VOLUME 2

AMERICAN BEETLES

Polyphaga: Scarabaeoidea through Curculionoidea

Ross H. Arnett, Jr. • Michael C. Thomas
Paul E. Skelley • J. Howard Frank

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Edited by
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To Ross H. Arnett, Jr.
1919-1999

and

Mary Arnett
1919-2002

Preface

It has been nearly 40 years since Ross H. Arnett, Jr. published the first fascicle of *The Beetles of the United States: A Manual for Identification*. It quickly became an indispensable tool for professional and amateur coleopterists, general entomologists, and naturalists. Although there were four additional printings it has long been out of print and difficult to obtain. It was prepared to replace Bradley's *A Manual of the Genera of Beetles of America, North of Mexico*, which itself was some 30 years out of date in 1960. *American Beetles* is, in turn, designed to replace *The Beetles of the United States*. It is hoped that it will prove to be as useful as its predecessor.

Ironically, much of the preface to the original edition applies today as well as it did 40 years ago:

> Many genera have since been described and reported within the area concerned, and many families have been revised. Extensive changes have been made in the family classification of the beetles of the United States during this period.
>
> The aim of this series of fascicles is to provide a tool for the identification of adult beetles of the United States to family and genus with the aid of illustrations, keys, descriptions, and references to sources for keys and descriptions of the species of this area. All of the genera known to inhabit this area are included in the keys and lists of genera which follow.

The design and format of this work follow closely that of the original edition, but the way it was put together was quite different. Its predecessor was very much the work of one man, Ross H. Arnett, Jr. With a few exceptions (George Ball wrote the carabid treatment for both the 1960 edition and for this one), Dr. Arnett wrote the family treatments of *The Beetles of the United States*. Many specialists reviewed those chapters, but they were almost entirely Dr. Arnett's work.

When Dr. Arnett announced plans to prepare a work to replace *The Beetles of the United States*, coleopterists literally lined up to volunteer their time and expertise in preparing the family treatments. Ultimately, more than 60 coleopterists participated in the preparation of *American Beetles*. This has truly been a community project.

Due to the size of the ensuing work, *American Beetles* is being printed in two volumes. Volume 1 includes the introductory material, and family treatments for the Archostemata, Myxophaga, Adephaga, and Polyphaga: Staphyliniformia. The remainder of the Polyphaga and the keys to families appear here in Volume 2.

Sadly, although Dr. Arnett initiated this project and was instrumental in its planning, he did not live to see its fruition. He became seriously ill in late 1998 and died on July 16, 1999 at the age of 80. We hope he would be pleased with the outcome.

Michael C. Thomas, Ph.D.
Gainesville, Florida
April 3, 2002

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Acknowledgments for Volume II

Originally, Ross Arnett was to have authored many of the family treatments, especially for those families with no specialists available. His death in 1999 left many families without an author. Several volunteers stepped forward, but Dan Young of the University of Wisconsin took responsibility for more than his fair share and got several of his enthusiastic graduate students involved in the project also. The members of the Editorial Board, listed in the Introduction, provided guidance, advice, and constructive criticism, but J. Howard Frank of the University of Florida has been outstanding in his unwavering demands for scholarship and proper English, and joined Paul E. Skelley and Michael C. Thomas, both of the Florida Department of Agriculture and Consumer Services, as an editor of Volume II. John Sulzycki of CRC Press has been more than helpful throughout some trying times.

Many of the excellent habitus drawings beginning the family treatments were done by Eileen R. Van Tassell of the University of Michigan for *The Beetles of the United States*, and for Volume 2 of *American Beetles* she produced excellent new ones for families 100, 108, and 119.

Authors of the family treatments often have acknowledgments in their respective chapters throughout the body of the text.

Ross Arnett's widow, Mary, was always his support staff throughout his long and productive career. After Ross' death, she helped by providing free and gracious access to Ross' files, and by her steady encouragement and quiet conviction that we would indeed be able to finish this, Ross Arnett's last big project. Unfortunately, Mary Arnett did not live to see Volume II published. She became ill in the fall of 2001 and died on January 3, 2002.

And I would like to again acknowledge my wife, Sheila, for her patience and forbearance during the long and sometimes difficult path that led to this volume.

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Editorial Board

Series SCARABAEIFORMIA Crowson 1960

(= Lamellicornia)

Superfamily SCARABAEOIDEA Latreille 1802

INTRODUCTION

by Mary Liz Jameson and Brett C. Ratcliffe

Common name: The scarabaeoid beetles

The superfamily Scarabaeoidea is a large, diverse, cosmopolitan group of beetles. Scarabaeoids are adapted to most habitats, and they are fungivores, herbivores, necrophages, coprophages, saprophages, and some are carnivores. They are widely distributed, even living in the Arctic in animal burrows. Some scarabs exhibit parental care and sociality. Some are myrmecophilous, termitophilous, or ectoparasitic. Many possess extravagant horns, others are able to roll into a compact ball, and still others are highly armored for inquiline life. Some are agricultural pests that may destroy crops while others are used in the biological control of dung and dung flies. Scarabaeoids are popular beetles due to their large size, bright colors, and interesting natural histories. Early Egyptians revered the scarab as a god, Jean Henri Fabre studied their behavior, and Charles Darwin used observations of scarabs in his theory of sexual selection.

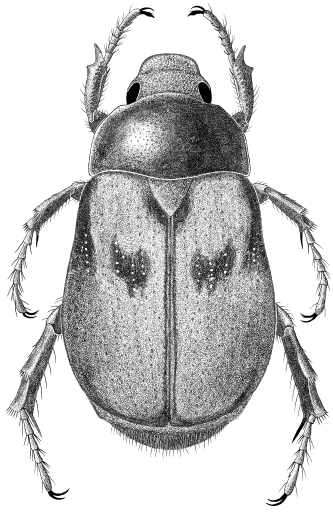

FIGURE 1. *Anomala binotata* (Gyllenhal) (Scarabaeidae) (Used by permission of University of Nebraska State Museum)

Description. Antennal club lamellate. Prothorax can be highly modified for burrowing, with large coxae (most with concealed trochantins and closed coxal cavities). Protibiae dentate with a single spur in most. Wing venation reduced and with a strong intrinsic spring mechanism for folding. Tergite 8 forming a true pygidium and not concealed by tergite 7. Four Malpighian tubules. Larvae scarabaeiform (cylindrical, C-shaped). Superfamily classification: Lawrence and Britton 1991; Lawrence and Newton 1995.

Status of the classification. The hierarchical level of families and subfamilies within the Scarabaeoidea is in disarray and remains unresolved. In the previous rendition of this work (Arnett's *The Beetles of the United States*, 1968), the Scarabaeoidea included three families: Passalidae, Lucanidae, and Scarabaeidae. This three-family system of classification was the "traditional" North American system and had several practical and conceptual advantages. First, it recognized the shared, derived characters that unite subfamilies within the family Scarabaeidae. Second, it provided a classification system that allowed easy retrieval of hierarchical information based on the fact that subfamilies were part of the family Scarabaeidae (*e.g.*, life history, morphology, larval type). Phylogenetic research indicates that the family Scarabaeidae (in the traditional sense) is not a monophyletic group. Therefore, we have chosen to follow the 12-family system established by Browne and Scholtz (1995, 1999) and Lawrence and Newton (1995). This system places emphasis on the differences that separate taxa rather than the similarities that unite them. Whereas families, subfamilies, and tribes in the staphylinoids and curculionoids are being combined because of shared characters (thus increasing efficient data retrieval), the scarabaeoids are being split into numerous families because of supposed differences (thus, in our view, decreasing information retrieval). The debate concerning scarabaeoid classification systems illustrates the weak phylogenetic foundation of the superfamily. This problem is the result of a number of factors including (1) lack of thorough study of all scarabaeoid taxa, (2) lack of diagnostic characters for all taxa, (3) lack of phylogenetic study of all taxa, (4) prevailing philosophies regarding categorical levels, and (5) emphasis in research on the less speciose groups of scarabaeoids and lack of research on the more speciose groups (such as the subfamilies of Scarabaeidae including the Melolonthinae, Rutelinae, Dynastinae, Aphodiinae, and Cetoniinae).

Acknowledgments. Mary Liz Jameson and Brett Ratcliffe thank our scientific illustrators, Mark Marcuson and Angie Fox, for their fine work. Al Newton, Margaret Thayer, Philip Harpootlian, and Andrew Smith are especially acknowledged for assistance with resolving authorship of some taxa and numerous grammatical corrections. For assistance with the keys and other aspects of the manuscript, we thank Andrew Smith, Federico Ocampo, William Warner, and Charles Brodel. Our development of the scarabaeoid chapters was supported by a NSF/PEET grant (DEB9712447) to B. C. Ratcliffe and M. L. Jameson. Parts of the Dynastinae treatment were supported by a NSF/BS&I grant (DEB9870202) to B. C. Ratcliffe.

Within the Scarabaeoidea there is a disparity in the knowledge between less speciose basal lineages and the more speciose groups of "higher" Scarabaeidae. For example, the family Trogidae includes approximately 300 species in four genera. Excellent revisionary, larval, and phylogenetic studies are available for this group (Baker 1968; Scholtz 1982, 1986, 1990, 1991, 1993; Scholtz and Peck 1990). Excellent monographs are also available for the approximately 600 species of Geotrupidae (Howden 1955, 1964, 1979, 1985a-b, 1992; Howden and Cooper 1977; Howden and Martínez 1978) and the Trogidae (Vaurie 1955), and these will provide the foundation for addressing relationships within this group. In comparison, the family Scarabaeidae (*sensu* Lawrence and Newton 1995) includes approximately 91% of the species (ca 27,800) of Scarabaeoidea. Within the Scarabaeidae, approximately 21,000 species are in the subfamilies Melolonthinae, Dynastinae, Rutelinae, and Cetoniinae (the "higher" scarabs). Only a few phylogenetic analyses have addressed relationships of pleurostict subtribes, genera, or species (Ratcliffe 1976; Ratcliffe and Deloya 1992; Jameson 1990, 1996, 1998; Jameson *et al.* 1994; Krell 1993), and only one analysis has been conducted to address tribal or subfamilial relationships (Browne and Scholtz 1999).

Historically, the superfamily Scarabaeoidea was divided into two generalized groups based on the position of the abdominal spiracles; the Laparosticti and Pleurosticti. Pleurostict scarabs were characterized by having most of the abdominal spiracles situated on the upper portion of the sternites (Ritcher 1969; Woodruff 1973) and included taxa whose adults feed on leaves, flowers and pollen, and whose larvae feed primarily on roots and decaying wood. Laparostict scarabs, on the other hand, were characterized by having most of the abdominal spiracles located on the pleural membrane between the tergites and sternites (Ritcher 1969) and included taxa whose adults and larvae feed on dung, carrion, hides, and feathers. The position of the spiracles, however, is not a consistent character (Ritcher 1969), and, in recent years, subfamilies and tribes that were once included in the Laparosticti have been raised to higher taxonomic status (family and subfamily, respectively).

The composition of the Scarabaeoidea remains a topic of debate. Lawrence and Newton (1995) proposed 13 families (12 found in the Nearctic, Belohinidae are Madagascan), and Scholtz and Browne (1996) and Browne and Scholtz (1995, 1998, 1999) proposed 13 families (all Nearctic, including Bolboceratidae; Belohinidae were not addressed). In this work we follow, with some hesitation, the system of Lawrence and Newton (1995) and treat the Scarabaeoidea as including 12 Nearctic families (eight or nine of which were previously considered subfamilies of the family Scarabaeidae, and one of which was previously considered a subfamily of the Lucanidae). Our reluctance to accept elevation of new families within the Scarabaeoidea stems from the fact that: 1) there have been no comprehensive taxonomic treatments of all higher categories of scarabaeoids (families and subfamilies) and, 2) there are few comprehensive, rigorous, phylogenetic analyses of higher scarabaeoid groups and, thus, a lack of synapomorphic characters that establish a basis for uniform familial and subfamilial levels. We *prefer* to see clades delimited by shared derived characters before the elevation of certain taxa to family level. Despite our reluctance to accept this classification system, we have little basis for disputing the validity of current taxonomic conclusions other than the fact that some of these taxonomic conclusions have been based on narrow taxonomic frameworks (only scarab taxa from certain geographic regions rather than all scarab groups) or based on few characters or suites of characters.

Underlying the classification problem is, of course, the fact that we are dealing with constructs that are 200 years old and that pre-date evolutionary theory. Linnaean classifications were based on overall morphological similarity rather than shared, derived characters. Thus, some groups within the scarabaeoids are not monophyletic lineages; instead, they are groups that were created historically because they superficially resembled each other. Our system of classification needs to convey information and concepts and allow for easy retrieval of information. Whether a certain taxon is classified at the level of family or subfamily may be trivial if we can continue to convey the needed information. We remain apprehensive that the trend of elevation to many families within the Scarabaeoidea will result, at least in the short term, in a net loss in retrievability of information.

Despite the considerable debate, phylogenetic analyses of scarabaeoid higher categories are on-going and their results bring us closer to understanding relationships of the groups. A preliminary "total evidence" phylogenetic analysis of 13 families of Scarabaeoidea (excluding Belohinidae, including Bolboceratidae) and most of the subfamilies was conducted using 134 adult and larval characters (Brown and Scholtz 1999). Results of this analysis showed that the superfamily Scarabaeoidea is comprised of three major lineages: the glaresid lineage that consists of only the family Glaresidae; the passalid lineage that consists of two major lines--a glaphyrid line (containing Glaphyridae, Passalidae, Lucanidae, Diphyllostomatidae, Trogidae, Bolboceratidae, and Pleocomidae), and a geotrupid line (containing Geotrupidae, Ochodaeidae, Ceratocanthidae, and Hybosoridae); and the scarab lineage (containing Aphodiinae, Scarabaeinae, Orphninae, Melolonthinae, Rutelinae, Dynastinae, and Cetoniinae).

The series Scarabaeiformia is comprised exclusively of the superfamily Scarabaeoidea. Monophyly of the group is well founded and undisputed (Lawrence and Britton 1991). The sister group for the Scarabaeoidea, however, is not resolved and continues to be debated. Two groups are considered: the Staphyliniformia and the Dascilloidea. The Scarabaeoidea and Staphyliniformia share characters of the wing venation and the abdomen that are not present in the dascilloids (Kukalová-Peck and Lawrence 1993). The Scarabaeoidea and Dascilloidea share similar larval characters (lack of urogomphi that are present in Staphyliniformia, cribriform spiracles, separate galea and lacinia) and adult characters (form of the ommatidium, male genitalia, mouthparts) (Scholtz *et al.* 1994). Lawrence and Newton (1982) argued that similarities in the Dascilloidea and Scarabaeoidea are attributable to either plesiomorphic or convergent characters that are associated with soil-dwelling habits.

Distribution. The superfamily Scarabaeoidea is one of the largest superfamilies in the Coleoptera and includes approximately 2,200 genera and about 31,000 species worldwide (Dalla Torre 1912-1913; Endrödi 1985; Hanski and Cambefort 1991; Krikken 1984; Lawrence 1982; Machatschke 1972; Scholtz 1982). While some of the smaller groups are well known worldwide (*e.g.,* Geotrupidae and Trogidae), some other groups (*e.g.,* Scarabaeidae that comprises 91% of the Scarabaeoidea) cannot be identified to even genus-level with reliability.

In the Nearctic region, the taxonomy of most scarabaeoids is now fairly well known although there remain a few areas of uncertainty. For example, the phylogenetic position of both the Pleocomidae and the Hopliini needs to be addressed. In this work, there are numerous changes in the author and/or date of many genera and even some higher categories since Arnett (1968). These are the result of greater scrutiny of the original literature rather than accepting at face value the often erroneus or incomplete information provided in older catalogs and faunal works.

There are approximately 170 genera and 2,000 species in the United States, Canada, and Nearctic Mexico. Smith (2001) provided a checklist of Nearctic scarabaeoids. Regional works: Blatchley 1910; Loding 1945; Saylor 1948; Edwards 1949; Helgesen and Post 1967; Hatch 1971; Woodruff 1973; Kirk and Balsbaugh 1975; Shook 1978; Lago *et al.* 1979; Ratcliffe 1991; Downie and Arnett 1996; Morón *et al.* 1997; Harpootlian 2001.

Summary of the Families and Subfamilies of Scarabaeoidea of the United States, Canada, and Nearctic Mexico

23. Lucanidae
    - Lucaninae
    - Nicaginae
    - Syndesinae
24. Diphyllostomatidae
25. Passalidae
26. Glaresidae
27. Trogidae
28. Pleocomidae
29. Geotrupidae
    - Bolboceratinae
    - Geotrupinae
30. Ochodaeidae
    - Ochodaeinae
    - Chaetocanthinae
31. Hybosoridae
32. Ceratocanthidae
33. Glaphyridae
34. Scarabaeidae
    - Aphodiinae
    - Scarabaeinae
    - Melolonthinae
    - Rutelinae
    - Dynastinae
    - Cetoniinae

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23. LUCANIDAE Latreille 1804

by Brett C. Ratcliffe

Family common name: The stag beetles

Stag beetles range in size from less than 1 cm to 9 cm. The largest Nearctic species attains a length of 6 cm. Most males possess greatly enlarged, curving mandibles that are sometimes used in combat with male opponents during fights to establish dominance. Female lucanids lack enlarged mandibles. In most, male development of the mandibles is allometric, that is, the size of the mandibles is proportional to the size of the body. Those males with the largest mandibles are referred to as "male majors" and those with the smallest mandibles are called "male minors."

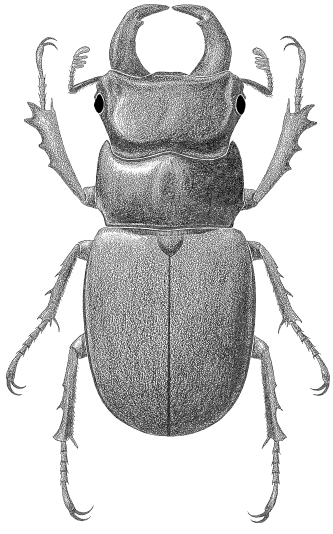


FIGURE 23.1. *Lucanus capreolus* (Linnaeus) (Used by permission of University of Nebraska State Museum)

Description. Length 8.0-60.0 mm. Shape usually weakly convex, subdepressed, or cylindrical, elongate. Color testaceous to reddish brown to black.

Head prognathus, not deflexed. Antennae geniculate or straight, 10-segmented, with 3-7 segmented club (all antennomeres unopposable and tomentose); first antennomere often subequal to remaining antennomeres. Eyes with eucone or acone ommatidia; eye canthus present or absent. Clypeus and labrum fused to frons. Mandibles produced beyond apex of labrum, prominent (males often with large, curved, elongate mandibles). Maxillae with 4-segmented palpi; labium with 3-segmented palpi.

Pronotum weakly convex, base narrower than elytral base, lacking tubercles, ridges, horns, or sulci. Elytra weakly convex, with or without impressed striae. Scutellum exposed, triangular or parabolic. Pygidium concealed by elytra or only weakly exposed. Legs with coxae transverse, mesocoxae separated; protibiae dentate on outer margin, apex with one spur; meso- and metatibia with ridges, apex with 2 spurs; tarsi 5-5-5; claws equal in size, simple; empodium present, extending weakly beyond fifth tarsomere or extending nearly one half claw length, with 2 to several setae. Profemora with tomentose patch anteriorly.

Abdomen with 5 visible sternites; 8 functional abdominal spiracles situated in pleural membrane. Wings well developed, with M-Cu loop and two, apical, detached veins. Male genitalia trilobed. References: Didier and Seguy 1953; Scholtz 1990.

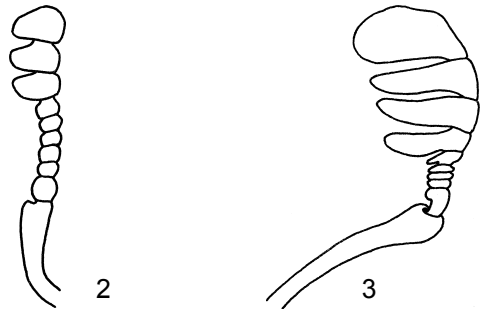
Larvae are scarabaeiform (c-shaped, subcylindrical). Color creamy-white or yellowish (except at caudal end which may be darkened by accumulated feces). Cranium heavily sclerotized, lightly pigmented. Antennae 3-4 segmented, last segment greatly reduced in size. Stemmata absent (present in *Platycerus*). Frontoclypeal suture present. Labrum at apex rounded or weakly lobed. Epipharynx rounded or lobed, with symmetrical tormae. Maxilla with galea and lacinia distinctly separate; maxillary stridulatory teeth absent (present in *Platycerus*); maxillary palpus 4-segmented. Mandibles elongate, asymmetrical. Abdominal segments 3-7 with 2 annuli, each with 1 or more transverse rows of short setae. Spiracles cribriform. Anal opening Y-shaped or longitudinal, surrounded by 2 fleshy lobes. Legs 4-segmented. Stridulatory apparatus on meso- and metathoracic legs present; claws present. References: Ritcher 1966; Scholtz 1990.

Habits and habitats. Lucanids are usually associated with decaying wood and logs in coniferous and deciduous forest habitats. Adults of some species are attracted to lights at night and some feed at sap flows from fluxing trees. Adults of some smaller species have been observed feeding on flowers. The eggs are customarily laid in crevices in bark or logs, and the larvae feed on decaying wood. The larvae resemble those of Scarabaeidae, but in lucanids the anal opening is longitudinal or Y-shaped transverse or Y-shaped in a few. References: Ratcliffe 1991.

Status of the classification. The family Lucanidae has long been considered one of the most primitive groups in the Scarabaeoidea (Crowson 1967; Howden 1982; Ritcher 1966), and scarabaeoid classifications and evolutionary hypotheses have generally regarded the Lucanidae as basal to all scarabaeoids (Howden 1982; Iablokoff-Khnzorian 1977; Lawrence and Newton 1995). However, based on comparison with "primitive" scarabaeoid groups, Scholtz *et al.* (1994) hypothesized that the scarabaeoid family Glaresidae, rather than the Lucanidae, is the most primitive scarabaeoid. According to this hypothesis, the Lucanidae is a member of a clade including the Passalidae, Diphyllostomatidae, Glaphyridae, Trogidae, Pleocomidae, and Bolboceratinae (Geotrupidae).

Prior to the taxonomic elevation of the genus *Diphyllostoma* to the family Diphyllostomatidae (Holloway 1972), the Lucanidae was hypothesized to be most closely related to the Passalidae (Howden 1982). Based on shared characters, it is now thought that the Lucanidae is most closely related to the Diphyllostomatidae (Caveney 1986; Browne and Scholtz 1995).

The world Lucanidae (about 800 species) have been treated in checklists by Benesh (1960) and Maes (1992) and in illustrated



FIGURES 2.23-3.23. Right antenna dorsal view of: 2. *Ceruchus piceus* and 3. *Platycerus* sp.

catalogs by Didier and Seguy (1953) and Mizunuma and Nagai (1994). The latter is spectacular for its colored plates of the world fauna. Benesh (1960) recognized eight subfamilies, four of which occurred in the United States. The classification of the North American species had been relatively stable until Howden and Lawrence (1974) proposed a significant rearranging of genera within subfamilies based partly on the work of Holloway (1960, 1968, 1969). This newer classification is followed here, with three subfamilies now recognized as occurring in North America: Nicaginae, Syndesinae, and Lucaninae.

Distribution. The world fauna consists of about 800 species (Mizunuma and Nagai 1994) with more species found in Asia than in other areas. In North America there are three subfamilies with eight genera and 24 species. Keys to adults: Benesh 1946; Blatchley 1910; Howden and Lawrence 1974; Ratcliffe 1991. Keys to larvae: Ritcher 1966; Smith 2001. World catalog: Krajcik 2001. Regional works: Edwards 1949; Hatch 1971; Kirk and Balsbaugh 1975; Ratcliffe 1991. Biology: Milne 1933; Hoffman 1937.

Key to the Nearctic Subfamilies, Tribes, and Genera of Lucanidae

1. Antenna straight, not geniculate (Fig. 2); body form oval or cylindrical; prosternal process narrow, anterior coxae nearly contiguous 2
— Antenna geniculate (Fig. 3); body form elongate, weakly flattened; prosternal process broad, anterior coxae distinctly separated (Lucaninae) . 4

2(1). Form short, oval, convex; elytra coarsely punctate with conspicuous bristles; antenna with club lamellate (Nicaginae) ..... *Nicagus*
— Form elongate, cylindrical; elytra striate and nearly glabrous; antenna with club only weakly lamellate (Syndesinae)..... 3

3(2). Head of male with long, median horn; female with median tubercle; mandibles in both sexes small and inconspicuous (Sinodendrini) . *Sinodendron*
— Head in both sexes lacking median horn or tubercle; mandibles large, conspicuous, especially in male (Ceruchini) ..... *Ceruchus*

4(1). Eye nearly entire, canthus absent or very short; antenna weakly geniculate, scape lacking groove at apex; body length mostly less than 15 mm (Platycerini) 5
— Eye divided by canthus, canthus more than 1/4 as long as eye; antenna strongly geniculate, scape with apical groove; body length more than 15 mm 7

5(4). Body robust, obovate, strongly convex; posterior tibia stout, expanded at apex, triangular in cross section; apical spurs spatulate ..... *Platyceropsis*
— Body distinctly depressed; posterior tibia narrow, not expanded at apex, not triangular in cross section; apical spurs slender, not spatulate 6

6(5). Anterior margin of head semicircularly excised; clypeus mostly concealed; mandibles subequal to length of head; club of antenna with 4 segments in male, 3 segments in female ..... *Platycerus*
— Anterior margin of head lacking excision on front; clypeus distinctly produced; mandibles about half length of head; club of antenna 3-segmented in both sexes ..... *Platyceroides*

7(4). Elytra nearly smooth; pronotum with lateral margin strongly arcuate or angulate; posterior tibia with 0, 2, or 3 spines along outer edge (Lucanini) .... *Lucanus*
— Elytra striate-punctate; pronotum with lateral margins subparallel; posterior tibia with 1 spine on outer edge (Dorcini) ..... *Dorcus*

Classification of the Nearctic Genera

Lucanidae Latreille 1804

Lucaninae Latreille 1804

Characteristics: Eye partly or completely divided by canthus. Antenna geniculate. Body form elongate, weakly flattened. Pronotal process broad between procoxae, coxae distinctly separated. Internal sac of aedeagus permanently everted.

Most of the lucanids of the world are found in this subfamily although many of the tribes are poorly or inconsistently characterized (Howden and Lawrence 1974). The classification of the North American genera seems now to be stable.

Lucanini Latreille 1804

Characteristics: Antenna strongly geniculate, scape with apical groove. Elytra nearly smooth or with minute and irregular punctation. Pronotum with lateral edges arcuate or angulate. Metatibia lacking spines or with 2 or 3 spines along outer edge. Most with body length greater than 25 mm.

This tribe consists of two genera in the New World. One genus, *Cantharolethrus*, is found from Mexico to South America. Keys to U.S. species: Fuchs 1882; Dillon and Dillon 1961. Keys to larvae: Ritcher (1966) was unable to distinguish between the three U.S. species he examined.

Lucanus Scopoli 1763
Hexaphyllus Mulsant 1839
Pseudolucanus Hope 1845
The genus *Lucanus* (Fig. 1) contains about 50 species distributed in Asia, Europe, and North America (Benesh 1960). Most of the species occur in Asia while five species occur in the United States and northern Mexico. Three species are restricted to the eastern United States while the other two are found in the Southwest and northern Mexico. Keys to species: Dillon and Dillon 1961. Biology: Milne 1933.

Dorcini Parry 1864

Characteristics: Antenna strongly geniculate, scape with apical groove. Elytra striate-punctate. Pronotum with lateral edges subparallel. Metatibia with 1 spine on outer edge. Body length more than 15 mm.

There is only one genus of Dorcini represented in North America: *Dorcus*. The tribe Dorcini has six genera, five of which are endemic to Asia.

Dorcus MacLeay 1819
The genus *Dorcus* contains about 30 species; most occur in Asia and India although two are also found in southern Europe, one in Mexico, and two in the United States (Benesh 1937). The two U.S. species are found in the eastern half of the country, and one species occurs in Quebec. Key to species: Downie and Arnett 1996.

Platycerini Mulsant 1842

Characteristics: Antenna weakly geniculate, scape lacking apical groove. Eye nearly entire, eye canthus absent or very short. Elytra striate in most. Most with body length less than 15 mm.

The tribe Platycerini consists of three genera in North America, with *Platycerus* also being found in Asia, Europe, and North Africa. Key to genera: Benesh 1946; Howden and Lawrence 1974.

Platyceroides Benesh 1946
This genus contains seven species, all of which are found in Washington, Oregon, and northern California. Key to species: Benesh 1946.

Platyceropsis Benesh 1946
This monobasic genus contains one species, *P. keeni* (Casey), which occurs from British Columbia to northern California.

Platycerus Geoffroy 1762
Systenocerus Weise 1883
Systenus Sharp and Muir 1912
Eight species are found in this genus, and five of these occur in the United States. Four of the U.S. species are found in the Pacific Northwest while the fifth species is found in the eastern United States and Canada. Key to species: Benesh 1946. Larval description: Ritcher 1966. Biology: Hoffman 1937.

Nicaginae LeConte 1860

Characteristics: Antenna not geniculate, instead straight, with strongly lamellate club. Eye entire (lacking canthus). Pronotum with lateral margins strongly crenulate. Elytra coarsely punctate, with conspicuous bristles. Prosternal process narrow so that anterior coxae almost contiguous. Aedeagus with internal sac eversible. Body form short, oval, convex.

According to Howden and Lawrence (1974), the Nicaginae contain two genera: *Ceratognathus* from Australia and New Zealand and *Nicagus* from North America and Japan. Previously, these genera were included in the subfamily Aesalinae.

Nicagus LeConte 1860
One species, *N. obscurus* LeConte, occurs in the eastern half of the United States.

Syndesinae MacLeay 1819

Characteristics: Antenna straight, not geniculate; club weakly lamellate. Eye entire (lacking canthus). Elytra striate, nearly glabrous. Prosternal process narrow, anterior coxae nearly contiguous. Aedeagus with internal sac eversible. Body form elongate, cylindrical.

This subfamily is composed of three tribes: Syndesini with the genera *Syndesus* (from Australia, Tasmania, New Caledonia, and Africa) and *Psilodon* (from South America); Sinodendrini with the genus *Sinodendron* (from North America); and Ceruchini with the single Holarctic genus *Ceruchus*.

Sinodendrini Mulsant 1842

Characteristics: Head of male with long, median horn; female with median tubercle. Mandibles in both sexes small and inconspicuous.

Sinodendron Hellwig 1894
Ligniperda Fabricius 1801
This genus contains two species and one, *S. rugosum* Mannerheim, is found in the Pacific Northwest. Generic overview: Hatch 1928.

Ceruchini Jacquelin du Val 1857

Characteristics: Head lacking median horn or tubercle in both sexes. Mandibles large, conspicuous (especially in male).

Ceruchus MacLeay 1819
Seven species occur in this Holarctic genus (Benesh 1960), and three species are found in North America. One species occurs in southeastern Canada and the northeastern quadrant of the United States while the other two species are found from California to

Vancouver Island. Larval description: Ritcher 1966. Biology: Hoffman 1937.

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24. DIPHYLLOSTOMATIDAE Holloway 1972

by Mary Liz Jameson and Brett C. Ratcliffe

Family common name: The false stag beetles

The family Diphyllostomatidae includes three species in the genus *Diphyllostoma*. The group is endemic to the west coast of California in the United States. The natural history of the group is poorly known, and larvae have not been described.

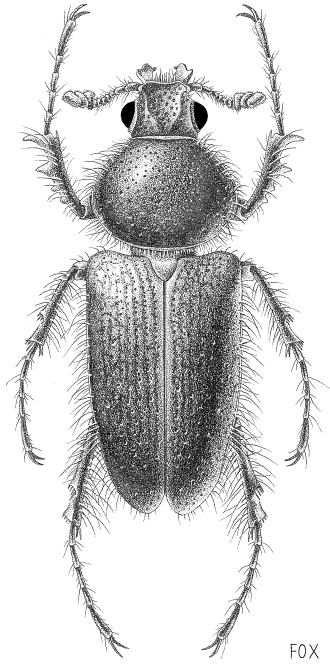

FIGURE 1.24 *Diphyllostoma fimbriata* (Fall) (Used by permission of University of Nebraska State Museum)

Description. Length 5.0-9.0 mm. Shape elongate-oval. Color brown to reddish-brown, without metallic reflections.

Head prognathous, not deflexed. Antennae straight (not geniculate), with 10 antennomeres including a 3-segmented, unopposable club (all antennomeres tomentose). Eyes with acone ommatidia, lacking canthus. Clypeus lacking tubercle or horn. Labrum concealed beneath clypeus. Mandibles prominent, quadrate or rounded at apex, produced beyond apex of labrum. Maxillae with 4-segmented palpi; labium with 4-segmented palpi.

Pronotum weakly convex, base narrower than elytral base, lacking tubercles, ridges, horns, or sulci. Elytra elongate, weakly convex, with weakly impressed, punctate striae. Pygidium concealed by elytra. Scutellum exposed, parabolic. Legs with protrochantin exposed, procoxae subconical, mesocoxae virtually contiguous; protibiae serrate on outer margin, apex lacking articulated spur; meso- and metatibia with ridges, apices with 2 spurs; tarsi 5-5-5; claws equal in size, simple; empodium present, extending to apex of fifth tarsomere, with 2 setae.

Abdomen with 7 visible sternites; 7 functional abdominal spiracles situated in pleural membrane. Wings well developed in male (vestigial in female), M-Cu loop and one apical detached vein present. Male genitalia trilobed. References: Holloway 1972; Scholtz 1990.

Larvae are not known but are probably of the scarabaeoid form and probably live in the soil.

Habits and habitats. Females differ from males in having greatly reduced eyes and vestigial wings. Life history information is scant. The adults are diurnal.

Status of the classification. The genus *Diphyllostoma* was originally placed in the family Lucanidae by Fall (1901) based on the 10-segmented antenna and lack of an eye canthus (typical characteristics of the family Lucanidae). However, several significant characters of *Diphyllostoma* are not found in other members of the family Lucanidae or other scarabaeoids. These include abdomen with 7 ventrites, exposed second abdominal segment, exposed protrochantin, and protibial spur lacking. Holloway (1972) proposed the family Diphyllostomatidae for the genus *Diphyllostoma* because of these unique characters.

Based on comparative studies, Holloway (1972) suggested the Diphyllostomatidae may be most closely related to the family Geotrupidae. Browne and Scholtz (1995, 1996, 1999) and Scholtz (1990) hypothesized that the family Diphyllostomatidae is the sister group to the Lucanidae. Diphyllostomatids and lucanids are the apical clade in a clade composed of the families Passalidae, Trogidae, Pleocomidae, Bolboceratidae, and Glaphyridae (Browne and Scholtz 1999).

Distribution. The genus *Diphyllostoma* includes three species that are found only in California in the western United States.

Classification of the Nearctic Genera

Diphyllostomatidae Holloway 1972

Diphyllostoma Fall 1901
Phyllostoma Fall 1901

This genus (Fig. 1) of fairly rare beetles includes only three species, all of which are found in California. Key: Linsley 1932; Fall 1932. Morphology: Holloway 1972.

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25. PASSALIDAE Leach 1815

by Jack C. Schuster

Family common name: The bess beetles

The bess beetle family has a limited distribution in the Nearctic Region; most species occur in tropical regions rather than temperate regions. Members of this family in the United States are typically large beetles (20 to 43 mm long) with a sublamellate antennal club. The form of body (elongate and dorsoventrally depressed) and form of the mentum (deeply emarginate apically) help to distinguish this family from other scarabaeoids. Adults and larvae live together in subsocial groups in rotting logs.

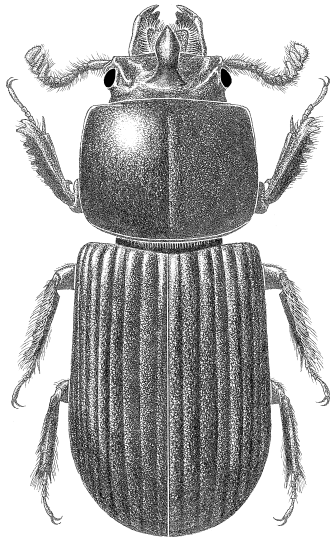

FIGURE 1.25 *Odontotaenius disjunctus* (Illiger)

Description. Length 20.0-43.0 mm. Shape elongate-cylindrical and depressed. Color black (tenerals orange to deep maroon); ventral surface with or without erect, moderately dense, yellow setae.

Head prognathous, narrower than thorax, often with dorsomedian horn. Antennae with 10 antennomeres including a 3-segmented club that is not opposable and not geniculate (but is capable of being rolled together); club antennomeres tomentose; antennae inserted under a prominent frontal margin. Eyes divided in half by canthus, with exocone ommatidium. Clypeus reduced, separated from frons by suture, or vertical and hidden beneath frons. Labrum distinct, prominent, projecting beyond apex of front of head, clypeal apex deeply emarginate, bisinuate, or truncate. Mandibles projecting beyond apex of labrum, large, curved, toothed, blunt. Maxillae with 4-segmented palpi; galea with apical hook; submentum large, prominent; mentum large, emarginate at apex; labium with 3-segmented palpi.

Pronotum broader than head, quadrate, surface smooth with median, longitudinal groove. Elytra elongate, sides parallel, apices rounded, with striae well developed. Pygidium concealed by elytra. Scutellum triangular, small (exposed only in groove between pronotum and elytra). Legs with transverse coxae, mesocoxae closed; protibiae with several external teeth on outer margin, apex with 1 spur; meso- and metatibiae with ridges, apices with 2 spurs; tarsal formula 5-5-5; claws equal in size, simple; empodium present, not extending beyond fifth tarsomere, with 2 setae.

Abdomen with 5 visible sternites; 7 functional abdominal spiracles situated in pleural membrane. Wings well developed without M-Cu loop, with 1 apical detached vein. Male genitalia trilobed. Female genitalia with paraprocts, proctiger, and styli absent; valvifers and coxite present. References: Scholtz 1990; Sharp and Muir 1912; Tanner 1927; Williams 1938.

Larvae are elongate, subcylindrical, slightly curved (not C-shaped). Color creamy white or blue-white (except at caudal end which may be darkened by accumulated feces). Cranium lightly sclerotized. Antennae 2-segmented with protruding fleshy base, short. Lateral ocelli lacking. Frontoclypeal suture distinct. Labrum rounded, setiferous at apex; maxilla with galea and lacinia distinctly separate, stridulatory area present, palpi 2-segmented (apparently 3-segmented). Abdominal segments without annuli. Spiracles cribriform with C-shaped peritremes. Venter of last abdominal segment with 2 anal lobes. Pro- and mesothoracic legs 4-segmented, with long, curved claw; metathoracic leg unsegmented, reduced to a stub with several apical teeth that rub against stridulatory area on coxa of mesothoracic leg. References: Bøving and Craighead 1930-1931; Krause and Ryan 1953; Ritcher 1966; Scholtz 1990. Keys to larvae: Schuster 1992; Schuster and Reyes-Castillo 1981.

Habits and habitats. Passalid adults live in well decayed logs and stumps with their larvae and subsocial family groups. All stages are found in galleries in wood that are excavated by the adults. Eggs are usually placed together in a "nest" of frass. In many species, recently oviposited eggs are red; as they mature, they change to brown, then to green. Adults and larvae communicate by stridulating and can produce 14 different calls. Adults care for larvae and prepare food by chewing it and presumably mixing it with saliva. Adults and larvae need to feed on adult feces that are predigested by microflora (essentially an external rumen). Biology: Reyes-Castillo 1970; Reyes-Castillo and Halffter 1984; Schuster 1975a, 1975b, 1983b; Gray 1946; Schuster and Schuster 1997; Ratcliffe 1991.

Status of the classification. Taxonomy of the species in the United States, Mexico and Central America is well known, although new species are still being found. Taxonomy of passalids in other regions of the world needs further study. Monophyly of the family is supported by larval and adult characteristics (see Scholtz 1990; Browne and Scholtz 1995). According to the phylogenetic analysis of Browne and Scholtz (1996), the family Passalidae is the basal member of a clade that includes the Diphyllostomatidae, Lucanidae, Glaphyridae, Trogidae, Bolboceratinae (Geotrupidae), and Pleocomidae. World catalog:

Acknowledgments: Jack Schuster thanks Enio Cano and Brett Ratcliffe for reviewing the passalid chapter.

Hincks and Dibb 1935. North American catalog: Smith 2001. Keys to Nearctic genera: Reyes-Castillo 1970; Schuster 1983a. Keys to genera of larvae: Schuster 1992. Regional works: Blatchley 1910; Edwards 1949; Hatch 1971; Ratcliffe 1991; Downie and Arnett 1996.

Distribution. There are over 500 described species, nearly all of which are tropical. Four extant species in two genera are recorded from the United States, and 90 species occur in Mexico. The presence of species in Texas, often cited, is highly doubtful, although one species, *Ptichopus angulatus* (Percheron), the only passalid obligatorially inhabiting leaf-cutter ant (*Atta* sp.) detritus chambers, is found on the Mexican side of the Rio Grande. The only confirmed U.S. species other than *Odontotaenius disjunctus* (Illiger) and *Odontotaenius floridanus* Schuster are *Passalus punctatostriatus* (Percheron) and *P. punctiger* LePeletier and Serville. *Passalus punctatostriatus* and *P. punctiger* were collected at the turn of the century in Arizona and have not been recorded since. *Odontotaenius disjunctus* is distributed from Nebraska, southern Manitoba and east Texas throughout the eastern U.S. and Canadian deciduous forests, south to the middle of Florida and north to Massachusetts and southern Ontario. *Odontotaenius floridanus* is endemic to certain sandhill areas of central Florida. A fossil passalid beetle, *Passalus indormitus* Cockerell, is known from Oligocene deposits of Oregon (Reyes-Castillo 1977). It is very similar to *P. punctiger*.

Key to The Genera of The Family Passalidae From The United States, Canada, and Northernmost Mexico

1. Anterior margin of labrum bisinuate; antennal lamellae curved; mandibles with 2 apical teeth; eyes reduced, canthus produced posteriorly more than radius of eye ..... *Ptichopus*
— Anterior margin of labrum straight or concave; antennal lamellae straight, lying in one plane; mandibles with 3 apical teeth; eyes not reduced, canthus not produced posteriorly more than radius of eye 2

2(1). Frons with few to many large, disc-shaped punctures; frontoclypeal suture not visible; width of antepenultimate antennomere greater than 3/4 width of penultimate lamella ..... *Passalus*
— Frons smooth, lacking disc-shaped punctures; frontoclypeal suture visible; width of antepenultimate antennomere 1/2 to 2/3 width of penultimate lamella ..... *Odontotaenius*

Classification of the Genera

Passalidae Leach 1815

Passalinae Leach 1815

Proculini Kaup 1868

Characteristics: Frontal horn pedunculate or greatly raised, without lateral extensions. Frontoclypeal suture visible dorsally. Eastern U.S. and Canada.

Odontotaenius Kuwert 1896
Two species in North America: *O. disjunctus* (Illiger) (Fig. 1) is distributed in the eastern United States and Canada. It is commonly called the "horned passalus" or "bess-beetle." *Odontotaenius floridanus* Schuster is restricted to Florida (see Schuster 1994).

Passalini Leach 1815

Characteristics: Frontal horn absent or not pedunculate, with lateral extensions in basal half. Frontoclypeal suture not visible dorsally. Arizona and possibly Texas.

Passalus Fabricius 1792
Two species are recorded from Arizona: *P. punctiger* (LePeletier and Serville) and *P. punctatostriatus* Percheron. Two species are recorded from Texas, but these are probably erroneous.

Ptichopus Kaup 1869
One species, *P. angulatus* (Percheron) is distributed from Mexico to South America.

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26. GLARESIDAE Semenov-Tian-Shanskii and Medvedev 1932

by Mary Liz Jameson

Family common name: The enigmatic scarab beetles

The beetle family Glaresidae contains one genus, *Glaresis*, that is found on all major continents except Australia. The family includes about 50 species worldwide, most of which inhabit arid and sandy regions. Members of the family are small (2.5-6.0 mm long) and light brown to dark brown. Adults are collected at lights. Larvae and biology of species in the family are not known.

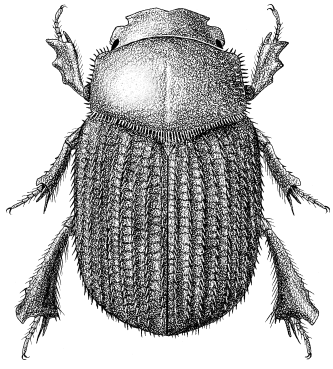

FIGURE 1.26. *Glaresis dakotensis* Gordon (Used by permission of University of Nebraska State Museum)

Description. Length 2.5-6.0 mm. Shape oblong-oval, convex. Color tan to dark brown; dorsal surface with moderately dense, short setae.

Head deflexed. Antennae 10-segmented with 3-segmented, opposable club; first antennomere of club often hollowed to receive club antenomeres 2 and 3; second and third antennomeres of club tomentose. Eyes divided in half by canthus, with eucone ommatidia. Clypeus lacking tubercle or horn. Labrum truncate, projecting weakly beyond apex of clypeus. Mandibles toothed and projecting weakly beyond apex of clypeus; maxillae with 4-segmented palpi; labium with 4-segmented palpi.

Pronotum short, broad, convex. Elytra convex with 10 distinct costae, intercostae with or without distinct punctures. Pygidium concealed by elytra. Scutellum exposed. Legs with coxae transverse; protibia fossorial, outer margin toothed, apex with one spur; meso- and metatibia with 2 apical spurs; metafemora and metatibiae enlarged to cover abdomen in retracted position; tarsi 5-5-5; claws equal in size, simple; empodium absent.

Abdomen with 5 free sternites; 8 functional abdominal spiracles situated in pleural membrane. Wings well developed, M-Cu loop present, without apical detached veins. Male genitalia trilobed. References: Cooper 1983; Scholtz 1990.

Larvae are not known but are probably of the scarabaeoid form.

Habits and habitats. Adults are found in dry, sandy areas and are attracted to lights. Adults stridulate weakly when handled (Scholtz *et al.* 1987). Based on the form of the lacinia, Scholtz *et al.* (1987) hypothesized that *Glaresis* species feed on subterranean fungi. Efforts to establish a laboratory culture from adults have not been successful (Scholtz *et al.* 1987).

Status of the classification. The genus *Glaresis* was traditionally placed in the family Trogidae (or the subfamily Troginae in the family Scarabaeidae) based on the trilobed male genitalia and five visible abdominal sternites. *Glaresis* has long been compared with primitive scarabaeoids (Ochodaeinae, Geotrupidae, Lucanidae, Hybosorinae) based on shared primitive characters. *Glaresis* shares no demonstrable, derived characters with any group and, as such, the family Glaresidae was established for the genus *Glaresis* (Scholtz *et al.* 1987). Based on plesiomorphic characters and comparison with "primitive" scarabaeoid groups, Scholtz *et al.* (1994) argued that the glaresids are the most primitive living scarabaeoids and that the family Glaresidae is the sister group to all other Scarabaeoidea (*e.g.,* Browne and Scholtz 1995, 1999; Scholtz *et al.* 1994).

Distribution. About 50 species are distributed on all major continents except Australia (Scholtz 1982), and about 15 species are found in Nearctic North America. North American catalog: Smith 2001. Regional works: Hatch 1971; Ratcliffe 1991; Downie and Arnett 1996.

Classification of the Genera of Glaresidae

Glaresidae Semenov-Tian-Shanskii and Medvedev 1932

The genus *Glaresis* (Fig. 1) is the sole member of the family Glaresidae. The tribe Glaresini was created by Semenov-Tian-Shanskii and Medvedev (1932) to accommodate the genus *Glaresis* and elevated to family status by Scholtz *et al.* (1987). Catalog: Scholtz 1982. Key to species of the United States: Gordon 1970, 1974; Warner 1995.

Glaresis Erichson 1848
- *Eoglaresis* Semenov-Tian-Shanskii and Medvedev 1932
- *Afroglaresis* Petrovitz 1968

Fifteen species in the genus occur from the western Great Plains to the west coast, and from Manitoba to northern Mexico and Baja California, Mexico.

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27. TROGIDAE MacLeay 1819

by Mary Liz Jameson

Family common name: The hide beetles

The family Trogidae is a small group (about 300 species worldwide) occurring on all major continents. Adults of the family are easily recognized by their overall warty, brown to gray to black, dirt-encrusted appearance, and their flat abdomen. The family includes three genera, two of which are present in North America. The genus *Trox* is widespread in the Holarctic and Ethiopian regions, and the genus *Omorgus* occurs primarily in arid regions in the southern continents. Adults and larvae can be found on the dry remains of dead animals (they are usually among the last of the succession of insects that invade carcasses) or in the nests of birds and mammals where they feed on hair, feathers, and skin.

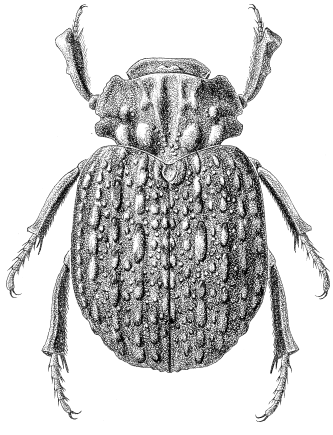


FIGURE 1.27. *Omorgus scabrosus* (Palisot de Beauvois) (Used by permission of University of Nebraska State Museum)

Description. Length 2.5-20.0 mm. Shape oblong-oval, convex. Color brown or gray to black, often with short, moderately dense, gray or brown setae; dorsal surface often greasy or encrusted with dirt.

Head deflexed. Antennae 10-segmented with 3-segmented, opposable club (all antennomeres tomentose); basal antennomere robust. Eyes with variable ommatidia (eucone, duocone, and exocone), not divided by canthus. Clypeus lacking tubercle or horn. Labrum truncate, not projecting beyond apex of clypeus. Mandibles with mandibular brush and prostheca, projecting weakly beyond apex of clypeus. Maxillae with 4-segmented palpi; labium with 4-segmented palpi.

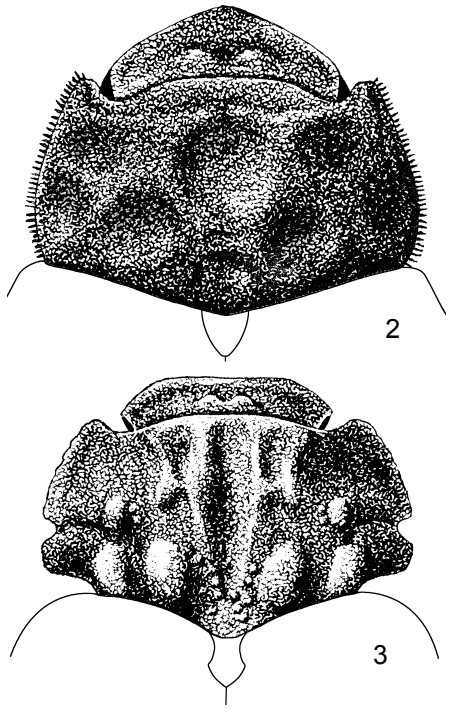
Pronotum short, broad, convex; sculptured with ridges, depressions, or tubercles; with or without setae. Elytra convex with striae impressed and intervals ridged or tuberculate. Pygidium concealed by elytra. Scutellum exposed; shape hastate or oval. Legs with coxae transverse, mesocoxae contiguous or nearly so; protibia more or less slender, outer margin weakly toothed, apex with one spur; meso- and metatibia with 2 apical spurs; profemora enlarged (concealing or partially concealing head when deflexed); meso- and metafemora not enlarged; tarsi 5-5-5; claws equal in size, simple; empodium absent.

Abdomen with 5 free sternites; 7 or 8 functional abdominal spiracles situated in pleural membrane. Wings well developed, M-Cu loop present, with 1 or 2 apical detached veins. Male genitalia trilobed. References: Cooper 1983; Scholtz 1986, 1990.

Larvae are scarabaeiform (C-shaped, cylindrical). Color creamy-white or yellow (except at caudal end which may be darkened by accumulated feces). Cranium heavily sclerotized, brown to black. Antennae 3-segmented with apical segment much reduced. Lateral ocelli present. Frontoclypeal suture distinct or faint. Labrum bilobed. Epipharynx with an oval pedium often surrounded by phobae; heli absent, tormae united. Maxilla with galea and lacinia distinctly separate; maxillary stridulatory area with a row or patch of minute teeth; maxillary palp 4-segmented. Abdominal segments 1 to 6 with 3 annuli, each with one or more transverse rows of short, stiff setae. Spiracles with closing apparatus; cribriform or biforous. Ventral surface of last abdominal segment with bare, fleshy lobes surrounding anus. Legs 4-segmented, well developed, lacking stridulatory apparatus, each with a long, curved claw that has 2 setae at its base. References: Ritcher 1966, Baker 1968, Scholtz 1990.

Habits and habitats. Trogids are most diverse in temperate and subtropical regions and are most common in drier habitats. Adults and larvae are among the last scavengers that visit the dry remains of dead animals where they feed on feathers, fur, and skin. They also feed on organic matter found in nests of mammals and birds (*i.e.,* feces, feathers, and fur). Adults of many species are attracted to lights at night. The life histories of many species remain poorly known because of specialized associations with bird nests and mammal nests. Much biological information could be gathered by collecting from burrows and nests. When disturbed or frightened, adults feign death and remain motionless. This, in combination with their dirt-encrusted appearance, enables them to evade potential predators that might be scavenging at a carcass. Because organic debris and soil often adhere to the surface of these beetles, cleaning is necessary in order to see important characters such as sculpturing and setae. Adults stridulate by rubbing a plectrum (located on the penultimate abdominal segment) against a file (located on the internal margin of the elytra) (Lawrence and Britton 1994). Larvae of carcass-feeding species live in short, vertical burrows beneath the carcass (Baker 1968). Larvae do not stridulate.

Status of the classification. The Trogidae are considered either as a family within the Scarabaeoidea or as a subfamily of the family Scarabaeidae. This work follows Scholtz (1986) and Lawrence and Newton (1995) who treat the Trogidae as a family. Monophyly of the Trogidae is suggested by the fact that all larvae share well developed, lateral ocelli (unique in the Scarabaeoidea). The group is generally regarded as among the primitive groups of scarabaeoids (*e.g.*, Crowson 1954, 1981) based on the trilobate



FIGURES 2.27-3.27. Dorsal view of pronotum and base of elytra showing: 2. *Trox* sp., scutellum oval, not narrowed at base; 3. *Omorgus* sp., scutellum hastate, distinctly narrowed at base (Used by permission of University of Nebraska State Museum).

form of the male genitalia. According to phylogenetic analyses, the family Trogidae is basal in a clade that includes the Pleocomidae and Bolboceratinae (Geotrupidae) (Browne and Scholtz 1995) or the Passalidae, Lucanidae, and Diphyllostomatidae (Browne and Scholtz 1999).

Distribution. About 51 species of trogids are known in the Nearctic region. In North America 43 species in 2 genera are known (Scholtz 1982). North American catalog: Smith 2001. Regional works: Blatchley 1910; Edwards 1949; Vaurie 1955; Hatch 1971; Kirk and Balsbaugh 1975; Lago *et al.* 1979; Ratcliffe 1991; Downie and Arnett 1996; Harpootlian 2001.

Key to the Genera of the Family Trogidae From the United States, Canada, and Nearctic Mexico

1. Scutellum oval, not narrowed at base (Fig. 2); base of pronotum not constricted; posterior tibia with lateral teeth or spines ..... *Trox*
— Scutellum hastate, distinctly narrowed at base (Fig. 3); base of pronotum sharply constricted; posterior tibia without lateral teeth or spines ..... *Omorgus*

Classification of the Genera of Trogidae

Trogidae MacLeay 1819

Omorgus Erichson 1847
Chesas Burmeister 1876
Lagopelas Burmeister 1876
Megalotrox De Borre 1886

Sixteen species of *Omorgus* (Fig. 1) are generally distributed in southern Canada, the United States, and Mexico. Key: Vaurie 1955. Catalog: Scholtz 1982.

Trox Fabricius 1775
Pseudatrox Robinson 1948

Twenty five species are found in southern Canada, the United States, and Mexico. Keys: Vaurie 1955; Howden and Vaurie 1957. Catalog: Scholtz 1982.

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28. PLEOCOMIDAE LeConte 1861

by Frank T. Hovore

Family common name: The rain beetles

This family contains a single genus, *Pleocoma*, and includes 26 species that are generally distributed from southern Washington southward to northern Baja California, Mexico. As the generic name implies ("*pleos*" from the Greek, meaning full or abundant, and "*kome,*" Greek for hair), adult rain beetles are densely pubescent ventrally, on the appendages, and at the margins of the elytra and thorax.

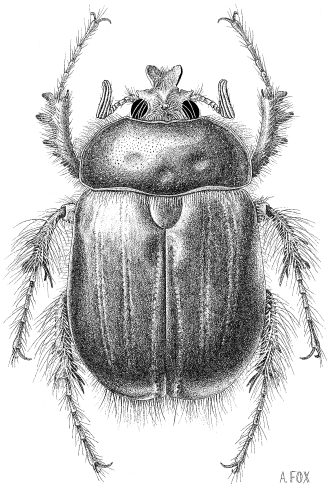

FIGURE 1.28. *Pleocoma fimbriata* LeConte

Description. Length: males 16.5-29.0 mm; females 19.5-44.5 mm. Body form robust, broadly oval in outline, strongly convex dorsally, dorsum glossy, venter densely clothed with long, fine hairs. Color variable, reddish-brown to piceous-black with setae variably colored (golden, reddish, chocolate-brown, black).

Head not deflexed or retractile. Clypeal process deeply bifurcated, outer angles produced and acute in males, broadly bilobed in females; vertex with a conical tubercle or erect horn medially. Antennae 11-segmented, scape subconical, antennomere 2 short and moniliform, antennomere 3 elongated and subcylindrical (angulated anteriorly in some), antennomeres 4-11 variable (moniliform, angulated anteriorly, or variously produced to form lamellae); antennal club of male elongate and comprised of 4 to 8 full lamellae; antennal club of female with 4-8 lamellae shorter and stouter than those of male. Eyes with exocone or duocone ommatidia, partially divided by canthus. Mouthparts partially fused and reduced; labrum connate with clypeus. Mandibles non-functional; esophageal opening closed by a membrane. Maxillary palpi 4-segmented, elongate; labial palpi shorter, 4-segmented.

Pronotum broad, evenly convex or depressed anteromedially, widest at or behind middle, lacking tubercles, horns or sulci, but some species with a low, transverse median ridge; mesothoracic spiracles primitive, slipper-shaped, with 2 intersegmentalia on each side. Scutellum exposed, subtriangular, narrowly to broadly rounded apically, lightly to densely pubescent. Elytra convex with variable sculpturing (costal striae lacking, feebly indicated, coriaceous, and/or strongly indicated); lateral margins rounded to sutural angle, sutural margins contiguous to apices. Pygidium exposed in both sexes. Legs with procoxae large, conical and prominent, procoxal cavities open; mesocoxae contiguous, prominent; protibiae strongly toothed on outer margin; meso- and metatibiae strongly ridged externally; tarsi simple and subcylindrical, elongate, 5-5-5, tarsomeres 1-4 subequal in length, tarsomere 5 longer than preceding 2 together; empodium present, produced beyond apex of tarsomere 5, with 2-3 setae.

Abdomen with 8 functional spiracles in pleural membrane. Male genitalia simple, trilobed, internal sac small, unarmed, setose. Female genitalia unsclerotized or with a few small, separated sclerites, ovipositor with styli, ovariole numbers 14-25 per ovary. Wings with M-Cu loop and 2 apical detached veins. Karyotype 9+Xyp. References: Ritcher 1969a, 1969b; Stemwedel 1973; Yadav *et al.* 1979; Ritcher and Baker 1974; Scholtz 1990; Browne and Scholtz 1995; Hovore 1977a, 1977b.

Larvae are scarabaeiform (C-shaped, cylindrical). Color creamy white except at caudal end which may be darkened by accumulated feces. Cranium heavily sclerotized, glossy, yellowish or reddish-brown. Mandibles piceous. Antennae 3-segmented, terminal segment minute, penultimate segment with apical sensory area. Frontoclypeal suture distinct. Galea and lacinia distinctly separate. Epipharynx with plegmatia and with prominent chaetoparia and acanthoparia; haptomerum with a longitudinal group of heli. Hypopharynx without oncyli. Maxillary palpi 4-segmented. Leg with apical claw bearing 2 basal setae; trochanters and femora of meso- and metathoracic legs with stridulatory organs. Spiracles cribriform, lacking closing apparatus, concavities of respiratory plates oriented ventrad. Terga of abdominal segments 3-7 each with 4 dorsal annulets. Anal opening V or Y-shaped, not surrounded by fleshy lobes. References: Ritcher 1947, 1966; Scholtz 1990.

Habits and habitats. *Pleocoma* larvae feed externally upon roots and often are found deep within the soil beneath their host plants. Although the duration of the larval stage is not known for most species, some species have nine or more instars and require from 8-13 years to reach adulthood. Pupation occurs in late summer in a simple, elongate cell. After pupation, both sexes dig to the surface and emerge more or less synchronously. Some species emerge at the onset of fall or winter rains while others are active during mid-winter or early spring. Above-ground activity of adults closely corresponds to rainfall or snowmelt, depending upon the species, elevation, and specific weather conditions. Most species are active during or immediately following precipitation. Because of the precipitation-oriented timing of adult activity, the common name for all members of the genus *Pleocoma* is "rain beetles."

Both sexes possess strongly toothed protibiae, and most species also have the clypeus and ocular canthi modified for digging through well-consolidated soils. Only male *Pleocoma* species are fully winged and capable of flight. Although the adults of most species have crepuscular flights, some fly in late morning and others fly in the night during rain. Males may be strongly attracted to light, particularly early in the flight season. Females generally are much larger than males, more heavy-bodied, and have the hind wings reduced to vestigial stubs. Females release pheromones that attract flying males, often in large numbers. Mating takes place either at the soil surface or within the female's larval burrow. Mated females return to the bottom of their burrow and wait for their eggs to mature (a process that may require several months) before depositing the eggs in a spiral pattern at the lower end of the burrow. Adult *Pleocoma* lack functional mouthparts or digestive tract, so the period of adult activity is relatively brief, dependent upon timing with conspecifics, temperature, and amount of precipitation during the emergence season. References: Hovore 1972, 1979; Fellin 1975, 1981.

Status of the classification. The genus *Pleocoma* has had a turbulent classification history. Previous authors placed *Pleocoma* in the subfamily Geotrupidae, the subfamily Melolonthinae, in its own subfamily (Pleocominae), or, in the current usage, its own family. The genera *Acoma* and *Benedictia* (currently in the subfamily Melolonthinae) were often treated in conjunction with *Pleocoma (e.g.*, Lawrence and Newton 1995). Browne and Scholtz (1995) consider the Pleocomidae to be a sister group to the Bolboceratinae (Geotrupidae) based primarily upon a series of minor structural synapomorphies. There are many basic structural dissimilarities between *Pleocoma* and the bolboceratines, however, and their respective larval characters, biologies, and geographical distributions are completely discordant, suggesting that any such putative relationship must have had an ancient point of divergence. Clearly, *Pleocoma* is a monophyletic and taxonomically isolated genus, and the relationship of the Pleocomidae to other scarabaeoids remains to be fully resolved.

The various forms of *Pleocoma* have been treated as species or subspecies with most taxa differing from one another by quantitative characters. Modern collecting methods have revealed considerable intraspecific variation in some taxa, resulting in synonymies and status changes. The only "revision" for the group was by Davis (1935). This work is out-dated and contains fewer than half of the present valid taxa. Linsley (1946) provided a provisional key to species. Currently there are 26 described species and 6 subspecies, and several additional new taxa await description.

Distribution. The genus *Pleocoma* is found from southern Washington through most of montane Oregon, southward through the Sierra Nevada and coast ranges of California, and into extreme northern Baja California Norte. The putative record of *Pleocoma* from Alaska is not considered valid. Regional work: Hatch 1971.

Classification of the Genera of Pleocomidae

Pleocomidae LeConte 1861

Pleocoma LeConte 1856

The genus *Pleocoma* (Fig. 1) includes 26 species and 6 subspecies that are restricted to regions of the west coast (from southern Washington to Baja California Norte). Key: Davis 1935. North American catalog: Smith 2001.

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29. GEOTRUPIDAE Latreille 1802

by Mary Liz Jameson

Family common name: The earth-boring scarab beetles

As the name implies, the geotrupids are burrowers in the soil ("*geos*" from Greek meaning earth and "*trypetes*" from Greek meaning borer). In Europe, geotrupids are referred to as dor beetles. Adults of most species provision earthen burrows with dead leaves, cow dung, horse dung, or humus for their larvae.

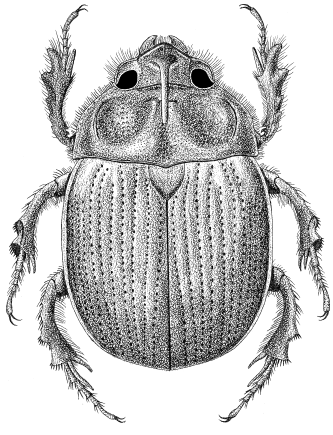


FIGURE 1.29. *Bolboceras filicornis* (Say) (Used by permission of University of Nebraska State Museum)

Description. Length 5.0-45.0 mm. Shape oval or round. Color yellowish, brown, orange-brown, reddish-brown, purple, brown, or black (with or without metallic reflections).

Head not deflexed. Antennae 11-segmented with 3-segmented, opposable club (all antennomeres tomentose). Eyes with eucone or exocone ommatidia, completely or partially divided by canthus. Clypeus often with tubercle or horn. Labrum truncate, prominent, produced beyond apex of clypeus. Mandibles produced beyond apex of labrum, prominent. Maxillae with 4-segmented palpi; labium with 3-segmented (Lethrinae) or 4-segmented (remaining taxa) palpi.

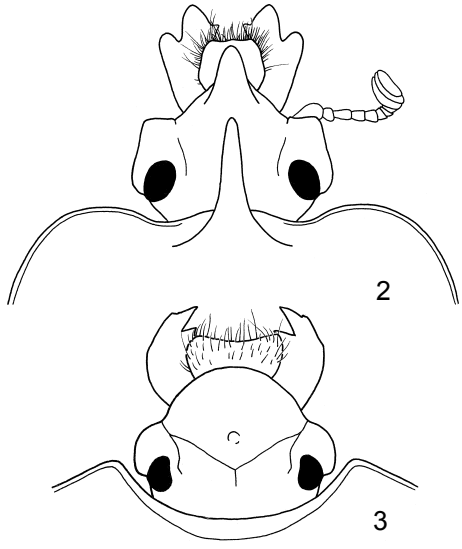
Pronotum convex with base wider than or subequal to elytral base and with or without tubercles, ridges, horns, or sulci. Elytra convex, with or without striae. Pygidium concealed by elytra. Scutellum exposed, triangular. Legs with coxae transverse, mesocoxae separated or contiguous; protibiae serrate on outer margin, apex with 1 spur; meso- and metatibia with ridges, apex with 2 spurs; tarsi 5-5-5; claws equal in size, simple; empodium present, extending beyond fifth tarsomere, with 2 setae.

Abdomen with 6 free sternites; 7 functional abdominal spiracles situated in pleural membrane (spiracles 1-7) and vestigial spiracle in pleural membrane (spiracle 8) [Bolboceratinae] or with 8 functional spiracles situated in the pleural membrane (spiracles 1-7) and the 8th pair in the tergite [Geotrupinae]. Wings well developed, M-Cu loop and two apical detached veins present. Male genitalia variable. References: Howden 1955; Scholtz 1990; Scholtz and Browne 1996.

Larvae are scarabaeiform (C-shaped, cylindrical). Color creamy-white or yellow (except at caudal end which may be darkened by accumulated feces). Cranium heavily sclerotized, brown to dark brown. Antennae 3-segmented, penultimate segment bearing 1 or more distal sense organs, last segment reduced in diameter. Lateral ocelli absent. Frontoclypeal suture absent (Geotrupinae and Bolboceratinae) or present (Taurocerastinae). Labrum at apex with 3 weak lobes or rounded. Epipharynx in most trilobed with symmetrical tormae. Maxilla with galea and lacinia distinctly separate; maxillary stridulatory area with teeth; maxillary palpi 4-segmented. Abdominal segments 3 to 7 with 2 annuli, each with one or more transverse rows of short setae. Spiracles cribriform (Geotrupinae and Lethrinae) or biforous (Bolboceratinae and Taurocerastinae). Venter of last abdominal segment V-shaped or Y-shaped, surrounded by fleshy lobes in some taxa. Legs 4-segmented (some Bolboceratinae) or pro- and mesothoracic legs 3-segmented and metathoracic leg reduced in size and 2-segmented (Geotrupinae and Taurocerastinae); stridulatory apparatus on meso- and metathoracic legs present (some Geotrupinae, some Bolboceratinae, some Taurocerastinae) or absent (some Geotrupinae, some Bolboceratinae, and Lethrinae); claws absent (Geotrupinae, Taurocerastinae, and some Bolboceratinae) or present (*Eucanthus* and *Bolbocerosoma*). References: Ritcher 1966; Scholtz 1990; Scholtz and Browne 1996.

Habits and habitats. Life histories of the geotrupids are diverse, and food habits vary from saprophagous to coprophagous and mycetophagous, and some adults apparently do not feed. Adults of most species are secretive, living most of their life in burrows. Although adults do not tend larvae, adults provision food for larvae in brood burrows. There is overlapping of generations in some species. For example, in the genus *Bolboceras*, eggs, larvae, pupae, and adults have been observed together in a single branching burrow. Adults dig vertical burrows (15-200 cm in depth) and provision larval cells with dead leaves, cow dung, horse dung, or humus. Burrows of some species extend to a depth of 3.0 meters. In restricted habitats, some species are semicolonial. Geotrupids are not of economic importance, although their burrowing has occasionally caused damage in lawns. Adults of many geotrupids are nocturnal and are frequently attracted to lights at night. Some species are attracted to fermenting malt and molasses baits. Most adults and larvae stridulate. The natural history and behavior of many species, especially the Bolboceratinae, are poorly known. References: Howden 1955; Woodruff 1973.

Status of the classification. There is considerable debate concerning the classification of the Geotrupidae. The diversity in structure in both adults and larvae has led to differences of opinion regarding classification, evolution, and monophyly of the group and the genera assigned to it. There is evidence that the group (as defined in this work) includes two distinct lineages: the Bolboceratinae and Athyreinae forming one lineage, and the Geotrupinae, Taurocerastinae, and Lethrinae forming the other.



FIGURES 2.29-3.29. Dorsal view of head and apex of pronotum showing: 2. *Ceratophyus gopherinus* Cartwright, apex of mandibles deeply bidentate and pronotum with central horn; 3. *Geotrupes splendidus* (Fabricius) apex of mandibles rounded and pronotum without central horn.

Scholtz and Browne (1996) proposed the family Bolboceratidae for the former lineage. In addition to the possible division of the group into two families, the geotrupids are often considered as a subfamily of the family Scarabaeidae. In this volume, we follow Lawrence and Newton (1995) and consider the group a family. There is ample evidence that the group is not monophyletic, but the taxa that should be included, characters that support the groupings, and the ranking of the groupings are still debated. Past workers (*e.g.*, Davis 1935; Ritcher 1947) have also included the genus *Pleocoma* (treated in the family Pleocomidae in this work) in the Geotrupidae based on the 11-segmented antenna. However, *Pleocoma* species differ from the geotrupids based on the open procoxal cavities (closed in geotrupids) and 4 to 7-segmented club (3-segmented in geotrupids).

Howden (1982) hypothesized that the Geotrupinae (Geotrupini, Athyreini, Bolboceratini, and Lethrini) form a monophyletic lineage that is most closely related to the Pleocominae (= Pleocomidae) based on characters such as the form of the antennal club, adult provisioning, and diet. Alternatively, it was hypothesized (Browne and Scholtz 1995, 1999; Scholtz and Browne 1996; Scholtz and Chown 1995) that the geotrupids are a polyphyletic group: the Bolboceratidae (including Athyreinae) is the sister taxon of Pleocomidae in a clade including the Glaphyridae, Trogidae, Passalidae, Lucanidae, and Diphyllostomatidae while the family Geotrupidae (including Geotrupinae, Taurocerastinae, and Lethrinae) is part of a separate clade that includes the Ochodaeidae, Hybosoridae, and Ceratocanthidae. The placement of the unusual South American genera *Taurocerastes* and *Frickius* has also been a source of much debate. These genera were placed in the Geotrupini (*e.g.*, Howden 1982; Howden and Peck 1987) or in their own group, the Taurocerastinae (*e.g.*, Zunino 1984a; Browne and Scholtz 1995).

Taxonomy of the world Geotrupidae is well established, primarily due to the prolific work of Howden (*e.g.*, Howden 1955, 1964, 1974, 1980, 1984). Taxonomy of the North American geotrupids is treated in Howden (1955, 1964).

Distribution. The family Geotrupidae includes 68 genera and about 620 species worldwide (Scholtz and Browne 1996). The subfamily Geotrupinae (including Geotrupini, Taurocerastini, and Lethrini) is distributed in the Holarctic region. In the New World, the subfamily Geotrupinae occurs from Canada to El Salvador. The subfamily Bolboceratinae (including Bolboceratini and Athyreini) is best represented in Australia, Africa, and South America. In the New World, the subfamily Bolboceratinae is distributed from Canada to Central America.

Twelve genera and 28 species of geotrupids occur in the United States, Canada, and Nearctic Mexico. Keys to genera and species: Howden 1955; Olson *et al.* 1954; Howden 1964. Reference: Scholtz and Browne 1996; Zunino 1984b. Biology: Howden 1955. Catalog of the U.S. species: Howden 1984; Smith 2001. Regional works: Blatchley 1910; Edwards 1949; Helgesen and Post 1967; Hatch 1971; Woodruff 1973; Ratcliffe 1991; Downie and Arnett 1996; Harpootlian 2001. Larvae: Ritcher 1966.

Key to the Subfamilies and Genera of the United States, Canada, and Nearctic Mexico

1. Antennal club large (about as long as antennomeres 1 through 8), round; mentum not noticeably emarginate at apex (Bolboceratinae) 2
— Antennal club small (about half as long antennomeres 1 through 8), elongate; mentum deeply emarginate at apex (Geotrupinae) 9

2(1). Mesocoxal separation greater than width of labrum ..... *Neoathyreus*
— Mesocoxal separation half or less than half width of labrum 3

3(2). Eyes entirely divided by canthus; dorsal color in some variegated 4
— Eyes only partially divided by canthus; dorsal color uniform brown to black 5

4(3). Color brownish orange with discrete areas of black or dark brown; mesocoxae narrowly separated by slender projection of mesosternal plate ..... *Bolbocerosoma*
— Color uniformly brown to black; mesocoxae contiguous, not separated by projection of mesosternal plate ..... *Bolboceras*

5(3). Elytra each with 5 striae between suture and humeral umbone; humeral angle of elytron not broadly rounded, margin almost always produced into tubercle ..... *Eucanthus*
— Elytra each with 7 striae between suture and humeral umbone; humeral angle of elytron broadly rounded, margin never produced into tubercle 6

6(5). Mesocoxae nearly contiguous, intercoxal process less than 0.3 mm wide and linear ... *Bolbelasmus*

— Mesocoxae well separated, intercoxal process more than 0.3 mm wide and never linear 7

7(6). Base of elytra margined; pronotum without postapical carina 8
— Base of elytra not margined; pronotum with postapical carina extending almost to side margins ..... *Bolborhombus*

8(7). Apex of middle and hind tibiae truncate; prosternal spine (behind anterior coxae) transverse ..... *Bolbocerastes*
— Apex of middle and hind tibiae deeply emarginate; prosternal spine lacking ..... *Bradycinetulus*

9(1). Mandible with apex deeply bidentate (Fig. 2) ..... *Ceratophyus*
— Mandible with apex rounded, at most with weak apical tooth (Fig. 3) 10

10(9). Elytra fused, surface roughly granulate; wings vestigial ..... *Mycotrupes*
— Elytra not fused, or if fused not roughly granulate; wings fully developed 11

11(10). Posterior tibia on outer edge with apex cariniform; lateral margin of elytra not widely flared at base ..... *Geotrupes*
— Posterior tibia on outer edge with apex eroded, not cariniform; lateral margin of elytra widely flared at base ..... *Peltotrupes*

Classification of the Subfamilies and Genera

Geotrupidae Latreille 1802

Bolboceratinae Mulsant 1842

Characteristics: Antennal club large, about as long as antennomeres 1-8, round, convex on both sides. Mesocoxae separated.

This subfamily contains 13 genera and over 300 species and occurs on all continents except Antarctica. Nearctic species belong to eight genera, over half of which belong to *Bolbocerosoma* and *Bolboceras*. Adults feed on fungi, and some are attracted to fermenting malt. Larval food consists of a brood ball of fine humus in *Eucanthus, Bolboceras*, and *Bolbocerosoma*. References: Howden 1955, 1964; Woodruff 1973. Biology: Woodruff 1973, Howden 1955. Larvae: Ritcher 1966; Howden 1964.

Bolbelasmus Boucomont 1911
Kolbeus Boucomont 1911
Four species occur in California, Arizona, Texas, and Nearctic Mexico. Keys: Cartwright 1953; Howden 1964.

Bolboceras Kirby 1819
Odonteus Samouelle 1819
Odontaeus Dejean 1821
The genus (Fig. 1) includes ten species that are generally distributed from southern Canada to the southern United States. A proposal is currently pending with the International Commission of Zoological Nomenclature to conserve the generic name *Bolboceras* Kirby because the senior synonym, *Odonteus* Samouelle, has not been used in the primary literature for over 70 years (Jameson and Howden in press). Keys: Wallis 1928; Howden 1964.

Bolbocerastes Cartwright 1953
Four species are distributed from Kansas and Oklahoma to the west coast and south to Mexico. Keys: Cartwright 1953; Howden 1964.

Bolbocerosoma Schaeffer 1906
Includes twelve species that are widely distributed east of the Rocky Mountains and southward into Mexico. Keys: Howden 1955, 1964. (Volume 1, Color Figure 10).

Bolborhombus Cartwright 1953
Three species occur in Texas, New Mexico, Arizona, and Nearctic Mexico. Keys: Cartwright 1953; Howden 1964.

Bradycinetulus Cockerell 1906
Amechanus Horn 1870
Bradycinetus Horn 1871
Three species occur in the mid-United States and southeastern United States. Key: Cartwright 1953.

Eucanthus Westwood 1848
Five species are widely distributed from southern Canada to Mexico. Key: Howden 1964.

Neoathyreus Howden and Martínez 1963
The genus *Neoathyreus* is the only representative of the tribe Athyreini in the Nearctic region. Two species, *N. mixtus* Howden and *N. fissicornis* (Harold), are found in northeastern Mexico. Reference: Howden 1964; Howden and Gill 1984.

Geotrupinae Latreille 1802

Characteristics: Antennal club small, about half as long as the antennomeres 1-8, elongate, not convex on the sides. Mesocoxae almost contiguous.

This subfamily contains eight genera distributed throughout the northern hemisphere. They are absent from South America, South Africa, and Australia. In the United States, species in the subfamily occur mostly east of the Rocky Mountains with only *Certatophyus gopherinus* Cartwright found in California. References: Howden 1955, 1964, 1974; Woodruff 1973; Ritcher and Duff 1971. Larvae: Ritcher 1966; Howden 1955, 1964.

Ceratophyus Fischer von Waldheim 1823
One species, *C. gopherinus* Cartwright (Fig. 2), occurs in California. Larvae feed on leaf litter and twigs. Reference: Zunino 1973.

Geotrupes Latreille 1796
subgenus *Geotrupes* Latreille 1796
subgenus *Anoplotrupes* Jekel 1865
subgenus *Cnemotrupes* Jekel 1865
Onychotrupes Jekel 1865
subgenus *Geohowdenius* Zunino 1984
subgenus *Megatrupes* Zunino 1984

The genus includes ten species that are generally distributed from southern Canada to Texas. Adults feed on carrion, fungi, leaf litter, and dung. *Geotrupes stercorarius* (L.) was introduced to North America from Europe. Keys: Howden 1955, 1964.

Mycotrupes LeConte 1866

Five species in the genus are distributed in Georgia, Florida, and South Carolina. Adults are wingless and isolated in sandy areas. Keys: Olson *et al.* 1954; Woodruff 1973.

Peltotrupes Blanchard 1888

The genus includes two species, *P. profundus* (Howden) and *P. youngi* Howden, that live in the sandy ridges of northern and peninsular Florida. Larvae feed on leaves, twigs, bark, and male pine cones. Key: Howden 1955.

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30. OCHODAEIDAE Mulsant and Rey 1870

by David C. Carlson

Family common name: The sand-loving scarab beetles

The family Ochodaeidae is relatively small and widely distributed. Adults are small, mostly brown, non-metallic beetles that are predominately active at night. They are most often collected at lights, sometimes in large numbers. Adults of a few species are active during the day. Many species prefer sandy areas, and many stridulate. Woodruff (1973) suggested that adults may spend the daylight hours in subterranean burrows, and that they might feed on fungi. Little else is known about the habits of adult or immature stages.

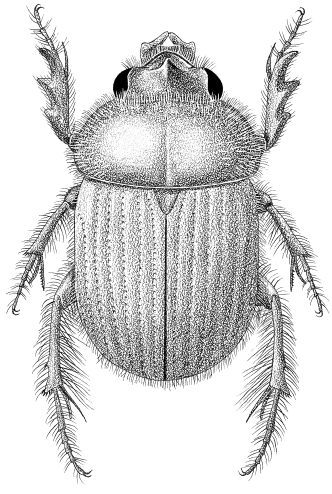

FIGURE 1.30. *Ochodaeus mandibularis* Linell

Description. Length 3.0-10.0 mm. Shape elongate and convex. Color yellowish, brown, reddish-brown, brown, or black; infrequently bicolorous.

Head not deflexed. Antennae 9 or 10-segmented, with 3-segmented, opposable, club (all antennomeres tomentose). Eyes with eucone ommatidia, not divided by canthus. Clypeus simple or with tubercle(s) on anterior margin. Labrum produced beyond apex of clypeus, often bilobed and emarginate, prominent. Mandibles produced beyond apex of labrum, prominent. Maxillae with 4 or 5-segmented palpi; labium with 3 or 4-segmented palpi.

Pronotum convex, subquadrate; most punctate and setose; without tubercles, ridges, horns, or sulci. Elytra convex, with or without striae, often punctate or granulate and setose, some smooth. Scutellum exposed, triangular. Pygidium exposed or concealed by elytra. Legs with procoxae conical or transverse; meso- and metacoxae transverse, mesocoxae separated or contiguous; protibia dentate on outer margin, apex with 1 spur; meso- and metatibia with 2 apical spurs; 1 mesotibial spur pectinate/crenulate, pro- and metatibial spur crenulate/pectinate in some; tarsi 5-5-5; claws equal in size, simple; empodium absent.

Abdomen with 6 visible sternites; stridulatory peg present in some; 8 functional abdominal spiracles with spiracles 1-6 situated in pleural membrane and spiracles 7-8 situated in tergites; tergite, pleurite, and sternite of female 9th abdominal segment visible as distinct sclerites. Wings well developed, M-Cu loop and two apical detached veins present. Male genitalia with divided basal piece, symmetrical parameres, partially sclerotized membranous median lobe and large internal sac; internal sac armed with spines, hooks, and toothed sclerites in many. Female genitalic hemisternites with styli present. Six ovarioles per ovary. References: Browne and Scholtz 1995; Carlson 1975; Carlson and Ritcher 1974; Ritcher 1969a, 1969b; Ritcher and Baker 1974; Scholtz 1990; Scholtz *et al.* 1988.

Larvae are scarabaeiform (C-shaped, cylindrical). Color whitish (except at caudal end which may be darkened by accumulated feces). Cranium sclerotized, yellow-brown to red-brown. Antennae 3 or 4-segmented, penultimate and apical segment with sense organs. Ocelli absent. Frontoclypeal suture absent. Labrum trilobed. Epipharynx with complete, symmetrical zygum; tormae fused and symmetrical. Maxilla with galea and lacinia distinctly separate. Maxillary palpi 4-segmented; maxillary and mandibular stridulatory areas present. Abdominal segments 1-7 with 3 dorsal lobes, anterior 2 lobes with transverse row of setae. Spiracles cribriform, inconspicuous. Anal opening Y-shaped, surrounded by fleshy lobes. Legs well developed, 4-segmented, with well-developed claws, stridulatory apparatus lacking. References: Carlson and Ritcher 1974; Medvedev 1960; Scholtz 1990.

Habits and habitats. Little is known about the biology of Ochodaeidae. There are few recorded observations of adult or larval habits except that adults of most species are nocturnal and are attracted to light, sometimes in large numbers. Adults of a few species are diurnally active and have been collected infrequently with sweep nets, malaise traps, or seining flumes. Adults of one species have been found associated with detritus deposits of harvester ants. Adults of another species were found to have basidiomycete spores in the midgut and hindgut. References: Arrow 1912; Carlson 1975; Carlson and Ritcher 1974; Deloya 1988.

Status of the classification. The ochodaeids have long been recognized as a distinct group. Their status has vacillated between the subfamily and family levels, but more recent works have tended to favor familial status (Scholtz 1990; Scholtz and Evans 1987; Scholtz and Chown 1995; Scholtz *et al.* 1988). Two subfamilies, Chaetocanthinae and Ochodaeinae are currently recognized (Lawrence and Newton 1995; Scholtz *et al.* 1988).

The phylogenetic position of the Ochodaeidae within the Scarabaeoidea has been discussed by numerous authors. Current views consider the ochodaeids to be an "intermediate" scarabaeoid family (Browne and Scholtz 1995; Scholtz 1990). A close relationship with the Hybosoridae was suggested by Carlson and Ritcher (1974). Recent studies suggest a close relationship between the Ochodaeidae, Hybosoridae, and Ceratocanthidae and consider the Ochodaeidae to be the sister group to the Hybosoridae plus

FIGURES 2.30-3.30. Spur at apex of metatibia of: 2. *Pseudochodaeus estriatus* (Schaeffer), pectinate; 3. *Ochodaeus* sp., not pectinate.

Ceratocanthidae (d'Hotman and Scholtz 1990; Scholtz *et al.* 1988; Browne and Scholtz 1995). The presence of a pectinate/crenulate mesotibial spur in the Ochodaeidae is unique among the Scarabaeoidea and, according to Scholtz (1990), establishes the monophyly of the group. Within the Ochodaeidae, d'Hotman and Scholtz (1990) consider *Ochodaeus* and *Codocera* to be the most primitive based on the structure of the male genitalia, and *Chaetocanthus* and *Namibiotalpa* are considered the most derived.

Taxonomy of the world Ochodaeidae is fairly well established for the Chaetocanthinae and the tribe Enodognathini (Ochodaeinae) (Scholtz and Evans 1987; Scholtz *et al.* 1988). The tribe Ochodaeini, however, is in a state of flux due to Nikolayev's (1995) description of two new genera. Nikolayev (1995) did not fully assign species to the new genera, and it is likely that more of the North American species currently included in *Ochodaeus* will be assigned to these genera. Nikolayev (1995) based these genera on characters that are well-recognized as separating groups (Fall 1909; Horn 1876; Carlson 1975).

Distribution. The family Ochodaeidae includes ten extant and two fossil genera and about 80 species worldwide (Arrow 1912; Scholtz and Evans 1987; Scholtz *et al.* 1988; Nikolayev 1995). In the Nearctic region, the family includes four genera and 35 species. North American catalog: Smith 2001. Regional works: Blatchely 1910; Edwards 1949; Woodruff 1973; Kirk and Balsbaugh 1975; Ratcliffe 1991; Downie and Arnett 1996.

Key to the Nearctic Subfamilies and Genera of the Family Ochodaeidae of the United States, Canada, and Nearctic Mexico

1. Metatibial spur not crenulate or pectinate (Fig. 3); metatibia cylindrical or flattened; abdominal stridulatory peg present in most (Ochodaeinae) 2

— Metatibial spur crenulate or pectinate (Fig. 2); metatibia flattened; abdominal stridulatory peg absent (Chaetocanthinae) ..... *Pseudochodaeus*

2(1). Sutural angle of elytra dentiform; propygidium with pair of tubercles at midline that interlock with dentiform elytral apices ..... *Parochodaeus*

— Sutural angle of elytra not dentiform; propygidium without tubercles at midline 3

3(2). Propygidium with longitudinal groove at midline that interlocks with medial edge of elytron. ..... *Neochodaeus*

— Propygidum with distal margin modified into transverse ridge that interlocks with distal elytral margin ..... *Ochodaeus*

Classification of the Subfamilies and Genera

Ochodaeidae Mulsant and Rey 1870

Ochodaeinae Mulsant and Rey 1870

Characteristics: Antennae 10-segmented. Pronotal surface punctate or granulate. Mesotibial spur crenulate or pectinate. Abdominal stridulatory peg present on sternum.

This subfamily contains six genera and about 70 species worldwide. Its members occur on all continents except Australia and Antarctica. North American species belong to three genera. Until Nikolayev (1995) described the genera *Neochodaeus* and *Parochodaeus*, *Ochodaeus* was the only genus from this subfamily represented in the Nearctic. Little is known about adult or larval habits. References: Horn 1876; Fall 1909; Arrow 1912; Howden 1968; Carlson 1975; Scholtz *et al.* 1988; Nikolayev 1995.

Neochodaeus Nikolayev 1995
Two species are distributed in the southwestern and southeastern United States and Mexico. References: Carlson 1975; Nikolayev 1995.

Ochodaeus Dejean 1821
This genus (Fig. 1) includes about 26 Nearctic and Neotropical species distributed from southern Canada to South America. References: Carlson 1975. Keys: Fall 1909; Woodruff 1973; Ratcliffe 1991.

Parochodaeus Nikolayev 1995
Six species are found in the southwestern and midwestern United States and Mexico. References: Carlson 1975; Nikolayev 1995.

Chaetocanthinae Scholtz 1988

Characteristics: Antennae 9 (*Chaetocanthus* only) or 10-segmented. Pronotal surface granulate in most. Meso- and metatibial spurs pectinate/crenulate. Abdominal stridulatory peg absent from sternum.

This subfamily contains four genera, three of which are found only in Africa. The fourth genus (*Pseudochodaeus*) is limited to the west coast of the United States. Little is known about the adult or larval habits. References: Carlson and Ritcher 1974; Scholtz *et al.* 1988.

Pseudochodaeus Carlson and Ritcher 1974

The genus *Pseudochodaeus* is monobasic. The single species, *P. estriatus* (Schaeffer), is distributed at mid-elevations from southern Oregon to central California. Reference: Carlson and Ritcher 1974.

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31. HYBOSORIDAE Erichson 1847

by Mary Liz Jameson

Family common name: The scavenger scarab beetles

Members of the Hybosoridae are distinguished from other scarabaeoids by their prominent mandibles and labrum and by their 10-segmented antenna with a 3-segmented club in which the basal antennomere of the club is hollowed out to receive the penultimate and ultimate antennomeres (Fig. 2). Other than adults being attracted to lights, little is known about their biology. In the Nearctic region, only two genera occur, one of which was adventive.

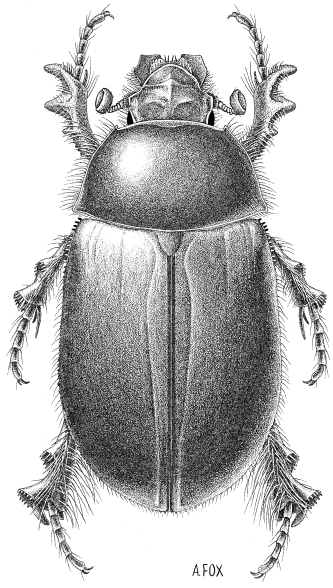

FIGURE 1.31. *Pachyplectrus laevis* (LeConte)

Description. Length 5.0-7.0 mm. Shape oval, dorsal surface convex. Color light brown to black, glossy.

Head not deflexed. Antennae 10-segmented with 3-segmented, opposable club (last 2 antennomeres tomentose), first antennomere of club hollowed to receive club antennomeres 2 and 3 (Fig. 2), basal antennomere expanded apically. Eyes with eucone ommatidia, divided by reduced canthus. Clypeus generally lacking tubercle or horn (*Pachyplectrus laevis* LeConte has a small tubercle on the frontoclypeal suture). Labrum truncate, produced beyond apex of clypeus, prominent. Mandibles produced beyond apex of labrum, prominent, external edge rounded, apex pointed. Maxillae with 4-segmented palpi; labium with 4-segmented palpi.

Pronotum convex, base wider than elytral base. Elytra convex, surface polished, glabrous. Pygidium concealed by elytra. Scutellum exposed, triangular. Legs with anterior coxae conical, contiguous; mesocoxae contiguous; protibiae tridentate on outer margin, apex with one spur; meso- and metatibia with prominent, oblique ridge, apex with 2 spurs; tarsi 5-5-5; claws equal in size, simple; empodium short, not extending beyond fifth tarsomere, with 2 setae.

Abdomen with 6 free sternites (first sternite obscured by hind coxae except at lateral edges); 8 functional abdominal spiracles, situated in pleural membrane (spiracles 1-7) and in tergite (spiracle 8). Wings well developed, with 2 apical, detached veins and M-Cu loop present. Male genitalia variable. References: Cooper 1983, Scholtz 1990.

Larvae are scarabaeiform (C-shaped, cylindrical). Color creamy-white or yellow (except at caudal end which may be darkened by accumulated feces). Cranium heavily sclerotized, brown to dark brown. Antennae 3 or 4-segmented (if 3-segmented, then third and fourth segments fused). Frontoclypeal suture distinct. Labrum at apex with 3 truncate lobes. Epipharynx with row of setae on each chaetoparia, a blunt tooth in the haptomeral region, and united tormae. Maxilla with galea and lacinia distinctly separate; maxillary stridulatory area consisting of a row of conical teeth; maxillary palp 3- or 4-segmented. Abdominal segments 1-6 with 3 annuli, each with 1 or more transverse rows of short setae. Spiracles cribriform, with closing apparatus. Venter of last abdominal segment with raster consisting of 2 curved rows of many short setae that converge caudally. Legs 4-segmented, well developed, with stridulatory apparatus on pro- and mesothoracic legs, each with a well-developed claw. References: Ritcher 1966; Scholtz 1990.

Habits and habitats. Little life history information is known for hybosorids. Adults feed on both invertebrate and vertebrate carrion in the early stages of decomposition; some species are found in dung, and others are attracted to lights at night. Adults of *Hybosorus illigeri* have been reported from turf in golf courses. Adults of *Hybosorus* are known to stridulate. Larvae stridulate by rubbing the front legs against the anterior margin of the epipharynx, a trait unique to the Hybosoridae (Paulian 1939). Larvae have been collected in decomposing plant material.

Status of the classification. The Hybosoridae are considered as a family within the Scarabaeoidea or as a subfamily of the family Scarabaeidae. In this volume, we follow Gardner (1935), Paulian (1939), and Lawrence and Newton (1995) and consider the group a family. Hybosorid larvae are distinct, and this is the primary reason that the group is treated as a family. Larvae possess prothoracic and mesothoracic stridulatory structures and three truncate lobes at the apex of the labrum, both of which are unique to this group. In adults, the form of the antenna (10-segmented with a 3-segmented club, the first club antennomere hollowed to receive club antennomeres two and three) is unique. The family Hybosoridae is hypothesized to be intermediate between the Ochodaeidae and Ceratocanthidae (Scholtz *et al.* 1988) or intermediate between the Trogidae and Ceratocanthidae (Howden and Gill 1988). Phylogenetic analyses of Browne and Scholtz (1995, 1999) hypothesize that the Hybosoridae and Ceratocanthidae are sister taxa. Aside from revisions of some genera and catalogs, little systematics work has been conducted on this group.

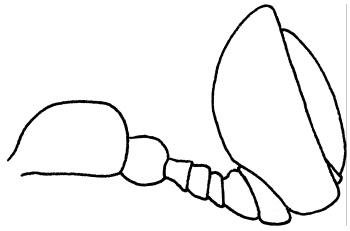

FIGURE 2.31. Right antenna, dorsal view of *Hybosorus illigeri* Reiche.

Distribution. The family Hybosoridae contains 33 genera world-wide and about 210 species (Allsopp 1984; Martínez 1994). Species are widely distributed in the tropics. Two genera and two species occur in the Nearctic region. *Phaeochrous emarginatus* Castelnau, a species that occurs in Asia, Australia, and India, was once reported from California, but the species is not established in California and the record was probably in error (Art Evans, personal communication 1998). Regional works: Hatch 1971; Woodruff 1973; Ratcliffe 1991; Downie and Arnett 1996; Harpootlian 2001.

Key to the Genera of Hybosoridae of The United States, Canada, and Nearctic Mexico

1. Mandibles narrow, falciform; frontoclypeal suture without tubercle ..... *Hybosorus*
— Mandibles wide, outer edge angular; frontoclypeal suture with tubercle..... *Pachyplectrus*

Classification of the Nearctic Genera

Hybosoridae Erichson 1847

Hybosorus MacLeay 1819

Hybosorus illigeri Reiche was inadvertently brought to the United States, apparently arriving before the 1840s from Europe. Its distribution now includes the southern United States, Caribbean, and Mexico. Adults are attracted to lights and have been reported from turf in golf courses. Larvae are not described. Key: Kuijten 1983.

Pachyplectrus LeConte 1874

The genus includes only *P. laevis* (LeConte) (Fig. 1). Specimens are rare and are distributed in Arizona and southern California. Adults have been taken at lights, on the crests of sand dunes, and in the burrows of kangaroo rats (Hardy 1977). Larvae remain unknown. Reference: Woodruff 1973.

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32. CERATOCANTHIDAE Martínez 1968

by Mary Liz Jameson

Family common name: The pill scarab beetles

Family synonym: Acanthoceridae Lacordaire 1856

Members of the Ceratocanthidae are distinguished from other scarabaeoids by the ability of the adult to form a nearly compact sphere. When disturbed, adults deflect the head, pronotum, and legs, thus forming a tight ball.

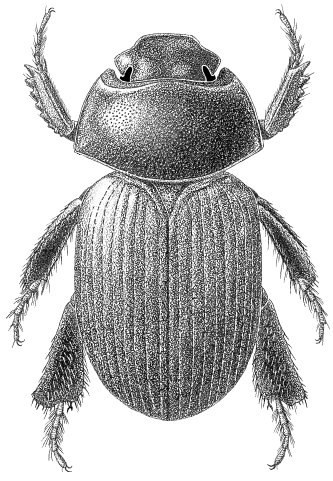

FIGURE 1.32. *Germarostes aphodioides* (Illiger) (Used by permission of University of Nebraska State Museum)

Description. Length 2.0-9.0 mm. Shape nearly spherical when head and pronotum deflexed. Color black, greenish black, or purplish, often with metallic luster.

Head deflexed. Antenna 9 or 10-segmented with 3-segmented, opposable club (all antennomeres tomentose); basal antennomere triangular and enlarged. Eyes partially divided by canthus, with eucone ommatidia. Clypeus lacking tubercle or horn. Labrum truncate, partially exposed beyond apex of clypeus. Mandibles partially exposed beyond apex of clypeus. Maxillae with 4-segmented palpi. Labium with 4-segmented palpi.

Pronotum broad, compressed laterally. Elytra convex, surface highly polished and glabrous. Pygidium concealed by elytra. Scutellum exposed, triangular. Legs with anterior coxae conical, prominent; mesocoxae transverse; tibiae (especially meso- and metatibae) horizontally flattened and broad (concealing sternites when contracted in spherical form), external surface striated; protibia with outer margin serrately toothed, apex with one spur; meso- and metatibia with 2 apical spurs; tarsi 5-5-5; claws equal in size, simple; empodium absent.

Abdomen with 5 free sternites; 8 functional abdominal spiracles situated in pleural membrane (spiracles 1-7) and in tergite (spiracle 8). Wings well developed, M-Cu loop reduced or absent, with 1 apical detached vein. Male genitalia variable. References: Cooper 1983; Scholtz 1990.

Larvae are scarabaeiform (C-shaped, cylindrical). Color creamy-white or yellow (except at caudal end which may be darkened by accumulated feces). Cranium heavily sclerotized, yellow-brown to dark brown. Antenna 4-segmented. Frontoclypeal suture distinct. Labrum with apical margin serrate, palpi 1-2 segmented. Epipharynx with dextral, beak-like process. Maxilla with galea and lacinia separate; maxillary stridulatory area with a row of conical teeth; maxillary palp 4-segmented. Abdominal segments 1-6 with 3 annuli, each with one or more transverse rows of short setae. Spiracles cribriform. Venter of last abdominal segment with transverse palidium of spatulate setae. Legs 4-segmented, well developed, with stridulatory apparatus on all legs or on meso- and metathoracic legs, each with a well-developed claw. References: Ritcher 1966; Scholtz 1990.

Habits and habitats. Adult ceratocanthids can be collected on the bark and branches of dead trees and vines, on fungi, in the burrows of passalid beetles, and occasionally at lights. Adults have also been found in association with termites and ants. When disturbed, these beetles are able to deflex their head and pronotum, thus concealing the entire ventral side. When contracted in this manner, they resemble spherical seeds. This behavior probably allows them to evade potential predators. This trait occurs in a lesser degree in some Hybosoridae. Adults probably feed on fungi (Nel and Scholtz 1990) or on rotting wood (Ohaus 1909). Larvae have been collected under bark (Ritcher 1966), reared from frass in passalid burrows (*Germarostes*, Woodruff 1973), and reared from wet tree holes (*Ceratocanthus*, Choate 1987). Adults and larvae of at least some species stridulate.

Status of the classification. The Ceratocanthidae are considered a family within the Scarabaeoidea or a subfamily of the family Scarabaeidae. In this volume, we follow Lawrence and Newton (1995) and consider the group a family. The group was previously referred to as the Acanthoceridae (Lacordaire 1856), a junior homonym that required replacement. The family name Ceratocanthidae has been erroneously attributed to Cartwright and Gordon (1971). Martínez (1968) first used the name at the family group level and should be credited as the author.

Based on phylogenetic analyses and character data, the family Ceratocanthidae is hypothesized to be the sister group to the Hybosoridae (Browne and Scholtz 1995, 1999; Lawrence and Britton 1994). However, Cooper (1983) postulated that the Ceratocanthidae are most closely related to the Trogidae. Aside from the work of Paulian (1982) for the South American Ceratocanthidae, little systematics work has been conducted on genera in the group. Howden and Gill (2000) provided a key to the New World genera, thus creating an excellent foundation for future studies.

Distribution. The family is widely distributed in the tropics. No ceratocanthids are known from Europe, and only three are known from Australia. In North and South America, the

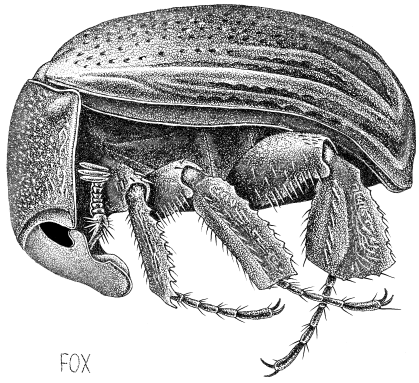

FIGURE 2.32. *Germarostes aphodioides* (Illiger) lateral view.

group includes 11 genera and about 155 species (Howden and Gill 2000). Two genera and three species occur in the Nearctic region. North American catalog: Smith 2001. Regional works: Woodruff 1973; Ratcliffe 1991; Downie and Arnett 1996; Harpootlian 2001.

Key to the Genera of the United States, Canada, and Nearctic Mexico

1. Middle and hind tibiae thickened at apical edge; posterior angles of pronotum nearly right-angled ..... *Germarostes*
— Middle and hind tibiae flat, blade-like; posterior angles of pronotum rounded ..... *Ceratocanthus*

Classification of the Nearctic Genera

Ceratocanthidae Martínez 1968

Ceratocanthus White 1842
Acanthocerus MacLeay 1819
Sphaeromorphus Germar 1843

One species, *C. aeneus* (MacLeay), occurs in the southeastern United States. Specimens have been collected by beating dead vegetation; they are rare in collections (Howden and Gill 2000). Choate (1987) discussed the biology of this species.

Germarostes Paulian 1982

Two species of *Germarostes, G. aphodioides* (Illiger) (Figs. 1-2) and *G. globosus* (Say), occur in the Nearctic region. Previously, these species were placed in the genus *Cloeotus* but were removed by Paulian (1982). The two species occur from southern Ontario to Indiana, south to Florida and Texas, and west to Nebraska. Specimens can be collected by beating dead vines, from fungi and carrion, at lights at night, and in flight intercept traps. Larvae have been collected from the frass of passalid burrows in logs. Key: Woodruff 1973.

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33. GLAPHYRIDAE MacLeay 1819

by David C. Carlson

Family common name: The bumble bee scarab beetles

Glaphyrid beetles are active fliers during the day. Adults of many species are brightly colored and hairy and often possess markings and coloration resembling bees and bumble bees. They are strong fliers and are often observed hovering near flowers or foliage or flying over sandy areas.

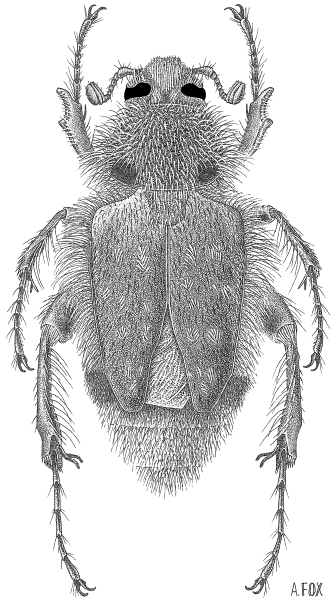

FIGURE 1.33 *Lichnanthe rathvoni* LeConte

Description. Length 6.0-20.0 mm. Shape elongate. Color testaceous to black, often with metallic reflections; setae dense, moderately long, color variable (white, yellow, orange, red, brown, or black).

Head deflexed. Antennae 9 or 10-segmented with 3-segmented, opposable club (all antennomeres tomentose). Eyes with eucone ommatidia, completely or partially divided by a canthus. Clypeus in most simple, anterior margin with or without teeth. Labrum emarginate, truncate or rounded, produced beyond apex of clypeus, prominent. Mandibles produced beyond apex of labrum, prominent. Maxillae filiform, plumose or truncate, with 4 or 5-segmented palpi. Labium with 4-segmented palpi.

Pronotum convex, most subquadrate, often densely punctate and setose, without tubercles, ridges, horns, or sulci. Elytra elongate, often thin and dehiscent at apex, without striae, often setose. Pygidium visible beyond elytra in most. Scutellum exposed, U-shaped or triangular. Legs with procoxae conical or transverse, meso- and metacoxae transverse; mesocoxae separated or contiguous; protibiae dentate on outer margin, apex with one spur; meso- and metatibia generally simple but some with apical modifications (spines or emarginations), apex with 2 spurs; tarsi 5-5-5, foretarsi modified medially (pectinate) in some Old World genera; claws equal in size with 1 tooth; empodium exposed beyond fifth tarsomere, dorso-ventrally flattened, with 2 setae.

Abdomen with 6 free sternites, most with 8 pairs of spiracles; spiracles 1-6 or 1-7 situated in pleural membrane, spiracles 7 or 8 in tergites (Glayphyrinae and some Lichniinae) or spiracles 1-8 in pleural membrane (some Lichniinae). Wings well developed, M-Cu loop present with 1 apical, detached vein. Male genitalia with well sclerotized, strongly arched basal piece, basal piece large relative to parameres; internal sac variable. Ovary with 6 ovarioles. References: Chapin 1938; Ritcher 1969; Ritcher and Baker 1974; Carlson 1980; d'Hotman and Scholtz 1990; Scholtz 1990; Browne and Scholtz 1995.

Larvae are scarabaeiform (C-shaped, cylindrical). Color bluish-white to yellow (prepupae) (except at caudal end which may be darkened by accumulated feces). Head capsule heavily sclerotized, reddish-brown (*Lichnanthe* with conspicuous median, circular depression on frons). Antennae 4-segmented, third segment with small sensory pits. Stemmata present or absent. Frontoclypeal suture present. Labrum trilobed. Epipharynx with asymmetrical tormae not fused. Maxilla with galea and lacinia separate; maxillary palpi 4-segmented; labial palpi 2-segmented; maxillary and mandibular stridulatory areas present. Abdominal segments 1 to 8 with 3 dorsal annuli. Spiracles cribriform. Anal slit transverse, located caudally on dorsum of last abdominal segment. Legs well developed, 4-segmented, lacking stridulatory organs; claws present. References: Ritcher 1966; Scholtz 1990.

Habits and habitats. Except for a few species, life histories of the glaphyrids are poorly documented. Adults are often brightly colored, densely setose, active diurnally, and strong fliers. Many species have colored setal bands on the abdomen and resemble various Hymenoptera (bumble bees and metallic bees). They have been observed frequenting flowers and foliage. Larvae are free living in sandy areas (riparian and coastal dunes) where they feed on decaying leaf litter and detritus that is layered in the sand. Larvae of *Lichnanthe vulpina* (Hentz) may be a pest of cranberry bogs in the northeastern United States. References: Ritcher 1966; Westcott 1976; Carlson 1977, 1980.

Status of the classification. The uniqueness of the glaphyrids has been recognized for a very long time, and the genera included in the group have changed little. However, the status of the group has been the subject of debate. Superfamily status was proposed by Machatschke (1959) but was not generally accepted. Workers have vacillated between using subfamily or family status, and familial status is now generally accepted (d'Hotman and Scholtz 1990; Scholtz 1990; Browne and Scholtz 1995).

The phylogenetic position of the Glaphyridae within the Scarabaeoidea has been discussed by numerous authors and is currently considered by most to be among the intermediate scarabaeoid families (d'Hotman and Scholtz 1990; Scholtz 1990; Browne and Scholtz 1995). Browne and Scholtz (1995) consider the Glaphyridae to be a monophyletic sister group of the trogid subgroup (Trogidae, Bolboceratinae [Geotrupidae] and Pleocomidae) based on characters of wing articulation.

Taxonomy of the world Glaphyridae is not well-established. Comprehensive taxonomic treatments are available for *Lichnanthe* (Carlson 1980), *Anthypna* (Endrödi 1952), and *Pygopleurus* (Petrovitz 1958). Most other genera have not been reviewed comprehensively. The taxonomy and nomenclature of the group were discussed by Chapin (1938) and Machatschke (1959). The extreme color polymorphism exhibited by many species has resulted in a proliferation of form, variety, or color morph names for some species, many of which are synonyms. The most recent world catalog for the family was Arrow (1912).

Distribution. The family Glaphyridae includes eight genera and about 80 species worldwide (Arrow 1912; Chapin 1938; Yawata 1942). The subfamily Lichniinae (including three genera) is limited to western South America, and the subfamily Glaphyrinae (including five genera) is widely distributed in the Holarctic region. One genus and eight species of glaphyrids occur in the United States, Canada, and Nearctic Mexico. Key to genera and subgenera: Chapin 1938. Key to U.S. species: Carlson 1980. Regional works: Edwards 1949; Hatch 1971; Downie and Arnett 1996. North American catalog: Smith 2001. Larvae: Ritcher 1966.

Classification of the Nearctic Genera

Glaphyridae MacLeay 1819

Glaphyrinae MacLeay 1819

Characteristics: Antennae 10-segmented, maxillary palpi truncate. This subfamily consists of five genera with about 68 species and is widely distributed in the Holarctic region. North American species belong to a single genus, *Lichnanthe* Burmeister. Adults are active diurnal fliers and frequent foliage and flowers. Adults of many species resemble various Hymenoptera (bumble bees and metallic bees). References: Chapin 1938; Westcott 1976; Carlson 1977, 1980. Larvae: Ritcher 1966.

Lichnanthe Burmeister 1844

This genus (Fig. 1) includes eight extant species and one fossil species that are Nearctic in distribution and primarily restricted to the continental United States. Species are distributed in the east coast states and western states. Key: Carlson 1980. (Volume 2, Color Figure 22)

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34. SCARABAEIDAE Latreille 1802

by Brett C. Ratcliffe, Mary Liz Jameson and Andrew B. T. Smith

Family common name: The scarab beetles

Scarab beetles comprise a speciose group, and they are a conspicuous component of the beetle fauna in the Nearctic region. Adults of many scarab beetles are noticeable due to their relatively large size, bright colors, often elaborate ornamentation, and interesting life histories. The family includes the goliath beetle from Africa [*Goliathus goliathus* (L.)], known as one of heaviest insects (up to 100 grams). It also includes the elephant beetle [*Megasoma elephas* (Fabricius)] and hercules beetle [*Dynastes hercules* (L.)], both from the American tropics, that are known for their large size (up to 160 mm for the hercules beetle) and highly developed horns in the males. The group includes over 27,800 species, an intriguing array of life histories, and many interesting adaptations.

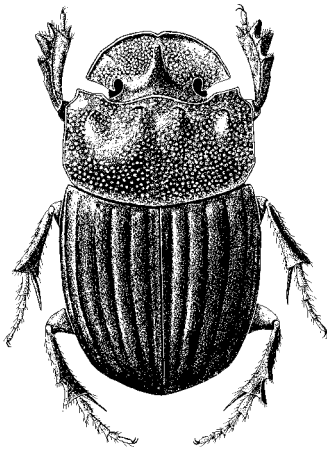


FIGURE 1.34. *Copris fricator* (Fabricius) (Used by permission of University of Nebraska State Museum)

Description. Length 2.0-60.0 mm (Nearctic species). Shape variable; ovate, obovate, quadrate, cylindrical. Color variable, with or without metallic reflections or metallic coloration; with or without vestiture.

Head weakly deflexed or not deflexed. Antennae 10-segmented (some 7-12 segmented) with 3 to 5-segmented, opposable club; club with apical antennomeres nearly glabrous [Melolonthinae, Dynastinae, Rutelinae, Cetoniinae] or with all antennomeres tomentose [Aphodiinae, Scarabaeinae]. Eyes with eucone ommatidia, partially divided by a canthus. Clypeus with or without tubercle or horn. Labrum distinct in most, produced beyond apex of clypeus or not. Mandibles variable, produced beyond apex of labrum or not. Maxillae with 4-segmented palpi. Labium with 3-segmented palpi.

Pronotum variable, with or without horns or tubercles. Elytra convex or flattened, with or without striae. Pygidium concealed by elytra [Aphodiinae, Scarabaeinae] or exposed [Scarabaeinae, Melolonthinae, Dynastinae, Rutelinae, Cetoniinae]. Scutellum exposed or not; shape triangular or parabolic. Legs with coxae transverse or conical; protibiae tridentate, bidentate, or serrate on outer margin, apex with one spur; meso- and metatibia slender or robust, apex with 1 or 2 spurs; tarsi 5-5-5, anterior tarsi absent in some Scarabaeinae; claws variable, equal in size or not, simple or toothed; empodium present, extending beyond fifth tarsomere, with 2-5 setae or with setae absent.

Abdomen with 6 free sternites; 7 functional abdominal spiracles situated in pleural membrane [Aphodiinae, Scarabaeinae] or in pleural membrane, in sternites and in tergite [Melolonthinae, Dynastinae, Rutelinae, Cetoniinae]. Wings well developed, M-Cu loop and 1 apical, detached vein present. Male genitalia variable, bilobed, or fused. References: Cooper 1983; Scholtz 1990.

Larvae are scarabaeiform (C-shaped, cylindrical), some humpbacked [Scarabaeinae]. Color creamy-white or yellow (except at caudal end which may be darkened by accumulated feces). Cranium heavily sclerotized, testaceous to brown to black. Antennae 4-segmented, last segment bearing 1 or more sensory spots. Ocelli absent, present [some Dynastinae, Cetoniinae], or with distinct pigmented spots. Frontoclypeal suture present. Labrum at apex variable, rounded or lobed. Epipharynx rounded or lobed, asymmetrical. Maxilla with galea and lacinia distinctly separate [Aphodiinae, Scarabaeinae], fused proximally and free distally [Melolonthinae], or fused to form mala [Dynastinae, Rutelinae, Cetoniinae]; maxillary stridulatory area present in most; maxillary palpus 4-segmented. Abdomen with segments 9 and 10 fused dorsally [Cetoniinae], segments 1-6 or 7 mostly with 3 annuli, each with 1 or more transverse rows of setae. Spiracles cribriform. Venter of last abdominal segment with or without fleshy lobes, apex with or without palidia, anal opening with transverse or Y-shaped slit. Legs 2-segmented [Scarabaeinae] or 4-segmented [Aphodiinae, Melolonthinae, Dynastinae, Rutelinae, Cetoniinae], lacking stridulatory process; claws present or absent with 1-2 setae. References: Ritcher 1966; Scholtz 1990.

Habits and habitats. Life histories of scarab beetles are incredibly diverse and include adults that feed on dung, carrion, fungi, vegetation, pollen, fruits, compost, or roots. Some scarab beetles live in the nests of ants (myrmecophiles), in the nests of termites (termitophiles), or in the nests of rodents or birds. Some species of dung beetles (Scarabaeinae) care for their larvae or the larval brood ball (*e.g.,* species of *Canthon* and *Copris*). Adults of some scarab beetles are diurnal and can be observed on flowers or vegetation (*e.g., Euphoria, Cotinis* [Cetoniinae]) while many species are nocturnal and attracted to lights at night (*e.g., Dynastes* [Dynastinae], *Chrysina* [Rutelinae], *Polyphylla* [Melolonthinae]). Adults and larvae of a few species of scarabs are economically important and may cause considerable damage due to defoliation or root-feeding (*e.g., Popillia japonica* Newman [Rutelinae]). Many scarabs are beneficial because they pollinate plants, recycle plant material, and are valuable dung recyclers. In 1968, for example, several species of dung beetles were introduced into Australia to

aid in the decomposition of cattle feces (Waterhouse 1974). Domesticated cattle produce feces different from native Australian herbivores. Native Australian dung beetles were not adapted to feed on the dung of domesticated cattle. As a result, cattle feces accumulated at such a rate that grasses and forbes were smothered and killed. Dung beetles were introduced from Africa, and these beetles readily fed on cattle dung, enriched the soil with the dung, and allowed the grasses and forbes to thrive. The dung beetles also reduce breeding sites for pest flies.

"Dung beetle" is a common name applied to beetles in the subfamilies Scarabaeinae and Aphodiinae. Species in these groups often have specific ecological requirements. For example, *Dialytes* spp. and *Aphotaenius carolinus* (Van Dyke) (both Aphodiinae) are specialists on deer dung. Some dung beetles, the so-called "tumble bugs" (*e.g., Canthon pilularius* (L.) [Scarabaeinae]), form a ball of dung and roll it away from potential competition at a dung pat. Other dung beetles make a ball of dung under the dung pile (*e.g., Copris fricator* (Fabricius), *Phanaeus vindex* (MacLeay), *Onthophagus hecate* (Panzer), *Onthophagus subaeneus* (Palisot de Beauvois) [all Scarabaeinae]). Scarab beetles that live in the nests of vertebrates include: *Onthophagus polyphemi* Hubbard (Scarabaeinae) that lives in the nest of gopher tortoises in Florida and South Carolina; *Ataenius sciurus* Cartwright (Aphodiinae) that lives in the nest of tree squirrels in Florida, and many species of *Aphodius* (Aphodiinae) that live in the nests of prairie dogs and pocket gophers. Although most dung beetles feed on dung, some, such as *Onthophagus striatulus* (Palisot de Beauvois) (Scarabaeinae), defy their common name and feed on fungi.

Some scarabs, such as *Euparia castanea* LePeletier and Serville (Aphodiinae) and *Cremastocheilus* spp. (Cetoniinae) are inquilines in the nests of ants. Species in the genus *Valgus* (Cetoniinae: Valgini) are inquilines in the nests of termites. The life history of these beetles, their adaptations, and their body form is intimately intertwined with their hosts.

Most species in the subfamilies Melolonthinae, Dynastinae, Rutelinae, and Cetoniinae feed on plant products. Larvae of many dynastines and rutelines feed on rotting wood. Larvae of many melolonthines (*e.g., Phyllophaga* species), rutelines (*e.g., Anomala* species), and dynastines (*e.g., Cyclocephala* species) feed on grass roots. Some of these larvae may be lawn pests (*e.g., Popillia japonica* Newman [Rutelinae], *Cyclocephala borealis* Arrow [Dynastinae], *Amphimallon majalis* Razoumowski, *Plectris aliena* Chapin, and *Phyllophaga* species [all Melolonthinae]). As adults, most species in these subfamilies feed on leaves or fruits. Adults of *Phyllophaga falsa* (LeConte) (Melolonthinae) occasionally defoliate pine trees. Some adults in these subfamilies are also attracted to sap flows.

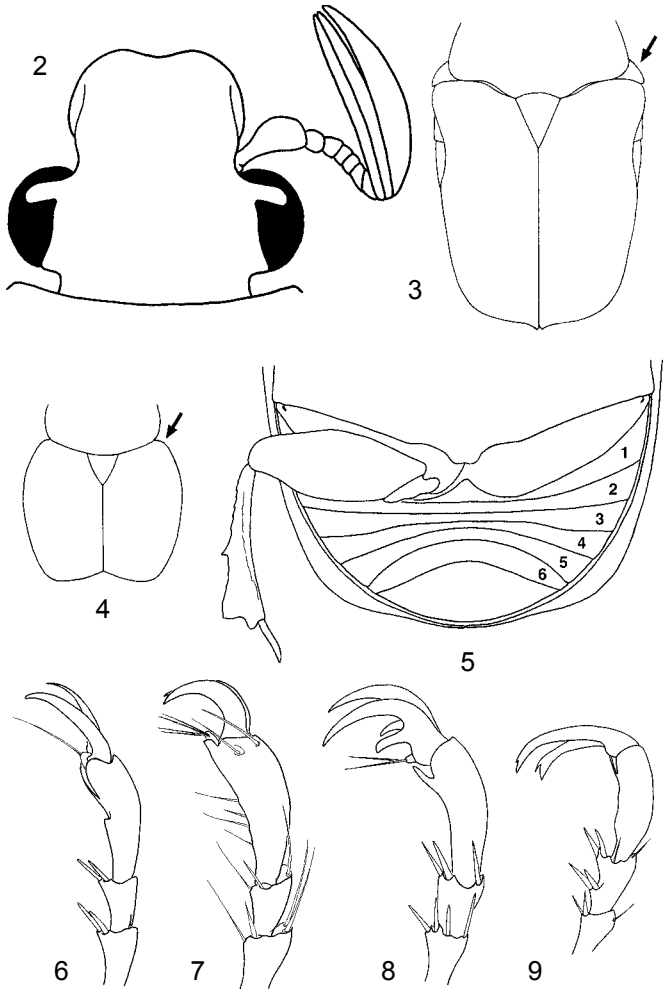
The larvae of most scarab beetles develop similarly. Eggs are deposited by the adult female in suitable soil, dung, compost, or other organic material. After hatching, the C-shaped grubs feed and grow, molting twice. In areas with cold winters, larvae overwinter below the frost line. As temperatures rise in the spring, larvae become active and feed until pupation. Emergence of the adults from pupal cells often occurs in response to environmental cues such as rainfall or temperature. After emergence, adults mate and begin the cycle anew. The biology and behavior of many species of scarabs are not known, and much remains to be studied. References: Woodruff 1973; Ratcliffe 1991.

Status of the classification. The past thirty years have seen many changes and debates in the classification of the Scarabaeidae. In the "traditional" North American system, the category Scarabaeidae has been treated as including the all scarabaeoid families except the Passalidae and Lucanidae. Old World scarab workers have tended to split the Scarabaeidae into several families. While the debate continues, we follow Lawrence and Newton (1995) and consider the family Scarabaeidae to include the subfamilies Aphodiinae, Scarabaeinae, Melolonthinae, Dynastinae, Rutelinae, and Cetoniinae. Several smaller subfamilies that are not present in the Nearctic region are also included in the Scarabaeidae: Orphninae, Phaenomeridinae, Pachypodinae, Allidiostomatinae, Dynamopodinae, Aclopinae, and Euchirinae. No phylogenetic analyses have addressed the relationships of all of these taxa. However, most hypotheses generally consider the Aphodiinae and Scarabaeinae as the sister group to the Melolonthinae, Dynastinae, Rutelinae, and Cetoniinae. The former Trichiinae and Valginae are here considered tribes of the Cetoniinae.

The family Scarabaeidae is sometimes referred to as the family Melolonthidae, especially by some of the Latin American workers. In this usage, the family includes the subfamilies Melolonthinae, Euchirinae, Phaenomeridinae, Dynastinae, Cetoniinae, Glaphyrinae, and Systellopodinae (Endrödi 1966) whereas the Scarabaeidae refers to everything else except Passalidae, Lucanidae, and Trogidae. This classification is not in wide use today and is incorrect. The family group names Rutelinae and Dynastinae were established by MacLeay in 1819, and the family group name Melolonthinae was established by Samouelle in 1819. However, the family group name Cetoniinae was established a few years earlier in 1815 by Leach. Thus, the family group name Cetoniidae has priority over Melolonthidae. Therefore, if one wants to consider all of these subfamilies in the same family (exclusive of Scarabaeinae, which was established by Latreille in 1802), then the valid name would be Cetoniidae! Accordingly, the family name Scarabaeidae (including Melolonthinae, Scarabaeinae, Dynastinae, Cetoniinae, etc.) is the correct family group name for these taxa and *not* Melolonthidae.

Classification of the world Scarabaeidae is variably known. The classification of the world Dynastinae is fairly well established due to the work of Endrödi (1985). Most Melolonthinae, Rutelinae, and Cetoniinae are so poorly known taxonomically that many New World genera cannot be reliably identified. Classification of the Scarabaeinae (Hanski and Cambefort 1991) and Aphodiinae are fairly well established (Dellacasa 1987, 1988a, 1988b, 1991, 1995). The taxonomy of the North American scarab beetles is relatively stable although no one volume is available for identification. Regional works (see listing) are sometimes the best sources for identification of Nearctic scarab beetles.

Distribution. The family Scarabaeidae includes about 91% of all scarabaeoids and includes about 27,800 species worldwide. Within the Scarabaeidae, the Aphodiinae and Scarabaeinae include approximately 6,850 species worldwide (about 22% of scarabaeoids and 25% of Scarabaeidae). The subfamilies



FIGURES 2.34-9.34. 2. Head and antenna (dorsal view) of *Euphoria* sp. showing clypeal sides constricted and with antennal insertion visible; 3. Cetoniini mesepimeron visible from above (arrow); 4. Trichiini mesepimeron not visible from above; 5. Abdomen and posterior leg of *Copris* sp. (Scarabaeinae). 6-9. Claws of posterior tarsi; 6. *Anomala* sp. (Rutelinae) (claws simple and unequal in length); 7. *Xyloryctes jamaicensis* (Drury) (Dynastinae) (claws simple and equal in length); 8. *Polyphylla* sp. (Melolonthinae); 9. *Dichelonyx* sp. (Melolonthinae) (claws cleft or toothed and equal in length) (Used by permission of University of Nebraska State Museum).

Orphninae, Melolonthinae, Dynastinae, Rutelinae, and Cetoniinae include approximately 20,950 species (about 69% of scarabaeoids and 75% of Scarabaeidae).

About 125 genera and 1,700 species of scarab beetles occur in the United States, Canada, and Nearctic Mexico. Keys to genera and species: Helgesen and Post 1967; Woodruff 1973; Ratcliffe 1991; Harpootlian 2001. Biology: Ritcher 1958. Catalog of the U.S. species: Blackwelder and Arnett 1974; Smith 2001. Regional works: Blatchley 1910; Loding 1945; Saylor 1948b; Edwards 1949; Helgesen and Post 1967; Hatch 1971; Woodruff 1973; Kirk and Balsbaugh 1975; Shook 1978; Lago *et al.* 1979; Ratcliffe 1991; Downie and Arnett 1996; Morón *et al.* 1997; Harpootlian 2001. Larvae: Ritcher 1966. Reference: Cooper 1983.

Classification of the Scarabaeidae of the United States, Canada, and Nearctic Mexico

The family Scarabaeidae is among the largest beetle families and is relatively well known. Despite the popularity of the group, there is no comprehensive treatment on the family as a whole. A comprehensive survey of this group is badly needed. The following subfamilies and tribes occur in the Nearctic region.

I. APHODIINAE
- 1. Aegialiini
- 2. Aphodiini
- 3. Didactyliini
- 4. Eupariini
- 5. Psammodiini

II. SCARABAEINAE
- 6. Canthonini
- 7. Coprini
- 8. Dichotomiini
- 9. Oniticellini
- 10. Onitini
- 11. Onthophagini
- 12. Phanaeini
- 13. Sisyphini

III. MELOLONTHINAE
- 14. Hopliini
- 15. Oncerini
- 16. Podolasiini
- 17. Sericini
- 18. Chasmatopterini
- 19. Melolonthini
- 20. Diplotaxini
- 21. Macrodactylini
- 22. Pachydemini
- 23. *Incertae Sedis* (*Acoma*)

IV. RUTELINAE
- 24. Anomalini
- 25. Rutelini

V. DYNASTINAE
- 26. Cyclocephalini
- 27. Pentodontini
- 28. Oryctini
- 29. Phileurini
- 30. Dynastini

VI. CETONIINAE
- 31. Gymnetini
- 32. Cetoniini
- 33. Cremastocheilini
- 34. Osmodermini
- 35. Trichiini
- 36. Valgini

KEY TO THE SUBFAMILIES OF THE UNITED STATES, CANADA, AND NEARCTIC MEXICO

1. Pygidium completely covered (or nearly so) by apex of elytra; length 1.5-13.0 mm I. Aphodiinae, p. 42
— Pygidium completely exposed; length longer than 5.0 mm 2

2(1). Antennal insertion visible from above; clypeus with sides constricted medially just before eyes (Fig. 2) ..... VI. Cetoniinae, p. 68
— Antennal insertion not visible from above; clypeus with sides not constricted (*e.g.* Fig. 1, Superfamily Scarabaeoidea) 3

3(2). Abdominal sternites distinctly narrowed at midline (Fig. 5); length of all sternites shorter than length of metasternum; scutellum hidden in most ..... II. Scarabaeinae, p. 48
— Abdominal sternites normal, not narrowed at midline; length of all sternites longer than length of metasternum; scutellum visible in most 4

4(3). Claws of both middle and posterior tarsi unequal in length and independently movable (Fig. 6) (exception: all legs in *Leptohoplia* with only one claw or with one claw greatly reduced); tarsomere 5 at apex with ventral, median, longitudinal cleft .... IV. Rutelinae, p. 60
— Claws of both middle and posterior tarsi equal in length and not independently movable (Figs. 7-9) (exception: posterior tarsi in *Hoplia* with only one claw); tarsomere 5 at apex lacking ventral, median, longitudinal cleft, instead with 2 parallel clefts either side of middle on ventral side 5

5(4). Claws of middle and posterior tarsi simple (Fig. 7); base of pronotum and elytra subequal in width; apex of posterior tibia always with 2 spurs; mandibles often exposed in dorsal view ..... V. Dynastinae, p. 64
— Claws of middle and posterior tarsi cleft, toothed (Figs. 8-9), or simple (if simple, base of pronotum much narrower than base of elytra); apex of posterior tibia with 1-2 spurs or spurs absent; mandibles hidden in dorsal view ..... III. Melolonthinae, p. 51

I. APHODIINAE LEACH 1815

by Paul E. Skelley and Robert D. Gordon

Common name: The aphodiine dung beetles

Characteristics: Clypeus dilated to cover mouthparts (except Aegialiini and *Annegialia* [Eupariini]), most medially emarginate. Mandibles hardened, most concealed by clypeus. Antennae with 9 segments, club 3-segmented. Mesocoxae contiguous or nearly so. Metatibiae with 2 apical spurs. Elytra nearly or entirely covering pygidium. Abdomen with 6 visible sternites. Tarsi with distinct claws, few with claws reduced.

Marco Dellacasa (1987, 1988a, 1988b, 1991, 1995) reviewed the current classification scheme for this subfamily on a world basis, provided a computer generated catalog of all taxa of Aphodiinae (or Aphodiidae) (1987), and gave a bibliography of authors and publications for all taxa (1988a). Additions and corrections to these works are in Dellacasa 1988b, 1991, 1995. These publications are the only comprehensive references on the subfamily.

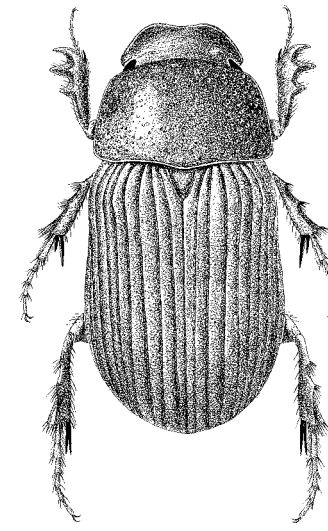


FIGURE 10.34. *Aphodius concavus* Say (Used by permission of University of Nebraska State Museum).

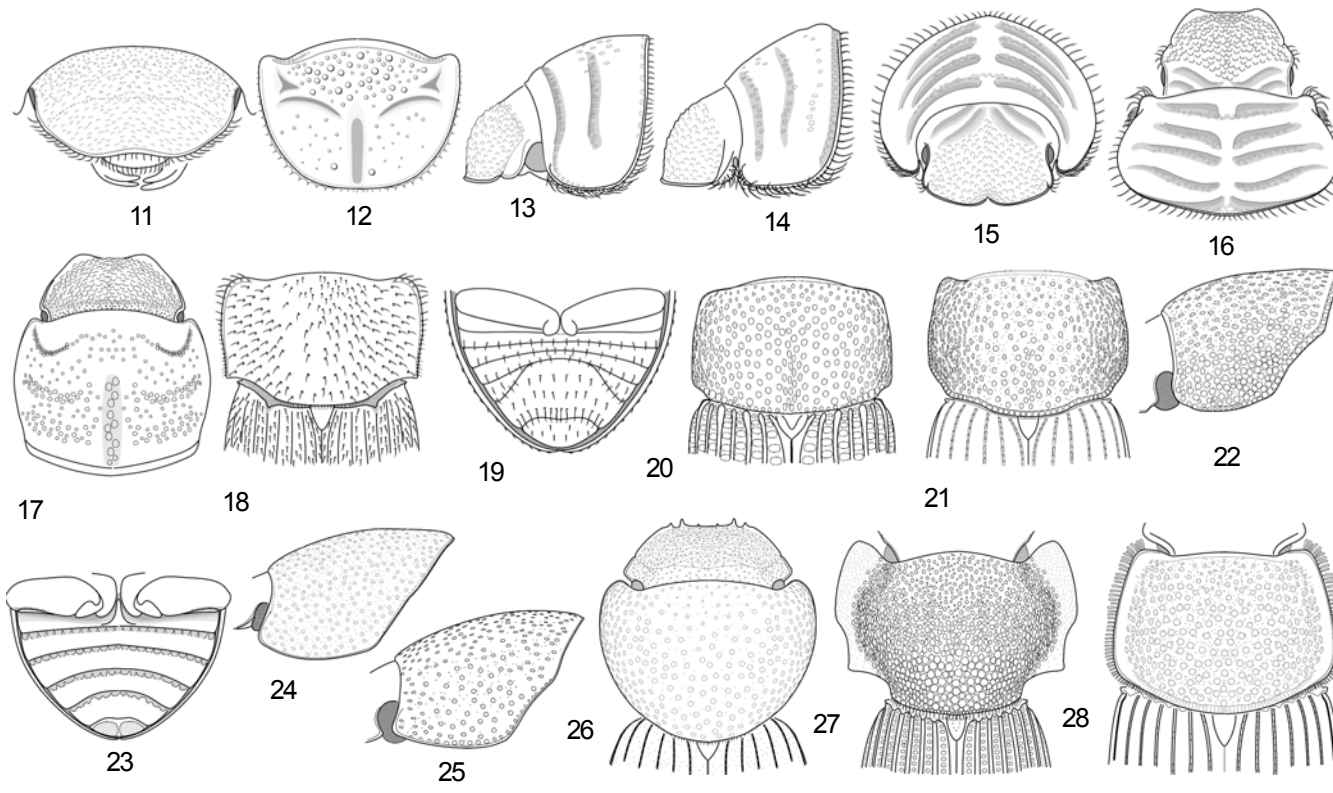
In the Nearctic region, the subfamily includes 26 genera and over 350 species. Keys to specific groups or revisionary studies are cited under the appropriate taxa. Regional works: Blatchley 1910 (Indiana); Helgesen and Post 1967 (North Dakota); Hatch 1971 (Pacific Northwest); Woodruff 1973 (Florida); Ratcliffe 1991 (Nebraska); Downie and Arnett 1996 (northeastern North America); Harpootlian 2001 (South Carolina). Faunal studies for other regions are in progress (see especially Dellacasa *et al.* in press). Larvae: Jerath 1960; Ritcher 1966. Biology: Jerath and Ritcher 1959.

KEY TO THE GENERA FROM THE UNITED STATES, CANADA, AND NEARCTIC MEXICO

1. Apical spurs of posterior tibiae separated; basal tarsomere articulated between spurs (Figs. 29-31) 2
— Apical spurs of posterior tibiae adjoining basally so basal tarsomere not articulated between spurs (Figs. 32-41) 3

2(1). Labrum and mandibles clearly visible beyond clypeus (Fig. 11) (Aegialiini) 5
— Labrum and mandibles concealed beneath clypeus (as in Fig. 15) (Aphodiini) 6

3(1). Abdominal sternites mostly separated by transverse band of short, longitudinal carinae (Fig. 23); pygidium with transverse ridge or carina dividing it into anterior and posterior halves, posterior half frequently eroded; middle and posterior tibia with variably arranged setae (Figs. 33-41) 4
— Abdominal sternites not separated by band of short, longitudinal carinae; pygidium lacking transverse ridge, surface entire; middle and posterior tibia with 4-5 setae on lateral edge, often with weak



FIGURES 11.34-28.34. 11. *Aegialia montana* Brown, anterior view of head; 12. *Annegialia ataeniformis* Howden, pronotum (after Howden 1971a); 13. *Leiopsammodius malkini* (Cartwright), lateral view of head and pronotum; 14. *Geopsammodius relictillus* (Deyrup and Woodruff), lateral view of head and pronotum; 15. *Psammodius basalis* (Mulsant and Rey), anterior view of head and pronotum; 16. *P. basalis*, dorsal view of head and pronotum; 17. *Pleurophorus caecus* (Creutzer), dorsal view of head and pronotum; 18. *Euparia castanea* LePeletier and Serville, dorsal view of pronotum and elytral base; 19. *Micraegialia pusillus* (Horn), abdominal sternites; 20. *Oxyomus silvestris* (Scopoli), dorsal pronotum and elytral base; 21. *Dialytellus dialytoides* (Fall), dorsal view of pronotum and elytral base; 22. *D. dialytoides*, lateral view of pronotum; 23. *Aphotaenius carolinus* (Van Dyke), abdominal sternites; 24. *Aphodius erraticus* (Linnaeus), lateral view of pronotum; 25. *Aphodius badipes* Melsheimer, lateral view of pronotum; 26. *Aphodius pyriformis* Brown, pronotum and elytral base; 27. *Euparixia duncani* Brown, dorsal view of pronotum and elytral base; 28. *Martineziella dutertrei* (Chalumeau), pronotum and elytral base.

transverse carina (Fig. 32) (Didactyliini) .... *Didactylia*

4(3). Pronotum with transverse furrows separated by swellings (Figs. 13-17), furrows can be weak with only traces of impressions remaining, at least visible near eyes; head granular (Figs. 13-17); posterior tarsomeres of many triangularly expanded, especially basal tarsomere (Figs. 35-40) (Psammodiini) 11

— Pronotum without transverse swellings (except *Annegialia*, Fig. 12), some with weak transverse impressions (Figs. 18, 27-28); head lacking granules in most; posterior tarsomeres elongate, in a few triangularly expanded (Figs. 33-34, 41) (Eupariini) 20

5(2). Intervals of elytron with short setae; abdominal sternites narrowed medially, 5th sternite obliterated medially by 6th sternite (Fig. 19) .... *Micraegialia*

— Intervals of elytra without short setae; abdominal sternites not narrowed medially, 5th sternite not obliterated medially by 6th sternite ..... *Aegialia*

6(2). Lateral elytral margin disappears beneath carinate interval midway to apex, carinate interval becomes lateral margin at apex; other intervals not carinate ..... *Hornietus*

— Lateral elytral margin complete from base to apex; intervals carinate or not 7

7(6). Anterior tibia with 4 teeth, apical tooth parallel to apical spur of tibia, lateral 3 teeth feeble, can be barely visible (Fig. 42) ..... *Dialytes*

— Anterior tibia with 3 or fewer teeth, lacking apical tooth 8

8(7). Elytral striae each consisting of single row of large punctures; punctures of elytral striae wider than intervals; pronotum with longitudinal depression at base (Fig. 20) ..... *Oxyomus*

— Elytral striae variable, each composed of distinctly impressed line with punctures single, doubled, or absent; elytral intervals wider than punctures of striae; pronotal disc lacking distinct depression 9

9(8). Posterior tarsomeres short, triangular; posterior tibia broadly, evenly expanded to strongly oblique apex (Fig. 29) ..... *Xeropsamobeus*

— Posterior tarsomeres cylindrical, elongate in most; posterior tibia slender or often abruptly expanded to transverse apex (Figs. 30-31) 10

10(9). Posterior angle of pronotum emarginate (Figs. 21-22); basal pronotal margin much narrower than anterior margin and strongly defined with row of large punctures; pronotum not noticeably wider at apex; clypeal teeth absent ..... *Dialytellus*

— Posterior angle of pronotum entire in most, rarely with posterior angle obsolete (Figs. 24-26); if angle obsolete then basal margin not strongly defined and pronotum distinctly wider at apex than at base (Fig. 26); clypeus with or without teeth .... *Aphodius*

11(4). Posterior tibia with weak transverse carina or row of tubercles (Figs. 35-36) 12

— Posterior tibia lacking transverse carina or row of tubercles (Figs. 37-40) 13

12(11). Apical clypeal angle with 1 small, sharp, clearly upturned tooth on each side of apical emargination ..... *Odontopsammodius*

— Clypeus rounded or angled at each side of median emargination, without teeth ..... *Tesarius*

13(11). Pronotal sculpture with at least 5 transverse ridges, ridges either continuous or broken into discrete granules, most with as many transverse furrows (Figs. 15-16) 14

— Pronotal sculpture with at most 3 weak, transverse ridges and furrows (Figs. 13-14, 17) 17

14(13). Posterior tarsomeres with at least basal tarsomere broad, strongly asymmetrically widened apically (*e.g.*, Figs. 35-36) 15

— Posterior tarsomeres elongate, basal tarsomere subcylindrical, slightly symmetrically or asymmetrically widened apically (Fig. 37) 16

15(14). Vertex of head with 1 or 2 pairs of oblique ridges arranged in chevron, ridges either continuous or broken into discrete tubercles (Figs. 15-16) .... *Psammodius*

— Vertex of head without oblique ridges .... *Neopsammodius*

16(14). Elytra with scale-like setae on raised intervals .... *Trichiorhyssemus*

— Elytra lacking setae ..... *Rhyssemus*

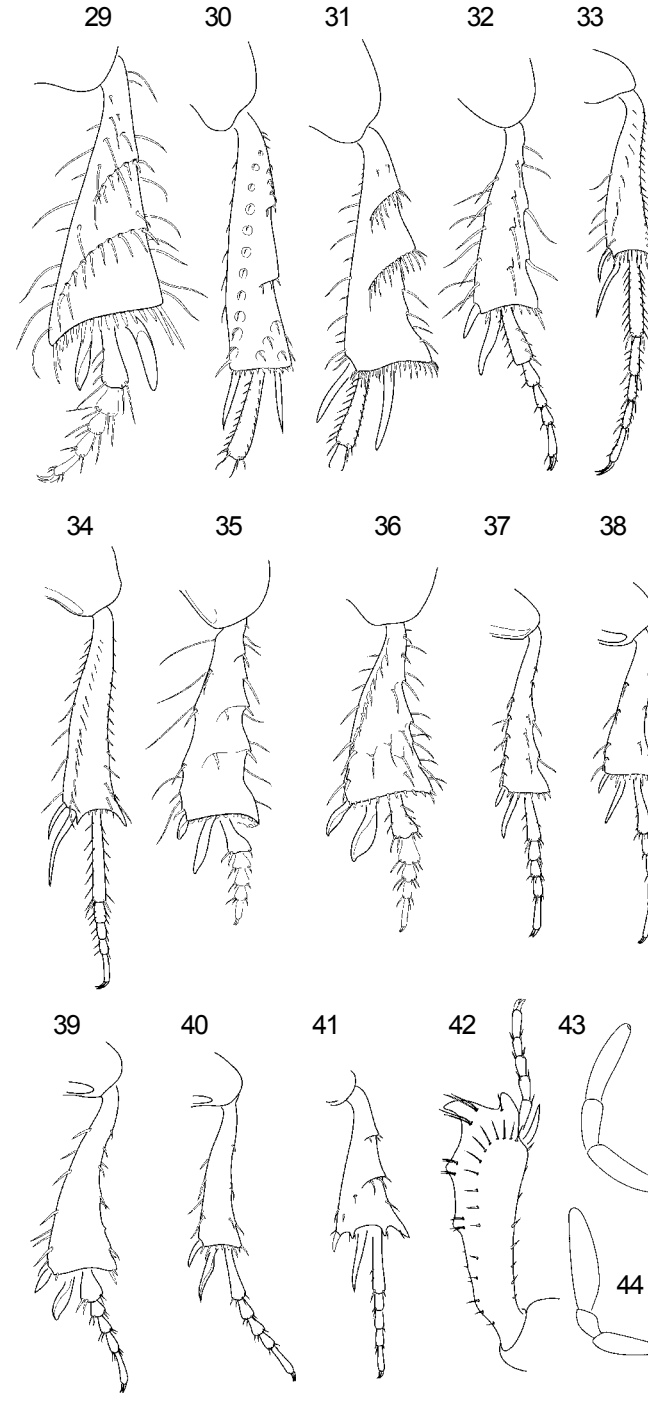
17(13). Posterior tarsus short, tarsomeres 1-4 triangular (*e.g.*, Figs. 35-36); body short, robust, visibly dilated posteriorly; elytral base not margined .. 18

— Posterior tarsus elongate or somewhat shortened, all tarsomeres elongate or with basal 1 or 2 tarsomeres asymmetrically widened apically (Figs. 38-40); body slender, elongate, either suboval or subparallel, slightly dilated posteriorly; elytral base margined 19

18(17). Eye normal (Fig. 13); frontal suture distinct in most; hindwing normally developed; tarsal claw corneous ..... *Leiopsammodius*

— Eye small, poorly developed (Fig. 14); frontal suture lacking, vertex lacking transverse ridge; hindwing vestigial; tarsal claws greatly reduced, setaceous ..... *Geopsammodius*

19(17). Posterior tarsus elongate, at least as long as tibia; first tarsomere subequal in length to long spur,



FIGURES 29.34-44.34. 29-41. Posterior tibiae and tarsi. 29. *Xeropsamobeus desertus* (Van Dyke); 30. *Dialytellus dialytoides* (Fall); 31. *Aphodius erraticus* (Linnaeus); 32. *Didactylia parcus* (Horn); 33. *Pseudataenius contortus* Cartwright; 34. *Ataenius rhyticephalus* (Chevrolat); 35. *Tesarius oregonensis* (Cartwright); 36. *Odontopsammodius cruentus* (Harold); 37. *Rhyssemus californicus* Horn; 38. *Pleurophorus caesus* (Creutzer); 39. *Platytomus micros* (Bates); 40. *Platytomus caelicollis* (Cartwright); 41. *Aphotaenius carolinus* (Van Dyke). 42. *Dialytes striatulus* (Say), anterior view of protibia; 43. *Pseudataenius contortus* Cartwright, maxillary palp; 44. *Ataenius rhyticephalus* (Chevrolat), maxillary palp.

cylindrical, slightly widened apically (Fig. 38) ... . *Pleurophorus*

— Posterior tarsus weakly to strongly shortened, visibly shorter than tibia; first tarsomere shorter than long spur, weakly to visibly widened at apex and slightly asymmetrical (Figs. 39-40) ... *Platytomus*

20(4). Pronotal disc with a T-shaped groove (Fig. 12) .... *Annegialia*

— Pronotal disc lacking groves or depressions 21

21(20). Elytral base notched (Fig. 18) ..... *Euparia*

— Elytral base not notched (Figs. 27-28) 22

22(21). Pronotum constricted basally and flared in front (Fig. 27); middle coxa touching base of elytra .... *Euparixia*

— Pronotum not constricted basally, sides parallel or evenly rounded, most not flared; middle coxa separated from elytral base 23

23(22). Posterior tibial apex with 4 distinct, spinose processes (Fig. 41); clypeus with 2 spiniform teeth ..... *Aphotaenius*

— Posterior tibial apex with 2 or fewer processes and fringed with many small spinules (Figs. 33-34); clypeus with or without spiniform teeth 24

24(23). Lateral pronotal margin flared for entire length and fringed with long, flattened setae (Fig. 28) .... *Martineziella*

— Lateral pronotal margin not flared for entire length, with or without flattened setae, without the above combination of characters 25

25(24). Mesosternum not carinate; terminal maxillary palpomere slender (Fig. 43); abdominal sternites with weakly developed, transverse band of longitudinal carinae; middle and posterior tarsus longer than tibia ..... *Pseudataenius*

— Mesosternum carinate; terminal maxillary palpomere thickened at middle (Fig.44); abdominal sternites separated by transverse band of short, longitudinal carinae, most strongly developed (*e.g.*, Fig. 23); middle and posterior tarsus subequal to or shorter than tibia ..... *Ataenius*

Classification of the Tribes and Genera of Aphodiinae

Aphodiinae Leach 1815

Aegialiini Laporte 1840

Characteristics: Head flat or slightly convex, surface granulate or punctate. Mandibles not covered by clypeus. Pronotum lacking ridges or grooves. Elytral base not bordered. Pygidium smooth, unmodified. Femora lacking grooves on anterior or posterior margin. Metatibia variable, broadly dilated at apex or not. Metatibial spurs separated by metatarsus. Metatarsomere 1 variable, broadly triangular or not.

Six of the nine genera and subgenera of the world Aegialiini are represented in North America. The tribe is composed of cold-adapted species with no truly tropical representatives. Only two species are known from the Southern Hemisphere: one from Tasmania and one from Argentina. Members of this tribe for which biological information is known are all detritivores, usually associated with sandy conditions, riparian, or littoral habitats.

Aegialia Latreille 1807
- subgenus *Aegialia* Latreille 1807
- subgenus *Caelius* Lewis 1895
  - *Leptaegialia* Brown 1931
- subgenus *Psammoporus* Thomson 1863
  - *Dimalia* Mulsant and Rey 1869
- subgenus *Rhysothorax* Bedel 1911
  - *Anomalaegialia* Brown 1931

The genus *Aegialia* (Fig. 11) is comprised of 41 species worldwide. In North America, the genus includes 31 species in four subgenera that are distributed from northeastern Canada to Alaska and south to South Carolina and southern California. Gordon and Cartwright (1988) revised the North American Aegialiini presenting keys and illustrations to all taxa as well as known habitat data. Gordon (1990) and Gordon and Rust (1997) described two additional species of *Aegialia*. The subgenera *Leptaegialia* and *Anomalaegialia* were placed as junior synonyms of *Caelius* and *Rhysothorax*, respectively, by M. Dellacasa (1987). Biology: Rust and Hanks 1982.

Micraegialia Brown 1931

The genus *Micraegialia* includes only *M. pusilla* (Horn), which is found in Manitoba, Minnesota, North Dakota, Washington, and British Columbia. This genus was described and illustrated in Gordon and Cartwright (1988).

Aphodiini Leach 1815

Characteristics: Head convex, surface granulate or punctate. Mandibles covered by clypeus. Pronotum lacking ridges or grooves. Elytral base not bordered. Pygidium smooth, unmodified. Femora not grooved at anterior or posterior margin. Metatibia broadly dilated at apex, may be slender, with 1-2 transverse carina in most. Metatibial spurs separated by metatarsus. Metatarsomere 1 slender, may be weakly triangular.

Six genera occur in North America according to the current classification, and some of these, especially *Aphodius*, are distributed worldwide. Keys to taxa: Horn 1887; Schmidt 1922; Helgesen and Post 1967; Hatch 1971; Woodruff 1973; Ratcliffe 1991. Keys to larvae: Jerath 1960.

Aphodius Illiger 1798

In North America this genus (Fig. 10) contains about 200 species with new species being discovered frequently. *Aphodius* is a tremendously large genus of more than 900 species worldwide. It has been variously divided into numerous subgenera. Poole and Gentili (1996) presented an extensive list of 138 subgeneric names associated with *Aphodius*. Dellacasa (1987, 1988a, 1988b, 1991, 1995) provided recent subgeneric placement of *Aphodius* species for the world. To date, no subgeneric classification has proved

satisfactory for North America. Reclassification efforts in progress will soon redefine most of our concepts, hence no subgeneric listing is included here. Keys to species of various North American groups can be found in Horn (1887); Brown (1927, 1928a, 1928b, 1929a); Fall (1932); Saylor (1940c); Cartwright (1972); Woodruff (1973); Gordon (1976, 1977, 1983); Ratcliffe (1991); Skelley and Gordon (2001).

As expected from the large number of species, *Aphodius* species occupy numerous niches. Many common species are generalist dung feeders. Many other species are highly specialized to feed on a specific type of dung or dung in specific situations (*e.g.,* animal burrows). Other species are detritivores, feeding on decaying plant materials. Gordon (1983) presented a key to the eastern species and discussed their feeding preferences. Skelley and Gordon (2001) readdress Gordon's (1983) ideas on their feeding preferences.

Dialytellus Brown 1929

Dialytellus contains only two species, both of which are endemic to North America. *Dialytellus dialytoides* (Fall) and *D. humeralis* (LeConte) are found in southeastern Canada, Massachusetts, Michigan, Maryland, North Carolina, and Virginia. Dellacasa and Gordon (1997) transferred *Dialytellus* from Eupariini to Aphodiini. Members of this genus feed on deer dung in shaded conditions but will also utilize sheep dung. Downie and Arnett (1996) diagnosed the species.

Dialytes Harold 1869

There are four species of *Dialytes*, all found in North America, *D. criddlei* Brown, *D. striatulus* (Say), *D. truncatus* (Melsheimer), and *D. ulkei* (Horn). Species are distributed from southeastern Canada to Virginia, west to Manitoba and Oklahoma. Stebnicka (1994) transferred *Dialytes* from Eupariini to Aphodiini and transferred all Old World members to other genera. Members of this genus feed on deer dung in shaded conditions and have also been found in sheep dung. Key: Downie and Arnett 1996.

Hornietus Stebnicka 2000

The genus *Hornietus* includes only one species, *H. ventralis* (Horn). It is known from eastern North America from the District of Columbia to Indiana and south to Kentucky and Alabama. *Hornietus ventralis* is a rare species that has been associated with logs containing passalid burrows and frass, but extensive efforts to survey this niche have been unsuccessful. The natural history of the species is unknown. This species was recently transferred from the genus *Saprosites* by Stebnicka (2000).

Oxyomus Laporte 1840

Xenoheptaulacus Hinton 1934

The genus *Oxyomus* is distributed in the Old World and consists of 27 species. One adventive species from the Old World, *O. silvestris* (Scopoli), has been recorded in New York, Pennsylvania, and Washington. It is known to live in dung of domestic animals and adults are attracted to lights.

Xeropsamobeus Saylor 1937

The genus is endemic to western North America and includes two species, *X. desertus* (Van Dyke) and *X. ambiguus* (Fall), that occur in California and New Mexico. Dellacasa and Gordon (1994) cite *Xeropsamobeus* as a subgenus of *Aphodius*. Because it traditionally has been considered a valid genus and because the current reclassification studies mentioned under *Aphodius* indicate it is valid, we choose to list it here with generic ranking. Members of *Xeropsamobeus* are detritivores and psammophilic (sand-loving).

Didactyliini Pittino 1984

Characteristics: Head slightly convex, surface punctate. Mandibles covered by clypeus. Pronotum lacking ridges or grooves. Elytral base not bordered. Pygidium smooth, unmodified. Femora lacking grooves on anterior or posterior margin. Metatibia dilated at apex, some with weak transverse carina. Metatibial spurs not separated by metatarsus. Metatarsomere 1 elongate, may be weakly triangular.

Pittino (1984) established the subtribe Didactyliina in the tribe Eupariini, and it was given tribal rank by Dellacasa (1987).

Didactylia d'Orbigny 1896

Worldwide, the genus *Didactylia* includes 31 species. Three species, *D. parcus* (Horn), *D. knausii* (Fall), and an undescribed species occur in the eastern and central United States. The taxonomy of American *Didactylia* is uncertain and is currently being studied (for pertinent comments see Woodruff 1973). The species are psammophiles and detritivores. Keys: Brown 1929b; Woodruff 1973.

Eupariini LePeletier and Serville 1828

Characteristics: Head slightly to strongly convex, surface variable, granulate to smooth with fine punctures. Mandibles covered by clypeus. Pronotum lacking ridges or grooves. Elytral base bordered in most. Pygidium modified, with transverse ridge and longitudinal grove at base (elytral locking mechanism). Femora with grooves on anterior or posterior margin, may be weakly developed. Metatibia slender, apically dilated in a few. Metatibial spurs not separated by metatarsus. Metatarsomere 1 slender in most.

Many genera and species worldwide are assigned to the Eupariini, but the genus *Ataenius* is by far the most significant taxon in terms of number of species, especially in the Western Hemisphere.

Annegialia Howden 1971

The genus *Annegialia* includes only *A. ataeniformis* Howden from Utah. *Annegialia* was described by Howden (1971a) in the Aegialiini and transferred to the Eupariini by Gordon and Cartwright (1988).

Aphotaenius Cartwright 1952

Five New World species are included in the genus and one species, *A. carolinus* (VanDyke), is widespread in the eastern United

States. Cartwright (1974) presented a description and other information. Woodruff (1973) illustrated an adult *A. carolinus*. *Aphotaenius* species are known to feed on deer dung in forested areas.

Ataenius Harold 1867

The genus *Ataenius* includes hundreds of species worldwide and is in need of taxonomic study. North of Mexico, the genus consists of about 65 species, occurring mostly in the eastern and southern United States. Cartwright (1974) revised the genera *Aphotaenius, Ataenius,* and *Pseudataenius*, providing keys to all taxa. Chalumeau (1992) transferred *Ataenius simulator* (Harold) to the genus *Parataenius* Balthasar. Additional species may be transferred to *Ataeniopsis* Petrovitz, *Phalangochaeta* Martínez, or other genera. Because of the amount of taxonomic work in progress on the Eupariini, the traditional classification (*sensu* Cartwright 1974) within *Ataenius* is maintained here. The majority of the known species are detritivores, while some species specialize on various types of dung. Many adults are attracted to lights.

Euparia LePeletier and Serville 1828

Worldwide, the genus *Euparia* includes 18 species. One species, *E. castanea* LePeletier and Serville, occurs in the southeastern U.S.: Florida, Alabama, and Louisiana. Woodruff (1973) provided a description and illustration. *Euparia castanea* lives primarily with native fire ants, *Solenopsis* species. Wojcik *et al.* (1977, 1978) and Wojcik and Habeck (1977) discussed the biology of the species.

Euparixia Brown 1927

Five species of *Euparixia* occur in the New World, and two species occur in the Nearctic region: *E. duncani* Brown in southern Arizona and *E. moseri* Woodruff and Cartwright in eastern Texas and Louisiana. The host of *E. duncani* is unknown, but *E. moseri* and several other members of *Euparixia* live in fungal gardens of leaf cutter ants (*Atta* sp.). Woodruff and Cartwright (1967) discussed this association (for additional information see Hinton 1936).

Martineziella Chalumeau 1986

Martinezia Chalumeau 1983

The genus *Martineziella* includes six American species. One adventive species, *M. dutertrei* (Chalumeau), known from South America and the West Indies, is widespread in the southeastern United States. It lives with imported fire ants (*Solenopsis* sp.). Woodruff (1973) provided a detailed description and illustrations. Wojcik *et al.* (1977, 1978), Wojcik and Habeck(1977), Vander Meer and Wojcik (1982), and Lanciani and Wojcik (1991) provided information on its biology in the United States.

Pseudataenius Brown 1927

The genus contains only three species that are endemic to the New World: *P. contortus* Cartwright, *P. socialis* (Horn), and *P. waltherhorni* (Balthasar). These species are known from New Jersey to Nebraska south to Florida and Texas and are primarily detritivores. Key: Cartwright 1974.

Psammodiini Mulsant 1842

Characteristics: Head strongly convex, surface with tubercles. Mandibles covered by clypeus. Pronotum with ridges or grooves, may be reduced to weak impressions. Elytral base bordered in most, may be weakly developed. Pygidium modified, with transverse ridge and longitudinal groove at base (elytral locking mechanism). Femora with grooves on anterior or posterior margin, may be weakly developed. Metatibia slender or broadly dilated. Metatibial spurs not separated by metatarsus. Metatarsomere 1 triangular or slender.

Cartwright (1955) revised North American "*Psammodius*" in the broad sense. Rakovic (1981, 1984, 1986, 1990) reclassified the tribe Psammodiini. Pittino and Mariani (1986) divided Psammodiini into two subtribes, Psammodiina for *Psammodius*, *Leiopsammodius, Tesarius* and several Old World genera, and Rhyssemina for *Platytomus, Pleurophorus, Rhyssemus, Trichiorhyssemus*, and several Old World genera. Marco Dellacasa (1988b) elevated Psammodiini to subfamily rank and the two subtribes to tribal status. Gordon and Pittino (1992) summarized the status of American taxa and provided a key to American genera. They treated Psammodiini as a tribe and disregarded the subtribe concept. All members of the Psammodiini are detritivores. A number of species are adventive, probably being transported in ships' ballast.

Geopsammodius Gordon and Pittino 1992

The genus *Geopsammodius* includes three species: *G. hydropicus* (Horn) from the Atlantic coast states; *G. relictillus* (Deyrup and Woodruff) from Central Florida; and *G. sabinae* Lavalette from French Guiana. Deyrup and Woodruff (1991) illustrated *G. relictillus*. Several undescribed species are known from the southeastern U.S., west to Texas.

Leiopsammodius Rakovic 1981

Thirty one species of *Leiopsammodius* are known worldwide with 15 occurring in the New World. There are four described and one undetermined species in the southeastern U.S.: *L. malkini* (Cartwright), *L. acei* Harpootlian *et al.*, *L. ocmulgeei* Harpootlian *et al.*, and *L. deyrupi* Harpootlian *et al.* Woodruff (1973) illustrated *L. malkini*, and Harpootlian *et al.* (2000) reviewed the genus in North America.

Neopsammodius Rakovic 1986

This genus includes nine species that are distributed in the western U.S. and Mexico. Five species occur in the western states and Nearctic region: *N. blandus* (Fall), *N. interruptus* (Say), *N. mimeticus* (Fall), *N. quinqueplicatus* (Horn), and *N. werneri* (Cartwright). In Cartwright's (1955) key, couplets 7-13 correspond to *Neopsammodius*.

Odontopsammodius Gordon and Pittino 1992

Odontopsammodius is comprised of 14 species in the New World. Three species occur in the southeastern United States: *O. armaticeps*

(Fall), *O. bidens* (Horn), and *O. cruentus* (Harold). In Cartwright's (1955) key, couplets 27-34 correspond to *Odontopsammodius*.

Platytomus Mulsant 1842
Of the 24 species in the genus, six are widely distributed in the United States: *P. atlanticus* (Cartwright), *P. caelicollis* (Cartwright), *P. longulus* (Cartwright), *P. micros* (Bates), *P. notialis* (Cartwright), and *P. tibialis* (Fabricius). Cartwright (1948) provided a key to Nearctic *Platyomus* species using the traditional generic name *Pleurophorus* for members of this group. Pittino and Mariani (1986) transferred all of the North American species, except *P. caesus*, to *Platytomus*.

Pleurophorus Mulsant 1842
The genus *Pleurophorus* contains 32 species that are distributed worldwide. Only one species, *P. caesus* (Creutzer), occurs in the United States, and it is widely distributed. Of the species included in *Pleurophorus* by Cartwright (1948), only *P. caesus* remains (see the genus *Platytomus*).

Psammodius Fallén 1807
Psammobius Heer 1841
The genus *Psammodius* includes approximately 19 Old World species and four New World species. Three species, *P. basalis* (Mulsant and Rey), *P. laevipennis* Costa, and *P. pierotti* Pittino occur in the northeastern United States. Couplets 2-4 in Cartwright's (1955) key correspond to the current definition of *Psammodius* as defined by Gordon and Pittino (1992).

Rhyssemus Mulsant 1842
Boucardius Petrovitz 1967
The genus *Rhyssemus* is a large (approximately 168 species), worldwide genus. The six species in the Nearctic region are widely distributed: *R. brownwoodi* Gordon and Cartwright, *R. californicus* Horn, *R. germanus* (L.), *R. neglectus* Brown, *R. scaber* Haldeman, and *R. sonatus* LeConte. Notes on the biology of *R. scaber* were given by Steiner (1980). Key: Gordon and Cartwright 1980.

Tesarius Rakovic 1981
The genus *Tesarius* includes five species, one of which is Australian and four of which are North American. *Tesarius caelatus* (LeConte), *T. oregonensis* (Cartwright), *T. mcclayi* (Cartwright), and *T. doyeni* (Cartwright) occur in the western United States. Couplets 22-23 in Cartwright's (1955) key correspond to species of *Tesarius*, with the exception of *T. doyeni*, which was described later. *Tesarius caelatus* is adventive to other continents, probably in ships' ballast (Skelley 2000).

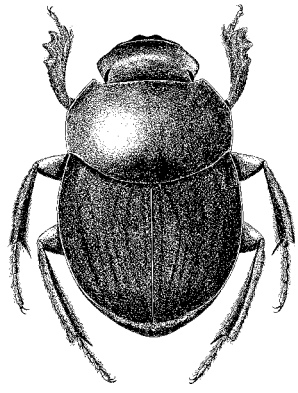


FIGURE 45.34. *Canthon pilularius* (Linnaeus) (Used by permission of University of Nebraska State Museum).

Trichiorhyssemus Clouet 1901
Trichiorhyssemus includes 33 species worldwide with only three known in the Americas. One species, *T. riparius* (Horn), occurs in the United States: Arizona, California, Nevada, New Mexico. Two species, *T. alternatus* Hinton and *T. cristatellus* (Bates), occur in Mexico. Key: Gordon and Cartwright 1980.

II. Scarabaeinae Latreille 1802

by Bruce D. Gill

Common name: The dung beetles

Characteristics: Clypeus expanded, covering mouthparts. Mandibles lamelliform, mostly membranous, with only outer margin hardened. Antennae with 8 or 9 antennomeres, club with 3. Middle coxae widely separated. Posterior tibiae nearly always with single apical spur. Elytra exposing pygidium, 6 visible, fused abdominal sternites. Anterior tarsi may be absent either in females or in both sexes.

This subfamily was divided by Cambefort (1991) into 12 tribes, eight of which are represented in the Nearctic (the Eucraniini and Eurysternini are strictly Neotropical, whereas the Gymnopleurini and Scarabaeini are limited to the Old World). Montreuil (1998) proposed significant changes to the classification of the Coprini and Dichotomiini by eliminating the Dichotomiini and transferring the genera to the Ateuchini and Coprini.

Members of this subfamily are commonly called dung beetles. Although many species feed on mammalian dung, others specialize to varying degrees upon the dung of other vertebrates and invertebrates, as well as on carrion, mushrooms, rotting fruit, and other decomposing plant material. The World fauna includes slightly over 5,000 described species in 234 genera, with close to 1,800 of these species belonging to the genus *Onthophagus*. In the Nearctic region, there are 17 genera and about 150 species. Biology: Halffter and Matthews 1966, Halffter and Edmonds 1982, Hanski and Cambefort 1991. Regional works: Woodruff 1973; Ratcliffe 1991; Downie and Arnett 1996; Harpootlian 2001. Keys to larvae: Ritcher 1966; Edmonds and Halffter 1978.

Key to the Tribes and Genera from the United States, Canada, and Nearctic Mexico

1. Middle and posterior tibiae slender, curved, only slightly expanded apically 2
— Middle and posterior tibiae strongly and often abruptly expanded apically 7

2(1). Body compressed laterally, sides of prothorax flattened, vertical (Sisyphini) ..... *Sisyphus*
— Body not compressed laterally, sides of prothorax rounded (Canthonini) 3

3(2). Scutellum visible ..... *Malagoniella*
— Scutellum hidden 4

4(3). Posterior edge of vertex rounded, not margined .. .. *Pseudocanthon*
— Posterior edge of vertex sharply margined, carinate 5

5(4). Anterior tarsi absent; elytral disc with humeral carina and apical tubercles ..... *Deltochilum*
— Anterior tarsi present; elytral disc lacking carina and apical tubercles 6

6(5). Posterior tibia with 2 apical spurs . *Melanocanthon*
— Posterior tibia with 1 apical spur ..... *Canthon*

7(1). Scutellum visible although can be small 8
— Scutellum completely hidden 10

8(7). Pronotum with pair of basal pits near midline; antenna with 9 antennomeres (Onitini) ..... *Onitis*
— Pronotum lacking basal pits; antenna with 8 antennomeres (Oniticellini) 9

9(8). Sides of head abruptly notched at junction of clypeus and gena ..... *Euoniticellus*
— Sides of head evenly rounded from clypeus to gena ..... *Liatongus*

10(7). Basal antennomere of club cup-shaped, enclosing last 2 antennomeres (Phanaeini) 11
— Basal antennomere of club similar to other club antennomeres, not cup-shaped 12

11(10). Anterior margin of clypeus sharply bidentate medially ..... *Coprophanaeus*
— Anterior margin of clypeus rounded or slightly emarginate ..... *Phanaeus*

12(10). Third labial palpomere small or inconspicuous (Onthophagini) ..... *Onthophagus*
— Third labial palpomere distinct 13

13(12). Elytron with 9 discal striae (Coprini) ..... *Copris*
— Elytron with 7 or 8 discal striae (Dichotomiini) .. 14

14(13). First posterior tarsomere triangular 15
— First posterior tarsomere slender or broadly rectangular 16

15(14). Abdominal sternites greatly compressed longitudinally along midline ..... *Ontherus*
— Abdominal sternites not compressed along midline ..... *Dichotomius*

16(14). Mesosternum very short; basal posterior tarsomere elongate, scarcely enlarged at apex ..... *Canthidium*
— Mesosternum distinct; basal posterior tarsomere gradually enlarged towards apex ..... *Ateuchus*

Classification of the Tribes and Genera of Scarabaeinae

Canthonini Péringuey 1901

Characteristics: Body size small to large (length 2-25 mm), shape round or oval. Head and pronotum lacking horns or carinae. Antenna with 9 segments. Middle and posterior tibiae slender, curved, only slightly expanded apically. Sexual dimorphism minimal.

The New World has 340 species in 27 genera, which equates to a third of the World fauna. Adults of most species are ball-rollers, and they shape carrion or dung into balls that are rolled away and buried at a distance from the food source. Key to genera: Halffter and Martínez 1977. Biology: Gordon and Cartwright 1974; Halffter and Halffter 1989.

Canthon Hoffmansegg 1817
Glaphyrocanthon Martínez 1948
Geocanthon Pereira and Martínez 1956
Boreocanthon Halffter 1958

Canthon (Fig. 45) is the most species-rich genus of the New World Canthonini with nearly 150 species distributed from southern Canada to Argentina. Twenty-one species are found in the Nearctic region. Keys to adults: Halffter 1958, 1961. Biology: Matthews 1963; Favila and Díaz 1996. Larval description: Ritcher 1966.

Deltochilum Eschscholtz 1822

Deltochilum is a New World genus with over 80 described species. Four species occur in northern Mexico and the southeastern United States, ranging as far north as Kentucky. Many of the species feed upon carrion. Key to adults: Howden 1966. Biology: Howden and Ritcher 1952. Larval description: Ritcher 1966.

Malagoniella Martínez 1961

There are nine species in the genus, eight of which are restricted to South America. *Malagoniella astyanax yucateca* (Harold) is widely distributed in Central America and reaches southern Texas. Adults are nocturnally active and frequently attracted to ultraviolet light. Key to adults: Martínez 1961; Halffter and Martínez 1966.

Melanocanthon Halffter 1958

Four species comprise this genus, all of which are restricted to the United States east of the Rocky Mountains. Key to adults: Halffter 1958.

Pseudocanthon Bates 1887
Opiocanthon Paulian 1947

Eight species occur in the Neotropics, and only *Pseudocanthon perplexus* (LeConte) extends into the eastern United States, ranging as far north as Arizona, Texas, Illinois and North Carolina. Reference: Bates 1887.

Coprini Leach 1815

Characteristics: Body 8-20 mm in length, elongate, robust, convex, generally black in color. Head or pronotum often with horns or tubercles, especially in males. Elytra with 9 discal striae. Scutellum hidden. Antenna with 9 segments. Middle and posterior tibia strongly expanded apically.

The tribe Coprini is a relatively small tribe with ten genera and slightly under 400 species worldwide. *Copris* is the only representative of the tribe in the New World.

Copris Geoffroy 1762
A widespread genus, *Copris* (Fig. 1) has nearly 200 species worldwide. Of the 28 species recorded from the New World, 14 are found from southern Canada to northern Mexico. Keys to adults: Matthews 1961; Matthews and Halffter 1968; Warner 1990. Keys to larvae: Ritcher 1966. Biology: Matthews 1961; Anduaga and Halffter 1991.

Dichotomiini Halffter and Matthews 1966

Characteristics: Body small and compact or large and robust (length 4-30 mm). Elytra with 7 or 8 discal striae. Scutellum hidden. Antenna with 9 segments. Middle and posterior tibia strongly expanded apically.

The tribe Dichotomiini is a diverse tribe with approximately 30 genera and 750 species worldwide. The New World has a large proportion of this diversity with close to 600 species in 23 genera.

Ateuchus Weber 1801
Choeridium LePeletier and Serville 1828
There are about 81 species in this New World genus. Five species are known from the eastern United States and northern Mexico. Key to adults: Balthasar 1939; Kohlmann 1984, Génier 2000. Larval description: Ritcher 1966. Phylogeny: Kohlmann and Halffter 1988.

Canthidium Erichson 1847
Canthidium is a Neotropical genus with over 150 described species and many more awaiting description. Several undescribed species occur in northern Mexico, at least one of which reaches southern Arizona. There is no modern taxonomic treatment for this group. The only revision (Harold 1867) treated just 38 species.

Dichotomius Hope 1838
Brachycopris Haldeman 1845
Pinotus Erichson 1847
Dichotomius is a New World genus with about 150 described species. Three or four species are found in northern Mexico, Arizona, and the eastern United States as far north as New York. The genus is in need of revision as the last complete study (Harold 1869c) is out of date. Taxonomic notes: Martínez 1951; Woodruff 1973.

Ontherus Erichson 1847
Ontherus is a Neotropical genus with 58 species, of which only *Ontherus mexicanus* Harold ranges into northeastern Mexico. Key to adults and phylogeny: Génier 1996.

Oniticellini d'Orbigny 1916

Characteristics: Body 7-14 mm in length, elongate, most flattened. Pronotum without basal pits near midline. Scutellum visible. Antenna with 8 segments.

Most of the 14 genera and 165 species in the tribe are found in Africa and Asia although *Anoplodrepanus* is restricted to the West Indies (Simonis 1981). Key to adults: Janssens 1953. Biogeography: Zunino 1982.

Euoniticellus Janssens 1953
Euoniticellus intermedius (Reiche) is an African species introduced into California and Texas (Fincher 1990), and it has spread into northern Mexico. There is a possibility that a native Cuban species may occur in Florida (Woodruff 1973). Key to adults: Janssens 1953. Biology and larva: Blume 1984.

Liatongus Reitter 1893
Two native species are found in California and northwestern Mexico. An African species, *L. militaris* (Laporte), has been introduced into the southern United States and may be established (Fincher 1990). Key to adults: Janssens 1953. Biology: Anduaga and Halffter 1993.

Onitini Laporte 1840

Characteristics: Body 10-20 mm in length, oblong, robust. Pronotum with pit on each side of midline near base. Scutellum small but visible. Elytron with prominent lateral carina. Antenna with 9 segments. Anterior tarsi lacking in both sexes. Middle and posterior tibiae strongly expanded at apex.

The tribe Onitini is an Old World group with 18 genera and about 200 species.

Onitis Fabricius 1798
Onitis is the largest genus in the tribe with over 150 described species in Africa, Asia, and Europe. Two African species have been released in the southern United States, although only *O. alexis* Klug is known to be established in California (Fincher 1990). Key to adults: Janssens 1937.

Onthophagini Lacordaire 1856

Characteristics: Body 2-12 mm in length, oval, convex. Head and/or pronotum often with horns or carinae. Scutellum hidden. Elytra with 7 discal striae. Third labial palpomere small or inconspicuous. Antenna with 9 segments. Tarsi and tarsal claws present on all legs. Middle and posterior tibiae broadly expanded at apex.

Sexual dimorphism is well developed in most *Onthophagus* species. Males typically have large horns on the head and/or pronotum (females with only carinae or rudimentary horns) or males have elongated protibiae with a long setal brush at the apex. The world fauna includes over 2,200 species in 34 genera.

Onthophagus Latreille 1807
Chalcoderus Erichson 1848
Monapus Erichson 1848
Psilax Erichson 1848
Gonocyphus Lansberg 1885
Tauronthophagus Shipp 1895
Digitonthophagus Balthasar 1959

Onthophagus is the largest genus of Scarabaeinae with representatives in nearly all parts of the world. Approximately 130 species are known from the New World, 40 of which occur from southern Canada to northern Mexico. An introduced species, *Onthophagus gazella* (Fabricius), has spread rapidly in the southern Nearctic realm. Adults commonly feed on mammalian dung, although some species feed on carrion, fungi, rotting plant material, or live in association with ground-burrowing mammals or tortoises. Keys to adults: Howden and Cartwright 1963; Zunino and Halffter 1988; additional species described by Howden 1973. Key to larvae: Ritcher 1966. Adventive species: Hoebeke and Beucke 1997. Biology: Hunter *et al.* 1996; Lobo and Halffter 1994.

Phanaeini Kolbe 1905

Characteristics: Body length 12-25 mm, robust, often with metallic coloration. Antenna with 9 segments, basal antennomere of club cup-shaped, enclosing distal 2 antennomeres. Tarsal claws absent. Anterior tarsi lacking in males, present or absent in females.

This tribe is restricted to the New World with most of the 9 genera and 150 species found in the Neotropics. Many species exhibit strong sexual dimorphism with the males possessing long horns on the head and/or pronotum. Zunino (1985) considered the Phanaeini to be a subtribe of the Onitini. Key to genera: Edmonds 1972, 1994.

Coprophanaeus d'Olsoufieff 1924

This Neotropical genus includes 32 species. Several species occur in northern Mexico, one of which (*C. pluto* [Harold]) reaches southern Arizona and Texas. Adults typically feed on carrion. Key to adults: d'Olsoufieff 1924.

Phanaeus MacLeay 1819
Lonchophorus Germar 1824
Onthurgus Gistel 1857
Paleocopris Pierce 1946

Nearly half of the 50 recognized species of *Phanaeus* are recorded from Mexico. Six species occur in northern Mexico and the eastern United States, extending as far north as Arizona in the west and Vermont in the east. Adults generally feed on mammalian dung. Key to adults: Edmonds 1994. Biology: Fincher 1972; Halffter and Lopez 1972; Halffter *et al.* 1974.

Sisyphini Mulsant 1842

Characteristics: Body length 6-10 mm, oval, compressed laterally with sides of pronotum and metasternum vertical. Color reddish brown to gray, surface matte, with setae on dorsum. Scutellum hidden. Antenna with 8 segments. Middle coxae very widely separated, forming lateral margin of body. Middle and posterior tibiae elongate, curved, barely enlarged at apex.

This tribe includes three genera of ball-rolling dung beetles. Most of the 60 species in the tribe are found in Africa and Asia, with only a few representatives in Europe and the New World.

Sisyphus Latreille 1807

Only two of the 30 species in the genus are native to the New World, and of these only *S. submonticolus* Howden reaches the Nearctic (Durango, Mexico). One African species (*S. rubrus* Paschalidis) has been introduced to the southern United States but is not known to be established (Fincher 1990). Key to adults: Haaf 1955; Howden 1965.

III. Melolonthinae Samouelle 1819

by Arthur V. Evans

Common names: The May beetles, June beetles, and chafers

Characteristics. Adults 3-58 mm in length. Dorsal surface often conspicuously setose or scaled; color reddish brown or black (*i.e.*

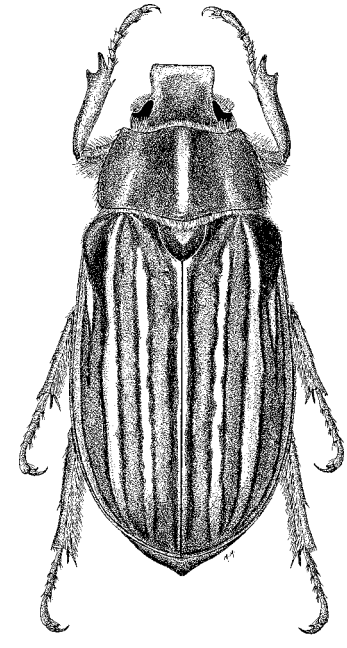


FIGURE 46.34. *Polyphylla decemlineata* (Say) (Used by permission of University of Nebraska State Museum).

Diplotaxis, Phyllophaga, Serica), some with metallic blue or green luster (*Dichelonyx*) or distinctly marked with patches of scales (*Hoplia, Polyphylla*). Head unarmed (except in *Chaunocolus*), most with mandibles well developed, sclerotized, completely concealed from above, or nearly so. Antennal insertions not visible from above; antennae 7 to 10-segmented, antennal lamellae folding tightly into a 3 to 7-segmented club, club oval to elongate, glabrous or with only a few setae. Labrum located below clypeus or on apical clypeal margin (Oncerini, Sericini), transverse, narrowed, or conical.

Thorax with pronotum unarmed; scutellum exposed. Elytral margins straight, without notch posterior to humerus. Mesepimeron covered by base of elytra (slightly exposed in *Gymnopyge*). Legs with claws simple; claws cleft, toothed, serrate or pectinate; metatarsal claws paired in most, equal in thickness and length or single (*Hoplia*).

Abdomen with 7 or fewer pairs of abdominal spiracles, most with posterior abdominal spiracles located in sternites, tergites or pleural membrane (see *Acoma* and *Podolasia*), with 1 pair exposed beneath edge of elytra; 5 or 6 visible sternites fused, most with sutures visible at least laterally, or completely effaced (Chasmatopterini), the sixth sternite (when present) can be partially or completely retracted within fifth (Diplotaxini); trace of suture between fifth sternite and propygidium evident in most, entirely absent in Diplotaxini; pygidium exposed. Sexual dimorphism not strongly developed; most males with abdomen less convex, with longer tarsi and antennal club than females, some genera with males having specialized front claws (*Hypotrichia*) or with protibial and metatibial spurs absent (some male Macrodactylini).

Ritcher (1966) characterized the soil dwelling, C-shaped larvae of North American melolonthines as follows: Head with mandibles lacking stridulatory area, or indistinct, with patch of minute granules; scissorial area of mandible with distal, blade-like portion which is separated from proximal tooth by scissorial notch. Galea and lacinia of maxilla fused proximally but separated distally; rarely galea and lacinia separated but tightly fitted together; lacinia with longitudinal row of 3 unci; maxillary stridulatory area without anterior process. Antennae 4-segmented; last antennal segment with single, elliptical, dorsal sensory spot. Thorax with all legs well developed, 4-segmented; each claw bearing 2 setae. Abdomen with anal opening angulate or Y-shaped in most. Lower anal lip of most with sagittal cleft or grooves. Keys to larvae: Bøving 1936, 1937, 1942b, 1942c; Ritcher 1949, 1966 (see also Bøving 1942a; King 1984).

Habits and habitats. Adults and larvae of the Melolonthinae are generally phytophagous, although some adults apparently do not feed. Adults and larvae of some genera may be of considerable economic importance (*i.e., Amphimallon, Diplotaxis, Phyllophaga, Polyphylla, Maladera, Serica*), damaging a wide variety of crops, pastures, and turf. Adult *Phyllophaga* may be so abundant locally that deciduous trees may be completely defoliated by their nocturnal feeding activities (Ritcher 1966). Many adults of flower or pollen-feeding species are diurnal (*Chnaunanthus, Gymnopyge, Hoplia, Macrodactylus, Oncerus*), but almost all melolonthines are crepuscular or nocturnal. Primarily nocturnal species in the genera *Diplotaxis, Phyllophaga, Polyphylla*, and *Serica* are usually encountered in numbers flying about lights or copulating, feeding, or resting on the foliage of host plants.

Status of the classification. Recognition of taxa as tribes or subfamilies has not been applied consistently (see discussion under Chasmatopterini and Oncerini). Moreover, the tribal classification is in a relative state of confusion due to the lack of definition and inconsistent use of characters (Hardy 1978b; Ratcliffe 1991). This state of affairs is further exacerbated by the fact that descriptions of the majority of genera and species published before 1940 are largely inadequate and seldom accompanied by illustrations, making reliable determinations difficult without examination of type specimens. Early workers rarely consulted types, resulting in numerous synonymies and incorrect placements. The present work is not designed to resolve these issues but is intended to make North American melolonthine genera recognizable. Not until the completion of a comparative analysis of all genera, including the larvae, will the higher classification of the Melolonthinae achieve some stability and begin to reflect the phylogenetic relationships of the group.

The North American melolonthines have not been considered in their entirety for more than 140 years, although many genera have subsequently been revised. Early attempts at establishing schemes of higher classification for the melolonthines were based primarily on taxa found outside of the Nearctic region. LeConte (1856) recognized the following tribes in the United States under the family Melolonthidae: Macrophyllae (*Phobetus*); Melolonthinae (*Polyphylla, Thyce*); Rhizotrogi (*Phyllophaga sensu latu*); Diplotaxes (*Diplotaxis*); Sericae (*Serica*); Macrodactyli (*Macrodactylus*); Dichelonychae (*Dichelonyx*); Lasipodes (*Podolasia, Oncerus*); Hopliae (*Hoplia*); Glaphyri (*Lichnanthe*). LeConte (1861) later modified his classification as follows: Macrophyllini, Melolonthini, Rhizotrogi, Diplotaxini, Sericini, Sericoidini (*Hypotrichia*), Macrodactylini, Dichelonychini, Oncerini (for *Lasipodes*), Hopliini, and Glaphyrini.

Harold (1869a) recognized the following tribes with North American taxa under the family Scarabaeidae: Glaphyrini (LeConte's Glaphyrini and Lasipodes, *Chnaunanthus*); Melolonthini (LeConte's Hopliini, Sericini, Dichelonychini, Macrodactylini, Diplotaxini, Rhizotrogini, Melolonthinae, Macrophyllini). The catalog of Dalla Torre (1912, 1913) listed the following tribes with Nearctic representatives under the subfamily Melolonthinae: Chasmatopterini (including LeConte's Oncerini); Sericini; Liparetrini (*Plectrodes, Hypotrichia*); Melolonthini (LeConte's Melolonthini, Rhizotrogini, Diplotaxini); Pachydemini (LeConte's Macrophyllini); Macrodactylini (LeConte's Macrodactylini, Dichelonychini); Hopliini. These tribes were not formally characterized by Dalla Torre, leading to considerable confusion of the higher classification of the subfamily. With the subsequent addition of hundreds of genera and species since its publication,

Acknowledgments. Art Evans thanks Paul Skelley, Paul Lago, James Hogue, Juan Limón and William Warner for checking the melolonthine keys and adding information and Rosser Garrison for assistance with the illustrations.

there is little basis for much of the systematic content of Dalla Torre's catalog although it remains a valuable bibliographic tool. The catalogues of Leng (1920), Leng and Mutchler (1927, 1933) and Blackwelder (1944) followed the classification of Dalla Torre. Saylor (1937b, 1938) removed the tribes Chasmatopterini and Oncerini from the Melolonthinae and considered them as separate subfamilies. On the basis of characters of known larvae, Ritcher (1966) recognized the following tribes: Sericini, Diplotaxini, Dichelonycini, Macrodactylini, Hopliini, Pachydemini, Melolonthini, and Plectrini. Hatch (1971) recognized the Diplotaxini and Dichelonycini. Arnett (1968) followed the system of Dalla Torre, with the exception of combining Saylor's Oncerinae and Chasmatopterinae within the Chasmatopterini of the Melolonthinae. Morón *et al.* (1997) presented the following tribal and subtribal classification for the melolonthines of Mexico: Melolonthini (Diplotaxina, Melolonthina, Rhizotrogina), Macrodactylini (Ceraspina, Macrodactylina), Hopliini (Hopliina), Sericini (Sericina), Chasmatopterini, and Pachydemini.

Useful faunal surveys, systematic catalogs, biogeographical analyses, or conservation notes on Nearctic Melolonthinae include: CANADA: Bousquet 1991; MEXICO: Morón 1996; Morón *et al.* 1997; Baja California peninsula: Saylor 1948b; Chiapas: Morón *et al.* 1985; Durango: Morón 1981, Morón and Deloya 1991; Hidalgo: Morón 1994; Jalisco: Morón *et al.* 1988; Morelos: Deloya *et al.* 1995; Mexico: Morón and Zaragoza 1976; Veracruz: Morón 1979; UNITED STATES: Arnett 1968; Alaska: Bousquet 1991; Colorado: Zimmerman *et al.* 1991; Florida: Woodruff and Deyrup 1994; Indiana: Blatchley 1910; Nebraska: Ratcliffe 1991; North Dakota: Lago *et al.* 1979; South Carolina: Harpootlian 2001; Northeast: Downie and Arnett 1996; Pacific Northwest: Hatch 1971; western sand dune systems: Andrews *et al.* 1979. Catalogs: Loding 1945; Edwards 1949; Kirk and Balsbaugh 1975; Shook 1978.

Distribution. The cosmopolitan subfamily Melolonthinae is one of the largest and most diverse subfamilies in the Scarabaeoidea, with approximately 750 genera and nearly 11,000 species worldwide (Houston and Weir 1992). There are nine tribes, 30 genera, and more than 1,000 species in North America. The greatest diversity of North American Melolonthinae appears to be in the southwestern United States and Mexico.

Key to the Tribes and Genera of the United States, Canada, and Mexico

Genera included in this key are from Nearctic *and* Neotropical Mexico.

1. Metatarsus with two claws 2
— Metatarsus with single claw (Hopliini) ..... *Hoplia*

2(1). Labrum not readily visible or located beneath clypeus (Figs. 47-48) 3
— Labrum distinct, located on apical margin of clypeus (Fig. 49) (Oncerini) 10

3(2). Labrum indistinct (in the Sericini, labrum located on apical margin of clypeus, suture barely indicated by differences in sculpturing on dorsal surface and by faintly indicated notches on margin) (Fig. 47) 4
— Labrum visible, located below the clypeus (Fig. 48) 5

4(3). Metatibial spurs subcontiguous, located below tarsal articulation (Fig. 77) (Podolasiini) 12
— Metatibial spurs set apart, below and above tarsal articulation (Fig. 78) (Sericini) 13

5 (3). Sutures between abdominal sternites distinct, at least laterally 6
— Sutures between abdominal sternites with sutures obliterated (Chasmatopterini) 11

6(5). Anterior pronotal margin with membranous border (Fig. 58); if border absent, then metacoxae widely separated (Fig. 68) 7
— Anterior pronotal margin without membranous border (Fig. 59); metacoxae contiguous or subcontiguous (Fig. 69) (Melolonthini) 21

7(6). Fifth abdominal sternite and propygidium separated by partial or complete suture (Fig. 86) 8
— Fifth abdominal sternite and propygidium not separated by suture (Fig. 87) (Diplotaxini) . *Diplotaxis*

8(7). Metatibial spurs set apart, located above and below tarsal articulation, separated by tarsal articulation (Fig. 78) 9
— Metatibial spurs absent, or with 1 or 2 subcontiguous spurs located below tarsal articulation (Fig. 77) (Macrodactylini) 15

9(8). Claws bifid or toothed (Figs. 81-82); labrum distinct, transverse, not fused to labrum (Fig. 48) (Pachydemini) 38
— Claws simple (Fig. 79); labrum reduced, conical, fused to labrum ..... *Acoma* (*incertae sedis*)

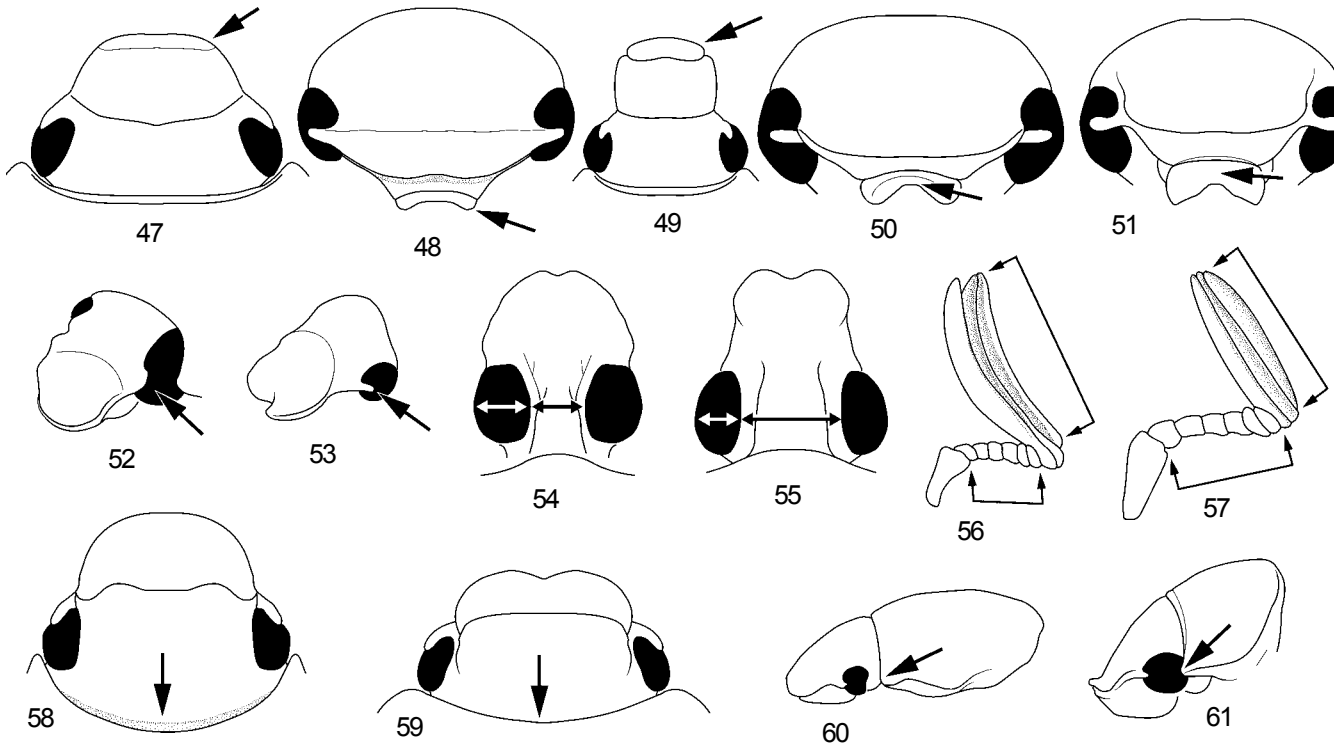
10(2). Lateral margins of clypeus parallel; metatibial spurs apical, subcontiguous ..... *Oncerus*
— Lateral margins of clypeus convergent anteriorly; metatibial spurs subapical, subcontiguous ..... *Nefoncerus*

11(5). Base of clypeus armed with erect horn; pronotum abruptly declivous anteriorly ..... *Chaunocolus*
— Base of clypeus lacking horn; pronotum simply convex ..... *Chnaunanthus*

12(4). Eye canthus obsolete or nearly so (Fig. 52); eyes separated ventrally by less than width of 1 eye (Fig. 54) ..... *Podolasia*
— Eye canthus present (Fig. 53); eyes separated ventrally by more than width of 1 eye (Fig. 55) ..... *Podostena*

13(4). Antennae with 10 antennomeres ..... *Maladera*
— Antennae with 8 or 9 antennomeres 14

14(13). Elytra without apical, membranous border .. *Serica*
— Elytra with apical, membranous border ..... *Nipponoserica*



FIGURES 47.34-61.34. 47-55. Heads. 47. Dorsal view with labrum indistinct, located on apical margin of clypeus; 48. Frontal view with labrum located beneath clypeus; 49. Dorsal view with labrum distinct, located on apical margin of clypeus; 50. Frontal view with labrum and labral notch almost approaching clypeus; 51. Frontal view with labrum and labral notch distinctly separated from clypeus; 52. Oblique view with eye canthus nearly obsolete (after Howden 1997); 53. Oblique view with eye canthus present (after Howden 1997); 54. Ventral view with eyes separated by less than one eye width (after Howden 1997); 55. Ventral with eyes separated by more than one eye width (after Howden 1997). 56-57. Antennae. 56. Dorsal view with club twice the length of pedicel; 57. Dorsal view with antennal club subequal to length of pedicel. 58-59. Heads. 58. Dorsal view with anterior pronotal margin membranous; 59. Dorsal view with anterior pronotal margin lacking membranous border. 60-61. Head and pronotum, lateral view. 60. Anterior pronotal angle not reaching eyes; 61. Anterior, pronotal angle partially covering eyes.

15(8). Anterior pronotal angles never reaching eyes (Fig. 60) 16
— Anterior pronotal angles partially covering eyes (Fig. 61) 17

16(15). Apical margin of terminal tarsomeres entire (Fig. 75) ..... *Macrodactylus*
— Apical margin of terminal tarsomere deeply notched (Fig. 76) ..... *Dichelonyx*

17(15). Metacoxae contiguous or subcontiguous (Fig. 69) 18
— Metacoxae widely separated (Fig. 68) ..... *Ceraspis*

18(17). Claws cleft (Fig. 80) 19
— Claws bifid (Fig. 81) ..... *Isonychus*

19(18). Claws distinctly cleft in lateral view 20
— Claws not cleft in lateral view ..... *Coenonycha*

20(19). Antennae with 8 or 9 antennomeres .. *Gymnopyge*
— Antennae with 10 antennomeres ..... *Plectris*

21 (6). Metepisternum narrow (Fig. 64) 22
— Metepisternum wide (Fig. 65) 32

22(21). Labrum narrow, less than half width of clypeus 23
— Labrum wide, more than half width of clypeus . 24

23(22). Clypeal suture carinate ..... *Fossocarus*
— Clypeal suture not carinate ..... *Gronocarus*

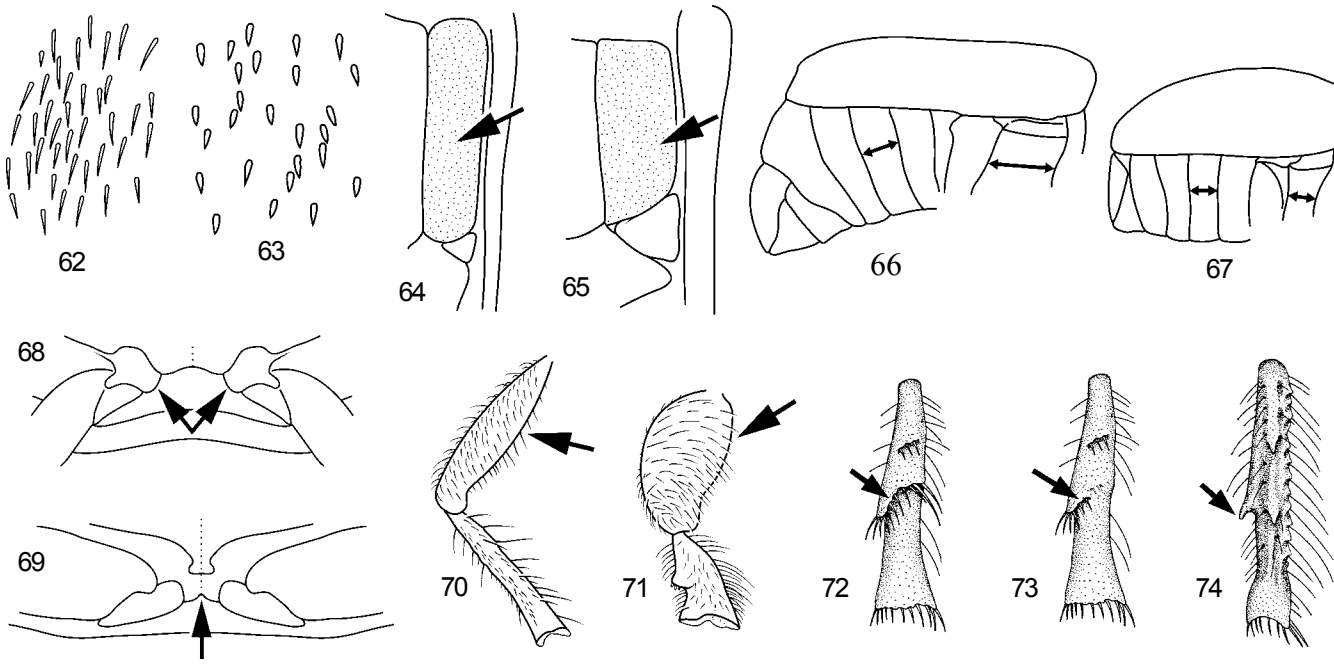
24(22). Labral notch almost approaching clypeus (Fig. 50) (orient specimen to achieve narrowest distance between notch and clypeus) (*Phyllophaga sensu lato*) 25
— Labral notch distinctly separated from clypeus (Fig. 51) ..... *Amphimallon*

25(24). Outer surface of metatibiae with complete, oblique, transverse carina or dentiform processes (Figs. 72, 74) 26
— Outer surface of metatibiae with incomplete carina (Fig. 73) ..... *Phyllophaga* (*Cnemarachis*)

26(25). Outer surface of mesotibiae with complete, oblique, transverse carina (Fig. 72) 27
— Outer surface of mesotibiae with dentiform processes (Fig. 74) ..... *Phyllophaga* (*Triodonyx*)

27(26). Claws simple, bifid, or toothed (Figs. 79, 81-82) 28
— Claws serrate or pectinate (Figs. 84-85) .... *Phyllophaga* (*Listrochelus*)

28(27). All claws bifid or toothed 29
— Pro- and mesotarsal claws simple, metatarsal claws toothed ..... *Phyllophaga* (*Chirodines*)



FIGURES 62.34-74.34. 62-63. Elytral vestiture. 62. Pubescent, or with hairs; 63. With scales or scale-like hairs. 64-65. Metathoraces, ventral view of left side. 64. Metepisternum narrow (after Lacroix 1989); 65. Metepisternum wide (after Lacroix 1989). 66-67. Lateral views of abdomen. 66. Metasternum longer than second abdominal sternite; 67. Metasternum subequal in length to second abdominal sternite. 68-69. Ventral views of metathorax and first abdominal sternite. 68. Metacoxae widely separated; 69. Metacoxae contiguous. 70-71. Hind legs, ventral view (after Britton 1957). 70. Metafemur slender; 71. Metafemur greatly enlarged. 72-74. Metatibiae, outer surface (after Morón 1986). 72. With complete, oblique, transverse carina; 73. With incomplete, transverse carina; 74. With dentiform process.

29(28). Claws bifid (Fig. 81) 30
— Claws toothed (Fig. 82) 31

30(29). Tarsi moderately to densely pilose beneath, less so in females; color light testaceous in most .... *Phyllophaga* (*Chlaenobia*)
— Tarsi sparsely setose beneath, never pilose; color variable ..... *Phyllophaga* (*Phytalus*)

31(29). Metasternum longer than second abdominal sternite (Fig. 66) ..... *Phyllophaga* (*Phyllophaga*)
— Metasternum subequal in length to second abdominal sternite (Fig. 67) .... *Phyllophaga* (*Tostegoptera*)

32(21). Antennal club with 5 (female) or 7 (male) segments ..... *Polyphylla*
— Antennal club with 3 segments 33

33(32). Ventral abdominal sutures mostly distinct, imbricate, or with suture between sternites 4 and 5 obliterated only at midline 34
— Ventral abdominal sutures never imbricate, often obliterated medially 35

34(33). Outer tarsal claw on each leg with acute basal tooth; metafemora slender, less than or subequal in width to second abdominal sternite (Fig. 70) .... *Plectrodes*
— Inner tarsal claw of anterior and middle legs with large, oval, basal lobe; metafemora greatly enlarged, greater in width than second abdominal sternite (Fig. 71) ..... *Hypotrichia*

35(33). Metafemora of males slender, less than or subequal in width to second abdominal sternite (Fig. 70). 36
— Metafemora of males enlarged, greater in width than second abdominal sternite (Fig. 71) 37

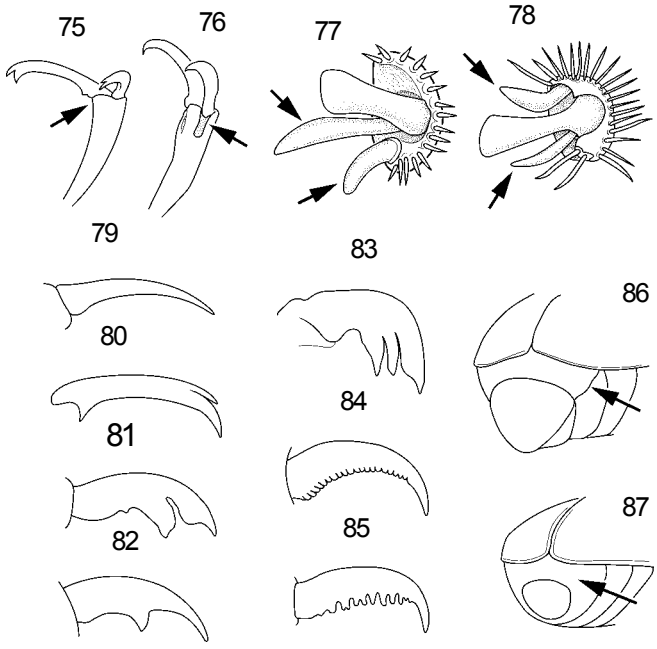
36(35). Antennal club of male twice length of pedicel (Fig. 56) ..... *Dinacoma*
— Antennal club of male subequal in length to pedicel (Fig. 57) ..... *Parathyce*

37(35). Dorsally pubescent, without scales or scale-like hairs (Fig. 62) ..... *Hypothyce*
— Dorsally with at least some scales or scale-like hairs (Fig. 63) ..... *Thyce*

38(9). Claws bifid (Fig. 81) ..... *Phobetus*
— Claws tridentate (Fig. 83) ..... *Benedictia*

Classification of the Tribes and Genera

The published distribution of each genus is indicated by country and state or province. The retrieval of generic provincial and state records was greatly facilitated by Bousquet (1991) and Morón *et al.* (1997). The inclusion of state and provincial records will readily identify range extensions and assist in compiling North American distributions.



FIGURES 75.34-87.34. 75-76. Apices of terminal tarsomere, ventral view. 75. With apical margin without notched; 76. With apical margin deeply notched. 77-78. Apices of metatibia (after Britton 1957). 77. Metatibial spurs contiguous, located below tarsal articulation; 78. Metatibial spurs set apart, located above and below tarsal articulation. 79-85. Tarsal claws. 79. Simple; 80. Cleft (after Hardy 1977); 81. Bifid; 82. Toothed (after Morón 1986); 83. Tridentate; 84. Serrate (after Morón 1986); 85. Pectinate (after Morón 1986). 86-87. Caudal view of pygidium and abdomen. 86.With fifth abdominal sternite and propygidium separated by suture; 87. With fifth abdominal sternite and propygidium not separated by suture.

Melolonthinae Samouelle 1819

Hopliini Burmeister 1855

Characteristics: Antennae 9-segmented, club 3-segmented. Labrum located below clypeus, distinct. Fifth abdominal sternite and propygidium separated by suture. Protibiae with spurs, meso- and metatibiae without apical spurs. Opposing pro- and mesotarsal claws subequal, metatarsi with single claw.

The tribe Hopliini is predominately Afrotropical, with representatives in the Oriental and Palearctic regions. *Hoplia* is the sole representative of the tribe in the New World. The tribe has been considered as a separate subfamily. Saylor (1935) described the genus *Leptohoplia* and placed it within the Hopliini. The genus was later transferred to the Anomalini of the subfamily Rutelinae by Howden and Hardy (1971).

Hoplia Illiger 1803
This genus has 24 species found from CANADA: Alberta, British Columbia, Manitoba, New Brunswick, Nova Scotia, Ontario, Quebec; MEXICO: Baja California, Hidalgo, Oaxaca, Puebla, Tabasco, Veracruz; USA: generally distributed but not Alaska, Arkansas, Kansas, Louisiana, Oklahoma. Keys: Boyer 1940; Hardy 1977. Larvae: Ritcher 1966.

Oncerini LeConte 1861

Characteristics: Antennae 9-segmented, club 3-segmented. Labrum coplanar with clypeus. Fifth abdominal sternite and propygidium separated by suture. Protibiae without apical spurs, meso- and metatibiae with 2 apical spurs. Metatibial spurs subcontiguous, inserted below tarsal articulation; opposing tarsal claws similar, cleft apically.

Saylor (1938) placed *Oncerus* and *Nefoncerus* in the subfamily Oncerinae on the basis of the placement of the abdominal spiracles (entirely within the pleural membrane) and the apical attachment of the labrum to the clypeus. Both genera were included in the Chasmatopterini (Arnett 1968). The subfamily is restricted to the Nearctic region where there are two monotypic genera.

Nefoncerus Saylor 1938
One species, *N. convergens* (Horn), is found in MEXICO: Baja California Sur. Discussion: Saylor 1938; Morón *et al.* 1997.

Oncerus LeConte 1856
One species, *O. floralis* LeConte, is found in MEXICO: Baja California; USA: California. Discussion: Saylor 1938; Morón *et al.* 1997.

Podolasiini Howden 1997

Characteristics: Antennae 8 or 9-segmented, club 3-segmented. Labrum not visible, located below and fused to clypeus. Fifth abdominal sternite and propygidium separated by suture. Protibiae without apical spurs, meso- and metatibiae with 2 apical spurs. Metatibial spurs subcontiguous and located below tarsal articulation; opposing tarsal claws equal, simple.

Podolasia (as *Lasiopus*) and *Oncerus* were grouped in the Lasiopodes by LeConte (1856) and later the Oncerini (LeConte 1861). Harold (1869b) noted the preoccupation of *Lasiopus* and proposed the new name *Podolasia*. Harold (1869a) placed *Podolasia* and *Oncerus* in the tribe Glaphyrini. Dalla Torre (1912) listed both of these genera under the Chasmatopterini, but inexplicably listed LeConte's tribe Lasipodes as a synonym of the Pachydemini. Leng (1920) followed the classification of Dalla Torre. Both of these genera were later placed in the subfamily Oncerinae by Saylor (1938), but *Podolasia* was removed from the Oncerinae and placed *incertae sedis* by Howden (1954). Ritcher (1969) concurred with Howden, noting that the abdomen of *Podolasia* has seven pairs of functional spiracles and a vestigial eighth pair. All of the abdominal spiracles are located in the pleural membrane. Howden (1997) erected the tribe Podolasiini for *Podolasia* and included *Podostena*. The females are apparently flightless (Howden 1954, 1997).

Podolasia Harold 1869
Lasiopus LeConte 1856
Nine species occur from MEXICO: Baja California, Baja California Sur, Chihuahua, Durango, San Luis Potosí; USA: New Mexico, Texas, Utah. Keys: Howden 1954, 1997.

Podostena Howden 1997
Four species are found in MEXICO: Baja California Sur; USA: Texas. Key: Howden 1997.

Sericini Kirby 1837

Characteristics: Antennae 9 or 10-segmented, club 3-segmented. Labrum not easily visible, fused to apical margin of clypeus. Fifth abdominal sternite and propygidium separated by suture. Protibiae with apical spurs, meso- and metatibiae with 2 spurs. Metatibial spurs separated, inserted above and below tarsal articulation. Posterior femora broadly flattened. Opposing tarsal claws similar, cleft apically.

This large, cosmopolitan tribe contains many genera in all zoogeographical regions but primarily in the Afrotropical and Oriental regions. *Serica* is the only genus native to North America. Species of adult sercines are best identified by the configuration of the male genitalia. In California, adult *Serica* are known to damage the foliage of various fruit trees. The Asiatic garden beetle, *Maladera castanea* (Arrow), originally known from Japan, was first recorded from North America in New Jersey in 1921. Adult Asiatic garden beetles feed on the foliage of many plants, while the larvae damage the roots of lawns, strawberries, vegetable seedlings, and flowers. *Nipponoserica peregrina* (Chapin), another Japanese species, was described from specimens collected, in part, from Long Island, New York in 1937. Descriptions: Dawson 1919a, 1919b, 1920, 1921, 1922, 1932, 1933, 1947, 1952.

Maladera Mulsant and Rey 1870
Aserica Lewis 1895
Autoserica Brenske 1897
One species, *M. castanea* (Arrow), is found in the USA: Connecticut, Delaware, Georgia, Maryland, Massachusetts, Michigan, New Jersey, New York, North Carolina, Pennsylvania, Rhode Island, South Carolina, Vermont, Virginia, West Virginia (also Japan, Taiwan, and Korea). Description: Dawson 1967. Larvae: Ritcher 1966. Nomenclature: Pope 1961.

Nipponoserica Nomura 1973
One species, *N. peregrina* (Chapin), is found in USA: Connecticut, Maryland, Massachusetts, New Jersey, New York, Pennsylvania, Virginia, West Virginia (also Japan). Descriptions: Chapin 1938, Dawson 1952. (See Nomura 1976 for *Serica peregrina* transferred to *Nipponoserica*).

Serica MacLeay 1819
Stilbolemma Harris 1827
Camptorhina Kirby 1837
There are 99 species in CANADA: widely distributed, except Newfoundland and Yukon; USA: widely distributed, except Alaska: MEXICO: Baja California, Baja California Sur, Coahuila (also Afrotropical, Palearctic, Oriental regions). Keys: Dawson 1919-1967; Gordon 1975; Hardy and Andrews 1987; Ratcliffe 1991. Larvae: Ritcher 1966. Biology: Evans 1985. (See Nikolayev 1979 for additional nomenclatural commentary).

Chasmatopterini Lacordaire 1856

Characteristics: Antennae 9-segmented, club 3-segmented. Labrum located beneath and not fused to clypeus. Abdomen with sternites entirely fused, sutures indistinct except for apical sternite; fifth abdominal sternite and propygidium separated by suture. Protibiae without apical spurs, meso- and metatibiae with 2 apical spurs. Metatibial spurs subcontiguous, located below tarsal articulation. Opposing tarsal claws similar, cleft apically.

Two genera inhabit the Nearctic region and a third genus is found in the western Palearctic. Saylor (1937b) stated that the Chasmatopterini did not belong in the Melolonthinae and elevated the tribe to the rank of subfamily (see also Baraud and Branco 1990) on the basis that the abdominal spiracles in *Chnaunanthus* and the Palearctic genus *Chasmatopterus* are located in the pleural membrane. In erecting *Chaunocolus*, Saylor (1937a) related it to *Oncerus*, *Podolasia*, and *Chnaunanthus* but did not include it in his treatment of the Chasmatopterini. *Oncerus* and *Nefoncerus* became the basis for the subfamily Oncerinae (Saylor 1938). Arnett (1971) and Morón *et al.* (1997) recognized the Chasmatopterini as including all of the aforementioned genera. Ritcher (1969) found that the abdominal spiracles of *Chnaunanthus* were not entirely in the pleural membrane, bringing into question Saylor's assertion that the tribe could not be considered as part of the Melolonthinae.

Chaunocolus Saylor 1937
One species, *C. cornutus* Saylor, is found in MEXICO: Baja California Sur. Discussion: Saylor 1937b; Morón *et al.* 1997.

Chnaunanthus Burmeister 1844
Acratus Horn 1867
Pseudacratus Dalle Torre 1912
Four species occur in MEXICO: Baja California; Baja California Sur, Guanajuato, Michoacan, Mexico, Morelos, Nayarit, Oaxaca, Puebla; USA: Arizona, California, Oregon, Utah Key: Saylor 1937b. Discussion: Morón *et al.* 1997.

Melolonthini Samouelle 1819

Characteristics: Antennae 9 or 10-segmented, club 3, 5 or 7-segmented. Labrum located below clypeus, distinct in most. Fifth abdominal sternite and propygidium separated by suture. Protibiae with apical spurs, meso- and metatibiae with 2 spurs. Metatibial spurs contiguous, located below tarsal articulation. Opposing tarsal claws equal (protarsal claws unequal in *Hypotrichia*), simple, cleft, toothed, serrate or pectinate.

The tribe Melolonthini is the largest tribe of the subfamily. Its species are generally distributed throughout the world and include many of economic importance. The European chafer, *Amphimallon majalis* (Razoumowski), was inadvertently introduced from the western Palearctic. The larvae may cause damage to pastures, lawns, grain, and legumes (Ritcher 1966). The larvae of *Phyllophaga* and *Polyphylla* are also considered to be serious crop and turf pests as a result of their root-feeding activities, while the nocturnal feeding activities of some adult *Phyllophaga* may result in the defoliation of deciduous trees in the eastern United States.

LeConte's (1861) placement of *Hypotrichia* in the Sericoidini resulted in its subsequent listing under the Liparetrini by Dalla Torre (1912). Leng (1920) retained *Hypotrichia* in the Liparetrini but placed *Plectrodes* in the Melolonthini. Howden (1968a) placed *Hypotrichia* in the Melolonthini and added the new genus *Hypothyce*. Hardy (1974a) later added *Parathyce* and *Polylamina* to the tribe, but Coca-Abia (2000) synonymized *Polylamina* with *Polyphylla*. *Fossocarus* Howden and *Gronocarus* Schaeffer, previously placed in the Pachydemini, are placed here in the Melolonthini on the basis of the contiguous metatibial spurs located beneath the tarsal articulation and the partially obliterated abdominal sutures.

Amphimallon LePeletier and Serville 1828
One species, *A. majalis* (Razoumowski), is found in CANADA: Ontario, Quebec; USA: Connecticut, New York, West Virginia. Key: Baraud 1992. Larvae: Böving 1942c; Ritcher 1966. Discussion: Butt 1944; Gyrisco *et al.* 1954.

Dinacoma Casey 1889
Two species occur in the USA: California. Key: Hardy 1974a.

Fossocarus Howden 1961
One species, *F. creoleorum* Howden, is from the USA: Texas. Discussion: Howden 1961, 1971a.

Gronocarus Schaeffer 1927
Two species are from the USA: Alabama, Florida. Discussion: Howden 1961; Woodruff and Deyrup 1994.

Hypothyce Howden 1968
Two species occur in the USA: Georgia, Texas. Key: Hardy 1974a. Larvae: Ritcher 1973. Biology: Barfield and Gibson 1975.

Hypotrichia LeConte 1861
One species, *H. spissipes* LeConte, is from the USA: Florida. Discussion: Hardy 1974a; Woodruff and Deyrup 1994.

Parathyce Hardy 1974
Six species occur in MEXICO: Baja California; USA: California Key: Hardy 1974a. Larvae: Erwin 1970. Discussion: Morón *et al.* 1997.

Plectrodes Horn 1867
One species, *P. pubescens* Horn, occurs in the USA: California. Discussion: Hardy 1974a.

Phyllophaga Harris 1827
- subgenus *Phytalus* Erichson 1847. Key: Saylor 1939. Discussion: Frey 1975, Morón and Rivera 1992.
- subgenus *Chlaenobia* Blanchard 1850. Key: Chapin 1935. Discussion: Morón 1992.
- subgenus *Listrochelus* Blanchard 1851. Key: Saylor 1940a.
- subgenus *Chirodines* Bates 1888. Key: Morón 1991.
- subgenus *Cnemarachis* Saylor 1942. Key: Saylor 1942.
  - *Abcrana* Saylor 1942
  - *Clemora* Saylor 1942
- subgenus *Phyllophaga* Harris 1827. Keys: Luginbill and Painter 1953, Morón 1986, Woodruff and Beck 1989.
  - *Ancyclonycha* Dejean 1833
  - *Lachnosterna* Hope 1837
  - *Trichesthes* Erichson 1847
  - *Endrosa* LeConte 1856
  - *Gynnis* LeConte 1856
- subgenus *Tostegoptera* Blanchard 1851
  - *Eugastra* LeConte 1856
- subgenus *Triodonyx* Saylor 1942. Key: Warner and Morón 1992.

There are 400+ species generally distributed in North America except in: Alaska, Nunavut, Northwest Territories, and Yukon. Keys: Reinhard 1950; Luginbill and Painter 1953; Butler and Werner 1961; Morón 1986, 1993; Woodruff and Beck 1989; Ratcliffe 1991. Larvae: Bøving 1942a, 1942b; Ritcher 1949, 1966; Rosander and Werner 1970. Bibliography: Pike *et al.* 1976; Woodruff and Beck 1989. Discussion: Saylor 1940b; Wolcott 1948; Sanderson 1951; Frey 1975; Garcia-Vidal 1975, 1978, 1984, 1987; Chalumeau and Gruner 1976; Chalumeau 1983; King 1984; Woodruff and Deyrup 1994.

Polyphylla Harris 1841
- *Macranoxia* Crotch 1873
- *Polylamina* Hardy 1974

There are 31 species of *Polyphylla* (Fig. 46) distributed from CANADA: Alberta, British Columbia, Manitoba, Ontario, Quebec, Saskatchewan; MEXICO: Aguascalientes, Baja California, Chihuahua, Coahuila, Durango, Hidalgo, Jalisco, Morelos, Oaxaca, Puebla, Sonora; USA: widely distributed, except Ohio, Michigan, West Virginia. Keys: Hardy 1981; Young 1988. Larvae: Ritcher 1966. Discussion: Woodruff and Deyrup 1994; Morón *et al.* 1997.

Thyce LeConte 1856
Two species occur in MEXICO: Chihuahua; USA: California, New Mexico, Texas. Key: Hardy 1974a. Discussion: Morón *et al.* 1997.

Diplotaxini Burmeister 1855

Characteristics: Antennae 9 or 10-segmented, club 3-segmented. Labrum located below clypeus. Abdominal sutures distinct; fifth abdominal sternite and propygidium not separated by suture; sixth abdominal sternite nearly completely retracted beneath fifth sternite. Protibiae with apical spurs, meso- and metatibiae with 2 spurs; metatibial spurs contiguous, located below tarsal articulation. Opposing tarsal claws equal, toothed, or cleft apically.

The tribe Diplotaxini is found in the Afrotropical, Neotropical, and Oriental regions with one genus found in the Nearctic region. Adults are mostly nocturnal, feeding on the foliage of various plants. The larvae of some species may damage seedlings of commercially grown trees. *Diplotaxis* species occur from Canada to Panama and reach their greatest diversity in the southwestern United States and the central highlands of Mexico (Vaurie 1958).

Diplotaxis Kirby 1837
Alobus LeConte 1856
Orsonyx LeConte 1856
Diazus LeConte 1860
This genus includes 212 species from CANADA: generally distributed except Newfoundland, Northwest Territories, and Yukon; MEXICO: widely distributed; USA: widely distributed. Keys: Vaurie 1958, 1960, 1963; Ratcliffe 1991. Larvae: Ritcher 1966. Biology: Evans 1985. Discussion: Delgado-Castillo 1990; McCleve 1993; Woodruff and Deyrup 1994; Morón *et al.* 1997.

Macrodactylini Burmeister 1855

Characteristics: Antennae 7 to 10-segmented, club 3-segmented. Labrum located below clypeus. Fifth abdominal sternite and propygidium separated by suture. Protibiae with or without apical spurs, meso- and metatibiae with or without spurs; if present, paired metatibial spurs contiguous, located below tarsal articulation. Opposing tarsal claws equal or subequal, simple, cleft apically, or bifid.

The tribe Macrodactylini is primarily Neotropical, with species also occurring in the Oriental region. One species of *Plectris* has become established in Australia. Seven genera are known from North America, including one introduced species of the genus *Plectris*. The diurnal adults of *Gymnopyge, Macrodactylus*, and some *Dichelonyx* feed on flowers or pollen, while the nocturnal *Coenonycha* and most *Dichelonyx* feed on foliage. Ritcher (1966) provided a key to the tribe based on larvae. Both Ritcher (1966, 1969) and Hatch (1971) placed *Coenonycha* and *Dichelonyx* in the Dichelonycini.

Ceraspis LePeletier and Serville 1828
Faula Blanchard 1850
There are four species from MEXICO: Chiapas, Guerrero, Oaxaca, Tabasco, and Veracruz; Saylor (1935) reported a specimen from Arizona, but this record is undoubtedly erroneous. Key: Frey 1962. Biology: Capistran and Aquino 1992. Discussion: Delgado-Castillo *et al.* 1987; Morón *et al.* 1997.

Coenonycha Horn 1876
This genus has 34 species from MEXICO: Baja California; USA: Arizona, California, Nevada, Oregon, Utah, and Washington. Keys: Cazier and McClay 1943; Evans and Smith 1986; Evans and D'Hotman 1988. Larvae: Ritcher 1966. Biology: Tilden and Mansfield 1944; Evans 1985. Discussion: Morón *et al.* 1997.

Dichelonyx Harris 1827
Dichelonycha Kirby 1837
There are 29 species from CANADA: generally distributed except Newfoundland and Yukon; MEXICO: Baja California, Baja California Sur; USA: generally distributed. Keys: Saylor 1945a; Brown 1946. Larvae: Ritcher 1966. Biology: Evans 1985. Discussion: Morón *et al.* 1997.

Gymnopyge Linell 1895
There are four species from the USA: Arizona, California, Oregon, and Utah. Discussion: Linell 1896; Cazier 1939.

Isonychus Mannerheim 1829
This genus contains nine species from MEXICO: Durango, Guerrero, Sinaloa, Jalisco, Mexico, Michoacan, Morelos; Nayarit, and Oaxaca; USA: Arizona. Discussion: Howden 1959; Morón *et al.* 1997.

Macrodactylus Dejean 1821
Stenothorax Harris 1827
Macrodactylus has 27 species from CANADA: Ontario, Quebec; MEXICO: widely distributed; USA: Arizona, eastern and southern states. Keys: Horn 1876; Carrillo and Gibson 1960; Arce-Perez and Morón 2000. Larvae: Ritcher 1966. Discussion: Morón *et al.* 1997.

Plectris LePeletier and Serville 1828
One species, *P. aliena* Chapin, is found in the USA: Alabama, Georgia, Florida, South Carolina (also Paraguay). Key: Frey 1967. Larvae: Bøving 1936; Ritcher 1966. Discussion: Chapin 1934.

Pachydemini Reitter 1902

Characteristics: Antennae 10-segmented, club 3 to 5-segmented. Labrum located below clypeus. Fifth abdominal sternite and propygidium separated by suture. Protibiae with apical spurs, meso- and metatibiae with 2 spurs; metatibial spurs separated, located on either side of tarsal articulation. Opposing tarsal claws equal, toothed, or cleft apically.

Sanderson (1939) described the genus *Benedictia* and placed it in the Pleocominae (Pleocomidae). Hardy (1978b) transferred *Benedictia* to the Pachydemini and commented that this tribe had become a dumping ground for genera that are difficult to place elsewhere, attributing this situation to the lack of a formal definition of the tribal concept by Dalla Torre (1913). *Fossocarus*, and *Gronocarus* were provisionally placed in the Pachydemini at the time of their description, but they are treated as members of the Melolonthini in this work.

Benedictia Sanderson 1939
One species, *B. pilosa* Sanderson, is from MEXICO: Chihuahua, Coahuila; USA: Texas. Discussion: Sanderson 1939; Hardy 1978b.

Phobetus LeConte 1856
Eleven species are found in CANADA: British Columbia; MEXICO: Baja California; USA: California, Oregon, Washington. Key: Hardy 1978a. Larvae: Ritcher 1966. Biology: Evans 1985. Discussion: Morón *et al.* 1997.

Incertae Sedis

Acoma Casey 1889
There are 24 species from MEXICO: Baja California, Baja California Sur, Chihuahua, Durango, Sonora; USA: Arizona, California, New Mexico, and Texas. Keys: Cazier 1953; Howden 1958, 1962.

Characteristics: Antennae 9- or 10-segmented, club 3- to 5- or 7-segmented. Labrum located below and fused to clypeus. Abdomen with sutures distinct; fifth abdominal sternite and propygidium separated by suture. Protibiae with apical spurs, meso- and metatibiae with 2 apical spurs; 2 metatibial spurs separated by tarsal articulation. Opposing claws equal, simple.

Casey (1889) and Davis (1935) placed *Acoma* next to *Podolasia*. Arrow (1909, 1912) and Leng (1920) placed *Acoma* under the Pleocominae (Pleocomidae). Blackwelder (1944) placed *Acoma* under the Chasmatopterini in the subfamily Melolonthinae, whereas Cazier (1953) kept it in the Pleocominae (Pleocomidae). Females are believed to be apterous (Van Dyke 1928; Cazier 1953). Howden (1958) stated that the phylogenetic placement would remain in doubt until the morphology of the female became known. Ritcher (1969) recorded the functional abdominal spiracles on segments 1-5, all of which are situated in the pleural membrane. Spiracles corresponding with abdominal segments 6-8 are vestigial. Spiracles associated with segments 6 and 8 are located in the membrane, while the spiracles on segment 7 are located in the sternite.

IV. Rutelinae MacLeay 1819

by Mary Liz Jameson

Common name: The shining leaf chafers

Characteristics: Form elongate oval. Labrum produced weakly beyond apex of clypeus (except in *Anomalacra* [Anomalini]). Antenna with 8-10 segments, antennal club with 3 segments. Anterior coxae transverse. Scutellum exposed. Tarsal claws on all legs independently movable, claws unequal in length or size and frequently weakly split at apex, 1 claw of each pair greatly reduced (1 claw lacking on all legs in *Leptohoplia* [Anomalini]). Onychium laterally flattened. Pygidium exposed beyond apices of elytra.

The subfamily Rutelinae is composed of approximately 200 genera and 4,100 species that are distributed worldwide (Machatschke 1972), although many taxa remain to be described.

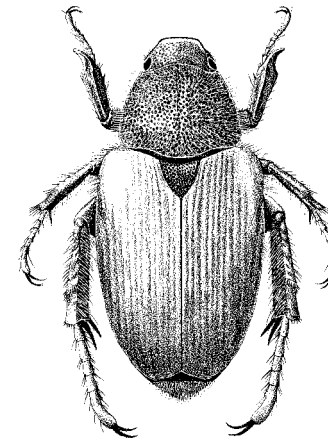


FIGURE 88.34. *Strigoderma arboricola* (Fabricius) (Used by permission of University of Nebraska State Museum).

Adult rutelines are phytophagous and feed on leaves, flowers, or flower parts. Larvae feed on roots, compost, and decaying vegetation. Some taxa, such as *Popillia japonica* Newman and *Anomala* species (both Anomalini), are agricultural pests. The common name of the subfamily, the shining leaf chafers, reflects the fact that many members of the subfamily are brightly colored, beautifully patterned, and often brilliantly metallic leaf-feeding beetles. Others in the subfamily, such as the genus *Anomala*, are small, obscure beetles. The subfamily is divided into six tribes, two of which occur in the United States. The tribe Spodochlamyini is found only in Central and South America; the tribe Anoplognathini occurs in the Australia and Central and South America; the tribe Adoretini is distributed throughout the Old World; the tribe Geniatini is distributed in Central and South America. The two remaining tribes, Rutelini and Anomalini, are the most speciose ruteline tribes and both occur in the Nearctic region. The tribe Rutelini is widely distributed but is most speciose in the Neotropics. The tribe Anomalini is widely distributed and is most speciose in the Old World. In the Nearctic region, the subfamily includes 14 genera and 95 species. Keys to genera and species: Casey 1915; Cooper 1983; Jameson 1990, 1998. Keys to larvae: Ritcher 1966; Jameson *et al.* 1994, Jameson 1998. United States catalog: Hardy 1991; Smith 2001. Regional works: Blatchley 1910; Loding 1945; Saylor 1948b; Edwards 1949; Hatch 1971; Kirk and Balsbaugh 1975; Lago *et al.* 1979; Ratcliffe 1991; Downie and Arnett 1996; Morón *et al.* 1997; Harpootlian 2001. World catalog: Machatschke 1972.

Key to the Tribes and Genera from the United States, Canada, and Nearctic Mexico

1. Lateral margin of elytra with membranous border (Fig. 89) (Anomalini) 2
— Lateral margin of elytra lacking membranous border (Fig. 90) (Rutelini) 6

2(1). Protibial spur absent; lacinia reduced, with 2 or fewer teeth ..... *Leptohoplia*
— Protibial spur present; lacinia not reduced, with more than 2 teeth 3

3(2). Base of pronotum tri-emarginate (Fig. 91); pygidium and abdominal sternites at sides with patches of dense, white setae ..... *Popillia*
— Base of pronotum rounded posteriorly (Figs. 92-93); pygidium and abdominal sternites at sides without patches of dense, white setae 4

4(3). Clypeus parabolic; apex of labrum thin, narrowly exposed beneath clypeus apex ..... *Anomalacra*
— Clypeus rounded or quadrate; apex of labrum moderately thick, broadly exposed beneath clypeal apex 5

5(4). Mesepimeron narrowly exposed in front of elytra (Fig. 93); base of pronotum narrower than base of elytra ..... *Strigoderma*
— Mesepimeron not exposed in front of elytra (Fig. 92); base of pronotum subequal to width of elytra at base ..... *Anomala*

6(1). Frontoclypeal suture complete, separating frons from clypeus (obsolete medially in *Paracotalpa deserta* Saylor) 7
— Frontoclypeal suture obsolete or lacking at middle 13

7(6). Mandible on external edge rounded 9
— Mandible on external edge with acute, apical tooth 8

8(7). Apex of mentum weakly emarginate; posterior border of metafemur in male without medial spine . ..... *Homoiosternus*
— Apex of mentum with U-shaped emargination; posterior border of metafemur in male with medial spine ..... *Plesiosternus*

9(7). Antenna with 10 antennomeres 10
— Antenna with 8 or 9 antennomeres .. *Parachrysina*

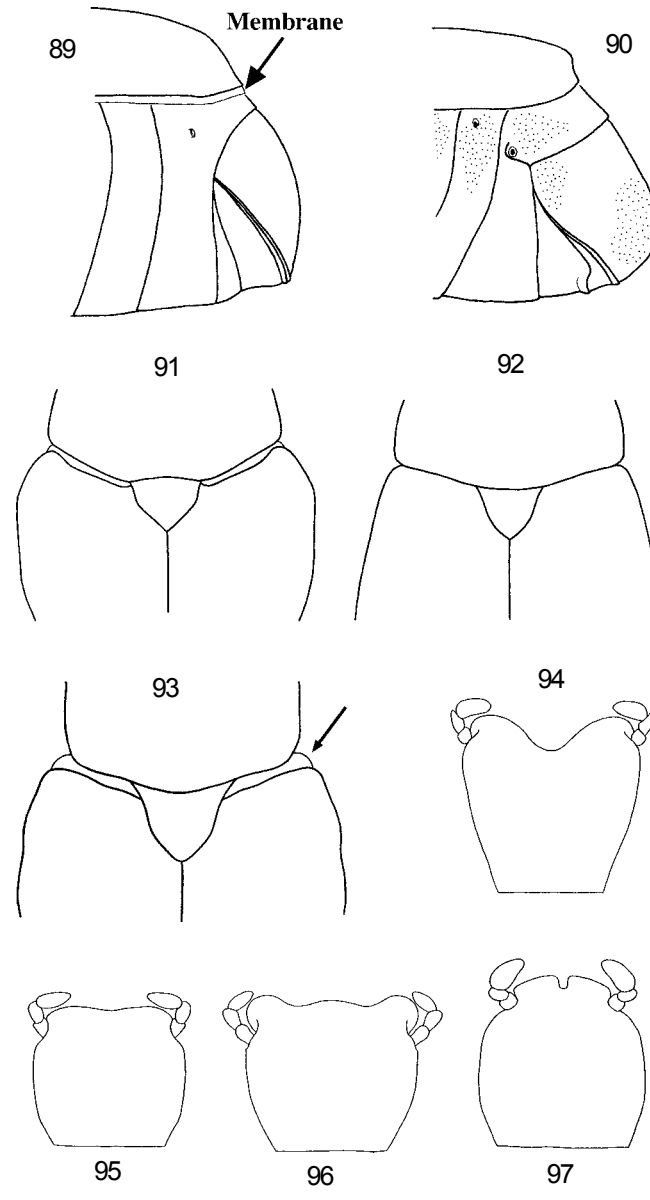
10(9). Terminal maxillary palpomere as long or longer than antennal club ..... *Pseudocotalpa*
— Terminal maxillary palpomere shorter than antennal club (nearly as long as antennal club in *Cotalpa subcribrata* Wickham) 11

11(10). Apex of mentum sinuate or bisinuate or emarginate (Figs. 94-96) 12
— Apex of the mentum notched (Fig. 97) ..... *Parabyrsopolis*

12(11). Pronotum glabrous; clypeus subrectangular, anterior angles narrowly rounded; large claw of at least metatarsus cleft in males, all claws simple in females ..... *Cotalpa*
— Pronotum setose (at least in places); clypeus semicircular (widest at base), angles broadly rounded (*P. deserta* with subrectangular clypeus); claws of both sexes simple ..... *Paracotalpa*

13(11). Frontoclypeal suture raised laterally; mandible on external edge with 1 acute, apical tooth 14
— Frontoclypeal suture not raised laterally; mandible on external edge rounded on bidentate 15

14(13). Antennal club 2 times longer than antennomeres 2-7; ventral apex of metatarsomere 4 with acute projection and 4 setae ..... *Parastasia*



FIGURES 89.34-97.34. 89-90. Apex of pygidium and elytra. 89. Anomalini, margin of elytra with membranous border; 90. Rutelini, margin of elytra without membranous border. 91-93. Dorsal view of pronotum and elytra showing form of pronotal base. 91. *Popillia japonica* Newman; 92. *Anomala* sp.; 93. *Strigoderma* sp. 94-97. Mentum, showing apical margins. 94. *Paracotalpa* sp., deeply sinuate; 95. *Cotalpa* sp., weakly sinuate; 96. *Cotalpa consobrina* Horn, bisinuate; 97. *Parabyrsopolis chihuahuae* (Bates), notched.

— Antennal club subequal in length to antennomeres 1-7; ventral apex of metatarsomere 4 truncate and with 4 spines ..... *Rutelisca*

15(13). Base of scutellum depressed below plane of elytron; elytron with marginal bead, epipleuron shelf-like 17
— Base of scutellum planar, extending anteriorly beneath pronotum; elytron without marginal bead, epipleuron rounded 16

16(15). Apex of metatibia with 10-18 spinules; mandibles rounded on external edge ..... *Calomacraspis*
— Apex of metatibia with 0-3 spinules; mandibles bidentate on external edge ..... *Rutela*

17(16). Apex of metatibia with 6-20 spinules ..... *Chrysina*
— Apex of metatibia with 0-1 spinules 18

18(17). Posterior tibia apicolaterally with small, articulated bristle; color rufous ..... *Ectinoplectron*
— Posterior tibia apicolaterally lacking small, articulated bristle; color testaceous, castaneous, or black ..... *Pelidnota*

Classification of the Tribes and Genera

Rutelinae MacLeay 1819

Anomalini Mulsant 1842

Characteristics: Antennae with 9 segments. Protibiae bidentate (rarely unidentate or tridentate), inner protibial spur subapical (lacking in *Leptohoplia*). Elytra with membranous border at lateral margin. Terminal spiracle not positioned in pleural suture.

The tribe Anomalini includes one of the largest genera in the Animal Kingdom: the genus *Anomala,* which includes approximately 1,000 species worldwide. Adult anomalines feed primarily on flowers and floral parts. Larvae feed primarily on plant roots. One adventive member of the tribe in North America, the Japnaese beetle (*Popillia japonica* Newman), causes economic damage to agricultural crops and ornamental plants. Because of potential damage to crop species, life histories of anomalines have been fairly well studied in the United States. Key to genera: Cooper 1983; Potts 1974, 1977a, 1977b. Key to larvae: Ritcher 1966.

Anomala Samouelle 1819
Phyllopertha Stephens 1830
Spilota Burmeister 1844
Callistethus Blanchard 1851
Pachystethus Blanchard 1851
Blitopertha Reitter 1903
Exomala Reitter 1903
Anomalepta Casey 1915
Anomalopus Casey 1915
Hemispilota Casey 1915
Oliganomala Casey 1915
Paranomala Casey 1915
Rhombonalia Casey 1915
Anomalopides Strand 1928

The genus *Anomala* (Fig. 1, Superfamily Scarabaeoidea) contains a heterogeneous assemblage of species and is in serious need of taxonomic study. In the United States and Canada 48 species are widely distributed. *Anomala marginata* (Fabricius) is considered a member of the genus *Callistethus* by some authors, and *A. orientalis* (Waterhouse) is placed in the genus *Exomala* by some authors. Adults feed on foliage and flowers, including the florets of grasses, and are diurnal and nocturnal. Larvae are subterranean root feeders and can be found in fields of oats, wheat, and corn, but they are also found under logs, rocks, and dried cow dung. Key to adults: Potts 1974, 1977a, 1977b. Larvae: Ritcher 1966.

Anomalacra Casey 1915
Anomalacra is a monotypic genus that includes only *A. clypealis* Schaeffer, and it occurs in Arizona and northern Mexico. Key: Potts 1974.

Leptohoplia Saylor 1935
Leptohoplia is a monotypic genus that includes only *L. testaceipennis* Saylor. The species occurs in the Colorado Desert of California and bordering regions in Arizona. In some specimens, one posterior claw may be so reduced as to appear absent. The genus *Hoplia* (subfamily Melolonthinae, tribe Hopliini) possesses only one posterior claw and, based on this character, *Leptohoplia* was previously placed in the Melolonthinae. Taxonomy and biology: Howden and Hardy 1971; Potts 1974.

Popillia Dejean 1821
The genus *Popillia* includes over 300 species in Asia and Africa. The Japanese beetle, *P. japonica* Newman, arrived from Asia into New Jersey in the roots of nursery stock in 1916. The species has expanded its range from the eastern regions (including Ontario) to as far west as Nebraska. Adults are severe pests of fruits and vegetables, field and forage crops, and ornamental plants. Larvae feed on various plant roots including ornamentals, grasses (including turfgrass), and vegetables. Larvae: Ritcher 1966.

Strigoderma Burmeister 1844
Alamona Casey 1915
Strigodermella Casey 1915

Five species occur in the United States and Canada, and an additional four species occur in Nearctic Mexico. Adults of *S. arboricola* (Fabricius) (Fig. 88) may cause damage to rose blossoms and are commonly encountered on many flowering plants. Keys to adults: Bader 1992. Larvae: Ritcher 1966.

Rutelini MacLeay 1819

Characteristics: Antennae with 10 segments (8 or 9 in *Parachrysina*). Protibiae tridentate, inner protibial spur apical. Elytral margin entirely chitinous. Terminal spiracle positioned in pleural suture.

The tribe Rutelini is distributed worldwide but is most speciose in the Neotropics. A wide array of morphological forms is exhibited by members of the tribe including taxa with enlarged, horn-like mandibles (*Fruhstorferia* from Asia), backward-projecting thoracic horns (*Peperonota* from Asia), enlarged hind femora (*Heterosternus* and *Chrysina* from the New World), and strikingly-colored, metallic silver and gold beetles (*Chrysina* from the New World). Keys to adults: Cooper 1983; Jameson 1990. Keys to larvae: Ritcher 1966; Jameson *et al.* 1994; Jameson 1998.

Calomacraspis Bates 1888
Calomacraspis splendens (Burmeister) is the only species of four in the genus that is distributed in the Nearctic region; it extends from southern Mexico to the southern limit of Nearctic Mexico. Adults are bright metallic green, diurnal, and feed on foliage, pollen, and floral parts (Jameson *et al.* 1994). Key to adults, biology, and larvae: Jameson *et al.* 1994.

Chrysina Kirby 1828
Plusiotis Burmeister 1844
Plusiotina Casey 1915
Pelidnotopsis Ohaus 1915
The genus *Chrysina* is well-known for its beautiful, metallic colors and relatively large size. Species in the genus are found from the southern United States to northern South America, and the genus includes 95 species (Hawks in press). Six species in this large genus occur in Arizona, New Mexico, Texas, and northern Mexico. *Chrysina gloriosa* (LeConte), a beautiful green and silver ruteline, occurs in Arizona, New Mexico, and Texas and feeds on juniper foliage. In some species, males possess greatly enlarged hind femora (such as *C. erubescens* Bates from northern Mexico). *Chrysina plusiotina* (Ohaus) is endemic to the Sierra Madre Oriental in Mexico and is rare in collections. Based on morphological and molecular data, Hawks *et al.* (in press) synonymized the genera *Plusiotis* and *Pelidnotopsis* with *Chrysina*. Key to adults: Cazier 1951; Morón 1990; Hawks and Bruyea 1999. Biology: Young 1957; Morón *et al.* 1997. Catalog: Hawks in press. Larvae: Ritcher 1966. (Volume 2, Color Figure 23)

Cotalpa Burmeister 1844
Ciocotalpa Saylor 1940 (subgenus)
The genus includes six species that are widely distributed in the United States. The goldsmith beetle, *Cotalpa lanigera* (L.), is found in sandy areas and feeds on the foliage of various trees including aspen, cottonwood, and willow. Key to adults: Saylor 1940d; Young 2002. Larvae: Ritcher 1966.

Ectinoplectron Ohaus 1915
Ectinoplectron includes only *E. oryctoides* (Ohaus) (= *Pelidnota howdeni* Hardy). This species is found only in northwestern Mexico. References: Morón 1990; Morón *et al.* 1997.

Homoiosternus Ohaus 1934
Homoiosternus includes two species and one of these, *H. beckeri* Ohaus, occurs in the Nearctic region. This species is found only in oak and pine/oak forests in the southern Sierra Madre Occidental mountain range of Mexico. Reference: Morón 1983a; Morón *et al.* 1997; Delgado and Blackaller-Bages 1997.

Parabyrsopolis Ohaus 1915
Byrsopolis Burmeister 1844
Parareoda Casey 1915
The genus *Parabyrsopolis* includes only *P. chihuahuae* (Bates). This species occurs in the Huachuca and Patagonia mountains of Arizona in the United States and in the Sierra Madre Occidental mountains in Mexico. The species is found in pine-oak forests and is attracted to lights at night. Reference: Jameson 1990.

Parachrysina Bates 1888
One species, *P. borealis* Jameson, occurs in the Sierra Madre Oriental mountains in Nuevo Leon, Mexico. The genus is unique in the Rutelini for its 8- or 9-segmented antenna. Key to adults: Jameson 1991.

Paracotalpa Ohaus 1915
Pocalta Casey 1915
Species in the genus are commonly called "little bears" due to their dense, long hair. The genus includes four species that are distributed west of the Rocky Mountains in the United States: *P. ursina* (Horn), *P. deserta* Saylor, *P. granicollis* (Haldeman), and *P. puncticollis* (LeConte). Larvae of *P. ursina* have been recorded feeding on sage brush (*Artemisia* sp.) (Ritcher 1966). Key to adults: Saylor 1940d. Larvae: Ritcher 1966.

Parastasia Westwood 1842
Barymorpha Guérin-Méneville 1843
Polymoechus LeConte 1856
Urleta Westwood 1875
Echmatophorus Waterhouse 1895
Ohkubous Sawada 1938
One species, *P. brevipes* (LeConte), is distributed in the eastern United States. The remaining species of *Parastasia* are distributed in Asia. Ratcliffe (1991) synonymized *P. conicicollis* (Casey) with *P. brevipes*. Adults are collected from lights at night. Key to adults: Kuijten 1992. Larva: Ritcher 1966.

Pelidnota MacLeay 1819
Aglycoptera Sharp 1885
Pelidnotidia Casey 1915
The genus *Pelidnota* includes about 100 species and is most speciose in South America. Six species are distributed in Nearctic North America. The spotted pelidnota, *P. punctata* (L.), occurs east of the Rocky Mountains. Adults feed on the foliage and fruits of grapes, and larvae feed on decaying roots and tree stumps. Key to adults: Hardy 1975. Larvae: Ritcher 1966.

Plesiosternus Morón 1983
Two species in the genus *Plesiosternus* are known, and *P. setosus* Morón occurs in the Nearctic region. The species is distributed from the Mexican states of Tamaulipas to Hidalgo and occurs in pine-oak forests. Reference: Morón 1983a; Morón and Howden 1992.

Pseudocotalpa Hardy 1971
The genus includes three species (*P. giulianii* Hardy, *P. andrewsi* Hardy, *P. sonorica* Hardy) that are distributed in sandy regions in California, Nevada, and Sonora, Mexico. Key to adults: Hardy 1974b. Biology: Hardy 1976, 1986.

Rutela Latreille 1802

Diabasis Hoffmansegg 1817

One species, *R. formosa* Burmeister, occurs in Florida, Georgia, the Bahamas, and Cuba. Keys, biology, larvae: Jameson 1998.

Rutelisca Bates 1888

This genus includes two species, one of which (*R. durangoana* Ohaus) is found in the Nearctic region. This species occurs in the pine/oak forests of the Sierra Madre Occidental mountains of Mexico. Key to adults: Jameson 2000. Larvae: Morón and Deloya 1991.

V. Dynastinae MacLeay 1819

by Brett C. Ratcliffe

Common names: The rhinoceros beetles and their hornless kin

Characteristics: Labrum hidden beneath clypeus. Clypeus with apex bidentate, rounded, acuminate, or truncate. Mandibles variable: Cyclocephalini and U.S. Phileurini lack teeth on lateral edge of mandibles, other tribes with teeth or lobes. Antennae 9-10 segmented, club small in most and with 3 segments. Scutellum normal, never enlarged. Procoxae transverse. Tarsal claws all subequal in size except for males of most Cyclocephalini and some Pentodontini with protarsal claws enlarged. Male genitalia diagnostic in nearly all species.

The sexes of most species are dimorphic (except Phileurini, some Cyclocephalini, and some Pentodontini) with males having either horns or enlarged tubercles or enlarged protarsi. The subfamily is divided into eight tribes, and five occur in the Nearctic region. Members of the Agaocephalini are Neotropical, while those of the Hexodontini are restricted to Madagascar and the Oryctoderini are found in the Australian and Oriental regions. In the United States, Canada, and northern Mexico there are 18 genera and about 62 species. Keys to adults: Endrödi 1985. Keys to larvae: Ritcher 1966. United States catalog: Hardy 1991; Smith 2001. Regional works: Blatchley 1910; Loding 1945; Saylor 1948a, 1948b; Edwards 1949; Hatch 1971; Kirk and Balsbaugh 1975; Shook 1978; Lago *et al.* 1979; Gordon and Anderson 1981; Ratcliffe 1991; Downie and Arnett 1996; Morón *et al.* 1997; Harpootlian 2001.

Key to the Tribes and Genera from the United States, Canada, and Nearctic Mexico

1. Head and pronotum lacking tubercles, carina, horn, or fovea; most males with anterior tarsomeres enlarged (Cyclocephalini) 5
— Head and pronotum with tubercles, carina, horn, or fovea; males with anterior tarsomeres slender or, if enlarged, with distinct transverse carina on head 2

2(1). Mentum greatly enlarged to cover bases of labial palps; clypeus sharply acuminate (Phileurini) . 7
— Mentum not enlarged, bases of labial palps visible; clypeal apex acuminate or not, but not sharply pointed 3

3(2). Apex of posterior tibia truncate or crenulate, upper apical angle not prolonged into large tooth (Fig. 99) (Pentodontini) 9
— Apex of posterior tibia crenulate or with triangular teeth or with prolonged tooth on upper apical angle (Fig. 100) 4

4(3). Mandibles concealed beneath clypeus or exposed; if exposed, then with 1-2 broadly rounded lobes or teeth (basal and subapical); males with median declivity on pronotum, females with or without declivity (Oryctini) 17
— Mandibles exposed at sides of clypeus and with 2 narrowly elongate teeth; neither males nor females with pronotal declivity (Dynastini) 18

5(1). Apex of clypeus angularly parabolic; mentum with apex deeply emarginate ..... *Ancognatha*
— Apex of clypeus rounded or truncate; mentum with apex entire or weakly emarginate 6

6(5). Clypeus trapezoidal; color black ..... *Dyscinetus*
— Clypeus rounded at apex; color testaceous or dark brown in some ..... *Cyclocephala*

7(2). Apex of posterior tibia truncate, without teeth (dorsal angle also not spiniformly produced) .... *Archophileurus*
— Apex of posterior tibia with dorsal angle spiniformly produced into a tooth 8

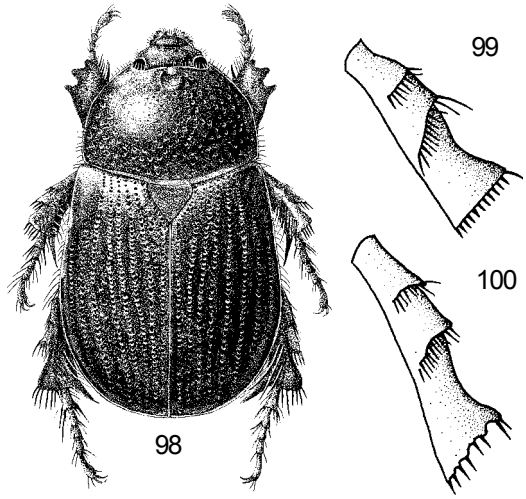
8(7). Tubercles or horns of frons located just either side of middle, removed from lateral margin of head; pronotum without fovea in front of longitudinal furrow ..... *Hemiphileurus*
— Tubercles or horns of frons located on lateral margin of head; pronotum with subapical fovea behind tubercle and in front of longitudinal furrow ..... *Phileurus*

9(3). Antenna with 9 antennomeres . *Aphonides* (in part)
— Antenna with 10 antennomeres 10

10(9). Small, black species, most less than 15 mm in length; head with 2 small, transverse tubercles; pronotum lacking tubercles or fovea; posterior tibia strongly broadened to apex ..... *Euetheola*
— Larger, reddish brown or black species generally greater than 15 mm in length; head with or without carina, tubercles, or horn; pronotum with or without tubercles or fovea; posterior tibia not strongly broadened apically 11

11(10). Clypeal apex acute and with subapical margins cariniform ..... *Oxygrylius*
— Clypeal apex bidentate, truncate, or rounded; subapical margins not cariniform 12

12(11). Clypeus with high, transverse carina *immediately* behind apex 13
— Clypeus lacking high, transverse carina *immediately* behind apex 14



FIGURES 98.34-100.34. 98. *Tomarus gibbosus* (DeGeer). 99-100. Posterior tibia. 99. Pentodontini, apex truncate or crenulate; 100. Oryctini, apex crenulate or with triangular teeth (All used by permission of University of Nebraska State Museum).

13(12). Transverse carina just behind apex of clypeus tridentate. Pronotum lacking subapical tubercle. Protibia with apex truncate. Size mostly less than 17 mm ..... *Aphonus*

— Transverse carina just behind apex of clypeus bidentate or entire. Pronotum with subapical tubercle or not. Protibia with apex rounded. Size mostly greater than 17 mm ..... *Orizabus*

14(12). Frontoclypeal region with tubercles or carina; posterior tarsus shorter than femur 15

— Frontoclypeal region lacking tubercles or carina; posterior tarsus as long as or longer than femur ..... *Coscinocephalus*

15(14). Elytron with sutural stria and 3 feebly indicated discal striae; clypeus strongly convex on dorsal surface ..... *Gillaspytes*

— Elytron with sutural striae as well as 5-7 clearly indicated, punctate striae; clypeus not strongly convex on dorsal surface 16

16(15). Frontoclypeal region with 2 tubercles; apex of clypeus with 2 small, reflexed teeth ... *Tomarus*

— Frontoclypeal region with strong, arcuate, transverse carina ..... *Aphonides* (in part)

17(4). Anterior tibia with 3 teeth; frons in male with horn, female with a single tubercle; pronotum in females simply convex ..... *Xyloryctes*

— Anterior tibia with 4 teeth; frons in both sexes with 2 tubercles; pronotum in females with subapical fovea ..... *Strategus*

18(4). Clypeal apex broadly bidentate; elytra dark brown to black, some with conspicuous setae; pronotum at middle in males with tubercle, short horn, or simply rounded; base of horn or tubercle (if present) lacking 2 small teeth; anterior angles of pronotum often produced into small tubercle or horn ..... *Megasoma*

— Clypeal apex narrowly bidentate or emarginate; elytra greenish gray and mottled with dark spots, glabrous; pronotum at middle in males produced into long, forward projecting horn, horn with brush of tawny setae beneath; base of horn with 2 teeth; anterior angles of pronotum lacking horns or tubercles ..... *Dynastes*

Classification of the Tribes and Genera

Dynastinae MacLeay 1819

Cyclocephalini Laporte 1840

Characteristics: Head and pronotum lacking tubercles, horns, carinae, or foveae in both sexes. Club of antennae longer in some males of *Cyclocephala*. Mandibles without teeth or lobes on lateral edge. Legs with all tarsi cylindrical, never subtriangular. Anterior tarsi enlarged in males of most species. Prosternal process prominent in most. Onychium at apex with two setae.

This tribe of 13 genera is restricted to the New World except for one monobasic genus, *Rutelorycte*s, in Africa. In the U.S., there are three genera. Most species are Neotropical in distribution. Keys to species: Saylor 1945b; Endrödi 1985; Ratcliffe 1991.

Ancognatha Erichson 1847

One species, *A. manca* (LeConte), is found in Arizona, New Mexico, and northern Mexico.

Cyclocephala Dejean 1821

Mononidia Casey 1915
Diaptalia Casey 1915
Stigmalia Casey 1915
Ochrosidia Casey 1915
Spilosota Casey 1915
Halotosia Casey 1915
Homochromina Casey 1915
Aclinidia Casey 1915
Plagiosalia Casey 1915
Isocoryna Casey 1915
Graphalia Casey 1915
Dichromina Casey 1915
Aspidotites Höhne 1922
Aspidodella Prell 1936
Albridarollia Bolivar, Jiminez and Martínez 1963
Paraclinidia Martínez 1965

This is a large genus with more than 250 species with most of the species occurring in Central and South America. Fifteen species occur in the United States with about four more species in northern Mexico. The U.S. species are generally distributed except for the Pacific Northwest and extreme north where they are absent. Keys to adults: Saylor 1945b; Endrödi 1985. Key to larvae: Ritcher 1966. (Volume 1, Color Figure 6).

Dyscinetus Harold 1869
Chalepus MacLeay 1819
Palechus Casey 1915
There are 15 species in this genus, most of which are found in Central and South America. Two species, *D. morator* (Fabricius) and *D. picipes* Burmeister, occur in the southern and midwestern United States. Keys to adults: Saylor 1945b; Endrödi 1985. Larval description: Ritcher 1966.

Pentodontini Mulsant 1842

Characteristics: Head and pronotum with carina, tubercles, or fovea. Club of antenna small in most. Mandibles with 1-3 lateral lobes or teeth in most. Apex of posterior tibiae generally truncate or finely crenulate (Fig. 99), not toothed. Prosternal process long, columnar. Onychium at apex with two setae in most.

The Pentodontini is the largest tribe of Dynastinae, and its species occur everywhere except for the polar regions. There are 25 genera in the New World, and eight occur in the United States. In the last version of this work (Arnett 1968), the tribe Pentodontini was not recognized. Keys to genera: Ratcliffe 1981; Endrödi 1985. Keys to species: Saylor 1946a-b, 1948a (as Oryctini); Endrödi 1985.

Aphonides Rivers 1889
Anoplognatho Rivers 1889
One species, *A. dunnianus* (Rivers), is found in Arizona, New Mexico, Texas, and northern Mexico. This species has 9 or 10-segmented antennae.

Aphonus LeConte 1856
The genus *Aphonus* contains eight species. Six species are generally distributed from southeastern Canada, through the eastern United States, and to the southern U.S. and west to Texas. Key to adults: Gill and Howden 1985. Key to larvae: Ritcher 1966.

Coscinocephalus Prell 1936
Anoplocephalus Schaeffer 1906
Two species occur in northern Mexico with one, *C. cribrifrons* Schaeffer, reaching southern Arizona. This genus was transferred from the tribe Cyclocephalini to the tribe Pentodontini by Morón and Ratcliffe (1996). Key to adults and larval description: Morón and Ratcliffe 1996.

Euetheola Bates 1888
Euetheola is composed of four species. The genus contains two species in the Nearctic region, *E. subglabra* (Schaeffer) in Arizona and Mexico and *E. humilis* (Burmeister) in the southeastern U.S. and northern Mexico. Key to adults: Endrödi 1985. Larval description: Ritcher 1966.

Gillaspytes Howden 1980
One rare species, *G. janzeni* Howden, is found in Nearctic Tamaulipas state and also in Veracruz, Mexico.

Orizabus Fairmaire 1878
Pseudaphonus Casey 1915
Aztecalius Casey 1915
Eight species of *Orizabus* occur from the central U.S. to Central America. Three species occur in the southwestern and southcentral U.S. Key to adults: Endrödi 1985. Larval description: Ritcher 1966 (as *Cheiroplatys*).

Oxygrylius Casey 1915
One species, *O. ruginasus* (LeConte), occurs in the southwestern U.S. and northern Mexico.

Tomarus Erichson 1847
Ligyrus Burmeister 1847
Ligyrodes Casey 1915
Euligyrus Casey 1915
Grylius Casey 1915
Anagrylius Casey 1915
Ligyrellus Casey 1915
The genus *Tomarus* (Fig. 98) contains 25 species that occur from Canada through South America. There are four species, some generally distributed, in the Nearctic region.

Both *Tomarus* Erichson and *Ligyrus* Burmeister were described in 1847. Ever since the 1850s, *Ligyrus* has been used as the senior name while *Tomarus* has been used as a subgenus. The forward in Burmeister's *Handbuch der Entomologie* (volume 5) is dated February 1847, and it was received in the library of the Entomologischen Vereine zu Stettin in September 1847. But, the paper following Erichson's in the Archiv für Naturgeschichte is dated January 1847, and it was received in the library in Stettin in April 1847. *Tomarus* has priority although Lacordaire stated in 1859, for reasons known only to him, that *Tomarus* was described after *Ligyrus*. The confusion over the correct name for this genus seems to stem from this point.

Key to adults (as *Ligyrus*): Endrödi 1985. Larval description: Ritcher 1966.

Oryctini Mulsant 1842

Characteristics: Head and pronotum with tubercles or horns (especially males) and pronotum of most with fovea (especially females). Club of antenna small. Mandibles with lateral lobes or teeth. Apex of posterior tibia strongly crenulate or with teeth (including apical tooth)(Fig. 100). Prosternal process prominent, columnar. Onychium with 3 or more setae at apex.

The tribe Oryctini is world wide in distribution. There are 13 genera in the New World, and two of these are found in the United States. Key to genera and species: Endrödi 1985.

Strategus Kirby 1828
Anastrategus Casey 1915
Strategodes Casey 1915
Strategopsis Chapin 1932
The genus *Strategus* contains 31 extant species and one fossil species that occur from the southcentral U. S. through South

America. Five species are found in the southern U.S. with one species reaching central Kansas. Key to adults: Ratcliffe 1976a. Key to larvae: Ritcher 1966. Biology: Ratcliffe 1976a.

Xyloryctes Hope 1837
Ten mostly Mexican species occur in the genus, and two species are found in the eastern and southwestern U.S. Key to adults: Endrödi 1985. Larval description: Ritcher 1966.

Phileurini Burmeister 1847

Characteristics: Head with tubercles or short horns, pronotum with median sulcus and most with apical tubercle. Club of antenna small. Mandibles exposed, narrowly subtriangular, lacking teeth. Mentum large, covering base of labial palps. Clypeus with apex acute. Apex of posterior tibia truncate or with teeth. Apex of basal tarsomere on posterior leg with long spine.

Phileurines are found in all regions of the world although most species are found in the tropics. There are 21 genera in the New World, and three genera occur in the United States. Key to genera: Endrödi 1985.

Archophileurus Kolbe 1910
Amblyophileurus Kolbe 1910
Periphileurus Kolbe 1910
Anisophileurus Prell 1912
There are about 25 primarily Neotropical species of *Archophileurus*, and one species, *A. cribrosus* (LeConte), occurs in Texas.

Hemiphileurus Kolbe 1910
Epiphileurus Kolbe 1910
This genus is composed of about 40 species, all of which are Neotropical. One species, *H. illatus* (LeConte), is distributed northward into the southwestern U.S.

Phileurus Latreille 1807
Two species, *P. valgus* (Olivier) and *P. truncatus* (Palisot de Beauvois), occur in the southern United States and Mexico. The 19 species in the genus are mostly Neotropical in distribution. Key to adults: Endrödi 1985. Larval description: Ritcher 1966.

Dynastini MacLeay 1819

Characteristics: Head and pronotum with horn (males) or head with tubercle (females) in most species. Prosternal process flattened, subtriangular, generally adpressed to prosternum, most short. Onychium at apex multisetose.

The tribe Dynastini is comprised of three genera in the New World, and two are found in the United States and northern Mexico. Members of the Dynastini are among the largest insects on Earth, and the males of some species possess very large horns.

Dynastes MacLeay 1819
Theogenes Burmeister 1847
Six species are found in the New World, and three species are found in the U.S. and Mexico: *D. tityus* (L.) in the southeastern U.S., *D. granti* Horn in the southwestern U.S., and *D. hyllus* Chevrolat in Mexico (extending northward as far as Tamaulipas state). Key to adults: Endrödi 1985. Photographic synopsis of adults: Lachaume 1985. Key to larvae: Ritcher 1966. Biology: Glaser 1976.

Megasoma Kirby 1825
Megalosoma Burmeister 1841
Lyphontes Bruch 1910
Megasominus Casey 1915
Seven species are found in the southwestern U.S. and northern Mexico. Key to adults: Hardy 1972; Endrödi 1985. Photographic synopsis of adults: Lachaume 1985.

VI. Cetoniinae Leach 1815

by Brett C. Ratcliffe

Common name: The flower chafers

Characteristics: Mandibles weakly developed, hidden by clypeus. Labrum membranous in most, hidden. Antenna 10-segmented, club with 3 segments (these can be elongated); antennal insertion visible from above (Fig. 2) on side of clypeus. Eye canthus long, narrow. Elytron with distinct post-humeral emargination (Gymnetini, Cetoniini, Cremastocheilini) (Fig. 3) that reveals the mesepimeron at the base of elytron or lacking post-humeral emargination (Trichiini and Valgini) (Fig. 4). Pygidium exposed. Propygidium rigidly connected to fifth visible sternite. Procoxae protruding conically downward. Posterior coxae contiguous or nearly so in Trichiini. Tarsal claws simple and subequal in size.

The subfamily Cetoniinae was redefined by Krikken (1984) to include twelve tribes (citing Trichiini and Valgini as tribes). Previously, Schenkling (1921) had recognized seven tribes in the *Coleopterorum Catalogus* (not including the Trichiini and Valgini). Of the twelve tribes recognized by Krikken, five occur in North America. The tribes not occurring in North America are: Xiphoscelidini (Africa and Madagascar), Stenotarsiini (Madagascar), Schizorhinini (Australia, Oriental), Goliathini (Africa, Oriental, Madagascar, two genera and three species in southern Mexico), Diplognathini (Africa, Oriental), Phaedimini (Oriental), and Taenioderini (Oriental, Australia, Palearctic).

In the United States, Canada, and northern Mexico, there are 18 genera and about 105 species. Keys to adults: Casey 1915; Goodrich 1966; Howden 1968b, 1971b; Krikken 1976, 1984 (to subtribes); Hardy 1988; Harpootlian 2001. North American catalog: Smith 2001. Regional works: Blatchley 1910; Lago *et al.* 1979; Ratcliffe 1991; Morón *et al.* 1997; Harpootlian 2001. World Catalog: Schenkling 1921; Krikken 1984 (genera); Krajcík 1998, 1999. Larvae: Ritcher 1966.

Key to the Tribes and Genera from the United States, Canada, and Nearctic Mexico

1. Posthumeral elytral emargination present; mesepimeron visible from above (Fig. 3) 2
— Posthumeral elytral emargination lacking; mesepimeron not visible from above (Fig. 4) ... 4

2(1). Pronotum with basomedian lobe enlarged, covering scutellum (Fig. 102) (Gymnetini) 5
— Pronotum without enlarged basomedian lobe; scutellum visible (Fig. 101) 3

3(2). Labium not enlarged or cup shaped, less than half as wide as head (Cetoniini) 8
— Labium cup shaped, one half to three quarters as wide as head (Cremastocheilini) 11

4(1). Posterior coxae contiguous or nearly so; protibia with 1-3 teeth (Fig. 103) (Trichiini) 15
— Posterior coxae widely separate; protibia with 3-5 teeth (Fig. 104) (Valgini) ..... *Valgus*

5(2). Apex of clypeus with median, upturned, lobiform process; vertex and frons with ridge-like, longitudinal process, often developed into distinct horn (Fig. 102) ..... *Cotinis*
— Apex of clypeus subtruncate, rounded, or weakly emarginate; vertex and frons never armed 6

6(5). Dorsal surface shiny black, with or without cream colored band on lateral edge of pronotum, traversing elytra just past middle; elytral band occasionally reduced to spots ..... *Gymnetina*
— Dorsal surface velutinous, either black with yellow markings or dusky brown, grey, yellowish green, or greyish green 7

7(6). Dorsal surface black with variable yellow markings on pronotum and elytra; prosternal process (in front of forecoxae) long ..... *Gymnetis*
— Dorsal surface a monochrome brown, grey, yellowish green, or greyish green; prosternal process absent ..... *Hologymnetis*

8(3). Clypeus with apex quadridentate or bidentate; pronotum on posterior margin entire or weakly emarginate in front of scutellum ... *Stephanucha*
— Clypeus with apex subtruncate to rounded, lacking teeth; pronotum on posterior margin distinctly emarginate in front of scutellum in most 9

9(8). Apex of elytra spiniformly produced at suture ..... *Protaetia*
— Apex of elytra rounded or angulate, not spiniformly produced 10

10(9). Prosternal process (in front of forecoxae) well-developed, almost as produced as coxae; body with dorsal surface conspicuously flattened; anterior tibia with 2 apical teeth very close together .... *Chlorixanthe*
— Prosternal process weakly developed, not noticeable in most; body of most with dorsal surface convex, not conspicuously flattened; anterior tibia with 3 teeth subequally spaced .. *Euphoria*

11(3). Pronotum with posterolateral angles produced, either acute or knob-like; trichomes present on basal or apical margin of pronotum 12
— Pronotum with posterolateral angle not produced, obtusely angulate or rounded in most; trichomes on pronotum absent 13

12(11). Pronotum with anterior angles acute; apex on sides with deep groove containing dense mat of setae ..... *Cremastocheilus*
— Pronotum with apex entire, lateral grooves absent ..... *Centrochilus*

13(11). Tarsomeres with numerous, small, longitudinal carinae; dorsal surface of pronotum and elytra smooth ..... *Lissomelas*
— Tarsomeres smooth, punctate, or irregularly punctate; lacking numerous longitudinal carinae; dorsal surface punctate in most 14

14(13). Antennal scape concave, surface smooth and glossy; elytra glossy ..... *Psilocnemis*
— Antennal scape flat or convex, surface finely to heavily punctate or rugose; elytra partly opaque or, if glossy, with chalky, white marks ..... *Genuchinus*

15(4). Protibia with basomedial angle and adjacent femoral part acute; clypeus in males with horn-like projection; eye canthus angulate on anterior edge ..... *Inca*
— Protibia lacking acute basomedial angle; clypeus in males without horn 16

16(15). Body dorsally unicolorous brown to black, without markings or chalky, white marks .... *Osmoderma*
— Body dorsally distinctly bicolored or with chalky, white marks on either elytra, pygidium, metasternum or all 3 (Fig. 103) 17

17(16). Disc of pronotum with impression in form of triangle ..... *Trigonopeltastes*
— Disc of pronotum without triangle-shaped impression 18

18(17). Disc of elytra with setae ..... *Trichiotinus*
— Disc of elytra lacking setae ..... *Gnorimella*

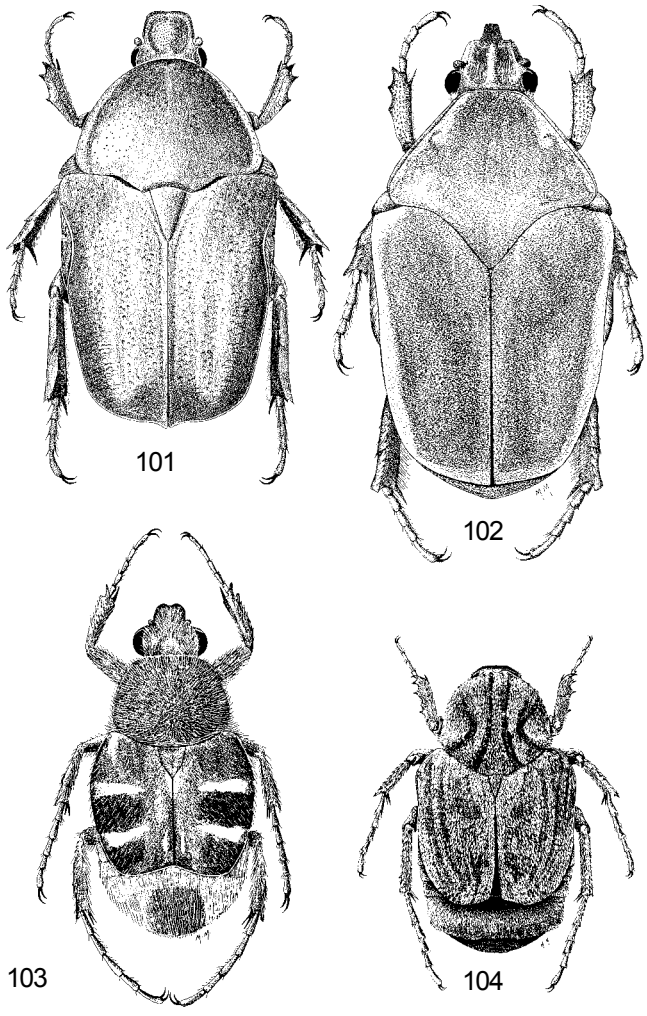
Classification of the Tribes and Genera

Cetoniinae Leach 1815

Gymnetini Kirby 1827

Characteristics: Pronotum with basomedian lobe strongly expanded, apex rounded, covering most of scutellum. Mesepimeron distinct. Posthumeral emargination of elytra distinct. Surface velutinous in most. Mesometasternal protrusion developed.

This tribe consists of approximately 29 genera, and 25 of these are restricted to the New World. In the U.S. there are four genera. Most of the species in the tribe are Neotropical in distribution. The taxa in this tribe are in great need of study, and Ratcliffe (in prep.) is working on this. Key to species: Casey 1915.



FIGURES 101.34-104.34. 101. *Euphoria fulgida* (Fabricius); 102. *Cotinis nitida* (Linnaeus); 103. *Trichiotinus assimilis* (Kirby); 104. *Valgus seticollis* (Palisot de Beauvois) (All used by permission of University of Nebraska State Museum).

Cotinis Burmeister 1842
- subgenus *Cotinis* Burmeister 1842
  - *Latemnis* Thomson 1880
  - *Cotinorrhina* Schoch 1895
- subgenus *Criniflavia* Goodrich 1966
- subgenus *Liberocera* Deloya and Ratcliffe 1988

Eight species of *Cotinis* (Fig. 102) occur in the southern half of the United States and northern Mexico. Key: Goodrich 1966; Deloya and Ratcliffe 1988. Larvae: Ritcher 1966.

Gymnetina Casey 1915
One species, *G. cretacea* (LeConte), is found in Arizona.

Gymnetis MacLeay 1819
- *Paragymnetis* Schürhoff 1937
- *Gymnetoides* Martínez 1949

One species, *G. sallei* Schaum, is found in the southwestern U.S. and Mexico. Larvae: Ritcher 1966.

Hologymnetis Martínez 1949
Two species, *H. argenteola* (Bates) and *H. cinerea* (Gory and Percheron), are found in southern Arizona and northern Mexico. Key: Ratcliffe and Deloya 1992. Larvae: Micó *et al.* 2001.

Cetoniini Leach 1815

Characteristics: Pronotum lacking basomedian lobe, scutellum visible. Mesepimeron distinct. Posthumeral emargination of elytra distinct. Elytra glabrous, setose, velutinous, or with cretaceous patches. Mesometasternal protrusion developed.

The large tribe Cetoniini consists of about 107 genera. These beetles are widely distributed around the world although not as commonly in the Neotropics, Madagascar, or Australasia. The African and Neotropical taxa are in need of revision. There are five genera in the United States, Canada, and northern Mexico (*Protaetia* is adventive in Florida). Keys: Casey 1915; Hardy 1988; Ratcliffe 1991. Larvae: Ritcher 1966.

Chlorixanthe Bates 1889
Two species occur in the genus, and one species, *C. propinqua* (Gory and Percheron) (= *C. chapini* Cartwright), is found in Mexico and the southwestern U.S. Key: Hardy 1988.

Euphoria Burmeister 1842
- *Erirhipis* Burmeister 1842
- *Euryomia* Lacordaire 1856
- *Euphoriaspis* Casey 1915
- *Erirhipidia* Casey 1915
- *Euphorhipis* Casey 1915
- *Haplophoria* Casey 1915
- *Isorhipina* Casey 1915
- *Rhipiphorina* Casey 1915

The genus *Euphoria* (Fig. 101) is badly in need of revision, and even some of the U.S. species cannot be reliably identified. There are approximately 73 species in the genus, and about 20 species are broadly distributed in the United States. Key: Casey 1915 (not reliable due to its typological concept). Larvae: Ritcher 1966; Ratcliffe 1976b; Micó *et. al* 2000.

Protaetia Burmeister 1842
Protaetia is a huge genus with about 250 species that occur in the Oriental, Australian, and Palearctic regions. One species, *P. fusca* (Herbst), widely distributed in Asia, has become established in southeastern Florida (Thomas 1998) and Hawaii (Miksic 1987). Key: Miksic 1987 (for all Old World species).

Stephanucha Burmeister 1842
- *Anatropis* Casey 1915

Stephanucha has six species that occur in the eastern United States west to Colorado, New Mexico, and Arizona and with two species in Mexico. Key: Casey 1915. Generic commentary: Hardy 1988. Immature stages and biology: Skelley 1991. (Volume 1, Color Figure 5).

Cremastocheilini Burmeister 1842

Characteristics: Labium cup-shaped, one half to three fourths as wide as head. Maxillary galea and lacinia dentate in most. Antenna with scape conspicuously enlarged into flattened, triangular shape. Middle coxae never separated by a broad protrusion. Body form of most subquadrate, flattened dorsally. Color black or brown.

The tribe Cremastocheilini contains about 51 genera. About 60% of the genera are found in Africa while none occur in Madagascar or Australia. In the New World there are ten genera, and five occur in North America. Most species are myrmecophilous. Keys: Potts 1945; Howden 1971b; Krikken 1976. Larvae: Ritcher 1966.

Centrochilus Krikken 1976
One species, *C. howdeni* Krikken, is known from Durango state in Mexico.

Cremastocheilus Knoch 1801
subgenus *Cremastocheilus* Knoch 1801
subgenus *Myrmecotonus* Mann 1914
Myrmecicon Mann 1914
subgenus *Macropodina* Casey 1915
subgenus *Trinodia* Casey 1915
subgenus *Anatrinodia* Casey 1915
The genus *Cremastocheilus* is restricted to North America and includes about 35 species. Most of these species are uncommonly encountered. The genus is in need of a modern synopsis. Keys: Potts 1945; Alpert 1994. Larvae: Ritcher 1966; Ratcliffe 1977.

Genuchinus Westwood 1873
Nine species are placed in this genus, and two species are found in Arizona and California. The remainder are primarily South American in distribution. Key: Krikken 1981.

Lissomelas Bates 1889
Only one Neotropical species is known, *L. flohri* Bates, and its distribution extends northward to southern Arizona.

Psilocnemis Burmeister 1842
One species is known, *P. leucostictica* Burmeister. It is found from Maryland to North Carolina in the United States.

Trichiini Fleming 1821

Characteristics: Procoxae projecting conically. Pronotum evenly convex or with weakly impressed midline or pre-discal impression. Mandibles either weakly or strongly sclerotized. Galea of maxilla penicillate in most. Protibia with 1-3 teeth. Dorsum uniformly dark brown or black or bicolored or with cretaceous spots or bands or metallic.

Until relatively recently, the trichiines have been considered as a subfamily (frequently as a family in Europe). The tribe Trichiini consists of 43 genera that are found nearly worldwide except Australia and Madagascar. Thirteen genera are found in the New World with five genera occurring in North America. Key: Howden 1968b; Morón and Krikken 1990.

Gnorimella Casey 1915
Only one species is known, *G. maculosa* (Knoch), and it occurs in the eastern United States and Canada. Larvae: Ritcher 1966.

Inca LePeletier and Serville 1828
The genus contains six species, one of which (*Inca clathratus sommeri* Westwood) is found in Mexico's Tamaulipas state in the Sierra Madre Oriental. Distribution: Morón *et al.* 1997. Biology: Boos and Ratcliffe 1985. Larvae: Morón 1983b.

Osmoderma LePeletier and Serville 1828
Gymnodi Kirby 1827 (*nomen oblitum*)
Gymnodus Kirby 1837 (unjustified emendation; *nomen oblitum*)
This genus contains nine species, three of which occur in North America. Keys: Hoffmann 1939; Howden 1968b. Larvae: Ritcher 1966; Ratcliffe 1977.

Trichiotinus Casey 1915
Eight species of *Trichiotinus* (Fig. 103) are found throughout the United States (except the far west) and southern Canada. Keys: Hoffmann 1935; Howden 1968b. Larvae: Ritcher 1966.

Trigonopeltastes Burmeister 1840
Archimedii Kirby 1827 (*nomen oblitum*)
Euclidii Kirby 1827 (*nomen oblitum*)
Roplisa Casey 1909
This genus has 15 species distributed in Mexico and Central America. Six species are found in the Nearctic realm, and two species, *T. delta* (Forster) and *T. floridana* (Casey), are found in the southeastern United States. Key: Howden 1968b. Larvae: Ritcher 1966. (Volume 1, Color Figure 12).

Valgini Mulsant 1842

Characteristics: Antennal insertion visible from above. Pronotum narrower than elytra and most with 2 distinct, parallel, longitudinal ridges. Posthumeral elytral emargination absent. Mesepimeron not visible in dorsal view. Propygidium and pygidium exposed. Metacoxae widely separated. Protibia with 5 teeth. Body size small, generally less than 10 mm.

The tribe Valgini consists of 33 genera found nearly worldwide. One genus, *Valgus*, is found in the Nearctic region. Key: Krikken 1978. Overview: Arrow 1944.

Valgus Scriba 1790
Acanthurus Kirby 1827
Homovalgus Kolbe 1897
The genus *Valgus* (Fig. 104) contains about 11 species in the Oriental, Palearctic, and Nearctic regions, and five species, including an adventive one from Europe, are found in the eastern United States and California. Most species seem to be

termitophilous. *Valgus canaliculatus* (Olivier) adults are found on flowers nectar-feeding in late spring and again in late summer, and their larvae and pupae are found in termite galleries of soft-wood logs. Keys: Casey 1915; Cazier 1937. Larvae: Ritcher 1966.

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