REVISION OF *BLEDIUS*. PART IV. CLASSIFICATION OF SPECIES GROUPS, PHYLOGENY, NATURAL HISTORY, AND CATALOGUE (COLEOPTERA, STAPHYLINIDAE, OXYTELINAE)

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CONTENTS

TABLES

ABSTRACT

The purpose of this monograph is to review and reinterpret what is known about *Bledius* with the goal of prompting further study of the genus. Included are a new infrageneric classification for the world; discussions of the life cycle, habitat, distribution, enemies, chemical secretions, economic importance, immature stages, fossils, and phylogeny; and a cross-indexed annotated catalogue to the taxonomic names and associated literature.

Formal taxonomic changes include the following: *Bledius minniensis* from Armenia is a **New Species**, *Neobledius* is a **New Synonym** of *Bledius* and *Elbidus*, and *Microbledius* and *Psamathobledius* are **New Synonyms** of *Bledius*. **New Combinations** include *B. karachiensis* transferred from *Neobledius* and *actitus, litoreus*, and *playanus* transferred from *Microbledius*. **New Names** include *albanicus* and *jutlandensis* which replace the preoccupied *nebulosus* Koch and *atlanticus* Lohse, respectively. The following names are labeled as **New Status**: *B. castaneipennis* Mannerheim is elevated from synonymy with *opacus* Block; *atramentarius* Rottenberg is elevated from synonymy with and replaces *bos* Fauvel which was described a year later; *limicola* Tottenham is elevated from synonymy with and replaces *germanicus* Wagner which is preoccupied by *germanicus* Gravenhorst; *minor* Mulsant and Rey is elevated from synonymy with and replaces *devillei* Bondroit which was an unnecessary replacement name. Two names are **emended**: *cariniceps* for *carinlceps* and *ghesquierei* for *guesquierei*. Six names, *bubalus* Gistel, *castaneus* Mulsant and Rey, *chimerinus* Gistel, *germanicus* Gravenhorst, *gyllenhalii* Laporte, and *westerhauseri* Gistel are used herein for the first time since their original publication.

All eight currently recognized subgenera are treated as synonyms of *Bledius*. In their place a classification of 34 species groups is proposed. This classification is based on examination of 422 of the 439 species of *Bledius*. The species were assigned to species groups based on examination of type material or subsequently identified specimens. Nine species were assigned to species groups from characters in the original description—each such assignment is clearly indicated. Eight species are listed as incertae sedis for one or more of the following reasons: material was unavailable for study, the description did not cite sufficient information for placement in a species group, the types were lost, or the species was unknown. Descriptions, illustrations, a list of included species and localities, and a distributional map are provided for each species group along with a key to the group. No effort was made to define or revise species.

The monophyly of *Bledius* is established by the presence of a cluster of secretory pores in a prosternal pit or depression and the possession in females of a pair of elongate, undivided genital sclerites on segment IX. Both *Bledius* and its sister genus *Eppelsheimius* have a central row of spine-like setae on the hypopharynx; they share other characters as well. The relationships among the species groups are shown in a cladogram on which many characters are homoplasic.

Bledius comprises two main lineages. One with 14 species groups and 88 species includes, among others, the large robust species with horns. Most species of this branch live in saline habitats. Two of the species groups are restricted to the New World. The sister lineage includes the remaining 20 species groups and more than 340 species. A terminal cluster of species groups along with species in three other groups live in saline habitats; the others, including the four most speciose groups, live in freshwater habitats. In this lineage 3 species groups are confined to the New World, 11 to the Old, and the remaining 6 are widespread in both hemispheres.

The primitive habitat for *Bledius* was near salt water. One descendent remains there; the other adapted to the freshwater habitat. In this second lineage some highly speciose groups developed near freshwater and there was a reinvasion of the saline habitat.

Bledius is a large genus of 439 species, some of which occur in huge populations. Species are found on all continents except Antarctica and on most continental islands but are absent from most oceanic islands. Although only a third of the species lives in saline habitats (inland as well as coastal), these species represent two-thirds of the species groups. Two-thirds of the species live in freshwater habitats, representing the remaining third of the species groups.

Bledius may have lived as far back as the Cretaceous. Nine fossil species have been described as belonging in *Bledius,* however, two of these are no longer included. Of the remaining seven only *Bledius glaciatus* from the Pleistocene and *B. primitiarum* of the Oligocene are likely to be *Bledius.* Another probable member of *Bledius* is *Staphylinus lesleyi* Scudder also of the Oligocene; this species has not been moved to *Bledius.* Although the oldest probable fossils of *Bledius* are about 35 million years old, evidence suggests that the Oxytelinae existed about 150 million years ago during the Jurassic.

Species of *Bledius* are most abundant in unvegetated or lightly vegetated, sunny, moist sand adjacent to rivers, lakes, and oceans. They prefer-

entially select their habitat based on soil moisture, salinity, texture, and, indirectly at least, size of the sand grains, availability of food, and amount of shade. The pressure of predators may influence habitat limits but that may be partly due to the physiological weakening of a *Bledius* that is not living in its optimal habitat. Although as yet undemonstrated, food plant specificity may influence habitat selection by *Bledius*.

Bledius lives in burrows which adults excavate with their mandibles and strengthen with their protibiae. The burrows are several millimeters to about 40 cm deep and about 1 to 5 mm in diameter. Larvae also construct and live in burrows. Eggs are laid in special egg chambers; some species cache food in the burrow. The burrow serves not only as living quarters for *Bledius* but helps protect them. *Bledius* can live at a relative humidity of 100 percent to no less than 93 percent. The humidity within the burrow is nearly 100 percent. Some seacoastal species live in the intertidal zone where they remain during high tide. Individuals that stay in the burrow during high tide live in an air bubble, which acts as a physical gill, and are immediately active after the tide recedes. Individuals exposed directly to seawater fly away or survive by becoming comatose and recover only slowly when removed from the water; most, however, die after a few hours of immersion.

Usually the adults overwinter in deep burrows. Eggs are deposited during spring or early summer and develop in two to three weeks. The larval stage lasts for six to eight weeks and the five instars are each of undetermined length. Pupae exist for about a week. Egg to adult then is two to three months. During the summer adults live for three to six weeks. Females oviposit several times; the number of generations per year is unclear but may vary according to species and climate. Larval characters have been published for 19 species.

Adults and larvae feed on algae and diatoms that live in the moisture surrounding each sand grain. The green algae there are said to be stunted filamentous forms. Some *Bledius* facultatively store algae.

Some species are said to exhibit subsocial behavior by attending to their offspring. Evidence for this interpretation is inconclusive.

Carabid beetles of *Dyschirius* are regarded as the principal predators of *Bledius*. However, little evidence is found to support a species-specific host-prey relationship. More likely, the relationship of *Bledius* and *Dyschirius* is based on geographical distribution and habitat preference. Over 50 species of *Dyschirius* are reported with over 80 species of *Bledius*. Other Carabidae reported as actual or probable predators of *Bledius* include species of *Cillenum, Bembidion, Pogonus, Dicheirotrichus, Clivina,* and *Schizogenius*. The ichneumonid wasp, *Barycnemis blediator,* is a parasitoid of *Bledius spectabilis*. Sandpipers and rainbow trout also eat *Bledius*. Fungi of the order Laboulbeniales commonly infest *Bledius* and, although usually regarded as benign, one report suggests otherwise.

Species of *Bledius* secrete a characteristic, penetratingly fragrant chemical of five components. That this secretion functions as a defensive chemical is debatable. No experimentally supported hypotheses have explained the function of this compound.

One species in Japan was reported to do economically significant damage to clay beds used to produce salt by evaporation of seawater.

The literature for and taxonomic names used in *Bledius* are summarized in a catalogue. Fifteen generic-level names have been used in *Bledius*; 646 species-level names have been used, 439 of which are presently listed as valid and extant. All names that have been included in *Bledius* are listed in the catalogue. The species names are cross-indexed and the references annotated.

INTRODUCTION

The purpose of this paper is to summarize, reorganize, and draw new conclusions about what is known for *Bledius*; to answer some questions and ask others; and to provide a springboard for new studies. The present investigation focuses on the species groups' classification, phylogeny, distribution, and natural history, and it provides a guide to the literature for *Bledius*. This paper is the culmination of an odyssey that began with a casual remark by George Ball (University of Alberta) to me in 1964, that if someone doesn't study *Bledius*, he might. Since then I have studied for 20 years a genus whose first species was described over 200 years ago in 1784.

Bledius is a speciose genus whose members are found in most parts of the world in small to stupendously large populations. With more than 430 species and tens of thousands of specimens in collections, what is the most efficacious plan for taxonomic study? In the past, since Erichson's world revision (1840), the answer has been to study the fauna of a region. This inevitably leads to the redescription of species under different names, to parallel or even divergent classifications, to the impossibility of recognizing monophyletic groups and sister taxa, and to false ideas about distribution. But how can one begin to study all of over 400 species of a genus as taxonomically complex as *Bledius*? The approach proposed herein is to assign all species to species groups and then revise the latter. To that end, I have divided the species of *Bledius* among 34 groups that range in size from 1 to about 70 species. Twenty-nine of the groups have fewer than 30 species each, 27 of them have fewer than 20. So divided, *Bledius* is then manageable. The genus can be grasped as a whole. Work can be done regionally or by monophyletic groups. Most natural history studies have focused on ecological questions. Now questions can be asked about the "biological" reality and characteristics of the groups. One can think more clearly about the speciation and evolution of the genus, about comparative natural history of closely related and more distantly related forms. We may begin to understand the distributional history of the genus.

METHOD

To accomplish this classification of species groups, all specimens were relegated to groups without regard to their species identity. The assignment of species to groups for North American species is based on my determinations of species. Group assignments for other parts of the world are based on examination of types, holotypes, lectotypes, syntypes, and paratypes, or where necessary, on determination of species by other staphylinid workers, especially Max Bernhauer, Malcolm Cameron, Henri Coiffait, Eduard Eppelsheim, Gaston Fagel, Albert Fauvel, Peter Hammond, Otto Scheerpeltz, and David Sharp. Where primary type material was used, any error in the accuracy of group assignment must be attributed to my carelessness or flaws in the classification. Where assignments are based on subsequent identification of species, I have endeavored to reduce the inaccuracy of group assignment by adopting the consensus of the identity of a species. If all identifications of a species result in its assignment to the same species group, I have accepted those determinations as accurate (for placement to group). When there were identifications that resulted in various group assignments, I used my own judgment. For example, I saw no type material of *Bledius opacus* but all workers identified the specimens so they fell in my *annularis* group. On the other hand most specimens of *Bledius akinini* were identified so they fell in my *semiferrugineus* group but a few belong with the *kochi* or *immaturus* group. In the final analysis, though, my species groups are hypotheses that will be reexamined and adjusted where new evidence warrants it. These species groups are a means of bringing order to an immense amount of information. Their reality will continually be tested.

LOCALITIES AND DISTRIBUTION

One of the drawbacks to the approach I have used to define the groups of species of *Bledius* is that, in contrast to my work on the North American species, I have relied on other workers for the identification of most of the material examined. For purposes of this paper I was interested in whether the specimen was in one species group or another. The effect is that I am unable to vouch for the accuracy of identification of most species. I have, however, published a list of localities for each species I examined. These localities are the basis of the maps that summarize the distribution of each species group. The maps are largely accurate for the distribution of species groups. The value of citing the material studied for each species is that readers are presented with an approximation of the currently known distribution of each species. Knowing the material bases for my decisions concerning species group composition and distribution permits reexamination. Doubts can be easily satisfied: we now have a summary, in one place, of what is known and can decide where we will go from there.

ORGANIZATION

The paper is divided into four major sections, namely Natural History, Phylogeny, Taxonomy, and Catalogue. For each section there are introductory remarks but their general theme is the same—to provide a platform for future work. For the Natural History and Catalogue sections, although I attempted to include all the major literature, some has been inadvertently, or occasionally purposely, excluded. The literature cited in the catalogue is briefly annotated. For the Taxonomic section, all species are assigned to group. Most were assigned by examination of specimens, however a few were assigned by examination of the original description; these are appropriately annotated. Included in the Taxonomic section are a key to species groups, and a description, illustrations, discussion, material examined and species composition for each group.

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Mickevich (University of Maryland) who ran my phylogenetic data through the PHYSYS program and to the University of Maryland Systematic Program for use of the PHYSYS program and their computer. I also thank Mr. Mike Pogue, a Predoctoral Fellow at the Smithsonian Institution, for helping me with use of the computer. I thank Ms. Beatrice Brewster who translated various articles from French and German, Mr. Sarfraz Lodhi who helped with the library work, and Ms. Lauren Duffy for assistance with the scanning electron microscope. I also extend my appreciation to the librarians of the American Museum of Natural History, particularly Mss. Mary Genett and Lynn Wiley, the Department of Agriculture at Beltsville, the Museum of Comparative Zoology at Harvard University, the Smithsonian Institution, and the U.S. Geological Survey. More than 97 percent of the references included in the bibliography were found in my personal library or that of the American Museum, but these other four libraries supplied me with the remaining difficult to locate references. Finally, I am grateful to Dr. J. Howard Frank who generously reviewed part of this manuscript.

ABBREVIATIONS

AMNH, American Museum of Natural History, New York
BMNH, British Museum of Natural History, London
BPBM, Bernice P. Bishop Museum, Honolulu
CMP, Carnegie Museum of Natural History, Pittsburgh
CNC, Canadian National Collection, Ottawa
FMNH, Field Museum of Natural History, Chicago
GLC, Gustav Lohse Collection, Hamburg
HCC, Henri Coiffait Collection
HNHM, Hungarian Natural History Museum, Budapest
IRSN, Institut Royal des Sciences Naturelles, Brussels
MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts
MGHN, Musée Guimet d'Histoire Naturelle, Lyon
MNHP, Muséum National d'Histoire Naturelle, Paris
MNHU, Museum für Naturkunde der Humboldt Universität
MNHV, Naturhistorisches Museum Wien, Vienna
MSNM, Museo Civico di Storia Naturale, Milano
MTC, Marc Tronquet Collection
MVA, National Museum of Victoria, Australia
MZUT, Museo ed Istituto di Zoologia Sistematica della Università di Torino
SAM, South Australia Museum, Adelaide
SNMB, Slovenské Narodné Muzeum v Bratislave, Czechoslovakia
STM, Stavanger Museum, Stavanger, Rogaland, Norway
TNC, Takehoko Nakane Collection
UKP, University of Karachi
USNM, National Museum of Natural History, Washington, D.C.
YSC, Yasutoshi Shibata Collection
ZMLS, Zoological Museum, Lund University, Sweden
ZMUH, Zoological Museum of the University, Helsinki
ZMUM, Zoological Museum, University of Moscow

TAXONOMIC HISTORY

AUTHOR AND DATE

Bledius was first used without distinguishing characters but in combination with one available species in Samouelle's 1819 *The Entomologist's Useful Compendium*.... Samouelle both cites Leach as author of *Bledius* and seems to credit the name to Leach by stating, "To my kind and valuable friend Dr. Leach I am indebted for the above and following notice of new genera, as lately established by the celebrated entomologists whose names are affixed" (p. 172). Samouelle attributes the arrangement of the taxa to Leach in the title to his book with the following: "... The Modern Method of arranging the Classes Crustacea, ... and Insects, from their Affinities and structure, according to the views of Dr. Leach ...." On page 45 Samouelle indicates he is adopting Leach's system of classification in his work. Indeed, from the first publication of characters for *Bledius* (Curtis, 1826, p. 143) until 1857 all subsequent writers[1] cited Leach as the author. Despite these facts, for about 100 years Mannerheim or more recently Samouelle have been considered the author of *Bledius*. Why?

During the early years, *Bledius* Leach was often followed by a reference to descriptions published by Mannerheim (1831) or Stephens (1834). Jacquelin du Val (1857, p. 54) omitted Leach and simply cited Mannerheim as though he were author of the name. In 1859 (p. 76) he again omitted Leach but cited Stephens as author.[2] Fauvel (1868, p. 26) used *Bledius* without the author's name following but cited a publication by Mannerheim as the first reference; in 1872 (p. 184) he cited Mannerheim as though he were the author of *Bledius*. Since 1872 most workers have cited Mannerheim as the author.[3] Samouelle seems to have been cited as author for the first time by Blackwelder (1943, p. 112; 1944, p. 106), then Kloet and Hincks (1945), Tottenham (1949, p. 363; 1954, p. 48), and Pope (1977, p. 24). Blackwelder in 1952 (p. 77) cited Leach as author.

It is clear that early writers regarded Leach as author of *Bledius*. They cited Mannerheim (1831) or Stephens (1834) perhaps because both provided descriptions of the genus and described some species. It is less certain whether Jacquelin du Val (1857) omitted Leach and cited instead only what he thought to be the first description of *Bledius* because it was less cumbersome a citation or because he thought that the author of a genus should be the first who gives characters. Since Jacquelin du Val's work the author of *Bledius*, and therefore date of publication, was rarely cited correctly.

Bledius in 1819 was validly published and was available [I.C.Z.N. Art. 16(a)(v)] by the inclusion of *Oxytelus armatus* Panzer (1799). Neither Mannerheim nor Stephens can be the author. Only Samouelle and Leach remain. If we accept Samouelle's attribution of *Bledius* to Leach, then Leach is author; if not, then Samouelle is. It matters little which we choose since both authors are associated with the same publication. I choose Leach since Samouelle cites Leach as author and credits the genus to him [I.C.Z.N., Art. 50].

SPECIES

Bledius was first established (Leach, 1819) with one species, *armatus*, that had been for-

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[1] Stephens (1829, p. 292; 1834, p. 307), Mannerheim (1831, p. 458), Boisduval and Lacordaire (1835, p. 455), Runde (1835, p. 17), Dejean (1837, p. 76), Heer (1839, p. 209), Erichson (1839, p. 578; 1840, p. 760), Sturm (1843, p. 52), Gaubil (1849, p. 257), Redtenbacker (1849, p. 737; 1858, p. 227), Fairmaire and Laboulbène (1856, p. 599), Lacordaire (1854, p. 114), Kraatz (1858, p. 816), Waterhouse (1858, p. 29), Thomson (1859, p. 12; 1861, p. 118), LeConte (1877, p. 217), Lynch (1884, p. 351), Casey (1889, p. 41), Blatchley (1910, p. 403), Blackwelder (1952, p. 77), Herman (1970, p. 375), Coiffait (1973, p. 122).

[2] Stephens was cited as author of *Bledius* by LeConte (1863, p. 51), Gemminger and Harold (1863, p. 643), and Hochhuth (1872, p. 158).

[3] Mulsant and Rey (1878, p. 551), Sharp (1887, p. 685), Heyden et al. (1891, p. 115; 1906, p. 143), Ganglbauer (1895, p. 610), Reitter (1909, p. 165), Bernhauer and Schubert (1911, p. 125), Kuhnt (1912, p. 203), Fowler and Donisthorpe (1913, p. 71), Johansen (1914, p. 534), Leng (1920, p. 97), Winkler (1925, p. 345), Portevin (1929, p. 409), Cameron (1930, p. 270), Scheerpeltz (1933, p. 1109), Hansen et al. (1939, p. 30), Hatch (1957, p. 98), Horion (1963, p. 251), Lohse (1964, p. 89), Scheerpeltz (1968, p. 31).

merly in *Staphylinus,* then *Oxytelus.* Curtis (1826) provided the first characters for *Bledius,* transferred another species from *Oxytelus,* and added a new species. In 1829 Curtis and then Stephens a few months later both published *Hesperophilus* without description but with the same list of four available valid species. Stephens included another available name as a junior synonym and both included some nomina nuda. In *Bledius* they both included the same two valid species but Stephens also listed some synonyms and nomina nuda. Mannerheim (1831, pp. 458–460) redescribed *Bledius* again and transferred species into the genus so that 11 species were in *Bledius* including most of those Stephens had put in *Hesperophilus.* In 1834 Stephens described *Bledius* and *Hesperophilus* and some of the included species. Gistel (1834, p. 9), in a list of generic and specific names, published *Dicarenus* with 10 species (three of them nomina nuda), most of which had been in *Bledius* and/or *Hesperophilus* but neither of which he mentions. His paper was forgotten. Boisduval and Lacordaire (1835, pp. 455–458) redescribed four species and described a new one from near Paris. In 1839 Erichson described five new species and redescribed five others from Germany and in the same year Heer described seven new species and redescribed six others from Switzerland.

Before Erichson (1840) published his classic *Genera et Species Staphylinorum,* in which he described and/or classified all of the known species of Staphylinidae and provided the basis for higher classification of the family, 43 species names had been cited in *Bledius* (not including nomina nuda). Erichson (1840, pp. 760–780) missed only 12 names: *divisus* Marsham, *germanicus* Gravenhorst, *bicornis* Olivier, *stephensii* Westwood, *haemopterus* Stephens, and the seven species described a year earlier by Heer. He transferred, without examining specimens, two species from *Staphylinus* that had been described by Fabricius from India and six from *Oxytelus* described by Say from the United States. He described 20 new species from various parts of the world and cited 6 species as synonyms. He regarded *Hesperophilus* as a junior synonym of *Bledius* and overlooked *Dicarenus* Gistel.

Erichson's work was a milestone; he summarized what was known about the genus. Including the 12 species he overlooked, 57 valid taxa were included in *Bledius* after his work. Today, 145 years later, 439 valid extant species are listed and 646 names have been used in the genus.

Nearly 90 people have contributed to this explosion. Seventy-six authors added one to 10 species. Fauvel, between 1864 and 1904, described 36 species only one of which is a synonym. LeConte in two papers (1863, 1877) added 34 species from the United States; eight are now synonyms. The much maligned Thomas L. Casey described 27 species from the United States; 19 of them still stand. Sharp (1874–1913) added 22 and Eppelsheim (1881–1894) 15 species. Fall (1901–1919) in three papers described 21 species; only seven are still valid. Bernhauer (1901–1943) and Cameron (1912–1951) added 89 and 41 species, respectively. Fourteen of Bernhauer's and four of Cameron's names have fallen. Koch in three papers and Herman in four articles added 20 and 22 species level names, respectively. Scheerpeltz, Hatch, and Coiffait added 19, 14, and 13 names, respectively.

While the work of most writers was confined to one region, a few described species from many parts of the world. Most notable among the latter were Erichson, Fauvel, Bernhauer, and Cameron.

CLASSIFICATION

Of particular relevance to the present task are the investigators who tried to make sense of the increasing variation included in *Bledius* as the number of species proliferated. Most authors added species with little attempt to recognize groups. Their additions, however, made possible the increasingly refined perception of groups of similar species.

The earliest worker simply listed the species. In the nonalphabetic lists it is clear that the linear order reflected the authors' thoughts that adjacent species were most similar. Many lists were published and the proximity of similar species must have helped precipitate the recognition of named groups. In spite of the importance of these lists I will concentrate on the formal attempts to classify the variation, that is, the subgenera and named species groups.

After Linnaeus (1758) described *Staphylinus* with 19 species he and others continued to add more species making the group increasingly diverse. Later, others trying to contend with this variation split off new genera. In 1802 Gravenhorst separated some species, calling the group *Oxytelus* and in turn Leach, 1819, separated some species from *Oxytelus* and put one of them (*armatus*) in *Bledius*. Curtis (1826) described *Bledius*. A few years later in 1929 both Curtis and Stephens listed a few species in *Bledius* and each named a new group, *Hesperophilus*. Curtis included two species in *Bledius* and four in *Hesperophilus*. *Hesperophilus* had species that looked like *Bledius* but lacked the cephalic and prothoracic horns. Characters were given to distinguish these two taxa by Stephens (1834). In 1834 Stephens had only four names in *Bledius* (he left *armatus* out) and five in *Hesperophilus* (he dropped one included in 1829 and added another).

Gistel (1834, p. 9) cited *Dicarenus*, without description, in a list that included seven available species. *Dicarenus* was forgotten until Blackwelder resurrected it in 1952. Erichson (1840) presented no formal classification within *Bledius* but he did cite *Hesperophilus* as a junior synonym of *Bledius*. Between 1829 and 1840 few workers cited *Hesperophilus*—the species that had been included there were listed in *Bledius*. Westwood (1838, p. 17) designated *fracticornis* as the type species of *Hesperophilus*. Waterhouse (1858, p. 29) listed both as separate genera.

In 1859 a new type species designation changed the concept of *Hesperophilus* and began a confusion that lasted for nearly a century. Thomson (1859), overlooking Westwood's designation, cited *arenarius* as the type species of *Hesperophilus*. He also described *Astycops*, designating *talpa* as the type species, and redescribed *Bledius*. Later he (1861, pp. 118–122) published longer descriptions of the three genera. In *Hesperophilus* and *Astycops* he included only the type species. Among the six species he cited with *Bledius* was *fracticornis*, the species Westwood designated as type species for *Hesperophilus*. Thomson's concept of *Hesperophilus* was followed for decades.

The seeds of misconception planted by Thomson flourished as Schiødte (1866, pp. 145–151) employed a classification of five genera. He moved *fracticornis* from *Bledius* to *Tadunus* (along with *crassicollis* and *atricapillus*). *Hesperophilus* remained with only *arenarius*. Schiødte also described *Bargus* (including in it *erraticus, opacus, pallipes, rastellus,* and *terebrans*) but failed to designate a type species for either *Bargus* or *Tadunus*. To *Astycops* Schiødte added another species.

Bledius remained the group of horned species. *Bargus* and *Tadunus* both included species with broadly crossed mandibles whereas species with porrect mandibles that crossed only at the tips were in *Hesperophilus* and *Astycops*.

Fauvel (1872, pp. 185–212) combined Schiødte's five genera into three groups within *Bledius*. Group 1 was *Bledius* (s. str.), the horned species. Group 2 was *Hesperophilus* and still included *arenarius*. In Group 3 he put *Astycops, Bargus,* and *Tadunus* where he included both *fracticornis* and *talpa*. He added species to each of the three groups. In the first catalogue to reflect a formal classification of *Bledius*, Fauvel (1875, pp. XII, XIII) added more species to his three groups. Each group was now a substantial taxon of many species. Group 1 included 17 species, Group 2 twelve, and Group 3 twenty-seven. The diversity in these groups was increasing markedly.

Writing about the French fauna, Mulsant and Rey (1878, pp. 551–661) proposed a classification of seven subgenera that is largely followed today. They continued to use *Bledius, Astycops,* and *Hesperophilus* but added *Elbidus, Pucerus, Belidus,* and *Blediodes*. Their work in effect represented a revision of Fauvel's classification of 1872.

Mulsant and Rey divided Fauvel's Group 1 (*Bledius*) into two subgenera, *Bledius* and *Elbidus*. These were the horned species. They reallocated the species that Fauvel (1872) put in Group 2 (*Hesperophilus*). Two species, including *arenarius*, went to *Hesperophilus*. Two were put in two new subgenera *Belidus* and *Pucerus*. Another species was added to *Pucerus*. Mulsant and Rey separated *Astycops* and four species from Fauvel's Group 3 and added to it the two species that remained in Fauvel's Group 2. Mulsant and Rey assigned the name *Blediodes* to the species that remained in Fauvel's Group 3 after *Astycops* had been removed. Inexplicably they failed to mention *Bargus* Schiødte or *Tadunus* Schiødte which Fauvel (1872) had combined with *Astycops* to form Group 3. They must have known of Schiødte's names since Fauvel's paper is cited throughout their revision.

Their oversight led them to name as *Blediodes,* a group that represented a combination of *Bargus* and *Tadunus.* This omission along with the continuing concept of *Hesperophilus* as including *arenarius* further compounded the misunderstanding of the groups of *Bledius.*

After Mulsant and Rey's work we had a classification that recognized two groups of horned species (*Bledius* and *Elbidus*), four with porrect mandibles that crossed only slightly at the tips (*Hesperophilus, Astycops, Pucerus,* and *Belidus*), and one with mandibles that cross broadly (*Blediodes*). Other characters were given to separate these subgenera.

Except for the addition of species names, the use of *Elbidus, Pucerus,* and *Belidus* remained unchanged. *Bledius* (s. str.) was modified slightly in 1929 when Znojko extracted several species to form *Euceratobledius.* These four subgenera were stable though many authors[4] used them. Most of these people were working with the same species, those in Europe.

Hesperophilus, Astycops, and *Blediodes* faced indefinite futures because of the acceptance of the wrong type species designation. *Hesperophilus* was being used for a group of species that included *arenarius.* It should have been applied to *Blediodes* of Mulsant and Rey or Schiødte's *Tadunus.*

Hesperophilus and *Astycops* share mandibular characteristics so while some authors separated them,[5] others[6] combined them.

A few papers included *Bargus* and *Tadunus.* Heyden et al. (1891, p. 115) cited them as junior synonyms of *Blediodes.* Seidlitz (1891a, 1891b) and Stierlin (1900, p. 392) considered them separate genera. Most authors[7] continued with *Blediodes* for this group of species until it was recognized that *Hesperophilus* has been misinterpreted.

Hesperophilus had had two type species designations, one in 1838 by Westwood (*H. fracticornis*) and another in 1859 by Thomson (*H. arenarius*). Everyone followed Thomson's usage for 80 years. Finally, though, Tottenham (1939, p. 225) correctly cited *fracticornis* as the type species of *Hesperophilus* then designated *fracticornis* as the type species of *Blediodes* (p. 228). By so designating the type species of *Blediodes* he made it an objective synonym of *Hesperophilus.* Sharp (1911c) had already designated *fracticornis* as the type of species for *Tadunus* thereby making it an objective synonym of *Hesperophilus* and *Blediodes.* In the same paper Sharp designated *B. pallipes* as the type species of *Bargus.* Since *pallipes* was included in *Blediodes* by most authors, *Bargus* was now a subjective synonym of *Hesperophilus,* the senior synonym of *Blediodes.* Tottenham (1949, p. 364) was first to outline this synonymy clearly (see table 8).

Tottenham (1939, p. 225), while pointing out the correct type species of *Hesperophilus,* recognized that the group that had had this name required a new one. He called it *Cotysops* and designated *arenarius* as the type species. This meant that the group referred to as *Hesperophilus* by authors for 80 years was now *Cotysops.*

Cotysops was short-lived, though. Another name was available. After being neglected for nearly 120 years *Dicarenus* Gistel was resurrected by Blackwelder (1952) in his landmark generic name catalogue. Blackwelder designated *arenarius* as the type species of *Dicarenus* thereby making *Cotysops* a junior objective synonym. Despite Blackwelder's

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[4] Ganglbauer (1895, pp. 610–627); Heyden et al. (1906, pp. 143–144); Reitter (1909, pp. 165–168); Winkler (1925, pp. 345–347); Porta (1926, pp. 45–48); Cameron (1930, pp. 270–278); Koch (1934, pp. 58–63; 1937, pp. 255–271); Tottenham, 1949, pp. 363–364, 410–411; 1954, pp. 48–55); Horion (1963, pp. 251–295); Lohse (1964, pp. 89–99); Scheerpeltz (1968, pp. 31–34); Coiffait (1973, p. 122); Shibata (1973, pp. 33–35).

[5] Heyden et al. (1891, p. 115); Seidlitz (1891a, 1891b); Sainte-Claire Deville (1907, p. 90); Tottenham (1954, pp. 52–55); Lohse (1964, pp. 92–99); Coiffait (1973, p. 122).

[6] Ganglbauer (1895, p. 624); Heyden et al. (1906, p. 143); Winkler (1925, pp. 346, 347); Porta (1926, p. 48); Horion (1963, pp. 288–294); Scheerpeltz (1968, pp. 33–34).

[7] Ganglbauer (1895, pp. 617–623); Heyden et al. (1906, p. 143); Sainte-Claire Deville (1907, pp. 90–92); Winkler (1925, p. 345); Porta (1926, pp. 46–47); Koch (1938a, pp. 130–140); Benick (1943, pp. 94, 95); Horion (1963, pp. 260–287); Scheerpeltz (1968, pp. 31–34).

resurrection of *Dicarenus*[8] Tottenham (1954) and Lohse (1964) continued to use *Cotysops.* Coiffait (1973) used *Dicarenus.*

The remaining history of subgeneric names is simple and direct. Znojko (1929) described *Euceratobledius* and designated *furcatus* as the type species. Herman (1972) removed a group of seven species and another of three and named them *Microbledius* and *Psamathobledius,* respectively. The type species are *playanus* and *punctatissimus,* respectively. A new genus, *Neobledius,* with one new species was described by Abdullah and Qadri (1968).

In North America a parallel classification with informal species group designations was being constructed. LeConte (1877, pp. 217–234), in the first of only two revisions of North American *Bledius,* stated (p. 217) the following:

> The species of this genus [*Bledius*] may be naturally divided into several groups, which have already been recognized in part by Schiødte [1866, 1867], and described by him as distinct genera.[9] The characters upon which these groups are defined have been determined by the study of very limited material, and will by no means serve for the natural arrangement of our [North American] species. The first dichotomous character of Schiødte . . . [Then characters are given] . . . would divide our large testaceous species which seems so closely allied . . . into two widely separated groups. The other characters used by that excellent observer are also of difficult observation, or visible with certainty only on dissection. I have therefore rejected them in great part and propose instead the following; the groups are named after the best known species pertaining to each.

LeConte then goes on with a key and description of five species groups[10] and all but 2 of the 44 species known from North America in 1877. Most Americans who used infrageneric groups followed LeConte (Casey, 1889; Fall, 1910; Notman, 1920; Herman, 1972, 1976, 1983a). The lone exception was Hatch (1957) who placed all of the Pacific Northwestern species in *Hesperophilus.*

The remarkable fact is that LeConte and European workers (Schiødte, Thomson, Curtis) independently produced exactly equivalent classifications excluding the two endemic groups, *mandibularis* in North America and *Bledius* (s. str.) in Eurasia; the four remaining species groups of LeConte represent the same concepts as the four genera (or subgenera) of the Europeans. The two classifications have never been reconciled. But that is in part the purpose of the present article.

The only changes made in LeConte's classification were by Herman (1972, 1976, 1983a)[11] who added three groups (*aequatorialis, melanocephalus,* and *emarginatus*) and separated out two genera: *Microbledius* and *Psamathobledius.*

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[8] However unfortunate Blackwelder's unearthing of Gistel's 1834 paper, the name *Dicarenus* has not been suppressed by the Commission on Zoological Nomenclature. We can either ignore it or use it. Having found and used the name, Blackwelder's choice of type species was not the best. The most appropriate type species for this ancient, forgotten name would have been one that made *Dicarenus* a junior synonym. As it happens there were three species that would have had this result. Gistel included 10 nominal species, 3 of which are nomina nuda. Of the remaining, 7 designation of either *armatus* or *tricornis* would have made *Dicarenus* either an isogenotypic or subjective synonym respectively of *Bledius* (s. str.).

Designation of *fracticornis* would have made *Dicarenus* an isogenotypic synonym of *Hesperophilus.* If *pallipes* or *castaneipennis* had been designated then *Dicarenus* would have replaced *Bargus* as the senior objective or subjective synonym, respectively, but would have been the subjective synonym of *Hesperophilus.* There would have been no further confusion or misuse. But from the remaining two species Blackwelder's choice of *arenarius* resulted in the synonymy of *Cotysops* which was only 13 years old and that had only been used in two papers by Tottenham. Had Blackwelder designated *talpa* then *Astycops,* a name used since 1859, would have fallen.

[9] Note: The genera cited by Schiødte were *Bledius, Tadunus, Bargus, Astycops,* and *Hesperophilus.*

[10] LeConte's species groups were: *mandibularis, armatus, semiferrugineus, annularis,* and *cordatus.*

[11] Herman also in these publications inadvertently changed LeConte's *cordatus* group to *basalis* group. The species composition is nearly the same.

NATURAL HISTORY

The most commonly known information about the life of *Bledius* is that they make burrows in moist sand, eat algae, and are eaten by species of *Dyschirius* (Carabidae). One textbook notes that one species is subsocial.

But what more can be said? Has so little work been done on the life story of so large a genus as *Bledius*? How and where are the burrows made? Where do the larvae live? How many larval instars are there? What is the ecological role of *Bledius*? What kind of algae are eaten? What is the nature of the *Dyschirius-Bledius* relationship? What eats *Bledius* besides *Dyschirius*? What are the characteristics of their "subsocial" behavior?

These and many other questions have been addressed by a number of investigators. The most noteworthy works are those of Larsen (1936, 1952, 1953), Paulian (1942), Matsuzawa (1964), Wyatt (1982), and Griffiths and Griffiths (1983). Many others have added important information. The following chapter will summarize much of the published literature along with some of my observations. Reviewing the literature and reflecting on my own experiences of collecting *Bledius* for 20 years prompted many other questions, some of which are included herein.

The purpose of the chapter is to provide an overview of what is known about the natural history of *Bledius* in the hope that it will stimulate further work. As a systematist, I want to know the natural historical "reality" of my anatomically based species groups.

NUMBER OF SPECIES

There are 439 valid, extant species presently listed in *Bledius.* I know of perhaps a dozen undescribed New World species and Drs. D. N. Biswas and T. Sen Gupta are working on a paper in which they will add perhaps six or eight new species from India. How many more are there? After years of studying a group some authors hazard a guess at how many more species there might be. Frank and Curtis (1979) showed the difficulty with "rule-of-thumb" estimates and with more quantitative estimates. I cannot guess how many more *Bledius* are yet to be discovered but there are certainly many names that should be synonymized.

POPULATION SIZE

Individuals of *Bledius* have often been reported in immense numbers. Rudd (1835) was the first to comment that he was able to fill a large pill box with *B. arenarius* (=*fergussoni*) with one sweep of his net. In two hours on three successive nights, 25,000 specimens of *Bledius mandibularis* were collected each night at a light trap set near a mangrove swamp on Little Cayman Island (Blackwelder, 1947). Ortenburger and Bird (1933) reported 285 galleries per square foot of a then undescribed species (*Bledius playanus*) inhabiting a salt flat in north central Oklahoma. The salt flat has an area of 43 square miles. The animals are certainly not evenly distributed over the whole surface and not all of the burrows are occupied. Nevertheless, even if there is only an average of one *Bledius playanus* per square foot (adult, larvae, or pupa), there are 1.2×10^9 individuals on this one salt flat. *Bledius mandibularis* is found on this same salt flat but in unknown abundance. Matsuzawa (1964), in an article discussing some economically significant damage accomplished by *Bledius salsus,* noted that 5,000 to 10,000 individuals can be collected at a light trap in one evening. Matsuzawa said that in a single clay bed (about 2 m wide and 25 m long) there were over 29,000 burrows and more than 8,500 beetles. At the localities where Matsuzawa was working there were many such clay beds occupied by *Bledius salsus* and the species was also found abundantly in nearby sandy-clay soil.

Bledius spectabilis in England was found in intertidal zones in concentrations of up to 1000 individuals per square meter (Wyatt, 1982).

Griffiths and Griffiths (1983) studied *Bledius punctatissimus* (then in *Psamathobledius*) on an island off the coast of South Carolina. The species was confined at one cove to an area about 12 m by 40 m adjacent to the ocean. They found 8000 adults per shore length meter and a peak population of 2260 beetles/m^2 at about 4 m from the drift line. Using their figures the size of the population at that cove can be estimated at about 320,000 adults and about 41,600 larvae; this at only one small beach.

In 20 minutes, P. M. Hammond (personal commun.) caught an estimated 250,000 specimens of *Bledius pilicollis* that flew to a light trap near the ocean in Cape Province, South Africa. He counted a cubic centimeter of specimens and extrapolated it to an estimate of 60,000 specimens per pint.

While collecting on a sand bar of the Platte River in eastern Nebraska in less than an hour more than 15 quarts of 10 species of *Bledius* were attracted to an ultraviolet light. Most of the specimens were *Bledius bellicus,* a species of about 4 to 7 mm long; eight of the other nine were smaller species (Herman, personal observ.). *Bledius pilicollis* is larger than *B. bellicus,* so using Hammond's estimate of 60,000 *pilicollis* per pint, there may have been as many as 1.8×10^6 *Bledius* in the 15 quarts of beetles that flew to the light on that quiet, sultry Nebraska evening.

But, however large the population of *Bledius* may be, the numbers are a mere pittance compared to nematodes for which Kevan (1962) cites densities of 0.2 to 20 million/m^2.

DISTRIBUTION

ISLANDS: Where is *Bledius* found? The genus is considered to be cosmopolitan by some (Scudder, 1900; Eichelbaum, 1909; Cameron, 1930; Herman, 1970) but careful examination reveals conspicuous gaps in a worldwide distribution. Species are found between at least −292 ft and 10,000 ft elevation and on all continents except Antarctica and on some continental islands. They are absent from most oceanic islands. In the Atlantic, no species have been reported from Iceland (West, 1937; Henriksen, 1939; Lindroth, 1957; Larsson and Gigja, 1959); the Faroes or Greenland (West, 1937; Lindroth, 1957), Baffin (Brown, 1937; Lindroth, 1957), the Azores (Bernhauer, 1940d; Méquignon, 1942; Smetana, 1970), Madeira (Wollaston, 1857; Bernhauer, 1940d; Smetana, 1963, 1970), or St. Helena (Wollaston, 1877a) nor have I seen any from these islands. Neither have I studied *Bledius* from Bermuda, Fernando Noronha, Ascension, Trinidad, or Tristan da Cunha. Similarly, *Bledius* is absent from any mid-Pacific islands, including Samoa (Cameron, 1927), the Marquesas Islands (Cameron, 1933a, 1936a; Coiffait, 1980a), or the Society Islands (Cameron, 1933b; Coiffait, 1980a). An undetermined species of *Bledius* was reported from Oahu, Hawaii (Moore, 1975) but it was a misidentification of *Carpelimus* (Herman, unpublished data). In 1984 I tried for two weeks to find *Bledius* in Hawaii and although I was unsuccessful there are many reef-sheltered beaches that would provide perfect habitat for *Bledius.* I have seen no specimens from most islands of the Indian Ocean, nor any of the islands of the southern parts of the Atlantic, Indian, or Pacific oceans. Hammond (1976) reported that the Oxytelinae are unknown from islands south of 45°S. The islands from which species of *Bledius* are known are all on the continental shelves or are oceanic islands that are around the perimeter of the oceans. In the Atlantic regions, nine species are reported in the West Indies (Blackwelder, 1943, 1947), eight from the Scilly Islands (Blair, 1931), one from the Shetland Islands (West, 1937), three from the Inner Hebrides (Welch, 1983) and Outer Hebrides (Waterston et al., 1981), three from the Canary Islands (Wollaston, 1864; Fauvel, 1897, 1902), and one from the Cape Verde Islands (Wollaston, 1877b). Around the Pacific species are known from some of the Aleutian Islands (Herman, 1983) and Japan, Taiwan, the Philippines, New Guinea, Indonesia, New Britain, New Ireland, Solomon Islands, New Hebrides, New Caledonia, New Zealand, and the Galapagos Islands (see figs. 1–12). In the Indian Ocean *Bledius* are found on Madagascar, the Aldabra Islands, the Laccadive Islands, and Chagos Archipelago (see figs. 1–3, 8–12). The Galapagos, New Caledonia, New Hebrides, New Zealand, Chagos Archipelago, and the Cape Verde and Canary Islands are noteworthy because they are so isolated from continental areas.

The Canary Islands have three species, *B. vitulus, B. unicornis,* and *B. corniger* (Fauvel, 1902), the Cape Verde Islands have only *B. vitulus* (Wollaston, 1877b) and *B. incertus* (localities cited herein), and the Galapagos have *B. aequatorialis* and *B. punctatissimus*

(Coiffait, 1981c). Diego Garcia Island of the Chagos Archipelago has *B. pulchellus,* New Caledonia has *B. circularis,* and species of the *verres* group are on both New Caledonia and New Hebrides. New Zealand has three species, *B. amplicollis, B. bidentifrons,* and *B. salinus* (reported herein). The unifying feature of these species is that they all live in seashore habitats. The species from the Canary, Cape Verde, and Galapagos Islands, and Diego Garcia, New Hebrides, and New Caledonia also occur on the nearest continent. The species from New Zealand are known nowhere else but revisionary work is required for them. These New Zealand species may occur in Australia and/or may be conspecific with other species.

Are these isolated island distributions natural or synanthropic? Lindroth (1957) listed characteristics he thought would help an insect survive transport across the Atlantic in ballast. The species should be ground dwelling, nonhygrophilous, prefer open ground of waste place character, nonhalobiontic, not dependent on special kinds of food, flightless, and parthenogenetic. *Bledius* are ground dwelling and some do not require saline habitats but they require moist conditions, require algae to eat (and therefore sunlight to grow them), fly, and are bisexual. Larsen (1936) was frustrated by the difficulty of maintaining live cultures of *Bledius.* When living conditions deteriorate, individuals leave the burrows and fly away or run around on the surface, eventually to die. *Bledius* probably tolerates accidental transport by man poorly.

Do they fly or float to isolated islands? That adults of *Bledius* fly is well known. As early as 1835, Rudd collected them in large numbers in flight with a sweep net. Many specimens of *Bledius* in museums were collected when they flew to a light. How far can or do they fly? There seem to be no data on this point. However, Blackwelder (1947) reported that more than 75,000 specimens of *Bledius mandibularis* were collected at a light trap placed near a mangrove swamp while, a quarter of a mile away, none were attracted to a light trap in a pasture nor to another near the top of a beach. *Bledius mandibularis* seems to fly only within its habitat. Above Tallulah, Louisiana, unnamed species of *Bledius* were captured at altitudes of 200 to 2000 ft; 88 percent of 125 specimens were collected at 200 to 500 ft. In these collections, *Bledius* represented 10 percent of the Staphylinidae which were 39 percent of the Coleoptera (Glick, 1939). Glick thought most of the insects were alive. Linsley Gressitt and his colleagues published papers in early volumes of *Pacific Insects* concerning insects collected by airplane over the Pacific but the published lists were identified only to family. There is no convincing evidence that *Bledius* fly to oceanic islands.

It is unclear whether saline tolerant *Bledius* spp. can survive sufficiently prolonged immersion in the ocean that they can be carried by sea currents to isolated islands. Experiments on saline tolerant species suggest that *B. spectabilis* could survive up to 10 hours of submergence (Evans et al., 1971), and that *B. punctatissimus* could live for 6 hours under water but that they all died after 8 hours (Griffiths and Griffiths, 1983). Nevertheless since all of the species reported from these oceanic islands are maritime and salt tolerant, they may have floated or rafted (or even been blown) to them. The *Bledius* fauna of these nearby oceanic islands does not include all the salt tolerant species from the nearest mainland, nor are there any freshwater species known.

The three species in New Zealand and one of those from the Galapagos (*B. punctatissimus*) belong to a species group in which most of the species are restricted to coastal, saline habitats around the world. It is one of the groups I would most expect to be on Pacific islands.

CONTINENTS: The distributions of the species of *Bledius* are known best in North America (Herman, 1972, 1976, 1983a), Europe, and perhaps North Africa, but for the latter two areas there are no publications that provide maps and/or detailed locality lists for all the species. Knowledge of distribution of species from these areas has been published piecemeal by many authors. The localities cited in the present paper are all from specimens I examined and are fairly representative of the known distribution. The distributions of each of the 34 species groups are summarized in maps and discussed briefly following the description of each group. All of the groups certainly occur more widely than shown herein.

Only six groups have species in the Old and New Worlds. The *punctatissimus* group has the widest distribution (fig. 11). It is found on all continents and New Zealand and some of the Indonesian islands. Species have not been reported from Madagascar but they may be there. The *emarginatus* group occurs widely in Central and South America and the West Indies with a few species getting into eastern North America (fig. 5). Species are in Australia and South Africa and a few specimens are known from northern India and possibly New Zealand. The *semiferrugineus* group is also widespread (fig. 7). Most species of this large group are found in the Holarctic region but a complex of several species related to *rubiginosus* extend into Central and South America. In the Old World a complex related to *ganglbaueri* (that resemble the *rubiginosus* complex in form, color, and sculpturing) is found in northern and subsaharan Africa. The *annularis* (fig. 5) and *albonotatus* (fig. 6) groups are both restricted to the Holarctic region, especially in cooler areas. Finally, the *basalis* group is amphiatlantic in the northern hemisphere (fig. 9). Most of the species are in the New World.

Five groups are restricted to the New World. The *armatus* group is found only in the Nearctic region where species extend onto the central Mexican plateau (fig. 8). The *aequatorialis* group is found only in and around the Caribbean, Ecuador, and the Galapagos (fig. 1). Most of the species of the *mandibularis* group are found along the coasts of North America (fig. 1). Some species are also found inland. The *bonariensis* group is restricted to southern Brazil, Uruguay and northern Argentina (fig. 10). The *forcipatus* group is found in both North and South America but most of the species are from the southern hemisphere (fig. 12)

Thus, 11 species groups incorporating 139 species are found in the New World, but only 5 of the groups are confined there.

The vast preponderance of the species groups and species are found in the Old World. Twenty-nine groups are found in the Old World; 23 are restricted to this hemisphere.

The largest and most widespread of the Old World groups is the *verres* group (fig. 9). That group has a paleotropical distribution with some species extending into temperate regions. It is absent from northern Europe, central and northern Asia, and New Zealand. It may occur only in northern Australia.

The *debilis* group is largely circummediterranean (fig. 10) and the *tibialis* group occurs from Europe to India (fig. 12). The *furcatus* (fig. 2), *minniensis* (fig. 1), *immaturus* (fig. 1), and *angustus* (fig. 12) groups have Eurasian distributions. The *kochi* (fig. 4) and *gigantulus* (fig. 3) groups are also Eurasian but extend into Africa. The *infans* group is in North Africa but may occur eastward to southeast Asia (fig. 10). The *fratellus* (fig. 10) and *lamelliceps* (fig. 2) groups are confined to Africa and the *lugubris* (fig. 10) group to Madagascar. The *compressicollis* (fig. 1), *rugosicollis* (fig. 1), *pulchellus* (fig. 10), *kosempoensis* (fig. 8), and *bispinus* (fig. 12) groups are known from southeastern Asia including India and Indonesia. The *bellicosus* (fig. 2) and *lucidus* (fig. 8) groups are found in that southeast Asian area but also reach Australia. The *hamifer* (fig. 1) and *minax* (fig. 1) groups are confined to *Australia* and *circularis* (fig. 1) is also in *Australia* but reaches New Caledonia and New Hebrides.

Table 1 summarizes the regional distribution of the species groups. Twenty groups are in Asia, 15 in Africa, 13 in Europe and India. One of the smallest regions is North Africa where 11 groups occur. Australia has eight groups. The West Indies and Madagascar, both so near large continents, each only have four groups. Eleven groups are found in the New World but 29 in the Old World. In the Old World 300 species are described and in the New World 139.

SALINE HABITATS: Most species of *Bledius* live in moist soil near freshwater or saltwater streams, rivers, and lakes, or near the ocean. The majority, about two-thirds, of the *species* live in freshwater habitats, but most of the species of about two-thirds of the *species groups* live in saline habitats. The names of groups found in saline habitats are marked with an asterisk in table 1. The habitat for

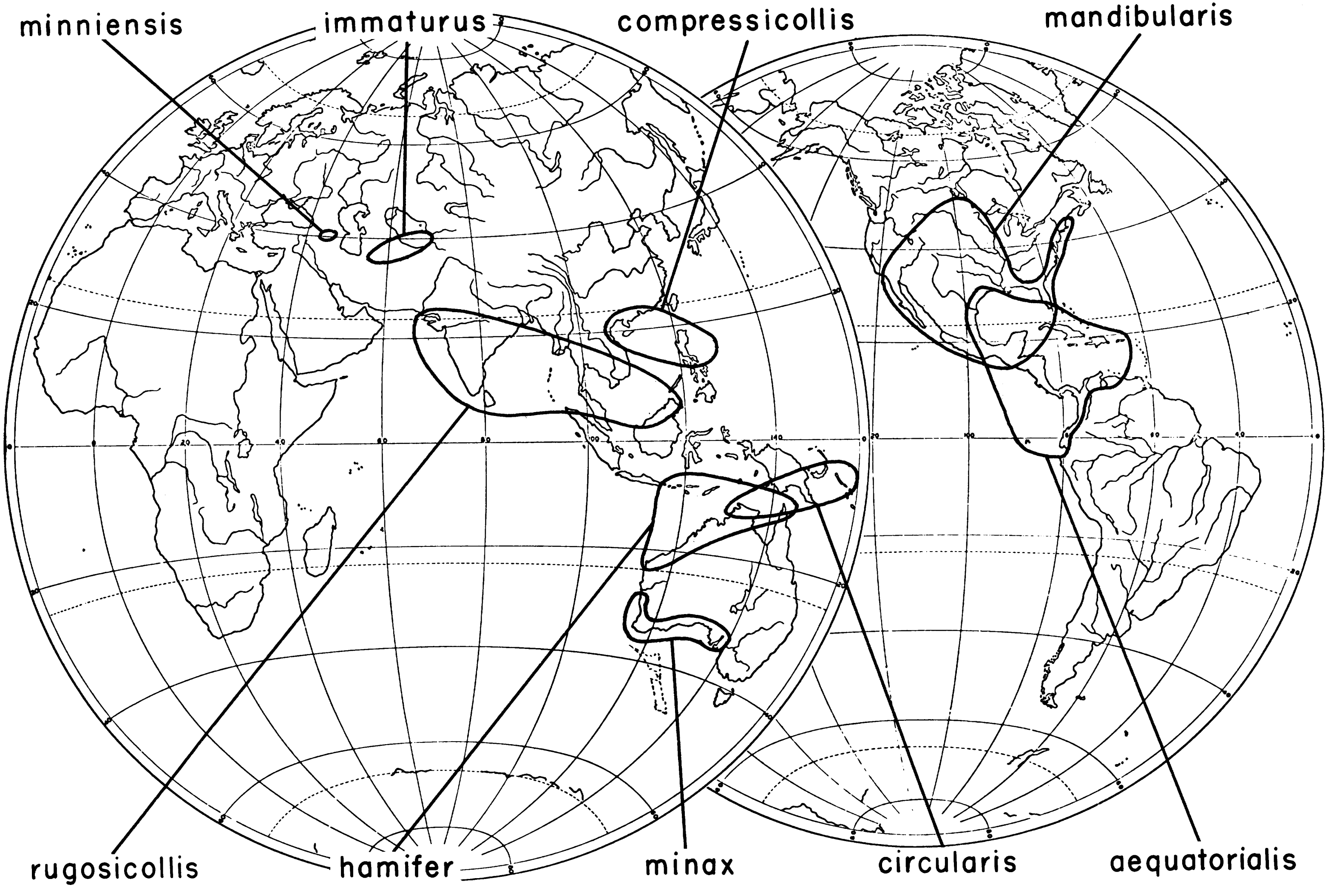

FIG. 1. Distribution of the *aequatorialis, circularis, compressicollis, hamifer, immaturus, mandibularis, minax, minniensis,* and *rugosicollis* groups.

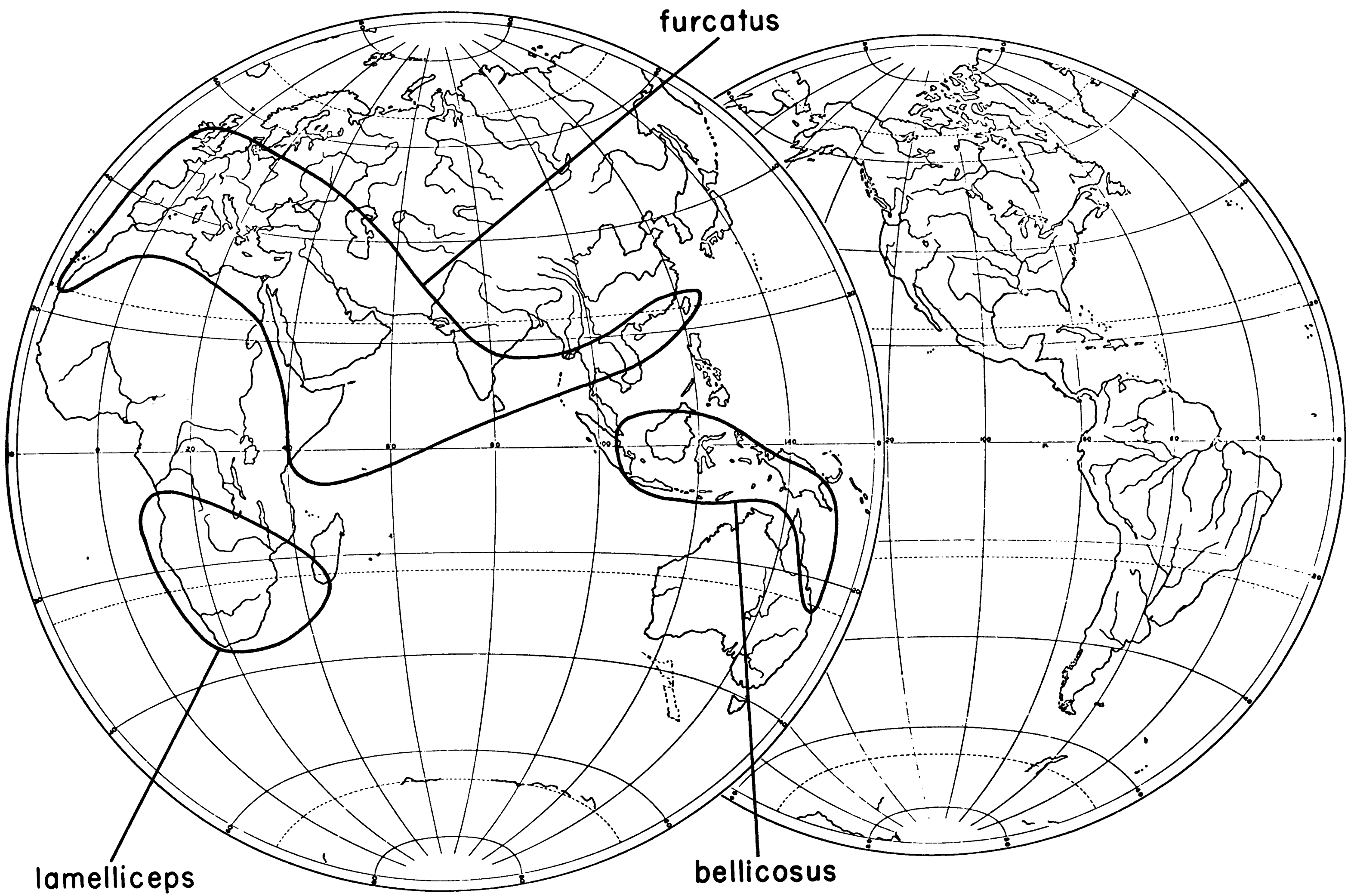

FIG. 2. Distribution of the *bellicosus*, *furcatus*, and *lamelliceps* groups.

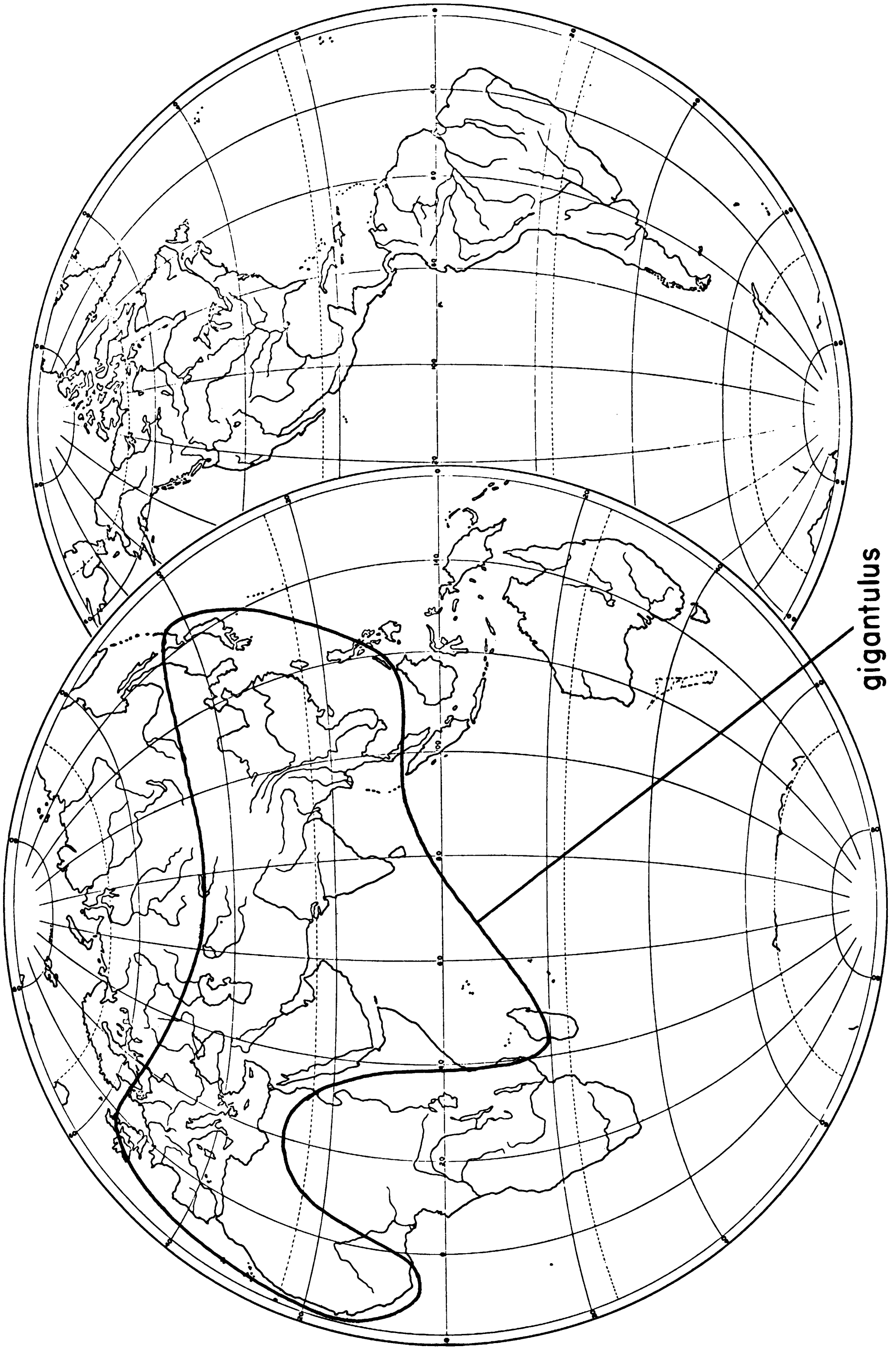

FIG. 3. Distribution of the *gigantulus* group.

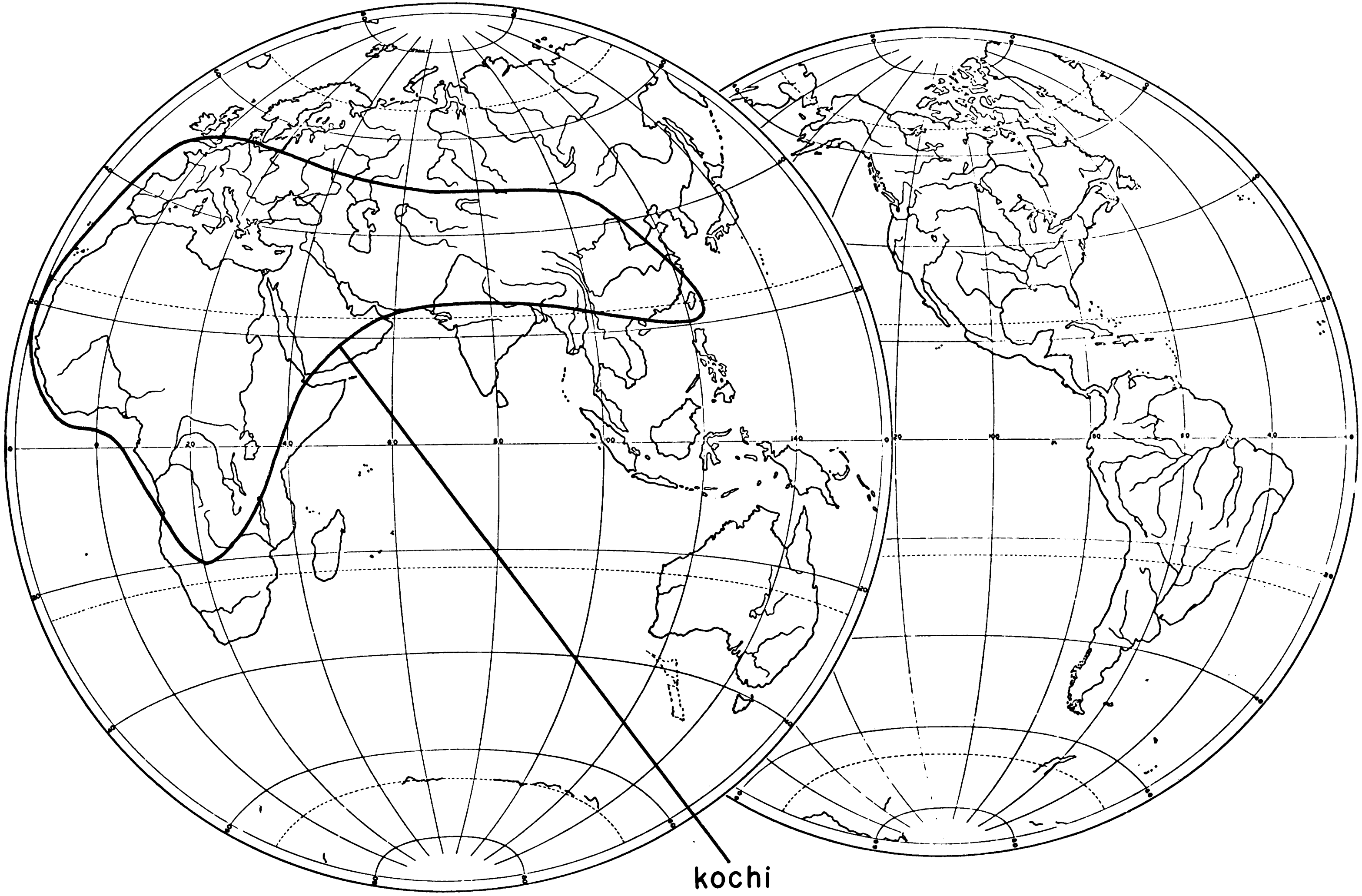

FIG. 4. Distribution of the *kochi* group.

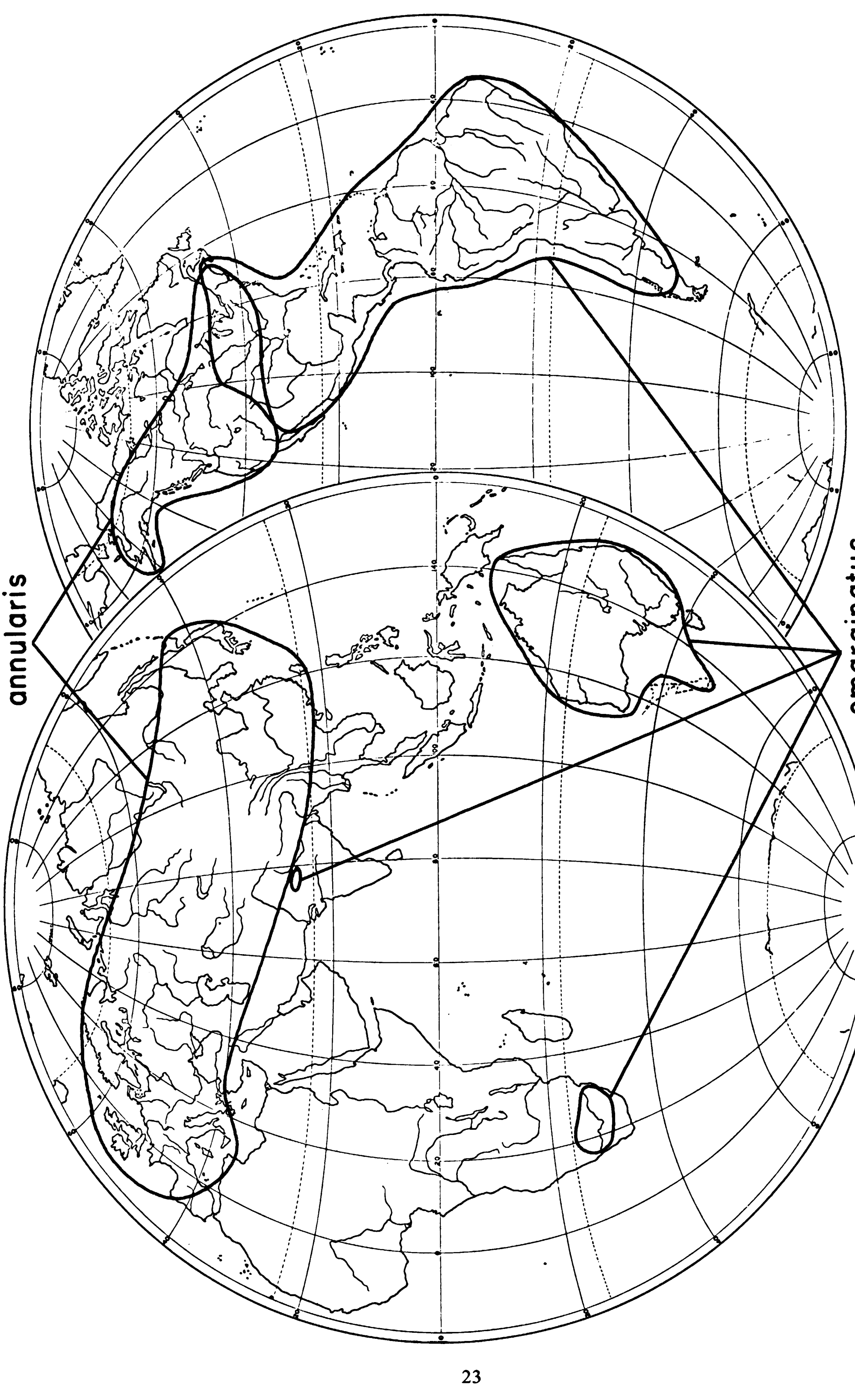

FIG. 5. Distribution of the *annularis* and *emarginatus* groups.

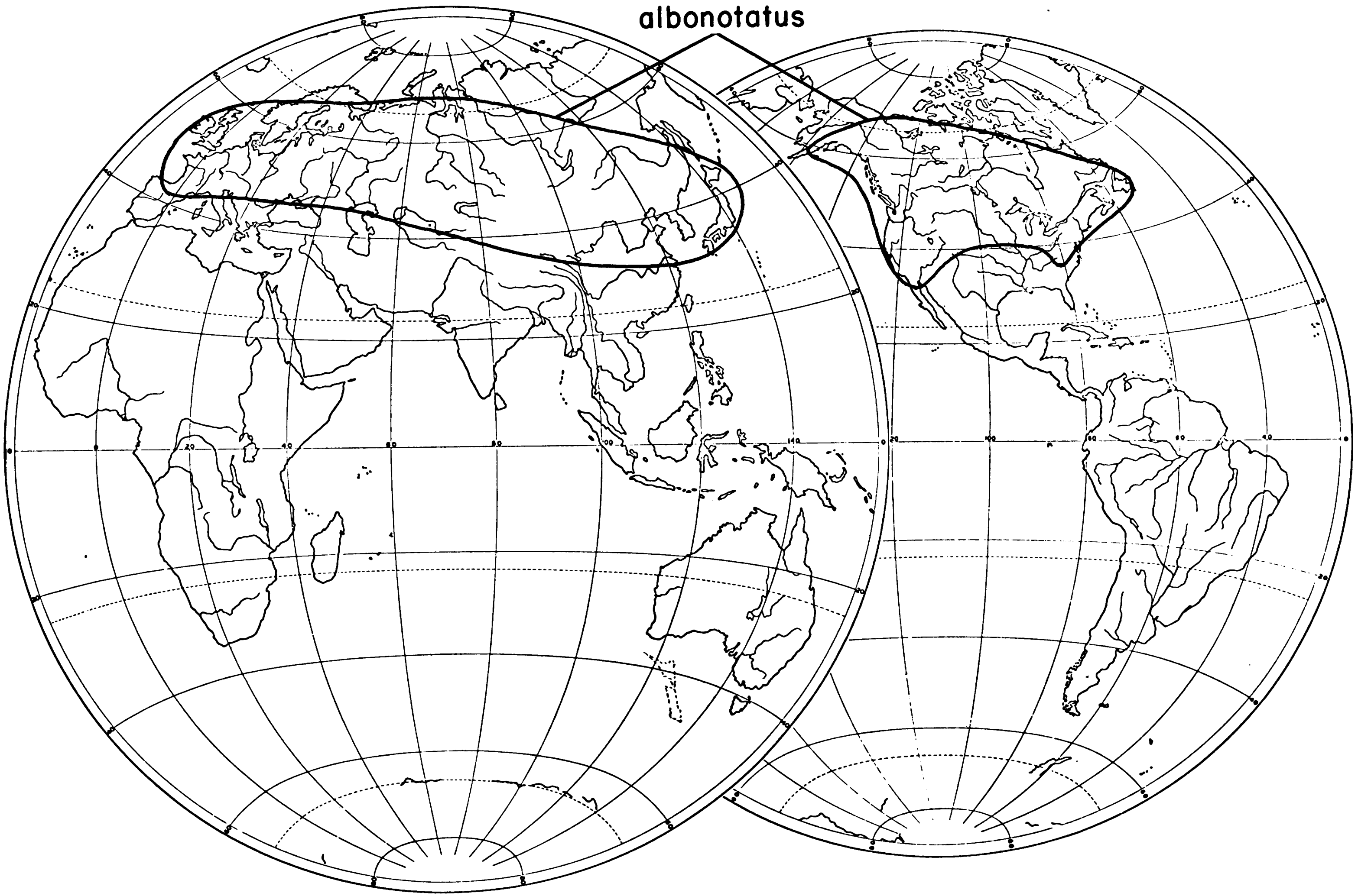

FIG. 6. Distribution of the *albonotatus* group.

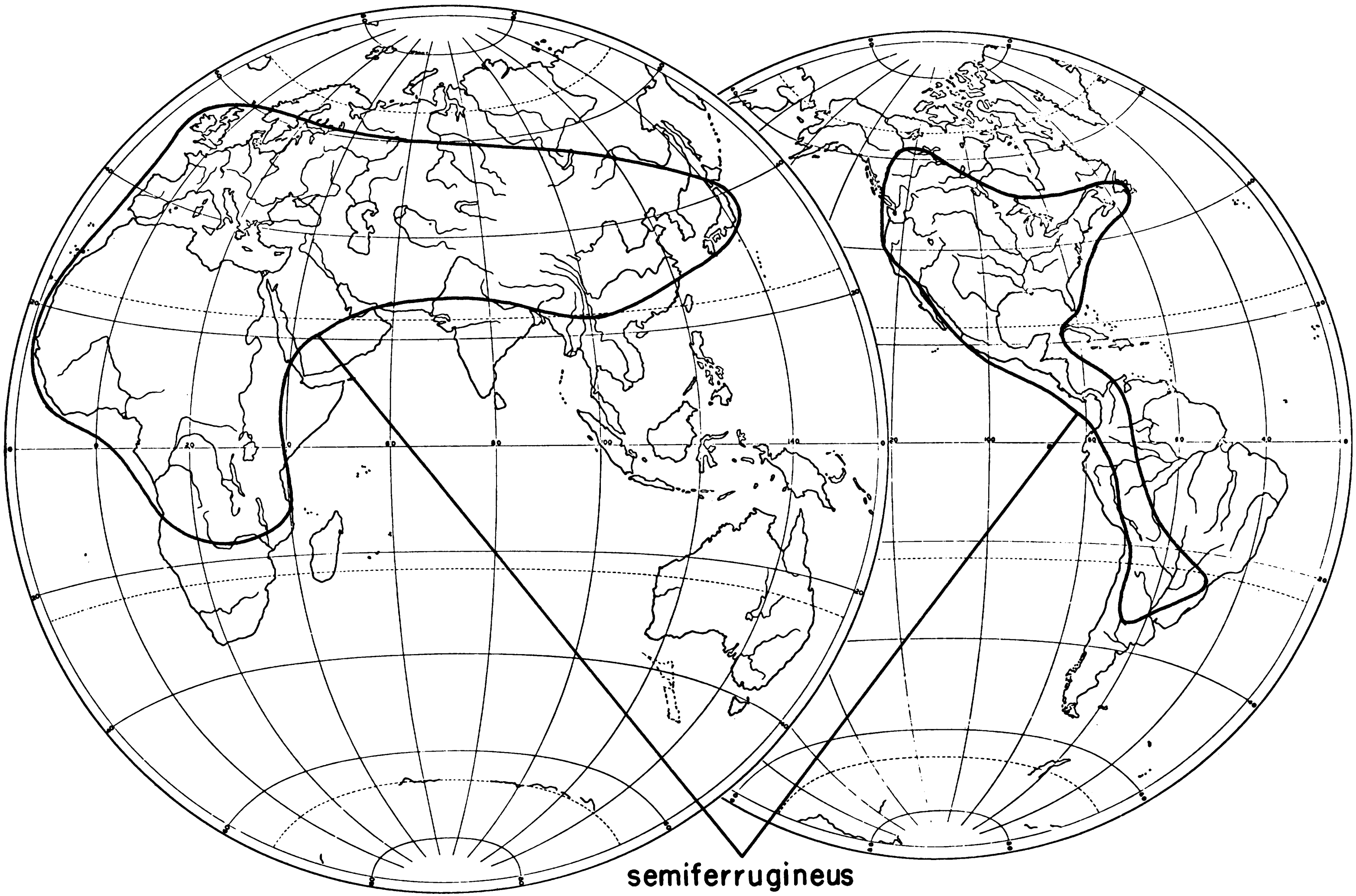

FIG. 7. Distribution of the *semiferrugineus* group.

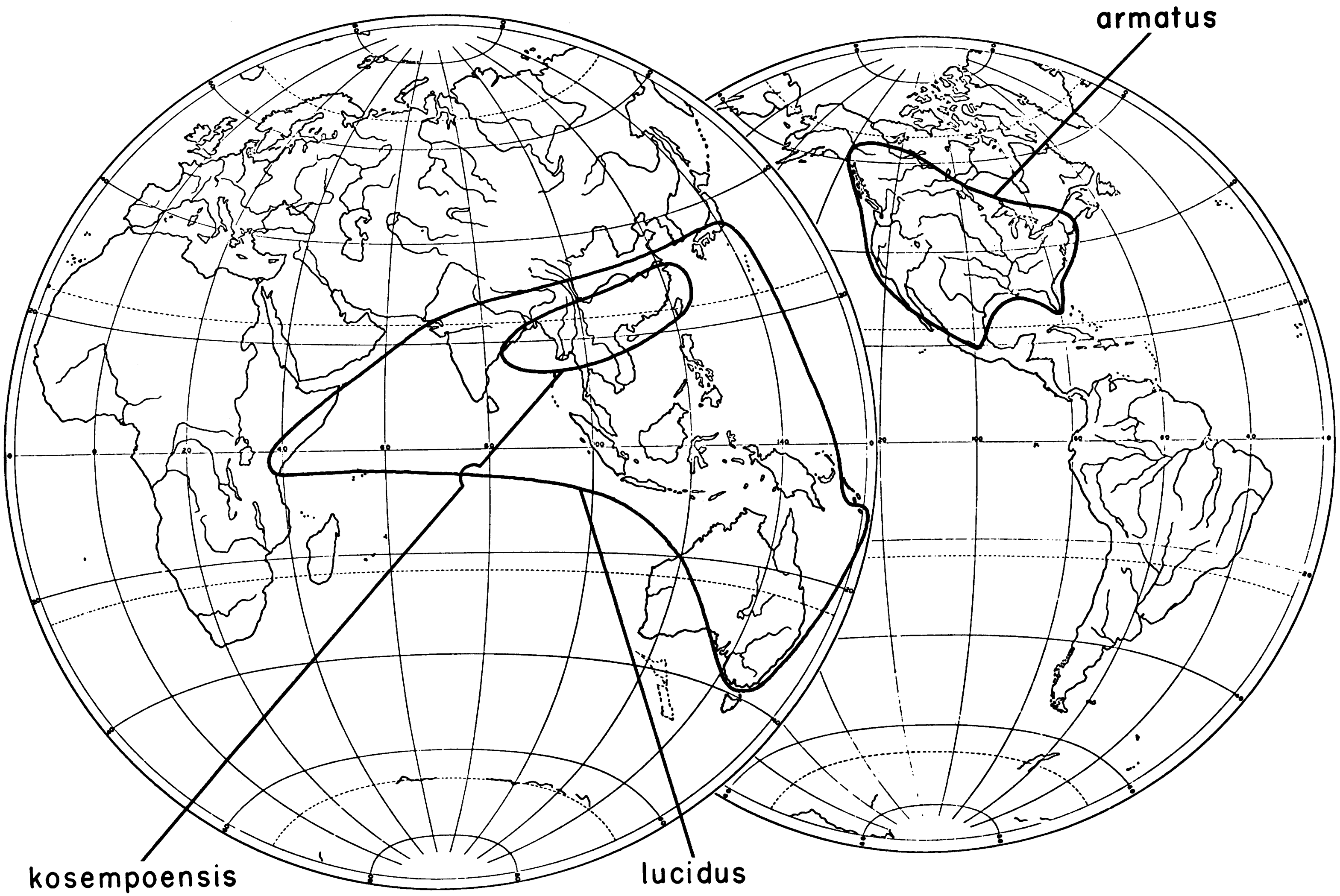

FIG. 8. Distribution of the *armatus*, *kosempoensis*, and *lucidus* groups.

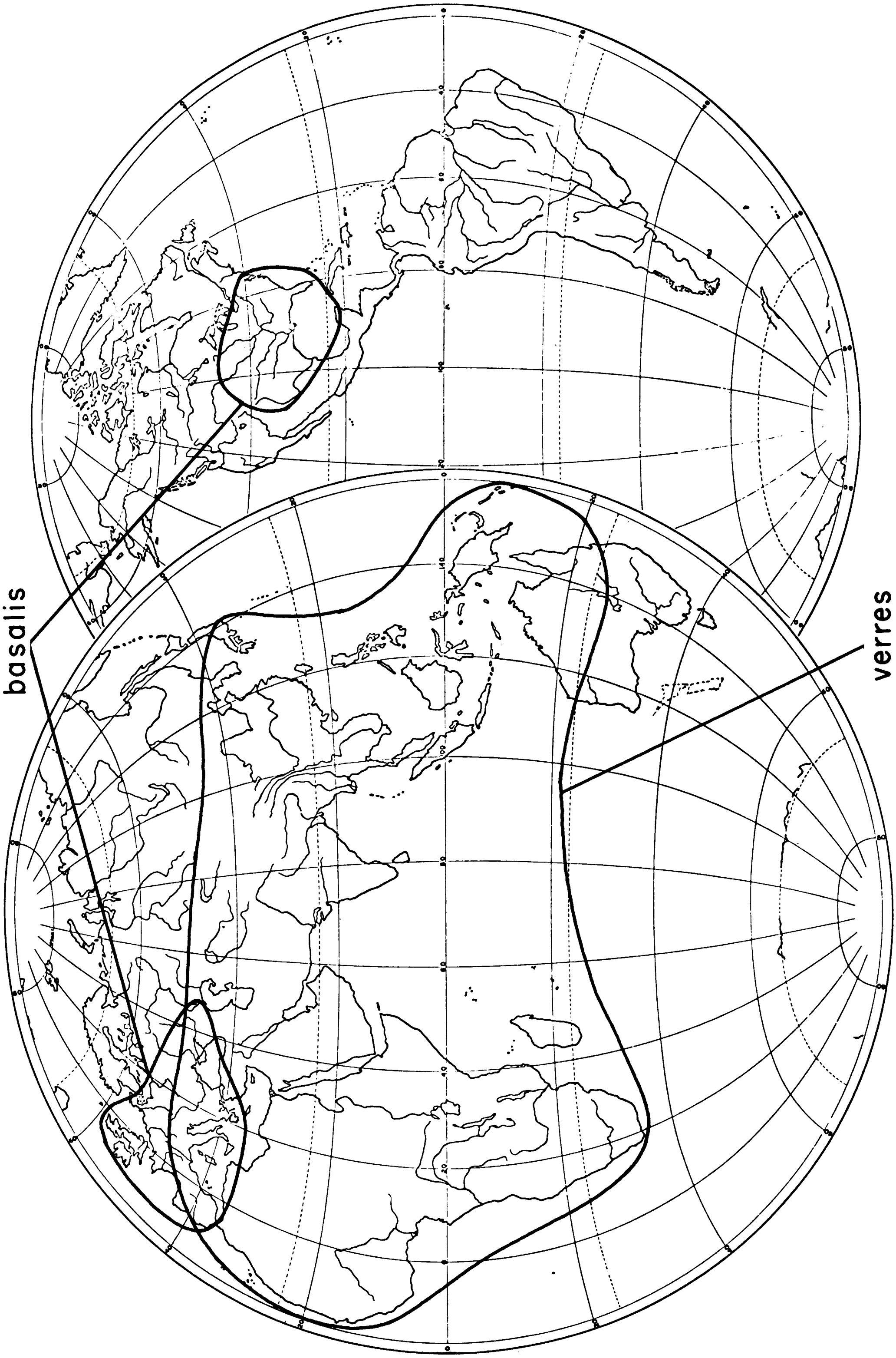

FIG. 9. Distribution of the *basalis* and *verres* groups.

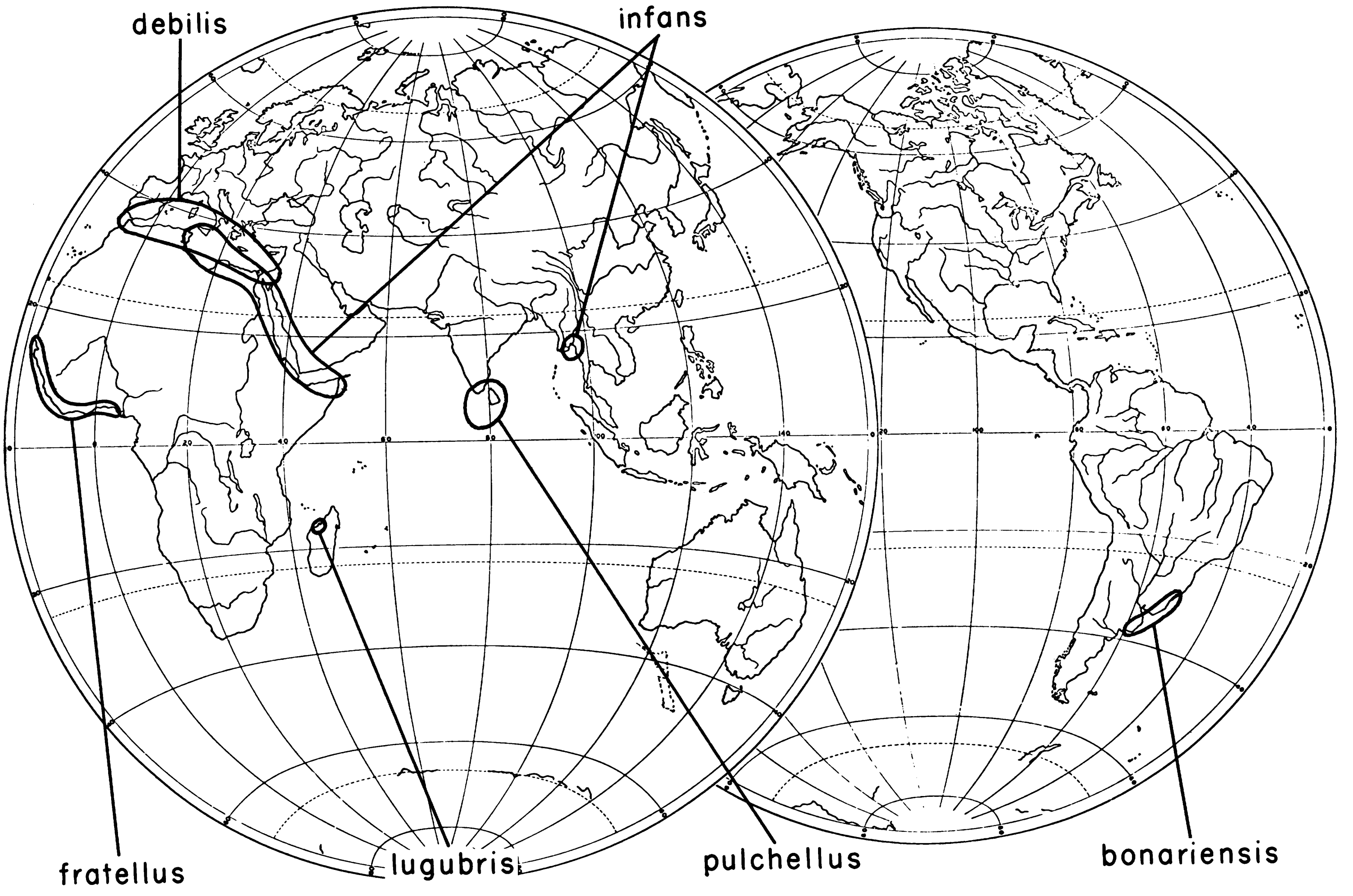

FIG. 10. Distribution of the *bonariensis, debilis, fratellus, infans, lugubris,* and *pulchellus* groups.

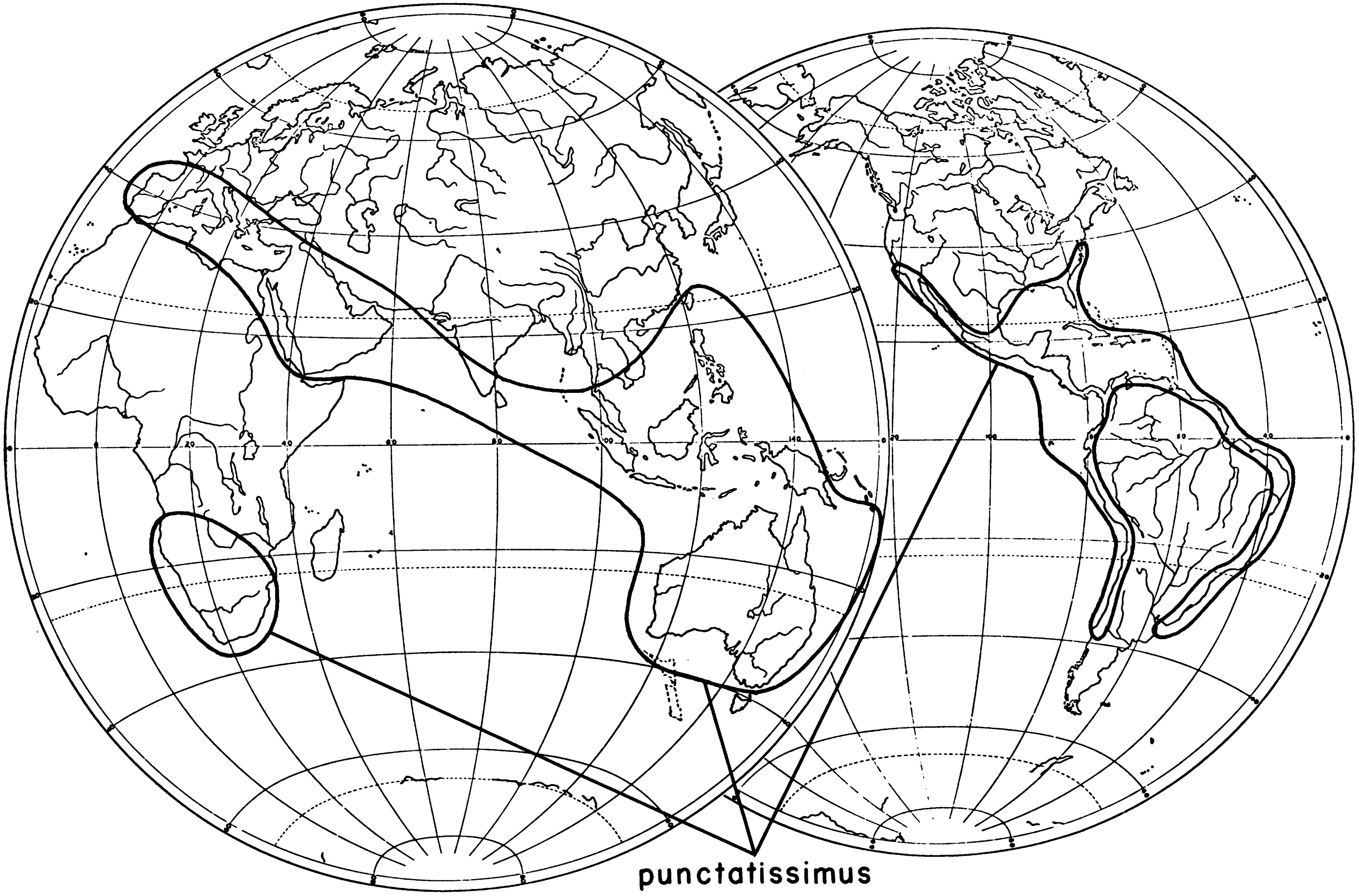

FIG. 11. Distribution of the *punctatissimus* group.

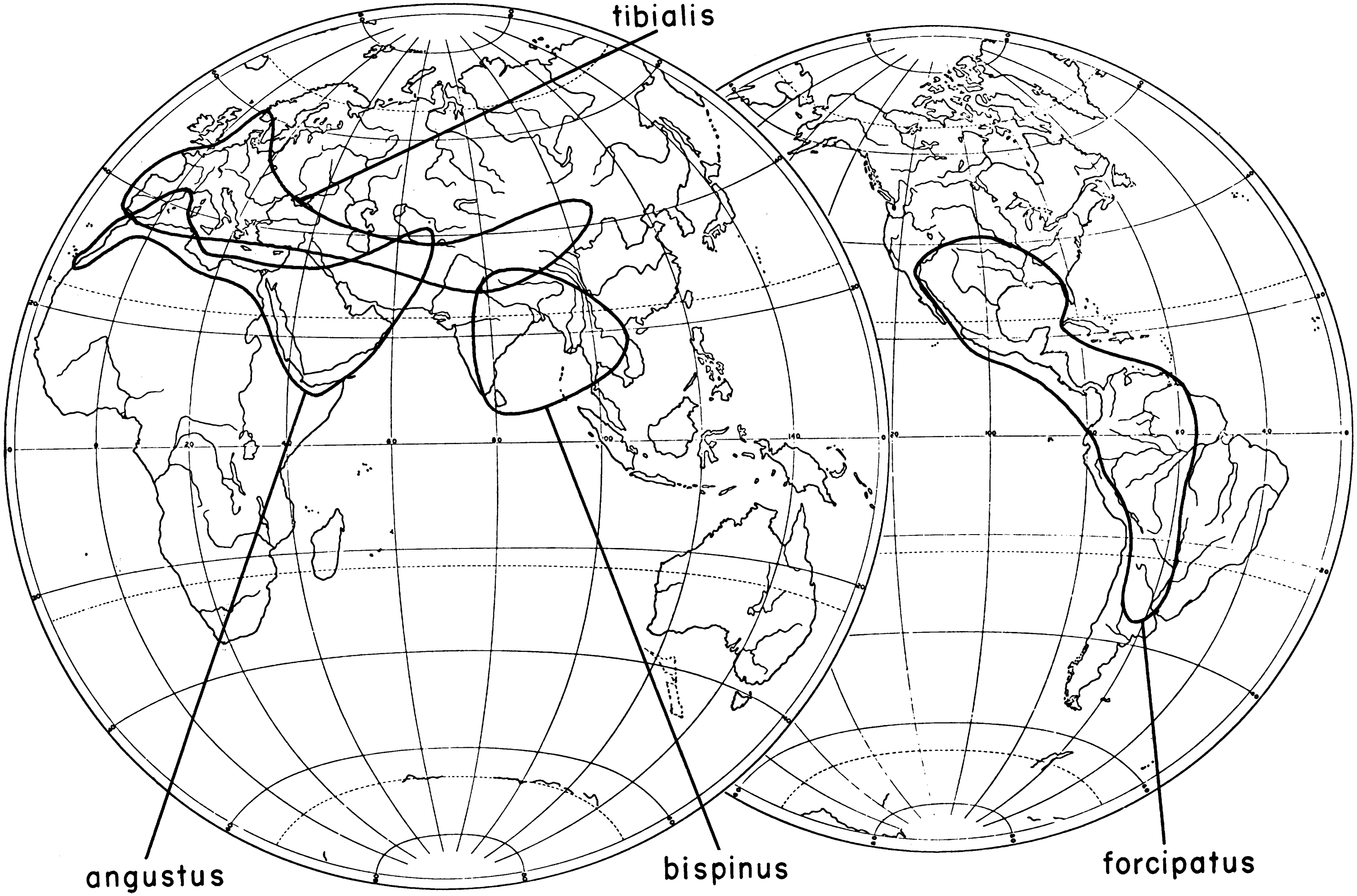

FIG. 12. Distribution of the *angustus, bispinus, forcipatus,* and *tibialis* groups.

most species is surmised by the locality. The *minniensis, bellicosus, kosempoensis, lugubris,* and *bispinus* groups are listed as from freshwater habitat because of the locality but each is known from few localities.

Most of the species of the four largest species groups, namely, the *emarginatus, annularis, semiferrugineus,* and *verres* groups, live in freshwater habitats but some may be in saline habitats. These groups are widespread around the world.

The groups with species that live in saline habitats are small to moderately large. The *kochi* and *punctatissimus* groups have the most species. Some groups, for example the *mandibularis, punctatissimus,* and *basalis* groups, include a few species that live in freshwater habitats. With the exception of the *immaturus* group, all of the saline tolerant groups have some species that are found at or are restricted to sea coastal habitats.

For salt tolerant *Bledius,* the most continuous habitat is the seacoast. The major breaks are between the New and Old Worlds and Australia. The inland salt lakes, also called athalassohaline lakes (Williams, 1981), are more scattered.

There are huge gaps in the known distributions of most salt tolerant species of *Bledius.* The gaps in sea coastal distributions are mostly artifacts of collecting. For species from athalassic salt lakes these gaps may either represent lack of collecting or absence of salt lakes. What is the distribution and origin of salt lakes? What is a salt lake? Presumably knowledge of where salt lakes are will help to fill the gaps in distribution of species that live near saline lakes. Establishing the distribution of saline tolerant *Bledius* that live near the ocean or even large salt lakes is relatively direct. However, surmising where to search for species that live near inland saline lakes requires knowledge of the distribution of salt lakes. Some saline tolerant species occur in somewhat unexpected places. For example, *Bledius* is found in claybeds used to evaporate seawater for commercial production of salt (Matsuzawa, 1964) or near salt mining regions of interior Germany.

SALT LAKES: Normally one thinks of salt lakes as rare—most of us would probably be able to list at most a few dozen, but there are hundreds. The volume of inland saline water has been estimated at 1.04×10^3 km^3 and for inland freshwater at 1.25×10^3 km^3 (Williams, 1981 citing Vallentyne) so that inland salt water accounts for about 45 percent of the inland water. The volume of freshwater is 0.009 percent of the water in the world, and inland salt water is 0.008 percent (Williams, 1981). Since all water contains dissolved salts, the definition of salt water is arbitrary but in practice salinity of 3–5 percent is accepted as saline (Williams, 1981).

Athalassic saline lakes (=athalassohaline lakes and inland salt lakes) are found on all continents including Antarctica (Williams, 1981). Their occurrence tends to coincide with the distribution of steppes and deserts on both sides of the equator. Most salt lakes are closed systems with an endorheic drainage (Williams, 1981). The conditions required for their formation are that the loss of water by evaporation exceed the total added by precipitation and fluvial runoff. The factors that influence that equation are a complex interaction of latitude, altitude, winds, ocean currents, and distance from the sea. Latitude and altitude help determine temperature; the higher the temperature the greater the amount of water needed to saturate the air and the higher the rate of evaporation. Of nearly equal importance is precipitation which is governed by the distribution of land, especially mountains, and sea, winds, and ocean currents (Borchert and Muir, 1964).

Salt lakes are related to the deposition of salt, not only chloride salts but also carbonate and sulfate salts. Understanding the origin and distribution of evaporites will help us locate present and past salt lakes and one hopes the present and perhaps former distribution of saline tolerant *Bledius.*

Evaporitic lakes include salt lakes, alkali lakes, and bitter lakes. Salt lakes, although often used to include all evaporitic lakes, may be defined as those with chloride precipitates, alkali lakes as those with carbonate precipitates, and bitter lakes as those with sulfate precipitates (Chapman, 1974; Borchert and Muir, 1964). A playa is a dry lake basin but if the soil is kept wet by capillary seepage this basin is referred to as a salina (Chapman, 1974). Inland marshes may also be saline.

EVAPORITES: Deposition of salts and evaporites has taken place on all continents. About

TABLE 1

Regional Distribution of Species Groups of *Bledius*

Asterisk indicates most species in group are salt tolerant.

	North America	South America	West Indies	Europe	Africa	North Africa	Madagascar	Asia	S.W. Asia	S.E. Asia	India	Indonesia New Guinea Philippines	Australia	New Zealand	Number of Old World species	Number of New World species	Total number of species
**mandibularis*	x	—	x	—	—	—	—	—	—	—	—	—	—	—	—	5	5
bellicosus	—	—	—	—	—	—	—	x	—	x	—	x	x	—	3	—	3
**compressicollis*	—	—	—	—	—	—	—	x	—	x	—	x	—	—	1	—	1
**hamifer*	—	—	—	—	—	—	—	—	—	—	—	x	x	—	1	—	1
**minax*	—	—	—	—	—	—	—	—	—	—	—	—	x	—	1	—	1
**aequatorialis*	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	4	4
**circularis*	—	—	—	—	—	—	—	—	—	—	—	—	x	—	1	—	1
minniensis	—	—	—	—	—	—	—	x	x	—	—	—	—	—	1	—	1
**rugosicollis*	—	—	—	—	—	—	—	x	—	x	x	—	—	—	3	—	3
**gigantulus*	—	—	—	x	x	x	x	x	x	x	x	x	—	—	22	—	22
**immaturus*	—	—	—	—	—	—	—	x	x	—	—	—	—	—	1	—	1
**furcatus*	—	—	—	x	x	x	—	x	x	—	x	—	—	—	10	—	10
**lamelliceps*	—	—	—	—	x	—	x	—	—	—	—	—	—	—	4	—	4
**kochi*	—	—	—	x	x	x	—	x	x	—	x	—	—	—	31	—	31
emarginatus	x	x	x	—	x	—	—	x	—	—	x	—	x	x	10	33	43
lucidus	—	—	—	—	x	—	—	—	—	x	x	x	x	—	3	—	3
kosempoensis	—	—	—	—	—	—	—	x	—	x	x	—	—	—	4	—	4
semiferrugineus	x	x	—	x	x	x	—	x	x	x	x	—	—	—	41	15	56
**armatus*	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15	15
albonotatus	x	—	—	x	—	—	—	x	—	—	—	—	—	—	5	10	15
annularis	x	—	—	x	—	x	—	x	x	—	—	—	—	—	44	29	73
**debilis*	—	—	—	x	x	x	—	—	—	—	—	—	—	—	2	—	2
**basalis*	x	—	—	x	x	x	—	—	—	—	—	—	—	—	6	8	14
**infans*	—	—	—	x	x	x	—	x	—	x	—	—	—	—	3	—	3
**fratellus*	—	—	—	—	x	—	—	—	—	—	—	—	—	—	1	—	1
**forcipatus*	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	10	10
**punctatissimus*	x	x	x	x	x	x	—	x	x	—	x	x	x	x	20	6	26
lugubris	—	—	—	—	—	—	x	—	—	—	—	—	—	—	1	—	1
**angustus*	—	—	—	x	x	x	—	x	x	—	—	—	—	—	3	—	3
bispinus	—	—	—	—	—	—	—	x	—	x	x	—	—	—	3	—	3

TABLE 1—(*Continued*)

	North America	South America	West Indies	Europe	Africa	North Africa	Madagascar	Asia	S.W. Asia	S.E. Asia	India	Indonesia New Guinea Philippines	Australia	New Zealand	Number of Old World species	Number of New World species	Total number of species
tibialis	–	–	–	x	x	x	–	x	x	–	x	–	–	–	4	–	4
**bonariensis*	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
**pulchellus*	–	–	–	–	–	–	–	x	–	–	x	–	–	–	1	–	1
verres	–	–	–	x	x	x	x	x	x	x	x	x	x	–	65	–	65
Incertae sedis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	3	8
Totals	10	6	4	13	15	12	4	20	11	10	13	7	8	2	300	139	439

25 percent of all continental areas may be underlain by evaporites. The preponderance of saline deposits are in the northern hemisphere where more than half the sedimentary areas are underlain by evaporites—about 60 percent of these as chloride salts. Some areas have repeatedly served as loci for salt deposition—for example, the Persian Gulf (Kozary et al., 1968; see their fig. 12 for a composite illustration of salt deposits). Lefond (1969) has brought together maps and information on a vast number of salt deposits around the world. He includes some salt lakes along with salt springs, salt mines, brine fields, playas, salinas, salt domes, salt basins, salt evaporation beds, and other salt deposits. His book will help one to locate actual or possible salt lakes.

Basically there are marine and continental evaporitic depositions. The optimal conditions for the formation of marine evaporites exist where a relatively shallow, marginal sea exists in an arid or semiarid region and retains only a shallow, narrow connection to the open sea. This basin should not receive an abundant influx of water from more humid surrounding areas. These conditions are often found near newly uplifted mountains. At present there are no areas with marginal seas that fulfill the requirements for deposition of marine evaporites (Borchert and Muir, 1964).

Continental evaporites are accumulating on all continents now. Basins that are fed by streams in more humid areas have carbonate deposits but in more arid areas have sulfate deposits. Ground water drawn to the surface in arid regions results in chloride precipitates (Borchert and Muir, 1964).

Evaporitic depositions in continental interiors have various origins. *Marginal salt pan deposits* form in low-lying areas that are flooded by the sea occasionally—they evaporate and are reflooded repeatedly. Unless permanently wet they are of little importance to *Bledius.*

Ocean spray may be blown as much as 500 miles inland by onshore winds. Some of the broad shallow lakes in the Rajputana region of India are derived thus. *Salina deposits* can form in depressions on coastal plains if the surface of the basin is below sea level and the soil is sufficiently permeable to permit seawater to percolate through. Lake Assal, 9 miles from the Gulf of Aden in Djibouti, is of this origin.

Lakes of marine origin are marginal seas once connected to the ocean but were separated by tectonic uplift or falling sea level. The Salton Sea, and the Caspian Sea are examples. The Caspian Sea has shrunk considerably, leaving behind hundreds of small saline lakes. *Lagoonal deposits* form in shallow lakes that are nearly cut off from a larger lake where evaporation exceeds influx. The classic example of this phenomenon is Karga Bogaz on the eastern edge of the Caspian. Kara Bogaz has a surface area of 8000 square miles but has a maximum depth of 50 ft. The link to the Caspian is about 3 miles long, a few hundred yards wide, and as shallow as 3 ft in places. Here salt is deposited at the rate of about 350,000 tons per day (Borchert and Muir, 1964). The processes seen at Kara Bogaz must resemble those which result in deposition in marginal seas.

Where lake waters are not of marine origin, the composition of the salts deposited depends on the kinds of salts found in the drainage basin. Thus there are chloride, alkali, bitter, borate, and nitrate lakes. Such lakes are filled by fluvial runoff, local precipitation, and rising ground water or springs. These waters dissolve and bring to the lake salts found in the surrounding drainage basin and/or dissolve the in situ salts that are trapped within the pore space of the soil or form a layer beneath the surface (Borchert and Muir, 1964).

The location or references to the location of specific saline lakes or salt deposits can be found in Lefond (1969), and in two symposia published in the journal *Hydrobiologia* (1981, vol. 81 and 1983, vol. 105), particularly the article by Williams (1981). These references do not list all salt lakes and salt deposits and more information is continually being published (for example, Pierce, 1981, on deposits in Arizona).

HABITAT

The point of the preceding paragraphs was not the origin of salt lakes or salt deposits but how to find saline habitats, particularly the isolated scattered ones of continental interiors. Where does one begin to look? However, *Bledius* spp. do not live on or in water; they live in the moist soil adjacent to bodies of water. But what is this habitat? *Bledius* spp. live near both fresh and saline water, but are species restricted to one or the other? Are all species found adjacent to bodies of water or do some live at some distance from water? Where exactly are the species? Do they just occur randomly near water? Do species select different habitats at a given locality? And, if they do, on what basis is the selection made? All species construct burrows, but do they burrow in all kinds of soil? Do characteristics of the substrate have any influence on which species occur where? Is there an optimal habitat for *Bledius* and if so what might be the characteristics of it? Is a species found in the same habitat throughout its geographic range? Are saline tolerant species influenced by the type of evaporites? How much salinity can species tolerate? Can some tolerate more than others? Do halophilic species require or do they tolerate salinity? How are species adapted physiologically to salinity? Are some species restricted to athalassic salt lake habitats and others to marine habitats? How do they travel from one salt lake to another?

DESCRIPTION: That species of *Bledius,* like other congeneric organisms, partition habitats among themselves is easily shown by a multiplicity of examples. Among the earliest descriptions of where *Bledius* live are that *B. tricornis* (Burrell, 1812a) and *B. arenarius*[12] (Rudd, 1835) were found in the intertidal zone and remained there during tidal flooding. The most typical habitat of *Bledius* is moist, unvegetated or lightly vegetated sand flats near rivers, streams, lakes, or oceans and the most unusual is within decaying masses of seaweed that have been cast high upon the beach.

I agree with Larsen (1936) and Andersen (1970) that though a species may occur in more than one habitat at a given locality, only those where eggs or larvae are found should be taken as the true habitat. Adults can be more opportunistic, sampling various habi-

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[12] Normally data for *arenarius* are referred to its senior synonym, *fergussoni*; however, in this case the species may be *subniger* which was confused with *arenarius* and which, according to Hollander and Etten (1974) lives nearer the water than *arenarius.*

tats and moving on if the conditions are not satisfactory.

Most descriptions of the habitat are very general. Thus, *B. brunneipennis* and *B. maindroni* are from the sand of estuaries (Fauvel, 1903a); *B. fossiventris* is from wet sand at the mouth of a brackish stream under debris (Fauvel, 1903b); *B. bedeli* is in deep burrows in mud after the melting snow, and *B. furcatus* and *B. corniger* are from littoral and interior saline areas (Fauvel, 1902); *B. analis* is from a sand flat of a river (Baranowski, 1980, in letter); *B. ornatus* is at the edge of a freshwater stream along the seashore (Moore, 1964).

Most maritime, saline tolerant species evidently live in the supralittoral zone. Some examples include the maritime species of the *basalis, aequatorialis, armatus, mandibularis, punctatissimus,* and *forcipatus* groups in North America (Herman, 1972, 1976), *B. tristis* in Israel (Kugler, 1980, in letter), *B. pilicollis* in South Africa (Griffiths, 1982, in letter); and *B. bonariensis* in Brazil (Gianuca, 1983, 1984, in letters).

Some species of *Bledius* are intertidal; they live in sand between the high and low tide lines and remain in their burrows during high tide. This phenomenon has been reported for *B. tricornis* (Burrell, 1812a), *B. arenarius* (=*subniger*) by Rudd (1835), *B. spectabilis* (Larsen, 1936, 1952), *B. unicornis* (Steel, 1955), and *B. punctatissimus* (Griffiths and Griffiths, 1983). Do other species live in similar circumstances? Some collecting data are suggestive. *Bledius caribbeanus* is found right at the edge of the water of a reef-enclosed bay on Virgin Gorda in the British Virgin Islands and *Bledius neglectus* was also collected near the tidal line of a shore protected from the surf on Assateague Island, Maryland (Herman, 1972, and unpublished data). *Bledius subniger* was found near the tidal line (Hollander and Etten, 1974) as was *Bledius pruinosulus* in South Africa (Griffiths, 1982, 1983, in letters).

Brief habitat descriptions were published for many British (Tottenham, 1954) and central European species (Horion, 1963).

More can be said to describe a habitat. Is a species on sand flats or banks? Is the sand unvegetated or vegetated? Is the vegetation sparse or light? Is the habitat sunny or shaded? Is the soil sand, silt, or clay, or a mixture? Is there variation in moisture and salinity of the soil? Some such descriptive information was published for most of the North American species (Herman, 1972, 1976, 1983a).

PREFERENCE: Many observations show that species of *Bledius* select different habitats at a given locality. Brunier (1931), collecting from a sand pit, found *B. nanus* in pure sand, *B. opacus* in clayey sand, *B. crassicollis* in cool sandy clay, *B. pallipes* in almost pure clay, and *B. dissimilis* very near the water. Over the years I have accumulated many similar examples but the data were not published in a form that emphasized habitat selection at one locality. Some examples include the following. Near a stream that flows onto a large salt flat in north central Oklahoma, *B. mandibularis* is abundant in wet unvegetated sand near the stream while *B. playanus* is found further from the stream in higher, drier sand. In eastern Nebraska on the Platte River, *Bledius bellicus* is abundant on the open, unvegetated moist sand bars, *B. pallipennis* on the lightly vegetated parts of the sand bars, and *B. emarginatus* in the sides of moist, vegetated sandy banks. Near Sandpoint, Idaho, *B. suturalis* is on wet, unvegetated sands near the water's edge and *B. foraminosus* is further from the water in drier, vegetated sand. At McElroy Lake in Washington, adults, larvae, and pupae of *B. eximius* live in moist salt-encrusted soil; larvae are found in vegetated soil whereas adults are found in both vegetated and unvegetated sand. At the same lake, *B. foraminosus* is found in vegetated and unvegetated soil but there are no salt accumulations on the surface. At Lake Abert in Oregon, *B. eximius* (adults and larvae) were in moist, unvegetated soil that had no or only slight salty accumulations on the soil, whereas adults and larvae of *B. strenuus* were found in soft, vegetated and unvegetated, salt encrusted soil. On the Cuyama River north of Ojai, California, *B. laticollis* was in very wet, unvegetated gravelly sand that was salt- or algae-encrusted and close to the water, *B. venus* was in moist, unvegetated sand near the water, *B. opacifrons* was in slightly moist salt encrusted sand or a slightly moist, vegetated, fine-grained sand bank, and *B. clarus* was also in a vegetated fine-grained sand bank.

Numerous similar examples have been recorded. More than one species can be in the open unvegetated sand or in the vegetated, shaded sand and in these instances habitat separation was difficult to see.

Moore (1964) working at a lagoon in northern Baja California near the ocean, divided the habitat into four zones. He characterized each in terms of plant density and predominance, kind of soil, and whether it was salt encrusted or not. Three species of *Bledius* were found in three zones. *Bledius ornatus* was in the same zone in which *Bledius punctatissimus* was the predominant species. In another zone, *B. ferratus* was most abundant but there were some *B. punctatissimus.*

Most of the above examples involved species from different species groups. Some data concerning habitat selection by species in the same species group are available. Steel (1955) described the habitats in Britain for *B. spectabilis, B. germanicus, B. tricornis,* and *B. unicornis*—all of the *gigantulus* group. His data are from various localities; there is little comparison of collections at one place. Moore (1978) attempted to point out habitat selection (or microhabitat differentiation) for two closely related species, *B. fenyesi* and *B. monstratus.* Both species are found in clumps of seaweed[13] cast ashore by high tides or by storms. Moore (1978) stated that *fenyesi* is found in large masses of well decayed wrack whereas *monstratus* is in small fresh clumps of wrack brought in by the previous high tide. Moore's data for *monstratus*[14] contradict evidence from my experience. I have found larvae and thousands of adults of *monstratus* in large and medium-size masses of well-decayed wrack that are often partly covered by sand and never found them in fresh seaweed (Herman, 1976). Moore (1978) collected larvae of neither species.

Andersen (1970) presented a classification of riparian habitats for rivers in central Norway. He recognized seven habitats each defined on the basis of elevation (above the stream), exposure, vegetation type and density, type of substrate, and moisture of soil. He subdivided each habitat. Later he (Andersen, 1982) used this classification to describe the habitat of seven species (*arcticus, denticollis, fontinalis, fuscipes, littoralis, longulus,* and *poppiusi*) of the *annularis* group and one (*talpa*) of the *albonotatus* group but he collected them from more than one river. One of the many possible examples from my own collecting is in the *mandibularis* group which has five species. One species, *pallipennis,* is found in freshwater locales of the Mississippi drainage where it lives in open, unvegetated or lightly vegetated, moist sand flats and sand bars. The other four species all live in saline habitats. *Bledius mandibularis* and *B. fortis* both live on the eastern North American coasts but *fortis* is only on the shore of the Gulf of Mexico. *B. mandibularis* occurs from Maine to Mexico and also at various inland salt lakes into Canada. Near Rockport, Texas, on a saline sand flat about a quarter of a mile from the sea, *B. mandibularis* is in open, unvegetated, moist sand but *fortis* is in low, hummocky patches of dense vegetation in drier sand. *B. ferratus,* a species of the western coasts of North America, also occurs near interior salt lakes. At a salt lake in southeastern New Mexico, *B. ferratus* is found with *B. mandibularis.* Here *B. ferratus* is found near the edge of small salty ponds and on open, unvegetated wet flats. *Bledius mandibularis* is in the vegetated drier flats that has a layer of salt several inches under the surface. I have no firsthand habitat data for the

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[13] Clumps of seaweed are an unusual habitat for *Bledius.* The only other species that I know to have been collected from seaweed is *B. michaelseni* in South Africa (Griffiths, 1983, in letter). This record should be corroborated, however, by more sampling, Finding larvae with the adults would help to affirm the habitat. I suspect that seaweed is not the habitat of *michaelseni.*

[14] Moore (1978) also stated that Point Conception separates the distribution of *fenyesi* and *monstratus.* My work (Herman, 1976) suggested that the break in distribution was further north at a bulge in the California coast west of San Luis Obispo known as Buchon Peninsula. *Bledius monstratus* was found at Morro Beach north of Point Buchon and *fenyesi* at Avila Beach south of the Point. At the time I was unable to collect on the Buchon Peninsula because of the construction of a nuclear power plant at Diablo Canyon. Mr. Derrick Lavoie collected there later and found *fenyesi* at five pocket beaches between Avila beach and Coon Creek Beach at Point Buchon and *monstratus* from south of Morro Beach to a beach at Hazard Canyon north of Coon Creek (Lavoie, 1980, personal commun.). The two species have not been collected at the same beach.

fifth species, *jacobinus,* which lives on the western coast of Mexico.

There are few experimental data to show habitat preference and limits. Papers by Larsen (1936, 1953) and Griffiths and Griffiths (1983) are notable exceptions.

HABITAT LIMITS: Griffiths and Griffiths (1983) showed that the availability of food and texture of the substrate controlled the distribution and density of *B. punctatissimus.* The species lives in a band between the high and low tide lines. It is absent from very wet and hard or well-drained and soft sand or from places with low food content. The seaward limit was indirectly determined by the duration of tidal cover since the animals closer to the low tide line had less time to feed. Shoreward extension was limited by lower moisture, looser sand texture, and reduction of food. Longshore limits were imposed by the texture of the sand. The beetles will live in a variety of sediment textures but the density in each is controlled by abundance of food. The species can only inhabit the intertidal zone of beaches that are protected from heavy surf (Griffiths and Griffiths, 1983).

Larsen (1936) tried to discover the factors that imposed habitat limits on 11 species of *Bledius.* In a follow-up study she examined alterations of the locale she had studied 6 years earlier and discussed how the changes affected the distribution of the fauna and flora (Larsen, 1953).

Larsen (1936) constructed salt and moisture gradients and found that species would preferentially select soil that had salinity and water content similar to that in which they live in the field. Species differentiated degrees of salinity and moisture. Initially individuals of all species burrowed anywhere but after a few days arranged themselves in areas of preferred moisture and salinity (Larsen, 1936).

Although the species of *Bledius* can detect a moisture gradient, and will select preferred moisture, the relative humidity within the burrow may be near 100 percent. Kevan (1962, citing Palmen) points out that in drier soil a burrowing animal may prefer lower temperature because the humidity may be higher. Larsen (1936) was less successful in showing the influence of the size of the sandgrains alone because the moisture content was related to grain size.

Larsen (1936) studied *Bledius taurus, B. spectabilis, B. tricornis, B. diota, B. opacus, B. longulus, B. rastellus, B. opacus, B. longulus, B. rastellus* (*=fuscipes*), *B. pygmaeus, B. fracticornis, B. subniger,* and *B. arenarius* (*=fergussoni* and *subniger*).

Bledius taurus (*furcatus* group) was in sand or clay-covered sand that was partly covered by *Salicornia* or was unvegetated. The water content was high and the salinity was 20–60 percent.

Bledius spectabilis and *B. tricornis* are both of the *gigantulus* group. One, *spectabilis,* was in the tidal zone that is vegetated with *Salicornia* or is bare or is covered by algal mats. The preferred salinity was 20–30 percent and moisture about 30 percent. *Bledius tricornis* was in overgrown meadows where *Plantago* was especially abundant. The habitat of *tricornis* is rarely flooded, and has 8–15 percent moisture content. Larsen (1936) found two peaks of preference for salinity 0–5 percent and 30–50 percent and suggested there may be two ecological races.

Bledius diota of the *kochi* group was in barren algae-covered flats that were often flooded in spring. This species lived in soil of 30–100 percent salinity and could tolerate 200 percent salinity. During spring floods the beetles could remain in their burrows for a week at a time.

Bledius opacus, pygmaeus, and *rastellus* of the *annularis* group all preferred loose dry sand without salt. The moisture content for each varied between 0 and 5 percent and the density of vegetation varied.

Larsen's results for *arenarius* included two species, *subniger* and *fergussoni* both in the *basalis* group. She separated them as forms. Both live in pure unvegetated firm sand that lacks algal covering or a clay layer. She found *subniger* in soil of 17–30 percent water content and *arenarius* in 4–16 percent moisture; the latter is always in drier sand, results corroborated by Hollander and Etten (1974). Larsen found *subniger* closer to the water in more saline soil. Her results for salinity were not published in a form that made clear the preference of each. She said *arenarius* reproduced well in 0–4 percent salinity as well as 20–60 percent salinity, but it is unclear whether both "forms" were included. Might one of her "forms" reproduce in the lower salinity and the other in the higher? Larsen's 1953 paper provides diagrammatic profiles of each habitat in 1934 and again 6 years later. She documented detailed changes of the vegetation, position of dunes and flats, the moisture and salinity, and the faunal composition of each habitat. She showed which *Bledius* were present in the habitat at these different times, their particular location and abundance or their absence in cases where the habitat changed beyond the tolerance of the species. Her data documented a natural test of habitat preference.

EDAPHIC FACTORS: What is the nature of the habitat within the soil? What are some of the characteristics that make sand and silt a suitable habitat for the genus?

The moisture content of soil is dependent in part on the size of the particles; the finer they are the more water the soil can hold. Each particle holds a thin layer of water that is resistant to drying and that provides habitat for small plants and animals. Moisture in the soil helps to ameliorate fluctuation of temperature—the water absorbs heat when the air temperature is high and releases heat when the air temperature falls. Variation in soil temperature decreases quickly with increased depth (Kühnelt, 1976).

Collectors may mention that the substrate is clay, silt, or sand or some combination of them. Each is defined by diameter. Coast sand is 2 to 0.2 mm, fine sand 0.2 to 0.02 mm, silt 0.02 to 0.002 mm, and clay less than 0.002 mm (Burges, 1967). The larger the particles the faster water percolates down through the substrate and the finer the particles the more moisture the soil can hold and the higher ground water can rise through capillary action. Soils with particles larger than 0.2 mm (coarse sand) will not hold water but below that (size) will hold it firmly (Kühnelt, 1976). Particles of 0.2 to 0.1 mm (fine sand) will bring ground water from 50 cm down; a grain size of of 0.1 to 0.05 (fine sand) will bring water up from 100 cm; and particles of 0.05 to 0.02 (silt) will bring water from 200 cm (Kühnelt, 1976).

At the minimum, therefore, *Bledius* lives in fine sand (0.2 to 0.02 mm). Species are reported in sand, silt, clay or a mixture of these. Those living in fine sand may either live in areas where the water table is near the surface (50 cm or less) or must be able to tolerate drier conditions. Those that live in silt or clay silt either require or can tolerate more moisture.

Although from the above discussion it is clear that some of the factors determining where *Bledius* lives include vegetation, light, moisture, salinity, and soil composition, are there others? What about food, parasites, predators, epizootics—do any of these control where species are found? Are there other factors? What about soil pH? What are the effects of living among the roots of plants?

FOOD: Griffiths and Griffiths (1983), measuring the amount and distribution of chlorophyll *a* in the soil, showed that the abundance of food in part controlled the density and distribution of a species of *Bledius* at one locality. Do different species of *Bledius* eat different algae? Larsen (1936) examined this question cursorily. To a mixed culture of five species of *Bledius*, three saline tolerant species and two freshwater species, Larsen (1936) added a clump of alga-covered sand from the nonsaline habitat of *B. rastellus* (=*fuscipes*). Almost immediately individuals of all five species gathered round the clump to eat. She concluded that differences of food exert no influence on the distribution and presence of different species. However, she also pointed out that it is unclear whether different algae are preferred over others. But further, will *Bledius* eat whatever alga is offered if nothing else is available? Will they select if given an option? What is the effect on development of eating any kind of alga? What is the correspondence between the distribution and habitat requirements of species of *Bledius* and algae? The question of food preference and its influence on the distribution and abundance of *Bledius* requires investigation.

SALINITY: Larsen (1952) reported that although the salt tolerant species *spectabilis*, *diota*, and *taurus* could all be found in microhabitats of lower salinity, at these localities they were attacked more frequently by parasites and fungi. In places of lower salinity the rate of fungal infection (Laboulbeniales) was as high as 40 percent but only one among hundreds of beetles was infested in soil of higher salinity. The salt tolerant *Bledius arenarius* was reported with higher fungal infection after heavy rainfall (Foster and Treherne, 1976, citing Green). Further, Larsen (1936) reported a high incidence of ichneumonid parasitism of saline tolerant species when the salt content of soil is lowered, but almost none when salt content is high.

An appreciable list of habitats for individual species can be made, but without an organizing theme it is difficult to do much beyond listing them. Relatively few habitat data are available through the entire geographical range of a species, nor are there detailed data for all the species of any species group. Ecological studies such as those of Larsen (1936, 1953) and Andersen (1968, 1970, 1982) are interesting and important, but they focus on how a more or less random selection of species are dividing a locale. From another view the habitats of species in monophyletic groups could be examined. From such data one might find similarities and differences of the habitats that might help us understand the ecological characteristics of a species group and the conditions to which each species is adapting. Since the species are closely related, we might detect factors that led to the origin of each. Knowing that one of the species of the *mandibularis* group or two of the *basalis* group live in freshwater habitats and the others live in saline ones, we can begin to think about the factors involved in this split.

LIFE HISTORY

The habitat of *Bledius,* except when washed away or prolongedly covered by floods, seems to present an admirable milieu with stable moisture, temperature, and food. But what does *Bledius* do? How do they live? How long do they live? How do they make burrows? Where are the eggs, larvae, pupae, and adults?

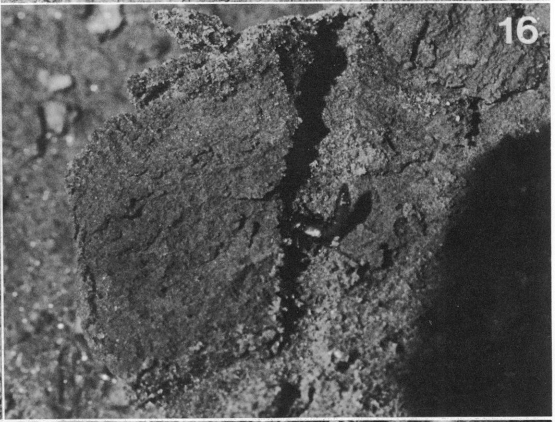
BURROWS: As with most staphylinids, *Bledius* are ordinarily hidden from view. All species make burrows in the soil. We know generally where *Bledius* live but one can't dig randomly in sand and expect to find the beetles consistently. Unlike most staphylinids, *Bledius* leave external telltale clues to where they live in the form of a cast or tumulus on the surface above the entrance of a burrow. This cast takes at least two forms, a circular, hemispherical mound of about 2 mm to 3 cm in diameter (for example, figs. 19–24, 27–34, 39, 40), or a slender stringlike tunnel (figs. 25, 37, 38). The tumulus is paler and lighter colored than the surrounding soil because it dries quickly. At some places the ground may be saturated with casts and the surface covered with light-colored powdery sand over the darker, wet sand. In dense concentrations the surface can be described as mealy, lacy, or foamy. The casts occur singly, separated from others, or in a dense clustered mass. They are very distinctive once recognized. In an article in a popular magazine, Emsley (1983) noted "meandering ribbonlike tracks" on a beach as the tide withdrew. He mentioned a small staphylinid. It was almost certainly *Bledius,* and may have been *B. caribbeanus.*

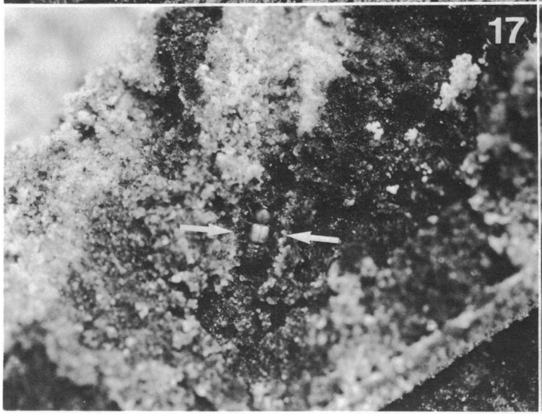
By excavating the sand (fig. 13) several centimeters under and around the cast and putting it in a bucket of water (fig. 14) one can collect the beetles that float to the surface. If, instead, one bisects the mass of sand vertically through the center of the tumulus, a profile of the burrow with beetles is often revealed (for example, figs. 15–17, 35, 36). Adults and larvae make burrows and both use similar techniques. What are these techniques?

BURROWING: The protibiae of adult *Bledius* are characteristically enlarged and fitted with one, two, or three rows of strong, spinelike setae. These protibiae have led some, for example Schiødte (1867), to postulate that *Bledius* digs burrows with its legs (see also Larsen, 1936, for a list of others who suggest that the protibiae are fossorial). One need only casually observe the digging activity of *Bledius* to discover that the mandibles are used to construct the burrows.

Animals can make burrows by peristaltic contractions of the whole body or by using appendages such as their mouth parts or legs (Kühnelt, 1976). According to one classification of burrowing animals (Kevan, 1962), adults and larvae of *Bledius* are excavators because they move soil mechanically and deposit it elsewhere. Burrows made by excavators are called galleries (Kevan, 1962). [Many other staphylinids that live in the soil would, by Kevan's classification, by tunnellers because they insinuate their body into or through preexisting spaces.]

If a *Bledius* is placed on the surface of the moist sand, it will run about for a while but will usually soon begin constructing a bur-



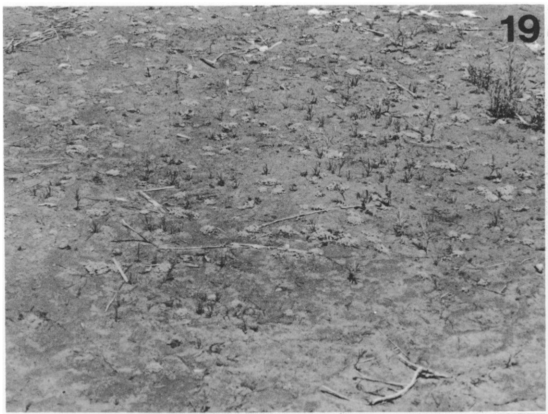


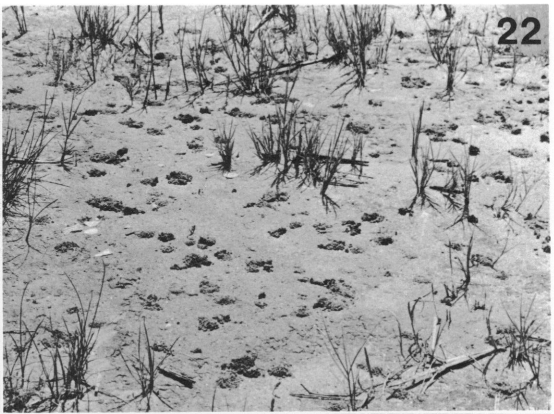
FIGS. 13, 14. Author using flotation method of collecting *Bledius*. **13.** Excavate soil containing tumulus, burrow, and beetle. **14.** Place soil in bucket of water where beetle floats to surface.

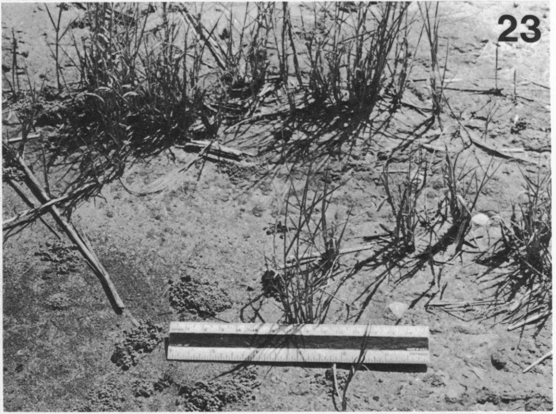
FIGS. 15–17. Bisected burrow of *Bledius mandibularis*. **15.** Note horizontal section of burrow. **16.** Burrow with adult. **17.** Burrow with adult. Note width of burrow and beetle. Width of burrow shown between arrows.

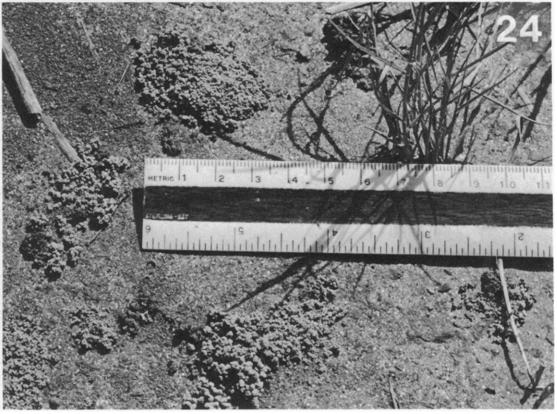
FIG. 18. Pupa of *Bledius mandibularis* in pupal chamber.

row. It grasps one or several grains of sand with its mandibles, turns its head and places the sand to one side. A hole is formed from which the *Bledius* repeatedly removes sand, which is placed on the surface around the excavation. With a microscope I have watched *B. mandibularis* construct this initial part of the burrow. As the hole becomes









FIGS. 19–21. Habitat and tumuli of burrows of *Bledius mandibularis* on sparsely vegetated sand at coast of Connecticut, USA. **20.** Enlargement of fig. 19. **21.** Enlargement of fig. 20.

FIGS. 22–24. Habitat and tumuli of burrows of *Bledius mandibularis* on moderately vegetated soil at coast of Connecticut, USA. **23.** Enlargement of fig. 22. **24.** Enlargement of fig. 23. Note variation in size of tumuli which results from the size of the animal and/or depth of the burrow.

deeper, *Bledius* enters it, continuing to remove sand which is placed around and over the entrance finally forming an igloo of sand (Larsen, 1936; Griffiths and Griffiths, 1983; Herman, personal observ.).

Beneath the surface *Bledius* continues moving sand from the tunnel. Some of it is carried to the surface, thereby enlarging the tumulus; other sand grains are pressed into the wall of the tunnel. The walls are touched

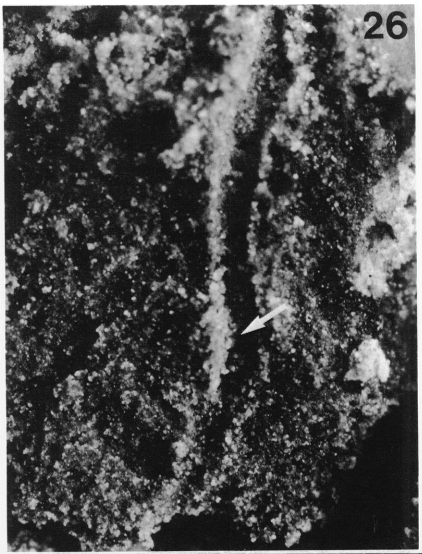


FIG. 25. Tumuli of burrows of *Bledius punctatissimus* in sand at Hatteras Island, North Carolina, USA. Arrow points to elongate tumulus of horizontal burrow near surface.

FIG. 26. Bisected burrow of *Bledius mandibularis* from Hatteras Island, North Carolina, USA. Arrow points to cache of algae in slightly wider portion of burrow.

FIGS. 27, 28. Habitat and tumuli of burrows of *Bledius mandibularis* at coast of Connecticut, USA. Note density compared to figs. 19 and 22.

in search of places to insert sand grains between those already there by pressure from the head and/or forelegs (Larsen, 1936). The forelegs may even tamp sand into place (Griffiths and Griffiths, 1983). The burrows are sufficiently strengthened by this wedging that those abandoned by *Bledius pallipennis,* for example, remain intact but fragile even when dug up from sand that is dry (Herman, personal observ.). Larsen (1936) noted the same phenomenon for other species. No glue is used but some species, for example *B. diota,* may occasionally coat the lower portion of the burrow with mud from above (Larsen, 1936).

Larger *Bledius* dig more slowly but remove more sand grains with each bite. A large *Bledius* may remove a clump of several sand grains that adhere together and with its forelegs press the grains into a coherent mass before carrying it away (Larsen, 1936). Small *Bledius* work more quickly and *B. arenarius,* for example, can move about 150 sand grains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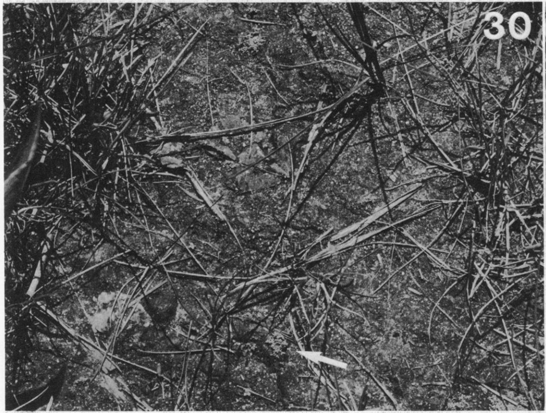
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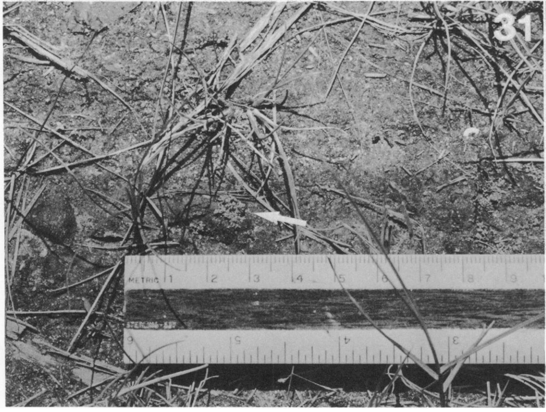
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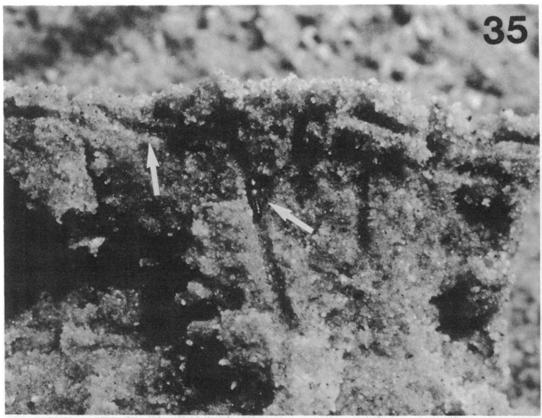
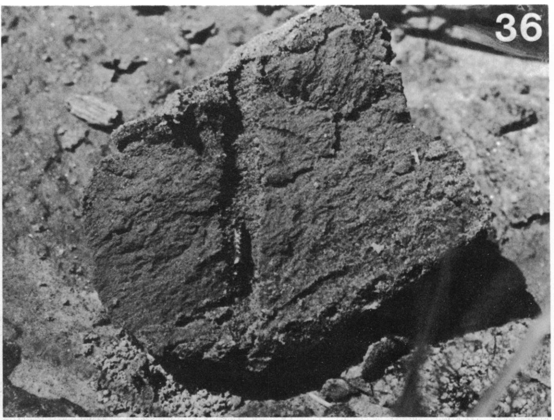
FIGS. 29–31. Habitat and tumuli of burrows of *Bledius philadelphilus* in Connecticut, USA. Arrows point to same tumulus. **29.** Habitat. **30.** Tumuli in upper and lower center and lower right corner. **31.** Tumulus with scale.

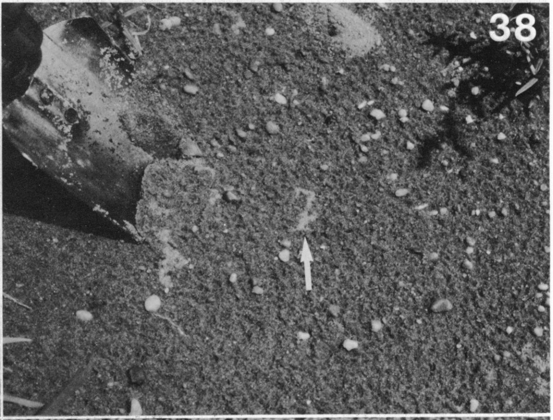
FIGS. 32–34. Habitat and tumuli of burrows of *Bledius politus* at coast of Connecticut, USA. **34.** Enlargement of fig. 33.

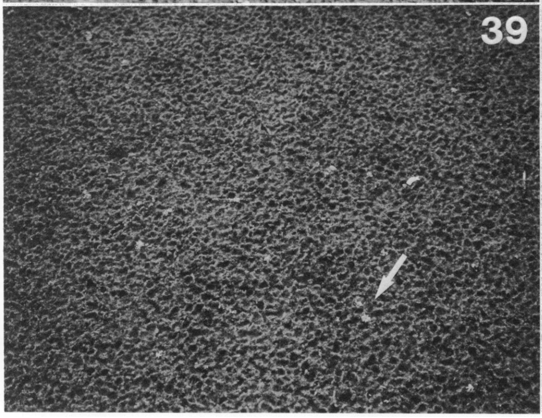
in 3 or 4 minutes (Larsen, 1936). Larsen, however, provided no figures for the rate at which larger *Bledius* move sand grains.

A small *Bledius* like *punctatissimus* starts its burrow by digging a trench on the margins of which the beetle piles sand grains to create









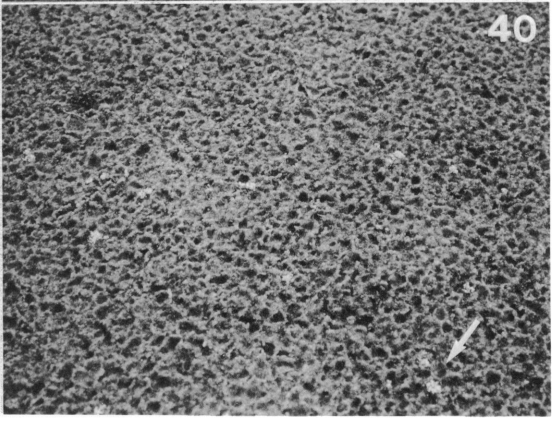


FIG. 35. Bisected burrow of *Bledius politus* with adult. One arrow points to beetle and another to horizontal portion of burrow.

FIG. 36. Bisected burrow of *Bledius mandibularis* with adult.

FIGS. 37, 38. Tumuli of burrow of *Bledius neglectus* at Hatteras Island, North Carolina. Figure 38 enlargement of fig. 37. Arrows point to same tumulus.

FIGS. 39, 40. Tumuli of burrows of *Bledius neglectus* at Hatteras Island, North Carolina. Arrows point to same tumulus. Depressions on surface of sand were produced by rain drops.

two parallel walls. It then pushes its head against the end of the trench to raise an arch over a gallery. The trench is then roofed over with sand removed from the interior (fig. 25).

After about 5 minutes the horizontal tunnel completely obscures the beetle. At about the middle of the horizontal tunnel, *B. punctatissimus* digs a vertical shaft. Sand is moved to the surface or tamped into the wall (Griffiths and Griffiths, 1983). The reason for the horizontal trench is unclear.

The legs are used to support *Bledius* while it digs. When *Bledius* grasps sand with the mandibles, it fixes the prolegs against the substrate for support. When turning to the side with its load of sand, the head and prothorax swivel on the elongate mesothorax while the middle legs are set into the soil (Larsen, 1936). The spinelike setae of the legs help *Bledius* gain purchase on the sides of the burrow (Larsen, 1936).

In a like manner, larval *Bledius* construct burrows with their mandibles. Testing for the stimuli that prompt this digging behavior, Paulian (1942) noted that if the setae of the anterior cephalic margin are touched, the larva will grasp a grain of sand, turn the head to one side, then drop the sand. If the stimulus is repeated, so is the action, but if not there is no further burrowing movement. [Paulian (1942) pointed out that larval *Ocypus* grasps prey animals that touch the cephalic setae; the prey are eaten, not released.]

In the field the complete movement, grasp-turn-deposit, ceases after one time unless one or more of the legs are higher than those of the other side. Once the larva has dug a gallery of sufficient length, then tactile pressure on the tergum from the wall of the burrow replaces the disposition of the legs to stimulate further digging (Paulian, 1942). Larvae also use the spinelike setae to cling to the walls of the burrow (Larsen, 1936).

Note that the larvae, with their legs that are slender and have few spinelike setae, and adults, with mildly to strongly expanded densely setate protibiae, both construct burrows similarly and both are said to use their tibiae to gain purchase. But why are the protibiae of adults so enlarged? The adults have been noted to tamp sand grains into the walls, and to use the forelegs to help mold a cluster of sand grains into a more coherent mass. But is this the reason for such broad protibiae? And why are the protibiae of some species of *Bledius* broader than others?

Some other beetles have been seen digging burrows with their mandibles but they have slender tibiae and few or no spinelike setae. Some examples are *Diglotta mersa,* a staphylinid, and *Cillenum laterale,* a carabid (Larsen, 1936). She also states that *Carpelimus* dig with their mandibles but most often creep around in cracks and crevices. The protibiae of species of *Eppelsheimius* are very enlarged and have numerous spinelike setae and also may be burrowers (Herman, 1983b).

Bledius can move backward and forward in the burrow with equal ease and in the soil they move with agility. Fossorial animals are often cylindrical (Kühnelt, 1976) and *Bledius* has a cylindrical or subcylindrical form.

Paulian (1942) was unable to provoke digging behavior in adults as he had for larvae. He also reported that variations of temperature and light had no effect on burrowing activity. However, *Bledius pallipennis* moves sluggishly at 20°C and requires about an hour or more to make a burrow but at 35°C works nearly four times as fast (Smith and Hein, 1971). Larsen (1936) showed experimentally that burrows are constructed toward the light, even if, as in a covered terrarium, the light comes from the side. If no light reaches the terrarium, then *Bledius* is unable to find the surface. Larsen (1936) thought that gravity might enable the beetles to make the burrow straight vertically.

Cessation of burrowing may be linked to humidity or food, Paulian (1943) suggested, but without specifying how. *Bledius* require a minimum degree of humidity and may burrow deeply enough to reach the desired level. The optimal humidity may be near the dew-point (Larsen, 1936). Some adults of *Bledius ineptus* were put in a petri dish lined with wet filter paper and others in one lined with dry filter paper. Those in the dry petri dish died within 2 hours; those in the wet dish lived for many hours thereafter (Herman, unpublished observ.). *Bledius arenarius* lives for a long time at 93 to 100 percent humidity but dies within 10 hours at 0–93 percent (Larsen, 1936). Less direct but still suggestive is the fact that adults of *Bledius* often appear on the surface on humid, windless evenings. They are attracted to light traps at this time. The humidity increases in the evening and near the surface above the sand the air is nearly saturated (Larsen, 1936). Whatever the humidity of the air outside the burrow, what is it inside? In moist or wet soil the intraburrow atmosphere is likely near 100 percent humidity but what is the atmospheric humidity in burrows of species like *opacus, pygmaeus,* and *fuscipes* that live in sand of 1 to 5 percent moisture content? Do these species require as high a humidity as *arenarius*?

Burrowing activity is almost constant (Evans et al., 1971). Working with *B. pallipennis* and *B. bellicus,* Smith and Hein (1971) recorded the appearance of an average of 40 new casts per square meter daily; in one plot 189 new ones were counted.

IMPORTANCE OF BURROW: The burrow protects *Bledius* from desiccation as well as drowning. Adults of some species have been shown to survive prolonged but not indefinite submersion in water by becoming comatose. *Bledius spectabilis* recovers in less than 10 minutes after 2 hours' submersion in seawater and in 40 minutes after 10 hours underwater (Evans et al., 1971). *Bledius punctatissimus,* submerged in seawater for 30 minutes, recovered in several minutes. If underwater for 4 hours, recovery took 10 to 50 minutes with 35 percent of the beetles dying. After 6 hours 39 percent of the beetles died and those that lived required 1 or 2 hours to revive. All *B. punctatissimus* died after 8 hours under water. On the other hand, *B. punctatissimus,* a species that lives in the intertidal zone, when collected from their burrows after being flooded by the tide for 4 hours, recover in *30 seconds* (Griffiths and Griffiths, 1983). As long ago as 1812, Burrell noted that the intertidal *B. tricornis* was active almost immediately after retreat of the tide as was *B. arenarius* (Rudd, 1835). *B. arenarius* may be able to remain in their submerged burrows for 9 or 10 days (Krogerus, 1932) and *B. diota* may stay underwater for a week at a time during spring floods (Larsen, 1936).

To survive tidal inundation of their habitat, *Bledius* avoid direct contact with water by remaining in the bubble that forms in the burrow during flooding (Larsen, 1936; Evans et al., 1971; Griffiths and Griffiths, 1983). For the intertidal *B. spectabilis,* the burrow must be 2 mm or less in diameter or have a neck of that diameter in the upper portion of the burrow for a bubble to form (Wyatt, 1982).

Griffiths and Griffiths (1983), calculating the rate of respiration of *B. punctatissimus* and the volume of oxygen in a burrow, showed that it would take 12 hours for the oxygen level to drop to 80 percent of the ambient oxygen. However, if the bubble were acting as a physical gill, then some of the oxygen would be replaced (Hinton, 1976). According to Hinton's (1976) classification, this would be a shrinking physical gill similar to one that forms on the back of aquatic insects that lack a plastron. Hinton (1976) noted that such a bubble of air can form in a cavity or crack in the substrate and that the life of a shrinking physical gill is based on the rate of loss of nitrogen. A bubble trapped in a burrow could also serve as a shrinking physical gill but would be effective only in well-aerated conditions, not in poorly drained anaerobic soil (Foster and Treherne, 1976). Thus, it is probable that *Bledius* lives in a shrinking physical gill, thereby explaining why some species can remain underwater for a week or more.

According to Wyatt (1982), *B. spectabilis* inserts a plug of sand into the entrance just before tidal flooding. He noted that the beetle is never taken unaware by abnormal flooding but does not understand how this happens. Working with *B. punctatissimus,* Griffiths and Griffiths (1983) watched the cast collapse or subside into the entrance of the burrow upon inundation, thereby sealing the burrow automatically.

Almost anyone who has collected *Bledius* in their habitat will protest that "washing" the shore with water will cause the beetles to run to higher ground. In these cases it may be that the burrow system was destroyed, that the air escaped (Larsen, 1936), or that the diameter of the burrow was too large (Wyatt, 1982).

Beetles caught outside of or forced out of their burrows by flooding usually float to the surface. *Bledius spectabilis* may remain underwater, hang onto the substrate until the tide retreats, and breathe with a bubble of air that is trapped when it flexes its abdomen over its head (Wyatt, 1982). Some, such as *B. albonotatus* (Moore, 1972), *B. punctatissimus* (Griffiths and Griffiths, 1983), *B. caribbeanus* (Herman, personal observ.), and probably many or most other species, if not wetted, fly directly from the surface. But if wetted then most adults of possibly all species flex their abdomen dorsally toward their head to form a ring or semicircle and float on the surface until they can climb out of the water onto something from which to fly away (Herman, personal observ.). Those that remain in the water may hold a bubble of air between the elytra and dorsally flexed abdomen (Griffiths and Griffiths, 1983 for *B. punctatissimus*) until the flooding recedes.

Larvae of *B. punctatissimus* can remain submerged for 4 or 6 hours and recover in 7 or 30 minutes, respectively, with about 50 percent mortality (Griffiths and Griffiths, 1983). According to these authors, the larvae possess no air bubble and slowly sink to the bottom. At least some of the larvae of probably all species do float to the surface and usually attempt to climb upon something to wait out the flood (Herman, personal observ.).

The burrow also helps *Bledius* survive extreme temperature. In temperate regions the fluctuation of temperature is gradual and seldom extreme below about 23 cm (Kevan, 1962). On exposed sand flats in hot regions, species of *Bledius* crawl deeper into their burrows as the temperature increases through the day (Herman, unpublished observ.). Similarly, at the onset of cold weather in Maine, during early October, the burrows of *B. mandibularis* were deeper than 18 cm (Herman, unpublished observ.). *Bledius arenarius* was found overwintering at depths of about 40 cm in Denmark (Larsen, 1936).

The burrows of *Bledius* then serve to ameliorate the effects of the physical environment including temperature, humidity, and flooding. The burrow also functions as a home, breeding site, nursery, and dining area and provides protection from predators and parasites.

ARCHITECTURE OF BURROW: Burrows of *Bledius* have been classified as simple and unbranched, complicated and unbranched with food and brood chambers, branched with brood but no food chambers (Larsen, 1936); or as single adult, maternal, or larval (Griffiths and Griffiths, 1983). One classification is based on use and structure, the other on use.

The burrows of adult *Bledius* are simple, more or less vertical tubes with or without branches or they have specialized chambers in the sides. The diameter and length of the burrow depends on a variety of factors including the species constructing it, the purpose for which it is used, and the environmental conditions. The diameter is as small as 0.8 mm (Griffiths and Griffiths, 1983) to 5 mm (Larsen, 1936) and the depth as little as 2 cm to as deep as 40 cm (Larsen, 1936).

The simplest burrows slope for a short distance from the surface or have a short passageway horizontal to and just under the surface, then plunge directly downward (fig. 15) or fork near the surface before descending (fig. 35). The forked burrow is made by a variety of small species including *arenarius, longulus, pygmaeus,* and *opacus* (Larsen, 1936). For *arenarius* the summer burrows have long forked branches, 4 to 5 cm and a short vertical gallery, about 2 to 5 cm. The beetles feed in the long branches which are in the subsurface algal layer. These branches may anastomose with the horizontal branches of burrows of other individuals in thickly populated areas. The fork may be used to turn around. The overwintering burrow can be 40 cm deep but the fork is short, about 0.5 to 1 mm.

The simplest burrow made by adults of *B. punctatissimus* is about 0.8 to 1.2 mm wide in the upper portion and expands to about 5 mm near the bottom and varies in length from 38 to 68 mm (Griffiths and Griffiths, 1983, fig. 2). The burrow of *B. taurus* (=*furcatus*) can be about 5 mm in diameter and be about 40 cm deep. The entrance may be narrow but it widens about 1 cm below the surface. The burrows of *tricornis* can be 30 cm deep whereas those of *pygmaeus* are scarcely 2 cm deep but their horizontal feeding burrows are 4–6 cm long (Larsen, 1936). *B. salsus* is found to depths of at least 10 cm in summer (Matsuzawa, 1964). *B. spectabilis* has been found to depths of about 7 cm during the summer in England (Evans et al., 1971).

Larvae construct similarly simple burrows.

The burrows of some species, for example *B. diota,* consist of a main vertical branch with various side galleries (Larsen, 1936). That of *B. spectabilis* may be in the form of a sinuous loop with a short vertical branch to the surface (Evans et al., 1971).

Breeding or maternal burrows are those with small oval egg chambers that are resistant to collapse and carved into the wall of the burrow using the same techniques as are used to excavate the burrow (Larsen, 1936). These chambers are usually connected to the main burrow by a narrow passageway that remains completely open or is partially filled with loose sand (for example, *taurus, tricornis, diota*). The egg chambers are often adjacent to the main vertical burrow but *diota* may construct a horizontal branch beside which are the egg chambers (Larsen, 1936). *Bledius arenarius* digs the chamber and lays an egg but later the egg chamber is seen to be disconnected from the main burrow (Larsen, 1936). Is the connection lost because the female fills it or does the connecting passageway collapse?

Reproduction and Life Cycle: Individuals of *Bledius* are usually in the burrow alone. At the beginning of the reproductive period males and females are often in the same burrow. Since the burrow of each individual rarely interconnects with that of another, pairing probably begins on the surface, perhaps when the adults leave their burrows on warm humid evenings (Larsen, 1936). [It is unclear how in dense populations an individual avoids breaking into another's burrow.] Burrell (1812a) watched a male of *B. tricornis* drag ". . . the female from her burrow, . . . to the distance of one inch . . . ." The two lay parallel for a moment, then the female ". . . fled into her hole, pursued close [*sic*] by the male." On digging them out Burrell found them mating.

After mating eggs are deposited in the egg chambers. The eggs are 0.70 to 1.46 mm long and 0.30 to 0.79 mm wide, depending on the species (Larsen, 1936). The eggs are white or yellow, and elongate. From 1 to 10 eggs are placed in each egg chamber (Larsen, 1936). One egg is attached to one or several grains of sand on the floor or suspended from the wall or ceiling of the egg chamber (Larsen, 1936). If more than one egg is placed in the chamber, the second is attached to the side of the first, the third to the second, etc. (Larsen, 1936). The end of the egg attached to the sand grain may be surrounded by a hornlike pedestal and for some species a sand grain is glued to the top of the egg (Larsen, 1936). By being glued to a sand grain the egg stands free in the chamber and is protected from the dampness of the soil (Larsen, 1936).

Eggs of *B. punctatissimus* are suspended from the ceiling singly or in pairs (Griffiths and Griffiths, 1983). *B. salsus* places one egg in each of 5 to 10 chambers (Matsuzawa, 1964). *B. rastellus* deposits two eggs in each chamber, one attached to a clump of algae and the second egg attached to the first (Larsen, 1936). The following unreplicated observations show *B. tau* and *gravidus* each depositing two eggs per chamber, *B. strenuus* with four, five, or six per chamber, *B. eximius* with five or six and *B. ineptus* with nine eggs per chamber (Herman, unpublished data).

Two eggs mature simultaneously (one in each ovary) in *B. rastellus* (=*fuscipes*); in other species investigated the eggs matured one at a time (Larsen, 1936). *B. spectabilis* evidently lays one egg per day (Wyatt, 1982).

Does the number of eggs in a chamber reflect the number that mature simultaneously and/or the number of ovarioles? Is there geographic or seasonal variation in the number of eggs laid by each species? How many eggs does a female lay in her lifetime and how many maternal burrows does she make? How many eggs will she put in one burrow and does this vary by season, geography, or species? Does each species actually place its egg(s) in the egg chamber in a characteristic fashion?

The eggs of *B. salsus* develop in about 14 to 20 days (Matsuzawa, 1964) and those of *B. spectabilis* take about 12 days in August (Paulian, 1942). Seasonal and geographic variation in the length of time required for the eggs of each species to develop is probable.

Larvae of *B. spectabilis* can be seen in the egg 12 to 24 hours before hatching. The larva moves slowly and discontinuously, the body pulsating, the mandibles opening and closing. The tips of the mandibles rub against the internal wall of the egg and in about 15 hours wear through a hole (Paulian, 1942).

Five larval instars were reported for *B. salsus* (Matsuzawa, 1964) and *B. punctatissimus* (Griffiths and Griffiths, 1983). The number of larval instars for both species was deduced by counting the number of classes of measured larval head capsules. The number of instars contrasts with those of other staphylinids for which three larval instars are reported [see, for example, *Oxyporus maxillosus* (Campbell, 1969, citing Scheerpeltz), *Creophilus maxillosus* (Dajoz and Caussanel, 1968;. Kramer, 1955), *Philonthus decorus* (Frank, 1968); *Quedius picipes* (Frank, 1969), *Anotylus latiusculus* (Hafez, 1942), *Platystethus arenarius* (Hinton, 1944), and various Omaliinae (Steel, 1970). *Paederus alfieri,* however, has only two larval instars (Ahmed, 1957). Howard Frank (personal commun.) informs me that all other paederine genera for which data are available have two larval instars.

No one seems to have reared larvae of *Bledius* so the duration of each instar is unknown.

To pupate, the larva constructs a cavity several centimeters below the surface (fig. 18). The pupa is covered with long processes that prop it off the substrate (Larsen, 1936). Illustration of these processes can be seen for *B. talpa* (Krogerus, 1925b, fig. 4), *B. tricornis* (Schiødte, 1864, tab. 12, fig. 14) and *B. punctatissimus* (Griffiths and Griffiths, 1983, fig. 3c).

After pupation the adult of *B. spectabilis* takes about three days to become fully pigmented. During the first day its movements are feeble, the wings are extended. By the second day the teneral adult digs a burrow and the abdomen is beginning to fold the wings (Paulian, 1942).

I have seen no information on how soon after emergence the adult begins laying eggs.

Larsen (1936) thought the larval period was about 3 weeks but according to Wyatt (1982) just the first instar larva of *B. spectabilis* lasts for 2 weeks. *B. salsus* remains a larva for 40 to 50 days, a prepupal larva for 2 to 4 more, and a pupa for 6 to 8 days (Matsuzawa, 1964). For *salsus* about 70 days elapse from egg to adult; development is shortest in midsummer (Matsuzawa, 1964). During the summer adults of *B. salsus* live for about 20 to 40 days and the female oviposits two or three times during her life, laying 5 to 10 eggs each time (Matsuzawa, 1964).

The number of generations per year is unclear. Larsen (1936), working with Danish species, stated that some may have two and others only one but further south, in Japan, Matsuzawa (1964) thought that *salsus* has three or even four generations. For *arenarius* eggs were found in April–May and again in August, for *tricornis* in April–May, for *diota* and *taurus* in June–July, *opacus, rastellus, longulus* in July–August (Larsen, 1936), and for *salsus* in April–May, June–July, and August–September (Matsuzawa, 1964). But were the investigators careful to distinguish the new broods of a single female (or generation of females) from the offspring of a new generation of females? Noting only the appearance of eggs will tell nothing about which generation produced them. Is there variation by species in the number of broods or generations per year? Might a species in cool parts of its geographical range have fewer generations and/or fewer broods per generation than in the warmer parts of its range? Matsuzawa (1964) pointed out that the duration of the life cycle (of *B. salsus*) is shorter in warmer weather. At the minimum this would allow time for more generations and broods in warmer regions. How does the difference in temperature between intensely hot interior continental regions and somewhat cooler, but still hot, coastal regions affect the duration of the life cycle of a species that lives in both circumstances?

The first specimens of *Bledius* collected after winter are adults and usually have no internal fat, whereas those collected in fall in cool areas are filled with fat (Herman, unpublished observ.). During early October in Maine adults of *Bledius mandibularis* are in deep burrows and when dug up move very sluggishly (Herman, personal observ.). Some species, for example, *ruficornis* in January near San Diego and *mandibularis* in December in Florida, have active adults in winter (Herman, personal observ.). Adults of *Bledius fenyesi* can be collected year round in California (Herman, 1976) and at one locality are especially abundant in February to August (Orth et al., 1978). Most *Bledius salsus* overwinter as adults but some remain in the pupal stage (Matsuzawa, 1964). In cool temperate areas where some overwintering adults may remain quiescent, they may do so in deep burrows which may be at some place other than their normal living-breeding grounds (Larsen, 1936). Larsen reported that some Danish populations of *B. arenarius* move to higher ground to overwinter and dig burrows about 40 cm deep. They were found there in dense concentrations of up to 46,700 animals per square meter. Her data for overwintering adults show that adults migrate to higher ground if the habitat is flooded during the winter. Some species move only after prolonged flooding (Larsen, 1936). It is unclear, however, whether the adults remain quiescent during the winter or whether some are and others are not active. Larsen (1936) found casts during early winter but says nothing about activity through the winter. Finally, some larval *Bledius* have been found in early spring and may have overwintered in that stage (Andersen, 1982).

FEEDING: Occasionally someone suggests that *Bledius* feed on other insects (see, for example, Moore, 1964 and Scheerpeltz cited by Lengerken, 1929) but those, including the present writer, who have examined the gut contents of *Bledius* always find algae and diatoms and never animal parts. Paulian (1941) reported the digestive tract of larval *B. spectabilis* to contain algae, diatoms, and abundant sand. The gut of *Bledius* spp. is filled with algae after rainfall (Larsen, 1936). Adults and larvae feed on green algae such as *Oocystis solitaria* Wittr., *Oocystis parva* West., *Anchistrodesmus falcatus* Ralfs, and *Conferva minor* Klebs, blue-green algae such as *Oscillatoria amphibia* Ag. and *Anabaena* sp., and various undetermined diatoms (Lengerken, 1929).

The algae upon which *Bledius* feed grow in the interstices between sand grains in the moist, jellylike mass surrounding each sand grain. The algal cells there are single-celled or in small groups but if cultured will grow into long filaments. When *Bledius* are grown in cultures in which the algae have become filamentous, they starve; their guts are empty despite there being individuals with algal filaments hanging from the mouth (Larsen, 1936).

In captivity adults of *Bledius* emerge in evening and choose a sand grain from which they rasp the algal covering. The mandibles are usually held apart and the sand grain manipulated with other mouthparts. Eventually the sand grain is pushed away with the forelegs and a new grain selected. If *Bledius* is put on pure sand and a clump of alga-bearing sand is placed on the surface, the animals immediately flock to the lump and begin grazing the algae. Similar feeding behavior can be observed in the upper part of the tunnels in the field (Larsen, 1936).

According to Larsen (1936) some species, such as *spectabilis* and *tricornis,* make a food chamber in the burrow which they provision with clumps of algae, each clump corresponding to the amount an animal can drag in at one time. Both *taurus* (=*furcatus*) and *diota* also store algae but not in special chambers. She suggests that these caches are used to feed the larvae and by adults and larvae to live on when the locality is too dry or is flooded. She also considered this behavior to be an adaptation to specific conditions which might explain why Wyatt (1982) reported *spectabilis* provisioning the burrow in the intertidal zone in Britain, but Paulian (1942) observed no such behavior by *spectabilis* in France. *Bledius mandibularis* at times makes what appears to be an algal cache (Herman, unpublished observ. and fig. 26).

Larsen (1936) reported that other species such as *opacus, rastellus, longulus,* and *pygmaeus* make small algal collections after rainy weather and that *rastellus* glues its egg to a large clump of algae. *Bledius arenarius* never stores algae, presumably because it lives in a constantly moist habitat (Larsen, 1936). Larsen noted that *arenarius* is often in places that lack algal growth but have abundant diatoms. Upon hatching the small larvae dig upward into the algal layer, where present, to feed. Do the species that eschew provisioning make galleries in the algal layer to find food? Certainly this would help to explain the burrows of *Bledius* that are horizontal and resemble those made by moles (figs. 25, 38). Do most species store algae facultatively as Larsen suggests some, such as *opacus,* do after rainfall?

Autotrophic plants of the soil such as green algae, blue green algae, and diatoms are found only on the surface and in the top layers. In sandy soil a thickly colonized layer of green algae is concentrated just under the surface (Kühnelt, 1976) down to several inches below the surface (Alexander, 1961). Some algae have been found down to 50 or 100 cm, but the algal population is largest 5 to 10 cm below the surface (Alexander, 1961). Francé (cited by Kühnelt, 1976) stated that algal groups are distributed at different depths according to their pigments; thus green algae occur at 0 to 5 cm deep, diatoms to 20 cm deep, and blue green algae down to 50 cm. Is there sufficient light at these greater depths for photosynthesis or do these plants become heterotrophic? Alexander (1961) pointed out that some species of algae are facultative heterotrophs that resume photosynthesis when sufficient light is present. Vertical transportation of algae is thought to be effected by rainfall and earthworms (Lund, 1967). Algae are in soils everywhere (Lund, 1967; Alexander, 1961) and the species is any given area may coexist rather than compete (Forest et al., 1963). Alexander (1961) pointed out that each taxon has its optimum range of pH. Thus diatoms are uncommon in acidic soils whereas green algae are common and abundant there and blue green algae are common in alkaline and saline soils (Alexander, 1961; Lund, 1967).

Although Larsen (1936) suggested that *Bledius* eat any species of algae, are certain types preferred? What is the effect of the vertical distribution of algae on feeding behavior, or is there an effect? Do they run out of food in a given burrow then make a new burrow or new feeding galleries? Does the tamping of sand grains into the walls of the burrows change, perhaps reduce, the algae available in the walls of the burrow? Presumably the species of algae upon which *Bledius* feed exhibit distinct geographical distributions and habitat requirements and are not cosmopolitan in distribution. Do these factors affect *Bledius*?

SUBSOCIAL BEHAVIOR: At least one species, *B. spectabilis,* has been thought to exhibit subsocial behavior (Larsen, 1952). Hinton (1944) defined infrasocial animals as those that make provision for their offspring even if only to lay their egg in or near a food supply. He cited *Bledius* spp. as showing infrasocial behavior. Subsocial animals are those that not only provide food for their offspring at birth but continue to do so and also protect or tend the young after hatching (Hinton, 1944). If the data on provisioning by *spectabilis, taurus, diota, tricornis,* and *rastellus* (Larsen, 1936) are correct, then these species at least would be infrasocial animals, but those species such as *opacus, longulus,* and *pygmaeus,* that bring clumps of algae into the burrow only after rainy weather (Larsen, 1936) would probably not be. The larvae of these animals and *arenarius* may harvest their own algae (Larsen, 1936).

In 1936 Larsen reported nothing about adults of *spectabilis* caring for the larvae beyond providing a store of algae. By 1952, however, she said the adult female of *spectabilis,* in addition to simply gathering food, stays with the larvae, ventilates the nest, collects new food at intervals, and sometimes defends the entrance of the burrow against intruders. She did not elaborate on these actions beyond stating that they occur. If the female of *spectabilis* is providing all these services to the larvae does she ever leave the burrow and if she leaves how does she return to the same burrow? Is she only defending and ventilating the burrow and gathering food for herself (and the larvae happen to be there) and if she left the larvae would they be able to fend for themselves (unless a different female entered the burrow)? Wyatt (1982) pointed out that the first instar larval *spectabilis* leaves the maternal burrow after the first 8 of its 14-day life to construct its own burrow. He also noted that by remaining in the parental burrow the larva is less exposed to parasitic and predatory attack. Wyatt (1982) also indicated that the larvae of *spectabilis* were able to develop normally even if the females were removed. The burrow of *spectabilis* is regularly covered by tidal flooding. Prior to this flooding the female plugs the entrance of the burrow, thereby helping to trap air in the burrow (Wyatt, 1982). This air bubble permits *B. spectabilis* to live under the tidal-water covering and also aerates the surrounding soil (Wyatt, 1982). It may be that any protection the larvae receive from the adult is incidental to the adult's normal behavior. If the adult gathers food and prepares the burrow against inundation when no larva is present, can it be said then that when these tasks are carried out in the presence of larva that the adult is providing or caring for the larva?

SALT TOLERANCE: What is the effect of environmental salinity on *Bledius*? The species of *Bledius* that are consistently found in saline habitats select and collect at places of higher concentrations of salt when given a choice (Larsen, 1952). Species such as *spectabilis, diota,* and *taurus* (*=furcatus*) can be found in habitats with lower salinity but fare poorly because they are attacked by parasites, predators, and fungi more frequently (Larsen, 1952). Larsen goes on, however, to say that high salinity doesn't enhance the salt tolerant species but the enemies of *Bledius* do poorly. How do freshwater species survive parasitic, predatory, and fungal attack? Are they attacked more frequently? Are the salt-preferring species physiologically weakened by being in freshwater habitats? Perhaps their osmotic balance cannot cope with freshwater.

The halophilic species of *Bledius* evidently have physiological and behavioral means of dealing with high concentrations of salt. *Bledius spectabilis,* for example, stores algae with up to 4 percent salt content and will eat but not store algae with 5 to 6 percent salt (Larsen, 1952). *Bledius diota* and *B. taurus* (*=furcatus*) avoid high salt content in their food by gathering it after rainfall (Larsen, 1952). Evidently some species move if salinity increases too much (Larsen, 1936). *Bledius spectabilis,* whether it eats algae with 0.25, 3.5, or 6.1 percent salt content, maintains the amount of salt in its hemolymph at 1.1 to 1.5 percent (Larsen, 1952). Some salt tolerant species of plants can grow normally in soil with salinities below 0.5 percent but do not compete well with other plants in that kind of soil (Ungar, 1966). On the other hand, plants that are normally in nonsaline soil cannot withstand high salinities, thereby leaving the area open for colonization by salt tolerant species (Ungar, 1966). But by contrast, salt tolerant species select salt concentrations and survive poorly in habitats of low salinity.

SURFACE ACTIVITY: Although species of *Bledius* remain underground for most of their lives, surface activity is of major importance to distribution, habitat selection, reproduction, and survival. Beetles will swarm after (or during) rainfall even in full sunshine. *Bledius caribbeanus* left their burrow en masse on one of the British Virgin Islands during a midday shower (Herman, personal observ.) and *Bledius ferratus* swarmed about 2 hours after heavy rainfall on a playa in eastern New Mexico (David Larson, in letter). Flooding the shores of streams and rivers will provoke *Bledius* to seek higher ground. Larsen (1936) reported that with the onset of winter some maritime species emigrate to habitats that remain unflooded during the winter.

Bledius, however, also leave their burrows more routinely. Many collectors report that *Bledius* fly in the early evening when they often are attracted to lights. Activity often declines as the evening progresses. Blackwelder (1947) reported that 25,000 individuals were collected during the first 2 hours of the evening but only 1500 in the next 2 hours. Their evening appearance resulted in the application of the generic name *Hesperophilus* [evening-loving] to some species. The implication of the name is that *Bledius* are reacting to twilight or a reduction of light. More likely though, increased humidity is prompting the swarming (Larsen, 1936). On warm, humid, windless days *Bledius arenarius* shows two peaks (at about 0800 h and 2000 h) of surface activity (Larsen, 1936). While above ground the beetles take off and land repeatedly, thereby permitting individuals to move to more preferable habitat (Larsen, 1936). Mates may be sought during swarming (Larsen, 1936). The peak of larval activity on the surface is between 0200 h and 0400 h for *B. spectabilis* (Wyatt, 1982).

FLIGHTLESSNESS: Although adults of *Bledius* fly, at least four species, *actitus, playanus, monstratus,* and *susae,* show dimorphism for the length of the metathoracic wings. The shortwinged form does not fly. The reason for short metathoracic wings in *Bledius* is unclear. Might the species be blown from its habitat? Possibly, but the flightless forms are found in the same place with other species of *Bledius* that can fly. Further, the habitat of *Bledius* is nearly always a narrow linear strip adjacent to water; why aren't more species flightless therefore? *Bledius actitus* and *B. playanus* are quite small (about 2 mm long) and might more easily be blown away perhaps. But there are many equally small flying species including some related to these two (in the *forcipatus* species group). Many Carabidae in cool or high mountain areas are flightless (Thiele, 1977). Loss of flight in carabids may be a response to living in stable habitats (Thiele, 1977, citing Lindroth and Darlington). The four flightless species of *Bledius* live in the same habitat as other flying species and the habitat of these four species is likely to be no more stable than for other species. In fact the flightless *monstratus* lives in the same microhabitat as its geographically separated sister species, *fenyesi.* All of the flightless *Bledius* live in saline habitats; three of them, *actitus, susae,* and *monstratus,* are maritime species. The fourth species, *playanus,* lives on inland salt flats and the only flying individuals were attracted to a light at the edge of a nearby river. For *actitus* and *susae* the flying and flightless forms seem to occur together. The individuals with the longest flying wings for *monstratus* are in the northernmost part of the range.

HORNS: The males of at least 100 species of *Bledius* have cephalic and/or pronotal horns. Included among those with both are species of the *furcatus, lamelliceps, kochi, gigantulus, aequatorialis, minax, compressicollis, hamifer,* and *bellicosus* groups. Species with only cephalic horns on the supraantennal ridge are in the *lucidus, forcipatus, verres,* and *rugosicollis* groups and some in the *kochi* group. Males of some species of the *verres* group have small clypeal horns or a ridge. Males of the *armatus* groups often have clypeal horns. No species have only a pronotal horn although some "minor" males have severely reduced supraantennal horns and the female of *B. susae* has a pronotal horn but lacks cephalic ones. For all species represented by a sufficient number of specimens, both minor and major males were seen. The major males have larger and longer horns and a more robust body than do the minor males.

What is the function of these horns? For some beetles the horns of the male have been shown to be useful for dislodging rival conspecific males from the substrate or burrow to win the female (Eberhard, 1978, 1980). For *Bledius tricornis* the horns of the male were thought to enable the male ". . . to overcome his reluctant female, in her subterraneous retreats" (Haworth, 1812). Perhaps the horns are used to push intruders out of the burrow (Howard Frank, personal commun.).

If any of these hypotheses applies to the purpose of *Bledius*'s horns why do so few species possess them? All species of *Bledius* live in essentially the same kind of habitat. Except for the three species of the *bellicosus* group all of the horned *Bledius* live in interior or coastal saline habitats. Many other species that lack horns also live in saline habitats. If the horns of the males are used to secure a female, why does the female of *Bledius susae* from Texas have a horn? Equally unclear is why some horned species have two cephalic horns, others four, and others five.

ENVIRONMENTAL EFFECT: What is the effect of *Bledius* on the environment? Burrowing animals are generally credited with improving the aeration and drainage of soil and participating in a gradual turnover of soil (Kevan, 1962); *Bledius* is no exception. That the burrows of *Bledius* help to aerate the soil is shown by the fact that when the burrows are in or pass through blue-black anoxic soil, the sand adjacent to the burrow becomes rusty brown and is oxygenated (Larsen, 1936, 1952; Wyatt, 1982). Matsuzawa (1964) was concerned with the loss of seawater that drained through the burrows of *Bledius salsus* in clay beds (that are used to concentrate salt water). When *Bledius* excavate galleries they carry to the surface some of the soil. *Bledius pallipennis* may bring up 2 g and *B. bellicus* about 0.5 g with each burrow and they may construct a burrow each 24 hours (Smith and Hein, 1971). One *Bledius pallipennis* removes an estimated 300 g of soil in 5 months and one *B. bellicus* moves about 75 g per individual per season (Smith and Hein, 1971). Assume for the moment that these estimates are correct. I collected 15 quarts of *bellicus* near where Smith and Hein did their work. P. M. Hammond (personal commun.) estimated that he collected 60,000 specimens per pint of *B. pilicollis,* a species that is larger than *B. bellicus.* Extrapolating to my collection of 15 quarts of *B. bellicus,* there may have been 1.8×10^6 individuals attracted to my light from a few hundred yards radius. If that many beetles are each excavating 75 grams per year then these beetles could be moving as much as 1.35×10^8 grams (or 149 tons) of sand in 5 months in an area of a few thousand square yards. The flaw in these calculations is the estimate of the number of beetles and the assumption that each beetle makes a new burrow each day. I doubt that each individual makes a new burrow each day. If we assume that each *bellicus* moves only one gram of soil per season, then 1.8×10^6 beetles will move nearly 4000 pounds. The point remains, however, that *Bledius* moves quantities of loose easily eroded sand to the surface where it is dispersed by wind and transformed into small aeolian ripples (Smith and Hein, 1971).

SUCCESS: Judging from the large numbers of species, large populations, and numerous widespread species, *Bledius* is a successful group. What factors contribute to this success? Certainly one of the major reasons must be their construction of burrows. In it *Bledius* is protected from some physical hazards and predators, parasites, and fungi. Within the burrow temperature and humidity are stable. By making adjustments in the structure of the burrow, the beetles receive some degree of protection from flooding. The adults and larvae remain near their food supply. They are able to survive moderately prolonged submersion, can float for many hours and survive, can take flight from the surface of the water, and they are adapted to saline or nonsaline habitats.

PREDATORS AND PARASITES

DYSCHIRIUS: "Whilst investigating the habits of *Hesperophilus* [=*Bledius*], I was accidentally led to detect those of a large species of *Dyschirius* . . . . On turning up the sandy tracks, or burrows . . . to uncover the *Hesperophili*, I found their ferocious enemy, the aforesaid *Dyschirius*, pursuing his work of destruction. These *Dyschirii* burrow after, seize, shake, . . . and devour the luckless *Hesperophili*: so intent are they on their purpose, that I have frequently observed them continuing to shake their victim after they were both brought to light," (Rudd, 1835). Thus was the first of many authors to comment on the *Bledius-Dyschirius* association (for example, Lengerken, 1929; Krogerus, 1928; Brunier, 1931; Deville, 1924; Paulian, 1943). Noting that *Dyschirius* eats *Bledius*, Schiødte (1867) remarked, ". . . *Dyschirius* constantly in motion . . . hunting their prey [*Bledius*] . . . exhibit upon the whole the same wild, restless insatiably rapacious nature as the shrewmouse and mole." That these evidently highly active ground beetles are so often found with *Bledius* may have led some writers to hint at an exclusive association or that *Bledius* is the main prey for *Dyschirius*.

One stated that for some *Dyschirius* there seems to be host specificity (Paulian, 1943); another wrote, " . . . the majority of species are constantly associated with . . . *Bledius*" (Lindroth, 1961); a third, " . . . *Dyschirius* species prey(ing) largely on *Bledius*" (Crowson, 1981). Most authors, however, deny host specificity. What is the evidence?

What is the nature of the *Dyschirius-Bledius* association? Are there any one-to-one relationships? Which species of each genus are associated? Does the association reflect preference for prey or habitat? Which stages of *Dyschirius* attack which stages of *Bledius*? Have *Dyschirius* actually been observed eating *Bledius*? How many of the associations are based on the incidental collection of *Dyschirius* in the same or nearby habitat as *Bledius*?

Dyschirius is a moderately large genus of about 280 species of scaritine Carabidae. The species are distributed on all continents except Antarctica (Csiki, 1927) and Ball (1963) estimated that 80 percent of the species are from temperate regions. That species of the genus feed on *Bledius* is noted frequently, but they also feed on other organisms (Thiele, 1977, citing Lindroth) such as *Heterocerus, Carpelimus,* and *Platystethus* (Paulian, 1943). A larval individual of *Dyschirius* sp. was observed entering the egg chamber of a *Heterocerus,* seizing an egg and exiting with it, then returning later for another (Larsen, 1936). In nature, *Dyschirius* may eat nematodes which they readily accept in the laboratory (Larsen, 1936).

Larsen (1936) stated that larvae of *Bledius* seldom remain long in a culture of *Dyschirius* and, citing Krogerus, noted that remains of *Bledius* were found in the gut of *Dyschirius.* She observed that when *Dyschirius* attacks *Bledius,* the predator raises its forebody, extends its prolegs, seizes the *Bledius* beneath the wings, bites a hole between the fore and hind bodies, then consumes the hind body. Frank (in press) found fragments of what he thought were larval *Bledius* in the gut of *Dyschirius exochus.*

If *Bledius arenarius* is added to a culture of hungry *Dyschirius thoracicus* and *D. obscurus,* they fall upon and devour the *Bledius* immediately. But despite their not having eaten for a month, the *Dyschirius* did not eat one another (Larsen, 1936).

Once Larsen (1936) saw a *Dyschirius* enter the burrow of a *Bledius*. The burrow of *Bledius* was so narrow that *Dyschirius* had to enlarge it. *Bledius,* further down in the burrow, working slowly to improve the sides, upon discovering the *Dyschirius* increased its rate of digging by five times. *Bledius* dug straight down for a distance then turning sharply upward continued digging toward the surface. In pursuit, *Dyschirius* continued digging downward staying in the *Bledius* burrow but going past, missing where *Bledius* had turned upward.

Clearly, *Bledius* is eaten by *Dyschirius*. Is there a species-specific predation?

Deville (1924), Larsen (1936), and Thiele (1977) agree that each species of *Dyschirius* is not adapted to a particular species of *Bledius,* that there is no obligatory dependence of *Dyschirius* on *Bledius*. Paulian (1943) thought that for some species environmental factors determined which species were associated but that for others there was host preference.

Table 2 shows some of the species of *Dyschirius* that have been found with species of *Bledius*. The data for the table were culled from Paulian (1943), Larsen (1936), Brunier (1931), Deville (1924), Evans (1980), and Herman (1976, 1983a). Scanning down the table shows *D. thoracicus* and *D. angustus* with 15 and 10 species of *Bledius,* and *D. impunctus, D. politus, D. salinus,* and *D. septentrionum* associated with six or more species of *Bledius*. Reading in the other direction, most species of *Bledius* are associated with two to seven species of *Dyschirius*. There are, in fact, 12 species of *Dyschirius* found with only one species of *Bledius*. But it is unclear what this means. Does it reflect host specificity or paucity of collecting? At least 7 of those 12 associations are the result of sampling a single host-predator population each.

Another view of the table is possible. An asterisk marks species of *Bledius* that live in saline habitats; the others live in freshwater habitats. Of the 29 species of *Dyschirius,* 3 are found exclusively with salt tolerant *Bledius,* 16 are only with "freshwater" species. Nine species of *Dyschirius* are found with salt tolerant or freshwater *Bledius*. However, Larsen (1936) demonstrated that *B. arenarius* and *B. tricornis* are found in habitats with low salinity (though they can survive well in higher salinity). With this in mind, on reexamination of the nine *Dyschirius* found with both fresh and salt water *Bledius,* four species (*D. angustatus, D. impunctipennis, D. obscurus, D. politus*) are found with freshwater species and *B. arenarius* and/or *B. tricornis,* and one species (*D. salinus*) is found with only one species of *Bledius,* that lives in a freshwater habitat. Three species (*D. macroderus, D. thoracicus,* and *D. sphaericollis*) of these nine *Dyschirius* were found with saline tolerant species of *Bledius* (*neglectus, tristis, unicornis*) for which we have no data concerning the degree of salinity of their habitat. Only *D. septentrionum* is found both with freshwater *Bledius* and with *Bledius spectabilis* that lives in a highly saline environment.

Tables 3 and 4 summarize the *Bledius-Dyschirius* associations in North America. Table 3 cites the number of localities at which a particular pair of species has been collected together and table 4 lists the localities along with the *Bledius-Dyschirius* collections. The North American data also support a lack of prey preference by *Dyschirius*. Only *Dyschirius arizonensis* and *D. curvispinus* were found with only one species of *Bledius*. Both associations are represented by one collection each. Widespread species such as *Dyschirius sphaericollis, D. sellatus,* and *D. politus* were found with 25, 18, and 21 species of *Bledius,* respectively.

Frank (1985) collected *Dyschirius exochus* with *Bledius thinopus, B. turbulentus,* and *B. punctatissimus* in Florida. I have similar associations with *D. exochus* (tables 3 and 4) but not including *B. punctatissimus*.

Review of tables 2, 3, and 4 suggests that the *Bledius-Dyschirius* association is based on habitat preference rather than host preference and that *Dyschirius* is an opportunistic predator that eats what it can catch. Different parts of the geographical range of a species of *Dyschirius* may overlap the ranges of several species of *Bledius*; if in the same habitat, the *Dyschirius* would eat the *Bledius*.

Paulian (1943) suggested that environmental factors govern the *Dyschirius-Bledius* association in some cases but asserted some host specificity. Lindroth also thought habitat was important to the association when he said ". . . The almost complete dependence

TABLE 2
Bledius-Dyschirius Associations, Published Data

Bledius \ *Dyschirius*	*aeneus*	*affinis*	*angustatus*	*arenosus*	*chalceus*	*chalybaeus*	*globosus*	*globulosus*	*helleni*	*impunctipennis*	*integer*	*interior*	*intermedius*	*laevifasciatus*	*laeviusculus*	*ludersi*	*macroderus*	*marinus*	*nitidus*	*numidicus*	*obscurus*	*pallipennis*	*politus*	*quadrimaculatus*	*ruficornis*	*salinus*	*septentriomum*	*sphaericollis*	*subarcticus*	*substriatus*	*thoracicus*
arcticus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—
**arenarius*	—	—	x	x	—	—	—	—	—	x	—	—	—	—	—	—	—	—	—	x	—	x	—	—	x	—	—	—	—	x	—
atricapillus	—	—	x	x	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	x	—	—	—	—	—	—	—	x	—
cribricollis	—	—	—	—	—	—	—	—	—	—	—	—	x	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
**diota*	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—
emarginatus	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
fontinalis	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—
fracticornis	—	—	—	x	—	—	—	—	—	—	—	—	—	—	x	x	—	—	—	—	—	x	—	—	—	—	—	—	—	x	—
frater	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—
**furcatus*	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—
hispidulus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
littoralis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—
longulus	—	—	x	—	—	—	—	—	x	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—	—	x	—	—	—	x	—
**monstratus*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—
morio	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—
**neglectus*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	x	—	—	—	—
occidentalis	—	—	—	x	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	x	—	—	—	—	—	—	—	x	—
opacus	—	—	x	—	—	—	—	—	—	x	—	—	—	—	—	—	—	x	—	x	—	x	—	—	x	—	—	—	—	x	—
pallipes	—	—	x	—	—	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	x	—	—	—	x	—	—	—	—	—
poppiusi	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—
procerulus	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
pusillus	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
pygmaeus	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
rastellus	—	—	—	—	—	—	—	—	—	x	—	—	x	—	x	—	—	—	x	x	—	—	—	—	—	—	—	—	—	x	—
**spectabilis*	—	—	—	—	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—
subterraneus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—	x	—	x	—	x	—	—	—	x	—	—	—	x	—
suturalis	—	—	—	—	—	—	—	—	—	—	—	x	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
talpa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—	—	—	x	—

TABLE 2—(*Continued*)

Dyschirius / *Bledius*	*aeneus*	*affinis*	*angustatus*	*arenosus*	*chalceus*	*chalybaeus*	*globosus*	*globulosus*	*helleni*	*impunctipennis*	*integer*	*interior*	*intermedius*	*laevifasciatus*	*laeviusculus*	*ludersi*
terebrans	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—
tibialis	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—
**tricornis*	—	—	x	—	x	—	—	—	—	—	—	—	—	—	—	—
**tristis*	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—
turgidus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
**unicornis*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
verres	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—

Dyschirius / *Bledius*	*macroderus*	*marinus*	*nitidus*	*numidicus*	*obscurus*	*pallidipennis*	*politus*	*quadrimaculatus*	*ruficornis*	*salinus*	*septentriomum*	*sphaericollis*	*subarcticus*	*substriatus*	*thoracicus*
terebrans	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
tibialis	—	—	—	—	—	—	—	—	—	—	—	—	x	x	—
**tricornis*	—	—	—	x	—	—	—	—	x	—	—	—	—	x	—
**tristis*	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—
turgidus	—	—	—	—	—	x	—	—	—	—	—	—	—	—	—
**unicornis*	x	—	—	—	—	—	—	—	x	—	—	—	—	—	—
verres	—	—	x	—	—	—	—	—	—	—	—	—	—	x	—

Asterisks denote species in saline habitats.

of *D. obscurus*—and of *D. impunctipennis*—on *Bledius arenarius* is undoubtedly connected with the . . . largely similar demands of these three species with regard to type of sand" (Thiele, 1977, p. 113, citing Lindroth). More is involved, however, than just the type of sand. What are the habitat requirements for *Dyschirius*? What are the distributions of the species of *Dyschirius*? Can the species of *Dyschirius* be divided into species groups and if so what are the distributions of these groups? How are the geograpical distributions of the species and species groups of *Dyschirius* related to those of *Bledius*? What would be the results of sampling the species of *Bledius* found with a species of *Dyschirius* over its entire geographical range and vice versa? Answers to these questions may help us to begin understanding the limits of the *Bledius-Dyschirius* association.

OTHER PREDATORS: Other Carabidae have been observed as predators of *Bledius*. *Cillenum laterale* and *Bembidion pallidipenne* hunt *Bledius arenarius* (Larsen, 1936). *Bembidion pallidipenne* was observed attacking and eating *Bledius* in the same manner as described for *Dyschirius* (Larsen, 1936). *Bembidion* appears to be narrowly connected to *Bledius* communities (Larsen, 1936) and may eat *Bledius* as often as does *Dyschirius*. *Pogonus* sp. (Paulian, 1942) and *Dicheirotrichus pubescens* (=*gustavi*) will eat *Bledius* although the latter may not be an important predator of the genus according to Larsen (1936) but Wyatt (1982) suggested otherwise. *Cicindela* has also been offered as a predator of *Bledius* (Ortenburger and Bird, 1933; Willis, 1967). Certainly since *Bledius* and *Cicindela* sometimes occur in the same habitat, the tiger beetles may feed on *Bledius*. However, most *Cicindela* are diurnally active animals whereas *Bledius* is regarded as active on the surface at twilight. However, *Bledius* can be seen running on the surface at other times. *Bledius mandibularis* was seen on the surface near Long Island Sound in Connecticut at about 11:00 AM in early June (Herman, unpublished observ.) but I have seen such activity infrequently. Tiger beetles are not the most common predaceous beetles found in the habitat of *Bledius* nor are there published observations of them eating *Bledius*. Frank (1985) reports finding *Bledius lateralis* to-

TABLE 3
Bledius-Dyschirius Association in North America, New Data

Numbers represent number of localities for each association.

Dyschirius *Bledius*	*aratus*	*arizonicus*	*campicola*	*compactus*	*consobrinus*	*curvispinus*	*duplicatus*	*edentulus*	*exochus*	*filiformis*	*frigidus*	*gibbipennis*	*globulosus*	*integer*	*interior*	*montanus*	*pacificus*	*pallipennis*	*pilosus*	*politus*	*salivaganus*	*sellatus*	*setosus*	*sphaericollis*	*subarcticus*	*terminatus*	*tridentatus*	*truncatus*	*varidens*
albonotatus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
analis	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	2	—	—	1	—	—	—	1	4	—	—	—	—	—
annularis complex	—	—	—	1	1	—	1	—	—	—	1	—	1	1	1	5	—	—	3	18	—	1	1	3	1	1	1	1	2
**basalis*	—	—	—	—	—	1	—	—	1	4	—	—	—	—	—	—	—	1	—	—	—	2	—	2	—	—	—	—	—
bellicus	1	—	1	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—
bicolor	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
cedarensis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
confusus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—
**consimilis*	—	—	3	—	—	—	—	1	—	—	—	—	—	—	1	—	—	—	—	—	—	2	—	4	—	—	—	—	—
**cordatus*	—	—	—	—	—	—	—	—	1	3	—	—	—	—	—	—	—	1	—	—	—	1	—	1	—	—	—	—	—
coulteri	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	—	—	—	—	—
emarginatus	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	1	1	—	—	1	—	2	—	1	—	—	—
**eximius*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—
**flavipennis*	1	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
foraminosus	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	1	—	—	—	—	—	—	—	—	2
**forcipatus*	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	1	—	2	—	—	—
gracilis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1	—	2
gravidus	1	—	1	—	—	—	2	—	—	—	—	—	—	2	—	3	—	1	—	10	—	1	1	4	—	—	—	—	—
habrus	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
ineptus	1	—	1	—	—	—	2	—	—	—	—	—	—	—	1	4	—	1	—	3	—	1	1	5	—	—	—	—	—
jucundus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—
**mandibularis*	1	—	1	—	—	—	—	2	—	2	—	—	—	—	—	—	—	—	—	—	1	2	—	2	—	—	—	—	—
melanocephalus	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	2	—	2	—	—	—
monticola	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
nardus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
**neglectus*	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—	—	2	—	1	—	—	—	—	—
newelli	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	—	—	2	—	—	—	—	—	—	—	—	—
nitidiceps	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
nitidicollis	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
notialus	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	1	—	1	—	—	—

TABLE 3—(*Continued*)

Dyschirius / *Bledius*	*aratus*	*arizonicus*	*campicola*	*compactus*	*consobrinus*	*curvispinus*	*duplicatus*	*edentulus*	*exochus*	*filiformis*	*frigidus*	*gibbipennis*	*globulosus*	*integer*	*interior*	*montanus*	*pacificus*	*pallipennis*	*pilosus*	*politus*	*salivaganus*	*sellatus*	*setosus*	*sphaericollis*	*subarcticus*	*terminatus*	*tridentatus*	*truncatus*	*varidens*
omega	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	2	—	1	—	1	—	1	—	3	—	—	—	—	—
opacifrons	—	—	—	—	—	1	—	—	—	—	—	—	—	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	2
**opaculus*	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	2	—	1	—	—	—	—	—
pallipennis	1	1	3	—	—	—	—	1	—	—	—	—	—	1	—	—	—	1	—	—	—	3	—	5	—	2	—	—	—
**playanus*	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	2	—	—	—	—	—
**politus*	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	2	—	—	—	—	—	2	—	—	—	—	—
**punctatissimus*	—	—	—	—	—	—	—	—	—	4	—	—	—	—	—	—	—	—	—	—	—	2	—	1	—	—	—	—	—
rotundicollis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	2	—	—	—	—	—
rubiginosus	—	—	2	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	2	—	1	—	—	—
ruficornis	—	—	—	—	—	—	—	—	—	—	2	1	1	—	—	—	—	—	—	1	—	—	—	—	—	—	1	—	1
**strenuus*	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	1	—	—	—	—	—	—	—	—
suturalis	1	—	3	—	—	—	—	—	—	—	—	—	—	—	2	5	—	—	—	8	—	1	—	4	—	—	1	—	4
tallaci	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
tarandus	—	—	—	1	—	—	—	—	—	—	—	1	—	—	—	3	—	—	—	9	—	—	—	—	—	—	—	—	—
tau	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1	—
**thinopus*	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
**turbulentus*	—	—	—	—	—	—	—	—	1	2	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
turgidus	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	8	—	—	—	—	1	—	—	—	—
villosus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1
viriosus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	4	—	—	—	—	—	—	—	—	—
zophus	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	2

Asterisks denote species in saline habitats.

TABLE 4
***Bledius-Dyschirius* Associations—North American Records**

Locality	*Bledius*	*Dyschirius*
Northwest Territories:		
Hay River, Hay River	*annularis* complex, *gravidus, tarandus*	*politus*
Paradise Gardens, nr Hay River, Hay River	*annularis* complex, *turgidus*	*subarcticus*
British Columbia:		
nr. Chetwynd, Pine River	*annularis* complex, *habrus, tarandus, turgidus*	*compactus, politus*
Valemount	*annularis* complex, *gravidus, tarandus, turgidus, zophus*	*politus*
Alberta:		
nr. Bonnyville, Moose Lake	*analis, annularis* complex, *gravidus, ineptus, strenuus, turgidus*	*montanus*
nr. Bonnyville, Beaver River	*annularis* complex, *gravidus, tarandus, turgidus*	*politus*
nr. Slave Lake, Otauwau River	*annularis* complex, *confusus, gravidus, turgidus, viriosus*	*politus*
nr. Grande Prairie, Smoky River	*annularis* complex, *gravidus, suturalis, tarandus*	*politus*
nr. High Level, Ponton River	*annularis* complex, *suturalis, tarandus, turgidus*	*montanus*
nr. Hinton, Athabasca River	*annularis* complex, *gravidus, suturalis, tarandus, turgidus*	*politus*
nr. Edson, McLeod River	*annularis* complex, *gravidus, suturalis, turgidus*	*politus*
105 mi. W Rocky Mountain House, Thompson Creek	*annularis* complex, *turgidus, viriosus*	*politus*
nr. Rocky Mountain House, North Saskatchewan River	*annularis* complex, *gravidus, ineptus, suturalis, tarandus*	*politus*
Washington:		
McElroy Lake	*flavipennis, foraminosus*	*integer*
Packwood, Cowlitz River	*annularis* complex, *ruficornis* *suturalis*	*frigidus, politus* *politus*
Elbe, Nisqually River	*annularis* complex, *suturalis*	*politus, montanus*
American River	*annularis* complex	*tridentatus*
Raymond	*annularis* complex, *bicolor*	*consobrinus*
Ocean Shores	*newelli*	*frigidus, politus*
nr. Ocean City	*albonotatus, newelli*	*pacificus*
nr. Sappho, Camp Creek	*annularis* complex, *cedarensis, nardus*	*politus*
Oregon:		
Winchester Bay	*albonotatus, newelli, tarandus, zophus* *ruficornis, tarandus, zophus*	*politus* *gibbipennis*
Lake Abert	*eximius, strenuus*	*salivagans*
nr. Lakeview, Crooked Creek	*annularis* complex, *foraminosus, opacifrons*	*integer, politus, varidens*
nr. Cave Junction, East Fork Illinois River	*gracilis, opacifrons, suturalis*	*varidens*
nr. Brookings, Harris Beach State Park	*ruficornis*	*frigidus*
S of Crater Lake National Park, Anne Creek	*suturalis, zophus*	*varidens*

TABLE 4—(*Continued*)

Locality	*Bledius*	*Dyschirius*
California:		
nr. Sierra City, North Yuba River	*annularis* complex, *monticola, tallaci, zophus*	*varidens*
nr. McCloud, Elm Creek	*foraminosus, suturalis, villosus*	*politus, varidens*
nr. Quincy	*gracilis, opacifrons, suturalis*	*politus*
nr. Yorkville	*ruficornis*	*varidens*
	gracilis, ruficornis, suturalis	*tridentatus, varidens*
New Mexico:		
Quemado	*ineptus, suturalis*	*interior*
Logan, Canadian River	*pallipennis*	*arizonicus*
nr. Loving, Pecos River	*mandibularis*	*aratus*
Texas:		
nr. Dalhart, Canadian River	*consimilis, pallipennis, suturalis*	*campicola, sphaericollis*
Goose Island State Park, nr. Rockport	*mandibularis*	*edentulus*
	basalis	*curvispinus*
Utah:		
nr. Cedar City	*flavipennis, ineptus, nitidiceps*	*aratus*
nr. Salt Lake City, Great Salt Lake	*eximius, mandibularis*	*salivagans*
Colorado:		
nr. Brush, South Platte River	*gravidus*	*integer*
nr. Loveland	*ineptus, strenuus*	*campicola*
nr. Pueblo, Huerfano River	*consimilis, suturalis*	*campicola, interior, sphaericollis*
nr. Dolores, West Dolores River	*annularis* complex, *jucundus, omega, suturalis, tarandus, turgidus*	*montanus*
Wyoming:		
nr. Leiter, Clear Creek	*analis, annularis* complex, *gravidus, ineptus*	*duplicatus, setosus, sphaericollis*
Oklahoma:		
nr. Pond Creek	*pallipennis*	*sphaericollis*
nr. Ponca City, Arkansas River	*forcipatus, notialus, rubiginosus*	*campicola*
nr. Cleo, Cimarron River	*consimilis, forcipatus, ineptus, mandibularis, pallipennis, playanus, rubiginosus*	*sellatus, sphaericollis*
Hugo, Red River	*notialus*	*campicola, sphaericollis, pallipennis*
nr. Jet, Salt Fork Arkansas River	*consimilis, mandibularis, pallipennis, playanus*	*edentulatus, campicola, sellatus, sphaericollis*
	rubiginosus	(*Clivina bipustulata*)
Arkansas:		
nr. Ozark, Arkansas River	*forcipatus, melanocephalus, notialus, pallipennis*	*pallipennis, terminatus*
Fort Smith, Arkansas River	*forcipatus, melanocephalus, pallipennis, rubiginosus*	*terminatus*
Nebraska:		
nr. Hay Springs, Niobrara River	*analis, ineptus, melanocephalus, suturalis*	*sphaericollis*
Oshkosh, North Platte River	*analis, bellicus, gravidus, ineptus, pallipennis, suturalis*	*campicola, integer, sellatus, sphaericollis*
	analis, annularis complex, *ineptus, suturalis*	*aratus, sphaericollis*

TABLE 4—(*Continued*)

Locality	*Bledius*	*Dyschirius*
Montana:		
Forsyth, Yellowstone River	*emarginatus, gravidus, ineptus, melanocephalus, nitidicollis, omega*	*duplicatus, sphaericollis, pallipennis*
Townsend	*annularis* complex	*politus*
nr. West Yellowstone	*annularis* complex, *confusus, jucundus, turgidus*	*politus*
nr. Havre	*analis, nitidicollis, opacifrons*	*duplicatus*
Saskatchewan:		
north of Prince Albert, Bittern Creek	*annularis* complex, *confusus, gravidus, ineptus, turgidus, viriosus*	*politus*
Montreal River at Rt. 2	*gravidus, ineptus, viriosus*	*politus*
Manito Lake, SE of Lloydminster	*ineptus, strenuus, suturalis*	*montanus*
Manitoba:		
nr. Richer	*gravidus, ineptus*	*montanus*
nr. Shilo	*analis, coulteri, gravidus, ineptus, rotundicollis*	*montanus, sphaericollis*
Wisconsin:		
nr. New Lisbon	*annularis* complex, *tau*	*truncatus*
Clam Lake	*annularis* complex, *viriosus*	*integer*
nr. Ashland, Marengo River	*annularis* complex, *omega*	*politus*
	omega, rotundicollis	*sphaericollis*
	omega	*sellatus*
	omega	*montanus*
	annularis complex, *emarginatus, omega*	*sellatus*
	annularis complex	*sphaericollis*
Ontario:		
nr. Massey, Birch Creek	*annularis* complex, *suturalis, tau*	*montanus*
New York:		
Croton Point Park, Hudson River	*annularis* complex, *ruficornis*	*globosus*
Pennsylvania:		
Delaware Water Gap, Delaware River	*annularis* complex, *emarginatus*	*terminatus*
Ohio:		
nr. Zanesville, Muskinghum River	*annularis* complex, *nitidicollis*	*sphaericollis*
nr. McConnelsville, Muskinghum River	*analis, annularis* complex, *emarginatus*	*pilosus, sphaericollis*
West Virginia:		
nr. Grafton, Cheat River	*annularis* complex	*pilosus*
New Jersey:		
Sandy Hook State Park	*neglectus*	*filiformis*
Maryland:		
Assateague Island	*mandibularis, neglectus, politus, punctatissimus*	*filiformis*
	basalis, cordatus, neglectus, opaculus, punctatissimus	*filiformis, sellatus, sphaericollis*

TABLE 4—(*Continued*)

Locality	*Bledius*	*Dyschirius*
North Carolina:		
Cape Hatteras, Oregon Inlet	*cordatus, neglectus, punctatissimus*	*filiformis*
	basalis, emarginatus, neglectus, punctatissimus	*filiformis, sellatus*
Cape Hatteras	*opaculus*	*sellatus*
	basalis, politus	*sphaericollis*
Florida:		
Punta Gorda Beach, nr. Englewood	*basalis, cordatus, thinopus, turbulentus, politus*	*pallipennis*
nr. Grove City	*cordatus, punctatissimus*	*filiformis*
Fort Desoto Park, nr. St. Petersburg	*basalis, cordatus, thinopus, turbulentus*	*exochus*
Palmetto	*basalis, turbulentus*	*filiformis*
Lower Matecumbe Key	*punctatissimus, turbulentus*	*filiformis*
St. George Island	*basalis, politus, thinopus*	*filiformis*

gether with *Clivina oblita* and *Schizogenius impressicollis* in northern Venezuela.

Specimens of *Bledius ruficornis* were removed from the stomach of a rainbow trout [*Salmo gairdneri*] in California (Herman, unpublished data). When *Bledius* are washed into streams, rivers, ponds, or the ocean then they are susceptible to predation by fish.

In a photograph of the casts of the burrows of *Bledius bellicus* published by Smith and Hein (1971) the burrow of a mole traversing a patch of *Bledius* burrows is visible. These animals may also eat some *Bledius*.

Birds, particularly those that feed from the shores of rivers, lakes, and oceans, are potential predators of *Bledius*. *Bledius spectabilis* was taken from the stomach of a sandpiper, *Calidris alba*, in Afghanistan (reported here from specimen in BMNH).

PARASITOIDS: Paulian (1941) mentioned that larvae of *Bledius spectabilis* were parasitized by an unnamed ichneumon wasp. In the original description of the ichneumonid *Leptopygus blediator* Aubert (1970) from France, *Bledius* was reported as the host. Wyatt (1982) reported the same species, *Barycnemis blediator* (Aubert), as a parasite [actually parasitoid] of *Bledius spectabilis* in England. He found that *B. blediator* sits on the cast at the entrance of a burrow of *Bledius* touching the cast with its antennae. Then after searching for the burrow with its ovipositor, spends 5 to 90 seconds in the burrow before reemerging to search for another burrow. A wasp may examine as many as 60 burrows and travel 20 m in 90 minutes. The parasite enters about 8 percent (1 of 12) of the burrows occupied by the female of *Bledius spectabilis* with larvae and eggs but will enter about 50 percent (32 of 64) of the burrows occupied by first instar larvae alone. Of these first instar burrows entered, about 94 percent of the occupants were parasitized while second and third instar larvae were parasitized less frequently. Wyatt (1982) suggested that the longer a larva delays leaving the parental burrow, the greater its chances of survival.

FUNGI: *Bledius* are infested by fungi (Foster and Treherne, 1976) which include species of the order Laboulbeniales (Larsen, 1952; Frank, 1982). These Ascomycetes are highly specialized, obligate superficial ectoparasites whose hosts are principally insects (Madelin, 1966; Whitney, 1982). Most of the 1500 species are associated with Coleoptera, especially Carabidae and Staphylinidae (Madelin, 1966). The animals most commonly infested are those living in damp habitats (Madelin, 1966). The spores of these fungi are formed in asci which develop in long, hollow perithecia. The spores, released from the perithecium when brushed by an insect, stick to the host and degrade the host's exoskeleton with an enzyme to permit penetration by a haustorium. The haustorium pen-

TABLE 5
***Bledius*-Laboulbeniales Associations**

Laboulbeniales	*Bledius*																			
	annularis	*assimilis*	*nitidicollis*	*subterraneus*	*bellicus*	Probably *strenuus*	*niloticus*	*emarginatus*	**bicornis*	**albonotatus*	*cribricollis*	*gallicus*	*opacus*	*rubiginosus*	**spectabilis*	**graellsi*	**unicornis*	**basalis*	**jacobinus*	**fergussoni*
Peyritschiellaceae																				
Cantharomyces																				
bledii		x	x	x	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
occidentalis		—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—	—
sp. nr. *platystethi*		—	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—	—
Dimorphomyces																				
bledii		—	—	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—
Haplomyces																				
californicus		—	—	—	—	—	—	—	x	x	—	—	—	—	—	—	—	—	—	—
texanus		—	—	—	x	—	—	—	—	—	x	x	x	x	x	x	x	—	—	—
virginianus		—	—	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	—	—
Peyritschiella																				
protea		—	—	—	—	—	—	—	x	—	—	—	—	—	x	—	—	—	—	—
Laboulbeniaceae																				
Dioicomyces																				
floridanus		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—	—
Laboulbenia																				
bledii		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	x	—
parraudi		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—	—	x
Misgomyces																				
dyschirii		—	—	—	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—

Asterisks indicate species found in saline habitats.

etrates only to the epidermal cells of most species where the fungus obtains nutrients (Whitney, 1982). That body liquids are removed by these fungi has been shown by the uptake of a dyed fluid (Frank, 1982, citing Scheloske).

The mode of infestation within and between species is debatable. Some say the spores are transferred from an infected individual to an uninfested one during social or sexual interaction (Whitney, 1982). Frank (1982) suggested that intraspecific contact may be of greater duration but of no greater frequency than interspecific contact. Spores may remain in the soil to be picked up by the host but the spores may live for only a few weeks in most environments and, although infection by spores in insects' surroundings has been experimentally induced, this may be a minor source of infestation in nature (Whitney, 1982).

Laboulbeniales are most often seen on adult insects but if present on larvae the fungi are shed during molting (Frank, 1982). Since the fungi are on adults and the spores remain viable for only a short time, the Laboulbeniales are restricted to hosts with overlapping generations (Whitney, 1982).

Bledius spp. may be perfect hosts for Laboulbeniales. *Bledius* occur in damp habitats, have overlapping generations, live in large groups, and remain in the same spot for long periods. In an excellent review of the parasites of the Staphylinidae, Frank (1982) cited 12 species of 2 families (Peyritschiellaceae and Laboulbeniaceae) of fungi that infest 19 species of *Bledius*. Table 5 summarizes Frank's data. The *Bledius* names preceded by an asterisk live in saline habitats.

The parasite-host relationship seems to be based more on habitat than phylogenetic affinity. Of the seven genera reported on *Bledius* only *Haplomyces* is restricted to that genus. Seventeen of 18 species of the *Cantharomyces* are on species of the Oxytelinae but most species of the other five genera attack non-Oxyteline species (Frank, 1982). One interesting anomaly is that *Misgomyces dyschirii* was found on species of *Bledius* and *Dyschirius* (Frank, 1982).

Most fungi are found exclusively on freshwater species or saltwater species. The exception is *Haplomyces texanus* which is found on five freshwater species and two saline species. All four species of the Laboulbeniaceae, along with *Haplomyces californicus* and *Peyritschiella protea,* infest only salt tolerant *Bledius.* The others are found on freshwater species.

The species of *Bledius* can be sorted by species group. Here we find *Cantharomyces* from five species groups, *Haplomyces* from six, *Peyritschiella* from two, and *Laboulbenia* from three. One species group may be attacked by parasites in different families and/or genera.

Infestation of natural populations of insects may run between 5 and 50 percent (Frank, 1982, citing Hincks). Larsen (1952) working with saline tolerant *Bledius* found that when they were in habitats of low salinity the fungal infestation ran to 40 percent or more while at the same time in nearby spots of higher salt content only one among hundreds was infested. Foster and Treherne (1976) suggested that fungal infection of *Bledius spectabilis* and *Bledius arenarius (=fergussoni)* is reduced in anaerobic soil. *Bledius spectabilis* has been reported in poorly oxygenated soil (Larsen, 1952) but *arenarius* has not been.

Laboulbeniales infection is thought to be a contagious, nonfatal, cutaneous, social disease (Madelin, 1966); these fungi are true parasites that do not kill their hosts (Frank, 1982, citing Hincks). However, Larsen (1952) cited observations that infested beetles move sluggishly, walk on the surface eating almost nothing, and she reported high mortality in infected cultures, especially when the mouthparts and antennae are attacked. The importance of Laboulbeniales infection is unclear. However, earlier (Larsen, 1936) she mentioned the difficulty of keeping *Bledius* alive in cultures. Perhaps here her animals were already dying or weakened and happened also to have fungal infections because the conditions were good for fungi but not for *Bledius.* How, though, does *Bledius* defend itself against these parasites: by physiological tolerance, grooming behavior, secreting antifungal fluids, living in habitats that cannot be tolerated by the fungi (Howard Frank, personal commun.)? Under what conditions are these defenses ineffective?

PROTOZOANS: Finally, *Entaphelencus bledii,* a microsporidan endoparasite, was found in *Bledius opacus.* These protozoans may be important insect pathogens. Infected individuals may be more subject to attack by predators and parasites than are healthy animals. A synergistic effect may be produced in hosts by a microsporidan and another parasite (Frank, 1982). Might this effect be found in individuals infested with Laboulbeniales?

CHEMICAL SECRETIONS

Various authors have commented briefly on the penetratingly odorous substance produced by *Bledius.* In a short historical review of this phenomenon, Larsen (1936) noted that the chemical can be variously regarded as corrosive, of sweetish, orangelike, Russian-leather-like, or violet-like odor, or is nauseatingly penetrating. I experience the odor as sweet and pleasant. She went on to say that the odor clings to one's fingers for a long time, and that the greasy chemical is produced from two large bladders at the posterior end of the abdomen. Similar bladders that open into grooves on tergites IX are characteristic of all Oxytelinae (Herman, 1970).

The structure of these pygidial glands is similar for *Bledius spectabilis* (Araujo, 1973) and *Bledius mandibularis* (Happ and Happ, 1973). The glands are paired, each having three parts. A *secretory cell mass* is linked by an efferent duct to an *intermediate tubular chamber* from which a duct runs to a lightly musculated *storage reservoir.* The two large dark-colored storage reservoirs are the structures generally reported as the abdominal glands. Each secretory cell mass contains several hundred secretory units. Each unit has two types of secretory cells, a *cortical* and *medullary* cell, that differ in position, nuclear morphology, and enclosed central cavity. The cortical or outer cell has an elongate central cavity and a rounded nucleus that includes one prominent nucleolus. The medullary or inner cell has an ovoid central cavity, an oval nucleus characterized by small scattered masses of chromatin. Both cells are drained by the same fine cuticular ductule. This ductule arises in the cavity of the cortical cell and runs into the cavity of the medullary cell where it loops several times before exiting to converge with 10 to 20 other such ductules to empty eventually into efferent ducts that drain the secretory mass into the storage reservoir. The chemical is secreted by contraction of the muscles of the reservoir (Happ and Happ, 1973). In contrast to some other staphylinids, such as those of the Staphylininae, the pygidial glands are not evaginated when the chemical is secreted.

Happ and Happ (1973) offered two hypotheses to explain the function of each cell but favored the following. The cortical cell accumulates precursors from the hemolymph and mediates some of the intermediate biosynthetic steps before expelling the primary secretory product into its central cavity. The primary product passes through the ductule into the cavity of the medullary cell where it is modified by injections of enzymes to produce the final product. In such a two-cell unit, relatively nontoxic products are produced in the cell and oxidized to more toxic ones in the central cavities.

The chemical secreted by both *B. mandibularis* and *B. spectabilis* is composed of different proportions of the same five compounds, namely: 1-undecene, methyl *p*-benzoquinone, the terpene aldehydes neral and geranial, and γ-dodecalactone. The major component for both *mandibularis* and *spectabilis* is γ-dodecalactone and represents 70 and 77 percent respectively of their secretions. This particular lactone had never been found in insects before, has a fruity odor, and is found in fruits and butterfats (Wheeler et al., 1972).

What is the function of the secretion? Happ and Happ (1973) remarked that the reactive nature of the terpenes suggests a repellent role and Araujo (1973) stated that the presence of the quinone may serve as defensive functions since quinones are known to be toxic. Because *Bledius* bends the tip of its abdomen forward and applies some of the secretion to the attacker when menaced by another insect or pair of forceps, Wheeler et al. (1972) believed the chemical to be defensive. They also thought it possible that one or more components may regulate algal growth upon which *Bledius* feed (Wheeler et al., 1972). These same three authors in the same paper pointed out that lactones have been reported as queen pheromones in hornets, and sex-related recognition pheromones in male black-tailed deer. They even went on to report that the γ-dodecalactone of *Bledius* differs from the lactone pheromone of the deer by one double bond (Wheeler et al., 1972). They failed, however, to propose that one or more of the components may serve as a sex pheromone or aggregative chemical. Further, they tested none of their hypotheses as to whether the secretion serves as an allomone and/or pheromone.

Duffy (1977) pointed out that allomones or defensive chemicals should be tested in the field using natural predators. He goes on to say that there is little evidence that allomones confer the hypothesized advantage or even that they are primarily for defending the secreting animal against large predators, and that predators often do eat organisms that produce defensive chemicals. He indicated that benzoquinones can interfere with certain bacterial growth and can mix with chemicals in the soil to produce antifungal chemicals.

Larsen (1936) seemed to have been the only scientist to have tested the function of the chemical secreted by *Bledius*. She wondered if the chemical repels enemies or attracts conspecifics, or perhaps serves as a lubricant that renders *Bledius* water resistant. To assess the defensive function of the chemical, Larsen (1936) kept a culture of *Dyschirius thoracicus* and *Dyschirius obscurus* that had not eaten for a month. Since there were no bits and pieces of exoskeleton lying about she surmised that the *Dyschirius* were not eating one another. When a *Bledius arenarius* (=*fergussoni*) was added, the *Dyschirius* immediately fell upon and devoured it. She then took a *Dyschirius obscurus* and rubbed it with the secretion from the abdominal tip of *Bledius tricornis.* This specimen was quickly torn apart and eaten when introduced into the culture of hungry *Dyschirius.* The same results were obtained when the test was repeated. As a control, a *Dyschirius* without the *Bledius* secretion was added to the culture but it remained unharmed. She concluded that the secretion serves poorly as a defensive chemical. One flaw in these tests may have been the use of *Dyschirius* that had not eaten for a month. Duffy (1977) suggested that hunger may transform a formerly offensive organism into a tolerable food item for a predator.

Wheeler et al. (1972) showed that for two species of *Bledius* the components of the secretion are the same; only the proportions vary. Do the proportions or components vary in other species? What is the variation of the secretion among species of the same species-group? Or between groups? Is there seasonal, age, geographic, or habitat difference? What is the function of the chemical and/or the components?

Economic Importance

Most Staphylinidae are regarded as beneficial or benign. The beneficial ones include those that eat other insects especially those that we designate as pests. A few are noxious. Species of *Paederus* are of medical importance in the tropics because they secrete "pederin," a chemical that produces a long-lasting blister that may be subject to secondary infection.

Bledius would seem an unlikely candidate as a pest, and certainly not one that produces damage of any economic significance. However, in Japan, *Bledius salsus* damages the clay beds over which salt water is flooded repeatedly to be concentrated (Miyatake, 1963; Matsuzawa, 1964). In an article describing the damage caused by *Bledius salsus,* Matsuzawa (1964) stated that this species "... is the most injurious insect to the clay bed ... in the sloping salt fields of Japan, although several other harmful insects are found there."

Clay beds of about 50 m^2 and 9–10 cm thickness with a gradual slope of 1/120 to 1/150 are repeatedly flooded with seawater to concentrate the salt by solar evaporation. The upper one- to two-thirds of the clay beds are riddled with as many as 29,000 galleries of *B. salsus* on a surface area of 32 m^2. In some places the density reached nearly 7000 galleries/m^2. The diameter of the holes varied from 1.0 to 10.0 mm with 90 percent of them 1.0 to 6.0 mm and 62 percent 1.1 to 3.0 mm. These holes allowed the seawater to leak through the clay bed causing heavy loss of seawater and reducing the efficiency of production in the amount of salt. The annual losses in salt production [in 1964] due to the damage were estimated to be 10,000 to 50,000 yen/hectare. Actual loss may be even greater since many beds were lying idle because of damage. Damage was stated to be increasing in all the salt fields throughout Japan (Matsuzawa, 1964).

It is surprising that only in 1964 was *Bledius salsus* reported as a pest of these salt fields. Although the species was first reported (and described) in Japan in 1963 it must have been there for longer than salt was produced in these salt fields. Why was the species not found there before 1963–1964 and why was the damage increasing? Although Matsuzawa (1964) considered it imperative that the beetle be controlled I was unable to discover how salt producers accomplished this.

Since *Bledius* eat algae and many of those eaten by *Bledius* require sunlight to survive, shading the habitat of species requiring full sunlight may force *Bledius* to move. Wyatt (1982) noted that when *Halimione* sp. shades the habitat of *Bledius spectabilis,* the beetle leaves. A similar approach is possible for these clay evaporation beds. These clay beds are simply salt flats to *Bledius,* but *B. salsus* may well require a habitat in full sunlight. Since *B. salsus* occupies the upper portion of the clay beds, perhaps that part can be shaded from the sun, thereby reducing algal growth and perhaps forcing *Bledius salsus* to seek more amenable habitat.

No other species of *Bledius* have been reported to be pests. The clay beds used to concentrate salt happened to be perfect habitats for species of *Bledius* that live in saline habitats. Solar evaporation of seawater to produce salt is practiced in many countries including, for example, Korea, China, Burma, India, Sri Lanka, France, Spain, Kenya, Tanzania, Mozambique, Angola, Namibia, etc. (Lefond, 1969) where there are species of the size and having habits and habitats similar to *Bledius salsus*. If the concentrating beds are made of clay then some other saline tolerant species of *Bledius* are potentially damaging species.

IMMATURE STAGES

The most accurate means of identifying the immature stages of Staphylinidae is by rearing them through to the adult stage. Although adult and larval staphylinids often occur in the same habitat, there is no way of being certain that the larvae and adults are conspecific short of rearing the larvae. *Bledius* may be exceptional in this regard because of two characteristics.

The eggs, larvae, pupae, and adults of each species of *Bledius* are often in the same or adjacent galleries. The species of *Bledius* live in dense aggregations or colonies that are usually composed of single species although other species may live in adjacent habitats. The occurrence of all life stages together and the aggregative habits of *Bledius* make identification of larvae by association with adults relatively accurate. Assurance of correct identification is improved by wide geographical sampling of each species.

Descriptions or a few characters have been published for *Bledius hinnulus, tricornis, fracticornis* (*=gallicus*), *pallipes, talpa* (Schiødte, 1864), *atricapillus* (Fauvel, 1873b), *opacus, fuscipes, arenarius* (*=fergussoni*), *subterraneus* (Krogerus, 1925b), *spectabilis, unicornis, furcatus,* and *fuscicornis* (Paulian, 1941), *ferratus, ornatus, punctatissimus,* and *diagonalis* (Moore, 1964). Matsuzawa (1964) published photographs of eggs, larvae, and pupae of *Bledius salsus*. Schiødte (1864) described the pupa of *tricornis*. Krogerus (1925b) described the pupa, larva, and egg for *talpa*. Griffiths and Griffiths illustrated the larva and pupa of *B. punctatissimus*. Moore and Legner (1974) described larval *ornatus* (*=albonotatus*) which Moore (1964) had characterized earlier. Pototskaya (1967) provided a key in Russian to *pallipes, opacus, furcatus, tricornis, unicornis, spectabilis, arenarius* (*=fergussoni*?), *talpa,* and *subterraneus*.

Generic characters for larval *Bledius* were described by Schiødte (1864) who examined five species. He divided these species into two groups, one with *hinnulus, tricornis,* and *fracticornis,* and the other with *pallipes* and *talpa*. Ganglbauer (1895) repeated Schiødte's work. Böving and Craighead (1931) provided a few generic characters for the larval *Bledius*. Paulian (1941) also provided a generic description, in this case based on *spectabilis, unicornis, furcatus,* and *fuscicornis*. In the same publication Paulian included a key to genera that separated larval *Bledius* from other staphylinid genera. Kasule (1968) published a key to the British genera of the Oxytelinae where he separated *Bledius* from six other genera.

Many of the species for which larvae have been described are represented in the British Museum of Natural History along with a few as yet undescribed ones. These collections represent seven of the species groups that are recognized herein. The collections of the American Museum of Natural History include over 40 species of larval *Bledius*. These species represent all of the 12 species groups from the New World. Work is planned that will describe these 40+ species with the goal of testing the adult-based classification and phylogeny that is proposed in the present work.

FOSSILS

FOSSIL ANIMALS: Fossils of the Staphylinidae have been reported from the Jurassic deposits of Kara Tau in Soviet Central Asia. Among the 10 genera and 16 species in this material are two species in the fossil genus *Mesoxytelus* of the Oxytelini (Tikhomirova, 1973). These fossils suggest that the Oxytelinae are at least as old as early or middle Jurassic. *Bledius,* however, is not reported until the Eocene deposits of Green River, Wyoming (Scudder, 1890, 1900).

Nine species of *Bledius* have been described from fossil deposits. Included are *adamus* (Scudder, 1890) and *faecorum* (Scudder, 1900) from the Green River Eocene shales; *osborni, primitiarum,* and *soli* from the Oligocene shales of Florissant,[15] Colo-

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[15] Different authors have referred to the Florissant deposits as being of either Miocene or Oligocene age. Durden (1966) alluded to this controversy and stated that "Vertebrate fossils . . . have indicated an early Oligocene

rado (Scudder, 1900); *speciosus* from lake deposits of Oeningen, Switzerland (Heer, 1862); and *glaciatus* from Pleistocene clay beds of Scarboro, Ontario (Scudder, 1890). These seven species of fossils are currently listed in *Bledius*. Two other species of fossils have also been cited in *Bledius*. Scudder (1900) described *morsei* from Florissant, Colorado and at the same time moved Heer's (1856) *Stenus prodromus* from Aix, France (Oligocene deposits) into *Bledius*. Handlirsch (1907) rejected Scudder's action and continued to include *prodromus* in *Stenus*. *Bledius morsei*, which Scudder thought to be similar to *prodromus*, clearly belongs to *Stenus* and was so transferred (Wickham, 1913). The antennae of *morsei* are slender, the legs slender and without spinelike setae, and the body is densely punctate, all typical characteristics of *Stenus*.

As for the other seven species none of them is unequivocally in *Bledius* but some are suggestive of the genus.

Bledius glaciatus is represented by an elytron (Scudder, 1890, pl. 1, fig. 35) similar to some species of *Bledius* with regard to punctation and the curved apical portion of the medial margin. This fossil may represent *Bledius* but it is only of Pleistocene age. Most of the post-Pliocene fossils of *Bledius* seem to belong to extant species. Elytra alone of *Bledius* are relatively uninformative for identification to species.

Bledius primitiarum (Scudder, 1900, pl. 8, fig. 13) may be a *Bledius*. The tibiae are expanded apically and one of them shows what appear to be spinelike setae. No features exclude *primitiarum* from *Bledius* but none clearly argue for inclusion.

The illustrations of *B. soli* (Scudder, 1900, p. 8, figs. 10, 14) are similar to that of *B. moresei* (pl. 8, fig. 8) which was moved to *Stenus*. The punctation of the body and form of the legs and antennae of *soli* are as suggestive of *Stenus* as they were for *moresei*. *Bledius soli* is probably not a *Bledius*.

Scudder (1890, pl. 8, fig. 10) illustrated *Bledius adamus* which he had described earlier (1878). This figure is more like *Osorius* than *Bledius*. However, the appendages are missing.

Bledius faecorum (Scudder, 1900, pl. 8, fig. 9) has the appearance of some Omaliinae. Scudder suggested it may be near *Oxytelus*!

Bledius osborni (Scudder, 1900, pl. 8, figs. 11, 12) has one too few abdominal segments even to be in the Oxytelinae. Even if the species is in the subfamily there is little to support putting it in *Bledius*. It could as well be *Carpelimus* since the tibiae are slender and lack spinelike setae.

Bledius speciosus (Heer, 1862, Taf. III, figs. 2, 2b–d), as illustrated, has what appear to be the abdominal tergites IX extended into long, cylindrical cerci-like structures. Such a configuration is common in some genera of the Staphylininae, but is found in no *Bledius*. Further, no second abdominal sternum is shown and the procoxae are elongate and free. *Bledius speciosus* is probably not in the correct genus.

Scudder (1900) tried to place his fossils in LeConte's (1877) classification of species groups. He regarded *adamus* as near the *semiferrugineus* group, *primitiarum* near the *annularis* group, and placed *faecorum* in the *armatus* group nearest the living species *flavipennis* LeConte. *B. moresei, osborni,* and *soli* were not placed in or near extant species groups. Only *glaciatus* and *primitiarum*, however, may belong in *Bledius*. There is little reason to include the others.

One of the fossils described by Scudder that is most reminiscent of *Bledius* is *Staphylinus lesleyi* (1900, p. 51, pl. 6, fig. 6). The illustration of this species shows apically expanded tibiae with spinelike setae, a possibly elongate first antennomere, a possible abdominal sternite II, absence of a neck, and possible subcylindrical body. In the description of the species, Scudder wrote that *lesleyi* is one of the most common species of the family at Florissant. The Florissant deposits are in and adjacent to a former lake. One would expect that *Bledius* could be abundant in such deposits, certainly more abundant than *Staphylinus*, normally an inhabitant of forest litter.

[On the same note, Scudder (1900, p. 59, pl. 7, fig. 11) described *Leptacinus rigatus*. The illustration shows and description mentions cephalic carinae. The carinae plus the shape of the pronotum are suggestive of *Pseu-*

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age for the Florissant lake bed . . . ." Scudder (1890, p. 36) drew similar conclusions from evidence of plants and vertebrates but Brues (1910), Handlirsch (1907), and Leng (1920) all assigned the Florissant deposits to the Miocene.

dopsis. Leptacinus has no cephalic carinae (Coiffait, 1972, Smetana, 1982).]

Handlirsch (1907) cited a reference to an unidentified species of *Bledius* from Oligocene amber and Spahr (1981) cited several other such references. I have neither seen the specimens nor illustrations of them and cannot comment on their inclusion in *Bledius.*

FOSSIL BURROWS: Some beetles (scarabaeids, for example, Retallack, 1984; cicindelids and heterocerids by Stanley and Fagerstrom, 1974) have been implicated as responsible for some fossilized burrows. Since species of *Bledius* saturate some habitats with burrows one would expect that some would turn up as ichnogenera. In a cursory examination of the literature on fossil burrows I saw no illustrations of burrows that unequivocably resembled those made by *Bledius.* Fossilized burrows of *Bledius* would have at least some of the following features. The diameter would be 0.8 to 5 mm, the length from 2 to 40 cm, and they would be in silt or fine to moderately coarse sand near former bodies of water. Most burrows are straight and perpendicular to the surface but some species make burrows with branches and sometimes the burrow has a characteristic fork or sloping branch near the surface (for examples see figs. 15 and 35 and also Larsen, 1936, figs. 42–50; Matsuzawa, 1964, fig. 6; Evans et al., 1971, figs. 5, 6a; Griffiths and Griffiths, 1983, fig. 2). Some burrows may have small, globular chambers adjacent and usually connected to the main burrows (Larsen, 1936, figs. 43b, c, 47, 48; Griffiths and Griffiths, 1983, fig. 2b; see also the information under the heading Architecture of Burrow).

Burrows of such size, from alluvial deposits in the Miocene of western Nebraska were described by Stanley and Fagerstrom (1974). These authors attributed these trace fossils to cicindelids and/or heterocerids but also mentioned that rove beetles are possibilities. The rove beetles to which they allude but do not cite are probably *Bledius.* Stanley and Fagerstrom (1974) found the vast majority of the trace burrows to be vertical and straight or slightly curved, with a diameter of 1–2 or 3–4 mm and length of 5 to 10 cm to as long as 45 cm.

SUBFOSSILS: Dr. Allan Ashworth of North Dakota State University provided an opportunity to study some more recent fossils of *Bledius* from 18 Mile River, Ontario, near Lake Huron. The material was collected in flood debris from which a piece of wood was radiocarbon-dated at 10,600 years (Ashworth, 1977). The two identifiable species were *B. turgidus* and *B. tarandus.* Both species now have boreal transcontinental distributions and for both the fossil site is near the southern edge of their present distribution in eastern Canada (Herman, 1983, figs. 104, 245). Kelley and Osborne (1965) reported *Bledius annae* from alluvial deposits (4800 B.P.) from near Shustoke in south central England and Morgan (1969) listed *Bledius fuscipes* from near Northampton, England, in deposits dated at about 28,000 years B.P.

What conclusions can be drawn from the fossil *Bledius*? If *Bledius primitarium* and *Staphylinus lesleyi* are in fact species of *Bledius,* then the genus existed at least 35 million years ago. Since there is evidence that Oxytelini existed about 150 million years ago during the Jurassic, then *Bledius* may have arisen during the Cretaceous along the edges of the extensive maritime coasts of that Period.

NATURAL HISTORY AND SPECIES GROUPS

One of the goals of the present paper is to delineate the species groups of *Bledius.* These groups are defined by anatomical characters, but are there features of their natural history that would similarly circumscribe them? Can the natural history of the species groups add anything to our understanding of the phylogeny of *Bledius*?

For most of the 34 species groups recognized herein, little is known beyond anatomy, geographical locality, and general habitat. The works of a few people have supplied data about factors affecting habitat selection, structure of the burrow, reproduction, life cycle, egg laying, and feeding behavior for about a dozen species in six species groups. Four of the groups are represented by data for one species each, so few generalizations can be made. Two other groups include information for three and four species. The data collected by these authors served to illuminate ecological questions, not phylogenetic or classificatory ones. These authors were seeking differences, whereas to classify we need differences and similarities.

Furcatus group. Bledius taurus (=*furcatus*) digs a broad, deep burrow and collects food in the burrow but evidently does not construct a food chamber. It lives outside the tidal zone in unvegetated or sparsely vegetated clay-covered sand. The soil is highly saline and has a high moisture content. The passageway to the egg chamber is very loosely filled with sand (Larsen, 1936).

Kochi group. Bledius diota constructs deep, complexly branched burrows. Horizontal galleries just under the algal layer serve as provision or maternal burrows. Special food chambers are not constructed but alga is stored. Egg chambers are connected to the maternal gallery by passageways that are loosely filled with sand. The species lives in alga-covered, barren flats in highly saline, very moist sand. They live above the tidal zone but during spring floods remain in their burrows (Larsen, 1936).

Basalis group. Bledius arenarius makes simple burrows that are forked near the surface. It feeds in these subsurface forks and store no food. The egg chamber is isolated from but near the retreat burrow. This species lives in slightly saline to mildly saline, moderately moist, clean, unvegetated sand (Larsen, 1936, 1953). Although there is a confusion in the early literature, and including the data of Larsen (1936, 1953), about *arenarius* (=*fergussoni*) and *subniger,* one of them (probably *subniger*) lives in the intertidal zone. Some of the North American species may also live in the intertidal zone. Most of the species are maritime; two, *dimidiatus* and *melanocephalus,* are found at inland freshwater localities.

Punctatissimus group. Bledius punctatissimus lives in simple burrows that have subsurface horizontal galleries. It inhabits clean, unvegetated, moderately saline, moist sand of the intertidal zone. The egg chamber is connected to the retreat burrow (Griffiths and Griffiths, 1983). This species probably stores no food. Other species, for example *caribbeanus,* may live in the intertidal zone and most of the species occur near the seacoast. The Chilean species, *maculipennis* and *puelches,* live inland and some inland records are known for species in northern Australia.

Gigantulus group. Some details of the natural history of this group are known for *salsus, tricornis,* and *spectabilis.* Both *spectabilis* and *tricornis* construct unbranched vertical burrows that include food and egg chambers (Larsen, 1936). *Bledius spectabilis* was reported to make burrows with a complex of branches (Paulian, 1941, 1942), or in the form of a sinuous loop (Evans et al., 1971). Both *spectabilis* and *tricornis* may store algae in the food chamber (Larsen, 1936). Wyatt (1982) also reported that *spectabilis* stores food but Paulian (1942) never observed that behavior. For *salsus* both unbranched and branched burrows are illustrated but nothing is written concerning its feeding behavior (Matsuzawa, 1964). The passages to the egg chambers of *spectabilis* and *tricornis* are loosely filled with sand. *B. tricornis* lives in densely vegetated meadows in soil of low salinity and moderately high water content, whereas *spectabilis* lives on unvegetated or vegetated moderately to highly saline soil with moderate water content. *B. tricornis* can live in highly saline soil. *B. spectabilis* lives in the intertidal zone (Larsen, 1936). Other species of the group, for example *tricornis, germanicus,* and *unicornis,* also are reported from saline habitats (Steel, 1955).

Annularis group. Larsen's (1936) study included four species of this group, namely *opacus, longulus, pygmaeus,* and *rastellus* (=*fuscipes*). They all excavated simple unbranched burrows that fork near the surface. They probably do not construct food chambers but do lay their eggs in small cavities. *B. rastellus* (=*fuscipes*) deposits its egg on top of a small cache of algae. After rainfall the four species accumulate small mounds of algae in the burrow. Their feeding burrows are the subsurface forks. They live in slightly to moderately vegetated loose sand that lacks salt and has low moisture. Larsen (1936) calls them xerophilous species. The North American species live in densely vegetated to unvegetated, wet to slightly moist sand near freshwater. Many species make horizontal subsurface burrows.

Armatus group. Many of the species of this group live in saline or alkaline soil; some live in soil devoid of appreciable evaporites. The soil may be vegetated or unvegetated and wet to moist. *B. ineptus, strenuus,* and *eximius* have been found with nine, five to six, and four to six eggs, respectively, in each egg chamber.

Habitat and geographical data for the above-cited groups and for all the species groups are summarized following the description of each in the section on Classification and Descriptions. Other information concerning the life history is unknown.

What more can be done with the existing data? Can a phylogeny be inferred or species groups characteristics be deduced? No, in my opinion. However, Larsen (1936) did speculate. She thought that xerophily in *Bledius* is a primitive condition and that burrows with food chambers and branches are more specialized that those without. Based on her natural history data, she concluded that *arenarius* (my *basalis* group) is the least specialized, that *taurus* (*furcatus* group), *spectabilis* and *tricornis* (*gigantulus* group), and *diota* (*kochi* group) are the most specialized, and that *longulus, pygmaeus,* and *rastellus* (*annularis* group) fall in between.

Larsen's hypotheses are based on the assumption that simple equals unspecialized or primitive and complex the opposite. But what does the sister taxon *Eppelsheimius* do? What is its natural history? If we are going to use characters of natural history, behavior, life cycle, etc., to deduce phylogeny, we must determine direction of change without a priori assumptions about polarity. The same methods used to assign character state polarity to anatomical characters should be used for other features.

Similarly, if we are going to treat features of the life cycle and behavior as taxonomic characters should we not study them in the same way we study anatomical ones? To determine anatomical limits of taxa we concern ourselves with, for example, individual, geographic, and abnormal variation as well as differences and similarities of groups. Do characters of the life cycles and behavior exhibit any less variation? Although investigating variation of anatomy is more readily accomplished than similar studies for behavior and natural history, that fact does not preclude the necessity of discovering that range for each character in order to define taxa.

PHYLOGENY

This chapter is divided into two parts. The first discusses structures of *Bledius,* some of which are used to support the phylogenetic hypotheses presented in the second part. The boldface numbers beside the character states in the section on morphology refer to the numbers and characters cited in tables 6 and 7 and the cladograms (figs. 41, 42). Table 6 summarizes the distribution of character states among species groups of *Bledius.* Table 7 describes each character state, gives its polarity, and refers to a figure that illustrates it.

MORPHOLOGY

Bledius is a large group of subcylindrical species that lack a neck (fig. 126), have "geniculate" antennae (fig. 296), prominent mandibles and eyes (fig. 126), expanded protibiae with many spinelike setae (figs. 59, 60), and a dehiscent elytral suture. The genus is easily recognized, so much so that few species of *Bledius* were described in other genera once the genus was segregated. Beyond this superficial uniformity is a wealth of anatomical diversity, some of it useful for classification and for supporting phylogenetic hypotheses.

In addition to *Bledius, Eppelsheimius* has a long first antennal segment. This configuration is often referred to as geniculate, which, strictly interpreted, is a misnomer. Geniculate antennae not only have a long first segment but the flagellum should flex forward from the first segment. In *Bledius* and *Eppelsheimius,* it flexes posteriorly. The first antennal segment is longest in the other oxyteline genera but this elongation is most pronounced in *Bledius* and *Eppelsheimius* and in *Bledius* reaches its maximum in some species of the *verres* group. Prominent eyes, common to all *Bledius,* are rare in other Oxytelinae.

The males of nearly a quarter of the species of *Bledius* have supraantennal horns (**1**). Females in two groups also have these horns (**3**). The other males and all females lack them as do species of other oxyteline genera. The form, number, and size of the horns vary. Males of the *rugosicollis* group and of *Bledius susae* (fig. 148) have small pointed bumps on the supraantennal ridge that represent reduced horns. The horns are dorsally directed (as for example in the *furcatus* group; fig. 207), anterodorsally directed (for example the *gigantulus* group; fig. 178), or anteriorly directed (as in some species of the *forcipatus* group; figs. 377–379). Most species possess one pair of horns; the four species of the *aequatorialis* group have two (fig. 157). The form varies. They may resemble rabbit ears (fig. 207), or be hatchetlike (*B. auriculicollis*), pointed (figs. 178, 378), apically truncate (fig. 377), or lamelliform (fig. 66). Some, perhaps all, of the horned species exhibit "major" and "minor" males. The major males are larger and more robust, with longer and larger horns; the minor males are correspondingly smaller.

The supraantennal ridge of some species of the *armatus* group are enlarged and robust, especially in the male, but there is no horn. Some males of the *verres* group have an elongate, tuberclelike supraantennal ridge at the end of which is the antennal insertion (fig. 473).

The males of the *bellicosus, compressicollis,* and *hamifer* groups have a midbasal cephalic horn (**2**) that varies in size and form. Such a horn is found nowhere else in *Bledius* or the Oxytelinae.

The head of the *bellicosus, compressicollis, hamifer, minax, circularis,* and *lamelliceps* groups and some species of the *aequatorialis* group has a postocular lateral carina (**4**; fig. 66) that is well developed in the male and weak in the female. The precursor of this carina may be the dorsal edge of a glabrous strip that extends posteriorly from the eye on the lateral side of the head of most species of *Bledius.* The development of this carina seems to be unique in the subfamily.

The anterior and lateral margins of the clypeus are reflexed (**5**) in three groups of species (fig. 66). The reflexion is well developed in the *lamelliceps* and *furcatus* groups and in some species of the *kochi* group; for some species of the latter group it is poorly developed. The character is unique in the subfamily.

Clypeal tubercles of the anterior margin, when present, are usually rounded, conical structures. In the *bispinus* group they are flattened and extend along the anterior margin

TABLE 6
Distribution of Character States in *Bledius* and *Eppelsheimius*[a]

Taxon, group	Character																										
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
mandibularis	–	–	–	–	–	+	–	–	+	–	–	–	+	–	–	b	+	b	+	–	–	+	–	+	–	–	b
bellicosus	+	+	–	+	–	–	–	–	–	–	–	+	–	–	–	–	+	a	+	–	–	–	–	+	–	b	–
compressicollis	+	+	–	+	–	–	–	–	–	+	?	?	?	?	?	?	+	?	?	?	?	?	?	?	?	b	a
hamifer	+	+	–	+	–	–	–	–	–	–	?	?	?	?	?	?	+	?	?	?	?	?	?	?	?	b	c
minax	+	–	–	+	–	–	–	–	–	+	?	?	?	?	?	?	+	?	?	?	?	?	?	?	?	b	–
aequatorialis	+	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	+	a	+	–	–	–	–	+	–	b	–
circularis	–	–	–	+	–	–	–	–	–	–	?	?	?	?	?	?	+	?	?	?	?	?	?	?	?	c	b
minniensis	–	–	–	–	–	–	–	–	–	–	?	?	?	?	?	?	+	?	?	?	?	?	?	?	?	–	b
rugosicollis	+	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	+	a	+	–	–	–	–	+	–	–	a
gigantulus	+	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	+	a	+	–	–	–	–	+	–	a	–
immaturus	+	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	+	a	+	–	–	–	–	+	?	–	–
furcatus	+	–	+	–	b	–	–	–	–	–	–	–	+	+	–	–	+	a	+	–	–	–	–	+	–	a	–
lamelliceps	+	–	+	+	b	–	–	–	–	–	–	–	+	+	–	–	+	a	–	–	–	–	–	+	–	a	–
kochi	+	–	–	–	b	–	–	–	–	–	–	–	+	+	–	–	+	a	+	–	–	–	–	+	–	c	–
emarginatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	c	–	–	–	+	–	–	–
lucidus	+	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	+	a	+	a	–	–	–	+	–	–	–
kosempoensis	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	+	a	+	a	–	–	–	+	?	–	–
semiferrugineus	–	–	–	–	–	–	–	–	+	–	–	–	+	–	–	–	+	a	+	a	–	–	–	+	–	–	–
armatus	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–
albonotatus	–	–	–	–	–	–	–	–	+	–	–	+	–	–	–	–	+	–	+	a	–	–	–	+	–	–	–
annularis	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	+	–	+	c	–	–	–	+	–	–	–
debilis	–	–	–	–	–	–	–	–	–	–	+	+	–	–	–	a	+	–	+	a	–	–	–	+	?	–	–
basalis	–	–	–	–	–	–	–	–	–	+	+	+	–	–	–	a	+	–	+	a	–	–	+	+	–	–	–
infans	–	–	–	–	–	–	–	–	–	–	?	?	?	?	?	?	+	?	?	?	?	?	?	?	?	–	c
fratellus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	a	+	–	+	–	+	+	–	–	–	–	–
forcipatus	+	–	–	–	–	–	–	–	–	–	–	+	–	–	–	a	+	–	–	–	+	+	–	–	–	–	c
punctatissimus	–	–	–	–	–	–	–	+	–	–	–	+	–	–	–	a	+	–	+	–	+	+	–	–	–	–	–
lugubris	–	–	–	–	–	–	–	–	–	–	?	?	?	?	?	a	+	?	?	?	?	?	?	?	?	–	–
angustus	–	–	–	–	–	–	–	–	–	+	–	+	–	–	–	a	+	a	–	–	+	+	–	–	+	–	b
bispinus	–	–	–	–	a	–	–	–	+	–	?	?	?	?	?	?	+	?	?	?	?	?	?	?	?	–	–
tibialis	–	–	–	–	a	–	–	–	+	–	–	+	–	–	–	a	+	–	+	b	+	+	–	–	–	–	a
pulchellus	–	–	–	–	–	–	–	–	+	+	–	+	–	–	–	a	+	–	+	c	+	+	–	–	–	–	b
bonariensis	+	–	–	–	–	–	+	+	+	–	–	+	–	–	–	a	+	–	–	a	+	+	–	–	–	–	–
verres	–	–	–	–	–	–	–	–	+	–	–	+	–	–	–	a	+	–	+	c	+	+	–	–	–	–	–
Eppelsheimius	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+	a	–	–	–	–	–	–	–	–	–

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[a] The minus sign (–) refers to the character states in the left column of table 7; the +, a, b, c, e refer to the character states in the right column of table 7.

TABLE 6—(*Continued*)

Taxon, group	Character																									
	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53
mandibularis	+	+	a	−	b	a	−	−	−	−	+	−	−	a	−	−	−	−	−	−	+	−	−	a	−	+
bellicosus	−	−	a	−	b	a	+	−	−	+	+	−	+	a	+	−	−	−	−	−	+	−	−	a	−	+
compressicollis	−	−	a	−	?	?	?	?	?	+	+	−	+	a	+	−	−	−	−	−	?	?	?	?	?	?
hamifer	−	−	a	−	?	?	?	?	?	+	+	−	+	a	+	−	−	−	−	−	?	?	?	?	?	?
minax	+	−	a	−	?	?	?	?	?	+	+	−	+	a	+	−	−	−	−	−	+	−	−	a	−	+
aequatorialis	−	−	a	−	b	a	+	−	−	+	+	−	+	a	+	−	−	−	−	−	+	−	−	a	−	+
circularis	+	−	a	−	?	?	?	?	?	−	+	−	+	a	+	−	−	−	−	−	+	−	−	a	−	+
minniensis	−	−	a	−	?	?	?	?	?	−	?	−	+	a	−	−	+	−	−	−	+	−	−	?	−	+
rugosicollis	−	−	a	−	b	a	−	−	−	−	+	−	+	a	−	−	+	−	−	−	+	−	−	a	−	+
gigantulus	−	−	a	−	b	a	−	−	−	−	+	−	+	a	−	−	+	−	−	−	+	−	−	a	−	+
immaturus	−	−	a	−	?	?	?	?	?	−	+	−	+	a	−	−	+	−	−	−	+	−	−	a	−	+
furcatus	−	−	a	−	b	a	−	−	−	−	+	−	+	a	−	−	+	−	−	−	+	−	−	a	−	+
lamelliceps	−	−	a	−	a	a	−	−	−	−	+	−	+	a	−	−	+	−	−	−	+	−	−	a	−	+
kochi	−	−	a	−	a	a	−	−	−	−	+	−	+	a	−	−	+	−	−	−	+	−	−	a	−	+
emarginatus	−	−	a	−	a	a	−	−	−	−	+	−	+	a	−	−	−	−	−	−	+	−	−	a	−	−
lucidus	+	−	a	−	a	a	−	−	−	−	+	−	+	a	−	−	−	−	−	−	+	−	−	b	−	−
kosempoensis	+	−	a	−	a	a	−	−	−	−	+	−	+	a	−	−	−	−	−	+	+	−	−	b	−	−
semiferrugineus	+	−	a	−	a	a	−	−	−	−	+	−	+	a	−	−	−	−	−	−	+	−	−	b	−	−
armatus	+	+	a	−	a	a	−	−	−	−	+	−	+	a	−	−	−	−	+	−	+	−	−	b	−	−
albonotatus	−	−	b	−	b	b	−	a	−	−	+	−	+	a	−	−	−	−	−	−	+	−	−	b	−	−
annularis	−	−	b	−	b	b	−	a	−	−	+	−	+	a	−	−	−	−	−	−	+	−	−	b	−	−
debilis	+	−	b	−	b	b	−	a	−	−	+	−	+	a	−	−	−	−	−	−	+	−	−	b	−	−
basalis	+	+	b	−	b	b	−	a	−	−	+	−	+	a	−	−	−	+	−	−	+	+	−	b	+	−
infans	−	+	b	−	?	?	?	?	?	−	−	+	−	b	−	a	−	+	−	−	+	+	+	e	−	−
fratellus	−	−	b	−	b	b	−	a	+	−	−	+	−	b	−	a	−	+	−	−	+	+	+	e	−	−
forcipatus	−	−	b	−	b	b	−	b	−	−	+	+	−	b	−	−	−	+	−	−	+	+	+	e	−	+
punctatissimus	−	−	b	+	b	b	−	a	−	−	−	−	−	b	−	−	−	+	−	−	+	+	−	d	+	−
lugubris	+	−	b	−	?	?	?	?	?	−	?	+	?	b	−	?	−	−	−	?	?	?	?	?	?	?
angustus	+	+	b	−	b	b	−	a	−	−	+	−	+	b	−	−	−	−	−	−	+	−	−	a	−	−
bispinus	−	−	b	−	?	?	?	?	?	−	?	−	−	a	−	−	−	−	−	−	+	−	−	d	−	−
tibialis	−	−	b	−	b	b	−	a	?	−	−	−	+	a	−	−	−	−	−	−	+	+	−	c	−	−
pulchellus	−	−	b	−	b	b	−	a	+	−	+	−	−	b	−	b	−	+	−	−	+	+	+	d	−	−
bonariensis	+	+	b	+	b	b	−	b	?	−	−	−	+	b	−	−	−	+	−	−	+	−	−	e	−	−
verres	−	−	b	−	b	b	−	a	+	−	−	−	−	b	−	−	−	+	−	−	+	−	+	d	−	−
Eppelsheimius	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−

TABLE 7
Character State Polarity in *Bledius*

	Plesiomorphic (−)	Apomorphic (+)
1	Supraantennal horn absent—male (fig. 392)	Supraantennal horn present—male (figs. 125, 157, 188, 207, 214, 224, 377–379, 441)
2	Head without midbasal horn—male	Head with midbasal horn—male (figs. 125–127)
3	Supraantennal horn absent in female	Supraantennal horn present in female (figs. 201, 212, 218)
4	Head without postocular lateral carina	Head with postocular lateral carina (fig. 66)
5	Clypeal margin not reflexed and tubercles cylindrical or absent	a. Clypeal tubercles flattened and broad and joined or tending to join medially to form carina on anterior margin b. Clypeal margin reflexed (fig. 66)
6	Submentum unmodified	Submentum excavated (figs. 117–120)
7	Head without subantennal pockets	Head with pocket under each antennal base that extends into head capsule (figs. 176, 441)
8	Gular sutures fused anteriorly (fig. 380)	Gular sutures separated anteriorly (figs. 395–397, 446)
9	Labrum fused medially (fig. 168)	Labrum with midlongitudinal incision (fig. 304)
10	Labral margin not reflexed	Labral margin reflexed (fig. 338)
11	Epipharynx with apically lobed median cuticular processes (fig. 288)	Epipharynx with clavate median cuticular processes (figs. 54, 330, 341)
12	Epipharyngeal lobe short (fig. 288)	Epipharyngeal lobe long and broad (fig. 391)
13	Epipharynx with numerous slender cuticular processes on lateral side (fig. 391)	Epipharynx with few thick, multiramous cuticular processes on lateral side (fig. 191)
14	Galea with dense cluster of setae of equal thickness on apex	Galea with some stouter setae on apex
15	Galea without setae on ventral surface	Galea with setae on ventral surface
16	Labial palps with segments of nearly equal length (fig. 190)	a. Labial palps with second segment shortest (fig. 361) b. Labial palps with second segment longest (fig. 115)
17	Hypopharyngeal disk without central row of setae (figs. 67–69)	Disk with central rows of spinelike setae (figs. 492, 509, 514, 557, 591)
18	Hypopharyngeal disk without setae (fig. 514)	a. Disk with setae (fig. 497) b. Disk with many setae (figs. 485, 488)
19	Hypopharyngeal disk without cuticular processes (figs. 509, 566)	Disk with cuticular processes (figs. 487, 493, 515, 536)
20	Hypopharyngeal cuticular processes scattered or in loose clusters (figs. 499, 541)	a. Cuticular processes arranged in palmate clusters (figs. 515, 522, 536, 547) b. Cuticular processes arranged in rows (figs. 575, 576) c. Cuticular processes of palmate cluster fused to form lobe (figs. 515, 599)
21	Hypopharyngeal lateral rows of setae widely separated and gradually convergent (figs. 491, 502, 512, 520)	Lateral rows of setae narrowly separated and strongly convergent (figs. 566, 572, 578, 595)
22	Hypopharyngeal basal setae arranged in row (figs. 505, 514, 520)	Basal setae arranged in cluster (figs. 554, 560, 564, 572, 582, 594)
23	Hypopharyngeal basal setae numerous	Basal setae reduced to two (figs. 548–552)
24	Hypopharyngeal basal setae slender, of nearly same diameter as those of central row (figs. 554, 561, 582)	Basal setae thick, much thicker than those of central row (figs. 491, 505, 521, 531, 552)
25	Hypopharyngeal coronal peg with central peg and coronal of equal length (figs. 518, 565, 576)	Coronal peg with central peg extending beyond corona with appearance of long seta (figs. 561–563)
26	Pronotal horn absent—male	a. Pronotal horn straight (figs. 182, 203) b. Pronotal horn deflexed (figs. 131, 145) c. Pronotum with anterior margin tumescent
27	Pronotal marginal bead complete and dividing notum and hypomeron (figs. 182, 228)	a. Pronotal marginal bead on hypomeron (fig. 169) b. Pronotal marginal bead incomplete (figs. 116, 458) c. Pronotal marginal bead absent (figs. 382, 417)
28	Procoxal fissure open (fig. 145)	Procoxal fissure closed (fig. 252)
29	Protergosternal suture present (fig. 252)	Protergosternal suture absent (fig. 339)

TABLE 7—(*Continued*)

Plesiomorphic (−)	Apomorphic (+)
30 Prosternum with setae scattered (figs. 91, 642)	a. Prosternum with setae clustered in or near depression (figs. 601, 616) b. Prosternum with setae clustered in or near pit (figs. 672, 678, 690)
31 Prosternal setae slender and cylindrical (fig. 655)	Prosternal setae broad and flattened (figs. 699, 700, 723)
32 Prosternal secretory pores scattered over surface (figs. 643, 646)	a. Secretory pores arranged in several clusters (figs. 638, 641) b. Secretory pores arranged in one cluster (figs. 609, 611, 620, 717)
33 Prosternal secretory pores on flat surface (figs. 642, 645)	a. Secretory pores in impression (figs. 616, 617, 622–624) b. Secretory pores in well-defined pit (figs. 672, 675, 691, 698, 708, 725, 726)
34 Prosternal secretory pores not behind ridge (figs. 602, 615)	Secretory pores behind ridge (figs. 608, 609, 620)
35 Prosternal secretory pores separated from setae (figs. 602, 611, 623, 624)	a. Secretory pores adjacent to setae (figs. 657, 664) b. Secretory pores among setae (figs. 695, 723)
36 Prosternal secretory pore not surrounded by collar (figs. 662, 665)	Secretory pores each surrounded by collar (figs. 717, 727)
37 Prosternal margin entire (figs. 169, 181)	Prosternal margin notched anterior to procoxae (figs. 131, 145)
38 Prosternal process short and carinate (figs. 363, 399, 400, 434)	Prosternal process elongate and broad (figs. 180, 181)
39 Elytral epipleural ridge complete (fig. 297) or incomplete (figs. 250, 414)	Elytral epipleural ridge absent
40 Elytra without membranous lobe on posterior margin	Elytra with membranous lobe on posterior margin (fig. 290)
41 Tarsi five segmented	a. Tarsi four segmented b. Tarsi three segmented
42 Protibia with one or two rows of spinelike setae and other scattered between	Protibia with three rows of spinelike setae
43 Metatibia with setae gradually tapered to one apex	a. Metatibia with some setae bifid at apex (fig. 366) b. Metatibia with some setae flattened and expanded toward apex
44 Tergum VII with fine fringe on posterior margin (fig. 55)	Tergum VII with coarse setiform fringe at middle of posterior margin (fig. 57)
45 Tergum VIII with emarginate posterior margin (fig. 344)	Tergum VIII with truncate posterior margin (fig. 477)
46 Tergum VIII with posterior margin entire (fig. 344)	Tergum VIII with posterior margin serrate or serrulate (figs. 298, 299)
47 Tergum IX tapered to apex on each side (fig. 478)	Tergum IX with each apex lobed (fig. 262)
48 Sternum IX (female) with coxites and valvifers differentiated (Herman, 1983b, fig. 33)	Sternum IX (female) with pair of elongate sclerites, valvifers and coxites not separate sclerites (fig. 401)
49 Tergum X (female) with struts on anterior margin (fig. 418)	Tergum X (female) without struts on anterior margin (fig. 437)
50 Glandular canal of genital segments open dorsally (fig. 437)	Glandular canal of genital segments closed dorsally (figs. 387, 478)
51 Paramere long and stout, median surface sclerotized and apex rounded (Herman, 1983b, fig. 32)	a. Paramere long and slender, median surface sclerotized and apex rounded (figs. 122, 183, 204, 415) b. Paramere long and broad, median surface membranous, and apex rounded (figs. 263, 276, 308) c. Paramere long and stout, median surface sclerotized, apex truncate (fig. 432) d. Paramere short and slender, median surface sclerotized, apex rounded (figs. 402, 461, 476) e. Parameres absent (figs. 354, 369, 383, 451)
52 Spermatheca with bipartite receptacle, each	Spermatheca with long slender membranous receptacle (fig. 403)

TABLE 7—(*Continued*)

	Plesiomorphic (−)	Apomorphic (+)
	end sclerotized and connected together by membranous tube (figs. 137, 195, 265, 320, 435)	
53	Spermatheca lightly sclerotized and tripartite	Spermatheca strongly sclerotized and tripartite

as a carina and in at least one species the carinae join medially forming a cariniform ridge on the anterior margin (**5**). Species of the *tibialis* have a similar cariniform ridge on the anterior clypeal margin. The ridge is unique in the Oxytelinae.

The submentum of the *mandibularis* group is excavated (**6**). The excavation is of varied form (figs. 117–120) and found nowhere else in the subfamily. The function is unknown.

The males of the *bonariensis* group have deep pits (fig. 152) beneath the antennal insertion (**7**). These pockets, also present but smaller in the female, are unique. The function is unknown.

For all species of *Bledius* the gular sutures are separated at the base of the head and, for most species, fused from there to the submentum. For some species of the *punctatissimus* group the sutures are separated from the submentum posteriorly (**8**); the length of the separation varies (figs. 395–397). This particular configuration of the separation of the gular suture is unique in the Oxytelinae in which the separation or confluence of the sutures is variable.

The labrum of 10 species groups (table 6) of *Bledius* is midlongitudinally divided (**9**; fig. 466). This incision is feebly developed in a few species of the *gigantulus, furcatus,* and *kochi* groups. The labrum remains fused at the base for all species of *Bledius* that have this incision. At least six genera of the Oxytelinae (including *Blediotrogus, Pareiobledius, Carpelimus, Apocellagria, Aploderus, Trogactus,* and *Thinodromus* and probably several others not presently available for study) have a medially divided labrum but in each of these genera the division is complete—the labrum is separated into two parts. This complete versus partial separation suggests independent origin of the incision. Other genera of the Oxytelinae lack the median incision. All but one species of the *basalis* group have a reflexed anterior labral margin (**10**; fig. 338). This character is distinctive in this group. In four other groups (*compressicollis, minax, angustus,* and *pulchellus* groups) the labral margin is feebly reflexed.

The clavate, apically rounded median cuticular processes of the epipharynx (**11**) are unique to the *basalis* (fig. 54) and *debilis* groups (fig. 330). In other species groups and oxyteline genera these processes are lobed apically. The epipharynx of most *Bledius* and most other Oxytelinae is short (fig. 112). For 11 species groups (table 6) and probably three others (that were not dissected), the epipharynx is extended into a long, broad lobe (**12**). The epipharynx of *Manda* and *Planeustomus* and one of *Eppelsheimius* is long and slender. The epipharyngeal enlargement of *Bledius* seems to be independent. The thick multiramous cuticular processes on the epipharynx (**13**) and the stout setae on the apex of the galea (**14**) seem to be unique to some groups of *Bledius.* The ventral surface of the galea has a small patch of setae (**15**) in the *lucidus* group of *Bledius* that is probably independently derived and is dissimilar to the row of spinelike setae on the ventral surface of the galea in *Eppelsheimius.*

The length of the segments of the labial palps are of subequal length (fig. 173) in most of the subfamily. In 11, perhaps 14, species groups of *Bledius* (table 6), the second segment is notably shorter than the others (**16**; fig. 115). In the *mandibularis* group the second segment is longer than the others (**16**).

The hypopharynx of *Bledius* is more variable than in other genera of the subfamily but further investigation is needed. Some of the intrasubfamilial variation is shown in figures 67–74 and 76–78. *Oxypius* was illustrated by Newton (1982) and *Eppelsheimius* by Herman (1983b). The hypopharynx in the Oxytelinae consists of broad bilobed structure. Extending from each lobe is a lateral row of spinelike setae that converge posteriorly (fig. 67). Between the proximal ends of these lateral rows of setae is a transverse row or cluster of spinelike setae (fig. 68). The region enclosed by these rows of spinelike setae is the disk which is divided into the central region (fig. 69) and the lateral lobes (fig. 70). On the disk are coronal pegs (fig. 72), cuticular processes, and setae (fig. 71) and in *Bledius* and *Eppelsheimius* a central row of spinelike setae (fig. 509).

One of the more curious structures on the hypopharynx is that resembling a peg in a donut (fig. 78). First illustrated by Herman (1972), it was referred to later as a *sensillum basiconicum* by Hammond (1976), *basiconic* peg by Bellamy and Zucharuk (1976), coronal peg by Doane and Klingler (1978), and mechanosensory nipple by Hallberg (1982). This structure is on the hypopharynx of at least some other oxyteline genera besides *Bledius,* and probably on the apex of the labial and/ or maxillary palps (figs. 49, 50) of all staphylinids, perhaps all beetles. Figure 54 shows coronal pegs on the dorsal surface of the pharynx. Figures 649 to 652 illustrate minute prosternal structures (note magnification) that resemble coronal pegs. Hallberg (1982) suggested that this structure is a mechanoreceptor. Doane and Klingler (1978) considered it improbable that coronal pegs are chemoreceptors for CO_2. The suggested function of this structure seems to have been arrived at by surmise, rather than experimentation. However, it should be noted that classification of most small sensilla is based on histological studies that reveal the thickness of the integumentary wall and its porosity (Zacharuk, 1980). I refer to the structure as a *coronal peg* since that term implies no function.

Coronal pegs are on the hypopharynx of all species of *Bledius, Eppelsheimius, Manda* (figs. 73, 74), *Deleaster* (figs. 76–78), *Platystethus* (figs. 70–72), and *Apocellus* (figs. 67, 68) that were examined. Other oxyteline genera were not examined. Within *Bledius,* the density, position, and number varies among species groups. In the *mandibularis* group they are found only in a small denuded patch near the apex of the disk near the central row of setae (figs. 485, 486). By contrast, coronal pegs are found widely over the surface of the disk in the *annularis* (fig. 521), *albonotatus* (fig. 547), *emarginatus* (fig. 518), and *verres* (fig. 599) groups. They are scattered sparsely on the disk in the *armatus* group. In the *kochi* (fig. 503), *gigantulus* (fig. 506), *furcatus* (fig. 498), *lamelliceps* (fig. 510), *bellicosus* (fig. 493), *aequatorialis* (fig. 495), *semiferrugineus* (fig. 533), and *armatus* (fig. 542) groups, coronal pegs are on the central portion of the disk near the central row of spines; the number and density vary. The coronal pegs are restricted to a narrow strip beside the central row of setae or are among these setae in the *bonariensis* (fig. 581), *basalis* (fig. 551), *forcipatus* (fig. 557), *punctatissimus* (fig. 588), *angustus, tibialis* (fig. 575), *fratellus,* and *pulchellus* groups. The peg of the coronal peg extends beyond the top edge of the corona in only the *mandibularis* (slightly; fig. 486), the *forcipatus* (slightly; fig. 565), and *angustus* (strongly; figs. 561–563) groups. In the *angustus* group the peg is so long that is resembles a seta or cuticular process (**25**).

Cuticular processes (**19**) are on the central, lateral, or anterior regions of the disk in every group examined except *forcipatus* and *angustus.* The cuticular processes are in linear clusters (**20**) of about three or more (figs. 500, 501, 504, 546) in all groups examined except evidently the *mandibularis* and *lamelliceps* group in which they occur singly. The processes of these linear clusters are loosely associated in the *kochi, gigantulus, furcatus, rugosicollis, bellicosus,* and *aequatorialis* groups. They occur as palmate clusters (fig. 546) in the *armatus, semiferrugineus, lucidus, albonotatus, pulchellus,* and *punctatissimus* groups and in some species of the *emarginatus, annularis,* and *verres* groups. In other species of the *emarginatus, annularis,* and *verres* groups the individual processes of the palmate cluster have evidently fused to form a tonguelike lobe (fig. 522). See figure 515 where all of the cuticular processes are tonguelike lobes except one which is a palmate cluster. In the *basalis* (fig. 549) and *fratellus* (fig. 556) groups the palmate cluster of cuticular processes arises from a plaquelike structure. In the *tibialis* group the separate palmate clusters have become linear rows (fig. 576) adjacent to the central row of setae.

Variation of the size of the disk depends on the relative proximity of the two lateral rows of spinelike setae (**21**). For almost all of the species groups of *Bledius* and for all other genera of the Oxytelinae (figs. 67–74, 76–78) examined, the disk occupies nearly the entire surface of the hypopharynx. For the *bonariensis* (fig. 578), *angustus* (fig. 560), *forcipatus* (fig. 566), *punctatissimus, tibialis* (fig. 572), *fratellus* (fig. 554), *verres,* and *basalis* (fig. 550) groups the disk is narrow and restricted to the anterior margin and midlongitudinal region of the hypopharynx, and the lateral rows of spinelike setae converge strongly.

Basal setae (**22**) are arranged in a large cluster (fig. 554) or in a transverse row (fig. 491) between the proximal ends of the two lateral rows of setae. The basal setae may be distinguished from the lateral rows and setae of the disk by thickness and/or density, or be identical to the discal and lateral setae. *Deleaster* (figs. 76, 77) has a dense cluster of setae that are the same size as those of the lateral row. *Manda* (fig. 73) has a transverse row that is continuous with the lateral row. *Apocellus* (fig. 68) has a transverse row of thick setae. *Eppelsheimius* has basal setae that are slightly thicker than those of the lateral and central rows. Within *Bledius* the basal setae are thick and peglike in contrast to the slender setae of the lateral rows. The basal setae are represented by a transverse row in the *kochi, gigantulus* (fig. 513), *lamelliceps, bellicosus* (fig. 491), *rugosicollis* (fig. 499), *aequatorialis, annularis, emarginatus* (fig. 517), *armatus, albonotatus, lucidus, kosempoensis,* and *semiferrugineus* (fig. 531) groups. The basal setae of these groups are especially stout (**24**). The *mandibularis* (figs. 485, 488) group also with notably massive basal setae are arranged in a transverse cluster. The *verres, angustus* (fig. 560), *forcipatus* (fig. 564), *punctatissimus* (fig. 584), *fratellus* (fig. 554), *pulchellus, bonariensis* (fig. 578), and *tibialis* (fig. 572) groups have a basal cluster of setae that are thicker than those of the lateral row but more slender (**24**) than the basal setae of the 14 species groups cited above. The *basalis* group has a pair (**23**) of exceptionally enlarged setae (fig. 548) in place of a basal cluster or row.

Among the Oxytelinae, only *Bledius* and *Eppelsheimius* have a midlongitudinal row of setae on the disk (**17**). The central region of the disk can have a single row (*bonariensis,* fig. 578; *fratellus,* fig. 557; *tibialis,* fig. 572) or a continuous (most of the species group, figs. 505, 509) or interrupted linear cluster (*bellicosus,* fig. 492; *parcissimus,* fig. 517; *chilensis,* fig. 514; *actitus,* fig. 566). The central row of spines is confined to the anterior discal margin in some species of the *verres* and *kochi* groups. At least one species of the *punctatissimus* group has compound setae in the central row (fig. 589).

The basal setae of the species groups with a transverse basal row are significantly more massive than those of the central row (fig. 509). The basal setae of most species groups with a basal cluster are nearly the same thickness as those of the central row (fig. 564).

In addition to the lateral, basal, and central rows of setae, the disk may have other setae scattered over the surface. For purpose of discussion they are named discal setae. *Apocellus* (fig. 68) and *Platystethus* (fig. 71) have two rows of short thick setae, *Aploderus* (fig. 69) has similar such setae scattered over the surface, and *Deleaster* (fig. 77) and *Manda* (fig. 74) lack these discal setae. The discal setae of *Eppelsheimius* are slender. Within *Bledius,* discal setae (**18**) are found in the *kochi, gigantulus, bellicosus, aequatorialis, mandibularis, lamelliceps, furcatus, rugosicollis, lucidus,* and *semiferrugineus* groups. Species of the *mandibularis* group are exceptional in that the disk is densely covered by setae (**25**; fig. 485). Species of the *angustus, fratellus, forcipatus, basalis, punctatissimus,* and *bonariensis* groups have discal setae only along the anterior margin.

In summary, the general features of the hypopharynx of *Bledius* include the presence of two lateral rows and a group of basal setae that are thicker than those of the lateral row and are arranged in a cluster or a transverse row. The disk has a central row of setae that are more slender than or as thick as the setae of the basal group. The disk has coronal pegs and may have cuticular processes and discal setae; each of these three features varies. No hypopharyngeal structure is unique to *Bledius.* The central row of setae, however, is found only in *Bledius* and *Eppelsheimius.*

Eppelsheimius has two lateral rows of setae and a larger cluster of basal setae that is continuous with the numerous setae of the central row. The lateral, basal, and central groups of setae are all of about the same length and diameter. The disk has scattered discal setae, some coronal pegs near the central row of setae, and lacks cuticular processes on the disk (Herman, 1983b, figs. 3, 4).

Herman (1972) illustrated on the fourth segment of the maxillary palpus of adult *Bledius* (and present in adults of other oxyteline genera) a series of pegs in grooves referred to as a chordotonal organ (Hammond, 1976), or digitiform organ or sensillum (Bellamy, 1973; Zacharuk et al., 1977; Honomichl, 1980). Digitiform sensilla are widespread in the Staphylinidae on the maxillary palpus. In species with an enlarged fourth segment, the peg-groove components of the sensillum are widely distributed over the surface and form a variety of patterns. Species with an enlarged fourth segment have an arc-shaped digitiform sensillum (figs. 43, 44), those with a conical or aculeate fourth palpal segment have a fan-shaped digitiform sensillum (figs. 45–47, 53), and in species with slender, acicular fourth palpal segment the sensillum is at the apex of the third segment (for example, *Thinodromus, Xerophygus, Carpelimus,* and *Parosus*). Digitiform sensilla may be widespread in Coleoptera and can be on either the maxillary or labial palps of adults and/or larvae. Bellamy (1973) suggested the organ functioned as a vibratory receptor. Later, in a more detailed analysis, Zacharuk et al. (1977) described and illustrated the sensillum, noting that the entire peg may be extended outward from the groove naturally or by external manipulation (see also figs. 47 and 48 for *Aploderus*). These authors stated that electrophysiological results indicate that the digitiform pegs respond only to mechanostimulation despite the presence of a subapical pore which is typical of some chemoreceptors. To them the digitiform sensillum is neither a typical mechanoreceptor or chemoreceptor but has characteristics of both. They believed that the subapical pore is a molting scar and that the sensillum is a vibratory receptor that receives stimuli from the substrate. If true, then how are the stimuli received; must the pegs be in contact with the substrate? By contrast, other investigators disputed the vibratory function and suggested that the digitiform sensilla function not as mechanoreceptors, but as receptors of temperature, humidity, or carbon dioxide (Honomichl, 1980; Honomichl and Guse, 1981).

The prothorax exhibits considerable variation in form and structure, including pronotal armature, sutures, carinae, pits, procoxal fissure, furcasternum, punctation, pubescence, and sculpturing. The shape, punctation, vestiture, and sculpturing, major examples of which were illustrated by Herman (1972, 1976, 1983a), are principally useful for species identification and there tend to be variations of a theme for each character in any given species group. A few of numerous examples include the shape of the prothorax within the *mandibularis, forcipatus, angustus,* and *verres* groups. The punctation is coarse in most species of the *semiferrugineus* group and fine for the *punctatissimus* group. The pronotum of species of the *punctatissimus* group is densely pubescent. Species of eight species groups (table 6) have a pronotal horn (**26**) that may be straight (*gigantulus, furcatus,* and *lamelliceps* groups) or deflexed (**26**) (*bellicosus, minax, aequatorialis, hamifer,* and *compressicollis* groups), thick or slender, long or short. The males of these eight groups possess the horn; only one female, *B. susae* of the *aequatorialis* group, has a distinct, slender pronotal horn (see Herman, 1983a) and the females of at least some species of the *lamelliceps* group have a short broad process on the anterior pronotal margin (fig. 217). The size of the horn varies in males—major males have longer, thicker horns and the prothorax is more robust and more convex than in the smaller, more delicate-looking minor males. One group of species, the *kochi* group, which is related to species with pronotal horns, has a median tumescence (**26**) in place of the horn. Pronotal horns are uncommon in staphylinids.

A carina, designated as the pronotal lateral marginal bead, normally divides the pronotum from the prohypomeron, that is, it is at the bend of the notum and hypomeron. The marginal bead is below this bend, on the hypomeron (**27**) in the *compressicollis, rugosicollis,* and *tibialis* groups. The marginal bead may be present and complete, separated or partially present (**27**), or absent (**27**). The hypomeron has an incision, the procoxal fissure, that when open reveals the protrochantin but when closed (**28**) conceals it. Dividing the hypomeron from the prosternum is a ridge, the prosternal suture, that is absent (**29**) in species of seven groups. The open procoxal fissure and presence of the marginal bead and prosternal suture are plesiomorphic in the Oxytelinae (Herman, 1970; Newton, 1982). Both the generalized and derived states of these three characters are scattered throughout the species groups of *Bledius.*

Unique to *Bledius* is a prosternal pit (**33**) anterior to the procoxa that is packed with setae, pores, and cuticular processes. This prosternal pit occurs in about half of the species groups of *Bledius.* The pit (fig. 75) is replaced in most other groups by a depression (**33**) and in a few groups the prosternal surface anterior to the procoxa is flat (fig. 648). Whether in a pit or depression or on a flat surface, one or more clusters of pores are common to all *Bledius. Eppelsheimius* (figs. 103–108), *Deleaster* (figs. 79–81), *Homalotrichus* (figs. 82–84), *Aploderus* (figs. 85–87), and *Anotylus* (figs. 88–90) have scattered pores that are not clustered together and lack a pit, depression, and concentration of setae. *Blediotrogus* (figs. 91–93), *Carpelimus* (figs. 97–99), and *Thinodromus* (figs. 100–102) have a series of small clusters of pores near a ridge that extends along the anterior margin of the pronotum; they lack a pit, depression, and concentration of setae. *Ochthephilus* (figs. 94–96) evidently lacks pores.

In the Oxytelinae there may be (at least) two independent developments toward clustering of these prosternal pores, one in genera related to *Carpelimus* and one in *Bledius.* Within *Bledius* the *semiferrugineus* (figs. 642–644), *emarginatus* (figs. 631–635), and *armatus* (figs. 648, 649, 653) groups have the pores arranged in scattered, loosely organized clusters (**32**) on an unimpressed or slightly impressed surface (**33**). In the *kosempoensis* (figs. 636–638) and *lucidus* (figs. 639–641) groups the pores are in several closely associated groups in a shallow depression. Each of these five species groups have setae scattered in a broad patch surrounding the pores (**30**). In the *mandibularis* (figs. 604–606), *gigantulus* (figs. 601–603), *rugosicollis* (figs. 613–615), *kochi, furcatus* (figs. 616–618), *lamelliceps, aequatorialis* (figs. 607–612), and *bellicosus* groups the pores are grouped in a tight cluster (**32**) in a depression (**33**). This cluster of pores is behind a ridge in the *aequatorialis* (figs. 609–611) and *bellicosus* (figs. 620, 621) groups. The prosternal setae of these eight groups form a broad, sparse patch behind the depression. In the *annularis* and *albonotatus* groups (figs. 654–665) the pores are in a dense cluster in a well-defined depression or moderately developed pit (**32, 33**). Associated with this pit/depression is a cluster of setae (**30**). The *basalis, debilis, tibialis, bonariensis, forcipatus, verres, fratellus, pulchellus, punctatissimus,* and *angustus* groups all have a dense cluster of setae in a moderately to well-developed pit. The pores are behind and/or among the clustered setae. The setae (**31**) of the *punctatissimus* and *bonariensis* groups are broad and flat. The pores in the *verres, fratellus* (fig. 688), and *pulchellus* groups are each surrounded by a lip or ridge (**36**). The pores of the *punctatissimus* (fig. 700) and *angustus* (fig. 706) groups have associated processes and ridges. Raspberry-like structures of unknown function are found near the pit in the *basalis* (figs. 680, 681) and *debilis* groups and in the pit among the pores in the *fratellus* and *punctatissimus* (figs. 700, 701) groups. The prosternum of *Bledius bellicus* has what appears to be a cluster of minute coronal pegs (figs. 649–652).

The prosternal pores are probably the external openings of secretory structures in the prothorax. Figures 612 and 633 support this premise; they each illustrate strands extending from the pores. The strands likely represent chemicals that were being secreted as the animal died. The clustering of the prosternal secretory pores is evidently a means of bringing the secretion to one place. The development of a depression or pit seems to permit a further garnering of the chemical. The setae associated with the pore may be a means of bringing the chemical from the surface. The clustering of setae might function to wick the chemical away from the body. In this regard it should be noted that when the setae are arranged in a tight cluster the secretory pores are closely associated with the setae (**35**).

Apparently unique to *Bledius* is the notch on the anterior prosternal margin in front of the procoxa (**37**); this notch is present in five species groups (table 6). The furcasternum has a prosternal process extending between the procoxae that is short to moderately long and cariniform to long, and ventrally curved (**38**). Other oxytelines either lack a distinct prosternal process or it is short and cariniform (figs. 79, 82, 85, and 103).

The elytral feature most characteristic of *Bledius* is the dehiscent elytral suture which is also found in *Eppelsheimius, Thinobius,* and some *Platystethus.* The epipleural ridge, common in most Oxytelinae, is absent (**39**), in the *infans, fratellus, forcipatus,* and *lugubris* groups and some species of the *angustus* group. The ridge is incomplete in some groups (figs. 114, 250). The posterior elytral margin of most species groups of *Bledius* has a small membranous lobe (**40**). A similar membranous lobe is found in *Planeustomus, Blediotrogus, Pareiobledius, Xerophygus, Thinodromus,* and some *Carpelimus.*

The tarsi of most *Bledius* have four segments (**41**), those of nine groups (table 6) have three (**41**). The plesiomorphic condition in the Oxytelinae is five segmented. Some large tropical species of the *verres* group have a faint, incomplete suture on the basal tarsomere that appears to be an incompletely separated fourth segment.

Bledius has expanded protibiae armed with numerous spinelike setae (**42**) of which there may be one, two (fig. 58), or three (fig. 60) rows. Most species have one or two rows with other spinelike setae scattered over the surface. Six species groups (table 6) have three rows (**42**). In the Oxytelinae only *Bledius* and *Eppelsheimius* have strongly expanded, spinous protibiae. The protibial spinelike setae of *Eppelsheimius* are scattered over the surface (Herman, 1983a, fig. 6). *Pareiobledius* and *Blediotrogus* both have feebly expanded protibiae with some scattered spinelike setae. Some other genera, *Manda, Planeustomus, Oxytelus, Anotylus,* and *Sartallus,* for example, have spinelike setae on the protibiae but the tibiae are not enlarged in the same way. The setae of legs are usually gradually tapered apically. Some metatibial setae are flattened and apically bifid (**43**) in the *infans* and *fratellus* groups and in some species of the *punctatissimus* group.

Abdominal tergum VII of all *Bledius* has a fringe of microtrichiae (figs. 55–57), the palisade fringe (Hammond, 1979), including those that are flightless and have reduced wings, elytra, and pterothorax. The palisade fringe of most *Bledius* (and most Oxytelinae) is composed of many slender processes that appear to be soft and flexible (fig. 55) but for seven species groups (table 6) of *Bledius* the central portion of the fringe is replaced by (fig. 57) coarse spiniform processes (**44**). Tergum VIII of most *Bledius* has an emarginate posterior margin; species of eight groups (table 6) have a truncate margin (**45**) and for two groups (table 6) the posterior margin is serrate to serrulate (**46**). The duct which carries the chemical compounds produced by the pygidial glands passes through a canal on the surface of tergite IX. In five groups (table 6) the canal is sclerotized (**50**) across the dorsal surface. At the posterior end of tergite IX, the apex is usually tapered but in the *kosempoensis* group the apex is prominently lobed (**47**) and forms part of what appears to be a gutter. A structure common to all *Bledius* is the pair of long, flattened genital appendages of segment IX of the female (**48**). There is no evidence of a stylus, valvifer, or coxite. It is unclear how the structure was formed. Is it the result of the fusion of the coxite and valvifer or the loss of one of these structures? Only the female's genital appendages in *Aploderus* are similar but the structural differences suggest they are analogous, not homologous, structures. *Eppelsheimius* and many other genera of the Oxytelinae have distinct valvifers and coxites (Herman, 1983a, fig. 33).

Among species groups of *Bledius* the aedeagus and spermatheca exhibit considerable difference but within groups they vary little. The parameres are short and slender (**51**; *basalis, punctatissimus, bispinus, pulchellus,* and *verres* groups) and fitted close to the median lobe or long and cylindrical (**51**; *mandibularis, bellicosus, minax, aequatorialis, circularis, rugosicollis, gigantulus, immaturus, furcatus, lamelliceps, kochi, emarginatus, angustus* groups and a species of the *basalis* and *annularis* groups). The parameres are broad with a membranous median surface (**51**) in the *lucidus, kosempoensis, semiferrugineus, armatus, albonotatus, annularis,*

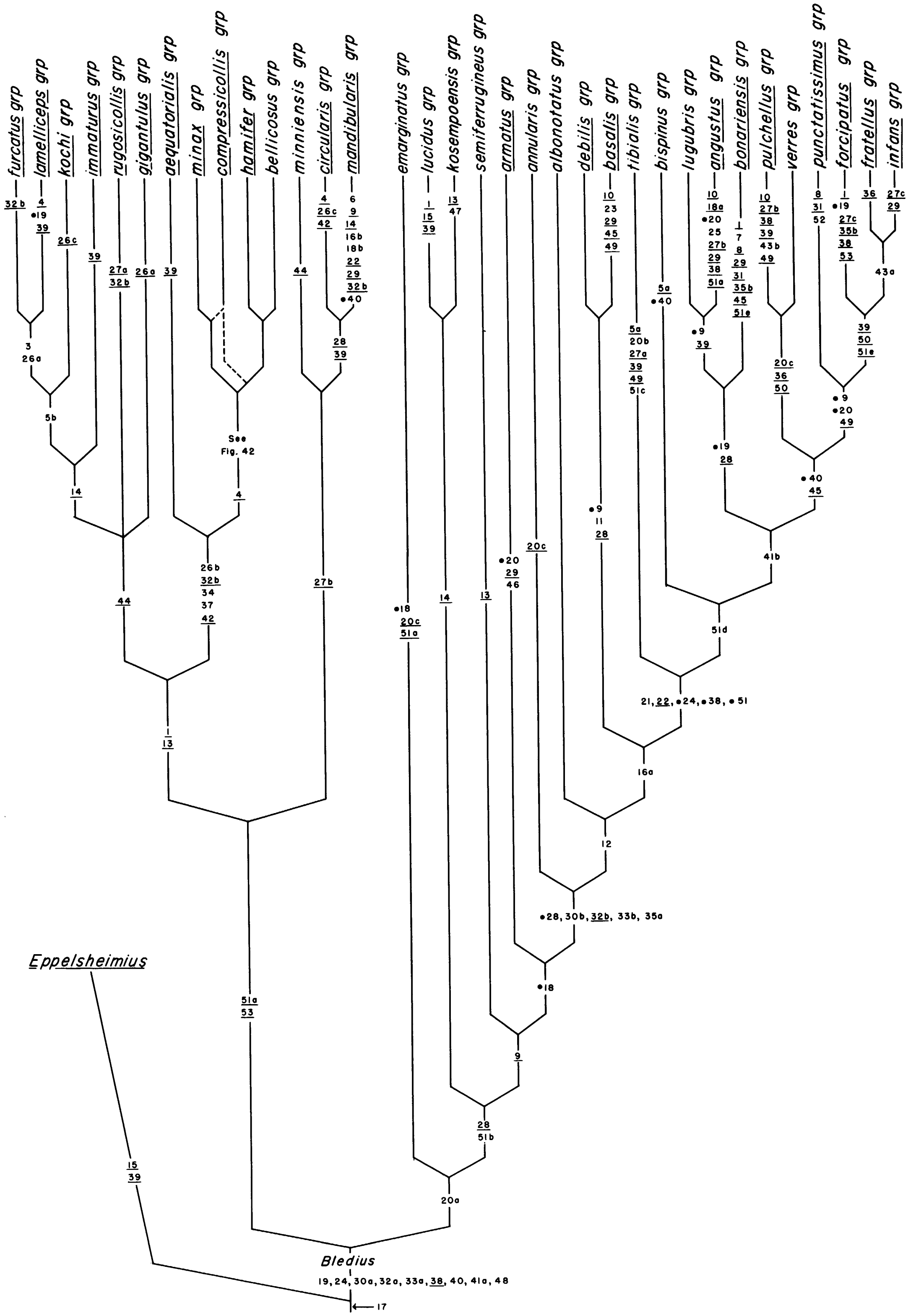


FIG. 41. Cladogram for the species groups of *Bledius*. The numbers refer to the character states in table 7. Homoplasious states are represented by the underlined numbers for parallelisms and numbers with an adjacent dot for reversals. Underlined taxa occur in saline habitats.

debilis, and *basalis* groups. Parameres are absent (**51**) in the *infans, fratellus, forcipatus,* and *bonariensis* groups. The median lobe is heavily sclerotized in the *forcipatus* group. The form of the aedeagus is unique in the *bellicosus, forcipatus,* and *kosempoensis* groups.

The spermatheca of *Bledius* is usually sclerotized, in some groups heavily so (**53**) and is divided into two parts, which I call the spermathecal gland, and receptacle. The receptacle is usually further divided in two parts connected by an accordionlike tube. The receptacle of the *punctatissimus* group is long, slender, and earthwormlike (**52**). In the *forcipatus* group one part of the receptacle is absent and the remaining part heavily sclerotized. In the *kosempoensis* and *debilis* groups and in some species of the *semiferrugineus, armatus, albonotatus, annularis,* and *basalis* groups one or both parts of the receptacle possess a brimlike ridge. The shape and relative size of the spermathecal gland and two parts of the receptacle vary among and within groups.

RELATIONSHIPS

Hypotheses concerning the relationships among the species groups of *Bledius* are illustrated in figures 41 and 42. The numbers on each internode indicate the character states that justify each branch. Numbers that lack a dot to the left refer to the apomorphic character states listed in table 7; those with a dot designate character state reversals and are listed in the plesiomorphic column of table 7. An underlined number signifies parallelisms. The distribution of character states among the 34 species groups of *Bledius* and the outgroup, *Eppelsheimius,* is presented in table 6 where the characters are identified by the numbers across the top (and keyed to the numbers in table 7), the pleisomorphic states are designated by a minus (−) and the apomorphic by a plus (+) for two state characters or by a letter for multistate characters. Question marks within the matrix identify characters that were not examined, usually because no specimens were available for dissection.

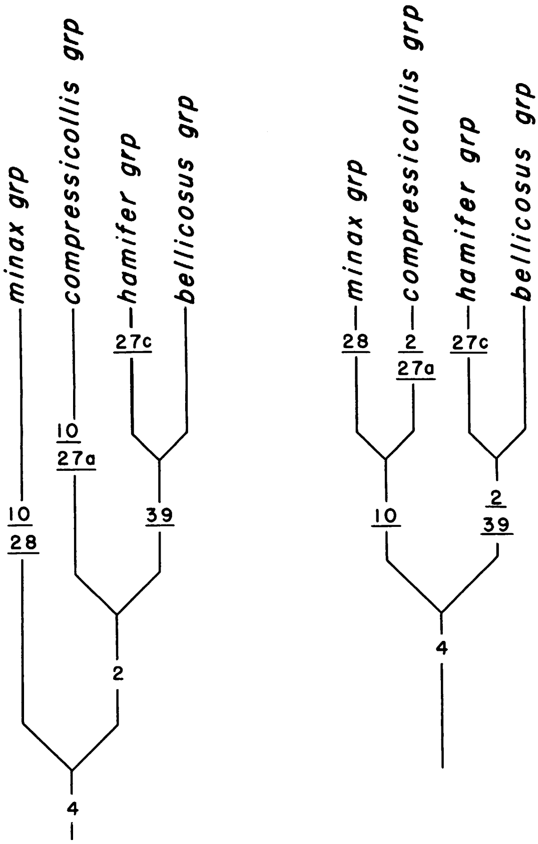


FIG. 42. Two cladograms depicting alternative hypotheses for four species groups of *Bledius.* The underlined numbers represent parallelisms.

Some character states are present in both the plesiomorphic and apomorphic condition within some groups. For example, within the *gigantulus, furcatus,* and *kochi* groups a few species have a feebly developed labral incision (**9**), most species lack the incision; I have coded the character state as plesiomorphic. Also designated as plesiomorphic in table 6 but present, if only weakly, in the more derived condition in some species are **4** (*aequatorialis* group), **12** (*Eppelsheimius*), **13** (*annularis* group), **27** (*aequatorialis* group), **28** (*forcipatus* and *punctatissimus* groups), **29** (*punctatissimus* group), **39** (*lamelliceps, punctatissimus,* and *angustus* groups), **43** (*punctatissimus* group), and **46** (*semiferrugineus* group). Marked as derived but present in a few species of a species group in the plesiomorphic state are characters **8** (*punctatissimus* group), **40** (*emarginatus, albonotatus, annularis,* and *basalis* groups), **44** (*furcatus* group), and **45** (*basalis* and *punctatissimus* groups). In the *emarginatus, an-*

nularis, and *verres* groups the hypopharyngeal cuticular processes **(20)** are lobes in most cases but palmate clusters in some. In the *basalis* group the parameres **(51)** may be broad with a membranous median surface, long and slender, or reduced to short stubs. In the *annularis* group the parameres **(51)** of most species are broad with a membranous median surface; in at least one species they are long and slender.

Attempts to construct a cladogram by hand revealed so much homoplasy that to obtain the most parsimonious hypothesis of relationships I was compelled to analyze my data using the University of Maryland's PHYSYS program and the generous help of one of the originators of PHYSYS, Dr. Mary F. Mickevich. The computer-generated cladogram (redrawn as figs. 41 and 42) includes 158 character states to support the branches; 118 states are homoplasious (reversals or parallelisms). Nonetheless, this was the most parsimonious tree found for the data and bears many similarities to my earlier hand-drawn tree which was based on fewer characters. Discrepancies in the two trees form the basis for some suggestions in later paragraphs for alternative placements of some species groups. Despite the high degree of homoplasy, the tree is largely resolved. There is one trifurcation (at the branch that includes *furcatus* through *gigantulus*) and one branch (that includes *minax* through *bellicosus*) for which there are two equally possible trees (fig. 42).

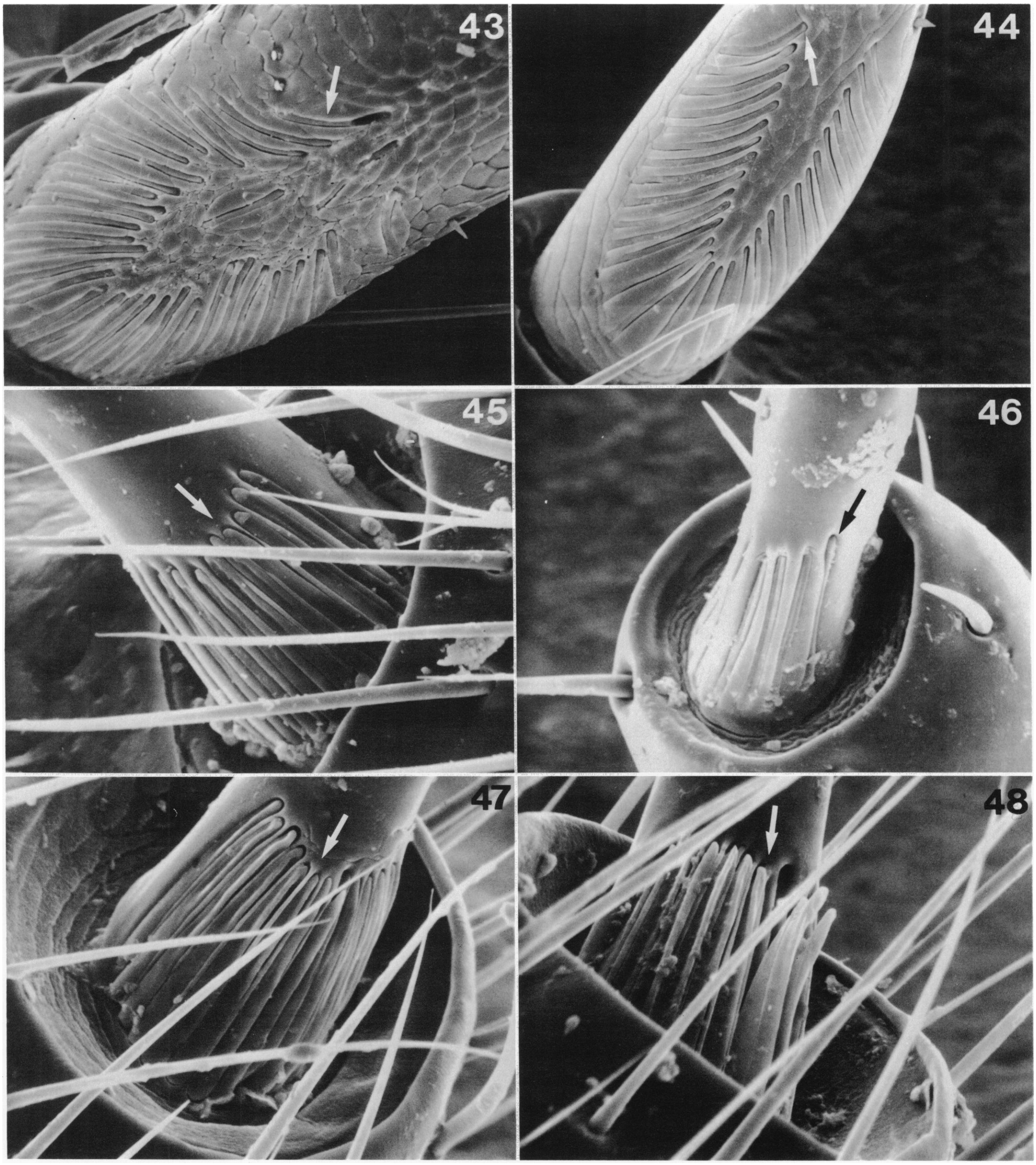
Five terminal branches exhibit no apomorphies. One of them, the *albonotatus* group, can be supported by the unique presence of a deeply emarginate labrum, a feature not included in my phylogenetic analysis. The *bellicosus* group is recognized in part by the incomplete elytral ridge, a state that had it been included in the character matrix would have been derived but highly homoplasious. The *debilis* group is the plesiomorphic member of a pair and might better be included with the *basalis* group. Little is known about the undissected *lugubris* group; when further studied it might be found to be in or the sister of the *punctatissimus* group. The most serious breach is the lack of an apomorphy for the large *verres* group. One possibility is to expand slightly the limits of the *verres* group to include the *pulchellus* group with only one species.

Previously (Herman, 1983b) I suggested that *Eppelsheimius* was this sister group of *Bledius.* The characters cited to justify that relationship were the confluent gular sutures, absence of a neck, expanded protibiae, a seta on the dorsal surface of the epipharyngeal lobe, the dehiscent elytra, and the geniculate antennae, of which all except the expanded protibiae are found scattered among five other genera of the Oxytelinae (Herman, 1983b). Added to the protibial feature is the presence of a midlongitudinal row of hypopharyngeal seta **(17)** found among the Oxytelinae only in *Bledius* and *Eppelsheimius.*

The monophyly of *Bledius* is supported by several unique characters including the tendency to develop a cluster of secretory pores **(32)** and associated setae **(30)** that are in a depression or pit **(33)** on the prosternum. The valvifers and coxites are fused into two long sclerites **(48)**; a similar such fusion of the genital appendages occurs in *Aploderus* but structural differences suggest parallel development. *Eppelsheimius* has scattered secretory pores on the prosternum (figs. 105, 108) and they are not in a depression or pit and the female's genital appendages are divided into coxites and valvifers (Herman, 1983b, fig. 33).

Bledius is divided into two main lineages. The smaller one, supported by features of the aedeagus **(51a)** and spermatheca **(53)**, includes 87 species in 14 species groups of which many species are robust and/or possess horns and most live in saline habitats. Five groups (*minax, compressicollis, hamifer, minniensis,* and *circularis*) are known from too few specimens to permit dissection. The *minax, compressicollis,* and *hamifer* groups belong to an incompletely resolved branch for which alternative trees are possible and *minniensis* and *circularis* may belong with other lineages as discussed in later paragraphs.

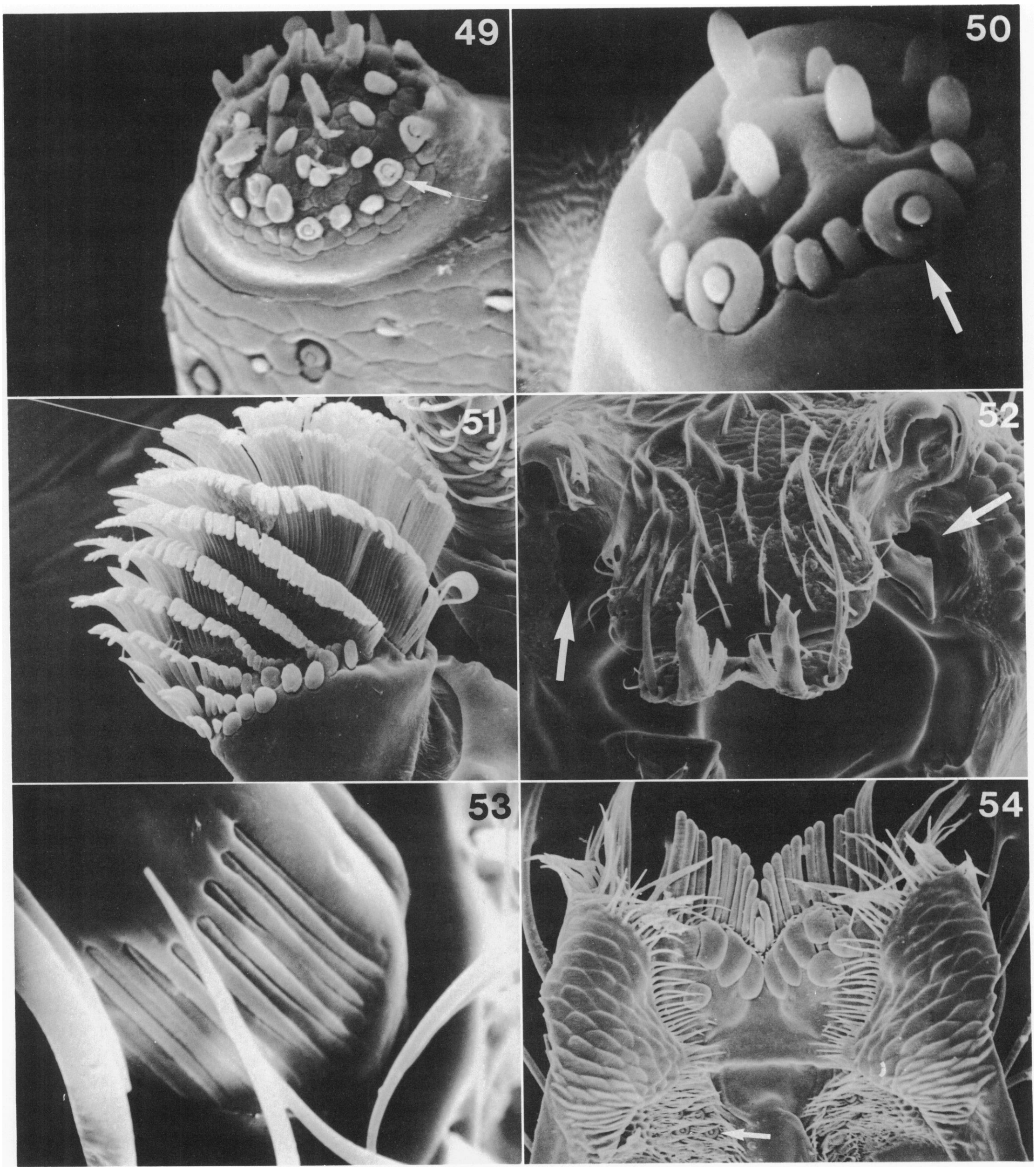
The branch leading to *furcatus* through *gigantulus* is supported by the condition of the palisade fringe **(44)**. This character state is found also in the *minniensis* group, which when studied further may be found to be part of the *furcatus-gigantulus* lineage. The *minniensis* group is known from one female of



FIGS. 43–48. Maxillary palpus, fourth segment. Arrows point to digitiform sensilla. **43.** *Deleaster trimaculatus,* 560 ×. **44.** *Manda mandibularis,* 800 ×. **45.** *Apocellus* sp., 1440 ×. **46.** *Platystethus americanus,* 1440 ×. **47.** *Aploderus* sp., 1280 ×. **48.** *Aploderus* sp., 1600 ×.

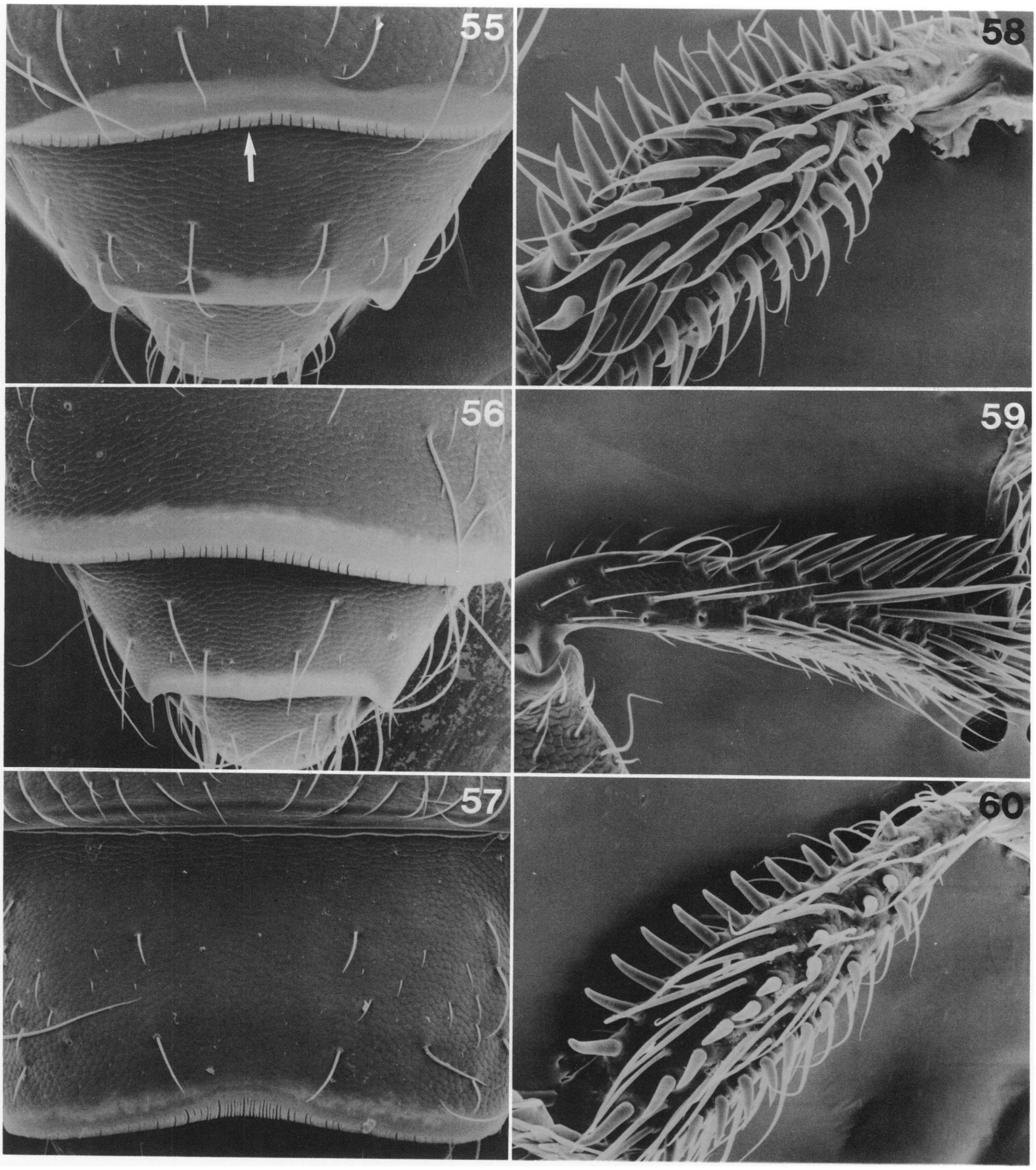
one species. Within this lineage is a trifurcation (which I had also encountered in my hand-drawn tree). The *furcatus-lamelliceps-kochi* branch includes species with a reflexed clypeal margin (5).

The *aequatorialis* through *bellicosus* lineage is based on five character states, two of which are homoplasious and three of which are unique in *Bledius.* Within this lineage there are alternative trees (fig. 42). In one, the



FIGS. 49–54. **49.** *Deleaster trimaculatus,* maxillary palpus, apex, arrows point to coronal pegs, 1600×. **50.** *Bledius fortis,* labial palpus, apex, arrow points to coronal pegs. **51.** *Bledius maindroni,* galea, 424×. **52.** *Bledius bonariensis,* head, anterior view, 176×; arrows point to subantennal pockets. **53.** *Bledius rubiginosus,* digitiform sensilla of fourth segment of maxillary palpus. **54.** *Bledius turbulentus,* labrum, ventral surface, arrow points to coronal peg.

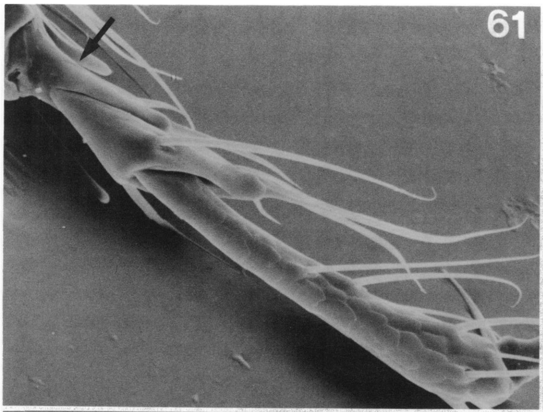
compressicollis, hamifer, and *bellicosus* groups are linked by the presence of a midcephalic horn (**2**) or alternatively *minax-compressicollis* with a reflexed labral margin (**10**) are the sister of *hamifer-bellicosus* branch with two homoplasious characters (**2** and **39a**). The first tree seems the more probable because the midcephalic horn is then unique to

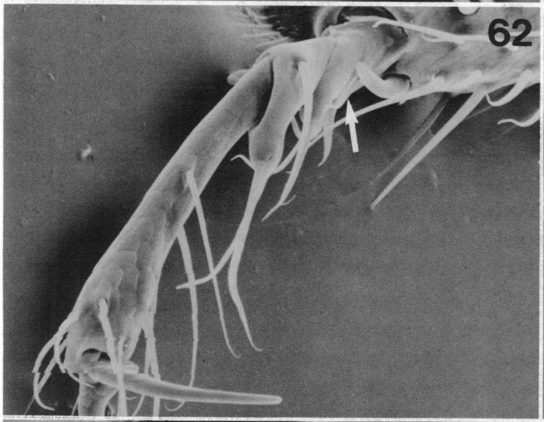


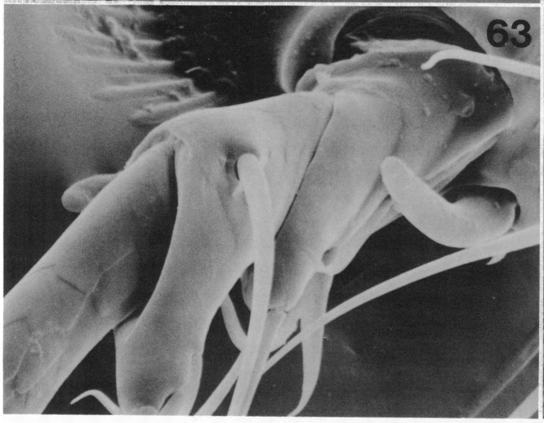
FIGS. 55–60. **55.** *Bledius ruficornis,* tergum VII–X, 124×, arrow points to palisade fringe. **56.** *Bledius pilicollis,* tergum VII–X, 80×. **57.** *Bledius gigantulus,* tergum VII, 82×. **58.** *Bledius pilicollis,* protibia, 136×. **59.** *Bledius gigantulus,* protibia, 108×. **60.** *Bledius beattyi,* protibia, 128×.

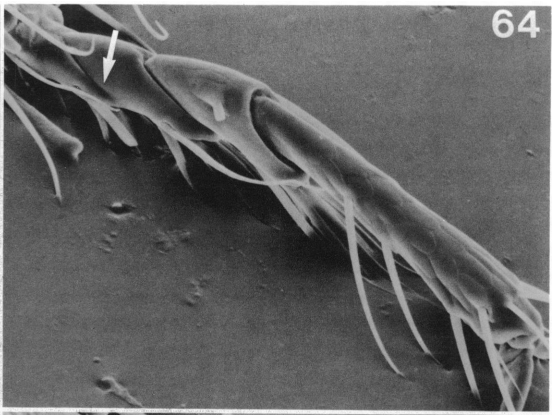
one branch. The reflexed labral margin in this branch is so feebly developed as to be of dubious value. Three of the five groups of the *aequatorialis-bellicosus* lineage have not been dissected. Also undissected and but lacking the deflexed pronotal horn (**26b**) and prosternal marginal notch (**37**) is the poorly known *circularis* group. This group might be placed at the base of the *aequatorialis-bellicosus* branch because both share a protibial character (**4**).

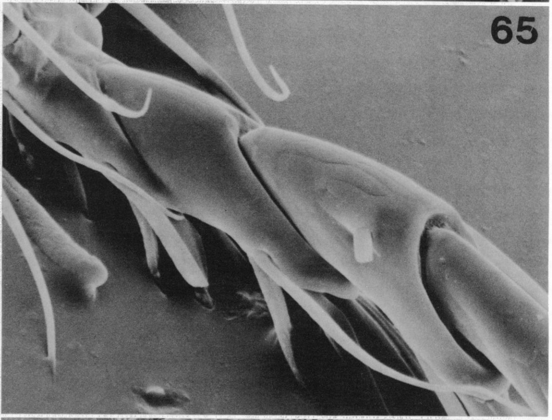
Finally, the branch leading to the *mandib-*

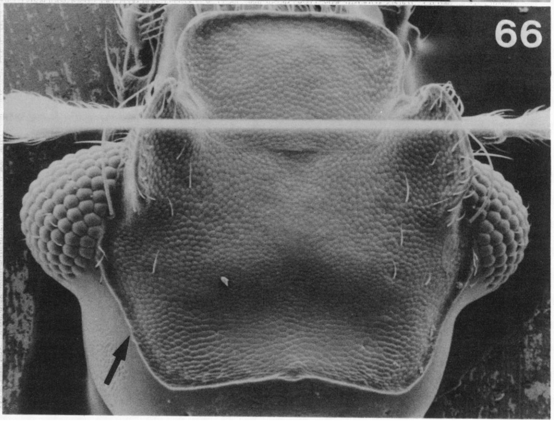










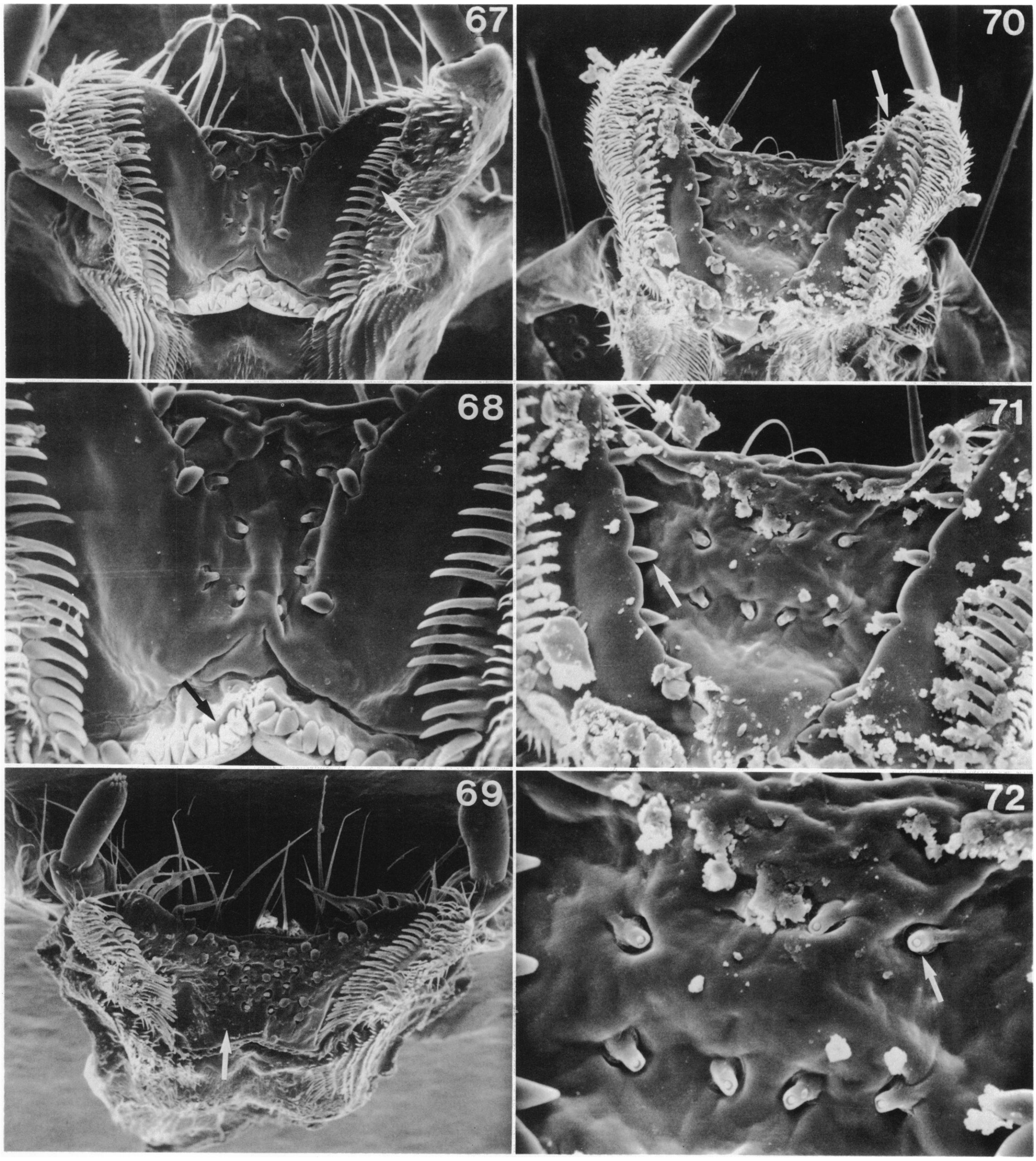


FIGS. 61–65. *Bledius* spp., *verres* group. **61.** Metatibia, laterodorsal view, arrow points to feeble separation of first article, 256 ×. **62.** Metatibia, anterolateral view, arrow points to partial separation of first and second articles, 252 ×. **63.** Metatibia, enlargement of basal articles, 630 ×. **64.** Mesotibia, arrow points to moderately developed separation of first and second articles, 264 ×. **65.** Mesotibia, enlargement of basal articles, 470 ×.

FIG. 66. *Bledius pilicollis,* head, dorsal, arrow points to postocular carina, 60 ×.

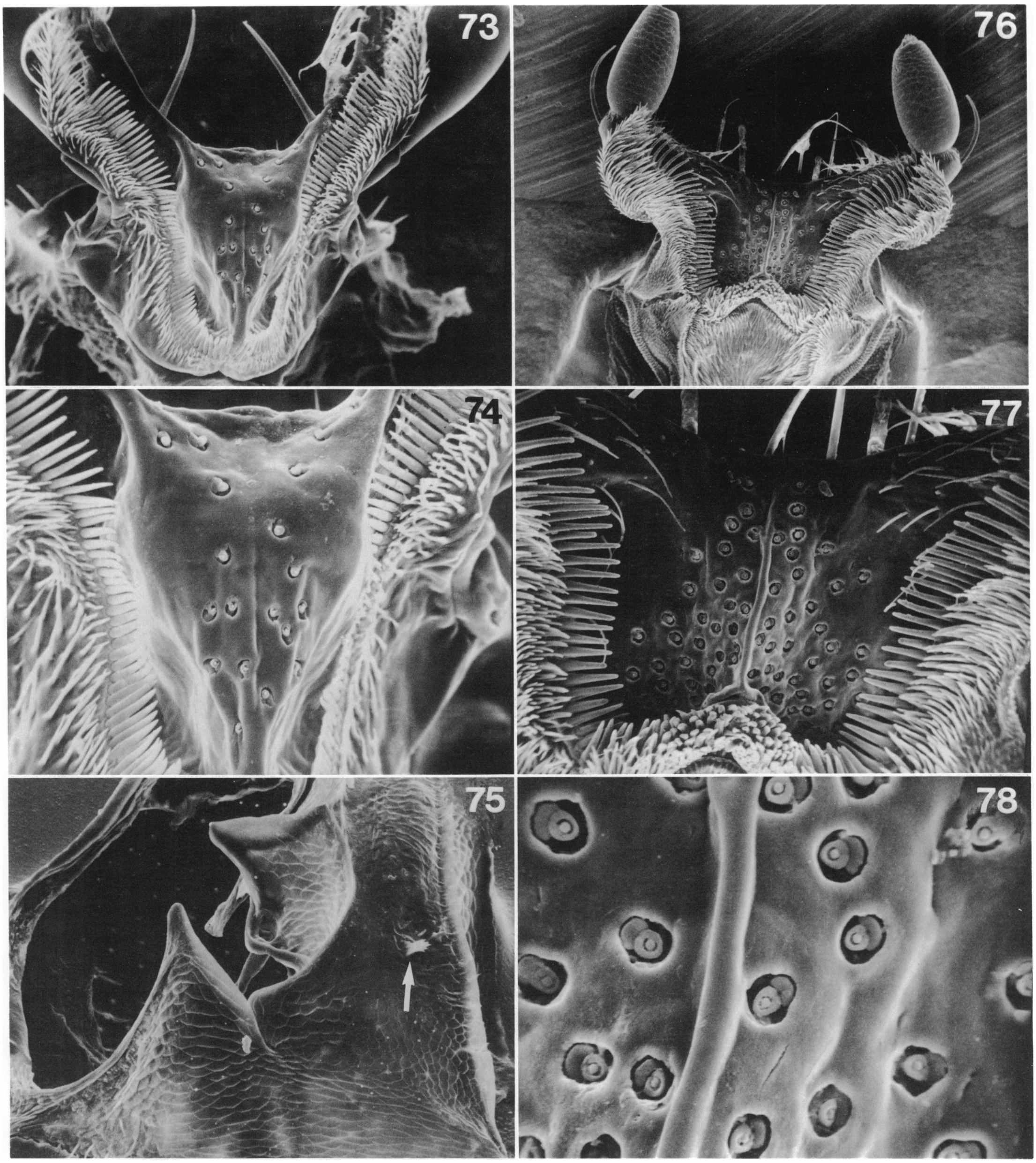
ularis group, which questionably includes the *minniensis* and *circularis* groups, is the sister branch to *furcatus* through *bellicosus.*

In the *furcatus-mandibularis* branch only *mandibularis* and *aequatorialis* occur in the New World (figs. 1–4). The sister group of



FIGS. 67–72. Hypopharynx. **67.** *Apocellus* sp., arrow points to lateral row of spinelike setae, 360×. **68.** *Apocellus* sp., arrow points to basal row of spinelike setae, 700×. **69.** *Aploderus* sp., arrow points to disk, 320×. **70.** *Platystethus americanus,* arrow points to anterior lobe of disk, 320×. **71.** *Platystethus americanus,* arrow points to discal seta, 640×. **72.** *Platystethus americanus,* arrow points to coronal peg, 1280×.

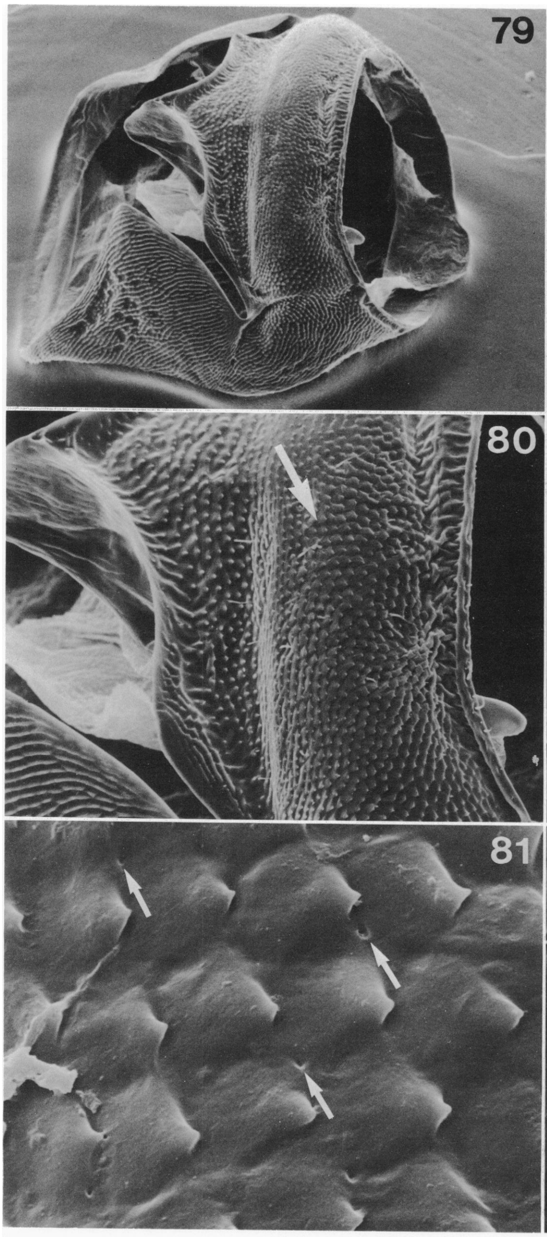
the New World *aequatorialis* group is the Indo-Australian *minax* through *bellicosus* branch. Also restricted to the Indo-Australian region is the *circularis* group which, if placed at the base of the *aequatorialis* through *bellicosus* branch, would produce a distributional tree with an Indo-Australian group (*circularis*) as the sister to an Indo-Australian

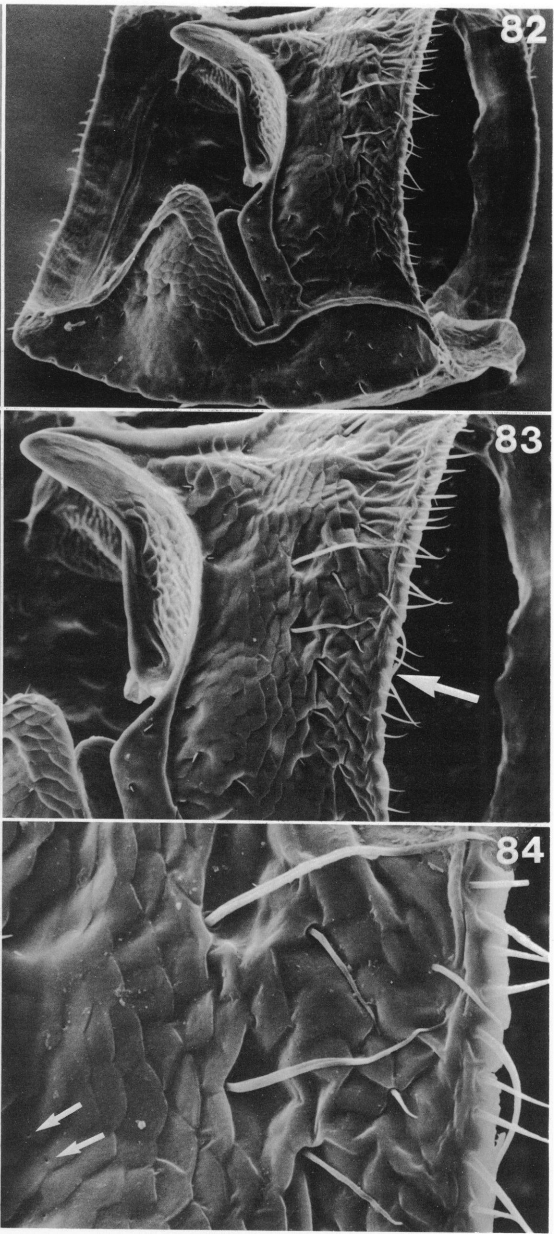


FIGS. 73–78. **73.** *Manda mandibularis,* hypopharynx, 320 ×. **74.** *Manda mandibularis,* hypopharynx, disk, 640 ×. **75.** *Bledius bonariensis,* prothorax, arrow points to setae of secretory pit, 152 ×. **76.** *Deleaster trimaculatus,* hypopharynx, 160 ×. **77.** *Deleaster trimaculatus,* hypopharynx, 320 ×. **78.** *Deleaster trimaculatus,* hypopharynx, disk, 1280 ×.

group (*minax* through *bellicosus*) and Caribbean-Galapagos group (*aequatorialis*).

The remaining seven groups are Afro-Eurasian; three of them (*furcatus, kochi,* and *gigantulus*) occur widely in the region; one is African (*lamelliceps*); two are central Asian



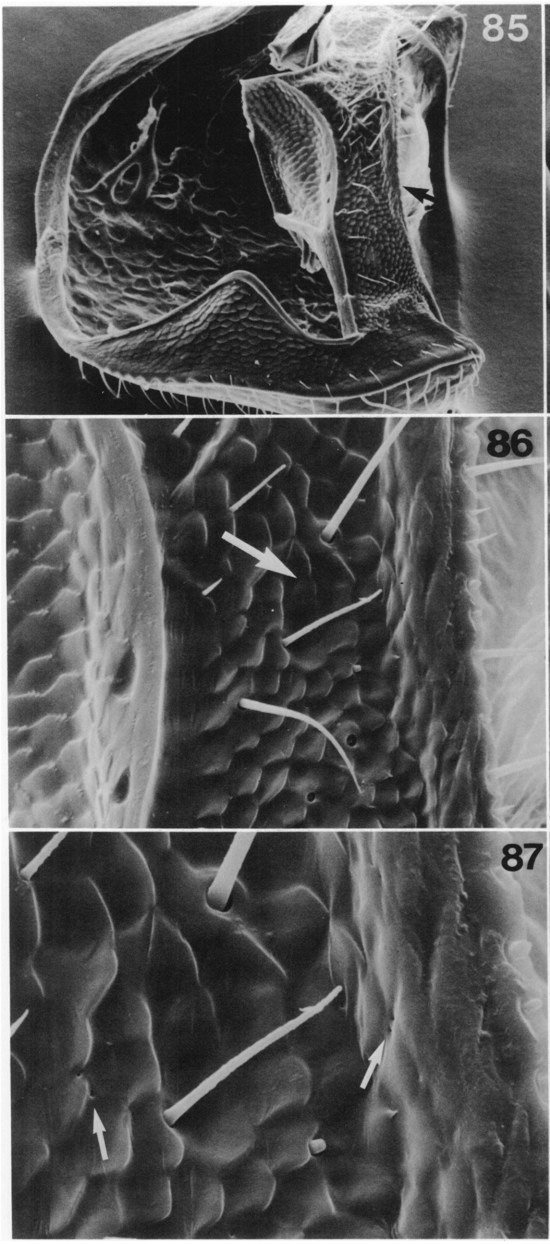


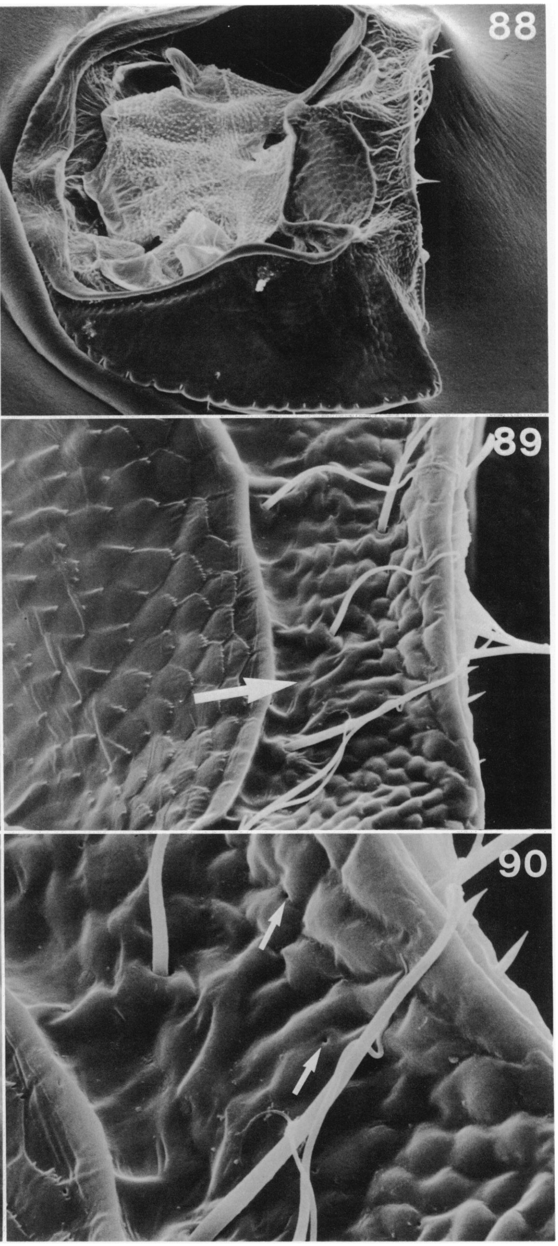
FIGS. 79–81. *Deleaster trimaculatus.* **79.** Prothorax, ventral, 64×. **80.** Prosternum, arrow points to area enlarged in next photo, 148×. **81.** Prosternum, arrows point to secretory pores, 1460×.

FIGS. 82–84. *Homalotrichus* sp. **82.** Prothorax, ventral, 126×. **83.** Prosternum, arrow points to area enlarged in next photo, 208×. **84.** Prosternum, arrows point to secretory pores, 520×.

(*immaturus* and *minniensis*); and one is south Asian (*rugosicollis*).

Nomenclaturally, three groups of the *furcatus-mandibularis* branch have been named as subgenera, namely, the *furcatus* group (*Euceratobledius*), the *kochi* group (*Elbidus*), and



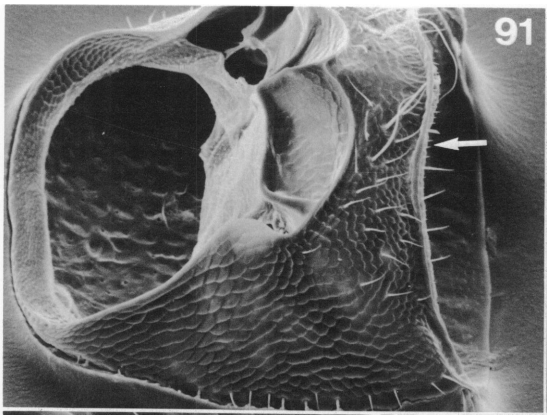


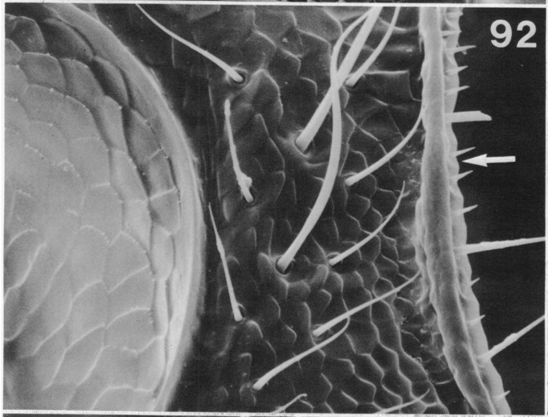
FIGS. 85–87. *Aploderus caelatus.* **85.** Prothorax, ventral, arrow points to area enlarged in next photo, 104×. **86.** Prosternum, arrow points to area enlarged in next photo, 520×. **87.** Prosternum, arrows point to secretory pores, 1040×.

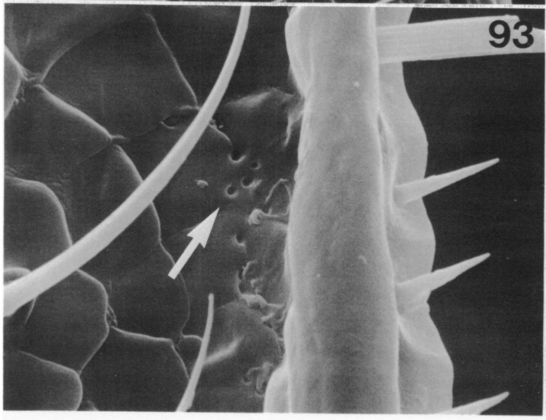
FIGS. 88–90. *Anotylus insignitus.* **88.** Prothorax, ventral, 110×. **89.** Prosternum, arrow points to area enlarged in next photo, 540×. **90.** Prosternum, arrows point to secretory pores, 1240×.

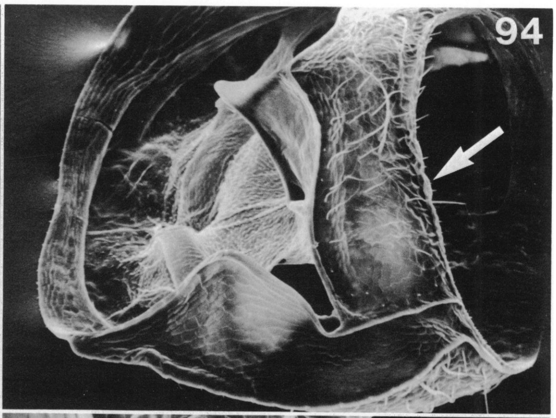
the *gigantulus* group (*Bledius* s. str.). A few species of one or another of these groups were included in one of the three subgenera (for details see table 9 and the discussion following the description of each group).

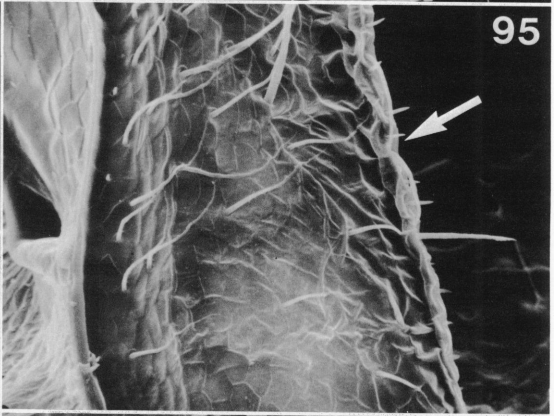
The sister of the branch that includes the

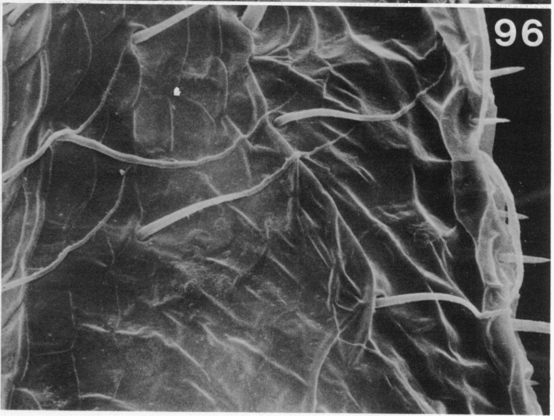








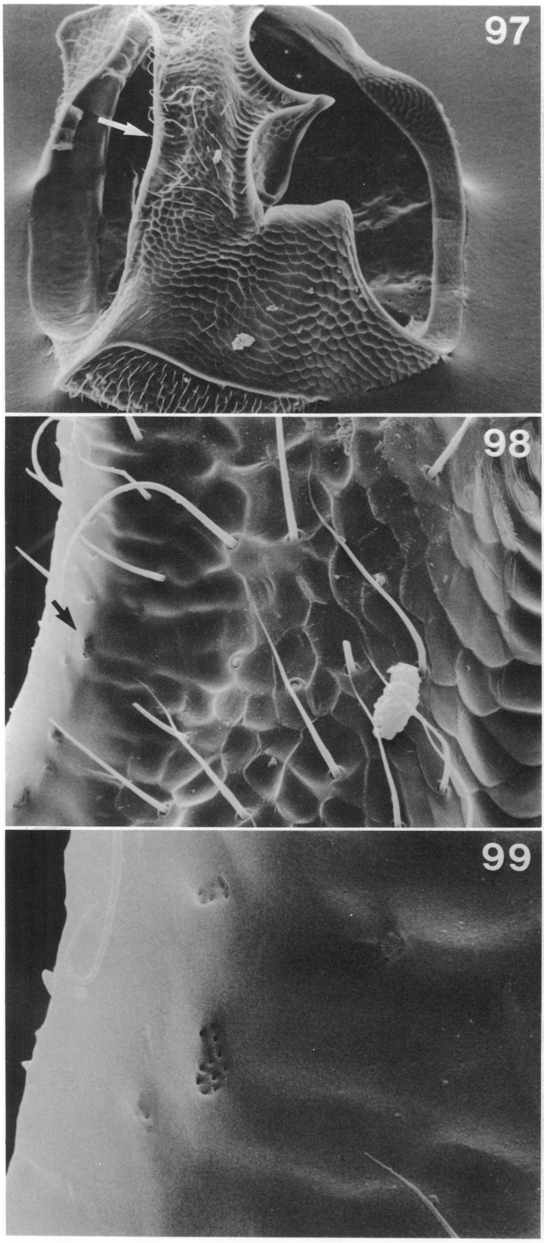


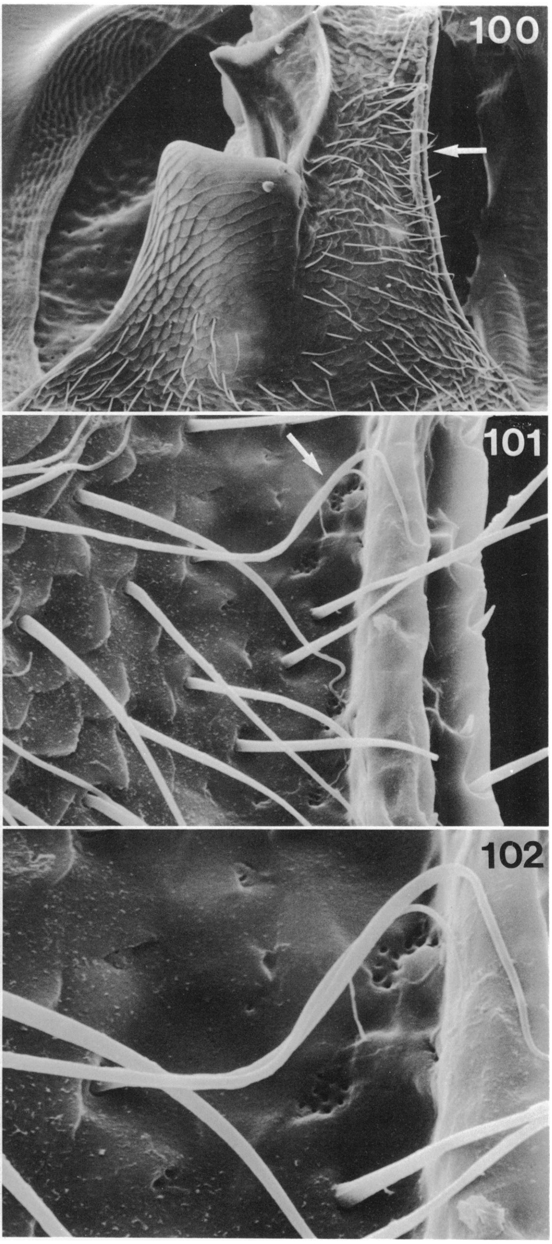


FIGS. 91–93. *Blediotrogus* sp. **91.** Prothorax, ventral, arrow points to area enlarged in next photo, 148×. Fig. **92.** Prosternum, arrow points to area enlarged in next photo, 520×. **93.** Prosternum, arrow points to cluster of secretory pores, 2080×.

FIGS. 94–96. *Ochthephilus longipennis.* **94.** Prothorax, ventral, arrow points to area enlarged in next photo, 148×. **95.** Prosternum, arrow points to area enlarged in next photo, 420×. **96.** Prosternum, 840×.

large, horned species, is the speciose lineage, *emarginatus* through *infans,* with 20 species groups and over 340 species. Ten of the species groups live in saline habitats; most of the species of the other ten groups live in freshwater habitats. For three groups (*bispi-*



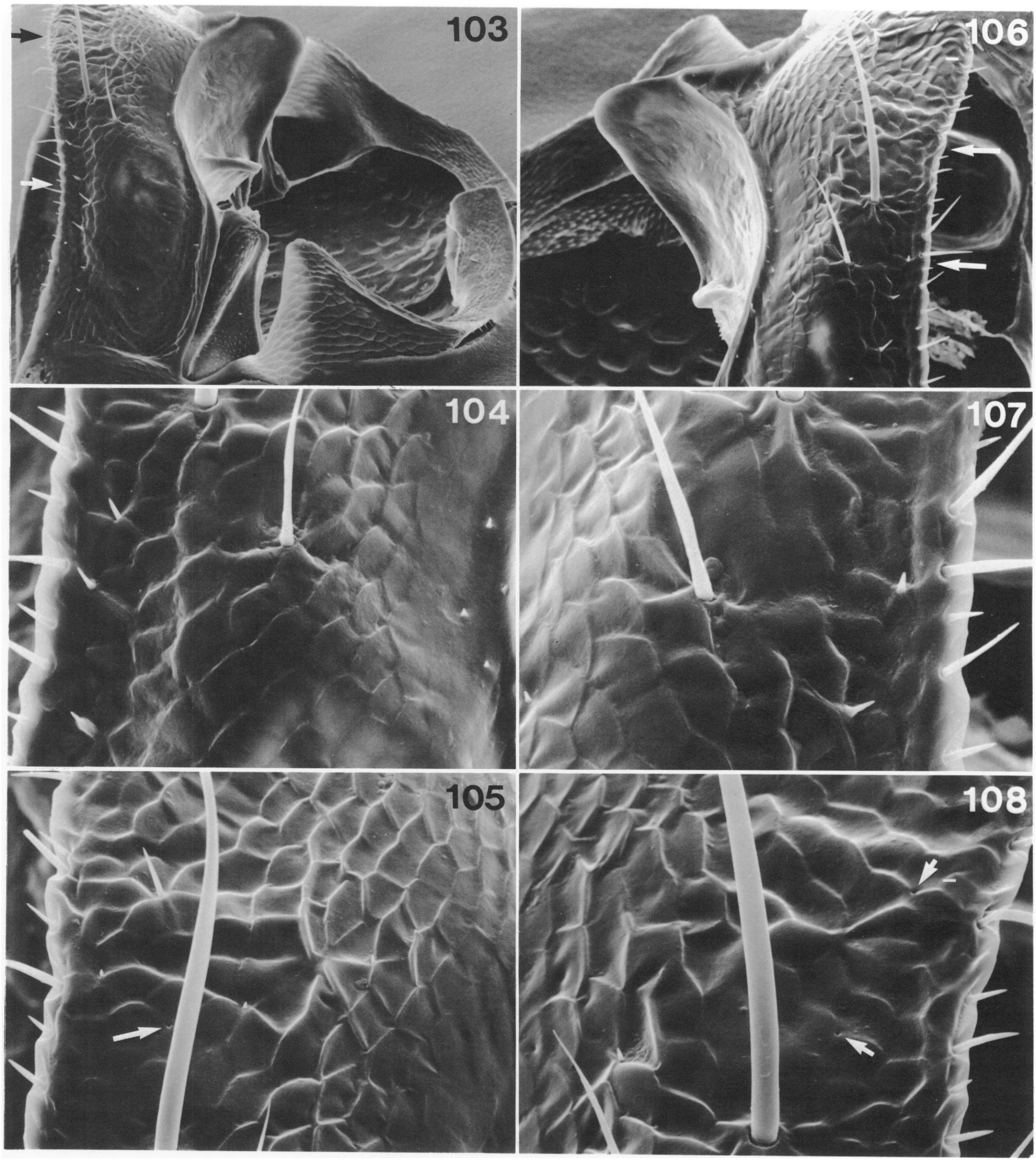


FIGS. 97–99. *Carpelimus correctus*. **97.** Prothorax, ventral, arrow points to area enlarged in next photo, 162×. **98.** Prosternum, arrow points to cluster of secretory pores enlarged in next photo, 880×. **99.** Secretory pores of prosternum, 2960×.

FIGS. 100–102. *Thinodromus* sp. **100.** Prothorax, ventral, arrow points to area enlarged in next photo, 164×. **101.** Prosternum, arrow points to cluster of secretory pores enlarged in next photo, 1280×. **102.** Secretory pores of prosternum, 2560×.

nus, lugubris, and *infans*) there was insufficient material for dissection, but of these only *lugubris* might better be placed elsewhere (near *punctatissimus*).

Moving up this second main lineage, the species groups are successively separated off until we reach first the internode for the *debilis* through *infans* branch which is sup-



FIGS. 103–108. *Eppelsheimius pirazzolii.* **103.** Prothorax, ventral, bottom arrow points to area enlarged in next photo, top arrow points to area enlarged in fig. 105, 120×. **104.** Prosternum, 512×. **105.** Prosternum, arrow points to secretory pore, 508×. **106.** Prosternum, bottom arrow points to area enlarged in fig. 108, 194×. **107.** Prosternum, 620×. **108.** Prosternum, arrows point to secretory pores, 620×.

ported by the presence of a shortened second labral segment (**16a**), then further up to a major cluster of species groups (*lugubris* through *infans*) which is based on the presence of only three tarsomeres (**41b**); all other *Bledius* have four. Beyond this point most of the internodes are justified by few nonhomoplasious character states. With the exception of the *lugubris* through *infans* branch, there are no major clusters of species groups in the second main lineage.

The *armatus, bonariensis,* and *forcipatus* groups are restricted to the New World. The *emarginatus, semiferrugineus, annularis, albonotatus, basalis,* and *punctatissimus* groups are found in both eastern and western hemispheres. The *emarginatus* group occurs largely in the southern hemisphere. The *punctatissimus* group includes species that are largely sea coastal around the world in both southern and northern hemispheres. The other four groups are holarctic and the *basalis* group is amphiatlantic. All of the remaining groups are restricted to the Old World.

Beginning with the *fratellus-infans* branch, these two African groups are sister to the largely Central and South American *forcipatus* group. Sister to these three groups is the widespread but largely tropical coastal *punctatissimus* group. Sister to them are the *verres-pulchellus* group of the Old World tropics. Excluding the dubiously placed *lugubris* group, the sister group to the *pulchellus* through *infans* branch is the *angustus* group (Afro-Asian) and the *bonariensis* group (South American). For the distributions of the remaining groups consult figures 5 to 12.

Eight of the 20 species groups of the second branch of *Bledius* have been named formally. They included the *semiferrugineus* (*Hesperophilus*), *annularis* (*Bargus*), *basalis* (*Dicarenus*), *angustus* (*Belidus*), *verres* (*Pucerus*), *punctatissimus* (*Psamathobledius*), and *forcipatus* (*Microbledius*) groups. Some species of the other groups have been included in these subgenera (table 9).

The species of *Eppelsheimius,* the sister group of *Bledius,* live in saline habitats (Herman, 1983b). The primitive *Bledius* likely occupied similar circumstances in sand near the ocean and/or salt lakes. In the cladogram (fig. 41) the groups that live or are thought to live in saline habitats are underlined. In the *furcatus-mandibularis* branch nearly all the species live near the ocean or salt lakes. In the second lineage, the less derived groups live in freshwater habitats and adaptation to saline habitats reappeared three times. In the *armatus* group many species live near salt or alkali lakes, a few near the ocean. Most of the species of the *basalis-debilis* branch live near the ocean. The species of at least seven groups of the *lugubris-infans* branch live near salt water. However, the vast majority of the species of the *emarginatus-infans* branch live in freshwater habitats because four (*emarginatus, semiferrugineus, annularis,* and *verres* groups) of the ten freshwater groups are highly speciose (with a total of 237 species).

CLASSIFICATION AND DESCRIPTIONS

INTRODUCTION

The principal purpose of the taxonomic portion of this paper is to recognize, define, and describe monophyletic groups of species in *Bledius,* to reveal the diversity of the genus, and to prompt revisionary studies.

Two infrageneric classifications are currently available. One with eight subgenera is used primarily by Europeans for Old World species but Hatch (1957), Coiffait and Saiz (1968), and Saiz (1973) applied it to some North American and Chilean species. Coiffait (1973) published a key to all the subgenera and Lohse's (1964) key excluded only *Belidus.* The second classification is used by North American workers and includes eight species groups, plus *Microbledius* and *Psamathobledius.* If *Microbledius* and *Psamathobledius* are reduced to subgenera and *Bargus* elevated from synonymy with *Hesperophilus,* then the subgeneric classification would have 11 groups.

The 95 species assigned to species groups prior to the present paper are listed by Herman (1983a, pp. 121–122). Subgeneric assignments on the other hand can be found in no one place. To rectify this and to clarify the composition of the subgenera, table 9 is constructed. The subgeneric assignments are taken from the literature—references to which are found in the Catalogue of *Bledius* of the World which is included herein as a separate chapter. Two hundred eighty-six species are included in subgenera. *Microbledius, Psamathobledius,* and *Neobledius,* all described as genera, are included because I have moved them all into *Bledius. Dicarenus* replaces the earlier erroneous use of *Hesperophilus.* Species formerly in *Blediodes* are now in *Hesperophilus*[16] as it is now understood. In parentheses and to the right of the species name is the species group assignment as determined herein.

Casual examination of table 9 quickly reveals the disparity between the composition of the species groups and subgenera. Note that *Microbledius* is monophyletic, *Psamathobledius* and *Neobledius* are paraphyletic, but the remainder are all polyphyletic.

If the subgenera were revised to include only and all the species most closely related to the type species, then they would be equivalent to some of the species groups used herein. Table 8 outlines the equivalency. Note that in this table *Bargus* remains a synonym of *Hesperophilus* where all authors currently place it, *Neobledius* is a synonym of *Elbidus* where I place it, and *Microbledius* and *Psamathobledius* are listed as subgenera.

If species can be simply transferred among the existing subgenera to make the subgenera monophyletic, why then not reallocate species and use a subgeneric classification? Why not reduce *Microbledius* and *Psamathobledius* to subgenera, elevate *Bargus,* synonymize *Neobledius,* and place the unassigned species in subgenera? Were this to be done, nearly 25 percent of the species would remain unassigned. These 100+ species I place in 23 additional species groups. Should then 23 new subgeneric names be proposed? Should the limits of the existing subgenera be expanded to accommodate these 23 other groups? The purpose of this paper is to expose the infrageneric diversity and monophyletic groups of *Bledius.* Will a proliferation of generic group or subsuming of variation help or hinder this goal? Binomens are efficacious to find our way about the literature and give us a handle to discuss taxa. Informal group designations permit us to develop concepts and to point out similarity and variation without the burden of subgeneric names and rules of formal nomenclature. The use of subgeneric names would permit no greater insight into the similarities and differences in *Bledius.*

Therefore, I adopt a species group classification here. The presently available subgeneric names are simply disregarded. Although if reconstituted the subgenera represent real biological entities, they are nomenclatural synonyms of *Bledius* and as such are treated as synonyms herein. *Psamathobledius* and *Microbledius,* both well-defined distinct taxa, are moved into *Bledius* and similarly treated as nomenclatural synonyms. *Neobledius* is likewise moved to *Bledius* but it also represents the same group of

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[16] See the section entitled Taxonomic History for the previous usage of these subgenera.

species as does *Elbidus* and is therefore a junior synonym of that name. The names of the groups are based on the name of an arbitrarily selected species. The composition of each group is based on examination of specimens of each species. For 79 percent of the species, holotypes, lectotypes, paratypes, syntypes were examined. Nine species were assigned to species group by characters given in the description; eight species remain unassigned. The status of the specimens upon which the group assignment is based is cited beside each species. **H** refers to holotype, **L** to lectotype, **P** to paratype, **Co** to cotype, **Syn** to syntype, **T** to type (that is usually a syntype), and **Sp** to subsequently identified material. The institutions to which the specimens belong are included as are the localities from which they were collected. These localities are the bases of the distributional maps of the species groups. Species may be misidentified but the assignment of specimens to species groups is correct. To reassign any of the specimens I examined would require revision of the characters of a species group. Some characters are visible only by dissecting the species. For some species groups I omit these characters because of the lack of sufficient material for dissection. For the other groups these characters are based on the dissection of one or a few species with the exception of the species groups found in North America. Specimens of nearly all the North American species were completely disarticulated for study with a compound microscope. If no material was available for dissection, the species groups are identified in table 6 by question marks in place of the character state polarity (see for example the *minax* group, table 6). To study properly the hypopharynx and the prosternal secretory pores, a scanning electron microscope (SEM) is required. The hypopharynx for nearly all the North American species is illustrated (Herman, 1972, 1976, 1983a). For species from other parts of the world, material was available for SEM study for few species. However, the hypopharynx is important to defining the species group and an effort should be made to acquire sufficient specimens to study this structure.

Most species groups now include only one or a few species. For most of these smaller groups, however, I have studied undetermined new species that belong in the groups. Nearly all of the species groups require revision. Much undetermined material is available in museums now but additional material is needed from some parts of the world.

Finally, I hope the infrageneric classification of *Bledius* presented in the succeeding pages will improve understanding and facilitate further study of this large, interesting genus.

Bledius

Type species: Bledius armatus (Panzer), junior synonym of *Bledius tricornis* (Herbst).

Synonymy: For the synonymic and subgeneric names in *Bledius,* see the Catalogue of *Bledius* of the World included in the present work.

DIAGNOSIS: *Bledius* can be separated from other genera of the Oxytelinae by the subcylindrical form of the body, the geniculate antennae (fig. 296), the presence of the procoxal fissure (figs. 116, 131), the spinous tibiae (figs. 58–60), the three or four segmented tarsi (figs. 61–65, 392), and the dehiscent elytral suture.

Bledius is similar to *Eppelsheimius.* The two genera share all of the features in the preceding paragraph except the number of tarsomeres (which number five in *Eppelsheimius*). *Bledius* lacks or has small submental processes on the lateral anterior edge that are enlarged in *Eppelsheimius* (Herman, 1983b, figs. 13, 30). The ventral genital sclerites of abdominal segment IX of the females of *Bledius* consist of a pair of elongate flattened sclerites (fig. 401). Those of *Eppelsheimius* are paired and transversely divided (Herman, 1983b, fig. 33).

DESCRIPTION: Length 1.5 to 12.0 mm. Form subcylindrical. Body sparsely to densely pubescent.

Head with lateral margins gradually convergent from eyes toward base (fig. 126); neck absent; postocular transverse depression present or absent. Epistomal suture present (fig. 126) and straight. Eyes strongly protruding from sides of head and not extending onto ventral surface. Supraantennal ridge small to large and well developed; horns present (figs. 126, 157, 377–379) or absent on males; horn absent on females. Dorsal tentorial arms present; anterior tentorial arm absent. Antenna with first segment elongate and geniculate (fig. 296). Gular sutures divergent near base of head and usually confluent for remainder of length (figs. 118, 380); some species with gular sutures separated anteriorly (figs. 395–397, 446). Submentum with or without small process (figs. 120, 380, 395, 396) on lateral anterior margin. Labium (figs. 166, 328) with trapezoidal mentum; palpal segments of variable length. Hypopharynx (figs. 492, 514, 517) with median row of spinelike setae and basal transverse row or cluster of spinelike setae. Hypopharyngeal disk with cuticular processes and setae present or absent, and coronal pegs present. Labrum (figs. 112, 130) with or without midlongitudinal incision. Epipharynx with short to long anteriorly directed membranous lobe. Mandibles edentate (fig. 459), bidentate (figs. 113, 128), tridentate (fig. 146), or quadridentate (fig. 493).

Pronotal shape variable; width usually greater than length. Pronotal horn present (fig. 131) or absent in males; horn usually absent in female, present only in *B. susae* (fig. 154). Pronotal lateral marginal bead present and complete (fig. 182) or incomplete (fig. 116) or absent (fig. 145); bead usually dividing hypomeron and notum (fig. 159), some species with bead on hypomeron (fig. 169). Protergosternal suture present (fig. 131) or absent (fig. 116) or obsolete (fig. 145). Procoxal fissure present and open (fig. 131) or closed (fig. 116). Protrochantin concealed or exposed. Postprocoxal lobe present (fig. 116). Prosternal intercoxal process present (figs. 131, 363) or absent; length and form variable. Prosternum with setigerous pit (figs. 363, 678), setigerous depression (figs. 601, 613), or patch of setae anterior to procoxae (fig. 648). Prosternum with cluster of pores associated with setae (figs. 615, 624, 726).

Scutellum concealed by pronotum or with apex slightly exposed. Elytral length variable; suture dehiscent at apex; apex with or without membranous lobe; epipleural ridge present and complete (fig. 297) or incomplete (fig. 193) or absent; surface without longitudinal striae. Mesosternal moderately long, carinate at apex and extending between mesocoxae. Mesocoxae contiguous. Metasternum without process between mesocoxae but with low, rounded ridge separating mesocoxal depressions. Mesendosternite variable; lateroposterior arm present or absent. Metendosternite

TABLE 8

Comparison of Classifications

Equivalency based on species group assignment of subgeneric type species.

Subgenus	Species group
Bledius (s. str.) Leach, 1819 Type species: *armatus* (=*tricornis*)	*gigantulus*
Hesperophilus Curtis, 1829 Type species: *fracticornis* (=*gallicus*)	*semiferrugineus* and *annularis*
Tadunus Schiødte, 1866 Type species: *fracticornis*	(*semiferrugineus*)
Blediodes Mulsant and Rey, 1878 Type species: *fracticornis*	(*semiferrugineus*)
Bargus Schiødte, 1866 Type species: *pallipes*	(*annularis*)
Dicarenus Gistel, 1834 Type species: *arenarius* (=*fergussoni*)	*basalis*
Cotysops Tottenham, 1939 Type species: *arenarius* (=*fergussoni*)	
Astycops Thomson, 1859 Type species: *talpa*	*albonotatus*
Elbidus Mulsant and Rey, 1878 Type species: *bicornis*	*kochi*
Neobledius Abdullah and Qadri, 1968 Type species: *karachiensis*	
Belidus Mulsant and Rey, 1878 Type species: *angustus*	*angustus*
Pucerus Mulsant and Rey, 1878 Type species: *verres*	*verres*
Euceratobledius Znojko, 1929 Type species: *furcatus*	*furcatus*
Microbledius Herman, 1972 Type species: *playanus*	*forcipatus*
Psamathobledius Herman, 1972 Type species: *punctatissimus*	*punctatissimus*

TABLE 9

Subgeneric and Species Group Assignments

(Subgeneric assignments of species as of Jan. 1985 in left column and species groups assignments as presented in the present monograph in right column)

Species	Species group	Species	Species group
		Bledius (s. str.)	
aequatorialis	(*aequatorialis* grp)	*limicola*	(*gigantulus* grp)
bison	(*furcatus* grp)	*paradoxus*	(*gigantulus* grp)
brunnipennis	(*rugosicollis* grp)	*pilicollis*	(*lamelliceps* grp)
chinensis	(*gigantulus* grp)	*ponticus*	(*gigantulus* grp)
corniger	(*gigantulus* grp)	*quadricornis*	(*bellicosus* grp)
ensifer	(*gigantulus* grp)	*salsus*	(*gigantulus* grp)
graellsi	(*gigantulus* grp)	*sarmaticus*	(*gigantulus* grp)
hauseri	(*kochi* grp)	*sauteri*	(*gigantulus* grp)
hoplites	(*gigantulus* grp)	*setonis*	(*gigantulus* grp)
immaturus	(*immaturus* grp)	*simulator*	(*gigantulus* grp)
lacustris	(*kochi* grp)	*spectabilis*	(*gigantulus* grp)
lamelliceps	(*lamelliceps* grp)	*tricornis*	(*gigantulus* grp)
		unicornis	(*gigantulus* grp)
		Hesperophilus	
afghanicus	(*semiferrugineus* grp)	*denticollis*	(*annularis* grp)
afrus	(incertae sedis)	*dissimilis*	(*semiferrugineus* grp)
agricultor	(*annularis* grp)	*elongatus*	(*semiferrugineus* grp)
akinini	(*semiferrugineus* grp)	*emarginatus*	(*emarginatus* grp)
albonotatus	(*albonotatus* grp)	*erraticus*	(*annularis* grp)
annae	(*annularis* grp)	*eximius*	(*armatus* grp)
annularis	(*annularis* grp)	*externus*	(*emarginatus* grp)
apfelbecki	(*annularis* grp)	*femoralis*	(*semiferrugineus* grp)
arcticus	(*annularis* grp)	*fennicus*	(*annularis* grp)
argentinus	(*semiferrugineus* grp)	*filipes*	(*annularis* grp)
atratus	(*semiferrugineus* grp)	*flavipennis*	(*armatus* grp)
atricapillus	(*semiferrugineus* grp)	*fontinalis*	(*annularis* grp)
baudii	(*annularis* grp)	*foraminosus*	(*semiferrugineus* grp)
bedeli	(*semiferrugineus* grp)	*fuscipes*	(*annularis* grp)
berlandi	(*semiferrugineus* grp)	*gallicus*	(*semiferrugineus* grp)
bernhaueri	(*annularis* grp)	*glasunovi*	(*semiferrugineus* grp)
bipustulatus	(*verres* grp)	*gravidus*	(*semiferrugineus* grp)
bolsonensis	(*emarginatus* grp)	*heterocerus*	(*semiferrugineus* grp)
bosnicus	(*annularis* grp)	*hindustanus*	(*kosempoensis* grp)
breretoni	(*annularis* grp)	*ignobilis*	(*annularis* grp)
brincki	(*emarginatus* grp)	*ignotus*	(*emarginatus* grp)
castaneus	(*semiferrugineus* grp)	*johnstoni*	(*semiferrugineus* grp)
cedarensis	(*annularis* grp)	*koenigsbaueri*	(*emarginatus* grp)
chinkiangensis	(*annularis* grp)	*kutsae*	(*annularis* grp)
clavatus	(*annularis* grp)	*laticollis*	(*annularis* grp)
claviventris	(*emarginatus* grp)	*lativentris*	(*annularis* grp)
cordicollis	(*annularis* grp)	*littoralis*	(*annularis* grp)
coulteri	(*semiferrugineus* grp)	*lividipes*	(*emarginatus* grp)
crassicollis	(*semiferrugineus* grp)	*longulus*	(*annularis* grp)
cribratus	(*semiferrugineus* grp)	*lucidus*	(*lucidus* grp)
cribricollis	(*semiferrugineus* grp)	*minarzianus*	(*semiferrugineus* grp)
curtipennis	(*emarginatus* grp)	*minax*	(*minax* grp)
decorsei	(*verres* grp)	*monstratus*	(*armatus* grp)
defensus	(*annularis* grp)	*mysticus*	(*annularis* grp)
dehnerti	(*semiferrugineus* grp)	*nanus*	(*semiferrugineus* grp)

TABLE 9—(*Continued*)

Species	Species group	Species	Species group
Hesperophilus			
newelli	(*annularis* grp)	*rectangulus*	(*albonotatus* grp)
norquincoensis	(*emarginatus* grp)	*rossicus*	(*annularis* grp)
obscurus	(*annularis* grp)	*roubali*	(*semiferrugineus* grp)
obsoletus	(*annularis* grp)	*ruficornis*	(*annularis* grp)
obtusus	(*semiferrugineus* grp)	*rugosicollis*	(*rugosicollis* grp)
occidentalis	(*semiferrugineus* grp)	*rugosulus*	(*annularis* grp)
opacicollis	(*annularis* grp)	*salinus*	(*punctatissimus* grp)
opacifrons	(*armatus* grp)	*secessus*	(*annularis* grp)
opacinus	(*verres* grp)	*semiopacus*	(*emarginatus* grp)
opacus	(*annularis* grp)	*strenuus*	(*armatus* grp)
orphanus	(*verres* grp)	*strictus*	(*annularis* grp)
osiris	(*annularis* grp)	*suturalis*	(*annularis* grp)
pallipes	(*annularis* grp)	*tenebricosus*	(*punctatissimus* grp)
papuanus	(*verres* grp)	*terebrans*	(*annularis* grp)
parisii	(*annularis* grp)	*transcaspicus*	(*semiferrugineus* grp)
parvicollis	(*albonotatus* grp)	*turgidus*	(*annularis* grp)
pechlaneri	(*annularis* grp)	*validepunctatus*	(*semiferrugineus* grp)
picipennis	(*semiferrugineus* grp)	*vilis*	(*annularis* grp)
poppiusi	(*annularis* grp)	*villosus*	(*annularis* grp)
procerulus	(*semiferrugineus* grp)	*vitaensis*	(*annularis* grp)
pusillus	(*annularis* grp)	*washingtonensis*	(*annularis* grp)
pygmaeus	(*annularis* grp)		
Dicarenus			
alfierii	(*verres* grp)	*lateripennis*	(*verres* grp)
beesoni	(*verres* grp)	*latus*	(*verres* grp)
birmanus	(*verres* grp)	*lucens*	(*kosempoensis* grp)
bispinus	(*bispinus* grp)	*lucidulus*	(*verres* grp)
bonariensis	(*bonariensis* grp)	*madagascariensis*	(*verres* grp)
buehleri	(*punctatissimus* grp)	*maindroni*	(*punctatissimus* grp)
capensis	(*punctatissimus* grp)	*marginalis*	(*verres* grp)
championi	(*bispinus* grp)	*michaelseni*	(*punctatissimus* grp)
dartevellei	(*punctatissimus* grp)	*niger*	(*verres* grp)
debilis	(*debilis* grp)	*parens*	(*verres* grp)
dilutipennis	(*verres* grp)	*peraffinis*	(*verres* grp)
doderoi	(*basalis* grp)	*perplexus*	(*verres* grp)
ealanus	(*verres* grp)	*pruinosulus*	(*punctatissimus* grp)
fergussoni	(*basalis* grp)	*pulchellus*	(*pulchellus* grp)
fernandezi	(*punctatissimus* grp)	*roettgeri*	(*verres* grp)
fraterculus	(*verres* grp)	*scheerpeltzi*	(*punctatissimus* grp)
fuscicornis	(*bispinus* grp)	*sellatus*	(*albonotatus* grp)
gradensis	(*basalis* grp)	*subniger*	(*basalis* grp)
helferi	(*infans* grp)	*transversemaculatus*	(*debilis* grp)
incertus	(*verres* grp)	*tristis*	(*punctatissimus* grp)
indicus	(*tibialis* grp)		
Astycops			
auripennis	(*tibialis* grp)	*morio*	(*tibialis* grp)
buettikeri	(*punctatissimus* grp)	*puelches*	(*punctatissimus* grp)
chilensis	(*emarginatus* grp)	*rufipes*	(*emarginatus* grp)
fossor	(*verres* grp)	*subterraneus*	(*albonotatus* grp)
frater	(*verres* grp)	*talpa*	(*albonotatus* grp)
limbatus	(*albonotatus* grp)	*tenebaumi*	(*albonotatus* grp)
maculipennis	(*punctatissimus* grp)	*tibialis*	(*tibialis* grp)

TABLE 9—(*Continued*)

Species	Species group	Species	Species group
Elbidus			
amplithorax	(*kochi* grp)	*naja*	(*kochi* grp)
bicornis	(*kochi* grp)	*naxius*	(*kochi* grp)
biskrensis	(*kochi* grp)	*ouzbekiscus*	(*kochi* grp)
bituberculatus	(*rugosicollis* grp)	*persicus*	(*kochi* grp)
carinicollis	(*kochi* grp)	*postmaculatus*	(*kochi* grp)
coiffaiti	(*furcatus* grp)	*puglialis*	(*kochi* grp)
convexicollis	(*kochi* grp)	*richteri*	(*kochi* grp)
diffinis	(*semiferrugineus* grp)	*sareptanus*	(*kochi* grp)
diota	(*kochi* grp)	*simplicifrons*	(*kochi* grp)
femineus	(*kochi* grp)	*taruensis*	(*kochi* grp)
formosanus	(*kochi* grp)	*tuniseus*	(*kochi* grp)
hinnulus	(*kochi* grp)	*turcmenus*	(*kochi* grp)
immarginatus	(*kochi* grp)	*vitulus*	(*kochi* grp)
kochi	(*kochi* grp)	*xiphias*	(*kochi* grp)
loeffleri	(*kochi* grp)		
Belidus			
angustus	(*angustus* grp)	*lindbergianus*	(*angustus* grp)
fratellus	(*fratellus* grp)	*magniceps*	(*angustus* grp)
infans	(*infans* grp)	*renominatus*	(*infans* grp)
Pucerus			
aethiops	(*verres* grp)	*latior*	(*verres* grp)
africanus	(*verres* grp)	*lepineyi*	(*verres* grp)
albomaculatus	(*verres* grp)	*louwerensi*	(*verres* grp)
albopubescens	(*verres* grp)	*mauritanicus*	(*verres* grp)
arabicus	(*verres* grp)	*negrei*	(*verres* grp)
bredoi	(*semiferrugineus* grp)	*niloticus*	(*verres* grp)
capicola	(*verres* grp)	*nodieri*	(*verres* grp)
cariniceps	(*verres* grp)	*palliatus*	(*verres* grp)
curvicornis	(*verres* grp)	*petzi*	(*verres* grp)
distans	(*verres* grp)	*rhinocerus*	(*verres* grp)
filipponii	(*semiferrugineus* grp)	*schoutedeni*	(*semiferrugineus* grp)
formosae	(*furcatus* grp)	*somalianus*	(*verres* grp)
fragilis	(*semiferrugineus* grp)	*splendens*	(*verres* grp)
ganglbaueri	(*semiferrugineus* grp)	*subopacus*	(*verres* grp)
gracilicornis	(*verres* grp)	*tenuiverres*	(*verres* grp)
haarlovi	(*semiferrugineus* grp)	*transversus*	(*verres* grp)
husseini	(*verres* grp)	*tuberculatus*	(*verres* grp)
klapperichi	(*verres* grp)	*verres*	(*verres* grp)
kosempoensis	(*kosempoensis* grp)	*yemenicus*	(*semiferrugineus* grp)
Euceratobledius			
andresi	(*furcatus* grp)	*dinoceros*	(*furcatus* grp)
atramentarius	(*furcatus* grp)	*eckerleini*	(*furcatus* grp)
bellicosus	(*bellicosus* grp)	*furcatus*	(*furcatus* grp)
capra	(*furcatus* grp)	*rudebecki*	(*lamelliceps* grp)
Microbledius			
actitus	(*forcipatus* grp)	*litoreus*	(*forcipatus* grp)
albidus	(*forcipatus* grp)	*miles*	(*forcipatus* grp)
albipennis	(*forcipatus* grp)	*minutissimus*	(*forcipatus* grp)
bifasciatus	(*forcipatus* grp)	*playanus*	(*forcipatus* grp)
forcipatus	(*forcipatus* grp)	*weiseri*	(*forcipatus* grp)

TABLE 9—(*Continued*)

Species	Species group	Species	Species group
Psamathobledius			
caribbeanus	(*punctatissimus* grp)	*punctatissimus*	(*punctatissimus* grp)
microcephalus	(*punctatissimus* grp)		
Neobledius			
karachiensis	(*kochi* grp)		
Unassigned			
aculeatus	(*semiferrugineus* grp)	*fasciatus*	(incertae sedis)
acuticollis	(*emarginatus* grp)	*fenyesi*	(*armatus* grp)
addendus	(*emarginatus* grp)	*ferratus*	(*mandibularis* grp)
albomarginatus	(*punctatissimus* grp)	*fortis*	(*mandibularis* grp)
amplicollis	(*punctatissimus* grp)	*fossiventris*	(*punctatissimus* grp)
analis	(*semiferrugineus* grp)	*fumatus*	(*semiferrugineus* grp)
aquilonarius	(*armatus* grp)	*gabonensis*	(*verres* grp)
arenicola	(*verres* grp)	*gebieni*	(*emarginatus* grp)
assimilis	(*semiferrugineus* grp)	*gemellus*	(*gigantulus* grp)
aterrimus	(*emarginatus* grp)	*gentilis*	(*annularis* grp)
aurantius	(*annularis* grp)	*gigantulus*	(*gigantulus* grp)
auriculicollis	(*kochi* grp)	*gomezi*	(*emarginatus* grp)
australis	(*lucidus* grp)	*gracilis*	(*annularis* grp)
austrinus	(*verres* grp)	*gregarius*	(*emarginatus* grp)
basalis	(*basalis* grp)	*gyllenhalii*	(*basalis* grp)
beattyi	(*aequatorialis* grp)	*gyotokoi*	(*gigantulus* grp)
bellicus	(*armatus* grp)	*habrus*	(*annularis* grp)
bicolor	(*annularis* grp)	*hamifer*	(*hamifer* grp)
bidentifrons	(*punctatissimus* grp)	*hasticeps*	(*lamelliceps* grp)
bruchi	(*emarginatus* grp)	*hlisnikowskii*	(*semiferrugineus* grp)
bubalus	(incertae sedis)	*honestus*	(*annularis* grp)
caroli	(*punctatissimus* grp)	*ineptus*	(*armatus* grp)
castaneipennis	(*semiferrugineus* grp)	*infantilis*	(*emarginatus* grp)
cavus	(*verres* grp)	*injucundus*	(*punctatissimus* grp)
ceratus	(*aequatoralis* grp)	*inornatus*	(*semiferrugineus* grp)
chimerinus	(incertae sedis)	*insignicornis*	(*verres* grp)
circularis	(*circularis* grp)	*jacobinus*	(*mandibularis* grp)
clarus	(*annularis* grp)	*jacobsoni*	(*verres* grp)
cognatus	(*emarginatus* grp)	*jadarensis*	(*annularis* grp)
compressicollis	(*compressicollis* grp)	*jamaicensis*	(*emarginatus* grp)
condensus	(*annularis* grp)	*japonicus*	(*annularis* grp)
confusus	(*annularis* grp)	*jucundus*	(*annularis* grp)
congoensis	(*verres* grp)	*lateralis*	(*semiferrugineus* grp)
conicicollis	(*kosempoensis* grp)	*leai*	(*emarginatus* grp)
consimilis	(*armatus* grp)	*longipennis*	(incertae sedis)
convexifrons	(*emarginatus* grp)	*lugubris*	(*lugubris* grp)
cordatus	(*basalis* grp)	*mandibularis*	(*mandibularis* grp)
cowleyi	(*lucidus* grp)	*marinus*	(*gigantulus* grp)
cubensis	(*emarginatus* grp)	*maritimus*	(*furcatus* grp)
curticornis	(*verres* grp)	*melanocolus*	(*annularis* grp)
derasus	(*armatus* grp)	*militaris*	(*emarginatus* grp)
diagonalis	(*albonotatus* grp)	*minniensis*	(*minniensis* grp)
dimidiatus	(*basalis* grp)	*minor*	(*basalis* grp)
episcopalis	(*armatus* grp)	*minutus*	(*emarginatus* grp)
erythraenus	(*semiferrugineus* grp)	*modestus*	(*emarginatus* grp)
exiguus	(*punctatissimus* grp)	*monticola*	(*annularis* grp)

TABLE 9—(*Continued*)

Species	Species group	Species	Species group
Unassigned			
muticus	(*emarginatus* grp)	*rubiginosus*	(*semiferrugineus* grp)
naius	(*annularis* grp)	*sanguinicollis*	(*kochi* grp)
nardus	(*albonotatus* grp)	*sanguinithorax*	(*semiferrugineus* grp)
nebulosus	(*annularis* grp)	*santschii*	(incertae sedis)
neglectus	(*basalis* grp)	*semicircularis*	(*bellicosus* grp)
nitidiceps	(*armatus* grp)	*semiferrugineus*	(*semiferrugineus* grp)
nitidicollis	(*semiferrugineus* grp)	*similis*	(*emarginatus* grp)
notialus	(*armatus* grp)	*simplex*	(*emarginatus* grp)
obihiroensis	(*annularis* grp)	*sinuatus*	(*annularis* grp)
omega	(*albonotatus* grp)	*stabilis*	(*annularis* grp)
opaculus	(*basalis* grp)	*susae*	(*aequatorialis* grp)
orientalis	(*punctatissimus* grp)	*tallaci*	(*semiferrugineus* grp)
orion	(*semiferrugineus* grp)	*tarandus*	(*albonotatus* grp)
ovensensis	(*emarginatus* grp)	*tau*	(*albonotatus* grp)
pallidipennis	(*emarginatus* grp)	*testaceipennis*	(*emarginatus* grp)
pallipennis	(*mandibularis* grp)	*thinopus*	(*basalis* grp)
parcissimus	(*emarginatus* grp)	*trinidadensis*	(*emarginatus* grp)
parvulus	(*emarginatus* grp)	*turbulentus*	(*basalis* grp)
perrieri	(*verres* grp)	*ugandae*	(*verres* grp)
persimilis	(*annularis* grp)	*venus*	(*albonotatus* grp)
philadelphicus	(*semiferrugineus* grp)	*verticalis*	(incertae sedis)
philippinus	(*gigantulus* grp)	*victoriae*	(*emarginatus* grp)
phytosinus	(*annularis* grp)	*viriosus*	(*annularis* grp)
politus	(*armatus* grp)	*westerhauseri*	(incertae sedis)
pontilis	(*punctatissimus* grp)	*withycombei*	(*emarginatus* grp)
porcellus	(*verres* grp)	*wombaliensis*	(*verres* grp)
pumilio	(*emarginatus* grp)	*wudus*	(*emarginatus* grp)
rarus	(*emarginatus* grp)	*yezoensis*	(*gigantulus* grp)
rotundicollis	(*semiferrugineus* grp)	*zophus*	(*albonotatus* grp)

with long, narrow stalk and furcal arms; furcal arms sclerotized and anteriolaterally directed; anterior tendons close to one another and arising from median body. Protibia expanded and with one to three rows of spinelike setae and often with other scattered spinelike setae. Mesotibia with two rows of spinelike setae. Tarsal formula 3-3-3 (fig. 479) or 4-4-4.

Abdominal sternite II well developed. Terga without basolateral ridges. Tergum VII with fringe on posterior margin. Tergum VIII with posterior margin truncate or emarginate. Segments II to VII each with two pairs of laterosclerites. Tergum IX divided by tergum X (fig. 387); canal for abdominal glands with dorsal surface membranous (fig. 423) or sclerotized (fig. 371). Segment IX of female with genital appendages (ventral) paired, elongate, and flattened (fig. 401); segment IX of male with sternum flattened and elongate. Aedeagus (figs. 122, 133, 253, 424, 451) with or without parameres; median lobe of variable shape.

Spermatheca bipartite (figs. 367, 386) or tripartite (fig. 121).

SPECIES INCLUDED: As of this writing there are 439 extant species in the genus. Included in the present work is a catalogue of the species along with their synonyms. The genus is divided into 34 species groups. The species that comprise each group are listed following the description of each group and under Conspectus of the Classification.

DISTRIBUTION: *Bledius* is known from all continents except Antarctica and from most continental islands; it is absent from most oceanic islands (figs. 1 to 12). The species are most common in warm, open, sunny, moist sand near bodies of water. Details of the habitat are discussed in the chapter on Natural History. The localities from which specimens have been examined are listed following the description of each species group.

SYNONYMS: *Neobledius* is a synonym of *Bledius* and *Elbidus.* It shares with *Bledius* all the characters that define the group and possesses none that would separate it from other *Bledius.* Further, it shares characters with *Elbidus,* which I call the *kochi* group.

Microbledius and *Psamathobledius* were separated from *Bledius* because they both possess three segmented tarsi and have unique genitalic characters (Herman, 1972). Further study shows that the tarsal formula of *Bledius* can be 3-3-3 or 4-4-4. Both *Microbledius* and *Psamathobledius* still represent distinct groups but are renamed herein as the *forcipatus* and *punctatissimus* groups, respectively, because I have chosen to designate the infrageneric groups with species group rather than subgeneric names.

That being said then, all the names of the heretofore recognized subgenera are replaced by species group names and many species groups are designated that have no corresponding subgeneric name. This decision is discussed in the introductory remarks of the present chapter. Table 8 lists the generic group names included in *Bledius* along with their species group equivalent.

KEY TO THE SPECIES GROUPS OF *BLEDIUS* FOR THE WORLD

1. Pronotal lateral marginal bead absent (fig. 382) or largely incomplete (figs. 116, 458) 2
Pronotal lateral marginal bead present (fig. 216) and complete or largely complete (figs. 131, 169) 11
2(1). Elytral epipleural ridge complete (as in fig. 279) .... 8. *minniensis* group
Elytral epipleural ridge incomplete (fig. 250) or absent 3
3(2). Tergum VIII with truncate posterior margin (fig. 477) 4
Tergum VIII with emarginate posterior margin (fig. 344) 6
4(3). Labrum with median incision (fig. 457) .... 33. *pulchellus* group
Labrum without median incision (fig. 374) 5
5(4). Old World species (fig. 10); prosternal process short and cariniform (as in fig. 363) .... 24. *infans* group
New World species (fig. 12); prosternal process elongate (fig. 382) .... 26. *forcipatus* group
6(3). Elytra with membranous lobe on posterior margin (fig. 251) 7
Elytra without membranous lobe on posterior margin 8
7(6). Procoxal fissure open (fig. 159) 9
Procoxal fissure closed (fig. 417) ... 10
8(6). Prosternum with patch of setae anterior to procoxae (fig. 604); labrum with median incision (fig. 112) .... 1. *mandibularis* group
Prosternum with setigerous pit anterior to procoxae (fig. 702); labrum without median incision (fig. 413) .... 29. *angustus* group
9(7). Old World species (fig. 1); males with one pair of cephalic horns .... 4. *hamifer* group
New World species (fig. 1); males with two pairs of cephalic horns[17] (fig. 157) ... . 6. *aequatorialis* group
10(7). Protergosternal suture absent (fig. 417); postocular carina absent .... 29. *angustus* group
Prosternal suture present; postocular carina present but only weakly on female .... 7. *circularis* group
11(1). Elytral epipleural ridge incomplete or absent (fig. 250) 12
Elytral epipleural ridge complete (fig. 297) 21
12(11). Elytra with membranous lobe on posterior margin (fig. 251) 13
Elytra without membranous lobe on posterior margin 17
13(12). Procoxal fissure closed (fig. 252) .... 16. *lucidus* group
Procoxal fissure open[18] (fig. 216) ... 14
14(12). Clypeus with anterior margin reflexed (figs. 66, 215) .... 13. *lamelliceps* group, *B. hasticeps*
Clypeal margin not reflexed 15
15(14). New World species (fig. 1) .... 6. *aequatorialis* group
Old World species 16
16(15). Protibia with three rows of spinelike setae (as in fig. 60); males with supraantennal

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[17] Supraantennal horns of *B. susae* and some individuals of the other species are reduced to small swellings on the anterior and posterior edges of the supraantennal ridge.

[18] Procoxal fissure of *B. bellicosus* is narrowly open.

and pronotal horns (figs. 127, 131) .... 2. *bellicosus* group

Protibia with two rows of spinelike setae (as in fig. 59); males without supraantennal and pronotal horns .... 11. *immaturus* group

17(12). Tergum VIII with posterior margin truncate (fig. 477) 18

Tergum VIII with posterior margin emarginate (fig. 344) 19

18(17). Gular sutures separated anteriorly (figs. 395, 396) ... 27. *punctatissimus* group

Gular sutures fused anteriorly (as in fig. 380) .... 25. *fratellus* group

19(17). Clypeus with anterior margin reflexed .... 31. *tibialis* group

Clypeal margin not reflexed 20

20(19). Elytral epipleural ridge absent; Old World species .... 28. *lugubris* group

Elytral epipleural ridge incomplete (fig. 394); New World species .... 27. *punctatissimus* group

21(11). Gular sutures strongly separated anteriorly (fig. 395, 396) 22

Gular sutures fused anteriorly (as in fig. 380) 24

22(21). Tergum VIII with posterior margin emarginate (as in fig. 344) .... 27. *punctatissimus* group

Tergum VIII with posterior margin truncate (fig. 477) 23

23(22). Labrum with median incision (fig. 442) .... 32. *bonariensis* group

Labrum without median incision (fig. 391) .... 27. *punctatissimus* group

24(21). Procoxal fissure closed (fig. 449) ... 25

Procoxal fissure open (fig. 203) 34

25(24). Labrum with median incision (fig. 442) 26

Labrum without median incision (fig. 391) 28

26(25). Tergum VIII with posterior margin truncate (as in fig. 477) .... 32. *bonariensis* group

Tergum VIII with posterior margin emarginate (figs. 271, 299) 27

27(26). Protergosternal suture absent; hypopharynx with long cuticular processes (figs. 537, 539, 541) ... 19. *armatus* group

Protergosternal suture present and hypopharynx with short cuticular processes (figs. 531–539) .... 18. *semiferrugineus* group[19]

28(25). Protergosternal suture absent (fig. 339) .... 23. *basalis* group

Protergosternal suture present (figs. 331, 398) 29

29(28). Tergum VIII with truncate posterior margin (as in fig. 477) .... 27. *punctatissimus* group

Tergum VIII with emarginate posterior margin (fig. 344) 30

30(29). Prosternum with patch of setae (figs. 631, 636) 32

Prosternum with setigerous pit (figs. 144, 696) 31

31(30). Tarsal formula 3-3-3 (fig. 392) .... 27. *punctatissimus* group

Tarsal formula 4-4-4 ... 22. *debilis* group

32(30). Tergum IX (fig. 262) with lobed apex (dorsal view) .... 17. *kosempoensis* group

Tergum IX (as in fig. 387) convergent to apex (dorsal view) 33

33(32). Elytra with membranous lobe on posterior margin (as in fig. 290) .... 5. *minax* group

Elytra without membranous lobe on posterior margin .... 15. *emarginatus* group[20]

34(24). Labrum without median incision (fig. 168) 42

Labrum with median incision (figs. 304, 314) 35

35(34). Clypeal margin reflexed (as in fig. 66) 36

Clypeal margin not reflexed 38

36(35). Prosternum with small setigerous pit anterior to procoxa (as in fig. 724) .... 30. *bispinus*

Prosternum with broad, shallow setigerous depression anterior to procoxa (fig. 625) 37

37(36). Metatibia with one subapical spinelike seta on lateral surface ... 14. *kochi* group

Metatibia with row of 3 to 5 subapical spinelike setae on lateral surface (fig. 202 .... 12. *furcatus* group

38(35). Tergite VII with coarse fringe on posterior margin (fig. 57) 10. *gigantulus* group

Tergite VII with fine fringe on posterior margin (as in fig. 55) 39

39(38). Tergum VIII with truncate posterior margin (fig. 477) ...... 34. *verres* group

Tergum VIII with emarginate posterior margin (fig. 344) 40

40(39). Labrum with deeply emarginate, bilobed

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[19] Three species of the *armatus* group have the protergosternal suture and will therefore run to the *semiferrugineus* group. The *armatus* group is found only in the New World. Separation of the three species is discussed in the Diagnosis of the *armatus* group.

[20] One species of the *emarginatus* group, *B. ovensensis*, has a narrowly open procoxal fissure that might be considered as closed; therefore that species is brought out in this couplet.

anterior margin (figs. 303, 304) .... 20. *albonotatus* group
Labrum with truncate or shallowly to moderately deeply emarginate anterior margin (fig. 288) 41
41(40). Labrum with broad midlongitudinal depression ...... 30. *bispinus* group
Labrum flat, without midlongitudinal depression ... 21. *annularis* group[21]
42(34). Clypeal margin reflexed (fig. 66) 43
Clypeal margin not reflexed 45
43(42). Head with postocular carina on lateral margin (figs. 66, 212, 215) .... 13. *lamelliceps* group
Head without postocular carina on lateral margin 44
44(43). Metatibia with 1 subapical spinelike seta on lateral surface ... 14. *kochi* group
Metatibia with row of 3 to 5 subapical spinelike setae on lateral surface (fig. 202) .... 12. *furcatus* group
45(42). Pronotal lateral marginal bead on prohypomeron (fig. 169) 46
Pronotal lateral marginal bead dividing pronotum and prohypomeron, not on prohypomeron (fig. 182) 48
46(45). Pronotum with horns (males) .... 3. *compressicollis* group
Pronotum without horns 47
47(46). Tergum VII with fine fringe (females) (as in fig. 55) .. 3. *compressicollis* group
Tergum VII with coarse fringe (as in fig. 57) .... 9. *rugosicollis* group
48(45). Tergum VII with coarse fringe on posterior margin (fig. 57) .... 10. *gigantulus* group[22]
Tergum VII with fine fringe on posterior margin (fig. 55) 49
49(48). Protrochantin clearly exposed for entire length of procoxal fissure (fig. 235) .. .. 15. *emarginatus* group
Protrochantin largely concealed, exposed only at slightly open ventral portion of fissure (fig. 331) ... 22. *debilis* group[23]

1. *mandibularis* group

Figures 1, 15–28, 36, 50, 109–124, 485–490, 604–606

DIAGNOSIS: Unique to this group and separating it from all others is the excavation of the submentum (figs. 117–120).

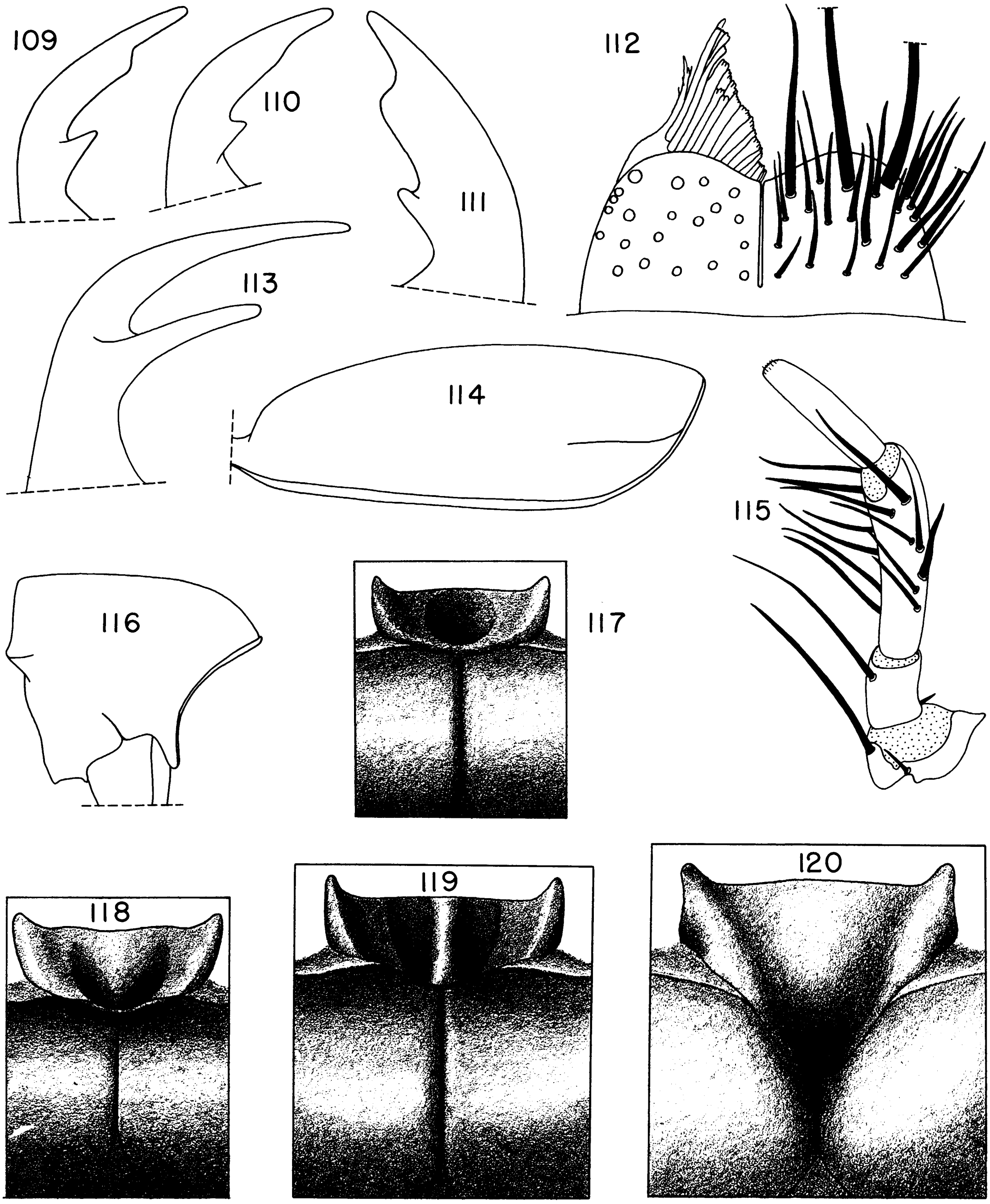
The group can be separated from all others by the incomplete pronotal marginal bead (fig. 116) and elytral epipleural ridge (fig. 114), absence of the protergosternal suture (fig. 116) and membranous lobe of the elytral margin, the closed procoxal fissure (fig. 116), the emarginate eighth tergum, and presence of the median labral incision and absence of the setigerous prosternal pit.

DESCRIPTION: Supraantennal ridge low, not enlarged, and without horns. Head without subantennal pockets; midbasal horn absent; postocular lateral carina absent. Clypeal margin not reflexed; anterior margin with or without tubercles; clypeal middle without spines, tubercles, or ridges. Gular sutures fused. Labral margin emarginate (fig. 112); margin not reflexed; median incision present (fig. 112); dorsal surface flat, without midlongitudinal impression. Epipharyngeal lobe short (fig. 112); dorsal surface with one long and one short seta; median processes with lobed apices; lateroapical processes numerous, slender, and branched or unbranched. Labial palps (fig. 115) with first segment shortest, second segment longest, and third segment of intermediate length; first and second segments of subequal thickness; first segment with two setae, second with many. Submentum with surface excavated (figs. 117–120). Mentum trapezoidal; surface with more setae laterally than medially. Hypopharynx (figs. 485–490) with lateral rows of spines gradually convergent toward base; basal setae stout and arranged in transverse basal cluster; cluster not on plate; central row of setae dense throughout and row indistinguishable from setae on disk; disk with setae densely covering entire surface; disk covered with long slender cuticular processes; coronal pegs present in bare patch near apex. Prementum with four sclerites, one medial, one basal, and two lateral. Galea with cluster of scattered, thick, long setae, and dense cluster of more slender setae; denser cluster with setae arranged in fanlike rows; ventral surface without setae; dorsomedial edge with lobe. Man-

[21] A few species, such as *B. turgidus*, *B. litoralis*, *B. ruficornis*, and *B. viriosus*, have the dorsal portion of the procoxal fissure closed. The ventral portion, however, is open and the protrochantin exposed.

[22] *B. convexicollis*, and a few other species which belong in the *kochi* group, run here to the *gigantulus* group. They can be separated from the *gigantulus* group by the absence of the pronotal horn in the male and by the feeble carinules on the lateral margin of the clypeus.

[23] The *debilis* group is brought out here and in couplet 31 because the procoxal fissure is closed to narrowly open. Based on characters of the epipharynx and hypopharynx, the group is clearly related to the *basalis* group.



FIGS. 109–120. The *mandibularis* group. **109.** Mandible, left (*ferratus*). **110.** Mandible, left (*mandibularis*). **111.** Mandible, right (*mandibularis*). **112.** Labrum, left setae and right epipharyngeal lobe removed (*fortis*). **113.** Mandible, left (*pallipennis*). **114.** Elytron, lateral (*mandibularis*). **115.** Labial palpus (*fortis*). **116.** Prothorax, lateral view (*ferratus*). 117–120. Submentum and gular region. **117.** (*jacobinus*). **118.** (*mandibularis*). **119.** (*fortis*). **120.** (*pallipennis*).

dibles bidentate; apical denticle often with flattened, subapical lobe (figs. 109–111, 113).

Pronotal horn absent. Marginal bead incomplete, present only anteriorly (fig. 116). Protergosternal suture absent (fig. 116). Procoxal fissure closed. Protrochantin concealed.

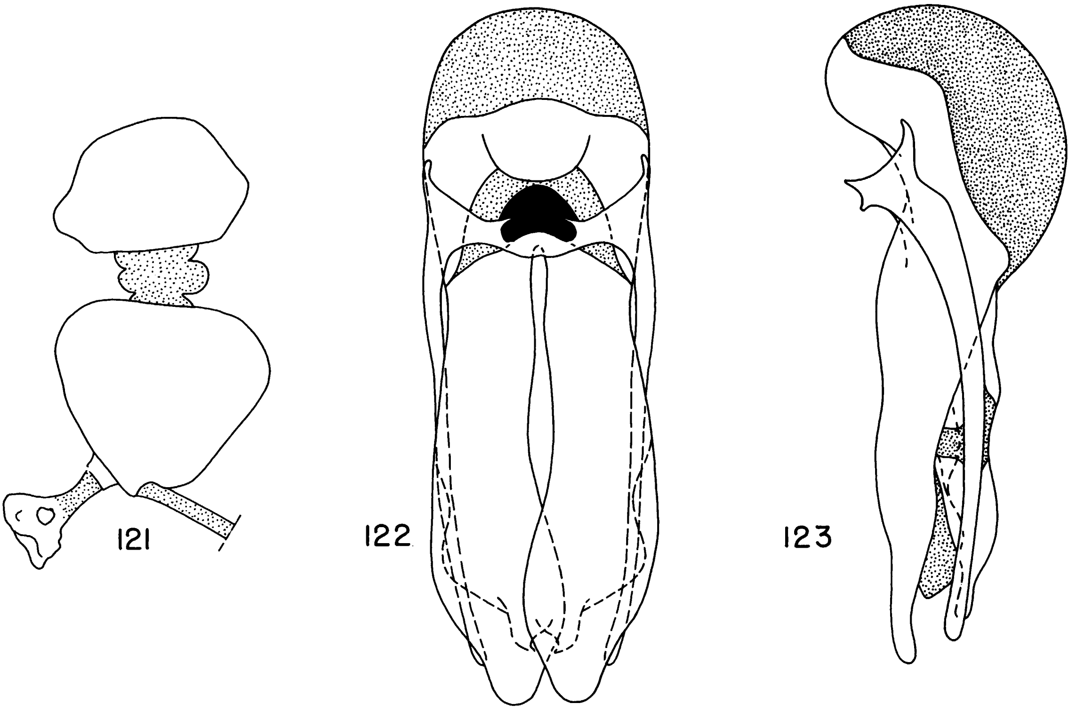


FIG. 121–123. The *mandibularis* group. **121.** Spermatheca. 122–123. Aedeagus (*mandibularis*). **122.** Dorsal view. **123.** Lateral view.

Prosternal process elongate. Prosternal setigerous pit absent; sternum with patch of setae surrounding shallow depression (figs. 604–606); depression with a few pores; anterior margin entire, without notch. Elytral epipleural ridge incomplete, present only apically (fig. 114); posterior margin without membranous lobe.

Tarsi four segmented. Protibia with one row of spinelike setae and with others scattered on posterior surface.

Abdominal tergum VII with fine fringe on posterior margin. Tergum VIII with posterior margin emarginate; margin entire, not serrate. Tergum IX with glandular canal widely open dorsally. Tergum X with struts on anterior margin.

Aedeagus (figs. 122, 123) with parameres. Parameres slender and with median surface sclerotized; parameres extending to near but not beyond apex of median lobe. Median lobe long; base bulbous, apical portion flattened; ventral surface midlongitudinally divided.

Spermatheca (fig. 121) tripartite. Receptacle sclerotized and divided by accordian tube into two parts; basal part larger than distal part; distal part without invagination. Spermathecal gland sclerotized; shape and surface irregular.

DISTRIBUTION AND HABITAT: This group is restricted to North America from southern Canada to southern Mexico. One species is reported from one West Indian and two Bahamian islands (fig. 124).

Four of the five species are restricted to coastal and inland saline habitats where they may be abundant. The fifth species is found along the Mississippi Drainage but evidently is restricted to the western portion of it. I have one doubtful, unspecified record from Ohio, but if the freshwater species is found east of the Mississippi it must be uncommon.

DISCUSSION: This species group was originally separated by LeConte (1877). He included all of the species presently placed there. None of the species have been included in subgenera. Herman (1972) provided a revision of the group and a key to the species.

Species Included and Material Examined

ferratus LeConte T(MCZ), Sp(AMNH); type country: USA.

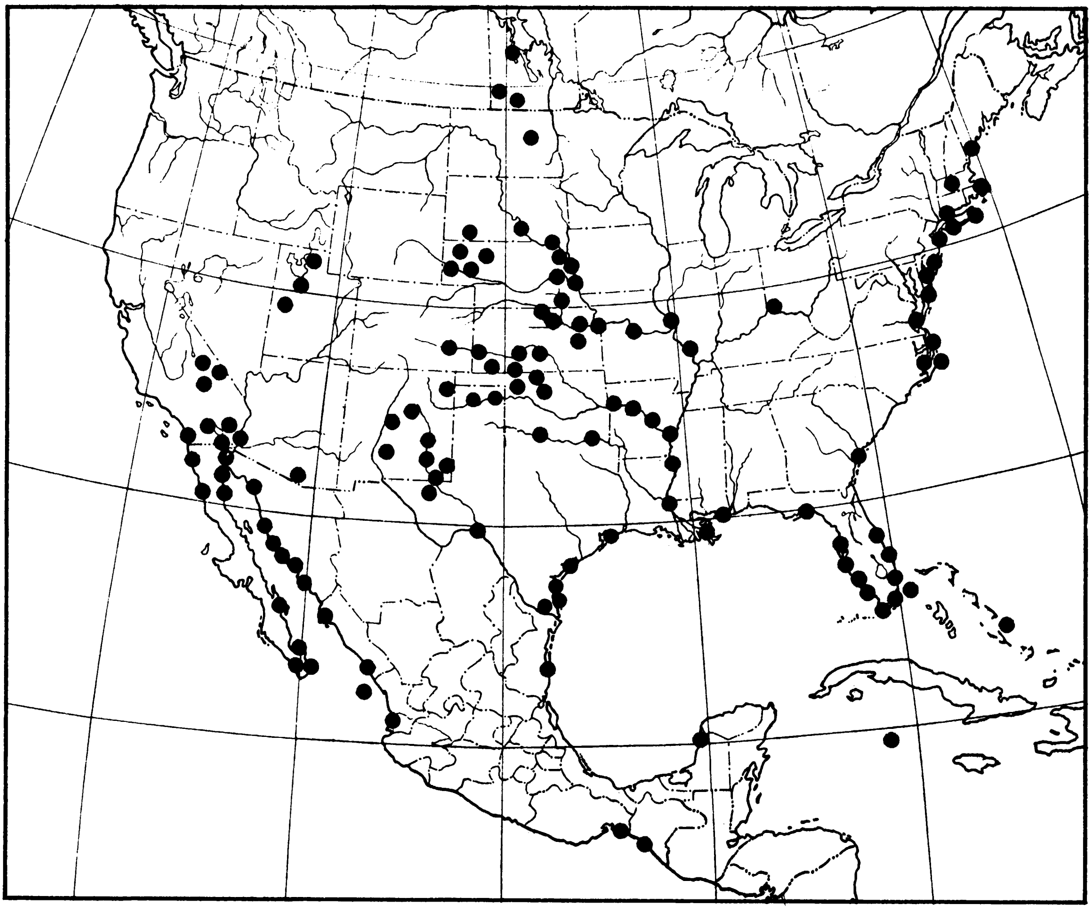


FIG. 124. Distribution of the *mandibularis* group in North America.

Southwestern **USA** and western **Mexico** (Herman, 1972, 1983a).

fortis LeConte T(MCZ), Sp(AMNH); type country: USA.

Coast of Texas, **USA** and Tamaulipas, **Mexico** (Herman, 1972, 1983a). New record: Texas: Cameron Co., South Padre Island (AMNH).

jacobinus LeConte T(MCZ), Sp(AMNH); type country: USA.

Western **Mexico** and southwestern **USA** (Herman, 1972, 1983a).

mandibularis Erichson Sp(AMNH); type country: USA.

Eastern and southern coastal and central interior **USA** and **West Indies** (Herman, 1972, 1983a).

pallipennis (Say) Sp(AMNH); type country: USA.

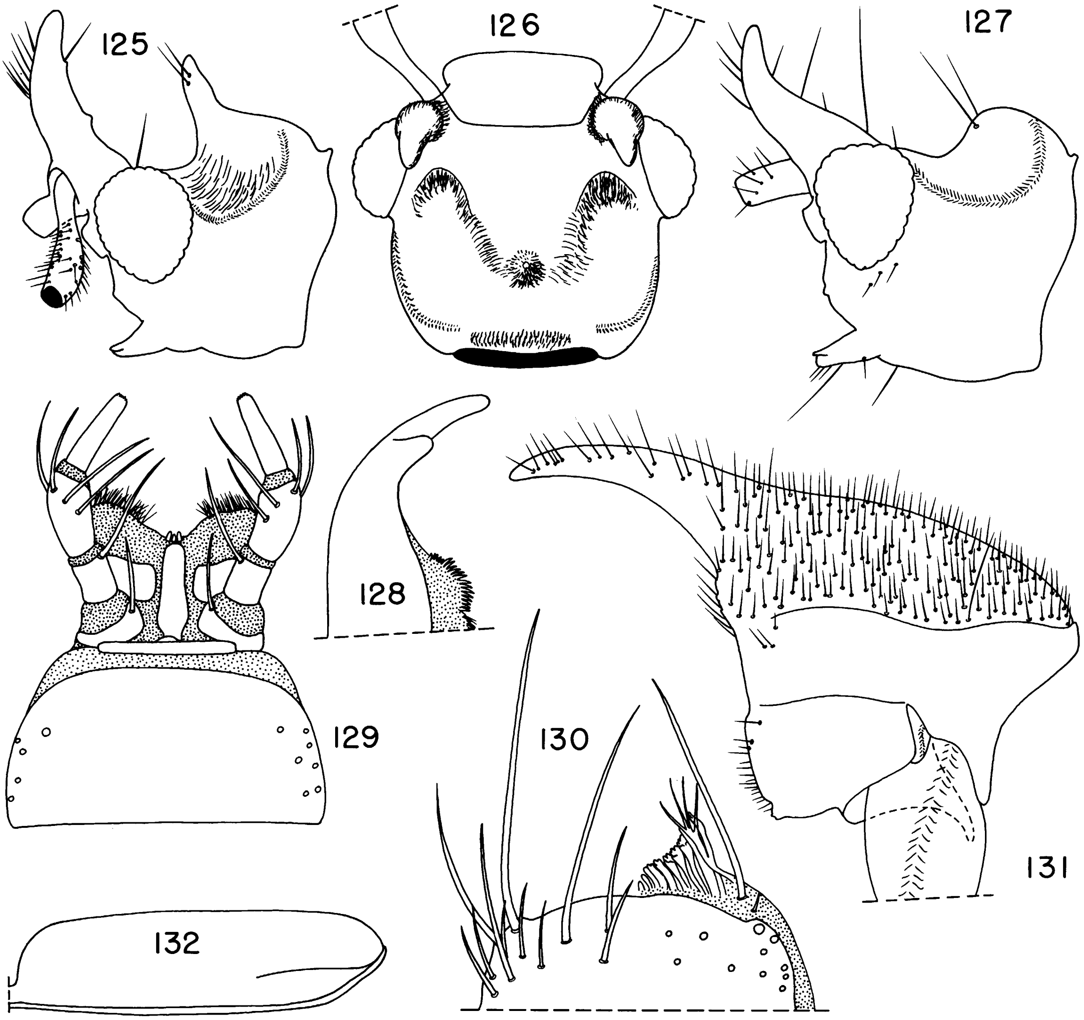
Central **USA** (Herman, 1972, 1983a).

2. *bellicosus* group

Figures 2, 125–139, 491–493, 619–621

DIAGNOSIS: The males of this group have a median horn (figs. 125, 126) or tumescence (fig. 127) at the base of the head and can therewith be separated from the males of all other groups except the *compressicollis* group from which the *bellicosus* group can be separated by its incomplete elytral epipleural ridge (fig. 132). Also useful for recognizing the males of the *bellicosus* group are the presence of one pair of supraantennal horns (figs. 125–127), a postocular cephalic carina (figs. 125–127), and a deflexed pronotal horn (fig. 131). The aedeagus (figs. 133–136) is distinctive in that the base of the paramere is large and envelops the median lobe.

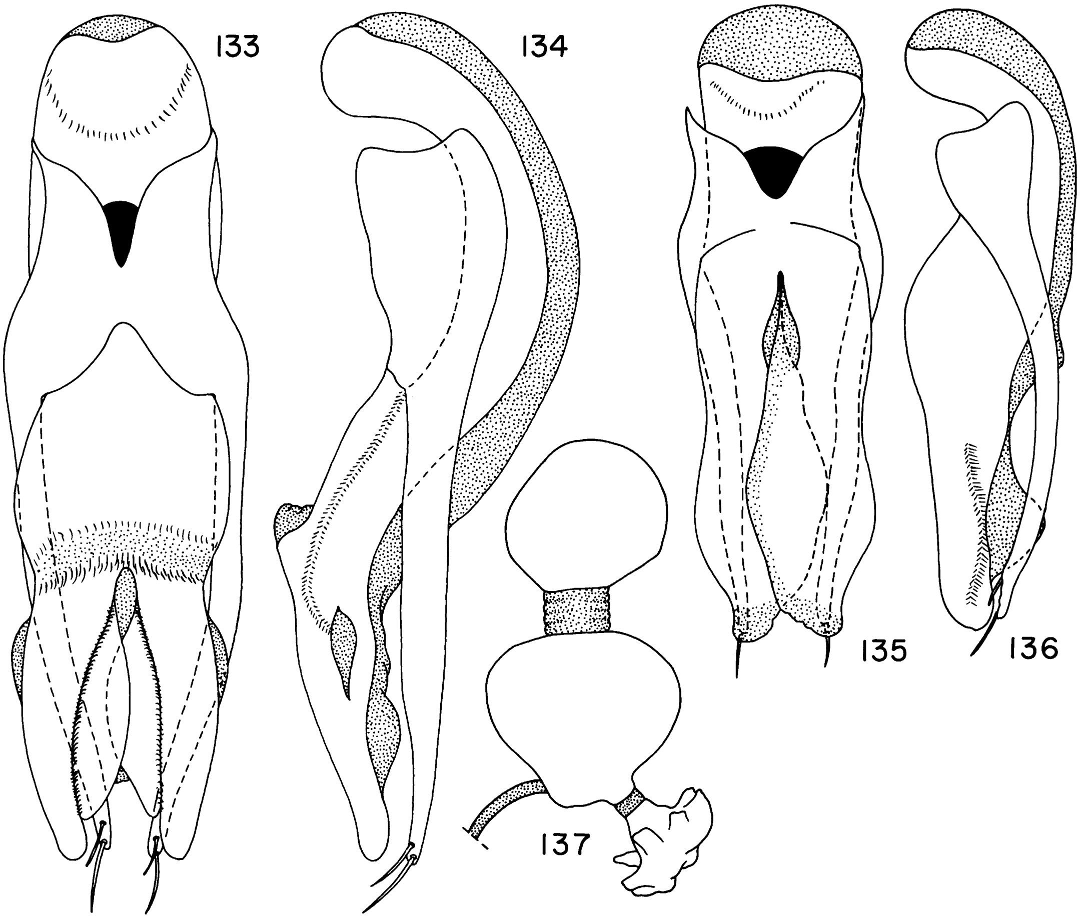
The females are separated from other groups except the *aequatorialis* group by the complete pronotal marginal bead (fig. 131),



FIGS. 125–132. The *bellicosus* group. **125.** Head, lateral, male, mouthparts removed (*bellicosus*). **126.** Head, dorsal, male, mouthparts removed (*bellicosus*). **127.** Head, lateral, male, antenna and mouthparts removed (n. sp.). **128.** Mandible, left (n. sp.). **129.** Labium (*bellicosus*). **130.** Labrum (*bellicosus*). **131.** Prothorax, lateral, male (*bellicosus*). **132.** Elytron, lateral (*bellicosus*).

the incomplete elytral epipleural ridge (fig. 132), the open procoxal fissure (fig. 131), the presence of a membranous lobe on the posterior margin of the elytra, and the three rows of spinelike setae on the protibia (as in fig. 60). The females of this group can be separated from those of the *aequatorialis* group by distribution. The *bellicosus* group is Old World (fig. 2), the *aequatorialis* group New World (fig. 1).

DESCRIPTION: Supraantennal ridge of male with one dorsally directed horn (figs. 125–127); female without horn. Head without subantennal pocket; midbasal horn (figs. 125, 127) present in male (absent or small in minor males) and absent in female; postocular lateral carina present in male (figs. 125–127), absent or weak in female. Clypeal margin not reflexed; anterior margin without tubercles; clypeal middle without spines, ridges, or tubercles. Gular sutures fused. Labrum (fig. 130) with anterior margin entire; anterior margin not reflexed; median incision absent; dorsal surface flat, without broad midlongitudinal impression. Epipharyngeal lobe short; dorsal surface with one long and one short seta; me-



FIGS. 133–137. The *bellicosus* group. **133.** Aedeagus, dorsal (*bellicosus*). **134.** Aedeagus, lateral (*bellicosus*). **135.** Aedeagus, dorsal (n. sp.). **136.** Aedeagus, lateral (n. sp.). **137.** Spermatheca (*bellicosus*).

dian processes with lobed apices; lateroapical portion with one thick multiramous process. Labial palps (fig. 129) with first segment shortest, second and third of subequal thickness; first segment with two setae, second with four or five. Submentum without excavation. Mentum (fig. 129) with setae present laterally and absent medially. Hypopharynx (figs. 491–493) with lateral rows of setae gradually convergent toward base; basal setae stout and arranged in transverse row; basal setae not on plate; central row of setae dense distally, absent medially and proximally; discal setae scattered on lateral and apical portion; disk covered with short, slender cuticular processes; coronal pegs on median portion of disk. Prementum (fig. 129) with four sclerites, one medial, two lateral, and one basal. Galea with dense cluster of setae on apex; ventral surface without setae; dorsomedial edge with lobe. Mandibles bidentate (fig. 128).

Pronotum of male with deflexed horn (fig. 131); female without horn. Marginal bead present (fig. 131) and complete; bead dividing notum and hypomeron, not on hypomeron. Protergosternal suture present (fig. 131). Bead and suture parallel (fig. 131). Procoxal fissure widely to narrowly open. Protrochantin exposed. Prosternal process elongate (fig. 131). Prosternal setigerous pit absent; sternum with patch of setae present around depression (figs. 619–621); depression with dense cluster of pores behind ridge (figs. 620, 621); anterior margin notched, more strongly so in male than female. Elytral epipleural ridge present and incomplete, present only on apical region

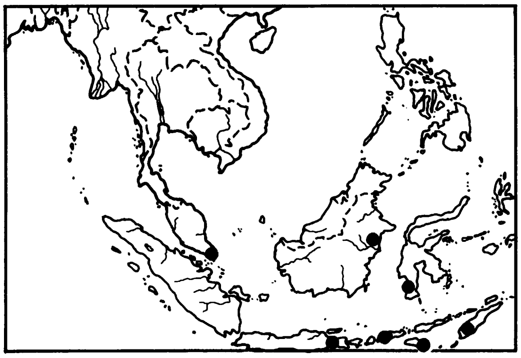


FIG. 138. Distribution of the *bellicosus* group in Indonesia.

(fig. 132); posterior margin with membranous lobe.

Tarsi four segmented. Protibia with three rows of spinelike setae. Metatibia with spinelike setae scattered over lateral surface near apex.

Abdominal tergum VII with fine fringe on posterior margin. Tergum VIII with posterior margin emarginate; margin entire, not serrate. Tergum IX with glandular canal widely open dorsally. Tergum X with struts on anterior margin.

Aedeagus (figs. 133–136) with parameres. Parameres slender and with medial surface sclerotized; parameres extending to apex of median lobe; base of parameres large and enveloping median lobe. Median lobe long; base bulbous, apical portion flattened, ventral surface midlongitudinally divided.

Spermatheca (fig. 137) tripartite. Receptacle sclerotized and divided into two parts by accordion tube; basal part larger than distal part; distal part without invagination; receptacle without brimlike ridges. Spermathecal gland sclerotized; shape and surface irregular.

DISTRIBUTION AND HABITAT: This group occurs in the western Pacific from the Malayan peninsula eastward to New Guinea and northern Australia (figs. 138, 139).

DISCUSSION: This group is recognized for the first time herein. One species was formerly in *Bledius* (s. str.), another in *Euceratobledius,* and the third was unassigned (table 9). They should be revised.

Although the female of this group can be separated from those of the *aequatorialis* group only by distribution, the males of the two groups are readily distinguished by several characters.

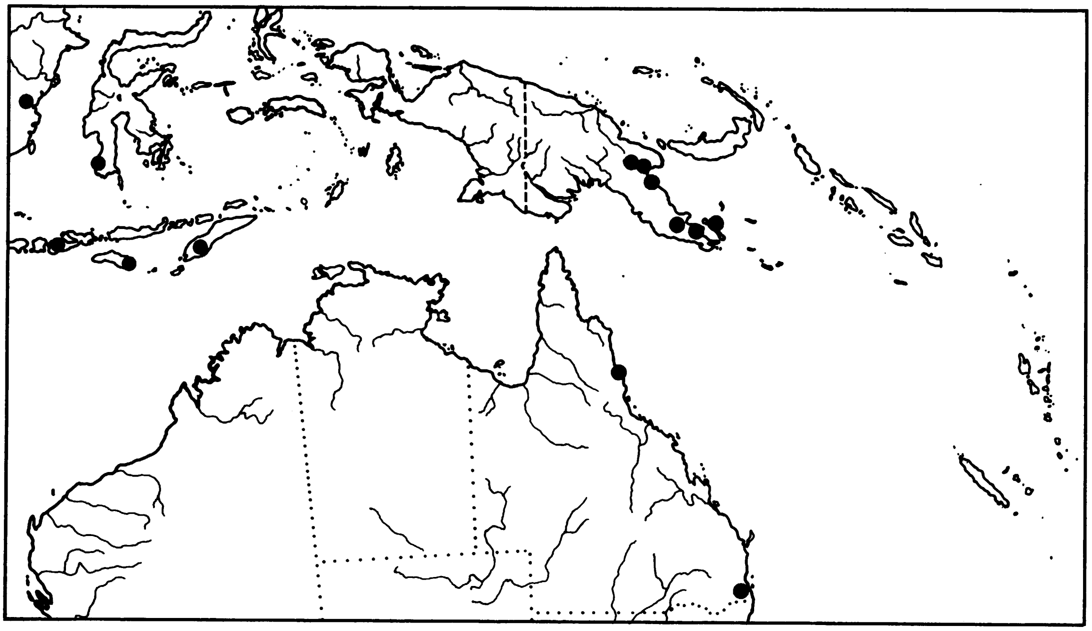


FIG. 139. Distribution of the *bellicosus* group in Indonesia, Papua New Guinea, and Australia.

The group is represented on the Cape York Peninsula of Australia by an undescribed species whose males have an interrupted pronotal marginal bead. The interruption is small; the marginal bead is mostly complete so I include it in the *bellicosus* group. Another new species represented by one male from "West Australia" has characters of both the *hamifer* and *bellicosus* groups. Both of these groups and the West Australian specimen have the postocular lateral carina. The West Australian specimen has a midbasal cephalic horn, which the *bellicosus* group has and the *hamifer* group lacks, and it lacks the pronotal marginal bead, which is present in the *bellicosus* group and absent in the *hamifer* group. The aedeagus of the West Australian specimen is similar to that of the *bellicosus* group. I have not been able to dissect for the aedeagus of the *hamifer* group. In my key to groups, this West Australian specimen runs to the *hamifer* group from which it can be separated by the presence of a midbasal cephalic horn.

Whether or not the West Australian specimen should be recognized as a separate group or combined with the *bellicosus* group (or even the *hamifer* group) will have to await more detailed analysis of the *bellicosus, hamifer, minax,* and *compressicollis* groups. In all of these groups there is a total of only six species, plus several undescribed ones, and I have had few specimens available for examination or dissection.

Species Included and Material Examined

bellicosus Fauvel Syn(IRSN), Sp(BMNH, FMNH); type country: Indonesia.

Borneo: (IRSN) (Batoe Panggal ? IRSN). (Tiboga? FMNH). **Indonesia:** Sumbawa (IRSN, MNHV, FMNH); Sumbawa (B. Aroe Hassa ? BMNH); Java (Toerabaya? IRSN); Sulawesi, Makassar (IRSN); Java, Malang (IRSN); Sumba, Melolo (MNHV); Sumba, Baing (MNHV). **Singapore:** (BMNH).

quadricornis Bernhauer T(FMNH); type country: Indonesia.

Indonesia: Java (Mis. Kawlo ? FMNH).

semicircularis Lea Syn(SAM); type country: Australia.

Australia: Queensland, Brisbane (SAM).

Undetermined.

Australia: (BMNH); Queensland, Cairns (BMNH). **Indonesia:** Timor (Gng. Leo, Ned.? BMNH); Sulawesi (BMNH). **Papua New Guinea:** Markham Valley, 11 mi. W Lae (CNC); Peria Creek, Kwagira River (AMNH); Cape Vogel Peninsula, Menapi (AMNH); Morobe, Umi River, Markham Valley, 95 mi. from Lae (AMNH); (Biniguni, Gwariu River ? AMNH); Fergusson Island, Iamelele (AMNH); Morobe District (BMNH); (Torricelli Mountains, Mobitei? BPBM).

3. *compressicollis* group

Figures 1, 140

DIAGNOSIS: The presence of the pronotal marginal bead on the hypomeron rather than dividing the pronotum from the prohypomeron will separate this group from all others but the *rugosicollis* and *tibialis* groups. The *tibialis* group has a reflexed anterior clypeal margin, a median labral incision, and an incomplete elytral epipleural ridge. The anterior margin of the clypeus of the *compressicollis* group is not reflexed, the labrum lacks a median incision, and the epipleural ridge is complete. The *compressicollis* group has a notch on the anterior margin of the prosternum and tergum VII has a fine fringe on the posterior margin. The *rugosicollis* group lacks the notch on the prosternal margin and the fringe of tergum VII is coarse.

The males of the *compressicollis* group have one pair of supraantennal horns, a postocular lateral carina, a midbasal carinate cephalic tumescence, and a deflexed pronotal horn. The *bellicosus* and *hamifer* groups are similar. The *hamifer* group lacks the midbasal cephalic tumescence, lacks a pronotal marginal bead, and has an incomplete elytral epipleural ridge. The *compressicollis* group has an entire elytral epipleural ridge. The elytral epipleural ridge of the *bellicosus* group is also incomplete and the pronotal marginal bead divides the notum and hypomeron.

DESCRIPTION. Supraantennal ridge of male with one dorsally directed horn; female without horn. (Subantennal pocket—no data.) Postocular lateral carina present. Midbasal cariniform horn present on male, absent on female. Clypeal margin not reflexed; anterior margin without tubercles; clypeal middle without spines, ridges, or tubercles. Gular sutures fused. Labrum with anterior margin en-

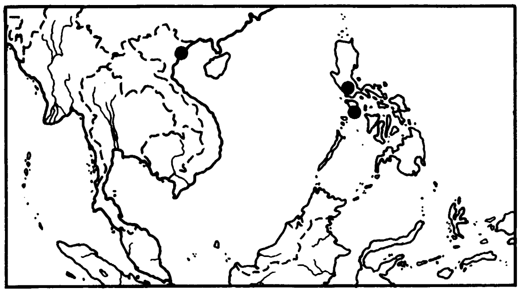


FIG. 140. Distribution of the *compressicollis* group in Vietnam and the Republic of the Philippines.

tire; anterior margin feebly reflexed; median incision absent; dorsal surface flat, without broad midlongitudinal impression. (Epipharyngeal lobe—no data.) (Labial palps—no data.) Submentum not excavated. (Mentum—no data.) (Hypopharynx—no data.) (Prementum—no data.) (Galea—no data.) Mandibles edentate or tridentate.

Pronotum of male with deflexed horn; female without horn. Marginal bead present and complete; bead on hypomeron. Protergosternal suture present. Bead and suture parallel or slightly convergent. Procoxal fissure open. Protrochantin exposed. Prosternal process elongate. Prosternal setigerous pit absent; sternum with patch of setae present around depression (no data on pores of depression); anterior margin notched, more strongly so in male than female. Elytral epipleural ridge present and complete; posterior margin with membranous lobe.

Tarsi four segmented. Protibia with three rows of spinelike setae. Metatibia with spinelike setae scattered over lateral surface near apex.

Abdominal tergum VII with fine fringe on posterior margin. Tergum VIII with posterior margin emarginate; margin entire, not serrate. (Tergum IX—no data.) (Tergum X—no data.)

(Aedeagus—no data.)

(Spermatheca—no data.)

DISTRIBUTION AND HABITAT: This group is known only from the Philippines and Vietnam (fig. 140).

DISCUSSION: The only named species in this group has not been included in a subgenus. The group has some unique features. This group is known by six specimens, none of which I was able to dissect.

B. compressicollis, from the Philippines, has edentate mandibles. An undescribed species from Vietnam has tridentate mandibles.

Species Included and Material Examined

compressicollis Bernhauer T,Sp(FMNH), Sp(MNHV; IRSN); type country: Philippine Islands.

Philippines: Luzon, Manila (MNHV, FMNH); Luzon, Mt. Maquiling (FMNH); Luzon, Los Banos (FMNH).

Undetermined.

Philippines: Mindoro, San Jose (BMNH). **Vietnam:** Haiphong (IRSN).

4. *hamifer* group

Figures 1, 141

DIAGNOSIS: This group can be separated from all groups except the *aequatorialis* group by the absence of the pronotal marginal bead, the incomplete elytral epipleural ridge, the presence of a membranous lobe on the posterior elytral margin, the emarginate tergum VIII, and the open procoxal fissure. In the *hamifer* group the males have one pair of supraantennal horns and the group is restricted to the Old World, whereas the *aequatorialis* group occurs in the New World and the males have two pairs of supraantennal horns. The *hamifer* group is also similar to the *bellicosus* and *compressicollis* groups. The absence of a pronotal marginal bead separates this group from both the *bellicosus* and *compressicollis* groups (see also Discussion under the *bellicosus* group).

DESCRIPTION: Supraantennal ridge of male with one dorsally directed horn; supraantennal ridge of female low and without horn. (Subantennal pocket—no data.) Head of male with midbasal pimplelike bump; bump with one seta; female without midbasal cephalic horn or pimple. Postocular lateral carina present. Clypeal margin not reflexed; anterior margin without tubercles; clypeal middle without tubercles, spines, or ridges. Gular sutures fused. Labrum with anterior margin entire; anterior margin not reflexed; median incision absent; dorsal surface flat, without broad midlongitudinal impression. (Epipharyngeal lobe—no data.) (Labial palps—no

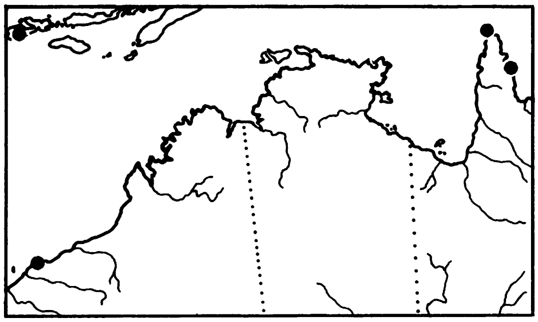


FIG. 141. Distribution of the *hamifer* group in Indonesia and Australia.

data.) Submentum not excavated. (Mentum—no data.) (Hypopharynx—no data.) (Prementum—no data.) (Galea—no data.) Mandibles tridentate.

Pronotum of male with deflexed horn; female without pronotal horn. Marginal bead absent. Protergosternal suture present. Procoxal fissure open. Protrochantin exposed. Prosternal process elongate. Prosternal setigerous pit absent; sternum with patch of setae present around depression (no data for pores of depression); anterior margin with notch. Elytral epipleural ridge present and incomplete, present only at apex; posterior margin with membranous lobe.

Tarsi four segmented. Protibia with three rows of spinelike setae. Metatibia with one spinelike seta on lateral side near apex.

Abdominal tergum VII with fine fringe. Tergum VIII with posterior margin emarginate; margin entire, not serrate. (Tergum IX—no data.) (Tergum X—no data.)

(Aedeagus—no data.)

(Spermatheca—no data.)

DISTRIBUTION AND HABITAT: This group is known only from Indonesia and northern Australia (fig. 141).

DISCUSSION: The sole species in this group has never been assigned to an infrageneric group. Little is known about the Indo-Australian *Bledius*, but this species is quite distinctive.

This group is known by four specimens: the holotype of the only described species, *B. hamifer*; an undetermined female from Sumbawa; an undetermined male from the Cape York Peninsula in Australia; and an undetermined female from Prince of Wales Island, Australia. The undetermined male differs from *B. hamifer* by the more narrowly open procoxal fissure.

The females of the *hamifer* group are difficult to separate from those of the *aequatorialis* group, but the males of the two groups are separated by the number of supraantennal horns.

The base of the head of the males of the *hamifer* group lack the median horn but in its place there is a small pimple with one seta. This may be homologous with the median horn of the *bellicosus* and *compressicollis* groups (see also the Discussion under the *bellicosus* group).

Species Included and Material Examined

hamifer Fauvel. T(BMNH); type country: Australia.
Australia: Nickol Bay (BMNH).
Undetermined.
Australia: Queensland, Iron Range, Cape York (BMNH); Prince of Wales Island (BPBM). **Indonesia:** Sumbawa (MNHV).

5. *minax* group

Figures 1, 142–144

DIAGNOSIS: This group can be separated from all others by the presence of a deflexed pronotal horn and one pair of supraantennal horns in the males, a complete pronotal marginal bead and elytral epipleural ridge, the presence of a patch of setae in a broad prosternal depression, the closed procoxal fissure, the presence of a protergosternal suture and a membranous lobe on the posterior elytral margin, and the emarginate eighth tergum. The *minax* group is easily separated from the other Indo-Australia groups in which the males have supraantennal horns and a deflexed pronotal horn (*hamifer, bellicosus,* and *compressicollis*) because the males of the *minax* group have no midbasal cephalic horn or even a suggestion of one (as for example the setose pimple of the *hamifer* group). The *minax* group has a closed procoxal fissure; the other three groups have an open fissure.

DESCRIPTION: Supraantennal ridge of male with one dorsally directed horn; female without horn. (Subantennal pocket—no data.) Postocular lateral carina present but weakly developed. Head without midbasal horn or tumescence. Clypeal margin not reflexed; anterior margin without tubercles; clypeal middle without ridges, spines, or tubercles. Gular sutures fused. Labrum with anterior margin entire; anterior margin feebly reflexed; median incision absent; dorsal surface flat, without broad midlongitudinal impression. (Epipharynx—no data.) (Labial palps—no data.) Submentum not excavated. (Mentum—no data). (Hypopharynx—no data.) (Prementum—no data.) (Galea—no data.) Mandibles tridentate.

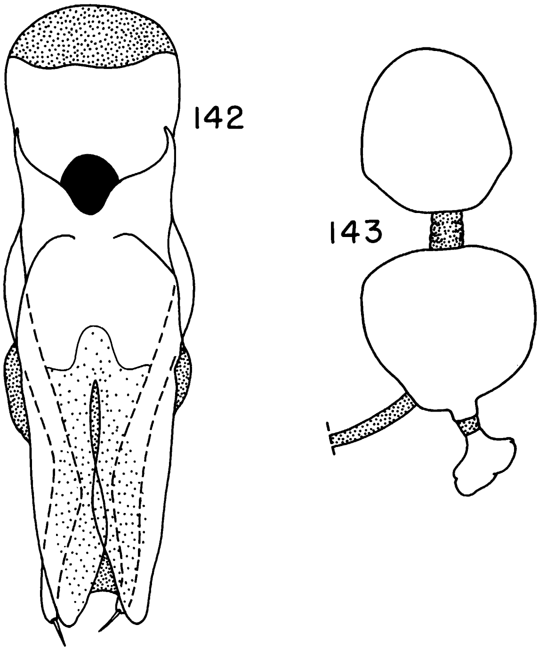
Pronotum of male with deflexed horn; female without horn. Marginal bead present and complete; bead dividing notum and hypomeron, not on hypomeron. Protergosternal suture present. Bead and suture nearly parallel. Procoxal fissure closed. Protrochantin concealed. Prosternal process elongate. Prosternal setigerous pit absent; sternum with patch of setae present around depression (no data for pores in depression); anterior margin of male notched and of female entire. Elytral epipleural ridge present and complete; posterior margin with membranous lobe present.

Tarsi four segmented. Protibia with three rows of spinelike setae. Metatibia with spinelike setae scattered on lateral surface near apex.

Abdominal tergum VII with medium fringe on posterior margin. Tergum VII with posterior margin emarginate, margin entire, not serrate. Tergum IX with glandular canal widely open dorsally. Tergum X with struts on anterior margin.

Aedeagus (fig. 142) with parameres. Parameres slender, with medial surface sclerotized, and extending to near apex of median lobe; base of parameres moderately large and enveloping median lobe moderately. Median lobe long; base bulbous, apical portion flattened; ventral surface midlongitudinally divided.

Spermatheca (fig. 143) tripartite. Receptacle sclerotized and divided into two parts; basal part larger than distal part; distal part without invagination; receptacle without brimlike ridges. Spermathecal gland sclerotized; shape and surface irregular.



FIGS. 142–143. The *minax* group. *Bledius minax*. **142.** Aedeagus, dorsal. **143.** Spermatheca.

DISTRIBUTION AND HABITAT: This group is known only from southern and western Australia (fig. 144).

DISCUSSION: The only species in this group had been assigned to *Hesperophilus*. Since so little is known about the Indo-Australian *Bledius* and this species is so distinctive, I have segregated it from others.

Species Included and Material Examined

minax Blackburn Sp(BMNH, MCZ, FMNH, IRSN); type country: Australia.
Australia: Albany (IRSN); Gawler (IRSN); Yanchep, 32 mi. N Perth (BMNH); (Vasse? BMNH, FMNH): Western Australia, Mt. William (BPBM); Western Australia, Mullewa (MCZ).

6. *aequatorialis* group

Figures 1, 60, 145–160, 494, 495, 607–612

DIAGNOSIS: The males of this group are separated from all other groups by the presence of two pairs of supraantennal horns (fig. 157) that in one species are reduced to two

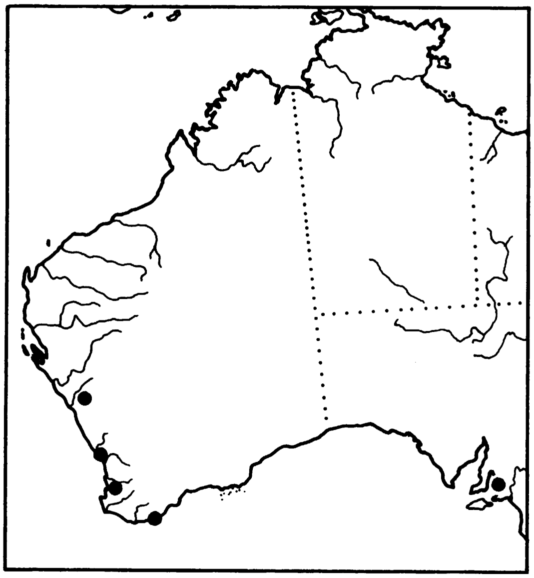


FIG. 144. Distribution of the *minax* group in Australia.

pairs of small swellings (figs. 148, 149). This group is the only one in the New World with a pronotal horn (figs. 151, 154, 159).

The group is separated from all other groups by the absence of a median labral incision (fig. 152), absence of a setigerous prosternal pit, the open procoxal fissure (figs. 145, 147), incomplete elytral epipleural ridge, presence of a membranous lobe on the elytral margin, the emarginate eighth tergum, and by its restriction to the New World (fig. 1).

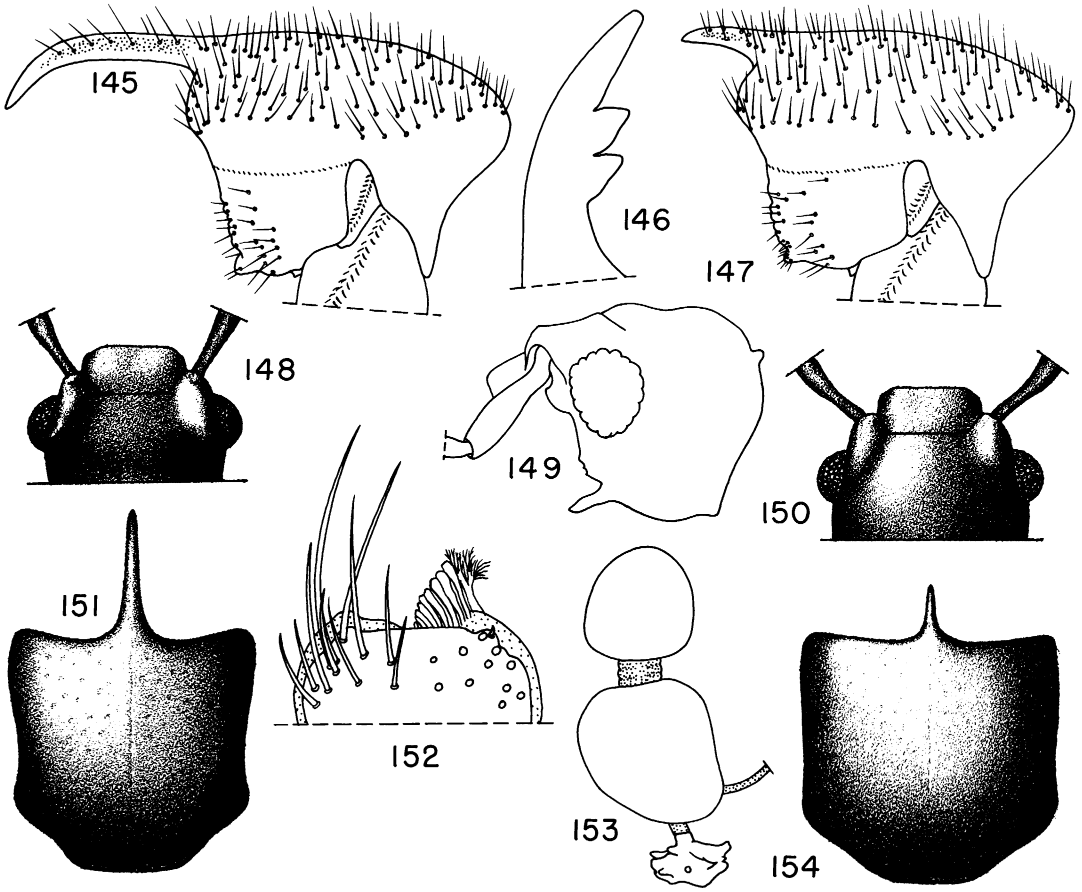
The females of the *aequatorialis* group can be separated from the *hamifer* and *bellicosus* groups by the geographical distribution. The *immaturus* group is separated by the presence of only two rows of protibial spines and by the coarser fringe on Tergum VIII.

DESCRIPTION: Supraantennal ridge of male with two dorsally directed horns (fig. 157) in one species reduced to small swellings on anterior and posterior ends of supraantennal ridge (figs. 148, 149); female without horns, ridge low. Head without subantennal pocket; midbasal horn absent; postocular lateral carina absent or present but weak. Clypeal margin not reflexed; anterior margin without tubercles; clypeal middle without spines, ridges, or tubercles. Gular sutures fused. Labrum (fig. 152) with anterior margin entire or slightly emarginate; anterior margin not reflexed; median incision absent (fig. 152); dorsal surface flat, without broad midlongitudinal impression. Epipharyngeal lobe (fig. 152) short; dorsal surface with one long and one minute seta; median processes with lobed apices; lateroapical portion with thick multiramous processes. Labial palps (fig. 158) with segments of subequal length; segments 1 and 2 of subequal thickness; first segment with two setae, second segment with three or four. Submentum not excavated. Mentum with setae present laterally and absent or sparse medially. Hypopharynx (figs. 494, 495) with lateral rows of setae gradually convergent toward base; basal setae arranged in curved, transverse row; basal setae stout, not on plate; central row of setae dense distally and sparser proximally; disk with setae scattered over surface; disk with cuticular processes scattered over surface; coronal pegs scattered over surface. Prementum with four sclerites, two lateral, one medial, and one basal. Galea with dense cluster of setae arranged in fanlike rows on apex; ventral surface without setae; dorsomedial edge with lobe. Mandibles bidentate or tridentate (fig. 146).

Pronotum of male with deflexed horn (figs. 145, 151, 159); female without horn or one species with short, slender, slightly deflexed horn (figs. 147, 154). Marginal bead present and complete (fig. 159) or incomplete or absent (fig. 145); bead dividing notum and hypomeron, not on hypomeron. Protergosternal suture present (fig. 159). Bead and suture parallel. Procoxal fissure open. Protrochantin exposed. Prosternal process elongate (fig. 159). Prosternal setigerous pit absent; sternum with patch of setae present around depression (figs. 607–612); depression with dense cluster of pores behind ridge; anterior margin with procoxal notch (figs. 145, 147), notch stronger in male than female. Elytral epipleural ridge present and incomplete; posterior margin with membranous lobe.

Tarsi four segmented. Protibia with three rows of spinelike setae. Metatibia with spinelike setae scattered on lateral surface near apex.

Abdominal tergum VII with fine fringe on posterior margin. Tergum VIII with posterior margin emarginate; margin entire, not serrate. Tergum IX with glandular canal widely



FIGS. 145–154. The *aequatorialis* group. *Bledius susae*. **145.** Prothorax, male, lateral view. **146.** Left mandible. **147.** Prothorax, female, lateral view. **148.** Head, male, dorsal view. **149.** Head, male, lateral view. **150.** Head, female, dorsal view. **151.** Prothorax, male, dorsal view. **152.** Labrum. **153.** Spermatheca. **154.** Prothorax, female, dorsal view.

open dorsally. Tergum X with struts on anterior margin.

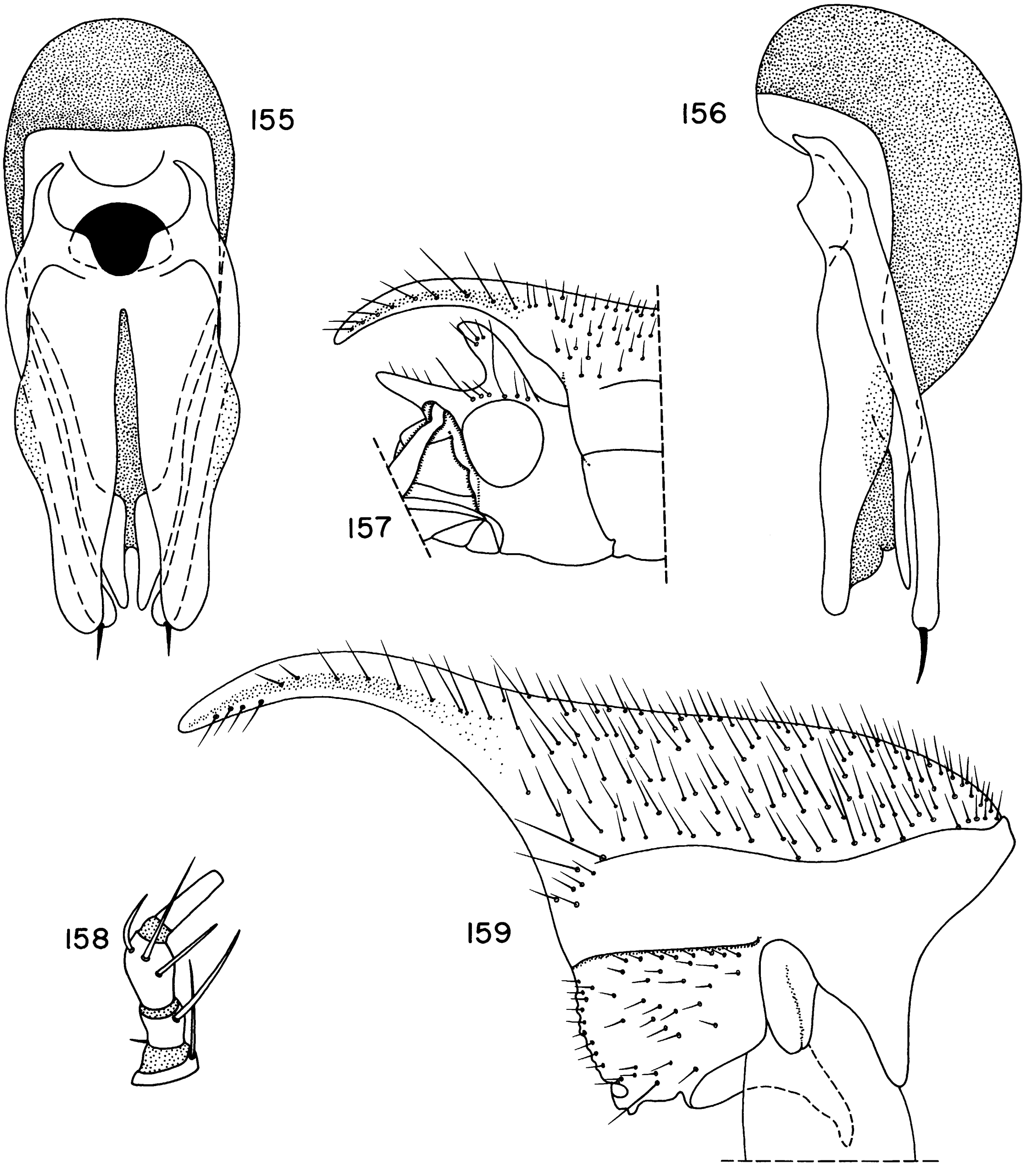
Aedeagus (figs. 155, 156) with parameres. Parameres slender and with medial surface sclerotized; parameres extending to apex of median lobe. Median lobe long; base bulbous, apical portion flattened; ventral surface midlongitudinally divided.

Spermatheca (fig. 153) tripartite. Receptacle sclerotized and divided into two parts by accordion tube; basal part larger than or equal to distal part; distal part without invagination; receptacle without brimlike ridges. Spermathecal gland sclerotized; shape and surface irregular.

DISTRIBUTION AND HABITAT: This group is known from coastal localities on the continental edges of the Caribbean Sea and the West Indies, and from the coasts of Ecuador and the Galapagos Islands (fig. 160).

DISCUSSION: This group was originally recognized by Herman (1972) who included three species. Later (Herman, 1983a) a fourth, *B. susae,* was added. Coiffait (1981c) put *B. aequatorialis* in the nominate subgenus. If a subgenus *Bledius* were recognized and species like *aequatorialis* included, then one would probably have to include in that subgenus all the species with pronotal horns along with those of the *kochi, rugosicollis, immaturus,* and *circularis* groups.

Descriptions of the four species are found



FIGS. 155–159. The *aequatorialis* group. **155.** Aedeagus, dorsal view (*aequatorialis*). **156.** Aedeagus, lateral view. **157.** Head and apex of prothorax, male, lateral view (*aequatorialis*). **158.** Labial palpus (*susae*). **159.** Prothorax, male, lateral view (*beattyi*).

in Herman, 1972 and 1983a; a revised Key to species is in the latter publication.

Species Included and Material Examined

aequatorialis Mutchler T,SP(AMNH); type country: Galapagos Islands. **Ecuador** and **Galapagos Islands** (Herman, 1972).

beattyi Blackwelder T(USNM), Sp(AMNH); type country: Virgin Islands: St. Croix. **West Indies** and **Colombia** (Herman, 1972, 1983a).

ceratus Blackwelder T(USNM), Sp(AMNH); type country: Haiti.

West Indies, Florida, USA, and **Bahamas** (Herman, 1972, 1983a).

susae Herman T,P,Sp(AMNH); type country: USA.

Coastal Texas, USA (Herman, 1983a). New record: Texas: Cameron Co., South Padre Island (AMNH).

7. *circularis* group

Figures 1, 161, 162, 164

DIAGNOSIS: The incomplete pronotal marginal bead and elytral epipleural ridge, emarginate eighth tergum, closed procoxal fissure, and presence of a protergosternal suture will separate this group from all others. The presence of the postocular cephalic carina and three rows of spinelike setae place this group near the *minax, hamifer, compressicollis, bellicosus,* and *aequatorialis* groups. The *circularis* group is separated from these groups by the absence of a complete pronotal marginal bead and the closed procoxal fissure. Furthermore, the male lacks supraantennal and pronotal horns.

DESCRIPTION: Supraantennal ridge without horn. (Subantennal pocket—no data.) Head without midbasal horn. Head with postocular lateral carina present; carina weaker in female than male. Clypeal margin not reflexed; anterior margin without tubercles; clypeal middle without tubercles, spines, or ridges. Gular sutures fused. Labrum with anterior margin entire; anterior margin not reflexed; median incision absent; dorsal surface flat, without broad midlongitudinal impression. (Epipharyngeal lobe—no data.) (Labial palps—no data.) Submentum not excavated. (Mentum—no data.) (Hypopharynx—no data.) (Prementum—no data.) (Galea—no data.) Mandibles bidentate.

Pronotum of female without horn or tumescence; male with broad tumescence on anterior margin. Marginal bead present and incomplete; bead divides notum and hypomeron. Protergosternal suture present. Suture convergent anteriorly with remnant of bead. Procoxal fissure closed. Protrochantin concealed. Prosternal process elongate. Prosternal setigerous pit absent; sternum with patch of setae present near depression (no data for pores in depression); anterior margin without notch. Elytral epipleural ridge incomplete, present only at apex; posterior margin with membranous lobe.

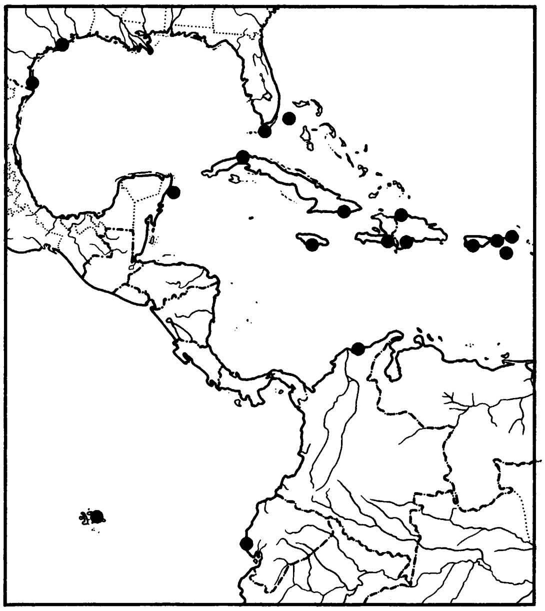


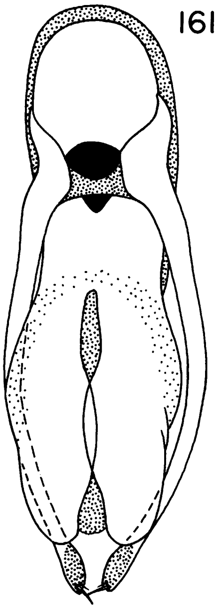
FIG. 160. Distribution of the *aequatorialis* group in the region of the Caribbean Sea, Gulf of Mexico, Ecuador, and the Galapagos Islands.

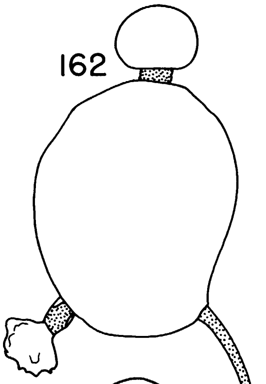
Tarsi four segmented. Protibia with three rows of spinelike setae. Metatibia with one spinelike seta on lateral subapical surface.

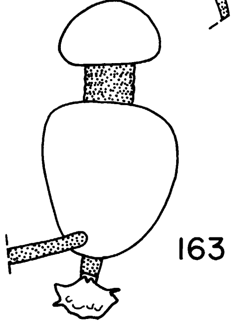
Abdominal tergum VII with fine fringe. Tergum VIII with posterior margin emarginate; margin entire, not serrate. Tergum IX with glandular canal open dorsally. Tergum IX with struts on anterior margin.

Aedeagus (fig. 161) with parameres. Parameres long, slender, and with most of medial surface sclerotized; apical portion with membranous medial surface; parameres extending beyond apex of median lobe; median portion of base of parameres membranous. Median lobe long; base bulbous; apical portion flattened; ventral surface midlongitudinally divided.

Spermatheca (fig. 162) tripartite. Receptacle sclerotized and divided into two parts by accordion tube; basal part larger than distal part; distal part without invagination; receptacle without brimlike ridges. Spermathecal gland sclerotized; shape and surface irregular.







FIGS. 161–162. The *circularis* group. *Bledius circularis.* **161.** Aedeagus, dorsal. **162.** Spermatheca.

FIG. 163. The *minniensis* group. *Bledius minniensis.* Spermatheca.

DISTRIBUTION AND HABITAT: This group is known by four specimens from three localities in New Caledonia and northern Australia (fig. 164).

DISCUSSION: *Bledius circularis* has not been included in an infrageneric group previously and is segregated here because of the presence of a membrane that connects each paramere over the median foramen. The male I studied has a median pronotal tumescence which may represent the vestigial pronotal horn of a minor male. If true there may be males of the species of this group with pronotal and perhaps supraantennal horns.

Species Included and Material Examined

circularis Fauvel T(IRSN); type country: New Caledonia.

New Caledonia: Koné (IRSN); (Ouano Beach ? BPBM).

Undetermined.

Australia: Cape York Peninsula, Iron Range, East Claudie River (AMNH); Darwin (AMNH).

8. *minniensis* group

Figures 1, 163, 165

DIAGNOSIS: The incomplete pronotal marginal bead and the presence of the elytral epipleural ridge will distinguish this group from all others. Additional characters that aid the recognition of this group include the absence of a labral incision, open procoxal fissure, presence of the protergosternal suture, presence of a membranous lobe on the elytral margin, and the emarginate eighth tergum.

DESCRIPTION: Supraantennal ridge without horn. (Subantennal pocket—no data.) Head without midbasal horn; postocular lateral carina absent. Clypeal margin not reflexed; anterior margin without tubercles; clypeal middle without tubercles, spines, or ridges. Gular sutures fused. Labrum with anterior margin entire; anterior margin not reflexed; median incision absent; dorsal surface flat, without broad midlongitudinal impression. (Epipharyngeal lobe—no data.) (Labial palps—no data.) Submentum not excavated. (Mentum—no data.) (Hypopharynx—no data.) (Prementum—no data.) (Galea—no data.) Mandibles bidentate.

Pronotum without horn. Marginal bead incomplete, present anteriorly. Protergosternal suture present. Suture and remnant of bead parallel. Procoxal fissure open. Protrochantin exposed. (Prosternal process—no data.) Prosternal setigerous pit absent; sternum with patch of setae present near broad depression (no data for pores of depression); anterior margin entire, not notched. Elytral epipleural ridge present and complete; posterior margin with membranous lobe present.

Tarsi four segmented. Protibia with two rows of spinelike setae. Metatibia with one spinelike seta on lateral side near apex.

Abdominal tergum VII with medium fringe on posterior margin. Tergum VIII with posterior margin emarginate; margin entire, not serrate. Tergum IX with glandular canal widely open dorsally. Tergum X with struts on anterior margin.

(Aedeagus—no data.)

Spermatheca (fig. 163) tripartite. Receptacle strongly sclerotized and divided into two parts by accordion tube; basal part larger than

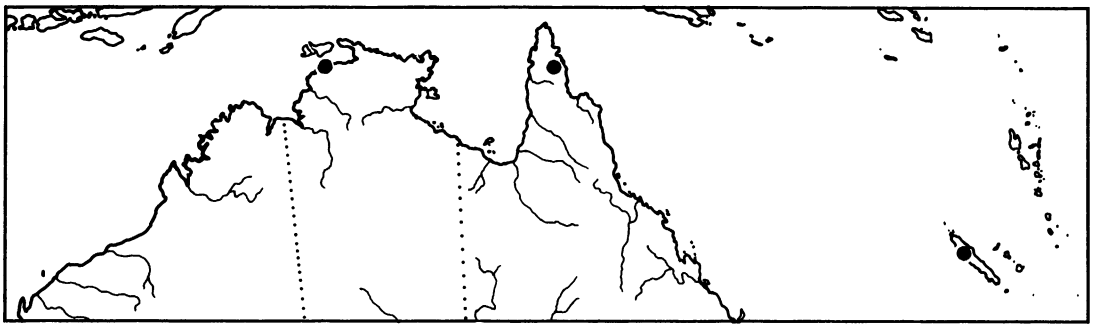


FIG. 164. Distribution of the *circularis* group in Australia and New Caledonia.

distal part; distal part not invaginated; brimlike ridges absent. Spermathecal gland sclerotized; shape irregular and surface tuberculate.

DISTRIBUTION AND HABITAT. The one specimen of the only species in this group is known from Armenia in the Soviet Union (fig. 165).

DISCUSSION. The combination of an incomplete pronotal marginal bead and complete elytral epipleural ridge in this species is unique in the genus.

Species Included and Material Examined

minniensis Herman type locality: **USSR:** Armenia (BMNH).

Bledius minniensis, new species
Figures 1, 163, 165

HOLOTYPE: Armenia [label in Russian, part of it translated for me by Peter Hammond] July 16; female; deposited in the British Museum [Natural History], London.

DIAGNOSIS: The diagnosis given for the species group will separate *Bledius minniensis* from all other species in the genus.

DESCRIPTION: *Minniensis* group. Length: 3 mm. Color dark reddish brown with paler brown elytra; legs and antenna pale brown.

Dorsum of head shining dully, not polished; ground sculpturing well developed; punctation moderately dense and moderately deep; pubescence moderately long; dorsum of head with shallow midbasal punctiform impression and without transverse postocular depression. Clypeus with well-developed ground sculpturing; punctation feeble; anterior margin without tubercles. Eyes moderately large. Width of head 1.02 mm; interocular width 0.75 mm; head width/interocular width 1.37. Labrum with truncate anterior margin. Mandibles bidentate; second denticle large. Antennomeres 3 to 7 without ridge or carina encircling apex.

Pronotum 1.0 mm long, and 1.0 mm wide; pronotum moderately convex; lateral margins nearly parallel to one another on anterior two-thirds and strongly convergent at basal third; basal angles rounded but distinct; anterior angles rounded and even with anterior margin. Pronotal surface shining dully, not polished; ground sculpturing moderately strong; punctation moderately dense and deep; pubescence moderately long; midlongitudinal groove well developed. Elytra 1.32 mm long; elytral length/pronotal length 1.32; elytral punctation distinct and moderately dense; posterior margin with large membranous lobe.

Abdomen with moderately long pubescence; ground sculpturing weak.

Spermatheca as in figure 163.

DISCUSSION: Although I have set aside many other undescribed species of *Bledius,* this one

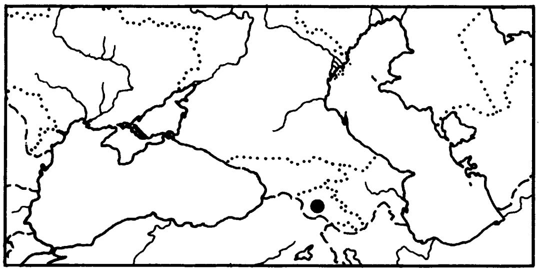


FIG. 165. Distribution of the *minniensis* group in the Transcaucasian region of the USSR.

is of particular interest because it represents a separate species group and is therefore described. *Bledius minniensis* is known from only one female. Its lack of a complete pronotal marginal bead coupled with the complete elytral epipleural ridge is a unique combination among all presently described *Bledius*. When discovered, the male might be found to possess pronotal and supraantennal horns.

ETYMOLOGY: The name is derived from *Minni,* the Biblical name for Armenia, the region from which the species was collected.

MATERIAL EXAMINED: Known only from the holotype female.

9. *rugosicollis* group

Figures 1, 166–172, 499–501, 613–615

DIAGNOSIS: The *rugosicollis* group can be separated from all but the *tibialis* and *compressicollis* groups by the presence of the pronotal marginal bead on the hypomeron (fig. 169). The marginal bead divides the notum and hypomeron in the other groups. The *tibialis* group has a median labral incision (fig. 428), reflexed clypeal margin, and incomplete elytral epipleural ridge. The *rugosicollis* group lacks the labral incision (fig. 168) and clypeal reflexion and the epipleural ridge is entire. The *compressicollis* group has three rows of protibial spinelike setae and a fine fringe on the posterior margin of tergum VII. The males of the *compressicollis* group have a pronotal horn. The *rugosicollis* group has two rows of protibial spinelike setae and a coarse fringe on tergum VII. The males of the *rugosicollis* group have a strongly convex pronotum but lack a pronotal horn (fig. 169).

Other characters that aid recognition of this group include the fused gular sutures, open procoxal fissure, presence of a protergosternal suture (fig. 169), presence of a membranous lobe on the elytral margin, and the emarginate eighth tergum.

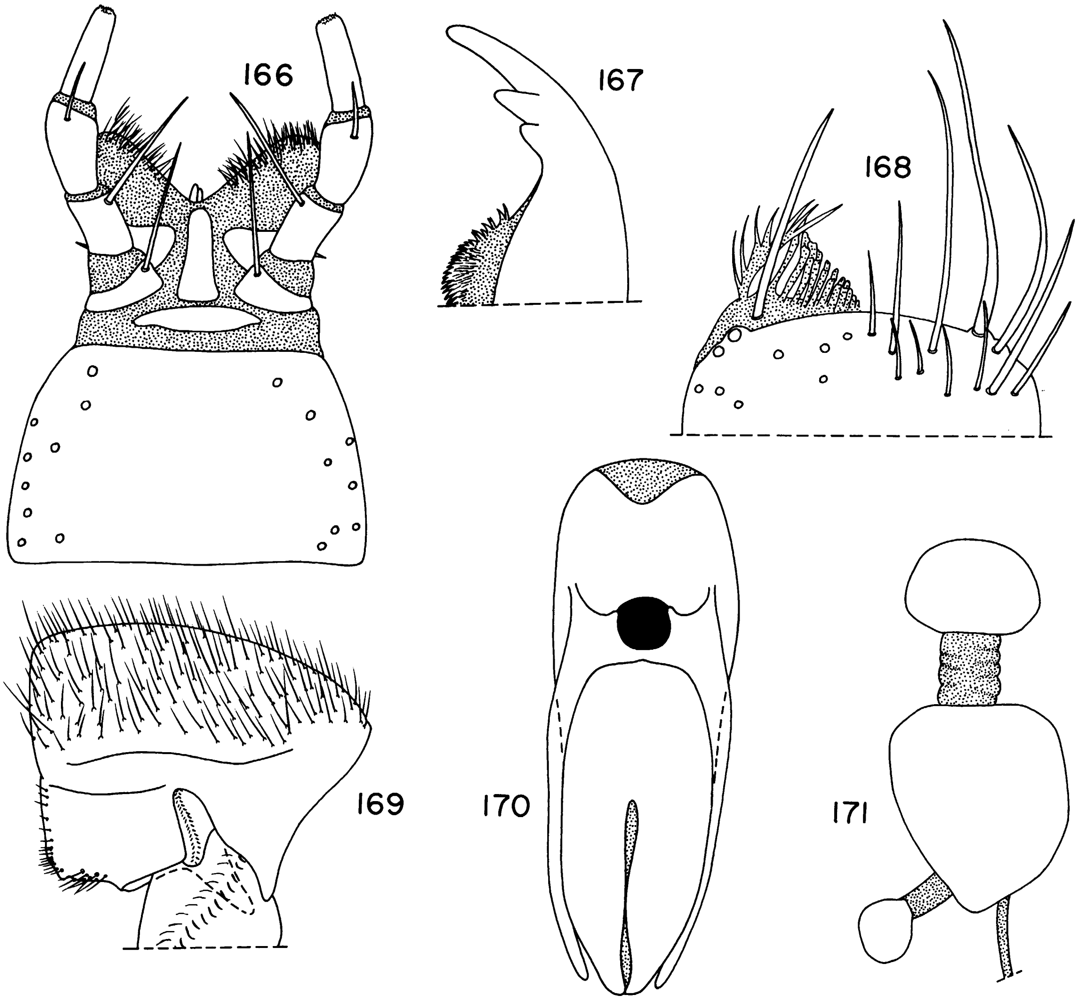
DESCRIPTION: Supraantennal ridge of female low, not enlarged, and without horns; supraantennal ridge of male enlarged moderately and with small, acute, dorsally directed, spiniform horn on posterior portion behind eye. Head without subantennal pockets; midbasal horn absent; postocular lateral carina absent. Clypeal margin not reflexed; anterior margin without tubercles; clypeal middle without spines, ridges, or tubercles. Gular sutures fused. Labrum (fig. 168) with anterior margin entire; margin not reflexed; median incision absent; dorsal surface flat, without midlongitudinal impression. Epipharyngeal lobe short; dorsal surface with one long and one minute seta; median processes with lobed apices; lateroapical region with one thick, multiramous cuticular process. Labial palps (fig. 166) with first segment shortest and with second and third of subequal length; first and second segments of subequal thickness; first segment with two setae, second with one seta. Submentum not excavated. Mentum (fig. 166) with setae present laterally and absent medially. Hypopharynx (figs. 499–501) with lateral row of setae gradually convergent toward base; basal setae arranged in transverse row; basal setae stout; basal setae not on plate; central row of setae dense distally and sparse medially; disk with setae scattered over central portion and denser on apical portion; disk covered with short cuticular processes; coronal pegs present on central part of disk. Prementum (fig. 166) with four sclerites, one medial, two lateral, and one basal. Galea with dense cluster of fanlike setae on apex; ventral surface without setae; dorsomedial edge with lobe. Mandibles tridentate (fig. 167).

Pronotal horn absent. Marginal bead present and complete; bead on hypomeron (fig. 169), not dividing notum and hypomeron. Protergosternal suture present. Bead and suture parallel in female and anteriorly divergent in male. Procoxal fissure open. Protrochantin exposed. Prosternal process elongate (fig. 169). Prosternal setigerous pit absent; sternum with patch of setae near depression (figs. 613, 614); depression with cluster of pores (fig. 615); anterior margin entire, without notch. Elytral epipleural ridge present and complete; posterior margin with membranous lobe.

Tarsi four segmented. Protibia with two rows of spinelike setae. Metatibia with one spinelike seta on lateral surface near apex.

Abdominal tergum VII with coarse fringe on posterior margin. Tergum VIII with posterior margin emarginate; margin entire, not serrate. Tergum IX with glandular canal widely open dorsally. Tergum X with struts on anterior margin.

Aedeagus (fig. 170) with parameres. Para-



FIGS. 166–171. The *rugosicollis* group. *Bledius* sp. **166.** Labium. **167.** Mandible, right. **168.** Labrum. **169.** Prothorax, lateral view. **170.** Aedeagus, dorsal view. **171.** Spermatheca.

meres slender and with medial surface sclerotized; parameres just reaching apex of median lobe. Median lobe long; base bulbous, apical portion flattened; ventral surface midlongitudinally divided.

Spermatheca (fig. 171) tripartite. Receptacle sclerotized and divided into two parts by accordion tube; basal part larger than distal part; distal part not invaginated. Spermathecal gland sclerotized; shape and surface irregular.

DISTRIBUTION AND HABITAT: The species of this group have been found at coastal localities from Pakistan to Thailand. The group has also been collected from inland localities in India (fig. 172).

DISCUSSION: This taxon is recognized herein for the first time. Until now the three species were placed in *Elbidus*, *Bledius* (s. str.), and *Hesperophilus* (table 9). The species require revision.

Species Included and Material Examined

bituberculatus Cameron T(BMNH); type country: Malaysia.

Malaysia: Langkawi Island (BMNH).

brunnipennis (Fabricius) Sp(BMNH, FMNH, IRSN, MNHV); type country: ? India orientali.

(Belgian Indies: Kanaza? IRSN). **India:** Malabar, Mahé (BMNH, IRSN); Parikud

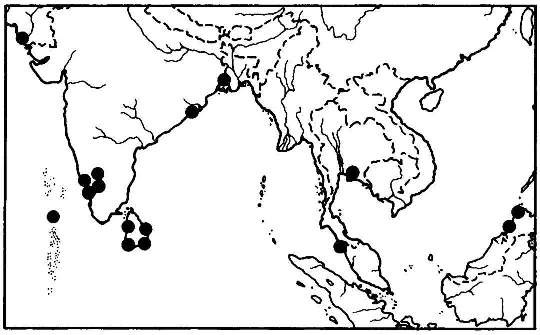


FIG. 172. Distribution of the *rugosicollis* group in southern Asia from Pakistan to Malaysia.

Island, Chika Lake (BMNH); Malabar, Calicut (IRSN, FMNH); Coonoor, Nilghiris (IRSN). **Laccadive Islands:** Minicoy Island (BMNH). **Sri Lanka:** (Ham District, Palutapana? BMNH).

rugosicollis Bernhauer T,Sp(FMNH); type country: Sri Lanka.

India: Calcutta (FMNH). **Pakistan:** Malir City (FMNH). **Sri Lanka:** Weligama (FMNH).

Undetermined.

India: Mysore, Bangalore, Karnataka (AMNH). **Malaysia:** Sabah, 7 km NNW Kudat, Tanjung Tajau (USNM): Sabah, Kuala Penyu (USNM). **Sri Lanka:** (Ruhunu National Park, near Altents ? USNM); N. W. Province, Arukallu, Eluamkulum, Puttalam (AMNH); Eastern Province, Anicuit, Punanai, Maduru Oya (USNM); Arugam Bay (AMNH); (Madawachchiya? AMNH). **Thailand:** (BMNH); Muok-Lek? MNHV).

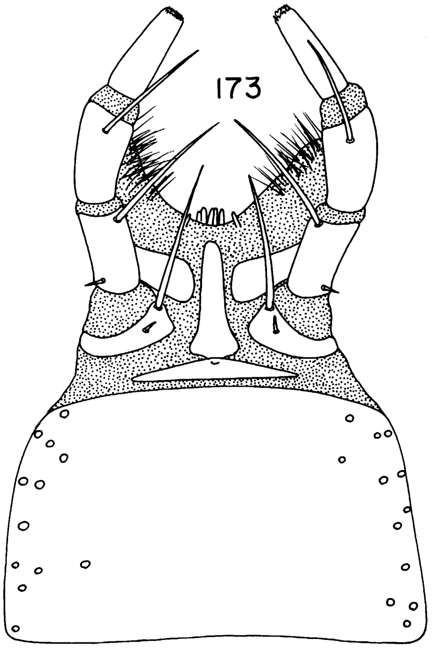
10. *gigantulus* group

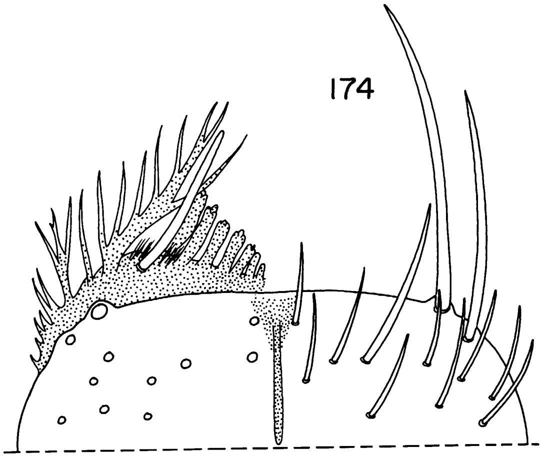
Figures 3, 57, 59, 173–189, 505–507, 601–603

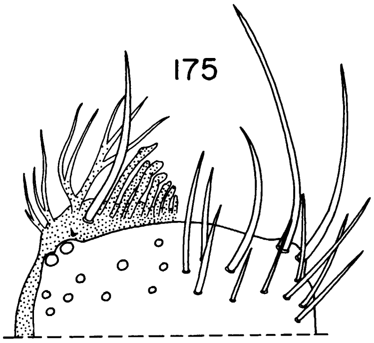
DIAGNOSIS: This group is separated from all others by the pronotal marginal bead that is complete (fig. 181) and that divides the notum and hypomeron, the complete epipleural ridge, the open procoxal fissure (fig. 182), the unreflexed clypeal margin, and the coarse fringe of tergum VIII (fig. 57). The males of this group can be separated from the males of all other groups by the presence of a straight pronotal horn (figs. 181, 182). The supraantennal ridge of the males often is enlarged as a short (fig. 178) to long horn that is anterodorsally directed.

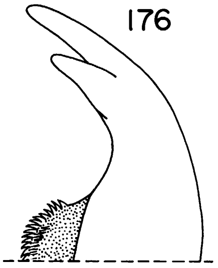
DESCRIPTION: Supraantennal ridge of female low, not enlarged, and without horns; supraantennal ridge of male moderately (fig. 179) to strongly enlarged and in some species enlarged further as small (fig. 178) to large dorsoanteriorly directed horn. Head without subantennal pockets; midbasal horn absent; postocular lateral carina absent. Clypeal margin not reflexed; anterior margin without tubercles; clypeal middle without tubercles, spines, or ridges. Gular sutures fused. Labrum (figs. 175) with anterior margin entire or weakly emarginate; anterior margin not reflexed; median incision present and feebly to moderately developed or absent; dorsal surface flat, without broad midlongitudinal impression. Epipharyngeal lobe short; dorsal surface with one long and one minute seta; median processes with lobed apices; lateroapical portion with thick, multiramous to simple processes. Labial palps (fig. 177) with segments of subequal length; first and second segments of subequal thickness; first segment with two setae, second with one or more setae. Submentum not excavated. Mentum (fig. 177) with setae present laterally but absent medially. Hypopharynx (figs. 505–507) with lateral row of setae gradually convergent toward base; basal setae arranged in transverse row, stout, not on plate; central row of setae dense distally; disk with short, slender cuticular processes on apical region; coronal pegs present on disk. Prementum (fig. 177) with four sclerites, one median, two lateral, and one basal. Galea with dense cluster of setae on apex; ventral surface without setae; dorsomedial edge with lobe. Mandibles bidentate (fig. 176).

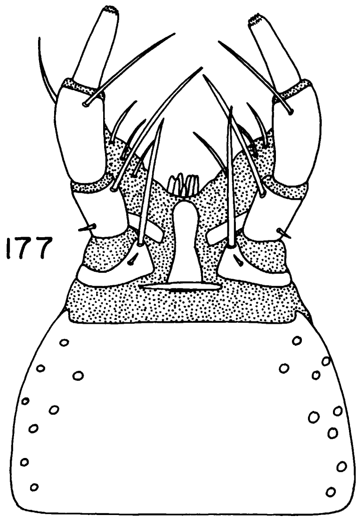
Pronotal horn present on male (figs. 181, 182) and straight or slightly deflexed; female without horn. Marginal bead present (fig. 182) and complete; bead dividing notum and hypomeron, not on hypomeron. Protergosternal suture present (fig. 182). Bead and suture parallel to slightly divergent anteriorly. Procoxal fissure open (fig. 182). Protrochantin exposed. Prosternal process elongate. Prosternal setigerous pit absent (fig. 180). Sternum with patch of setae (fig. 601) near shallow depression; depression with cluster of pores (figs. 602, 603); anterior margin entire,

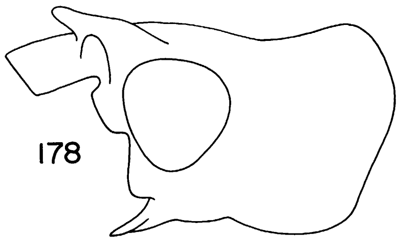


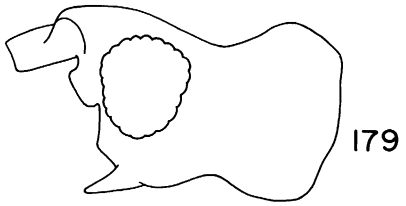








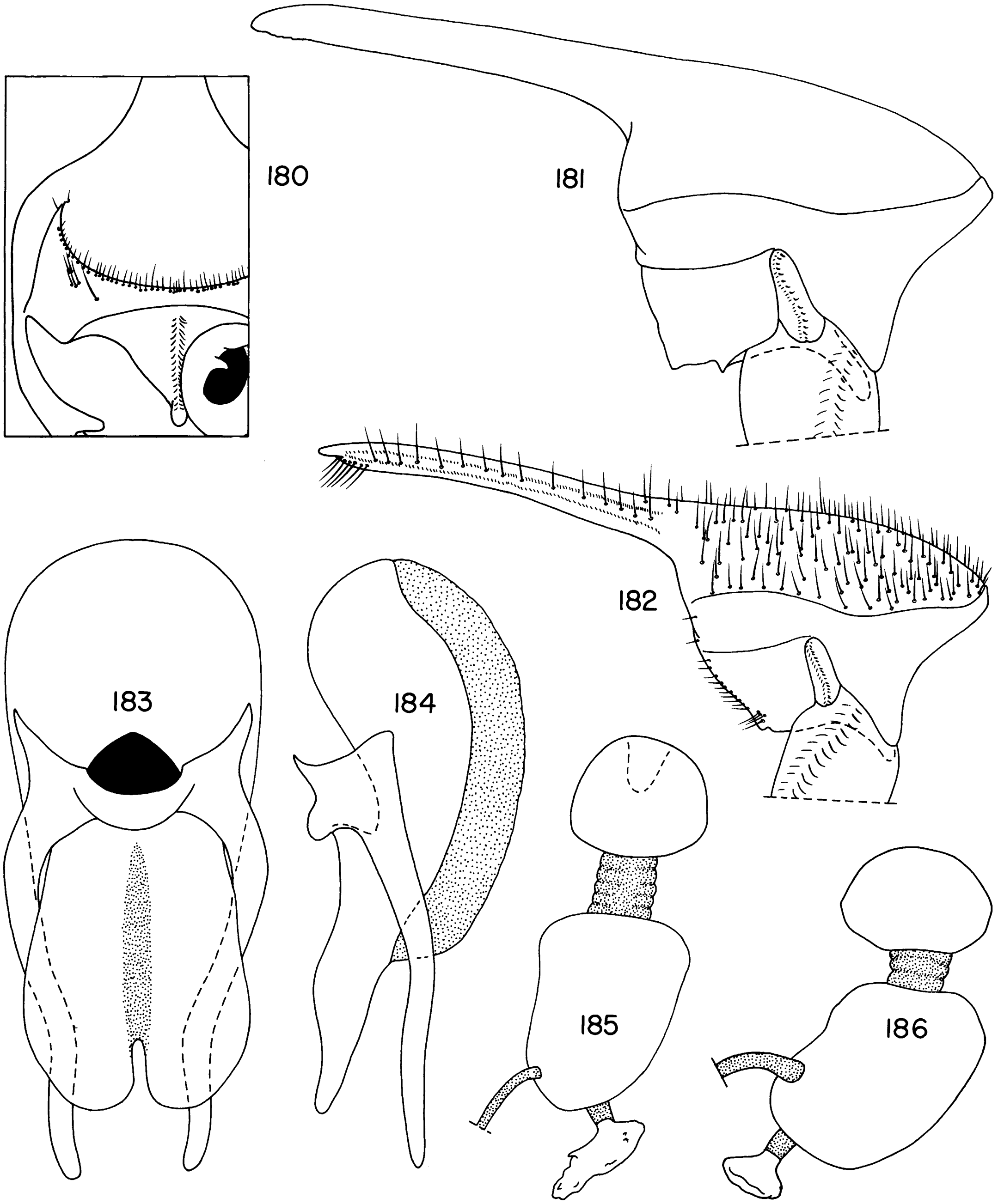




FIGS. 173–179. The *gigantulus* group. **173.** Labium (*graellsi*). **174.** Labrum (*graellsi*). **175.** Labrum (*unicornis*). **176.** Mandible, right (*unicornis*). **177.** Labium (*unicornis*). **178.** Head, male, lateral view, mouthparts and antenna removed (*graellsi*). **179.** Head, male, lateral view, mouthparts and antenna removed (*unicornis*).

not notched. Elytral epipleural ridge present and complete; posterior margin with membranous lobe.

Tarsi four segmented. Protibia with two rows of spinelike setae. Metatibia with one spinelike seta on lateral surface near apex.



FIGS. 180–186. The *gigantulus* group. **180.** Prothorax, male, ventral view of right two-thirds (*unicornis*). **181.** Prothorax, male, lateral view, setae removed (*graellsi*). **182.** Prothorax, male, lateral view (*unicornis*). **183.** Aedeagus, dorsal view (*graellsi*). **184.** Aedeagus, lateral view (*graellsi*). **185.** Spermatheca (*graellsi*). **186.** Spermatheca (*unicornis*).

Abdominal tergum VII with coarse fringe on posterior margin (fig. 57). Tergum VIII with posterior margin emarginate; margin entire, not serrate. Tergum IX with glandular canal widely open dorsally. Tergum X with struts on anterior margin.

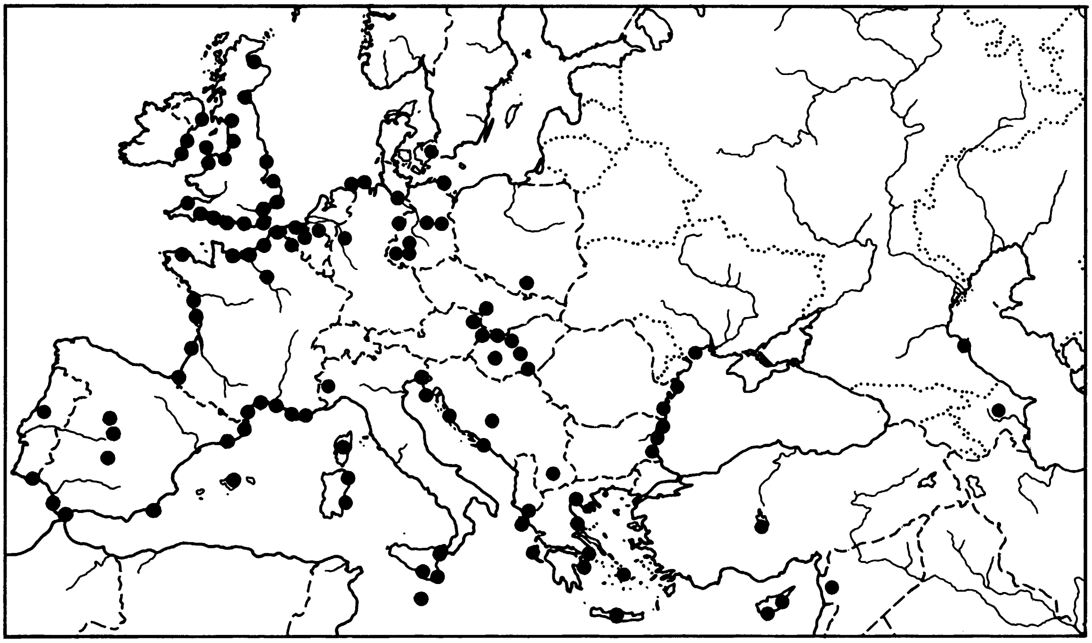


FIG. 187. Distribution of the *gigantulus* group in Europe.

Aedeagus (figs. 183, 184) with parameres. Parameters slender and with medial surface sclerotized; parameres extending beyond apex of median lobe. Median lobe long; base bulbous, apical portion flattened; ventral surface midlongitudinally divided.

Spermatheca (figs. 185, 186) tripartite. Receptacle sclerotized and divided into two parts by accordion tube; basal part larger than distal part; distal part with or without apical invagination; receptacle without brimlike ridges. Spermathecal gland sclerotized; shape and surface irregular.

DISTRIBUTION AND HABITAT: This group is known from Europe and northern Africa eastward across Asia to China and Japan. Species are also known from Taiwan, the Philippines, Sri Lanka, the Aldabra Island, Madagascar, and both western and coastal Ethiopia (figs. 187–189). Many of the specimens were taken from coastal localities and from inland salt lakes. Most of all of the species may be restricted to saline habitats.

DISCUSSION: If nine species currently included in *Bledius* (s. str.) were removed (table 9) and six added, then the subgenus would be equivalent to the *gigantulus* group. *Bledius gemellus, gigantulus, gyotokui, marinus, philippinus,* and *yezoensis* are included in an infrageneric group for the first time. The group is in need of revision.

Within the *gigantulus* group smaller complexes of species can be identified. One of these, the *unicornis* complex, includes *B. corniger, B. ensifer, B. paradoxus, B. ponticus, B. sarmaticus,* and *B. unicornis.* The males of the *unicornis* complex all have a straight pronotal horn that is flattened at the base (in lateral view) and broad in dorsal view. The supraantennal ridge of the males lacks a horn but it is knobbier than on the female. In contrast, the *tricornis* complex (which includes *B. chinensis, B. gigantulus, B. hoplites, B. philippinus, B. salsus, B. sauteri, B. setonis,* and *B. tricornis*) has a straight pronotal horn that is cylindrical and more slender at the base. The supraantennal ridge has a long, broad, anterodorsally directed horn. Most of the species of the *tricornis* complex are found in eastern Asia, Japan, and Taiwan. One of the species is European. The *unicornis* complex occurs in Europe eastward to the Transcaspian region and Iran and across northern Africa with some specimens reported from Ethiopia.

Partially bridging the gap between the *unicornis* and *tricornis* complexes are *B. gemellus, B. graellsi,* and *B. spectabilis* which

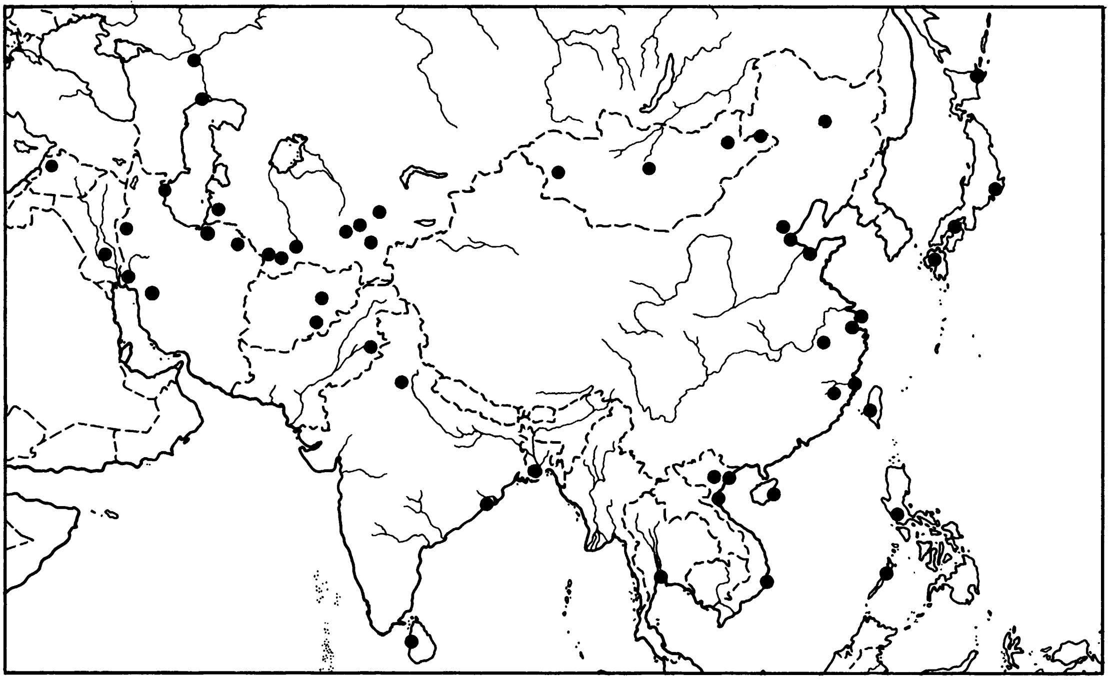


FIG. 188. Distribution of the *gigantulus* group in Asia.

have short supraantennal horns on major males; these horns are even shorter on minor males. The pronotal horn of these three species is similar to that in the *tricornis* complex. Further closing the gap, the males of *B. marinus* have knobbed supraantennal ridges and a slightly flattened pronotal horn.

Species Included and Material Examined

chinensis Bernhauer Co,Sp(FMNH); Sp(BMNH, CNC, MNHV); type country: China.

China: Ting-hai (BMNH); (Jentschoufu? BMNH, FMNH); Tientsin [=Tianjin] (MNHV, FMNH); Harbin (FMNH); (Yantz our ? FMNH). **Mongolia:** Cojbalsan [= Dornod or Choybalsan] aimak, SW corner of Bujr Nur [= Buyr Nuur] (CNC); Cojbalsan [=Dornod] aimak, Somon Chalchin [=Halfin] Gol (CNC).

corniger Rosenhauer Co,Sp (MNHV), Sp(BMNH, FMNH, IRSN); type country: Spain.

Algeria: Oued Bechar (MNHV); Bone [='Annaba] (IRSN); Aïn Sefra (IRSN); Biskra (IRSN, FMNH); Constantine, fountain of the Gazelles, 30 km NW Biskra (IRSN); (Zibane, Oasis of Chetma ? IRSN). **France:** La Nouvelle (IRSN). **Greece:** Corfu (MNHV, IRSN, FMNH). **Italy:** Sicily (MNHV, FMNH); Sicily, Gela (MNHV). **Jordan:** Araq Shishan, 200 km W Amman (MNHV). **Malta:** (BMNH, IRSN). **Morocco:** Taourirt (MNHV). **Spain:** La Linea (BMNH); Andalusia (MNHV). **Tunisia:** Souk el Arba (IRSN); (Rekba? IRSN); Mateur (IRSN). (Bou Skoura ? BMNH).

ensifer Fauvel Syn,Sp(IRSN), Sp(MNHV); type country: Algeria.

Algeria: Ouargla (MNHV); Oran, Es Senia (IRSN); Constantine (IRSN). **Italy:** Sicily, Gela (MNHV).

gemellus Eppelsheim Co,Sp(MNHV), Sp(BMNH, FMNH, IRSN); type country: Cape Verde.

Ghana: (FMNH, MNHV); Quittah [=Keta] (MNHV). **Senegal:** (FMNH, IRSN); (Cayon? BMNH); Thies (BMNH); Dakar (MNHV); Rufisque (MNHV); St. Louis (IRSN). (Senegambia? BMNH).

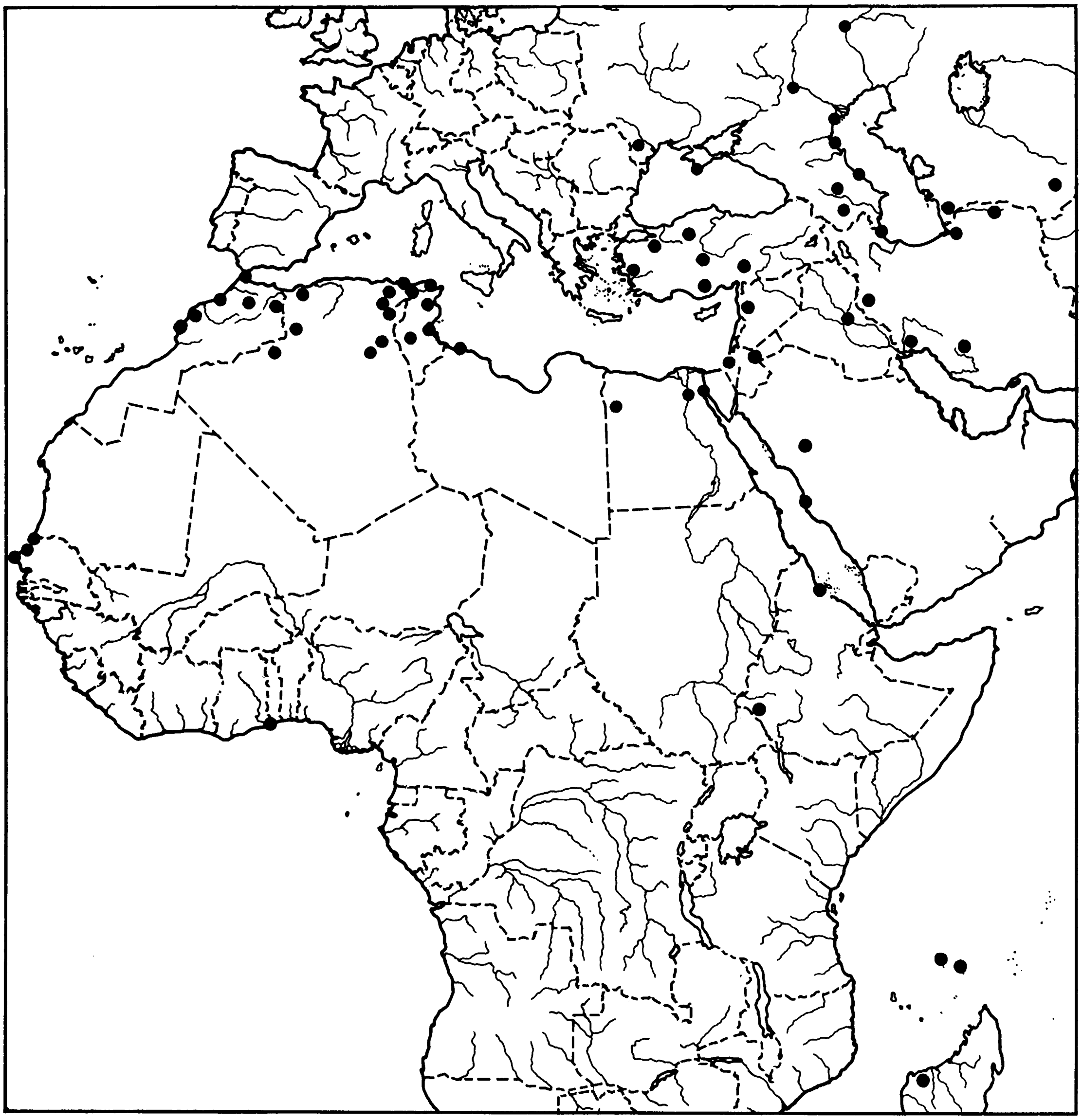


FIG. 189. Distribution of the *gigantulus* group in Africa.

gigantulus Bernhauer T,Co,Sp(FMNH), Co,Sp(BMNH), Sp(MNHV); type country: Taiwan.
China: Tientsin [=Tianjin] (FMNH, BMNH); Fo-kien, Ting-hai (BMNH). **Japan:** Tokyo (BMNH). **Mongolia:** Cojbalsan aimak, Somon Chalchingol (BMNH). **Taiwan:** An-ping (FMNH, BMNH); (Suisharyo? FMNH, BMNH).

graellsi Fauvel Sp(BMNH, FMNH, IRSN, MNHV, HCC); type country: ?
Albania: Butrintit (BMNH). **Algeria:** Touggourt (IRSN); Bone [='Annaba] (IRSN). **France:** Hyères (MNHV, FMNH, BMNH); La Franqui (FMNH); Morlaix (BMNH, FMNH, IRSN); Marseilles (IRSN); Corsica (Corbara? IRSN); Ile de Ré (IRSN). **Greece:** Corfu (MNHV,

FMNH); Volos (MNHV); Attiki, Phaleron (MNHV, FMNH); Naxos (MNHV, FMNH); Salonich [=Thessaloniki], Vardar plains (FMNH); Thessalia, Volos (FMNH); Poros (FMNH); Cyklades [=Kikladhes] (FMNH); Athens (FMNH); Crete (FMNH). **Italy:** Grado (FMNH); Piemonte (IRSN). **Morocco:** (Esmir? IRSN); (Meija Bokka). **Saudi Arabia:** Khaybar, Hedjaz (HCC). **Spain:** (FMNH, BMNH) Barcelona (MNHV); Catalonia, Rosas (MNHV); El Escorial (MNHV, IRSN); Aranjuez (IRSN). **Tunisia:** Kebili (MNHV, IRSN); Gabes (IRSN). **Turkey:** Taurus [= Toros Daglari] (FMNH). **Yugoslavia:** Metkovic (MNHV); Zara [=Zardar] (MNHV); Bosnie [Bosna and Hercegovina] (IRSN).

gyotokui Nakane H(TNC); type country: Japan.

Japan: Fukuoka, Yoshii (TNC).

hoplites Fauvel Syn,Sp(BMNH, IRSN), Sp(FMNH, MNHV); type country: ?

Bangladesh: Sunderbans, Khulna District, Ganges Delta, Bosondhur (FMNH). **India:** Parikud Island, Chilka Lake (BMNH). **Philippines:** Manila (IRSN); Pampanga (IRSN). **Thailand:** Bangkok (IRSN, BMNH). **Vietnam:** (Phu Lang Thuong ? MNHV).

limicola Tottenham Sp(BMNH, IRSN); type country: United Kingdom.

Belgium: St. Jan in Eremo (IRSN). **Iraq:** Mesopotamia (BMNH). **United Kingdom:** widespread maritime localities (P. M. Hammond, BMNH, unpublished notes).

marinus Bernhauer T(BMNH, FMNH), Sp(BMNH); type country: Aldabra Islands.

Aldabra Islands: (FMNH); South Island: Takamaka Grove, Cing Casas (BMNH); West Island, West Settlement (BMNH).

[*paradoxus* Gridelli] No specimens examined; type country: Italy.

In the original description Gridelli (1936) placed *paradoxus* in the nominate subgenus and provided illustrations of the species. The form of the pronotum, the suggestion of a pronotal horn, the transverse basal impression of the head, the knobby supraantennal ridge, and the suggestion of a coarse fringe on tergum VII all support assignment of *paradoxus* to the *gigantulus* group. Further, the species apparently belongs with the *unicornis* complex.

philippinus Bernhauer T,Co,Sp(FMNH), Sp(BMNH, MNHV); type country: Philippines.

Philippines: Luzon, Manila (FMNH, BMNH, MNHV).

ponticus Znojko Co(ZMUH); type country: USSR.

USSR: Odessa (ZMUH).

salsus Miyatake Sp(AMNH, MNHV); type country: Japan.

Japan: Kagawa, Utazu (AMNH). Kagawa, Utatsu (AMNH); Okayama, Mizushima (AMNH).

sarmaticus Znojko Co(ZMUH), Sp(HCC); type country: USSR.

USSR: Odessa (HCC, ZMUH).

sauteri Bernhauer T,Co,Sp(FMNH); Co,Sp(BMNH); type country: Taiwan.

China: Kui Kiang (BMNH); Haining (FMNH, BMNH); Shanghai (FMNH, BMNH); Tientsin [=Tianjin] (FMNH, BMNH). **Taiwan:** An-p'ing (FMNH, BMNH); Suisharyo (FMNH). **Vietnam:** Haiphong (FMNH).

[*setonis* Miyatake] no specimens examined; type country: Japan.

Miyatake (1963) put this species (then named *rotundicollis*) in the nominate subgenus. His illustrations show the pronotal and cephalic horns, and absence of a reflexed clypeus. These features support placing *setonis* in the *gigantulus* group and in the *gigantulus* complex.

simulator Eppelsheim Co,Sp(MNHV), Sp(FMNH, BMNH); type country: USSR.

Syria: (Mujunkum? FMNH). **USSR:** Uzbekistan, Margelan (MNHV); Uzbekistan, Fergana (FMNH); Turkmeniya, Gr. Balachan [= Great Balkan], Dschebell [=Dzhebel] (FMNH, MNHV); Turkestan (BMNH).

spectabilis Kraatz Sp(BMNH, FMNH, IRSN, MNHV); type country: Greece.

Afghanistan: Ab-i-Istada (BMNH). **Algeria:** Aïn Sefra (IRSN). **Austria:** Neusiedler Sea (FMNH, MNHV); Wien (FMNH); Korneuburg (FMNH). **Bulgaria:** Varna (MNHV). **China:** (Schansi? FMNH). **Cyprus:** (FMNH, IRSN); Larnaca (FMNH); Limassol (FMNH). **France:** (FMNH); Bay of the Somme (MNHV); Camargue (MNHV); Cette [=Sète] (IRSN); Ile de Ré (IRSN); Le Crotoy (IRSN); Herault (IRSN); Hyères (IRSN); Arcachon (IRSN). **Germany, East:** Laucha (FMNH); Eisleben (MNHV). **Germany, West:** Borkum Island (FMNH, MNHV); Norderney (MNHV). **Greece:** Cyklades [=Kikladhes] (FMNH); Thessalia Province (FMNH); Naxos (FMNH, MNHV); Crete (IRSN); Athens (BMNH). **Hungary:** Siofok (FMNH). **Iran:** Kopet Dagh (FMNH); Khuzistan, Shadegan (MNHV). **Iraq:** Mesopotamia (FMNH); Baghdad (MNHV). **Italy:** Grado (FMNH). **Malta:** (FMNH). **Portugal:** Coimbra (FMNH). **Romania:** Black Sea (MNHV); Mangalia (BMNH, MNHV). **Spain:** Cadiz (FMNH). **Syria:** (Mujunkum? FMNH). **Turkey:** Smyrna [=Izmir] (FMNH); Kizicahamam (MNHV). **United Kingdom:** Coastal localities in Ireland, Wales, and southern England (P. M. Hammond, BMNH, unpublished notes). **USSR:** Merv [=Mary] (FMNH, MNHV, IRSN); Crimea, Sevastopol (FMNH); Turkestan (FMNH); Transcaspian (Splichal? FMNH); Repetek (FMNH, MNHV) Aulie Atta [=Dzhambul] (FMNH); Transcaspian (Imam? FMNH); Transcaspian (New Saratov ? MNHV); Transcaspian (Saramskli); Sarepta (IRSN, MNHV); Bessarabia (MNHV); Turkmeniya, Bayram-Ali (IRSN). **Yugoslavia:** Istria (MNHV).

tricornis (Herbst) Sp(BMNH, CNC, FMNH, IRSN, MNHV); type country: Germany.

Afghanistan: 30 km NW Kabul, Paghman (MNHV). **Austria:** Neusiedler Sea (IRSN, MNHV); Korneuburg (FMNH); Illmitz (FMNH). **Belgium:** Wemmel (IRSN); St. Jan in Eremo (IRSN); Antwerpen (IRSN); Blankenberghe (IRSN). **China:** Tientsin [=Tianjin] (FMNH); Shanghai (FMNH); Foochow [=Fuzhou] (FMNH); Beijing (FMNH); Hainan Dao (BMNH). **Czechoslovakia:** Brandeis [=Brandys] (MNHV) Cejc (u Hod ? BMNH). **Denmark:** Copenhagen (MNHV). **France:** Dieppe (IRSN); Paris (IRSN); Cabourg (IRSN); Lille (IRSN); Caen (IRSN); Versailles (IRSN); Trouville (IRSN); Camargue (MNHV, FMNH); Vendee Department (Rougeville? BMNH). **Germany, East:** Eisleben (MNHV); Stotternheim (MNHV); Vilm Island (FMNH). **Germany, West:** Berlin (IRSN, MNHV); Braunschweig (Jerxheim? MNHV); Borkum Island (MNHV); Hamburg (FMNH). **Greece:** Saloniki [=Thessaloniki] (MNHV, BMNH); Corfu (MNHV). **Hungary:** (BMNH) Györ (FMNH); Esztergom (FMNH); Szeged (FMNH); Neusiedler Sea (MNHV): Ujpest (IRSN). **Iran:** (Kohistan? IRSN). **Mongolia:** Chovd [=Hovd] aimak, Jamatin Dolon, 40 km N Somon Manchan [=Manhan], SW corner of Char [=Har] Us Nuur (CNC); Cojbalsan [= Choybalsan or Dornod], Somon Chalchin [=Halhïn] Gol (CNC); Central [=Töv] aimak, 2–7 km W Somon Lün (CNC). (Additional localities: Smetana, 1975.) **Poland:** Krakow (MNHV). **Romania:** Sulina (BMNH). **Spain:** Catalonia, Rosas (MNHV). **Syria:** (MNHV); (Mujunkum? FMNH). **Turkey:** Biledjek (FMNH). **USSR:** Caucasus (Aresch? IRSN, FMNH); Repetek (IRSN, BMNH); Kazakhstan, Tashkent (IRSN); Astrakhan (IRSN); Sarepta (IRSN, MNHV, FMNH); Kazakhstan, Ural'sk (MNHV); Transcaspian (New Saratov ? MNHV); Transcaspian (Baiga-Kum? MNHV); Turkestan (MNHV); Aulie-Ata [=Dzhambul] (MNHV); Transcaspian (Tapskyu? FMNH); Golodnaja Steppe (FMNH); Elizabethpol [=Kirovabad] (FMNH); Turkestan (Geok-cepa? BMNH). **Vietnam:** Hue (IRSN); Thanh-Hoa (IRSN); Haiphong (IRSN); Hanoi (IRSN). **Yugoslavia:** Sarajevo (MNHV); Macedonia, Vardar River (MNHV).

unicornis (Germar) Sp(BMNH, FMNH, IRSN); type country: Yugoslavia.

Algeria: (FMNH); Biskra (IRSN); Touggourt (BMNH, IRSN). **Austria:** Neusiedler Sea (MNHV, IRSN, FMNH); Thüringen (MNHV); Arbe Island (MNHV). **Belgium:** Nieuwpoort (IRSN). **Bulgaria:** Nessebar [=Nesebur] (MNHV); Burgas (FMNH). **Canary Islands:** (IRSN). **Cyprus:** (IRSN); Akrotiri Bay (BMNH). **Egypt:** Siwa (BMNH); Pozuelo de Calatrava (IRSN); Helwan (IRSN, MNHV, FMNH); Suez (IRSN); (Meaddich? FMNH). **Ethiopia:** Neum (FMNH); Massaua [=Mits'iwa] (FMNH). **France:** Carantec (IRSN); St. Jean de Luz (IRSN); Hyères (IRSN, MNHV, FMNH); Collioure (IRSN); Camargue

(MNHV, IRSN); Corsica, Aleria (IRSN); Corsica (MNHV); Mallorca, Rabassa (MNHV, FMNH); Mallorca, La Albufera (FMNH). **Germany, East:** Eisleben (IRSN); Magdeburg (FMNH). **Germany, West:** Düsseldorf (FMNH). **Greece:** Corfu (FMNH, BMNH, MNHV); Kefallinia (MNHV); Attiki (MNHV); Thessalia, Volos (MNHV, FMNH); Naxos (FMNH); Cyclades [=Kikladhes] (FMNH); Attiki, Phaleron (FMNH). **Italy:** Sardinia, Lanusei (IRSN); Sardinia (MNHV); Sardinia, Aranci Golfo (BMNH); Sicily, Galatz [=Galati] (BMNH); Trieste (MNHV); Sicily, Pachino (MNHV); Grado (FMNH). **Iraq:** Mesopotamia. **Israel:** Wadi Ghuzzeh (BMNH). **Libya:** Tripoli (BMNH, MNHV). **Malta:** (BMNH). **Morocco:** Mogador [=Essaouira] (BMNH, FMNH); Tanger (FMNH, BMNH, IRSN); Fedala-barene [=Mohammedia] (MNHV); Fes (Douiete? MNHV). **Portugal:** Figueira da Fox (MNHV); Faro (FMNH). **Romania:** Sulina (BMNH); Mangalia (MNHV). **Saudi Arabia:** Ieddah [=Jiddah] (BMNH). **Senegal:** Thies (BMNH). **Syria:** (IRSN). **Spain:** Cartagena (BMNH, IRSN); Andalusia (IRSN); Tarifa (IRSN); Cadiz (MNHV); Algeciras (FMNH). **Tunisia:** Souk el Arba (IRSN); Tunis (IRSN); Kebili (IRSN, MNHV); Gabes (IRSN); Kairouan (IRSN). **Turkey:** Tzu Gölü (MNHV); (Karapinar? MNHV). **United Kingdom:** Coastal England from Lancashire south to southern coast then north to Norfolk and on Meath coast of Ireland (P. M. Hammond, BMNH, unpublished notes). **USSR:** Caucasus (FMNH); Caucasus (Geok-Tapa? IRSN); Sarepta (IRSN); Transcaspian (Dortkuju? MNHV); Odessa (MNHV); Transcaspian (Kisil-Arvat? MNHV); Transcaspian (Splichal? FMNH); Repetek (FMNH). **Yugoslavia:** Vardar River (MNHV).

yezoensis Nakane H(TNC); type country: Japan.

Japan: Hokkaido, Otaito (TNC).

Undetermined.

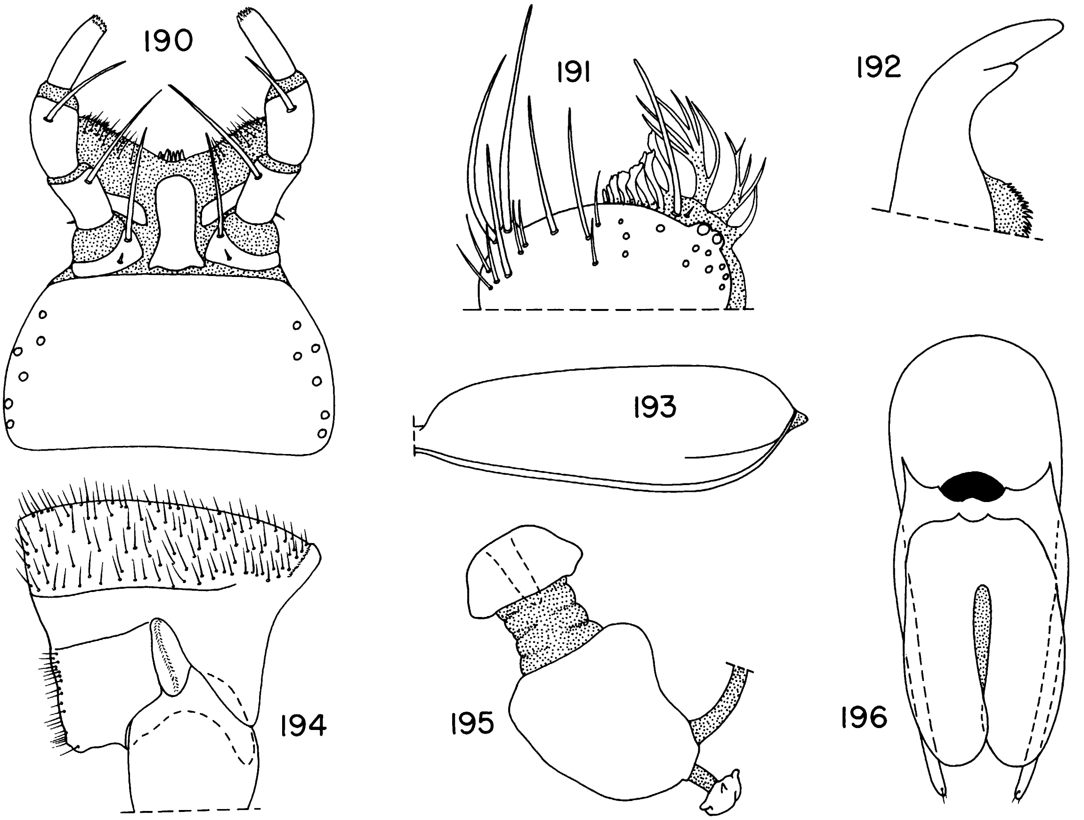
China: Shandong, Tsintao (AMNH); Fujian Yungan (BPBM). **Hungary:** Kecskemet (BMNH). **India:** New Delhi (USNM); **Iran:** Azerbaijan, Astara (USNM); Kermanshah (USNM); Mazandaran, 25 km W Gorgan (USNM); Fars, 13 km SE Shiraz (USNM). **Iraq:** Baghdad (USNM). **Japan:** Tokyo (USNM). **Jordan:** Azraq Shishan (BMNH). **Madagascar:** (Ifaty? MNHV). **Pakistan:** Lahore (USNM). **Philippines:** Palawan (Tarumpitao Point ? BPBM). **Spain:** Andalusia (MNHV); Cartagena (MNHV). **Sri Lanka:** NW Province, Arukallu, Eluamkulum, Puttalam (AMNH). **Turkey:** Efsus [=Afsin] (BMNH). **USSR:** Dagestan, Kraynovka (BMNH). Crimea (MNHV); Derbent (MNHV); Elizabethpol [=Kirovabad] (Geok-Tapa? BMNH). **Vietnam:** Nha Trang (BPBM).

11. *immaturus* group

Figures 1, 190–197

DIAGNOSIS: This group can be separated from the others by the presence of a pronotal (fig. 194) marginal bead, open procoxal fissure (fig. 194), the incomplete elytral epipleural ridge (fig. 194), presence of a membranous lobe on the elytral margin, the unreflexed clypeal margin, and the two rows of spinelike setae on the protibiae. The coarse fringe on the poterior margin of tergum VII is shared with groups in which the males have pronotal and supraantennal armature. The males of the *immaturus* group lack a pronotal horn but the supraantennal ridge is cariniform with a small tumescence on the anterior and posterior ends.

DESCRIPTION: Supraantennal ridge of male cariniform with small tumescence on anterior and posterior ends; supraantennal ridge of female low and without horns. Head without subantennal pockets; midbasal horn absent; postocular lateral carina absent. Clypeal margin not reflexed; anterior margin without tubercles; clypeal middle without tubercles, spines, or ridges. Gular sutures fused. Labrum (fig. 191) with anterior margin entire; anterior margin not reflexed; median incision absent; dorsal surface flat, without broad midlongitudinal impression. Epipharyngeal lobe short; dorsal surface with one long and one minute seta; median processes with lobed apices; lateroapical portion with thick multiramous process. Labial palps (fig. 190) with segments of subequal length; first and second segments of subequal thickness; first segment with two setae, second with one. Submentum not excavated. Mentum (fig. 190) with setae present laterally and absent medially. Hy-



FIGS. 190–196. The *immaturus* group. *Bledius immaturus*. **190.** Labium. **191.** Labrum, left setae and right epipharyngeal removed. **192.** Mandible, left. **193.** Elytron, lateral view, setae removed. **194.** Prothorax, lateral. **195.** Spermatheca. **196.** Aedeagus, dorsal view.

popharynx with lateral rows of setae gradually convergent toward base; basal setae arranged in transverse row; basal setae not on plate; central row of setae dense distally and absent proximally; disk with setae scattered over medial and lateral surfaces; disk with short slender cuticular processes on lateral and apical regions; coronal pegs present on disk. Prementum (fig. 190) with four sclerites, one medial, two lateral, and one basal. Galea with row of stout spinelike setae on lateral part and dorsal edge of apex and with dense cluster of setae on remainder of apex; ventral surface without setae; dorsomedial edge with lobe. Mandibles bidentate (fig. 195).

Pronotum (fig. 194) without horn. Marginal bead present and complete; bead dividing notum and hypomeron, not on hypomeron. Protergosternal suture present. Bead and suture anteriorly divergent. Procoxal fissure open. Protrochantin exposed. Prosternal process elongate. Prosternal setigerous pit absent; sternum with patch of setae present near depression (no data for pores in depression); anterior margin entire, not notched. Elytral (fig. 193) epipleural ridge present and incomplete, present only apically; posterior margin with membranous lobe.

Tarsi four segmented. Protibia with two rows of spinelike setae. Metatibia with one spinelike seta on lateral side near apex.

Abdominal tergum VII with coarse fringe on posterior margin. Tergum VIII with posterior margin emarginate; margin entire, not serrate. Tergum IX with glandular canal widely open dorsally. Tergum X with struts on anterior margin.

Aedeagus (fig. 196) with parameres. Parameres slender and with medial surface sclerotized; parameres extending just beyond apex

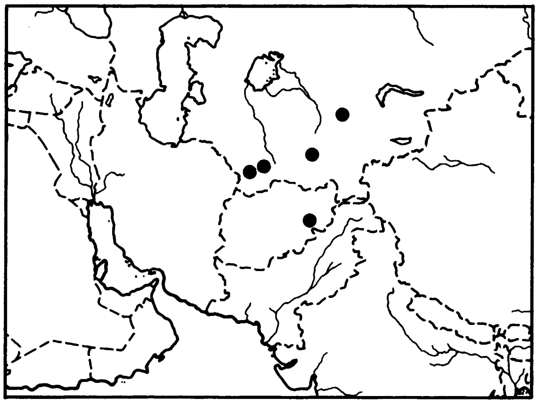


FIG. 197. Distribution of the *immaturus* group in Afghanistan and the USSR.

of median lobe. Median lobe long; base bulbous; apical portion flattened; ventral surface midlongitudinally divided.

Spermatheca (fig. 195) tripartite. Receptacle sclerotized and divided into two parts by accordion tube; basal part larger than distal part; distal part with invagination; receptacle without brimlike ridges. Spermathecal gland sclerotized; shape and surface irregular.

DISTRIBUTION AND HABITAT: This group is known from the Transcaspian region in south central Soviet Union southward into Afghanistan (fig. 197).

DISCUSSION: *Bledius immaturus,* which lacks pronotal or cephalic horns, was previously included in *Bledius* (s. str.). It is easily separated from all groups.

Species Included and Material Examined

immaturus Eppelsheim Co,Sp(MNHV), Sp(FMNH); type country: USSR. **Afghanistan:** Kabul (MNHV). **USSR:** Golodnaya Steppe (FMNH); (Transcaspian, Zapgocyu? FMNH); Transcaspian, Tschardshui [=Tcharjui] (FMNH, MNHV); (Transcaspian, Dortkuju? MNHV); Bukhara (MNHV); Turkestan [=Kazakhstan] (MNHV); Repetek, Turkmeniya (BMNH).

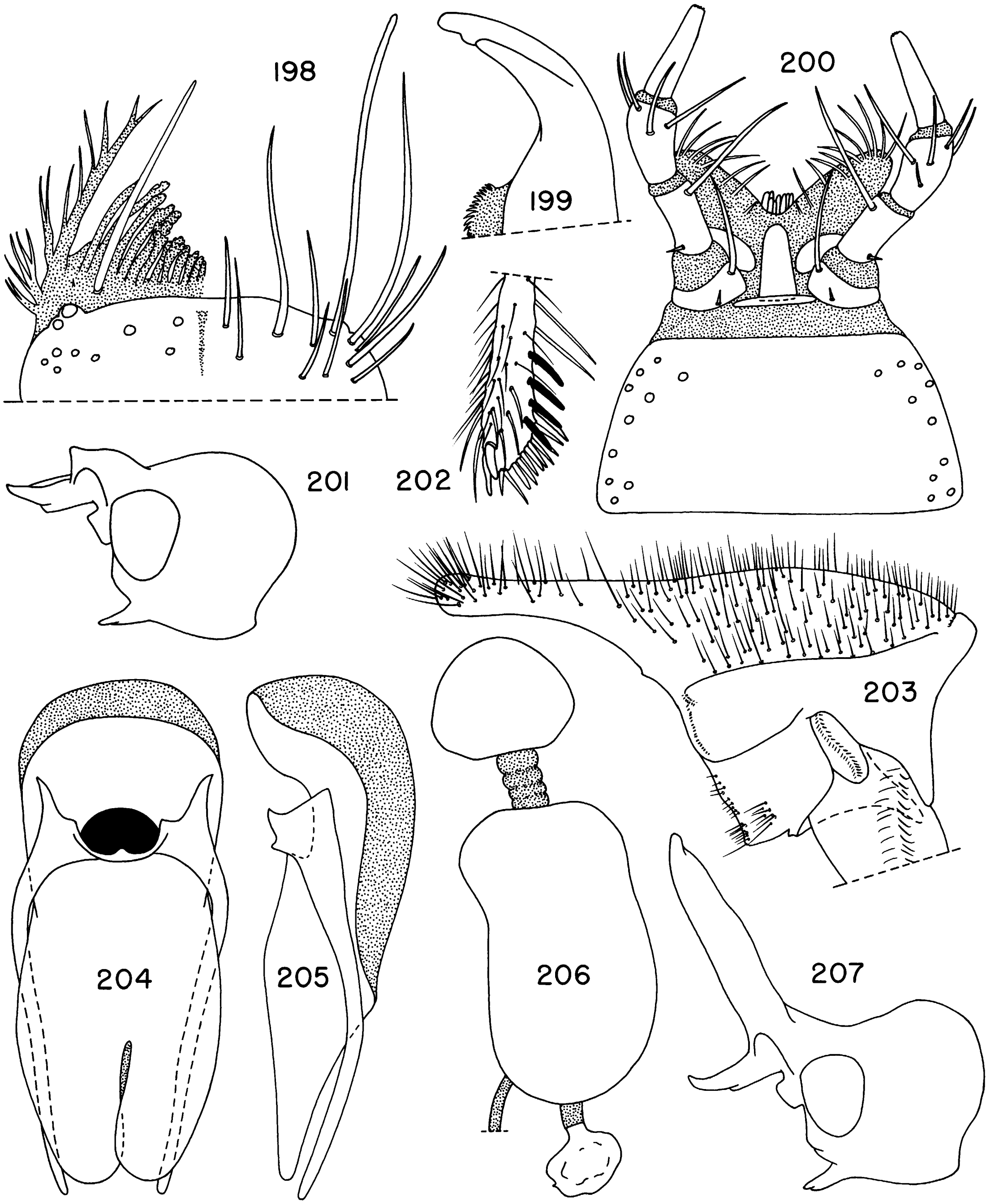
12. *furcatus* group

Figures 2, 198–210, 496–498, 416–418

DIAGNOSIS: This group can be separated from all groups except the *tibialis, kochi,* and *lamelliceps* groups by the reflexed clypeal margin (fig. 207). The *tibialis* group has an incomplete elytral epipleural ridge; the *furcatus* group has a complete epipleural ridge. The *lamelliceps* group is separated by the presence of a postocular cephalic carina (figs. 214, 215) which is absent (fig. 207) in the *furcatus* group. The *kochi* group has one subapical spinelike seta on the lateral side of the metatibia; the *furcatus* group has a row of three to five spinelike setae (fig. 202; blackened setae). The clypeal margin is notably more reflexed in the *furcatus* group than in the *kochi* group. The males of the *furcatus* group have a pronotal horn (fig. 203); the males of the *kochi* group (except *B. auriculicollis*) have one or a pair of tumescences on the midanterior margin of the pronotum. *B. auriculicollis* has a large, broad, thick hornlike tumescence.

Other characters that help to recognize the *furcatus* group include the presence of supraantennal horns, the open procoxal fissure (fig. 203), the presence of a protergosternal suture (fig. 203), the complete pronotal marginal bead and elytral epipleural ridge, the presence of a membranous lobe on the posterior margin of the elytra, the coarse fringe on the posterior margin of tergum VII, and the emarginate posterior margin of tergum VIII.

DESCRIPTION: Supraantennal ridge of female (fig. 201) with one dorsally directed cariniform horn; supraantennal ridge of male with one flattened, dorsally directed horn (fig. 207). Head without subantennal pocket; midbasal horn absent; postocular lateral carina absent. Clypeal margin reflexed; anterior margin without tubercles; clypeal middle without spines, ridges, or tubercles. Gular sutures fused. Labrum (fig. 198) with anterior margin entire; anterior margin not reflexed; median incision present and weak, or absent; dorsal surface flat, without broad midlongitudinal impression. Epipharyngeal lobe short; dorsal surface with one long and one minute seta; median processes with lobed apices; lateroapical portion with thick multiramous process. Labial palps (fig. 200) with segments of subequal length; first and second segments of subequal thickness; first segment with two setae, second with four or five. Submentum not excavated. Mentum (fig. 200) with setae present laterally and absent medially. Hypopharynx (figs. 496–498) with lateral rows



FIGS. 198–207. The *furcatus* group. *Bledius furcatus*. **198.** Labrum, right epipharyngeal lobe and left setae removed. **199.** Mandible, right. **200.** Labium, setae of mentum removed. **201.** Head, female, lateral view, mouthparts and antenna removed. **202.** Metatibia, apex. **203.** Prothorax, male, lateral view. **204.** Aedeagus, dorsal view. **205.** Aedeagus, lateral view. **206.** Spermatheca. **207.** Head, male, lateral view, mouthparts and antenna removed.

of setae gradually convergent toward base; basal setae arranged in transverse row; basal setae stout; basal setae not on plate; central row of setae dense distally and sparser proxi-

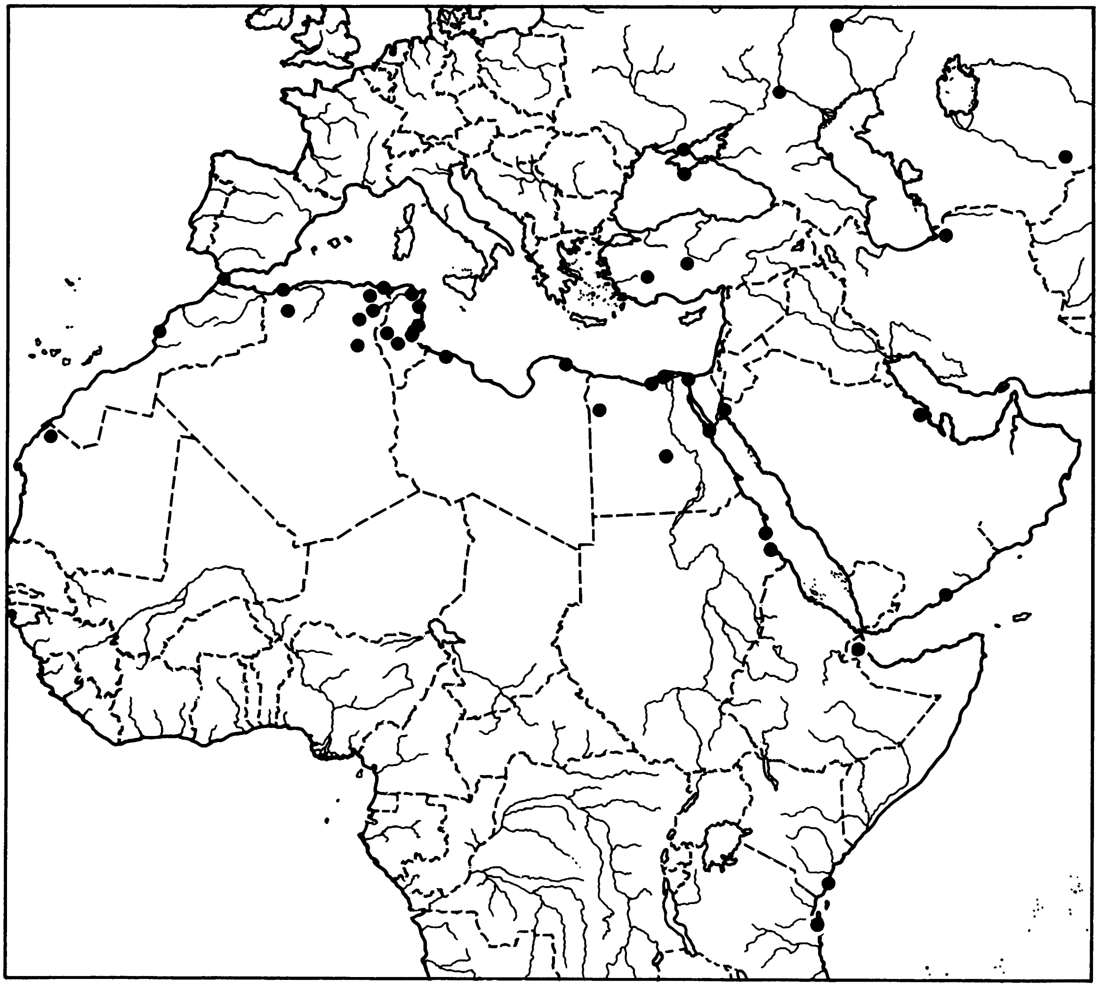


FIG. 208. Distribution of the *furcatus* group in Africa and western Asia.

mally; disk with setae scattered over medial and apical surfaces; disk with moderately long cuticular processes on apical region; coronal pegs present on disk. Prementum (fig. 200) with four sclerites; two lateral, one medial, and one basal. Galea with row of long stout setae on dorsal edge of apex and with dense cluster of setae on remainder of apex; ventral surface without setae; dorsomedial edge with lobe. Mandibles bidentate (fig. 199).

Pronotum (fig. 203) of male with straight horn; female without horn. Marginal bead present (fig. 203) and complete; bead dividing notum and hypomeron, not on hypomeron. Protergosternal suture present (fig. 203). Bead and suture parallel to divergent anteriorly. Procoxal fissure open (fig. 203). Protrochantin exposed. Prosternal process elongate (fig. 203). Prosternal setigerous pit absent (figs. 616, 617); sternum with patch of setae near depression (fig. 618); depression with cluster of pores; anterior margin entire, not notched. Elytral epipleural ridge present and complete; posterior margin with membranous lobe.

Tarsi four segmented. Protibia with two rows of spinelike setae. Metatibia with row of three or more spinelike setae on lateral surface beginning near apex (fig. 202).

Abdominal tergum VII with coarse fringe on posterior margin. Tergum VIII with posterior margin emarginate; margin entire, not serrate. Tergum IX with glandular canal

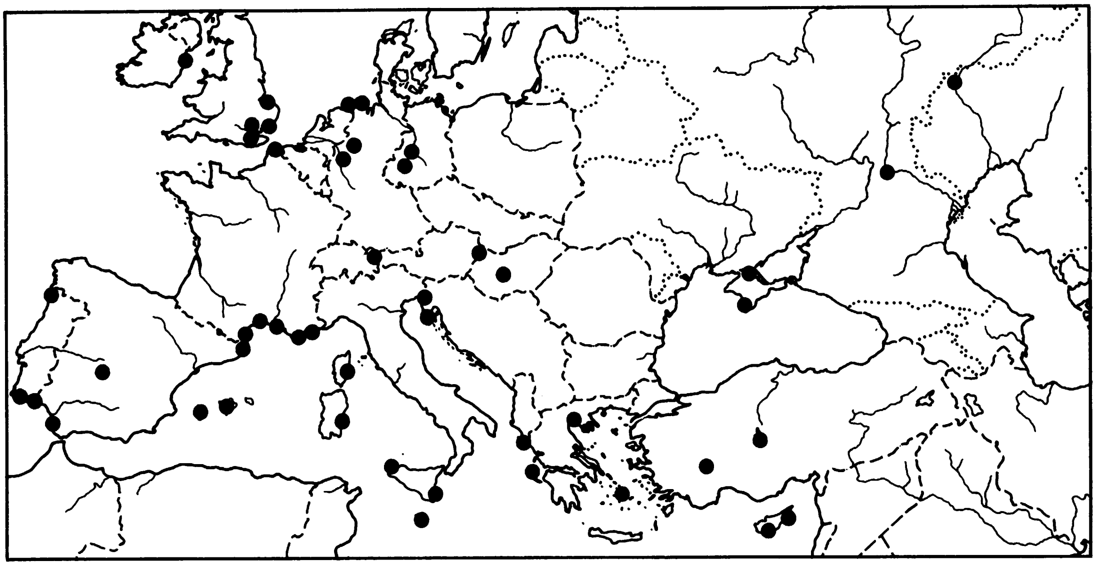


FIG. 209. Distribution of the *furcatus* group in Europe.

widely open dorsally. Tergum X with struts on anterior margin.

Aedeagus (figs. 204, 205) with parameres. Parameres slender and with median surface sclerotized; parameres extending to or just beyond apex of median lobe. Median lobe long; base bulbous, apical portion flattened; ventral surface midlongitudinally divided.

Spermatheca (fig. 206) tripartite. Receptacle sclerotized and divided into two parts by accordion tube; basal part larger than distal part; distal part without apical invagination; receptacle without brimlike ridges. Spermathecal gland sclerotized; shape and surface irregular.

DISTRIBUTION AND HABITAT: This group is known from Europe across Asia to Taiwan and in north Africa southward along the east African coast to Tanzania (figs. 208–210). Most of the species are from Europe and north Africa. The localities are near the seacoast or near salt lakes so the species may be restricted to saline habitats.

DISCUSSION: Six of the species formerly placed in *Euceratobledius* (table 9), and including its type species *B. furcatus*, are members of the *furcatus* group. A seventh species had been in the nominate subgenus, the eighth in *Elbidus*, and the ninth in *Pucerus*; the tenth, *maritimus*, had no previous subgeneric assignment. The group is in need of revision.

Species Included and Material Examined

andresi Bernhauer T(FMNH); type country: Egypt.

Algeria: Ziban, dunes of Biskra (IRSN); Touggourt (BMNH). **Egypt:** Mariout [=Maryut] (FMNH).

atramentarius Rottenberg [= *bos* Fauvel] Sp(BMNH, FMNH, MNHV, IRSN), type country: Italy.

Algeria: (BMNH); Oran (La Sinia? IRSN); Constantine (MNHV, FMNH). **Italy:** (FMNH); Sicily, Siracusa (IRSN); Sicily, Trapani (IRSN); Sicily (BMNH, MNHV, FMNH); Sardinia (FMNH). **Morocco:** Mogador [=Essaouira] (FMNH). **Tunisia:** Tunis (IRSN, MNHV); La Goulette

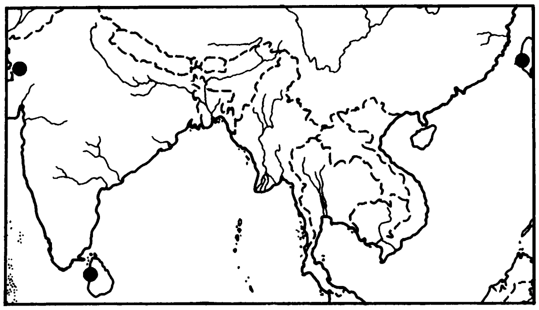


FIG. 210. Distribution of the *furcatus* group in India, Sri Lanka, and Taiwan.

(IRSN); Gabes (IRSN); Kebili (IRSN); (Gazom? IRSN); Soussa (BMNH).

bison Cameron T(BMNH); type country: India Or.

East India: (BMNH).

capra Fauvel Syn,Sp(IRSN), Sp(BMNH, FMNH, MNHV); type country: Egypt.

Algeria: (IRSN). **Arabia:** (Dakha? BMNH). **Djibouti:** Obock (BMNH). **Egypt:** (Giraffalosta? IRSN); Mariout [= Bahra Maryut] (IRSN, FMNH); Dakhel (IRSN); (Barrage? IRSN); Port Said (MNHV, IRSN, BMNH); Idku Lake (BMNH, FMNH); Siwa, Khamissa (BMNH); Ghardaga [=Hurghada] (FMNH). **Kenya:** Kilifi (BMNH). **Saudi Arabia:** Gulf of 'Aqaba (IRSN, FMNH). **Sudan:** Port Sudan (IRSN, BMNH, FMNH); Saukin (MNHV, FMNH). **Tanzania:** Dar-es-salam (FMNH). **Tunisia:** Kerkennah Island, El Ataya (MNHV); Sfax (MNHV). **Yemen:** (IRSN, BMNH); Al Mukalla (BMNH).

coiffaiti Irmler P(HCC); type country: Tunisia.

Tunisia: Kebili (HCC).

dinoceros Znojko Sp(BMNH, CNC, HCC); type country: USSR.

USSR: Crimea, Sivash (BMNH, HCC, CNC).

eckerleini Scheerpeltz H(MNHV); type country: Algeria.

Algeria: Massif de l'Aures, 5 km S Khanga, Sidi Nadji (MNHV).

formosae Bernhauer T,Co(FMNH); Co,Sp(BMNH, MNHV); type country: Taiwan.

Taiwan: An-p'ing (BMNH, FMNH); (Suisharyo? BMNH, FMNH).

furcatus (Olivier) Sp(BMNH, FMNH, IRSN, MNHV); type country: France.

Algeria: Oran (MNHV); Kralfallah (IRSN); Bone [='Annaba] (IRSN); Touggourt (IRSN); Oran (La Senia ? IRSN); Constantine Province (IRSN). **Austria:** Neusiedler Sea (MNHV); Arbe Island (MNHV); Thuringen (FMNH). **Cyprus:** Akrotiri (BMNH). **Egypt:** Alexandria (FMNH); Mariout [= Bahra Maryut] (FMNH); (Meaddish? FMNH); Port Said (IRSN); (Lake Aboukis ? IRSN). **France:** Var Department, La Seyne (MNHV); Herault Department (MNHV); Cette [=Sète] (IRSN); Calais (IRSN); Camargue (IRSN); Hyères (IRSN); Var Department (IRSN); Corsica, Aleria (IRSN); Port Vendres (IRSN); La Nouvelle (BMNH); Aigues Mortes (BMNH). **Germany, East:** Magdeburg (MNHV, FMNH); Eisleben (MNHV). **Germany, West:** Borkum Island (MNHV, FMNH); Halle (FMNH); Düsseldorf (FMNH); Langeroog Island (MNHV). **Greece:** (MNHV, FMNH, BMNH); Corfu (MNHV, FMNH, IRSN, BMNH); Kefallinia (MNHV, FMNH); Naxos (MNHV, FMNH); Kikladhes (MNHV, FMNH); Saloniki (Emgre? BMNH). **Hungary:** (IRSN). **Italy:** (FMNH) Grado (MNHV); Sardinia (BMNH, FMNH), Sicily, Trapani (IRSN); Monfalcone (IRSN); Siracusa (MNHV). **Libya:** Tripoli (FMNH, BMNH); Gulf of Bunbah, Cyrenaica (FMNH). **Malta:** (BMNH). **Mauritania:** Boulanouar (MNHV). **Morocco:** (FMNH, BMNH); Tanger (IRSN); Mogador [=Essaouira] (BMNH). **Portugal:** Fao (MNHV); (Mt. Cordova ? MNHV); Faro (FMNH); Portimao (IRSN). **Spain:** Mallorca (lagoon near Torre de la Porrassa ? BMNH); Mallorca, Rabassa (MNHV, FMNH); Ibiza (FMNH); Rosas, Catalonia (MNHV); Pozuelo de Calatrava (IRSN). **Sweden:** (FMNH). **Tunisia:** Tozeur (FMNH); Kebili (IRSN); Zarzis (IRSN). **Turkey:** Tuz Gölü Lake (MNHV); (50 km W Errgli, Karapinar? MNHV); Bornova, near Smyrna [=Izmir] (FMNH, BMNH). **United Kingdom:** southeastern England (P. M. Hammond, BMNH, unpublished notes). **USSR:** Sarepta (FMNH, IRSN, MNHV); Turkestan (MNHV); Ural'sk (FMNH); Sevastopol (FMNH). **Yugoslavia:** (Dalmatia, Vranjica, Karaman? MNHV); Pula (IRSN).

maritimus Bernhauer Co(FMNH), Sp(BMNH, MNHV); type country: Sudan.

Sudan: (Khor Arbeat Delta ? BMNH); Port Sudan (FMNH).

Undetermined.

Cyprus: Famagusta (MNHV). **Egypt:** Burg el Arab (USNM). **India:** Barmer, Thar Desert (BMNH). **Iran:** Mazandaran, 25 km W Gorgan (USNM). **Saudi Arabia:** Eastern Province, E of Khobar [= Al Khubar] (MCZ). **Sri Lanka:** (Willpattu Park, Marai Villa ? AMNH); Northwest Province, Arukallu, Eluamkulum, Pattalam (AMNH);

(Ham District, Palutapana? BMNH). **Turkey:** Aci-gol Lake, near Denizli (BMNH).

13. *lamelliceps* group

Figures 2, 56, 58, 66, 211–221,
508–511, 622–624

DIAGNOSIS: This group can be separated from all others by the reflexed clypeal margin (figs. 66, 215) and the postocular cephalic carina (figs. 66, 212, 214). Other characters that help to recognize the group include the open procoxal fissure (fig. 216), the presence of a protergosternal suture (fig. 216), the complete pronotal marginal bead (fig. 216), the presence of a membranous lobe on the posterior margin of the elytra, and the emarginate posterior margin of tergum VIII (fig. 56). The males have well-developed pronotal (fig. 216) and supraantennal horns (figs. 214, 215). The female also has supraantennal horns (figs. 212, 218) and, further, the pronotum has a short, broad, triangular, apically acute horn (fig. 217). The only other female with a pronotal horn is *B. susae* but it is slender and there are no supraantennal horns.

DESCRIPTION: Supraantennal ridge of male with one flattened, dorsally directed horn (figs. 214, 215); female with one flattened, cariniform horn (figs. 212, 218); horn of female smaller than that of male. Head without subantennal pockets; midbasal horn absent; postocular lateral carina present. Clypeal margin reflexed (figs. 66, 215); anterior margin without tubercles; clypeal middle without spines, ridges, or tubercles. Gular sutures fused. Labrum (fig. 213) with anterior margin entire or weakly emarginate; anterior margin not reflexed; median incision absent; dorsal surface flat, without broad midlongitudinal impression. Epipharyngeal lobe short; dorsal surface with one long and one minute seta; median processes with lobed apices, lateroapical region with thick multiramous process. Labial palps (fig. 211) with segments of subequal length; segments one and two of subequal thickness; first segment with two setae, second with three. Submentum not excavated. Mentum (fig. 211) with setae present laterally and medially. Hypopharynx (figs. 508–513) with lateral rows of setae gradually convergent toward base; basal setae arranged in transverse row; basal setae stout; basal setae not on plate; central row of setae dense throughout; disk with setae over most of surface; disk without cuticular processes; coronal pegs scattered over medial surface of disk. Prementum (fig. 211) with four sclerites, two lateral, one basal, and one medial. Galea with dense cluster of setae on apex and with long, stout setae on dorsal and lateral edge of apex; ventral surface without setae; dorsomedial edge with lobe. Mandibles bidentate.

Pronotum of male (fig. 216) with straight or slightly deflexed horn; female with short, broad, triangular median process (fig. 217). Marginal bead present and complete (fig. 216); bead dividing notum and hypomeron, not on hypomeron. Protergosternal suture present (fig. 216). Bead and suture anteriorly divergent. Procoxal fissure open (fig. 216). Protrochantin exposed. Prosternal process elongate. Prosternal setigerous pit absent; sternum (figs. 622, 623) with patch of setae present near shallow depression; depression with cluster of pores (fig. 624); anterior margin entire, not notched. Elytral epipleural ridge present and complete or incomplete; posterior margin with membranous lobe.

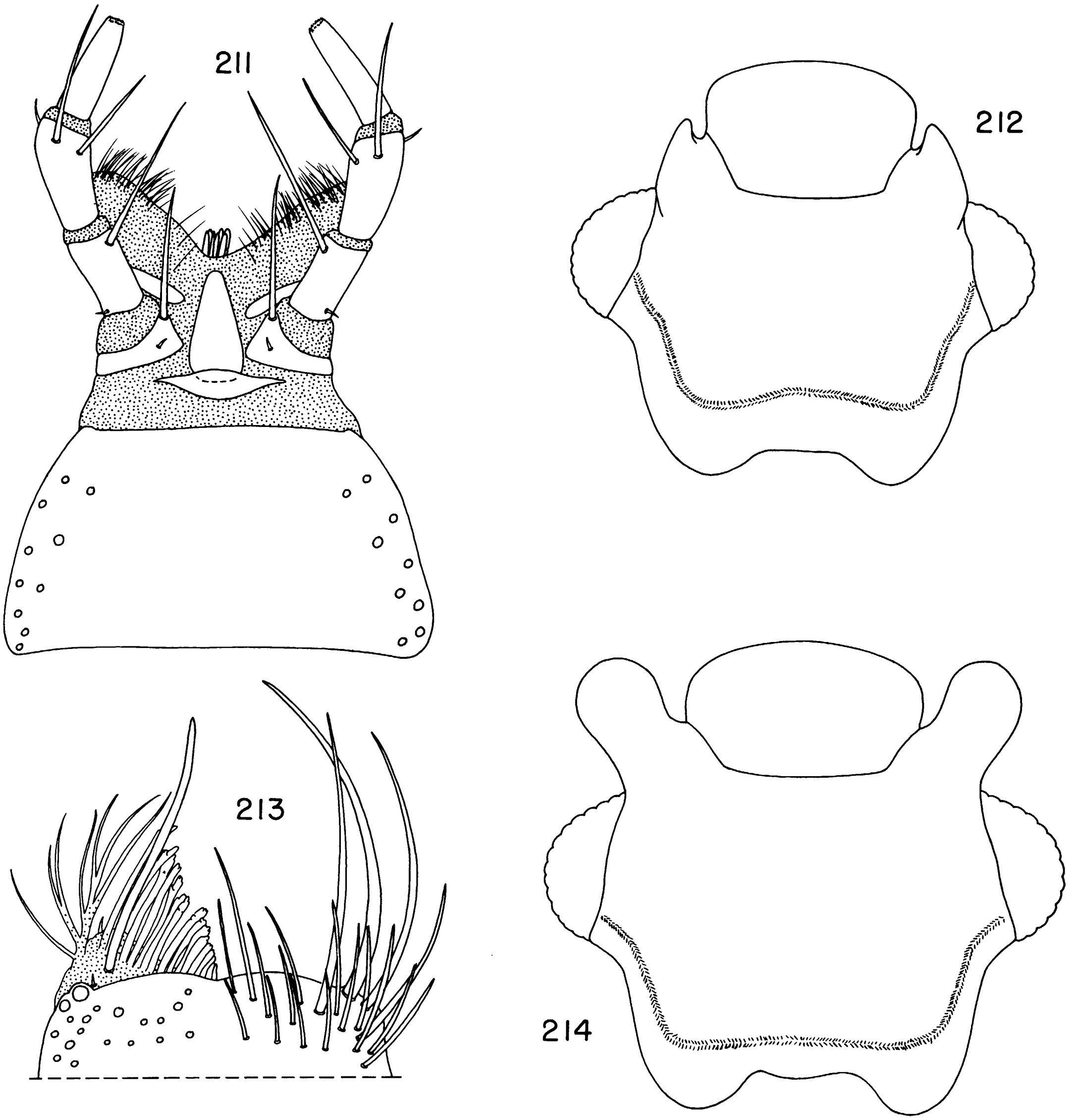
Tarsi four segmented. Protibia with two rows of spinelike setae. Metatibia with one spinelike seta on lateral surface near apex.

Abdominal tergum VII with medium to fine fringe on posterior margin. Tergum VIII with posterior margin emarginate; margin entire, not serrate. Tergum IX with glandular canal widely open dorsally. Tergum X with struts on anterior margin.

Aedeagus (fig. 219) with parameres. Parameres slender and with medial surface sclerotized; parameres extending to or just beyond apex of median lobe. Median lobe long; base bulbous, apical portion flattened; ventral surface midlongitudinally divided.

Spermatheca (fig. 220) tripartite. Receptacle sclerotized and divided into two parts by accordion tube; basal part larger than distal part; distal part without invagination; receptacle without brimlike ridges. Spermathecal gland sclerotized; shape and surface irregular.

DISTRIBUTION AND HABITAT: This group is known from the southern half of Africa and Madagascar (fig. 221). Since the locality records are all from near salt lakes and the seacoast, the species are probably restricted to saline habitats.



FIGS. 211–214. The *lamelliceps* group. *Bledius pilicollis*. **211.** Labium, setae of mentum removed. **212.** Head, female, dorsal view, mouthparts and antenna removed. **213.** Labrum, setae of left and epipharyngeal lobe of right removed. **214.** Head, male, dorsal view, mouthparts and antenna removed.

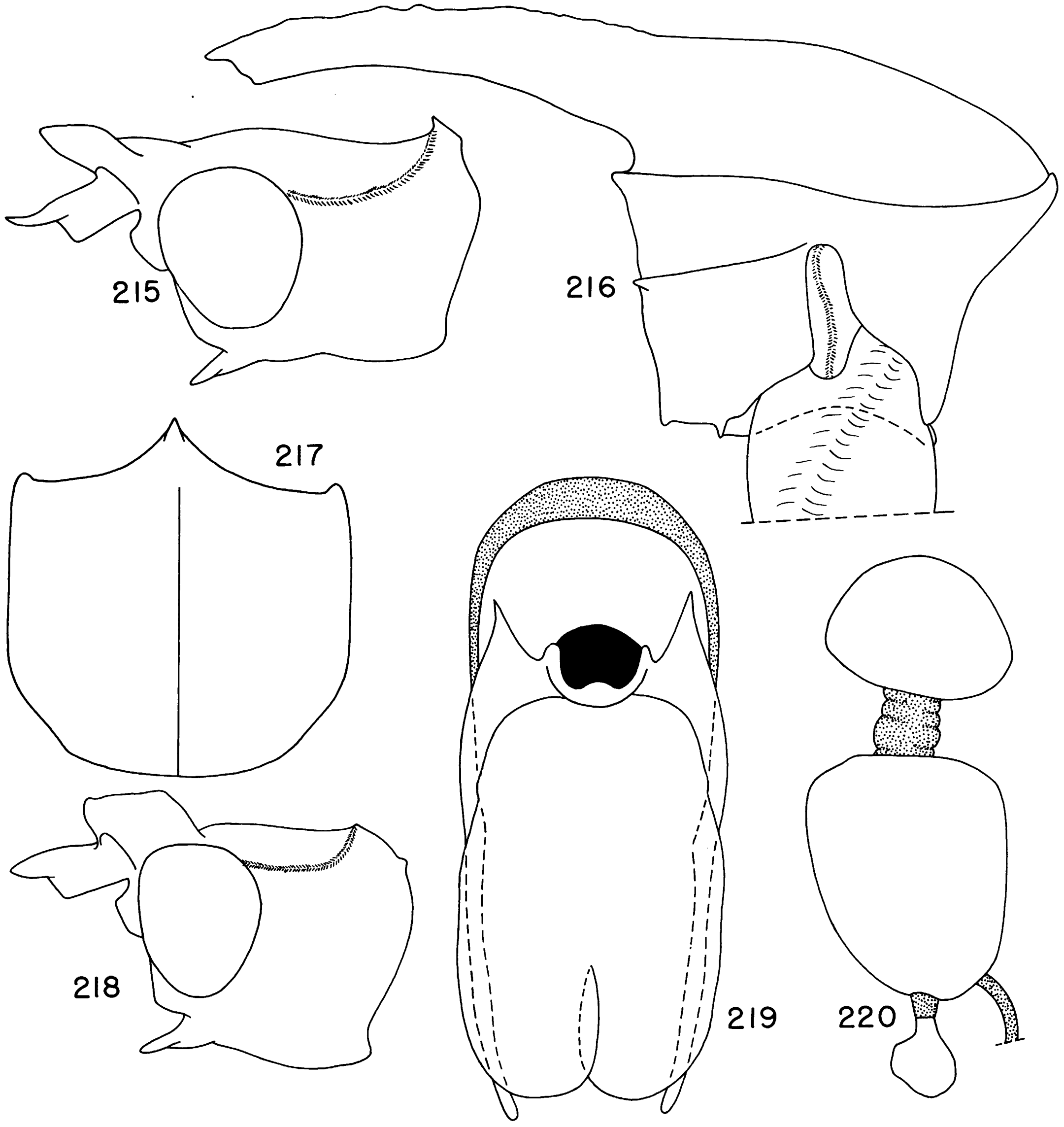
DISCUSSION: This group of species is separated for the first time herein. Two of the species had been in *Bledius* (s. str.), one in *Euceratobledius*, and the fourth had not been put in a subgenus (table 9). The group requires revision.

The females of this group and the female of *B. susae* are the only species known to have pronotal horns.

Species Included and Material Examined

hasticeps Bernhauer T(FMNH), Sp(MNHV); type country: Tanzania.
Madagascar: Tulear [=Toliara] (MNHV).
Tanzania: Dar-es-salam (FMNH).

lamelliceps Bernhauer T(FMNH, BMNH), Sp(BMNH); type country: South Africa.
South Africa: Milnerton (BMNH, FMNH);



FIGS. 215–220. The *lamelliceps* group. *Bledius pilicollis*. **215.** Head, male, lateral view, mouthparts and antenna removed. **216.** Prothorax, male, lateral view, setae removed. **217.** Prothorax, female, dorsal view, setae removed. **218.** Head, female, lateral view, mouthparts and antenna removed. **219.** Aedeagus, dorsal view. **220.** Spermatheca.

Grahamstown (BMNH); Port Alfred (BMNH).

pilicollis Bernhauer T,Co,Sp(FMNH), Co,Sp(BMNH), Sp(IRSN); type country: Angola.

Angola: Benguela (IRSN); Lobito (FMNH); Ambrizette [=N'zeto] (FMNH). **South Africa:** Rondebosch District (IRSN). **West Africa:** (IRSN). **Zaire:** Banana (IRSN, FMNH).

rudebecki Scheerpeltz H,Sp(MNHV); type country: South Africa.

South Africa: Transvaal, Capetown (MNHV); Milnerton, lagoon (MNHV).

Undetermined.

Angola: 7 mi. NE Porto Alexandre, Curoca

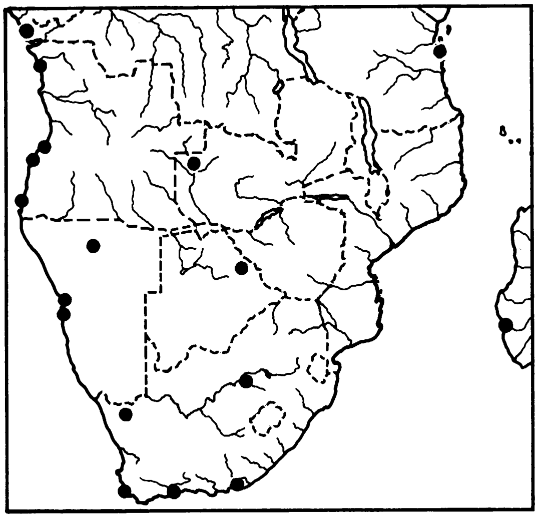


FIG. 221. Distribution of the *lamelliceps* group in southern Africa and Madagascar.

River (BMNH). **Botswana:** Makarikar Pan [= Makgadikgadi Pan] (BMNH); 2 mi. N Gweta (BMNH). **Namibia:** Swakopmund (BMNH); Walvis Bay (BMNH); Onguma fm., 55 mi. NW Tsumeb (BMNH); Otjitambi fm., 27 mi. ESE Kamanjab (BMNH); Homeb, 10 mi. ESE Gobabeb (BMNH). **South Africa:** Cape Province: Mosselbaai (BMNH, FMNH); Cape Province, Fish Hoek Valley (BMNH); Port Alfred (BMNH, IRSN); Capetown (IRSN); Cape Colony, Koeberg (IRSN); Orange Free State, Bothaville (FMNH); Cape Province, Rosebank (AMNH); Cape Province, Die Panne Nature Reserve (BMNH). **Zambia:** Zambezi (IRSN).

14. *kochi* group

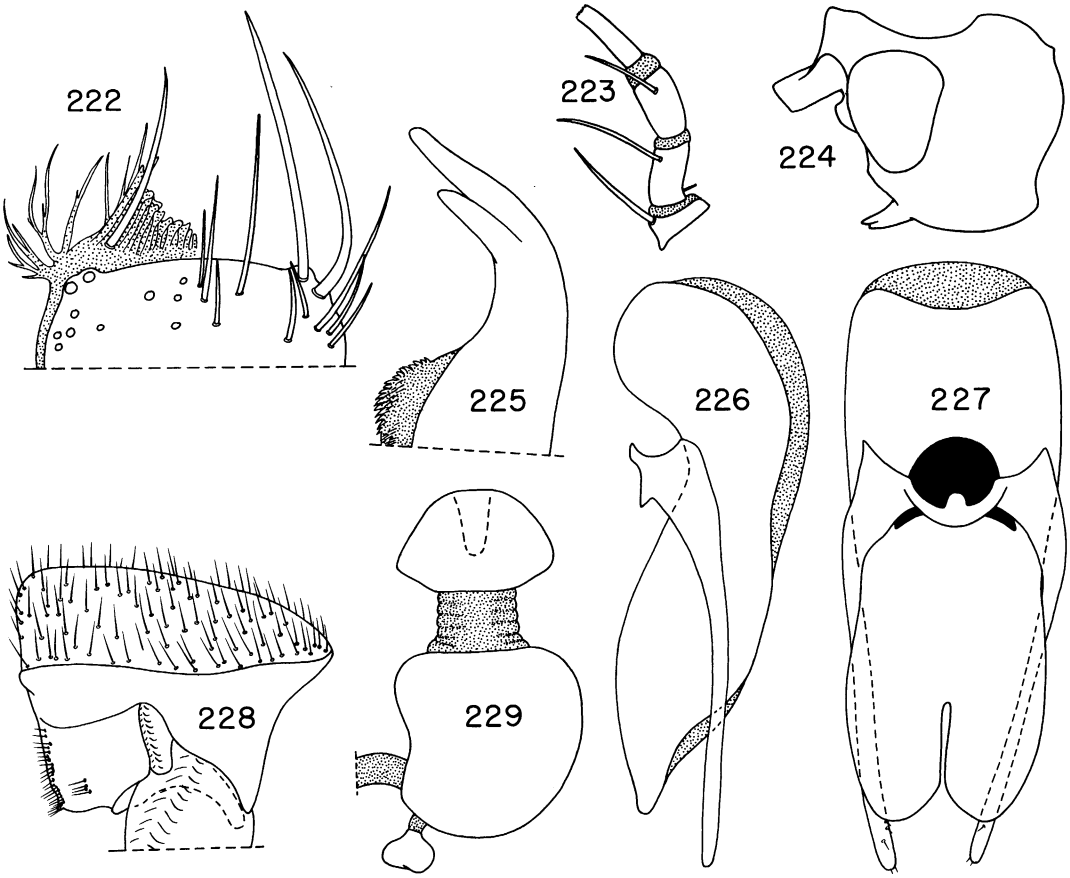
Figures 4, 222–232, 502–504, 625–630

DIAGNOSIS: Most of the species of this group can be separated from all other groups by the reflexed clypeal margin, the presence of only one subapical spinelike seta on the lateral surface of the metatibia, the complete elytral epipleural ridge, and the absence of a postocular carina (fig. 224). The males of this group have cariniform supraantennal ridges (fig. 224) and a midanterior tumescence on the pronotum.

The *furcatus* group, which has a well-developed clypeal reflexion, has four subapical spinelike setae on the lateral metatibial surface (fig. 202); the males have well-developed pronotal and supraantennal horns (fig. 207). The *lamelliceps* group, also with a reflexed clypeal margin, has a postocular cephalic carina (figs. 214, 215).

A few species of the *kochi* group with a feebly reflexed clypeal margin can be confused with the *gigantulus* group but can be separated because the males of the *gigantulus* group have pronotal horns and the males of the *kochi* group lack the horn but may have a large to feeble midanterior tumescence.

DESCRIPTION: Supraantennal ridge of male (fig. 224) with moderately to strongly developed cariniform, dorsally directed horn; female with enlarged supraantennal ridge but without horn. Head without subantennal pockets; midbasal horn absent; postocular lateral carina absent. Clypeal margin moderately to weakly to feebly reflexed; clypeus more strongly reflexed in male than female; clypeal reflexion often present only on lateral margin and absent on midanterior margin; clypeal reflexion evident in some species only as small carinules at anterolateral angles; anterior margin without spines; ridges, or tubercles. Gular sutures fused. Labrum (fig. 222) with anterior margin entire; anterior margin not reflexed; median incision present and feeble, or absent; dorsal surface flat, without broad midlongitudinal impression. Epipharyngeal lobe short; dorsal surface with one long and one minute seta; median processes with lobed apices; lateroapical portion with thick multiramous processes. Labial palps (fig. 223) with segments of subequal length; first and second segments of subequal thickness; first segment with two setae, second with one. Submentum not excavated. Mentum with setae present laterally and absent medially. Hypopharynx (figs. 502–504) with lateral rows of setae gradually convergent toward base; basal setae arranged in transverse row; basal setae stout; basal setae not on plate; central row of setae dense distally and sparse proximally; disk with setae scattered over central portion; disk with short cuticular processes on apical region; coronal pegs scattered on central portion of disk. Prementum with four sclerites, two lateral, one medial, and one basal. Galea with dense cluster of setae on apex and with row of long stout setae on dor-



FIGS. 222–229. The *kochi* group. *Bledius bicornis*. **222.** Labrum, setae of left and epipharyngeal lobe of right removed. **223.** Labial palpus. **224.** Head, male, lateral view, mouthparts and antenna removed. **225.** Madible, right. **226.** Aedeagus, lateral view. **227.** Aedeagus, dorsal view. **228.** Prothorax, male, lateral view. **229.** Spermatheca.

sal edge of apex; ventral surface without setae; dorsomedial edge with lobe. Mandibles bidentate (fig. 225).

Pronotum (fig. 228) of male with broad midanterior tumescence or with anterior middle bitumescent, or anterior margin unmodified; pronotum of female unmodified. Marginal bead present and complete (fig. 228); bead dividing notum and hypomeron, not on hypomeron. Protergosternal suture present (fig. 228). Bead and suture divergent anteriorly. Procoxal fissure open (fig. 228). Protrochantin exposed. Prosternal process elongate (fig. 228). Prosternal setigerous pit absent; sternum with patch of setae near shallow depression (figs. 625, 626); depression with cluster of pores in a pit (figs. 627–630); anterior margin entire, not notched. Elytral epipleural ridge present and complete; posterior margin with membranous lobe.

Tarsi four segmented. Protibia with two rows of spinelike setae. Metatibia with one spinelike seta on lateral surface near apex.

Abdominal tergum VII with coarse to moderately coarse fringe on posterior margin. Tergum VIII with posterior margin emarginate; margin entire, not serrate. Tergum IX with glandular canal widely open dorsally. Tergum X with struts on anterior margin.

Aedeagus (figs. 226, 227) with parameres. Parameres slender and with medial surface

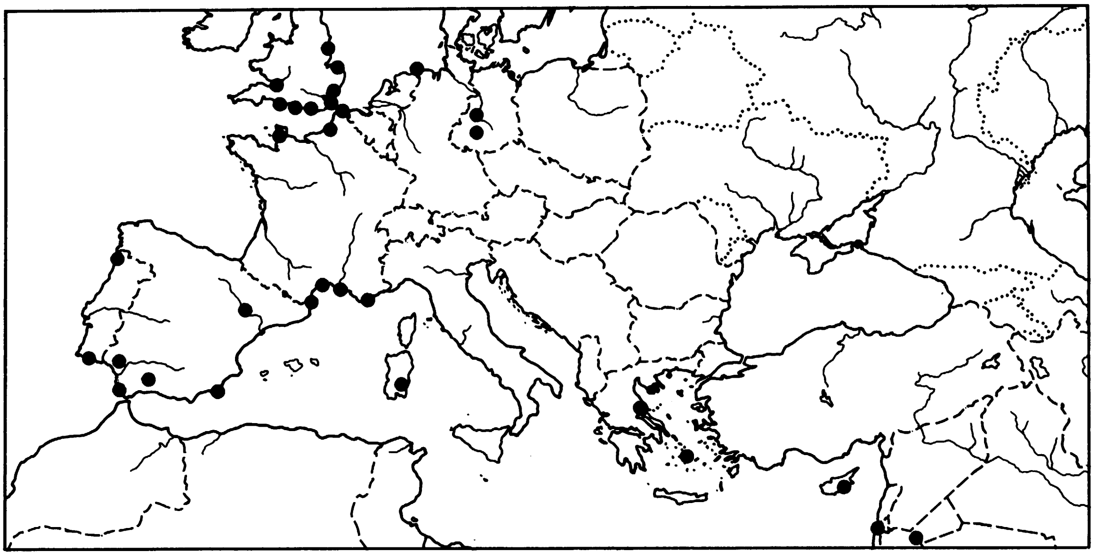


FIG. 230. Distribution of the *kochi* group in Europe.

sclerotized; parameres extending beyond apex of median lobe. Median lobe long; base bulbous, apical portion flattened; ventral surface midlongitudinally divided.

Spermatheca (fig. 229) tripartite. Receptacle sclerotized and divided into two parts by accordion tube; basal part larger than distal part; distal part with apical invagination; receptacle without brimlike ridges. Spermathecal gland sclerotized; shape and surface irregular.

DISTRIBUTION AND HABITAT: This moderately large group of species is found from Europe eastward across Asia to Taiwan and from north Africa south to Namibia and Botswana (figs. 230–232). The Chinese locality is indeterminant. The specimen from Namibia is undetermined. A new species of the group is from Noordhoek which I cannot find.

Most of the localities are near the ocean or salt lakes or in arid regions. The species may be found in saline habitats.

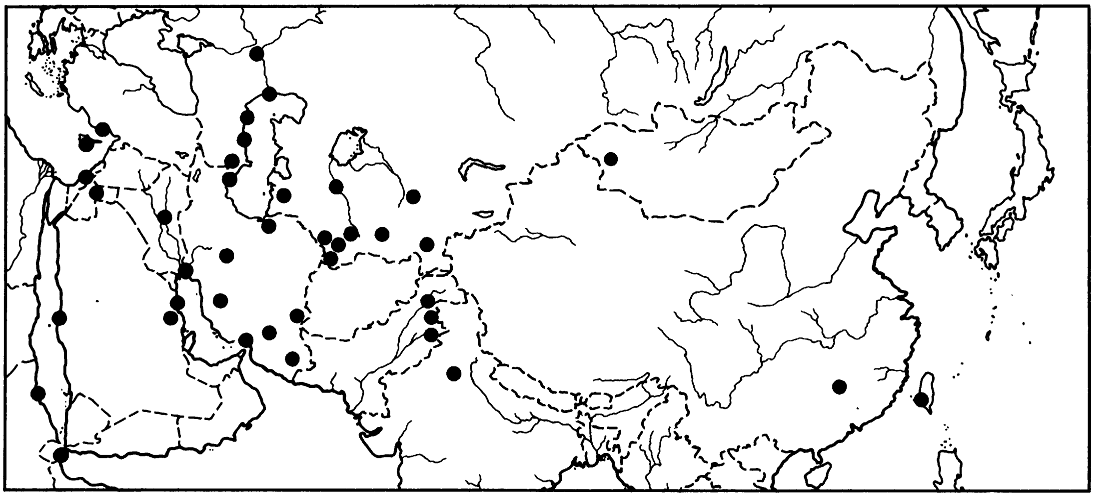


FIG. 231. Distribution of the *kochi* group in Asia.

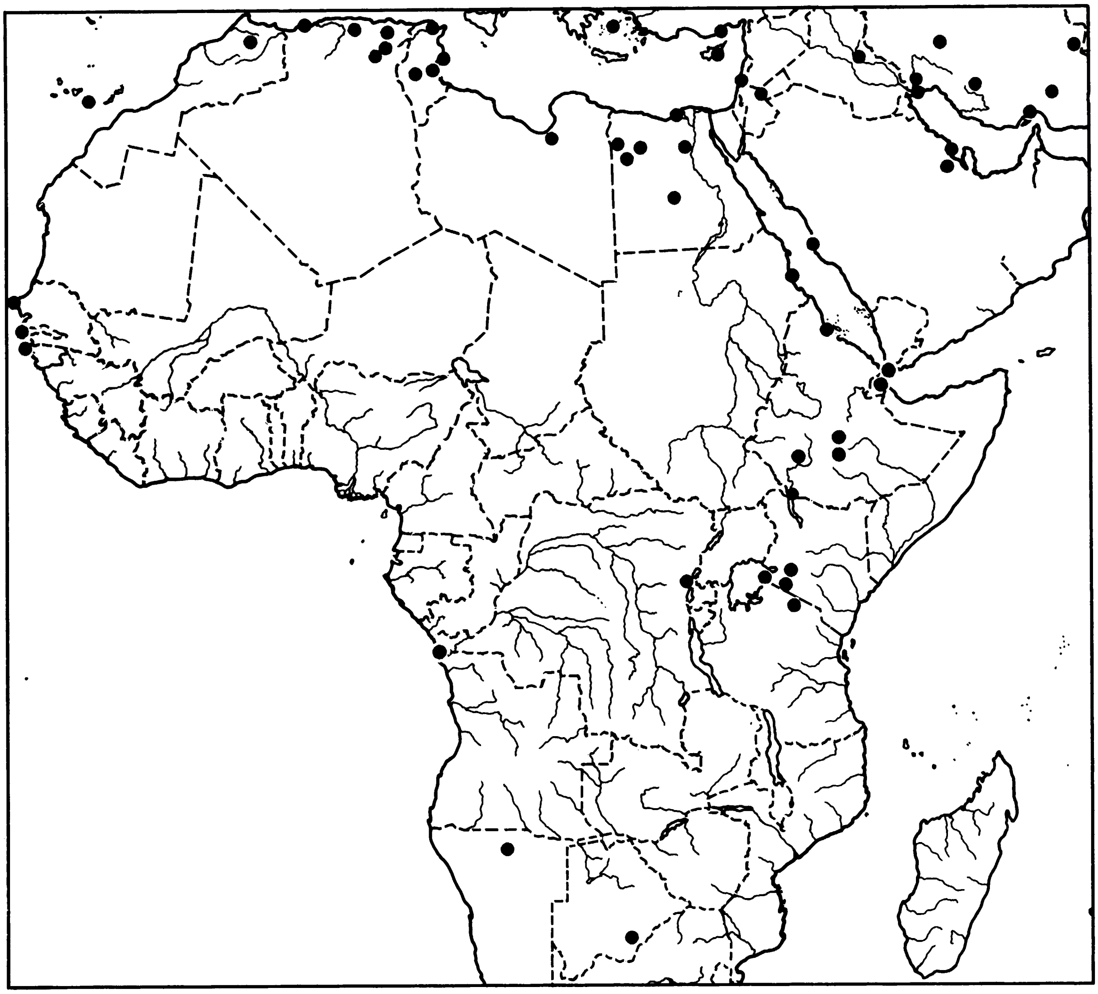


FIG. 232. Distribution of the *kochi* group in Africa.

DISCUSSION: This species group comprises most of the species that were in the subgenus *Elbidus* (table 9). Two species included in that subgenus are now in other species groups. *Bledius hauseri* and *lacustris* had been included in *Bledius* (s. str.) and *karachiensis* had been included in *Neobledius* which is now a junior synonym of the genus *Bledius* (synonymy herein). Two species, *auriculicollis* and *sanguinicollis,* are assigned to an infrageneric group for the first time.

Although this taxon has been correctly recognized for many years, many species have been added without benefit of a comprehensive analysis. The group is in serious need of revision.

The clypeal margin of this group is moderately to feebly reflexed. On some species (for example *B. auriculicollis, B. lacustris, B. sanguinicollis,* and *B. vitulus*) the reflexion extends over the whole anterior and lateral clypeal margin. The clypeal reflexion of *B. carinicollis* includes both the lateral and anterior margin but is broken into a series of carinules. Many European and Asian species have the clypeal reflexion moderately well developed on the lateral margin but weakly developed or absent on the anterior margin. Often the reflexion is absent only on the median portion of the anterior margin. Species with this partially reflexed clypeal margin include *B. bicornis, B. formosanus, B. hinnu-*

lus, B. naxius, B. ouzbekiscus, B. persicus, B. simplicifrons, and others. *Bledius hauseri* has a feebly reflexed clypeal margin that in some individuals is restricted to the lateral margin.

Bledius convexicollis and *B. taruensis* have feeble carinules on the lateral clypeal margin. They run to the *gigantulus* group in couplet 48 of the key to species groups. I include these two species in the *kochi* group because the males have cariniform supraantennal horns and a broad tumescence on the midanterior portion of the pronotum (both characteristic of the males of the *kochi* group). The presence of carinae on the clypeal margin, however faint, I take as further support for inclusion in the *kochi* group. The reduction of the clypeal reflexion has already been noted for other species.

Abdullah and Qadri (1968) described *Neobledius karachiensis. Neobledius* is a synonym of *Elbidus* and the species belongs in the *kochi* group where it is near or conspecific with *B. vitulus.* Both species have a well-developed clypeal reflexion, a bipronged supraantennal horn, a bitumescent anterior pronotal margin, and anteriorly produced pronotal angles.

Species Included and Material Examined

amplithorax Coiffait H(HCC); type country: USSR.

USSR: Turkmenia, Kouchka (HCC).

auriculicollis Bernhauer T(FMNH), Co,Sp(BMNH), Sp(MNHV); type country: Tanzania.

Botswana: Kanye (MNHV). **Kenya:** Magadi (BMNH); Ngong (BMNH). **Tanzania:** Natron Lake (FMNH, BMNH); (Kamballa? BMNH, FMNH).

bicornis (Germar) Sp(BMNH, FMNH, IRSN, MNHV); type country: East Germany.

Algeria: Arzew near Oran (IRSN); (La Senia, Oran, Lac Salé ? IRSN); the lake between Constantine and Batna (IRSN). **China:** (Tchenly, Yangtz? FMNH). **France:** Camargue (MNHV); Manche Dept. (Lingreville? IRSN); Cette [=Sète] (IRSN); Calais (IRSN); St. Valery sur Somme (IRSN); Banyuls sur Mer (IRSN). **Germany, East:** Sülldorf near Magdeburg (MNHV); Eisleben (MNHV). **Germany, West:** Borkum Island (MNHV, FMNH). **Iraq:** Mesopotamia (FMNH, BMNH). **Italy:** Sardinia (MNHV). **Senegal:** Dakar (IRSN). **Spain:** Cartagena (IRSN). **Syria:** (Mujunkum? FMNH). **Taiwan:** An-p'ing (FMNH); (Suisharyo? FMNH). **Tunisia:** Gabes (IRSN); Tunis (IRSN). **United Kingdom:** southern coast of England (P. M. Hammond, unpublished notes). **USSR:** Sarepta (FMNH); Repetek, Turkmeniya (FMNH); Tschardschui [=Tcharjui] (FMNH); Merv [=Mary], Turkmeniya (FMNH); Transcaspian (Dortkuju? FMNH); Transcaspian (Splichal? FMNH); Transcaspian, Aulie Ata [=Dzhambul] (FMNH); Transcaspian (Imam? FMNH); Turkestan (FMNH). Country unknown: (Saemiretschj Ilijsk ? FMNH). (Salziger See ? FMNH).

biskrensis Fagel H,P(IRSN); type country: Algeria.

Algeria: Ziban, Biskra Oasis, Touggourt route (IRSN); Biskra (IRSN); Touggourt (IRSN). **Tunisia:** Kebili (IRSN).

carinicollis Fauvel Syn,Sp(IRSN), Sp(BMNH, FMNH, MNHV); type country: Algeria.

Algeria: Bou Saâda (IRSN); Constantine, Gazelle fountain, 30 km NW Biskra (IRSN); (Nza-ben-Rzig, Oued-Rirh? IRSN); Biskra (MNHV, IRSN, FMNH); Touggourt (IRSN); plain of Hodna (IRSN). **Iran:** (BMNH, FMNH). **Iraq:** Mesopotamia (BMNH); Baghdad (BMNH). **Tunisia:** Gabes (IRSN).

convexicollis Bernhauer T,Co(FMNH), Sp(BMNH); type country: USSR.

USSR: Turkmeniya, Tedzen (BMNH); Tschardshui [=Tcharjui] (FMNH); Transcaspian (Kuschka? FMNH).

diota Schiødte Sp(BMNH, IRSN, MNHV); type country: Denmark.

Algeria: Oran (BMNH). **Egypt:** El Bahrein (BMNH); Sitra (BMNH). **Germany, East:** Eisleben (IRSN). **Germany, West:** Borkum Island (MNHV). **Sudan:** (Khor Arbaat Delta ? BMNH). **United Kingdom:** southeastern coastal England (P. M. Hammond, BMNH, unpublished notes).

femineus Coiffait P(HCC); type country: Saudi Arabia.

Saudi Arabia: Ad Dammam (HCC); Hofuf [= Al Hufuf](HCC); (Bahara? HCC).

formosanus Bernhauer T(FMNH); type country: Taiwan.

Taiwan: (Suisharyo? FMNH).

hauseri Eppelsheim T(MNHV), Sp(IRSN); type country: USSR.

USSR: Buchara (MNHV); Turkmeniya, Repetek (IRSN).

hinnulus Erichson Sp(BMNH, FMNH, IRSN, MNHV); type country: USSR.

Iran: Khuzistan, Shadegan (MNHV); (Poucht-e-Kouh? IRSN). **Iraq:** Baghdad (MNHV). **Mongolia:** Chovd [=Hovd] aimak, Jamatin Dolon, 40 km N Somon Manchan [=Manhan], SW corner of char [=Har] Us Nuur (CNC) (additional localities: Smetana, 1975). **Pakistan:** Rawalpindi (MNHV). **Syria:** (Mujunkum? FMNH). **USSR:** Turkestan (MNHV, BMNH, IRSN); Uzbekistan, Margelan (MNHV, FMNH); Turkmeniya, Bayram-Ali (IRSN); Turkmeniya, Repetek (FMNH, IRSN, MNHV); Astrakhan, Caspian Sea (IRSN, MNHV); Sarepta (IRSN, MNHV); Caucasus, Araxes-Thal [= Aras Valley] (MNHV); Transcaspian (New Saratov ? MNHV); Merv [=Mary] (MNHV, BMNH); Turkmeniya, Imambaba (MNHV); Transcaspian (Dortkuju? MNHV); Transcaspian (Ljutfabad? MNHV); Transcaspian (Saramsakli? MNHV); Syrdarja Region, Uzbekistan (MNHV); Great Balakhan, Dschebell [=Dzhebel] (MNHV); Aulie-Ata [=Dzhambul] (FMNH, MNHV); Turkestan, Ketmen (Sussamyr? MNHV); Azerbaydzhan, Lenkoran, Astara (IRSN); Buchara (FMNH).

immarginatus Koch Sp(MNHV); type country: Egypt.

Algeria: Massif de l'Aure, 5 km S Kanga, Sidi Nadji (MNHV); Boghari (MNHV). **Egypt:** Fayum [= El Faiyûm] (MNHV). **Iran:** Khuzistan, Shadegan (MNHV). **North Africa:** (MNHV). **Sudan:** (MNHV).

karachiensis (Abdullah and Qadri) H,P(UKP); type country: Pakistan.

Pakistan: Karachi (UKP).

kochi Cameron Syn(BMNH); type country: Egypt.

Egypt: Siwa (Khormissa? BMNH).

lacustris Bernhauer T,Sp(BMNH), Co(FMNH); type country: Ethiopia.

Ethiopia: Hora Abyate Lake (FMNH, BMNH). **Kenya:** Lake Elmenteita (BMNH); (Lake Ndutu ? BMNH); (Lake Hannington ? BMNH). **Zaire:** Vitshumbi, Lake Edward (IRSN, BMNH).

loeffleri Coiffait P(HCC); type country: Iran.

Iran: Kerman Province (HCC).

[*naja* Koch] no specimens examined; type country: USSR.

Koch (1938b) assigned this species to the subgenus *Elbidus*. He illustrated it and compared it to *carinicollis*. The carinate pronotal tumescence shown in Koch's figure of *naja* is characteristic of some species of the *kochi* group.

naxius Bernhauer T,Co(FMNH), Co(BMNH), Sp(MNHV); type country: Greece.

Greece: Naxos (FMNH, MNHV, BMNH).

ouzbekiscus Coiffait H,P(HCC); type country: USSR.

USSR: Uzbekistan, Urgench (HCC).

persicus Bernhauer T(FMNH), Sp(MNHV); type country: Iran.

Iran: (FMNH); Iranshahr (MNHV).

postmaculatus Fagel H,P(IRSN); type country: USSR.

USSR: Buchara (IRSN); Turkestan (IRSN); Turkmeniya, Bayram Ali (IRSN).

puglialis Coiffait H(HCC); type country: Spain.

Spain: Andalusia, Cape Trafalgar (HCC).

richteri Scheerpeltz T,Co(MNHV); type country: Iran.

Iran: Khuzistan, Shadegan (MNHV).

sanguinicollis Bernhauer T(FMNH, BMNH); type country: Kenya.

Kenya: Homa, South Kavirondo Gulf (BMNH, FMNH).

sareptanus Fagel H,P(IRSN); type country: USSR.

USSR: Sarepta (IRSN).

simplicifrons Coiffait Sp(HCC); type country: Saudi Arabia.

Saudi Arabia: Hofuf [= Al Hufuf] (HCC).

taruensis Cameron Syn,Sp(BMNH); type country: Pakistan.

Iraq: Baghdad (BMNH). **Pakistan:** Peshawar (Taru? BMNH).

tuniseus Fagel P(IRSN); type country: Tunisia.

Tunisia: Kebili (IRSN).

turcmenus Fagel H,P(IRSN); type country: USSR.

USSR: Turkmeniya, Bayram-Ali (IRSN).

vitulus Erichson Sp(BMNH, FMNH, IRSN,

MNHV, HCC); type country: Saudi Arabia.

Algeria: Biskra (FMNH); Oran (La Senia, salt lake ? IRSN); Touggourt (IRSN); Oran (FMNH). **Canary Islands:** Grand Canary: Maspalomas (BMNH). **Cyprus:** (IRSN); Larnaca (MNHV). **Djibouti:** Obock (IRSN). **Egypt:** Siwa Depression (BMNH); Sitra (BMNH); (Sennoures? FMNH); Fayum Province (FMNH); Bahra Maryut (FMNH); (Lake Aboukiz ? IRSN). **Ethiopia:** (BMNH); Massawa (FMNH, IRSN); Nanoropus, Lake Rudolf (FMNH). **Gambia:** (Keneba? BMNH); (Tambanaa? BMNH). **Germany, East:** salt lake near Eisleben (MNHV). **Germany, West:** Borkum Island (MNHV). **Guinea-Bissau:** Cacheu (BMNH). **Greece:** Volos, Thessalia (MNHV). **Iran:** Khuzistan, Shadegan (MNHV). **Iraq:** Mesopotamia (BMNH, FMNH). **Israel:** Haifa (FMNH). **(Italian Somaliland:** Disei? BMNH). **Jordan:** Azraq Shishan, 200 km E Amman (MNHV). **Libya:** Cyrenaica (FMNH). **Morocco:** Fès (Douiete? MNHV). **Persian Gulf:** (BMNH). **Portugal:** Fao (BMNH, FMNH). **Saudi Arabia:** Iedda [=Jiddah] (BMNH, FMNH); (Dakhla? BMNH, FMNH). **Senegal:** (FMNH); (Sebikotan? BMNH); Dakar (IRSN). **South Yemen:** Perim Island (BMNH). **Spain:** Andalusia (MNHV); Murcia Province (FMNH); Andalusia, Laguna Antequera (HCC); Sastago, Salina de Retallon (HCC); Sevilla (San Lucar ? MNHV). **Sudan:** (Khor Arbaat Delta? BMNH); Port Sudan (FMNH). **Tunisia:** Tunis (MNHV); Kebili (IRSN); (Fedjadi? IRSN); Kerkenna Island (IRSN). **Turkey:** Silifke (BMNH). **USSR:** Sarepta (MNHV).

[*xiphias* Koch] no specimens examined; type country: Tunisia.

Koch (1938b) placed this species in the subgenus *Elbidus.* It is unusual in the *kochi* group because Koch illustrates the species with a long, slender pronotal horn; such modification is more characteristic of the *furcatus* group. The supraantennal horn shown for *xiphias* by Koch, however, is more characteristic of the *kochi* than the *furcatus* group. The more definitive means of separating the *kochi* [=*Elbidus*] and *furcatus* [=*Euceratobledius*] group is the number of subapical metatibial spinelike setae. Koch knew this and probably placed *xiphias* correctly in *Elbidus.*

Undetermined.

Afghanistan: (Dahlah? MNHV). **Egypt:** (Amrieh?); Dakha Oasis (USNM). **Ethiopia:** Arba Minch (BMNH); Shoa, Awasa Lake (BMNH); Shoa, Langana Lake (BMNH). **France:** Hyères. **Gambia:** Toniataba (USNM). **India:** New Delhi (USNM). **Iran:** Fars Province, 13 km SE Shiraz (USNM); Mazandaran, 25 km W Gorgan (USNM); Baluchistan, 85 km W Zahedan (USNM); Kerman, 5 km NE Bandar Abbas (USNM); Shiraz (MNHV); 30 km S Esfahan (MNHV); Abadan (MNHV). **Jordan:** (Wadi er Ratam? BMNH). **Kenya:** Nakuru District, Lake Nakuru (AMNH). **Pakistan:** Lahore (USNM). **Saudi Arabia:** El Katif (IRSN). **Tunisia:** Sfax (BMNH). **USSR:** Daghestan, Kraynovka (BMNH); Daghestan, Biryuchek (BMNH); Daghestan, Novobiryuzyak (BMNH); Daghestan, Derbent (MNHV); Turkmeniya (Kouchka, Broussailles River ? HCC). **Zaire:** Banana (IRSN).

15. *emarginatus* group

Figures 5, 233–245, 514–519, 524, 525, 631–635

DIAGNOSIS: This group is separated from all others by the characters given in the key. The only external feature that distinguishes the *emarginatus* from the *annularis* group is the absence of the median incision of the labrum (fig. 234). Some of the features that characterize the *emarginatus* group include: the open procoxal fissure (fig. 235), presence of the protergosternal suture (fig. 235), complete pronotal marginal bead and elytral epipleural ridge, and emarginate posterior margin of tergum VIII.

DESCRIPTION: Supraantennal ridge low, not enlarged and without horns. Head without subantennal pocket; midbasal horn absent; postocular lateral carina absent. Clypeal margin not reflexed; anterior margin with or without tubercles; clypeal middle without spines, ridges, or tubercles. Gular sutures fused. Labral margin (fig. 234) entire or emarginate; margin not reflexed; median incision absent (fig. 234); dorsal surface flat, without midlongitudinal impression. Epipharyngeal lobe (fig. 234) short; dorsal surface with one long and one short seta; median processes with lobed apices; lateroapical processes numerous, slender, and unbranched or branched. Labial palps (fig. 233) with segment of subequal length; first and second segments of subequal thickness; first segment with two setae, second segment with one. Submentum not excavated. Mentum (fig. 233) with setae sparse laterally and absent or absent from narrow median strip. Hypopharynx (figs. 514–519, 524, 525) with lateral rows of spines gradually convergent toward base; basal setae arranged in transverse row; basal setae stout; basal setae not on plate; central row of setae dense distally and proximally, sparse or absent medially; disk without setae; disk with or without short cuticular processes over most of surface; cuticular processes lobed or in palmate clusters (fig. 515); coronal pegs scattered over most of surface of disk. Prementum with three sclerites, one median and two lateral; basal sclerite absent. Galea with dense cluster of fanlike rows of setae on apex; ventral surface without setae; dorsomedial edge with lobe. Mandibles edentate, bidentate, or tridentate (fig. 236).

Pronotal horn absent. Marginal bead present (fig. 235) and complete; bead dividing notum and hypomeron, not on hypomeron. Protergosternal suture present (fig. 235); suture weak in some species. Bead and suture parallel. Procoxal fissure open (fig. 235). Protrochantin exposed. Prosternal process elongate. Prosternal setigerous absent; prosternum with shallow depression surrounded by scattered setae (figs. 631, 632); depression with small cluster of pores (figs. 633–635); anterior margin entire, without notch. Elytral epipleural ridge present and complete; posterior margin with or without membranous lobe.

Tarsi four segmented. Protibia with two rows of spinelike setae.

Abdominal tergum VII with fine fringe on posterior margin. Tergum VIII with posterior margin emarginate; margin entire, not serrate. Tergum IX with glandular canals widely open dorsally. Tergum X with struts on anterior margin.

Aedeagus (figs. 238, 239) with parameres. Parameres slender and with median surface sclerotized; parameres extending beyond apex of median lobe. Median lobe long; base bulbous, apical portion flattened; ventral surface midlongitudinally divided.

Spermatheca (figs. 240, 241) tripartite. Receptacle sclerotized or membranous and divided by accordion tube into two parts; basal and distal parts of nearly equal size; distal part invaginated; distal and basal parts each with or without brimlike ridge. Spermathecal gland weakly sclerotized; shape nearly spherical; surface smooth.

DISTRIBUTION AND HABITAT: Most of the species in this group are found in the southern hemisphere in southern Africa (fig. 245), Australia (fig. 244), and South America. In the New World some species are found in Central America and the West Indies (fig. 242) with three species reaching the United States and one to Canada (fig. 243). However, although the group is distributed in both the New and Old World, most of the species are in North and South America. Only 10 species are described for the Old World, 7 in Australia, and 3 in Africa. One undescribed species is found in northern India (fig. 5). The group is probably more speciose in the Old World than the data now show.

Species for which habitat information is available are found near freshwater.

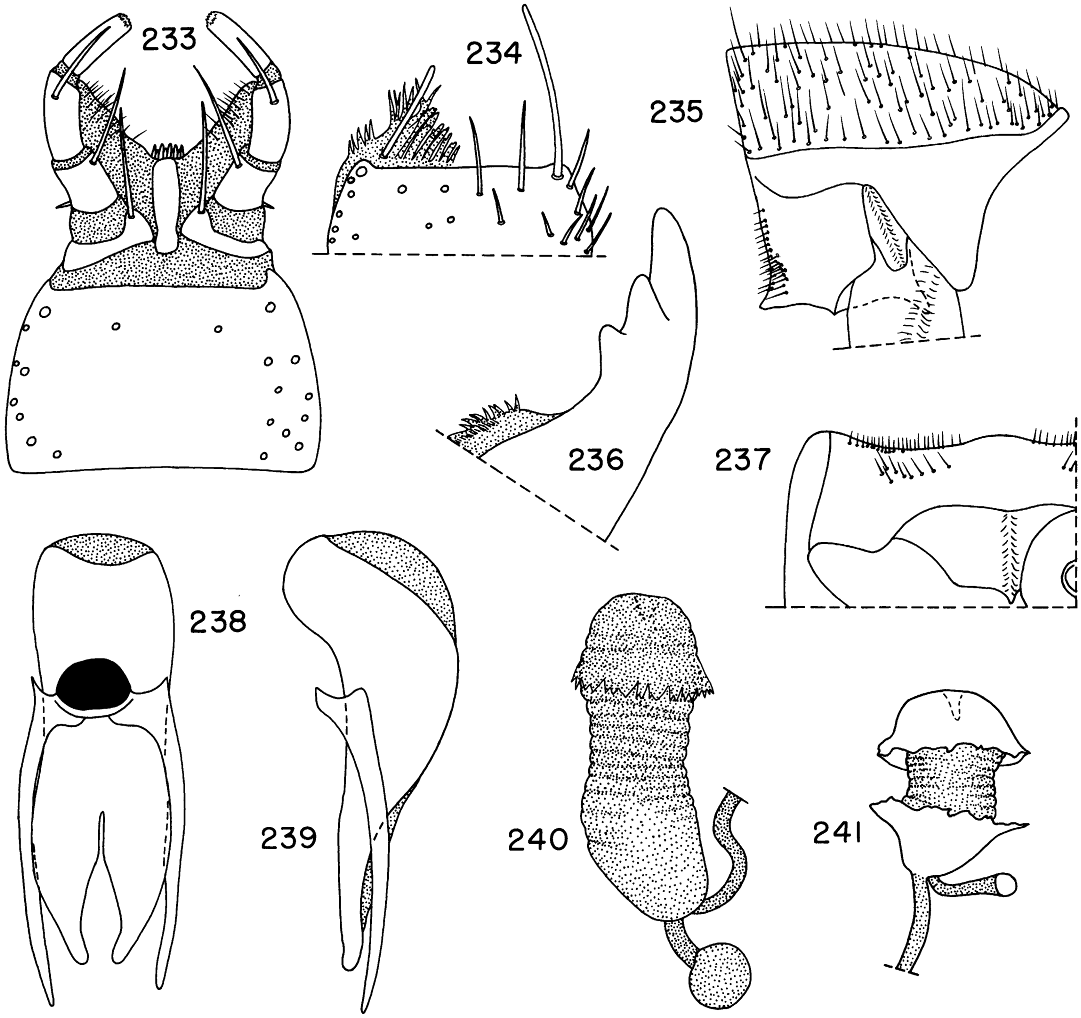
DISCUSSION: This group was first segregated with only three North American species by Herman (1983a). Herein I move 2 from *Astycops* and 11 from *Hesperophilus* (table 9). The remaining 27 were previously unassigned to any infrageneric group.

Some species of this group form complexes but they are characterized by similarity of appearance rather than more objective features. Some of these groups may be composed of related species but seeking to substantiate these complexes is beyond the scope of this paper. I list these species and groups merely as a starting point for revising the group.

The *bruchi* complex has three species: *acuticollis, bruchi,* and *testaceipennis.* The anterior pronotal angles of each are produced and acute. They are all from Argentina and may in fact represent one species.

Bledius konigsbaueri and *semiopacus* are similar species from Namibia and may be conspecific.

Bledius bolsonensis, chilensis, norquincoensis, and *rufipes* are from Chile and Ar-



FIGS. 233–241. The *emarginatus* group. *Bledius externus.* **233.** Labium, setae of mentum removed. **234.** Labrum, setae of left and epiphryngeal lobe of right removed. **235.** Prothorax, lateral view. **236.** Mandible, right. **237.** Prothorax, ventral view, right anterior two-thirds. **238.** Aedeagus, dorsal view. **239.** Aedeagus, lateral view. **240.** Spermatheca. **241.** Spermatheca (*B. emarginatus*).

gentina. They are black, lack the median pronotal groove, and the pronotal surface has a matte appearance. *Bledius bolsonensis* and *rufipes* may be conspecific. *Bledius chilensis* and *norquincoensis* may be synonyms.

Bledius addendus, curtipennis, and *simplex,* all from South America, have distinct but rounded pronotal basal angles, the surface of the pronotum shines dully, and the species are yellowish brown.

The next group is large but I find no easily examined characters to define it. I base the group on appearance but there may be other characters that can be seen upon dissection. The group is found in North America, South America, and the West Indies. It includes: *cognatus, cubensis, emarginatus, gebieni, gregarius, infantilis, jamaicensis, pumilio, trinidadensis, withycombei,* and *wudus.*

Bledius ovensensis, from Australia, has narrowly open procoxal fissures and is included in this group because it shares other characters with species in the *emarginatus* group.

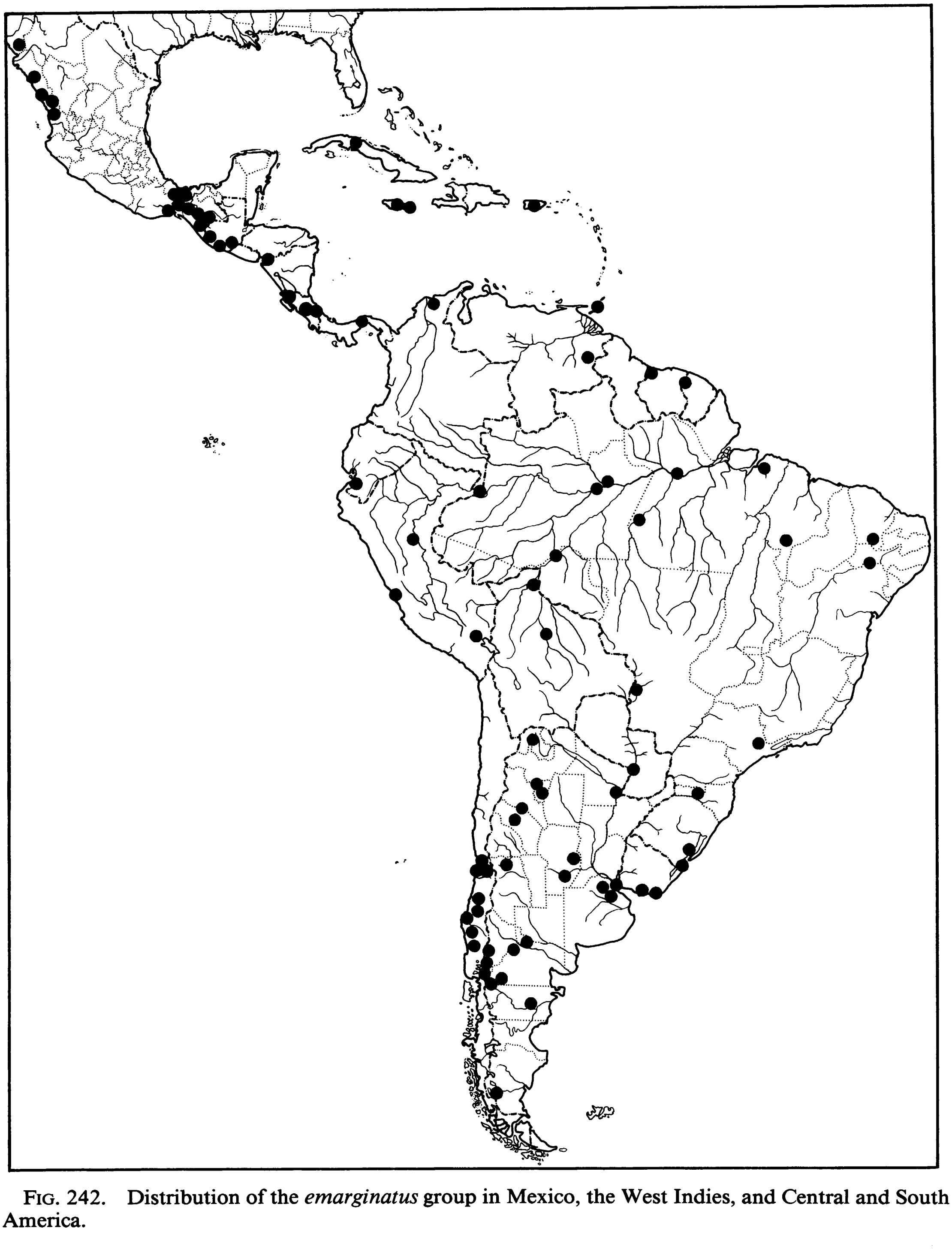


FIG. 242. Distribution of the *emarginatus* group in Mexico, the West Indies, and Central and South America.

Bledius aterrimus, also from Australia, is included here pending further study. This species is black, has bidentate mandibles, and a deeply emarginate labrum that has a broad, midlongitudinal impression. It is difficult to be certain that the median incision of the

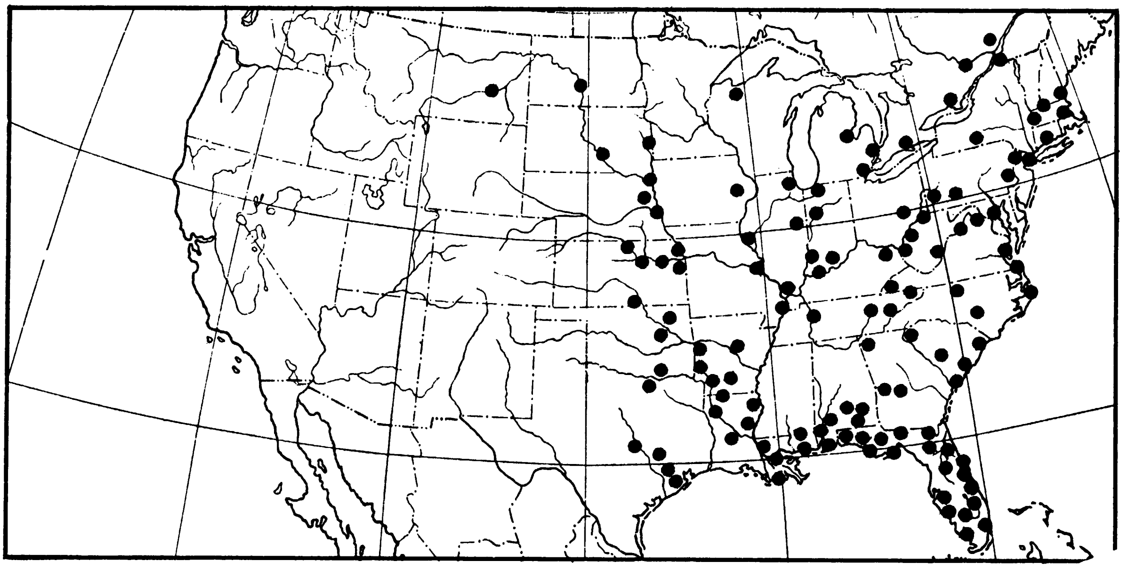


FIG. 243. Distribution of the *emarginatus* group in North America.

labrum is absent. More specimens are needed for dissection so that the species can be assigned to the proper group.

Species Included and Material Examined

acuticollis Bernhauer T(FMNH); type country: Argentina.

Argentina: Cordoba Province (FMNH).

addendus Sharp T(BMNH); type country: Brazil.

Brazil: Rio Solimoes (BMNH).

aterrimus Fauvel Syn,Sp(IRSN), Sp(BMNH); type country: Australia.

Australia: King George Sound (BMNH); Albany (IRSN); Sydney (IRSN); New South Wales, Cumberland (BMNH); South Australia, Margaret River (MCZ).

bolsonensis Scheerpeltz Co(MNHV); type country: Argentina.

Argentina: Rio Negro, El Bolson (MNHV).

brincki Scheerpeltz H,P(ZMLS); type country: Namibia.

Namibia: Kaokoveld, Omutati, 70 mi. WSW Ohopoho (ZMLS).

bruchi Bernhauer T(FMNH); type country: Argentina.

Argentina: Cordoba Province (FMNH).

chilensis Coiffait and Saiz Sp(AMNH); type country: Chile.

Argentina: Rio Negro, 20 km E San Carlos de Bariloche (AMNH); Neuquen, 16 km from Rahue, route 46 (AMNH). **Chile:** Nuble, Las Trancas (CAS).

claviventris Fairmaire and Germain T(BMNH), Sp(IRSN, AMNH); type country: Chile.

Chile: (BMNH); Angola (AMNH); Concepcion (AMNH).

cognatus LeConte T(MCZ), Sp(AMNH); type country: USA.

Southeastern **USA** (Herman, 1983a).

convexifrons Fauvel Syn(BMNH, IRSN); type country: Australia.

Australia: Swan River (BMNH, IRSN).

cubensis Blackwelder P(USNM, FMNH); type country: Cuba.

Cuba: Cayamas (USNM).

curtipennis Bernhauer T(FMNH); type country: Argentina.

Argentina: Tucuman Province (FMNH); Jujuy Province (FMNH).

emarginatus (Say) Sp(AMNH); type country: USA.

Eastern half of **USA** and southern **Canada** (Herman, 1983a).

externus Lynch T(IRSN), Sp(FMNH); type country: Argentina.

Argentina: Buenos Aires Province; Chacabuco (IRSN); Mendoza (FMNH); (Chaunar? FMNH). **Uruguay:** Montevideo (FMNH).

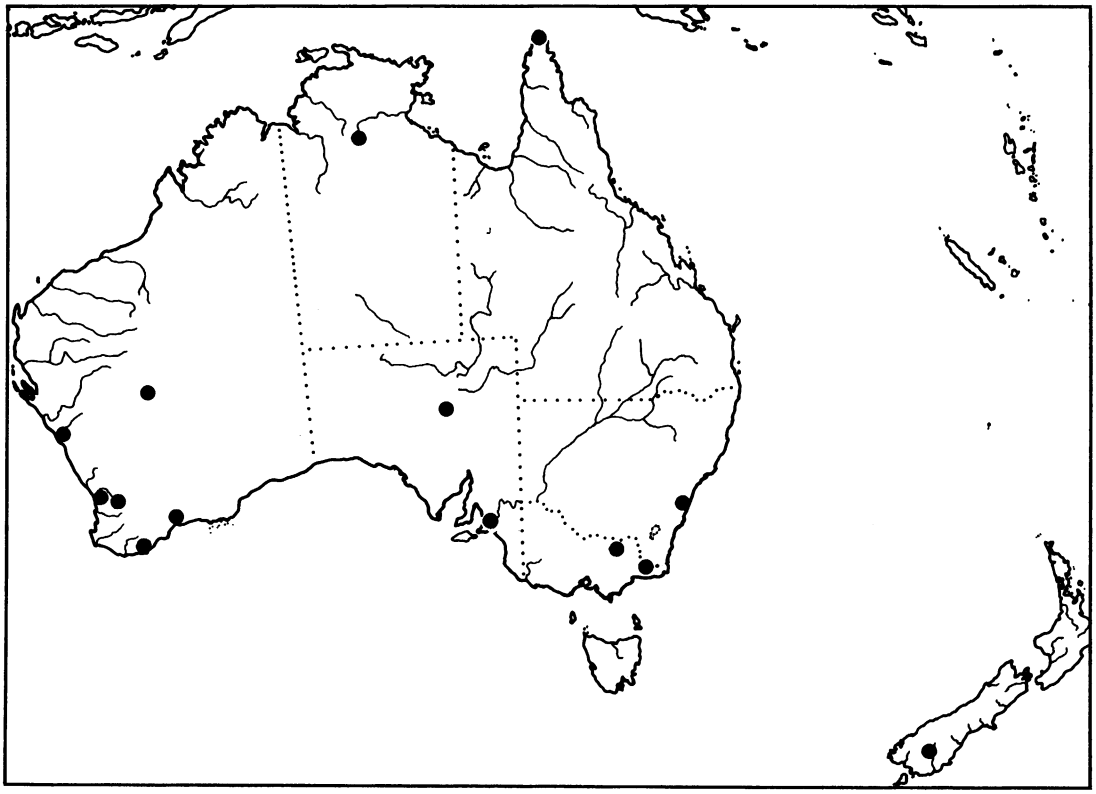


FIG. 244. Distribution of the *emarginatus* group in Australia and New Zealand.

gebieni Bernhauer T(FMNH); type country: Costa Rica.

Costa Rica: Hamburg Farm, Reventazon, Limon plain (FMNH).

gomezi Bernhauer T(FMNH); type country: Argentina.

Argentina: La Rioja (FMNH).

gregarius Sharp T,Sp(BMNH), Co(FMNH); type country: Guatemala.

French Guiana: Maroni River (BMNH). **Guatemala:** Duenas (BMNH, FMNH).

ignotus Saiz P(AMNH); type country: Chile.

Chile: (AMNH).

infantilis Sharp T,Sp(BMNH), Co,Sp (FMNH); type country: Mexico.

Brazil: Mato Grosso, Corumba (BMNH). **Mexico:** Presidio (BMNH, FMNH). *Vera Cruz:* Tres Valles (FMNH). **Trinidad:** St. Augustine (FMNH).

jamaicensis Blackwelder H,P(USNM); type country: Jamaica.

Jamaica: Spanishtown (FMNH, USNM); Trinityville (FMNH, USNM); Troy (USNM); Santa Cruz (USNM).

koenigsbaueri Scheerpeltz T(MNHV); type country: Namibia.

Namibia: Otjikondo (MNHV); Okahandja (MNHV).

leai Scheerpeltz Syn(SAM), SP(BMNH); type country: Australia.

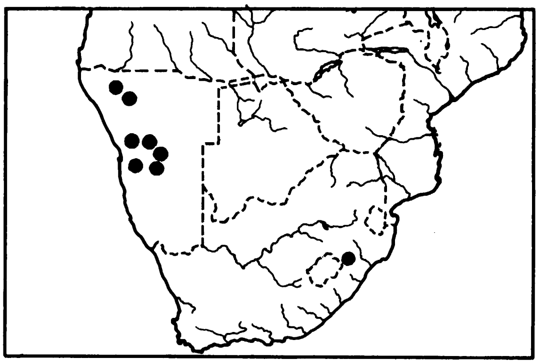


FIG. 245. Distribution of the *emarginatus* group in southern Africa.

Australia: (Mundaring? BMNH); Beverley, Western Australia (SAM).

lividipes Fairmaire and Germain T(BMNH, IRSN), Sp(FMNH, AMNH); type country: Chile.

Argentina: Jujuy Province (FMNH). **Chile:** (BMNH); Santiago (IRSN).

militaris Oke, P(MVA); type country: Australia.

Australia: Victoria, Belgrave (MVA).

minutus Bernhauer T,Co(FMNH); type country: Australia.

Australia: Queensland (Tolga? FMNH).

modestus Sharp T(BMNH); type country: Brazil.

Brazil: Amazonas, Madeira River (BMNH).

muticus Sharp T,Sp(BMNH); type country: Brazil.

Brazil: Amazonas, Madeira River (BMNH).

norquincoensis Scheerpeltz Co(MNHV); type country: Argentina.

Argentina: Rio Negro, Norquinco (MNHV).

ovensensis Blackburn Co(BMNH); type country: Australia.

Australia: (BMNH).

pallidipennis Bernhauer T(FMNH); type country: Argentina.

Argentina: (Chaunar? FMNH).

parcissimus Bernhauer T(FMNH); type country: Argentina.

Argentina: Catamarca (Pampa Grande ? FMNH). *Tucuman:* San Pedro de Colalao (AMNH). *La Rioja:* 5 km E Chilecito (AMNH).

parvulus Erichson T(ZMHU); type country: Venezuela.

Type examined; no locality data with types but type locality is Valencia, Venezuela.

pumilio Erichson T(MNHU), Sp(FMNH); type country: Colombia.

Brazil: Mato Grosso (FMNH). **Colombia:** (MNHU). **French Guiana:** (MNHV). **Peru:** Rio Sivia (FMNH).

rarus Sharp T(BMNH); type country: Brazil.

Brazil: (Ega? BMNH).

rufipes Germain T,Sp(BMNH), Syn(IRSN), Sp(FMNH); type country: Chile.

Chile: (BMNH, IRSN); Santiago (IRSN); Calera (AMNH); Valparaiso (AMNH); Quillota (FMNH).

semiopacus Bernhauer T,Co(FMNH), T,Sp(BMNH); type country: South Africa.

South Africa: Natal, Frere (FMNH, BMNH); Natal, Estcourt (FMNH, BMNH).

similis Sharp T(BMNH); type country: Brazil.

Brazil: Rio Purus (BMNH).

simplex Sharp T,Sp(BMNH); type country: Brazil.

Brazil: Rio Solimoes (BMNH).

testaceipennis Lynch T(IRSN), Sp(MNHV); type country: Argentina.

Argentina: Chacabuco (IRSN); Buenos Aires Province (IRSN); Cordoba Province (MNHV).

trinidadensis Blackwelder P(USNM, FMNH); type country: Trinidad.

Trinidad: St. Augustine (FMNH, USNM); near Tunapuna (USNM).

victoriae Bernhauer and Schubert T(BMNH); type country: Australia.

Australia: (BMNH).

withycombei Bernhauer T(FMNH); type country: Trinidad.

Trinidad: St. Augustine (FMNH).

wudus Herman H,P(AMNH); type country: USA.

Southeastern **USA** (Herman, 1983a).

Undetermined.

Argentina: delta of Parana, near Buenos Aires (BMNH); Chubut (BMNH). *La Rioja:* 1 km SW San Blas, Rio de los Sauces (AMNH); near Villa Union (AMNH). *Tucuman:* 15 km N Tucuman (AMNH). *Cordoba:* 5 km W La Carlota (AMNH). *Chaco:* Barranqueras, Punto Vilelas (USNM). *Rio Negro:* various localities (AMNH). *Neuquen:* various localities (AMNH). *Santa Cruz:* Lago Argentina (BMNH). **Australia:** Perth (BMNH); Swan River (IRSN); Albany (IRSN); Burnside (MNHV); Cape York peninsula, Lockerbie, 10 mi. WSW Somerset (AMNH); 32 km N Elliot (USNM); Cape York, Top Rock Yard, Rocky River, NE of Coen (BPBM). South Australia, Adelaide (MCZ); Victoria, Cann River (MCZ); Victoria, Mirboo National Park (MCZ); Western Australia, Wiluna (MCZ); Western Australia, Geraldton (MCZ); Western Australia, Culham (MCZ). **Bolivia:** Sara Province (CMP); Beni, Mamore River, Guayaramerin (AMNH);

Trinidad (USNM). **Brazil:** Pelotas (USNM); Sao Paulo, Piracicaba (AMNH); Para, Jacareacanga (AMNH); Cachoeira (CMP); near Belem (AMNH); NNE Manaus (AMNH). **Chile:** 20 km E Temuca (CAS); Curico, Mataquito (MCZ); 40 km E San Carlos. **Colombia:** Leticia (CNC); Rio Frio (MCZ). **Costa Rica:** San Jose (AMNH); near Liberia (USNM). **Guatemala:** 2.5 km S La Maquina (CNC); Duenas (AMNH). **Honduras:** near Choluteca (USNM). **India:** Uttar Pradesh, Kumaun, Haldwani District (BMNH). **Mexico:** *Chiapas:* 25 mi. E Zanatepec (CNC). *Oaxaca:* 19 mi. S Matias Romero (CNC). *Vera Cruz:* 2 mi. S Acayucan (CNC). *Chiapas:* 32 mi. E Comitan. *Chiapas:* 20 mi. N Huixtla (CNC). *Sonora:* Alamos (CAS, CNC). *Sinaloa:* 26 mi. N Pericos (CAS); 16 mi. N Mazatlan (CAS). *Nayarit:* Acaponeta (CAS). *Oaxaca:* Tehuantepec. **Namibia:** Okahandja (BMNH); Omaruru (AMNH); Windhoek (BMNH); Kuiseb Canyon (BMNH); Swakop River, 3 mi. S Okahandja (BMNH); Otjitambi fm., 27 mi. ESE Kamanjab (BMNH). **New Zealand:** Otago (BMNH). **Panama:** Canal Zone (USNM). **Paraguay:** Asuncion (AMNH). **Peru:** Lima (USNM); near Pucallpa (AMNH). **Puerto Rico:** Ponce (USNM). **South Africa:** Kahn River, 5 mi. N Usakos (BMNH). **Surinam:** Nickerie (USNM). **Uruguay:** Maldonado (USNM). **Venezuela:** El Dorado, Rio Cuyuni (USNM).

16. *lucidus* group

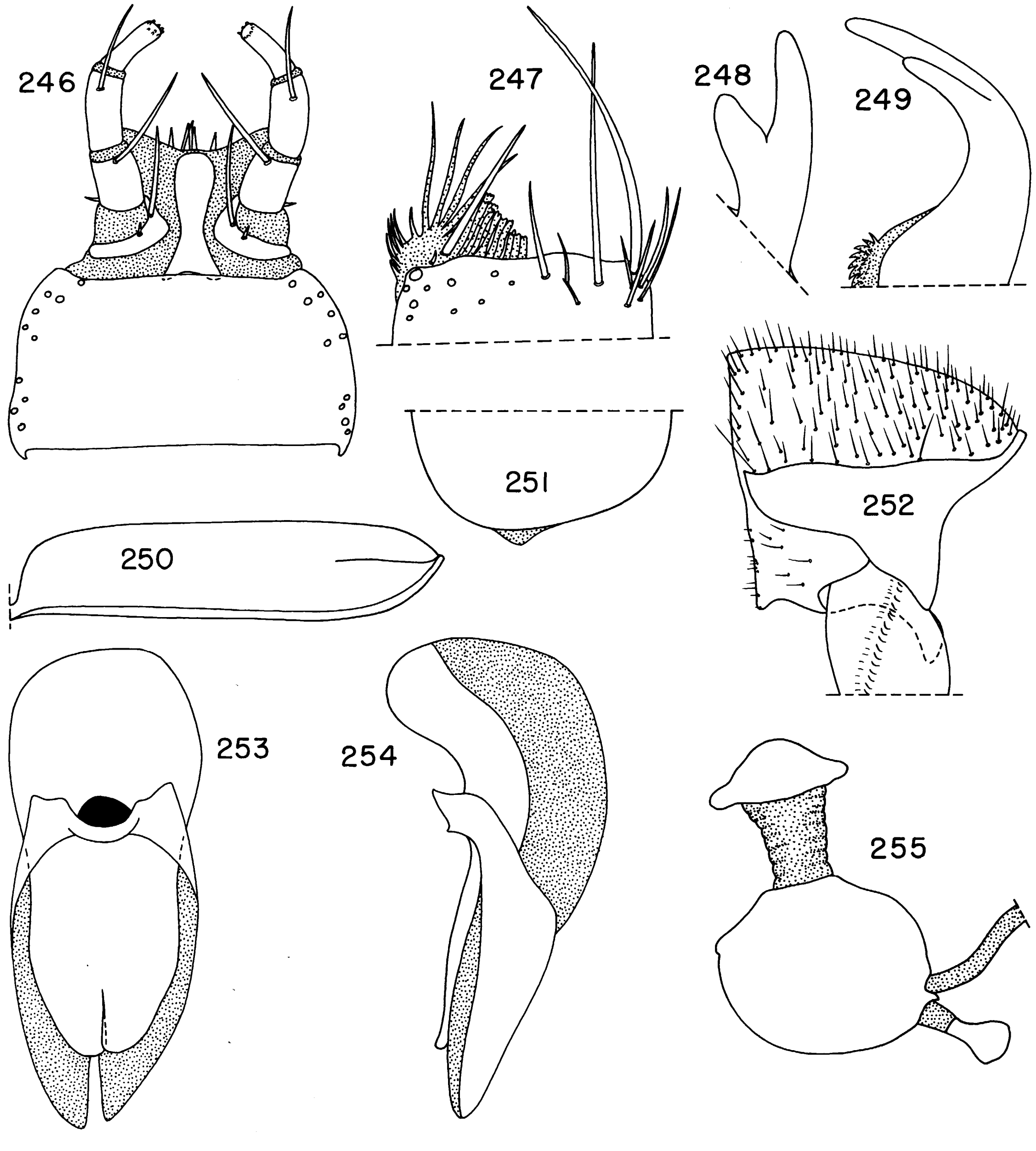
Figures 8, 246–257, 526–528, 639–641

DIAGNOSIS: The presence of a complete pronotal marginal bead (fig. 252), incomplete elytral epipleural ridge (fig. 250), membranous lobe on the elytral margin (fig. 251), and the closed procoxal fissure (fig. 252) will separate this group from all others. Other characters useful for its recognition include the absence of the labral incision (fig. 247), absence of a setigerous pit on the prosternum, and presence of the protergosternal suture. The males have a small to large, anteriorly directed supraantennal horn. Unique to the group are the setae on the ventral surface of the galea.

The *lucidus* group is similar to the *semiferrugineus* and *kosempoensis* groups but is separated from both by the incomplete elytral epipleural ridge. The apex of tergum IX of the *lucidus* group is tapered apically, not lobed as in the *kosempoensis* group. The *semiferrugineus* has a median labral incision; the *lucidus* group does not.

DESCRIPTION: Supraantennal ridge of male moderately enlarged and with small to large anteriorly directed horn; supraantennal ridge of female low, not enlarged, and without horn. Head without subantennal pocket; midbasal horn absent; postocular lateral carina absent. Clypeal margin not reflexed; anterior margin without tubercles; clypeal middle without spines, ridges, or tubercles. Gular sutures fused. Labral (fig. 247) margin entire, margin not reflexed; median incision absent; dorsal surface flat, without midlongitudinal impression. Epipharyngeal lobe short; dorsal surface with one long and one short seta; median processes with lobed apices; lateroapical processes numerous, slender, and unbranched. Labial palps (fig. 246) with second segment longest; first and third segments of subequal length; first and second segments of subequal thickness; first segment with two setae, second segment with one seta. Submentum not excavated. Mentum (fig. 246) with channel surrounding broad plateaulike median region; surface with setae present laterally and absent medially. Hypopharynx (figs. 526–528) with lateral rows of setae gradually convergent toward base; basal setae arranged in transverse row; basal setae stout; basal setae not on plate; central row of setae dense distally and sparse proximally; disk with a few scattered thick spinelike setae; disk with both separate cuticular processes and palmate clusters of cuticular processes over entire surface (no data for coronal pegs). Prementum (fig. 246) with one median sclerite; basal and lateral sclerites absent. Galea with row of long, stout setae on dorsal edge of apex and with small cluster of setae near middle of apex; ventral surface with setae; dorsomedial edge with lobe. Mandibles bidentate (figs. 248, 249).

Pronotal horn absent. Marginal bead (fig. 252) present and complete; bead dividing notum and hypomeron, not on hypomeron. Protergosternal suture present (fig. 252). Bead and suture anteriorly convergent (fig. 252). Procoxal fissure closed (fig. 252). Protro-



FIGS. 246–255. The *lucidus* group. *Bledius lucidus*. **246.** Labium, setae of mentum removed. **247.** Labrum, setae of left and epipharyngeal lobe of right removed. **248.** Mandible, right, lateroapical view of apical portion. **249.** Mandible, right, dorsal view. **250.** Elytron, left, lateral view, setae removed. **251.** Elytron, left, apical quarter, setae removed. **252.** Prothorax, lateral view. **253.** Aedeagus, dorsal view. **254.** Aedeagus, lateral view. **255.** Spermatheca.

chantin concealed. Prosternal process elongate (fig. 252). Prosternum with patch of setae near shallow depression (figs. 639, 640); setigerous pit absent; depression with small clusters of pores (fig. 641); anterior margin entire, without notch. Elytral epipleural ridge incomplete, present only at apical portion (fig. 250); posterior margin with membranous lobe (fig. 251).

Tarsi four segmented. Protibia with two rows of spinelike setae.

Abdominal tergum VII with fine fringe on

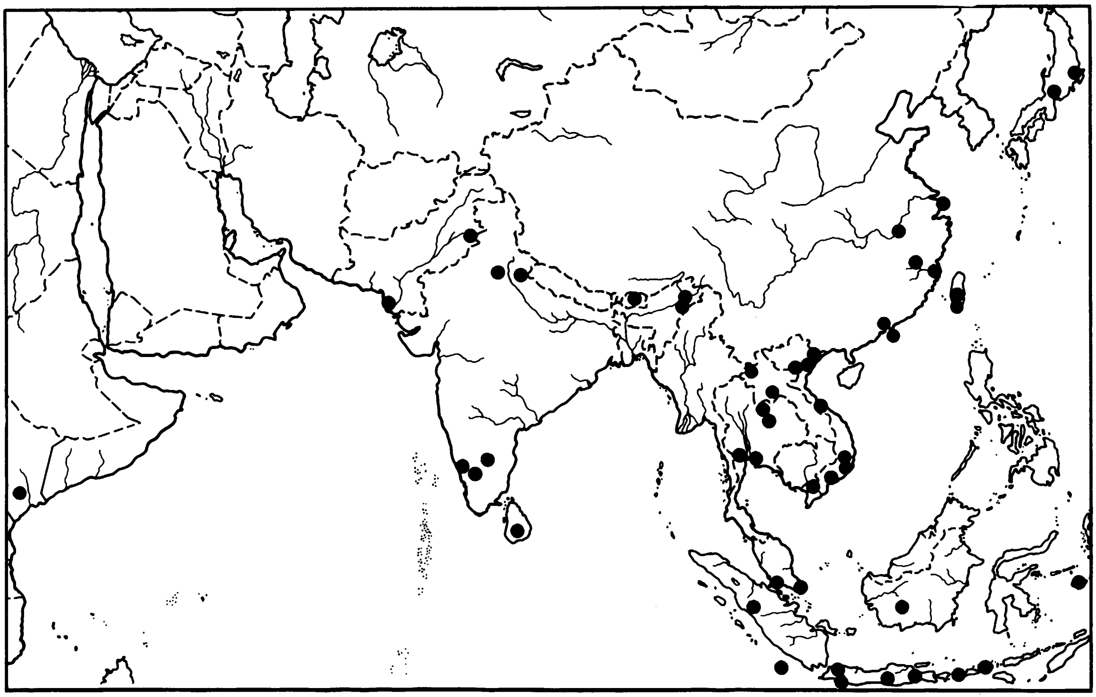


FIG. 256. Distribution of the *lucidus* group in Asia and Indonesia.

posterior margin. Tergum VIII with posterior margin emarginate; margin entire, not serrate. Tergum IX with glandular canal moderately widely open dorsally. Tergum X with struts on anterior margin.

Aedeagus (fig. 253, 254) with parameres. Parameres broad and with median surface membranous; parameres extending beyond apex of median lobe. Median lobe long; base bulbous; apical portion flattened; ventral surface midlongitudinally divided at apex.

Spermatheca (fig. 255) tripartite. Receptacle sclerotized and divided by accordion tube into two parts; basal part larger than distal part; distal part without invagination; distal part with brimlike ridge; basal part without brimlike ridge. Spermathecal gland sclerotized; shape and surface irregular.

DISTRIBUTION AND HABITAT: This group is found from Pakistan eastward across southern Asia to China and Japan, and through Indonesia to New Guinea and northern Australia (figs. 256, 257). I have examined a few specimens from Africa and there are reports of other localities in the literature.

DISCUSSION: This group is recognized for the first time here. *Bledius lucidus* had been in *Hesperophilus*; *australis* and *cowleyi* were unassigned to infrageneric groups.

Species Included and Material Examined

australis Oke P(MVA); type country: Australia.

Australia: Victoria, Caulfield (MVA).

cowleyi Blackburn T(BMNH); type country: Australia.

Australia: (BMNH).

lucidus Sharp T,Sp(BMNH), Sp(FMNH, IRSN, MNHV); type country: Japan.

Australia: Queensland, Port Denison (IRSN); Kimberley District (FMNH). **Bhutan:** (Samchi? BMNH). **Borneo:** (Teland? IRSN). **China:** Kiukiang (IRSN); Foochow [=Fuzhou] (FMNH); Shaowu, Fujien (FMNH); Shanghai (MNHV). **India:** Malabar, Mahe (IRSN); Nilgiris Hills (BMNH); Assam, Patkai Hills (BMNH); Assam (Shugun? BMNH); Uttar Pradesh, Kumaun, Haldwani (FMNH). **Indonesia:** Sumbawa, Gunung Tambora (IRSN); Java, Malang (IRSN); Lombok, Pringabaja (BMNH); Java, Buitenzorg (BMNH, MNHV); Enggano (Bua Bua ? FMNH,

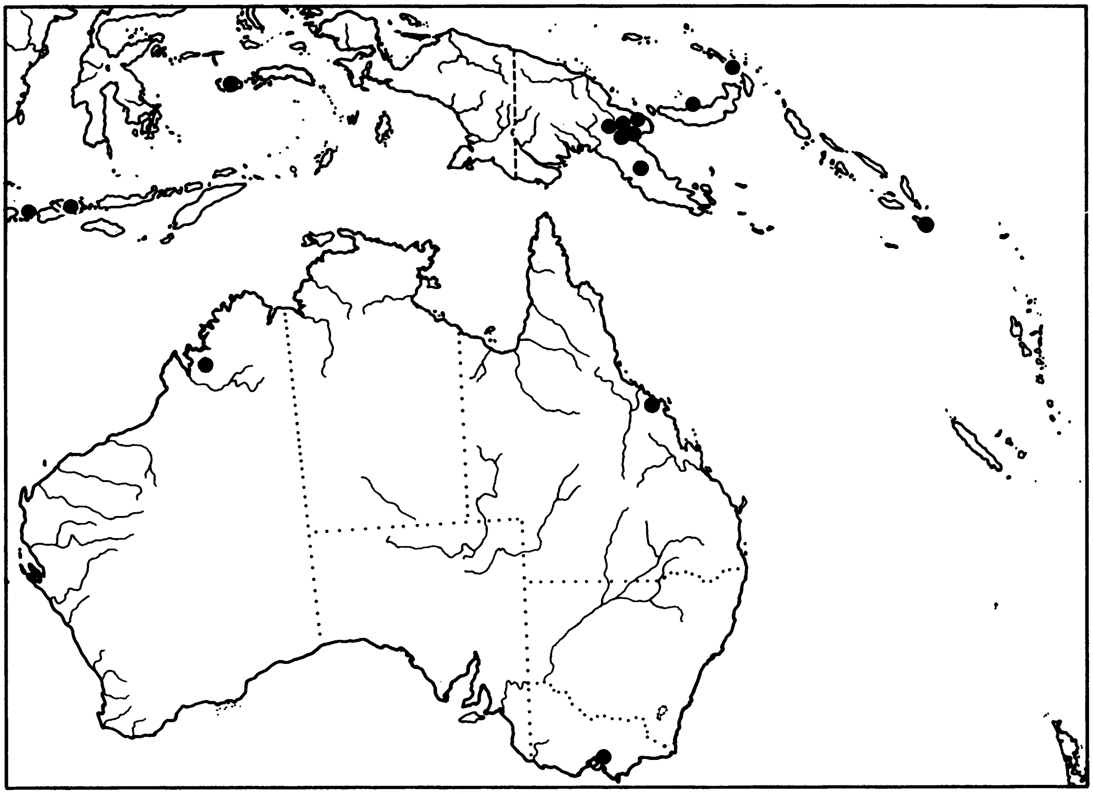


FIG. 257. Distribution of the *lucidus* group in Australia, Indonesia, and Papua New Guinea.

IRSN); Java, Batavia [=Jakarta] (FMNH); Java, Preanger (Tjigembong? FMNH); Java, Djokjakarta [=Yogyakarta] (FMNH); Moluccas, Buru Island (FMNH); Sumatra, Fort de Kock [=Bukittinggi] (FMNH, MNHV). **Japan:** Tokyo (BMNH); Kanagawa (FMNH); Gifu (IRSN). **Kenya:** (Ramissi? FMNH). **Pakistan:** Karachi (IRSN, BMNH). **Papua New Guinea:** Kokoda (BMNH). **Singapore:** (BMNH). **Thailand:** Bangkok (IRSN, BMNH); (Renong? BMNH). **Vietnam:** Quang Binh (IRSN); Long-Xuyen (IRSN); Thanh-Moi (IRSN); Hanoi (IRSN); Hoa Binh (FMNH); (Cho Ganh ? FMNH).

Undetermined.

India: Mysore, Bangalore, Karnataka (AMNH); Assam, Chabua (USNM); New Delhi (USNM). **Indonesia:** Sumbawa (Aroe Hassa ? AMNH). **Japan:** Tokyo, Machida, near Tsurukawa (AMNH); Sagamihara, Kanagawa (AMNH). **Malaysia:** Port Dickson (BMNH). **New Britain:** Volupai, Willaumez (BPBM). **New Ireland:** Schleinitz Mountains, Lelet Plateau (BPBM). **Pakistan:** Lahore (USNM). **Papua New Guinea:** Lae, near mouth of Markham River (AMNH); Morobe, Umi River, Markham Valley, 95 mi. from Lae (AMNH); Kassam in Kratke Mts. on Lae-Goroka Road (AMNH); Morobe District, Herzog Mts., Vagau (BMNH); Madang District, Finisterre Ra Range (BMNH). **Solomon Islands:** San Cristobal (Napagiwae? BPBM); San Cristobal (Wugiroga? BPBM). **Sri Lanka:** (Ruhunu National Park, near Altents? AMNH). **Taiwan:** (Sun-Moon Lake ? AMNH); Puli (BPBM); Kwantzeling, Tainan Hsien (BPBM); Liukue, Kaohsiung Hsien (BPBM). **Thailand:** Khon Kaen; Muang Loei. **Vietnam:** Saigon [= Ho Chi Minh] (USNM).

17. *kosempoensis* group

Figures 8, 258–266, 529, 530, 636–638

DIAGNOSIS: This group is separated from all others by the lobed apex of tergite IX (fig.

262). The aedeagal configuration (dissected herein for only one species) may also be unique (figs. 263, 264). Other characters useful for recognition of the group are the absence of the median labral incision (fig. 259), presence of the protergosternal suture (fig. 260), the closed procoxal fissure (fig. 260), the complete pronotal marginal bead (fig. 260) and elytral epipleural ridge, presence of a membranous lobe on the elytral margin, and the emarginate tergum VIII.

The *kosempoensis* group is most similar to the *semiferrugineus* and *lucidus* groups. The *semiferrugineus* group has the median labral incision (fig. 267) and the *lucidus* group has an incomplete elytral epipleural ridge (fig. 250).

DESCRIPTION: Supraantennal ridge low, not enlarged, and without horns. Head without subantennal pocket; midbasal horn absent; postocular lateral carina absent. Clypeal margin not reflexed; anterior margin with tubercles; clypeal middle without spines, ridges, or tubercles. Gular sutures fused. Labral (fig. 259) margin entire; margin not reflexed; median incision absent; dorsal surface flat, without midlongitudinal impression. Epipharyngeal lobe short; dorsal surface with one long and one short seta; median processes with lobed apices; lateroapical processes slender and unbranched and thick and multiramous. Labial palps (fig. 258) with segments of subequal length; first and second segments of subequal thickness; first segment with two setae, second with four or five setae. Submentum not excavated. Mentum (fig. 258) with setae present laterally and present less densely medially but absent from narrow median strip. Hypopharynx (figs. 529, 530) with lateral rows of setae gradually convergent toward base; basal setae stout; basal setae arranged in transverse row; basal setae not on plate; central row of setae dense throughout length; disk with scattered setae; disk with short cuticular processes on anterior portion (coronal pegs—no data). Prementum (fig. 258) with three sclerites, one medial and two minute lateral sclerites; basal sclerite absent. Galea with row of long stout setae on dorsal edge of apex and with cluster of long stout setae over surface of apex; ventral surface without seta; dorsomedial edge with lobe. Mandibles bidentate (fig. 261).

Pronotal (fig. 260) horn absent. Marginal bead present and complete; bead dividing hypomeron and notum, not on hypomeron. Protergosternal suture present (fig. 260). Bead and suture convergent anteriorly (fig. 260). Procoxal fissure closed (fig. 260). Protrochantin concealed. Prosternal process elongate (fig. 260). Prosternum with patch of setae near shallow depression (figs. 636, 637); setigerous pit absent; depression with small clusters of pores (fig. 638); anterior margin entire, without notch. Elytral eipleural ridge present and complete; posterior margin with membranous lobe present.

Tarsi four segmented. Protibia with two rows of spinelike setae.

Abdominal tergum VII with fine fringe on posterior margin. Tergum VIII with posterior margin emarginate; margin entire, not serrate. Tergum IX (fig. 262) with glandular canal widely open dorsally; apex modified into rounded lobe (fig. 262). Tergum X with struts on anterior margin (fig. 262).

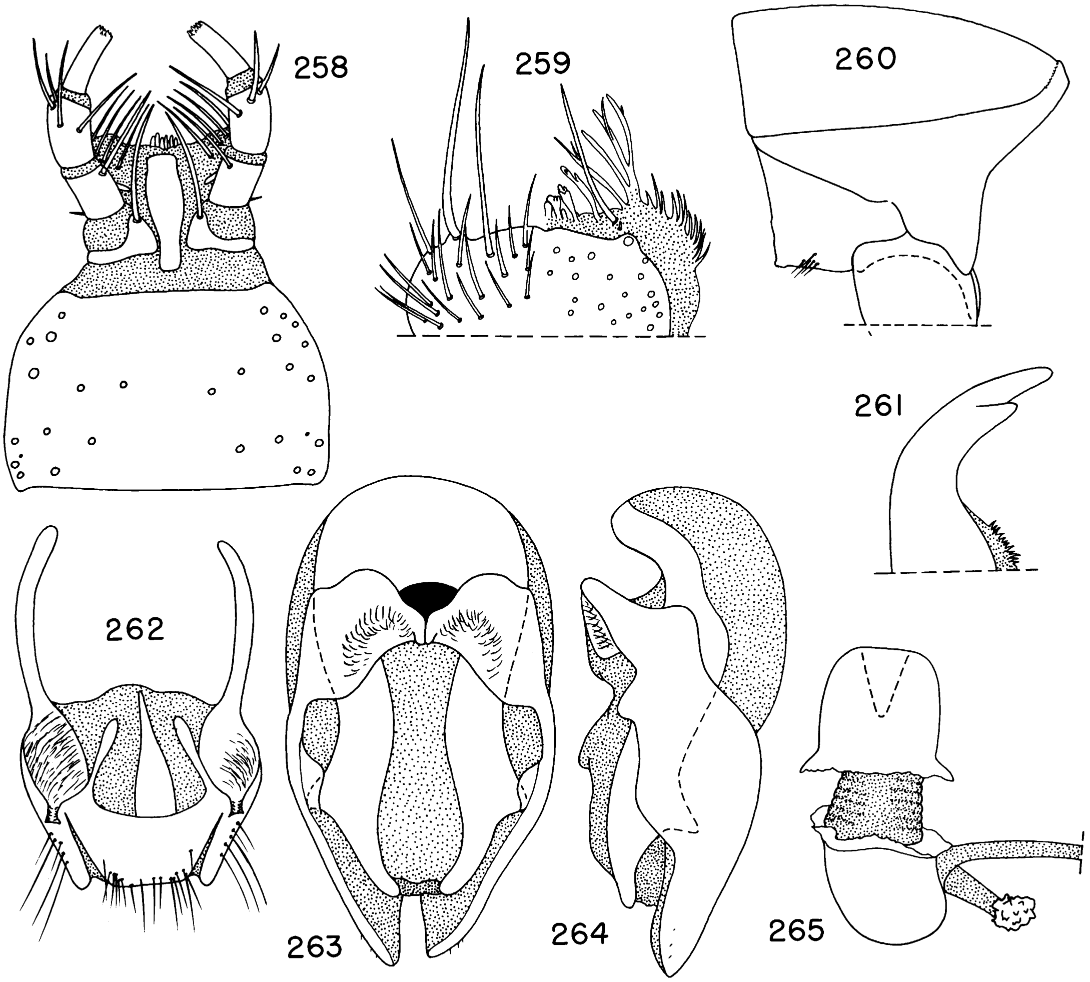
Aedeagus (figs. 263, 264) with parameres. Parameres broad and with median surface membranous; parameres extending beyond apex of median lobe. Median lobe long; base bulbous; apical portion flattened; ventral surface midlongitudinally divided.

Spermatheca (fig. 265) tripartite. Receptacle sclerotized and divided by accordion tube into two parts; distal and basal parts of nearly equal size; distal part invaginated; distal and basal parts each with brimlike ridge. Spermathecal gland sclerotized; shape and surface irregular.

DISTRIBUTION AND HABITAT: This group is known from Taiwan, eastern China, Vietnam, and India (fig. 266).

DISCUSSION: These four species are separated as a group for the first time herein. Previously, one species had not been included in a subgenus, one was in *Hesperophilus,* one in *Dicarenus,* and one in *Pucerus.*

The most problematically included species is *Bledius hindustanus.* Only one specimen of it was available for study; therefore, the problems may be resolved by dissection when other specimens are available. The labrum of the type of *hindustanus* seems to have a faint labral incision and the apex of tergum IX is poorly developed and difficult to see. If there is a labral incision and if tergum IX is unlobed then the species should be placed in the *semiferrugineus* group.



FIGS. 258–265. The *kosempoensis* group. *Bledius kosempoensis*. **258.** Labium, setae removed from mentum. **259.** Labrum, setae of right and epipharyngeal lobe of left removed. **260.** Prothorax, lateral view, setae removed. **261.** Mandible, left. **262.** Abdominal segments IX and X, male, dorsal view. **263.** Aedeagus, dorsal view. **264.** Aedeagus, lateral view. **265.** Spermatheca.

Species Included and Material Examined

conicicollis Fauvel T(IRSN); type country: Vietnam.

Vietnam: Tonkin (IRSN).

hindustanus Cameron T(BMNH); type country: India.

India: (Ferrapore? BMNH).

kosempoensis Bernhauer T,Co(FMNH), Co,Sp(BMNH); type country: Taiwan.

Taiwan: (Kisan? BMNH); (Rokki? BMNH); (Kosempo? BMNH, FMNH); Nan-t'ou, Hsien, near Wushe (MNH).

lucens Cameron T(BMNH); type country: China.

China: Shanghai (BMNH).

Undetermined.

China: Hunan, Li [River], Tsinshih [=Sangzhi?] (BPBM).

18. *semiferrugineus* group

Figures 7, 53, 267–285, 531–536, 642–647

DIAGNOSIS: This group is separated from all others by the complete pronotal marginal bead (fig. 269) and elytral epipleural ridge (fig. 268), presence of a medial labral incision (fig. 267) and protergosternal suture (fig. 269), emarginate tergum VIII, and closed procoxal fissure (fig. 269). The group is similar to the *lucidus* and *kosempoensis* groups. The *lucidus* group has an incomplete elytra epipleural ridge (fig. 250), lacks the median labral incision (fig. 247), and has setae on the ventral surface of the galea. The *kosempoensis* group lacks the median labral incision (fig. 259) and has a lobe on the apex of each tergite IX (fig. 262). The *semiferrugineus* group has a median labral incision, a complete elytral epipleural ridge, and lacks the lobes on tergites IX and setae on the ventral surface of the galea.

Most species of the *armatus* group, which is restricted to the New World, lack a protergosternal suture (fig. 289) and are thereby easily separated from the *semiferrugineus* group. Three species of the *armatus* group have the suture and can be confused with the *semiferrugineus* group. See the Diagnosis of the *armatus* group for separation of these species. The most reliable, but not easily viewed, characters are on the hypopharynx.

DESCRIPTION: Supraantennal ridge low, not enlarged, and without horns. Head without subantennal pocket; postocular lateral carina absent; midbasal horn absent. Clypeal margin not reflexed; anterior margin with tubercles; clypeal middle with (rarely) or without spines, or tubercles and without ridges. Gular sutures fused. Labral margin shallowly emarginate (fig. 267); margin not reflexed; median incision present (fig. 267); dorsal surface flat, with midlongitudinal impression. Epipharyngeal lobe (fig. 267) short; dorsal surface with one long and one short seta; median processes with lobed apices; lateroapical processes few, thick, and branched. Labial palps with second segment longer than first and third; first and third segments of subequal length; first and second segments of subequal thickness; first segment with two setae, second segment with one seta. Submentum not excavated. Mentum with setae dense laterally and absent medially. Hypopharynx (figs. 531–536) with lateral rows of setae gradually convergent toward base; basal setae arranged in transverse row; basal setae stout; basal setae not on plate; central row of setae dense throughout length; disk with setae scattered over surface; disk with palmate clusters of short cuticular processes on most of surface (fig. 536); coronal pegs scattered over surface of disk. Prementum with two sclerites, one medial and one basal; lateral sclerites absent. Galea with moderately dense cluster of setae on apex; ventral surface without setae; dorsomedial edge with lobe. Mandibles bidentate or tridentate (fig. 270).

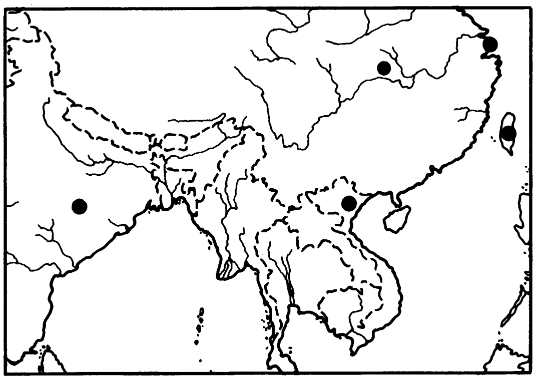


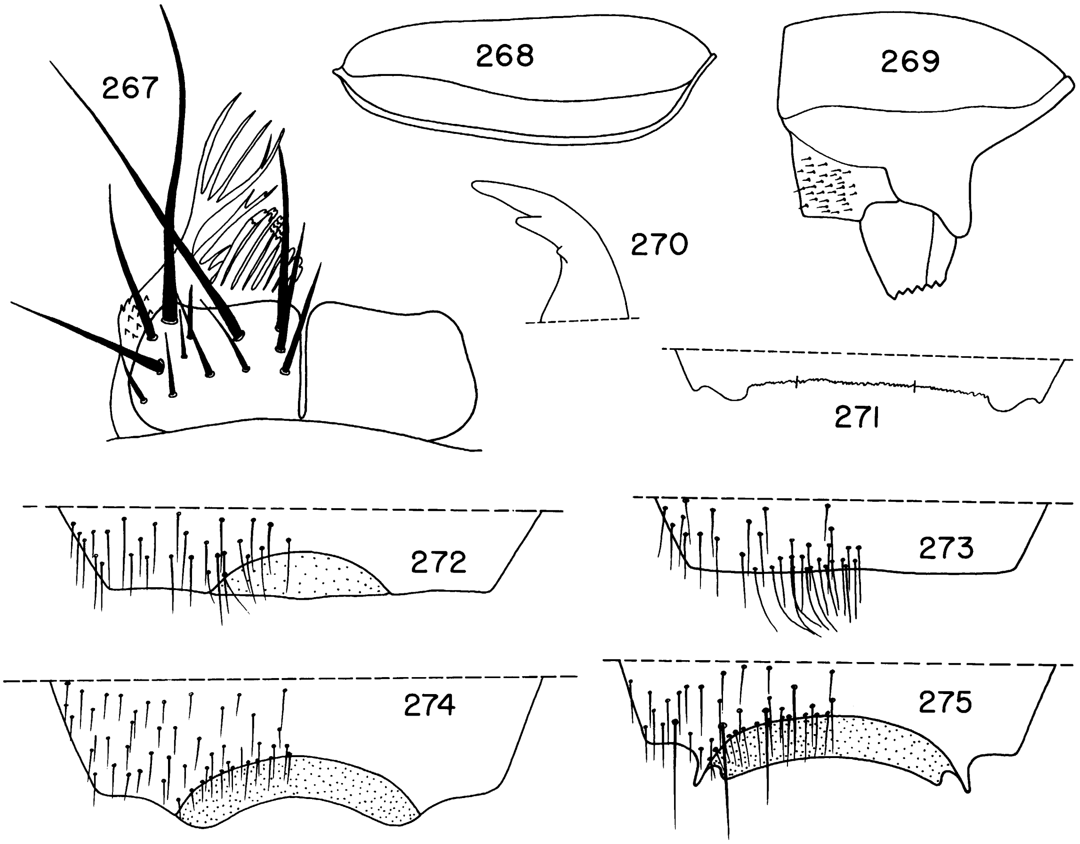
FIG. 266. Distribution of the *kosempoensis* group in southeastern Asia.

Pronotal horn absent. Marginal bead present and complete; bead dividing notum and hypomeron, not on hypomeron. Protergosternal suture present (fig. 269). Bead and suture convergent anteriorly. Procoxal fissure closed (fig. 269). Protrochantin concealed. Prosternal process elongate. Prosternal setigerous pit absent; sternum with patch of setae (figs. 642, 643, 645, 647); sternum without depression but with small clusters of pores anterior to patch of setae (figs. 643, 644, 646); anterior sternal margin entire, without notch. Elytral epipleural ridge present and complete (fig. 268); posterior margin with membranous lobe.

Tarsi four segmented. Protibia with two rows of spinelike setae.

Abdominal tergum VII with fine fringe on posterior margin (fig. 271). Tergum VIII with posterior margin emarginate; margin serrulate or entire. Tergum IX with glandular canal widely open dorsally. Tergum X with struts on anterior margin.

Aedeagus (figs. 276, 278) with parameres. Parameres broad and with median surface membranous (fig. 276); parameres extending



FIGS. 267–275. The *semiferrugineus* group. **267.** Labrum, setae and epipharyngeal lobe of right removed (*semiferrugineus*). **268.** Elytron, left, lateral view, setae removed (*analis*). **269.** Prothorax, lateral view, setae removed (*analis*). **270.** Mandible, right (*philadelphicus*). **271.** Tergum VIII, apical margin (*rubiginosus*). **272.** Sternum VII, apical margin (*philadelphicus*). **273.** Sternum VII, apical margin (*analis*). **274.** Sternum VII, apical margin (*coulteri*). **275.** Sternum VII, apical margin (*assimilis*).

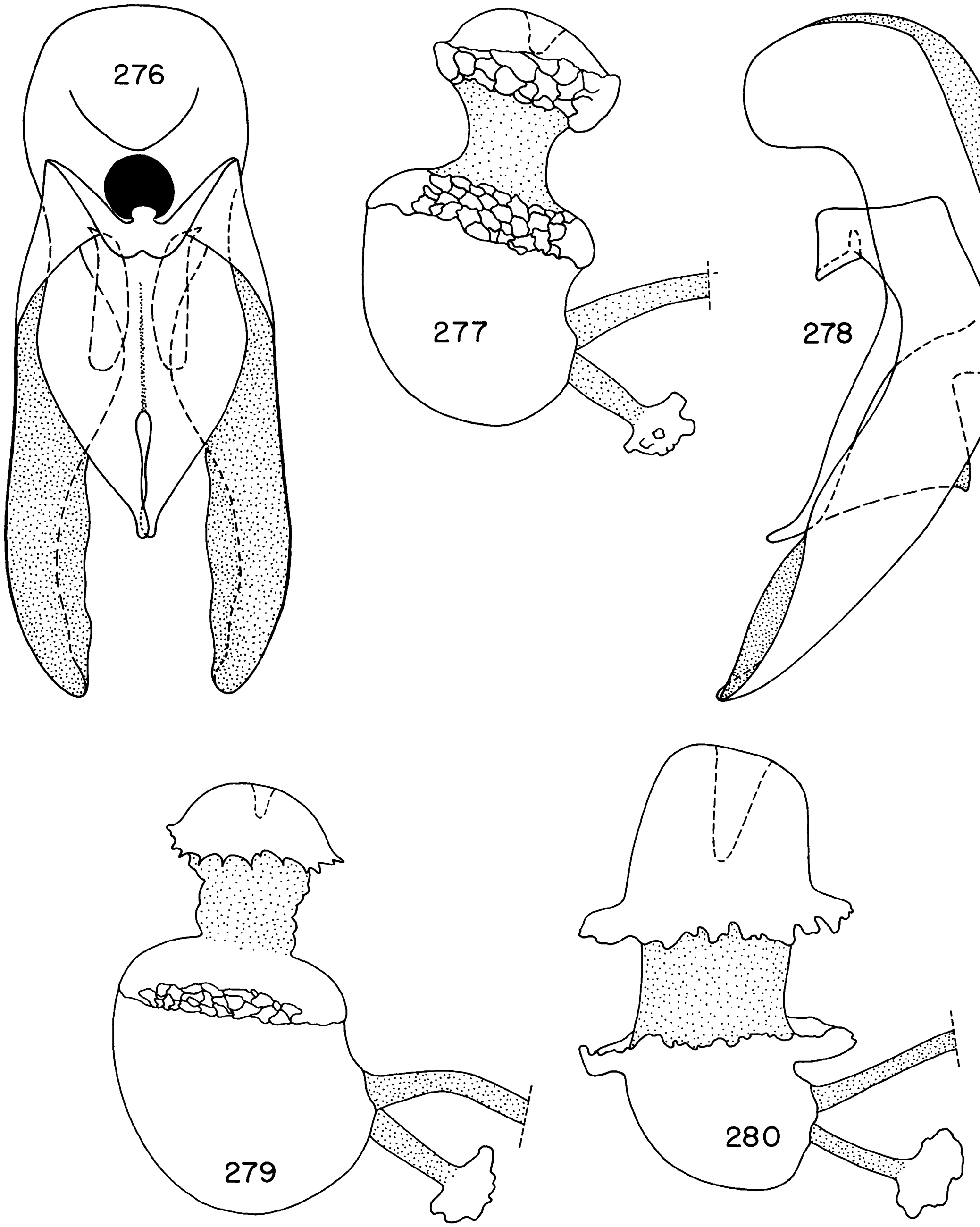
beyond apex of median lobe. Median lobe long; base bulbous; apical portion flattened; ventral surface midlongitudinally divided.

Spermatheca (figs. 277, 279, 280) tripartite. Receptacle sclerotized and divided by accordion tube into two parts; distal part larger than, equal to, or smaller than basal part; distal part invaginated; distal and basal parts with brimlike ridges. Spermathecal gland sclerotized; shape and surface irregular.

Distribution and Habitat: This group has a holarctic distribution (figs. 281–285) with some species occurring southward into southern Africa (fig. 285) and southern South America (fig. 282). There is a conspicuous absence of the group from southern India, southeastern Asia, Indonesia, New Guinea, and Australia. Most of the species are found in freshwater habitats.

After completion of the maps, I received specimens of *Bledius semiferrugineus* from an unspecified locality in Cuba; this record is not included on the general map of distribution for the *semiferrugineus* group (fig. 7) but is on the specific map (fig. 282). This Cuban record needs confirmation by further collection. The species is common in Florida and likely an inhabitant of Cuba.

DISCUSSION: The type species of *Hesperophilus* along with 30 species currently listed in that subgenus (table 9) are placed in the *semiferrugineus* group. This reallocation of species is part of the breakup of the large, heterogeneous *Hesperophilus*. Seven species



FIGS. 276–280. The *semiferrugineus* group. **276.** Aedeagus, dorsal view (*gravidus*). **277.** Spermatheca (*coulteri*). **278.** Aedeagus, lateral view (*gravidus*). **279.** Spermatheca (*assimilis*). **280.** Spermatheca (*rubiginosus*).

are transferred here from *Pucerus,* one from *Elbidus,* and 17 others were not previously assigned to subgenus (table 9). Nine of the unassigned species were part of the *semiferrugineus* group which was first recognized by LeConte (1877).

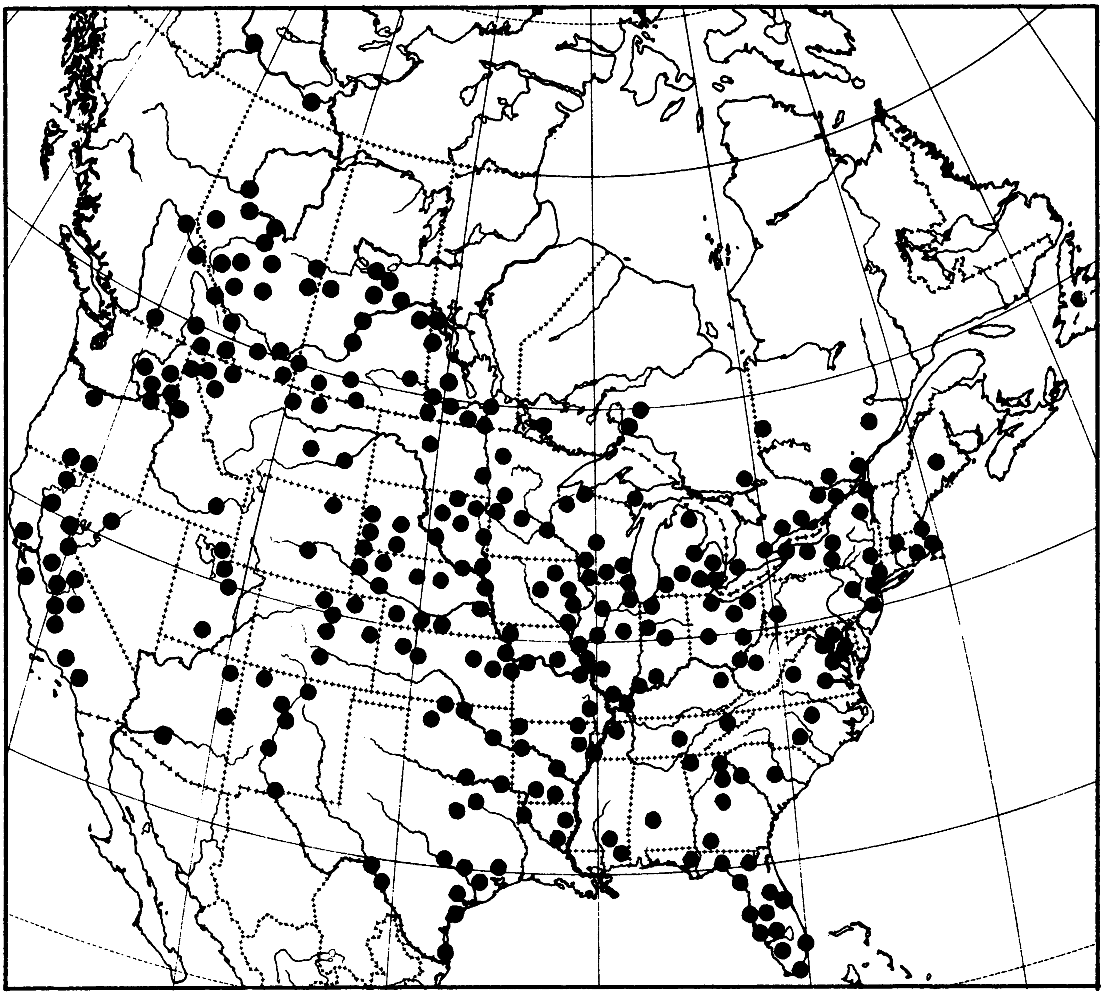


FIG. 281. Distribution of the *semiferrugineus* group in North America.

The *semiferrugineus* group can be divided into at least six complexes. These complexes are based on male secondary sexual characters or body sculpturing.

The *assimilis* complex includes: *assimilis, atratus, castaneus, crassicollis, cribratus, cribricollis, dissimilis, femoralis, fragilis, minarzianus, obtusus, occidentalis, picipennis,* and *roubali.* The complex is recognized by the presence of a membrane-filled emargination of sternite VII that is bordered by a spine on each side (fig. 275). The pronotal median groove is absent or weakly developed. One species is found in North America, the remaining 13 occur from Europe to Japan. Three are in Japan; 10 are in Europe and southwestern Asia. I have also examined an undescribed species of the complex from Nigeria and another from Ethiopia.

One of the species in the complex, *castaneus,* was heretofore overlooked. It was described and named conditionally in a brief paragraph. The code of zoological nomenclature permits availability of such conditional names before 1961.

The *gallicius* complex includes: *bedeli, coulteri, elongatus, gallicus, heterocerus, orion, philadelphicus, procerulus,* and *sanguinithorax.* It is distinguished by the membrane-filled emargination of sternite VII that is devoid of bordering spines (figs. 272, 274). The pronotal median groove is well devel-

FIG. 282. Distribution of the *semiferrugineus* group from Mexico to Argentina.

oped. Two of the species occur in North America, four are European, two North African, and one occurs in southwestern Asia.

The inclusion of *heterocerus* in this complex is somewhat problematical. One of the three cotypes of *heterocerus* in the Eppelsheim collection has the membrane-filled emargination but lacks the spines adjacent to the emargination. (The other two cotypes are females.) However, 11 specimens in the Eppelsheim collections follow the three cotypes and are presumably thought to be *heterocerus*. The males in this series have the spine adjacent to the membrane-filled emargination; they should be included in the *assimilis* complex. The three cotypes should be included in the *gallicus* complex. Specimens identified as *heterocerus* in other collections all belong with the *assimilis* complex.

The *fumatus* complex includes: *foraminosus, fumatus, gravidus, rotundicollis, semiferrugineus,* and *tallaci.* This complex is segregated by an emargination of sternite VII that is surrounded by pubescence. The species

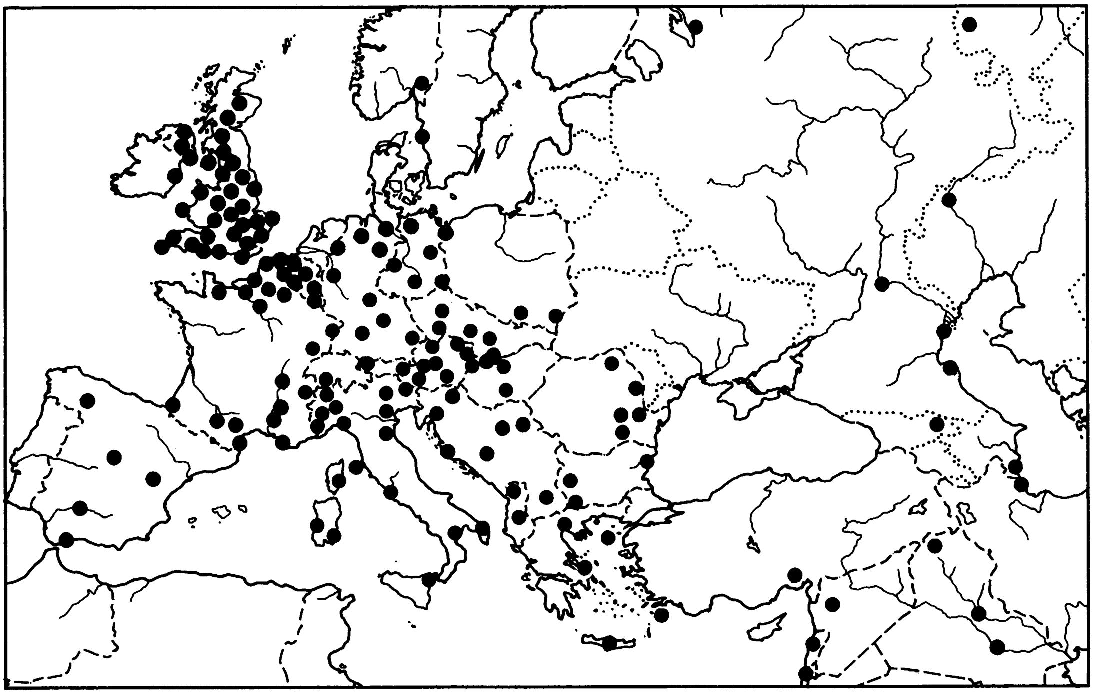


FIG. 283. Distribution of the *semiferrugineus* group in Europe.

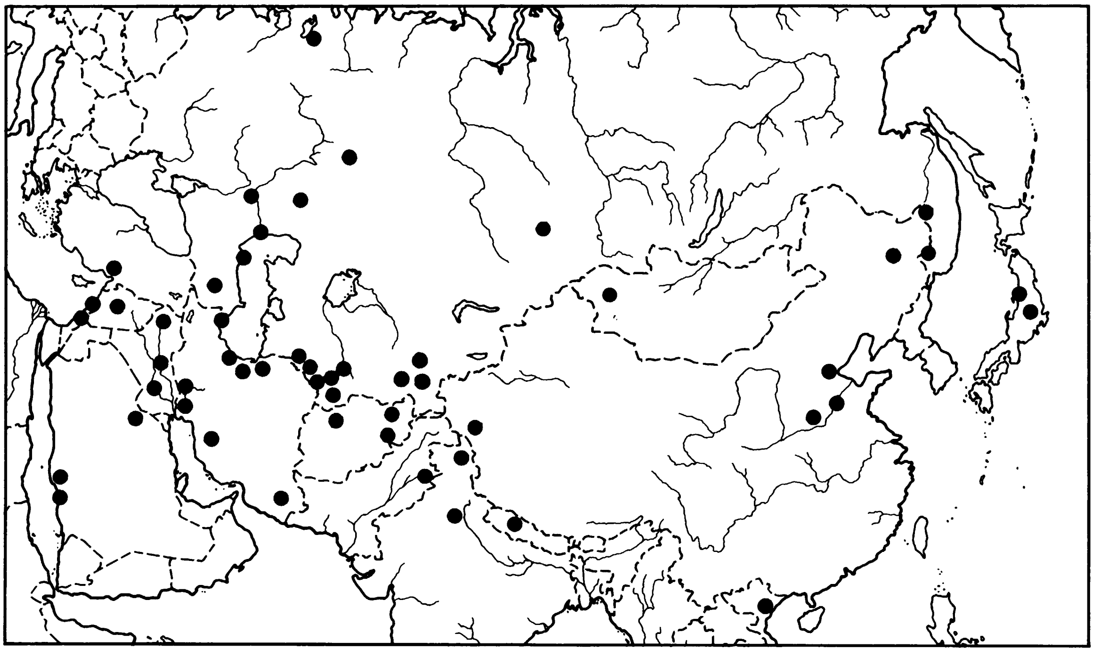


FIG. 284. Distribution of the *semiferrugineus* group in Asia.

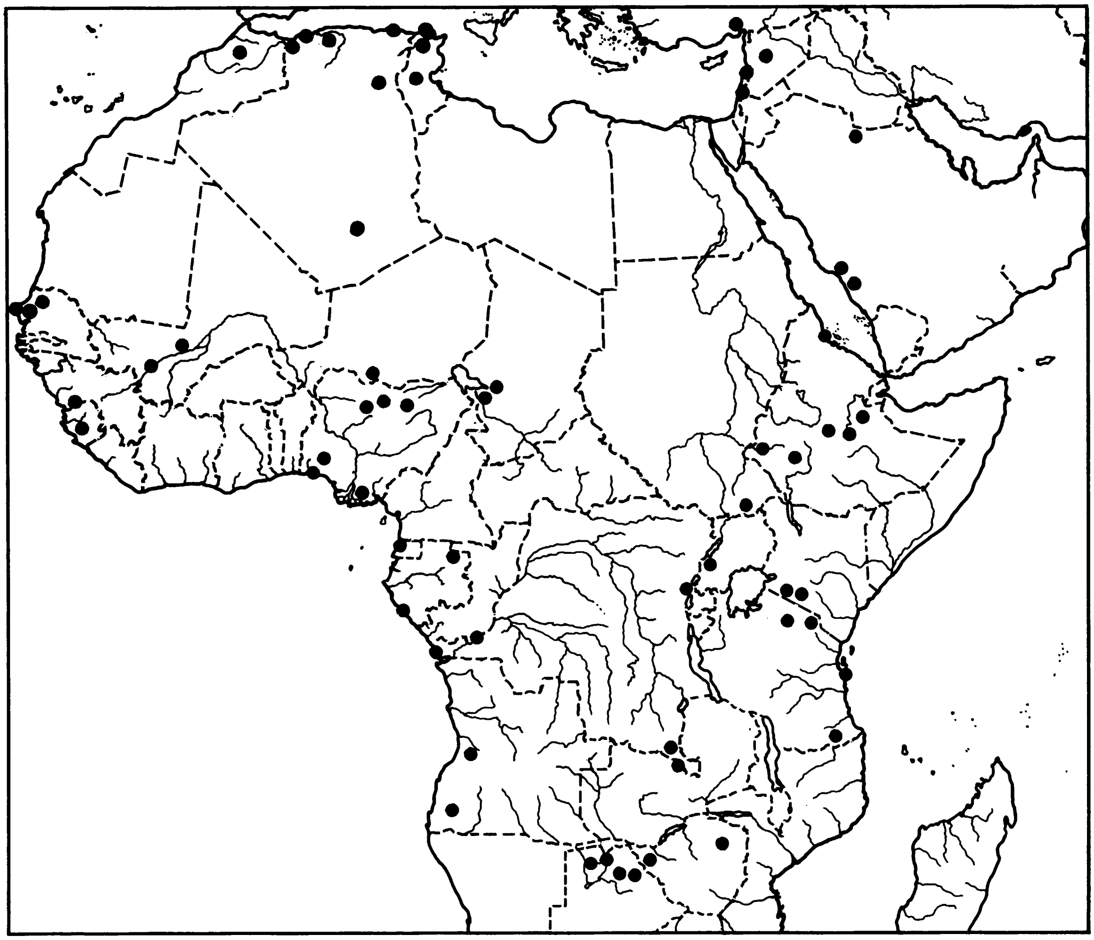


FIG. 285. Distribution of the *semiferrugineus* group in Africa.

are all larger on average than most species of the *semiferrugineus* group. The complex is restricted to North America.

The *rubiginosus* complex includes: *argentinus, inornatus, lateralis,* and *rubiginosus.* These species have a black head and orange to reddish orange pronotum and elytra. The pronotum is slightly wider than to nearly equal to the length. The species are found from the southern United States to central Argentina. This complex is the only part of the *semiferrugineus* group that lives in Mexico and Central and South America.

The *ganglbaueri* complex includes: *aculeatus, berlandi, bredoi, diffinis, erythraeanus, filipponii, ganglbaueri, johnstoni, schoutedeni, validepunctatus,* and *yemenicus.* As in the *rubiginosus* complex, this one also has a black or dark reddish brown head and orange to reddish orange to reddish brown pronotum and elytra. The pronotum is strongly transverse and strongly convex. The pronotal punctation is coarse. The clypeal middle has well-developed spiniform tubercles, the presence of which leads to the placement of *filipponii* and *yemenicus* in the subgenus *Pucerus. Bledius diffinis* lacks these clypeal tubercles and may not belong in this complex. The species in this group are African with some reaching the Arabian peninsula to Pakistan.

The preceding two complexes both extend into the southern hemisphere and tropical region, and have similar color patterns and body sculpturing.

The *akinini* complex includes: *akinini, atricapillus, glasunovi,* and *hlisnikowskii* and possibly *afghanicus* and *haarlovi*. This complex is more ill-defined than the others but careful observation reveals shared characters. The pronotal punctation is weak, and the sculpturing of the head and pronotum is strongly microgranulate. The head is dark reddish brown, the pronotum is pale reddish brown to yellowish brown, and the elytra are paler and usually yellowish brown. The complex is found in Europe and southwestern Asia. *Bledius nanus* and *B. transcaspicus* may belong with the group because of the similarity of the pronotal punctation, sculpturing, and shape but both are more darkly pigmented.

The *analis* complex includes: *analis* and *nitidicollis*. The males of both have a feeble emargination of sternite VII that is bordered by a patch of long setae (fig. 273). The pronotal median groove is feeble. Both species are from central North America.

Species Included and Material Examined

aculeatus Fauvel Syn(IRSN); type country: ?

Gabon: [Petit] Loango (IRSN). **Sierra Leon:** (Rhobomp? IRSN). **Zaire:** Kinshasa (IRSN).

afghanicus Scheerpeltz Co(MNHV); type country: Afghanistan.

Afghanistan: Kabul (MNHV).

akinini Eppelsheim Co,Sp(MNHV), Sp (FMNH, BMNH, IRSN); type country: USSR.

Afghanistan: (Margowüste? MNHV). **China:** Tientsin [=Tianjin] (FMNH); Chinkiang [=Xinjiang] (FMNH). **Iran:** (Anbar-Abad? MNHV). **Iraq:** Baghdad (MNHV). **Mongolia:** (FMNH). **USSR:** Aulia Ata [=Dzhambul] (FMNH, MNHV); Transcaspian (FMNH); Ashkabad (FMNH, IRSN); Repetek (FMNH, MNHV); Kasalinsk (MNHV); Margelan (MNHV); Buchara (MNHV); Turkmeniya (MNHV); Turkestan (Djizak? MNHV); Turkestan (MNHV, FMNH).

analis LeConte L(MCZ), Sp(AMNH); type country: USA.

Eastern two-thirds of **North America** (Herman, 1972, 1983a).

argentinus Bernhauer T,Sp(FMNH), Sp(BMNH); type country: Argentina.

Argentina: Tucuman Province (BMNH, FMNH); Salta Province (FMNH). **Bolivia:** (FMNH). **Brazil:** Sao Paulo (FMNH).

assimilis Casey L(USNM), Sp(AMNH); type country: USA.

Eastern **USA** and **Canada** (Herman, 1972, 1983a).

atratus Fauvel Syn(IRSN); type country: Italy.

Italy: Sardinia: Tertenia (IRSN).

atricapillus (Germar) Sp(BMNH, FMNH, IRSN, MNHV); type country: East Germany.

Austria: Wien (MNHV); Stockerau (FMNH); Thüringen (FMNH); Ulrichskirchen (FMNH); Lake Enzersdorf (FMNH); Korneuberg (FMNH). **Belgium:** Brussels (IRSN, BMNH); Forest (IRSN); St. Jan in Eremo (IRSN). **Bulgaria:** Varna (FMNH). **Czechoslovakia:** Trencin (FMNH). **France:** Nyons (IRSN); St. Jean de Luz (IRSN); Bavay (IRSN); Calvados (MNHV); Carcassonne (MNHV); Cape Alprech (BMNH); Avignon (IRSN). **Germany, West:** Bergstrasse (MNHV); Darmstadt (FMNH); Pfarrkirchen (FMNH). **Hungary:** Pest (IRSN); Buda (FMNH). **Iraq:** Baghdad (IRSN). **Italy:** (MNHV); Piemonte (IRSN); Oriolo (FMNH); Rome (FMNH). **Poland:** Jaroslaw (IRSN); Stettin [=Szczecin] (IRSN, MNHV). **Romania:** Vaslui (MNHV); Galatz (BMNH). **Spain:** Albarracin (MNHV); Madrid (FMNH). **Turkey:** Diarbekir (IRSN). **United Kingdom:** maritime and estuarian localities throughout (P. M. Hammond, BMNH, unpublished notes). **USSR:** Merv [=Mary] (IRSN, FMNH); Turkestan (IRSN); Ashkabad (IRSN); Caucasus (Aresch? IRSN); Aulie-Ata [=Dzhambul] (MNHV); Sarepta (MNHV); Repetek (MNHV, FMNH); Transcaspian (New Saratov ? MNHV); Transcaspian (Ljutfabad? MNHV); Namangan, Fergana (FMNH); (Dortkuju? FMNH); Tedzhen (FMNH); Golodnaja-Steppe (FMNH). **Yugoslavia:** Sarajevo (MNHV); Dalmatia (FMNH); Ruma (FMNH).

bedeli Fauvel Syn,Sp(IRSN), Sp(FMNH, MNHV); type country: Algeria.

Algeria: Daya (MNHV, IRSN); Alger (MNHV); Oran (FMNH, MNHV); Tlemcen (IRSN). **Lebanon:** Beirut (IRSN); Nahr el Kelb (IRSN). **Turkey:** Adana (IRSN).

berlandi Cameron P,Sp(BMNH), Sp(MNHV); type country: Senegal.

Guinea: Kindia (Friguiagbe? MNHV). **Mali:** Bamako (MNHV). **Nigeria:** Ibadan (BMNH). **Senegal:** Dakar (BMNH); Thies (BMNH).

bredoi Bernhauer T(FMNH); type country: Zaire.

Zaire: Elizabethville [=Lubumbashi] (FMNH).

castaneipennis Mannerheim Syn(ZMUH); type country: ?

Syntypic specimens without locality labels (ZMUH).

[*castaneus* Mulsant and Rey]—no specimens examined; type country: France.

This species was proposed conditionally and described in a paragraph at the end of a redescription of *Bledius femoralis.* Mulsant and Rey (1878, p. 596) mentioned long divergent spines on the sixth abdominal segments which suggests that *castaneus* is a member of the *assimilis* complex of the *semiferrugineus* group.

Dr. Joël Clary of the Musée Guimet d'Histoire Naturelle Lyon informed me (in a letter) that there are no specimens of *Bledius castaneus* in the Rey collection but that one of the four specimens of *femoralis* is labeled as "variété." On the chance that this variety of *femoralis* was a specimen of *castaneus,* Dr. Clary sent the specimen to me. Unfortunately, the specimen is a female; the authors of *castaneus* clearly stated that the specimens are male.

coulteri Hatch H(USNM), Sp(AMNH); type country: USA.

Western **USA** and **Canada** (Herman, 1972, 1983a).

crassicollis Boisduval and Lacordaire Sp(FMNH, BMNH, IRSN, MNHV); type country: France.

Austria: Wien (FMNH, MNHV); Linz (MNHV); Vorarlberg (MNHV); Wolfsgraben (FMNH); Hall (FMNH); Stockerau (FMNH); Windischgarsten (MNHV). **Belgium:** Angre (IRSN); Renaix [=Ronse] (IRSN). **Czechoslovakia:** Teschen (MNHV); Brno (BMNH); Brandeis [=Brandys] (MNHV). **France:** Reims (IRSN); Elbeuf (IRSN); Rouen (IRSN); Noyon (BMNH); Avignon (IRSN). **Germany, East:** Mecklenburg (IRSN). **Germany, West:** Berlin (IRSN, FMNH, BMNH); Heilsbronn (MNHV). **Hungary:** (BMNH); Neusiedler Sea (MNHV). **Italy:** Piemonte (IRSN); Sicily, Milazzo (IRSN); Emilia (MNHV). **Poland:** Krakow (MNHV). **Sweden:** (MNHV). **United Kingdom:** scattered mostly coastal localities in southern England (P. M. Hammond, BMNH, unpublished notes). **USSR:** Riazan (IRSN). **Yugoslavia:** Ruma (FMNH); Krapina (FMNH).

cribratus Sharp T(BMNH); type country: Japan.

Japan: Nikko (BMNH).

cribricollis Heer Sp(BMNH, FMNH, IRSN, MNHV); type country: Switzerland.

Albania: Elbasan (FMNH); Shkoder (BMNH). **Algeria:** Bone [=Annaba] (IRSN). **Austria:** Lake Enzersdorf (MNHV, FMNH); Wien (MNHV, FMNH); Stockerau (MNHV, FMNH); Graz (MNHV); Vorarlberg (MNHV); Korneuburg (FMNH); Neusiedler Sea (FMNH); Floridsdorf (FMNH). **Belgium:** Angre (IRSN); Tervueren (IRSN). **Czechoslovakia:** Brandeis [=Brandys] (MNHV); Trencin (FMNH). **France:** Chambery (IRSN); Lyon (IRSN); Nyons (IRSN); Perpignan (FMNH). **Greece:** Saloniki [=Thessaloniki] (FMNH). **Iraq:** Mesopotamia (IRSN). **Italy:** Taufers (FMNH); Aosta (BMNH); Novoli (IRSN); Carnia, Tolmezzo (IRSN); Rovereto (BMNH). **Poland:** Krakow (MNHV). **Spain:** Sierra de Cordoba (FMNH); Andalusia, San Pedro de Alcantara (IRSN). **Switzerland:** Ragaz (BMNH). **Tunisia:** Souk el Arba (IRSN); Oued Zarga (IRSN). **Turkey:** Adana (IRSN). **USSR:** Caucasus (IRSN); Sarepta (FMNH); Lenkoran (MNHV). **Yugoslavia:** Ivanscica (MNHV); Krapina (FMNH).

dehnerti Korge Sp(GLC); type country: Germany.

France: Voiron region, Isère Dept. (GLC).

diffinis Baudi Syn(MZUT); type country: Cyprus.

Cyprus (MZUT; types lack labels but as described originally the species is presumably from Cyprus).

dissimilis Erichson Sp(BMNH, FMNH, IRSN, MNHV); type country: ?

Austria: Mödling (MNHV); Stockerau (MNHV, FMNH); Wien (MNHV); Korneuburg (FMNH). **Belgium:** Brussels (IRSN); Wemmel (IRSN); Boitsfort (IRSN); Roisin (IRSN). **France:** Lille (MNHV, IRSN); Avignon (IRSN); Paris (IRSN); Toulouse (IRSN); Carcassonne (FMNH). **Germany, East:** Lobau (FMNH). **Germany, West:** Pforzheim (MNHV). **Greece:** Evvoia Island (FMNH); Salonica [=Thessaloniki] (BMNH). **Hungary:** Ujpest (MNHV); Sopron (MNHV); Herkulesbad (MNHV); (Tifel? IRSN); Esztergom (FMNH); Györ (FMNH); Siebenbürgen (MNHV). **Iran:** Elburz Mts. (FMNH). **Iraq:** Mesopotamia (FMNH, BMNH). **Italy:** Torino (IRSN); Oriolo (FMNH); Carnia, Tolmezzo (IRSN). **Luxembourg:** Maas River (MNHV). **Romania:** Galatz [=Galati] (MNHV, BMNH, IRSN); Bucharest (IRSN). **Spain:** Ponferrada (FMNH). **USSR:** Barnaul (MNHV); Sarepta (IRSN, FMNH); Enzeli [= Bandar Anzeli] (IRSN); Caucasus (FMNH); Caucasus (Aresch? IRSN). **Yugoslavia:** Vardar River (MNHV, IRSN, FMNH); Visegrad (FMNH, IRSN).

elongatus Mannerheim H(ZMUH), Sp(FMNH, MNHV); type country: USSR.

Austria: Neudorf (MNHV). **Italy:** Colli-Euganei (MNHV). **USSR:** Petropoli [= St. Petersburg] (ZMUH).

erythraeanus Bernhauer T(FMNH); type country: Ethiopia.

Ethiopia: Massawa (FMNH).

femoralis (Gyllenhal) Sp(BMNH, FMNH, IRSN, MNHV); type country: Sweden.

Belgium: Lamorteau (IRSN). **Czechoslovakia:** Trencin (FMNH). **France:** (MGHN); Marly (IRSN); Lille (IRSN). **Germany, West:** Huntlosen (FMNH); Darmstadt (FMNH); Köln (MNHV). **United Kingdom:** southeastern England, and Cumbria and Yorkshire (P. M. Hammond, BMNH, unpublished notes).

filipponii Coiffait H,P(HCC); type country: Saudi Arabia.

Saudi Arabia: (Wadi Jizan ? HCC).

foraminosus Casey L(USNM), Sp(AMNH); type country: USA.

Western **USA** and **Canada** (Herman, 1972, 1983a).

fragilis Sharp T(BMNH); type country: Japan.

Japan: (BMNH).

fumatus LeConte L(MCZ), Sp(AMNH); type country: USA.

Central **USA** and south central **Canada** (Herman, 1972).

gallicus (Gravenhorst) Sp(BMNH, FMNH, IRSN, MNHV); type country: France.

Algeria: Philippeville [=Skikda] (IRSN). **Austria:** Feldkirch (MNHV); Mödling (MNHV); Wien (MNHV); Enzersdorf (MNHV); Neusiedler Sea (MNHV); Burgenland (MNHV); Graz (MNHV); Kitsbuhel (MNHV); Schladming (MNHV); Horn (FMNH); Stockerau (FMNH); Korneuburg (FMNH); Hohen Tauern, Koetschach Valley (IRSN). **Belgium:** Brussels (IRSN); Forêt de Soignes (IRSN); Anderlecht (IRSN); Wemmel (IRSN); Antwerpen (IRSN); Mazy (IRSN); Heysel (IRSN); Jette (IRSN); Seilles (IRSN); Gembloux (IRSN); Ben-Ahin (IRSN); Dieuxville (IRSN). **China:** Ussuri River (FMNH). **Czechoslovakia:** Brandeis [=Brandys] (MNHV); Nymburk (MNHV). **Denmark:** (MNHV). **Finland:** Lojo (FMNH). **France:** Paris (IRSN); Lille (IRSN); Marseille (IRSN); St. Germain (IRSN); Corsica (IRSN); Meysse (IRSN); Corsica, Ghisonaccia (IRSN); Savoie (Belmont? MNHV); Fontainebleau (FMNH). **Germany, East:** Birkenwerder (FMNH). **Germany, West:** Hannover (MNHV); Freiweinheim (FMNH); Hamburg (MNHV). **Greece:** Crete (FMNH, MNHV). **Hungary:** Sopron (MNHV); Ujpest (MNHV). **Israel:** Haifa (IRSN); Palestine (MNHV). **Italy:** Sardinia: Oristano (MNHV); Carnia, Tolmezzo (IRSN); Carnia, Arta (IRSN); Valdieri (MNHV). **Lebanon:** Beirut (IRSN). **Mongolia:** Choud [=Hovd] aimak, Jamatin Dolon, 40 km N Somon Manchan [=Manhan], SW corner of Char [=Har] us Nuur (CNC) (additional localities: Smetana, 1975). **Norway:** Oslo (MNHV). **Poland:** Jaroslaw (IRSN, FMNH). **Romania:** Sinaia (IRSN); Brosteni (IRSN). **Spain:** Escorial (IRSN); Andalusia (IRSN); San Pedro de Alcantara (IRSN); Ponferrada (FMNH). **Switzerland:** (BMNH); Martigny, Valais (IRSN). **Syria:** (Mujunkum? FMNH). **Tunisia:** Teboursouk (IRSN). **United Kingdom:** widespread throughout (P. M. Hammond, BMNH, unpublished notes). **USSR:** Sarepta (IRSN, MNHV, FMNH); Onega Lake [= Ozero Onezhskoye] (MNHV); Uralsk (MNHV); Aulie-Ata [=Dzhambul] (MNHV); Golodnaja-Steppe (FMNH); Astrakhan (BMNH); Hanka Lake [= Ozero Khanka] (IRSN). **Yugoslavia:** Morovic (MNHV); Ruma (FMNH); Fruska Gora (FMNH).

ganglbaueri Bernhauer T,Co,Sp(FMNH), Co,Sp(BMNH), Sp(MNHV); type country: Tanzania.

Chad: Massakori (FMNH); Fort Lamy [=N'Djamena] (MNHV, BMNH); Moyen Chari (BMNH). **Ethiopia:** Harar (FMNH). **Niger:** Maradi (BMNH). **Nigeria:** Azare (FMNH, BMNH). **Saudi Arabia:** Hedjaz (BMNH). **Sudan:** Wadi Medani (FMNH, BMNH); (Dahr el Ghazal ? MNHV). **Tanzania:** Nachingwea (BMNH); Dar-es-Salaam (FMNH, BMNH); Kilimanjaro (FMNH, BMNH); Ngorongoro (MNHV). **Uganda-Zaire:** Ruwenzori (Watalinga? FMNH). **Zimbabwe:** Salisbury (FMNH, BMNH).

glasunovi Luze Co(BMNH), Sp(MNHV); type country: USSR.

Afghanistan: Qades (MNHV); (Dahlah? MNHV); Kunduz (BMNH). **China:** Karakorum, Hotan (BMNH). **[China-Tibet]:** source of the Indus (FMNH). **Iran:** Anbar-Abad (MNHV); Baluchistan, Iranshahr (MNHV). **Iraq:** Mesopotamia (FMNH, BMNH). **USSR:** Repetek (MNHV, FMNH, BMNH); Merv [=Mary] (MNHV, BMNH, FMNH); Imambaba (MNHV, FMNH); Transcaspian (Dortkuju? MNHV); (New Saratov ? MNHV); Transcaspian (Ljutfabad? MNHV); Aulie Ata [=Dzhambul] (FMNH); Transcaspian (BMNH). **Yugoslavia:** Ruma (FMNH).

gravidus Casey L(USNM), Sp(AMNH); type country: USA.

Canada and western **USA** (Herman, 1972, 1983a).

haarlovi Scheerpeltz H,P(MNHV); type country: Afghanistan.

Afghanistan: Panjao (MNHV); Qades (MNHV).

heterocerus Eppelsheim Co,Sp(MNHV), Sp(FMNH); type country: Yugoslavia.

Austria: Stockerau (MNHV); Wien (MNHV). **Hungary:** Nagymihaly (MNHV). **Italy:** Toscana (MCC). **Yugoslavia:** Vardar (MNHV); Croatia (MNHV).

hlisnikowskii Roubal L,Sp(SNMB); type country: USSR.

USSR: Kiev (SNMB).

inornatus Sharp T(BMNH), Sp(FMNH); type countries: Costa Rica, Panama.

Costa Rica: near San José (FMNH); Irazu (BMNH). **Mexico:** *Tabasco:* Teapa (BMNH). **Panama:** Bugaba (BMNH).

johnstoni Cameron T,Sp(BMNH); type country: Sudan.

Kenya: Magadi (BMNH). **Saudi Arabia:** Al Khadra (BMNH). **Senegal:** Linguere (BMNH). **Sudan:** (Khor Arbaat Delta ? BMNH).

lateralis Erichson T(MNHV), Sp(MNHV, AMNH, IRSN); type country: Venezuela.

Argentina: Cordoba (IRSN); Tucuman (IRSN). **Costa Rica:** Santa Clara (IRSN). **Ecuador:** Napo Province (IRSN). **Mexico:** Tabasco (IRSN); Durango (IRSN). **Venezuela:** Miranda, Panaquire, Rio Tuy (AMNH); Puerto Cabello (MNHU).

minarzianus Bernhauer T(FMNH); type country: USSR.

USSR: Ural Mts. (FMNH).

nanus Erichson Sp(FMNH, BMNH, IRSN, MNHV); type country: Austria.

Austria: Wien (MNHV); Mödling (MNHV); Graz (MNHV); Prossnitz (MNHV, IRSN); Ulrichskirchen (IRSN). **Belgium:** Schaerbeek (BMNH); Forest (IRSN). **Czechoslovakia:** Brandeis [=Brandys] (MNHV). **Denmark:** Nykjobing (BMNH). **France:** Seine and Oise Rivers (MNHV); Paris (BMNH); Vitry sur Seine (BMNH); Strasbourg (BMNH). **Germany, East:** Leipzig (FMNH). **Germany, West:** Heilbronn (MNHV); Darmstadt (MNHV). **Greece:** Limnos Island (BMNH). **Hungary:** Neusiedler Sea (MNHV); Budapest (MNHV); Kalocsa (MNHV); Ujpest (MNHV). **Iraq:** Baghdad (MNHV). **Italy:** Imola (MNHV). **USSR:** Namangan, Fergana (FMNH).

nitidicollis LeConte L(MCZ), Sp(AMNH); type country: USA.

Eastern two-thirds of **USA** and southern **Canada** (Herman, 1972, 1983a).

obtusus Sharp T,Sp(BMNH); type country: Japan.

Japan: Niigata (BMNH).

occidentalis Bondroit Sp(BMNH, MNHV); type country: Netherlands.

Austria: Hall (MNHV). **France:** Carcassonne (MNHV). **Germany:** (MNHV). **Italy:** Toscana (MCC). **Netherlands:** Hengelo (MNHV). **Sweden:** Säro, Halland (MNHV). **United Kingdom:** scattered in southern England (P. M. Hammond, BMNH, unpublished notes). **Yugoslavia:** Croatia (BMNH).

[*orion* Normand]—no specimens examined; type country: Tunisia.

Normand (1939) described the presence of a large triangular lobe on the penultimate sternite [VII] and discussed the similarity of *orion* with *elongatus* and *fracticornis* [=*gallicus*]. Further, Normand stated that *orion* is the species mentioned in a catalogue by Fauvel as *B. fracticornis* var. *elongatus.* Normand's comparison and discussion and the lobe of sternite VII lead me to think that *orion* is part of the *gallicus* complex of the *semiferrugineus* group.

philadelphicus Fall L(MCZ), Sp(AMNH); type country: USA.

Northeastern **USA** and southeastern **Canada** (Herman, 1972, 1983a).

[*picipennis* Hochhuth] no specimens examined; type country: USSR.

Hochhuth (1849) compared this species to *crassicollis* but, more importantly, mentioned the presence of a pair of spines adjacent to an emargination of the sixth abdominal segment [Sternum VII]. The only species of *Bledius* so armed are those of the *assimilis* complex which is part of the *semiferrugineus* group.

procerulus Erichson Sp(BMNH, FMNH, IRSN, MNHV); type country: Austria.

Austria: Wien (MNHV); Neusiedler Sea (MNHV, FMNH); Korneuburg (MNHV). **Bulgaria:** Samokov (MNHV). **France:** (BMNH, IRSN); Fontainebleau (MNHV, FMNH, IRSN); St. Germain (IRSN); Dieppe (IRSN). **Germany, West:** Taunus Mts. (MNHV); Hamburg (MNHV); Wimpfen (MNHV). **Italy:** Emilia (MNHV). **USSR:** Sarepta (IRSN). **Yugoslavia:** Ivanscica (MNHV).

rotundicollis LeConte L(MCZ), Sp(AMNH); type country: USA.

Central **USA** and south central **Canada** (Herman, 1972, 1983a).

roubali Horion Sp(BMNH, MNHV); type country: Czechoslovakia.

Albania: Elbasan (MNHV). **Austria:** Wien (MNHV). **Czechoslovakia:** Cejc (BMNH); Levice (BMNH). **Romania:** Giurgevo (MNHV). **USSR:** Turkestan, Geok-Tepe (BMNH). **Yugoslavia:** Ivanscica (MNHV).

rubiginosus Erichson L(ZMHU), Sp(AMNH); type country: USA.

Eastern **USA** and south central **Canada** (Herman, 1972, 1983a).

sanguinithorax Bernhauer T,Sp(FMNH); type country: USSR.

USSR: Transcaspian (FMNH); (Chiva? FMNH).

schoutedeni Cameron Co,Sp(BMNH), Sp(FMNH); type country: Zaire.

Angola: Quirimbo (BMNH, FMNH); (Congulu? FMNH, FMNH). **Zaire:** Kivu (BMNH); Elisabethville [=Lubumbashi] (FMNH); Leopoldville [=Kinshasa] (FMNH). **Zambia:** Nchanga (BMNH).

semiferrugineus LeConte L(MCZ), Sp(AMNH); type country: USA.

Eastern **USA** and southeastern **Canada** (Herman, 1972, 1983a). New record: **Cuba:** (MNHU) [This record is represented by two species collected long ago. *Bledius semiferrugineus* is very common in Florida and likely to be in Cuba but I would like corroboration of the record].

tallaci Fall L(MCZ), Sp(AMNH); type country: USA.

California, **USA** (Herman, 1972, 1983a).

transcaspicus Bernhauer T,Co,Sp(FMNH), Sp(BMNH); type country: USSR.

USSR: Transcaspian (Kuschk? FMNH); Transcaspian, Bayram Ali (FMNH); Repetek (FMNH); Transcaspian (Dortkuju? BMNH); Merv [=Mary] (BMNH).

validepunctatus Scheerpeltz H(ZMLS); type country: South Africa.

South Africa: Natal, Estcourt (ZMLS).

yemenicus Coiffait H(HNHM); type country: Yemen.

Yemen: Wadi Zabid (HNHM).

Undetermined.

Algeria: Dellys (IRSN, det. as *atricapillus*); Oued Rhiou (IRSN, det. as *atricapillus*); Touggourt (IRSN, det. as *atricapillus*); Hoggar, Guelta Issakarassene (MNHV).

Angola: Tundavala, Lubango (BMNH). **Bolivia:** Santa Cruz (MNHV); Cochabamba, Chapare River (MNHV); Beni (Blancaflor? USNM). **Botswana:** Kanyu (MNHV); 2 mi. N Gweta (BMNH); Moremi Reserve (BMNH); Xugana, Okavango Swamp (USNM). **China:** Harbin (BMNH); Shandong Province, Jinan. **Costa Rica:** San Jose (AMNH); San Isidro de General (USNM). **Equatorial Guinea:** Bata (MNHV). **Ethiopia:** Massawa (IRSN); Saati (FMNH); Kaffa, Jima (BMNH); Harer, Errer Hotel (BMNH); Ilubador, Gambela (BMNH); Shewa, Awash (BMNH); Harer, 30.5 km NE Dire Dawal (BMNH). **Gabon:** Belinga (HCC). **Guinea:** (IRSN). **Honduras:** Colon, 3 mi. SW Sonaguera (AMNH). Progreso (BMNH). **India:** (Bengal, Sarda? BMNH); New Delhi (USNM). **Iran:** Khuzestan, Shush (MNHV); Mazandaran, 25 km W of Gorgan (USNM); 11 km S Chalus (USNM); Fars, 13 km SE Shiraz (USNM); Ahwaz (BMNH). **Iraq:** Mosul (MNHV). **Kenya:** Magadi (BMNH). **Korea:** Gensan (FMNH). **Mali:** (R. Diaka, Kara? BMNH); Ke Macina (BMNH). **Mexico:** *San Luis Potosi:* Tamazunchale (USNM); Jicaltepec (MCZ). *Vera Cruz:* 3 mi. S Tecolutla (CNC). *Sonora:* 40 mi. NW Santa Ana (CNC); 40 km SW Sonora, Ciudad Obregon, San Jose Beach (CNC). *Nayarit:* Tepic (AMNH); Acaponeta. *Sinaloa:* 21 mi. E Villa Union (CNC); near Palmito (CNC). *Oaxaca:* Papaloapam (AMNH). **Morocco:** Fes, Sebou River (MNHV). **Nepal:** Royal Chitwan National Park (USNM). **Nigeria:** Ibadan (BMNH); Zaria (BMNH); Kano, Rio Galma (BMNH); Lagos (BMNH); Umuahia (BMNH). **Pakistan:** Lahore (USNM). **Saudi Arabia:** Gumfuda [= Al Qunfudhah] (BMNH); Wadi Al Lith (BMNH). **South Africa:** Natal, Pietermaritzburg (FMNH). **Sudan:** Torit (BMNH). **Tunisia:** Kebili (IRSN, det. as *atricapillus*). **Turkey:** Makri Gulf (MNHV). **USSR:** Kraynovka (BMNH). **Zaire:** Banana (BMNH). **Zimbabwe:** Wankie National Park, Pan (BMNH).

19. *armatus* group

Figures 8, 286–302, 537–542, 648–653

DIAGNOSIS: This group can be separated from all others by the absence of the protergosternal suture (fig. 289), presence of the median labral incision (fig. 288), the complete elytral epipleural ridge (fig. 297), and the emarginate tergum VIII (fig. 298). Other useful characters include the closed procoxal fissure (fig. 289), the absence of a setigerous pit on the pronotum (figs. 289, 648), and the presence of a membranous lobe on the elytral margin.

Three of the 15 species of the *armatus* group have a protergosternal suture and will run to the *semiferrugineus* group in my key. Each of the three species has hypopharyngeal characters that are typical of and confined to the *armatus* group (as in figs. 537–542). The three species are *B. opacifrons, B. nitidiceps,* and *B. strenuus.* All have tridentate mandibles and the posterior margin of sternum VII is truncate; these two characters will separate the three species from most species of the *semiferrugineus* group. Since these species are found in the New World, I have made the following comparison to New World species of the *semiferrugineus* group. *Bledius strenuus,* which has a feeble protergosternal suture, is recognized by the bituberculate tumescence on the dorsum of the head and by the coarsely serrate posterior margin of tergum VIII (as in fig. 299). *Bledius nitidiceps* is separated by the long pubescence on the body, the ridge on the apex of antennomeres 3 to 7, and the coarsely serrate posterior margin of tergum VIII (as in fig. 299). *Bledius opacifrons* is separated by the fine, sparse punctation of the head and pronotum.

DESCRIPTION: Supraantennal ridge low to moderately enlarged, and without horns. Head without subantennal pocket; midbasal horn absent; postocular lateral carina absent. Clypeal margin not reflexed; anterior margin with tubercles (figs. 292, 293); clypeal middle without spines, ridges, or tubercles. Gular sutures fused. Labral margin emarginate (fig. 288); margin not reflexed; median incision present (fig. 288); dorsal surface flat, without midlongitudinal impression. Epipharyngeal lobe short (fig. 288); dorsal surface with one long and one short seta; median processes with lobed apices; lateroapical processes few, slender, and branched. Labial palps (fig. 291) with segments of subequal length; segments one and two of subequal thickness; first segment with two setae, second segment with one seta. Submentum not excavated. Mentum with setae present laterally and absent medially. Hypopharynx (figs. 537–542) with lateral rows of setae gradually convergent toward base; basal setae arranged in transverse row; basal setae stout; basal setae not on plate; central row of setae dense distally and proximally, sparse medially; disk without setae; disk with long and short cuticular processes; coronal pegs on median portion of disk and each in a hole. Prementum with three sclerites, one medial and two lateral; basal sclerite absent. Galea with dense cluster of setae on apex; ventral surface without setae; dorsomedial edge with lobe. Mandibles bidentate (fig. 286) or tridentate (fig. 287).

Pronotal horn absent. Marginal bead present and complete; bead dividing notum and hypomeron, not on hypomeron. Protergosternal suture absent (fig. 289) or present. Bead and suture (when present) anteriorly convergent. Procoxal fissure closed (fig. 289). Protrochantin concealed. Prosternum without setigerous pit; sternum with patch of setae near shallow depression (figs. 648, 649); depression with scattered clusters of pores (figs. 649, 653) and with small patch of coronal pegs (figs. 649–652); anterior margin entire, not notched. Elytral epipleural ridge present and complete (fig. 297); posterior margin with membranous lobe (fig. 290).

Tarsi four segmented. Protibia with one row of spinelike setae and numerous others scattered on surface.

Abdominal tergum VII with fine fringe on posterior margin. Tergum VIII with posterior margin emarginate; margin serrulate or serrate (figs. 298, 299). Tergum IX with glandular canal widely open dorsally. Tergum X with struts on anterior margin.

Aedeagus (figs. 294, 295) with parameres. Parameres broad and with median surface membranous; parameres extending beyond apex of median lobe. Median lobe long; base bulbous; apical portion flattened; ventral surface midlongitudinally divided.

Spermatheca (figs. 300, 301) tripartite. Receptacle sclerotized and divided by accordion tube into two parts; distal part larger than, equal to, or smaller than basal part; distal part invaginated; distal and basal parts with or without brimlike ridges. Spermathecal gland sclerotized; shape and surface irregular.

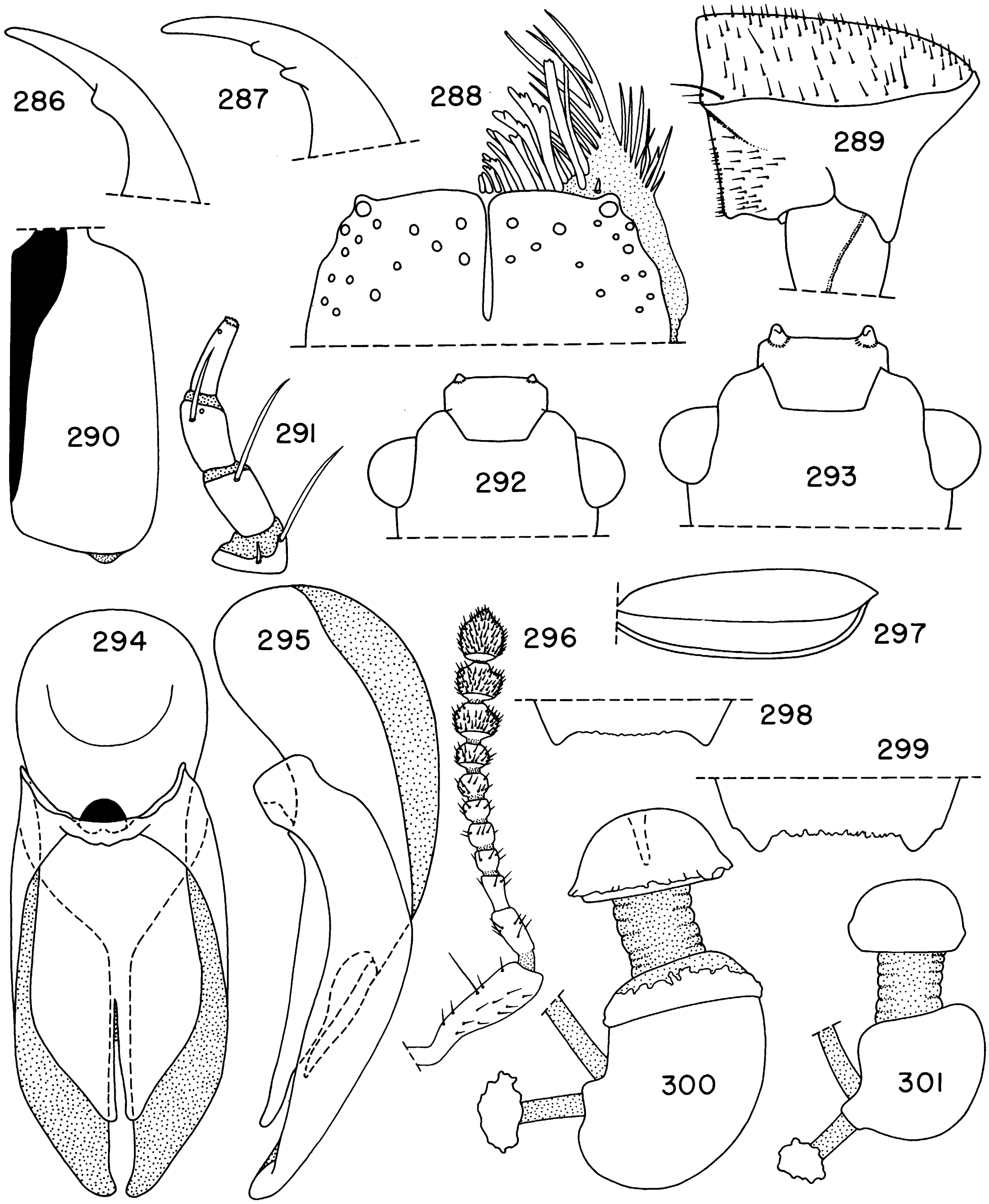
DISTRIBUTION AND HABITAT: The *armatus* group is confined to North America from Canada to southern Mexico (fig. 302). Most of the species are found in the western half of the United States and Canada. Only four are found in the east, one is found on the eastern coast from New York to northern Mexico, one has a transcontinental Canadian distribution, and the other two are western species with a few populations in the midwestern United States.

The species are found in the more arid parts of the continent, most in saline or alkaline habitats. One is found in saline, alkaline, and freshwater habitats. Two species have been collected only on the shore of freshwater rivers. Two species, *B. monstratus* and *B. fenyesi,* have a unique habitat. They live in decaying, sand covered piles of seaweed.

DISCUSSION: This group was first segregated by LeConte (1877). Herman (1976) revised the group and all the species except *derasus* which is added herein. Five species (or their junior synonyms) had been included in *Hesperophilus* (table 9).

Separation of the *armatus* and *semiferrugineus* groups using external characters is unsatisfactory. Species of the *semiferrugineus* group have a protergosternal suture. Although most of those of the *armatus* group lack the suture, three species of the *armatus* group have it. Separation of them from the *semiferrugineus* group was discussed previously (Herman, 1972, p. 155). However, more to the point, why not put these three species in the *semiferrugineus* group? Two of the three species were originally included in the *semiferrugineus* group, but during my investigations of the North American species I became suspicious about their placement because their form was more similar to that of the *armatus* group. Further study revealed the hypopharynx to have characters found only in the *armatus* group. These hypopharyngeal characters (figs. 537–542), which include the long cuticular processes on the apical lobes of the disk and their absence on the central region of the disk and the presence of the coronal pegs in holes, are the strongest argument for continued recognition of the *armatus* group. Even if the *armatus* and *semiferrugineus* groups were combined, the species of the *armatus* group would be separated as a monophyletic lineage.

Most species of *Bledius* make burrows in



FIGS. 286–301. The *armatus* group. **286.** Mandible, female, right (*bellicus*). **287.** Mandible, male, right (*bellicus*). **288.** Labrum, setae and left epipharyngeal lobe removed (*strenuus*). **289.** Prothorax, lateral (*politus*). **290.** Elytron, right, setae removed (*politus*). **291.** Labial palpus (*strenuus*). **292, 293.** Head, dorsal view, antennae and mouthparts removed (*flavipennis*). **294.** Aedeagus, dorsal view (*strenuus*). **295.** Aedeagus, lateral view (*strenuus*). **296.** Antenna (*fenyesi*). **297.** Elytron, lateral view (*politus*). **298.** Tergum VIII, apical margin (*monstratus*). **299.** Tergum VIII, apical margin (*opacifrons*). **300.** Spermatheca (*opacifrons*). **301.** Spermatheca (*aquilonarius*).

sand. Two of them, *B. monstratus* and *B. fenyesi,* live under and in piles of decaying sand-covered seaweed. This habitat is unique in the group. These two species are also anatomically separated from the others. Might there be one or more undiscovered Asian species that live in similar coastal habitats and might they be the sister group to these two North American species?

Species Included and Material Examined

aquilonarius Herman H,P(CNC), P,Sp(AMNH); type country: Canada.
Transcanadian (Herman, 1976, 1983a).

bellicus Blackwelder Sp(AMNH); type country: USA.
Central **USA** (Herman, 1976).

consimilis Fall L(MCZ), Sp(AMNH); type country: USA.
Central and southwestern **USA** (Herman, 1976, 1983a).

derasus Sharp T,Sp(BMNH); type country: Mexico.
Mexico: *Durango:* Ciudad Lerdo (BMNH).

episcopalis Fall L(MCZ), Sp(AMNH); type country: USA.
California and Nevada, **USA** (Herman, 1976).

eximius Casey L(USNM), Sp(AMNH); type country: USA.
Western **USA** (Herman, 1976).

fenyesi Bernhauer and Schubert L(MCZ), Sp(AMNH); type country: USA.
Western coastal **North America** from Coon Creek Beach at Point Buchon, San Luis Obispo County, California (new record), south to southern Baja, **Mexico** (Herman, 1976).

flavipennis LeConte L(MCZ), Sp(AMNH); type country: USA.
Western half of **USA** and southern **Canada** (Herman, 1976, 1983a).

ineptus Casey L(USNM), Sp(AMNH); type country: USA.
Central two-thirds of **USA** and southern **Canada** (Herman, 1976, 1983a).

monstratus Casey L(USNM), Sp(AMNH); type country: USA.
Western coastal **North America** from Hazard Canyon Beach, San Luis Obispo County, California (new record) north to Queen Charlotte Island, **Canada** (Herman, 1976, 1983a).

nitidiceps LeConte L(MCZ), Sp(AMNH); type country: USA.
Southwestern **USA** and northern **Mexico** (Herman, 1976, 1983a).

notialus Herman H,P(AMNH); type country: USA.
Central **USA** (Herman, 1976, 1983a).

opacifrons LeConte L(MCZ), Sp(AMNH); type country: USA.
Western **USA** and **Canada** (Herman, 1976, 1983a).

politus Erichson L(ZMHU), Sp(AMNH); type country: USA.
Eastern coastal **USA** from near Westport, Connecticut (new record) south to Texas (Herman, 1976, 1983a).

strenuus Casey L(USNM); Sp(AMNH); type country: USA.
Western two-thirds of **North America** (Herman, 1976, 1983a).

20. *albonotatus* group

Figures 6, 303–313, 543–547, 654–659

DIAGNOSIS: This group is separated from all others by the deeply emarginate labrum (figs. 303, 304), emarginate tergum VIII, complete elytral epipleural ridge, and open procoxal fissure (fig. 306). Other useful characters include the presence of a setigerous prosternal pit (figs. 654, 655, 658) and protergosternal suture, and complete pronotal marginal bead.

DESCRIPTION: Supraantennal ridge low, not enlarged, and without horns. Head without subantennal pocket; midbasal horn absent; postocular lateral carina absent. Clypeal margin not reflexed; anterior margin with tubercles; clypeal middle without spines, ridges, or tubercles. Gular sutures fused. Labral margin deeply emarginate (figs. 303, 304); margin not reflexed; median incision present (fig. 304); dorsal surface with or without midlongitudinal impression. Epipharyngeal lobe (figs. 303, 304) moderately long to long; dorsal surface with one long and one short seta; median processes with lobed apices; lateroapical processes numerous, slender, and branched or unbranched. Labial palps with segments of subequal length; first and second segments of subequal thickness; first segment with one seta, second segment with one or two setae. Submentum not excavated. Mentum with setae laterally and present medially but sparser and absent on narrow median stripe. Hypopharynx (figs. 543–547) with lateral rows of

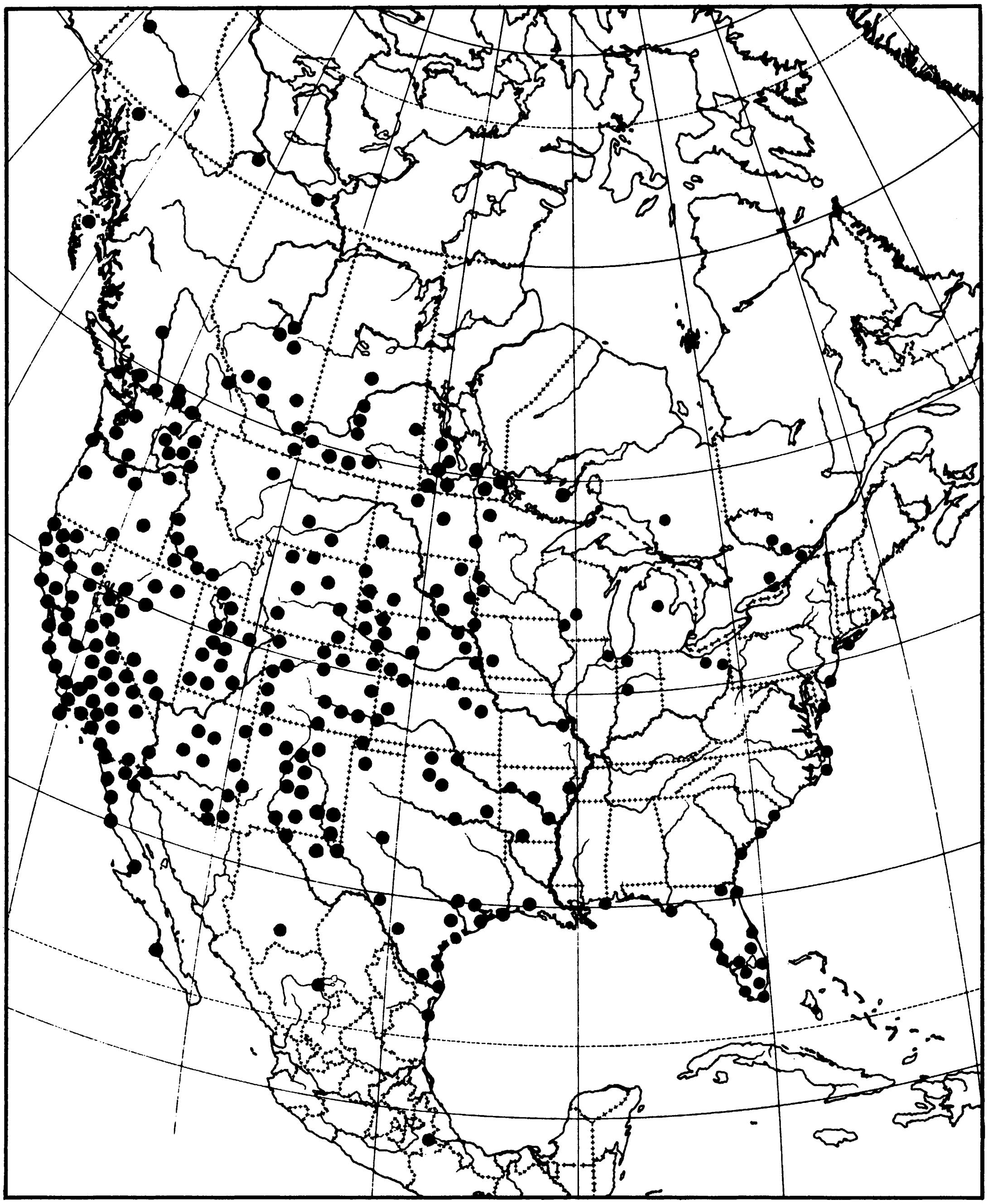
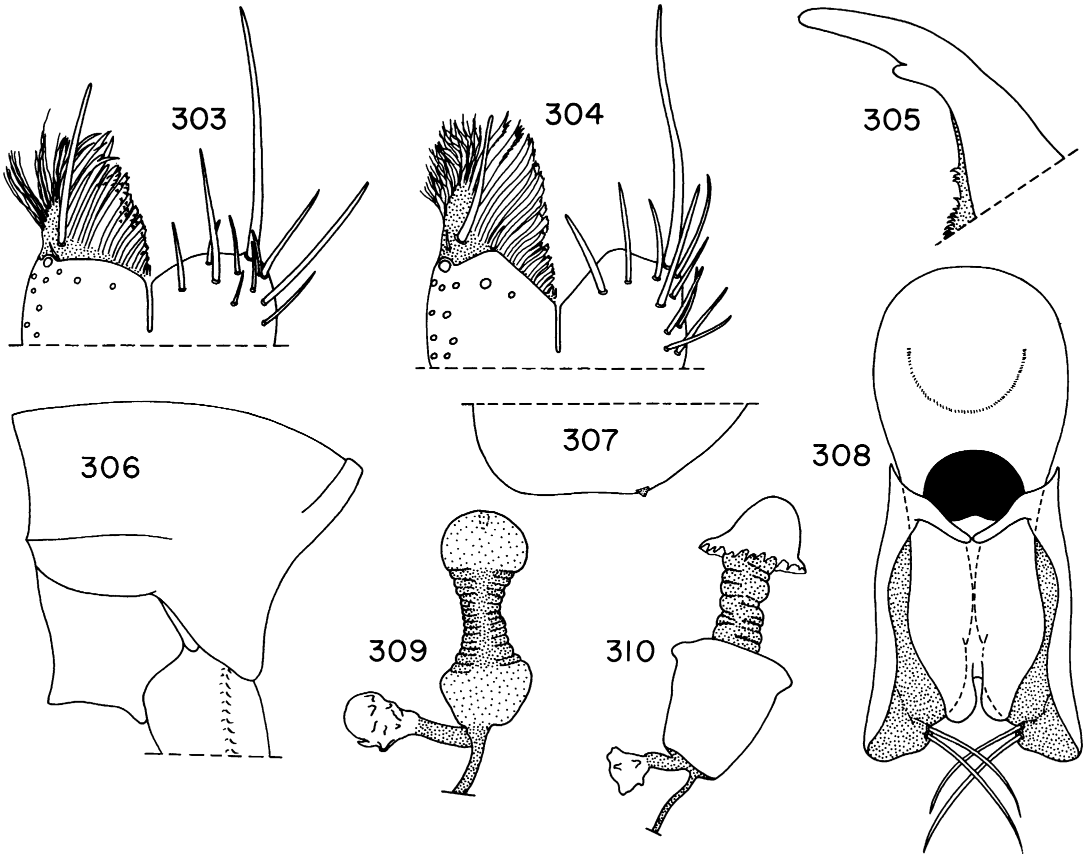


FIG. 302. Distribution of the *armatus* group in North America.

spines gradually convergent toward base; basal setae arranged in cluster or transverse row; basal setae stout; basal setae not on plate; central row of setae dense distally and sparse medially and proximally; disk without setae; disk covered with palmate clusters of cutic-



FIGS. 303–310. The *albonotatus* group. **303.** Labrum, setae of left and epipharyngeal lobe of right removed (*diagonalis*). **304.** Labrum, setae of left and epipharyngeal lobe of right removed (*albonotatus*). **305.** Mandible, right (*parvicollis*). **306.** Prothorax, lateral, setae removed (*nardus*). **307.** Elytron, right, apex (*albonotatus*). **308.** Aedeagus, dorsal view (*albonotatus*). **309.** Spermatheca (*diagonalis*). **310.** Spermatheca (*albonotatus*).

ular processes; coronal pegs scattered on median portion of disk. Prementum with three sclerites, one medial and two lateral; basal sclerite absent. Galea with dense cluster of fanlike rows of setae on apex; ventral surface without setae; dorsomedial edge with lobe. Mandibles bidentate (fig. 305).

Pronotal horn absent. Marginal bead present and complete, incomplete in *nardus*; bead dividing notum and hypomeron, not on hypomeron. Protergosternal suture present. Bead and suture parallel. Procoxal fissure open widely or narrowly (fig. 306). Protrochantin exposed. Prosternal process elongate. Prosternum with setigerous pit (figs. 654, 655, 658, 659); pit with pores among and behind setae (figs. 656, 657); anterior margin entire, without notch. Elytral epipleural ridge present and complete; posterior margin without membranous lobe or with minute, dorsally directed lobe surrounded by sclerite (fig. 307).

Tarsi four segmented. Protibia with one row of spinelike setae and with others scattered on lateral surface.

Abdominal tergum VII with fine fringe on posterior margin. Tergum VIII with posterior margin emarginate; margin entire, not serrate. Tergum IX with glandular canal widely open dorsally. Tergum X with struts on anterior margin.

Aedeagus (fig. 308) with parameres. Parameres broad and with membranous median

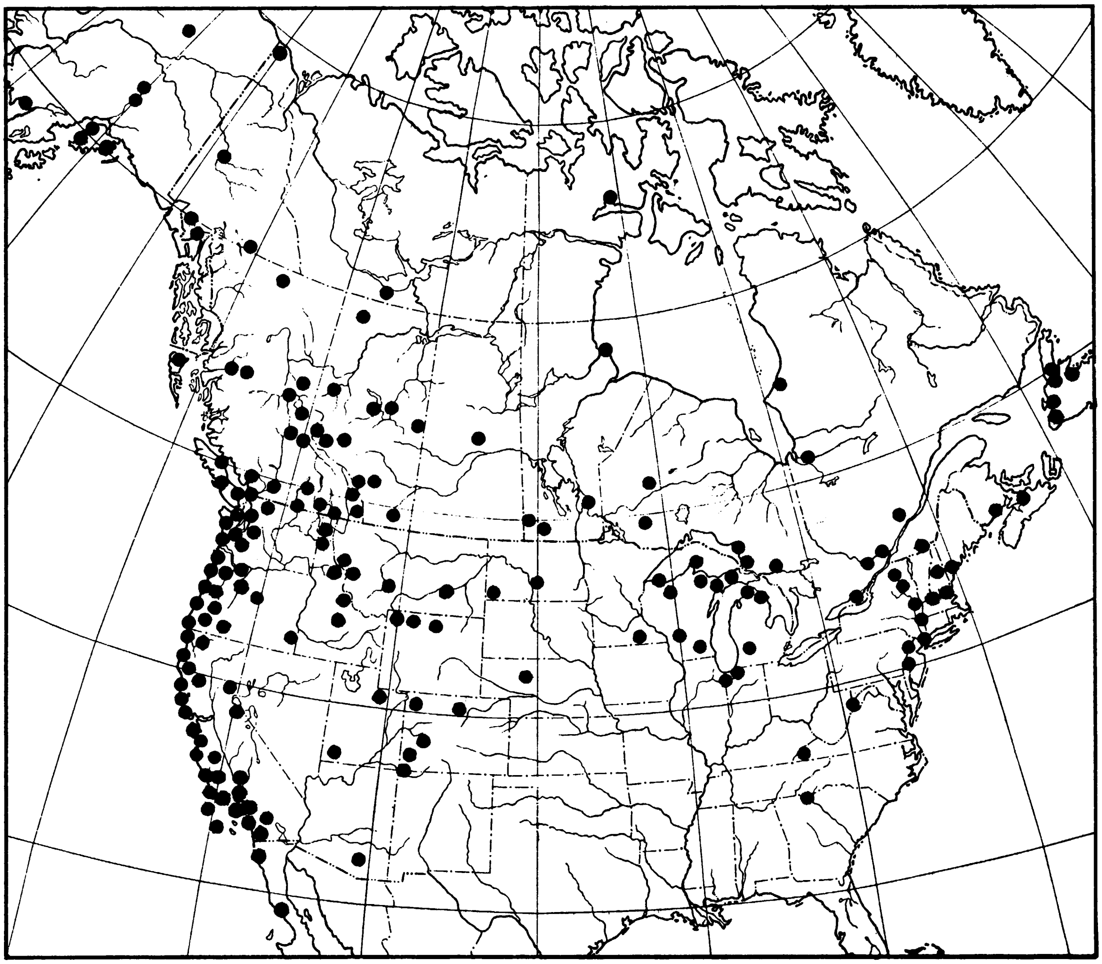


FIG. 311. Distribution of the *albonotatus* group in North America.

surface; parameres extending beyond apex of median lobe. Median lobe long; base bulbous; apical portion flattened; ventral surface midlongitudinally divided.

Spermatheca (figs. 309, 310) tripartite. Receptacle sclerotized and divided by accordion tube into two parts; basal part larger than or nearly equal to distal part; distal part invaginated; distal and basal parts with or without brimlike ridges. Spermathecal gland sclerotized; shape and surface irregular.

DISTRIBUTION AND HABITAT: This group has a holarctic distribution and the species are among the most northerly (figs. 311–313). The species are found in freshwater habitats. One, *albonotatus*, is nearly confined to the seashore but always occurs adjacent to a freshwater stream or river that empties into the ocean. *Bledius diagonalis* and *B. venus* can live near slightly saline streams or rivers.

DISCUSSION: The type species and three European species included in *Astycops* are moved herein to the *albonotatus* group (table 9) which is recognized herein for the first time. An oriental species was in *Dicarenus,* in east Asian and two North American ones were in *Hesperophilus,* and seven North American species were not placed in a subgenus (table 9).

Earlier I included the North American species of this group in the *annularis* group (Herman, 1983a) even though two obvious groups were evident. At the time I had regarded *suturalis, melanocolus,* and *gentilis* to

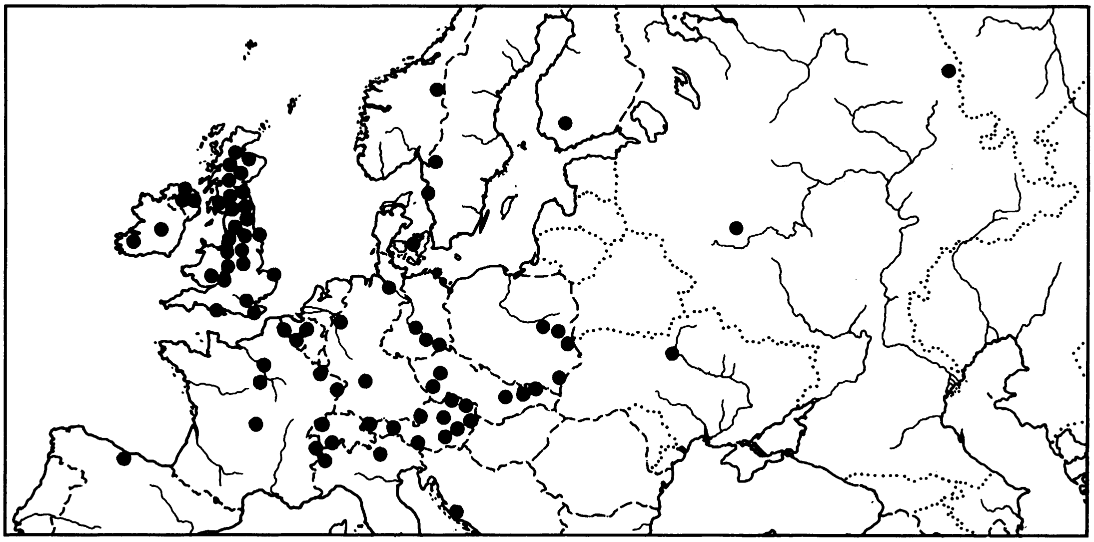


FIG. 312. Distribution of the *albonotatus* group in Europe.

be species that connected the *albonotatus* and *annularis* groups. These three species have a deeply emarginated labrum; it is not as deeply emarginate as the species of the *albonotatus* group but more deeply so than the *annularis* group.

The two groups are clearly separated by characters of the hypopharynx. In the *albonotatus* group the mandibles are bidentate, the labral emargination is deep, the elytral margin either lacks a membranous lobe or has a minute one surrounded by sclerotization, and the epipharyngeal lobe is moderately long to long. The disk of the hypopharynx is covered in palmate clusters of short cuticular processes (figs. 543–547). In the *annularis* group the mandibles are bidentate or tridentate, the elytral margin either has or lacks a membranous lobe but there is not a minute membranous lobe surrounded by a sclerite, the labral margin is shallowly to moderately emarginate or truncate with a small median notch, and the epipharyngeal lobe is small. The disk of the hypopharynx is covered with broad, flattened cuticular processes or palmate clusters of cuticular processes (figs. 520–523).

This group can be divided into several ill-defined subgroups of species that are probably related. The most obvious one includes *nardus, talpa,* and *zophus. Bledius sellatus* and *parvicollis* seem to be related as do *diagonalis* and *venus.* A large group seems to include *rectangulus, subterraneus, tarandus,* and *tenenbaumi* as one part along with *limbatus, omega,* and *tau. Bledius albonotatus* is the least easily placed species.

Species Included and Material Examined

albonotatus Mäklin T(MZUH); type country: USA.

Western coastal **North America** from Alaska south to Baja, **Mexico** (Herman, 1983a).

diagonalis LeConte L(MCZ), Sp(AMNH); type country: USA.

California and Arizona, **USA** and Baja, **Mexico** (Herman, 1983a).

limbatus Hochhuth Sp(BMNH, FMNH, IRSN, MNHV); type country: USSR.

Poland: (Zegre? BMNH, FMNH); Kijowiec (BMNH); (Urle? FMNH). **USSR:** Kiyev (BMNH, MNHV, FMNH).

nardus Herman H,P(AMNH); type country: USA.

Northwestern **USA** and southwestern **Canada** (Herman, 1983a).

omega Herman H,P(AMNH); type country: USA.

Northern **USA** and southern **Canada** (Herman, 1983a).

parvicollis Casey L(USNM), Sp(AMNH); type country: USA.

Western **USA** (Herman, 1983a).

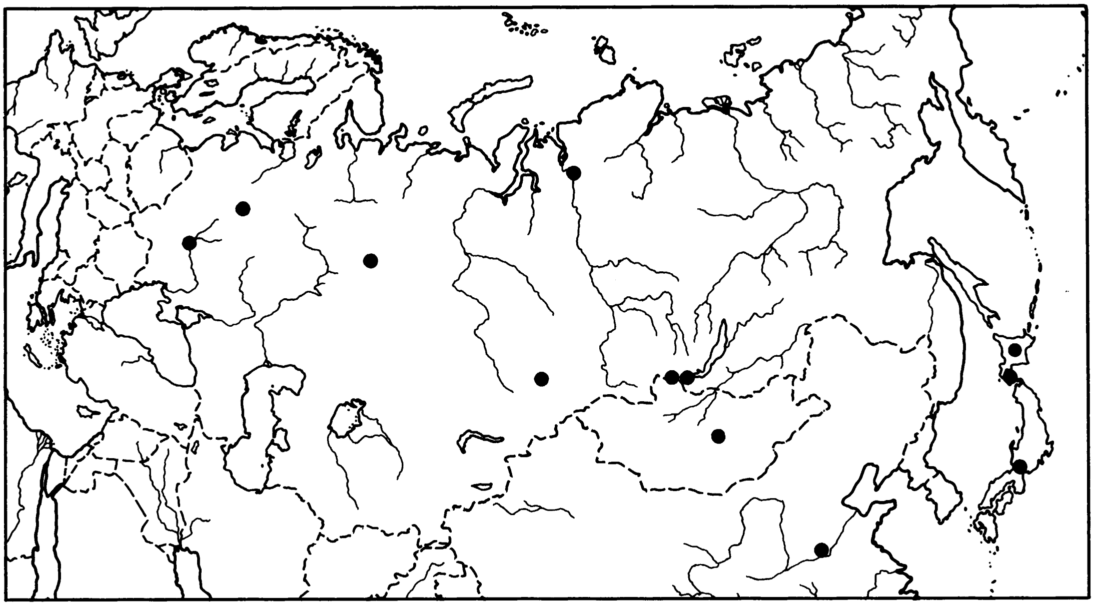


FIG. 313. Distribution of the *albonotatus* group in Asia.

rectangulus Eppelsheim Co,Sp(MNHV), Sp(FMNH, BMNH, IRSN); type country: USSR.

Mongolia: (MNHV). **Poland:** (Zegre? FMNH). **USSR:** source of the Irkut (BMNH, MNHV); eastern Siberia (BMNH, MNHV, FMNH, IRSN); Lake Baikal (BMNH); Transbaikal (IRSN); Dudinka (FMNH); Perm (FMNH).

sellatus Sharp Syn,Sp(BMNH), Sp(FMNH, IRSN, MNHV); type country: Japan.

China: Chinkiang [=Xinjiang] (FMNH). **Japan:** (FMNH); Hakodate (BMNH); Gifu (IRSN); (Vita? MNHV). **Korea:** Gensan (FMNH).

subterraneus Erichson Sp(BMNH, FMNH, IRSN, MNHV, ZMUH); type country: West Germany.

Austria: Gars (MNHV); Waidhofen (MNHV); Murz River (MNHV); Steyr (MNHV); Obdach (MNHV); Gars, Kamp Valley (FMNH); Horn (FMNH); Styria (St. Johann Ob Hohenburg ? FMNH); Wien (MNHV). **Belgium:** Brussels (BMNH); Angre (IRSN). **Czechoslovakia:** Teschen (FMNH); Trencin (FMNH); Cestice (BMNH); Brandeis [=Brandys] (MNHV). **France:** Le Bourget (IRSN); Metz (IRSN); Strasbourg (IRSN); Paris (IRSN); Lake Chambon (IRSN); Lille (IRSN); Savoie, Argentieres (BMNH); Briare (IRSN). **Germany, East:** Leipzig (MNHV); Wechselburg (FMNH); Dessau (FMNH); Furstenburg, Oder River (FMNH); Dresden (MNHV); Saxony (ZMUH). **Germany, West:** Hamburg (MNHV); Düsseldorf (IRSN). **Greece:** Cyclades [=Kikladhes] (FMNH). **Italy:** Courmayeur (BMNH); Pinzolo (BMNH). **Poland:** Poprad River (Rylvu? FMNH); (Zegre? FMNH); Jaroslaw (IRSN). **Portugal:** Runa (FMNH). **Romania:** Herkulesbad (FMNH). **Spain:** Potes (IRSN). **Sweden:** Klarälven River (Värenland? FMNH). **Switzerland:** Zermatt (MNHV). **United Kingdom:** widespread throughout (P. M. Hammond, BMNH, unpublished notes). **USSR:** Barnaul (FMNH). **Yugoslavia:** Dalmatia (MNHV).

talpa (Gyllenhal) Sp(BMNH, FMNH, IRSN, MNHV); type country: Sweden.

Austria: Salzburg (MNHV); Innsbruck (MNHV); Koetschach Valley, Hohen Tauern (MNHV, FMNH); Koetschach Valley, Bad Gastein (MNHV); Thuringen (FMNH); Wien (BMNH). **Czechoslovakia:** Tatry Mts. (MNHV); Tatry Mts. (Koprova dolins ? BMNH). **Denmark:** (MNHV); Halsskov Odde (BMNH). **Finland:** (FMNH); (Heteoja-Nauzi-Pazuki? MNHV). **Germany, East:** Dresden (FMNH, MNHV, IRSN). **Germany, West:** Neuhütten. **Norway:** (FMNH). **Poland:** (Nanosy, Navoszy? FMNH). **Sweden:** Mölndal (MNHV). **USSR:** Lake Baikal (MNHV); Moscow (MNHV); Dorpat (FMNH). **Yugoslavia:** Sarajevo (MNHV).

tarandus Herman L(MCZ), Sp(AMNH); type country: USA.

Transcanadian and south in western **USA** to Utah and Colorado (Herman, 1983a). New record: **Canada:** Yukon Territory, British Mountains, Teal Lake (CNC).

tau LeConte L(MCZ), Sp(AMNH); type country: USA.

Northeastern to midwestern **USA** and southern **Canada** (Herman, 1983a).

tenenbaumi Bernhauer T,Co,Sp(FMNH), Sp(BMNH, IRSN); type country: Poland.

Poland: (Zegre? BMNH, FMNH); Warsaw, Swider River (FMNH, IRSN); Warsaw (FMNH).

venus Herman H,P(AMNH); type country: USA.

California, **USA** (Herman, 1983a).

zophus Herman H,P(AMNH); type country: USA.

Northwestern **USA** and western **Canada** (Herman, 1983a).

Undetermined.

Czechoslovakia: Mähren (MNHV). **Japan:** Hokkaido, Shikaribetsu (YSC). **Switzerland:** Murtensee (MNHV).

21. *annularis* group

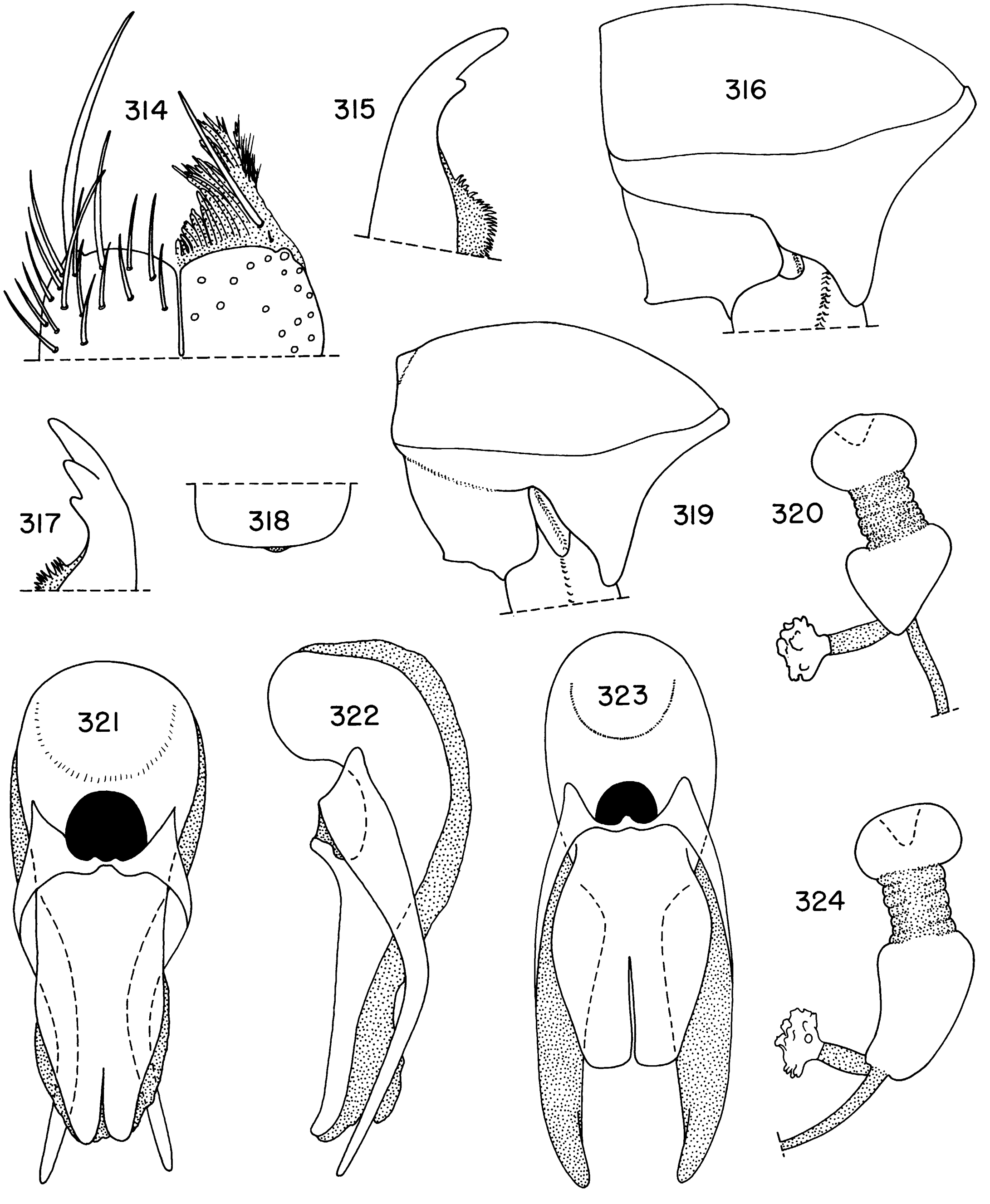
Figures 5, 55, 314–327, 520–523, 660–671

DIAGNOSIS: This group can be distinguished from all others by the characters given in the key. The *annularis* group is one of only a few in which the parameres of the aedeagus are broad and have a membranous median surface (fig. 323). The hypopharynx is covered with broad flattened cuticular processes which are found in two other groups (figs. 520–522).

DESCRIPTION: Supraantennal ridge low, not enlarged, and without horns. Head without subantennal pocket; midbasal horn absent; postocular lateral carina absent. Clypeal margin not reflexed; anterior margin with or without tubercles; clypeal middle without tubercles; spines, or ridges. Gular sutures fused. Labral margin emarginate (fig. 314); margin not reflexed; median incision present (fig. 314); dorsal surface flat, without midlongitudinal impression. Epipharyngeal lobe (fig. 314) short; dorsal surface with one long and one short seta; median processes with lobed apices; lateroapical processes numerous, slender, and branched or few, thick, and branched. Labial palps with segments of subequal length, or with second segment longest and segments one and three of subequal length; first and second segments of subequal thickness; first segment with two setae, second segment with one seta. Submentum not excavated. Mentum with setae present laterally and absent medially. Hypopharynx (figs. 520–523) with lateral rows of spines gradually convergent toward base; basal setae arranged in transverse row; basal setae stout; basal setae not on plate; central row of setae dense distally, sparse medially and proximally; disk without setae; disk with palmate clusters of cuticular processes covering surface (fig. 523) or with some palmate clusters of cuticular processes near anterior margin and covered with broad, flattened cuticular lobes (figs. 520–522); coronal pegs scattered over surface. Prementum with three sclerites, one medial and two lateral; basal sclerite absent. Galea with dense cluster of fanlike rows of setae on apex; ventral surface without setae; dorsomedial edge with lobe. Mandibles bidentate (fig. 315) or tridentate (figs. 317).

Pronotal horn absent. Marginal bead (fig. 316) present and complete; bead dividing hypomeron and notum, not on hypomeron. Protergosternal suture present (fig. 316). Bead and suture parallel to anteriorly convergent. Procoxal fissure usually open for entire length (fig. 319), in a few species closed for most of length and open only on ventral portion (fig. 316). Protrochantin exposed for entire length of fissure or occasionally exposed only at ventral portion of fissure. Prosternal process elongate. Prosternum usually with setigerous pit (figs. 660, 663, 666, 669), some species with small patch of setae on sternum; pit with dense cluster of pores behind setae (figs. 661–668, 671); anterior margin of sternum entire, without notch. Elytral epipleural ridge present and complete; posterior margin with (fig. 318) or without membranous lobe.

Tarsi four segmented. Protibia with one



FIGS. 314–324. The *annularis* group. **314.** Labrum, setae of right and epipharyngeal lobe of left removed (*villosus*). **315.** Mandible, left (*melanocolus*). **316.** Prothorax, lateral, setae removed (*turgidus*). **317.** Mandible, right (*habrus*). **318.** Elytron, right, apex (*monticola*). **319.** Prothorax, lateral, setae removed (*newelli*). **320.** Spermatheca (*ruficornis*). **321.** Aedeagus, dorsal view (*persimilis*). **322.** Aedeagus, lateral view (*persimilis*). **323.** Aedeagus, dorsal view (*suturalis*). **324.** Spermatheca (*newelli*).

row of spinelike setae and with many others scattered over lateral surface.

Abdominal tergum VII with fine fringe on posterior margin. Tergum VIII with posterior

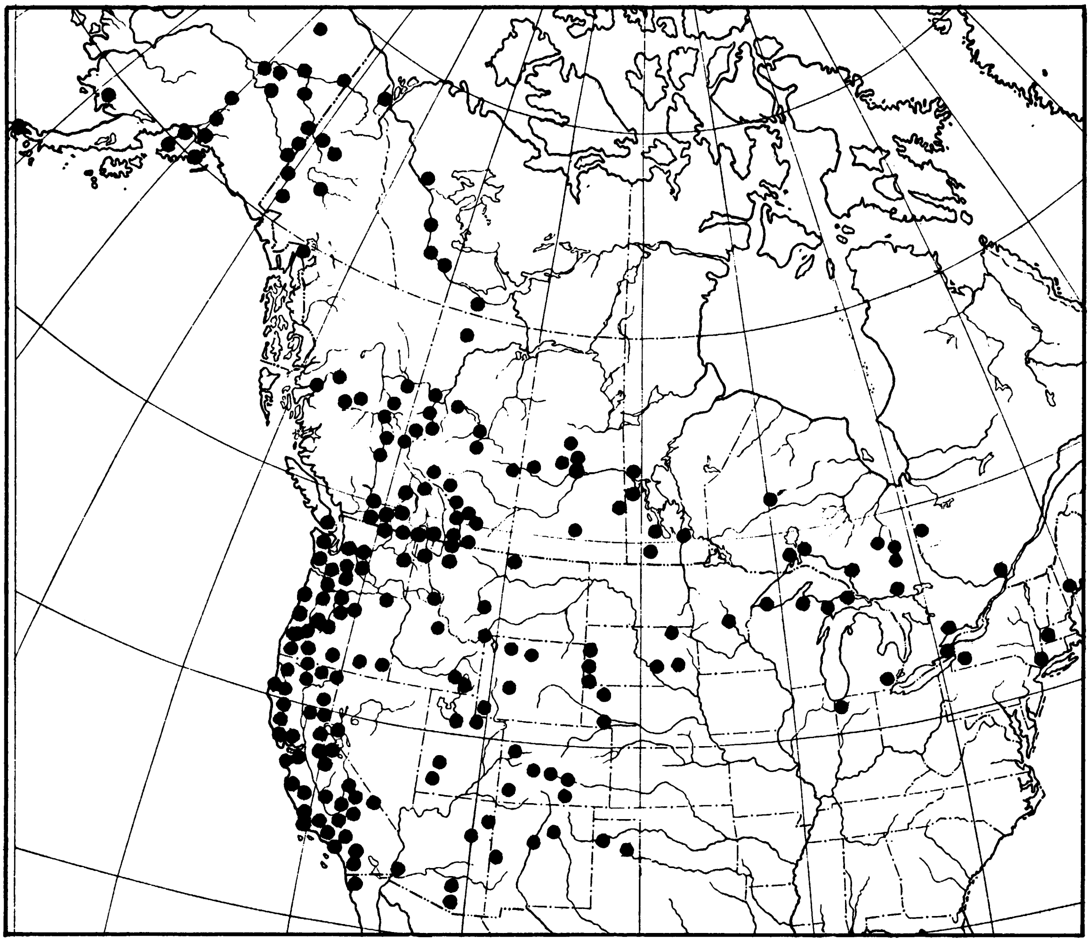


FIG. 325. Distribution of the *annularis* group in North America.

margin emarginate; margin entire, not serrate. Tergum IX with glandular canal widely open dorsally. Tergum X with struts on anterior margin.

Aedeagus (figs. 321–323) with parameres. Parameres broad and with median surface membranous (fig. 323) or rarely, parameres slender and median surface sclerotized (figs. 321, 322); parameres extending beyond apex of median lobe. Median lobe long; base bulbous; apical portion flattened; ventral surface midlongitudinally divided.

Spermatheca (figs. 320, 324) tripartite. Receptacle sclerotized and divided by accordion tube into two parts; basal part larger than or nearly equal to distal part; distal part invaginated; distal part with or without brimlike ridge; basal part without brimlike ridge. Spermathecal gland sclerotized; shape and surface irregular.

DISTRIBUTION AND HABITAT: This group has a holarctic distribution (figs. 325–327). Some of the species are found at the highest altitudinal and latitudinal localities for the genus. Most or all of the species are found near freshwater habitats and for many species the habitat is shaded.

DISCUSSION: Fifty-one of the species in this group were taken from *Hesperophilus* (the old *Blediodes*) as it is currently used (table 9). Removal of these 51 species represents part of a major reorganization of *Hesperophilus*. The type species of *Bargus* falls in the *annularis* group (table 9). The remaining 22 species had not been previously placed in a subgenus, but 18 of them had been in the

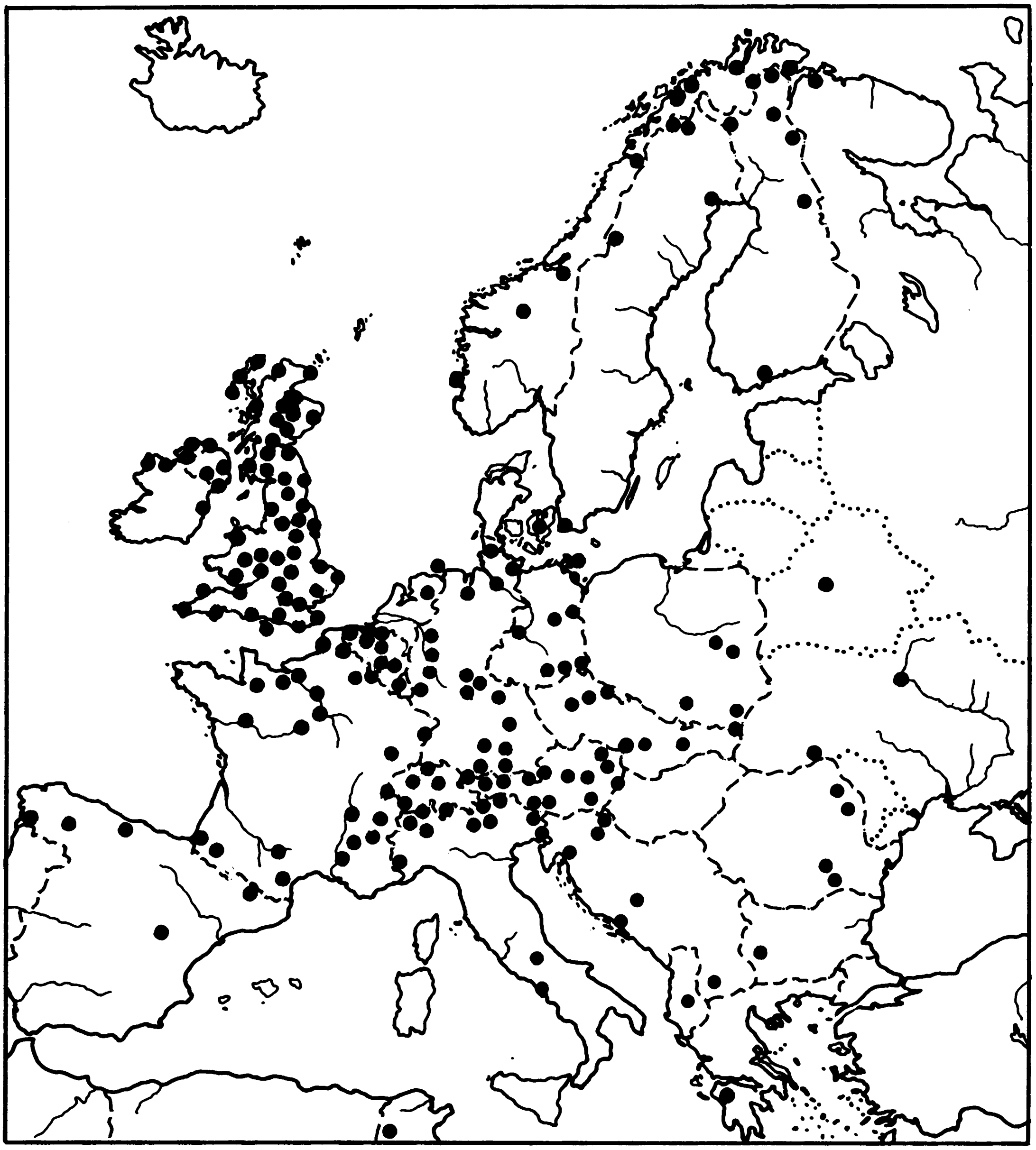


FIG. 326. Distribution of the *annularis* group in Europe.

annularis group which was first named by LeConte (1877). Both he and Herman (1983a) included some species in the *annularis* group that are herein placed in the *albonotatus* group.

Most of the species in this group are difficult to identify. For the North American species I discussed the *annularis* complex, which is a heterogeneous assemblage of unidentified species (Herman, 1983a, pp. 93–95). Although I was able to distinguish more than a dozen species I was neither able to communicate the differences nor to identify all specimens to species. At any given locality I could sort most specimens to one or more species and could even combine specimens from several localities together into homogeneous groups. However, it was impossible

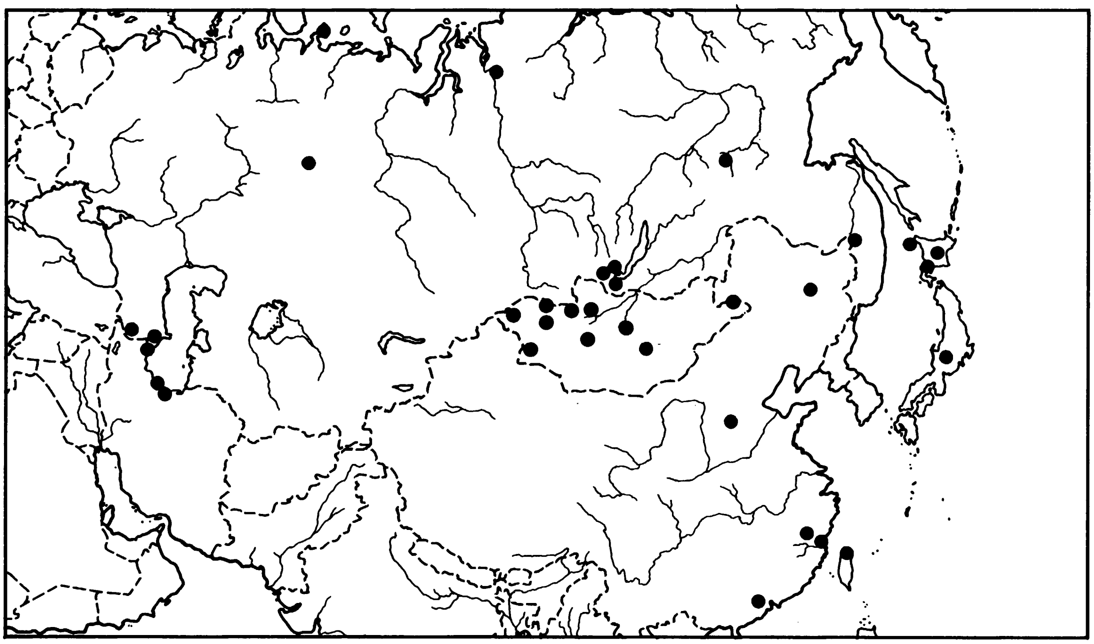


FIG. 327. Distribution of the *annularis* group in Asia.

to assign all specimens to a species and as more specimens from other areas were added to a species the heterogeneity increased.

In North America I studied more than 7000 specimens from the entire New World range of the *annularis* complex. Although I have seen fewer specimens of the Old World species in the *annularis* complex, the identical problems exist in the Eurasian material that I encountered in the North American species. What are the anatomical limits of each species? How can all specimens be clearly identified? How can the results be communicated objectively to other workers?

The species of the complex all have tridentate mandibles, rectangulate or strongly angulate basal angles of the pronotum, a midlongitudinal pronotal groove, a membranous lobe on the posterior margin of the elytra, and the absence of particularly distinguishing characters. The species of this complex are not necessarily related; they are simply the species that remain after the more easily recognized species have been set aside. Within the complex the punctation, sculpturing, size, proportions, form, color, and pubescence vary.

In North America there are eight nominal species in the complex: *annularis, breretoni, honestus, mysticus, nebulosus, sinuatus, stabilis,* and *washingtonensis.* In addition there are six or eight more undescribed species in the complex. The Eurasian species in the complex include: *annae, arcticus, bernhaueri, cordicollis, defensus, denticollis, filipes, fuscipes, ignobilis, jadarensis, obihiroensis, opacicollis, opacus, pallipes, poppiusi, rossicus, strictus, terebrans, vilis* and others.

In the literature it is difficult to detect that the Eurasian species constitute a problem. Two of the more recent keys to European species of *Bledius* (Tottenham, 1954, pp. 53, 54; Lohse, 1964, pp. 92–95) used the same characters (for species in the *annularis* complex) that I tried so unsuccessfully to use. Yet there is no indication of the variability that I found in these characters. I suspect that part of the lack of appreciation of the problems of this complex is caused by the limited number of specimens and localities and restricted geographical range evident in each collection. Were someone to study the Old World species of the complex for all of Europe and Asia and use many specimens, I predict they would discover the same difficulties that I encountered. W. O. Steel (1952, 1956) touched on the problem for *B. arcticus* and *B. opacus* (determined as *denticollis*) and for *B. denticollis* and *B. opacus.* Throughout his discussion of how to separate these species, despite his remark that *opacus* and *denticollis* are easily separated, he uses such words and phrases as: "... pronotum a little more transverse ..."; "... punctation somewhat coarser ..."; "Eyes more prominent" vs. "Eyes less prominent"; "Pronotum more narrowed behind" vs. "Pronotum less narrowed behind," etc. These differences, although they might work for the material Steel used, did not consider geographical variation. Also, it is unclear how many specimens Steel used. The variation seen in *opacus* (with the named variety *subsinuatus*) is typical of the species of this complex. The point is that a difficult problem exists that has yet to be solved for either the North American or Eurasian fauna of the *annularis* group.

Several other species seem to fall together as complexes and may be related. These include: *baudii, obsoletus, pusillus,* and *pygmaeus*; *erraticus* and *fontinalis*; *confusus* and *lativentris*; *laticollis* and *obscurus*; *littoralis* and *turgidus.* Along with *littoralis* and *turgidus* several other species might be included, namely *viriosus, newelli,* and *cedarensis.*

In the complex that includes *baudii,* the species all have rectangulate basal angles of the pronotum, have a membranous lobe on the elytral margin, and lack the pronotal midlongitudinal groove. Both *erraticus* and *fontinalis* have the same characters but are larger. The other groups are largely based on gestalt; they look similar. *Bledius littoralis* and *turgidus* are sufficiently similar that they might be conspecific.

Species Included and Material Examined

agricultor Heer Sp(FMNH); type country: Switzerland.

Austria: Innsbruck (MNHV). **Denmark:** (Hvorup? BMNH).

annae Sharp Syn,Sp(BMNH), Sp(MNHV); type country: United Kingdom.

Germany, West: Borkum Island (MNHV). **Norway:** Jaederen (MNHV). **United Kingdom:** widespread throughout Scotland and England (P. M. Hammond, BMNH, unpublished notes).

annularis LeConte L(MCZ), Sp(AMNH); type country: USA.

USA (Herman, 1983a).

apfelbecki Koch Sp(FMNH, BMNH); type country: Yugoslavia.

Yugoslavia: Krapina (BMNH).

arcticus Sahlberg H(ZMUH), Sp(BMNH, FMNH, IRSN, MNHV); type country: Finland.

Algeria: (Medjuez-Amar? IRSN). **Belgium:** Halle (IRSN). **Czechoslovakia:** Tatry Mts. (Koprova dolina ? BMNH). **Finland:** Kuusamo (FMNH); Muonio (ZMUH). **Norway:** Sør Varanger (BMNH, MNHV); Dovre (MNHV, FMNH); Lakselv (MNHV, IRSN); Fokstua (MNHV, IRSN); Kirkestuen (IRSN); Stabburselv (IRSN). **Sweden:** Abisko (BMNH). **United Kingdom:** Highland Scotland and Outer Hebrides (P. M. Hammond, BMNH, unpublished notes). **USSR:** Kultuk, Lake Baikal (IRSN); eastern Siberia (Sotka Gora ? FMNH). (Lutto River ? FMNH).

aurantius Herman H,P(AMNH); type country: USA.

California, **USA** (Herman, 1983a).

baudii Fauvel Sp(BMNH, FMNH, IRSN, MNHV); type country: ?

Algeria: (Medjez-Amar? IRSN). **Austria:** Enzersdorf (FMNH, MNHV); Stockerau (FMNH); Gesause Valley (MNHV); Grünberg (MNHV, FMNH); Kärnten (MNHV). **Belgium:** Halle (IRSN). **Bulgaria:** Samokov (MNHV). **Czechoslovakia:** Sudetic Mts. (MNHV); Teschen (FMNH, MNHV); Trencin (MNHV, FMNH); Moravia (IRSN). **France:** Vienne (MNHV); Lyon (MNHV, IRSN); Grenoble (IRSN); Merville (IRSN); Drôme (IRSN); Lyonnaise (IRSN). **Germany, West:** Oberstdorf (BMNH); Wolfratshausen (BMNH). **Hungary:** (FMNH). **Italy:** Monfalcone (FMNH); Garda (FMNH); Piemonte (MNHV, IRSN). **Poland:** (Diwinogröd? FMNH). **Switzerland:** Heitenried (MNHV); Roveredo (MNHV). Laupen (IRSN). **USSR:** (Kuzy, Podk? BMNH). **Yugoslavia:** Sarajevo (MNHV, IRSN); Ilidza (FMNH).

bernhaueri Poppius T(ZMUH), Sp(FMNH, BMNH, MNHV); type country: USSR.

Mongolia: Bajanchongor [=Bayanhongor] aimak, Changaj Mountains [= Hangay Nuruu], Somon Dzag, Dzag River (CNC).

Norway: Dovre (MNHV); Lakselv (MNHV). **Sweden:** Abisko (FMNH). **USSR:** Kanin (FMNH, MNHV, BMNH).

bicolor Casey L(USNM), Sp(AMNH); type country: USA.

California, Washington, Oregon, **USA** (Herman, 1983a).

bosnicus Bernhauer T,Sp(FMNH); type country: Yugoslavia.

Austria: Enzersdorf Lake (FMNH); Korneuburg (FMNH). **Yugoslavia:** Sarajevo (FMNH).

breretoni Hatch H(USNM); type country: USA.

USA (Herman, 1983a).

cedarensis Hatch H(USNM), Sp(AMNH); type country: USA.

Washington and Idaho, **USA** (Herman, 1983a).

chinkiangensis Bernhauer T(FMNH); type country: China.

China: Chinkiang [=Xinjiang] (FMNH).

clarus Fall L(MCZ), Sp(AMNH); type country: USA.

California, **USA** (Herman, 1983a).

clavatus Eppelsheim T(MNHV); type country: USSR.

USSR: Siberia, source of the Irkut (MNHV).

[*condensus* Kangas] no specimens examined; type country: Finland.

This species was named by Kangas (1938) for *fuscipes* as used by Finnish authors. No type was designated nor description given; it is in effect a replacement name. Presumably Finnish workers were identifying a species as *fuscipes* that was actually similar to the true *fuscipes*. With this assumption I assign *condensus* to the *annularis* group.

confusus LeConte L(MCZ), Sp(AMNH); type country: USA.

Canada and northern **USA** (Herman, 1983a).

cordicollis Motschulsky Syn(ZMUM); type country: USSR.

USSR: Dauria, Turkinsk (ZMUM).

defensus Fauvel Syn,Sp(IRSN), Sp(FMNH, BMNH, MNHV); type country: France.

Austria: Reisach (FMNH). **Belgium:** Brussels (BMNH); Mazy, Orneau Valley (IRSN); Ittrebeek, Pede Valley (IRSN); Namur (IRSN); Forêt de Soigues (IRSN). **France:** Avignon (BMNH); Lisieux (IRSN). **Germany, West:** Darmstadt (MNHV). **Poland:** Jaroslaw (MNHV). **Switzerland:** Burgdorf (IRSN). **United Kingdom:** north central England (P. M. Hammond, BMNH, unpublished notes). **USSR:** Czernowitz [=Chernovtsy] (MNHV). **Yugoslavia:** Agram [=Zagreb] (MNHV); Sarajevo (IRSN).

denticollis Fauvel T,Sp(IRSN), Sp(FMNH, BMNH, MNHV); type country: France.

Austria: Enzersdorf Lake (MNHV); Grünburg (MNHV); Korneuburg (FMNH). **Belgium:** Brussels (FMNH). **Czechoslovakia:** Brandeis [=Brandys] (FMNH); Trencin (FMNH). **France:** Lyon (MNHV, IRSN); Merlay (IRSN); Lisieux (IRSN); Rouen (IRSN); Strasbourg (IRSN); Nyons (IRSN); Elbeuf (IRSN); Chambery (IRSN). **Germany, East:** Dresden (IRSN). **Germany, West:** München (BMNH); Wolfratshausen (BMNH); Hamburg (FMNH). **Hungary:** (MNHV). **Italy:** Carnia, Tolmezzo, near Mt. Armariana (BMNH); Abruzzese (IRSN); Piemonte (IRSN); Torino (IRSN); (Castelnovale, Torr. Talvera ? IRSN). **Mongolia:** Chovd [Hovd] aimak, Bulgan Gol, 15 km N Somon Bulgan (CNC) (additional localities: Smetana, 1975). **Netherlands:** (Dinkel? BMNH). **Norway:** Malselv (BMNH). **Poland:** (Zegre? FMNH); Swider River (FMNH); Jaroslaw (IRSN). **Romania:** Bucharest (IRSN). **USSR:** source of the Irkut (BMNH, MNHV, IRSN); (Kuzy? BMNH); Dudinka (FMNH); Lake Baikal (FMNH). **Yugoslavia:** Dalmatia (FMNH); Lokve (FMNH).

erraticus Erichson Sp(BMNH, FMNH, IRSN, MNHV); type country: West Germany.

Albania: Epirus (MNHV); Elbasan (MNHV). **Austria:** Wolkersdorf (MNHV); Innsbruck (MNHV); Spittal (MNHV); Görz (MNHV); St. Gallen (MNHV); Salzburg (MNHV); Wien (FMNH); Enzersdorf Lake (FMNH); Korneuburg (FMNH); Hohentauern, Nassfeld (FMNH); Grünburg (FMNH); Liezen (FMNH); Lunz am See (FMNH); Tirol (BMNH, MNHV); Carniola (MNHV); Golling (MNHV); Kärnten (IRSN). **Belgium:** Uccle (IRSN); Forest (IRSN); Sielles (IRSN). **Czechoslovakia:** Mähren (MNHV); Teschen (FMNH); Moravia (FMNH); Brandeis [=Brandys] (MNHV). **Denmark:** Sjaeland Island

(MNHV); (Tidsvilde? BMNH). **Finland:** (Paanajarvi? MNHV, BMNH). **France:** Lyon (IRSN); Grenoble (IRSN); Boulogne sur Mer (FMNH); Orleans (IRSN). **Germany, East:** Lobau (MNHV). **Germany, West:** Berlin (MNHV); Hallstadt (BMNH); Hamburg (BMNH); Wolfratshausen (BMNH); Elberfeld [=Wuppertal] (MNHV). **Greece:** Olympia (IRSN). **Hungary:** Neusiedler Sea (MNHV). **Italy:** Piemonte (IRSN); Taufers (MNHV); Rovereto (MNHV); Garda (MNHV); Carnia, Moggio, Fella River (IRSN); Carnia, Tolmezzo, near Mt. Amariana (IRSN). **Norway:** Mälselv (MNHV); (Rundhaug? MNHV). **Poland:** Kroscienko, Dunajec River (FMNH). **Switzerland:** Geneve (IRSN, MNHV). **United Kingdom:** northern England and Ireland and southern Scotland (P. M. Hammond, BMNH, unpublished notes). **USSR:** Riazan (IRSN). **Yugoslavia:** Ilidza (MNHV, BMNH); Sarajevo (FMNH, MNHV); Podgora (FMNH).

fennicus Kangas T(ZMUH); type country: Finland.

Finland: Nuorgam (ZMUH); Yläluostari (ZMUH).

filipes Sharp Syn,Sp(BMNH); type country: United Kingdom.

Germany, West: Eckernförde (BMNH). **Sweden:** Malmö (BMNH); Skanör (BMNH).

fontinalis Bernhauer T,Sp(FMNH), Co,Sp(BMNH), Sp(IRSN, MNHV); type country: Austria.

Austria: Hohentauern, Nassfeld (BMNH, MNHV, IRSN). **Finland:** Kuusamo (FMNH). **Italy:** Champolus (BMNH). **Sweden:** Abisko (FMNH); Frostviken (FMNH).

fuscipes Rey Syn,Sp(BMNH), Sp(FMNH, IRSN, MNHV); type country: United Kingdom.

Belgium: Brussels (BMNH); St. Margriet (IRSN); Anvers (IRSN); St. Jan in Eremo (IRSN); Assenede (IRSN). **France:** Le Crotoy (BMNH). **Germany, West:** Bayern (FMNH); Bonn (FMNH), Borkum Island (MNHV). **Norway:** Lakselv (FMNH, BMNH); Malselv (FMNH); Fokstua (BMNH); Jaederen (BMNH). **Switzerland:** Silvretta (MNHV). **United Kingdom:** maritime localities throughout (P. M. Hammond, BMNH, unpublished notes).

gentilis Casey L(USNM), Sp(AMNH); type country: USA.

Western **USA** (Herman, 1983a).

gracilis Casey L(USNM), Sp(AMNH); type country: USA.

California and Oregon, **USA** (Herman, 1983a).

habrus Herman H,P(AMNH); type country: Canada.

Northwestern **North America** (Herman, 1983a).

honestus Casey L(USNM), Sp(AMNH); type country: USA.

USA (Herman, 1983a).

ignobilis Eppelsheim Co(MNHV); type country: USSR.

USSR: Caucasus, Kura River (near Michialow? MNHV).

jadarensis Helliesen Syn(STM); type country: Norway.

Norway: (STM).

japonicus Bernhauer T,Sp(FMNH), Sp(BMNH); type country: Japan.

China: Jujien, Shaowu (BMNH, FMNH). **Japan:** Takakijama (FMNH).

jucundus Herman H,P(AMNH); type country: USA.

Rocky Mountains, **USA** (Herman, 1983a).

kutsae Kangas T(ZMUH); type country: Finland.

Finland: Salla, Kutsa (ZMUH).

laticollis LeConte L(MCZ), Sp(AMNH); type country: USA.

California, Oregon, Washington, **USA** (Herman, 1983a).

lativentris Jansson Sp(FMNH, BMNH, MNHV); type country: Sweden.

Sweden: Torneträsk (BMNH); Abisko (BMNH, MNHV).

littoralis Heer Sp(BMNH, FMNH, IRSN, MNHV); type country: Switzerland.

Austria: Lofer (FMNH, MNHV); Innsbruck (MNHV); Feldkirsch (MNHV); Zillertaler Alpen (MNHV); Karawanken (MNHV); Spittal (MNHV); Hohen Tauern, Nassfeld (FMNH); Steiermark (FMNH). **Belgium:** Halle (FMNH). **France:** Albertville (IRSN). **Germany, East:** Eisleben (MNHV). **Germany, West:** Hallstadt (BMNH). **Italy:** Aosta (BMNH). **Mongolia:** (IRSN); Chövsgol [=Hövsgol] aimak, 7 km WSW Somon Cecerleg [=Tsetserleg], Tesijn [=Tesiyn] Gol (CNC); Uvs aimak, Somon Öndörchangaj (CNC); Uvs aimak, Baruunturuun Gol, Baruunturuun (CNC). **Norway:** Stjørdal (MNHV); Saltdal (MNHV); Kirkenstuen (MNHV). **Poland:** Warsaw (BMNH); Jaroslaw (IRSN). **Pyrenees:** (MNHV, BMNH, IRSN). **Romania:** Moldavia (IRSN). **Switzerland:** Büren, Mt. Bern (MNHV); Stalden (MNHV). **USSR:** Slyudyanka River, near Lake Baikal (IRSN); Caucasus (IRSN); Siberia, Lake Baikal (FMNH, MNHV, BMNH); east Siberia (Werchne Udinsk ? MNHV); Minsk (IRSN) Czernowitz [=Chernovtsy] (MNHV); Aldan (BMNH, MNHV).

longulus Erichson Sp(FMNH, BMNH, IRSN, MNHV); type country: West Germany.

Austria: Wien (MNHV, FMNH); Kärnten (MNHV); Grünberg (FMNH, Korneuburg (FMNH); Hohen Tauern, Nassfeld (FMNH); Hohen Tauern, Koetschach (FMNH); Liezen (FMNH); Stockerau (FMNH); Lake Enzersdorf (FMNH); Horn (FMNH); Hohen Tauern (BMNH); (Tullnerbach? MNHV). **Belgium:** Angre (IRSN); Forest (IRSN); Uccle (IRSN). **Czechoslovakia:** Teschen (FMNH); Brandeis [=Brandys] (MNHV). **France:** Marly (IRSN); St. Julien (IRSN); Lyon (IRSN); Normandie (MNHV). **Germany, East:** Rügen Island (FMNH). **Germany, West:** Elberfeld [=Wuppertal] (IRSN); Darmstadt (MNHV, FMNH); Borkum Island (MNHV, FMNH); Krefeld (FMNH); Lichterfelde (FMNH); Ulm (IRSN). **Hungary:** Banat (MNHV). **Norway:** Haugesund (MNHV); (Rundhaug? MNHV). **Poland:** Jaroslaw (IRSN); Krakow (MNHV). **Romania:** Sinaia (IRSN). **Spain:** Potes (IRSN). **Sweden:** Alvsbyn (FMNH). **Switzerland:** Valais, Mattmark Lake (IRSN); Lucern (MNHV); Heitenried (MNHV). **United Kingdom:** widespread (P. M. Hammond, BMNH, unpublished notes). **Yugoslavia:** Dalmatia (FMNH); Krapina (FMNH).

melanocolus Herman H,P(AMNH); type country: USA.

Southern California, **USA** (Herman, 1983a).

monticola Casey L(USNM), Sp(AMNH); type country: USA.

California and Oregon, **USA** (Herman, 1983a).

mysticus Fall L(MCZ); type country: USA.

USA (Herman, 1983a).

naius Herman H(CNC); type country: USA.

Arizona, **USA** (Herman, 1983a).

nebulosus Casey L(USNM), Sp(AMNH); type country: USA.

USA (Herman, 1983a).

newelli Hatch H(USNM), Sp(AMNH); type country: USA.

Washington and Oregon, **USA** (Herman, 1983a).

obihiroensis Nakane H(TNC); type country: Japan.

Japan: Hokkaido, Obihiro (TNC).

obscurus Motschulsky Sp(FMNH, MNHV); type country: Mongolia.

Mongolia: Archangaj [=Arhangay] aimak, Changaj [=Hangay] Mountains near Somon Urd Tamir (CNC); Cojbalsan [=Dornod] aimak, Somon Chalchin [=Halhïn] Gol (CNC) (additional localities: Smetana, 1975). **USSR:** Ussur River (Kassa Kewitsch ? MNHV, FMNH).

obsoletus Fauvel Syn,Sp(IRSN), Sp(FMNH, MNHV); type country: France.

France: Albi (IRSN); Pau (IRSN). **Pyrenees:** (IRSN, MNHV).

opacicollis Eppelsheim Co,Sp(MNHV); type country: USSR.

Mongolia: Bajan-Ölgij [=Bayanölgiy] aimak, Chavcalyn Gol valley, 24 km W Somon Cagannuur [=Tsaganuur] (CNC). **USSR:** Siberia, source of Irkut (MNHV).

opacus (Block) Sp(BMNH, FMNH, IRSN, MNHV); type country: Germany.

Austria: Horn (FMNH); Korneuburg (FMNH); Stockerau (FMNH); Lake Enzersdorf (FMNH); Grünberg (FMNH, MNHV); Lunz (FMNH); Lofer (FMNH); Krems (FMNH); Floridsdorf (FMNH): Wien (MNHV); Wienerwald (MNHV); Kamp Valley (MNHV); Weikendorf (MNHV); Feldkirch (MNHV). **Belgium:** Anvers (IRSN); Braine l'Alleud (IRSN); Sielles (IRSN); Uccle (IRSN); Forest (IRSN); La Hulpe (IRSN). **Bulgaria:** Samokov (MNHV). **China:** Yunan (IRSN). **Czechoslovakia:** Brandeis [=Brandys] (MNHV); Jungbunzlau (MNHV); Modrany (MNHV); Nymburk (MNHV). **Den-**

mark: (MNHV). **Finland:** Ivalo (FMNH); Helsinki (FMNH). **France:** Villier (FMNH); Lille (IRSN); St. Jean d'Luz (IRSN); Nyons (IRSN); Villeneuve sur Lot (IRSN); Grenoble (MNHV). **Germany, East:** Wechselburg (FMNH, MNHV); Velten (FMNH). **Germany, West:** Hamburg (MNHV); Borkum Island (MNHV); Berlin (MNHV). **Hungary:** (FMNH); Neusiedler Sea (MNHV); Herkulesbad (MNHV). **Iran:** Elburz Mts. (FMNH). **Italy:** Garda Sea (FMNH, MNHV); Fucine (FMNH); Bolzano (IRSN); L'Aquila (IRSN); Carnia, Moggio, Fella River (IRSN); Carnia, Tolmezzo (IRSN); Camonica Valley (MNHV). **Mongolia:** Central [=Töv] aimak, Kerulen River, 40 km W Somon Bajandelger (CNC); Chövsgol [=Hövsgöl] aimak, 8 km N Somon Burenchaan, Delgermörön River (CNC); Uvs aimak, Baruunturuun (Additional localities: Smetana, 1975). **Norway:** Haugesund (MNHV). **Poland:** Swider River (FMNH); Bransberg [=Braniewo] (MNHV). **Romania:** Brosteni (IRSN). **Spain:** Ponferrada (FMNH); Cangas (IRSN); Catalonia, Seo de Urgel (IRSN); Albarracin (MNHV). **United Kingdom:** widespread (P. M. Hammond, BMNH, unpublished notes). **USSR:** Kiyev (FMNH); Caucasus, Lenkoran (IRSN); Czernowitz [=Chernovtsy] (MNHV). **Yugoslavia:** Krapina (FMNH); Sarajevo (FMNH); Titel (IRSN); Treska River (MNHV); Sarajevo (MNHV).

osiris Normand Sp(MTC); type country: Tunisia.

Tunisia: Le Kef (MTC).

pallipes (Gravenhorst) Sp(BMNH, FMNH, IRSN, MNHV); type country: Germany.

Austria: Korneuburg (FMNH); Horn (FMNH); Graz (MNHV). **Belgium:** Seilles (IRSN); Mazy, Orneau Valley (IRSN); Anderlecht (IRSN); Grimbergen (IRSN); Anvers (IRSN); Angre (IRSN); Uccle (IRSN); Auderghem (IRSN); La Hulpe (IRSN); Jette (IRSN); Woluwe (IRSN); Brusseghem (IRSN); Berg (IRSN); Schaerbeek (BMNH). **Czechoslovakia:** Trencin (FMNH). **Finland:** Ivalo (FMNH). **France:** Valmondois (BMNH); Achères (BMNH); Lille (IRSN); Paris (IRSN). **Germany, West:** Huntlosen (FMNH); Borkum Island (FMNH); Darmstadt (FMNH); Travemünde (IRSN). **Netherlands:** Ommen (FMNH). **Norway:** Malselv (MNHV); Lakselv (IRSN). **USSR:** Perm (FMNH); Dudinka (IRSN); Caucasus (IRSN); Minsk (IRSN).

parisii Koch H(MSNM); type country: Yugoslavia.

Yugoslavia: Arbe [=Rab] Island (MSNM).

pechlaneri L. Benick Sp(GLC); type country: Germany.

Italy: S. Tirol, Brixen (GLC).

This species was sent to me by Dr. Gustav Lohse who informed me in a letter that *pechlaneri* is a synonym of *secessus*. Since this synonymy has not been published, I am listing these two names as separate species for purposes of this paper. My having listed them separately is not intended to dispute Dr. Lohse's assessment of the species.

persimilis Fall H(MCZ), Sp(AMNH); type country: USA.

California, **USA** (Herman, 1983a).

phytosinus LeConte T(MCZ), Sp(AMNH); type country: USA.

California, **USA** (Herman, 1983a).

poppiusi Bernhauer T(FMNH, ZMUH), Sp(BMNH, IRSN, MNHV, ZMUH); type country: USSR?

Finland: Ivalo (BMNH). **Norway:** Karasjok (MNHV); Tromsdalen (IRSN). **Sweden:** Abisko (BMNH).

pusillus Erichson Sp(BMNH, FMNH, IRSN, MNHV); type country: Germany.

Austria: Ulrichskirchen (IRSN). **Czechoslovakia:** Praha (MNHV). **France:** (FMNH); Bouray (IRSN); Poissy (IRSN); St. Germain (IRSN); Fontainebleau (IRSN); Paris (BMNH). **Germany, West:** Wimpfen (MNHV). **Italy:** Macugnaga, Mt. Rosa (FMNH). **Yugoslavia:** Dalmatia (IRSN).

pygmaeus Erichson Sp(FMNH, IRSN, MNHV); type country: West Germany.

Austria: Innsbruck (MNHV); Marchfeld (MNHV); Wien (MNHV); Lech Valley (MNHV). **Belgium:** Rixensart (IRSN). **Czechoslovakia:** Mutenice (BMNH). **France:** (FMNH); Anjou (IRSN); Carcassonne (IRSN); St. Laurent du Pont (IRSN); Fontainebleau (MNHV); Paris (MNHV). **Germany, East:** Oderburg (BMNH). **Ger-**

many, West: Darmstadt (FMNH); München (MNHV, FMNH); Wimpfen (IRSN); Bensheim (MNHV); Frankfurt (BMNH). **Italy:** Piemonte (IRSN). **Pyrenees:** (IRSN). **Switzerland:** Laupen (IRSN); Aarau (IRSN). **Yugoslavia:** Dalmatia (MNHV, IRSN).

rossicus Bernhauer and Schubert Sp(ZMUH); type country: USSR.

[Locality on label illegible.]

ruficornis LeConte L(MCZ), Sp(AMNH); type country: USA.

Transcontinental **USA** and **Canada** (Herman, 1983a).

rugosulus Eppelsheim Co(MNHV); type country: USSR.

USSR: Siberia, source of Irkut (MNHV).

secessus Bondroit Sp(BMNH, MNHV); type country: Italy.

Germany, West: Niederbayern (Vilahofen? BMNH); Niederbayern (Gelbersdorf? BMNH). **Italy:** Brixen [=Bressanone] (MNHV).

sinuatus LeConte L(MCZ), type country: USA.

USA (Herman, 1983a).

stabilis Casey L(USNM); type country: USA.

USA (Herman, 1983a).

strictus Fauvel Syn,Sp(IRSN), Sp(FMNH, BMNH, MNHV); type country: ?

Austria: Innsbruck (FMNH, MNHV); Haiming (BMNH); Admont (MNHV). **Bulgaria:** Izvor (FMNH). **Italy:** Valdieri, Piemonte (IRSN). **Switzerland:** Martigny-ville (IRSN).

suturalis LeConte L(MCZ), Sp(AMNH); type country: USA.

Western two-thirds of **Canada** and **USA** (Herman, 1983a).

terebrans (Schiødte) Sp(BMNH, FMNH, IRSN, MNHV); type country: Denmark.

Austria: Wiener Wald (MNHV). **Belgium:** Beverlo (FMNH, MNHV); Nieuwpoort (BMNH, IRSN); Genval (IRSN). **Germany, West:** Bensberg (FMNH); Kordel (FMNH); Berlin (MNHV, IRSN). **Norway:** Sør Varanger (FMNH). **Sweden:** (BMNH). **United Kingdom:** scattered throughout (P. M. Hammond, BMNH, unpublished notes). **USSR:** Minsk (IRSN).

turgidus Casey L(USNM); Sp(AMNH); type country: USA.

Transcontinental **USA** and **Canada** (Herman, 1983a).

vilis Mäklin Sp(BMNH, FMNH, IRSN, MNHV); type country: Finland.

Finland: (MNHV). **Germany, West:** Oldenburg (BMNH, MNHV); Huntlosen (IRSN, FMNH). **Netherlands:** Overijssel (BMNH). **Norway:** Sør Varanger (BMNH, MNHV, IRSN). **USSR:** Petsamo [=Pechenga] (BMNH).

villosus Casey L(USNM), Sp(AMNH); type country: USA.

Oregon and California, **USA** (Herman, 1983a).

viriosus Herman H,P(AMNH); type country: USA.

Transcanadian and north central **USA** (Herman, 1983a).

vitaensis Bernhauer T(FMNH); type country: Japan.

Japan: (Vita? FMNH).

washingtonensis Hatch H(USNM); type country: USA.

USA (Herman, 1983a).

Undetermined.

China: Heilongjiang, Charbin (BMNH); Foochow [=Fuzhou] (FMNH). **Iran:** Mazandaran, 11 mi. S Chalus (USNM). **Italy:** Patria Lake (MNHV); Fiume Sesia, Carpignano (MNHV). **Japan:** Rishiri Island, Himenuma (YSC); Hokkaido, Ishikari (YSC). **Mongolia:** (Shangai? MNHV); Uvs aimak, Baruunturuun Gol, Baruunturuun (CNC; misidentified as *transcaspicus*). **Taiwan:** Taipei Hsien (Yehlin Beach ? BPBM). **USSR:** Lenkoran (MNHV). **Vietnam:** Saigon [= Ho Chi Minh] (IRSN).

22. *debilis* group

Figures 10, 328–335, 676–677

DIAGNOSIS: This group is separated from all others by the presence of a complete pronotal marginal bead and elytral epipleural ridge; presence of the protergosternal suture (fig. 331), the setigerous prosternal pit, the four segmented tarsi, the fused gular sutures, and the emarginate eighth tergum; and the absence of a labral incision (fig. 330). The most similar group is the *basalis* group. The *debilis* group has a protergosternal suture and an unreflexed labral margin (fig. 330); the *basalis* group lacks the suture and the anterior margin of the labrum is reflexed (figs. 338, 341).

DESCRIPTION: Supraantennal ridge low, not enlarged, and without horns. Head without subantennal pockets; midbasal horn absent; postocular lateral carina absent. Clypeal margin not reflexed; anterior margin with two tubercles; clypeal middle without tubercles, spines, or ridges. Gular sutures fused. Labrum (fig. 330) with anterior margin truncate; anterior margin not reflexed; median incision absent; dorsal surface flat, without midlongitudinal impression. Epipharyngeal lobe moderately long; dorsal surface with one long seta; median processes with rounded, slightly clavate, unlobed apices; lateroapical processes numerous, slender, and unbranched. Labial palps (fig. 328) with second segment shortest, first segment longest, third segment of intermediate length; first segment thickest; first segment with three setae, second with one seta. Submentum not excavated. Mentum (fig. 328) trapezoidal and transverse; setae evenly distributed over surface. Hypopharynx with lateral rows of setae gradually convergent toward base; basal setae arranged in bisinuate row; median setae of basal row large and thick; basal setae not on plate; central row of setae dense distally and sparse proximally; disk with setae on anterior portion; disk with short cuticular processes arranged in palmate groups and covering surface; coronal pegs scattered over median portion. Prementum (fig. 328) with three sclerites, one medial and two lateral. Galea with fanlike rows of setae on apex; ventral surface without setae; dorsomedial edge with lobe. Mandibles tridentate (fig. 329).

Pronotal horn absent. Marginal bead present and complete. Ptergosternal suture present but weakly developed anteriorly (fig. 331). Procoxal fissure closed or narrowly open. Protrochantin concealed or narrowly exposed. Prosternal process elongate. Prosternal setigerous pit present; pit with cluster of pores behind setae; prosternal margin entire, without notch. Elytral epipleural ridge present and complete; posterior margin with membranous lobe.

Tarsi four segmented. Protibia with two rows of spinelike setae and others scattered between rows (fig. 333).

Abdominal tergum VII with fine fringe on posterior margin. Tergum VIII with emarginate posterior margin; margin not serrate. Tergum IX with glandular canal widely open dorsally. Tergum X with slender struts on anterior margin.

Aedeagus (fig. 332) with parameres. Parameres broad and with median surface membranous and extending beyond apex of median lobe. Median lobe bulbous basally, apical portion flattened; ventral surface midlongitudinally divided.

Spermatheca (fig. 334) tripartite. Receptacle divided by accordion tube into two parts; basal part membranous and larger than lightly sclerotized distal part; distal and basal parts each encircled by delicate brimlike ridge; distal part without invagination. Spermathecal gland sclerotized; of irregular shape and with irregular surface.

DISTRIBUTION AND HABITAT: Most of the localities for this group are along the coasts of southern Europe and northern Africa (fig. 335). A few localities are inland. I have examined some specimens from unspecified places in Norway but these may be erroneous records.

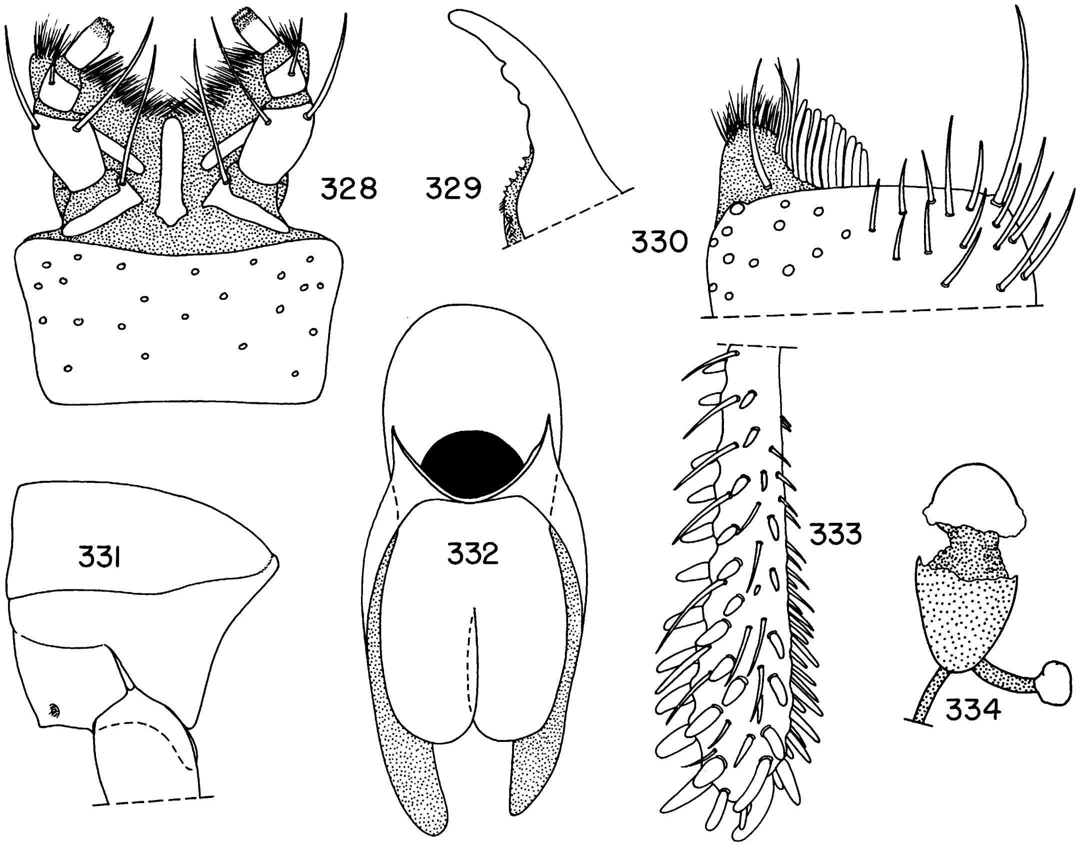
The species of this group may be found in saline habitats since most of the localities are adjacent to the Mediterranean Sea or Atlantic Ocean or are near salt flats or lakes.

DISCUSSION: The two species that constitute this group are two of the many that were removed from *Dicarenus* (table 9).

Species Included and Material Examined

debilis Erichson Sp(BMNH, FMNH, IRSN, MNHV); type country: USSR.

Algeria: Oran: Aïn Sefra (IRSN); Bone [='Annaba] (IRSN; BMNH). **Gibraltar:** (BMNH). **Italy:** Sicily, Trapani (IRSN); Messina (MNHV; FMNH). **Morocco:** Mogador [=Essaouira] (MNHV); Tanger (FMNH); (Esmir? IRSN). **Norway:** (MNHV; doubtful locality). **Portugal:** (MNHV). **Spain:** Andalusia Region (IRSN; FMNH); Algeciras (IRSN); Barcelona (IRSN); Cadiz (FMNH); San Roque District (BMNH). **Spain-France:** Pyrenees (MNHV). **Tunisia:** Gafsa Oasis (FMNH); Mateur (IRSN); Sousse (IRSN; BMNH);



FIGS. 328–334. The *debilis* group. *Bledius debilis*. **328.** Labium, setae removed from mentum. **329.** Mandible, right. **330.** Labrum, left setae and right epipharyngeal lobe removed. **331.** Prothorax, lateral view, setae removed. **332.** Aedeagus, dorsal view. **333.** Protibia. **334.** Spermatheca.

Teboursouk (IRSN); Tunis (BMNH). **Yugoslavia:** Sarajevo (MNHV).

transversemaculatus Koch Co(FMNH); type country: Egypt.

Egypt: Ismailia [=Ismâ'iliya] (AMNH).

23. *basalis* group

Figures 9, 54, 336–353, 548–553, 678–683

DIAGNOSIS: The most distinctive features of this group are the reflexed anterior margin of the labrum (figs. 338, 341) and the absence of a median incision on the labrum (fig. 341). Those characters will separate the group from all others. The anterior labral margin of the *Bledius melanocephalus* group is feebly reflexed (fig. 341). Other useful features are the complete pronotal marginal bead (fig. 339) and elytral epipleural ridge, the absence of the protergosternal suture (fig. 339), the closed procoxal fissure (fig. 339), the fused gular sutures, the presence of a setigerous pit on the prosternum, and the emarginate posterior margin of tergum VIII (fig. 344).

DESCRIPTION: Supraantennal ridge low, not enlarged, and without horns. Head without subantennal pockets; midbasal horn absent; postocular lateral carina absent. Clypeal margin not reflexed; anterior margin with two tubercles; clypeal middle without tubercles, spines, or ridges. Gular sutures fused. Labrum (figs. 338, 341) with anterior margin sinuotruncate to entire and broadly rounded; anterior margin strongly to moderately strongly reflexed (figs. 338, 341); median incision absent (fig. 341); dorsal surface flat, without midlongitudinal impression. Epipharyngeal lobe moderately long; dorsal surface with one long seta or one long and one minute seta; median processes with rounded, slightly clavate or simple, unlobed apices; lateroapical processes numerous, slender, and simply branched or unbranched. Labial palps (fig. 337) with second segment shortest, first segment longest, third segment intermediate; first segment thickest; first segment with two setae; second segment with one seta. Submentum not excavated. Mentum trapezoidal and transverse; setae sparsely and evenly distributed over surface. Hypopharynx (figs. 548–553) with lateral rows of setae gradually convergent toward base; basal row of setae reduced to two large, stout setae; basal setae on plate; central row of setae dense distally and medially, absent proximally; disk with many setae on apical portion; disk with long slender cuticular processes arranged in palmate groups or short slender processes covering surface; coronal pegs scattered on midbasal part of disk. Prementum with three or four sclerites, one medial, two lateral, and one basal; basal sclerite weakly sclerotized or absent. Galea with fanlike rows of setae on apex; ventral surface without seta; dorsomedial edge with lobe. Mandibles (figs. 336, 343) edentate, bidentate, or tridentate.

Pronotal horn absent. Marginal bead present and complete. Protergosternal suture absent (fig. 339). Procoxal fissure closed (fig. 339). Protrochantin concealed. Posternal process elongate. Prosternal setigerous pit present (figs. 678, 679, 682); pit with cluster of pores behind setae (fig. 680); prosternal margin entire, without notch anterior to procoxa. Elytral epipleural ridge present and complete; posterior margin with or without membranous lobe.

Tarsi four segmented. Protibia with two rows of spinelike setae and others scattered between rows.

Abdominal tergum VII with fine fringe on posterior margin. Tergum VIII with strongly (fig. 344) to weakly emarginate posterior margin (some individuals of *basalis* and *melanocephalus* with truncate margin); margin not serrate. Tergum IX with glandular canal widely to narrowly open dorsally. Tergum X without struts on anterior margin.

Aedeagus (figs. 346–351) with parameres. Parameres broad with median surface membranous or slender with sclerotized median surface; parameres extending beyond apex of median lobe or short and not reaching apex of median lobe (fig. 348). Median lobe bulbous basally, apical portion flattened; ventral surface midlongitudinally divided.

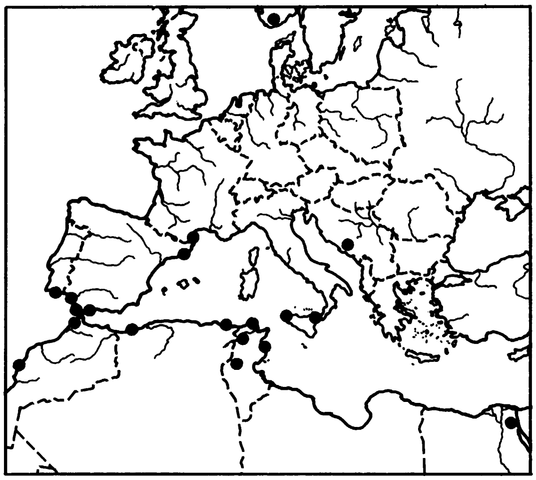
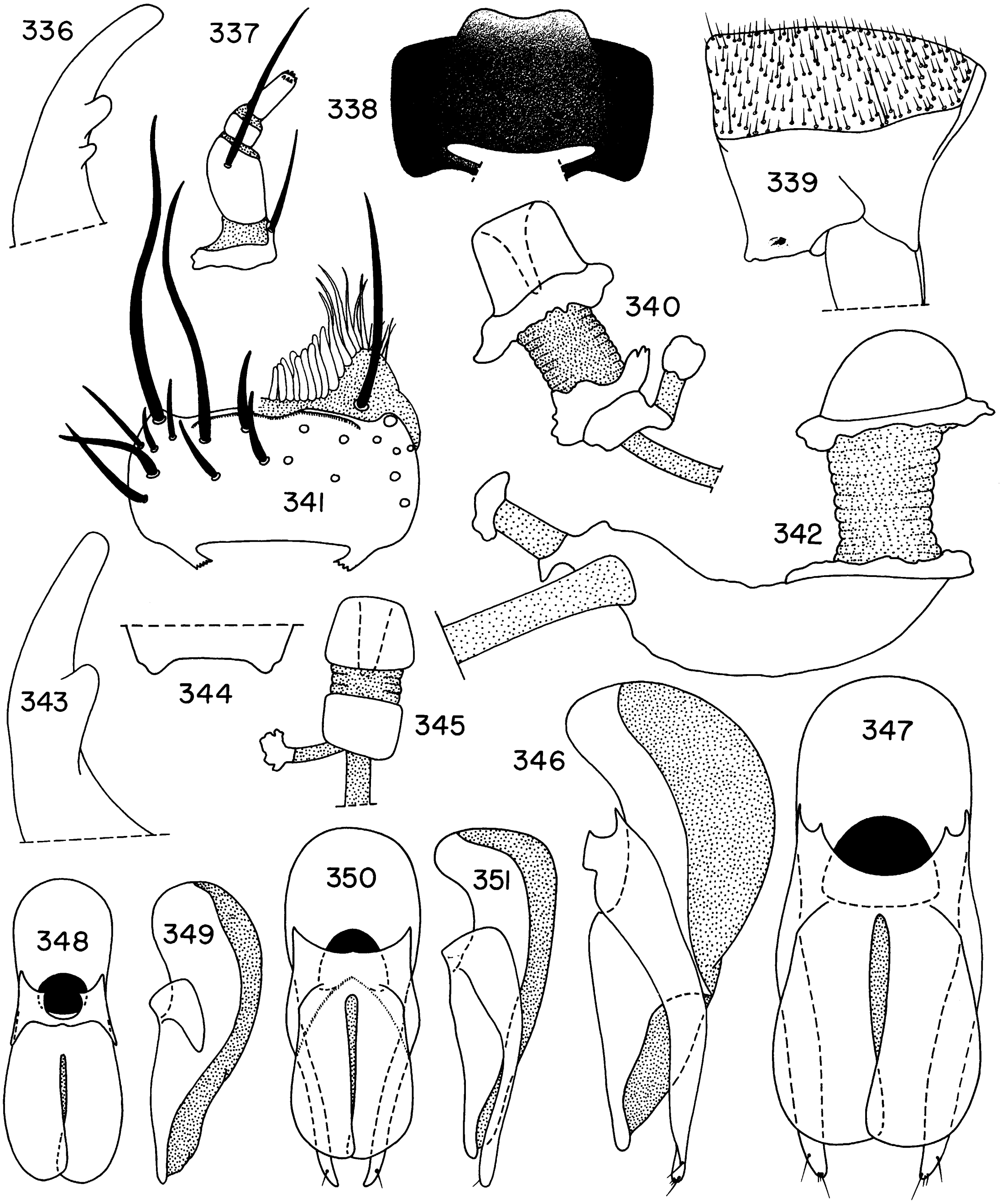


FIG. 335. Distribution of the *debilis* group in Europe and North Africa.

Spermatheca tripartite (figs. 340, 345). Receptacle sclerotized and divided by accordion tube into two parts; distal and basal parts subequal in size or with basal or distal part larger; basal and distal parts each encircled by brimlike ridge or without such ridges; distal part with invagination. Spermathecal gland sclerotized, or irregular shape, and with irregular surface.

DISTRIBUTION AND HABITAT: Most of the species are known only from saline habitats along the seacoasts of North America (fig. 352), Europe, and northern Africa (fig. 353). *Bledius dimidiatus* is found only in inland, nonsaline habitats in Florida and some European species have been taken inland as well as near the coast. *Bledius melanocephalus* is found along freshwater rivers and streams in the central portion of North America. Six species are in the Old World and eight are found in the New World.

DISCUSSION: This species group was first separated by LeConte (1877) who called it the *cordatus* group. Herman (1972) used *basalis* to designate the same group and revised 8 of the 14 species now in it. Four Old World species, *doderoi, fergussoni, gradensis,* and *subniger* were formerly part of *Dicarenus* (table 9). The type species of *Dicarenus, arenarius* (=*fergussoni*) is part of the *basalis*



FIGS. 336–351. The *basalis* group. **336.** Mandible, left (*opaculus*). **337.** Labial palpus (*melanocephalus*). **338.** Labrum (*opaculus*). **339.** Prothorax, lateral view (*melanocephalus*). **340.** Spermatheca (*dimidiatus*). **341.** Labrum, right setae and left epipharyngeal lobe removed (*melanocephalus*). **342.** Spermatheca (*cordatus*). **343.** Mandible, left (*melanocephalus*). **344.** Tergum VIII, apex (*basalis*). **345.** Spermatheca (*melanocephalus*). **346.** Aedeagus, lateral (*neglectus*). **347.** Aedeagus, dorsal (*neglectus*). **348.** Aedeagus, dorsal (*melanocephalus*). **349.** Aedeagus, lateral (*melanocephalus*). **350.** Aedeagus, dorsal (*basalis*). **351.** Aedeagus, lateral (*basalis*).

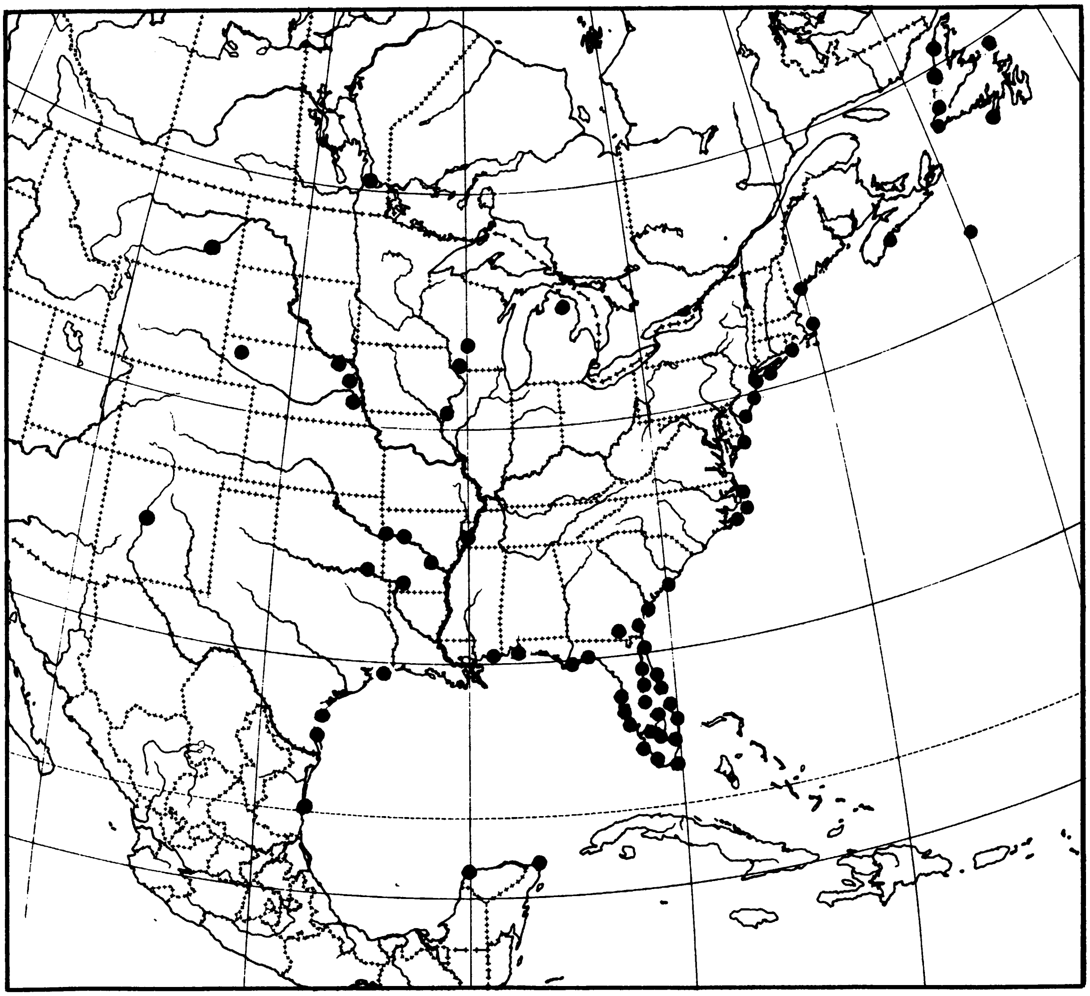


FIG. 352. Distribution of the *basalis* group in North America.

group. Two species, *minor* and *gyllenhalii,* had not been part of an infrageneric group.

Previously I had segregated *Bledius melanocephalus* as a group because it lacks a membranous lobe on the posterior margin of the elytron, has short parameres, and lacks setae on the second segment of the labial palps (Herman, 1976). Subsequently collected specimens reveal that some individuals do have a small membranous lobe on the posterior elytral margin. Further, I overlooked a small seta on the second segment of the labial palps. *Bledius melanocephalus* lacks the brimlike ridges on the spermatheca (fig. 345) that are evident in the *basalis* group, has fewer mandibular denticles, and is found only in freshwater habitats. The species, however, is clearly related to those in the *basalis* group and without some distinct external differences I am reluctant to continue recognizing it as separate.

Species Included and Material Examined

basalis LeConte L(MCZ), Sp(AMNH); type country: USA.

Eastern and southern coastal USA (Herman, 1972, 1983a).

cordatus (Say) Sp(AMNH); type country: USA.

Eastern coastal **USA** (Herman, 1972, 1983a).

dimidiatus LeConte L(MCZ), Sp(AMNH); type country: USA.

Southeastern **USA** (Herman, 1972, 1983a).

doderoi Bondroit Sp(FMNH, BMNH, NHMV); type country: Greece.

Greece: Kikladhes, Naxos (BMNH, MNHV). **Italy:** Venezia Prov. (BMNH, MNHV); Riccione (MNHV); (Lucania, Metaponto Lido ? MNHV).

fergussoni Joy Sp(FMNH, BMNH, IRSN, NHMV); type country: United Kingdom.

Belgium: Anver (IRSN). **France:** LeCrotoy (IRSN); Dunkerque (IRSN); Calais (IRSN); Morlaix (IRSN, MNHV); Carteret (IRSN); Cette [=Sète] (IRSN); Landes Dept. (IRSN). **Germany, West:** Borkum Island (MNHV). **Morocco:** (Esmir?) (TRSN). **Norway:** Jaederen District (MNHV). **Poland:** Swinemunde [=Swinoujscie] (IRSN, FMNH); Stettin [=Szczecin] (BMNH). **Romania:** Sulina (BMNH). **Spain:** Andalusia, Tarifa (IRSN). **Sweden:** Öland Island (MNHV). **Tunisia:** Mateur (IRSN); Tabarka (MNHV). **United Kingdom:** western coast on Kintyre peninsula in Strathclyde south to Channel coast north on eastern coast to Grampian, on Outer Hebrides, and from Londonderry, Down, and Cork in Ireland (P. M. Hammond, BMNH, unpublished notes). **USSR:** Sarepta (IRSN).

gradensis Bernhauer T,Co,Sp(FMNH), Co(BMNH); type country: Italy.

Italy: Grado (FMNH); Montfalcone [=Monfalcone] (BMNH).

[*gyllenhalii* Laporte] no specimens examined, type country: Sweden.

This species was named by Laporte (1840) for *arenarius* var. *b* reported by Gyllenhal (1810). The species seems never to have been mentioned again. I made no effort to find the type of "var. *b*" and place *gyllenhalii* in the *basalis* group solely because it was originally cited as a variation of *arenarius* (=*fergussoni*), a member of the *basalis* group.

melanocephalus (Say) Sp(AMNH); type country: USA.

Central **USA** (Herman, 1972, 1983a).

minor Mulsant and Rey Sp(FMNH, BMNH, NHMV); type country: France.

Albania: Valona [=Vlorë] (BMNH). **Italy:** Riccione (MNHV).

neglectus Casey L(USNM), Sp(AMNH); type country: USA.

Eastern coastal **USA** and **Canada** (Herman, 1976).

opaculus LeConte L(MCZ), Sp(AMNH); type country: USA.

Northeastern coastal **USA** and **Canada** (Herman, 1972, 1983a).

subniger Schneider Sp(FMNH, BMNH, NHMV); type country: West Germany.

Germany, West: Borkum Island (MNHV). **Spain:** San Roque District (BMNH). **Tunisia:** Soliman (MNHV). **United Kingdom:** Rum Island and Cumbria on western coast south to Channel coast and north on eastern coast to Grampian and in Ireland on coast of Waterford and Kerry (P. M. Hammond, BMNH, unpublished notes).

thinopus Herman H,P,Sp(AMNH); type country: USA.

Southern coastal **USA** (Herman, 1976).

turbulentus Casey L(USNM), Sp(AMNH); type country: USA.

Mexico and southern coastal **USA** (Herman, 1972, 1983a).

Undetermined.

Denmark: Röm Island (FMNH). **France:** Brittany, Morgat (BMNH). **Germany, East:** Rügen Island (FMNH). **Germany, West:** Berlin (FMNH); Nordernay (FMNH). **Libya:** Tripoli (FMNH). **Poland:** Swider (FMNH); Zegre (FMNH). **Sweden:** Skane Region.

24. *infans* group

Figures 10, 354–360

DIAGNOSIS: The *infans* group can be separated from all other groups except the *forcipatus* group by the absence of the pronotal lateral marginal bead, elytral epipleural ridge, and midlongitudinal labral incision; and by the truncate posterior margin of tergum VIII. The *infans* group has a short, carinate prosternal process and is found only in the Old World, whereas the New World *forcipatus* group has an elongate prosternal process (fig. 382). The aedeagus of the *forcipatus* group is more heavily sclerotized and the ventral surface is sclerotized; in the *infans* group the aedeagus (figs. 354, 355) is more lightly sclerotized and the ventral surface is membra-

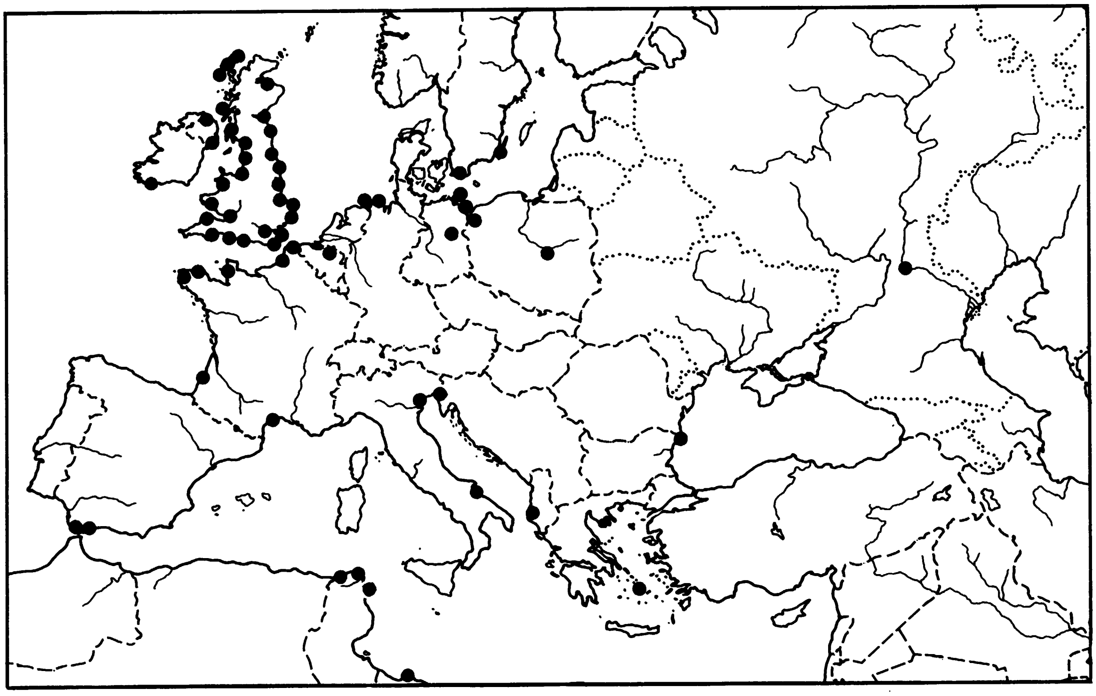


FIG. 353. Distribution of the *basalis* group in Europe and North Africa.

nous. The spermatheca is bipartite in both groups but in the *forcipatus* group it is spherical and heavily sclerotized (fig. 386); in the *infans* group it is moderately heavily sclerotized, and more elongate (fig. 357) than in the *forcipatus* group.

Other characters useful for recognition of the *infans* group include the absence of the protergosternal suture, presence of the prosternal setigerous pit, open procoxal fissure, absence of a membranous lobe on the posterior margin of the elytron, and the three-segmented tarsi.

DESCRIPTION: Supraantennal ridge low, not enlarged, and without horns (subantennal pocket—no data). Midbasal cephalic horn absent; postocular lateral carina of head absent. Clypeal margin not reflexed and without tubercles; clypeal middle without tubercles, spines, or ridges. Gular sutures fused. Labral margin truncate and not reflexed; median incision absent; dorsal surface flat, not impressed midlongitudinally, and with anterior half deflexed. (Epipharynx—no data.) (Labial palp—no data.) Submentum not excavated. Mentum transverse and trapezoidal; setae evenly distributed over surface. (Hypopharynx—no data.) (Prementum—no data.) (Galea—no data.) Mandibles tridentate; subapical denticle evident as flattened lobe on medial edge of apical denticle.

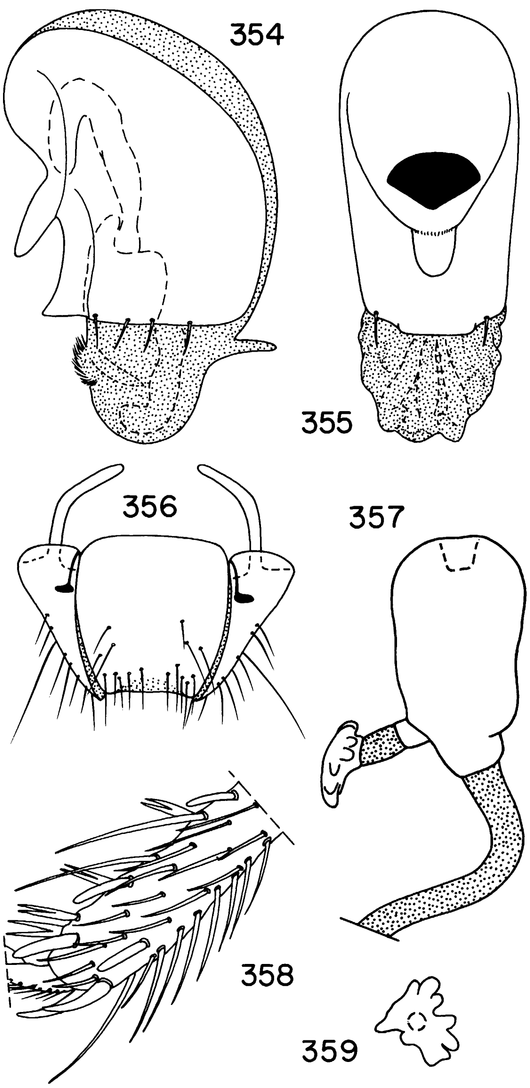
Pronotal horn absent. Marginal bead absent. Protergosternal suture absent. Procoxal fissure open. Protrochantin exposed. Prosternal process short and carinate. Prosternal setigerous pit present (no data for secretory pores); anterior margin entire, notch absent. Elytral epipleural ridge absent; posterior margin without membranous lobe.

Tarsi three segmented. Protibia with two rows of spines and others scattered between rows. Metatibia with apically bifid setae near apex (fig. 358).

Abdominal tergum VII with fine fringe on posterior margin. Tergum VIII with truncate posterior margin; margin entire, not serrate. Tergum IX with glandular canal fused and closed dorsally (fig. 356). Tergum X without struts on anterior margin (fig. 356).

Aedeagus (figs. 354, 355) without parameres. Median lobe bulbous, short; ventral surface sclerotized and not divided midlongitudinally.

Spermatheca (fig. 357) bipartite. Recepta-



FIGS. 354–359. The *infans* group. **354.** Aedeagus, lateral (*infans*). **355.** Aedeagus, dorsal (*infans*). **356.** Segments IX and X, male, dorsal (*infans*). **357.** Spermatheca (*renominatus*). **358.** Metatibia, apex (*renominatus*). **359.** Spermathecal gland, dorsal view (*renominatus*).

cle moderately elongate and moderately heavily sclerotized; accordion tube absent; distal end invaginated; brimlike ridge absent.

DISTRIBUTION AND HABITAT: Two species of this group have been collected from coastal localities along the Mediterranean Sea, Red Sea, and Gulf of Aden. One species (*helferi*) is reported from Burma. If the Burmese record is accurate, *B. helferi* probably also lives on the coast and the *infans* group may occur at many coastal localities from Africa to southeastern Asia (fig. 360). However, the three species may be difficult to find since they are uncommon in collections—but their rarity may be caused in part by their small size.

DISCUSSION: These three species are brought together for the first time. Two had been in *Belidus,* the other in *Dicarenus* (table 9).

Bledius helferi, as determined in the collections of the Field Museum and the British Museum, is in the *verres* group. However, examination of the holotype of *helferi* unequivocably places it in the *infans* group—it is difficult to distinguish from the other two species of the group. Misinterpretation of species is common and normally causes no problems. However, in this case, inclusion of *helferi* in the *infans* group extends the range of the group from northern Africa to Burma. No geographical intermediates are known. The *verres* group is common in Burma. The occurrence of the *infans* group in Burma needs corroboration and an effort should be made to find the group in the region between Africa and Burma.

Additional specimens of the group are needed for more detailed anatomical examination. I was able only to dissect for the aedeagus and spermatheca. Material was insufficiently abundant to permit dissection of the mouthparts.

Species Included and Material Examined

helferi Fauvel T(IRSN); type country: Burma.

Burma: (IRSN).

infans Rottenberg Co,Sp(MNHV), Sp(BMNH, FMNH, IRSN); type country: Italy.

Italy: Sicily, Siracusa (IRSN, MNHV). **South Yemen:** (BMNH). **Tunisia:** Sousse (BMNH); Carthage (IRSN); Rades (IRSN); Tunis (FMNH, MNHV); Bizerte (MNHV); Sfax (MNHV).

renominatus Cameron Co,Sp(BMNH), Sp(FMNH); type country: Ethiopia.

Ethiopia: Dalak [=Dahlak] (FMNH). **Somalia:** (Disei? BMNH, IRSN).

25. *fratellus* group

Figures 10, 361–372, 554–559, 684–689

DIAGNOSIS: The *fratellus* group can be distinguished from all other groups by the fused

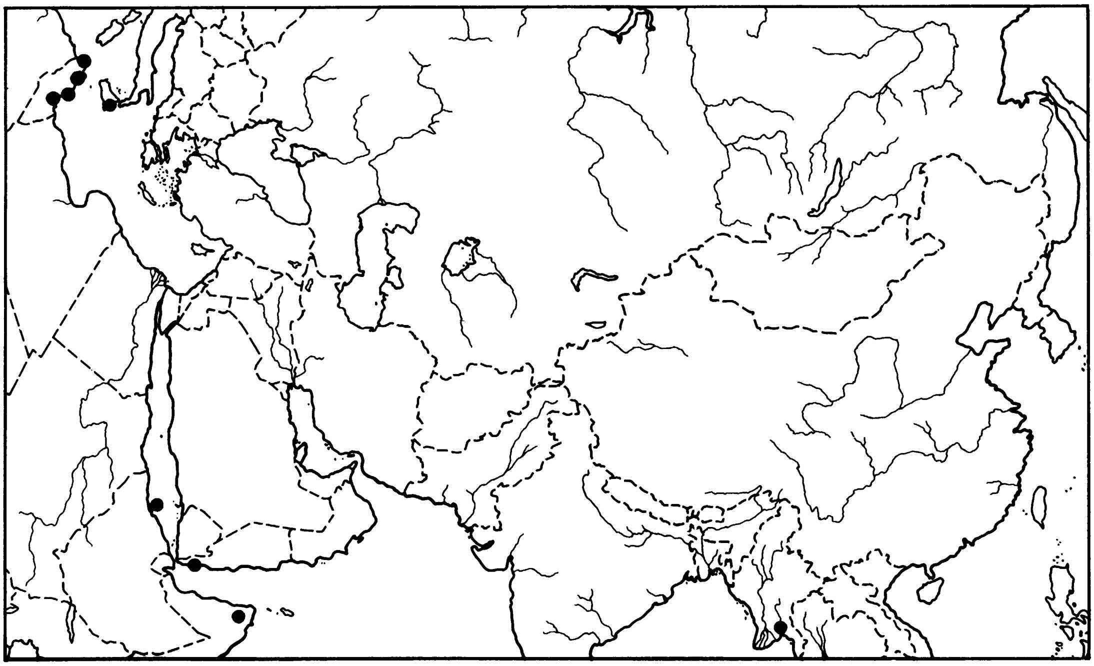


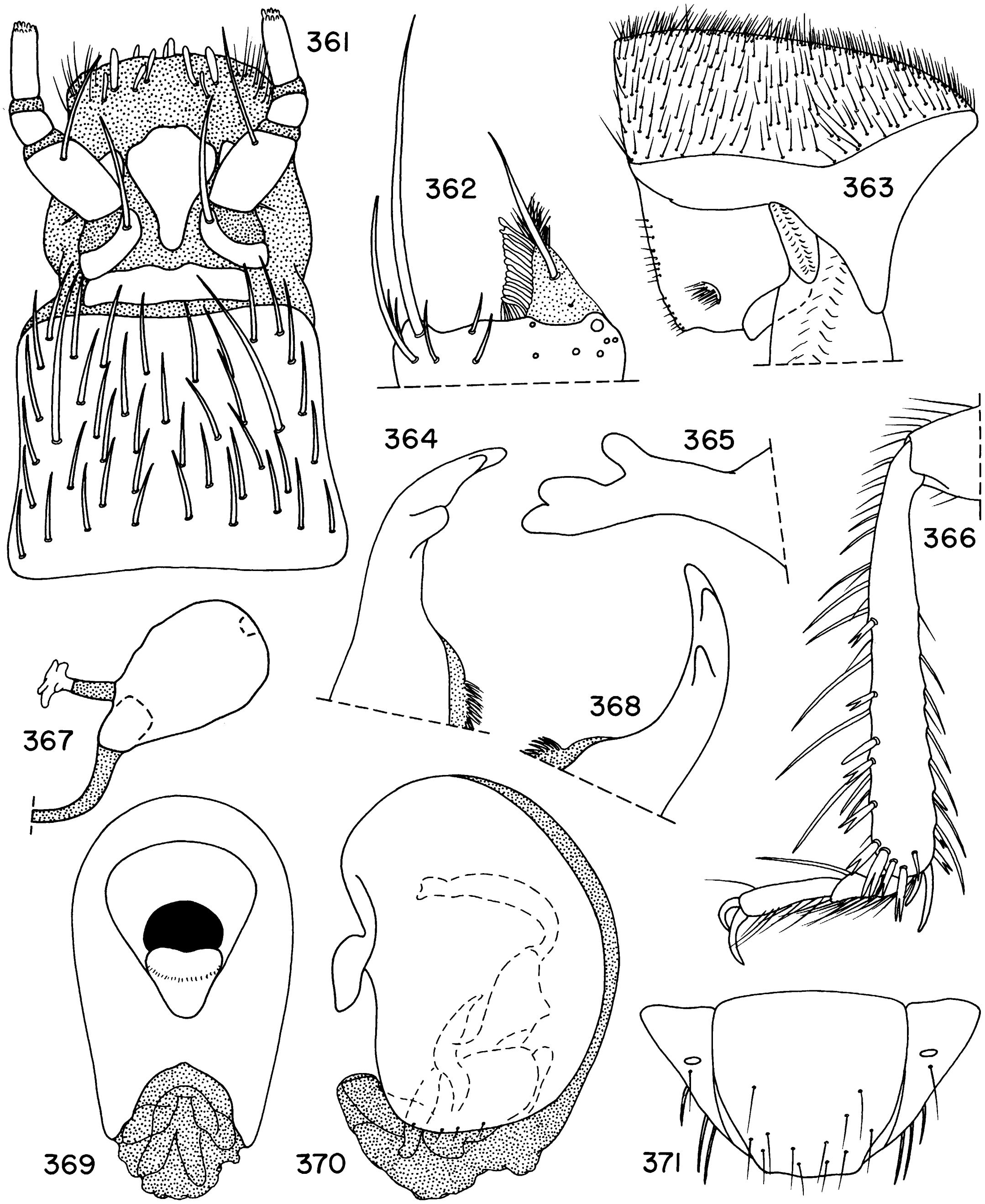
FIG. 360. Distribution of the *infans* group in North Africa and Burma.

gular sutures, presence of the pronotal marginal bead and protergosternal suture (fig. 363), absence of the elytral epipleural ridge and membranous lobe on the posterior elytral margin, the open procoxal fissure (fig. 363), and the truncate posterior margin of tergum VIII. Other useful features include the presence of the prosternal setigerous pit (figs. 363, 684, 685), the short, carinate prosternal process (fig. 363), and the three-segmented tarsi (fig. 366).

DESCRIPTION: Supraantennal ridge low, not enlarged, and without horns. Head without subantennal pocket; midbasal horn absent; postocular lateral carina absent. Clypeal margin not reflexed and without tubercles; clypeal middle without tubercles, spines, or ridges. Gular sutures fused. Labral margin (fig. 362) sinuotruncate; margin not reflexed; median incision absent; dorsal surface flat, without midlongitudinal impression. Epipharyngeal lobe long; dorsal surface with two setae, one long and one minute; median processes with lobed apices; lateroapical process numerous, slender, and unbranched or branched. Labial palps (fig. 361) with second segment shortest, first segment longest, and third segment intermediate; first segment thickest; first segment with two setae, second segment without setae. Submentum not excavated. Mentum trapezoidal and transverse; setae evenly distributed over surface (fig. 361). Hypopharynx (figs. 554–559) with lateral rows of setae strongly convergent toward base; basal setae arranged in large cluster; basal setae slender; cluster of basal setae on plate; central row of setae dense distally, sparse medially and basally; disk with setae on apical region; disk with long, slender cuticular processes on anterior half; disk with a few coronal pegs midbasally beside setae of central row. Prementum (fig. 361) with four sclerites, two lateral, one medial, and one basal. Galea with a few fanlike rows of setae; ventral surface without setae; dorsomedial edge with lobe. Mandibles tridentate; subapical denticle lobelike (figs. 364, 365, 368).

Pronotal (fig. 363) horn absent. Marginal bead present and complete. Protergosternal suture present; bead and suture parallel. Procoxal fissure open. Protrochantin exposed. Prosternal process short and carinate. Prosternal setigerous pit present (figs. 684–686); pit with cluster of pores behind setae (figs. 687–689); anterior margin entire. Elytral epipleural ridge absent; posterior margin without membranous lobe.

Tarsi three segmented. Protibia with one



FIGS. 361–371. The *fratellus* group. *Bledius fratellus*. **361.** Labium. **362.** Labrum, right setae and left epipharyngeal lobe removed. **363.** Prothorax, lateral view. **364.** Mandible, male, left, dorsal view. **365.** Mandible, male, left, anterolateral view. **366.** Metaleg. **367.** Spermatheca. **368.** Mandible, female, right, dorsal view. **369.** Aedeagus, dorsal view. **370.** Aedeagus, lateral view. **371.** Segments IX and X, female, dorsal view.

row of spinelike setae, others scattered. Metatibia with row of apically bifid setae (fig. 366).

Abdominal tergum VII with fine fringe on posterior margin. Tergum VIII with truncate posterior margin; margin not serrate. Tergum IX with glandular canal closed dorsally (fig. 371). Tergum X without struts on anterior margin (fig. 371).

Aedeagus (figs. 369, 370) without parameres. Median lobe with ventral surface membranous; median lobe slightly enlarged basally; distal portion tubular and slightly compressed laterally.

Spermatheca (fig. 367) bipartite. Receptacle moderately elongate and moderately heavily sclerotized; basal end with short internal tube at juncture with spermathecal duct; distal end invaginated; brimlike ridges absent; spermathecal gland with irregular shape and surface.

DISTRIBUTION AND HABITAT: The species of this group are known from a few coastal localities in West Africa (fig. 372).

DISCUSSION: *Bledius fratellus* was formerly in *Belidus*.

The *fratellus* and *infans* groups are easily separated by the presence of the pronotal marginal bead and protergosternal suture in *fratellus* and their absence in the *infans* group. The two groups are similar in most other respects including aedeagal and spermathecal features. Both groups have apically bifid metatibial setae. I have been able to study the hypopharynx of only the *fratellus* group.

Species Included and Material Examined

fratellus Eppelsheim Co,Sp(MNHV), Sp(FMNH, BMNH, IRSN); type country: West Africa.

Ghana: Adda [=Ada] (BMNH, FMNH, IRSN); Quittah [=Keta] (MNHV). **Nigeria:** Lagos (BMNH). **Senegal:** (BMNH).

26. *forcipatus* group

Figures 12, 373–389, 564–567, 690–695

DIAGNOSIS: The absence of the pronotal lateral marginal bead (fig. 382) and elytral epipleural ridge, the truncate posterior margin of tergum VIII, and the medially fused labrum (fig. 374) will distinguish the *forcipatus* from all other groups except *infans*. The elongate prosternal process (fig. 382) will separate the New World *forcipatus* group from the Old World *infans* group. In both groups the aedeagus lacks parameres. In the *forcipatus* group the ventral surface of the median lobe is sclerotized but is membranous in the *infans* group. In the *forcipatus* group the spermatheca (fig. 386) is spherical, heavily sclerotized, and bipartite; in the *infans* group it is elongate, moderately heavily sclerotized, and bipartite (fig. 357).

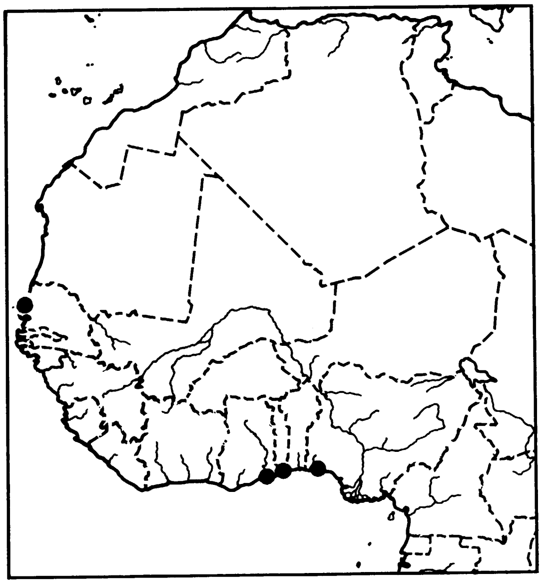
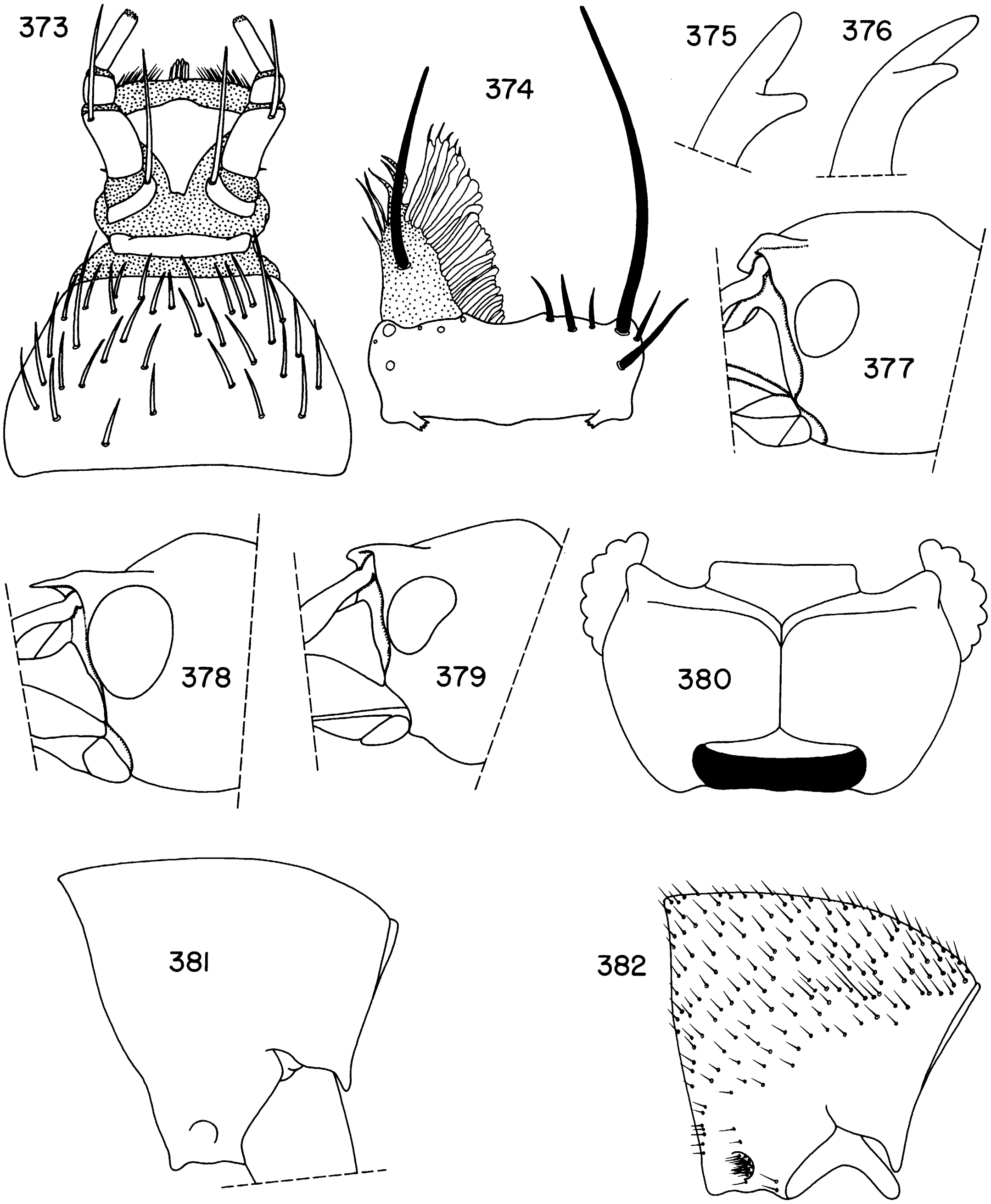


FIG. 372. Distribution of the *fratellus* group in western Africa.

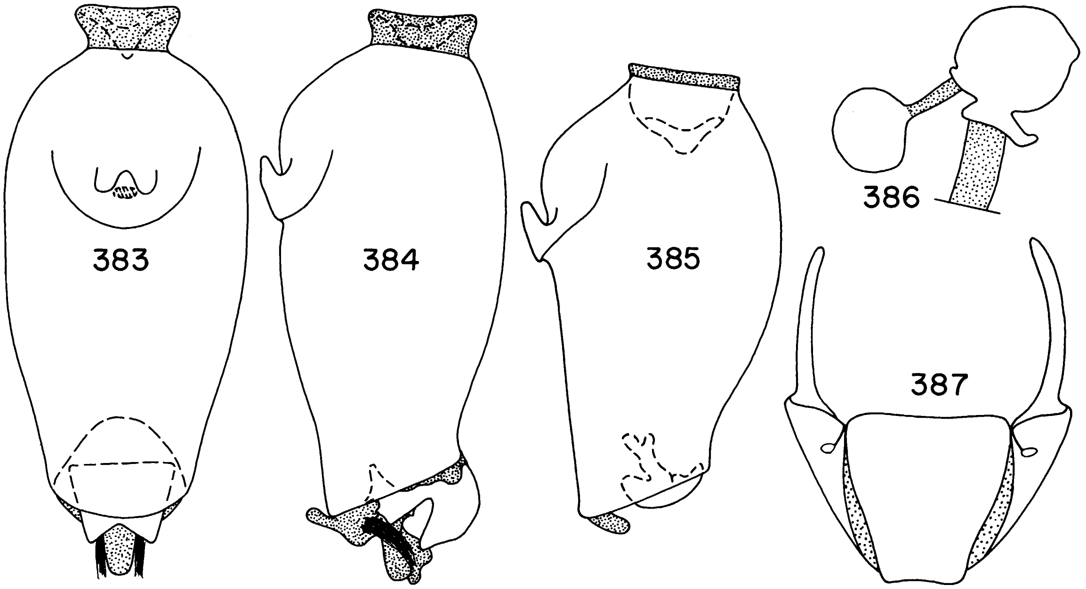
Other features that are useful for recognition of the *forcipatus* group are the absence of the protergosternal suture (figs. 381, 382), presence of the prosternal setigerous pit (figs. 382, 690, 691), fused gular sutures, absence of a membranous lobe on the elytral margin, and the three-segmented tarsi. The *forcipatus* group is also similar to the *angustus* group. The *forcipatus* group lacks the membranous lobe on the elytral margin, has a truncate margin on tergum VIII, lacks parameres (fig. 383), and is restricted to the New World. The *angustus* group has a membranous lobe on the elytral margin, has an emarginate posterior margin of tergum VIII, has parameres (fig. 415), and is found in the Old World (fig. 420).

DESCRIPTION: Supraantennal ridge of male modified as anteriorly directed horn (figs. 377–379); supraantennal ridge of female low, not enlarged, and without horns. Head without subantennal pockets; midbasal horn absent; postocular lateral carina absent. Clypeal margin not reflexed and without tubercles; clypeal middle without tubercles, spines, or



Figs. 373–382. The *forcipatus* group. **373.** Labium (*actitus*). **374.** Labrum, left setae and right epipharyngeal lobe removed (*forcipatus*). **375.** Mandible, left, apex, anterolateral view (*actitus*). **376.** Mandible, left, dorsal view (*actitus*). **377.** Head, lateral view (*actitus*). **378.** Head, lateral view (*forcipatus*). **379.** Head, lateral view (*litoreus*). **380.** Head, ventral view, mouth parts removed (*forcipatus*). **381.** Prothorax, lateral, setae removed (*litoreus*). **382.** Prothorax, lateral (*forcipatus*).

ridges. Gular sutures fused (fig. 380). Labral margin (fig. 374) emarginate and not reflexed; median incision absent (fig. 374); dorsal surface flat, not midlongitudinally impressed.



Figs. 383–387. The *forcipatus* group. **383.** Aedeagus, dorsal (*forcipatus*). **384.** Aedeagus, lateral (*forcipatus*). **385.** Aedeagus, lateral (*actitus*). **386.** Spermatheca (*litoreus*). **387.** Segments IX and X, male, dorsal view (*actitus*).

Epipharyngeal lobe (fig. 374) long; dorsal surface with one long seta; median processes with lobed apices; lateroapical processes numerous, slender, and unbranched. Labial palps (fig. 373) with second segment shortest; first and third segments of subequal length; first segment thickest; first segment with two setae, second segment with one seta. Submentum not excavated. Mentum (fig. 373) transverse and trapezoidal; pubescence sparser medially than laterally. Hypopharynx (figs. 564–567) with lateral rows of setae sharply convergent from apex to near middle of disk, then nearly parallel to base; basal setae arranged in one or two clusters; basal setae slender; basal setae not on plate; central row of setae dense anteriorly and sparsely present medially or absent; disk without setae; disk without cuticular processes; coronal pegs present medially. Prementum (fig. 373) with two sclerites, one medial and one basal. Galea with a few fanlike rows of setae on apex; ventral surface without setae; dorsomedial edge with lobe. Mandibles bidentate (figs. 375, 376).

Pronotal horn absent. Marginal bead absent (fig. 382). Protergosternal suture absent (fig. 382). Procoxal fissure open (fig. 381) or closed (fig. 382). Protrochantin exposed or concealed. Prosternal process elongate (fig. 382). Prosternal setigerous pit present (figs. 690–692); pit with pores among setae (figs. 693–695); anterior margin entire, without notch anterior to procoxa. Elytral epipleural ridge absent; posterior margin without membranous lobe.

Tarsi three segmented. Protibia with one row of spines and others scattered.

Abdominal tergum VII with fine fringe on posterior margin. Tergum VIII with truncate posterior margin; margin entire, not serrate. Tergum IX with glandular canal closed dorsally (fig. 387). Tergum X without struts on anterior margin (fig. 387).

Aedeagus (figs. 383–385) without parameres. Median lobe tubular, larger basally than apically and sclerotized on dorsal and ventral surfaces.

Spermatheca (fig. 386) bipartite. Receptacle pot-shaped and heavily sclerotized; accordion tube absent; distal end invaginate; brimlike ridge absent. Spermathecal gland sclerotized, irregularly spherical, and with more or less smooth surface.

Distribution and Habitat: The *forcipatus* group is restricted to the New World where

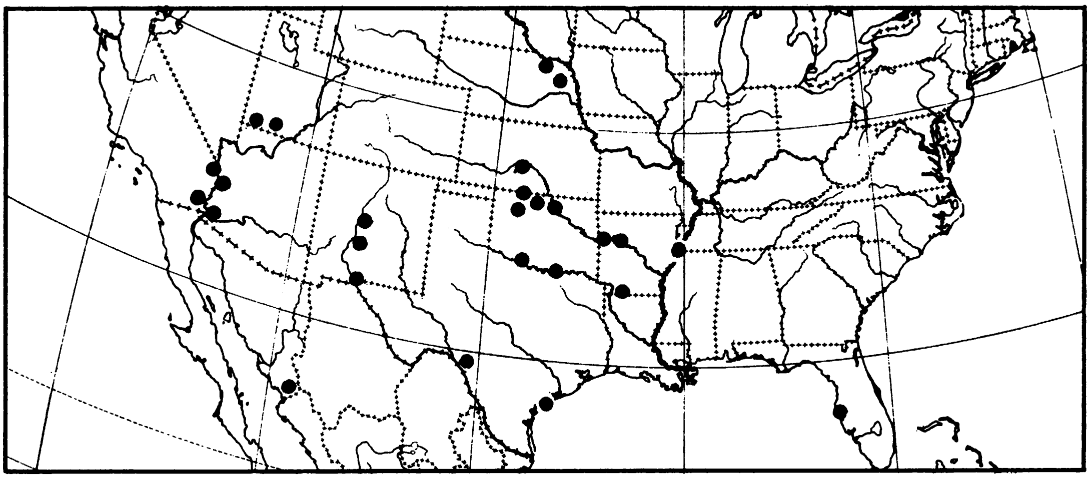


FIG. 388. Distribution of the *forcipatus* group in the USA.

it occurs from the central and western parts of North America south to central Argentina (figs. 388, 389). More thorough collecting in Central and South America should extend and fill in the range of this group. The group is unkown from the Caribbean Islands, but will likely be found there.

Species are found in freshwater and saline habitats, on salt flats, and near the ocean. The group probably will be found in most of the coastal and arid parts of Central and South America. The small size of the species and the need for specialized collecting make discovery difficult.

DISCUSSION: In 1972 I segregated the species of this group as a genus—*Microbledius*—in part because these species have three-segmented tarsi. In support of this decision were characters of the aedeagus and spermatheca. Further investigation revealed 11 other groups to have the same tarsal formula. Rather than fragment *Bledius* into smaller more difficult to identify taxa, I have opted to move *Microbledius* back into *Bledius*.

Species Included and Material Examined

actitus (Herman) H,P,Sp(AMNH); type country: USA.

Coast of Texas, **USA** (Herman, 1972, 1983a).

albidus Sharp Syn(BMNH), Sp(FMNH); type country: Brazil.

Argentina: Tucuman Province (FMNH).

Brazil: Amazonas, Jurua (BMNH).

albipennis Bernhauer T,Sp(FMNH), Sp(BMNH); type country: Argentina.

Argentina: *La Rioja:* Patquia (BMNH, FMNH); La Rioja (Iliar? FMNH).

bifasciatus Sharp L,P(BMNH); Sp(FMNH, AMNH); type country: Guatemala.

Guatemala: Rio Naranjo (BMNH); Pantaleon (BMNH).

forcipatus LeConte H(MCZ), Sp(AMNH); type country: USA.

Central and southwestern **USA** and northwestern **Mexico** (Herman, 1972, 1983a).

litoreus (Herman) H,P(CU), P(AMNH); type country: USA.

Coastal Florida, **USA** (Herman, 1972).

miles Bernhauer T,Sp(FMNH); type country: Argentina.

Argentina: Mendoza (FMNH); Cordoba Province (FMNH). *Catamarca:* La Cienega, Belen (FMNH); Buenos Aires (FMNH).

minutissimus Bernhauer T(FMNH); type country: Argentina.

Argentina: Tucuman Province (FMNH).

playanus (Herman) H,P,Sp(AMNH; type country: USA.

Central and southwestern **USA** (Herman, 1972).

weiseri Bernhauer T,Sp(FMNH); type country: Argentina.

Argentina: Catamarca (Pampa Grande ? FMNH). (Cienega Quebrada ? FMNH).

FIG. 389. Distribution of the *forcipatus* group from Mexico to Argentina.

Undetermined.

Argentina: *Buenos Aires:* Chascomus (AMNH). *Catamarca:* 5 km NW Alpasinche, Rio Salado (AMNH). *La Rioja:* 5 km NW Vinchina, Rio Vinchina (AMNH); 10 km NW Vinchina (AMNH); Villa Union, Rio Vinchina (AMNH); 5 km E Chilecito (AMNH); Los Corrales, 15 km NW Famatina (AMNH). *Salta:* 34 km SE Angastaco, Rio Calchaqui (AMNH); Seclantes, Rio Calchaqui (AMNH); 7 km SE Rosario de la Frontera (AMNH); 7 km NW Juramento, Rio Juramento (AMNH). *Santiago del Estero:* Rio Hondo, Termas del Rio Hondo (AMNH). *Tucuman:* 15 km N Tucuman (AMNH); Antiguo Quilmes, Rio Santa Maria (AMNH). **Bolivia:** Beni, Guayaramerin, Rio Mamore (AMNH); Province of Sara (CMP); Trinidad (AMNH). **Brazil:** Para, Jacareacanga (AMNH); Bahia (Copixaba? AMNH). **Colombia:** *Atlantico:* east of Salgar, near Sabanilla (AMNH); Puerto Colombia (AMNH). **Honduras:** 12 km W Olanchito

(CNC); Rio Humuya, NW Comayagua (USNM). **Mexico:** *Chiapas:* 7.8 mi. E Pichucalco (USNM). *Guerrero:* Teloloapan. *Nayarit:* San Blas (CAS). *San Luis Potosi:* 1 mi. W Tamazunchale (USNM). *Sinaloa:* Mazatlan (USNM). **Peru:** San Jorge, 40 mi. W Pucallpa (CAS); Cuzco, 15 km SW Limatambo (USNM). **Trinidad:** Manzanilla (AMNH).

27. *punctatissimus* group

Figures 11, 51, 390–409, 584–589, 593, 594, 696–701

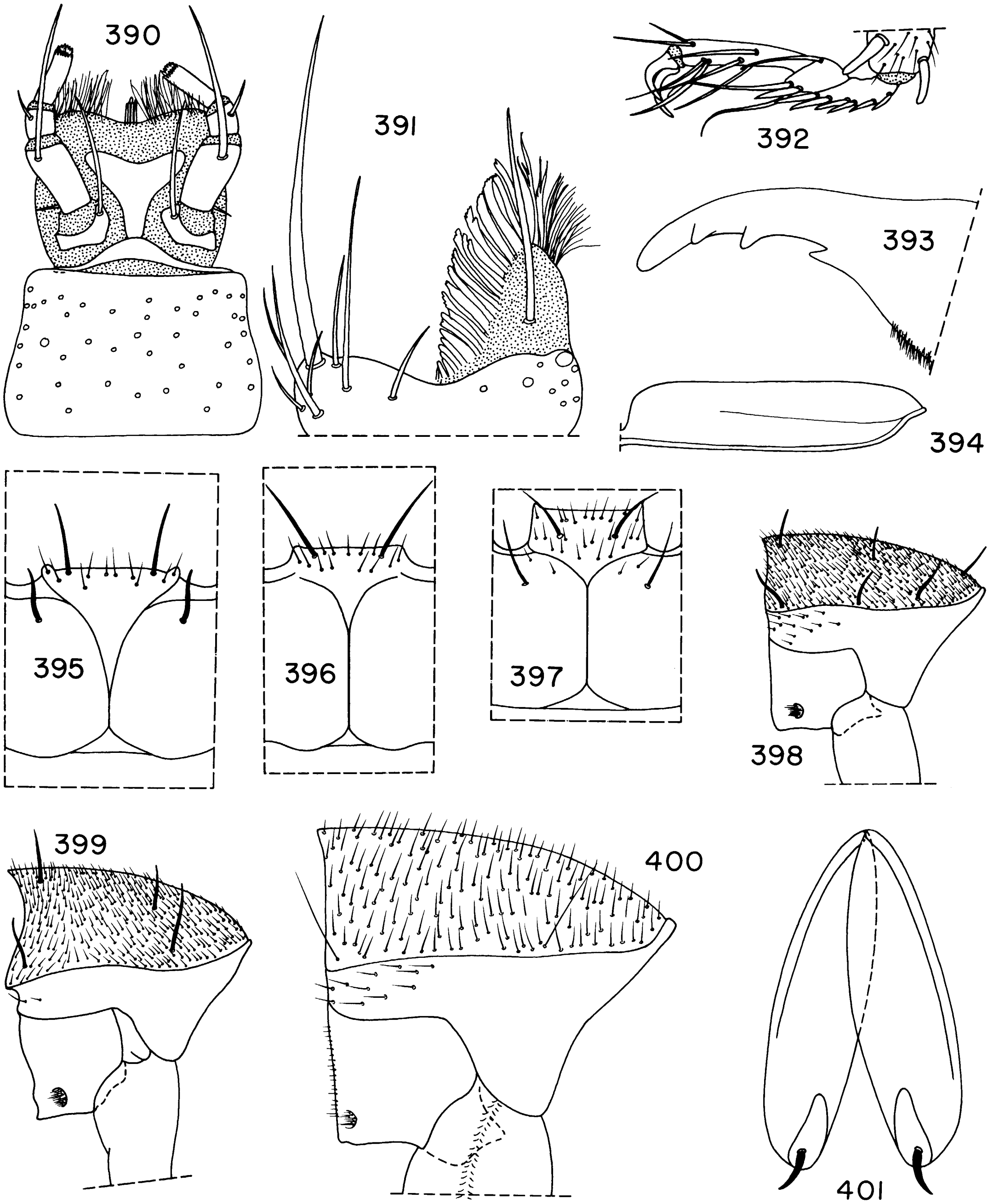
DIAGNOSIS: The annelidoid spermatheca is unique to this group (fig. 403). To separate the *punctatissimus* group from other groups requires a combination of external characters none of which is unique to this group. The labral incision is absent (fig. 391), the pronotal marginal bead is present and complete (figs. 399, 400), the prosternal setigerous pit is present (figs. 399, 696), the prosternal process is short and carinate, the elytral posterior margin lacks a membranous lobe, and the tarsi are three segmented (fig. 392). The protergosternal suture is present (fig. 400) or absent (absent in one species and feeble in another), the gular sutures are fused anteriorly (fig. 397) separated at the very anterior end (fig. 396), or separated for most of their length (fig. 395), the elytral epipleural ridge is present and complete or incomplete (fig. 394), and the posterior margin of tergum VIII is truncate or emarginate. The emargination is broad and shallow and (except for *albomarginatus*), lacks the lobes on the lateral portion of the margin. The procoxal fissure is open (fig. 399) or closed (fig. 398).

DESCRIPTION: Supraantennal ridge low, not enlarged, and without horns. Head without subantennal pocket. Head without midbasal horn; postocular lateral carina absent. Clypeal margin not reflexed; margin without tubercles; middle without tubercles, spines, or ridges. Gular sutures fused (fig. 397) anteriorly to separated for part (fig. 396) or most (fig. 395) of length. Labrum with broad, moderately deep emargination (fig. 391); margin usually not reflexed (margin slightly reflexed in *B. michaelseni*); median incision absent (fig. 391); dorsal surface impressed or flat. Epipharyngeal lobe (fig. 391) long; dorsal surface with one long and one or two minute setae; median processes of anterior margin with divided or undivided apices; lateroapical processes numerous, slender, and unbranched or biramous. Labial palps (fig. 390) with second segment shortest, first segment shorter or subequal to length of third; first segment thickest; first segment with two setae and second segment with one seta. Submentum not excavated. Mentum (fig. 390) transverse and trapezoidal; setae evenly distributed over surface. Hypopharynx (figs. 584–589) with lateral row of setae gradually convergent; basal setae clustered on median plate; basal setae slender; central row of setae dense apically and arranged in narrow row medially and basally; disk with dense cluster of setae on apical edge and without setae medially; disk with long cuticular processes medially; disk with coronal pegs near central row of setae. Prementum (fig. 390) with two sclerites, one medial and one basal. Galea with a few fanlike rows of setae on apex; ventral surface without setae; dorsomedial edge with lobe. Mandibles bidentate, tridentate, or quadridentate (fig. 393).

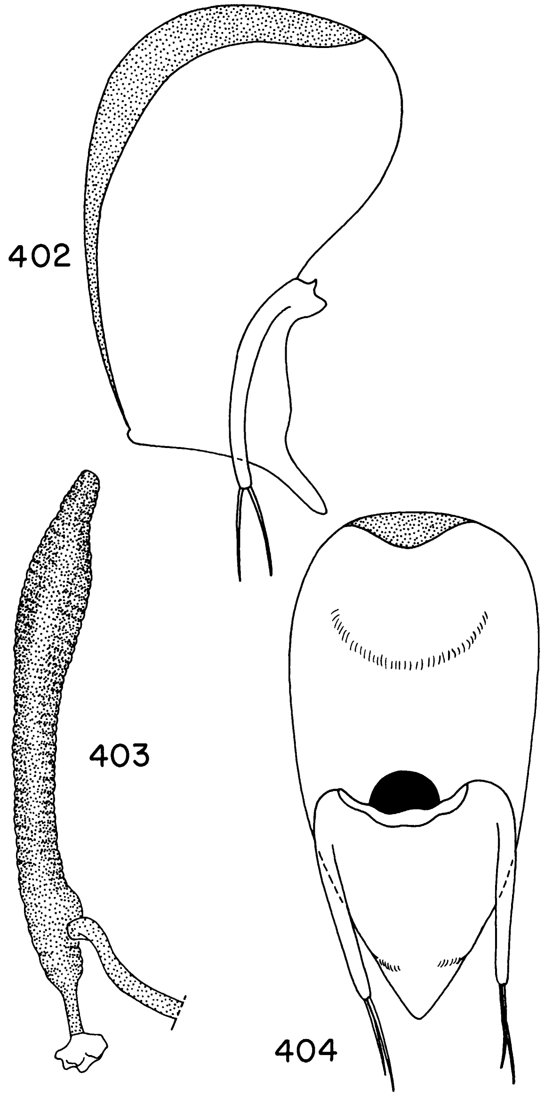
Pronotal horn absent. Marginal bead present and complete (fig. 398); bead dividing notum and hypomeron, not on hypomeron. Protergosternal suture absent or present (figs. 399, 400) and moderately well defined and more or less parallel to bead. Procoxal fissure open (fig. 399) or closed (figs. 400). Protrochantin exposed or concealed. Prosternal process short and carinate (fig. 400). Prosternal setigerous pit present (figs. 696–701); setae flattened (fig. 699); pit with cluster of pores behind setae; anterior margin entire. Elytral epipleural ridge present and complete or incomplete and present only at apex or on apical two-thirds (fig. 394); posterior margin without membranous lobe.

Tarsi three segmented (fig. 392). Protibia with one row of spinelike setae and others scattered on surface.

Abdominal tergum VII with fine fringe on posterior margin. Tergum VIII with posterior margin truncate or emarginate; emargination broad and shallow, usually with lobes on lateral portion of margin; margin entire, not serrate. Tergum IX with glandular canal nar-



FIGS. 390–401. The *punctatissimus* group. **390.** Labium, setae removed from mentum (*puelches*). **391.** Labrum, right setae and left epipharyngeal lobe removed (*puelches*). **392.** Metatarsus (*punctatissimus*). **393.** Mandible, right (*puelches*). **394.** Elytron, lateral view (*puelches*). **395.** Gular region (*caribbeanus*). **396.** Gular region (*microcephalus*). **397.** Gular region (*punctatissimus*). **398.** Prothorax, lateral (*punctatissimus*). **399.** Prothorax, lateral (*caribbeanus*). **400.** Prothorax, lateral (*puelches*). **401.** Genital appendages of segment IX, female (*caribbeanus*).



FIGS. 402–404. The *punctatissimus* group. *Bledius puelches*. **402.** Aedeagus, lateral. **403.** Spermatheca. **404.** Aedeagus, dorsal.

rowly to widely open dorsally. Tergum X without struts on anterior margin.

Aedeagus (figs. 402, 404) with parameres. Parameres slender, cylindrical, median surface sclerotized, and not or just reaching apex of median lobe. Median lobe short, bulbous, and with midventral surface fused.

Spermatheca (fig. 403) bipartite and annelidoid. Receptacle membranous, elongate, and without differentiation of proximal and distal part from accordion tube; apex with or without invagination; brimlike ridges absent. Spermathecal gland sclerotized, or irregular shape, and with irregular surface.

DISTRIBUTION AND HABITAT: Most species of this group have been collected from sea coastal localities throughout the world (figs. 405–409). Some species are reported from the intertidal zone of the seacoast. They remain in this zone during high tide. Two species from Chile (*maculipennis* and *puelches*), one from Congo (*dartevillei*), and one from Zimbabwe (*pruinosulus*) were collected from inland localities. A few unidentified specimens have been taken a short distance from the coast in northern Australia. Most of the species are small to minute and easily overlooked by collectors. Only 6 of the 26 species are reported from the New World.

DISCUSSION: This group was first separated as the genus *Psamathobledius* and included three New World species (table 9). The group was separated because it had three-segmented tarsi along with some unique genitalic and hypopharyngeal characters. *Psamathobledius* shares unique characters with *Bledius*. The three-segmented tarsi are found in 11 other species groups. *Psamathobledius* is recognized herein as the *punctatissimus* group.

Nine species in the *punctatissimus* were removed from *Dicarenus*, three from *Psamathobledius*, two from *Hesperophilus*, and three from *Astycops*; nine were never assigned to an infrageneric taxon (table 9).

This is one of the more interesting species groups and is in dire need of revision. The Chilean, North American, and Caribbean species have been revised (Saiz, 1973; Herman, 1972).

The variable condition of the gular sutures, procoxal fissure, elytral epipleural ridge, and posterior margin of tergum VIII led me to attempt to divide the *punctatissimus* group into smaller groups. This variation is reflected in a preliminary key to the species of the group. The main problems with recognizing smaller species groups were that *B. punctatissimus* (from America) was grouped with species found in South Africa, India, Indonesia, Formosa, and Australia. Of these species, *pontilis, caroli,* and *maindroni* (from Australia, Australia, and India), were notably similar to species from New Zealand that were

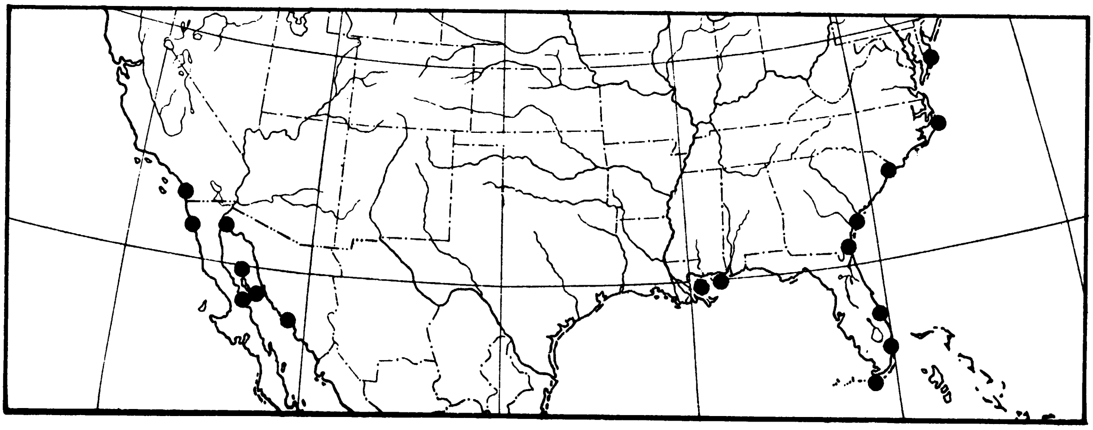


FIG. 405. Distribution of the *punctatissimus* group in Mexico and the USA.

in a different group. Two characters (condition of the gular sutures, and margin of tergum VIII) are sufficiently variable that doubt arises for the placement of some species.

PRELIMINARY KEY TO THE *PUNCTATISSIMUS* AND *LUGUBRIS* GROUPS (*ORIENTALIS* OMITTED)

1. Elytral epipleural ridge present and complete or incomplete (fig. 394) 2
   Elytral epipleural ridge absent .... *lugubris* Fauvel (Madagascar)

2(1). Elytral epipleural ridge complete 3
   Elytral epipleural ridge incomplete (fig. 394) 7

3(2). Procoxal fissure open (fig. 399) .... *buettikeri* Coiffait (Saudi Arabia), *caribbeanus* Blackwelder (West Indies), *microcephalus* Fauvel (Colombia)
   Procoxal fissure closed (figs. 398, 400) ... 4

4(3). Gular sutures fused anteriorly (fig. 397) 5
   Gular sutures separated anteriorly (figs. 395, 396) 6

5(4). Tergum VIII truncate ... *exiguus* (Australia), *punctatissimus* (USA), *tenebricosus* (South Africa)
   Tergum VIII emarginate .... *albomarginatus* (Formosa), *buehleri* (Indonesia), *caroli* (Australia), *maindroni* (India), *pontilis* (Australia)

6(4). Tergum VIII truncate .... *fossiventris* (New Caledonia)
   Tergum VIII emarginate .... *amplicollis* (New Zealand), *bidentifrons* (New Zealand), *fernandezi* (Uruguay), *injucundus* (Australia), *salinus* (New Zealand)

7(2). Protergosternal suture absent .... *dartevellei* (Congo)
   Protergosternal suture present (fig. 400) .. 8

8(7). Procoxal fissure closed (fig. 400) .... *maculipennis* (Chile), *puelches* (Chile)
   Procoxal fissure open (fig. 399) 9

9(8). Mandibles bidentate .. *scheerpeltzi* (Egypt)
   Mandibles tridentate .... *capensis* (South Africa), *michaelseni* (Namibia), *pruinosulus* (South Africa), *tristis* (Europe)

Species Included and Material Examined

albomarginatus Bernhauer, T,Co(FMNH), Sp(BMNH); type country: Taiwan.

Taiwan: (Alikang? BMNH; AMNH).

amplicollis Fauvel Syn(IRSN); type country: New Zealand.

New Zealand: Tairua (IRSN).

bidentifrons Broun T,Sp(BMNH); type country: New Zealand.

New Zealand: Kerikeri (BMNH); Wanganui Beach (BMNH).

buehleri Scheerpeltz Co(MNHV); type country: Indonesia.

Indonesia: Sumba, Baing (MNHV); Sumba, Melolo (MNHV).

buettikeri Coiffait P(HCC); type country: Saudi Arabia.

Saudi Arabia: (El Shoiba ? HCC).

capensis Cameron H,Sp(BMNH); type country: South Africa.

FIG. 406. Distribution of the *punctatissimus* group from Mexico to Chile and Uruguay.

South Africa: Simonstown (BMNH).

caribbeanus Blackwelder H(USNM), Sp(AMNH); type country: Trinidad and Tobago.

West Indies: (see Herman, 1972, 1983a).

caroli Blackburn Co(BMNH), Sp(IRSN); type country: Australia.

Australia: (BMNH); Victoria (BMNH).

dartevillei Bernhauer T,Co(FMNH), Co(BMNH); type country: Congo.

Congo: Malembe (FMNH, BMNH).

exiguus Scheerpeltz T(FMNH); type country: Australia.

Australia: Queensland, Laura (AMNH).

fernandezi Bernhauer T,Co(FMNH); type country: Uruguay.

Uruguay: Atlantica, Canelones (FMNH).

fossiventris Fauvel Syn,Sp(IRSN); type country: New Caledonia.

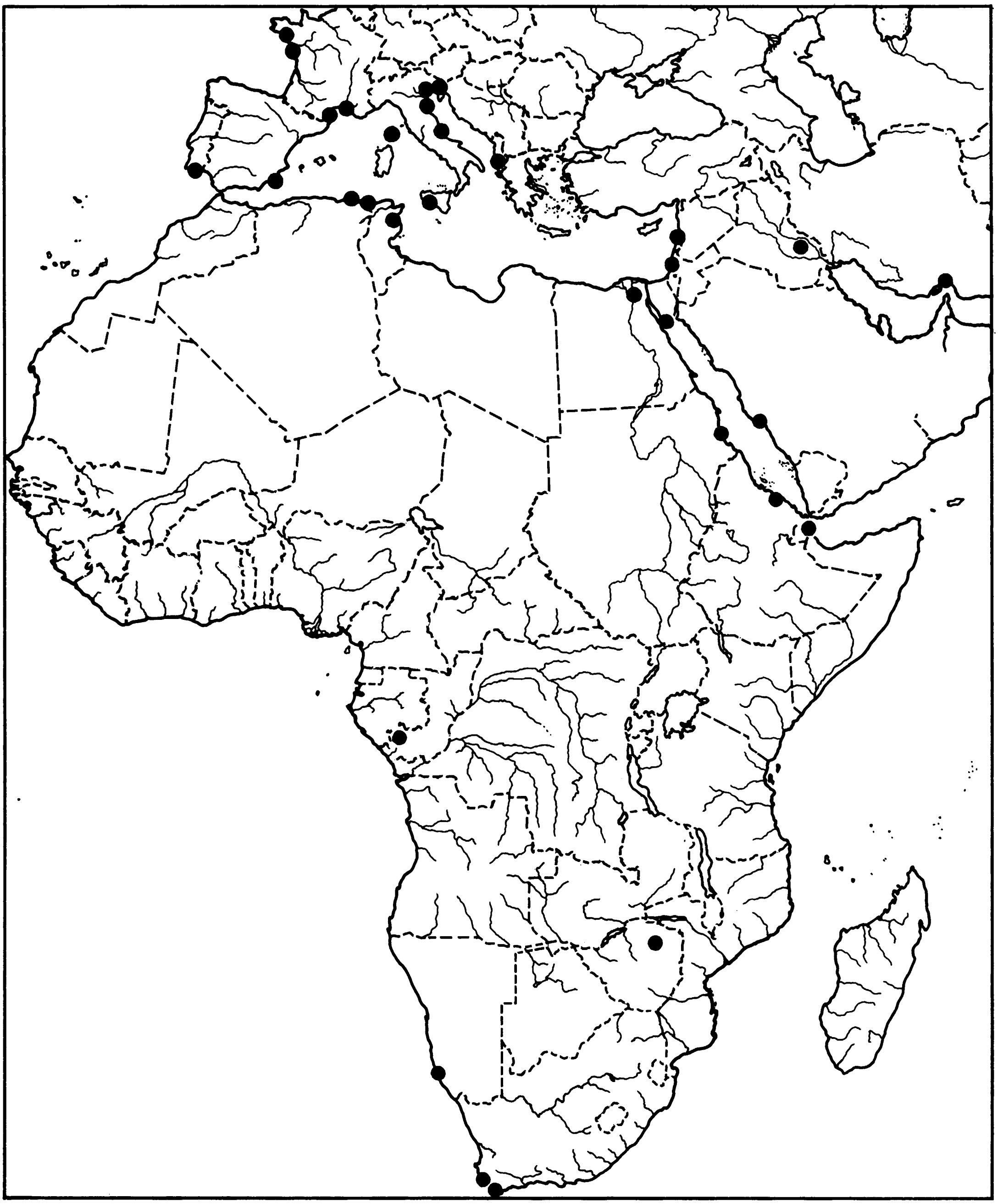


FIG. 407. Distribution of the *punctatissimus* group in Europe and Africa.

New Caledonia: Noumea (IRSN). (Hedesbin? IRSN).

injucundus Blackburn T(BMNH); type country: Australia.

Australia: (BMNH); Port Lincoln (BMNH).

maculipennis (Solier) Syn(IRSN), Sp(AMNH, BMNH, FMNH, IRSN); type country: Chile.

Chile: (BMNH, FMNH); Santiago (IRSN); Santiago Prov., La Reina (AMNH).

maindroni Fauvel Syn(IRSN), Sp(BMNH); type country: India.

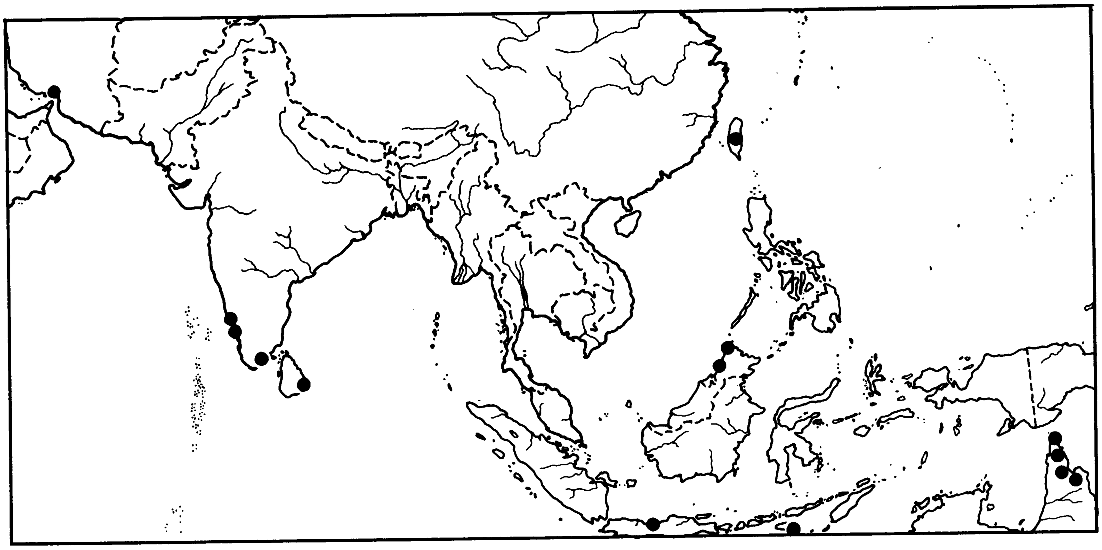


FIG. 408. Distribution of the *punctatissimus* group in the Indo-Pacific region.

India: Tuticorin (BMNH); Malabar, Mahe (IRSN); Malabar, Calicut (IRSN).

michaelseni Bernhauer Co(FMNH); type country: Namibia.

Namibia: Pinguin Island, Lüderitz Bay (FMNH).

microcephalus Fauvel H(IRSN), Sp(AMNH); type country: Colombia.

Colombia: (Herman, 1972, 1983a).

orientalis Bernhauer and Schubert Sp(MNHP); type country: Djibouti.

Djibouti: Obock (MNHP).

pontilis Blackburn T,Sp(BMNH); type country: Australia.

Australia: (BMNH).

puelches Fauvel Syn(IRSN), Sp(AMNH, FMNH, IRSN); type country: Chile.

Chile: San Antonio (IRSN); Santiago, Calera (FMNH); Valparaiso Prov., between Concon and Quintero (AMNH); Rio Mataquito, Tonlemo, Huaquen, Curico (MCZ); Nuble, Rio Pinto, E of Chillan (USNM).

pruinosulus Bernhauer Syn(FMNH, BMNH); type country: Zimbabwe.

Zimbabwe: Mashonaland, Salisbury (BMNH, FMNH).

punctatissimus LeConte L(MCZ), Sp(AMNH); type country: USA.

Coastal **Colombia, Ecuador, Mexico, USA** and **West Indies** (see Herman, 1972, 1983a).

salinus Cameron P,Sp(BMNH); type country: New Zealand.

New Zealand: N. Auckland, Ruakaka, beach (BMNH); Whangaparapara, Great Barrier Island, Huaraki Gulf (BMNH).

scheerpeltzi Koch Co,Sp(FMNH), Co(MNHV); type country: Egypt.

Egypt: El Tur, Sinai (FMNH, MUHV); Cairo (FMNH). **Iraq:** Mesopotamia (FMNH).

tenebricosus Scheerpeltz Co(MNHV); type country: South Africa.

South Africa: Cape Prov., Franschhoek, Bosreserve, Upper Berg River (MNHV).

tristis Aube Sp(FMNH, AMNH, BMNH, IRSN, MNHV); type country: Italy.

Albania: Valona [=Vlorë] (BMNH, MNHV). **Algeria:** Philippeville [=Skikda] (IRSN); Algiers [=Alger] (MNHV); Bone [='Annaba] (FMNH, IRSN). **France:** Ile de Ré (BMNH, IRSN); Narbonne (MNHV); Ile de la Camargue (FMNH); St. Gilles sur Vie, Vendée Dept. (FMNH); Corsica (FMNH, det. as *minarzi*). **Italy:** Friuli Region, Lignano (BMNH); Rimini (IRSN, MNHV); Giulianova (IRSN); Riccione, Emilia (MNHV), Mt. Argentario, Tombolo di Feniglla (MNHV); Siclly, Porto Empedocle (MNHV); Grado (FMNH, det. as *minarzi*); Venezia (BMNH, det. as *minarzi*). **[Portugal]**: Faro (MNHV, det. as *minarzi*). **Spain:** Cartagena, Cabo de Palos

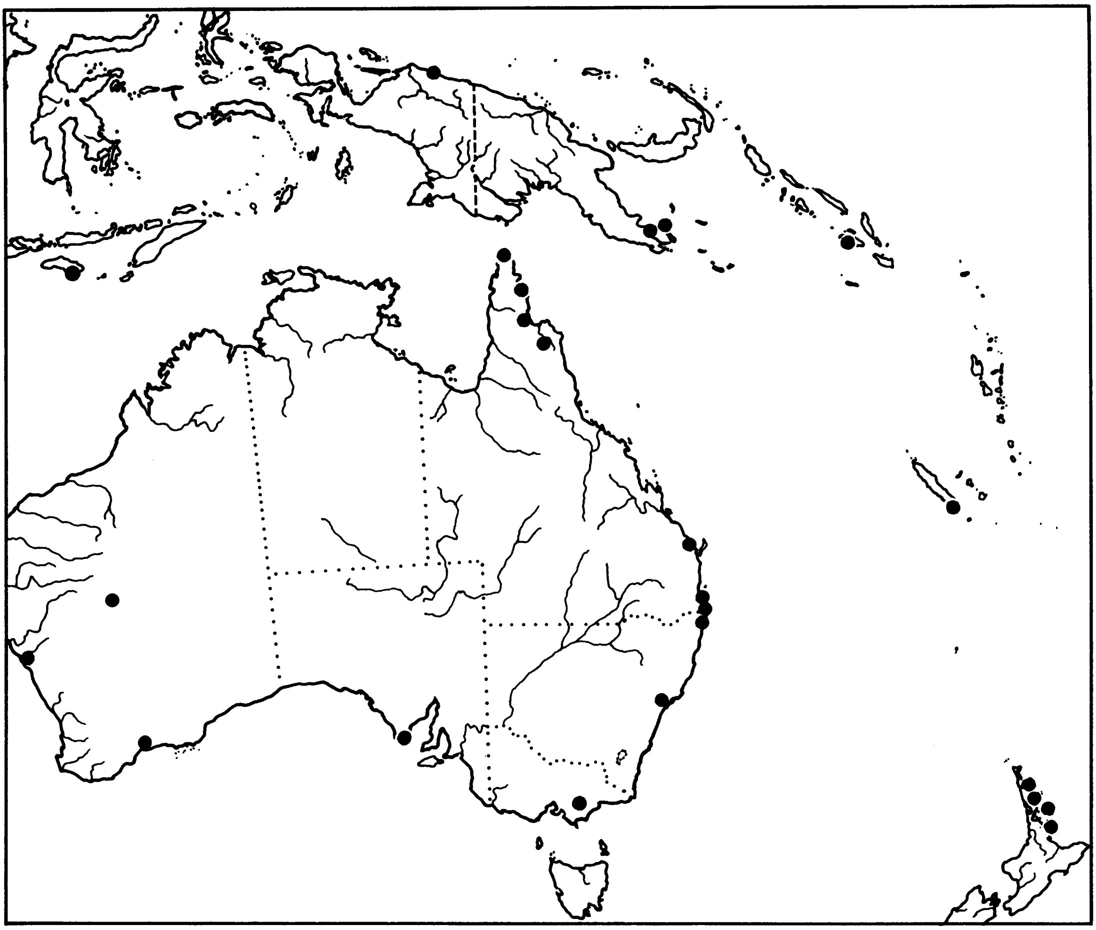


FIG. 409. Distribution of the *punctatissimus* group in the Indo-Australian region and New Zealand.

(MNHV). **Sudan:** Port Sudan (BMNH). **Tunisia:** Kairouan (IRSN); (Cape Kamart ?) (IRSN); (Gamarth? MNHV).

Undetermined.

Australia: Bundaberg (BPBM); Sandgate (BPBM); Murwillumba (BPBM); Blue Mountains (BPPM); Coolangatta (BPBM); Tweedshead (BPBM); Cape York Peninsula, Iron Range, east bank of East Claudie River (AMNH); Cape York Peninsula, Ebagoola, about 26 mi. from Coen (AMNH); Cape York Peninsula, Lockerbie, 10 mi. WSW Somerset (AMNH); Queensland, Claudie River, near Iron Range (MCZ); Victoria, Mirboo National Park (MCZ); Western Australia, Wiluna (MCZ); Western Australia, Culham (MCZ); Western Australia, Geraldton (MCZ). **Brazil:** Rio de Janeiro, Mangaratiba (AMNH). Rio Grande do Sul: Cassino Beach (AMNH). **Djibouti:** Obock (IRSN). **Ethiopia:** (Ras Gheden ? IRSN). **France:** Ile de la Camarque, St. Maries (BMNH). **French Guiana:** Cayenne (IRSN). **Indonesia:** Java (BPBM). **Iran:** Kerman, 5 km NE Bandar Abbas (USNM). **Irian Jaya:** Mouth of Tor River, 4 km E Hol Maffen (BPBM). **Israel:** Ma'agan Mikha'el (MNHV). **Italy:** Abruzzo, Descara (MNHV). **Lebanon:** Beirut (MNHV). **Malaysia:** Sabah, 7 km NNW Kudat, Tanjung Tajau (USNM); Sabah, Kuala Penya (USNM). **Mexico:** Gulf of Mexico, Isla Partida (CAS); Gulf of Mexico, Angeles Bay (CAS); Gulf of Mexico, Punta Refugio (CAS); Sonora, Punta Sargento (CAS). **New Caledonia:** (Ouano Beach ? BPBM). **Papua New Guinea:** Cape Vogel Peninsula, Menapi (AMNH); D'Entrecasteaux Islands, Fergusson Island, Deidei, Gomwa Bay (AMNH). **Solomon Island:** Guadalcanal, Honiara (BMNH). **Sri Lanka:** Arugam Bay (AMNH). **South Africa:** Kleinmond (BMNH); Capetown (IRSN). **Uruguay:** Maldonado Dept. (AMNH).

28. *lugubris* group

Figures 10, 410

DIAGNOSIS: This species is similar to those in the *punctatissimus* group. It is separated from the *punctatissimus* group by the absence of the elytral epipleural ridge. Other characters useful for recognition of this group are the absence of a median labral incision, presence of the pronotal marginal bead and protergosternal suture, open procoxal fissure, and presence of a setigerous prosternal pit.

DESCRIPTION: Supraantennal ridge low, not enlarged, and without horns. (Subantennal pockets—no data.) Head without midbasal horn; postocular lateral carina absent. Clypeal margin not reflexed; margin without tubercles; middle without tubercles, spines, or ridges. Gular sutures fused. Labral margin emarginate and not reflexed; median incision absent; dorsal surface flat, without midlongitudinal impression. (Epipharynx—no data.) Labial palps with second segment shortest and first segment thickest (no other data for palps). (Mentum—no data.) (Hypopharynx—no data.) (Prementum—no data.) (Galea—no data.) Mandibles tridentate; subapical denticle modified as flattened lobe.

Pronotal horn absent. Marginal bead present and complete; bead dividing notum and hypomeron, not on hypomeron. Protergosternal suture present; bead and suture parallel. Procoxal fissure closed. Protrochantin concealed. (Prosternal process—no data.) Prosternal setigerous pit present (no data for pores); anterior margin entire elytral epipleural ridge absent; posterior margin without membranous lobe.

Tarsi three segmented. Protibia with one row of spinelike setae, others scattered over posterior surface.

Abdominal tergum VII with fine fringe on posterior margin. Tergum VIII with posterior margin emarginate; margin entire, not serrate. (Tergum IX—no data.) (Tergum X—no data.)

(Aedeagus—no data.)

(Spermatheca—no data.)

DISTRIBUTION AND HABITAT: This group is known only from Madagascar (fig. 410).

DISCUSSION: *Bledius lugubris* may belong with those in the *punctatissimus* group but is separated from them by the absence of the elytral epipleural ridge. Since I was unable to examine the spermatheca of *lugubris* I am separating it from the *punctatissimus* group pending further study.

The species previously was not assigned to an infrageneric taxon.

Species Included and Material Examined

lugubris Fauvel Sp(MNHV); type country: Madagascar.

Madagascar: Mahavatsy [Mahavavy River ?] (MNHV).

29. *angustus* group

Figures 12, 411–420, 560–563, 702–706

DIAGNOSIS: The *angustus* group is separated from all other groups by the absence of the pronotal marginal bead (fig. 417), the incomplete elytral epipleural ridge (fig. 414), the emarginate posterior margin of tergum VIII, the medially fused labrum (fig. 413), closed procoxal fissure (fig. 417), presence of the prosternal setigerous pit (figs. 417, 702, 703), and absence of the postocular cephalic carina. Other useful features are the fused gular sutures, absence of the protergosternal suture, moderately long, carinate prosternal process (fig. 417), and presence of long, slender parameres (figs. 415, 416).

DESCRIPTION: Supraantennal ridge low, not enlarged, and without horns. Head without subantennal pocket; midbasal horn absent; postocular lateral carina absent. Clypeal margin not reflexed and without tubercles; clypeal middle without tubercles, spines, or ridges. Gular sutures fused. Labrum (fig. 413) with feebly emarginate anterior margin; anterior margin narrowly reflexed; median incision absent; dorsal surface flat, not impressed midlongitudinally. Epipharyngeal lobe long; dorsal surface with two long setae; median processes with divided or undivided apices; lateroapical processes numerous, slender, and unbranched. Labial palps (fig. 411) with second segment shortest, first segment longest, and third segment intermediate; first segment thickest; first segment with two setae, second segment with one seta. Submentum not excavated. Mentum (fig. 411) transverse and trapezoidal; setae sparser medially and laterally. Hypopharynx (figs. 560–563) with lateral row of setae sharply convergent from apex of disk to middle then nearly parallel to base; basal setae arranged in large cluster of setae on basal third of disk; basal setae slender; basal setae not on plate; central row of setae dense anteriorly and slightly less so medially; disk with setae scattered over surface including middle of disk; disk without cuticular processes; coronal pegs among central row of setae; coronal peg with peg extending much beyond corona (figs. 561–563). Prementum (fig. 411) with four sclerites, one basal, one median, and two lateral. Galea with many fanlike rows of setae on apex; ventral surface without setae; dorsomedial edge with lobe. Mandibles bidentate (fig. 412).

Pronotal (fig. 417) horn absent. Marginal bead incomplete, present only near base, or present near base and on anterior portion but interrupted medially. Protergosternal suture absent. Procoxal fissure closed. Protrochantin concealed. Prosternal process moderately long and carinate. Prosternal setigerous pit present (figs. 702, 703); pit with pores behind and among setae (figs. 704–706); anterior margin entire. Elytral epipleural ridge absent or present and incomplete but present only on apical portion (fig. 414); posterior margin with small membranous lobe (this lobe on *lindbergeanus* is difficult to see) or absent.

Tarsi three segmented. Protibia with two rows of spinelike setae and others scattered between.

Abdominal tergum VII with fine fringe on posterior margin. Tergum VIII with emarginate posterior margin; margin not serrate. Tergum IX with glandular canal open dorsally (fig. 418). Tergum X with long, slender struts on anterior margin (fig. 418).

Aedeagus (figs. 415, 416) with parameres. Parameres slender, cylindrical, median surface sclerotized, and extending to just beyond apex of median lobe. Median lobe long, base bulbous, apical portion flattened; ventral surface largely membranous.

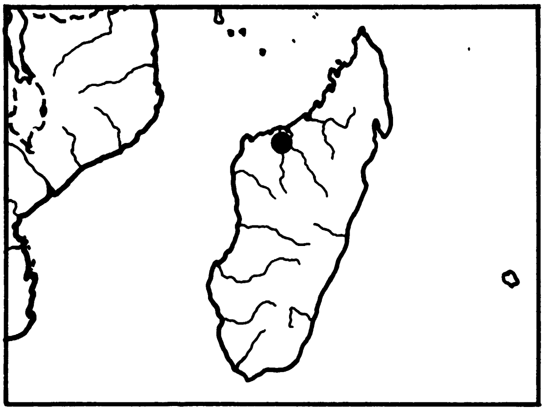


FIG. 410. Distribution of the *lugubris* group in Madagascar.

Spermatheca (fig. 419) bipartite. Receptacle folded at middle, and distal and proximal ends only slightly differentiated from accordion tube; distal portion sclerotized, basal and middle portion membranous; apex with small invagination; brimlike ridges absent. Spermathecal gland sclerotized, of irregular shape, and with irregular surface.

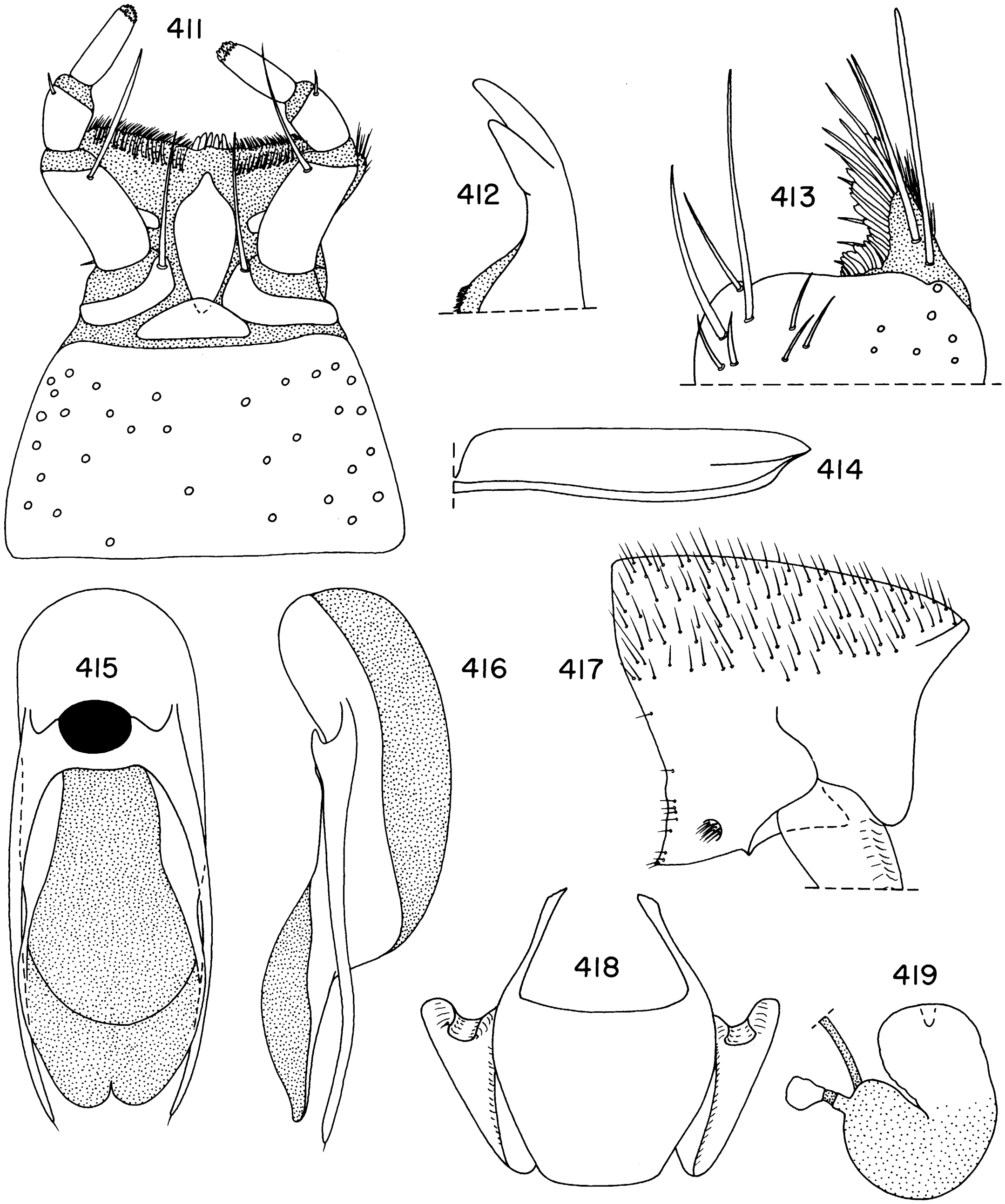
DISTRIBUTION AND HABITAT: The *angustus* group is known from arid and semiarid regions in Spain, France, and the western Sahara eastward to eastern Iran, Afghanistan, and the Karakum in the Soviet Union (fig. 420). Some specimens were collected from coastal localities in France, Saudi Arabia, and Djibouti. The species are probably found in saline habitats.

DISCUSSION: The three species included in this group are those that remain in *Belidus* after *fratellus* and *infans* have been moved to their own group (table 9).

Species Included and Material Examined

angustus Mulsant and Rey Sp(AMNH, FMNH, BMNH, IRSN, MNHV); type country: France.

Algeria: Touggourt (BMNH, IRSN); El Goliah [=El Goléa] (IRSN); Massif de l'Aures, 5 km S Kanga (MNHV); Biskra (FMNH, IRSN, MNHV). **Djibouti:** Obock (IRSN). **Egypt:** Siwa Depression, Tenterad Depression (BMNH). Zagazig (HCC); Cairo, Helwân (FMNH, MNHV); Khamissa



FIGS. 411–419. The *angustus* group. *Bledius angustus*. **411.** Labium, setae of mentum removed. **412.** Mandible, right. **413.** Labrum, right setae and left epipharyngeal lobe removed. **414.** Elytron, lateral. **415.** Aedeagus, dorsal. **416.** Aedeagus, lateral. **417.** Prothorax, lateral. **418.** Segments IX and X, female, dorsal view. **419.** Spermatheca.

(BMNH). **France:** Cette [=Sète] (IRSN). **Iran:** Baluchestan, Iranshahr (MNHV); Kerman Prov. (HCC). **Iraq:** Mesopotamia (FMNH, BMNH). **Mauritania:** Trarza Bagzleilag (HCC). **Oman:** Muscat (IRSN, BMNH). **Saudi Arabia:** Jiddah (BMNH);

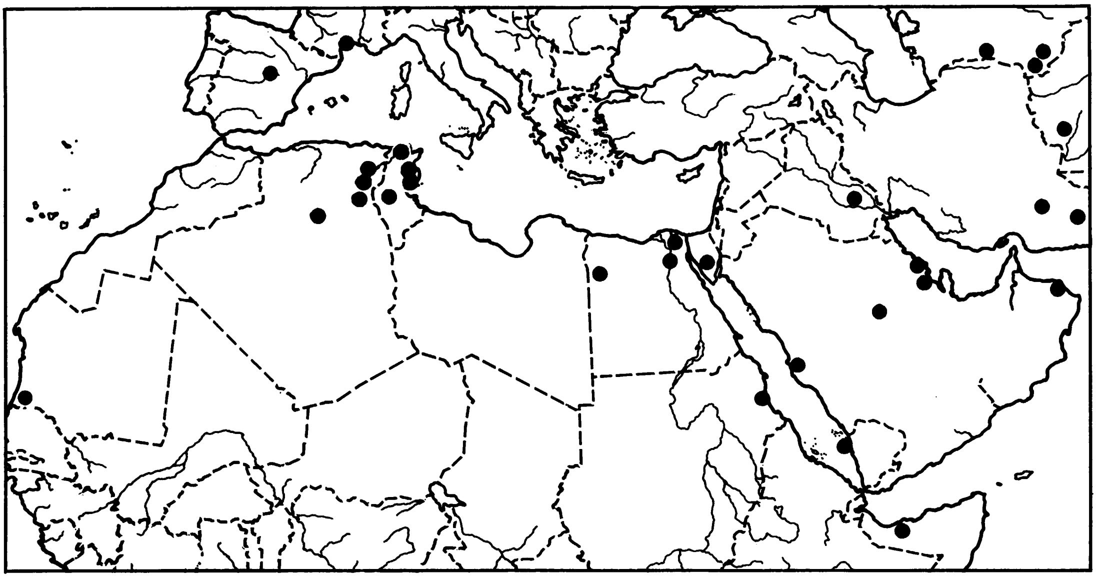


FIG. 420. Distribution of the *angustus* group in Europe, Africa, and southwestern Asia.

Hofuf [= Al Hufuf] (HCC); Riyadh (HCC); (Wadi Gaanah ? HCC). **South Yemen:** Kamaran Island (BMNH). **Spain:** Madina Cali [=Medinaceli] (IRSN). **Sudan:** Port Sudan (MNHV, FMNH). **Tunisia:** Kebili (IRSN); Kairouan (IRSN, FMNH); Mateur (IRSN); Sfax (IRSN). **USSR:** [Turkmeniya]: Merv [=Mary] (MNHV); Kopet Dagh [= Khrebet Mts.] (MNHV); Repetek (FMNH).

lindbergianus Scheerpeltz H,P(MNHV); type country: Afghanistan.

Afghanistan: Dilaram (MNHV).

magniceps Reitter Sp(FMNH, IRSN); type country: USSR.

USSR: Transcaspian [= Turkmenskaya + Kazakhskaya] (IRSN).

Undetermined.

Saudi Arabia: Eastern Province, E of Khobar [= Al Khubar] (MCZ). **Somalia:** Biyo Gora Gorge, SE Berbera (BMNH).

30. *bispinus* group

Figures 12, 421–426

DIAGNOSIS: The species of this group are similar to those of the *verres* group but can be separated by the emarginate posterior margin of tergum VIII (fig. 422) and the four-segmented tarsi. Also similar is the *pulchellus* group from which *bispinus* group is separated by the characters listed above but also by the complete elytral epipleural ridge. The elytral epipleural ridge is complete in the *bispinus* group but incomplete in the *tibialis* group.

Other characters to help recognize the *bispinus* group are the complete pronotal marginal bead, open procoxal fissure, fused gular sutures, labral incision, partially reflexed clypeal margin, fine fringe of tergum VII, the shallowly to moderately emarginate labral margin, the midlongitudinal labral impression, the prosternal setigerous pit, absence of a membranous lobe on the elytra, presence of a protergosternal suture, and the short, slender parameres (figs. 424, 425).

DESCRIPTION: Supraantennal ridge low, not enlarged, and without horns. (Subantennal pockets—no data.) Head without midbasal horn; postocular lateral carina absent. Clypeal margin partially reflexed, lateral portion of margin with flattened, tuberclelike reflexions that join or are near one another medially; clypeal middle without tubercles, spines, or ridges; gular sutures fused. Labral margin emarginate; anterior margin not reflexed; median incision present; dorsal surface with midlongitudinal impression. (Epipharynx—no data.) (Labial palps—no data.) Submentum not excavated. (Mentum—no data.) (Hypopharynx—no data.) (Prementum—no data.) (Galea—no data.) Mandibles bidentate or tridentate.

Pronotal horn absent. Marginal bead present and complete. Protergosternal suture present. Bead and suture slightly divergent anteriorly. Procoxal fissure open. Protrochantin exposed. (Prosternal process—no data.) Prosternum with setigerous pit anterior to procoxae (no data for pores); anterior margin entire, without notch. Elytral epipleural ridge present and complete; posterior margin without membranous lobe.

Tarsi four segmented. Protibia with one row of spinelike setae and with others scattered over posterior surface.

Abdominal tergum VII with fine fringe on posterior margin. Tergum VIII (fig. 422) with posterior margin broadly emarginate; margin not serrate. Tergum IX with glandular canal open dorsally (fig. 423). Tergum X with small struts on anterior margin (fig. 423).

Aedeagus (figs. 424, 425) with parameres. Parameres slender, short, appressed to median lobe, with median surface sclerotized, and not extending beyond apex of median lobe. Median lobe bulbous; apical portion cylindrical; ventral surface midlongitudinally membranous.

Spermatheca (fig. 426) tripartite. Receptacle divided into two portions separated by accordian tube; basal part membranous and slightly larger than lightly sclerotized apical part; receptacle without brimlike ridges; apical part without invagination. Spermathecal gland sclerotized; surface irregular; shape irregularly spheroidal.

DISTRIBUTION AND HABITAT: This group is known from several localities in north central India and from unspecified localities in Burma and Sri Lanka (fig. 427).

DISCUSSION: The males of the three species of this group have a pair of processes on the posterior margin of sternum VII (fig. 421). These processes are long in *fuscicornis* and *bispinus* (see Cameron, 1930, pp. 279, 280) and reduced to nubs in *championi* (fig. 421). These three species were included in the subgenus *Dicarenus* (the earlier version of *Hesperophilus*) by Cameron (1930).

Species Included and Material Examined

bispinus Kraatz Sp(BMNH, FMNH, IRSN); type country: India.

Burma: (IRSN). **India:** Uttar Pradesh, Kumaon, Tanakpur (BMNH, FMNH); W Almora (FMNH).

championi Bernhauer T(FMNH), Sp(BMNH); type country: India.

Burma: (IRSN). **India:** Haldwani District, Kumaon (FMNH); Uttar Pradesh, Mussourie (FMNH); Dehra Dun (Nim Nadi, Lachiwala, Nun Nadi ? BMNH).

fuscicornis Cameron T(BMNH); type country: India.

India: Uttar Pradesh, Almora, Dhauli Ganga (BMNH).

Undetermined.

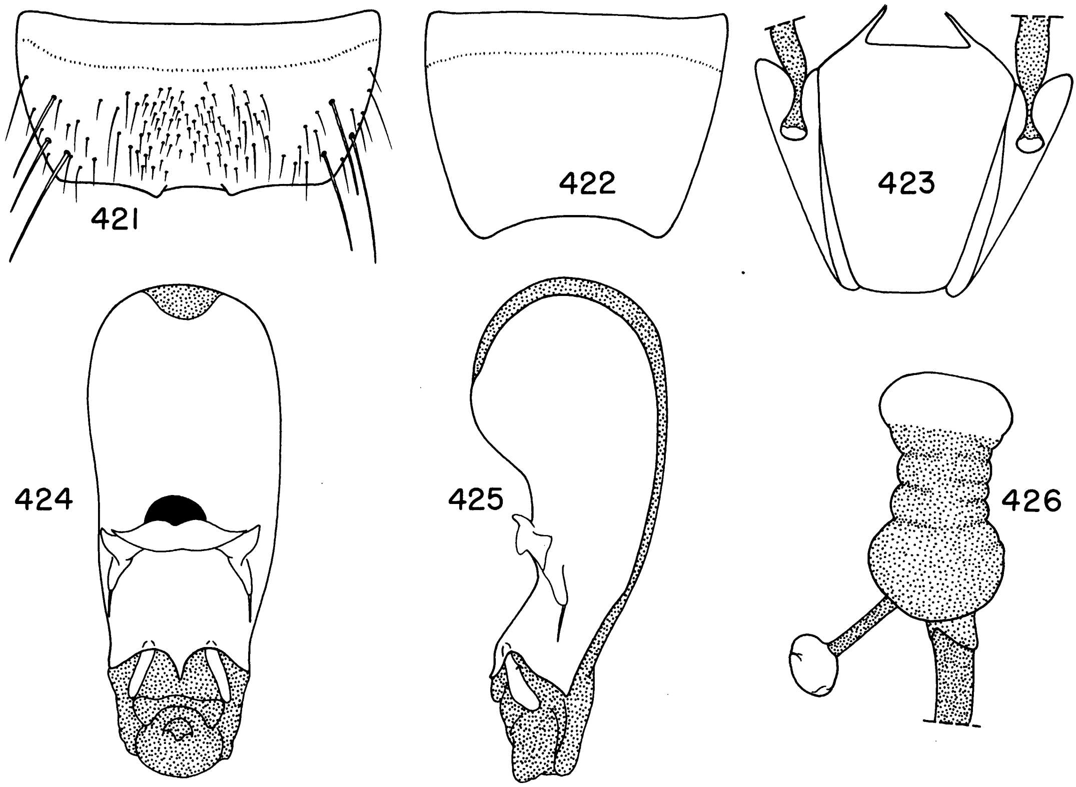
India: Vizagapatam [=Vishakhapatnam] District, Chipurupalle (BMNH, as *gracilicornis*); Malabar, Calicut (BMNH, as *gracilicornis* and *tuberculatus*). **Laos:** Vientiane (BPBM). **Nepal:** Bagmati Province, 3 km N Bahunepati, 900 m [16 km NE Kathmandu] (CNC). **Sri Lanka:** (BMNH, as *gracilicornis* and *tuberculatus*).

31. *tibialis* group

Figures 12, 428–439, 572–577, 707–712

DIAGNOSIS: The *tibialis* group can be distinguished from all others by the reflexed anterior clypeal margin, incomplete elytral epipleural ridge (fig. 433), and presence of setigerous pits on the prosternum (figs. 434, 707, 708). Other useful characters include the presence of the pronotal marginal bead (fig. 434), absence of the membranous elytral lobe, emargination of the posterior margin of tergum VIII, and the median incision of the labrum (fig. 428).

DESCRIPTION: Supraantennal ridge low, unmodified, without horn. Subantennal pocket absent. Head without midbasal horn. Postocular carina absent. Clypeal margin reflexed; anterior margin without tubercles; middle without tubercles, spines, or ridges. Gular sutures fused anteriorly. Labral (fig. 428) margin broadly and deeply to moderately deeply emarginate; margin not reflexed; median incision present; surface with median impression. Epipharyngeal lobe long; dorsal surface with one long and one minute seta; median processes of anterior margin with lobed or simple apices; lateroapical portion with many long, slender, unbranched, or biramous processes. Labial palp (fig. 431) with second segment shortest, first segment long-



FIGS. 421–426. The *bispinus* group. **421.** Sternum VII, male (*championi*). **422.** Tergum VIII, setae removed (*championi*). **423.** Terga IX and X, female (*bispinus*). **424.** Aedeagus, dorsal (*championi*). **425.** Aedeagus, lateral (*championi*). **426.** Spermatheca (*bispinus*).

est, third segment intermediate; first segment thickest, second and third of subequal thickness; first segment with two setae, second with one. Submentum not excavated. Mentum transverse and rectangulotrapezoidal; setae nearly evenly distributed. Hypopharynx (figs. 572–577) with lateral row of setae gradually convergent; basal setae arranged in cluster; basal setae slender; cluster on plate; central row of setae dense anteriorly and reduced to narrow row from middle to base; disk with many setae on anterior portion and without setae medially; disk with rows of numerous short palmate cuticular processes adjacent to central row of setae; coronal pegs scattered over median swath near central row of setae. Prementum with two sclerites; median one well developed, basal one feebly sclerotized and difficult to see. Galea with a few fanlike rows of setae on apex; ventral surface without setae; dorsomedial edge with lobe. Mandibles bidentate, tridentate (fig. 430), or quadridentate (fig. 429).

Pronotum (fig. 434) without horn. Marginal bead present and complete; bead on hypomeron or dividing hypomeron and notum. Protergosternal suture present, well developed, and more or less parallel to bead. Procoxal fissure open. Protrochantin exposed. Prosternal process short and carinate. Prosternum with setigerous pit (figs. 707, 708); pit with cluster of pores behind setae (figs. 709–712); anterior margin entire. Elytral epipleural ridge (fig. 433) present and incomplete, present on apical third to half; posterior margin with minute, dorsally directed membranous lobe.

Tarsi four segmented. Protibia with two rows of spinelike setae and others scattered between.

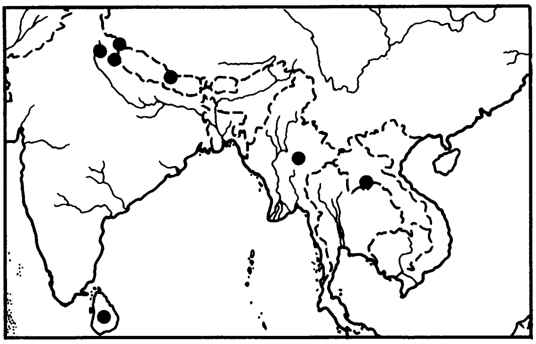


FIG. 427. Distribution of the *bispinus* group in Southeast Asia.

Abdominal tergum VII with fine posterior fringe. Tergum VIII with posterior margin emarginate; margin entire. Tergum IX (fig. 437) with glandular canal open dorsally. Tergum X without struts on anterior margin (fig. 437).

Aedeagus (fig. 432) with parameres present. Parameres long, extending beyond apex of median lobe; parameres slender for most of length then expanded near apex, apex truncate; median surface sclerotized. Median lobe with ventral surface fused medially; base bulbous, apical half more flattened.

Spermatheca (figs. 435, 436) tripartite. Receptacle with apical and basal portion weakly sclerotized, of nearly equal diameter, basal portion longer; apical and basal portions moderately differentiated from accordion tube; receptacle without brimlike ridges; distal portion without invagination. Spermathecal gland sclerotized, of irregular shape and surface strongly tuberculate.

DISTRIBUTION AND HABITAT: This group is known from Europe and northern Africa eastward to Mongolia and north central India (figs. 438, 439). The two European species comprise most of the records which extend as far north as northern Norway. Most of the localities are in cool temperate and montane regions.

DISCUSSION. Three of the species in this group have been placed in the subgenus *Astycops* (table 9), which includes such species as *B. talpa, B. fossor,* and *B. subterraneus.* I separated the *tibialis* group because of the reflexed clypeal margin, short prosternal process, and incomplete elytral epipleural ridge as well as differences of the aedeagus and spermatheca. The fourth species, *indicus,* was included in the subgenus *Dicarenus* from which it is excluded because of the characters listed in the preceding sentence in addition to the open procoxal fissure.

Species Included and Material Examined

auripennis Coiffait P(HCC); type country: Afghanistan.

Afghanistan: Parum Valley (HCC); Pech Valley, between Gusalik and Wama (HCC).

indicus Cameron H(BMNH); type country: India.

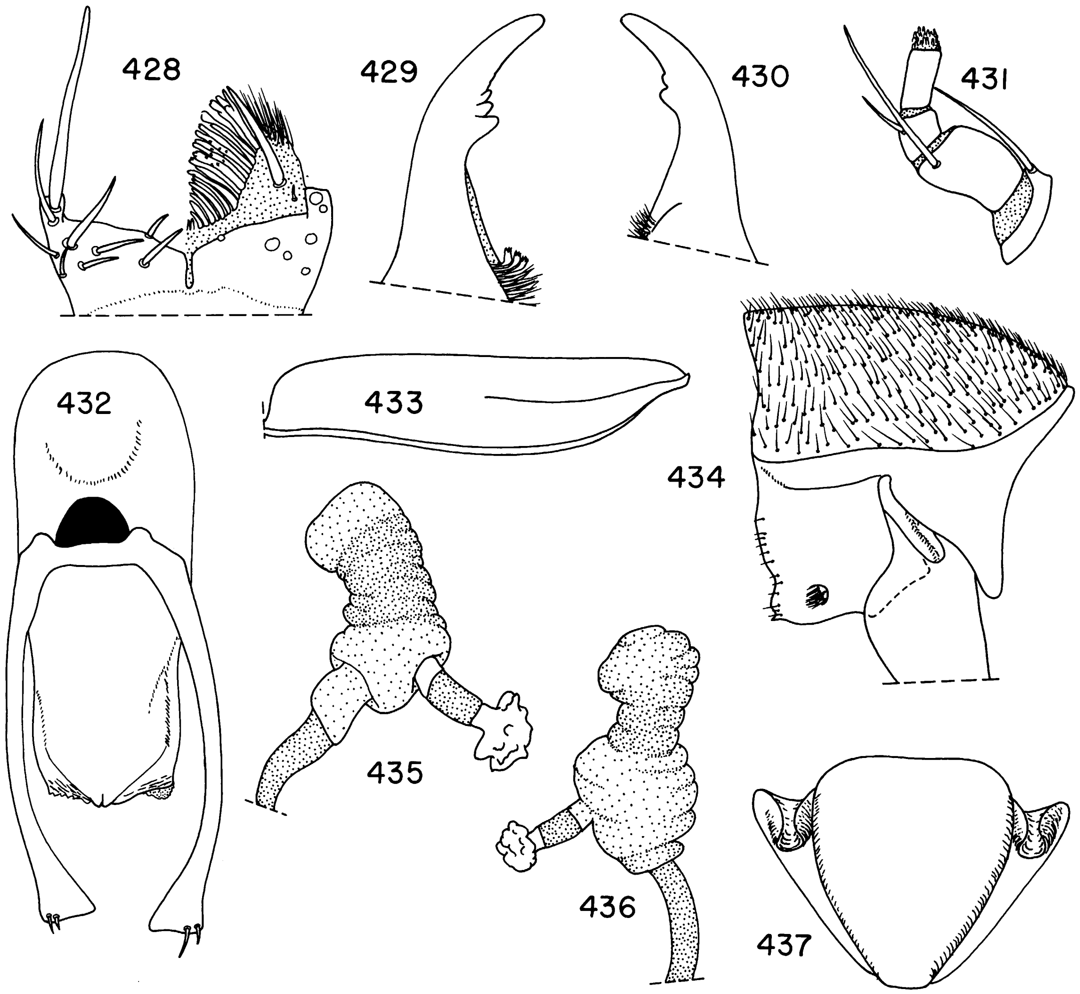
India: Uttar Pradesh: Kumaon, Haldwani (BMNH).

morio Heer Co(BMNH), Sp(BMNH, FMNH, IRSN); type country: Switzerland.

Algeria: (Clouet des Pesruches ä Medjez-Amar ? IRSN); La Calle (FMNH). **France:** Taussat, Gironde (BMNH); Vernet les Bain (IRSN); Lyon (IRSN); Montpellier (IRSN); St. Medard en Jalles, Gironde (IRSN); Lot-et, Garonne (MNHV); Savoie Dept., Belmont (MNHV); Biarritz (MNHV); Bourdeaux (MNHV). (Gironde, Fracture ? IRSN). **Spain:** Andalousia, San Pedro, Alcantara (IRSN); Andalousia, Lanjaron (IRSN); Malaga (IRSN); Arragon, Albarracin (MNHV); Ponferrada (FMNH); El Pardo (FMNH). **Switzerland:** Genève (IRSN). **Tunisia:** Sousse (IRSN); Fernana (MNHV).

tibialis Heer Co(BMNH), Sp(BMNH, FMNH, IRSN); type country: Switzerland.

Albania: Fushë e Arrësit (BMNH). **Algeria:** Bône ['Annaba] (IRSN). **Austria:** Kärnten Prov. (BMNH); Linz (IRSN); Neudorf (MNHV); Baumgarten (MNHV); Grünberg (MNHV); Graz, Styria (MNHV); Schladming (MNHV); Niedere Tauern Mountains (MNHV); Spittal (MNHV); Ferlach, Carinthia, Drau River (MNHV); Sachsenberg, Carinthia (MNHV); Wien (MNHV); Mödling (MNHV); Tirol Prov. (FMNH); Grünberg (FMNH). **Czechoslovakia:** Trencsen [=Trencin] (FMNH); Jablonica, Herzegovia (FMNH). **France:** Amelie les Bain (BMNH, IRSN); Chambery (IRSN); Limoges (IRSN); Lyon



FIGS. 428–437. The *tibialis* group. **428.** Labrum, right setae and left epipharyngeal lobe removed (*tibialis*). **429.** Mandible, left (*morio*). **430.** Mandible, right (*tibialis*). **431.** Labial palpus (*tibialis*). **432.** Aedeagus, dorsal (*tibialis*). **433.** Elytron, lateral (*tibialis*). **434.** Prothorax, lateral (*tibialis*). **435.** Spermatheca (*morio*). **436.** Spermatheca (*tibialis*). **437.** Terga IX and X, female (*morio*).

(IRSN); Landes Dept. (IRSN); Compiegne (IRSN); Prades (IRSN). **Germany, East:** Haringodorf, Usedom Island (MNHV). **Italy:** Aosta (BMNH); Trento (IRSN); Bozen [=Bolzano] (MNHV); Tarcento (FMNH); (Castelnovale, Talvera River ? IRSN). **Mongolia:** Chovd [=Hovd] aimak, 34 km N Somon Uenc [=Üyönch], Uenc [=Üyönch] Gol (CNC). **Norway:** Karasjok (MNHV); Kongsberg (MNHV); Haugesund (FMNH, MNHV). **Portugal:** Coimbra (IRSN). **Switzerland:** Laupen (IRSN); Heitenried (MNHV). **[Tibet?]:** Headwaters of Indus (FMNH). **Turkey:** Broussa (IRSN). **USSR:** Caucasus (FMNH). **Yugoslavia:** Sarajevo (MNHV); Visegrad (MNHV).

Undetermined.

Cyprus: Galatia (MNHV). **France:** Nyons (IRSN). **Nepal:** Bagmati Prov., 4 km S Tarang Marang, 900 m [16 km NE Kathmandu] (CNC). **Spain:** Madrid (BMNH); Guadarrama (BMNH); La Granja (BMNH); Potes (BMNH); Torrelodones (MNHV).

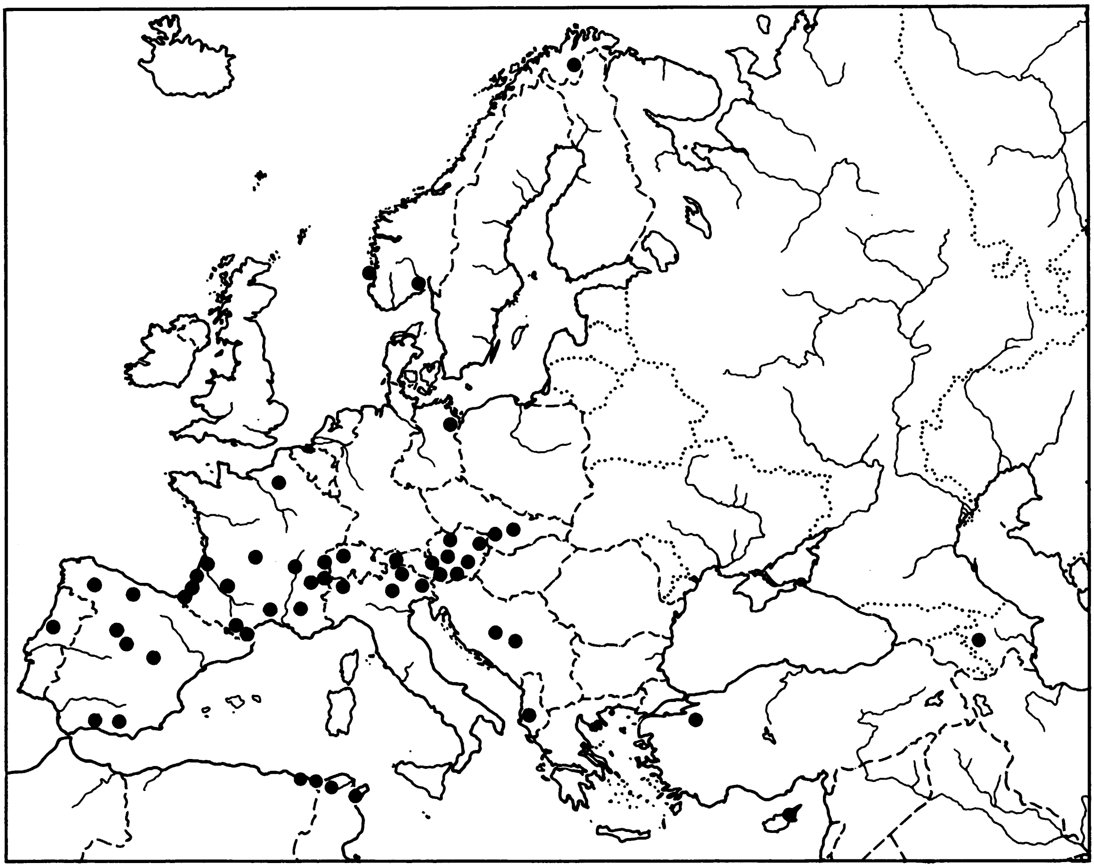


FIG. 438. Distribution of the *tibialis* group in Europe and North Africa.

32. *bonariensis* group

Figures 10, 52, 440–455,
578–583, 718–723

DIAGNOSIS: The presence of a nearly complete pronotal marginal bead (fig. 449), complete elytral epipleural ridge, and median incision of the labrum (fig. 442), the closed procoxal fissure (fig. 449), and the truncate posterior margin of tergum VIII will separate *B. bonariensis* from all other groups of *Bledius*. Unique to *bonariensis* are the subantennal pockets (figs. 52, 441) which can be seen only by clearing the head capsule; the absence of parameres (fig. 451) will distinguish *bonariensis* from all other groups but the *infans* and *forcipatus* groups. The supraantennal ridge of *bonariensis* is extended anteriorly into a broad horn (fig. 441), the gular sutures (fig. 446) are separated for a short distance from the submentum, the prosternum has a setigerous pit (figs. 449, 718, 719), and the tarsi are three segmented (fig. 450).

DESCRIPTION: Supraantennal ridge of male enlarged as short, broad, anteriorly directed horn; supraantennal ridge of female moderately developed and not extended anteriorly as horn. Head (figs. 52, 441) with internal subantennal pocket; pocket larger in male than female; midbasal cephalic horn absent. Postocular lateral carina absent. Clypeal margin not reflexed; margin without tubercles; middle without tubercles, spines, or ridges. Gular suture (fig. 446) separated anteriorly, more so in male than in female. Submentum without process on lateroapical margin. Labral margin (fig. 442) broadly emarginate; margin not reflexed; median incision present; surface with median impression. Epipharyngeal lobe long (fig. 442); dorsal surface with one long and one minute seta; median processes of anterior margin with lobed apices; lateroapical portion of lobe with many long, slender, unbranched, or biramous processes. Labial palps (fig. 440) with second segment shortest; first and third segments of subequal length; third segment narrowest, first and second of subequal thickness; first segment with two setae, second segment with one seta. Submentum not excavated. Mentum (fig. 440) elongate and trapezoidal; setae evenly distributed over surface. Hypopharynx (figs. 578–583) with lateral row of setae strongly and gradually convergent; basal setae arranged in basal cluster; basal setae slender; basal cluster of setae not on a plate; central row of setae numerous and densely clustered distally and arranged as single row medially; disk with setae present on apical edge and absent medially; disk without cuticular processes; disk with a few coronal pegs scattered over median surface. Prementum with four sclerites; lateral sclerites feebly sclerotized. Galea with a few fanlike rows of setae on apex; ventral surface without setae; dorsomedial edge with weakly developed lobe. Mandibles quadridentate in female (fig. 443) and tridentate (figs. 444, 445) in male; basal denticle short and stout.

Pronotum (figs. 447, 449) without horn. Marginal bead present and slightly interrupted near base; bead separating notum and hypomeron, bead not on hypomeron. Protergosternal suture absent. Procoxal fissure closed. Protrochantin concealed. Prosternal process short and carinate. Prosternum with setigerous pit (figs. 718, 179); setae flattened (figs. 722, 723); pit with pores among setae (figs. 720–723); anterior margin entire. Elytral epipleural ridge present and complete; posterior margin thinly sclerotized along most of width, appears to be broad membranous marginal strip.

Tarsi three segmented (fig. 450). Protibia with one row of spinelike setae and others scattered (fig. 448).

Abdominal tergum VII with fine posterior fringe on posterior margin. Tergum VIII with posterior margin truncate; margin entire. Tergum IX with glandular canal narrowly open dorsally (fig. 453). Tergum X of female and male with short, poorly developed struts on anterior margin (fig. 453).

Aedeagus (figs. 451, 452) without parameres. Median lobe with ventral surface fused medially; basal half bulbous and enlarged; distal half flattened.

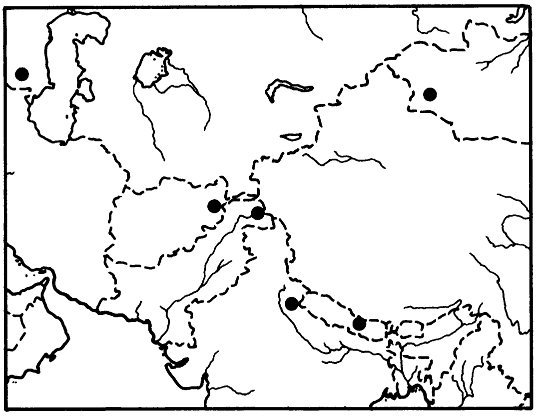


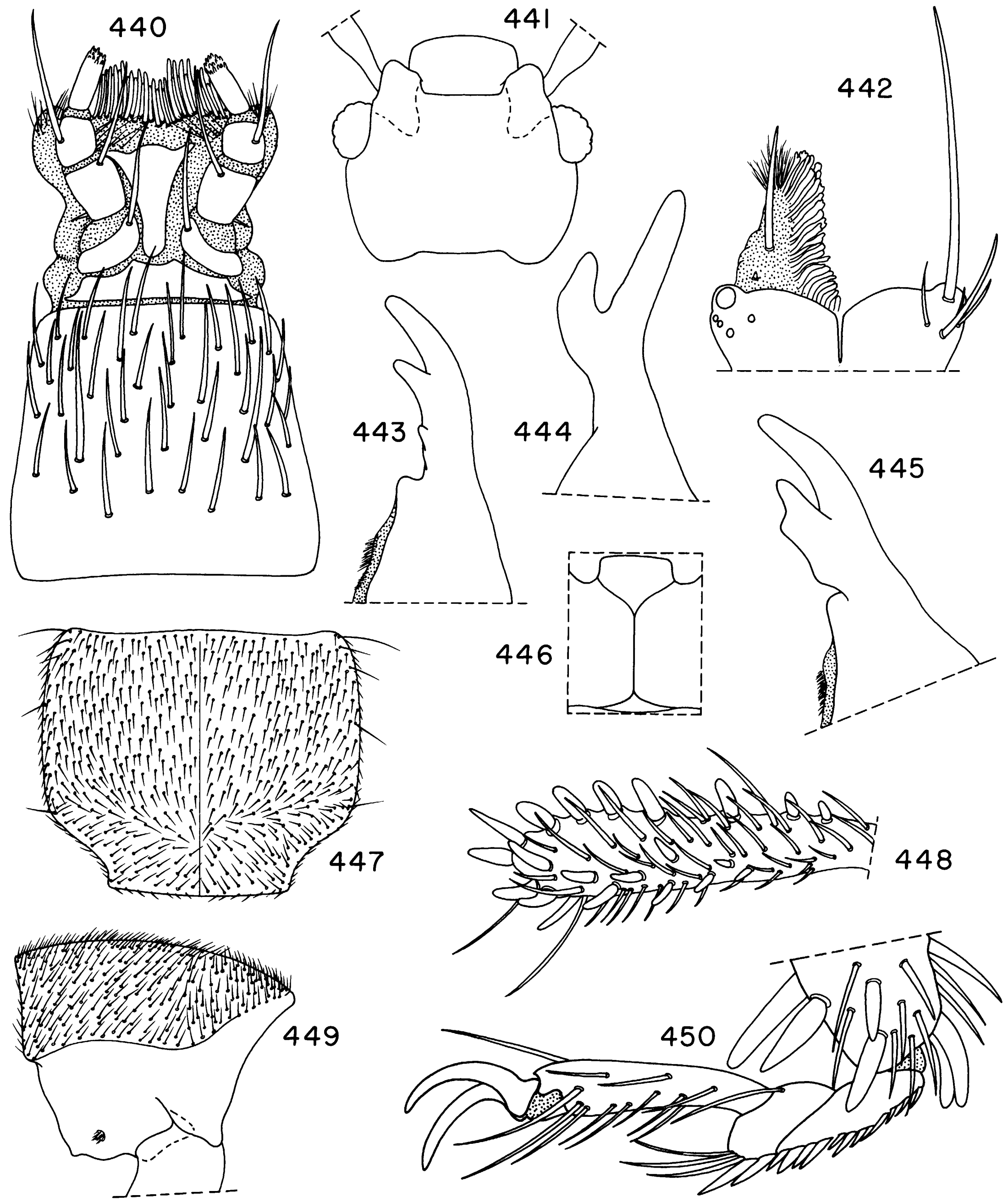
FIG. 439. Distribution of the *tibialis* group in Central Asia.

Spermatheca (fig. 454) tripartite. Receptacle with basal portion enlarged and feebly sclerotized; distal portion membranous and only slightly differentiated from accordion tube; receptacle without brimlike ridges; distal end not invaginated. Spermathecal gland sclerotized and with irregular surface and shape.

DISTRIBUTION AND HABITAT: This species is known only from Argentina, Brazil, and Uruguay, where it was collected from coastal localities. The collections suggest that the species lives in a saline habitat (fig. 455).

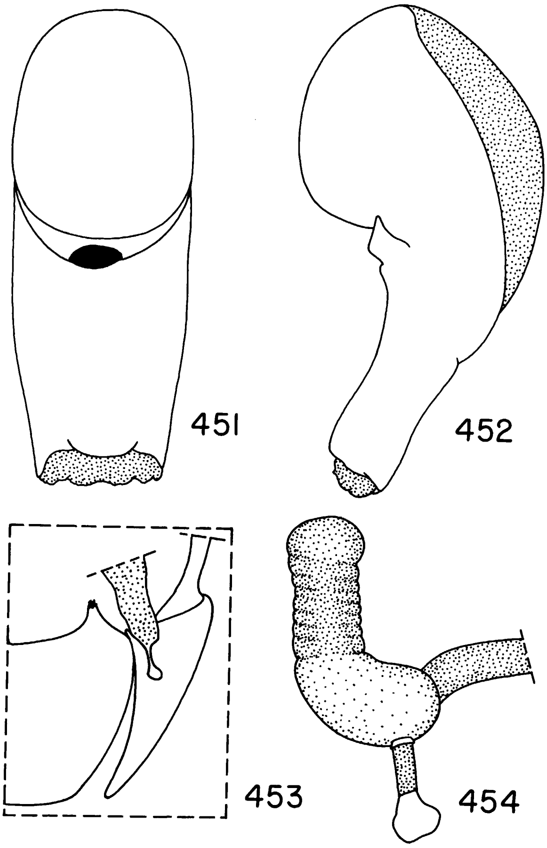
DISCUSSION: *Bledius bonariensis* was included in the older version of *Hesperophilus*, a concept replaced by *Dicarenus*. *Dicarenus* is composed of many disparate elements. *Bledius bonariensis* is unique in several respects and is therefore segregated from other *Bledius.*

The males have an enlarged supraantennal ridge; the mandibles are tridentate with the second denticle enlarged, flattened, and the margin lobed. The supraantennal ridges of the female are normally developed and the mandible quadridentate. The second (subapical) mandibular denticle of the female is slender. Unique to the group are the pair of subantennal pockets which are larger in the male than the female. The gular sutures are separated at the very anterior portion in this species, therefore suggesting inclusion in the



FIGS. 440–450. The *bonariensis* group. *Bledius bonariensis*. **440.** Labium. **441.** Head, dorsal, male, mouthparts removed; dotted lines indicate limits of subantennal pockets. **442.** Labrum, left setae and right epipharyngeal lobe removed. **443.** Mandible, right, dorsal, female. **444.** Mandible, right, lateral, male. **445.** Mandible, right, dorsal, male. **446.** Gular region. **447.** Prothorax, lateral. **448.** Protibia. **449.** Prothorax, lateral. **450.** Metatarsus.

punctatissimus group. I separate it because the labrum has a median incision, the head has subantennal pockets, the protergosternal suture is absent, the aedeagus lacks para-



FIGS. 451–454. The *bonariensis* group. *Bledius bonariensis.* **451.** Aedeagus, dorsal. **452.** Aedeagus, lateral. **453.** Right tergite IX and right half of tergum X. **454.** Spermatheca.

meres, the spermatheca is tripartite, and there are several differences of the hypopharynx.

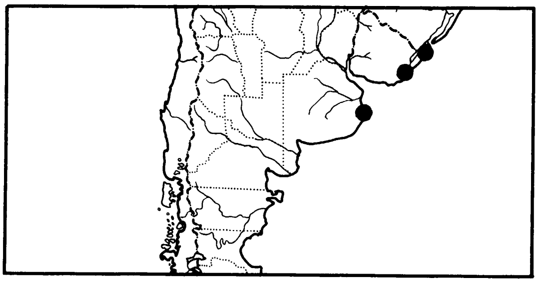


FIG. 455. Distribution of the *bonariensis* group from Brazil to Argentina.

The holotype of *B. bonariensis* Bernhauer is so badly eaten by dermestids that only a few fragments (of the abdominal sternites; eighth, ninth, and tenth tergites; metalegs; and pterosterna) remain. However, the posterior margin of tergum VIII is truncate. Among the species in South America only those in the *punctatissimus, caribbeanus,* and *forcipatus* group and a species from San Clemente, Argentina, have a truncate margin of tergum VIII. A specimen in the Naturhistorisches Museum Wien from Canciones, Atlantica, Uruguay, determined as *B. bonariensis* by Bernhauer, is conspecific with the species from San Clemente. Furthermore, the description states that basal angles of the pronotum are sharply angulate. None of the species in the *punctatissimus, caribbeanus,* and *forcipatus* groups have angulate basal angles of the pronotum, but the species from San Clemente and the specimen in Vienna do.

Species Included and Material Examined

bonariensis Bernhauer H(FMNH), Sp(AMNH, NHMV); type country: Argentina.

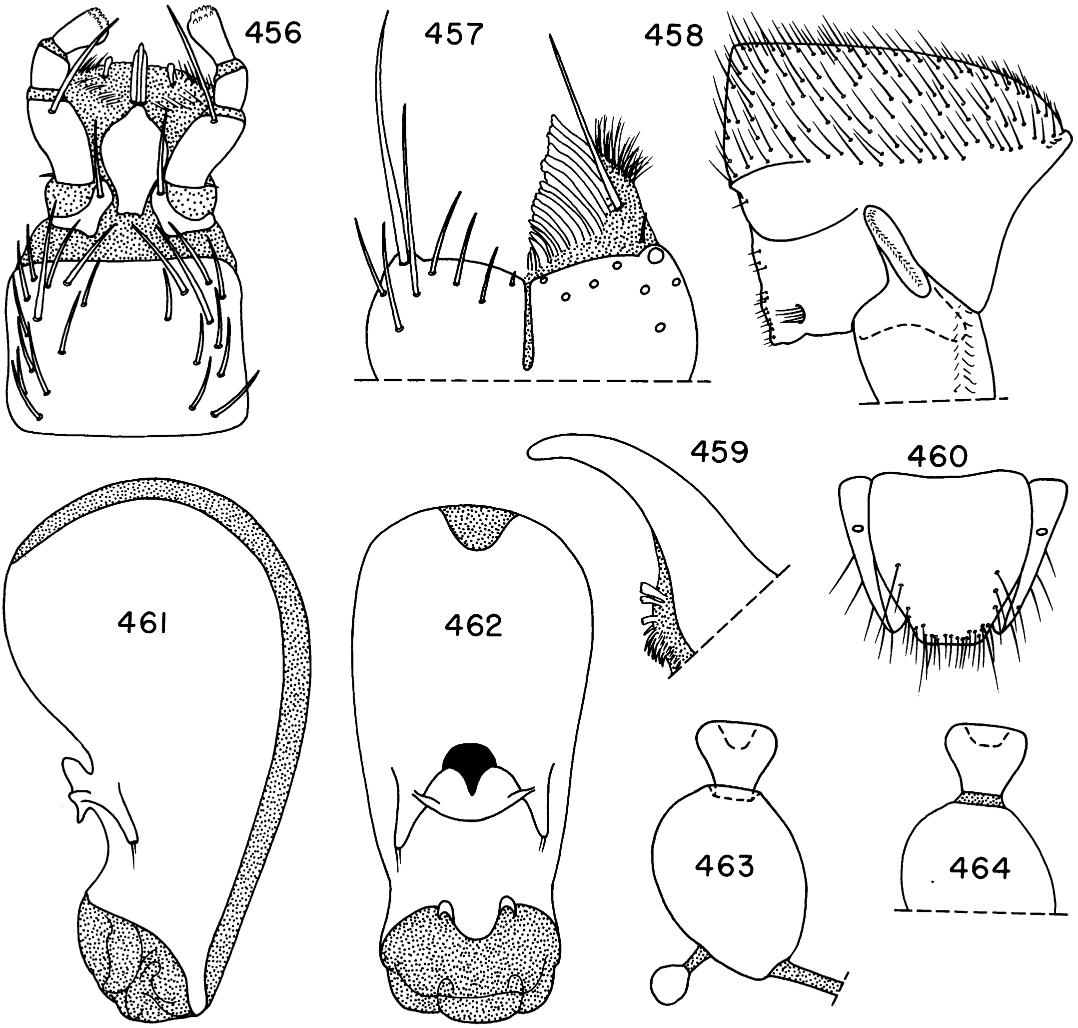
Argentina: Buenos Aires Prov., San Clemente (AMNH). **Brazil:** Rio Grande do Sul, Cassino Beach (AMNH). **Uruguay:** Rocha Prov., Atlantica, Canciones (MNHV).

33. *pulchellus* group

Figures 10, 456–465, 568–571, 713–717

DIAGNOSIS: The incomplete pronotal marginal bead (fig. 458) and elytral epipleural ridge, the median labral incision (fig. 457), and the truncate posterior margin of tergum VIII will separate *pulchellus* from all other groups. Other useful characters include presence of the prosternal setigerous pit (figs. 458, 713, 714), presence of the protergosternal suture that is anteriorly divergent from the pronotal marginal bead, and the absence of the membranous lobe from the posterior margin of the elytra. Two similar groups are the *verres* and *bispinus* groups, both of which have a complete elytral epipleural ridge.

DESCRIPTION: Supraantennal ridge of male moderately enlarged and without horns; supraantennal ridge of female low, not enlarged, and without horns; subantennal pockets absent. Head without midbasal horn; postocular lateral carina absent. Clypeal margin not reflexed and without tubercles; clypeal middle without tubercles, spines, or ridges. Gular sutures fused. Labral (fig. 457) margin



FIGS. 456–464. The *pulchellus* group. *Bledius pulchellus*. **456.** Labium. **457.** Labrum, right setae and left epipharyngeal lobe removed. **458.** Prothorax, lateral. **459.** Mandible, right, female. **460.** Tergites IX and Tergum X, female. **461.** Aedeagus, lateral. **462.** Aedeagus, dorsal. **463.** Spermatheca. **464.** Spermatheca.

emarginate; anterior margin slightly reflexed; median incision present; dorsal surface flat and without midlongitudinal impression or some individuals with slight midlongitudinal impression. Epipharyngeal lobe long; dorsal surface with one long and one short seta; median processes of anterior margin with lobed or simple apices; lateroapical portion with numerous long, slender, unbranched processes. Labial palps (fig. 456) with second segment shortest, first segment longest, third segment intermediate; first segment slightly thicker than second; first segment with two setae; second segment without setae. Submentum not excavated. Mentum (fig. 456) transverse and rectangular; setae present laterally and absent medially. Hypopharynx (figs. 568–571) with lateral row of setae gradually and strongly convergent; basal setae arranged in cluster; cluster not on plate; basal setae broad and flattened; central row of setae absent medially and dense anteriorly; disk with some setae on anterior portion, setae absent medially; disk covered with short broad cuticular processes; coronal pegs scattered over surface of disk. Prementum (fig. 456) with one median sclerite. Galea with fanlike rows of setae on apex; ventral surface without setae. Mandibles bidentate in male, edentate in female (fig. 459).

Pronotal (fig. 458) horn absent. Marginal bead present and incomplete (fig. 458). Protergosternal suture present. Bead and suture divergent. Procoxal fissure open. Protrochantin exposed. Prosternal process elongate and carinate. Prosternal setigerous pit present (figs. 713–715); pit with pores among and behind setae (figs. 716, 717); anterior margin entire, without notch. Elytral epipleural ridge present and incomplete, present only on apical portion; posterior margin without membranous lobe.

Tarsal formula 3-3-3. Protibia with one row of spines, others scattered over posterior surface. Metatibia with row of apically expanded and flattened setae.

Abdominal tergum VII with fine fringe on posterior margin. Tergum VIII with posterior margin truncate; margin not serrate. Tergum IX with glandular canal closed dorsally (fig. 460). Tergum X without struts on anterior margin (fig. 460).

Aedeagus (figs. 461, 462) with parameres present. Parameres short, flattened, appressed to median lobe, and sclerotized on medial surface. Median lobe with ventral surface membranous; base bulbous and apical half cylindrical.

Spermatheca (figs. 463, 464) tripartite. Receptacle with apical and basal portions sclerotized; basal portion larger than apical portion, apical and basal portions separated by short membranous tube; receptacle without brimlike ridges; distal portion with invagination. Spermathecal gland sclerotized, spheroidal, and with nearly smooth surface.

Distribution and Habitat: This group is known only from a few coastal localities in southern India and Sri Lanka and from Diego Garcia in the Chagos Archipelago (fig. 465).

Discussion: The sole species in this group was included in the older interpretation of *Hesperophilus* which was replaced by *Dicarenus*. This species is actually near the *verres* group from which it is easily separated.

Bledius pulchellus shares many characters with the *verres* group. These include the moderately enlarged supraantennal ridge of the male and the long setae on the medial side of antennomeres 4 to 8 of the male, the edentate mandibles of the female, the presence of a median labral incision, the anteriorly divergent protergosternal suture and pronotal marginal bead, the absence of the membranous lobe of the posterior margin of the elytron, and the truncate posterior margin of tergum VIII. The incomplete pronotal marginal bead and elytral epipleural ridge and the flat dorsal surface of the labrum lead me to separate *pulchellus* from the *verres* group.

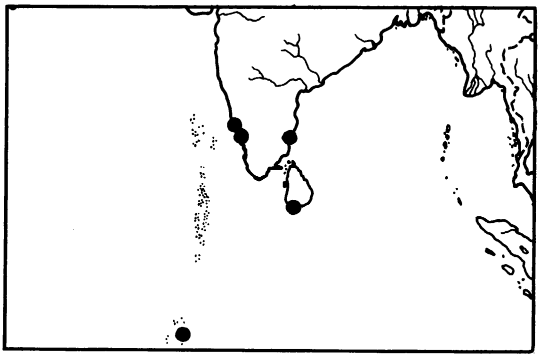


Fig. 465. Distribution of the *pulchellus* group in India, Sri Lanka, and the Chagos Archipelago.

Species Included and Material Examined

pulchellus Kraatz Sp(FMNH, IRSN); type country: Sri Lanka.
Chagos Archipelago: Diego Garcia (BMNH). **India:** Calicut (BMNH); Malabar (BMNH); Pondichery (BMNH). **Sri Lanka:** Weligama (BMNH, FMNH).

34. *verres* group

Figures 9, 61–65, 466–484, 590–592, 595–600, 724–728

Diagnosis: This large group of species is separated from all other groups by the complete pronotal marginal bead (fig. 474) and elytral epipleural ridge, the open procoxal fissure, the fused gular sutures, the presence of a median labral incision (fig. 466), and unreflexed clypeal margin, the fine fringe of tergum VII, the shallowly to moderately emarginate labral margin (fig. 466), the presence of a midlongitudinal labral impression, the truncate margin of tergum VIII, and the three-segmented tarsi (figs. 479, 480). The *verres* group is most similar to the *pulchellus* and *bispinus* groups. Characters to separate these groups from *verres* are also discussed in the Diagnoses of these groups.

Other useful characters include the presence of a prosternal setigerous pit (figs. 474, 724), the absence of a membranous lobe on the elytral margin, the presence of a protergosternal suture (fig. 474), and the short median lobe and short slender parameres (fig. 476).

DESCRIPTION: Supraantennal ridge of male enlarged (fig. 473) or not enlarged, and without horns; supraantennal ridge of female low, not enlarged, and without horns. Head without subantennal pockets; midbasal horn absent; postocular lateral carina absent. Clypeal margin not reflexed; anterior margin with or without tubercles; clypeal middle of male with or without tubercles, spines, ridges; clypeal middle of female unmodified. Gular sutures fused. Labral (fig. 466) margin truncate or emarginate; anterior margin not reflexed; median incision present; dorsal surface flat or with broad midlongitudinal impression. Epipharyngeal lobe long; dorsal surface with one long seta and one minute seta; median processes with lobed apices; lateroapical processes numerous, slender, and unbranched or simply branched. Labial palps (fig. 467) with second segment shortest, first segment longest, third segment intermediate; first segment thickest; first segment with two setae, second segment with one. Submentum not excavated. Mentum transverse and trapezoidal; surface with more setae laterally than medially. Hypopharynx (figs. 590–592, 595–600) with lateral rows of setae gradually and strongly convergent toward base; basal setae arranged in cluster; basal setae slender; basal cluster of setae on plate; central row of setae dense distally and absent medially and proximally; disk with setae scattered on apical portion; disk covered with short cuticular processes arranged in palmate groups or fused to form broad, flattened process; coronal pegs scattered over most of central portion of disk. Prementum with three sclerites, one medial and two lateral; lateral sclerites weakly sclerotized. Galea with numerous fanlike rows of setae on apex; ventral surface without setae; dorsomedial edge with lobe. Mandibles edentate, bidentate (figs. 468, 469), or tridentate (figs. 470–472).

Pronotal (fig. 474) horn absent. Marginal bead present and complete. Protergosternal suture present. Bead and suture parallel. Procoxal fissure open. Protrochantin exposed. Prosternal process moderately elongate and carinate. Prosternal setigerous pit present (figs. 724, 725); pit with pores among and behind setae (figs. 726–728); margin entire, without notch. Elytral epipleural ridge present and complete; posterior margin without membranous lobe.

Tarsi three segmented (figs. 479, 480); some of large Asian species with fourth segment or pseudosegment. Protibia with one row of spinelike setae and with others scattered over posterior surface.

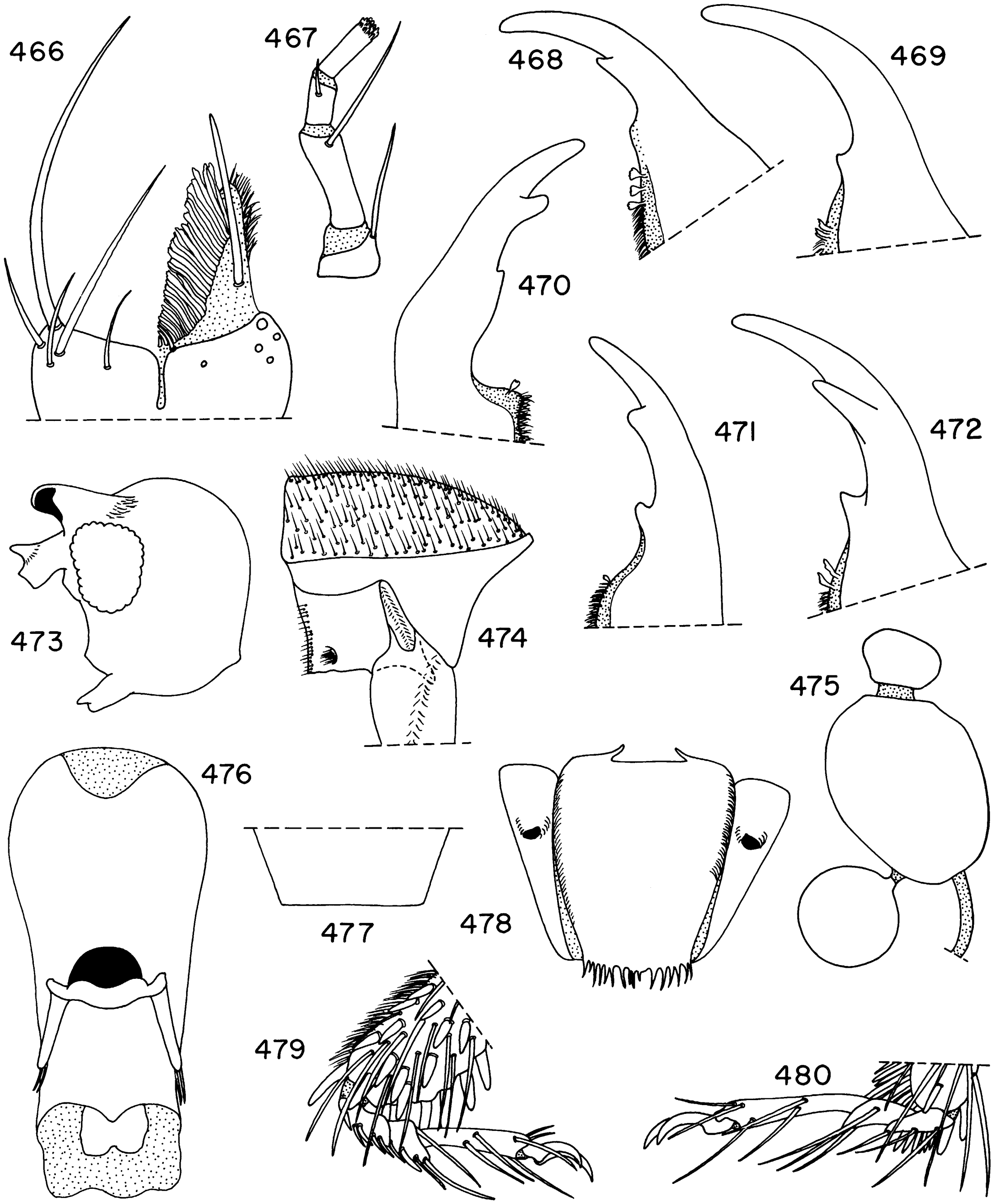
Abdominal tergum VII with fine fringe on posterior margin. Tergum VIII with truncate posterior margin (fig. 477); margin not serrate. Tergum IX (fig. 478) with glandular canal closed dorsally. Tergum X with small struts on anterior margin (fig. 478).

Aedeagus (fig. 476) with parameres. Parameres slender, with sclerotized median surface; parameres not extending beyond apex of median lobe. Median lobe bulbous; apical portion more or less cylindrical; ventral surface midlongitudinally membranous.

Spermatheca (fig. 475) tripartite. Receptacle sclerotized and divided by accordion tube into two parts; basal part larger than distal part; basal and distal parts without brimlike ridges; distal part with invagination. Spermathecal gland sclerotized; surface smooth or irregular; shape spherical or irregular; size greater than or less than distal part of receptacle.

DISTRIBUTION AND HABITAT: The species of this group are found in the Old World tropics and subtropics with some species living in more temperate regions. The group occurs from the Cape Verde Islands eastward across Africa and southern Europe, southern Asia, Indonesia, the Philippines to Japan, New Guinea, and Australia. The Australian records are few but there are probably a number of species in the northern areas and few in the south (figs. 481–484).

DISCUSSION: Twenty-nine species that were



FIGS. 466–480. The *verres* group. **466.** Labrum, right setae and left epipharyngeal lobe removed (*verres*). **467.** Labial palpus (*verres*). **468.** Mandible (*curticornis*). **469.** Mandible, female (*verres*). **470.** Mandible, male (*Bledius* sp.). **471.** Mandible, female (*Bledius* sp.). **472.** Mandible, male (*verres*). **473.** Head, lateral, male, mouthparts and antenna removed (*verres*). **474.** Prothorax, lateral (*verres*). **475.** Spermatheca (*verres*). **476.** Aedeagus, dorsal (*verres*). **477.** Tergum VIII, apex (*verres*). **478.** Segments IX and X, female, dorsal (*verres*). **479.** Protarsus (*verres*). **480.** Metatarsus (*verres*).

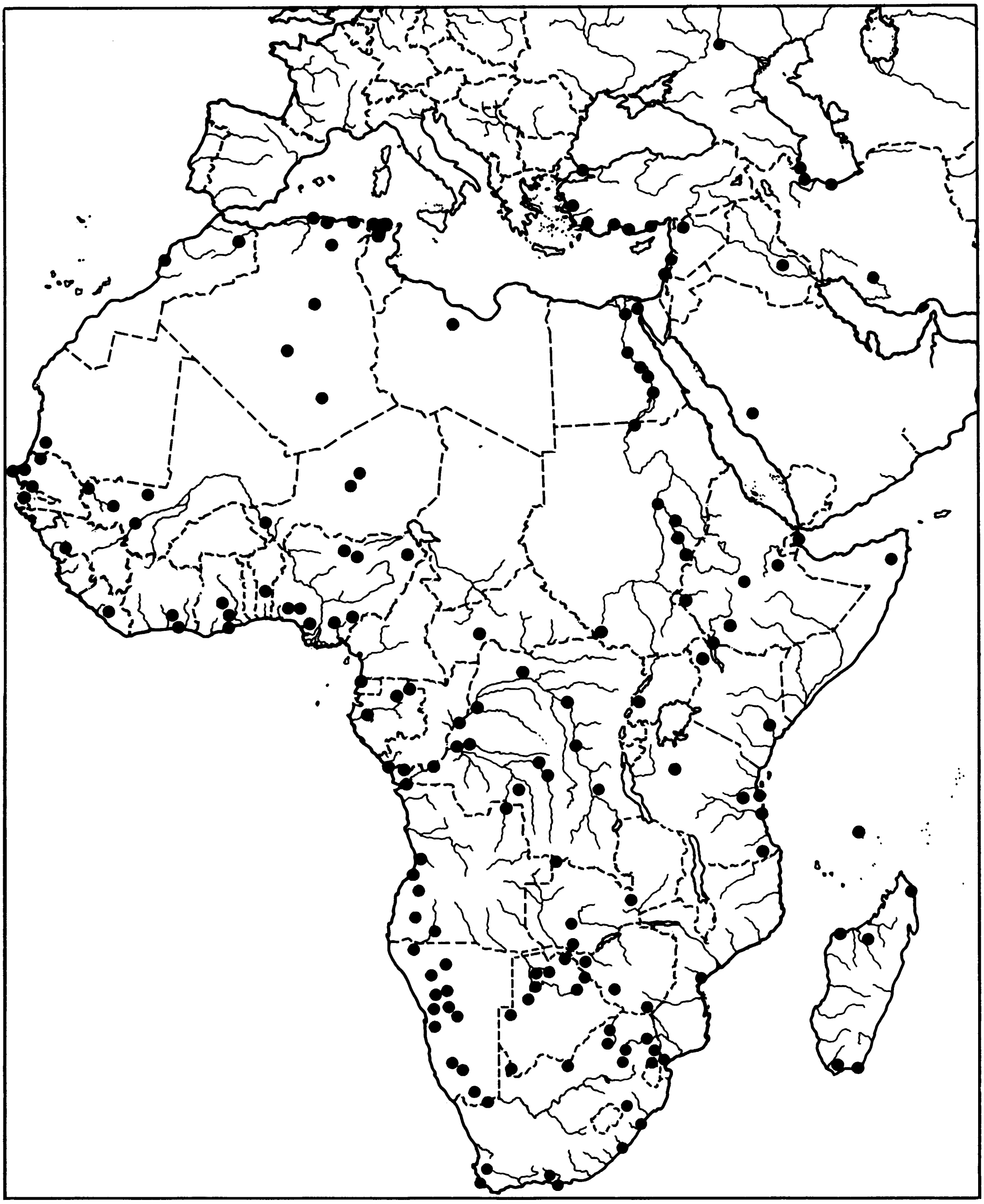


FIG. 481. Distribution of the *verres* group in Africa.

in *Pucerus,* including the type species of that subgenus, 17 species that were in *Dicarenus,* 5 from *Hesperophilus,* 2 from *Astycops,* and 12 species previously unassigned to an infrageneric taxon (table 9) compose the *verres* group. Recognition of the *verres* group represents a major enlargement of *Pucerus* and a major disassembling of *Dicarenus.*

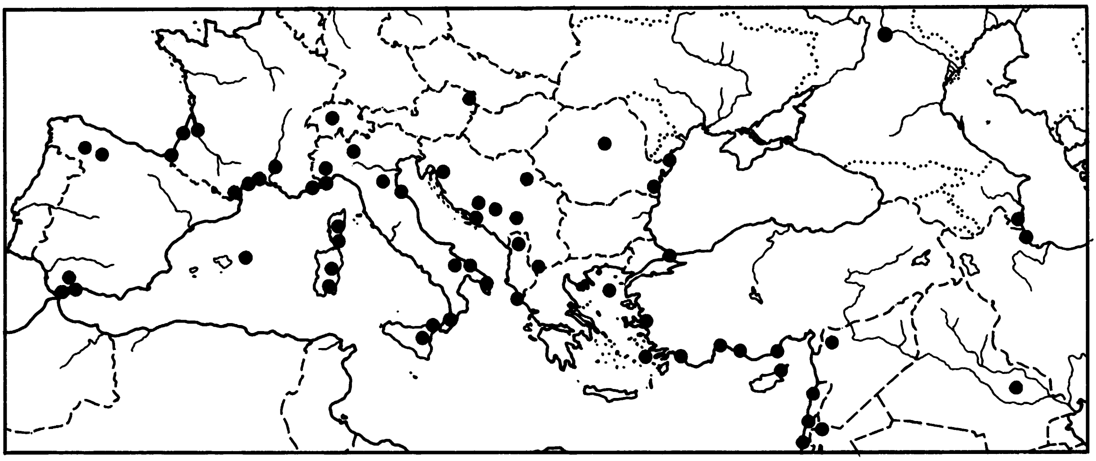


FIG. 482. Distribution of the *verres* group in Europe.

About half of the species included in the *verres* have a bifurcate tubercle, a pair of tubercles, or a transverse ridge on the middle of the clypeus. The others lack such clypeal armature. Most species with these structures were placed in *Pucerus* (for a list see *Pucerus* in table 9); species without them were placed elsewhere (table 9). Combining these two

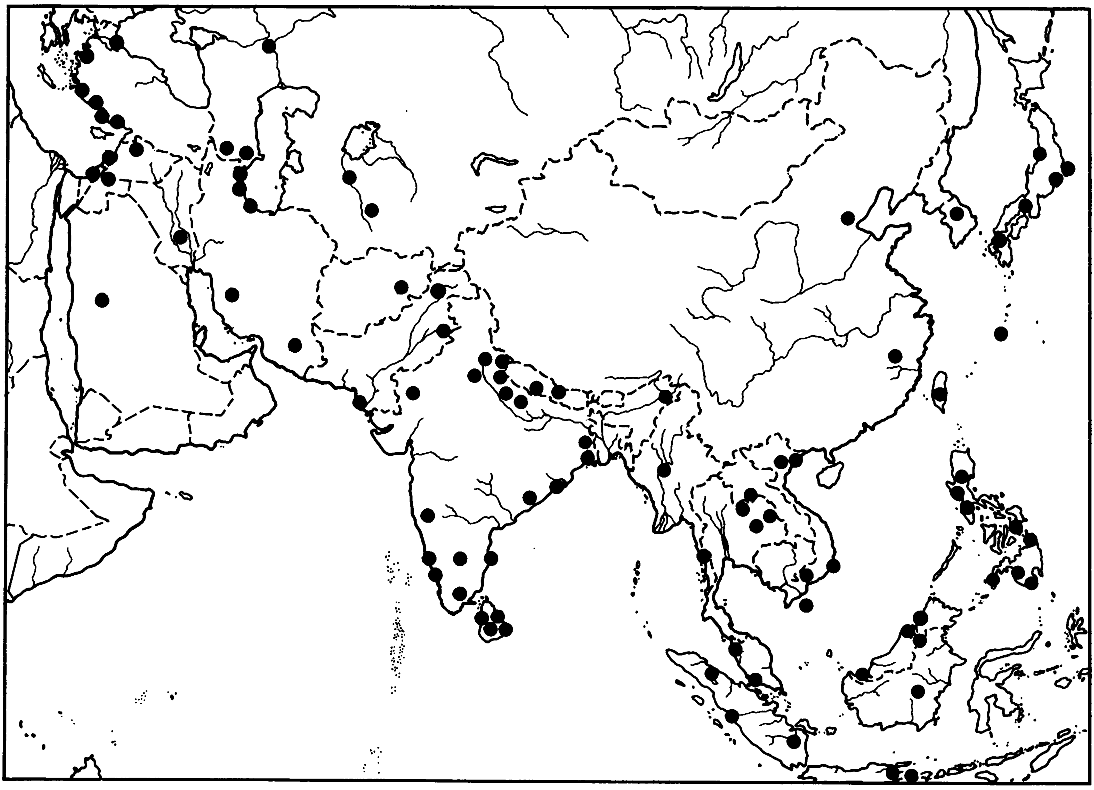


FIG. 483. Distribution of the *verres* group in Asia and the Indo-Pacific region.

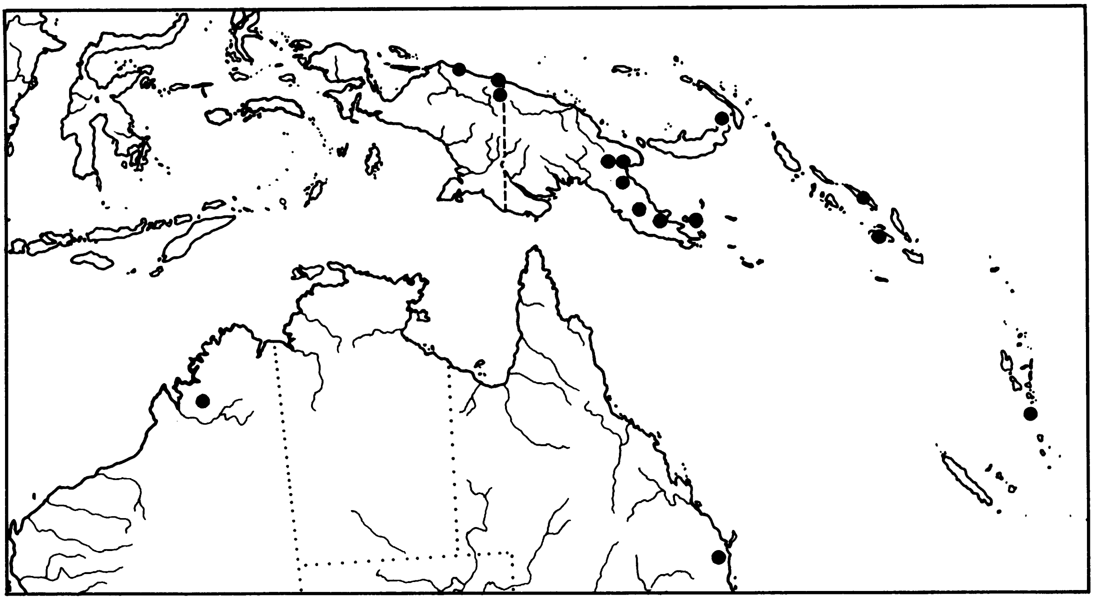


FIG. 484. Distribution of the *verres* group in the Indo-Australian region.

groups represents a significant departure from the existing subgeneric classification. It is unclear how species with the modified clypeus are related to one another or to those lacking the armature. Three species, from India and Burma, *B. bispinus* Kraatz, *B. championi* Bernhauer, and *B. fuscicornis* Cameron, are similar to species in the *verres* group in all respects but two. These three species have four-segmented tarsi and an emarginate posterior margin of tergum VIII; the species of the *verres* group have three-segmented tarsi and the posterior margin of tergum VIII is truncate. Pending further study, I have segregated the three aforementioned species into the *bispinus* group. I have reservations about this decision because some of the larger Asian species have a line across the middle of the basal tarsomere, which I interpret to be a false segment (figs. 61–65).

Species Included and Material Examined

aethiops Bernhauer T(FMNH); type country: Congo.

Congo: (Kunungu? FMNH). **Equatorial Guinea:** Bata (MNHV). **Guinea:** Kindia (MNHV).

africanus Cameron T(BMNH); type country: Zaire.

Zaire: Bena Dibele (BMNH).

albomaculatus Bernhauer T(FMNH); type country: Tanzania.

Tanzania: Dar-es-salam (FMNH).

albopubescens Cameron T(BMNH); type country: Philippines.

Philippines: Manila (BMNH).

alfierii Koch Sp(MNHV); type country: Egypt.

Sudan: Wadi Halfa (MNHV).

arabicus Coiffait P,Sp(HCC); type country: Saudi Arabia.

Saudi Arabia: (Bahara? HCC); Village Qaraah Khamis (HCC); (Wadi Jiran ? HCC).

arenicola Fauvel Syn(IRSN); type country: India.

India: Malabar, Mahé (IRSN).

austrinus Herman Sp(FMNH); type country: Australia.

Australia: Kimberley District (FMNH).

beesoni Cameron T,Sp(BMNH), Co(FMNH); type country: India.

India: Rajpur (Arni Gad ? BMNH); Kheri Rau, Siwaliks (BMNH, FMNH); Dehra Dun, Nim Nadi (BMNH); Mohan Rau, Siwaliks (BMNH).

bipustulatus Bernhauer T,Sp(FMNH), Sp(BMNH, MNHV); type country: eastern Africa.

Kenya: Tana [= Tana River ?] (FMNH, MNHV); Turkana District (Kacheliba, West Suk ? FMNH). **South Africa:** Natal, Estcourt (BMNH); Natal (Weenen? BMNH).

birmanus Cameron T,Sp(BMNH), Sp(FMNH); type country: Burma.

Burma: Tavoy (BMNH). **Malaysia:** Port Dickson, Negeri Sembilan (BMNH).

capicola Cameron T(BMNH); type country: South Africa.

Central African Republic: Fort Sibut [=Sibut] (BMNH). **South Africa:** Simonstown (BMNH).

cariniceps Bernhauer T,Co,Sp(FMNH), Co,Sp(BMNH); type country: Zaire.

Zaire: Leopoldville [=Kinshasa] (FMNH); Boma (FMNH); Sankuru River (Komi? (FMNH); Lusambo (FMNH).

cavus Eppelsheim T(MNHV), Sp(FMNH); type country: West Africa.

Ghana: (FMNH, MNHV).

congoensis Cameron Co,Sp(BMNH, FMNH); type country: Zaire.

Angola: Malemba [=Malembo, Cabinda] (FMNH). **Zaire:** Mushie (BMNH, FMNH).

curticornis Fauvel Syn(IRSN), Sp(MNHV); type country: Zaire.

Mali: Badoumbe (BMNH). **Nigeria:** Kano (MNHV). **Zaire:** Kindu (FMNH); Leopoldville [=Kinshasa] (FMNH); Stanleyville [=Kisangani] (FMNH); Kasai River (FMNH) (Ed Luja, Kondue? MNHV).

curvicornis Sharp Syn,Sp(BMNH), Sp(FMNH, MNHV); type country: Japan.

China: Fukien, Shaowu (FMNH). **Japan:** Kanagawa (FMNH); Niigata (BMNH, MNHV); Wakamatsu, Fukushima Prefecture (BMNH). **Korea:** (Gensu? FMNH).

decorsei Cameron H(MNHP); type country: Central African Republic.

Central African Republic: Dar Banda Merid. Krebedje (Fort Sibut) (MNHP).

dilutipennis Motschulsky Sp(BMNH, FMNH, IRSN, MNHV); type country: East Indies.

Burma: (IRSN). **India:** Kumaon, Uttar Pradesh, Tankapur (FMNH); Dehra Dun (FMNH, BMNH); Madras (MNHV). **Iran:** Iranshahr (MNHV).

distans Fauvel Syn,Sp(IRSN); type country: Madagascar.

Madagascar: Fort Dauphin [=Taolanarp] (IRSN); Vohimarina (IRSN).

ealanus Cameron Co(BMNH, IRSN); type country: Zaire.

Zaire: Eala (BMNH, IRSN).

fossor Heer Sp(FMNH, BMNH, IRSN, MNHV); type country: Switzerland.

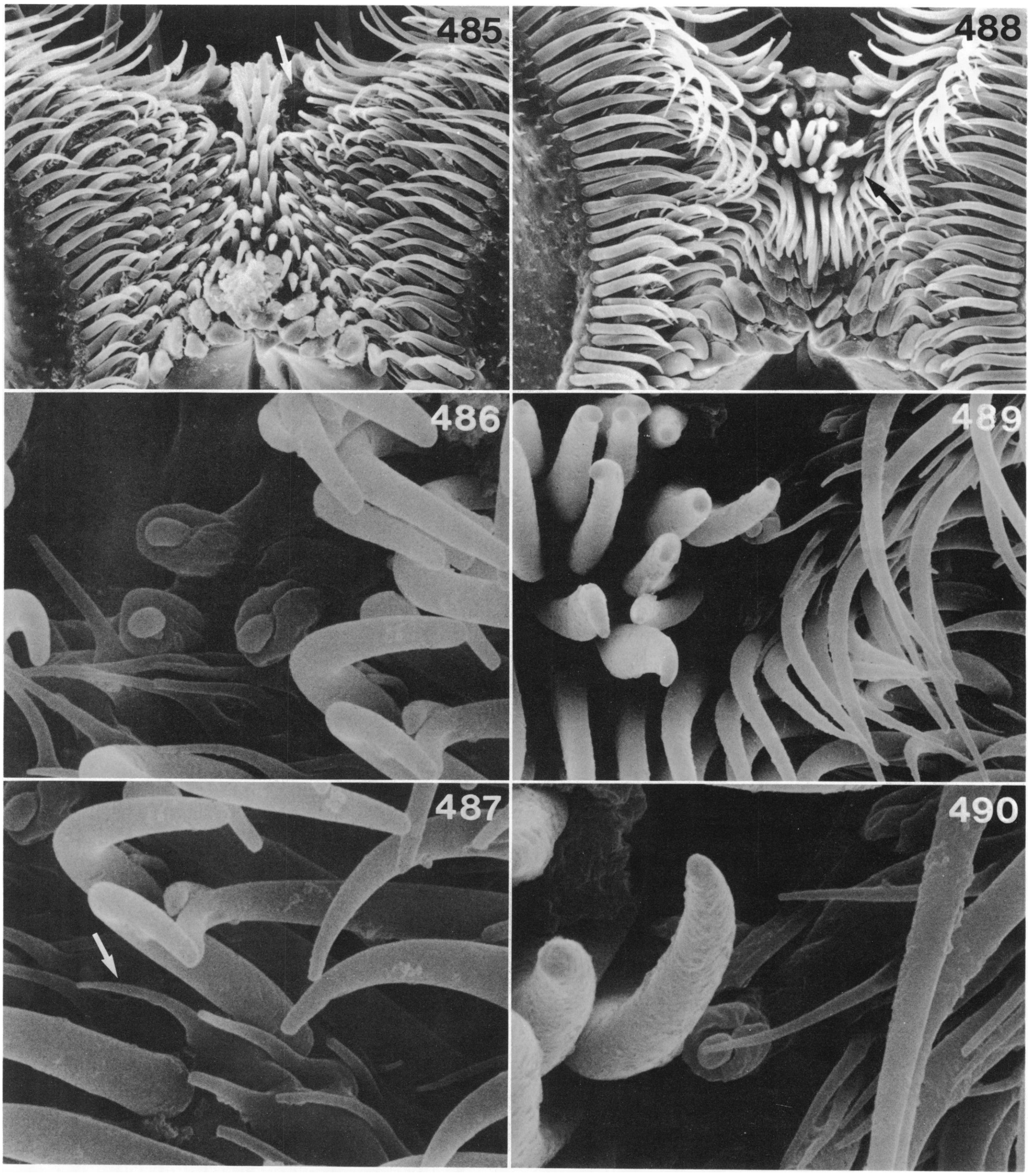
Algeria: Philippeville [=Skikda] (IRSN). **Austria:** Baumgarten (MNHV); Enzerdorf (MNHV). **Bulgaria:** (FMNH); Nessebar [=Nesebur] (MNHV); Pirin, Macedonia (BMNH); (Mittl. Struma, Central Macedonia, Kresana-Defile? MNHV). **France:** Corsica, Ghisonaccia, Gravier du Fiumorbo (IRSN); Amelie les Bains (IRSN, BMNH); Avignon (IRSN); Montpellier (IRSN); Nice (IRSN); Millas, Pyrenees Oriental (FMNH); Béziers (MNHV). **Gibraltar:** (IRSN); La Linea (BMNH). **Greece:** Corfu (MNHV, FMNH); Limnos Island (BMNH). **Iran:** (IRSN). **Italy:** Leece (IRSN); Novoli (IRSN); Bari (IRSN); Milan (MNHV); Sicily (IRSN); Sicily, Bauso (FMNH); Sicily, Alcantara [River] (MNHV); Calabria, Antonimina (FMNH); Gesso [River] (FMNH); Piemonte (IRSN). **Lebanon:** Beirut (IRSN, FMNH). **Morocco:** (Urica? MNHV). **Romania:** (Rotemtm. Pass, Transylvania? MNHV). **Spain:** Andalusia, Marbella (IRSN); Ponferrada (FMNH; MNHV); Turcia (FMNH). **Switzerland:** (BMNH). **Tunisia:** Teboursouk (IRSN); Kairouan (IRSN); Mateur (IRSN). **Turkey:** Alanya (Dim Irmak ? IRSN); Smyrna [=Izmir], Hermos River (IRSN); Istanbul (MNHV). **USSR:** Sarepta (MNHV, FMNH); Caucasus (Aresch? IRSN). **Yugoslavia:** Sarajevo, Kobinger (FMNH); Metkovic, Dalmatia (MNHV); Croatia (MNHV); Ilidza (MNHV, FMNH).

frater Kraatz Sp(BMNH, FMNH, IRSN, MNHV); type country: Italy.

Albania: Skutari [=Shkodër], Bojana River (IRSN, MNHV); (Tumor-Burang? FMNH). **Italy:** Emilia (FMNH); Emilia, Reno River (MNHV); Sicily, Alcantara [River] (MNHV); Basilicata (Lavello? IRSN). **Yugoslavia:** Priboj (FMNH); Croatia (MNHV).

fraterculus Cameron T,Sp(BMNH), Sp(AMNH); type country: Malaysia.

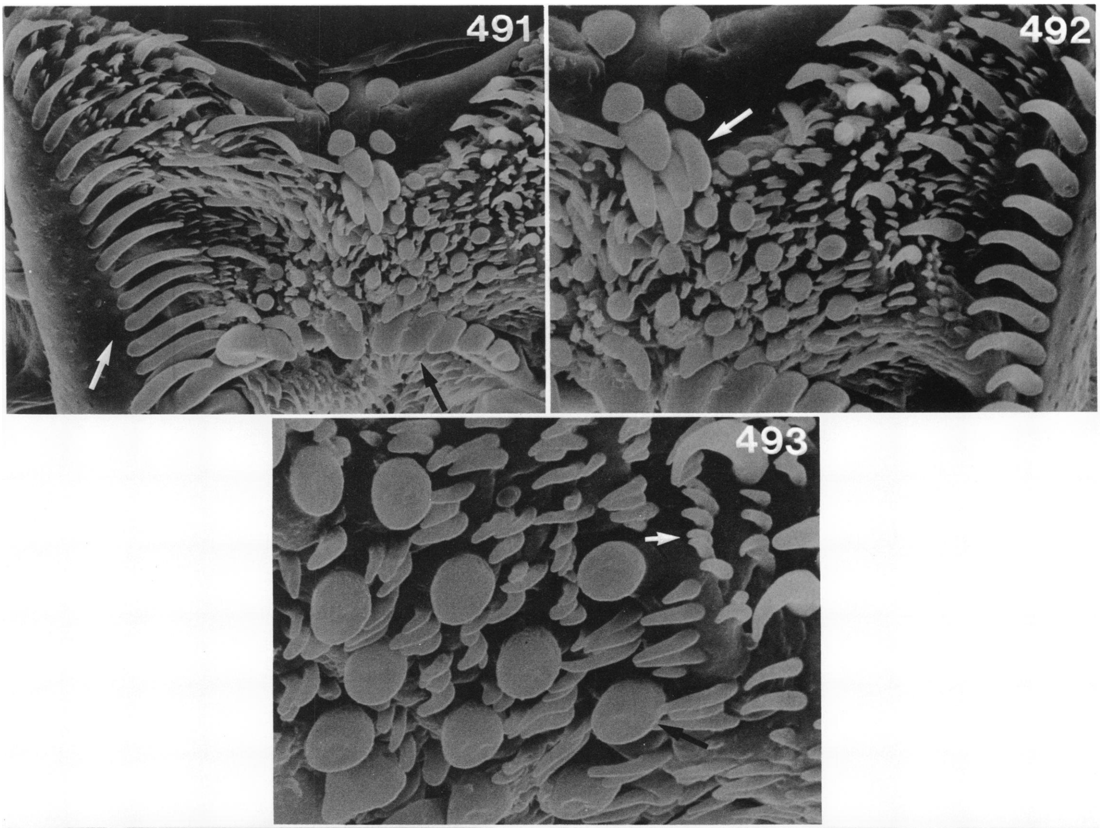
Malaysia: Negeri Sembilan, Port Dickson (BMNH).

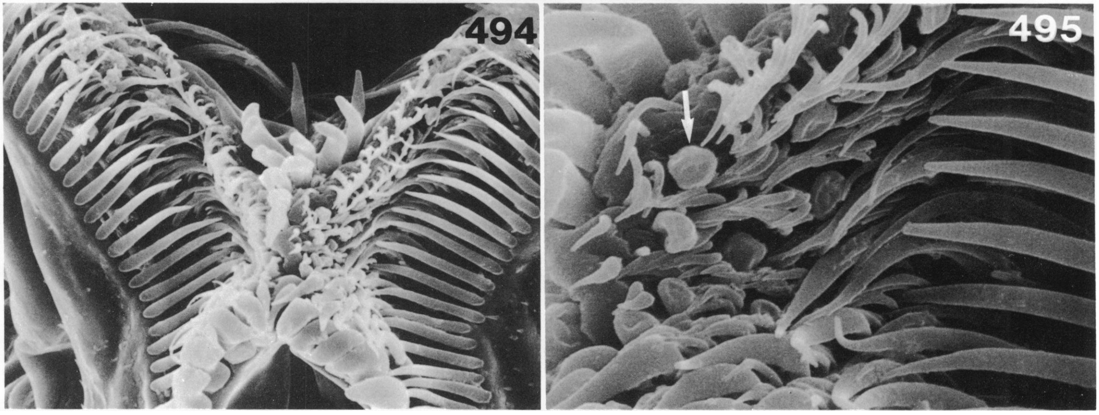


FIGS. 485–490. The *mandibularis* group. Hypopharynx. **485.** *Bledius mandibularis,* general aspect, arrow points to area enlarged in following photo, 440×. **486.** *Bledius mandibularis,* enlargement of anteromedial part of disk, 3800×. **487.** *Bledius mandibularis,* enlargement of part of disk, arrow points to cuticular process, 3800×. **488.** *Bledius fortis,* general aspect, arrow points to area enlarged in following photo, 430×. **489.** *Bledius fortis,* enlargement of anteromedial part of disk, 1600×. **490.** *Bledius fortis,* enlargement of anteromedial part of disk, 3200×.

gabonensis Fauvel Syn (IRSN, BMNH); type country: Congo.

[Congo]: Loango (IRSN). **Gabon:** (BMNH, FMNH). **Zaire:** Kinshasa (BMNH, IRSN).



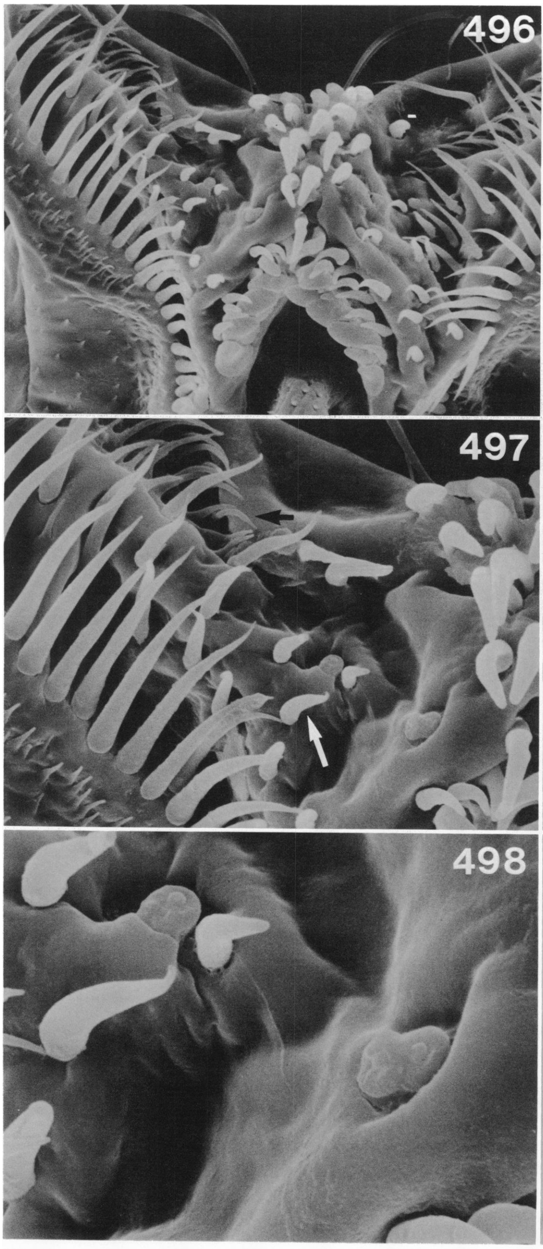


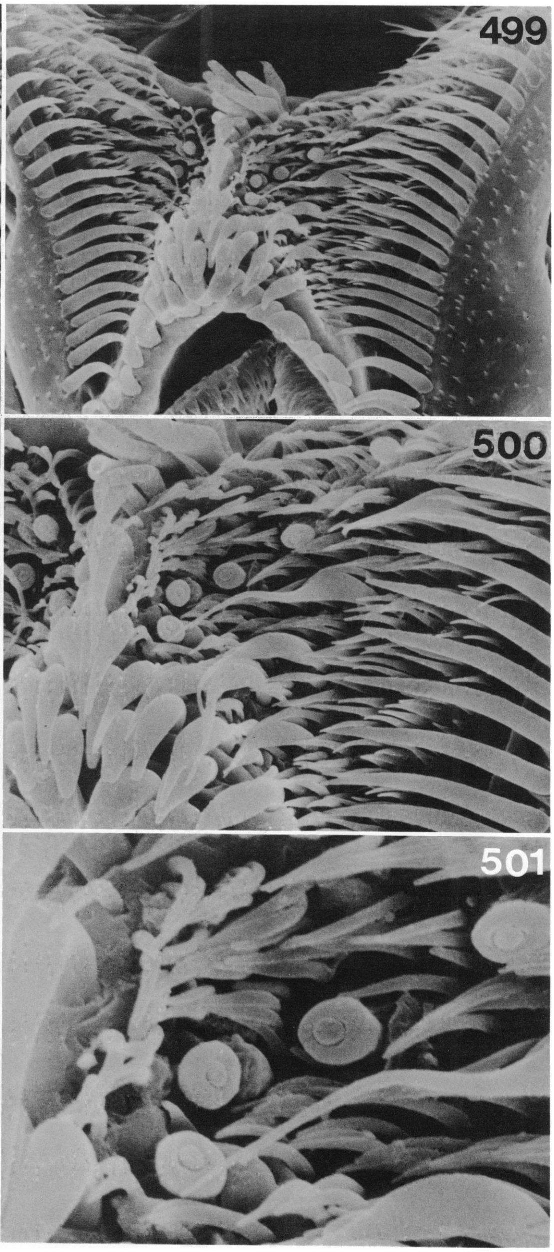
FIGS. 491–493. The *bellicosus* group. *Bledius bellicosus.* Hypopharynx. **491.** General aspect, white arrow points to lateral row of setae, black arrow points to basal row of setae, 880×. **492.** Disk, enlarged, arrow points to central row of spinelike setae, 1280×. **493.** Disk, enlarged, black arrow points to coronal peg, white arrow points to cuticular process, 3000×.

FIGS. 494–495. The *aequatorialis* group. *Bledius beattyi.* Hypopharynx. **494.** General aspect, 700×. **495.** Disk, enlarged, arrow points to coronal peg, 2000×.

gracilicornis Kraatz Syn,Sp(FMNH), Sp(BMNH, IRSN, MNHV); type country: Sri Lanka.

Burma: Irrawaddy (IRSN). **India:** Assam (BMNH); Uttar Pradesh, Fyzabad (BMNH); Calcutta (BMNH); Belgaum

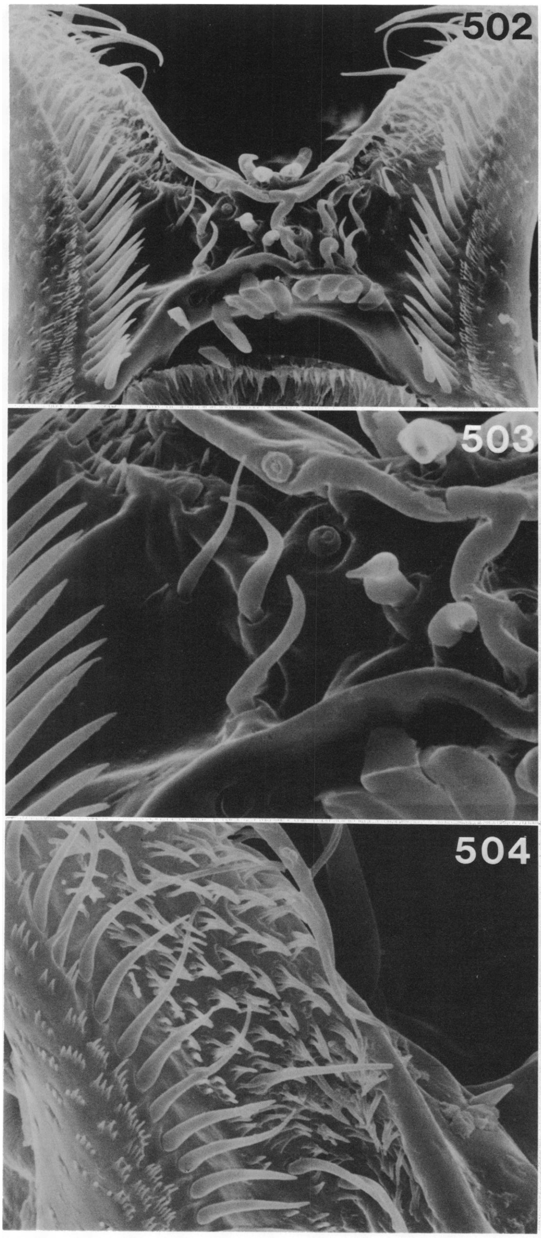


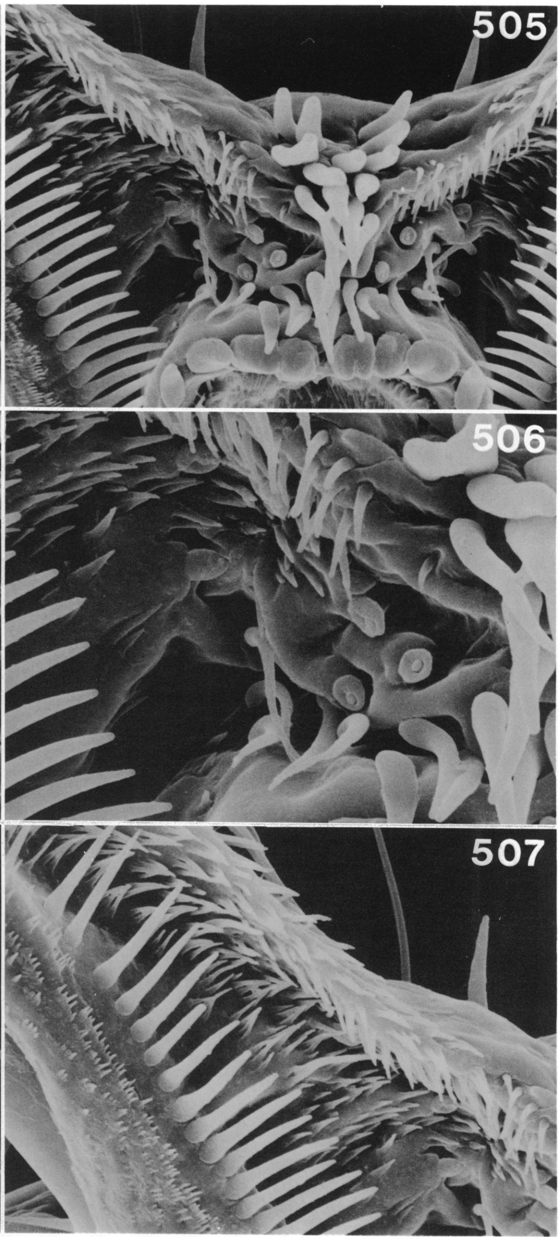


FIGS. 496–498. The *furcatus* group. *Bledius furcatus*. Hypopharynx. **496.** General aspect, 620×. **497.** Disk, enlarged, black arrow points to cuticular process, white arrow points to discal seta, 1240×. **498.** Disk, enlarged, 3200×.

FIGS. 499–501. The *rugosicollis* group, *Bledius rugosicollis*. Hypopharynx. **499.** General aspect, 640×. **500.** Disk, enlarged, 1280×. **501.** Disk, enlarged, 3300×.

(BMNH); Malabar, Calicut (IRSN). **Irian Jaya:** (Lake Sentani, Iffar? BMNH); (Cyclops Mts., Sabron? BMNH). **Papua New Guinea:** Kokoda (BMNH). **Sri Lanka:** (FMNH, IRSN, MNHV). **Vietnam:** Haiphong (IRSN); Hanoi (IRSN); Saigon [= Ho Chi Minh] (IRSN); Phuc-Yen (IRSN). *husseini* Quedenfeldt Co(MNHV),



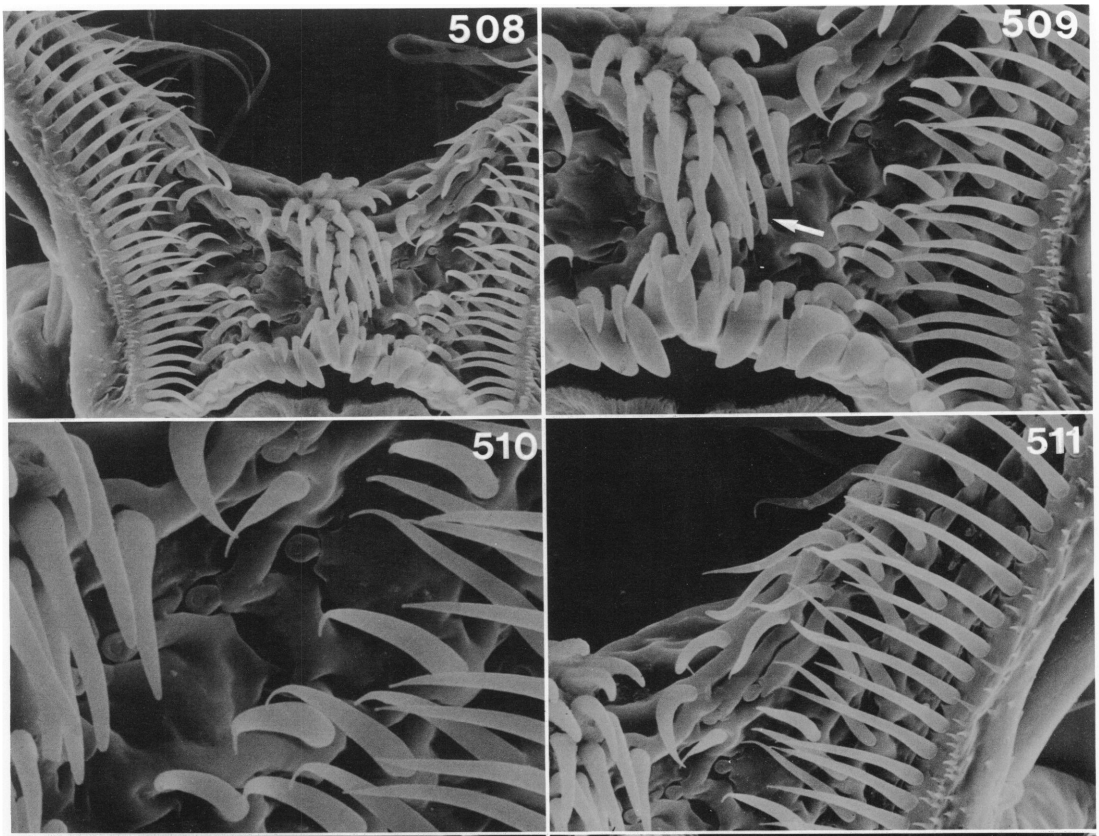


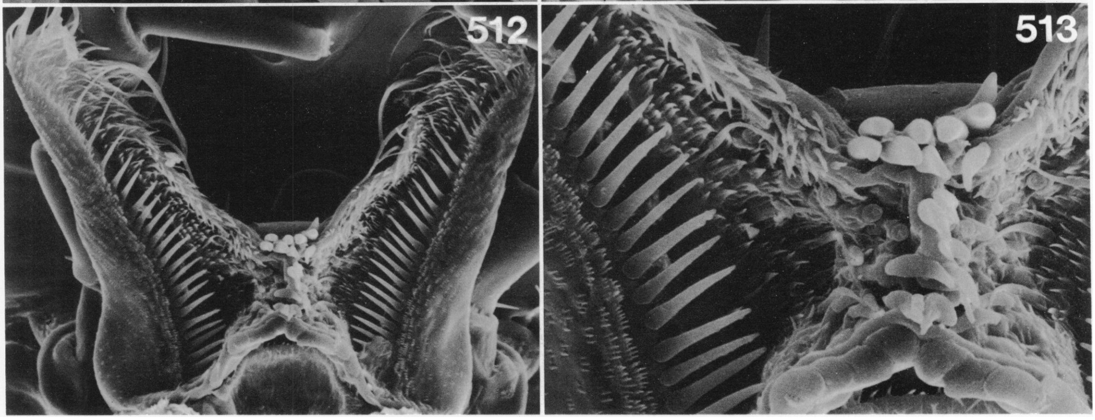
FIGS. 502–504. The *kochi* group. *Bledius kochi.* Hypopharynx. **502.** General aspect, 580×. **503.** Disk, median region, 1760×. **504.** Disk, anterior lobe, 1220×.

FIGS. 505–507. The *gigantulus* group. *Bledius* sp. Hypopharynx. **505.** General aspect, 760×. **506.** Disk, median region, 1520×. **507.** Disk, anterior lobe, 920×.

Sp(BMNH, FMNH, IRSN); type country: Morocco.

Algeria: Hoggar, Tihentekot (FMNH); Bou Saâda (MNHV); El Goliah [= El Golea] (IRSN); (Oued Saoura, Ouarourout, Seguia? IRSN). **Egypt:** Asyut (BMNH); Cairo (IRSN); (Barrage? FMNH). **Gabon:** (Mocquery? BMNH); Lambarene (IRSN). **Lib-**

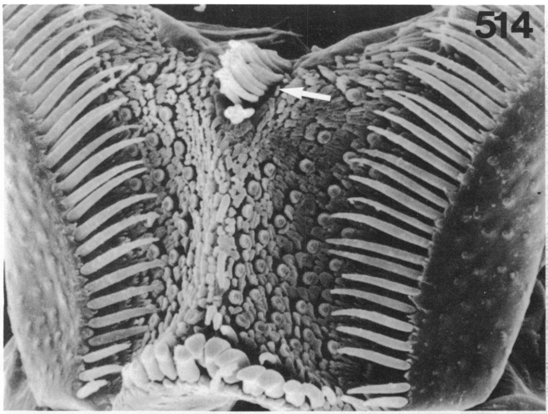


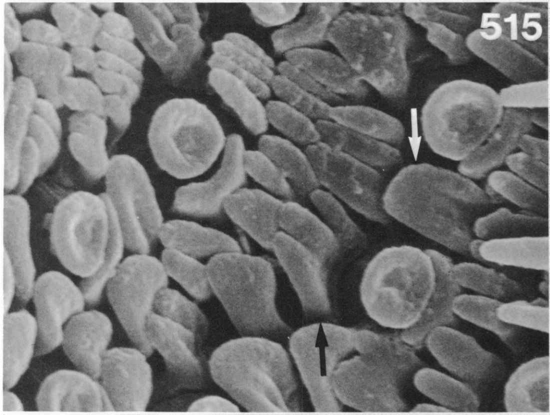


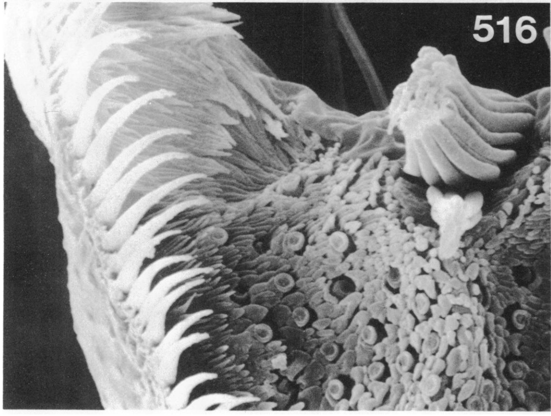
FIGS. 508–511. The *lamelliceps* group. *Bledius pilicollis.* Hypopharynx. **508.** General aspect, 460×. **509.** Disk, arrow points to central row of spinelike setae, 840×. **510.** Disk, median region, 1680×. **511.** Disk, anterior lobe, 840×.

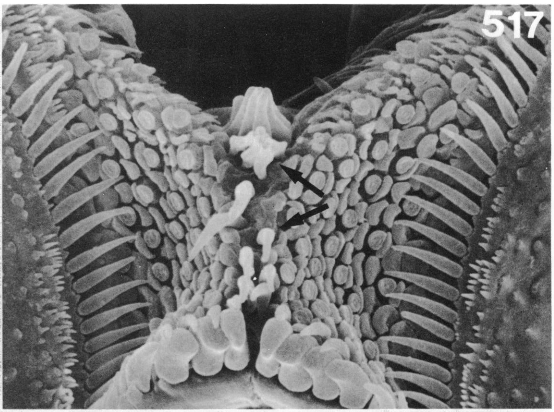
FIGS. 512–513. The *gigantulus* group. *Bledius tricornis.* Hypopharynx. **512.** General aspect, 272×. **513.** Disk, 720×.

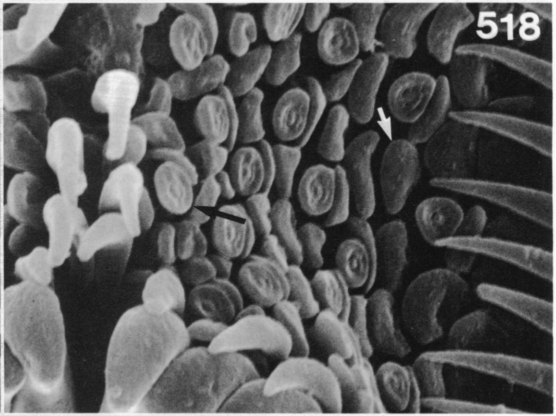
ya: Hun (FMNH). **Mali:** Badoumbe (IRSN). **Morocco:** (Issil River ? MNHV); Guercif (Oued Moulouja ? MNHV); Mogador [=Essaouira] (IRSN); (Urica? IRSN, FMNH). **Senegal:** Dakar (BMNH). **Zaire:** Katanga, Katompi (FMNH).









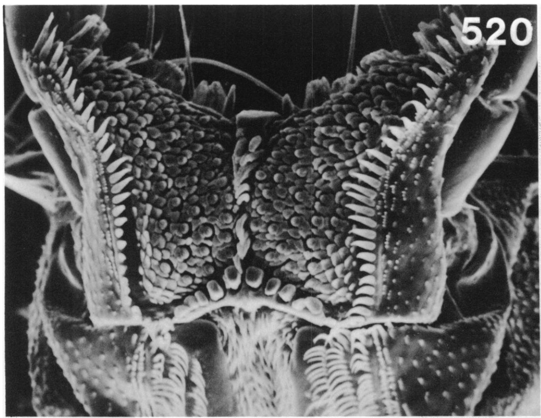


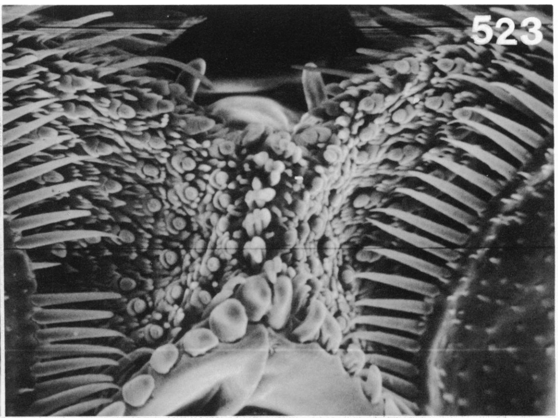
FIGS. 514–516. The *emarginatus* group. *Bledius chilensis.* Hypopharynx. **514.** General aspect, arrow points to central row of setae, 760×. **515.** Disk, median region; white arrow points to cuticular lobe, black arrow points to palmate cluster of cuticular processes, 4600×. **516.** Disk, median region and part of anterior lobe, 1180×.

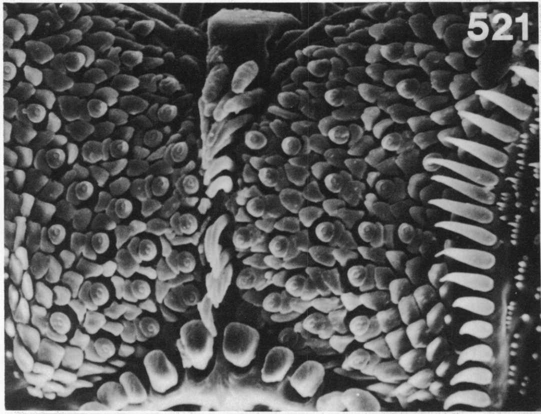
FIGS. 517–519. The *emarginatus* group. *Bledius parcissimus.* Hypopharynx. **517.** General aspect, arrows point to central row of setae, 1080×. **518.** Disk, median region; black arrow points to coronal peg, white arrow points to cuticular lobe, 2880×. **519.** Disk, base of anterior lobe, 2160×.

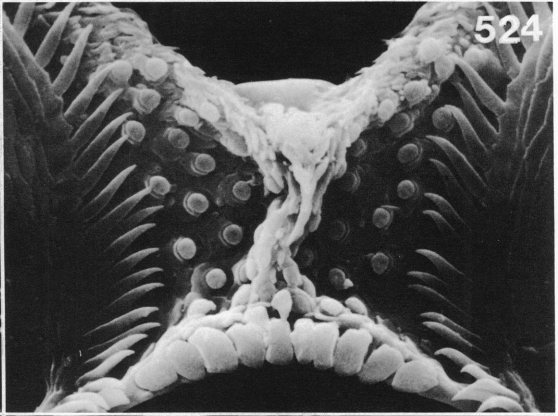
incertus Cameron P,Sp(BMNH), Sp(FMNH, MNHV); type country: Mauritania.

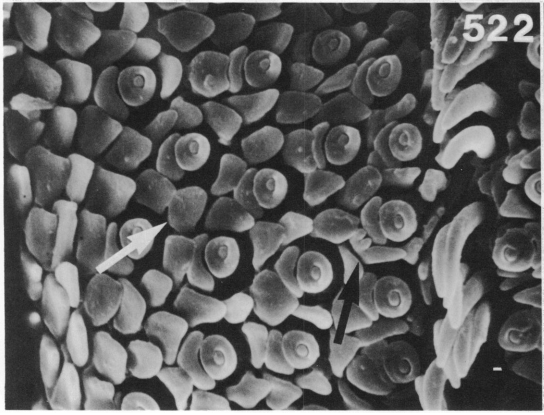
Cape Verde: Sao Tiago (Orgaos Grandes ? FMNH); (Pedra Badejo ? FMNH, BMNH,

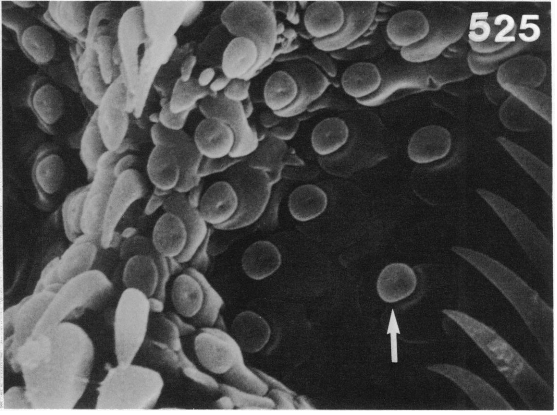












FIGS. 520–522. The *annularis* group. *Bledius confusus.* Hypopharynx. **520.** General aspect, 376×. **521.** Disk, 740×. **522.** Disk, median region, black arrow points to palmate cluster of cuticular processes, white arrow points to cuticular lobe, 1480×.

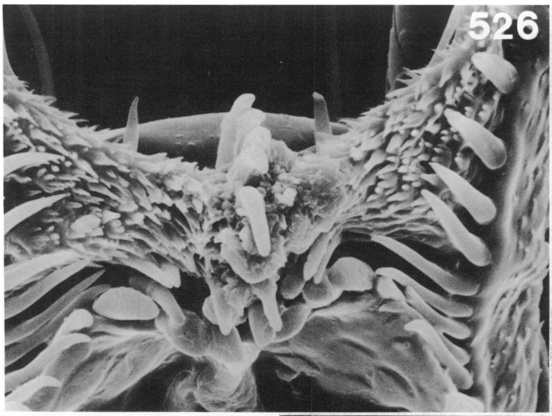
FIG. 523. The *annularis* group. *Bledius newelli.* Hypopharynx, general aspect, 540×.

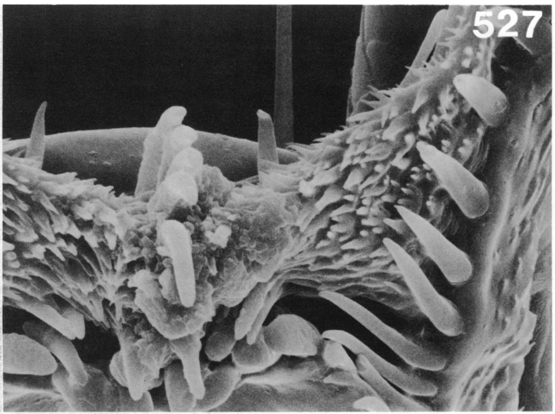
FIGS. 524–525. The *emarginatus* group. *Bledius cognatus.* Hypopharynx. **524.** General aspect, 960×. **525.** Disk, median region, arrow points to coronal peg, 1800×.

MNHV). **Mauritania:** (Tergit? BMNH); (Hamdoum? BMNH). **Nigeria:** Azare (BMNH).

insignicornis Blackburn T(BMNH), Sp(IRSN); type country: Australia.

Australia: (BMNH).


526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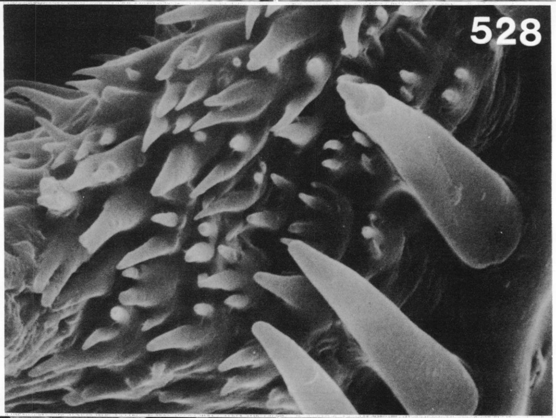
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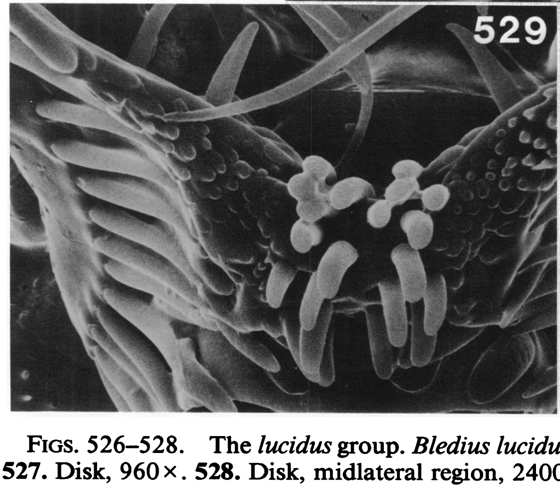
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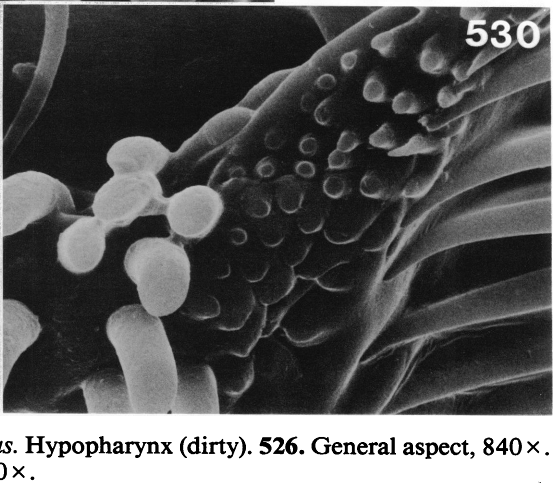

530

FIGS. 526–528. The *lucidus* group. *Bledius lucidus.* Hypopharynx (dirty). **526.** General aspect, 840×. **527.** Disk, 960×. **528.** Disk, midlateral region, 2400×.

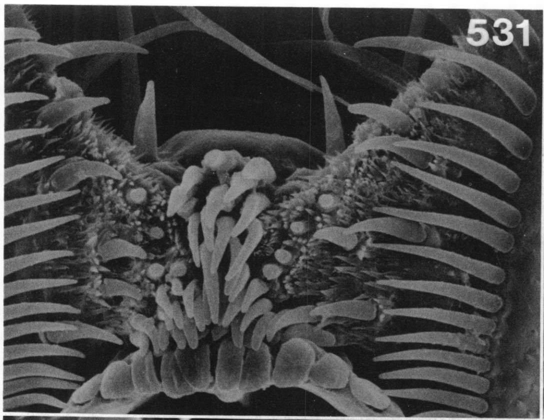
FIGS. 529–530. The *kosempoensis* group. *Bledius kosempoensis.* Hypopharynx (dirty). **529.** Disk, 840×. **530.** Disk, median region, 1680×.

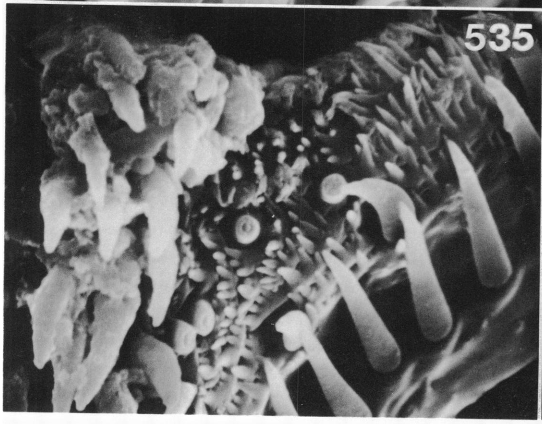
jacobsoni Cameron T(BMNH); type country: Indonesia.

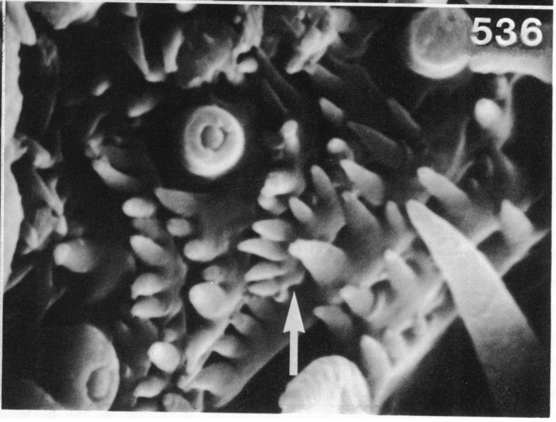
Indonesia: Sumatra, Fort de Koch [=Bukittinggi] (BMNH).

klapperichi Coiffait P(HCC); type country: Iran.

Iran: Bandar Palavi [= Bandar Anzali], Caspian Sea (HCC).







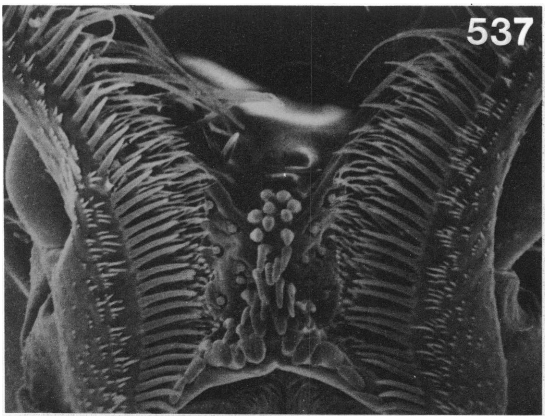
FIGS. 531–533. The *semiferrugineus* group. *Bledius semiferrugineus*. Hypopharynx. **531.** General aspect, 660×. **532.** Disk, median region, arrow points to discal seta, 1320×. **533.** Disk, median region.

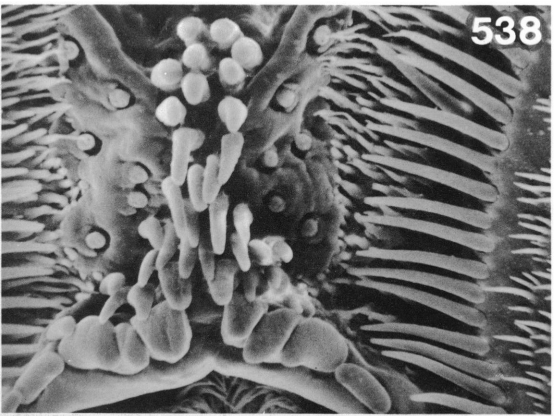
FIG. **534.** The *semiferrugineus* group. *Bledius foraminosus*. Hypopharynx, disk, median region.

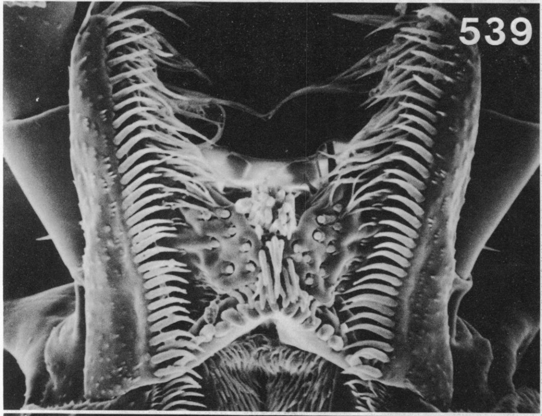
FIGS. 535–536. The *semiferrugineus* group. *Bledius nitidicollis*. Hypopharynx. **535.** Disk, median region. **536.** Disk median region enlarged, arrow points to palmate cluster of cuticular processes.

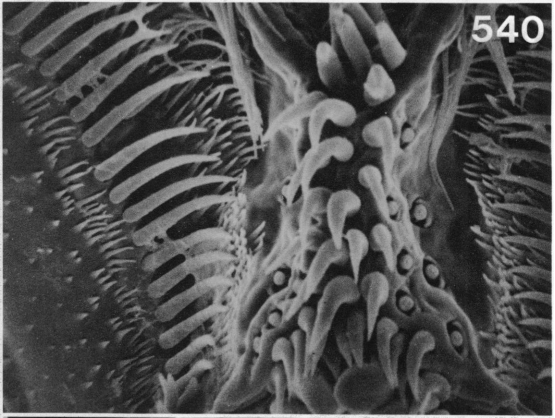
lateripennis Bernhauer T,Co(FMNH), Co,Sp(BMNH), Sp(MNHV); type country: South Africa.

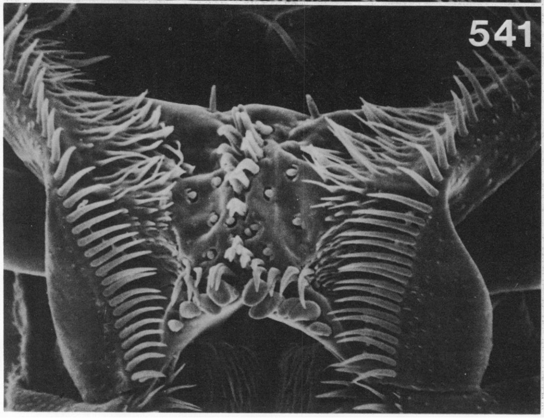
Mauritania: (Hamdoum? BMNH). **Namibia:** Kaokoveld, Omutati, 70 mi. WSW Ohopoho (BMNH). **South Africa:** Trans-

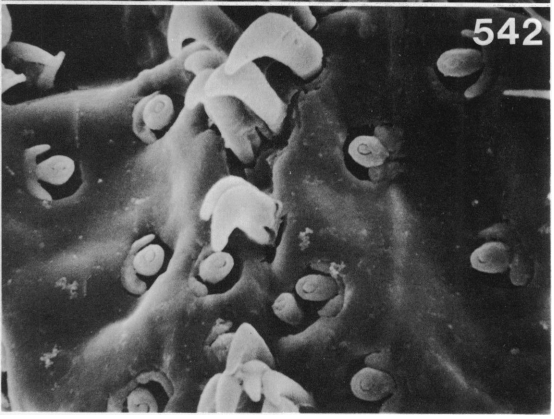










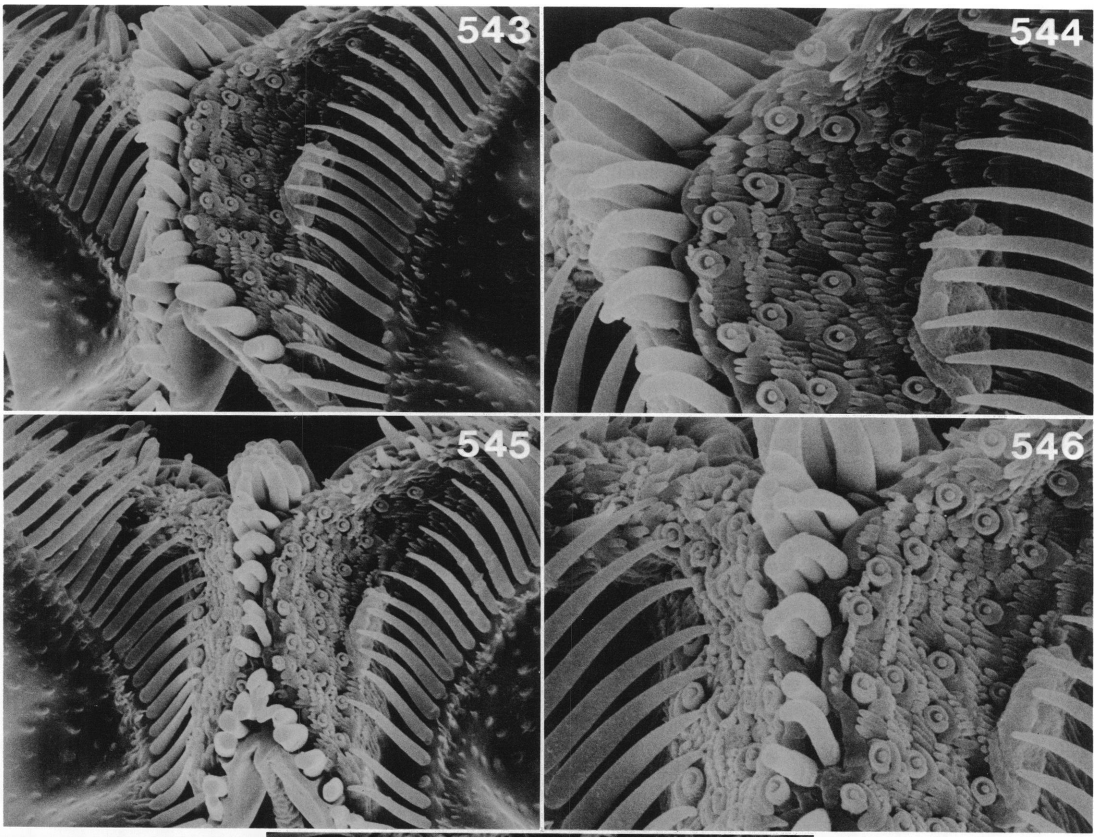


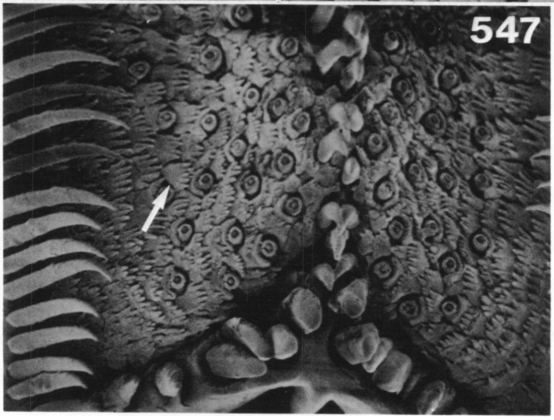
FIGS. 537–538. The *armatus* group. *Bledius strenuus.* Hypopharynx. **537.** General aspect. **538.** Disk.
FIG. 539. The *armatus* group. *Bledius politus.* Hypopharynx, general aspect.
FIGS. 540. The *armatus* group. *Bledius episcopalis.* Hypopharynx, disk.
FIGS. 541–542. The *armatus* group. *Bledius bellicus.* Hypopharynx. **541.** General aspect. **542.** Disk.

vaal, Kruger National Park, Letaba Camp (BMNH); Pondoland (FMNH); Port St. Johns (FMNH, MNHV).

latior Bernhauer T,Sp(FMNH); type country: Zaire.

Zaire: Boma (FMNH).





FIGS. 543–546. The *albonotatus* group. *Bledius tarandus*. Hypopharynx. **543.** General aspect, 920×. **544.** Disk, median region, 1800×. **545.** General aspect, 900×. **546.** Disk, median region, 1800×.

FIG. 547. The *albonotatus* group. *Bledius diagonalis*. Hypopharynx, median region of disk, arrow points to palmate cluster of cuticular processes, 3200×.

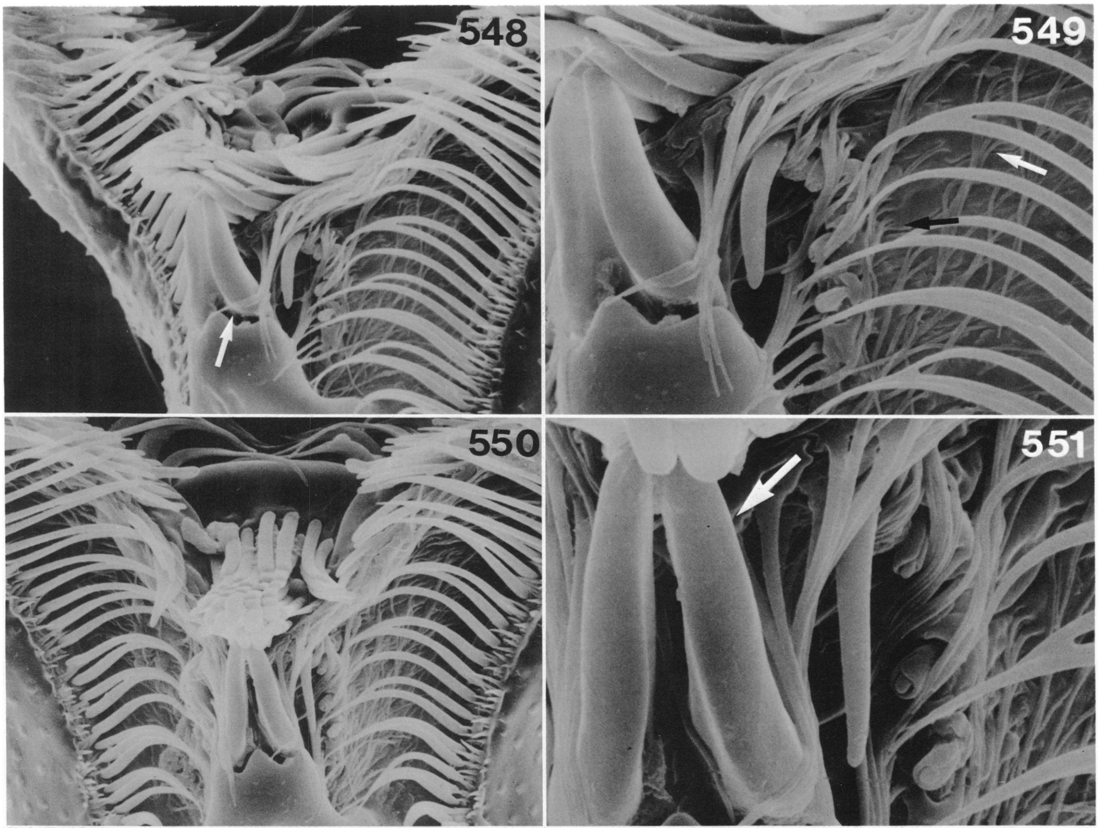
latus Bernhauer Sp(FMNH); type country: USSR.

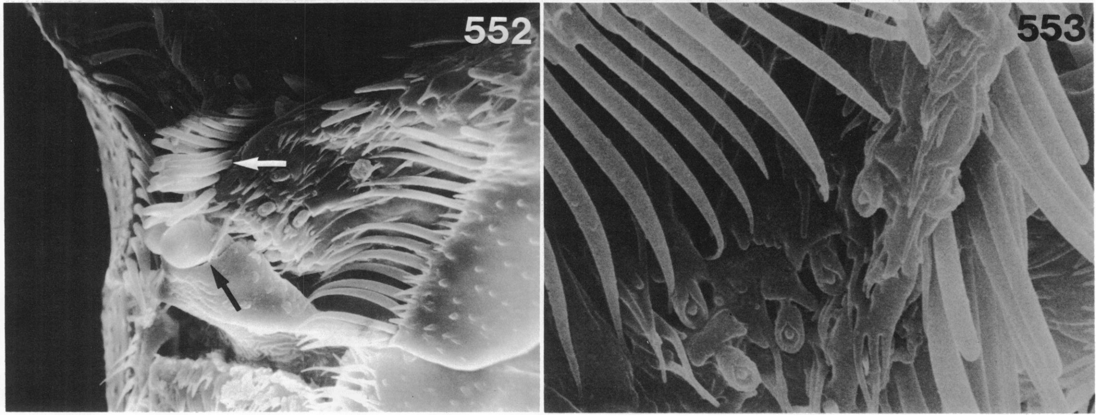
[USSR?]: (Chiva or. ? FMNH).

lepineyi Scheerpeltz T(MNHV), Sp(BMNH); type country: Mali.

Mali: Sokolo, Cle de Macina (MNHV). **Niger:** Agadez, Aïn Sud (BMNH). **Senegal:** Thies (BMNH).

louwerensi Cameron P,Sp(BMNH); type country: Indonesia.





FIGS. 548–551. The *basalis* group. *Bledius thinopus.* Hypopharynx. **548.** General aspect, arrow points to basal seta, 780×. **549.** Disk, median region, arrows point to cuticular processes, 1560×. **550.** General aspect, 800×. **551.** Disk, median region, arrow points to basal seta, 2760×.

FIGS. 552–553. The *basalis* group. *Bledius melanocephalus.* Hypopharynx. **552.** General aspect, white arrow points to central row of setae, black arrow points to basal seta. **553.** Disk, median region, 3100×.

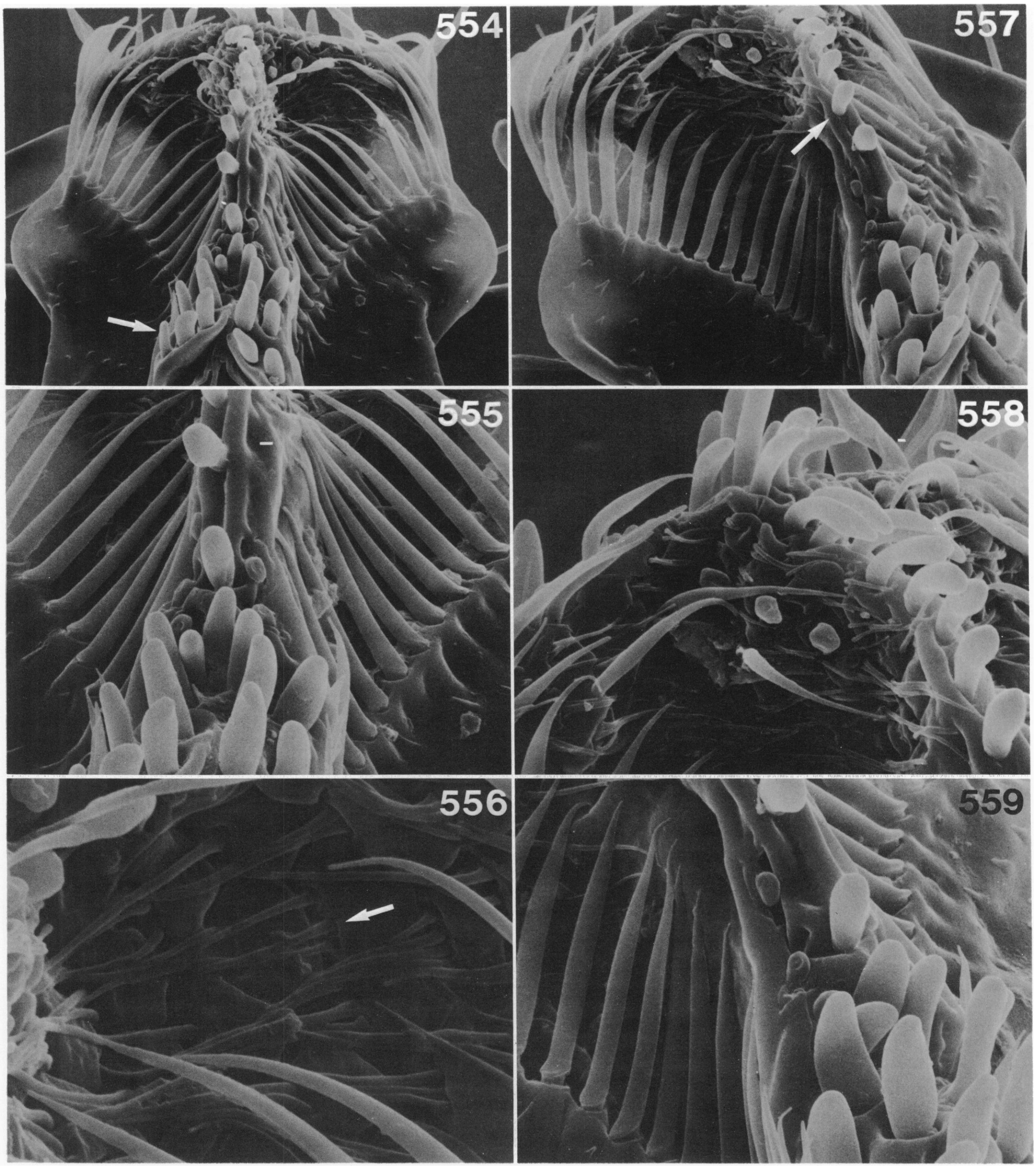
Indonesia: Java, Kediri (Samberbajem Res. ? BMNH); Djember (BMNH).

lucidulus Cameron T(BMNH); type country: Con Son.

Pulo Condore Island [= **Con Son**] (BMNH).

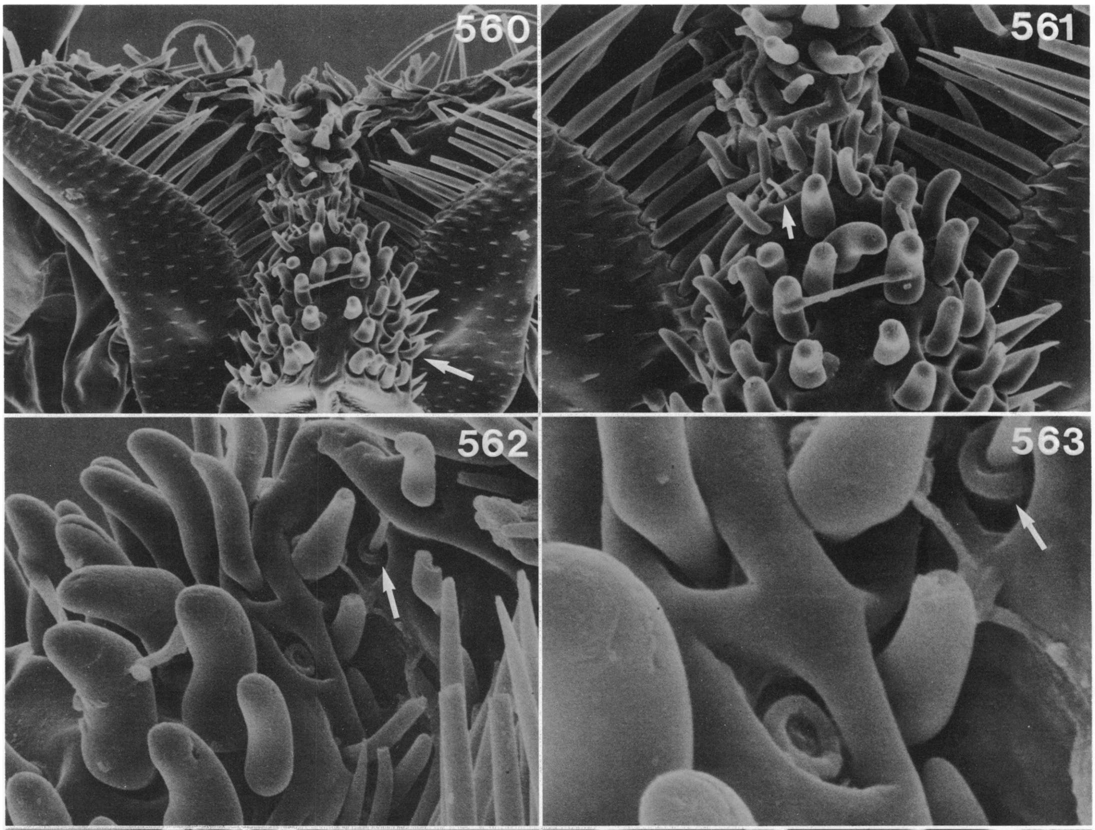
madagascariensis Bernhauer T(BMNH); type country: Madagascar.

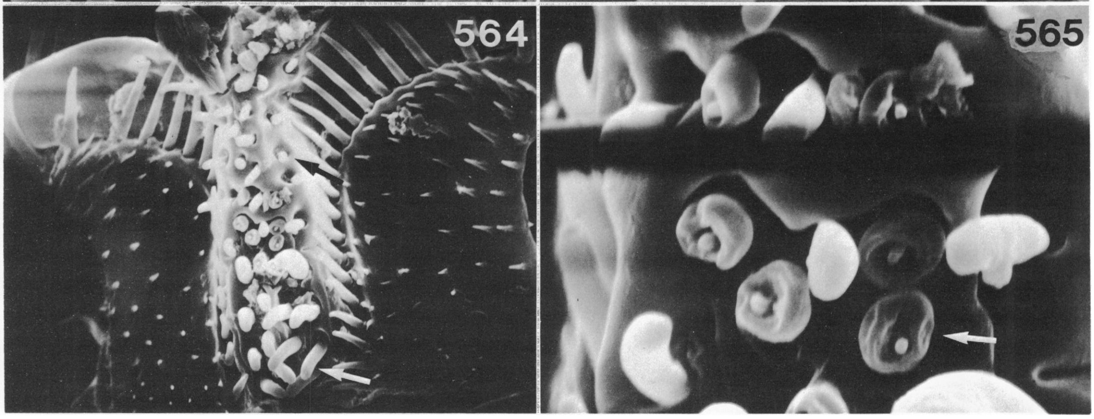
Madagascar: Fort Dauphin [=Toalanarp] (FMNH).



FIGS. 554–559. The *fratellus* group. *Bledius fratellus*. Hypopharynx. **554.** General aspect, arrow points to seta of basal cluster, 700×. **555.** Disk, basal cluster, and central row of setae, 1400×. **556.** Disk, midanterior region, arrow points to cuticular processes, 3500×. **557.** General aspect, arrow points to seta of central row, 880×. **558.** Disk, midanterior region, 1760×. **559.** Disk, basal cluster, and central row of setae, 1760×.

marginalis Cameron T(BMNH); type country: South Africa.
South Africa: Simons Town (BMNH).
mauritanicus Coiffait H,P(HCC); type country: Mauritania.
Mauritania: Trarza Gana (HCC).
negrei Coiffait H(HCC); type country: USSR.
USSR: Uzbekistan, Urgench (HCC).
niger Cameron T,Sp(BMNH); type country: South Africa.



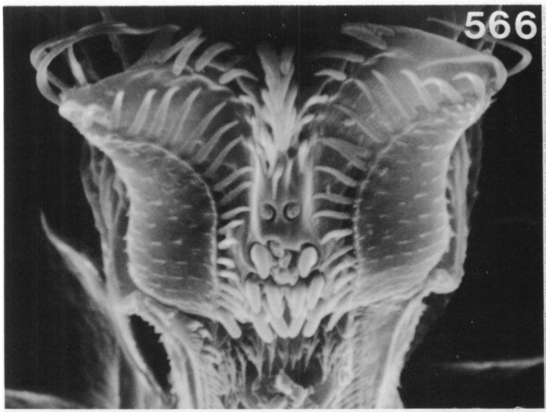


FIGS. 560–563. The *angustus* group. *Bledius* sp. Hypopharynx. **560.** General aspect, arrow points to seta of basal cluster, 470×. **561.** Disk, basal cluster and central row of setae, arrow points to coronal peg, 940×. **562.** Disk, setae of basal cluster and central row, arrow points to coronal peg, 1800×. **563.** Disk, setae of central row, arrow points to coronal peg, 4800×.

FIGS. 564–565. The *forcipatus* group. *Bledius playanus.* Hypopharynx. **564.** General aspect, black arrow points to seta of central row, white arrow points to seta of basal row. **565.** Disk, central row, arrow points to coronal peg.

Angola: Dundo (BMNH). **South Africa:** Simons Town (BMNH).

niloticus Erichson Sp(BMNH, FMNH, IRSN, MNHV); type country: Egypt.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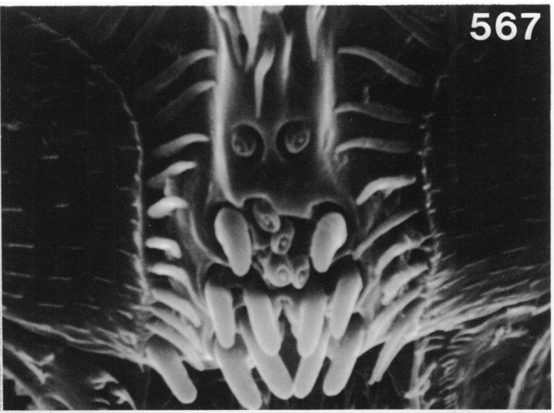
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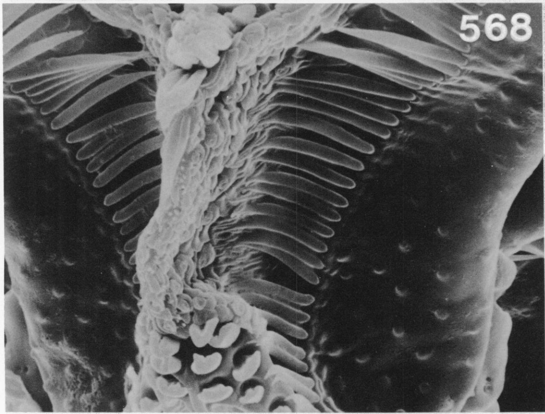
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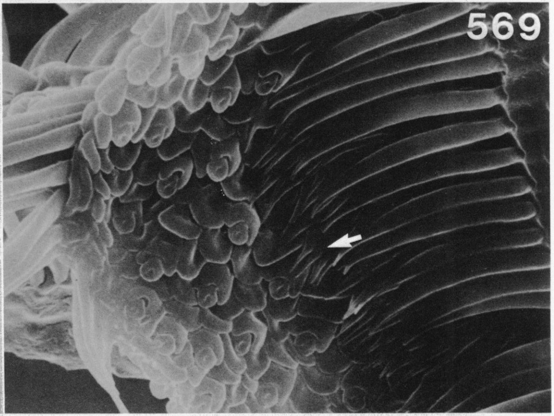
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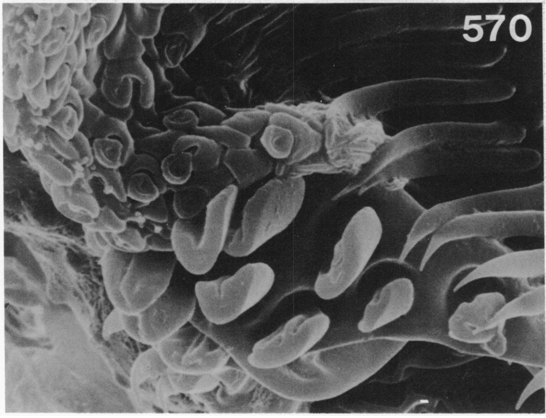
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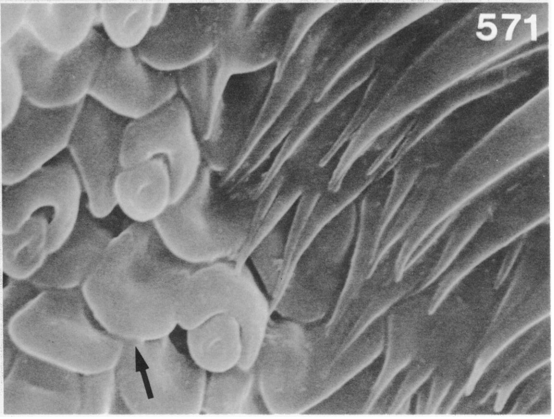
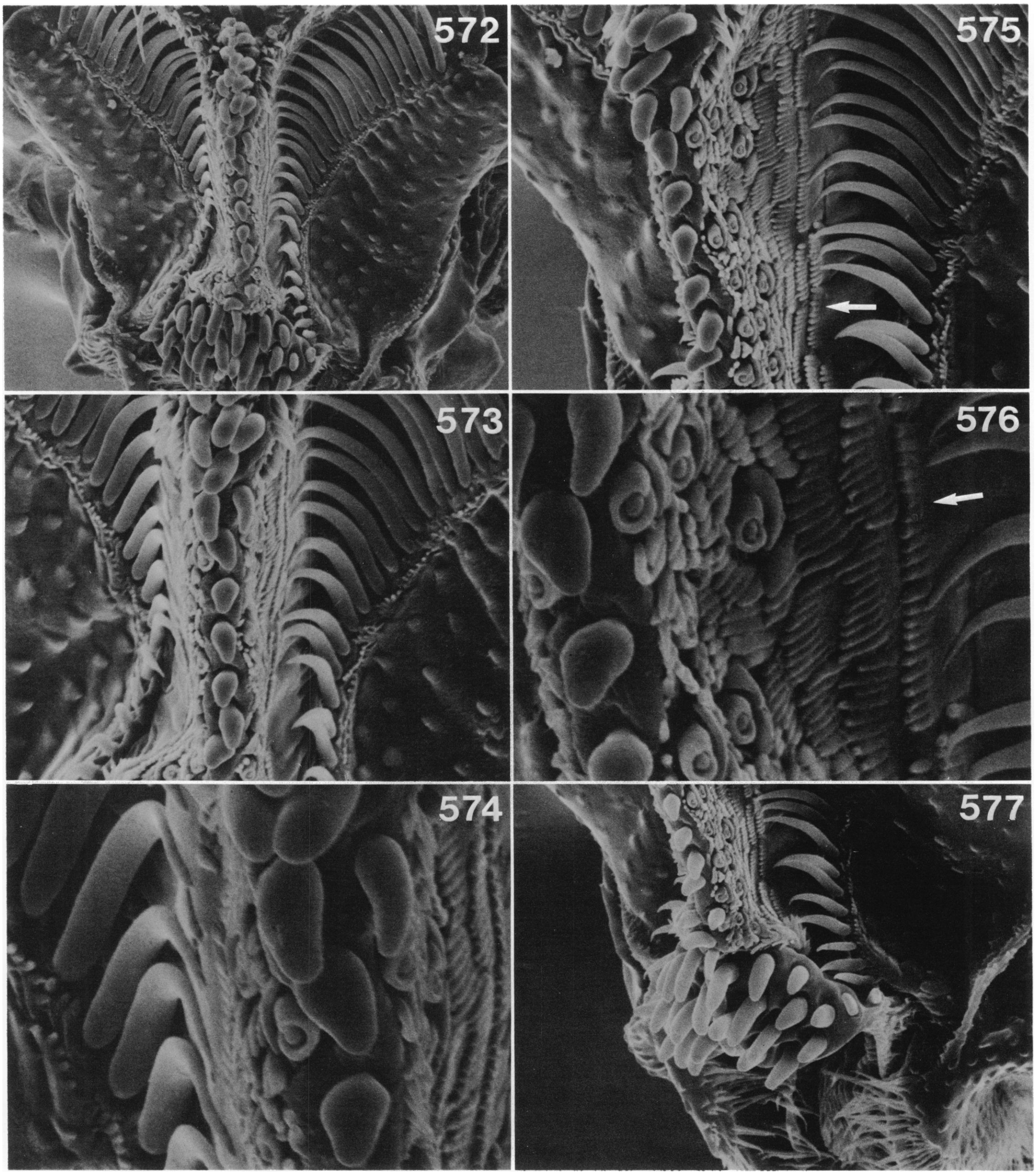

571

FIGS. 566–567. The *forcipatus* group. *Bledius actitus.* **566.** General aspect. **567.** Disk, central region and setae of basal cluster.

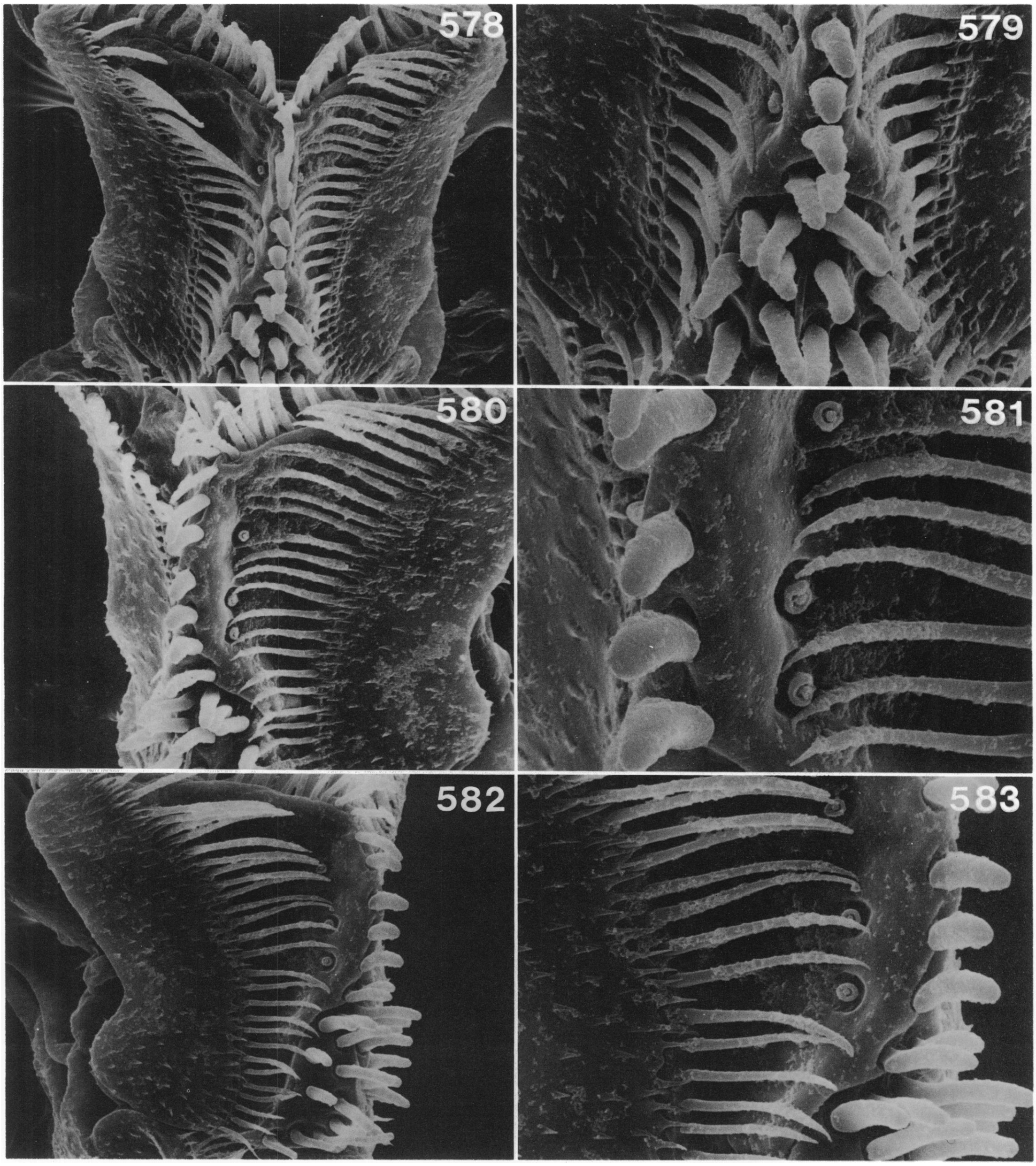
FIGS. 568–571. The *pulchellus* group. *Bledius pulchellus.* **568.** General aspect, 980×. **569.** Disk, midanterior region, arrow points to palmate cluster of cuticular processes, 1480×. **570.** Disk, central region and setae of basal cluster, 2240×. **571.** Disk, midanterior region, arrow points to cuticular lobe, 3800×.

Angola: Quirimbo (BMNH). **Congo:** Loango (IRSN). **Egypt:** (BMNH, FMNH); Aswân (MNHV); Cairo, Meadi (MNHV, IRSN); Girgeh (IRSN); Luxor (IRSN). **Ethiopia:** Harrar [= Harerge Prov.] (FMNH). **Gabon:** (FMNH). **Ghana:**



FIGS. 572–577. The *tibialis* group. *Bledius tibialis*. Hypopharynx. **572.** General aspect, 696×. **573.** Disk, central region and setae of central row, 1400×. **574.** Disk, central region and setae of central row, 3500×. **575.** Disk, central region, arrow points to linear row of cuticular processes, 1400×. **576.** Disk, central region, arrow points to linear row of cuticular processes, 3500×. **577.** Disk, setae of basal cluster and part of central row, 960×.

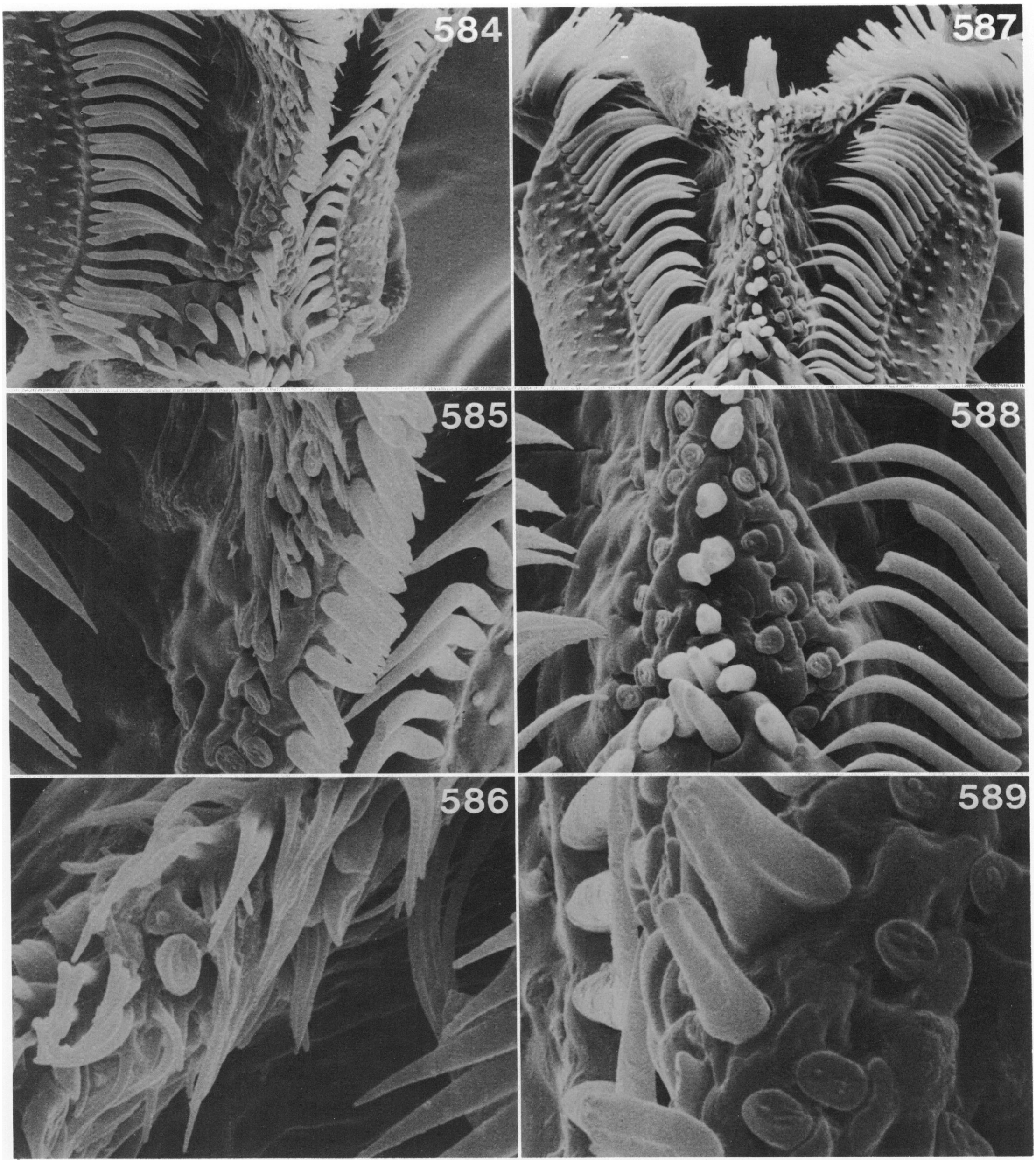
(FMNH). **Israel:** Jaffa (IRSN); Haifa (IRSN). **Ivory Coast:** Grand Bassam (IRSN). **Lebanon:** Beirut (IRSN). **Morocco:** Souk el Arba (IRSN). **Niger:** Agadez, Aïn Sud (BMNH). **Senegal:** (Sebikotane? BMNH). **South Africa:** Natal, Isipingo (BMNH). **Sudan:** Khartoum (FMNH). **Tanzania:** Dar-es-salam (BMNH, FMNH).



FIGS. 578–583. The *bonariensis* group. *Bledius bonariensis.* Hypopharynx. **578.** General aspect, 590×. **579.** Disk, setae of basal cluster and part of central row, 1200×. **580.** Disk, right lateral side, 730×. **581.** Disk, right lateral side, 2000×. **582.** Disk, left lateral side, 600×. **583.** Disk, setae of central row and basal cluster, 1200×.

Tunisia: (Birbou Rekba, pres. Hammaneuf ? IRSN). **Zaire:** Leopoldville [=Kinshasa] (FMNH, BMNH); Kasenye (FMNH); Moleka (FMNH); Tshela (FMNH); Kasai River (FMNH); Lisala Territory, Modjuambe [=Modjamboli] (FMNH); Stanleyville [=Kisangani] (FMNH); Boma (FMNH, IRSN); (Kisimba? BMNH).

nodieri Cameron P(BMNH); type country: Mali.



FIGS. 584–589. The *punctatissimus* group. *Bledius maindroni.* Hypopharynx. **584.** General aspect, anterior portion omitted, 680×. **585.** Disk and central row of setae, 1800×. **586.** Disk, anterior region with cuticular processes, 3400×. **587.** General aspect, basal portion omitted, 620×. **588.** Disk, part of basal cluster and central row of setae, 1680×. **589.** Disk, setae of central row showing compound seta, 3600×.

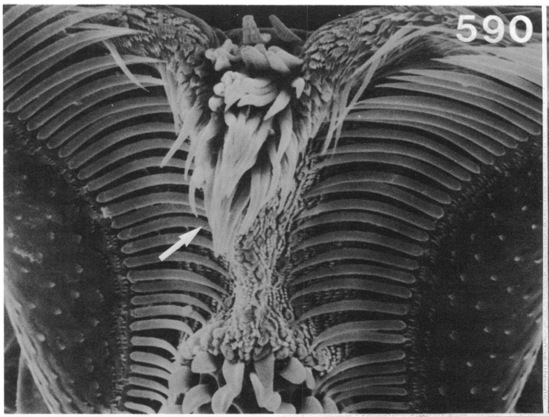
Mali: Badoumbe (BMNH).

opacinus Scheerpeltz H(MNHV); type country: Afghanistan.

Afghanistan: Kabul (MNHV).

orphanus Sharp T(BMNH), Sp(FMNH); type country: Japan.

China: Fukien (Kwangtseh? FMNH). **Japan:** Kobe (BMNH).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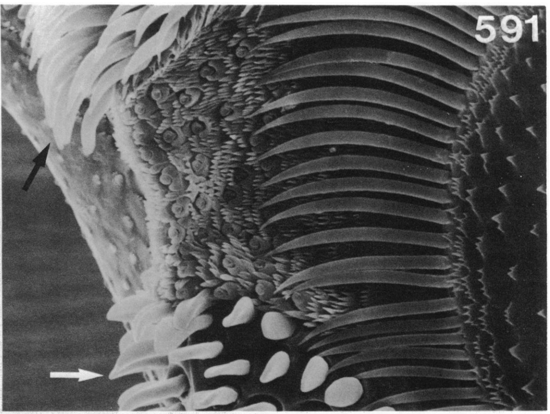
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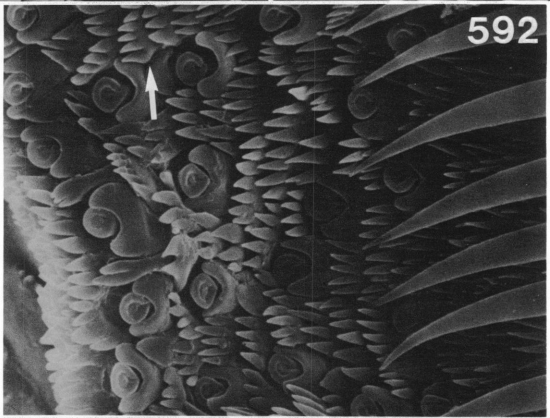
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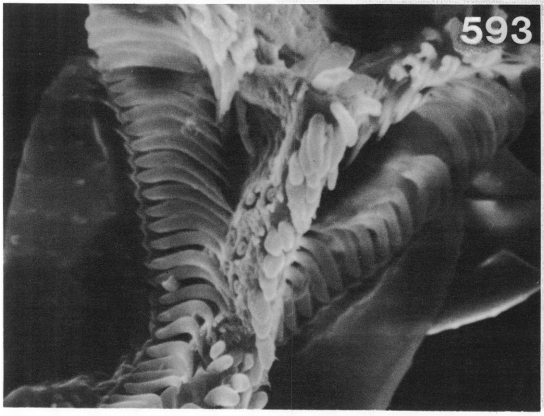
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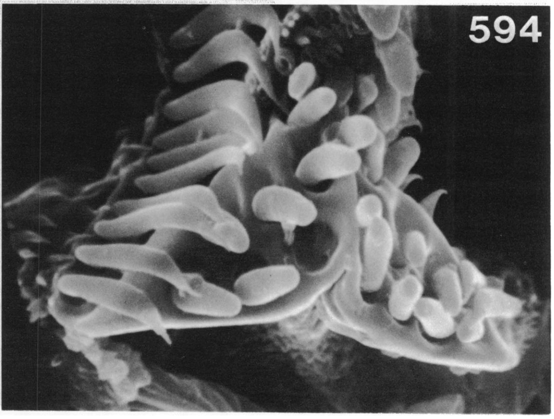
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FIGS. 590–592. The *verres* group. *Bledius verres*. Hypopharynx. **590.** General aspect, arrow points to seta of central row, 480×. **591.** Disk, median region, right lateral side, black arrow points to seta of central row, white arrow points to seta of basal cluster, 640×. **592.** Disk, central region, arrow points to palmate cluster of cuticular processes, 1920×.

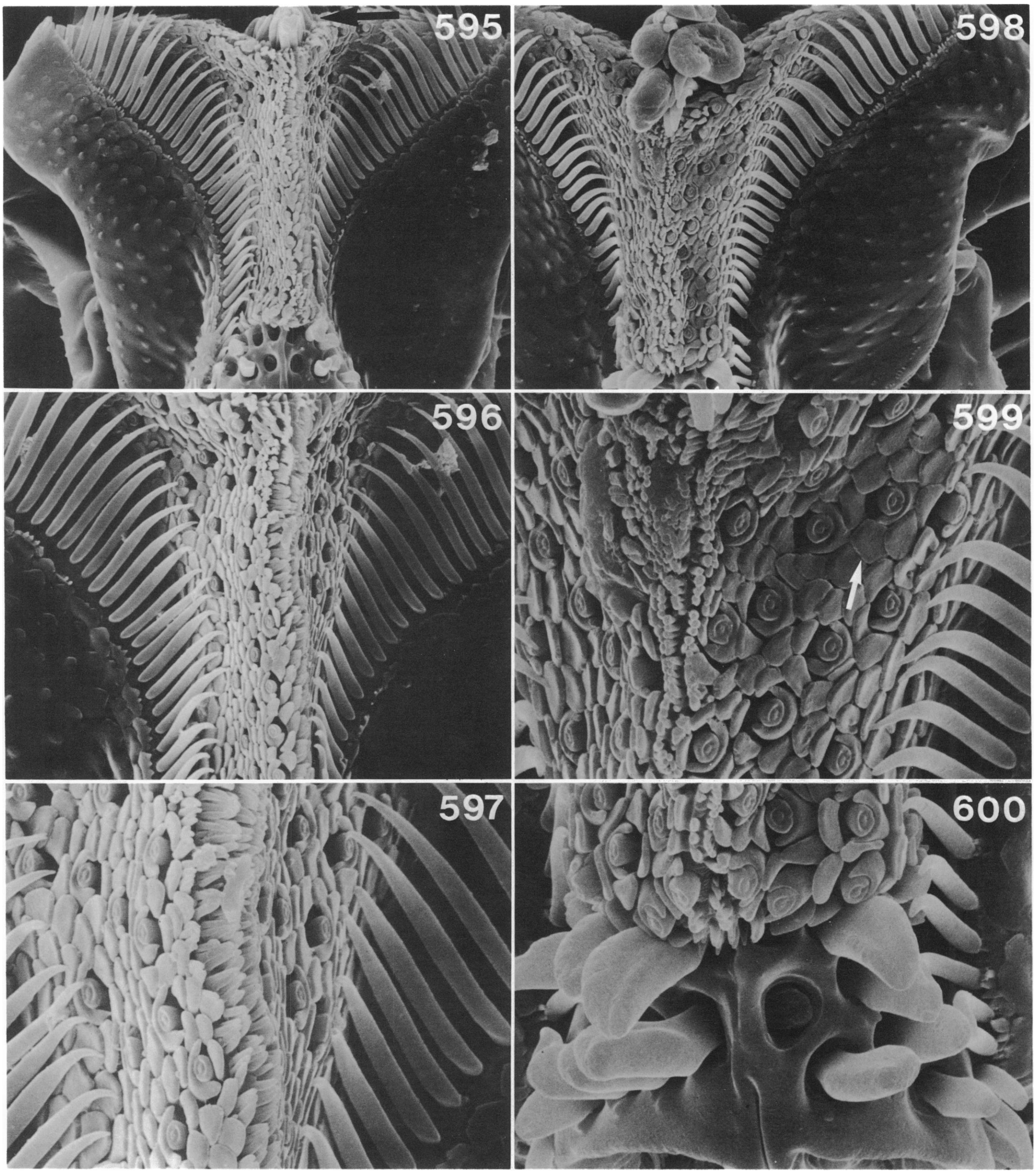
FIGS. 593–594. The *punctatissimus* group. *Bledius punctatissimus*. Hypopharynx. **593.** General aspect. **594.** Basal cluster of setae and part of lateral row of setae.

palliatus Fauvel Syn,Sp(IRSN); type country: Burma.

Burma: Myeenkyan [=Myingyan] (IRSN).

papuanus Cameron T(BMNH); type country: Papua New Guinea.

Papua New Guinea: Kokoda (BMNH).



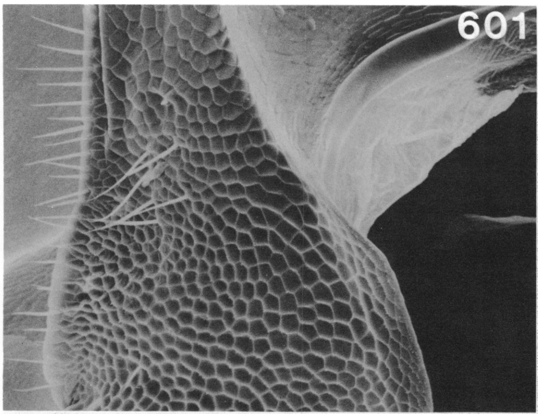
FIGS. 595–600. The *verres* group. *Bledius* sp. Hypopharynx. **595.** General aspect, arrow points to setae of central row, 680×. **596.** Disk, central region, 1220×. **597.** Disk, central region, 2400×. **598.** General aspect (midanterior region with debris), 760×. **599.** Disk, central region, arrow points to cuticular lobe, 2440×. **600.** Basal cluster of setae, 2480×.

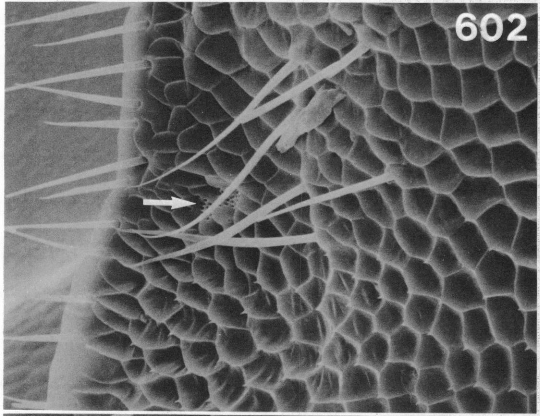
parens Cameron T(BMNH); type country: Philippines.

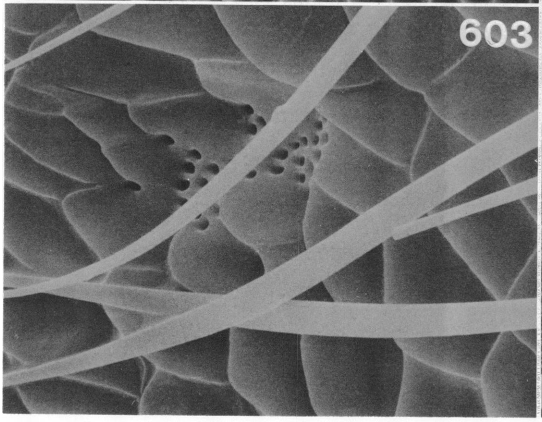
Philippines: Manila (BMNH).

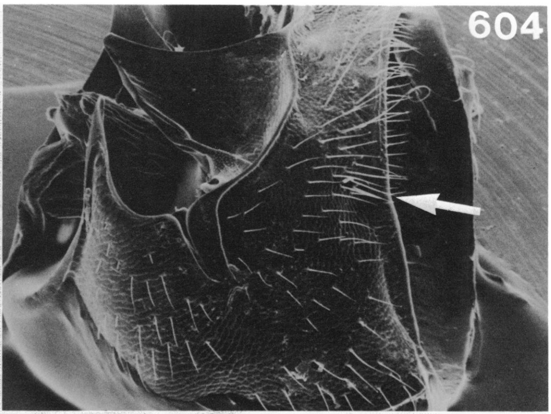
peraffinis Cameron T,Sp(BMNH); type country: Con Son.

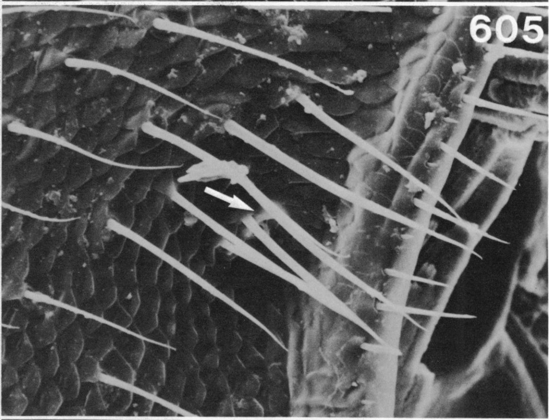
Pulo Condore [= **Con Son**] (BMNH).

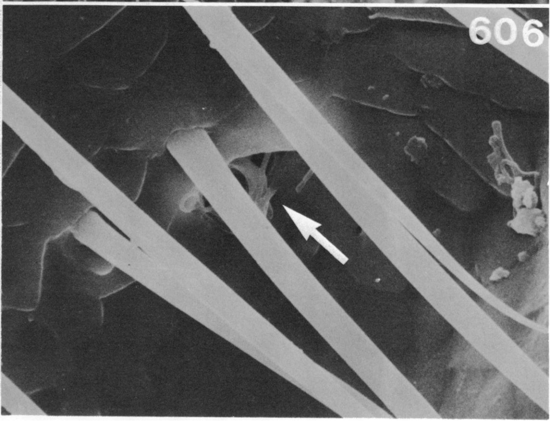












FIGS. 601–603. The *gigantulus* group. *Bledius gigantulus.* **601.** Prosternum, 168×. **602.** Prosternum, arrow points to secretory pores, 420×. **603.** Secretory pores of prosternum, 1600×.

FIGS. 604–606. The *mandibularis* group. *Bledius mandibularis.* **604.** Prothorax, ventral, arrow points to area enlarged in next photo, 55×. **605.** Prosternum, arrow points to secretory pore, 300×. **606.** Prosternum, arrow points to secretion, 1200×.

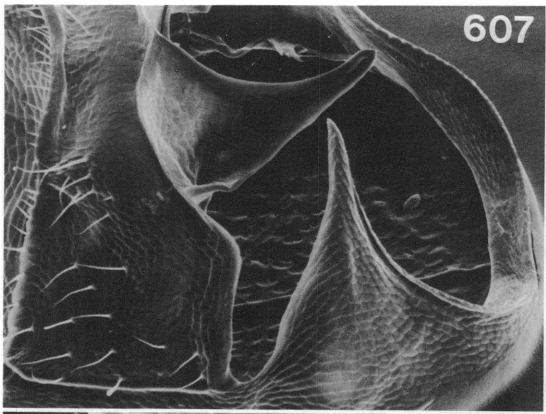
perplexus Cameron T,Sp(BMNH); type country: Taiwan.

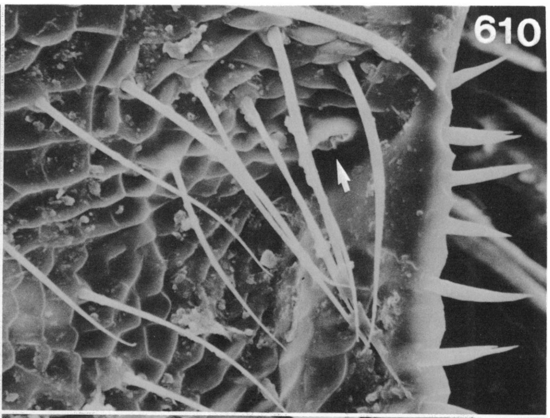
Taiwan: (Suisharyo? BMNH).

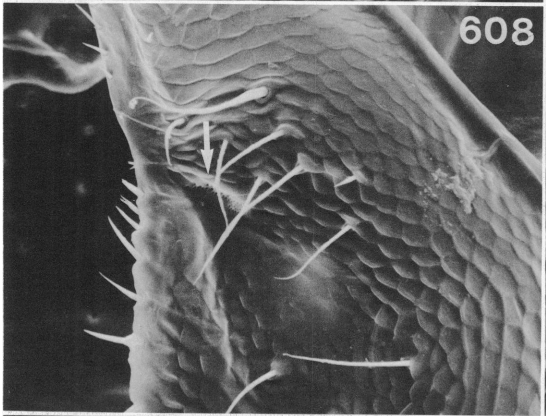
perrieri Fauvel Syn(IRSN); type country: Madagascar.

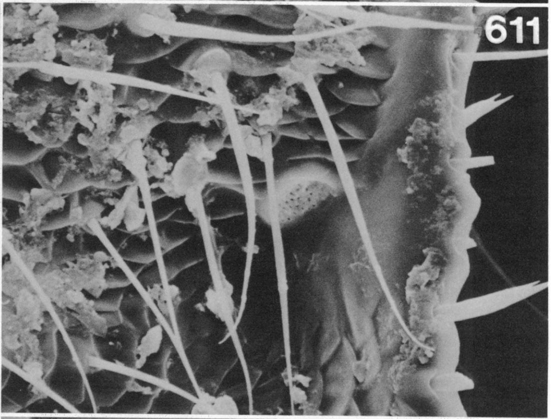
Madagascar: Soalala (IRSN); (Suberbieville? IRSN).

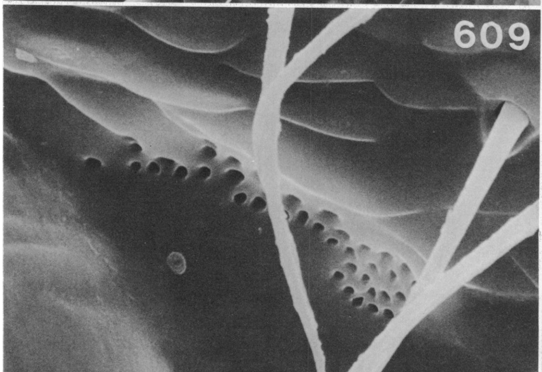
petzi Bernhauer T,Sp(FMNH), Sp(BMNH, MNHV); type country: Tanzania.

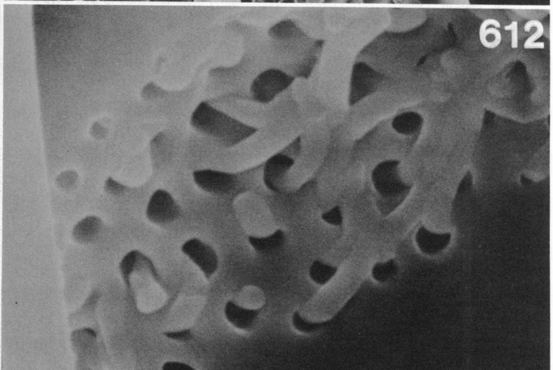












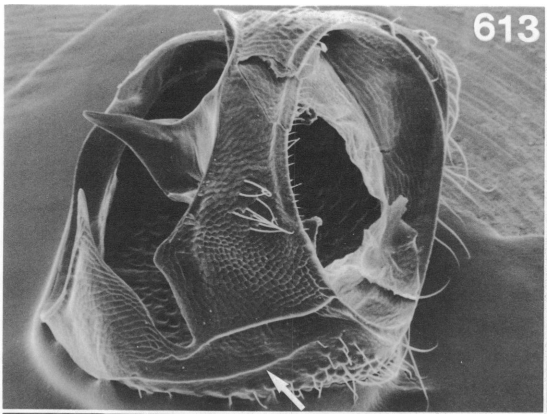
FIGS. 607–609. The *aequatorialis* group. *Bledius aequatorialis*. **607.** Prothorax, ventral, 110×. **608.** Prosternum, arrow points to secretory pores, 290×. **609.** Secretory pores, 1720×.

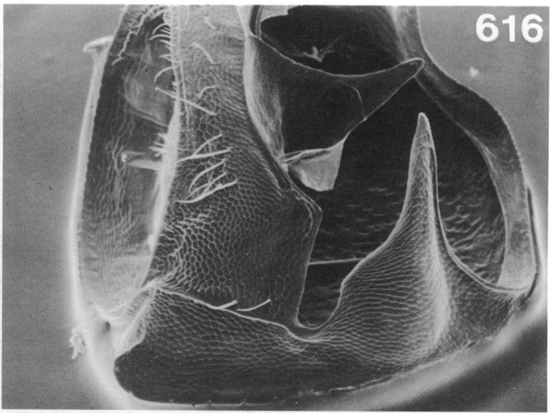
FIGS. 610–612. The *aequatorialis* group. *Bledius beattyi*. **610.** Prosternum, arrow points to secretory pores, 470×. **611.** Prosternum, 510×. **612.** Secretory pores with secretion, 5100×.

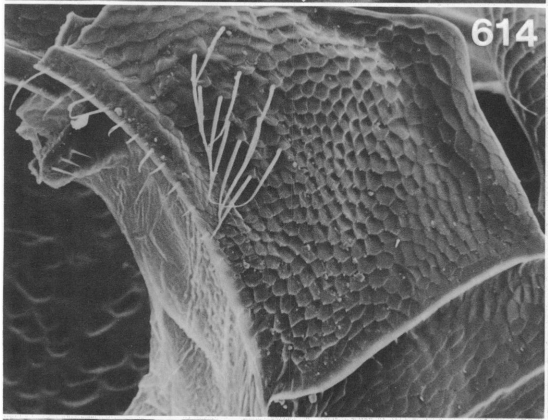
Tanzania: Dar-es-salam (FMNH, BMNH, MNHV).

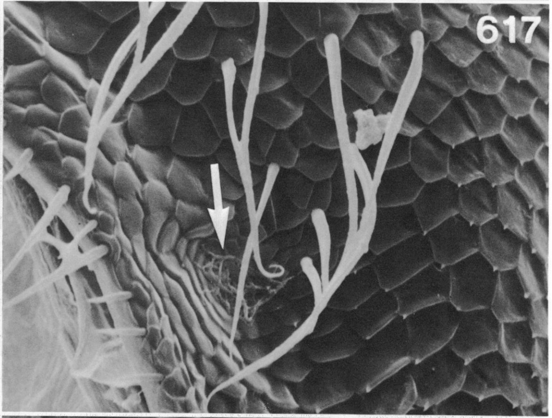
porcellus Bernhauer T,Co,Sp(FMNH), Co,Sp(BMNH), Sp(MNHV); type country: Indonesia.

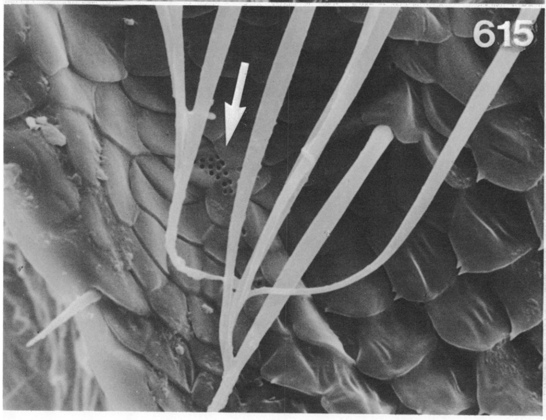
Borneo: (MNHV). **Indonesia:** Sumatra, Medan (FMNH); Sumatra, Palembang (FMNH). **Malaysia:** Perak (FMNH, MNHV, BMNH). **Philippines:** Mindanao, Surigao (BMNH). **Taiwan:** (Takezaki, nr. Mt. Ari ? BMNH).

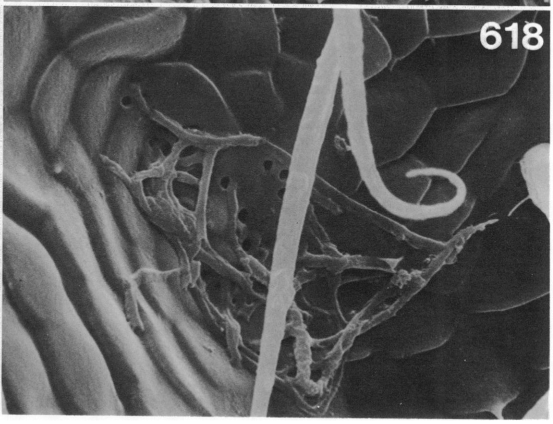










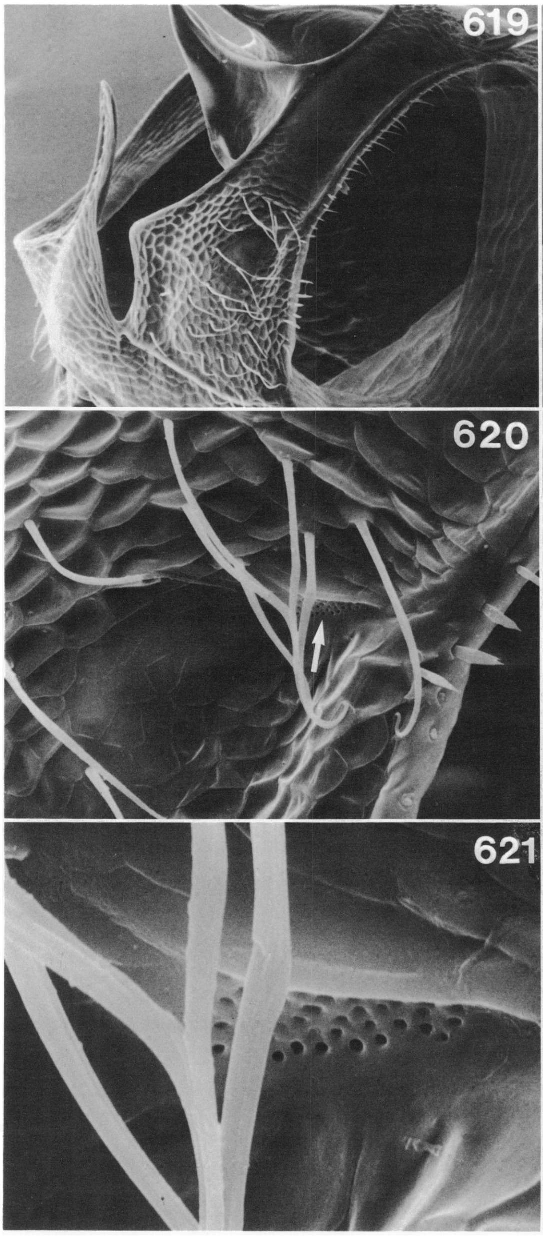


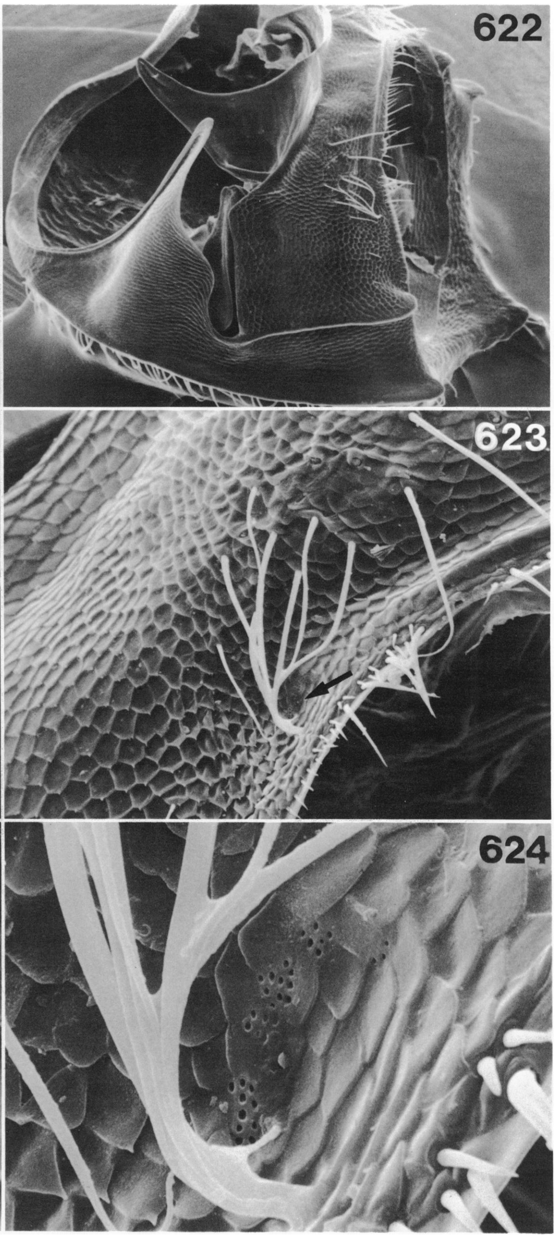
FIGS. 613–615. The *rugosicollis* group. *Bledius rugosicollis*. **613.** Prothorax, ventral, arrow points to pronotal marginal bead on hypomeron, 71×. **614.** Prosternum, 178×. **615.** Prosternum, arrow points to secretory pores, 940×.

FIGS. 616–618. The *furcatus* group. *Bledius furcatus*. **616.** Prothorax, ventral, 64×. **617.** Prosternum, anterior view of secretory depression, arrow points to secretory pores, 460×. **618.** Secretory pores of prosternum with secretion, 1880×.

rhinocerus Cameron T,Sp(BMNH); type country: ?
India: Assam (BMNH).

roettgeni Bernhauer T(FMNH), Sp(BMNH, MNHV); type country: Iraq.
Iraq: Mesopotamia (FMNH). **USSR:** Cau-





FIGS. 619–621. The *bellicosus* group. *Bledius,* n. sp. **619.** Prothorax, anteroventral, 132×. **620.** Prosternum, arrow points to secretory pores, 670×. **621.** Secretory pores of prosternum, 2640×.

FIGS. 622–624. The *lamelliceps* group. *Bledius pilicollis.* **622.** Prothorax, ventral, 57×. **623.** Prosternum, anterior view, arrow points to secretory pores, 236×. **624.** Secretory pores of prosternum, 1160×.

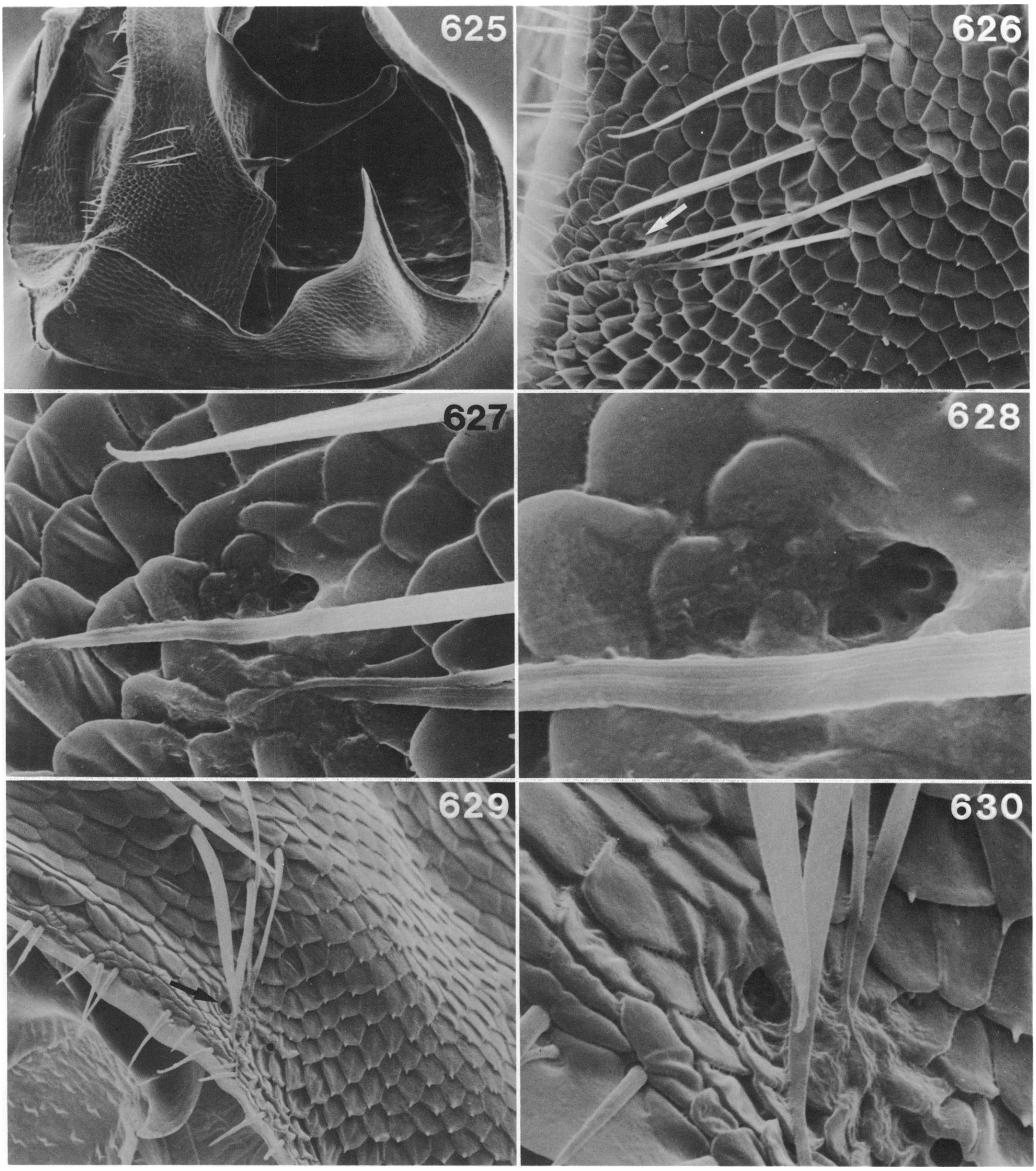
casus, Araxesthal [= Aras Valley] (BMNH, MNHV); Armenia (BMNH, MNHV).

somalianus Cameron T(BMNH); type country: Somalia.

Somalia: Gai Mudugh Province (BMNH).

splendens Bernhauer T,Sp(FMNH); type country: Zaire.

Zaire: Leopoldville [=Kinshasa] (FMNH).



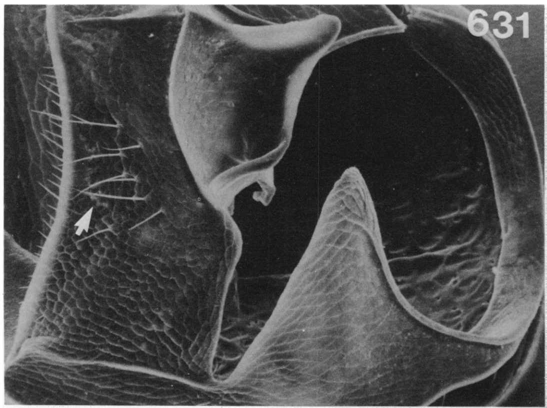
FIGS. 625–630. The *kochi* group. *Bledius bicornis*. **625.** Prothorax, ventral, 88×. **626.** Prosternum, arrow points to secretory pores, 440×. **627.** Prosternum, 1760×. **628.** Secretory pores of prosternum, 4300×. **629.** Prosternum, anterior view, arrow points to secretory pores, 420×. **630.** Prosternum with secretory pores, 1680×.

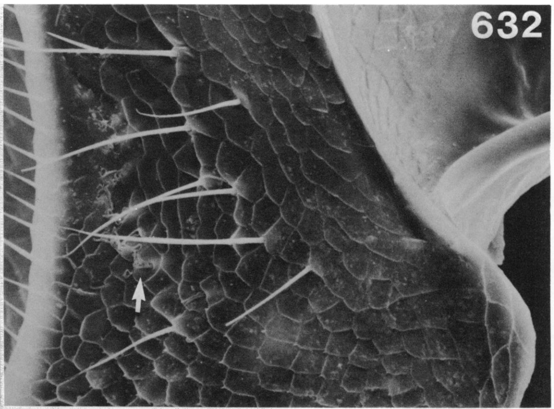
subopacus Bernhauer Co,Sp(BMNH), Sp(FMNH); type country: Namibia.

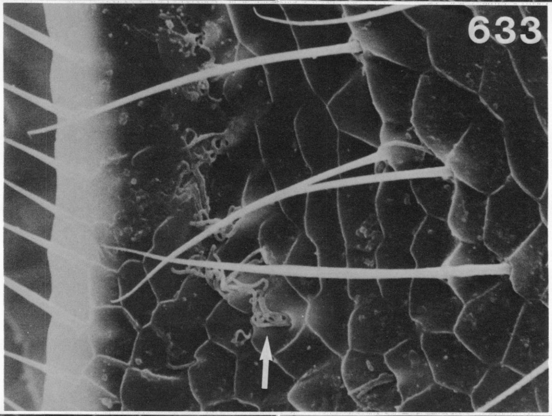
Angola: Lobito (FMNH). **Ethiopia:** Nanoropus, shore of Lake Rudolf (BMNH). **Madagascar:** Tulear [=Toliara] (FMNH). **Namibia:** Okahandja (BMNH, FMNH). **South Africa:** Pretoria (FMNH); Natal, Weenen (FMNH); Transvaal (Botshabelo? FMNH).

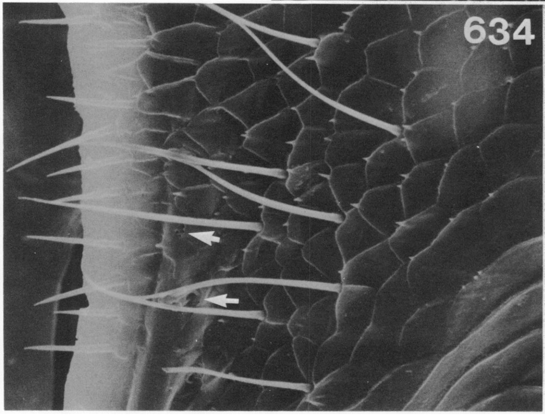
tenuiverres Scheerpeltz Co(BMNH, MNHV); type country: South Africa.

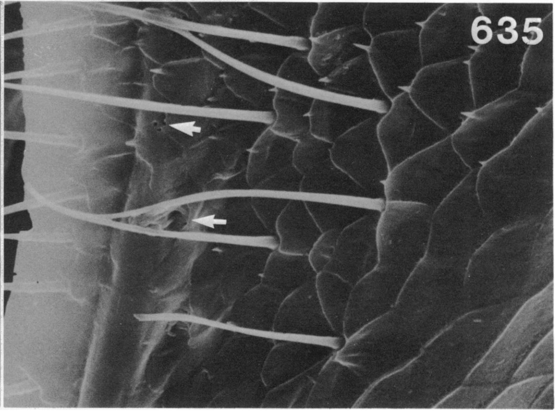
South Africa: Cape Province, Skurfteberg,











FIGS. 631–633. The *emarginatus* group. *Bledius parcissimus*. **631.** Prothorax, ventral, arrow points to secretory pores, 144×. **632.** Prosternum, arrow points to secretory pores, 380×. **633.** Prosternum, arrow points to secretory pores and secretion, 760×.

FIGS. 634–635. The *emarginatus* group. *Bledius chilensis*. **634.** Prosternum, arrows point to secretory pores, 640×. **635.** Prosternum, arrows point to secretory pores, 900×.

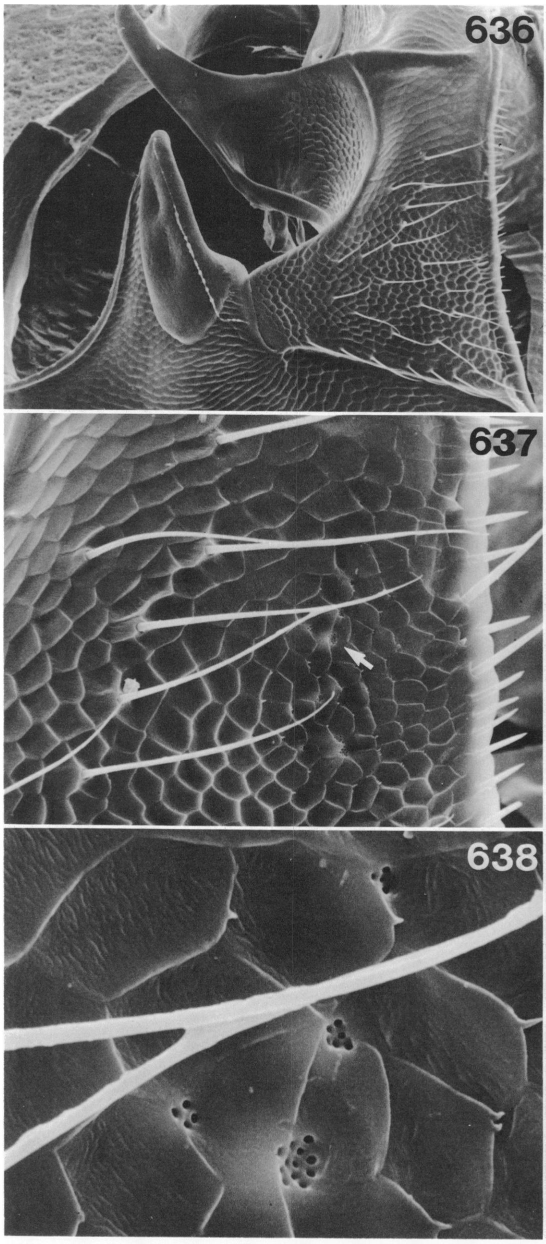
Alfreds Berg Pass, NNW Ceres (BMNH, MNHV).

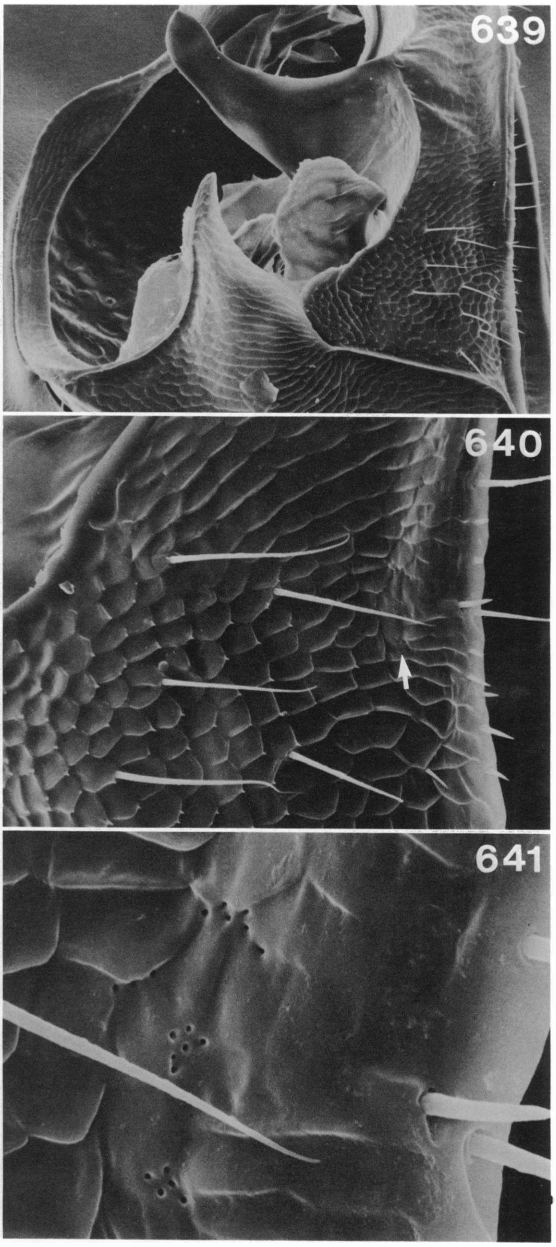
transversus Cameron T(BMNH); type country: India.

India: Dehra Dun (BMNH).

tuberculatus (Fabricius) Sp(BMNH, FMNH, MNHV, IRSN); type country: India.

Egypt: (FMNH, BMNH, IRSN); Ismailia

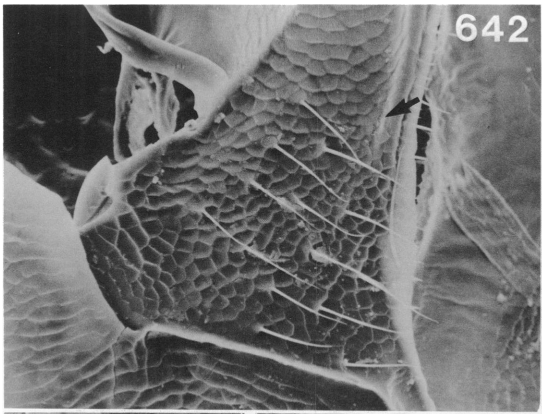


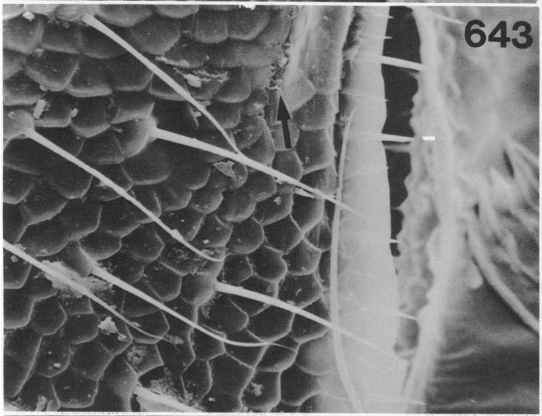


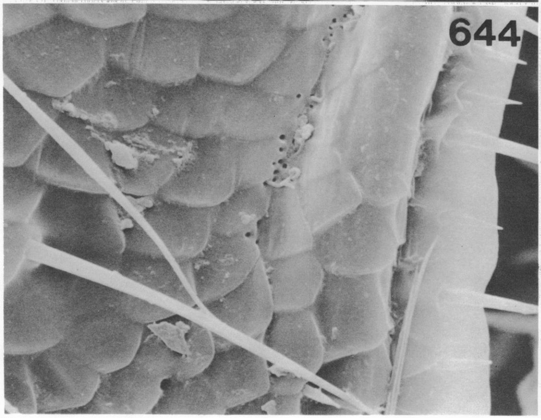
FIGS. 636–638. The *kosempoensis* group. *Bledius kosempoensis*. **636.** Prothorax, ventral, 100 ×. **637.** Prosternum, arrow points to secretory pores, 380 ×. **638.** Secretory pores of prosternum, 1960 ×.

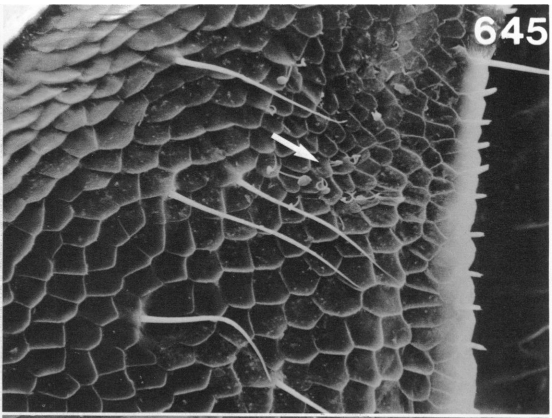
FIGS. 639–641. The *lucidus* group. *Bledius lucidus*. **639.** Prothorax, ventral, 136 ×. **640.** Prosternum, arrow points to secretory pores, 460 ×. **641.** Secretory pores of prosternum, 1840 ×.

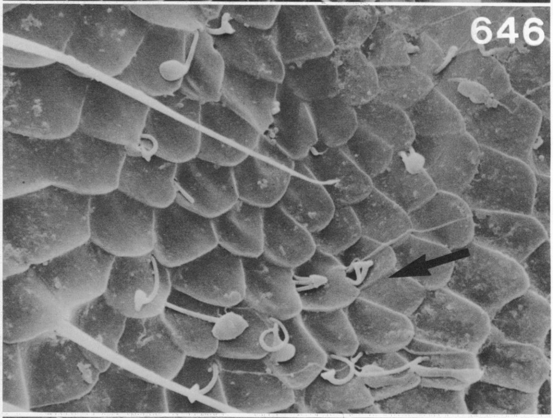
[=Ismâ'ilîya] (BMNH). **India:** Parikud Island, Chilka Lake, Ganjam District (BMNH); Mysore [=Karnatake] (BMNH); Madura (BMNH); Puri, Orissa Coast (FMNH); Balighai, near Puri (FMNH); Madras (MNHV); Malabar, Mahé (MNHV, IRSN). **Philippines:** Luzon, Los Banos (FMNH); Luzon, Mt. Maquiling (FMNH). **South Africa:** Setlagodi District (IRSN). **Sri Lanka:** (FMNH, IRSN).

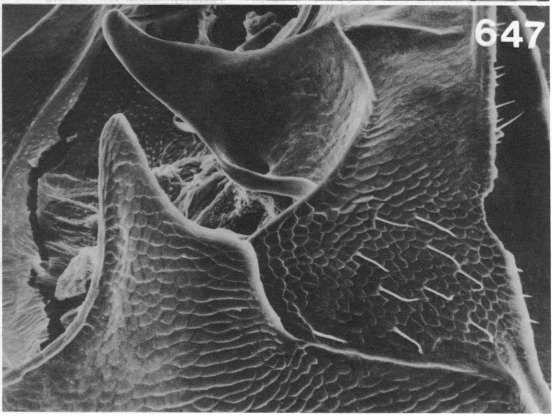












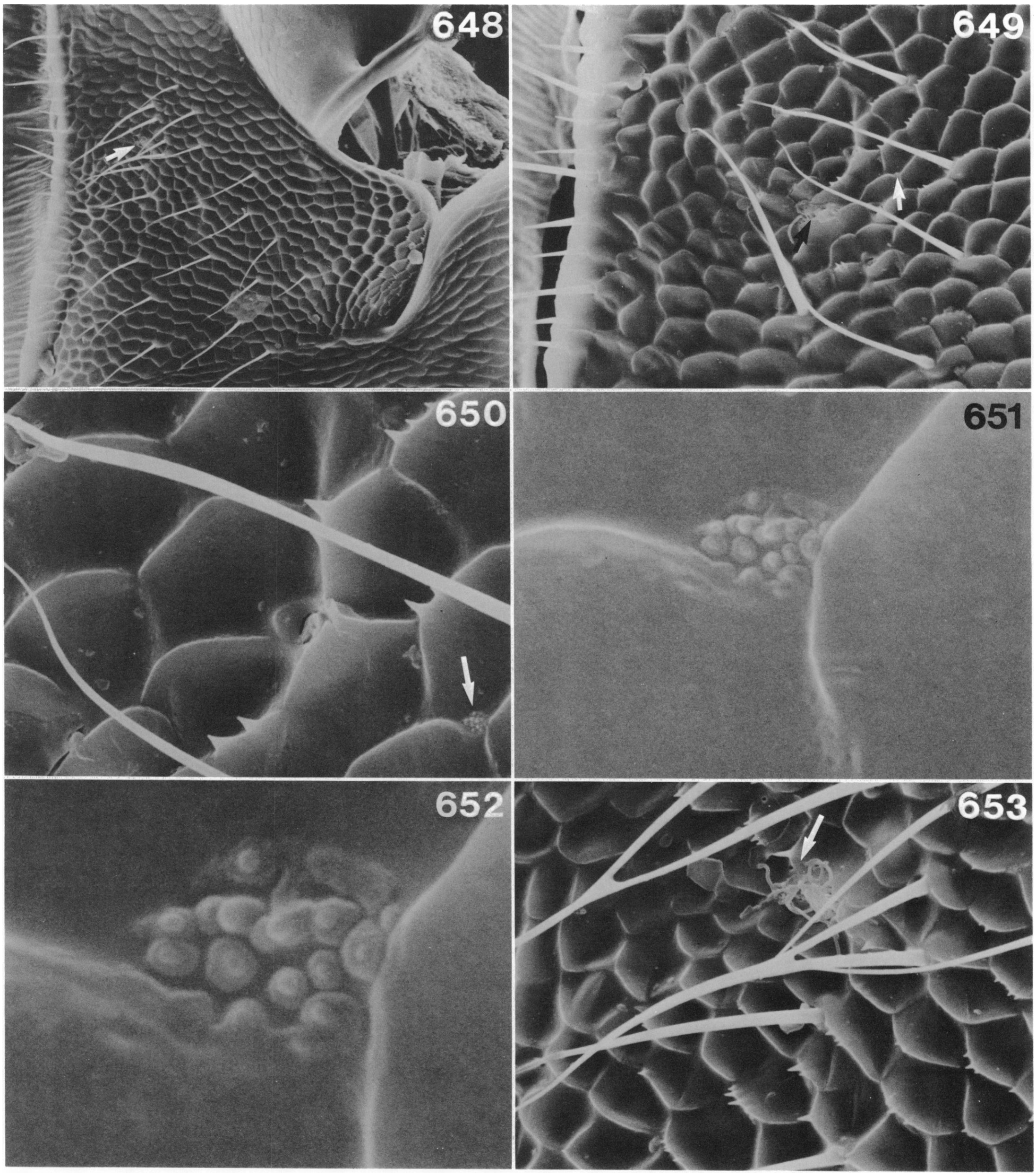
FIGS. 642–644. The *semiferrugineus* group. *Bledius* nr. *validepunctatus*. **642.** Prosternum, arrow points to secretory pores, 208 ×. **643.** Prosternum, arrow points to secretory pores, 520 ×. **644.** Prosternum and secretory pores with secretion, 1040 ×.

FIGS. 645–646. The *semiferrugineus* group. *Bledius semiferrugineus*. **645.** Prosternum, arrow points to secretory pores, 310 ×. **646.** Prosternum, arrows point to secretory pores and their secretion, 820 ×.

FIG. 647. The *semiferrugineus* group. *Bledius analis*. Prothorax, ventral, 136 ×.

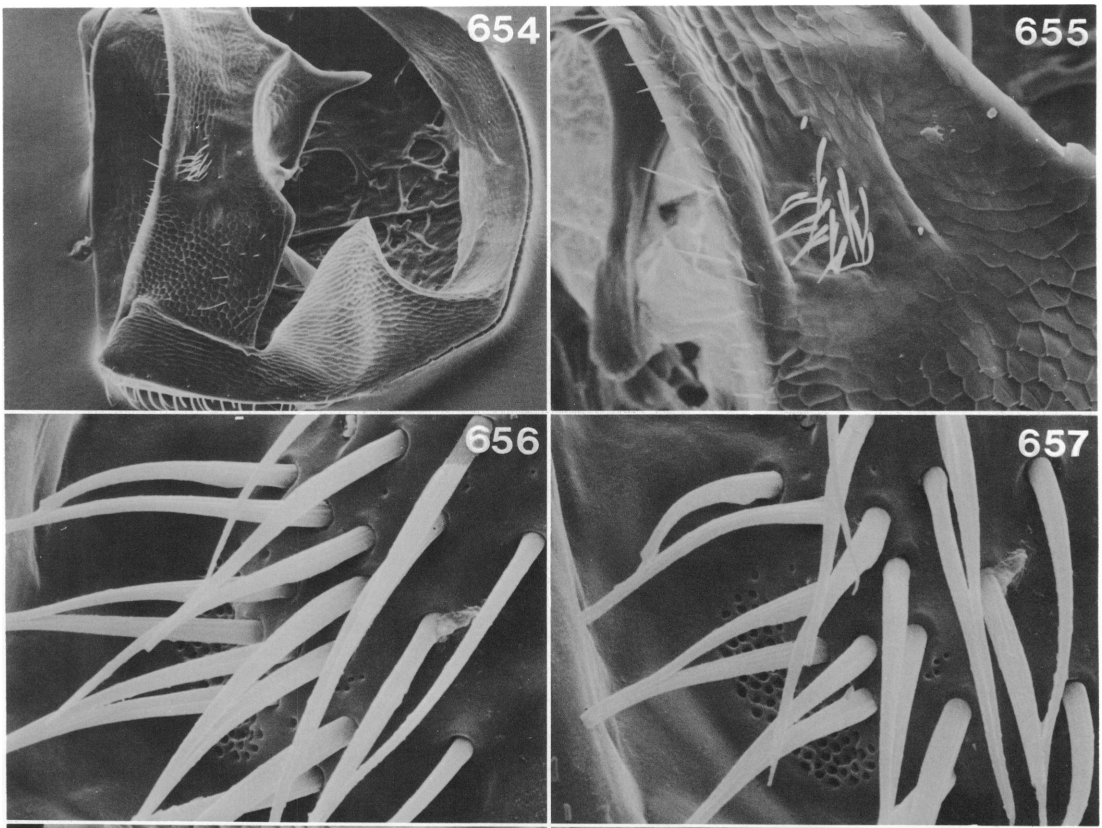
ugandae Bernhauer T,Co,Sp(FMNH), T,Sp(BMNH); type country: Kenya. **Kenya:** mouth of Kerio River (BMNH). **Tanzania:** Nachingwea (BMNH).

verres Erichson Sp(BMNH, FMNH, MNHV, IRSN); type country: Italy.

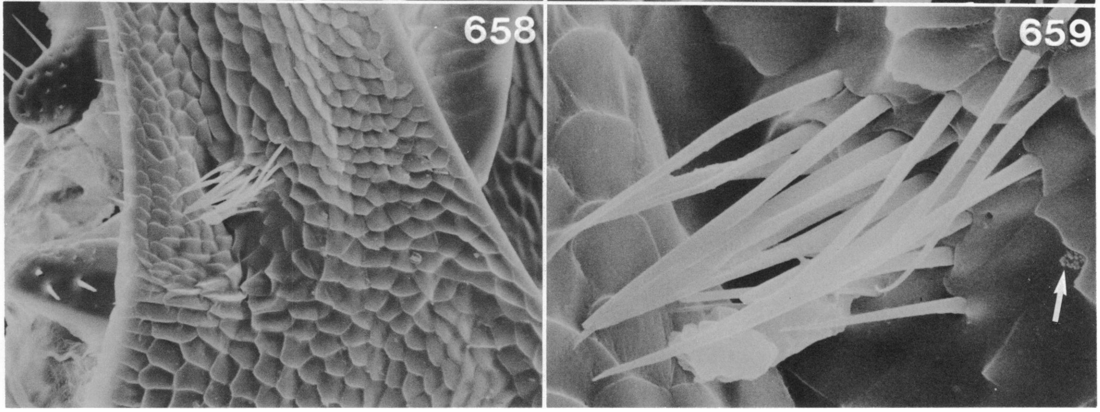


FIGS. 648–653. The *armatus* group. *Bledius bellicus*. **648.** Prosternum, arrow points to secretory pores, 168×. **649.** Prosternum, black arrow points to secretory pores covered by secretion, white arrow points to sensory structure, 470×. **650.** Prosternum, arrow points to sensory structure, 1920×. **651.** Prosternal sensory structure, 10,000×. **652.** Prosternal sensory structure, 18,800×. **653.** Prothorax, arrow points to secretory pores and secretion. 840×.

Algeria: Alger (IRSN); Philippeville [=Skikda] (IRSN); Great Kabylie, Azazga, Oued Dis (IRSN). **Bulgaria:** Nessebur [=Nesebur] (MNHV). **Cyprus:** (IRSN). **Ethiopia:** Nanoropus, Lake Rudolf (FMNH). **France:** Bordeaux (FMNH); Corsica (FMNH, MNHV); Corsica, Salice (FMNH); Provence, Menton (FMNH); La

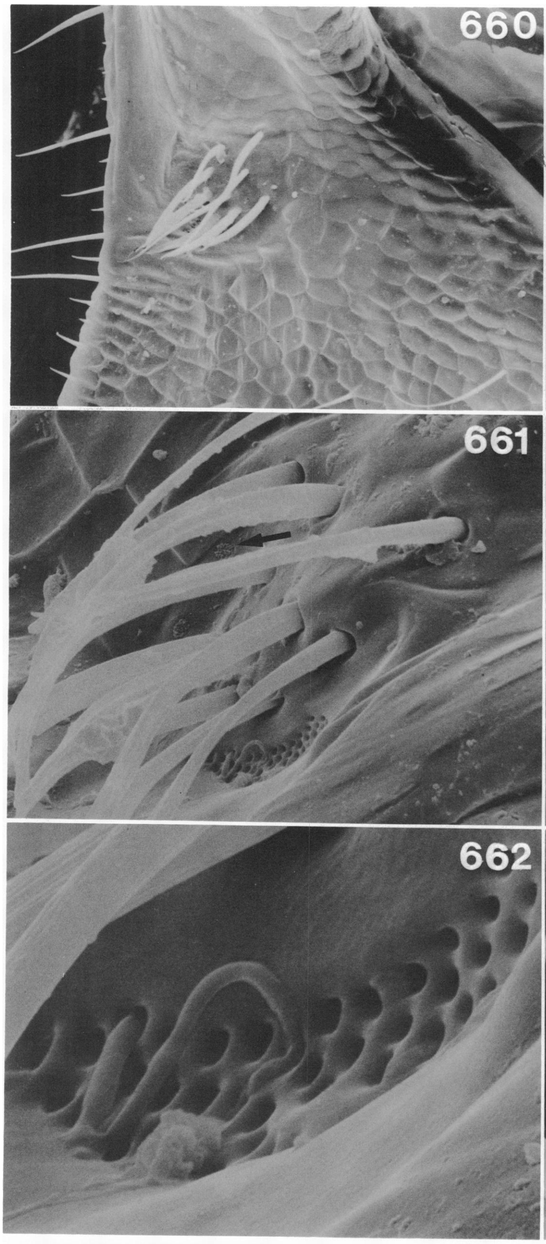


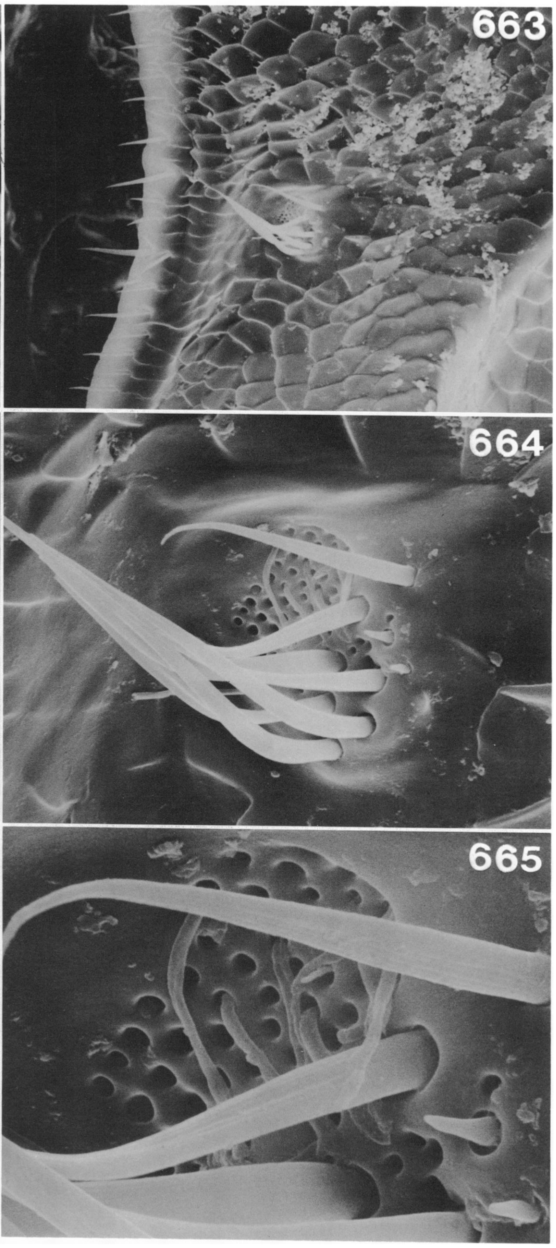
FIGS. 654–657. The *albonotatus* group. *Bledius diagonalis*. **654.** Prothorax, ventral, 92×. **655.** Prosternum, anterior view, 352×. **656.** Secretory pores and associated setae of prosternum, lateral view, 1600×. **657.** Secretory pores and associated setae of prosternum, anterior view, 1760×.



FIGS. 658–659. The *albonotatus* group. *Bledius nardus*. **658.** Prosternum, 310×. **659.** Cluster of setae associated with secretory pores, arrow points to sensory structure, 1560×.

Teste (IRSN); Corsica, Porto Vecchio (IRSN); St. Jean [de Luz] (IRSN); Nice (IRSN); Cazaux (IRSN); Corsica, Ghisonaccia, Gravier du Fiumorbo (IRSN). **Gibraltar:** (IRSN). **Greece:** Corfu, Potamos (FMNH, MNHV); Corfu (Boromera? FMNH); Corfu (IRSN); Kos Island (BMNH). **India:** Uttar Pradesh, Kumaon,

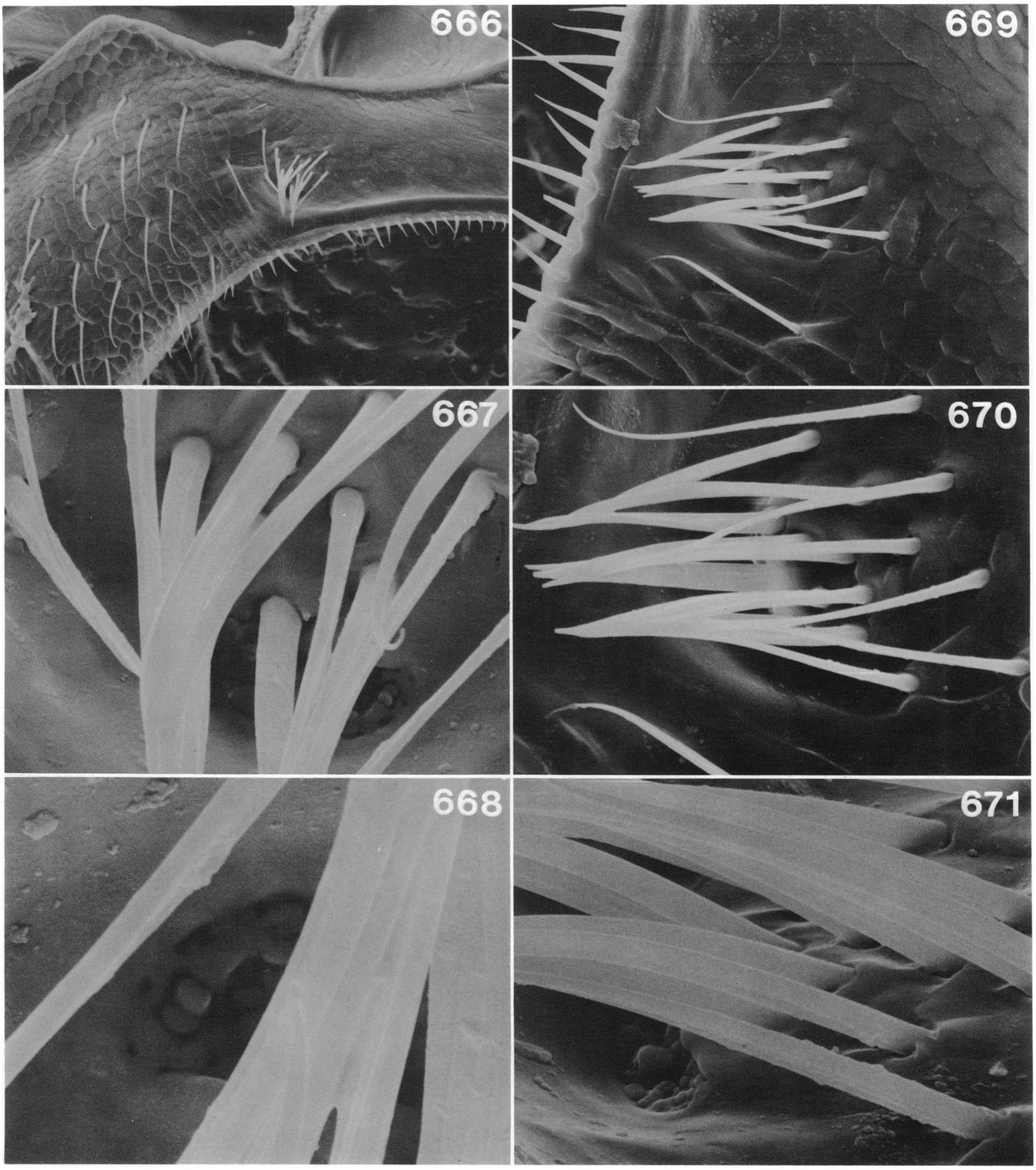




FIGS. 660–662. The *annularis* group. *Bledius newelli.* **660.** Prosternum with setae near secretory pores, 300×. **661.** Secretory pores and associated setae of prosternum, arrow points to sensory structure, 1200×. **662.** Secretory pores of prosternum with strand of secretion shown, 5600×.

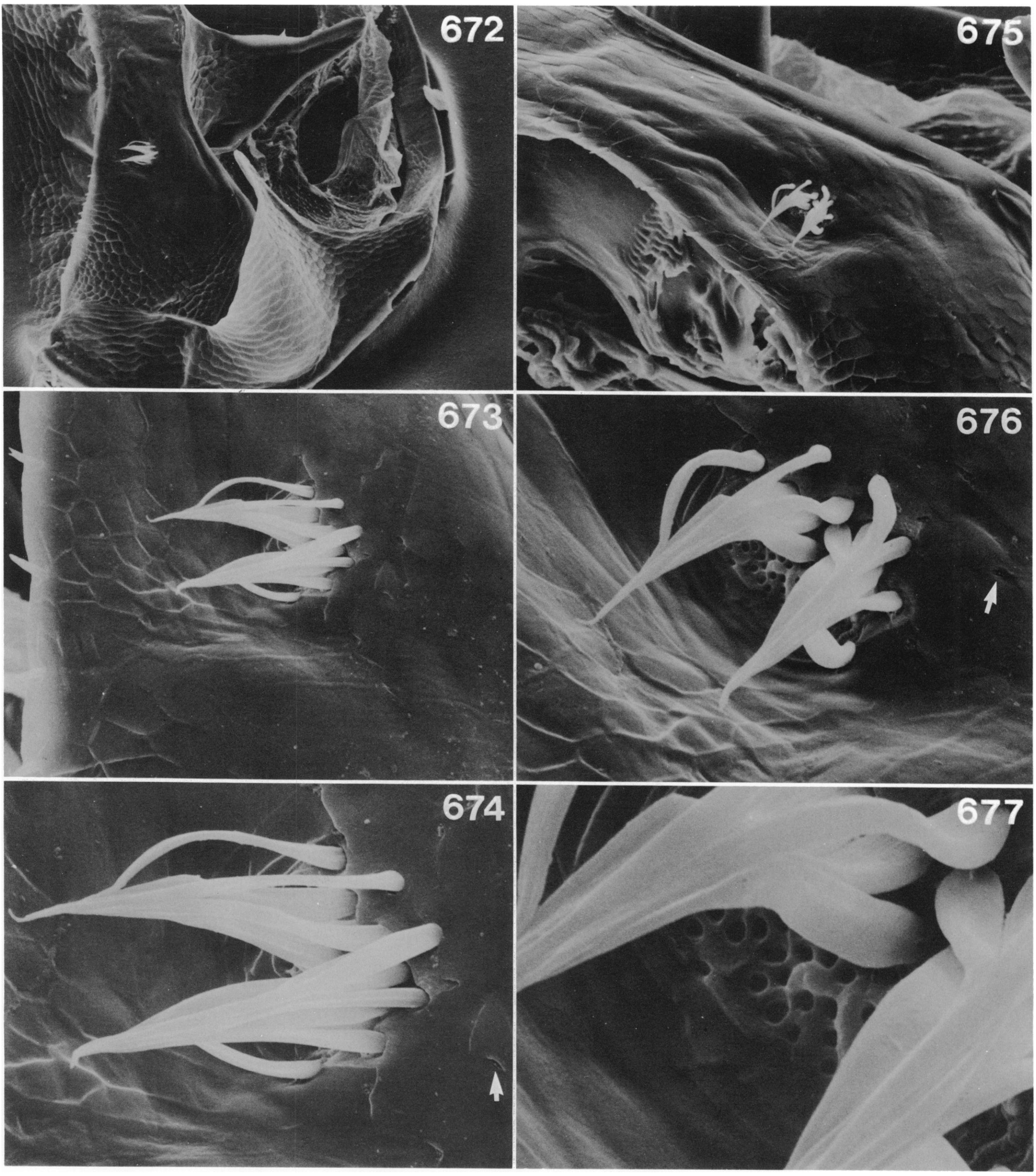
FIGS. 663–665. The *annularis* group. *Bledius suturalis.* **663.** Prosternum with setae near secretory pores, 400×. **664.** Secretory pores and associated setae of prosternum, 1640×. **665.** Secretory pores shown with strands of secretion, 4100×.

Ranikhet (FMNH); Dehra Dun (FMNH); Dehra Dun (Nim Nadi ? BMNH); (Lachiwala, Siwaliks ? BMNH). **Italy:** Sicily (FMNH, IRSN, MNHV); Sardinia (Assuni? FMNH); Sardinia, Dorgali (FMNH); Calabria, Antonimina (FMNH); Emilia, Riccione (MNHV); Ventimiglia, Roia (MNHV); Sardinia, Flumendosa River,



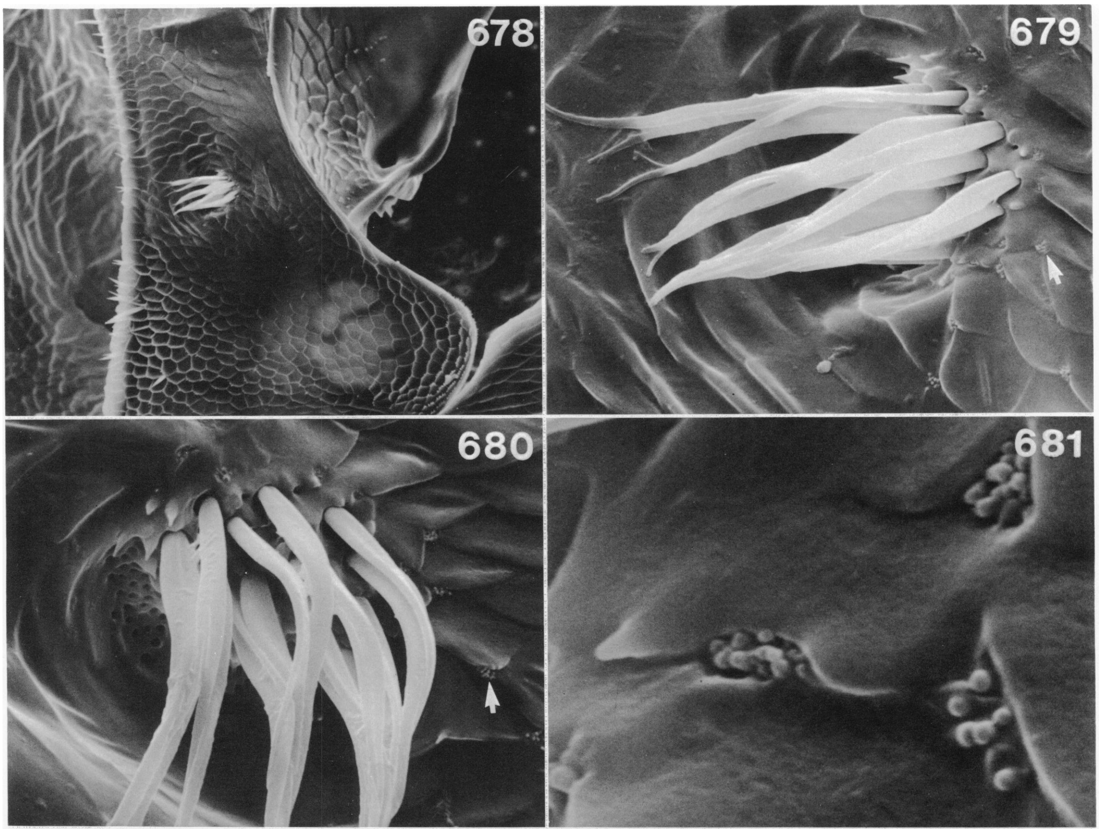
FIGS. 666–671. The *annularis* group. *Bledius ruficornis*. **666.** Prosternum, anterior view of left half, 200×. **667.** Secretory pores and associated setae of prosternum, anterior view, 2000×. **668.** Secretory pores, anterior view, 4960×. **669.** Cluster of setae associated with prosternal secretory pores, 500×. **670.** Setae near secretory pores of prosternum, 1000×. **671.** Secretory pores of prosternum, 2000×.

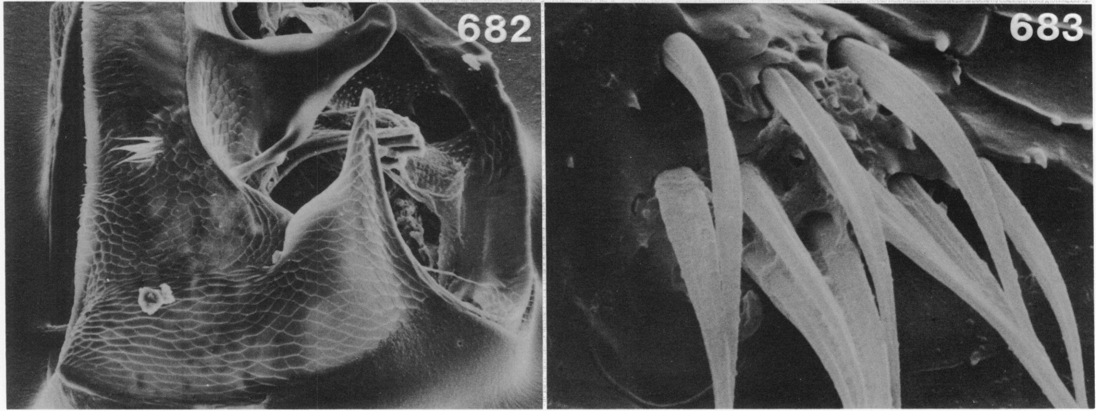
near Foce al Ponte (MNHV); Milan (MNHV); Leece (IRSN). **Jordan:** east bank of Jordan River, near Sea of Galilee [=Tiberias] (FMNH). **Lebanon:** Beirut (IRSN). **Madagascar:** Port Daufin [=Taolanaro] (FMNH). **Morocco:** Mogador [=Essaouira] (IRSN, MNHV); (Urica? MNHV). **Philippines:** Luzon, Mt. Maquiling (FMNH). **Romania:** Sulina (BMNH). **South Africa:** Natal, Isipingo (BMNH). **Spain:** Marbella



FIGS. 672–677. The *debilis* group. *Bledius debilis*. **672.** Prothorax, ventral, 144×. **673.** Cluster of setae associated with secretory pores, lateral view, 740×. **674.** Setae near secretory pores of prosternum, arrow points to sensory structure, 1480×. **675.** Prosternum, anterior view, right side, 360×. **676.** Setae and secretory pores of prosternum, arrow points to sensory structure, 1520×. **677.** Secretory pores and associated setae, 3800×.

(MNHV); Ponferrada (FMNH); Algeciras (FMNH); Andalusia, Ronda, Rio Grande (IRSN); Andalusia, Ronda, Arriate, Rio Guadalcobacin (IRSN); Andalusia, Marbella (San Pedro Alcantara ? IRSN); San Roque District (BMNH). **Syria:** Aleppo (FMNH). **Tanzania:** Tabora (FMNH). **Tunisia:** Souk el Arba (MNHV); Teboursouk

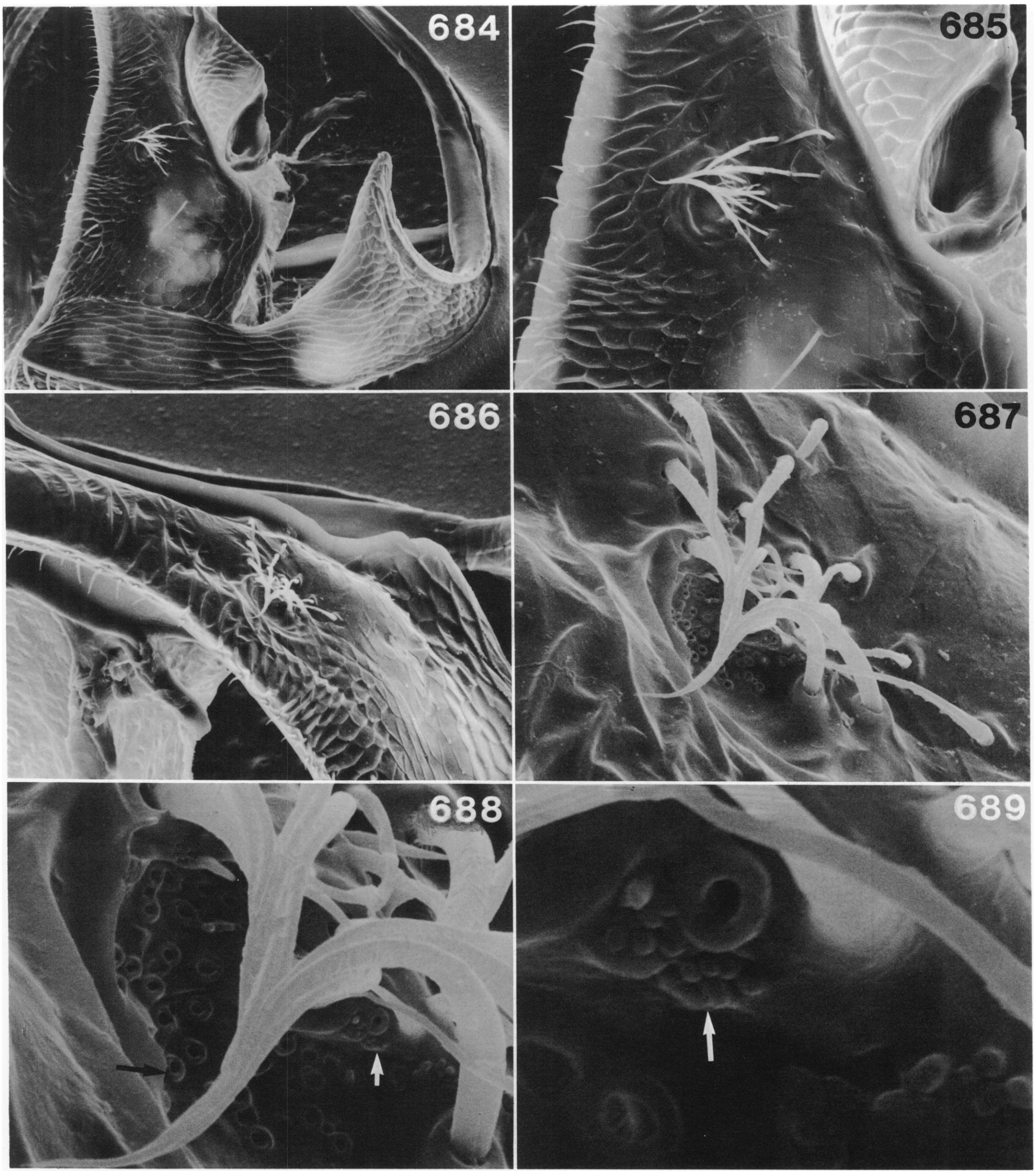




FIGS. 678–681. The *basalis* group. *Bledius opaculus*. **678.** Prosternum, lateral view, 196×. **679.** Prosternal setae associated with secretory pores, arrow points to sensory structure, 1120×. **680.** Secretory pores and adjacent setae of prosternum, anterior view, arrow points to sensory structure, 1460×. **681.** Sensory structures on prosternum, 9800×.

FIGS. 682–683. The *basalis* group. *Bledius melanocephalus*. **682.** Prothorax, ventral, 156×. **683.** Setae associated with secretory pores of prosternum, anterior view, 2320×.

(FMNH, MNHV, IRSN); Tabarka Oued (MNHV). **Turkey:** Alanya (Dim Irmak ? IRSN). **Uganda:** mouth of Kerio River (BMNH). **USSR:** Buchara (MNHV); Lenkoran, Azerbaidzhan (MNHV, IRSN); Sarepta (IRSN); Caucasus (Aresch? IRSN).



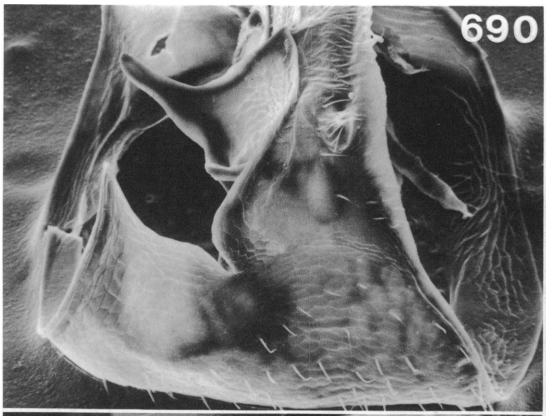
FIGS. 684–689. The *fratellus* group. *Bledius fratellus*. **684.** Prothorax, ventral, 1524×. **685.** Prosternum, lateral view, 380×. **686.** Prosternum, anterior view, right side, 350×. **687.** Secretory pores and associated setae of prosternum, anterior view, 1400×. **688.** Secretory pores and adjacent setae of prosternum, anterior view, black arrow points to collar around secretory pore, white arrow points to sensory structure, 3400×. **689.** Secretory pores of prosternum, arrow points to sensory structure, 13,600×.

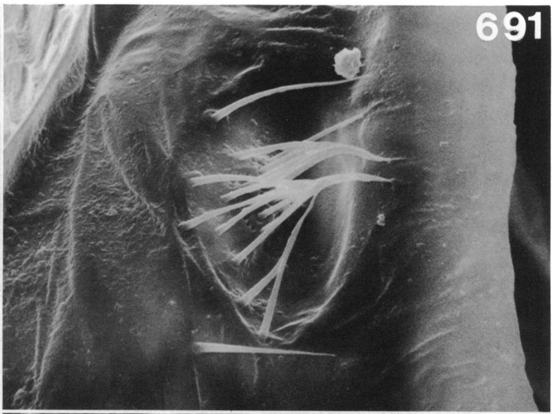
Yugoslavia: Zara [=Zadar] (Grande Lago ? MNHV); Serbia, Struga (FMNH); Bosnie [=Bosna] (IRSN); Beograd, near Danubio (MNHV).

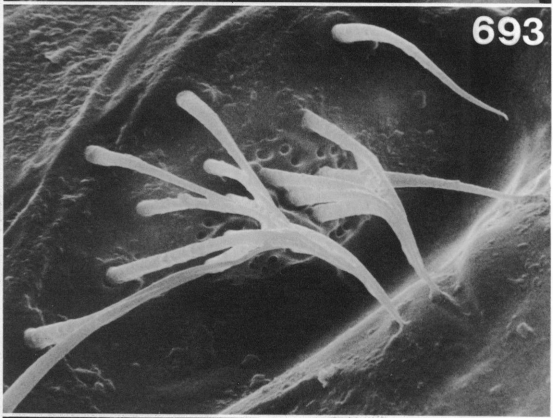
wombaliensis Bernhauer T(FMNH); type country: Congo.

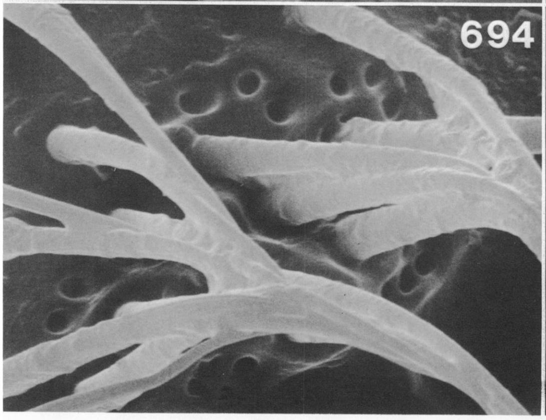
(**Congo:** Wombali? FMNH).

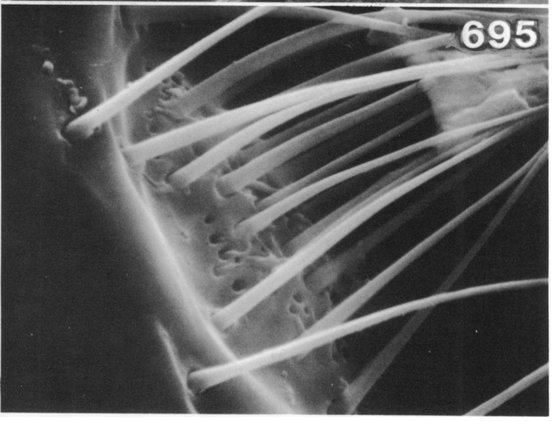
Undetermined.







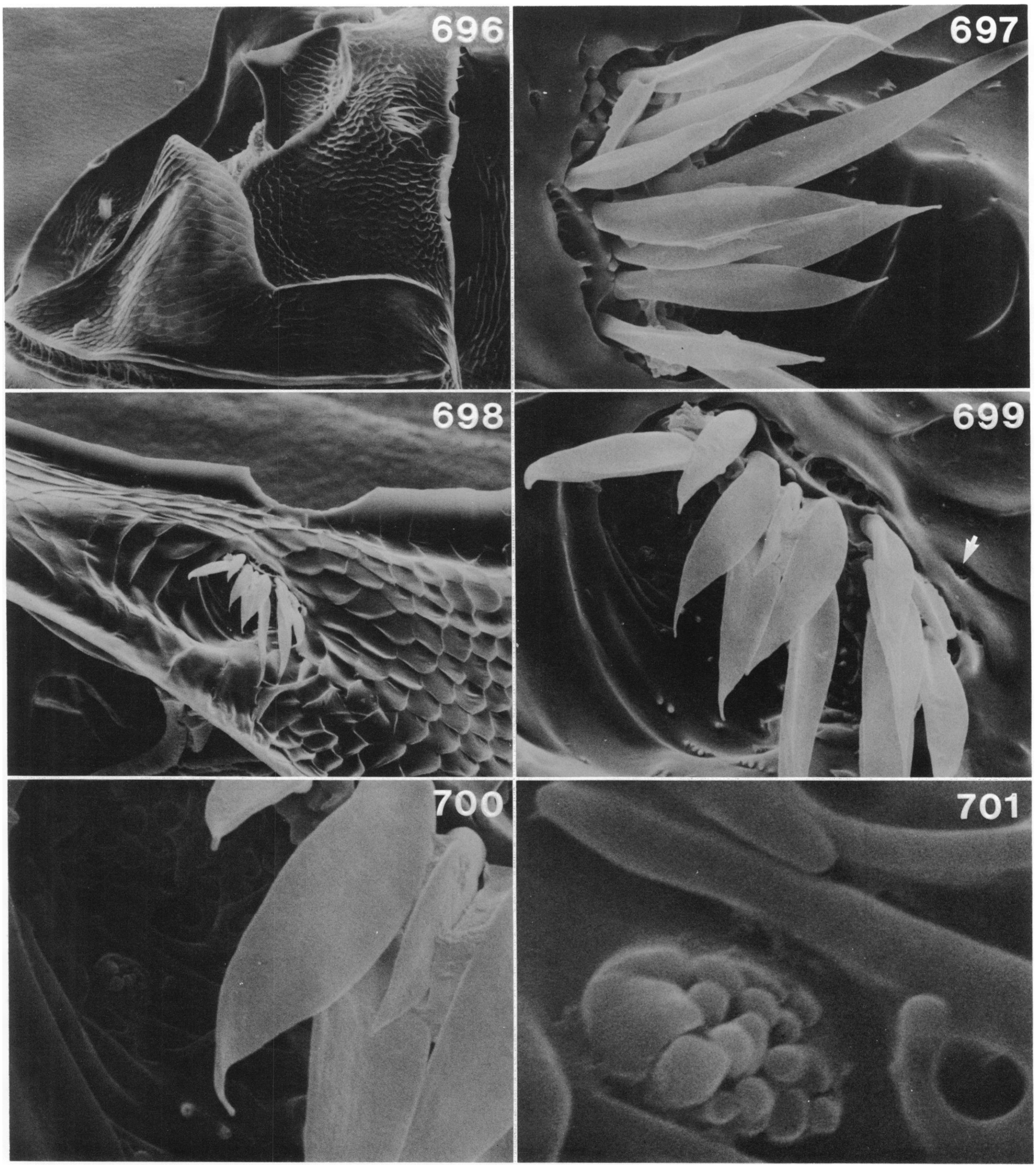




FIGS. 690–694. The *forcipatus* group. *Bledius actitus*. **690.** Prothorax, ventral, 184×. **691.** Setae of prosternum associated with secretory pores, lateral view, 880×. **692.** Setae of prosternum associated with secretory pores, anterior view, 940×. **693.** Secretory pores and associated setae, anterior view, 1880×. **694.** Secretory pores among setae, 4700×.

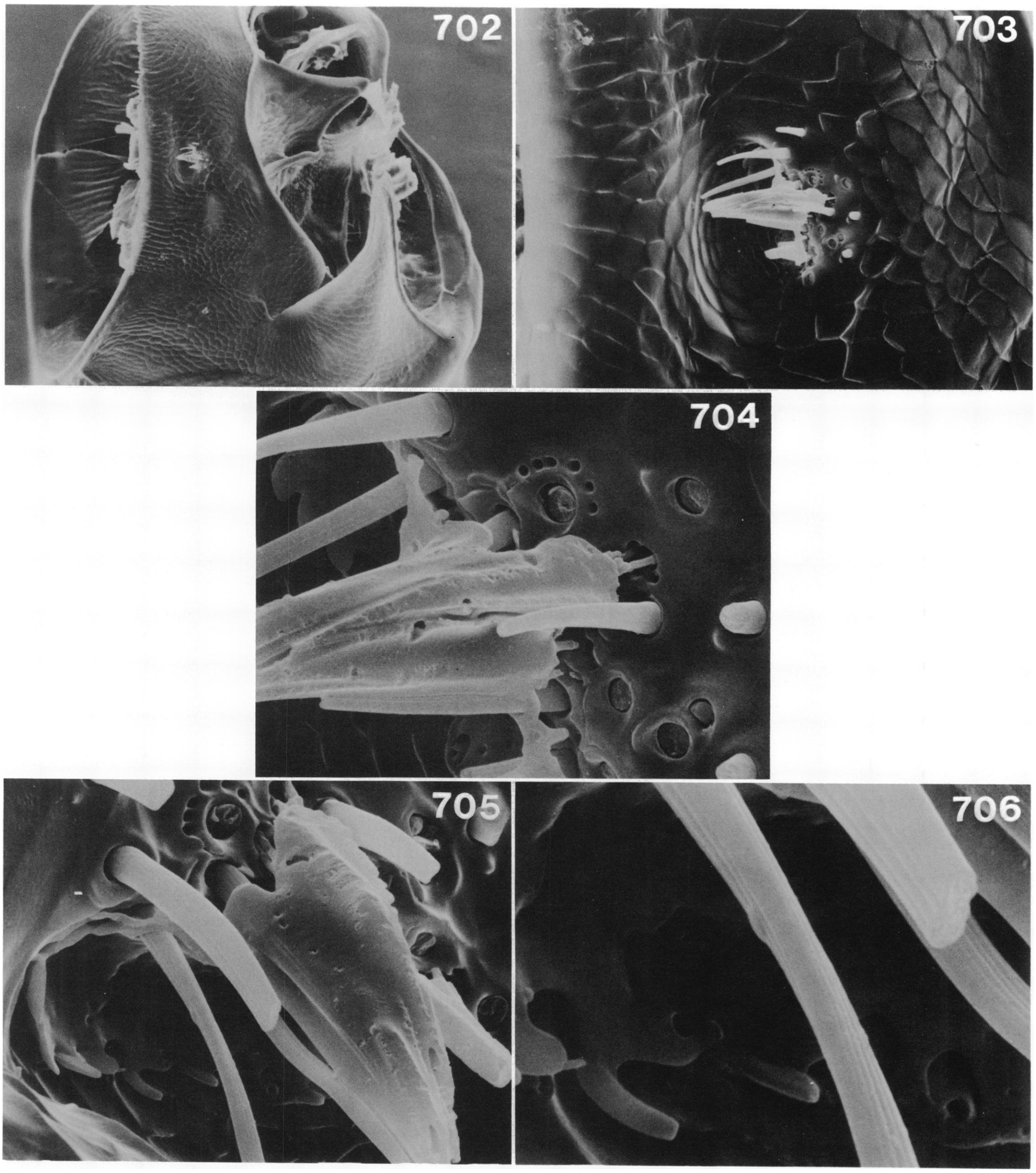
FIG. 695. The *forcipatus* group. *Bledius forcipatus*. Secretory pores and associated setae.

Afghanistan: Pul-e-Charkhi, 22 km ENE Kabul (HCC); Kabul (MNHV). **Aldabra Islands:** (USNM); South Island, Cinq Casas (BMNH, USNM). **Algeria:** In Salah (MNHV). **Angola:** Joao de Almeida (BMNH); (3 mi. N Santa Clara ? BMNH); Hanha (AMNH); Cachoeiras, 20 mi. SW Gabela (BMNH); Roçadas, Cunene River



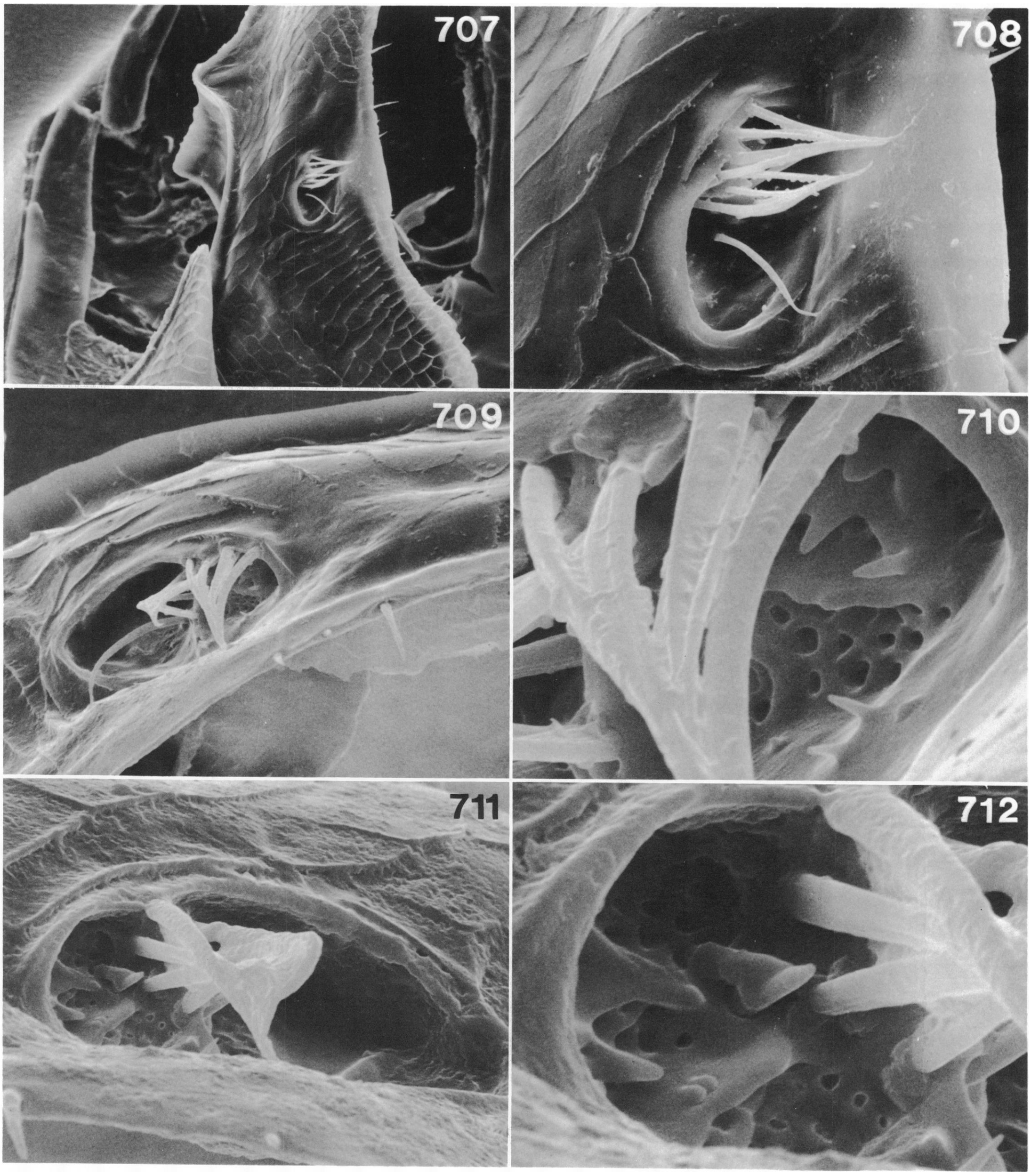
FIGS. 696–701. The *punctatissimus* group. *Bledius maindroni*. **696.** Prothorax, ventral, 132×. **697.** Setae of prosternum associated with secretory pores, lateral view, 1520×. **698.** Prosternum, right side, anterior view, 430×. **699.** Setae of prosternum and secretory pores, anterior view, arrow points to sensory structure, 1720×. **700.** Secretory pores of prosternum, anterior view, 3900×. **701.** Sensory structure among secretory pores of prosternum, 17,200×.

(BMNH). **Australia:** Queensland, 14 km N Gympie (USNM); Victoria, Mirboo National Park (MCZ). **Benin:** (Central Region, Zizonkame ? USNM). **Botswana:** Lake Ngami, 12 mi. NE Sehithwa (BMNH); Thamalakane River, 7 mi. NE Maun (BMNH); Moremi Reserve (BMNH); Toteng, 42 mi. SW Maun (BMNH); Nata Riv-



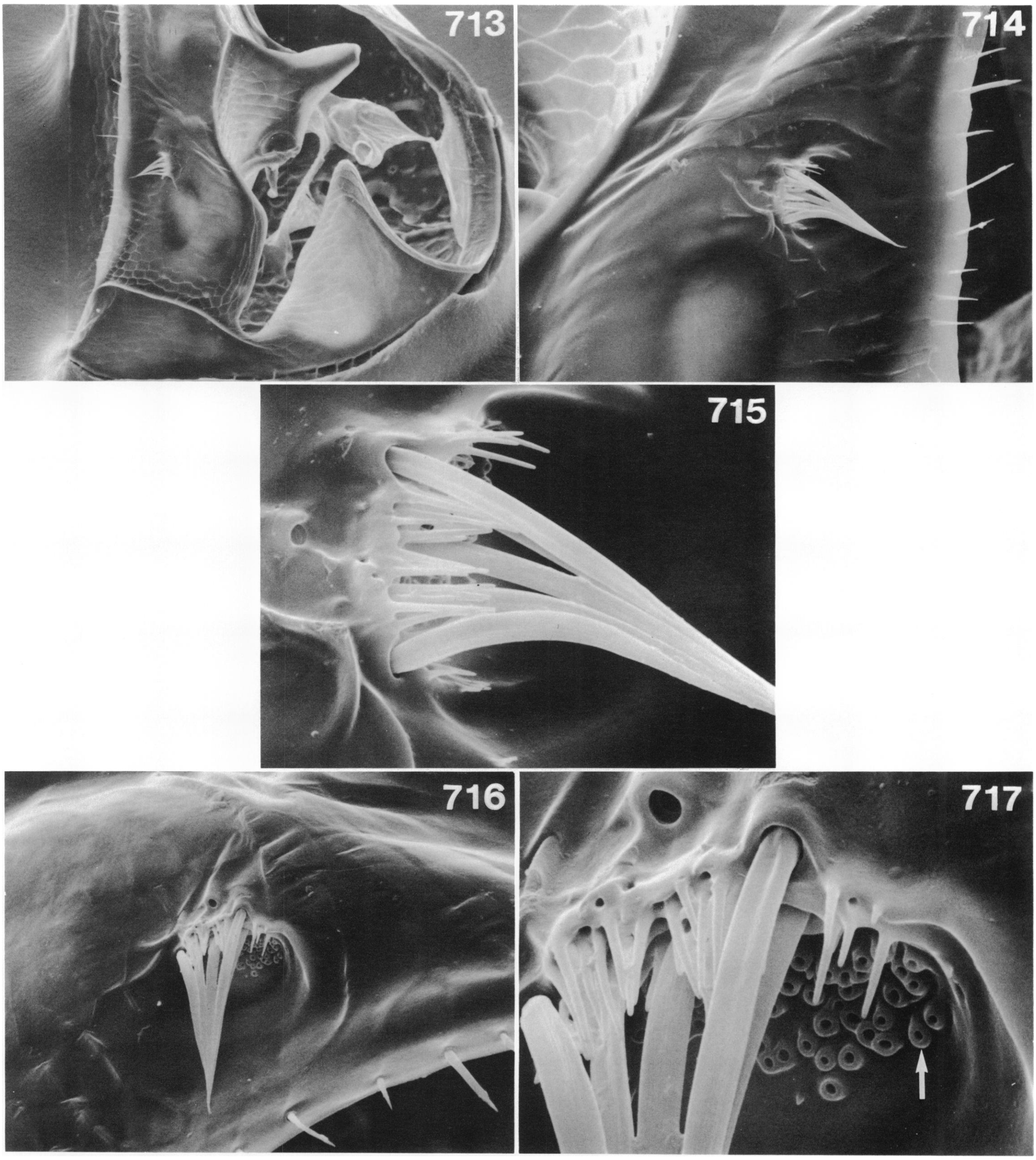
FIGS. 702–706. The *angustus* group. *Bledius* sp. **702.** Prothorax, 100×. **703.** Prosternum, lateral view, 510×. **704.** Setae of prosternum associated with secretory pores, lateral view, 2080×. **705.** Secretory pores and associated setae of prosternum, anterior view, 2120×. **706.** Secretory pores of prosternum, 5300×.

er (BMNH, MNHV); Makgadikgadi Salt Pan (BMNH); Xugana, Okavango Swamp (USNM); Kuke Pan (BMNH); Semowane River (BMNH); Moremi Reserve (BMNH); Maun, Ngamiland (BMNH); Chobe District, Shaile (BMNH); 2 mi. N Gweta (BMNH); 42 mi. W Kalkfontein (BMNH). **Brunei:** Seria (BMNH). **Bulgaria:** Levunovo (BMNH); (Goce Delcev-Mesta ? BMNH). **China:** Beijing (USNM). **Cyprus:** Galata [=Galatia] (MNHV). **Djibouti:** Obock (IRSN). **Ethiopia:** Ilubador, Gambela



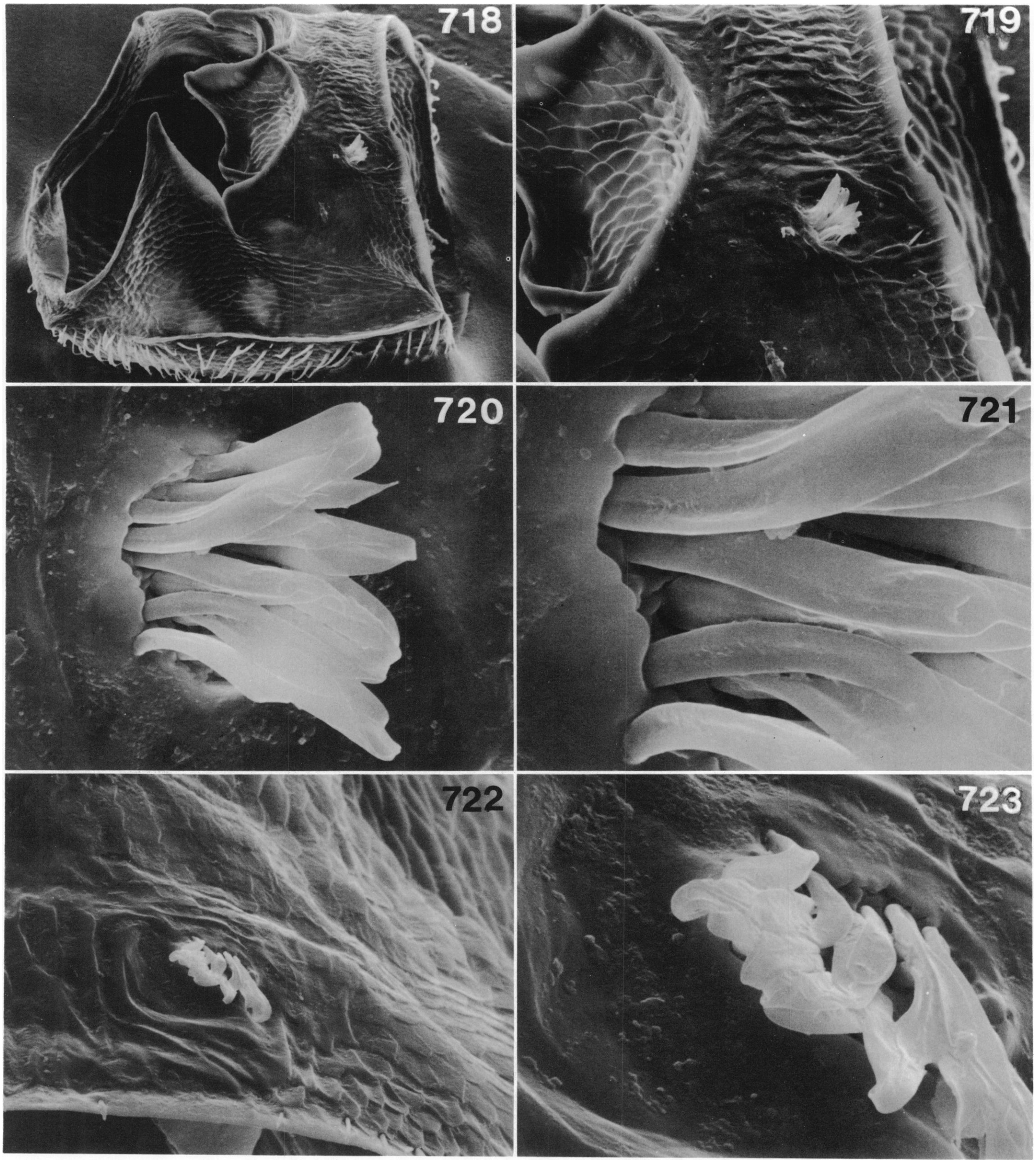
FIGS. 707–712. The *tibialis* group. *Bledius tibialis*. **707.** Prothorax, ventral, 256×. **708.** Prosternum, left lateral view, 860×. **709.** Prosternum, left anterior view, 900×. **710.** Secretory pores and associated setae of prosternum, 4500×. **711.** Prosternum, right anterior view, 1800×. **712.** Secretory pores and associated setae of prosternum, 4400×.

(BMNH); Arba Minch (BMNH); Shewa, Gibbe River (BMNH); Harerge Prov., 30.5 km NE Dire Dawa (BMNH). **Gabon:** Belinga (HCC); Makokou (HCC); Lambarene (IRSN). **Gambia:** (Keneba? BMNH). **Ghana:** Tafo (AMNH). **Guinea:** Kindia (Mt. Gangan ? MNHV); Kindia (Segueia? MNHV). **India:** Uttar Pradesh, Sitapur (FMNH); Jodhpur (BMNH); Uttar Pradesh, Haldwani District, Sudlimah



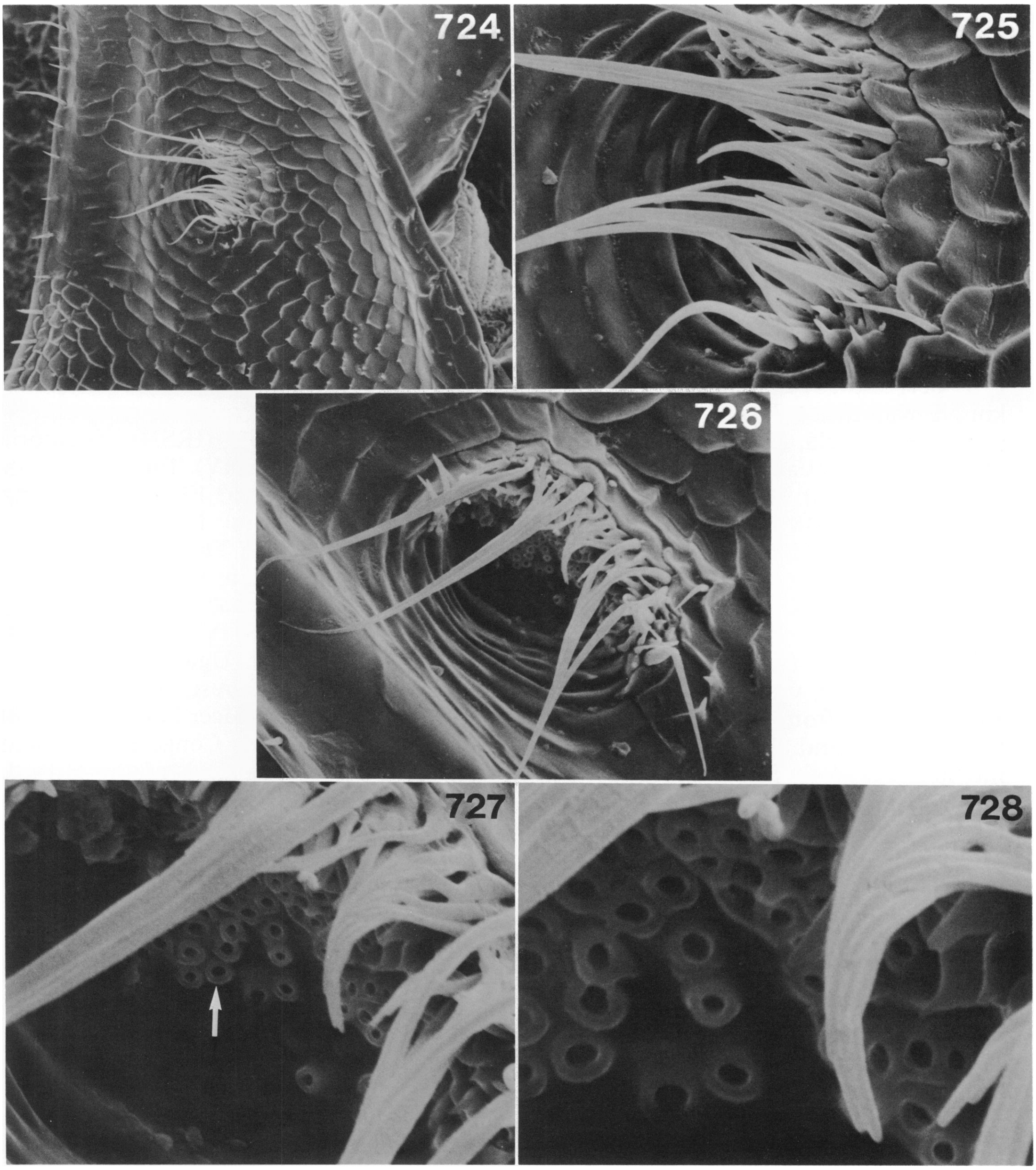
FIGS. 713–717. The *pulchellus* group. *Bledius pulchellus*. **713.** Prothorax, ventral, 150×. **714.** Prosternum, left lateral view, 480×. **715.** Setae of prosternum associated with secretory pores, 1920×. **716.** Setae of prosternum and secretory pores, anterior view, 760×. **717.** Secretory pores and associated setae of prosternum, arrow points to collar around pore, 3040×.

(BMNH); Assam, Chabua (USNM); New Delhi (USNM); Mysore, Bangalore, Karnataka (AMNH); West Bengal, Birbhum District, Santiniketan (BPBM). **Iran:** Mazandaran, 11 km S Chalus (USNM); Fars, 13 km SE Sharaz (USNM); Azerbaijan Province, Astara (USNM). **Irian Jaya:** Hollandia [=Jayapura] (USNM); Waris, S of Hollandia (BPBM); Mouth of Tor River, 4 km E Hol Maffen (BPBM). **Ivory Coast:**



FIGS. 718–723. The *bonariensis* group. *Bledius bonariensis*. **718.** Prothorax, ventral, 124×. **719.** Prosternum, left lateral view, 288×. **720.** Setae of prosternum associated with secretory pores, 1660×. **721.** Base of cluster of setae associated with secretory pores, 3760×. **722.** Prosternum, right anterior view, 580×. **723.** Setae of prosternum associated with secretory pores, anterior view, 2320×.

17 km NW Abidjan; 25 km N Bouake. **Japan:** Beppu (No-Kiushiu? FMNH); Okinawa, Chizuka (USNM); Chiba Prefecture (Cape Futtsu ?). **Laos:** Vientiane (BPBM); Vientiane Prov. (Tha Ngone ? BPBM). **Liberia:** (Suakoko? USNM). **Madagascar:** Tulear Province, 16 km W Tsihombe (USNM); Majunga Province, 25 km SW Ambalanjanakomby (USNM). **Malaysia:** Pahang, 19 mi. N Kuantan (BMNH); Sabah (Karamuak River, 7 mi. SSE Telupid ?) (BMNH); Sabah (Tanjung Aru Beach)



FIGS. 724–728. The *verres* group. *Bledius* sp. **724.** Prosternum, right lateral view, 300×. **725.** Setae of prosternum associated with secretory pores, lateral view, 1200×. **726.** Setae of prosternum and secretory pores, anterior view, 980×. **727.** Secretory pores and associated setae, arrow points to collar around pore, 2920×. **728.** Secretory pores of prosternum, 6200×.

(USNM); Sabah, Kuala Penyu (USNM); Sarawak, Mulu National Park (BMNH); Perak (IRSN); Sarawak, Kuching, Santubong (BPBM); (Pahang Kuala Tahan ? BPBM). **Mali:** Bamako (MNHV); Khayes (IRSN). **Mauritania:** Trarza (HCC). **Mozambique:** Lourenzo [=Maputo] (IRSN); Beira (BMNH). **Namibia:** Ameib Farm, 19 mi. NW Karibib (BMNH); Windhoek (BMNH); Otjikoko sub fm; 33 mi. NE

Omaruru (BMNH); Otjitambi fm; 27 mi. ESE Kamanjab (BMNH); Onguma fm; 55 mi. NW Tsumeb (BMNH); Orange River, near Onseepkans (BMNH); Fish River Canyon (BMNH); Homeb, 10 mi. ESE Gobabeb (BMNH); Barby fm; 25 mi. W Helmeringhausen (BMNH); Okahandja River, 1 mi. S Okahandja (BMNH); Noachabeb, 27 mi. NNE Grunau (BMNH); Kahn River, 5 mi. N Usakos (BMNH); Kuiseb Canyon (BMNH); Swakops River, 3 mi. S Okahandja (BMNH). **Nepal:** (Royal Chitwan National Park ? USNM); Bagmat Province, 3 km N Bahunepati, 900 m [16 km NE Kathmandu] (CNC). **New Britain:** Gazelle Peninsula, Keravat (BPBM). **New Hebrides:** Efate Island, Maat (BPBM). **Niger:** Warri (IRSN); Niamey (BMNH); (Air Mts., Italemen? BMNH). **Nigeria:** Central State, Katsina (USNM); Western State, Ife (USNM); Maiduguri (CNC); Enugu (CNC); Ibadan (BMNH); Kano (BMNH, MNHV). **Pakistan:** Lahore (USNM); Malir City (AMNH); Saidu (AMNH). **Papua New Guinea:** Morobe, Guakor, Wampit River Valley, 45 mi. from Lae (AMNH); D'Entrecasteaux Island, Fergusson Island, Iamelele, 1.5 mi. from Seymour Bay (AMNH); Eastern Highlands, Kassam, Kratke Mts., Lae-Goroka Rd. (AMNH); Morobe, Umi River, Markham Valley, 95 mi. from Lae (AMNH); Morobe, Oomsis 22 mi. W Lae (AMNH); Peria Creek, Kwagira River (AMNH); 64 km N Lae, Bulem River (BPBM); Wau, Morobe District (BPBM); Mt. Lamington (BPBM). **Philippines:** Luzon, Bambang (MNHV); Leyete, Abuyog, 35 mi. S Tacloban (AMNH); Mindanao, Zamboanga del Sur, Zamboanga (BPBM); Mindanao, Cotabato, General Santo (BPBM); Luzon, Camarines Sur Prov. (Esperanza, Bayugan, Matibog creek ? BPBM); Leyete (Makaplag? BPBM). **Romania:** Mamaia (MNHV). **Senegal:** Thies (IRSN); Nioro (FMNH); Richard Toll (USNM). **Solomon Islands:** Guadalcanal (Kukun? BMNH); Honiara (BMNH); Santa Isabel (Kolotuve? BPBM); Guadalcanal, nr. Tetere, Roroni (BPBM); Guadalcanal, 9.6 km SE Honiara, Lunga River (BPBM). **South Africa:** Transvaal, Naboomspruit (MNHV); Cape Province, Fish Hoek (MNHV); Magalakwena River (BMNH); Transvaal (Nylsvley Nat. Res. ? BMNH); Cape Prov., Assegaaibosch (BMNH); Transvaal, 5 km W Kaapmuiden (USNM); Transvaal, 5 km W Warmbad (USNM); Transvaal, Lyttelton, Pretoria; Cape Province, Humansdorp District, Van Staadens Pass (BMNH); Skukuza, Kruger National Park (BMNH). **Spain:** Menorca, Mahon (MNHV). **Sri Lanka:** Kurunegala (USNM); (Ruhunu National Park, near Altents ? AMNH); Wilpattu National Park, 30 mi. N Puttalam; Eastern Province, Punani Anicuit, Maduru Oya (AMNH); Arugam Bay (AMNH). **Sudan:** Rahad River and Blue Nile (IRSN); Prov. of Sennar (IRSN); Roseires, Blue Nile (IRSN); Equatoria, Tambura Wau (MNHV). **Taiwan:** An-p'ing (FMNH); (Suisharyo? FMNH); (Alikang? FMNH). **Tanzania:** Kilindi (BMNH); Morogoro (FMNH). **Thailand:** Khonkaen; Muang Sakon, Nakan; Muang Loei; (Trang Prov., Khaophappha? BPBM). **Turkey:** Gulf of Makri (MNHV); Silifke (BMNH); Antalya (BMNH). **Uganda:** Ruwenzori Range (Semliki Forest, Hot Springs ? BMNH). **Vietnam:** Tiger Lake, Cam Rahn Bay (USNM). **Zaire:** Congo River, Lukolela (AMNH). **Zambia:** Mufulwe Hills, L. V. Locus (BMNH); Mwinilunga District, Ikelenge, near Kalene, Zambeze Rapids (BMNH); Katambora, 40 mi. W Victoria Falls (BMNH); Namwala (BMNH). **Zimbabwe:** Wankie National Park, Pan (BMNH); (Nuanets River, Malipati? BMNH); Matopo Hills, Maleme Dam (BMNH); (Nuanets River, Majinji Pan ? BMNH).

Incertae Sedis

No specimens of the following species were examined, nor were the characters published with the original description sufficient to place the species clearly in my classification.

afrus Herman (= *africanus* Cameron, 1948) The type is supposed to be in the Muséum National d'Histoire Naturelle, Paris, but Curator Mlle. Nicole Berti was unable to find the specimens.

Cameron, in his description, put the species in the subgenus *Blediodes* which is now divided among several of my species groups. This African species may be in either the *semiferrugineus* or *verres* species groups. Cameron compared the species to *nanus.*

bubalus Gistel

Gistel's collection is said to be in Munich at the Zoologische Staatssammlung but the curator, Dr. Gerhard Scherer, informed me that he has been able to find nearly nothing of the collection. Searching at my request, he was unable to find specimens of *Bledius bubalus, B. chimerinus,* or *B. westerhauseri,* all described by Gistel in 1957 and all uncited since then.

Bledius bubalus is said to have cephalic horns but no mention is made of a pronotal horn so it may be part of the *kochi* group.

chimerinus Gistel

See above under *bubalus.* The Gistel collection was not found in the Zoologische Staatssammlung in Munich nor was *B. chimerinus* found. The characters cited in the original description are insufficient to place the species in my classification.

fasciatus (Say)

The type of this North American species is probably lost. The species was discussed by Herman (1983a), who was unable to deduce its identity.

longipennis Mäklin

The type of this North American species is supposed to be in the Zoological Museum of the University of Helsinki. Although Dr. H. Silfverberg searched several times for this specimen, it was not found.

Some North American workers have identified specimens as *longipennis* that I classify as belonging in the *albonotatus* group. Two species have been confused under what was called *longipennis* by these specialists; the characters given in the original description do not permit unequivocal selection of one of these two species as *longipennis.* See Herman (1983a) for further discussion of this problem.

santschii Bondroit

The type of this species is supposed to be in the Institut Royal des Sciences Naturelles de Belgique, Brussels, but Dr. Leon Baert informed me that it has disappeared from the collections. Bondroit made no comparison of the Tunisian *santschii* with other species nor did he put it into a subgenus. The characters are not sufficient to place it clearly but it may be part of the *semiferrugineus* or *verres* groups.

verticalis Notman

The type of this species is supposed to be in the Staten Island Museum of Art and Science, New York City, but was not found despite repeated searching. Herman (1983a, p. 97) discussed the identity of the species.

westerhauseri Gistel

See discussion above under *bubalus.* Neither the Gistel collection nor the type of *westerhauseri* were found at the Zoologische Staatssammlung, Munich. The characters in the description do not allow me to place the species to species group.

CONSPECTUS OF CLASSIFICATION

Following is a summary of the species included in each species group. Species enclosed by brackets are those which are placed in a species group based on characters taken from the original description. Reasons for such placements are discussed for each species in the section "Species Included and Material Examined" that follows the description of each species group. All other assignments to species groups are based on examination of type material or subsequently identified specimens.

mandibularis group
ferratus LeConte
fortis LeConte
jacobinus LeConte
mandibularis Erichson
pallipennis (Say)

bellicosus group
bellicosus Fauvel
quadricornis Bernhauer
semicircularis Lea

compressicollis group
compressicollis Bernhauer

hamifer group
hamifer Fauvel

minax group
minax Blackburn

aequatorialis group
aequatorialis Mutchler
beattyi Blackwelder
ceratus Blackwelder
susae Herman

circularis group
circularis Fauvel

minniensis group
minniensis Herman

rugosicollis group
bituberculatus Cameron
brunnipennis (Fabricius)
rugosicollis Bernhauer

gigantulus group
chinensis Bernhauer
corniger Rosenhauer
ensifer Fauvel
gemellus Eppelsheim
gigantulus Bernhauer
graellsi Fauvel
gyotokui Nakane
hoplites Fauvel
limicola Tottenham
marinus Bernhauer
[*paradoxus* Gridelli]
philippinus Bernhauer
ponticus Znojko
salsus Miyatake
sarmaticus Znojko
sauteri Bernhauer
[*setonis* Miyatake]
simulator Eppelsheim
spectabilis Kraatz
tricornis (Herbst)
unicornis (Germar)
yezoensis Nakane

immaturus group
immaturus Eppelsheim

furcatus group
andresi Bernhauer
atramentarius Rottenberg
bison Cameron
capra Fauvel
coiffaiti Irmler
dinoceros Znojko
eckerleini Scheerpeltz
formosae Bernhauer
furcatus (Olivier)
maritimus Bernhauer

lamelliceps group
hasticeps Bernhauer
lamelliceps Bernhauer
pilicollis Bernhauer
rudebecki Scheerpeltz

kochi group
amplithorax Coiffait
auriculicollis Bernhauer
bicornis (Germar)
biskrensis Fagel
carinicollis Fauvel
convexicollis Bernhauer
diota Schiodte
femineus Coiffait
formosanus Bernhauer
hauseri Eppelsheim
hinnulus Erichson
immarginatus Koch
karachiensis (Abdullah and Qadri)
kochi Cameron
lacustris Bernhauer
loeffleri Coiffait
[*naja* Koch]
naxius Bernhauer
ouzbekiscus Coiffait
persicus Bernhauer
postmaculatus Fagel
puglialis Coiffait
richteri Scheerpeltz
sanguinicollis Bernhauer
sareptanus Fagel
simplicifrons Coiffait
taruensis Cameron
tuniseus Fagel
turcmenus Fagel
vitulus Erichson
[*xiphias* Koch]

emarginatus group
acuticollis Bernhauer
addendus Sharp
aterrimus Fauvel
bolsonensis Scheerpeltz
brincki Scheerpeltz
bruchi Bernhauer
chilensis Coiffait and Saiz
claviventris Fairmaire and Germain
cognatus LeConte
convexifrons Fauvel
cubensis Blackwelder
curtipennis Bernhauer
emarginatus (Say)
externus Lynch
gebieni Bernhauer
gomezi Bernhauer
gregarius Sharp
ignotus Saiz
infantilis Sharp
jamaicensis Blackwelder
koenigsbaueri Scheerpeltz
leai Scheerpeltz
lividipes Fairmaire and Germain
militaris Oke
minutus Bernhauer
modestus Oke
muticus Sharp
norquinocoensis Scheerpeltz
ovensensis Blackburn
pallidipennis Bernhauer
parcissimus Bernhauer
parvulus Erichson
pumilio Erichson

emarginatus group (cont.)
- *rarus* Sharp
- *rufipes* Germain
- *semiopacus* Bernhauer
- *similis* Sharp
- *simplex* Sharp
- *testaceipennis* Lynch
- *trinidadensis* Blackwelder
- *victoriae* Bernhauer and Schubert
- *withycombei* Bernhauer
- *wudus* Herman

lucidus group
- *australis* Oke
- *cowleyi* Blackburn
- *lucidus* Sharp

kosempoensis group
- *conicicollis* Fauvel
- *hindustanus* Cameron
- *kosempoensis* Bernhauer
- *lucens* Cameron

semiferrugineus group
- *aculeatus* Fauvel
- *afghanicus* Scheerpeltz
- *akinini* Eppelsheim
- *analis* LeConte
- *argentinus* Bernhauer
- *assimilis* Casey
- *atratus* Fauvel
- *atricapillus* (Germar)
- *bedeli* Fauvel
- *berlandi* Cameron
- *bredoi* Bernhauer
- *casteneipennis* Mannerheim
- [*castaneus* Mulsant and Rey]
- *coulteri* Hatch
- *crassicollis* Boisduval and Lacordaire
- *cribratus* Sharp
- *cribricollis* Heer
- *dehnerti* Korge
- *diffinis* Baudi
- *dissimilis* Erichson
- *elongatus* Mannerheim
- *erythraeanus* Bernhauer
- *femoralis* (Gyllenhal)
- *filipponii* Coiffait
- *foraminosus* Casey
- *fragilis* Sharp
- *fumatus* LeConte
- *gallicus* (Gravenhorst)
- *ganglbaueri* Bernhauer
- *glasunovi* Luze
- *gravidus* Casey
- *haarlovi* Scheerpeltz
- *heterocerus* Eppelsheim
- *hlisnikowskii* Roubal
- *inornatus* Sharp
- *johnstoni* Cameron
- *lateralis* Erichson
- *minarzianus* Bernhauer
- *nanus* Erichson
- *nitidicollis* LeConte
- *obtusus* Sharp
- *occidentalis* Bondroit
- [*orion* Normand]
- *philadelphicus* Fall
- [*picipennis* Hochhuth]
- *procerulus* Erichson
- *rotundicollis* LeConte
- *roubali* Horion
- *rubiginosus* Erichson
- *sanguinithorax* Bernhauer
- *schoutedeni* Cameron
- *semiferrugineus* LeConte
- *tallaci* Fall
- *transcaspicus* Bernhauer
- *validepunctatus* Scheerpeltz
- *yemenicus* Coiffait

armatus group
- *aquilonarius* Herman
- *bellicus* Blackwelder
- *consimilis* Fall
- *derasus* Sharp
- *episcopalis* Fall
- *eximius* Casey
- *fenyesi* Bernhauer and Schubert
- *flavipennis* LeConte
- *ineptus* Casey
- *monstratus* Casey
- *nitidiceps* LeConte
- *notialus* Herman
- *opacifrons* LeConte
- *politus* Erichson
- *strenuus* Casey

albonotatus group
- *albonotatus* Mäklin
- *diagonalis* LeConte
- *limbatus* Hochhuth
- *nardus* Herman
- *omega* Herman
- *parvicollis* Casey
- *rectangulus* Eppelsheim
- *sellatus* Sharp
- *subterraneus* Erichson
- *talpa* (Gyllenhal)
- *tarandus* Herman
- *tau* LeConte
- *tenenbaumi* Bernhauer
- *venus* Herman
- *zophus* Herman

annularis group
- *agricultor* Heer
- *annae* LeConte
- *annularis* LeConte
- *apfelbecki* Koch
- *arcticus* Sahlberg
- *aurantius* Herman
- *baudii* Fauvel
- *bernhaueri* Poppius
- *bicolor* Casey
- *bosnicus* Bernhauer
- *breretoni* Hatch
- *cedarensis* Hatch
- *chinkiangensis* Bernhauer
- *clarus* Fall
- *clavatus* Eppelsheim
- [*condensus* Kangas]
- *confusus* LeConte
- *cordicollis* Motschulsky
- *defensus* Fauvel
- *denticollis* Fauvel
- *erraticus* Erichson
- *fennicus* Kangas
- *filipes* Sharp
- *fontinalis* Bernhauer
- *fuscipes* Rey
- *gentilis* Casey
- *gracilis* Casey
- *habrus* Herman
- *honestus* Casey
- *ignobilis* Eppelsheim
- *jadarensis* Helliesen
- *japonicus* Bernhauer
- *jucundus* Herman
- *kutsae* Kangas
- *laticollis* LeConte
- *lativentris* Jansson
- *littoralis* Heer
- *longulus* Erichson
- *melanocolus* Herman
- *monticola* Casey
- *mysticus* Fall
- *naius* Herman
- *nebulosus* Casey
- *newelli* Hatch
- *obihiroensis* Nakane
- *obscurus* Motschulsky
- *obsoletus* Fauvel
- *opacicollis* Eppelsheim
- *opacus* (Block)
- *osiris* Normand
- *pallipes* (Gravenhorst)
- *parisii* Koch
- *pechlaneri* L. Benick
- *persimilis* Fall
- *phytosinus* LeConte
- *poppiusi* Bernhauer
- *pusillus* Erichson
- *pygmaeus* Erichson
- *rossicus* Bernhauer and Schubert
- *ruficornis* LeConte

annularis group (cont.)
rugosulus Eppelsheim
secessus Bondroit
sinuatus LeConte
stabilis Casey
strictus Fauvel
suturalis LeConte
terebrans (Schiødte)
turgidus Casey
vilis Mäklin
villosus Casey
viriosus Herman
vitaensis Bernhauer
washingtonensis Hatch

debilis group
debilis Erichson
transversemaculatus Koch

basalis group
basalis LeConte
cordatus (Say)
dimidiatus LeConte
doderoi Bondroit
fergussoni Joy
gradensis Bernhauer
[*gyllenhalii* Laporte]
melanocephalus (Say)
minor Mulsant and Rey
neglectus Casey
opaculus LeConte
subniger Schneider
thinopus Herman
turbulentus Casey

infans group
helferi Fauvel
infans Rottenberg
renominatus Cameron

fratellus group
fratellus Eppelsheim

forcipatus group
actitus (Herman)
albidus Sharp
albipennis Bernhauer
bifasciatus Sharp
forcipatus LeConte
litoreus (Herman)
miles Bernhauer
minutissimus Bernhauer
playanus (Herman)
weiseri Bernhauer

punctatissimus group
albomarginatus Bernhauer
amplicollis Fauvel
bidentifrons Broun
buehleri Scheerpeltz
buettikeri Coiffait
capensis Cameron
caribbeanus Blackwelder
caroli Blackburn
dartevillei Bernhauer
exiguus Scheerpeltz
fernandezi Bernhauer
fossiventris Fauvel
injucundus Blackburn
maculipennis (Solier)
maindroni Fauvel
michaelseni Bernhauer
microcephalus Fauvel
orientalis Bernhauer and Schubert
pontilis Blackburn
pruinosulus Bernhauer
puelches Fauvel
punctatissimus LeConte
salinus Cameron
scheerpeltzi Koch
tenebricosus Scheerpeltz
tristis Aube

lugubris group
lugubris Fauvel

angustus group
angustus Mulsant and Rey
lindbergianus Scheerpeltz
magniceps Reitter

bispinus group
bispinus Kraatz
championi Bernhauer
fuscicornis Cameron

tibialis group
auripennis Cameron
indicus Cameron
morio Heer
tibialis Heer

bonariensis group
bonariensis Bernhauer

pulchellus group
pulchellus Kraatz

verres group
aethiops Bernhauer
africanus Cameron
albomaculatus Bernhauer
albopubescens Cameron
alfierii Koch
arabicus Coiffait
arenicola Fauvel
austrinus Herman
beesoni Cameron
bipustulatus Bernhauer
birmanus Cameron
capicola Cameron
cariniceps Bernhauer
cavus Eppelsheim
congoensis Cameron
curticornis Fauvel
curvicornis Sharp
decorsei Cameron
dilutipennis Motschulsky
distans Fauvel
ealanus Cameron
fossor Heer
frater Kraatz
fraterculus Cameron
gabonensis Fauvel
gracilicornis Kraatz
husseini Quedenfeldt
incertus Cameron
insignicornis Blackburn
jacobsoni Cameron
klapperichi Coiffait
lateripennis Bernhauer
latior Bernhauer
latus Bernhauer
lepineyi Scheerpeltz
louwerensi Cameron
lucidulus Cameron
madagascariensis Bernhauer
marginalis Cameron
mauritanicus Coiffait
negrei Coiffait
niger Cameron
niloticus Erichson
nodieri Cameron
opacinus Scheerpeltz
orphanus Sharp
palliatus Fauvel
papuanus Cameron
parens Cameron
peraffinis Cameron
perplexus Cameron
perrieri Fauvel
petzi Bernhauer
porcellus Bernhauer
rhinocerus Cameron
roettgeni Bernhauer
somalianus Cameron
splendens Bernhauer
subopacus Bernhauer
tenuiverres Scheerpeltz
transversus Cameron
tuberculatus (Fabricius)
ugandae Bernhauer
verres Erichson
wombaliensis Bernhauer

Incertae Sedis
afrus Herman
bubalus Gistel
chimerinus Gistel
fasciatus (Say)
longipennis Mäklin
santschii Bondroit
verticalis Notman
westerhauseri Gistel

QUESTIONS

The preceding pages bring together what is known about the natural history of *Bledius* and provide a new infrageneric classification, some hypotheses concerning phylogenetic relationships, and an entrée to the literature. If this monograph is intended as a starting point, where then might we go from here?

Bledius is a large, predominantly Old World genus. Two-thirds of the species groups and species are confined to that region. Only five species groups are restricted to the New World. Six species groups occur in both hemispheres.

Despite there being a literature of hundreds of papers, most species are poorly known. The majority were described once, never illustrated or included in a key, and were not compared with their nearest relatives. Although 167 names are listed as synonyms or homonyms, most of them are for North American or European species. Certainly many other synonyms remain undetected. Some species presently regarded as synonyms, particularly among those synonymized in the 19th century, are probably valid species.

The best known *Bledius* faunas are those of North America, Europe, and probably North Africa. The North American species were recently revised and keys, maps, descriptions, and illustrations provided. For Europe and North Africa no such revision exists. Neither fauna has been tackled in its entirety. Most of the species of these two regions have not been illustrated and the keys are regional, usually by country. No one has brought together all the available specimens for study and comparison. The full geographical ranges of most species are unknown. The *Bledius* of India are moderately well known; a key to most of the species was published but illustrations are needed and probably many species will be added. Numerous species are described from Africa and Asia; most are poorly known, yet many others remain undescribed. Knowledge of the *Bledius* of southeastern Asia, Indonesia, Philippines, New Guinea, Australia, and New Zealand is dismal. Not only is taxonomic study needed but also new collections from previously unsampled areas need to be made.

A profitable route to resolving the taxonomic problems in *Bledius* will be to revise *species groups.* Most of the 34 species groups are small. Twenty-two groups have fewer than 5 species, seven have 10 to 26, and five have 30 to 73 species. The 29 smaller groups are easily handled; the most difficult problem is acquiring sufficient material to understand the variation. The five larger groups present more problems. Most of the problems in the *kochi* and *semiferrugineus* groups (with 31 and 56 species) can, with adequate material, be resolved. In the *semiferrugineus* group there are several complexes, such as the *gallicus, assimilis, ganglbaueri, rubiginosus,* etc., that should be carefully examined to sort geographical and populational variation from interspecific variation. The *emarginatus, verres,* and *annularis* groups are not only large (43, 65, and 73 species respectively) but have some knotty problems. Almost no species in the *emarginatus* or *verres* groups have been compared with the most nearly related species nor have they been included in keys; only about half of those in the *annularis* group are included in keys. In the *emarginatus* group there are some difficult problems of species limits centered around the *emarginatus* complex and similar problems exist elsewhere in the group. One of the most difficult problems is in the *annularis* group: in North America the *annularis* complex, with 10 species, remains unresolved. The same complex exists in Europe and Asia: here the problems center around such species as *pallipes, fuscipes,* and *opacus* to name a few. These species and several others are part of the *annularis* complex (defined by Herman, 1983a, p. 93). This complex defies solution in North America and remains unaddressed in Eurasia.

The distribution of each species group is described. Are there broader patterns? What is the distributional history of the groups? *Bledius* is found on all continents (except Antarctica), most continental islands, and a few oceanic islands. Are they absent from most oceanic islands? If so, why?

Throughout this monograph questions are asked and hypotheses proposed—any and all of them require further testing. As species in each of the species groups are studied more thoroughly, the monophyly of species groups and the interrelationships among the groups should be tested. The hypopharynx will continue to provide characters important to phylogenetic analysis as material becomes available for examination and dissection. Are there new characters? Can some of those used be reinterpreted?

The genus may be ancient. Did it arise during or before the Cretaceous? Is *Staphylinus lesleyi* a *Bledius*? Are there any fossilized burrows or trace fossils (named as Ichnogenera) that belong to *Bledius*? If so, where and when? Is the primitive habitat in saline soil? Is that why species of so many different species groups are salt tolerant?

Some details of the life history of *Bledius* are discussed herein but many questions remain—simple questions, like the number of generations per year or the length of each larval instar. Is there geographical (or climatic) variation in the number of generations or length of larval instars? Are there five larval instars? Larvae for only 19 species are described. As others are studied, will a classification of larvae be concordant with that based on adults? What about a cladogram using larval characters? *Bledius* eats algae and diatoms. Is there host specificity? Some descriptive and observational data are available concerning habitat and ecological limits. What is the role of algae in limiting *Bledius* beyond simple presence or absence of the plants? Does the availability of particular species of algae impose ecological and distributional limits on particular species of *Bledius*? What factors other than soil texture and moisture, shade, and salinity circumscribe where *Bledius* lives and how do species divide up a locality? At a given locality there can be two to a dozen species of *Bledius* and four to six are common. Two species, *fenyesi* and *monstratus*, occupy a peculiar habitat on western coastal North America. They live in decaying sand-covered kelp that has been thrown ashore. Do they eat this kelp? What is the sister group of these species and what is their (or its) habitat? Are there other *Bledius* in a similar habitat? *Bledius monstratus* has flightless populations; *B. fenyesi* does not. Why? Is there differential deposition of kelp? Are the wind patterns different? A few other species are known to have flightless populations. Why? What is the advantage of the loss of flight in *Bledius*? A few beetles, wasps, birds, and fish are known to eat *Bledius*. Are there others such as reptiles? One of the major predators of *Bledius* is regarded to be the scaritine ground beetles of *Dyschirius*. Is the *Bledius*-*Dyschirius* association based on predator-prey affinity or are *Dyschirius* opportunistic predators that share ecological requirements with *Bledius*? All *Bledius* secrete a strong, sweet smelling chemical from pygidial glands. Is the function of the chemical defensive as has been suggested (though the evidence so far is negative)? The chemical has five components. Might each serve the species differently? *Bledius* has minimum humidity requirements but might this secretion help to aggregate it in suitable habitats? Is the chemical a fungicide against perhaps Laboulbeniales infection? Is *Dyschirius* attracted to the odor?

In contrast to many staphylinids, *Bledius* is fairly colorful. If they are in burrows during most of the day, and active on the surface in the evening and night, why the color? Why is the head of all species black or darker than the remainder of the body? Is there a geographical correlation for color? Most species of the lineage with *furcatus* through *mandibularis,* those of *forcipatus, bonariensis, lucidus,* and some of those in the *verres* group have cephalic and/or pronotal horns. What is the function of these horns? Why the variation in shape, number, and position? Some point forward, some upward; why? There are major and minor males. Some species of the *verres* groups have enlarged, tuberclelike supraantennal ridges, why? The function of many structures can be questioned but a few deserve special attention. Why is the hypopharynx so variable? On it and the ends of the palaps are coronal pegs; what is their function? The maxillary palps have digitiform sensillae; are they humidity or gas receptors? Why are the antennae geniculate, the body subcylindrical, the eyes so enlarged, the protibiae expanded, the labrum divided (or fused)? The prosternum has setigerous pits or depressions that contain secretory pores. What is the function of the secretion? Why in some are these pores and setae concentrated in a pit and others in a depression, and in still others the surface nearly flat? Do the depressions and pits help concentrate the secretion and the setae help to bring the chemical to the surface? The wing folding fringe of tergum VII may be composed in part of spines; why? How are the subantennal pockets in *Bledius bonariensis* used?

While not all questions are answered with equal ease, the number and diversity are limited only by one's time and imagination. Despite the size of the genus and the difficulty of identifying some species, *Bledius* is an excellent group for investigation. Species are found nearly everywhere. Usually several species can be found at any one locality. They are easy to collect and some species occur in large populations.

CATALOGUE OF *BLEDIUS* OF THE WORLD

INTRODUCTION

The literature for *Bledius* began over two centuries ago in 1784 with Herbst's description of *Staphylinus tricornis* which was later moved to *Bledius*. Over 200 other writers have contributed hundreds of articles about *Bledius*. Six hundred forty-five species names are cited in the genus between 1784 and 1984, of which 438 are valid extant species, 167 are synonyms (or subspecies) or homonyms, 7 are fossil species, 23 are nomina nuda, and 10 have been removed from *Bledius*. Beyond the original descriptions there have been redescriptions, illustrations, keys, geographical range extensions, larval and pupal descriptions, discussion of natural history, checklists, catalogues, revisions, etc. Most of the subsequent and some of the original literature have never been cited in a catalogue.

Most catalogues that include *Bledius* are lists of species with references only to their original descriptions. Many such lists have been published and most are regional. Some examples are: Stephens (1829), Gaubil (1849), Waterhouse (1858), Jacquelin du Val (1859), Geminger and Harold (1868), Fauvel (1875), Heyden, Reitter, and Weise (1891; 1906), Leng (1920), Winkler (1925), Blackwelder (1944), Kloet and Hincks (1945), Strand (1946), Tottenham (1949), Shibata (1973; 1976), and Pope (1977). Erichson (1840) revised or listed nearly all of the known species. Bernhauer and Schubert (1911) published a catalogue that includes most of the species, their original descriptions, synonyms, many subsequent references, and a summary of the distribution of each species. Scheerpeltz (1933) supplemented this catalogue. Since 1933 over 185 names have been added and many important studies have appeared.

The present catalogue includes all of the names that have been used in *Bledius*, their first description or citation, and important subsequent publications. The purpose of the catalogue is to stimulate new studies of the genus. To facilitate revision and updating, the catalogue is stored electronically.

MATERIAL INCLUDED: The catalogue contains the following: generic and specific group names, reference to the original and subsequent publications, brief annotation of subsequent publications, notation of the genus in which the species were originally described, the original and subsequent subgeneric assignments, and the type locality. All names that have been used in *Bledius* are listed, including nomina nuda, subspecies, homonyms, and synonyms (and aberrations or varieties). The catalogue is cross indexed for species names.

The catalogue reflects the published literature and, except where indicated, no unpublished nomenclature changes are made. Some names are followed by **New Combination**, **New Status**, **New Synonym**, or **New Name**. These designate changes made herein and they are explained in the present work. **New synonyms** include *Microbledius, Psamathobledius, Neobledius, bos, devillei,* and *germanicus.* **New combinations** include *actitus, litoreus, playanus,* and *karachiensis.* **New Names** include *albanicus* and *jutlandensis.* Four names have been **resurrected** from synonymy, namely, *atramentarius, castaneipennis, limicola,* and *minor.* Six names, *bubalus* Gistel, *castaneus* Mulsant and Rey, *chimerinus* Gistel, *gyllenhalii* Laporte, *germanicus* Gravenhorst, and *westerhauseri* Gistel, are cited herein for the first time since they were described.

FORMAT: All species names are listed alphabetically. Valid species presently in the genus are in boldface type. Species names that represent cross indexing for homonyms, synonyms, subspecies, and species that have been transferred out of *Bledius* are italicized. Indented chronologically under the valid names are: (1) synonyms (italic type) and (2) subspecies (boldface type).

The first author, date, and page number following a species group name is the original description of citation. Following this, in parentheses, is the genus in which the species was originally cited and, the original subgeneric assignment—if the author made one. Next is the type locality. Following the type locality are the subsequent references for which I cite the author, date, and page only. Most subsequent references are briefly annotated in parentheses.

The last item for each valid species is the group assignment that I make in the present study (in boldface type).

CROSS INDEXING: Although beetle catalogues are not generally cross indexed, this is a useful tool to facilitate finding names that are no longer valid species or that have been transferred to other genera. It may also obviate publication of new homonyms. Misspelled and misidentified names are excluded from the index.

AUTHOR'S NAME: The author's name is fully spelled. Abbreviations are not universally understood. In some cases, after naming only one species, cataloguers have abbreviated an author's name. Abbreviations are variable and therefore open to misinterpretation. Bernhauer's name has been abbreviated as "Bernh", "Bnh", "Brnh", and there may be others. One may know who is represented by "F." or "L." but who are "Parf.", "Kng.", "Kol.", or "Rosh."?

Parentheses enclose an author's name if the species was originally described in a genus other than *Bledius*. The parentheses exclude the date of publication. Article 51d of the code on zoological nomenclature states that parentheses should enclose the author's name when a species is transferred from the genus in which it was originally described but says nothing about including the date.

LITERATURE CITATION: For each reference only the author, date, and page number are included. The complete citation is found in the Literature Cited. I have examined every reference cited. For Fauvel, 1871 and 1873a, and West, 1937, the date of publication cited herein differs from the generally used date. Each is annotated in the Literature Cited.

TYPE SPECIES: For each generic group name I cite the type species along with reference to its first designation. The type species is cited as the name originally used in the designation. For example, *armatus* was the name first validly cited as the type species of *Bledius*. Often the name *tricornis* is cited as the type species of *Bledius* because it is the senior synonym of *armatus*. The synonym is subjective; therefore, at any time someone might decide that *armatus* and *tricornis* are different species. This would necessitate changing the name of the type species if *tricornis* had been cited as the type species. Further, the name *tricornis* was not one of the originally included names.

TYPE LOCALITY: The locality published with the original description is given herein as the "type locality" whether or not a holotype or lectotype was designated. If more than one locality is cited with the original description and no type was designated, then all are listed as "type localities." In most cases I cite the locality in the language and political geography of the original publication but I have been inconsistent in this and some localities are anglicized or some towns or regions are listed in their present countries. For some species no localities were included in the original publications.

SYNONYMS: Junior synonyms are indented and chronological under the senior name. Efforts were made to find the earliest publication that refers a name to synonymy. Except where I explicitly cite my own studies, I have not verified the zoological accuracy of the synonymy. However, in nearly all cases corroboration is needed by the study types. For example, after examination of the type of *B. castaneipennis,* I found it necessary to resurrect it from synonymy with *opacus.*

Some names have been presented as the synonym of more than one species, or the name has been regarded by some as a junior synonym and by others a valid species. For these I have arbitrarily and probably inconsistently chosen a published decision. The annotated subsequent references give a brief history of these changes and should signal the existence of a problem. Two examples are *rastellus* and *subsinuatus.*

HOMONYMS: Two names, *albanicus* and *jutlandensis,* are proposed to replace preoccupied primary homonyms. They are annotated as "new name."

Pope (1977) brought to notice two names that he effectively recommended be regarded as nomina oblita. Olivier used *bicornis* and Nicolai named *atricapillus* in *Oxytelus.* Later Germar described a *bicornis* and *atricapillus* in *Oxytelus.* Germar's names were transferred to *Bledius* and now have a long history of publication. Olivier's and Nicolai's names were not used thereafter in *Oxytelus* or *Bledius.* I follow Pope's lead on these names.

Another problem of homonymy involves *germanicus.* The name was first used by

Gravenhorst (1806) along with *gallicus* as two forms of *pallipes*. Later, after *pallipes* was transferred to *Bledius, gallicus* was elevated and considered a different species. *Bledius gallicus* is now a commonly used name. Gravenhorst's *germanicus* was never cited again but is presumably an objective synonym of *pallipes*. Gravenhorst cited two only localities, France and Germany, for *pallipes*. Presumably Gravenhorst's *pallipes gallicus* is the French form and *pallipes germanicus* the German one. With the elevation of the French form *gallicus* then *germanicus* is logically equivalent to *pallipes*.

Wagner (1935), unaware of an earlier use of the name, proposed *germanicus* for a subspecies of *spectabilis*. Tottenham (1940) described *limicola* as a new species. After *germanicus* and *spectabilis* were recognized to be separate species, *limicola* was placed as a junior synonym of *germanicus*.

Since *germanicus* Wagner is a junior homonym of *pallipes germanicus*, Wagner's name must be replaced. Tottenham's *limicola* is therefore resurrected as the replacement name.

In contrast to *bicornis* Germar and *atricapillus* Germar, the literature for *germanicus* is minute. There is little reason not to replace *germanicus* Wagner.

A number of "pseudo homonyms" were cited as synonyms by Bernhauer and Schubert (1911) and Scheerpeltz (1933). Some examples include *pygmaeus* and *pusillus* cited by Fauvel (1872), *pallipes* used by Boisduval and Lacordaire (1835), and *agricultor* by Kraatz (1858). These are really only misidentifications or misuses of names. They were not intended as new taxa when they were redescribed. For each misidentification the author of the paper cites the original author of the name and in no case does he cite the name as his own new species. To cite these misidentifications as though they were newly described species is inaccurate and misleading. In this catalogue the reference to the misidentified species is listed under the correct species and is appropriately annotated.

EMENDATIONS: Two names required emendation. These are annotated in the catalogue. A few other names have been cited in the past with more than one spelling. Unless good reason was found to emend the name, I use the original spelling. An example is *littoralis* which is often cited with one "t". The Latin root is *litus* but its use in scientific names is often with a double "t" and was so used by Heer.

SUBSEQUENT REFERENCES: I made an effort to find what I regard as important subsequent references, particularly among the more recent publications. Included among these are revisionary and natural history studies, and descriptions, keys, transfer of species, new subgeneric assignments, recognition of synonyms, and distributional data. I may have missed some important references and I certainly have not cited every publication that includes *Bledius*.

Most subsequent references are annotated briefly in parentheses. Often there is more and other information in the reference. The references may be annotated for distributional data, notes (usually taxonomic), descriptions, keys, discussion of characters, synonymy, generic transfers, subgeneric assignments, larval descriptions, and natural history information. The latter may include habitat data or ecological, behavioral, or physiological studies.

DISTRIBUTION: No distributional data are given beyond the type locality.

NOMINA NUDA: At least 23 names have been cited in *Bledius* but have never been described. I list them with their earliest citation in a separate section at the end of the catalogue.

FOSSILS: Nine species of fossils have been included in *Bledius*; two were transferred to *Stenus*. Since names for extant and extinct forms compete as homonyms, the fossil names are included alphabetically in the list. Each fossil species if followed by an asterisk and is annotated.

PROPOSED CLASSIFICATION: The species group name in brackets is the group in which I place the species as a result of the present work. This notation is to facilitate finding a species in my classification.

BLEDIUS

Bledius Leach, 1819, p. 174. Type species: *B. armatus* (Panzer). Fixed by: Leach, 1819, p. 174 by monotypy. — Curtis, 1826, p. 234 (description of genus, two species). — Curtis, 1829, p. 29 (list). — Stephens, 1829, p. 292 (list includes 2 species, 5 names). — Mannerheim, 1831, pp. 458–460 (generic description, 11 species). — Stephens, 1834, pp. 307–311 (generic description, 3 species, 4 names). — Boisduval and Lacordaire, 1835, pp. 455–458 (redescription of 5 species). — Runde, 1835, pp. 17–19 (includes 7 species). — Curtis, 1837, p. 39 (list). — Dejean, 1837, p. 76 (list). — Audouin, 1837 (synonym of *Oxytelus*). — Erichson, 1839, pp. 578–585 (redescribes 5 species, describes 5 species). — Heer, 1839, pp. 209–212 (redescribes 6 species, describes 7 species). — Erichson, 1840, pp. 760–780 (redescribes, lists most of known species, transfers 8 to *Bledius,* describes new species, cites synonyms). — Laporte, 1840, pp. 187–188 (species descriptions). — Heer, 1841, pp. 575–576 (1 new species). — Sturm, 1843, p. 52 (list). — Gaubil, 1849, p. 257 (catalogue—Europe, Algeria). — Redtenbacher, 1849, pp. 732–735, 873 (key, list; Austria). — Fairmaire and Laboulbène, 1856, pp. 599–606 (descriptions). — Lacordaire, 1854, pp. 114–115 (descriptions). — Dohrn, 1855 (list of species). — Kraatz, 1858, pp. 816–838 (species redescribed). — Redtenbacher, 1858, pp. 227–230 (key; Austria). — Waterhouse, 1858, p. 29 (list). — Jacquelin du Val, 1857–1859, pp. 54–55 (generic description). — Jacquelin du Val, 1859, pp. 76–77 (catalogue; Europe). — Thomson, 1861, pp. 118–122. — Fairmaire and Germain, 1861, pp. 445–446. — LeConte, 1863, pp. 51–54 (American species). — Schiødte, 1864, pp. 121–124, tab. XII (larvae, pupae). — Schiødte, 1866, pp. 142–143 (classification, discussion). — Gemminger and von Harold, 1868, pp. 643–646 (catalogue). — Fauvel, 1872, pp. 185–212 (classification, descriptions, synonyms). — Fauvel, 1873c, pp. 33–35 (notes, distribution). — Fauvel, 1873d, pp. 57–59 (notes, distribution). — Fauvel, 1875, pp. xii–xiii (catalogue; Europe, north Africa). — LeConte, 1877 (revision; American species). — Mulsant and Rey, 1878, pp. 551–661 (classification). — Mulsant and Rey, 1879, pp. 109–219 (identical to Mulsant and Rey, 1878, pp. 551–661). — Heyden et al., 1883, p. 59 (catalogue; Europe). — Fauvel, 1886, pp. 24–27 (north African species). — Fowler, 1888, pp. 362–373 (British species). — Casey, 1889 (American species). — Heyden et al., 1891, p. 115 (catalogue; Europe, Russia). — Seidlitz, 1891a, pp. 380–382 (key; Europe). — Seidlitz, 1891b, pp. 356–359 (key; Europe). — Ganglbauer, 1895, pp. 610–625 (key, descriptions; Europe). — Fauvel, 1897, pp. 259–263 (catalogue). — Everts, 1898, pp. 330–335 (key; Europe). — Stierlin, 1900, pp. 392–395 (key; Europe). — Fauvel, 1902, pp. 68–72 (catalogue). — Heyden et al., 1906, pp. 143–144 (catalogue; Europe, Russia). — Deville, 1907, pp. 82–92 (key, descriptions; France). — Handlirsch, 1907, pp. 728–729 (fossils). — Betis, 1908–1926, pp. 234–246 (key, list, collecting data; Europe). — Reitter, 1909, pp. 165–168 (key; Germany). — Gerhardt, 1910, pp. 61–62 (annotated list; Europe). — Bernhauer and Schubert, 1911, pp. 125–137 (world catalogue). — Sharp, 1911c, p. 57 (type species). — Kuhnt, 1912, pp. 203–206 (key; Germany). — Johansen, 1914, pp. 534–549 (key, redescriptions; Denmark). — Eichelbaum, 1914, p. 223 (anatomy). — Leng, 1920, pp. 97, 352 (catalogue; North America). — Everts, 1922, pp. 138–144 (notes, localities, discussions). — Deville, 1924, pp. 23–24 (*Bledius-Dyschirius* relationship). — Winkler, 1925, pp. 345–347 (catalogue, classification; Palearctic). — Krogerus, 1925b (key, natural history, larvae). — Krogerus, 1925a (natural history). — Porta, 1926, pp. 45–48 (key, classification; Italy). — Leng and Mutchler, 1927, p. 20 (catalogue, North America supplement). — Krogerus, 1928 (natural history). — Lengerken, 1929, pp. 33–35, 38, 71–80 (natural history). — Portevin, 1929, pp. 409–414 (key; France). — Cameron, 1930, pp. 270–286 (description, key; India). — Böving and Craighead, 1931, pp. 9, 27, 28 (larva). — Brunier, 1931 (natural history). — Joy, 1932, pp. 140–144, pls. 40, 41 (key; British species). — Scheerpeltz, 1933, pp. 1109–1124 (catalogue, world; supplement). — Leng and Mutchler, 1933, p. 19 (catalogue, North America; supplement). — Koch, 1934, pp. 58–63 (key; Egypt). — Porta, 1934, pp. 116–117 (catalogue, Italy; supplement). — Blackwelder, 1936, pp. 50, 55, 62, 71, 73, 74, 79, 80 (anatomy). — Larsen, 1936 (natural history). — Breddin, 1936 (natural history). — Hansen et al., 1939 (catalogue; north Europe). — Lengerken, 1939, pp. 131–135 (natural history). — Blackwelder, 1939, pp. 22, 100 (catalogue, North America; supplement). — Glick, 1939, pp. 31, 68 (natural history). — Paulian, 1941, pp. 169–174 (larvae). — West, 1942 (catalogue; Denmark). — Paulian, 1942 (natural history). — Paulian, 1943 (natural history). — Blackwelder, 1943, pp. 112–119 (description, key; West Indies). — Blackwelder, 1944, p. 106 (checklist; Central and South America). — Hinton, 1944, pp. 116–117 (natural history). — Kloet and Hincks, 1945, pp. 162–163 (checklist; Britain). — Strand, 1946, pp. 239–241 (catalogue; north Europe). — Kangas, 1948 (genitalia). — Porta, 1949, pp. 139–140 (catalogue; Italy; supplement). — Tottenham, 1949, pp. 363–364, 410–411 (type species; checklist, Britain; classification). — Blackwelder, 1952, pp. 77–78 (type species; synonyms; subgenera). — Larsen, 1952 (natural history). — Larsen, 1953 (natural history). — Tottenham, 1954, pp. 48–55 (key; Britain). — Steel, 1955 (natural history). — Klefbeck and Sjoberg, 1957, p. 60 (checklist; Sweden). — Kocker, 1958, pp. 105–110 (catalogue; Morocco). — Hansen et al., 1960, pp. 118–119 (checklist; north Europe). — Horion, 1963, pp. 251–295 (catalogue, annotated, central Europe). — Moore, 1964 (natural history, larvae). — Lohse, 1964, pp. 89–99 (key; central Europe). — Kasule, 1968, p. 120 (genus in larval key to Oxytelinae). — Scheerpeltz, 1968, pp. 31–34 (catalogue; Austria). — Herman, 1970, pp. 354–355, 375–379 (relationships, description, checklist). — Evans et al., 1971 (natural history). — Smith and Hein, 1971 (natural history). — Herman, 1972 (revision, key; North America). — Tikhomirova, 1973, pp. 146–147 (checklist; USSR). — Coiffait, 1973, p. 122 (subgeneric key). — Shibata, 1973, pp. 33–35 (checklist; Taiwan). — Coiffait and Saiz, 1968, pp. 423–427 (descriptions, key; Chile). — Saiz, 1973 (revision; Chile). — Moore and Legner, 1974 (natural history, larva). — Hollander and Van Etten, 1974 (natural history). — Shibata, 1976, pp. 133–141 (catalogue; Japan). — Herman, 1976 (revision, key; North America). — Pope, 1977, p. 24 (checklist; Britain). — Spahr, 1981, p. 94 (references to *Bledius* from amber and copal). — Frank, 1982, pp. 10–12 (parasites, references). — Newton, 1982, p. 23 (larval characters). — Griffiths and Griffiths, 1983 (natural history). — Herman, 1983a (revision, key; North America). — Herman, 1983b (relationships).

Hesperophilus Curtis, 1829, p. 29. Type species: *Hesperophilus fracticornis* (Paykull). Fixed by: Westwood, 1838, p. 17; subsequent designation. Subgenus. — Stephens, 1829, p. 292 (includes 4 species, 6 names). — Stephens, 1834, pp. 307–311 (includes 5 species). — Curtis, 1837, p. 39 (list). — Waterhouse, 1858, p. 29 (list). — Thomson, 1861. — Schiødte, 1866, p. 151. — Fauvel, 1872, pp. 196–198 (classification). — Fauvel, 1875, p. xiii (catalogue; classification). — Mulsant and Rey, 1878 (classification). — Seidlitz, 1891a, p. 382. — Ganglbauer, 1895, pp. 624–626. — Deville, 1907, p. 90. — Tottenham, 1949, pp. 364, 410 (type species; checklist, Britain). — Blackwelder, 1952, p. 183 (type species).

Tadunus Schiødte, 1866, pp. 144, 147. Type species: *Tadunus fracticornis* (Paykull). Fixed by: Sharp, 1911, p. 57, subsequent designation. Junior synonym of *Hesperophilus.* — Seidlitz, 1891a, p. 382. — Stierlin, 1900, pp. 393–394. — Tottenham, 1949, p. 364 (type species). — Blackwelder, 1952, p. 372 (type species).

Bargus Schiødte, 1866, pp. 145, 148. Type species: *Bargus pallipes* (Gravenhorst). Fixed by: Sharp, 1911, p. 57, subsequent designation. Junior synonym of *Hesperophilus.* — Seidlitz, 1891a, p. 382. — Stierlin, 1900, pp. 394–395. — Tottenham, 1949, p. 364 (type species). — Blackwelder, 1952, p. 72 (type species).

Blediodes Mulsant and Rey, 1878, p. 576. Type species: *Blediodes fracticornis* (Paykull). Fixed by: Tottenham, 1939, p. 228, subsequent designation. Junior synonym of *Hesperophilus.* — Ganglbauer, 1895, pp. 617–623. — Deville, 1907, pp. 90–92. — Reitter, 1909, pp. 166–168. — Benick, 1943, p. 94 (list of species). — Tottenham, 1949, p. 364 (type species). — Blackwelder, 1952, p. 77 (type species).

Dicarenus Gistel, 1834, p. 9. Type species: *Dicarenus arenarius* (Paykull). Fixed by: Blackwelder, 1952, p. 124, subsequent designation. Subgenus. — Blackwelder, 1952, p. 124 (type species).

Cotysops Tottenham, 1939, p. 225. Type species: *Cotysops arenarius* (Paykull). Fixed by: Tottenham, 1939, p. 225, original designation. Junior synonym of *Dicarenus.* — Tottenham, 1949, pp. 364, 411 (type species; checklist, Britain). — Blackwelder, 1952, p. 109 (type species).

Astycops Thomson, 1859, p. 43. Type species: *Astycops talpa* (Gyllenhal). Fixed by: Thomson, 1859, p. 43, original designation and monotypy. Subgenus. — Schiødte, 1866, p. 150. — Fauvel, 1872, pp. 199–212 (classification). — Fauvel, 1875, p. xiii (catalogue; classification). — Mulsant and Rey, 1878 (classification). — Seidlitz, 1891a, p. 382. — Stierlin, 1900, p. 395. — Deville, 1907, p. 90. — Tottenham, 1949, pp. 364, 411 (type species; checklist, Britain). — Blackwelder, 1952, p. 66 (type species). — Szujecki, 1968 (characters, species, key; Europe).

Elbidus Mulsant and Rey, 1878, p. 572, Type species: *Elbidus bicornis* (Germar). Fixed by: Blackwelder, 1943, p. 112 by subsequent designation. Subgenus. — Reitter, 1909, p. 165. — Tottenham, 1949, pp. 364, 411 (type species; checklist, Britain). — Blackwelder, 1952, p. 145 (type species).

Neobledius Abdullah and Qadri, 1968, p. 394. Type species: *N. karachiensis* Abdullah and Qadri. **[New Synonym]**

Pucerus Mulsant and Rey, 1878, p. 654. Type species: *Pucerus verres* (Erichson). Fixed by: Blackwelder, 1943, p. 112, by subsequent designation. Subgenus. — Ganglbauer, 1895, p. 627. — Blackwelder, 1952, p. 332 (type species).

Belidus Mulsant and Rey, 1878, p. 657. *Belidus angustus* (Mulsant and Rey). Fixed by: Mulsant and Rey, 1878, p. 657, monotypy. Subgenus. — Blackwelder, 1952, p. 74 (type species).

Euceratobledius Znojko, 1929, p. 203. Type species: *E. furcatus* (Olivier). Fixed by: Znojko, 1929, p. 204, original designation. Subgenus. — Tottenham, 1949, pp. 364, 410 (type species; checklist, Britain). — Blackwelder, 1952, p. 154 (type species).

Microbledius Herman, 1972, p. 118. Type species: *M. playanus* Herman. **[New Synonym]**

Psamathobledius Herman, 1972, p. 136. Type species: *P. punctatissimus* (LeConte). **[New Synonym]**

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actitus (Herman), 1972, p. 127. **New Combination** (*Microbledius*). Type locality: Texas: 9 mi. N Rockport, Aransas Co., Copano Bay. — Herman, 1983a, p. 134 (distribution). **[forcipatus group]**

actus Herman, 1970, see: *jacobinus* LeConte, 1877.

aculeatus Fauvel, 1900, p. 69 (*Bledius*). Type localities: Congo: Kinchassa. Gabon: Loango. Sierra Leon: Rhobomp. **[semiferrugineus group]**

acuticollis Bernhauer, 1927, p. 233 (*Bledius*). Type locality: Argentina: Prov. Cordoba. **[emarginatus group]**

*adamus** Scudder, 1878, p. 762 (*Bledius*). Type locality: Utah: Green River (Fossil; Eocene). Scudder, 1890, p. 504 (redescription, illustration).

addendus Sharp, 1876, p. 394 (*Bledius*). Type locality: Brazil: Rio Solimoes. **[emarginatus group]**

adelaidae Blackburn, 1888, see: *Carpelimus.*

adustus Casey, 1889, see: *gentilis* Casey, 1889.

aequatorialis Mutchler, 1925, p. 225 (*Bledius*). Type locality: Galapagos Islands: South Seymour. — Herman, 1972, pp. 169–173 (*aequatorialis* group; redescription, key, illustrations, distribution). — Coiffait, 1981c, p. 290 (subg. *Bledius*; distribution). — Herman, 1983a, p. 101 (key). **[aequatorialis group]**

aethiops Bernhauer, 1932, p. 83 (*Bledius*; subg. *Pucerus*). Type locality: Congo: Kunungu. **[verres group]**

affinis Motschulsky, 1860, see: *dissimilis* Erichson, 1840.

afghanicus Scheerpeltz, 1960, p. 71 (*Bledius*; subg. *Blediodes*). Type locality: Afghanistan: Kabul. **[semiferrugineus group]**

africanus Cameron, 1933, p. 383 (*Bledius*; subg. *Pucerus*). Type locality: Belgian Congo: Bena-Dibele. **[verres group]**

africanus Cameron, 1948, see: *afrus* Herman, 1970.

afrus Herman, 1970, p. 376 (*Bledius*). (Replacement name for *africanus* Cameron, 1948, not Cameron, 1933.) **[incertae sedis]**

africanus Cameron, 1948, p. 39 (*Bledius*; subg. *Blediodes*). Type locality: Dar-Banda Merid.

agonus Casey, 1889, see: *flavipennis* LeConte, 1863.

agricultor Heer, 1841, p. 576 (*Bledius*). Type locality: Switzerland: Geneva, Arve River. — Fauvel, 1872, p. 206 (synonym of *pygmaeus* which was cited as *pusillus*). — Seidlitz, 1891, p. 381 (synonym of *pygmaeus*). — Benick, 1937, pp. 75–78 (valid species, characters, key). — Benick, 1943, p. 95 (subg. *Blediodes*; characters). — Horion, 1963, p. 187 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 97 (subg. *Hesperophilus*; key). — Scheerpeltz, 168, p. 31 (subg. *Blediodes*; catalogue). **[annularis group]**

ajjer Jarrige, 1960, see: *bicornis* Germar, 1822.

akinini Eppelsheim, 1888, p. 65 (*Bledius*). Type locality: Central Asia: Kasalinsk. — Fauvel, 1895, p. 118 (synonym of *atricapillus*). — Bondroit, 1913, p. 297 (notes). — Winkler, 1925, p. 346 (subg. *Blediodes*). **[semiferrugineus group]**

albanicus Herman, **New Name**, see: *tristis* Aube, 1843.

albidipennis Bernhauer, 1912, see: *albonotatus* Mäklin, 1853.

albidus Sharp, 1876, p. 393 (*Bledius*). Type locality: Brazil: Jurua. — Bernhauer, 1927a, p. 234 (key). — Scheerpeltz, 1933, p. 1110 (subg.

Bledius). — Herman, 1972, p. 120 (*Microbledius*). **[forcipatus group]**

albipennis Bernhauer, 1933, p. 330 (*Bledius*). Type locality: Argentina: La Rioja. — Herman, 1972, p. 120 (*Microbledius*). **[forcipatus group]**

albomaculatus Bernhauer, 1937, p. 583 (*Bledius*). Type locality: German East Africa: Daressalam. **[verres group]**

albomarginatus Bernhauer, 1922, p. 225 (*Bledius*). Type localities: Formosa: Alikang, Suisharyo. — Shibata, 1973, p. 35 (subg. *Pucerus*; distribution). **[punctatissimus group]**

albonotatus Mäklin, 1853, p. 193 (*Bledius*). Type locality: Fort Nicolajevsk, Kenai Peninsula. — Keen, 1895, p. 170. — Herman, 1983a, pp. 23–26 (*annularis* group; redescription, key, illustration, distribution, natural history, synonyms). **[albonotatus group]**

ornatus LeConte, 1863, p. 53 (*Bledius*). Type locality: California: San Francisco. — LeConte, 1877, pp. 226, 230 (*annularis* group; redescription, key). — Fall, 1901, p. 75. — Hatch, 1957, p. 104 (subg. *Hesperophilus*; key). — Moore, 1964 (key, larva, distribution, natural history). — Moore, 1972 (natural history). — Moore and Legner, 1974 (natural history, larva). — Frank, 1982, p. 11 (parasites, references). — Herman, 1983a, pp. 23, 25, 119 (junior synonym of *albonotatus*, lectotype).

albidipennis Bernhauer, 1912, p. 171 (*Bledius*). Type locality: California: Laguna Beach. — Herman, 1983a, pp. 23, 25 (junior synonym of *albonotatus*).

albopubescens Cameron, 1941, p. 434 (*Bledius*; subg. *Pucerus*). Type locality: Manila. **[verres group]**

alfierii Koch, 1934, p. 53 (*Bledius*; subg. *Hesperophilus*). Type localities: Egypt: Ismailia; Tor (east coast of Red Sea, southern Sinai). — Scheerpeltz, 1974a, p. 9 (distribution). **[verres group]**

alpestris Heer, 1839, see: *fracticornis* (Paykull), 1790.

alutellus Bernhauer, 1934, see: *Pareiobledius*.

amplicollis Fauvel, 1900, p. 185 (*Bledius*). Type locality: New Zealand, Tairua. **[punctatissimus group]**

amplithorax Coiffait, 1985, p. 209 (*Bledius*; subg. *Elbidus*). Type locality: USSR. Turkmenia, Kouchka. **[kochi group]**

analis LeConte, 1863, p. 52 (*Bledius*). Type locality: Illinois. — LeConte, 1877, pp. 223, 225 (*semiferrugineus* group; redescription, key). — Casey, 1889, p. 52. — Blatchley, 1910, p. 464. — Notman, 1920, p. 697 (key). — Herman, 1972, pp. 230–234 (*semiferrugineus* group; redescription, key, illustrations, distribution, natural history). — Herman, 1983a, pp. 118, 134 (lectotype; distribution). **[semiferrugineus group]**

andresi Bernhauer, 1927, p. 90 (*Bledius*). Type locality: Egypt: Mariout. (Described as subspecies of *capra* Fauvel.) — Znojko, 1929, p. 204. — Koch, 1934, pp. 50, 58 (elevated, key, notes) (*Euceratobledius*). **[furcatus group]**

angolensis Cameron, 1950, see: *niger* Cameron, 1945.

angustus Mulsant and Rey, 1861, p. 168 (*Bledius*). Type locality: Cette. — Fauvel, 1872, p. 196 (group 2—*Hesperophilus*). — Fauvel, 1875, p. xiii (group 2—*Hesperophilus*). — Mulsant and Rey, 1878 (subg. *Belidus*). — Fauvel, 1886, p. 26 (distribution, notes). — Fauvel, 1897, p. 261 (distribution, notes). — Fauvel, 1902, p. 70 (distribution, notes). — Winkler, 1925, p. 347 (subg. *Belidus*). — Porta, 1926, p. 48 (subg. *Belidus*; key). — Koch, 1934, pp. 57, 61 (subg. *Belidus*). — Koch, 1937 (subg. *Belidus*). — Kocker, 1958, p. 110 (distribution). — Scheerpeltz, 1961c, p. 251 (distribution, notes). — Coiffait, 1966, p. 340 (distribution). — Coiffait, 1981a, p. 237 (distribution). **[angustus group]**

annae Sharp, 1911, p. 31 (*Bledius*). Type localities: Britain: Nith; Moray, Nethy River. — Bondroit, 1912a, p. 63 (characters, notes). — Winkler, 1925, p. 345 (subg. *Blediodes*). — Lindroth, 1935, pp. 595, 596 (synonym of *arcticus*). — Tottenham, 1949, p. 411 (subg. *Hesperophilus*). — Tottenham, 1954, p. 54 (subg. *Hesperophilus*; key, distribution, habitat). — Andersen, 1983, p. 429 (distribution, natural history). **[annularis group]**

larseni Hansen, 1940, p. 581 (*Bledius*). Type locality: Denmark: Jutland, Sneum rivulet. — West, 1941, pp. 142, 635 (distribution, habitat). — Benick, 1943, p. 94 (subg. *Blediodes*; characters). — Horion, 1963, p. 265 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 93 (subg. *Hesperophilus*; key). — Pope, 1977, p. 24 (synonym of *annae*). — Lohse, 1982, p. 117 (synonym of *pallipes*).

annularis LeConte, 1863, p. 53 (*Bledius*). Type locality: Lake Superior. — LeConte, 1877, pp. 226, 228 (*annularis* group; redescription, key). — Casey, 1889, p. 62. — Blatchley, 1910, p. 466. — Hatch, 1957, p. 102 (subg. *Hesperophilus*; key). — Frank, 1982, p. 10 (parasites, references). — Herman, 1983a, pp. 93, 94, 118 (*annularis* complex; discussion; lectotype). **[annularis group]**

languidus Casey, 1889, p. 63 (*Bledius*: *annularis* group). Type locality: Oregon: Huntington. — Fall, 1910, p. 112. — Hatch, 1957, p. 102

(junior synonym of *annularis*). — Herman, 1983a, pp. 94, 119 (junior synonym, lectotype).

antilope Peyron, 1858, see: *graellsi* Fauvel, 1865.

apfelbecki Koch, 1938a, p. 132 (*Bledius*; subg. *Blediodes*). Type locality: Croatia, Krapina. **[annularis group]**

apicalis Fall, 1910, see: *diagonalis* LeConte, 1863.

aquarius Erichson, 1840, see: *littoralis* Heer, 1839.

aquilonarius Herman, 1976, p. 121 (*Bledius*; *armatus* group). Type locality: Ontario: Bourget, La Rose Forest. — Herman, 1983a, p. 135 (distribution). **[armatus group]**

arabicus Coiffait, 1979, p. 178 (*Bledius*; subg. *Pucerus*). Type locality: Saudi Arabia: Bahara. Coiffait, 1981a, p. 237 (distribution). **[verres group]**

arcticus J. Sahlberg, 1890, p. 12 (*Bledius*). Type locality: Muonio. — Bernhauer and Schubert, 1911, p. 125 (catalogue, references). — Winkler, 1925, p. 345 (subg. *Blediodes*). — Krogerus, 1925b (key). — Lindroth, 1935, pp. 595–596 (natural history, distribution). — Benick, 1943, p. 94 (subg. *Blediodes*; characters). — Strand, 1946, p. 239 (distribution). — Steel, 1952 (characters). — Tottenham, 1954, p. 54 (subg. *Hesperophilus*; key, distribution, habitat). — Andersen, 1968 (natural history). — Andersen, 1982, p. 64 (natural history). — Andersen, 1983, p. 429 (distribution, natural history). **[annularis group]**

arenarius (Paykull), 1800, see: *arenoides* Tottenham, 1939.

arenicola Fauvel, 1904, p. 112 (*Bledius*). Type locality: Coast of Malabar: Mahe. **[verres group]**

arenoides Tottenham, 1939, see: *fergussoni* Joy, 1912.

argentinus Bernhauer, 1912, p. 167 (*Bledius*). Type locality: Argentina: Salta Province. — Bernhauer, 1927a, p. 233 (key). — Scheerpeltz, 1933, p. 1111 (subg. *Blediodes*). **[semiferrugineus group]**

arizonensis Fall, 1910, see: *strenuus* Casey, 1889.

armatus (Panzer) 1799, see: *tricornis* (Herbst), 1784.

armatus (Say), 1823, see: *bellicus* Blackwelder, 1944.

assimilis Casey, 1889, p. 55 (*Bledius*; *semiferrugineus* group). Type locality: Iowa. — Fall, 1910, p. 109. — Notman, 1920, p. 697 (key). — Hatch, 1957, p. 100. — Herman, 1972, pp. 243–246 (*semiferrugineus* group; redescription, key, illustrations, distribution). — Frank, 1982, p. 10 (parasites, references). — Herman, 1983a, pp. 119, 135 (lectotype, distribution). **[semiferrugineus group]**

aterrimus Fauvel, 1877, p. 204 (*Bledius*). Type locality: Australia: Nouvelle Galles du Sud, Sydney. **[emarginatus group]**

atlanticus Koch, 1938, see: *tristis* Aube, 1843.

atlanticus Lohse, 1978, see: *jutlandicus* Herman, **New Name.**

atomus Saulcy, 1864, see: *Carpelimus exiguus* Erichson, 1839.

atramentarius Rottenberg, 1870, p. 35 (*Bledius*). Type locality: Sicily. **New Status.** — Fauvel, 1872, p. 190 (junior synonym of *bos*). — Fauvel, 1873a, p. 32. **[furcatus group]**

bos Fauvel, 1871, p. 20 (*Bledius*). Type locality: Algeria: Oran. **New Synonym.** Fauvel, 1872, p. 190 (group 1—*Beldius*). — Fauvel, 1873a, p. 32. — Fauvel, 1875, p. xii (group 1—*Bledius*). — Fauvel, 1886, p. 24 (distribution, notes). — Fauvel, 1897, p. 259 (distribution, notes). — Fauvel, 1902, p. 68 (distribution, notes). — Winkler, 1925, p. 345 (subg. *Bledius*). — Porta, 1926, p. 45 (subg. *Bledius*; key). — Znojko, 1929, p. 204 (*Euceratobledius*). — Koch, 1937 (subg. *Euceratobledius*).

atratus Fauvel, 1875, p. xiii (*Bledius*). Type locality: Sardinia, Tertenia. — Winkler, 1925, p. 346 (subg. *Blediodes*). — Porta, 1926, p. 46 (subg. *Blediodes*; key). **[semiferrugineus group]**

atricapillus (Germar), 1825, fasc. 11, nr. 4 (*Oxytelus*). Type locality: Mansfeldensis. — Mannerheim, 1831, p. 459 (*Bledius*). — Runde, 1835, p. 18. — Erichson, 1840, p. 773. — Schiødte, 1866, p. 147 (*Tadunus*). — Fauvel, 1872, p. 203 (group 3—*Astycops-Bargus-Tadunus*). — Fauvel, 1873b, p. 18 (larva). — Fauvel, 1875, p. xiii (group 3 — *Astycops-Bargus-Tadunus*). — Mulsant and Rey, 1878 (subg. *Blediodes*). — Fauvel, 1884, p. 78 (synonymy). — Fauvel, 1886, p. 26 (distribution, notes). — Fowler, 1888, p. 370. — Seidlitz (1891, p. 381 (key, subg. *Tadunus*). — Ganglbauer, 1895, p. 620 (subg. *Blediodes*). — Fauvel, 1895, p. 118 (synonymy). — Fauvel, 1897, p. 262 (distribution, notes). — Fauvel, 1902, p. 72 (distribution, notes). Deville, 1907, p. 91 (subg. *Blediodes*). — Reitter, 1909, p. 168 (subg. *Blediodes*; key). — Everts, 1922, p. 140 (notes, distribution). — Winkler, 1925, p. 346 (subg. *Blediodes*). — Porta, 1926, p. 46 (subg. *Blediodes*; key). — Lengerken, 1929, p. 80 (natural history, distribution). — Portevin, 1929, p. 414 (key). — Breddin, 1936 (natural history). — West, 1942, p. 143 (distribution, habitat). — Benick, 1943, p. 94 (subg. *Blediodes*; characters). — Tottenham, 1949, p. 411 (subg. *Hesperophilus*). — Tottenham, 1954, p. 53 (subg. *Hesperophilus*; key, distribution, habitat). — Kocker, 1958, p. 108 (distribution). — Hicks, 1959, p. 112 (natural history). — Horion, 1963, p. 270 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 95 (subg. *Hesperophilus*; key). — Coiffait, 1966, p. 340 (distribution). — Coiffait, 1968, p. 138 (distribution). — Scheerpeltz, 1968, p. 31 (subg. *Blediodes*; catalogue). — Lohse, 1982, pp. 117–118 (notes). **[semiferrugineus group]**

praetermissus Williams, 1929, p. 28 (*Bledius*; subg. *Blediodes*). Type locality: Isle of Wight. — Tottenham, 1949, p. 410 (subg. *Hesperophilus*). — Tottenham, 1954, p. 53 (subg. *Hesperophilus*; key, distribution, habitat). — Horion, 1963, pp. 271–272 (synonym of *atricapillus*). — Lohse, 1964, p. 95 (variety of *atricapillus*; key). — Scheerpeltz, 1968, p. 31 (synonym of *atricapillus*). — Pope, 1977, p. 24 (synonym of *atricapillus*). — Lohse, 1982, pp. 117–118 (notes).

aurantius Herman, 1983, p. 63 (*Bledius*; *annularis* group). Type locality: California: Ventura Co.: 41 mi. N Ojai, Cuyama River. **[annularis group]**

auriculicollis Bernhauer, 1915, p. 103 (*Bledius*). Type localities: Deutsche Ostafrika: Kamballa; Natronsee. — Scheerpeltz, 1933, p. 1111 (cited as *auricollis*). **[kochi group]**

auripennis Coiffait, 1978, p. 567 (*Bledius*; subg. *Astycops*). Type locality: Afghanistan: Nouristan: Valley of Parum. **[tibialis group]**

australis Oke, 1933, p. 109 (*Bledius*). Type localities: Australia: Victoria: Caulfield, Emerald, Warburton. **[lucidus group]**

austrinus Herman, 1970, p. 376 (*Bledius*). (Replacement name for *mandibularis* MacLeay.) **[verres group]**

mandibularis MacLeay, 1873, p. 150 (*Bledius*). Type locality: Australia: Gayndah, Burnett River, abt. 150 mi. inland from Wide Bay.

basalis LeConte, 1863, p. 54 (*Bledius*). Type locality: New York: Coney Island. — LeConte, 1877, p. 232 (*cordatus* group; redescription, key). — Casey, 1889, pp. 67–71. — Fall, 1910, p. 114. — Notman, 1920, p. 698. — Herman, 1976, pp. 96–98 (*basalis* group; redescription, key, illustrations, distribution, natural history, synonyms). — Frank, 1982, p. 10 (parasites, references). — Herman, 1983a, pp. 118, 135 (lectotype, distribution). **[basalis group]**

ignavus Casey, 1889, p. 67 (*Bledius*; *cordatus* group). Type locality: Rhode Island. — Herman, 1976, pp. 96, 97 (*basalis* group; junior synonym of *basalis*). — Herman, 1983a, p. 119 (lectotype).

misellus Casey, 1889, p. 68 (*Bledius*; *cordatus* group). Type locality: Texas: Galveston. — Herman, 1976, pp. 96, 97 (*basalis* group; junior synonym of *basalis*). — Herman, 1983a, p. 120 (lectotype).

baudii Fauvel, 1872, p. 205 (*Bledius*). Type localities: Calvados; Merville; La London; Geneva; Vevey; Lyon; Pau; Germany; Piemonte. — Kraatz, 1858, pp. 205, 837 (misinterpretation of *agricultor* Heer). — Fauvel, 1873a, p. 47 (cited as new species). — Fauvel, 1875, p. xiii (group 3—*Astycops, Bargus, Tadunus*). — Mulsant and Rey, 1878 (subg. *Blediodes*). — Fauvel, 1890, p. 331 (synonymy). — Ganglbauer, 1895, p. 623 (subg. *Blediodes*). — Deville, 1907, p. 92 (subg. *Blediodes*). — Reitter, 1909, p. 166 (subg. *Blediodes*; key). **[annularis group]**

neuter Mulsant and Rey, 1878, p. 608 (*Bledius*; subg. *Blediodes*). Type locality: not cited, presumably France. (Species cited in paragraph at end of description of *baudii*.) — Fauvel, 1890, p. 331 (junior synonym of *baudii*). — Ganglbauer, 1895, p. 623 (synonym of *baudii*).

bavaricus Koch, 1938, see: *denticollis* Fauvel, 1872.

beattyi Blackwelder, 1943, p. 117 (*Bledius*). Type locality: St. Croix, 1 mi. NE of Sprat Hill Estate. — Blackwelder, 1944, p. 106 (checklist). — Herman, 1972, pp. 160–164 (*aequatorialis* group; redescription, key, illustrations, distribution). — Herman, 1983a, pp. 101, 135 (key, distribution). **[aequatorialis group]**

bedeli Fauvel, 1878, p. 99 (*Bledius*). Type locality: Algeria: Daya. — Fauvel, 1886, p. 27 (distribution, notes). — Fauvel, 1897, p. 263 (distribution, notes). — Fauvel, 1902, p. 72 (distribution, notes). — Winkler, 1925, p. 346 (subg. *Hesperophilus*). — Koch, 1938a, p. 140 (notes). — Kocker, 1958, p. 109 (distribution). **[semiferrugineus group]**

beesoni Cameron, 1930, p. 285 (*Bledius*). Type localities: India: Dehra Dun: Nim Nadi; Arni Gad. — Scheerpeltz, 1933, p. 1111 (subg. *Hesperophilus*). **[verres group]**

bellicosus Fauvel, 1904, p. 111 (*Bledius*). Type localities: Sumatra. Borneo Orientale: Batoe Panggal. Java: Soerabaja; Ardjoeno. Sumbawa. Celebes: Macassar; Bangka. — Scheerpeltz, 1933, p. 1111 (subg. *Bledius*). — Scheerpeltz, 1957, p. 226 (subg. *Euceratobledius*; distribution). **[bellicosus group]**

bellicus Blackwelder, 1944, p. 106 (*Bledius*). (Replacement name for *armatus* Say.) — Smith and Hein, 1971 (cited in error as *bellicosus*). — Herman, 1976, pp. 133–136 (*armatus* group; redescription, key, illustrations, distribution, natural history). — Frank, 1982, p. 11 (parasites, references). — Herman, 1983a, p. 135 (distribution). **[armatus group]**

armatus (Say), 1823, p. 155 (*Oxytelus*). Type locality: not cited. — Erichson, 1840, p. 779 (*Bledius*; list). — Fall, 1910, pp. 102–103. — Herman, 1976, p. 134. — Frank, 1982, p. 11 (parasites, references).

berlandi Cameron, 1938, p. 182 (*Bledius*; subg. *Blediodes*). Type locality: Senegal: Dakar. **[semiferrugineus group]**

bernhaueri Cameron, 1912a, see: *renominatus* Cameron, 1914.

bernhaueri Poppius, 1909b, p. 17 (*Bledius*; subg. *Blediodes*). Type locality: Kanin Island. — Winkler, 1925, p. 345 (subg. *Blediodes*). — Benick, 1943, p. 94 (subg. *Blediodes*; characters). — Strand, 1946, p. 239 (distribution). — Smetana, 1975, p. 161 (distribution, notes). **[annularis group]**

bicolor Casey, 1889, p. 64 (*Bledius*; *annularis* group). Type locality: California: Napa Co.: Yountville. — Fall, 1901, p. 76. Herman, 1983a, pp. 84–86, 119 (*annularis* group; redescription, key, illustrations, distribution, synonyms, lectotype). **[annularis group]**

rusticus Fall, 1901, p. 229 (*Bledius*; *annularis* group). Type locality: California: Pomona. — Herman, 1983a, pp. 84, 85, 120 (junior synonym of *bicolor,* lectotype).

bicornis (Germar),[24] 1822, fasc. 6, nr. 15 (*Oxytelus*). Type locality: Mansfeldensis. — Runde, 1835, p. 18 (*Bledius*). — Heer, 1839, p. 209. — Erichson, 1840, p. 762. — Schiødte, 1866, p. 146 (*Bledius*). — Fauvel, 1872, p. 191 (group 1—*Bledius*). — Fauvel, 1873a, p. 33. — Fauvel, 1873b, p. 19 (distribution). — Fauvel, 1875, p. XII (group 1—*Bledius*). — Mulsant and Rey, 1878 (subg. *Elbidus*). — Fauvel, 1886, p. 25 (distribution, notes). — Fowler, 1888, p. 366. — Seidlitz, 1891, p. 381 (subg. *Bledius*; key). — Ganglbauer, 1895, p. 617 (subg. *Elbidus*). — Fauvel, 1897, p. 260 (distribution, notes). — Stierlin, 1900, p. 393 (subg. *Bledius*; key). — Fauvel, 1902, p. 69 (distribution, notes). Deville, 1907, p. 89 (subg. *Bledius*; key). — Reitter, 1909, p. 165 (subg. *Elbidus*; key). — Bondroit, 1913, p. 298 (notes). — Everts, 1922, p. 139 (notes, distribution). — Winkler, 1925, p. 345 (*Elbidus*). — Porta, 1926, p. 46 (subg. *Elbidus*; key). — Lengerken, 1929, p. 76 (natural history, distribution). — Portevin, 1929, p. 410 (key). — Koch, 1934, pp. 50, 60 (subg. *Elbidus*; key, notes). — Benick, 1934, p. 190 (key). — Koch, 1937 (*Elbidus*). — West, 1942, p. 145 (distribution, habitat). — Tottenham, 1949, p. 411 (subg. *Elbidus*). — Tottenham, 1954, p. 52 (subg. *Elbidus*; key, distribution, habitat). — Bückmann, 1955b (natural history). — Kocker, 1958, p. 107 (distribution). — Scheerpeltz, 1961c, p. 250 (distribution, notes). — Horion, 1963, p. 258 (subg. *Elbidus*; distribution, notes). — Lohse, 1964, p. 91 (subg. *Elbidus*; key). — Coiffait, 1966, p. 340 (distribution). — Smetana, 1967, p. 322 (distribution, notes). — Scheerpeltz, 1968, p. 31 (subg. *Elbidus*; catalogue). — Shibata, 1973, p. 34 (subg. *Elbidus*; distribution). — Lohse, 1978, pp. 11–12 (characters). — Frank, 1982, p. 11 (parasites, references). **[kochi group]**

ajjer Jarrige, 1960, p. 39 (*Bledius*; subg. *Elbidus*). Type locality: Issaouane (described as subspecies of *bicornis*).

dama Motschulsky, 1857, p. 507 (*Bledius*). Type locality: Algeria. — Fauvel, 1872, p. 191 (junior synonym of *bicornis*). — Fauvel, 1873a, p. 33. — Fowler, 1888, p. 366 (synonym of *bicornis*). — Fauvel, 1897, p. 260 (synonym of *bicornis*). — Fauvel, 1902, p. 69 (synonym of *bicornis*).

jutlandensis Herman, **New Name** [replacement name for *atlanticus* Lohse, 1978].

atlanticus Lohse, 1978, p. 12 (*Bledius*; subg. *Elbidus*). Type locality: West Germany: Büsum. (Subspecies of *bicornis.*) [Name **preoccupied** by *atlanticus* Koch, 1938].

bidentifrons Broun, 1912, p. 401 (*Bledius*). Type locality: New Zealand: Wanganui Beach. **[punctatissimus group]**

bifasciatus Sharp, 1887, p. 686 (*Bledius*). Type locality: Guatemala: Pantaleon, Rio Naranjo. — Herman, 1972, pp. 120, 136 (*Microbledius*; diagnosis). **[forcipatus group]**

bipustulatus Bernhauer, 1905, p. 14 (*Bledius*). Type locality: Africa orientalis. — Bernhauer and Schubert, 1911, p. 126 (subg. *Blediodes*). — Scheerpeltz, 1974a, p. 9 (distribution). **[verres group]**

birmanus Cameron, 1930, p. 283 (*Bledius*). Type locality: Burma: Tavoy. — Scheerpeltz, 1933, p. 1111 (subg. *Hesperophilus*). **[verres group]**

biskrensis Fagel, 1970, p. 6 (*Bledius*; subg. *Elbidus*). Type locality: Algeria: Biskra Oasis. **[kochi group]**

bison Cameron, 1930, p. 273 (*Bledius*; subg. *Bledius*). Type locality: India Orientali. **[furcatus group]**

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[24] This name was cited earlier (in *Oxytelus*) by Olivier, 1812, p. 615 but inexplicably was not used thereafter (except Pope, 1977, p. 24) despite the subsequent use of other of Olivier's names (for example *furcatus*) cited in the same publication. For the purpose of this catalogue I have chosen to follow Pope (1977) and ignore the earlier citation and regard it as a *nomen oblitum.* It is unclear whether the two uses of this name represent one or two species.

bispinus Kraatz, 1859, p. 169 (*Bledius*). Type locality: India Orientali. — Cameron, 1930, p. 279 (key, redescription). — Scheerpeltz, 1933, p. 1111 (subg. *Hesperophilus*). **[bispinus group]**

bituberculatus Cameron, 1940, p. 183 (*Bledius*; subg. *Elbidus*). Type locality: Malaya: West Coast, Langkawi Island. **[rugosicollis group]**

boddyi Hatch, 1957, see: *eximius* Casey, 1889.

bolsonensis Scheerpeltz, 1972, p. 94 (*Bledius*; subg. *Hesperophilus*). Type locality: Argentina: Rio Negro. **[emarginatus group]**

bonariensis Bernhauer, 1912, p. 168 (*Bledius*; subg. *Hesperophilus*). Type locality: Argentina: Prov. Buenos Aires. — Bernhauer, 1927a, p. 234 (keys). **[bonariensis group]**

borealis Blatchley, 1910, see: *turgidus* Casey, 1889.

bos Fauvel, 1871, see: *atramentarius* Rottenberg, 1870.

bosnicus Bernhauer, 1902, p. 700 (*Bledius*). Type locality: Yugoslavia: Sarajevo. — Porta, 1926, p. 47 (subg. *Blediodes*; key). — Benick, 1937, pp. 73–74 (subspecies of *erraticus*). — Benick, 1943, p. 95 (subg. *Blediodes*; characters). — Strand, 1946, p. 240 (distribution). — Scheerpeltz, 1968, p. 31 (subg. *Blediodes*; catalogue). **[annularis group]**

bowronensis Hatch, 1957, see: *turgidus* Casey, 1889.

bredoi Bernhauer, 1943, p. 280 (*Bledius*; subg. *Pucerus*). Type locality: Cogo: Elisabethville. **[semiferrugineus group]**

breretoni Hatch, 1957, p. 100 (*Bledius*; subg. *Hesperophilus*). Type locality: Washington: Pullman. — Herman, 1983a, pp. 93–95 (*annularis* complex; discussion). **[annularis group]**

brevicollis Mulsant and Rey, 1861, see: *tristis* Aube, 1843.

brevidens LeConte, 1877, see: *mandibularis* Erichson, 1840.

brincki Scheerpeltz, 1974, p. 78 (*Bledius*; subg. *Hesperophilus*). Type locality: Southwest Africa: Kaokoveld, Omutati, 70 mi. WSW Ohopoho. **[emarginatus group]**

bruchi Bernhauer, 1927, p. 233 (*Bledius*). Type locality: Argentina: Cordoba. **[emarginatus group]**

brunnipennis (Fabricius), 1801, p. 596 (*Staphylinus*). Type locality: India Orientali. — Erichson, 1840, p. 779 (*Bledius*; list). — Fauvel, 1903a, p. 151 (distribution, notes, synonymy). — Fauvel, 1904c, p. 46 (synonymy). — Cameron, 1930, pp. 272, 273 (subg. *Bledius*; key, redescription). **[rugosicollis group]**

productus (Walker), 1858, p. 205 (*Oxytelus*). Type locality: Ceylon. — Fauvel, 1903a, p. 151 (synonym of *brunneipennis*). — Fauvel, 1904c, p. 46 (synonym of *brunneipennis*).

rudis (Walker), 1858, p. 205 (*Oxytelus*). Type locality: Ceylon. — Fauvel, 1903a, p. 151 (synonym of *brunneipennis*). — Fauvel, 1904c, p. 46 (synonym of *brunneipennis*).

bubalus Gistel, 1857, pp. 18, 49 (*Bledius*). Type locality: Corfu. **[incertae sedis]**

buehleri Scheerpeltz, 1957, pp. 226, 245 (*Bledius*; subg. *Hesperophilus*). Type locality: Sumba: Melolo. **[punctatissimus group]**

buettikeri Coiffait, 1981, p. 241 (*Bledius*; subg. *Astycops*). Type locality: Saudi Arabia: El Shoiba. **[punctatissimus group]**

burlinii Koch, 1938, see: *osiris* Normand, 1934.

campi Bondroit, 1907, see: *terebrans* (Schiødte), 1866.

canaliculatus Notman, 1920, see: *semiferrugineus* LeConte, 1863.

capensis Cameron, 1945, p. 708 (*Bledius*; subgen. *Hesperophilus*). Type locality: South Africa: Simon's Town. **[punctatissimus group]**

capicola Cameron, 1945, p. 708 (*Bledius*; subg. *Pucerus*). Type locality: South Africa: Simon's Town. **[verres group]**

capitalis Fauvel, 1877, see: *lucidus* Sharp, 1874.

capra Fauvel, 1875, p. XII (*Bledius*). Type locality: Egypt: Port Said. — Fauvel, 1886, p. 24 (distribution, notes, synonymy). — Fauvel, 1902, p. 69 (distribution, notes). — Winkler, 1925, p. 345 (subg. *Bledius*). — Znojko, 1929, p. 204 (*Euceratobledius*). — Koch, 1934, pp. 49, 59 (subg. *Euceratobledius*; key, notes). — Smetana, 1967, p. 322 (distribution, notes). **[furcatus group]**

giraffa Costa, 1875, p. 21 (*Bledius*). Type locality: Egypt. — Fauvel, 1886, p. 24 (junior synonym of *capra*). — Fauvel, 1902, p. 69 (synonym of *capra*).

seurati Peyerimhoff, 1924, p. 158 (*Bledius*). Type locality: Tunisia: Kerkennah Island. (Described as subspecies of *capra*.) — Znojko, 1929, p. 204 (*Euceratobledius*).

caribbeanus Blackwelder, 1943, p. 113 (*Bledius*). Type locality: Tobago, 3 mi. SW Scarborough. — Blackwelder, 1944, p. 106 (checklist). — Herman, 1972, pp. 145–148 (*Psamathobledius*; redescription, key, illustrations, distribution). — Herman, 1983a, p. 134 (distribution). **[punctatissimus group]**

cariniceps Bernhauer, 1932, p. 82 (*Bledius*; subg. *Pucerus*). Type locality: Congo: Leopoldville; Komi. (**Emendation**, original spelling *carinlceps*.) **[verres group]**

ghesquierei Bernhauer, 1932, p. 82 (*Bledius*; subg. *Pucerus*). Type locality: Congo: Lusambo. (Described as variety of *cariniceps*.) (**Emendation**; original spelling was *guesquierei* but the name is a patronym of the collector I. Ghesquiere.)

carinicollis Fauvel, 1875, p. XII (*Bledius*). Type locality: Biskra. — Fauvel, 1886, p. 25 (distribution, notes). — Fauvel, 1897, p. 260 (distribution, notes). — Fauvel, 1902, p. 69 (distribution, notes). — Winkler, 1925, p. 345 (subg. *Elbidus*). **[kochi group]**

caroli Blackburn, 1888, p. 13 (*Bledius*). Type locality: Australia: Adelaide, Port River. **[punctatissimus group]**

castaneipennis Mannerheim, 1831, p. 459 (*Bledius*). **[New Status]**. — Stephens, 1829, p. 292 (nomen nudum). — Gistel, 1934, p. 9 (*Dicarenus*). — Boisduval and Lacordaire, 1835, p. 457 (*Bledius*). — Erichson, 1939, p. 581 (junior synonym of *opacus*). — Seidlitz, 1891, p. 381 (synonym of *opacus*). — Ganglbauer, 1895, p. 619 (synonym of *opacus*). **[semiferrugineus group]**

castaneus Mulsant and Rey, 1878, p. 596 (*Bledius*; subg. *Blediodes*). Type locality: not cited, presumably France [cited in paragraph at end of redescription of *femoralis*]. **[semiferrugineus group]**

cavus Eppelsheim, 1885, p. 143 (*Bledius*). Type locality: West Africa. **[verres group]**

cedarensis Hatch, 1957, p. 101 (*Bledius*; subg. *Hesperophilus*). Type locality: Washington: Cedar Mountain. — Herman, 1983a, pp. 78–79 (*annularis* group; redescription, key, illustrations, distribution). **[annularis group]**

ceratus Blackwelder, 1943, p. 118 (*Bledius*). Type locality: Haiti: Port-au-Prince. — Blackwelder, 1944, p. 106 (checklist). — Herman, 1972, pp. 164–169 (*aequatorialis* group; redescription, key, illustrations, distribution). — Herman, 1983a, pp. 101, 135 (key, distribution). **[aequatorialis group]**

championi Bernhauer, 1926, p. 23 (*Bledius*). Type locality: India: Kumaon: Haldwani District. — Cameron, 1930, pp. 279, 281 (key, redescription). — Scheerpeltz, 1933, p. 1112 (subg. *Hesperophilus*). **[bispinus group]**

chilensis Coiffait and Saiz, 1968, p. 426 (*Bledius*; subg. *Astycops*). Type locality: Chile: Curico. — Saiz, 1973, p. 230 (key, discussion). **[emarginatus group]**

chimerinus Gistel, 1857, p. 73 (*Bledius*). Type locality: Tyrolis. **[incertae sedis]**

chinensis Bernhauer, 1928, p. 8 (*Bledius*; subg. *Bledius*). Type locality: China: Schantung: Jentschoufu. — Smetana, 1975, p. 160 (distribution, notes). **[gigantulus group]**

chinkiangensis Bernhauer, 1938, p. 24 (*Bledius*; subg. *Blediodes*). Type locality: China: Chinkiang. **[annularis group]**

cinctus Motschulsky, 1860, see: *verres* Erichson, 1840.

circularis Fauvel, 1889, p. 251 (*Bledius*). Type locality: New Caledonia: Kone. — Fauvel, 1903b, p. 261 (distribution). **[circularis group]**

clarus Fall, 1901, p. 228 (*Bledius*). Type locality: California: Pomona. — Herman, 1983a, pp. 62–63, 120 (*annularis* group; redescription, key, illustrations, distribution, natural history, lectotype). **[annularis group]**

clavatus Eppelsheim, 1893, p. 60 (*Bledius*). Type locality: Baikal Region: Quellgebiet des Irkut. — Winkler, 1925, p. 346 (subg. *Blediodes*). **[annularis group]**

claviventris Fairmaire and Germain, 1861, p. 445 (*Bledius*). Type locality: Chile: Quillota. — Coiffait and Saiz, 1968, p. 425 (*Hesperophilus*; key, redescription). — Saiz, 1973, p. 229 (key, notes). **[emarginatus group]**

cognatus LeConte, 1877, p. 231 (*Bledius*; *annularis* group). Type locality: North Carolina. — Herman, 1983a, pp. 11–14, 118 (*emarginatus* group; redescription, key, illustrations, distribution, natural history, lectotype). **[emarginatus group]**

coiffaiti Irmler, 1979, p. 115 (*Bledius*; subg. *Elbidus*). Type locality: Tunisia: Kebili. **[furcatus group]**

compressicollis Bernhuaer, 1912, p. 247 (*Bledius*). Type locality: Luzon: Manila. **[compressicollis group]**

condensus Kangas, 1938, p. 127 (*Bledius*). Type locality: not given (proposed for *fuscipes* as used by Finnish authors). **[annularis group]**

condonensis Hatch, 1957, see: *opacifrons* LeConte, 1877.

confinis Fall, 1910, see: *melanocephalus* (Say), 1823.

confusus LeConte, 1877, p. 228 (*Bledius*; *annularis* group). Type locality: Lake Superior. — Blatchley, 1910, p. 466. — Herman, 1983a, pp. 65–67, 118 (*annularis* group; redescription, key, illustrations, distribution, natural history, lectotype). **[annularis group]**

congoensis Cameron, 1928, p. 19 (*Bledius*). Type locality: Belgian Congo: Mushie. **[verres group]**

conicicollis Fauvel, 1904, p. 111 (*Bledius*). Type locality: Tonkin. **[kosempoensis group]**

consimilis Fall, 1910, p. 105 (*Bledius*). Type locality: New Mexico: Thornton. — Notman, 1920, p. 695 (key). — Herman, 1976, pp. 111–114 (*armatus* group; redescription, key, illustrations, distribution, natural history). — Herman, 1983a, pp. 120, 136 (lectotype, distribution). **[armatus group]**

convexicollis Bernhauer, 1912, p. 259 (*Bledius*). Type locality: Transcaspian: Kuschka. — Winkler, 1925, p. 345 (subg. *Bledius*). — Koch, 1938b, p. 40 (subg. *Elbidus*; notes). **[kochi group]**

convexifrons Fauvel, 1878, p. 498 (*Bledius*). Type locality: Australia occidentale: Swan River. **[emarginatus group]**

cordatus (Say), 1834, p. 461 (*Oxytelus*). Type locality: Virginia. — Erichson, 1840, p. 780 (*Bledius*; list). — LeConte, 1877, pp. 232, 233 (*cordatus* group; redescription, key). — Casey, 1889, p. 67. — Fall, 1910, p. 114. — Blatchley, 1910, p. 467. — Notman, 1920, p. 698. — Herman, 1976, pp. 81–85 (*basalis* group; redescription, key, illustrations, distribution, natural history). — Herman, 1983a, p. 136 (distribution). **[basalis group]**

cordicollis Motschulsky, 1860, p. 555 (*Bledius*). Type locality: N la Daourie, Tourkinsk, near Baical. — Fauvel, 1875, p. xiii (group 2—*Hesperophilus*). — Bondroit, 1913, p. 297 (notes). — Winkler, 1925, p. 346 (subg. *Blediodes*). **[annularis group]**

corniger Rosenhauer, 1856, p. 77 (*Bledius*). Type locality: Spain: Cartama. — Fauvel, 1872, p. 192 (group 1—*Bledius*). — Fauvel, 1875, p. xii (group 1—*Bledius*). — Fauvel, 1886, p. 25 (distribution, notes). — Champion, 1898, p. 100 (distribution). — Fauvel, 1902, p. 70 (distribution, notes). — Winkler, 1925, p. 345 (subg. *Bledius*). — Porta, 1926, p. 46 (subg. *Bledius*; key). — Kocher, 1958, p. 106 (distribution). — Bordoni, 1973, p. 665 (distribution). **[gigantulus group]**

cornutissimus Wollaston, 1864, p. 594 (*Bledius*). Type localities: Canary Islands: Lanzerote: the Salinas; Arrecife. Fuerteventura: Puerto de Cabras. — Fauvel, 1872, p. 192 (junior synonym of *corniger*). — Fauvel, 1897, p. 260 (synonym of *unicornis*). — Fauvel, 1902, p. 70 (synonym of *corniger*).

cornutissimus Wollaston, 1864, see: *corniger* Rosenhauer, 1856.

coulteri Hatch, 1957, p. 99 (*Bledius*; subg. *Hesperophilus*). Type locality: Washington: Cheeney, Turnbull Slough. — Herman, 1972, pp. 240–243 (*semiferrugineus* group; redescription, key, illustrations, distribution). — Herman, 1983a, p. 136 (distribution). **[semiferrugineus group]**

cowleyi Blackburn, 1902, p. 22 (*Bledius*). Type locality: Australia: Queensland: Cairns. **[lucidus group]**

crassicollis Boisduval and Lacordaire, 1835, p. 456 (*Bledius*). Type locality: Paris. Erichson, 1839, p. 580. — Erichson, 1840, p. 770. — Thomson, 1861. — Schiødte, 1866, p. 147 (*Tadunus*). — Thomson, 1867 (*Bledius*). — Fauvel, 1872, p. 208 (group 3—*Astycops, Bargus, Tadunus*). — Fauvel, 1873a, p. 50. — Fauvel, 1875, p. xiii (group 3—*Astycops, Bargus, Tadunus*). — Mulsant and Rey, 1878 (subg. *Blediodes*). — Fowler, 1888, p. 371 (synonymy). — Seidlitz, 1891, p. 382 (subg. *Tadunus*; key). — Ganglbauer, 1895, p. 621 (subg. *Blediodes*). — Stierlin, 1900, p. 394 (subg. *Tadunus*; key). — Deville, 1907, p. 92 (subg. *Blediodes*). — Reitter, 1909, p. 167 (subg. *Blediodes*; key). — Everts, 1922, p. 141 (notes, distribution, key). — Winkler, 1925, p. 346 (subg. *Blediodes*). — Porta, 1926, p. 47 (subg. *Blediodes*; key). — Portevin, 1929, p. 413 (key). — Brunier, 1931, pp. 43–44 (natural history). — Breddin, 1936 (natural history). — West, 1942, pp. 144, 635 (distribution, habitat). — Benick, 1943, p. 95 (subg. *Blediodes*; characters). — Horion, 1963, p. 276 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 97 (subg. *Hesperophilus*; key). — Scheerpeltz, 1968, p. 31 (subg. *Blediodes*; catalogue). **[semiferrugineus group]**

filum Heer, 1839, p. 211 (*Bledius*). Type locality: Switzerland: Geneva, Arve River. — Fauvel, 1872, p. 208 (junior synonym of *crassicollis*). Fauvel, 1873a, p. 50. — Fowler, 1888, p. 371 (synonym of *crassicollis*). — Seidlitz, 1891, p. 382 (synonym of *crassicollis*).

crenulatus Stierlin, 1867, see: *unicornis* (Germar), 1825.

cribratus Sharp, 1889, p. 413 (*Bledius*). Type locality: Japan: Nikko. — Winkler, 1925, p. 346 (subg. *Blediodes*). — Shibata, 1976, p. 134 (distribution, catalogue). **[semiferrugineus group]**

cribricollis LeConte, 1877, see: *fenyesi* Bernhauer and Schubert, 1911.

cribricollis Heer, 1839, p. 210 (*Bledius*). Type localities: Switzerland: Geneva, Arve River; Aigle. — Jacquelin du Val, 1859, p. 76 (junior synonym of *rufipennis*). — Fauvel, 1872, p. 209 (group 3—*Astycops, Bargus, Tadunus*). — Fauvel, 1873a, p. 51. — Fauvel, 1873b, p. 22 (distribution). — Fauvel, 1875, p. xiii (group 3—*Astycops, Bargus, Tadunus*). — Mulsant and Rey, 1878 (subg. *Blediodes*). — Fauvel, 1886, p. 27 (distribution, notes). — Seidlitz, 1891, p. 382 (key, subg. *Tadunus*). — Ganglbauer, 1895, p. 621 (subg. *Blediodes*). — Fauvel, 1897, p. 263 (distribution, notes). — Stierlin, 1900, p. 394 (subg. *Tadunus*; key). — Fauvel, 1902, p. 72 (distribution, notes). — Reitter, 1909, p. 167 (subg. *Blediodes*; key). — Everts, 1922, p. 141 (notes, distribution, key). — Winkler, 1925, p. 346 (subg. *Blediodes*). — Porta, 1926, p. 46 (subg. *Blediodes*; key). — Portevin, 1929, p. 413 (key). — Breddin, 1936 (natural history). — Koch, 1938a, p. 137 (notes). — West, 1942, p. 145 (distribution, habitat). — Benick, 1943, p. 95 (subg. *Blediodes*; characters). — Kocker, 1958, p. 108 (distribution). — Smetana, 1959, p. 201 (distribution). — Horion, 1963, p. 278 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 97 (subg. *Hesperophilus*; key). — Scheerpeltz, 1968, p. 32 (subg. *Blediodes*; catalogue). — Smetana, 1975, p. 162 (distribution, notes). — Frank, 1982, p. 11 (parasites, references). **[semiferrugineus group]**

rufipennis Erichson, 1840, p. 770 (*Bledius*). Type locality: Austria. — Jacquelin du Val, 1859, p. 76. — Fauvel, 1872, p. 209 (junior synonym of *cribricollis*). — Fauvel, 1873a, p. 51. — Seidlitz, 1891, p. 382 (synonym of *cribricollis*).

dissecticollis Roubal, 1918, p. 9 (*Bledius*). (Described as a variety of *cribricollis*.)

cubensis Blackwelder, 1943, p. 115 (*Bledius*). Type locality: Cuba: Cayamas. **[emarginatus group]**

curticornis Fauvel, 1900, p. 68 (*Bledius*). Type locality: Congo: Kinchasa. **[verres group]**

curtipennis Bernhauer, 1921, p. 172 (*Bledius*). Type locality: Argentina: Prov. Tucuman. — Bernhauer, 1927a, p. 233 (key). — Scheerpeltz, 1933, p. 1113 (subg. *Hesperophilus*). **[emarginatus group]**

montanus Bernhauer, 1921, p. 172 (*Bledius*). Type locality: Argentina: Prov. Jujuy. (Described as variety of *curtipennis*.) — Bernhauer, 1927a, p. 233 (key).

curvicornis Sharp, 1889, p. 412 (*Bledius*). Type locality: Japan: Niigata. — Winkler, 1925, p. 347 (subg. *Pucerus*). — Shibata, 1976, p. 134 (distribution, catalogue). **[verres group]**

cuspidatus LeConte, 1877, see: *flavipennis* LeConte, 1863.

dama Motschulsky, 1857, see: *bicornis* (Germar), 1822.

dartevellei Bernhauer, 1943, p. 279 (*Bledius*; subg. *Hesperophilus*). Type locality: Congo: Malembe. **[punctatissimus group]**

debilis Erichson, 1840, p. 778 (*Bledius*). Type locality: Russia meridionali. — Fauvel, 1866, p. 107. — Fauvel, 1872, p. 197 (group 2—*Hesperophilus*). — Fauvel, 1873a, p. 39. — Fauvel, 1875, p. xiii (group 2—*Hesperophilus*). — Mulsant and Rey, 1878 (subg. *Astycops*). — Fauvel, 1886, p. 26 (distribution, notes). — Ganglbauer, 1895, p. 625 (subg. *Hesperophilus*). — Fauvel, 1897, p. 262 (distribution, notes). — Champion, 1898, p. 100 (distribution). — Fauvel, 1902, p. 71 (distribution, notes). — Reitter, 1909, p. 168 (subg. *Blediodes*; key). — Everts, 1922, p. 139 (notes, distribution). — Winkler, 1925, p. 346 (subg. *Hesperophilus*). — Porta, 1926, p. 48 (subg. *Hesperophilus*; key). — Porta, 1949, p. 140 (distribution). — Kocker, 1958, p. 109 (distribution). — Horion, 1963, p. 293 (subg. *Hesperophilus*; distribution, notes). — Szujecki, 1968, p. 294 (notes, does not occur in Poland). — Bordoni, 1973, p. 666 (distribution). **[debilis group]**

mulsanti Rosenhauer, 1856, p. 80 (*Bledius*). Type locality: Spain: Cadiz. — Fauvel, 1866, p. 107 (junior synonym of *debilis*). — Fauvel, 1872, p. 197 (synonym of *debilis*). — Fauvel, 1873a, p. 39. — Mulsant and Rey, 1878 (subg. *Astycops*).

deceptivus Fall, 1901, see: *foraminosus* Casey, 1889.

decorsei Cameron, 1948, p. 39 (*Bledius*; subg. *Blediodes*). Type locality: Dar-Banda merid. Krebedje; Fort Sibut. **[verres group]**

defensus Fauvel, 1872, p. 212 (*Bledius*). Type localities: France: Calvados; Firfol near Lisieux. — Fauvel, 1873a, p. 54 (cited as new species). — Fauvel, 1875, p. xiii (group 3—*Astycops, Bargus, Tadunus*). — Mulsant and Rey, 1878 (subg. *Blediodes*). — Ganglbauer, 1895, p. 618 (subg. *Blediodes*). — Bondroit, 1913, p. 297 (synonymy). — Everts, 1922, p. 141 (notes, distribution). — Winkler, 1925, p. 345 (subg. *Blediodes*). — Porta, 1926, p. 46 (subg. *Blediodes*; key). — Portevin, 1929, p. 411 (key). — Breddin, 1936 (natural history). — Hansen, 1940, p. 583 (key). — West, 1942, pp. 141, 635 (distribution, habitat). — Benick, 1943, p. 94 (subg. *Blediodes*; characters). — Tottenham, 1949, p. 411 (subg. *Hesperophilus*). — Tottenham, 1954, p. 54 (subg. *Hesperophilus*; key, distribution, habitat). — Horion, 1963, p. 267 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 92 (subg. *Hesperophilus*; key). — Scheerpeltz, 1968, p. 32 (subg. *Blediodes*; catalogue). **[annularis group]**

gulielmi Sharp, 1913, p. 1 (*Bledius*). Type locality: Britain: Yorkshire. — Sharp, W., 1913, p. 14. — Bondroit, 1913, p. 297 (synonym of *defensus*). — Tottenham, 1949, p. 411 (synonym of *defensus*).

dehnerti Korge, 1959, p. 26 (*Bledius*). Type locality: Germany: Niederrodenbacher Kalksteinbruch bei Hanau. — Lohse, 1964, p. 96 (subg. *Hesperophilus*; key). **[semiferrugineus group]**

denticollis Fauvel, 1872, p. 202 (*Bledius*). (Replacement name for *obscurus* Mulsant and Rey.) — Fauvel, 1873a, p. 44 (replacement name). — Fauvel, 1875, p. xiii (group 3—*Astycops, Bargus, Tadunus*). — Mulsant and Rey, 1878 (subg. *Blediodes*). — Ganglbauer, 1895, p. 618 (subg. *Blediodes*). — Fauvel, 1895, p. 118 (synonymy). — Deville, 1907, p. 91 (subg. *Blediodes*). — Reitter, 1909, p. 166 (subg. *Blediodes*; key). — Everts, 1922, pp. 142, 143 (notes, distribution, key). — Winkler, 1925, p. 345 (subg. *Blediodes*). — Krogerus, 1925a (natural history). — Porta, 1926, p. 46 (subg. *Blediodes*; key). — Portevin, 1929, p. 411 (key). — Benick, 1943, p. 94 (subg. *Blediodes*; characters). — Strand, 1946, p. 238 (distribution). — Tottenham, 1949, p. 411 (subg. *Hesperophilus*). — Steel, 1956 (characters). — Horion, 1963, p. 260 (subg. *Blediodes*; distribution, notes). — Lohse, 1963, p. 94 (subg. *Hesperophilus*; key). — Andersen, 1968 (natural history). — Scheerpeltz, 1968, p. 32 (subg. *Blediodes*; catalogue). — Smetana, 1975, p. 160 (distribution, notes). — Andersen, 1982, p. 67 (natural history). — Andersen, 1983, p. 429 (distribution, natural history). **[annularis group]**

obscurus Mulsant and Rey, 1870, p. 111 (*Bledius*). Type locality: Lyon, Saône River. — Fauvel, 1872, p. 202 (preoccupied). — Fauvel, 1873a, p. 44 (preoccupied).

bavaricus Koch, 1938, p. 45 (*Bledius*; subg. *Blediodes*). Type locality: Germany: Bavaria. (Described as subspecies of *rastellus*.) — Lohse, 1964, p. 94 (synonym of *denticollis*). — Scheerpeltz, 1968, p. 32 (subg. *Blediodes*; catalogue).

obtusicollis Koch, 1938, p. 48 (*Bledius*; subg. *Blediodes*.) (Described as variety of subspecies *bavaricus*).

derasus Sharp, 1887, p. 800 (*Bledius*). Type locality: Mexico: Durango: Villa Lerdo. **[armatus group]**

devillei Bondroit, 1912, see: *minor* Mulsant and Rey.

diagonalis LeConte, 1863, p. 52 (*Bledius*). Type locality: California: San Diego. — LeConte, 1877, pp. 226, 230 (*annularis* group; redescription, key). — Casey, 1889, p. 65. — Fall, 1901, p. 75. — Moore, 1964, pp. 277, 280. — Herman, 1983a, pp. 28–32, 118 (*annularis* group; redescription, key, illustrations, distribution, natural history, synonyms, lectotype). **[albonotatus group]**

apicalis Fall, 1910, p. 112 (*Bledius*). Type locality: California: Raymond. — Herman, 1983a, pp. 28, 31, 120 (junior synonym of *diagonalis*, lectotype).

dickersoni Notman, 1922, see: *philadelphicus* Fall, 1919.

diffinis Baudi, 1869, p. 398 (*Bledius*). Type locality: Cyprus (?). — Fauvel, 1875, p. XIII (group 1—*Bledius*). — Winkler, 1925, p. 345 (subg. *Elbidus*). **[semiferrugineus group]**

dilutipennis Motschulsky, 1857, p. 507 (*Bledius*). Type locality: Indes orientales. — Cameron, 1930, pp. 278, 284 (key, redescription). — Scheerpeltz, 1933, p. 1113 (subg. *Hesperophilus*). — Coiffait, 1981d, p. 350 (distribution). **[verres group]**

dimidiatus LeConte, 1877, p. 232 (*Bledius*; *cordatus* group). Type locality: Florida: Enterprise. — Notman, 1920, p. 698. — Herman, 1976, pp. 85–86 (*basalis* group; redescription, key, illustrations, distribution). — Herman, 1983a, pp. 118, 136 (lectotype, distribution). **[basalis group]**

dinoceros Znojko, 1929, p. 200 (*Bledius*; subg. *Euceratobledius*). Type locality: Odessa. — Blinshtein, 1976, pp. 80–81 (female described, notes, natural history, distribution). **[furcatus group]**

diota Schiødte, 1866, p. 146 (*Bledius*). Type locality: Denmark. — Fauvel, 1875, p. xii (group 1—*Bledius*). — Fauvel, 1884, p. 78 (junior synonym of *tricornis*). — Ganglbauer, 1895, p. 615 (synonym of *tricornis*). — Bernhauer and Schubert, 1911, p. 136 (synonym of *tricornis*). — Sharp, 1911, p. 34 (valid species; natural history). — Everts, 1922, p. 139 (notes, distribution). — Krogerus, 1925b (key, natural history). — Benick, 1934, p. 190 (key). — Larsen, 1936 (natural history). — Lengerken, 1939, pp. 131–136 (natural history). — West, 1942, p. 141 (distribution, habitat). — Tottenham, 1949, p. 411 (subg. *Elbidus*). — Larsen, 1952 (natural history). — Larsen, 1953 (natural history). — Tottenham, 1954, p. 52 (subg. *Elbidus*; key, distribution, habitat). — Horion, 1963, p. 259 (subg. *Elbidus*; distribution, notes). — Lohse, 1964, p. 91 (subg. *Elbidus*; key). — Lipkow, 1968, p. 210 (natural history). **[kochi group]**

dissecticollis Roubal, 1918, see: *cribricollis* Heer, 1839.

dissimilis Fall, 1910, see: *philadelphicus* Fall, 1919.

dissimilis Erichson, 1840, p. 769 (*Bledius*). Type localities: Germany, Austria, Hungaria, Istria, France. — Fauvel, 1872, p. 210 (group 3—*Astycops, Bargus, Tadunus*). — Fauvel, 1873a, p. 52. — Fauvel, 1875, p. xiii (group 3—*Astycops, Bargus, Tadunus*). — Mulsant and Rey, 1878 (subg. *Blediodes*). — Fowler, 1888, p. 372. — Seidlitz, 1891, p. 382 (key, subg. *Tadunus*). — Ganglbauer, 1895, p. 622 (subg. *Blediodes*). — Reitter, 1909, p. 167 (subg. *Blediodes*; key). — Everts, 1922, p. 141 (notes, distribution). — Winkler, 1925, p. 346 (subg. *Blediodes*). — Porta, 1926, p. 47 (subg. *Blediodes*; key). — Portevin, 1929, p. 413 (key). — Brunier, 1931, pp. 44–46 (natural history). — West, 1942, p. 143 (distribution, habitat). — Benick, 1943, p. 95 (subg. *Blediodes*; characters). — Porta, 1949, p. 140 (synonyms). — Tottenham, 1949, p. 411 (subg. *Hesperophilus*). — Tottenham, 1954 (subg. *Hesperophilus*; key, distribution, habitat). —

Horion, 1963, p. 279 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 98 (subg. *Hesperophilus*; key). — Scheerpeltz, 1968, p. 32 (subg. *Blediodes*; catalogue). **[semiferrugineus group]**

simpliciventris Apfelbeck, 1907, p. 638 (*Bledius*). Type locality: Ufer der Drina bei Visegrad im Sandigen Lehmboden. — Bondroit, 1912a, p. 66 (synonym of *nigricans*).

nigricans Erichson, 1840, p. 769 (*Bledius*). Type locality: Russia meridionali. — Fauvel, 1875, p. XIII (group 3—*Astycops, Bargus, Tadunus*). — Ganglbauer, 1895, p. 622 (variety of *dissimilis*). — Bondroit, 1912a, p. 66 (characters, notes, synonymy).

affinis Motschulsky, 1860, p. 556 (*Bledius*). Type localities: Dschanghi-Tau, Khirghiz Steppes; Lake Inderskoe, near Volga River. — Fauvel, 1875, p. XIII (group 2—*Hesperophilus*). — Winkler, 1925, p. 347 (subg. *Pucerus*). — Znojko, 1929, p. 206 (synonym of *dissimilis* var. *nigricans*).

sulcicollis Koch, 1938a, p. 135 (*Bledius*; subg. *Blediodes*). Type locality: Italy: Emilia; Bosnia: Visegrad (described as variety of *dissimilis*). — Porta, 1949, p. 140 (distribution).

erythropeplus Koch, 1938a, p. 137 (*Bledius*; subg. *Blediodes*). Type locality: Italy: Emilia. (Described as an aberration of *dissimilis*.) — Porta, 1949, p. 140 (distribution).

distans Fauvel, 1904, p. 304 (*Bledius*). Type locality: Madagascar: Fort Dauphin. — Bernhauer and Schubert, 1911, p. 129 (subg. *Pucerus*). **[verres group]**

divisus Marsham, 1802, see: *opacus* (Block), 1799.

divisus LeConte, 1863, see: *tarandus* Herman, 1970.

doderoi Bondroit, 1912, p. 66 (*Bledius*). Type locality: Cyclades. — Winkler, 1925, p. 346 (subg. *Hesperophilus*). — Porta, 1949, p. 139 (distribution, synonyms). **[basalis group]**

ealanus Cameron, 1947, p. 4 (*Bledius*; subg. *Hesperophilus*). Type locality: Belgian Congo: Eala. **[verres group]**

eckerleini Scheerpeltz, 1972, p. 154 (*Bledius*; subg. *Euceratobledius*). Type locality: Algeria: Massiv de l'Aures, 5 km sudlich Khanga-sidi-Nadji, nordoestlich des Shott Melrir. **[furcatus group]**

elongatus Mannerheim, 1831, p. 459 (*Bledius*). Type locality: Petropoli [= St. Petersburg]. — Erichson, 1840, p. 779 (list). — Seidlitz, 1891, p. 381 (synonym of *fracticornis*?). — Bernhauer and Schubert, 1911, p. 130 (variety of *fracticornis*). — Bondroit, 1912a, p. 65 (characters, notes). — Everts, 1922, p. 140 (synonym of *fracticornis*). — Winkler, 1925, p. 346 (subg. *Blediodes*). — Porta, 1926, p. 46 (synonym of *elongatus*). — Benick, 1943, p. 94 (subg. *Blediodes*; characters). **[semiferrugineus group]**

emarginatus (Say), 1834, p. 461 (*Oxytelus*). Type locality: Indiana. — Erichson, 1840, p. 780 (*Bledius*; list). — LeConte, 1877, pp. 226, 231 (*annularis* group; redescription, key). — Blatchley, 1910, p. 466. — Bernhauer and Schubert, 1911, p. 129 (subg. *Blediodes*). — Frank, 1982, p. 11 (parasites, references). — Herman, 1983a, pp. 14–16 (*emarginatus* group; redescription, key, illustrations, distribution, natural history, synonyms). **[emarginatus group]**

troglodytes Erichson, 1840, p. 774 (*Bledius*). Type locality: Carolina meridionali. — LeConte, 1877, p. 231 (junior synonym of *emarginatus*). — Casey, 1889, p. 56. — Herman, 1983a, p. 14.

ensifer Fauvel, 1898, p. 96 (*Bledius*). Type localities: Algeria: Oran, La Senia; Constantine: Les Lacs. — Fauvel, 1897, p. 260 (nomen nudum; distribution). Fauvel, 1902, p. 70 (distribution, notes). — Winkler, 1925, p. 345 (subg. *Bledius*). — Kocker, 1958, p. 107 (distribution). **[gigantulus group]**

episcopalis Fall, 1910, p. 104 (*Bledius*; *armatus* group). Type locality: California: Bishop. — Notman, 1920, p. 696 (key). — Herman, 1976, pp. 109–111 (*armatus* group; redescription, key, illustration, distribution). — Herman, 1983a, pp. 120, 136 (lectotype, distribution). **[armatus group]**

erraticus Erichson, 1839, p. 582 (*Bledius*). Type locality: [Germany]: Mark. — Heer, 1839, p. 575. — Erichson, 1840, p. 772. — Schiødte, 1866, p. 148 (*Bargus*). — Fauvel, 1872, p. 203 (group 3—*Astycops, Bargus, Tadunus*). — Fauvel, 1873a, p. 45. — Fauvel, 1875, p. XIII (group 3—*Astycops, Bargus, Tadunus*). — Mulsant and Rey, 1878 (subg. *Blediodes*). — Fowler, 1888, p. 372. — Seidlitz, 1891, p. 382 (subg. *Bargus*; key). — Ganglbauer, 1895, p. 622 (subg. *Blediodes*). — Stierlin, 1900, p. 394 (subg. *Bargus*; key). — Reitter, 1909, p. 166 (subg. *Blediodes*; key). — Everts, 1922, p. 142 (notes, distribution). — Winkler, 1925, p. 346 (subg. *Blediodes*). — Porta, 1926, p. 47 (subg. *Blediodes*; key). — Portevin, 1929, p. 412 (key). — Breddin, 1936 (natural history). — Benick, 1937, pp. 73–74 (taxonomic notes). — West, 1942, pp. 143, 635 (distribution, habitat). — Benick, 1943, p. 95 (subg. *Blediodes*; characters). — Tottenham, 1949, p. 411 (subg. *Hesperophilus*). — Tottenham, 1954 (subg. *Hesperophilus*; key, distribution, habitat). — Horion, 1963, p. 281 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 96 (subg. *Hesperophilus*; key). — Andersen, 1968 (natural history). — Scheerpeltz, 1968, p. 32 (subg. *Blediodes*; catalogue). **[annularis group]**

erythraeanus Bernhauer, 1933, p. 54 (*Bledius*). Type locality: Eritrea: Massaua. **[semiferrugineus group]**

erythropeplus Koch, 1938, see: *dissimilis* Erichson, 1840.

erythropterus Kraatz, 1858, see: *fracticornis* (Paykull) 1790.

esposus Blackwelder, 1943, see: *punctatissimus* LeConte, 1877.

exiguus Scheerpeltz, 1933, p. 1114 (*Bledius*). (Replacement name for *minor* Bernhauer.) **[punctatissimus group]**

minor Bernhauer, 1920, p. 6 (*Bledius*). Type locality: Australia: Laura.

eximius Casey, 1889, p. 47 (*Bledius*; *armatus* group). Type locality: California: San Diego. — Fall, 1910, p. 105. — Notman, 1920, p. 696 (key). — Herman, 1976, pp. 136–140 (*armatus* group; redescription, key, illustrations, distribution, natural history, synonyms). — Herman, 1983a, pp. 119, 136 (lectotype, distribution). **[armatus group]**

boddyi Hatch, 1957, p. 102 (*Bledius*; subg. *Hesperophilus*). Type locality: Oregon: Abert Lake. — Herman, 1976, pp. 137, 140 (junior synonym of *eximius*).

gradatus Fall, 1910, p. 104 (*Bledius*). Type locality: California: near Keeler. — Notman, 1920, p. 696 (key). — Herman, 1976, pp. 137, 140 (junior synonym of *eximius*). — Herman, 1983a, p. 120 (lectotype).

extensus Motschulsky, 1860, see: *opacus* (Block), 1799.

externus Lynch, 1884, p. 353 (*Bledius*). Type locality: Argentina: Buenos Aires: Chacabuco. — Bernhauer and Schubert, 1911, p. 129 (subg. *Blediodes*). — Bernhauer, 1927a, p. 233 (key). **[emarginatus group]**

*faecorum** Scudder, 1910, p. 74 (*Bledius*). Type locality: Wyoming: Green River (Fossil; Eocene).

falli Wendeler, 1928, see: *philadelphicus* Fall, 1919.

fasciatus (Say), 1823, p. 156 (*Oxytelus*). Type locality: Engineer Cantonment. — Erichson, 1840, p. 780 (*Bledius*; list). — Herman, 1983a, p. 96 (type locality: Nebraska, north of Omaha, Missouri River) (species unknown; discussion). **[incertae sedis]**

fauveli Bernhauer and Schubert, 1911, see: *Blediotrogus*.

femineus Coiffait, 1979, p. 177 (*Bledius*; subg. *Elbidus*). Type locality: Saudi Arabia: Damman. — Coiffait, 1981a, p. 237 (distribution). **[kochi group]**

femoralis (Gyllenhal), 1827, p. 497 (*Oxytelus*). Type locality: Sweden (Suecia). — Mannerheim, 1831, p. 459 (*Bledius*). — Erichson, 1840, p. 768. — Jacquelin du Val, 1859, p. 76. — Thomson, 1861. — Thomson, 1867. — Fauvel, 1872, p. 211 (group 3—*Astycops, Bargus, Tadunus*). — Fauvel, 1873a, p. 53. — Fauvel, 1875, p. xiii (group 3—*Astycops, Bargus, Tadunus*). — Mulsant and Rey, 1878 (subg. *Blediodes*). — Fowler, 1888, p. 370. — Seidlitz, 1891, p. 381 (key, subg. *Tadunus*). — Ganglbauer, 1895, p. 620 (subg. *Blediodes*). — Stierlin, 1900, p. 394 (subg. *Tadunus*; key). — Reitter, 1909, p. 167 (subg. *Blediodes*; key). — Sharp, 1911c, p. 59 (characters). — Everts, 1922, p. 140 (notes, distribution). — Winkler, 1925, p. 346 (subg. *Blediodes*). — Porta, 1926, p. 46 (subg. *Blediodes*; key). — Portevin, 1929, p. 414 (key). — Blair, 1931, p. 1231 (distribution). — West, 1942, p. 143 (distribution, habitat). — Benick, 1943, p. 94 (subg. *Blediodes*; characters). — Porta, 1949, p. 140 (distribution). — Tottenham, 1949, p. 140 (subg. *Hesperophilus*). — Tottenham, 1954, p. 53 (subg. *Hesperophilus*); key, distribution, habitat). — Horion, 1963, p. 273 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 95 (subg. *Hesperophilus*; key). — Scheerpeltz, 1968, p. 32 (subg. *Blediodes*; catalogue). **[semiferrugineus group]**

sus Aube, 1850, p. 320 (*Bledius*). Type locality: Compiegne. — Jacquelin du Val, 1859, p. 76 (junior synonym of *femoralis*). — Fauvel, 1872, p. 211 (synonym of *femoralis*). — Fauvel, 1873a, p. 52. — Seidlitz, 1891, p. 381 (synonym of *femoralis*).

fennicus Kangas, 1937, p. 189 (*Bledius*; subg. *Blediodes*). Type localities: Finland: Utsjoki, Nuorgam; Petsamo, Ylaeluostari. **[annularis group]**

fenyesi Bernhauer and Schubert, 1911, p. 129 (*Bledius*). (Proposed as replacement name for *lecontei* Bernhauer.) — Notman, 1920, p. 695 (key). — Herman, 1976, pp. 143–144 (*armatus* group; redescription, key, illustrations, distribution, natural history). — Orth et al., 1978 (natural history). — Moore, 1978 (natural history). — Herman, 1983a, p. 136 (distribution). **[armatus group]**

cribricollis LeConte, 1877, p. 221 (*Bledius*; *armatus* group). Type locality: California: San Diego. — Casey, 1889, p. 46. — Fall, 1901, p. 75. — Herman, 1976, p. 143. — Herman, 1983a, p. 118 (lectotype).

lecontei Bernhauer, 1905, p. 14 (*Bledius*). (Proposed as replacement for *cribricollis* LeConte.) — Herman, 1976, p. 143.

fergussoni Joy, 1912, p. 44 (*Bledius*). Type locality: Britain: Knoweside, Aryshire (described as variety of *arenarius*). — Newbery, 1912, p. 64 (synonym of *minor* Rey). — Winkler, 1925, p. 346 (synonym of *minor*; subg. *Hesperophilus*). — Tottenham, 1949, p. 411 (subg. *Cotycops*). — Tottenham, 1954, p. 55 (variety of *arenoides*; key). — Frank, 1982, p. 11 (parasites, references). **[basalis group]**

arenoides Tottenham, 1939, p. 230 (*Bledius*). (Replacement name for *arenarius* Paykull.) — Tottenham, 1949, p. 411 (variety of *fergussoni*). — Tottenham, 1954, p. 55 (subg. *Cotysops*; key, distribution, habitat).

arenarius (Paykull), 1800, p. 382 (*Staphylinus*). Type locality: Westrogothia. — Gyllenhal, 1810, p. 448 (*Oxytelus*). — Gyllenhal, 1827. — Curtis, 1829, p. 29 (*Hesperophilus*). — Stephens, 1829, p. 292 (*Hesperophilus*). — Mannerheim, 1831, p. 460 (*Bledius*). — Stephens, 1834 (*Hesperophilus*). — Gistel, 1834, p. 9 (*Dicarenus*). — Erichson, 1839, p. 585 (*Bledius*). — Erichson, 1840, p. 778. — Laporte, 1840, p. 188. — Thomson, 1861 (*Hesperophilus*). — Schiødte, 1866, p. 150 (*Hesperophilus*). — Thomson, 1867 (*Hesperophilus*). — Fauvel, 1872, p. 197 (group 2—*Hesperophilus*). — Fauvel, 1873a, p. 39. — Fauvel, 1873b, p. 19 (distribution). — Fauvel, 1875, p. xiii (group 2—*Hesperophilus*). — Mulsant and Rey, 1878 (subg. *Hesperophilus*). — Fowler, 1888, p. 367. — Fauvel, 1890, p. 331 (synonymy). — Seidlitz, 1891, p. 382 (key, subg. *Hesperophilus*). — Ganglbauer, 1895, p. 624 (subg. *Hesperophilus*). — Champion, 1898, p. 100 (distribution). — Fauvel, 1902, p. 71 (distribution, notes). — Deville, 1907, p. 90 (subg. *Hesperophilus*; key). — Reitter, 1909, p. 166 (subg. *Blediodes*; key). — Eichelbaum, 1914, p. 223 (anatomy). — Winkler, 1925, p. 346 (subg. *Hesperophilus*). — Krogerus, 1925b (key, natural history, larva). — Krogerus, 1925a (natural history). — Porta, 1926, p. 48 (subg. *Hesperophilus*; key). — Krogerus, 1928 (natural history). — Lengerken, 1929, pp. 34, 38, 78–80 (natural history, distribution). — Portevin, 1929, p. 412 (key). — Blair, 1931, p. 1231 (distribution). — Larsen, 1936 (natural history). — Lengerken, 1939, pp. 131–135 (natural history). — West, 1942, p. 145 (distribution, habitat). — Paulian, 1943, p. 206 (natural history). — Strand, 1946, p. 241 (distribution). — Tottenham, 1949, p. 411 (synonym of *arenoides*). — Larsen, 1953 (natural history). — Kocker, 1958, p. 109 (distribution). — Horion, 1963, p. 290 (subg. *Hesperophilus*; distribution, notes). — Lohse, 1964, p. 98 (subg. *Cotysops*; key). — Potoskaya, 1967, p. 33 (larva). — Lipkow, 1968, p. 210 (natural history). — Szujecki, 1968, p. 193. — Hollander and van Etten, 1974 (natural history).

fuscipennis Koch, 1934, p. 56 (*Bledius*; subg. *Hesperophilus*). Type locality: Libya: Tripolis (subspecies). — Koch, 1938a, p. 141 (notes).

fernandezi Bernhauer, 1939, p. 234 (*Bledius*; subg. *Hesperophilus*). Type locality: Uruguay: Canelones. **[punctatissimus group]**

ferratus LeConte, 1877, p. 220 (*Bledius*; *mandibularis* group). Type locality: California: San Diego. — Fall, 1901, p. 75. — Moore, 1964 (natural history, larva, key, redescription). — Herman, 1972, pp. 189–191 (*mandibularis* group; redescription, key, illustrations, distribution, natural history). — Herman, 1983a, pp. 118, 136 (lectotype, distribution). **[mandibularis group]**

filipes Sharp, 1911, p. 32 (*Bledius*). Type locality: Britain: Norfolk, Overstrand, nr. Cromer. — Bondroit, 1912a, p. 65 (character, notes). — Winkler, 1925, p. 345 (subg. *Blediodes*). — West, 1942, p. 145 (distribution, habitat). — Tottenham, 1949, p. 411 (subg. *Hesperophilus*). — Tottenham, 1954, p. 54 (subg. *Hesperophilus*; key, distribution, habitat). — Horion, 1963, p. 262 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 93 (subg. *Hesperophilus*; key). — Scheerpeltz, 1968, p. 32 (subg. *Blediodes*; catalogue). **[annularis group]**

filipponii Coiffait, 1982, p. 205 (*Bledius*; subg. *Pucerus*). Type locality: Saudi Arabia: Wadi Jizan. **[semiferrugineus group]**

filum Heer, 1839, see: *crassicollis* Boisduval and Lacordaire, 1835.

fiorii Bernhauer, 1902, see: *frater* Kraatz, 1858.

fischeri Bernhauer, 1903, see: *lucidus* Sharp, 1874.

flavipennis LeConte, 1863, p. 52 (*Bledius*). Type locality: California: San Diego. — LeConte, 1877, pp. 221, 222 (*armatus* group; redescription, key). — Casey, 1889, p. 50. — Fall, 1901, p. 75; 1910, p. 105. — Notman, 1920, p. 695 (key). — Blackwelder, 1944, p. 106. — Herman, 1976, pp. 114–121 (*armatus* group; redescription, key, illustrations, distribution, natural history, synonyms). — Herman, 1983a, pp. 118, 136 (lectotype, distribution). **[armatus group]**

agonus Casey, 1889, p. 48 (*Bledius*; *armatus* group). Type locality: Utah. — Notman, 1920, p. 695 (key). — Herman, 1976, pp. 114, 119 (junior synonym of *flavipennis*). — Herman, 1983a, p. 119 (lectotype).

cuspidatus LeConte, 1877, p. 222 (*Bledius*; *ar-*

matus group). Type locality: Dacota. — Casey, 1889, p. 48. — Fall, 1910, p. 106. — Notman, 1920, p. 696 (key). — Herman, 1976, pp. 114, 119 (junior synonym of *flavipennis*). — Herman, 1983a, p. 118 (lectotype).

nelsoni Hatch, 1957, p. 101 (*Bledius*; subg. *Hesperophilus*). Type locality: Washington: Deep Lake. — Herman, 1976, pp. 114, 119 (junior synonym of *flavipennis*).

tenuis Casey, 1889, p. 50 (*Bledius, armatus* group). Type locality: Nevada. — Fall, 1910, p. 106. — Notman, 1920, p. 696 (key). — Herman, 1976, pp. 114, 119 (junior synonym of *flavipennis*). — Herman, 1983a, p. 120 (lectotype).

flexicornis Apfelbeck, 1907, see: *frater* Kraatz, 1858.

fontinalis Bernhauer, 1929, p. 181 (*Bledius*). Type locality: Austria: Hohen Tauern, Salzberg. — Horion, 1963, p. 283 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 96 (subg. *Hesperophilus*; key). — Scheerpeltz, 1968, p. 32 (subg. *Blediodes*; catalogue). — Andersen, 1982, p. 65 (natural history). — Andersen, 1983, p. 429 (distribution, natural history). **[annularis group]**

sparsicollis Koch, 1938a, p. 138 (*Bledius*; subg. *Blediodes*). (Described as subspecies of *bosnicus*.) — Porta, 1949, p. 140 (distribution). — Lohse, 1964, p. 97 (synonym of *fontinalis*).

foraminosus Casey, 1889, p. 53 (*Bledius*; *semiferrugineus* group). Type locality: California: Lake Co. — Fall, 1901, p. 76; 1910, p. 107. — Notman, 1920, p. 697 (key). — Hatch, 1957, p. 99 (subg. *Hesperophilus*; key). — Herman, 1972, pp. 209–217 (*semiferrugineus* group; redescription, key, illustrations, distribution, natural history, synonyms). Herman, 1983a, pp. 119, 137 (lectotype, distribution). **[semiferrugineus group]**

deceptivus Fall, 1901, p. 227 (*Bledius*; *semiferrugineus* group). Type locality: California: Kern Co. — Notman, 1920, p. 697 (key). — Fall, 1910, p. 107. — Herman, 1972, pp. 209, 216 (junior synonym of *foraminosus*). — Herman, 1983a, p. 120 (lectotype).

relictus Fall, 1901, p. 228 (*Bledius*; *semiferrugineus* group). Type locality: California: Pomona. — Fall, 1910, p. 107. — Notman, 1920, p. 697 (key). — Herman, 1972, pp. 209, 216 (junior synonym of *foraminosus*). — Herman, 1983a, p. 120 (lectotype).

forcipatus LeConte, 1863, p. 54 (*Bledius*). Type locality: California: Fort Yuma. — LeConte, 1877, pp. 232, 233 (*cordatus* group; redescription, key). — Casey, 1889, p. 67. — Fall, 1901, p. 75. — Herman, 1972, pp. 131-136 (*Microbledius*; redescription, key, illustrations, distribution, natural history). — Herman, 1983a, pp. 118, 134 (lectotype, distribution). **[forcipatus group]**

formosae Bernhauer, 1922, p. 223 (*Bledius*). Type localities: Formosa: Anping, Suisharyo. — Shibata, 1973, p. 35 (subg. *Pucerus*; distribution). **[furcatus group]**

formosanus Bernhauer, 1940, p. 627 (*Bledius*; subg. *Elbidus*). Type locality: Formosa: Suisharyo. — Shibata, 1973, p. 35 (subg. *Pucerus*; distribution). **[kochi group]**

fortis LeConte, 1877, p. 219 (*Bledius*; *mandibularis* group). Type locality: Texas: Galveston. — Herman, 1972, pp. 180–189 (*mandibularis* group; redescription, key, illustrations, distribution). — Herman, 1983a, pp. 118, 137 (lectotype, distribution). **[mandibularis group]**

fossiventris Fauvel, 1889, p. 252 (*Bledius*). Type locality: New Caledonia: Noumea. — Fauvel, 1903b, p. 261 (distribution, notes). — Bernhauer and Schubert, 1911, p. 129 (as *fossiventrls*). **[punctatissimus group]**

fossor Heer, 1839, p. 211 (*Bledius*). Type locality: Switzerland: Geneva, Arve River. — Fairmaire and Laboulbene, 1854, p. 603 (misidentified as *opacus* var. B). — Jacquelin du Val, 1859, p. 76. — Fauvel, 1872, p. 197 (group 2—*Hesperophilus*). — Fauvel, 1873a, p. 39. — Fauvel, 1873b, p. 19 (distribution). — Fauvel, 1875, p. xiii (group 2—*Hesperophilus*). — Mulsant and Rey, 1878 (subg. *Astycops*). — Fauvel, 1884, p. 78 (synonymy). — Fauvel, 1886, p. 26 (distribution, notes). — Ganglbauer, 1895, p. 626 (subg. *Hesperophilus*). — Fauvel, 1897, p. 262 (distribution, notes). — Champion, 1898, p. 100 (distribution). — Stierlin, 1900, p. 395 (subg. *Astycops*; key). — Fauvel, 1902, p. 71 (distribution, notes). — Reitter, 1909, p. 167 (subg. *Blediodes*; key). — Winkler, 1925, p. 347 (subg. *Hesperophilus*). — Porta, 1926, p. 48 (subg. *Hesperophilus*; key). — Portevin, 1929, p. 414 (key). — Kocker, 1958, p. 109 (distribution). — Smetana, 1959, p. 201 (distribution). — Horion, 1963, p. 294 (subg. *Hesperophilus*; distribution, notes). — Lohse, 1964, p. 99 (subg. *Astycops*; key). — Smetana, 1967, p. 323 (distribution, notes). — Szujecki, 1968, p. 297 (subg. *Astycops*; key). — Scheerpeltz, 1968, p. 33 (subg. *Hesperophilus*; catalogue). — Smetana, 1975, p. 163 (distribution, notes). **[verres group]**

grandicollis Motschulsky, 1857, p. 507 (*Bledius*). Type locality: [Austria]: Styria. — Fauvel, 1875, p. XIII (var.? of *fossor*).

triangulum Baudi, 1848, p. 143 (*Bledius*). Type locality: Piemonte, Italy. — Jacquelin du Val, 1859, p. 76 (junior synonym of *fossor*). — Fauvel, 1872, p. 197 (synonyn of *fossor*). — Fauvel, 1873a, p. 39.

funestus Eppelsheim, 1883, p. 271 (*Bledius*; subg. *Pucerus*). Type locality: Turkey; Merkl. — Fauvel, 1884, p. 78 (junior synonym of *fossor*). — Bernhauer and Schubert, 1911, p. 129 (variety of *fossor*).

fracticornis Paykull, 1790, see: *gallicus* Gravenhorst, 1806.

fragilis Sharp, 1874, p. 90 (*Bledius*). Type locality: Japan: Simbara. — Winkler, 1925, p. 347 (subg. *Pucerus*). — Shibata, 1973, p. 35 (subg. *Pucerus*; distribution). — Shibata, 1976, p. 135 (distribution, catalogue). **[semiferrugineus group]**

fratellus Eppelsheim, 1885, p. 144 (*Bledius*). Type locality: West Africa. — Bernhauer and Schubert, 1911, p. 130 (subg. *Belidus*). **[fratellus group]**

fratellus Fall, 1910, see: *transitus* Fall, 1919.

frater Kraatz, 1858, p. 827 (*Bledius*). Type locality: Nizza, Var River. — Fauvel, 1872, p. 197 (junior synonym of *fossor*). — Fauvel, 1873a, p. 39. — Mulsant and Rey, 1878 (subg. *Astycops*). — Winkler, 1925, p. 347 (subg. *Hesperophilus*). — Lohse, 1964, p. 99 (subg. *Astycops*; key). — Szujecki, 1968, p. 297 (subg. *Astycops*; key). **[verres group]**

flexicornis Apfelbeck, 1907, p. 638 (*Bledius*; subg. *Pucerus*). Type localities: Südostbosnien: Lim River near Uvac on the Turkish border; near Priboj; Drina River near Visegrad. — Bernhauer and Schubert, 1911, p. 129 (junior synonym of *frater* Kraatz). — Winkler, 1925, p. 347 (synonym of *frater*).

fiorii Bernhauer, 1902, p. 60 (*Bledius*). Type locality: Italy: Emilia Prov., Saliceto. — Bernhauer and Schubert, 1911, p. 130 (synonym of *frater*). — Porta, 1926, p. 48 (subg. *Hesperophilus*; key).

fraterculus Cameron, 1936, p. 40 (*Bledius*; subg. *Hesperophilus*). Type locality: Malay Peninsula: Negri Sembilan: Port Dickson. **[verres group]**

frisius Lohse, 1978, see *spectabilis* Kraatz, 1858.

fumatus LeConte, 1863, p. 52 (*Bledius*). Type locality: western states. — LeConte, 1877, p. 224 (*semiferrugineus* group; redescription, key). — Casey, 1889, p. 53, 54. — Blatchley, 1910, p. 464. — Notman, 1920, p. 697 (key). — Hatch, 1957, p. 99 (note). — Herman, 1972, pp. 219–221 (*semiferrugineus* group; redescription, key, illustrations, distribution, natural history). — Herman, 1983a, pp. 118, 135 (lectotype, distribution). **[semiferrugineus group]**

funestus Eppelsheim, 1883, see: *fossor* Heer, 1839.

furcatus (Olivier), 1812, p. 616 (*Oxytelus*). Type locality: France. — Erichson, 1840, p. 761 (*Bledius*; junior synonym of *taurus*). — Jacquelin du Val, 1859, p. 76 (junior synonym of *taurus*). — Fauvel, 1873b, p. 18 (distribution, synonyms). — Ganglbauer, 1895, p. 615 (subg. *Bledius*). — Fauvel, 1897, p. 259 (distribution, notes). — Fauvel, 1902, p. 68 (distribution, notes). — Deville, 1907, p. 88 (subg. *Bledius*; key). — Reitter, 1909, p. 165 (subg. *Bledius*; key). — Bondroit, 1913, p. 299 (notes). — Winkler, 1925, p. 345 (subg. *Bledius*). — Porta, 1926, p. 45 (subg. *Bledius*; key). — Znojko, 1929, p. 204 (*Euceratobledius*). — Lengerken, 1929, p. 73 (natural history, distribution). — Paulian, 1941, p. 172 (larva). — West, 1942, p. 141 (distribution, habitat). — Tottenham, 1949, p. 410 (subg. *Euceratobledius*). — Tottenham, 1954, p. 50 (subg. *Euceratobledius*; key, distribution, habitat). — Kocker, 1958, p. 106 (distribution). — Horion, 1963, p. 251 (distribution, notes, natural history). — Lohse, 1964, p. 90 (subg. *Euceratobledius*; key). — Potoskaya, 1967, p. 32 (larva). — Lipkow, 1968, p. 210 (natural history). — Scheerpeltz, 1968, p. 31 (subg. *Euceratobledius*; catalogue). — Bordoni, 1973, p. 664, distribution). **[furcatus group]**

taurus (Germar), 1825, fasc. 12, nr. 2 (*Oxytelus*). Type localities: Dalmatia; Illyria. — Stephen, 1829, p. 292 (*Bledius*; junior synonym of *skrimshirii*). — Mannerheim, 1831, p. 458 (*Bledius*; valid species). — Stephens, 1834 (*Bledius*; valid species). — Runde, 1835, p. 18. — Erichson, 1840, p. 760. — Jacquelin du Val, 1859, p. 76. — Fauvel, 1872, p. 190 (group 1—*Bledius*). — Fauvel, 1873a, p. 32. — Fauvel, 1875, p. XII (group 1—*Bledius*). — Mulsant and Rey, 1878 (subg. *Bledius*). — Fauvel, 1886, p. 24 (distribution, notes). — Fowler, 1888, p. 365. — Seidlitz, 1891, p. 380 (key, subg. *Bledius*). — Ganglbauer, 1895, p. 615 (synonym of *furcatus*). — Fauvel, 1897, p. 259 (synonym of *furcatus*). — Champion, 1898, p. 100 (distribution). — Stierlin, 1900, p. 392 (subg. *Bledius*; key). — Fauvel, 1902, p. 68 (synonym of *furcatus*). — Portevin, 1929, p. 410 (key). — Larsen, 1936 (natural history). — Larsen, 1952 (natural history). — Larsen, 1953 (natural history).

haedus Baudi, 1857, p. 110 (*Bledius*). Type locality: Cyprus. — Fauvel, 1875, p. XII (group 1—*Bledius*). — Fauvel, 1886, p. 24 (distribution, notes). — Fauvel, 1897, p. 259 (distribution, notes). — Fauvel, 1902, p. 68 (synonym of *furcatus*). — Koch, 1934, p. 59 (subg. *Euceratobledius*; key).

skrimshirii Curtis, 1826, pl. 143 (*Bledius*). Type locality: Britain: Holkham. — Stephens, 1829, p. 292. — Stephens, 1834 (junior synonym of *taurus*). — Erichson, 1840, p. 761 (junior synonym of *taurus*). — Jacquelin du Val, 1859, p. 76 (synonym of *taurus*). — Ganglbauer, 1895, p. 615 (synonym of *furcatus*). — Fauvel, 1895, p. 118 (synonymy). — Fauvel, 1897, p. 259 (synonym of *furcatus*). — Fauvel, 1902, p. 68 (synonym of *furcatus*). — Koch, 1934, p. 59 (subg. *Euceratobledius*; key). — Tottenham, 1954, p. 50 (key, distribution, habitat).

ruddii Stephens, 1832, p. 308 (*Bledius*). Type locality: Britain: Yorkshire, Coatham Marshes. — Stephens, 1834. — Erichson, 1840, p. 761 (junior synonym of *taurus*). — Jacquelin du Val, 1859, p. 76 (synonym of *taurus*). — Fauvel, 1872, p. 191 (junior synonym of *bicornis*). — Fauvel, 1873b, p. 18 (synonym of *taurus*). — Fauvel, 1873a, p. 33. — Fowler, 1888, p. 366 (synonym of *bicornis*). — Ganglbauer, 1895, p. 615 (synonym of *furcatus*). — Fauvel, 1895, p. 118 (junior synonym of *skrimshirii*).

stephensii Westwood, 1827, p. 61 (*Bledius*). Type locality: Britain: Norfolk. — Stephens, 1829, p. 292 (junior synonym of *skrimshirii*). — Jacquelin du Val, 1859, p. 76 (synonym of *taurus*). — Ganglbauer, 1895, p. 615 (synonym of *furcatus*).

furtivus Casey, 1889, see: *strenuus* Casey, 1889.

fuscicornis Cameron, 1930, p. 280 (*Bledius*). Type localities: India: Almora: Dhauli Ganga; Kumaon: Tanakpur. — Scheerpeltz, 1933, p. 1116 (subg. *Hesperophilus*). — Paulian, 1941, p. 173 (larva). **[bispinus group]**

fuscipennis Koch, 1934, see: *arenarius* (Paykull), 1880.

fuscipes Rye, 1865, p. 154 (*Bledius*). Type locality: Britain: Firth of Forth near Aberlady. — Fauvel, 1872, p. 201 (junior synonym of *pallipes*). — Fauvel, 1873a, p. 43 (synonym of *pallipes*). — Fauvel, 1873b, p. 20 (synonym of *pallipes*). — Fowler, 1888, p. 368. — Seidlitz, 1891, p. 382 (synonym of *subterraneus*). — Ganglbauer, 1895, p. 618 (synonym of *pallipes*). — Bernhauer and Schubert, 1911, p. 134 (synonym of *pallipes*). — Sharp, 1911, p. 33 (valid species). — Bondroit, 1912a, p. 64 (characters, notes). — Everts, 1922, pp. 142, 143 (notes, distribution, key). — Winkler, 1925, p. 345 (subg. *Blediodes*; synonym of *rastellus* Thomson). — Krogerus, 1925b (key, natural history, larva). — Krogerus, 1925a (natural history). — Krogerus, 1928 (natural history). — Blair, 1931, p. 1231 (distribution). — West, 1942, p. 145 (distribution, habitat). — Tottenham, 1949, p. 411 (subg. *Hesperophilus*). — Tottenham, 1954, p. 54 (subg. *Hesperophilus*; key, distribution, habitat). — Horion, 1963, p. 264 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 93 (subg. *Hesperophilus*; key). — Lipkow, 1968, p. 210 (natural history). — Scheerpeltz, 1968, p. 33 (synonym of *rastellus*). — Andersen, 1982, p. 65 (natural history). — Andersen, 1983, p. 429 (distribution, natural history). **[annularis group]**

rastellus (Schiødte), 1866, p. 149 (*Bargus*). — Thomson, 1867, p. 291. (*Bledius*; this reference is most often cited as the original description of *rastellus* but Thomson refers to Schiødte as the author.) — Kraatz, 1868, p. 292 (characters). — Fauvel, 1869 (synonym of *pallipes*). — Taylor, 1870 (natural history). — Fauvel, 1872, p. 201 (synonym of *pallipes*). — Fauvel, 1873a, p. 43 (synonym of *pallipes*). — Fauvel, 1873b, p. 20 (synonym of *pallipes*). — Fowler, 1888, p. 367 (junior synonym of *pallipes*). — Seidlitz, 1891, p. 382 (synonym of *subterraneus*). — Ganglbauer, 1895, p. 624 (synonym of *subterraneus*). — Bernhauer and Schubert, 1911, p. 135 (as junior synonym of *subterraneus* Erichson). — Bernhauer and Schubert, 1911, p. 134 (cited with Thompson, 1867 as author and as a junior synonym of *pallipes* Gravenhorst). — Sharp, 1911, p. 33 (synonym of *fuscipes*). — Winkler, 1925, p. 345 (subg. *Blediodes*; valid species with Thomson as author and *fuscipes* as junior synonym). — Benick, 1936 (key, notes). — Larsen, 1936 (natural history). — Kangas, 1938, p. 126 (valid species). — Lengerken, 1939, pp. 131–135 (natural history). — Hansen, 1939, p. 584 (key). — West, 1942, p. 142 (distribution, habitat). — Benick, 1943, p. 94 (subg. *Blediodes*; characters). — Tottenham, 1949, p. 411 (synonym of *fuscipes* with Thomson as author). — Larsen, 1953 (natural history). — Lohse, 1964, p. 93 (synonym of *fuscipes* with Thomson as author). — Scheerpeltz, 1968, p. 33 (subg. *Blediodes*; Thomson as author; catalogue). — Pope, 1977, p. 24 (synonym of *fuscipes*; Thomson as author). — Scheerpeltz, 1933, p. 1121 (cited with Thompson, 1867 as author and as a valid species with *fuscipes* Rye as a junior synonym). — Scheerpeltz, 1968, p. 32 (cited as in Scheerpeltz, 1933, p. 1121). — Pope, 1977, p. 24 (cited as junior synonym of *fuscipes* Rye but with Thompson, 1867, as author).

gabonensis Fauvel, 1900, p. 68 (*Bledius*). Type localities: Congo: Kinchassa: Boma; Loango. **[verres group]**

galeatus Wollaston, 1864, see: *unicornis* (Germar), 1825.

gallicus (Gravenhorst), 1806, p. 198 (*Oxytelus*). Type locality: France. (Originally described as form of *pallipes*.) — Erichson, 1840, p. 767 (*Bledius*; junior synonym of *fracticornis*). — Jacquelin du Val, 1859, p. 76 (junior synonym of *fracticornis*). — Tottenham, 1939, pp. 229–230 (elevated to replace the preoccupied *fracticornis*). — Tottenham, 1949, p. 410 (subg. *Hesperophilus*). — Tottenham, 1954, p. 53 (subg. *Hesperophilus*; key, distribution, habitat). — Frank, 1982, p. 11 (references, parasites). **[semiferrugineus group]**

fracticornis (Paykull), 1790, p. 135 (*Staphylinus*). Type locality: Vestrogothia. — Paykull, 1800 (redescription). — Gyllenhal, 1810, p. 446 (*Oxytelus*). — Gyllenhal, 1810. — Curtis, 1829, p. 29 (*Hesperophilus*). — Stephens, 1829, p. 292 (*Hesperophilus*). — Mannerheim, 1831, p. 459 (*Bledius*). — Stephens, 1834 (*Hesperophilus*). — Gistel, 1834, p. 9 (*Dicarenus*). — Runde, 1835, p. 18 (*Bledius*). — Boisduval and Lacordaire, 1835, p. 458 (misidentified as *pallipes*). — Erichson, 1839, p. 579. — Heer, 1839, p. 209. — Erichson, 1840, p. 767. — Thomson, 1861. — Schiødte, 1864, p. 123, tab. XII (larva). — Schiødte, 1866, p. 147 (*Tadunus*). — Thomson, 1867 (*Bledius*). — Fauvel, 1872, p. 210 (group 3—*Astycops, Bargus, Tadunus*). — Fauvel, 1873b, p. 22 (distribution). — Fauvel, 1873a, p. 52. — Fauvel, 1875, p. xiii (group 3—*Astycops, Bargus, Tadunus*). — Mulsant and Rey, 1878 (subg. *Blediodes*). — Fowler, 1888, p. 369. — Kraatz, 1889, p. 220 (synonymy). — Fauvel, 1890, p. 331 (synonymy). — Seidlitz, 1891, p. 381 (subg. *Tadunus*; key). — Ganglbauer, 1895, p. 620 (subg. *Blediodes*). — Stierlin, 1900, p. 383 (subg. *Tadunus*; key). — Fauvel, 1902, p. 72 (distribution, notes). — Reitter, 1909, p. 167 (subg. *Blediodes*; key). — Sharp, 1911c, p. 57 (discussion, natural history, type species). — Bondroit, 1913, p. 297 (notes). — Notman, 1920, p. 189 (distribution). — Everts, 1922, p. 140 (notes, distribution). — Winkler, 1925, p. 346 (subg. *Blediodes*). — Krogerus, 1925b (key, natural history). — Porta, 1926, p. 26 (subg. *Blediodes*; key). — Portevin, 1929, p. 414 (key). — Blair, 1931, p. 1231 (distribution). — Larsen, 1936 (natural history). — Breddin, 1936 (natural history). — Donisthorpe, 1937, p. 122 (natural history). — West, 1942, p. 143 (distribution, habitat). — Benick, 1943, p. 94 (subg. *Blediodes*; characters). — Strand, 1946, p. 240 (distribution). — Tottenham, 1949, p. 410 (synonym of *gallicus*). — Kocker, 1958, p. 108 (distribution). — Hicks, 1959, p. 112 (natural history). — Horion, 1963, p. 273 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 95 (subg. *Hesperophilus*; key). — Scheerpeltz, 1968, p. 32 (subg. *Blediodes*; catalogue). — Smetana, 1975, p. 162 (distribution, notes).

alpestris Heer, 1839, p. 210 (*Bledius*). Type locality: Switzerland: Bevers, Inn River. — Fauvel, 1872, p. 210 (junior synonym of *fracticornis*). — Fauvel, 1873a, p. 52.

erythropterus Kraatz, 1858, p. 831 (*Bledius*). Type locality: Bavarian Alps. — Fauvel, 1875, p. xiii (group 3—*Astycops, Bargus, Tadunus*). — Kraatz, 1889, p. 220 (junior synonym of *fracticornis*). — Fauvel, 1889, p. 192 (synonym of *fracticornis*).

laetior Mulsant and Rey, 1878, p. 593 (*Bledius*; subg. *Blediodes*). (Described in paragraph of notes under description of *fracticornis*.) — Fauvel, 1890, p. 331 (junior synonym of *fracticornis*). — Sharp, 1911c, p. 58 (valid species). — Everts, 1922, p. 140 (notes, distribution). — Winkler, 1925, p. 346 (subg. *Blediodes*). — Tottenham, 1954, p. 53 (key).

sharpi Fowler and Donisthorpe, 1913, p. 74 (*Bledius*). (Described as variety.) Type locality: not cited. — Tottenham, 1954, p. 53 (key).

ganglbaueri Bernhauer, 1908, p. 103 (*Bledius*; subg. *Pucerus*). Type locality: German East Africa: Dar es Salam. — Scheerpeltz, 1974a, p. 9 (distribution). **[semiferrugineus group]**

gebieni Bernhauer, 1942, p. 6 (*Bledius*). Type locality: Costa Rica, Reventazon, Ebene Limon, Hamburgfarm. **[emarginatus group]**

gemellus Eppelsheim, 1885, p. 140 (*Bledius*). Type locality: Cape Verde. — Bernhauer and Schubert, 1911, p. 130 (subg. *Bledius*). **[gigantulus group]**

gentilis Casey, 1889, p. 59 (*Bledius*; *annularis* group). Type locality: California: Sonoma County: Santa Rosa. — Fall, 1901, p. 76. — Fall, 1910, p. 111. — Herman, 1983a, pp. 49–51, 119 (*annularis* group; redescription, key, illustrations, distribution, natural history, synonyms, lectotype). **[annularis group]**

adustus Casey, 1889, p. 62 (*Bledius*; *annularis* group). Type locality: Colorado: Garland. — Fall, 1910, p. 113. — Herman, 1983a, pp. 49, 50, 119 (junior synonym of *gentilis*, lectotype).

transitus Fall, 1919, p. 26 (*Bledius*). (Replacement name for *fratellus* Fall.) — Herman, 1983a, pp. 49, 50 (junior synonym of *gentilis*).

fratellus Fall, 1910, p. 112 (*Bledius*). Type locality: California: Pasadena. — Herman, 1983a, pp. 49, 50, 120 (junior synonym, lectotype).

germanicus Gravenhorst, 1806, see: *pallipes* (Gravenhorst), 1806.

germanicus Wagner, 1935, see: *limicola* Tottenham, 1940.

ghesquierei Bernhauer, 1932, see: *cariniceps* Bernhauer, 1932.

gigantulus Bernhauer, 1922, p. 224 (*Bledius*). Type localities: Formosa: Anping, Taihorin. — Shibata, 1973, p. 33 (subg. *Bledius*; distribution). — Shibata, 1976, p. 135 (distribution, catalogue). **[gigantulus group]**

giraffa Costa, 1875, see: *capra* Fauvel, 1875.

*glaciatus** Scudder, 1890, p. 505 (*Bledius*). Type locality: Ontario: Scarboro. (Fossil; Pleistocene).

gladiator Normand, 1934, see: *unicornis* (Germar), 1825.

glasunovi Luze, 1904, p. 87 (*Bledius*). Type localities: Jagnob: Ansob; Iskander-Kul: Iskander-darja. — Winkler, 1925, p. 346 (subg. *Blediodes*). — Benick, 1943, p. 94 (subg. *Blediodes*; characters). — Scheerpeltz, 1961c, p. 250 (distribution, notes). — Smetana, 1975, p. 162 (distribution, notes). **[semiferrugineus group]**

gomezi Bernhauer, 1933, p. 330 (*Bledius*). Type locality: Argentina: La Rioja. **[emarginatus group]**

gracilicornis Kraatz, 1859, p. 169 (*Bledius*). Type locality: Ceylon. — Bernhauer and Schubert, 1911, p. 130 (subg. *Pucerus*). — Cameron, 1930, pp. 275–276 (subg. *Pucerus*; key, redescription). — Scheerpeltz, 1961b, p. 134 (distribution, notes). **[verres group]**

gracilicornis Poppius, 1907, see: *rossicus* Bernhauer and Schubert, 1911.

gracilis Casey, 1889, p. 60 (*Bledius*; *annularis* group). Type locality: California: Mendocino Co.: Anderson Valley, Soda Springs. — Fall, 1910, pp. 76, 111. — Herman, 1983a, pp. 59–60, 119 (*annularis* group; redescription, key, illustrations, distribution, natural history, lectotype). **[annularis group]**

gradatus Fall, 1910, see: *eximius* Casey, 1889.

gradensis Bernhauer, 1929, p. 183 (*Bledius*; subg. *Hesperophilus*). Type localities: Italy: Grado; Monfalcone. Rab Island: Arbe. — Porta, 1934, p. 116 (subg. *Hesperophilus*; distribution). — Porta, 1949, p. 139 (synonym of *devillei*). **[basalis group]**

graellsi Fauvel, 1865, p. 309 (*Bledius*). Type localities: France: Marseille. Italy: Piemonte. Spain: Aranjuez. Algeria: Bone. — Fairmaire and Laboulbene, 1854, p. 600 (misapplication of *tricornis* Herbst *var. B*). — Fauvel, 1872, p. 194 (group 1—*Bledius*). — Fauvel, 1873a, p. 36. — Fauvel, 1873b, p. 19 (distribution). — Fauvel, 1875, p. xii (group 1—*Bledius*). — Fauvel, 1886, p. 25 (distribution, notes). — Ganglbauer, 1895, p. 616 (subg. *Bledius*). — Fauvel, 1897, p. 261 (distribution, notes). — Fauvel, 1902, p. 70 (distribution, notes). — Winkler, 1925, p. 345 (subg. *Bledius*). — Porta, 1926, p. 45 (subg. *Bledius*; key). — Portevin, 1929, p. 410 (key). — Kocker, 1958, p. 106 (distribution). — Bordoni, 1973, p. 664 (distribution). — Lohse, 1978, pp. 13, 14 (characters). **[gigantulus group]**

antilope Peyron, 1858, p. 431 (*Bledius*). Type locality: Caramanie. — Fauvel, 1872, p. 194 (junior synonym of *gracilis*). — Fauvel, 1873a, p. 36.

hedjazensis Coiffait, 1981, p. 241 (*Bledius*; subg. *Bledius*). Type locality: Saudi Arabia: Nord Hedjaz, Khaybar. Subspecies.

grandicollis Motschulsky, 1857, see: *fossor* Heer, 1839.

grandipennis Bernhauer, 1938, see: *sellatus* Sharp, 1889.

gravidus Casey, 1889, p. 54 (*Bledius*; *semiferrugineus* group). Type locality: New Mexico: Albuquerque. — Fall, 1910, pp. 107, 108. — Notman, 1920, p. 697 (key). — Herman, 1972, pp. 217–219 (*semiferrugineus* group; redescription, key, illustrations, distribution, natural history, synonyms). — Herman, 1983a, pp. 119, 137 (lectotype, distribution). **[semiferrugineus group]**

missionensis Hatch, 1957, p. 99 (*Bledius*; subg. *Hesperophilus*). Type locality: British Columbia: Mission Flats, near Kamloops. — Herman, 1972, pp. 217, 218 (junior synonym of *gravidus*).

gregarius Sharp, 1887, p. 685 (*Bledius*). Type locality: Guatemala, Duenas. **[emarginatus group]**

gularis LeConte, 1877, see: *pallipennis* (Say), 1823.

gulielmi Sharp, 1913, see: *defensus* Fauvel, 1872.

gyllenhalii Laporte, 1840, p. 188 (*Bledius*). Type locality: Sweden. (Name proposed for *arenarius* var. *b* Gyllenhal.) **[basalis group]**

arenarius var. *b* (Gyllenhal), 1810, p. 449 (*Oxytelus*).

gyotokui Nakane, 1963, p. 21 (*Bledius*). Type locality: Japan: Kyushu, Fukuoka, Yoshii. — Nakane et al., 1965, p. 84, pl. 42, fig. 25. — Shibata, 1976, p. 136 (distribution, catalogue). **[gigantulus group]**

haarlovi Scheerpeltz, 1960, p. 42 (*Bledius*; subg. *Pucerus*). Type locality: Afghanistan: Panjao. **[semiferrugineus group]**

habrus Herman, 1983, p. 86 (*Bledius*; *annularis* group). Type locality: British Columbia: 22 mi. W Chetwynd, Pine River. **[annularis group]**

haedus Baudi, 1857, see: *furcatus* Olivier, 1812.

haemopterus (Stephens), 1832, see: *opacus* (Block), 1799.

hamifer Fauvel, 1878, p. 499 (*Bledius*). Type locality: Australia occidentale: Nichol Bay. **[hamifer group]**

hasticeps Bernhauer, 1937, p. 583 (*Bledius*). Type locality: German East Africa: Daressalam. **[lamelliceps group]**

hauseri Eppelsheim, 1894, p. 40 (*Bledius*). Type locality: Buchara. — Winkler, 1925, p. 345 (subg. *Bledius*). **[kochi group]**

hedjazensis Coiffait, 1981, see: *graellsi* Fauvel, 1865.

helferi Fauvel, 1904, p. 112 (*Bledius*). Type locality: Birmanie. — Cameron, 1930, pp. 278, 284 (key, redescription). — Scheerpeltz, 1933, p. 1117 (subg. *Hesperophilus*). — Shibata, 1973, p. 34 (subg. *Hesperophilus*; distribution). **[infans group]**

heterocerus Eppelsheim, 1889, p. 180 (*Bledius*). Type locality: Croatia. — Ganglbauer, 1895, p. 622 (subg. *Blediodes*). — Winkler, 1925, p. 346 (subg. *Blediodes*). — Porta, 1926, p. 47 (subg. *Blediodes*; key). — Benick, 1943, p. 95 (subg. *Blediodes*; characters). — Lohse, 1964, p. 97 (subg. *Hesperophilus*; key). — Scheerpeltz, 1968, p. 32 (subg. *Blediodes*; catalogue). **[semiferrugineus group]**

hindustanus Cameron, 1942, p. 108 (*Bledius*; subg. *Hesperophilus*). Type locality: India: Ferrapore. **[kosempoensis group]**

hinnulus Erichson, 1840, p. 762 (*Bledius*). Type localities: Russia meridionali; Grusinia. — Schiødte, 1864, p. 122, tab. XII (larva). — Fauvel, 1875, p. XII (group 1—*Bledius*). — Mulsant and Rey, 1878 (subg. *Elbidus*). — Sharp, 1911, p. 35 (discussion). — Everts, 1922, p. 139 (synonym of *diota*). — Winkler, 1925, p. 345 (subg. *Elbidus*). — Scheerpeltz, 1960c, p. 2 (distribution). — Scheerpeltz, 1961c, p. 250 (distribution, notes). — Smetana, 1975, p. 160 (distribution, notes). **[kochi group]**

hispidulus Fairmaire and Laboulbene, 1856, see: *morio* Heer, 1839.

hispidus Parfitt, 1857, see: *unicornis* (Germar), 1825.

hlisnikowskii Roubal, 1939, p. 136 (*Bledius*). Type locality: Russia: Kiev. **[semiferrugineus group]**

honestus Casey, 1889, p. 66 (*Bledius*; *annularis* group). Type locality: New York: Catskill Mountains, Shokan. — Herman, 1983a, pp. 93–95, 119 (*annularis* complex; discussion, lectotype). **[annularis group]**

hoplites Fauvel, 1886, p. 146 (*Bledius*). Type localities: Philippines: Manila. Siam: Bangkok. Annam: Hue. — Cameron, 1930, pp. 272, 274 (subg. *Bledius*; key, redescription). — Scheerpeltz, 1961b, p. 134 (distribution, notes). **[gigantulus group]**

husseini Quedenfeldt, 1884; p. 377 (*Bledius*). Type locality: Morocco: Urica, Issil River. — Fauvel, 1886, p. 26 (distribution, notes). — Fauvel, 1897, p. 262 (distribution, notes). — Fauvel, 1902, p. 71 (distribution, notes). — Bernhauer and Schubert, 1911, p. 131 (subg. *Hesperophilus*). — Winkler, 1925, p. 346 (subg. *Hesperophilus*). — Koch, 1934, pp. 55, 60 (subg. *Pucerus*; key, notes). — Koch, 1937 (subg. *Pucerus*). — Koch, 1938a, p. 146 (notes). — Kocker, 1958, p. 109 (distribution). **[verres group]**

scutellaris Cameron, 1928, p. 19 (*Bledius*). Type locality: Belgian Congo: Mushie. (Described as variety of *husseini*.)

ignavus Casey, 1889, see: *basalis* LeConte, 1863.

ignobilis Eppelsheim, 1880, p. 508 (*Bledius*). Type locality: Caucasus: Kura near Michailowo. — Winkler, 1925, p. 346 (subg. *Blediodes*). **[annularis group]**

ignotus Saiz, 1973, p. 232 (*Bledius*; subg. *Hesperophilus*). Type locality: Chile: Valparaiso: Caleu-La Dormida. **[emarginatus group]**

immarginatus Koch, 1934, p. 51 (*Bledius*; subg. *Elbidus*). Type locality: Egypt: Mersa Halaib. **[kochi group]**

immaturus Eppelsheim, 1892, p. 345 (*Bledius*). Type locality: Djizak. — Winkler, 1925, p. 345 (subg. *Bledius*). — Coiffait, 1970, p. 144 (distribution). **[immaturus group]**

incertus Cameron, 1952, p. 823 (*Bledius*; subg. *Hesperophilus*). Type locality: Mauritania: Terjit. **[verres group]**

indicus Cameron, 1930, p. 282 (*Bledius*). Type locality: India: Kumaon, Haldwani. — Scheerpeltz, 1933, p. 1117 (subg. *Hesperophilus*). **[tibialis group]**

ineptus Casey, 1889, p. 48 (*Bledius*; *armatus* group). Type locality: New Mexico: Albuquerque. — Notman, 1920, p. 695 (key). — Herman, 1976, pp. 123–126 (*armatus* group; redescription, key, illustrations, distribution, natural history). Herman, 1983a, pp. 119, 137 (lectotype, distribution). **[armatus group]**

infans Blackburn, 1891, see: *victoriae* Bernhauer and Schubert, 1912.

infans Rottenberg, 1870, p. 36 (*Bledius*). Type locality: Sicily. — Fauvel, 1875, p. xiii (group 2—*Hesperophilus*). — Fauvel, 1897, p. 261 (distribution, notes). — Fauvel, 1902, p. 70 (distribution, notes). — Bernhauer and Schubert, 1911, p. 131 (subg. *Belidus*). — Winkler,

1925, p. 347 (subg. *Belidus*). — Porta, 1926, p. 48 (subg. *Hesperophilus*; key).
[infans group]

reductus Koch, 1937, p. 266 (*Bledius*; subg. *Belidus*). Type locality: Libya: Zuara. (Described as subspecies of *infans*.)

infantilis Sharp, 1887, p. 686 (*Bledius*). Type locality: Mexico: Presidio.
[emarginatus group]

injucundus Blackburn, 1888, p. 14 (*Bledius*). Type locality: Australia: Port Lincoln.
[punctatissimus group]

inornatus Sharp, 1887, p. 685 (*Bledius*). Type localities: Costa Rica: Irazu; Panama: Bugaba.
[semiferrugineus group]

insignicornis Blackburn, 1891, p. 75 (*Bledius*). Type locality: Australia: Victoria: Ovens River.
[verres group]

irmleri Coiffait, 1980, see: *vitulus* Erichson, 1840.

irroratus Fauvel, 1864, see: *maculipennis* (Solier), 1849.

jacobinus LeConte, 1877, p. 220 (*Bledius*; *mandibularis* group). Type locality: California: San Diego. — Sharp, 1887, p. 685. — Fall, 1901, p. 75. — Moore, 1964, p. 275. — Herman, 1972, pp. 200–204 (*mandibularis* group; redescription, key, illustrations, natural history, synonyms). — Frank, 1982, p. 11 (parasites, references). — Herman, 1983a, pp. 118, 138 (lectotype, distribution).
[mandibularis group]

actus Herman, 1970, p. 376 (*Bledius*). (Replacement name for *lecontei* Sharp.) — Herman, 1972, pp. 200, 203 (junior synonym of *jacobinus*).

lecontei Sharp, 1887, p. 685 (*Bledius*). Type locality: Mexico: Tres Marias Islands. — Casey, 1889, p. 71. — Blackwelder, 1944, p. 106 (checklist). — Herman, 1970, p. 376 (preoccupied). — Herman, 1972, pp. 200, 203 (junior synonym of *actus* and *jacobinus*).

jacobsoni Cameron, 1928, p. 106 (*Bledius*). Type locality: Sumatra: Fort de Kock.
[verres group]

jadarensis Helliesen, 1913, p. 4 (*Bledius*). Type locality: Norway. — Koch, 1938a, p. 131 (notes). **[annularis group]**

jamaicensis Blackwelder, 1943, p. 117 (*Bledius*). Type locality: Jamaica: between Spanish Town and Kingston. **[emarginatus group]**

januvianus Wollaston, 1864, see: *vitulus* Erichson, 1840.

japonicus Bernhauer, 1936, p. 305 (*Bledius*). Type locality: Japan: Takakijama. — Shibata, 1976, p. 136 (distribution, catalogue).
[annularis group]

javanus Bernhauer, 1915, see: *quadricornis* Bernhauer, 1915.

johnstoni Cameron, 1950, p. 213 (*Bledius*; subg. *Blediodes*). Type locality: Sudan: Khor Arbaat Delta. **[semiferrugineus group]**

jucundus Herman, 1983, p. 89 (*Bledius*; *annularis* group). Type locality: Utah: Summit Co.: 8.4 mi. ESE Kamas, Beaver Creek.
[annularis group]

jutlandensis Herman, **New Name**, see: *bicornis* (Germar), 1822.

juvencus Erichson, 1840, see: *unicornis* (Germar), 1825.

karachiensis (Abdullah and Qadri), 1968, p. 395 (*Neobledius*). Type locality: Pakistan: Karachi. **New combination.** **[kochi group]**

kincaidi Hatch, 1957, see: *parvicollis* Casey, 1889.

klapperichi Coiffait, 1981, p. 22 (*Bledius*; subg. *Pucerus*). Type locality: Iran: Bander Palevi, Caspian Sea. **[verres group]**

koenigsbaueri Scheerpeltz, 1966, p. 63 (*Bledius*; subg. *Blediodes*). Type locality: South West Africa: Okahandja, Otjkondo.
[emarginatus group]

kochi Cameron, 1951, p. 280 (*Bledius*; sub. *Elbidus*). Type locality: Egypt: Siwa.
[kochi group]

kosempoensis Bernhauer, 1922, p. 225 (*Bledius*). Type locality: Formosa: Kosempo. — Shibata, 1973, p. 35 (subg. *Pucerus*; distribution).
[kosempoensis group]

krogeri Scheerpeltz, 1933, see: *opacus* (Block), 1799.

kutsae Kangas, 1937, p. 185 (*Bledius*; subg. *Blediodes*). Type locality: Finland: Salla, Kutsajoki. — Benick, 1943, p. 94 (subg. *Blediodes*; characters). **[annularis group]**

lacustris Bernhauer, 1931, p. 568 (*Bledius*; subg. *Bledius*). Type locality: Abyssinia: Lake Hora Abjata. **[kochi group]**

laetior Mulsant and Rey, 1878, see: *fracticornis* Paykull, 1790.

lamelliceps Bernhauer, 1934, p. 493 (*Bledius*; subg. *Bledius*). Type locality: South Africa: Cape Town: Milnerton. **[lamelliceps group]**

languidus Casey, 1889, see: *annularis* LeConte, 1863.

larseni Hansen, 1940, see: *annae* Sharp, 1911.

lateralis Erichson, 1840, p. 766 (*Bledius*). Type locality: Venezuela: Puerto Cabello.
[semiferrugineus group]

lateripennis Bernhauer, 1934, p. 494 (*Bledius*; subg. *Hesperophilus*). Type locality: South Africa: Pondoland: Port St. Johns. **[verres group]**

laticollis LeConte, 1877, p. 227 (*Bledius*; *annularis* group). Type locality: California: San Diego. — Casey, 1889, pp. 57, 58. — Hatch, 1957, p. 101 (subg. *Hesperophilus*; key). — Herman, 1983a, pp. 67–71, 119 (*arenarius* group; redescription, key, illustrations, natural history, lectotype). **[annularis group]**

latior Bernhauer, 1943, p. 280 (*Bledius*; subg. *Pucerus*). Type locality: Congo: Boma. **[verres group]**

lativentris Jansson, 1928, p. 214 (*Bledius*). Type locality: Lappland: Abisko. — Benick, 1943, p. 94 (subg. *Blediodes*; characters). — Strand, 1946, p. 240 (distribution). **[annularis group]**

latus Bernhauer, 1928, p. 9 (*Bledius*; subg. *Hesperophilus*). Type locality: Transcaspian, Tschardshui. **[verres group]**

leai Scheerpeltz, 1933, p. 1117 (*Bledius*). (Replacement name for *parvulus* Lea.) **[emarginatus group]**

parvulus Lea, 1910, p. 124 (*Bledius*). Type locality: W. Australia: Beverley, Pinjarrah.

lecontei Duvivier, 1883, see: *phytosinus* LeConte, 1877.

lecontei Bernhauer, 1905, see: *fenyesi* Bernhauer and Schubert, 1911.

lecontei Sharp, 1887, see: *actus* Herman, 1970.

lectus Casey, 1889, see: *opacifrons* LeConte, 1877.

lepineyi Scheerpeltz, 1934, p. 94 (*Bledius*; subg. *Pucerus*). Type locality: Sudan: Sokolo, Cle de Macina. — Coiffait, 1968, p. 138 (distribution). **[verres group]**

limbatus Hochhuth, 1872, p. 158 (*Bledius*). Type locality: Russia: Dnepr River. (Original spelling is *limbalus*.) — Fauvel, 1875, p. xiii (group 2—*Hesperophilus*). — Winkler, 1925, p. 347 (subg. *Hesperophilus*). — Szujecki, 1968 (subg. *Astycops*; emended from *limbalus* to *limbatus*; key, redescription). **[albonotatus group]**

limicola Tottenham, 1940, p. 38 (*Bledius*). Type locality: England: Highcliffe. **New Status.** — Tottenham, 1949, p. 410 (subg. *Bledius*). — Tottenham, 1954, p. 51 (synonym of *germanicus*). **[gigantulus group]**

germanicus[25] Wagner, 1935, p. 109 (*Bledius*). Type locality: Germany. (Described as subspecies of *spectabilis* Kraatz.) **New Synonym.** — Benick, 1939, pp. 25–26 (race). — Tottenham, 1954, p. 51 (subg. *Bledius*; key, distribution, habitat). — Steel, 1955, p. 240 (natural history). — Horion, 1963, p. 256 (cited as subspecies of *spectabilis*). — Lohse, 1964, p. 91 (subg. *Bledius*; key). — Smetana, 1967, p. 321 (distribution, notes). — Scheerpeltz, 1968, p. 31 (synonym of *spectabilis*). — Pope, 1977, p. 24 (cited as valid species). — Lohse, 1978, p. 14 (characters).

lindbergianus Scheerpeltz, 1963, p. 8, 24 (*Bledius*; subg. *Belidus*). Type locality: Afghanistan: Dilaram. **[angustus group]**

litoreus (Herman), 1972, p. 129 (*Microbledius*). Type locality: Florida: Passe Grille. **New Combination.** **[forcipatus group]**

littoralis Heer, 1839, p. 209 (*Bledius*). Type localities: Switzerland: Geneva, Arve River; Bevers, Inn River. (This name is often spelled with one "t" but Heer used two.) — Jacquelin du Val, 1859, p. 76 (junior synonym of *aquarius*). — Fauvel, 1872, p. 204 (group 3—*Astycops, Bargus, Tadunus*). — Fauvel, 1873a, p. 46. — Fauvel, 1875, p. xiii (group 3—*Astycops, Bargus, Tadunus*). — Mulsant and Rey, 1878 (subg. *Blediodes*). — Seidlitz, 1891, p. 382 (subg. *Bargus* key). — Ganglbauer, 1895, p. 617 (subg. *Blediodes*). — Stierlin, 1900, p. 395 (subg. *Bargus*; key). — Reitter, 1909, p. 166 (as *litoralis*; subg. *Blediodes*; key). — Poppius, 1909a, p. 10 (subg. *Blediodes*; notes). — Bernhauer and Schubert, 1911, p. 131 (as *litoralis*). — Winkler, 1925, p. 345 (subg. *Blediodes*; as *litoralis*). — Krogerus, 1925b (key, natural history, larva). — Krogerus, 1925a (natural history). — Porta, 1926, p. 46 (subg. *Blediodes*; key). — Portevin, 1929, p. 411 (key). — Benick, 1943, p. 94 (subg. *Blediodes*; characters). — Strand, 1946, p. 238 (distribution). — Horion, 1963, p. 260 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 93 (subg. *Hesperophilus*; key). — Andersen, 1968 (natural history). — Scheerpeltz, 1968, p. 32 (subg. *Blediodes*; catalogue). — Smetana, 1975, p. 160 (distribution, notes). — Andersen, 1982, p. 65 (natural history). — Andersen, 1983, pp. 421, 429 (distribution, natural history). **[annularis group]**

aquarius Erichson, 1840, p. 766 (*Bledius*). Type locality: Geneva. — Jacquelin du Val, 1859, p. 76. — Fauvel, 1872, p. 204 (junior synonym of *littoralis*). — Fauvel, 1873a, p. 46. — Seidlitz, 1891, p. 382 (junior synonym of *littoralis*).

lugubris Poppius, 1909a, p. 10 (*Bledius*; subg. *Blediodes*). Type locality: East Siberia: Lena Valley. (Described as variety.)

vulneratus Reitter, 1909, p. 166 (*Bledius*). (Described as variety of *littoralis*.)

lividipes Fairmaire, 1892, see: *orientalis* Bernhauer and Schubert, 1912.

lividipes Fairmaire and Germain, 1861, p. 445 (*Bledius*). Type locality: Chile: Quillota. — Coiffait and Saiz, 1968, p. 425 (subg. *Hesperophilus*; key, redescription). — Saiz, 1973, p. 230 (key, notes). **[emarginatus group]**

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[25] The name *germanicus* was used by Gravenhorst, 1806 as a form of *pallipes*. The name evidently was never used again. Furthermore, two forms of that species were then recognized and named. One of them, *gallicus*, was discovered to be a different species and later elevated; the other one, *germanicus*, seems to be the same as the nominate form.

loeffleri Coiffait, 1973, p. 121 (*Bledius*; subg. *Elbidus*). Type locality: Iran: Kerman Prov. **[kochi group]**

longipennis Mäklin, 1852, p. 318 (*Bledius*). Type locality: Sitka Island. — Herman, 1983a, pp. 95–96 (species unknown; discussion). **[incertae sedis]**

longulus Erichson, 1839, p. 579 (*Bledius*). Type locality: Mark. — Heer, 1839, p. 575. — Erichson, 1840, p. 768. — Fauvel, 1872, p. 207 (group 3—*Astycops, Bargus, Tadunus*). — Fauvel, 1873a, p. 49. — Fauvel, 1873b, p. 22 (distribution). — Fauvel, 1875, p. xiii (group 3—*Astycops, Bargus, Tadunus*). — Mulsant and Rey, 1878 (subg. *Blediodes*). — Fowler, 1888, p. 369. — Seidlitz, 1891, p. 382 (subg. *Bargus*; key). — Ganglbauer, 1895, p. 619 (subg. *Blediodes*). — Stierlin, 1900, p. 394 (subg. *Bargus*; key). — Deville, 1907, p. 91 (subg. *Blediodes*). — Reitter, 1909, p. 167 (subg. *Blediodes*; key). — Everts, 1922, pp. 142, 143 (notes, distribution, key). — Winkler, 1925, p. 345 (subg. *Blediodes*). — Krogerus, 1925b (key, natural history). — Porta, 1926, p. 46 (subg. *Blediodes*; key). — Portevin, 1929, p. 413 (key). — Blair, 1931, p. 1231 (distribution). — Larsen, 1936 (natural history). — Breddin, 1936 (natural history). — Benick, 1937, pp. 74–75 (taxonomic notes). — Koch, 1938, p. 131 (notes). — Lengerken, 1939, pp. 131–136 (natural history). — West, 1942, p. 142 (distribution, habitat). — Benick, 1943, p. 94 (subg. *Blediodes*; characters). — Strand, 1946, p. 240 (distribution). — Tottenham, 1949, p. 411 (subg. *Hesperophilus*). — Tottenham, 1954, p. 54 (subg. *Hesperophilus*; key, distribution, habitat). — Horion, 1963, p. 268 (subg. *Hesperophilus*; distribution, notes). — Andersen, 1968 (natural history). — Scheerpeltz, 1968, p. 32 (subg. *Blediodes*; catalogue). — Andersen, 1982, p. 65 (natural history). — Andersen, 1983, p. 429 (distribution, natural history). **[annularis group]**

ruficornis Mulsant and Rey, 1878, p. 597 (*Bledius*; subg. *Blediodes*). Type locality: France: Lyon. — Ganglbauer, 1895, p. 619 (synonym of *longulus*).

nigripennis Bernhauer, 1910, p. 256 (*Bledius*). Type locality: Austria: Hochwassers der Steyr in Grunburg. (Described in aberration.)

nigripennis Gabriel, 1929, p. 8 (*Bledius*). Type locality: Nassfeld near Gastein (described as aberration of *longulus*). Roubal, 1933, p. 189 (junior synonym of *longulus nigripennis* Bernhauer).

pflaundleri Benick, 1937, p. 74 (*Bledius*). Type locality: Germany. (Described as variety.)

louwerensi Cameron, 1938, p. 148 (*Bledius*; subg. *Pucerus*). Type locality: E. Java: Res. Kediri, Pandan Aroem, Samberbajem. **[verres group]**

lucens Cameron, 1940, p. 184 (*Bledius*; subg. *Hesperophilus*). Type locality: China: Shanghai. **[kosempoensis group]**

lucidulus Cameron, 1929, p. 445 (*Bledius*; subg. *Hesperophilus*). Type locality: Pulo Condore. — Scheerpeltz, 1957, p. 226 (subg. *Hesperophilus*; distribution). **[verres group]**

lucidus Sharp, 1874, p. 90 (*Bledius*). Type localities: Japan: Tomatzu, Nagasaki. China. — Fauvel, 1903a, p. 152 (synonymy). — Fauvel, 1904c, p. 46 (synonymy, distribution). — Winkler, 1925, p. 347 (subg. *Hesperophilus*). — Cameron, 1930, p. 179 (key, redescription). — Scheerpeltz, 1957, p. 226 (subg. *Hesperophilus*; distribution). — Shibata, 1973, p. 34 (subg. *Hesperophilus*; distribution). — Shibata, 1976, p. 136 (distribution, catalogue). **[lucidus group]**

capitalis Fauvel, 1877, p. 204 (*Bledius*). Type locality: Australia: Queensland, Port Denison. — Fauvel, 1903a, p. 152 (synonym of *lucidus*). — Fauvel, 1904c, p. 46 (synonym of *lucidus*).

fischeri Bernhauer, 1903, p. 35 (*Bledius*). Type locality: Sumatra.

lugubris Poppius, 1909, see: *littoralis* Heer, 1839.

lugubris Fauvel, 1904, p. 305 (*Bledius*). Type locality: Madagascar: Baie de Saint-Augustin. **[lugubris group]**

luteipennis LeConte, 1877, see: *suturalis* LeConte, 1863.

maculipennis (Solier), 1849, p. 332 (*Teropalpus*). Type locality: Chile: in the lower mountains of Coquimbo. — Fairmaire and Germain, 1861 (*Bledius*). — Coiffait and Saiz, 1968, pp. 425, 427 (subg. *Astycops*; key, redescription). — Saiz, 1973, p. 230 (key, discussion, notes). **[punctatissimus group]**

irroratus Fauvel, 1864, p. 127 (*Bledius*). Type locality: Chile. — Fauvel, 1868, p. 26 (junior synonym of *maculipennis*). — Blackwelder, 1944, p. 106. — Coiffait and Saiz, 1968, p. 427 (junior synonym of *maculipennis*).

madagascariensis Bernhauer, 1901, p. 169 (*Bledius*). Type locality: Madagascar: Port Daufin. — Bernhauer and Schubert, 1911, p. 132 (subg. *Hesperophilus*). **[verres group]**

magniceps Reitter, 1902, p. 186 (*Bledius*; subg. *Belidus*). Type locality: Transcaspien: Askhabad. — Winkler, 1925, p. 347 (subg. *Belidus*). **[angustus group]**

maindroni Fauvel, 1903a, p. 151 (*Bledius*). Type localities: India: Mahe, Calicut. — Cameron, 1930, pp. 278, 282 (key, redescription). — Scheerpeltz, 1933, p. 1118 (subg. *Hesperophilus*). **[punctatissimus group]**

mandibularis Erichson, 1840, p. 765 (*Bledius*). Type locality: America septentrionali. — LeConte, 1877, pp. 218, 219 (*mandibularis* group; redescription, key). — Casey, 1889, p. 42. — Bernhauer and Schubert, 1911, p. 133 (junior synonym of *pallipennis*). — Leng, 1920, p. 97 (junior synonym of *pallipennis*). — Blackwelder, 1947, pp. 119–121 (redescription, resurrection, distribution, natural history, synonyms). — Herman, 1972, pp. 191–200 (*mandibularis* group; redescription, key, illustrations, distribution, natural history, synonyms). — Wheeler et al., 1972 (physiology). — Happ and Happ, 1973 (anatomy, histology). — Herman, 1983a, p. 138 (distribution). **[mandibularis group]**

brevidens LeConte, 1877, p. 219 (*Bledius*; *mandibularis* group). Type locality: New York. — — Duvivier, 1883, p. 186. — Casey, 1889, p. 42. — Blackwelder, 1947, p. 119 (junior synonym of *mandibularis*). — Herman, 1972, pp. 192, 199 (junior synonym of *mandibularis*). — Herman, 1983a, p. 118 (lectotype).

mandibularis MacLeay, 1873, see: *austrinus* Herman, 1970.

marginalis Cameron, 1945, p. 707 (*Bledius*; subg. *Hesperophilus*). Type locality: South Africa: Simon's Town. **[verres group]**

marinus Bernhauer, 1922, p. 168 (*Bledius*). Type locality: Aldabra: Takamaka.[26] Scott, 1922, p. 187. **[gigantulus group]**

maritimus Bernhauer, 1923, p. 176 (*Bledius*). Type locality: Sudan: Port Sudan. **[furcatus group]**

mauritanicus Coiffait, 1966, p. 349 (*Bledius*; subg. *Pucerus*). Type locality: Mauritania: Trarza Gana. **[verres group]**

maxillosus Sperk, 1835, see: *Anotylus inustus* Gravenhorst, 1806.

medialis Fall, 1910, see: *suturalis* LeConte, 1863.

melanocephalus (Say), 1823, p. 156 (*Oxytelus*). Type locality: Missouri River above confluence of Platte River. — Erichson, 1840, p. 780 (*Bledius*; list). — Herman, 1976, pp. 99–104 (*melanocephalus* group; redescription, key, illustrations, distribution, natural history, synonyms). — Herman, 1983a, p. 138 (distribution). **[basalis group]**

confinis Fall, 1910, p. 114 (*Bledius*; *cordatus* group). Type locality: Texas: El Paso. — Herman, 1976, pp. 99, 101 (junior synonym of *melanocephalus*). — Herman, 1983a, p. 120 (lectotype).

melanocolus Herman, 1983, p. 51 (*Bledius*; *annularis* group). Type locality: California: San Bernardino Co.: 30 mi. ENE Redlands, South Fork Campground, Santa Ana River. **[annularis group]**

michaelseni Bernhauer, 1915, p. 313 (*Bledius*; subg. *Hesperophilus*). Type locality: Southwest Africa: Pinguin Island, near Luederitzbucht. **[punctatissimus group]**

microcephalus Fauvel, 1901, p. 72 (*Bledius*). Type locality: Colombia. — Blackwelder, 1944, p. 100 (checklist). — Herman, 1972, pp. 148–153 (*Psamathobledius*; redescription, key, illustrations, distribution). — Herman, 1983a, p. 134 (distribution). **[punctatissimus group]**

miles Bernhauer, 1909, p. 232 (*Bledius*). Type locality: Argentina: Buenos Aires. — Bernhauer, 1927a, p. 234 (key). — Herman, 1972, p. 120 (*Microbledius*). **[forcipatus group]**

militaris Oke, 1933, p. 108 (*Bledius*). Type localities: Australia: Ringwood, Belgrave. **[emarginatus group]**

minarzi Bernhauer, 1929, see: *tristis* Aube, 1843.

minarzianus Bernhauer, 1943, p. 74 (*Bledius*; subg. *Blediodes*). Type locality: Urals. **[semiferrugineus group]**

minax Blackburn, 1888, p. 14 (*Bledius*). Type locality: Australia: 35 mi. NW Port Lincoln. **[minax group]**

minniensis Herman, described in the present work. Type locality: Armenia. **[minniensis group]**

minor Bernhauer, 1920, see: *exiguus* Scheerpeltz, 1933.

minor Krogerus, 1925, see: *opacus* (Block), 1799.

minor[27] Mulsant and Rey, 1878, p. 634 (*Bledius*;

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[26] The type locality is cited here as it is in the original Description. There is a Takamaka on Mahe Island in the Seychelles. Scott (1922) and Bernhauer (1922) cite *marinus* in the Aldabra Islands. The type has the label "Aldabra: South Island: Takamaka Grove."

[27] The name *devillei* Bondroit was proposed unnecessarily as a replacement name for *minor* Mulsant and Rey. Bondroit, while incorrectly citing the author and date for Mulsant and Rey's *minor,* also stated that *minor* had been used as a variety of *fracticornis.* Erichson (1840, p. 767), Fairmaire and Laboulbène (1854, p. 603), Jacquelin du Val (1859, p. 76), and Fauvel (1872, p. 210) cite *tricornis* var. *minor* Gravenhorst as a junior synonym of *fracticornis.* Gravenhorst is stated to have used the name on page 196 of his 1806 publication. I find the name *minor* neither there nor in his 1802 book and so resurrect *minor* Mulsant and Rey to replace *devillei.*

Scheerpeltz cited *minor* under *arenarius* (p. 1110) and under *devillei* (p. 1113). For the first he cited Mulsant and Rey, 1879 and the other Rey, 1877. These publications are identical. The 1877 publication is actually subg. *Hesperophilus*). Type locality: not cited, presumably France. (Cited in paragraph of description of *arenarius.*) **New Status.** — Fauvel, 1890, p. 331 (junior synonym of *arenarius*). — Newbery, 1912, p. 64 (synonym of *fergusoni*). — Porta, 1949, p. 139 (synonym of *devillei*). **[basalis group]**

devillei Bondroit, 1912, p. 67 (*Bledius*). (Replacement name for *minor* Mulsant and Rey.) **New Synonym.** — Winkler, 1925, p. 346 (subg. *Hesperophilus*). — Porta, 1926, p. 47 (subg. *Blediodes*; key). — Porta, 1949, p. 139 (subsp. of *doderoi*).

minusculus Motschulsky, 1861, see: *Carpelimus exiguus* (Erichson), 1839.

minutissimus Bernhauer, 1921, p. 171 (*Bledius*). Type locality: Argentina: Prov. Tucuman. — Bernhauer, 1927a, p. 232 (key). — Herman, 1972, p. 120 (*Microbledius*). **[forcipatus group]**

minutus Bernhauer, 1920, p. 6 (*Bledius*). Type locality: Australia: Tolga. **[emarginatus group]**

misellus Casey, 1889, see: *basalis* LeConte, 1863.

missionensis Hatch, 1957, see: *gravidus* Casey, 1889.

mixtus Notman, 1922, see: *philadelphicus* Fall, 1919.

modestus Sharp, 1876, p. 396 (*Bledius*). Type locality: Brazil: Rio Madeira. **[emarginatus group]**

monachus Bernhauer, 1915, see: *verres* Erichson, 1840.

monachus Cameron, 1930, see: *verres* Erichson, 1840.

monoceros Rosenhauer, 1856, see: *unicornis* (Germar), 1825.

monstratus Casey, 1889, p. 46 (*Bledius*; *armatus* group). Type locality: California: San Francisco. — Fall, 1901, p. 76. — Notman, 1920, p. 695 (key). — Blackwelder, 1936, p. 60 (illustration). — Hatch, 1957, p. 105 (subg. *Hesperophilus*; key, cited as *monstrosus*). — Herman, 1976, pp. 140–143 (*armatus* group; redescription, key, illustration, distribution, natural history). — Moore, 1978 (natural history). — Herman, 1983a, pp. 120, 138 (lectotype, distribution). **[armatus group]**

montanus Bernhauer, 1921, see: *curtipennis* Bernhauer, 1921.

monticola Casey, 1889, p. 58 (*Bledius*; *annularis* group). Type locality: California: Lake Tahoe. — Fall, 1901, p. 76. — Fall, 1910, p. 111. — Herman, 1983a, pp. 79–81, 120 (*annularis* group; redescription, key, illustration, distribution, natural history, lectotype). **[annularis group]**

morio Heer, 1839, p. 211 (*Bledius*). Type localities: Switzerland: Zurich, Sihl River; Geneva, Arve River. — Jacquelin du Val, 1859, p. 59 (junior synonym of *tibialis*). — Fauvel, 1900b, p. 161 (synonymy). — Fauvel, 1902, p. 72 (distribution, notes). — Deville, 1907, p. 90 (subg. *Astycops*; key). — Everts, 1922, p. 139 (synonym of *tibialis*). — Winkler, 1925, p. 346 (subg. *Hesperophilus*). — Porta, 1934, p. 116 (subg. *Hesperophilus*; distribution). — Kocker, 1958, p. 109 (distribution). — Horion, 1963, p. 293 (subg. *Hesperophilus*; distribution, notes). — Lohse, 1964, p. 99 (subg. *Astycops*; key). — Scheerpeltz, 1968, p. 33 (subg. *Hesperophilus*; catalogue). **[tibialis group]**

hispidulus Fairmaire and Laboulbene, 1856, p. 601 (*Bledius*). Type localities: Fontainebleau; Compiegne; la Teste; Arcachon. — Fauvel, 1872, p. 199 (group 3—*Astycops, Bargus, Tadunus*). — Fauvel, 1873a, p. 41. — Fauvel, 1875, p. xiii (group 3—*Astycops, Bargus, Tadunus*). — Mulsant and Rey, 1878 (subg. *Astycops*). — Fauvel, 1886, p. 26 (distribution, notes). — Ganglbauer, 1895, p. 625 (subg. *Hesperophilus*). — Fauvel, 1897, p. 262 (distribution, notes). — Fauvel, 1900, p. 161 (junior synonym of *morio*). — Fauvel, 1902, p. 72 (synonym of *morio*).

*morsei** Scudder, 1900, see: *Stenus* (transferred by Wickham, 1913, p. 289).

mulsanti Rosenhauer, 1856, see: *debilis* Erichson, 1840.

muticus Sharp, 1876, p. 395 (*Bledius*). Type locality: Brazil: Rio Madeira. **[emarginatus group]**

mysticus Fall, 1910, p. 111 (*Bledius*; *annularis* group). Type locality: Washington. — Hatch, 1957, p. 102 (subg. *Hesperophilus*; key). — Herman, 1983a, pp. 93–95, 120 (*annularis* complex; discussion, lectotype). **[annularis group]**

naius Herman, 1983, p. 91 (*Bledius*; *annularis* group). Type locality: Arizona: Santa Rita Mountains: Madera Canyon. **[annularis group]**

naja Koch, 1938, p. 39 (*Bledius*; subg. *Elbidus*). Type locality: Turkmenia. **[kochi group]**

nanus Erichson, 1840, p. 773 (*Bledius*). Type locality: Austria. — Fauvel, 1872, p. 203 (junior synonym of *atricapillus*). — Fauvel, 1873a, p. 45. — Mulsant and Rey, 1878 (subg. *Blediodes*). — Fauvel, 1884, p. 78 (junior synonym of *atricapillus*). — Seidlitz, 1891, p. 381

Mulsant and Rey, 1878 (see my Literature Cited) which was republished by the same authors in 1879. Since Bondroit (1912) recognized *minor* as a separate species, it is cited as such herein.

(subg. *Tadunus*; key). — Ganglbauer, 1895, p. 620 (subg. *Blediodes*). — Stierlin, 1900, p. 393 (subg. *Tadunus*; key). — Deville, 1907, p. 91 (synonym of *atricapillus*). — Reitter, 1909, p. 167 (subg. *Blediodes*; key). — Bernhauer and Schubert, 1911, p. 126 (variety of *atricapillus*). — Bondroit, 1912a, p. 66 (characters, notes). — Everts, 1922, p. 140 (notes, distribution). — Winkler, 1925, p. 346 (subg. *Blediodes*). — Porta, 1926, p. 46 (subg. *Blediodes*; key). — Brunier, 1931, pp. 2–4 (natural history). — Scheerpeltz, 1933, pp. 1111, 1118 (valid species). — Koch, 1934, p. 61 (subg. *Blediodes*; key). — Breddin, 1936 (natural history). — West, 1942, p. 143 (distribution, habitat). — Benick, 1943, p. 94 (subg. *Blediodes*; characters). — Smetana, 1959, p. 201 (distribution). — Horion, 1963, p. 272 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 96 (subg. *Hesperophilus*; key). — Scheerpeltz, 1968, p. 33 (subg. *Blediodes*; catalogue). **[semiferrugineus group]**

nardus Herman, 1983, p. 41 (*Bledius*; *annularis* group). Type locality: Washington: Clallam Co.: 18 mi. E Clallam Bay, Deep Creek. **[albonotatus group]**

naxius Bernhauer, 1940, p. 626 (*Bledius*; subg. *Elbidus*). Type locality: Greece: Naxos. **[kochi group]**

nebulosus Casey, 1889, p. 57 (*Bledius*; *annularis* group). Type locality: Iowa. — Herman, 1983a, pp. 93–95, 120 (*annularis* complex; discussion, lectotype). **[annularis group]**

nebulosus Koch, 1938, see: *albanicus* Herman, **New Name.**

neglectus Casey, 1889, p. 69 (*Bledius*; *cordatus* group). Type locality: Rhode Island. — Herman, 1976, pp. 90–94 (*basalis* group; redescription, key, illustration, distribution, natural history). — Herman, 1983a, p. 120 (lectotype). **[basalis group]**

negrei Coiffait, 1970, p. 147 (*Bledius*; subg. *Pucerus*). Type locality: USSR: Uzbekistan: Urgench. **[verres group]**

nelsoni Hatch, 1957, see: *flavipennis* LeConte, 1863.

neuter Mulsant and Rey, 1878, see: *baudii* Fauvel, 1872.

newelli Hatch, 1957, p. 105 (*Bledius*; subg. *Hesperophilus*). Type locality: Oregon: Lane Co.: Winchester Bay. — Herman, 1983a, pp. 77–78 (*annularis* group; redescription, key, illustration, distribution, natural history). **[annularis group]**

niger Cameron, 1945, p. 707 (*Bledius*; subg. *Hesperophilus*). Type locality: South Africa: Simon's Town. **[verres group]**

angolensis Cameron, 1950, p. 115 (*Bledius*). Type locality: Angola: Dundo. (Described as variety.)

nigricans Erichson, 1840, see: *dissimilis* Erichson, 1840.

nigriceps Notman, 1920, see: *politus* Erichson, 1840.

nigripennis Bernhauer, 1910, see: *longulus* Erichson, 1839.

nigripennis Gabriel, 1929, see: *longulus* Erichson, 1839.

niloticus Erichson, 1840, p. 776 (*Bledius*). Type locality: Egypt. — Fauvel, 1975, p. xiii (group 2—*Hesperophilus*). — Mulsant and Rey, 1878 (subg. *Pucerus*). — Fauvel, 1886, p. 25 (distribution, notes). — Fauvel, 1897, p. 262 (distribution, notes). — Fauvel, 1902, p. 71 (distribution, note). — Winkler, 1925, p. 347 (subg. *Pucerus*). — Koch, 1934, pp. 57, 60 (subg. *Pucerus*; key, notes). — Frank, 1982, p. 11 (parasites, references). **[verres group]**

nitidicollis Eppelsheim, 1885, p. 142 (*Bledius*). Type locality: West Africa. — Fauvel, 1902, p. 71 (junior synonym of *niloticus*).

nitidiceps LeConte, 1877, p. 224 (*Bledius*; *semiferrugineus* group). Type locality: California: Los Angeles. — Fall, 1901, p. 75. — Notman, 1920, p. 697. — Herman, 1976, pp. 150–153 (*armatus* group; redescription, key, illustrations, distribution, natural history). — Herman, 1983a, pp. 119, 138 (lectotype, distribution). **[armatus group]**

nitidicollis Eppelsheim, 1885, see: *niloticus* Erichson, 1840.

nitidicollis LeConte, 1863, p. 52 (*Bledius*). Type locality: New York. — LeConte, 1877, pp. 223, 225 (*semiferrugineus* group; redescription, key). — Casey, 1889, p. 56. — Blatchley, 1910, pp. 464, 465. — Notman, 1920, p. 697 (key). — Herman, 1972, pp. 229–230 (*semiferrugineus* group; redescription, key, illustrations, distribution, natural history). — Frank, 1982, p. 11 (parasites, references). — Herman, 1983a, pp. 119, 138 (lectotype, distribution). **[semiferrugineus group]**

nodieri Cameron, 1939, p. 205 (*Bledius*; subg. *Pucerus*). Type locality: Senegal: Badoumbe. **[verres group]**

normandi Koch, 1938, see: *tristis* Aube, 1843.

norquincoensis Scheerpeltz, 1972, p. 91 (*Bledius*; subg. *Hesperophilus*). Type locality: Argentina: Rio Negro. **[emarginatus group]**

notialus Herman, 1976, p. 131 (*Bledius*; *armatus* group). Type locality: Oklahoma: Kay Co.: Ponca City. — Herman, 1983a, p. 138 (distribution). **[armatus group]**

nuchicornis Mulsant and Rey, 1861, see: *tricornis* (Herbst), 1784.

obihiroensis Nakane, 1963, p. 21 (*Bledius*). Type locality: Japan: Hokkaido, Tokachi, Obihiro. — Nakane et al., 1965, p. 84, pl. 42, fig. 23. — Shibata, 1976, p. 137 (distribution, catalogue). **[annularis group]**

obscurus Mulsant and Rey, 1870, see: *denticollis* Fauvel, 1872.

obscurus Motschulsky, 1860, p. 556 (*Bledius*). Type locality: Mongolia: Selenga River near Kiahta. — Fauvel, 1875, p. XII (group 1—*Bledius*). — Winkler, 1925, p. 346 (subg. *Blediodes*). — Smetana, 1975, p. 162 (distribution, notes). **[annularis group]**

obsoletus Fauvel, 1872, p. 207 (*Bledius*). Type localities: France: Albi; Haut Pyrenees. — Fauvel, 1873a, p. 49 (cited as new species). — Fauvel, 1873b, p. 21 (distribution). — Fauvel, 1875, p. xiii (group 3—*Astycops, Bargus, Tadunus*). — Mulsant and Rey, 1878 (subg. *Blediodes*). — Winkler, 1925, p. 346 (subg. *Blediodes*). — Portevin, 1929, p. 412 (key). — Benick, 1843, p. 95 (subg. *Blediodes*; characters). **[annularis group]**

obtusicollis Koch, 1938, see: *bavaricus* Koch, 1938.

obtusus Sharp, 1889, p. 413 (*Bledius*). Type locality: Japan: Niigata. — Winkler, 1925, p. 346 (subg. *Blediodes*). — Shibata, 1976, p. 137 (distribution, catalogue). **[semiferrugineus group]**

occidentalis Bondroit, 1907, p. 245 (*Bledius*). Type locality: Holland: Zwijn. — Everts, 1922, p. 141 (notes, distribution, key). — Winkler, 1925, p. 346 (subg. *Blediodes*). — Koch, 1938a, p. 136 (notes). — West, 1942, p. 145 (distribution, habitat). — Benick, 1943, p. 95 (subg. *Blediodes*; characters). — Tottenham, 1949, p. 410 (subg. *Hesperophilus*). — Tottenham, 1954, p. 52 (subg. *Hesperophilus*; key, distribution, habitat). — Horion, 1963, p. 277 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 97 (subg. *Hesperophilus*; key). — Scheerpeltz, 1968, p. 33 (subg. *Blediodes*; catalogue). **[semiferrugineus group]**

omega Herman, 1983, p. 45 (*Bledius*; *annularis* group). Type locality: Wisconsin: Ashland Co.: Marengo River. **[albonotatus group]**

opacicollis Eppelsheim, 1893, p. 59 (*Bledius*). Type locality: Baikal Region: Quellgebiet des Irkut. — Poppius, 1909a, p. 10 (subg. *Blediodes*; distribution). — Winkler, 1925, p. 346 (subg. *Blediodes*). — Smetana, 1975, p. 162 (distribution, notes). **[annularis group]**

opacifrons LeConte, 1877, p. 224 (*Bledius*; *semiferrugineus* group). Type locality: California: San Diego. — Fall, 1901, p. 75. — Notman, 1920, p. 697. — Hatch, 1957, p. 99 (subg. *Hesperophilus*; key). — Herman, 1976, pp. 153–156 (*armatus* group; redescription, key, illustrations, distribution, natural history, synonyms). — Herman, 1983a, pp. 119, 139 (lectotype, distribution). **[armatus group]**

condonensis Hatch, 1957, p. 98. (*Bledius*; subg. *Hesperophilus*). Type locality: Oregon: Condon. — Herman, 1976, pp. 153, 156 (junior synonym of *opacifrons*).

lectus Casey, 1889, p. 49 (*Bledius*; *armatus* group). Type locality: California: Sonoma Co. — Fall, 1910, p. 76. — Notman, 1920, p. 696 (key). — Herman, 1976, pp. 153, 156 (junior synonym of *opacifrons*). — Herman, 1983a, p. 119 (lectotype).

piceus Fall, 1910, p. 108 (*Bledius*; *semiferrugineus* group). Type locality: California: Pasadena. — Notman, 1920, p. 697. — Herman, 1976, pp. 153, 156 (junior synonym of *opacifrons*). — Herman, 1983a, p. 120 (lectotype).

regularis Fall, 1910, p. 109 (*Bledius*; *semiferrugineus* group). Type locality: California: Siskiyou Co.: Cole. — Notman, 1910, p. 697. — Hatch, 1957, p. 98. — Herman, 1976, pp. 153, 156 (junior synonym of *opacifrons*). — Herman, 1983a, p. 120 (lectotype).

specularis Fall, 1910, p. 109 (*Bledius*; *semiferrugineus* group). Type locality: California: Point Reyes. — Notman, 1920, p. 697. — Herman, 1976, pp. 153, 156 (junior synonym of *opacifrons*). — Herman, 1983a, p. 121 (lectotype).

opacinus Scheerpeltz, 1960, p. 73 (*Bledius*; subg. *Hesperophilus*). Type locality: Afghanistan: Kabul. **[verres group]**

opaculus LeConte, 1863, p. 54 (*Bledius*). Type locality: Maine. — LeConte, 1877, pp. 232, 233 (*cordatus* group; redescription, key). — Casey, 1889, p. 67. — Herman, 1976, pp. 88–90 (*basalis* group; redescription, key, illustrations, distribution, natural history). — Herman, 1983a, pp. 119, 139 (lectotype, distribution). **[basalis group]**

opacus (Block), 1799, p. 117 (*Staphylinus*). — Erichson, 1839, p. 581 (*Bledius*). — Heer, 1839, p. 210. — Erichson, 1840, p. 771. — Thomson, 1861. — Schiødte, 1866, p. 148 (*Bargus*). — Thomson, 1867 (*Bledius*). — Fauvel, 1872, p. 204 (group 3—*Astycops, Bargus, Tadunus*). — Fauvel, 1873a, p. 46. — Fauvel, 1873b, p. 21 (distribution). — Fauvel, 1875, p. xiii (group 3—*Astycops, Bargus, Tadunus*). — Mulsant and Rey, 1878 (subg. *Blediodes*). — Fauvel, 1886, p. 27 (distribution, notes). — Fowler, 1888, p. 370. — Seidlitz, 1891, p. 381 (key). — Ganglbauer, 1895, p. 619 (subg. *Blediodes*). — Fauvel, 1897, p. 263 (distribution, notes). — Stierlin, 1900, p. 363 (key). — Fauvel, 1902, p. 72 (distribution, notes). — Deville, 1907, p. 91 (subg. *Blediodes*). — Reitter, 1909, p. 167 (subg. *Blediodes*; key). — Everts, 1922, p. 139 (notes, distribution). — Winkler, 1925, p. 346 (subg. *Blediodes*). — Krogerus, 1925b (key, natural history, larva). — Krogerus, 1925a (natural history). — Porta, 1926, p. 46 (subg. *Blediodes*; key). — Portevin, 1929, p. 414 (key). — Blair, 1931, p. 1231 (distribution). — Brunier, 1931, pp. 41–42 (natural history). — Larsen, 1936 (natural history). — Breddin, 1936 (natural history). — Lengerken, 1939, pp. 131–135 (natural history). — West, 1942, p. 143 (distribution, habitat). — Benick, 1943, p. 94 (subg. *Blediodes*; key). — Tottenham, 1949, p. 411 (subg. *Hesperophilus*). — Larsen, 1953 (natural history). — Tottenham, 1954, p. 53 (subg. *Hesperophilus*; key, distribution, habitat). — Steel, 1956 (characters). — Horion, 1963, p. 269 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 95 (subg. *Hesperophilus*; key). — Potoskaya, 1967, p. 32 (larva). — Scheerpeltz, 1968, p. 33 (subg. *Blediodes*; catalogue). — Smetana, 1975, p. 161 (distribution, notes). — Frank, 1982, p. 11 (parasites, references). — Lohse, 1982, pp. 116, 117 (characters). **[annularis group]**

divisus (Marsham), 1802, p. 510 (*Staphylinus*). — Curtis, 1829, p. 29 (*Hesperophilus*). — Stephens, 1829, p. 292 (*Hesperophilus*). — Stephens, 1834 (*Hesperophilus*). — Ganglbauer, 1895, p. 619 (synonym of *opacus*).

haemopterus (Stephens), 1832, p. 310 (*Hesperophilus*). Type localities: Britain: Suffolk; Norfolk; Yorkshire. — Curtis, 1829, p. 29 (*Hesperophilus,* nomen nudum). — Stephens, 1829, p. 292 (nomen nudum). — Stephens, 1834 (*Hesperophilus*). — Ganglbauer, 1895, p. 619 (synonym of *opacus*).

extensus Motschulsky, 1860, p. 555 (*Bledius*). Type locality: Daourie. — Fauvel, 1872, p. 204 (group 3—*Astycops, Bargus, Tadunus*). — Fauvel, 1873a, p. 46. — Winkler, 1925, p. 346 (variety of *opacus*).

sinuatocollis Gerhardt, 1899, p. 218 (*Bledius*) (Described as variety of *opacus*.) — Koch, 1938a, p. 131 (synonym of *subsinuatus*). — Steel, 1952 (characters, cited as *denticollis*). — Lohse, 1964 (synonym of *subsinuatus*).

subsinuatus Mulsant and Rey, 1878, p. 602 (*Bledius*; subg. *Blediodes*). Type locality: Grande Chartreuse. (Cited in paragraph at end of description of *opacus*.) — Fauvel, 1895, p. 118 (synonym of *denticollis*). — Koch, 1938a, p. 131 (variety of *opacus*). — Lohse, 1963, p. 94 (variety of *opacus*?; key). — Scheerpeltz, 1968, p. 32 (synonym of *denticollis*). — Lohse, 1982, pp. 116, 117 (synonym of *opacus*).

krogeri Scheerpeltz, 1933, p. 1119 (*Bledius*). (Replacement name for *minor* Krogerus.)

minor Krogerus, 1925, p. 117 (*Bledius*). (Described as variety of *opacus*.)

oregonensis Hatch, 1957, see: *suturalis* LeConte, 1863.

orientalis Bernhauer and Schubert, 1911, p. 133 (*Bledius*). (Replacement name for *lividipes* Fairmaire.) **[punctatissimus group]**

lividipes Fairmaire, 1892, p. 90 (*Bledius*). Type locality: Obock.

orientalis Roubal, 1934, see: *roubali* Horion, 1963.

orion Normand, 1939, p. 485 (*Bledius*). Type localities: Tunisia: Fernana; Souk-el-Arba. **[semiferrugineus group]**

ornatus LeConte, 1863, see: *albonotatus* Mäklin, 1853.

orphanus Sharp, 1874, p. 91 (*Bledius*). Type locality: Japan: Kobe. — Winkler, 1925, p. 347 (subg. *Hesperophilus*). — Nakane et al., 1965, p. 84, pl. 42, fig. 22 (cited as *orphinus*). — Shibata, 1973, p. 34 (subg. *Hesperophilus*; distribution). — Shibata, 1976, p. 138 (distribution, catalogue). **[verres group]**

*osborni** Scudder, 1900, p. 72 (*Bledius*). Type locality: Colorado: Florissant. Fossil; Miocene.

osiris Normand, 1934, p. 361 (*Bledius*). Type locality: Tunisia: Le Kef.

burlinii Koch, 1938a, p. 140 (*Bledius*; subg. *Blediodes*). Type locality: Italy: Lovadina near Treviso. (Subspecies). — Porta, 1949, p. 140 (distribution). **[annularis group]**

ouzbekiscus Coiffait, 1970, p. 145 (*Bledius*; subg. *Elbidus*). Type locality: USSR: Uzbeckistan: Urgench. **[kochi group]**

ovensensis Blackburn, 1891, p. 76 (*Bledius*). Type locality: Australia: Victoria: Ovens River. — Bernhauer and Schubert, 1911, p. 133 (cited as *ovensis*). **[emarginatus group]**

palliatus Fauvel, 1895, p. 203 (*Bledius*). Type locality: Birmanie: Myeenkyan. — Cameron, 1930, pp. 275, 278 (subg. *Pucerus*; key, redescription). **[verres group]**

pallidipennis Bernhauer, 1927, p. 234 (*Bledius*). Type locality: Argentina: Chaunar Region. **[emarginatus group]**

pallipennis (Say), 1823, p. 155 (*Oxytelus*). Type locality: Missouri River below confluence of the Platte River. — Erichson, 1840, p. 779 (*Bledius*; list). — LeConte, 1877, p. 218 (*mandibularis* group; redescription, key). — Blatchley, 1910, p. 464. — Blackwelder, 1947, p. 119. — Herman, 1972, pp. 173–180 (*man-*

dibularis group; redescription, key, illustrations, distribution, synonyms). — Herman, 1983a, p. 139 (distribution).
[mandibularis group]

gularis LeConte, 1877, p. 218 (*Bledius*; *mandibularis* group). Type locality: Middle States. — Blatchley, 1910, p. 463. — Herman, 1972, pp. 174, 177 (*mandibularis* group; junior synonym of *pallipennis*). — Herman, 1983a, p. 118 (lectotype).

pallipes[28] (Gravenhorst), 1806, p. 197 (*Oxytelus*). Type locality: Germany. — Gyllenhal, 1810, p. 447. — Gyllenhal, 1827. — Stephens, 1829, p. 292 (*Hesperophilus*; junior synonym of *fracticornis*). — Mannerheim, 1831, p. 459 (*Bledius*). — Gistel, 1834, p. 9 (*Dicarenus*). — Runde, 1835, p. 18. — Erichson, 1840, p. 772. — Thomson, 1861. — Schiødte, 1864, p. 124, tab. XII (larva). — Schiødte, 1866, p. 149 (*Bargus*). — Thomson, 1867 (*Bledius*). — Fauvel, 1869 (synonymy with *fuscipes*). — Fauvel, 1872, p. 201 (group 3—*Astycops, Bargus, Tadunus*). — Fauvel, 1873a, p. 43. — Fauvel, 1873b, p. 20 (characters, synonyms, distribution, discussion). — Fauvel, 1875, p. xiii (group 3—*Astycops, Bargus, Tadunus*). — Mulsant and Rey, 1878 (subg. *Blediodes*). — Fauvel, 1884, p. 78 (synonymy). — Fowler, 1888, p. 367. — Seidlitz, 1891, p. 382 (subg. *Bargus*; key). — Ganglbauer, 1895, p. 618 (subg. *Blediodes*). — Stierlin, 1900, p. 394 (subg. *Bargus*; key). — Deville, 1907, p. 91 (subg. *Blediodes*; key). — Reitter, 1909, p. 166 (subg. *Blediodes*; key). — Sharp, 1911a, p. 31 (notes). — Sharp, 1911c, p. 57 (type species). — Bondroit, 1912a, p. 63 (characters, notes). — Everts, 1922, pp. 142, 143 (notes, distribution, key). — Winkler, 1925, p. 345 (subg. *Blediodes*). — Krogerus, 1925b (key). — Porta, 1926, p. 46 (subg. *Blediodes*; key). — Portevin, 1929, p. 411 (key). — Blair, 1931, p. 1231 (distribution). — Benick, 1936 (key, notes). — Larsen, 1936 (natural history). — Hansen, 1940, p. 583 (key). — West, 1942, p. 142 (distribution, habitat). — Benick, 1943, p. 94 (subg. *Blediodes*; characters). — Tottenham, 1949, p. 411 (subg. *Hesperophilus*). — Tottenham, 1954, p. 54 (subg. *Hesperophilus*; key, distribution, habitat). — Potoskaya, 1967, p. 32 (larva). — Scheerpeltz, 1968, p. 33 (subg. *Blediodes*; catalogue). — Shibata, 1976, p. 138 (distribution, catalogue). — Lohse, 1982, pp. 116–117 (characters). **[annularis group]**

germanicus (Gravenhorst), 1806, p. 198 (*Oxytelus*). Type locality: Germany. (Originally described as a form of *pallipes*.)

papuanus Cameron, 1937, p. 90 (*Bledius*; subg. *Hesperophilus*). Type locality: New Guinea: Kokoda. **[verres group]**

paradoxus Gridelli, 1936, p. 60 (*Bledius*; subg. *Bledius*). Type locality: Italy: Basilicata, Leoni a Lavello. — Porta, 1949, p. 139 (distribution). **[gigantulus group]**

parcissimus Bernhauer, 1927, p. 232 (*Bledius*). Type locality: Argentina: Catamarca, Pampa Grande. **[emarginatus group]**

parens Cameron, 1941, p. 434 (*Bledius*; subg. *Hesperophilus*). Type locality: Manila.
[verres group]

parisii Koch, 1938, p. 335 (*Bledius*; subg. *Blediodes*). Type locality: Dalmatia: Arbe Island. — Porta, 1949, p. 139 (distribution).
[annularis group]

parvicollis Casey, 1889, p. 65 (*Bledius*; *annularis* group). Type locality: California: Mendocino Co.: Gualala. — Fall, 1901, p. 76. — Herman, 1983a, pp. 32–35, 120 (*annularis* group; redescription, key, illustration, distribution, natural history, synonyms, lectotype).
[albonotatus group]

kincaidi Hatch, 1957, p. 103 (*Bledius*; subg. *Hesperophilus*). Type locality: Washington: Chehalis. — Herman, 1983a, pp. 32, 34 (junior synonym of *parvicollis*).

parvulus Erichson, 1840, p. 775 (*Bledius*). Type locality: Colombia [Venezuela]: Valenciae.
[emarginatus group]

parvulus Lea, 1910, see: *leai* Scheerpeltz, 1933.

pechlaneri[29] Benick, 1943, p. 91 (*Bledius*; subg. *Blediodes*). Type locality: Germany: Leifers, Umgebung Bozen. — Horion, 1963, p. 282 (notes). **[annularis group]**

peraffinis Cameron, 1940, p. 184 (*Bledius*; subg. *Hesperophilus*). Type locality: South China Sea, Pulo Condore. **[verres group]**

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[28] Gravenhorst (1806) cited two forms in his description of *pallipes*. One, *gallicus*, is now the senior synonym of *fracticornis* (Paykull), the other, *germanicus*, was never used again. Gravenhorst cited only the two names and indicated that *pallipes* is from France and Germany; therefore *gallicus* is from France and *germanicus* is from Germany. Presumably, therefore, the nominate *pallipes* is also from Germany and is therefore an objective senior synonym of the form *germanicus*. If *gallicus* is to be used then there is no reason not to use *germanicus*.

[29] Dr. Gustav Lohse informed me in a letter that this species is a synonym of *B. secessus* Bondroit. Since this synonymy has not been discussed in publication, I list the two names as though they are separate species.

perplexus Cameron, 1940, p. 184 (*Bledius*; subg. *Hesperophilus*). Type locality: Formosae: Suisharyo. — Shibata, 1973, p. 34 (subg. *Hesperophilus*; distribution). **[verres group]**

perrieri Fauvel, 1904, p. 305 (*Bledius*). Type localities: Madagascar: Suberbieville; Soalala. **[verres group]**

persicus Bernhauer, 1940, p. 627 (*Bledius*; subg. *Elbidus*). Type locality: Persia. **[kochi group]**

persimilis Fall, 1910, p. 110 (*Bledius*). Type locality: California: Pomona. — Herman, 1983a, pp. 57–59, 120 (*annularis* group; redescription, key, illustrations, distribution, natural history, lectotype). **[annularis group]**

petzi Bernhauer, 1908, p. 104 (*Bledius*; subg. *Pucerus*). Type locality: German East Africa: Dar es Salam. **[verres group]**

pflaundleri Benick, 1937, see: *longulus* Erichson, 1839.

philadelphicus Fall, 1919, p. 26 (*Bledius*). (Replacement name for *dissimilis* Fall.) — Notman, 1920, p. 697 (*semiferrugineus* group; key). — Herman, 1972, pp. 234–239 (*semiferrugineus* group; redescription, key, illustrations, distribution, synonyms). — Herman, 1983a, p. 139 (distribution). **[semiferrugineus group]**

dissimilis Fall, 1910, p. 107 (*Bledius*). Type locality: Pennsylvania: Philadelphia. — Herman, 1972, p. 234. — Herman, 1983a, p. 120 (lectotype).

falli Wendeler, 1928, p. 298 (*Bledius*). (Replacement for *dissimilis* Fall.) — Herman, 1972, p. 234.

dickersoni Notman, 1922, p. 105 (*Bledius*; *semiferrugineus* group). Type locality: New Jersey: Newark. — Herman, 1972, pp. 234, 239 (junior synonym of *philadelphicus*).

mixtus Notman, 1922, p. 104 (*Bledius*; *semiferrugineus* group). Type locality: New Jersey: Newark. — Herman, 1972, pp. 234, 239 (junior synonym of *philadelphicus*).

philippinus Bernhauer, 1912, p. 248 (*Bledius*). Type locality: Philippines: Luzon: Manila. **[gigantulus group]**

phytosinus Fauvel, 1878b, see: *Blediotrogus*.

phytosinus LeConte, 1877, p. 231 (*Bledius*; *annularis* group). Type locality: southern California. — Casey, 1889, p. 71. — Fall, 1901, p. 75. — Herman, 1983a, pp. 87–89, 119 (*annularis* group; redescription, key, illustrations, distribution, synonyms, lectotype). **[annularis group]**

lecontei Duvivier, 1883, p. 187 (*Bledius*). (Replacement name for *phytosinus* LeConte.) — Herman, 1983a, p. 87.

piceus Fall, 1910, see: *opacifrons* LeConte, 1877.

picipennis Hochhuth, 1849, p. 182 (*Bledius*). Type locality: Caucasus. — Fauvel, 1875, p. xiii (group 3—*Astycops, Bargus, Tadunus*). — Winkler, 1925, p. 346 (subg. *Blediodes*). **[semiferrugineus group]**

pilicollis Bernhauer, 1908, p. 103 (*Bledius*). Type locality: Angola: Ambrizette, Walfisch Bai. **[lamelliceps group]**

playanus (Herman), 1972, p. 121 (*Microbledius*). Type locality: Oklahoma: Alfalfa Co.: 6 mi. E, 3 mi. S Cherokee, Great Salt Plains National Wildlife Refuge. **[New Combination]**. — Ortenberger and Bird, 1933, pp. 61, 62. **[forcipatus group]**

pleuralis LeConte, 1877, see: *suturalis* LeConte, 1863.

politus Erichson, 1840, p. 766 (*Bledius*). Type locality: Carolina meridionali. — LeConte, 1877, p. 220 (*armatus* group; redescription, key). — Casey, 1889, p. 49. — Notman, 1920, p. 696 (key). — Hatch, 1957, p. 102. — Herman, 1976, pp. 126–131 (*armatus* group; redescription, key, illustrations, distribution, natural history, synonyms). — Herman, 1983a, p. 140 (distribution). **[armatus group]**

nigriceps Notman, 1920, p. 696 (*Bledius*; *armatus* group). Type locality: Florida: Fort Myers. — Herman, 1976, pp. 126, 130 (junior synonym of *politus*).

ponticus Znojko, 1929, p. 204 (*Bledius*; subg. *Bledius*). Type localities: Odessa; Krim: Eupatoria. **[gigantulus group]**

pontilis Blackburn, 1902, p. 22 (*Bledius*). Type locality: S. Australia: Murray Bridge. **[punctatissimus group]**

poppiusi Bernhauer, 1902, p. 248 (*Bledius*). Type locality: Northern Russia: Lutto River. — Poppius, 1909a, p. 10 (subg. *Blediodes*; distribution). — Krogerus, 1925b (key, natural history). — Benick, 1943, p. 94 (subg. *Blediodes*; characters). — Strand, 1946, p. 239 (distribution). — Andersen, 1982, p. 65 (natural history). — Andersen, 1983, p. 429 (distribution, natural history). **[annularis group]**

porcellus Bernhauer, 1927, p. 7 (*Bledius*). Type localities: Sumatra: Medan; Tjinta Radja; Palembang. **[verres group]**

postmaculatus Fagel, 1970, p. 9 (*Bledius*; subg. *Elbidus*). Type locality: Turkestan: Bairam-Ali. **[kochi group]**

praetermissus Williams, 1929, see: *atricapillus* (Germar), 1825.

*primitiarum** Scudder, 1900, p. 73 (*Bledius*). Type locality: Colorado: Florissant. Fossil; Miocene.

procerulus Erichson, 1840, p. 768 (*Bledius*). Type locality: Austria. — Fauvel, 1872, p. 208

(group 3—*Astycops, Bargus, Tadunus*). — Fauvel, 1873a, p. 50. — Fauvel, 1875, p. xiii (group 3—*Astycops, Bargus, Tadunus*). — Mulsant and Rey, 1878 (subg. *Blediodes*). — Seidlitz, 1891, p. 381 (subg. *Tadunus*; key). — Ganglbauer, 1895, p. 621 (subg. *Blediodes*). — Deville, 1907, p. 92 (subg. *Blediodes*). — Reitter, 1909, p. 167 (subg. *Blediodes*; key). — Winkler, 1925, p. 346 (subg. *Blediodes*). — Porta, 1926, p. 47 (subg. *Blediodes*; key). — Portevin, 1929, p. 413 (key). — West, 1942, p. 145 (distribution, habitat). — Benick, 1943, p. 94 (subg. *Blediodes*; characters). — Horion, 1963, p. 275 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 95 (subg. *Hesperophilus*; key). — Scheerpeltz, 1968, p. 33 (subg. *Blediodes*; catalogue). **[semiferrugineus group]**

*prodromus** (Heer), 1856, p. 14, see: *Stenus*. [This species is an Oligocene fossil from Aix en Provence, France. Scudder, 1900, pp. 70, 72, moved it to *Bledius* but Handlirsch, 1907, retained it in *Stenus*.]

productus (Walker), 1858, see: *brunnipennis* (Fabricius), 1801.

pruinosulus Bernhauer, 1934, p. 494 (*Bledius*; subg. *Hesperophilus*). Type locality: South Africa: Mashonaland. **[punctatissimus group]**

pruinosus Bernhauer, 1912f, see: *Parieobledius*.

pubescens Kolenati, 1846, see: *tibialis* Heer, 1839.

puelches Fauvel, 1868, p. 28 (*Bledius*). Type locality: Chile: San Antonio. — Bernhauer and Schubert, 1911, p. 134 (cited as *pueches*). — Coiffait and Saiz, 1968, pp. 425, 426 (subg. *Astycops*; key, redescription). — Saiz, 1973, p. 230 (key, notes, discussion). **[punctatissimus group]**

puglialis Coiffait, 1976, p. 57 (*Bledius*; subg. *Elbidus*). Type locality: Spain: Andalusia, Cape Trafalgar. **[kochi group]**

pulchellus Kraatz, 1859, p. 169 (*Bledius*). Type locality: Ceylon. — Cameron, 1930, pp. 278–283 (key, redescription). — Scheerpeltz, 1933, p. 1120 (subg. *Hesperophilus*). **[pulchellus group]**

pumilio Erichson, 1840, p. 775 (*Bledius*). Type locality: Colombia. **[emarginatus group]**

punctatissimus LeConte, 1877, p. 226 (*Bledius*; *annularis* group). Type locality: southern California. — Casey, 1889, p. 56. — Fall, 1901, p. 75. — Notman, 1920, p. 698. — Moore, 1964 (habitat, larva, key, redescription). — Herman, 1972, pp. 140–145 (*Psamathobledius*; redescription, key, illustrations, distribution, natural history, synonyms). — Coiffait, 1981c, p. 290 (distribution). — Griffiths and Griffiths, 1983 (natural history). — Herman, 1983a, pp. 119, 134 (lectotype, dis-distribution). **[punctatissimus group]**

esposus Blackwelder, 1943, p. 114 (*Bledius*). Type locality: Antigua, St. Johns. Blackwelder, 1947, p. 119 (distribution). — Herman, 1972, pp. 140, 141, 142 (*Psamathobledius*; junior synonym of *punctatissimus*).

pusillus Erichson, 1839, p. 583 (*Bledius*). Type locality: [Germany]: Mark. — Erichson, 1840, p. 773. — Fauvel, 1872, p. 205 (misidentified as *pygmaeus* Erichson). — Fauvel, 1873a, p. 47 (cited as *pygmaeus*). — Fauvel, 1873b, p. 21 (distribution). — Fauvel, 1875, p. xiii (group 3—*Astycops, Bargus, Tadunus*). — Mulsant and Rey, 1878 (subg. *Blediodes*). — Seidlitz, 1891, p. 381 (key). — Ganglbauer, 1895, p. 623 (subg. *Blediodes*). — Stierlin, 1900, p. 393 (key). — Deville, 1907, p. 92 (subg. *Blediodes*). — Reitter, 1909, p. 166 (subg. *Blediodes*; key). — Everts, 1922, p. 140 (notes, distribution). — Winkler, 1925, p. 346 (subg. *Blediodes*). — Porta, 1926, p. 47 (subg. *Blediodes*; key). — Portevin, 1929, p. 412 (key). — Benick, 1937, pp. 75–78 (characters, key). — West, 1942, p. 144 (distribution, habitat). — Benick, 1943, p. 94 (subg. *Blediodes*, characters). — Horion, 1963, p. 285 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 97 (subg. *Hesperophilus*; key). — Scheerpeltz, 1968, p. 33 (subg. *Blediodes*; catalogue). **[annularis group]**

pygmaeus Erichson, 1939, p. 583 (*Bledius*). Type locality: [Germany]: Mark. — Erichson, 1840, p. 774. — Fauvel, 1872, p. 206 (misidentified as *pusillus* Erichson). — Fauvel, 1873a, p. 48 (cited as *pusillus*). — Fauvel, 1875, p. xiii (group 3—*Astycops, Bargus, Tadunus*). — Mulsant and Rey, 1878 (subg. *Blediodes*). — Seidlitz, 1891, p. 381 (key). — Ganglbauer, 1895, p. 623 (subg. *Blediodes*). — Stierlin, 1900, p. 393 (key). — Reitter, 1909, p. 166 (subg. *Blediodes*; key). — Winkler, 1925, p. 346 (subg. *Blediodes*). — Porta, 1926, p. 47 (subg. *Blediodes*; key). — Portevin, 1929, p. 412 (key). — Larsen, 1936 (natural history). — Benick, 1937, pp. 75–78 (characters, key). — Lengerken, 1939, pp. 131–135 (natural history). — West, 1942, p. 144 (distribution, habitat). — Benick, 1943, p. 95 (subg. *Blediodes*; characters). — Horion, 1963, p. 286 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 97 (subg. *Hesperophilus*; key). — Scheerpeltz, 1968, p. 33 (subg. *Blediodes*; catalogue). **[annularis group]**

quadricornis Bernhauer, 1915, p. 135 (*Bledius*). Type locality: E. India: Madura. — Cameron, 1930, p. 272 (subg. *Bledius*; key, redescription). **[bellicosus group]**

javanus Bernhauer, 1915, p. 136 (*Bledius*). Type locality: Java: Mt. Kawlo. (Described as aberration of *quadricornis.*)

rarus Sharp, 1876, p. 394 (*Bledius*). Type locality: Brazil: Ega. **[emarginatus group]**

rastellus Schiødte, 1866, see: *fuscipes* Rye, 1865.

rectangulus Eppelsheim, 1893, p. 61 (*Bledius*). Type locality: Baikal Region: Quellgebiet des Irkut. — Winkler, 1925, p. 346 (subg. *Hesperophilus*). **[albonotatus group]**

rectangulus tenenbaumi Bernhauer: Szujecki, 1968, p. 295. Elevated to species level.

reductus Koch, 1937, see: *infans* Rottenberg, 1870.

regularis Fall, 1910, see: *opacifrons* LeConte, 1877.

relictus Fall, 1901, see: *foraminosus* Casey, 1889.

renominatus Cameron, 1914, p. 203 (*Bledius*). (Replacement name for *bernhaueri.*) — Scheerpeltz, 1933, p. 1121 (subg. *Belidus*). **[infans group]**

bernhaueri Cameron, 1912a, p. 28 (*Bledius*; subg. *Belidus*). Type locality: Dahlak Island.

rhinoceros Cameron, 1930, p. 277 (*Bledius*; subg. *Pucerus*). Type localities: Assam. Burma: Tienzo. — Coiffait, 1978, p. 554 (distribution). **[verres group]**

richteri Scheerpeltz, 1961, pp. 2, 9 (*Bledius*; subg. *Elbidus*). Type locality: Iran, Khuzistan, Shadegan. **[kochi group]**

roettgeni Bernhauer, 1928, p. 9 (*Bledius*; subg. *Hesperophilus*). Type locality: Mesopotamia. — Koch, 1938a, p. 146 (notes). **[verres group]**

rossicus Bernhauer and Schubert, 1911, p. 135 (*Bledius*). (Replacement name for *gracilicornis* Poppius.) — Winkler, 1925, p. 345 (subg. *Blediodes*). — Benick, 1943, p. 94 (subg. *Blediodes*; characters). **[annularis group]**

gracilicornis Poppius, 1907, p. 313 (*Bledius*). Type locality: Russia: Ustj-Zylma.

rotundicollis LeConte, 1877, p. 223 (*Bledius*; *semiferrugineus* group). Type locality: Nebraska: Fort Pierre. — Notman, 1920, p. 697 (key). — Hatch, 1957, p. 99 (notes). — Miyatake, 1967, p. 94. — Herman, 1972, pp. 228–229 (*semiferrugineus* group; redescription, key, illustrations, distribution). — Herman, 1983a, pp. 119, 140 (lectotype, distribution). **[semiferrugineus group]**

rotundicollis Miyatake, 1963, see: *setonis* Miyatake, 1967.

roubali Horion, 1963, p. 278 (*Bledius*; subg. *Blediodes*). (Replacement name for *orientalis* Roubal; cited by Horion with Scheerpeltz as author but Scheerpeltz did not use the name until 1968.) — Lohse, 1964, p. 98 (subg. *Hesperophilus*; key). — Scheerpeltz, 1968, p. 33 (subg. *Blediodes*; catalogue; cited as new name to replace *orientalis*). **[semiferrugineus group]**

orientalis Roubal, 1934, p. 17 (*Bledius*). Type localities: Czechoslovakia: Slovakia: Levice. Rumania: Nadlak, Pecica. — Koch, 1938a, p. 136 (notes). — Horion, 1963, p. 278 (preoccupied name). — Lohse, 1964, p. 98 (synonym of *roubali*).

rubiginosus Erichson, 1840, p. 765 (*Bledius*). Type locality: Carolina meridionali. — LeConte, 1877, pp. 223, 224 (*semiferrugineus* group; redescription, key). — Casey, 1889, p. 55. — Notman, 1920, p. 697 (key). — Herman, 1972, pp. 224–225 (*semiferrugineus* group; redescription, key, illustrations, distribution, natural history). — Frank, 1982, p. 11 (parasites, references). — Herman, 1983a, p. 140 (distribution). **[semiferrugineus group]**

ruddii Stephens, 1832, see: *furcatus* (Olivier), 1812.

rudebecki Scheerpeltz, 1974, p. 74 (*Bledius*; subg. *Euceratobledius*). Type locality: South Africa: Transvaal, Barberspan, 45 mi. SW Lichtenburg. **[lamelliceps group]**

rudis (Walker), 1858, see: *brunnipennis* (Fabricius), 1801.

ruficornis LeConte, 1863, p. 53 (*Bledius*). Type locality: California: San Francisco. — LeConte, 1877, pp. 226, 229 (*annularis* group; redescription, key). — Casey, 1889, pp. 63, 64. — Fall, 1901, p. 75. — Fall, 1910, pp. 112, 113. — Hatch, 1957, p. 100 (subg. *Hesperophilus*; key). — Herman, 1983a, pp. 81–84, 119 (*annularis* group; redescription, key, illustrations, distribution, natural history, lectotype). **[annularis group]**

ruficornis Mulsant and Rey, 1878, see: *longulus* Erichson, 1839.

rufipennis Erichson, 1840, see: *cribricollis* Heer, 1839.

rufipes Germain, 1855, p. 390 (*Bledius*). Type locality: not cited, presumably Chile. — Fairmaire and Germain, 1861. — Coiffait and Saiz, 1968, pp. 424, 426 (subg. *Astycops*; key, redescription). — Saiz, 1973, p. 230 (key, discussion). **[emarginatus group]**

rugosicollis Bernhauer, 1902, p. 43 (*Bledius*). Type locality: Ceylon: Weligama. — Cameron, 1930, p. 285 (redescription). — Scheerpeltz, 1933, p. 1121 (subg. *Hesperophilus*). **[rugosicollis group]**

rugosulus Eppelsheim, 1893, p. 61 (*Bledius*). Type locality: Baikal Region: Quellgebiet des Irkut. — Winkler, 1925, p. 346 (subg. *Blediodes*). **[annularis group]**

rusticus Fall, 1901, see: *bicolor* Casey, 1889.

salinus Cameron, 1947, p. 704 (*Bledius*; subg. *Blediodes*). Type locality: New Zealand: N. Auckland, Ruakaka Beach. **[punctatissimus group]**

salsus Miyatake, 1963, p. 106 (*Bledius*; subg. *Bledius*). Type locality: Japan: Utayu, Kagawa Pref., Shikoku. — Shibata, 1976, p. 139 (distribution, catalogue). **[gigantulus group]**

sanguinicollis Bernhauer, 1937, p. 291 (*Bledius*). Type locality: Kenya: Homa: Sud-Kavirondo. **[kochi group]**

sanguinithorax Bernhauer, 1911, p. 235 (*Bledius*). Type locality: Oestl: Chiva. **[semiferrugineus group]**

santschii Bondroit, 1913, p. 297 (*Bledius*). Type locality: Tunisia: Kairouan. **[incertae sedis]**

sareptanus Fagel, 1970, p. 11 (*Bledius*; subg. *Elbidus*). Type locality: Sarepta. Russia meridionali. **[kochi group]**

sarmaticus Znojko, 1929, p. 206 (*Bledius*; subg. *Bledius*). Type localities: Odessa; Transdnepr Region: Aleshki; Askania-Nova; Stroganovka am Sivash; Krim: Eupatoria; Caucasus Black Sea Coast: Anapa. **[gigantulus group]**

sauteri Bernhauer, 1922, p. 224 (*Bledius*). Type locality: Formosa. — Shibata, 1973, p. 33 (subg. *Bledius*; distribution). **[gigantulus group]**

sparsior Bernhauer, 1929, p. 182 (*Bledius*). Type localities: China: Tientsin, Shanghai. (Described as variety.)

scheerpeltzi Koch, 1934, p. 54 (*Bledius*; subg. *Hesperophilus*). Type locality: Egypt: Tor (east coast of Red Sea, southern Sinai). **[punctatissimus group]**

schoutedeni Cameron, 1928, p. 20 (*Bledius*; subg. *Pucerus*). Type locality: Belgian Congo: Kivu, Kibati. **[semiferrugineus group]**

scutellaris Cameron, 1928, see: *husseini* Quedenfeldt, 1884.

secerdendus Joy, 1911, see: *subniger,* Schneider, 1898.

secernendus Joy, 1912, see: *subniger* Schneider, 1898.

secessus Bondroit, 1912, p. 68 (*Bledius*). Type locality: Emilie. — Winkler, 1925, p. 346 (subg. *Blediodes*). — Porta, 1926, p. 47 (subg. *Blediodes*; key). — Koch, 1938a, pp. 134–136 (discussion). — Benick, 1943, p. 94 (subg. *Blediodes*; characters). — Horion, 1963, p. 284 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 95 (subg. *Hesperophilus*; key). **[annularis group]**

sellatus Sharp, 1889, p. 413 (*Bledius*). Type locality: Japan: Hakodate. — Winkler, 1925, p. 347 (subg. *Hesperophilus*). — Shibata, 1976, p. 140 (distribution, catalogue). **[albonotatus group]**

grandipennis Bernhauer, 1938, p. 26 (*Bledius*). Type localities: Nordwestl. China: Chinkiang. Japan: Vita. (Described as variety.)

semicircularis Lea, 1910, p. 123 (*Bledius*). Type locality: Australia: Queensland, Brisbane. **[bellicosus group]**

semiferrugineus LeConte, 1863, p. 52 (*Bledius*). Type locality: Middle States. — LeConte, 1877, p. 223 (*semiferrugineus* group; redescription, key). — Casey, 1889, p. 52. — Fall, 1910, p. 108. — Blatchley, 1910, p. 464. — Notman, 1920, p. 697 (key). — Herman, 1972, pp. 205–209 (*semiferrugineus* group; redescription, key, illustrations, distribution, natural history, synonyms). — Herman, 1983a, pp. 119, 140 (lectotype, distribution). **[semiferrugineus group]**

canaliculatus Notman, 1920, p. 698 (*Bledius*: *semiferrugineus* group). Type locality: Florida: Fort Myers. — Herman, 1972, pp. 205, 209 (junior synonym of *semiferrugineus*).

semiopacus Bernhauer, 1934, p. 493 (*Bledius*; subg. *Blediodes*). Type localities: South Africa: Natal: Frere; Estcourt. **[emarginatus group]**

setonis Miyatake, 1967, p. 94 (*Bledius*; subg. *Bledius*). (Replacement name for *rotundicollis.*) — Shibata, 1976, p. 140 (distribution, catalogue). **[gigantulus group]**

rotundicollis Miyatake, 1963, p. 109 (*Bledius*; subg. *Bledius*). Type locality: Japan: Ohmishima Island, Ehime Pref., Seto Sea.

seurati Peyerimhoff, 1924, see: *capra* Fauvel, 1875.

sharpi Fowler and Donisthorpe, 1913, see: *fracticornis* (Paykull), 1790.

similis Sharp, 1876, p. 396 (*Bledius*). Type locality: Brazil: Rio Purus. **[emarginatus group]**

simplex Sharp, 1876, p. 395 (*Bledius*). Type locality: Brazil: Rio Solimoes. **[emarginatus group]**

simplicifrons Coiffait, 1979, p. 175 (*Bledius*; subg. *Elbidus*). Type locality: Saudi Arabia: Damman. — Coiffait, 1981a, p. 237 (distribution). **[kochi group]**

simpliciventris Apfelbeck, 1907, see: *dissimilis* Erichson, 1840.

simulator Eppelsheim, 1892, p. 344 (*Bledius*). Type localities: Tashkent; Condradt in Altai Mountains. — Winkler, 1925, p. 345 (subg. *Bledius*). **[gigantulus group]**

sinuatocollis Gerhardt, 1899, see: *opacus* Block, 1799.

sinuatus LeConte, 1877, p. 228 (*Bledius*; *annularis* group). Type locality: Illinois. — Casey, 1889, pp. 59, 60. — Fall, 1910, p. 111. — Herman, 1983a, pp. 93–95, 119 (*annularis* complex; discussion, lectotype). **[annularis group]**

skrimshirii Curtis, 1826, see: *furcatus* (Olivier), 1811.

*soli** Scudder, 1900, p. 71 (*Bledius*). Type locality: Colorado: Florissant (Fossil; Miocene).

somalianus Cameron, 1950, p. 182 (*Bledius*; subg. *Pucerus*). Type locality: Somalia: Gai Mudugh Province. **[verres group]**

sparsicollis Koch, 1939, see: *fontinalis* Bernhauer, 1929.

sparsior Bernhauer, 1929, see: *sauteri* Bernhauer, 1922.

*speciosus** Heer, 1862, p. 46 (*Bledius*). Type locality: Oeningen, Baden (Fossil; Tortonian, Miocene).

spectabilis Kraatz, 1858, p. 821 (*Bledius*). Type locality: Greece. — Fairmaire and Laboulbène, 1854, p. 600 (misidentified as *tricornis* Herbst). — Fauvel, 1865, p. 309 (variety of *tricornis*). — Fauvel, 1872, p. 195 (group 1—*Bledius*). — Fauvel, 1873a, p. 37. — Fauvel, 1873b, p. 19 (distribution). — Fauvel, 1875, p. XII (group 1—*Bledius*). — Mulsant and Rey, 1878 (subg. *Bledius*). — Fauvel, 1886, p. 25 (distribution, notes). — Fowler, 1888, p. 365. — Plateau, 1890, pp. 248, 249 (natural history). — Ganglbauer, 1895, p. 616 (subg. *Bledius*). — Fauvel, 1897, p. 261 (distribution, notes). — Champion, 1898, p. 100 (distribution). — Fauvel, 1902, p. 70 (distribution, notes). — Deville, 1907, p. 89 (subg. *Bledius*; key). — Reitter, 1909, p. 165 (subg. *Bledius*; key). — Everts, 1922, p. 139 (notes, distribution). — Winkler, 1925, p. 345 (subg. *Bledius*. — Porta, 1926, p. 45 (subg. *Bledius*; key). — Lengerken, 1929, p. 73 (natural history, distribution). — Portevin, 1929, p. 410 (key). — Koch, 1934, p. 59 (subg. *Bledius*; key). — Larsen, 1936 (natural history). — Lengerken, 1939, pp. 131–135 (natural history). — Benick, 1939, pp. 25–26 (race). — Paulian, 1941, p. 170 (larva). — West, 1942, pp. 141, 635 (distribution, habitat). — Paulian, 1942, pp. 62–72 (natural history). — Paulian, 1943, pp. 154, 207 (natural history). — Tottenham, 1949, p. 410 (subg. *Bledius*). — Larsen, 1952 (natural history). — Larsen, 1953 (natural history). — Tottenham, 1954, p. 51 (subg. *Bledius*; key, distribution, habitat). — Steel, 1955, p. 240 (natural history). — Bückmann, 1955a, p. 79 (natural history). — Lindroth, 1957, pp. 179, 187, 205 (natural history, distribution). — Kocker, 1958, p. 106 (distribution). — Scheerpeltz, 1961c, p. 250 (distribution, notes). — Horion, 1963, p. 254 (distribution, notes, natural history). — Lohse, 1964, p. 92 (subg. *Bledius*; key). — Smetana, 1965, p. 168 (distribution). — Potoskaya, 1967, p. 32 (larva). — Smetana, 1967, p. 321 (distribution, notes). — Lipkow, 1968, p. 211 (natural history). — Scheerpeltz, 1968 (subg. *Bledius*; catalogue). — Evans et al., 1971 (natural history). — Wheeler et al., 1972 (physiology). — Araujo, 1973 (anatomy, histology). — Bordoni, 1973, p. 664 (distribution). — Lohse, 1978, pp. 13, 14 (characters). — Wyatt, 1982 (natural history). — Frank, 1982, p. 11 (parasites, references). — Elliott et al., 1983, p. 578 (natural history). **[gigantulus group]**

frisius Lohse, 1978, p. 14 (*Bledius*). Type locality: Sylt, Ellenbogen. Subspecies.

specularis Fall, 1910, see: *opacifrons* LeConte, 1877.

splendens Bernhauer, 1932, p. 82 (*Bledius*; subg. *Pucerus*). Type locality: Congo: Leopoldville. **[verres group]**

stabilis Casey, 1889, p. 61 (*Bledius*; *annularis* group). Type locality: Pennsylvania: Allegheny Co. — Herman, 1983a, pp. 93–95, 120 (*annularis* complex; discussion, lectotype). **[annularis group]**

stephensii Westwood, 1827, see: *furcatus* (Olivier), 1811.

strenuus Casey, 1889, p. 44 (*Bledius*; *armatus* group). Type locality: California: San Francisco. — LeConte, 1863, pp. 51, 52 (cited as *armatus* Say). — LeConte, 1877, p. 221 (cited as *armatus* Say). — Casey, 1889, pp. 43, 44, 45, 64 (cited as *armatus* Say). — Fall, 1901, pp. 103, 104. — Notman, 1920, p. 695 (key). — Hatch, 1957, p. 105 (subg. *Hesperophilus*; key). — Herman, 1976, pp. 144–150 (*armatus* group; redescription, key, illustrations, natural history, synonyms). — Herman, 1983a, pp. 120, 140 (lectotype, distribution). **[armatus group]**

furtivus Casey, 1889, p. 45 (*Bledius*; *armatus* group). Type locality: Oregon: The Dalles. — Notman, 1920, p. 105. — Hatch, 1957, p. 105 (junior synonym of *strenuus*). — Herman, 1976, pp. 144, 149 (junior synonym of *strenuus*). — Herman, 1983a, p. 119 (lectotype).

arizonensis Fall, 1910, p. 103 (*Bledius*; *armatus* group). Type locality: Arizona: Flagstaff. — Notman, 1920, p. 695 (key). — Herman, 1976, pp. 144, 149 (junior synonym of *strenuus*). — Herman, 1983a, p. 120 (lectotype).

strictus Fauvel, 1872, p. 211 (*Bledius*). Type localities: Switzerland; Piemont; Syria. — Fauvel, 1873a, p. 53 (cited as new species). — Fauvel, 1875, p. xiii (group 3—*Astycops, Bargus, Tadunus*). — Ganglbauer, 1895, p. 619 (subg. *Blediodes*). — Winkler, 1925, p. 346

(subg. *Blediodes*). — Porta, 1926, p. 46 (subg. *Blediodes*; key). — Koch, 1938, p. 131 (notes). — Benick, 1943, p. 94 (subg. *Blediodes*; characters). — Horion, 1963, p. 269 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 94 (subg. *Hesperophilus*; key). — Scheerpeltz, 1968, p. 33 (subg. *Blediodes*; catalogue). **[annularis group]**

subniger Schneider, 1898, p. 62 (*Bledius*). Type localities: Juist; Norderney; Wangeroog. (Described as variety of *arenarius*.) — Bernhauer and Schubert, 1911, p. 126 (synonym of *arenarius*). — Bondroit, 1912b, p. 450 (synonymy). — Winkler, 1925, p. 346 (subg. *Hesperophilus*). — Blair, 1931, p. 1231 (distribution). — Tottenham, 1949, p. 411 (subg. *Cotysops*). — Tottenham, 1954, p. 55 (subg. *Cotysops*; key, distribution, habitat). — Lohse, 1964, p. 98 (subg. *Cotysops*; key). — Hollander and van Etten, 1974 (natural history). **[basalis group]**

secerdendus Joy, 1911, p. 269 (*Bledius*). Type localities: Dovercourt; Dawlish; Tresco, Scilly Isles; Cloghane Co., Kerry. — Bondroit, 1912b, p. 450 (synonym of *subniger*). — Tottenham, 1949, p. 411 (synonym of *subniger*).

secernendus Joy, 1912, p. 44 (*Bledius*). (Emendation of *secerdendus* Joy.) — Winkler, 1925, p. 346 (synonym of *subniger*).

subopacus Bernhauer, 1908, p. 104 (*Bledius*). Type localities: South West Africa: Gr. Namaland, Chamis, nördlich von Bethanien am Koankip; Okahandja. **[verres group]**

subsinuatus Mulsant and Rey, 1878, see: *opacus* (Block), 1799.

subterraneus Erichson, 1839, p. 584 (*Bledius*). Type locality: [Germany]: Mark. — Heer, 1839, p. 211. — Erichson, 1840, p. 777. — Thomson, 1861, p. 119 (misidentification, cited as *pallipes* Gravenhorst). — Schiødte, 1866, p. 150 (*Astycops*). — Fauvel, 1872, p. 200 (group 3—*Astycops, Bargus, Tadunus*). — Fauvel, 1873a, p. 42. — Fauvel, 1873b, p. 19 (characters, distribution). — Fauvel, 1875, p. xiii (group 3—*Astycops, Bargus, Tadunus*). — Mulsant and Rey, 1878 (subg. *Astycops*). — Fowler, 1888, p. 368. — Seidlitz, 1891, p. 381 (subg. *Bargus*; key). — Ganglbauer, 1895, p. 624 (subg. *Hesperophilus*). — Stierlin, 1900, p. 394 (subg. *Bargus*; key). — Deville, 1907, p. 90 (subg. *Blediodes*; key). — Reitter, 1909, p. 166 (subg. *Blediodes*; key). — Poppius, 1909a, p. 10 (subg. *Hesperophilus*; distribution). — Everts, 1922, pp. 142 (notes, distribution, key). — Winkler, 1925, p. 346 (subg. *Hesperophilus*). — Krogerus, 1925b (key, natural history, larva). — Krogerus, 1925a (natural history). — Porta, 1926, p. 48 (subg. *Hesperophilus*). — Portevin, 1929, p. 411 (key). — Benick, 1936, pp. 8–9 (key, notes). — Hansen, 1940, p. 583 (key). — West, 1942, p. 145 (distribution, habitat). — Strand, 1946, p. 241 (distribution). — Tottenham, 1949, p. 411 (subg. *Astycops*). — Tottenham, 1954, p. 54 (subg. *Astycops*; key, distribution, habitat). — Horion, 1963, p. 289 (subg. *Hesperophilus*; distribution, notes). — Lohse, 1964, p. 99 (subg. *Astycops*; key). — Potoskaya, 1967, p. 33 (larva). — Szujecki, 1968, p. 296 (subg. *Astycops*; key). — Scheerpeltz, 1968, p. 34 (subg. *Hesperophilus*; catalogue). — Frank, 1982, p. 12 (parasites, references). **[albonotatus group]**

sulcicollis Koch, 1938, see: *dissimilis* Erichson, 1840.

sus Aube, 1850, see: *femoralis* Gyllenhal, 1827.

susae Herman, 1983, p. 98 (*Bledius*; *aequatorialis* group). Type locality: Texas: Aransas Co.: 4 mi. S Rockport. **[aequatorialis group]**

suturalis LeConte, 1863, p. 54 (*Bledius*). Type locality: Arizona: Gila River. — LeConte, 1877, pp. 226, 231 (*annularis* group; redescription, key). — Fall, 1910, p. 113. — Herman, 1983a, pp. 53–57, 119 (*annularis* group; redescription, key, illustrations, distribution, natural history, synonyms, lectotype). **[annularis group]**

luteipennis LeConte, 1877, p. 227 (*Bledius*; *annularis* group). Type locality: California: San Bernardino. — Fall, 1901, p. 75. — Herman, 1983a, pp. 53, 56, 119 (junior synonym of *suturalis*, lectotype).

pleuralis LeConte, 1877, p. 229 (*Bledius*; *annularis* group). Type locality: California: San Bernardino. — Fall, 1901, p. 75. — Herman, 1983a, pp. 53, 56, 119 (junior synonym of *suturalis*, lectotype).

medialis Fall, 1910, p. 113 (*Bledius*). Type locality: British Columbia: Vancouver Island. — Hatch, 1957, p. 103 (subg. *Hesperophilus*; key). — Herman, 1983a, pp. 53, 56, 120 (junior synonym of *suturalis*, lectotype).

oregonensis Hatch, 1957, p. 103 (*Bledius*; subg. *Hesperophilus*). Type locality: Oregon: Condon. — Herman, 1983a, pp. 53, 56 (junior synonym of *suturalis*).

tallaci Fall, 1910, p. 106 (*Bledius*). Type locality: California: Lake Tahoe, Tallac. — Notman, 1920, p. 697 (*semiferrugineus* group; key). — Herman, 1972, pp. 221–224 (*semiferrugineus* group; redescription, key, illustrations, distribution). — Herman, 1983a, pp. 121, 141 (lectotype, distribution). **[semiferrugineus group]**

talpa (Gyllenhal), 1810, p. 448 (*Oxytelus*). Type locality: Sweden. — Gyllenhal, 1827. — Curtis, 1829, p. 29 (*Hesperophilus*). — Stephens, 1829, p. 292 (*Hesperophilus*). — Mannerheim, 1831, p. 459 (*Bledius*). — Stephens, 1834 (*Hesperophilus*). — Gistel, 1834, p. 9 (*Dicarenus*). — Boisduval and Lacordaire, 1835, p. 458 (*Bledius*). — Erichson, 1840, p. 777. — Thomson, 1861 (*Astycops*). — Schiødte, 1864, p. 124, tab. XII (larva). — Schiødte, 1866, p. 150 (*Astycops*). — Thomson, 1867 (*Astycops*). — Fauvel, 1872, p. 200 (group 3—*Astycops, Bargus, Tadunus*). — Fauvel, 1873a, p. 42. — Fauvel, 1873b, p. 19 (note). — Fauvel, 1875, p. xiii (group 3—*Astycops, Bargus, Tadunus*). — Mulsant and Rey, 1878 (subg. *Astycops*). — Seidlitz, 1891, p. 382 (subg. *Bargus*; key). — Ganglbauer, 1895, p. 624 (subg. *Hesperophilus*). — Stierlin, 1900, p. 395 (subg. *Astycops*; key). — Reitter, 1909, p. 166 (subg. *Blediodes*; key). — Winkler, 1925, p. 346 (subg. *Hesperophilus*). — Krogerus, 1925b (key, natural history, egg, larva, pupa). — Porta, 1934, p. 116 (subg. *Hesperophilus*; distribution). — West, 1942, p. 145 (distribution, habitat). — Strand, 1946, p. 241 (distribution). — Horion, 1963, p. 288 (subg. *Hesperophilus*; distribution, notes). — Lohse, 1964, p. 99 (subg. *Astycops*; key). — Potoskaya, 1967, p. 33 (larva). — Szujecki, 1968, p. 296 (subg. *Astycops*; key). — Scheerpeltz, 1968, p. 34 (subg. *Hesperophilus*; catalogue). — Andersen, 1982, p. 65 (natural history). **[albonotatus group]**

tarandus Herman, 1970, p. 379 (*Bledius*). (Replacement name for *divisus* LeConte, not Marsham.) — Herman, 1983a, pp. 35–39 (*annularis* group; redescription, key, illustrations, distribution, natural history, synonyms). **[albonotatus group]**

divisus LeConte, 1863, p. 53 (*Bledius*). Type locality: Nebraska: Platte River Valley. — LeConte, 1877, pp. 226, 229 (*annularis* group; redescription, key). — Hatch, 1957, p. 104 (cited as *albonotatus*). — Herman, 1983a, p. 35, 118 (junior synonym, lectotype).

taruensis Cameron, 1920, p. 144 (*Bledius*; subg. *Elbidus*). Type locality: India: Pesawar, Taru. — Cameron, 1930, p. 274 (subg. *Elbidus*; redescription). **[kochi group]**

tau LeConte, 1877, p. 230 (*Bledius*; *annularis* group). Type locality: New York. — Herman, 1983a, pp. 43–45, 119 (*annularis* group; redescription, key, illustrations, distribution, natural history, lectotype). **[albonotatus group]**

taurus (Germar), 1825, see: *furcatus* (Olivier), 1811.

tenebricosus Scheerpeltz, 1974, p. 77 (*Bledius*; subg. *Hesperophilus*). Type locality: South Africa: Cape Province: Franschhoek Bosreserve, Upper Berg Reserve. **[punctatissimus group]**

tenenbaumi Bernhauer, 1936, p. 239 (*Bledius*). Type locality: Poland: Swider. (Described as subspecies of *rectangulus* Eppelsheim.) — Szujecki, 1968, pp. 293, 294, 295, 296 (subg. *Astycops*; elevated to species, key, redescription). **[albonotatus group]**

tenuis Casey, 1889, see: *flavipennis* LeConte, 1863.

tenuiverres Scheerpeltz, 1974, p. 80 (*Bledius*; subg. *Pucerus*). Type locality: South Africa: Franschhoek Bosreserve; Upper Berg River. **[verres group]**

terebrans (Schiødte), 1866, p. 149 (*Bargus*). Type locality: Denmark. — Fowler, 1888, p. 367 (junior synonym of *pallipes*). — Ganglbauer, 1895, p. 618 (synonym of *pallipes*). — Bernhauer and Schubert, 1911 (synonym of *pallipes*). — Sharp, 1911, p. 33 (valid species). — Cameron, 1912b, p. 89 (synonymy). — Bondroit, 1912a, p. 64 (synonymy, characters). — Everts, 1914 (notes). — Everts, 1922, pp. 142, 143 (notes, distribution, key). — Winkler, 1925, p. 345 (subg. *Blediodes*). — Krogerus, 1925b (key, natural history). — Lindroth, 1935 (key, notes). — Koch, 1938a, p. 130 (notes). — Hansen, 1940, p. 583 (key). — West, 1942, p. 142 (distribution, habitat). — Benick, 1943, p. 94 (subg. *Blediodes*; characters). — Strand, 1946, p. 239 (distribution). — Tottenham, 1949, p. 411 (subg. *Hesperophilus*). — Tottenham, 1954, p. 54 (subg. *Hesperophilus*; key, distribution, habitat). — Scheerpeltz, 1963, p. 263 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 92 (subg. *Hesperophilus*; key). **[annularis group]**

campi Bondroit, 1907, p. 24 (*Bledius*). Type locality: Belgium: Beverloo. — Cameron, 1912b, pp. 89–90 (synonym of *terebrans*). — Bondroit, 1912a, p. 66 (synonym of *terebrans*). — Bondroit, 1913, p. 297 (notes).

testaceipennis Lynch, 1884, p. 355 (*Bledius*). Type locality: Argentina: Buenos Aires: Chacabuco. — Bernhauer, 1927a, p. 233 (key). **[emarginatus group]**

thinopus Herman, 1976, p. 86 (*Bledius*; *basalis* group). Type locality: Florida: Wakulla Co.: Alligator Point. **[basalis group]**

tibialis Heer, 1839, p. 212 (*Bledius*). Type locality: Switzerland: Geneva, Arve River. — Jacquelin du Val, 1859, p. 76. — Fauvel, 1872, p. 198 (group 3—*Astycops, Bargus, Tadunus*). — Fauvel, 1873a, p. 41. — Fauvel, 1875, p. xiii (group 3—*Astycops, Bargus, Tadunus*). — Mulsant and Rey, 1878 (subg. *Astycops*). — Ganglbauer, 1895, p. 626 (subg. *Hesperophilus*). — Stierlin, 1900, p. 395 (subg. *Astycops*; key). — Reitter, 1909, p. 168 (subg. *Blediodes*;

key). — Everts, 1922, p. 139 (notes, distribution). — Winkler, 1925, p. 346 (subg. *Hesperophilus*). — Porta, 1926, p. 48 (subg. *Hesperophilus*; key). — Krogerus, 1928 (natural history). — Portevin, 1929, p. 414 (key). — West, 1942, pp. 145, 635 (distribution, habitat). — Smetana, 1959, p. 201 (distribution). — Horion, 1963, p. 292 (subg. *Hesperophilus*; distribution, notes). — Lohse, 1964, p. 99 (subg. *Astycops*; key). — Szujecki, 1968, p. 296 (subg. *Astycops*; key). — Scheerpeltz, 1968, p. 34 (subg. *Hesperophilus*; catalogue). — Smetana, 1975, p. 162 (distribution, notes). **[tibialis group]**

pubescens Kolenati, 1846, p. 25 (*Bledius*). Type localities: Caucasus Region: Elisabethopol; Karabagh. — Jacquelin du Val, 1859, p. 76 (junior synonym of *tibialis*).

transcaspicus Bernhauer, 1913, p. 220 (*Bledius*). Type localities: Transcaspian: Kuschk; Merv; Dortkuju. — Winkler, 1925, p. 346 (subg. *Blediodes*). — Smetana, 1975, p. 161 (distribution, notes). **[semiferrugineus group]**

transitus Fall, 1919, see: *gentilis* Casey, 1889.

transversemaculatus Koch, 1934, p. 52 (*Bledius*; subg. *Hesperophilus*). Type localities: Egypt: El Wasfya; Ismailia. **[debilis group]**

transversus Cameron, 1930, p. 277 (*Bledius*; subg. *Pucerus*). Type locality: India: Dehra Dun. **[verres group]**

triangulum Baudi, 1848, see: *fossor* Heer, 1839.

tricornis (Herbst), 1784, p. 149 (*Staphylinus*). Type locality: Germany: Berlin. — Gravenhorst, 1802, p. 109 (*Oxytelus*). — Gravenhorst, 1806, p. 196 (*Oxytelus*). — Gyllenhal, 1810, p. 444 (*Oxytelus*). — Olivier, 1811. — Haworth, 1812, p. 97 (*Staphylinus*). — Burrell, 1812, p. 236 (*Staphylinus*). — Burrell, 1812, pp. 310–311 (natural history). — Curtis, 1826, pl. 143 (*Bledius*). — Gyllenhal, 1827. — Stephens, 1829, p. 292. — Mannerheim, 1831, p. 458 (*Bledius*). — Stephens, 1834 (*Bledius*). — Gistel, 1834, p. 9 (*Dicarenus*). — Boisduval and Lacordaire, 1835, p. 456 (*Bledius*). — Runde, 1835, p. 17 (*Bledius*). — Audouin, 1837 (*Oxytelus*). — Erichson, 1839, p. 578 (*Bledius*). — Erichson, 1840, p. 763. — Laporte, 1840, p. 188. — Jacquelin du Val, 1859, p. 76. — Mulsant and Rey, 1861, p. 165 (synonym of *nuchicornis*). — Thomson, 1861. — Schiødte, 1864, p. 123, tab. XII (larva, pupa). — Schiødte, 1866, p. 145 (*Bledius*). — Thomson, 1867. — Kraatz, 1868, pp. 346–347 (synonymy). — Fauvel, 1872, p. 193 (group 1—*Bledius*). — Fauvel, 1873a, p. 35. — Fauvel, 1873b, p. 19 (distribution). — Fauvel, 1875, p. XII (group 1—*Bledius*). — Mulsant and Rey, 1878 (subg. *Bledius*). — Fauvel, 1884, p. 78 (synonyms). — Fowler, 1888, p. 366. — Plateau, 1890, pp. 248–249 (natural history). — Seidlitz, 1891, p. 380 (subg. *Bledius*; key). — Ganglbauer, 1895, p. 615 (subg. *Bledius*). — Stierlin, 1900, p. 392 (subg. *Bledius*; key). — Deville, 1907, p. 89 (subg. *Bledius*; key). — Reitter, 1909, p. 165 (subg. *Bledius*; key). — Everts, 1922, p. 139 (notes, distribution). — Winkler, 1925, p. 345 (subg. *Bledius*). — Krogerus, 1925b (natural history, key). — Porta, 1926, p. 45 (subg. *Bledius*; key). — Lengerken, 1929, pp. 35, 76 (natural history, distribution). — Portevin, 1929, p. 410 (key). — Benick, 1934, p. 190 (key). — Larsen, 1936 (natural history). — Lengerken, 1939, pp. 131–135 (natural history). — West, 1942, p. 141 (distribution, habitat). — Paulian, 1943, p. 206 (natural history). — Strand, 1946, p. 238 (distribution). — Tottenham, 1949, p. 410 (subg. *Bledius*). — Larsen, 1953 (natural history). — Tottenham, 1954, p. 50 (subg. *Bledius*; key, distribution, habitat). — Steel, 1955, p. 240 (natural history). — Kocker, 1958, p. 106 (distribution). — Smetana, 1959, p. 200 (distribution). — Hick, 1959, p. 112 (natural history). — Scheerpeltz, 1961c, p. 250 (distribution, notes). — Horion, 1963, p. 252 (distribution, notes, natural history). — Lohse, 1964, p. 91 (subg. *Bledius*; key). — Potoskaya, 1967, p. 32 (larva). — Lipkow, 1968, p. 210 (natural history). — Scheerpeltz, 1968, p. 31 (subg. *Bledius*; catalogue). — Bordoni, 1973, p. 665 (distribution). — Smetana, 1975, p. 160 (distribution, notes). — Lohse, 1978, pp. 13, 14 (characters). **[gigantulus group]**

armatus (Panzer), 1799, p. 17 (*Staphylinus*). — Gravenhorst, 1802, p. 110 (*Oxytelus*; synonym of *tricornis*). — Gyllenhal, 1810, p. 444 (junior synonym of *tricornis*). — Leach, 1819, p. 172 (*Bledius*). — Gyllenhal, 1827. — Gistel, 1834, p. 9 (*Dicarenus*). — Erichson, 1839, p. 578 (*Bledius*; junior synonym of *tricornis*). — Erichson, 1840, p. 763.

nuchicornis Mulsant and Rey, 1861, p. 165 (*Bledius*). Type locality: Versailles. — Kraatz, 1868, pp. 346–347 (junior synonym of *tricornis*). — Fauvel, 1873a, p. 35. — Seidlitz, 1891, p. 381 (synonym of *bicornis*). — Ganglbauer, 1895, p. 615 (synonym of *tricornis*).

trinidadensis Blackwelder, 1943, p. 116 (*Bledius*). Type locality: Trinidad, St. Augustine, St. George Co., Ward of Tacarigua, **[emarginatus group]**

tripolitanus Koch, 1934, see: *tristis* Aube, 1843.

tristis Aube, 1843, p. 92 (*Bledius*). Type locality: Sicily. — Fauvel, 1872, p. 198 (group 2—*Hesperophilus*). — Fauvel, 1873a, p. 40. — Fauvel, 1873b, p. 19 (distribution). — Fauvel, 1875, p. xiii (group 2—*Hesperophilus*). — Mulsant and Rey, 1878 (subg. *Hesperophilus*). — Fauvel, 1886, p. 26 (distribution, notes). — Ganglbauer, 1895, p. 626 (subg. *Hesperophilus*). — Fauvel, 1897, p. 262 (distribution, notes). — Fauvel, 1902, p. 71 (distribution, notes). — Winkler, 1925, p. 347 (subg. *Hesperophilus*). — Porta, 1926, p. 48 (subg. *Hesperophilus*; key). — Portevin, 1929, p. 412 (key). — Koch, 1934, p. 63 (subg. *Hesperophilus*; key). — Koch, 1938a, p. 142 (notes). **[punctatissimus group]**

tripolitanus Koch, 1934, p. 53 (*Bledius*; subg. *Hesperophilus*). Type locality: Libya: Tripolis. Subspecies.

minarzi Bernhauer, 1929, p. 182 (*Bledius*; subg. *Hesperophilus*). Type localities: Italy: Grado. Corsica. — Porta, 1934, p. 116 (subg. *Hesperophilus*; key). — Koch, 1938a, p. 142 (subspecies of *tristis*). — Porta, 1949, p. 140 (distribution).

normandi Koch, 1938a, p. 144 (*Bledius*; subg. *Hesperophilus*). Type locality: Tunisia: Djerba. Subspecies.

atlanticus Koch, 1938c, p. 336 (*Bledius*; subg. *Hesperophilus*). Type locality: France: St. Gilles s. Vie nella Vendee. Subspecies.

brevicollis Mulsant and Rey, 1861, p. 170 (*Bledius*). Type locality: Hyeres. — Fauvel, 1872, p. 198 (junior synonym of *tristis*). — Fauvel, 1873a, p. 40. — Koch, 1938a, p. 142 (notes). — Porta, 1949, p. 140 (distribution).

albanicus Herman, **New Name** (replacement name for *nebulosus* Koch).

nebulosus Koch, 1938a, p. 143 (*Bledius*; subg. *Hesperophilus*). Type locality: Albania: Valona. Subspecies. (Name **preoccupied** by *nebulosus* Casey, 1899.)

troglodytes Erichson, 1840, see: *emarginatus* (Say), 1834.

tuberculatus (Fabricius), 1798, p. 181 (*Staphylinus*). Type locality: India. — Erichson, 1840, p. 779 (*Bledius*; list). — Fauvel, 1882 (*Bledius*). — Bernhauer and Schubert, 1911, p. 136 (subg. *Pucerus*). — Winkler, 1925, p. 347 (subg. *Pucerus*). — Cameron, 1930, pp. 275–276 (subg. *Pucerus*; key, redescription). — Koch, 1934, pp. 57, 61 (subg. *Pucerus*; key, notes). **[verres group]**

tuniseus Fagel, 1970, p. 7 (*Bledius*; subg. *Elbidus*). Type locality: Tunisia: Kebili. **[kochi group]**

turbulentus Casey, 1889, p. 70 (*Bledius*; *basalis* group). Type locality: Florida. — Herman, 1976, pp. 94–96 (*basalis* group; redescription, key, illustrations, distribution, natural history). — Herman, 1983a, pp. 120, 141 (lectotype, distribution). **[basalis group]**

turcmenus Fagel, 1970, p. 10 (*Bledius*; subg. *Elbidus*). Type locality: USSR: Turkmenistan: Bairam-Ali. **[kochi group]**

turgidus Casey, 1889, p. 52 (*Bledius*; *semiferrugineus* group). Type locality: Colorado: Fort Garland. — Snow, 1906, p. 171 (cited as *B. ornatus*). — Fall and Cockerell, 1907, p. 168 (cited as *ornatus*). — Notman, 1920, p. 696. — Herman, 1983a, pp. 71–73, 120 (*annularis* group; redescription, key, illustrations, distribution, natural history, synonyms, lectotype). **[annularis group]**

borealis Blatchley, 1910, p. 465 (*Bledius*). Type locality: Indiana: Lake Co.: Pine. — Herman, 1983a, pp. 71, 73 (junior synonym of *turgidus*).

bowronensis Hatch, 1957, p. 105 (*Bledius*; subg. *Hesperophilus*). Type locality: British Columbia: Bowron Lake. — Herman, 1983a, pp. 72, 73 (junior synonym of *turgidus*).

ugandae Bernhauer, 1940, p. 344 (*Bledius*). Type locality: Kenya: Kerio Rivermouth. **[verres group]**

unicornis (Germar), 1825, fasc. 12, nr. 3 (*Oxytelus*). Type locality: Illyria. — Mannerheim, 1831, p. 459 (*Bledius*). — Runde, 1835, p. 18. — Erichson, 1840, p. 764. — Fauvel, 1872, p. 192 (group 1—*Bledius*). — Fauvel, 1873a, p. 34. — Fauvel, 1875, p. XII (group 1—*Bledius*). — Mulsant and Rey, 1878 (subg. *Bledius*). — Fauvel, 1886, p. 25 (distribution, notes). — Fowler, 1888, p. 365. — Seidlitz, 1891, p. 381 (subg. *Bledius*; key). — Ganglbauer, 1895, p. 616 (subg. *Bledius*). — Fauvel, 1897, p. 260 (distribution, notes). — Champion, 1898, p. 100 (distribution). — Fauvel, 1902, p. 70 (distribution, notes). — Deville, 1907, p. 89 (subg. *Bledius*; key). — Reitter, 1909, p. 165 (subg. *Bledius*; key). — Winkler, 1925, p. 345 (subg. *Bledius*). — Porta, 1926, p. 45 (subg. *Bledius*; key). — Lengerken, 1929, p. 75 (natural history, distribution). — Portevin, 1929, p. 410 (key). — Blair, 1931, p. 1231 (distribution). — Koch, 1937 (subg. *Bledius*). — Paulian, 1941, p. 171 (larva). — Tottenham, 1949, p. 410 (subg. *Bledius*). — Tottenham, 1954, p. 50 (subg. *Bledius*; key, distribution, habitat). — Kocker, 1958, p. 106 (distribution). — Horion, 1963, p. 257 (distribution, notes). — Lohse, 1964, p. 91 (subg. *Bledius*; key). — Potoskaya, 1967, p. 32 (larva). — Smetana, 1967, p. 322 (distribution, key). — Scheerpeltz, 1968, p. 31 (subg. *Bledius*; catalogue). — Bordoni, 1973, p. 666 (distribution). — Coiffait, 1981a, p. 237 (distribution). — Frank, 1982, p. 12 (parasites, references). **[gigantulus group]**

gladiator Normand, 1934, p. 52 (*Bledius*). Type locality: Tunisia: Sousse. (Described as subspecies of *unicornis*.)

hispidus Parfitt, 1857, p. 5409 (*Bledius*). Type locality: Britain: Exmouth. — Ganglbauer, 1895, p. 616 (synonym of *unicornis*).

juvencus Erichson, 1840, p. 763 (*Bledius*). Type locality: Russia meridionali. — Fauvel, 1875, p. XII (group 1 — *Bledius*). — Mulsant and Rey, 1878 (subg. *Elbidus*). — Fauvel, 1902, p. 70 (synonym of *unicornis*).

monoceros Rosenhauer, 1856, p. 78 (*Bledius*). Type locality: Spain: Cadiz. — Fauvel, 1872, p. 192 (junior synonym of *unicornis*). — Fauvel, 1873a, p. 34. — Mulsant and Rey, 1878 (subg. *Bledius*). — Fowler, 1888, p. 366 (synonym of *unicornis*). — Ganglbauer, 1895, p. 616 (synonym of *unicornis*).

galeatus Wollaston, 1864, p. 594 (*Bledius*). Type locality: Canary Islands: Lanzarote, the Salinas. — Fauvel, 1897, p. 260 (distribution, notes). — Fauvel, 1902, p. 70 (synonym of *unicornis*). — Koch, 1934, pp. 50, 59 (subg. *Bledius*; key, notes).

winkleri Bernhauer, 1905, p. 588 (*Bledius*). Type locality: Kephallenia. — Müller, 1908, p. 236 (geographic form of *unicornis*).

crenulatus Stierlin, 1867, p. 222 (*Bledius*). Type locality: Sarepta. — Fauvel, 1873b, p. 19 (junior synonym of *unicornis*). — Ganglbauer, 1895, p. 616 (synonym of *unicornis*). — Fauvel, 1902, p. 70 (synonym of *unicornis*).

validepunctatus Scheerpeltz, 1974, p. 76 (*Bledius*; subg. *Blediodes*). Type locality: South Africa: Natal: Estcourt. **[semiferrugineus group]**

venus Herman, 1983, p. 26 (*Bledius*; *annularis* group). Type locality: California: San Luis Obispo Co.: 13.6 mi. ENE Arroyo Grande, Huasna Creek. **[albonotatus group]**

verres Erichson, 1840, p. 776 (*Bledius*). Type locality: Sardinia. — Fauvel, 1872, p. 196 (group 2—*Hesperophilus*). — Fauvel, 1873a, p. 38. — Fauvel, 1875, p. xiii (group 2—*Hesperophilus*). — Mulsant and Rey, 1878 (subg. *Pucerus*). — Fauvel, 1886, p. 25 (distribution, notes). — Ganglbauer, 1895, p. 627 (subg. *Pucerus*). — Fauvel, 1897, p. 261 (distribution, notes). — Champion, 1898, p. 100 (distribution). — Fauvel, 1902, p. 71 (distribution, notes). — Winkler, 1925, p. 347 (subg. *Pucerus*). — Porta, 1926, p. 47 (subg. *Pucerus*; key). — Portevin, 1929, p. 413 (key). — Cameron, 1930, pp. 270–286 (subg. *Pucerus*; key, redescription). — Koch, 1934, p. 60 (key). — Kocker, 1958, p. 110 (distribution). — Smetana, 1959, p. 201 (distribution). — Scheerpeltz, 1961c, p. 251 (distribution, notes). — Horion, 1963, p. 294 (subg. *Pucerus*; distribution, notes). — Lohse, 1964, p. 99 (subg. *Pucerus*; key). — Smetana, 1967, p. 323 (distribution, notes). — Scheerpeltz, 1968, p. 34 (subg. *Pucerus*; catalogue). — Scheerpeltz, 1974a, p. 9 (distribution). **[verres group]**

cinctus Motschulsky, 1860, p. 555 (*Bledius*). Type localities: Piatigorsk; Caucasus; Station Gorskaja, Volga River.

monachus Bernhauer, 1914, p. 9 (*Bledius*). Type locality: Corfu. (Described as subspecies.) — Winkler, 1925, p. 347 (variety of *verres*).

monachus[30] Cameron, 1930, p. 275 (*Bledius*; subg. *Pucerus*). Type localities: Siwaliks: Lachiwala. Kumaon: Ranikhet. (Described as variety of *verres*.)

verticalis Notman, 1921, p. 148 (*Bledius*; *annularis* group). Type locality: New York: Chautauqua Co.: Westfield. — Herman, 1983a, pp. 97–98 (species unknown; discussion). **[incertae sedis]**

victoriae[31] Bernhauer and Schubert, 1911, p. 137 (*Bledius*). (Replacement name for *infans* Blackburn.) **[emarginatus group]**

infans Blackburn, 1891, p. 76 (*Bledius*). Type locality: Australia: Victoria, Ovens River.

vilis Mäklin, 1876, p. 22 (*Bledius*). Type locality: Anträffend en enda gang söder om Troitzskoj under 65°45′N lat. — Fauvel, 1884, p. 78 (junior synonym of *pallipes*). — Ganglbauer, 1895, p. 618 (synonym of *pallipes*). — Bernhauer and Schubert, 1911, p. 134 (synonym of *pallipes*). — Bondroit, 1912a, p. 63 (characters, notes). — Everts, 1922, pp. 142–143 (notes, distribution, key). — Winkler, 1925, p. 345 (subg. *Blediodes*). — Krogerus, 1925b (key). — Krogerus, 1925a (natural history). — Benick, 1934, pp. 8–9 (key, notes). — Hansen, 1940, p. 584 (key). — West, 1942, p. 145 (distribution, habitat). — Benick, 1943, p. 94 (subg. *Blediodes*; characters). — Strand, 1946, p. 240 (distribution). — Horion, 1963, p. 266 (subg. *Blediodes*; distribution, notes). — Lohse, 1964, p. 93 (subg. *Hesperophilus*; key). — Andersen, 1983, p. 429 (distribution, natural history). **[annularis group]**

villosus Casey, 1889, p. 57 (*Bledius*; *annularis* group). Type locality: California. — Fall, 1901, p. 76. — Hatch, 1957, pp. 100, 103 (subg. *Hesperophilus*; key). — Herman, 1983a, pp. 60–62, 120 (*annularis* group; redescription,

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[30] This variety was described by Cameron but cited as "*monachus* Bernhauer, *in litt.*"

[31] "*victoriae* n. sp." was inadvertently used by Oke, 1933, p. 117, fig. 66 for *B. australis* and is a nomen nudum.

key, illustrations, distribution, natural history, lectotype). **[annularis group]**

viriosus Herman, 1983, p. 73 (*Bledius*; *annularis* group). Type locality: South Dakota: Pennington Co.: 5.7 mi. SSW Hill City, Spring Creek. **[annularis group]**

vitaensis Bernhauer, 1938, p. 25 (*Bledius*; subg. *Blediodes*). Type locality: Japan: Vita. — Shibata, 1976, p. 141 (distribution, catalogue). **[annularis group]**

vitulus Erichson, 1840, p. 761 (*Bledius*). Type locality: Arabia. — Fauvel, 1875, p. XII (group 1—*Bledius*). — Wollaston, 1877, p. 253 (distribution). — Fauvel, 1886, p. 25 (distribution, notes). — Fauvel, 1897, p. 259 (distribution, notes). — Winkler, 1925, p. 345 (subg. *Bledius*). — Koch, 1934, pp. 50, 60 (subg. *Elbidus*; key, notes). — Scheerpeltz, 1960c, p. 2 (distribution). — Coiffait, 1966, p. 340 (distribution). **[kochi group]**

januvianus Wollaston, 1864, p. 593 (*Bledius*). Type locality: Canary Islands: Lanzarote, salt lake of Januvio. — Fauvel, 1875, p. XII (junior synonym of *vitulus*). — Fauvel, 1897, p. 259 (synonym of *vitulus*).

irmleri Coiffait, 1980, p. 49 (*Bledius*; subg. *Elbidus*). Type locality: Andalusia: Salz, Lagune de Antequara. (Described as variety of *vitulus*.)

vulneratus Reitter, 1909, see: *littoralis* Heer, 1839.

washingtonensis Hatch, 1957, p. 102 (*Bledius*; subg. *Hesperophilus*). Type locality: Washington: Cedar Mountain. — Herman, 1983a, pp. 93–95 (*annularis* complex; discussion). **[annularis group]**

weiseri Bernhauer, 1927, p. 234 (*Bledius*). Type locality: Argentina: Catamarca, Pampa Grande. — Herman, 1972, p. 120 (*Microbledius*). **[forcipatus group]**

westerhauseri Gistel, 1857, p. 58 (*Bledius*). Type locality: Tyrolis. **[incertae sedis]**

winkleri Bernhauer, 1905, see: *unicornis* (Germar), 1825.

withycombei Bernhauer, 1934, p. 157 (*Bledius*). Type locality: Trinidad: St. Augustine. — Blackwelder, 1943, pp. 113, 115 (key, redescription, distribution). **[emarginatus group]**

wombaliensis Bernhauer, 1932, p. 83 (*Bledius*). Type locality: Congo: Wombali. **[verres group]**

wudus Herman, 1983, p. 16 (*Bledius*; *emarginatus* group). Type locality: Florida: Leon Co.: 20 mi. N Tallahassee, Tall Timbers Research Station. **[emarginatus group]**

xiphias Koch, 1938, p. 41 (*Bledius*; subg. *Elbidus*). Type locality: Tunisia: Tunis; Kairouan. **[kochi group]**

yemenicus Coiffait, 1981, p. 22 (*Bledius*; subg. *Pucerus*). Type locality: Yemen: Wadi Zabid. **[semiferrugineus group]**

yezoensis Nakane, 1963, p. 21 (*Bledius*). Type locality: Japan: Hokkaido, Nemuro, Otaito. — Nakane et al., 1965, p. 84, pl. 42, fig. 24. — Shibata, 1976, p. 141 (distribution, catalogue). **[gigantulus group]**

zophus Herman, 1983, p. 39 (*Bledius*; *annularis* group). Type locality: Wyoming: Sheridan Co.: 42 mi. W Sheridan, Prune Creek, at Prune Creek Campground. **[albonotatus group]**

NOMINA NUDA

These names were published but have no description, definition, or indication. Names first published as nomina nuda but later made available are not included. Names that are clearly misspellings of available names are excluded. The author of the nomen nudum is cited as the author of the paper in which it appears even if the name is attributed to another person, unless that person published the name earlier. Some nomina nuda have been published repeatedly but only their first publication is cited herein.

adriaticus Gridelli, 1936, pp. 59, 60.
aegyptiacus Koch, 1934, p. 59.
agnatus Heyden, 1892, p. 100.
cribrarius Dejean, 1833, p. 67.
cylindricollis Znojko, 1929, p. 206.
dorsalis Dejean, 1833, p. 67.
erichsoni Sturm, 1843, p. 52.
fuscus Motschulsky, 1858, p. 71.
illyricus Dejean, 1833, p. 67.
laevicollis Dejean, 1833, p. 67.
laevipennis Koch, 1938, p. 134.
litigiosus Dejean, 1833, p. 67.
obscurellus Kraatz, 1858, p. 826.
obscurior Gridelli, 1936, p. 59.
procerus Dejean, 1833, p. 67.
pudens Kangas, 1939, pp. 172, 174.
punctatus Dejean, 1833, p. 67.
sachsei Kraatz, 1858, p. 838.
simplexiventris Herman, 1970, p. 379.
subcornutus Stephens, 1829, p. 292.
subnitidus Kraatz, 1858, p. 827.
volgens Everts, 1922, p. 140.
zischkai Zischka, 1949, p. 16.

NOMENCLATURAL CHANGES

The following list is intended to make more accessible the nomenclatural changes proposed in this article. The changes of species names are presented and discussed in the Catalog. The generic synonyms are discussed in the introductory remarks for the chapter entitled Classification and Descriptions and in the discussion following the formal description of *Bledius*. The new species, *minniensis*, is described within the chapter Classification and Descriptions and can be found by consulting the Table of Contents or the Index to Scientific Names.

actitus Herman—New Combination, transferred from *Microbledius*.
albanicus—New Name, proposed herein to replace *nebulosus* Koch.
atlanticus Lohse—Preoccupied, replaced by *jutlandensis*.
atramentarius Rottenberg—New Status, elevated to replace *bos* Fauvel which was published later.
bos Fauvel—New Synonym, replaced by *atramentarius* Rottenberg, which was published earlier.
bubalus Gistel—Used herein for the first time since its original publication.
cariniceps Bernhauer—Emendation to replace *carinlceps* Bernhauer, a *lapsus calami*.
carinlceps Bernhauer—*Lapsus calami*, replaced by *cariniceps* Bernhauer.
castaneipennis Mannerheim—New Status, elevated from synonymy with *opacus* Block.
castaneus Mulsant and Rey—Used herein for the first time since its original publication.
chimerinus Gistel—Used herein for the first time since its original publication.
devillei Bondroit—New Synonym of *minor* Mulsant and Rey; it was an unneeded replacement name.
germanicus Wagner—Preoccupied, replaced by *limicola* Tottenham.
ghesquierei Bernhauer—Emendation, replacing *guesquierei* Bernhauer.
guesquierei Bernhauer, *Lapsus calami*, replaced by *ghesquierei* Bernhauer.
gyllenhalii Laporte—Used herein for the first time since its original publication.
jutlandensis—New Name, proposed herein to replace *atlanticus* Lohse.
karachiensis Abdullah and Qadri—New Combination, transferred from *Neobledius*.
limicola Tottenham—Elevated, replacement name from *germanicus* Wagner.
litoreus Herman—New Combination, transferred from *Microbledius*.
Microbledius Herman—New Synonym of *Bledius*.
minor Mulsant and Rey—New Status, elevated from synonymy with *devillei* which was an unnecessary replacement name.
nebulosus Koch—Preoccupied, replaced by *albanicus*.
Neobledius Abdullah and Qadri—New Synonym of *Bledius* and *Elbidus*.
playanus Herman—New Combination, transferred from *Microbledius*.
Psamathobledius Herman—New Synonym of *Bledius*.
westerhauseri Gistel—Used herein for the first time since its original publication.

ADDENDUM

Nearly two months after I read proof for this article, a new species, *Bledius* (*Elbidus*) *pitcheri* from Saudi Arabia, was published by Henri Coiffait (1985. Quatrième contribution à la connaissance des Staphylinides d'Arabie Saoudite. Nouv. Rev. Ent. (n.s.), vol. 2, fasc. 4, pp. 393–396, 3 figs.). I have not examined specimens of *B. pitcheri*; the description and subgeneric assignment leave little doubt that the species is a member of the *kochi* group. This new species increases the number of species of *Bledius* to 440 and of the *kochi* group to 32.

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GEOGRAPHICAL INDEX

This index will permit preparation of lists of species by country.

INDEX OF SCIENTIFIC NAMES

Page numbers in boldface indicate the main reference or description of the taxon and species group assignments. This index excludes names in the catalogue, which is alphabetical and cross-indexed. Unless indicated otherwise, all of the species listed in the index are in *Bledius.*

SUBJECT INDEX

The section on Natural History and part of that on Phylogeny are indexed here.

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CONTENTS OF VOLUME 184