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A generic-level phylogenetic review of the Macroductylini  
(Coleoptera: Scarabaeidae: Melolonthinae)

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(Coleoptera: Scarabaeidae: Melolonthinae)

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**Abstract.** A revision of the generic classification of the tribe Macroductylini is provided using morphological characters of adults. The revision is based on a taxonomic analysis of 80 genera historically placed in the tribe and a cladistic analysis of 32 genera conforming to the new tribal definition. Synapomorphies for the newly defined Macroductylini include: the length of the fifth ventrite longer than the fourth ventrite when viewed ventrally, fifth ventrite lacking a complete suture between the tergite and sternite, and the metathoracic tibial spurs (if present) offset, allowing the metatarsus to move past them. Thirty-two genera constitute the newly defined Macroductylini: *Agaocnemis* Moser, *Alvarinus* Blanchard, *Ancistrosoma* Curtis, *Anomonyx* Saylor, *Anoplosiagum* Blanchard, *Astaenosiagum* Martínez, *Barybas* Blanchard, *Calodactylus* Blanchard, *Ceraspis* Le Peletier and Serville, *Ceratolontha* Arrow, *Chariodactylus* Moser, *Chariodema* Blanchard, *Chremastodus* Solier, *Clavipalpus* Laporte, *Ctenotis* Burmeister, *Dasyus* Le Peletier and Serville, *Dicrania* Le Peletier and Serville, *Gama* Blanchard, *Gastrohoplus* Moser, *Hercitis* Burmeister, *Hieritis* Burmeister, *Isonychus* Mannerheim, *Issacaris* Fairmaire, *Macroductylus* Dejean, *Manodactylus* Moser, *Manopus* Laporte, *Oedichira* Burmeister, *Pectinosoma* Arrow, *Plectris* Le Peletier and Serville, *Priesterophora* Harold, *Rhinaspis* Perty, and *Schizochelus* Blanchard. Sixteen genera are removed or their removal is confirmed from the historical Macroductylini: *Coenonycha* Horn, *Dichelonyx* Harris, and *Gymnopyge* Linell (to *Dichelonychini*), *Homalochilus* Blanchard, *Homoliogenys* Gutiérrez, *Liogenys* Guérin-Méneville, and *Pacuvia* Curtis (to *Diploctaxini*), *Diphycerus* Deyrolle and Fairmaire (to *Diphycerini*), *Hyperius* Deyrolle and Fairmaire (to *Melolonthini*), *Apterodemidea* Gutiérrez (to *Sericoidini*), *Blepharotoma* Blanchard (to *Liparetrini*), *Diaphylla* Erichson (removed from Macroductylini, and currently unplaced into existing melolonthine tribes), *Hilarianus* Blanchard, *Manonychus* Moser, *Pseudoisonychus* Frey (removed from Macroductylini, and currently unplaced into existing melolonthine tribes) and *Zabacana* Saylor (to *Epectinaspis* (Rutelinae)). Nine new generic synonyms are proposed: *Corminus* Burmeister, junior synonym of *Alvarinus* Blanchard; *Ctilocephala* Burmeister, *Eubarybas* Gutiérrez, and *Pseudohercitis* Moser, each a junior synonym of *Barybas* Blanchard; *Byrasba* Harold, *Rhinaspoides* Moser, and *Ulomenes* Blanchard, each a junior synonym of *Rhinaspis* Perty; *Demodema* Blanchard, a junior synonym of *Plectris* Le Peletier and Serville; and *Pachyloptoma* Blanchard, junior synonym of *Gama* Blanchard. Eight previously proposed synonyms are confirmed: *Amphicrania* Burmeister, junior synonym of *Clavipalpus* Laporte; *Chlaeobia* Blanchard a junior synonym of *Phyllophaga* Harris; *Dioplia* Burmeister, junior synonym of *Calodactylus* Blanchard; *Faula* Blanchard junior synonym of *Ceraspis* Le Peletier and Serville; *Dejeania* Blanchard, preoccupied name and junior synonym of *Dichelomorpha* Burmeister; *Harpodactyla* Burmeister, junior synonym of *Gama* Blanchard; and *Microcrania* Burmeister, junior synonym of *Barybas* Blanchard. The removal of *Philochloenia* (junior synonym of *Dichelonyx*) is noted. Fifteen genera remain *incertae sedis* due to lack of adequate study material or insufficient information on their possible removal from Macroductylini: *Acanthosternum* Philippi (junior synonym of *Modialis*, Smith and Evans 2005), *Anomalochilus* Blanchard, *Astaenoplia* Martínez, *Aulanota* Moser, *Canestera* Saylor, *Dichelomorpha* Burmeister, *Diphydactylus* Thomson, *Hadrocerus* Guérin-Méneville, *Hamatoplectris* Frey, *Mallotarsus* Blanchard, *Metaceraspis* Frey, *Paulosawaya* Martínez and D'Andretta, *Pseudodicrania* Gutiérrez, *Pseudoleuretra* Martínez and D'Andretta and *Xenoceraspis* Arrow. A diagnosis for the thirty-two genera comprising the Macroductylini is presented and key characters are illustrated. A key to the genera and hypothesized phylogeny of Macroductylini is provided.

## Introduction

The tribe Macroductylini has historically comprised approximately 10% of the Melolonthinae. Until this work, the tribe lacked a clear definition and had never been subjected to a formal cladistic analysis. A review of the literature revealed 80 genera (73 Neotropical and Nearctic and seven Oriental) and ap-

proximately 1,000 species assigned to the tribe. Nearly a third of the species belong to two genera, *Plectris* Le Peletier and Serville and *Isonychus* Mannerheim. Most genera (58% of the historically conceived tribe) are endemic to Brazil. Adding to the historical context is the fact that 41% of the genera are monotypic and 59% of the generic and species descriptions date from the 1800s; most are exceedingly brief, incomplete, and uninformative for even diagnostic, much less comparative, purposes.

The objectives of this work were to: critically examine the type species for each of the 80 genera historically assigned to the Macroductylini (including previous synonyms and genera previously removed from the tribe); seek a monophyletic interpretation of Macroductylini based upon an analysis of morphological characters from adults; provisionally redefine Macroductylini on the basis of a cladistic analysis; produce a key to the genera (based on types only); and redescribe, illustrate, and photograph the genera of Macroductylini.

## History of Macroductylini

The classification history of the tribe began with Latreille in 1825, who discussed the North American "*Macroductyle*" (*Macroductylus*) as being "different" from the European *Melolontha*, into which it was originally placed by Fabricius (1775). Latreille did not provide a complete description of *Macroductylus* or designate any species in this work. Le Peletier and Serville later provided a complete description of the genus in 1828. The genus is credited to Dejean (1821) who designated the species *Melolontha subspinosus* Fabricius and *Melolontha angustus* Fabricius as members of *Macroductylus*, but did not discuss them in a relational sense. Kirby (1837) placed *M. subspinosus* (Fabricius) into a newly erected family, Macroductylidae. It is unclear why Kirby did this; presumably he reasoned that this unique North American species differed substantially from other European species of *Melolontha*, the genus into which it had historically been placed. Le Peletier and Serville (1828) described *Ceraspis*, *Dasyus*, *Dicrania*, and *Plectris*. This work provided substantial descriptions of the genera and included a thorough generic description of *Macroductylus*. Harris (1827) established the genus *Dichelonyx* from North America for *Melolontha linearis* Gyllenhal (1817) and suggested it was related to the macroductyline scarabs. Much confusion has surrounded this genus. Schönherr (1817) noted *Melolontha elongata* Fabricius (1792) was a primary junior homonym of *Melolontha elongata* Olivier (1789), renaming the former *Melolontha elongatula*. In 1837, Harris recognized that *M. elongatula* Schönherr was the senior synonym of *M. linearis* Gyllenhal (1817), the generic type species of *Dichelonyx* at this time. Therefore, the appropriate type species of the genus is *Dichelonyx elongatula* (Schönherr 1817). Kirby (1837) inappropriately emended the generic name to *Dichelonycha*, and named three new species. This spelling error was repeated until 1920 when Leng correctly brought back the original spelling. The 1820s ended with Mannerheim (1829) describing *Isonychus*.

The 1830s saw a series of monotypic genera described: *Hadrocerus* Guérin-Ménéville (1831), *Clavipalpus* Laporte (1832), *Rhinaspis* Perty (1833), *Ancistrosoma* Curtis (1835), and *Liogenys* Guérin-Ménéville (1838).

The 1840s saw little work in the macroductylines. Laporte (1840) described the monotypic *Manopus*, Curtis (1844) described the monotypic *Pacuvia*, and Erichson (1847) described the monotypic *Diaphylla*. In 1848, Erichson placed two European genera, *Macrophylla* Hope 1837 and *Onochaeta* Erichson 1848, into his newly erected Macroductylidae, under the broader group Melolonthidae. He expressed that several North and South American genera reside within this family (*Ancistrosoma*, *Ceraspis*, *Dasyus*, *Dichelonycha*, *Isonychus*, *Liogenys*, *Macroductylus*, *Plectris*, and *Rhinaspis*). Subsequent workers have not placed *Macrophylla* and *Onochaeta* in the Macroductylini.

The mid-1800s saw the most taxonomic work on the Macroductylini. Solier (1851) described the monotypic *Chremastodus*. Between 1850 and 1851 Blanchard described numerous genera within the Melolonthinae. Blanchard placed five previously described genera and four newly described genera (*Barybas*, *Calodactylus*, *Dejeania*, *Schizochelus*) into his "Omalopliitae" and seven previously described genera and 14 newly described genera (*Alvarinus*, *Anomalochilus*, *Anoplosiagum*, *Blepharotoma*, *Chariodema*, *Chlaenobia*, *Demodema*, *Faula*, *Gama*, *Hilarianus*, *Homalochilus*, *Mallotarsus*, *Pachylotoma*, *Philochloenia*) in his "Melolonthitae." Blanchard did not provide clear definitions for these groups.

Burmeister (1855) produced the first substantial work on the macroductylines. Burmeister's work was mainly a response to Blanchard's work, but he did not acknowledge the Blanchard genera. He pro-

vided the first diagnosis of the macrodactyline group as well as the first keys to a number of genera. Burmeister is credited with the first description of the present day tribe Macrodactylini, but he did not use this term. He designated this group as the Macrodactylidae, and included seven subgroups: Ceraspidae (*Ancistrosoma* and *Ceraspis*); Dichelonychidae (*Dasyus*, *Dichelonycha*, and *Dioplia* Burmeister); Dicraniadae (*Dicrania* and *Rhinaspis*); Isonychidae (*Amphicrania* Burmeister, *Corminus* Burmeister, *Diaphylla*, *Hadrocerus*, *Isonychus*, *Macrodactylus*, *Manopus* and *Philochloenia sensu* Burmeister); Liogenyidae (*Barybas sensu* Burmeister, *Ctenotis* Burmeister, *Harpodactyla* Burmeister, and *Liogenys*); Microcraniadae (*Ctilocephala* Burmeister, *Hercitis* Burmeister, and *Microcrania* Burmeister); and Plectridae (*Oedichira* Burmeister and *Plectris*). Within this work Burmeister attributed the name Macrodactylidae to Kirby (1837).

Lacordaire (1856) provided the most complete treatment of the macrodactylines yet produced. His *Genera des Coléoptères* provided extensive redescriptions of genera, including the Blanchard genera, to which Lacordaire had access at the Paris Museum. Although his treatment of genera was global, with keys and definitions of upper level divisions down to genera, he did not cover the Burmeister genera in his work. The Macrodactylides were designated along with a description of the subtribe. Within this subtribe, genera were placed into four groups: Ceraspides (*Ancistrosoma*, *Ceraspis*, *Chariodema*, *Dejeania*, and *Manopus*), Dicranides (*Dasyus* and *Dicrania*), Macrodactylides (*Calodactylus*, *Isonychus*, *Macrodactylus*, and *Schizochelus*), and Philochlenides (*Alvarinus*, *Anomalochilus*, *Anoplosiagum*, *Barybas* (*sensu* Blanchard), *Blepharotoma*, *Chlaenobia*, *Demodema*, *Gama*, *Mallotarsus*, *Philochloenia* (*sensu* Blanchard), *Plectris*, *Rhinaspis*, and *Ulomenes*). Genera previously within the historic Macrodactylini fell into two additional subtribes: Sericoides, in which he placed *Diaphylla* under his Heteronyces group and *Dichelonycha* into his Sericoides group; *Clavipalpus*, *Liogenys*, *Hilarianus*, *Homalochilus*, and *Pachylotoma* were placed in the Clavipalpides group. The significance of Lacordaire's work is best thought of in two respects. The first is the global treatment of genera and tribes along with the inclusion of descriptions at all taxonomic levels. The second effect of this work is the redescriptions of Blanchard's genera. Blanchard's descriptions were exceedingly short and uninformative, but after Lacordaire's work these genera could be more clearly understood. LeConte (1856), paralleling Lacordaire's work, designated for the first time the Macrodactylini, containing *Macrodactylus*, and separated several genera into newly formed tribes, such as Dichelonychini, containing *Dichelonyx*. The 1850s ended with Thomson (1858) describing the monotypic *Diphydactylus*.

The 1860s saw only one new genus described in the Macrodactylini. Philippi (1861), described the monotypic *Acanthosternum*. The first substantial catalogue of Scarabaeidae was produced during this time period by Harold (1869a). He treated many of the historic genera as belonging to the Melolonthini. Not all genera historically associated with Macrodactylini were included within this work, and no clear reasons were provided for this classification.

In the 1870s the North American worker Horn (1876) established *Coenonycha* and placed into it *Dichelonyx rotundata* (LeConte), indicating the close relationship to *Dichelonyx*. In 1878, Fairmaire and Deyrolle described five species in two genera from Asia: *Diphycerus* and *Hyperius*. Fairmaire (1889) described the monotypic *Issacaris*, and the century ended with Linell (1896) describing the North American *Gymnopyge*.

Dalla Torre (1913) cataloged the Macrodactylini, and several historical macrodactyline genera were placed back into or removed from the tribe without justification. Numerous synonyms relevant to Macrodactylini were recorded: *Dioplia* synonymous with *Calodactylus*, *Amphicrania* (in part) and *Pacuvia* synonymous with *Liogenys*, *Amphicrania* (in part) synonymous with *Clavipalpus*, *Microcrania* synonymous with *Barybas*, *Faula* (in part) synonymous with *Ceraspis*, and *Faula* (in part) synonymous with *Ancistrosoma*. The justification for these synonyms and changes in tribal status were not provided, nor was a clear explanation given for the multiple synonyms of genera, such as *Faula* and *Amphicrania*. Several genera not placed previously into this tribe were included without justification as well, including *Epicaulis* Dejean and *Oxychirus* Quedenfeldt. Subsequent workers have considered *Oxychirus* a member of Phaenomerinae. *Epicaulis* has not been discussed, likely due to the lack of adequate descriptions and type material.

Arrow (1913) described the monotypic *Pectinosoma*. He later (1920) placed it into the "Macrodactylides" and provided a detailed discussion of the Asian genera *Dichelomorpha* Burmeister, *Diphycerus* Fairmaire, and *Xenoceraspis* (new genus and species) from India. The German worker Moser described nine South

American genera (1918, 1919a, 1919b, 1921a, 1921b and 1924): *Agaocnemis*, *Anomonyx*, *Aulanota*, *Chariodactylus*, *Gastrohoplus*, *Manodactylus*, *Manonychus*, *Pseudohercitis*, and *Rhinaspoides*.

The North American worker Saylor (1938) described *Canestera*. In 1940, he corrected a homonym, replacing Mosers's *Anomolonyx* (1921) with *Anomonyx*.

The 1940s saw little work on Macroductylini, with two genera described during this time period: Saylor (1946) described *Zabacana* and Arrow (1948) described the monotypic *Ceratolontha*. Blackwelder (1944) produced a checklist of Coleoptera in Mexico, Central America, West Indies, and South America. Notable in the checklist was the removal of *Chlaenobia* from the macroductylines and placement as a synonym of *Phyllophaga* Harris (Melolonthini) and the inclusion of *Isoceraspis* Ohaus (1911) as a genus. *Isoceraspis* has subsequently been treated as a subgenus of *Ceraspis* as it was originally designated. Several South American genera are absent from the list without explanation.

Janssens (1949) proposed a classification of Scarabaeidae, including a key to tribes (including Macroductylini). This key was based on what Janssens described as European members of these tribes, but Macroductylini (non-European) were included. This work was one of the first to provide significant tribal level characters for Macroductylini.

In the 1950s the Chilean worker Gutiérrez (1952) described the monotypic *Eubarybas*; he also moved the Chilean *Apterodema paraguayensis* Arrow 1903 to the new genus *Apterodemidea*, and *Liogenys tarsalis* Moser 1921 to the new genus *Homoliogenys*. Gutiérrez provided a key to these genera and species along with several other Chilean melolonthine genera. The Argentinean worker Martínez (1957) described *Astaenoplia* and moved *Schizochelus longipes* Philippi to his new genus *Astaenosiagum*.

In the 1960s Frey began working on the Macroductylini, describing the monotypic *Metaceraspis* (1962). In 1967 he added the monotypic *Hamatoplectris*, and in 1971 the monotypic *Pseudoisonychus*. Frey described numerous species within existing "macroductylines" genera. His works also included regional keys for *Ceraspis* (Frey 1962), *Dicrania* (Frey 1972a), *Isonychus* (Frey 1964, 1965, 1970), *Liogenys* (Frey 1969), and *Plectris* (Frey 1967). Frey (1972b) removed *Blepharotoma* Blanchard from Macroductylini, placing it in Sericoidini. Ritcher (1966) proposed the tribe Plectrini, composed of *Plectris*, based on larval characters. He demonstrated that the tribes Macroductylini, Dichelonychini (*sensu* LeConte), and Plectrini were separable based on larval characters. This was based on the few known larvae of *Macroductylus*, *Dichelonyx*, *Coenonycha*, and *Plectris*. North and South American workers treating the tribes have apparently overlooked or discounted this work.

In 1975 Martínez transferred two genera from the Pachydemini and placed them into the Macroductylini: *Paulosawaya* Martínez and D'Andretta 1956, and *Pseudoleuretra* Martínez and D'Andretta 1956. Since 1975 no new macroductylines have been described. There have been numerous species-level contributions, mainly for Central American and Caribbean species. Notable works have included regional generic keys: Carrillo and Gibson (1960), Garcia-Vidal (1982), Arce-Pérez and Morón (2000).

Britton's (1957, 1978) work on Australian Melolonthinae included a tribal description of Macroductylini, due the presence of an invasive *Plectris* in Australia. Baraud (1992) included Macroductylinae in his key to Palearctic subfamilies of Melolonthidae, but provided no comment on the subfamily, which is absent from Europe. The characters used in this tribal description are similar to those of Janssens (1946).

Evans (2003) published a catalogue of South American Melolonthinae; this was supplemented in 2005 (Smith and Evans 2005), and an updated catalogue was published in 2005 (Evans and Smith 2005). Numerous changes were made to the Macroductylini: *Homalochilus* Blanchard, *Homoliogenys* Gutiérrez, *Liogenys* Guérin-Méneville, and *Pacuvia* Curtis were moved to the re-erected Diplotaxini; *Apterodemidea* Gutiérrez was placed in the Sericoidini; and *Acanthosternum* Philippi 1861 was placed as a junior synonym of *Modialis* Fairmaire and Germain 1860 in Melolonthini.

### Distribution of Macroductylini

The newly defined Macroductylini are distributed across the New World. The vast majority of macroductylines are centered in Southern Brazil, with several genera extending into Central and North America. Distributional limits remain unclear for the vast majority of genera, with adequate distributional information recorded only for a modest number of North American, Caribbean, and Central American species.

## General Life History of Macroductylini

Little is known of the life histories or food plant associations of macroductyline species. Limited information suggests members of this tribe feed on root tissues as larvae and plant parts (leaves and flowers) as adults. Anecdotal evidence suggests larvae prefer well-drained soils with some organic materials in which to develop and feed. Adults of this tribe are known to exhibit both nocturnal and diurnal activity patterns.

## Taxonomic Methodology and Materials

Specimens used in this study were provided by 14 primary institutions. Acronyms for loan institutions follow Arnett et al. (1993). Syntypes and homeotypes examined by the author were labeled with a species identification label and their location is noted. Holotypes and paratypes examined were not labeled; their location is provided in this manuscript.

LACM Arthur V. Evans Collection (AVEC), subsequently placed at the LACM, Los Angeles, CA, USA  
BMNH The Natural History Museum, London, England (M. Kerley)  
BPBM Bishop Museum, Honolulu, HI, USA (G. Samuelson)  
CASC California Academy of Sciences, San Francisco, CA, USA (R. Brett)  
CMNC Canadian Museum of Nature, Ottawa, Canada (R. Anderson)  
CNCI Canadian National Collection of Insects, Ottawa, ON, Canada (L. LeSage)  
FMNH Field Museum of Natural History, Chicago, IL, USA (A. Newton)  
FSCA Florida State Collection of Arthropods, Gainesville, FL, USA (P. Skelley)  
MLUH Wissenschaftsbereich Zoologie, Sektion Biowissenschaftler Martin-Luther-Universität Halle, Halle, Germany (K. Schneider)  
MNHN Muséum National d'Histoire Naturelle, Paris, France (N. Berti)  
MNNC Colección Nacional de Insectos, Santiago, Chile (M. Elgueta)  
UDECE Universidad de Concepción, Museo de Zoología, Concepción, Chile (V. Jerez)  
USNM United States National Museum, Washington, D.C., USA (the late N. Adams)  
ZMHB Museum für Naturkunde der Humboldt Universität zu Berlin, Berlin, Germany (M. Uhlig and J. Willers)

## Methods for generic diagnosis

Generic diagnoses were based on a consistent format. The holotype of the generic type species (if located or designated) was used along with the original description. Dissections for the purpose of viewing internal structures were done on homeotypes, lectotypes, or syntypes if appropriate material was available. If the holotype was not directly available or did not exist, then a syntype of the generic type species was chosen for the redescription. In several cases no primary types were located, but other specimens of the generic type species were located. These were then compared with the original description and redescriptions by later authors to confirm the identifications. If considered identical, they were used. In most cases, species were arguably authoritatively identified by previous macroductyline workers (Moser, Frey, Arrow, etc.). In the course of this research, I was able to “rediscover” material for several “missing” genera. Such cases are clearly stated within each pertinent generic redescription and should be considered when evaluating any subsequent analyses.

## Taxonomic analysis

Tribal morphological synapomorphies were investigated to develop a working, monophyletic hypothesis for Macroductylini. Generic representatives in the historical Macroductylini were redescribed and presented in this manuscript as abbreviated diagnoses. Seventy-seven morphological characters were recorded and compared to presumed macroductyline genera and genera representing additional tribes of Melolonthinae. Genera occurring (if possible) in both the New World and Old World from 12 tribes were obtained, and salient tribal morphological characters were recorded. Melolonthinae tribes and genera

examined included: Chasmatopterini (*Chasmatopterus*), Dichelonychini (*Dichelonyx*), Diphucephalini (*Diphucephala*), Diplotaxini (*Diplotaxis*), Hopliini (*Hoplia*), Liparetrini (*Colpochila*, *Heteronyx*, *Liparetrus*), Maechidiini (*Maechidius*), Melolonthini (*Hypotrachia*, *Phyllophaga*, *Melolontha*, *Rhizotrogus*), Pachydemini (*Sparrmannia*), Sericoidini (*Sericoides*), Sericini (*Serica*, *Maladera*), Stethaspini (*Modialis* (disputably placed within this tribe), *Stethaspis*). Hypothesized synapomorphies were noted if found to be uniform for a specific tribe, including Macroductylini. Genera historically placed in Macroductylini were then compared to these tribes. Genera were retained in Macroductylini if they conformed to the new, presumed monophyletic definition of the tribe. Genera not conforming to the new, global, tribal definition were removed from Macroductylini and placed into other existing tribes (see Disposition of Historic Macroductylina Genera).

### Disposition of Historic Macroductylina Genera

Thirty-two genera constitute the newly redefined Macroductylini based on three tribal-level synapomorphies: length of the fifth ventrite longer than the fourth ventrite when viewed ventrally, fifth ventrite lacking a complete suture between the tergite and sternite, metathoracic tibial spurs (if present) offset, allowing the metatarsus to move past them. *Agaocnemis* Moser, *Alvarinus* Blanchard, *Ancistrosoma* Curtis, *Anomonyx* Saylor, *Anoplosiagum* Blanchard, *Astaenosia* Martínez, *Barybas* Blanchard, *Calodactylus* Blanchard, *Ceraspis* Le Peletier and Serville, *Ceratolontha* Arrow, *Chariodactylus* Moser, *Chariodema* Blanchard, *Clavipalpus* Laporte, *Chremastodus* Solier, *Ctenotis* Burmeister, *Dasyus* Le Peletier and Serville, *Dicrania* Le Peletier and Serville, *Gama* Blanchard, *Gastrohoplus* Moser, *Hercitis* Burmeister, *Hieritis* Burmeister, *Isonychus* Mannerheim, *Issacaris* Fairmaire, *Macroductylus* Dejean, *Manodactylus* Moser, *Manopus* Laporte, *Oedichira* Burmeister, *Pectinosoma* Arrow, *Plectris* Le Peletier and Serville, *Pristerophora* Harold, *Rhinaspis* Perty, and *Schizochelus* Blanchard comprise the newly defined Macroductylini. Nine new generic synonyms are proposed: *Corminus* Burmeister, junior synonym of *Alvarinus* Blanchard; *Ctilocephala* Burmeister, *Eubarybas* Gutiérrez, and *Pseudohercitis* Moser, each a junior synonym of *Barybas* Blanchard; *Byrasba* Harold, *Rhinaspoides* Moser, and *Ulomenes* Blanchard, each a junior synonym of *Rhinaspis* Perty; *Demodema* Blanchard, a junior synonym of *Plectris* Le Peletier and Serville; and *Pachylotoma* Blanchard, junior synonym of *Gama* Blanchard. Eight previously proposed synonyms are confirmed: *Chlaeobia* Blanchard, a junior synonym of *Phyllophaga* Harris; *Dioplia* Burmeister, junior synonym of *Calodactylus* Blanchard; *Faula* Blanchard, junior synonym of *Ceraspis* Le Peletier and Serville; *Amphicrania* Burmeister, junior synonym of *Clavipalpus* Laporte; *Dejeania* Blanchard, preoccupied name and junior synonym of *Dichelomorpha* Burmeister (Arrow 1907); *Harpodactyla* Burmeister, junior synonym of *Gama* Blanchard; and *Microcrania* Burmeister, junior synonym of *Barybas* Blanchard. *Philochloenia* has been placed within the Macroductylini and has historically been misapplied to several genera. Smith and Evans (2005) discussed *Philochloenia*, placing it as a junior synonym of *Dichelonyx*.

Twelve genera remain *incertae sedis* within Macroductylini due to lack of adequate study material or insufficient information at this time regarding their possible removal from the tribe: *Acanthosternum* Philippi, type specimen not located during this study, noted as a junior synonym of *Modialis* (Melolonthini) by Smith and Evans (2005); *Anomalochilus* Blanchard, type specimen located at the NMNH, single specimen did not allow for a detailed diagnosis; *Astaenoplia* Martínez, not located during this study; *Aulanota* Moser, type specimen located at the ZMHB, single specimen did not allow for a detailed diagnosis; *Canestera* Saylor, type specimen located at the BMNH, single specimen did not allow for a detailed diagnosis; *Diphydactylus* Thomson, type specimen not located during this study; *Hadrocerus* Guérin-Méneville, type specimen located at the NMNH, single specimen did not allow for a detailed diagnosis; *Hamatoplectris* Frey, type specimen not located during this study (Frey (1967) indicated this genus resembles *Plectris*); *Mallotarsus* Blanchard, type specimen located at the NMNH, single specimen did not allow for a detailed diagnosis, but a preliminary look suggests this genus is very close to *Gama*, differing in the mesothoracic spurs and ventral surface of the prementum; *Metaceraspis* Frey, type specimens not located during this study (Frey (1962) indicated this genus resembles *Ceraspis*); *Paulosawaya* Martínez and D'Andretta, type specimen was not located during this study; and *Pseudoleuretra* Martínez and D'Andretta, type specimen was not located during this study.

Thirty-two genera were removed and placed into existing tribes, *Incertae sedis* within Macroductylini, removed from Macroductylini and currently unplaced into existing melolonthine tribes, or their previous removal from the historical Macroductylini was confirmed: *Coenonycha* Horn, *Dichelonyx* Harris, and *Gymnopyge* Linell to Dichelonychini; *Homalochilus* Blanchard, *Homoliogenys* Gutiérrez, *Liogenys* Guérin-Méneville, and *Pacuvia* Curtis to Diplotaxini (in accordance with Evans 2003); *Diphycerus* Fairmaire to Diphycerini (in accordance with Medvedev 1952); *Apterodemidea* Gutiérrez to Sericoidini (in accordance with Evans 2003); *Blepharotoma* Blanchard to Liparetrini (in accordance with Evans and Smith 2005); *Zabacana* Saylor to *Epectinaspis* (Rutelinae) (in accordance with Paucar-Cabrera 2003); *Diaphylla* Erichson removed from Macroductylini, its current placement unknown (in accordance with Evans and Smith 2005); *Dichelomorpha* Burmeister, *Hilarianus* Blanchard, *Hyperius* Deyrolle and Fairmaire, *Manonychus* Moser, *Pseudodictyria* Gutiérrez, *Pseudoisonychus* Frey, and *Xenoceraspis* Arrow, current placement remains unknown.

### Justification for removal of genera from Macroductylini

*Coenonycha* Horn, *Dichelonyx* Harris, and *Gymnopyge* Linell are moved to Dichelonychini. This tribe was established in 1856 by LeConte based on the following characters: labrum distinct, large and deeply emarginate; ligula connate with the mentum; ventrites not connate and with distinct sutures; the prelabrum often visible in *Dichelonyx*; sternum not prominent; posterior tibia with 0-2 apical spurs, the spurs, when present, placed close together below the tarsal articulation so that the basal segment of the tarsus passes above the spurs; claws split; width of 5<sup>th</sup> visible ventrite equal to that of the width of the 4<sup>th</sup> visible ventrite; ventrite and tergite of the propygidium with a complete, straight suture, with the spiracle placed below the suture. *Coenonycha* and *Dichelonyx* have elongate, rather rectangular bodies and large prominent eyes. *Gymnopyge* contains small, compact, square beetles that do not agree much in appearance with the aforementioned genera. The move to Dichelonychini is based loosely on similarities in geographic similarity to other Dichelonychini distributions, mouthparts, and abdominal ventrite characteristics. This genus remains troublesome in its phylogenetic placement. The phylogenetic analysis supports the distinctness of this tribe from the newly envisioned Macroductylini (Fig. 167).

*Homalochilus* Blanchard, *Homoliogenys* Gutiérrez, *Liogenys* Guérin-Méneville, and *Pacuvia* Curtis were moved to Diplotaxini by Evans (2003). The tribe was defined by LeConte (1856) and Evans (2002). An additional character shared by these genera was discovered during this study: the bilobed molar surface, similar to that of Melolonthini and lacking in Macroductylini.

The Asian *Diphycerus* Fairmaire was placed into Diphycerini by Medvedev in 1952. *Diphycerus* has all of the characteristics of the Macroductylini, including an autapomorphy not seen in any other current member (labrum produced anteriorly so that it is visible in dorsal view). This genus was not well-known to western workers, but the uniqueness of the characters in relation to the South East Asian melolonthine fauna and the uniqueness of the labrum support its placement into this tribe.

*Apterodemidea* Gutiérrez was moved to Sericoidini by Evans (2002). *Apterodemidea* has a Sericoidini-like labrum (labrum produced anteriorly so that it is visible in dorsal view) and propygidial characteristics (spiracle placed on suture line). The metathoracic femora and tibiae are moderately large, but not as dramatic as described for Sericoidini by LeConte (1856). The metathoracic tibia lacks paired apical spurs, resulting in confusion of its overall tribal placement.

*Blepharotoma* Blanchard is currently placed within Liparetrini (Evans and Smith 2005). It has a small but distinct labrum that is not produced anteriorly (unlike Sericoidini), and the apical spurs of the metathoracic tibiae are similar to Sericoidini. The metathoracic femora and tibiae are large, as described for Sericoidini by LeConte (1856). Liparetrini is poorly defined and lacks a consistent definition encompassing the world fauna. The metathoracic femora and tibiae of Liparetrini are noted as thin, unlike *Blepharotoma*. The current placement of this genus will be clarified when we have a better understanding of the relationship between Liparetrini and other tribes.

The initial placement of *Zabacana* Saylor in the Macroductylini was clearly in error. This genus belongs in Rutelinae, and Paucar-Cabrera (2003) corrected this.

*Diaphylla* lacks the characteristics of the newly envisioned Macroductylini, but it remains unclear as to its tribal status. *Diaphylla* shows a Sericoidini-like labrum but lacks the spur characteristics to pro-

vide information as to their tribal placement. It currently remains unplaced in the New World melolonthine tribes.

*Dichelomorpha* Burmeister is an Asian genus; the type species *D. ochracea* was not located at the MLUH. Analysis of the genus is based on a dissected homeotype of the presumptive syntype of *D. alsiosia* Blanchard, located at the MNHC, and identified with a Blanchard label. This Asian genus demonstrates all of the tribal characters of the newly envisioned Macroductylini, but it demonstrates a combination of characters not found in any of the New World Macroductylini (clypeus in dorsal view semicircular; metathoracic femur broadly ovate, widest medially, ventral margin distally with a pair of acute lobes). Based on this and its Asian distribution, this genus is likely a case of convergence with Macroductylini. The tribal placement of *Dichelomorpha* remains uncertain at this time until more comprehensive tribal descriptions of Asian taxa are provided.

*Hilarianus* Blanchard is similar in appearance to Diplotaxini due to the 5<sup>th</sup> visible ventrite equal in width to 4<sup>th</sup> visible ventrite and the fifth ventrite and sternite lacking a complete suture. However, this genus has the pygidium wider than long, and the metatarsal spur placement is more similar to Pachydemini (paired apical metatibial spurs placed close together, spurs placed within the notch and preventing the tibia from moving past the spurs). This genus also lacks a clear bilobed molar area of Diplotaxini. Its tribal status remains uncertain, and its placement will remain unclear until the relationships of the South American melolonthine tribes are clarified.

The Asian genus *Hyperius* shows characters similar to Melolonthini (labrum well developed, deeply emarginated, suture between the fifth and sixth ventrite complete, sigmoidal in shape, and the spiracle positioned centrally at the angle), but it lacks the mandibular characteristics noted during this study for the Melolonthini as well as Diplotaxini (bilobed molar area). The placement of this genus into Melolonthini was chosen based on the predominance of Melolonthini characters, and its placement will be clarified as the Asian melolonthine tribes are defined.

*Manonychus* has a slightly produced labrum similar to Sericoidini, and the metathoracic apical tibial spur placement relative to the tarsal articulation is the same as in the Sericoidini. The remaining morphological characters provide little additional tribal-level support. Its tribal placement remains unclear at this time, but it is likely to be placed into Liparetrini.

*Pseudodicrania* Gutiérrez demonstrates a series of characters similar to those of the Australian and New Zealand tribe Stethaspini (distinct labrum, posterior tibial apical spur placement and articulation with tarsus, and most apparently, the mesosternum and metasternum together forming a forward directed peg-like process). This study also found very similar mouthparts, notably in the mentum, mandibles and labium. The tribal status remains debatable and may simply be a case of convergence or possibly an example of a disjunct distribution. For the purposes of this work, the genus remains unplaced into an existing tribe.

The Asian *Pseudoisonychus* Frey shows a mix of characters, with a labrum similar to Sericini and propygidial and pygidial characteristics of Diplotaxini. Its tribal status remains uncertain, and its placement will be clear as the Asian melolonthine tribes are clarified.

The type of *Xenoceraspis* Arrow (*Xenoceraspis dispar* Arrow) was located at the BMNH. This Asian genus demonstrates all of the tribal characters of the newly envisioned Macroductylini, but it demonstrates several unique characters not seen in any of the New World Macroductylini (labrum visible in the dorsal view, in lateral profile subtriangular, prominently produced from clypeus; elytra with lateral margin weakly concave in anterior 1/2, medially produced outward into a flange, rounded in posterior 1/2). Based on this and its Asian distribution, this genus is a likely case of convergence with Macroductylini. The tribal placement of *Xenoceraspis* remains uncertain at this time, and its placement will be clear as the Asian melolonthine tribes are clarified.

## Phylogenetic Analysis

The possible phylogenies of Macroductylini were reconstructed using 77 adult anatomical characters. The character matrix was constructed using MacClade 4.03 (Maddison and Maddison 1992) and analyzed using the computer program algorithms Phylogenetic Analysis Using Parsimony (PAUP) version 4.09b (Swofford 1993). Five genera representing five New World tribes composed the outgroups for direct com-

parison with the Macroductylini. Dichelonychini (*Dichelonyx*), Diplotaxini (*Diplotaxis*), Melolonthini (*Phyllophaga*), Sericoidini (*Sericoides*), and Sericini (*Serica*) composed the outgroup taxa.

### Cladistic Methods

A total of 77 adult anatomical characters was recorded in the matrix, 46 of which were coded as binary and 31 as multistate characters. All characters were initially unordered and unweighted.

The large data set for Macroductylini did not allow for the implementation of an exhaustive search for the most parsimonious trees using “Branch and Bound” or “Exhaustive” search options in PAUP. A “Heuristic” search option was used with the following options: 1) minimal trees kept, 2) zero-length branches collapsed, 3) starting tree obtained by stepwise addition, 4) branches swapped on minimal trees, 5) simple addition sequence, 6) TBR branch swapping. Ambiguous character optimizations were resolved to favor reversal or secondary loss over convergence (ACCTRAN optimization) to minimize homoplasy, and all characters were treated as unordered and of equal weight. Branch swapping was used to address the problem of tree islands produced by the heuristic search. One hundred replicates of branch swapping were performed. This number was chosen to increase the probability that the shortest tree(s) were produced. Tree length, consistency index, retention index, and homoplasy index were reported for the optimal trees located with this search strategy.

A strict consensus tree was produced from the resulting trees in the previous analysis. Successive approximations character weighting (Farris 1969) was used to further evaluate phylogenetic relationships. This was implemented on the strict consensus tree. While this method increases assumptions in the analysis, it allows for more hypothetical resolution in the cladogram. Weighting was based on the retention index. The final trees produced from the reweighted analyses are presented. The trees produced are in two formats: traditional cladogram and phylogram.

### Out-group Analysis

The cladistic relationships of Melolonthinae are themselves unresolved, thus offering no clear out-groups for this study. Out-groups were, therefore, taken from a subset of New World genera representing five tribes within the Melolonthinae. Out-group comparison was based on the following methods (Nixon and Carpenter 1993): 1) in-group taxa were defined on the basis of presumed synapomorphies, 2) out-groups were selected on the basis of synapomorphies at a higher taxonomic level, 3) an unrooted parsimony analysis was performed (see previous section), 4) cladograms were then rooted between the presumed out-group and in-group, 5) character polarity was then hypothesized from this analysis.

### Character Definition

The following definitions were used for scoring the character state for the phylogenetic analysis. The complete character matrix is provided in Appendix 1.

**Measurements.** The regions measured in the diagnoses are the prothorax at widest point, measured across the dorsum; elytra at widest, dorsal point; total length, measured from the anterior margin of clypeus to the basal or proximal edge of the pygidium.

**Color and Vestiture.** Based on dried pinned specimen(s). The color and vestiture were recorded for the individual specimen and should not be considered representative of the entire genus or even species. Punctuation and setal characteristics were noted only if they appeared unique or significant.

### Adult Morphological Characters

1. Ligula in ventral profile (0) = visible, (1) = not visible.
2. Ligula medially narrowed and produced anteriorly (0) = no, (1) = yes.
3. Apex of ligula deeply emarginate (0) = yes, (1) = no.
4. Apex of prementum (0) = obtuse or acute, (1) = emarginate.

5. Prementum shape in ventral profile (0) = quadrate, (1) = trapezoidal, (2) = rectangular, (3) = subtriangular, (4) = elongate.
6. Anterior angle of prementum (0) = broadly rounded, (1) = acute, (2) = obtuse.
7. Ventral surface of prementum (0) = transverse carina only, (1) = transverse carina and medially raised carina, (2) = grooved medially, (3) = flattened, (4) = medial carina or lobe only.
8. Size of apical labial palpomere (0) = 1 and 2 = 3, (1) = 3 > 1 and 2.
9. Labrum in frontal view (0) = broadly ovate, (1) = narrowly ovate, (2) = thin or absent from view.
10. Labrum, overall size (0) = absent or much reduced, (1) = small and semicircular, (2) = large and ovate.
11. Clypeal shape (0) = rectangular, (1) = square, (2) = semicircular or ovate.
12. Clypeo-labral interface (0) = labrum produced outwardly, (1) = labrum connate, (2) = labrum fused above, not clearly visible.
13. Labrum to clypeus angle (0) = labrum not coplanar with clypeus, (1) = labrum coplanar with clypeus.
14. Labrum emargination (0) = labrum deeply emarginate, (1) = labrum flattened or moderately emarginate.
15. Clypeus to frons angle (0) = clypeus not coplanar with frons, (1) = clypeus coplanar with frons.
16. Adoral ventral groove of dististipes (0) = present, (1) = absent.
17. Shape of last maxillary palpomere (0) = ovate, (1) = conical, (2) = broad and spatulate.
18. Apical maxillary palpomere grooved on ventral surface (0) = no, (1) = yes.
19. Number of teeth on galea (0) = 6 or more, (1) = 5, (2) = 4 to 1, (3) = teeth absent.
20. Orientation of galea (0) = 0-30 degrees, (1) = 31-60 degrees, (2) = 61-90 degrees.
21. Lacinia with a well-developed apical tooth (0) = yes, (1) = no.
22. Mandible in lateral profile (0) = 1:1 length to height, (1) = 2:1, (2) = 3:1, (3) = 4:1.
23. Scissorial area of mandible (0) = broad, (1) = bluntly produced or acute.
24. Scissorial area appearance (0) = sinuate or toothed, (1) = raised carina or emarginate, (2) = unmodified or rounded.
25. Molar surface in lateral profile (0) = well developed, separated, (1) = bilobed, (2) = well-developed quadrate, (3) = reduced, narrow.
26. Adoral margin of mandible membranous (0) = no, (1) = yes.
27. Edge of adoral lateral margin of mandible (0) = raised, (1) = not raised.
28. Aboral lateral margin of mandible grooved (0) = yes, (1) = no.
29. Number of antennomeres (0) = ten, (1) = nine, (2) = eight.
30. Length of antennomeres 3-5 (0) = unequal, (1) = equal.
31. Number of antennomeres in club (0) = 4 or more, (1) = 3.
32. Canthus of eye (0) = canthus > 2/3<sup>rd</sup> ocular width, (1) = canthus < 2/3<sup>rd</sup> ocular width.
33. Eye size (0) = small (length less than width), (1) = large (length greater/equal width).
34. Presence of ocular ridge (0) = no, (1) = yes.
35. Declivity of head (0) = 0-30 degrees, (1) = 31-60 degrees.
36. Number of visible abdominal segments (excluding pygidium) (0) = 6, (1) = 5.
37. Abdominal segment 5 width vs. width of 4<sup>th</sup> segment (0) = subequal, (1) = 5<sup>th</sup> > 4<sup>th</sup>, (2) = 5<sup>th</sup> < 4<sup>th</sup>.
38. Membrane on posterior of propygidium (0) = no, (1) = yes.
39. Propygidium division (0) = complete suture, (1) = partial suture or depression, (2) = not divided.
40. Position of spiracle on propygidium (0) = medial, no suture, (1) = on suture line, (2) = above suture line, (3) = below suture line.
41. Propygidium coverage by elytron (0) = total coverage, (1) = half coverage, (2) = no coverage.
42. Pygidial shape: 0 = width equal to length, 1 = width < length, 2 = width > length.
43. Pygidial posterior margin: 0 = rounded, 1 = concave.
44. Membrane on posterior margin of 6<sup>th</sup> abdominal segment: 0 = no, 1 = yes.
45. Anterior margin of scutellum: 0 = entire, 1 = deeply emarginate.
46. Pronotal width: 0 = wider than long, 1 = equal, 2 = longer than wide.
47. Anterior margin of pronotum: 0 = straight, 1 = convex, 2 = concave.
48. Anterior margin of pronotum membranous: 0 = no, 1 = yes.
49. Posterior margin of pronotum (medial): 0 = convex, 1 = bidentate, 2 = narrowly acuminate, 3 = multi-toothed, 4 = bi-emarginate, 5 = straight, 6 = concave.
50. Dorsal surface of pronotum grooved: 0 = no, 1 = yes.
51. Prosternal process produced posteriorly over mesosternum: 0 = no, 1 = yes.
52. Prothoracic coxa: 0 = transverse, 1 = elongate.
53. Prothoracic coxa with transverse carina: 0 = yes, 1 = no.
54. Tibial spur present on prothoracic tibia: 0 = no, 1 = yes.
55. Number of teeth on the prothoracic tibia: 0 = 2, 1 = 1, 2 = 0.
56. Prothoracic pretarsal claws: 0 = even, 1 = uneven.
57. Outer pretarsal claw of prothoracic leg: 0 = simple, 1 = split, 2 = toothed and split.

58. Prothoracic pretarsal claw with secondary tooth: 0 = yes, 1 = no.  
 59. Prothoracic pretarsal empodium length: 0 = short-broad, 1 = elongate-narrow, 2 = empodium absent.  
 60. Prothoracic pretarsal empodial shape: 0 = subtriangular, 1 = trapezoidal or rectangular, 2 = ovate, 3 = narrowly acute, 4 = absent.  
 61. Elytral sutural margin distinctly raised in posterior region: 0 = no, 1 = yes.  
 62. Elytral epipleuron: 0 = rounded, slightly flattened distally, 1 = distally flattened.  
 63. Membrane along elytral margin: 0 = absent, 1 = present.  
 64. Anterior elytral umbone: 0 = absent, 1 = weak, 2 = strong.  
 65. Posterior elytral umbone: 0 = absent, 1 = weak, 2 = strong.  
 66. Metepimeron visibility: 0 = not visible or partially so, 1 = visible, >25%.  
 67. Transverse ridges on mesothoracic tibia: 0 = 2, 1 = 1, 2 = 0.  
 68. Mesothoracic tibia with dorsal pocket: 0 = no, 1 = yes.  
 69. Mesothoracic coxal separation: 0 = wide, 1 = narrow (coxae in contact or nearly so).  
 70. Metathoracic coxal separation: 0 = wide, 1 = narrow (coxae in contact or nearly so).  
 71. Metathoracic tibial spur(s) and tarsi: 0 = spurs to one side, same level, 1 = spurs to one side, one above, 2 = tarsi pass through spurs, 3 = spurs blocking tarsal movement, 4 = spurs lacking, 5 = single spur only.  
 72. Distoventral posterior margin of metathoracic tibia: 0 = deeply grooved, 1 = shallow groove.  
 73. Shape of metathoracic femur: 0 = narrowly elongate, ovate, 1 = broadly ovate.  
 74. Transverse ridges on metatibia: 0 = 2, 1 = 1, 2 = 0.  
 75. Pretarsal claws of metathoracic leg: 0 = even, 1 = uneven.  
 76. Pretarsal claws of metathoracic leg: 0 = simple, 1 = split, 2 = toothed.  
 77. Pretarsal claws of metathoracic leg paired: 0 = no, 1 = yes.

## Dissection and Illustration

Examination of various anatomical characters often required removal of specific anatomical structures. Dried specimens were placed into warm ammonia for several minutes to soften structures for removal then placed into 70% ethyl alcohol for several minutes to remove the ammonia. All structures were then card-mounted in an orientation facilitating optimal views. These cards were then placed below the specimen. Illustrations were made of all salient visible adult anatomy, including mouthparts. Illustrations herein are limited to those relevant for generic diagnosis.

## Photographs

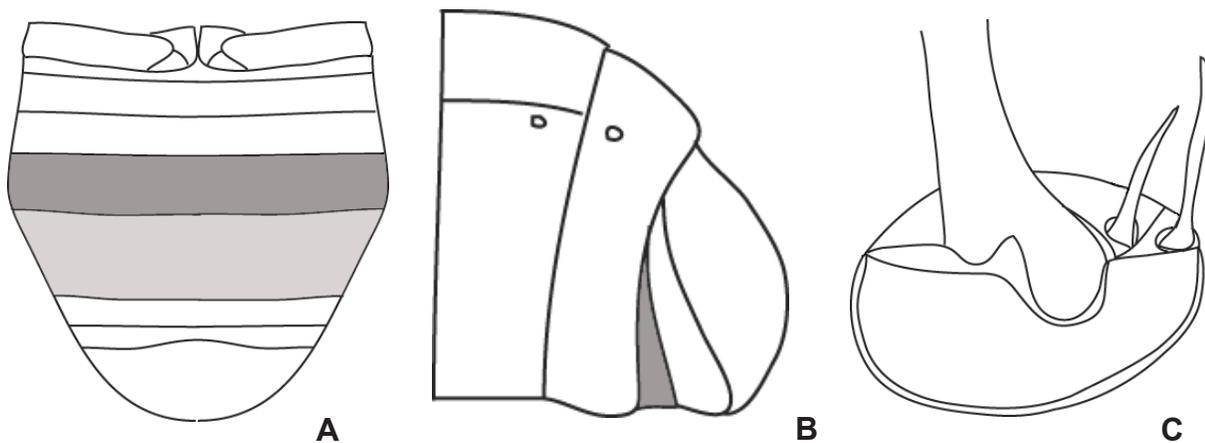
Photographs of types were taken with a Nikon digital camera at their respective collections. While these lack the desired photographic quality, they do document the type's general appearance. If loaned material of lectotypes, syntypes, or homeotypes was available, they were photographed using a Syncrosopy Auto-montage 3D imaging system. Dorsal and left lateral habitus images were taken to demonstrate general appearance.

## Key to the Macroductylini Genera

The key is based on the type species only and is representative primarily of males. Specific characters are illustrated to facilitate identification. All Macroductylini can be distinguished from other melolonthine tribes by the following: length of the fifth ventrite longer than the fourth ventrite when viewed ventrally (Fig. A), fifth ventrite lacking a complete suture between the tergite and sternite (Fig. B), and the metathoracic tibial spurs (if present) offset, allowing the metatarsus to move past them (Fig. C).

1. Mesosternal process extending anteriorly to prosternum (Fig. 144); 5<sup>th</sup> ventrite (=propygidium) raised medially along anterior aspect, posteriorly raised into a prominent process (Fig. 145) ..  
 ..... *Pectinosoma*
- Mesosternal process never extending anteriorly to prosternum; 5<sup>th</sup> ventrite (=propygidium) variable, never raised into a prominent process. .... 2

- 2(1). Pronotum with posterior margin bearing a single, narrow, acuminate process medially (Fig. 15); 1<sup>st</sup> abdominal ventrite with posterior margin bearing a narrow, blunt acuminate process medially, process extending nearly to posterior margin of 3<sup>rd</sup> ventrite (Fig. 16) ..... **Ancistrosoma**  
 — Pronotum with posterior margin variable, never with a single narrow, acuminate process medially; 1<sup>st</sup> abdominal ventrite with posterior margin straight, never with an acuminate process medially ..... **3**
- 3(2). Clypeus with dorsolateral angles strongly projecting dorsally, forming “horns” (Fig. 51), in dorsal view anterior angles strongly produced dorsoanteriorly, forming a pair of long “horns” ..... **Ceratolontha**  
 — Clypeus often produced forwardly into a trapezoidal process, but not forming “horns” ..... **4**
- 4(3). Clypeus projecting anteriorly, with lateral margins strongly indented (Fig. 158), surface of prementum with raised carinae, one medial and one U-shaped (Fig. 160) ..... **Rhinaspis**  
 — Clypeus with lateral margin never strongly indented; prementum variable ..... **5**
- 5(4). Meso- and metathoracic claws simple ..... **6**  
 — Meso- and metathoracic claws split ..... **7**
- 6(5). Elytra often clothed in scale-like setae; 5<sup>th</sup> ventrite with medial surface bearing a semicircular, recessed pocket, margins of which are raised ..... **Calodactylus**  
 — Elytra not clothed in scale-like setae; 6<sup>th</sup> ventrite with medial surface bearing a semicircular-shaped pocket, margins of which are raised (Fig. 81) ..... **Dasyus**
- 7(5). Pronotum widest anteriorly, posterior angles acute (Fig. 103); pygidium longer than wide, posterior margin concave (Fig. 104); prementum elongate and flattened (Fig. 102); small beetles (5.5-5.8 mm long) ..... **Hercitis**  
 — Pronotum widest medially or posteriorly, posterior angles variable; pygidium variable, if longer than wide, never with the posterior margin concave; prementum variable, if elongate and flattened, always with the pygidium wider than long; beetles usually greater than 5.6 mm long ..... **8**
- 8(7). Prementum rectangular, ligula narrowed between labial palpi, strongly produced anteriorly, often appearing bilobed (Fig. 149 and 150); pretarsus of meso- and metathoracic claws often unequal in length ..... **Plectris**



**Figure A-C.** Key characters. **A)** Abdominal ventrites five (lightly shaded) and four (darkly shaded). **B)** Ventrites 4, 5, 6, and 7 (pygidium) and 4<sup>th</sup> tergite in lateral view. **C)** Metathoracic tibia and tibial spurs in posteroventral view.

- Prementum and ligula variable, but the ligula is never strongly produced anterior and never bilobed; pretarsus of meso- and metathoracic claws variable ..... 9
- 9(8). Prementum quadrate with a raised U-shaped longitudinal carina (Fig. 37); ocular canthus > 2/3 ocular width; frons in lateral profile strongly angled at 90° (Fig. 35); elytra in dorsal view rectangular, quadrate, surface uneven, often with scale-like setae; small beetles (4.0-8.0 mm long) ..... ***Barybas***
- Prementum variable, if quadrate never with a raised U-shape longitudinal carina; ocular canthus < 2/3 ocular width; frons variable; elytra in dorsal view never rectangular, quadrate, surface variable, beetles variable in size ..... 10
- 10(9). Metathoracic tibia strongly clavate, distal margin broadly rounded, setose (Fig. 5); prementum quadrate, ventral surface lobed (Fig. 3) ..... ***Agaocnemis***
- Metathoracic tibia never strongly clavate, distal margin not as above; prementum shape and ventral surface variable ..... 11
- 11(10). Prementum elongate (length > width) ..... 12
- Prementum quadrate, rectangular or subtriangular ..... 21
- 12(11). Prementum flattened; pygidium distinctly subtriangular in shape; small, elongate beetles (5.2-5.7 mm in length) ..... ***Pristerophora***
- Prementum medially grooved; pygidium variable in shape, if subtriangular then never a small, elongate beetle ..... 13
- 13(12). Pronotum cordiform, widest medially (Fig. 128), body glabrous, black ..... ***Manodactylus***
- Pronotum variable, never cordiform; body color variable ..... 14
- 14(13). Pronotum elongate (length > width), widest medially or anteriorly, narrowing at anterior and posterior margins ..... 15
- Pronotum rectangular or quadrate, widest medially or posteriorly ..... 16
- 15(14). Pronotum hexagonal, oblong, posterior margin convex (Fig. 57); scutellum elongate, subtriangular ..... ***Chariodactylus***
- Pronotum hexagonal, transverse, posterior margin weakly concave (Fig. 123); scutellum subtriangular but not elongate ..... ***Macroductylus***
- 16(14). Pronotum widest medially (width > length), anterior and posterior margins not distinctly narrowed ..... 17
- Pronotum widest posteriorly, width of anterior margin less than width of posterior margin ... 18
- 17(16). Elytral surface uneven, mottled, brownish in color, striae present, posterior umbones prominent ..... ***Chremastodus***
- Elytral surface never uneven, often greenish, sometimes setose, striae absent, posterior umbones well developed (Fig. 62); pronotum often medially grooved ..... ***Chariodema***
- 18(16). Elytra broadly ovate, width equal to or greater than length; anterior elytral angles often toothed (Fig. 86); metathoracic femora often greatly enlarged, broadly ovate ..... ***Dicrania***
- Elytra elongate or, if ovate, not broadly so; anterior angles of elytra not toothed; metathoracic femora never greatly enlarged ..... 19
- 19(18). Body shape ovate in dorsal view, rotund in lateral view, often clothed in scale-like setae; pronotum transverse, anterior angles acute (Fig. 113) ..... ***Isonychus***
- Body elongate, never rotund, never covered in scale-like setae ..... 20

- 20(19). Propygidium of male elongate laterally, forming two long subtriangular plates (Fig. 98); prothoracic tibia with tooth present ..... ***Gastrohoplus***  
 — Propygidium of males not as above; prothoracic tibia with spur, but lacking teeth (Fig. 165) ..... ***Schizochelus***
- 21(11). Prementum quadrate (length = width) or rectangular (length < width) ..... **23**  
 — Prementum subtriangular (Figs. 25 and 117) ..... **22**
- 22(21). Prementum medially grooved; clypeus narrowly ovate; antennae with 8 antennomeres ..... ***Issacaris***  
 — Prementum not medially grooved; clypeus broadly rounded, antennae with 9 antennomeres ..... ***Anoplosiagum***
- 23(21). Prementum grooved medially ..... **24**  
 — Prementum flattened, medially lobed or with a raised U-shaped carina ..... **28**
- 24(23). Labrum small, subtriangular; clypeus elongate in frontal view (Fig. 9); antennomeres 7-9 forming an elongate club; club lamellae equal to the length of antennomeres 2-6, combined (Fig. 11) .. ***Alvarinus***  
 — Labrum ovate or semicircular, never small and subtriangular; clypeus not noticeably elongate in frontal view; antennal club lamellae never elongate as above ..... **25**
- 25(24). Posterior margin of pronotum lobed medially (Fig. 30); elytral surface with weak striae, interstitial regions slightly raised, surface with short white setae; pygidium large, subtriangular (Fig. 32) ..... ***Astaenosiagum***  
 — Posterior margin of pronotum bi-emarginate or bidentate, never lobed; elytral surface variable, pygidium variable ..... **26**
- 26(25). Pronotum with posterior margin medially bi-emarginate (Fig. 135); scutellum densely covered with white setae; elytra mottled in coloration; prelabrum often visible (Fig. 133) .... ***Manopus***  
 — Pronotum with posterior margin medially tridentate (Fig. 46), scutellum and elytra variable; prementum not visible ..... **27**
- 27(26). Prothoracic sternum with posterior margin not bearing a process, not extending over mesosternum; scutellum not chordate, mesothoracic tarsi in males highly modified, often hook-like (Fig. 92); antennal club often greatly elongate ..... ***Gama***  
 — Prothoracic sternum with posterior margin medially bearing a process extending posterad of the coxae, extending over mesosternum (Fig. 47); scutellum chordate (Fig. 48), mesothoracic tarsi never hook-like, antennal club not noticeably elongate ..... ***Ceraspis***
- 28(23). Ventral surface of prementum with a weakly raised U-shaped carina (Fig. 19) ..... ***Anomonyx***  
 — Ventral surface of prementum flattened or medially raised (lobed) ..... **29**
- 29(28). Antennal club 5-segmented (Fig. 139); meso- and metathoracic tarsal segments enlarged ..... ***Oedichira***  
 — Antennal club 3 or 4-segmented, meso- and metathoracic tarsal segments variable, never distinctly enlarged ..... **30**
- 30(29). Antennal club 4-segmented (Fig. 75), large, rotund beetles (7.5 mm or greater); clypeus semicircular in dorsal view; labial palpi not noticeably elongate; pronotum with anterior margin narrower than posterior margin (Fig. 76) ..... ***Ctenotis***  
 — Antennal club 3-segmented, body size and shape variable, if large and rotund (7.5 mm or greater), clypeus ovate (bilobed in frontal view), in dorsal view; labial palpi elongate; pronotum with anterior margin equal to posterior margin ..... **31**

- 31(30). Ligula not extended anteriorly (Fig. 69); elytra slightly wider than long, widest in posterior 1/4, medium to large, rotund beetles ..... *Clavipalpus*  
 — Ligula extending anteriorly (Fig. 107); elytra longer than wide, small, elongate beetles (7.0 to 7.5 mm long) ..... *Hercitis*

### Genera Comprising the Tribe Macroductylini

#### *Agaocnemis* Moser, 1918

(Figure 1-6)

*Agaocnemis* Moser, 1918: 115. Type species *Agaocnemis pruina* Moser, 1918, by monotypy.

#### Taxonomic Notes

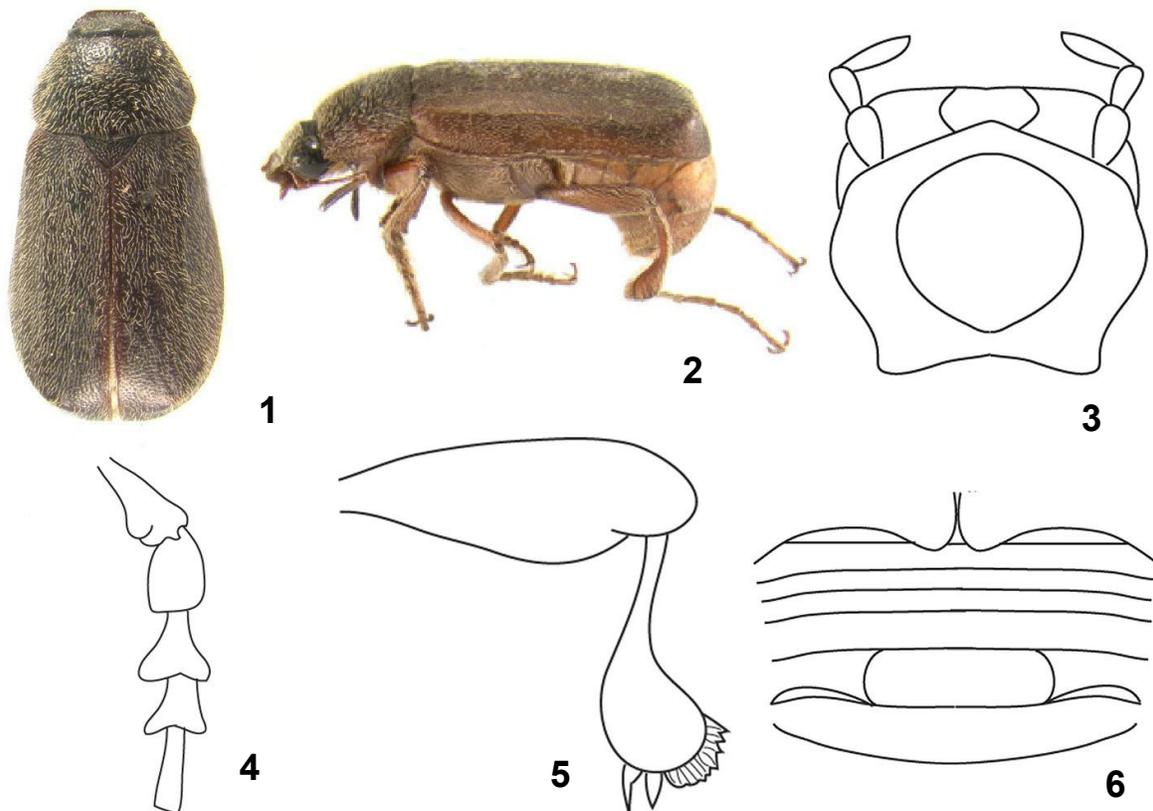
The following generic diagnosis is based on a single dissected male paratype of the type species, *A. pruina* (ZMHB).

#### Generic diagnosis

This genus is characterized by its elongate body, quadrate prementum with lobed ventral surface, strongly clavate metathoracic tibia, with distal margin broadly rounded, setose; 6<sup>th</sup> ventrite equal in length to 4<sup>th</sup> ventrite, flattened medially, forming an ovate region.

#### Generic redescription

*Measurements*: prothorax at widest point 4.7 mm, elytra at widest point 5.8 mm, elytral length 12.7 mm.



**Figure 1-6.** *Agaocnemis pruina* Moser (male). **1)** Dorsal habitus. **2)** Left lateral view. **3)** Prementum, ligula and labial palpi, ventral view. **4)** Prothoracic tibia (male). **5)** Left metathoracic femur and tibia (male). **6)** Visible abdominal segments, ventral view.

*Color and vestiture:* Body dark brown, vestiture consisting of small reddish-brown setae.

*Head:* Clypeus not coplanar with frons; frons angled at 30°; labrum in frontal view broadly ovate, deeply emarginate, labrum coplanar with clypeus; labium with prementum quadrate, ventral surface raised medially (Fig. 3); mandibles in dorsal view narrowly rectangular, scissorial area bluntly produced, molar area well developed; maxillary palpi with apical palpomeres broadly ovate; antennae with 10 antennomeres, antennomeres 8-10 forming an elongate club, the length of the lamellae equal to combined length of segments 3-7.

*Prothorax:* Pronotum oblong, transverse, widest in posterior 1/4, anterior angles acute, lateral margins convex, posterior angles obtuse, posterior margin convex, medially lobed, dorsal surface rounded; prothoracic leg with coxa transverse; tibia with dorsal margin bidentate; tarsomeres broadly clavate (Fig. 4); pretarsus with claws divergent, equal in length, both claws narrowly split, upper and lower lobes of individual claw narrow.

*Mesothorax:* Scutellum subtriangular; elytra longer than wide, widest in posterior 1/4, elytral epipleuron flattened, dorsal surface lacking striae, anterior and posterior umbones well developed; pretarsus similar to prothoracic pretarsus.

*Metathorax:* Coxae contiguous; femur ovate, widest in distal 1/2; tibia very strongly clavate, narrow in proximal 1/2, widest in distal 1/2, posteroventral margin with two stout, long spurs, each arising at same level as tarsal articulation joint, posterior margin with a shallow, U-shaped groove (Fig. 5); pretarsus with claws similar to those of prothoracic legs.

*Abdomen:* Ventrites 2-4 equal in length, 5<sup>th</sup> ventrite (= propygidium) equal in length to combined lengths of ventrites 3-4, ventrite and sternite of 5<sup>th</sup> abdominal segment not separated by a distinct suture, spiracle placed medially at the anterior region of a shallow groove-like depression, 6<sup>th</sup> ventrite equal in length to that of ventrite 4, flattened medially, forming an ovate region (Fig. 6); pygidium subtriangular, wider than long.

### Diversity and Geographic Distribution

*Agaocnemis* is monotypic, with *A. pruina* recorded only from Brazil.

### *Alvarinus* Blanchard, 1850

(Figure 7-11)

*Alvarinus* Blanchard, 1850: 123. Type species *Alvarinus hilarii* Blanchard, 1850, by subsequent designation (Evans 2003).

*Corminus* Burmeister, 1855: 39. Type species *Corminus canescens* Burmeister, 1855, by subsequent designation (Evans 2003). [New Synonym]

### Taxonomic Notes

The following generic diagnosis is based on a homeotype of the presumptive syntype of the type species *A. hilarii*, located at the NMNH and identified with a Blanchard label. A syntype of *C. canescens*, type species of *Corminus* Burmeister (MLUH) was also used to verify the generic limits of *Alvarinus*.

### Generic diagnosis

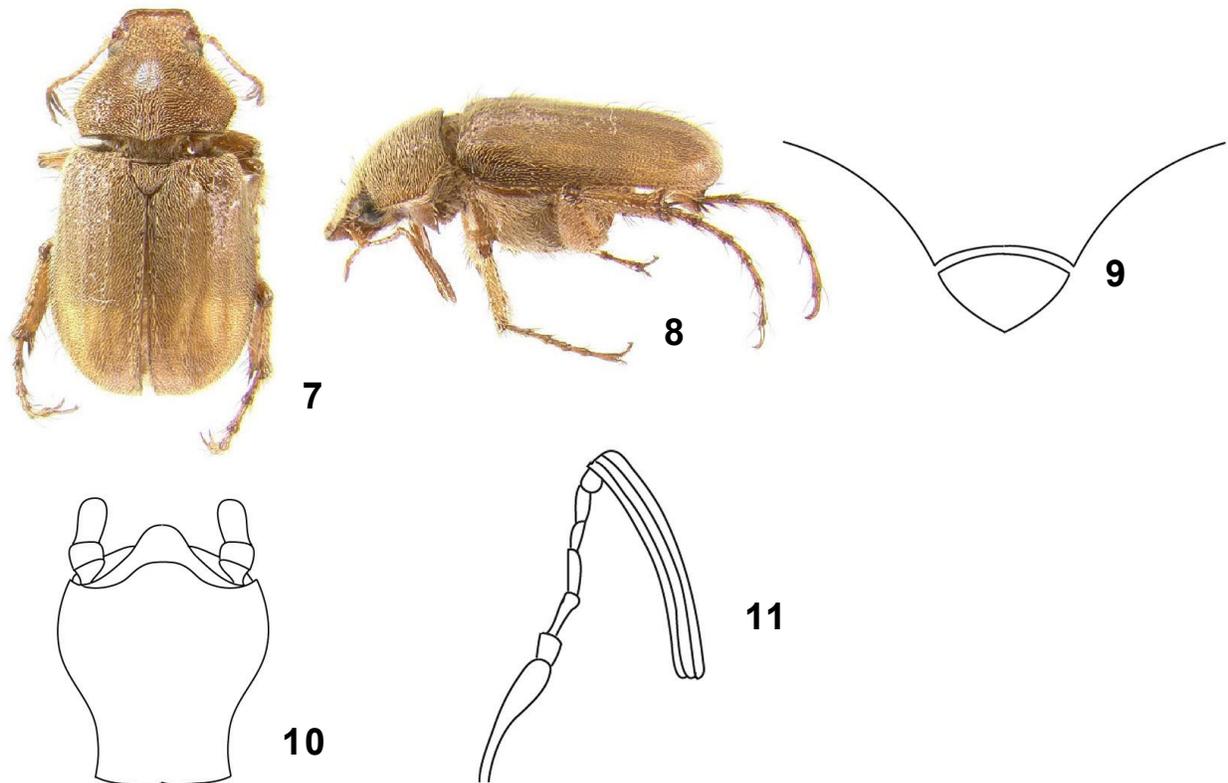
The genus is characterized by its elongate body, semicircular labrum and elongated clypeus in frontal view, quadrate prementum, with ventral surface medially lobed; the antennae with nine antennomeres, with antennomeres 7-9 forming an elongate club, the length of which equals the combined length of antennomeres 2-6.

### Generic redescription

*Measurements (Alvarinus hilarii):* Prothorax at widest point 3.5 mm, elytra at widest point 4.4 mm, elytral length 8.6 mm.

*Color and vestiture (Alvarinus hilarii):* Body dark brown to black, vestiture consisting of dense, yellow to gold setae.

*Head:* Clypeus not coplanar with frons; frons angled at 45°; labrum in frontal view semicircular, small, slight medial groove (Fig.9), labrum not coplanar with clypeus; labium with prementum quadrate,



**Figure 7-11.** *Alvarinus canescens* (Burmeister) (male). **7)** Dorsal habitus. **8)** Left lateral view. **9)** Clypeus and labrum, frontal view. **10)** Prementum, ligula and labial palpi, ventral view. **11)** Antenna.

medially lobed, surface flattened (Fig. 10); mandibles in dorsal view rectangular, scissorial area bluntly produced into a thin rectangular process, molar area prominent; maxillary palpi with apical palpus ovate, equal to length of 2<sup>nd</sup> segment, apex obtuse; antennae with 9 antennomeres, antennomeres 7-9 forming the elongate club, equal to the length of antennomeres 2-6 combined (Fig. 11).

**Prothorax:** Pronotum oblong, transverse, widest medially, anterior angle obtuse, lateral margins convex, posterior angle obtuse, posterior margin convex, medially lobed, dorsal surface rounded; prothoracic leg with coxa transverse; tibia dentate or bidentate, pretarsus with claws divergent, equal in length, both claws narrowly split, upper lobe narrow, lower lobe broad on individual claw.

**Mesothorax:** Scutellum subtriangular; elytra longer than wide, widest in posterior 2/3, elytral epipleuron forming a narrow bead, dorsal surface with two weak, vertical striae, striae smooth, interstitial region punctate, anterior umbone prominent, posterior umbone weak; pretarsus similar to prothoracic pretarsus.

**Metathorax:** Coxae clearly separated; femur ovate, widest medially; tibia triangular, narrow proximally, widest medially, posteroventral margin with a pair of large, stout spurs, anterior spur shorter than posterior spur, spurs arising at same level as tarsal articulation joint, posterior margin with a shallow, U-shaped groove; claws similar to prothoracic claws.

**Abdomen:** Ventrites 2-4 subequal in length, 5<sup>th</sup> ventrite (= propygidium) equal to length of ventrites 3-4 combined, ventrite and sternite of 5<sup>th</sup> abdominal segment not separated by a distinct suture, partial groove present, spiracle located medially, 6<sup>th</sup> ventrite equal to length of 4<sup>th</sup> ventrite length, posterior margin concave medially; pygidium subtriangular, wider than long.

### Diversity and Geographic Distribution

*Alvarinus* currently comprises 16 Brazilian, Argentinean, Bolivian, and Ecuadorian species. No species level key is currently available for members of this genus.

**Ancistrosoma** Curtis, 1835

(Figure 12-16)

*Ancistrosoma* Curtis, 1835: 307. Type species *Ancistrosoma klugi* Curtis, 1835, by monotypy.**Taxonomic Notes**

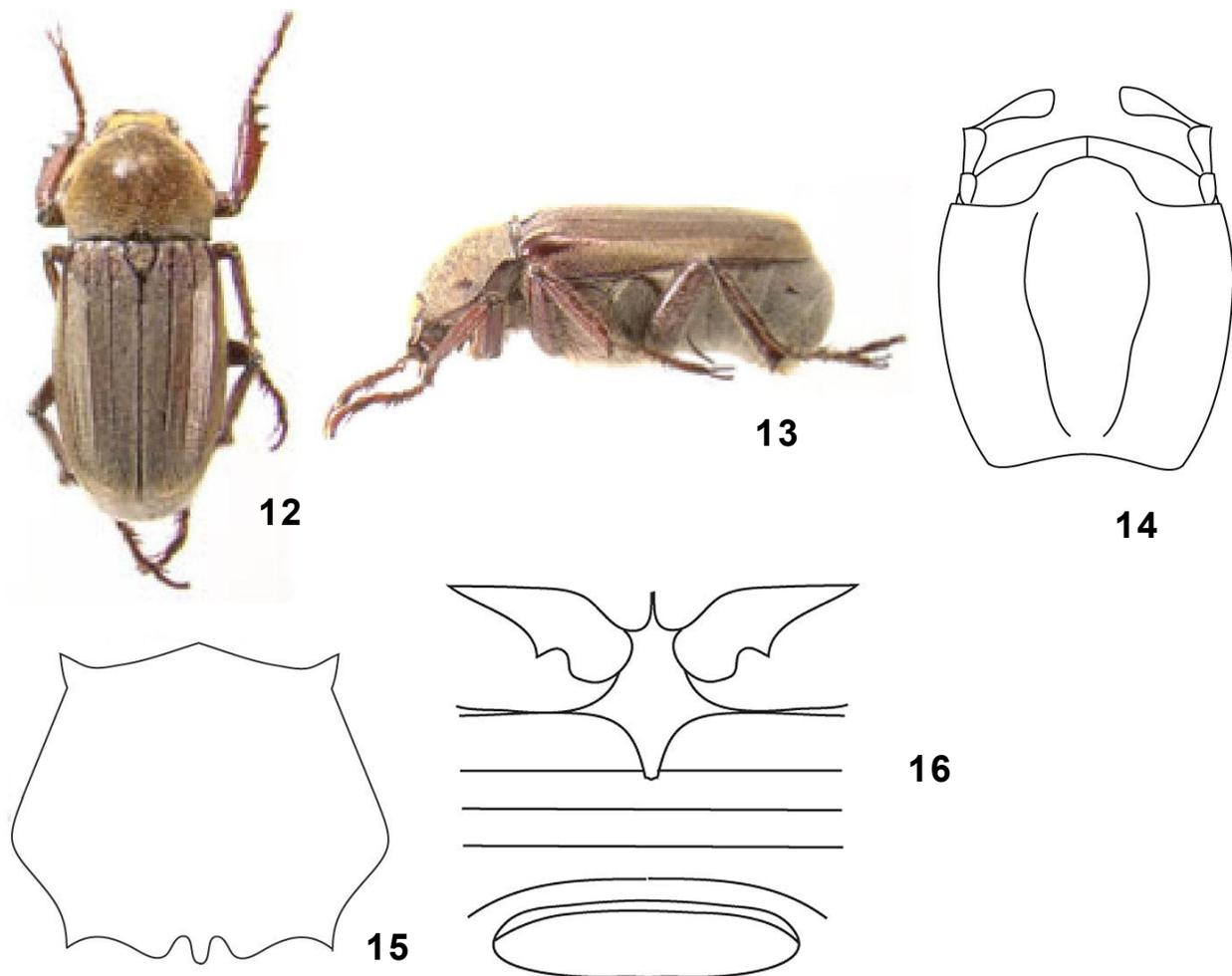
The diagnosis is based on a dissected homeotype of *A. trinitatis* Arrow (IRC). Specimens were compared with the type species located at the BMNH. The type species, *A. klugi* Curtis, was not located at the BMNH. Specimens of *A. klugi* were located at several collections and a comparison of generic characters was made with *A. trinitatis*.

**Generic diagnosis**

The genus is characterized by its large size, elongate body, pronotum with the posterior margin bearing a single, narrow acuminate medial process; mesosternum medially interrupted by a broad triangular extension of the prosternum; 1st abdominal ventrite with posterior margin bearing a narrow, blunt acuminate process medially in males.

**Generic redescription**

*Measurements*: Prothorax at widest point 6.2 mm, elytral at widest point 9.6 mm, elytral length 20.0 mm.



**Figure 12-16.** *Ancistrosoma trinitatis* Arrow (male). **12)** Dorsal habitus. **13)** Left lateral view. **14)** Prementum, ligula and labial palpi, ventral view. **15)** Pronotum, dorsal view. **16)** Visible abdominal segments, ventral view.

*Color and vestiture:* Body brown, surface glabrous, vestiture consisting of yellowish setae.

*Head:* Clypeus not coplanar with frons; frons angled at 30°; labrum in frontal view narrowly ovate, weakly emarginate, labrum not coplanar with clypeus; labium with prementum quadrate, ventral surface medially grooved (Fig. 14); mandibles rectangular, scissorial area bluntly produced, narrow, concave, molar area bluntly produced adorally; maxillary palpi with apical palpus ovate, apex acute; antennae with 9 antennomeres, antennomeres 7-9 forming the elongate club, equal in length to antennomeres 2-6 combined.

*Prothorax:* Pronotum oblong, transverse, width subequal to length, widest medially, anterior angle acute, appearing toothed, lateral margin convex, posterior angle acute, appearing toothed, posterior margin weakly concave, medially with a narrow acuminate process, dorsal surface rounded (Fig. 15); prothoracic leg with coxa elongate; tibia bidentate; pretarsus with claws divergent, equal in length, both claws broadly split, upper lobe narrow, slightly longer than narrow, lower lobe of individual claw.

*Mesothorax:* Scutellum subtriangular, anterior margin convex, medially with a deep emargination; elytra longer than wide, widest in anterior 1/4, elytral epipleuron flattened, membranous, dorsal surface with three weakly raised striae, interstrial regions setose, anterior and posterior umbones strongly produced; pretarsus similar to prothoracic pretarsus.

*Metathorax:* Coxae widely separated; femur ovate, width subequal along entire length; tibia subtriangular, narrow proximally, widest distally, posteroventral margin with a pair of elongate spurs, anterior spur short, spurs arise from same plane as tarsal segment articulation joint, posterior margin with a shallow, U-shaped groove; pretarsus with claw articulation grooves present; claws similar to prothoracic claws.

*Abdomen:* First ventrite equal in length to ventrites 2-4, posterior margin medially with a narrow, blunt acuminate process, process extends approximately to posterior margin of 3<sup>rd</sup> ventrite (Fig. 16), 2<sup>nd</sup> ventrite length equal to length of ventrites 3-4 combined, partially obscured by 1<sup>st</sup> ventrite, ventrites 3-4 equal in length, 5<sup>th</sup> ventrite (= propygidium) equal to 1.5X length of 4<sup>th</sup> ventrites, ventrite and sternite of 5<sup>th</sup> abdominal segment of propygidium not separated by a suture, spiracle placed in anterior 1/4, 6<sup>th</sup> ventrite equal in length to 5<sup>th</sup> ventrite, flattened, posterior margin straight, membranous; pygidium subtriangular, wider than long, posterior margin weakly concave.

### Diversity and Geographic Distribution

*Ancistrosoma* comprises 15 species. Their distributions are centered in Colombia, Ecuador, Peru, Venezuela, Trinidad and Tobago, and a single species is recorded from Argentina. Keys to species are provided by Arrow (1913).

### *Anomonyx* Saylor, 1940

(Figure 17-21)

*Anomonyx* Saylor, 1940: 46. Type species *Anomolonyx uruguayensis* Moser, 1921, by monotypy.

### Taxonomic Notes

The following generic diagnosis is based on a single dissected paratype of the generic type species *A. uruguayensis* (ZMHB).

### Generic diagnosis

This genus is characterized by its rotund body and rounded elytral shape; long labial palpi, ventral surface of the quadrate prementum with a raised U-shape surface, and the antennae with 8 antennomeres, with antennomeres 6-8 forming the elongate club, club length equal to length of antennomeres 2-5 combined.

### Generic redescription

*Measurements:* Prothorax at widest point 6.0 mm, elytra at widest point 8.0 mm, length 14.2 mm.

*Color and vestiture:* Body reddish brown, vestiture consisting of golden setae dorsally and ventrally, strongly setose ventrally.

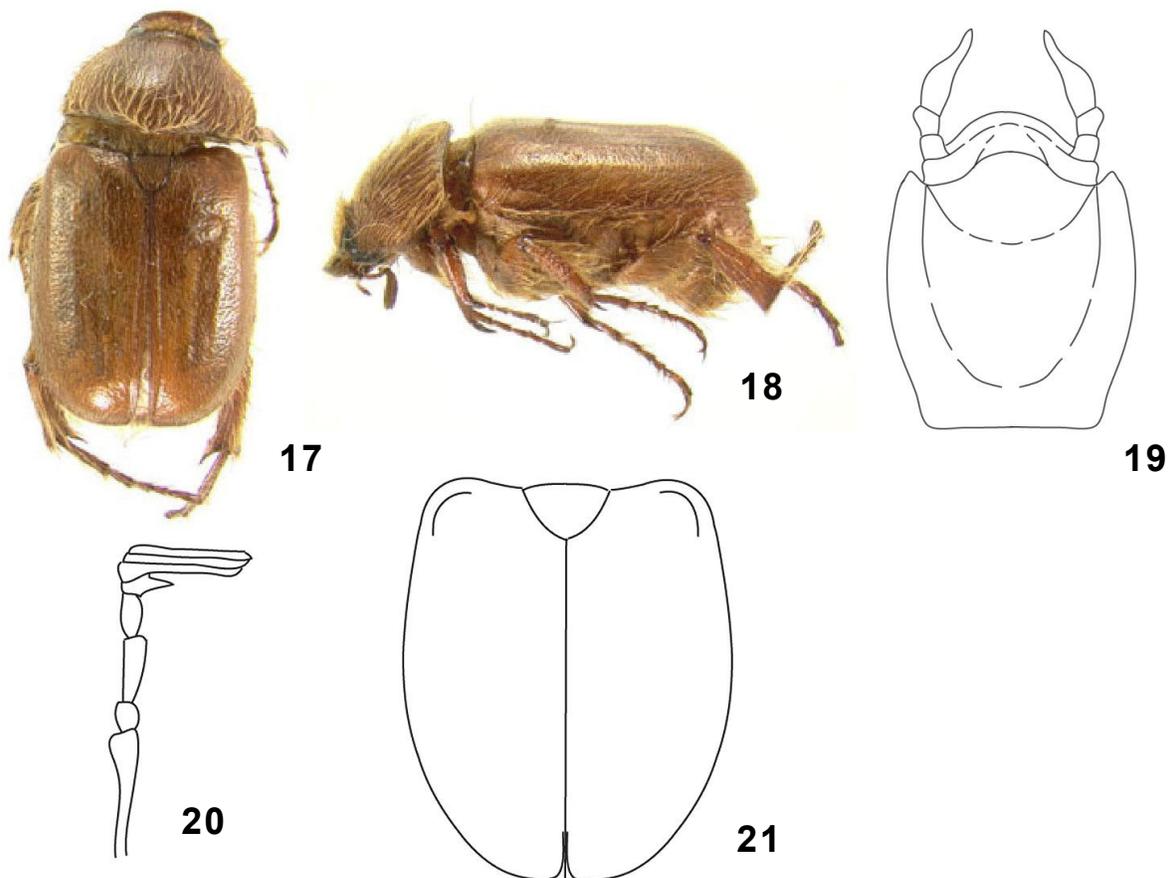
**Head:** Clypeus not coplanar with frons; frons angled at 60°; labrum in frontal view ovate, medially with a deep emargination, labrum not coplanar with clypeus; labium with prementum quadrate, ventral surface forming a raised, U-shaped transverse ridge (Fig. 19); mandibles in dorsal view semicircular, scissorial area bluntly produced, medially with a slight emargination, posterior margin of scissorial area produced into a blunt point, molar area lobed, weakly sclerotized; maxillary palpi with apical palpus ovate, equal to segments 2-3, apically blunt, surface flattened on adoral margin; antennae 8-segmented, segments 6-8 forming the club, equal to length to segments 2-5 combined (Fig. 20).

**Prothorax:** Pronotum oblong, transverse, widest in posterior 1/3, anterior angle obtuse, lateral margin convex, posterior angle obtuse, posterior margin straight, medially lobed, dorsal surface rounded; prothoracic legs with coxa transverse; tibia dentate, pretarsus with claws slightly divergent, equal in length, both claws narrowly split, upper and lower lobes of each claw narrow, base of claw weakly toothed.

**Mesothorax:** Scutellum narrowly subtriangular; elytra longer than wide, width fairly uniform (Fig. 21), elytral epipleuron flattened, weakly grooved, dorsal surface lacking striae, anterior umbone weakly produced, posterior umbone absent; pretarsus similar to prothoracic pretarsus.

**Metathorax:** Coxa narrowly separated; femur ovate, widest in proximal 1/4; tibia triangular, narrow in proximal 1/4, widest medially, posteroventral margin with a single long spur, spur arising at same level as tarsal articulation joint, posterior margin with a deep, U-shaped groove; pretarsus with claws similar to prothoracic claws.

**Abdomen:** Ventrites 2-4 equal in length, sutures distinct, 5<sup>th</sup> ventrite (= propygidium) equal to length of ventrites 1-4 combined, posterior margin membranous, ventrite and sternite of 5<sup>th</sup> abdominal segment lacking suture, spiracle in posterior 1/4, situated at apex of triangular groove, 6<sup>th</sup> ventrite 1/2 length of 5<sup>th</sup> ventrite length, slight membranous margin on posterior margin; pygidium subtriangular, wider than long, posterior margin rounded.



**Figure 17-21.** *Anomolonyx uruguayensis* Moser (male). **17)** Dorsal habitus. **18)** Left lateral view. **19)** Prementum, ligula and labial palpi, ventral view. **20)** Antenna. **21)** Elytra, dorsal view.

### Diversity and Geographic distribution

The monotypic *Anomonyx* (*A. uruguayensis*) is recorded only from Uruguay.

### *Anoplosiagum* Blanchard, 1850

(Figure 22-26)

*Anoplosiagum* Blanchard, 1850: 119. Type species *Anoplosiagum rufipenne* (Fabricius), 1801, by subsequent designation (Lacordaire 1856: 264).

### Taxonomic Notes

The following generic diagnosis is based on a dissected homeotype of the presumptive syntype of *A. sulcatum* Blanchard located at the MNHC, and identified with a Blanchard label. Type specimens of the type species, *A. rufipenne* (Fabricius), were not located at the MNHC.

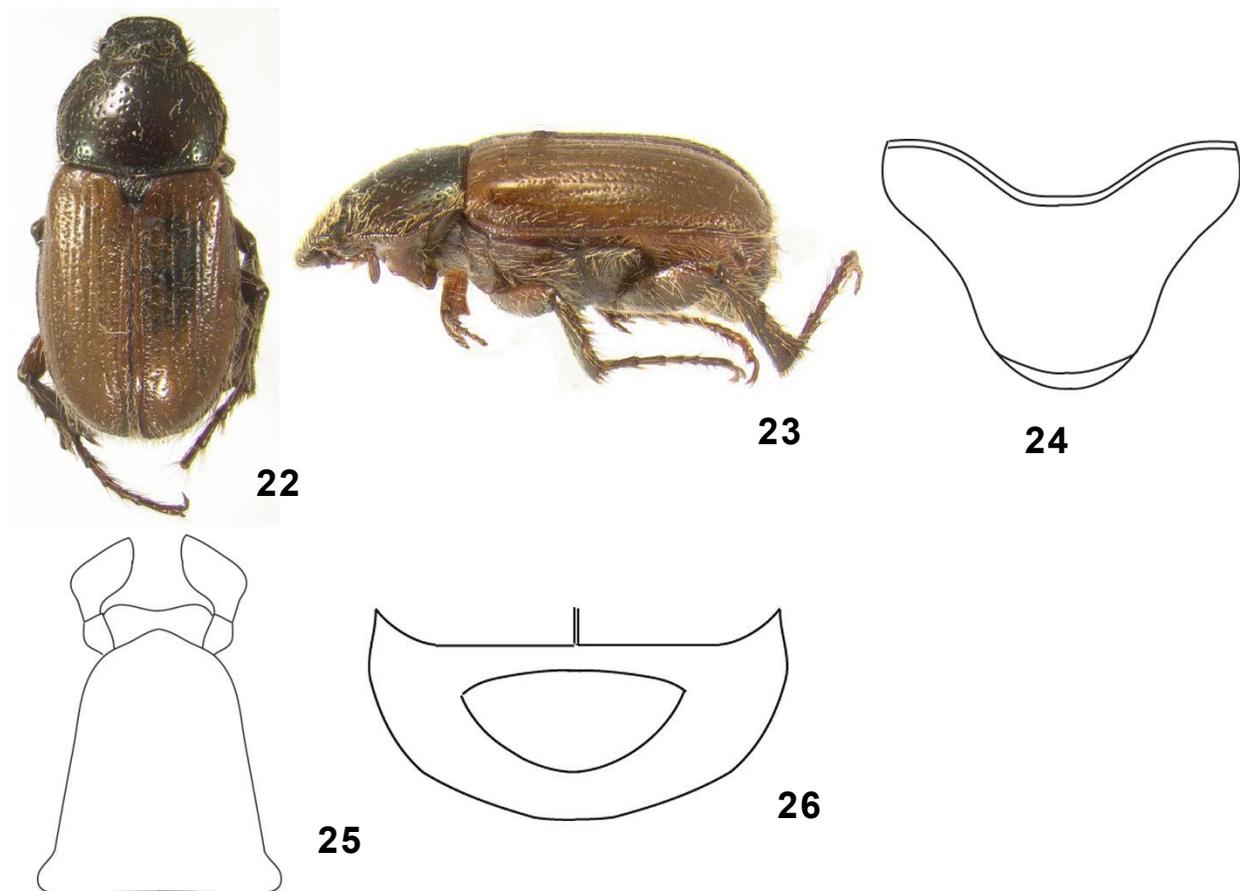
### Generic diagnosis

This genus is characterized by its elongate shape, flattened lateral profile, often rounded clypeus in dorsal view, small, ovate or semicircular labrum in frontal view, subtriangular prementum.

### Generic redescription

*Measurements*: Prothorax at widest point 5.3 mm, elytra at widest point 6.7 mm, length 14.0 mm.

*Color and vestiture*: Pronotum black, glabrous, elytra black to dark reddish-brown, ventral surface reddish-brown, vestiture consisting of scattered long reddish setae.



**Figure 22-26.** *Anoplosiagum sulcatum* Blanchard. **22)** Dorsal habitus. **23)** Left lateral view. **24)** Clypeus and labrum, frontal view. **25)** Prementum, ligula and labial palpi, ventral view. **26)** Pygidium, dorsal view.

*Head:* Clypeus not coplanar with frons; frons angled at 30°; labrum in frontal view small, ovate to semicircular, medially with a shallow emargination (Fig. 24); labium with prementum trapezoidal, elongate, ventral surface flattened (Fig. 25); mandibles in dorsal view rectangular, scissorial region sinuate, weakly lobed distally, molar area well sclerotized; maxillary palpi with apical palpus narrowly elongate, ovate, weakly flattened on ventral margin; antennae with 9 antennomeres, antennomeres 7-9 forming the elongate club, equal to length of antennomeres 2-6 combined.

*Prothorax:* Pronotum oblong, transverse, anterior angles strongly acute, appearing toothed, lateral margin convex, beaded, posterior angle obtuse, posterior margin straight, medially lobed, beaded, dorsal surface rounded; prothoracic leg with coxa transverse; tibia distal 1/4 with a tooth, distal 1/4 with an acute spur; pretarsus with tarsal claws divergent, equal in length, both claws broadly split, upper and lower lobes narrow on each claw.

*Mesothorax:* Scutellum subtriangular; elytra longer than wide, width fairly even, in lateral profile elytral epipleuron flattened, dorsal surface distinctly striate, striae margins raised, smooth, anterior umbone slightly produced, posterior umbone weak; pretarsus similar to prothoracic pretarsus.

*Metathorax:* Coxa widely separated; femur ovate, widest medially; tibia triangular, narrow proximally, widest medially, posteroventral margin with pair of equal, long spurs, spurs at same level as tarsal articulation joint, posterior margin with a deep, U-shaped groove; pretarsus with tarsal claws similar to prothoracic claws.

*Abdomen:* With ventrites 2-4 equal in length, sutures distinct, 5<sup>th</sup> ventrite equal to length of 3<sup>rd</sup> and 4<sup>th</sup> ventrites combined, margin membranous, ventrite and sternite of 5<sup>th</sup> abdominal segment lacking suture, spiracle situated in posterior 1/4, at apex of a weak groove, 6<sup>th</sup> ventrite semicircular in ventral view, posterior margin lower than remaining ventrite; pygidium subtriangular, wider than long, posterior margin rounded (Fig. 26).

### Diversity and Geographic distribution

*Anoplosiagum* comprises 31 species, recorded from Brazil, Colombia, Cuba, and Paraguay. Keys to the Cuban species are available (Chapin 1932).

### *Astaenosiagum* Martínez, 1957

(Figure 27-32)

*Astaenosiagum* Martínez, 1957: 50. Type species *Schizochelus longipes* F. Philippi, 1861, by original designation.

### Taxonomic Notes

The following generic diagnosis is based on a dissected homeotype of *S. longipes*, the generic type species. The type species and homeotypes designated by Martínez were borrowed from the MNNC.

### Generic diagnosis

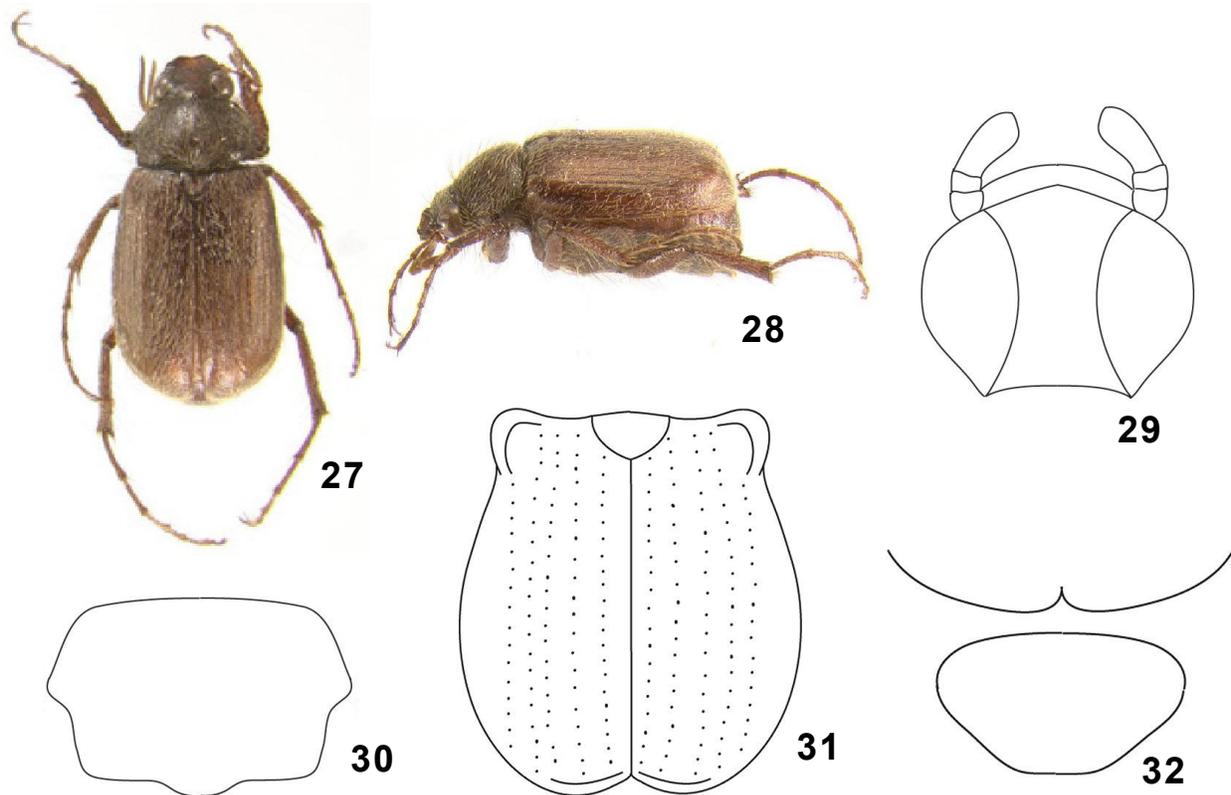
This genus is characterized by its elongate body, small size, body flattened in lateral profile, quadrate prementum, with ventral surface medially grooved; oblong pronotum, with lateral margins serrate; elytra with vestiture of long, whitish setae; large, subtriangular pygidium.

### Generic redescription

*Measurements:* Prothorax at widest point of pronotum 3.8 mm, elytra at widest point 6.0 mm, length 10.5 mm.

*Color and vestiture:* Head and pronotum reddish brown, with vestiture consisting of long whitish setae covering body.

*Head:* Clypeus coplanar with frons; frons angled at 30°; labrum in frontal view narrow, ovate, weakly emarginate, labrum coplanar with clypeus; labium with prementum quadrate, ventral surface with a broad, shallow, medial groove (Fig. 29); mandibles in dorsal view subtriangular, scissorial area weakly developed, slightly concave, weakly sclerotized, molar region weakly developed; maxillary palpi with api-



**Figure 27-32.** *Astaenosiagum longipes* (F. Philippi). **27)** Dorsal habitus. **28)** Left lateral view. **29)** Prementum, ligula and labial palpi, ventral view. **30)** Pronotum, dorsal view. **31)** Scutellum, and elytra, dorsal view. **32)** Pygidium dorsal view.

cal palpus elongate, ovate, thin in profile, apex with a sensory spot; antennae with 9 antennomeres, antennomeres 7-9 forming the club, club equal to length of antennomeres 2-6 combined.

*Prothorax:* Pronotum oblong, transverse, widest medially, anterior angle obtuse, lateral margin convex, serrate, posterior angle obtuse, posterior margin straight, medially lobed (Fig. 30); prothoracic leg with coxae transverse; tibia dentate, long spur in distal 1/4; pretarsus with claws slightly divergent, equal in length, both claws widely split, upper lobe narrow, lower lobe broad on individual claw, base of claw toothed.

*Mesothorax:* Scutellum subtriangular; elytra longer than wide, widest medially (Fig. 31), epipleuron narrow, flattened, dorsal surface with weak striae, interstrial regions slightly raised, surface with short white setae, anterior umbone moderately prominent, posterior umbone absent; pretarsus similar to prothoracic pretarsus.

*Metathorax:* Coxa narrowly separated; femur narrow, widest medially; tibia vase shape, widest in medially, narrowed in proximal 1/4, posteroventral margin lined with long setae, lacking spurs, posterior margin with a shallow, U-shaped groove; pretarsus with claws similar to prothoracic claws.

*Abdomen:* Ventrites 1-3 equal in length, sutures distinct, 4<sup>th</sup> ventrite (= propygidium) with anterior region equal to length of ventrites 2-3 combined, posterior region of ventrite angled dorsally, membranous, ventrite and sternite of 4<sup>th</sup> abdominal segment not separated by distinct suture, spiracle placed in posterior 1/4, situated in slight groove, weak sutural line visible, 5<sup>th</sup> ventrite length equal to length of 2<sup>nd</sup> ventrite, posterior margin membranous; pygidium large, subtriangular, width subequal to length (Fig. 32).

#### Diversity and Geographic distribution

The monotypic *Astaenosiagum* is recorded exclusively from Chile.

***Barybas* Blanchard, 1850**

(Figure 33-38)

*Barybas* Blanchard, 1850: 94. Type species *Barybas nana* Blanchard, 1850, by subsequent designation (Bates 1887: 150).

*Ctilocephala* Burmeister, 1855: 78. Type species *Ctilocephala pellucens* Burmeister, 1855, by monotypy.

**[New Synonym]**

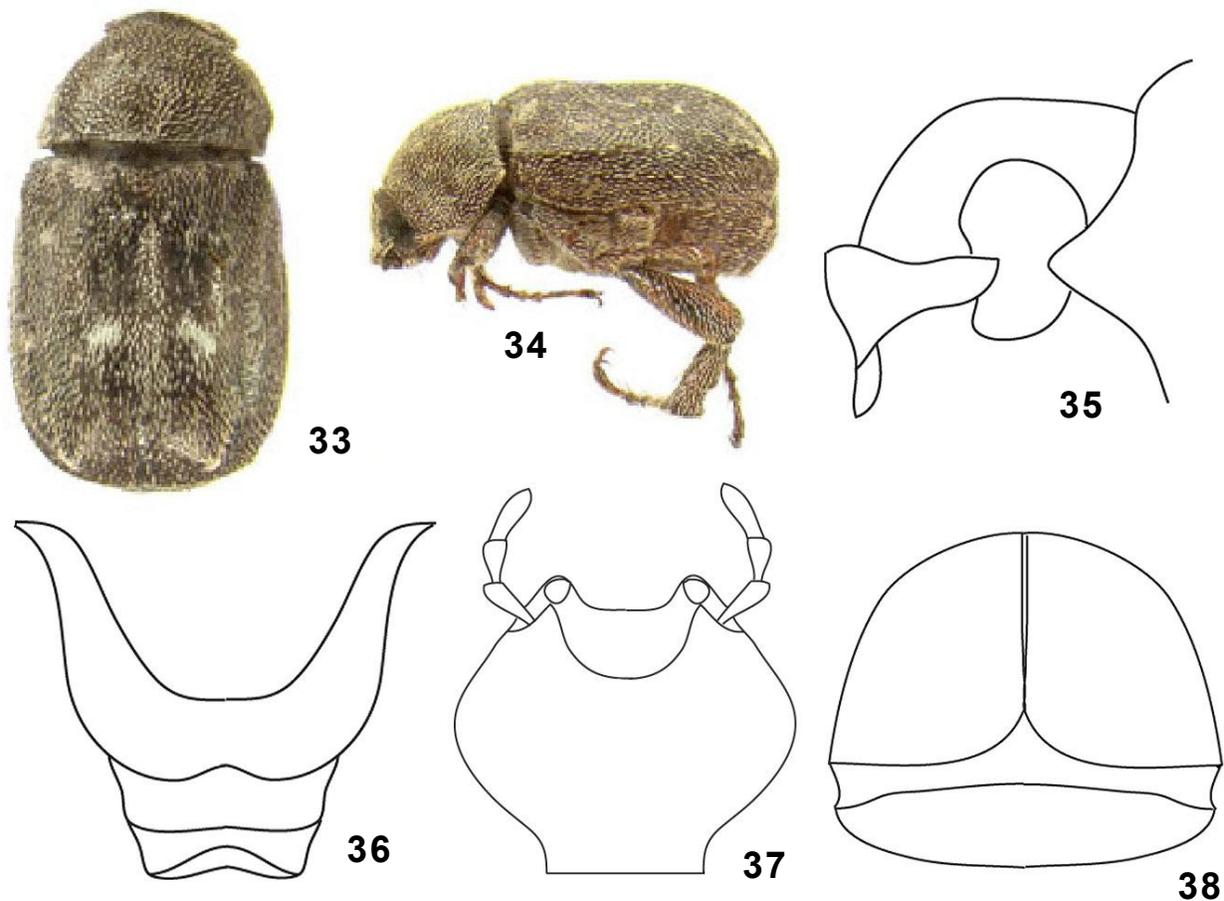
*Eubarybas* Gutiérrez, 1952: 216. Type species *Eubarybas asper* Gutiérrez, 1952, by original designation. **[New Synonym]**

*Microcrania* Burmeister, 1855: 75. Type species *Philochloenia compacta* Erichson, 1847, by subsequent designation (Evans 2003: 230).

*Pseudohercitis* Moser, 1921: 174. Type species *Pseudohercitis viridiaenea* Moser, 1921b, by subsequent designation (Evans 2003: 343). **[New Synonym]**

**Taxonomic Notes**

The following generic diagnosis is based on a dissected homeotype of the generic type species *B. nana* Blanchard located at the NHMN and identified with a Blanchard label. The type species of *Ctilocephala* Burmeister (MLUH), *Eubarybas* Gutiérrez (MNNC), and *Pseudohercitis* Moser (ZMHB) were critically examined to help form the generic limits of this genus. Of all the above generic type species, syntypes, paratypes, or homeotypes were used for dissections. The only exception was *Eubarybas*, for which no additional material was located, hence it was not dissected.



**Figure 33-38.** *Barybas nana* Blanchard. **33)** Dorsal habitus. **34)** Left lateral view. **35)** Clypeus, labrum, frons and ocular canthus, left lateral view. **36)** Clypeus and labrum, frontal view. **37)** Prementum, ligula and labial palpi, ventral view. **38)** Pygidium, dorsal view.

### Generic diagnosis

The genus is characterized by the small body size, rotund appearance; frons angled at 90°, ocular canthus 2/3 ocular width, prementum with a unique U-shaped raised longitudinal carina; elytra often quadrate in dorsal view; vestiture of the elytra often with scattered hairs or scales.

### Generic redescription

*Measurements:* Prothorax at widest point 2.5-3.2 mm, elytra at widest point 3.0-3.2 mm, length 5.7-8.6 mm.

*Color and vestiture:* Body reddish-brown to black, surface with vestiture consisting of scattered white, orange or golden setae, setae often scale-like.

*Head:* Ocular canthus 2/3 ocular width (Fig. 35); clypeus not coplanar with frons; frons strongly angled at 90°; labrum in frontal view, narrowly ovate, moderately emarginate (Fig. 36), labrum not coplanar with clypeus; labium with prementum quadrate, ventral surface with a raised, transverse U-shaped ridge, ridge lined with long setae (Fig. 37); mandibles in dorsal view rectangular, scissorial area bluntly produced, broadly rounded, occasionally emarginate, well sclerotized, molar area bluntly produced; maxillary palpi with apical palpus conical, elongate, occasionally ovate, equal to length of segments 1-2 combined, apex obtuse, narrow in lateral profile; antennae with 8- to 9 antennomeres, antennomeres 7-9 forming the elongate club, club equal in length to antennomeres 2-6 combined.

*Prothorax:* Pronotum oblong, transverse, widest medially, anterior angles acute or obtuse, often appearing toothed, lateral margins convex, posterior angle acute, weakly toothed, posterior margin straight, medially lobed; prothoracic leg with coxa transverse; tibia with dorsal margin often serrate, mono-tridentate, ventral margin medially with a stout spur; pretarsus with claws weakly divergent, equal in length, both claws narrowly split, upper lobe narrow, lower lobe broad on individual claw, base of claw toothed.

*Mesothorax:* Scutellum subtriangular; elytra quadrate, width equal to length, in lateral profile epipleuron flattened, angled inwardly, dorsal surface striate, surface uneven, grooved vertically along elytral suture, surface often covered with scale-like setae, anterior and posterior umbones well developed; pretarsus similar to prothoracic pretarsus.

*Metathorax:* Coxa narrowly separated; femur broadly ovate, widest medially; tibia subtriangular, narrow proximally, widest medially, posteroventral margin with a pair of long, stout spurs, posterior spur slightly longer than anterior spur, spurs arising from same level as tarsal articulation joint, posterior margin with a deep, U-shaped groove; pretarsus with claws unequal, weakly divergent, outer claw longer than inner claw, both claws narrowly split, lobes equal in length, occasionally with a small basal tooth.

*Abdomen:* With ventrites 2-4 equal in length, 5<sup>th</sup> ventrite (= propygidium) equal to 2X length of 4<sup>th</sup> ventrite length, ventrite and sternite of 5<sup>th</sup> abdominal segment divided by a partial suture, weakly defined groove, or lacking any distinct suture, spiracle placed medially, 6<sup>th</sup> ventrite narrow, equal in length to 1/3 length of 4<sup>th</sup> ventrite; pygidium subtriangular, wider than long, posterior margin broadly rounded (Fig. 38).

### Diversity and Geographic Distribution

*Barybas* currently comprises 49 species recorded from Bolivia, Brazil, Colombia, Ecuador, French Guiana, Nicaragua, Panama, Peru, Trinidad, and Venezuela. No species level key is available for this genus.

### *Calodactylus* Blanchard, 1850

(Figure 39-42)

*Calodactylus* Blanchard, 1850: 91. Type species *Calodactylus tibialis* Blanchard, 1850, by monotypy.

*Dioplia* Burmeister, 1855: 70. Type species *Dioplia sulphurea* Burmeister, 1855, by subsequent designation (Evans 2003: 234). Synonymy by Harold (1869a).

### Taxonomic Notes

The following generic diagnosis is based on a dissected homeotype of the generic type species *C. tibialis* located at the MNHC, and identified with a Blanchard label. Type material of *Dioplia sulphurea* Burmeister (MLUH) was examined to confirm generic synonymy with *Calodactylus*.

### Generic diagnosis

The genus is characterized by the elongate, narrow, ovate body; elongate prementum, medially grooved; metathoracic tarsi vase-shaped, meso- and metathoracic legs having simple pretarsal claws only; the elytra often with scale-like setae; ventromedial surface of the 5<sup>th</sup> ventrite of males bearing a semicircular, recessed pocket.

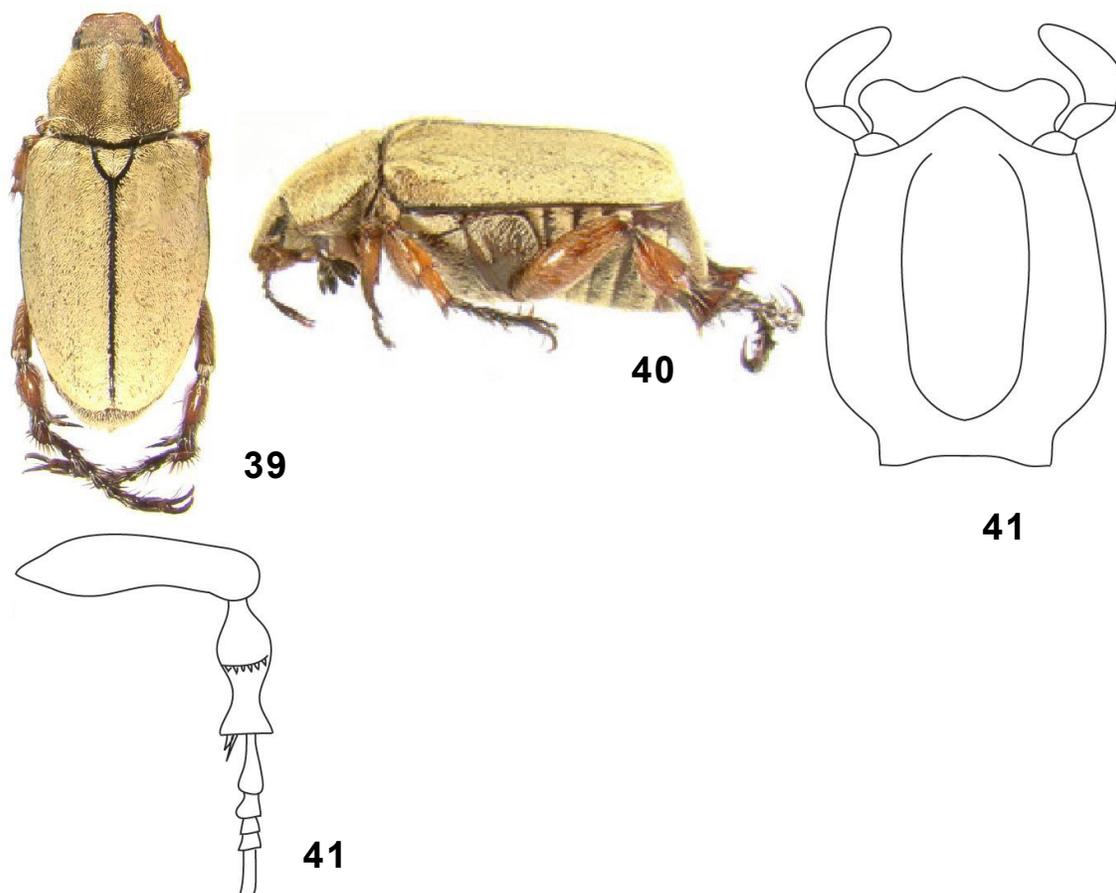
### Generic redescription

*Measurements:* Prothorax at widest point 3.8 mm, elytra at widest point 5.2 mm, length 12.0 mm.

*Color and vestiture:* Head and abdomen reddish-brown, vestiture consisting of short, yellow scale-like setae, femora reddish-brown, tibiae and tarsomeres reddish-brown.

*Head:* Clypeus coplanar with frons; frons angled at 30°; labrum in frontal view narrowly ovate, weakly emarginate, labrum coplanar with clypeus; labium with prementum elongate, ventral surface with medial groove (Fig. 41); mandibles in dorsal view subtriangular, scissorial area bluntly produced, medially emarginate, molar area well developed; maxillary palpi with apical palpus ovate, elongate, equal to 3X length of 2<sup>nd</sup> segment; antennae with 9 antennomeres, antennomeres 7-9 forming the elongate club, equal to length of antennomeres 2-6 combined.

*Prothorax:* Pronotum oblong, transverse, widest medially, anterior angle obtuse, lateral margin convex, posterior angle obtuse, in dorsal view strongly rounded; prothoracic leg with coxa elongate; tibia



**Figure 39-42.** *Calodactylus tibialis* Blanchard (male). 39) Dorsal habitus. 40) Left lateral view. 41) Prementum, ligula and labial palpi, ventral view. 42) Metathoracic femur and tibia.

dentate, distal 1/2 medially with a stout spur; pretarsus with claws divergent, equal in length, both claws narrowly split, upper lobe narrow, lower lobe broad on individual claw.

*Mesothorax*: Scutellum subtriangular; elytra ovate, elongate, widest medially, narrowing posteriorly, elytral epipleuron forming a rounded bead, margin with a slight membranous border, dorsal surface covered with dense, yellow scale-like setae; anterior umbone prominent, posterior umbone moderately produced; pretarsus similar to prothoracic pretarsus.

*Metathorax*: Coxa clearly separated; femur ovate, widest medially; tibia vase-shaped, widest medially, narrow in proximal 1/4 (Fig. 42), posteroventral margin with a pair of long, stout spurs, spurs of equal length, arising from same level as tarsal articulation joint, posterior margin with a deep, U-shaped groove; tarsal claws similar to mesothoracic legs.

*Abdomen*: Ventrites 2-4 subequal in length, 5<sup>th</sup> visible ventrite (= propygidium) equal in length to ventrites 3-4 combined, ventrite and sternite of 5<sup>th</sup> abdominal segment lacking a complete suture, spiracle placed medially, sixth ventrite equal in length to 4<sup>th</sup> and 5<sup>th</sup> ventrites combined, ventromedial surface with a semicircular pocket, margins of which are raised, posterior margin sinuate; pygidium subtriangular, width equal to length, posterior margin rounded.

### Diversity and Geographic Distribution

*Calodactylus* comprises 10 species from Brazil, Bolivia, Ecuador, and Peru. No species level key is available for this genus.

### *Ceraspis* Le Peletier and Serville, 1828

(Figure 43-48)

*Ceraspis* Le Peletier and Serville, 1828: 370. Type species *Melolontha bivulnerata* Germar, a senior synonym of *Ceraspis pruinosa* Le Peletier and Serville, 1828, by subsequent designation (Lacordaire 1856: 252).

*Faula* Blanchard, 1850: 124. Type species *Faula cornuta* Blanchard, 1850, by present designation. Synonym proposed by Bates (1887).

Subgenus: *Isoceraspis* Ohaus, 1911: 669. Type species *Ceraspis duckei* Ohaus, 1911, by monotypy.

### Taxonomic Notes

The following generic diagnosis is based on two dissected homeotypes of *C. pilatei* (Harold) (BMNH). The generic type specimen *C. bivulnerata* or *C. pruinosa* were not located at the NMHC. Specimens representing *C. pruinosa* were located at several collections, and a comparison to the original description was made to confirm the generic limits of this genus were uniform.

### Generic diagnosis

The genus is characterized by the elongate, narrow, ovate body; posterior margin of the pronotum medially with bidentate acuminate processes, prothoracic sternum with a posterior margin bearing a medially flattened acuminate process, extending posteriad of the coxae and extending over the mesosternum; cordate scutellum, elytra often with a vestiture of scale-like setae.

### Generic redescription

*Measurements*: Prothorax at widest point 4.7 mm, elytra at widest point 6.0 mm, total length 13.7 mm.

*Color and vestiture*: Body dark reddish-brown to black, vestiture consisting of short, scale-like white setae.

*Head*: Clypeus not coplanar with frons; frons angled at 45°; labrum in frontal view narrowly ovate, weakly emarginate, labrum not coplanar with clypeus; labium with prementum quadrate, ventral surface medially with a broad groove, surface raised in a semicircular transverse ridge (Fig. 45); mandibles in dorsal view subtriangular or semicircular, scissorial area bluntly produced, thin, bidentate, strongly angled adorally, molar area bluntly produced adorally; maxillary palpi with apical palpus broadly ovate,

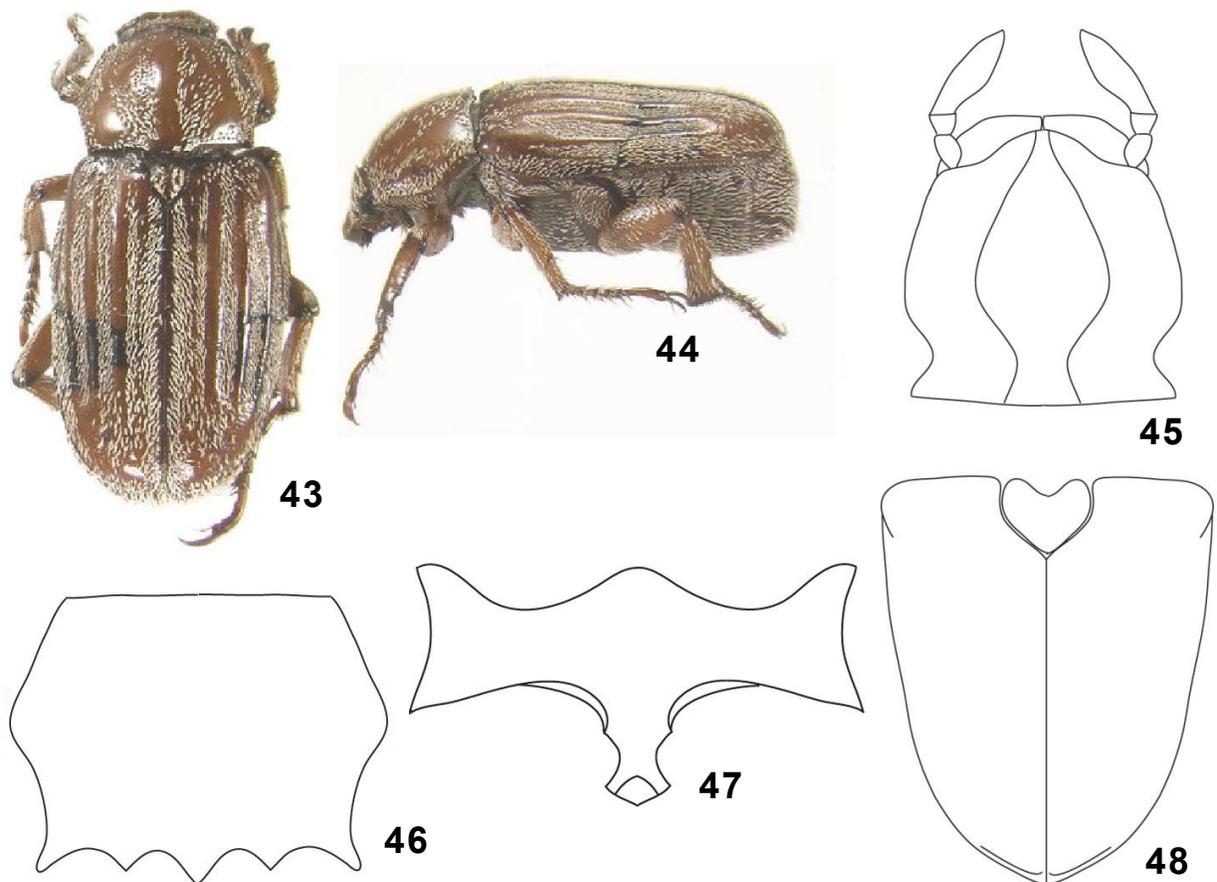
apex obtuse; antennae with 9 antennomeres, antennomeres 7-9 forming an elongate club, the length of which is equal to antennomeres 3-7 combined.

*Prothorax*: Pronotum oblong, transverse, widest medially, anterior angles acute, lateral margins convex, posterior angles acute, appearing toothed, posterior margin convex, medially tridentate (Fig. 46); prothoracic sternum with a posterior margin bearing a medially flattened acuminate process, extending posteriorly of the coxae and extending over the mesosternum (Fig. 47); prothoracic leg with coxa transverse; tibia weakly bidentate, ventral margin medially with a small spur; pretarsus with claws weakly divergent, equal in length, narrowly split, appearing simple, upper lobe narrow, lower lobe very narrow on individual claw.

*Mesothorax*: Scutellum cordate; elytra longer than wide, widest medially (Fig. 48), in epipleuron flattened, margin lined with a narrow membrane, dorsal surface with four striae, interstrial regions rounded, smooth, setose, strial margins raised, smooth, anterior umbone moderate, posterior umbone weak; pretarsus similar to prothoracic pretarsus.

*Metathorax*: Coxa widely separated; femur broadly ovate, widest medially; tibia subtriangular, narrowest proximally, widest distally, distoposteroventral margin with pair of stout spurs, anterior spur shorter than posterior spur, spurs arising from above tarsal articulation joint, posterior margin with a shallow, U-shaped groove; pretarsus with claws similar to those of prothoracic legs.

*Abdomen*: Ventrites 2-4 equal in length, 5<sup>th</sup> ventrite (= propygidium) equal in length to ventrites 3-4 combined, ventrite and sternite of 5<sup>th</sup> abdominal segment not separated by a suture, spiracle placed medially, 6<sup>th</sup> ventrite equal in length to ventrites 2-4 combined, posterior margin concave; pygidium oblong, transverse, wider than long, posterior margin lobed.



**Figure 43-48.** *Ceraspis pilatei* (Harold). 43) Dorsal habitus. 44) Left lateral view. 45) Prementum, ligula and labial palpi, ventral view. 46) Pronotum, dorsal view. 47) Prothoracic sternum, ventral view. 48) Scutellum and elytra, dorsal view.

### Diversity and Geographic Distribution

*Ceraspis* contains 101 species distributed from Mexico south through Central America, into Colombia, Guyana, and Brazil. There is no species level key currently available for the entire genus. Regional keys to the genus do exist (Frey 1962, Delgado 2001).

### *Ceratolontha* Arrow, 1948

(Figure 49-53)

*Ceratolontha* Arrow, 1948: 372. Type species *Ceratolontha venezuelae* Arrow, 1948, by monotypy.

### Taxonomic Notes

The following generic diagnosis is based on a dissected female paratype of the type species, *C. venezuelae* (BMNH).

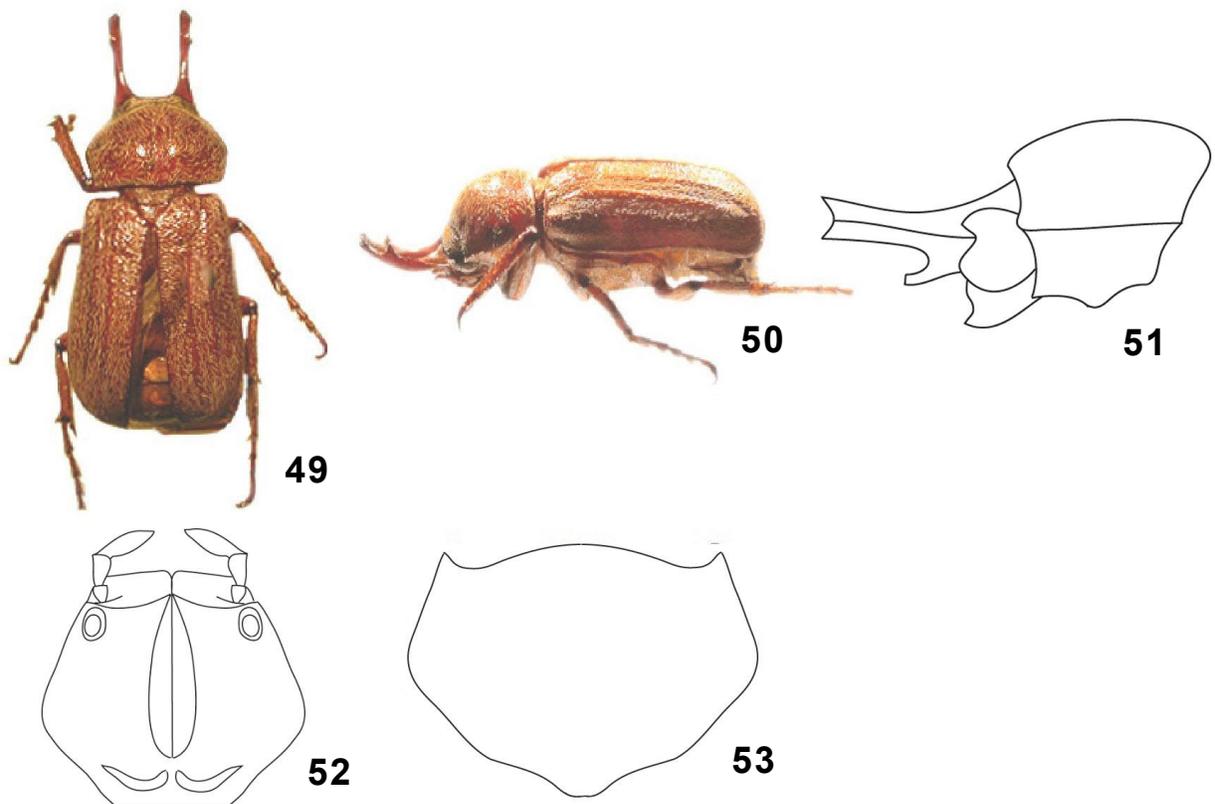
### Generic diagnosis

This genus is characterized by its elongate body, clypeus in males forming a pair of horns, in frontal view very narrow, dorsolateral angles strongly projecting upwards into a short horn, in dorsal view anterior angles strongly produced anteriorly and dorsally, forming a pair of long horns, dorsal surface with a deep medial U-shaped depression in males; quadrate prementum, ventral surface with a raised U-shaped transverse ridge, medially with a raised anterior ridge.

### Generic redescription

*Measurements*: Prothorax at widest point 6.0 mm, elytra at widest point 6.5 mm, length 15.0 mm.

*Color and vestiture*: Body brown, surface with vestiture consisting of scattered fine yellow setae.



**Figure 49-53.** *Ceratolontha venezuelae* Arrow. **49)** Dorsal habitus. **50)** Left lateral view. **51)** Clypeus, labrum and pronotum, lateral view. **52)** Prementum, ligula and labial palpi, ventral view. **53)** Pronotum, dorsal view.

**Head:** Clypeus not coplanar with frons, clypeus in males forming a pair of horns (Fig. 51), in frontal view very narrow, dorsolateral angles strongly projecting upwards into a short horn, in dorsal view anterior angles strongly produced anteriorly and dorsally, forming a pair of long horns; frons angled 10°; labrum in frontal view narrowly ovate, deeply emarginate, labrum not coplanar with clypeus; labium with prementum quadrate, ventral surface with a raised U-shaped transverse ridge in posterior 3/4, medially with a raised ridge in anterior 1/2 (Fig. 52); mandibles rectangular, scissorial area bluntly produced, medially with a small tooth, molar area bluntly produced; maxillary palpi 4-segmented, 4<sup>th</sup> segment narrowly ovate, apex acute, elongate, equal to length of segments 1-2 combined; antennae with 9 antennomeres, antennomeres 7-9 forming the elongate club, club equal to length of antennomeres 2-6 combined.

**Prothorax:** Pronotum oblong, transverse, widest medially, anterior angle acute, lateral margin convex, posterior angle obtuse, posterior margin weakly convex, medially lobed (Fig. 53), dorsal surface strongly rounded; prothoracic leg with coxa transverse; tibia bidentate; pretarsus with claws divergent, equal in length, both claws narrowly split, upper lobe narrow, lower lobe broad on individual claw.

**Mesothorax:** Scutellum semicircular; elytra longer than wide, widest in anterior 1/4, epipleuron flattened, medially grooved, margin lined with a slight membrane, dorsal surface flattened, three weak striae, intervals shallowly punctured, punctures with small white setae, anterior and posterior umbones moderate; pretarsus similar to prothoracic pretarsus.

**Metathorax:** Coxa clearly separated; femur narrowly ovate, width uniform; tibia narrowly rectangular, narrow proximally, widest medially, posteroventral margin with pair of long, stout spurs, spurs equal in length, arising at same level as tarsal articulation joint, posterior margin with broad, shallow, U-shaped groove; pretarsus with claws similar to claws of prothoracic legs.

**Abdomen:** Ventrites 2-4 subequal in length, 5<sup>th</sup> ventrite (= propygidium), equal to length of ventrites 3-4 combined, ventrite and sternite of 5<sup>th</sup> abdominal segment with a weak fold, complete suture lacking, spiracle located medially; 6<sup>th</sup> ventrite equal to length of 4<sup>th</sup> ventrite, posterior margin membranous; pygidium subtriangular, wider than long, posterior margin rounded.

### Diversity and Geographic Distribution

*Ceratolontha* is monotypic, with *C. venezuelae* known only from Venezuela.

### *Chariodactylus* Moser, 1919

(Figure 54-57)

*Chariodactylus* Moser, 1919a: 45. Type species *Chariodactylus chacoensis* Moser, 1919a, by subsequent designation (Evans 2003: 247).

### Taxonomic Notes

The following generic diagnosis is based on a dissected paratype of the type species, *C. chacoensis* (ZMHB).

### Generic diagnosis

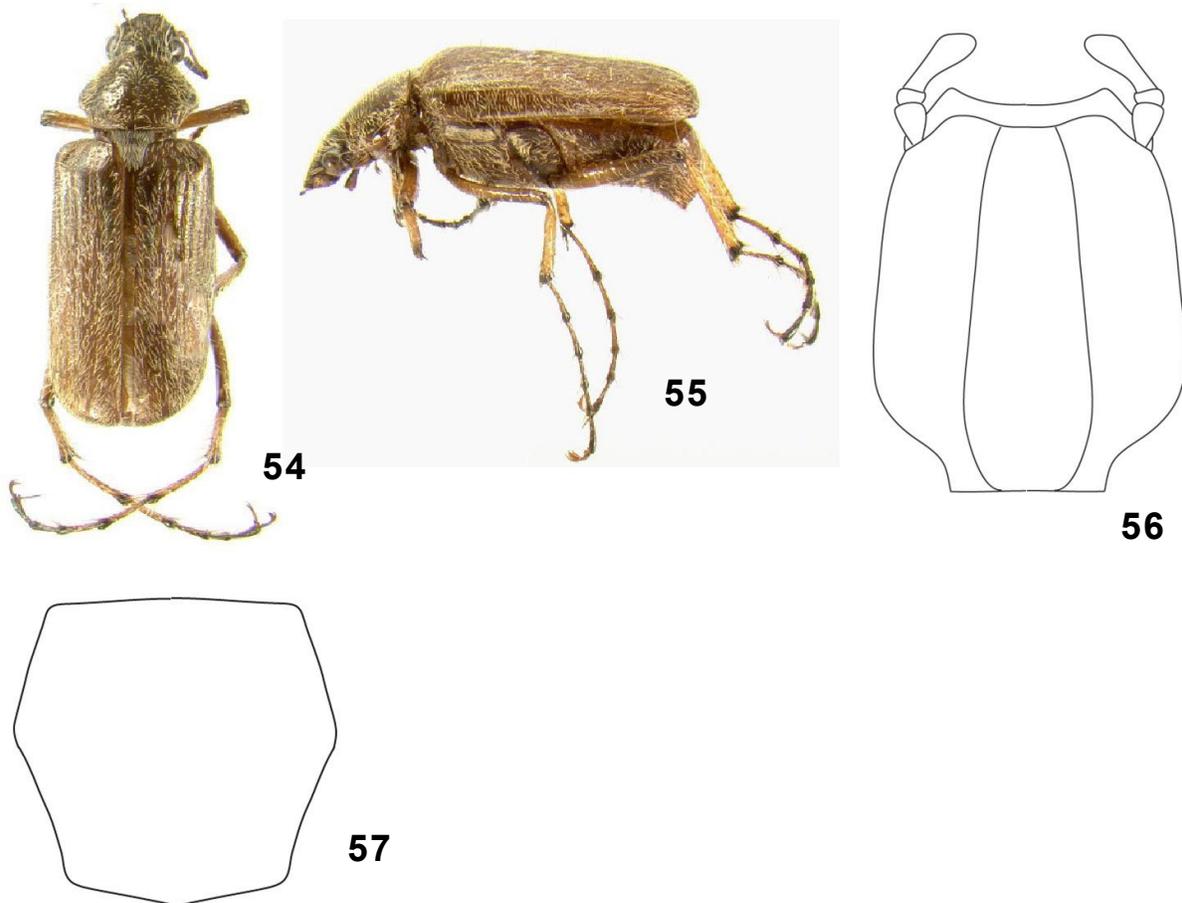
This genus closely resembles *Macroductylus*, but is characterized by the hexagonal pronotum, elongate, subtriangular scutellum; and the elongate metatarsus of the metathoracic legs.

### Generic redescription

**Measurements:** Prothorax at widest point of prothorax 3.0 mm, elytra at widest point 4.2 mm, length 11.0 mm.

**Color and vestiture:** Body reddish-brown, surface covered with a vestiture consisting of short and long white setae.

**Head:** Clypeus coplanar with frons, angled at 30°; labrum in frontal view oval, narrow, weakly emarginate, labrum coplanar with clypeus; labium with prementum rectangular, elongate (2X longer than wide), ventral surface with medial groove (Fig. 56); mandibles in dorsal view triangular, narrowest anteriorly, scissorial area reduced to a membrane, lined with dense setae, molar area well developed, bluntly



**Figure 54-57.** *Chariodactylus chacoensis* Moser (male). **54)** Dorsal habitus. **55)** Left lateral view. **56)** Prementum, ligula and labial palpi, ventral view. **57)** Pronotum, dorsal view.

produced adorally; maxillary palpi with apical palpus ovate, equal to length of 3<sup>rd</sup> segment, apex obtuse, distally with a sensory region; antennae with 9 antennomeres, antennomeres 7-9 forming the elongate club, lamellae thin, equal to length of antennomeres 3-6 combined.

**Prothorax:** Pronotum hexagonal, oblong, transverse, widest medially, anterior angles obtuse, lateral margin convex, posterior angles obtuse, posterior margin convex (Fig. 57), in dorsal view rounded; prothoracic leg with coxa elongate; tibia weakly dentate; pretarsus with claws divergent, equal in length, both claws narrowly split, upper lobe narrow, lower lobe broad on individual claw, base of claw toothed.

**Mesothorax:** Scutellum subtriangular; elytra longer than wide, widest at anterior margin, elytral epipleuron flattened, margin lined with a thin membrane, dorsal surface with distinct striae, intervals punctate, slightly convex, surface covered with short and long setae, anterior umbone strongly developed, posterior umbone weakly developed; pretarsus similar to prothoracic pretarsus.

**Metathorax:** Coxa widely separated; femur narrowly ovate, width uniform; tibia narrowly subtriangular, broader distally, posteroventral margin lacking spurs, posterior margin lacking tarsal articulation groove; pretarsus with claws similar to prothoracic legs.

**Abdomen:** Ventrites 2-4 subequal in length, 5<sup>th</sup> visible ventrite (= propygidium) equal to length of 4<sup>th</sup> and 1/2 length of 3<sup>rd</sup> ventrite combined, ventromedial surface transitioning to membranous posterior margin, ventrite and sternite of 5<sup>th</sup> abdominal segment lacking a complete suture, spiracle placed medially; 6<sup>th</sup> ventrite equal in length to 5<sup>th</sup> ventrite, ventromedially transitioning to membranous posterior margin, in lateral view broadly triangular; pygidium subtriangular, longer than wide, posterior margin rounded.

### Diversity and Geographic Distribution

*Chariodactylus* comprises two species recorded from Bolivia and Peru.

### *Chariodema* Blanchard, 1850

(Figure 58-62)

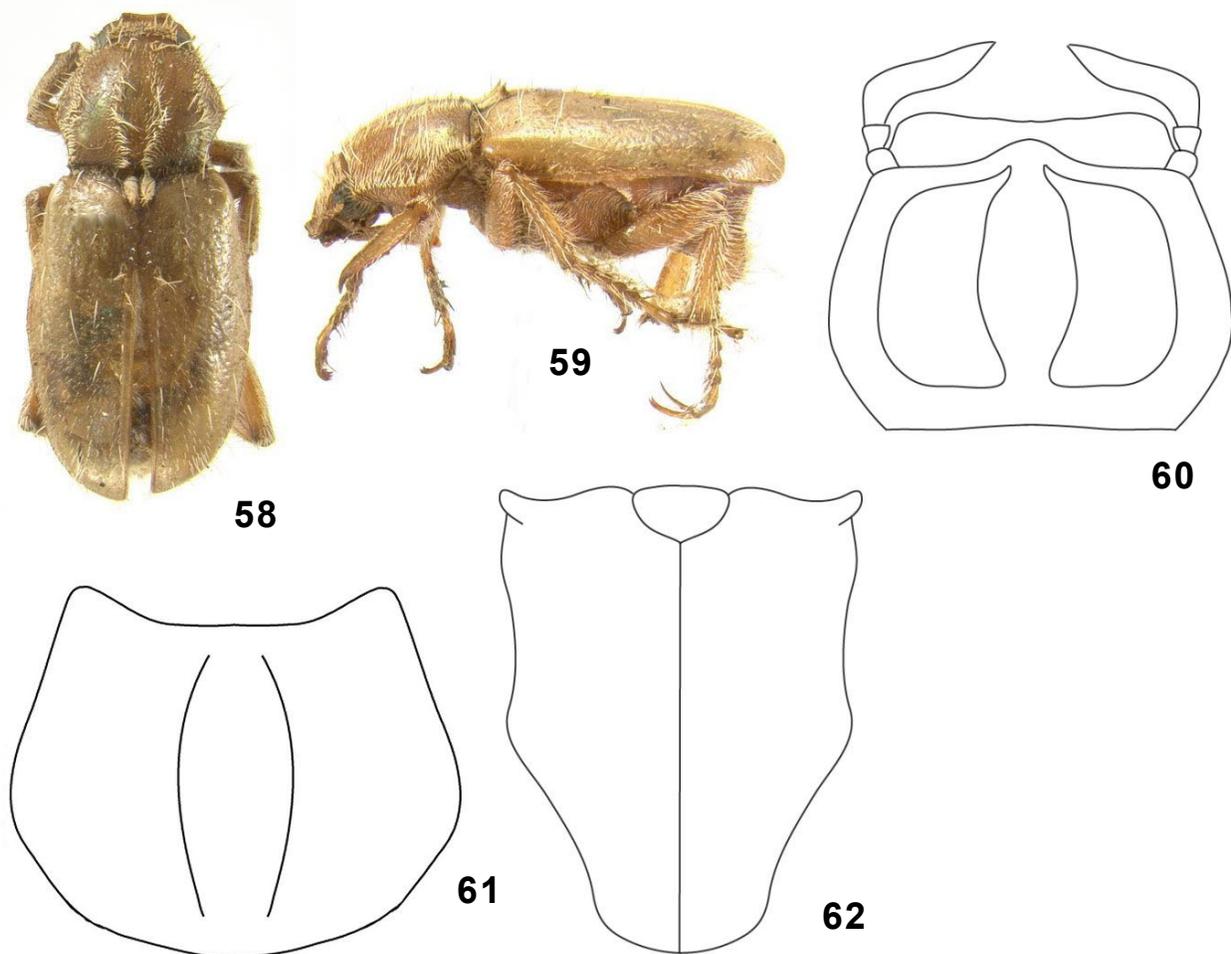
*Chariodema* Blanchard, 1850: 117. Type species *Philochloenia virescens* Blanchard, 1850, by subsequent designation (Evans 2003: 247).

### Taxonomic Notes

The following generic diagnosis is based on a dissected homeotype of the presumptive syntype of *C. xyлина* Blanchard located at the MNHC and identified with a Blanchard label. The generic type of *C. virescens* Blanchard was located at the MNHC, identified by a Blanchard label. The generic limits of the genus were compared to *C. xyлина*.

### Generic diagnosis

This genus is characterized by the wide, hexagonal pronotum; elongate prementum, with ventral surface medially grooved; elytra with strong anterior umbones, weak posterior umbones.



**Figure 58-62.** *Chariodema virescens* (Blanchard). **58)** Dorsal habitus. **59)** Left lateral view. **60)** Prementum, ligula and labial palpi, ventral view. **61)** Pronotum, dorsal view. **62)** Scutellum, and elytra, dorsal view.

### Generic redescription

*Measurements:* Prothorax at widest point 3.0 mm, elytra at widest point 3.7 mm, length 8.6 mm.

*Color and vestiture:* Body brown, surface with a vestiture consisting of short white setae.

*Head:* Clypeus not coplanar with frons; frons angled with clypeus at 20°; labrum in frontal view trapezoidal, broad, weakly emarginate, labrum evenly transitioning with clypeus; labium with prementum quadrate, ventral surface with medial groove, ventromedially forming a weak U-shaped pocket, ventroposterior region flattened, ventromedially with an incomplete raised transverse ridge (Fig. 60); mandible in dorsal view rectangular, scissorial area bluntly produced, bidentate, strongly deflexed dorsally, molar area well developed, bluntly produced adorally; maxillary palpi with apical palpus ovate, equal to length of 2<sup>nd</sup> segment, apex acute, distally with a small sensory spot; antennae with 9 antennomeres, antennomeres 7-9 forming the elongate club, lamellae thin, equal to length of antennomeres 2-6 combined.

*Prothorax:* Pronotum hexagonal, oblong, transverse, widest medially, anterior angle acute, lateral margin convex, posterior angle obtuse, posterior margin convex, dorsal surface rounded, with a weak medial groove (Fig. 61); prothoracic leg with coxa transverse; tibia bidentate, spur present in other species; pretarsus with claws missing in *C. virescens*, in *C. xylina*, claws are weakly divergent, equal in length, both claws are narrowly split, upper lobe narrow, lower lobe broad on individual claw.

*Mesothorax:* Scutellum subtriangular; elytra longer than wide, widest medially (Fig. 62), elytral epipleuron narrowly flattened, margin lacking a membrane, dorsal surface lacking striae, anterior umbone strongly developed, posterior umbone weakly developed; pretarsus similar to prothoracic pretarsus.

*Metathorax:* Coxa widely separated; femur narrowly ovate, narrow proximally, width uniform; tibia subtriangular, narrow proximally, widest distally, posteroventral margin with a pair of long, stout spurs, anterior spur shorter than posterior spur, spurs arising from same level as tarsal articulation joint, posterior margin with a deep U-shaped tarsal articulation groove; pretarsus with claws similar to prothoracic legs.

*Abdomen:* Ventrites 2-4 subequal in length, 5<sup>th</sup> visible ventrite (= propygidium) equal to length of 4<sup>th</sup> ventrite and sternite of 5<sup>th</sup> abdominal segment not separated by a suture, spiracle placed medially, 6<sup>th</sup> ventrite equal in length to 2X 5<sup>th</sup> ventrite length, posteromedial margin membranous; pygidium subtriangular, longer than wide, posterior margin rounded.

### Diversity and Geographic distribution

*Chariodema* contains 12 species, distributed from Bolivia, Brazil, and Colombia. There is no species level key currently available for this genus.

### *Chremastodus* Solier, 1851

(Figure 63-66)

*Chremastodus* Solier, 1851: 103. Type species *Chremastodus pubescens* Solier, 1851, by subsequent designation (Evans 2003: 248).

*Cremastodus* Solier, 1851, Dalla Torre, 1913 [spelling error]

### Taxonomic Notes

The following generic diagnosis is based on a dissected specimen of *C. marmoratus* (Curtis) located at the BMNH and identified with a Curtis determination label. The type of *C. marmoratus* was not located at the BMNH. The type species *C. pubescens* Solier was located at the MNHC, but it was not dissected because it was a single specimen. The generic limits of the genus were compared to *C. marmoratus*.

### Generic diagnosis

This genus resembles *Macrodactylus*, but is characterized by the uneven, mottled elytral surface, oblong pronotum, and prominent umbones.

### Generic redescription

*Measurements:* Prothorax at widest point 3.0 mm, elytra at widest point of elytra 4.0 mm, length 7.5 mm.

*Color and vestiture:* Body dark brown to mottled black, vestiture consisting of long, scale-like white setae.

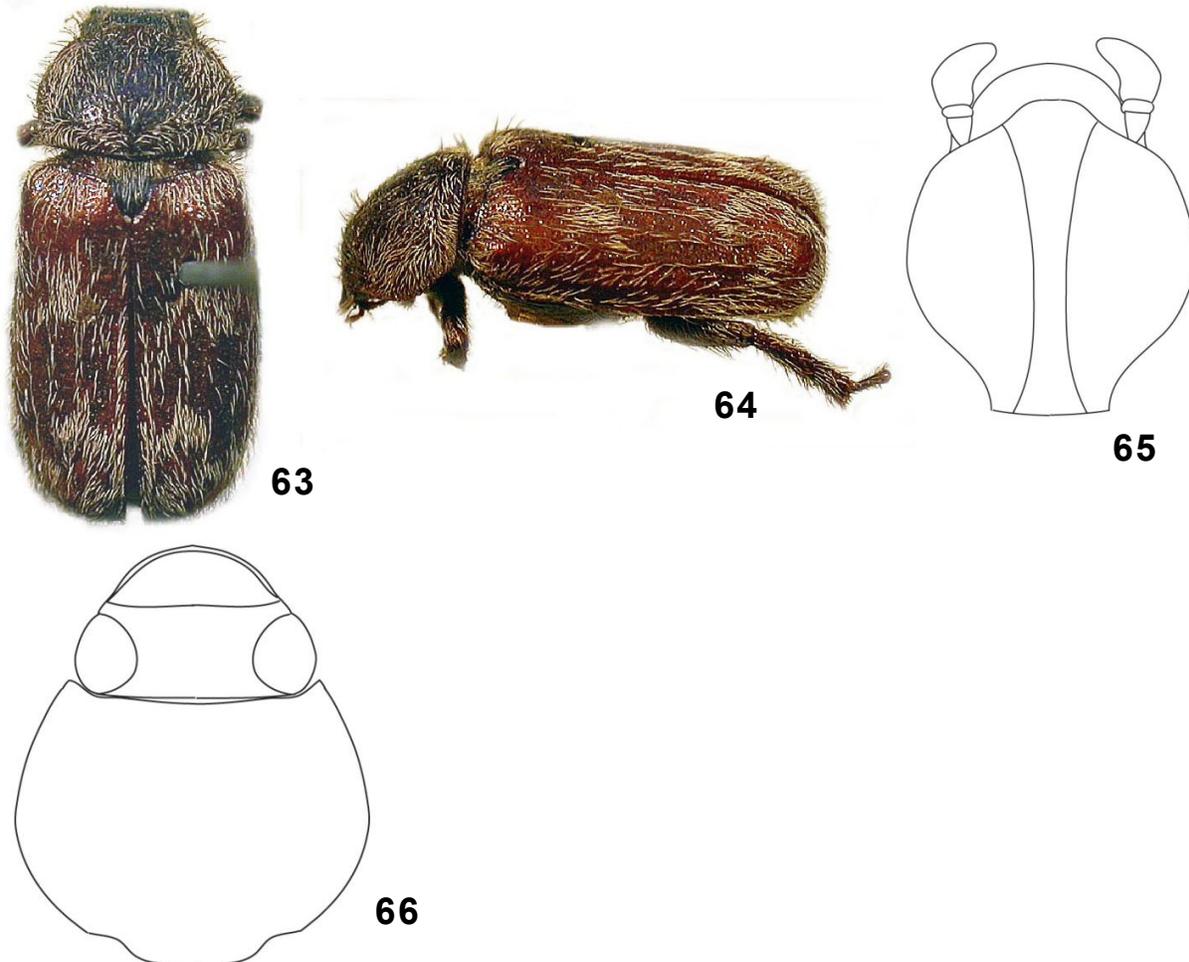
*Head:* Clypeus coplanar with frons, frons angled at 45°; labrum in frontal view, narrowly ovate, weakly emarginate; labium with prementum rectangular, elongate, medially grooved (Fig. 65); mandibles in dorsal view rectangular, scissorial area reduced to a membrane, lined with dense setae, molar area reduced; maxillary palpi with apical segment ovate, equal to segments 2-3, apex obtuse, with blunt sensory region; antennae with antennomeres, antennomeres 7-9 forming the elongate club, lamellae thin, equal in length to antennomeres 2-5 combined.

*Prothorax:* Pronotum oblong, transverse, wider than long, widest medially, anterior angles acute, lateral margin convex, posterior angles obtuse, posterior margin weakly convex, medially obtuse (Fig. 66); coxa transverse, tibia dentate; pretarsus with claws divergent, equal in length, both claws narrowly split, outer lobe narrow, slightly longer than lower lobe, lower lobe narrow on individual claw.

*Mesothorax:* Scutellum subtriangular; elytra longer than wide, width uniform, elytral epipleuron flattened, margin setose, dorsal surface with three weakly raised striae, anterior and posterior umbones strongly developed; pretarsus similar to prothoracic pretarsus.

*Metathorax:* Metathoracic leg with coxa contiguous; femur broadly ovate, widest medially; tibia subtriangular, narrow proximally, widest distally, posteroventral margin lacking spurs, posterior margin with a deep U-shaped groove; pretarsus with claws similar to prothoracic legs.

*Abdomen:* Ventrites 2-4 subequal in length, 5<sup>th</sup> visible ventrite (= propygidium) equal in length to ventrites 3-4 combined, posterior margin membrane like, ventrite and sternite of 5<sup>th</sup> abdominal segment



**Figure 63-66.** *Chremastodus marmoratus* (Curtis). **63)** Dorsal habitus. **64)** Left lateral view. **65)** Prementum, ligula and labial palpi, ventral view. **66)** Head and pronotum, dorsal view.

with suture lacking, spiracle placed medially, 6<sup>th</sup> ventrite equal to length of 3/4 5<sup>th</sup> ventrite length, triangular in lateral profile; pygidium subtriangular, width equal to length, posterior margin rounded.

#### Diversity and Geographic distribution

*Chremastodus* contains two species, both of which are recorded only from Chile.

#### *Clavipalpus* Laporte, 1832

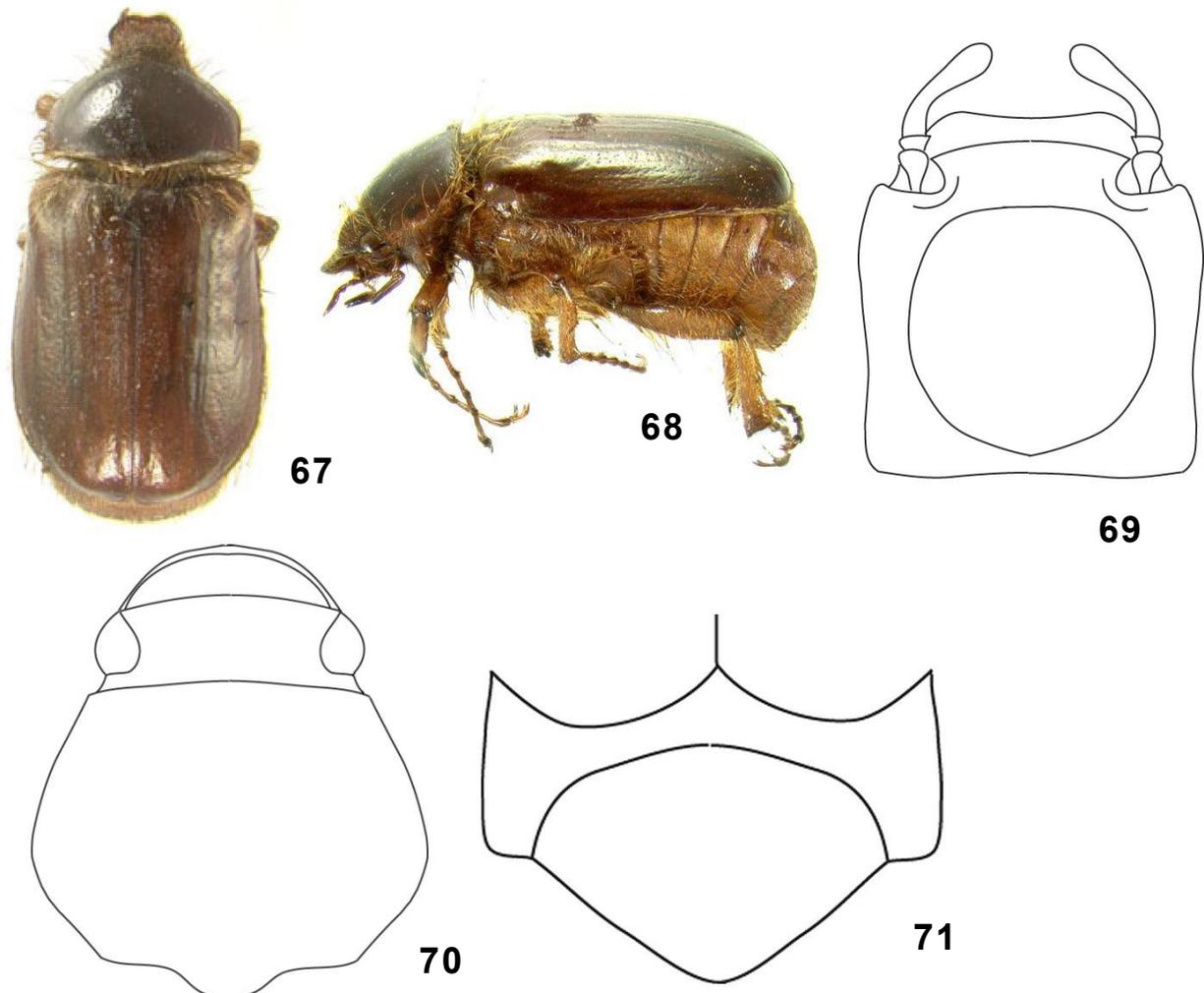
(Figure 67-71)

*Clavipalpus* Laporte, 1832: 406. Type species *Clavipalpus dejeani* Laporte, 1832, by monotypy.

*Amphicrania* Burmeister, 1855: 26. Type species *Amphicrania ursina* Burmeister, 1855, by subsequent designation (Evans 2003: 249). Synonym proposed by Dalla Torre (1913).

#### Taxonomic Notes

The following generic diagnosis is based on four dissected homeotypes of the presumptive syntype of *Clavipalpus ursinus* Blanchard located at the MNHC and identified with a Blanchard label. The type species *C. dejeani* Laporte was not located at the MNHC during this study. A syntype of *A. ursina* (MLUH) was examined to confirm synonymy. The holotype of *Clavipalpus aequatorialus* Moser, 1918 (ZMHB) was also examined to investigate the generic limits of this genus.



**Figure 67-71.** *Clavipalpus ursinus* (Burmeister). **67)** Dorsal habitus. **68)** Left lateral view. **69)** Prementum, ligula and labial palpi, ventral view. **70)** Head and pronotum, dorsal view. **71)** Pygidium, dorsal view.

### Generic diagnosis

This genus is characterized by its large, ovate size, rotund body; prementum quadrate, ventral surface with a weakly raised lobe; small, semicircular labrum in frontal view, elongate clypeus in frontal view, elongate labial palpi.

### Generic redescription

*Measurements:* Prothorax at widest point 6.2 mm, elytra at widest point 8.4 mm, length 15.0 mm.

*Color and vestiture:* Head and pronotum reddish brown, dorsal surface smooth, with vestiture consisting of scattered golden setae, ventrally yellowish brown, with scattered golden setae.

*Head:* Clypeus not coplanar with frons; frons angled at 60°; labrum in frontal view small, ovate, deeply emarginate, in lateral profile labrum vertical, produced outward from clypeus; labrum with prementum quadrate, ventral surface with a weak medially raised lobe; apical palpus of labial palp ovate, narrowly elongate, apically acute, dorsally grooved (Fig. 69); mandibles in dorsal view hourglass shaped, scissorial area bluntly produced, glabrous, heavily sclerotized, molar area well developed; maxillary palpi with apical palpus broadly ovate, adoral margin sinuate, broader proximally, distal apex acute; antennae with 9 antennomeres, antennomeres 7-9 forming the club, lamellae thin, elongate, equal to length of antennomeres 3-6 combined.

*Prothorax:* Pronotum oblong, transverse, widest medially, anterior angle obtuse, lateral margins convex, narrowing anteriorly, posterior angle obtuse, posterior margin convex, medially with a broad, rounded lobe (Fig. 70), dorsal surface strongly rounded; prothoracic legs with coxa transverse; tibia dentate; pretarsus with claws divergent, equal in length, both claws broadly split, upper lobe narrow, lower lobe broad on individual claw.

*Mesothorax:* Scutellum broadly subtriangular; elytra slightly wider than long, widest in posterior 1/4, epipleuron flattened, weakly grooved, lacking membranous border, dorsal surface weakly striate, striae smooth, glabrous, intervals glabrous, punctate, punctures small and shallow, anterior and posterior umbones prominent; pretarsus similar to prothoracic pretarsus.

*Metathorax:* Metathoracic leg with coxa contiguous; femur ovate, widest medially, narrow proximally; tibia triangular, narrow proximally, widest medially, posteroventral margin with pair of long, stout spurs, anterior spur shorter than posterior spur, posterior margin with a shallow U-shaped groove; claws similar to prothoracic claws.

*Abdomen:* Ventrites 2-4 equal in length, 5<sup>th</sup> ventrite (= propygidium) equal to length of ventrites 3-4 combined, ventrite and sternite of 5<sup>th</sup> abdominal segment lacking a suture, spiracle placed slightly anteromedially in a slight depression, 6<sup>th</sup> ventrite equal to length of 4<sup>th</sup> ventrite, posterior margin membranous; pygidium wider than long, subtriangular, posterior margin rounded (Fig. 71).

### Diversity and Geographic Distribution

*Clavipalpus* currently contains 20 species. There is no species level key available for this genus. Distribution is poorly understood, apparently centered in northern South America (Colombia, Brazil, and Ecuador).

### *Ctenotis* Burmeister, 1855

(Figure 72-76)

*Ctenotis* Burmeister, 1855: 20. Type species *Ctenotis obesa* Burmeister, 1855, by monotypy.

### Taxonomic Notes

The following generic diagnosis is based on a dissected syntype of the generic type species, *C. obesa* (MLUH).

### Generic diagnosis

This genus is characterized by its large size, and rotund body; prementum quadrate, anteromedial region bulbous; elongate labrum and semicircular clypeus, antennae with 10 antennomeres, with

antennomeres 6-10 forming an elongate club; pronotum with anterior margin less in width than posterior margin.

### Generic redescription

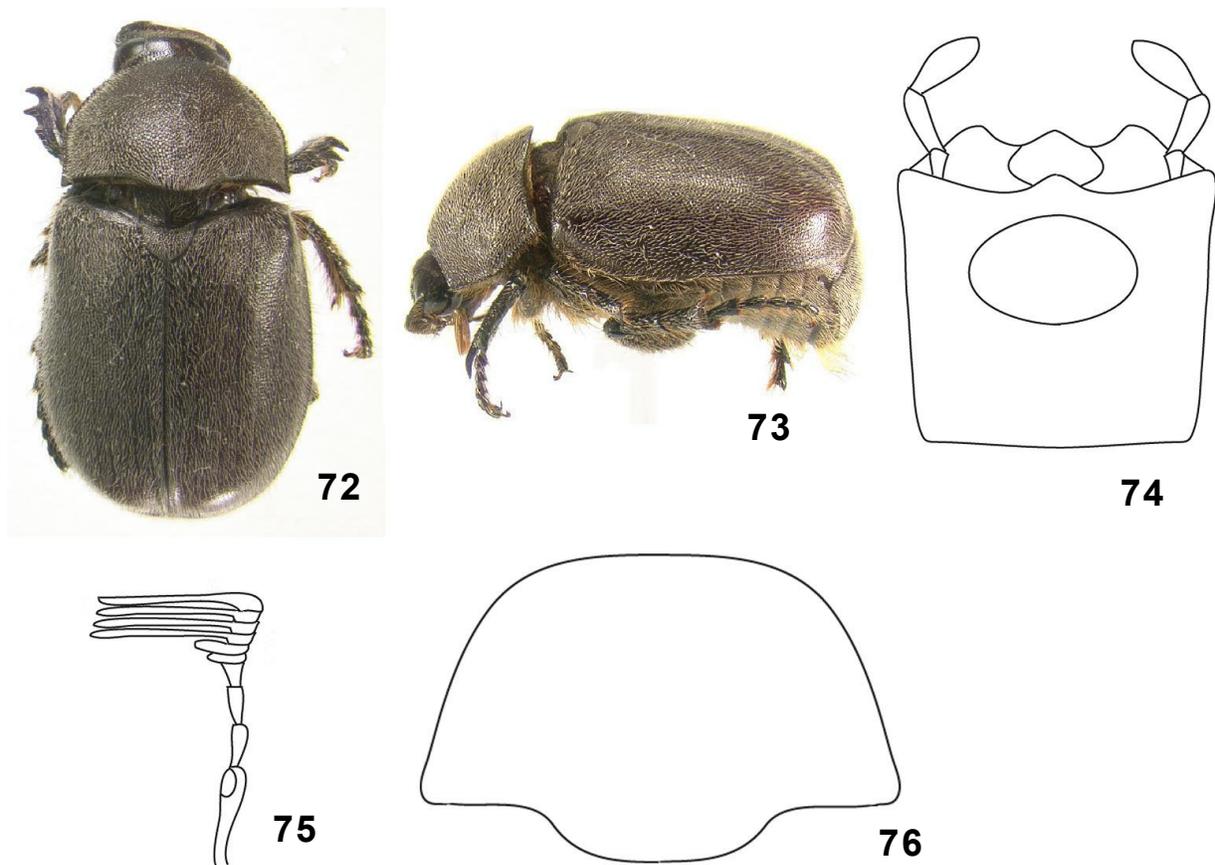
*Measurements:* Prothorax at widest point 6.5 mm, elytra at widest point of elytra 9.0 mm, length 18.0 mm.

*Color and vestiture:* Body dark brown, pronotum and elytra covered with a vestiture consisting of small fine grey setae, ventrites of thorax with long golden setae, abdomen with small grey setae and patches of long golden setae.

*Head:* Clypeus not coplanar with frons; frons angled at 30°; labrum in frontal view, broadly oval, deeply emarginate, labrum not coplanar with clypeus; labium with prementum quadrate, anteromedial region of mentum bulbous, posterior region flat (Fig. 74); mandibles in dorsal view semicircular, scissorial area bluntly produced adorally, thin in lateral profile, bilobed, molar area bluntly produced, well sclerotized; maxillary palpi with apical palpus broadly ovate, flattening distally in lateral profile, 2X length of 3<sup>rd</sup> segment, apex with a circular sensory region; antennae 10-segmented (Fig. 75), segments 6-10 broadly ovate, forming the elongate club, 6<sup>th</sup> segment smaller, 1/4 length of 7<sup>th</sup> segment, segments 7-10 equal to length of segments 1-6 combined.

*Prothorax:* Pronotum oblong (Fig. 76), transverse, widest medially, anterior angle obtuse, lateral margins gradually narrowing anteriorly, straight posteriorly, posterior angle acute, posterior margin straight, medially lobed; prothoracic leg with coxa transverse; tibia bidentate, thin spur present at distal 3/4; pretarsus with claws widely divergent, equal in length, both claws narrowly split, outer lobe narrow, lower lobe broad on individual claw.

*Mesothorax:* Scutellum subtriangular; elytra wider than long, widest in posterior 3/4, elytral epipleuron flattened, margin lacking membrane, dorsal surface lacking striae, densely covered with fine setiferous



**Figure 72-76.** *Ctenotis obesa* Burmeister. **72)** Dorsal habitus. **73)** Left lateral view. **74)** Prementum, ligula and labial palpi, ventral view. **75)** Antenna. **76)** Pronotum, dorsal view.

punctures, anterior umbone prominent, posterior umbones weakly developed; pretarsus similar to prothoracic pretarsus.

*Metathorax:* Metathoracic leg with coxa narrowly separated; femur ovate, widest distally, gradually widening toward distal margin; tibia rectangular, width uniform, posteroventral margin with pair of large spurs, spurs of equal length, arising from same level as tarsal articulation joint, posterior margin with a deep, U-shaped tarsal articulation groove; pretarsus with claws similar to prothoracic legs.

*Abdomen:* Ventrites 2-4 subequal in length, 5<sup>th</sup> ventrite (= propygidium) slightly larger than 4<sup>th</sup> ventrite length, ventrite and sternite of 5<sup>th</sup> abdominal segment not separated by a suture, spiracle placed medially, 6<sup>th</sup> ventrite equal to length of 4<sup>th</sup> ventrite, posterior margin membranous; pygidium broadly triangular, wider than long, posterior margin rounded.

### Diversity and Geographic Distribution

*Ctenotis* is monotypic, with *C. obesa* known only from Brazil.

### *Dasyus* Le Peletier and Serville, 1828

(Figure 77-81)

*Dasyus* Le Peletier and Serville, 1828: 369. Type species *Dasyus collaris* Le Peletier and Serville, 1828, by monotypy.

### Taxonomic Notes

The following generic diagnosis is based on two dissected male homeotypes of the presumptive syntype of the type species *D. collaris* located at the MNHC and identified with a Le Peletier label.

### Generic diagnosis

This genus is characterized by its ovate body; prementum elongate, ventral surface medially grooved; pretarsus of meso and metathoracic legs with claws equal, divergent, simple; ventromedial surface of 6<sup>th</sup> ventrite with a semicircular shaped pocket, margins of which are raised, posterior margin sinuate; pygidium subtriangular, width equal to length, posterior margin blunt.

### Generic redescription

*Measurements:* Prothorax at widest point 3.0 mm, elytra at widest point 3.6 mm, length 8.0 mm.

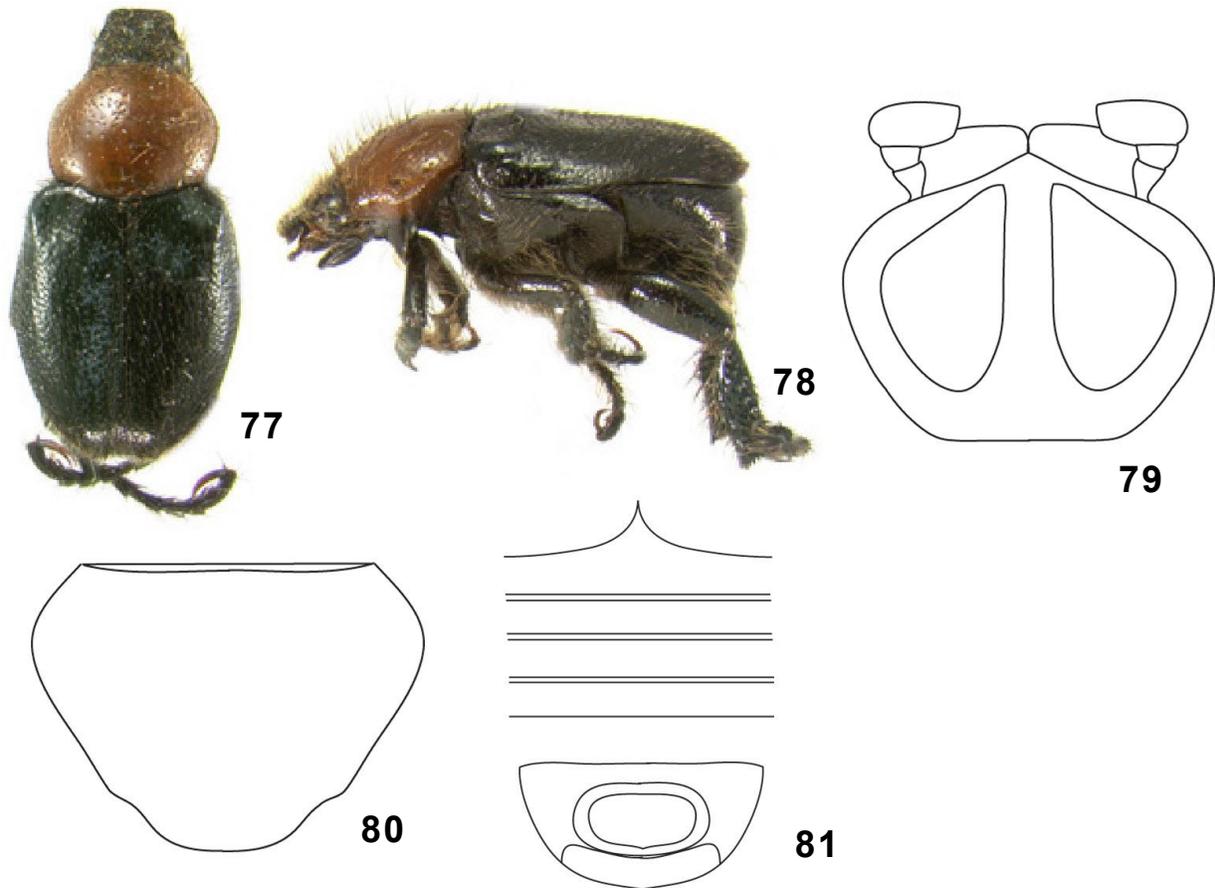
*Color and vestiture:* Head and abdomen black, thorax red, vestiture consisting of short, yellow setae, femora reddish-brown, tibiae and tarsomeres black.

*Head:* Clypeus coplanar with frons, frons angled at 30°; labrum in frontal view narrowly ovate, weakly emarginate, slightly produced anteriorly from clypeus, labrum not coplanar with clypeus; labium with prementum elongate, ventral surface with medial groove (Fig. 79); mandibles in dorsal view subtriangular, scissorial area bluntly produced, angled adorally, weakly concave, medially with a small acuminate point, molar area well developed; maxillary palpi with apical palpus ovate, elongate, equal to 3X length of 2<sup>nd</sup> segment, distally with a small sensory spot; antennae with 9 antennomeres, antennomeres 7-9 forming the elongate club, equal to length of antennomeres 2-6 combined.

*Prothorax:* Pronotum oblong, transverse, widest medially, anterior angle obtuse, lateral margin convex, posterior angle obtuse, posterior margin convex, medially lobed (Fig. 80), in dorsal view strongly rounded; prothoracic leg with coxae elongate; tibia lacking teeth, medially with a stout spur; pretarsus with claws strongly divergent, equal in length, both claws narrowly split, outer lobe narrow, inner lobe broad on individual claw.

*Mesothorax:* Scutellum subtriangular; elytra ovate, width equal to length, elytral epipleuron forming a rounded bead, margin with a slight membranous border, dorsal surface with raised striae absent, surface punctate, punctures in distinct vertical lines, anterodorsal region weakly raised, anterior umbone prominent, posterior umbone moderately produced; pretarsus of mesothoracic leg with claws equal, divergent, simple.

*Metathorax:* Metathoracic leg with coxae clearly separated; femur broadly ovate, widest medially; tibia subtriangular, widest medially, narrow proximally, posteroventral margin with a pair of long, stout



**Figure 77-81.** *Dasyus collaris* Le Peletier and Serville. **77)** Dorsal habitus. **78)** Left lateral view. **79)** Prementum, ligula and labial palpi, ventral view. **80)** Pronotum, dorsal view. **81)** Visible abdominal segments, ventral view.

spurs, anterior spur slightly above posterior spur, spurs arise above tarsal articulation joint, posterior margin with a deep U-shaped groove; pretarsus with claws similar to mesothoracic legs.

**Abdomen:** Ventrites 2-4 subequal in length, 5<sup>th</sup> visible ventrite (= propygidium) equal in length to ventrites 2-4 combined, ventrite and sternite of 5<sup>th</sup> abdominal segment lacking a complete suture, slight depression present posterad of spiracle, spiracle placed medially, sixth ventrite equal to length of 5<sup>th</sup> and 4<sup>th</sup> ventrite combined, ventromedial surface with a semicircular shaped pocket, margins of which are raised, posterior margin sinuate (Fig. 81); pygidium subtriangular, width equal to length, posterior margin blunt.

#### Diversity and Geographic distribution

*Dasyus* contains two species, both known only from Brazil.

#### *Dicrania* Le Peletier and Serville, 1828

(Figure 82-87)

*Dicrania* Le Peletier and Serville, 1828: 371. Type species *Dicrania nigra* Le Peletier and Serville, 1828, by monotypy.

*Monocrania* Laporte, 1832: 410. Type species *Monocrania luridipennis* Laporte, 1832, by subsequent designation (Evans 2003: 263). Synonymized by Dalla Torre (1913).

### Taxonomic Notes

The following generic diagnosis is based on two dissected homeotypes (one male and one female) of the presumptive syntype of the type species *D. nigra* located at the MNHC, and identified with a Le Peletier label.

### Generic diagnosis

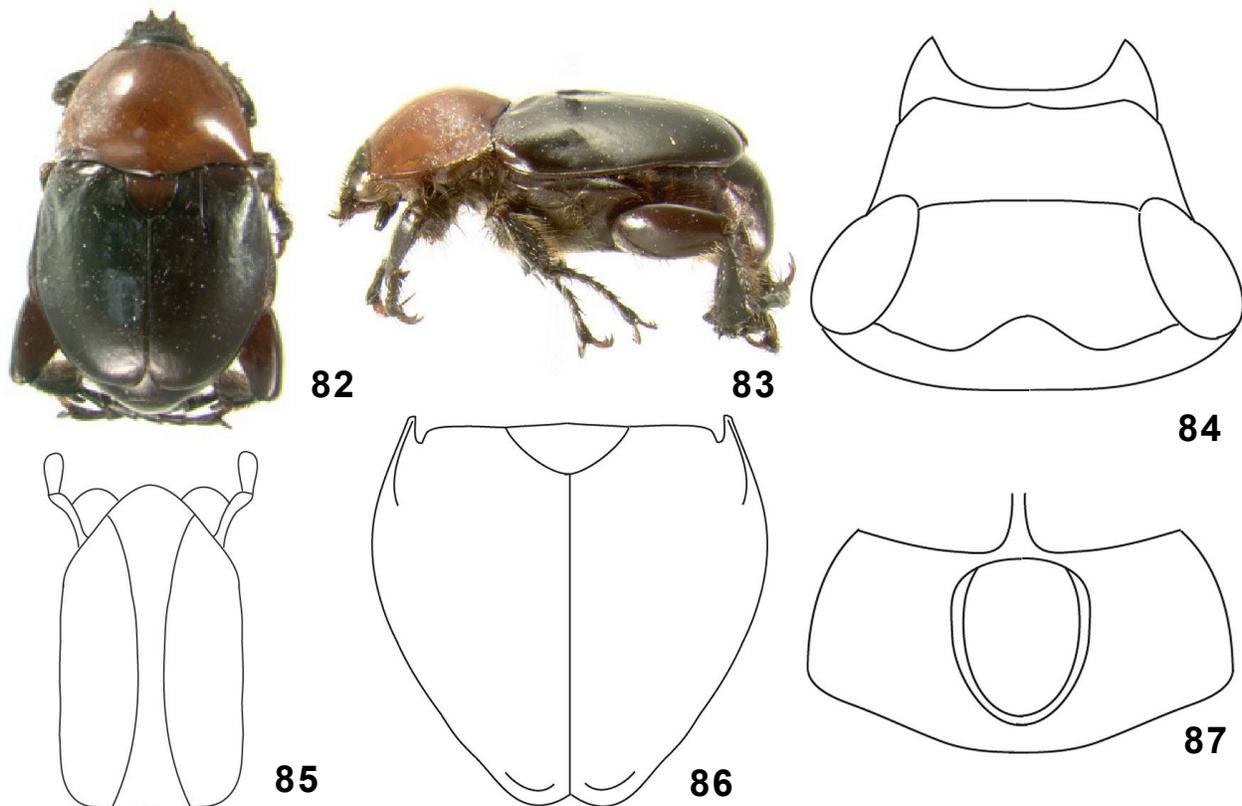
This genus is characterized by its elongate prementum, medially grooved; clypeus with anterior angles often produced into narrow teeth, strongly deflexed; pronotum, trapezoidal oblong, posterior margin often lobed; elytra ovate, widest in anterior 1/4, anterior angles often appearing toothed; metathoracic femur often broadly ovate; pygidium small, ovate.

### Generic redescription

*Measurements:* Prothorax at widest point 5.2 mm, elytra at widest point 6.4 mm, length 13.0 mm.

*Color and vestiture:* Body of male black, dorsal surface glabrous, ventrally with a vestiture consisting of reddish setae. Female with body black, glabrous dorsally, prothorax red, ventrally with a vestiture consisting of reddish setae.

*Head:* Clypeus coplanar with frons, anterior angles often produced into narrow teeth, strongly deflexed (Fig. 84); frons angled at 30°; labrum in frontal view narrowly rectangular, weakly emarginate, labrum coplanar with clypeus; labium with prementum elongate, ventral surface medially with a broad, shallow groove (Fig. 85); mandibles in dorsal view subtriangular, scissorial area rounded, membranous, molar area bluntly produced adorally; maxillary palpi with apical palpus ovate, equal in length to segments 2-3 combined, flattened ventrally, apex obtuse, forming a small sensory spot; antennae with 9 antennomeres, antennomeres 7-9 forming the elongate club, the length of which is equal to antennomeres 3-6 combined.



**Figure 82-87.** *Dicrania nigra* Le Peletier and Serville. 82) Dorsal habitus. 83) Left lateral view. 84) Head, dorsal view. 85) Prementum, ligula and labial palpi, ventral view. 86) Scutellum and elytra, dorsal view. 87) Pygidium, dorsal view.

*Prothorax*: Pronotum trapezoidal, widest posteriorly, anterior angle obtuse, lateral margin rounded, posterior angle obtuse, posterior margin convex, medially lobed; prothoracic leg with coxa transverse; tibia dentate; pretarsus with claws divergent, equal in length, both claws narrowly split, upper lobe narrow, slightly shorter than lower lobe, lower lobe broad on individual claw, base of claw toothed.

*Mesothorax*: Scutellum subtriangular; elytra oblong, widest in anterior 1/4, narrowing in posterior 1/2, anterior angle produced into an acute anteriorly directed tooth (Fig. 86), epipleuron with a slight bead, membranous margin in posterior 1/2, dorsal surface lacking striae, glabrous, anterior and posterior umbones slightly produced; pretarsus similar to prothoracic pretarsus.

*Metathorax*: Metathoracic leg with coxa widely separated; femur broadly ovate, widest medially; narrow proximally, tibia broadly clavate, widest distally, posteroventral margin with a pair of stout, long spurs, anterior spur short, arising above level of posterior spur tarsal articulation joint, posterior spur long, arising from same plane as tarsal articulation joint, posterior margin shallow, broadly grooved; pretarsus with claws similar to prothoracic and mesothoracic claws.

*Abdomen*: Ventrites 2-4 equal in length, sutures distinct, 5<sup>th</sup> ventrite (= propygidium) broad, equal to length of ventrites 2-4 combined, medially ridged, posterior margin clear, membrane-like, ventrite and sternite of 5<sup>th</sup> abdominal segment lacking a distinct suture, spiracle placed medially in a slight groove, 6<sup>th</sup> ventrite equal to 1/2 length of 5<sup>th</sup> ventrite; pygidium small, ovate, longer than wide (Fig. 87).

### Diversity and Geographic Distribution

*Dicrania* contains 43 species. Distribution is recorded from Argentina, Bolivia, Brazil, Colombia, French Guiana, Guyana, Paraguay, and Peru. Regional keys were provided by Frey (1972a).

### *Gama* Blanchard, 1850

(Figure 88-93)

*Gama* Blanchard, 1850: 118. Type species *Gama grandicornis* Blanchard, 1850, by subsequent designation (Lacordaire 1856: 265).

*Harpodactyla* Burmeister, 1855: 118. Type species *Harpodactyla grandicornis* Burmeister, 1855, by subsequent designation (Evans 2003: 268). Synonym proposed by Dalla Torre (1913).

### Taxonomic Notes

The following generic characterization is based on two syntypes of *Gama viridifusca* Moser, located at ZMHB. The type of *G. grandicornis* Blanchard was not located at the MNHC. Additional *Gama* species described by Blanchard were located at the MNHC. The generic limits were compared with the syntypes of *G. viridifusca*. Additionally, a syntype of the generic type species *G. grandicornis* (Burmeister) (MLUH) was examined.

### Generic diagnosis

This genus is recognized by its elongate body; prementum quadrate, ventral surface often medially grooved; pronotum oblong, with posterior margin medially with a pair of short, acute, teeth; mesothoracic leg of males with an elaborate metatarsus, often hook-like.

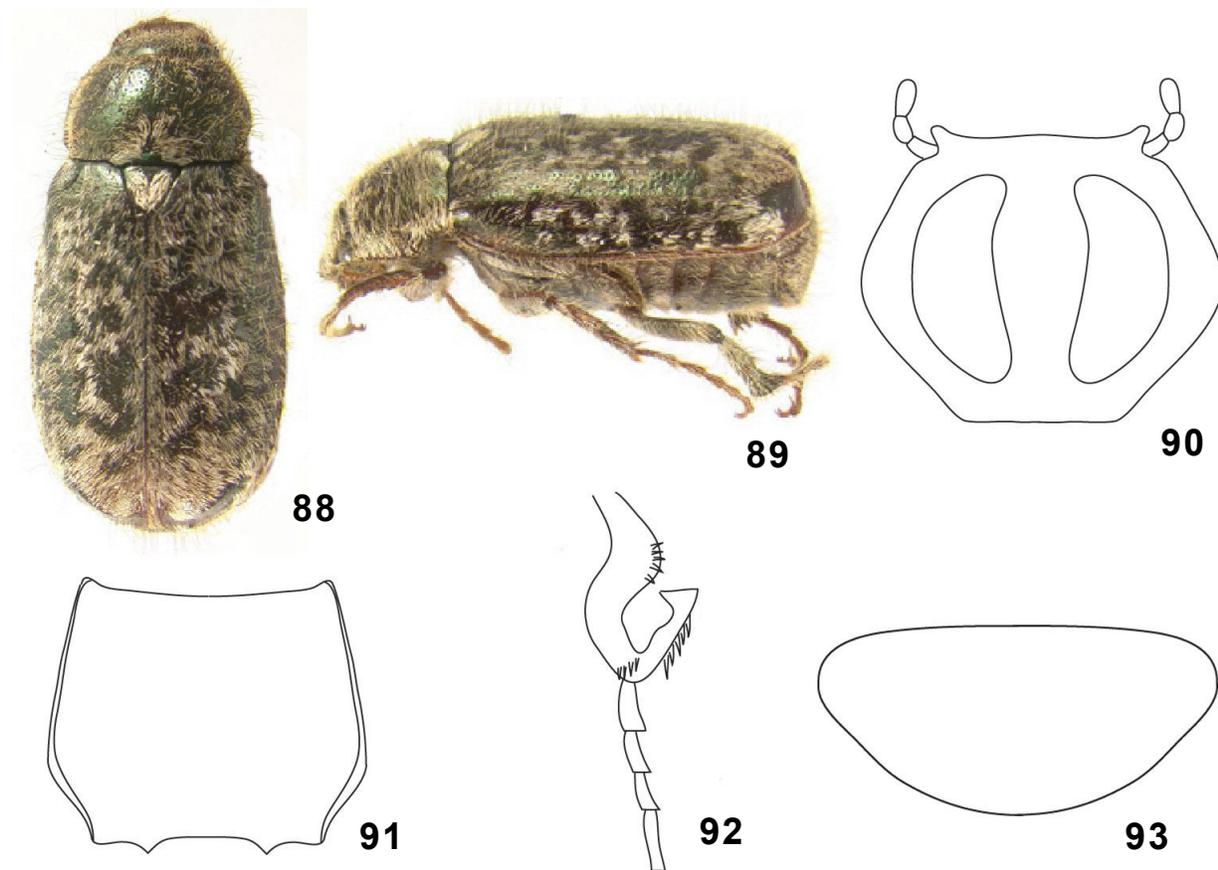
### Generic redescription

*Measurements*: Prothorax at widest point 4.0 mm, elytra at widest point 4.2 mm, length 10.5 mm.

*Color and vestiture*: Body mottled brown and green, surface shiny and reflective, vestiture lacking.

*Head*: Clypeus not coplanar with frons; frons angled at 45°; labrum in frontal view ovate, medially with a deep emargination, labrum coplanar with clypeus; labium with prementum quadrate, ventral surface raised slightly, rounded, (medially grooved in *G. grandicornis*) (Fig. 90); mandibles in dorsal view rectangular, scissorial region directed aborally, medially lobed, molar area well sclerotized, prominent; maxillary palpi with apical segment elongate, ovate; antennae with 9 antennomeres, antennomeres 7-9 forming the elongate club, equal to antennomeres 2-6 combined.

*Prothorax*: Pronotum oblong, transverse, widest medially, anterior angle obtuse, lateral margin convex, posterior angle acute, posterior margin straight, weakly bidentate (Fig. 91); prothoracic leg with



**Figure 88-93.** *Gama viridifusca* Moser (male syntype). **88)** Dorsal habitus. **89)** Left lateral view. **90)** Prementum, ligula and labial palpi, ventral view. **91)** Pronotum, dorsal view. **92)** Mesothoracic tibia and tarsi. **93)** Pygidium, ventral view.

coxa transverse; tibia weakly dentate; pretarsus with claws widely divergent, equal in length, both claws broadly split, upper lobe narrow, lower lobe broad on individual claw.

**Mesothorax:** Mesothoracic leg with metatarsus oblong, transverse, broadly arrow shaped, angled dorsally, dorsal margin straight, rounded on dorsoventral margin, anterior ventral margin produced in a flange, posterior ventral margin with a narrow hook, posterior surface scooped out, width equal to 2<sup>nd</sup> tarsomere width (Fig. 92); scutellum subtriangular; elytra longer than wide, width uniform, dorsal surface with weak striae, patches of broad white setae, anterior umbone slightly produced, posterior umbone prominent; pretarsus similar to prothoracic pretarsus.

**Metathorax:** Metathoracic leg with coxae widely separated; femur narrowly ovate, widest medially; tibia vase-shaped, narrow proximally, widest in proximal 1/4, narrowing in distal 1/4, distoventral margin with pair of equal, long, flattened spurs, spurs arise at same level as tarsal articulation joint, posterior margin with a deep, U-shaped groove; pretarsus with claws similar to prothoracic and mesothoracic claws.

**Abdomen:** Ventrites 2-4 equal in length, sutures distinct, length of 5<sup>th</sup> ventrite equal to length of 3<sup>rd</sup> and 4<sup>th</sup> ventrites combined, posterior margin concave, ventrite and sternite of 5<sup>th</sup> abdominal segment lacking a suture, spiracle situated in posterior 1/4, 6<sup>th</sup> ventrite ovate in ventral profile; pygidium subtriangular, wider than long, posterior margin rounded (Fig. 93).

### Diversity and Geographic Distribution

*Gama* comprises 29 species, primarily from Brazil, with a limited number of species from Argentina, Colombia, and Venezuela. No key to species currently exists.

***Gastrohoplus* Moser, 1921**

(Figure 94-99)

*Gastrohoplus* Moser, 1921b: 165. Type species *Gastrohoplus mirabilis* Moser, 1921b, by monotypy.**Taxonomic Notes**

The following generic diagnosis is based on a single dissected syntype of the generic type species *G. mirabilis* (ZMHB).

**Generic diagnosis**

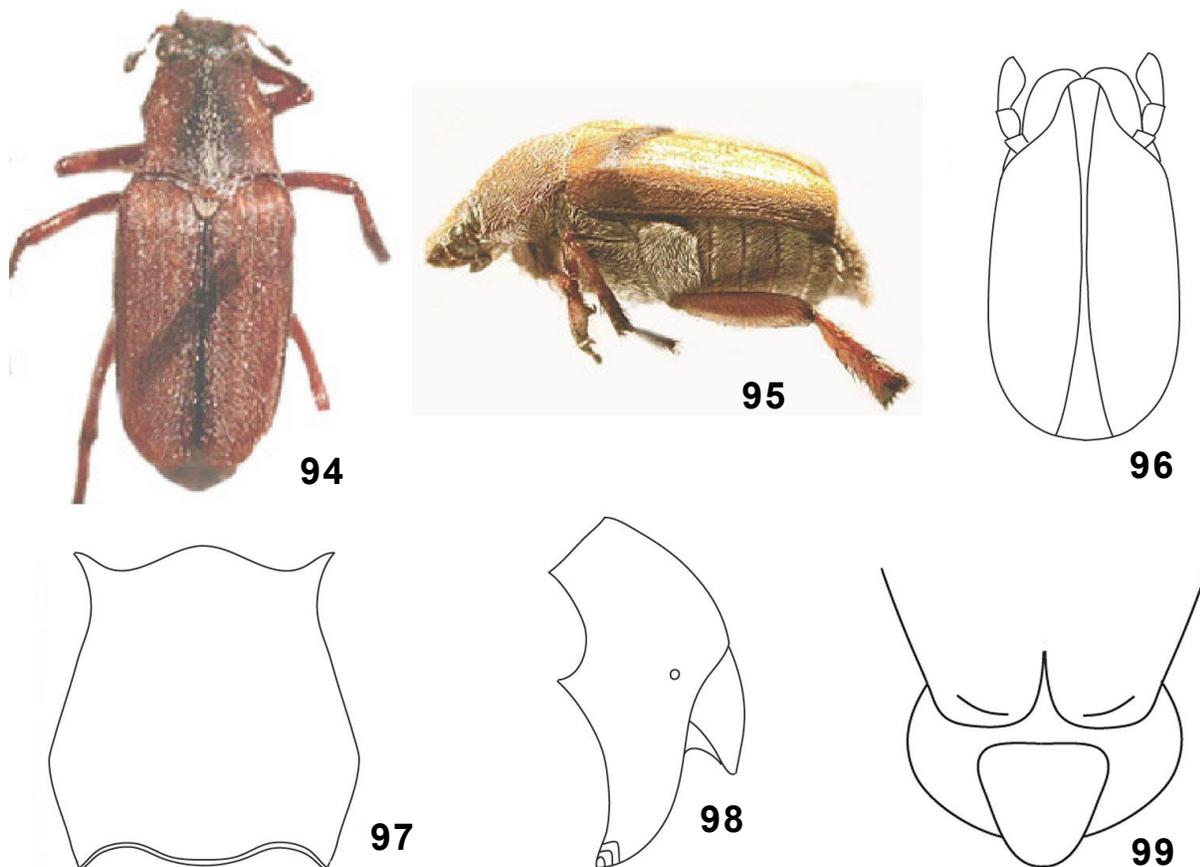
This genus closely resembles *Macroductylus*, it is characterized by the quadrate pronotum, widest in the posterior 1/4, anterior angles toothed; males with propygidium elongate laterally, forming two long subtriangular plates.

**Generic redescription**

*Measurements:* Prothorax at widest point 3.25 mm, elytra at widest point 5.0 mm, length 10.0 mm.

*Color and vestiture:* Head black, vestiture consisting of whitish scale-like setae and fine orange setae, pronotum medially with white, scale-like setae, elytra brown, with a vestiture consisting of fine orange setae, abdomen dark brown, covered with a vestiture consisting of short, white setae.

*Head:* Clypeus coplanar with frons; frons angled at 30°; labrum in frontal view narrowly ovate, weakly emarginate, labrum coplanar with clypeus; labium with prementum rectangular, elongate (2X longer than wide), ventral surface with medial groove (Fig. 96); mandibles in dorsal view rectangular,



**Figure 94-99.** *Gastrohoplus mirabilis* Moser (female). **94)** Dorsal habitus. **95)** Left lateral view. **96)** Prementum, ligula and labial palpi, ventral view. **97)** Pronotum, dorsal view. **98)** Propygidium and pygidium, left lateral view. **99)** Pygidium, dorsal view.

scissorial area reduced to a membrane, lined with dense setae, molar area well developed; maxillary palpi with apical segment conical, equal to length of segments 1 and 2 combined, apex obtuse; antennae with 9 antennomeres, antennomeres 7-9 forming the club, lamellae thin, elongate, equal to antennomeres 3-6 combined.

*Prothorax*: Pronotum quadrate, widest in posterior 3/4, anterior angles acute, appearing toothed, lateral margin concave in anterior 1/2, convex in posterior 1/2, posterior angle acute, appearing toothed, posterior margin concave, medially lobed (Fig. 97); prothoracic leg with coxa elongate; tibia lacking a tooth, ventral margin with a small spur in distal 1/4; pretarsus with claws divergent, equal in length, both claws broadly split, upper lobe broad, longer than lower lobe, lower lobe broad on individual claw.

*Mesothorax*: Scutellum subtriangular; elytra longer than wide, widest medially, elytral epipleuron narrowly flattened, dorsal surface with striae indistinct, anterior umbone strongly developed, posterior umbone weakly developed; pretarsus similar to prothoracic pretarsus.

*Metathorax*: Metathoracic leg with coxa narrowly separated; femur ovate, widest medially, narrowing distally; tibia vase-shaped, narrow proximally, widest in proximal 1/4, posteroventral margin with two spurs arising from same plane as tarsal articulation, posterior margin lacking groove; pretarsus with claws similar to prothoracic and mesothoracic legs.

*Abdomen*: Ventrites 2-4 subequal in length, 5<sup>th</sup> visible ventrite (= propygidium) 1.5X length of 4<sup>th</sup> ventrite, horizontal ridge medially, ventrite and sternite of 5<sup>th</sup> abdominal segment lacking a suture, spiracle placed medially, male with propygidium elongate laterally, forming two long subtriangular plates (Fig. 98); 6<sup>th</sup> ventrite equal in length to 5<sup>th</sup> ventrite, posterior margin weakly concave; pygidium subtriangular, longer than wide, posterior margin rounded (Fig. 99).

### Diversity and Geographic Distribution

*Gastrohoplus* is monotypic, with *G. mirabilis* known only from Brazil.

### *Hercitis* Burmeister, 1855

(Figure 100-104)

*Hercitis* Burmeister, 1855: 79. Type species *Hercitis pygmaea* Burmeister, 1855, by monotypy.

### Taxonomic Notes

The following generic diagnosis is based on a single dissected syntype of the generic type species, *H. pygmaea* (MLUH).

### Generic diagnosis

This genus is characterized by its elongate, body and very small size; prementum elongate, ventral surface flattened; pronotum oblong, widest in anterior 1/4, posterior angles acute; anterior and posterior umbones prominent; 6<sup>th</sup> ventrite with posterior margin medially bidentate, raised dorsally; pygidium tear-shaped, posterior margin blunt, concave.

### Generic redescription

*Measurements*: Prothorax at widest point 2.3 mm, elytra at widest point 2.6 mm, length 5.5 mm.

*Color and vestiture*: Body dark brown, dorsally with a vestiture consisting of scattered white setae.

*Head*: Clypeus coplanar with frons, angled at 45°; labrum in frontal view very narrow, rectangular, with a slight, broad groove medially, labrum coplanar with clypeus; labium with prementum elongate, ventral surface flattened in posterior 3/4, apically with small medial groove (Fig. 102); mandibles in dorsal view semicircular, scissorial area narrow, concave, posterior angle of region toothed, molar area prominent, weakly sclerotized; maxillary palpi with apical palpus elongate, ovate, equal to length of segments 1-3 combined; antennae with 8 antennomeres, antennomeres 6-8 forming the club, equal to length of antennomeres 3-5 combined, club rounded.

*Prothorax*: Pronotum oblong, transverse, widest medially, anterior angle obtuse, lateral margin convex in anterior 1/2, concave in posterior 1/2, posterior angle acute, appearing toothed, posterior margin concave, medially lobed (Fig. 103); prothoracic leg with coxa elongate; tibia dentate, ventral margin with

a large spur in distal 1/4; pretarsus with claws divergent, equal in length, both claws narrowly split, upper and lower lobes narrow on individual claw.

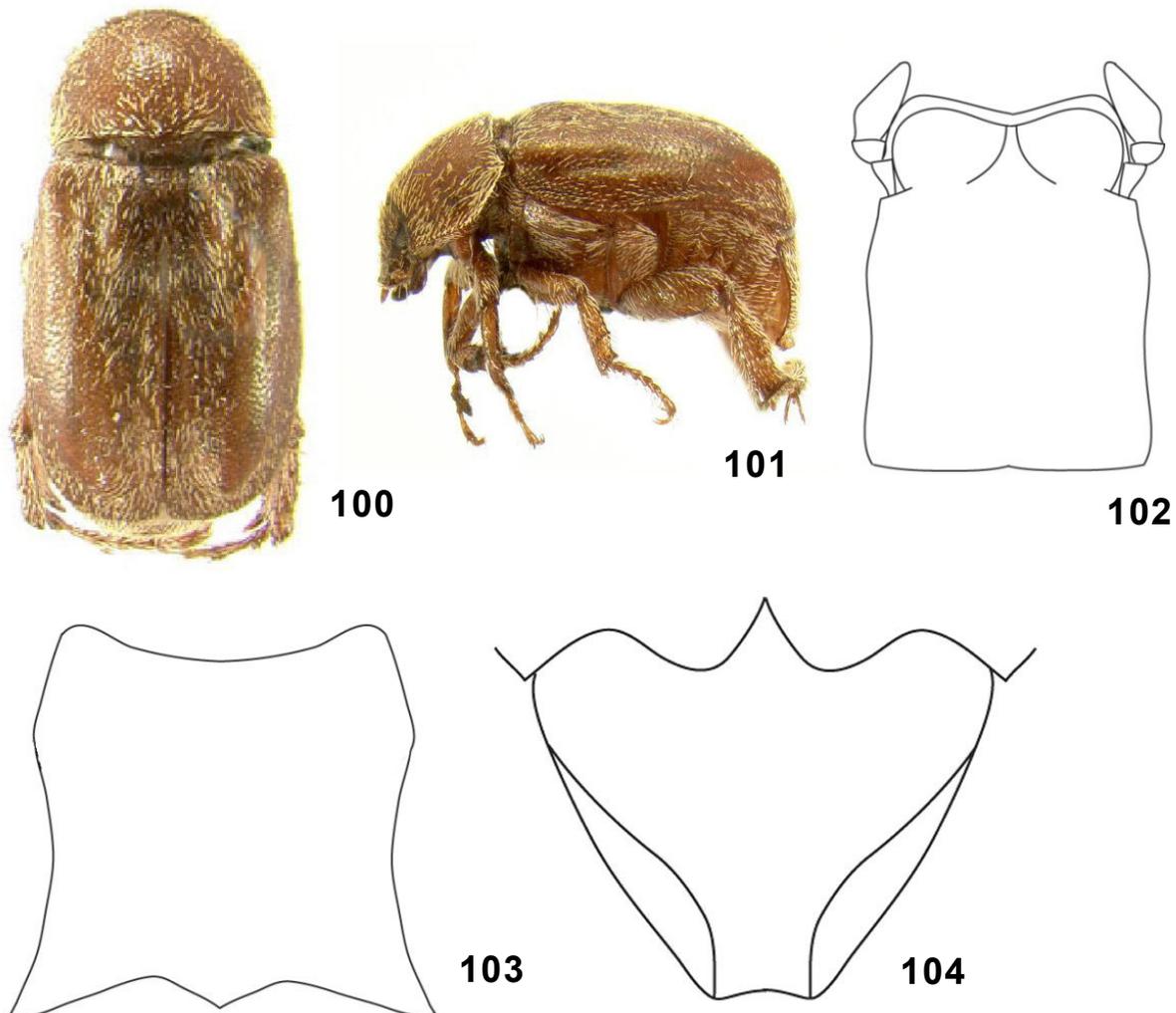
*Mesothorax*: Scutellum subtriangular; elytra longer than wide, widest in posterior 3/4, epipleuron narrow, smooth, appearing membranous, dorsal surface weakly striate, interstitial areas smooth, anterior and posterior umbones prominent; pretarsus similar to prothoracic pretarsus.

*Metathorax*: Metathoracic leg with coxa narrowly separated; femur ovate, widest in proximal 1/3; tibia vase shaped, narrow proximally, widest medially, posteroventral margin with pair of spurs, ventral spur broad, short, slightly raised above tarsal articulation joint, posterior spur long, narrow, arising from same plane as tarsal articulation joint, posterior margin with a deep, U-shaped groove; pretarsus with claws similar to claws of prothoracic and mesothoracic claws.

*Abdomen*: Ventrites 2-4 equal in length, 5<sup>th</sup> ventrite (= propygidium) slightly longer than 4<sup>th</sup> ventrite length, posterior margin membrane-like, ventrite and sternite of 5<sup>th</sup> abdominal segment lacking a suture, spiracle placed medially, 6<sup>th</sup> ventrite length equal to 5<sup>th</sup> ventrite length, posterior margin sinuate, medially bidentate, raised dorsally; pygidium tear-shaped, longer than wide, posterior margin blunt, concave (Fig. 104).

### Diversity and Geographic Distribution

*Hercitis* comprises four species, all known only from Brazil. There is currently no key to species.



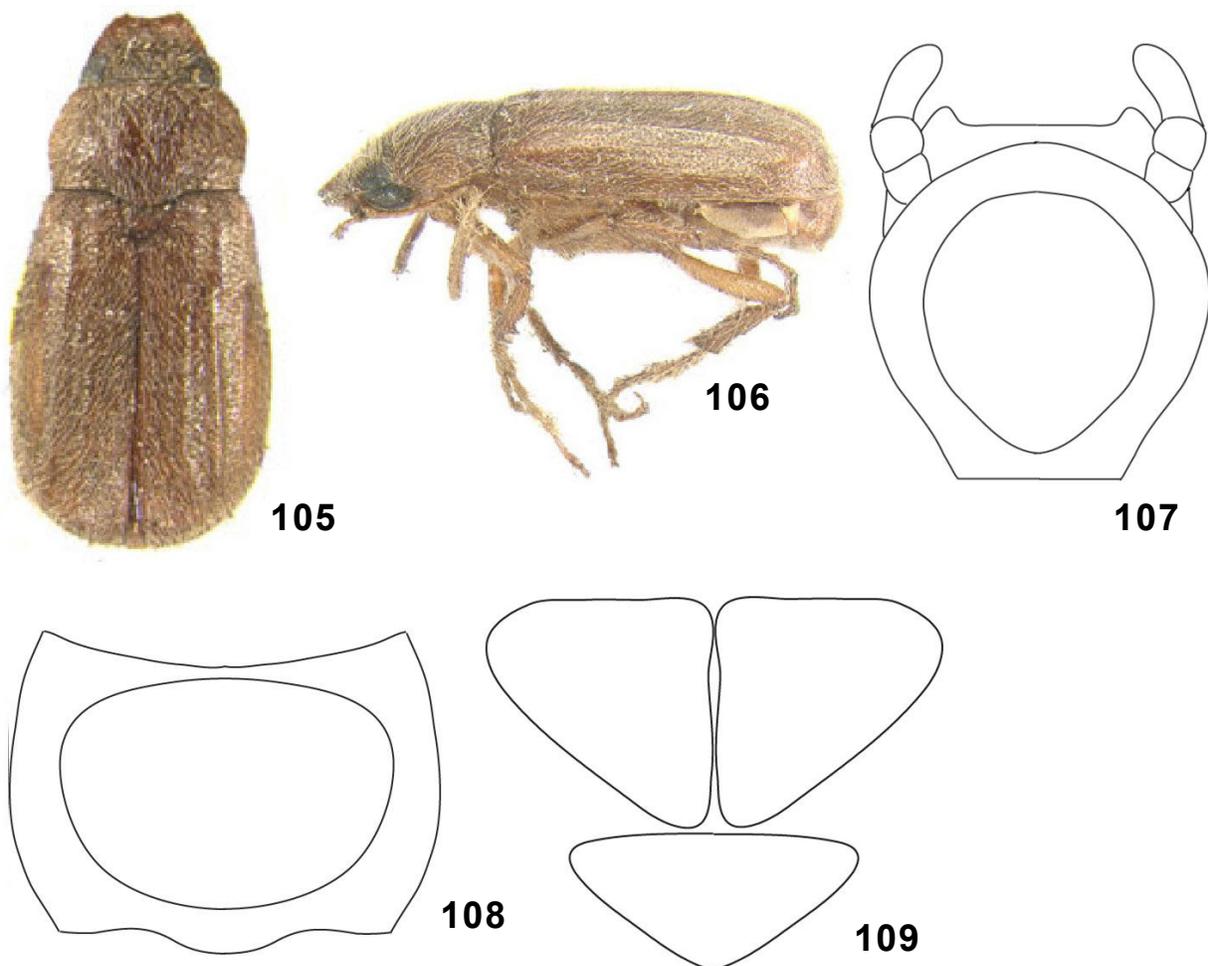
**Figure 100-104.** *Hercitis pygmaea* Burmeister. **100)** Dorsal habitus. **101)** Left lateral view. **102)** Prementum, ligula and labial palpi, ventral view. **103)** Pronotum, dorsal view. **104)** Pygidium, dorsal view.

***Hieritis* Burmeister, 1855**

(Figure 105-109)

*Hieritis* Burmeister, 1855: 41. Type species *Hieritis macrocera* Burmeister, 1855, by monotypy.**Taxonomic Notes**The following generic diagnosis is based on a single dissected syntype of the generic type species, *H. macrocera* (MLUH).**Generic diagnosis**

This genus is characterized by its very small size; quadrate prementum, ventral surface raise; oblong, transverse pronotum; pygidium subtriangular, wider than long.

**Generic redescription***Measurements*: Prothorax at widest point 2.2 mm, elytra at widest point 3.0 mm, length 7.2 mm.*Color and vestiture*: Body brown, surface with vestiture consisting of fine yellow setae.*Head*: Clypeus not coplanar with frons; frons angled at 60°; labrum in frontal very narrowly ovate, slightly emarginate medially, labrum not coplanar with clypeus; labium with prementum quadrate, ventral surface raised medially (Fig. 107); mandibles in dorsal view broadly rectangular, scissorial area bluntly produced, medially emarginate, molar region flush with adoral lateral margin, not bluntly produced; maxillary palpi with apical palpus conical, elongate, equal to 1<sup>st</sup> and 2<sup>nd</sup> segments combined, apex**Figure 105-109.** *Hieritis macrocera* Burmeister. **105)** Dorsal habitus. **106)** Left lateral view. **107)** Prementum, ligula and labial palpi, ventral view. **108)** Pronotum, dorsal view. **109)** Pygidium, dorsal view.

acute; antennae with 10 antennomeres, antennomeres 8-10 forming the elongate club, club length equal to length of antennomeres 2-7 combined.

*Prothorax*: Pronotum oblong, transverse, widest medially, anterior angles acute, lateral margins convex, posterior angle obtuse, posterior margin straight, medially lobed (Fig. 108); prothoracic leg with coxa transverse; tibia dentate, ventral with a small spur present in distal 1/4; pretarsus with claws divergent, equal in length, both claws narrowly split, upper lobe narrow, lower lobe broad on individual claw.

*Mesothorax*: Scutellum cordate; elytra longer than wide, width uniform, elytral epipleuron flattened, grooved in lateral view, dorsal surface with three weak striae, surface covered with fine setae, anterior and posterior umbones weakly produced.

*Metathorax*: Metathoracic leg with coxa clearly separated; femur narrowly ovate, narrow proximally, widest medially; tibia rectangular, narrowed proximally, widest medially, posteroventral margin with a pair of long, stout spurs, spurs subequal in length, arising at same plane as tarsal articulation joint, posterior margin with a deep, U-shaped groove; pretarsus with claws similar to claws of prothoracic and mesothoracic legs.

*Abdomen*: Ventrites 2-4 equal in length, ventrite 5 (= propygidium) equal to length of ventrites 3-4 combined, ventrite and sternite of 5<sup>th</sup> abdominal segment not separated by a suture, spiracle located medially, length of ventrite six equal to 4<sup>th</sup> ventrite length; pygidium subtriangular, wider than long, posterior margin rounded (Fig. 109).

### Diversity and Geographic Distribution

*Hieritis* is currently monotypic, with *Hieritis macrocera* known only from Brazil.

### *Isonychus* Mannerheim, 1829

(Figure 110-114)

*Isonychus* Mannerheim, 1829: 69. Type species *Isonychus sulphureus* Mannerheim, 1829, by original designation.

*Colporhina* Curtis, 1844: 200. Type species *Colporhina bifoveolata* Curtis, 1844, by monotypy. Synonymized by Dalla Torre (1913).

### Taxonomic Notes

The following generic diagnosis is based on a single dissected specimen of the generic type species, *I. sulphureus*. Specimens were authoritatively identified by Moser, Arrow, and the author with the aid of the original description. The type was not seen during this study.

### Generic diagnosis

This genus is characterized by its ovate, rotund body shape; body often covered with scale-like hairs; prementum elongate, ventral surface medially grooved; pronotum oblong, transverse, anterior angles acute, appearing toothed; pygidium subtriangular, width equal to length.

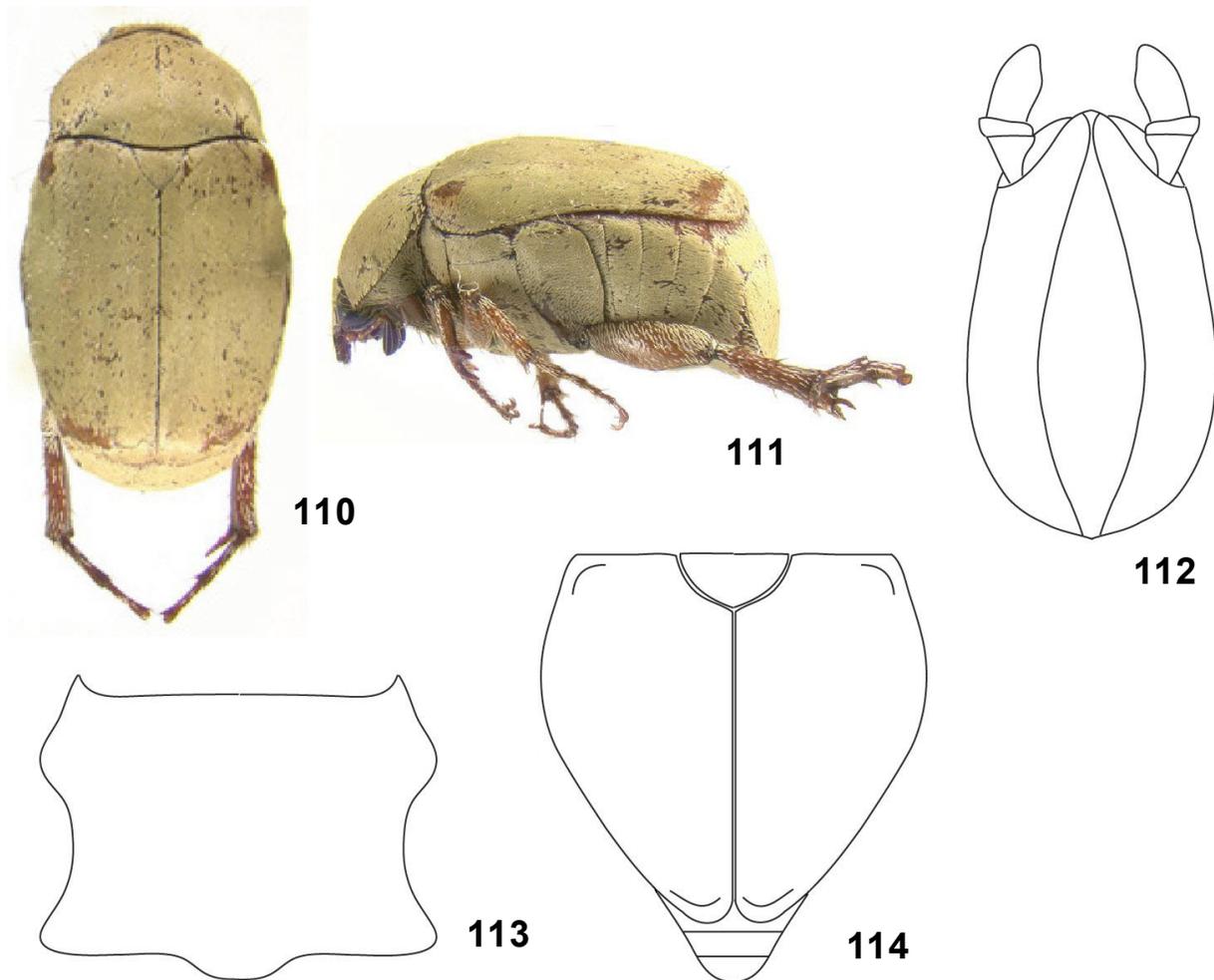
### Generic redescription

*Measurements*: Prothorax at widest point 3.6 mm, elytra widest point 4.8 mm, length 9.3 mm.

*Color and vestiture*: Head and pronotum black, legs reddish brown, body with a vestiture consisting of sulphur-colored scales.

*Head*: Clypeus coplanar with frons; frons angled at 60°; labrum in frontal view narrow, ovate, slightly emarginate medially, labrum coplanar with clypeus; labium with prementum rectangular, elongate, ventral surface medially grooved (Fig. 112); mandibles in dorsal view broadly rectangular, anterior margin broadly rounded, scissorial area reduced to a membrane, molar region prominent, well sclerotized; maxillary palpi with apical palpus ovate, elongate, equal to length of 2<sup>nd</sup> and 3<sup>rd</sup> segments combined, thin in lateral profile, blunt apically; antennae with 9 antennomeres, antennomeres 7-9 forming the club, equal to length of antennomeres 2-6 combined.

*Prothorax*: Pronotum oblong, transverse, widest medially, anterior angles acute, lateral margin convex, posterior 1/4 of margin straight, posterior angles acute, posterior margin weakly concave, medially



**Figure 110-114.** *Isonychus sulphureus* Mannerheim. **110)** Dorsal habitus. **111)** Left lateral view. **112)** Prementum, ligula and labial palpi, ventral view. **113)** Pronotum, dorsal view. **114)** Elytra, propygidium and pygidium, dorsal view.

with a broad lobe (Fig. 113); prothoracic leg with coxa elongate; tibia dentate, ventral margin with spur present in distal 3/4; pretarsus with claws divergent, equal in length, both claws narrowly split, upper lobe narrow, lower lobe broad on individual claw, base of claw toothed.

*Mesothorax:* Scutellum subtriangular; elytra slightly longer than wide, widest in anterior 1/2 (Fig. 114), elytral epipleuron absent, membrane lining lateral margin, dorsal surface with seven weak sutural striae present, surface covered with dense, sulfur colored scales anterior umbone moderately prominent, posterior umbone weak; pretarsus similar to prothoracic pretarsus.

*Metathorax:* Metathoracic leg with coxa contiguous; femur elongate, ovate, narrow proximally, widest medially; tibia vase-shaped, proximally narrowed, widest medially, narrowing in distal 1/4, posteroventral margin with two long, stout spurs, ventral spur slightly shorter than posterior spur, arising from same plane as tarsal articulation joint, posterior margin with a deep, U-shaped groove; pretarsus with claws similar to claws of prothoracic and mesothoracic legs.

*Abdomen:* Ventrites 2-4 equal in length, 5<sup>th</sup> ventrite (= propygidium) equal to length of ventrites 2-4 combined, posterior margin membranous, below plane of sclerotized 5<sup>th</sup> ventrite, ventrite and sternite of 5<sup>th</sup> abdominal segment lacking a suture, spiracle located in the posterior 1/4, 6<sup>th</sup> ventrite triangular, glabrous, posterior margin appearing membranous, surface of all ventrites covered with dense, sulfur colored scales; pygidium subtriangular, width equal to length, posterior margin rounded.

### Diversity and Geographic Distribution

*Isonychus* comprises 147 species, distributed from Argentina, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, French Guiana, Guatemala, Guyana, Honduras, Mexico, Nicaragua, Panama, Peru, Surinam, United States, Uruguay, and Venezuela. Regional keys are provided by Frey (1964, 1965, 1970) and Morón (1994).

### *Issacaris* Fairmaire, 1889

(Figure 115-119)

*Issacaris* Fairmaire, 1889: 117. Type species *Issacaris petalophora* Fairmaire, 1889, by monotypy.

### Taxonomic Notes

The following generic diagnosis is based on a single dissected male homeotype of the presumptive syntype of the type species *I. petalophora* located at the MNHC and identified with a Fairmaire label.

### Generic diagnosis

This genus is characterized by its large size, rectangular shape of elytra; large, globose eyes; pronotum oblong, transverse, widest medially; prementum elongate weakly subtriangular, medially grooved; clypeus semicircular in dorsal view, labrum narrowly ovate in frontal view; pygidium subtriangular, wider than long.

### Generic redescription

*Measurements*: Prothorax at widest point 7.0 mm, elytra at widest point 10.0 mm, length 17.0 mm.

*Color and vestiture*: Head black, pronotum dark reddish brown, elytra light brown, abdomen and thorax reddish brown, ventral surface with vestiture consisting of long, golden setae.

*Head*: Clypeus not coplanar with frons; frons angled at 10°; labrum in frontal view narrowly ovate, weakly emarginate, labrum not coplanar with clypeus; labium with prementum elongate, weakly subtriangular, ventral surface medially grooved (Fig. 117); mandibles in dorsal view subtriangular, scissorial area reduced to a rounded apex, not prominently produced adorally, molar area not produced adorally, weakly sclerotized; maxillary palpi with apical palpus ovate, equal to length of segments 2-3, apex acute; antennae with 8 antennomeres, antennomeres 6-8 forming the very elongate club, club length equal to length of antennomeres 1-5 combined (Fig. 118).

*Prothorax*: Pronotum oblong, transverse, widest medially, anterior angle obtuse, lateral margins convex, margins with a narrow bead, posterior angle obtuse, posterior margin straight, medially lobed, dorsal surface weakly lobed (Fig. 119); prothoracic leg with coxa transverse; tibia dentate, distal 1/3 with a long spur; pretarsus with claws not divergent, equal in length, both claws narrowly split, outer lobe narrow, slightly longer than lower lobe, lower lobe broad on individual claw, base of claw toothed.

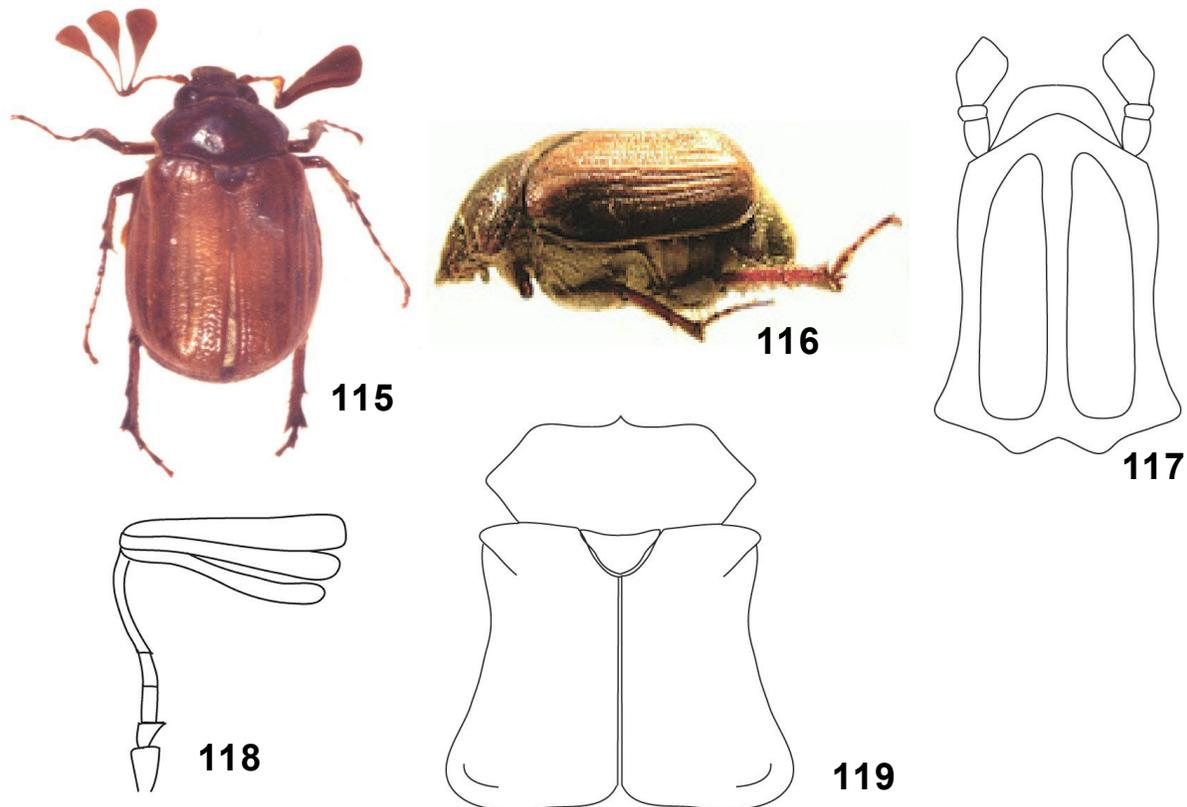
*Mesothorax*: Scutellum subtriangular; elytra wider than long, widest in posterior 3/4, elytral epipleuron flattened, grooved, dorsal surface with several weak, punctate striae, strial intervals slightly raised anterior umbone strong, posterior umbone weak; pretarsus similar to prothoracic pretarsus.

*Metathorax*: Metathoracic leg with coxa widely separated; femur broadly ovate, widest medially; tibia rectangular, proximally narrow, width uniform, posteroventral margin lacking spurs, posterior margin with a broad, shallow U-shaped groove; pretarsus similar to pro- and mesothoracic legs.

*Abdomen*: Ventrites 2-4 equal in length, 5<sup>th</sup> ventrite (= propygidium) equal to length of ventrites 2-3 combined, posterior margin membranous, ventrite and sternite of 5<sup>th</sup> abdominal segment with a partial suture, spiracle placed medially, at apex of suture, length of 6<sup>th</sup> ventrite equal to 1/2 length of 5<sup>th</sup> ventrite; pygidium subtriangular, wider than long, posterior margin rounded.

### Diversity and Geographic Distribution

*Issacaris* comprises three species, all known only from Chile. A key is provided by Gutiérrez (1952).



**Figure 115-119.** *Issacaris petalophora* Fairmaire (male). **115)** Dorsal habitus. **116)** Left lateral view. **117)** Prementum, ligula and labial palpi, ventral view. **118)** Antenna. **119)** Pronotum, scutellum and elytra, dorsal view.

### ***Macroductylus* Dejean, 1821**

(Figure 120-124)

*Macroductylus* Dejean, 1821: 58. Type species *Melolontha subspinosus* Fabricius, 1775, by subsequent designation (Evans 2003: 290).

*Stenothorax* Harris, 1827: 8. Type species *Stenothorax subspinosus* (Fabricius), 1775, by monotypy.

### **Taxonomic Notes**

The following generic diagnosis is based on four dissected homeotypes of the presumptive syntype of the type species *M. subspinosus* located at the MNHC, and identified with a Fabricius label.

### **Generic diagnosis**

This genus is characterized by its elongate body, often with a vestiture consisting of scale-like setae; prementum elongate, medially grooved; pronotum hexagonal, longer than wide, widest medially.

### **Generic redescription**

*Measurements:* Prothorax at widest point 2.4 mm, elytra at widest point 3.7 mm, length 10.0 mm.

*Color and vestiture:* Head, thorax and abdomen dark brown; body with a vestiture consisting of short, broad, dense yellow recumbent setae.

*Head:* Clypeus coplanar with frons; frons angled at 30°; labrum in frontal view, oval, narrow, weakly emarginate, labrum coplanar with clypeus; labium with prementum rectangular, elongate, ventral surface with medial groove (Fig. 122); mandibles in dorsal view triangular, scissorial area reduced to a membrane, lined with dense setae, molar area well developed, weakly sclerotized; maxillary palpi with apical palpus oval, equal to length of segments 1-2 combined, apex with blunt sensory region; antennae

with 9 antennomeres, antennomeres 7-9 forming the club, lamellae thin, elongate, equal to length of antennomeres 3-6 combined.

*Prothorax*: Pronotum hexagonal, transverse, widest medially, anterior angle obtuse, lateral margin convex medially, posterior angle obtuse, posterior margin weakly concave (Fig. 123); prothoracic leg with coxa elongate; tibia dentate, with a small spur (absent in males) 1/4 distance from distal apex; pretarsus with claws divergent, equal in length, both claws narrowly split, outer lobe narrow, slightly longer than lower lobe, lower lobe broad on individual claw.

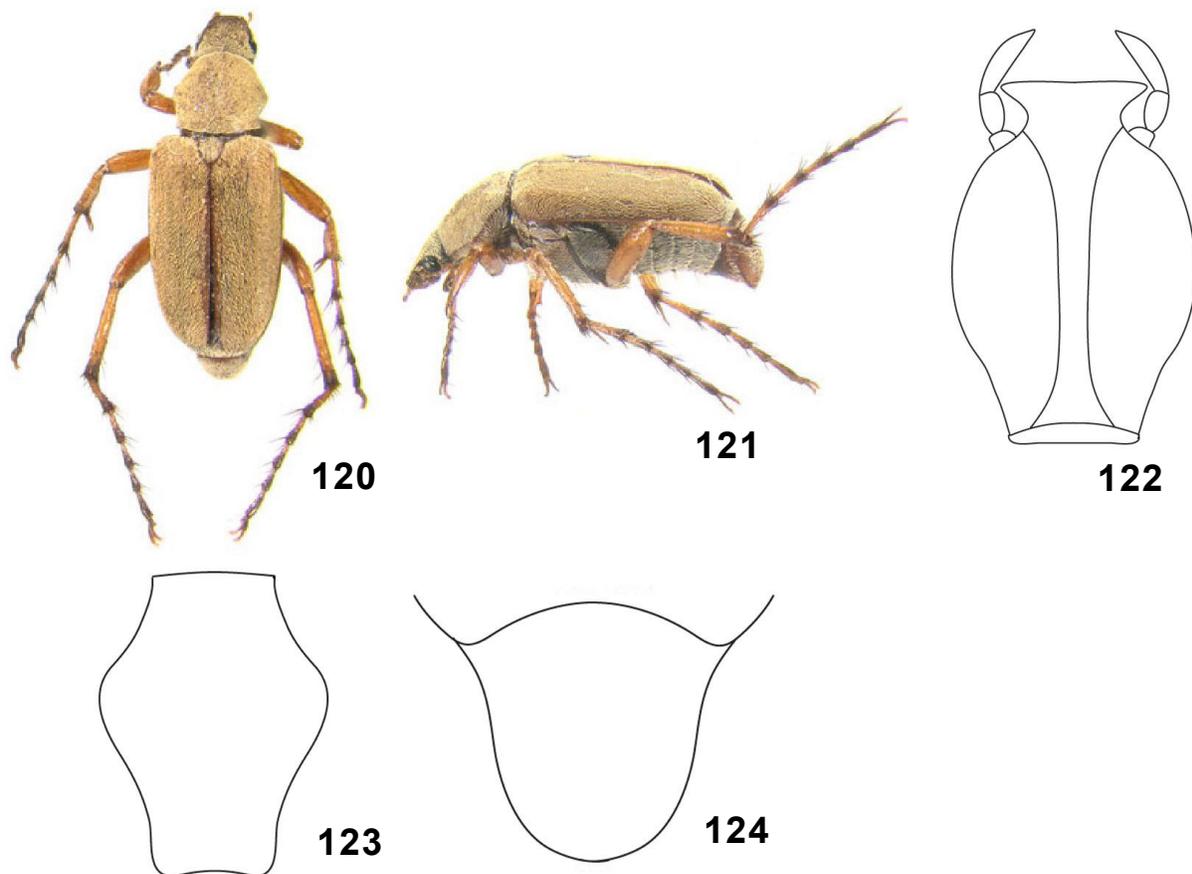
*Mesothorax*: Scutellum cordiform; elytra longer than wide, width uniform, elytral epipleuron narrowly flattened, membranous, dorsal surface with striae distinct, intervals slightly convex, surface covered with short, broad, yellow setae, anterior umbone strongly developed, posterior umbone very weakly developed; pretarsus similar to prothoracic pretarsus.

*Metathorax*: Metathoracic leg with coxae clearly separated; femur elongate, weakly ovate, widest medially; tibia triangular, broader distally; posteroventral margin with subequal spurs (absent in males), spurs arising from same plane as tarsal articulation joint, posterior margin lacking a U-shape groove; pretarsus with claws similar to prothoracic and mesothoracic legs and empodium.

*Abdomen*: Ventrites 2-4 subequal in length, 5<sup>th</sup> visible ventrite (= propygidium) 1.5X length of ventrite 4 length, 5<sup>th</sup> visible ventrite and sternite of 5<sup>th</sup> abdominal segment with suture lacking, spiracle placed medially, 6<sup>th</sup> ventrite triangular, posterior 1/2 membranous; pygidium triangular, posterior margin rounded, longer than wide in males (Fig. 124).

### Diversity and Geographic Distribution

*Macrodactylus* comprises 109 species, distributed from Argentina, Belize, Bolivia, Brazil, Canada, Chile, Colombia, Costa Rica, Ecuador, Guatemala, Mexico, Nicaragua, Panama, Paraguay, Peru, United



**Figure 120-124.** *Macrodactylus subspinosus* (Fabricius) (female). **120)** Dorsal habitus. **121)** Left lateral view. **122)** Prementum, ligula and labial palpi, ventral view. **123)** Head, pronotum, scutellum, dorsal view. **124)** Pygidium, dorsal view.

States, and Venezuela. Regional keys provided by Horn (1876), Carrillo and Gibson (1960), Morón (1994), and Arce-Pérez and Morón (2000).

### ***Manodactylus* Moser, 1919**

(Figure 125-129)

*Manodactylus* Moser, 1919: 43. Type species *Manodactylus gaujoni* Moser, 1919, by monotypy.

#### **Taxonomic Notes**

The following generic diagnosis is based on a single dissected syntype of the type species, *M. gaujoni* (ZMHB).

#### **Generic diagnosis**

This monotypic genus closely resembles *Macroactylus*, but is characterized by its black, glabrous color and the cordate pronotum, widest medially.

#### **Generic redescription**

*Measurements*: Prothorax at widest point 3.0 mm, elytra at widest point 3.6 mm, length 8.7 mm.

*Color and vestiture*: Body black, glabrous, lacking vestiture.

*Head*: Clypeus coplanar with frons; angled at 30°; labrum in frontal view narrowly ovate, weakly emarginate; labrum coplanar with clypeus; labium with prementum elongate, ventral surface with a deep medial groove (Fig. 127); mandibles in dorsal view triangular, scissorial area rounded, membranous, molar area weakly produced adorally, well sclerotized; maxillary palpi missing; antennae with 9 antennomeres, antennomeres 7-9 forming the elongate club, club length equal to antennomeres 3-6 combined.

*Prothorax*: Pronotum cordiform, widest medially, anterior angle obtuse, lateral margin strongly convex, posterior angle obtuse, posterior margin weakly convex (Fig. 128); prothoracic leg with coxa elongate; tibia weakly dentate; pretarsus with claws not divergent, equal in length, both claws narrowly split, upper lobe narrow, longer than lower lobe, lower lobe broad on individual claw; pretarsus similar to prothoracic pretarsus.

*Mesothorax*: Scutellum subtriangular; elytra longer than wide, width uniform, in lateral profile epipleuron narrow, rounded, dorsal surface with five weak striae, anterior umbone moderately produced, posterior umbone absent.

*Metathorax*: Metathoracic leg with coxae narrowly separated; femur narrowly ovate, narrow proximally, width uniform; tibia clavate, narrow proximally, widest in distal 1/4, posteroventral margin lined with short and long setae, lacking spurs, posterior margin lacking a U-shaped groove; pretarsus with claws similar to claws of prothoracic and mesothoracic claws.

*Abdomen*: Ventrites 2-4 equal in length, margins deflexed dorsally, 4<sup>th</sup> ventrite equal to 1/4 length of 5<sup>th</sup> ventrite, 5<sup>th</sup> ventrite (= propygidium) 4X length of 4<sup>th</sup> ventrite length, posterior 1/3 membrane-like, distinctly margined giving the appearance of a separate ventrite, membrane-like region deflexed ventrally, ventrite and sternite of 5<sup>th</sup> abdominal segment separated with a partial suture, spiracle placed medially at anterior of suture, 6<sup>th</sup> ventrite triangular, length equal to 5<sup>th</sup> ventrite length, posterior 1/2 membranous; propygidium broadly subtriangular, slightly wider than long, posterior margin rounded (Fig. 129).

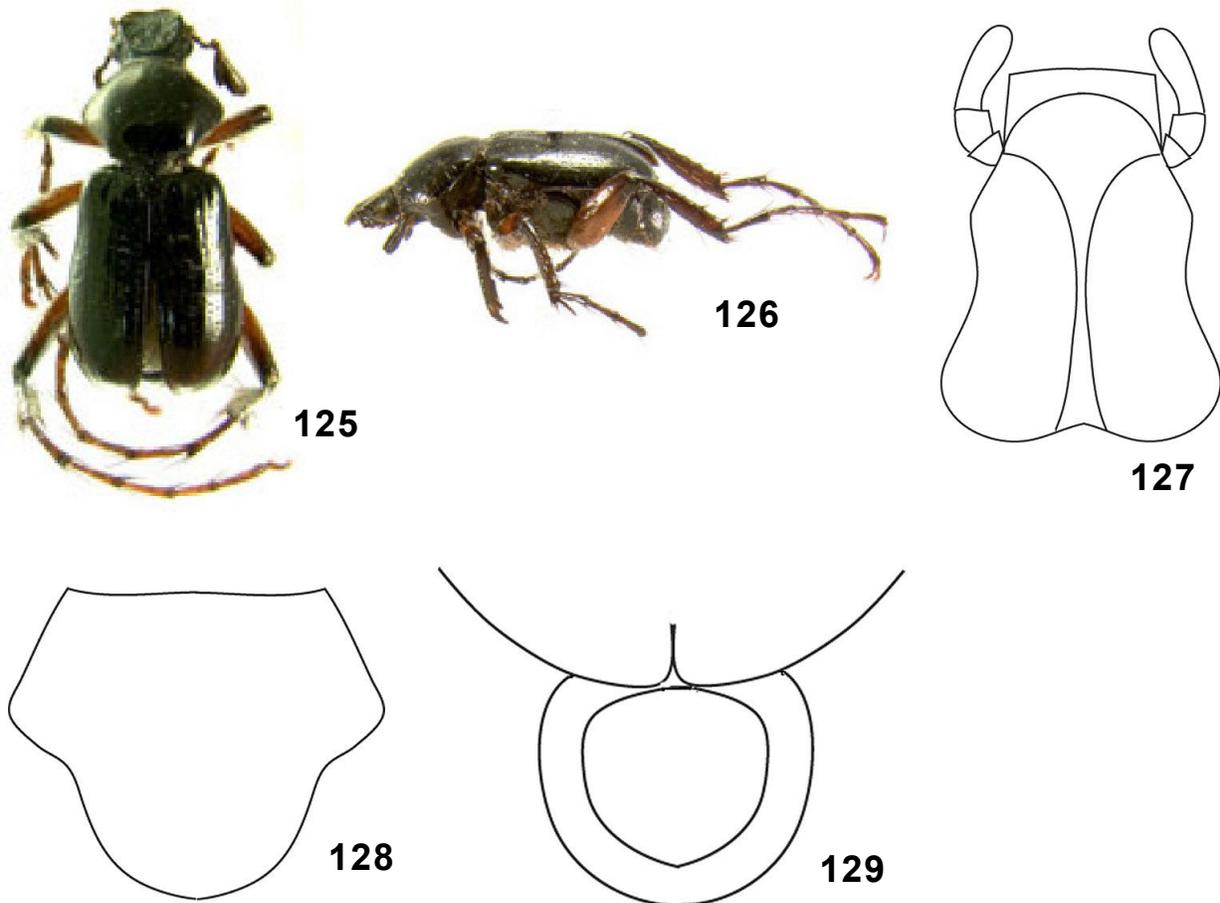
#### **Diversity and Geographic Distribution**

*Manodactylus* is monotypic, with *M. gaujoni* known only from Ecuador.

### ***Manopus* Laporte, 1840**

(Figure 130-135)

*Manopus* Laporte, 1840: 147. Type species *Manopus biguttatus* Laporte, 1840, by monotypy.



**Figure 125-129.** *Manodactylus gaujoni* Moser. **125)** Dorsal habitus. **126)** Left lateral view. **127)** Prementum, ligula and labial palpi, ventral view. **128)** Pronotum, dorsal view. **129)** Pygidium, dorsal view.

#### Taxonomic Notes

The following generic diagnosis is based on two dissected homeotypes of the presumptive syntype of the type species *M. biguttatus* located at the MNHC and identified with a Laporte label.

#### Generic diagnosis

This genus is characterized by its elongate body; mottled coloration; prementum quadrate, medially grooved; clypeus with anterior angles acute, prelabrum partially visible; pronotum cordate, widest medially, posterior margin straight, medially concave; pygidium tear-shaped.

#### Generic redescription

*Measurements:* Prothorax at widest point 3.3 mm, elytra at widest point 4.5 mm, length 13.3 mm.

*Color and vestiture:* Head and pronotum dark brown, vestiture consisting of white setae, scutellum dark brown, densely covered with white setae, elytra golden brown, mottled, ventral surface dark brown.

*Head:* Clypeus coplanar with frons, with anterior angles acute (Fig. 132); frons angled at 30°; labrum in frontal view oval, slightly grooved ventrally, labrum not coplanar with clypeus, prelabrum visible (Fig. 133); labium with prementum quadrate, medially grooved (Fig. 134); mandibles triangular, scissorial area well sclerotized, bidentate, molar area quadrate, well sclerotized; maxillary palpi with apical palpus oval, equal to segments 2-3 combined; antennae with 9 antennomeres, antennomeres 7-9 forming the club, club thin, length equal to antennomeres 3-6 combined, antennal insertions not visible in dorsal view.

*Prothorax*: Pronotum cordate, widest medially, anterior angle obtuse, lateral margin convex, posterior angle acute, posterior margin straight, medially concave (Fig. 135); coxa transverse; tibia bidentate; pretarsus with claws weakly divergent, equal in length, both claws narrowly split, upper lobe slightly longer than lower lobe, narrow, lower lobe narrow on individual claw.

*Mesothorax*: Scutellum broadly triangular; elytra longer than wide, widest medially, elytral epipleuron narrowly rounded, dorsal surface flattened, lacking striae, anterior and posterior umbones prominent; pretarsus similar to prothoracic pretarsus.

*Metathorax*: Metathoracic leg with coxa widely separated; femur ovate, narrowing distally; tibia clavate, widest medially, narrowing in distal 1/4, widening at distal margin, posteroventral distal margin with two large spurs, spurs above tarsal articulation joint, posterior distal margin with deep, broad U-shaped groove; pretarsus with claws similar to prothoracic and mesothoracic claws.

*Abdomen*: Ventrites 2-4 subequal in length, 5<sup>th</sup> visible ventrite (= propygidium) length equal to the length of ventrites 3-4 combined, 6<sup>th</sup> ventrite equal in length to 5<sup>th</sup> ventrite length, posterior margin with a slight membranous margin, ventrite and sternite of 5<sup>th</sup> abdominal segment lacking a complete suture; propygidium tear-shaped, longer than wide, narrowing posteriorly, posterior margin blunt.

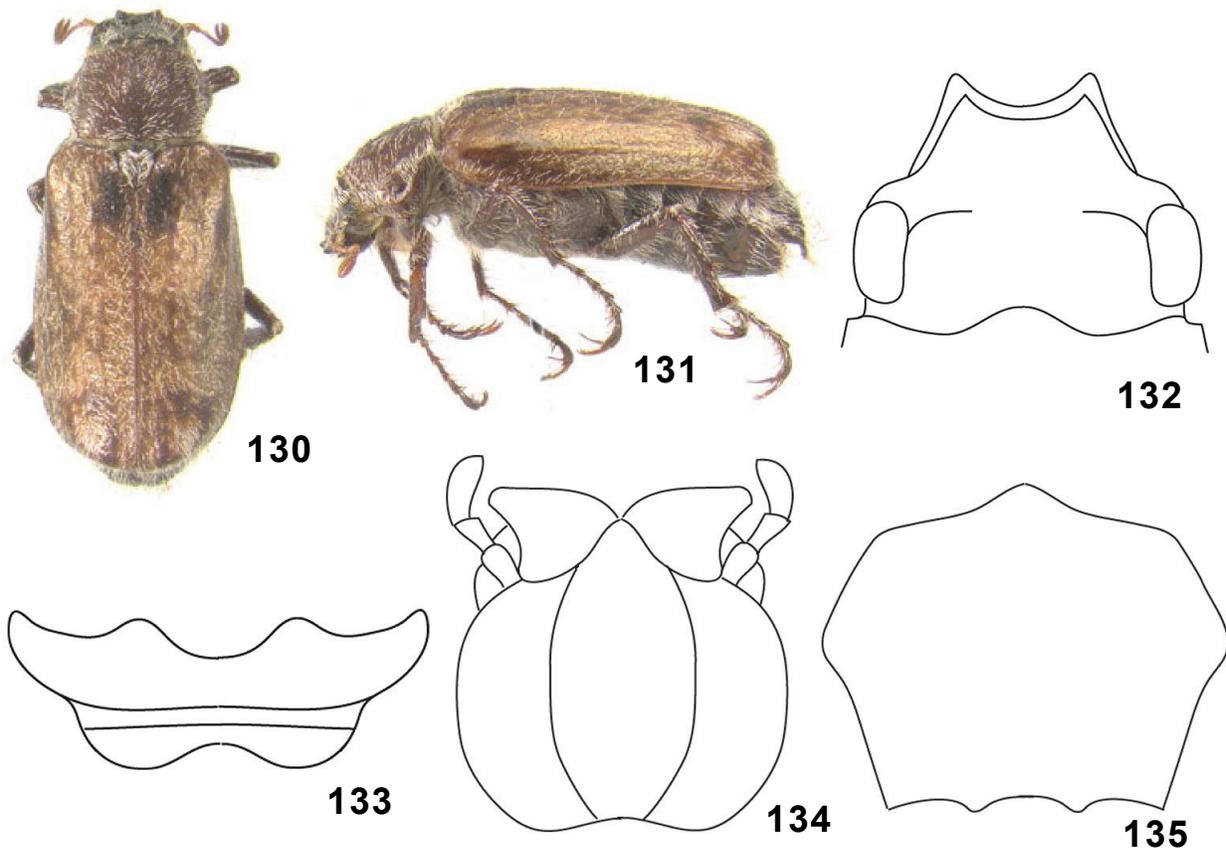
### Diversity and Geographic Distribution

*Manopus* comprises two species, both restricted to Colombia.

#### *Oedichira* Burmeister, 1855

(Figure 136-140)

*Oedichira* Burmeister, 1855: 80. Type species *Oedichira pachydactyla* Burmeister, 1855, by subsequent designation (Evans 2003: 303).



**Figure 130-135.** *Manopus biguttatus* Laporte. **130)** Dorsal habitus. **131)** Left lateral view. **132)** Clypeus and head, dorsal view. **133)** Prelabrum and labrum, lateral view. **134)** Prementum, ligula and labial palpi, ventral view. **135)** Pronotum, dorsal view.

### Taxonomic Notes

The following generic diagnosis is based on a single dissected syntype of *Oedichira crassipes* Burmeister (MLUH). The generic type species was located at the MLUH, but it was not dissected because it was a single specimen.

### Generic diagnosis

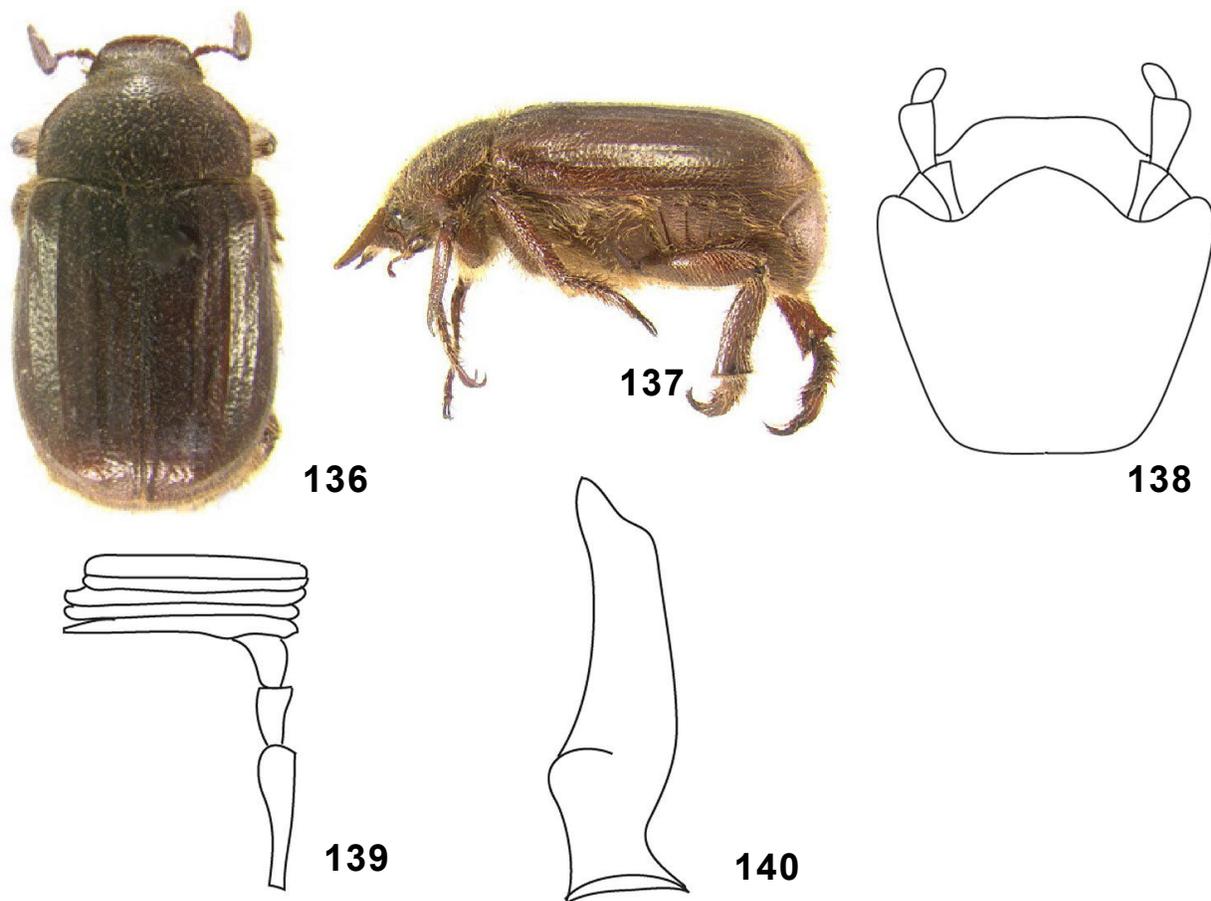
This genus is characterized by its large size, rotund body; antennae with 8 antennomeres, with antennomeres 4-8 forming an elongate club, with lamellae long and thin; prementum trapezoidal, ventral surface flattened; pretarsus of all legs with claws uneven.

### Generic redescription

*Measurements:* Prothorax at widest point of prothorax 8.2 mm, elytra at widest point 11.0 mm, length 18.5 mm.

*Color and vestiture:* Body reddish brown, ventral surface with a vestiture consisting of dense golden setae.

*Head:* Clypeus not coplanar with frons; frons slightly bulbous, angled at 45°; labrum in frontal view oval, small, deeply emarginate, labrum not coplanar with clypeus; labium with prementum trapezoidal, ventral surface flattened (Fig. 138); mandibles in dorsal view rectangular, scissorial area weakly bilobed, moderately sclerotized, molar area strongly produced adorally, well sclerotized; maxillary palpi with apical palpus narrow, oval, with a sensory patch at distal margin; antennae with 8 antennomeres, antennomeres 4-8 forming club, lamellae long and thin, 4<sup>th</sup> antennomere shorter than antennomeres 5-8 combined, remaining lamellae subequal in length to antennomeres 1-4 combined (Fig. 139).



**Figure 136-140.** *Oedichira crassipes* Burmeister (male). **136)** Dorsal habitus. **137)** Left lateral view. **138)** Prementum, ligula and labial palpi, ventral view. **139)** Antenna. **140)** Metathoracic tibia.

*Prothorax*: Pronotum oblong, widest medially, anterior angle acute, weakly appearing toothed, lateral margin convex, posterior angle obtuse, posterior margin straight, medially lobed; prothoracic legs with coxa elongate; tibia dentate; pretarsus with claws weakly divergent, uneven in length, inner claw slightly smaller than outer claw, both claws narrowly split, upper lobe shorter than lower lobe, narrow, inner lobe long, narrow on individual claw.

*Mesothorax*: Scutellum triangular; elytron wider than long, widest medially, elytral epipleuron flattened, dorsal surface with three weak striae, intervals flat, surface smooth, scattered transverse rows of declivous fine golden setae humeral umbones slightly produced; pretarsus similar to prothoracic pretarsus.

*Metathorax*: Metathoracic leg with coxa widely separated; femur narrowly ovate, widest in distal 1/4; tibia rectangular, narrow proximally, widest medially, narrowing to a wide distal margin, posteroventral margin with a single blunt tooth on anteroventral margin, posterior margin with broad, deep U-shaped groove (Fig. 140); pretarsus with claws similar to those of prothoracic and mesothoracic legs.

*Abdomen*: Ventrites 2-4 subequal in length, 5<sup>th</sup> ventrite (= propygidium), equal to length of ventrites 3-4 combined, ventrite and sternite of 5<sup>th</sup> abdominal segment with partial suture, spiracle medially at anterior point of suture, 6<sup>th</sup> ventrite subequal in length to 4<sup>th</sup> ventrite length, crescent-shaped; pygidium triangular, broader than long, posterior margin narrow, rounded.

### Diversity and Geographic Distribution

*Oedichira* comprises two species, known only from Brazil.

### *Pectinosoma* Arrow, 1913

(Figure 141-145)

*Pectinosoma* Arrow, 1913: 430. Type species *Pectinosoma elongatum* Arrow, 1913, by monotypy.

### Taxonomic Notes

The following generic diagnosis is based on a single dissected male syntype of the type species, *P. elongatum* (BMNH).

### Generic diagnosis

This genus is characterized by its elongate body, large size, distinct coloration pattern; prementum elongate, ventral surface with a medial groove; mesosternum trapezoidal, flattened, anteriorly obscured by an elevated process; 5<sup>th</sup> ventrite raised medially, posteriorly raised into a prominent process; pretarsus with all claws simple. The type species name was changed to *P. elongata* and is here changed back to the original gender-neutral *P. elongatum*.

### Generic redescription

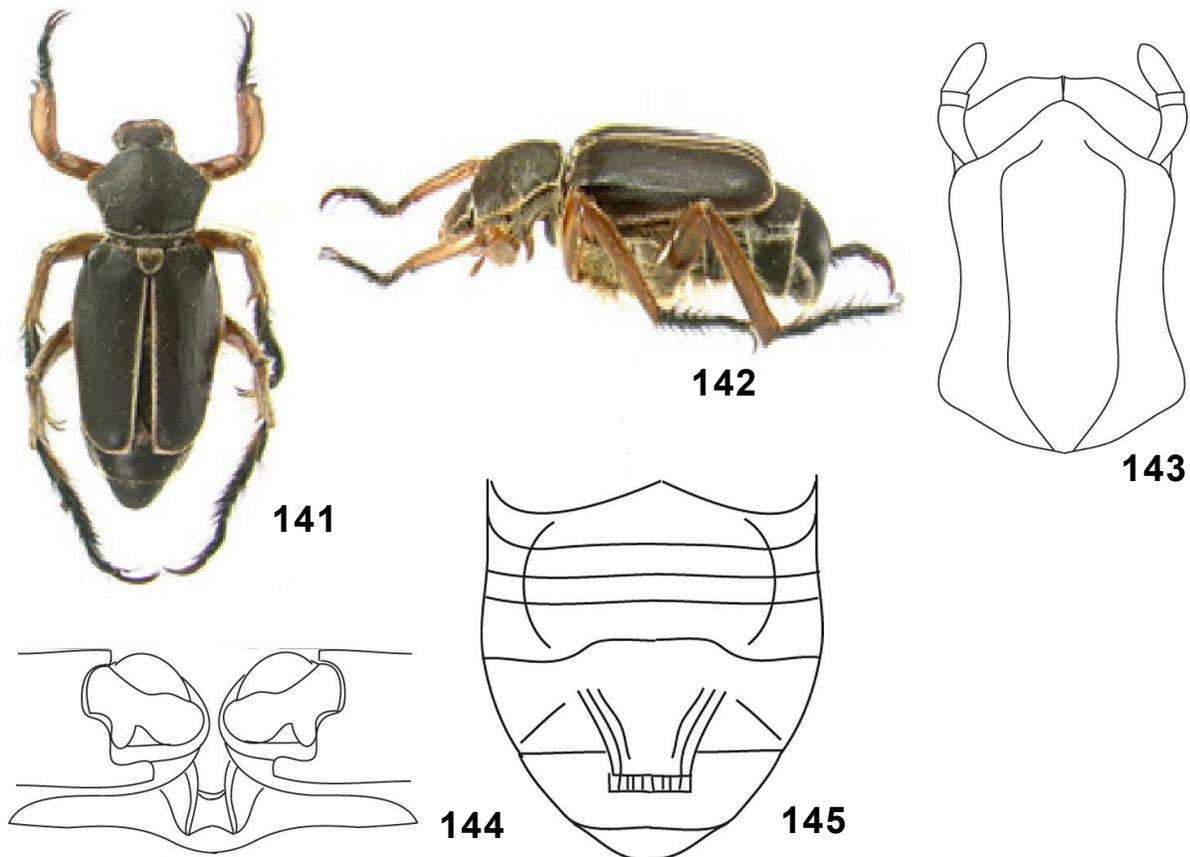
*Measurements*: Prothorax at widest point 5.0 mm, elytra at widest point 4.8 mm, length 18.0 mm.

*Color and vestiture*: Head and pronotum black, abdomen and elytra black, legs reddish brown, margins of elytra and pronotum lined with white setae.

*Head*: Clypeus not coplanar with frons; frons angled at 30°; labrum in frontal view narrow, rectangular, emarginate, labrum not coplanar with clypeus; labium with prementum elongate, ventral surface with a medial groove (Fig. 143); mandibles in dorsal view semicircular, scissorial area very narrow, blunt, directed aborally, thin in lateral profile, well sclerotized, molar area produced aborally, well sclerotized; maxillary palpi with apical palpus ovate, equal to segments 2-3; antennae with 9 antennomeres, antennomeres 7-9 forming the club, equal in length to antennomeres 3-6 combined.

*Prothorax*: Pronotum oblong, longer than wide, widest at 2/3 distance from anterior, anterior angle acute, appearing toothed, lateral margin convex, margin with a slight bead, in posterior 1/3, posterior angle obtuse, posterior margin weakly convex, margin with a slight bead; prothoracic leg with coxa transverse; tibia dentate; pretarsus with claws not divergent, equal in length, both claws simple, base of claw toothed.

*Mesothorax*: Mesosternum trapezoidal, flattened, anteriorly obscured by bifurcate prosternal process, posterior margin convex (Fig. 144); scutellum subtriangular; elytra longer than wide, widest in anterior 1/4, epipleuron with slight deflexed margin, slight membrane along margin, elytral surface



**Figure 141-145.** *Pectinosoma elongatum* Arrow (male). 141) Dorsal habitus. 142) Left lateral view. 143) Prementum, ligula and labial palpi, ventral view. 144) Mesosternum, ventral view. 145) Visible abdominal segments.

lacking clear striae, anterior umbones prominent, posterior umbone very weakly developed; pretarsus similar to prothoracic pretarsus.

*Metathorax:* Metathoracic leg with coxa widely separated; femur ovate, widest in distal 1/4; tibia clavate, narrow proximally; posteroventral margin with pair of spurs, ventral spur short, broad, dorsal spur elongate, narrow, spurs raised above level of tarsal articulation joint, posterior margin with several elongate setae, margin with a deep, U-shaped groove; pretarsus with claws and empodium similar to prothoracic and mesothoracic claws.

*Abdomen:* First ventrite strongly angled dorsally, 2<sup>nd</sup> ventrite equal to length of 1<sup>st</sup> ventrite, ventrites 3-4 subequal in length, hollowed out medially, 5<sup>th</sup> ventrite (= propygidium) subequal in length to ventrites 3-4 combined, raised medially in anterior, posteriorly raised into a prominent trapezoidal process, process with distal margin lined with cylindrical elements, lateral margins of process grooved (Fig. 145), ventrite and sternite of 5<sup>th</sup> abdominal segment not separated by a suture, spiracle placed anteriorly, 6<sup>th</sup> ventrite equal to length of 4<sup>th</sup> ventrite, flattened; pygidium longer than wide.

### Diversity and Geographic Distribution

*Pectinosoma* is monotypic, with *P. elongatum* known only from Guyana.

### *Plectris* Le Peletier and Serville, 1828

(Figure 146-150)

*Plectris* Le Peletier and Serville, 1828: 369. Type species *Plectris tomentosa* Le Peletier and Serville, 1828, by monotypy.

*Euryaspis* Blanchard, 1851: 130. Type species *Euryaspis gaudichaudii* Blanchard, 1851, by monotypy. Synonymized by Dalla Torre (1913).

*Junkia* Dalla Torre, 1913: 310. (for *Trichoderma* Nonfried) Type species *Trichoderma ceylanica* Nonfried, 1894, by monotypy.

*Trichoderma* Nonfried, 1894: 11. (preoccupied name), Type species *Trichoderma ceylanica* Nonfried, 1894, by monotypy.

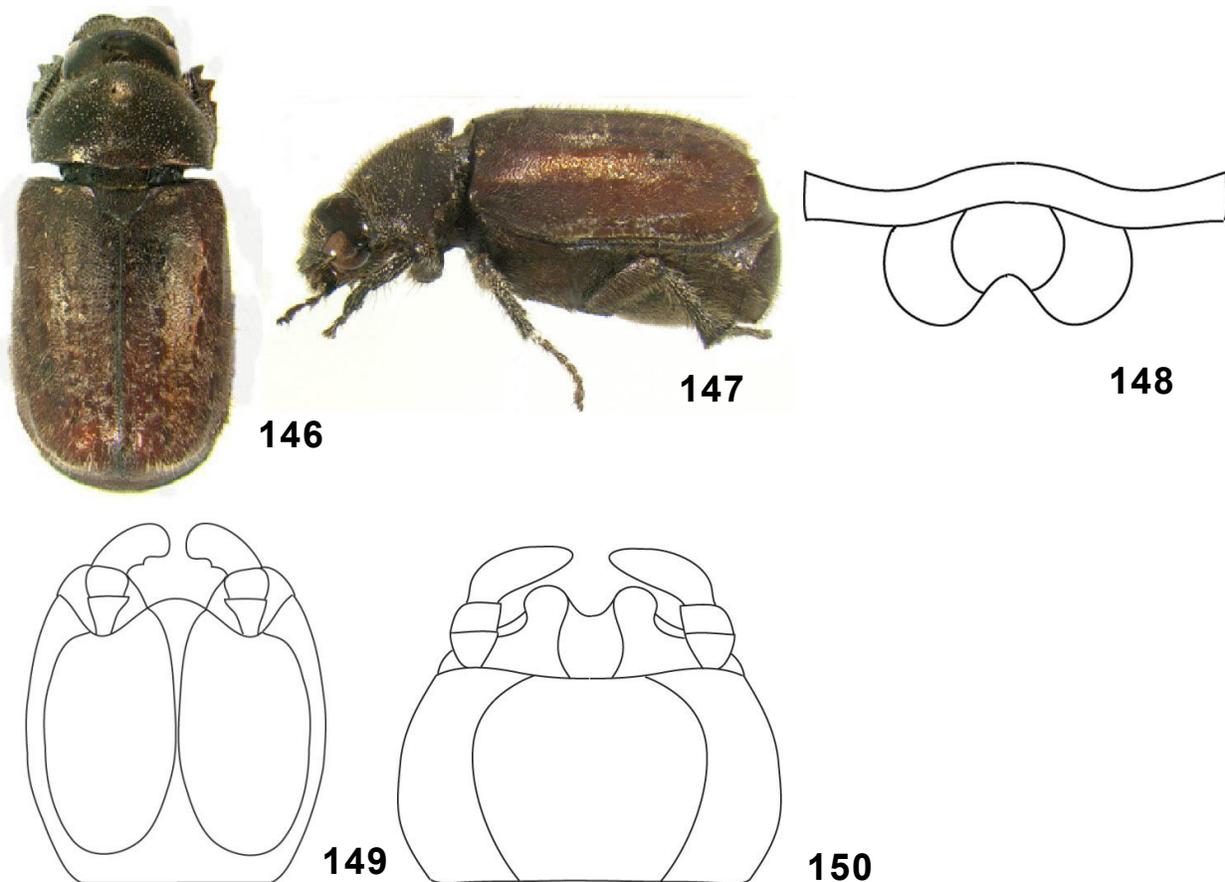
*Pseudoserica* Guérin-Méneville, 1830: 86. Type species *Pseudoserica marmorea* Guérin-Méneville, 1830, by monotypy. Synonymized by Dalla Torre (1913).

### Taxonomic Notes

The following generic diagnosis is based on a dissected homeotype of *P. micans* (Bates), type located at the BMNH. The generic limits of this genus were compared to a dissected homeotype of the presumptive syntype of the generic type species, *P. tomentosa* Le Peletier and Serville located at the MNHC and identified with a Le Peletier label. *Plectris micans* was used for the generic diagnosis based on the poor photo quality of *P. tomentosa* and its rarity.

### Generic diagnosis

This genus is characterized by its elongate body; prementum rectangular, ventral surface flattened, occasionally lobed or weakly grooved; prominent ligula, appearing bilobed, a shallow groove present medially; pretarsus of meso and metathoracic legs with claws often unequal.



**Figure 146-150.** *Plectris micans* (Bates). **146)** Dorsal habitus. **147)** Left lateral view. **148)** Clypeus and labrum, frontal view. **149)** Prementum, ligula and labial palpi, ventral view. **150)** *Plectris tomentosa* Le Peletier and Serville prementum, ligula and labial palpi, ventral view.

### Generic redescription

*Measurements:* Prothorax at widest point 6.0 mm, elytra at widest point 8.0 mm, length 15.0 mm.

*Color and vestiture:* Body reddish brown, metallic, vestiture consisting of fine, white setae, sutural striae with tufts of white setae.

*Head:* Clypeus not coplanar with frons; frons angled at 30°; labrum in frontal view ovate, large, with a deep medial groove (Fig. 148), labrum not coplanar with clypeus; labium with prementum rectangular, ventral surface medially grooved, prominent ligula, appearing bilobed, (Fig. 149 and 150); mandibles in dorsal view rectangular, scissorial area bluntly produced into broadly rounded process, posteriorly with a raised process, molar area prominent, mandible in lateral profile triangular; maxillary palpi with apical palpus ovate, elongate, apex obtuse; antennae with 10 antennomeres, antennomeres 7-10 forming the elongate club, equal to length of antennomere one.

*Prothorax:* Pronotum oblong, transverse, widest medially, anterior angle acute, lateral margins convex, serrate, posterior angle obtuse, posterior margin concave, medially lobed; prothoracic leg with coxa transverse; tibia dentate, ventral margin with a small, broad spur; pretarsus with claws weakly divergent, equal in length, both claws broadly split, upper lobe narrow, lower lobe broad.

*Mesothorax:* Scutellum subtriangular; elytra longer than wide, widest medially, in lateral profile epipleuron forming a narrow flattened margin, elytral surface with three weak vertical striae, striae smooth, with scattered long white setae, inter striae regions rugose, setose, anterior umbone moderate, posterior umbone weak; pretarsus with claws equal, weakly divergent, both claws broadly split, upper lobe narrow, lower lobe broad.

*Metathorax:* Metathoracic leg with coxae narrowly separated; femur narrowly ovate, widest medially; tibia vase-shaped, narrow proximally, widest medially, posteroventral margin with a pair of stout spurs, arising at same level as tarsal articulation joint, posterior margin with a distinct U-shaped groove; pretarsus with claws equal, weakly divergent, both claws broadly split, upper lobe narrow, lower lobe broad.

*Abdomen:* Ventrites 2-4 subequal in length, 5<sup>th</sup> ventrite (= propygidium) equal to length of ventrites 3-4 combined, ventrite and sternite of 5<sup>th</sup> abdominal segment with a groove appearing as a partial suture, spiracle located medially, at apex of groove, 6<sup>th</sup> ventrite length equal to length of 4<sup>th</sup> ventrite; pygidium subtriangular, wider than long, posterior margin rounded.

### Diversity and Geographic Distribution

*Plectris* comprises 353 species, distributed in Argentina, Australia (exotic), Brazil, Bolivia, Colombia, Ecuador, French Guiana, Guatemala, Guyana, Martinique, Mexico, Nicaragua, Panama, Paraguay, Peru, Saint Vincent, United States (exotic), Uruguay, and Venezuela. Regional keys are provided by Frey (1967) and Chalumeau (1982).

### *Pristerophora* Harold, 1869

(Figure 151-155)

*Pristerophora* Harold, 1869b: 123. Replacement name for *Prionophora* Solier, 1851: 101. (Preoccupied name). Type species *Prionophora picipennis* Solier, 1851, by monotypy.

### Taxonomic Notes

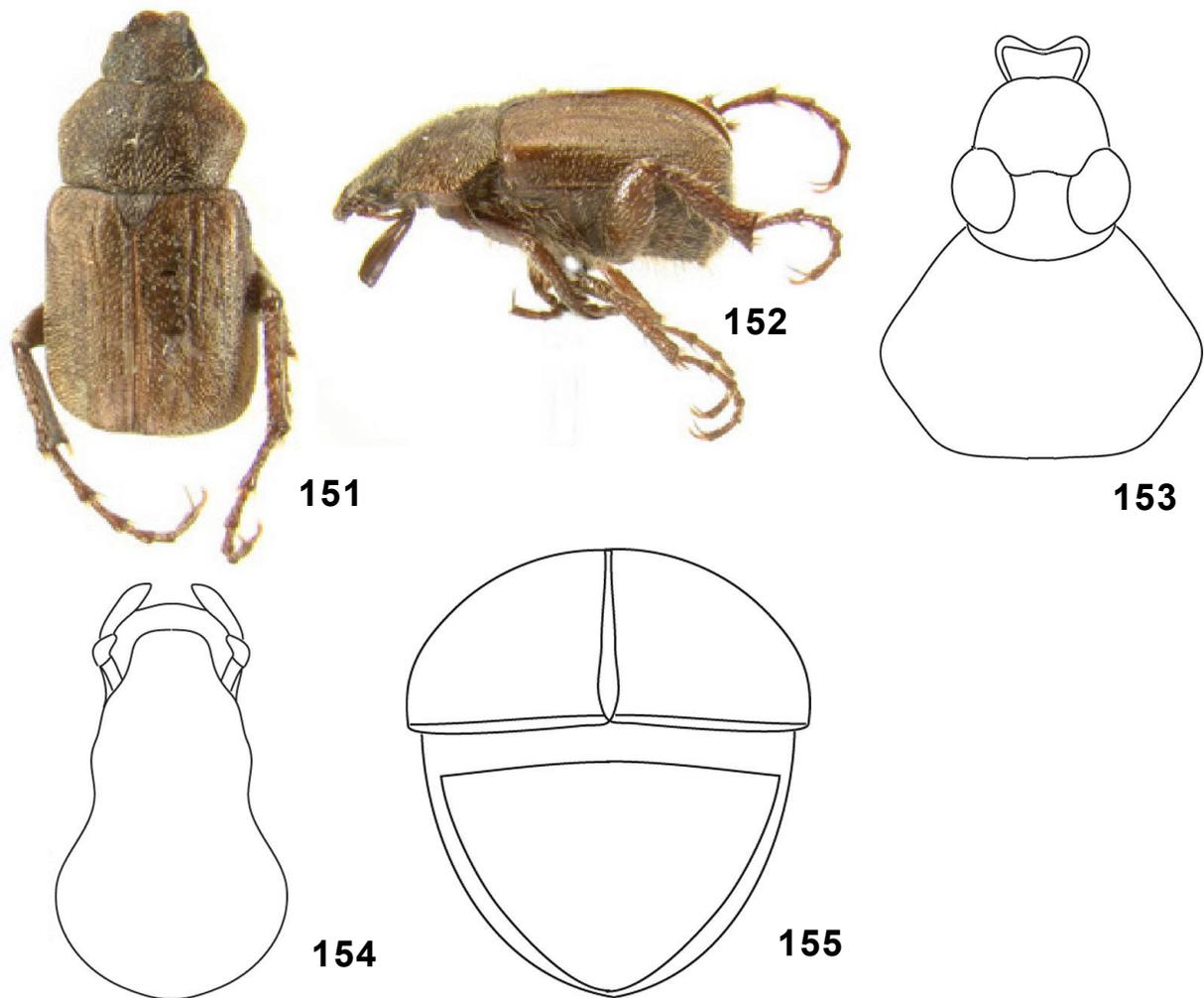
The following generic diagnosis is based on two dissected specimens of the generic type species, *P. picipennis* (ZMHB). Specimens were authoritatively identified by Moser and the author with the aid of the original description. The type was not located at ZMHB or the MNHC during this study.

### Generic diagnosis

This genus is characterized by its elongate body, very small size; prementum rectangular, ventral surface flattened; pygidium subtriangular, posterior margin rounded.

### Generic redescription

*Measurements:* Prothorax at widest point 2.3 mm, elytra at widest point 2.4 mm, length 5.7 mm.



**Figure 151-155.** *Pristerophora picipennis* Solier. **151)** Dorsal habitus. **152)** Left lateral view. **153)** Clypeus and head, dorsal view. **154)** Prementum, ligula and labial palpi, ventral view. **155)** Elytra, propygidium and pygidium, dorsal view.

*Color and vestiture:* Body dark brown, vestiture consisting of scattered white setae.

*Head:* Clypeus coplanar with frons, (Fig. 153); frons angled at 30°; labrum in frontal view, narrowly ovate, not emarginate, labrum coplanar with clypeus; labium with prementum rectangular, elongate, ventral surface flattened (Fig. 154); mandibles in dorsal view rectangular, scissorial area reduced to a rounded, membrane, lined with setae, molar area weakly sclerotized, bluntly produced adorally; maxillary palpi with apical palpus conical, equal to length of segments 1-2 combined, apex acute; antennae with 9 antennomeres, antennomeres 7-9 forming the elongate club, lamellae thin, equal to length of antennomeres 3-6 combined.

*Prothorax:* Pronotum hexagonal, oblong, transverse, widest medially, anterior angle acute, lateral margin convex, posterior angle obtuse, posterior margin weakly convex (Fig. 155); prothoracic leg with coxa elongate; tibia serrate in medial region, dentate, ventral margin with a long spur in the distal 1/4; pretarsus with claws divergent, equal in length, both claws narrowly split, upper lobe narrow, longer than lower lobe, lower lobe slightly broader on individual claw.

*Mesothorax:* Scutellum subtriangular; elytra longer than wide, width subequal over entire length, elytral epipleuron flattened, dorsal surface lacking striae, anterior umbone well developed, posterior umbone weak; pretarsus similar to prothoracic pretarsus.

*Metathorax*: Metathoracic leg with coxa widely separated; femur ovate, widest medially; tibia rectangular, narrow proximally, widest medially, posteroventral margin lacking spurs, posterior margin with a broad, deep U-shaped groove; pretarsus with claws similar to prothoracic and mesothoracic legs.

*Abdomen*: Ventrites 2-4 subequal in length, 5<sup>th</sup> visible ventrite (= propygidium) equal to length of ventrites 2-4 combined, ventromedial surface transitioning to membranous posterior margin, ventrite and sternite of 5<sup>th</sup> abdominal segment lacking a suture, spiracle placed medially, 6<sup>th</sup> ventrite equal in length to 4<sup>th</sup> ventrite; pygidium subtriangular, wider than long, posterior margin rounded (Fig. 155).

### Diversity and Geographic Distribution

*Pristerophora* comprises two species, both known only from Chile.

### *Rhinaspis* Perty, 1833

(Figure 156-160)

*Rhinaspis* Perty, 1833: 46. Type species *Rhinaspis schranki* Perty, 1833 (a junior synonym of *Rhinaspis aenea* [Billberg]), by monotypy.

### Taxonomic Notes

The following generic diagnosis is based on a single dissected male specimen of *R. aenea*, the senior synonym of the generic type species. Specimens were authoritatively identified by Burmeister, Arrow, and Moser, and confirmed by the author with the original description. The type species was not located during this study.

### Generic diagnosis

This genus is characterized by its elongate body and often large size; clypeus in dorsal view with anterior margin straight, in males, narrowed, produced forward, lateral margins deeply indented; prementum quadrate, in ventral profile raised in posterior 3/4, transverse ridge present, medially with a distinct suture, labrum in frontal view broadly ovate, deeply grooved, directed vertically.

### Generic redescription

*Measurements*: Prothorax at widest point 10.0 mm, elytra at widest point 11.2 mm, length 24.0 mm.

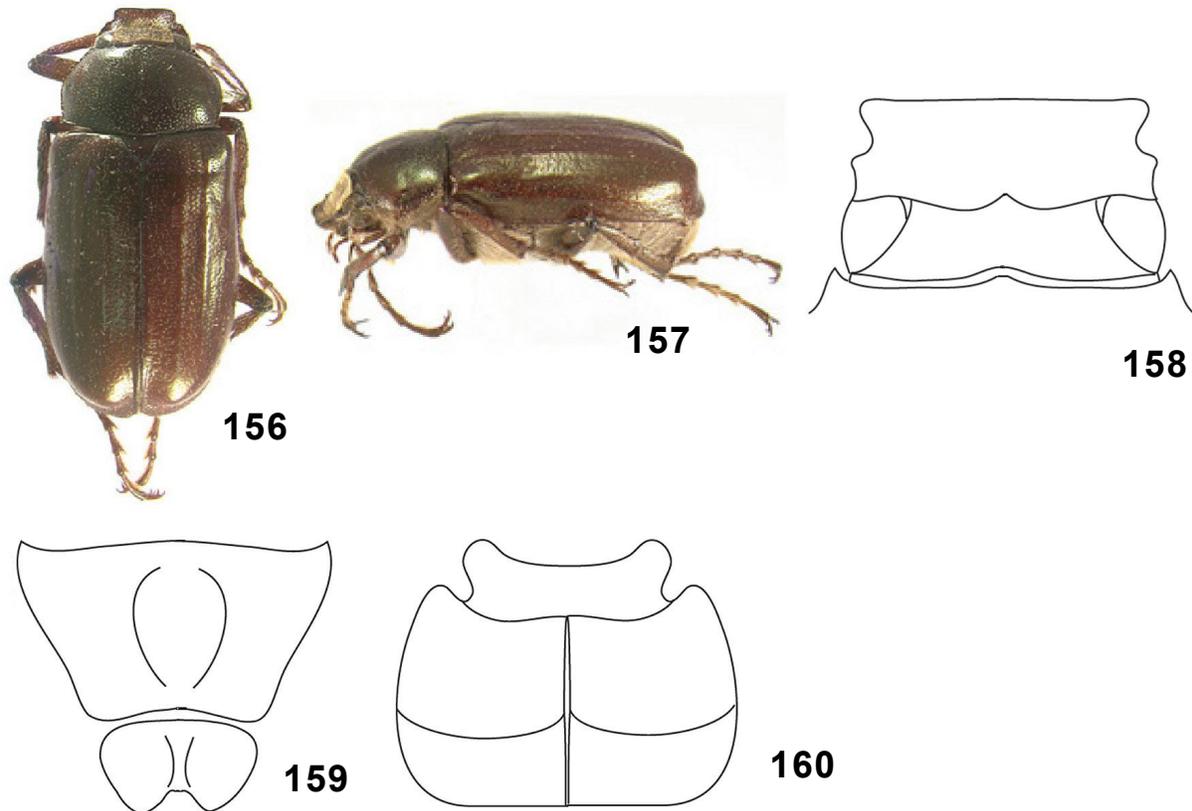
*Color and vestiture*: Body bronze, venter bronze, vestiture consisting of fine yellow setae.

*Head*: Clypeus not coplanar with frons, clypeus in dorsal view with anterior margin straight, in males, narrowed, produced forward, lateral margins deeply indented (Fig. 158); frons angled 60°; labrum in frontal view broadly ovate, deeply grooved, directed vertically (Fig. 159), labrum not coplanar with clypeus; labium with prementum quadrate, in ventral profile raised in posterior 3/4, transverse ridge present, medially with a distinct suture (Fig. 160); mandibles in dorsal view rectangular, scissorial area bluntly produced, well sclerotized, weakly bidentate, molar area bluntly produced, well sclerotized; maxillary palpi with apical segment ovate, apex obtuse, distally with a sensory spot; antennae with 10 antennomeres, antennomeres 8-10 forming the club, club equal to length of antennomeres 3-6 combined.

*Prothorax*: Pronotum oblong, transverse, widest medially, anterior angle obtuse, lateral margin convex, posterior angle acute, posterior margin weakly convex, medially lobed; prothoracic leg with coxa transverse; tibia bidentate, ventral margin with spur in distal 3/4; pretarsus with claws divergent, equal in length, both claws broadly split, upper lobe longer than lower lobe, broad, lower lobe narrow on individual claw.

*Mesothorax*: Scutellum cordate; elytra longer than wide, widest in posterior 1/4, in lateral profile, epipleuron flattened, produced outward, in dorsal view elytra flattened, three weak striae present, intervals shallowly punctured, punctures with small yellow setae, anterior and posterior umbones prominent; pretarsus similar to prothoracic pretarsus.

*Metathorax*: Metathoracic leg with coxa contiguous; femur narrowly ovate, widest in proximal 1/3; tibia narrowly figure-8 shaped, narrow proximally, widest medially, narrowing in distal 1/4, posteroventral margin with pair of long, stout spurs, anterior spur slightly shorter than posterior spur, arising above



**Figure 156-160.** *Rhinaspis aenea* (Billberg) (male). **156)** Dorsal habitus. **157)** Left lateral view. **158)** Clypeus and head, dorsal view. **159)** Labrum and clypeus, frontal view. **160)** Prementum, ligula and labial palpi, ventral view.

tarsal articulation joint, posterior spur arising at same level as tarsal articulation joint, posterior margin with deep, U-shaped groove; pretarsus with claws similar to those of prothoracic and mesothoracic legs.

*Abdomen:* Ventrites 2-4 subequal in length, 5<sup>th</sup> ventrite (= propygidium), 2X length of 4<sup>th</sup> ventrite, ventrite and sternite of 5<sup>th</sup> abdominal segment not separated by a complete suture, spiracle located posterolaterally; 6<sup>th</sup> ventrite narrow, 1/3 length of 5<sup>th</sup> ventrite length; pygidium tear-shaped, wider than long, posterior margin rounded.

### Diversity and Geographic Distribution

*Rhinaspis* comprises 10 species, all known only from Brazil or Argentina. There is no key to species available.

### *Schizochelus* Blanchard, 1850

(Figure 161-166)

*Schizochelus* Blanchard, 1850: 89. Type species *Schizochelus flavescens* Blanchard, 1850, by subsequent designation (Evans 2003: 346).

### Taxonomic Notes

The following generic diagnosis is based on a dissected homeotype of the presumptive syntype of the type species *S. flavescens* located at the MNHC, identified with a Blanchard label.

### Generic diagnosis

This genus is similar in appearance to *Macroductylus*, but can be characterized by its oblong, transverse pronotum, widest in anterior 1/4.

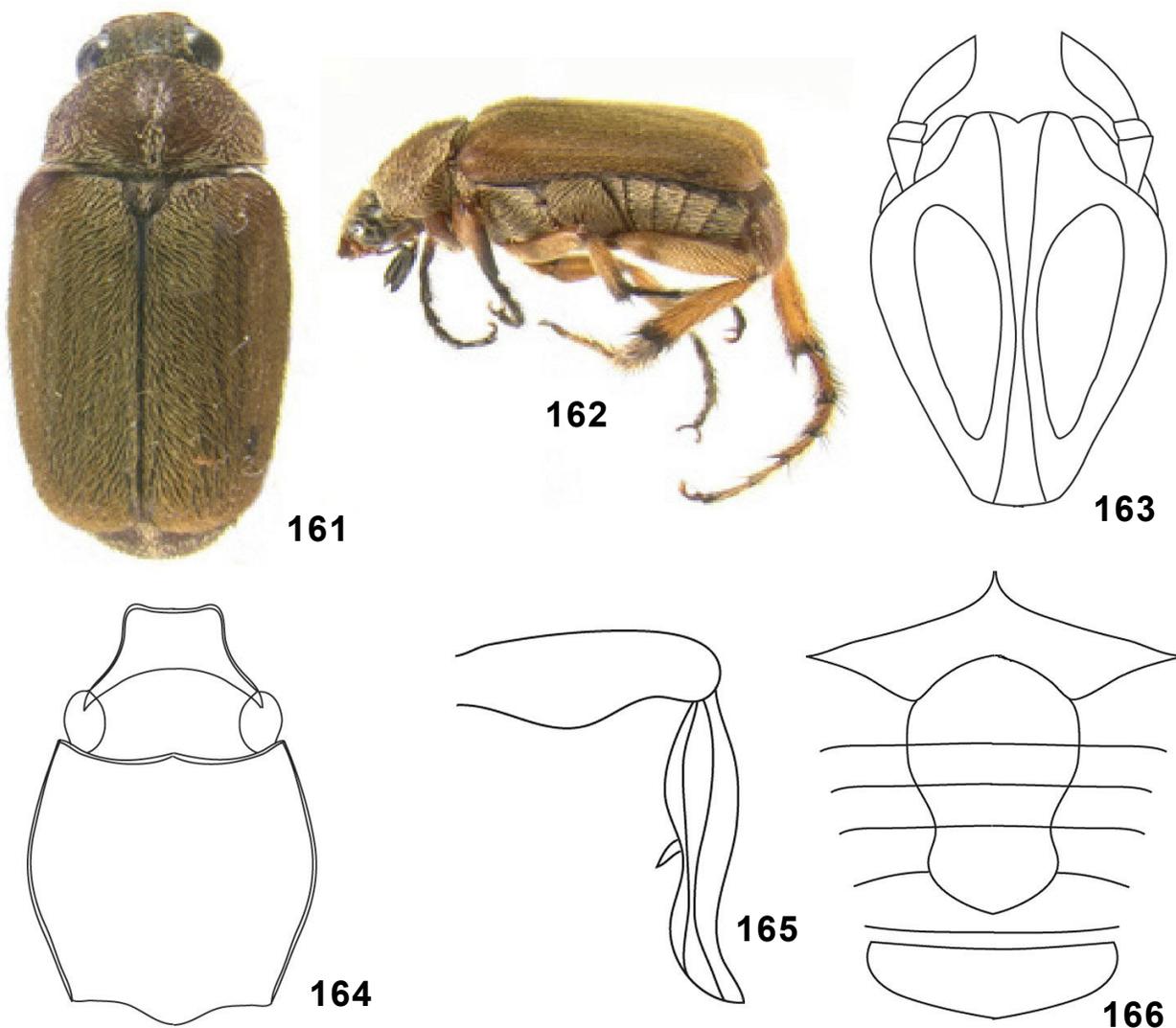
**Generic redescription**

*Measurements:* Prothorax at widest point of prothorax 2.5 mm, elytra at widest point of elytra 3.2 mm.

*Color and vestiture:* Body brown, elytral surface with a vestiture consisting of dense yellow setae, remaining surface of body with scattered yellowish setae.

*Head:* Clypeus not coplanar with frons; frons angled at 30°; labrum in frontal view, narrowly ovate, weakly emarginate, labrum coplanar with clypeus; labium with prementum rectangular, elongate (2X longer than wide), ventral surface with medial groove (Fig. 163); mandibles in dorsal view rectangular, scissorial area reduced to a membrane, lined with dense setae, molar area bluntly produced, weakly sclerotized; maxillary palpi with apical palpus ovate, equal to length of segments 2-3 combined, apex acute, with blunt sensory region; antennae with 10 antennomeres, antennomeres 7-9 forming the elongate club, lamellae thin, equal to length of antennomeres 2-7 combined.

*Prothorax:* Pronotum oblong, transverse, wider than long, widest in anterior 1/4, anterior angle acute, lateral margin convex, posterior angle acute, posterior margin concave, medially lobed (Fig. 164); prothoracic leg with coxa elongate; tibia lacking tooth, ventral margin medially with a spur (Fig. 165);



**Figure 161-166.** *Schizochelus flavescens* Blanchard (male). **161)** Dorsal habitus. **162)** Left lateral view. **163)** Prementum, ligula and labial palpi, ventral view. **164)** Head and pronotum, dorsal view. **165)** Prothoracic tibia. **166)** Visible abdominal segments.

pretarsus with claws divergent, equal in length, both claws narrowly split, upper lobe narrow, slightly longer than lower lobe, lower lobe narrow on individual claw, base of claw toothed.

*Mesothorax*: Scutellum narrowly subtriangular; elytra longer than wide, widest medially, in lateral profile epipleuron flattened, membranous, dorsal surface with six weakly raised striae, anterior and posterior umbones strongly developed; pretarsus similar to prothoracic pretarsus.

*Metathorax*: Metathoracic leg with coxa widely separated; femur narrowly ovate, narrow proximally, widest medially; tibia subtriangular, narrow proximally, widest medially, posteroventral margin lacking spurs, posterior margin with a deep, U-shaped groove; pretarsus with claws similar to those of prothoracic and mesothoracic legs.

*Abdomen*: Ventrites 2-4 subequal in length, medially grooved (Fig. 166), 5<sup>th</sup> visible ventrite (= propygidium) equal to length of ventrites 3-4 combined, posterior margin membrane-like, ventrite and sternite of 5<sup>th</sup> abdominal segment lacking suture, spiracle placed posteromedially, 6<sup>th</sup> ventrite equal to length of 5<sup>th</sup> ventrite, triangular in lateral profile; pygidium subtriangular, width equal to length, posterior margin rounded.

### Diversity and Geographic Distribution

*Schizochelus* comprises seven species, all known only from Brazil or Chile. No key to species exists.

### Results of cladistic analysis

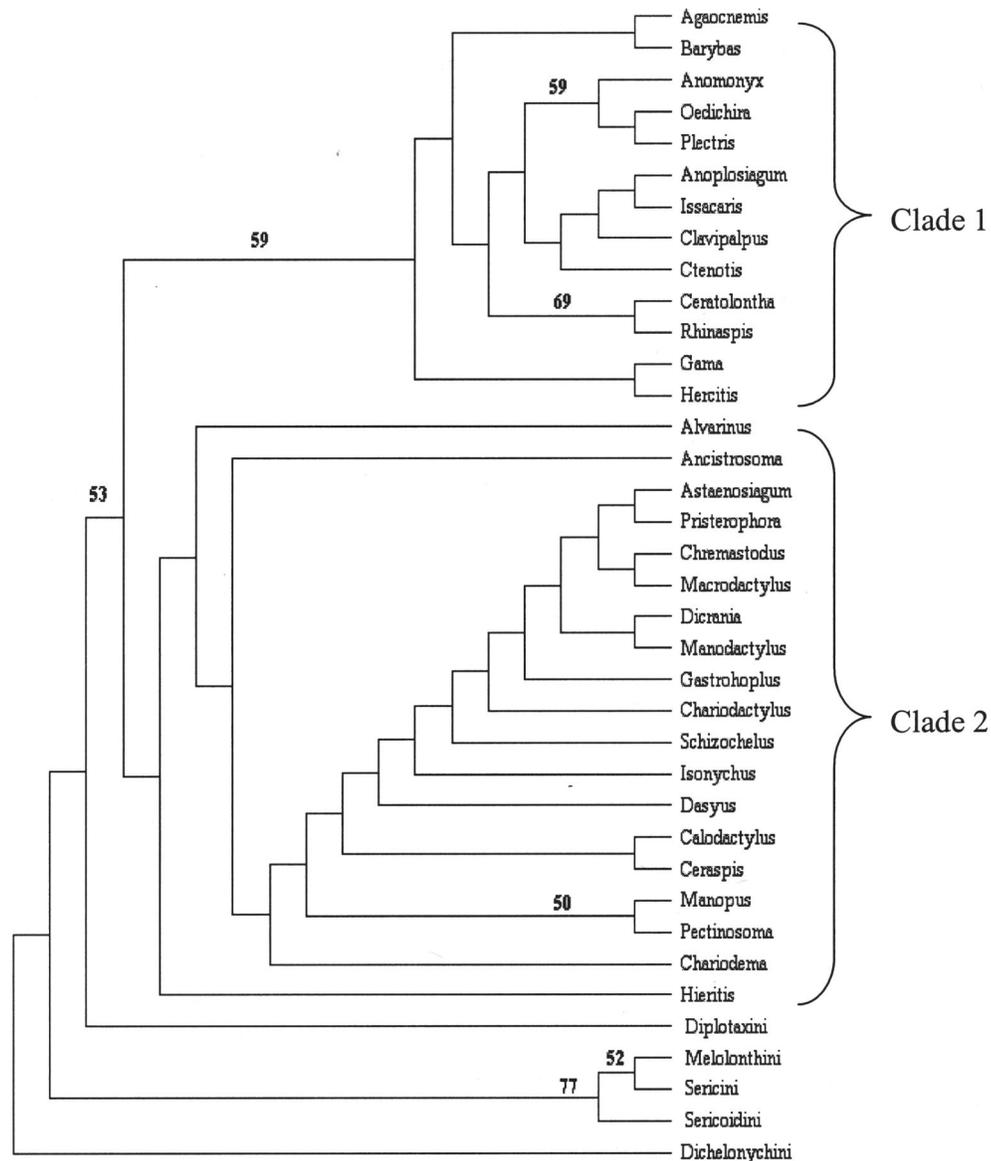
The initial cladistic analysis produced 186 most parsimonious trees of 500 steps. A strict consensus tree was produced and the characters reweighted by the maximum value of the rescaled consistency index. A second heuristic search produced one single tree of 47.336 steps. The consistency index was 0.240 and the retention index was 0.448. Bootstrap values were placed on the second tree. A cladogram and corresponding phylogram demonstrating maximum parsimony are presented as the hypothetical relationships within the Macroductylini (Fig. 167-168).

### Discussion

Given the character range of the newly envisioned Macroductylini, the hypothetical ancestral members of the tribe most closely resemble in physical appearance the tribes Melolonthini and Diplotaxini. Diplotaxini consistently comes out as the sister taxon to Macroductylini. The primary reason for this is the similarity in the propygidium, which lacks an apparent suture line separating the sternite and ventrite. Ancestral members of the Macroductylini are hypothesized to have exhibited the following characters: body form rotund; head with frons and clypeus not coplanar, clypeus and labrum not coplanar, labrum prominent and well-developed; mandibles large, length less than width, scissorial area toothed, molar area well developed, with a deep, medial groove; prementum quadrate or rectangular, ventral surface flattened; maxillae well developed and toothed. This revision demonstrates Macroductylini monophyly based on three synapomorphies: fifth visible ventrite longer than fourth visible ventrite, propygidium lacking a complete suture between the ventrite and tergite, and posterior tibiae with one or two closely placed apical spurs, inserted below the tarsal articulation, so that the metatarsus moves past them (occasionally spurs are secondarily absent). While none of these characters are unique, in concert they are unique to this tribe. The phylogenetic analysis demonstrates moderate support for monophyly (bootstrap value of 53%).

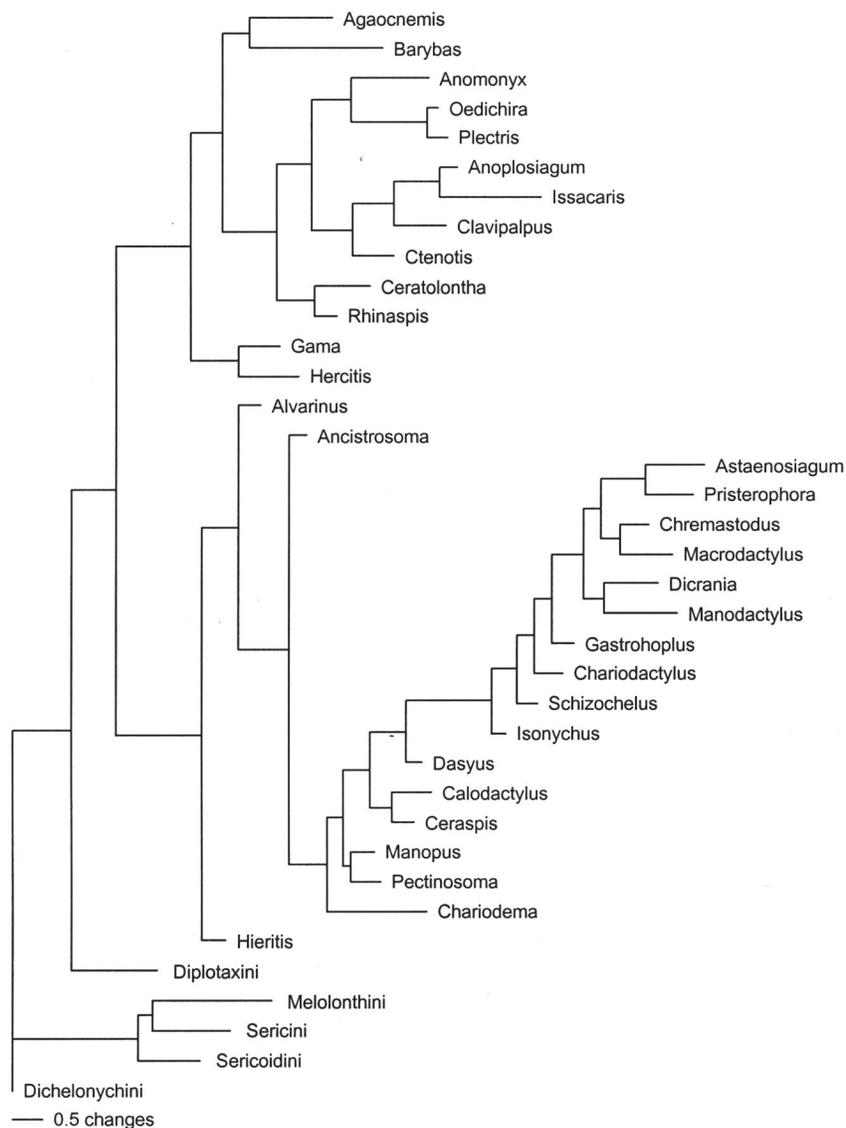
A consistency index of 0.240 and retention index of 0.448 are not unusual for a matrix of this size. The bootstrap values demonstrate moderate support for the tribe, but at the basal branches there is little to no significant support. The terminal branches show only a few points of support. The low level of basal support suggests that more parsimony-informative characters are needed. The low support at the terminal branches would indicate that the fine scale relationships among the genera are unclear and require more characters and a more extensive understanding of the generic limits for individual genera than were available for this study.

The hypothetical phylogeny indicates two primary clades within the Macroductylini (Fig. 167). Initial branching for clade one and two demonstrates a weak trend in the declivity of the head remaining similar



**Figure 167.** Single most parsimonious tree based on 77 morphological characters of 32 genera conforming to the revised Macrodactylini, including five outgroups. Numerical values demonstrate bootstrap values.

to the outgroups (declivity of head  $> 30^\circ$ ) in clade one and declivity of head  $< 30^\circ$  in clade two. In both clade one and two there is an apparent trend in mouthpart elongation and reduction in size: prementum shape quadrate or rectangular to elongate; reduction in height of the mandible, with a length to height ratio of 1:1 to 3:1. An additional trend, the elongation of the thorax and abdomen, is most evident in the genera of clade two but can also be seen in some members of clade one. However, there is a lack of clear synapomorphies within the clades, and within the individual clades, genera are often difficult to distinguish due to a similar lack of autapomorphies. Numerous genera appear to grade into each other. This gradation of genera is not unexpected, and similar trends appear to be the case in several melolonthine tribes. In the current absence of data relative to larvae and larval microhabitats and microecological requirements, it is hypothesized that the primary driving force in Macrodactylini generic differentiation and diversification is foliage feeding by the adults. Clades one and two suggest different feeding strategies, and subsequent changes in morphology provide insight into their strategies. Feeding information is all but absent in this tribe making further speculation on this topic difficult.



**Figure 168.** Phylogram of the single most parsimonious tree based on 77 morphological characters of 32 genera conforming to the revised Macrodactylini, including five outgroups.

Clade one (Fig. 167) contains thirteen genera. Most genera resemble the hypothetical outgroup taxa in general body appearance. Basal changes include the labrum moving from produced outward to connate, molar surface moving from bilobed to quadrate, and the length of the 5<sup>th</sup> visible ventrite moving from equal in length to the 4<sup>th</sup> visible ventrite to the 5<sup>th</sup> greater in length than the 4<sup>th</sup>. The basal members of clade one are *Gama* and *Hercitis*. *Hercitis* is elongate in shape and small in size. It has an undifferentiated ventral surface of the prementum and mandibles designed with a well-developed scissorial area, linking it to the outgroups. *Gama* features characters similar to those of the outgroups (quadrate prementum), but is clearly identified by a strong autapomorphy, males possess highly modified mesothoracic basitarsi that is species specific in design.

*Agaoenemis* and *Barybas* form an unlikely sister group within clade one. In general body appearance they are similar to members of the outgroups. Their placement will likely be clarified with further investigation of the genera in clade one to which they show obvious similarities. *Barybas* demonstrates an autapomorphy, prementum with a ventral, raised, U-shaped carina. The genus contains small, rather rotund beetles that resemble the very smallest members of the more terminal genus *Plectris*. *Barybas* appears to be a distinct genus with numerous species. The monotypic *Agaoenemis* also resembles larger

members of *Plectris* and differs mainly in the sexually dimorphic male metathoracic tibia (strongly clavate, with dorsal margin rounded and setose). The generic validity of this genus seems questionable, and it will likely be synonymized into *Plectris* as our understanding of the character range of *Plectris* develops.

The remaining members of clade one are distinguished by the deeply emarginate labrum and rectangular mandibles with a scissorial area more heavily sclerotized than other Macroductylini and the molar area well developed. Basal members of this clade include the closely related *Ceratolontha* and *Rhinaspis*. Diagnostics of these sister genera are the prementum with medial and basal U-shaped carinae and a distinct ocular ridge. Both genera often show distinct sexual dimorphism in the clypeus, with males often having elaborated extensions of the clypeus, most prominent in *Ceratolontha*. These two genera show similarities to the very speciose *Plectris* and the monotypic *Oedichira*. The terminal members of clade one are divided into two branches. This division is based on one branch containing genera that show an increase in labial palpus size and the other branch containing genera that show an increase in the number of antennal segments of males.

Like *Oedichira*, *Anomonyx* is a possible transitional representative, or it may simply illustrate character range within the more terminal *Plectris*. Further work on *Plectris* and the related monotypic genera of this clade will provide a clearer understanding of character range. *Plectris* resembles the hypothetical outgroups in general body form (ovate, robust bodies, well developed mandibles, quadrate to rectangular prementa). Given the species richness of *Plectris* and the potential range of characters, apomorphies for this genus are currently based on the type species. *Plectris* appears to have at least three fairly strong apomorphies: ligula narrowed and produced anteriorly, clypeus dorsally ovate, and labrum connate. Additionally it appears that the presence of uneven metathoracic tarsal claws may also be diagnostic in many members of this genus.

The second division comprises the monotypic *Ctenotis*, a poorly defined genus that appears to be a transitional form. The remaining genera demonstrate a trend in the ventral surface of the prementum from flattened to medially grooved, the development of a membranous border along the elytral margin, and the mesocoxal separation moving from narrow to wide. *Clavipalpus* is fairly distinct: ventral surface of prementum with a medial lobe, elongate labial palpi, and an overall large, rotund body. It demonstrates mouthparts adapted for feeding in a hypognathous fashion. In frontal view, members of this genus have a semicircular labrum and elongated clypeus. *Anoplosiagum* and *Issacaris* demonstrate similar mouthpart characteristics but differ in a trend toward slightly more dorsoventrally flattened bodies.

Clade two contains 19 genera. These genera show the strongest trends related to mouthpart elongation: mandible in lateral profile becoming thinner, scissorial area reduced from a distinct cutting region to a broader cutting surface, labrum produced outwardly transitioning to one connate with the clypeus, declivity of the head moving to  $\sim 30^\circ$ . These changes have resulted in the beetles feeding in a prognathous manner. *Hieritis* demonstrates a transitional member with mouthpart similarities to members of clade one. Its small size complicates the character appearance of this genus. *Alvarinus* represents a second transitional form in clade two. It appears to demonstrate a change from a large labrum to a smaller labrum and the retention of the quadrate prementum with the ventral surface medially lobed. The long antennal club length is most distinctive.

The remaining genera in clade two show a grooved medial surface of the prementum, reduction in overall labral size, reduction in the declivity of the frons, and elongation of the body and legs.

*Ancistrosoma* is a well-defined genus with several strong autapomorphies (see generic diagnosis). *Chariodema* is difficult to distinguish among other clade three macroductylines when looked at in its entirety, the only noticeable difference being the diagnostically hexagonal pronotum. The generic validity of *Chariodema* is unclear and will likely be illuminated as additional species beyond the type are studied. The remaining genera in clade one demonstrate fairly strong generic characters. *Pectinosoma* closely resembles *Ancistrosoma*, but it is clearly separated by several apomorphies and appears to be an example of convergence. *Manopus* is intermediate in character range between *Ancistrosoma* and the more terminal genera of clade one such as *Ceraspis*.

*Calodactylus* and *Ceraspis* resemble *Manopus* and *Pectinosoma*. *Calodactylus* is well supported with an autapomorphy of a semicircular-shaped pocket on the ventromedial surface of ventrite (5<sup>th</sup> ventrite). *Ceraspis* is a speciose genus that seems well defined by a combination of characters: anterior margin of scutellum deeply emarginate, posterior margin of pronotum bidentate, and prosternal process produced

posteriorly over the mesosternum. *Dasyus* appears very similar to *Calodactylus*, and although it also has a semicircular-shaped pocket on the ventromedial surface of the ventrites, the pocket is located on a different ventrite (6<sup>th</sup> ventrite).

The speciose genus *Isonychus* lies within this clade and is characterized by several strong apomorphies. There is a large amount of variation in *Isonychus*, but most variation is in body length and the degree to which the body is covered with scale-like setae.

*Schizochelus*, *Chariodactylus*, and *Gastrohoplus* represent possible transitional genera. *Gastrohoplus* is a monotypic genus that is easily distinguished from other genera of clade two by the strongly quadrate pronotum, and the male has a striking autapomorphy: paired, well-developed parallel propygidial plates. The generic validity of all three genera remains questionable. They differ primarily in pronotal shape and length. The possibility that these genera will be synonymized remains open until more specimens can be evaluated. While beyond the scope of the present study, the inclusion of *Gastrohoplus* with *Chariodactylus* or *Schizochelus* would not be surprising with further investigation of these genera.

The terminal genera of clade two appear to be some of the most highly derived as implied in the phylogram (Fig. 188). *Manodactylus* appears very similar to *Macrodactylus*, differentiated only by the pronotal shape (cordate, widest anteriorly). As suggested for the previous genera, this may simply be another example of character variation. It would not be surprising in the future to see *Manodactylus* synonymized under *Macrodactylus*. *Dicrania* forms a sister taxon that is well supported by several apomorphies. *Chremastodus* and *Macrodactylus* are sister genera, differing most significantly in the pronotal shape and dorsal elytral surface. Again, it is possible that a more broadly conceived *Macrodactylus* could subsume *Chremastodus*. However, this would significantly expand the character range of *Macrodactylus*, and this is beyond the scope of this study. *Pristerophora* contains species that are small in size, and it is distinct from the other genera in the terminal clade. The terminal and arguably most derived member of the Macrodactylini is *Astaenosiagum*. This genus shows a reduction in the complexity of mouthparts, reversal in the elongation of the prementum to a quadrate shape, and a dorsoventral flattening of the body.

It is likely that with additional analysis, the generic relationships, limits among the genera, and the composition of this tribe will continue to change. The relationships of Melolonthinae will also continue to shape the composition of the Macrodactylini. It is possible that some members of Macrodactylini may be moved into other existing tribes. As more material is carefully examined, the character ranges of numerous genera will obviously be expanded, and perhaps more of the monotypic genera will be synonymized. This analysis is considered a starting point, a logical first step in the process of understanding this tribe. Numerous problems clearly exist in the present analysis. The lack of clear tribal definitions for outgroups is a concern and will require considerable attention from subsequent workers. The difficulty in obtaining type material has discouraged numerous workers in this field. It is hoped that many of these problems will be rectified over time, as type material is located. It is likely that several genera will need to have their characters re-evaluated once the types are located. The framework of this revision is designed to be flexible, so that changes can be incorporated and misinterpretation rectified. The phylogeny produced by the cladistic analysis should be considered a working hypothesis, with much room for clarification and future revision.

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Appendix 1. Character matrix used in the phylogenetic revision.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
<i>Agaocnemis pruina</i>	0	0	1	0	0	1	3	0	0	2	0	0	0	1	0	0	0	0	0
<i>Alvarinus hilarii</i>	0	0	1	1	0/2	1	3	0	0	1	0/1	1	0	1	1	1	0	0	0/3
<i>Ancistrosoma trinitatis</i>	0	0	1	0	0	2	2	0	0	2	0	0	0	1	1	1	0	0	0
<i>Anomonyx uruguayensis</i>	0	1	1	1	0	1	5	0	0	1	2	0	0	0	0	0	0	0	3
<i>Anoplosiagum sulcatum</i>	0	0	1	0	3	2	3	1	0	1	2	0	0	1	1	1	0	0	3
<i>Astaenosiagum longipes</i>	1	0	1	0	0	0	2	1	1	0	1	1	1	1	1	1	0	0	3
<i>Barybas nana</i>	1	0	1	1	0	0/2	0	0	1	2	0	0	0	1	0	0	0/1	0	0
<i>Calodactylus tibialis</i>	0	0	1	0	4	2	2	0	1	2	0	0	1	1	1	0	2	1	0
<i>Ceraspis pilatei</i>	0	0	1	0	0	2	2	0	1	2	0	0	1	1	1	0	0	0	0
<i>Ceratolontha venezuelae</i>	0	0	1	1	0	1	1	0	1	2	0	1	0	0	0	0	0	0	1
<i>Chariodactylus chacoensis</i>	1	0	1	1	4	2	2	0	1	0	1	1	1	1	1	1	0	0	0
<i>Chariodema xyliina</i>	0	0	1	0	0	2	2	0	0	2	1	1	1	1	0	1	0	0	0
<i>Clavipalpus ursinus</i>	0	1	1	0	0	1	4	1	0	1	0	0	0	0	1	0	0	0	3
<i>Chremastodus marmoratus</i>	0	0	1	0	4	0	2	0	1	0	2	1	1	1	1	0	0	0	1
<i>Ctenotis obesa</i>	0	1	1	1	0	1	3	1	0	2	2	0	0	0	0	1	0	0	0
<i>Dasyus collaris</i>	0	0	1	0	0	0	2	0	1	2	1	0	1	1	1	1	0	0	0
<i>Dicrania nigra</i>	0	0	1	0	4	0	2	0	1	0	0	0	1	1	1	1	0	1	0
<i>Gama viridifusca</i>	1	0	1	1	2	2	2	0	0	2	0	1	0	1	0	1	0	0	0
<i>Gastrohoplus mirabilis</i>	0	0	1	0	4	0/2	2	0	1	0	1	0	1	1	1	0	1	0	0
<i>Hercitis pygmaea</i>	0	0	1	1	0	2	3	0	1	0	0	1	1	1	1	1	0	0	0
<i>Hieritis macrocera</i>	0	1	1	0	0	0	3	0	0	2	0	1	0	1	1	1	0	0	2
<i>Isonychus sulphureus</i>	0	0	1	1	4	2	2	0	1	0	1	0	1	1	1	1	0	0	0
<i>Issacaris petalophora</i>	0	0	1	0	4	2	2	1	1	1	2	0	0	1	1	0	0	0	2
<i>Macroactylus subspinosus</i>	1	0	1	1	4	1	2	0	1	0	0	0	1	1	1	1	0	0	1
<i>Manodactylus gaujoni</i>	0	0	1	0	4	0	2	0	1	0	1	0	1	1	1	1	0	0	3
<i>Manopus biguttatus</i>	0	0	1	0	0	2	2	0	0	2	1	0	0	1	1	1	0	0	0
<i>Oedichira crassipes</i>	0	0	1	1	0	1	3	0	0	2	2	1	0	0	0	0	0	0	0
<i>Pectinosoma elongatum</i>	0	0	1	0	4	1	2	0	0	2	1	0	1	1	1	1	0	0	0
<i>Plectris tomentosa</i>	0	1	0/1	1	0/2	1/2	2/3	0	0	2	0	0	0	0	0	0/1	0/1	0	0/2
<i>Pristerophora picipennis</i>	0	0	1	0	4	0	3	1	1	0	1	0	1	1	1	1	0	0	3
<i>Rhinaspis aenea</i>	0	0	1	1	0/2	1	1	0	0	2	0	1	0	1	0	0	0	0	0
<i>Schizochelus flavescens</i>	0	0	1	1	4	2	2	0	1	0	1	0	1	1	1	0	0	0	0
Dichelonychini	0	0	1	0	0	0	2	0	0	2	0	0	0	1	1	1	2	1	2
Diplotaxini	0	0	1	0	2	1	0	0	0	2	0	0	0	1	0	1	0	0	2
Melolonthini	0	0	0	0	2	1	0	0	0	2	0	0	1	0	1	0	0	1	1
Sericini	0	0	1	1	4	1	0	0	2	0	2	0	1	1	1	0	0	0	1
Sericoidini	1	0	1	1	4	2	0	0	0	2	0	1	0	1	1	0	2	0	1

## Appendix 1. Character matrix used in the phylogenetic revision (Cont.).

	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
<i>Agaocnemis pruina</i>	0	1	1	1	0	2	1	1	0	0	1	1	1	1	0	0	0
<i>Alvarinus hilarii</i>	1/2	0/1	0/1	1	1/2	2	1	0/1	0/1	0/1	1	1	1	1	0	0/1	0
<i>Ancistrosoma trinitatis</i>	2	0	1	1	1	2	1	1	0	1	1	1	1	1	0	0	0
<i>Anomonyx uruguayensis</i>	0	0	0	1	1	2	1	1	1	2	0	1	0	1	1	1	0
<i>Anoplosiagum sulcatum</i>	0	0	0	1	2	2	0	1	1	1	1	1	1	1	0	0	0
<i>Astaenosiagum longipes</i>	1	1	3	0	2	3	1	1	1	1	1	1	1	1	0	0	0
<i>Barybas nana</i>	1	0	2	1	2	2	1	0	0	1/2	1	1	0	0	0	1	0
<i>Calodactylus tibialis</i>	2	0	2	1	0	2	1	1	1	1	1	1	1	1	0	0	0
<i>Ceraspis pilatei</i>	1	0	1	1	1	2	1	0/1	1	1	1	1	1	0	0	0	0
<i>Ceratolontha venezuelae</i>	2	0	0	1	0	2	1	1	0	1	1	1	1	1	1	0	0
<i>Chariodactylus chacoensis</i>	2	0	2	0	1	2	1	1	1	1	1	1	1	1	1	0	0
<i>Chariodema xyliina</i>	2	0	1	1	1	2	1	0	0	1/2	1	1	1	0	0	0	0
<i>Clavipalpus ursinus</i>	0	0	1	1	1	2	0	1	1	1	0	1	1	0	0	1	0
<i>Chremastodus marmoratus</i>	0	1	3	0	2	3	1	1	1	1	1	1	1	1	0	0	0
<i>Ctenotis obesa</i>	1	0	0	1	0	2	1	0	0	0	0	0	1	1	0	1	0
<i>Dasyus collaris</i>	2	0	2	1	2	2	1	1	1	1	1	1	1	1	0	0	0
<i>Dicrania nigra</i>	0	1	1	0	2	2	1	1	1	1	1	1	1	1	0	0	0
<i>Gama viridifusca</i>	2	0	1	1	0	2	1	0	1	1	1	1	1	1	0	1	0
<i>Gastrohoplus mirabilis</i>	2	0	2	0	2	2	1	1	1	1	1	1	1	1	0	0	0
<i>Hercitis pygmaea</i>	2	0	2	1	0	2	1	1	1	2	0	1	1	1	0	0	1
<i>Hieritis macrocera</i>	0	1	2	1	0	2	1	1	0	0/1	1	1	1	1	0	0	0
<i>Isonychus sulphureus</i>	2	1	1	0	2	2	1	1	1	1	1	1	1	1	0	1	0
<i>Issacaris petalophora</i>	1	1	0	0	0	2	1	1	0	2	0	1	1	1	0	0	0
<i>Macroctylus subspinosus</i>	2	1	3	0	2	3	1	1	1	1	1	1	1	0	0	0	0
<i>Manodactylus gaujoni</i>	0	0	3	0	2	2	1	0	1	1	1	1	1	0	0	0	0
<i>Manopus biguttatus</i>	2	0	1	1	1	2	1	0	1	2	0	1	1	1	0	0	0
<i>Oedichira crassipes</i>	0	0	0	1	0	2	1	1	0	2	0	0	1	1	0	0	0
<i>Pectinosoma elongatum</i>	2	0	1	1	2	2	1	0	1	1	0	1	1	0	0	0	0
<i>Plectris tomentosa</i>	2	0	0/1	1	0/2	2	1	0/1	0/1	0/1/2	0	1	1	0/1	0	0/1	0
<i>Pristerophora picipennis</i>	0	1	1	0	2	3	1	1	1	1	1	1	1	0	0	0	0
<i>Rhinaspis aenea</i>	1/2	0	0/1	1	0/1	2	1	1	0	0	1	1	1	1	1	0/1	0
<i>Schizochelus flavescens</i>	2	0	1	0	2	2	1	1	1	1	1	1	0	1	0	0	0
Dichelonychini	2	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	0
Diplotaxini	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	1	0
Melolonthini	1	0	0	1	2	0	0	1	1	0/1	1	1	1	1	0	0	0
Sericini	2	1	1	1	2	2	1	1	1	1	1	1	1	1	0	0	1
Sericoidini	2	0	0	0	2	2	0	1	1	2	0	1	1	1	0	0	1

Appendix 1. Character matrix used in the phylogenetic revision (Cont.).

	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54
<i>Agaocnemis pruina</i>	1	0	1	1	2	2	0	1	0	0	1	0	0	0	0	0	0	0
<i>Alvarinus hilarii</i>	1	0	1/2	0	1/2	2	0	0/1	0	0	0	0	0	0	0	0	0	1
<i>Ancistrosoma trinitatis</i>	1	0	2	0	1	2	0	0	1	1	2	0	2	0	1	1	1	1
<i>Anomonyx uruguayensis</i>	1	1	1	1	1	2	0	1	0	0	2	0	0	0	0	0	0	1
<i>Anoplosiagum sulcatum</i>	1	1	1/2	0/1	0/1	2	0	0/1	0	0	2	0/1	0	0	0	0	0	0/1
<i>Astaenosiagum longipes</i>	1	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0
<i>Barybas nana</i>	1	0	1	1	0	2	0	0	0	0	2	1	0	0	0	0	0	0
<i>Calodactylus tibialis</i>	1	0	2	0	0	1	0	1	0	0	2	0	0	0	0	0	0	0
<i>Ceraspis pilatei</i>	1	0	2	0	0/1	2	0	1	1	0	2	0	1	0	1	0	0	0
<i>Ceratolontha venezuelae</i>	1	0	1	2	1	2	0	1	0	0	2	1	0	0	1	0	0	1
<i>Chariodactylus chacoensis</i>	1	1	2	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0
<i>Chariodema xyliina</i>	0	0	2	0	0	1	0	1	0	2	2	0	0	1	0	0	0	1
<i>Clavipalpus ursinus</i>	1	1	1	0	1	2	0	1	0	0	2	1	0	0	0	0	1	1
<i>Chremastodus marmoratus</i>	1	1	2	0	2	1	0	0	0	0	2	1	0	0	1	0	0	1
<i>Ctenotis obesa</i>	1	0	2	0	0	2	0	1	1	0	1	0	0	0	0	0	0	0
<i>Dasyus collaris</i>	1	0	2	0	1	0	0	0	0	1	2	1	0	0	0	1	0	0
<i>Dicrania nigra</i>	1	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0	0	1
<i>Gama viridifusca</i>	1	1	2	0	1	2	0	1	0	0	2	0	1	0	0	0	0	0
<i>Gastrohoplus mirabilis</i>	1	1	2	0	2	1	0	0	0	2	2	1	0	0	1	1	0	0
<i>Hercitis pygmaea</i>	1	1	2	0	1	2	1	1	0	2	2	1	0	0	0	0	0	0
<i>Hieritis macrocera</i>	1	0	2	0	0	2	0	0	0	0	2	0	0	0	0	0	0	0
<i>Isonychus sulphureus</i>	1	1	2	0	2	0	0	0	0	0	2	0	0	0	0	1	0	0
<i>Issacaris petalophora</i>	1	1	1	0	1	2	0	0	0	0	2	1	0	0	0	0	1	0
<i>Macroactylus subspinosus</i>	1	0	2	0	2	1	0	0	0	2	0	0	5	0	1	1	0	0&1
<i>Manodactylus gaujoni</i>	1	0	1	1	0	2	0	0	0	0	0	1	0	0	1	1	0	1
<i>Manopus biguttatus</i>	1	0	2	0	0	1	1	0	0	0	1	0	6	0	0	0	0	1
<i>Oedichira crassipes</i>	1	1	1	1	1	2	0	1	0	0	2	0	0	0	0	0	0	1
<i>Pectinosoma elongatum</i>	1	0	2	0	2	1	0	0	0	2	0	0	5	0	1	0	0	1
<i>Plectris tomentosa</i>	1	0/1	1/2	0/1	1	2	0	0/1	0	0	2	0/1	0/7	0	0	0	0	1
<i>Pristerophora picipennis</i>	1	1	2	0	2	2	0	0	0	0	2	0	0	0	0	1	0	0
<i>Rhinaspis aenea</i>	1	0	2	0	0/1	2	0	0	0	0	2	0	0	0	0	0	0	0/1
<i>Schizochelus flavescens</i>	1	1	2	0	1	0	0	0	0	0	2	1	0	0	0	1	0	0
Dichelonychini	0	0	0	3	0	2	0	0	0	0	2	1	0	0/1	0	0	0	0
Diplotaxini	0	0	2	0	1	2	0	0	0	0	0	1	0	0	0	0	0	0
Melolonthini	0	0	0	3	0	2	0	0	0	0	2	0	0	0	0	0	1	0
Sericini	0	0	0	3	0	2	0	0	0	0	2	0	0	0	0	0	1	0
Sericoidini	0	0	0	3	0	2	0	1	0	0	2	0	0	0	0	0	0	0

## Appendix 1. Character matrix used in the phylogenetic revision (Cont.).

	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71
<i>Agaocnemis pruina</i>	0	0	1	1	0	1	1	0	0	2	2	0	2	0	1	1	0
<i>Alvarinus hilarii</i>	1	0	1	1	0	1	1	0	0	2	1	0&1	2	0	0	0/1	0/1
<i>Ancistrosoma trinitatis</i>	0	0	0	1	1	3	1	1	1	2	2	1	1/2	0	0	0	0
<i>Anomonyx uruguayensis</i>	1	0	1	1	0	3	1	1	0	1	0	1	1	0	1	0	5
<i>Anoplosiagum sulcatum</i>	1	0	1	0	0	0/1	0/1	1	0	1/2	1	1	0/1	0	1	0/1	0
<i>Astaenosiagum longipes</i>	1	0	1	0	0	2	0	0	1	1	0	0	0	0	1	1	4
<i>Barybas nana</i>	3	0	1	0	0	0	0	1	0	2	2	1	2	0	1	1	0
<i>Calodactylus tibialis</i>	1	0	1	1	1	3	0	0	1	2	2	0	1	0	0	0	0
<i>Ceraspis pilatei</i>	0/1	0	0/1	1	1	3	0/1	1	1	2	1	1	1/2	0	0	0	1
<i>Ceratolontha venezuelae</i>	1	0	1	1	0	0	0	1	1	1	1	1	1	0	1	0	0
<i>Chariodactylus chacoensis</i>	1	0	1	0	0	0	0	1	1	2	1	1	2	0	0	2	4
<i>Chariodema xyliina</i>	1	0	1	1	1	3	0	1	0	2	1	1	2	0	0	0	0
<i>Clavipalpus ursinus</i>	1	0	1	1	0	1	1	1	0	2	1	0	2	1	1	2	0
<i>Chremastodus marmoratus</i>	1	0	1	1	0	0	0	1	0	2	2	1	1	0	1	1	4
<i>Ctenotis obesa</i>	0	0	1	1	0	1	1	1	0	2	1	1	1	0	1	1	0
<i>Dasyus collaris</i>	2	0	1	1	1	3	0	0	1	2	1	1	1	0	1	1	1
<i>Dicrania nigra</i>	1	0	1	1	0	0	0	0	1	1	1	1	1	0	0	0	1
<i>Gama viridifusca</i>	2	0	1	1	0	0	0	0	0	1	1	1	1	0	1	1	0
<i>Gastrohoplus mirabilis</i>	1	0	1	0	0	0	1	0	1	2	2	1	1	0	1	1	0
<i>Hercitis pygmaea</i>	1	0	1	1	0	0	0	0	0	1	1	0	1	0	1	1	0
<i>Hieritis macrocera</i>	1	0	1	1	0	1	0	1	0	1	1	1	2	1	1	0	0
<i>Isonychus sulphureus</i>	1	0	1	0	0	0	0	0	1	1	1	0	1	0	1	2	1
<i>Issacaris petalophora</i>	1	0	1	0	0	1	0	1	0	2	1	1	1	0	0	0	4
<i>Macrodactylus subspinosus</i>	1	0	1	1	0	1	0	1	1	2	0	1	2	0	0	1	0
<i>Manodactylus gaujoni</i>	1	0	1	1	0	1	0	0	0	1	0	1	2	0	0	1	4
<i>Manopus biguttatus</i>	0	0	1	1	1	3	0	1	1	2	1	1	0	0	0	0	1
<i>Oedichira crassipes</i>	1	1	1	1	0	0	1	1	1	1	1	1	2	1	1	0	5
<i>Pectinosoma elongatum</i>	1	0	0	1	1	3	0	1	0	2	1	1	2	0	0	0	1
<i>Plectris tomentosa</i>	0/1	0/1	1	0/1	0/1	0/3	0/1	1	0	1	0/1	1	1	0	1	1	1/5
<i>Pristerophora picipennis</i>	1	0	1	1	0	0	0	0	0	2	0	0	2	0	1	0	4
<i>Rhinaspis aenea</i>	0/1	0	1	1	0	0	0/1	1	0	1/2	2	0/1	1/2	0	1	1	0/1
<i>Schizochelus flavescens</i>	2	0	1	0	0	1	0	1	1	2	2	1	2	0	1	1	4
Dichelonychini	0	0	1	1	1	3	0	1	0	2	1	0	1	0	2	1	0
Diplotaxini	0	0	1	1	0	1	0	1	1	1	1	1	1	0	1	1	0
Melolonthini	0	0	2	1	0	0	0	1	1	1	1	0	1	0	1	1	1
Sericini	0	0	1	1	0	0	0	1	0	1	0	0	2	0	0	2	2
Sericoidini	1	0	1	1	0	1	0	1	0	1	0	1	0	1	1	4	1

Appendix 1. Character matrix used in the phylogenetic revision (Cont.).

	72	73	74	75	76	77
<i>Agaocnemis pruina</i>	1	0	2	0	1	1
<i>Alvarinus hilarii</i>	0	1	1/2	0	1	1
<i>Ancistrosoma trinitatis</i>	0	0	2	0	1	1
<i>Anomyx uruguayensis</i>	0	1	1	0	1	1
<i>Anoplosiagum sulcatum</i>	0	1	0/1	0	1	1
<i>Astaenosiagum longipes</i>	1	0	1	0	1	1
<i>Barybas nana</i>	0	1	2	1	1	1
<i>Calodactylus tibialis</i>	0	0	1	0	0	1
<i>Ceraspis pilatei</i>	1	1	1/2	0/1	0/1	1
<i>Ceratolontha venezuelae</i>	1	0	1	0	1	1
<i>Chariodactylus chacoensis</i>	1	0	2	0	1	1
<i>Chariodema xyliina</i>	0	0	2	0	1	1
<i>Clavipalpus ursinus</i>	0	0	1	0	1	1
<i>Chremastodus marmoratus</i>	1	1	1	0	1	1
<i>Ctenotis obesa</i>	0	1	1	0	1	1
<i>Dasyus collaris</i>	0	1	2	0	0	1
<i>Dicrania nigra</i>	1	1	1	0	1	1
<i>Gama viridifusca</i>	0	0	1	0	1	1
<i>Gastrohoplus mirabilis</i>	1	0	1	0	1	1
<i>Hercitis pygmaea</i>	0	0	1	0	1	1
<i>Hieritis macrocera</i>	1	0	2	0	1	1
<i>Isonychus sulphureus</i>	0	0	2	0	1	1
<i>Issacaris petalophora</i>	1	1	1	0	1	1
<i>Macroactylus subspinosus</i>	1	0	1	0	1	1
<i>Manodactylus gaujoni</i>	1	0	2	0	1	1
<i>Manopus biguttatus</i>	0	0	2	0	1	1
<i>Oedichira crassipes</i>	0	0	1	1	1	1
<i>Pectinosoma elongatum</i>	0	0	2	0	0	1
<i>Plectris tomentosa</i>	0/1	0	2	1	1	1
<i>Pristerophora picipennis</i>	1	0	2	0	1	1
<i>Rhinaspis aenea</i>	0/1	0/1	1/2	0	1	1
<i>Schizochelus flavescens</i>	1	0	2	0	1	1
Dichelonychini	1	0	1	0	1	1
Diplotaxini	0	0	0	0	1	1
Melolonthini	0	0	1	0	2	1
Sericini	1	0	0	0	1	1
Sericoidini	1	1	0	1	1	1