VOLUME 1

AMERICAN BEETLES

Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia

Ross H. Arnett, Jr. • Michael C. Thomas

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The late Ross H. Arnett, Jr.
and
Michael C. Thomas

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To Ross H. Arnett, Jr.
1919-1999

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to replace Bradley's *A Manual of the Genera of Beetles of America, North of Mexico*, which itself was some 30 years out of date in 1960.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 will appear 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
September 15, 2000

Acknowledgments

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. 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 Michigan State University for *The Beetles of the United States*.

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. Since Ross' death, she has 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.

And I would like to 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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Family 8

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Table of Contents

Introduction

The beetles comprise the largest and most diverse order of life on Earth. Beetles occupy almost every conceivable habitat except for the purely marine. The immense number of species and great diversity have resulted in an equally immense literature that can be daunting even to the professional systematist. Relatively few works have attempted to treat the entire Order Coleoptera, and then usually only for a restricted geographical area or at the family level only. One of those few was Ross H. Arnett, Jr.'s *The Beetles of the United States (A Manual for Identification)*, published in fascicles from 1960 to 1963 and then reprinted in 1963, 1968, 1971, and 1973. It has been out of print for many years.

This publication is a direct descendant of that volume and attempts to build on that work and to bring it up to date with current thoughts on the classification of the Coleoptera and recent phylogenetic analyses.

The area covered by this publication is North America, minus the Nearctic area of Mexico. The classification adopted here is that of Lawrence and Newton (1995) with the exception that Bruchidae are treated here as a full family rather than as a subfamily of the Chrysomelidae. This first volume covers the suborders Archostemata, Myxophaga, and Adephaga, plus the series Staphyliniformia of the suborder Polyphaga. The second volume includes the family keys and covers the remainder of the Polyphaga. Much of the following introductory material is adopted from Arnett (1960-1963).

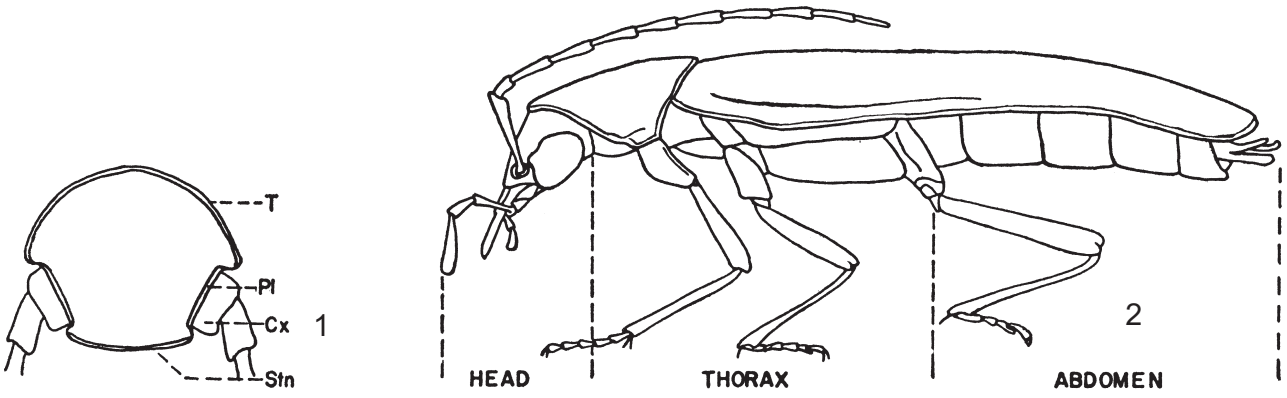
Family treatments

The family chapters have a consistent format and are arranged as follows:

Family name, author, date
Common name
Synonymy
Diagnosis
Description (shape, size, color, vestiture, head, antennae, mouthparts, eyes, thorax, legs, elytra, wings, abdomen, male and female genitalia, larvae)
Habits and habitats
Status of the classification
Distribution and number of species
Key to the genera of the United States
Classification of the genera of the United States
Bibliography

The family names are those used by Lawrence and Newton (1995). The common name has been selected by the individual authors, or based on common usage, or because they were used in Arnett (1960-1963). The common name is to be applied to the family and not to individual species that are already named in the common name list published by the Entomological Society of America. In this sense, then, it is believed that they are appropriate, and may be useful in certain works, i.e., works of a popular nature, or occasionally in titles of reports, and the like, directed to the general public.

The general features particularly useful for the spot identification of a member of a family are given as a diagnosis to the recognition of a group. This will help in determining if a specimen has been keyed to the proper family. There then follows a partial description of the family as a whole. This is the most useful section of the book because it attempts to define a family,



FIGURES 1-2. Fig. 1, cross-section of hypothetical arthropod segment; Fig. 2, *Oxacis taeniata* (LeConte), lateral view, showing tagmata (Oedemeridae).

not simply to distinguish a family. At the same time, it is recognized that these definitions are often incomplete. It is hoped that these descriptions will provide the basis for further, more complete and comprehensive descriptions. Meanwhile their usefulness will be a further aid in checking identifications to family. They will provide the user with some idea of the range and variety of structures in a family. Caution must be exercised, however. The assumption that a particular structure is not found in a family should be made only after a careful evaluation of all of the features discussed in the description.

Ecological information about beetles still is distressingly limited. A large volume of the literature, plus the field experience of the authors, have been condensed into this brief section of the family characterization. Many specialists have a wealth of information on the habits and habitats of beetles which they have not made available in published form. They should be urged to publish these data piecemeal if necessary so that a permanent record is available to future students. Also many of the published statements should be reexamined for accuracy, and erroneous notions be eliminated from the literature wherever possible.

The status of the classification is given as an aid for the evaluation of the work accomplished to date on the family and an indication of research yet to be done. Obviously, revisions that are now underway, but as yet unpublished, will outdate these comments. Where it is known that studies are underway, this is indicated. Also, a brief history of the group is included, and suggestions are sometimes given for possible further studies. When determinations are being made, these comments should be kept in mind.

Most families have a worldwide distribution, but often groups are more concentrated in certain areas. This is indicated, along with estimates on the size of the family for the world and the approximate number of species found in the United States.

The keys to the genera have been compiled by the individual authors, some are modified from those used by Arnett (1960-1963); many are original. In all cases, the keys have been brought up to date by the inclusion of new genera and genera new to the United States.

The classification of the genera proposed here is not to be construed as final in any sense.The number of species occurring in the United States is indicated for each genus, and a brief summary of the range of the genus is given. This will be an aid in the identification of specimens. Those genera with only one species have included also the name of the species. It is possible to make some specific determinations with this manual because of this, but before the determination is accepted, a description of the species should be consulted.

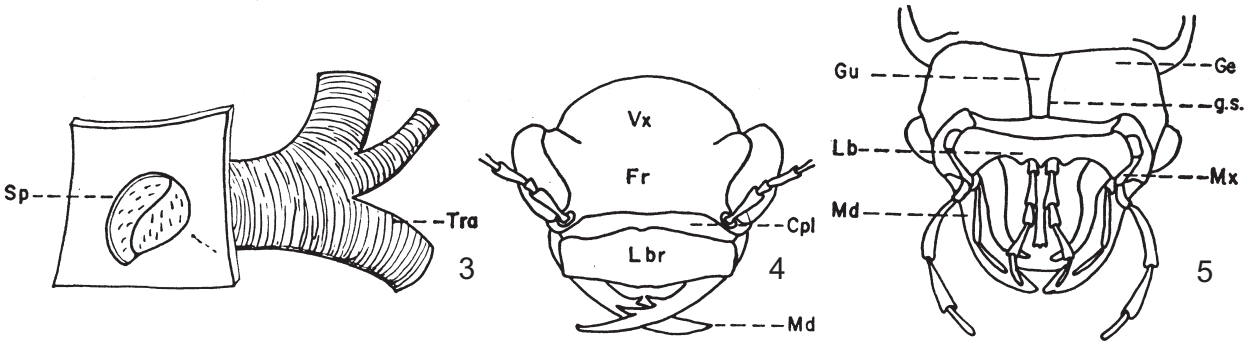
A major change from Arnett (1960-1963) is the addition of a detailed bibliography with each family. The completeness of the bibliographies varies from family to family, but at a minimum they provide an entry into the literature on the family. It is sincerely hoped that there are no serious omissions.

Keys for the identification of organisms, at best, are only guides. As a practical method, the use of external anatomical characters in keys has served us admirably as a means of identification of specimens. Some of the more obvious anatomical features of the various classification groups have been singled out and organized into what we call "keys." These keys are intended to be a short cut to the literature on a particular group by giving us a classification name. The keys on the following pages are meant for this purpose alone and do not reflect the natural classification of the group. It is not possible, under present circumstances, to write "perfect" keys. Not enough is known about a given group, especially at the family level. Mistakes will be found in these keys, as well as any other key. If this were not so, there would be no need for this book. We would be using the "perfect" one already available.

For those who have not had previous experience in using keys for identification, the following brief explanation should suffice. A key is an elimination device. The numbered sections are couplets, or sometimes triplets.

The external anatomy of adult beetles

For practical reasons, the foundation upon which classification is based is anatomy, even though as many biological features as possible are also employed. Each group of animals has its



FIGURES 3-5. Fig. 3, section of body wall showing spiracle and tracheae, diagrammatic; Fig. 4, head of *Cicindela* sp. (Carabidae), anterior view; Fig. 5, head of Carabidae, ventral view.

own set of terms peculiar to the anatomy of the group, as well as a number of terms that are common to many groups. It is necessary to have a good working background in beetle anatomy in order to understand the classification and identification descriptions of the beetles discussed in the following sections.

It must be borne in mind that even though the homologies of insect parts have been worked out fairly well, the names used in various groups for various parts have been handed down to us before these homologies were recognized. Therefore, it is frequently more convenient to use the terms as they are found in the early literature rather than to attempt to bring all morphological terms into uniformity. Also, the names for these parts are, even today, likely to change as our knowledge increases with further morphological study.

The following discourse on the external anatomy of beetles is not intended to be anything other than a brief introduction to "traditional" beetle structure, mainly those features generally used in identification keys.

Like all arthropods, the body of a beetle is segmented with a hard exoskeleton. This integument is composed of sclerites or plates separated by a suture, a thin, flexible groove in the exoskeleton. The fundamental pattern of a segment is four sclerites arranged in a ring, the dorsal *tergum* (Fig. 1, T), lateral *pleura* (Fig. 1, Pl), and a ventral *sternum* (Fig. 1, Stn). Various segmented appendages are found on some of the segments located on the pleuron, e.g., the *coxa* (Fig. 1, Cx). This plan is the same from segment to segment and from group to group, but varies in detail.

Beetles have six legs in the adult stage, and the body is divided into three parts: the head, the thorax, and the abdomen (Fig. 2). They breath by means of *tracheae* (Fig. 3, Tra), a series of ramifying tubes which run throughout the body much the same as arteries do in vertebrate animals. The entrance to these tubes is a valve-like arrangement under muscular control, the *spiracle* (Fig. 3, Sp). By means of this respiratory system there is an exchange of the gasses, oxygen and carbon dioxide, with the cells and the external atmosphere. In addition, beetles have one pair of antennae, usually two pairs of wings, and the external organs of copulation near the posterior or caudal end of the body. These characteristics they share with almost all other insects. The following anatomical details will serve to characterize the order Coleoptera and serve to separate this order from the other insects.

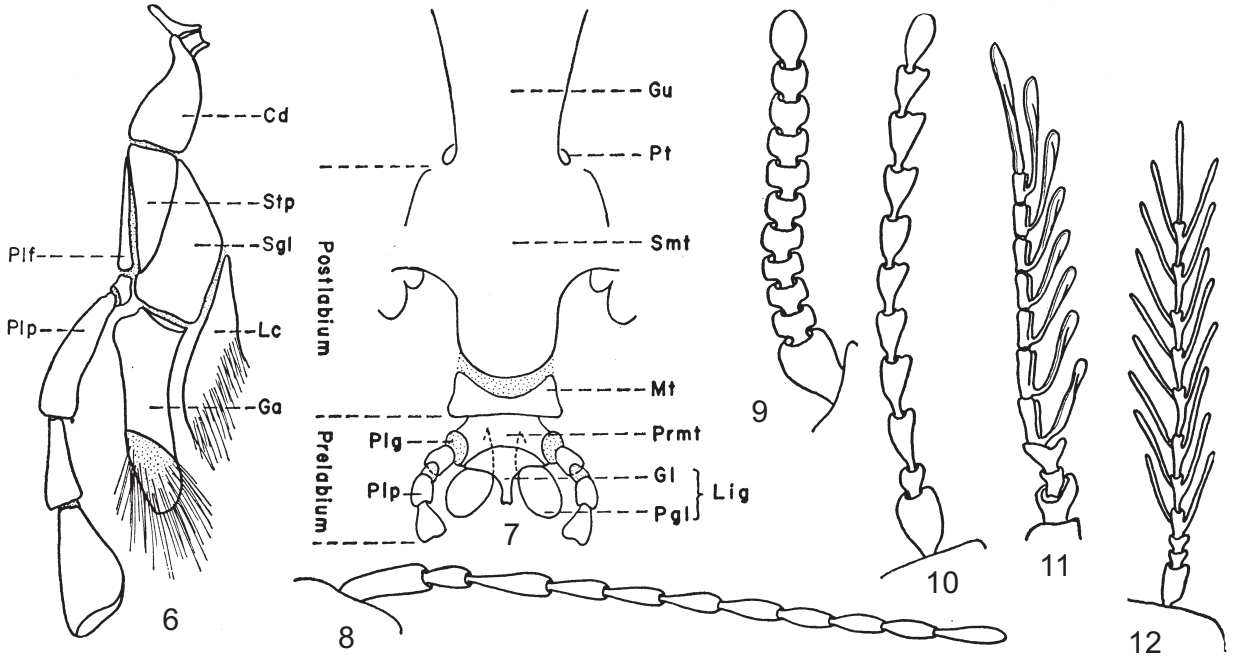
Head, thorax, and abdomen

The head and its appendages

The anterior portion of the body is the head. It varies greatly in form, and is joined to the prothorax by a membrane. It is always sunken into the prothorax which covers it to a varying degree. Usually the hind portion is but slightly narrowed; sometimes the part behind the eyes is suddenly narrowed and constricted, forming a neck, or gradually narrowed and much prolonged. One large group commonly known as the snout beetles (Curculionidae) have the head elongate in front of the eyes. This is not definitive for this group; however, for some of the snout beetles do not have snouts, and almost every other major group throughout the order have one or two genera which have the head prolonged into a snout.

The top surface of the head is called the *vertex* (Fig. 4, Vx). In other insects the head may be composed of several sclerites limited by distinct sutures. In some beetles (e.g., Hydrophilidae) there may be secondary folding which gives the appearance of sutures, but these are not true sutures and are not homologous with those of other insects. Below the vertex is the *frons* (Fig. 4, Fr) and attached to the frons is the *clypeus* (Fig. 4, Clp) to which is attached the *labrum* (Fig. 4, Lbr), the dorsal movable, flap-like covering of the mouthparts. Usually the clypeus is not separated from the frons by a distinct suture, but often there is a line which may be called the epistomal sulcus.

On the under surface of the head in many species there are two grooves, or sutures, which interrupt the *genae* (Fig. 5, Ge). These are the *gular sutures* (Fig. 5, g.s.) and the area between these is the *gula* (Fig. 5, Gu). This sclerite is interposed between the labium and the *foramen magnum* in beetles. Sometimes the two sutures are joined on the median line so that the gula is no longer evident. This characteristic is used in identifying certain groups and is especially characteristic of the snout beetles mentioned above. The head bears the antennae, the eyes, and the mouthparts.



FIGURES 6-12. Fig. 6, maxilla of *Sisenes championi* Horn (Oedemeridae); Fig. 7, labium of *Sisenes championi* Horn (Oedemeridae), ventral view; Fig. 8, filiform antenna, *Harpalinus* sp. (Carabidae); Fig. 9, moniliform antenna of *Clinidium sculptiltis* Newm. (Rhysodidae); Fig. 10, serrate antenna of *Ctenicera* sp. (Elateridae); Fig. 11, pectinate antenna of *Calochromus* sp. (Lycidae); Fig. 12, bipectinate antenna of *Pityobius* sp. (Elateridae).

Eyes. The eyes show comparatively little variation throughout the order. They differ in size and shape, usually round or oval, sometimes kidney-shaped, or sausage-shaped, and rarely absent. In a few groups, the eyes are divided so that they form four eyes. This is characteristic of one family, the Gyrinidae, and some genera of several other families. Ocelli are rarely present in the adult (see Staphylinidae and Dermestidae).

Mouthparts. The mouthparts are similar to those of the grasshopper, but the various parts show considerable variation throughout the order and have been used by early workers as a basis for the classification of beetles. The position of the parts is referred to morphologically, the assumption being that the head is segmented from anterior to posterior, even when it is hypognathus.

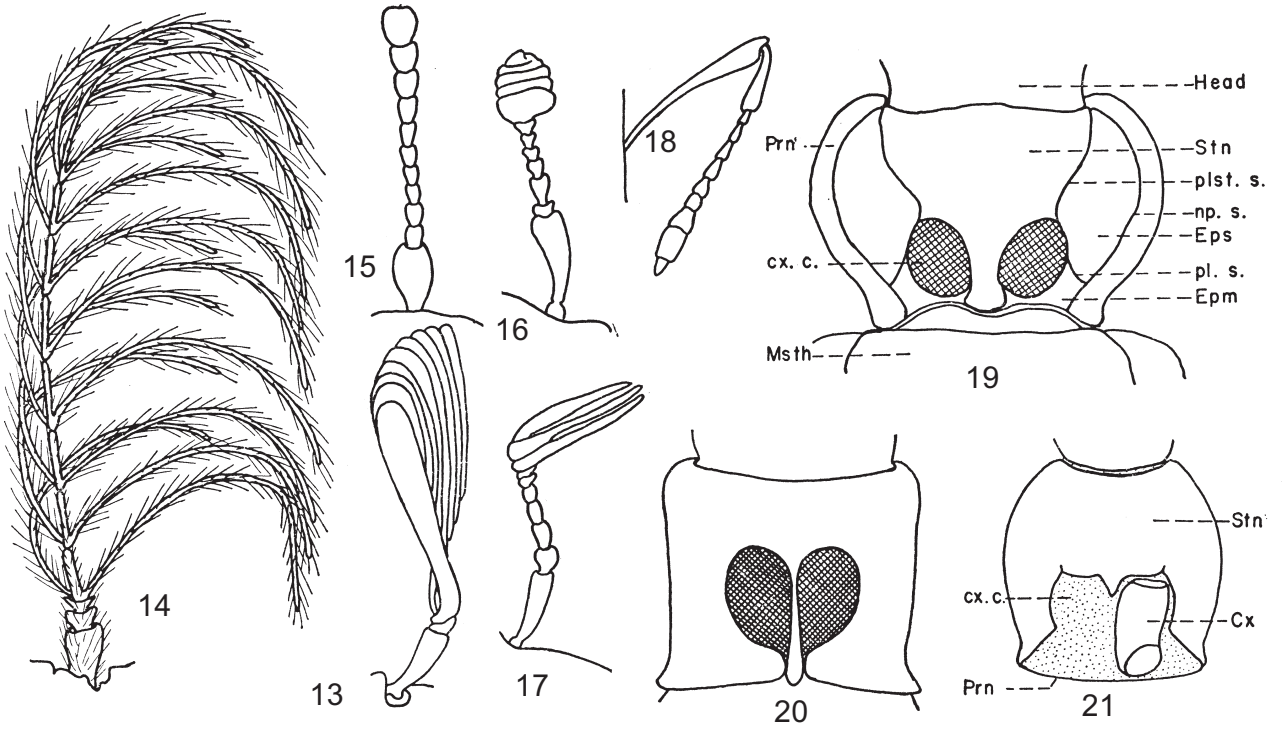
Anterior to the mouth opening is a small, more or less transverse, piece: the labrum mentioned above. It is variable in form, and is in nearly all of the families distinctly visible. It may, however, be solidly united with the clypeus, or retracted beneath it. In the snout beetles, except for some groups, it is entirely absent.

Immediately posterior to the labrum are the *mandibles* (Fig. 4, Md). They also vary much in shape and size but are usually curved, often toothed on the inner side, and, in the males of certain Lucanidae, they are long and branched like the antlers of a deer. In some, they are partly membranous, and in one group, the beaver parasites, they are atrophied. The motion of the mandibles is from side to side. They are used to grasp and crush the food, often as defense organs, and rarely as clasping organs.

Posterior to the mandibles is a second pair of horizontally moving pieces, the *maxillae* (Fig. 5, Mx). They are of complex structure and are of importance in the classification of certain groups. The basal portion of the maxilla is composed of four pieces: the first articulates with the side of the head near the labium, the *cardo* (Fig. 6, Cd); the second is the *stipes* (Fig. 6, Stp) and articulates, usually, at a more or less acute angle with the first; the third, which lies on the inner side of the stipes is the *subgalea* (Fig. 6, Sgl); and the fourth is the *palpifer* (Fig. 6, Plf) which bears the maxillary palpus. The subgalea bears the *lacinia* (Fig. 6, Lc) which is modified in various ways, sometimes comb-like, sometimes sharp and mandible-like. The *galea* (Fig. 6, Ga), if distinct, is often palpus-like, usually of two segments. The *maxillary palpi* (Fig. 6, Plp) are usually composed of four segments, rarely three-segmented, and in at least one case (the genus *Aleochara*, family Staphylinidae) they are five-segmented.

The development and shape of the maxillae of beetles, as of other insects, depend very largely upon the nature of the food, as those organs serve not only to seize and hold the food in the mouth, but also as accessory jaws, aiding the mandibles in the rendering of the food into a form more suitable for swallowing. Their palpi are not only organs of touch, but in many cases act as hands in prehending and carrying morsels of food to the mouth.

The posterior portion of the mouth, the *labium* (Fig. 5, Lb) has at its base, the *submentum* (Fig. 7, Smt) which is attached to the gula. Distal to the submenturn is another piece, the *mentum* (Fig. 7, Mt). These two sclerites together comprise the *postlabium* (Fig. 7) or, as it is sometimes called, the *postmentum*. The apical portion



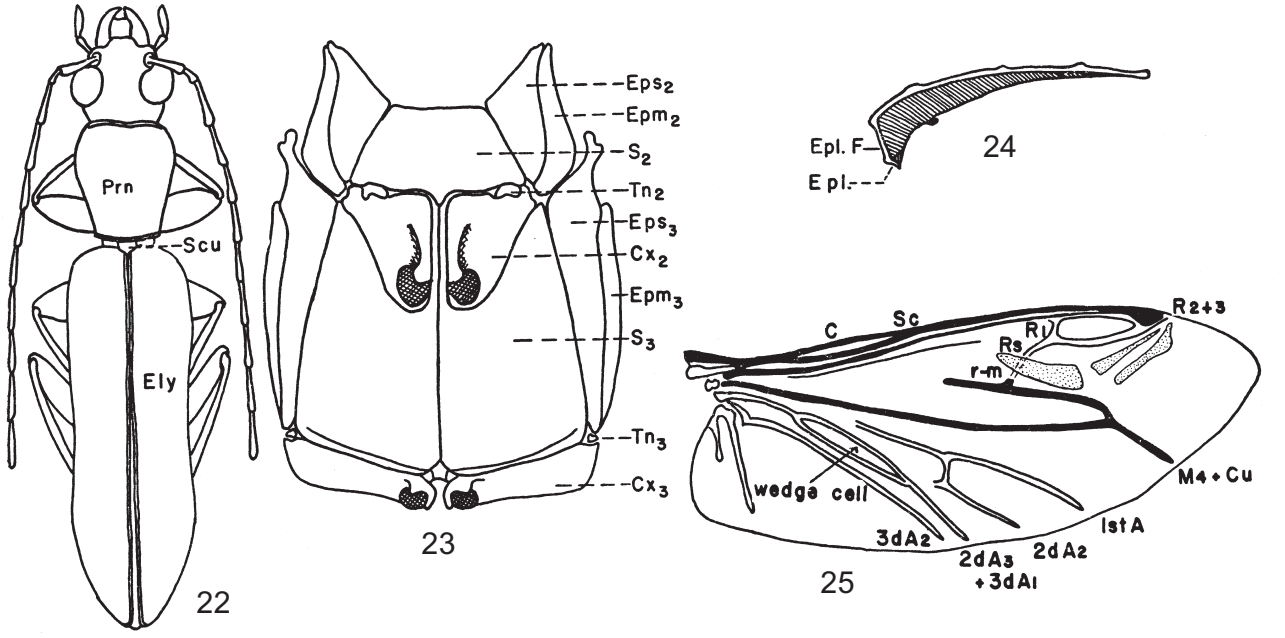
FIGURES 13-21. Fig. 13, flabellate antenna of *Sandalus* sp. (Rhipiceridae); Fig. 14, plumose antenna of *Phengodes* sp. (Phengodidae); Fig. 15, clavate antenna of *Ostoma* sp. (Trogossitidae); Fig. 16, capitate antenna of *Nicrophorus* sp. (Silphidae); Fig. 17, lamellate antenna of *Phyllophaga* sp. (Scarabaeidae); Fig. 18, geniculate antenna of *Rhyssematus* sp. (Curculionidae); Fig. 19, prothorax, ventral view, of *Patrobus* sp. (Carabidae); Fig. 20, prothorax, ventral view, of *Statira* sp. (Tenebrionidae); Fig. 21, prothorax, ventral view, of *Dendroides* sp. (Pyrochroidae).

of the labium is, in the primitive forms, divided into three pieces, a basal portion, the *prementum* (Fig. 7, Prmt), a central portion composed of two lobes, the *glossae* (Fig. 7, Gl), and two side-pieces, the *paraglossae* (Fig. 7, Pgl). The glossae and paraglossae together comprise the *ligula* (Fig. 7, Lig). The *labial palpi* (Fig. 7, Plp) are borne on lobes of the prementum, the palpigers (Fig. 7, Plg). These are similar to the maxillary palpi and are usually three-segmented, but may be reduced to two segments, or less; there are rarely four segments. The entire portion of the labium distal to the mentum is called the *prelabium* (Fig. 7) but this term is not often used in the Coleoptera. There frequently is no suture separating the submentum from the gula, but the two regions may be separated for descriptive purposes by locating the *posterior tentorial pits* (Fig. 7, pt). A line drawn between these pits separates the two regions.

Antennae. The antennae of beetles are borne at the side of the head, usually between the eyes and the base of the mandibles, but the position is variable, depending on the group. The size and shape of the antennae are exceedingly diverse, almost every type of antennae found in the insect class is represented in this single order. The number of segments also varies depending on the species. The usual number is 11, and in rare cases 12 segments may be present by the division of the apical segment into two apparent segments which are rarely freely articulated. In a few cases, the number of segments may be thirty or more and vary somewhat with individuals.

The principal forms of the antennae are defined below (figs. 8 to 17). These terms are fairly precise and are extensively used as key characters. The types of antennae are often characteristic of families. Some of the often used terms are defined as follows:

1. **Filiform** (Fig. 8): the simplest form, thread-like, the segments are cylindrical and uniform in shape, or nearly so.
2. **Moniliform** (Fig. 9): bead-like, the segments are nearly uniform in size and rounded, thus resembling a string of beads.
3. **Serrate** (Fig. 10): saw-like, the segments are triangular and compressed.
4. **Pectinate** (Fig. 11): comb-like, the segments are short with the front angles of each much prolonged.
5. **Bipectinate** (Fig. 12): each segment has a comb-like tooth on each side.
6. **Flabellate** (Fig. 13): fan-like, the prolongations of each segment are long and fold together like a fan.
7. **Plumose** (Fig. 14): feather-like, the prolongations are long, slender, and flexible.
8. **Clavate** (Fig. 15): the outer segments are gradually enlarged, forming a distinct club.
9. **Capitate** (Fig. 16): some of the apical segments separated into a round or oval part, distinct from the basal segments.
10. **Lamellate** (Fig. 17): the outer segments are flattened plates which are capable of close approximation, forming a special type of club.



FIGURES 22-25. Fig. 22, *Oxacis xerensis* Arn. (Oedemeridae), dorsal view; Fig. 23, pterosternum of *Sisenes championi* Horn (Oedemeridae); Fig. 24, cross-section view of elytra looking toward the anterior articulation, diagrammatic; Fig. 25, *Sisenes championi* Horn (Oedemeridae), wing.

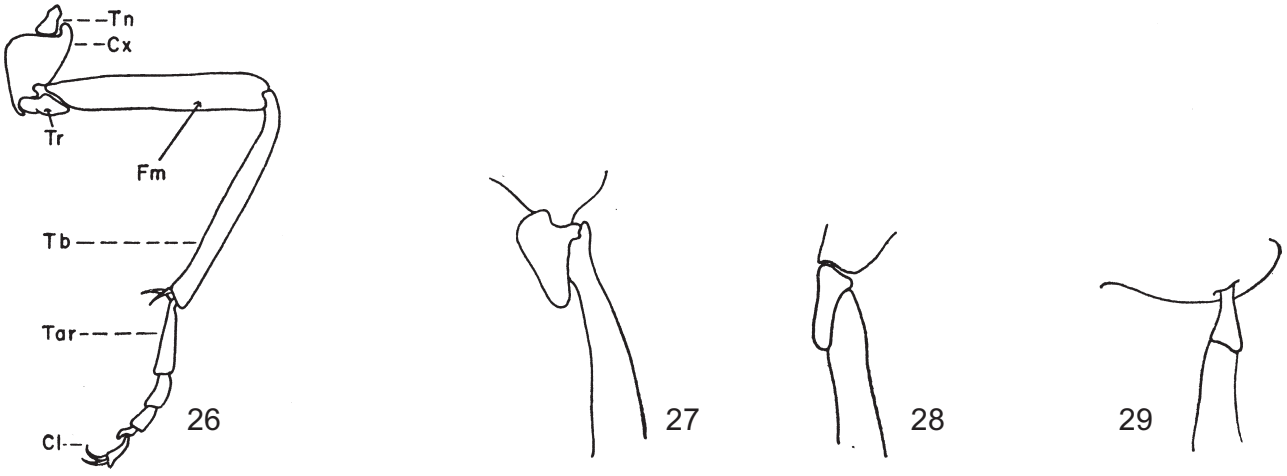
The antennae are said to be *geniculate* (Fig. 18) or elbowed when the second segment is attached to the first in such a way as to make an obtuse angle, the segments after the second following the same line as the latter. In this form the first or basal segment is usually much longer, and is called the scape. When the geniculate form is at the same time capitate, the segments intermediate between the scape and the club form the *funicle* (Fig. 16).

The antennae of beetles are supposed to be primarily organs of smell, but they also bear organs of touch. In a number of species they are put to other uses. Certain Cerambycidae use the antennae as balancing poles, much the same as a tightwire walker. Many aquatic species use the antennae for gathering in air and passing it under the body for storage while submerged. The males of some of the blister beetles use the antennae as clasping organs. Some species have been observed using their antennae as defense organs, flailing their opponents unmercifully, or others use them in the same manner during courtship procedures.

The thorax and its appendages

The thorax, the middle portion of the beetle body, is divided into three segments, the first of which is always distinct, the other two, the pterothorax, are more or less firmly united. The prothorax, or first thoracic segment, has as appendages only the front legs. The head is attached to the front part over which it may project to varying degrees, sometimes hiding the head entirely from view from above. Located between the head and the thorax, in the neck region are, in most species, two pairs of articulating sclerites, the cervical sclerites, the exact nature of which remain obscure. The prothorax is often freely movable, or it may be firmly united with the other two thoracic segments. The dorsal surface of the segment is called the *pronotum* (Fig. 22, Prn). Its shape and modifications are very frequently used as specific, generic, and even family characters. Beneath are attached the front or fore legs. The method and position of attachment of these legs serve as useful characters in separating genera and families. Often there are grooves present on the underside of the prothorax for the reception of the antennae, legs, and rarely, the mouthparts. The lateral part of the lower surface of the prothorax is called the *propleura* (Fig. 19); the central portion, the *prosternum* (Fig. 19, Stn). The pleural region is separated from the tergum by the *notopleural suture* (Fig. 19, np. s.) and the sternum by the *pleurosternal suture* (Fig. 19, plst. s.). The presence or absence of lobes, ridges, etc. on the intercoxal piece of the prosternum (also called the *spinasternum*) is useful in beetle classification. When the propleurae have a *pleural suture* (Fig. 19, pl. s.) dividing them into two sclerites, the anterior sclerite is called the prosternal *episternum* (Fig. 19, Eps). The posterior sclerite is the prosternal *epimeron* (Fig. 19, Epm). More frequently, all of these sclerites are solidly fused to the pronotum; in which case, the lower surface is simply referred to as the prosternum. Members of the suborder Adephaga have a distinct suture separating the protergal region from the pleural region of the prothorax, the *notopleural suture* (Fig. 19, np. s.).

The cavities in which the anterior legs are inserted are called anterior coxal cavities. An extremely useful, but difficult character is to be found in the relationship of the sclerites which surround the coxal cavities. If they are enclosed behind by the junction of the prosternum and the epimeron, or by the meeting of the epimera, they are referred to as "anterior coxal cavities closed behind" (Fig. 20). If there is no sclerite exposed behind the coxal cavities, but rather, the cavities open directly on the next thoracic segment, they are referred to as "anterior coxal cavities open be-



FIGURES 26-29. Fig. 26, *Sisenes championi* Horn (Oedemeridae), middle leg; Fig. 27, *Nebria* sp. (Carabidae), hind leg, part; Fig. 28, *Chauliognathus pennsylvanicus* (DeGeer) (Cantharidae), middle leg, part; Fig. 29, *Lyctus* sp. (Bostrichidae), hind leg, part.

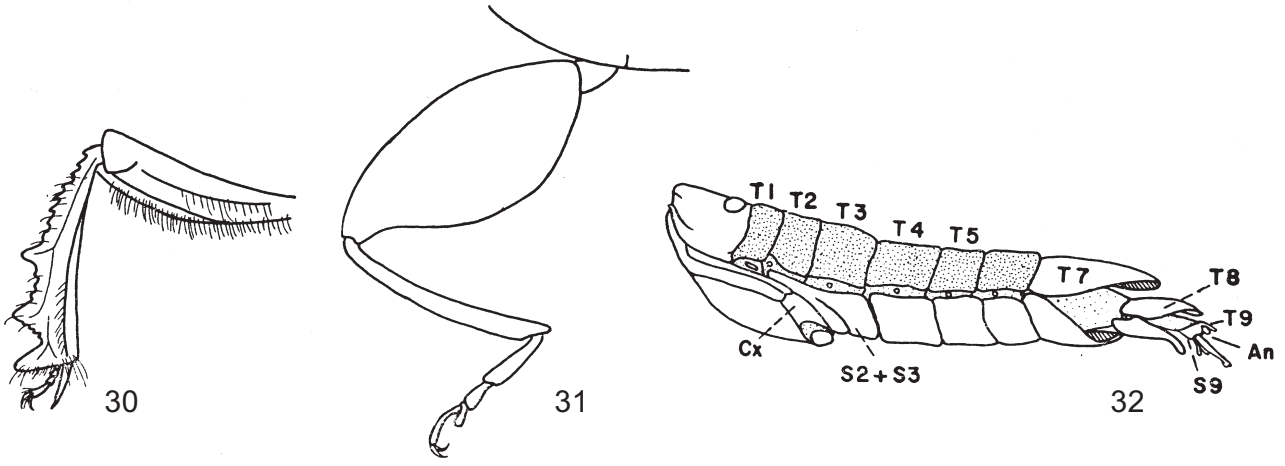
hind" (Fig. 21). These two conditions serve to distinguish families, subfamilies, and tribes.

The middle thoracic segment, or mesothorax, bears the middle pair of legs and the anterior pair of wings, which in beetles are hardened, or leathery and are called *elytra* (singular *elytron*) (Fig. 22, Ely). The dorsal surface is hidden by the elytra when they are in repose, except for a small shield-like portion, appropriately called the *scutellum* (Fig. 22). The scutellum, the shape of which is very useful in distinguishing some genera or groups of genera, is always located immediately behind the pronotum, between the elytra. It varies considerably in size and shape and is rarely entirely hidden. The lower surface of the *mesothorax*. (Fig. 23) has essentially the same parts as the prothorax, which are distinguished by adding the prefix meso- to the terms *episternum* (Fig. 23, Eps_2), *epimera* (Fig. 23, Epm_2) and *sternum* (Fig. 23, S_2). The mesothorax is firmly united to the last thoracic segment, sometimes without distinct sutures separating the two segments. The characters offered by this thoracic segment are rarely used in the classification of the groups. The location of the middle *coxae* (Fig. 23, Cx_2) is the best criterion for determining the posterior limit of the mesothorax. The mesocoxal cavities are always closed behind by the metasternum. There can sometimes be located a small *trochantin* (Fig. 23, Tn_2) on the middle coxae.

The hind thoracic segment, the *metathorax*, bears the flight wings, which are usually present, and the hind pair of legs. The most important characters are to be found in the manner of insertion of the hind legs, and in the shape, position, and modifications of the posterior portion of the *metepimeron* (Fig. 23, Epm_3). The exposed portion of this sclerite is usually a small plate lying at the lateral extremities of the *metacoxae* (Fig. 23, Cx_3), the remaining portion is hidden by the elytra. The *metepisternum* (Fig. 23, Eps_3) is a long sclerite lying lateral to the long and broad *metasternum* (Fig. 23, S_3). The hind coxae are usually transverse. A small sclerite lateral to the coxae and articulating with the metepisternum, the *trochantin* (Fig. 23, Tn_3) is sometimes evident. These sclerites are modified by the general shortening of the metathorax in wingless forms. A transverse sclerite is sometimes formed by the presence of a sulcus anterior to the coxae. This is also referred to as the antecoxal piece (see especially Carabidae).

Wings. The anterior *wings* (elytra, Fig. 22, Ely) of Coleoptera are greatly modified as protective covers for the hind wings. Usually they are hard or horny, sometimes soft, but always opaque. They are held side by side over the abdomen, and the morphological hind edges generally join forming a median line along the abdomen. When the elytra are in repose this junction point along the hind edge is termed the suture. The morphological front edge is called the lateral margin, and the inflexed portion of the elytra, that is, the portion of the elytra along the lateral margin which is bent down, is called the *epipleural fold* (Fig. 24, Epl. F). Bordering the inner edge of this is a piece of varying width, sometimes extending from the base to the apex, called the *epipleura* (Fig. 24, Epl). The elytra usually cover most of the abdomen and often extend slightly beyond the apex. In one large group, in particular, the Staphylinidae, and in many other widely separated groups, the elytra are shortened, exposing several of the abdominal segments. In a few groups the elytra are small, fleshy flaps (Rhipiphoridae and Stylopidae). Striae and intervals, as well as costae are present on many elytra and are useful characters for identification.

The posterior wings, or flying wings are membranous with supporting structures, called *veins* (Fig. 25), crossing their surface. These veins are so constructed as to allow the wings to be folded under the elytra when they are not in use. Both the arrangement of the veins and the folding patterns of the wings are uniform for a given taxon. This is best described by Forbes (1922 and 1926). However, the characters furnished by the flying wings are difficult to use, and are seldom employed in the characterization of species or genera. They are rarely used in descriptions. The flying wings are lacking in many desert and cave species, in which case, the metathorax is short, and the elytra closely united or connate.



FIGURES 30-32. Fig. 30, foreleg of *Canthon* sp. (Scarabaeidae); Fig. 31, hind leg of *Disonycha* sp. (Chrysomelidae); Fig. 32, male abdomen of *Sessinia decolor* (Fairmaire) (Oedemeridae) (redrawn from Arnett, 1949).

Legs. The fundamental structure of insect legs consists of six parts, the trochantin, coxa, trochanter, femur, tibia, and tarsus. This is fairly uniform throughout the class. The *trochantin* (Fig. 26, Tn) is a small sclerite at the base of the coxa, usually partly hidden, or entirely hidden by the base of the coxa when the leg is in normal position. The *coxae* (Fig. 26, Cx) vary considerably in shape. They may be round, oval, elongate, conical, or rarely cylindrical. Inserted between the coxa and the femur is a small piece called the *trochanter* (Fig. 26, Tr). Its point of attachment is a useful character in classification. There are four types of trochanters in beetles. In the Caraboid type (Fig. 27) the trochanter of the hind leg lies entirely to one side of the femur. In the "normal" type, the trochanter is triangular (Fig. 28) and the femur is attached near the base. In the heteromerous type (Fig. 26, Tr) the femur is attached along the side of the trochanter, and in the elongate type (Fig. 29) the femur is attached to the truncate apex of the trochanter. The *femur* (Fig. 26, Fm) is a large piece, sometimes swollen apically or otherwise modified depending on the species and group. As in grasshoppers those beetles that are good jumpers have a greatly enlarged femur. The *tibia* (Fig. 26, Tb) is more slender, often adorned with spines, particularly at the apex. The presence, absence, or size of these spines is useful in determining groups or species. The *tarsi* (Fig. 26, Tar) are the most useful classification structures of the legs. They are always segmented, and end in *claws* (Fig. 26, Cl). The number of tarsal segments, or tarsomeres, varies from one to five, depending on the group, or sometimes, the sex. The early classifications were dependent on the number of tarsomeres, and family groups were named according to their number. It is now believed that the tarsal formula is not really basic to the classification. The number of tarsomeres is always constant for a particular genus or higher group. The number of tarsomeres for the different pairs of legs may also vary. These numbers are expressed as tarsal formulae in this manner. If the front tarsi have five segments, the middle tarsi five segments, and the hind tarsi four segments, the formula is written in this form: 5-5-4. Or further reductions, or arrangements thus: 5-5-5, 4-4-4, 5-4-5, etc. This is extremely useful and is employed in all family keys. The tarsomeres vary greatly in shape, some may be lobed beneath, some may have spongy or brushlike pads beneath, or the length of each tarsomere in relation to the length of another tarsomere may be quite different.

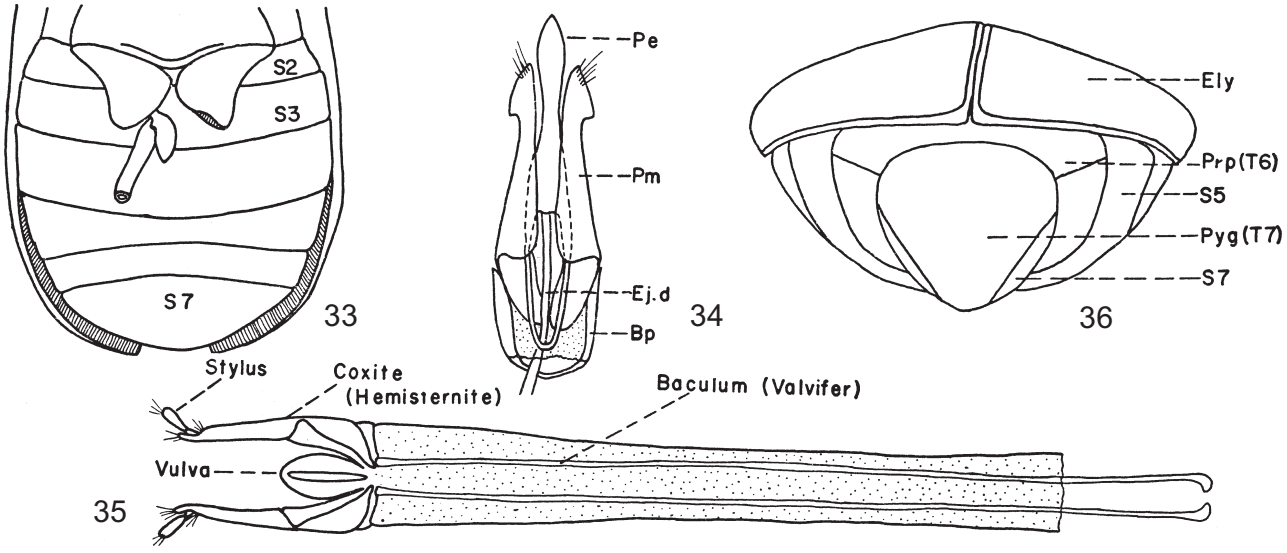
The claws are attached to the apex of the last tarsomere and are paired. The shape of an individual claw may differ on different legs, or different groups. Some are toothed, cleft, serrate, comb-like, bifid, or with ventral pads. However, the usual condition is simple, i.e., unmodified, without the forementioned characteristics. These differences are always used for the separation of species, genera, and whenever possible, even families because such characteristics are not variable with individuals. When the claws are capable of being drawn back upon the last tarsal segment, they are chelate, a condition often found in the family Scarabaeidae. Sometimes there may be a small pad, or a hair, between the claws, but this is not often a useful descriptive character.

In some descriptions the legs are given various names according to their form. Legs fitted for walking are termed ambulatorial (Fig. 2); digging, fossorial (Fig. 30); swimming, natatorial (Fig. 47) (this term is rarely used); jumping, saltatorial (Fig. 31). A few others similarly designate the particular function, but are rarely used.

Abdomen

The portion of the body behind the metathorax, the *abdomen* (Fig. 32), is a series of rings, or partial rings, each ring with a pair of *spiracles* (Fig. 3, Sp), the openings to the *tracheae* (Fig. 3, Tra). There are no abdominal appendages, but some species may have articulating sternal lobes (see Mordellidae).

Each segment of the abdomen shows the four fundamental sclerites: the tergum, the pleura, and the sternum (Fig. 1). The tergum is usually soft and more or less membranous except for one or two (sometimes more) apical tergites. The pleura are very small and are usually more or less hidden. Each pleuron has a



FIGURES 33-36. Fig. 33, ventral view of abdomen of *Nebria* sp. (Carabidae); Fig. 34, dorsal view of male genitalia of *Melanotus* sp. (Elateridae); Fig. 35, ventral view of ninth segment (female genitalia) of *Melanotus* sp. (Elateridae); Fig. 36, posterior view of abdomen of *Saprinus* sp. (Histeridae).

spiracle opening on its surface. Often the pleura are fused with the sternum so that the spiracle appears to be on the sternum. The sternum is a more or less heavily scleritized plate and is the most visible portion of the abdomen, the tergum usually is hidden by the wings and elytra except when the beetle is in flight position.

The usual number of abdominal segments is nine. This may be demonstrated by counting the pairs of spiracles, and counting the terga. The first spiracle is large, the ninth is usually very obscure or absent. There are often only five abdominal sterna visible. The first abdominal sternum is absent or fused with the metasternum of the thorax. The second and third sterna are usually fused and appear as one. In the suborder Adephaga, the second sternum is visible as two triangular pieces lying at the side and in front of the third *sternum* (Fig. 33). The eighth sternum is usually visible, but partly drawn into the seventh segment. The ninth abdominal segment is usually invisible, being covered by the eighth abdominal segment. Often both the eighth and ninth segments are modified in various ways and function as a part of the copulatory organs. The last visible abdominal tergum is referred toas the *pygidium* (tergum 7) (Fig. 36, Pyg), and the next to the last is the *propygidium* (Fig. 36, Prp) (tergum 6).

The genitalia (*aedeagus*) of the male consists of two parts: the intromittent organ, the *penis* (or median lobe), and the *tegmen*, composed of a *pars basalis* and one pair of *parameres* (or lateral lobes) and rarely the *tegminite*. The parameres may be fused to form a single median structure. Four main types of male genitalia (Tuxen, 1956) have been described, of which only one, the trilobate type (Fig. 34), is shown here. There are many variations of these types. The genitalia of the female is a tube composed of the ninth segment, and is poorly known (Fig. 35). These parts have been variously named; the system used by Tanner (1928) differs considerably from that of Lindroth (1957). (See Tuxen, 1956, pp. 69 to 76, and Lindroth, 1957, for further details and a standardized system of nomenclature.)

The genitalia project from the membrane which connects the ninth sternite below the anus, the terminal opening of the alimentary tract, and the tenth sternite. The tenth sternite is rarely visible as a scleritized structure in insects. The tenth tergite has been demonstrated only in a few groups (Arnett, mss.). It is believed, however, that in the primitive insect form there were ten or more abdominal segments. This is borne out by the form of the abdomen in many primitive existing insects. In many groups the male genitalia are extremely useful for separating species and higher categories. The female genitalia have been studied at the family level, but only a few papers have been published using the female genitalia as the basis for the separation of species (e.g., Arnett, 1944).

Classification

Order Coleoptera Linnaeus 1758

(**Note:** *Families surrounded by brackets ({ }) are not known to occur in the area covered by this book. They are listed here but not further treated.*)

Suborder **ARCHOSTEMATA** Kolbe, 1908
- Family 1. **CUPEDIDAE** Laporte 1836; The reticulated beetles
  - {Ommatidae Sharp and Muir 1912}
  - {Crowsonellidae Iablokoff-Khnzorian 1983}
- Family 2. **MICROMALTHIDAE** Barber 1913, The telephone-pole beetles

Suborder **MYXOPHAGA** Crowson 1955
- {Lepiceridae Hinton 1936}
- Family 3. **MICROSPORIDAE** Crotch 1873, The minute bog beetles
- Family 4. **HYDROSCAPHIDAE** LeConte 1874, The skiff beetles
  - {Torridincolidae Steffan 1964}

Suborder **ADEPHAGA** Schellenberg 1806
- Family 5. **RHYSODIDAE** Laporte 1840, The wrinkled bark beetles
- Family 6. **CARABIDAE** Latreille 1802, The ground beetles
- Family 7. **GYRINIDAE** Latreille 1810, The whirligig beetles
- Family 8 **HALIPLIDAE** Aubé 1836, The crawling water beetles
- Family 9. **TRACHYPACHIDAE** C. G. Thomson 1857, The false ground beetles
- Family 10. **NOTERIDAE** C. G. Thomson 1860, The burrowing water beetles
- Family 11. **AMPHIZOIDAE** LeConte 1853, The trout-stream beetles
  - {Hygrobiidae Regimbart 1878}
- Family 12. **DYTISCIDAE** Leach 1815, The predacious diving beetles

Suborder **POLYPHAGA** Emery 1886

Series **STAPHYLINIFORMIA** Lameere 1900

Superfamily **HYDROPHILOIDEA** Latreille 1802
- Family 13. **HYDROPHILIDAE** Latreille 1802, The water scavenger beetles
- Family 14. **SPHAERITIDAE** Shuckard 1839, The false clown beetles
  - {Synteliidae Lewis 1882}
- Family 15. **HISTERIDAE** Gyllenhal, The clown beetles

Superfamily **STAPHYLINOIDEA** Latreille 1802
- Family 16. **HYDRAENIDAE** Mulsant 1844, The minute moss beetles
- Family 17. **PTILIIDAE** Erichson 1845, The feather-winged beetles
- Family 18. **AGYRTIDAE** C. G. Thomson 1859, The primitive carrion beetles
- Family 19. **LEIODIDAE** Fleming 1821, The round fungus beetles
- Family 20. **SCYDMAENIDAE** Leach 1815, The antlike stone beetles
- Family 21. **SILPHIDAE** Latreille 1807, The carrion beetles
- Family 22. **STAPHYLINIDAE** Latreille 1802, The rove beetles

Series **SCARABAEIFORMIA** Crowson 1960

Superfamily **SCARABAEOIDEA** Latreille 1802
- Family 23. **LUCANIDAE** Latreille 1804, The stag beetles
- Family 24. **DIPHYLLOSTOMATIDAE** Holloway 1972, The diphyllostomatid beetles
- Family 25. **PASSALIDAE** Leach 1815, The bess beetles
- Family 26. **GLARESIDAE** Semenovrlan-Shanskii and Medvedev 1932; The glaresid beetles
- Family 27. **TROGIDAE** MacLeay 1819, The skin beetles
- Family 28. **PLEOCOMIDAE** LeConte 1861, The rain beetles
- Family 29. **GEOTRUPIDAE** Latreille 1802, The earth-boring dung beetles
  - {Belohinidae Paulian 1959}
- Family 30. **OCHODAEIDAE** Mulsant and Rey 1871, Theochodaeid scarab beetles
- Family 31. **HYBOSORIDAE** Erichson 1847, The hybosorid scarab beetles

Family 32. **CERATOCANTHIDAE** Cartwright and Gordon 1971, The ceratocanthid scarab beetles
Family 33. **GLAPHYRIDAE** MacLeay 1819, The glaphyrid scarab beetles
Family 34. **SCARABAEIDAE** Latreille 1802, The scarab beetles

Series **ELATERIFORMIA** Crowson 1960
[Podabrocephalidae]
[Rhinorhipidae]

Superfamily **SCIRTOIDEA** Fleming 1821
[Decliniidae Nikitsky *et al.* 1994]
Family 35. **EUCINETIDAE** Lacordaire 1857, The plate-thigh beetles
Family 36. **CLAMBIDAE** Fischer 1821, The minute beetles
Family 37. **SCIRTIDAE** Fleming 1821, The marsh beetles

Superfamily **DASCILLOIDEA** Guérin-Méneville 1843
Family 38. **DASCILLIDAE** Guérin-Méneville 1843
Family 39. **RHIPICERIDAE** Latreille 1834, The cicada parasite beetles

Superfamily **BUPRESTOIDEA** Leach 1815
Family 40. **SCHIZOPODIDAE** LeConte 1861, The schizopodid beetles
Family 41. **BUPRESTIDAE** Leach 1815, The metallic wood-boring beetles

Superfamily **BYRRHOIDEA** Latreille 1804
Family 42 **BYRRHIDAE** Latreille 1804, The pill beetles
Family 43. **ELMIDAE** Curtis 1830, The riffle beetles
Family 44. **DRYOPIDAE** Billberg 1820, The long-toes beetles
Family 45 **LUTROCHIDAE** Kasap and Crowson 1975, The robust marsh-loving beetles
Family 46. **LIMNICHIDAE** Erichson 1846, The minute marsh-loving beetles
Family 47. **HETEROCERIDAE** MacLeay 1825 The variegated mod-loving beetles
Family 48. **PSEPHENIDAE** Lacordaire 1854, The water penny beetles
[Cneoglossidae Champion 1897]
Family 49. **PTILODACTYLIDAE** Laporte 1836, The toe-winged beetles
Family 50. **CHELONARIIDAE** Blanchard 1845, The turtle beetles
Family 51. **EULICHADIDAE** Crowson 1973, The eulichadid beetles
Family 52. **CALLIRHIPIDAE** Emden 1924, The cedar beetles

Superfamily **ELATEROIDEA** Leach 1815
Family 53. **ARTEMATOPODIDAE** Lacordaire 1857, The soft-bodied plant beetles
Family 54. **BRACHYPSECTRIDAE** Leconte and Horn 1883, The Texas beetles
Family 55. **CEROPHYTIDAE** Latreille 1834, The rare click beetles
Family 56. **EUCNEMIDAE** Eschscholtz 1829, The false click beetles
Family 57. **THROSCIDAE** Laporte 1840, The false metallic wood-boring beetles
Family 58. **ELATERIDAE** Leach 1815, The click beetles
[Plastoceridae Crowson 1972]
[Drilidae Blanchard 1845]
[Omalisidae Lacordaire 1857]
Family 59. **LYCIDAE** Laporte 1836, The net-winged beetles
Family 60. **TELEGEUSIDAE** Leng 1920, The long-lipped beetles
Family 61. **PHENGODIDAE** LeConte 1861, The glowworm beetles
Family 62. **LAMPYRIDAE** Latreille 1817, The firefly beetles
Family 63. **OMETHIDAE** LeConte 1861, The false firefly beetles
Family 64. **CANTHARIDAE** Imhoff 1856, The soldier beetles

Series **BOSTRICHIFORMIA** Forbes 1926
Family 65. **JACOBSONIIDAE** Heller 1926, The Jacobson's beetles

Superfamily **DERODONTOIDEA** LeConte 1861
Family 66. **DERODONTIDAE** LeConte 1861, The tooth-necked fungus beetles

Superfamily **BOSTRICHOIDEA** Latreille 1802
Family 67. **NOSODENDRIDAE** Erichson 1846, The wounded-tree beetles
Family 68. **DERMESTIDAE** Latreille 1804, The skin and larder beetles
Family 69. **BOSTRICHIDAE** Latreillew 1802, The horned powder-post beetles
Family 70. **ANOBIIDAE** Fleming 1821, The death-watch beetles

Series **CUCUJIFORMIA** Lameere 1938
- Superfamily **LYMEXYLOIDEA** Fleming 1821
  - Family 71. **LYMEXYLIDAE** Fleming 1821, The ship-timber beetles
- Superfamily **CLEROIDEA** Latreille 1802
  - [Phloiophilidae Kiesenwetter 1863]
  - Family 72. **TROGOSSITIDAE** Latreille 1802, The bark-gnawing beetles
    - [Chaetosomatidae Crowson 1952]
  - Family 73. **CLERIDAE** Latreille 1802, The checkered beetles
    - [Acanthocnemidae Crowson 1964]
    - [Phycosecidae Crowson 1952]
    - [Prionoceridae Lacordaire 1857]
  - Family 74. **MELYRIDAE** Leach 1815, The soft-winged flower beetles
- Superfamily **CUCUJOIDEA** Latreille 1802
  - [Protocucujidae Crowson 1954]
  - Family 75. **SPHINDIDAE** Jacquelin du Val 1860, The dry-fungus beetles
  - Family 76. **BRACHYPTERIDAE** Erichson 1845, The short-winged flower beetles
  - Family 77. **NITIDULIDAE** Latreille 1802, The sap-feeding beetles
  - Family 78. **SMICRIPIDAE** Horn 1879, The palmetto beetles
  - Family 79. **MONOTOMIDAE** Laporte 1840, The root-eating beetles
    - [Boganiidae Sen Gupta and Crowson 1966]
    - [Helotidae Reitter 1876]
    - [Phloeostichidae Reitter 1911]
  - Family 80. **SILVANIDAE** Kirby 1837, The silvanid flat bark beetles
  - Family 81. **PASSANDRIDAE** Erichson 1845, The parasitic flat bark beetles
  - Family 82. **CUCUJIDAE** Latreille 1802, The flat bark beetles
  - Family 83. **LAEMOPHLOEIDAE** Ganglbauer 1899, The lined flat bark beetles
    - [Propalticidae Crowson 1952]
  - Family 84. **PHALACRIDAE** Leach 1815, The shining flower beetles
    - [Hobartiidae Sen Gupta and Crowson 1966]
    - [Cavognathidae Sen Gupta and Crowson 1966]
  - Family 85. **CRYPTOPHAGIDAE** Kirby 1837, The silken fungus beetles
    - [Lamingtoniidae Sen Gupta and Crowson 1969]
  - Family 86. **LANGURIIDAE** Crotch 1873, The lizard beetles
  - Family 87. **EROTYLIDAE** Latreille 1802, The pleasing fungus beetles
  - Family 88. **BYTURIDAE** Jacquelin du Val 1858, The fruitworm beetles
  - Family 89. **BIPHYLLIDAE** LeConte 1861, The false skin beetles
  - Family 90. **BOTHRIDERIDAE** Erichson 1845, The dry bark beetles
  - Family 91. **CERYLONIDAE** Billberg 1820, The minute bark beetles
    - [Alexiidae Imhoff 1856]
    - [Discolomatidae Horn 1878]
  - Family 92. **ENDOMYCHIDAE** Leach 1815, The handsome fungus beetles
  - Family 93. **COCCINELLIDAE** Latreille 1807, The ladybird beetles
  - Family 94. **CORYLOPHIDAE** LeConte 1852, The minute fungus beetles
  - Family 95. **LATRIDIIDAE** Erichson 1842, The minute brown scavenger beetles
- Superfamily **TENEBRIONOIDEA** Latreille 1802
  - Family 96. **MYCETOPHAGIDAE** Leach 1815, The hairy fungus beetles
  - Family 97. **ARCHEOCRYPTICIDAE** Kaszab 1964, The archeocryptic beetles
    - [Pterogeniidae Crowson 1953]
  - Family 98. **CIIDAE** Leach 1819, The minute tree-fungus beetles
  - Family 99. **TETRATOMIDAE** Billberg 1820, The polypore fungus beetles
  - Family 100. **MELANDRYIDAE** Leach 1815, The false darkling beetles
  - Family 101. **MORDELLIDAE** Latreille 1802, The tumbling flower beetles
  - Family 102. **RHIPIPHORIDAE** Gemminger and Harold 1870, The wedge-shaped beetles
  - Family 103. **COLYDIIDAE** Erichson 1842, The cylindrical bark beetles
  - Family 104. **MONOMMATIDAE** Blanchard 1845, The opossum beetles

Family 105. **ZOPHERIDAE** Solier 1834, The ironclad beetles
[Ulodidae Pascoe 1869]
[Perimylopidae St. George 1939]
[Chalcodryidae Watt 1974]
[Trachelostenidae Lacordaire 1859]
Family 106. **TENEBRIONIDAE** Latreille 1802, The darkling beetles
Family 107. **PROSTOMIDAE** C. G. Thomson 1859, The jugular-horned beetles
Family 108. **SYNCHROIDAE** Lacordaire 1859, The synchroa beetles
Family 109. **OEDEMERIDAE** Latreille 1810, The pollen-feeding beetles
Family 110. **STENOTRACHELIDAE** C. G. Thomson 1859, The false long-horned beetles
Family 111. **MELOIDAE** Gyllenhal 1810, The blister beetles
Family 112. **MYCTERIDAE** Blanchard 1845, The palm and flower beetles
Family 113. **BORIDAE** C. G. Thomson 1859, The conifer bark beetles
[Trictenotomidae Blanchard 1845]
Family 114. **PYTHIDAE** Solier 1834, The dead log bark beetles
Family 115. **PYROCHROIDAE** Latreille 1807, The fire-colored beetles
Family 116. **SALPINGIDAE** Leach 1815, The narrow-waisted bark beetles
Family 117. **ANTHICIDAE** Latreille 1819, The antlike flower beetles
Family 118. **ADERIDAE** Winkler 1927, The antlike leaf beetles
Family 119. **SCRAPTIIDAE** Mulsant 1856, The false flower beetles

Superfamily **CHRYOMELOIDEA** Latreille 1802
Family 120. **CERAMBYCIDAE** Latreille 1802, The long-horned beetles
Family 121. **BRUCHIDAE** Latreille 1802, the pea and bean weevils
Family 122. **MEGALOPODIDAE** Latreille 1802
Family 123. **ORSODACNIDAE** C. G. Thomson 1859
Family 124. **CHRYSOMELIDAE** Latreille 1802, The leaf beetles

Superfamily **CURCULIONOIDEA** Latreille 1802
Family 125. **NEMONYCHIDAE** Bedel 1882, The pine-flower snout beetles
Family 126. **ANTHRIBIDAE** Billberg 1820, The fungus weevils
Family 127. **BELIDAE** Schönherr 1826, The primitive weevils
Family 128. **ATTELABIDAE** Billberg 1820, The tooth-nosed snout beetles
Family 129. **BRENTIDAE** Billberg 1820, The straight-snouted weevils
[Caridae Thompson 1992]
Family 130. **ITHYCERIDAE** Schönherr 1823, The New York weevils
Family 131. **CURCULIONIDAE** Latreille 1802, The snout beetles and true weevils

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Suborder ARCHOSTEMATA Kolbe, 1908

1. CUPEDIDAE Laporte, 1836

by Daniel K. Young

Family common name: The reticulated beetles

Family synonyms: Cupesidae Alluaud, 1900.

Extant cupedids are but relictual members of a once more diverse lineage dating from the Triassic (Carpenter 1992). Adults can sometimes be found around and beneath bark of dead logs, the general habitat of larvae, or in the evening at light. The western Priacma serrata (LeConte) can frequently be attracted in large numbers to bleach containing sodium hypochlorite (Edwards 1951; Atkins 1957). They are easily distinguished by their flattened, parallel-sided body, rows of closely placed, square elytral "window punctures," and vestiture of broad scale-like setae.

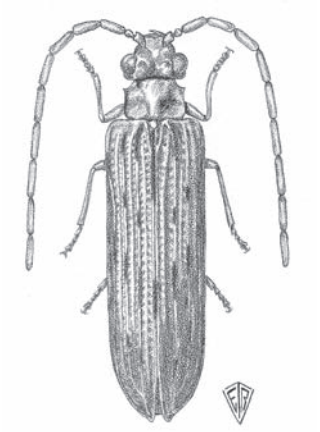

FIGURE 1.1. *Tenomerga cinereus* (Say).

Description: Body elongate, length 5-25 mm, more or less parallel-sided, moderately to strongly flattened, the dorsal surface irregularly sculptured; color brownish or black and gray; vestiture consisting of broad scale-like setae nearly covering body.

Head usually short, subquadrate with dorsal protuberances; antennae 11-segmented, filiform but thick, longer than combined head and prothorax, situated dorsally, with insertions elevated; mandibles short, blunt, with a single apical tooth; palpi small, apical segment of maxillary palpi bearing exposed, digitiform sensillae [sensillae enclosed in deep pit in Micromalthidae and Ommatidae (Australia, South America) and lacking in Crowsoniellidae (Italy)]; eyes usually large, protruding, entire, finely faceted.

Thorax: Pronotum irregularly sculptured, with more or less distinct lateral margins and acute subapical angles; notopleural suture always distinct; prosternum with distinct protarsal grooves (absent in *Priacma*); legs slender, prothoracic coxae separated by prosternum which is extended behind and fits into small, mesoventral cavity; tarsal formula 5-5-5, tarsomeres tomentose beneath, penultimate tarsomere expanded, apically emarginate and/or with ventral lobe; elytra broader than pronotum, elongate, strongly costate, with rows of quadrate "window punctures," parallel-sided; elytral epipleura narrow, lacking cells.

Abdomen with five visible, distinctly overlapping sterna; male genitalia usually with bifurcate V-shaped sclerite between tergite nine and aedeagus, parameres usually with supplementary subapical lobes and long, attenuate ventromarginal spines; female genitalia with styli on the coxites and with valvifers mostly membranous. Three thoracic and eight abdominal ganglia present in *Priacma serrata*; four Malpighian tubules in *Priacma serrata* (as in Adephaga).

Larvae of known Cupedidae [*Distocupes* (Australia), *Priacma serrata* (first instar only), and *Tenomerga*] lack stemmata, have a single stemma on either side of the head capsule, or possess a few poorly developed eye spots; possess a single, simple median endocarina; have six-segmented legs; and possess a median sclerotized process on the ninth abdominal tergum.

Habits and habitats. Larvae are wood-borers, living in fairly firm, but fungal-infested wood through which they navigate with the aid of their asperate thoracic and abdominal ampullae. Sometimes they have been found in structural timbers. *Priacma serrata* males have been attracted in great numbers to chlorine bleaches. Adults of *Tenomerga* are occasionally attracted to lights at night.

Status of the classification. Cupedid classification has had a colorful history, starting with Fabricius who described the first species as a chrysomelid, presumably because of the hispine-like elytral punctures. Latreille (1810) realized it was not a leaf-beetle and placed it in the lampyroid complex because of the 5-5-5 tarsal formula, but later suggested it might belong near Rhysodidae. Lacordaire did not agree, and placed the group near Ptinidae (= Anobiidae) because of the similarly inserted antennae. Ganglbauer (1903) placed them in Adephaga. Kolbe (1908) recognized the distinctiveness of these beetles and erected Archostemata, including it in his division Symphytogastra of the suborder Heterophaga. Sharp and Muir (1912) placed Cupedidae in Byrrhoidea. In 1920, Leng concluded that they should be in a superfamily by themselves, but placed it near Lymexylidae. Forbes (1926) placed Cupedidae together with Micromalthidae in Archostemata as a separate suborder, based on the spiral rolling of the distal metathoracic wings during folding. Bøving and Craighead (1931) supported the suborder treatment based upon larval structures. Since the 1930s, Cupedidae has generally been placed as one of the most primitive beetle families, in the suborder Archostemata. Ommatidae, based on the Australiam *Omma*

FIGURE 2.1. *Priacma serrata* (LeConte) (after Hatch 1953).

was first proposed as a family distinct from Cupedidae on the basis of male genitalia (Sharp and Muir 1912), but most subsequent works continued to include it in Cupedidae until 1976, when Crowson supported elevation of his Ommatini (*Omma* Newman) to Ommatidae and combined his Tetraphalerini (*Tetraphalerus* Waterhouse, South America) with the Italian *Crowsoniella* to form the family Tetraphaleridae. Lawrence and Newton (1995) noted the putitive maxillary palpal synapomorphy (digitiform sensillae enclosed in a deep pit) in uniting *Omma* and *Tetraphalerus* in Ommatidae, but excluding *Crowsoniella* (as Crowsoniellidae). In the most recent classification (Lawrence 1999), Cupedidae has three subfamilies: Mesocupedinae (Lower Triassic to Lower Cretaceous), Priacminae (Upper Jurassic to Recent) and Cupedinae (Oligocene to Recent).

Distribution. Cupedidae exhibits an ancient, Pangean distribution with species known from all continents and most of the larger continental islands. The extant world fauna consists of approximately 30 species. Four genera, each with a single species, are known from the United States and Canada.

Only nine genera are known: *Adinolepis* Neboiss has four Australian species; *Ascioplaga* Neboiss is represented by two species endemic to New Caledonia; *Cupes capitatus* Fabricius (monotypic) is indigenous to eastern North America; *Distocupes varians* (Lea) is known only from eastern Australia; *Paracupes brasiliensis* Kolbe occurs in Brasil and Ecuador; the monotypic *Priacma serrata* (LeConte) is known from montane forests of western North America; *Prolixocupes* Neboiss consists of *P. laterillei* (Solier) from the mountains of Argentina and Chile, while *P. lobiceps* (LeConte) is known from California and the southern regions of Arizona; *Rhipsideigma* Neboiss is represented by one East African and three Malagesian species. The most diverse, extant genus is *Tenomerga* Neboiss, with 10 widely distributed species.

Key to the Nearctic Genera and Species

1. Prosternum without distinct tarsal grooves; antennae short, scarcely half as long as body (Fig. 1.2) ..... *Priacma serrata* (LeConte)
— Prosternum with distinct tarsal grooves; antennae longer, usually distinctly longer than half length of body (Fig. 1.1) 2

2 (1). All four head tubercles obtuse, posterior pair distinctly larger than anterior pair; antennae slightly serrate; tarsal grooves of prosternum separated anteriorly by nearly entire width of prosternum ..... *Prolixocupes lobiceps* (LeConte)
— One or both pairs of head tubercles conical, of subequal size; antennae filiform; tarsal grooves of prosternum separated anteriorly by one or two mesal carinae or low ridges 3

3(2). Prosternal tarsal grooves separated anteriorly by a pair of low ridges near the meson ..... *Cupes capitatus* Fabricius
— Prosternal tarsal grooves separated anteriorly by a distinct, single mesal carina ..... *Tenomerga cinereus* (Say)

Classification of the Nearctic Genera

Cupedidae

Cupes Fabricius, 1801, one species, *C. capitatus* Fabricius, Eastern United States and Canada.

Priacma LeConte, 1874, one species, *P. serrata* (LeConte), mountains of Western United States and Canada (BC, WA, OR, ID, MT, CA).

Prolixocupes Neboiss, 1959, one species, *P. lobiceps* (LeConte), southern Arizona and California.

Tenomerga Neboiss, 1984, one species, *T. cinereus* (Say), Eastern United States and Canada.

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2. MICROMALTHIDAE Barber, 1913

by T. Keith Philips and Daniel K. Young

Common name: The telephone-pole beetles

These very small beetles are easily recognized by their cantharid-like appearance. Unlike cantharids, they have large heads, and moniliform antennae. They are dark brown to black in color with yellowish legs and antennae.

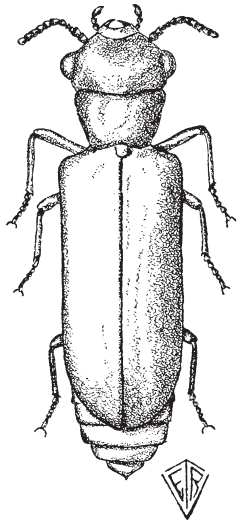

FIGURE 1.2. *Micromalthus debilis* LeConte.

Description: Elongate, somewhat depressed, and relatively soft bodied, 1.5 to 2.5 mm in length; dark brown to piceous, with pale yellow legs and antennae: vestiture sparse, limited to scattered long, erect, pale setae on lateral margin of elytra and pronotum, front, antennae, legs, and apex of abdomen.

Head (Stickney 1923) large and prognathous, broader than thorax, with large round eyes protruding from head; antennae short with eleven antennomeres, moniliform, first two antennomeres large, third small, 4 to 11 gradually increasing in diameter with 11th nearly as large as 2nd; mandibles large, curved toward each other with apices acutely three-toothed; clypeus and labium small, labial and maxillary palpi large, apical maxillary palpomere with digitiform appendages located in a large cavity.

Thorax with pronotum small, flattened above, oval, slightly narrower than the head, without margins or sutures, also lacking prosternal process and both notopleural and sternopleural sutures; legs with 5-5-5 tarsi; trochanters interstitial; hind coxae cylindrical, separate, metatrochantins exposed; elytra with prominent shoulders, flattened above, sides parallel, apices rounded, shortened, exposing about five abdominal tergites; wings with apical half spirally rolled, venation reduced, oblongum cell absent (Forbes 1926).

Abdomen with six overlapping ventrites, with the second sternite exposed, the male has ventrites 3-5 each with large median setose cavities; male genitalia distinctive and similar to other Archostemata in shape of pregenital ring, lack of phallobase, and parameres from near base with two long slender spines (Paterson 1938).

Larvae: [Micromalthidae exhibits hypermetamorphic development; the following description is based largely on the actively feeding, cerambycoid instars, unless specifically noted otherwise] vestiture sparse but stout on most segments; color white. Head enlarged, larger than prothorax, occasionally with a single stemma on each side. Antennae three-segmented, with an elongate third segment and well-developed sensorium. Clypeus and free labrum present; mandibles robust, longer than wide; apices bidentate, mola transversely ridged, protheca distinct, elongate, narrow, and sclerotized. Maxilla short, with short, transverse cardo, stipes distinct with three-segmented palpi; lobe-like setiferous articulated galea, and small fixed lacinia. Mentum with a large ligular sclerome, and one-segmented palpi, with an elongate appendage at their base. Thorax three-segmented, transverse, dorsal and ventral ampullae beginning on the mesothorax; legs when present (caraboid 1st instar) four-segmented and long, with a very long and narrow tarsus and two pretarsal claws, each with a long basal seta. Abdomen nine-segmented, anal region surrounded by opposing, sclerotized, distally toothed dorsal and ventral acuminations, with an additional pair of large, fleshy lobes bilaterally. Spiracles annular, small, on mesothorax and abdominal segments one to eight (Bøving and Craighead 1931, Lawrence 1991, Peterson 1951).

Habits and habitats. The larvae are wood borers, feeding in moist, decaying oak or chestnut logs in the red-rotten or yellowish-brown stage of decay, and are reported as causing damage to buildings and poles. They may be common, but are seldom recognized and individual collecting events appear rare. The complicated life cycle involves paedogenesis and several types of parthenogenesis. The larvae exhibit several stages and shapes in their development, including caraboid, cerambycoid, and curculionoid larval types. The caraboid larva is very mobile and molts into a cerambycoid larva. Perhaps the most unusual feature is that the cerambycoid larva can either develop into an adult female, or a paedogenetic female-producing larva which gives birth to caraboid larvae. The cerambycoid larva can also develop into a male producer. These individuals produce eggs which hatch as a curculionoid larvae and later develop into haploid adult males (Barber 1913a, b; Pringle 1938; Scott 1936, 1938, 1941).

Status of the classification. This family, represented by a single described species, has been subject to much discussion and controversy. This species has even recently been considered part of the Polyphaga and included in the Lymexylidae (Lymexyloidea), the Telegusidae (Cantharoidea), or as a separate family in the Cantharoidea (or Elateroidea *sensu* Lawrence

and Newton [1995]). But based on overwhelming evidence from larval, wing, and male genitalic characters, the family is now placed in the suborder Archostemata (Lawrence 1999). Although the family contains only one described species (Schenkling 1915), what may be a second species is known from first instars discovered in Hong Kong. Fossils (Cretaceous through to perhaps Miocene in age) representing additional species are known from amber collected in Mexico, Lebanon, the Baltic, and the Dominican Republic (Rozen 1971, Ivie and Miller, *in litt*.).

Distribution. Native to the eastern United States and perhaps Belize, the single species has been widely distributed by commerce, and its range now includes British Columbia, New Mexico and the overseas localities of Brazil, Cuba, Hong Kong, Hawaii, and South Africa (Borror *et al.* 1986, Downie and Arnett 1996, Marshall and Thornton 1963, Philips 2000, Scholtz and Holm 1985). Although there is no reason why it may not be present in Europe, this record is in error as Silvestri (1941) only thought the species should be found there due to the importation of timber from the New World.

Classification of the Nearctic Genus

Micromalthidae

Micromalthus LeConte, 1879, 1 sp., *M. debilis* LeConte, 1878, eastern United States, Belize.

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Suborder MYXOPHAGA Crowson, 1956

3. MICROSPORIDAE Crotch, 1873

by W. Eugene Hall

Family common name: The minute bog beetles

Family synonym: Sphaeriidae Erichson, 1845

The small, obscure beetles of this family resemble the Orthoperidae, but may be distinguished from other families by the comparatively large and prominent head, capitate antennae, design of meso- and metasternum, large posterior coxal plates and the unequal length of the visible abdominal sternites.

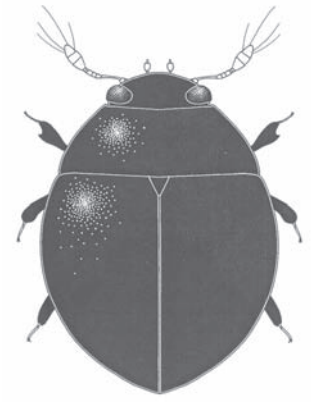

FIGURE 1.3. *Microsporus* sp.

Description: Form greatly convex, subhemispherical, color dark brown or black, body dorsal surface smooth, glabrous, glossy, occasional markings, head prominent, antennae yellowish with long setae on terminal segments. Length: 0.5 - 1.2 mm.

Head large, somewhat produced; antennae inserted near eyes, extended well beyond margin of head, 11 antennomeres, segment I large, segment II nearly as large, segment III long and slender, as long as segments I and II combined, segments IV - VI nearly equal in length, but combined shorter than segment III, segments VII and VIII short, segments IX - VI forming a conical club, segment XI with long setae and sensorial discs on apices; labrum nearly as long as wide; mentum widest at base, narrowed anteriorly; mandibles bifid, curved, prostheca present on left mandible; maxillary palp 4-segmented, segment I small, segment II long, slender, segment III large, suboval, segment IV slender, dilated at apicex; galea and lacinia forming a single mala; eyes prominent, interfacetal setae absent.

Prothorax expanded posteriorly, widest at hind angles; prosternum short, procoxae moderately separated, coxal cavities open, procoxae globular, prosternal process present between procoxae, narrow; notopleural suture present. Mesosternum reduced in size, fused to larger metasternum, forming a large plate, mesocoxae widely separated. Metacoxae nearly contiguous, coxal plates large, covering hind femur and first visible abdominal sternite, trochanters of legs short, femora robust, widely grooved on under side with edge of grooves acutely angulated near middle; tibiae broadly dilated, widest near middle, outer margin deeply excised near apex and armed with short spines in the upper angle of excision, tarsi 3-3-3, first long, subcylindrical, second much smaller than first, third elongate, claws moderate, simple, unequal.

Elytra complete, covering all abdominal segments, with distinct epipleural fold. Wing membrane large, wide, fringed with long setae along margin of membrane, possessing a distinct closed cell close to the posterior margin near middle.

Abdomen with three visible sternites, first large and long, second narrow, third wide and long; adominal tergite VIII extended anteriorly, medially narrowing segments VI - VII. Male and female genitalia undescribed.

Larva: Description based on synopsis by Beutel *et al*. (1999) and Britton (1966): Body small, flattened, 0.65 mm in length, head large, posteroventral area of head retracted into prothorax, head broader than long, deflexed, 4 large stemmata present lateral to antennae, labrum articulated, frontoclypeal, frontal and coronal sutures absent, clypeal area smooth, labrum well developed, covering mandibles and maxillary mala, antennae short but well developed, directed posteriorly, segment I long and broad, segments II and III fused, sensorial appendage elongate, narrow, mandibles small, molar well developed, apical teeth and subapical prostheca reduced or absent, maxilla deeply inserted into articulatory area, cardo short, palpifer well developed, 2-segmented, proximal palpomere possessing sensory structures, galea and lacinia fused and forming sclerotized mala, mentum and submentum fused, prementum unsclerotized, ligula large and divided, hypopharynx covered by labrum. Thorax broader than head, rounded laterally, approximately half the length of abdomen, pronotum 2.5 times broader than long with lateral extensions, legs short, 5-segmented, widely separated, coxae large, trochanter indistinct, femur and tibiotarsus short, single claw, mesothorax broad, shorter than pronotum, sternum broad, unsclerotized, metathorax broad, shorter than mesonotum. Abdomen nearly as broad as thorax, narrowed posteriorly, lancet-shaped setae on tergites I - V, segments I - VIII possessing lateral projections and balloon-shaped spiracular gills, sternum unsclerotized, segment IX with posterolateral projections, urogomphi absent, gills and lancet-shaped setae absent, sternum well developed, segment X inserted on ventral side of seg-

ment and possessing 3 membranous lobes, each with a pair of hooks.

Habits and habitats. These beetles occur in mud, under stones or on algae along the edge of streams and rivers, among the roots of plants, in mosses associated with bogs, or inhabiting moist leaf litter further away from bodies of water (Löbl, 1995). Adult microsporids store air beneath their elytra, but lack a dense mat of setae forming a plastron as in *Hydroscapha* (Beutel 1998/1999; Britton 1966; Hinton 1967; Messner and Joost 1984). Females produce a large, single egg at a time (Britton 1966). Adults and larvae feed on algae.

Status of the classification. This small group of beetles has long been recognized as a distinct family, but in the past has been placed in various suborders and superfamilies. While it is generally agreed upon that Microsporidae currently belong in the suborder Myxophaga, controversy remains regarding the family-group name (Jach, 1999).

LeConte and Horn (1883) placed Microsporidae (=Sphaeriidae) between Hydroscaphidae and Scaphidiidae, and stated rather prematurely: "The relations between this family and Trichopterygidae (=Ptiliidae) are so obvious as to require no further elucidation." Matthews (1899) placed the microsporids near the hydroscaphids. Kolbe (1901) and Ganglbauer (1903) both placed Microsporidae within Staphylinoidea. Stickney (1923) and Williams (1938), using Leng's catalog (1920), include microsporids within Staphylinoidea, and briefly comment on shared characters between microsporids and ptiliids. On the basis of hind wing venation, Forbes (1926) compared "the spring-like structure which closes the wing" to adephagans, but conceded that the body structures lacked adephagan attributes, yet placed microsporids in the adephagan superfamily Hydradephaga. Bøving and Craighead (1931) and Jeannel and Paulian (1944) placed microsporids among the Staphylinoidea. Crowson (1955) erected a new suborder, Myxophaga, partially based on the presence of notopleural sutures. Myxophaga currently contain the families Microsporidae, Hydroscaphidae, Lepiceridae and Torridincolidae. Hinton (1967) proposed the type of respiratory system in larval myxophagans, including the presence of spiracular gills, validates the suborder. Reichardt (1973) presents evidence suggesting Myxophaga represent a primitive group of beetles possessing characters intermediate between Adephaga and Polyphaga. Based on characters of the hind wing and other morphological and ecological features, Kukalova-Peck and Lawrence (1993) recognize Myxophaga as a sister group to Adephaga. Recent coleopteran classifications (Lawrence, 1982; Lawrence and Newton 1995, 1982) retain Microsporidae within Myxophaga. Phylogenetic analyses of adult and larval morphological characters (Beutel 1998/1999; Beutel *et al.* 1999) support the monophyly of Myxophaga.

Distribution. Microsporidae consist of 19 species that in Africa (including Madagascar), Asia, Australia, Europe and North and Central America (Endrödy-Younga 1997).

Classification of the Nearctic Species

Microsporus Kolenati 1846

Sphaerius Waltl 1838

Three nominal species are known from Texas, Arizona, California, and Washington. The genus is in need of revision.

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4. HYDROSCAPHIDAE LeConte, 1874

by W. Eugene Hall

Family common name: The skiff beetles

These small beetles somewhat resemble tachyporine staphylinids, but the presence of a distinct notopleural suture and aquatic habits immediately separates the two groups. The hind femora are partially covered by metacoxal plates.

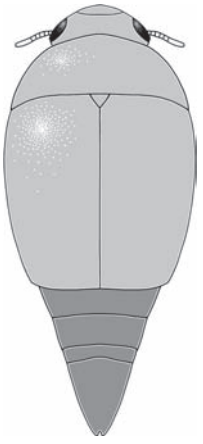

FIGURE 1.4. *Hydroscapha natans* LeConte.

Description: Body fusiform, elongate, somewhat depressed; length 1.0 - 2.0 mm; color tan to brown, margins darkened; pubescence fine, recumbent, sparse on body, longer and somewhat denser on appendages.

Head moderate, prognathous, anteriorly arcuate with pronounced frontal ridge; surface with moderately shallow punctures. Antennae sub-clavate, cylindrical, extended beyond anterolateral margins of head, possessing 9 antennomeres, segment IX enlarged, nearly as long as segments V - VIII combined, antennae inserted beneath the frontal ridge, between eyes and base of mandibles; labrum well-developed, fused to clypeus, apically arcuate. Mandibles small, apices blunt, prostheca present on left mandible. Maxillary palpi prominent, possessing four palpomeres, apical one small, no longer than wide, apex acute; penultimate enlarged and three times as long as apical. Labial palpi possessing three palpomeres, small and obscure; gular sutures present, widely separated then converging anteriorly. Eyes small, oval, widely separated, not protuberant, interfacetal setae absent.

Pronotum broader than head, broadened posteriorly and widest at hind angles, nearly as wide as elytra; anterior margin excavated to receive head; lateral margins arcuate, sides deeply explanate, posterior margin arcuate. Prosternum short, spinasternum depressed, obscure. Procoxal cavities open posteriorly, procoxae conical, prominent. Mesosternum short, mesocoxal cavities widely separated, mesocoxae small, ovate. Metasternum long, metacoxal cavities widely separated, metacoxae transverse, posteriorly enlarged and forming a coxal plate partially covering hind femora. Trochanters small, triangular. Femora and tibiae normal. Tarsi 3-3-3; claws moderate.

Elytra truncate, exposing three or four abdominal tergites. Wings fringed with long setae along margin; venation reduced, oblong cell absent. Epipleural fold prominent basally, narrowing apically.

Abdomen narrowed posteriorly, possessing a dense mat of recumbent setae on tergite III, forming a plastron beneath elytra; six visible sternites, sternite VI of female tapered at posterior margin, male with segment VI possessing two widely separated, acute teeth along posterior margin; genitalia as in Reichardt and Hinton (1976).

The following synopsis of larval characters is based on Beutel and Haas (1998) and Beutel *et al*., (1999) for *Hydroscapha natans* LeConte 1874, which occurs in North America. Body small, flattened anteriorly, 1.1 - 1.3 mm in length, narrowed toward posterior apex. Head subprognathous, broad compared to body size, posteriorly retracted into prothorax, stemmata in two rows of three and two, labrum extended and fused with clypeus, clypeolabrum nearly covering mandibles, frontal suture distinct and lyriform, antennae short, two segmented, segment I broad and short, segment II slender, sensorial appendage present, mandibles short and flattened, mola well-developed, subapical pseudomola present, apical and subapical teeth present, maxilla maxillary articulatory area and membrane well-developed, cardo moderate in size, stipes elongated, galea and lacinia fused, forming hook-like mala, palpifer absent, two palpomeres present, mentum and submentum fused, prementum semimembranous, ligula broad, hypopharynx separated from dorsal wall of prementum by a distinct fold. Thorax slightly broader than head, longer than half the length of abdomen, more than twice as broad as abdominal segments V - IX, prothorax 2 times broader than long and possessing lateral extension, balloon-like spiracular gill present on posterolateral margin, sternum weakly sclerotized, legs nearly adjacent, 5-segmented, coxae large and conical, trochanter inconspicuous, femur long, tibiotarsus short, single claw elongate, mesonotum as broad but shorter than pronotum, spiracular gill absent, metanotum similar to mesonotum. Abdomen narrowed posteriorly, tergite I narrower and shorter than thoracic terga, lateral extensions present, lancet-shaped setae present posteriorly, spiracular gills present posterolaterally, sternum moderately broad, segment II narrower than segment I, spiracular gills absent, lateral extensions indistinct, lancet-shaped setae present posteriorly, sternum as broad as tergum, segments III - VII narrowed posteriorly, lateral extensions and spiracular gills absent, lancet-shapes setae present posteriorly, sternum broad, segment VIII longer than preceding segments, balloon-shaped spiracular gills present posterolaterally, lancet-shaped setae absent posteriorly,

segment IX narrower than segment VIII, posterior margin with row of long setae, urogomphi absent, segment X composed of a flat, opercular plate possessing numerous spines, thin hooks attached dorsally.

Habits and habitats. Skiff beetles are abundant in streams, on filamentous algae growing on rocks, especially in the marginal shallows. Adults and larvae are non-predacious, feeding on algae. Hydroscaphids can tolerate a wide range of water temperatures ranging from icy streams to hot springs. Reproduction occurs with one large egg being produced at a time and the eggs are then laid on mats of algae. The developing larvae of *Hydroscapha* are entirely aquatic (Beutel 1998/1999; Beutel and Haas 1998; Bøving 1914). Adults carry a supply of air under the elytra via recumbent setae that act as a plastron on tergite III, assisting in respiration (Beutel 1998/1999; Messner and Joost 1984).

Status of the classification. Upon describing the type species *Hydroscapha natans*, LeConte (1874) proposed placing the new genus within its own family. Matthews (1884: 114-116) believed the group deserved tribal ranking within Ptiliidae (=Trichopterygidae) based on morphological characters, including the form of the hindwing. Later, Matthews (1900: 13-16) determined Hydroscaphidae deserved family status representing a "connecting link" between Staphylinidae and Ptiliidae. Lameere (1900), Kolbe (1901) and Ganglbauer (1903) placed Hydroscaphidae among families of the Staphyliniformia. Based on larval characters, Bøving (1914) placed the hydroscaphids as a subfamily within Hydrophilidae. Stickney (1923), using Leng's (1920) catalog, included the hydroscaphids as a subfamily of hydrophilids. Forbes (1926) included Hydroscaphidae in the suborder Adephaga within the superfamily Hydradephaga. Bøving and Craighead (1931) and Jeannel and Paulian (1944) placed Hydroscaphidae as a family within the suborder Polyphaga, superfamily Staphylinoidea. D'Orchymont (1945) retained hydroscaphids within Staphyliniformia. Crowson (1955) included Hydroscaphidae within the new suborder Myxophaga, which currently includes the families Hydroscaphidae, Lepiceridae, Microsporidae and Torridincolidae. Reichardt (1973) suggested that Myxophagans possess primitive characteristics intermediate between Adephaga and Polyphaga. Reichardt (1974) discusses the close relationship of Hydroscaphidae and Torridincolidae. Reichardt and Hinton (1976) reviewed Hydroscaphidae from the New World. Based on characters of the hindwing, Kukalova-Peck and Lawrence (1993) recognize Myxophaga as a sister group to Adephaga. Recent coleopteran classifications (Lawrence 1982; Lawrence and Newton 1995, 1982) retain Hydroscaphidae within Myxophaga. Phylogenetic analyses based on larval and adult morphological characters (Beutel 1998/1999; Beutel and Haas 1998; Beutel *et al.*, 1999) support the monophyly of Myxophaga and inclusion of Hydroscaphidae.

Distribution. Hydroscaphidae contain three genera: *Hydroscapha* LeConte 1874, *Scaphydra* Reichardt 1973 and *Yara* Reichardt and Hinton 1976. The genus *Hydroscapha* contains 11 species and occurs in North America, Mexico, Eurasia, North Africa and Madagascar (Arce-Perez *et al.*, 1996; Arce-Perez and Novelo-Gutierrez 1990; Lawrence and Newton 1995; Löbl 1994; Reichardt 1973; Reichardt and Hinton 1976). The remaining genera of Hydroscaphidae that occur outside the United States include *Scaphydra* (Brazil) and *Yara* (Brazil, Panama).

Classification of the Nearctic Species

Hydroscapha LeConte, 1874

One species, *H. natans* LeConte, 1874, has been described in the United States from Arizona, southern California, and southern Nevada.

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5. RHYSODIDAE Laporte, 1840

by Ross H. Arnett, Jr. and Michael A. Ivie

Family Common Name: The wrinkled bark beetles

Family synonym: Rhyssodidae Jacquelin du Val, 1857

The members of this small family closely resemble in a superficial way, some of the species of the family Colydi idae and Brentidae. However, they are really highly specialized members of the suborder Adephaga, and recent workers have included them in this suborder. The notopleural suture and divided first visible sternite will clearly distinguish this group from any of the similar looking Polyphaga, and the moniliform antennae combined with the distinctively grooved prothorax and head will separate them from other members of the Adephaga.

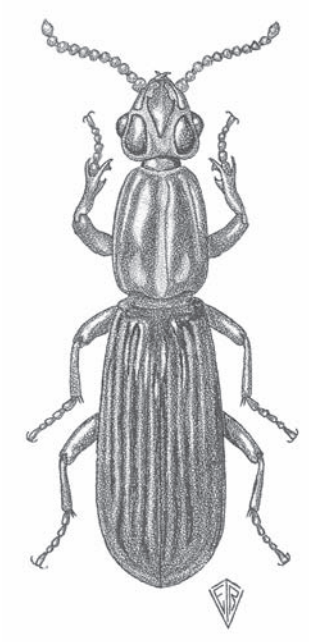

FIGURE 1.5. *Clinidium sculptile* Newman.

Description: Shape cylindrical, elongate; size 5-8 mm; color testaceous to dark, immaculate; vestiture absent except for sparse, moderate hairs on antennae and abdomen.

Head moderate, grooved dorsally, constricted behind into a neck which forms a ball and socket joint with the prothorax; antennae short, 11-segmented, each segment as broad as long, bead-like; mouthparts unique, labrum triangular, bi- to quadrisetose; mandibles nonfunctional, lacking cutting edges, each with a scrobal seta and hollowed external tooth; maxillae, except tip of palps, hidden by mentum, galea and lacinia styliform; labial palpi reduced, hidden by mentum; mentum fused laterally to the head capsule, extending anteriorly beyond other mouthparts to form cutting edge; labial palpi reduced, hidden by mentum when the jaws are closed but emerge when the jaws are open; maxillae and their palpi also completely hidden when jaws are shut, except for tip of palpus; galea and lacinia of maxillae converted into stylets; eyes narrow, obscure, facets obscure, or round, with more or less distinct facets.

Prothorax with notopleural sutures; elongate with sides arcuate, narrowed in front and behind, dorsal surface with deep longitudinal grooves; legs slender, tarsi 5-5-5, claws simple; elytra covering abdomen, rounded behind, sides parallel, surface with deep longitudinal grooves; wings when present with oblong area absent, as in Cicindellidae, m-cu straight.

Abdomen with five visible sternites, the first visible sternite divided into 3 pieces, one on each side of the coxae, and one between the coxae; sternites in *Clinidium* with pollinose sulci, the arrangment of which is important in species identification; male genitalia a modified trilobed type, the parameres short and concave, closely resembling certain Carabidae.

The grub-like larvae are of caraboid type with labial palpi. latent, prementum and ligula fused into an unpaired anteriorly bilobed piece, retracted ventral mouthparts, one claw, urogomphi absent.

Habits and habitats. Both adults and larvae are found in moist rotten logs infested with slime molds (Myxomycetes), which are their presumed food (Bell 1991, Lawrence and Britton 1994). Both hard woods and conifers are commonly inhabited. Feeding is done in a unique manner (Bell 1994). The mandibles cannot be used to bite, and the anterior margin of the mentum is used as a cutting edge. The mentum and mandibles enclose the rest of the mouthparts when the mandibles are closed, but opening the mandibles exposes/extends the maxillary stylets and labial palps.

Status of the classification. The hard body and unusual wrinkled appearance led early authors to place this family near the Colydiidae and Cucujidae, at that time both extremely diverse groups themselves. Modern workers have recognized the clearly adephagan membership of this group from the notopleural sutures, divided first abdomenal segment, fused hind coxae, and unambiguous characters of the wing and larva. The current controversy is whether to continue to recognize the rhysodids as a family, or as a member of the Carabidae. Bell and Bell (1962), Bell (1970), and Forsyth (1970) provided strong evidence for placement in the Carabidae based on characters of the tactile setae, antenna cleaner, and pygidial defense glands. Beutel (1990) and Bell (1998) went even further, showing support for a specific relationship with the carabid tribe Scaritini. However, consideration of larval characters leaves a less clear picture, leading Beutel (1992, 1993, 1995) to reverse himself, and follow larval workers Grandi (1972), Burakowski (1975), and Costa *et al*. (1988) in considering rhysodids as a full family, placing them as the sister-group of the rest of the Carabidae. The final answer is still out on the question of the phylogenetic placement of this family, but we are following Lawrence and Newton (1995). The family has been relatively recently revised for the world by Bell and Bell (1978, 1979,1982,1985), and cataloged for North America by Bell (1985).

Distribution. Approximately 170 species in 20 genera are described nearly worldwide, with the richest concentration in the Southeast Asia-New Guinea area. There are 8 species in 2 genera in North America north of Mexico.