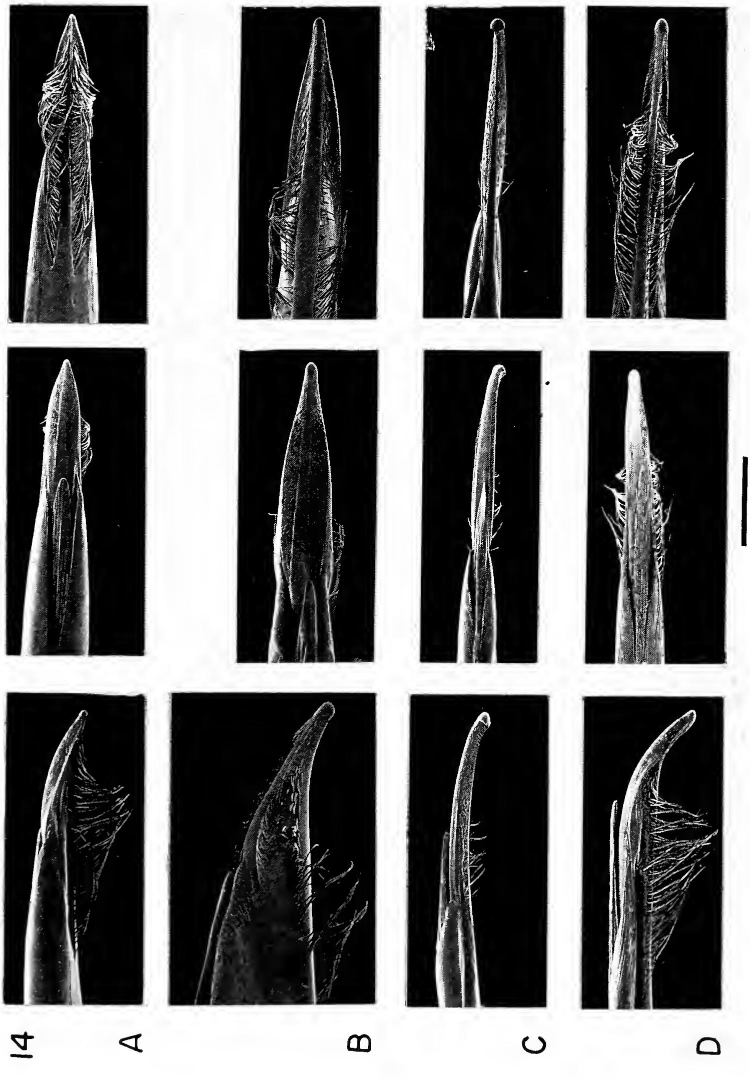


Fig. 14. Scanning electron micrographs of apex of median lobe of males of species of *Dytiscus* Linnaeus. Lateral, dorsal and ventral views. A, *D. verticalis* Say; B, *D. harrisii* Kirby; C, *D. hybridus* Aubé; D, *D. marginicollis* LeConte.

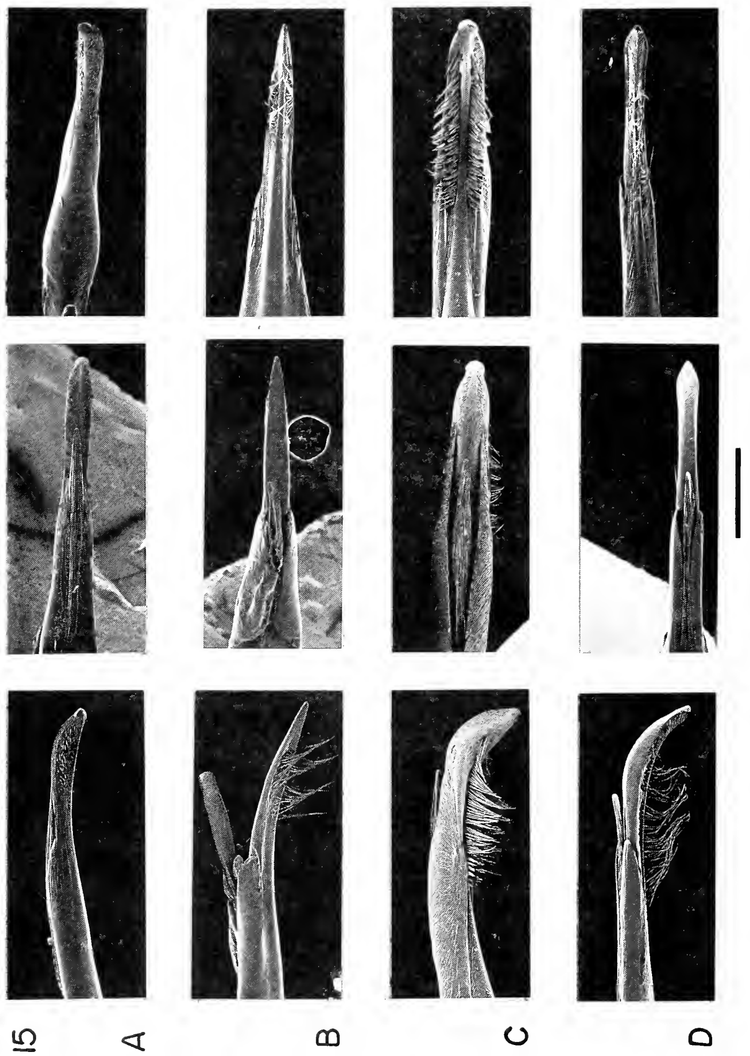


Fig. 15. Scanning electron micrographs of apex of median lobe of males of species of *Dytiscus* Linnaeus. Lateral, dorsal and ventral views. A, *D. habilis* Say; B, *D..semisulcatus* Müller; C, *D. sharpi* Wehncke; D, *D. carolinus* Aubé.

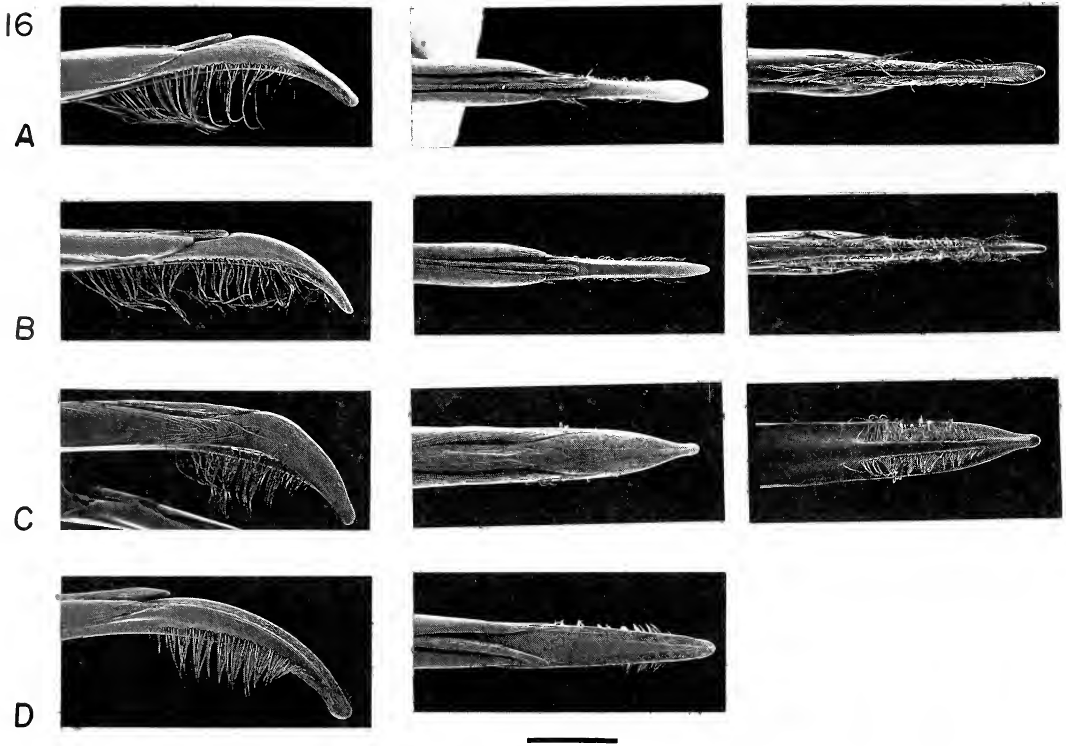


Fig. 16. Scanning electron micrographs of apex of median lobe of males of species of *Dytiscus* Linnaeus. Lateral, dorsal and ventral views. A, *D. fasciventris* Say; B, *D. hatchi* Wallis; C, *D. cordieri* Aubé; D, *D. mutinensis* Pederzani.

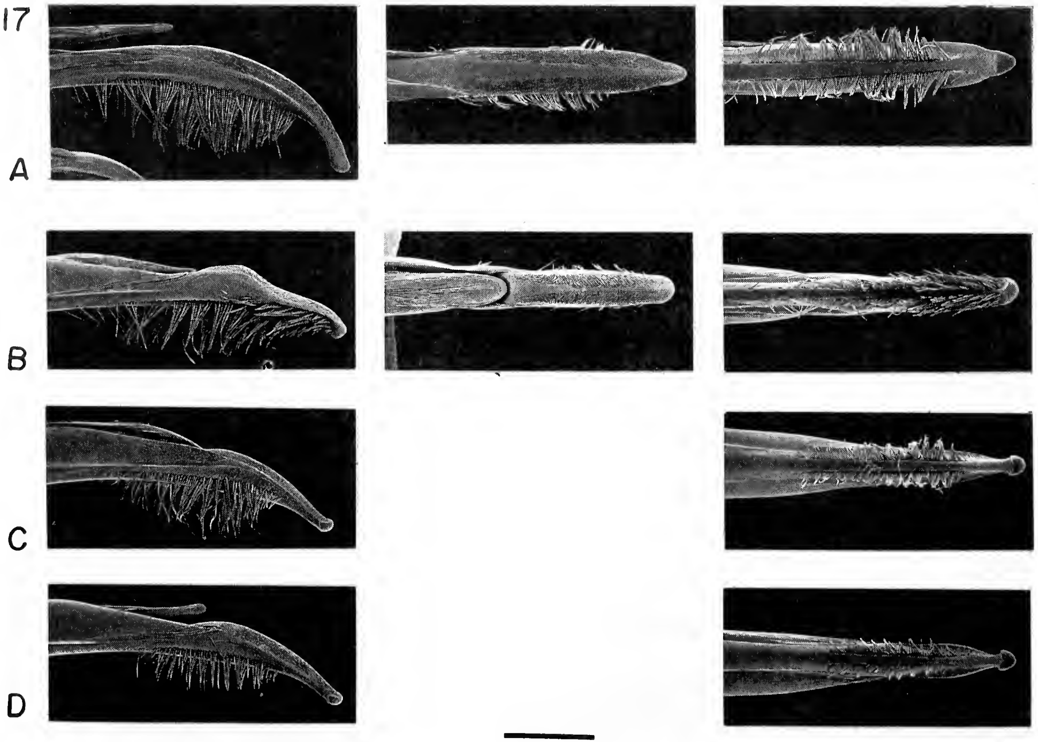


Fig. 17. Scanning electron micrographs of apex of median lobe of males of species and subspecies of *Dytiscus* Linnaeus. Lateral, dorsal and ventral views. A, *D. dimidiatus* Bergsträsser; B, *D. pisanus* Castelnau; C, *D. marginalis marginalis* Linnaeus; D, *D. marginalis czerskii* Zaitsev.

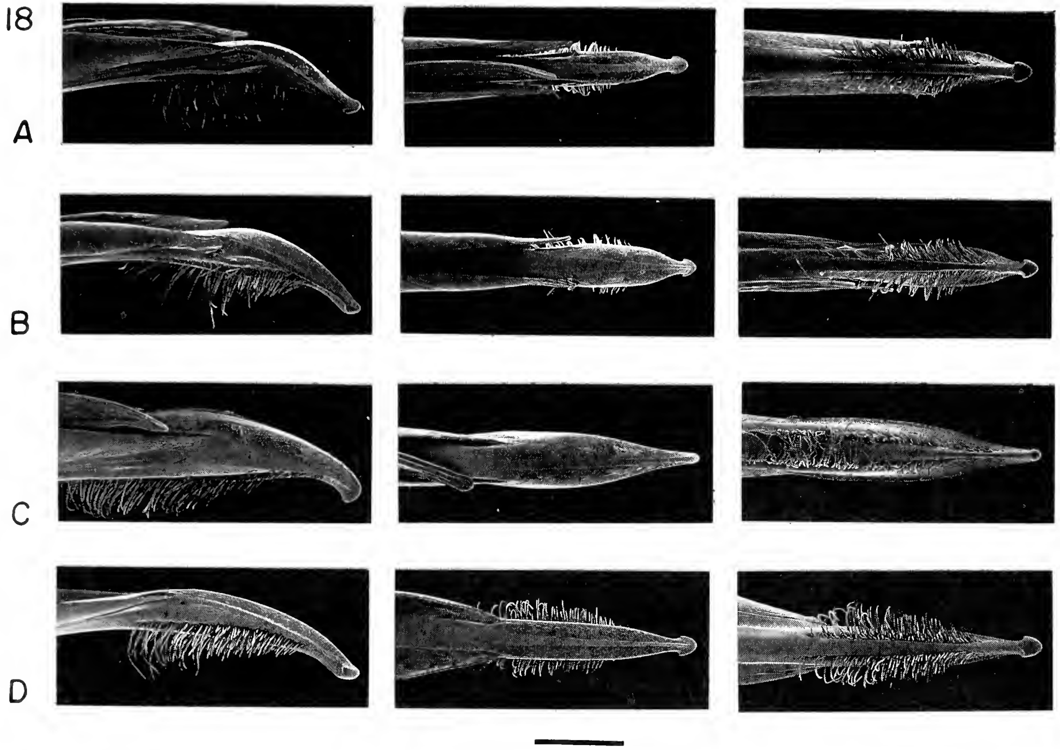


Fig. 18. Scanning electron micrographs of apex of median lobe of males of species of *Dytiscus* Linnaeus. Lateral, dorsal and ventral views. A, *D. persicus* Wehncke; B, *D. delictus* (Zaitzev); C, *D. latissimus* Linnaeus; D, *D. circumcinctus* Ahrens; Palearctic specimen.

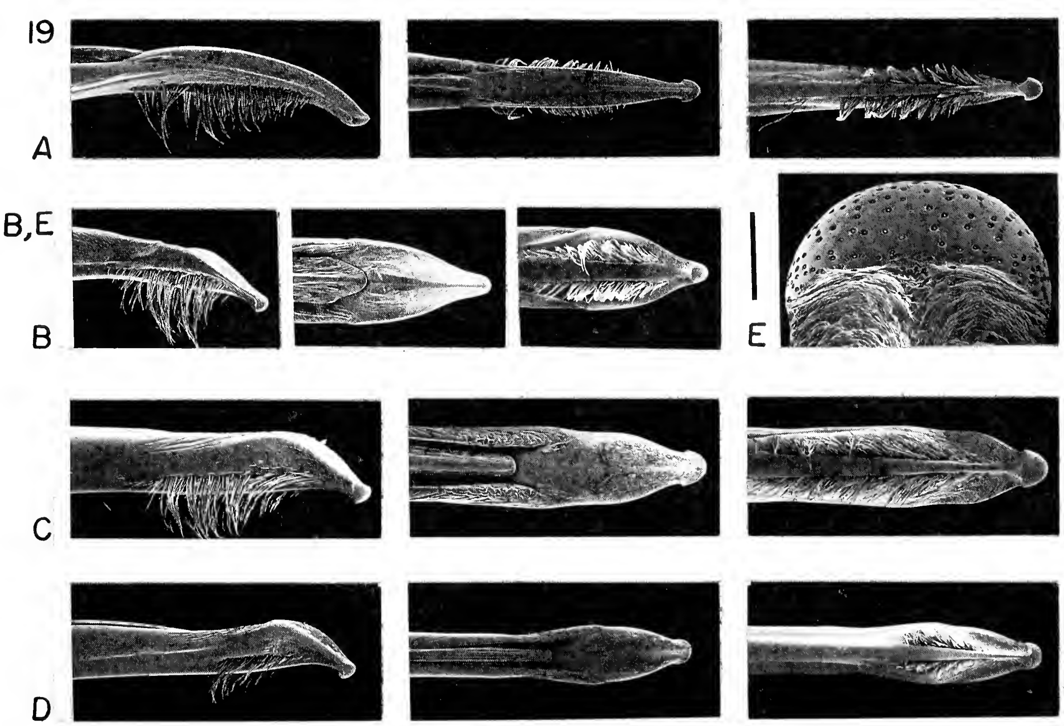


Fig. 19. Scanning electron micrographs of apex of median lobe of males of species and subspecies of *Dytiscus* Linnaeus. Lateral, dorsal and ventral views. A, *D. circumcinctus* Ahrens, Nearctic specimen; B, *D. alaskanus* J. Balfour-Browne; C, *D. dauricus* Gebler; D, *D. lapponicus lapponicus* Gyllenhal. E, Underside of apical knob of median lobe of *D. lapponicus lapponicus* Gyllenhal.

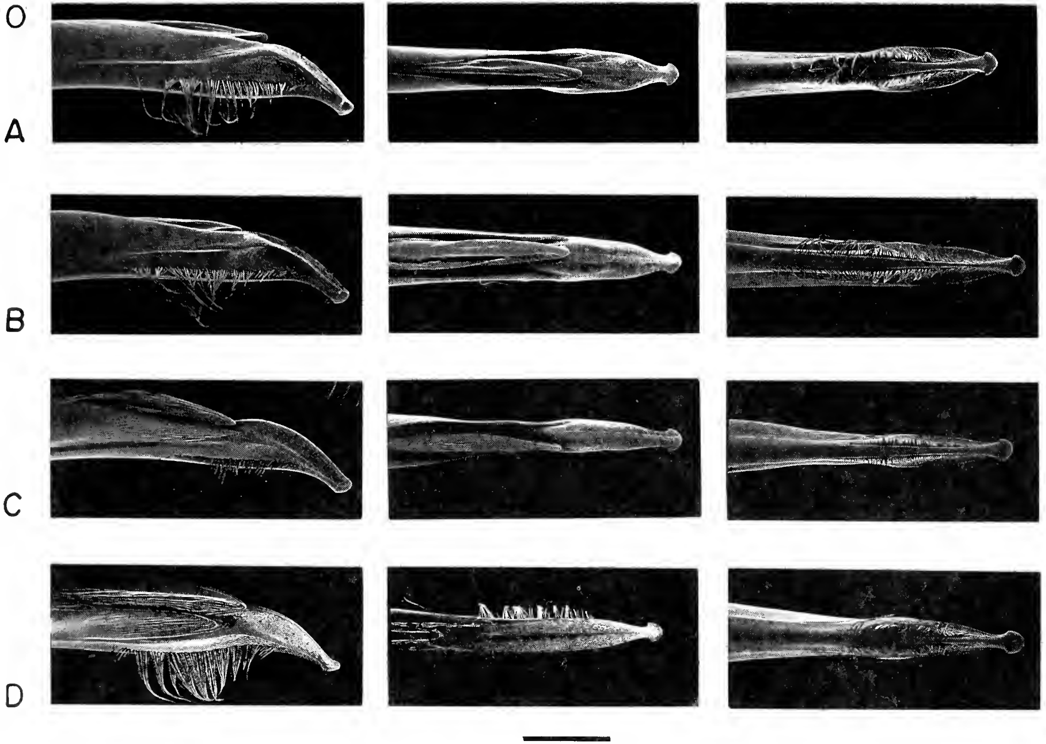


Fig. 20. Scanning electron micrographs of apex of median lobe of males of species of *Dytiscus* Linnaeus. Lateral, dorsal and ventral views. A, *D. circumflexus* Fabricius; B, *D. thianshanicus* Gschwendtner; C, *D. latro* Sharp; D, *D. sinensis* Feng.

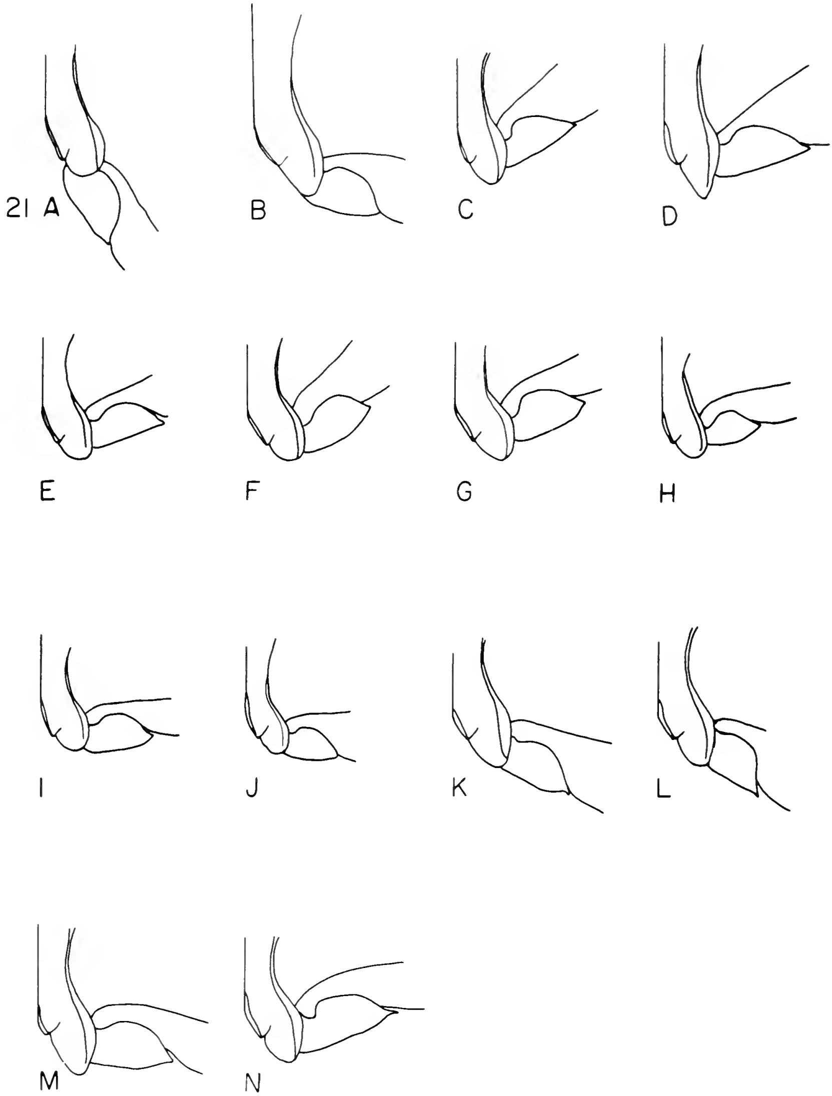


Fig. 21. Left metacoxal process, trochanter and base of metafemur of species of *Dytiscus* Linnaeus. A, *D. verticalis* Say; B, *D. harrisii* Kirby; C, *D. hybridus* Aubé; D, *D. marginicollis* LeConte; E, *D. habilis* Say; F, *D..semisulcatus* Müller; G, *D. sharpi* Wehncke; H, *D. carolinus* Aubé; I, *D. fasciventris* Say; J, *D. hatchi* Wallis; K, *D. cordieri* Aubé; L, *D. mutinensis* Pederzani; M, *D. dimidiatus* Bergsträsser; N, *D. pisanus* Castelnau.

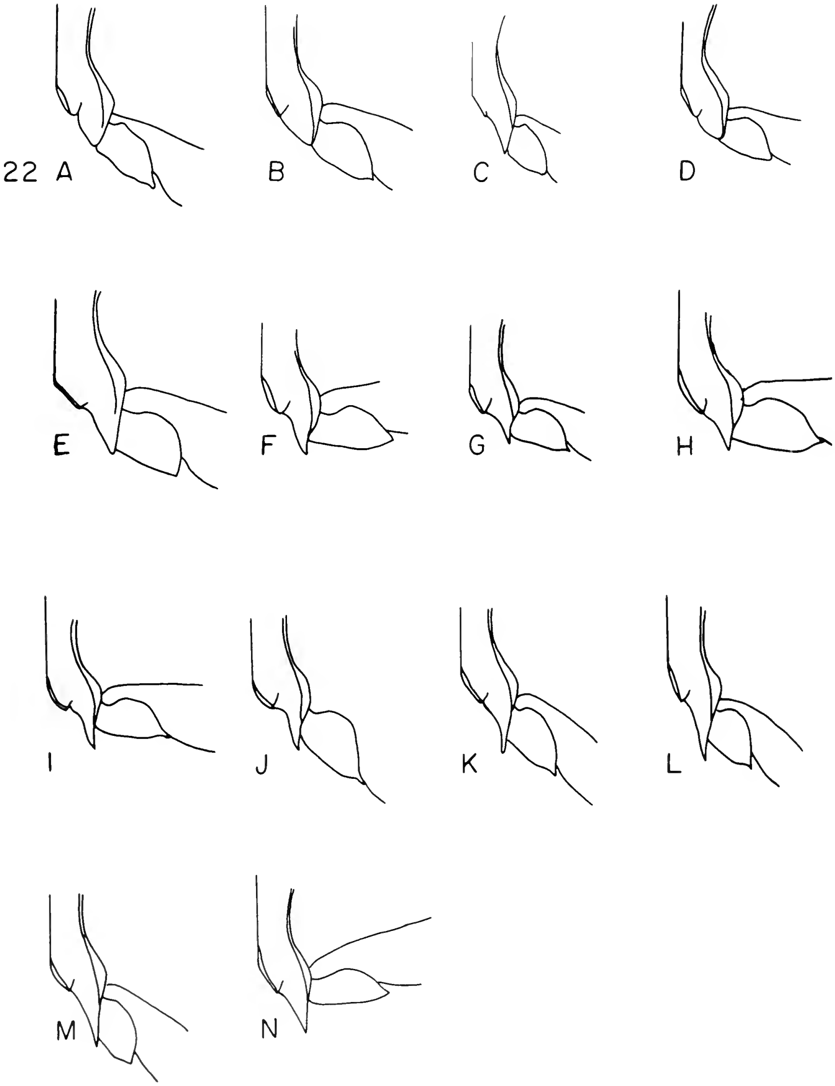


Fig. 22. Left metacoxal process, trochanter and base of metafemur of species of *Dytiscus* Linnaeus. A, *D. marginalis marginalis* Linnaeus; B, *D. marginalis czerskii* Zaitsev; C, *D. persicus* Wehncke; D, *D. delictus* (Zaitzev); E, *D. latissimus* Linnaeus; F, *D. circumcinctus* Ahrens; G, *D. alaskanus* J. Balfour-Browne; H, *D. dauricus* Gebler;; I, *D. lapponicus lapponicus* Gyllenhal; J, *D. lapponicus disjunctus* Camerano; K, *D. circumflexus* Fabricius; L, *D. thianshanicus* Gschwendtner; M, *D. latro* Sharp; N, *D. sinensis* Feng.

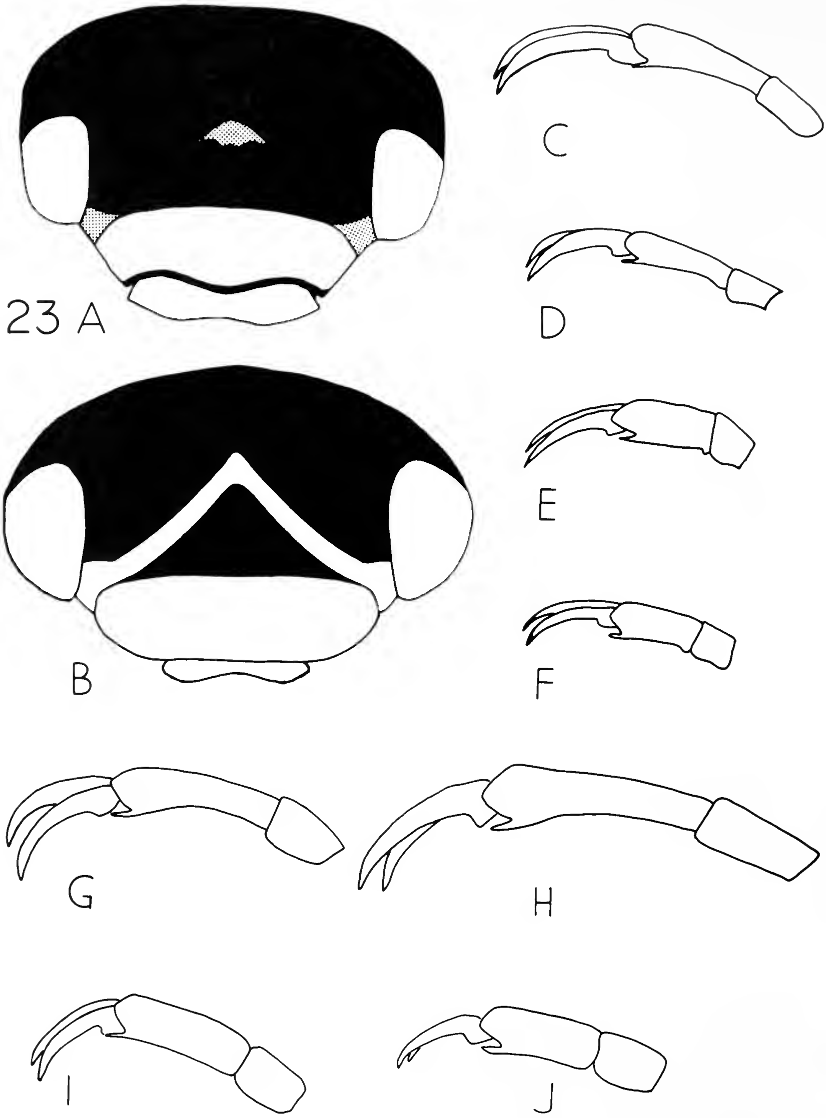


Fig. 23. Structural features of species of *Dytiscus* Linnaeus. A, frontal view of head of *D. harrisii* Kirby. B, frontal view of head of *D. cordieri* Aubé. C, protarsomere IV and V plus claws of male of *D. hatchi* Wallis. D, protarsomere IV and V plus claws of male of *D. fasciventris* Say. E, mesotarsomere IV and V plus claws of female of *D. hatchi* Wallis. F, mesotarsomere IV and V plus claws of female of *D. fasciventris* Say. G, protarsomere IV and V plus claws of male of *D. mutinensis* Pederzani. H, protarsomere IV and V plus claws of male of *D. dimidiatus* Bergsträsser. I, mesotarsomere IV and V plus claws of female of *D. pisanus* Castelnau; J, mesotarsomere IV and V plus claws of female of *D. delictus* (Zaitzev)

Key to Adults of Palearctic Species of *Dytiscus* Linnaeus

1 (0) Metacoxal process with inner margin convex, apex rounded to obtusely angulate, not acuminate (Figs. 21F, G, L-N)..........2

1' Metacoxal process with inner margin convex, apex acutely angulate and more or less acuminate (Figs. 22E-N)................11

2 (1) Pronotum with anterior and posterior yellow bands absent, OR, less than 0.33 width of lateral band (Figs. 2A, B, 3B, C)....3

2' Pronotum with anterior and posterior yellow bands present and at least 0.50 width of lateral band (Fig. 3D)....................6

3 (2) Pterothoracic sterna piceous to black (Figs. 8B, C); smaller specimens, 24 to 30 mm)..4

3' Pterothoracic sterna predominantly yellow (Figs. 9D, 10A); larger specimens, 28 to 39 mm.......................................5

4 (3) Metatrochanter with apex rounded (Fig. 21F); body narrowly oval (TL/GW 1.97 to 2.01); distributed from Europe, east to Kazakh SSR (Fig. 29), and New Zealand.. *D. semisulcatus* Müller, p. 444

4' Metatrochanter with apex acuminate (Fig. 21G); body broadly oval (TL/GW 1.84 to 1.94); distributed in Japan, Maritime USSR, northeastern China (Fig. 30)..*D. sharpi* Wehncke, p. 445

5 (3') Body oblong (TL/GW 1.98 to 2.00); male with protarsomere V about 1.3 length of longer claw (Fig. 23G), and about 30 punctures on anterior surface; smaller specimens, 28 to 35 mm; distributed in Italy, Corfu, Yugoslavia (Fig. 35)...*D. mutinensis* Pederzani, p. 458

5' Body more elongate (TL/GW 1.84 to 1.95); male with protarsomere V about 1.5 length of longer claw (Fig. 23H), and about 60 punctures on anterior surface; larger specimens, 32 to 39 mm; distributed from Europe to Transcaucasia, Asia Minor and Syria (Fig. 36)..*D. dimidiatus* Bergsträsser, p. 459

6 (2') Metacoxal process with apex rounded (Figs. 21N, 22D)..........7

6' Metacoxal process with apex acute (Figs. 22A-C)..................8

7 (6) Metatrochanter with apex acuminate (Fig. 21N); male with protarsomere V about 1.3 times width of protibia; male with median lobe broadly rounded at apex (Fig. 17B); female with mesotarsomere V about 2.0 times length of IV (Fig. 23I); most females with elytron sulcate; distribution circum-Mediterannean (Fig. 37)...*D. pisanus* Laporte de Castelnau, p. 461

7' Metatrochanter obtusely rounded or acute (males, Fig. 22D); male with protarsomere V about equal in length to width of protibia; male with median lobe notched laterally at apex (Fig. 18B); female with mesotarsomere V about 1.5 times length of IV (Fig. 23J); no sulcate females known; distributed in Maritime USSR (Fig. 40).......*D. delictus* (Zaitzev), p. 471

8 (6') Venter with at least abdominal sterna II, II and VI with large, transverse, baso-lateral infuscation (Fig. 10D, 11A).............9

8' Venter with abdominal sterna II to V without baso-lateral infuscation, or, with only narrow baso-lateral infuscation (Fig. 10C) 10

9 (8) Head with chevron extended antero-laterally to yellow spot at antennal base; distributed in Maritime USSR and Japan (Fig. 38) ....*D. marginalis czerskii* Zaitsev (in part), p. 469

9' Head with chevron not extended antero-laterally, not connected to yellow spot at antennal base; distributed in Caucasus Mountains, Transcaucasia and Crimean USSR, northeastern Turkey and Iran (Fig. 39)............................ ....*D. persicus* Wehncke, p. 470

10 (8') Head with chevron extended antero-laterally to yellow spot at antennal base; distributed in Maritime USSR and Japan (Fig. 38) ....*D. marginalis* czerskii Zaitsev (in part), p. 467

10' Head with chevron not extended antero-laterally, not connected to yellow spot at antennal base; distributed from Portugal and southern Spain north to Scotland and east Siberia (Fig. 38).. ....*D. marginalis marginalis* Linnaeus, p. 467

11 (1') Elytron with epipleuron greatly widened into a flange (Fig. 4B); clypeus of most specimens with anterior margin shallowly bisinuate; distributed from France through Ukrainian SSR to western Siberia (Fig. 41)...................... ....*D. latissimus* Linnaeus, p. 476

11' Elytron with epipleuron not widened into flange; clypeus with anterior margin evenly curved.................................. 12

12 (11') Pronotum very broadly margined with yellow, anterior orposterior bands wider than or almost as wide as discal infuscation (Fig. 5C); elytral disc of many specimens with infuscation reduced to numerous lines of spots (Fig. 5C); metacoxal processes with apical spine very long (Figs. 22I, J) ...(*D. lapponicus*) 13

12' Pronotum more narrowly margined with yellow, anterior and posterior bands much narrower than discal infuscation (Fig. 5D); elytral disc piceous to black (Fig. 5D); metacoxal processes of various lengths (Figs. 22K-N) 14

13 (12) Pronotum with quadrangular infuscation (Fig. 5C); distributed in northern Europe to USSR (Fig. 47)............................ ....*D. lapponicus lapponicus* Gyllenhal, p. 486

13' Pronotum with infuscation greatly reduced, almost linear, in shape of printers bracket, opening posteriorly; distributed in Italian Alps (Fig. 47).. ....*D. lapponicus disjunctus* Camerano, p. 490

14 (12') Metacoxal process with apical spine very long (Figs. 22K N).... 16

14' Metacoxal process with apical spine shorter (Figs. 22F-H) 15

15 (14') Eye enclosed dorsally by narrow yellow band, or, some specimens with band narrowly broken near inner posterior margin of eye; pterothoracic and abdominal sterna testaceous to pale rufous, basal margins of sterna testaceous to pale rufous, basal margins of sterna I to III very narrowly infuscate in some specimens (Fig. 11D); male with apex of median lobe not sinuate in dorsal view (Fig. 18D) ....

.................................*D. circumcinctus* Ahrens, p. 477

15' Eye not enclosed dorsally by narrow yellow band, some specimens with inner margin margined with yellow or red; pterothoracic sterna with at least metasternum medially infuscate (Fig. 12B), abdominal sterna variable in colour pattern; male with apex of median lobe sinuate in dorsal view (Fig. 19C)..........................*D. dauricus* Gebler, p. 483

16 (14) Abdominal sterna with broad fasciae (Fig. 13A left, D)..17

16' Abdominal sterna without, or with narrow fasciae (Fig. 13A right, B,C) 19

17 (16) Distributed in Europe, Great Britain, southern Scandinavia and northern Africa (Fig. 48); male with protarsal claw about 0.50 length of protarsomere V; male with knob of median lobe not spatulate in lateral view (Fig. 20A) .... *D. circumflexus* Fabricius (in part), p. 490

17' Distributed from central USSR eastward (Figs. 49, 51); male protarsal claw about 0.67 length of protarsomere V; male with median lobe in lateral view spatulate or not (Figs. 20B, D) 18

18 (17') Distributed in Peoples Republic of China (Fig. 51); male with knob of median lobe spatulate in lateral view (Fig. 20D)....... ....*D. sinensis* Feng, p. 493

18' Distributed in central USSR, Afghanistan and Kashmir (Fig. 49); male with knob of median lobe not spatulate in ateral view (Fig. 20B)........*D. thianshanicus* Gschwendtner, p. 493

19 (16') Distributed in western Palearctic region (Fig. 48) ....*D. circumflexus* Fabricius (in part), p. 490

19' Distributed in central and eastern Palearctic region (Figs. 49, 50) 20

20 (19') Head with chevron extended to antero-lateral margin; male with median lobe in dorsal view with pre-apical portion narrow (Fig. 20C); distributed in far eastern USSR (Fig. 50)... ....*D. latro* Sharp, p. 494

20' Head with chevron not extended to antero-lateral margin; male with median lobe in dorsal view with pre-apical portion broader (Fig. 20B); distributed in central USSR, Afghanistan and Kashmir (Fig. 49) ....*D. thianshanicus* Gschwendtner, p. 493

Species Treatments

Dytiscus verticalis Say, 1823

Figs. 1A, 7A, 14A, 21A, 24, and 52

Dytiscus verticalis Say, 1823:92 (Type area- not stated, but presumably from eastern United States. Type specimens probably lost, see below). -Zimmermann, 1920:255. -Hatch, 1929:226. -Wallis, 1950:51. -Wallis and Larson, 1973:110 -Larson, 1975:396.

Derivation of specific epithet.— Unclear but probably derived from Latin, meaning at the vertex, directly overhead or upright, possibly referring to the chevron on the vertex of the head.

Notes about type material.— As with most of the typical material of Thomas Say, original specimens are probably lost (Lindroth and Freitag 1969).

However, Say's original description is sufficiently diagnostic to indicate that this is indeed the taxon to which he was referring. Therefore a neotype is not needed.

Diagnostic combination.— Large size, sub-apical transverse fascia of elytron of most specimens (Fig. 1A), infuscate venter, and pronotum with broad yellow lateral margins only, permit easy recognition of adults of this Nearctic species.

Description.— Measurements of largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of the body is shown in Fig. lA; coloration of pterothoracic sterna and abdominal terga in Fig. 7A; median lobe of male in Fig. 14A; and metacoxal processes in Fig. 21A.

Variation.— Adults are relatively uniform in coloration. Pronota and elytra of a very few specimens have a dark greenish cast. The sub-apical transverse fascia of the elytron varies in width and distinctness and is absent from a few specimens. Pronota of a few specimens have the anterior and posterior margins marked with yellow bands, less than 10% of width of lateral bands. Some other specimens have piceous anterior and posterior margins of the pronotum.

Natural history.— This species seems to be most common in ponds in the eastern deciduous forest and adjacent areas. Young (1966) discussed methods for laboratory rearing of *D. verticalis.* Formanowicz and Brodie (1981) present information about pupation.

Brodie and Formanowicz (1981, 1983), Brodie *et al.* (1978), Formanowicz (1982, 1986, 1987), Leclair *et al.* (1986) and Formanowicz and Bobka (1989) analyzed aspects of predation of larval *D. verticalis* on amphibian larvae of *Rana* spp. (Ranidae), *Hyla* spp. (Hylidae), *Bufo* spp. (Bufonidae), *Ambystoma* spp. (Ambystomidae) and *Notopthalmus* sp. (Salamandridae). In general, larvae of *D. verticalis* are avid predators of immature amphibians and consume several prey daily.

Data on labels are interpreted as evidence for an autumnal dispersal after emergence from the pupal stage (Table 4). Autumnal dispersal could take place soon after emergence from the pupa, as a teneral specimen from Ann Arbor, Michigan, was taken at a porch light in July (Tables 4 and 5). Other data suggestive for an autumnal dispersal flight are listed in Table 5. No information is available about overwintering sites, *i.e.*, in water or on land, but adults of *D. verticalis* appear to have a vernal dispersal (Table 5) which could be associated with movement to temporary vernal ponds as well as permanent ponds where larval development occurs (see above), although label records for definitely temporary ponds are scarce (Ontario, near Huntsville 31.v.72 and 7.vi.66 [2 ROMC]).

Distribution. (Fig. 24).— This is a species of eastern North America which ranges as far west as western Manitoba and western Wisconsin and as far south as North Carolina with one dubious unmapped record from Homestead, Florida (1 MCZC). Records of this species from the State of California [Stan. U. 19.iv. - (2 CASC) and a state record only (1 ICCM)] are probably in error. The majority of records are from Connecticut, Massachusetts and New York.

Chorological relationships.— *Dytiscus verticalis* is broadly sympatric with all other Nearctic species which occur in eastern North America except the more northerly *D. dauricus* and *D. alaskanus.*

Phylogenetic relationships.— The basal segment of the labial palpus of third instar larvae of *D. verticalis* lacks the false segmentation of every other known third stage larva of *Dytiscus* (Wilson 1923, Fig. 37 and Roughley, unpublished data) and in this state they are similar to third stage larvae of *Hyderodes shuckardi* Hope (Watts 1964, Fig. 16). Because of the distribution of this character state, I suggest that *D. verticalis* is the sister group to the remainder of *Dytiscus* (Fig. 52).

Material examined.— A total of 993 adult specimens were examined of which 349 are males, 420 are females, and for 224 specimens sex was not determined.

Dytiscus harrisii Kirby, 1837
Figs. 1B, 7B, 14B, 21B, 23A, 25, and 52

Dytiscus harrisii Kirby, 1837:76 (Type area- "taken in the Journey from New York to Cumberland-house." Holotype- see Larson 1975:397.). -Zimmermann, 1920:242, 248. -Hatch, 1929:277. -Hatch, 1953:238. -Gordon and Post, 1965:25. -Wallis and Larson 1973:110. -Larson, 1975:397.

Derivation of specific epithet.— Kirby named this species in honour of T.W. Harris, "...a very eminent American entomologist."

Diagnostic combination.— Bisinuate anterior margin of clypeus, large size, and combination of distinctive dorsal and ventral colour pattern (Figs. 1B, 7B, and 23A) allow easy recognition of adults of this species.

Description.— Measurements for largest and smallest specimens are given in Table 2. States of taxonomically important characters of adult males and females are given in Table 3. Dorsal view of the body is shown in Fig. 1B; coloration of pterothoracic sterna and abdominal terga in Fig. 7B; median lobe of male in Fig. 14B; and metacoxal processes in Fig. 21B.

Variation.— Adults are relatively uniform in coloration. Pronota and elytra of a very few specimens have a dark green cast. Colour of legs varies, with the posterior faces of the pro- and mesofemora testaceous in some specimens, rather than the usual piceous to black. This difference is not completely correlated with geographic locality of the specimen but is more common in eastern North America. The subapical transverse fascia of the elytron varies in width and distinctness but is present in all specimens examined.

Larson (1975) commented about the small size of specimens from Alberta and Northwest Territories compared to specimens from Ontario and Wisconsin. A similar difference was found by me, and is interpreted as indicative of sampling bias (see Measurements). Differences in length can be explained by a greater size range for adult *D. harrisii* in northwestern North America with smaller specimens being more often captured; whereas, in eastern North America the size range is less and therefore the adult stage appears to be larger within this area.

Natural history.— I have evidence from western Canada that larval development takes place in or near running water (Roughley, in prep.). The remainder of the life cycle can be inferred from information on labels of adult specimens examined. Adults probably overwinter in relatively permanent water bodies [Vermont, Burlington, 22.ii.49, taken through fishing hole in ice, L. Champlain, (1, UVCC)]. Depending on local climatic and other factors, larval development is completed by June or July as indicated by occurrence of teneral adult specimens (Table 4), and mature, field-collected pupae [Alberta, Kneehills Creek near Acme, pupa coll'd. 23.vi.80, adult emg'd. 6.vii.80, (1, JBWM); British Columbia 1 km N Golden, prepupa coll'd. 21.vi.80, adult emg'd. 10.vii.80 (1, JBWM)]. The adult teneral specimen from southern Alberta, 3.ix.61, reported by Larson (1975:398) probably represents an exceptional situation. Following shortly after adult emergence is a dispersal flight (Table 5), presumably to overwintering sites but possibly to localities where feeding takes place before overwintering begins. During these dispersal flights, specimens are collected in non-typical habitats such as beach drift, and swimming pools (Table 5).

Distribution (Fig. 25).— The range of this species is transcontinental in the Nearctic region, from Newfoundland to Alaska. The northern limit of distribution is probably coincident with treeline and the southern limit appears to be the latitude of southern Pensylvania, central Nebraska and northern Washington. Most specimens are from states and provinces in the vicinity of the Great Lakes.

Chorological relationships.— *Dytiscus harrisii* is sympatric with all other Nearctic species of *Dytiscus* except *D. habilis* and *D. carolinus.*

Phylogenetic relationshipships.— This species is probably related to a species complex which includes *D. habilis*, *D. hybridus*, and *D. marginicollis* (Fig. 52).

Material examined.— A total of 571 adult specimens was examined of which 270 are males, 285 are females, and for 14 specimens sex was not determined.

Dytiscus hybridus Aubé, 1838
Figs. 1D, 7C, 14C, 21C, 26, and 52

Dytiscus hybridus Aubé, 1838:116 (Type area -"États Unis d'Amérique." Type not seen.). -Zimmermann, 1920:248. -Hatch 1929:226. -Hatch 1933:11. -Wallis 1950:51. -Gordon and Post 1965:24. -Wallis and Larson 1973:110. -Larson 1975:398.

Leionotus compar Melsheimer, 1844:26 (Type area - "Pennsylvania and Massachusetts." Type not seen.). -Zimmermann 1920:248.

Derivation of specific epithet.— From the Latin hybrida meaning a hybrid or an indication of hybridization, presumably because, to Aubé, adults of this species demonstrated a mixture of the characteristics of other species.

Notes about type material.— I searched for, but was unable to find, any type material within the R. Oberthür collection in MNHN.

Diagnostic combination.— Adults of *D. hybridus* are distinguished from adults of other species of *Dytiscus* with piceous to black venters, by smaller size, non-explanate pronotal margins, and presence of wide yellow margins laterally only on pronotum. Females not sulcate. Males with mesotarsomeres I to III ventrally with longitudinal glabrous area.

Description.— Measurements of largest and smallest specimens are given in Table 2. States of taxonomically important characters of adult males and females are given in Table 3. Dorsal view of the body is shown in Fig. 1D; coloration of pterothoracic and abdominal sterna in Fig. 7C; median lobe of male in Fig. 14C; and metacoxal processes in Fig. 21C.

Variation.— The most conspicuous variation of adult *D. hybridus* is in coloration of the pronotal margin. The most common condition is absence of posterior pronotal yellow band but with a very narrow anterior band. Some specimens have both the anterior and posterior bands obliterated and still others have both of these bands present and distinct. In examples of the latter, the anterior band is wider than the posterior band, and both are less than 0.33 width of a lateral band.

Other than pronotal bands, adults of this species are quite uniform in colour and in structural features. Most other differences in colour (*e.g.* piceous rather than black venter) are probably due to age of specimens when collected (*e.g.* fully sclerotized versus teneral). Compared to most other species of *Dytiscus*, *D. hybridus* occupies a smaller geographic range and is structurally more homogeneous.

Natural history.— Apparently this is a species which prefers mature ponds within the eastern deciduous forests of North America. Collection of an adult female in December at Ithaca, New York could be interpreted as evidence that the adult stage overwinters in water. However, specimens have been collected in flight in Pennsylvania in December and in Illinois in January, and may indicate dispersal from any over-wintering habitat. Teneral specimens from the more southerly portions of the range were taken in June and July (Table 4). Specimen data indicative of flight period are inconclusive (Table 5); adults may have only an extended late-season flight (July to January) depending on geographic location, or a late season flight (July to September) and a very early season flight (December to January).

Distribution (Fig. 26).— This strictly Nearctic species appears to be common only east of the 100th meridian. Scattered localities, perhaps indicating range expansion (Larson 1975:398), extend the range to Oregon and northward into Alberta. The southern limit is represented by specimens from Missouri, Tennessee, and South Carolina. The hiatus in locality information in the eastern USA, which coincides with the eastern mountain chains, could be indicative of less collecting effort, lack of suitable habitat within the area, or of avoidance of montane habitats by adults of this species. The more north- central and north-eastern "limits" are probably artificial and due to insufficient collecting.

Chorological relationships— Within the *D. hybridus* species-group, *D. hybridus* is broadly sympatric with *D. harrisii* only.

Phylogenetic relationships.— Adults of this species exhibit a high number of plesiotypic character states when compared to other members of the *D. hybridus* species-group. As such, of the four extant taxa, it is probably the most similar to the hypothetical ancestor of this clade.

Material examined.— A total of 1636 adult specimens were examined, of which 852 are males, 778 females, and 6 are of undetermined sex.

Dytiscus marginicollis LeConte, 1845
Figs. 7D, 14D, 21D, 27, and 52

Dytiscus marginicollis LeConte 1845:209, Fig. 10, plate XVIII (Type locality -"*in flumine* Missouri". Holotype female in LeConte collection of MCZC labelled as follows: [green circular label] Type 6091 [red label] *D. marginicollis* Lec., albionicus Motsch.). -Zimmermann 1920:252 (*ex parte*). -Hatch 1929:226, 1933:11. -Leech 1941:290, 1948:414. -La Rivers 1951:404. -Hatch 1953:238. -Leech and Chandler 1956:323. -Anderson 1962:73. -Larson 1975:398.

Dytiscus albionicus Motschulsky 1859:166 (Type locality - Fort Ross near San Francisco, California, U.S.A.) (Holotype female in ZILR labelled as follows: 81.; *Dytiscus albionicus* Motsch; *D. marginicollis* Lec., Zaicev det.; HOLOTYPE, Dytiscus albionicus, Motschulsky 1859 examined R.E. Roughley). -Zimmermann 1920:244.

Dytiscus anxius; Gemminger and Harold 1868:461, *nec* Mannerheim 1843:218.

Dytiscus anxius var. *albionicus*; Gemminger and Harold 1868:461. -Zimmermann 1920:244; *nec* Mannerheim 1843:218, *nec* Motschulsky 1859:166.

Dytiscus vexatus; Hatch 1929:226, *nec* Sharp 1882:643.

Derivation of specific epithet.— From Latin, *marginare*, to enclose within a border, and *collum* meaning neck, in reference to the yellow margins of the pronotum.

Notes about type material.— My interpretation of the placement of *D. albionicus* Motschulsky differs from that of Larson (1975:401), and other authors who have placed this name as a junior synonym of *D. circumcinctus*. Reassignment is based on absence of *D. circumcinctus* from California, USA, from which Motschulsky described *D. albionicus*. Also, the type of *D. albionicus* was examined and it is a typical female of *D. marginicollis*.

Diagnostic combination.— Distinctive pronotal and ventral coloration (Fig. 7D) separate adults of this Nearctic species from those of all other species except *D. habilis*. Adult males of *D. marginicollis* are distinguished from males of *D. habilis* by mid-ventral glabrous areas on mesotarsomeres II and III. Males and females of *D. marginicollis* also have an increased area of the pronotal disc infuscate and the posterior margin of this infuscation is sinuate. Adults of *D. marginicollis* are longer than those of *D. habilis* (Table 2). Females of both taxa are not sulcate. The range of *D. habilis* is south of that of *D. marginicollis* (Fig. 27; *cf.* Fig. 28).

Description.— Measurements for largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of the body is not shown; coloration of pterothoracic sterna and abdominal terga is shown in Fig. 7D; median lobe of male in Fig. 14D; and metacoxal processes in Fig. 21D.

Taxonomic notes.— Leech (1948) noted that two male specimens which he examined from Baja California, México, might represent a distinct subspecies as they are more parallel-sided than other specimens. I have seen these specimens and judge them to be within the range of variation shown by more northern specimens.

Variation.— One of the most consistent character states shown by adult specimens of *D. marginicollis* is sinuation of anterior and posterior margins of the discal infuscation of the pronotum. This state has permitted rapid and efficient sorting of members of this taxon. In contrast, there is extreme variation in colour of the scutellum and, to a lesser extent, of legs. The scutellum varies from completely yellow to completely piceous in most population samples. Leg colour varies similarly, and these two states are not completely correlated, although there are general trends to extremes of both states in some specimens. Some specimens have elytral disc with obsolete irrorations. Post-mortem changes can discolor ventral and dorsal colour patterns. These are usually easily overcome by proper cleaning of specimens. Other structural and colour characters are relatively uniform.

Natural history.— Most habitats where I have collected adults of this species are characterized by high salinity, typical of ponds in grassland areas, and stands of *Scirpus* species. Larson (1975:399) noted an affinity for what were presumed to be permanent prairie sloughs in conjunction with *Typha* and *Juncus*.

Adults and larvae of *D. marginicollis* are able to use hot springs as habitats. Brues (1928: 152, 153, 176) recorded adults from a group of springs near Battle Mountain, Nevada in which the temperature was 30°C. Brues (1932:272) recorded a large larva of *Dytiscus*, which is presumably that of *D. marginicollis*, from a cooler (17°C) spring in Yellowstone National Park, Wyoming.

Holomuzki (1986) records *D. marginicollis* at elevations between 1500 and 2500 m in east central Arizona where it coexists with tiger salamanders. In this region, *D. dauricus* occurs with the same salamander but at higher elevations (2500+ m). The record of a larval *Dytiscus* killing a young garter snake (Drummond and Wolfe 1981) is almost certainly for *D. marginicollis* (Roughley unpubl.) although garter snakes are not likely normal prey for them.

Flight records are available for many months of the year, with July predominating (Table 5). Dispersal could follow shortly after emergence from pupae, as records of teneral specimens range from May to August (Table 4).

Distribution (Fig. 27).— The range of this species is perhaps significantly, if broadly, described as west of that of *D. hybridus* and north of that of *D. habilis*. The eastern-most record is from Aweme, Manitoba, Canada, and the southern-most from San Dimas, Durango, México. Records of this taxon from Alaska (*e.g.* Hatch 1929, Leech 1948, Larson 1975) are suspect, and could stem from the inclusion of *D. marginicollis* as a junior synonym of *D. anxius*, the type locality of which is Sitka, or from Hatch's inclusion of *D. vexatus* as a junior synonym of *D. marginicollis*. However, further collecting could well extend the range of this species northward along the British Columbia coast and perhaps into southernmost Alaska. The northernmost records of adult specimens are from Calgary and Lethbridge, Alberta, Canada, although I have seen mature larvae from George Lake, near Dunstable, Alberta. The record for the state of Durango, México, mentioned above, may seem inconsistent except that I have many larval records from Baja California, México (and none for *D. habilis*, Roughley, in prep.) and the Durango specimen may represent dispersal from Baja California del Sur.

Chorological relationships. - The exclusively western North American distribution of *D. marginicollis* excludes sympatry with *D. carolinus* and *D. verticalis*. It is only narrowly sympatric or parapatric with *D. hybridus* and *D. habilis*.

Phylogenetic relationships.— Within the *D. hybridus* assemblage, adults of *D. marginicollis* are most similar in colour pattern to those of *D. habilis* and these two species are more similar to *D. harrisii* than to *D. hybridus* Despite these similarities, *D. marginicollis* is probably the sister species to *D. hybridus* based on common possession of glabrous areas on the male mesotarsomeres (Table 3 and Fig. 52).

Material examined.— A total of 972 adult specimens was examined, of which 443 are male, 526 female, and sex was not determined for 3 specimens.

Dytiscus habilis Say, 1834
Figs. 1C, 8A, 15A, 21E, 28, and 52

Dytiscus habilis Say 1834:441 (Type area -"...in the river beyond Vera Cruz...", México. Type probably lost.). -Zimmermann 1920:248. -Darlington 1938:84. -Wallis 1950:51.

Derivation of specific epithet.— This name is derived from the Latin, *habilis*, meaning apt, fit, suitable (Brown, 1956).

Notes about type material. - Say's types are probably lost (see equivalent section under *D. verticalis*). Because Say's original description agrees well with the present concept of this taxon (specimens within the LeConte collection, MCZC, belong to this taxon), and considering that *D. habilis* is the only species which is widespread in México, a neotype is not required.

Diagnostic combination.— See discussion under equivalent section in treatment of *D. marginicollis*.

Description.— Measurements for largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of the body is shown in Fig. 1C; coloration of pterothoracic sterna and abdominal terga in Fig. 8A; median lobe of male in Fig. 15A; and metacoxal processes in Fig. 21E.

Variation.— Most of the types of variation discussed under *D. marginicollis* apply equally well to *D. habilis.*

Natural history.— Nothing has been published concerning natural history of this species. Available flight records are for April and October in Chihuahua, México, and June in Arizona, USA (Table 5). From limited specimen label data it appears that specimens are taken at increasing elevations further south in the range. For instance, in Arizona [Cochise Co., SW Res. Stn., 5 mi S Portal (FNYC, USNM)] specimens were taken at 1645 m, whereas specimens from northern México [Chihuahua, 5.1 km n Colonia Garcia, 23.vii.79 (1 JBWM)] were taken at 2010 m and at 2560 m in Guatemala (Huehuetenango, 7 mi N Santa Eulalia on road to San Mateo Ixtatán, 5.ii.65 (4 CASC)]. Other label information is scarce but the specimen mentioned above was taken at the margin of a creek, and another Méxican specimen [Chiapas, San Cristöbal de las Casas, 6.vii.64 (1 CASC] was taken in a habitat characterized as "pond and spring".

Distribution (Fig. 28).— From southwestern Arizona, southeastern New Mexico, and southwestern Texas, USA, this species ranges southward to Guatemala.

Chorological relationships.— Along the northern edge of its range, *D. habilis* is either narrowly sympatric or allopatric with *D. marginicollis.* It is not sympatric with, nor does its range closely approach, that of any other species of *Dytiscus.*

Phylogenetic relationships.— The similarity to specimens of *D. marginicollis* was noted in discussion of that species. *Dytiscus habilis* is interpreted as representative of sister lineage to that of *D. hybridus* plus *D. marginicollis* (Fig. 52).

Material examined.— A total of 240 adult specimens was examined, of which 148 are males, 90 females, and 2 are of undetermined sex.

Fig. 24. Known distribution of *Dytiscus verticalis* Say.

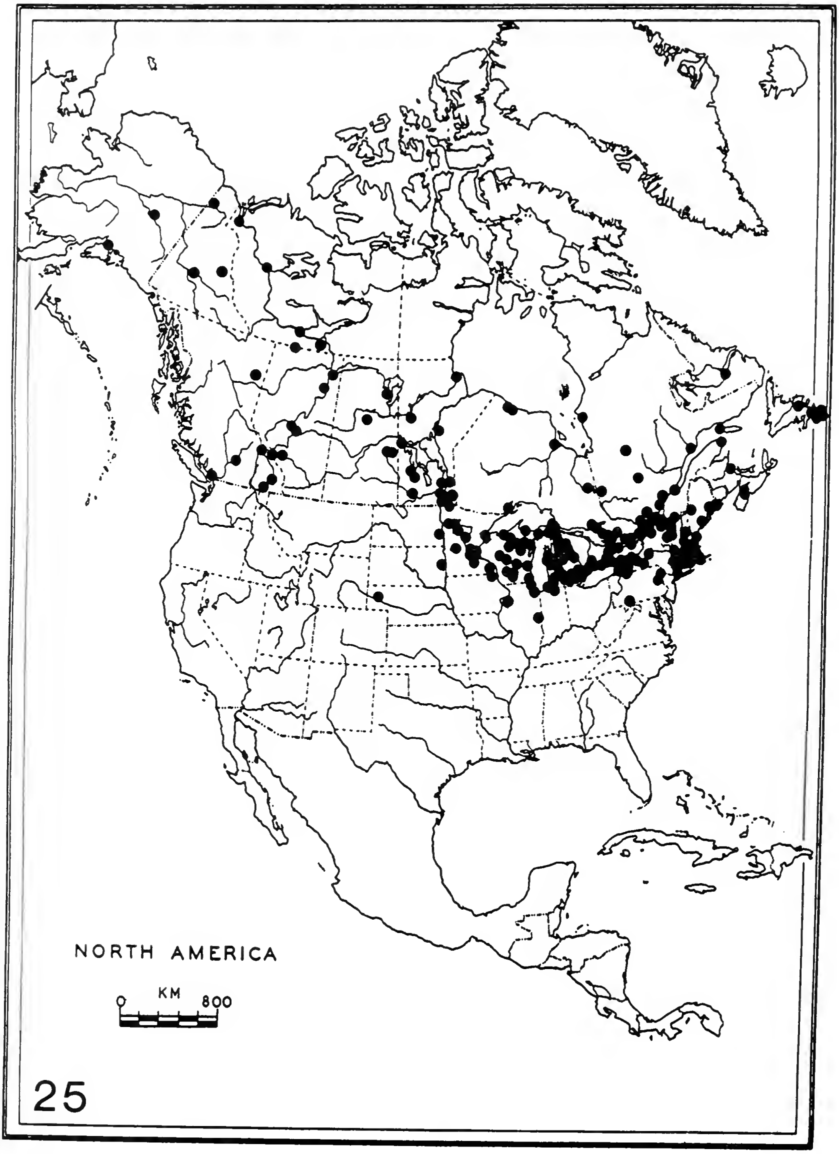


Fig. 25. Known distribution of *Dytiscus harrisii* Kirby.

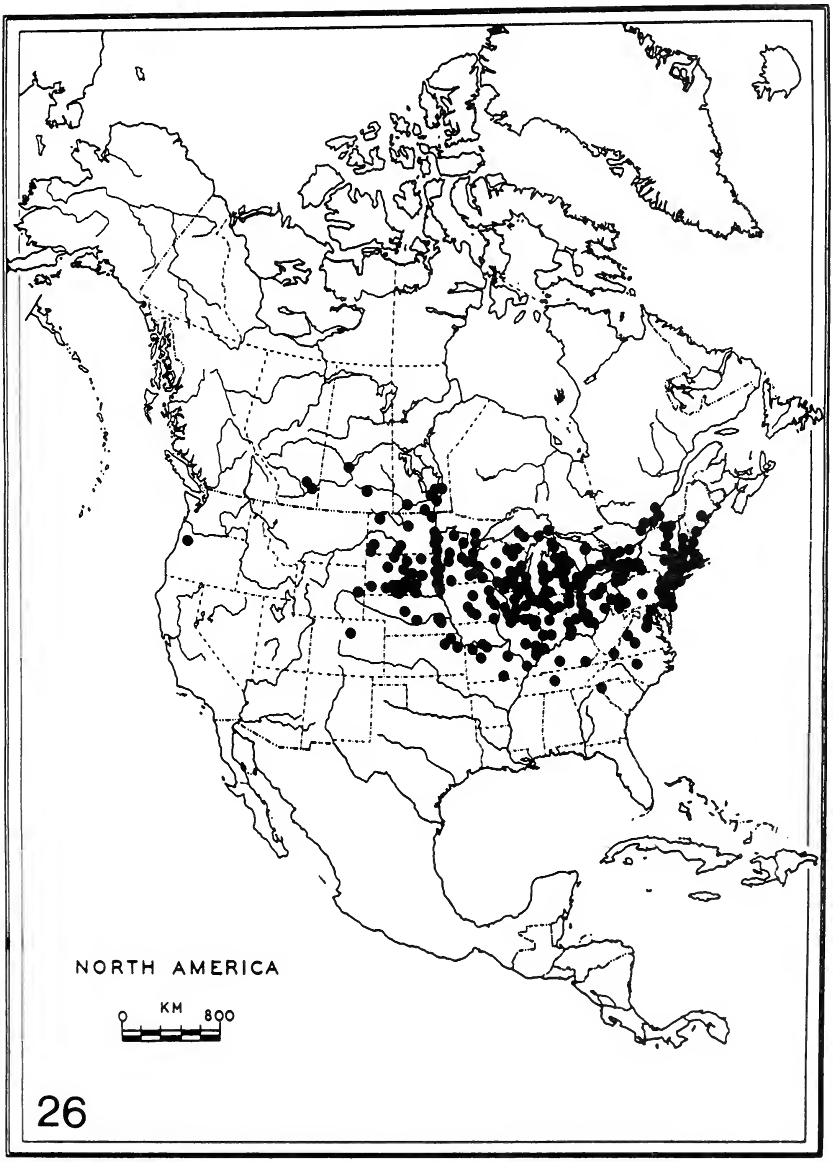


Fig. 26. Known distribution of *Dytiscus hybridus* Aubé.

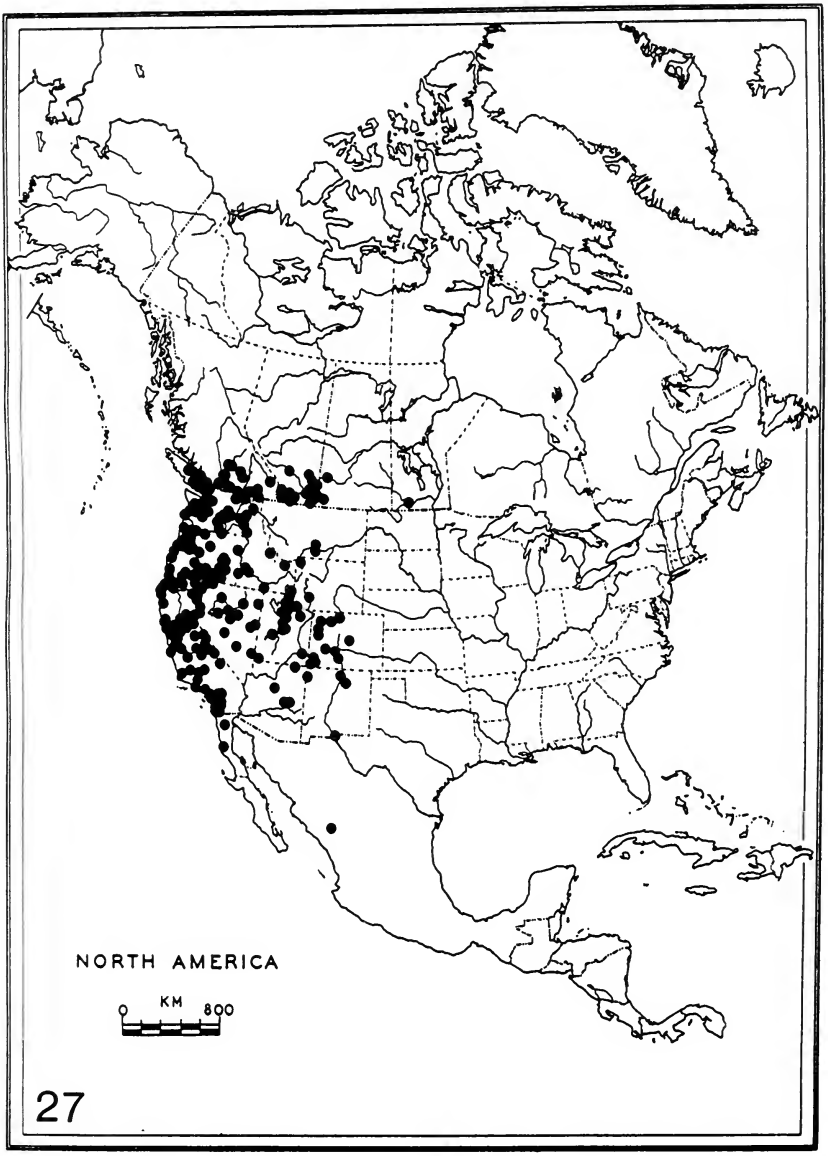


Fig. 27. Known distribution of *Dytiscus marginicollis* LeConte.

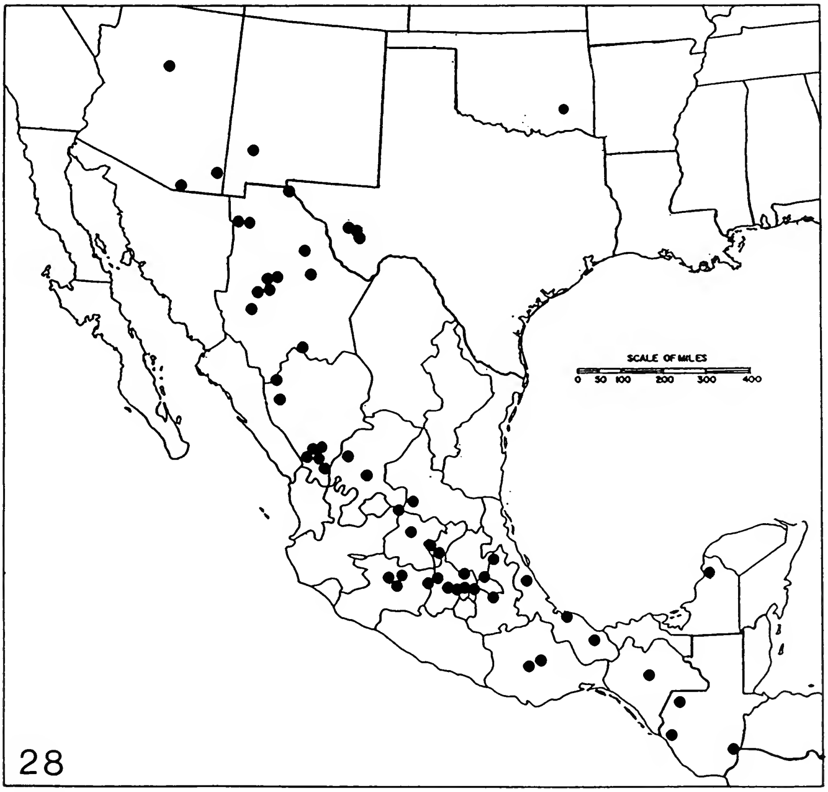


Fig. 28. Known distribution of *Dytiscus habilis* Say.

Dytiscus semisulcatus Müller, 1776
Figs. 2A, 8B, 15B, 21F, 29, and 52

Dytiscus semisulcatus Müller 1776:70 (Type area-Denmark. Type not seen). -Zimmermann 1920:253. -Guignot 1932:709. -Houlbert 1934:132. -Zimmermann and Gschwendtner 1938:38. -Guignot 1947a:242. -F. Balfour-Browne 1950:268. -F. Balfour-Browne 1953:27. -Zaitsev 1953:324. -Guignot 1961:857. -Ordish 1966:254. -Ordish 1967:6. -Galewski 1971a:100. -Schaeflein 1971:87. -Franciscolo 1979:662. -Régil and Salgado 1984:134,135.

Dytiscus punctulatus Fabricius 1777:238 (Type area - "Chilonii in rivulus". Type not seen.). -Zimmermann 1920:253.

Dytiscus frischi Bergsträsser 1778:43 (Type locality -Hanau area of Hessen, West Germany. Type not seen.). -Zimmermann 1920:254.

Dytiscus stagnalis Fourcroy 1785:66 (Type locality -Paris, France. Type not seen.). -Zimmermann 1920:254.

Dytiscus porcatus Thunberg 1794:74 (Type area -"Uplandiae," Sweden. Type not seen.). -Zimmermann 1920:254.

Dytiscus punctatus Olivier 1795:12 (Type locality -not stated. Type not seen.). -Zimmermann 1920:254.

Dytiscus punctulatus ab. *maurus* Schaufuss 1882:clxxiii (Type locality -Dresden in Dresden, West Germany. Type not seen.). -Zimmermann 1920:254. -Guignot 1932:709. -Zimmermann and Gschwendtner 1938:38. -F. Balfour-Browne 1950:268. -Zaitzev 1953:324. -Guignot 1961:857.

Dytiscus punctulatus var. *expectata* Peyerimhoff 1905:229 (Holotype female from Algeria in MNHN labelled as follows: Lac de Mouzaïa, 15 Juin 1905; v. expectatus type unique; HOLOTYPE, *Dytiscus punctulatus* var. *expectata* Peyerimhoff, examined R.E. Roughley 1981.).

Dytiscus punctulatus var. *expectatus* Peyerimhoff. **Justified emendation.** -Zimmermann 1920:254. -Guignot 1932:709. -Zimmermann and Gschwendtner 1938:38. -Guignot 1947a:242. -F. Balfour-Browne 1950:268. -Zaitsev 1953:324. Guignot 1961:858. -Schaeflein 1971:87. -Franciscolo 1979:662.

Dytiscus punctulatus var. *laevis* Engert 1911:19 (Type locality-Corfu, Greece. Type not seen.). -Zimmermann 1920:254. -Zimmermann and Gschwendtner 1938:38. -Guignot 1961:858.

Derivation of specific epithet.— From Latin, in reference to the short sulci or grooves on the female elytra.

Diagnostic combination.— European distribution, infuscate venter (Fig. 8B) and pronotum with lateral yellow margins only (Fig. 2A) easily distinguish adults of this taxon.

Description.— Measurements for largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of the body is shown in Fig. 2A; coloration of pterothoracic sterna and abdominal sterna in Fig. 8B; median lobe of male in Fig. 15B; and metacoxal processes in Fig. 21F.

Variation.— Guignot (1961:857) suggested that the completely piceous colour of specimens of *D. semisulcatus* which Schaufuss described as ab. *maurus* is the result of post-mortem changes. Pronotal colour pattern (Fig. 2A) is quite uniform in specimens that I have seen. Only very few specimens have the anterior margin of pronotum narrowly reddish or yellowish. Most specimens have the legs completely infuscate, except for anterior faces of protibia and protarsus of both sexes, and the femoral-tibial juncture of the hind two pairs of legs is marked by a rufous spot. The venter is piceous to black. Throughout most of its range, adult females exhibit sulcate elytra. Only in Palearctic Africa do non-sulcate females make up a significant proportion of population samples.

Natural history.— *Dytiscus semisulcatus* is the only species of *Dytiscus* known to overwinter in the larval stage. Blunck (1916a) discussed the life cycle of this species in detail, indicating pupation in May. This is in contradistinction to the implication by F. Balfour-Browne (1950:270) that the life cycle in England is biomodal. F. Balfour-Browne (1950) provides other natural history notes, as does Guignot (1932), and the former author records the majority of teneral specimens for July, August and September. It is apparently a species of strictly fresh-water habitats.

Distribution (Fig. 29).— This species ranges throughout Europe except in the north, but also occurs in northern Africa (Guignot 1961). The eastern-most record is from Turkestan, Kazakh SSSR. It occurs northward as far as southern Sweden based on locality information from specimens examined. Apparently it has been introduced into New Zealand (Ordish 1966).

Chorological relationships.— *Dytiscus semisulcatus* is broadly sympatric with most other European species of *Dytiscus*. Available distribution records suggest only narrow sympatry with *D. mutinensis* and *D. lapponicus*.

Phylogenetic relationships.— I interpret this taxon, based on adult characters, to be the most plesiotypic of the extant species of *Dytiscus* of which females have sulcate elytra (Fig 52).

Material examined.— A total of 469 specimens was examined of which 242 are males and 217 are females.

Dytiscus sharpi Wehncke, 1875
Figs. 2B, 8C, 15C, 21G, 30, and 52

Dytiscus sharpi Wehncke 1875:500 (Type area - "Japan". Lectotype male designated here from the Wehncke collection, MNHN, labelled as follows: LECTOTYPE; SYNTYPE; Japonia [yellow label, black edging]; Thoiry; sharpi mihi.). -Zimmermann 1920:254. -Zimmermann and Gschwendtner 1938:40 -Zaitsev 1953:325.

Dytiscus validus Régimbart 1899:311 (Type locality - "Nagahama, Japan". Lectotype male designated here in the Régimbart collection, MNHN, labelled as follows: LECTOTYPE; SYNTYPE; Nagahama, July 1886, Leech; LECTOTYPE, *Dytiscus* validus Régimbart R.E. Roughley.). -Zimmermann 1920:254. -Zaitsev 1953:325. **NEW SYNONYMY.**

Derivation of specific epithet.— Not specifically stated by Wehncke, but obviously named in honour of the British entomologist, David Sharp. Sharp had begun to accumulate the specimens for his 1882 monograph as early as 1875 according to Severin (1892) and would have been well known to Wehncke.

Diagnostic combination.— Adults of this species are most similar to those of *D. semisulcatus*. These are the only two Palearctic species with adults with yellow borders only on lateral margins of pronotum and infuscate venter. This species is found only in the eastern part of the Palearctic Region. In addition to differences in body shape, specimens of these taxa are easily separated on the basis of tarsal character states presented in the key.

Description.— Measurements for largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of the body is shown in Fig. 2B; coloration or pterothoracic sterna and abdominal terga in Fig. 8C; median lobe of male in Fig. 15C; and metacoxal processes in Fig. 21G.

Variation.— Too few specimens were seen to identify geographic patterns of variation. Few specimens have the anterior margin of the pronotum narrowly reddish. All females I have seen have sulcate elytra, but the female syntype from Wehncke's collection is sulcate basally only, the grooves are only about half as long as in other specimens of the same sex. Some specimens (teneral?) have legs completely brownish-yellow and abdominal terga indistinctly maculate (Fig. 8C). Most specimens have legs and venter black.

Natural history.— I can find nothing published about the natural history of this species, nor does the scanty label data supply any information.

Distribution (Fig. 30).— I have seen records for the People's Republic of China and Japan only. This species is expected to occur also in the extreme southeastern corner of the USSR.

Chorological relationships.—*Dytiscus sharpi* is broadly sympatric only with *D. delictus*, *D. dauricus* and *D. marginalis czerskii.*

Phylogenetic relationships.— This taxon and *D. semisulcatus* form the sister group to a Nearctic complex of species which includes *D. fasciventris*, *D. carolinus* and *D. hatchi* (Fig. 52).

Material examined.— A total of 21 specimens was examined of which 10 are males and 11 are females.

Dytiscus carolinus Aubé, 1838
Figs. 2C, 8D, 15D, 21H, 31, and 52

Dytiscus carolinus Aubé 1838:120 (Type area-"États Unis d'Amérique". Type not seen.). **NEW STATUS.**

Dytiscus fasciventris; *auctorum*, *nec* Say 1824:270. -LeConte 1859:177 (*ex parte*). -Crotch 1873:408 (*ex parte*). Wickham 1895 (*ex parte*). -Roberts 1905:106 (*ex parte*). Blatchley 1910:231 (*ex parte*). -Zimmermann 1919:233 (*ex parte*). -Zimmermann 1920:248 (*ex parte*). -Hatch 1929:226 (*ex parte*). -Wallis 1950:51 (*ex parte*). -Hatch 1953:237 (*ex parte*). -Michael and Matta 1977:41.

Dytiscus sp.; Young 1954:26.

? *Dytiscus fasciventris*; -Folkerts 1978:346.

Derivation of specific epithet.— Not stated by Aubé, but presumably referring to the type area which is presumably the east coast of the USA in the region occupied by the states of North and South Carolina.

Notes about type material. - I acknowledge the help of Dr. F.N. Young, Bloomington, Indiana who first pointed out the validity of this taxon. I have not seen Aubé's type(s), but the original description makes it clear that this is indeed the taxon to which he was referring.

Diagnostic combination.— Characters presented in the key, and the more southern distribution provide a reliable distinction among adults of *D. fasciventris* and *D. carolinus.*

Description.— Measurements for largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of the body is shown in Fig. 2C; coloration of pterothoracic sterna and abdominal terga in Fig. 8D; median lobe of male in Fig. 15D; and metacoxal processes in Fig. 21H; structure of protarsi in Fig. 23D and of mesotarsi in Fig. 23F.

Taxonomic notes.— See equivalent section in the treatment of *D. fasciventris.*

Variation.— See notes under variation in the treatment of *D. fasciventris.*

Natural history.— Dr. J.F. Matta, Old Dominion University, Norfolk, Virginia, USA, has provided unpublished collecting notes for this species in Virginia. Adults were collected at sites in which the dominant aquatic vegetation was: l. *Ludwigia palustris* and *Lemna gemsa*; 2. *Utricularia* sp.; and 3, no vegetation. Proportion of surface of ponds covered by vegetation varied from zero to complete. Each site was characterized by a large amount of detritus. Sites varied from relatively unshaded to ponds under a closed canopy.

One teneral adult male specimen (Table 4) was seen and bears the additional information: larva coll. 21.iv.73, pupa 2.v.73, ad. emerged 11.v.73. Flight records (Table 5) are two each for April and June, and one each for July and October.

Distribution (Fig. 31).— Distributed in a broad U-shape, from southern New England, south along the Atlantic and Gulf Coast to southern Georgia, and north along the Mississippi River drainage system to southern Michigan and extreme southeastern Wisconsin, USA. As for *D. hybridus*, absence of records for *D. carolinus* in eastern mountains is notable.

Chorological relationships.— Dytiscus carolinus seems most broadly sympatric with *D. verticalis* and *D. hybridus*. Zones of parapatry with *D. fasciventris* are noted under variation and taxonomic notes in the treatment of that species.

Phylogenetic relationships.— Closely related to *D. fasciventris* and *D. hatchi, D. carolinus* is the most plesiotypic of the Nearctic species females of which have sulcate elytra (Fig. 52).

Material examined.— A total of 91 specimens was examined of which 35 are males and 56 are females.

Dytiscus fasciventris Say, 1824
Figs. 2D, 9A, 16A, 21I, 32, and 52

Dytiscus fasciventris Say 1824:270 (Type area-"Lake Superior". Type probably lost). -Zimmermann 1920:248 (*ex parte*). -Hatch 1929:226 (*ex parte*). -Wallis 1950:51 (*ex parte*). -Hatch 1953:237 (*ex parte*). -Wallis and Larson 1973:110. -Larson 1975:399.

Derivation of specific epithet. — From the Latin fascia, band or stripe, and venter, belly (Brown 1956), in reference to the alternating black and yellow fasciae on the abdomen of adult specimens.

Notes about type material.— Say's type is probably lost (Larson 1975:400). Although the separation of *D. carolinus* would seem to require a type designation for one of these taxa, I hesitate to do so until it can be determined convincingly that type material of *D. carolinus* is no longer extant. I am confident of assignment of these two names because of the differing type areas for these taxa.

Diagnostic combination.— Characters presented in the key and mentioned below in the section on variation should be adequate to distinguish among specimens of the three closely related species: *D. fasciventris, D. hatchi* and *D. carolinus*.

Description.— Measurements for largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of the body is shown in Fig. 2D; coloration of pterothoracic sterna and abdominal terga in Fig. 9A; median lobe of male in Fig. 16A; and metacoxal processes in Fig. 21I.

Taxonomic notes.— Specimens of *D. fasciventris* have long been confused with those of *D. carolinus*, but I recognize two species. Possible introgression between *D. fasciventris* and *D. carolinus* in eastern North America, and between *D. fasciventris* and *D. hatchi* in western North America (see below) is problematic in that if all three are reproductively isolated but closely related taxa, then one would expect character displacement rather than character convergence within areas of sympatry. Despite limited convergence, I retain specific level status for each of these taxa because: 1, introgression has not been conclusively demonstrated; and 2, convergence is limited to a few characters only among *D. fasciventris* and *D. carolinus*. I do not treat *D. carolinus* and *D. fasciventris* as subspecies because: 1, the area where maximum similarity apparently occurs is north of the known range of *D. carolinus*; 2, there is no convergence in at least two characters (colour of metacoxal plates and shape of median lobe); and 3, difference in amount of character convergence among samples of specimens from Michigan and from the north-eastern United States.

No evidence suggests that introgression occurs now. In fact, variation in degree of character convergence is suggestive of an alternative hypothesis. Much of the apparent similarity could be derived from compression, fragmentation and broad overlap of ranges which would have been necessary adjustments to, for instance, the Wisconsinan glacial epoch. Thus the apparent convergence could be indicative of Wisconsinan rather than Holocene introgression. More extensive collections of specimens from the zones of parapatry and sympatry, and attempts to cross these putative specifically distinct taxa in laboratory and field situations will determine their ultimate taxonomic fate.

The major consistent differences among adult specimens of *D. fasciventris* and *D. carolinus* are given in the key to species. Other differences are length and width (Table 2), differences in form of the apex of the median lobe (compare Figs. 15D and 16A), and leg colour (generally darker in *D. carolinus*).

Wallis (1950:51) listed a number of subtle differences among specimens of *D. fasciventris* and *D. hatchi*, other than those used in the key. These are: 1, males of *D. hatchi* with elytra more distinctly punctate basally; 2, median lobe of male *D. hatchi* more linear than that of males of *D. fasciventris*; 3, infuscate markings of abdominal sterna touching the inter-sternal suture in *D. fasciventris*, as compared to isolated central blotches in *D. hatchi*; and 4, broader anterior and posterior bands of yellow of pronotum on specimens of *D. hatchi*.

Variation.— Specimens from central and northern portions of the range exhibit little variation. However, specimens occurring sympatrically with *D. carolinus* exhibit limited convergence with that species, mainly with respect to coloration. In southern New England and adjacent areas of the USA, specimens of *D. fasciventris* are more extensively marked with reddish colour on the abdominal sterna and thus are more similar to north-eastern specimens of *D. carolinus*. As well, north-eastern specimens of *D. carolinus* are larger than more southern specimens, and therefore these two taxa are more similar in size in this region. Specimens from this area are recognized by yellow versus infuscate metacoxal plates, females with protarsal claws shorter or subequal versus longer than protarsomere V, and shape of the median lobe of males (see key).

The other major area of sympatry, notably in Michigan, is more problematic. Most specimens from Michigan and Wisconsin are easily assigned to one or other of the names on the basis of the characters listed above. However, a few females that I have assigned to *D. fasciventris* [Michigan, Cheboygan Co., Douglas Lake, 16.vii.1978 (JBWM)] have protarsal claws longer than protarsomere V, expanded infuscation on metasternal wings, and extensive areas of red colour on abdominal sterna. Other Michigan specimens show similar traits, especially with respect to length of female claws and sternal colour. Most of these specimens are from localities north of the known range of *D. carolinus*, but still within the potential dispersal range of this species. In Michigan, then, specimens from a few localities have character states indicative of limited introgression among *D. fasciventris* and *D. carolinus*.

A similar but less complex situation is indicated among specimens of *D. fasciventris* and *D. hatchi*. Pronota of eastern specimens of *D. fasciventris* lack or have very narrow anterior and posterior yellow margins. Specimens from Alberta and British Columbia have much wider anterior and posterior yellow margins. In some examples, the anterior yellow margin is 0.2 of pronotal length (Wallis 1950:51). Thus, western specimens of *D. fasciventris* are more similar to *D. hatchi* in this character, although other characters are consistently different among these two taxa. Therefore, there is a possibility that introgression is occurring or has occurred among western populations of *D. fasciventris* and *D. hatchi.*

Natural history.— James (1961, 1970) and Larson (1975) provide natural history notes about this species in Ontario and Alberta, Canada, respectively. Adults probably reproduce quite early in the spring and are avid predators of early spring mosquitoes. James (1970) discusses parasitoids of pupae of *D. fasciventris.*

Flight records are roughly divisible into a vernal dispersal flight from April to late June, and a post-emergence flight from July to November (Table 5). All available records for teneral specimens are for the month of July (Table 4 and Larson 1975:400).

Distribution. (Fig. 32).— Transcontinental in North America, from the Maritime Provinces to Vancouver Island in Canada, this species extends southward to extreme southern Indiana, USA. The northern-most record is for Dawson City in Canada's Yukon Territory.

Chorological relationships.— Throughout its entire range, *D. fasciventris* is sympatric (at least narrowly so) with every other Nearctic species of *Dytiscus* except *D. habilis.*

Phylogenetic relationships.—*Dytiscus fasciventris* forms, in conjunction with *D. carolinus* and *D. hatchi*, a closely related assemblage of relatively recent origin (Fig. 52), judging by the relatively small amount of structural divergence of adults, evidence of possible introgression, and geographical replacement of these taxa with only narrow zones of sympatry.

Material examined.— A total of 1,257 specimens was examined of which 610 are males, 645 females, and sex was not determined for 2 specimens.

Dytiscus hatchi Wallis, 1950
Figs. 2E, 9B, 16B, 21J, 23C, 33, and 52

Dytiscus hatchi Wallis 1950:50 (Type locality - as below. Holotype male in CNIC, labelled as follows: Pond N. of Bethel, Washington, Apr. 21, 1940; holotype male *Dytiscus hatchi* Wallis; holotype *Dytiscus hatchi* Wallis No. 5880). -Hatch 1953:237. -Leech and Chandler 1956:323. -Larson 1975:400.

Derivation of specific epithet.— Wallis named this taxon in honour of Melville Hatch, the noted coleopterist.

Diagnostic combination.— Character states presented in the key and distribution, supplemented by characters mentioned in taxonomic notes under treatment of *D. fasciventris* allow accurate determination of adult specimens of *D. hatchi.*

Description.— Measurements for largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of the body is shown in Fig. 2E; coloration of pterothoracic sterna and abdominal terga in Fig. 9B; median lobe of male in Fig. 16B; and metacoxal processes in Fig. 21J; and mesotarsal structures in Fig. 23C.

Taxonomic notes.— See equivalent section in treatment of *D. fasciventris.*

Variation.— Important aspects of variation are discussed in section about variation in the treatment of *D. fasciventris.*

Natural history.— Nothing substantial is published, nor can much be inferred from label information about the natural history of this taxon. Teneral specimens are known from the month of August (Table 4). Two flight records are available for the month of July (Table 5). Because of the phylogenetic affinities of this taxon to *D. fasciventris*, it probably represents the ecological replacement of *D. fasciventris* in western North America.

Distribution (Fig. 33).— The range of this species extends from British Columbia, Canada, south to California, USA. All records are from localities west of the Rocky Mountains.

Chorological relationships.— *Dytiscus hatchi* is broadly sympatric only with *D. marginicollis*. It is narrowly sympatric with its closest relative, *D. fasciventris*, in southern British Columbia, Canada.

Phylogenetic relationships.— See notes under equivalent section in treatment of *D. fasciventris* and (Fig. 52).

Material examined.— A total of 222 specimens was examined of which 107 are males, 112 females, and sex was not determined for 3 specimens.

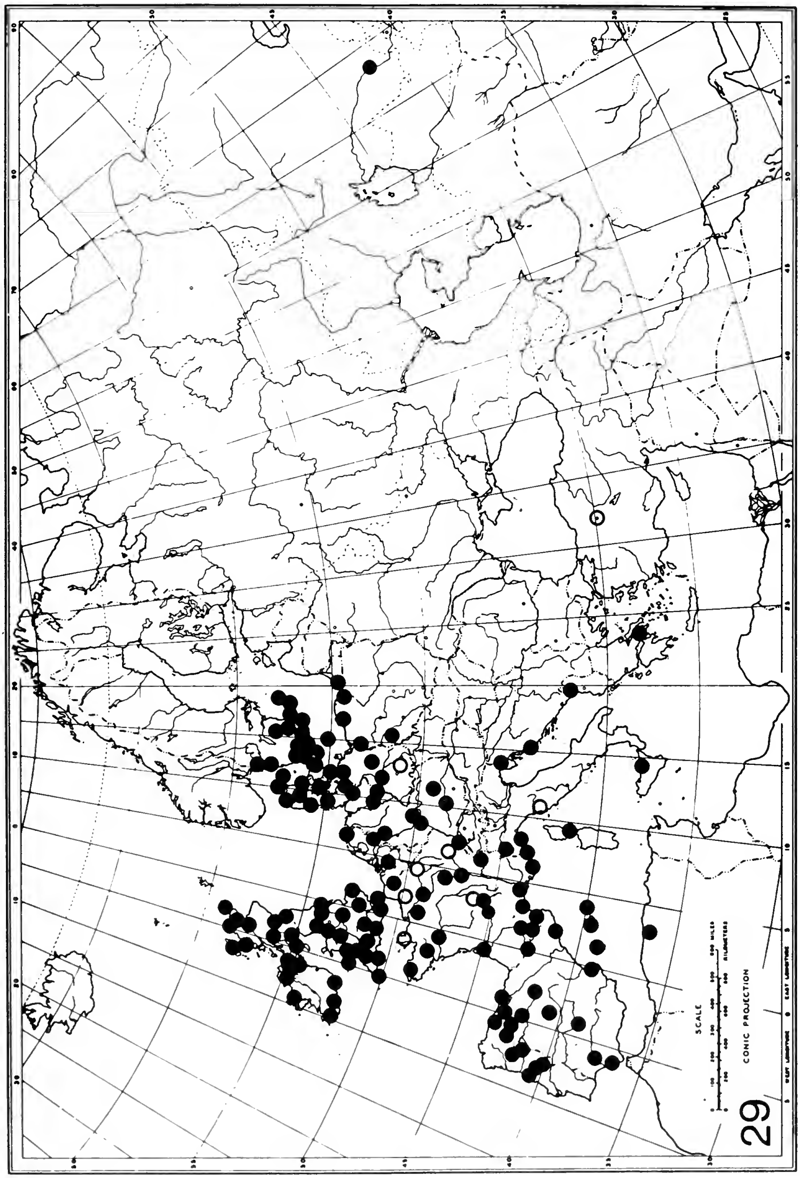


Fig. 29. Known distribution of *Dytiscus semisulcatus* Müller.

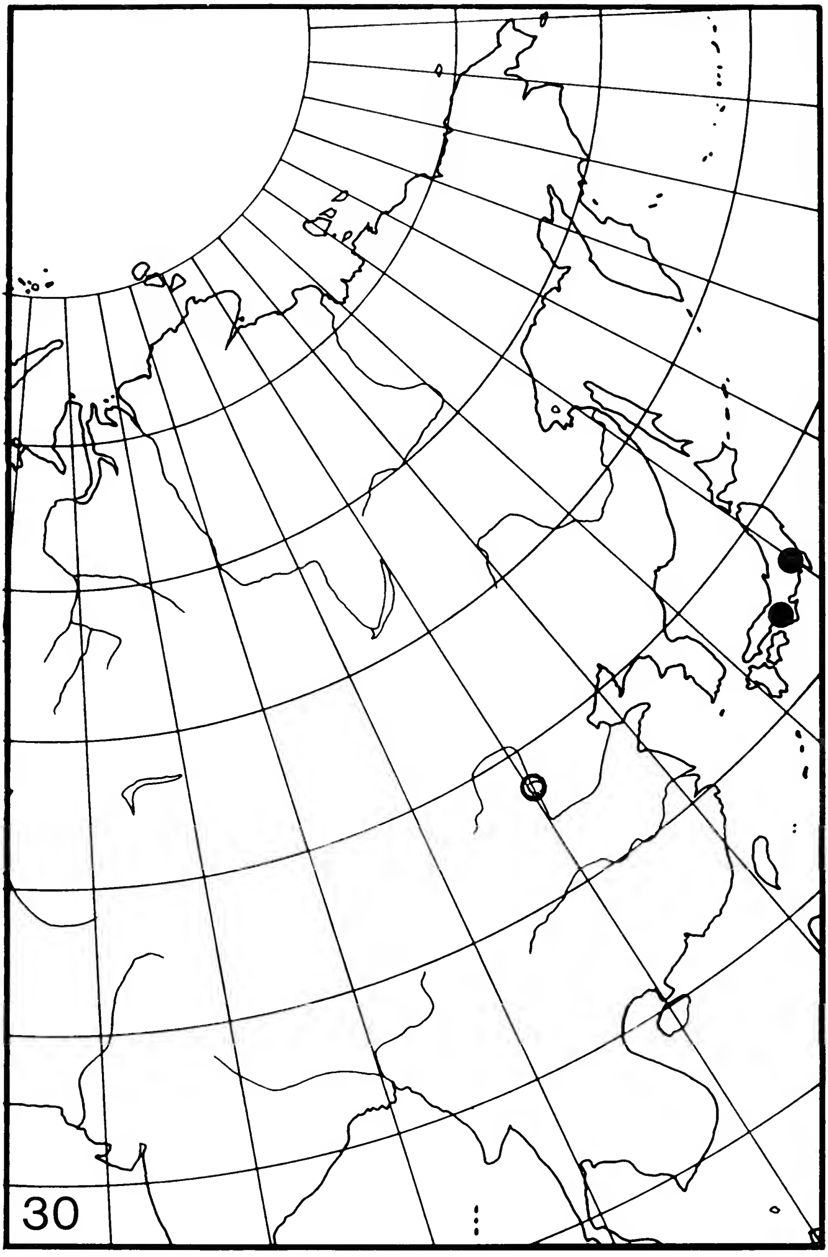


Fig. 30. Known distribution of *Dytiscus sharpi* Wehncke

Fig. 31. Known distribution of *Dytiscus carolinus* Aubé.

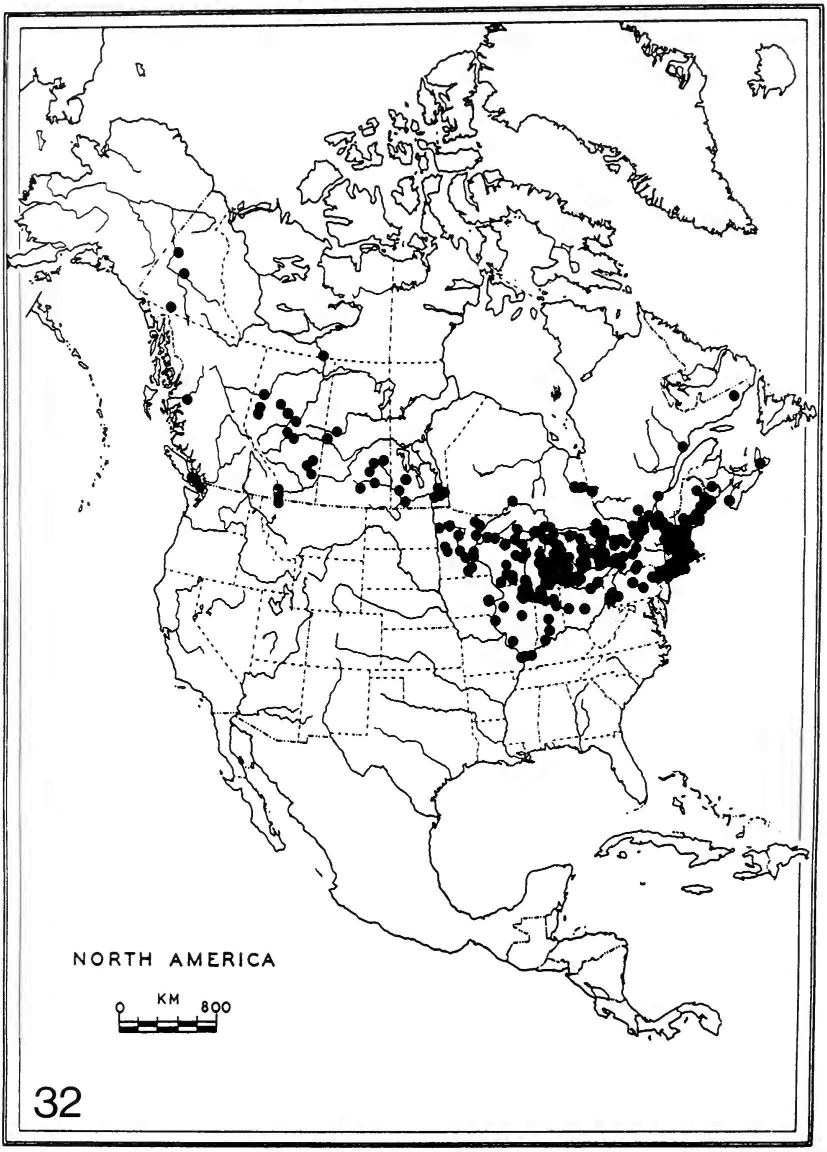


Fig. 32. Known distribution of *Dytiscus fasciventris* Say.

Fig. 33. Known distribution of *Dytiscus hatchi* Wallis.

Dytiscus cordieri Aubé, 1838
Figs. 3A, 9C, 16C, 21K, 23B, 34, and 52

Dytiscus cordieri Aubé 1838:108 (Type locality - "Boston...", Mass., USA. Type not seen). -Zimmermann 1920:246. -Wallis, 1950:51. -Hatch 1953:238. -Gordon and Post 1965:25. -Wallis and Larson 1973:110. -Larson 1975:400.

Dytiscus sublimbatus LeConte 1857:34 (Type locality - "Prairie Paso", Oregon Territory. Holotype female in LeConte collection, MCZC, labelled as follows: "Or.; D. sublimbatus Lec; Horn Coll H. 1485"). -Zimmerman 1920:246. -Hatch 1929:226. -Wallis and Larson 1973:110.

Dytiscus marginalis; *auctorum, nec* Linnaeus 1758. **Misidentification.** Sharp 1882:641 (*ex parte*). -Ganglbauer 1892:515 (*ex parte*). -Wickham 1895:151 (*ex parte*). -Roberts 1905:106 (*ex parte*). -Csiki 1908:508 (*ex parte*). -Reitter 1908:233 (*ex parte*). -Reitter 1909:46 (*ex parte*). -Gozis 1910:12 (*ex parte*). -Blunck 1913:47 (*ex parte*). -Schaufuss 1916:138 (*ex parte*). -Zimmermann 1920:250 (*ex parte*). -Guignot 1932:718 (*ex parte*). -Houlbert 1934:133 (*ex parte*). -Zimmermann and Gschwendtner 1938:47 (*ex parte*). -Guignot, 1947a:243 (*ex parte*). -F. Balfour-Browne 1950:270 (*ex parte*). -Zaitsev 1953:327 (*ex parte*). -Galewski 1971a:100 (*ex parte*). -Franciscolo 1979:665 (*ex parte*).

Derivation of specific epithet.— The meaning of this name is not mentioned specifically by Aubé (1838) but possibly it was derived to honour the French geologist, Pierre L.A. Cordier.

Notes about type material. - I have not seen the type(s) of *D. cordieri*. Severin (1892) records a syntype in the Royal Museum in Brussels, Belgium. Aubé's type locality, Boston, Massachusetts, USA, is based on a single male specimen provided by Chevrolat.

Sharp (1882:773) states that he had seen the holotype, but that it was a very mutilated specimen of *D. fasciventris*. Sharp wrote, "Aubé's description does not agree well with this individual, or with any other species, and I think it must have been made from this individual and supplemented or corrected from another species...". This is in contrast to the statement by Aubé (1838:108) that "...Je n'ai vu de ce Dytique qu'un seul individu...". Sharp (1882:638) used the LeConte name, *D. sublimbatus*, presumably because of this confusion over the type. After the holotype and more specimens from Aubé's original series are studied, his concept will be better understood, and nomenclatural changes may be necessary.

LeConte's *D. sublimbatus* was described from a specimen from Prairie Paso, "Oregon Territory". However, I have been unable to find this locality. The type of this name is a nonsulcate female.

Diagnostic combination.— Distinct in North America as the only species of which adults possess obtuse apices of metacoxal lobes and a yellow venter (Figs. 21K and 9C). The only other Nearctic species with venter of adults yellow are *D. circumcinctus* and *D. alaskanus* (some specimens); members of both species have acuminate metacoxal lobes.

Description.— Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 3A; coloration of pterothoracic and abdominal sterna in Fig. 9C; median lobe of male in Fig. 16C; metacoxal processes in Fig. 21K; and frontal view of head in Fig. 23B.

Taxonomic notes.— I believe most records of *D. marginalis* in North America are based on specimens of *D. cordieri*, or on mislabelled specimens. Adult *D. cordieri* are most easily distinguished from *D. marginalis* by an elongate chevron (Fig. 23B) on the frons extended to the antennal bases. In addition, adult male specimens of these two taxa are easily separated by pronotal structure (not explanate in *D. cordieri*, explanate in *D. marginalis*), and shape of apex of median lobe (rounded in *D. cordieri*, Fig. 16C, with distinct apical knob in *D. marginalis*, Fig. 17C). Adult females are more similar because those of *D. cordieri* are shallowly or indistinctly explanate laterally, while those of *D. marginalis* are more distinctly explanate. Female adults are best separated by association with males and distribution. Further discussion of the confusion between *D. cordieri* and *D. marginalis* is provided within the treatment of the latter.

Variation.— There is a geographic basis to the occurrence of sulcate females. Most eastern specimens are sulcate and most western specimens are nonsulcate. For example 59 of 67 adult females from Ontario were sulcate, while of 142 specimens examined by Larson (1975) and me from Alberta, British Columbia, Manitoba and Saskatchewan, 11 are sulcate.

Almost all adult specimens of *D. cordieri* have the distinctively elongate chevron of the frons. In a few specimens, however, this is difficult to see because of *post-mortem* discoloration. Once these specimens are sufficiently cleaned, it is quite distinctive.

Pterothoracic sternal coloration is predominantly yellowish. The darkest specimen seen, which is quite outside the normal range of variation, is illustrated in Fig. 9C. Infuscation is restricted to the central area of the metasternum and sutures of the sterna in most specimens.

Natural history.— Larval development is completed probably between mid-July and mid-August, because teneral adults have been collected in late July and throughout August (Table 4). I have no information about overwintering sites of adults, except one specimen from Aweme, Manitoba, 26.iv.30 (1 CNIC) was "taken under logs out of water". This record could represent an overwintering site, but could indicate just as easily an example of a poor choice for a landing during dispersal. Label data indicative of dispersal are presented in Table 5. Records predominate for April in the spring and post-emergence flight takes place from July to October.

Larson (1975:401) noted that adults of *D. cordieri* occur in a wide variety of types of water body, and furthermore, that most records of *D. cordieri* are represented by individuals, with the longest series he had seen from Alberta being three specimens. Larson suggested that this was because either of low population densities or of insufficient knowledge of microhabitat of adults.

Using data from museum specimens, I tallied the number of adult specimens collected on a single day by a single collector, hereafter referred to as a sample. Of 335 samples from almost the entire range of the species, the average was 1.6 specimens. A similar tally for adult *D. alaskanus* yielded 202 samples averaging 3.4 specimens. The latter perhaps is more typical of *Dytiscus* adults. Less than 20 of these samples of adult *D. cordieri* were of more than five specimens, including bottle-trapped samples, and most of these are from April or from late August to early October, and were probably collected during or shortly after dispersal flight. By inference, I conclude that adults of *D. cordieri* occur at a lower population density than do those of other species.

Distribution (Fig. 34).— This species is transcontinental in North America, ranging from Alaska and the Northwest Territories, south to central California and northern Colorado, with the most southern record being from Gastonia, North Carolina.

Chorological relationships.— In some part of its range, *D. cordieri* is sympatric with every other Nearctic species of *Dytiscus* except the Méxican *D. habilis*.

Phylogenetic relationships.— In my phylogenetic interpretation of *Dytiscus* (Fig. 52), I have placed this species in the *D. dimidiatus*-group on the basis of presence of rounded metacoxal processes, rounded apex of the median lobe, and absence of a distinct knob at the apex of the median lobe. Specimens of *D. cordieri* are phenetically quite distinct from other members of the *D. dimidiatus*-group and represent the only Nearctic members of the group.

Material examined.— A total of 691 adult specimens was examined of which 362 were males, 328 were females, and for one specimen sex was not determined.

Dytiscus mutinensis Pederzani, 1971
Figs. 3B, 9D, 16D, 21L, 23G, 35, and 52

Dytiscus dimidiatus ab. *mutinensis* Fiori 1881:276 (Information about types below). -Zimmermann 1920:248. -Müller 1926:298. -Guignot 1932:715 (*ex parte*). -Zimmermann and Gschwendtner 1938:40. -F. Balfour-Browne 1950:285. - Zaitsev 1953:325. -Schaeflein 1971:87. -Franciscolo 1979:663.

Dytiscus pisanus var. *mutinensis*; -Guignot 1931a:7 (**Misidentification** of *D. dimidiatus*), *quod vide*. -Richoux and Dufay 1986: 421.

Dytiscus mutinensis Pederzani 1971:220 (Information about types below). Schaeflein 1973:74.

Derivation of specific epithet.— From "Mutina", the Latin name of Modena, Italy, which is Fiori's type locality.

Notes about type material. — Fiori's type is discussed by Pederzani (1971). Pederzani, when elevating this taxon to specific rank, retained the same epithet, presumably to provide continuity in use of this name. For his new, species-level taxon, Pederzani designated a new type specimen from Italy for which he gives the following information: "Holotypus [male symbol]; Ravenna, pineta di S. Vitale, 20.ix.1970, leg. Pederzani." It is deposited in the Museo Civico di Storia Naturale de Milano, Italy (Pederzani, 1971:222).

Diagnostic combination.— Adults of this species are best separated by characters presented in the key. Supplemental character states distinguishing it from *D. dimidiatus* and *D. pisanus* are provided by Pederzani (1971).

Description.— Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 3B; coloration of pterothoracic and abdominal sterna in Fig. 9D; median lobe of male in fig. 16D; metacoxal processes in Fig. 21L; and sturcture of protarsi in Fig. 23G.

Taxonomic notes.— This taxon has been confused with members of *D. dimidiatus* because adults are quite similar in external features. Pederzani (1971) was the first to distinguish this taxon as being of specific rank. As such, a new holotype was needed, and a specimen was so designated by that author.

Part of the taxonomic confusion arose because non-sulcate females of *D. dimidiatus* were assigned to *D. dimidiatus* ab. *mutinensis*. Guignot's (1931a, 1932) record of this aberration from France, Department of Bouches-du-Rhône, St. Rémy (1 MNHN) is such a non-sulcate female. Both *D. dimidiatus* and *D. mutinensis* have sulcate and non-sulcate states of elytra of females.

Franciscolo (1979:663-664) expresses reservations about the species-level separation of *D. mutinensis* and *D. dimidiatus*. As he infers, the longer metatarsomere V of male *D. dimidiatus* would be expected to have more punctures (approximately 60) than that of the shorter one of *D. mutinensis* (approximately 30), and this is one of the major differences used by Pederzani (1971) and me. Franciscolo notes that other differences between these putative species are very subtle.

In the south of France, females of *D. dimidiatus* have both sulcate and non-sulcate females. Furthermore, specimens from southern France and particularly those from the Camargue region are somewhat shorter, narrower and less robust. I interpret this variation as only a populational difference but such specimens are more similar to those of *D. mutinensis*. Some females from this region are non-sulcate; however, Leblanc (1982) has described sulcate females of this population as *D. mutinensis* var. *striatus*. Through the courtesy of P. Leblanc (Troyes, France) and F. Bameul (Bordeaux, France) I have studied three paratypes of this variety and I assign them to *D. dimidiatus*. I have not seen a specimen of my concept of *D. mutinensis* from France.

Richoux and Dufay (1986) conducted a detailed study of variation among specimens of *D. mutinensis* and *D. dimidiatus* from the south of France, Greece and Italy. They concluded that *D. mutinensis* is a variety of *D. dimidiatus* because population samples from the south of France and Greece exhibit intermediate character states.

I have maintained the separation of these taxa as species for the following reasons: 1, consistent, if slight, differences in shape of median lobe of males; 2, information provided by Franciscolo (1979) that specimens assignable to both taxa were taken in the same ponds; and 3, lack of intermediate specimens among the limited sample I have seen. Obviously, it will require further study of specimens from an array of localities as well as carefully constructed hypotheses to establish confidently the status of these names.

Variation.— I saw slight variation in external features of adults in 12 specimens of *D. mutinensis*. Of the five males examined in detail, number of punctures on the anterior surface of protarsomere V ranged between 24 and 34.

Presence or absence of the anterior yellow band of the pronotum varies, but when present, this band is quite narrow, in most less than 10% of width of lateral bands. Two of the four females from Corfu have slightly impressed grooves.

Natural history.— Pederzani (1971) notes a preference of adult specimens of *D. mutinensis* for lentic habitats with much vegetation and detritus. Adults occur in both open and shaded habitats, but locally. Angelini (1978) provides more detailed notes about habitats where specimens of *D. mutinensis* were collected, and adds occurrence in slowly moving water.

Distribution (Fig. 35).— This species occurs throughout Italy and around the Adriatic Sea. Guignot's record from France is discussed above. I suspect that the records from southern France provided by Thérond (1975:106) will also prove to be non-sulcate females of *D. dimidiatus*. Therefore, the records from France do not appear on Fig. 35.

Chorological relationships.— Even though it occupies a small range, *D. mutinensis* is sympatric with all other European species except *Dytiscus lapponicus*.

Phylogenetic relationships.— I have interpreted *D. mutinensis* as the sister species of *D. dimidiatus* (Fig. 52), both of which are allied to *D. cordieri* and *D. pisanus* .

Material examined.— A total of 13 adult specimens was examined, of which 8 were males, and 5 were females.

Dytiscus dimidiatus Bergsträsser, 1778
Figs. 3C, 10A, 17A, 21M, 23H, 36, and 52

Dytiscus dimidiatus Bergsträsser 1778:33 (Type locality -Hanau area of Hessen, West Germany. Type not seen). -Zimmermann 1920:247. -Guignot 1932:712. -Houlbert 1934:132.

Zimmermann and Gschwendtner 1938:40. -Guignot 1947a:242. -F. Balfour-Browne 1950:285. -F. Balfour-Browne 1953:27. -Zaitsev 1953:325. -Galewski 1971a:100. -Schaeflein 1971:87. -Pederzani 1971:222. -Franciscolo 1979:663. -Régil and Salgado 1984:134,135.

Dytiscus dimidiatus ab. *mutinensis*; Guignot 1932:715. -Guignot 1947a:242.

Dytiscus pisanus ab. *mutinensis*; Guignot 1931a:7.

Dytiscus mutinensis; Thérond 1975: 106.

Dytiscus mutinensis var. *striatus* Leblanc 1982:239. (Type locality -"Étang du Charnier, près de Gallician, commune de Vauvert (Gard)", France. Type repository -MNHN). **NEW SYNONYMY.**

Derivation of specific epithet.— Latin for 'halved', presumably in reference to length of elytral sulci of adult females (Fig. 3C). - Adults of this species are best separated by characters presented in the key.

Description.— Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 3C; coloration of pterothoracic and abdominal sterna in Fig. 10A; median lobe of male in fig. 17A; metacoxal processes in Fig. 21M; and protarsi in Fig. 23H.

Taxonomic notes.— For a discussion of the confusion of species among *D. mutinensis* and *D. dimidiatus* by previous taxonomists, see the equivalent section in the treatment of the former species.

Variation.— Slight variation in external features of adults was noted and consisted mostly of presence, absence and width of anterior and posterior yellow bands of the pronotum. The anterior yellow band was consistently less than 30% of the width of the lateral bands of the pronotum.

Most females have sulcate elytra. For a discussion of records of non-sulcate females, see taxonomic notes under *D. mutinensis.*

Natural history.— F. Balfour-Browne (1950) stated that adults of this species are typically found in fens with occasional records from more temporary or disturbed habitats. He also gives a flight record for May and a record of a teneral specimen for September.

Brancucci (1979) reported a maximum density of adults in marshes during the month of June near Cudrefin, Switzerland. Borchert (1938:17) characterizes this species in Europe as a resident of lowland habitats where occasional specimens are found over a wide variety of habitats. Pederzani (1971) implies that specimens live in both open, disturbed habitats as well as more mature ponds. Neither this species nor *D. mutinensis* are found as adults in lotic habitats in anything but very slowly running water. Korschelt (1923, 1924) gives further details about natural history of this species.

Distribution (Fig. 36).— This species occurs throughout Europe. In Scandinavia, I have no records north of about 62°N. The easternmost record is at about 41°E. I have seen specimens labelled simply "Africa" (CASC) but have not been able to find any precise locality records for Africa. Leblanc (1982) mentions that it is found in Saudi Arabia but I have not seen specimens from there.

Chorological relationships.—*Dytiscus dimidiatus* is sympatric with every other species of *Dytiscus* occurring in Europe.

Phylogenetic relationships.— See equivalent section under treatment of *D. mutinensis* (Fig. 52).

Material examined.— A total of 305 adults was examined, of which 156 are males and 149 are females.

Dytiscus pisanus LaPorte Compte de Castelnau, 1835
Figs. 3D, 10B, 17B, 21N, 23I, 37, and 52

Dytiscus pisanus LaPorte Compte de Castelnau 1835:98 (Type locality - "Pise", Italy. Lectotype, here selected - male in BMNH labelled: LECTOTYPE; SYNTYPE; Sharp coll., 1905-313; *Dytiscus pisanus* Lap., Italia [male symbol]; LECTOTYPE, *Dytiscus pisanus* LaPorte de Castelnau 1835, selected R.E. Roughley.). -Zimmermann 1920:253. -Guignot 1932:719. -Houlbert 1934:134. -Zimmermann and Gschwendtner 1938:44. -Guignot 1947a:244. -Guignot 1961:859. -Pederzani 1971:224. -Franciscolo 1979:666. -Régil and Salgado 1984:134,135.

Dytiscus ibericus Rosenhauer 1856:47 (Type locality - Algeciras, Spain. Type not seen.). -Zimmermann 1920:253.

Dytiscus pisanus var. *ibericus*; -Guignot 1931a:7. -Guignot 1932:719. -Zimmermann and Gschwendtner 1938:44. -Guignot 1947a:244. -Guignot 1961:859. -Franciscolo 1979:667.

Dytiscus pisanus var. *nonsulcatus* Zimmermann 1919:233 (Type locality - not given. Holotype in Zimmermann collection, ZSBS, labelled as follows:♀; Tanger, Rolph; Type; Holotypus, Dytiscus pisanus ♀ var. nonsulcatus Zim., Staatssamml. München.). -Zimmermann 1920:253. -Pederzani 1971:219.

Derivation of specific epithet.—"*pisanus* " is the adjectival form of the name of the type locality, Pisa, Italy.

Diagnostic combination.— European distribution, pronotum broadly margined with yellow on all sides, combined with rounded lobe of metacoxal process and detailed features presented in the key allow accurate determination of adult specimens. Also, the form of the median lobe of male adults is quite distinctive (Fig. 17B).

Description.— Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 3D; coloration of pterothoracic and abdominal sterna in Fig. 10B; median lobe of male in Fig. 17B; metacoxal processes in Fig. 21N; and mesotarsi of females in Fig. 23I.

Taxonomic notes.— Guignot (1932) states that certain (unnamed) authors proposed to make *D. pisanus* a variety of *D. marginalis*. He provides several minor distinctions among adults of these species, and a major difference in form of the median lobe. These distinctions, in conjunction with those presented in the key, demonstrate that two species are represented, especially when supplemented with the information that *D. pisanus* is widely sympatric with *D. marginalis*.

Zimmermann (1919) erected *D. pisanus* var. *nonsulcatus* for female forms with smooth elytra. Many authors have used the name *ibericus* for this form, but Pederzani (1971) examined five specimens from MNHN determined as *Dytiscus ibericus* and states that they were sulcate.

Variation.— I have seen too few specimens of this taxon to assess patterns of variation. More than half of the specimens seen have the pterothoracic sterna piceous ventrally as in Fig. 10B. Associated with this coloration in most specimens is a darkening of abdominal sterna. Conversely, those specimens with lighter pterothoracic sterna tend to be closer to uniformly yellow in ventral coloration.

Guignot (1932:720) states that the non-sulcate form is quite rare. To his list of localities for non-sulcate females, I add only Godelleta, Spain (1 MCZC). Thus, the non-sulcate form is restricted to the southern and western parts of the range (southern France, Spain, Morocco and Algeria).

Natural history.— Guignot (1932) states that adults of *D. pisanus* live in calm, clear water. However, Pederzani (1971) notes a preference for running water or for pools in stream beds.

The larva of *D. pisanus* was described and compared to those of *D. circumflexus* and *D. semisulcatus* by Bertrand (1928). This species may complete larval development early in the year as Bertrand (1928: 17) records (presumably) mature larvae from April in Montpellier (Dept. Hérault, France).

Distribution (Fig. 37).— This species has a Mediterranean distribution, but does not occur as far north as 50°. The easternmost record is for the island of Crete, and the southernmost records are from Algeria and Morocco.

Chorological relationships.— Apparently sympatric with every other European species of *Dytiscus*. If its preference for running water is correct though, it may well occupy a distinctly different microhabitat from that of most co-occurring taxa.

Phylogenetic relationships.— The rounded apex of the median lobe indicates a close relationship to *D. mutinensis* and *D. dimidiatus*.

Material examined.— A total of 129 specimens was examined of which 50 were males and 79 females.

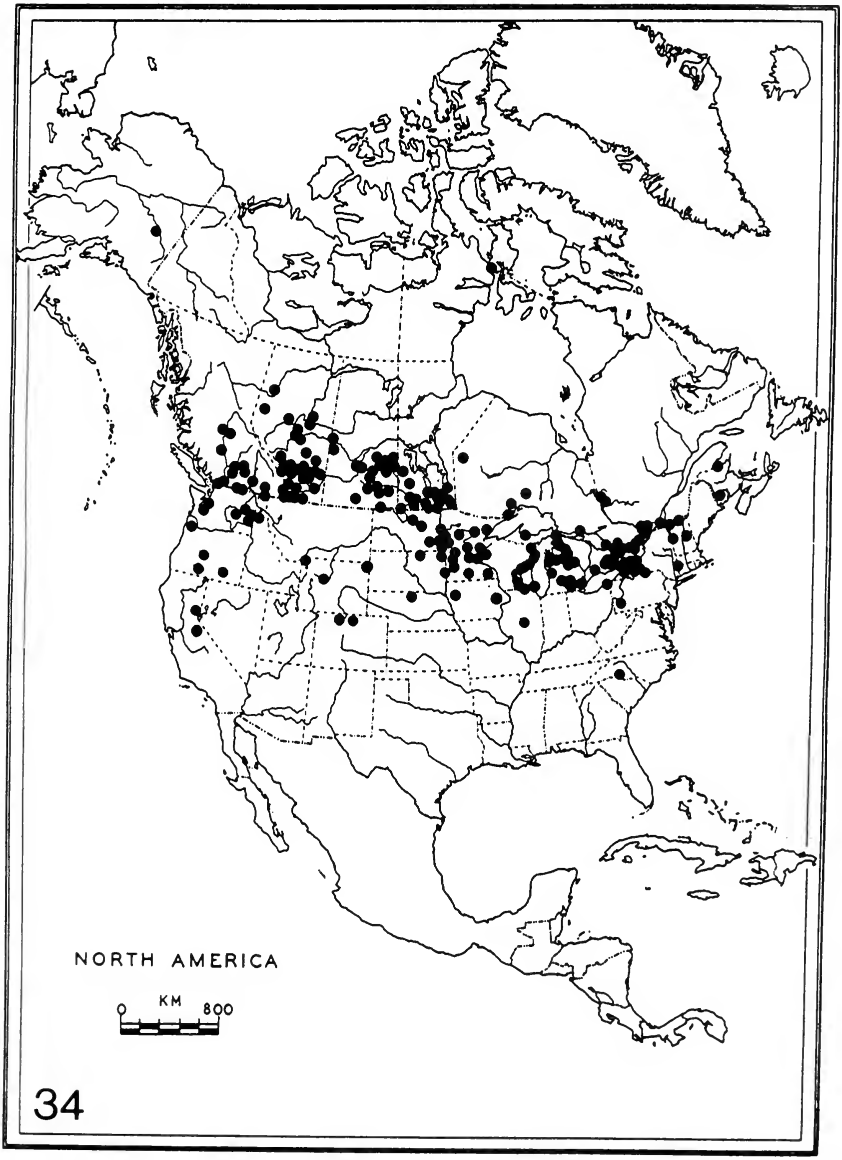


Fig. 34. Known distribution of *Dytiscus cordieri* Aubé.

35

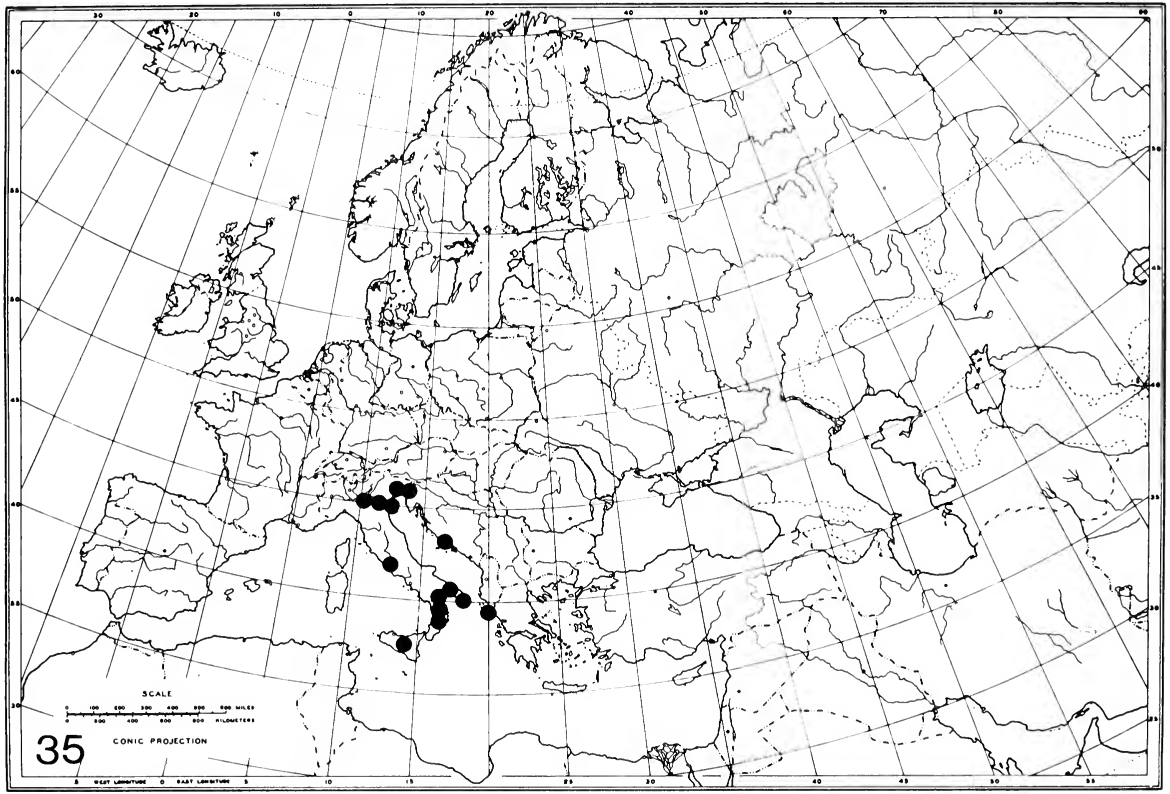


Fig. 35. Known distribution of *Dytiscus mutinensis* Pederzani.

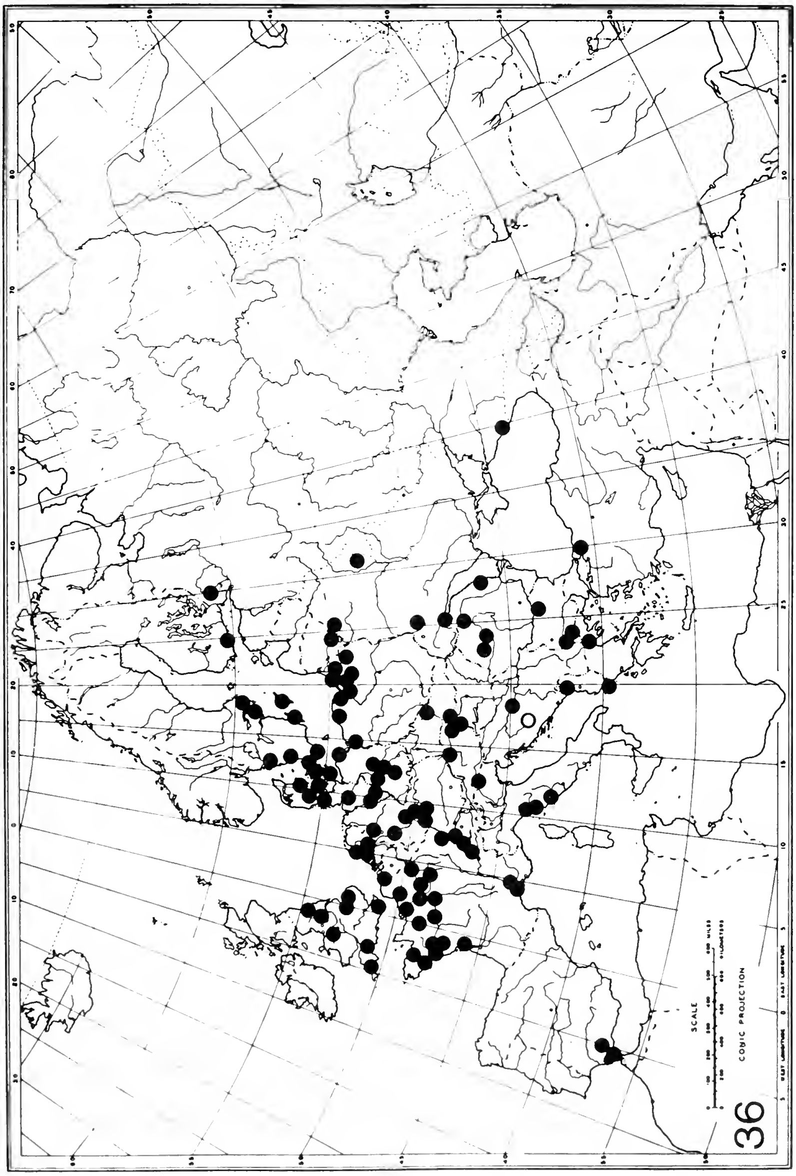
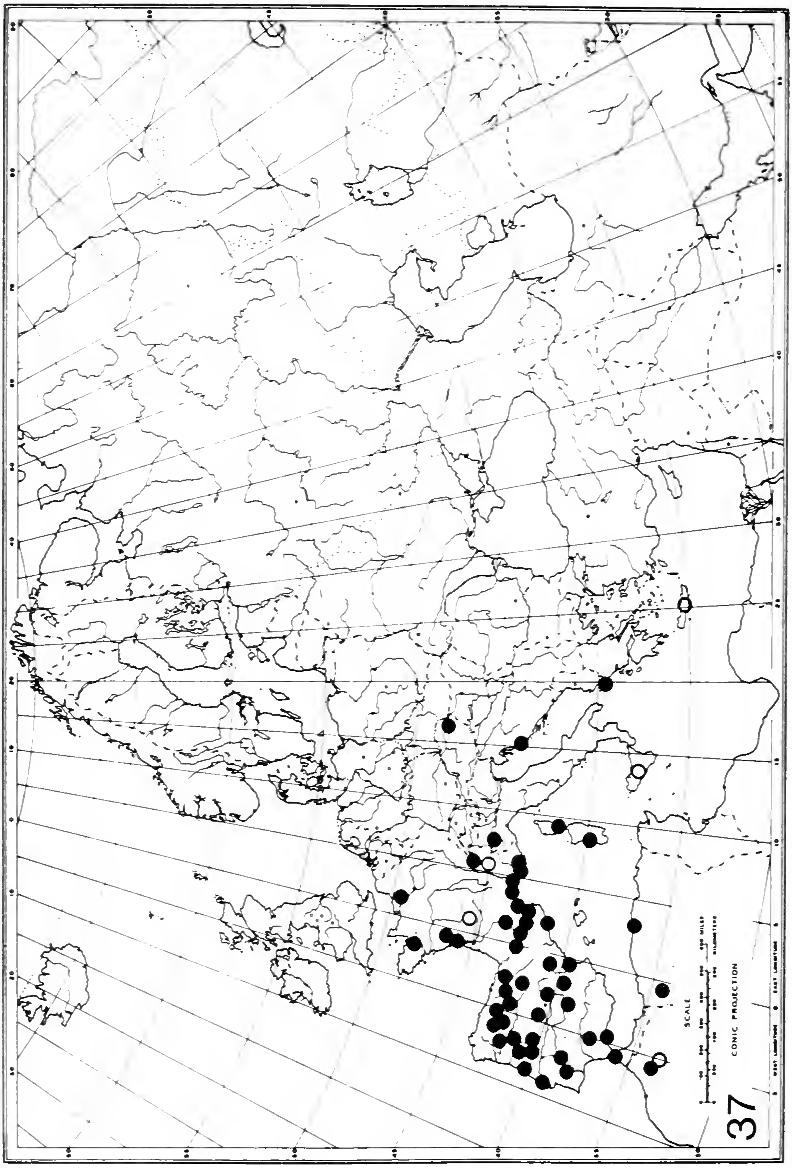


Fig. 36. Known distribution of *Dytiscus dimidiatus* Bergsträsser.



37

Fig. 37. Known distribution of *Dytiscus pisanus* Castelnau.

Dytiscus marginalis Linnaeus, 1758
Figs. 3E, 10C, 17C–D, 22A–B, 38, and 52

Dytiscus marginalis Linnaeus 1758:411.

Derivation of specific epithet.— With reference to all sides of the pronotum, or alternatively, lateral edges of elytra being margined with yellow.

Diagnostic combination.— The combination of Palearctic distribution, acute but not acuminate metacoxal lobes, pronotum with yellow margin on all sides, and form of median lobe of males distinguish males of this taxon.

Taxonomic notes.—Some notes about confusion among *D. marginalis* and *D. cordieri* are presented under the treatment of the latter. Sharp (1882:641) was the first to ascribe *D. marginalis* to the Nearctic fauna based on a female specimen labelled "am. bor. int., montagnes rocheuses", and another individual "...said to be from North America, in Murray's collection." The latter record refers to a specimen of *D. cordieri.* The former specimen, provided by Castelnau, is deposited in BMNH and is a sulcate female of *D. marginalis*. I believe this specimen to be mislabelled. Similarly, I have seen the following specimens of *D. marginalis* which presumably have incorrect locality information: America (1 HNHM), "Ind." (1 CNIC), Canada? (1 MCZC), Detroit, Mich. (3 ICCM), Grand Portage, Labr. 2.vi.17 (1 ICCM), Montreal, Quebec (1 ICCM), Allegheny Co., Pa., vi.25 (1 ICCM), Quebec (1 ICCM), Ridgeway, Ont. (1 ICCM), and Toronto, Ont., vi.14 (1 ICCM).

As Brinck (1946:146) pointed out, there is little difference in form of the median lobe among eastern and western Palearctic specimens of *D. marginalis*. However, there are major differences in ventral coloration, and these colour forms are geographically vicariant. Thus, I have decided to treat *D. marginalis* as two subspecies: 1, the nominate, western Palearctic form, characterized by predominantly yellow pterothoracic sterna; and 2, an eastern Palearctic form for which the name *D. czerskii* is available and in which adults have the pterothoracic sterna appreciably marked with black or piceous. The two forms are allopatric and could represent taxa of specific level. However, differences in form of the median lobe are too slight to support such a conclusion, without additional supporting evidence. I have not seen intermediates in type of ventral coloration.

Distribution.— This ubiquitous Palearctic species, when the combined ranges of both subspecies are considered, includes most of the Palearctic region.

Chorological relationships.— The aggregate range of both subspecies of this species suggest that it is sympatric with every other Palearctic species of *Dytiscus* except possibly *D. sinensis*.

Phylogenetic relationships.— Presence of character states such as acute metacoxal lobes, margined pronotum, as well as those found in form of the median lobe of males, indicate that it is closest to *D. persicus* and *D. delictus* (Fig. 52).

Dytiscus marginalis marginalis Linnaeus, 1758, NEW STATUS

Dytiscus marginalis Linnaeus 1758:411 (Type area - "Europae". Type not seen.). -Zimmermann 1920:249. -Müller 1926:298. Guignot 1932:715. -Houlbert 1934:133. -Zimmermann and Gschwendtner 1938:47. -Guignot 1947a:243. - F. Balfour-Browne 1950:270. -F. Balfour-Browne 1953:27. -Zaitsev 1953:327. -Galewski 1971a:100. -Schaeflein 1971:88. -Franciscolo 1979:665. -Régil and Salgado 1984:134,135.

D. marginalis, auctorum. Nearctic records are *D. cordieri, quod vide*. **Misidentification**.

Dytiscus semistriatus Linnaeus 1758:412 (Type area - "Europae". Type not seen.). - Zimmermann 1920:250.

Dytiscus totomarginalis DeGeer 1774:391 (Type locality not stated. Type Material - see Notes, below). -Zimmermann 1920:250.

Dytiscus conformis Kunze 1818:58 (Type locality - "Leipzig". Type not seen.). -Zimmermann 1920:250.

Dytiscus marginalis var. *conformis* Kunze; -Zimmermann 1920:250. Müller 1926:298. -Guignot 1932:715. -Zimmermann and Gschwendtner 1938:47. -Guignot 1947a:243. - F. Balfour-Browne 1950:250. -Zaitsev 1953:327. -Schaeflein 1971:88. -Franciscolo 1979:665.

Dytiscus submarginalis Stephens 1828:90 (Type locality - "taken near London, England". Lectotype male, selected here, in BMNH, labelled as follows: "LECTOTYPE; SYNTYPE; LECTOTYPE, *Dytiscus submarginalis* Stephens, selected R.E. Roughley").

Dytiscus circumductus Serville 1830:90 (Type locality - near Paris, France. Type not seen.). Zimmermann 1920:251.

Dytiscus marginalis form *semicostata* Reineck 1921:117 (Type locality - "...in Kurland in der Misse-Niederung." Type not seen.). -Guignot 1932:715. -Zimmermann and Gschwendtner 1938:47. -Guignot 1947a:243. - F. Balfour-Browne 1950:240. -Zaitsev 1953:327.

Notes about type material.— A lectotype of *D. submarginalis* is designated above. Type material for most other junior synonyms was not seen. However, three specimens of *D. totomarginalis* were examined from the DeGeer collection, Riksmuseet, Stockholm. The header label for these specimens reads: "2. D. totomarginalis p. 391, D. marginal. L. ♂ - D. semistri. L. ♀". Two males and a female are in the series and each bears a square, orange label which is white on the lower surface. All specimens are missing parts of legs but otherwise are in good condition. No lectotype is designated.

Diagnostic combination.— The yellow pterothoracic sterna and western Palearctic distribution, in combination with the diagnostic combination of the species, are sufficient to identify adult members of *D. marginalis marginalis*.

Description.— Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 3E; coloration of pterothoracic and abdominal sterna in Fig. 10C; median lobe of male in Fig. 17C; and metacoxal processes in Fig. 22A.

Variation.— As noted above, form of the median lobe of adult males varies only slightly among subspecies, and variation within subspecies is even less. Other aspects of variation include pronotal width, coloration of pterothoracic sterna, and sulcate or non-sulcate elytra of females.

Males and females from higher elevations in the Pyrenees and Cantabrian Mountains have the pronota narrower than the base of the elytra. In lowland specimens, pronota are distinctly broader than elytral bases. The latter is true for lowland specimens from central Spain, and I have therefore not treated this form as subspecifically distinct. It is more likely that the change in pronotal form is due to dietary and thermal effects of cold, oligotrophic alpine lakes and ponds.

Sharp (1882) discussed a specimen, which I have seen, of *D. marginalis marginalis* with expanded dark fasciae on the abdominal sterna. This specimen is a male and the median lobe is protruding, but the apex is damaged. After detailed comparison of this specimen with specimens of other Palearctic species, I judge the specimen to belong to *D. persicus* , even though labelled as coming from Europe. Others (*e.g.*, Zaitsev 1953) have mentioned increased infuscation of the abdominal sterna. In all specimens that I have seen there is virtually no infuscation of the abdominal venter except for very narrow infuscation along abdominal sutures ventrally (Fig. 10C). Thus, adults of this subspecies are best separated from members of *D. marginalis czerskii* on the basis of lack of appreciable pterothoracic infuscation and distribution. See also notes under variation of *D. marginalis czerskii.*

Females of *D. marginalis marginalis* with non-sulcate elytra appear sporadically throughout the entire range of this taxon. There may be geographic patterns to the frequency of occurrence of the two female forms. For instance, F. Balfour-Browne (1950) states that the non-sulcate form is quite rare in Britain, or at least has been since 1828. Guignot (1932) states that the non-sulcate form occurs throughout France but is more common in central and western France. The non-sulcate form occurs throughout Italy, but Franciscolo (1979) noted a trend for it to become slightly more common in the south. For central Europe, Schaeflein (1971) characterizes the grooved female as most common, but that at certain localities in the northern and northeastern regions, the smooth form is more numerous than the grooved form. Guignot (1933) mentions that the smooth form is more common in the southern USSR, while Zaitzev (1953) apparently extends this trend to all of the USSR.

Natural history.— The natural history of adult and larval stages of this subspecies has been intensively studied for many years in Europe. Many of the publications are cited by Zimmermann (1920:251), and are discussed and augmented in the treatment edited by Korschelt (1923, 1924).

Distribution (Fig. 38).— This subspecies is widespread in the western and central parts of the Palearctic region.

Material examined.— A total of 1382 adult specimens was examined, of which 619 were males, 762 were females, and sex of one specimen was not determined.

Dytiscus marginalis czerskii Zaitsev 1953, NEW STATUS

Dytiscus marginalis, auctorum; Sharp 1874;417. -Sharp 1882:641 (*ex parte*). -Brinck 1946:146. -J. Balfour-Browne 1946:453. -Guignot 1947a:244 (*ex parte*).

Dytiscus czerskii Zaitsev 1953:328. **NEW SYNONYMY**. (Type locality - not specified, but all localities listed are in Primorskij Kraj (Maritime Territory), USSR.).

Derivation of subspecific epithet.—Named in honour of A.I. Cherskii, who collected the type specimen.

Notes about type material. - I have not seen Zaitzev's type of this taxon, which, according to his preface, is deposited in the Zoological Institute of the Academy of Sciences of the USSR in Leningrad. I have, however, seen specimens authenticated by Zaitzev.

Diagnostic combination.— The infuscate pterothoracic sterna and eastern Palearctic distribution, in combination with the diagnostic combination of the species, are sufficient to identify adult members of *D. marginalis czerskii.*

Description.— Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is not shown; coloration of pterothoracic and abdominal sterna in Fig. 10D; median lobe of male in Fig. 17D; and metacoxal processes in Fig. 22B.

Taxonomic notes.— The slight character differences mentioned by Zaitsev (1953) among specimens of *D. marginalis* and *D. czerskii* are insufficient in themselves to warrant species-level status. This is true also of differences in form of the median lobe, and I have therefore used subspecific rank for these two forms.

Variation.— I have seen too few specimens of this taxon to assess patterns of variation. Zaitsev (1953) writes that the ventral colour of *D. czerskii* is similar to that of *D. marginalis*. All specimens of *D. marginalis czerskii* that I have seen have a much greater development of infuscation on the venter than is typical of more western populations of *D. marginalis*. All specimens have sternum VI broadly infuscate, and most specimens have a broad infuscate band on sternum II.

As noted under the section concerning variation in *D. marginalis marginalis*, Zaitsev implies that the non-sulcate form is the most common in the USSR. This is in marked contrast to the condition of female *D. marginalis czerskii*. Zaitsev (1953) states that all 16 females which he had seen were sulcate. I have seen an additional eight female specimens, all of which have sulcate elytra.

Natural history.— Nothing has been published about natural history of this subspecies.

Distribution (Fig. 38).— This subspecies is found in the Amur and Maritime regions of the USSR, and in Japan, and is to be expected in the northeastern regions of China. In addition, the records cited by Yoon and Ahn (1988) for North Korea may well refer to this subspecies.

Material examined.— A total of 20 adult specimens was examined, of which six are males and l4 are females.

Dytiscus persicus Wehncke, 1876
Figs. 11A, 18A, 22C, 39, and 52

Dytiscus persicus Wehncke 1876:52 (Type area - "Persien". Holotype female in Wehncke collection, MNHN, labelled as follows: "Persia, settente., 1862-63, Coll. G. Doria; type; Persia; HOLOTYPE, *Dytiscus persicus* Wehncke, examined R.E. Roughley"). -Zimmermann 1920:-235. -Zimmermann and Gschwendtner 1938:46. -Zaitsev 1953:327.

Dytiscus marginalis; Sharp 1882:641 (*ex parte*). **Misidentification.**

Derivation of specific epithet.— Named for "Persia", the type area.

Notes about type material. — Wehncke's description indicates that he had seen only one non-sulcate female of this species from the Dohrn collection. The holotype was placed beside a large label reading "*persicus* mihi" in Wehncke's handwriting. The BMNH contains two other non-sulcate female specimens labelled: "Co-type; Persia, settente., 1862-63, coll. G. Doria; Sharp coll., 1905-313 [label inverted]; Ispahan. Persia. J. Doria 1862-63, *persicus* ", the bottom label in David Sharp's handwriting. These BMNH specimens cannot be considered part of the type series of *D. persicus* because, based on Wehncke's original description, they were not seen by him, even though they are part of the same series of specimens. Sharp may have obtained the specimens from Doria. Sharp (1882) states that these specimens may be from Isfahan (=Esfahan), Iran, but does not mention the source of this information.

Diagnostic combination.— This is the only western Palearctic species other than *D. pisanus*, *D. circumcinctus* and *D. lapponicus* of which adults have transverse black fasciae on the abdominal venter. The latter two have longer metacoxal proccesses, while *D. persicus* and *D. pisanus* have quite separate ranges.

Description.— Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is not shown; coloration of pterothoracic and abdominal sterna in Fig. 11A; median lobe of male in Fig. 18A; and metacoxal processes in Fig. 22C.

Taxonomic notes.— See notes provided under *D. marginalis*.

Variation.— I have seen only 19 specimens assignable to this name, and have therefore little information about variation. Of the ten females examined, four have sulcate elytra.

Natural history.— Unknown.

Distribution Map, Fig. 39.— Zaitsev (1953:328) records this species from Iran, northeastern Turkey and from the southern coast of Crimea, Dagestan and Transcaucasia in the USSR. I have assigned a specimen from Narin, Afghanistan to this species.

Chorological relationships.— I have seen few specific locality records for any species from the range of *D. persicus* , and cannot make a confident statement of co-occurence with other taxa. However, it may be sympatric with *D. semisulcatus*, *D. dimidiatus*, *D. marginalis*, *D. circumflexus* and *D. thianshanicus*.

Phylogenetic relationships.— Adult members of this species show characteristics indicating that *D. persicus* is related to *D. marginalis* and *D. delictus*.

Material examined.— A total of 19 adult specimens was examined, of which nine are male and 10 are females.

Dytiscus delictus (Zaitzev, 1906)
Figs. 4A, 11B, 18B, 22D, 23J, 40, and 52

Macrodytes delictus Zaitzev 1906:28 (Type locality - Chaborovsk, Chaborovsk Kraj, RSFSR, USS. Type not seen).

Dytiscus delictus; -Zimmermann 1920:247. -Zimmermann and Gschwendtner 1938:43. -Zaitsev 1953:326.

Derivation of specific epithet.— Not stated by Zaitzev. The Latin word *delictus* means "faulted" or "failed", but the significance of this epithet is not apparent.

Notes about type material. - I have not seen type specimens of this species, but have seen specimens authenticated by Zaitzev.

Diagnostic combination.— Eastern Palearctic distribution, acute metacoxal lobes, and fasciate abdominal sterna distinguish adults of this taxon from those of other species of *Dytiscus*.

Description.— Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 4A; coloration of pterothoracic and abdominal sterna in Fig. 11B; median lobe of male in Fig. 18B; metacoxal processes in Fig. 22D; and mesotarsi of females in Fig. 23J.

Taxonomic notes.— Zaitzev (1906) accepted *Macrodytes* as a distinct genus, and assigned his species, *delictus*, to it.

Variation.— I have seen too few specimens to assess patterns of variation.

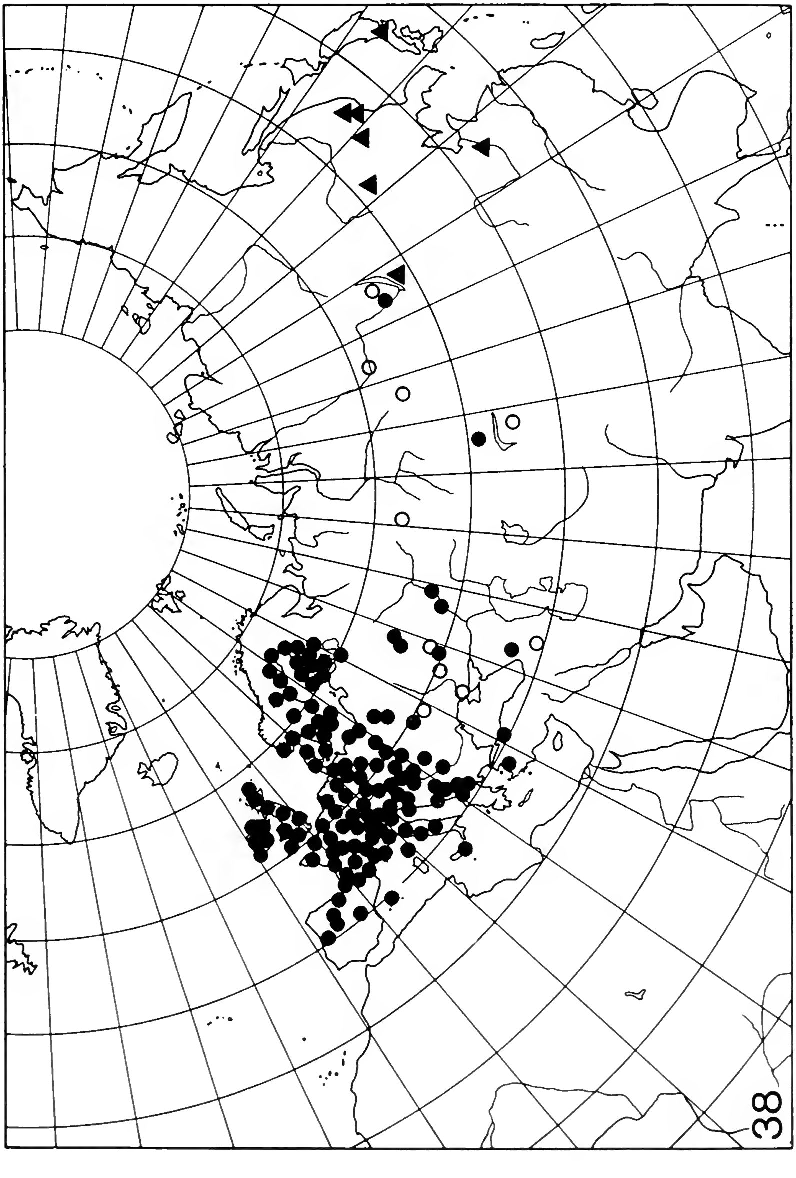
Natural history.— Unknown.

Distribution Map, Fig. 40.— I have seen specimens from Chabarovsk Kraj, Primorskij Kraj, and Sachalin Oblast of the eastern USSR. Zaitsev (1953) reports specimens from the same general area. This species may also occur in northeastern China and Japan.

Chorological relationships.— *Dytiscus delictus* is sympatric with *D. sharpi*, *D. marginalis czerskii*, *D. dauricus*, *D. circumcinctus*, and *D. thianshanicus.*

Phylogenetic relationships.— This species is the eastern vicar of *D. persicus* (Fig. 52).

Material examined.— A total of 20 adult specimens was examined, of which nine are males and 11 are females.



38

Fig. 38. Known distribution of *Dytiscus marginalis marginalis* Linnaeus (circles) and *D. marginalis czerskii* Zaitsev (triangles).

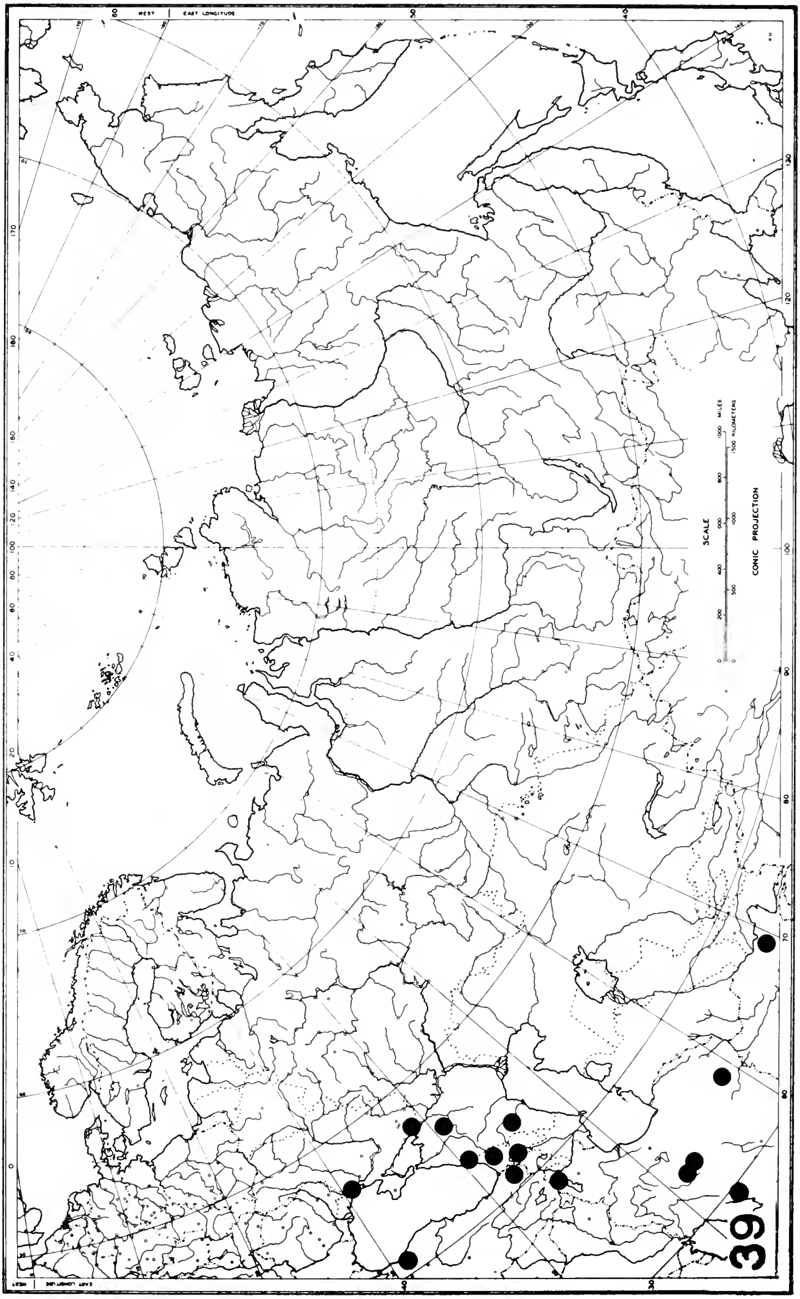


Fig. 39. Known distribution of *Dytiscus persicus* Wehncke

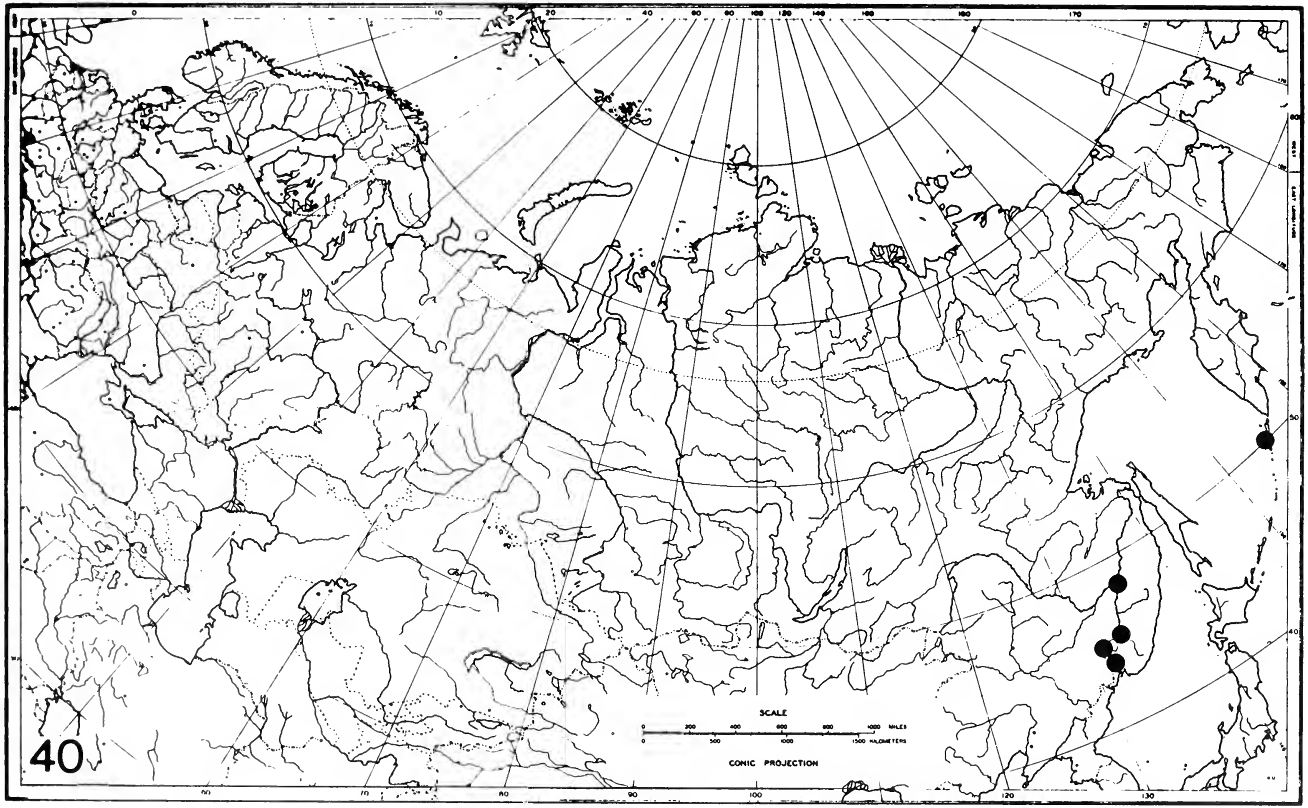


Fig. 40. Known distribution of *Dytiscus delictus* (Zaitzev).

Dytiscus latissimus Linnaeus, 1758
Figs. 4B, 11C, 18C, 22E, 41, and 52

Dytiscus latissimus Linnaeus 1758:411 (Type area - "Europae". Type not seen.). -Zimmermann 1920:242. -Guignot 1932:730. -Houlbert 1934:132. -Zimmermann and Gschwendtner 1938:35. -Guignot 1947a:247. -Zaitsev 1953:321. -Schaeflein 1971:86. -Franciscolo 1979:671.

Dytiscus amplissimus Müller 1776:69 (Type area - not stated, presumably Denmark). -Zimmermann 1920:243.

Dytiscus anastomozans Well 1781:386 (Type locality - not known to me. Type not seen.). -Zimmermann 1920:244.

Derivation of specific epithet.— This name is derived from the superlative form of Latin latus, meaning "broad" or "wide". It is an apt name for this taxon because of the great width of the body of adults.

Diagostic combination.— The great width of the body and widening of the elytral epipleura are sufficient to distinguish adults of this taxon.

Description.— Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 4B; coloration of pterothoracic and abdominal sterna in Fig. 11C; median lobe of male in Fig. 18C; and metacoxal processes in Fig. 22E.

Taxonomic notes.— Most recent European workers have arranged the species of *Dytiscus* in two subgenera: the nominate subgenus, and subgenus *Macrodytes* Thomson. Members of *D. latissimus* have traditionally been placed in subgenus *Dytiscus*. The type species of *Dytiscus*, however, is *D. marginalis*, and the group of species generally treated as belonging to *Macrodytes* should in fact be assigned to subgenus *Dytiscus*. Despite such nomenclatural problems, it is clear that the intention of earlier authors was to isolate *D. latissimus* in a separate subgenus because of its distinctiveness. I do not believe that any subgeneric distinction is necessary within *Dytiscus*, and based on phylogenetic analysis it is not warranted for members of *D. latissimus*. For further discussion of this nomenclatural confusion, see the generic treatment.

Variation.— Non-sulcate females of *D. latissimus* are not known. This is unique among Palearctic taxa of *Dytiscus* except possibly for *D. marginalis czerskii*. However, only a few specimens of the latter taxon are known. Such a uniform condition of sulcate females suggests that females are under strong selective pressure for grooved elytra. Study of the behavioural function, and hydrodynamic importance of sulci in this species may provide the key to understanding evolution of grooved elytra among members of *Dytiscus*.

Natural history.— Guignot (1932), Zaitsev (1953), and other European authors characterize the habitat of this species as large bodies of water; that is, large ponds and lakes, although I am not sure whether or not this species occurs in open water within this habitat. Many specimens have been recorded as being collected in fish weirs.

Distribution (Fig. 41). — Occurs in the northern portions of the Palearctic region, except Great Britain. The easternmost record that I have seen is from USSR, RSFSR, Altajskij Kraj, Utkul' (52° 43'N 84° 36'E) but this species is undoubdtedly more widespread in USSR. The southernmost record is from Yugoslavia, probably associated with long range dispersal (Apfelbeck 1904:308).

Chorological relationships.— I have few records from the far eastern Palearctic Region, and it is therefore difficult to assess areas of sympatry with such species as *D. sharpi*, *D. delictus*, *D. marginalis czerskii*, *D. thianshanicus*, *D. latro* and *D. sinensis*. The known range of *D. latissimus* indicates sympatry with *D. semisulcatus*, *D. dimidiatus*, *D. pisanus*, *D. marginalis marginalis*, *D. circumcinctus*, *D. dauricus*, *D. lapponicus* and *D. circumflexus*.. It is not sympatric with *D. mutinensis* and *D. persicus* .

Phylogenetic relationships.— Members of *D. latissimus* have the metacoxal processes acuminate, but less so than more advanced members of the genus such as *D. lapponicus*, *D. circumflexus*, *etc*. However, the median lobe is without an apical knob, which I interpret as a secondary loss, which has also occurred in *D. alaskanus*. I have placed *D. latissimus* as the most plesiotypic of those taxa which have acuminate metacoxal lobes (Fig. 52).

Material examined.— A total of 428 specimens was examined, of which 208 are males and 220 are females.

Dytiscus circumcinctus Ahrens, 1811
Figs. 4C, 11D, 18D, 19A, 22F, 42, 43, and 52

Dytiscus circumcinctus Ahrens 1811:67 (Type locality - not known to me. Type not seen.). -Zimmermann 1920:244. -Hatch 1929:227. - Guignot 1932:720. -Houlbert 1934:134. -Zimmermann and Gschwendtner 1938:54. -Guignot 1947a:244. - F. Balfour-Browne 1950:275. -LaRivers 1951:404. - F. Balfour-Browne 1953:27. -Hatch 1953:238. -Zaitsev 1953:331. -Gordon and Post 1965:25. -Galewski 1971a:88. -Schaeflein 1971:88. -Larson 1975:401. -Franciscolo 1979:669.

Dytiscus flavocinctus Hummel 1823:17 (Type area - "Livonie". Type not seen.). -Zimmermann 1920:245.

Dytiscus circumcinctus var. *flavocinctus* Hummel; -Zimmermann 1920:245. -Guignot 1932:720. -Zimmermann and Gschwendtner 1938:54. -Guignot 1947a:244. - F. Balfour-Browne 1950:277. -Zaitsev 1953:331. -Schaeflein 1971:88. -Franciscolo 1979:669.

Dytiscus angustatus Stephens 1828:88 (Type locality - "Bomere, Salop.", England. Lectotype male selected here from Stephens collection, BMNH, and labelled as follows: LECTOTYPE; SYNTYPE; LECTOTYPE, Dytiscus angustatus Stephens selected R.E. Roughley). -Zimmermann 1920:245.

Dytiscus dubius Gyllenhal 1827:372 (Type locality - not stated. Type not seen.). -Zimmermann 1920:245.

Dytiscus ooligbuckii Kirby 1837:74 (Type locality - "Great Bear Lake River", N.W.T., Canada. Type - see Larson 1975:401.). -Zimmermann 1920:247.

Dytiscus circumscriptus Boisduval and Lacordaire 1835:300 (Type locality - near Paris, France. Type not seen.). Zimmermann 1920:245. -Houlbert 1934:134.

Dytiscus anxius Mannerheim 1843:218 (Type locality - "Sitkha", Alaska. Type not seen.). -Zimmermann 1920:244. - F. Balfour-Browne 1950:277. -Leech and Chandler 1956:323. -Wallis and Larson 1973:110. -Larson 1975:401.

Dytiscus fusco-striatus Motschulsky 1859:167 (Type locality - Fort Ross near San Francisco, California, U.S.A. Type not seen). -Zimmermann 1920:248.

Dytiscus confusus Motschulsky 1860:101 (Type area - "...dans toute la Sibérie orientale, jusqu'au Kamtschatka, et a été rapporté du fl. Amour..." Syntype male in MNHM labelled: SYNTYPE; Dytiscus confusus Mots., Dauria, [illegible], 52° [or 62°] [yellow circular label]; 1; Dytiscus ♂ confusus Daur. Motsch.; Museum Paris, coll de Marseul 1890; SYNTYPE, Dytiscus confusus Motschulsky 1860, examined R.E. Roughley). -Zimmermann 1920:245.

Dytiscus circumcinctus ab. ♂ *striatus* Bruce 1931: 190 (Type locality - "Kalmar, Ljungbyholm", Sweden. Type repository - not stated. Type not seen.).

Dytiscus albionicus; *auctorum, nec* Motschulsky 1859:166. **Misidentification** of *D. marginicollis, quod vide*.

Dytiscus dauricus; *auctorum, nec* Gebler 1832:39. **Misidentification**. -Zimmermann and Gschwendtner 1938:55 (*ex parte*).

Derivation of specific epithet.— This epithet is formed from the Latin words *circum* meaning around or on all sides, and *cinctum*, girdle or belt (Brown

1956). The name possibly refers to the yellow band around the dorsal edge of the eye of adults.

Notes about type material.— F. Balfour-Browne (1950) discussed many of the taxonomic problems associated with this species. Larson (1975) provides details about the type of *D. ooligbuckii*. I examined the type series of *D. angustatus* within the Stephens collection, BMNH. A lectotype is designated above, but because of the short pins used for Stephens' specimens, these are pinned beside the lectotype. In addition, there is a sulcate female specimen which is a syntype.

As noted above, I have seen a male syntype of *D. confusus* Motschulsky. My reasons for considering this specimen to be a part of the type series are: 1, the label on the box in de Marseul's collection as discussed under the treatment of *D. dauricus*; 2, the name *D. confusus* is on this list; 3, one of the labels ("*Dytiscus* ♂ *confusus* Daur., Motsch.") appears to be in Motschulsky's handwriting, by comparison with handwriting samples shown in Horn and Kahle (1935-37, Plate XVI, Fig. 23, and Plate XXI, Fig. 33); and 4, Motschulsky, in his discussion of this species, implies that he had seen a number of specimens from diverse localities. I have not designated this syntype as lectotype because it is incomplete, lacking its head, and having only the right foreleg complete.

Diagnostic combination.— Adults possess the following combination of character states: pronotum margined with yellow on all sides, acuminate metacoxal processes, predominantly yellow pterothoracic sterna, and eyes dorsally surrounded by narrow yellow band.

Description.— Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 4C; coloration of pterothoracic and abdominal sterna in Fig. 11D; median lobe of male in Figs. 18D and 19A; and metacoxal processes in Fig. 22F.

Taxonomic notes.— Many names have been proposed for this species, presumably because it is very widespread and exhibits a certain amount of colour and structural variation. Samples from particular localities are generally uniform in colour and size and if compared with samples from adjacent localities, then assignment is usually not difficult. Taxonomic problems arise when comparing specimens from widely separated localities. In the latter example I have referred consistently to shape of the median lobe for evidence on which to make taxonomic judgments. Median lobes shown in Figs. 18D and 19A are typical of the variation in form of the median lobe; yet, the specimens are from localities (Edmonton, Alberta, Canada and Berlin, West Germany) from more than half of the Holarctic Region apart. The form of the median lobes of these specimens is very similar and therefore I have assigned them both to the same taxon. Another factor which has led to a proliferation of names is the occurrence of both sulcate and non-sulcate females in most populations of *D. circumcinctus*. Most early workers considered the two forms to be representative of separate taxa (see Blunck 1913 for discussion).

As noted above in the discussion of *D. marginicollis*, I have transferred the name *D. albionicus* from a junior synonym of *D. circumcinctus* to a junior synonym of *D. marginicollis*. One reason for this transfer was that *D. circumcinctus* is absent from California. Nevertheless I have retained the name *D. fuscostriatus* as a junior synonym of *D. circumcinctus* even though it was described from the same type locality (San Francisco). I have followed Larson (1975) in the present placement of *D. fuscostriatus* in part because Motschulsky

(1859) describes the venter of the type female as testaceous and the elytra as sulcate. Study of Motschulsky's types will be needed to clarify this problem.

Variation.— As noted above there is very little variation in form of the median lobe of male specimens from throughout the entire, Holarctic range of *D. circumcinctus*. One of the major features of variation in the median lobe of adult males is positive correlation among size of specimens and length of the median lobe. Increased or shortened length of the median lobe does not significantly affect shape of the apical portion of the median lobe.

Colour of pterothoracic sterna of adults is predominantly yellow in all specimens seen. Some specimens become discolored by breakdown of fat body and other viscera but without exception these conform to the generalized pattern once thoroughly cleaned.

The majority of specimens of *D. circumcinctus* which I have seen from the Nearctic region are from western Canada and adjacent areas. Within these areas, there is some suggestion of a geographic pattern to relative frequency of elytral sulcation of females. For instance, of 309 females from Alberta, Manitoba, Northwest and Yukon Territories, Saskatchewan, and North Dakota, only 33 or 11% are sulcate. The number of specimens from other areas is much less, but of 28 females from Alaska, British Columbia, and Washington, 22 or 79% are sulcate.

Guignot (1932:722) and F. Balfour-Browne (1950:277) state that specimens of *D. circumcintus* are rarely collected in France and Great Britain, respectively. Of those adult females collected, they mention that sulcate specimens are scarce. Guignot writes that sulcate specimens are more common in Sweden. Available information supports his claim: of 73 females from Sweden, 64 or 88% are sulcate, and of 87 females from Finland, 65 or 75% are sulcate. In these areas, *D. circumcinctus* is collected more commonly than it is in France and Great Britain. Interestingly, Zaitsev (1953:354) states that sulcate and non-sulcate females occur in about equal abundance in the U.S.S.R., but does not mention whether he noted a regional disparity in dimorphism. He also records it as the commonest species of *Dytiscus* in the U.S.S.R.

In summary, within the western portions of the Palearctic region, specimens of *D. circumcinctus* are more scarce southward, but of these, non-sulcate females make up a greater proportion. Within North America, there is a similar trend in abundance, but most records of non-sulcate females are from east of the Rocky Mountains, with sulcate females predominating to the west. These trends are only preliminary, but suggest differences in dispersal rates and sources of fauna (*e.g.* western Nearctic populations may be derived from the Russian fauna via Beringia), or of physiological-genetic properties of non-sulcate females, or a combination of both features. Further information and investigation is warranted to achieve better understanding of the pattern.

Natural history.— Most of the comments presented below refer to my own collecting experiences in western Canada, label information from specimens examined, and some literature references. As more detailed collecting notes, natural history studies, larval identification and similar types of information become available, they will provide an interesting and informative comparison against, in particular, the seeming structural uniformity of adult *D. circumcinctus* throughout its range.

Larson (1975:402) noted the broad range of habitats in which he had collected adults of *D. circumcinctus* within Alberta. My experience suggests that this observation is true for most of western Canada, and can extend Larson's range of habitats to highly alkaline or saline habitats. Galewski (1971b) similarly recorded a wide ecological valence for this species in Poland as does Borchert (1938:17) for Germany; Borchert (1938) describes this species as scarce and sparsely distributed. However, Guignot (1932:722) implies that, in France, *D. circumcinctus* is restricted to cold clear aquatic habitats, and F. Balfour-Browne (1950-278) records it primarily as a locally distributed inhabitant of fens in Britain. In Sweden it is found primarily in eutrophic, lowland lakes (Nilsson, pers. comm). A wide habitat range would provide an adaptive advantage for this species, and presumably forms part of the reason for its Holarctic distribution pattern. Nevertheless, in certain areas, such as France and Great Britain, habitat diversity of *D. circumcinctus* may be curtailed by any number of features (*e.g.* local competition).

Galewski (1964) records a specimen of *D. circumcinctus* being taken from forest litter in Poland during winter. An adult male that I collected in Edmonton, Alberta on 23.v.79 was under a log on the south shore of the North Saskatchewan River ravine. Each year, this north-facing slope near the river is one of the last areas to lose snow cover, and temperatures are kept low because of the nearby ice on the river. Therefore, I suspect that this specimen overwintered at that particular site. Larson (1975:402) reported taking specimens through the ice in February. Thus, these few preliminary data suggest that adult specimens of *D. circumcinctus* may overwinter either on land or in water.

Galewski (1971b) discusses early season occurrence of this species in temporary pools where it feeds extensively before moving on to more permanent habitats for reproduction. Available flight records (Table 5 and Larson 1975) suggest one peak of dispersal in April and May and another in September and October. The majority of teneral specimens seen by Larson (1975) were from July, and in Table 4 there is one each for May, June, August and September. This variation may well indicate local topographic differences in habitats, such as availability of prey, water temperatures, *etc.*

Distribution (Figs. 42 and 43).— This species is widespread within the Holarctic Region. In North America it is transcontinental, with records from Maine to Alaska. It occurs as far south as North Carolina, and I have taken it at tree-line in Canada's Yukon Territory. In the Palearctic region it ranges from Norway and Great Britain south to Italy (Franciscolo 1979:69) and Bulgaria (Guéorguiev 1958) and westward throughout the region. I have been unable to find records for Spain excluding the Pyrenees. Apparently it is collected less commonly in the southern portions of its range.

Chorological relationships.—In some parts of its range, *D. circumcinctus* is sympatric with every other species of *Dytiscus* except *D. habilis* in the Nearctic Region, and, in the Palearctic, *D. sinensis.*

Phylogenetic relationships.— Adults of *D. circumcinctus* possess acuminate metacoxal processes and therefore belong to one of the more advanced grades within *Dytiscus.* The median lobe is not sinuate laterally, but has an apical knob with sensory pores. These synapotypic character states define adequately the relative position of *D. circumcinctus,* but the exact sister group relationship of the species is less certain. The only character I could find to separate the more advanced members of this clade from *D. circumcinctus* is the relatively abrupt bend in the lateral ridge of the median lobe of advanced members, compared to the evenly curved lateral ridge of the same structure in members of *D. circumcinctus.* I believe this to be a relatively weak character, and thus the hypothesized sister group relationship may change as new characters are found and incorporated into the analysis. Members of *D. latissimus*, *D. alaskanus* and *D. circumcinctus* are very difficult to place in the cladogram. The two former species probably have lost the apical knob of the median lobe secondarily.

Material examined.— A total of 1470 specimens of *D. circumcinctus* was examined: 283 males and 337 females from the Palearctic region, and 351 males, 381 females and 18 specimens of undetermined sex from the Nearctic region.

Dytiscus alaskanus J. Balfour-Browne, 1944
Figs. 5A, 12A, 19B, 22G, 44, and 52

Dytiscus parvulus Motschulsky 1852:77 (Lectotype male designated here, in UMHF, labelled as follows: LECTOTYPE; SYNTYPE; Kadjak; Holmberg; Dytiscus parvulus, Ménétr., Kadjak; LECTOTYPE, Dytiscus parvulus Motschulsky 1852, designated R.E. Roughley; Dytiscus alaskanus J.B.-B. det. R.E. Roughley 1982) *nec* Müller 1776:73. -Zimmermann 1920:253. -Hatch 1929:227. -Brown 1930:237. -Wallis and Larson 1973:110. Larson 1975:404.

Dytiscus alaskanus J. Balfour-Browne 1944:356. -Larson 1975:404.

Dytiscus ooligbuckii; J. Balfour-Browne 1948:161. -Gordon and Post 1965:25.

Dytiscus oolibuckii; Hatch 1953:238.

Dytiscus ooligbukii; Anderson 1962:73 *nec* Kirby 1837:74. -Larson 1975:404.

Dytiscus ooligubuckii; Kirby 1837:74. **Misidentification** of *D. circumcinctus, quod vide.*

Derivation of specific epithet.— The name of this taxon was proposed in honour of the State of Alaska, U.S.A., where it is abundant, and which contains the type locality of *D. parvulus*, for which *alaskanus* is a replacement name.

Notes about type material.— The type series of *D. alaskanus* in UMHF consists of six specimens: five males and one female. The female is non-sulcate. The type locality, Kodiak Island, is the western-most record I have for this species. All specimens have at least sterna II, III and VI with transverse dark fascia, and most, including the lectotype, have narrow markings on sterna IV and V.

Diagnostic combination.— Adults of *D. alaskanus* are known only from the Nearctic region. Only three species within the Nearctic region have acuminate metacoxal processes: *D. circumcinctus*, *D. alaskanus* and *D. dauricus*. Those specimens of *D. alaskanus* with a predominantly yellow venter are most easily separated from *D. circumcinctus* by absence of a yellow ring around the eye dorsally, by the fusion of inter-sulcal ridges apically on sulcate females (compare Figs. 4C and 5A). Specimens of *D. alaskanus* with fasciate abdominal sterna are most similar to specimens of *D. dauricus*, and are best separated by the characters presented in the key.

Description.— Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 5A; coloration of pterothoracic and abdominal sterna in Fig. 12A; median lobe of male in Fig. 19B; and metacoxal processes in Fig. 22G.

Taxonomic notes.— Larson (1975:404) provides a detailed history of the long, confused history of the nomenclature of this taxon.

Variation.— Larson (1975:404) provides notes about variation of this taxon within the province of Alberta, and therefore I confine this discussion to other geographic areas to variation of some taxonomically important characters. Further discussion is provided in the treatment of *D. dauricus*.

Colour of pterothoracic sterna varies geographically. Most specimens of *D. alaskanus* observed from British Columbia, Newfoundland, Northwest and Yukon Territories have completely yellow venters, whereas the majority of specimens from intervening localities have at least some degree of infuscation.

The median lobe of males of all these specimens is similar to that shown in Fig. 19B.

Larson (1975:404) mentions only one Alberta locality, near the Northwest Territories border, for non-sulcate females, and in excess of 99% of our combined samples are sulcate. Throughout most of its range, females of *D. alaskanus* are consistently sulcate, and where non-sulcate females do occur, they make up only a very small proportion of the total. The areas for which I have seen non-sulcate females, and the percentage of the total number of females seen from that geograhic area (localities for non-sulcate females in parentheses) are as follows: British Columbia - 5 of 56 or 9% (Kamloops area, Summit Lake, and Mile 627 on Alaska Highway); Manitoba - 3 of 13, or 23% (The Pas); Saskatchewan - 1 of 6, or 7% (Saskatoon); Ontario - 1 of 11, or 9% (Toronto); Colorado - 5 of 20, or 25% (Breckenridge and Science Lodge W., both in Summit Co.); Northwest Territories - 4 of 15, or 27% (Ft. Smith, Reindeer Depot, and Simpson Islands in Great Slave Lake); Alaska and Yukon Territory - 12 of 34, or 35% (Ft. Yukon, Kodiak and Fairbanks; Mile 629 and 681 on Alaska Hwy., Chappie Lake, Von Wilczek Lake, Watson Lake, and Whitehorse). As suggested by Larson (1975), this elytral form is more common in the northwestern position of the range of *D. alaskanus*. It is interesting, but as yet unexplained, that the co-occurring *D. circumcinctus* shows the reverse pattern over much of the same area (*i.e.*, non-sulcate form predominant southward). Low level occurrence of non-sulcate females in other widely separated areas such as Ontario and Colorado is perhaps associated with dispersal, but possibly also indicates independent loss of sulcation within these areas. None of the non-sulcate females is provided with label data giving precise habitat, and therefore the possibility of an ecophenotypic response cannot be ruled out.

Natural history.— Members of *D. alaskanus* are collected in very large numbers at various localities in western Canada. Many bottle traps left in George Lake, near Busby, Alberta, for two days yield 10 to 15 specimens per bottle, and have taken up to 80 specimens. Most localities where net-collecting has yielded only one or two specimens have produced many times this number when bottle traps were used subsequently. This confirms the observation made by Larson (1975) that adults are often numerically abundant at particular localities.

In northwestern North America, members of *D. alaskanus* have been collected from permanent ponds and lakes in prairie, aspen parkland and boreal forest. Specimens of *D. alaskanus* overwinter in bodies of water such as George Lake and are active quite early in the spring, often before the ice is off the lake. I have observed copulating pairs from mid-April to early June at this locality. Favoured oviposition sites are plants such as *Scirpus* and *Typha*. Held in captivity for a week to ten days, with a single plant available for oviposition, two or three females reduce a plant to shreds by constant slitting of the leaves and stem with the ovipositor. During this time, individual females lay up to 40 eggs within the plant tissue. It is not known whether females lay a similar number of eggs under field conditions, but the above number may be conservative, because availability and quality of oviposition sites, as well as quality of food is greater in the field than it is possible to provide in the laboratory.

Aiken (1985) discussed the correlation of life histories of the hydrachnellid mites (*Eylais* sp.) and *D. alaskanus*. Aiken (1986) and Aiken and Wilkinson (1985) provide a detailed life history of this species at George Lake, Alberta.

Larval development in natural conditions is probably dependent on amount and type of food available, and on water temperature. For instance, most teneral specimens were collected in August, but in seasonally more advanced and warmer areas such as Kamloops, British Columbia, teneral specimens were collected in late June (Table 4). Larson (1975) records a teneral specimen as late as mid-October.

Some dispersal occurs in spring (Table 5) and perhaps again in autumn. It is interesting that the number of flight records is so low, given local abundane of this species throughout its range.

Distribution (Fig. 44).— This species is transcontinental in North America with records from Newfoundland to Alaska. The southern limit of *D. alaskanus* is represented by an isolated population in south-central Wyoming and adjacent areas of Colorado. Most records are from south of tree-line, but some scattered records indicate possible extension onto tundra habitats.

Chorological relationships.— The range of *D. alaskanus* overlaps that of every other Nearctic species except *D. habilis* and *D. carolinus.*

Phylogenetic relationships.— As with *D. latissimus*, placement of *D. alaskanus* in the phylogenetic analysis is provisional because, in dorsal view, the median lobe of males of both species lack a distinct apical knob. In males of *D. alaskanus*, however, the knob is visible in ventral view, and therefore is most likely an example of reduction from the well differentiated state, unlike the condition of *D. latissimus*. Members of *D. alaskanus* and *D. dauricus* may represent a sister pair of species, but I have been unable to find a synapotypic character state linking them

The more advanced members of *Dytiscus*, as shown in the cladogram, are united by having the median lobe of males sinuate laterally. This is a condition absent from *D. alaskanus*. The lack of an apical knob in dorsal view and the absence of lateral sinuation of the median lobe could be part of the same evolutionary step. A shortening of the apical portion of the median lobe may have brought about changes in both character states simultaneously.

Material examined.— A total of 661 adult specimens were examined and the label information recorded from these. Of these, 387 are males and 274 are females. In addition, long series of this species from George Lake, Alberta were examined but the label information not recorded. The total number of adult specimens examined is thus in excess of 2000.

Dytiscus dauricus Gebler, 1832
Figs. 5B, 12B, 19C, 22H, 45, 46, and 52

Dytiscus dauricus Gebler 1832:39 (Type area - "le district des mines de Nertschinsk, dans la Sibérie orientale". Lectotype male selected here from Marseul collection, MNHM, labelled as follows: LECTOTYPE; SYNTYPE; *Dytiscus Dauricus* Gebler, Sib. or. 62; Dytiscus dauricus Gebl., Sib. or.; [indistinguishable mark similar to "q"]; Lectotype, *Dytiscus dauricus* Gebler selected by R.E. Roughley). -Zimmermann 1920:247. -Hatch 1929:227. -Brown 1930:237. -Hatch 1933:11. -Zimmermann and Gschwendtner 1938:55. -Brinck 1946:154. -J. Balfour-Browne 1946:452. -Hatch 1953:238. -Zaitsev 1953:331. -Leech and Chandler 1956:323. -Wallis and Larson 1973:110. -Larson 1975:402.

Dytiscus confluens Say 1834:440 (Type area - Maine. Type probably lost.).

Dytiscus franklinii Kirby 1837:77 (Type area - "Lat. 65°", boreal North America. Type - see Larson 1975:403.). -Zimmermann 1920:247.

Dytiscus dauricus var. *franklini; auctorum.* **Unjustified emendation** of *D. franklinii* Kirby 1837. -Zimmermann 1920:247. -Zimmermann and Gschwendtner 1938:55. -Zaitsev 1953:354

Dytiscus confluentus LeConte 1850:212. **Unjustified emendation** of *D. confluens* Say.

Dytiscus ooligbuckii; sensu LeConte 1850:212 *nec* Kirby 1837, *quod vide.*

Dytiscus ventralis Motshulsky 1855:79 (New name for *D. ooligbuckii, sensu* Mannerheim 1852:303 nec Kirby 1837. Type locality - "Tschishlkath", near present day Skagway, Alaska. Type not seen.). -Zimmermann 1920:255. -Zaitsev 1953:331. -Larson 1975:403.

Dytiscus dauricus var. *ventralis* Motschulsky; -Zimmermann 1920:247. -Zimmermann and Gschwendtner 1938:55.

Dytiscus frontalis Motschulsky 1859:489. *Nomen nudum.* J. Balfour-Browne 1944:356.

Dytiscus frontalis Motschulsky 1860:101 (Type locality -"Kamtschatka", Alaska. Type not seen.) *nec* Marsham 1802. -Zimmermann 1920:248.

Dytiscus vexatus Sharp 1882:643 (Type area - Russian America. Type - see Larson 1975:403). -Zimmermann 1920:255.

Dytiscus dauricus var. *obscurus* Gschwendtner 1922:93 (Type locality - "Berisovka in Transbaikalien", USSR. Type not seen). Zimmermann and Gschwendtner 1938:56. -Zaitsev 1953:354.

Dytiscus amurensis J. Balfour-Browne 1944:356. New name for *D. frontalis* Motschulsky 1860 *nec* Marsham 1802.

Derivation of specific epithet.— Named for 'Dauria', a region in eastern Asia east of Lake Baikal (now divided between the U.S.S.R. and China), which includes the type locality.

Notes about type material. - Three sources of information were used as the basis for selection of the above lectotype of *D. dauricus.* First, a male specimen of *D. dauricus* in BMNH is labelled "Siberia; Sharp coll., 1905-313 [inverted label]; Siberia or. [inverted yellow label]; *Dytiscus dauricus* according to a type in de Marseul's coll." The last label is in David Sharp's handwriting. Second, Horn and Kahle (1935-1937) state that the collection of F.A. von Gebler was transferred to the René Oberthür collection in MNHM, as was that of S.A. de Marseul. Third, in de Marseul's collection is a box-label which reads "Communiqué à. M. Sharp par M. Lewis le 8 1876" and in the following list is the name *D. dauricus.* From this information, I have inferred that this specimen is part of Gebler's material and available for designation as lectotype.

Diagnostic combination.— In the Nearctic region adults of only *D. dauricus* and *D. alaskanus* possess acuminate metacoxal processes and fasciate abdominal sterna. Members of these two taxa are best separated by the characters presented in the key to adults of the Nearctic region. In the Palearctic region, *D. dauricus* occurs abundantly only about as far west as the Lake Baikal region, although there is one record for Yining (Kuldja), China at 43° 55'N 81°14'E. This distribution, in combination with fasciate abdominal sterna, and acuminate but not spinose metacoxal processes will separate members of *D. dauricus* from other congeners in this area.

Description.— Measurements of representative specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 5B; coloration of pterothoracic and abdominal sterna in Fig. 12B; median lobe of male in Fig. 19C; and metacoxal processes in Fig. 22H.

Taxonomic notes.— Larson (1975) discussed most of the taxonomic problems associated with *D. dauricus.* Many names have been proposed for this taxon, in part because in most collections it is represented by only a few specimens, and if the specimens are from widely separated geographic localities they may appear to represent different taxa, especially if characteristics of the male median lobe are excluded. Also, and perhaps correlated with the above, authors' concepts of this taxon have been communicated inadequately over the years, and this has led to confusion concerning the naming of specimens.

Variation.— As noted under the treatment of Measurements (see also Table 2), there is a wide range in total length and associated measurements. However, specimens collected by bottle trap (Table 1) show a consistent size and are on average larger than those collected with dip nets. This suggests a size bias associated with collecting technique. As more series of specimens collected by bottle-trap become available for study, it will be valuable to test them against net-collected specimens from the same geographic area.

The predominantly yellow pterothoracic and abdominal sterna are marked consistently with infuscation in the material at hand. The mode of this pattern is darker than that of *D. alaskanus*, but the variation shown in the latter eliminates ventral colour pattern as a useful taxonomic character, except on a regional basis. In certain geographic areas, population samples have a majority of specimens with, for instance, expanded infuscation of metathoracic 'wing' *e.g.* Fig. 12B left combined with more yellow abdominal sterna (*e.g.* Fig. 12B right). I have been unable to find a pattern in this variation, and indeed, there may not be one. In general, darker specimens predominate and increased infuscation of any one sternum is correlated positively with increased infuscation of other sterna.

An important feature unique to females of *D. dauricus* is the distinct disjunction between the planes of clypeus and frons at the fronto-clypeal suture. The frons is markedly recessed from the clypeus (Larson 1975:403). Some female specimens of *D. alaskanus* show a slight planar disjunction in this area, and this is marked in some teneral specimens. Once specimens of both taxa have been seen, however, the difference in degree is sufficient to allow reliable use of this character for separation of female members of these taxa.

Another character used to distinguish among females of *D. alaskanus* and *D. dauricus* is arrangement of the inter-sulcal ridges of the apex of the elytron. Character state differences are presented in couplet 13 of the key to Nearctic species. I have seen no exceptions to this dichotomy, except where elytra have been malformed, presumably during eclosion from the pupal cell.

Of the 41 female specimens seen from the Palearctic region, 13, or 32%, show no trace of elytral sulci, 27 are distinctly sulcate, and one specimen has the sulci only slightly impressed. From the Nearctic region, 315 specimens were available for analysis. Distribution of sulcate and non-sulcate females from North American localities is given in Table 6. These data are presented in a northwest to southeast direction. While it will be more compelling when more specimens become available for study, these preliminary numbers suggest three areas of occurrence of non-sulcate females: 1, Alaska, Yukon and Northwest Territories, Ontario, and the western Provinces of Canada; 2, Newfoundland; and 3, high altitude sites in Colorado and Wyoming. These localities are just as suggestive of development of the non-sulcate form in refugia (*i.e.*, Beringia, Newfoundland, and alpine Colorado and Wyoming) as they are of environmental influence on proportion of non-sulcate females. The latter scenario is somewhat weakened when it is considered that samples of *D. dauricus* from presumably similar habitats in California, Idaho, Montana, Nevada and Utah contained no non-sulcate female specimens. Both hypotheses are weakened by the low proportion of non-sulcate females in Alaska and Yukon Territory.

Natural history.— Larval development of *D. dauricus* is completed by late July to early August in Alberta and Minnesota, as teneral specimens from the first half of August were seen by Larson (1975) and me (Table 4). This species seems to prefer permanent pond or lake habitats, and these are usually associated with some amount of tree cover (Larson, 1975).

Further north in its range, *D. dauricus* occurs at a broad range of altitudes including sea level. Further south in its Nearctic range, at least, it becomes restricted to higher elevation. Blake (1945) recorded *D. dauricus* from large permanent and moraine ponds at 3050 and 4011 m in the Medicine Bow Mountains of Wyoming. Holomuzki (1986) found specimens of this species only at elevations above about 2500 m in the White Mountains of Arizona. *Dytiscus dauricus* is sympatric with *D. marginicollis* in Arizona but Holomuzki (1986) reports that, among his study sites, *D. marginicollis* was found from 1500 to 2500 m whereas *D. dauricus* was found only at higher elevations.

Holomuzki (1985) discussed the life history of *D. dauricus* in east central Arizona where they are predators of larval tiger salamanders, *Ambystoma tigrinum nebulosum* (Ambystomatidae) (Holomuzki 1986). Blake (1945) observed mating in the first week of July at his high elevation study site in Wyoming.

Available flight records are for April, July, September and October (Larson, 1975, and Table 5). This species may overwinter in the permanent habitats which they inhabit because specimens were caught in bottle traps at George Lake near Busby, Alberta in late April, 1982, when the margins of the lake were ice-free, but most of the lake was still frozen. At this locality, *D. dauricus* occurs at a much lower density than does *D. alaskanus*; however, in Arizona Holomuzki (1986) estimated an abundance of 2.6 adults/m^3.

Distribution (Figs. 45 and 46).— This Holarctic species ranges from Newfoundland westward to Alaska, and occurs sporadically on the Aleutian Islands. In North America, most localities are from south of tree-line, but certain localities in northern Labrador, Ontario and Manitoba probably indicate that it occurs in tundra ponds. The range of *D. dauricus* extends southward along the western mountain ranges to Arizona and California and may occur in alpine and sub-alpine ponds in these areas. In the Palearctic region, most records are from east of Lake Baikal. The most southern and western record is for Yining, China.

Chorological relationships.— In North America, this species is sympatric with every other Nearctic species except *D. habilis* and *D. carolinus*. In the Palearctic it is sympatric with *D. sharpi*, *D. marginalis czerskii*, *D. delictus*, *D. circumcinctus*, *D. lapponicus lapponicus*, *D. latro* and possibly *D. latissimus*.

Phylogenetic relationships.— The robust form and markedly curved lateral margins of the median lobe of males of *D. dauricus* indicate close relationship of this taxon to *D. lapponicus*, *D. circumflexus*, *D. thianshanicus*, *D. latro* and *D. sinensis* (Fig. 52). Unlike these taxa, however, adults of *D. dauricus* do not have a spinose metacoxal process.

Material examined.— A total of 768 adult specimens of *D. dauricus* was examined. From the Palearctic region were 27 males and 41 females, and from the Nearctic region, 382 males and 336 females.

Dytiscus lapponicus Gyllenhal, 1808
Figs. 5C, 12C,D, 19D,E, 22I,J, 47, and 52

Dytiscus lapponicus Gyllenhal 1808:468.

Derivation of specific epithet.— Latin, referring to the type locality, Lapland.

Diagnostic combination.— The combination of Palearctic distribution, acuminate metacoxal lobes, pronotum with very broad yellow margins on all sides and elytra predominantly yellow with rows of black dots easily distinguish members of *D. lapponicus*.

Taxonomic notes.— I have arranged *D. lapponicus* in two subspecies: widespread nominate subspecies, and another restricted to the Italian Alps, for which the subspecific epithet *disjunctus* is available. The form of the median lobe of both subspecies is quite similar but there is a major difference in coloration of the prothoracic disc in the material I have seen (see couplet 13 of key to Palearctic species). I have chosen to treat these named forms as subspecies because: 1, they are allopatric; 2, other specimens of *D. lapponicus* from latitudes near or as far south as that of *D. disjunctus* (*e.g.* France, Germany and U.S.S.R.) do not exhibit its characteristics; and 3, distinctiveness of both groups judging from specimens I have seen. On the basis of colour characteristics studied, each specimen was assigned easily to one or the other subspecies, and subsequent use of geographic criteria showed this to be correlated. Other colour characteristics of *D. lapponicus disjunctus* not used in the key but perhaps correlated with reduced infuscation of the pronotum are greatly expanded yellow band around eye (more than 0.5 width of eye) and posterior extension and expansion of chevron such that it appears hour-glass shaped but with anterior portion wider. Other character differences are discussed by Zimmermann and Gschwendtner (1938:50).

Many Palearctic authors have commented on this form and most have suggested it to be an aberration. Below, I present a brief, selected history of the taxonomic treatment of this form.

Seidlitz (1887:111) accepted *D. disjunctus* as valid at the level of species. Zaitzev (1908) states that recognition of the form *disjunctus* as an alpine "race" is unjustified because he had seen specimens with similarly coloured pronota from northern Russia. Holdhaus (1912:423) states that *D. lapponicus* occurs in the typical or nominate form at La Grave, Isére (now in Dep't. Hautes-Alpes, France). Guignot (1932:726, 1947a:246) presents records for *D. lapponicus* ab. *disjunctus* from Meyrannes near Barcellonette (Dep't. Basses-Alpes, France) and "lac du col de Lauzanier". Interestingly, Guignot, in the former reference, records La Grave as a locality for the nominate form (perhaps following Holdhaus, above) but in later work suggested it as a locality for ab. *D. disjunctus* without providing an explanation for the change. Brundin (1934:252), citing earlier authors, gives, in addition, records for Mt. Cenis (Dep't. Savoie, France) and Simplon (Canton Valais, Switzerland). All of these localities are relatively close to the type locality of *D. lapponicus disjunctus*, but are on the northern and southwestern portions of the watershed of the Alps, whereas the type locality of *disjunctus*, Lago della Magdallena, is on the southern portion of the watershed. Re-examination of these specimens is very important. Because of the problems associated with the Guignot records, I have treated them all as belonging to the nominate subspecies. Also, I do not believe that the concept of this taxon has been well communicated among coleopterists within the region; specimens are not numerous and are restricted to only a few museums. I believe that area of collections was used previously for determination, rather than other characters. If these records do represent the nominate subspecies, then they must represent dispersal records from other areas (*e.g.* Germany) or at least be remnants of a different colonization of the Alps from that which gave rise to *D. lapponicus disjunctus*.

Zimmermann (1919:233) and Zimmermann and Gschwendtner (1938:50) cite *D. disjunctus* as an example of an inbred "race" formed by extreme geographic isolation. F. Balfour-Browne (1950:238) suggests that the main diagnostic feature of *D. disjunctus* is fragmentation of the pronotal infuscation and that Scottish specimens of the nominate form showed evidence of an "elementary stage" of development of this character state. Therefore, he judged *D. disjunctus* to represent a simple aberration. Zaitsev (1953:329) states that *D. disjunctus* is a psychrophilic form as he has seen specimens from Leningrad. I have not seen Zaitsev's specimens. As stated above, the paucity of available specimens may have influenced Balfour-Browne's and Zaitsev's concepts of *D. lapponicus disjunctus*. If they believed that it is only characterized by fragmentation of the infuscated portion of the pronotal disc, then they could have been misled by variation within *D. lapponicus lapponicus*.

The infuscated portion of the pronotum of specimens of the nominate subspecies varies in width, sinuation and fragmentation, but I have seen no extralimital specimens showing character states similar to that of members of *D. lapponicus disjunctus*. Furthermore, even if this character state is demonstrated to occur in other populations, it cannot be inferred that subspecies status in invalid - only that further analysis and characters are needed.

Distribution (Fig. 47).— This is a species of more northern distribution than other Palearctic species. It occurs sporadically in southern Europe, usually associated with montane, or at least cold, oligotrophic habitats. It is more common in northern Europe and is known from throughout the U.S.S.R. I have seen no reliable records for North America.

Chorological relationships.— Areally, the combined range of both subspecies suggests sympatry with most Palaearctic species except *D. sharpi*, *D. persicus* and *D. sinensis*, and possibly *D. delictus*. Differences in preferred habitat suggest that co-occurrence within habitats (or effective sympatry) could happen with *D. marginalis*, *D. circumcinctus*, *D. dauricus*, *D. latro* and *D. thianshanicus*.

Phylogenetic relationships.— Acuminate metacoxal processes, sinuate lateral margins of median lobe of male, with distinct sensory-type pores on apical knob indicate close affinity with *D. thianshanicus*, *D. latro* and *D. sinensis* (Fig. 52).

Dytiscus lapponicus lapponicus Gyllenhal 1808, NEW STATUS

Dytiscus lapponicus Gyllenhal 1808:468 (Type area - "habitat in aquis Lapponiae". Type not seen). -Zimmermann 1920:248. -Guignot 1932:48. -Houlbert 1934:134. -Zimmermann and Gschwendtner 1838:34. -F. Balfour-Browne 1953:27. -Zaitsev 1953:351. -Schaeflein 1971:88.

Dytiscus borealis Motschulsky 1860:101 (Type area - "Sibérie". Type not seen.).

Dytiscus septemtrionalis Gyllenhal 1827:373 (Type area - "Habitat in Finlandiae aquis". Type material -see Notes, below.).

Dytiscus lapponicus var. *septentrionalis*. **Unjustified emendation**. -Zimmermann 1920:249. -Guignot 1932:723. -Houlbert 1934-134. -Zimmermann and Gschwendtner 1938:48. -F.Balfour-Browne 1950:280. -F. Balfour-Browne 1953:27. -Zaitsev 1953:351. -Schaeflein 1971:88.

Notes about type material. — Type material of *D. septemtrionalis* was examined from the Gyllenhal collection in Riksmuseet, Stockholm. There is a male specimen labelled "Finlandia, Falander, ♂ in copula; Coll. Sahlberg" and a female specimen labelled "Finlandia, Falander, ♀ in copula; Coll. *Sahlberg*". Other notes associated with these specimens are "septentrionalis, Germ. in litt., lapponicus var B Gyll. Ins. Sve.; *Dytiscus septemtrionalis*, Gyllenhal Ins. Sve. IV app. p. 373 3-4, Habitat in Finlandiae aquis rarius, a Dom Vasastjerna in copula captus; Mus. Dom. Schönherr." These specimens are syntypes but I did not label them as such nor did I designate a lectotype.

Diagnostic combination.— The broad pronotal infuscation and distribution which excludes the Italian Alps, in conjunction with the diagnostic combination of the species, are sufficient to identify adult members of *D. lapponicus lapponicus*.

Description.— Measurements of largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 5C; coloration of pterothoracic and abdominal sterna in Fig. 12C; median lobe of male in Fig. 19D, E; and metacoxal processes in Fig. 22I.

Variation.— This is a relatively varied taxon, but the limits are defined and identification is usually easy because of several unique features. With respect to diagnostic features, pronotal infuscation is somewhat varied (see Taxonomic notes under *D. lapponicus*). The width of this infuscation is at most subequal to that of the width of an anterior or posterior yellow band. The anterior and/or posterior margins of the band are sinuate in some specimens. Some specimens have the pronotal infuscation arranged in three or more blocks by longitudinal incursions of yellow.

F. Balfour-Browne (1950:281-282) noted the trend for more northern samples of *D. lapponicus lapponicus* to have a greater proportion of non-sulcate females than more southern populations. Unfortunately, he does not provide relative proportions of sulcate and non-sulcate females for the Scottish and Irish samples that he studied. Other available data also suggest this trend. Guignot (1932:726) states that the non-sulcate form does not occur in France. Horion (1941:439-440)) does not mention the varietal name used for non-sulcate females (as he does for other species with dimorphic females) as occurring in Germany, although I have seen a few specimens of ungrooved females labelled only "Germania". Of 28 female specimens seen from Prussia and Poland, all are sulcate. From Sweden, I have seen 71 females of which 54 or 76% are sulcate; from Finland, 105 females of which 84 or 80% are sulcate; and from Norway, 4 of the 11 or 36% of the females studied are sulcate.

As noted elsewhere (*e.g. D. alaskanus*), the cause of geographic variation in proportion of the two types of females is unknown. The pattern suggests dispersal from particular refugia, but ecophenotypic phenomena cannot be ruled out, nor can a combination of both. The observation that all females of *D. lapponicus lapponicus* are sulcate even though they occupy cold, oligotrophic habitats in the Alps argues against the hypothesis of ecophenotypic expression. Further detailed information of occurrence and relative proportion of both states would be most helpful in attempting an explanation.

Natural history.— What is known of the natural history of this species is summarized adequately by F. Balfour-Browne (1913, 1950:283-284) and Jackson (1955:84-85); Eriksson (1972) discusses aspects of the life history of this species in Finland as do Brinck and Wingstrand (1949, 1951) in Sweden.

Distribution (Fig. 47).— Very locally distributed in high mountains of southern Europe, with sporadic records for Germany, Switzerland, Holland, Belgium, Scotland and Ireland. Poppius (1910:356) discounts previous records of this species from Iceland. I have seen the following records which I believe to represent incorrect labelling: "Hongric [ongrie], Roussel" (2 CASC, 1 HNHM), Spain (2 ICCM), and Sitka (1 MNHN). There are no recent nor reliable records for North America.

Material examined.— A total of 657 adult specimens was examined, of which 259 were males and 657 were females.

Dytiscus lapponicus disjunctus Camerano 1880, NEW STATUS

Dytiscus lapponicus var. *disjunctus* Camerano 1880:120 (Type locality - Argentara, Piemonte, Italy. Type not seen.). Zimmermann 1920:249. -Gschwendtner 1923:110. -Guignot 1932:726. -Zimmermann and Gschwendtner 1938-48. -F. Balfour-Browne 1950:280. -Zaitsev 1953:351. -Franciscolo 1979:667.

Derivation of specific epithet.— Presumably, Camerano proposed this name to reflect the isolation of this taxon within the Italian Alps.

Diagnostic combination.— Reduction of pronotal infuscation to a sinuate line across the pronotal disc and restricted range, in conjunction with the diagnostic combination for the species, are sufficient to identify adult members of *D. lapponicus disjunctus*.

Description.— Measurements of largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is not shown (see Franciscolo 1979:658, Fig. 2046); coloration of pterothoracic and abdominal sterna in Fig. 12D; median lobe of male not shown; metacoxal processes in Fig. 22J.

Variation.— Shape of pronotal markings of specimens of *D. lapponicus disjunctus* examined is relatively consistent and similar to that illustrated by Franciscolo (1979:658, Fig. 2046).

All of the 38 females seen are sulcate.

If fresh material can be obtained (but see natural history), it would be useful to determine whether or not flight muscles are present within members of this subspecies. Jackson (1955) suggested that absence of flight muscles from Scottish specimens of the nominate subspecies could have played a role in the limited distribution of that form in Scotland.

Natural history.— Most collection records have no dates associated with them. Available dates are: vii.1898, vii.21, 8.viii.21, viii.23, 22.viii.23. These correlate well with those mentioned by Franciscolo (1979), who further states that he has been unable to collect this subspecies at the type locality despite repeated attempts since 1954. Intensive collecting by Franciscolo and others has failed to find any other localities for *D. lapponicus disjunctus*. Franciscolo correlates the demise of this taxon with the introduction of trout into the type locality and similar lakes within the Italian Alps. This is very interesting, because F. Balfour-Browne (1913, 1950) mentions that in Scotland *D. lapponicus* is taken only in lochs from which trout are absent. Franciscolo mentions that trout could have preyed upon the immature forms of this subspecies and that it may already be extinct.

Distribution (Fig. 47).— All specimens that I have seen were labelled with part of the following compounded label information: Lago della Maddalena, Argenterra, Col de Larche, Valle Sture, Piemonte, Alpi Marittime, 2000 m. Other possible records are treated under Taxonomic notes for *D. lapponicus*.

Material examined.— A total of 50 adult specimens was examined, 12 males and 38 females.

Dytiscus circumflexus Fabricius, 1801

Figs. 5D, 13A, 20A, 22K, 48, and 52

Dytiscus circumflexus Fabricius 1801:258 (Type area - Tanger *fide* Guignot 1961:860. Type not seen.). -Zimmermann 1920:245. -Müller 1926:299. -Guignot 1932:722. -Houlbert 1934:135. -Zimmermann and Gschwendtner 1938:51. -Guignot 1947a:245. -F. Balfour-Browne 1950:273. -F. Balfour-Browne 1953:27. Zaitsev 1953:351. -Guignot 1961:860. -Schaeflein 1971:88. -Franciscolo 1979:669. -Régil and Salgado 1984:133,135.

Dytiscus flavomaculatus Curtis 1826:99 (Type area - not known to me. Type not seen.). -Zimmermann 1920:246.

Dytiscus flavoscutellatus Latreille 1806:331. (Type area - not known to me. Type not seen.). -Zimmermann 1920:246.

Dytiscus excrucians Stephens 1828:503 (Type area - not known to me. Type not seen.). -Zimmermann 1920:246.

Dytiscus dubius Serville 1830:90 *nec* Gyllenhal 1827:373 (Type area - near Paris, France. Type not seen.). -Zimmermann 1920:246.

Dytiscus circumflexus var. *dubius* Serville. -Zimmermann 1920:246. -Müller 1926:299. -Guignot 1932:722. -Houlbert 1934:135. -Guignot 1947a:245. -F. Balfour-Browne 1950:273. -F. Balfour-Browne 1953:27. -Zaitsev 1953:351. Guignot 1961:860. -Schaeflein 1971:88. -Franciscolo 1979:669.

Dytiscus perplexus Boisduval et Lacordaire 1835:302 (Type area - near Paris, France. Type not seen.). -Zimmermann 1920:246.

Dytiscus pisanus var. *kunstleri* Peytoreau 1894:xlii (Type area - not specifically stated, but probably near Bordeaux, France. Type not seen.). -Zimmermann 1920:246.

Derivation of specific epithet.— From Latin *circum* meaning "around" and *flexus*, meaning a "bending or turning". The significance of this epithet is unclear to me (perhaps a reference to the frontal chevron).

Notes about type material. — I have not seen the types of any of the various names applied to this species. Therefore, assignment of the names follows traditional usage (*e.g.* Zimmermann 1920). Explanation of Peytoreau's var. *kunstleri* is required. Most Palearctic workers such as Zimmermann have treated this name as if it were assigned species level status. This may be because these authors had not seen the original description published in a little known journal that is difficult to obtain. After reading the original description, I was unsure whether Peytoreau had described a specimen of *D. pisanus* or *D. circumflexus*.. Reference to Peytoreau's figure of metacoxal processes definitely indicates the latter, as the processes are much too aciculate for members of the former.

Diagnostic combination.— All but four of the specimens examined have maculate abdominal sterna. This, in combination with acuminate metacoxal processes and principally European and North African distribution, should allow easy separation of most specimens. For specimens difficult to identify using external features, reference to features of the median lobe of males is essential, and females are best determined by association with males from the same region.

Description.— Measurements of largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 5D; coloration of pterothoracic and abdominal sterna in Fig. 13A; median lobe of male in Fig. 20A; and metacoxal processes in Fig. 22K.

Taxonomic notes.— This species is the most varied in body shape, yet the form of the apex of the median lobe is quite constant. Far eastern Palearctic records of this species probably result from confusion with *D. sinensis*, which is quite similar in markings of the venter.

The species *D. circumflexus*, *D. thianshanicus*, *D. latro* and *D. sinensis* comprise a monophyletic group of some complexity. As presently interpreted, they form a geographical replacement series extending through the Palearctic Region, basically from west to east, the taxa in the sequence indicated above. Of these four species, *D. circumflexus* (except as noted under variation) and *D. sinensis* are similar in ventral colour pattern (*i.e.*, pterothoracic and abdominal sterna fasciate), while specimens of *D. thianshanicus* and *D. latro* have most of the venter yellow. The best characters for their separation are details of the form of the median lobe of males. Scanning electron micrographs of the apical portions of the median lobe of male specimens are presented in Figs. 20A-*D*. Taxonomically important character states of the median lobe for each species are as follows: 1, shape of posterior portion of knob in ventral view - notched (*D. circumflexus*), triangularly extended posteriorly and fading into the ventral ridge (*D. thianshanicus* and *D. sinensis*), or evenly truncate (*D. latro*); 2, width of apical knob relative to that of preapical portion - knob much narrower than preapical portion (*D. circumflexus* and *D. thianshanicus*), and knob somewhat narrower than preapical portion (*D. latro* and *D. sinensis*); 3, prominence of apical knob in lateral view - not very prominent (*D. circumflexus*, *D. thianshanicus* and *D. latro*), and very prominent or spatulate (*D. sinensis*); 4, widening of ventral ridge in ventral view - abruptly (*D. circumflexus*) or evenly tapered (*D. thianshanicus*, *D. latro* and (*D. sinensis*); 5, in lateral view, the relative width of dorsal and ventral portions of median lobe just anterior to its greatest width (using lateral ridge as a dividing line) - dorsal portion much narrower than ventral portion (*D. circumflexus* and *D. thianshanicus*), dorsal and ventral portions approximately equal (*D. latro*), and dorsal much wider than ventral portion (*D. sinensis*).

Variation.— Specimens of this species exhibit a great deal of variation in body shape or habitus. This may be part of the reason for proposal of many of the names listed above. For instance, most male specimens have pronota wider than elytra and most females have pronota equal or subequal to elytra at the base. However, some males have pronota only as wide as that of most females, and some females have very narrow pronota so that the pronotal-elytral juncture appears emarginate. Such differences in pronotal shape drastically alter overall appearance of specimens. These characters are consistent within many local populations, but population samples from surrounding areas may show opposite extremes.

Most specimens have the venter marked with black (Fig. 13A left). However a few specimens have a completely yellow venter (*e.g.* from Sweden (Skåne), Czeckoslovakia (Moravia), Hungary (Kolocsa), and Iran). There is little geographic correlation to this pattern except that the atypical specimens occur along the eastern edge of the range, although specimens with a typical pattern are found at the western-most locality in Afghanistan.

In Europe, excluding Great Britain, most female specimens are not sulcate. Scattered records of sulcate females are available for Sweden, France, Holland, Germany, Prussia or Poland, Corsica and Crete, as well as the Ahaggar Mountains of Algeria. In Great Britain, F. Balfour-Browne (1950:274) states that sulcate females predominate. Thus the trend is for more northern samples to be sulcate, whereas more southern samples are predominantly non-sulcate, and the most southern (but montane) samples are also sulcate.

Natural history.— A summary of the natural history of this species is presented by F. Balfour-Browne (1950:272-277), Alfes and Bilke (1977:104), and Aguesse and Bigot (1959). On the Iberian Peninsula, Régil and Salgado (1984:136) record it from altitudes ranging from 750 to 1250 m with most records of capture distributed from March to November with the latter predominant.

Distribution (Fig. 48).— All specimens of *D. circumflexus* that I have seen are from Europe, northern Africa and Asia Minor. Extralimital to Fig. 48 are records from various localities in the Ahaggar Mountains of southern Algeria. More eastern records (*e.g.* Siberia, by Zaitsev 1953:329) probably refer to *D. latro* and records for Kazakhstan (*e.g.* Konev 1976) need to be re-examined in light of the previously inadequately understood *D. thianshanicus*. Records of *D.*

circumflexus for the Canary Islands (F. Balfour-Browne 1950:276) need to be confirmed.

Chorological relationships.— Until the eastward extension of the range of *D. circumflexus* is better defined, it is difficult to list the taxa with which this species is sympatric. Within Europe, it is sympatric with *D. semisulcatus*, *D. mutinensis*, *D. dimidiatus*, *D. pisanus*, *D. marginalis*, *D. latissimus*, *D. circumcinctus* and *D. lapponicus*. It may be sympatric with *D. persicus* in Iran, but more records are needed to establish this with certainty.

Phylogenetic relationships.— *D. circumflexus* (if its distribution pattern is confirmed as suggested above), *D. thianshanicus* (south-central U.S.S.R., Afghanistan and Kashmir). *D. latro* (Siberia) and *D. sinensis* (northern China) seem to form a stepwise pattern suggesting vicariance and/or ecological replacement. This is supported by phylogenetic analysis (Fig. 52). These four taxa are united by common possession of a well-developed constriction of the apex of the median lobe just before the apical knob (Figs. 20A-D, dorsal view), and share with their sister group (*D. lapponicus*) very elongate metacoxal processes.

Material examined.— A total of 546 adult specimens of *D. circumflexus* was seen. Of these, 216 were males and 229 were females. Sex was not determined for one specimen.

Dytiscus thianshanicus Gschwendtner, 1923
Figs. 5E, 13B, 20B, 22L, 49, and 52

. *Dytiscus thianshanicus* Gschwendtner 1923:107 (Type locality - "Aksu-Tal am Südabhang des Thian-schan" = Jachsu River Valley, Kuljab district of Tadzik S.S.R. Holotype male in OLML labelled as follows: Prov.Kuliab, Ak-sou-Thal; Type, Gschw.; Coll., Gschwendtner; Macrodytes, thianshanicus, Gschw.). -Zimmermann and Gschwendtner 1938:53. -Zaitsev 1953:352.

Dytiscus latro; Brancucci 1981:184, *nec* Sharp 1882:644.

Notes about type material.— The genitalia of the holotype are dissected and mounted on a card beneath the specimen as are the last two visible abdominal sterna. Study of the holotype of this species has altered my concept of it. Previously, all specimens assigned to this name by me were predominantly yellow on the ventral surface. The colour of the ventral surface of the holotype is illustrated in Fig. 13B and it is broadly marked with infuscate areas.

Derivation of specific epithet.— Derived from the name of the mountain range in which the type locality is located.

Diagnostic combination.— A combination of south-central Palearctic distribution, spinose metacoxal processes, lack of narrow yellow ring around eye, and distinctive form of apex of median lobe of males distinguish members of this species.

Description.— Measurements of largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 5E; coloration of pterothoracic and abdominal sterna in Fig. 13B; median lobe of male in Fig. 20B; and metacoxal processes in Fig. 22L.

Taxonomic notes.— This species is still inadequately known. Members of *D. thianshanicus* are difficult to separate from those of *D. latro* except on the basis of form of the apex of the median lobe and distribution. The latter feature is of doubtful value, for ranges of both taxa are inadequately known. See also taxonomic notes under *D. circumflexus.* I have re-examined the specimens determined as *D. latro* by Brancucci (1981) and assign them to *D. thianshanicus.*

Variation.— Too few specimens were seen to establish whether or not there are geographic patterns of variation. No sulcate females were seen but this may be due to the small number of specimens studied. Similarly as noted above in the discussion of type material, the colour of the ventral surface appears to be highly varied in this species, if indeed, all specimens belong to a single taxon.

Natural history.— I can find nothing published about natural history of this species, nor does the scanty label data supply any information.

Distribution (Fig. 49).— I have seen specimens only from south-central U.S.S.R. and from Afghanistan and Kashmir; however the locality from Kashmir (Tangmarg Pir Panjal Gebirge, 2400 m, 21-25.v.76) is extralimital to Fig. 49.

Chorological relationships.— This species is known to be sympatric (but see above) with *D. marginalis marginalis*, *D. circumcinctus* and *D. latissimus.* It may also be sympatric with *D. semisulcatus*, *D. persicus* and *D. dauricus.*

Phylogenetic relationships.— See similar section in treatment of *D. latro* and Fig. 52.

Material examined.— A total of 11 specimens of *D. thianshanicus* was examined and of these 7 were males and 4 were females.

Dytiscus latro Sharp, 1882
Figs. 6A, 13C, 20C, 22M, 50, and 52

Dytiscus latro Sharp 1882:644 (Type locality - "Mantchuria". Holotype non-sulcate female in BMNH labelled as follows: Type [circular orange-rimmed label]: Mantchuria; Sharp Coll. 1905-313 [label inverted]; *Dytiscus latro*, Sharp type; Mantchuria Mus. Castelnau 948; HOLOTYPE, *Dytiscus latro* Sharp, examined R.E. Roughley 1981.). -Zimmermann 1920:249. -Zimmermann and Gschwendtner 1938:53. -J. Balfour-Browne 1946:453. -Zaitsev 1953:353.

Dytiscus piceatus Sharp 1882:644 (Type locality - "Eastern Siberia; (Irkutsk)". NEW SYNONYMY. Holotype male in BMNH labelled as follows: Type [circular orange-rimmed label]; Irkutsk, Siberia; Sharp Coll. 1905-313 [label inverted]; Dytiscus piceatus, Sharp type; Irkutsk, Siberia, 949; HOLOTYPE, Dytiscus piceatus Sharp, examined R.E. Roughley 1981). -Zimmermann 1920:253. -Zimmermann and Gschwendtner 1938:52.

Dytiscus stadleri Gschwendtner 1922:93 (Type locality -"Berisovka, Transbaikalien". Holotype male in ZSBS labelled as follows: "Type; [illegible handwriting, perhaps = Berisovka]; HOLOTYPE, Dytiscus stadleri Gschwendtner). -Zimmermann and Gschwendtner 1938:53. -J. Balfour-Browne 1946:453.

Derivation of specific epithet.— Latin *latro* means hireling, robber or brigand. The significance is not known.

Diagnostic combination.— A combination of eastern Palearctic distribution, predominantly yellow venter, spinose metacoxal processes, lack of narrow yellow ring around eye and distinctive form of apex of median lobe of males should adequately distinguish members of this species.

Description.— Measurements of largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 6A; coloration of paterothoracic and abdominal sterna in Fig. 13C; median lobe of male in Fig. 20C; and metacoxal processes in Fig. 22M.

Taxonomic notes.— The taxonomic problems associated with *D. latro* are a result of inadequate description (and therefore limited dissemination of Sharp's concept), association of sexes, and too few available specimens. The last feature remains the most critical. Sharp may have suspected that *D. latro* and *D. piceatus* were representative of the same taxon, but does not clearly state this. Gschwendtner would have had difficulty assigning his specimen to *D. latro* based on the original description, and therefore described *D. stadleri*. Either he or Zimmermann noticed the error and provided the synonymy, although this is not clearly indicated in their publication, nor are their reasons for synonomizing them.

Sharp discussed both *D. latro* and *D. piceatus* on the same page of his monograh but *D. latro* occurs first, and is thus the valid name for this taxon.

Based primarily on the form of the median lobe of the male, this species appears distinct. Assignment of females is more difficult because of their similarity to females of *D. thianshanicus*. The most reliable means I have found is association with males and distributional differences. More specimens need to be examined before the present arrangement is treated as more than provisional.

Variation.— Too few specimens were seen to establish whether or not there are geographic patterns of variation. No sulcate females were seen, but this may be due to the small number of specimens seen.

Natural history.— I can find nothing published about the natural history of this species, nor does the scanty label data supply any information.

Chorological relationships.— The entire range of this exclusively east Palearctic species is known insufficiently. However, it is known or inferred to be sympatric with *D. sharpi*, *D. marginalis czerskii*, *D. delictus*, *D. circumcinctus*, *D. lapponicus lapponicus* and *D. latissimus*. Establishment of the western limits of *D. latro* and the eastern limits of *D. thianshanicus* would be helpful in determining the taxonomic status of these two taxa.

Phylogenetic relationships.— The sinuate lateral margins and well developed sensory pores on the knob of the median lobe of males, and spinose metacoxal processes indicate close relationship to *D. lapponicus*, *D. circumflexus*, *D. thianshanicus*, and *D. sinensis*. In Fig. 52, I have interpreted *D. latro* as the eastern vicar of the central Palearctic *D. thianshanicus*.

Distribution (Fig. 50).— This taxon occurs in the eastern U.S.S.R. (described loosely as Siberia) and adjacent Manchuria.

Material examined.— A total of 17 specimens was examined, of which four are males and 13 females.

Dytiscus sinensis Feng, 1935
Figs. 6B, 13D, 20D, 22N, 51, and 52

Dytiscus sinensis Feng 1935:182 (Type locality - Yin-Kuan-Tsai, Szechuen, China. Holotype male in USNM labelled as follows: Szechuen, CHINA, DC Graham; Yin-Kuan-Tsai, 12300 ft, vii.21.30; Dytiscus sinensis (Type) H.T. Feng). -Feng 1937:14. -Zimmermann and Gschwendtner 1939:27.

Derivation of specific epithet.— The specific epithet means Chinese.

Diagnostic combination.— A combination of eastern Palearctic distribution, fasciate abdominal sterna, spinose metacoxal processes, and spatulate form of apex of median lobe of males (in side view) distinguish adequately members of this species.

Description.— Measurements of largest and smallest specimens are given in Table 2. States of taxonomically important characters are given in Table 3. Dorsal view of body is shown in Fig. 6B; coloration of pterothoracic and abdominal sterna in Fig. 13D; median lobe of male in Fig. 20D; and metacoxal processes in Fig. 22N.

Taxonomic notes.— This species appears to be quite distinctive despite the few specimens seen by both Feng and me.

Variation.— Too few specimens were seen to establish whether or not there are geographic patterns of variation. No sulcate females were seen but this may be due to the small number of specimens seen.

Natural history.— I can find nothing plublished on the natural history of this species, nor does the scanty label data supply any information.

Distribution (Fig. 51).— I have seen specimens from the type locality only. Feng (1937) adds Shensi (=Shanxi Province, China) and Manchuria.

Chorological relationships.— Generalizing from the distribution, this species may be sympatric with *D. marginalis czerskii*, *D. delictus*, *D. circumcinctus*, *D. lapponicus*, *D. latro* and possibly *D. latissimus*. The altitude given for the type specimen may indicate an affinity for high altitude habitats, reducing co-occurrence with other species.

Phylogenetic relationships.— The species of the *D. dauricus*-group comprise two subgroups. *Dytiscus sinensis* is in the more apotypic of these groups (characterized by the character states discussed under *D. latro*), and within this subgroup shows the highest number of apotypic features.

Material examined.— A total of 10 specimens of *D. sinensis* was examined, all from the type locality. Three are males and seven are females.

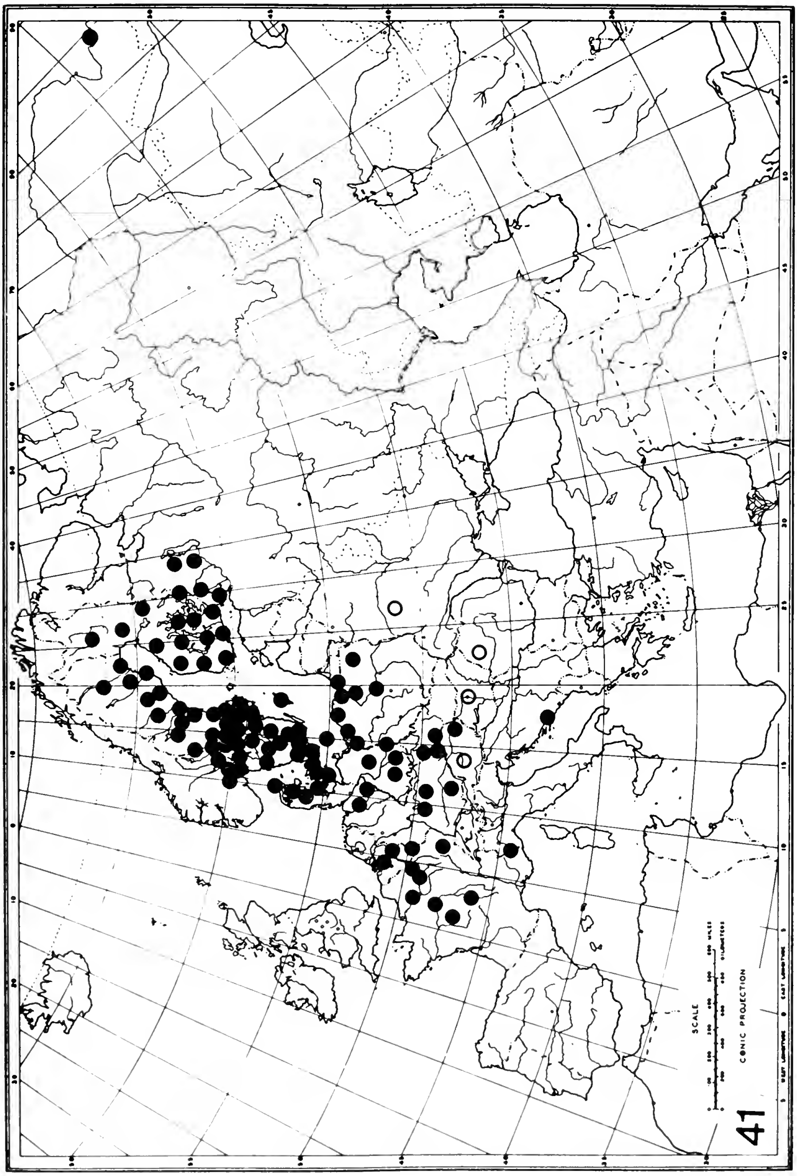


Fig. 41. Known distribution of *Dytiscus latissimus* Linnaeus.

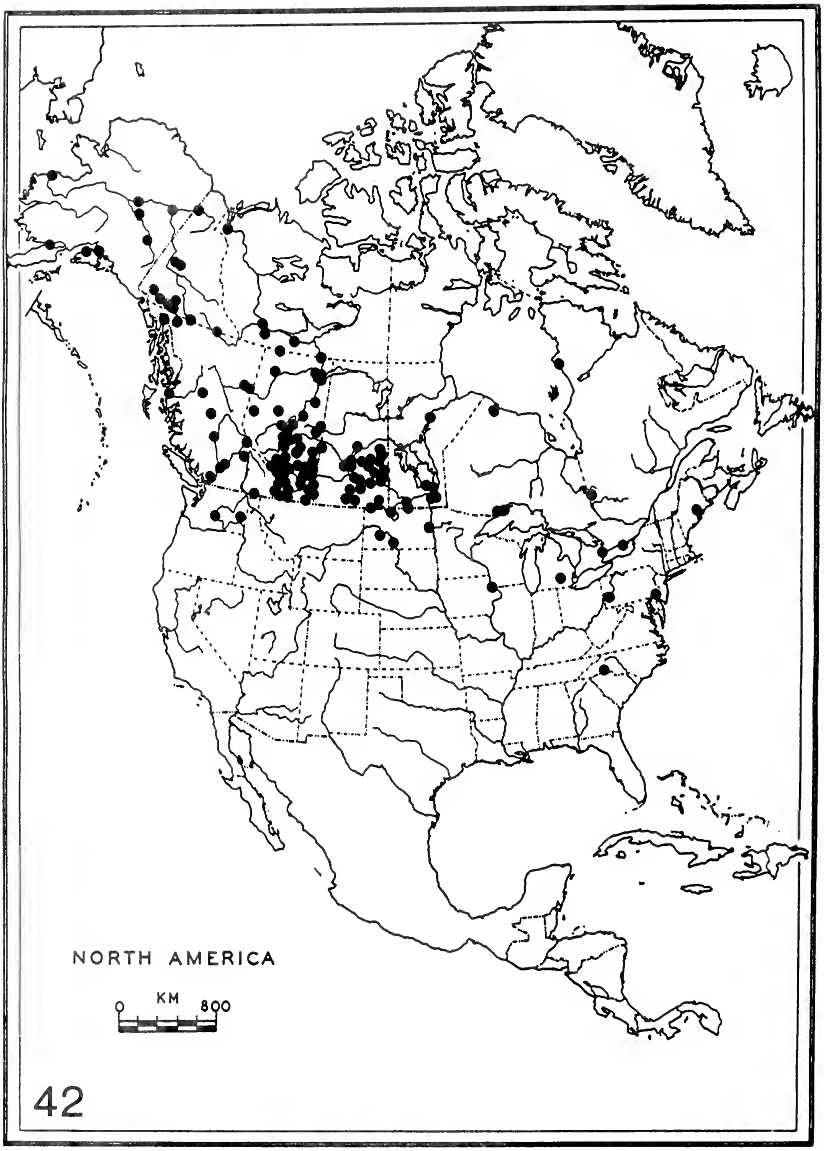
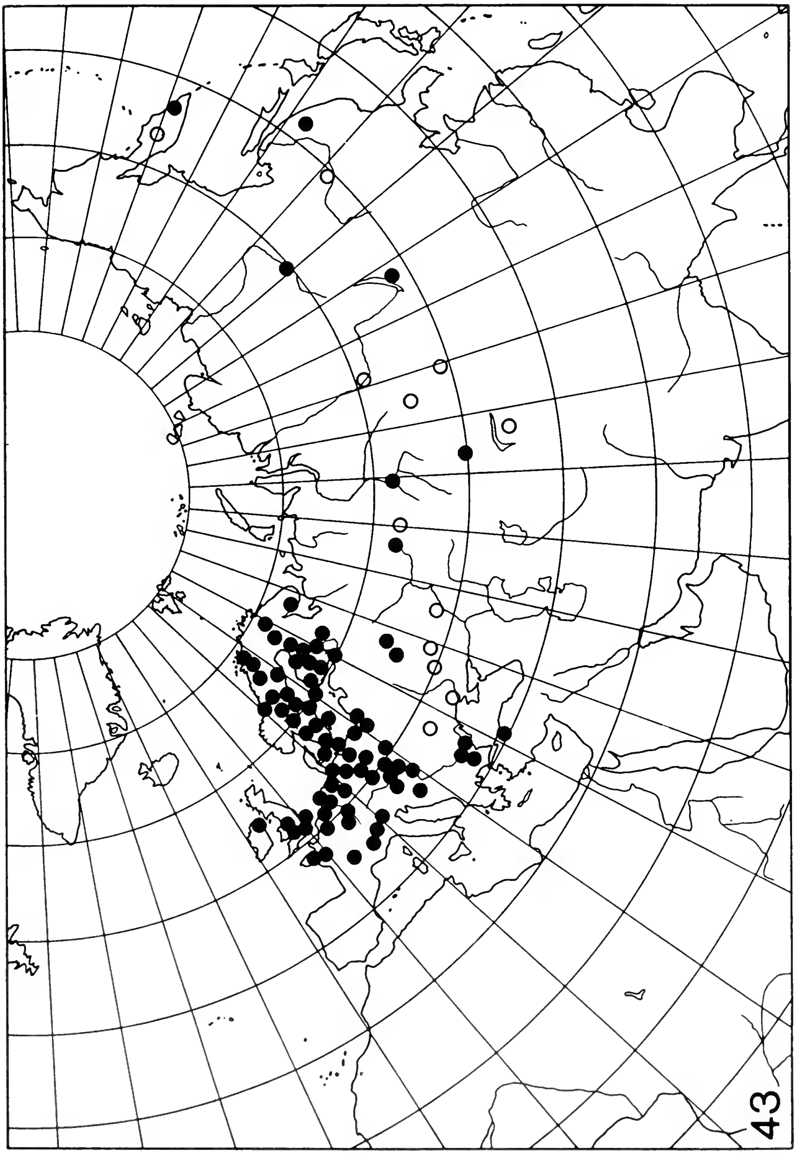


Fig. 42. Known distribution of *Dytiscus circumcinctus* Ahrens in the Nearctic region.



43

Fig. 43. Known distribution of *Dytiscus circumcinctus* Ahrens in the Palearctic region.

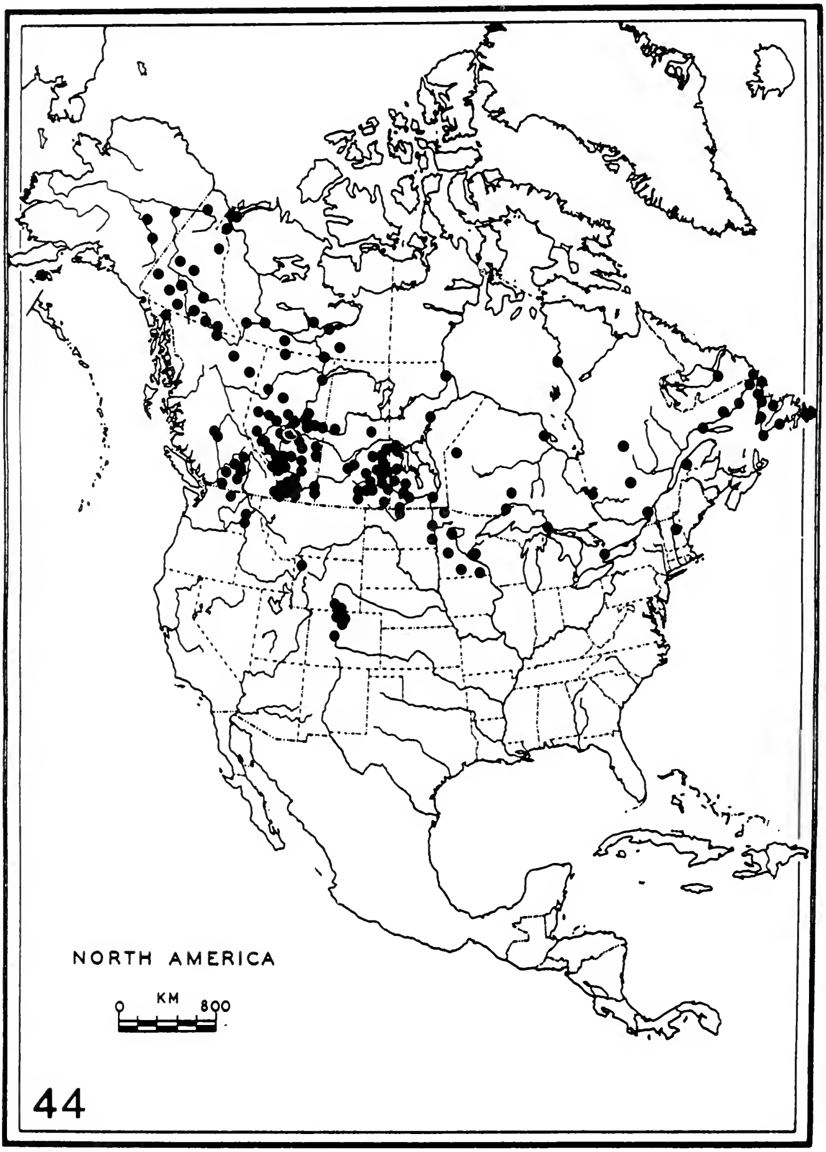


Fig. 44. Known distribution of *Dytiscus alaskanus* Balfour-Browne.

Fig. 45. Known distribution of *Dytiscus dauricus* Gebler in the Nearctic region.

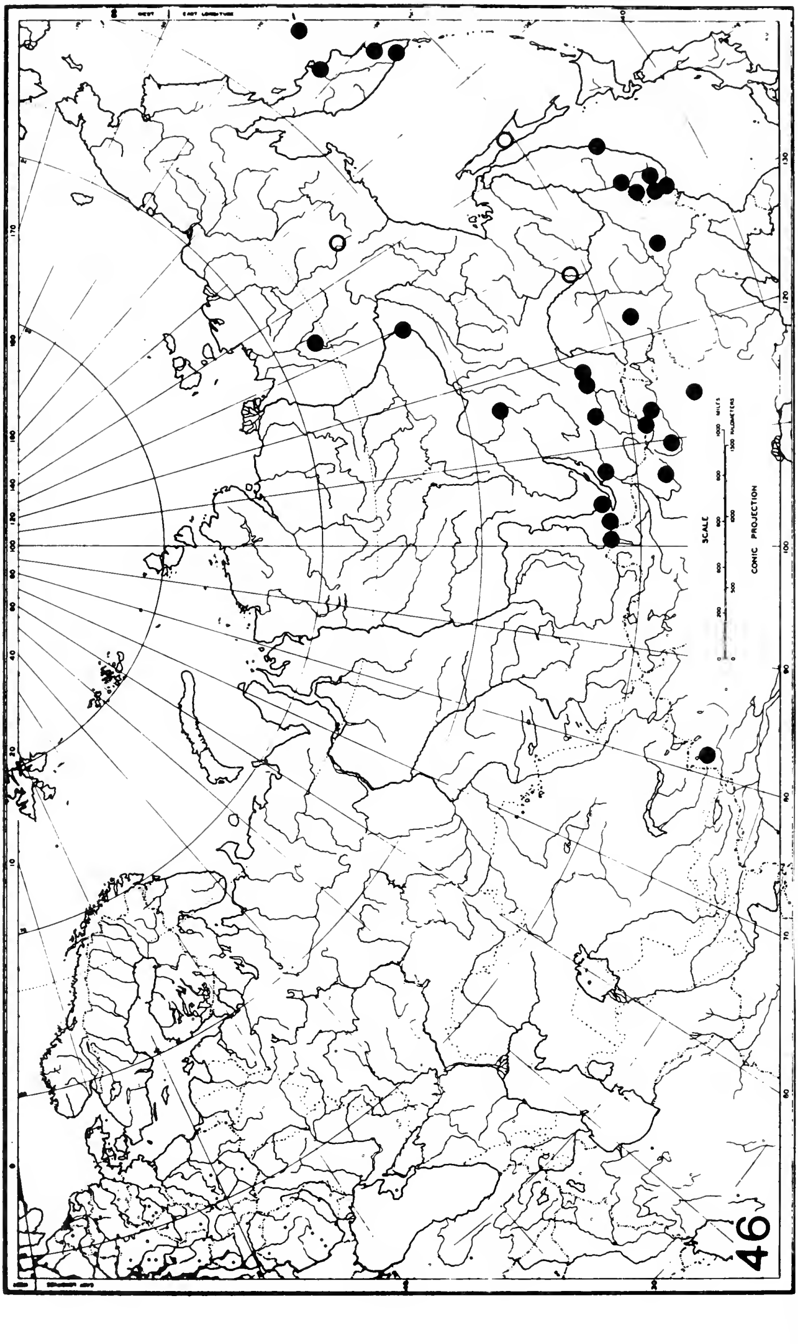


Fig. 46. Known distribution of *Dytiscus dauricus* Gebler in the Palearctic region.

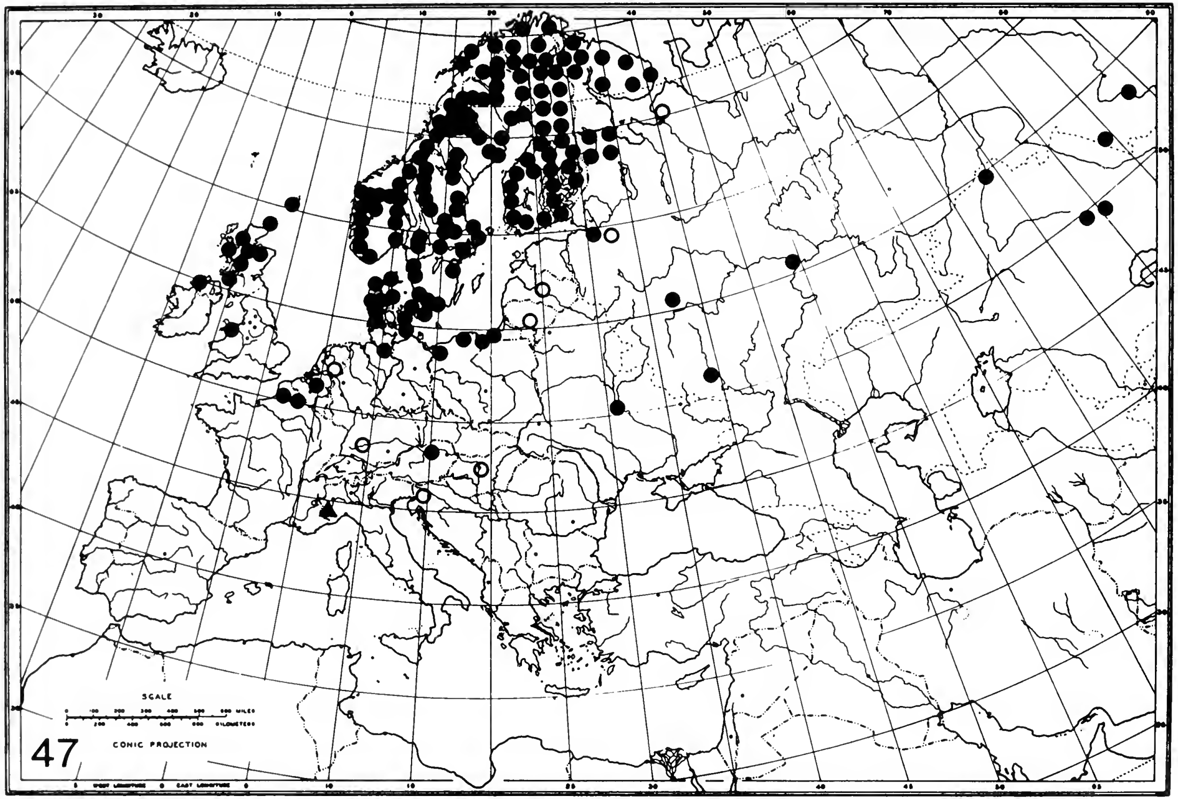


Fig. 47. Known distribution of *Dytiscus lapponicus lapponicus* Gyllenhal (circles) and *D. lapponicus disjunctus* Camerano (triangle).

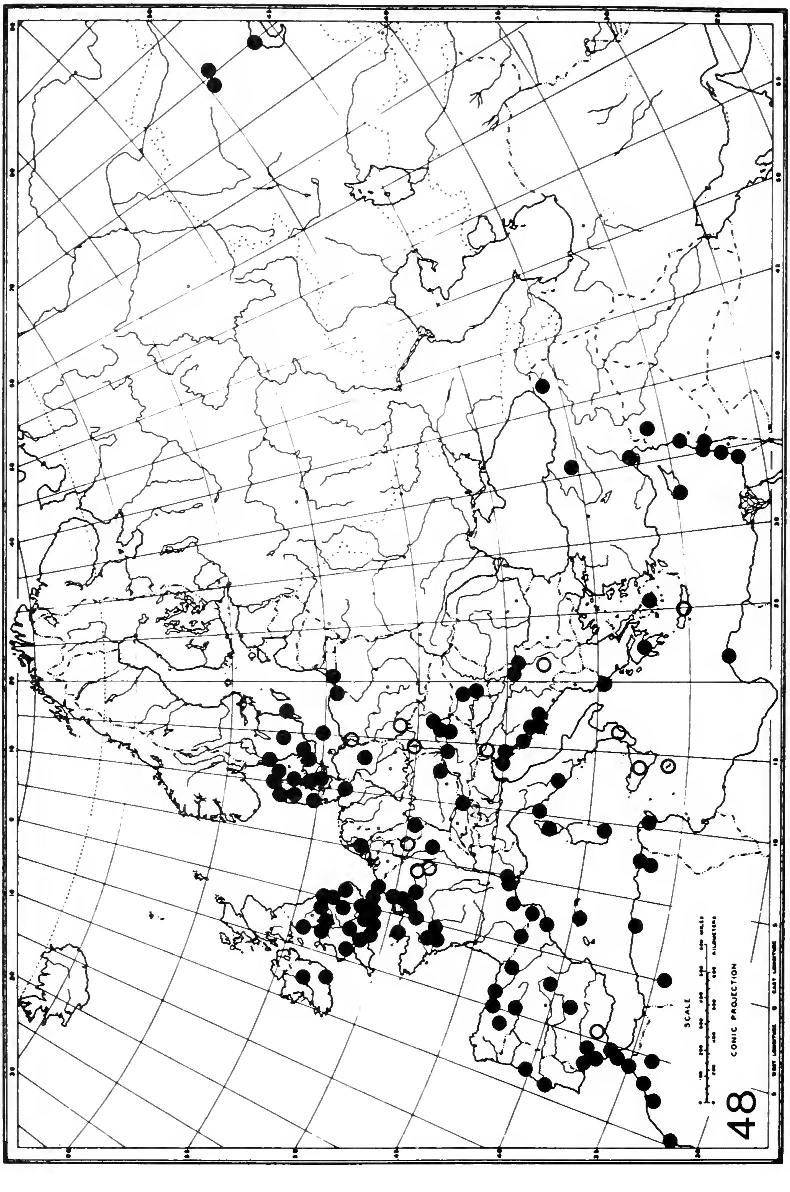


Fig. 48. Known distribution of *Dytiscus circumflexus* Fabricius.

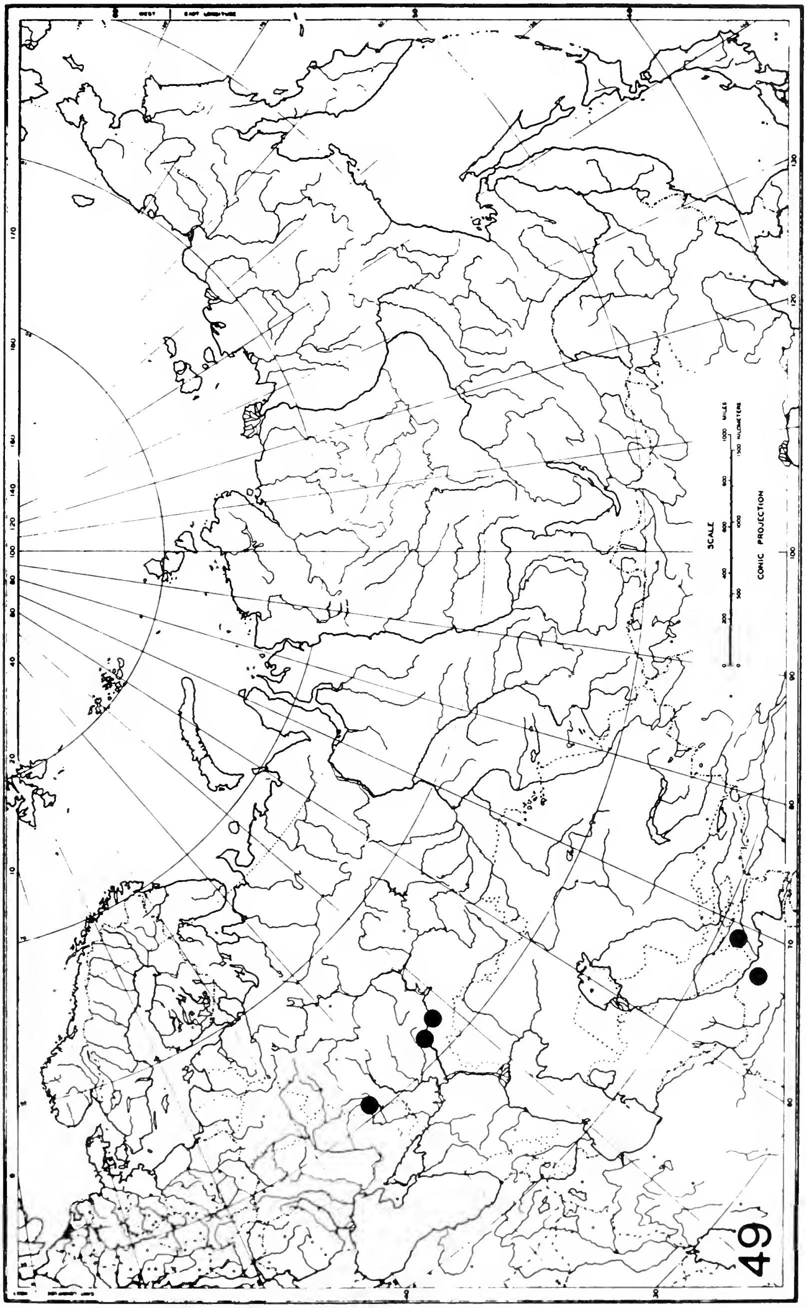


Fig. 49. Known distribution of *Dytiscus thianshanicus* Gschwendtner.

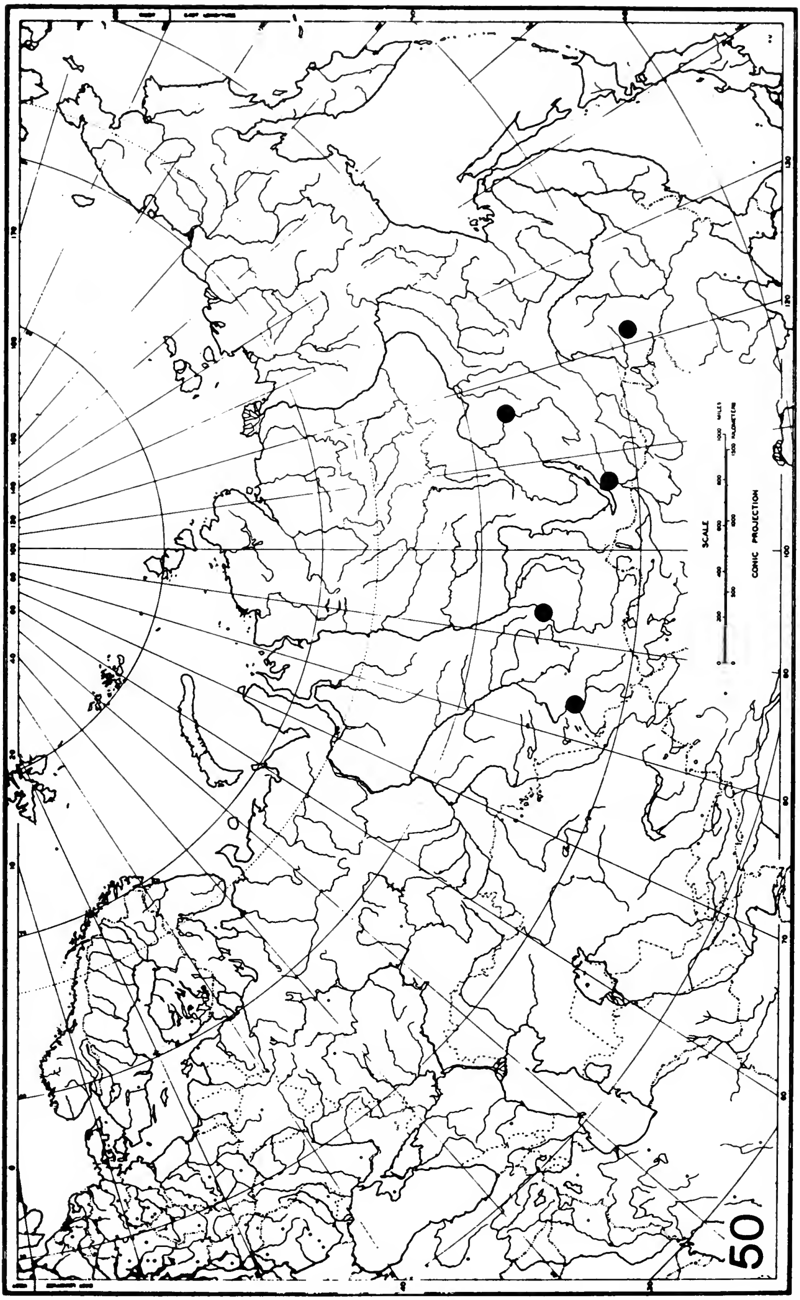


Fig. 50. Known distribution of *Dytiscus latro* Sharp.

51

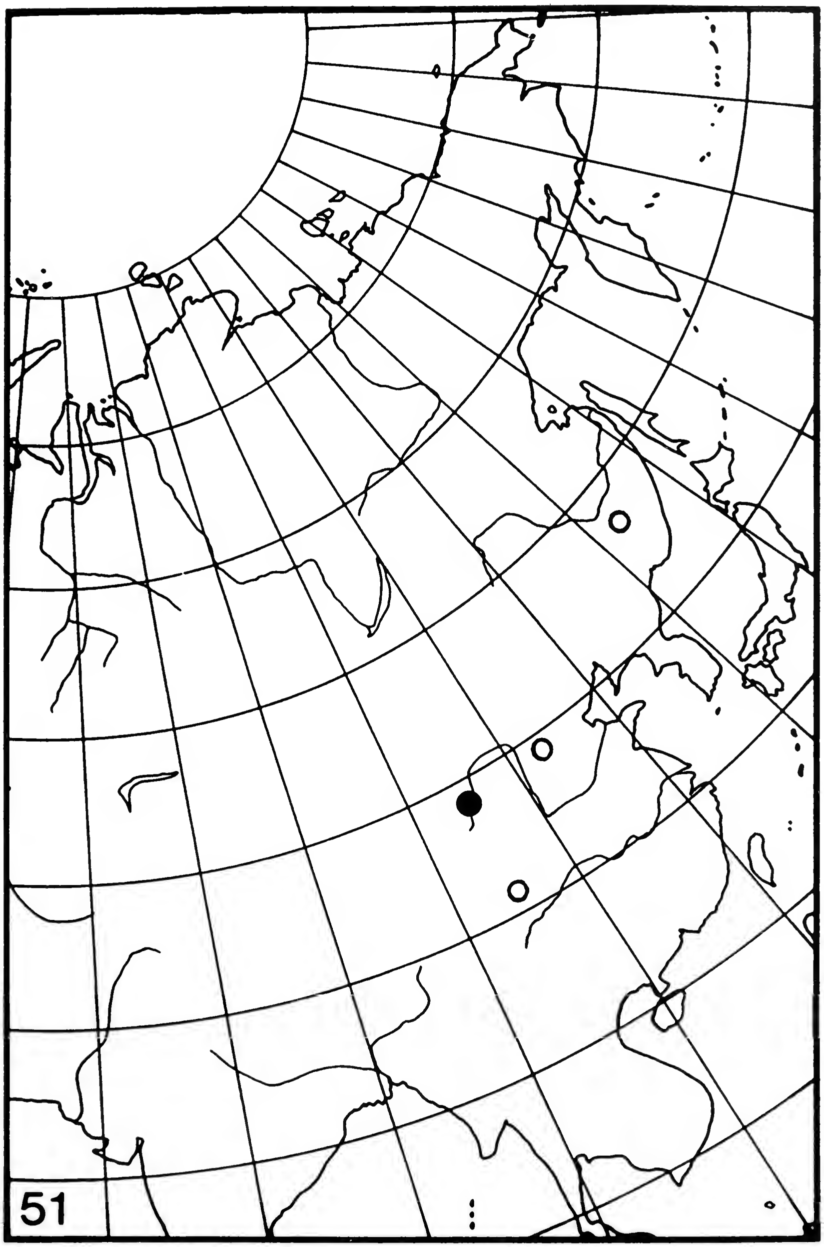


Fig. 51. Known distribution of *Dytiscus sinensis* Feng.

Incertae Sedis

One other name is available within *Dytiscus* but for which I am unable to determine a status nor can I assign specimens to this name. Therefore I have left it as *incertae sedis*. A brief statement about this name follows.

Dytiscus distantus Feng 1937:14 (Type locality - Manchuria. Type repository listed by Feng (1937:1, 15) as Musée Hoang Ho Pai Ho). Additional locality - Mongolia (T'ang Kia Yingze), June 13, 1927, a male paratype stated as being in the H.T. Feng collection.

Table 2. Range of measurements (mm) of total length (TL), greatest width (GW), and ratio of total length - greatest width (TL/GW) for specimens of each taxon within *Dytiscus* L. (Coleoptera: Dytiscidae).TL/GW not necessarily calculated from TL and GW presented here.

	Total Length	Greatest Width	TL/GW
D. verticalis	29.6 - 36.0	16.5 - 19.4	1.79 - 1.86
D. harrisii	32.4 - 39.0	16.4 - 21.9	1.78 - 1.98
D. hybridus	24.2 - 28.1	12.0 - 14.0	1.90 - 2.02
D. marginicollis	26.7 - 33.0	13.4 - 18.7	1.76 - 2.10
D. habilis	23.0 - 27.5	12.2 - 14.1	1.89 - 1.95
D. semisulcatus	22.8 - 31.6	11.6 - 15.7	1.97 - 2.01
D. sharpi	27.3 - 31.0	14.8 - 16.0	1.84 - 1.94
D. carolinus	22.0 - 26.1	11.8 - 14.0	1.85 - 1.92
D. fasciventris	22.0 - 27.9	11.5 - 15.0	1.80 - 2.10
D. hatchi	22.1 - 28.5	11.7 - 15.6	1.83 - 1.95
D. cordieri	26.3 - 32.5	13.6 - 18.1	1.77 - 2.10
D. mutinensis	28.0 - 31.7	14.0 - 16.0	1.98 - 2.00
D. dimidiatus	29.3 - 39.0	15.9 - 20.0	1.84 - 1.95
D. pisanus	28.0 - 33.9	14.6 - 18.0	1.88 - 1.92
D. m. marginalis	27.6 - 35.2	15.0 - 17.6	1.84 - 2.05
D. m. czerskii	28.7 - 32.6	15.7 - 17.4	1.83 - 1.88
D. persicus	29.3 - 32.4	15.3 - 16.0	1.92 - 2.03
D. delictus	27.5 - 30.6	14.7 - 16.5	1.85 - 1.87
D. latissimus	38.6 - 44.0	23.8 - 28.0	1.55 - 1.62
D. circumcinctus[1]	27.5 - 34.0	13.0 - 17.1	1.80 - 2.10
D. circumcinctus[2]	29.2 - 36.2	14.4 - 17.8	1.95 - 2.09
D. alaskanus	22.6 - 30.2	11.5 - 15.4	1.80 - 2.01
D. dauricus[1]	29.7 - 40.0	15.0 - 20.1	1.86 - 2.03
D. dauricus[2]	27.8 - 33.3	13.9 - 16.6	1.90 - 2.01
D. l. lapponicus	24.1 - 30.0	12.7 - 15.3	1.90 - 1.96
D. l. disjunctus	25.0 - 28.0	13.0 - 14.0	1.92 - 2.00
D. circumflexus	27.0 - 33.1	14.3 - 16.0	1.89 - 2.07
D. thianshanicus	29.3 - 30.5	14.5 - 15.7	1.94 - 2.02
D. latro	29.4 - 31.1	14.8 - 16.1	1.94 - 1.99
D. sinensis	26.5 - 31.0	13.6 - 16.0	1.94 - 1.95

[1] Nearctic specimens.

[2] Palearctic specimens.

Table 3. Character state matrix for taxa included within the genus *Dytiscus* L. (Coleoptera: Dytiscidae).Taxa are scored based on the most common state exhibited by specimens examined.Symbols: m = restricted to males; f = restricted to females; - = character absent from taxon; 1 = character state present; 0 = character state absent.Species names are abbreviated as follows: VERT=*D. verticalis;* HARR=*D. harrisii;* HYBR=*D. hybridus;* MARG=*D. marginicollis;* HABI=*D. habilis;* SEMI=*D. semisulcatus;* SHAR=*D. sharpi;* CARO=*D. carolinus;* FASC=*D. fasciventris;* HATC=*D. hatchi*, CORD=*D. cordieri;* MUTI=*D. mutinensis;* DIMI=*D. dimidiatus;* PISA=*D. pisanus;* MMAR=*D. marginalis marginalis;* MCZE=*D. marginalis czerskii;* PERS=*D. persicus;* DELI=*D. delictus;* LATI=*D. latissimus;* CICI=*D. circumcinctus;* ALAS=*D. alaskanus;* DAUR=*D. dauricus;* LLAP=*D. lapponicus lapponicus;* LDIS=*D. lapponicus disjunctus;* CIFL=*D. circumflexus;* THIAN=*D. thianshanicus;* LATR=*D. latro; and* SINE=*D. sinensis.*

Abbreviations of species epithets	VERT	HARR	HYBR	MARG	HABI	SEMI	SHAR	CARO	FASC	HATC	CORD	MUTI	DIMI	PISA	MMAR	MCZE	PERS	DELI	LATI	CICI	ALAS	DAUR	LLAP	LDIS	CIFL	THIA	LATR	SINE
Character state and descriptions																												
1 Clypeus																												
1.1 Suture																												
1.1.1 linear/curved	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
1.1.2 bisinuate	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
2 Frons																												
2.1 Chevron, extension																												
2.1.1 no	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1	0	1	1	0	0	1	1	1	1	0	1
2.1.2 yes	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	1	0
3 Pronotum																												
3.1 Explanate																												
3.1.1 yes	1	0	0	0	0	1	1	1	1	1	f	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
3.1.2 no	0	1	1	1	1	0	0	0	0	0	m	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

(continued on next page)

Table 3 (continued)

Abbreviations of species epithets	VERT	HARR	HYBR	MARG	HABI	SEMI	SHAR	CARO	FASC	HATC	CORD	MUTI	DIMI	PISA	MMAR	MCZE	PERS	DELI	LATI	CICI	ALAS	DAUR	LLAP	LDIS	CIFL	THIA	LATR	SINE
3.2 Anterior yellow band																												
3.2.1 absent	1	0	1	0	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3.2.2 present	0	1	0	1	1	0	0	0	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
3.3. Posterior yellow band																												
3.3.1 absent	1	0	1	0	0	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3.3.2 present	0	1	0	1	1	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
4 Ventral features																												
4.1 Metepisternum, colour																												
4.1.1 black	1	1	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.1.2 black/yellow	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
4.1.3 yellow	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	1
4.2 Metasternum, colour																												
4.2.1 black	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.2.2 black/yellow	0	1	0	1	1	0	0	0	1	1	0	1	1	1	0	1	1	1	0	0	1	1	0	0	1	0	0	1
4.2.3 yellow	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	1	0	1	1	0	1	1	0
4.3 Metacoxa, colour																												
4.3.1 black	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.3.2 black/yellow	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1	1	0	0	0	1	0	0	1	0	0	0
4.3.3 black/red	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.3.4 yellow	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	1	1	1	0	1	1	0	1	1	1

(continued on next page)

Table 3 (continued)

Abbreviations of species epithets	VERT	HARR	HYBR	MARG	HABI	SEMI	SHAR	CARO	FASC	HATC	CORD	MUTI	DIMI	PISA	MMAR	MCZE	PERS	DELI	LATI	CICI	ALAS	DAUR	LLAP	LDIS	CFIL	THIA	LATR	SINE
4.4 Abdominal sternum I, colour																												
4.4.1 infuscate	1	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.4.2 yellow	0	1	0	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
4.5 Abdominal sternum II–VI, colour																												
4.5.1 black	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.5.2 black/red	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.5.3 black/yellow	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	1	1	0	0	1	1	1	1	1	0	0	1
4.5.4 yellow	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	1	1	1	0	0	0	1	1	1	0
4.6 Metacoxal apex, shape																												
4.6.1 rounded	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.6.2 acute	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
4.6.3 acuminate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0
4.6.4 elongate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
4.7 Metacoxal apex, inner margin																												
4.7.1 convex	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
4.7.2 concave	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1

(continued on next page)

Table 3 (continued)

Abbreviations of species epithets	V E R T	H A R R	H Y B R	M A R G	H A B I	S E M I	S H A R	C A R O	F A S C	H A T C	C O R D	M U T I	D I M I	P I S A	M M A R	M C Z E	P E R S	D E L I	L A T I	C I C I	A L A S	D A U R	L L A P	L D I S	C I F L	T H I A	L A T R	S I N E
5 Elytra, female																												
5.1 Sulcation																												
5.1.1 absent	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1
5.1.2 present	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	0	0
6 Mesotarsus, male																												
6.1 Distribution of palettes																												
6.1.1 evenly distributed	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
6.1.2 glabrous area	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7 Median lobe of male																												
7.1 Lateral ridge, apically																												
7.1.1 present	1	1	0	0	0	0	1	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
7.1.2 absent	0	0	1	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7.2 Lateral ridge, curvature																												
7.2.1 even	1	1	-	-	-	-	0	-	1	-	-	1	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0
7.2.2 absent	0	0	-	-	-	-	1	-	0	-	-	0	0	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1
7.3 Pre-apex, laterally																												
7.3.1 linear	1	1	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7.3.2 curved	0	0	0	1	0	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1

(continued on next page)

Table 3 (continued)

Abbreviations of species epithets	VERT	HART	HYBR	MARG	HABI	SEMI	SHAR	CARO	FASC	HATC	CORD	MUTI	DIMI	PISA	MMAR	MCZE	PERS	DELI	LATI	CICI	ALAS	DAUR	LLAP	LDIS	CIFL	THIA	LATR	SINE
7.4 Pre-apex, dorsally																												
7.4.1 parallel	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
7.4.2 sinuous	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
7.5 Lateral and dorsal flanges																												
7.5.1 subequal in length	1	1	0	1	0	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
7.5.2 dorsal longer	0	0	1	0	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7.6 Tip shape																												
7.6.1 not rounded	1	1	1	1	0	1	0	1	1	1	0	0	0	0	1	1	1	1	0	1	0	1	1	1	1	1	1	1
7.6.2 narrowly rounded	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
7.6.3 broadly rounded	0	0	0	0	1	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
7.7. Tip shape																												
7.7.1 knob absent	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0
7.7.2 knob present	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0	1	1	1	1	1	1	1
7.8 Tip, well-developed pores																												
7.8.1 absent	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
7.8.2 present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1
7.9 Pre-knob, extension																												
7.9.1 absent	–	–	–	–	1	–	–	–	–	–	–	–	–	–	0	0	0	0	–	1	–	1	1	1	1	1	1	1
7.9.2 present	–	–	–	–	0	–	–	–	–	–	–	–	–	–	1	1	1	1	–	0	–	0	0	0	0	0	0	0

(continued on next page)

Table 3 (continued)

Abbreviations of species epithets	VERT	HARR	HYBR	MARG	HABI	SEMI	SHAR	CARO	FASC	HATC	CORD	MUTI	DIMI	PISA	MMAR	MCZE	PERS	DELI	LATI	CICI	ALAS	DAUR	LLAP	LDIS	CIFL	THIA	LATR	SINE
7.10 Knob, development																												
7.10.1 moderate	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	1	1	1	-	1	-	1	1	1	0	0	0	0
7.10.2 significant	-	-	-	-	0	-	-	-	-	-	-	-	-	-	0	0	0	0	-	0	-	0	0	0	1	1	1	1
7.11 Pre-apex, dorsally																												
7.11.1 wide	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0
7.11.2 thin	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1

Table 4. List of teneral specimens of selected species of *Dytiscus* Linnaeus (Coleoptera: Dytiscidae). # = Number and sex of specimens. Colln. = collection in which specimens are held.

Taxon / Locality	Date	#	Colln.
D. verticalis Say			
MI, Washtenaw Co., Ann Arbor	27.vii.30	1♀	UMMZ
NH, Coos Co., Bretton Wds.	1.ix.24	1♀	MCZC
NY, Ulster Co., Ashokan	3.viii.-	1♀	AMNH
MB, Hwy.10, 8 km N Overflowing R.	1.viii.86	1♀	JBWM
D. harrisii Kirby			
ONT, Goose Creek, nr. Severn R.	11.vi.56	2♂	ROMC
ONT, Pr. Edw. Co.	8.vii.39	1♂	UMMZ
"	19.vii.39	1♀	UMMZ
D. hybridus Aubé			
MO, Oregon Co., 12 mi. e. Alton	20.vi.40	1♂	FMNH
NY, Niagra Co., Olcott	16.vii.22	1♂	CUIC
MN, Nicollet Co., St. Peter	24.vii.22	2♂,4♀	DEFW
MI, Cheboygan Co., Douglas Lake	-.viii.17	1♂	ZSBS
D. marginicollis LeConte			
OR, Marion Co., Salem	31.v.28	1♀	USNM
OR, Lane Co., Siltcoos Outlet	7.vi.57	1♂	FMNH
BC, Vernon	12.vii.26	1♀	CNIC
CA, Amedee	21.vii.28	1♂	USNM
ALTA, Medicine Hat	25.viii.25	1♀	UMMZ
D. carolinus Aubé			
MA, Talbot Co., Wittman	11.v.73	1♂	USNM
D. fasciventris Say			
ONT, Belleville	8.vii.63	1♀	CNIC
MI, Cheboygan Co.	9.vii.19	1♂	UMMZ
NH, Cheshire Co., Jaffrey	13.vii.01	1♂	MCZC
ONT, Belleville	22.vii.63	2♂	CNIC
MI, Cheboygan Co., Douglas Lake	-.vii.23	1♂	DEFW
MI, Cheboygan Co.	-.vii.35	1♂	UMMZ
MI, Alpena Co., Bean Cr.	-.-.25	1♀	UMMZ

(continued on next page)

Table 4(continued)

Taxon / Locality	Date	#	Colln.
D. hatchi Wallis			
BC, Smithers	15.viii.51	1♂	UBCZ
"	28.viii.49	1	UBCZ
D. cordieri Aubé			
ONT. Belleville	26.vii.63	2♀	CNIC
MN, Douglas Co., Alexandria	1.viii.68	1♀	SCSU
MAN, Delta Res. Stn., L. Winnipeg	15.viii.50	1♀	UBCZ
MN, Saint Louis Co., Duluth	17.viii.42	1♂	AMNH
MAN, Winnipeg	28.viii.27	1♂	MCZC
D. circumcinctus Ahrens			
BC, Swift Creek, Mt. Robson	10.v.25	1♀	UBCZ
SASK, Pasqua	4-18.vi.73	1♀	CNIC
NWT, Fort Smith	3.viii.50	1♂	CNIC
ALTA, Waterways	12.ix.47	1♀	CUIC
D. alaskanus J. Balfour-Browne			
BC, Kamloops	23.vi.41	1♀	CASC
"	"	1♂	UBCZ
ALTA, Laggan	4.vii.94	1♀	AMNH
ONT, Port Arthur	10.vii.65	1♂	UGIC
MN, De Sota Lake	21.vii.38	1♂	DEFW
NWT, Yellowknife	3.viii.51	1♂	CNIC
NFLD, Sandbank Park	19.viii.78	1♀	MUIC
NWT, Ft. Resolution	22.viii.47	1	CUIC
"	"	1♀	CNIC
YUKON, Dawson	22.viii.49	1♂	CNIC
"	30.viii.49	1♀	CNIC
D. dauricus Gebler			
MN, Clearwater Co., Itasca St. Pk.	1.viii.72	1♂	ROMC

Table 5. List of specimens interpreted as undergoing dispersal flight, for selected species of *Dytiscus* Linnaeus (Coleoptera: Dytiscidae), with label data.(Abbreviated column headings: # = Number and sex of specimens [m = male, f=female]; Colln. = collection in which specimens are held [see Section 2.1 for definition of museum codes]).

Taxon / Locality	Date	#	Colln.	
D. verticalis Say				
MA, "East Mass".	-.iv.07	1♂	USNM	"mouse trap baited with meat"
MN, Stearns Co., St. Cloud	1.v.68	1♂	SCSU	lights
IN, Porter Co., Tremont	30.v.27	1♀	FMNH	alive in lower beach drift
MI, Washtenaw Co., Ann Arbor	27.vii.30	1♀	UMMZ	porch light
MI, Livingston Co., E.S. George Res.	26.vii.41	1♀	UMMZ	taken at light
ME, York Co., Old Orchard Beach	14.viii.39	1♂	UAIC	at country club on grass
NY, Tompkins Co., Ludlowville	29.viii.64	1♀	CUIC	at 15W uv blacklight
CT, Tolland Co., Storrs	26.ix.75	1♀	UCSE	migrating
MI, Livingston CO., E.S. George Res.	29.ix.38	1♂	UMMZ	taken at light
CT, New Haven Co., Guilford	9-10.x.73	1♀	PMNH	uv trap
CT, Litchfield Co., Litchfield	24.x.20	1♀	FMNH	house, at lights
MA, Hampshire Co., Belchertown	14.ix.50	1♂	UCRC	on tar roof
D. harrisii Kirby				
VT, Chittendon Co., S. Burlington	8.v.68	1♀	UVCC	dead on lawn
" "	-.v.68	1♂	UVCC	dead in backyard
NWT, Hay River	2.vi.64	1	UCIC	in flight
MN, Stearns Co., St. Cloud	22.vi.72	1♂	SCSU	lights
ONT., Pr. Edw. Co.	10.vii.37	1♂	CASC	at light
ONT., Chaffeys Locks	13.vii.64	1♂	ROMC	uv light

(continued on next page)

Table 5 (continued)

Taxon / Locality	Date	#	Colln.	
MI, Berrien Co., E.K. Warren Pres.	14.vii.20	1♀	UMMZ	L. Michigan beach drift
NY, Tompkins Co., Enfield St. Pk.	23.vii.39	1♂	USNM	swimming pool
MN, Stearns Co., St. Cloud	26.vii.75	1♀	SCSU	at light
" "	15.viii.75	1♂,1♀	SCSU	at light
WI, Douglas Co., Superior	-.viii.55	1♀	SCSU	shore of L. Superior
ALTA, Banff	6.x.81	1♀	UASM	in flight
D. hybridus Aubé				
IL, Champaign Co., Urbana	14.i.51	1♂	INHS	found alive, 7-7.30 PM on ground
DC, Washington	28.iii.05	1♂	USNM	electric light
NY, Tompkins Co., nr. Dryden	14.iv.67	1♂	GWSC	at uv light
IL, Cook Co., Chicago	28.iv.06	1♀	UANH	lake beach
DC, Washington	-.iv.-	1♀	USNM	electric light
SASK, Regina	18.v.80	1♂	UASM	at light
IN, Lake Co.,Pine	20.v.06	1♀	FMNH	lake beach
IL, Alexander Co., Cairo	10.vi.07	1♀	INHS	elec. light
MI, Berrien Co., St. Joseph	17.vi.06	1♀	FMNH	lake beach
IL, Mason Co., Havanna	28.vi.07	1♀	INHS	at light
NY, Tompkins Co., Ithaca	7.vii.25	1♂	CUIC	lantern trap
OH, Preble Co., W. Alexandria	7.vii.47	1♂	UVCC	in cattle tank
MI, Berrien Co., EK Warren Pres.	14.vii.20	4♂,10♀	UMMZ	L. Michigan beach drift
MI, Mason Co., Ludington	30.vii.32	1♂	FMNH	lake drift
IL, Lake Co., Beach St. Pk.	30-31.vii.75	1♂	WUBC	black light
MI, Emmet Co.	27.viii.29	1♀	UMMZ	on beach

(continued on next page)

Table 5 (continued)

Taxon / Locality	Date	#	Colln.	
SD, Brookings Co., Brookings	2.ix.43	1♀	UANH	light trap
IL, Peoria Co., Peoria	6.ix.41	1♀	INHS	at light, main streets
ONT, Port Credit	-.ix-65	1♂	ROMC	uv light
DC, Washington	21.ix.97	1♂	USNM	flying
PA, Allegheny Co., Moon Twp.	25.xii.40	1♂	ICCM	ground under light Xmas tree, pond & small stream @100 yd away
DC, Washington	12.5.05	1♂	USNM	electric light
D. marginicollis LeConte				
CA, Mendocina Co., Mendocino	3.i.55	1♀	CASC	flying
BC, Creston	9.iii.53	1	UBCZ	at light
BC, Vancouver	11.iii.39	1♀	CASC	on steps of building
BC, Merritt	15.vi.58	1♀	UBCZ	at light
Wa, Yakima Co., Toppenish	25.vi.57	1♀	OSUO	light trap
UT, Cache Co., Logan Canyon	3.vii.40	1	EMUS	at light
UT, Millard Co., Oak Creek Canyon	4.vii.37	1	CASC	at light
" "	"	1♀	EMUS	at light
WA, Yakima Co., Toppenish	10.vii.56	4,4♀	OSUO	light trap
OR, lake Co., 6 mi. ne Plush	12.vii.54	1,2♀	OSUO	dead on beach
CO, Rio Grande Co., Monte Vista	23.viii.40	1♀	DEFW	at light
BC, Salmon Arm	-.ix-35	1	CASC	flying at light in barn
ALTA, Lethbridge	1.x.29	1	CNIC	flight
CA, Contra Costa Co., Danville	8.xii.48	1	CASC	at light

(continued on next page)

Table 5 (continued)

Taxon / Locality	Date	#	Colln.	
D. habilis Say				
CHIHUAHUA, 6 mi. w. Encinillas, 5420'	16.iv.69	1♀	UCRC	uc light
AZ, COchise Co., 5 mi. w. Portal	-vi.56	1♀	FNYC	swimming pool
CHUHUAHUA, 22 mi. w. El Sueco	8.x.75	1	JRZC	tank
D. carolinus Aubé				
GA, Clarke Co., Whitehall Forest	9-15.iv.77	1♀	RHTC	black light trap
NC, Wake Co.	21.iv.49	1♂	CUIC	at light
DC, Washington	4.vi.02	1♀	USNM	electric light
MO, Scott Co., Sikeston	16.vi.56	1♂	USNM	at light
DC, Washington	13.vii.06	1♂	USNM	at light
"	4.x.05	1♂	USNM	electric light
D. fasciventris Say				
MI, Washtenaw Co., Ann Arbor	13.iv.38	1♀	UMMZ	at light
WI, Door Co., Sturgeon Bay	27.iv.71	1♂,1	WLHC	swimming pool
MA, Middlesex Co., Framingham	29.iv.40	1♀	UCSE	in flight, 12 noon
ONT, Dunrobin	28.iv.74	1♂,2	CNIC	at light
WI, Door Co., Sturgeon Bay	2.v.71	1♂,2	WLHC	swimming pool
MI, Washtenaw Co., Ann Arbor	19.vi.19	1♂	UMMZ	at light
MI, Ottawa Co., Hudsonville	22.vi.77	2♀	MSUC	black light
MI, Washtenaw Co., Ann Arbor	24.vi.21	1♀	UMMZ	at light
MI, Menominee Co.	24,vi,71	1♂	GWWC	electric light

(continued on next page)

Table 5 (continued)

Taxon / Locality	Date	#	Colln.	
MI, Ottawa Co.	25.vi.71	1♀	GWWC	electric light
ONT, Chaffeys Locks	1.vii.64	1♀	ROMC	uv light
”	6.vii.64	1♀	ROMC	uv light
MI, Cheboygan Co.	7.vii.52	2♂	USNM	at light
ONT, Chaffeys Locks	10.vii.64	1♀	ROMC	uv light
”	11.vii.64	1♀	ROMC	uv light
”	12.vii.64	1♀	ROMC	uv light
MN, Itasca State Park	12.vii.37	1♀	CASC	at light
MI, Berrien Co., E.K. Warren Pres.	14.vii.20	2♂,4♀	UMMZ	L. Michigan beach drift
MI, Cheboygan Co.	14.vii.52	1♀	USNM	at light
ME, Lincoln Co., Damariscotta	15.vii.69	1♀	CISC	black light
MI, Cheboygan Co., T38 R/E sec. 30	16.vii.66	2♀	MSUC	uv light
MI, Cheboygan Co., Douglas Lake	16.vii.78	1♂,1♀	UASM	beach drift
ONT, Chaffeys Locks	22.vii.71	1♀	ROMC	bl. light
PQ, Duparquet	26.vii.44	1♀	CASC	at light
”	27.vii.44	2♂	CASC	at light
ONT, Fraserburg	3.viii.71	1♀	ROMC	uv light
MI, Cheboygan Co.	5.viii.52	2♂	USNM	at light
MI, Schoolcraft Co., T42N R16W sec.13	6.viii.65	5♂,5♀	MSUC	uv light
ALTA, Edmonton	27.ix.70	1♂,1♀	UASM	light
ONT, Chaffeys Locks	2.xi.69	1♀	CNIC	uv light
WI, Waupaca Co., Clintonville	12.xi.39	1♂	CNIC	alive on street
CT, Tolland Co., Storrs	6.xii.73	1♂	UCSE	on road

(continued on next page)

Table 5 (continued)

Taxon / Locality	Date	#	Colln.	
D. hatchi Wallis				
OR, Washington Co., Forest Grove	17.vii.28	1♀	OSUO	flying at dusk
CA, Humboldt Co., Arcata	17.vii.69	1♂	CISC	black light trap
D. cordieri Aubé				
MN, Stearns Co., St. Cloud	30.iii.66	1♀	SCSU	lights
"	14.iv.70	1♂	SCSU	at lights, cool night
ALTA, Edmonton	18.iv.80	1♂	UASM	under street lights
ONT, Guelph	20.iv.75	1♂	UGIC	on sidewalk
MAN, Aweme	26.iv.30	1♀	CNIC	taken under logs, out of water
SASK, Regina	27.iv.80	1♂	UASM	in flight
SD, Brookings Co., Brookings	29.iv.57	1♂,1♀	SDSU	light trap
BC, Creston	29.v.48	1	UBCZ	at light
MI, Wexford Co., Cadillac	10.vii.21	1♀	MSUC	in swimming pool
MI, Emmett Co., Big Stone Bay	30.vii.65	1♀	UMMZ	beach
ND, Cass Co., Fargo	2.viii.56	1	NDSU	uv light trap
"	6.viii.56	1♀	FNYC	uv light trap
SD, Brookings Co., Brookings	2.ix.43	1♂,1♀	UANH	light trap
MN, Stearns Co., St. Cloud	24.ix.69	2♂	SCSU	lights
ALTA, Cereal	2.x.70	2-	UCIC	at light

(continued on next page)

Table 5 (continued)

Taxon / Locality	Date	#	Colln.	
D. circumcinctus Ahrens				
ALTA, Edmonton	18.iv.80	1♀	UASM	under street lights
"	27.iv.78	1♂,1♀	UASM	in flight
"	24.v.78	1♂	UASM	found under doorway light
AK, Fairbanks	4.vii.64	2♀	CASC	at electric light, 11:50 PM
SASK, Gandview Bch., Last Mtn. Lk.	11.viii.70	2♀	ROMC	uv light
ALTA, Edmonton	22.ix.73	1♀	UASM	on sidewalk
D. alaskanus J. Balfour-Browne				
MN, Roseau Co., Roseau	29.vi.63	1♂	DEFW	light trap
SASK, Regina	11.vii.80	1♂	at lights	
MN, Pope Co., Glacial Lks. St. Pk.	21.viii.71	1♀	DEFW	at black light
D. dauricus Gebler				
MN, Carlton CO., Cloquet	22.iv.58	1♂	UASM	at light
PQ, Duparquet	11.vii.43	1♂	CASC	at light
ALTA, Edmonton	10.x.73	1♂	UASM	at light

Table 6. Distribution of dimorphic elytral states of females of *Dytiscus dauricus* Gebler (Coleoptera: Dytiscidae), by political subdivisions of Canada and United States. Based on specimens examined assignable to particular subdivisions.

Province State	Total *Number*	Number *Sulcate*	Proportion *Sulcate*	Number *Non-sulcate*	Proportion *Non-slucate*
Alaska	78	77	99%	1	1%
Yukon	10	9	90%	1	10%
N.W.T.	13	8	62%	5	38%
British Columbia	20	16	60%	4	20%
Alberta	34	25	74%	9	26%
Saskatchewan	1	1	100%	0	0%
Manitoba	21	9	43%	12	57%
Ontario	7	4	57%	3	43%
Quebec, N.B.	7	7	100%	0	0%
P.E.I., Nova Scotia	4	4	100%	0	0%
Newfoundland	18	13	72%	5	28%
Washington, Oregon	10	10	100%	0	0%
California	18	18	100%	0	0%
Idaho, Montana	6	6	100%	0	0%
Nevada, Utah	11	11	100%	0	0%
Wyoming	5	4	80%	1	20%
Colorado	8	4	50%	4	50%
N., S. Dakota	2	2	100%	0	0%
Wis., Mich., Minn.	18	18	100%	0	0%
Vermont, New York	4	4	100%	0	0%
New Hamp., Maine	19	19	100%	0	0%
TOTAL	315	270	86%	45	14%

RECONSTRUCTED PHYLOGENY

Introduction

In this section, I present reasons for regarding the tribe Dytiscini and genus *Dytiscus* as monophyletic. Then, I deal in some detail with the evolution of *Dytiscus*, from a holomorphological point of view.

Methods used for reconstruction of the phylogeny of members of *Dytiscus* are discussed in Ball and Roughley (1982), Roughley and Pengelly (1982) and references cited therein. Also, see the excellent treatment by Ashe (1982:225-229). Characters and character state distribution by taxon are shown in Table 3. The reconstructed phylogeny is shown in Fig. 52. Character state polarity was deduced from ex-group occurrence in members of Dytiscinae. The most easily resolved character consists of two character states found in two groups of taxa. For example, members of Dytiscinae, exclusive of *Dytiscus*, possess rounded metacoxal lobes, whereas members of *Dytiscus* possess either rounded or variously elongated or pointed metacoxal lobes. The unique state expressed only by some members of *Dytiscus* is therefore considered apotypic for them (Watrous and Wheeler 1981).

Many character states are not discretely distributed, however. Various states of a character can evolve independently by reversal, parallelism, or even convergence (see discussion in Gauld and Mound 1982, and Wiley 1981:12-13, 120-122). Some features of subsets of *Dytiscus* (species-groups, sets of species-groups) were polarized and homoplasies established by means of in-group criteria discussed by de Jong (1980) and Watrous and Wheeler (1981). Most examples of characters of equivocal polarity could be analyzed because of their co-occurrence with more easily established (heavily weighted) character trends (de Jong 1980).

Holomorphological Aspects: Dytiscini and *Dytiscus*

Dytiscini as a monophyletic unit.— The tribe Dytiscini is comprised of two genera, the dibasic Australian and Tasmanian *Hyderodes* Hope (Watts 1978), and the more diverse Holarctic *Dytiscus*. Sharp (1882:939) was not convinced of the naturalness of this tribe: "... the resemblance or approximation between *Dytiscus* and *Hyderodes* does not arise from genetic connection (or common origin), but is due to a parallelism in the environment of the organisms during their evolution." Sharp does not mention what these environmental similarities might be.

I disagree with Sharp's hypothesis. This is in part based upon characters which Sharp himself has provided (1882:937-939). The first two characters, which I interpret as synapotypic for Dytiscini, is size. The total range of size within the tribe is from 19 to 44 mm, and is not approached by many groups of Hydradephaga except Cybistrini, which range from 13 mm (Brinck 1945) to 47.5 mm (Sharp 1882:713). Large size has evolved independently in members of Dytiscini and Cybistrini.

Sharp (1882:240, 938) discusses the much enlarged spiracular openings of the last two abdominal terga, which are unique to Dytiscini. This character state, then, is also a synapomorphy for the members of the tribe. The enlarged spiracular openings are not due solely to larger size of specimens of Dytiscini as larger members of Cybristini have relatively smaller openings.

Dytiscus as a monophyletic unit.— At least five characters indicate the monophyly of *Dytiscus*. Some of these are more difficult to polarize than others, but in totality they probably indicate the phylogenetic uniqueness of this genus.

1) Large size. Specimens of *Dytiscus* range from 22.6 to 40.0 mm (Table 2) in length, and most are in the range of 24 to 30 mm. Specimens of *Hyderodes* are 19 to 20 mm in length (Sharp 1882:633, 644 and Watts 1978:138; note-- the length of 10.9 mm given by Watts for specimens of *H. crassus* Sharp must be a misprint).

2) Clypeal-frontal suture entire. Sharp (1882:904) mentions that the clypeal suture is complete and distinct throughout its entire length. This is unique among members of the family Dytiscidae, and represents a state similar to that found within at least Hygrobiidae, Amphizoidae, Trachypachidae and Carabidae. Its presence in specimens of *Dytiscus* is interpreted as re-acquisition of this character.

3) Male mesotarsus with very numerous palettes. Male specimens of *Dytiscus* have more than 700 to 1000 palettes per mesotarsal acetabulum. This state is not approached by any other member of Dytiscini that I have examined. For instance, specimens of *Hyderodes* have 18 palettes per mesotarsal

acetabulum. Nevertheless, this character is difficult to polarize. It is unique within Dytiscinae, but is more similar to the state found in many members of Colymbetinae. Relatively numerous palletes probably represent a plesiotypic state (*e.g.* see discussion in Roughley and Pengelly 1982 for Hydaticini) in certain groups of Dytiscidae, but rarely, if ever, does it approach the numerical abundance found in males of *Dytiscus*. Therefore, I interpret the condition found in the genus as apotypic.

4) Very large spiracular stigma of two apical abdominal terga. Members of Dytiscini are characterized by large stigmata (see above), which in *Dytiscus* are much longer than those of *Hyderodes*.

5) Triangular shape, in cross-section, of apical portion of median lobe. In the discussion of character 7.3 used in the phylogenetic analysis, I characterize the plesiotypic form of the median lobe of male Dytiscinae. Male specimens of *Hyderodes* closely resemble this generalized form. In particular, the apical portion (posterior to flanges) is blade-like, and therefore oval in cross-section. Male specimens of *Dytiscus*, in contrast, have the median lobe more or less widened laterally, and thereby present a triangular cross section of the apical portion.

Holomorphological Aspects: Evolution of *Dytiscus*

Characters used in phylogenetic analysis.— In this section, I list each character in the order in which it appears on Fig. 52, although reference to the characters by numerals is as in Table 3. States of each character are listed along with the suggested transformation series they form, and the basis for this polarity. Character state changes are summarized in Table 7.

Character A. Segmentation of labial palpomere I of third-stage larva. Two states: plesiotypic, one-segmented; apotypic, two-segmented. Basis for classification: ex-group.

Character 3.1. Explanation of pronotum. Two states: plesiotypic, explanate; apotypic, not explanate. Basis for classification: in-group.

Character 5.1. Elytron of female. Two states: plesiotypic, not sulcate, and therefore male-like; apotypic, sulcate. Basis for classification: ex-group.

Character 7.1. Lateral ridges of median lobe. Two states: plesiotypic, present; apotypic, absent. Basis for classification: ex-group.

Character 6.1. Distribution of palettes on male mesotarsal acetabulum. Two states: plesiotypic, evenly distributed; apotypic, with glabrous area centrally. Basis for classification: ex-group.

Character 7.5. Relative length of dorsal and lateral flanges of median lobe of male. Two states: plesiotypic, dorsal equal to, or longer than laterals; apotypic, dorsal much longer than laterals. basis for classification: ex-group and in-group.

Character 4.6. Shape of apex of metacoxal process. Four states: plesiotypic, rounded; first apotypic, acute; second apotypic, acuminate; third apotypic, acuminate and elongate. Basis for classification, ex-group and in-group.

Character 4.7. Shape of inner margin of metacoxal process. Two states: plesiotypic, convex; apotypic, concave. Basis for classification: ex-group.

Character 7.3. Curvature of preapical portion of median lobe of male. Two states: plesiotypic, linear; apotypic, curved. Basis for classification: ex-group.

Characters 4.1 – 4.5. Colour of pterothoracic sterna. Three states: plesiotypic, black; first apotypic, black and yellow (fasciate); second apotypic, yellow. Basis for classification: ex-group and in-group.

Character 7.6. Roundedness of tip of median lobe of male. Three states: plesiotypic, not rounded; first apotypic, rounded; second apotypic, broadly rounded. Basis for classification: ex-group.

Character 7.7. Development of tip of median lobe of male. Two states: plesiotypic, without knob; apotypic, knobbed. Basis for classification: ex-group.

Character 7.9. Extension of pre-knob portion of median lobe of male. Two states: plesiotypic, not extended; apotypic, extended. Basis for classification: in-group.

Character 7.8. Development of sensory-type pores on tip of median lobe of male. Two states: plesiotypic, absent or, if present, small; apotypic, distinct. Basis for classification: ex-group and in-group.

Character 7.2. Curvature of apex of median lobe of male (lateral view). Two states: plesiotypic, straight; apotypic, curved. Basis for classification: ex-group and in-group.

Character 7.4. Profile of pre-apical portion of median lobe of male (dorsal view). Two states: plesiotypic, parallel-sided; apotypic, sinuate. Basis for classification: ex-group and in-group.

Character 7.10. Relative development of median lobe of male. Two states: plesiotypic, moderate; apotypic, significant. Basis for classification: in-group.

Character 7.11. Profile of pre-apical portion of median lobe (dorsal view). Two states: plesiotypic, wider or more robust; apotypic, thinner or less robust. Basis for classification: in-group.

Characters and homoplasy.— My interpretation of some characters is not completely apparent from simple description of the characters and their states. The following section explains more fully some characters and justifies my interpretation of others.

Character A. Segmentation of labial palpomere I of third-stage larva.

Blunck and Klynstra (1923) discuss the secondary or superimposed segmentation of head appendages of larval stages of species of *Dytiscus.* In the discussion of phylogenetic relationships of *D. verticalis*, the one-segmented labial palpomere I of larvae (Wilson 1923, Fig. 37) was noted to be similar to that of members of *Hyderodes shuckardi* (Watts 1964, Fig. 37). Subsequent study has confirmed the lack of false segmentation of this palpomere in larvae of both of these species.

I have associated adult and third-stage larvae of all Nearctic species except *D. hatchi* (Roughley, unpublished data), and larvae of European species of *Dytiscus* were described by Blunck and Klynstra (1923). Therefore, while known distribution of this character is incomplete (larvae of some eastern Palearctic species of *Dytiscus* are unknown), knowledge is sufficient to suggest use of the derived state as a synapotypy for all species of *Dytiscus* other than *D. verticalis.*

Character 3.1. Explanation of pronotum.

Laterally explanate pronota are unique to adult *Dytiscus* among Dytiscinae. As such, this character state is synapotypic for members of *Dytiscus*, though secondarily absent from members of the *D. hybridus*-group. This character is sexually dimorphic in adults of *D. cordieri* (pronotum explanate in females, only). I deem absence of the explanation in males as a loss of the apotypic condition, and thus an evolutionary reversal.

An alternate phylogeny suggested by the distribution of this character would be one in which the *D. verticalis*- and *D. hybridus*-groups were interchanged in Fig. 52. This would result in explanate pronota representing a synapotypy for all species-groups of *Dytiscus* except the *D. hybridus*-group, rather than for *Dytiscus* as a whole. Also, the derived state of Character A would be unique to a single monobasic species-group (*D. verticalis*). There is little corroborating evidence for either of these hypotheses. I have chosen the representation shown in Figure 52 because specimens of *D. verticalis* exhibit less derived character states than do members of the *D. hybridus*-group, and is thus closer to the hypothetical ancestor of the genus.

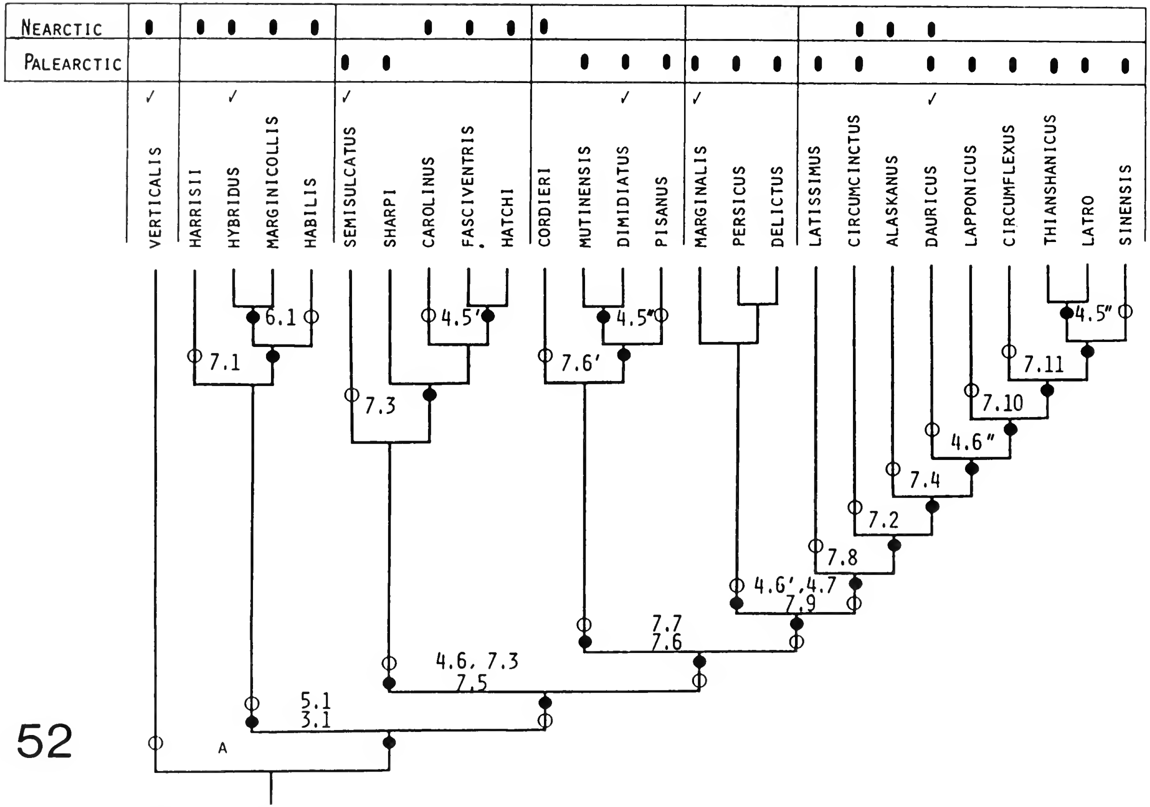
Character 6.1. Distribution of palettes on male mesotarsal acetabulum.

In all adult male dytiscines exmined, palettes of the mesotarsus are more or less evenly distributed. In specimens of *D. hybridus* and *D. marginicollis*, the acetabulum has a central, longitudinal glabrous area. This is considered an apotypic state. Given that these two members of the *D. hybridus*-group are the only extant species of *Dytiscus* which have such a glabrous area, and that it is achieved in a similar manner, suggests that, even though it is a loss, it is a structural synapotypy for these two taxa. As mentioned under the phylogenetic treatment of *D. hybridus*, this species represents my concept of the hypothetical ancestor of the group, except that it would have had evenly distributed tarsal palettes.

In the absence of this character, I would have rearranged the *D. hybridus*-group, placing *D. hybridus* as the sister group to a lineage including *D. harrisii*, *D. marginicollis* and *D. habilis*. This would have allowed simpler explanation of characters 3.2, 4.2-4.5, 7.1 and 7.5 (see Table 3). The first five of these characters are colour-related, and markedly variable (see Table 7 for Character 4.5). Character 7.2 is discussed elsewhere in this section as being of less phylogenetic weight, and character 7.5 would still require one withinin-species-group reversal for the state found in males of *D. habilis*. The question becomes one of whether or not seven synapotypies of less weight are more significant than one of more weight. My interpretation demands a negative answer to this question, or demonstration of a single character better than distribution of tarsal palettes. In the absence of the latter, I retain the arrangement shown in Figure 52.

Character 7.5. Relative length of dorsal and lateral flanges of median lobe.

Dorsal and lateral flanges of the median lobe are used as guides for the spermatophore during its transfer to, and deposition in, the female's bursa copulatrix (Demandt 1924). In most species of *Dytiscus*, and in species of *Hyderodes*, the two sets of flanges are subequal in length. In some members of both the *D. hybridus*- and *D. semisulcatus*-groups, there is a marked discrepancy in length, presumably brought about by a decrease in length of the lateral flanges. On Figure 52, I have used the apotypic state (dorsal flange longer than lateral flanges) to isolate the *D. semisulcatus*-group. This requires (Table 7) that the apotypic state be derived three times: once in *D. hybridus*, once in *D. habilis*, and once in the common ancestor of the *D. semisulcatus*-group. Furthermore, there is a reversal from the apotypic to the plesiotypic state in one member of the *D. semisulcatus*-group (*D. sharpi*). The alternate arrangement of grouping all species which possess the apotypic state (*D. hybridus*, *D. habilis*, *D. semisulcatus*, *D. carolinus*, *D. fasciventris*, and *D. hatchi*) seems unlikely,



52

Fig. 52. Reconstructed phylogeny of species of *Dytiscus* Linnaeus. Checkmark denotes the taxon used for the name of the species-group.

because it would mean that sulcate elytra had evolved more than once (Character 3.1).

Character 4.6 and 4.7. Shape of metacoxal process.

The most common form of metacoxal process of members of Dytiscinae is a rounded metacoxal lobe (*i.e.*, not angulate and with inner margin convex). Increasing angle of apex of metacoxal process is a heavily weighted character within my phylogenetic analysis. The three apotypic states represent a transition series easily polarized by comparison to specimens of *Hyderodes* and other Dytiscinae. The second apotypic state is conincident with concave inner margin of the metacoxal process. They are perhaps separate characters, because there is no intermediate character state for shape of the inner margin of the metacoxal process.

Heavy weighting of this character forces recognition of homoplasies in other characters. For example, presence of a knob at the apex of the median lobe of males (Character 7.7) isolates members of the *D. marginalis*- and *D. dauricus*-groups, except for *D. latissimus* and *D. alaskanus* of the latter group. A lesser weight placed on Characters 4.6 and 4.7 would allow these two species to be placed in a separate group as sister lineage to the remainder of the *D. marginalis*- plus *D. dauricus*-groups. This arrangement would suggest that acuminate metacoxal processes with a concave inner margin evolved more than once.

I have chosen to retain Characters 4.6 and 4.7 as heavily weighted because they form a clear morphocline which is easily polarized, and because other arrangements would precipitate recognition of many more homoplasies. For example, the re-arranged phylogeny suggested above would bring about two (as opposed to one) independent developments of the apotypic state of Character 7.8, four (as opposed to three) of Character 7.2, and two each (as opposed to one) of Characters 4.6 and 4.7, discussed above.

Character 7.3. Curvature of preapical portion of median lobe of male.

Roughley and Pengelly (1982:280) characterized the plesiotypic hydaticine median lobe as parallel-sided, with unmodified tip. These characters in conjunction with a generally blade-like form of the median lobe comprise the ancestral form of the median lobe of males of Dytiscinae.

Within *Dytiscus*, the apotypic state has evolved at least three times: in *D. hybridus*-group (*D. marginicollis*), in *D. semisulcatus*-group, and is also found in the more advanced species-groups, but lost in *D. pisanus*. . The sporadic parallelisms and the reversal of the apotypic state of this character are perhaps not surprising when it is considered that the change is simple and probably easily achieved in the evolution of various lineages. It is therefore to be considered a character of low importance for reconstruction of phylogeny.

Characters 4.1 - 4.5. Colour of pterothoracic sterna.

Ventral colouration among species of *Dytiscus* is variable within species as well as within species-groups, and both apotypic states have occurred independently in a number of lineages. Among members of *Dytiscus*, however, there is a generalized group trend from darker to lighter in all colour-related characters (2.1, 3.2, 3.3, 4.1-4.5: see Table 3). All are characters of low phylogenetic weight and they are highly variable (Table 7).

Character 7.7. Development of tip of median lobe of male.

The generalized ex-group form of the median lobe of dytiscines is discussed under the treatment of Character 7.3. The derived state of this character unites the *D. marginalis*- and *D. dauricus*-groups. Within the latter, absence of the apotypic state from male specimens of *D. latissimus* and *D. alaskanus* represent secondary, independent losses, as discussed under Characters 4.6 and 4.7, above.

Table 7. Number of changes of state (derivation of apotypic state or reversal to plesiotypic state) for the 19 charcters used for phylogenetic reconstruction of the genus *Dytiscus* L. (Coleoptera: Dytiscidae).All characters are scored as if existing in two states only.Based on Table 3 and Figure 52.

	Changes of state					
Character	1	2	3	4	5	6
A	X					
3.1	X	X				
4.5'	X	X				
4.5"	X	X	X	X	X	X
4.6	X					
4.7	X					
5.1	X	X	X			
6.1	X					
7.1	X	X	X	X		
7.2	X	X	X			
7.3	X	X	X	X		
7.4	X					
7.5	X	X	X	X		
7.6	X	X	X	X	X	
7.7	X	X	X	X		
7.8	X					
7.9	X					
7.10	X					
7.11	X	X				
Total number of characters undergoing given number of state changes.	8	3	2	4	1	1

Total number state changes = 47.

Character 7.9. Extension of pre-knob portion of median lobe of male.

The apotypic condition as represented by members of the *D. marginalis*-group consists of a narrowing and elongation of the pre-apical portion just before the apical knob. The apotypic condition of this character is distinct from that of Character 7.11, discussed below, in which the entire pre-apical portion is narrowed.

Character 7.2. Curvature of apex of median lobe of male (lateral view).

The primitive form of the median lobe is discussed under the treatment of Character 7.3. Subsequent modification of this basic plan has occurred many times in the history of the subfamily (group trend, *e.g.* see Roughley and

Pengelly 1982). Within *Dytiscus*, there is evidence of the plesiotypic state of this character in the plesiotypic members of two lineages (*D. verticalis* and *D. harrisii*) and of three independent derivations of the apotypic state (*D. sharpi*, *D. pisanus* , and all but two members of the *D. dauricus*-group). This character is similar to Character 7.3 in that conversion to the apotypic state probably is accomplished easily and thus is considered to be of low phylogenetic weight.

Character 7.10. Relative development of knob of median lobe of male (dorsal view).

The apotypic state of this character is relative and subjective. However, the distinctiveness of the change is apparent. The apotypic state of this character would be coincident with that of Character 7.11 if it were not for *D. circumflexus*, males of which have a very distinctive apical knob, but the apex is not excessivley narrowed.

Evolution of genitalia of males of Dytiscus.— I have assigned form of the median lobe of male genitalia some importance for both recognition of species level status and for phylogenetic analysis. The male genitalia are much more than simply a set of characters, and must be treated as a functional evolutionary unit. Therefore, the purpose of this section is to trace the history of male genitalia as detalied by the reconstructed phylogeny proposed (Figure 52). My method has involved description of a hypothetical type of genitalia, to which are assigned the characteristics I believe to be primitive, and then to discuss the form and modification of the median lobe from primitive through derived species-groups.

Ancestral dytiscines probably possessed a J-shaped median lobe with a longer portion, or shaft, parallel-sided, with an unmodified, straight, blade-like tip (based in part on Roughley and Pengelly 1882:280). Located dorsally on the median lobe are two lateral and one dorsal flange, which form a guide, or channel, for the spermatophore during copulation (Demandt 1924). This form of median lobe, except for the straight tip, is seen in extant *Prodaticus*, a basal hydaticine, and *Hyderodes*, a basal dytiscine.

Coincident with the origin of the genus *Dytiscus* was derivation of a median lobe with a triangular cross section. The plesiotypic, blade-like condition was modified by lateral extension of the sides and perhaps also by strengthening of the ventral ridge. These steps have created the triangular form of the apex. The form of the median lobe closest to this ancestral type within *Dytiscus* is seen in specimens of *D. verticalis* (Fig. 14A), and *D. harrisii* (Fig. 14B).

Earlier, I discussed the form of the apex of the median lobe as the major taxonomic criterion for delimiting species level taxa, and noted the uniformity of this character within species. This implies selection for uniformity within species, and that difference in form of the apex of the median lobe could be an isolating mechanism for species. This latter point is exemplified by members of the *D. hybridus*-group (Figs. 14B-D, 15A). As recorded above, *D. harrisii* (Fig. 14B) has the plesiotypic form within the group. The median lobe of *D. marginicollis* (Fig. 14D) is similar to that of *D. harrisii* except that the tip is abruptly deflexed. The allopatric *D. hybridus* (Fig. 14C) and *D. habilis* (Fig. 15A) have shortened lateral flanges, lack distinct lateral ridges, and have slightly (*D. hybridus*) or more prominently (*D. habilis*) modified tips. In addition, the pre-apical portion of the median lobe of *D. hybridus* is slender, whereas it is greatly thickened in male *D. habilis*. In summary, modification of five characteristics within three species has produced four markedly different forms of the median lobe.

Within the *D. semisulcatus*-group (Figs. 15B-D, 16A-B), the nominate species (Fig. 15B) has the median lobe similar to that of the plesiotypic form but less triangular and with the dorsal flange markedly elongate. An elongate dorsal flange is characteristic of three other species of the group (*D. sharpi* [Fig. 15C] is the exception). All but the nominate species have the tip abruptly deflexed, although it is more deflexed in *D. sharpi* than in the others, and males of this taxon also have the tip modified. The median lobe of *D. carolinus* (Fig. 15D) and *D. hatchi* (Fig. 16B) lack any remnant of a lateral ridge, whereas that of *D. fasciventris* exhibits it, although only apically. Conversely, the median lobe of males of *D. carolinus* and *D. fasciventris* (Fig. 16A) share a curious subapical depression in dorsal view.

It is interesting that the members of this group are largely allopatric and yet show a high degree of divergence in the form of the median lobe and that the three Nearctic species (*D. carolinus, D. fasciventris* and *D. hatchi*) have the most similar form of the median lobe. The former is probably the result of the long isolation of the species of this group, and the latter to more recent speciation among them than between them and the other members of the clade. Members of this group exhibit modifications in the same five characteristics found in the *D. hybridus*-group, but show more stages of some of these (*i.e.*, deflection of the tip, reduction of lateral flanges, and effacement of the lateral ridge) and added another characteristic (dorsal depression).

The *D. dimidiatus*-group is characterized by a rounded tip of the median lobe (Figs. 16C-D, 17A-B). All have the apex deflexed, and all but the Nearctic *D. cordieri* (Fig. 16C) have the tip quite broadly rounded, with distinct lateral ridges. Specimens of *D. cordieri* exhibit some characters of the plesiotypic form except those noted above, and the swollen area above the place the lateral ridges would normally be located. Specimens of the Palearctic species *D. mutinensis* (Fig. 16D) and *D. dimidiatus* (Fig. 17A) are very similar in form and, as argued in the text, this is perhaps best considered as an example of recent speciation. Co-occurring geographically with these latter two species is *D. pisanus* (Fig. 17B)of which the apical portion of the median lobe has a host of unique characteristics, such as very broad tip, sinuate lateral margin (in lateral view), and great development of ventral setation towards the apex. Members of the *D. dimidiatus*-group thus show, in form and subsequent modification of the median lobe, few similarities to the previously discussed species-groups of *Dytiscus*.

Both the *D. marginalis*- and *D. dauricus*-groups are characterized by presence of a distinct knob on the median lobe (secondarily lost from males of *D. alaskanus* (Fig. 19B) and *D. latissimus* (Fig. 18C) of the latter species-group). The *D. marginalis*-group (Figs. 17C-D, 18A-B) is unique because of the extension of the pre-apical knob portion (Character 7.9). All species have subequal flanges, distinct lateral ridges, and a general similarity in form. There are minor differences in shape of the knob when seen in ventral view, and the relative thickening of the ventral ridge. All of the four forms included in this group occur exclusively in the Palearctic region. Of these only *D. marginalis cerskii* and *D. delictus* are broadly sympatric. In the latter (Fig. 18B), the apex of the median lobe is stouter and the distance from the tip to the dorsal flange is appreciably shorter. Therefore, in this group of species, the integrity of taxa is perhaps more sustained by allopatry and other differences in life history than by divergence in form of the median lobe.

As mentioned previously, two members of the *D. dauricus*-group (Figs. 18C-D, 19A–D, 20A–D) have lost the apical knob of the median lobe, yet the median lobe of both species remains qualitatively different. All species have deflexed apices, distinct lateral ridges and subequal dorsal flanges. The apical portion of the median lobe is flatly arched in *D. circumcinctus* (using the lateral ridges as a reference point, Fig. 19A), and more abruptly arched in more advanced species (except *D. alaskanus,* Fig. 19B), which also have sinuate lateral margins (in dorsal view). Members of *D. circumcinctus* and all other advanced species have well-developed sensory-type pores on the apical knob (Fig, 19E). Their function is unknown to me. Males of *D. circumcinctus* (Fig. 19A), *D. thianshanicus* (Fig. 20B), *D. latro* (Fig. 20C) and *D. sinensis* (Fig. 20D) possess quite a prominent knob at the apex, and the latter three taxa have a distinctly thinner pre-apical portion (in dorsal view) which produces an even greater prominence of the apical knob.

As in the *D. marginalis*-group, the degree of differentiation among species based on the form of the apex of the median lobe is less dramatic within the *D. dauricus*-group than in the *D. hybridus*- and *D. semisulcatus*-groups. However, within the *D. dauricus*-group, unlike the *D. marginalis*-group, many of species of the former occur sympatrically. This could be interpreted as reflecting less reliance on the median lobe as an isolating mechanism, although the fact that each form of apex is distinctive somewhat negates this. It seems more reasonable to suggest that at least some members of the *D. dauricus*-group have arisen more recently than have species of some other groups, and therefore have had less time available for divergence. Other isolating factors associated with life history could be operating to augment the mechanical isolation supplied by genital differences.

Of the six species-groups recognized within *Dytiscus*, members of two (*D. verticalis*- and *D. hybridus*-groups) have a median lobe which appears quite similar to that reconstructed for the hypothetical ancestor of the genus. Plesiotypic members of the *D. semisulcatus*- and *D. dimidiatus*-groups show some but not extreme modification from the ancestral type. In the *D. marginalis*- and *D. dauricus*-groups, the common presence of an apical knob places them as quite derived from the ancestral type.

Parallel, dramatic changes in form of the apex of the median lobe characterize species in the *D. hybridus*- and *D. semisulcatus*-groups. A high degree of differentiation is found in members of the *D. dimidiatus*-group as well. The *D. marginalis*- and *D. dauricus*-groups show comparatively less within-group differentiation, and yet the presence of the apical knob is certainly a strong isolating mechanism between these two groups and the four more plesiotypic groups.

In summary, there is a transformation series shown by the species-groups of *Dytiscus* in the form of the apex of the median lobe. The series is disguised by within-group changes, and is apparent only after examination of the plesiotypic forms within each species-group. (That the plesiotypic member of each group exhibits a form of median lobe most similar to a hypothetical ancestor of that group probably reflects heavy emphasis on the median lobe for construction of the proposed phylogeny, within species-groups, in the first place! The same is not true, however, for comparisons between groups, where, as mentioned elsewhere, other characters such as form of the metacoxal processes were more heavily weighted).

CONCLUDING STATEMENT

The classification of species of *Dytiscus* is far from complete. Many type specimens of junior synonyms remain to be studied; of some 75 names treated herein type material has been studied recently of only 26. Further study will undoubtedly bring about re-assignment of some of these names (*e.g.* see discussion of *D. fuscostriatus* within the treatment of *D. circumcinctus*). Similarly types of the following senior names need to be carefully studied (if indeed they still exist): *D. carolinus* Aubé, *D. circumcinctus* Ahrens, *D. circumflexus* Fabricius, *D. cordieri* Aubé, *D. czerskii* Zaitsev, *D. delictus* Zaitzev, *D. dimidiatus* Bergsträsser, *D. distantus* Feng, *D. fasciventris* Say, *D. habilis* Say, *D. hybridus* Aubé, *D. lapponicus* Gyllenhal, *D. latissimus* Linnaeus, *D. marginalis* Linnaeus, *D. semisulcatus* Müller and *D. verticalis* Say. Therefore while some changes in nomenclature are to be expected I believe these are minor and that the overall classification is sound.

As mentioned elsewhere my studies of *Dytiscus* are not complete yet. Further analysis will be presented through study of immature stages and of zoogeography and reconstructed phylogeny. After that an advanced level of understanding of the systematics of *Dytiscus* will have been achieved. It is hoped that this understanding will provide the framework for further studies of other topics using *Dytiscus*. For instance, in terms of ecological studies there is a very unequal coverage. In the Palearctic realm, *D. marginalis* is well studied whereas in the Nearctic region the best studied species is *D. alaskanus* yet even casual comparison of the literature about these two species shows that the former is much better known than is the latter. Many interesting questions about the natural history of *Dytiscus* are yet to be resolved. For instance some but not all species are specialized predators of immature aquatic vertebrates (*e.g.* salamanders, frogs and fish) or of immature aquatic invertebrates (*e.g.* caddisflies) whereas other species appear to be predators of anything that they can overpower. How widespread is specialized predation and how did it evolve?

One feature of specimens of *Dytiscus* which makes them very suitable for further research is their large size. Their size renders them suitable for most kinds of studies carried out by entomologists. For instance, they are easy animals to observe, particularly when maintained in aquaria, and therefore study of their behaviour may yield interesting data.

One of the many fascinating evolutionary problems that remains unsolved is the purpose and function of the sulcate grooves of some females of *Dytiscus*. A variety of theories have been put forward to explain their existence but none of these stands up to critical analysis. Most species of *Dytiscus* are known to possess sulcate elytra; in only few species were all females sulcate, in other species sulcate females predominate in the southern portion of the geographic range whereas in other species the reverse is true. If these sulcae have an important role then why are they found only in females, what are the mechanisms be which sulcae are lost, *etc.*?

Considering that the classification of *Dytiscus* is relatively stabilized this should open the door for further study of many interesting and unique phenomena of these animals.

ACKNOWLEDGEMENTS

I express appreciation to my supervisor, G.E. Ball for his help and advice during my study. His constant enthusiasm and insight as well as his attitude toward teaching and research were of great value. The climate of learning which he has helped create in the Department of Entomology of the University of Alberta made the opportunity to study and conduct research there a very beneficial experience.

D.A. Craig, B.S. Heming, C. Schweger, J.R. Spence and H.B. Leech assisted by serving on my committee, by reading the thesis on which this paper was based, and in many other ways. E. Maw has assisted with some of the technical aspects of manuscript production, particularly during the early stages; D. Holder, D.A. Pollock and I.S. Askevold also assisted me in Winnipeg.

S. Wroot worked very efficiently and quickly to provide the habitus drawings; her effort and skill are greatly appreciated. G.D. Braybrook provided technical assistance with scanning electron microscope work. J.S. Scott provided valuable technical advice concerning arrangement and methods of presentation of the plates. M.G. McIntyre assisted in designing and building a mechanical microscope stage for measuring specimens and provided other technical expertise. F.A.H. Sperling and I.S. Askevold assisted with, or checked the accuracy of German translations, and J.F. and M. Landry provided similar help with French translations; G. Léger (Winnipeg) also assisted with French translations and with typing and computer formatting.

I express appreciation to the librarians in charge of the Inter-Library loans office both at the University of Manitoba and at the University of Alberta for their assistance in tracking down some of the more obscure literature sources. In this regard I owe a great debt to the librarians at the British Museum (Natural History) for their courtesy, helpfulness and efficiency during my visits to that institution.

To my former colleagues in the Department of Entomology, University of Alberta, I owe a great deal. They were most helpful in discussions of specific problems and of general theory and application of systematics, as well as providing many specimens of *Dytiscus* or other information. I thank them all, but certain of them deserve special mention for their detailed contributions. These are R.B. Aiken, J.S. Ashe, A. Borkent, H. Goulet, D. Kavanaugh, D. Lafontaine, F. Leggett, A.P. Nimmo and J.R. Spence, as well as J. Acorn, R.S. Anderson, J. Cumming, D.C. Currie, H. Frania, G.A.P. Gibson, J.F. Landry, E. Maw, J. O'Hara, K. Shaw and F.A.H. Sperling. Also, I greatly appreciate the assistance and enthusiasm of many colleagues from other institutions who assisted with obtaining obscure literature, specimens, *etc*. D. Larson (St. John's) and A. Nilsson (Umeå) provided vigorous and effective reviews of this manuscript.

As explained elsewhere, examination of specimens of *Dytiscus* involved visiting collections, and I express my appreciation to the respective curators for their assistance during my visit to their institutions. In particular, M.E. Bacchus and P.M. Hammond at BM(NH) and, J.J. Menier (MNHN) provided a good deal of assistance with types in their collections.

Travel, field work and other financial support was provided by NSERC Canada grant #A-1399 held by G.E. Ball. Field work in Yukon Territory in 1977 was supported by a grant to the Beringea Yukon Refugium Project administered by J.V. Matthews, Jr., Geological Survey of Canada, Ottawa. Field work in the eastern arctic of Canada during 1979 was supported by the Boreal Institute, University of Alberta. Subsequent research and museum travel and publication costs were supported by NSERC Canada grant #A0428 to RER.

I acknowledge also the forebearance and assistance of the faculty and staff of the Department of Entomology, University of Manitoba, during my dual status as student and faculty member.

Last, but foremost, was the support, help and enthusiasm of my wife Marsha. I am fortunate to share my life with a person who both understands and participates in my work.

REFERENCES CITED

(† indicates references used in compiling distribution records for taxa. Some are cited in the text; others are not).

†Abot, G. 1928. Catalogue des Coléoptères observés dans le Département de Maine-et-Loire. Paul Lechevalier, Paris. xv + 386 pp.

†Aguesse, P. and L. Bigot. 1959. Les Coléoptères Hydrocanthares de Camargue: essai écologique et faunistique. La Terre et la Vie, 106: 128–148.

Ahrens, A. 1811. Beschreibung der grossen Wasserkäfer-Arten in der Gegend um Halle in Sachsen (Dytici). Neue Schriften der naturforschenden Gesellschaft zu Halle, l (Heft VI): 47–58.

Aiken, R.B. 1985. Attachment sites, phenology, and growth of larvae of *Eylais* sp. (Acari) on *Dytiscus alaskanus* J. Balfour-Browne (Coleoptera: Dytiscidae). Canadian Journal of Zoology, 63: 267–271.

Aiken, R.B. 1986. Diel activity of a boreal water beetle (*Dytiscus alaskanus*: Coleoptera; Dytiscidae) in the laboratory and field. Freshwater Biology, 16: 155–159.

Aiken, R.B., and R.E. Roughley. 1985. An effective trapping and marking method for aquatic beetles. Proceedings of the Academy of Natural Sciences of Philadelphia, 137: 5–7.

Aiken, R.B. and C.W. Wilkinson. 1985. Bionomics of *Dytiscus alaskanus* J. Balfour-Browne (Coleoptera:Dytiscidae) in a central Alberta lake. Canadian Journal of Zoology, 63: 1316–1323.

†Alfes, C. and H. Bilke, 1977. Coleoptera Westfalica: Familia Dytiscidae. Abhandlungen aus dem Landesmuseum für Naturkunde zu Münster in Westfalen, 39: 1–109.

Anderson, R.D. 1962. The Dytiscidae (Coleoptera) of Utah: keys, original citation, types and Utah distribution. The Great Basin Naturalist, 22: 54–75.

†Angelini, F. 1975. Nuovi reperti di Hydroadephaga (Coleoptera: Haliplidae, Dytiscidae, Gyrinidae). Bollettino della Società Entomologica Italiana, 107: 56–70.

†Angelini, F. 1978. Haliplidae, Dytiscidae e Gyrinidae della Lucania. Entomologica (Bari), 14: 63–135.

†Angelini, F. 1984. Catalogo topografico dei Coleoptera Haliplidae, Hygrobiidae, Dytiscidae e Gyrinidae d'Italia. Memorie della Società Entomologica Italiana, 61A (1984): 45–216.

†Apfelbeck, V. 1904. Die Käferfauna der Balkanhalbinsel, mit Berücksichtigung Klein-Asiens und der Insel Kreta. Erster Band: Familienreihe Caraboidea. Friedländer & Sohn, Berlin. x + 422 p.

Ashe, J.S. 1982. Generic revision of the subtribe Gyrophaenina (Coleoptera: Staphylinidae: Aleocharinae) with a review of described subgenera and major features of evolution. *Quaestiones Entomologicae* 20: 129–349.

Aubé, C. 1838. Tome sixième. Spécies général des Hydrocanthares et Gyriniens. *In* Dejean, P.F.M.A. Spécies général des coléoptères de la collection de M. le compte Dejean. Mequignon, Paris. xvi + 804 pp.

†Auber, L. 1945. Atlas des Coléoptères de France. I. Carabes, Staphylins, Dytiques, Scarabées. N. Boubée & Cie, Paris. 83 pp + xii plates.

Baehr, M. 1979. Vergleichende Untersuchungen am Skelett und der Coxalmuskulature des Prothorax der Coleoptera. Ein Beitrag zu Klärung der phylogenetischen Beziehungen der Adephaga (Coleoptera, Insecta). Zoologica, 44: 1–76.

Balduf, W.V. 1935. The bionomics of entomophagous Coleoptera. [Reprinted 1969] E.W. Classey Ltd., Middlesex, England. i + 220 pp.].

†Balfour-Browne, F. 1913. The life history of a water beetle. Proceedings of the Royal Institution of Great Britain, 20: 754–764.

Balfour-Browne, F. 1932. A textbook of practical entomology. Edward Arnold & Co., London. viii + 191 pp.

Balfour-Browne, F. 1934. The proventriculus in the Dytiscidae (Col.) as a taxonomic character. Stylops [Proceedings of the Royal Entomological Society of London], 3: 241–244, 3 pl.

Balfour-Browne, F. 1944. The wing-venation of the Adephaga (Coleoptera) with special reference to the Hydradephaga and some homologies with the Polyphaga. Journal of the Royal Microscopical Society, 63: 55–84.

†Balfour-Browne, F. 1950. British water beetles. Volume 2. Ray Society Publications, No. 134. Bartholomew Press, London. xx + 394 pp.

†Balfour-Browne, F. 1951. The aquatic Coleoptera of Ireland with some remarks on the causes of their distribution. The Entomologist's Gazette, 2: 1–52.

Balfour-Browne, F. 1953. Handbooks for the identification of British Insects. Volume IV, Part 3. Coleoptera, Hydradephaga. Royal Entomological Society, London. 33 pp.

†Balfour-Browne, F. 1960. The aquatic Coleoptera of Scotland and their routes of arrival. The Entomologist's Gazette 11: 69–106.

Balfour-Browne, F. 1961. The metendosternite in the Coleoptera. Journal of the Linnaean Society of London, Zoology, 44: 337–354

Balfour-Browne, F. 1965. The metathorax of the Dytiscidae (Col.). The Entomologist's Monthly Magazine, 100: 188–189.

Balfour-Browne, F. 1967. A study of the metathorax and its principal muscles in dytiscid beetles. Proceedings of the Royal Entomological Society of London (Series A, General Entomology), 42: 155–166.

Balfour-Browne, J. 1944. New names and synonymies in the Dytiscidae (Col.). The Annals and Magazine of Natural History (Series 11), 11: 345–359.

Balfour-Browne, J. 1946. The aquatic Coleoptera of Manchuria (Weymarn collection). The Annals and Magazine of Natural History (Series 11), 13: 433–460.

Balfour-Browne, J. 1948. The aquatic Coleoptera of Newfoundland and Nova Scotia. The Canadian Entomologist, 80: 156–165.

Balfour-Browne, J. 1960. Proposed use of plenary powers to vary the ruling given in Opinion 522 so as to preserve the generic name *Acilius* Leach, 1817 (Class Insecta, Order Coleoptera). Bulletin of Zoological Nomenclature, 17: 250–253.

Ball, G.E., and R.E. Roughley. 1982. The *Hypherpes*-like taxa of southern México: Classification and evolutionary considerations (Coleoptera: Carabidae: Pterostichus). Transactions of the American Entomological Society, 108: 315–400.

Bartholomew, J. Editor. 1955-1959. The Times Atlas of the World. Mid-Century Edition. 1955. Volume III. Northern Europe. xii + plates 49-72 + 57 pp.; 1956. Volume IV. Southern Europe and Africa. xii + plates 73–96 + 50 pp.; 1957. Volume V. The Americas. xii + plates 97–120 + 57 pp.; 1958. Volume I. The World, Australasia, and East Asia. xxvii + plates 1–24 + 34 pp.; 1959. Volume II. South-West Asia and Russia. xv + plates 25–48 + 51 pp. The Times Publishing Company, London.

†Bedel, L.E.M. 1879-1881. Faune des Coléoptères du Bassin de la Seine (et de ses bassins secondaires). Tomus I. xxiv + 360 pp + 2 plates. [Sections published as appendices to Annales de la Société Entomologique de France. Pp. 257-288, incl. *Dytiscus*, appeared in Sér. V, 9(4) in 1881].

Bell, R.T. 1965. Coxal cavities and the phylogeny of the Adephaga. Proceedings of the XIIth International Congress of Entomology, London, July 1964, Volume 1: 80–81.

Bell, R.T. 1967. Coxal cavities and the classification of the Adephaga (Coleoptera). Annals of the Entomological Society of America, 60: 101–107.

†Bercio, H., and B. Folwaczny. 1979. Verzeichniss der Käfer Preussens. Verlag Parzeller & Co., Fulda. xxxi + 369 pp.

Bergsträsser, J.A.B. 1778. Nomenclator und Beschreibung der Insecten in der Grafschaft Hanau-Münzenberger, wie auch der Wetterau und der angrenzenden Nachbarschaft dies und jenseits des Mains, mit erleuchteten Kupfern. Jahrgang I. Coleoptera. Verfassers, Hanau. 88 pp. + 14 Tafeln.

†Bertrand, H. 1928. Note sur une larve de Dytique (*Dytiscus pisanus* Cast.) trouvée aux sources du Sébou (Maroc). Bulletin de la Société des Sciences Naturelles du Maroc, 8:16–18.

†Bertrand, H. 1949a. Récoltes de Coléoptères aquatiques (Hydrocanthares) dans les Alpes; observations écologiques. Bulletin de la Société Zoologique de France, 74: 330–341

†Bertrand, H. 1949b. Récoltes de Coléoptères aquatiques (Hydrocanthares) dans les Pyrénées; observations écologiques. Bulletin de la Société Zoologique de France, 74: 59–70.

†Bertrand, H. 1953. Récoltes de Coléoptères dans les Pyrénées; observations écologiques (Deuxième note). Bulletin de la Société Zoologique de France, 78:59–70.

†Bertrand, H. 1954. Récoltes de Coléoptères aquatiques (Hydrocanthares) dans les massifs montagneux de l'Espagne; observations écologiques. Bulletin de la Société Zoologique de France, 79: 91–105.

†Bertrand, H. 1956. Récoltes de Coléoptères aquatiques (Hydrocanthares) dans les massifs montagneux de l'Espagne; observations écologiques. (Deuxième note). Bulletin de la Société Zoologique de France, 81:12–23.

†Bertrand, H. 1957a. Récoltes de Coléoptères aquatiques (Hydrocanthares) dans les régions montagneuses de l'Espagne; observations écologiques (Troisième note). Bulletin de la Société Zoologique de France, 82: 149–157.

†Bertrand, H. 1957b. Récoltes de Coléoptères aquatiques (Hydrocanthares) dans les massifs montagneux de la Grèce; observations écologiques. Bulletin de la Société Zoologique de France, 81: 323–338.

†Bilardo, A. 1965. Ricerche sugli Hydroadephaga nella Provincia di Varese (Coleoptera). Memorie della Società Entomologica Italiana, 44: 109–152.

†Bilardo, A. 1969. Contributo alla conoscenza degli Hydroadephaga delle Alpi. (Alpi marittime ed Alpi cozie) (Coleoptera: Haliplidae, Dytiscidae). Bollettino della Società Entomologica Italiana, 99: 17–43.

Blackie, C. 1887. A Dictionary of Place-names, giving their derivations, (3rd edition). John Murray, London. [Reprinted 1968 by Gale Research Co., Detroit. xxxix + 243 pp.]

Blake, I.H. 1945. An ecological reconnaissance in the Medicine Bow Mountains. Ecological Monographs, 15:207–242.

Blatchley, W.S. 1910. An illustrated descriptive catalogue of the Coleoptera or beetles (exclusive of the Rhynchophora) known to occur in Indiana, with bibliography and descriptions of new species. Indiana Department of Geology and Natural Resources, Bulletin number l. 1386 pp.

†Blunck, H. 1913. Beiträge zur Naturgeschichte des *Dytiscus marginalis* L. (Historisches, Paläontologie, Systematik und Faunistik.) Zoologische Jahrbücher, Abteilung für Systematik, Geographie, und Biologie der Tiere, 35: 1–54.

Blunck, H. 1916a. Die art-individuellen biologischen Charaktere des *Dytiscus semisulcatus* Müller (=*punctulatus* Fabr.). Zoologischer Anzeiger, 46: 225–231.

Blunck, H. 1916b. Das Leben des Gelbrands (*Dytiscus marginalis* L.) (ohne die Metamorphose). Vorläufige Zusammenstellung. Zoologischer Anzeiger, 46: 271-285, 289–300.

Blunck, H. 1923a. Zur Kenntnis des "Breitrands" *Dytiscus latissimus* L. und seiner Junglarve. Zoologischer Anzeiger, 57: 157–168.

Blunck, H. 1923b. Krankheiten, Feinde und Schmarotzer des Gelbrands. Zoologischer Anzeiger, 57: 296–328.

Blunck, H. 1924. Die Metamorphose (Larven- und Puppenleben). Pp. 591–811 *in* E. Korschelt, *loc. cit.*

Blunck, H., and B.H. Klynstra. 1929. Die Kennzeichen der Jugenstände in Deutschland und Holland vorkommender *Dytiscus* Arten. Zoologischer Anzeiger, 81: 114–140.

Boisduval, J.B.A., and J.T. Lacordaire. 1835. Faune entomologique des environs de Paris, ou spécies général des insectes de quinze à vingt lieues aux alentours de Paris. Tome I. Coléoptères. Mequignon-Marvis, Paris. 696 pp.+ 3 planches.

†Borchert, W. 1938. Die Verbreitung der Käfer Deutschland Tatsachen und Folgerungen. The author, Schönebeck (Elbe). 6 + 137 + 9 pp + 94 maps.

†Borchert, W. 1951. Die Käferwelt des Madgeburger Raumes. Madgeburger Forschungen, Band II. 264 pp + 9 maps.

Brancucci, M. 1979. Considérations sur la faune des Dytiscidae de la grève de Cudrefin (VD) (Insecta:Coleoptera). Bulletin de la Société vaudoise des Sciences Naturelles, 74: 301–311.

†Brancucci, M. 1981. Dytiscidae aus Nepal, Kashmir und Ladakh (Insecta:Coleoptera). Senckenbergiana Biologica, 61 (1980): 179–186.

†Brancucci, M. 1982. Beitrag zur Kenntnis der Dytiscidae und der Haliplidae der Mongolei. Abhandlungen und Berichte der Museum für Natur in Gotha, 11: 69–70.

Brinck, P. 1945. Nomenklatorische und systematische Studien über Dytisciden. III. Die Klassifikation der Cybisterinen. Kungliga Fysiografiska Sällskapets Handlingar, (n.f.) 56(4): 1–20.

†Brinck, P. 1946. Water beetles from Manchuria. With some zoogeographical remarks. *Opuscula Entomologica*, 11: 146–156.

Brinck, P. and K.G. Wingstrand. 1949. The mountain fauna of the Virihaure area in Swedish Lapland. I. General Account. Kungliga Fysiografiska Sällskapets Handlingar, (n.f.) 60 (2): 1–70.

Brinck, P. and K.G. Wingstrand. 1951. The mountain fauna of the Virihaure area in Swedish Lapland. II. Special Account. Kungliga Fysiografiska Sällskapets Handlingar, (n.f.) 61 (2): 1–173.

Brodie, E.D. Jr. and D.R. Formanowicz Jr. 1981. Larvae of the predaceous diving beetle *Dytiscus verticalis* acquire an avoidance to skin secretions of the newt *Notophthalmus viridescens*. Herpetologica, 37: 172–176.

Brodie, E.D. Jr. and D.R. Formanowicz Jr. 1983. Prey size preference of predators: differential vulnerability of larval anurans. Herpetologica, 39: 67–75.

Brodie, E.D. Jr., D.R. Formanowicz Jr. and E.D. Brodie III.1978. The development of noxiousness of *Bufo americanus* tadpoles to aquatic insect predators. Herpetologica, 34: 302–306.

Brown, R.W. 1956. Composition of scientific words, (revised edition). Smithsonian Institute Press, Washington, D.C. 882 pp.

Brown, W.J. 1930. Coleoptera of the north shore of the gulf of the St. Lawrence. The Canadian Entomologist, 62: 231–237.

Bruce, N. 1931. Bidrag til kännedom om svenska coleopteras geografiska utbredning samt några för Sverige nya samt sällsyntare arter. Entomologisk Tidskrift, 52: 189-199.

Brues, C.T. 1928. Studies on the fauna of hot springs in the western United States and the biology of thermophilous animals. Proceedings of the American Academy of Arts and Sciences, 63: 139-228 + plates I–V.

Brues, C.T. 1932. Further studies on the fauna of North American hot springs. Proceedings of the American Academy of Arts and Sciences, 67: 185–303.

†Brundin, L. 1934. Die Coleopteren des Tornetraskgebietes. Ein Beitrag zur Ökologie und geschichte der Käferwelt in schwedisch-Lappland. Carl Bloms, Lund. 436 pp.

Buhlmann, E. 1923. Das Chitinskelett. Pp. 16–79 *in* E. Korschelt *loc. cit.*

Burmeister, E.-G. 1976. Der Ovipositor der Hydradephaga (Coleoptera) und seine phylogenetische Bedeutung unter besonderer Berücksichtigung der Dytiscidae. Zoomorphologie, 85: 165–257.

Burmeister, E.-G. 1980. Funktionsmorphologie und Evolution des Ovipositor der Adephaga (Coleoptera). Verhandlungen des naturwissenschaftlichen Vereines für Hamburg, (N.F.), 24: 89–184.

†Burmeister, E.-G. 1981. Zur Wasserkäferfauna Nordwestdeutschlands. Teil I: Adephaga (Haliplidae, Noteridae, Gyrinidae, Hygrobiidae, Dytiscidae) (Insecta: Coleoptera). Spixiana, 4: 73–101.

†Caillol, H. 1908. Catalogue des Coléoptères de Provence d'après des documents recueillis et groupés. 1re partie. Cicindelidae, Carabidae, Haliplidae, Hygrobiidae, Dytiscidae, Gyrinidae, Staphylinidae, Pselaphidae, Clavigeridae, Scydmaenidae. Annales de la Société Naturelles de Provence, 1: 73–584.

†Caillol, H. 1954. Catalogue des Coléoptrèes de Provence. D'après des documents recueillis et groupés. 5e partie (Additions et corrections). Muséum National d'Histoire Naturelle (Entomologie Agricole), Paris. 725 pp.

Camerano, L. 1880. Note intorno ai Dytiscini del Piemonte. Bulletino della Società Entomologica Italiana 12: 116–122.

†Caspers, H. 1951. Biozönotische Untersuchungen über die Strandarthropoden im bulgarischen Küstenbereich des Schwarzen Meeres. Hydrobiologica, 3: 131–193.

Chisholm, G.G. Editor. 1899. The Times Gazeteer of the World. The Times, London. 1788 pp.

Cronquist, A. 1978. Once again, what is a species? Pp. 3-20 *in* J.H. Romberger *et al., loc. cit.*

Crotch, G.R. 1873. Revision of the Dytiscidae of the United States. Transactions of the American Entomological Society, 4: 383–424.

Crowson, R.A. 1938. The metendosternite in Coleoptera. A comparative study. Transactions of the Royal Entomological Society, 87: 397–415.

Crowson, R.A. 1944. Further studies on the metendosternite in Coleoptera. Transactions of the Royal Entomological Society, 94: 273–310.

Csiki, M. 1908. Magyarorsag bogárfaunája. I Kotet. Bucharest. 546 pp.

†Cuni y Martorell, D.M. and D.M. Martorell y Peña. 1876. Catálogo metódico y razonado de los Coleópteros observados en Cataluña. Carlos Bailly-Bailliere, Madrid. viii + 359 pp.

Curtis, J. 1824-1840. British entomology: being illustrations and descriptions of the genera of insects found in Great Britain and Ireland containing coloured figures from nature of the most rare and beautiful species and in many instances of the plants upon which they are found. Privately printed, London. 12 volumes. [Volume 1, 1824, [4] + #1–50. Volume 2, 1825, [4] + #51–98. Volume 3, 1826, [4] + #99–146. Note - not paginated, each species treatment consists of text and plate numbered sequentially].

Darlington, P.J. 1938. *Dytiscus habilis* Say in Texas. Psyche 45: 84.

DeGeer, C. 1774. Mémoires pour servir à l'histoire des insectes. Volume IV. Pierre Hesselberg, Stockholm. 457 pp. + 19 planches.

Demandt, C. 1924. Der Geschlechtsapparat. Pp. 146-257 *in* E. Korschelt. *loc. cit.*

Deschamps, P.L.E. 1870. Dictionaire de géographie ancienne et modern...suivi de l'imprimerie hors l'Europe. Firmin Didot, Paris. [Reprinted 1964. Maison-neuve et Larose, Paris. 1592 col., 208 pp.].

†Dorsselaer, R. van. 1957. Catalogue des Coléoptères de Belgique. Fascicule III. Partie 4. Caraboidea Dytiscoidea. pp. 9–31. Siège social, Brussels pour la Société Royale d'Entomologie de Belgique. i + 36 pp.

Drummond, H., and G.W. Wolfe. 1981. An observation of a diving beetle larva (Insecta: Coleoptera: Dytiscidae) attacking and killing a garter snake, *Thamnophis elegans* (Reptilia: Serpentes: Colubridae). The Coleopterists' Bulletin 35: 121–124.

Duponchel, P.A.J. 1845. *In* C. d'Orbigny. Dictionaire Universel d'Histoire Naturelle. Volume 5. Renard, Martinet, et Cie., Paris.

Energy, Mines and Resources Canada. 1980. Canada Gazeteer Atlas. Macmillan of Canada and Canadian Government Publishing Centre, Supply and Services Canada, Ottawa. ix + 164 pp.

Engert, H. 1911. *Dytiscus punctulatus* F. var. nov. *laevis*. Entomologische Blätter, 7: 19.

Erichson, W.F. 1832. *Genera dyticeorum. (Dissertatio inauguralis).* C. Hold, Berlin. 48 pp.

Eriksson, U. 1972.The invertebrate fauna of the Kilpisjärvi area, Finnish Lapland. 10. Dytiscidae. *Acta Societatis pro Fauna et Flora Fennica*, 80: 121–160.

Erwin, T.L. 1970. A reclassification of bombardier beetles and a taxonomic revision of the North and Middle American species (Carabidae: Brachinida). *Quaestiones Entomologicae*, 6: 4–215.

Erwin, T.L. 1982. *Agra*, arboreal beetles of Neotropical forests: erythropus group systematics (Carabidae). Systematic Entomology, 7: 39–71.

Erwin, T.L., G.E. Ball, D.R. Whitehead and A.L. Halpern. Editors. 1979. Carabid beetles: their evolution, natural history, and classification. Dr. W. Junk, The Hague. f.p. + (5) + 635 pp.

†Escalera, M. Martinez de la. 1914. Los Coleópteros de Marruecos. Trabajos del Museo Nacional de Ciencias Naturales (Madrid), Ser. Zoológica, 11.

Evans, M.E.G. 1977. Locomotion in the Coleoptera Adephaga, especially Carabidae. Journal of Zoology, 181: 189–226.

Evans, M.E.G. 1985. Hydradephagan comparative morphology and evolution: some locomotor features and their possible phylogenetic implications. Proceedings of the Academy of Natural Sciences of Philadelphia, 137: 172–181.

Fabricius, J.C. 1775. *Systema Entomologiae, sistens Insectorum classes, ordines, genera, species, adjectis synonymus, locis, descriptionibus, observationibus*. Libraria Kortii, Flensburg et Lipsiae. [30] + 832 pp.

Fabricius, J.C. 1777. *Genera– Insectorum, eorumque characteres naturales secundum numerum, figuram, situm et proportionem omnivum partium oris adiecta mantissa specierum nuper detectarum*. M.F. Bartschii, Chilonii. [14] + 310 pp.

Fabricius, J.C. 1801. *Systema Eleutheratorum, secundum ordines, genera, species, adiectis locis, observationibus, descriptionibus*. Impensis Bibliopolii Academici Novi, Kiliae. Tomus I. xxiv + 506 pp. Tomus II. 687 pp.

†Falkenström, G. 1939. Halipliden und dytisciden aus der Iberischen Halbinsel, gesammelt im Sommer 1935 von Prof. Dr. O. Lundblad. Arkiv för Zoologi, 31A, (5): 1–22.

Feng, H.T. 1935. Aquatic insects of China. Article XIX. A new diving beetle from Szechuan (Order Coleoptera, Family Dytiscidae). Peking Natural History Bulletin, 9: 181–184.

Feng, H.T. 1937. Notes on some Dytiscidae from Musee Hoang Ho Pai Ho, Tientsin, with descriptions of eleven new species. Peking Natural History Bulletin, 11: 1–15.

†Fichtner, E. 1983. Beiträge zur Insektenfauna der DDR: Coleoptera - Dytiscidae (Insecta). Faunistische Abhandlungen staatliches Museum für Tierkunde in Dresden, 11: 1–48.

Fiori, A. 1881. Polimorfismo nella femmina del *Dytiscus dimidiatus* Berg. Bolletino della Società Entomologia Italiana, 13: 274–277.

Folkerts, G.W. 1978. A preliminary checklist of the Hydradephaga (Coleoptera) of Alabama. The Coleopterists' Bulletin, 32: 345–347.

Forbes, W.T.M. 1922. The wing venation of the Coleoptera. Annals of the Entomological Society of America, 15: 328-345 + plates XXIX-XXXV.

Forbes, W.T.M. 1926. The wing-folding patterns of the Coleoptera. Journal of the New York Entomological Society, 34: 42-68, 91–139.

Formanowicz, D.R. Jr. 1982. Foraging tactics of larvae of *Dytiscus verticalis* (Coleoptera: Dytiscidae): the assessment of prey density. Journal of Animal Ecology, 51: 757–767.

Formanowicz, D.R. Jr. 1986. Anuran tadpole/aquatic insect predator-prey interactions: tadpole size and predator capture success. Herpetologica, 42: 367–373.

Formanowicz, D.R. Jr. 1987. Foraging tactics of *Dytiscus verticalis* larvae (Coleoptera: Dytiscidae): prey detection, reactive distance and predator size. Journal of the Kansas Entomological Society, 60: 92–99.

Formanowicz, D.R. Jr. and M.S. Bobka. 1989. Predation risk and microhabitat preference: an experimental study of the behavioral responses of prey and predator. The American Midland Naturalist, 121: 379–386.

Formanowicz, D.R. Jr. and E.D. Brodie Jr. 1981. Prepupation behaviour and pupation of the predaceous diving beetle *Dytiscus verticalis* Say (Coleoptera: Dytiscidae). Journal of the New York Entomological Society, 89: 152–157.

Fourcroy, R.F. 1785. *Entomologia Parisiensis: sive Catalogus Insectorum quae in Agro Parisiensi reperiuntur; secundum methodum Geoffraeanan in sectiones, genera et species distributus: Cui addita sunt nomina triviata et fere trecentae novae species.* Paris. [Pars prima, viii + 231 pp., pars seconda, t.p. + 233–544.]

†Franciscolo, M.E. 1972. Hydroadephaga of Yugoslav Adriatic Islands. Acta Entomologica Jugoslavica, 8: 55–90.

†Franciscolo, M.E. 1979. Coleoptera: Haliplidae, Hygrobiidae, Gyrinidae, Dytiscide. Fauna d'Italia, 14. vi + 804 pp.

†de la Fuente, J.M. 1921. Catálogo sistemático- geográfico de los Colépteros observados en la Península Ibérica, Pirineos propiamente dichos y Baleares. Boletin de la Sociedad Entomologíca de España, 4: 262-265.

Galewski, K. 1964. The hibernation of the adults of the European species of Dytiscidae (Coleoptera) out of water. Polskie Pismo Entomologiczne, 34: 25–40.

Galewski, K. 1971a. Klucze do oznaczania owadow Polski. Cześć XIX Chrzaszcze - Coleoptera. Zeszyt 7 Plywakowate - Dytiscidae. Polskie Towarzystwo Entomologiczne. 112 pp.

Galewski, K. 1971b. A study on morphobiotic adaptations of European species of the Dytiscidae (Coleoptera). Polskie Pismo Entomologiczne, 41: 487–702.

†Galewski, K. 1976. Dytiscidae. Pp. 22-133 in B. Burakowski, M. Mroczkowski and J. Stefańska. Editors. Chrzszcze Coleoptera. Adephaga prócz Carabida, Myxophaga, Polyphaga: Hydrophiloidea. Katalog Fauny Polski, 28 (4): 1–275.

Ganglbauer, L. 1892. Die Käfer von Mitteleuropa. Die Käfer der österreichisch-ungarisch Monarchie, der Schweiz, sowie des franzöischen und italischen Alpengebietes. I. Familienreihe Caraboidea. Vienna. iii + 557 pp.

Gauld, I.D., and L.A. Mound. 1982. Homoplasy and the delineation of holophyletic genera in some insect groups. Systematic Entomology, 7: 73–86.

von Gebler, F.A. 1832. Notice sur les Coléoptères qui se trouvent dans le district des mines de Nertchinsk, dans la Sibérie orientale, avec la description de quelques espèces nouvelles. Mémoires de la Société Impériales des Naturalistes de Moscou, (Mémoires nouvelles 2), 8: 23–78.

Gemminger, M., and B. de Harold. 1868. Dytiscidae, Gyrinidae, Hydrophilidae, Staphylinidae, Pselaphidae, Gnostidae, Paussidae, Scydmaenidae, Silphidae, Trichopteryidae, Scaphididae. *Catalogus Coleopterorum hucusque descriptorum synonymicus et systematicus.* Tomus II. E.H. Gummi, Monachii pp. 425–752.

Geoffroy, E.L. 1762. Histoire abrégée des insectes qui se trouvent aux environs Paris, dans laquelle ces animaux sont rangés suivant un ordre méthodique. Volume I. Paris. xxviii + 523 pp. + planches i–x.

Goodliffe, F.D. 1939. The taxonomic value of wing venation in the larger Dytiscidae (Coleoptera). Transactions of the Society for British Entomology, 6: 23–38 + plate I.

Gordon, R.D., and R.L. Post. 1965. North Dakota Water Beetles. North Dakota Insects, 5: 1–53.

des Gozis, M. 1910-1916. Tableaux de détermination des dytiscides, notérides, hyphydrides, hygrobiides et haliplides de la faune Franco-rhéane. Miscellanea Entomologica 18–23.

Greenwood, P.H., and P.L. Forey. Editors. 1981. Chance, Change and Challenge. The Evolving Biosphere. British Museum (Natural History) and Cambridge University Press. viii + f.p. + 311 pp.

†Gridelli, E. 1930. Risultati zoologici della missione inviata dalla R. Società Geografica Italiana per l'esplorazione dell'oasi di Giarabub (1926–1927). Coleotteri. Annali del Museo Civico di Storia Naturale di Genova, 54. 487 pp + map.

Gschwendtner, L. 1922. Beiträge zur Kenntnis der Dytiscidae Transbaikaliens. Weiner entomologische Zeitung, 39: 92–94.

Gschwendtner, L. 1923. Einiges über Ost-Turkestan und dessen Dytisciden-Fauna. Archiv für Naturgeschichte, 8: 93–111.

Guéorguiev, V.B. 1958. Verzeichnis der Wasserkäfer Bulgariens. Entomologische Blätter für Biologie und Systematik der Käfer, 54: 44–51.

†Guéorguiev, V.B. 1971. Coleoptera Hydrocanthares et Palpicornia. *Catalogus faunae Jugoslaviae*, 3 (6): 1–45.

†Guignot, F. 1928. Notes de chasse nouveautés pour la faune Franco-Rhénane. Miscellanea Entomologica, 31: 82.

†Guignot, F. 1931a. Notes sur quelques Dytiscides. Miscellanea Entomologica, 33: 5-7.

†Guignot, F. 1931b-1933. Les Hydrocanthares de France. Hygrobiidae, Haliplidae, Dytiscidae et Gyrinidae de la France continentale avec notes sur les espèces de la Corse et de l'Afrique du Nord française. Douladoure, Toulouse. xv + 1057 pp. + planches I-VII. [Pp. 1–188 (1931), pp. 189–786 (1932), pp. 787–1057 (1933)].

Guignot, F. 1946. Génotypes des Dytiscoidea et des Gyrinoidea. Revue Française d'Entomologie, 13: 112–118.

†Guignot, F. 1947a. Coléoptères Hydrocanthares. Faune de France, 48. Lechevalier, Paris. 288 pp.

†Guignot, F. 1947b. Haliplides, Dytiscides et Gyrinides du haut atlas Marocain. Revue Française d'Entomologie, 13: 185–187.

†Guignot, F. 1961. Revision des Hydrocanthares d'Afrique (Coleoptera Dityscoidea). Troisième partie. Annales du Musée Royal du Congo Belge (Tervuren), Série Sciences Zoologiques, 90: 659–995.

Gyllenhal, L. 1808. *Insecta Suecia descripta Classis I. Coleoptera sive Eleutherata. Tomus I.* F.J. Leveventz. Scaris. VIII + 4 + 572 pp.

Gyllenhal, L. 1827. *Ibid. Tomus I. Pars IV. Cum appendice ad partes priores.* F. Fleischer, Lipsiae. viii + 2 + 762 pp.

Hammond, P.M. 1979. Wing-folding mechanisms of beetles, with special reference to investigations of adephagan phylogeny (Coleoptera). Pp. 113–180, *In* T.L. Erwin, *et al.*, *loc. cit.*

Hammond, P.M. 1981a. Speciation in the face of gene flow - sympatric-parapatric speciation. Pp. 37–48 (chapter 4) *in* P.H. Greenwood, and P.L. Forey, *loc. cit.*

Hammond, P.M. 1981b. The origin and development of reproductive barriers. Pp. 49–60 (chapter 5), *In* P.H. Greenwood, and P.L. Forey, *loc. cit.*

†Hardouin, R. 1933. Coléoptrèes aquicoles capturés dans les Départements de la Seine-et-Oise et de la Seine. Miscellanea Entomologica, 34: 85–87.

Hatch, M.H. 1929. Studies on Dytiscidae. Bulletin of the Brooklyn Entomological Society, 23 (1928): 217–229.

Hatch, M.H. 1933. Records of Coleoptera from Montana. The Canadian Entomologist, 65: 5–15.

Hatch, M.H. 1953. The beetles of the Pacific Northwest. Part I: Introduction and Adephaga. University of Washington Publications in Biology, Volume 16. University of Washington Press, Seattle. 340 pp.

Hennig, W. 1966. Phylogenetic Systematics. University of Illinois Press, Urbana. 263 pp.

†Hlisnikovský, J. 1954. Fauna dytiscidarum Bulgarica (Coleoptera). Acta Entomologica Musei Nationalis Pragae, 29: 93–103.

Holdhaus, K. 1912. Kritisches Verzeichnis der boreoalpin Teirformen (Glazialrelikte) der mittel- und südeuropäischen Hochgebirge. Annalen des Kaiserlich-Königlich Naturhistorischen Hofmuseums (Wien), 26: 399–440.

Holomuzki, J.R. 1985. Life history aspects of the predaceous diving beetle, *Dytiscus dauricus* (Gebler), in Arizona. The Southwestern Naturalist, 30: 485–490.

Holomuzki, J.R. 1986. Predator avoidance and diel patterns of microhabitat use by larval salamanders. Ecology, 67: 737–748.

Hope, F.W. 1839. The Coleopterist's manual, part the second, containing the predaceous land and water beetles of Linnaeus and Fabricius. H.G. Bohn, London. f.p. + xvi + 168 pp. + 3 plates.

†Horion, A. 1941. Faunistik der deutschen Käfer. Band I. Adephaga-Caraboidea. Hans Goecke Verlag, Krefeld. 464 pp.

Horn, W., and I. Kahle. 1935-1937. Über entomologische Sammlungen, Entomologen und Entomo-Museologie. (Ein Beitrag zur Geschichte der Entomologie). Teil I-III. [Reprinted from Entomologische Beihefte aus Berlin-Dahlem]. vi + 536 pp., 38 Tafeln.

†Houlbert, C. 1934. Faune entomologique Armoricaine. Coléoptères, Hydrocarabiques (Hydaticiformes). Bulletin de la Société Scientifique de Bretagne, 11: 1–147.

Hummel, A.-D. 1823. Observations sur les insectes de 1823. *Monographia pelophilarum. Novae species.* Essais entomologiques 3. Imprimerie de la Chancellerie privée du Ministère de l'Intérieur, St. Petersbourg. 48 pp.

†Ienistea, M-A. 1978. Hydradephaga und Palpicornia. Pp. 291-314 *in* J.Illies. Editor. Limnofauna Europaea. Verlag Stuttgart. Second edition. xvii + 532 pp. + map.

ICZN. 1985. International Code of Zoological Noememclature. British Museum (Natural History), London. Third Edition. xx + 338 pp.

Jackson, D.J. 1955. The capacity for flight of certain water beetles and its bearing on their origin in the western Scottish Isles. Proceedings of the Linnaean Society of London, 167: 76–96 + plate 7.

Jacquelin du Val, P.N.C., and J. Migneaux. 1857. Manuel entomologique. Genera des Coléoptères d'Europe comprenant leur classification en familles naturelles, la description de tous les genres, des tableaux dichotomiques destinés à faciliter l'étude, le catalogue de toutes les espèces de nombreux dessins au trait de caractères. Tome I. A. Deyrolle, Paris. cclxxvi + 140 pp. + 52 planches. [Cahier 3. Dytiscides, Gyrinides, pp. 69–84, planches 25–28].

†Jakobson, G.G. 1905. Coleoptera of Russia and western Europe [In Russian]. A.F. Devriena, St. Petersburg. iii + 1024 pp., 83 plates [incomplete].

James, H. G. 1961. Some predators of *Aedes stimulans* (Walk.) and *Aedes trichurus* (Dyar) (Diptera: Culicidae) in woodland pools. Canadian Journal of Zoology, 39: 533–540.

James, H.G. 1970. Immature stages of five diving beetles (Coleoptera: Dytiscidae), notes on their habits and life history, and a key to aquatic beetles of vernal woodland pools in southern Ontario. Proceedings of the Entomological Society of Ontario (1969), 100: 52–97.

†Jarrige, M.J. 1928. Contribution à la faune du Bassin de la Seine. Première note. Miscellanea Entomologica, 31: 77–79.

de Jong, R. 1980. Some tools for evolutionary and phylogenetic studies. Zeitschrift für zoologische Systematik und Evolutionsforschung, 18: 1–23.

Kavanaugh, D.H. 1979. Studies on the Nebriini (Coleoptera: Carabidae), III. New Nearctic Nebria species and subspecies, nomenclatoral notes, and lectotype designations. Proceedings of the California Academy of Sciences, 42: 87–133.

Kirby, W. 1837. Coleoptera. *In* J. Richardson. Fauna Boreali-Americana; or the zoology of the northern parts of British America. Part 4, The Insects. Josiah Fletcher, Norwich and London. xxix + 325 pp.

†Kocher, L. 1953. Localisations nouvelles ou intéressantes de Coléoptères marocains. Travaux de l'Institut Scientifique Chérifien, 7. 142 pp + map.

†Kocher, L. 1956. Catalogue commenté des Coléoptères du Maroc. Fascicule I. Préface, introduction, carte. Travaux de l'Institut Scientifique Chérifien, Série Zoologie, 7. 26 pp. + map.

†Kocher, L. 1958. *Ibid.* Fascicule II. Hydrocanthares, Palpicornes, Brachelytres. Travaux de l'Institut Scientifique Chérifien, Série Zoologie, 14. 246 pp.

†Konev, A.A. 1976. On the fauna of water-beetles of sub-order Adephaga (Coleoptera) of Central Kasakhstan. [In Russian] Entomologicheskoe Obozrenie, 55: 820–822.

Korschelt, E. Editor. 1923. Bearbeitung einheimischer Tiere. Erste Monographie: Der Gelbrand *Dytiscus marginalis* L. Band I. Verlag Wilhelm Engelmann, Leipzig. (6) + 863 pp.

Korschelt, E. Editor. 1924. *Ibid.* Band II. vii + 964 pp.

Kunze, G. 1818. Vermischte Bemerkungen und Zusätze zu den in dieser Schriften abgehandelten Gattungen und Arten der Käfer. Neue Schriften der naturforschenden Gesellschaft zu Halle, 2: 57–70.

Lafontaine, J.D. 1982. Classification and phylogeny of the *Euxoa detersa* group (Lepidoptera: Noctuidae). *Quaestiones Entomologicae*, 17: 1–20.

de LaPorte, F.L.N.C. (Compte de Castelnau). 1834, 1835. Études entomologiques, ou descriptions d'insectes nouveaux, et observations sur leur synonymie. Coléoptères carnassiers. Méquignon-Marvis, Paris. [Pp. 1–94 + planches 1-2 (1834). Pp. 95–159 + planches 3–4 (1835)].

La Rivers, I. 1951. Nevada Dytiscidae (Coleoptera). American Midland Naturalist, 45: 392–406.

†Larson, D.J. 1975. The predaceous water beetles (Coleoptera: Dytiscidae) of Alberta: systematics, natural history and distribution. *Quaestiones Entomologicae*, 11: 245–498.

Latreille, P.A. 1806-1809. *Genera Crustaceorum et Insectorum secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimus explicata.* Tomus I-IV. A. Koenig, Parisiis et Artgentorati. 4 volumes + 16 plates. [Tomus I. 302 pp. (1806)].

Latreille, P.A. 1810. Considérations générales sur l'ordre naturel des animaux composant les classes des Crustacés, des Arachnides, et des Insectes; avec un tableau méthodique de leurs genres, disposés en familles. J. Schoell, Paris. 444 pp.

Leblanc, P. 1982. A propos du *Dytiscus* (*Macrodytes*) *mutinensis* [Col. Dytiscidae]. L'Entomologiste, 38: 238–241.

LeConte, J.L. 1845. Descriptions of some new and interesting insects inhabiting the United States. Boston Journal of Natural History, 5: 203-209 + plate XVIII. [Separates of this paper paginated differently.]

LeConte, J.L. 1850. General remarks upon the Coleoptera of Lake Superior. Pp. 201–242 *in* J.L.R. Agassiz. Lake Superior: Its physical character, vegetation and animals compared with those of other and similar regions, with a narrative of the tour by J. Eliott Cabot, and contributions by other scientific gentlemen. Gould, Kendall and Lincoln, Boston. x + 248 pp. + plates 1–8 + unnumbered landscapes.

LeConte, J.L. 1857. Zoological Report No. 1. Report upon insects collected on the survey. Reports of explorations and surveys to ascertain the most practicable and economical route for a railroad from the Mississippi River to the Pacific Ocean. Made under the direction of the Secretary of War, in 1853-5, according to Acts of Congress of March 3, 1853, May 31, 1854, and August 5, 1854. Volume XII, Book II. Washington. Pp. 1–72, pl. 1 & 2.

LeConte, J.L. 1859. Editor. Insects of American Entomology: A description of the insects of North America, by Thomas Say, with illustrations drawn and colored after nature. Bailliere Bros., New York. [Volume 1, xxiv + 412 pp. + 55 pl. Volume 2, iv + 814 pp.].

Leech, H.B. 1941. The dates of the publication of two articles on Coleoptera by John L. LeConte, issued in 1845. Entomological News, 52: 290–291.

Leech, H.B. 1948. Contributions toward a knowledge of the insect fauna of Lower California. No. 11. Coleoptera: Haliplidae, Limnebiidae. Proceedings of the California Academy of Sciences (Series 4), 24: 375-484 + plates 21–22.

Leech, H.B., and H.P. Chandler. 1956. Aquatic Coleoptera. Pp. 293–371 *in* R.L. Usinger. Editor. Aquatic insects of California with keys to North American genera and California species. University of California Press. Berkeley and Los Angeles. ix + 508 pp.

Lindroth, C.H. 1969. The ground-beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Part I. *Opuscula Entomologica*, Supplementum 35. xlviii pp.

Lindroth, C.H., and R. Freitag. 1969. North American ground beetles (Coleoptera, Carabidae, excluding Cicindelinae) described by Thomas Say: Designations of lectotypes and neotypes. Psyche, 76: 326–361.

†Lindroth, C.H., V. Hansen, E. Klefbeck, O. Sjöberg, G. Stenius and A. Strand. 1960. Catalogus Coleopterorum Fennoscandiae et Daniae. Entomologiska Sällskapet, Lund. 476 pp + map.

Linnaeus, C. 1758. *Systema naturae per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata.* Stockholm. 823 + 1 pp. [Photographic facsimile, British Museum (Natural History), London].

Mannerheim, C.G. 1843. Beitrag zur Kaefer-fauna des Aleutischen Inseln, der Insel Sitkha, und neu-Californiens. Bulletin de la Société Impériale des Naturalistes de Moscou, 16: 175-314.

Mannerheim, C.G. 1852. Zweiter Nachtrag zur Kaefer-Fauna der Nord-Amerikanischen Laender des Russischen Reiches. Bulletin de la Société Impériale des Naturalistes de Moscou, 25: 283-387.

†Marcu, O. 1936. Die Wasserkäferfauna (Haliplidae, Hygrobiidae, Dytiscidae, Gyrinidae) der Bucovina. Festschrift zum 60. Geburgstage von Professor Dr. Embrik Strand 1: 629-637.

Marsham, T. 1802. *Entomologia Britannica, sistens Insecta Britanniae indigena secundum methodum Linnaeanam disposita. Tomus* I. Coleoptera. Wilks & Taylor. London. xxxi + 547 + [1] pp.

Mayr, E. 1942. Systematics and the origin of species from the viewpoint of a zoologist. Columbia University Press, New York. 334 pp.

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

Mayr, E. 1969. Principles of systematic zoology. McGraw-Hill, New York. 328 pp.

Melsheimer, F.E. 1844. Descriptions of new species of Coleoptera of the United States. Proceedings of the Academy of natural Sciences of Philadelphia, 2: 26-118, 134-160, 213-223, 302-318.

Michael, A.G., and J.F. Matta. 1977. The Dytiscidae of Virginia (Coleoptera: Adephaga) (Subfamilies: Laccophilinae, Colymbetinae, Dytiscinae, Hydaticinae and Cybistrinae). The Insects of Virginia, 12:1-53.

von Motschulsky, V. 1852. Nouveautés. Études Entomologiques, 1:77-80.

von Motschulsky, V. 1855. Synonymies. Études Entomologiques, 4:79.

von Motschulsky, V. 1859. Coléoptères nouveaux de la Californie. Bulletin de la Société Impériale des Naturalistes de Moscou, 32: 122-185, 357-410.

von Motschulsky, V. 1860. Coléoptères de la Sibérie orientale et en particulier des rives de l'Amour. Pp. 77–257, 6 Tafeln + map *in* L. von Schrenck. Reisen und Forschungen in Amurlande. Band 2, Leiferung 2. Coleopteren. Kaiserlichen Akademie der Wissenschaften.

†Müller, G. 1926. I Coleotteri della Venezia Giulia. Parte I: Adephaga. Studi Entomologici, 1(2): 3-306.

Müller, O.F. 1776. *Zoologicae Danicae prodromus, seu animalium Daniae et Norvegiae indigenarum characteres, nomina, et synonyma imprimis popularium.* Hallageriis, Havniae. xxxii + 282 pp.

Nilsson, A.N., R.E. Roughley and M. Brancucci. 1989. A review of the genus- and family-group names of the family Dytiscidae Leach (Coleoptera). Entomologica Scandinavica 20: 287-316.

Olivier, M. 1795. Entomologie, ou histoire naturelle des insectes, avec leurs caractères générique et spécifiques, leur descriptions, leur synonymie, et leur figure enluminée. Coléoptères. (3rd edition). Lanneau, Paris. 557 pp., 65 planches.

Opinion 619. 1961. *Acilius* Leach, 1817 (Insecta, Coleoptera); preservation by use of the plenary powers to vary the ruling given in opinion 522. Bulletin of Zoological Nomenclature, 18: 369-371.

Ordish, R.G. 1966. A systematic revision of the New Zealand water beetles (Coleoptera: Dytiscidae). Records of the Dominion Museum (Wellington, New Zealand), 5: 217-264.

Ordish, R.G. 1967. The identification of New Zealand water beetles (Dytiscidae). Tuatara, 15: 1-9.

†Paulin de Oliviera, M. 1887. Catalogue des insectes du Portugal. Coleoptères. Imprensa da Universidade Coimbra. 393 pp.

†Pederzani, F. 1971. Il *Dytiscus dimidiatus* Bergstr. var. *mutinensis* Fiori elevato al rango di specie. Bolletino della Società Entomologica Italiana, 103: 219-224.

Peyerimhoff, P. de. 1905. Nouveaux Coléoptères du Nord-Africain (Première note). Bulletin de la Société Entomologique de France, 1905: 229-230.

Peytoreau, A. 1894. Sur le *Dytiscus herbeti* (spec.nova) ♀ et ♂ et le *Dytiscus pisanus* Cast., var. *kunstleri* (var. nova) ♀. Comptes Rendu de la Société Linnéenne de Bourdeau, 47: xxxiii-xlii.

†Poppius, B. 1910. Die Coleopteren des arktischen Gebietes, Pp. 289-447 *in* F. Römer, F. Schaudlinn, A. Brauer and W. Arndt. Editors. Fauna Arctica. Eine Zusammenstellung der arktischen Tierformen mit besonderer Berücksichtigung des Spitzbergen Gebietes auf Grund der Ergebnisse der Deutschen Expedition in das Nördliche Eismeer im Jahr 1898. Band 5, Leiferung 1. G. Fischer, Jena. 447 pp. + 5 pl.

†Rapp, O. 1933. Die Käfer Thüringens unter besonderer Berücksichtigung der faunistisch-oekologischen Geographie auf Grund der Literatur, die Beiträge zahlreicher Entomologen und einer Beobachtungen im Aufrage der Akademie gemeinütziger Wissenschaften zu Erfurt. Die Natur der mitteldeutschen Landschaft Thüringen, Band I. xiii + 770 pp.

Régil, J.A. and J.M. Salgado. 1984. Identificación mediante el aparato genital feminio de las especies del género *Dytiscus* (subgen. *Macrodytes* Thomson) y su distribución en la provincia de Léon. Miscellánea Zoológica, 8: 133–137.

†Régil Cueto, J.A. and A. Veiga Fernandez. 1985. Primeras observaciones sobre la adefagofauna acuática de Palencia (Col.: Dytiscidae, Gyrinidae, Haliplidae e Hygrobiidae). Publicaciónes del Instituto Tello Téllez de Meneses, 53: 5–41.

Régimbart, M. 1899. Révision des Dytiscidae de la Région Indo-Sino-Malaise. Annales de la Société Entomologique de France, 68: 186–367.

Reineck, G. 1921. Über eine auffallende Form *Dytiscus marginalis* L. Deutsche entomologische Zeitschrift, 1921: 117.

Reitter, E. 1908. Fauna Germanica. Die Käfer des deutschen Reiches nach der analytischen Methode bearbeitet. Band I. Stuttgart. vii + 248 pp., 40 Tafeln.

Reitter, E. 1909. Coleoptera, Käfer. *In* A. Brauer. Editor. Die Süsswasserfauna Deutschlands, Heft 3 und 4. Gustav Fischer, Jena. 235 pp.

Richoux, P. and C. Dufay. 1986. Présence en Gréce continentale de *Dytiscus dimidiatus* Bergstr. var. *mutienensis* Fiori: statut taxinomique et répartition géographique (Coléoptères, Dytiscidae). Biologia Gallo-hellenica, 12: 421–431.

Ríha, P. 1955. Studies on the metathoracic furca of the Palearctic Dytiscidae (Coleoptera). Acta Entomologica Musei Nationalis Pragae, 30: 341-398, 14 plates.

Roberts, C. 1905. The distinctive characters of the eastern species of the genera *Dytiscus* and *Cybister*. Journal of the New York Entomological Society, 13: 103–107.

Romberger, J.A., R.H. Foote, L. Knutson, and P.L. Lentz. Editors. 1978. Biosystematics in agriculture. Beltsville symposia in agricultural research 2. Allenheld, Osmun and Company, Montclair, New Jersey (distributed by John Wiley and Sons, New York). xii + 340 pp.

Room, A. 1979. Place-name changes since 1900: A world gazetteer. Scarecrow Press, Metuchen, New Jersey. xxii + 202 pp.

Rosenhauer, W.G. 1856. Die Thiere Andalusiens nach dem Resultate einer Reise zusammengestellt, nebst den Beschreibungen von 249 neuen oder bis jetzt noch unbeschriebenen Gattungen und Arten. Blaesing, Erlangen. viii + 429 pp.+ 3 Tafeln.

Roughley, R.E., and D.H. Pengelly. 1982. Classification, phylogeny, and zoogeography of Hydaticus Leach (Coleoptera: Dytiscidae) of North America. *Questiones Entomologicae*, 17 (1981): 249–309.

†Sahlberg, J. 1913. *Coleoptera mediterranea orientali, quae in Aegypto, Palaestina, Syria, Caramania atque in Anatolia occidentali anno 1904 collegerunt John Sahlberg et Unio Saalas.* Finska Vetenskaps Societetens Förhandlingar, 55, Afd. A, No. 19:1–282.

Say, T. 1823. Descriptions of insects of the families of Carabici and Hydrocanthari of Latreille, inhabiting North America. Transactions of the American Philosophical Society (new series), 2: 1–109.

Say, T. 1824. Appendix to the narrative of an expedition to the source of the St. Peter's River, &c., under the command of Major S.H. Long, U.S.T.E. Western Quarterly Reporter, 2: 268–378.

Say, T. 1834. Descriptions of new North American insects and observations on some already described. Transactions of the American Philosophical Society (new series), 4: 409–470.

Schaeflein, H. 1971. 4. Fam. Dytiscidae. Pp. 16–89 + table *in* H. Freude, K.W. Harde, and G.A. Lohse. Editors. Die Käfer Mitteleuropas. Band 3. Goecke und Evers Verlag, Krefeld. 365 pp. + Table.

Schaeflein, H. 1973. *Dytiscus dimidiatus* Bergstr. var. ♀ *mutinensis* Fiori ist species propria (Coleoptera, Dytiscidae). Nachrichtenblatt der Bayerischen Entomologen, 22: 74–75.

†Schaeflein, H. and G. Wewalka. 1982. Ordn.: Coleoptera Fam.: Hygrobiidae, Haliplidae, Dytiscidae. *Catalogus Faunae Austriae*, Teil XV c:1–27.

Schaufuss, L.W. 1882. [*Dytiscus punctulatus* var. *maurus* n.v.] Bulletin de la Société Entomologique de France (series 6), 2: clxxiii.

Schaufuss, C. 1916. Calwer's Käferbuch, einführung in die Kenntnis der Käfer Europas. (Sechste Auflage). Schweizerbart'sche, Stuttgart. Band I. iii + 709 pp + 20 Tafeln.

†Scherdlin, P. 1920. Deuxième supplément au catalogue des Coléoptères de la chaine des Vosges et des régions limitrophes. Bulletin de la Société d'Histoire Naturelle de Colmar, 15: 1–255.

Schmiedlein, G.B. 1786. Einleitung in die nähere Kenntnis der Insektenlehre nach dem Linnéischen System, zum Gebrauch angehender Sammler. Boehme, Leipzig. 8 + 194 pp. + 2 Tafeln.

Seidlitz, G.C.M. 1887. Bestimmungs-Tabelle der Dytiscidae und Gyrinidae der europäischen Faunengebietes. Verhandlungen des Naturforschenden Vereines in Brünn. 25: 3–136 [Reprinted in same year *in* E.M. Reitter.

Editor. Bestimmungs-Tabelle des europäischen Faunengebietes No. 15. 136 pp.].

Seltzer, L.E. Editor. 1962. The Columbia Lippencott Gazetteer of the World. Columbia University Press, Morningside Heights, New York. x + 2148 + 22 pp.

Serville, J.G. Audinet-. 1830. *In* J.G. Audinet-Serville and A.L.M. Lepeletier. La partie qui a paru des insectes de la Faune française. Tome 3. Les Insectes. Les Coléoptères. Levrault, Paris. 240 pp.

Severin, G.A. 1892. Les collections d'articul s du Musée Royal d'Histoire Naturelle de Belgique. Annales de la Société Entomologique de Belgique, 36: 469–478.

Sharp, D. 1874. Some additions to the coleopterous fauna of Japan. Transactions of the Entomological Society of London, 1874: 417–422.

Sharp, D. 1882. On aquatic carnivorous Coleoptera or Dytiscidae. The Scientific Transactions of the Royal Dublin Society, 2 (new series), part II: 179–1003 + plates vii-xviii.

†Sharp, D. 1884. The water beetles of Japan. Transactions of the Entomological Society of London, 1884: 439–464.

Simpson, G.G. 1961. Principles of animal taxonomy. Columbia University Press, New York. 247 pp.

Stephens, J.F. 1828–1829. Illustrations of British entomology or, a synopsis of indigenous insects containing their generic and specific distinctions with an account of their metamorphoses, times of appearance, localities, food, and economy, as far as practicable. Mandibulata 2. Baldwin and Craddock, London. 200 pp., pl. 10–15.

†Thérond, J. 1975. Catalogue des Coléoptères de la Camarque et du Gard. 1ère partie. Société d'Étude des Sciences Naturelles de Nîmes, Mémoire 10.

Thomson, C.G. 1859. Skandinaviens Coleoptera, synoptiskt bearbetade. Tomus I. Berlingska, Lund. vi + 290 pp.

Thomson, C.G. 1860. *Ibid.* Tomus II. 304 pp.

Thunberg, C.P. 1794. *Dissertatio entomologica sistens, Insecta Suecica. Pars* VI. Edman, Upsala. ii + 73–82.

Wallis, J.B. 1950. A new species of *Dytiscus* Linnaeus (Coleoptera: Dytiscidae). The Canadian Entomologist, 82: 50–52.

Wallis, J.B., and D.J. Larson. 1973. An annotated list of the Hydroadephaga (Coleoptera: Insecta) of Manitoba and Minnesota. *Quaestiones Entomologicae*, 9: 99–114.

Ward, R.D. 1979. Metathoracic wing structures as phylogenetic indicators in the Adephaga (Coleoptera). Pp. 181–191 *in* T.L. Erwin *et al.*, *loc. cit.*

Watrous, L.E., and Q.D. Wheeler. 1981. The out-group comparison method of character analysis. Systematic Zoology, 30: 1–11.

Watts, C.H.S. 1964. The larvae of Australian *Cybister* spp. Curt., *Homeodytes* spp. Reg. and *Hyderodes schuckardi* Hope (Coleoptera: Dytiscidae). Transactions of the Royal Society of South Australia, 88: 145–156.

Watts, C.H.S. 1978. A revision of the Australian Dytiscidae (Coleoptera). Australian Journal of Zoology, Supplementary series, 57:1–166.

Wehncke, E. 1875. *Dytiscus sharpi* n. sp. Entomologische Zeitung 1875: 500.

Wehncke, E. 1876. Ein neuer *Dytiscus*. Stettiner entomologische Zeitung, 37: 52.

von Well, J. 1781. *Additamenta quaedam ad entomologiam.* Pp. 380–386 + plate 23. *In* N.J. von Jacquin. *Miscellanea Austriaca, ad Botanicum, Chemiam et Historiam Naturalam spectatia. Tomus 2.* Kraus, Vindobonae.

Wesenberg-Lund, C. 1912. Biologische Studien über Dytisciden. Internationalen Revue der gesamten Hydrobiologie und Hydographie, Biologische Supplemente V, Nr. XIV: 11–129, Tafeln I–IX.

Wesenberg-Lund, C. 1943. Biologie der Süsswasserinsekten. J. Springer, Berlin und Wien. [8] + 682 pp. + Tafeln I-XIII.

Westwood, J.O. 1838. Synopsis of the genera of British insects. Pp. 1–48 *in* J.O. Westwood. An introduction to the modern classification of insects, founded on the natural habits and corresponding organization of the different families. Longman, Orme, Brown, Green, and Longman, London. 2 volumes.

Whitehead, D.R. 1972. Classification, phylogeny, and zoogeography of *Schizogenius* Putzeys (Coleoptera: Carabidae: Scaratini). *Quaestiones Entomologicae*, 8: 131–348.

Wickham, H.F. 1895. The Coleoptera of Canada. X. The Dytiscidae (Dytiscini and Cybistrini) of Ontario and Quebec. The Canadian Entomologist, 27: 149–153.

Wiley, E.O. 1981. Phylogenetics. The Theory and Practice of Phylogenetic Systematics. John Wiley and Sons, New York. xv + 439 pp.

Wilson, C.B. 1923. Water beetles in relation to pondfish culture, with life histories of those found in fishponds at Fairport, Iowa. Bulletin of the U.S. Bureau of Fisheries (1923-1924), 39, Document No. 953: 231–345.

†Wu, C.F. 1937. *Catalogus insectorum sinensium*. Volume III. Fan Memorial Institute of Biology, Peiping, China. x + 1312 pp.

Yoon, Il-Byong and Kee-Jeong Ahn. 1988. A systematic study of Korean Dytiscidae III. Colymbetinae and Dytiscinae. The Korean Journal of Entomology, 18:251–268.

Young, A.M. 1966. The culturing of the diving beetle, *Dytiscus verticalis*, in the laboratory for observation of holometabolic development in aquatic insects. Turtox News, 44: 224–228.

Young, F.N. 1954. The water beetles of Florida. University of Florida Biological Series, 5(1): 1–238.

†Zaitsev, F.A. 1953. Families Amphizoidae, Hygrobiidae, Haliplidae, Dytiscidae, Gyrinidae. Fauna of the USSR Coleoptera Volume 4. Zoological Institute of the Academy of Sciences of the USSR, new series, No. 58. [Translated from Russian (1972), Israel Program for Scientific Translations, Jerusalem, 1972. iii + 401 pp.].

Zaitzev, P. 1906. Drei neue Dytisciden-Arten (Coleoptera). Revue Russe d'Entomologie, 6: 26-28.

Zaitzev, P. 1908. Berichtigungen and Zusätze zu den Haliplidae, Dytiscidae und Gyrinidae in der neuesten Katalogen der Coleoptera. Revue Russe d'Entomologie, 1907: 114-124.

†Zimmermann, A. 1919. Die Schwimmkäfer des deutschen entomologischen Museums in Berlin-Dahlem. Archiv für Naturgeschichte, 83(12): 68–249, 2 Tafeln.

Zimmermann, A. 1920. Pars 71: Dytiscidae, Haliplidae, Hygrobiidae, Amphizoidae. *In* W. Junk and S. Schenkling. Editors. *Coleoptorùm Catalogus*. Volume X, IV. W. Junk, Berlin and s'Gravenhage. 326 pp.

†Zimmermannn, A. 1925. Entomologische Ergebnisse der schwedischen Kamtchatka-Expedition 1920-1922. 9. Haliplidae und Dytiscidae. Arkiv för Zoologi, 18B (5):1-3.

Zimmermann, A., and L. Gschwendtner. 1938. Monographie der paläarktischen Dytisciden. IX. Dytiscinae. Koleopterologische Rundschau, 24: 33-76

[Reprinted in same year in Edm. Reitter. Bestimmungs-Tabellen der europäischen Coleoptera. Verlag Edm. Reitter, Troppau. Heft 121. 44 pp.].

Zimmermann, A., and L. Gschwendtner. 1939. Monographie der paläarktischen Dytisciden. X. Ergänzungen und Register. Koleopterologische Rundschau, 25: 23-69. [Reprinted in same year *in* Edm. Reitter. Bestimmungs-Tabellen der europäischen Coleoptera. Verlag Edm. Reitter, Troppau. Heft 122. 47 pp.].

INDEX TO NAMES OF TAXA

(Junior synonyms in italics)

Quaestiones
Entomologicae

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

VOLUME 26 NUMBER 4 FALL 1990

Publication of *Quaestiones Entomologicae* was started in 1965 as part of a memorial project for Professor E.H. Strickland, the founder of the Department of Entomology at the University of Alberta in 1922.

It is intended to provide prompt relatively low cost publication for comprehensive accounts of entomological research of greater than average length. However, shorter papers about insects in the Prairie Provinces of Canada are acceptable. Page charges are normally levied, the rate determined by printer's charges. For information about current page charges, consult the Editor.

Copy for all types of papers should conform to the Style Manual for Biological Journals, published by the American Institute of Biological Sciences, Second Edition, 1964, except that title of periodicals should be given in full. For style of taxonomic papers, the Editor should be consulted. Two copies of a manuscript are requested. All manuscripts will be reviewed by referees.

Abstracts are required, one in English and one in another language, preferably French.

Copy for illustrations must accompany the manuscript, and be of such character as to give satisfactory reproduction at page size (less 1/2 inch, or 1.2 cm on plates of full page size [7 X 4 1/4 inches or 17.8 X 10.7 cm]). Reprints must be ordered when proofs are returned, and will be supplied at cost.

Subscription rates are the same for institutions, libraries and individuals, $20.00* per volume of four issues, normally appearing at quarterly intervals; single issues $5.00**. Back volumes and issues are available at the same cost. These prices supersede those previously indicated, and are subject to change as required by inflationary pressure on the value of money.

Communications regarding subscriptions should be addressed to the Subscription Manager, and regarding manuscripts to the Editor.

* Same rate in U.S.$ for non-Canadian subscriptions.

** Single issues of more than 100 pages: $10.00; exception: volume 21(4) - $20.00.

Published quarterly by:

Department of Entomology
University of Alberta
Edmonton, Alberta, CANADA
T6G 2E3

Second Class Mail Registration Number 5222

Return Undeliverable mail to the address above. Return Postage Guaranteed

Issued December 1990

QUAESTIONES ENTOMOLOGICAE ISSN 0033-5037

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

Volume 26 Number 4 1990

CONTENTS

Revision of the *Anthonomus* Subgenus *Anthonomocyllus* Dietz (Coleoptera: Curculionidae)

Wayne E. Clark
Department of Entomology and
Alabama Agricultural Experiment Station
Auburn University
Auburn, Alabama, 36849-5413
USA

Quaestiones Entomologicae
26: 559–600 1990

ABSTRACT

The seventeen species of Anthonomus *Germar in the subgenus* Anthonomocyllus *Dietz include* Anthonomus tenuirostris *Champion (=* A. filirostris *Champion, new synonymy),* A. argentatus *Gyllenhal,* A. costulatus *Suffrian (=* A. elegans *LeConte),* A. contaminatus *Boheman,* A. dentipes *Hustache (=* A. murinofasciatus *Voss, new synonymy),* A. xanthoxyli *Linell,* A. leucostictus *Dietz,* A. aeroides *Champion,* A. caeruleisquamis *Champion, and eight new species:* A. acus, A. accola, A. azalus, A. guanita, A. pazmani, A. aeroides, A. cymatilis *and* A. caesius. *The species occur in the Southern United States, México, Central and South America and in the West Indies. Some are known to be associated with plants in the genus* Zanthoxylum *(Rutaceae). Lectotypes are designated for* A. tenuirostris, A. filirostris, *and* A. dentipes, *and a neotype is designated for* A. murinofasciatus. *Characters of the subgenus and of the species groups and included species are described and illustrated and a key to adults of the species is presented. The phylogenetic relationships of the species are reconstructed on the basis of apomorphic characters of adults.*

INTRODUCTION

Anthonomocyllus was established by Dietz (1891) as a subgenus of the genus *Anthonomus* Germar to include *A. elegans* LeConte from Florida, *A. leucostictus* Dietz and *A. pusillus* LeConte (= *A. hamiltoni* Dietz) from Texas. Later, *A. xanthoxyli* Linell from Texas, *A. atomarius* Blatchley from New Jersey, and *A. murinofasciatus* Voss from Brazil were added (Linell 1897, Blatchley and Leng 1916, Voss 1944). Burke (1968) and Ahmad and Burke (1972) noted that the subgenus thus constituted contained disparate elements, suggesting the need for a revision. Seventeen New World species of *Anthonomus*, eight of them new, are herein assigned to *Anthonomocyllus*. Descriptions, illustrations and keys are presented in this paper to facilitate identification of the species.

MATERIALS AND METHODS

Specimens of 485 adults, including the types of most of the previously described species, were examined. These were borrowed from the collections of the following individuals and institutions (letter codens identify the collections in the text):

AMNH	The American Museum of Natural History, New York, New York, USA, L. H. Herman, Jr.;
AUEM	Auburn University Entomological Collections, Auburn, Alabama, USA, W. E. Clark;
BMNH	The British Museum (Natural History), London, England, R. T. Thompson;

CMFP	M. Ferragu Collection, Paris, France;
CNCI	Canadian National Collection of Insects and Arachnids, Ottawa, Canada, D. E. Bright;
CWOB	Collection of C. W. O'Brien, Tallahassee, Florida, USA;
DEIC	Deutsches Entomologisches Institut, Eberswalde, DDR, L. Dieckmann;
DZUP	Universidade Federal do Paraná, Curitiba, Brazil, G. H. Rosado-Neto;
FSCA	Florida State Collection of Arthropods, Gainesville, Florida, USA, R. E. Woodruff;
HAHC	H. and *A* Howden Collection, Ottawa, Ontario, Canada;
IZAV	Universidad Central de Venezuela, Maracay, Venezuela, L. J. Joly;
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA, S. R. Shaw;
MHND	Museum Nacional de la Historia Natural, Santo Domingo, Republica Dominicana; *A* Zaglul;
MNHN	Muséum National d'Histoire Naturelle, Paris, France, H. Perrin;
MPEG	Museu Paraense Emilio Goeldi, Belém, Pará, Brazil, W. L. Overal;
MZSP	Museu de Zoología, Universidade de São Paulo, São Paulo, Brazil, U. R. Martins;
NHRS	Naturhistoriska Riksmuseum, Stockholm, Sweden, P. I. Persson;
RSAC	Robert S. Anderson Collection, College Station, Texas, USA;
TAMU	Texas A&M University, College Station, Texas, USA, H. R. Burke;
USNM	National Museum of Natural History, Washington, D. C., USA, D. R. Whitehead.
ZMHB	Museum für Naturkunde der Humboldt-Universität, Berlin, DDR, F. Hieke.

Measurements were made with an ocular micrometer in a dissecting microscope as follows: total body length from anterior margin of eye to elytral apex in lateral view; width across elytra at widest point; length of pronotum from anterior to posterior margins; length of rostrum from anteroventral margin of eye to apex, across arc, in lateral view; length of distal portion of rostrum from antennal insertion to apex in lateral view; width of frons at narrowest point between eyes; width of base of rostrum just distad of eyes in dorsal view; and width of pro- and metafemora, in anterior view, excluding inner marginal teeth. The range and, in parentheses, the mean and sample size of each measurement, are given for each species.

Subgenus *Anthonomocyllus* Dietz

Anthonomocyllus Dietz 1891: 191. Type species, *Anthonomus costulatus* Suffrian (= *A. elegans* LeConte), by original designation). Blatchley and Leng 1916: 287. Schenkling and Marshall 1934: 38. Voss 1944: 47-48. O'Brien and Wibmer 1982: 105. Wibmer and O'Brien 1986: 203.

Recognition.— The composition of the subgenus *Anthonomocyllus* is defended on the basis of hypotheses of phylogenetic relationships presented in the phylogeny section. Monophyly of the subgenus is indicated by a single apomorphic character shared by adults of most of the species:

Mesocoxae widely separated from each other by distance *ca.* 0.50 times wider than the diameter of a mesocoxa or more.

The mesocoxae are more narrowly separated in a monophyletic group composed of *A. tenuirostris*, *A. acus* and *A. accola*. The protibia in these three species is like that in species assigned to the *A. tenuirostris* group that have widely separated mesocoxae in having a slender, acute median tooth on the inner margin tooth (Figs. 53-59). The pronotum is flattened in the latter two species (Figs. 4, 6), as in the other species assigned to the *A. tenuirostris* group, and like those species it has a large dorsal macula of imbricated, pallid scales on the anterior and median portions of the dorsum (Figs. 8, 12, 14, 16, 18).

Included species.— The seventeen species of *Anthonomocyllus* are placed in three species groups.

- *A. tenuirostris* Species Group
  - *A. tenuirostris* Champion (Guatemala, México)
  - *A. acus*, new species (Bolivia, Brazil, México)
  - *A. accola*, new species (Venezuela)
  - *A. argentatus* Gyllenhal (Cuba, Jamaica, Hispaniola, Puerto Rico, St. Barthélemy, Trinidad, Venezuela)
  - *A. costulatus* Suffrian (= *A. elegans* LeConte) (Bahamas, Cuba, Florida)
  - *A. azalus*, new species (México)
  - *A. contaminatus* Boheman (Colombia, Venezuela)
  - *A. dentipes* Hustache (= *A. murinofasciatus* Voss) (Argentina, Brazil)
  - *A. guanita*, new species (Antigua, Guadeloupe, Hispaniola)
  - *A. pazmani*, new species (México)
  - *A. xanthoxyli* Linell (México, Texas)
- *A. leucostictus* Species Group
  - *A. leucostictus* Dietz (= *A. albopictus* Champion) (México, Texas)
- *A. caeruleisquamis* Species Group
  - *A. squamiger* Champion (Panamá, Venezuela)
  - *A. caeruleisquamis* Champion (Guatemala)
  - *A. aeroides* new species (Colombia, Venezuela)
  - *A. cymatilis*, new species (Brazil)
  - *A. caesius*, new species (Brazil)

Some species previously in *Anthonomocyllus* are excluded. The mesocoxae of *A. pusillus* LeConte (= *A. hamiltoni* Dietz) from Texas are not widely separated, and as Burke (1968) and Ahmad and Burke (1972) stated, the species is "obviously not very closely related" to the type species of *Anthonomocyllus*. Blatchley and Leng (1916: 290) placed *A. atomarius* Blatchley from New Jersey in *Anthonomocyllus*. No specimens of *A. atomarius* were examined, but Burke (pers. comm.) stated that the species is more closely related to *A. pusillus* than to any of the species of *Anthonomocyllus*. These two species may now properly be considered to belong to the subgenus *Anthonomus*.

Natural History.— *Anthonomocyllus* adults have been collected on the following plants:

- Euphorbiaceae
  - *Alchornea sidaefolia* Baill.
    - *A. acus*
- Rubiaceae
  - *Faramea occidentalis* A. Rich.
    - *A. argentatus*
- Rutaceae
  - *Zanthoxylum fagara* (L.) Sarg.
    - *A. leucostictus*
    - *A. xanthoxyli*
  - *Zanthoxylum spinifex* D.C.
    - *A. guanita*

Zanthoxylum sp.
  A. contaminatus
  A. tenuirostris
"rutaceous shrub"
  A. azalus

The *Zanthoxylum* records probably represent true hosts, *i.e.*, plants on which the larvae develop. Linell (1897: 49-50) noted that the types of *A. xanthoxyli* were found "living in the seeds" of *Z. fagara,* while Burke and Gates (1974: 325-326) noted that adults of that species have been collected along with those of *A. leucostictus* on *Zanthoxylum* plants. Townsend (1903) stated that larvae of both *A. xanthoxyli* and *A. leucostictus* develop in the fruit of *Z. fagara.*

The Euphorbiaceae and Rubiaceae records probably represent spurious occurrences. Anthonomine weevils are monophagous or oligophagous at the species level and several natural groups of species have relatively narrow host ranges (Burke 1976, Clark 1987a,b, 1988a,b,c,d, Clark and Burke 1985, 1986a,b, 1989). Thus, it seems likely that other species of *Anthonomocyllus* have species of Rutaceae, perhaps *Zanthoxylum*, as hosts. The species known to be associated with *Zanthoxylum* represent two of the three *Anthonomocyllus* species groups, but hosts of the species in the third species group, the *A. caeruleisquamis* group, are unknown.

Key to the *Anthonomocyllus* Species Groups

1 Mesotibia with outer apical angle rounded or angulate but not drawn out into an acute spine; femoral tooth short, acute or blunt (Figs. 53) ....*A. tenuirostris* group, p. 562

1' Mesotibia with acute outer apical spine (Fig. 67); femoral tooth (Fig. 67) long, slender, slightly curved, acute 2

2 Pronotal punctures separated by carinate interspaces, most with a narrow, fuscous scale, a few with broad, leucine scales; elytra with integument broadly visible between scattered leucine scales and inconspicuous, narrow, pallid fuliginous scales (Figs. 19, 20); elytral interstriae slightly convex, 3rd slightly elevated at base ....*A. leucostictus* group, p. 577

2' Pronotal punctures separated by flat interspaces, most with a large scale that does not extend beyond edge of puncture, a few with much narrower scales (Figs. 22-26); elytra with integument narrowly visible between small, rounded, cinereous to caeruleous scales; elytral interstriae flat, 3rd not elevated at base ....*A. caeruleisquamis* group, p. 578

The *Anthonomus tenuirostris* Species Group

Recognition (Figs. 1-18).— The pronotum has a large dorsal macula of broad, pallid scales that are replaced by dark, narrow scales on the posterolateral portions in adults of most of the species (Figs. 4, 6, 8, 10, 12), although this is not evident in *A. tenuirostris* (Fig. 2). The pronotum is flattened on the disc, especially in *A. accola* (Fig. 6) and *A. argentatus* (Fig. 8), but it is much less flattened in *A. acus* and is strongly rounded in *A. tenuirostris.* The inner margin of the protibia has a slender, acute, median tooth in *A. tenuirostris* (Fig. 53), *A. accola* (Fig. 54) and *A. argentatus* (Fig. 55). This is not evident in adults of the other members of the group which have a broad, blunt, median prominence on the inner protibial margin (Figs. 56-59).

Key to the Species in the *A. tenuirostris* Species Group

1 Mesocoxae narrowly separated by distance *ca.* 0.3-0.4 x width of a mesocoxa; pygidium of female with short, carinate, apicodorsal prominence (Figs. 30-32); abdominal sternum 5 of female with posteromarginal "clasp" that receives apicomedian prominence of pygidium (Figs. 44, 45) 2

1' Mesocoxae widely separated by distance *ca.* 0.5-0.8 x width of a mesocoxa; pygidium of female with dorsal, apicolateral extensions, apicodorsal excavation and middorsal concavity or channel (Figs. 33-39); abdominal sternum 5 of female straight (Fig. 46) or emarginate (Figs. 47-49), without posteromarginal "clasp" 4

2 (1) Pronotum flattened dorsally; metatibia with large inner marginal prominence (Fig. 61); mesosternum carinate between mesocoxae; endophallic sclerites large (Fig. 72); rostrum of female curved (Fig. 5)............. *A. accola, p. 567*

2' Pronotum rounded dorsally; metatibia without inner marginal prominence; mesosternum not carinate between mesocoxae; endophallic sclerites small (Fig. 70, 71); rostrum of female straight, slender (Fig. 1)... 3

3 (2') Eyes protruding (Fig. 3); protibia straight on outer margin, not widened medially, inner marginal tooth blunt; pronotum with broad, pallid scales in large fascia covering all but posterolateral portions (Fig. 4).................. *A. acus*, p. 566

3' Eyes not protruding (Fig. 1); protibia strongly curved on outer margin, widened medially to short, acute, inner marginal tooth (Fig. 53); scales on posterolateral portions of pronotum not strongly differentiated from those on other portions (Fig. 2).......................... *A. tenuirostris*, p. 564

4 (1') Sutural elytral interstriae without postscutellar patch of broad, pallid scales (Fig. 8); odd-numbered elytral interstriae slightly elevated; median inner marginal protibial prominence long, slender, acute (Fig. 55); abdominal sternum 5 of female without anteromedian fovea (Fig. 46) .... *A. argentatus*, p. 568

4' Sutural elytral interstriae with postscutellar patch of broad, pallid scales (Fig. 10); odd-numbered elytral interstriae not elevated; median inner marginal protibial prominence short, stout (Figs. 56-59); abdominal sternum 5 of female with anteromedian fovea (Figs. 47-49)..................................... 5

5 (4') Femora with long scales on inner margin that exceed ventral tooth (Figs. 56, 63); metatibia of male (Fig. 63) strongly excavated between inner marginal prominence, emarginate apicodorsally; pygidium of female with large apicodorsal excavation and broad, thin, apicolateral extensions (Fig. 34) .... *A. costulatus*, p. 569

5' Femora with short scales on inner margin that do not exceed inner marginal tooth (Figs. 57-59, 64, 65); metatibia of male weakly excavated (Fig. 65) or not excavated (Figs. 64, 66) between inner marginal prominence, not emarginate apicodorsally; pygidium of female without large apicodorsal excavation, apicolateral extensions stouter (Figs. 35-38) or minute (Fig. 39)..6

6 (5') Femora short, stout, *ca.* 3.1 x longer than wide (Figs. 58, 65); pygidium of female with broad dorsal excavation (Fig. 38); aedeagus with long, slender, apical extension (Fig. 78)..*A. guanita*, p. 574

6' Femora longer, more slender; pygidium of female with narrower dorsal excavation (Figs. 35-37); aedeagus without slender apical extension..7

7 (6') Metatibia of male with slight inner marginal prominence (Fig. 64)..8

7' Metatibia of male without inner marginal prominence (Fig. 66)..9

8 (7) Aedeagus symmetrical, not strongly expanded at apex (Fig. 88); adults 2.64-2.80 mm in length.......*A. dentipes*, p. 573

8' Aedeagus asymmetrical, strongly expanded at apex (Fig. 79); adult larger, 3.12 mm in length............*A. pazmani*, p. 575

9 (7') Protibia without preapical tooth (Fig. 59); aedeagus strongly asymmetrical, with apicodorsal carinae that converge apically to apicomedian prominences (Fig. 80); abdominal sternum 5 of female with u-shaped posteromedian emargination (Fig. 49); dorsolateral carinae of female pygidium extended posteriorly as slight, narrowly separated apicolateral prominences (Fig. 39).....*A. xanthoxyli*, p. 576

9' Protibia with well-developed preapical tooth; aedeagus symmetrical (Fig. 75) or only slightly asymmetrical (Fig. 76), without apicodorsal carinae; abdominal sternum 5 of female without posteromedian emargination (Fig. 47); dorsolateral carinae of female pygidium extended posteriorly as thick, apicolateral prominences (Figs. 35, 36)..................10

10 (9') Aedeagus symmetrical, subapicolateral expansions subangular (Fig. 75)...........................*A. azalus*, p. 571

10' Aedeagus slightly asymmetrical, subapicolateral expansion rounded (Fig. 76)........................ *A. contaminatus*, p. 572

Anthonomus (*Anthonomocyllus*) *tenuirostris* Champion

Figs. 1, 2, 30, 53, 60, 70

Anthonomus tenuirostris Champion 1903: 187-188, Tab. XI.,figs. 5, 5a, male; 6, female). *Lectotype* (here designated): GUATEMALA, male, on left hand side of card on which 2 males are mounted [♂] [Sp. figured] [Capetillo,/ Guatemala./ Champion.] [B.C.A. Col.IV.4./ Anthonomus/ tenuirostris,/ Champ.] [Type] (BMNH). *Paralectotypes*: GUATEMALA, 1 male, [♂] [Sp. figured] [Capetillo,/ Guatemala./ Champion.] [B.C.A. Col.IV.4./ Anthonomus/ tenuirostris,/ Champ.] [Type] (BMNH); 5 males [Duenas,/ Guatemala,/ G. C. Champion.] [B.C.A. Col.IV..4./ Anthonomus/ tenuirostris,/ Champ.] [♂] (BMNH); 2 females [Duenas,/ Guatemala,/ G. C. Champion.] [B.C.A. Col.IV..4./ Anthonomus/ tenuirostris,/ Champ.] (BMNH); 1 male, 1 female [♂ ♀] [Duenas,/ Guatemala,/ G. C. Champion.] [B.C.A. Col.IV..4./ Anthonomus/ tenuirostris,/ Champ.] (BMNH). Blackwelder 1947: 838. Schenkling and Marshall 1934: 60. O'Brien and Wibmer 1982: 107.

Anthonomus filirostris Champion 1910: 187. *Lectotype* (here designated): MEXICO, male [Mexico/ Rtt] [♂] [B.C.A. Col.IV.7./ Anthonomus/ filirostris,/ Champ.] [Anthonomus/ filirostris/ Ch] [LECTO-/ TYPE] [Type] [LECTOTYPE/ Anthonomus/ filirostris/ Ch./ design. by/ 1966 H. R. Burke] (BMNH). *Paralectotype*: MEXICO, female [Type] [♀] [Mexico/ Rtt] [B.C.A. Col.IV.7./ Anthonomus/ filirostris,/ Champ.] (BMNH). Blackwelder 1947: 838. Schenkling and Marshall 1934: 60. O'Brien and Wibmer 1982: 107. NEW SYNONYMY.

Recognition (Figs. 1, 2).— Adults of *A. tenuirostris* are unique among *Anthonomocyllus* in the following characters: protibia (Fig. 53) strongly curved, widened medially, with short, acute, inner marginal tooth; eyes (Fig. 1) not protruding; scales on posterolateral portions of pronotum (Fig. 2) similar to those on other portions; metatibia of male (Fig. 60) slightly sinuate, without inner marginal prominence. They resemble adults of *A. acus* in the following character: rostrum straight, that of female (Fig. 1) slender, glabrous; and they share the following characters with that species and with *A. accola*: mesocoxae separated by distance *ca.* 0.3 x width of one mesocoxa; pygidium of female (Fig. 30) with short, carinate, apicodorsal prominence; abdominal sternum 5 of female with small posteromarginal clasp that receives apicomedian prominence of pygidium; endophallus (Fig. 70) with three small sclerites.

Description.—

Male. *Length*: 1.84–3.32 mm (x̄ = 2.85, n = 10). Width: 1.18-1.76 mm (x̄ = 1.52, n = 10). *Head*: vertex with sparse, slender, pallid fuscescent scales; eyes large, narrowly separated by distance ca. 0.4 x width of rostrum at base. *Rostrum*: slender, nearly straight; length 1.34–1.95 x pronotal length (x̄ = 1.56, n = 10); smooth, sparsely punctate; glabrous except at extreme base; length of distal portion 31-38% of total rostral length (x̄ = 35, n = 10). *Prothorax*: pronotum without distinct subapical constriction; interspaces narrow, broadly exposed; with rounded, pallid, cinereous scales in diffuse middorsal and dorsolateral vittae and with slightly narrower, fuliginous scales in diffuse dorsolateral vittae; pleuron with broader, slightly imbricated, pallid cinereous scales. *Elytra*: interstriae nearly flat, 3rd widened at extreme base; dark integument broadly exposed between intermixed cinereous scales, fuliginous scales, and dark, fuscous scales; cinereous scales dense in postscutellar patch on sutural interstria. *Abdomen*: sternum 5 ca. 0.9 x as long as sternum 4, broadly, shallowly emarginate posteriorly, sparsely setose medially. *Legs*: profemur stout, ca. 1.1 x wider than metafemur; protibial uncus short, slender; metatibia with long, slender, oblique apical mucro. *Genitalia*: aedeagus symmetrical, widest basally, most strongly narrowed in distal 1/4, with slight apicolateral expansion.

Female. *Length*: 2.44-3.08 mm (x̄ = 2.76, n = 10). Width: 1.32-1.44 mm (x̄ = 1.36, n = 10). *Rostrum*: length 0.93-1.34 x pronotal length (x̄ = 1.26, n = 10); length of distal portion 36-46% of total rostral length (x̄ = 40, n = 10). *Abdomen*: sternum 5 with posterior margin slightly emarginate. *Legs*: protibia curved, with obtuse, median, inner marginal tooth; metatibia with inner marginal prominence; metatibial mucro obsolete.

Distribution.— In addition to the specimens in the type series of *A. tenuirostris* from Guatemala, and those of *A. filirostris* from México, 51 specimens (AUEM, TAMU) from the following localities were examined. GUATEMALA. *Guatemala*: Puerta Parada. MEXICO. *Morelos*: 4.4 mi. E Cuernavaca.

Natural History.— The specimens of *A. tenuirostris* from Puerta Parada, Guatemala, and Cuernavaca, México, were collected by beating *Zanthoxylum* plants in June and July.

Synonymy.— Direct comparison of the types revealed that the characters Champion (1910: 187) gave to distinguish *A. filirostris* from *A. tenuirostris*, namely the "not so coarse" vestiture and the dense white scales behind the scutellum, are not diagnostic. Champion himself correctly noted that some of the types of *A. tenuirostris* have white postscutellar scales. He also asserted that the rostrum in the types of *A. filirostris* is slightly more slender than that in the types of *A. tenuirostris*, but this appears to be a function of the smaller size of the *A. filirostris* types. The male lectotype of *A. filirostris* is slightly smaller than the smallest of a large series of *A. tenuirostris* from Puerta Parada, Guatemala, whereas the female paralectotype is a little larger than the smallest of that series. The types of *A. tenuirostris* are slightly larger than the largest members of the Puerta Parada series.

Anthonomus (*Anthonomocyllus*) *acus*, new species
Figs. 3, 4, 31, 44, 71

Type Series.— *Holotype*: BRAZIL, male [BRASIL, Bahia/ Encruzilhada/ 960m.XI-1073/ Alvarenga & Scabra (sic)] (DZUP). *Paratypes*: BOLIVIA, 1 female [Bolivien/ Germain] [Coll. Kraatz] [Coll. DEI/ Eberswalde]. BRAZIL, 1 male, 5 females [BRASIL, Bahia/ Encruzilhada/ 960m.XI-1073/ Alvarenga & Scabra (sic)]; 3 females [BRASIL, Bahia/ Encruzilhada/ 960m.XI-1073/ M. Alvarenga]; 1 male [Brasilien/ Nova Teutonia/ 27°11'B. 52°23'L/ Fritz Plaumann/ 14 XII 1949/ 300 W. 500 m.] [Euphorbiaceae/ Alchornea/ sidaefolia]. MEXICO, 1 male [Coyame/ Catemaco/ V.C., Mex.] [VI 15 54/ D G Kissinger] [5] [Anthonomus/ prob. filirostris Ch/ det. H. R. Burke 61] [1 ♂ in BM./ R.T.Thompson]. Total paratypes, 12 (AUEM, CWOB, DEIC, DZUP, MZSP, TAMU, USNM).

Recognition (Figs. 3, 4).— Adults of *A. acus* are similar to those of *A. tenuirostris* in having the rostrum of the female (*cf.* Fig. 1) straight, slender and glabrous and in having narrowly separated mesocoxae. They are distinguished from adults of that species by the following characters: eyes (Fig. 3) protruding; pronotum (Fig. 4) with broad, pallid scales in large fascia on all but posterolateral portions; protibia straight, inner marginal tooth blunt; metatibia of male with ventral margin straight. In general appearance, adults of *A. acus* are somewhat intermediate between adults of *A. tenuirostris* and those of the other species in the *A. tenuirostris* group. The elytra of *A. acus* are less strongly convex than those of *A. tenuirostris*, but more rounded than the other members of the subgenus. The vestiture of the pronotum and elytra of *A. acus* is also more like that of the other members of the subgenus.

Description.—

Male. *Length*: 2.20-2.72 mm ($\bar{x}$ = 2.50, n = 5). *Width*: 1.14–1.40 mm ($\bar{x}$ = 1.26, n = 5). *Head*: vertex with broad, dark fuscescent scales; eyes protruding, tilted forward, narrowly separated by distance *ca.* 0.5 x width of rostrum at base. *Rostrum*: slender, nearly straight; length 1.41–1.62 x pronotal length ($\bar{x}$ = 1.50, n = 5); carinae feebly developed; scales slender; length of distal portion 34-36% of total rostral length ($\bar{x}$ = 35, n = 5). *Prothorax*: pronotum with feebly developed subapical constriction; interspaces narrowly exposed; with broad, apically rounded, fulvoaeneous scales and sparsely admixed narrower, darker scales; pleuron with broadly imbricated, whitish scales. *Elytra*: interstriae nearly flat, 3rd widened at extreme base; dark integument narrowly exposed between intermixed white scales and pallid and dark fulvoaeneous scales; cinereous scales dense in postscutellar patch on sutural interstriae and in posteromedian fascicles. *Abdomen*: sternum 5 *ca.* 0.8 x as long as sternum 4, broadly, shallowly emarginate posteriorly, setose medially. *Legs*: profemur slender, *ca.* 1.2 x wider than metafemur; protibial uncus short, slender; metatibial uncus stout, conical, excavated. *Genitalia*: aedeagus symmetrical, widest basally, most strongly narrowed in distal 1/4, with slight apicolateral expansion.

Female. *Length*: 2.32–2.56 mm ($\bar{x}$ = 2.47, n = 8) *Width*: 1.22–1.32 mm ($\bar{x}$ = 1.24, n = 8). *Rostrum*: length 1.07–1.65 x pronotal length ($\bar{x}$ = 1.50, n = 8); length of distal portion 48-53% of total rostral length ($\bar{x}$ = 50, n = 8). *Legs*: protibia straight, with acute inner marginal tooth; metatibia straight, without inner marginal tooth; metatibial mucro obsolete.

Distribution.— *Anthonomus acus* is known only from the type series from widely separated localities in the states of Bahia and Santa Catarina, Brazil, and in the state of Veracruz, México.

Natural History.— Label data indicate that one of the paratypes of *A. acus* was collected on *Alchornea sidaefolia* in Nova Teutonia, Brazil. In view of the fact that several other members of the subgenus, including the closely related *A. tenuirostris*, are known to be associated with *Zanthoxylum* (Rutaceae), it seems unlikely that this member of the Euphorbiaceae is actually a host. Examined specimens were collected in June (México), November and December (Brazil).

Etymology.— The specific epithet, a Latin noun meaning needle, refers to the shape of the rostrum of the female.

Anthonomus (*Anthonomocyllus*) *accola*, new species
Figs. 5, 6, 32, 45, 54, 61, 72

Type Series.— *Holotype*: VENEZUELA, male, [Venezuela, Aragua/ El Limon 490m./ 14-VI-1977] [En la/ Luz] [F. Fernandez Y./ col.] (IZAV). *Paratypes*: VENEZUELA, 1 female [Venezuela, Aragua/ El Limon 450m./ 27-IV-1976] [S. Clavijo/ J. Clavijo] [Luz de/ Mercurio]; 1 female [Venezuela, Aragua/ El Limon 450m./ 18-IV-1977] [B. Bechyne/ leg.]; 2 females [Venezuela, Aragua/ El Limon 450m./ 24-IV-1977] [Luz de/ Mercurio] [F. Fernandez Y./ col.]; 1 female [Venezuela, Aragua/ El Limon 450m./ 28-IV-1977] [Luz de/ Mercurio] [F. Fernandez Y./ col.]; 1 male, 1 female [Venezuela, Aragua/ El Limon 450m./ 14-VI-1977] [B. Bechyne/ leg.]. Total paratypes, 7 (AUEM, IZAV, TAMU).

Recognition (Figs. 5, 6).— The relatively large adults of *A. accola* are distinguished by the following combination of characters: mesosternum carinate between mesocoxae; metatibia of male (Fig. 61) stout, with large inner marginal prominence; mesocoxae narrowly separated by distance *ca.* 0.3 x width of one mesocoxa; pygidium of female (Fig. 32) with short, carinate, apicodorsal prominence; abdominal sternum 5 of female (Fig. 45) with posteromarginal clasp that receives apicomedian prominence of pygidium; endophallus (Fig. 72) with three large sclerites.

Adults of *A. accola* are larger but otherwise resemble those of *A. argentatus*. Adults of both species have dark integument on the median portion of abdominal sternum 5 and slightly elevated odd-numbered elytral interstriae. Adults of *A. accola* are more like those of *A. tenuirostris* and *A. acus*, however, in the armature of the endophallus (*cf.* Figs. 70-72), the shape of the pygidium of the female (*cf.* Figs. 30-32), and in possession of a posteromarginal "clasp" on abdominal sternum 5 of the female (Figs. 44, 45) that receives an apicomedian prominence of the pygidium.

Description.—

Male. *Length*: 3.32-3.48 mm ($\bar{x}$ = 3.40, n = 2). *Width*: 1.14–1.40 mm ($\bar{x}$ =1.26, n = 2). *Head*: vertex with broad, rounded scales; eyes large, nearly round, strongly convex, separated by distance *ca.* 0.7 x width of rostrum at base. *Rostrum*: slender, slightly curved over antennal insertions; length 1.10–1.11 x pronotal length ($\bar{x}$ = 1.11, n = 2); scales dense, broad; carinae obsolete; length of distal portion 27–28% of total rostral length ($\bar{x}$ = 28, n = 2). *Prothorax*: pronotum flattened, with slight dorsolateral depressions and postocular prominences; with slightly imbricated, rounded, pallid scales, slightly narrower, subtruncate, fulvoaeneous scales and narrower, darker fuscoaeneous scales; broad scales dense apically, in transverse middorsal fascia, and on pleuron. *Elytra*: sutural, 3rd and 5th interstriae slightly convex; interstriae with imbricated, pallid scales, fulvescent to fuliginous scales and fuscous scales; dark scales dense on median portion of sutural interstriae and on basal portion of interstria 3; pallid scales subfasciculate throughout. *Abdomen*: sternum 5 broadly, shallowly emarginate posteriorly, flattened medially, with slight posteromarginal prominence. *Legs*: profemur *ca.* 1.0 x as wide as metafemur; protibia straight, inner margin concave between slender, acute median tooth and blunt, preapical tooth; protibial uncus slender, acute; metatibial mucro small, slender, truncate. *Genitalia*: aedeagus symmetrical, broad, narrowed to blunt apex, not constricted medially, without apicolateral prominences.

Female. *Length*: 3.44–3.80 mm (x̄ = 3.56, n = 6). *Width*: 1.64–1.80 mm (x̄ = 1.68, n = 6). *Rostrum*: slender, slightly, evenly curved; scales dense, broad; carinae obsolete; length 1.11–1.24 x pronotal length (x̄ = 1.20, n = 6); length of distal portion 36–42% of total rostral length (x̄ = 39, n = 6). *Abdomen*: sterna 3-5 ascending. *Legs*: metatibial mucro short, stout.

Distribution. — *Anthonomus accola* is known only from the type series from the state of Aragua, Venezuela.

Natural History.— Nothing is known about the life history and hosts of *A. accola*. Label data indicate that the specimens in the type series were collected at light in April and June.

Etymology.— The specific epithet, a Latin noun meaning neighbor, refers to the fact that this species lives near the home of Carlos Bordón in the community of El Limón, near Maracay, Venezuela.

Anthonomus (*Anthonomocyllus*) *argentatus* Gyllenhal
Figs. 7, 8, 33, 46, 55, 62, 73

Anthonomus argentatus Gyllenhal 1836: 343. *Holotype*: ST. BARTHELEMY, male [Typus] [St. Barthemeli/ Forss röm. (sic)] [17] [45/ 88] [Riksmuseum/ Stockholm] (NHRS). Boheman 1843: 219. Schenkling and Marshall 1934: 55. Blackwelder 1947: 838. O'Brien and Wibmer 1982: 106.

Recognition (Figs. 7, 8).— Adults of *A. argentatus* are distinguished by the following combination of characters: odd-numbered elytral interstriae slightly elevated; inner marginal protibial prominence (Fig. 55) long, slender, acute; aedeagus (Fig. 73) broadly constricted medially, with short apicolateral prominences; sutural elytral interstriae (Fig. 8) without postscutellar patch of broad, pallid scales; pygidium of female (Fig. 33) with widely separated apicolateral prominences, excavated in apicodorsal 1/4; mesocoxae widely separated by distance *ca.* 0.8 x width of one mesocoxa.

In lacking an anteromedian fovea on abdominal sternum 5, adult females of *A. argentatus* are like those of *A. accola*, *A. acus* and *A. tenuirostris*. Adults of *A. argentatus* are also similar to those of *A. accola* in having a dark patch of integument on abdominal sternum 5 and slightly elevated odd-numbered elytral interstriae. Adult females of *A. argentatus* have the pygidium more like that of *A. costulatus* (*cf.* Figs. 33, 34) than that of any of the aforementioned species, however, and like adult females of *A. costulatus*, they lack a posteromarginal clasp on abdominal sternum 5.

Description.—

Male. *Length:* 2.08–2.56 mm x̄ =2, 37; n = 10). *Width*: 1.04–1.32 mm (x̄ = 1.20, n = 10). *Head*: vertex with broad, rounded scales; eyes protruding, separated by distance *ca.* 0.5 x width of rostrum at base. *Rostrum*: slender, slightly curved over antennal insertions; length 1.33–1.59 x pronotal length (x̄ = 1.46, n = 10), with dense, broad scales; carinae obsolete; length of distal portion 27–35% of total rostral length (x̄ = 30, n = 10). *Prothorax*: pronotum flattened, with slight dorsolateral depressions and postocular prominences; with slightly imbricated, rounded, pallid whitish scales, narrower, subtruncate, fulvoaeneous scales and narrower, darker fuscoaeneous scales; broad scales dense apically, in transverse middorsal fascia, and on pleuron. *Elytra:* interstriae with imbricated, whitish scales, pallid fulvescent to fuliginous scales, and dark, fuscous scales that form diffuse discal macula; pallid scales dense in diffuse, transverse, posteromedian fascia. *Abdomen*: sternum 5 *ca.* 1.1 x longer than sternum 4, deeply emarginate posteriorly, with slight median concavity and posteromedian prominence. *Legs*: profemur *ca.* 1.0

x as wide as metafemur; protibia straight, protibial uncus slender, acute; metatibia slightly sinuate, inner margin broadly concave between small tooth in proximal 1/3 and small preapical tooth; metatibial mucro small, slender, curved. *Genitalia*: endophallus unarmed.

Female. *Length*: 2.20–2.60 mm (x̄ = 2.36, n = 5). *Width*: 1,10–1.30 mm (x̄ = 1.20, n = 5). *Rostrum*: slender, slightly, evenly curved; length 1.58–1.74 x pronotal length (x̄ = 1.69, n = 5); length of distal portion 43–51% of total rostral length (x̄ = 47, n = 5). *Abdomen:* sterna 3-5 ascending; sternum 5 broadly, shallowly concave medially. *Legs:* protibia with long, acute, inner marginal tooth; metatibia with obsolescent ventral marginal tooth in proximal 1/3; metatibial mucro obsolete.

Distribution.— In addition to the holotype of *A. argentatus* from the West Indian island of St. Barthélemy, 17 specimens (CWOB, HAHC, MHND, TAMU, USNM, ZMHB) from the following localities were examined. CUBA. *La Habana*: Cayamas. JAMAICA. *Manchester:* Skull Point. REPUBLICA DOMINICANA. *Distrito Nacional:* Boca Chica. PUERTO RICO. *Caribbean National Forest*: El Verde. *Guánica*: Highway 334 at Guánica Forest Ranger Station. *Ponce*: Ponce; Torres Finca. *San Juan*: Río Pedras. TRINIDAD. Arima Valley. VENEZUELA. *Distrito Federál*: Caracas.

Natural History.— A specimen of *A. argentatus* from Ponce, Puerto Rico, has a label indicating that it was collected on *Faramea occidentalis*. In view of the fact that several other members of the subgenus, including the closely related *A. tenuirostris*, are known to be associated with *Zanthoxylum* (Rutaceae), it seems unlikely that this member of the Rubiaceae is actually a host. Examined specimens were collected in March, May, July, August, and September.

Anthonomus (*Anthonomocyllus*) *costulatus* Suffrain
Figs. 9, 10, 34, 56, 63, 74

Anthonomus costulatus Suffrian 1871: 137. *Lectotype*: CUBA, male, designated by Burke 1975: 58. "Anth costulatus/ Cuba/ 39254; in ZIH" (Zoologisches Institut, Halle). Not examined. Gundlach 1891: 287. Schenkling and Marshall 1934: 38 (= *A. irroratus* Dietz). Ahmad and Burke 1972: 52-53 (= *A. irroratus* Dietz). Gates and Burke 1972: 1219-1221. Burke 1975: 58 (= *A. elegans* LeConte). O'Brien and Wibmer 1982: 106 (= *A. elegans* LeConte).

Anthonomus elegans LeConte 1876: 202. *Lectotype*: FLORIDA, male [Haulover/ March 10 Fla] [Type/ 1949] [J. L. Leconte/ Coll.] [LECTOTYPE/ Anthonomus/ elegans *LeC*./ design. by/ H. R. Burke] [*A. elegans* / Lec.] (MCZC), designated by Burke 1975: 58. *Paralectotype*: FLORIDA, 1 male [Haulover/ March 13 Fla] [48] [Type 1940] [J. L. Leconte/ Coll.] [PARALECTOTYPE/ *Anthonomus*/ *elegans* LeC./ des. H. R. Burke] (MCZC). Dietz 1891: 192. Blatchley and Leng 1916: 289. Blatchley 1925: 97. Schenkling and Marshall 1934: 38.

Recognition (Figs. 9, 10).— Adults of *A. costulatus* are distinguished by the following combination of characters: femora (Figs. 56, 63) with long scales on inner margin that exceed inner marginal tooth; metatibia of male (Fig. 63) strongly excavated between inner marginal prominence, outer margin emarginate apically; aedeagus (Fig. 74) abruptly widened subapically, truncate at apex, with shallow apicomedian emargination; inner marginal protibial prominence (Fig. 63) short, stout; pygidium of female (Fig. 34) with narrow, shallow, median concavity with long, broad scales and widely separated apicolateral prominences, excavated in apicodorsal 1/4; mesocoxae widely separated by distance *ca.* 0.8 x width of one mesocoxa; sutural elytral interstriae (Fig. 10) with postscutellar patch of broad, pallid scales; abdominal sternum 5 of female with anteromedian fovea.

The pygidium of the adult females of *A. costulatus* (Fig. 34) is very similar to that in *A. argentatus* (Fig. 33), but in other characters, notably the pygidial channel in the female (Fig. 34) and the anteromedian fovea of abdominal sternum 5 of the female, adult *A. costulatus* more closely resemble adults of *A. azalus* (Fig. 47), *A. contaminatus*, *A. dentipes*, *A. guanita*, *A. pazmani* and *A. xanthoxyli*.

Description.—

Male. *Length*: 2,40–2,76 mm (x̄ = 2.53, n = 10). *Width*: 1.26–1.42 mm (x̄ = 1.36, n = 10). *Head*: vertex with broad, rounded scales; eyes protruding, separated by distance *ca.* 0.7 x width of rostrum at base. *Rostrum*: slender, slightly, evenly curved, length 1.14–1.36 x pronotal length (x̄ = 1.26, n = 10); carinae obsolete; scales broad, sparse; length of distal portion 31–38% of total rostral length (x̄ = 34, n = 10). *Prothorax*: pronotum flattened, with slight dorsolateral depressions and postocular prominences; with imbricated, rounded, pallid scales, narrower, subtruncate, fulvoaeneous scales and narrower fuscoaeneous scales; broad scales dense apically, in transverse middorsal fascia, and on pleuron. *Elytra*: interstriae slightly convex, with imbricated, whitish scales, pallid fulvescent to fuliginous scales and dark, fuscous scales; dark scales dense medially on sutural interstriae, on basal portion of interstria 3, on posteromedian portion of interstria 2, and in diffuse posterolateral macula across interstria 2-10; pallid scales dense on large anterolateral fascia and on declivities. *Abdomen*: sternum 5 *ca.* 1.2 x longer than sternum 4, broadly emarginate posteriorly, with dense, broad scales laterally, slightly concave and setose medially. *Legs:* profemur *ca.* 1.3 x wider than metafemur; protibial uncus short, stout, perpendicular; metatibia straight, inner margin excavated between blunt inner marginal tooth and apex; metatibia with outer margin emarginate apically, with slender, curved, excavated mucro and large, blunt, apicodorsal tooth. *Genitalia*: endophallus unarmed.

Female. *Length*: 2.32–2.56 mm (x̄ = 2.44, n = 10). *Width*: 1.26–1.40 mm (x̄ = 1.34, n = 10). *Rostrum*: slender; length 1.31–1.45 x pronotal length (x̄ = 1.37, n = 10); length of distal portion 38–45% of total rostral length (x̄ = 41, n = 10). *Legs*: metatibia slightly sinuate, without inner marginal tooth; metatibial mucro obsolete, apicodorsal tooth absent.

Synonymy.—The four specimens Suffrian (1871: 137-138) stated were in the original type series of *A. costulatus* were not examined. The identity of the species was determined by comparison of specimens with the original description and with descriptive notes and photographs of the specimen designated by Burke (1975: 58) as lectotype. A photograph of a specimen in the Gundlach Collection in the Instituto de Ecología y Systemática, Academia de Ciencias de Cuba, Havana, identified as *A. costulatus*, was also examined. This specimen, pictured in dorsal view, has lost most of the scales on the dorsal surfaces, recalling Suffrian's (1871) statement that the syntypes were all "mehr oder weniger abgerieben". It was not possible to determine whether or not this specimen is conspecific with the lectotype.

Gates and Burke (1972: 1219-1220) noted that the name *A. costulatus* was considered to be a senior synonym of the name *A irroratus* Dietz by Schwarz (1913), Blatchley and Leng (1916), Leng (1920), Schenkling and Marshall (1934) and Ahmad and Burke (1972). Based on examination of the specimen that would subsequently be designated as lectotype of *A. costulatus* by Burke (1975: 58), they determined that this synonymy was incorrect and that *A irroratus* and *A. costulatus* are "separate and distinct species".

Distribution.— Suffrian (1871: 138) stated that *A. costulatus* was described from specimens "Von Dr. G. in den Bezirken *Cienfugos* (sic) und *Cardenas* im Mai gesammelt," and Gundlach (1891: 287) reported *A. costulatus* from Cardenas and Ciénaga de Zapata, Cuba. In addition to the lectotype and paralectotype of *A. elegans*, 51 specimens (AMNH, FSCA, TAMU, USNM, ZMHB) were examined in the present study. These are from the following localities. BAHAMAS. South Bimini. CUBA. *La Habana*: Cayamas. UNITED STATES. *Florida*: Everglades National Park. Dade Co.: Matheson Hammock. Monroe Co.: Key Largo. One examined specimen (USNM) bears the anomalous label [Banana leaf/ PANAMA/ N. Orleans/ L2 P.Q.#/ 6055/ Mch. 13-33'].

Natural History.— Blatchley and Leng (1916: 289) described *A. costulatus* (as *A. elegans*) as "very rare on oak shrubs; March 10". Blatchley (1925: 97) stated that the same species has been recorded as a submaritime Floridian species, found only on foliage near the sea. Examples are at hand from Palmdale and Royal Palm Park, both inland stations; also from Miami and Caxambus in addition to those previously mentioned. At Palmdale it was swept from a tall St. Johnswort.

Label data state that specimens from Key Largo, Florida, were taken by "beating hammock vegetation at night". Examined specimens were collected in November and December.

Anthonomus (*Anthonomocyllus*) *azalus*, new species

Figs. 35, 47, 75

Type Series.— *Holotype:* MEXICO, male [MEXICO: Baja Calif./ Sur, 1650' 2.4 mi. NE./ El Sauzal, 14-VIII-/ 1980, R. L. Westcott] [on rutaceous/ shrub] (CWOB). *Paratypes*: MEXICO, 9 males, 5 females [MEXICO: Baja Calif./ Sur, 1650' 2.4 mi. NE./ El Sauzal, 14-VIII-/ 1980, R. L. Westcott] [on rutaceous/ shrub]; 1 male [MEX Baja/ Calif Carrizal/ 6-6-74/ Foster & Slaten] [Jesus Nevarez/ cotton farm/ 74-8320]; 1 male [MEXICO: B.C.S./ El Triunfo/ 13.IX.1978/ D. R. Whitehead]; 1 male [MEX., Baja Calif. Sur/ arroyo .4 mi N,/ .6 mi E Migrino/ (18-21)-IV-1985/ R. L. Westcott]; 1 female [MEX: Baja Cal. Sur/ 9.4 mi. W. hwy. 1 on/ Ramal a San Felipe/ IX-10-11-88: E. Riley]. Total paratypes, 18 (AUEM, CWOB, RSAC, TAMU, USNM).

Recognition.— Adults of *A. azalus* are distinguished by the following combination of characters: aedeagus (Fig. 75) broadly constricted in distal 2/3, widened apically, apex subtruncate, broadly, shallowly emarginate medially; pygidium of female (Fig. 35) with apicodorsal concavity with long, broad scales and with thick apicolateral prominences; abdominal sternum 5 of female (Fig. 47) with anteromedian fovea; sutural elytral interstriae with postscutellar patch of broad, pallid scales; mesocoxae separated by distance *ca.* 0.6 x width of one mesocoxa; metatibia of male without inner marginal prominence; protibia with short, stout, inner marginal prominence and well-developed preapical tooth.

The relatively large, robust adults of *A. azalus* closely resemble adults of *A. dentipes*, *A. contaminatus* and *A. pazmani*. The structure of the pygidium of the female is nearly identical in these species (*cf.* Figs. 35-37).

Description.—

Male. *Length*: 2.48–3.48 mm ($\bar{x}$ = 3.03, n = 10). *Width*: 1.38–1.76 mm ($\bar{x}$ = 1.59, n = 10). *Head*: vertex with broad, rounded scales; eyes protruding, narrowly separated by distance *ca.* 0.4 x width of rostrum at base. *Rostrum*: stout, slightly curved distally; length 1.19–1.37 x pronotal length ($\bar{x}$ = 1.27, n = 10); scales broad, dense; carinae obsolete; length of distal portion 29–35% of total rostral length ($\bar{x}$ = 32, n = 10). *Prothorax*: pronotum flattened, with slight dorsolateral depressions and postocular prominences; with imbricated, rounded, pallid scales, narrower, subtruncate, fulvoaeneous scales and narrower, fuscoaeneous scales; broad scales dense apically, in transverse middorsal fascia, and on pleuron. *Elytra*: interstriae nearly flat, with imbricated, whitish scales, pallid fulvescent to fuliginous scales, and dark, fuscous scales; dark scales dense medially on sutural interstriae, on basal portion of interstria 3, on short posteromedian section of interstria 2, and in diffuse posterolateral macula across interstriae 2-10; pallid scales dense in short to elongate fascicles around posterolateral macula and in declivital fascia. *Abdomen*: sternum 5 *ca.* 0.9 x as long as sternum 4, broadly, deeply emarginate posteriorly, with dense scales laterally, slightly concave and setose medially. *Legs*: protibial uncus stout, long, curved; metatibial mucro short, curved, oblique. *Genitalia*: endophallus unarmed.

Female. *Length*: 2.80–3.20 mm (x̄ = 3.06, n = 5). *Width*: 1.60–1.72 mm (x̄ = 1.65, n = 5). *Rostrum*: slender; length 1.34–1.60 x pronotal length (x̄ = 1.47, n = 5); length of distal portion 41-44% of total rostral length (x = 42, n = 5). *Abdomen*: sternum 5 with shallow, subtruncate, apicomedian emargination. *Legs*: protibia with inner marginal tooth; metatibia without inner marginal tooth; metatibial mucro obsolete.

Distribution.— *Anthonomus azalus* is known only from the type series from Baja California Sur, México.

Natural History.— The holotype and some of the paratypes of *A. azalus* were collected, according to label data, on a "rutaceous shrub".

Etymology.— The specific epithet is an anagram of part of the name of the type locality.

Anthonomus (*Anthonomocyllus*) *contaminatus* Boheman
Figs. 11, 12, 36, 76

Anthonomus contaminatus Boheman 1843: 219-220. *Holotype*: BRAZIL, male [Brasilia/ Falderm.] [Typus] [contaminatus/ Boh.] [39/ 53] [68/ 84] [424/ 87] [Riksmuseum/ Stockholm] (NHRS). Schenkling and Marshall 1934: 56. Wibmer and O'Brien 1986: 203.

Recognition (Figs. 11, 12).— Adults of *A. contaminatus* are distinguished by the following combination of characters: aedeagus (Fig. 76) slightly asymmetrical, widened apically, with slight apicomedian emargination; metatibia of male without inner marginal prominence; sutural elytral interstriae (Fig. 12) with postscutellar patch of broad, pallid scales; protibia with well-developed preapical tooth; mesocoxae separated by distance *ca*. 0.7 x width of one mesocoxa; pygidium of female (Fig. 36) with narrow middorsal channel with long, broad scales and stout, narrowly separated, apicolateral prominences; abdominal sternum 5 of female with anteromedian fovea.

Anthonomus contaminatus is distinguished from *A. dentipes* by the shape of the aedeagus (*cf*. Figs. 76, 77) and by the absence of a prominence on the inner margin of the metatibia. The aedeagus of *A. contaminatus* is similar to that in *A. xanthoxyli* (*cf*. Figs. 76, 80), but in the latter species this has a shallow apicomedian emargination between two relatively narrowly separated apical prominences and two ridges extend basad from each prominence to the dorsal orifice.

Description.—

Male. *Length*: 2.60-3.16 mm (x̄ = 2.88, n=2). *Width*: 1.36-1.68 mm (x̄ = 1.52, n=2).Head: vertex with broad, rounded scales; eyes protruding, narrowly separated by distance ca. 0.4 x width of rostrum at base. Rostrum: slender, slightly curved distally; length 1.30-1.40 x pronotal length (x̄ = 1.35, n = 2); scales broad, dense; carinae well developed; length of distal portion 29-31% of total rostral length (x̄ = 30, n = 2). *Prothorax*: pronotum flattened, with slight dorsolateral depressions and slight postocular prominences; with imbricated, rounded, pallid scales, narrower, subtruncate, fulvoaeneous scales and narrower, fuscoaeneous scales; broad scales dense apically, in transverse middorsal fascia, and on pleuron. *Elytra*: interstriae nearly flat, with imbricated, whitish scales, pallid fulvescent to fuliginous scales, and dark, fuscous scales; dark scales dense on median portion of sutural interstriae, on basal portion of interstria 3, and on short posteromedian section of interstria 2; pallid scales dense in small, median fascicles and in declivital fascia. *Abdomen*: sternum 5 ca. 0.8 x as long as sternum 4, broadly emarginate posteriorly, sparsely setose medially. *Legs*: profemur ca. 1.0 x as wide as metafemur; protibia straight, inner margin concave between large, blunt, median tooth and conical preapical tooth; protibial uncus long, stout, curved; metatibial mucro short, slender, curved. *Genitalia*: endophallus unarmed.

Female. *Length*: 2,64 mm (n = 1). *Width*: 1.44 mm (n = 1). *Rostrum*: slender; length 1.50 x pronotal length (n = 1); length of distal portion 45% of total rostral length (n = 1).

Abdomen: sternum 5 with broad, shallow, subtruncate apicomedian emargination. *Legs*: protibia with inner marginal tooth; metatibia without inner marginal tooth; metatibial mucro obsolete.

Distribution.— In addition to the holotype from an unspecified locality in Brazil, two specimens (TAMU) of *A. contaminatus* from the following localities were examined. COLOMBIA. *Valle de Cauca*: 16 km. S Restrepo. VENEZUELA. *Falcón*: La Cruz de Taratara.

Natural History.— The specimens of *A. contaminatus* from Colombia and Venezuela were both collected by beating plants in June. The plants were well past the fruiting stage and weevils were not abundant.

Anthonomus (*Anthonomocyllus*) *dentipes* Hustache
Figs. 13, 14, 37, 57, 64, 77

Anthonomus dentipes Hustache 1940: 114-115. *Lectotype* (here designated): ARGENTINA, male [BUENOS AIRES ARGENTINA/ ISLA MARTIN GARCIA/ 6-1936 M. J. VIANA] [♂] [TYPE] [MUSEUM PARIS/ 1949/ Col. A HUSTACHE] [anthonomus/ (Leptarthrus)/ dentipes/ m.] (MNHN). *Paralectotype*: 1 female [BUENOS AIRES ARGENTINA/ ISLA MARTIN GARCIA/ 1938 M. J. VIANA] [♀] [MUSEUM PARIS/ 1949/ Col. A. HUSTACHE] [dentipes] (MNHN). Wibmer and O'Brien 1986: 203)

Anthonomus (*Anthonomocyllus*) *murinofasciatus* Voss 1944: 48. *Neotype* (here designated): BRAZIL, male [Brasilien/ Nova Teutônia/ 27°11'B . 52°23'L/ Fritz Plaumann/ VIII-1954/ 300-500 m] (MZSP). Weidner 1979: 398. Wibmer and O'Brien 1986: 204. NEW SYNONYMY.

Recognition.— (Figs. 13, 14). Adults of *A. dentipes* are distinguished by the following combination of characters: pygidium of female with narrow middorsal channel with long, broad scales and with stout, narrowly separated, apicolateral prominences; aedeagus (Fig. 77) with slight subapical constriction, subtruncate at apex; metatibia of male (Fig. 64) with slight inner marginal prominence; inner marginal protibial prominence (Fig. 57) short, stout; abdominal sternum 5 of female with anteromedian fovea; mesocoxae widely separated by distance *ca.* 0.5 x width of one mesocoxa; sutural elytral interstriae (Fig. 14) with postscutellar patch of broad, pallid scales.

Aside from the shape of the aedeagus (*cf.* Figs. 76, 77), *A. dentipes* differs from *A. contaminatus* only in possession of a slight inner marginal prominence on the metatibia.

Description.—

Male. *Length*: 2.64-2.72 mm ($\bar{x}$ = 2.68, n = 2). *Width*: 1.32-1.36 mm ($\bar{x}$ = 1.34, n = 2). *Head*: vertex with broad, rounded scales; eyes protruding, separated by distance *ca.* 0.7 x width of rostrum at base. *Rostrum:* slender, slightly curved distally; length 1.10-1.24 x pronotal length ($\bar{x}$ = 1.17, n = 2); carinae well-developed; scales broad, sparse; length of distal portion 33-37% of total rostral length ($\bar{x}$ = 35, n = 2). *Prothorax*: pronotum flattened, with slight dorsolateral depressions and postocular prominences; with imbricated, apically rounded, pallid scales, narrower, subtruncate, fulvoaeneous scales and narrower, fuscoaeneous scales; broad scales dense apically, in transverse middorsal fascia, and on pleuron. *Elytra*: interstriae nearly flat, with imbricated, whitish scales, pallid fulvescent to fuliginous scales and dark, fuscous scales; dark scales dense medially on sutural interstriae, on basal portion of interstria 3, on short posteromedian section of interstria 2, and in diffuse posterolateral macula across interstriae 2-10; pallid scales dense in short to elongate fascicles around posterolateral macula and in declivital fascia. *Abdomen*: sternum 5 *ca.* 0.8 x as long as sternum 4, broadly emarginate posteriorly, with dense, broad scales laterally, slightly concave and setose medially. *Legs*: profemur *ca.* 1.0 x as wide as metafemur; protibial uncus long, stout, curved; metatibial mucro short, stout, curved. *Genitalia*: endophallus unarmed.

Female. *Length*: 2.76-2.80 mm ($\bar{x}$ = 2.78, n = 2). *Width*: 1.34-1.46 mm ($\bar{x}$ = 1.40, n = 2). *Rostrum*: slender; length 1.37-1.46 x pronotal length ($\bar{x}$ = 1.42, n = 2); length of distal portion 44-45% of total rostral length (x̄ = 45, n = 2). *Legs*: protibia with inner marginal tooth, without preapical tooth; metatibia without inner marginal tooth; metatibial mucro obsolete.

Distribution.— In addition to the lectotype and one paralectotype of *A. dentipes* from the Isla Martín Garcia, Buenos Aires, Argentina, and the neotype of *A. murinofasciatus* from Nova Teutônia, Santa Catarina, Brazil, three additional specimens (MZSP) from Nova Teutônia were examined.

Natural History.— Nothing is known about the life history and hosts of *A. dentipes*. Examined specimens were collected in April, August, and November.

Neotype.— Voss (1944: 48) described *A. murinofasciatus* from a single male that he stated was in his own collection. Apparently that specimen, collected by F. Plaumann in Nova Teutônia, Santa Catarina, Brazil, no longer exists. Weidner (1979: 398) listed *A. murinofasciatus* as one of the species described by Voss whose types have been destroyed. Plaumann (in litt.) asserted that the species is not represented in his collection. The label data cited by Voss (1944: 48) for the holotype ("Brasilien: Nova Teutônia. 27°s. Br. 52–53°w. L. (15.10.1935. Plaumann leg.") are like those of the male specimen (MZSP) designated as neotype except for the date of collection. The neotype agrees with the original description except that the hind femur has a small tooth. This tooth is nearly concealed by long scales and could easily have been overlooked when the original description was prepared.

Anthonomus (*Anthonomocyllus*) *guanita*, new species
Figs. 15, 16, 38, 48, 58, 65, 78

Type Series.— *Holotype*: ANTIGUA, male [Antigua, BWI/ St. John/ Jan. 12/14, 1955/ A. M. Nadler] (AMNH). *Paratypes:* GUADELOUPE, 1 male, 1 female [GUADELOUPE/ St. François/ Anse la Boise/ 4-II-1966/ J. Bonfils] [sat/ Zanthoxylum/ spinifex D.C./ 542-08]. REPUBLICA DOMINICANA, 1 female [Los Ranchitos/ S. J. Ocoa, Prov./ Peravia, R.D./ 18-IX-1979/ Cols. Aquino - Reynoso]; Total paratypes, 3 (CMFP, MHND).

Recognition (Figs. 15, 16).— Adults of *A. guanita* are distinguished by the following combination of characters: femora (Figs. 58, 65) short, stout; metatibia of male (Fig. 65) slightly excavated between obtuse inner marginal prominence and apex, inner margin distended apically, with small, conical, preapical tooth; aedeagus (Fig. 78) with long, slender, apical extension; pygidium of female (Fig. 38) with broad median channel with long, broad scales and with widely separated apicolateral prominences; abdominal sternum 5 of female (Fig. 48) foveate, emarginate; mesocoxae widely separated by distance *ca.* 0.8 x width of one mesocoxa; sutural elytral interstriae (Fig. 16) with postscutellar patch of broad, pallid scales; inner marginal protibial prominence (Fig. 58) short, stout.

Description.—

Male. *Length* 2.16-2.28 mm (x̄ = 2.22, n = 2). *Width*: 1.16-1.24 mm (x̄ = 1.20, n = 2). *Head*: vertex with broad, rounded scales; enter with slightly broader, more pallid scales; eyes protruding, separated by distance *ca.* 0.5 x width of rostrum at base. *Rostrum*: slender, slightly curved over antennal insertions; length 1.14-1.37 x pronotal length (x̄ = 1.26, n = 2), with dense, broad scales; carinae obsolete; length of distal portion 25-27% of total rostral length (x̄ = 26, n = 2). *Prothorax*: pronotum flattened, with slight dorsolateral depressions and postocular prominences; with imbricated, rounded, pallid scales, narrower, subtruncate, fulvoaeneous scales and narrower, fuscoaeneous scales; broad scales dense apically, in transverse middorsal fascia, and on pleuron. *Elytra*: interstriae nearly flat, with imbricated, whitish scales, pallid fulvescent to fuliginous scales, and dark, fuscous scales that are dense on median portion of sutural interstriae, on basal portion of interstria 3, on short posteromedian section of interstria 2, and in diffuse posterolateral macula across interstriae 2-10; pallid scales dense in short to elongate fascicles around posterolateral macula and in declivital fascia. *Abdomen*: sternum 5 *ca*. 1.1 x longer than sternum 4, broadly, shallowly emarginate posteriorly, with dense scales laterally, slightly concave and setose medially. *Legs*: profemur *ca*. 1.1 x wider than metafemur; protibia with blunt preapical tooth; protibial uncus short, slender, acute; metatibial uncus short, acute.

Female. *Length*: 2.32-2.36 mm ($\bar{x}$ = 2.34, n = 2). *Width*: 1.24-1.26 mm ($\bar{x}$ = 1.25, n = 2). *Rostrum*: slender, slightly, evenly curved; length 1.29-1.44 x pronotal length ($\bar{x}$ = 1.37, n = 2); length of distal portion 39-46% of total rostral length ($\bar{x}$ = 43, n = 2). *Legs*: protibia with inner marginal tooth; metatibia with obsolescent inner marginal tooth in proximal 1/3; metatibial mucro obsolete.

Distribution.— *Anthonomus guanita* is known only from the type series from the West Indian islands of Antigua, Guadeloupe and Hispaniola.

Natural History.— One of the paratypes of *A. guanita* was collected on *Zanthoxylum spinifex* D.C.

Etymology.— The specific epithet is an anagram of the name of the type locality.

Anthonomus (*Anthonomocyllus*) *pazmani*, new species
Fig. 79

Type Series.— *Holotype*: MEXICO, male [MEXICO: Hgo., 12 mi/ S. Zimapan, 6700'/ V-28-1974 C. W. & L./ O'Brien & Marshall] (CWOB).

Recognition.— The holotype of *A. pazmani* is distinguished by the following combination of characters: aedeagus (Fig. 79) asymmetrical, strongly expanded at apex; metatibia of male with slight inner marginal prominence; inner marginal protibial prominence short, stout; mesocoxae widely separated by distance *ca*. 0.8 x width of one mesocoxa; sutural elytral interstriae with postscutellar patch of broad, pallid scales.

The holotype of *A. pazmani* is larger and stouter, but otherwise closely resembles adults of *A. dentipes* and *A. contaminatus*. The three species are distinguished by the shape of the aedeagus (*cf*. Figs. 76, 77, 79). The aedeagus of *A. pazmani* is similar to that in *A. contaminatus*, but the latter lacks the extreme apical expansion exhibited in *A. pazmani* (*cf*. Figs. 76, 79). The metatibia of the adult male of *A. pazmani* is similar to that of *A. dentipes* (Fig. 64) in having a slight inner marginal prominence not present in *A. contaminatus*.

Description.—

Male. *Length*: 3.12 mm (n = 1). *Width*: 1.70 mm (n = 1). *Head*: vertex with broad, rounded scales; eyes protruding, narrowly separated by distance *ca*. 0.4 x width of rostrum at base. *Rostrum*: slightly curved distally; length 1.35 x pronotal length (n = 1); scales broad, dense; carinae obsolete; length of distal portion 35% of total rostral length (n = 1). *Prothorax*: pronotum flattened, with slight dorsolateral depressions and postocular prominences; with imbricated, rounded, pallid scales, narrower, subtruncate, fulvoaeneous scales and narrower, fuscoaeneous scales; broad scales dense apically, in transverse middorsal fascia, and on pleuron. *Elytra*: interstriae nearly flat, with imbricated, whitish scales, pallid fulvescent to fuliginous scales, and dark, fuscous scales; dark scales dense on median portion of sutural interstriae, on basal portion of interstria 3, on short posteromedian section of interstria 2, and in diffuse posterolateral macula across interstriae 2-10; pallid scales dense in short to elongate fascicles around posterolateral macula, and in declivital fascia. *Abdomen*: sternum 5 *ca*. 0.8 x as long as sternum 4, deeply, broadly emarginate posteriorly, with dense scales laterally, slightly concave and setose medially. *Legs*: profemur ca. 1.2 x wider than metafemur; protibial uncus stout, long, curved; metatibial mucro short, acute, oblique. *Genitalia*: endophallus unarmed.

Female. Unknown.

Distribution.— *Anthonomus pazmani* is known only from the holotype from the state of Hidalgo, México.

Natural History.— Nothing is known about the life history and hosts of *A. pazmani.*

Etymology.— The specific epithet is an anagram of the name of the type locality.

Anthonomus (*Anthonomocyllus*) *xanthoxyli* Linell
Figs. 17, 18, 39, 49, 59, 66, 80

Anthonomus xanthoxyli Linell 1897: 49-50. *Holotype*: TEXAS, female [Type No. 1399/ U.S.N.M.] [San Diego/ 27.10 Tex.] [E. A Schwarz/ collector] USNM. *Paratypes*: TEXAS, 15 [San Diego/ 27.10 Tex.] [E. A. Schwarz/ collector] USNM; 1 [Victoria, Tex. 4, 6-11] [on Xanthoxylum/ clava-herculis] [J. D. Mitchell/ collector] USNM; 5 [Brownsville,/ Tex. III-20-08] USNM; [Rio Grande City/ Tex./ X-29-36] [in seed/ Fagara fagara] USNM. Townsend 1903. Schenkling and Marshall 1934: 38. Burke 1962: 204-205. Burke and Gates 1974: 325-326. O'Brien and Wibmer 1982: 108.

Recognition (Figs. 17, 18).— Adults of *A. xanthoxyli* are distinguished by the following combination of characters: abdominal sternum 5 of female (Fig. 49) with a u-shaped posteromedian emargination and an anteromedian fovea; aedeagus (Fig. 80) strongly asymmetrical, with apicodorsal carinae that converge apically to apicomedian prominences; pygidium of female (Fig. 39) with broad dorsomedian concavity with long, broad scales and with small apicolateral prominences; mesocoxae widely separated by distance *ca.* 0.6 x width of one mesocoxa; sutural elytral interstriae (Fig. 18) with postscutellar patch of broad, pallid scales; inner marginal protibial prominence (Figs. 59) feebly developed; metatibia of male (Fig. 66) straight on inner margin.

Description.—

Male. *Length*: 2.08-2.48 mm ($\bar{x}$ = 2.34, n = 10). *Width*: 1.32-1.44 mm ($\bar{x}$ = 1.31, n = 10). *Head*: vertex with broad, rounded scales; eyes protruding, narrowly separated by distance *ca.* 0.4 x width of rostrum at base. *Rostrum*: stout, slightly curved distally; length 1.15-1.77 x pronotal length ($\bar{x}$ = 1.28, n = 10); scales broad, dense; carinae obsolete; length of distal portion 24-36% of total rostral length ($\bar{x}$ = 31, n = 10). *Prothorax*: pronotum flattened, with slight dorsolateral depressions and postocular prominences; with imbricated, rounded, pallid scales, slightly narrower, apically subtruncate, fulvoaeneous scales and narrower, fuscoaeneous scales; broad scales dense apically, in transverse middorsal fascia, and on pleuron. *Elytra*: interstriae nearly flat, with imbricated, whitish scales, pallid fulvescent to fuliginous scales, and dark, fuscous scales; dark scales dense medially on sutural interstriae, on basal portion of interstria 3, on short posteromedian section of interstria 2, and in diffuse posterolateral macula across interstriae 2-10; pallid scales dense in short to elongate fascicles around posterolateral macula, and in declivital fascia. *Abdomen*: sternum 5 *ca.* 1.0 x as long as sternum 4, broadly emarginate posteriorly, with dense, broad scales laterally, slightly concave and setose medially. *Legs*: profemur *ca.* 1.1 x wider than metafemur; protibial uncus stout, long, curved; metatibial mucro short, curved, oblique. *Genitalia*: endophallus unarmed.

Female. *Length*: 2.28-2.72 mm ($\bar{x}$ = 2.44, n = 10). *Width*: 1.32–1.44 mm ($\bar{x}$ = 1.36, n = 10). *Rostrum*: slender; length 0.93–1.34 x pronotal length ($\bar{x}$ = 1.26, n = 10); length of distal portion 36–46% of total rostral length ($\bar{x}$ = 40, n = 10). *Legs*: protibia with inner marginal tooth; metatibia without inner marginal tooth; metatibial mucro obsolete.

Distribution.— The concept of *A. xanthoxyli* adopted here is based on specimens identified by H. R. Burke after examining the type series from Texas. The 202 examined specimens (TAMU) are from the following localities. MEXICO. *Chiapas*: Las Margaritas. *Nuevo León*: 7.5 mi. S Monterrey. *San Luis Potosí*: Ciudad Valles. *Tamaulipas*: 22 mi. SE Ciudad Victoria; Tampico; Municipio San Carlos, Cerro del Oriente. UNITED STATES. *Texas*: Cameron

Co.: Brownsville; Palmito Battleground; 10 mi. E Rio Hondo; Sabal Palm Grove Sanctuary near Southmost. Hidalgo Co.: Bentsen Rio Grande State Park; Santa Ana Wildlife Refuge. Kleberg Co.: Kingsville. Nueces Co.: Corpus Christi. Refugio Co.: 8 mi. S Woodsboro. San Patricio Co.: 3 mi. E Mathis; 7 mi. N Sinton. Starr Co.

Natural History.— Specimens of *A. xanthoxyli* have been collected on *Zanthoxylum fagara.* Linell (1897: 49-50) stated that the types of *A. xanthoxyli* were found "living in the seeds" of this plant, and Burke and Gates (1974: 325-326) noted that specimens of *A. xanthoxyli* occur along with those of *A. leucostictus* at the same time on the same *Z. fagara* plants in Texas. Townsend (1903) indicated that both species develop in the fruit of *Z. fagara*, stating that "larvae and pupae of *A. leucostictus* have been taken from fruits of *Zanthoxylum* during May through August," whereas those of *A. xanthoxyli* "occur during June and July". Referring to both species, the same authors stated that larvae feed on the white, fleshy inner portion of the fruits, devouring the tissue until only a thin outer shell remains. Infested fruits remain on the tree. Pupation occurs in the larval feeding cavity and the adult emerges through a small round hole in the fruit. One weevil develops in each fruit.

Examined specimens were collected in all months of the year except May and August.

The *Anthonomus leucostictus* Species Group

Recognition.— Adults of *A. leucostictus*, the only species in this species group, are distinguished by the following combination of characters: Pronotum with narrow, fuscous scales, and scattered, broad, leucine scales arising from punctures; elytral integument broadly visible between scattered leucine scales and inconspicuous, narrow, pallid fuliginous scales (Figs. 19, 20); elytral interstriae slightly convex, 3rd slightly elevated at base; head slightly constricted behind protruding eyes (Figs. 19); pronotum emarginate anterodorsally and anteroventrally; mesocoxae widely separated; femora relatively slender, each with a long, slender, slightly curved, acute inner marginal tooth (Fig. 67); mesotibia with acute outer apical spine (Fig. 67).

Anthonomus (*Anthonomocyllus*) *leucostictus* Dietz

Figs. 19, 20, 40, 67, 81

Anthonomus (*Anthonomocyllus*) *leucostictus* Dietz (1891: 193, pl. 5, figs. 7, 7a). *Holotype*: TEXAS, male [Tex.] [Type/ 1950] [W. G. Dietz/ Coll.] [Anthonomus/ leucostictus/ Dietz] (MCZC). Schenkling and Marshall 1934: 38. Burke 1971: 49 (= *A. albopictus*). Burke and Gates 1974: 325-326. O'Brien and Wibmer 1982: 108.

Anthonomus albopictus Champion 1903: 173. *Holotype:* MEXICO, female [Ventanas/ Durango, Höge.] [B.C.A. Col.IV.4./ Anthonomus/ albopictus, Champ.] [Holo-/ type] [Type] (BMNH). Schenkling and Marshall 1934: 55. Blackwelder 1947: 838.

Recognition (Figs. 19, 20).— This species is recognized by the characters listed for the *A. leucostictus* species group. The species is the sister group of the *A. caeruleisquamis* species group as indicated by the shared possession of the long, slender, acute femoral tooth (Fig. 67) and the acute, outer apical mesotibial spine (Fig. 67).

Description.—

Male. *Length*: 2.32-2.64 mm ($\bar{x}$= 2.45, n= 10). *Width*: 1.32-1.56 mm ($\bar{x}$= 1.42, n= 10). *Head*: vertex with large, leucine scales like those on lateral margins of frons between eyes and with narrow, pallid fuliginous scales; venter with broad, imbricated, white scales; eyes protruding, narrowly separated by distance *ca.* 0.8 x width of rostrum at base. *Rostrum*: slender, nearly straight proximally, slightly curved distally; distal portion tricarinate; length 1.33-2.26 x (x̄= 1.58, n= 10) total body length; length of distal portion 31-37% (x̄= 35, n= 10) of total rostral length. *Prothorax*: slightly constricted subapically, without dorsolateral depressions; emarginate anterodorsally, with well-developed postocular lobes; densely punctate, interspaces narrow, broadly exposed; dorsum with scattered, apically rounded, pallid leucine scales and with inconspicuous, narrow, pallid fuliginous scales; lower portion of pleuron with imbricated leucine scales. *Elytra*: subparallel-sided in basal 1/2; interstriae slightly convex, 3rd slightly elevated at base; dark integument broadly visible between narrow, pallid fuliginous scales and scattered, broad, leucine scales or small fascicles of such scales; striae deep, narrow, punctures with setiform scales. *Abdomen*: sternum 5 *ca.* 0.9 x as long as sternum 4, not emarginate posteriorly, not concave, densely setose medially. *Legs*: profemur *ca.* 1.0 x as wide as metafemur, with a single, slender inner marginal tooth; protibia straight, inner margin slightly concave between broad median prominence and slender apical uncus; metatibia nearly straight, without inner marginal prominence, widened at apex; metatibial mucro small, slender. *Genitalia*: aedeagus (Fig. 81) symmetrical, narrowed to subtruncate apex; endophallus unarmed.

Female. *Length*: 2.36-2.80 mm (x̄= 2.57, n= 10). *Width*: 1.30-1.58 mm (x̄= 1.44, n= 10). *Head: Rostrum*: slender, length 1.58-1.81 x (x̄= 1.67, n= 10) pronotal length; length of distal portion 43-55% (x̄= 47, n= 10) of total rostral length. *Pygidium* (Fig. 40): with broad, slightly rounded, apicomedian prominence. *Abdomen*: sternum 5 with small apicomedian prominence. *Legs*: protibia with slight inner marginal prominence; metatibia without inner marginal tooth; metatibial mucro obsolete.

Distribution.— *Anthonomus leucostictus* is known to occur in southern and western Texas and in northeastern and north-central México. In addition to the holotype of *A. leucostictus* from an unspecified locality in Texas, and that of *A. albopictus* from the state of Durango, México, 284 specimens (CNCI, CWOB, RSAC, TAMU, USNM) from the following localities were examined. MEXICO. *Durango*: 24 mi. W La Ciudad. *Hidalgo*: Sabinas. *México*: Bejuco, Temascaltepec. *Nuevo León*: 15.3 mi. E China; 15 and 18 mi. N Linares; 7.5 mi. S Monterrey; east slope Cerro de la Silla, near Guadalupe. *San Luis Potosí*: Río Verde; Media Luna. *Tamaulipas*: Tampico; 2 mi. E Tula. UNITED STATES. Texas. Bee Co.: 7 mi. SE Beeville. Bexar Co.: San Antonio. Brewster Co.: Big Bend National Park. Brazos Co. Cameron Co.: 10 mi. W Boca Chica; Brownsville; 8 mi. E Brownsville; 10 mi. E Rio Hondo; Palmito Battle Ground; Sabal Palm Grove. Hidalgo Co.: 2 mi. S Linn; Santa Ana Wildlife Refuge. Jim Wells Co.: 7 mi. W Alice. Kleberg Co.: Kingsville. La Salle Co.: 12 mi. N Cotulla. Live Oak Co.: 5 mi. E George West. Nueces Co.: Corpus Christi; 2 mi. S Corpus Christi. Refugio Co.: 8 mi. S Woodsboro. San Patricio Co.: Lake Corpus Christi State Park; 4 mi. SW Mathis; 6, 7 and 8 mi. N Sinton; Welder Wildlife Refuge. Victoria Co.: 7 mi. S Victoria.

Natural History.— Burke and Gates (1974: 325-326) noted that specimens of *A. leucostictus* occur along with those of *A. xanthoxyli* at the same time on the same *Zanthoxylum fagara* plants in *Texas*.

The *Anthonomus caeruleisquamis* Species Group

The *A. caeruleisquamis* group was established by Champion (1903: 157, 174-175) for two Central American species, *A. caeruleisquamis* Champion, and *A. squamiger* Champion.

Recognition (Figs. 21-26).— The species in this group are distinguished by the following characters: Pronotum and elytra broad, smooth, without elevations, prominences or distinct subapical constriction; pronotal punctures each with a large scale that does not extend beyond edge of puncture or with a much narrower scales; elytral interstriae flat, 3rd not elevated at base; elytral integument narrowly visible between dense vestiture of small, rounded, cinereous to caeruleous scales; femora and tibiae, except for distal portions, ferruginous to alizarine. They share the following characters with *A. leucostictus*: femora with a single long, slender, curved tooth (*cf.* Fig. 67); mesotibia with acute outer apical spine (*cf.* Fig. 67); head slightly constricted behind protruding eyes.

The group is a relatively homogeneous one and the following descriptions apply to all of the assigned species.

Description.—

Male. *Head*: vertex with small griseous to caeruleous scales; venter with densely imbricated white scales; eyes protruding. *Rostrum*: slender, more-or-less evenly curved from base to apex; proximal portion tricarinate, with sparse, slender scales; distal portion smooth, glabrous. *Prothorax*: broad at base, narrowed to shallow subapical constriction; each pronotal puncture with a broad scale that fills puncture but does not overlap interspace, or with a narrow, setiform scale; lower portion of pleuron with broader, white scales. *Elytra*: not vaulted medially, sides slightly widened in posterior 1/3; interstriae broad, flat, with dense, recumbent vestiture of small, rounded scales and median rows of smaller, narrower, scales; striae deep, narrow, with minute setiform scales; interstria 3 not prominent at base. *Abdomen:* sterna 3-5 shallowly, broadly concave medially, with dense, imbricated scales laterally, longer, setiform scales medially. *Legs*: femora ferruginous to alizarine in basal 3/4, piceous, like distal portions of tibiae and tarsi, in distal 1/4, with sparse, narrow scales that are replaced by broader caesious scales in distal 1/4; profemur with a single long, slender, slightly curved, acute inner marginal tooth.

Female. *Rostrum*: very slender; proximal portion smooth, shining, glabrous, except at extreme base; distal portion smooth, glabrous. *Pygidium*: with slight apicomedian marginal prominence; slightly excavated apicomedially, excavation with broad scales. *Abdomen*: sterna 1–4 slightly, broadly concave, with dense, imbricated white scales laterally, admixed longer, suberect white scales and erect setiform scales medially.

Key to Known Adult Males of the Species in the *A. caeruleisquamis* Group

1 Procoxa with acute internal tooth; pygidium not excavated; metatibia slightly constricted subapically, not excavated posteriorly, without subapical, inner marginal prominence; rostrum without midventral, subapical tooth .... *A. squamiger*, p. 580

1' Procoxa without internal tooth; pygidium excavated (Figs. 27-28); metatibia excavated posteriorly in apical 1/4 between broad, rounded, outer apical and inner apical expansions or with large, bluntly rounded, subapical, inner marginal prominence (Figs. 68, 69); rostrum with midventral, subapical tooth (Fig. 25) 2

2 Metatibia not excavated in apical 1/4, with large, bluntly rounded, subapical, inner marginal prominence (Fig. 69) .... *A. caesius*, p. 583

2' Metatibia excavated posteriorly in apical 1/4 between broad, rounded, outer apical and inner apical expansions, without subapical, inner marginal prominence (Fig. 68) 3

3 Pygidium deeply excavated, with long, acuminate, aureous scales that are much longer and broader in two contiguous middorsal clusters and in smaller, extreme lateral clusters (Fig. 27) .... *A. aeroides*, p. 581

3' Pygidium less deeply excavated, with long, acuminate, aureous scales that are longest and broadest in large, approximate, rounded dorsomedian clusters, without lateral clusters (Fig. 28)............................*A. cymatilis*, p. 582

Key to Known Adult Females of the Species in the *A. caeruleisquamis* Group

1 Abdominal sternum 5 without median fovea, depressed on each side of apicomedian carina (Fig. 50); protibia with obsolescent inner marginal prominence ....*A. squamiger*, p. 580

1' Abdominal sternum 5 with median fovea, without apicomedian carina (Figs. 51, 52); protibia with broad, low, inner marginal prominence 2

2 Abdominal sternum 5 slightly produced apicomedially (Fig. 51); broad scales on pronotum and elytra deep caeruleous...... ....*A. caeruleisquamis*, p. 581

2' Abdominal sternum 5 broadly emarginate apicomedially (Fig. 52); broad scales on pronotum and elytra pallid caesius to cinereous ....*A. cymatilis*, p. 582

Anthonomus (*Anthonomocyllus*) *squamiger* Champion
Figs. 21, 22, 41, 50, 82, 83

Anthonomus squamiger Champion 1903: 174-175. *Holotype*. PANAMA: female [San Miguel,/ Pearl Isl./ Champion.] [♀] [B.C.A. Col.IV.4./ Anthonomus/ squamiger,/ Champ.] [Type] (BMNH). Schenkling and Marshall 1934: 55. Blackwelder 1947: 839. O'Brien and Wibmer 1982: 110.

Recognition (Figs. 21, 22).— Adults of this relatively small member of the *A. caeruleisquamis* subgroup are distinguished from the other members of the subgroup by the deep caeruleous color of the scales on the pronotum and elytra, by the unmodified pygidium and metatibia of the male, and by the small, acute internal tooth on the procoxa of the male.

Descriptiom.—

Male. *Length*: 2.20 mm (n= 1). *Width*: 1.24 mm (n= 1). *Head*: eyes separated by distance *ca*. 0.8 x width of rostrum at base. *Rostrum*: length 1.90 x (n= 1) pronotal length; length of distal portion 32% (n= 1) of total rostral length. *Prothorax*: broad scales deep caeruleous. *Elytra*: broad scales deep caeruleous. *Abdomen*: sternum 4 ca. 1.2 x longer in middle than sternum 5. *Legs*: profemur *ca*. 1.1 x wider than metafemur; protibia slender, slightly curved, without inner marginal prominence; metatibia nearly straight, slightly constricted subapically, with short, oblique apical uncus. *Genitalia* (Figs. 82, 83): aedeagus slender, slightly constricted subapically, expanded at extreme apex; endophallus unarmed.

Female. *Length*: 2.24-2.40 mm (n= 2). *Width:* 51-53 mm (n= 2). *Rostrum*: length 1.89-2.09 x (n= 2) pronotal length; length of distal portion 51-53% (n= 2) of total rostral length. *Pygidium* (Fig. 41): not depressed apicodorsally, with slight apicomedian projection. *Abdomen*: sternum 5 depressed on each side of apicomedian carina (Fig. 50). *Legs*: protibia slender, with obsolescent inner marginal prominence; metatibia nearly straight, widened slightly at apex, unarmed apically.

Distribution.— In addition to the male holotype from Panamá, two specimens from the following localities were examined. PANAMA. *Panamá* (Archipélago de las Perlas): Isla Taboga (1 male, TAMU). VENEZUELA. *Táchira*: La Quinta (1 female, AUEM).

Natural History.— Nothing is known about the life history and hosts of *A. squamiger*. Examined specimens were collected in March and June.

Anthonomus (*Anthonomocyllus*) *caeruleisquamis* Champion
Figs. 23, 24, 42, 51

Anthonomus caeruleisquamis Champion 1903: 174, Tab. X. figs. 12,12a, female). *Holotype.* GUATEMALA: [♀] [Sp. figured] [Mirandilla,/ 1700 ft./ Champion.] [B.C.A. Col.IV.4./ Anthonomus/ caeruleisquamis,/ Champ.] [Type] (BMNH). Schenkling and Marshall 1934: 56. Blackwelder 1947: 838. O'Brien and Wibmer 1982: 106.

Recognition (Figs. 23, 24).—Champion (1903: 174) stated that *A. caeruleisquamis*, "one of the most remarkable forms of *Anthonomus* yet discovered", is "recognizable at a glance by the blue squamosity of the upper surface". The specimens examined also have distinctive ochreous scales on the mesepisternum, mesepimeron and metepisternum and the ochreous pads on the tarsi contrast sharply with the dark integument and griseous scales on the upper portions of the tarsi. The examined adults are also somewhat larger than those of the other species in the *A. caeruleisquamis* subgroup. Since the male of the species is unknown, the possibility that the specimens identified as *A. caeruleisquamis* are females of one of the other named species of the *A. caeruleisquamis* subgroup cannot be ruled out.

Description.—

Male. Unknown.

Female. *Length*: 3.20 mm (n= 2). *Width*: 1.66-1.72 mm (n= 2). *Head*: eyes small, separated by distance *ca.* 0.9 x width of rostrum at base. *Rostrum*: length 1.98-2.08 x (n= 2) pronotal length; length of distal portion 57-60% (n= 2) of total rostral length. *Prothorax*: broad scales deep caeruleous. *Elytra*: broad scales deep caeruleous in color. *Abdomen* (Fig. 51): sternum 5 rounded, not emarginate apicomedially, with deep median fovea. *Legs*: profemur *ca.* 1.3 x wider than metafemur; protibia slender, with broad, low, inner marginal prominence; metatibia nearly straight, slightly widened at apex, unarmed apically.

Distribution.— In addition to the holotype of *A. caeruleisquamis* from the Department of Escuintla, Guatemala, a specimen labelled "On ship from GUATEMALA Phila. Pa." (1 female, USNM) was examined.

Natural History.— Nothing is known about the life history and hosts of *A. caeruleisquamis*. Examined specimens were collected in February and November.

Anthonomus (*Anthonomocyllus*) *aeroides*, new species
Figs. 25, 26, 27, 84, 85

Type Series.— *Holotype:* VENEZUELA, male [Venezuela - AR/ Rancho Grande/ 900 m 3-VI-1966/ J. & B. Bechyne] (IZAV). *Paratype:* COLOMBIA, male [COLOM. Magd., 3000'/ Campana, 25 Km. S./ Sta. Marta, IV-29-1973/ Howden & Campbell] (HAHC).

Recognition (Figs. 25, 26).— This species is distinguished from the other members of the *A. caeruleisquamis* subgroup by the male having a relatively large, deeply excavated pygidium with long, acuminate, aureous scales that are much longer and broader in two contiguous middorsal clusters and in smaller, lateral clusters (Fig. 27). The metatibia of the male, as in the related *A. cymatilis*, is excavated posteriorly in the apical 1/4 between broad, rounded, apical, inner and outer marginal expansions (*cf.* Fig. 68).

Description.—

Male. *Length*: 2.60 mm (n= 2). *Width*: 1.54-1.56 mm (n= 2). *Head*: eyes separated by distance *ca.* 0.7 x width of rostrum at base. *Rostrum*: length 1.56-1.59 x (n= 2) pronotal length; distal portion with midventral, subapical tooth; length of distal portion 34% (n = 2) of total rostral length. *Prothorax*: broad scales pallid caesius. *Elytra*: broad scales pallid caesius in color.

Pygidium (Fig. 27): deeply excavated; with long, acuminate, aureous scales that are much longer and broader in two contiguous middorsal clusters and in smaller, extreme lateral clusters. *Abdomen*: sternum 4 *ca.* 2.0 x longer in middle than sternum 5. *Legs*: profemur subequal in width to metafemur; protibia slender, slightly curved basally, straight distally, with slight inner marginal prominence; metatibia stout, straight, excavated posteriorly in apical 1/4 between broad, rounded, apical, outer and inner marginal expansions. *Genitalia* (Figs. 84, 85): aedeagus sinuate in lateral view, slightly expanded medially, narrowed to broadly subtruncate apex; endophallus with minute median sclerite.

Female. Unknown.

Distribution.— This species is known only from the specimens in the type series from the Department of Magdalena, Colombia, and from the State of Aragua, Venezuela.

Natural History.— Nothing is known about the life history and hosts of *A. aeroides*. Examined specimens were collected in April and June.

Etymology.— The specific epithet means "like the sky" in Latin. It refers to the scales on the upper portion of the prothorax and on the elytra which are the color of a lightly overcast sky.

Anthonomus (*Anthonomocyllus*) *cymatilis*, new species

Figs. 28, 43, 52, 68, 86, 87

Type Series.— *Holotype*: BRAZIL, male [S. Roque SP/ 25-XII-71/ F. Lane Col.] (MCZC). *Paratypes*: BRAZIL, 1 male, 1 female [S. Roque SP/ 25-XII-71/ F. Lane Col.]; 1 female [Pouso Alegre/ M. Gerais - Brasil/ IX-962/ F. S. Pereira col.]; 1 male [BRAZIL: PARANA/ 5 Km E Foz do/ Iguacu: Jan. 27/ 83: E. G. Riley]; 1 male, 1 female [*P. Grossa*/ Pedreira/ G. chuva./ *9-44*] [*2039*] [Coleção/ F. Justus Jor] [Dept$^{\underline{o}}$ Zool/ UF-PARANA]; 1 female [MORUMBI/ São Paulo-Capital/ Dr. Nick. 22.10.44] [Gregorio Bondar/ Collection/ David Rockefeller/ Donor]; 1 female [MORUMBI/ São Paulo-Capital/ Dr. Nick. 24.9.44] [4991] [Gregorio Bondar/ Collection/ David Rockefeller/ Donor]. Total paratypes, 8 (AMNH, CWOB, DZUP, MZSP].

Recognition.— *A. cymatilis* is like *A. caesius* in having the metatibia of the male excavated in apical 1/4 (Fig. 69). The pygidium of the male of *A. cymatilis* has long, acuminate, aureous scales that are longest and broadest in large, approximate, rounded dorsomedian clusters (Fig. 28).

Description.—

Male. *Length*: 2.44-2.68 mm ($\bar{x}$= 2.58, n= 5). *Width*: 1.54-2.44 mm ($\bar{x}$= 1.76, n= 5). *Head*: eyes separated by distance *ca.* 0.7 x width of rostrum at base. *Rostrum*: length 1.53-1.77 x ($\bar{x}$= 1.62, n= 5) pronotal length; distal portion with median, midventral, subapical tooth; length of distal portion 31-34% ($\bar{x}$= 33, n= 5) of total rostral length. *Prothorax*: broad scales pallid caesius to cinereous. *Elytra*: broad scales pallid caesius to cinereous. *Pygidium* (Fig. 28): excavated, with long, acuminate, aureous scales that are longest and broadest in large, approximate, rounded dorsomedian clusters. *Abdomen*: sternum 4 *ca.* 2.0 x longer in middle than sternum 5. *Legs*: profemur subequal in width to metafemur; protibia slender, slightly curved basally, straight distally, with slight inner marginal prominence; metatibia stout, straight, excavated posteriorly in apical 1/4 between broad, rounded, outer apical and inner apical expansions (Fig. 68). *Genitalia* (Figs. 86, 87): aedeagus sinuate in lateral view, slightly expanded medially, constricted proximal to slight apicolateral expansions; struts expanded distally; endophallus with minute median sclerite.

Female. *Length*: 2.32-2.72 mm (n= 2). *Width*: 1.62-1.64 mm (n= 2). *Rostrum*: length 2.08-2.21 x (n= 2) pronotal length; length of distal portion 31-37% (n= 2) of total rostral length. *Abdomen*: sternum 5 with deep median fovea. *Legs*: protibia slender, with broad, low, inner marginal prominence; metatibia constricted subapically, widened slightly at apex; metatibial uncus obsolete, outer apical tooth present.

Distribution.— This species is known only from the type series from the States of Minas Gerais, Paraná and São Paulo, Brazil.

Natural History.— Nothing is known about the life history and hosts of *A. cymatilis*. Examined specimens were collected in January, September, November and December.

Etymology.— The specific epithet, a Latin adjective meaning blue, refers to the bluish color of the scales on the upper portion of the prothorax and on the elytra.

Anthonomus (*Anthonomocyllus*) *caesius*, new species

Figs. 29, 69, 88, 89

Type Series.— Holotype: BRAZIL, male [Chapada dos/ Guimarães/ 24-1-1961] [Brasil, MT/ J. & B. Bechyné] (MPEG).

Recognition.— *A. caesius* is distinguished from the other members of the *A. caeruleisquamis* subgroup that have the pygidium of the male excavated by not having the metatibia of the male excavated in apical 1/4, but armed with a large, bluntly rounded, subapical, inner marginal prominence (Fig. 69). The pygidium of the male (Fig. 29) has long, aureous scales that are longest and broadest in wide, approximate, dorsal bands and not forming such distinct middorsal clusters as in *A. cymatilis* (*cf.* Fig. 28).

Description.—

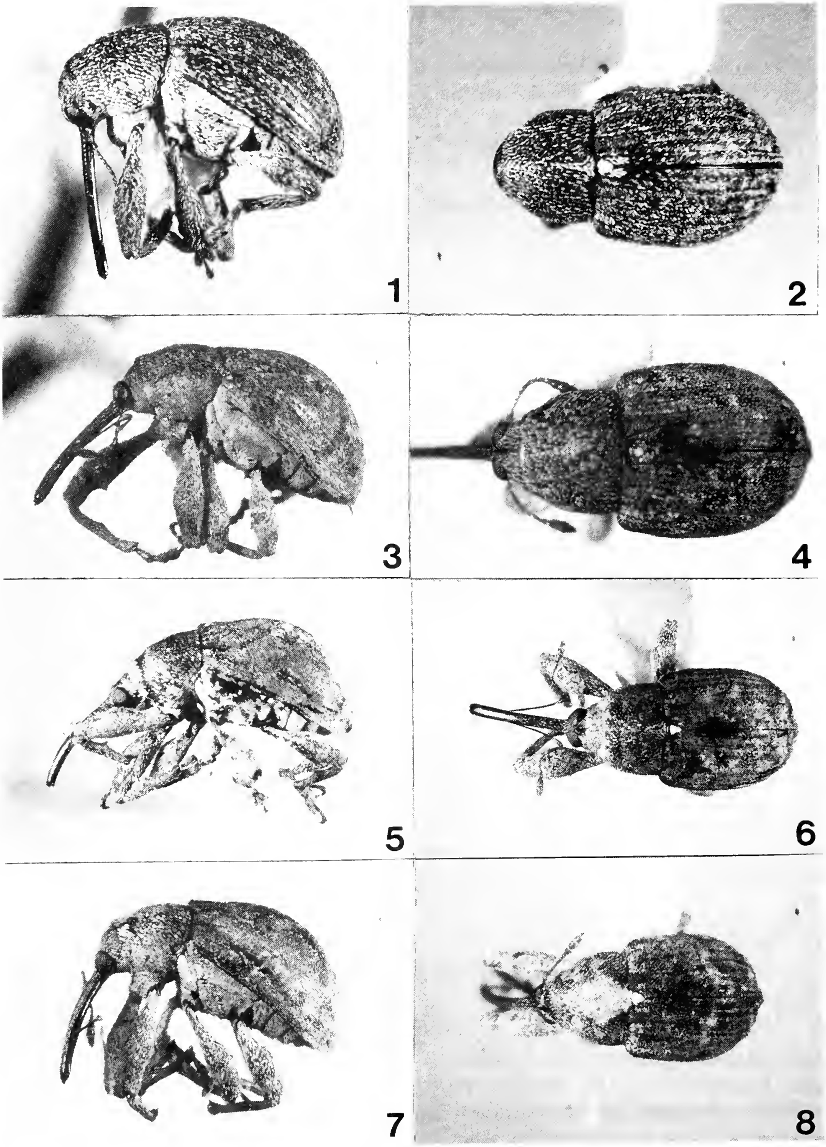
Male. *Length*: 2.32 mm (n= 1). *Width*: 1.60 mm (n= 1). *Head*: eyes separated by distance *ca.* 0.7 x width of rostrum at base. *Rostrum*: length 1.57 x (n= 1) pronotal length; distal portion with midventral, subapical tooth; length of distal portion 50% (n= 1) of total rostral length. *Prothorax*: broad scales pallid caesius. *Elytra*: broad scales pallid caesius in color. *Pygidium* (Fig. 29): excavated, with long, acuminate, aureous scales that are longest and broadest in wide, approximate, dorsal bands. *Abdomen*: sternum 4 *ca.* 2.0 x longer in middle than sternum 5. *Legs*: profemur subequal in width to metafemur; protibia slender, slightly curved basally, straight distally, with slight inner marginal prominence; metatibia stout, straight, with large, bluntly rounded, subapical, inner marginal prominence proximal to narrow, oblique, inner marginal channel (Fig. 69); metatibial uncus oblique, apically truncate. *Genitalia* (Figs. 88, 89): aedeagus sinuate in lateral view, slightly expanded medially then constricted proximal to slight apicolateral expansions; endophallus with minute median sclerite.

Female. Unknown.

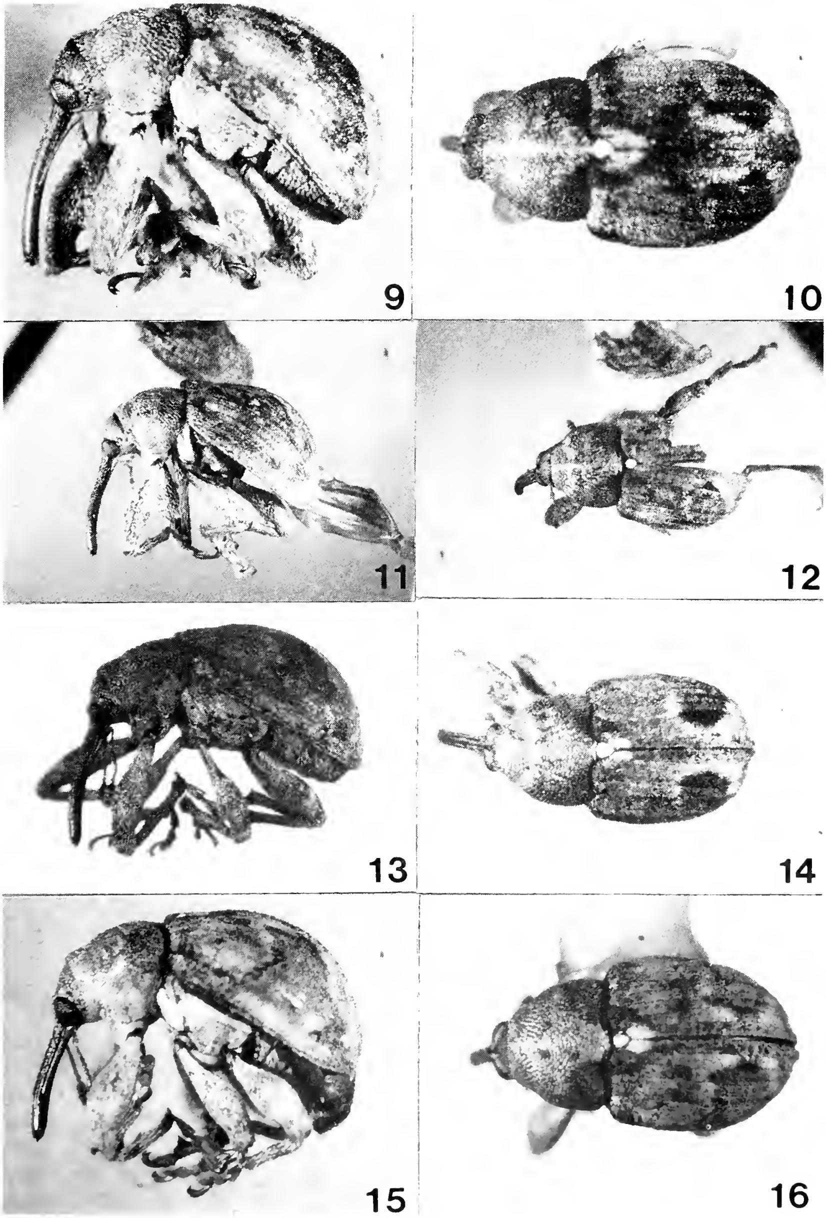
Distribution.— This species is known only from the holotype from the State of Mato Grosso, Brazil.

Natural History.— Nothing is known about the life history and hosts of *A. caesius*. The holotype was collected in January.

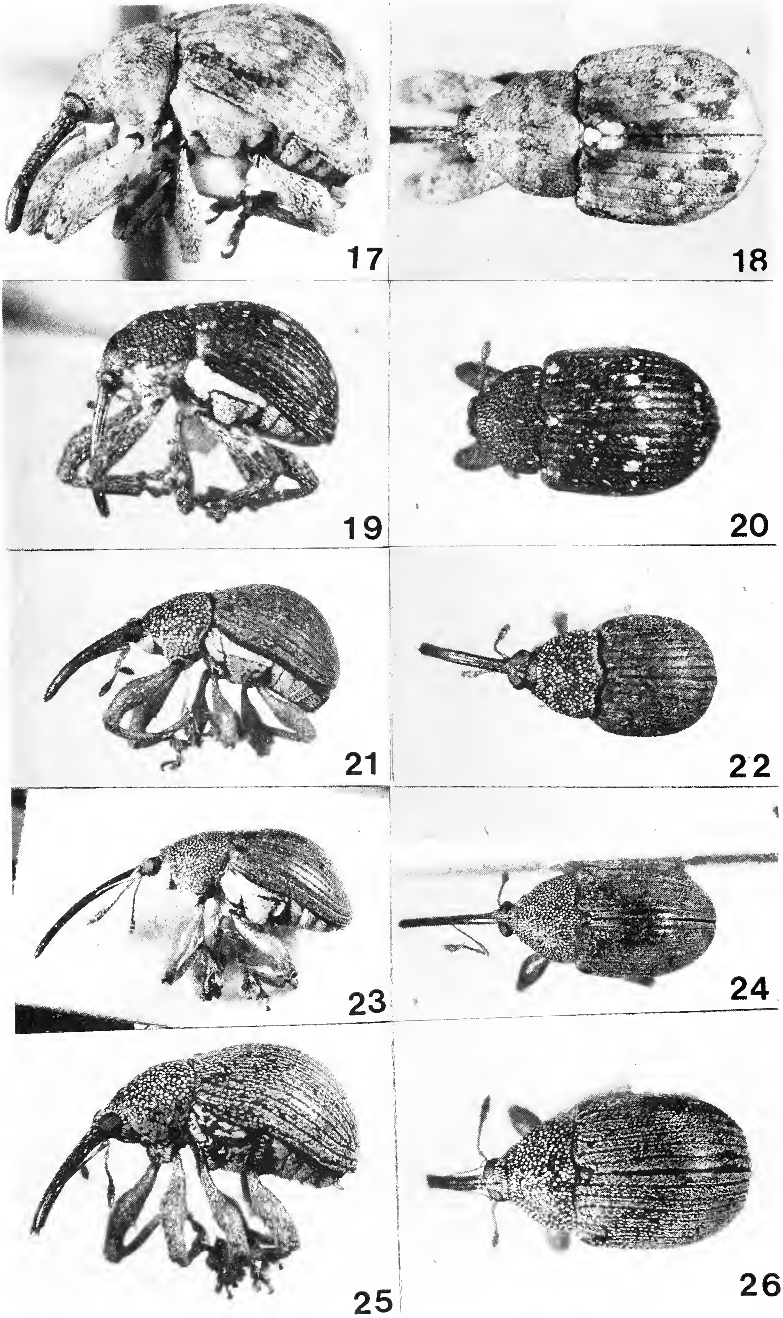
Etymology.— The specific epithet, a Latin adjective meaning bluish-gray, refers to the color of the scales on the upper portions of the prothorax and the elytra.



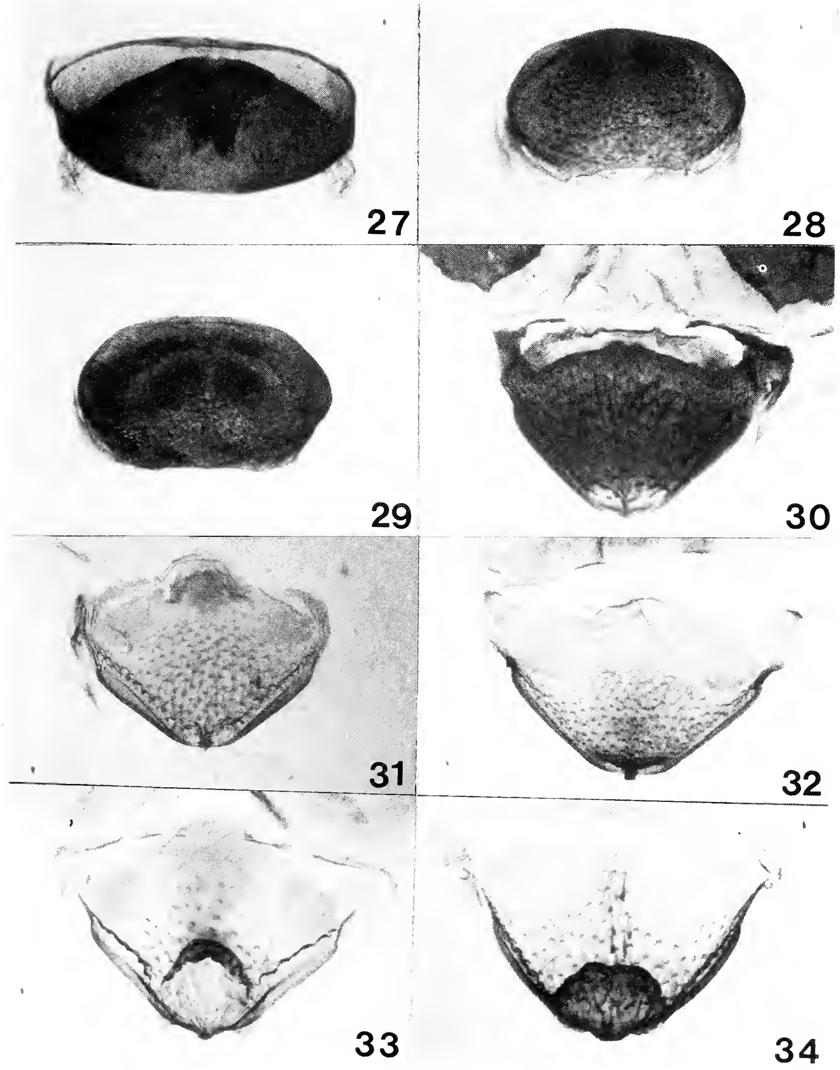
Figs. 1–8. Subgenus *Anthonomocyllus* spp., habitus of adults, lateral and dorsal views: 1, 2) *A. tenuirostris*, ♀, Puerta Parada, Guatemala; 3, 4) *A. acus*, ♂, Encruzilhada, Brazil; 5, 6) *A. accola*, ♀, El Limón, Venezuela; 7, 8) *A. argentatus*, ♂, Cayamas, Cuba.



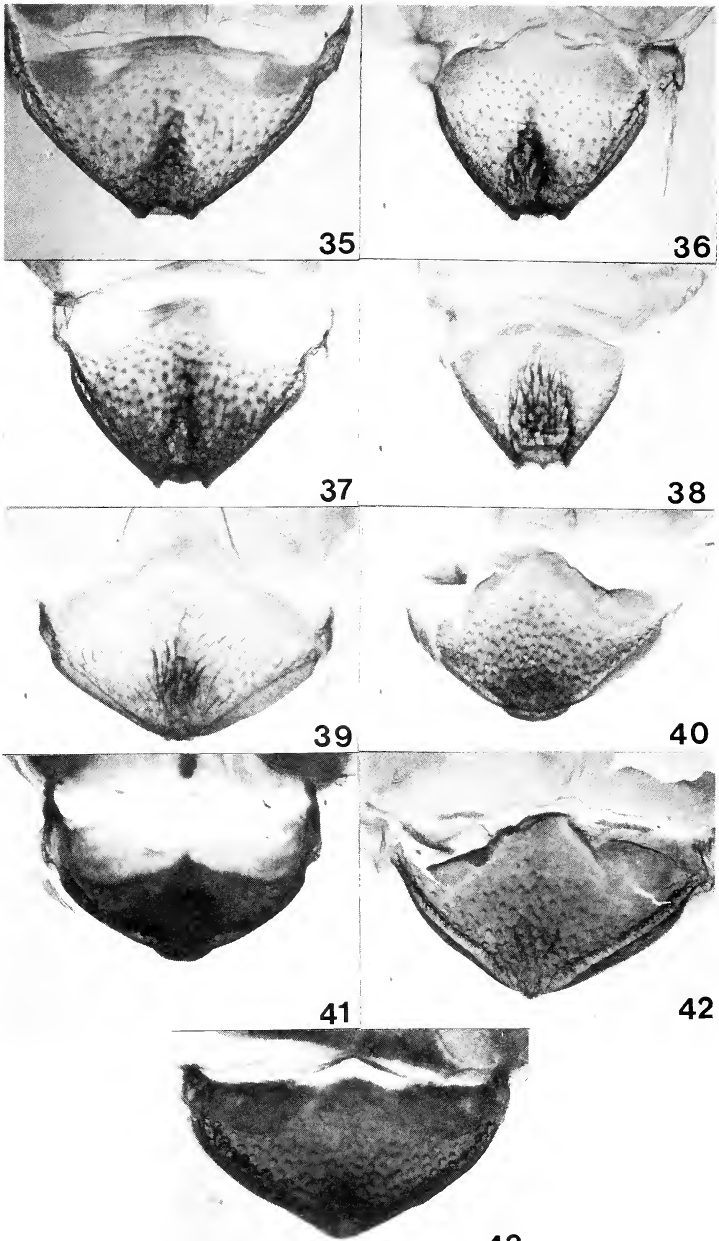
Figs. 9–16. Subgenus *Anthonomocyllus* spp., habitus of adults, lateral and dorsal views: 9, 10) *A. costulatus*, ♀, Matheson Hammock, Florida; 11, 12) *A. contaminatus*, ♂, holotype; 13, 14) *A. dentipes*, ♂, lectotype; 15, 16) *A. guanita*, ♂, holotype.



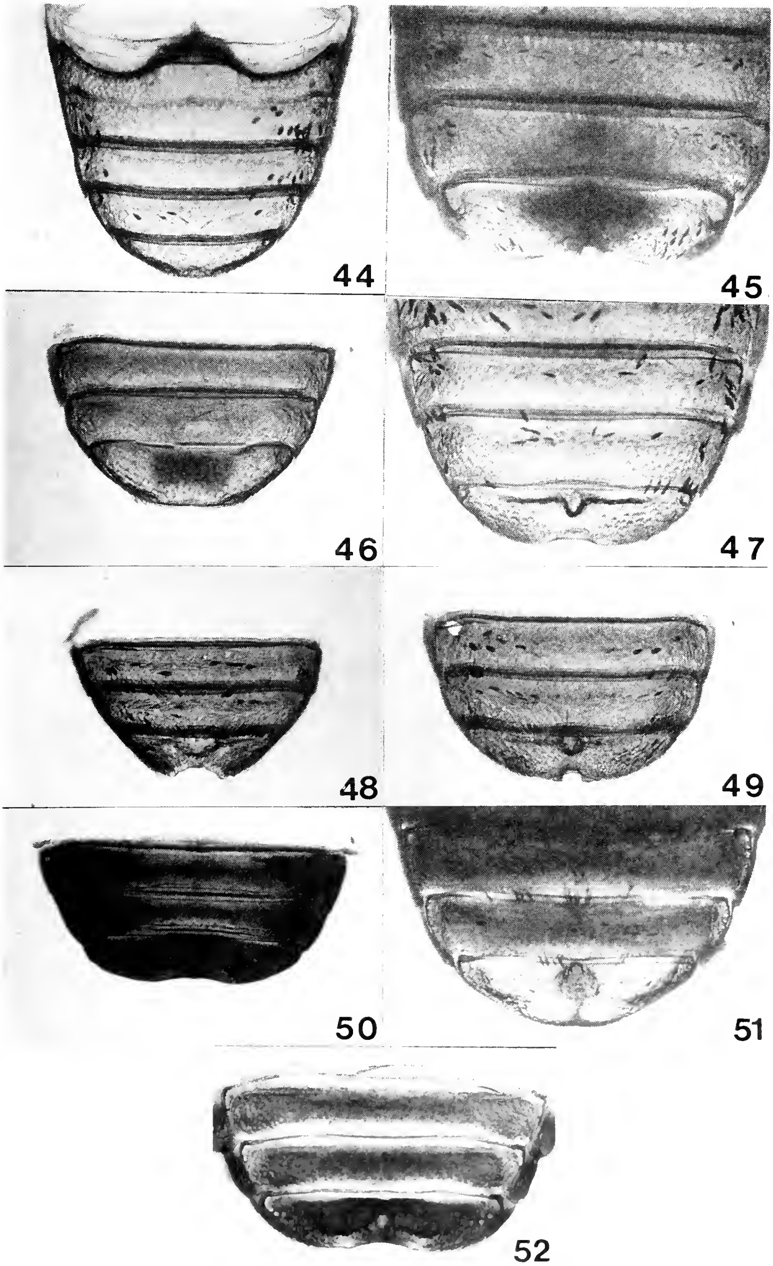
Figs. 17–26. Subgenus *Anthonomocyllus* spp., habitus of adults, lateral and dorsal views: 17, 18) *A. xanthoxyli*, ♂ Santa Ana Wildlife Refuge, Texas; 19, 20) *A. leucostictus*, ♀, Welder Wildlife Refuge, Texas; 21, 22) *A. squamiger*, ♂, 23, 24) *A. caeruleisquamis*, ♀ holotype; 25, 26) *A. aeroides*, ♂, Campana, Magdalena, Colombia.



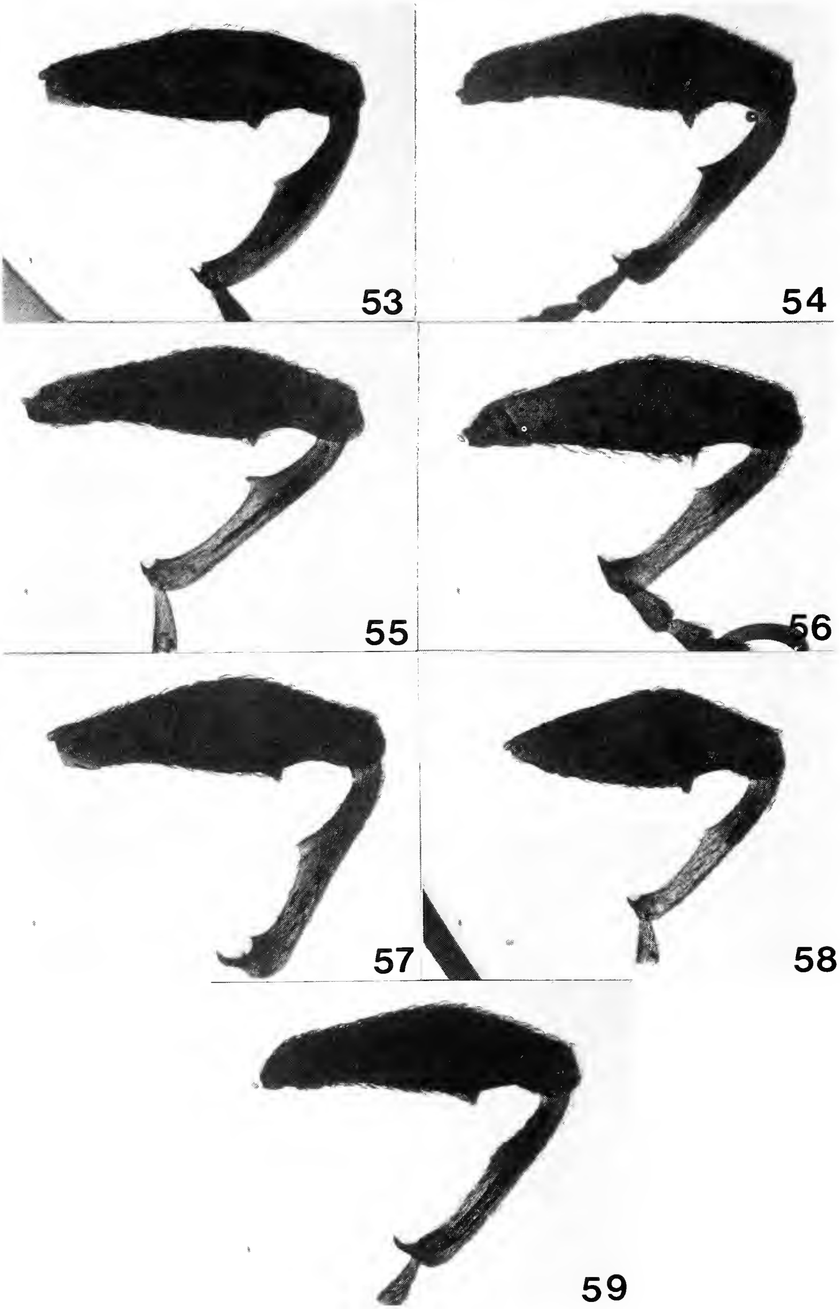
Figs. 27–34. Subgenus *Anthonomocyllus* spp., pygidium, dorsal view: 27) *A. aeroides*, ♂, Campana, Magdalena, Colombia; 28) *A. cymatilis*, ♂, holotype; 29) *A. caesius*, ♂ holotype; 30) *A. tenuirostris*, ♀, Puerta Parada, Guatemala; 31) *A. acus*, ♀, Encruzilhada, Brazil; 32) *A. accola*, ♀, El Limón, Venezuela; 33) *A. argentatus*, ♀ Boca Chica, Republica Dominicana; 34) *A. costulatus*, ♀, Matheson Hammock, Florida.



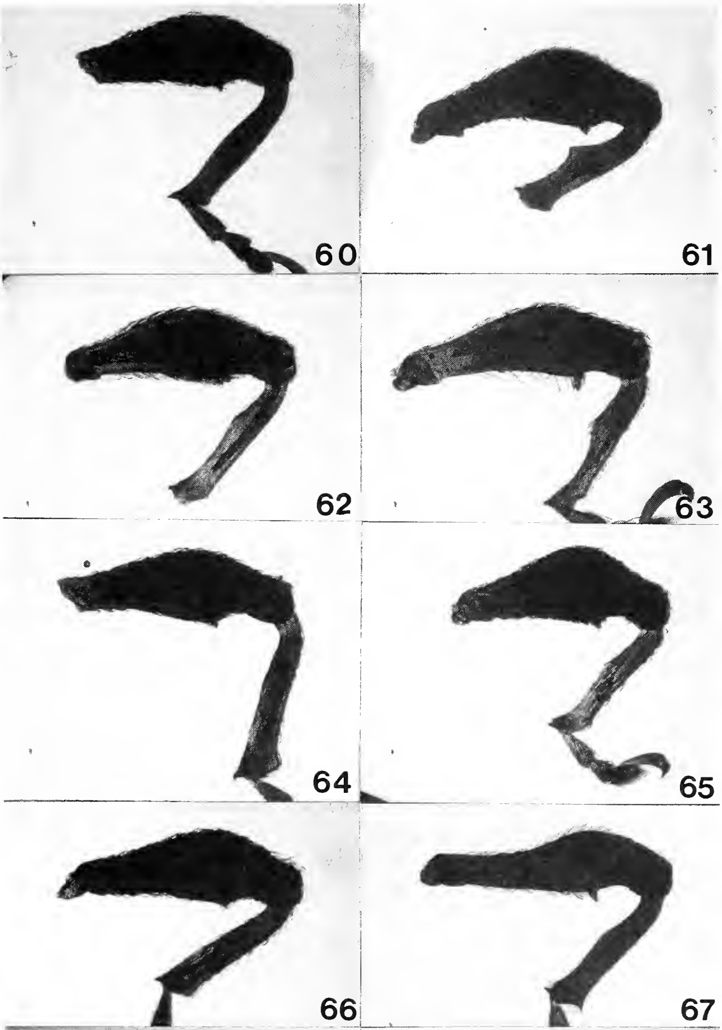
Figs. 35–43. Subgenus *Anthonomocyllus* spp., pygidium, dorsal view: 35) *A. azalus*, ♀, 2.4 mi. NE El Sauzal, México; 36) *A. contaminatus*, ♀, La Cruz de Taratara, Venezuela; 37) *A. dentipes*, ♀, Nova Teutônia, Brazil; 38) *A. guanita*, ♀, Anse la Boise, Guadeloupe; 39) *A. xanthoxyli*, ♀, Santa Ana Wildlife Refuge, Texas; 40) *A. leucostictus*, ♀, Welder Wildlife Refuge, Texas; 41) *A. squamiger*, ♀, La Quinta, Táchira, Venezuela; 42) *A. caeruleisquamis*, ♀, Guatemala; 43) *A. cymatilis*, ♀, São Roque, São Paulo, Brazil.

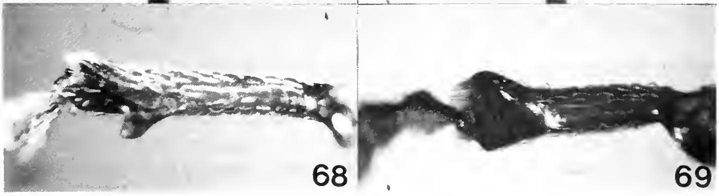


Figs. 44–52. Subgenus *Anthonomocyllus* spp., abdominal sternum of ♀, ventral view: 44) *A. acus*, Encruzilhada, Brazil; 45) *A. accola*, El Limón, Venezuela; 46) *A. argentatus*, Boca Chica, Republica Dominicana; 47) *A. azalus*, 2.4 mi.NE El Sauzal, México; 48) *A. guanita*, Anse la Boise, Guadeloupe; 49) *A. xanthoxyli*, Santa Ana Wildlife Refuge, Texas; 50) *A. squamiger*, La Quinta, Táchira, Venezuela; 51) *A. caeruleisquamis*, Guatemala; 52) *A. cymatilis*, São Roque, São Paulo, Brazil.



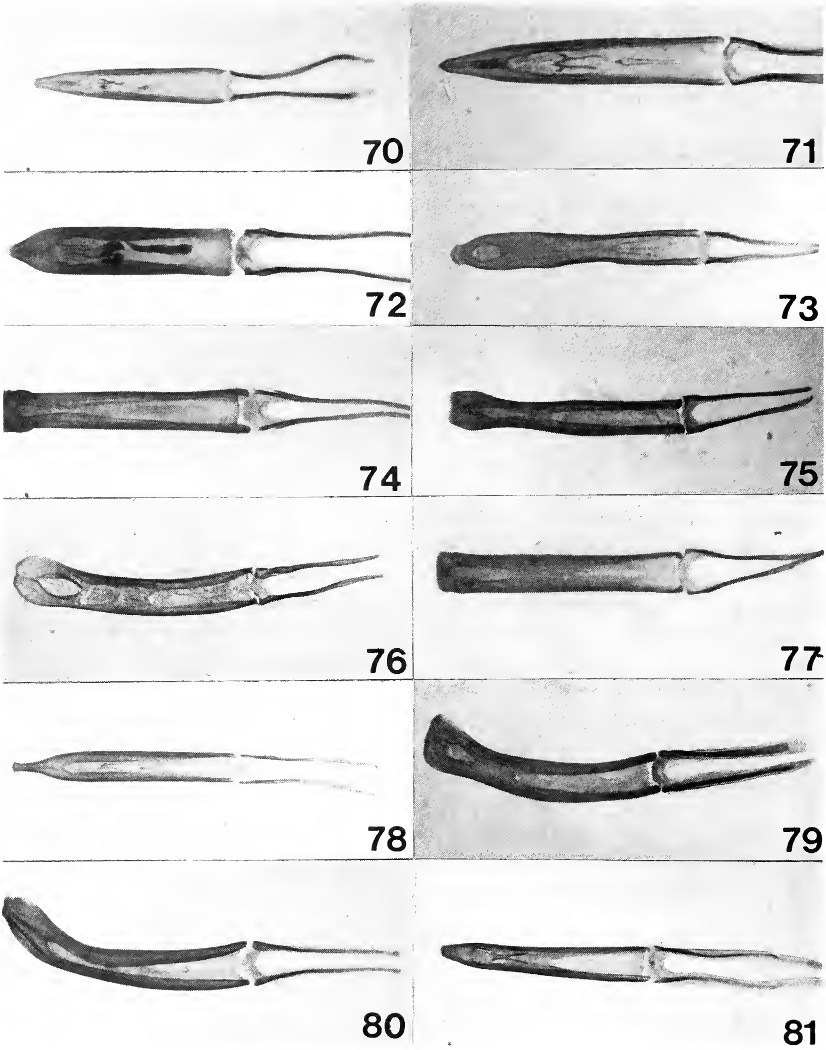
Figs. 53–59. Subgenus *Anthonomocyllus* spp., prothoracic legs, ♂, anterior view: 53) *A. tenuirostris*, Puerta Parada, Guatemala; 54) *A. accola*, holotype; 55) *A. argentatus*, Cayamas, Cuba; 56) *A. costulatus*, Matheson Hammock, Florida; 57) *A. dentipes*, Nova Teutônia, Brazil; 58) *A. guanita*, holotype; 59) *A. xanthoxyli*, Santa Ana Wildlife Refuge, Texas.



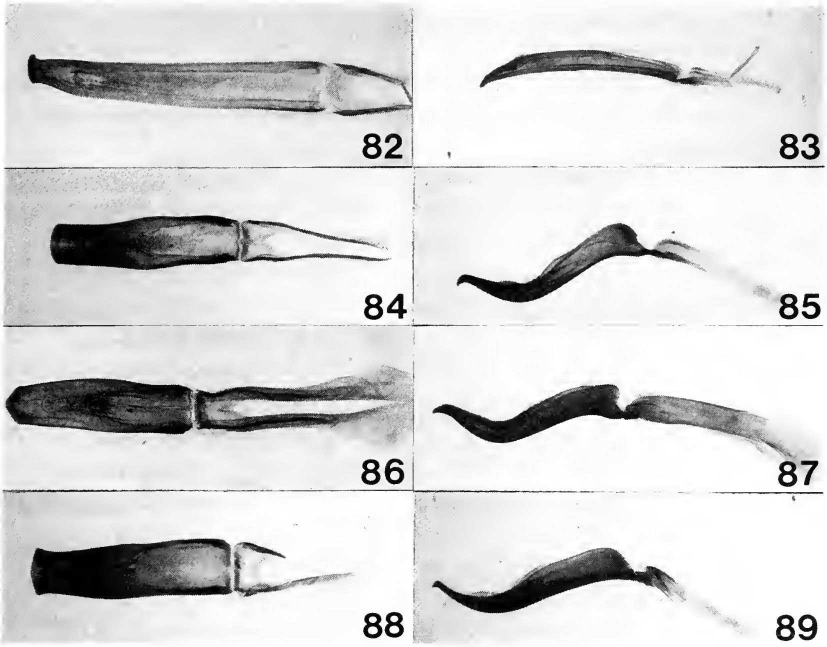


Figs. 60–67. Subgenus *Anthonomocyllus* spp., left metathoracic leg, anterior views: 60) *A. tenuirostris*, ♂, Puerta Parada, Guatemala; 61) *A. accola*, ♂ holotype; 62) *A. argentatus*, ♂, Cayamas, Cuba; 63) *A. costulatus*, ♂, Matheson Hammock, Florida; 64) *A. dentipes*, ♂, Nova Teutônia, Brazil; 65) *A. guanita*, ♂, holotype; 66) *A. xanthoxyli*, ♂, Santa Ana Wildlife Refuge, Texas; 67) *A. leucostictus*, ♀, Welder Wildlife Refuge, Texas.

Figs. 68–69. Subgenus *Anthonomocyllus* spp., left metatibia, ♂, ventral view: 68) *A. cymatilis*, holotype; 69) *A. caesius*, holotype.



Figs. 70–81. Subgenus *Anthonomocyllus* spp., ♂ genitalia, dorsal view: 70) *A. tenuirostris*, Puerta Parada, Guatemala; 71) *A. acus*, holotype; 72) *A. accola*, holotype; 73) *A. argentatus*, holotype; 74) *A. costulatus*, Matheson Hammock, Florida; 75) *A. azalus*, holotype; 76) *A. contaminatus*, holotype; 77) *A. dentipes*, holotype; 78) *A. guanita*, holotype; 79) *A. pazmani*, holotype; 80) *A. xanthoxyli*, Santa Ana Wildlife Refuge, Texas; 81) *A. leucostictus*, Welder Wildlife Refuge, Texas, dorsal view.



Figs. 82–89. Subgenus *Anthonomocyllus* spp., ♂ genitalia: 82) *A. aeroides*, Isla de Perlas, Panamá, dorsal view; 83) *A. aeroides*, Isla de Perlas, Panam , lateral view; 84) *A. aeroides*, Campana, Magdalena, Colombia, dorsal view; 85) *A. aeroides*, Campana, Magdalena, Colombia, lateral view; 86) *A. cymatilis*, holotype, dorsal view; 87) *A. cymatilis*, holotype, lateral view; 88) *A. caesius*, holotype, dorsal view; 89) *A. caesius*, holotype, lateral view.

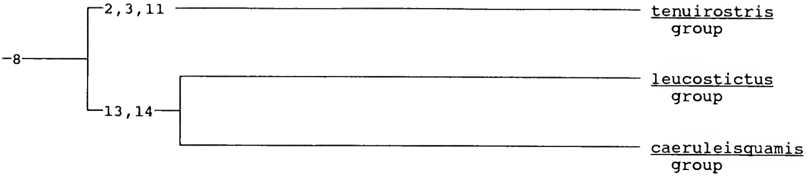


Fig. 90

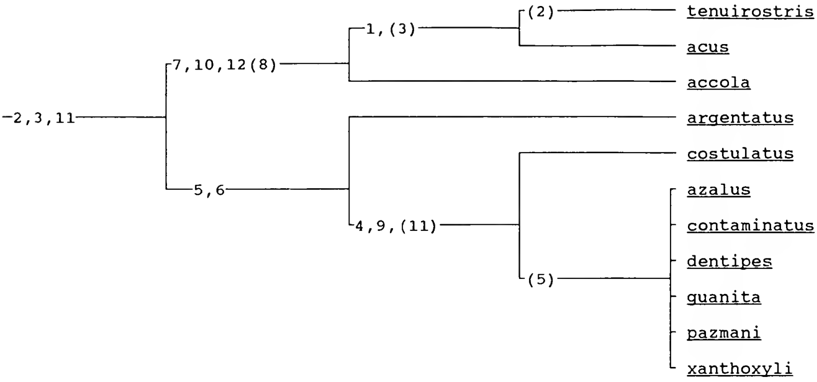


Fig. 91

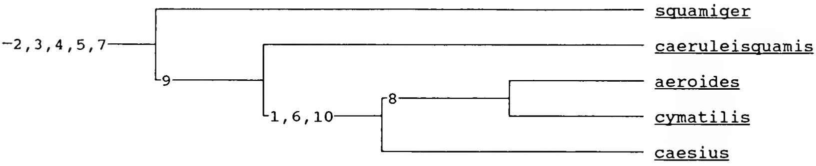


Fig. 92

Fig. 90. Phylogenetic tree depicting relationships of the species groups of the subgenus *Anthonomocyllus*.

Fig. 91. Phylogenetic tree depicting relationships of the species in the *A. tenuirostris* species group (homoplasious characters indicated by parentheses at assumed point of reversal).

Fig. 92. Phylogenetic tree depicting relationships of the species in the *A. tenuirostris* species group.

Table 1. Fourteen apomorphic characters and a matrix showing their distribution in eight of the species of *Anthonomus* in the subgenus *Anthonomocyllus*.

1) Rostrum of female (Fig. 1) slender, glabrous, straight.
2) Pronotum (Figs. 3-18) with large macula of imbricated, pallid scales on anterior and median portions of dorsum.
3) Pronotum flattened dorasally.
4) Pygidium of female (Figs. 34-39) with broad scales in middorsal concavity.
5) Pygidium of female (Figs. 33, 34) with broad apicodorsal excavation delimited by carina.
6) Pygidium of female (Figs. 33-39) with dorsal, apicolateral extensions.
7) Pygidium of female (Figs. 30-32) with short, apicodorsal, carinate prominence.
8) Mesocoxae separated by distance greater than 0.50 x width of one mesocoxa.
9) Sternum 5 of female abdomen (Figs. 47-49) with anteromedian fovea.
10) Sternum 5 of female abdomen (Figs. 44, 45) with posteromarginal "clasp" that receives apicomedian prominence of pygidium.
11) Protibia (Figs. 53-55) with slender, acute, median, inner marginal tooth.
12) Endophallus (Figs. 70-72) with 3 large sclerites.
13) Femoral tooth (Fig. 67) long, slender, slightly curved, acute.
14) Mesotibia (Fig. 67) with acute outer apical spine.

species	characters													
	0	0	0	0	0	0	0	0	1	1	1	1	1	1
	1	2	3	4	5	6	7	8	9	1	1	2	3	4
outgroup*	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A. accola	0	1	1	0	0	0	1	0	0	1	1	1	0	0
A. acus	1	1	0	0	0	0	1	0	0	1	1	1	0	0
A. argentatus	0	1	1	0	1	1	0	1	0	0	1	0	0	0
A. azalus	0	1	1	1	0	1	0	1	1	0	0	0	0	0
A. caeruleisquamis	0	0	0	0	0	0	0	1	0	0	0	0	1	1
A. costulatus	0	1	1	1	1	1	0	1	1	0	0	0	0	0
A. leucostictus	0	0	0	0	0	0	0	1	0	0	0	0	1	1
A. tenuirostris	1	0	0	0	0	0	1	0	0	1	1	1	0	0

0=character absent; 1=character present

Table 2. Ten apomorphic characters and a matrix showing their distribution in *A. leucostictus* and in the five species of *Anthonomus* in the *A. caeruleisquamis* species group.

1) Rostrum (Fig. 25) with midventral, subapical tooth.
2) Pronotum (Figs. 21, 23, 25) with subapical constriction obsolete.
3) Pronotal punctures each with a large scale that does not extend beyond edge of puncture or with a much narrower scale, separated by flat interspaces.
4) Elytral integument narrowly visible between dense vestiture of small, rounded, cinereous to caeruleous scales.
5) Elytral interstriae flat, 3rd not elevated at base.
6) Pygidium of male (Figs. 27-29) excavated, with long, acuminate, aureous scales that are long and dense in contiguous or approximate middorsal clusters.
7) Femora and tibiae, except for distal portions, ferruginous to alizarine.
8) Metatibia of male (Fig. 68) excavated posteriorly in apical 1/4 between broad, rounded, outer apical and inner apical expansions.
9) Abdominal sternum 5 of female (Fig. 51, 52) with median fovea.
10) Aedeagus (Figs. 85, 87, 89) sinuate in lateral view.

species	characters									
	01	02	03	04	05	06	07	08	09	10
*A. leucostictus**	0	0	0	0	0	0	0	0	0	0
A. squamiger	0	1	1	1	1	0	1	0	0	0
A. caeruleisquamis	0	1	1	1	1	9	1	9	1	9
A. aeroides	1	1	1	1	1	1	1	1	9	1
A. caesius	1	1	1	1	1	1	1	0	9	1
A. cymatilis	1	1	1	1	1	1	1	1	1	1

* = outgroup; 0= character absent; 1 = character present; 9 = unknown (male of *A. caeruleisquamis* unknown; females of *A. aeroides* and *A. caesius* unknown)

PHYLOGENY

The "chaotic" classification of the Anthonominae was discussed recently in reference to attempts to identify the sister groups of the genus *Loncophorus* Chevrolat (Clark 1988d) and the *Anthonomus ornatus* species group (Clark and Burke 1989). Since the sister groups of these taxa were not found, it was necessary to identify apomorphic characters by survey of a wide array of anthonomines, including types of most New World species and specimens in other recently revised groups. This same survey served as the basis for discovery of unique characters in the subgenus *Anthonomocyllus*. These characters and their distributions among the species in the subgenus are depicted in Tables 1 and 2. The data matrices presented in these tables were analyzed using the ALLTREES option of PAUP (Swofford 1985) to find the most parsimonious trees supported by the equally weighted characters. Analysis of the 14 characters in the 8 species listed in Table 1 produced four trees, one of which is depicted in two parts in Figures 91 and 92. This tree can be cited as justification for recognition of the *A. tenuirostris*, *A. leucostictus* and *A. caeruleisquamis* species groups. Monophyly of the *A. caeruleisquamis* subgroup was assumed prior to this analysis. Analysis of the ten characters of the 5 species in that group, listed in Table 2, produced one tree, depicted in Figure 93. This analysis also included *A. leucostictus*, which was designated as the outgroup because the previous analysis had shown the species to be the sister group of the *A. caeruleisquamis* subgroup.

ACKNOWLEDGMENTS

Thanks are extended to the individuals and institutions listed in the Materials and Methods section for arranging loans of the specimens used in this study. H. R. Burke initially suggested the group as suitable for revision and provided information and other assistance, along with performing a critical review of the manuscript. Larry J. Hribar and Michael L. Williams also reviewed the manuscript. This paper is published as Alabama Agricultural Experiment Station Journal Series No. 17-892145P.

REFERENCES CITED

Ahmad, M. and H. R. Burke. 1972. Larvae of the weevil tribe Anthonomini. Miscellaneous Publications of the Entomological Society of America 8: 31–80.

Blackwelder, R. E. 1947. Checklist of the coleopterous insects of Mexico, Central America, the West Indies and South America, Part 5. Bulletin of the U. S. National Museum (185): I-IV, 765–925.

Blatchley, W. S., and C. W. Leng. 1916. Rhynchophora or weevils of North Eastern America. pp. 1–682. Indianapolis.

Blatchley, W. S. 1925. Notes on the Rhynchophora of eastern North America with descriptions of new species, III. Journal of the New York Entomological Society 33: 87–113.

Boheman, C. H. 1843. (Description of *Anthonomus contaminatus*), pp. 219-220, *In* C. J. Schönherr. Genera et species curculionidum Roret, Paris; Fleischer, Lipsiae. Vol. 7, pt. 2, pp. 1–461.

Burke, H. R. 1962. Studies on the genus *Anthonomus* in North and Central America (Coleoptera: Curculionidae) I. Some new and little known species from Mexico. Southwestern Natturalist 7(3-4): 202–210.

Burke, H. R. 1968. Pupae of the weevil tribe Anthonominae (Coleoptera: Curculionidae).Texas Agricultural Experimental Station Technical Monograph 5, 92 pp.

Burke, H. R. 1971. New synonymy in North American *Anthonomus*. Journal of the New York Entomological Society 44(1): 46–50.

Burke, H. R. 1975. Nomenclatural changes in North American *Anthonomus* (Coleoptera: Curculionidae). Entomological News 86(3-4): 57–62.

Burke, H. R. 1976. Bionomics of the anthonomine weevils. Annual Reviews of Entomology 21: 283–303.

Burke, H. R., and D. B. Gates. 1974. Bionomics of several North American species of *Anthonomus* (Coleoptera: Curculionidae). Southwestern Naturalist 19: 313–327.

Champion, G. C. 1903. Curculionidae: Curculioninae, Volume 4, Part 4, pp. 145–312, *In*: F. D. Godman and O. Salvin (eds.). 1879-1911. Biologia Centrali-Americana, Insecta, Coleoptera, 7 volumes in 17 parts. London, Dulau.

Champion, G. C. 1910. Biologia Centrali-Americana. Insecta. Coleoptera. Rhynchophora. Curculionidae. Curculioninae (concluded) and Calandrinae, vol. 4, pt. 7, pp. 79–221.

Clark, W. E. 1987a. Revision of the *unipustulatus* group of the weevil genus *Anthonomus* Germar (Coleoptera: Curculionidae). Coleopterists Bulletin 41(1): 73–88.

Clark, W. E. 1987b. Revision of the *Anthonomus* subgenus *Anthomorphus* Weise (Coleoptera: Curculionidae). *Quaestiones Entomologicae* 23: 317–364.

Clark, W. E. 1988a. The species of *Anthonomus* in the *albolineatus* group (Coleoptera: Curculionidae). Transactions of the American Entomological Society 113: 309–359.

Clark, W. E. 1988b. Revision of the *furcatus* species group of the weevil genus *Anthonomus* Germar (Coleoptera: Curculionidae). Coleopterists Bulletin 42(4): 359–377.

Clark, W. E. 1988c. Review of the *Anthonomus alboscutellatus* species group, with description of a new species (Coleoptera: Curculionidae). Coleopterists Bulletin 42(4): 379–386.

Clark, W. E. 1988d. Revision of the weevil genus *Loncophorus* Chevrolat (Coleoptera: Curculionidae, Anthonominae). *Quaestiones Entomologicae* 24(3): 465-518.

Clark, W. E., and H. R. Burke. 1985. Revision of the *venustus* species group of the weevil genus *Anthonomus* Germar (Coleoptera: Curculionidae). Transactions of the American Entomological Society 111:103–170.

Clark, W. E., and H. R. Burke. 1986a. Revision of the *gularis* species group of the genus *Anthonomus* Germar (Coleoptera: Curculionidae). Coleopterists Bulletin 40(1): 1–26.

Clark, W. E., and H. R. Burke. 1986b. Phylogeny of the species of the *Anthonomus* subgenus *Anthonomorphus* Dietz, with discussion of relationships with *Anthonomus grandis* Boheman (Coleoptera: Curculionidae). Journal of the Kansas Entomological Society 59(3): 508–516.

Clark, W. E., and H. R. Burke. 1989. Revision of the *ornatus* species group of the genus *Anthonomus* Germar (Coleoptera: Curculionidae, Anthonominae). Proceedings of the Entomological Society of Washington 91(1): 88–111.

Dietz, W. G. 1891. Revision of the genera and species of Anthonomini inhabiting North America. Transactions of the American Entomological Society 18: 177–276.

Gates, D. B., and H. R. Burke. 1972. Review of gall-inhabiting weevils of the genus *Anthonomus*, with description and biology of a new species (Coleoptera: Curculionidae). Annals of the Entomological Society of America 65(5): 1215–1224.

Gundlach, J. 1891. Contribucion a la entomologia Cubana, vol. 3, 494 pp. Habana.

Gyllenhal, L. 1836. (Description of *Anthonomus argentatus*), p. 343, *In* C. J. Schönherr, Genera et species curculionidum .... Roret, Paris; Fleischer, Lipsiae. Vol. 3, pt. 1, pp. [I-II], 1-505; pt. 2, pp. 506–858.

Hustache, A. 1940. Curculionides nouveaux de l'Argentine et autres régions sud-américaines (deuxieme note). Anales de la Sociedad Cientificas Argentina 129: 112–144.

LeConte, J. L. 1876. (Description of *Anthonomus elegans*), p. 202, *In* J. L. LeConte and G. W. Horn, The Rhynchophora of America, north of Mexico. Proceedings of the American Philosophical Society 15(96): i-xvi, 1–455.

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

Linell, M. L. 1897. New genera and species of North American Curculionidae. Journal of the New York Entomological Society 5(2): 49–56.

O'Brien, C. W., and G. J. Wibmer. 1982. Annotated checklist of the weevils (Curculionidae *sensu lato*) of North America, Central America, and the West Indies (Coleoptera: Curculionoidea). Memoirs of the American Entomological Institute 34: i-ix + 1–382.

Schenkling, S., and G. A. K. Marshall. 1934. Coleopterorum Catalogus, Pars 139, Curculionidae: Anthonominae, pp. 3-82; Laemosaccinae, pp. 1-8. (vol. 29).

Schwarz, E. *A* 1913. *Anthonomus irroratus* Dietz developing in cecidomyiid galls. Proceedings of the Entomological Society of Washington 15: 43.

Suffrian, E. 1871. Verzeichniss der von Dr. Gundlach auf der Insel Cuba gesammelten Rüsselkäfer. Archiv für Naturgeschichte 37(1): 122–184.

Swofford, D. L. 1985. PAUP: Phylogenetic Analysis Using Parsimony. Users Manual, Illinois Natural History Survey, Champaign, Ill.

Townsend, C. H. T. 1903. Contribution to a knowledge of the coleopterous fauna of the Lower Rio Grande in Texas and Tamaulipas, with biological notes and special reference to geographic distribution. Transactions of Texas Academy of Sciience 5: 51–101.

Voss, E. 1944. Anthonominen-Studien (Col., Curc.) (97 Beitrag zur Kenntnis der Curculioniden). Stett. Entomol. Ztg. 105: 34–51.

Weidner, H. 1979. Die Entomologischen Sammlungen des Zoologischen Instituts und Zoologischen Museums der Universit t Hamburg. IX. Teil. Insecta VI. Mitteilungen Hamburgisches Zoologische Museum und Institut 76: 395–468.

Wibmer, G. J., and C. W. O'Brien. 1986. Annotated checklist of the weevils (Curculionidae *sensu lato*) of South America (Coleoptera: Curculionoidea). Memoirs of the American Entomological Institute 39: i-xvi, 1–563.

INDEX TO NAMES OF TAXA
(Junior synonyms in italics)

RECONSTRUCTED PHYLOGENY AND RECLASSIFICATION OF THE GENERA OF DONACIINAE (COLEOPTERA: CHRYSOMELIDAE).

Ingolf S. Askevold[1]
Department of Entomology
University of Manitoba
Winnipeg, Manitoba R3T 2N2
CANADA

Quaestiones Entomologicae
26: 601– 664 1990

ABSTRACT

Based on phylogenetic analysis of genera of Donaciinae, three tribes of Donaciinae are recognized: Plateumarini, new tribe, Donaciini Kirby and Haemoniini Chen. All described genus- and species-group taxa are placed within this tribal classification, except Donacia microcephala *Daniel and Daniel (uncertain generic assignment in Donaciini) and* Neohaemonia voronovae *Medvedev (uncertain generic assignment in Haemoniini).* Poecilocera *Schaeffer is removed from synonymy with* Sominella *Jacobson and includes a single Nearctic species,* P. harrisii *(LeConte).* Prodonacia *Chen and* Donaciocrioceris *Pic (both monobasic) are newly placed as junior subjective synonyms of* Donaciasta *Fairmaire.* Donacia *(*Donaciomima*) Medvedev is removed from synonymy with* Donacia, *and is recognized as a valid subgenus, including most species hitherto placed in* Donacia s. str. *(i.e., 22 Nearctic and 52 Palaearctic species). The fossil genus* Hemidonacia *Haupt is placed as junior subjective synonym of* Donacia *(*Cyphogaster*) Goecke;* Eodonacia *Haupt is placed as junior subjective synonym of* Donacia *(*s. str.*) Fabricius.* Donaciella *Reitter is elevated to generic status, with the Nearctic species* Donacia pubicollis *Suffrian and Palaearctic species* Donacia clavipes *Fabricius,* Donacia cinera *Herbst, and* Donacia tomentosa *Ahrens transferred to this genus.* Donacia reticulata *Gyllenhal and* D. kraatzi *Weise are transferred to* Sominella *from* Donacia, *and* Pseudodonacia *and* Plateumaroides *(both based on* D. kraatzi*) are removed from synonymy with* Donacia *and transferred to synonymy with* Sominella.

Among Palaearctic D. *(*Donaciomima*) species,* D. fukiensis *Goecke is placed as junior subjective synonym of* Donacia clavareaui *Jacobson, and* D. ochroleuca *Weise and* D. flavidula *Reitter are placed as junior subjective synonyms of* D. fennica *Paykull.* Donacia *(*Cyphogaster*)* tuberfrons *Goecke is placed as a junior subjective synonym of* D. transversicollis *Fairmaire, which is assigned to this subgenus.* Donacia *(*Donacia*)* clarki *Monrós and* D. indica *Clark are placed as junior subjective synonyms of* D. recticollis *Jacoby.* Haemonia piligera *Weise and* Haemonia incostata *Pic are placed as junior subjective synonyms of* Macroplea pubipennis *(Reuter).*

Relationship of sagroid subfamilies (Sagrinae + Criocerinae + Donaciinae) was examined to select an outgroup of Donaciinae. Criocerinae were found to show more synapomorphies in common with Donaciinae, and neither Criocerinae nor Donaciinae could be directly derived from Sagrinae. Despite lack of clarity of relationship, altered polarity of certain characters did not affect reconstruction of relationships of genera of Donaciinae.

---

[1] Present address: Entomology – Biological Control Division of Agricultural Sciences, Florida A & M University, Tallahassee, Florida 32307-2001, U. S. A.

TABLE OF CONTENTS

INTRODUCTION

Donaciinae, among the Chrysomelidae, is a relatively small group of aquatic beetles comprised of fewer than 160 species, but most of the world fauna has been confused taxonomically. Numerous faunistic treatments provide means of identification of regional faunas (*e.g.*, Gruev and Tomov 1984, Kimoto 1983, Hatch 1971, Mohr 1966, Gressitt and Kimoto 1961, Schaeffer 1925, and many others). No genus has been monographed in its entirety except *Plateumaris* Thomson (Askevold, in prep. a), *Donaciasta* Fairmaire (Askevold, in prep. d) and *Neohaemonia* Székessy (Askevold 1988); *Donaciasta* was incompletely treated by Monrós (1958) and Jolivet (1972), and *Donacia* (*Cyphogaster*) Goecke was treated by Goecke (1934, 1935, 1936, 1944).

The subfamily has not been monographed broadly at the genus level because authors of regional treatments have accepted existing classifications. Perhaps the closest attempt to propose a phylogeny of donaciines was by Goecke (1960b); no empirical basis was provided, and it was based essentially on his existing classification (Goecke 1960a). Failure to question existing classifications in catalogues has led to taxonomic confusion and incorrect generic assignment, as for *Donaciasta*. This acceptance has also led to ill-founded zoogeographic analysis (*e.g.* Borowiec 1984). *Donacia* Fabricius has appeared first in most catalogues and probably has been inferred to be most primitive among donaciines; Monrós (1959) alone placed *Plateumaris* first (*i.e.* most primitive), an arrangement reversed by Jolivet (1970).

The present study grew from research to monograph *Plateumaris* and to assess the limits and phylogenetic position of that genus. It became an attempt to revise the generic assignment of as many of the described Donaciinae as possible, to analyze relationships of the genera, and to develop a new classification of donaciines. Most members of the subfamily have been examined, several genera monographed (Askevold 1988, in prep. a,d), some taxonomic problems among members of *Donacia* were resolved (Askevold 1987a, b), fossils were studied (Askevold 1990) and the relationship of donaciines to their host plants was analyzed (Askevold, in prep. b). Results and reclassification presented here represent the collective product of these interrelated and interdependent efforts.

MATERIALS AND METHODS

Materials

All New World and most Old World taxa of Donaciinae were studied. Old World taxa examined are listed within the section on reclassification of genera. New World taxa examined, as now reclassified, are listed elsewhere (Askevold, in prep. c). Specimens were personally collected, borrowed, or exchanged from 85 collections and museums, a list of which is given elsewhere (Askevold in prep. a). This revision is based on study of 111 specimens of *Poecilocera harrisii* (LeConte), 48 specimens of *Donaciella pubicollis* (Suffrian), more than 42,000 specimens of the other described and undescribed Nearctic species of Donaciinae, and more than 4,000 specimens of 79 Old World taxa of Donaciinae (excluding 16, names of which are placed in synonymy). I have not examined specimens of 21 Palaearctic taxa which remain unknown to me (these indicated as such in section on reclassification of genera).

The following sagrines were examined: *Atalasis sagroides* Lacordaire, *Ametalla atenodera* Lacordaire, *Ametalla spinolae* Hope, *Megamerus femoralis* Lea, *Mecynodera coxalgica* Boisduval, *Carpophagus banksiae* McLeay, *Polyoptilus erichsoni* Germar, *Diaphanops westermanni* Boheman, and various Oriental and Afrotropical species of *Sagra* Fabricius. I referred also to unpublished data of Mann and Crowson (in prep.) on genitalia of sagrines.

A number of criocerine species in the genera *Lema, Oulema, Lilioceris* and *Crioceris* were examined for general structure, and some of these were examined also for male genitalic structures. I relied principally on the figures of male genitalia of Criocerinae presented in White (in prep.) to infer widespread presence of characters among criocerines. Other than members of Sagrinae and Criocerinae, I have studied many other Chrysomelidae and perhaps some statements (hypotheses or observations) I make take their study into account, though not explicitly.

Methods

A general comment about wording should be made, in view of the general truth observed by Ball (1977) that many phrases in literature of systematic biology are grammatically incorrect. Therefore, the reader is advised that certain phrases should be understood to have a specific meaning. In particular, the use of phrases such as "*Atalasis* Lacordaire is most similar to *Plateumaris*", should be understood to mean "Specimens of members of *Atalasis* are more similar to specimens of members of *Plateumaris* ". Similarly, with regard to sex of specimens, when I state "Endophallus of *Plateumaris aurifer* with... ", this should be understood to mean "Endophallus of male specimens of *P. aurifer* with... ". In other words, I write as though I am discussing taxa, but this should be understood to mean that I am discussing specimens of members of those taxa. I do not use these phrases uniformly; sometimes I use the "correct" form for variation. However, in general, I use the "incorrect" forms because I find the correct forms lengthy and cumbersome.

Techniques and drawings.— The technique used for study of genitalia was that given by Askevold (1988:367) and discussed at length by Askevold (in prep. a) and is not repeated in detail here.

Drawings and figures were made using a Wild M5 dissecting microscope with the aid of a camera lucida.

Philosophy of classification.— An important component of systematics is the observation that nested sets of derived character states form the basis of classification, only in the cladistic school of systematics. A classification based upon reconstruction of phylogeny is ostensibly more stable because there exists only one true pattern of evolution; the classification that most accurately mirrors this pattern should be least altered by future treatments, and addition of new data and/or taxa. From such stability can arise reproducible results, and particularly, predictability about other components of the biota upon which other sciences draw and rely.

Schools of systematics do not agree entirely on how or to what degree classification should be a reflection of evolutionary relationships. Strict cladism dictates development of a strict hierarchical classification from which a phylogeny can be derived directly. However, the evolutionary systematics school diverges from cladistics on this point, attempting to draw evolutionary divergence into the classification as well (Bock 1974). That is, cladistic classifications allow only holophyletic and monophyletic taxa, while evolutionary classifications accept paraphyletic taxa as valid (Ashlock 1974, Cronquist 1987) because characters are differentially weighted as to their significance in the evolution of organisms (Mayr 1974). Thus, an evolutionary classification can reflect aspects of evolutionary phenomena or important structural innovations that are responsible for radiation in a group of organisms, while a strictly cladistic classification reflects only pattern of phyletic relationship.

While I ascribe to cladistic methods of phylogenetic analysis, I am also forced to accept a non-cladistic philosophy relating to derivation of classifications, at least among donaciines at the supra-generic level. Hull's (1979:437) simple assessment sums up my conclusions, that "the cladists' rules for classifying are simple enough, but that the resulting classifications are not." Disney (1989) observed that "Paraphyletic taxa... are avoided on principle, but in practise one is always confronted by 'residual paraphyletic groups'."

Thus, I have accepted paraphyletic groups in the Donaciinae, partly because I am not able to resolve the relationships of all genera, or because some clades are not well defined. I do so because such a tribal classification is more useful in conveying information about the state of knowledge of the evolution of Donaciinae than is the lack of a tribal classification. This tribal classification also allows statements about the successive grades donaciines have achieved with respect to host plant use (Askevold, in prep. b). Such statements would be confused by a more complicated higher classification. I suspect similar treatments in other groups of Chrysomelidae would result once they are analyzed, because much of evolution proceeds in grades of adaptation (see Erwin 1981, for example). It is my opinion that no strictly cladistic classification for most groups of chrysomelids could be manageable at this time, and donaciines are no exception.

Methods of phylogenetic reconstruction.— Phylogenetic reconstruction was carried out according to the principles of Hennig (1965,1966), which have been discussed at length by many authors (*e.g.* Kavanaugh 1972; Ashlock 1974; DeJong 1980; Wiley 1981). These methods are simply the process of searching for characters, by comparison among a number of related taxa, that one would consider useful for cladistic analysis (phylogenetic reconstruction). Such characters should be shared-derived, or synapomorphies.

I used two methods of reconstructing phylogenies (*i.e.* manual and computer-aided), and eventually selected a compromised result that was consistent both with certain *a priori* views about donaciine evolution, and to some extent with general parsimony; I did not take exception to Neff's (1986) advocating of *a priori* weighting as Sharkey (1989) did. Initially, I used a manual method based on first selecting principal characters that I thought were significant to partially resolve a tree and then added the remaining characters to resolve more fully this tree to support groupings. PAUP [Phylogenetic Analysis Using Parsimony, Version 2.4.1 (Swofford, 1985)] was used to test these reconstructions, and to demonstrate alternate character distributions on trees.

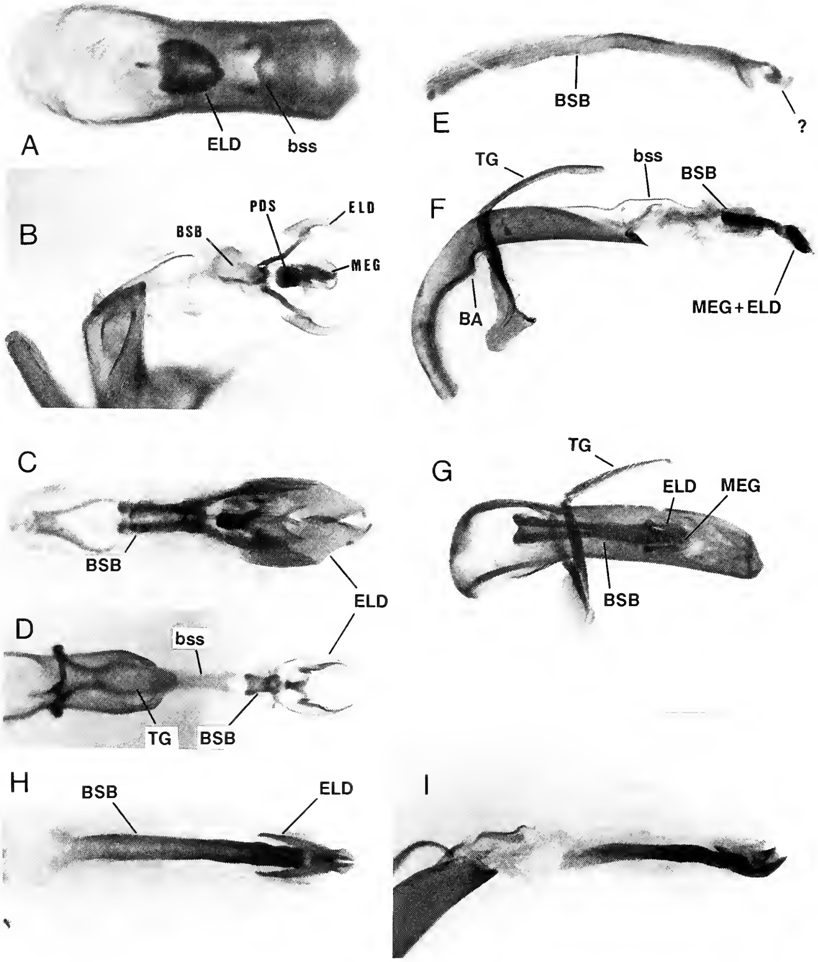
STRUCTURES USED IN CLASSIFICATION OF DONACIINAE

Elsewhere, I presented discussion of structures that are important in classification of donaciines (Askevold, in prep. a). I present here only some cursory remarks about endophallic structure in donaciines. Readers are referred to this reference for detailed information about endophallic structure in particular. In the character analysis, below, I give details about other structures as they pertain to reconstruction of phylogeny.

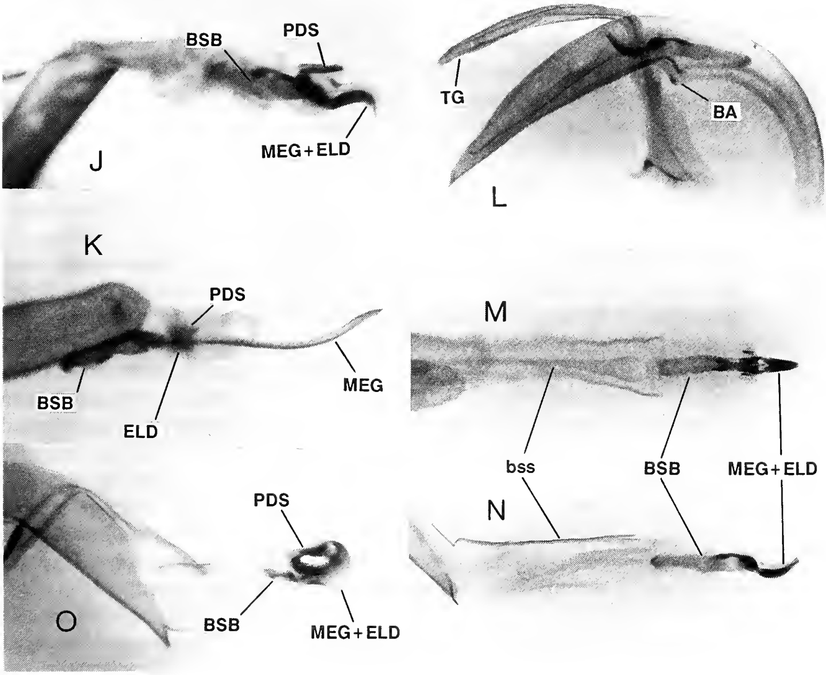
The endophallus consists of a several sclerites which are similar in arrangement among the sagroid subfamilies (*i.e.* the Sagrinae + Criocerinae + Donaciinae). I homologize them among genera of Donaciinae at least, though I am not fully convinced that all sclerites found in similar positions on the endophallus of sagrines and criocerines, are homologous with those found in donaciines. The important endophallic sclerites I use are assigned the following codens by which they are hereafter referred to in the text: BSB (basal supporting block), ELD (endophallic lateral digit), PDS (paired dorsal sclerite) and MEG (median ejaculatory guide) (see Photographs A-O). The BSB is a basal sclerite with which the remaining apical endophallic sclerites articulate (*i.e.* basal with respect to the apical sclerites; all sclerites are apical, except for those involved with sac-retracting - bss, Phots. A, M).

RECONSTRUCTED PHYLOGENY OF WORLD GENERA OF DONACIINAE

Reconstruction of relationships of donaciine genera proceeded, of necessity, along two lines of analysis. Character analysis requires understanding of out-group relationship. Some authors, such as Crowson (1945), have been rather explicit and have stated that certain sagrine genera are probably most closely related to donaciines. Others, such as Schmitt (1985a,b, 1988), have not made use of explicit out-group criteria in examining relationships among sagroid subfamilies. Therefore, the question of out-group to Donaciinae has not been examined critically. This problem is the first examined below because analysis of relationships of donaciine genera may depend upon the out-group



PHOTOGRAPHS A-I: Photographs of male genitalia of Sagrinae and Donaciinae. **A.** Dorsal aspect of median lobe of *Atalasis sagroides* Lacordaire, with endophallus in repose. **B.** Dorsal aspect of everted endophallus of *Plateumaris flavipes* (Kirby). **C.** Dorsal aspect of *Plateumaris robusta* (Schaeffer). *D.* Dorsal aspect of apex of median lobe, tegmen and everted endophallus of *Plateumaris neomexicana* (Schaeffer). **E.** Lateral aspect of endophallus of *Poecilocera harrisii* (LeConte). **F.** Lateral aspect of median lobe, tegmen and everted endophallus of *Donacia* (*Donaciomima*) *magnifica* LeConte. **G.** Dorsal aspect of median lobe and tegmen of *Sominella macrocnemia* (Fisch. v. Waldheim), with endophallus in repose. **H, I.** Dorsal and lateral aspects, respectively, of *Donacia* (*Donaciomima*) *hirticollis* Kirby. BA = subbasal angulation of median lobe; BSB = basal supporting block; ELD = endophallic lateral digit; MEG = median ejaculatory guide; PDS = paired dorsal sclerites; TG = tegmen.



PHOTOGRAPHS J-O: Photographs of male genitalia of Donaciinae. **J.** Lateral aspect of endophallus of *Donacia* (*Donaciomima*) *tuberculifrons* Schaeffer. **K.** Lateral aspect of endophallus of *Donaciasta perrieri* (Fairmaire). **L.** Lateral aspect of median lobe and tegmen of *Donacia* (*Donacia*) *cincticornis* Newman with endophallus in repose. **M, N.** Dorsal and lateral aspect, respectively, of endophallus of *Donacia cincticornis*. **O.** Lateral aspect of apex of median lobe and tegmen of *Macroplea pubipennis* (Reuter), with endophallus everted. BA = subbasal angulation of median lobe; BSB = basal supporting block; ELD = endophallic lateral digit; MEG = median ejaculatory guide; PDS = paired dorsal sclerites; TG = tegmen.

selected.

I develop hypotheses about sagroid subfamily (*i.e.* Sagrinae + Criocerinae + Donaciinae) relationships, which I use as a basis for determining polarity of characters. All characters considered for reconstruction of relationships are examined below, whether I find them useful as synapomorphies or not, and at what taxonomic level. I begin with the character analysis, proceeding to analysis of subfamily relationships, then to relationships of donaciine genera and problems in their classification.

Character analysis

Characters used in analysis of phylogenetic relationships of genera are coded in two ways. The plesiomorphic state is coded as 0, and states in a transformation series are coded as 1,2,3, in progressively derived apomorphic states. Some characters that have independently-derived apomorphic states (*e.g.* tegmen, ovipositor, tibial spurs, host plants) are divided into component characters (*e.g.* 24a-b, 27a-c, 30a-b). Character states and their polarities are summarized in accompanying tables: Tables 1 and 2 for sagroid relationships; and Tables 3 and 4 for donaciine generic relationships.

Character 1. Ligula of labium.— (see Askevold, 1988, Figs. 43-44). Two states: plesiomorphic, ligula membranous and bilobed; apomorphic, ligula not membranous, not bilobed.

Among members of Sagrinae and some other apparently primitive groups, (*e.g. Syneta* Dejean, *Orsodacne* Latreille, Aulacoscelinae and Megalopodinae) the ligula is bilobed and membranous (Crowson 1945), while in those of Donaciinae and Criocerinae this is not so. The derived, non-membranous, non-bilobed state could be considered synapomorphic for Criocerinae + Donaciinae, though Schmitt (1985a,b) did not consider this possibility. It is more parsimonious to consider a single, rather than parallel, reduction of ligular lobes among closely related groups, so it is arguable that the state found in criocerines and donaciines is synapomorphic. The derived state should be considered a reduction from the plesiomorphic state, and therefore could have occurred independently in many lineages, as appears to be so among other chrysomelid groups.

Tentatively I consider ligular form synapomorphic for the Donaciinae. On the basis of the hypothesis that donaciines are derived directly from a sagrine lineage, and not from a common ancestor of Criocerinae + Donaciinae, the non-bilobed ligula must be considered independently derived in criocerines.

Character 2. Tibial spurs.— Three states: plesiomorphic, all tibiae with two articulated spurs; apomorphic, only pro- and mesotibia with one articulated spur each, metatibia without articulated spur; apomorphic, all spurs lost.

Presence of two articulated spurs on all tibiae is probably the ground plan state in Chrysomelidae, retained in a few groups such as Megalopodinae, some *Syneta* (Synetinae) and certain Eumolpinae (*Hornius* Fairmaire, *Stenomela* Erichson). Three states are recognized in sagroids: criocerines retain the 2-2-2 state (some taxa with reduction) (Schmitt 1985a,b), while donaciines are 1-1-0 and sagrines have no articulated spurs [*i.e.* Sagrinae as defined by Seeno and Wilcox (1982), not as by Crowson (1945)].

If criocerines and donaciines are derived from sagrines, then they too should lack tibial spurs, by implication of Dollo's Law, and so this character presents a difficult problem in logic. It is unlikely that criocerines and donaciines re-evolved spurs. It is easier to consider that the reduced state, 1-1-0, is derived from the 2-2-2 state of an ancestor common to donaciines and criocerines, while sagrines independently lost tibial spurs subsequent to divergence from the remaining crioceriform lineage early in sagroid evolution. I have no explanation of this problem, in view of other characters that suggest alternate hypotheses of sagroid relationships, and I postulate tentatively that the 1-1-0 state is synapomorphic for donaciines.

Character 3. Larval spiracular hooks.— Three states: plesiomorphic, spiracular hooks on eighth abdominal segment absent; apomorphic 1, spiracular hooks present; apomorphic 2, spiracular hooks elongate.

Spiracles of the eighth abdominal segment of larvae with hooks are unique to donaciines. In members of *D.* (*Donacia*) and *D.* (*Cyphogaster*) these hooks are much more elongate than in other taxa; their state in *Donaciasta* is unknown. I hypothesize that greatly elongate hooks are synapomorphic for these two subgenera of *Donacia*, and that their length is related to use of host plants, the Nymphaeaceae. Larvae of *Donaciasta* also may be associated with Nymphaeaceae and therefore may have similar hook length.

Character 4. BSB of endophallus.— (Photographs A-O). Two states: plesiomorphic, BSB absent; apomorphic, BSB present. This structure was discussed in detail by Askevold (in prep a.).

In the sagrines examined, no sclerite resembling a BSB was found. Criocerines examined possess a BSB or a BSB-like sclerite. Figures of male genitalia of criocerines (White, in prep.), and those examined, show a structure that is similar to that of donaciines. I infer this occurs in all criocerines. Therefore, it is tempting to consider presence of a BSB as synapomorphic at least for Criocerinae + Donaciinae, and possibly for all sagroids.

Character 5. ELD of endophallus.— (Photographs A-O). Three states: plesiomorphic, ELDs absent; apomorphic 1, ELDs present, moveable, basally articulated with BSB, and easily distinguishable (Phot. A-D); apomorphic 2, ELDs contiguous at least apically (Phot. G), usually from base to apex, enclosing the MEG (Phot. E, J-O).

This character was discussed in detail by Askevold (in prep. a). Among sagrines and criocerines examined, in particular specimens of *Atalasis*, two sclerites that resemble the ELDs of *Plateumaris* are visible. Thus I hypothesize that the state possessed by *Plateumaris*, with ELDs separate and articulating, is plesiomorphic. In most other donaciines the ELDs are at least apically contiguous, and are generally contiguous from base to apex, enclosing the MEG. The contiguous state I hypothesize is synapomorphic for all members of Donaciini + Haemoniini. I could not interpret the state in *Poecilocera harrisii* because I was not able to homologize all endophallic sclerites with those of other genera.

Character 6. Basal angulation of median lobe.— (Photographs F, L). Two states: plesiomorphic, basal angulation of median lobe absent; apomorphic 1, basal angulation present (Phots. F, L); apomorphic 2, basal angulation lost.

In sagrines, *Plateumaris* and *Poecilocera* the median lobe does not have an angulation subbasally, and this state is hypothesized as plesiomorphic. Among Criocerinae and most Donaciini (except *Donaciasta* and some members of *Sominella* Jacobson) and Haemoniini, a basal angulation is present; its absence from *Donaciasta* and some members of *Sominella* is hypothesized as a secondary loss. If criocerines were considered an out-group, then absence of this structure in donaciines would have to be considered apomorphic. *Plateumaris* and *Poecilocera* then could be considered sister taxa on the basis of shared loss, with two species of *Sominella*, *Donaciasta*, and Sagrinae independently having lost this structure. However, shape and prominence of the angulation in criocerines is very different from that of donaciines, and I conclude they are derived independently.

Character 7. Underside of median lobe.— Two states: plesiomorphic states, surface of underside of median lobe smooth, or more commonly, striate; apomorphic, underside of median lobe with longitudinal furrow or flattened.

The apomorphic state is present only in members of *Donacia s.str.* and *D.* (*Cyphogaster*) [except *D.* (*Donaciomima*) *tuberculifrons* Schaeffer], and is hypothesized as synapomorphic for these two subgenera of *Donacia*.

Character 8. Elytral apex.— (see Askevold, in prep a, Figs. 9-13 and 1988, Figs. 34-35). Three states: plesiomorphic, apex of elytron rounded; apomorphic 1, elytral apex truncate; apomorphic 2, elytral apex with large spine at outer angle.

The elytral apex of most sagroids and *Plateumaris* is rounded. That of *Sominella reticulata* Gyllenhal, *Donacia microcephala* and members of *Donaciella* is also rounded, which I consider reversals. *Poecilocera* and most

Donaciini have truncate elytra, or with some slight modification, while Haemoniini are characterized by truncate elytra with an apical spine. The truncate condition I hypothesize is synapomorphic for *Poecilocera* + Donaciini + Haemoniini.

Character 9. Sutural interval of elytron.— (see Askevold, in prep. a, Figs. 10-13). Two states: plesiomorphic, sutural interval of elytron narrowed subapically, the inner and outer beads convergent and exposing an explanate lower sutural margin; apomorphic, inner and outer beads convergent only at apex, lower sutural margin only narrowly exposed.

The state hypothesized as plesiomorphic is present in *Plateumaris* and *Poecilocera*; it is also present in most sagrines (*cf.* Table 2), as well as a few criocerines, and is certainly a sagroid ground plan character. Monrós (1959) stated that this character is also present in *Donaciocrioceris dentatus* Pic (here transferred to *Donaciasta*), but the elytral apex in this species is not different from other members of *Donaciasta* and other Donaciini.

Character 10. Mandibular teeth.— (Figs. 8-10, see also Askevold, 1988, Figs. 45-46). Four states: plesiomorphic, mandible apically with single tooth, outer margin curved uniformly; apomorphic 1, mandible with two apical teeth, profile slender, apical teeth approximate, no prominent occlusal edge, the outer margin forming uniform curve; apomorphic 2, apical profile slightly explanate, the ventral apical tooth displaced from apex, forming short cutting edge, and outer margin rounded or slightly angulate; apomorphic 3, apical teeth more dramatically divergent and forming a long, finely serrate occlusal cutting edge, and outer margin distinctly angulate.

Sagrines (and cerambycids and bruchids) have only a single blunt or acute apical tooth and the mandible is sickle-like in shape. Among criocerines, most taxa examined possess a mandible which is distinctly bidentate apically, like that of donaciines (a few are tridentate). The mandible of criocerines is somewhat more robust, and less sickle-shaped than is found in *Plateumaris* and *Poecilocera*. It is tempting to consider the bidentate state synapomorphic for Criocerinae + Donaciinae. However, on the basis of selection of Sagrinae (*Atalasis*) as out-group, the bidentate mandible must be considered independently derived in criocerines. Similarly, the more complex, tridentate mandible found in many other chrysomelids is also independently derived.

In specimens of *Plateumaris* and *Poecilocera*, the apical teeth are slender, and the lateral surface is uniformly rounded; in the Donaciini and Haemoniini the apical teeth are at least slightly divergent. The ventral tooth is shorter and somewhat displaced basad, forming at least a short cutting occlusal edge. The mandible, therefore, is not so slender in profile, and rounded or a little angulate externally. I hypothesize that this state is synapomorphic for Donaciini + Haemoniini. In members of *D.* (*Donacia*) and *D.* (*Cyphogaster*), the apex is explanate, the ventral tooth markedly displaced ventrally and basad forming a prominent, serrate cutting edge; the outer margin in these taxa is prominently angulate. I hypothesize that this condition is synapomorphic for these two subgenera of *Donacia*.

One could consider several independent characters as comprising this series, but I think they are integrated as a single functional system that is related to host plant type and ovipositional behaviour. This is especially true of those members which are Nymphaeaceae-associated [*i.e.*, *Donacia s.str.* and *D.* (*Cyphogaster*)] Females of these species cut a hole in the leaf surface (floating) and lower the abdomen through this hole to oviposit. It seems a mandible of this shape, and with a serrate occlusal edge, would be effective in cutting a hole in a flat surface. Leaves of Nymphaeaceae are thick, and a long occlusal edge would be necessary in order to puncture the leaf.

Character 11. Hypomeral pubescence.— (see Askevold, 1988, Figs. 23, 27, and in prep. a, Figs. 14-17). Four states: plesiomorphic, pubescence above procoxa absent, hypomeron glabrous above sternal-hypomeral suture; apomorphic 1, sparse setae present; apomorphic 2, prominent quadrate pubescent area present above procoxa, may occupy entire hypomeron, but generally only half; apomorphic 3, hypomeral pubescence lost.

Askevold (1988:393, 407) discussed the hypothesized adaptive significance of supracoxal pubescence among Donaciinae, and presented a simplified transformation series of absence as plesiomorphic, and presence as derived, with *Macroplea* as having secondarily lost this pubescence. However, *Poecilocera harrisii*, *Sominella macrocnemia* (Fisch. v. Waldheim), and *S. reticulata* possess some sparse, inconspicuous pubescence that could be considered intermediate between complete absence in *Plateumaris* and *S. longicornis* (Jacoby) and other Donaciini and Haemoniini. I have found no single synapomorphy to define *Sominella* as a monophyletic unit; tentatively, I group the four species together in *Sominella* on the basis of gross similarity, and exclusion from other Donaciini, but note that alternative equally parsimonious explanations are possible (*cf.* Table 4, and Figs. 16-18).

Character 12. Clypeal length.— (Figs. 1-3; see also Askevold, 1988, Figs. 38-39). Two states: plesiomorphic, clypeus short; apomorphic, clypeus elongate. The clypeal length in donaciines is typically short, such that the mandibular articulation is proximal to the antennal bases. In *Donaciasta* the clypeus is elongate, the clypeogenal suture longer; in *Neohaemonia* mandibular insertion is slightly removed from the antennal bases, but in *Macroplea* it is much like that of *Donaciasta*. I hypothesize the derived state to have arisen independently in *Donaciasta* and Haemoniini.

Character 13. Clypeal depression.— (Fig. 3). Two states: plesiomorphic, surface of clypeus flat or somewhat convex; apomorphic, clypeus with triangular or ⊥-shaped depression. The derived state occurs only in members of *Donaciasta* (most specimens), in which there is a shallow transverse furrow just above the clypeolabral suture.

Character 14. Pygidial shape, ♀♀.— (Fig. 6). Two states: plesiomorphic, pygidium apically broadly rounded or emarginate, more or less quadrate in overall shape; apomorphic, pygidial apex acute or narrowly rounded, more or less triangular and elongate in overall shape. The pygidium of female donaciines is typically rounded or emarginate apically (extensive homoplasy in states), and in overall shape the tergum is rather quadrate. In members of *D.* (*Donacia*) and *D.* (*Cyphogaster*), the pygidium is elongated, in overall shape much longer than broad, and with apex acute or narrowly rounded. This state is considered synapomorphic for these two subgenera of *Donacia*.

Character 15. Dorsal colour.— Two states: plesiomorphic, metallic in colour; apomorphic, metallic pigmentation lost or reduced, colour therefore piceous, rufous, or testaceous.

Donaciines are typically brightly metallic in colour, dorsally and ventrally. A few species of *Plateumaris* may be piceous or testaceous, as are several *D.* (*Donaciomima*) Medvedev, but in most of these taxa only some specimens lack metallic colour, while most or many are typically metallic. In many *Donacia* exclusive of *D.* (*Donaciomima*), specimens are entirely rufous or testaceous, or they may have a slight metallic luster, while some are entirely metallic (*e.g. D.*

crassipes Fabricius, *D. ozensis* Nakane, *D. proxima* Kirby), or are largely metallic with some reduction of metallic colour [*e.g.* many *D.* (*Cyphogaster*)].

Haemoniini are typified by lack of metallic colour, for which the state is considered synapomorphic as a consequence of development of a fully aquatic life history (Askevold 1988). Loss of colour in other groups, including several *D.* (*Donaciomima*) and most other *Donacia* should be considered independently achieved; Members of *Donaciasta* virtually completely lack metallic colouration, save a faint lustre; they are otherwise rufous (*e.g. D. goeckei*) or piceous (*D. perrieri*) in colour ventrally and dorsally (but head black in *D. assama*). I note that this character correlates with others to support grouping of *Donaciasta* + Haemoniini as sister taxa, and include it as synapomorphic for this grouping.

Character 16. Abdominal tubercles ♂♂.— Two states: plesiomorphic, males without pair of glabrous tubercles medially on basal abdominal sternum; apomorphic, with pair of small glabrous tubercles medially on basal abdominal sternum.

Males of *D.* (*Cyphogaster*) possess a pair of small, glabrous tubercles medially on the basal abdominal sternum. These structures are unique to the subgenus *D.* (*Cyphogaster*), with the exception of *D.* (*Donaciomima*) *dentata* Hoppe. In this latter species the tubercles probably are derived independently; Goecke (1934) suggested that they are not homologous, but the possibility that they are cannot be discounted, for the subgenus *Donaciomima* may be paraphyletic.

Character 17. Tarsal claw segment.— (see Askevold, 1988, Fig. 31). Two states: plesiomorphic, length of claw-bearing segment shorter; apomorphic, claw-bearing segment elongate. Askevold (1988) discussed this character, and considered the elongate claw segment as synapomorphic for Haemoniini.

Character 18. Ovipositor, subapical setae.— (see Askevold, in prep a, Figs. 237-239). Two states: plesiomorphic, setae on sternum and tergum VIII; apomorphic, setae of sternum and tergum VIII absent.

Taxa with a sclerotized ovipositor also lack the fine setae present in other groups of donaciines (see next character). Loss of setae from these segments is considered to have occurred independently in *Plateumaris* and *Donaciella* Reitter, but it is synapomorphic for each of these genera. It seems that taxa which oviposit within plant tissue, as members of *Plateumaris* at least, appear to do, would not need sensory setae on the ovipositor surface because they would tend to be abraded anyway.

Character 19. Ovipositor sclerotized.— (see Askevold, in prep. a, Figs. 237-239). Two states: plesiomorphic, tergum and sternum VIII pliable, not sclerotized markedly, and truncate apically; apomorphic, tergum and sternum VIII prominently sclerotized and apically acute, sternum VIII often with serrate apical margins.

Members of *Plateumaris* possess the most heavily sclerotized ovipositor. Two species of *Donaciella*, the Nearctic species, *D. pubicollis*, and the Palaearctic species, *D. clavipes* (Fabricius), possess an ovipositor that is similar to that of *Plateumaris*. Two other species of *Donaciella*, *D. cinerea* (Herbst) and *D. tomentosa* (Ahrens), have the ventral valve acute, and more heavily sclerotized than is usual among *Donacia*. I consider the state possessed by *Plateumaris* as synapomorphic for the genus, and the state found in *Donaciella* as independently derived. The less developed state in the species of *Donaciella* is probably intermediate between the plesiomorphic state and the more highly derived state found in the other two members of the genus.

Character 20. Ovipositor valve length.— (see Askevold, in prep a, Figs. 237-239). Two states: plesiomorphic, dorsal valve (tergum VIII) and ventral valve (sternum VIII) of equal length; apomorphic, ventral valve longer than dorsal valve.

Donaciines, as well as other sagroids, normally have the tergum and sternum VIII of an equal length, and not functioning as discussed in the previous character (#19). The elongate ventral valve (sternum VIII) is clearly a derived character state.

Character 21. Mesosternal width.— (Fig. 5). Two states: plesiomorphic, mesosternum narrow between mesocoxae; apomorphic, mesosternum, especially of female specimens, broad between mesocoxae, wider than half the mesocoxal diameter.

The mesosternum of sagroids is typically narrow, and this state is retained by most donaciines. Members of *D.* (*Donacia*) and *D.* (*Cyphogaster*), especially females, possess a broad mesosternum; therefore these insects are broader across the humerus than is typical of other donaciines. This broader body form occurs similarly in a number of taxa of *D.* (*Donaciomima*) and in *Donaciasta*, but very prominently so in members of *D.* (*Donacia*) and *D.* (*Cyphogaster*). In general, it seems the species that live on plants with floating leaves are broader in body shape, and have a broader mesosternal process, but among species of *D.* (*Donaciomima*) there is considerable variation. However, the species of the former two subgenera of *Donacia* are typically so prominently widened that I consider the extreme state they possess as synapomorphic for members of those two subgenera.

Character 22. Metafemoral tooth.— Two states: plesiomorphic, metafemoral tooth present; apomorphic, metafemoral tooth absent.

Most sagrines, and donaciines, have an acute tooth on the metafemur, and this is certainly a ground plan state. Few criocerines possess a femoral tooth. Males of *Poecilocera*, some species of *D.* (*Donaciomima*), and most species of *D.* (*Donacia*) and *D.* (*Cyphogaster*), possess a second, shorter tooth more proximally placed. A number of taxa have lost the tooth independently, *e.g.* some members of *Plateumaris*, or the tooth is small or absent in some specimens of some species. Loss of metafemoral tooth is associated generally with decrease of metafemoral diameter. All members of the Haemoniini lack the metafemoral tooth, and therefore have very slender metafemora; this state is considered synapomorphic for the tribe Haemoniini. Similarly, species of *Donaciella* lack a tooth (and have slender metafemora), though some specimens of *D. clavipes* possess a small tooth; tentatively I consider the state in *Donaciella* as synapomorphic for members of the genus.

Character 23. Pronotal punctures.— Three states: plesiomorphic, punctation of pronotal disc fine or absent; apomorphic 1, pronotal disc more or less uniformly coarsely punctate; apomorphic 2, pronotal punctation diminished or lost completely.

Pronotal punctation is a variable character state among donaciines, and evidently it is subject to considerable homoplasy. Members of *Plateumaris* show a range of prominence of punctation, while all *Sominella*, *Donaciasta* and most *D.* (*Donaciomima*) are prominently punctate. Pronotal punctation in most *Donaciella* is concealed by pubescence, though punctation is somewhat finer. Coarse punctation could be considered independently derived in the various groups of Donaciini (*i.e.*, at least three times). Alternatively, it is more parsimonious to consider that coarse punctation is synapomorphic for Donaciini + Haemoniini, and that such punctation was lost no more than twice [not counting a few otherwise typical members of *D.* (*Donaciomima*)], perhaps once as synapomorphic for the Haemoniini, and once in the other two subgenera of *Donacia*. Members of *D.* (*Donacia*) and *D.* (*Cyphogaster*) show no coarse punctation that is uniformly distributed in a way that typifies other Donaciini. Largely on the basis of character correlation, lack of coarse punctation in *D.* (*Donacia*) and *D.* (*Cyphogaster*) is hypothesized as synapomorphic for these two sugenera. Askevold (1988) discussed punctation in Haemoniini, and suggested that diminished punctation probably was independent in the various groups of Haemoniini; whether independently lost or acquired by the taxa of Haemoniini that do or do not possess pronotal punctation requires the same degree of homoplasy. Thus, I consider the state of diminished punctation as synapomorphic for the Haemoniini, with subsequent independent additional reduction among other members of the tribe.

Character 24. Frontal and ocular grooves.— (Figs 1-4; see also Schmitt, 1985a, Fig. 41, 1985b, Fig. 10). Three states: plesiomorphic, frontal grooves absent; apomorphic (24a), frontal grooves complete, with grooves deep and connected with ocular grooves; apomorphic (24b), grooves mesad of eyes somewhat to well developed, extending behind eyes. I consider the term frontal grooves in a more restricted sense than have other authors, as detailed below.

Frontal (24a) and ocular grooves (24b) are, in my opinion, two separate structures. The former are actually deeply incised frontoclypeal suture, forming ^-shaped grooves. The latter are entirely unrelated grooves located mesad of the eyes and are usually \ /-shaped or exceptionally V-shaped. In some exceptional groups, such as *Sagra*, the frontal and ocular grooves meet at their apices, forming X-shaped furrows.

Schmitt (1985a,b, 1988) hypothesized that the members of Criocerinae and Sagrinae are sister taxa on the basis of the single character of presence of crossed frontal grooves (Character 24a). He noted that such complete grooves are not typical of all Sagrinae, but that they are typical of Criocerinae. However, he interpreted the character as synapomorphic for the two groups, stating that frontal grooves are absent from members of Donaciinae and the bruchids. However, many donaciines possess the lower, frontoclypeal half, and to some extent also the upper, ocular part of these grooves. Donaciines merely lack the X-shaped complete furrows and have prominent antennal calli (as do some sagrines that lack the X-shaped part).

Most genera of sagrines do not have ocular and frontoclypeal grooves typical of *Sagra*. In fact, of sagrines examined (Table 2), *Sagra* alone possesses complete frontal grooves, and *Carpophagus* MacLeay has short ocular grooves. Therefore I think a reassessment of this character is needed. The frontal and ocular grooves may indeed be derived, but cannot be synapomorphic for Sagrinae + Criocerinae exclusively, as Schmitt (1985a,b, 1988) suggested.

The lower, frontal portion of these grooves occurs in many sagroids, including many donaciines except some more highly derived taxa, despite contrary claims (*e.g.* Schmitt 1985a,b). Some of the more highly derived donaciines have slightly developed frontoclypeal grooves, but they are found in many taxa and should be considered part of the ground plan of donaciines.

The upper, or ocular grooves, are structures that vary in development among sagrines and criocerines (Table 2). At best, frontoclypeal and ocular grooves could be considered part of the ground plan of sagroids, or even variously derived within sagroids, but not of use in resolving relationships at the subfamily level.

In Donaciinae the ocular grooves are indicated by an indistinct glabrous line or shallow furrow. However, in *Donaciasta*, there is a more prominent furrow that extends from near the antennal callus to behind the eyes, much like in some criocerines, and is unique to this genus, among donaciines. The furrow may be homologous with the ocular grooves, but because it is unique among donaciines I must consider it a redevelopment of a groove similar to the ground-plan state, and therefore synapomorphic for the genus (character 24b).

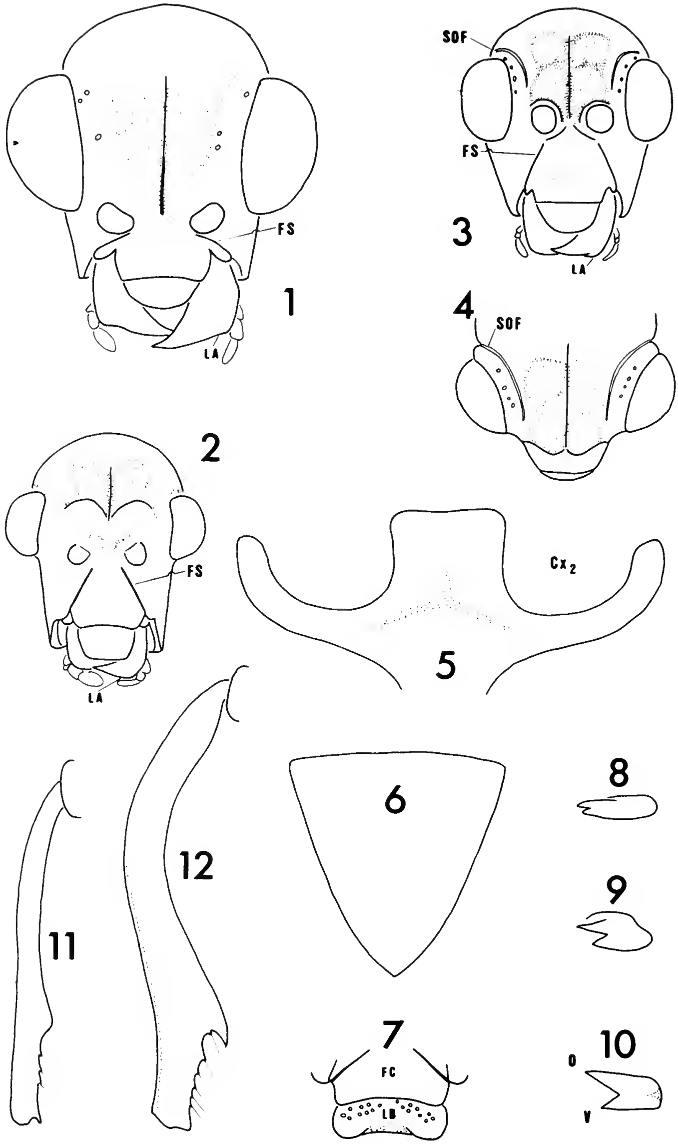
Character 25. Egg bursters.— Two states: plesiomorphic, egg bursters present in first instar larvae; apomorphic, egg bursters lost.

Cox (1988) reviewed the occurrence of egg bursters in the Chrysomeloidea, stating that Donaciinae examined lack them; however, only larvae of *D.* (*Donaciomima*) *semicuprea* Panzer and *D.* (*Donaciomima*) *bicolor* Zschach were examined. Cox (1988, p. 415) suggested that absence of egg bursters in the donaciines "may be correlated with the specialized extrachorion of the eggs." He supposed that first instar larvae must bite through the chorion in order to ingest bacteria that are contained in the extrachorion (*i.e.*, the gelatinous matrix into which Donaciini and Haemoniini oviposit). This loss correlates well with most Haemoniini and Donaciini, which oviposit under water in a gelatinous matrix. However, females of *Plateumaris* (but *Poecilocera* and *Sominella* oviposition behaviour unknown) do not oviposit in this way, and so their larvae may not achieve bacterial transmission in this way. While sagrines have not been investigated for egg bursters, criocerines do possess them, and oviposit on foliage. Primitive donaciines (*i.e. Plateumaris*) also oviposit on foliage (or insert their eggs into plant tissue), as opposed to under water in extrachorion. Thus I question whether primitive donaciines have egg bursters, namely *Plateumaris*, possibly *Poecilocera* and even *Sominella.* If so, then egg bursters should be found in the same location as in criocerines and bruchids (*i.e.*, on abdominal segment 1, dorsad of spiracle). Thus, I hypothesize tentatively that lack of eggbursters in donaciines is synapomorphic for Donaciini + Haemoniini. This interpretation is consistent with other characters that define the same grouping of genera, and with the historical scenario I have constructed summarizing the evolution of Donaciinae.

Character 26. Oviposition glands.— Two states: plesiomorphic, paired glands opening into common oviduct absent or not modified; apomorphic, sac-like glands, hypothesized to produce a gelatinous extrachorion, present.

Mann and Crowson (1983a) found that "gelatinous glands" are absent from females of *Plateumaris sericea* (Linnaeus) [(as *P. discolor* (Panzer)], but present in those of *D.* (*Donacia*) *crassipes.* These scanty data are hardly sufficient, but I observe that they are consistent with other characters, notably ovipositor and mandibular structure, egg bursters, oviposition behaviour, and host plants. Lack of such a gland is tentatively considered plesiomorphic, and I predict that most, if not all, Donaciini and Haemoniini should have them.

In another publication, Mann and Crowson (1983b) refered to "vaginal pouches", which were described as occurring in what seems to be the same position as their "gelatinous glands" (Mann and Crowson 1983a). They (Mann and Crowson 1983b) thought that these "pouches" are organs of symbiont transmission, though this may not preclude production of an ovipositional matrix. Their claim that vaginal pouches are absent from Donaciinae (Mann and Crowson 1983b) is contradicted by their recognition of "gelatinous glands" (Mann and Crowson 1983a) if the organs in question are in fact the same. Further, Stammer (1935) investigated symbiont transmission in donaciines, and found that "Mitteldarmblindsäcke" (four blind sacs of midgut, at junction of mid- and foreguts) of larvae harbour the bacteria, and that in the adult beetles bacteria are restricted to swellings of Malpighian tubules of females. At present, for want



FIGURES 1-12: 1. Frontal aspect of head of *Donacia hypoleuca* Lacordaire. **2.** Frontal aspect of head of *Macroplea pubipennis* (Reuter). **3.** Frontal aspect of head of *Donaciasta luridiventris* (Lacordaire). **4.** Dorsal aspect of head of *Donaciasta luridiventris*. **5.** Mesosternum of *Donacia cincticornis* Newman. **6.** Pygium of female of *Donacia cincticornis* **7.** Frontal aspect of frontoclypeus and labrum of *Sominella kraatzi* (Weise). **8.** Apical aspect of left mandible of *Plateumaris rufa* (Say). **9.** Apical aspect of left mandible of *Poecilocera harrisii* (LeConte). **10.** Apical aspect of left mandible of *Donacia cincticornis*. **11.** Lateral aspect of metatibia of female of *Sominella macrocnemia* (Fisch. v. Wald.). **12.** Lateral aspect of left metatibia of male of *Sominella macrocnemia*. Cx_2 = mesocoxa; D = dorsal apical tooth of mandible; FC = frontoclypeus; FS = frontoclypeal suture; LA = lateral angulation of mandible; LB = labrum; SOF = supraocular furrow; V = ventral apical tooth of mandible. Scale bar = 1.0 mm for Figs. 1-10, 0.5 mm for Figs. 11 and 12.

of more complete data, I postulate the above character sequence of absence = plesiomorphic, and presence = apomorphic. I observe that if this interpretation is correct, this character would be consistent with several other characters that I have suggested are integrated and related to other structures, general behaviour and host plant associations.

Character 27. Host plants.— Four states: plesiomorphic, hosts principally Cyperaceae; apomorphic 27a, hosts Gramineae; apomorphic 27b, hosts Nymphaeaceae; apomorphic 27c, hosts principally Zosteraceae and Haloragaceae. Each of the states, a, b and c, I postulate are derived host associations relative to the plesiomorphic association with vertical-emergent plants; each represents an independent shift to plant taxa in the same (Gramineae, for example) or another type (Nymphaeaceae, Zosteraceae) of growth form.

Based on study of host plant associations, I have postulated that host plant growth form is an important feature in the evolution of donaciines (Askevold, in prep. b). I postulated that donaciines are primitively associated with plants the leaves of which are vertical in growth form and emergent from the water, occurring along water body margins; *Plateumaris*, *Poecilocera* and most *D*. (*Donaciomima*) use these plants (mostly Cyperaceae). Also using vertical plants, are *Donaciella* (Gramineae); I hypothesize use of grasses as synapomorphic for the genus *Donaciella*.

Members of *D*. (*Donacia*) and *D*. (*Cyphogaster*) are restricted to floating plants, exclusively to the Nymphaeaceae. I consider tentatively use of pond lilies and related genera as synapomorphic for these two subgenera, and uses by some *D*. (*Donaciomima*) as independently derived associations.

Members of *Donaciasta* also appear to be restricted to floating plants, on the basis of two host records, from *Potamogeton* (Bertrand 1965) and "*Nymphaea* and *Trapa natans*" (Askevold, in prep. d). The Haemoniini are restricted to the Zosteraceae (with some records from Haloragaceae) (Askevold 1988).

Host plant data are useful in the ecological definition of certain genera and subgenera, but are not useful in grouping of genera, with the possible exception of state 27c, hosts of the Zosteraceae and Haloragaceae. In an ecological and adaptive sense, taxa using these plants conceivably are derived from an intermediate group, state 27b. That is, the floating-leaf category could be considered phylogenetically and adaptively intermediate between the vertical and submerged plants. Such a progression in donaciine phylogeny is supported by the character of colour loss (character 15) that is shared by Haemoniini, *Donaciasta* and many *D*. (*Donacia*) and *D*. (*Cyphogaster*), and a few *D*. (*Donaciomima*).

Character 28. Metatibia ventrally explanate.— (Figs. 11-12). Two states: plesiomorphic, metatibia ventrally with at most prominent denticles; apomorphic, metatibia ventrally prominently carinate or explanate, producing a large tooth in many males. Some species of *Donacia* (especially *s.str.*) have prominent denticles ventrally on the metatibia, as do some species of *D*. (*Donaciomima*). Otherwise, donaciines have no modification of the tibial underside except in two species of *Sominella*: *S. longicornis* and *S. macrocnemia*, especially males, have prominently carinate metatibiae, varying from having an explanate carina to a prominent tooth about midlength. I consider this structure synapomorphic for this species pair.

Character 29. Ratio of antennomeres 3:4.— Two states: plesiomorphic, antennomere 3 shorter than antennomere 4; apomorphic, antennomere 3 as long as or longer than 4.

Typically among donaciines, antennomere 3 is much shorter than 4. However, some specimens of *Poecilocera*, most specimens of *Sominella longicornis* and *S. macrocnemia*, and many specimens of *S. reticulata* and *S. kraatzi* have antennomere 3 as long as or longer than 4. The derived state is considered synapomorphic for at least *S. macrocnemia* + *S. longicornis*, and possibly independently derived in some specimens of other taxa. PAUP analysis selected character 29 as synapomorphic for Donaciinae exclusive of *Plateumaris*, with reversal at the node connecting the remaining Donaciini + Haemoniini, but I find such an explanation unsatisfactory. Rather, I must consider the state occurring homoplastically in at least *Poecilocera*, and possibly in *S. reticulata* and *S. kraatzi* also. However, it could also be argued that this character is synapomorphic for all four species of *Sominella*, but this would require homoplasy in some other characters that I weight more heavily.

Character 30. Form of tegmen.— (Photographs B, D, F, L, O). I consider two independent characters of this structure, divided into characters 30a and 30b. Four states: plesiomorphic, parameres complete, forming a ring around the median lobe, with dorsal cap robust (Phots. B, D); apomorphic 1 (30a), dorsal cap slender, of more or less uniform width and thickness (Phots. F, O); apomorphic 2 (30a) dorsal cap slender, but uniformly broadened (Phot. L); apomorphic (30b), dorsal cap portion absent.

Within donaciines, *Plateumaris* and *Poecilocera* have a robust dorsal cap similar to that of sagrines, and this is undoubtedly the plesiomorphic state. Donaciini and Haemoniini have a slender and thin dorsal cap, while in *D.* (*Donacia*) and *D.* (*Cyphogaster*) the cap is wide, but thin. I consider the slender state synapomorphic for Donaciini + Haemoniini, and the widened state synapomorphic for the two subgenera of *D.* (*Donacia*).

Sagroids exclusive of Criocerinae possess a complete tegmen. Criocerines appear to have lost the dorsal cap portion (30b), leaving only a V-shaped ventral strut portion, much like in Alticinae and Galerucinae. I consider the reduced tegmen synapomorphic for the Criocerinae.

Character 31. Form of epipleuron.— Two states: plesiomorphic, epipleuron more or less angulate from humerus to near apex; apomorphic, epipleuron flattened or rounded, not more prominent than the outer interval.

Most donaciines possess an angulate epipleuron, which is elevated and more prominent than the flat outer interval. Several groups possess a flattened epipleuron, for which the state appears to be synapomorphic. Members of *Donaciella*, *D. microcephala* Daniel and Daniel, *D.* (*Donacia*) and *D.* (*Cyphogaster*) possess this state, as do a few species of *D.* (*Donaciomima*) and *S. kraatzi*. The degree to which the epipleuron is flat varies within these groups, so I cannot consider the character synapomorphic for these groups together, even though character 32 (eye size) is consistent with such a grouping.

Character 32. Eye size.— (Fig. 1). Two states: plesiomorphic, eyes small and round; apomorphic, eyes large and oval or round. Most donaciines have eyes rather small in relation to overall head size or length of occiput.

Several groups in Donaciini have very prominent, large eyes, and it is tempting to consider the state synapomorphic for these groups: *Donaciella*, *D. microcephala*, *D.* (*Donacia*) and *D.* (*Cyphogaster*), and a few unrelated species of *D.* (*Donaciomima*). Rather, I choose to consider the state synapomorphic for *D.*

(*Donacia*) + *D.* (*Cyphogaster*), and as an independent synapomorphy for *Donaciella*.

Character 33. Male abdominal apex.— Two states: plesiomorphic, basal sternum and apical sternum without medial depression in males; apomorphic, abdominal apex and basal sternum with broad depression in males.

All male donaciines are recognized by adominal depressions medially on the basal sternite, and apically on the apical sternite. The same condition occurs in some sagrines (Table 2), but not among criocerines I examined. I consider presence of this depression synapomorphic for Donaciinae + *Atalasis* and perhaps some other sagrines.

Character 34. Pronotal lateral margin.— Two states: plesiomorphic, pronotum laterally margined; apomorphic, lateral margin absent.

All sagroids lack a lateral margin of the pronotum, whereas most Coleoptera possess a lateral margin. While the character is therefore one of loss, it could be considered synapomorphic for the sagroid subfamilies. Lack of this margin also occurs in widely unrelated chrysomelids: some Galerucinae (*e.g. Cyclotrypema* Blake), many Eumolpinae (*e.g.* most, if not all, Adoxini), Orsodacninae, Zeugophorinae and Megalopodinae; the latter three are generally considered relatively primitive groups.

Character 35. MEG.— Two states: plesiomorphic, ejaculatory duct (flagellum) slender, unmodified; apomorphic, flagellum shortened, not exceeding the median lobe in length, more heavily sclerotized and sheathed with membrane.

Many chrysomelids possess an elongate flagellar structure that protrudes from the median lobe; it is sclerotized, but is not part of an internal sac complex as in donaciines. In sagroids examined, the ejaculatory duct is not elongate, but forms part of a sclerotized complex on the internal sac apex. This ground plan seems to characterize sagroids, as far as I can ascertain, and I consider this state synapomorphic for the sagroid subfamilies.

Character 36. Basal sac sclerites.— (Photographs D, F, I, M, N). Two states: plesiomorphic, basal sac sclerites absent or slightly developed; apomorphic, basal sac sclerites well developed as a sac-retracting mechanism (*cf.* Askevold in prep. a, Figs. 4-6 and discussion).

I am not familiar with detailed internal sac structure in chrysomeloids other than those I have examined (sagroids and bruchids). However, the median lobe of many chrysomelids seems to possess apical structures about the orifice, that appear much like those of sagroids (internal sac in repose). In sagroids, when the internal sac is everted, these structures can be seen as basal sclerites on the sac, an elongate one dorsally, and one or more on each side which I interpret as functioning to facilitate sac retraction. Bruchids appear not to possess such sclerites (*cf.* Borowiec 1987), and so I suggest that presence of basal sac-folding sclerites is synapomorphic for the sagroids (not including bruchids).

Character 37. Pubescence of scutellum.— Two states: plesiomorphic, scutellum pubescent; apomorphic, scutellum glabrous.

Most sagrines possess a pubescent scutellum (see Table 2), as do all donaciines, while criocerines (at least most) have a glabrous scutellum. Two explanations are possible: either the pubescent scutellum is part of the ground plan of sagroids, and it is lost from some sagrines and the criocerines; or the pubescent scutellum is derived within sagroids, and synapomorphic for Donaciinae + some other sagrines. Partly on the basis of the common = primitive criterion (*i.e.*, widespread among sagroids), I conclude that it is a ground plan character, lost from criocerines and a few sagrines. Also it is more reasonable to infer that a few groups lost pubescence, rather than requiring multiple independent derivations of pubescence among sagroids.

Character 38. Pubescence of humerus.— The character is not polarized and was not used for analysis of relationships of sagroid subfamilies, but states are detailed in Table 2 for sagrines, to which could be added Criocerinae without, and Donaciinae with, humeral pubescence. Humeral pubescence is probably also a ground plan character, variously lost from Criocerinae and sagrines, but retained by the aquatic donaciines, perhaps as part of their plastron system.

Relationship of donaciines to other sagroid subfamilies

The sagroid subfamilies.— Traditionally, the Sagrinae, Criocerinae and Donaciinae are placed close to one another in classifications (*e.g.* Seeno and Wilcox 1982, Monrós 1959). Schmitt (1985a,b, 1988, 1989) considered these three subfamilies as comprising a single, monophyletic group, but the matter is not resolved satisfactorily.

Schmitt (1985a,b, 1988) has been the only author to approach the problem of relationship by methods of phylogenetic systematics; his work is therefore the most satisfactory point at which to begin. Polarity of certain synapomorphic characters and therefore inclusiveness of taxa by such synapomorphies, might be affected by choice of hypothesis about out-group. The hypothesis selected was that donaciines are derived from a lineage of sagrines, and that criocerines are independently derived from sagrines.

A discussion of donaciine generic relationships must first establish that the general hypothesis of progression of character states in donaciines is valid despite ambiguities about relationships of sagroid subfamilies. That is, reversal of polarity of the relatively few characters because of out-group choice does not alter relationships of donaciine genera significantly.

Some authors have considered Bruchidae to belong among the sagroids (*e.g.* Mann and Crowson 1981, 1983b, 1983c, Crowson 1960). Chen (1986) included the Bruchidae in this group (named the Crioceridae). Monrós (1959, Fig. 1, p. 20) used the term Crioceriformes for the grouping of these three subfamilies, but including also the Bruchidae as sister group to the Sagrinae. Schmitt (1989) considered that bruchids belong within Chrysomelidae, probably as sister group to the "Crioceriformes" + "Cryptostomes" (Cassidinae + Hispinae), largely on the basis of presence of bifid tarsal setae.

Bruchids have an internal sac structure and retraction musculature that bears little resemblance to any other sagroids I have examined (based on figures in Kingsolver 1970 and Borowiec 1987). I considered certain bruchid characteristics, but I find that these do not have much bearing either on relationships of sagroid subfamilies or on phylogeny of donaciine genera for the purpose of analyzing character polarity in sagroids.

Problematic characters and outgroup to Donaciinae.— Certain characters discussed above, some of which were used by Schmitt (1985a,b) to reconstruct the relationship among the Sagrinae, Criocerinae and Donaciinae, are problematic. These characters are: (1), ligular lobes; (2), tibial spurs; (4), BSB of endophallus; (6), basal angle of median lobe; (10), mandibular teeth; and (24), frontal grooves. Each of these characters is considered above, to rationalize sagroid subfamily relationships and selection of out-group. Character states are summarized in Tables 1 and 2.

Definition of an out-group to donaciines is problematic. If one were to echo Crowson's (1945) view that Sagrinae are a stem-group, then only one or a few genera of sagrines should be considered valid for proximal out-group purposes.

TABLE 1. CHARACTERS USED TO ASSESS PHYLOGENETIC RELATIONSHIP OF SAGROID SUBFAMILIES.

		TAXA							
CHARACTERS**		CRIOCERINAE		**SAGRINAE		*ATALASIS*		DONACIINAE	
(1-30 from Table 3)		state	code	state	code	state	code	state	code
1.	Ligular lobes	absent	1	GP- present	0	present	0	absent	1
2.	Tibial spurs	GP- 2-2-2	0	0-0-0	A	0-0-0	A	1-1-0	B
4.	BSB	present ?	1	absent	0	absent	0	present	1
5.	ELD	present ?	1	abs./pres.	0/1	present	1	present	1
6.	Med. lobe angulation	present	1	GP- absent	0	absent	0	abs./pres.	0/1
9.	El. suture explanate	no (yes)	1/0	GP- yes/no	0/1	yes	0	yes/no	0/1
10.	Mandibular teeth	bidentate	1	GP- unidentate	0	unidentate	0	bidentate	1
24a.	Frontoclypeal groove	present	1	GP- present	1	present	1	present	1
30b.	Tegmen, dorsal cap	reduced	1	GP- no	0	no	0	no	0
33.	♂ ♂ Sexual characters	no	1	GP- yes/no	0/1	yes	0	yes	0
34.	Pn. lat. margin	absent	1	GP- absent	1	absent	1	absent	1
35.	MEG	present	1	abs./pres.	0/1	present	1	present	1
36.	Basal sac sclerites	present	1	GP- present	1	present	1	present	1
37.	Scutellum pubescent	no	1	GP- yes/no	0/1	yes	0	yes	0
38.	Humeral pubescence	GP- no	*	GP- yes/no	*	no	*	yes	*

** Characters 30b to 37 are presented here for subfamilial level character assessment; for details of Sagrinae genera, see Table 2, for Donaciinae see Table 3. A and B = separate reductions from ground plan state. GP- = probable groundplan state. * = polarity undetermined.

TABLE 2. ASSESSMENT OF SOME PHYLOGENETIC CHARACTER STATES OF SAGRINAE.

		TAXA*							
Characters		*Diap*	*Carp*	*Poly*	*Mega*	*Mecy*	*Sagr*	*Amet*	*Atal*
4.	ELD	?	?	-	-	?	NH	NH	1
5.	BSB	?	?	-	-	?	NH	NH	0
9.	Elytral suture	0	1	0	0	0	0	1	0
24.	Ocular groove	no	yes(I)	no	no	no	yes	no	no
30b.	Tegmen	0(?)	0(?)	0(?)	0(?)	0(?)	0	0	0
33.	♂♂ Sexual characters	?	?	1	1	?	1	1	1
34.	Pronotal lateral margin	1	1	1	1	1	1	1	1
35.	MEG	?	?	-	-	?	1	NH	1
36.	Basal sac sclerites	?	?	?	?	?	1	1	1
37.	Scutellum pubescent	yes	yes	yes	yes	yes	no	yes	yes
38.	Humeral pubescence	yes	yes	no	no	no	no	yes	no

Characters stated as yes/no are not polarized.

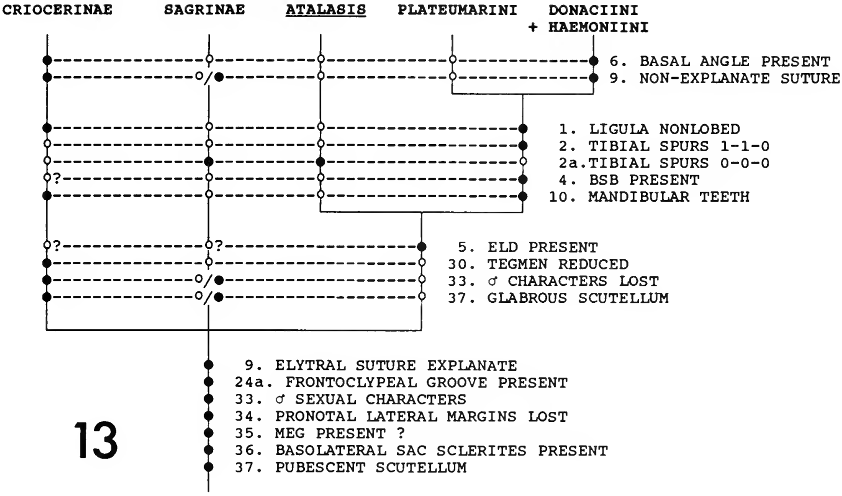
I= character more or less present, but incomplete in development.

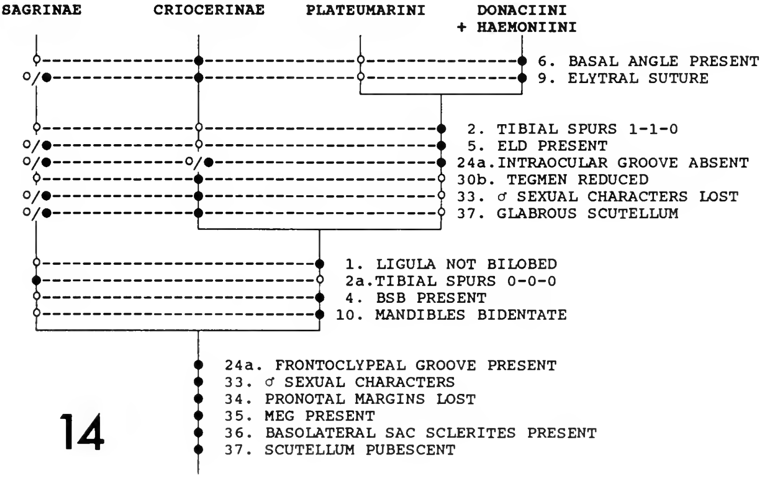
? = state unknown because no male specimens examined, or structure not identified (*Polyoptilus* and *Megamerus*).

- = internal sac without sclerites.

NH = sac sclerite not homologized.

*Names of taxa: *Amet* = *Ametalla; Atal* = *Atalasis; Carp* = *Carpophagus; Diap* = *Diaphanops; Mecy* = *Mecynodera; Mega* = *Megamerus; Poly* = *Polyoptilus; Sagr* = *Sagra.*





FIGURES 13, 14. Cladograms illustrating hypotheses of phylogenetic relationship of Donaciinae to Criocerinae and Sagrinae. Apomorphic states indicated on diagrams. ●= apomorphic character states; O= plesiomorphic character states. **13, Hypothesis 1.** The genus *Atalasis* is assumed to be the sister taxon to Donaciinae if apomorphic states in characters 1,4,6 and 10 in Criocerinae are considered independently derived. **14, Hypothesis 2.** The Criocerinae is assumed to be the sister taxon to Donaciinae because characters 1, 4 and 10 could be considered synapomorphic for the grouping Criocerinae + Donaciinae. This hypothesis requires reversal of character 6 in Plateumarini and most Sagrinae, or homoplasy of 6 between Donaciini and Criocerinae. Reduction of character 2 is more easily derived from the criocerine type than from the sagrine type.

Using Sagrinae as a whole might be misleading, for character state polarity would be ambiguous for the most part. The same could be said of the Criocerinae, if they were also derived from Sagrinae independently of Donaciinae. The principal purpose of this discussion is to rationalize use of *Atalasis* as closest out-group to Donaciinae. My preliminary view of relationships among the three sagroid subfamilies was that among *Atalasis*, the rest of Sagrinae, and Criocerinae, *Atalasis* possesses more derived character states in common with Donaciinae and should therefore be considered the closest out-group.

Results of analysis of sagroid groups (Figures 13, 14) using PAUP varied according to which out-group was defined. If either Criocerinae or *Atalasis* was defined as hypothetical out-group, PAUP presented *Atalasis* as sister taxon to Donaciinae because fewer character transformations were required **within** Donaciinae than among the three groups. However, if an additional hypothetical out-group (*i.e.* the remainder of Sagrinae) was defined, then PAUP selected Criocerinae as sister taxon to Donaciinae, based partly on a number of shared loss characters, or losses in Donaciinae from the plesiomorphic state in Criocerinae.

Several characters suggest that Criocerinae is indeed the sister group to Donaciinae: tibial spurs, mandibular teeth, ligular lobes, median lobe angulation and possibly certain endophallic sclerites. Other characters suggest a group of sagrines is the sister taxon: male sexual characters, pubescent scutellum and elytral humerus, toothed metafemora, and elytral suture explanate (at least primitively). However, none of these characters can be considered shared-derived (at least at this taxonomic level) because they constitute part of the ground plan of the sagroids, from which many character states can be derived.

The possible character state distributions, and relationships of sagroids, are presented in Figures 13 and 14. I am not satisfied that sagroid relationships are well resolved, but select sagrines as out-group as the hypothesis to proceed with. *However, I note that characters the polarity of which would be reversed by selection of criocerines as out-group would not alter the general donaciine generic relationships.*

RECLASSIFICATION OF GENERA OF DONACIINAE

This section comprises two parts. First, I discuss aspects of the hypothesis of reconstructed phylogeny of donaciine genera (Fig. 15), especially as relevant to their classification. Following, I summarize my ideas about higher classification of Donaciinae by means of a brief treatment of each tribe and its included genera. Both Old and New World supraspecific taxa are included: tribes, genera and subgenera are characterized and diagnosed; and genera and subgenera are keyed (Old and New World taxa separately). Analysis of the Haemoniini was examined previously (Askevold 1988), and is condensed here.

The classification of Donaciinae proposed herein is provisional. Clearly, problems at both generic and tribal levels persist because of lack of resolution of relationships (Figs. 15-18), subjectivity of character assessment, and perhaps also because I am reluctant to recognize multiple monobasic genera. These problems require a classification of donaciines that is not strictly phylogenetic. Therefore, the appertaining principles adopted are clarified briefly in the context of a discussion about the phylogeny.

Paraphyletic tribes

For tribal classification, it is clearly desirable to recognize only monophyletic taxa (Donoghue and Cantino 1988). However, among the tribes of Donaciinae, this is possible only for Haemoniini. To adhere strictly to cladistic classification, I would have to follow either a complicated and cumbersome arrangement, or none at all. Lack of a tribal classification would hinder discussion of such aspects as host plant relationship. I regard the reconstructed phylogeny as not fully resolved and consider that the classification derived from it justifiably is not fully resolved either.

The relationship of *Plateumaris* and *Poecilocera* is based largely on symplesiomorphy; additional characters may show them to be sister taxa, but there is no particular reason to expect this. I group them here on the basis of symplesiomorphy, structurally and in host plant use. Thus the Plateumarini constitutes a paraphyletic, grade-based taxon. *Poecilocera* could be placed in Donaciini just as readily on the basis of host relations because many taxa in Donaciini are associated with the same plants as are Plateumarini. However, it bears greater resemblance to *Plateumaris*, albeit plesiomorphically, and I am more comfortable with this assignment at this time.

The tribe Donaciini is a broad mixture of structurally generalized to specialized groups, and would be holophyletic only if Haemoniini were not recognized as a distinct tribe. As I discuss elsewhere (Askevold, in prep. b), the Donaciini consists ecologically of members that are generalized in host plant use [*i.e. Sominella*, most *D.* (*Donaciomima*)], as well as of lineages that have become highly specialized in host plant use [*i.e. Donacia* (*Cyphogaster*), *D.* (*Donacia*) and *Donaciasta*]. The former are mostly taxa that are structurally more generalized and most similar to the donaciine ground plan exmplified by *Plateumaris*; the latter are both structurally and ecologically specialized groups. The Donaciini is therefore a stem-group from which several lineages succeeded in attaining greater specialization.

One of these lineages is the Haemoniini which, as is supported by several characters (Table 3 and Fig. 15), is the sister taxon to *Donaciasta* of Donaciini. Haemoniini consists of members that are profoundly different from other lineages of donaciines, both ecologically and structurally (Askevold 1988), and I am reluctant to reject this group as a useful monophyletic taxon.

For Plateumarini and Donaciini then, two paraphyletic taxa are recognized. There is an inherent danger that such groups will be treated as monophyletic by subsequent investigators (Donoghue and Cantino 1988), but this classification should be recognized for what it represents: a provisional one that could be a staging-point for subsequent investigations. Many published classifications in chrysomelids have no apparent structural basis. Available classifications of almost all chrysomelid groups therefore must be regarded as fully unsubstantiated and effectively uninvestigated. The classification of Donaciinae proposed here is a solution to certain problems but creates others; however, it puts Donaciinae on a better foundation than is available for other subfamilies of chrysomelids. My classification can be reexamined and modified in the future as it becomes supplemented by additional and new kinds of data, both biochemical and structural.

TABLE 3. MATRIX OF CHARACTER STATES USED IN PHYLOGENETIC RECONSTRUCTION OF GENERA OF DONACIINAE.

	TAXA*										
Characters	*SAGR*	*CRIO*	*Plat*	*Poec*	*Somi*	*Donl*	*"Don"*	*Dona*	*Dona*	*Dona*	*Dont*	*HAEM*
							micr	*(Dim)*	*(Don)*	*(Cyp)*		
1. Labial ligula	0	1	1	1	1	1	1	1	1	1	1	1
2. Tibial spurs	0	0	1	1	1	1	1	1	1	1	1	1
3. Larval hooks	0	0	1	1	1	1	?	2	2	1	?	1
4. BSB	0(-1?)	1	1	1	1	1	1	1	1	1	1	1
5. ELD	1	1	1	1	2	2	2	2	2	2	2	2
6. M.L. basal angle	0	1	0	0	0-1	1	1	1	1	1	0(R)	1
7. M.L.furrowed	0	0	0	0	0	0	0	1	1	0	0	0
8. Elytral apex	0	0	0	1	1	1	0(R)	1	1	1	1	2
9. Sut. interval	0-1	0-1	0	0	1	1	1	1	1	1	1	1
10. Mandib. teeth	0	1	1	1	2	2	1(R)	3	3	2	2	2
11. Hypom. pubesc.	0	0	0	1	0-2	2	2	2	2	2	2	2^1-3
12 Clypeus length	NA	NA	0	0	0	0	0	0	0	0	1	1^1
13. Clyp. depress.	NA	NA	0	0	0	0	0	0	0	0	1	0
14. ♀♀ pygidium	0	0	0	0	0	0	0	1	1	0	0	0
15. Dorsal colour	0	0	0(1)	0	0	0	1	0-1	0-1	0(1)	1	1
16. Abd .tubercles	0	0	0	0	0	0	0	0	1	0(1)	0	0
17. Claw segment	0	0	0	0	0	0	0	0	0	0	0	1
18. Ovipos. setae	NA	NA	1	0	0	1	0	0	0	0	0	0
19. Ovipos. scler.	0	0	1	0	0	1	0	0	0	0	0	0
20. Valve length	NA	NA	1	0	0	1	0	0	0	0	0	0

(continued on next page)

Table 3 (continued)

	Characters	TAXA*											
		SAGR	*CRIO*	*Plat*	*Poec*	*Somi*	*Donl*	*"Don" micr*	*Dona (Dim)*	*Dona (Don)*	*Dona (Cyp)*	*Dont*	*HAEM*
21.	Mesost. width	0	0	0	0	0	0	0(1)	1	1	0(1)	0(1)	0
22.	Metafem. tooth	0	1(0)	0(1)	0	0	1(0)	0(1)	0(1)	0(1)	0(1)	0	1
23.	Pronot. punct.	NA	NA	0	0	1	1	1	2	2	1	1	1
24.	Ocular grooves	0(1)	0(1)	0	0	0	0	0	0	0	0	1	0
25.	Egg bursters	NA	NA	0(?)	0(?)	1(?)	1(?)	1(?)	1(?)	1(?)	1	1(?)	1(?)
26.	Ovipos. gland	NA	NA	0	0(?)	1(?)	1(?)	1(?)	1	1(?)	1	1(?)	1(?)
27a	Hosts	NA	NA	0	0	0(?)	1	?	0	0	0	0	0
27b.	Hosts	NA	NA	0	0	0(?)	0	?	1	1	0(1,2)	1,2	2
28.	Metatibia expl.	0	0	0	0	0(1)	0	0	0	0	0	0	0
29.	Antenn. 3:4	0	0	0	0(1)	1	0	0	0	0	0	0	0
30a.	Tegmen	0	0	0	0	1	1	1	2	2	1	1	1
31.	Elytral epipl.	0	NA	0	0	0-1	1	1	1	1	0(1)	0	0
32.	Eyes large	NA	NA	0	0	0	1	1	1	1	0(1)	0	0

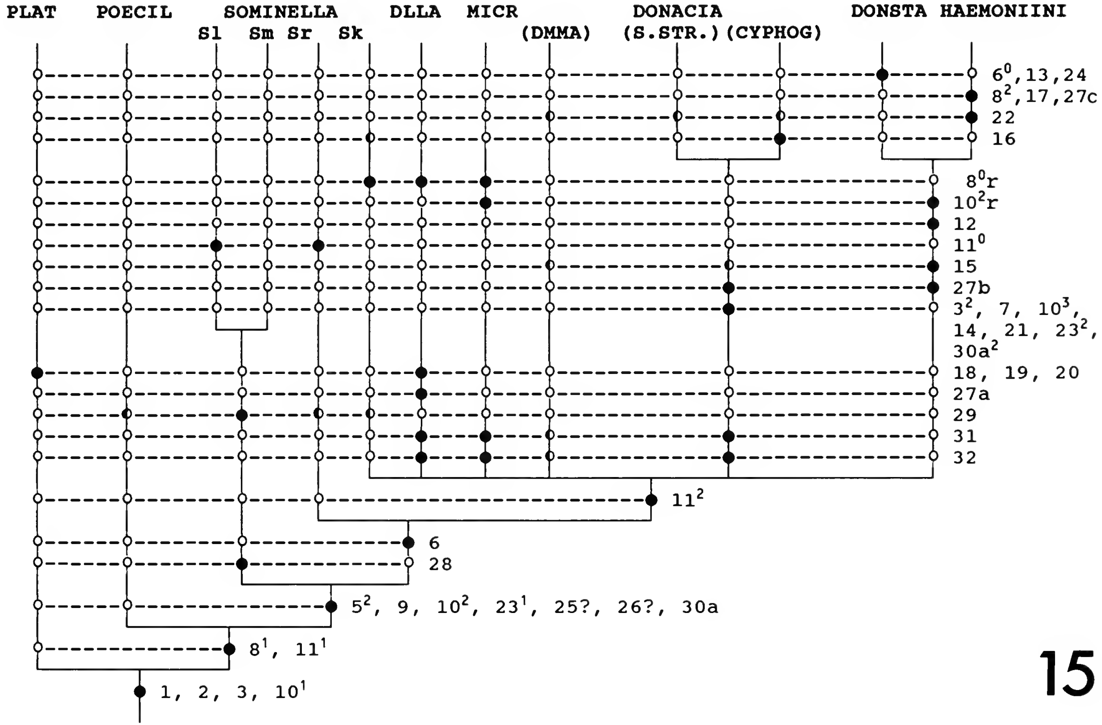
1 = state unknown in *Neohaemonia voronovae* Medvedev (for character 6). ? = state unknown.

R = postulated reversal to plesiotypic state, 0 or 1.

NA = character not assessed, not relevent to analysis.

(1) or (0) = some members possess state in parentheses, = homoplasy.

*Names of taxa: CRIO = Criocerinae; "Don" micr = "Donacia" microcephala; Dona (Cyp) = Donacia (Cyphogaster); Dona (Dim) = Donacia (Donaciomima); Dona (DDon) = Donacia (Donacia); Donl = Donaciella; Dont = Donaciasta; HAEM = Haemoniini; Plat = Plateumanis; Poec = Poecilocera; and SAGR = Sagrinae.



15

FIGURE 15. Reconstructed phylogeny of genera and some taxa of Donaciinae not assigned to genus. PLAT = *Plateumaris;* POECIL = *Poecilocera*; Sl = *Sominella longicornis*; Sm = *Sominella macrocnemia*; Sr = *Sominella reticulata*; Sk = *Sominella kraatzi*; DLLA = *Donaciella*; MICR = "*Donacia*" *microcephala*; DMMA = *D*. (*Donaciomima*); CYPHOG = *Donacia* (*Cyphogaster*); DONSTA = *Donaciasta*. ● = apomorphic character states; O= plesiomorphic character states; half-circles = specimens (or taxa) with both states occurring in that taxon; r = reversal.

Paraphyletic genera and subgenera

Donacia s.str. is probably paraphyletic because I have no synapomorphy for the group; the grouping of this subgenus and *D.* (*Cyphogaster*) is clearly defined, but without a synapomorphy for the nominate subgenus I cannot rule out the possibility that *D.* (*Cyphogaster*) could have arisen from some group within *D.* (*Donacia*). Similarly, *D.* (*Donaciomima*) is very likely a paraphyletic group from which the major lineage of the other two subgenera could have diverged ecologically and structurally, and become specialized to Nymphaeaceae-hosts. Among these subgenera, *D.* (*Cyphogaster*) alone is defined by a synapomorphy.

That these paraphyletic relationships exist is virtually a certainty for, as Disney (1989) observed, residual paraphyletic groups remain when the rank of a subset of species within a genus is raised to the generic (or subgeneric) level. The remainder, which belong in the group bearing the original genus name, cannot be defined by a synapomorphy. As long as relationships and limits of these groups remain confused, I am inclined to accept a relatively *status quo* approach rather than to elevate all apparently defined lineages to generic status.

The problem of *Sominella*, also a paraphyletic group, is discussed below. According to strict criteria of monophyly, *Sominella* would remain, consisting of two species, *S. longicornis* and *S. macrocnemia*; *S. kraatzi* and *S. reticulata* should be assigned to their own genera: *Pseudodonacia* Reitter and a new genus, respectively. However, this approach seems simply inappropriate for species which are not significantly unique from others.

Problems in classification of some genera

The reconstructed phylogeny of donaciine genera is partly clearly resolved. Some groupings, like the Haemoniini (see Askevold 1988) and the pair of subgenera *D.* (*Donacia*) and *D.* (*Cyphogaster*), are defined by many synapomorphies. The relationship of Haemoniini to *Donaciasta* is supported by at least one structural character (#12) as well as by host plant association (#27); an additional character (#15), loss of dorsal colour, supports this arrangement.

No synapomorphy was found for taxa grouped in *D.* (*Donaciomima*) and *Sominella*. Both groups are recognized on the basis of general similarity of included members. *Donacia microcephala* and *Neohaemonia voronovae* Medvedev also remain of uncertain relationship within Donaciini and Haemoniini, respectively. The relationships I have not been able to resolve satisfactorily are discussed in greater detail, below.

Problem of phylogeny and classification of Sominella.— On the basis of characters examined, no single primary synapomorphy was found for the group to which four species are here assigned, *Sominella*, except perhaps character 29 (antennomere 3:4 ratio). Even if character 29 was considered a primary synapomorphy, this arrangement would require homoplasy in characters 11 and 6. The species here placed in *Sominella* have a general facies that suggests their combination into one genus: occiput not constricted behind eye (or only slightly), eye therefore not protruding, elongate antenna, femora coarsely and closely punctured, vertexal calli at most slight, elytron sparsely but coarsely rugose. I cannot consider confidently any of these characters as synapomorphic.

Other characters constitute a confusing array of plesiomorphic and apomorphic characters: characters suggesting inclusion in the rest of Donaciini (elytral apex, median lobe angulation, hypomeral pubescence) by some taxa, but others retaining or reverting to plesiomorphic states. The elytral apex of these species varies: narrowly truncate in *S. longicornis*, toothed and emarginate in *S. macrocnemia*, produced into a narrowly rounded apex in *S. kraatzi*, and typical of

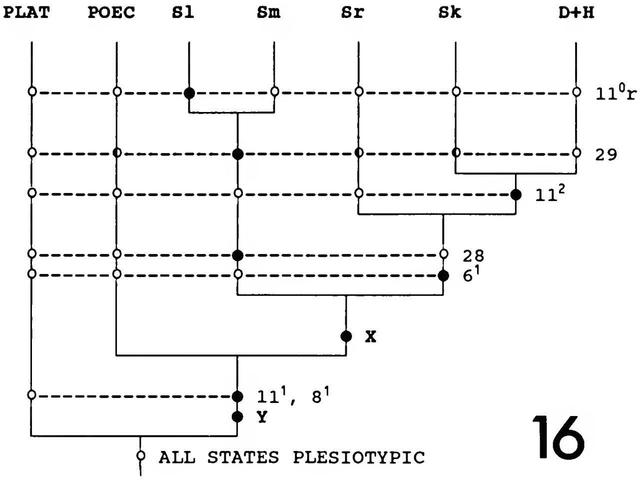
TABLE 4. DETAILS OF CHARACTER STATE DISTRIBUTION OF SOME HOMOPLASTIC CHARACTERS IN DONACIINAE.

CHARACTERS	TAXA*						
	Plat.	*Poec.*	*Sominella*				DONA+ HEM
			long.	*macr.*	*reti.*	*kraatzi*	
6. Median lobe angulation	0	0	0	0	1	1	1
11. Hypomeral pubescence	0	1(0)=1	0	1	1(0)=1	2	2(1)=2
28. Metatibial explanation	0	0	1	1	0	0	0
29. Antennomeres 3:4	0	0(1)=0	1	1	1(0)=1	1(0)=1	0

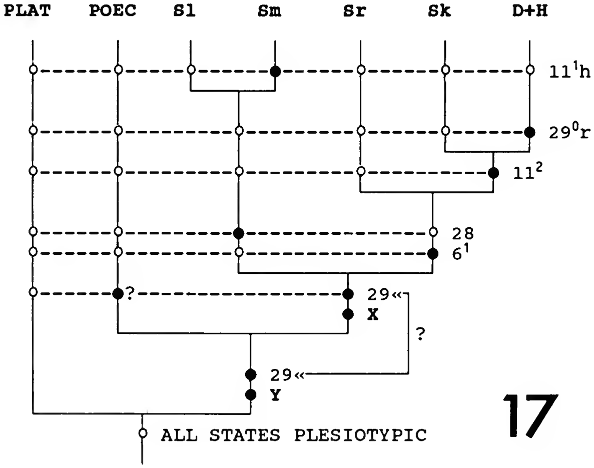
Characters and their states are taken from Table 3, with specific states in species of "*Sominella*" inserted.

See discussion of characters for analysis of polarity. Value in parentheses (e.g. 1(0)=1) = some specimens of that taxon, or some taxa in the group, have on alternate character state, and "=1" or "=2" indicates subsequent decisions about polarity.

*Names of Taxa: DONA = DONACIINI; HAEM = HAEMONIINI; *long* = *S. longicornis; macr* = *S. macrocnemia; Plat* = *Plateumaris; Poec* = *Poecilocera; reti* = *S. reticulata.*



16



17

FIGURES 16, 17: Possible relationships of members here assigned to *Sominella* to remaining Donaciini. X and Y indicate apomorphies defining these clades (see Fig. 15). **16, Hypothesis 1.** In this hypothesis, *S. reticulata* and *Poecilocera harrisii* are assumed to possess the derived state of character 11. Character 29 is selected by PAUP analysis to be derived at branch Y, and reversed on the D+H branch. **17, Hypothesis 2.** In this hypothesis, *S. reticulata* and *Poecilocera harrisii* are assumed to possess the plesiomorphic state of character 11. PAUP analysis did not select possible monophyly of *Sominella* based on 29 because of additional tree length caused by greater required homoplasy in characters 11 and 6; 29 was selected by PAUP analysis to be derived at branch Y (or X if *P. harrisii* does not possess 29), and reversed at the D+H branch.

● = apomorphic states, O= plesiomorphic states, and half-circles = specimens with both states occurring in this taxon. PLAT= *Plateumaris;* POEC= *Poecilocera*; Sl= *Sominella longicornis*; Sm= *Sominella macrocnemia*; Sr= *Sominella reticulata*; Sk= *Sominella kraatzi*; D+H= rest of Donaciini + Haemoniini; r= postulated reversal to plesiomorphic state, O; h= postulated homoplastic occurrence of derived state, 1.

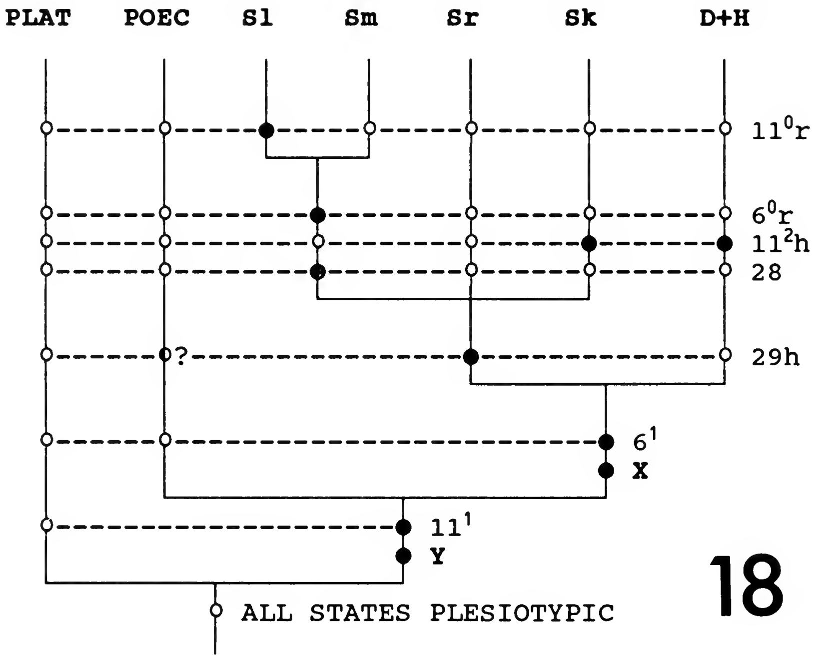


FIGURE 18. Possible relationship of members here assigned to *Sominella* to remaining Donaciini. **Hypothesis 3.** The derived state of character 11 is assumed to be possessed by *P. harrisii* and *S. reticulata.* PAUP analysis did not select possible monophyly of *Sominella* based on character 29 because of additional tree length caused by greater required homoplasy in characters 11 and 6. For explanation of abbreviations *etc*, see Figure 17.

Donaciini in *S. reticulata.* Median lobe and hypomeral characters are detailed in Table 4 and Figures 16-18.

There is no satisfactory resolution for the purposes of classifying these taxa. I am reluctant to erect a new monobasic genus to accommodate *S. reticulata*, while *Pseudodonacia* Reitter is available for *S. kraatzi.* Therefore I expand *Sominella* to include four species that are similar in general facies, and that can be excluded from other genera in Donaciini. Therefore, the genus constitutes a paraphyletic group as now defined by phylogenetic reconstruction.

Placement of Donacia microcephala Daniel and Daniel.— Donacia microcephala is known from the Middle East only. I examined a series of specimens from Iran. Specimens of *D. microcephala* possess most character states of Donaciini, with the notable exception of mandibular structure: the mandibles are slender in width and profile and each possesses only a single apical tooth, a reduction from the state typical of Donaciini. Specimens of the Nearctic *D.* (*Donaciomima*) *pubescens* LeConte are similar to those of *D. microcephala* in being totally pubescent dorsally; additionally, specimens of both species have rounded elytral apex, flat epipleuron, and are testaceous in colour. The species of *Donaciella* are similar to these two species in the flattened epipleuron, most species with rounded elytral apex, and dorsal pubescence in some species. Most species of *D.* (*Donacia*) and *D.* (*Cyphogaster*) have extremely dense ventral pubescence, through which the fine punctures are not visible; this is also so for *D. microcephala* and a few species of *D.* (*Donaciomima*). *Donaciella* and *D.* (*Donacia*) and *D.* (*Cyphogaster*) are similar to *D. microcephala* in size of eyes and general lack or slight development of antennal and vertexal calli. There was no single character that I considered convincing evidence for inclusion in any of the generic taxa of Donaciini as they are currently defined, though *D. microcephala* has several characters that suggest inclusion in *Donaciella*. I am reluctant to erect a monobasic genus because relationships are not resolved adequately.

Problem of placement of Neohaemonia voronovae Medvedev.— I have not examined specimens of this species. Askevold (1988) suggested it does not belong in any described genus, but the problem remains unresolved.

Treatment of tribes and genera

Details of reclassification of Donaciinae as proposed herein, based on phylogenetic analysis of the genera, are treated below. Jolivet (1970:1) listed all suprageneric names based on *Donacia* Fabricius; these are not relisted here but authorship of Donaciinae, and therefore Donaciini, is attributable to Kirby by implication of ICZN (1985) Articles 33b(ii), 43(a) and 36(a) bearing on the matter of family-group name authorship. Below, each tribe is diagnosed and included generic names are listed. Generic names for fossils proposed by Haupt (1956) are incorporated on the basis of my interpretation of their original descriptions and as suggested by Askevold (1990). Type species designations are stated for all genus-group taxa and are verified or corrected by me *by reference to original literature.*

For each genus and/or subgenus I list the Old World species that I assign to them. *The Palaearctic taxa listed are those of which I have examined specimens.*

To conserve space, *I do not present full bibliographic citation for all Old World species* (references are not given); I give date of original description, but most bibliographic details can be found in Jolivet (1970) and Borowiec (1984). I give full bibliographic information only for taxa described after Jolivet (1970), for taxa involved with new synonymies proposed here, and for those about which I report type specimen data (which indicates that I have examined these types). New World species are to be listed separately (Askevold, in prep. c).

DONACIINAE KIRBY, 1837

DONACIADAE KIRBY, 1837:22

TRIBE PLATEUMARINI, NEW TRIBE

Type genus.— *Plateumaris* Thomson, 1859.

Diagnosis.— Sutural margin of elytron explanate apically, inner sutural bead sinuate far from apex and joined to outer bead, and elytral apex rounded in most species; hypomeron of pronotum glabrous (or with few scattered setae); mandible with apical teeth approximate, lacking serrulate occlusal edge; median lobe without basal angulation, tegmen robust and tapered. Hosts typically Cyperaceae, but also a few other emergent plant types.

Plateumaris Thomson, 1859

Plateumaris Thomson (1859:154). Type species *Donacia nigra* Fabricius (1792), by original designation.

Juliusina Reitter (1920:41). Type species *Prionus braccatus* Scopoli (1772), designation by Monrós (1959).

Euplateumaris Iablokoff-Khnzorian (1966:121). Type species *Leptura sericea* Linnaeus, 1758, by original designation.

Donacocia Gistel (1857:12). Type species *Donacocia aenea* Gistel (1857:12), by monotypy. Application for suppression submitted to ICZN.

Juliusiana Mohr (1966: 108). Unjustified emendation.

The genus was monographed by Askevold (in prep. a) recognizing 26 species: 9 Old World, and 17 New World. Taxonomic details provided there are not repeated here.

Poecilocera Schaeffer, 1919. NEW STATUS

Poecilocera Schaeffer (1919:307), Type species *Donacia harrisii* LeConte, 1851, by monotypy.

Donacia (*Poecilocera*) Schaeffer (1919:307, 1925:120).

Sominella, *ex parte*: Goecke (1931, 1960a:10), Jolivet (1970:61), Wilcox (1975:3), Borowiec (1984:454).

Sominaella: Monrós and Bechyné (1956:1121). unjustified emendation

Plateumaris (*Sominaella*), *ex parte*: Monrós (1959:94,107). unjustified emendation

Etymology.— Not stated by Schaeffer. The name could be based on the Greek *poecil*, meaning variegated or coloured, and *keras*, meaning horns (or antennae) (Jaeger 1955). This may be the meaning Schaeffer intended, but such characters are not at all distinctive among donaciines.

Diagnosis.— Elytral apex emarginate or truncate, sutural interval narrowed before apex, lower margin explanate; pronotum with pubescence of anterior lateral parts of prosternum extended slightly and sparsely onto hypomeron; latter otherwise entirely glabrous; apical teeth of mandibles approximate; mesosternal process narrow between mesocoxae; eyes small, vertex not raised; median lobe without basal angulation, tegmen robust and tapered; ovipositor with ventral and dorsal valves of equal length, and with subapical surface finely setose.

Taxonomic history.— The name *Poecilocera* first was proposed for a subgenus of *Donacia* (*sensu lato*) by Schaeffer (1919) to accommodate a single Nearctic species, *Donacia harrisii* LeConte. As Schaeffer observed, this species possesses character states similar to *Plateumaris*, but also to *Donacia*. The name *Plateumaris* had not yet achieved common use as a genus name among North American coleopterists when Schaeffer revised the Nearctic Donaciinae (1919, 1925). Thus, *Poecilocera* subsequently was not recognized as a genus either. Goecke (1931) was the first and last author to examine the generic assignment of *Donacia harrisii*, and transferred it to the genus *Sominella* on the basis of gross similarity and antennomere proportion. Marx (1957) followed Schaeffer (1925) and considered *Poecilocera* a subgenus of *Donacia*, while Monrós (1959) considered *Sominella* (including *D. harrisii*) a subgenus of *Plateumaris*. Recent authors (*i.e.* Jolivet 1970, Borowiec 1984), retained genus status of *Sominella*, with *D. harrisii* placed in it, according to Goecke's (1931) arrangement.

Discussion of genus status.— Adult specimens of *Poecilocera* are characterized primarily by plesiomorphic character states: small eyes, undeveloped vertexal calli, lack of pubescence on pronotal hypomeron, rounded elytral apices (or apex depressed, and therefore appearing emarginate), robust, tapering tegmen, lack of subbasal angulation of median lobe, teeth of mandibles approximate, and mesosternal process narrow.

Adult specimens of *Sominella* also share most of these plesiomorphic states, but shape of elytral apex and hypomeral pubescence vary; the tegmen is slender, and mandible with apical teeth a little divergent. These character states are derived in relation to states possessed by *Poecilocera* (and *Plateumaris*), and are shared with other genera of Donaciini and the Haemoniini.

Additionally, specimens of *P. harrisii* have a slightly developed hypomeral pubescent area, which I consider a state intermediate between that shown by *Plateumaris* and most of the Donaciini and Haemoniini. Among the species placed in *Sominella*, a variety of states occur; specimens of *S. longicornis* lack hypomeral pubescence; those of *S. reticulata* have only a very few inconspicuous setae and could be equally considered as lacking, or having poorly developed, hypomeral pubescence; specimens of *S. macrocnemia* are much like those of *P. harrisii* in this character, while those of *S. kraatzi* have hypomeral pubescence fully developed, as in other Donaciini. I argued (Askevold 1988) that this character may have been important in donaciine evolution, its presence being apomorphic (but lost independently in the ancestor to *Macroplea*).

Goecke's (1931) observation that *Sominella* species (*i.e.*, *S. macrocnemia* and *S. longicornis*) are convincingly similar to *P. harrisii* is true. General similarity in body form and appearance would lead to the conclusion that they are congeneric: small eyes, antennomere 3 equal to or longer than 4, coarse but sparse transverse rugae on elytra, and apical teeth of mandibles approximate in *Poecilocera*, only a little divergent in *Sominella*. Specimens of *S. longicornis* have the apical sutural interval somewhat narrowed, similar to that of *P. harrisii* and members of *Plateumaris*, but this is not shared by *S. macrocnemia* or the two other species I tentatively place in the genus.

Character states possessed by members of *Sominella* therefore constitute a mosaic of plesiomorphic and apomorphic states. Apomorphic states suggest placement in Donaciini + Haemoniini, while the plesiomorphic states are shared with the Plateumarini. Plesiomorphies cannot be used to reconstruct relationships (Hennig 1966, Kavanaugh 1972), so despite substantial similarity of *P. harrisii* to members of *Sominella*, I cannot consider them contribal or congeneric. Therefore, I remove *P. harrisii* from *Sominella* and place it in a monobasic genus, for which the name *Poecilocera* was made available by Schaeffer (1919). I redescribe its single included member, below.

Poecilocera harrisii (LeConte 1851:316) NEW COMBINATION
Figures 19, 20, Phot. E.

Donacia harrisii LeConte (1851:316).
Donacia harrisii: Crotch (1873:20), Leng (1891:172).
Donacia harrisi: Jacoby and Clavareau (1904:8), Clavareau (1913:21), Wilcox (1954:372).
Donacia (*Poecilocera*) *harrisi*: Schaeffer (1919:308, 1925:120), Marx (1957:196).
Sominella harrisi: Goecke (1931:159), Jolivet (1970:61), Wilcox (1975:3), Borowiec (1984:454).
Plateumaris (*Sominaella*) *harrisi*: Monrós (1959:107).

Type specimen.— LECTOTYPE ♀, MCZ Type #4244. LeConte stated he had a male and female, and therefore had at leat two specimens before him. The single, remaining specimen found in the LeConte collection is here designated: "[pink disc] ♀, Type #4244 [red], D. Harrisii *Lec.* / LECTOTYPE ♀ Donacia harrisii LeConte design. I.S. Askevold 1990 [red]".

Type locality.— The LeConte pink disc indicates "Middle States, N.Y.", although LeConte states "Penn. rarissime".

Etymology.— Evidently named after T.W. Harris, from whom LeConte states he obtained the specimen under the manuscript name *D. inermis* Harris.

Taxonomic history.— *Poecilocera harrisii* has been long recognized by authors, there being no taxon with which to confuse it, although the *Donacia harrisi* [*sic*] that Blatchley (1910) recognized was described subsequently by Schaeffer (1925) as *D.* (*Plateumaris*) *diversa. Donacia harrisii* became emended to *D. harrisi*, it seems first by Jacoby and Clavareau (1904), and has been spelled as such since. Schaeffer recognized that *D. harrisii* was unusual among North American donaciines, and erected the subgenus (*Poecilocera*) to accommodate it. Goecke (1931) then moved it to the genus *Sominella* Jacobson because of antennomere proportions, and there it has remained in treatments by European authors, but has been assigned to *Donacia* by most American authors.

Diagnosis.— Elytral apex emarginate or truncate, sutural interval narrowed before apex, lower margin explanate; eyes small, vertex not raised, apical teeth of mandibles approximate; pronotum with pubescence of anterior lateral parts of prosternum extended slightly and sparsely onto hypomeron, latter otherwise entirely glabrous; elytra and disc of pronotum transversely rugose; mesosternal process narrow; metafemur extremely robust, almost hemispherical, ventral margin of metafemur of ♂ and metatibia of both sexes with denticles; colour above coppery, below entirely dark to entirely reddish; elytron of some specimens with epipleuron and/or suture narrowly reddish.

Description.— **Length.** Males: 6.90 - 7.74 mm, females: 8.23 - 8.64 mm

Colour. Coppery brown dorsally, similar ventrally, but with abdomen, pygidium, antennae and tarsi of most specimens fulvous.

Pronotum. Pubescence of prosternum extended only slightly onto area of hypomeron, of few scattered setae; anterolateral and posterolateral tubercles of tactile setae of most specimens fulvous; disc of moderate to fine punctures and punctulae confluent over much of disc in form of transverse rugae, like elytra but denser; disc of some specimens partly microreticulate in areas of diminished punctation.

Head. Eyes small, round; occiput hardly constricted, eyes therefore not markedly protruded, temporal area very short behind eyes and oblique to axis of head; mandibles with apical teeth approximate, of subequal length, mandibles therefore slender in apical and lateral views; antennae entirely reddish, antennomere 3 equal to or slightly greater than length of 4.

Legs. Metafemur metallic in apical half or more, reddish basally, tibia and tarsus reddish. Metafemur of male specimens with two subapical ventral spines and most specimens with several large denticles along ventral margin, that of female specimens without these; ventral margin of metafemur straight, dorsally curved, therefore in appearance almost hemispherical; metatibia conspicuously denticulate along ventral margin in both sexes, meso- and metatibia of both sexes without tibial tubercle, mesotibia of both sexes with small mucro, about same size as that of protibia.

Elytra. Coppery brown; strial punctures united transversely by strigations over most of the surface, these rather uniformly transverse except in areas of antemedial and postmedial depressions; intervening strial intervals more or less uniformly and densely punctulate; apex truncate, that concavely depressed, therefore in appearance slightly emarginate; epipleuron slightly reddish in most specimens; sutural interval indistinctly delimited except near apex, beads developed only toward apex, inner sutural bead in contact with outer lateral bead of sutural interval some distance from apex, lower sutural margin exposed, that reddish fulvous.

Males. Pygidium broadly emarginate; tegmen broad, robust; median lobe without subbasal angulation; BSB of endophallus extremely long, about half as long as median lobe; basal

19

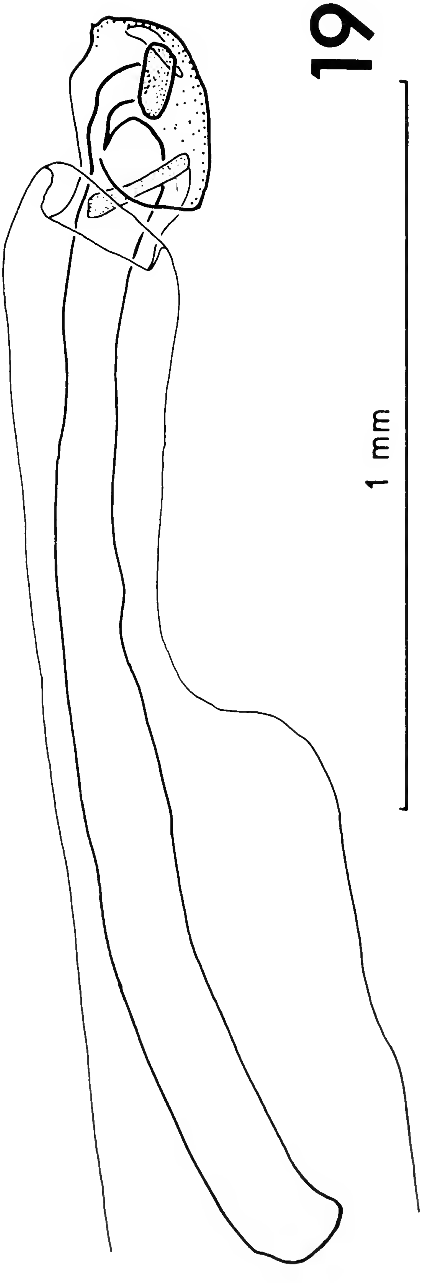


FIGURE 19. Lateral aspect of endophallus of *Poecilocera harrisii* (LeConte).

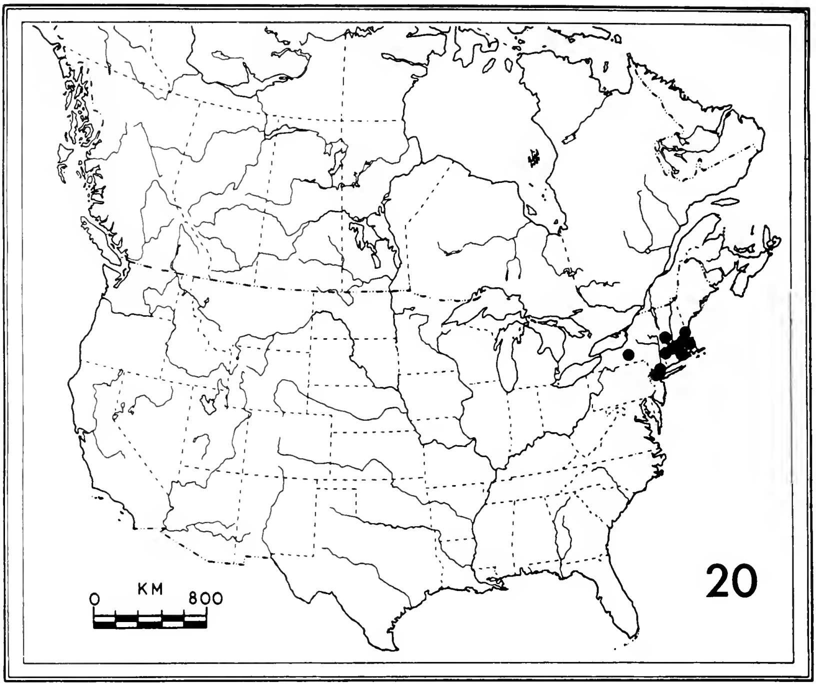


FIGURE 20. Known distribution in North America of *Poecilocera harrisii* (LeConte), based on specimens examined, and on published records (Schaeffer 1925). Each dot represents one collection record, or a group of very close records.

abdominal sternum flat, not impressed.

Females. Pygidium broadly emarginate; dorsal and ventral valves of ovipositor of equal length, both setose around apical area; apical sternum broadly truncate.

Sexual dimorphism.— Specimens of *P. harrisii* sexually dimorphic in size, armature of metafemur, and shape of apical abdominal sternum.

Variation.— Labrum, clypeus and antennal calli vary from fulvous to colour of rest of head; pro- to metasternum and anterior margin of pronotum fulvous in some specimens, in some specimens entire venter dark.

Natural history.— Few host records accompanied pinned specimens, but some collected by C.A. Frost indicate that *P. harrisii* occurs on sedges (probably *Carex* and *Scirpus* species). *Carex* was reported by Schaeffer (1925) according to collections made by Frost. Dates of collection are typically May to July. Judging by these data, the species probably overwinters in the adult stage, as do the species of *Plateumaris* and many *Donacia*, especially of the subgenus *Donaciomima*.

Distribution.— (Fig. 20). The known distribution is only from northern New Jersey to southern New Hampshire and Maine, mostly in areas close to the Atlantic coast.

Specimens examined.— 111 males and females, plus holotype.

UNITED STATES. CONNECTICUT: Fairfield Co.: Wilton, vi.24.1930 (AMNH 1); New London Co./Windham Co.: Pachaug State Forest, vi.29.47 (PMY 1). MASSACHUSSETTS: Berkshire Co.: Sheffield, vi.21.30 (MCZ 1); Essex Co.: Plum Isl., vi.12.1932 (MCZ 2); Middlesex Co.: Arlington, June.27.1897 (MCZ 1); Boston, no date (MCZ 1); Framingham, v.29 (USNM 1), 21.v.11 (UAE 1, MCZ 2, UMMA 2), vii.8.1917 (CAS 1), v.19.12 (UMMA 2); Natick, vi.8.46 (NMDC 1), vii.10.1926 (CAS 2), vi.18.49 (CAS 1), vi.16.1949 (CAS 1, USNM 1, UCR 2), vi.20.1950, "on sedge (or grass) in wet meadow" (OSUC 2), vi.20.50, "coll'd on heads of a sedge" (MCZ 1), vi.20.50 (UMMA 2); Sherborn, 28.vi.24 (CNC 1), vi.20.1931 (NMDC 1), vi.28.24 (USNM 3, ISAC 2), vii.1927 (USNM 4), vii.5 (USNM 1), 29.vi.24 (UAE 1, MCZ 2), v.16.09 (MCZ 1, UANH 2), vi.27.15 (UAE 1), vii.4.1924 (MCZ 1), vi.16.1923 (MCZ 1), vii.2.17 (UMMA 1), vi.22.15 (UMMA 1); Sudbury, vi.15.19 (MCZ 1), July.10.1892 (MCZ 1); Tyngsboro, 7.4.97 (MCZ 3), no date (MCZ 3). Norfolk Co.: Dover, II.22 (USNM 1); Wellesley, June.11.'95 (MCZ 1); Suffolk Co.: Winchendon, vi.28 (CMP 1); Worchester Co.: Berlin, vi.23.1937 (MCZ 2, OKS 1), vi.25.1937 (MCZ 2), 6.18.40 (UMMA 2), vi.26.1937 (CAS 1), vii.1.1935 (USNM 2, FMNH 1), vi.13.15 (UMMA 1), vii.1.1937 (CAS 7); Southboro, vi.22.24 (MCZ 2); Locality not found: Mt. Tom, Jy.'73 (MCZ 2), no date (MCZ 2); Miscellaneous: "Mass." no dates (WEEM 1, CAS 1). MICHIGAN: Wayne Co.: Detroit (ex Schaeffer 1925). NEW HAMPSHIRE: Rockingham Co.: Dover, vii.7.1934 (UNH 1); Exeter, vi.23.24 (MCZ 2); Strafford Co.: Milton, June.26-7.'09 (MCZ 1). NEW JERSEY: Morris Co.: Boonton, vi.12.01 (USNM 1); Miscellaneous: "N.J." no dates (MCZ 4). NEW YORK: Delaware Co.: Hamden [ex Schaeffer 1925, but stated as a locality in Pennsylvania; Rockland Co.: Suffern, no date (CUCC 1); Tompkins Co.: McLean, no date (USNM 1); Miscellaneous: "N.Y." no date (USNM 1). VERMONT: Bennington Co.: East Dorset, vi.4.1957 (CVCC 1), June.11/15.1935 (CVCC 1, ISAC 1). MISCELLANEOUS SPECIMENS: "Drac." 6.18.91 (MCZ 4); no data (FMNH 2). Schaeffer (1925) also gives Michigan and Pennsylvania, but I have not seen these specimens. The locality given for Pennsylvania was not found in Pennsylvania, but in New York, and I suppose this was an error by Schaeffer.

TRIBE DONACIINI Kirby (1837)

Type genus.— *Donacia* Fabricius (1775).

Diagnosis.— Sutural margin of elytron more or less straight to apex, beads in contact only at extreme apex, apex truncate in most species; hypomeron with broad pubescent area in most species; mandible with apical teeth slightly to markedly divergent with occlusal edge long, serrulate; median lobe with basal angulation in most species, tegmen thin and slender in most species. Hosts various, including most aquatic vascular plants.

Sominella Jacobson, 1908

Sominella Jacobson (1908:622). Type species *Donacia macrocnemia* Fischer v. Waldheim (1824), by original designation.

Pseudodonacia Reitter (1920:27). Type species *Donacia kraatzi* Weise (1882), by monotypy. **NEW SYNONYMY**

Plateumaroides Khnzorian (1962:116). Type species *Plateumaroides fastuosa* Khnzorian (1962), (= *Donacia kraatzi* Weise, 1882), by monotypy. **NEW SYNONYMY**

Pseudodonacia: Iablokoff-Khnzorian (1968:262).

Pseudonacia Jolivet (1970:9). unjustified emendation

Sominaella Monrós and Bechyné (1956:1121). unjustified emendation

Etymology.— Jacobson named this genus after O. Somina.

Diagnosis.— No single synapomorphy, really suffices to define the genus. Members here assigned to *Sominella* share a general facies: most specimens with antennomere 3 as long as or longer than 4, most specimens with elytra sparsely and coarsely rugose, with interspaces finely punctulate. Other character states, of hypomeral pubescence, metatibial tooth, shape of elytral apex, and density and coarseness of pronotal punctation are various.

Included taxa (examined by me).—

S. kraatzi (Weise, 1882), **NEW COMBINATION**

Plateumaroides fastuosa Khnzorian,1962. Synonymy with *Donacia kraatzi* was suspected by Iablokoff-Khnzorian (1968:262), and was listed, probably correctly, as a synonym by Borowiec (1984).

S. longicornis (Jacoby, 1890:84, plate I). Jacoby indicated "a few specimens"; two specimens were found in MCZ, and are here designated. Lectotype ♂, MCZ #8452: "Chang Yang A.E. Pratt. Coll. June 1888 / 1st Jacoby Coll. / TYPE [pink] / Type 8453 [red] / D. longicornis Jac. Type [blue] / LECTOTYPE ♂ Donacia longicornis Jacoby design. I.S. Askevold '90 [red]. Paralectotype ♀: "Chang Yang A.E. Pratt. Coll. June 1888 / 1st Jacoby Coll. / TYPE [pink] / PARALECTOTYPE ♀ Donacia longicornis Jacoby [red]".

S. macrocnemia (Fischer von Waldheim, 1824).

Plateumaris excisipennis Jacobson, 1894.

S. reticulata (Gyllenhal, 1817) **NEW COMBINATION**

Donacia appendiculata Ahrens, 1810 (not *Donacia appendiculata* Panzer, 1794, now in *Macroplea*; *cf.* Silfverberg, 1977:93).

Transfer of the two species, *Donacia kraatzi* and *Donacia reticulata* to *Sominella* is a compromise in classification which is discussed above.

I do not present further details about the included species here. Adults are easily identified using publications and the key to genera presented here. *Sominella reticulata* is identified easily using Mohr (1966); *S. kraatzi* is a distinctive species, one of rather few donaciines occurring in the area of the Black Sea, and the description given by Weise (1882), comments by Reitter (1920:27-28) and description of *Plateumaroides fastuosa* Khnzorian (1962) are adequate for identification; the two remaining species, *S. longicornis* and *S. macrocnemia*, are separable using the characters presented by Gressitt and Kimoto (1961), and more detailed discussion of the genus by Goecke (1931).

Donaciella Reitter, 1920. NEW STATUS

Donaciella Reitter (1920:38). Type species *Donacia tomentosa* Ahrens (1810), designation by Monrós (1959:94)

Donacia (*Donaciella*) Reitter 1920:38.

Donacia (*Donaciella*): Chûjô (1951:48), Müller (1949-53:259), Mohr (1966:107), Gruev and Tomov (1984:62).

Etymology.— Diminutive form of *Donacia*.

Diagnosis.— The species transferred to this genus have in common a general, slender facies, and characters as listed and discussed in the character analysis and used in the key to genera. Principally, members of the genus have a slender mesosternal process between the mesocoxae, elongate body and elytra, slender femora with absent or reduced metafemoral tooth, most members have well-sclerotized, acute, glabrous valves of the ovipositor (sternum VIII and tergum VIII) and the species are associated with grasses as host plants, principally *Phragmites*.

Taxonomic history.— *Donaciella* has been recognized as a subgenus by most authors since Reitter (1920) proposed the name to include two species with integument pubescent. Monrós (1959:107) and Jolivet (1970:9) placed the name *Donaciella* in synonymy with *Donacia s.str.* Other authors, cited above, used *Donaciella* as a subgenus of *Donacia*. Schaeffer (1925:120) realized that *D. pubicollis*, a Nearctic species, is similar in certain respects to *D. clavipes*, which is not pubescent dorsally; curiously, he made no comparison with the two pubescent Palaearctic species.

Donaciella is here elevated to genus status, and expanded to include four species, on the basis of monophyly and structural and ecological specialization of these included members.

Included Palaearctic taxa (examined by me).—
Donaciella clavipes (Fabricius, 1793). **NEW COMBINATION**
Donaciella cinerea (Herbst, 1784). **NEW COMBINATION**
Donaciella tomentosa (Ahrens, 1810). **NEW COMBINATION**

More detailed treatment of the single Nearctic species is given here of which I present taxonomic details, a brief description and outline its geographical distribution. The Palaearctic species are separable using keys provided by the authors cited.

Donaciella pubicollis (Suffrian, 1872). NEW COMBINATION
Fig. 21

Donacia pubicollis Suffrian, 1872:21. (not Crotch 1873).

Donacia pubicollis Crotch 1873:21. (not Suffrian 1872). Synonymized with *D. pubicollis* Suffrian by Marx (1957:247).

Donacia pubicollis:Leng 1891:165, Blatchley 1910:1100, Schaeffer 1925:119, Wilcox 1954:372, Marx 1957:247.

Type specimen.— The types of neither Suffrian nor Crotch were examined. No specimens that could be identified as types of Crotch's species were found in the MCZ in 1990. For this species, however, there is no doubt of assignment. The Suffrian type should be preserved in Berlin or Halle (MLU).

Type locality.— "Illinois".

Etymology.-- The specific epithet is in obvious reference to the finely pubescent pronotal disc.

Taxonomic history.— Crotch (1873) did not cite Suffrian (1872) as authority of *D. pubicollis*, and evidently thought it to be undescribed, and aptly named it *D. pubicollis*. Indeed, this is not at all surprising, in view of the possibility that Crotch may not have been aware of Suffrian's (1872) publication. Most authors since Crotch have listed Crotch as the author of *D. pubicollis*, without considering the possibility of inadvertent homonomy (*i.e.* Leng 1891,Blatchley 1910, Jacoby and Clavareau 1904, Clavareau 1913, Schaeffer 1925, Wilcox 1954, Jolivet 1970). I believe this to be so because Crotch specifically stated "*D. pubicollis* sp. n." (1873:21); interestingly enough, Crotch described *D. texana* on the following page, and that species has been recognized by authors since, but these same authors (except Marx, 1957) failed to recognize that "sp. n." applied to *D. pubicollis* probably indicated that Crotch was unaware of Suffrian's species by the same name. Be that as it may, it is obvious that there is a case of homonymy, and that Suffrian's name has priority.

Schaeffer (1925) recognized that *D. pubicollis* is similar in body form to the Palaearctic species *D. clavipes*, but did not mention *D. tomentosa* or *D. cinerea*, which bear an even greater resemblance. Reitter (1920) placed both *D. tomentosa* and *D. cinerea* together, constituting a new subgenus of *Donacia*, but the taxon has not been recognized consistently since, even by European authors.

Diagnosis.— large, elongate, coppery in colour; pronotum entirely finely pubescent; appendages slender, metafemora toothless, not clavate; mesosternal process narrow between mesocoxae; elytral disc coarsely reticulately wrinkled, apex rounded, apical punctures coarse, entirely confused, epipleuron rounded from base to apex; females with ventral valve of ovipositor sclerotized and apex acute.

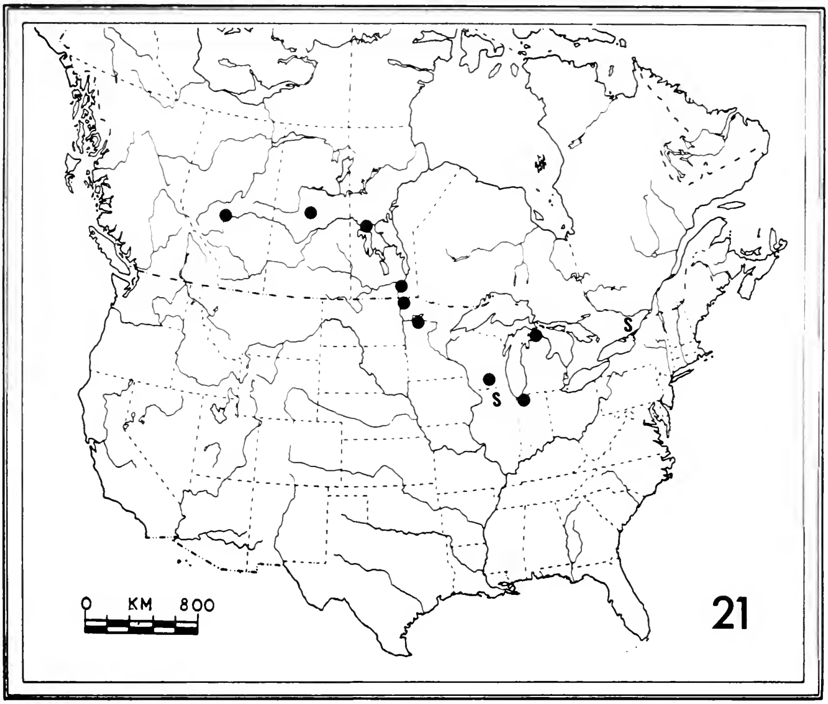


FIGURE 21. Known distribution in North America of *Donaciella pubicollis* (Suffrian), based on specimens examined, and on published records (Schaeffer 1925, Marx 1957). Each dot represents one collection record, or a group of very close records; S = state or provincial record.

Host.— *Phragmites; Nymphaea* reported, but most likely an adventitious record.

Distribution.— (Fig. 21). *Donaciella pubicollis* is known to occur narrowly from northern Indiana west to Alberta, exclusive of the prairies. The known distribution to date has included northernmost Indiana to Itasca State Park, Minnesota (Marx 1957, Schaeffer 1925).

Specimens examined.— 48 males and females.

CANADA: ALBERTA: Sturgeon River at Lac Sainte Anne, 53°90.43' N., 114°90.20' W., 1-3.vi.1982, "ex emergence traps", J.S. Richardson (ISAC 2). MANITOBA: Cedar Lake, July.5,12,26.1936, C.T. Parsons (MCZ 5), July.1936, Brues (MCZ 1); Winnipeg, June.24.1951, DH Groves (CNC 1). SASKATCHEWAN: Timber Bay, E. Montreal Lake, 1.vii.1985, C & A v.Nidek (ISAC 1). ONTARIO: "E. Ont.", Entomol. Branch (CNC 1, CAS 1, CMNH 1). UNITED STATES: ILLINOIS: Cook Co., Evanston, July 20 1900 (*ex* Marx 1957:249), county record, no date (MCZ 2); "Ill." (MCZ 11, CAS 1), "N. Ill." (CAS 1, ROM 1, UANH 1). INDIANA: Lake Co., Pine, May (*ex* Schaeffer 1925:120), Laporte Co., Laporte, no date (CMNH 2); Locality not found: Hessville, vii.1.12, AB Wolcott (FMNH 1). MICHIGAN: Cheboygan Co., Douglas Lake (*ex* Hoffman, 1940). MINNESOTA: Clearwater Co., Itasca State Park, 6.17.57, ex Phragmites (SCSU 2, ISAC 2), 6.14.1920, SA Graham (UMMZ 2, UASM 1, FMNH 5, CAS 1); Kittson Co., [county record], no date, OW Oestland (DEFW 1). WISCONSIN: Dane Co., (county record), April (*ex* Schaeffer 1925:120).

Donacia (*Donaciomima*) Medvedev, 1973. NEW STATUS

Plateumaris (*Donaciomima*) Medvedev (1973:876). Type species *Donacia clavareaui* Jacobson (1906), by original designation.

Etymology.— Diminutive form of *Donacia*.

Taxonomic history.— Medvedev (1973) apparently created this name as a subgenus of *Plateumaris* and based it on *Donacia clavreaui* Jacobson, though this is not clear from arrangement of taxa in that publication. Possibly he misidentified the type species as a species of *Plateumaris*, but I have examined the type (see below), and the species is similar to *D. simplex* Fabricius and *D. vulgaris* Zschach. Authors have not recognized *D. clavareaui*, and have recognized instead *D. fukiensis* Goecke (here synonymized). Borowiec (1984) synonymized the names *Donaciomima* and *Donacia s.str.*

Donaciomima is here removed from synonymy and accorded status as a subgenus of *Donacia*, because the included members cannot be assigned to either of the other subgenera of *Donacia*. To deny these subgenera status would be to deny that they include members that form a clearly defined, monophyletic group, and that are clearly defined ecologically (host plant use).

Diagnosis.— No single synapomorphy defines this subgenus. Most species share a general facies, but exceptions to all character states exist: most members have a coarsely punctate pronotum, the punctures confluent to form transverse rugae in many members, the spaces between the punctures alutaceous in many members, elytra of most members rugose, to rugulose, epipleuron of most members raised and sharply defined; most species are entirely metallic in colour, above and below, with metallic or dark appendages (but this varies greatly).

Included Palaearctic taxa (examined by me).—

D. aequidorsis Jacobson, 1894.

D. antiqua Kunze, 1818.

D. apricans Lacordaire, 1845.

D. aquatica Linnaeus, 1758.

D. aureocincta J. Sahlberg, 1921.

D. bactriana Weise, 1887.

D. bicolor Zschach, 1788.

D. bicoloricornis Chen, 1941.

D. brevicornis Ahrens, 1810.

D. brevitarsis Thomson, 1884.

D. clavareaui Jacobson (1906:311). Holotype ♂ MNHN: "Kjachta Siberie par Götzelmann [Clavareau's handwriting] / Donacia Clavareaui *TYPE* Jacob. [Clavareau's handwriting] / TYPE [red, added by N. Berti] / Museum Paris Coll. H. Clavareau 1932 / Donacia clavareaui Jac. ♂ typ. G. Jacobson det."

> *D. fukiensis* Goecke (1944:9). No type specimens of Goecke's species were examined, but *D. fukiensis* is a well known species in Japan, which are no different from specimens I have examined from China, and these are no different from the type of *D. clavareaui* Jacobson. **NEW SYNONMY**

D. delagrangei Pic (1896:35). Holotype ♀, MNHN: "Asie-Min. Anatolie CD. 1888 / type [written on underside of pink disc] / Donacia Delagrangei Pic [handwritten] / communique la returner [handwritten] / Goecke vidit. / HOLOTYPE ♀ [red] / vidit 1984 I.S. Askevold".

D. dentata Hoppe, 1795.

D. fennica Paykull (1800:70)

> *D. ochroleuca* Weise (1912:76). Holotype ♂, ZMHB: "Sibir or. Ertl / ♂ / TYPUS [orange] / Zool. Mus. Berlin / ochroleuca m." I added the label

"HOLOTYPE ♂ Donacia ochroleuca Weise [red]} and "Donacia fennica Paykull ♂ det. I.S. Askevold 1989". **NEW SYNONYMY**

D. flavidula Reitter (1913:124). This name has been placed in synonymy of *D. ochroleuca* by authors, and is therefore transferred. **NEW SYNONYMY**

D. flemola Goecke, 1944.

D. frontalis Jacoby (1893:261). Syntype BMNH. No further data recorded.

D. gracilicornis Jacobson, 1899.

D. gracilipes Jacoby (1885:191). Lectotype ♀ MCZ #8485, by present designation: "Japan Lewis / 1st Jacoby Coll. / Type 8485 [red] / LECTOTYPE ♀ Donacia gracilipes Jacoby design. IS Askevold 1990 [red]", and paralectotype ♀ "Japan Lewis / 1st Jacoby Coll. / PARALECTOTYPE ♀ Donacia gracilipes [red]". A syntype specimen is also labelled as type, BMNH (further data not recorded).

D. hirtihumeralis Komiya and Kobuta, 1987:41.

D. hiurai Kimoto, 1983:11.

D. impressa Paykull, 1799.

D. jacobsoni Semenov and Reichardt, 1927.

D. jacobsoniana Shavrov, 1946.

D. japana Chûjô and Goecke, 1956.

D. katsurai Kimoto, 1981:24.

D. kweilina Chen, 1941. [This reference missed by Jolivet, 1970]. Two paratypes examined (ISAC).

D. malinowskyi Ahrens, 1810.

D. marginata Hoppe, 1795.

D. mistshenkoi Jacobson, 1910.

D. nitidior (Nakane, 1963).

D. obscura Gyllenhal, 1813.

D. polita Kunze, 1818.

D. semenowi Jacobson (1907:5). Holotype ♂, MNHN: "Zaïdam (Thibet) Kozlow 1895 G. Jacobson / Donacia Semenovi *TYPE* Jacob. / Donacia ♂ semenovi Jac. typ G. Jacobson det. / TYPE [pink] / Museum Paris Coll. H. Clavareau 1932 / vidit 1984 I.S. Askevold".

D. semicuprea Panzer, 1796.

D. simplex Fabricius, 1775.

D. sparganii Ahrens, 1810.

D. springeri Müller, 1916.

D. thalassina Germar, 1811.

D. versicolorea Brahm, 1790.

D. vulgaris Zschach, 1788.

Taxa unknown to me.— *D. breviuscula* Jacobson, 1899, *D. fedtschenkoae* Jacobson, 1899, *D. freyi* Goecke, 1940, *D. galaica* Baguena, 1959, *D. humilis* Weise, 1912, *D. intermedia* Jacobson, 1899, *D. kirgizkaisaka* Jacobson, 1910, *D. knipowitschi* Jacobson, 1927, *D. koenigi* Jacobson, 1899, *D. mannerheimi* Lacordaire, 1845, *D. mediohirsuta* Chen, 1941, and *D. tschitscherini* Semenow, 1895 (= 12 taxa).

Donacia (*Donacia*) Fabricius, 1775

Donacia (*Donacia*) Fabricius (1775:195). Type species *Donacia crassipes* Fabricius (1775), designation by Curtis (1834), not Chapuis (1874).

Eodonacia Haupt (1956:54). Type species *Eodonacia goeckei* Haupt (1956), by original designation. Askevold (1990) presented reasons for synonymization of this name. **NEW SYNONYMY**

Etymology.— Based on the Greek *Donax*, for reed, reeds or other aquatic plants being host plants for the majority of species.

Taxonomic history and synonymies.— *Donacia* is the oldest genus-group name in the subfamily, which is based on this name. Most members of the subfamily were described in *Donacia*, which has gradually become restricted in composition. It is unfortunate that Curtis (1834) selected *Donacia crassipes* as type species, for the group of species to which *D. crassipes* belongs is a much smaller group of species in the genus. With resurrection of *D.* (*Donaciomima*) to subgenus status, the subgenus *Donacia* (*Donacia*) becomes restricted to a small group of 10 Nearctic species and five Old World species (one undescribed).

Diagnosis.— Species of this subgenus are recognized by their large and broad size (most members), with mesosternum broad, pygidium of females elongate and pointed (rounded apically in some species, but shape at least elongate), elytra partly to entirely rufous (most species) and tending toward diminished rugosity (most species), occiput of head with at least a pair of small rufous spots (most species), varying to entirely rufous, pronotum of most species rufous, underside with extremely dense pubescence, the punctation not visible, mandibles with prominent lateral angulation and widely splayed apical teeth (Figs. 1, 10), and median lobe with underside flat or sulcate.

Included Old World taxa (examined by me).—

D. crassipes Fabricius, 1775.

Donacia sp. nov., from Botswana.

D. ozensis Nakane, 1954.

D. recticollis Jacoby (1893:261). Syntypes (# not recorded), one labelled as holotype (sex not recorded), BMNH, Berhampur, India (and three possible syntypes also labelled simply "Berhampur", MCZ).

D. indica Clark (1866:1, not Melsheimer 1847). Holotype ♀, BMNH. The specimen is a composite. Elytra, pterothorax and abdomen undoubtedly represent the authentic type, but the prothorax and head belong to a specimen of *Sominella reticulata*. Nonetheless, Clark described the species from this composite specimen and drew particular attention to the curious green nature of the head and thorax, strongly contrasting with the testaceous elytra [as did Jacoby (1908:11)]. The body and elytra of the specimen agree fully with the type of *D. recticollis*, which is a large species with flavous elytra. **NEW SYNONYMY**

D. clarki Monrós (1959:115) (replacement name for *D. indica* Clark), **NEW SYNONYMY**

Taxon unknown to me.— *D. ussuriensis* Medvedev.

Donacia (*Cyphogaster*) Goecke, 1934.

Donacia (*Cyphogaster*) Goecke (1934:219). Type species *Donacia provostii* Fairmaire (1885), designation by Chen (1941).

Hemidonacia Haupt (1956:60). Type species *Hemidonacia insolita* Haupt (1956) by monotypy. Askevold (1990) presented reasons for synonymization of this name. **NEW SYNONYMY**

Etymology.— Not stated by Goecke; it appears to be based on the Greek *kyphos*, meaning bent or humb-backed, and *gaster*, or abdomen, but I do not know what this should be in reference to.

Taxonomic history.— The subgenus was erected by Goecke (1934) for most of the species listed below, and has been recognized in catalogues [Monrós (1959), Jolivet (1970), Borowiec (1984)] and faunistic treatments [Gressitt and Kimoto (1961), Chûjô (1951), Kimoto (1983)] as a subgenus since.

Diagnosis.— Members of this subgenus are recognized by the same characters of *Donacia s.str.*, but most members have elytra more uniformly dark or metallic. The only character that defines the subgenus is a pair of small, glabrous, raised tubercles about midlength, medially, on the basal abdominal sternum of male specimens (though *D.* (*Donaciomima*) *dentata* has a similar structure).

Included taxa (examined by me).—

D. australasiae Blackburn (1892:235). Holotype ♂, BMNH. Additional data not recorded.

D. delesserti Guérin-Méneville (1844:258). Type, BMNH. Additional data not recorded. Taxonomic status not evaluated, but I cannot determine consistent differences from *D. javana*.

D. inopinata Goecke, 1944.

D. javana Wiedemann, 1821.

D. lenzi Schönfeld (1888:33). Holotype ♂, SMF (Frankfurt): "Hiogo Jap. L. [white with black trim] / coll. v. Schönfeldt [white] / TYPUS [red with black trim] / Lenzi Schönf [white with black trim] / vidit 1984 I.S. Askevold".

D. papuana Gressitt (1971:607). Paratype ♀, BPBM. Additional data not recorded.

D. provostii Fairmaire (1885:LXIV). Holotype ♀, MNHN. Additional data not recorded.

D. transversicollis Fairmaire (1887:135) (new subgenus combination). Holotype ♀, MNHN. Fairmaire's type keys to *D. tuberfrons* Goecke, in the key to species of *D.* (*Cyphogaster*) presented by Goecke (1934:217), and agrees in detail with paratypes of *D. tuberfrons* examined.

D. tuberfrons Goecke (1934:221). Four paratypes, MNHN, examined. Additional data not recorded. **NEW SYNONYMY**

Taxon unknown to me.— *D. yuasi* Nakane, 1963.

Donaciasta Fairmaire, 1901

Donaciasta Fairmaire (1901b:233) (replacement name). Type species *Donacilla perrieri* Fairmaire (1901a), by ICZN (1985) Art. 67h.

Donacilla Fairmaire (1901a:127) (not Lamarck, 1818). Type species *Donacilla perrieri* Fairmaire (1901a), by monotypy.

Donaciocrioceris Pic (1936:10). Type species *Donaciocrioceris dentatus* Pic (1936), by monotypy. **NEW SYNONYMY**

Prodonacia Chen (1966:144). Type species *Prodonacia shishona* Chen (1966), by monotypy. **NEW SYNONYMY**

Etymology.— Unknown, probably merely a diminutive of *Donacia*, based on the Latin *donax*, a reed.

Taxonomic history.— *Donaciasta* is not well known taxonomically despite recent treatments, by Monrós (1958) and Jolivet (1972), both of whom described additional species but did not examine types of other described African and Madagascan donaciines. On examination of types of described species I find that African species hitherto placed in *Donacia* belong in *Donaciasta*. Taxonomic treatment is in progress (Askevold in prep. d); I list the revised synonymies below because of reassignment of species to this genus.

Borowiec (1984) synonymized the names *Prodonacia shishona* Chen and *Donacia vietnamensis* Gressitt and Kimoto (both species described from ♂♂), and the names *Prodonacia* Chen and *Donacia* Fabricius. The description of *Donacia assama* Goecke was based on a single female (holotype ♀, BMNH). On the basis of non-sexually dimorphic characters, the types of *Prodonacia shishona* and *Donacia vietnamensis* are conspecific with the type of *Donacia assama. Donacia assama* is the senior and valid name of the species. Specimens of this species possess the majority of characters that are typical of *Donaciasta*, and I transfer this species to *Donaciasta*.

Elytral structure of *Donaciocrioceris dentatus* Pic was interpreted incorrectly by Monrós (1959), who claimed that its elytral apex is like that of *Plateumaris* (*i.e.* like Fig. 9, Askevold, in prep. a). This is not so; the elytral apex is typical of Donaciini. This species is odd in other respects, however: in head and body shape it is similar to *Plateumaris*; in tarsal claw structure it is similar to certain criocerines that have connate claws (hence the name Pic created). It is highly autapomorphic and therefore it is not surprising that a genus was erected for it; however, it possesses the synapomorphies of *Donaciasta* as well, and is phylogenetically in an intermediate position in the genus (Askevold, in prep. b) (reflected by position in list of taxa, below).

Diagnosis.— Specimens of *Donaciasta* are recognized by the coarsely punctured pronotal disc (except *D. dentata*), presence of proepimeral pubescence, lack of tactile seta of anterolateral tubercles; mandible articulation remote from antennal bases (not especially in *D. assama*), the clypeus therefore somewhat elongate; colour of most species not metallic like most other Donaciinae, dorsum rufous, testaceous or piceous, and with at most a metallic luster; elytra of most members with supernumerary punctures in some intervals, and interval 8 at least a little costate (especially ♀♀); males with median lobe lacking subbasal angulation, tegmen slender, of uniform width and thickness from base to apex; legs and antennae at most partially infuscate.

Donaciasta is the only donaciine genus that occurs in Madagascar and tropical Africa, with the exception of a single, undescribed species of *Donacia* (*Donacia*) known from Botswana. Species are associated with the plants *Potamogeton*, *Trapa natans* L. and possibly *Nymphaea*, as indicated by the few available host records.

Included taxa.—[revised synonymies and details about type specimens examined are given by Askevold (prep. d), and are not repeated here].

D. assama (Goecke) (1936:224), **NEW COMBINATION**
  Prodonacia shishona Chen (1966:144, 146). **NEW SYNONYMY**
  Donacia vietnamensis Kimoto and Gressitt (1979:202). Placed in synonymy with *Prodonacia shishona* by Borowiec (1984). **NEW SYNONYMY**
D. dentata (Pic, 1936:10), **NEW COMBINATION**
D. perrieri (Fairmaire, 1901a).
D. luridiventris (Lacordaire, 1845).
D. abortiva (Fairmaire, 1899:27), **NEW COMBINATION**
  Donaciasta minuta Pic, 1936.
  Donacia madecassa Pic, 1944.
  Donacia notaticollis Pic, 1944.
D. goeckei Monrós, 1958.
  Donaciasta quioca Monrós. 1958.
  Donaciasta capensis Monrós, 1958.

Donaciasta garambana Jolivet, 1972.
Donaciasta monrosi Jolivet, 1972.

Taxon of uncertain placement within Donaciini.—
Donacia microcephala Daniel and Daniel (1904:89).

Donacia testaceipes Pic (1908:52). Holotype ♂, MNHN: "Adana [handwritten] / Type [handwritten] / Museum Paris Coll. M. Pic / HOLOTYPE [red] / testaceipes Pic [handwritten] / Lesne vidit (1926) / vidit 1984 I.S. Askevold".

TRIBE HAEMONIINI CHEN (1941)

Type genus.— *Haemonia* Dejean (1821).

Diagnosis.— Dorsum testaceous; legs almost entirely testaceous, metafemur edentate, slender, tarsi with apical tarsomere elongate, tarsomeres with reduced ventral pubescence; elytron apically with spine at outer angle (most species); hypomeron with pubescent area above coxa (lost in *Macroplea*, character state in *N. voronovae* unknown); mandible with apical teeth divergent, in form of serrate occlusal edge; median lobe with basal angulation, tegmen slender. Hosts Zosteraceae and Haloragaceae.

Macroplea Samouelle, 1819

Macroplea Samouelle (1819:211). Type species *Donacia zosterae* Fabricius (1801), designation by Curtis (1830) [Monrós (1959:102) stated that Barber and Bridwell (1940) designated the type species, but Curtis (1830) had already done so, as Barber and Bridwell (1940) had stated].

Apelma Billberg (1820:53). Type species *Donacia zosterae* Fabricius (1801), designation by Barber and Bridwell (1940).

Haemonia Dejean (1821:114). Type species *Donacia zosterae* Fabricius (1801), designation by Thomson (1859:154) [Monrós (1959:102) stated that Barber and Bridwell (1940) designated the type species, but Thomson (1859) had already done so].

Included taxa (examined by me).—
M. appendiculata (Panzer, 1794)
Donacia zosterae Fabricius, 1801
M. japana (Jacoby, 1885)
M. mutica (Fabricius, 1792)
M. pubipennis (Reuter, 1875)
Haemonia piligera Weise (1889:576). **NEW SYNONYMY**
Haemonia incostata Pic (1907:100). Holotype ♂, MNHN: "Ost-Turkestan, Aksu 1067 m, 5.1903 Coll. Hauser / type [handwritten] / Haemonia incostata Pic [handwritten]". This synonymy was suggested previously by Hellén (1937), but was not adopted by later authors. I have not found any differences among specimens of *M. piligera* from Turkestan (also collected by Hauser) and *M. pubipennis* from Finland, including genitalic structure. **NEW SYNONYMY**

Neohaemonia Székessy, 1941

Neohaemonia Székessy (1941:148). Type species *Haemonia nigricornis* Kirby (1837), by original designation.

Five species are known in this genus, which was treated in full by Askevold (1988); members are listed by Askevold (in prep. c).

Incertae sedis in Haemoniini.— Neohaemonia voronovae Medvedev (1977).

Nomen incertae sedis in Donaciinae.— Arundinarius Voet (1806:31). This name has been placed in synonymy with *Donacia* by previous authors. Most likely, the name would have included species now assigned to *Donaciomima*, most of the species of which are reed plant-associated (the origin of the name). Silfverberg (pers. comm. 27.6.1985) assured me that this work of Voet (1806) should be considered rejected because he did not adhere to the principle of binominality (using names inconsistently as binomials and trinomials) (ICZN 1985, Art. 11c (iii).

Key to Genera and Subgenera of New World Donaciinae

1 Prothorax of most specimens with broad, finely pubescent area above procoxa, disc of some specimens conspicuously pubescent also; sutural interval of elytron with inner and outer beads convergent only at apex, in form of a short apical carina in some specimens, lower sutural margin narrow, not explanate; eyes of most specimens set off from vertex by distinct sulcus, vertex of many specimens with two distinct calli; median lobe sub-basally with distinct angulation, tegmen thin and slender, and of uniform width 3

1' Prothorax without conspicuous broad pubescent area above procoxae (but *cf. Plateumaris aurifer*); sutural interval of elytron with sutural bead sinuate, and convergent with inner bead some distance from apex (sutural bead sinuate), exposing the lower, internal, explanate margin of elytron; vertex of head more or less flat in most specimens; median lobe sub-basally without angulation, tegmen robust, tapering apically..... 2

2 (1') Apex of elytron broadly rounded; antennomere 3 shorter than 4; metatibia and metafemur not denticulate on underside, metafemur untoothed or with only one tooth; underside metallic or not, but not largely rufous, except for all or apex of abdominal sterna, reddish; females with strongly sclerotized, acute ovipositor, in some specimens distinctly serrate, dorsal valve shorter than ventral valve.................. ....*Plateumaris* Thomson, p. 634

2' Apex of elytron truncate or emarginate; antennomere 3 as long as or longer than 4; metatibia and metafemur (especially males) distinctly denticulate on underside, metafemur of males with both a subapical ventral and a ventromesal tooth, females with only subapical ventral tooth; underside largely rufous; ovipositor of females not strongly sclerotized or acute, dorsal and ventral valves of equal length.................. ....*Poecilocera* Schaeffer, p. 634

3 (1) Outer apical angle of elytron with distinct spine; metafemur slender and untoothed, apical tarsomere elongate, about as long as preceding tarsomeres combined; legs, thorax, and elytron pale brown, most of underside, tarsi, scutellum, antenna, strial punctures, and head (except vertex of many specimens), black..............*Neohaemonia* Székessy, p. 648

3' Outer apical angle of elytron not toothed; metafemur of most specimens distinctly clavate, most specimens with 1 or 2 subapical ventral teeth, apical tarsomere much shorter than preceding tarsomeres combined; colour not as above, most specimens dorsally metallic, not entirely pale brown 4

4 (3') Pronotal disc distinctly and finely pubescent AND legs entirely rufous, at most with indistinct infuscation; metafemur without distinct subapical tooth below; epipleuron of elytron rounded, not angulate; elytral apex broadly rounded, apical punctation close, entirely confused; female with acute, sclerotized ovipositor; host *Phragmites* ....*Donaciella* Reitter, p. 640

4' Pronotal disc glabrous, if pubescent then elytral apex truncate or elytra pubescent also; legs rufous to entirely metallic, metafemur of most specimens with one or more subapical teeth; epipleuron of elytron rounded or distinctly angulate; elytral apex truncated, with obtuse to acute outer angle, punctures of striae finer, more widely spaced, and more or less regular in arrangement apically; hosts other than *Phragmites* 5

5 (4') Occiput of most specimens with two reddish spots, in many specimens spots expanded over entire occiput; legs (except *D. proxima*) with no more than dorsum of metafemur darkened; pronotal disc without coarse punctures, but many specimens with very fine transverse to irregular rugae, OR surface granulate, alutaceous, OR smooth and shiny between punctures; mesosternal process, especially in females, broad between the mesocoxae, at least half as broad as diameter of mesocoxal cavities; ventral punctation obscured by dense pubescence; pygidium of most females more or less elongately triangular, apically acute or narrowly rounded; host Nymphaeaceae.......*Donacia* (*Donacia*) Fabricius, p. 644

5' Head more or less unicolourous, not reddish in most specimens; legs entirely dark to entirely red, but not with only dorsum of metafemur dark; pronotal disc with coarse punctures, punctures typically contiguous to confluent laterally to form coarse to moderate rugae (except 2 pubescent species and *D. caerulea*-Group); mesosternal process no more than half diameter of mesocoxal cavities; ventral coarse punctation visible, at most obscured by pubescence (except *D. cuprea*); pygidium of females broadly rounded or emarginate, not elongate; hosts mostly Cyperaceae, Sparganiaceae, Zosteraceae, and Nymphaeaceae ....*Donacia* (*Donaciomima*) Medvedev, p. 642

Key to Tribes, Genera and Subgenera of Old World Donaciinae

1 Elytron with outer apical angle prolonged as spine; if only with obtuse or acute angulation, then elytra and pronotum with conspicuous sparse, long setae; apical tarsomere elongate, as long as basal 3 together, and tarsus with markedly reduced pubescence; elytra, pronotum and legs testaceous or brownish, with black strial punctures (most taxa); hosts Zosteraceae and Haloragaceae ....

HAEMONIINI 2

1' Elytron with outer apical angle not markedly produced, but truncate, rounded, or emarginate, pubescent or not; apical tarsomere shorter than remaining articles together, tarsi typically with dense and plush pubescence below; elytra and pronotum typically metallic, but colour various; host plants various 3

2 (1) Pronotal disc without individually distinct punctures; elytron with strial punctures black; geographical range from Europe to Japan............................*Macroplea* Samouelle, p. 648

2' Pronotal disc with individually distinct punctures; elytron with strial punctures not black; known only from Lake Ugii-Nur, Ara-Khankai Aimak, Mongolia; generic assignment not established.................*Neohaemonia voronovae* Medvedev

3 (1') Elytron with inner bead of sutural interval sinuate distinctly before apex, joined with outer bead as single bead, explanate sutural margin below exposed; pronotal hypomeron without broad pubescent area above procoxa; median lobe without subasal angulation, and tegmen robust and tapered; ovipositor of females acute and markedly sclerotized, serrate in most species, and with acute apex; (*Plateumaris* Thomson, single Palaearctic genus) .............PLATEUMARINI, p. 633

3' Elytron with beads of sutural interval in contact near apex only, or obscured, interval more or less uniformly wide to near apex, and explanate margin not broadly exposed; pronotal hypomeron typically broadly pubescent above procoxa; median lobe with or without prominent subbasal angulation (cannot be seen if uncleared!), tegmen typically slender, more or less parallel-sided, not thick; ovipositor of most female specimens not acute and markedly sclerotized..... ......DONACIINI..4

4 (3') Specimens from Madagascar or Africa south of 15° North latitude 5

4' Specimens not from tropical Africa or Madagascar..................6

5 (4) Pronotum with anterolateral tactile seta absent; elytron with interval 8 slightly to markedly costate, some intervals with unordered punctation; frons and vertex with calli distinct and largely glabrous (Fig. 3,4); metatibia not markedly carinate or denticulate below; punctures of pronotal disc, if individally distinct, not confluent to form irregular rugae. Geographical distribution: Senegal to Uganda, south to South Africa, and Madagascar .... *Donaciasta* Fairmaire, p. 646

5' Pronotum with anterolateral tactile seta prominent, of normal length; elytron with interval 8 not costate, intervals without punctation; frons and vertex uniformly pubescent, without distinct calli; metatibia markedly explanate and denticulate below; punctures of pronotal disc not individually distinct, the disc irregularly rugose. Geographical distribution: Botswana ....*Donacia* (*Donacia*) sp., undescribed

6 (4') Pronotum and elytra uniformly pubescent, like head and underside; mesosternal process slender between mesocoxa;

elytral epipleuron flat, or rounded and slightly raised, at most angulate at extreme base by humerus 7

6' Pronotum and elytra pubescent or not; mesosternal process typically broader, as much as half or more width of mesocoxae (especially ♀♀); epipleuron prominently angulate in most taxa from below humerus to near apex 8

7 (6) Body dorsally and ventrally bronzish or bright pale green; mandible distinctly and broadly bidentate apically; metafemur rather slender, hardly clavate, in most specimens edentate; female ovipositor of most species with acute, sclerotized ventral valve; hosts typically Gramineae. Geographical distribution: more northern Palaearctic region . ...*Donaciella* Reitter (part), p. 640

7' Entire body dorsally and ventrally testaceous, pronotal disc at most broadly darkened in middle; mandibles unidentate, therefore slender and sickle shaped; metafemur toothed; female ovipositor blunt, not sclerotized; host plant unknown. Geographical distribution: Middle East. Generic assignment undetermined... ....*Donacia microcephala* Daniel and Daniel

8 (6') Labrum with apex broadly and deeply emarginate (Fig. 7)..........9

8' Labrum with apex broadly rounded (Fig. 1)..........................11

9 (8) Pronotal disc of most specimens with fine, short pubescence; metafemur without subapical ventral tooth; pronotum wider across posterior margin than across anterior margin; elytral apex narrow and rounded. Geographical distribution: southwestern Caucasus............. *Sominella kraatzi* (Weise)

9' Pronotal disc without distinct setae; metafemur of most specimens with subapical tooth, legs largely rufous; pronotum of most specimens wider across anterior margin than across posterior margin; elytral apex various, most specimens with apex broadly truncate. Geographical distribution: almost Transpalaearctic, including Caucasus 10

10 (9') Elytron with epipleuron flat or slightly rounded from behind humerus to near apex; dorsum pale metallic green or bronzish ....*Donaciella clavipes* (Fabricius)

10' Elytron with epipleuron angulate from behind humerus to near apex; dorsum with colour various, testaceous or brown, very dark green, or pale green (or with elytron laterally reddish).... ....*Donacia* (*Donaciomima*) Medvedev (part), p. 642

11 (8') Pronotal disc more or less uniformly coarsely punctured (most taxa), and intervening spaces alutaceous or not; elytral disc typically coarsely rugose, and generally metallic in colour; female pygidium rounded or emarginate apically, similar to that of male in length; mandibular teeth not especially prominently divergent apically, and outer margin typically more or less uniformly arcuate; head of uniform colour, metallic to piceous; epipleuron typically raised and angulate along upper edge adjacent to outermost stria; hosts Cyperaceae, Zosteraceae, Nymphaeaceae and Trapaceae 12

11' Pronotal disc at most punctulate, shiny or alutaceous and smooth, or finely rugulose; elytral disc largely smooth and shiny, and punctulate, with few coarse rugae; elytra metallic, testaceous or brown in colour, then with or without metallic lustre; female pygidium prolonged and more or less triangular, acute or narrowly rounded at apex, very different from males; mandibular teeth very prominently explanate and divergent, lower tooth directed ventrally and inwards, in form of a broad, cutting edge; head typically with pair of small red spots behind eyes on occiput, or head partially to completely red; epipleuron typically rounded or flat, at most angulate near humerus; hosts Nymphaeaceae 14

12 (11) Pronotum with anterolateral tactile seta prominent, of normal length; dorsum entirely metallic; underside metallic, legs and antenna largely metallic, some specimens with ventral half of femora rufous; antennae densely and uniformly pubescent. Geographical distribution: Europe to Japan, some in China. Hosts various. 13

12' Pronotum with anterolateral tactile seta absent; dorsum except head brown or testaceous, at most somewhat piceous with pale metallic tinge; underside, antenna and legs largely rufous; antenna sparsely pubescent basally. Known only from three localities in southeast Asia. Host plant unknown, probably Trapaceae, Zosteraceae, or Nymphaeaceae .... *Donaciasta assama* (Goecke)

13 (12) Pronotal hypomeron without dense patch of pubescence above coxa (sparse setae in *S. macrocnemia* and *S. reticulata*), hypomeron very coarsely rugose longitudinally; elytral apex various, narrow and rounded, toothed at inner apical angle, some specimens also at outer angles, or narrowly truncate; specimens of two Oriental species with metatibia explanate to prominently toothed ventrally (Figs. 11, 12); elytral disc typically shiny, punctulate or not, but most specimens not coarsely and densely rugose; vertex of head flat or depressed, without pair of calli; antennomere 3 typically long, in most specimens with article 3 as long as or longer than 4 .... *Sominella* Jacobson (part), p. 639

13' Pronotal hypomeron typically with pubescent patch above coxa in most specimens, and hypomeron generally not so coarsely rugose; elytral apex generally broadly truncate, and disc generally densely rugose, shiny in some; metatibia at most denticulate along ventral margin; most specimens with calli of vertex convex to prominently raised; antennomere 3 not as long as 4 .... *Donacia* (*Donaciomima*) Medvedev (part), p. 642

14 (11') Male specimens without pair of small shiny tubercles on abdomen. Geographical distribution: Europe to Japan, and northern India...... *Donacia* (*Donacia*) Fabricius (part), p. 644

14' Male specimens with pair of small glabrous tubercles at middle of basal abdominal sternum. Geographical distribution: Japan to S.E. Asia, including Nepal, India and Sri Lanka, Java, Singapore, Mindanao, New Guinea, and northern Australia..... *Donacia* (*Cyphogaster*) Goecke, p. 645

ACKNOWLEDGEMENTS

Research leading to this publication was supported by an NSERC PGS Scholarship to me, and NSERC grant #AO4128 held by R.E. Roughley; I was also fortunate to be granted some financial assistance, made available by the former Dean of Agriculture, University of Manitoba, R.C. McGinnis, to support me during thesis writing.

I thank the members of my Ph.D. committee, R.E. Roughley, T.D. Galloway and R.J. Elias of the University of Manitoba, and G.E. Ball of the University of Alberta, for their efforts in reviewing the thesis from which this publication is extracted. Their valuable comments contributed greatly to its improvement. I also thank the anonymous reviewers for their useful comments.

I owe many individuals thanks for their repeated and invaluable assistance with loans of specimens; the many curators and collectors were acknowledged specifically previously (Askevold, in prep. a), and I thank them all again but do not list them all. However, I must acknowledge specifically N. Berti (Paris), R.D. Pope and S.L. Shute (London) and R. zur Strassen (Frankfurt) for their hospitality during museum visits in 1984 to study type specimens. I must also acknowledge certain individuals who exchanged specimens with me, whereby I was able to obtain many Old World specimens for study: C. Shaoguang (Beijing), Y. Komiya (Tokyo), H. Takizawa (Kanagawa), K. Harusawa (Osaka) L. Borowiec (Wroclaw), P. deWailly (Paris), M. Daccordi (Verona), and M. Döberl (Abensberg). Their contributions were essential to the material basis for this and other studies on donacines.

REFERENCES CITED

Ahrens, A. 1810. Beiträge zu einer Monographie der Rohrkäfer. Neue Schriften der naturforschenden Gesellschaft zu Halle 1:9-48.

Ashlock, P.D. 1974. The uses of cladistics. Annual Review of Ecology and Systematics 5:81-99.

Askevold, I.S. 1987a. The identity of *Donacia cuprea* Kirby, 1837, and *Donacia quadricollis* Say, 1827, with a taxonomic revision of members of the *Donacia subtilis* Kunze - group (Coleoptera: Chrysomelidae: Donaciinae). The Canadian Entomologist 119:629-645.

Askevold, I.S. 1987b. The identity of *Donacia caerulea* Olivier, 1795 (Coleoptera: Chrysomelidae: Donaciinae). The Coleopterists Bulletin 41:345-349.

Askevold, I.S. 1988. The genus *Neohaemonia* Székessy in North America (Coleoptera: Chrysomelidae: Donaciinae): systematics, reconstructed phylogeny and geographic history. Transactions of the American Entomological Society 113:360-430.

Askevold, I.S. 1990. Tertiary fossil Donaciinae of North America: implications for classification and evolution of the Donaciinae (Coleoptera: Chrysomelidae). Canadian Journal of Zoology, in press.

Askevold, I.S. in preparation a. Classification, reconstructed phylogeny and geographic history of the New World members of *Plateumaris* Thomson, 1859 (Coleoptera: Chrysomelidae). Submitted to the Canadian Entomologist.

Askevold, I.S. in preparation b. Host plant relationships of donaciine leaf beetles (Coleoptera: Chrysomelidae): coevolution by descent or association by colonization?

Askevold, I.S. in preparation c. Type specimens of Nearctic Donaciinae (Coleoptera: Chrysomelidae).

Askevold, I.S. in preparation d. A restudy of the austral genus *Donaciasta* Fairmaire (Coleoptera: Chrysomelidae: Donaciinae): systematics, reconstructed phylogeny, and geographic history.

Ball, G.E. 1977. Editorial - comments about a few words in the biological sciences. *Quaestiones Entomologicae* 13:1-4.

Barber, H.S. and J.C. Bridwell 1940. Dejean catalogue names (Coleoptera). Bulletin of the Brooklyn Entomological Society 35:1-12.

Bertrand, H. 1965. Contribution à l'étude des premiers états des Coléoptères aquatiques de la région éthiopienne (7e. note). Bulletin de l'Institut français d'Afrique noire (Ser. A, No.4) 27:1336-1393.

Billberg, G.J. 1820. Enumeratio Insectorum in Museo Billberg. Stockholm, Gadel 4:1-138.

Blackburn, T. 1892. Notes on Australian Coleoptera, with description of new species. Transactions of the Royal Society of South Australia 15:207-261. [not seen, cited in Jolviet 1970, incorrectly cited in Monrós 1959].

Blatchley, W.S. 1910. An illustrated descriptive catalogue of the Coleoptera or Beetles (exclusive of the Rhynchophora) known to occur in Indiana. Nature Publ. Co., Indianapolis. 1386 pp.

Bock, W.J. 1974. Philosophical foundations of classical evolutionary classification. Systematic Zoology 22:375-392.

Borowiec, L. 1984. Zoogeographical study on Donaciinae of the world (Coleoptera, Chrysomelidae). Polskie Pismo Entomologiczne 53:433-518.

Borowiec, L. 1987. The genera of seed-beetles (Coleoptera, Bruchidae). Polskie Pismo Entomologiczne 57:3-207.

Chapuis, F. 1874. Genera des Coléoptères, Vol. 10 *In* Lacordaire, T. Histoire naturelle des insectes. 455 pp, plates 111-123. Paris [not seen, cited in Jolivet 1970:5].

Chen, S.H. 1941. Notes on donaciine beetles. Sinensia 12:1-17.

Chen, S.H. 1966. Notes on Chinese Donaciinae. Acta Entomologica Sinica 15:137-147.

Chen, S.H. 1986. Fauna Sinica. Insecta. Coleoptera Hispidae. Science Press, Beijing. [only a few select pages were examined; a full bibliographic citation is not available].

Chûjô, M. 1951. A taxonomic study on the Chrysomelidae (Insecta-Coleoptera) from Formosa. Part II Subfamily Donaciinae. Technical Bulletin of the Kagawa Agricultural College 3:43-56.

Clark, H. 1866. A catalogue of Phytophaga (Coleoptera, Pseudotetramera). Appendix. Williams & Norgate, London and Edinburgh. 1 + 88 pp.

Clavareau, H. 1913. Sagrinae, Donaciinae and Criocerinae, *In* Junk, W. and S. Schenkling, *Editors*. Coleopterorum Catalogus 51:1-103.

Cox, M.L. 1988. Egg bursters in the Chrysomelidae, with a review of their occurrence in the Chrysomeloidea and Curculionoidea (Coleoptera). Systematic Entomology 13:393-432.

Cronquist, A. 1987. A Botanical critique of cladism. The Botanical Review 53:1-52.

Crotch, G. R., 1873. Materials for the study of the Phytophaga of the United States. Proceedings of the Academy of Natural Sciences of Philadelphia 25:19-83

Crowson, R.A. 1945. A revision of the chrysomelid group Sagrinae (Coleoptera). Transactions of the Royal Entomological Society of London 97:75-115.

Crowson, R.A. 1960. The phylogeny of Coleoptera. Annual Review of Entomology 5:111-134.

Curtis, J. 1830. British Entomology; being illustrations and descriptions of the genera of insects found in Great Britain and Ireland: containing coloured figures from nature of the most rare and beautiful species, and in many instances of the plants upon which they are found. Volume VII. Privately published, London [4] + #290-337. [Note: not paginated, instead each species treatment and plate are numbered sequentially].

Curtis, J. 1834. ibidem. Volume XI, loc. cit. [6] + #482-529.

Daniel, K. and J. Daniel. 1904. Neue paläarktische Koleopteren. Münchener koleopterologische Zeitung 2:76-93.

Dejean, P.F.M.A. 1821. Catalogue de la collection de Coléoptères de M. la baron Dejean. Crevot, Paris. 8. viii + 136 pp.

DeJong, R. 1980. Some tools for evolutionary phylogenetic studies. Zeitschrift für zoologische Systematik und Evolutionsforschung 18:1-23.

Disney, R.H.L. 1989. Antidote to taxonomic instability. Nature 342:488.

Donoghue, M.J. and P.D. Cantino. 1988. Paraphyly, ancestors, and the goals of taxonomy: a botanical defense of cladism. The Botanical Review 54:107-126.

Erwin, T.L. 1981. Taxon pulses, vicariance, and dispersal: an evolutionary synthesis illustrated by carabid beetles. pp 159-196. In Nelson, G. and D.E. Rosen, Editors. Vicariance Biogeography. A Critique. Columbia University Press xvi + 593 pp.

Fabricius, J.C. 1775. *Systema Entomologicae, sistens insectorum classes, ordines, genera, species, adjectis synonymis, locis, descriptionibus, observationibus.* Korte, Flensburgi et Lipsiae. 8. [30] + 832 pp [not seen]

Fabricius, J.C. 1792. *Entomologia Systematica emendata et aucta, secundum classes, ordines, genera, species adjectis synonimis, locis, observationibus.* C.G. Proft, Hafniae. Tomus I. Pars I. xx + 1-330 pp, Pars II. 1-538 pp. [not seen]

Fabricius, J.C. 1801. *Systema Eleutheratorum, ordines, genera, species, adjectis locis, observationibus, descriptionibus.* Volume II. Bibliopol. acad., Kiliae, 687 pp. [not seen]

Fairmaire, L. 1885. [untitled]. Bulletin de la Société Entomologique de France (6)5:64-65.

Fairmaire, L. 1887. Coléoptères de l'intérieur de la Chine. Annales de la Société Entomologique de Belgique 31:87-136. [not seen, cited in Monrós, 1959].

Fairmaire, L. 1899. Coléoptères de Madagascar. Mémoires de la Société Zoologique de France 12:27-28.

Fairmaire, L. 1901a. Descriptions de Coléoptères nouveaux, de Madagascar. Bulletin de la Société Entomologique de France 1901:126-128.

Fairmaire, L. 1901b. Matériaux pour la faune Coléoptèrique de la région Malgache. Revue d'Entomologie 20:101-248.

Fischer von Waldheim, G. 1824. *Entomographia Imperii Rossici; Genera Insectorum systematicae exposita et analysi iconographica instructa* Volumen II. Moscow. 262 pp, 40 plates.

Gistel, J.N.F.X. 1857. Achthundert und zwanzig neue oder unbeschriebene wirbellose Thiere. Vacuna 2:513-606. [Also published separately, Straubing, Schorner, 1857. 8:94 pp, under the title "Vacuna oder die

Geheimnisse aus der organischen und leblosen Welt." The former is usually cited.]

Goecke, H. 1931. Die Gattung *Sominella* Jacobson (Col. Chrys. Donaciini) (1. Beitrag zur Kenntnis der Donaciinen). Entomologische Blätter für Biologie und Systematik der Käfer. 27:152-161, 1 plate.

Goecke, H. 1934. Revision asiatischer Donaciinen (Col. Chrys.). I. (3. Beitrag zur Kenntnis der Donaciinen). Koleopterologische Rundschau 20:215-230, 1 plate.

Goecke, H. 1935. Zur geographischen Verbreitung der Donaciinen (Col. Chrys.) in Süd- und Ostasien. Archiv für Hydrobiologie und Planktonkunde, Suppl. 14:286-291.

Goecke, H.1936. Revision asiatischer Donaciinen (Col. Chrys.) II. 8. Beitrag zur Kenntnis der Donaciinen. Entomologische Blätter für Biologie und Systematik der Käfer. 32:220-228 + 1 plate.

Goecke, H. 1944. Revision asiatischer Donaciinen (Col. Chrys.) III. 14. Beitrag zur Kenntnis der Donaciinen. Entomologische Blätter für Biologie und Systematik der Käfer. 40:7-14.

Goecke, H. 1960a. Monographie der Schilfkäfer III. Die Gattungen und Arten der Donaciinae (Col. Chrys.) und Ihre Verbreitung. Entomologische Blätter für Biologie und Systematik der Käfer. 56:1-19.

Goecke, H. 1960b. Zur Gattungsystematik der Donaciinae (Col.Chrys.) 19. Beitrag zur Kenntnis der Donaciinae. Entomologische Blätter für Biologie und Systematik der Käfer 56:164-165.

Gressitt, J.L. 1971. Chrysomelid beetles from the Papuan Subregion, 7 (Donaciinae). Pacific Insects 13:607-609.

Gressitt, J.L. and S. Kimoto. 1961. The Chrysomelidae (Coleopt.) of China and Korea. Part 1. Pacific Insects Monograph 1:1-299.

Gruev, B. and V. Tomov. 1984. Coleoptera, Chrysomelidae. Part 1. Orsodacninae, Zeugophorinae, Donaciinae, Criocerinae, Clytrinae, Cryptocephalinae, Lamprosomatinae, Eumolpinae. Fauna Bulgarica 13:1-218. [in Bulgarian]

Guérin-Méneville, F.E. 1944. Iconographie du Règne Animal de G. Cuvier, représentation d'après nature de l'une des espèces les plus remarquables et souvent non encore figurées, de chaque genre d'animaux. Tome III. Paris, J.B. Baillière, 1829-1844. 8. 576 pp, 104 plates.

Hatch, M.H. 1971. The Beetles of the Pacific Northwest Part V. Rhipiceroidea, Sternoxi, Phytophaga, Rhynchophora, and Lamellicornia. University of Washington Publications in Biology Vol. 16. xiv + 662 pp.

Haupt, H. 1956. Beitrag zur Kenntnis der eozänen Arthropodenfauna des Geiseltales. Nova Acta Leopoldina (N.F.) 18: 90 pp.

Hellén, W. 1937. Über die Haemonia = Arten Finnlands (Col.). Notulae Entomologicae 17:1-4.

Hennig, W. 1965. Phylogenetic Systematics. Annual Review of Entomology 10:97-116.

Hennig, W. 1966. Phylogenetic Systematics. University of Illinois Press, Urbana. 263 pp.

Hoffman, C.E. 1940. Limnological relationships of some Northern Michigan Donaciini (Coleoptera: Chrysomelidae). Transactions of the American Microscopical Society 19:259-274.

Hull, D.L. 1979. The limits of cladism. Systematic Zoology 28:416-440.

Iablokoff-Khnzorian, S.M. 1966. Considérations sur l'édéage des Chrysomelidae et son importance phylogénique. L'Entomologiste 22:115-137.

Iablokoff-Khnzorian, S.M. 1968. Notes sur les Chrysomelidae de l-Arménie sovietique [Col.]. Annales de la Société entomologique de France (Nouvelles Série) 4:259-277.

International Commission on Zoological Nomenclature. 1985. International Code of Zoological Nomenclature, Third Edition. University of California Press, Berkeley and Los Angeles. xx + 338 pp.

Jacobson, G.G. 1906. *Donacia clavareaui spec. nova*. Annales de la Société Entomologique de Belgique 50:311-312.

Jacobson, G.G. 1907. *Donacia semenovi*, sp. nov. (Coleoptera, Chrysomelidae). Revue Russe d'Entomologie 7:5-6.

Jacobson, G.G. 1908. *De tribus generibus novis Chrysomelidarum faunae rossicae*. Horae Societatis Entomologicae Rossicae 38:619-662, Plate VII.

Jacoby, M. 1885. Descriptions of the phytophagous Coleoptera of Japan, obtained by Mr. George Lewis during his second Journey, from February 1880 to September 1881. - Part I. Proceedings of the Zoological Society of London 1885:190-211, + 1 plate. [reference not seen].

Jacoby, M. 1890. Descriptions of new species of phytophagous Coleoptera received by Mr. J.H. Leech, from Chang-Yang, China. The Entomologist 23:84-89 + plates I-II.

Jacoby, M. 1893. Descriptions of some new species of Donaciinae and Criocerinæ contained in the Brussels Museum and that of my own. Annales de la Société Entomologique de Belgique 37:261-271.

Jacoby, M. 1908. Coleoptera. Chrysomelidae. Vol. I. xx + 534 pp + 2 colour plates. *In* C.T. Bingham, *Editor*. The fauna of British India, including Ceylon and Burma. Taylor & Francis, London. [First Indian reprint edition, 1975, Today & Tomorrow's Printers and Publishers, New Delhi].

Jacoby, M. and H. Clavareau, 1904. Coleoptera Phytophaga Fam. Donacidae. *In* P. Wytsman, *Editor*. Genera Insectorum 21:1-14, 1 plate.

Jaeger, E.C. 1955. A source-book of biological names and terms. 3rd Edition, fourth printing. Charles C. Thomas, Publ. Springfield, Illinois. xxxv + 323 pp.

Jolivet, P. 1970. Donaciinae. *In* Junk, W. *Editor*. Coleopterorum Catalogus Supplementum. Pars 51. Fasc. 2. 71 pp. W.O. Steel, Gravenhage.

Jolivet, P. 1972. Coleoptera Chrysomelidae Donaciinae. Exploration du Parc National de la Garamba. Mission H. de Saeger, Bruxelles 56(3):43-58.

Kavanaugh, D.H. 1972. Hennig's principles and methods of phylogenetic systematics. The Biologist 54:115-127.

Khnzorian, S.M. 1962. [see also Iablokoff-Khnzorian]. New species of Coleoptera from Transcaucasus. Academy of Sciences of Armenian SSR Zoological Institute, Zoological Papers. 12:99-124.

Kimoto, S. 1981. New or little known Japanese Donaciinae (Coleoptera: Chrysomelidae). Bulletin of the Osaka Museum of Natural History 34:23-26.

Kimoto, S. 1983. Revisional study on Megalopodinae, Donaciinae and Clytrinae of Japan (Coleoptera: Chrysomelidae). Entomological Review of Japan 38:5-23.

Kimoto, S. and J.L. Gressitt. 1979. Chrysomelidae (Coleoptera) of Thailand, Cambodia, Laos and Vietnam I. Sagrinae, Donaciinae, Zeugophorinae, Megalopodinae and Criocerinae. Pacific Insects 20:191-256.

Kingsolver, J.M. 1970. A study of male genitalia in Bruchidae. Proceedings of the Entomological Society of Washington 72:370-386.

Kirby, W. 1837. Part the fourth and last. The Insects. *In* Richardson, J. Fauna Boreali-Americana; or the Zoology of the Northern Parts of British America: containing descriptions of the objects of natural history collected on the late northern land expedition under command of Cpt. Sir John Franklin, R.N. Norwich. xxxix + 325 pp, + 8 plates.

Komiya, Y. and M. Kubota. 1987. A new *Donacia* (Coleoptera, Chrysomelidae, Donaciinae) from Central Japan. Elytra 15:41-44.

Kunze, G. 1818. I. Beiträge zur Monographie der Rohrkäfer. Neue Schriften der naturforschenden Gesellschaft zu Halle. 2:1-56.

Lacordaire, Th. 1845. Monographie des coléoptères subpentamères de la famille des phytophages. Tome 1. Mémoires de la Société Royale des Sciences de Liège. Tome 3 (pt.1). xiii + 740 pp.

LeConte, J.L. 1851. Synopsis of the species of *Donacia* (Fabr.) inhabiting the United States. Proceedings of the California Academy of Sciences 5:310-316.

Leng, C. W. 1891. Revision of the Donaciae of Boreal America. Transactions of the American Entomological Society 18:159-176.

Linnaeus, C. 1758. *Systema Naturae per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum characteribus, differentiis, synonymis, locis.* Tomus I. Editio Decima. Laurentii Salvii, Holmiae. 824 pp. [photographic facsimile, published by British Museum (Natural History), 1939].

Mann, J.S. and R.A. Crowson. 1981. The systematic positions of *Orsodacne* Latr. and *Syneta* Lac. (Coleoptera: Chrysomelidae), in relation to characters of larvae, internal anatomy and tarsal vestiture. Journal of Natural History 15:727-749.

Mann, J.S. and R.A. Crowson. 1983a. Observations on the internal anatomy and classification of Donaciinae (Col., Chrysomelidae). Entomologist's Monthly Magazine 119:17-27.

Mann, J.S. and R.A. Crowson. 1983b. On the occurrence of mid-gut caeca, and organs of symbiont transmission in leaf beetles (Coleoptera: Chrysomelidae). The Coleopterists Bulletin 37:1-15.

Mann, J.S. and R.A. Crowson. 1983c. On the internal male reproductive organs and their taxonomic significance in the leaf beetles (Coleoptera: Chrysomelidae). Entomologia Generalis 9:75-99.

Mann, J.S. and R.A. Crowson. in preparation. Some observations on the genitalia of Sagrinae (Coleoptera: Chrysomelidae). unpublished manuscript, 1990.

Marx, E.J.F. 1957. A Review of the subgenus *Donacia* in the Western Hemisphere (Coleoptera: Donaciidae). Bulletin of the American Museum of Natural History 112:191-278.

Mayr, E. 1974. Cladistic analysis or cladistic classification? Zeitschrift für Zoologische Systematik und Evolutionsforschung 12:94-128.

Medvedev, L.N. 1973. New Leaf Beetles from Palaearctic. Entomological Review of Washington 52:562-568. [Translated from: Entomologicheskoe Obozrenie 52:876-885.]

Medvedev, L.N. 1977. Discovery of a representative of American genus *Neohaemonia* Szék. (Coleoptera, Chrysomelidae) in Mongolia. Doklady Akademii Nauk CCCP 236:488-490 [translated from: Akademii Nauk SSSR Doklady Biol. Sci. 236:447-449.]

Melsheimer, F.E. 1847. Descriptions of new species of Coleoptera of the United States. Proceedings of the California Academy of Sciences 3:158-181.

Mohr, K.H. 1966. 88. Fam. Chrysomelidae. *In* Freude H., K.W. Harde, and G.A. Lohse, *Editors*. Die Käfer Mitteleuropas. Goecke & Evers Verlag, Krefeld. Volume 9:95-280.

Monrós, F. 1958. Enumeración de las Donaciinae africanas con notas a algunas especies (Coleoptera: Chrysomelidae). Diamang (Companhia di Diamantes de Angola) 38:87-92.

Monrós, F. 1959. Los Generos de Chrysomelidae (Coleoptera). Opera Lilloana III:5-337 + 3 plates.

Monrós, F. and J. Bechyné 1956. Über einige verkannte Chrysomeliden-Namen. Entomologische Arbeiten aus dem Museum G. Frey 7:1118-1137

Müller, G. 1949-1953. I Coleotteri della Venezia Giulia. Volume II: Coleoptera Phytophaga (Cerambycidae, Chrysomelidae, Bruchidae). Trieste, Centro Sperimentale Agrario e Forestale 4:485 pp.

Neff, N.A. 1986. A rational basis for a priori character weighting. Systematic Zoology 35:110-123.

Pic, M. 1896. Coléoptères d'Asie Mineure et de Syrie. Miscellanées entomologiques 4:35-36.

Pic, M. 1908. Descriptions ou diagnoses et notes diverses. Échange 24:47-52. [not seen, cited in Monrós 1959].

Pic, M. 1907. Coléoptères paléarctiques nouveaux.Échange 23:100. [not seen, cited in Jolivet 1970, and Monrós 1959].

Pic, M. 1936. Nouveautés diverses. Mélange Exotico-Entomologiques 67:9-16.

Paykull, G. von. 1800. Fauna Suecica; Insecta 3. 459 pp. [not seen, cited in Monrós, 1959].

Reitter, E. 1913. Koleopterologische Novitaten der palaearktischen Fauna. Koleopterologische Rundschau 2:121-125. [not seen, cited by Monrós, 1959].

Reitter, E. 1920. Bestimmungs-Tabelle der europäischen Donaciini, mit Berücksichtigung der Arten der paläarktischen Region. Wiener entomologische Zeitung 38:21-43.

Samouelle, G. 1819. The entomologist's useful compendium; or an introduction to the knowledge of British insects, comprising the best means of obtaining and preserving them, and a description of the apparatus generally used; together with the genera of Linné, and the modern method of arranging the Classes Crutacea, Myriapoda, Spiders, Mites and Insects, from their affinities and structure, according to the views of Dr. Leach. Also an explanation of the terms used in entomology; a calendar of the times of appearance and usual situations of 3,000 species of British insects; with instructions for collecting and fitting up objects for the microscope. Thomas Boys, London 496 pp + 12 plates.

Schaeffer, C. 1919. Synonymical and other notes on some species of the family Chrysomelidae and descriptions of new species. Journal of the New York Entomological Society 27:307-340.

Schaeffer, C. 1925. Revision of the new world species of the tribe Donaciini of the Coleopterous family Chrysomelidae. Brooklyn Museum Science Bulletin 3:45-165.

Schmitt, M. 1985a. Versuch einer phylogenetischen-systematischen Analyse der Criocerinae (Coleoptera, Chrysomelidae). Zoologische Beiträge (N.F.) 29:35-85.

Schmitt, M. 1985b. On the phylogeny of the Criocerinae (Coleoptera, Chrysomelidae). Pp 393-401, *In* D.G. Furth and T.N. Seeno, *Editors*. First

International Symposium on the Chrysomelidae. Entomography 3:371-503.

Schmitt, M. 1988. 28. The Criocerinae: biology, phylogeny and evolution. Pp 475-495, *In* P. Jolivet, E. Petitpierre, and T.H. Hsiao, *Editors*. Biology of Chrysomelidae. Kluwer Academic Publishers.

Schmitt, M. 1989. On the phylogenetic position of the Bruchidae within the Chrysomeloidea (Coleoptera). Entomography 6:531-537.

Schönfeld, H. von. 1888. Eine neue *Donacia* aus Japan. Entomologische Nachrichten 14:33-34. [not seen, cited in Monrós 1959].

Scopoli, J.A. 1772. *Annus historico naturalis*. Lipsiae, Hilscher. Ann. 5, 128 pp.

Seeno, T.N. and J.A. Wilcox. 1982. Leaf Beetle Genera (Coleoptera: Chrysomelidae). Entomography 1:1-221.

Sharkey, M.J. 1989. A hypothesis-independent method of character weighting for cladistic analysis. Cladistics 5:63-86.

Silfverberg, H. 1977. Nomenclatoric notes on Coleoptera Polyphaga. Notulae Entomologicae 57:91-91.

Suffrian, E. 1872. Synonymische Miscellaneen. Stettiner entomologische Zeitung 33:11-22.

Swofford, D.L. 1985. Phylogenetic analysis using parsimony, version 2.4.1. Unpublished documentation.

Székessy, V. 1941. Die zur Gattung *Haemonia* Latr. gestellten Arten aus Amerika (Coleopt, Chrysomelidae). Münchner entomologische Gesellschaft, Mitteilungen, 31:148-154.

Thomson, C.G. 1859. Skandinaviens Coleoptera, Synoptisk Bearbetade I. Berlingska, Lund. iv + 1-161 + 1-290.

Voet, J.E. 1806. *Catalogus Systematicus Coleopterorum*. Tomus II. G. Bakhuysen, Haag. [Published simultaneously in three languages: Latin, pp 1-82; French, pp 1-85; Dutch, pp 1-87, plus index, 20 pp.]

Weise, J. 1881-1893. Chrysomelidae. *In* W.F. Erichson, *Editor*. Naturgeschichte der Insekten Deutschlands 6, XIV + 1161 pp, 1 plate. Berlin, Nicolai. [books have cover date of publication of 1893, but parts appeared as follows: 1881, 1-192; 1882, 193-368; 1884, 369-568; 1886, 569-768; 1888, 769-960; 1893, I-XIV + 961-1161, 1 plate.]

Weise, J. 1889. *Insecta, a Cl. G.N. Potanin in China et in Mongolia novissime lecta IX, Chrysomelidae et Coccinellidae*. Horae societatis entomologicae Rossicae 23:560-653. [not seen, cited in Monrós 1959].

Weise, J. 1912. Beitrag zur Kenntnis der Chrysomeliden. Archiv für Naturgeschichte. 78:76-98. [not seen, cited in Monrós, 1959].

White, R.E. in preparation. Revision of the Criocerinae of America North of Mexico (Coleoptera: Chrysomelidae) (unpublished manuscript).

Wilcox, J.A. 1954. Leaf Beetles of Ohio (Coleoptera: Chrysomelidae). Ohio Biological Survey Bulletin 3:353-506.

Wilcox, J.A. 1975. Checklist of the beetles of North and Central America and the West Indies. Vol. 8, fam. 129, Chrysomelidae. Flora and Fauna Publications, Gainesville, Florida. 166 pp.

Wiley, E.O. 1981. Phylogenetics: the theory and practise of phylogenetic systematics. John Wiley, New York xv + 439 pp.

INDEX TO NAMES OF TAXA

(Junior synonyms in italics)

SPECIES AND SUBSPECIES

CLASSFICATION, RELATIONSHIPS, LIFE HISTORY, AND EVOLUTION OF *EREBIA MAGDALENA* STRECKER (LEPIDOPTERA: SATYRIDAE)

Gerald J. Hilchie
Department of Entomology
University of Albertan
Edmonto, Alberta T6G 2E3
CANADA

Quaestiones Entomologicae
26: 665–693 1990

ABSTRACT

Several populations of Erebia magdalena *Strecker were discovered in Alberta and British Columbia, Canada, all within a limited geographic area. Specimens from the Rocky Mountain states and the sister species* E. mackinleyensis *Gunder from Alaska and Yukon Territory were compared with the newly discovered populations. Principal Component Analysis showed little evidence of introgression of the Alberta populations with populations of* E. mackinleyensis. *Populations of* E. magdalena *from the Rocky Mountain states clustered near and overlapped with the Alberta populations. Discriminant analysis demonstrated a clinal shift in character states within* E. magdalena *which were separate from those of* E. mackinleyensis. *These permitted recognition of different populations. Egg and larval characteristics show similarity between* Erebia magdalena *and* E. mackinleyensis. *Observable differences occur between the* E. magdalena/mackinleyensis *species pair eggs and larvae, and those of* E. fasciata *Butler.* Erebia magdalena saxicola *new subspecies is described. Type locality is Adams Lookout, Wilmore Wilderness Park (43 km southeast of Grande Cache), Alberta.* Erebia magdalena *females oviposit on rocks. Larval development appears univoltine with late instar larvae overwintering. Larvae feed on a variety of grasses.* Erebia magdalena *appears to have evolved from a common ancestor with* E. mackinleyensis *during a pre Wisconsinan glacial period. Subsequent dispersal and isolation resulted in fragmentation and subspeciation. In Alberta* E. magdalena *appears derived from ancestral populations formerly located in the Montana front ranges during the last glacial stage.*

INTRODUCTION

Erebia magdalena Strecker was known to inhabit high mountain boulder fields and talus slopes in alpine scree of northern New Mexico, Colorado, Wyoming, Utah, and southern Montana (Ferris and Brown, 1980). Inaccessibility and remoteness have limited collection of this species in many parts of its range. Its discovery in Alberta and adjacent British Columbia raises some interesting questions. What are the affinities of these populations with other populations of *E. magdalena* and those of its seemingly close relative *E. mackinleyensis* Gunder? Why has this butterfly species not been found in the mountain areas between Wilmore Wilderness Park (near Grande Cache), Alberta and Carbon County, southern Montana? Is it a relic of pre- or post- Wisconsinan dispersal? To attempt to answer these questions, populations of *E. magdalena* are compared with each other and with populations of *E. mackinleyensis*. Aspects of life history are included as further characterization.

MATERIAL AND METHODS

Material

Study material included: 242 adults, eggs, egg shells, larvae, 1 pupa, and photographic material of life stages of *Erebia magdalena*; 54 adults, eggs, egg shells and larvae of *E. mackinleyensis*; and and eggs, egg shells and larvae of *Erebia fasciata*.

The following codens designate collections cited in this paper. Names of curators or owners of private collections are in parentheses following the address of each collection.

ALME	Allyn Museum of Entomology, 3701 Bay Shore Road, Sarasota, Florida 33580. (L.D. Miller).
AMNH	American Museum of Natural History, Central Park West at 79 Street, New York, New York 10024. (F.H. Rindge).
AVER	Avery Collection, Hinton, Alberta. (K. Avery).
CNC	Canadian National Collection, Biosystematics Research Institute, Ottawa, Ontario, K1A 0C6. (J.D. Lafontaine).
HILC	Hilchie Collection, Department of Entomology, University of Alberta, Edmonton, Alberta, T6G 2E3. (G. J. Hilchie).
INHS	Illinois Natural History Survey, 172 Natural Resources Building, Urbana, Illinois 61800. (K.C. McGiffen).
PIKE	Pike Collection, Department of Biology, University of Calgary, Calgary, Alberta T2N 1N4 (E. M. Pike).
PRES	Preston Collection, Lawrence Kansas. (J. & F. Preston).
SHEP	Shepard Collection, Sproule Cr. Road, Nelson, B.C. (J. Shepard).
SPER	Sperling Collection, Department of Ecology and Systematics, Cornell University, Ithaca, New York, 14853. (F. A. H. Sperling).
UASM	University of Alberta, Strickland Museum, Edmonton, Alberta, T6G 2E3. (D. Shpeley).
USNM	United States National Museum, Smithsonian Institution, Washington, D.C. 20560. (R.K. Robbins).
YOUN	Young Collection, 256 Clear Falls Circle, Eagle River, Alaska 99577. (M. E. Young)

Methods

Several populations of *E. magdalena* were examined critically for similarities and differences to assist in recognizing species and subspecies boundaries. Characters used in the analysis include scale pattern and color, on the wings and antennae, measurements, structure of male genitalia and structure of the egg. Data generated from the study was examined statistically.

Measurements.— Specimens were examined using a Wild M5 microscope equipped with an ocular micrometer. Wing length measurements were made from base to margin at R4 for the forewing and from base to margin at M3 on the hindwing. Larval head capsule widths were measured frontally at the widest point. Egg capsules were measured for length (apex to base) and width (widest point).

Scale pattern and color.— Wing scale and hair counts were made on limited regions of the fore and hindwings. On the forewing the area was delimited by the veins R4 and R5 and the wing margin. On the hindwing the area was delimited by the veins M1 and M2 and the wing margin.

Medial band on the hind wing was indexed as three character states: present and clearly defined; present but faint and indistinctly defined; and absent. The presence and extent of pattern exhibited by rust coloured scales was indexed as five character states (only three listed): no rust scales; a few scattered scales; large well defined patch. Variation of pigmentation of the antennal club was indexed as seven character states dependent on colour and pattern of light and dark areas. Indexing of the antennal club did not use color patterns of the covering scales as these were badly abraded on many specimens. Index values were polarized to reflect recognized taxa, with low numbers assigned to *E. magdalena* and higher numbers to *E. mackinleyensis*

Male genitalia.— Male genitalia were studied by removing the terminal segments of the abdomen and placing them in hot 10% KOH solution until soft. Illustrations were made with the aid of a camera lucida on a Wild M5 microscope. Then genitalia and terminal segments of the abdomen were placed in glycerol in a microvial which was pinned through its cork beneath the specimen of origin.

Egg and larval structures .— Egg and larval structures were examined and photographed with the aid of a Zeiss Tessovar light microscope and Cambridge Stereoscan 250 and 100 Electron Scanning Microscopes.

Chromosome study.— Butterflies were brought to the lab alive, frozen at -20°C and stored until chromosome fixing. Frozen testes were dissected and fixed in 95% ethanol:acetic acid (3:1). Testes were Fuelgen stained, squashed in 50% acetic acid and preserved in Euparol.

Life history study.— Caged females were given substrate choices (rocks, lichens, grasses, willow twigs and leaves) on which to oviposit. Eggs were collected for rearing and taxonomic study. Larvae initially were given a choice of food until the food preference was determined. Larvae were reared to maturity in petri dishes, lined with absorbent toweling, and supplied with fresh leaves daily. Incubators were used to control environmental conditions for part of the rearing.

Statistical analysis.— Data obtained were subjected to Principal Component Analysis, Discriminant Analysis and Cluster Analysis for evaluation of variance and relationship between populations and individuals. Statistical manipulations were made with the Michigan Interactive Data Analysis System (MIDAS) on the Amdhal Computer at the University of Alberta.

The data were pooled to provide population samples of adequate size for statistical analysis. Small samples that could not be pooled were excluded from the initial analysis, then compared with the results on an individual basis.

CHARACTER ANALYSIS

Characters for species and subspecies designation in *Erebia* species are based on structural differences in genitalia, chromosome number, wing venation, wing shape, differences in maculation and scale types (Warren, 1936). Lesser levels of difference in maculation pattern with geographic isolation serve as criteria for subspecies discrimination.

Warren (1936) commented "There is obviously little possibility of showing variation" in reference to the uniform black colour of *E. magdalena*. This results in placing more emphasis on character states which do show variation.

Table 1. Comparison of males of *Erebia mackinleyensis* and *E. magdalena* adult males using measurements and character index values.

Character	Species													
	E. mackinleyensis		*E. magdalena*											
	Alaska & Yukon		Alberta to New Mexico		Alberta		Montana		Utah		Colorado		Colorado (south) & New Mexico	
	n=39		n=167		n=28		n=6		n=20		n=95		n=18	
	mean	range	mean	range	mean	range	mean	range	mean	range	mean	range	mean	range
Forewing														
-length (mm)	25.7	22.8-28.9	25.1	21.4-28.9	23.8	21.4-26.1	24.9	24.2-25.8	25.7	21.9-27.7	25.3	21.9-28.9	25.1	23.5-27.9
-white scale index	0.33	0-10	1.5	0-26	4.6	0-26	7.2	2-16	3.3	0-24	0.18	0-10	0.33	0-3
-white hair index	3.2	0-38	2.1	0-35	1.7	0-10	10.5	2-22	5.5	5.5-35	1.1	0-20	1.8	0-14
Hindwing														
-length (mm)	21.5	18.2-23.8	20.9	17.7-23.5	19.9	17.7-21.7	20.7	19.8-21.4	21.2	18.2-23.3	21.1	18.2-23.5	20.8	19.1-22.6
-white scale index	0.03	0-1	3.6	0-48	8.7	0-48	13.5	0-38	1.5	0-12	1.8	0-32	3.9	0-42
-white hair index	1.3	0-28	1.7	0-46	1.0	1-10	11.0	0-33	0.35	0-5	1.2	0-27	4.2	0-46
Wing markings														
-mesial band index	2.5	1-3	1.7	1-3	1	1	1	1	1	1	1.1	1-3	1.2	1-2
-dorsal rust patch	1.7	1-5	1	1	1	1	1	1	1	1	1	1	1	1
-ventral rust patch	3.2	1-6	1.02	1-3	1	1	1.5	1-3	1	1	1	1	1	1
Antennal club														
-color index	3.6	1-8	5.9	4-8	6.4	5-7	7.0	5-8	6.4	4-8	5.6	5-8	6.1	5-8

Table 2. Comparison of *Erebia mackinleyensis* and *E. magdalena* adult females using measurements and character index values.

Character	Species													
	E. mackinleyensis		*E. magdalena*											
	Alaska & Yukon n=15		Alberta to New Mexico n=75		Alberta n=20		Montana n=3		Utah n=4		Colorado n=42		Colorado (south) & New Mexico n=6	
	mean	range	mean	range	mean	range	mean	range	mean	range	mean	range	mean	range
Forewing														
-length (mm)	25.8	23.5-28.2	25.3	22.1-28.0	25.0	22.1-27.7	25.5	24.9-26.3	25.4	23.7-26.3	25.3	22.4-28.0	26.5	24.5-27.5
-white scale index	4.9	0-39	20.6	0-200	46.4	3-200	49.3	21-105	6.7	4-13	9.7	0-30	5.5	0-14
-white hair index	18.8	0-52	68.5	1-218	66.5	2-150	84	49-137	33	17-68	74.9	1-218	46	0-111
Hindwing														
-length (mm)	21.5	19.1-22.8	21.0	17.2-23.3	20.5	17.2-22.8	21.4	19.8-22.6	20.8	19.8-21.4	21.1	18.2-23.3	21.9	20.0-23.3
-white scale index	3.9	0-23	31.8	0-135	59.6	6-135	53.7	25-97	6.0	0-14	17.9	0-93	41.8	0-97
-white hair index	4.5	0-24	73.5	0-258	51.8	0-153	168.3	139-216	9.7	1-29	8.5	0-258	63.8	0-147
Wing markings														
-mesial band index	2.9	2-3	1.8	1-3	1	1	1	1	1	1	2.4	1-3	2	2
-dorsal rust patch	5.4	1-6	1.2	1-6	1.05	1-2	4	3-6	1.25	1-2	1.09	1-5	1	1
-ventral rust patch	5.0	1-6	1.1	1-5	1	1	1.7	1-3	1.25	1-2	1.09	1-5	1	1
Antennal club														
-color index	2.7	2-4	6.1	5-8	6.8	6-8	6.0	5-8	7	7	5.7	5-7	6.0	5-7

External Features

Erebia magdalena is one of the plainest butterfly species in North America, with adults uniformly black to dark brown. Other colours and patterns are absent from most specimens. Data on populations sampled are presented in Tables 1 and 2. Few females have a reddish flush (6.7%, n=75), with one population (Montana, Beartooth Plateau) in which all females examined (n=3) and one of the males (n=5) were marked. Ventral maculations are slightly developed to obsolete with considerable variation between localities. Most females from Colorado (80%, n=45) are banded (Figure 43) while females from Alberta, Montana, Utah, New Mexico (n=20, 3, 4, 4) were unbanded. Most males lack ventral banding. Degree of coverage by scattered white hairs and scales on the ventral wing surface varies markedly. When present in quantity the white scales and hairs dusted the ventral apex of the forewing and were more evenly distributed on the hind wing. In females from Colorado these scales enhance the banding pattern on the hind wing but do not do so on females from Alberta. Markings on the antennal club vary, but on average it has a dark piceous half partially bisected by a longitudinal strip lighter in colour. The remaining half of the club is paler on many adults. Scales obscure the boundaries of the markings (Figure 41).

Data for the Principal Component Analysis were placed in the following groups for comparative purposes (males, females):

E. magdalena

CANADA. Alberta, (Mount Hamell 11, 4; Adams Look Out 17, 15; Dore River, B.C. 0, 1). U.S.A. Montana (Beartooth Plateau of Montana and Wyoming 6, 3). Utah (Summit, Duchesne and Uintah Counties 20, 4). Colorado, northern (Larimer, Grand, Gilpin and Boulder Counties 42, 18). Loveland Pass, (central Colorado 40, 13). Colorado, southern (Gunnison, Park, Hinsdale, La Plata, Custer, *etc*. Counties 27, 14). New Mexico (Taos County 4, 3).

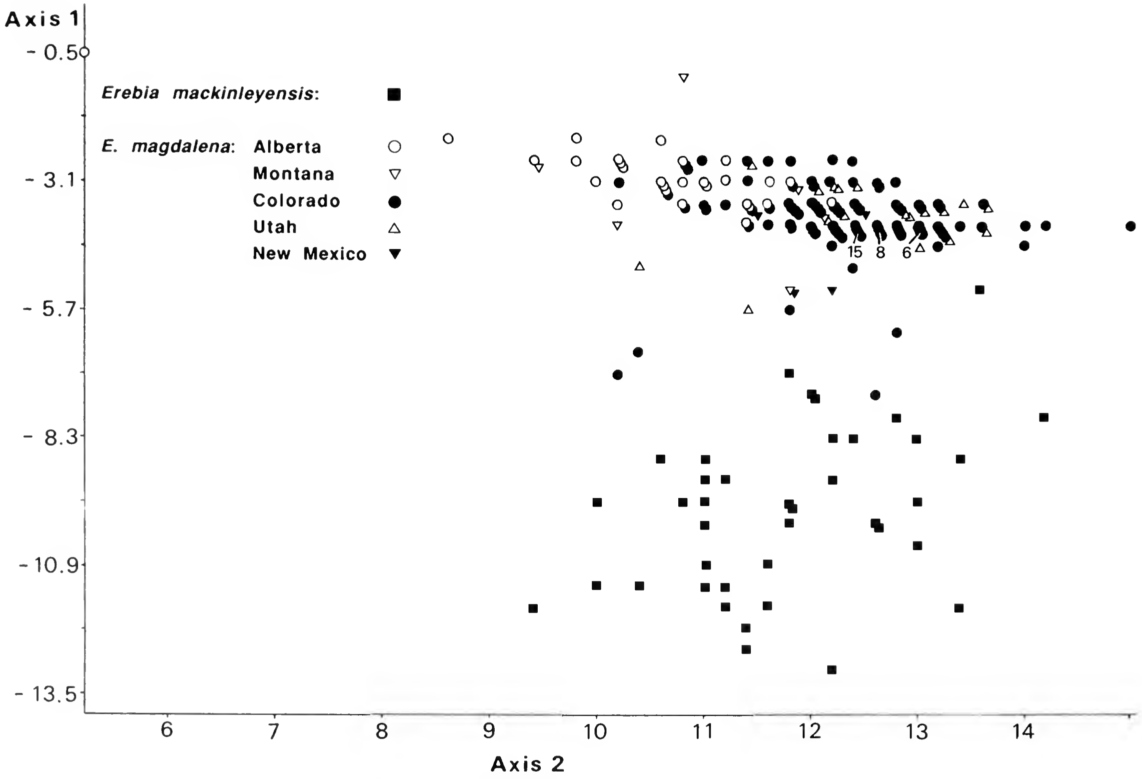
E. mackinleyensis

CANADA. Yukon (Dempster Highway 37, 11). U.S.A. Alaska (2, 4)

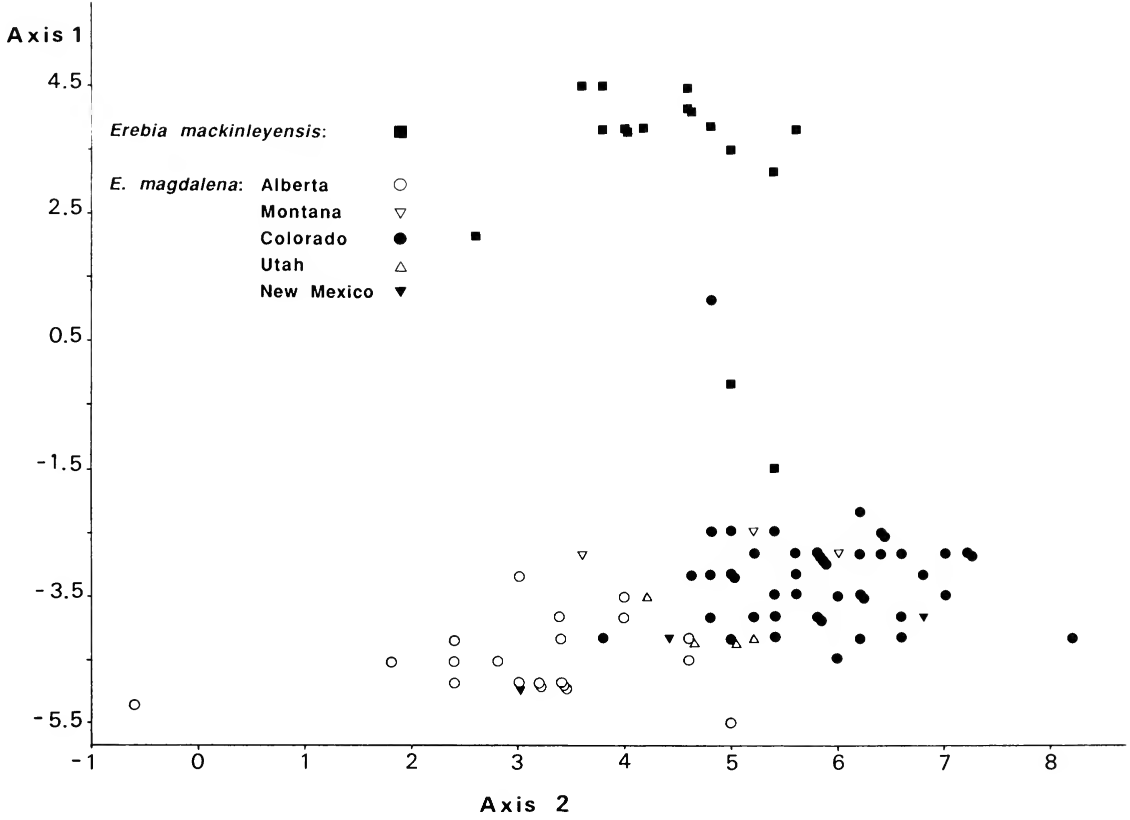
Results from Principal Component Analysis of the various populations support the idea that *E. magdalena* and *E. mackinleyensis* are separate and recognizable entities as shown in Graphs A and B. Tables 1 and 2 list the mean values for variables used in the analysis and their range of variation expressed by length, or indexed value. Populations of *E. magdalena* show a trend (Graphs A and B: Tables 1 and 2): data points cluster but are skewed geographically. Northern (Alberta) specimens appear as one end of a cline, with intermediate individuals forming a blend zone with southern (Colorado) specimens. Albeit the Montana sample is small, the specimens examined tend to be somewhat intermediate in placement, along with specimens from Utah. It is clear that these populations belong together; it is also clear that there are recognizable differences between the populations. Discriminant Analysis and Cluster Analysis exhibited similar results.

Male Genitalia

Males of *E. magdalena* (Figures 31–36) are very similar in genitalic structure to males of *E. mackinleyensis* (Figures 37 and 38). Spination of the claspers (Figures 32b-36b) is along the outer margin. In males of *E. mackinleyensis* (Figures 37b-38b) the spines are expanded onto the inner face. Warren (1981) reports the dorsal parts of the uncus and brachia are on a smaller



Graph A. Principal Component Analysis of adult females of *Erebia mackinleyensis* and several populations of *E. magdalena* from Alberta, Montana, Colorado, Utah and New Mexico. (Re-plotted from computer printout.)



Graph B. Principal Component Analysis of adult males of *Erebia mackinleyensis* and several populations of *E. magdalena* from Alberta, Montana, Colorado, Utah and New Mexico. (Re-plotted from computer printout.) Numbers refer to numbers of individuals whose scores fall on one plotting point.

scale in *E. mackinleyensis*. Variation in shape and size of parts of the male genitalia of *E. magdalena* as shown in Figures 32–36 (male claspers) indicate that size and shape do not discriminate these species reliably.

Conclusions

Erebia mackinleyensis and *E. magdalena* have been considered as conspecfic subspecies (*e.g.*, Ehrlich and Ehrlich 1961, Howe 1975). The distinct appearance of the adults, structural differences in male genitalia and vicariance strongly suggest separate gene pools. Until genetic compatibility is determined, I accept Warren's (1981) decision in recognition of *Erebia magdalena* and *Erebia mackinleyensis* as distinct species. Further I suggest that they are sister species.

Based on phenetic differences and geographical disjunction, the populations of *Erebia magdalena* form two identifiable groups. These groups deserve subspecific recognition, with the names that are given them serving as convenient designations for use by systematists and others. Although some individuals reject the formal recognition of a subspecies category, I accept the position taken by Willis (1967): "... if a subspecies reflects to some degree the actual pattern of variation, as well as being convenient 'handles' for reference, their value seems sufficient to justify their recognition".

TAXONOMIC TREATMENT

Erebia magdalena Species Group

Similarities in structure of the male genitalia place *Erebia magdalena* and *E. mackinleyensis* in a group with *E. fasciata* Butler, *E. semo* Grüm-Grschimailo and *E. erinnyn* Warren (Warren 1936,1981). The *magdalena* group is subdivided on the presence or absence of male androconial scales. *Erebia magdalena, mackinleyensis, semo* and *erinnyn* are included in the subgroup which possesses androconia (*erinnyn* is assumed by Warren to have androconia). Reduction of the

Table 3. Comparison of larval head capsule width, and egg diameter and length for *Erebia magdalena, E. mackinleyensis* and *E. fasciata*.

Stadia	**Species**							
	E. m. mag.		*E. m. sax.*		*E. mack.*		*E. fasc.*	
Egg dia.	1.23		1.22±0.07		1.10±0.09		1.03±0.05	
lgth.	1.36	n=3	1.45±0.07	n=25	1.28±0.05	n=11	1.27±0.08	n=11
Instar								
1st	0.74	n=3	0.81±0.02	n=25	0.74±0.03	n=13	0.69±0.03	n=12
2nd			1.18±0.04	n= 4	1.05±0.04	n=19	0.99±0.04	n=16
3rd			1.55±0.02	n= 5	1.51±0.07	n=19	1.41±0.05	n=36
4th	2.15	n=2	2.19±0.04	n=10	2.13	n= 3	2.00±0.06	n= 5
5th	3.15	n=2	3.00±0.10	n=10	3.00	n= 1	2.79	n= 3

Units are in mm, error limit is ± one standard deviation Abbreviations used: diam. = diameter; *E. m. mag. = E. m. magdalena; E. m. sax = E. m. saxicola; E. m. mack. = E. mackinleyensis; E. fasc. = E. fasciata.*

mesal banding pattern helps to unify the subgroup. The uniform black color of *E. magdalena* in both sexes differentiates the species from *E. mackinleyensis* and *E. erinnyn. Erebia erinnyn* is Asian while *E. mackinleyensis* is North American.

Erebia fasciata Butler 1868
(Figures 51 and 52, Table 3)

Eggs and larvae were examined and compared with immatures of *Erebia mackinleyensis* and *E. magdalena* .

Material Examined.—

Immatures. CANADA. Yukon; Dempster Highway, 14 eggs and egg shells, 11 first larvae, 4 second instar larvae, 38 third instar larvae, 4 fourth instar larvae, 3 fifth instar larvae and associated exuviae (HILC).

Erebia mackinleyensis Gunder 1932
Figures 37, 38, 40 and 44 - 50, Tables 1, 2 and 3)

Recognition.— Most adults are easily recognized by reddish wing patches to well marked bands on the wings. Geographic locality in Alaska and Yukon Territory further assists in identification.

Description.—

Adults (Figures 37, 38, 40 and 44). Form, shape and general appearance are similar to *E. magdalena* as mentioned by Gunder's original description (1932). Data are summarized in Tables 1 and 2. Maculations are more prevalent in both sexes. Most females (91%, n=15) display a conspicuous rust patch on the forewing (Figure 44) or at least scattered rust scales. Males show the same marking but at a lower frequency (74% n=39). Both sexes have a ventral mesial band on the hind wing (males 97%, n=39; females 100%, n=15). Few white hairs and scales are present on either sex. The antennal club is different from *E. magdalena* in that it tends to be testaceous to two-toned yellow (Figure 40). A few *E. mackinleyensis* adults had darker antennal clubs (7.5%, n= 39 males, 0%, n=15 females) resembling those of *E. magdalena.*

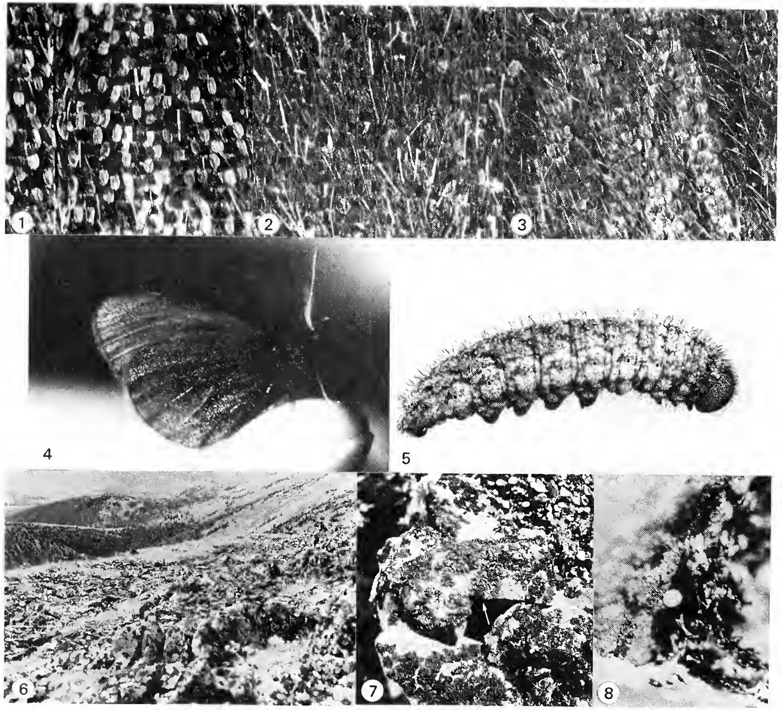
Male genitalia are similar to those of *E. magdalena* The spination on the uncus is expanded onto the inner surface (Figures 37 and 38).

Larvae (Figures 46–50, Table 3). Larvae were indistinguishable from those of *E. magdalena* but differed from those of *E. fasciata. Erebia fasciata* larvae were similar in body appearance structurally but differed in maculation pattern and first instar larvae (Figure 52) showed differences in the sculpture pattern of the head capsule. Measurements of head capsule are summarized in Table 3.

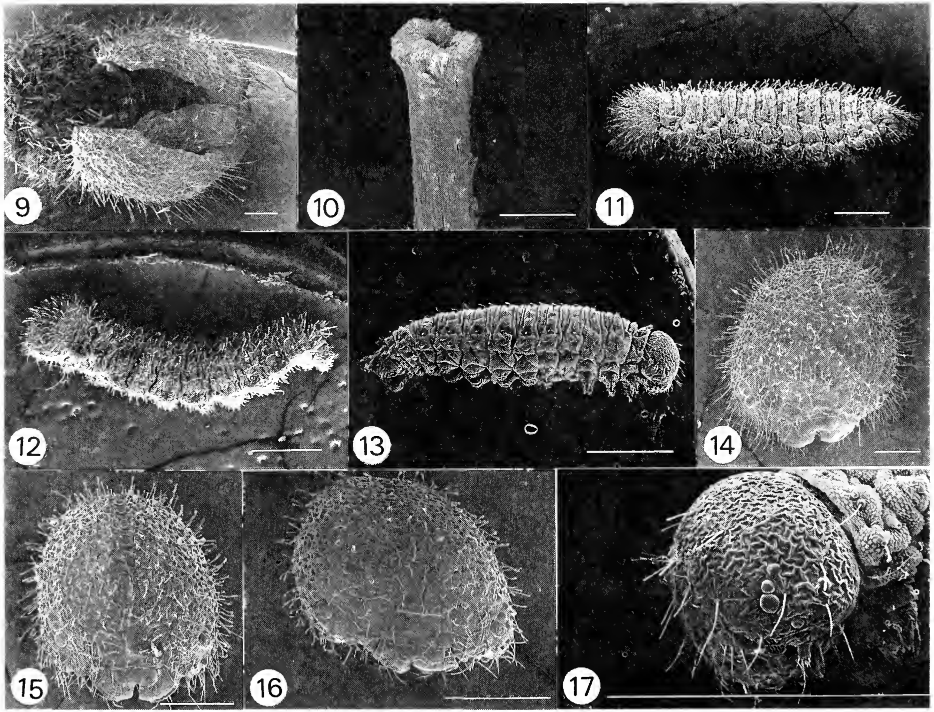
Egg (Figure 45). Sculpture and shape are very similar to that seen in eggs of *E. magdalena*, length 1.10 mm, diameter 1.28 mm, (n= 11). The area around the micropyle appears different; (compare Figures 24 and 45). The basic ground plan pattern is similar but differs in the number of micropyle holes (the differences could be due to individual variation). For comparative purposes the micropyle region of a third species of the *magdalena* group was examined, *E. fasciata* (Figure 51). On the eggs of this species the micropyle region is very similar to that seen on the eggs of *E. mackinleyensis* with only slight symmetry differences of the openings.

Geographical Distribution.— *Erebia mackinleyensis* is known from alpine tundra rock pile habitat in Alaska and Yukon Territory. The southern range limits in the mountain regions have not been documented.

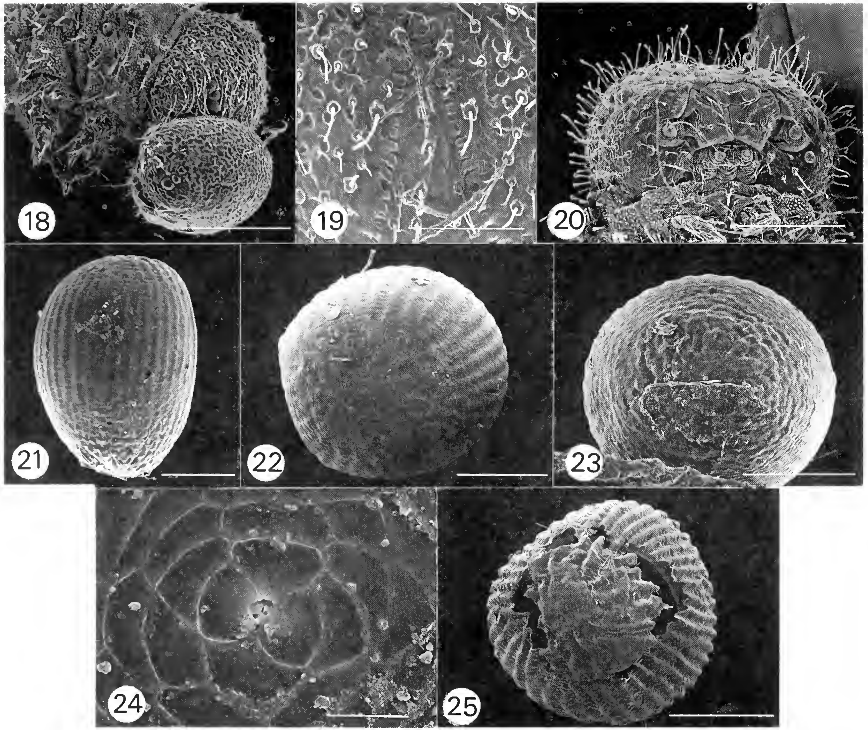
Chorological Affinities.— *Erebia mackinleyensis* occurs in areas inhabitated by other species of *Erebia*. *Erebia fasciata* is often found in close proximity. Ferris *et. al.* (1983) report on the occurrence of *E. erinnyn* in North America but the butterfly prefers low elevation moist meadow habitat and thus is not in contact with populations of, *E. magdalena* .



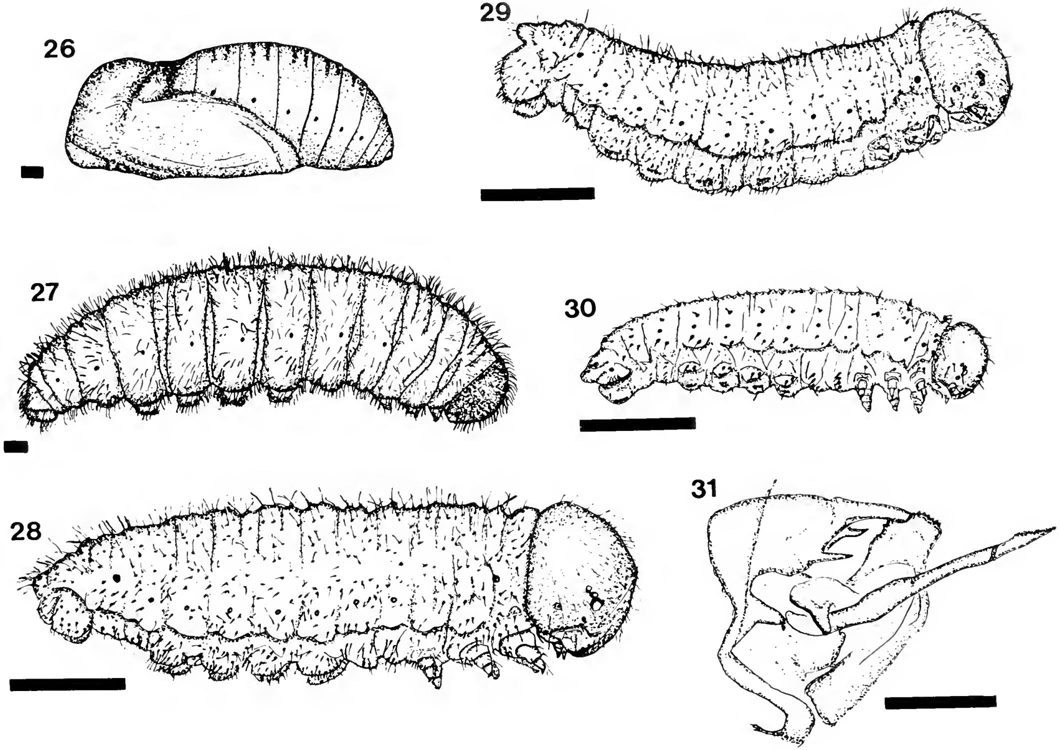
Figures 1-8. Fig. 1. White scales and hairs on ventral forewing surface of *E. magdalena saxicola* female. Fig. 2. White hairs on ventral hindwing surface of *E. m. saxicola* male. Fig. 3. Dark scales and hairs on ventral forewing surface of *E. m. magdalena* female. Fig. 4. Adult female of *E. m. saxicola*; note dusting of white on the wings. Fig. 5. Fifth instar larvae of *E. m. saxicola*. Fig. 6. View of type locality, Adams Lookout, Wilmore Wilderness Park, boulder field near top of mountain, interspersed with patches of vegetation. Fig. 7. Natural oviposition side, egg deposited under edge of rock near arrow. Fig. 8. Egg on underside of rock in Fig. 7.



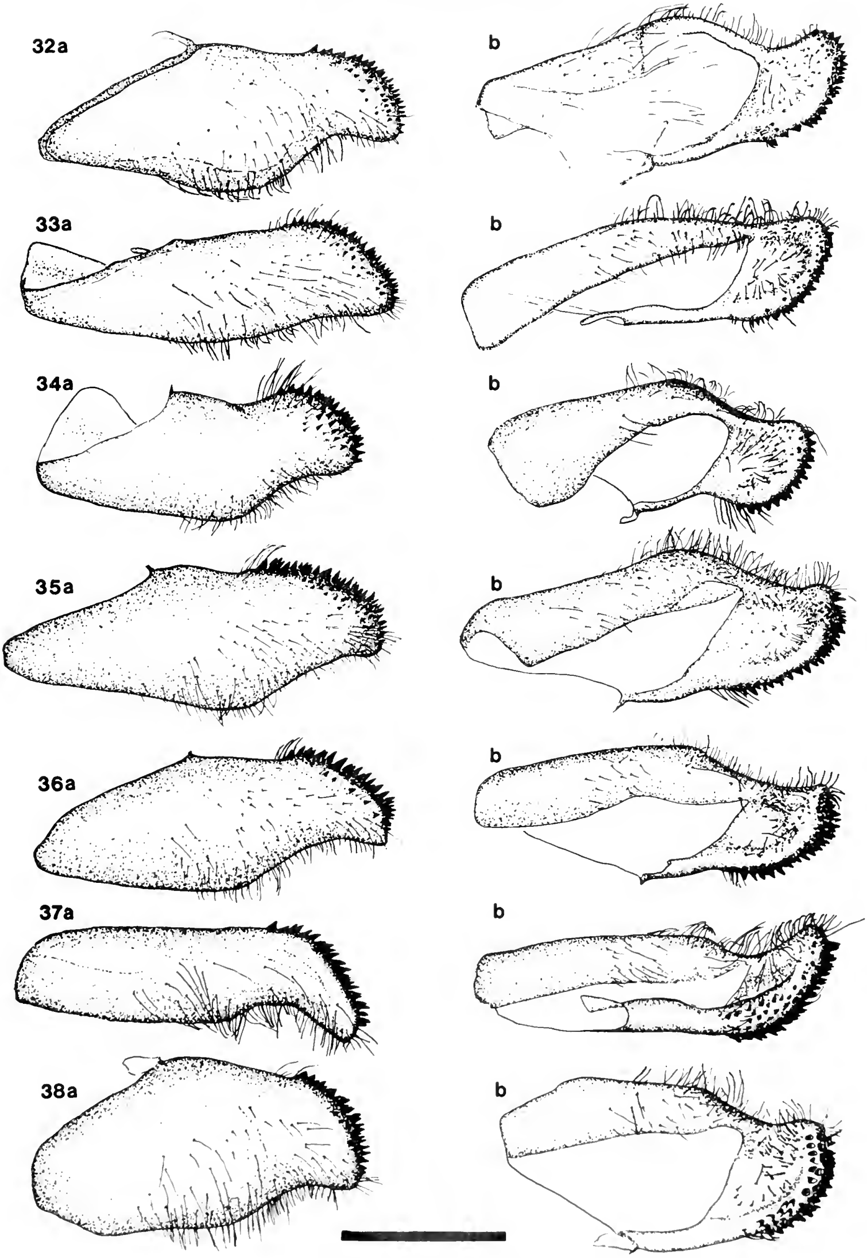
Figures 9-17. Scanning electron micrographs of *E. magdalena saxicola*. Scale line = 1 mm unless specified otherwise. Fig. 9. Cast cuticle from fifth instar larva. Fig. 10. Tip of fifth instar larval body hair; scale = 50 mm Fig. 11. Third instar larva. Fig. 12. Second instar larva. Fig. 13. First instar larva. Fig. 14. Fourth larval instar head capsule. Fig. 15. Third larval instar head capsule. Fig. 16. Second larval instar head capsule. Fig. 17. First larval instar head capsule.



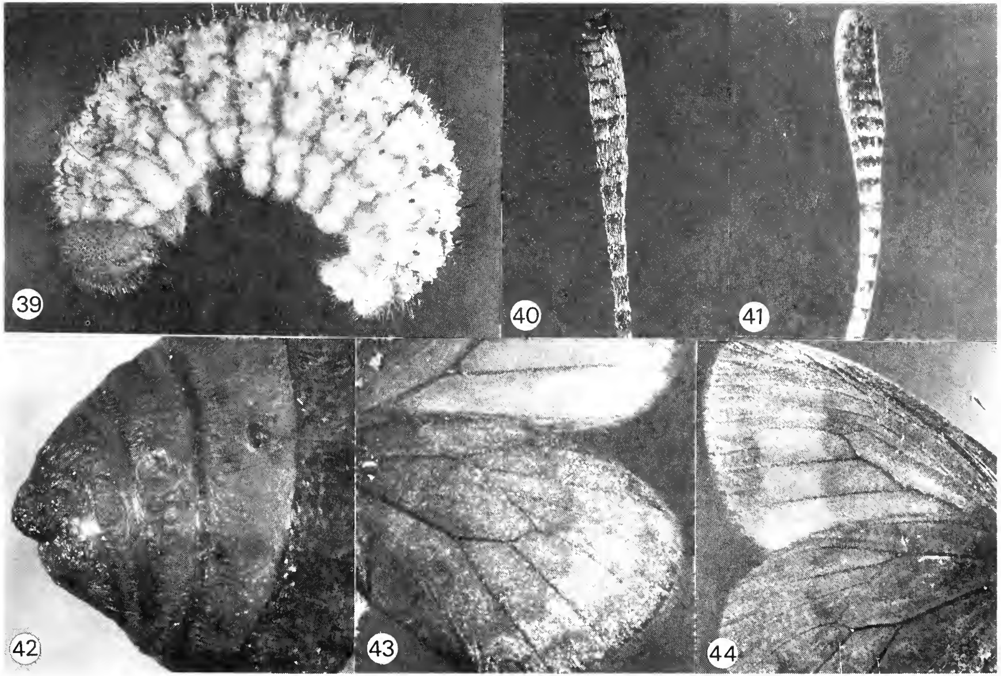
Figures 18-25. Scanning electron micrographs of *E. magdalena saxicola*. Scale line = 0.5 mm unless specified otherwise. Fig. 18. First instar molting to second instar larva. Fig. 19. Sutures on head of third instar larva. Fig. 20. Mouthparts of third instar larva. Fig. 21. Lateral view of egg. Fig. 22. Apical view of egg. Fig. 23. Basal portion of egg; note patch of adhesive material. Fig. 24. Micropyle on apex of egg; scale = 20 mm. Fig. 25. Egg after emergence of larva.



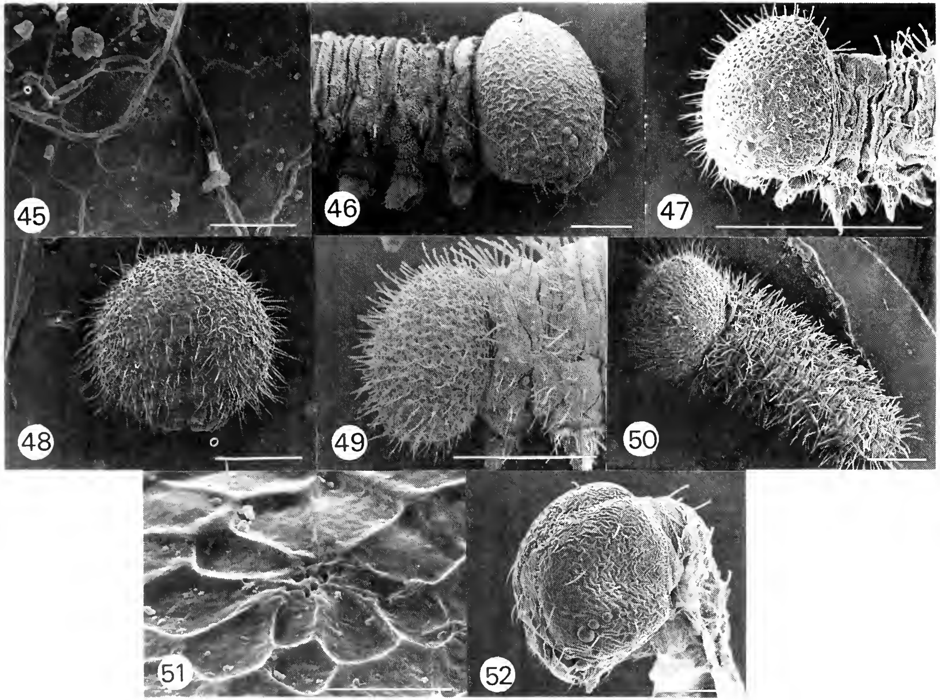
Figures 26-31. Line drawings of *E. magdalena saxicola*. Scale line = 1 mm. Fig. 26. Pupa. Fig. 27. Fifth instar larva. Fig. 28. Third instar larva. Fig. 29. Second instar larva. Fig. 30. First instar larva. Fig. 31. Male genitalia with left clasper removed.



Figures 32-38. Line drawings of the left clasper of male genitalia for *E. magdalena magdalena*, *E. m. saxicola* and *E. mackinleyensis*. Drawing **a**, view of outer surface, dorsal to the top of the page; drawing **b**, inner surface, dorsal side to bottom of page. Scale line = 1 mm. Fig. 32 *E. m. saxicola*, Adams Lookout. Fig. 33. *E. m. saxicola*, Adams Lookout. Fig. 34 *E. m. magdalena*, Utah. Fig. 35. *E. m. magdalena*, Maroon Pass, Colorado. Fig. 36. *E. m. magdalena*, Mount Audubon, Colorado. Fig. 37. *E. mackinleyensis*, Dempster Highway, km 131, Yukon. Fig. 38. *E. mackinleyensis*, Dempster Highway, Km 468, North West Territories.



Figures 39-44. Photographs of *E. magdalena magdalena*, *E. m. saxicola* and *E. mackinleyensis*. Fig. 39. Fifth instar larva of *E. m. magdalena*, reared from eggs collected at Wheeler Basin, Colorado by M. E. Young, 1973. Fig. 40. Left antennal club of *E. mackinleyensis*, *Dempster Highway, Yukon*. Fig. 41. Left antennal club of *E. m. saxicola* Adams Lookout, Alberta. Fig. 42. Abdomen of pupa of *E. m. saxicola*, reared from eggs from females collected at Adams Lookout, Alberta (adult emerged 1983, see Fig. 4.). Fig. 43. Ventral hind wing of female *E. m. magdalena*, showing enhanced banding pattern with white scales, Mount Kelso, Colorado. Fig. 44. Ventral forewing of female *E. mackinleyensis* with distinct rust patch, Dempster Highway, km 465, Yukon.



Figures 45-52. Eggs and reared larvae of *E. mackinleyensis* and *E. fasciata*. Eggs were collected by P. Ross from captive females, 1985, Dempster Highway, Yukon. Fig. 45. Egg micropyle of *E. mackinleyensis*. Scale line = 20 mm. Fig. 46. First instar larva of *E. mackinleyensis*. Scale line = 0.2 mm. Fig. 47. Second instar larva of *E. mackinleyensis*. Scale line = 1 mm. Fig. 48. Larval head capsule of third instar larva of *E. mackinleyensis*. Scale line = 1 mm. Fig. 49. Lateral view of third instar larvae of *E. mackinleyensis*. Scale line = 1 mm. Fig. 50. Dorsal view of third instar larvae of E. mackinleyensis. Fig. 51. Micropyle region on egg of *E. fasciata*. Scale line = 20 µm. Fig. 52. Head of first instar of *E. fasciata*. 0.2 mm.

Phylogenetic Relationships.— The *E. magdalena /mackinleyensis* species pair exhibits many characters which unite them as sister species: structure of male genitalia; lack of maculations from most adults; when maculations are present, a similarity of design; and presence of andriconial scales in the males. Other related species are *E. erinnyn* (Siberia, except for the presumed Canadian record); and *E. fasciata.*

Material Examined.—

Adults (males, females). CANADA: Yukon; Dempster Highway, Km 154 to 156, 34, 10 (CNC, HILC, PIKE, PRES, SHEP, SPER). Dempster Highway, Km 465 to 468, 3, 1 (CNC). U.S.A.: Alaska; Atigun Gorge, north ridge, 2, 4 (SHEP).

Immatures. CANADA: Yukon; Dempster Highway, Eggs 20 eggs and egg shells, 17 first instar larvae,16 second instar larvae, 12 third instar larvae, 2 fourth instar larvae, 1 fifth instar larvae and associated exuviae (HILC).

Erebia magdalena Strecker 1880
(Figures 1 – 5, 8 – 36, 39 and 41 – 43, Tables 1 – 3)

Recognition.— This is perhaps the plainest butterfly species in North America, most specimens exhibiting a uniform dull black to dark brown color.

Description.—

Adults (Figures 1–4, 31–36, and 41). Wings dark blackish brown, population variations occur with some individuals exhibiting banding ventrally, and others developing a rust colored patch. See the discussion on character states under Character Analysis. Body similar color to the wings. Antennae annulated with gray white, club ferruginous above, black below (Figure 41).

Male genitalia as illustrated (Figures 31–36). Spination of uncus not expanded to inner surface as in *E. mackinleyensis* (Figures 37 and 38). Chromosome numbers reported by Maeki and Remington (1960) for *E. magdalena* from Gunnison County, Colorado were 10 large, 11 medium and 8 small for a sum of 29.

Immatures (Figures 5, 9–28, 39, 42; Table 3). Pupa (Figures 26 and 42). Alberta specimen (n=1); Length, 14 mm long. Head and thorax regions olive to dark green with abdomen medium brown tinged with green, without distinct markings, spines or hairs. Cremaster blunt, rounded (Figure 42), sculpturing on abdominal sclerites is a series of short longitudinal lines (Figure 42). Silk not observed. Colorado specimen; (from photo, YOUN) similar to Alberta specimen.

Larva, fifth instar (Figures 5 and 27). Alberta specimens (n=10); Integument with numerous blunt hairs (Figure 10). Head capsule dark brown, ground color of body green with black mottled maculations (Figure 5). Head capsule width 3.00 ± 0.10 mm. Colorado specimens (n=2); head capsule lighter brown, photo of larvae show light green ground colour, head capsule width 3.15 mm.

Larva, fourth instar. Alberta (n=10); Similar to fifth instars except smaller and with fewer hairs. Head capsule (Figure 14), width 2.19 ± 0.04 mm, n= 10. Colorado specimens (n=2); Ground colour cream in preserved specimens, head capsule width 2.15 mm.

Larva, third instar (Figures 11 and 28). Alberta specimens (n=5); similar to fourth instars, with reduced maculation and fewer hairs. Head capsule (Figure 15) width 1.55 ± 0.02 mm. Colorado specimens not seen.

Larva, second instar (Figures 12 and 29). Alberta specimens (n=4); hairs very few, no obvious maculations, ground color green. Head capsule, brown, lightly rugose (Figure 16) width 1.18 ± 0.04 mm. Colorado specimens not seen.

Larva, first instar (Figures 13 and 30). Alberta specimens (n=25); hairs very few, in discrete pattern. Ground color various from cream to light green with no dark maculations. Head capsule (Figure 17) with markedly rugose sculpture. Head width measurements 0.812 ± 0.018 mm. Colorado specimens (n=2); Similar ground colour, cream in preserved specimens, head capsule width 0.743 mm. Published illustration in Edwards [1888, collected by Mr. Bruce at Hall Valley, Mount Bullion (Edwards 1951)].

Egg (Figures 8, 21–25). Alberta specimens (n=25); ovoid with rounded ridges on sides (Figure 21). Top and bottom with rounded bumps (Figures 22 and 23). Micropile centered at apex (Figure 24). Color cream, darkened just before hatching. Length 1.45 ± 0.07 mm with diameter of 1.22 ± 0.07 mm. Bottom glued to substrate during oviposition (adhesive pad on bottom of egg, Figure 23). Colorado specimens (n=3); Similar in appearance, length 1.36 mm, diameter 1.23 mm. Published illustration in Edwards (1888).

Geographical Distribution.— *Erebia magdalena* is known from the high alpine meadows of northern New Mexico, through Colorado, Utah and Wyoming north to southern Montana, and west central Alberta and adjacent British Columbia.

Chorological Affinities.— Few other species of butterflies share the high mountain slopes with *E. magdalena.* Other species of *Erebia* may be found as strays in high mountain habitat, but none are closely related to *E. magdalena.*

Phylogenetic Relationships.— As indicated, *E. mackinleyensis* and *E. magdalena* appear to be sister species. *Erebia magdalena* populations show recognisable differences which can be attributed to subspeciation on isolated mountains. Taxa included are *E. m. magdalena* Strecker and *E. m. saxicola* new subspecies.

Erebia magdalena magdalena Strecker 1880
(Figures 3, 4 - 36, 39 and 43, Tables 1 - 3)

Recognition.— These butterflies are dark brown to black, with individuals in southern populations exhibiting mesial bands (predominantly in females) and occasionally with rust colored scales, but seldom developed as a distinct patch.

Description.—As described for *E. magdalena.*

Geographical Distribution (Figure 58).— *Erebia magdalena magdalena* is known from northern New Mexico, through Colorado, eastern Utah, north to Wyoming and southern Montana.

Chorological Affinities.— Few other high elevation butterflies are found in the same habitat. Some of these are *Oeneis melissa* (*O. m. lucilla* Barnes and McDunnough, in Colorado *O. m. beani* Elwes, in Montana and Wyoming). Other high elevation species are found in adjacent habitats of moist meadows such as *O. polixenes* (Fabricius), *O. taygete* Geyer and *Colias nastes streckeri* Grüm-Grschimailo. No other species of *Erebia* shares the high mountain habitat with *E. magdalena.*

Phylogenetic Relationships.— The very local isolated populations scattered over many mountains has facilatated population differentiation. The analysis of the different populations shows a clinal type relationship (Graphs A and B), with individual character states showing no clear trends. The greatest shift is shown with the Alberta population, described below as a separate subspecies.

Material Examined.—

Adults (males, females). U.S.A.: Colorado; Boulder County; Arapahoe Pass 1, 0 (USNM). Arapahoe Pass Trail 3, 0 (YOUN). Boulder 3, 2 (USNM). Mount Audubon 11, 3 (ALME, AMNH, CNC, USNM). Mount Navajo, ridge east of, 1, 2 (ALME, USNM). Navajo Peak, 1, 0 (USNM). Needles Eye Tunnel, Corona Pass 1, 2 (ALME, SHEP). Niwot Ridge, near Ward 1, 0 (CNC). Clear Creek County; Loveland Pass 40, 11 (ALME, INHS). Mount Kelso 0, 2 (PIKE, YOUN). Custer County; Hermit Pass 1, 0 (PRES). Grand County; Berthoud Pass 2, 0 (YOUN). Corona Pass 2, 0 (ALME). Wheeler Basin 0, 2 (YOUN). Gilpin County; Corona Pass 4, 0 (ALME, AMNH, PRES). Gunnison County; Copper Lake, above 1, 0 (USNM). Cumberland Pass 2, 0 (SHEP). East Maroon Pass 9, 1 (SPER). Yule Pass 0, 1 (SPER). Hinsdale County; Mount Umcompadre 0, 1 (SPER). La Plata County; Chicago Basin 1, 0 (AMNH). Larimer County; (Rocky Mountain National Park) 6, 3 (ALME, CNC, USNM). Longs Peak 3, 1 (ALME, AMNH). Peacock Lake 1, 1 (ALME). Specimen Mountain 2, 2 (ALME, USNM). Park County; 2, 0

(USNM). Hall Valley 9, 9 (ALME, USNM). Hoosier Pass 0, 1 (AMNH). Bullion Peak 1, 0 (USNM). Pennsylvania Mountain 0, 1 (ALME). Storm Peak 1, 0 (ALME). Montana: Carbon County; Beartooth Plateau 5, 3 (SHEP). New Mexico: Taos County; Wheeler Peak 4, 3 (INHS). Utah: 3, 0 (ALME, UASM). Summit and Duchesne Counties; Bald Mountain 8, 1 (ALME, PRES). Summit County; 1, 0 (ALME). Uintah County; Leidy Peak 8, 3 (ALME). Wyoming: Fremont County; 1, 0 (USNM).

Immatures. U.S.A.: Colorado: Boulder County; Corona Pass, Eggs 3 (shells), 1st instar 1 (UASM). Grand County; 1st instar 1, 4th instar 1, 4–5th instar (died in moult) 1, 5th instar 1, photographs of larvae and pupa (YOUN).

Erebia magdalena saxicola, NEW SUBSPECIES
(Figures 1, 2, 4, 5, 8 - 33 and 41, Tables 1 - 3)

Derivation Of Subspecific Epithet — The subspecies is named for its association with rocky habitat. All specimens were captured on a boulder field on top of a mountain. *Saxicola* from Latin means 'inhabits rocks'.

Type Material.— Holotype: male, Adams Lookout, Alberta Forestry Service, Wilmore Wilderness Park, Alberta, 1.viii.81, G.J. HILCHIE. Allotype: 24.vii.81, same locality data.

Paratypes: 27 males, 19 females, Adams Lookout, AFS, Wilmore Wilderness Park, Alberta, 4.vii.81, K. AVERY; 1.viii.81, G.J. HILCHIE; 11.vii.82, F.A.H. SPERLING; 12.vii.82, F.A.H. SPERLING; 12.vii.82, E.M. PIKE; 13.vii.82, E.M. PIKE; 24.vii.82, G.J. HILCHIE; 25.vii.82, G.J. HILCHIE; 29.vii.84, G.J. HILCHIE; Mount Hamell, 23.vii.84, K. AVERY; 25.vii.84, K. AVERY; 30.vii.84, K. AVERY; 26.vii.85, G.J. HILCHIE; 27.vii.85, G.J. HILCHIE; 28,vii.85, G. HILCHIE; Dore River, near McBride, British Columbia, 15.viii.84, D. L. THREATFUL.

Type material is deposited in the following institutions: holotype, allotype, and 6 paratypes, CNC; 4 paratypes, USNM; 6 paratypes, UASM; 5 paratypes, Alberta Provincial Museum, Edmonton; 8 paratypes, AVER; 10 paratypes, HILC; 5 paratypes, SPER; 2 paratypes, PIKE. 2 paratypes, SHEP.

Type Locality.— Adams Lookout, Alberta Forestry Service, Wilmore Wilderness Park, 43 km southeast of Grande Cache, Alberta, Canada.

Recognition.—This subspecies is distinguished from *Erebia magdalena magdalena* by the following features: males have scattered white hairs on the ventral surface of the wings; females have scattered white scales and hairs on the ventral surface of the wings (Figures 1, 2 and 4) with concentrations near the apex of the forewing, mesial wing bands absent; geographic range confined to Alberta and B.C.

Description.—

Adults (Figures 4, 31–33 and 41). Male: wings with ground color, dorsal and ventral dark brown to black without pattern, androconial scales present; forewing length 23.8 ± 1.2 mm[1], range 21.4–26.1 mm; hind wing length 19.9 ± 0.9 mm, range 17.7–21.7 mm, n=28; ventral surface of wings with scattered white hairs near apex of forewing and on central area of hind wing (Figure 2). Genitalia typical for *E. magdalena* as illustrated in Warren (1936, Plate 35, Figure 327 and 330). Claspers various in shape (Figures 32 and 33). Gnathos, uncus and aedeagus typical for *E. magdalena* (Figure 31).

Haploid chromosome number is 29 (mode number from counts).

Female: wings with color similar to male; forewing length 25.0 ± 1.4 mm, range 22.1–27.7 mm; hindwing length 20.5 ± 1.3 mm, range 17.2–22.8 mm, n=20; ventral surface of wings with white hairs near tip of forewing and on most of hindwing (Figure 1). Twelve of 16 females examined had from a few to hundreds of white or very pale scales near the tip of the forewing and on the central area and margins of the hindwing. Four females appeared to have their wings dusted with white scales when viewed at low magnification.

Immatures (Figures 5–30). As figured and previously described.

---

[1] One standard deviation

Habitat.— *Erebia magdalena saxicola* inhabits alpine boulder fields (ca. 2200 to 3000 m), interspersed with patches of vegetation (Figure 6).

Geographic Distribution (Figure 58).— Known from Adams Lookout, (Wilmore Wilderness Park) and Mount Hamell in Alberta and in an adjacent area in British Columbia which are widely disjunct from the next nearest known populations, found in southern Montana.

Chorological Affinities .— *Erebia discoidalis* Butler, *E. epipsodea* Butler, and *E. disa* Thunberg overlap in range with *E. m. saxicola* None of these species share the high mountain habitat.

Phylogenetic Relationships.— *Erebia magdalena saxicola* is the sister group of *Erebia magdalena magdalena.*

Material Examined.— Type material only.

LIFE CYCLE AND BEHAVIOUR OF *EREBIA MAGDALENA SAXICOLA*

Behaviour of Adults

Males and females (about 1:1) are in the same flight area from July 4 to August 1. They fly over areas of rocks covered with the black lichens *Hypogymnia oroarctica* Krog., *Umbilicaria proboscidea* (L.) Schrad., *U. hyperborea* (Ach.) Hoffm., *Pseudephebe pubescens* (L.) Choisy, and the yellow crustose lichen *Rhizocarpon geographicum* (L.) DC. Rock areas are interspersed with patches of vegetation in the centers of polygon frost formations (Figure 6). Vegetation is high mountain alpine, with the ground cover dominated by *Dryas hookeriana* Juz., *Salix arctica* Pall. and *Silene acaulis* L. Other plant taxa are *Saxifraga oppositifolia* (L.), *Oxitropis podocarpa* A. Gray, *Cassiope tetragona* (L.), *Carex* spp. and various alpine grasses, *Festuca saximontana* Rydb. and *Poa alpina* (L.) (Porsild, 1974).

Erebia magdalena saxicola adults fly in association with many alpine butterfly species but only a few are found in the same habitat [*e.g., Boloria astarte* (Doubleday and Hewitson) and *Oeneis melissa* (Fabricius), see Table 4.]. Some of these species are near the limits of their ranges, *e.g., Boloria napaea alaskensis* (Holland) is at its southern limit and *Boloria alberta* (Edwards) at is at its northern known limit.

Adults fly in sunshine from about 1000 hr to 1730 hr. Females have a wandering flight over the rocks, periodically landing to bask or visit flowers. Males appear more directed in flight, and dark butterflies that pass near them are pursued with great vigor. These included female *E. magdalena*, other males, and males and females of *Oeneis melissa.*

Oviposition

Oviposition in the field occurs in areas of loose rock which are covered by black lichen. One female observed ovipositing backed down the side of a rock (Figure 7) and laid a single egg on the underside near an edge (egg shown on rock in Figure 8). Eggs laid in the field are not placed near plants.

Development

In the laboratory, females laid eggs on any substrate (rocks, cage, water container), preferring sides and lower surfaces. Oviposition normally occurred in the early morning, with some eggs being laid in late afternoon.

Table 4. List of butterflies collected at or near Adams Lookout, Alberta Forest service, Wilmore Wilderness Park, Alberta (1980-1983).

Species	Collection areas				
	Valley	Subalpine	Alpine [1]		
	willows, meadows	pine, fir, spruce	wet meadows	dry meadows	rocks, scree
Erynnis persius Scudder	++[2]				
Hesperia comma manitoba Scudder	+++	++			
Pyrgus centaurae freija Warren	++	+			+
Carterocephalus palaemon mandan Edw.	++				
Euchloe creusa Dbld.	+				
E. ausonides ausonides Lucas	+				
Anthocharis sara Lucas [3a]	+				
Colias meadii elis Strecker		+	+		
C. alexandra christina Edw.	+++	+			
C. nastes streckeri Gr. Gr.			+	+++	+
C. pelidne minisini Bean	+				
C. philodice philodice Godart	++				
C. interior interior Scudder	+				
Pieris napi oleracea Harris	+	+			
P. protodice occidentalis Reak.			+	++	+
Parnassius phoebus Fabricus [3a,b]		+++	++		
Papilio machaon L.	+				+
P. machaon X *zelicaon*					++
P. zelicaon Lucas	+				+
P. glaucus canadensis R. & J.	++	+			
Plebjus argyrognomon scudderii Edw.	++	+			
P. saepiolus amica Edw.	++				
P. aquilo megalo McD.	+	+	+	+	
Glausopsyche lygdamus Dbld.	+++	+			
Everes amyntula Boisduval	++				
Celastrina argiolus lucia Kby.	+	+			+
Lycaena phleas arethusa Dod.	+++	+	+	+	
L. cupreus snowi Edw.	+	+		+	
L. dorcas Kby.	++	+			
L. mariposa Reakirt	+				
Erebia disa mancinus Dbld.	+				
E. epipsodea epipsodea Butler	+++	+			
E. magdalena saxicola n.ssp.					+++

(continued on next page)

Table 4 (continued)

Species	**Collection areas**				
	Valley	Subalpine	Alpine[1]		
	willows, meadows	pine, fir, spruce	wet meadows	dry meadows	rocks, scree
Oeneis c. chryxus Dbld.	++	+++	+		
O. melissa beanii Elwes				+	+++
O. polixenes brucei Edw.				++	
O. taygete edwardsi dos Passos			+	+	
O. jutta chermocki Wyatt		+			
Boloria napaea alaskensis Holland				+++	+
Boloria epithore Edw.[3a]		+			
B. eunomia nichollae Barnes & Benjamin			+		
E. eunomia dawsoni B. & McD.	+++	++			
B. frigga saga Staudinger		+	+	+	
B. improba youngi Holland				++	
B. alberta Edw.					+
B. a. astarte Dbld.				+	++
B. titania grandis B. & McD.		+++	+		
B. freija freija Thunberg		+	+		
Speyeria mormonia eurynome Edw.		+	+	++	+
Phyciodes c. campestris Behr		++			
Euphydryas editha beani Skinner				+	
E. anicia anicia Dbld.		+++		+	
Nymphalis milberti Lat.	+	+	+	+	+
N. antiopa L.		+			
Vanessa cardui L.					+
Polygonia faunus rustica Edwards		+			

---

[1]. Some species collected are migrants from lower elevations "hill topping".

[2]. Key to symbols: + uncommon (1-3 specimens); ++ common (4-10 specimens); +++ abundant (11+ specimens) Numbers are based on specimens collected during visits to the alpine habitat.

[3]. Additional species from nearby mountains: 3a. Horn Ridge; 3b. Mount Hamell).

Table 5. Rates of development for immatures of *Erebia magdalena saxicola.*

Stadia	Development Time (days/stadia)		Sample Size
	Minimum	Maximum	
egg	11	12	110[1]
first	4	6	75
second	8	36	31
third	14	68	18
fourth	22	90	11
fifth	99[2]	-	1
pupa	7	-	1

[1]. Numbers refer only to those individuals which matured and moulted to the next stadium.

[2]. Includes time while in diapause in an incubator (33 days below +4°C)

Larvae were reared in the laboratory. Development from egg to adult required a minimum of 165 days. Eggs and early instar larvae were maintained at 20–23°C. Development was rapid and mortality high. Table 5 summarizes rates of development

Fourth, and especially fifth instar larvae were slower in development than the first 3 instars. The surviving fifth instar larva pupated after a 99 day stadium including 63 days at 20–25°C and 33 days at +4 to -2°C. During cold treatment larvae were provided with food. One larva continued to feed at +4°C for a few days. Upon removal from the incubator fifth instar larvae were given fresh food. The larvae did not resume feeding (T=20°C, photo period natural short day). Larvae were returned to the incubator for five days at +4°C then brought out in another attempt to stimulate feeding. The temperature was raised to 25°C and they were placed under artificial photoperiod of 16 hours of light and 8 hours of dark. All larvae resumed feeding. Of the 11 reared to fifth instar and brought through the incubation process, 10 contracted a fungal infection and died, one pupated and emerged as an adult. In the molt from fifth instar to pupa, the head capsule splits (Figure 9) and is shed posteriorly with the rest of the larval cuticle. Pupal period at 25°C had a duration of 7 days (n=1) and a female emerged.

By comparison with the natural time span available for development with the rate of development in Table 5, I infer that larvae falcultatively overwinter in Alberta as second or third instar larvae with potential for diapause in any larval instar. Rates of development barring diapause are sufficient that the species should normally complete one generation per year, but two or three years may be required pending unfavourable climatic conditions.

Food Plants.— Larvae were fed grasses throughout rearing. First instar larvae were given a choice of black lichen, fleabane, willow, dandeleon, larkspur, lawngrass clippings, and barley. Larvae readily ate grass clippings and barley. The lawn clippings were a mixture of creeping fescue and Kentucky blue grass. Judging from the oviposition site and non-specificity of food grasses, larvae will eat most grasses of the alpine zone.

EVOLUTION OF *EREBIA MAGDALENA* STRECKER

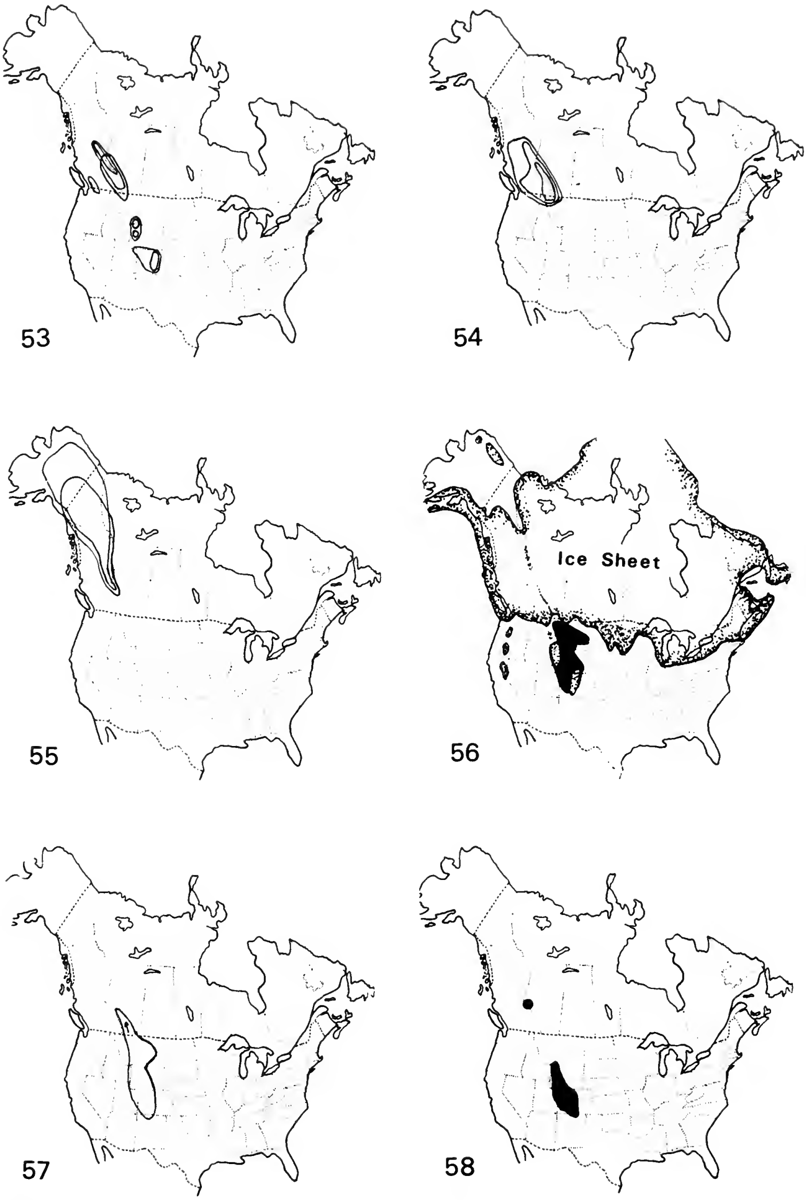
Erebia magdalena belongs to a group of Rocky Mountain arctic-alpine butterflies the components of which are distributed more or less discontinuously from Colorado to Alaska. *Erebia magdalena* is the southern sister-species of the Beringian *Erebia mackinleyensis*. This pair of vicars is likely the descendant of an ancestral arctic-alpine stock the range of which was interrupted by one of the pre-Wisconsinan glaciations, since it is unlikely that the surviving stocks would have differentiated to the species level in the time interval embraced by the Wisconsinan glacial stage plus the Holocene (See Whitehead, 1972:334-337, for a discussion of rates of speciation in insects).

Erebia magdalena/mackinleyensis stock dispersed into North America from Asia during one of the early glacials. Subsequent dispersal and isolation during glacial and interstadial periods caused speciation of *Erebia magdalena* and *Erebia mackinleyensis*.

Time of differentiation within *Erebia magdalena* could be comparatively recent, for the included taxa are very similar to one another. Two hypotheses have been proposed that would account for both the discontinuity in range between the two subspecies and their differentiation. Scudder (1979) proposed that the Alberta fauna has a southern affinity and dispersed northward from Wisconsinan-time refugia located south of the ice as the glacial ice melted and exposed the underlying soil. Subsequently, as the climate became more temperate, alpine stocks moved upward to suitable sites at higher altitude on the slopes of the Rockies, with consequent interruption of geographical ranges.

On the other hand, Pike (1980) proposed that various arctic-alpine stocks of butterflies of southern affinity survived the Wisconsinan glaciation on known nunataks and thus were isolated for an extended period of time from their counterparts which survived in suitable habitats south, or north of the ice. As a result of isolation, differentiation took place, at least to the subspecies level (see Kavanaugh (1979:39-40)), for discussion of rates of subspeciation in montane carabids). Although the geological evidence favoring existence of nunataks on the eastern slopes of the Rockies seems firm, and a few plants (Packer and Vitt 1974) exhibit distribution patterns consistent with survival in such areas (also proposed by Pike 1980, for two butterfly subspecies), I am not convinced that nunataks did serve as refugia for butterflies.

I have re-examined distribution data for alpine butterflies (Ferris and Brown 1980; Shepard, British Columbia butterfly distribution maps, pers. comm.; Bird *et. al.*, Alberta butterfly distribution maps, pers. com.; Ferris *et.al.*, 1983). Of the 12 taxa examined by Pike (1980), four are not restricted to above treeline (*E. editha beani, L. phleas arethusa, L. cupreus snowi*, and *B. e. nichollae*). The remaining eight may be considered true alpine/tundra insects. Mapping generalized ranges for each recognizable subspecies, six are distributed widely in the Alberta and British Columbia Rockies with some populations also in the Canadian coastal ranges and in the Rocky Mountain states of the United States (Figures 53 and 54), implying a refugium south of the ice. Two other species show a northern origin (Figure 55) with a distribution pattern extending along the mountains (personal collecting records show *B. improba* at several localities including, Alberta— Adams Lookout, Horn Ridge, British Columbia— Torrens River, Thunder Mountain and Pink Mountain) from the Yukon. This



Figures 53-58. Butterfly distribution and proposed Pleistocene scenerio maps. Fig. 53. Generalized distribution for *Oeneis polixenes brucei*, *O. taygete edwardsii*, and *O. melissa beani*. Fig. 54. Generalized distribution for *Colias nastes streckeri*, *Boloria astarte astarte*, and *B. alberta*. Fig. 55. Generalized distribution for *Boloria improba youngi* and *B. napea alaskensis*. Fig. 56. Posible distribution of *Erebia magdalena ca*. 1700 B.P. with continuous range in a Wisconsinan refugium. Fig. 57. Dispersal and movement of *E. magdalena ca*. 1200 B.P. north along the foothill ranges following retreating ice sheets. Fig. 58. Present range of *E. magdalena* following climatic readjustments, extinctions and isolation with subspecies differentiation. (dot = *E. m. saxicola*, black area = *E. m. magdalena*).

differs from Pike's proposed interpretation: the range of the one disjunct (*B. improba*), actually extends along the mountains and the one supposed endemic (*B. eunomia*) is not actually a true alpine species but has a wide ranging lowland form, surrounding the highland form that occurs in the Mountain Park area (Cadomin, Alberta).

In terms of available biogeographic data there is no firm support of the hypothesis that a few butterfly species survived on nunataks in northwestern Alberta between the ice sheets. All the alpine butterfly species found in Alberta have portions of their ranges in unglaciated areas south or north of the limits of the Wisconsinan Ice sheet.

If the character states of a population are intermediate between populations found in Alaska and Colorado, it would be reasonable to assume that this population is a relict of a former cline and may have moved to its present location from a nearby refugum. If character states of a geographically intermediate population are not intermediate between those of the geographically adjacent populations, but closely related to one of the populations it would then be more reasonable to assume that these populations share a common parental stock. Present distributions are the result of local extinctions, and migrations over time, creating the illusion of long distance dispersal. It would appear more parsimonious to propose that even for those taxa which show subspecific differentiation, and are not intermediates of a cline, that their parental stocks dispersed from refugia along the northern or southern margins of the ice sheet, and that their differentiation in Alberta is post-glacial in age. I believe this is true of *Erebia magdalena*, and the following scenario including the history of *Erebia mackinleyensis* is based on this belief.

At the zenith of the Wisconsinan Glacial stage the parent stock of *Erebia magdalena* is postulated to have occupied alpine-tundra habitat south of the ice in areas of Montana, Wyoming and Colorado (Figure 56). During melting of the ice mass, the butterflies followed newly developing habitat north along the Rocky Mountain foothills, probably in an ice free corridor (Prest 1969) (Figure 57). Dispersal rate would be affected by dispersal rate of host grasses. Continued climatic amelioration caused suitable lowland habitats to disappear, forcing populations up the east slopes of the Rockies. Isolation of butterfly populations occurred at this time (circa 10,000 years BP).

As the climate continued to ameloriate, alpine-tundra habitats were displaced higher up the mountains. Aridity in the alpine zone of southern Alberta and Montana may have led to shifts in floral composition resulting in local population extinctions of certain butterfly species possibly due to chinook conditions resulting in dry mild winters with very little protective snow cover. The vicariance of *Erebia magdalena* populations (Figure 58) is thus postulated. Three alpine butterfly species, *Oeneis polixenes brucei, Oeneis melissa beani*.and *Oeneis taygete edwardsii* have a similar vicariance with populations in the north (Alberta Rockies) and south (southern Montana, Wyoming and Colorado, Figure 53).

Isolation of relatively small populations of *Erebia magdalena* in the northern Rockies created conditions conducive for genetic drift, resulting in subspecfic differentiation.

CONCLUDING STATEMENT

Erebia magdalena is in the process of speciation, although isolation and speciation did not occur during, but after the Wisconsinan glacial and continues to the present. Other alpine-arctic butterflies in the Rockies of northern Alberta and British Columbia may be represented by unique populations as a result of recent isolation during the last 8,000 to 10,000 years. Additional study of the flora and fauna may reveal additional presently unrecognized subspecies with strong southern affiliations.

ACKNOWLEDGEMENTS

I thank C.D. Bird for identifying the lichens and D.R. Maddison for preparing chromosome slides from material provided by F.A.H. Sperling. Thanks are extended to K. Avery, E.M. Pike, J.&F. Preston, F.A.H. Sperling, J.H. Shepard, and D.L. Threatful for loan of material from their private collections and collecting data. Thanks are extended to the following museum curators for the loan of specimens: J.D. Lafontaine (CNC), K.C. McGiffen and M. Toliver (INHS), L.D. Miller (ALME), F.H. Rindge (AMNH), and R.K. Robbins (USNM).

Special thanks are extended to M.E. Young for the loan of adults and larvae of *Erebia magdalena* with photographic documentation of the immatures, and to J. Peter Ross for providing live eggs of *E. mackinleyensis* and *E. fasciata*

I thank G.E. Ball, C. Guppy and F.A.H. Sperling for critical review of this manuscript.

This research was supported with funds from the Strickland Memorial Trust Fund.

REFERENCES CITED

Butler, A.G. 1868. A catalogue of the diurnal Lepidoptera of the family Satyridae in the collection of the British Museum. London. 211 pp., 5 plates.

Edwards, W.H. 1887–1893. The butterflies of North America, third series. Boston; Houghton, Mifflin and Company. Part 5, May 28, 1888. Containing *Melitaea rubicunda, Erebia magdalena, Debis portlandia.*

Edwards, W.H. 1951. The entomological reminiscences of William Henry Edwards (with introduction and annotations by C.F. dos Passos). Journal of the New York Entomological Society. 59:129–186.

Ehrlich, P.R. and A.H. Ehrlich. 1961. How to know the butterflies. Wm. C. Brown Co. Pub., Dubuque Iowa. 262 pp.

Ferris, C.D. and F.M. Brown. 1980. Butterflies of the Rocky Mountain States. University of Oklahoma Press, Norman. 442 pp.

Ferris, C.D., C.F. dos Passos, J.A. Ebner and J.D. Lafontaine. 1983. An annotated list of butterflies (Lepidoptera) of the Yukon Territory, Canada. Canadian Entomologist 115:823–840.

Gunder, J.D. 1932.New Rhopalocera (Lepidoptera). Canadian Entomologist 64:276–284.

Howe, W.H. 1975. The butterflies of North America. Doubleday and Co. Inc. Garden City, New York. 633 pp.

Kavanaugh, D.H. 1979. Rates of taxonomically significant differentiation in relation to geographic isolation and habitat: examples from a study of the nearctic *Nebria* fauna. p. 35–57. *In* Carabid beetles: their evolution, natural history, and classification. Eds. Erwin, Ball, Whitehead and Halpern. Dr. W. Junk bv Publishers. The Hague 1979. 635 pp.

Maeki, K. and C.L. Remington. 1960. Studies of the chromosomes of North American Rhopalocera. 3. Lycaenidae, Danainae, Satyrinae. Journal of the Lepidopterists Society. 14:127–147.

Packer, J.G. and D.H. Vitt. 1974. Mountain Park: a plant refugium in the Canadian Rocky Mountains. Canadian Journal of Botany 52:1393–1409.

Pike, E.M. 1980. Origin of tundra butterflies in Alberta. *Quaestiones Entomologicae*. 16:555–596.

Porsild, A.E. 1974. Rocky mountain wild flowers. National Museums of Canada and Parks Canada. 454 pp.

Prest, V.K. 1969. Retreat of Wisconsin and recent ice in North America. Geological Survey of Canada Map 1257A.

Scudder, G.G.E. 1979. Present patterns in the fauna and flora of Canada. p. 87–179 *In* Danks, H.V. (Editor). 1979. Canada and its insect fauna. Memoirs of the Entomological Society of Canada. No. 108. 573 pp.

Simpson, G.G. 1961. Principles of animal taxonomy. Columbia Uinversity Press, New York. 247 pp.

Strecker, F.H. 1880. Descriptions of some new species and varieties of North American Lepidoptera. Bulletin of the Brooklyn Entomological Society. 3:33-36.

Warren, B.C.S. 1936. Monograph of the genus *Erebia*. London. 407 pp., 104 plates.

Warren, B.C.S. 1981. Supplement to monograph of the genus *Erebia* E.W. Classey, Faringdon, England. 17 pp.

Whitehead, D.R. 1972. Classification, phylogeny and zoogeography of *Schizogenius* Putzeys (Coleoptera: Carabidae: Scaritini). *Quaestiones Entomologicae*. 8:131-348.

Willis, H.J. 1967. Bionomics and zoogeography of tigerbeetles of saline habitats in central U.S.A. University of Kansas Science Bulletin 47:143-313.

COMMENTARY

[Commentary is a section of *Quaest. Ent.*that appears from time to time, and contains expressions of opinions about general items, controversial or otherwise, that ought to be of interest to many of our readers. These contributions are not refereed because they are intended to be free expressions of opinion. Changes by the Editor might be made to the form of presentation, but not to its substance. Remarks that are deliberately abusive or insulting will not be published. Rebuttals to previously expressed views will be considered, but the journal is under no obligation to publish them.

The Editor]

Linear, longitudinal markings on the outer elytral surface of beetles: interneurs or striae?

Kenneth W. Cooper
Department of Biology, University of California
Riverside, California 92521
U. S. A.

Quaestiones Entomologicae
26: 695–699 1990

The reasons given for the substitution of the neologism "interneur" for "stria", when used as a collective noun in English, are examined. They are based on a *non sequitur*, a mistaken idea that use of "interneur" solves an important problem that "stria" does not, and on the oversight that "interneur" requires redefinition to make it fully synonymous with "stria". The physical basis, homologies, and non-homology of striae are outlined. It is recommended that "interneur" be abandoned; it is an unsuitable replacement for the old and universally familiar "stria".

Only Erwin (1974) appears to have responded to Spilman's (1971) examination of the word "stria" as used in discussions and descriptions of the elytra of beetles. Spilman recommends that the longitudinal, linearly-impressed markings, such as grooves, rows of puncta, and related sculptural forms collectively be called "*elytral striae*". As Erwin is aware, major taxonomists writing in English, including among others G. H. Horn, Andrewes, Casey, Jeannel, Lindroth, and Darlington have all, at some point, found it convenient to use "stria(e)" in the collective sense of "elytral stria(e)", as well as in the structural sense. None subsequently appears to have been misled by their and other's double usage of "stria". In what follows, "*stria(e)" will be used to designate and shorten repeated use of "elytral stria(e)" and its grammatical derivatives.

Spilman points out that an alternative to his suggestion would be coinage of a new collective term, but he does not advocate doing so. Nevertheless, Erwin has proposed the new generic term "interneur" to encompass the various forms taken by elytral striae. His grounds for advancing that neologism lack force; as will be pointed out, "interneur" has a disadvantage that *stria does not. Even so, "interneur" is now widely used among an important North American school of workers on Carabidae, of which Erwin is an influential member, as well as by a few describing other forms of Coleoptera. As "interneur" has strongly been urged upon others, as I have been told, this discussion may serve as a useful retardant to its acceptance and continued use.

The following questions awakened by Erwin's (1974; pp. 3-5) justifications of "interneur" will be discussed: 1) Is the argument sound that stria "... should have a name equivalent to 'interval'"? 2) Does "interneur" serve any special purpose that "*stria" does not? 3) Is "interneur" handicapped in any way that "*stria" is not? 4) What in fact do most *striae and interneurs represent?

1) Should *striae have a name equivalent to "interval"?

Erwin's argument that a new name is *needed* for *stria maintains that "If the intervals are the derived character state of the wing veins of the primitive beetle wing, and if the structures between the intervals are the derived character state of the wing 'cells' or membranes, then the latter [!] should have a name equivalent to 'interval'." Although "interneur" may provide a pleasing counterpart to "interval", the argument is a *non sequitur*. Assuredly no such nomenclatural necessity would arise even were those suppositions proven correct (see section 4), or were all intervals separated by phyletically equivalent structures (which they are not; see section 3). Furthermore, the "structures" in question are of course already named.

For nearly two centuries they have been called "striae" by coleopterists, a misfortune as Erwin sees it. He states that " ... coleopterists have used 'stria' for this structure since a 'stria' (in its proper definition) on a beetle elytron is common to most coleopterous families and thus to most coleopterists [*sic*!]. When the unnamed elytral structure described above [in the "syllogism"] is a serial row of unconnected punctures some coleopterists retain the term 'stria' as a structural name, rather than a descriptive name. Therein lies the problem."

That "problem", in the past and present, has caused little if any difficulty for most coleopterists. As with such nouns as "man", context readily indicates whether "stria" is in use as a collective or as a specific noun. In any case, *if* a change in nomenclature is to be made, Spilman's (1971) specific proposal that "*elytral stria*" be used as a collective noun is an alternative that avoids all assumptions and is senior to "interneur".

2) Does "interneur" serve any special purpose that "*stria" does not?

As the main reason for proposing "interneur", Erwin contends that "One cannot state 'stria 7 absent' without meaning the plesiomorphic elytral structure was indeed a stria ...", namely "an impressed line or furrow". Assuredly that is not so; "*stria 7 absent" (just as does "interneur 7 absent") implies *only* that in the presumed plesiomorphic state the external surface of the elytron displays a linear structural marking of some *unspecified* sort. When it is desired " ... to make ... descriptions comparative within a broad taxonomic framework" and " ... to take into account evolutionary changes within taxa ...", then of course the physical nature of the plesiomorphic elytral marking must be specifically stated for interneur and *stria alike. In this respect, each term is without specific meaning, and synonymous.

An analogy: shall a new term be coined to encompass the varied forms of pronotal hind angles, say, to avoid a fancied implication that the plesiomorphic state was in fact a true angle (and not rounded off at its apex) when it is stated, as Lindroth (1966; p. 158) does, "Prothorax without trace of hind angles"? To do so would be to give an illusory solution to an illusory problem.

3) Are the terms "*stria" and "interneur" equally applicable?

*Striae are certain longitudinal modifications of elytral structure, and the term "*stria" is defined and may be used without a stated or implied evolutionary overtone. "Interneur", on the contrary, properly refers to a structure that is presumed to be "the derived character state of wing 'cells' or membranes", that lay between veins of the primitive beetle wing. Here then *is* a problem: the actual number of *striae may significantly exceed the possible number of interneurs marking the elytra of a fair number of not-primitive, living carabids.

Nine or ten *striae (possible interneurs) on an elytron is the probable modal number for beetles today, including carabids. How then are the five (some *Omophron* with 15 striae) to eight (some *Scaphinotus* with 18) extra sculptured elytral lineations[1] to be referred to under Erwin's proposal? It can be done only by altering the evolutionary definition and meaning of "interneur" to complete synonymy with *stria.

It has been shown by Kolbe (1886, 1893), Bonsdorff (1890), Ganglbauer (1909), Jeannel (e.g., 1925, 1940), and others that the extra impressed lineations are supernumerary formations that subdivide particular not-tracheated intervals, hence are not primitive. No problem arises by denoting these extras as "secondary", "tertiary", *etc.* *striae, as is done. However, "interneur" does not accept such modification without loss of consistency and meaning, for interneurs are characterized as sharing a primary homology (owing to their supposed origins). So far as the interneur concept is concerned, supernumerary *striae must represent one or more classes of unnamed structures.

4) What in fact do *striae and interneurs represent?[2]

Surface expressions of aligned trabeculae (= columnae, columellae) is the answer. Apart from the margins where the upper and lower lamellae of the elytron meet, the elytron is strengthened within and, unlike a flight wing, its two lamellae are held apart by more or less vertical skeletal pillars - the trabeculae. The haemocoel of the elytron is continuous through the interspaces between trabeculae, and is therefore much larger in volume than is that of the hind wing which remains confined to sinuses enclosed within certain veins (see Arnold, 1964).

When *striae are counted and their lengths measured, the *minimal* number and *least* lengths of the underlying longitudinal rows of trabeculae of an elytron have been estimated. This can be confirmed by examination of the inner surface of an elytron where the bases of the trabeculae ("endoreticulum" of Smrz, 1982) are ordinarily visible through the relatively thin surface of the lower lamella[1,3], a fact known since at least the observations of Heer (1847) and Erichson (1848). As trabeculae are not structures unique either to elytra or to Coleoptera (Weber, 1933), and may occupy sites scattered about an elytron (see below), they are very likely *not* homologous with structures of a flight wing above the level of specialized hypodermal cell products and not specifically with the sclerotized outer walls of wing veins.

---

[1] Or the 21 or 22 *striae on an elytron of the fossil *Calosoma heeri* Scudder, referred to by Ganglbauer (1909) in his analysis of supernumerary striae. Jeannel (1940) holds the elytron to be that of a carabid on the testimony of Lapouge who examined the specimen, but not a species of *Calosoma*. Supernumerary striae are not limited to Adephaga. I count 14 striae (thus 15 intervals) on the elytra of several species of *Eleodes* (Tenebrionidae). That count would have proved extremely difficult without examination of the aligned bases of the trabeculae on the elytral undersurface.

[2] The general statements of this and section 4 hold for the great majority of beetles, but not necessarily all.

[3] The presence or absence of lines of trabeculae visible on the undersurface of an elytron, so easily examined, in certain cases should make determination of the abbreviation or absence of lineations on the upper surface as plesio- or apomorphies a simple matter. If, for brevity's sake, a single word be desired for aligned trabeculae, *substria(e)* should do satisfactorily.

Where *striae (interneurs) are shortened, faint, or even absent externally in certain members of a group in which many species have *striated elytra, a complete complement of serially aligned trabeculae of full length may nevertheless be present in all, whether with *striated elytra or not. Rows of trabeculae therefore provide the morphological basis of externally visible *striae (and interneurs). Unaligned trabeculae provide a basis for scattered puncta that dot the surface of an otherwise smooth elytron. Puncta of intervals lying between *striae frequently (but not always[4]) have a different basis; in such cases, they are unrelated to trabeculae as Kolbe (1893) comments. Though evidently necessary for the production of *striae and most puncta, the presence of trabeculae is obviously not a sufficient cause for puncta.

However manifested on an elytral outer surface, *striae ("interneurs") therefore share structural homology, as do their underlying components with those of unaligned puncta (but not with seta-bearing or sensory pits).

CONCLUDING COMMENTS

Finally a minor point, perhaps, for today few scientists endeavor to compound new technical terms with attention to their construction: "interneur" is a compound of Latin and clipped Greek; it should be in plural form, for nothing can be between one thing.

It is a strange invention, arising from unsound premises, solving only an imaginary problem, and not literally applicable to all elytral striae. It merits suppression[5]. "Stria" has a long history of useful application, and its uses are readily understandable by all. In his excellent fieldguide, White defines "stria" in its generic sense: "A groove or impressed line or a row of punctures ... " (1983; see pp. 46, 342). And so new generations of budding coleopterists are welcomed with "stria", not "interneur"; may that tradition continue[6].

ACKNOWLEDGMENTS

Two reviewers, Dr. T. J. Spilman of the Systematic Entomology Laboratory, U.S.D.A., and Prof. John D. Pinto of the University of California at Riverside, provided meticulous critical reviews of the penultimate draft of this commentary. Prof. S. L. Straneo of Milano, Italy, and Dr. John F. Lawrence of the C.S.I.R.O. of Australia, were kind enough to comment on "interneur", and to read and express approval of the manuscript. To each I express warm gratitude for their observations. However, it must be noted that the analysis presented is mine alone.

REFERENCES CITED

Arnold, J. W. 1964. Blood circulation in insect wings. Memoirs of the Entomological Society of Canada, No. 38. 48 pp + 12 pls.

---

[4] Puncta on intervals in many carabids are not underlain by trabeculae; in some beetles they are produced by trabeculae, for example in the meloid *Pleuropompha carinata* (Le Conte).

[5] Bequaert (1929) has commented pointedly on new names for old familiar structures.

[6] Prof. S.L. Straneo has informed me that in his forthcoming paper about the South American species of *Loxandrus*, he too is offering objection to the use of "interneur" (1990 Annals of the Carnegie Museum, in press).

Bequaert, J. 1929. Present trends in systematic entomology. Descriptions. Bulletin of the Brooklyn Entomological Society, 24:98-102.

Bonsdorff, A. von 1890. Über die Ableitung der Sculpturverhältnisse bei den Deckflügeln der Coleopteren. Zoologische Anzeiger, 13:342-346.

Erichson, W. F. 1848. (Das Studium fossiler Coleopteren.) Bericht über die wissenschaftlichen Leistungen im Gebiete der Entomologie, 1847, Berlin, 1848:39-46.

Erwin, T. L. 1974. Studies of the subtribe Tachyina (Coleoptera: Carabidae: Bembidiini), Part II: A revision of the New World-Australian genus *Pericompsus* LeConte. Smithsonian Contributions to Zoology, No. 162. (iii + 96 pp.)

Ganglbauer, L. 1909. Über die Beziehungen der Skulptur zum Tracheenverlauf in den Elytren der Koleopteren. Verhandlungen der K. K. zoologischen-botanischen Gesellscheft in Wien, 59:(17)-(26).

Heer, O. 1847. Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatien. Abteilung l: Käfer. Leipzig. 230 pp. + 8 pls.

Jeannel, R. 1925. Morphologie de l'élytre des coléoptères adéphages. Archives de zoologie experimentale et générale, 64:1-84.

Jeannel, R. 1940. Les calosomes (Coleoptera Carabidae). Memoirés du Muséum National d'Histoire Naturelle, Paris (N.S.) 13:1-240 + 8 pls.

Kolbe, H. J. 1886. Die Zwischenräume zwischen den Punktstreifen der punktiertgestreiften Flügeldecken der Coleoptera als rudimentäre Rippen aufgefasst. Jahresbericht des Westfälischen Provinzialvereins für Wissenschaft und Kunst. Münster. 14:57-59 + 1 pl.

Kolbe, H. J. 1893. Einfährung in die Kenntnis der Insekten. Berlin. xii + 709 pp.

Lindroth, C. J. 1966. The ground beetles of Canada and Alaska. Pt. 4. Opuscula Entomologica Supplementum. xxix:409-648.

Smrz, J. 1982. Comparative anatomy of proventriculus and intraelytral structure of the suborder Adephaga (Coleptera). Acta Universitatis Carolinae-Biologica 1980:213-296.

Spilman, T. J. 1971. The longitudinal lines on beetle elytra: a definition of stria. Coleopterists Bulletin, 25:121-122.

Weber, H. 1933. Lehrbuch der Entomologie. Jena. xii + 726 pp.

White, R. E. 1983. A field guide to the beetles of North America. Boston. xii + 368 pp. + 12 pls.

NOTE

NEW NEARCTIC REGION RECORDS OF PALEARCTIC *MEGASELIA* SPECIES(DIPTERA: PHORIDAE)

Brian V. Brown
Department of Entomology
University of Alberta
Edmonton, Alberta, T6G 2E3
CANADA

Quaestiones Entomologicae
26: 701–702

In the summer of 1990 we conducted an informal survey of insects of the boreal region of Alberta (Brown *et al.* 1990), to document more fully the distribution of taxa of interest to us. Among the material collected in this survey, and in other Alberta collections, were specimens of five species of the paraphyletic genus *Megaselia* Rondani, all of which are new records for the Nearctic Region. These species are *M. coccyx* Schmitz, *M. eccoptomera* Schmitz, *M. gartensis* Disney, *M. humeralis* (Zetterstedt) and *M. sordescens* Schmitz. All except *M. humeralis* are similar to the Holarctic Region species *M. sordida* (Zetterstedt), but the differences between them are discussed by Disney (1985). Specimens of *M. sordida,* a species which is widely distributed in Alberta, were also collected in our survey.

All of the five newly recorded taxa are distinctive species, and are recognized easily using Disney's Handbook of the British *Megaselia* (Disney 1989; Brown 1989), a publication which is extremely useful even in Alberta, far outside of its intended area of coverage. I suggest that anyone attempting to identify North American specimens of *Megaselia* should spend some time becoming familiar with the illustrations of male terminalia found in Disney's book. This will help to supplement identifications based on the hopelessly out of date keys of Borgmeier (1964, 1966).

Most of the material is deposited in my collection, but some voucher specimens also will be placed in the collection of the Provincial Museum of Alberta and the Strickland Museum, University of Alberta. Some records for the above mentioned taxa are as follows:

M. coccyx Schmitz, 2♂ CANADA: Alberta, 8km W Edmonton, Wagner Natural Area, 27.vi.-5.vii.1990, B.V.Brown, Malaise trap, poplar/ spruce.

M. eccoptomera Schmitz, CANADA: Alberta, 1♂, 12km N Boyle, 19.v.-10.vi.1990, B.V.Brown, FIT 1a, *Populus/ Picea*; 3♂, 91km S Fort McMurray, 19.v.-10.vi.1990, B.V.Brown, FIT 1d, *Picea*; 1♂, 58km S Fort McMurray, 19.v.-10.vi.1990, B.V.Brown, FIT 1e, *Pinus/ Picea*; 1♂, 750km NW Edmonton, Bistcho Lake, 20-22.vi.1987, Malaise trap, leg. A.T. Finnamore; 1♂, Hondo, 29.v.-9.vii.1990, E.R.Fuller, FIT 2a, *Pinus/ Picea/ Populus*; 12♂, 10km N Slave Lake, Muskeg Lake, 29.v.-9.vii.1990, E.R.Fuller, FIT 2b, *Pinus/ Picea/ Populus*; 3♂, 30km N Slave Lake, Marten Mountain, 29.v.-9.vii.1990, E.R.Fuller, FIT 2c, *Picea/ Populus*; 2♂, 61km N Slave Lake, 29.v.-9.vii.1990, E.R.Fuller, FIT 2e, *Populus/ Picea*; 1♂, 13km N Hinton, 9-30.vi.1990, T.G.Spanton, FIT 3a, *Picea/ Populus*; 3♂, 48km N Hinton, 9-30.vi.1990, T.G.Spanton, FIT 3b, *Picea/ Pinus*; 5♂, 84km N Hinton, 9-30.vi.1990, T.G.Spanton, FIT 3c, *Picea/ Pinus*; 1♂, 8km W Edmonton, Wagner Natural Area, 4-13.vi.1990, B.V.Brown, Malaise trap, poplar/ spruce; 20km S Nordegg, 4♂, 27.v-24.vi., 7♂, 24.vi-23.vii.1990, D.A.Pollock, FIT 4e, *Picea/ Pinus/ Populus*; 21♂, 38km S Robb, 27.v.-24.vi.1990, D.A.Pollock, FIT 4c; 1♂, 10km S Nordegg, 24.vi-23.vii.1990, D.A.Pollock, FIT 4d.

M. gartensis Disney, 1♂, CANADA: Alberta, 190km S Fort McMurray, 10.vi.-22.vii.1990, B.V.Brown, FIT 1b.

M. humeralis (Zetterstedt), 2♂, 2♀, CANADA: Alberta, 61km N Slave Lake, 29.v.-9.vii.1990, E.R.Fuller, FIT 2e.

M. sordescens Schmitz, CANADA: Alberta, 2♂, 38km S Robb, 27.v-24.vi.1990, D.A.Pollock, FIT 4c; 4♂, 20km S Nordegg, 24.vi-23.vii.1990, D.A.Pollock, FIT 4e, *Picea/ Pinus/ Populus*; 2♂, 30km N Slave Lake, Marten Mountain, 29.v.-9.vii.1990, E.R.Fuller, FIT 2c, *Picea/ Populus*.

ACKNOWLEDGEMENTS

I thank R.H.L. Disney for confirming my identifications of the newly recorded taxa, my fellow collectors E.R. Fuller, D.A. Pollock, and T.G. Spanton for participating in the Alberta survey, and the Wagner Natural Area Society for permission to conduct research at the Wagner Natural Area. This research was supported by Natural Sciences and Engineering Research Council operating grant A–1399 to G.E. Ball, and a Max and Marjorie Ward Scholarship≥ to D. Pollock and T. Spanton.

REFERENCES CITED

Borgmeier, T. 1964. Revision of the North American phorid flies. Part II. The species of the genus *Megaselia*, subgenus *Aphiochaeta*. Studia Entomologica, 7: 257-416.

Borgmeier, T. 1966. Revision of the North American phorid flies. Part III. The species of the genus *Megaselia*, subgenus *Megaselia*. Studia Entomologica, 8(1965): 1-160.

Brown, B. V. 1989. Book review of Disney 1989, Scuttle flies (Diptera, Phoridae), genus *Megaselia*. Fly Times, 3: 12-13.

Brown, B. V., Fuller, E. R., Pollock, D. A. and Spanton, T. G. 1990. 1990 Alberta insect survey. Newsletter of the Biological Survey of Canada (Terrestrial Arthropods), 9: 46-48.

Disney, R. H. L. 1985. A new species of *Megaselia* Rondani (Diptera: Phoridae) from northern Britain. Entomologist's Record and Journal of Variation, 97: 200-202.

Disney, R. H. L. 1989. Scuttle flies- Diptera, Phoridae, Genus *Megaselia*. Handbooks for the Identification of British Insects, 10: 1-155.

EDITOR'S ACKNOWLEDGEMENTS AND FAREWELL

As noted previously, *Quaestiones Entomologicae* ceases publication with this volume. That note produced expressions of sympathy and condolence from subscribers, friends and associates. I appreciate the thoughtfulness of those who took the time to write. I appreciate also the efforts of the reviewers (names and abbreviated addresses listed below), whose comments and suggestions contributed significantly to the general quality of the publications in Volume 26.

I. S. Askevold
    Entomology-Biological Control, Florida A & M University
F. M. Atton
    412 Leslie Avenue, Saskatoon, Saskatchewan
V. Behan-Pelletier
    Biosystematics Research Centre, Agriculture Canada
R. G. Beutel
    Department of Zoology, Institut für Biologie II (Zool.), RWTH Aachen
O. Biström
    Entomology Division, Finnish Museum of Natural History
Y. Bousquet
    Biosystematics Research Centre, Agriculture Canada
D. R. Bright
    Biosystematics Research Centre, Agriculture Canada
T. L. Erwin
    Department of Entomology, Smithsonian Institution
T. Galloway
    Department of Entomology, University of Manitoba
T. J. Spilman
    Systematic Entomology Laboratory, U. S. Department of Agriculture
D. R. Whitehead (deceased)
    Systematic Entomology Laboratory, USDA
G. W. Wolfe
    Division of Mathematics and Science, Dobbs Hall, Reinhardt College
D. A. Wrubleski
    Department of Entomology, University of Alberta

I acknowledge especially the cooperation of R. B. Aiken and R. E. Roughley, organizers of the Hydradephaga Symposium that was held in 1988 as part of the program of the XVIII International Congress of Entomology, in Vancouver. It was a pleasure to work with them, in producing The Proceedings of their symposium, which were published in the Spring and Summer issues of *Quaest. Ent.*

The prompt, cheerful and efficient service provided by our printers, Hallis Graphics Ltd., has added to the pleasure of publication. I will miss the association with the President of Hallis, Mr. J. Haukedal. I take this opportunity to wish him well in these trying times for the smaller businesses.

Mrs. Suseela Subbarao has served for 10 years as the Publications Manager of *Quaest. Ent.* In that capacity, she kept us up to date as publishing operations became more complex and sophisticated. She developed and maintained good working relations with the various individuals and groups involved in production of our journal. She endeavored to satisfy the requirements of authors, even those who seemed to be unreasonably demanding. From time to time, she complained— with justification— but she did what was needed, taking satisfaction from the excellent issues that she produced. It is difficult for me to accept that our working relationship is at an end. She will be leaving the Department of Entomology, taking with her my gratitude and appreciation for a job well done.

For 26 years, *Quaest. Ent.* has been an integral part of the operations of our Department. During that period, the Editors (Brian Hocking first, and then me) have called upon our colleagues from time to time for assistance in one form or another. Our requests were met and our expectations fulfilled. For this cooperation, willingly given, I am very grateful.

The Cameron Library of the University of Alberta has been one of our staunch supporters. Subscriptions to *Quaest. Ent.* were offered in exchange for a wide variety of other journals. Thus, we were able to contribute toward development of what was hoped to be a great library in Western Canada. I appreciated the opportunity to be involved in this form of contribution to the general improvement of the University. I regret that this contribution must cease, and especially at this time, when the Library budget is being reduced.

One year ago in the "Editor's Acknowledgements", I noted that *Quaest. Ent.* had reached its 25th year of publishing, but that a celebration would be held off until 2014, the year of the 50th anniversary of the journal. I would have made more of it, had I known that Volume 25 was to be the penultimate, rather than the half-way mark to the Golden Anniversary. What happened? This year, the Department's budget was cut as part of a general reduction in University funding. Loss of our journal was deemed to be the most endurable of the many possible losses that were required in the face of the reduced budget.

I believe that I am at fault for not having foreseen the possibility of the loss of University funding through the departmental budget for *Quaest. Ent.* The handwriting was, so to speak, on the wall, but, like Belshazzar, the last ruler of the kingdom of Babylon, some 2500 years ago, I failed to understand the urgency of the message, a failure best described as complacency. After all, the journal had been in existence for more than 20 years. Surely, its continued existence was assured? Nothing in this world is assured, and an individual should be able to learn this before the near midpoint of his sixth decade of existence.

In the world of free enterprise, or perhaps I should say economic freebooting and buccaneering that has been foisted on us by the likes of Thatcher, Reagan, and lesser national leaders of similar right-wing persuasion, endeavors that do not pay directly for their operations must perish— in spite of other aspects of merit that might justify expenditures from the public purse. Because *Quaest. Ent.* had not become self-sustaining, it became a victim to financial exigency. However, its passing is symptomatic of the stifling of funding for the public institutions, such as universities, libraries, and museums, that contribute to the cultural life of the world.

It is claimed loudly by right-wing politicians (including some nearly brain-dead provincial ministers of education) and their wealthy supporters that there is not enough money to fund properly these institutions. Yet, some years ago, there was funding more adequate than at present. Where has it gone? It's there alright, available for corporate take-overs that contribute to destruction of the system through the looting of pension funds and other necessary reserves; available to purveyors of junk bonds and other unscrupulous manipulators of a nation's wealth; available to a host of lawyers intent on turning the legal system, developed originally as an instrument of justice, into a route to excessive personal financial gain; and available to large corporations as tax rebates made by grateful politicians who cannot distinguish their own private interests from the public interest.

This dislocation of funds has had a profound effect on citizens, generally. It has led to loss of jobs, and loss of opportunity for even modest gain, the reward for doing a job well. The effect of this period of unneeded financial upheaval on the unemployed and under-employed citizenry is encapsulated in a phrase I heard the other day: "their dreams are dying". As I write these words, the Canadian Broadcasting System is carrying Margaret Thatcher's last address as leader of the British Conservative Party. As one of the symbols of destruction of the dreams of the economically unprivileged, her political demise might be taken as a sign of hope that things are changing, but I doubt it. I expect her replacement to be of an ilk similar to that of the "Iron Lady".

In brief, I believe that the world is in the grip of a system based on excessive financial competition that encourages and rewards greed, and that is without respect for the institutions that enrich the process of living, and that is without regard for the environment in which living takes place. To paraphrase one of Sir Winston Churchill's wartime statements, the lights are going out, not only in Europe, but all over the world. When they come on again— whenever that kinder, gentler time may be— perhaps along with the reawakening of other dreams, someone will breathe life back into the remains of the entomological journal *Quaestiones Entomologicae*. Until then, *requiescat in pace*.

George E. Ball
Editor