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The Dynastine Scarab Beetles of Costa Rica and Panama (Coleoptera: Scarabaeidae: Dynastinae)

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The Dynastine Scarab Beetles of Costa Rica and Panama

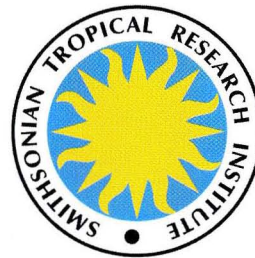
(Coleoptera: Scarabaeidae: Dynastinae)

Brett C. Ratcliffe



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Cover: A male hercules beetle, *Dynastes hercules* (L.), clinging to a liana with a bromeliad in the background. Mixed media illustration by Mark Marcuson.

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of Costa Rica and Panama
(Coleoptera: Scarabaeidae: Dynastinae)

by

Brett C. Ratcliffe



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DEDICATION

This work is dedicated to Dr. Dodge Engleman, Ratibor and Dinorah Hartmann, and Dr. Henry Stockwell, all of whom resided in Panama during the period of this study. All of these generous people were my hosts and companions in the field at one time or another during my expeditions to Panama, and they all provided the impetus for me to engage in this work. They gave freely of themselves to provide logistical support, and they graciously shared their extensive knowledge and wisdom about the extravagant tropical plants and animals that surrounded them. They were fortunate to live amongst such tropical splendor. And I was fortunate to know such fine individuals.



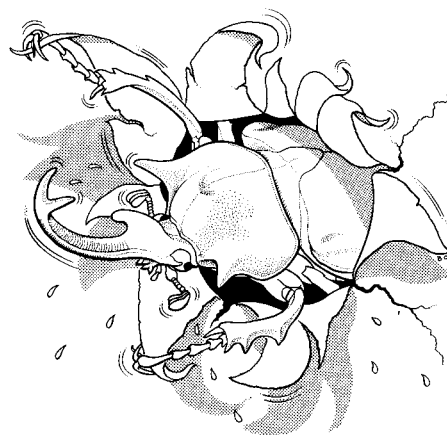
Dr. Dodge Engleman, Pipeline Road, Canal Zone, Panama, May 1977. Photo by BCR.



Ratibor and Dinorah Hartmann at their home near Santa Clara, Chiriqui, Panama, May 1980. Photo by BCR.



Dr. Henry Stockwell on the way to Isla Majé research station, Panama, May 1976. Photo by BCR.





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The Dynastine Scarab Beetles
of Costa Rica and Panama
(Coleoptera: Scarabaeidae: Dynastinae)

by

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Abstract. The 157 species of dynastine scarab beetles that occur in Costa Rica and Panama are comprehensively reviewed. Keys, descriptions, distributions, and notes on biology are provided for all species as well as illustrations and maps. The larvae of *Enema endymion*, *Heterogomphus chevrolati*, and *Dynastes hercules* are described for the first time. Also included are synopses of the higher-level taxa, a glossary, a gazetteer of place names, and a species checklist.

The following new species are described: *Cyclocephala alazona*, *C. enigma*, *C. labidion*, *C. maryliza*, *C. mustacha*, *C. stockwelli*, *C. unamas* (all Cyclocephalini); *Irazua dilicra* (Oryctini); *Amblyoproctus centroamericanus*, *Hemiphileurus curoei*, *H. dyscritus*, *H. nebulohylaeus*, *H. pygidiopunctissimus* (all Phileurini); *Golofa hirsuta* and *G. solisi* (Dynastini). *Irazua* is described as a new genus of Oryctini.

The following new synonyms are recognized: *Cyclocephala dissimulata* Ratcliffe (= *C. almitana* Dechambre), *C. howdeni* Endrödi (= *C. carbonaria* Arrow), *C. obscurata* Endrödi (= *C. castaniella* Bates), *C. conspicua gregaroides* Dechambre and *C. conspicua fusca* Dechambre (= *C. conspicua* Sharp), *C. mollis* Endrödi (= *C. epistomalis* Bates), *C. barroensis* Endrödi (= *C. herteli* Endrödi), *C. rorschachoides* Ratcliffe (= *C. krombeini* Endrödi), *C. pseudisabellina* Endrödi (= *C. mutata* Harold), *C. vitracelis* Dechambre (= *C. mutata* Harold), *Stenocrates difficilis* Endrödi (= *S. bicarinatus* Robinson) (Cyclocephalini); *Hemiphileurus variolosus striatus* Endrödi (= *H. variolosus* [Burmeister]) (Phileurini); and *Aegopsis westwoodi* Thomson (= *A. curvicornis* Burmeister) (Agaoccephalini).

The following names reflect a change in status because all are resurrected from synonymy: *Cyclocephala brevis* Höhne, *C. multiplex* Casey, *C. mutata* Harold, and *C. ovulum* Bates (Cyclocephalini).

The following names are combinations resulting from a change in genus from *Ligyris* to *Tomarus*: *Tomarus bituberculatus* (Palisot de Beauvois), *T. cicatricosus* (Prell), *T. ebenus* (DeGeer), *T. fossor* (Latreille), *T. gyas* Erichson, *T. laevicollis* (Bates), *T. maternus* (Prell), *T. nasutus* (Burmeister), *T. sallaei* (Bates), and *T. similis* (Endrödi).

Lectotype and paralectotype designations are made for the syntypes of *Hemiphileurus cylindroides* (Bates). The generic name *Enema* is designated a *nomen protectum*, and the generic name *Hoplites* is designated a *nomen oblitum*.

The following Cyclocephalini are reported for the first time from Costa Rica: *Ancognatha atacazo* Kirsch, *A. vexans* Ratcliffe, *Aspidolea kuntzeni* Höhne, *A. notaticollis* Höhne, *C. erotylina* Arrow, *C. fasciolata* Bates, *C. ligyrina* Bates, *C. prolongata* Arrow, *Erioscelis columbica* Endrödi, *Stenocrates bicarinatus* Robinson, *S. hardyi* Dechambre, and *S. laevicollis* Kirsch. The following Cyclocephalini are reported for the first time from Panama: *Cyclocephala epistomalis* Bates and *C. rogezi* Dechambre.

The following species have been reported from Costa Rica and/or Panama, but since they have never been collected since being reported, or they are so far out of their normal range, I consider the records to be erroneous, spurious, or otherwise suspect: *Cyclocephala cartwrighti* Endrödi, *C. freudi* Endrödi, *C. gregaria* Heyne and Taschenberg, *C. laminata* Burmeister, *C. lurida coahuilae* Bates, *C. obesa* Burmeister, *C. simulatrix* Höhne, *C. tutilina* Burmeister, and *C. warneri* Ratcliffe.

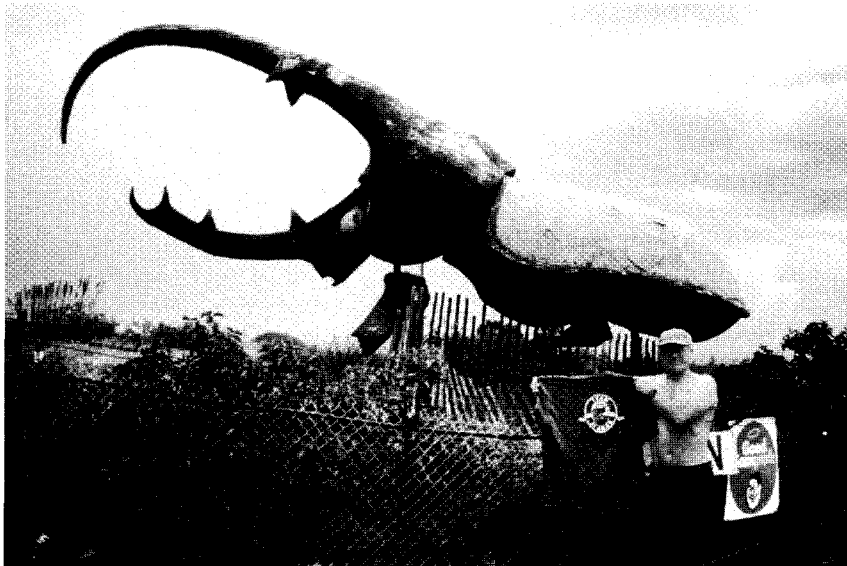
The following Pentodontini are reported for the first time from Costa Rica: *Euetheola bidentata* Burmeister, *Tomarus cicatricosus* (Prell), *T. laevicollis* (Bates), and *T. maternus* (Prell).

The following Oryctini are reported for the first time from Costa Rica: *Enema pan* (Fabr.) and *Xyloryctes splendidus* Prell.

The following Phileurini are reported for the first time from Costa Rica: *Amblyodus taurus* Westwood and *Hemiphileurus dejeani* (Bates).

The following Agaoccephalini are reported for the first time from Costa Rica: *Aegopsis curvicornis* Burmeister and *Spodistes beltianus* (Bates).

The following Dynastini is reported for the first time from Costa Rica: *Golofa tersander* Burmeister.



BCR with *Dynastes hercules* Team Scarab t-shirt and slightly larger *D. hercules* in background at May Museum of Natural History near Colorado Springs, CO, August 1999. Photo by Ian Ratcliffe.

Resumen. Se realizó una revisión comprehensiva de las 157 especies de escarabajos dinastinos que ocurren en Costa Rica y Panamá. Se proveen claves, descripciones, distribuciones y notas sobre la biología de todas las especies, también se presentan ilustraciones y mapas. Las larvas de *Enema endymion*, *Heterogomphus chevrolati*, y de *Dynastes hercules* son descritas por primera vez. Además, se incluyen sinópsis de los taxa de niveles superiores, un glosario, un gazetteer de las localidades y un listado de especies.

Se describen las siguientes especies nuevas: *Cyclocephala alazona*, *C. enigma*, *C. labidion*, *C. maryliza*, *C. mustacha*, *C. stockwelli*, *C. unamas* (todas Cyclocephalini); *Irazua dilicra* (Oryctini); *Amblyoproctus centroamericanus*, *Hemiphileurus curoei*, *H. dyscritus*, *H. nebulohylaeus*, *H. pygidiopunctissimus* (todas Phileurini); *Golofa hirsuta* y *G. solisi* (Dynastini). *Irazua* es descrito como un género nuevo de Oryctini.

Se reconocen los siguientes sinónimos: *Cyclocephala dissimulata* Ratcliffe (= *C. almitana* Dechambre), *C. howdeni* Endrödi (= *C. carbonaria* Arrow), *C. obscurata* Endrödi (= *C. castaniella* Bates), *C. conspicua gregaroides* Dechambre y *C. conspicua fusca* Dechambre (= *C. conspicua* Sharp), *C. mollis* Endrödi (= *C. epistomalis* Bates), *C. barroensis* Endrödi (= *C. herteli* Endrödi), *C. rorschachoides* Ratcliffe (= *C. krombeini* Endrödi), *C. pseudisabellina* Endrödi (= *C. mutata* Harold), *C. vitracelis* Dechambre (= *C. mutata* Harold), *Stenocrates difficilis* Endrödi (= *S. bicarinatus* Robinson) (Cyclocephalini), *Hemiphileurus variolosus striatus* Endrödi (= *H. variolosus* [Burmeister]) (Phileurini), y *Aegopsis westwoodi* Thomson (= *A. curvicornis* Burmeister) (Agacephalini).

Los siguientes nombres reflejan un cambio de estatus debido a que todos han sido resucitados de la sinonimia: *Cyclocephala brevis* Höhne, *C. multiplex* Casey, *C. mutata* Harold, y *C. ovulum* Bates (Cyclocephalini).

Los siguientes nombres son combinaciones como resultado del cambio de género, de *Ligyris* a *Tomarus*: *Tomarus bituberculatus* (Palisot de Beauvois), *T. cicatricosus* (Prell), *T. ebenus* (DeGeer), *T. fossor* (Latreille), *T. gyas* Erichson, *T. laevicollis* (Bates), *T. maternus* (Prell), *T. nasutus* (Burmeister), *T. sallaei* (Bates) y *T. similis* (Endrödi).

Se hacen designaciones de lectotipo y paralectotipo para los sintipos de *Hemiphileurus cylindroides* (Bates). El nombre genérico *Enema* es designado como *nomen protectum*, y el nombre genérico *Hoplites* es designado como *nomen oblitum*.

Los siguientes Cyclocephalini se reportan por primera vez para Costa Rica: *Ancognatha atacazo* Kirsch, *A. vexans* Ratcliffe, *Aspidolea kuntzeni* Höhne, *A. notaticollis* Höhne, *C. erotylina* Arrow, *C. fasciolata* Bates, *C. ligyrina* Bates, *C. prolongata* Arrow, *Erioscelis columbica* Endrödi, *Stenocrates bicarinatus* Robinson, *S. hardyi* Dechambre y *S. laevicollis* Kirsch. Los siguientes Cyclocephalini se reportan por primera vez para Panamá: *Cyclocephala epistomalis* Bates y *C. rogezi* Dechambre.

Las siguientes especies han sido reportadas para Costa Rica o Panamá pero no han sido colectas desde entonces, o se encuentran tan alejadas de sus rango de distribución que los considero registros erróneos o de algún modo

sospechosos: *Cyclocephala cartwrighti* Endrödi, *C. freudi* Endrödi, *C. gregaria* Heyne y Taschenberg, *C. laminata* Burmeister, *C. lurida coahuilae* Bates, *C. obesa* Burmeister, *C. simulatrix* Höhne, *C. tutilina* Burmeister, y *C. warneri* Ratcliffe.

Los siguientes Pentodontini se reportan por primera vez para Costa Rica: *Euethoela bidentata* Burmeister, *Tomarus cicatricosus* (Prell), *T. laevicollis* (Bates) y *T. maternus* (Prell).

Los siguientes Oryctini se reportan por primera vez para Costa Rica: *Enema pan* (Fabr.) y *Xyloryctes splendens* Prell.

Los siguientes Phileurini se reportan por primera vez para Costa Rica: *Amblyodus taurus* Westwood y *Hemiphileurus dejeani* (Bates).

Los siguientes Agacephalini se reportan por primera vez para Costa Rica: *Aegopsis curvicornis* Burmeister y *Spodistes beltianus* (Bates).

El siguiente Dynastini se reporta por primera vez para Costa Rica: *Golofa tersander* Burmeister.

INTRODUCTION

There will always be those who must look into the dark in order to see.

— McGlashan

The beetle family Scarabaeidae is a large, diverse, cosmopolitan group of beetles. It has about 30,000 described species, and about 200 new species are being described each year. Scarabs have diversified into most habitats, and they are fungivores, herbivores, necrophages, coprophages, saprophages, and carnivores. They are widely distributed, even living in the Arctic in animal burrows. Some scarabs exhibit various levels of parental care and sociality. Some are myrmecophilous, termitophilous, or ectoparasitic. Many possess extravagant horns, others are able to roll into a compact ball, and still others are highly armored for inquiline life. Some are important agricultural pests that may destroy crops while others are used in the biological control of dung and dung flies. Scarabs are some of the more popular beetles due to their large size, bright colors, and interesting natural histories. Early Egyptians revered the scarab as a symbol of god, Jean Henri Fabre studied their behavior, and Charles Darwin used observations of scarabs in his theory of sexual selection. Because of the popularity of the group, especially with amateurs, there exists a totally erroneous impression that the family is taxonomically well-known. However, even with this seemingly long history, the group is desperately in need of systematics studies.

The family Scarabaeidae is sometimes referred to as the family Melolonthidae, especially by some Latin American workers. In this usage, the family includes the subfamilies Melolonthinae, Euchirinae, Phaenomeridinae, Dynastinae, Cetoniinae, Glaphyrinae, and Systellopodinae (Endrödi 1966), whereas the Scarabaeidae refers to everything else except Passalidae, Lucanidae, and Trogidae. This classification is not in wide use today and is actually incorrect. The family group names Rutelinae and Dynastinae were established by MacLeay in 1819, and the family group name Melolonthinae was established

by Samouelle in 1819. However, the family group name Cetoniinae was established a few years earlier in 1815 by Leach. Thus, the family group name Cetoniidae has priority over Melolonthidae. Therefore, if one wants to consider all of these subfamilies in the same family (exclusive of Scarabaeinae, which was established by Latreille in 1802), then the valid name would be Cetoniidae and not Melolonthidae! Accordingly, the family name Scarabaeidae (including Melolonthinae, Dynastinae, Cetoniinae, etc. and Scarabaeinae) is the correct family group name for these taxa and not Melolonthidae. Most authors dealing with higher classification (*e.g.*, Browne and Scholtz 1995; Lawrence and Newton 1995; Jameson and Ratcliffe 2002) consider Scarabaeidae to include the Aphodiinae, Scarabaeinae, Melolonthinae, Rutelinae, Dynastinae, and Cetoniinae.

Subfamily Dynastinae: Literature Overview

Taxonomic monographs containing descriptions, illustrations, keys, nomenclature, and lists are the cornerstones of comparative biology (Anonymous 1995) because they document biodiversity, enable identifications, and provide the baseline data for subsequent avenues of research. The first attempt at an identification manual for the Central American Scarabaeoidea was written by Bates (1886-1890; Fig. 1) in the *Biologia Centrali-Americana* series. The scarab volume is still intensively used today because of its fine illustrations and lack of anything better specifically for the region. An identification manual for the world dynastine fauna was produced by Endrödi (1985a; Fig. 2). This work was an English-version condensation of Endrödi's series of 22 synoptic papers in German that he wrote between 1966-1978. Endrödi's 1985 work provided the first comprehensive classification of the subfamily as



Fig. 1. Henry Walter Bates, 1825-1892.



Fig. 2. Sebo Endrödi, 1903-1984.

well as enabling species identifications, and it is an indispensable tool.

However, the manual, as Endrödi stated in his preface, was not intended as a monographic treatment, especially since the world dynastine fauna was still far from known. For example, there have been at least 90 species of *Cyclocephala* alone described in the intervening 17 years since the manual was published, which tends to lower dramatically the utility of the *Cyclocephala* key in the manual. Moreover, the manual did not provide complete descriptions or synonymies, temporal distributions, life history data, habitat associations or detailed geographical distributions . . . and there were few illustrations other than male parameres. Even the original taxonomic papers in German lacked some of these important components because Endrödi was hurrying to finish, in a synoptic fashion, a huge amount of work in his elderly years. Dynastine workers today owe him a great debt of gratitude for his pioneering effort in

producing a complete taxonomic package for the subfamily. While this volume provided the framework for all future studies on the Dynastinae, it suffered from significant errors in key construction and language use, vagueness, and superficial distributional information (Ratcliffe 1987, 1989).

Aside from the works of Endrödi, the dynastine fauna in several parts of the Old World tropics have been reviewed with variable success (Arrow 1925; Dechambre 1986; Ferreira 1965; Nakamura 1974). In temperate areas, the Dynastinae are fairly well-known (Carne 1957; Ratcliffe 1991; Saylor 1945, 1946a-b, 1948a-b; Dechambre 1974; Paulian and Baraud 1982). However, the New World tropical fauna (where dynastines are most diverse) has remained poorly studied. Only those works on the Lesser Antilles (Chalumeau 1983) and Cuba (Chapin 1932) are comprehensive in their coverage. Ratcliffe (2000, 2002b) provided a brief overview of the Dynastinae occurring in Monteverde, Costa

Rica and a checklist of the Scarabaeoidea of Panama, respectively. There has never been a monographic, faunistic, or even an identification guide produced for the Dynastinae of any mainland country in the Neotropics. This survey of the Dynastinae of Costa Rica and Panama is the first of a three-phase study to document the taxonomic, geographic, and temporal distribution of all the dynastines in Central America. The second phase, currently ongoing (with Ronald Cave, recently of the Escuela Agrícola Panamericana, Zamorano, Honduras and now University of Florida), will survey the Dynastinae of Honduras, Nicaragua, and El Salvador. The third and final phase will be to survey the Dynastinae in Mexico, Guatemala, and Belize.

Dynastinae of Central America

Why Central America? Many of these countries (especially Panama, Costa Rica, Honduras, and Mexico) have become major natural history laboratories for the study of their organisms and their biology. These countries are also relatively familiar to biologists because of national organizations promoting biodiversity research (Instituto Nacional de Biodiversidad and the Organization for Tropical Studies in Costa Rica, Smithsonian Tropical Research Institute in Panama, Escuela Agrícola Panamericana in Honduras, Museo Nacional de Historia Natural in El Salvador, Institute of Ecology in Mexico, Universidad del Valle in Guatemala) as well as having established national parks and biological reserves and the many resident biologists that live there.

Most of these countries have, in addition, established infrastructures for assisting in research endeavors by national and foreign scientists. Lastly, the various habitats in these countries are usually accessible, and this is of special importance for any kind of country-wide inventory. My own field data from both Central and South America indicate that new species and a wealth of information not yet residing in museum collections awaits to be described and gathered. There is an urgency in conducting faunistic studies because burgeoning human populations and

associated human activities are rapidly eliminating natural habitats that sustain so much tropical biodiversity (Anonymous 1980; Blackmore 1996; McNeely *et al.* 1990; Myers 1980; National Science Board 1989; Savage 1982).

Collections of new material and inventories of existing collections are needed in order to explore and catalog biotic diversity and to facilitate further research. These are very different, but complementary, components of biotic surveys. There has not previously been an attempt to bring together the taxonomic, biological, ecological, and distributional data that currently exists in systematics research collections or that which can still be gathered in the field in order to provide a sound systematic treatment of the Dynastinae of Mesoamerica.

My target audience for these biotic surveys consists of:

- (1) fellow systematists conducting research on dynastines;
- (2) curators and collections managers responsible for organizing research collections in order to facilitate data retrieval;
- (3) Central American scientists and students studying their entomofauna;
- (4) ecologists who encounter dynastines during their studies and need identifications and information on biology and distribution;
- (5) biogeographers needing distributional data;
- (6) park and reserve managers needing to know the composition of faunal elements under their jurisdiction for establishing management plans, educational programs, or research opportunities;
- (7) applied entomologists requiring information about possible pest status;
- (8) the large community of scarab collectors.

MATERIALS AND METHODS

This study was based on the examination of 34,728 specimens from Costa Rica and Panama. The genus *Cyclocephala* alone comprised 22,501 of those records. This material

came from two sources: (1) 14 expeditions to Costa Rica and Panama between 1975-1996, and (2) the study of specimens from the following institutional collections (curators and/or collection managers in brackets following):

BMNH The Natural History Museum, London, England (Malcolm Kerley)
 CASC California Academy of Sciences, San Francisco, CA (Norm Penny)
 CDAE California State Collection of Arthropods, Sacramento, CA (Fred Andrews)
 CMNC Canadian Museum of Nature, Ottawa, Canada (François Génier)
 CNCI Canadian National Collection of Insects, Ottawa, Canada (Jean McNamara, Yves Bousquet, Anthony Davies)
 HNHM Hungarian Natural History Museum, Budapest, Hungary (Otto Merkl)
 INBC Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica (Angel Solís)
 MNHN Museum National d'Histoire Naturelle, Paris, France (Roger-Paul Dechambre, Jean Menier)
 SEMC Snow Entomological Museum, University of Kansas, Lawrence, KS (Steve Ashe, Rob Brooks)
 SMTD Staatliches Museum für Tierkunde, Dresden, Germany (Olaf Yaeger)
 UNSM University of Nebraska State Museum, Lincoln, NE
 USNM U.S. National Museum, Washington, D.C. (Robert D. Gordon, Gloria House, Nancy Adams)
 ZMHB Museum für Naturkunde, Berlin, Germany (Manfred Uhlig, Joachim Schulze, Hella Wendt)

Material was also studied from the following private collections:

AAAG Alan R. Gillogly Collection, College Station, TX
 ABTS Andrew B. T. Smith Collection, Lincoln, NE
 AJRC Alex Reifschneider Collection, Sierra Madre, CA

BCRC Brett C. Ratcliffe Collection, Lincoln, NE
 DCCC David C. Carlson Collection, Fair Oaks, CA
 DJCC Daniel J. Curoe, Palo Alto, CA
 EGRC Edward G. Riley Collection, College Station, TX
 HAHC Henry and Anne Howden Collection, Ottawa, Canada
 JEWJ James E. Wappes Collection, Bulverde, TX
 KJRC Keve J. Ribardo Collection, San Jose, CA
 MLJC Mary Liz Jameson Collection, Lincoln, NE
 PKLC Paul K. Lago Collection, University, MS
 RHTC Robert H. Turnbow Collection, Ft. Rucker, AL
 WBWC William B. Warner Collection, Chandler, AZ

My own numerous research/collecting expeditions between 1975 and 1995 were scheduled so as to sample during different seasons in the study area, although there was a clear preference for sampling during the onset of the rainy season in May and again in September. It is during these times when most adult dynastine activity occurs. In addition, many different habitats were surveyed in order to find as many species as possible, especially since some taxa are limited in their distribution by elevation or habitat type. The collecting methods that I used that are especially appropriate to dynastines are mercury vapor and ultraviolet light traps (Fig. 3), foliage gleaning (especially at night) (Fig. 4), excavating rotting logs and stumps (Fig. 5), and collecting in aroids. Flight intercept traps (Fig. 6) and rotting fruit traps (Fig. 7) were also used extensively, but these did not trap dynastines except on rare occasions.

Augmenting greatly the collecting and data-gathering were the parataxonomists (Fig. 8) in Costa Rica who operate under the guidance of INBio. The parataxonomists are local people in Costa Rica who receive training in insect collecting, identification, and biology, and they are constantly sampling the entomofauna in the areas in which they live.



Fig. 3. Light trapping at Pipeline Road, former Canal Zone, Panama, May 1995. From left: David Brzoska (tiger beetle specialist from Kansas), Brett Ratcliffe, and Mary Liz Jameson. Photo by Mark Moffett.



Fig. 5. Mary Liz Jameson excavating a rotten log at Hartmann's coffee finca, Chiriqui, Panama, July 1994. Photo by BCR.



Fig. 4. Foliage gleaning at Hartmann's coffee finca, Chiriqui, Panama, May 1977. From left: Dodge Engleman, Elizabeth Stockwell, Al Thurman. Photo by BCR.

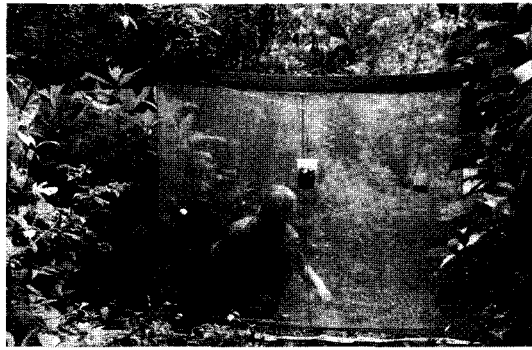


Fig. 6. Mary Liz Jameson tending a flight intercept trap at Rancho Naturalista near Tuis, Cartago, Costa Rica, May 1995. Photo by BCR.

The parataxonomists can sample from many areas throughout the year and over a several year span. This kind of coverage is simply not possible by a non-resident investigator. Even though the parataxonomists are not systematists, their contributions to our science are huge.

Collections-based research, both from institutional and private collections, completed the data for the survey. All the systematics collections in Costa Rica and Panama were examined, curated, and authoritatively identified. The principal collections in the United States and Canada containing Central American material were also studied.

Critical to the management of such a huge amount of information is electronic databasing. In Costa Rica, INBio (Fig. 9) captures label data using a system of bar codes placed on individual specimens that can be scanned for content. Each specimen has a unique bar code label in addition to the regular printed label. A large, electronic database was created for their collections, and these data are available on-line (www.inbio.ac.cr/bims/k02/p05/c029/o0122/f01094.htm). The



Fig. 7. Don Thomas with fruit-baited trap in Chiapas, Mexico, June 1991. Photo by BCR.



Fig. 8. Winnie Hallwachs (with soda can) and INBio parataxonomists at Parque Nacional Santa Rosa, Costa Rica, May 1995. Photo by M. L. Jameson.



Fig. 9. Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica, August 1995. Photo by BCR.

database for the Panamanian material is available at the University of Nebraska State Museum website (www-museum.unl.edu/research/entomology/database/dbpan.htm).

Conventional, artificial keys, both in English and Spanish, to all Dynastinae found in Costa Rica and Panama are presented. I have attempted to use characters that are consistently expressed, low in intrinsic variability, and easily observed with reasonable procedures. The keys and descriptions are accompanied by numerous illustrations to aid in correctly identifying specimens. Dot maps are provided that show distributions as exemplified by label data.

Each genus and species is introduced with its chronological, nomenclatural history. An abbreviated description for each species then follows. This consists of length and width measurements (from apex of clypeus to apex of elytra and across widest part of elytra), color (using transmitted light and not simply reflected light), and distinguishing characteristics of the head, pronotum, elytra, pygidium, legs, venter, and parameres. With regard to surface sculpturing, punctures are considered irregular in distribution and simple unless otherwise noted. Ocellate punctures are ringed with a slightly different color tone, and umbilicate punctures have a small, convex bump at the bottom of the puncture. Minute punctures are generally not seen with 10X magnification but are easily seen with 50X magnification. Small punctures are easily seen with 10X magnification and can be seen with the unaided eye. Large punctures are easily seen without instruments. Punctures are termed sparse if there are few of them or they are separated from one another by ten or more puncture diameters. Punctures that are moderate in density are separated from one another by about five puncture diameters, and dense punctures are separated by less than one to three puncture diameters.

For most species of Dynastinae, it is necessary to examine the form of the parameres of the male genitalia because, with rare exception, they are diagnostic. The parameres may be easily extracted from dried, pinned specimens in two ways. The first, which is more time-consuming and labor intensive, is to immerse the specimen in hot water for several minutes in order to soften it and then extract the parameres through the genital opening. Great care is needed when attempting this

because the parameres have also become softened and so may tear easily. This is especially true for species of *Stenocrates* and *Tomarus* whose parameres are fragile and parchment-like under any circumstances.

The second, and easier option in my opinion, is to gently “break” the “locked” position of the middle and hind legs so as to push them to the side and away from the sternites. Then, using a fine point forceps, insert the tip just behind the metacoxae at the extreme base of the first abdominal sternite and, while pushing down and toward the rear of the specimen, dislodge the entire abdomen. When this is done, simply remove the dried contents of the abdomen until you can grasp the parameres that are located just inside of the pygidium. With a small drop of water-soluble glue, put the abdomen back in place. Clean away the debris from the parameres and glue them on to an archival-quality mounting point that is placed beneath the specimen. Finally, gently push the middle and hind legs back into position.

An overall geographic distribution is then given followed by locality records (alphabetical by place names within each province), temporal distribution, a brief diagnosis, and remarks on biology, habitat preference, and elevational range. For temporal distribution, records are for the study area only and not range-wide. Species that also occur, for example, in South America may have significantly different times of adult activity due to seasonal displacement resulting from a different latitude or elevation.

This volume concludes with the 393 references cited in this work. By necessity, some technical terms referring primarily to body structure have been used. A brief glossary is provided in the back of this work for those unfamiliar with those words. Definitions used are primarily from Torre-Bueno (1937). Lastly, I have provided a checklist of all the species where you can even “check-off” those collected or observed for your “life list”; birders no longer have a monopoly on such lists.

The phylogenetic species concept as outlined by Wheeler and Platnick (2000) was

used in this work. This concept defines species as the smallest aggregation of populations diagnosable by a unique combination of character states. As Smith (2003) noted, each species description is, therefore, a scientific hypothesis. The number of specimens examined (given at the end of each description) is the number of replicates studied. Character states are used to support the hypothesis that all the individuals examined are of the same species. The different species can be recognized by a unique combination of character states because they are isolated genetically from other species. Different character states will become fixed in different species due to genetic isolation. The strength of the hypothesis (species description) increases with the number of replicates (specimens) examined. Not all species are equally diagnosable. Some are easily recognized by examining one individual with a unique set of characters (for example a male with radically different parameres), and some must be proposed only after many individuals from different populations are examined (when species have recently diverged or have not changed drastically since their divergence so fixed character states are difficult to recognize). These analyses must be done in the context of other closely related species. Examining intraspecific variation within closely related species is an important tool in distinguishing fixed character states from phenotypic traits that vary within a population or species. When traits are mistaken for fixed character states, the number of species can be overestimated.

Smith (2003) noted further that no species description (hypothesis) is accurate for all of the individuals in a species. There are sometimes anomalous individuals that have unusual traits or have been malformed during development. Size and coloration of some species may vary widely from year to year depending on the amount of rain, food availability, temperature, etc. Some populations also may exhibit phenotypic variation of certain traits at different levels from other populations as a result of, for example, composition of the substrate or different types of food plants.

THE STUDY AREA

Introduction

Although small countries, Costa Rica and Panama have some of the highest levels of biodiversity per area of any country in the world. Costa Rica and Panama have 12 different life zones (Fig. 10) ranging from tropical dry forest to subalpine rain páramo. These diverse habitats are home to hundreds of thousands of species. Their location on the isthmus between two large continents, combined with a tropical climate and mountainous terrain (Fig. 11), has contributed to this rich biodiversity. It has been suggested that Costa Rica has an estimated 5% of global species (Anonymous 1996)! Condit *et al.* (2002) documented patterns of beta diversity (using trees) in three different parts of the American tropics and demonstrated higher species turnover in Panama than in Amazonia, which correlated with the greater habitat diversity of the isthmus. Angehr (1989) compared Panama (87,000 square kilometers) with the state of Virginia in the United States (103,000 square kilometers) and found that smaller Panama had twice as many species of birds (900 versus 413), three times as many mammals (220 versus 75), three times as many reptiles and amphibians (376 versus 123), and four times as many flowering plants (10,000 versus 2,600). Ratcliffe (2002) recorded approximately 550 species of Scarabaeoidea found in just Panama whereas Jameson and Ratcliffe (2002b) calculated approximately 2,000 species in ALL of Canada, the United States and Nearctic Mexico.

With our fairly limited knowledge of most insects and their habitat associations, we should use some caution when attributing a certain species to a particular life zone. Some dynastines, for example species of *Dynastes*, *Golofa*, and *Cyclocephala* species, are found only at elevations above 1,500 meters in the study area whereas others (other *Cyclocephala* species) are broadly distributed from near sea level to 2,000 meters in elevation. Janzen (1983) pointed out that there are at least 220 species of breeding butterflies (excluding skippers, hairstreaks, and metalmarks) in Corcovado National Park (36,000

hectares) in Costa Rica. By contrast, Chirripo National Park (a larger 43,700 hectares) has only 30 species, and it is only 70 km north of Corcovado! The very nature of tropical habitats, often small and patchy, precludes gross generalizations regarding plant and animal distributions. Detailed studies, combined with extensive observations and collecting, are needed to accurately ascertain the distributions, both in space and time, of tropical organisms.

With the intense biodiversity survey activities conducted in Costa Rica during the past decade, most of the country is fairly well explored for scarab beetles, although not all places have been studied, particularly along the Atlantic lowlands in Limón province, some of the border areas with Nicaragua, the Nicoya peninsula, and the Osa peninsula. Consequently, we can expect new records and possible new species to be yet discovered. Much of Panama still remains to be entomologically sampled, especially the Azuero peninsula and most of San Blas and Darién provinces. It seems clear that in the Darién and eastern San Blas province there will be many taxa of South American affinities recorded as new for Panama. The absence of roads in the region, combined with the lawlessness engendered by the drug trade and rebel groups operating near the Colombian border, will make understanding the biota of extreme eastern Panama a challenge.

Paleobiogeography

The isthmus was not always so biotically diverse. Mesoamerica has been a land corridor for millions of years for the interchange of plants and animals between North and South America and has also been a nucleus for speciation and biotic diversification. Kimsey (1992) observed that the majority of insects in this region appear to have southern origins due to the similarity of habitats in the isthmus with those of nearby northern South America. The forest types of Panama differ little from those of Colombia (Golley *et al.* 1969). Pre-Miocene dispersal of the biota between North and South America probably occurred uncommonly. A small amount of biotic interchange agrees with the geologic evidence suggesting a relatively wide separation of the

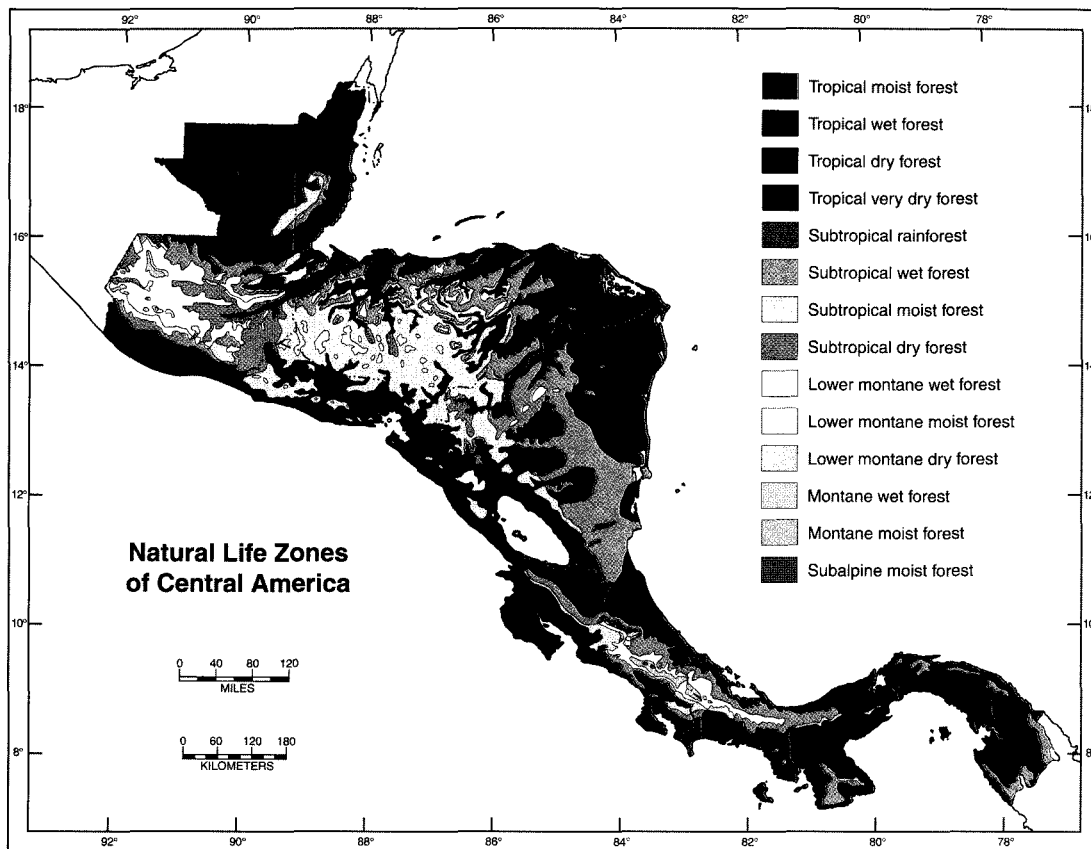


Fig. 10. Life zones of Central America. Modified from Campbell and Lamar (1989).

Americas in Cretaceous through Oligocene times (Raven and Axelrod 1974; Smith and Bredin 1977; Gose *et al.* 1980). Initial contact was probably through a filter route consisting of a peninsula and islands. Even after the formation of a continuous land connection, a filter bridge, rather than a corridor, was in operation due to probable unfavorable conditions along the route or at either end.

After Mesoamerica coalesced during the Pliocene 3.0 MYBP (Marshall 1988; Donnelly 1992; Iturralde-Vinent and MacPhee 1999) to 5.7 MYBP (Lloyd 1963; Kaneps 1979), an extensive faunal exchange began (Webb 1978; Stehli and Webb 1985a). Formation of the isthmian dispersal route permitted separate invasions of plants and animals at widely separated periods when climates and topographic features were different.

Webb (1978, 1985) provided an excellent analysis of the interamerican biotic exchange, appropriate parts of which are mentioned

here. The interval from 2.5–1.5 MYBP shows an extensive movement of savanna-adapted mammal faunas from south temperate to north temperate latitudes and vice versa. All of the animals that are known to have dispersed between the Americas in the late Tertiary were tolerant of, or specifically adapted to, savanna woodland habitats. The savanna elements were not incidental parts of the interchange but represent the vast majority of the taxa involved. Notable among them were horses, llamas, armadillos, and ground sloths. The extent of savanna adaptations among the land mammals of the interchange indicates the presence of a uniformly nonforested corridor or a moving mosaic of such habitats between South America and North America. The more arid conditions that must be postulated for the isthmian region during its early history probably supported seasonal forests grading into thorn scrub savannas. Similar habitats exist today in northern Venezuela

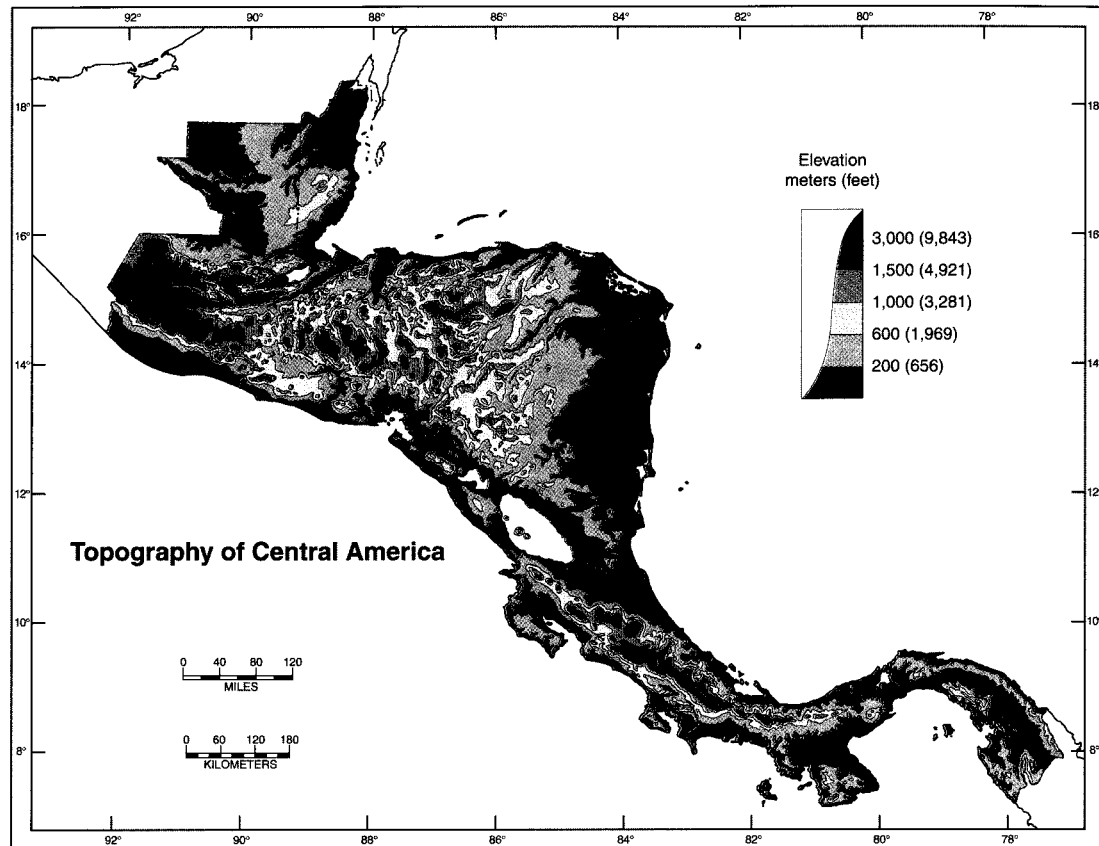


Fig. 11. Topography of Central America. Modified from Campbell and Lamar (1989).

and eastern Colombia and on the Pacific slopes of Central America from western Panama northward.

Less mesic conditions in the isthmian corridor were a result of a combination of factors having to do with climatic fluctuations associated with northern hemisphere glaciations, lowering of sea levels (with a concomitant increase in land area), regional uplift with large-scale volcanic extrusion, and creation of rainshadow regions. The data of Shackleton and Opdyke (1977) and Cronin (1981) indicate that glacial maxima at and following the emergence of the Panamanian land bridge, combined with the presence of a north-south corridor over the bridge, occurred only twice in the late Tertiary. These times (2.5 and 1.8 MYBP) represent "optimal ecological windows" that permitted dispersal of taxa living in savanna habitats between the Americas (Marshall 1985). The earliest known South American mammals to disperse to North

America across the Panamanian land bridge occur in rocks dated at 2.8–2.6 MYBP. This reciprocal event favoring savanna-adapted forms could not have occurred earlier due to absence of a suitable corridor, habitat, and climate. Subsequent opportunities did not exist until the next glacial maxima at about 2.0–1.9 MYBP (Marshall 1985).

The last glacial maximum permitting dispersal of savanna biotas over the land bridge occurred 12,000–1,000 year B.P. (Bradbury 1982; Markgraf and Bradbury 1982). A savanna corridor formed along the eastern side of the Andes connecting the now disjunct habitats in South America. The major obstacles to such dispersal were distance and potential competitive exclusion. According to Rich and Rich (1983), angiosperm floras of Central America today are most similar to those of South America, and sweepstakes dispersal from South America may have been more pronounced for plants than for animals.

Pleistocene cool periods in the tropics promoted dispersal of montane plant species such as gooseberries, currants, willows, and primroses. The dispersal of insects between the mid-continental regions of North and South America may have occurred in only a few thousand years with the availability of suitable habitat. The vertebrate fossil evidence clearly indicates that dispersal of savanna-adapted animals occurred twice in the late Tertiary. While it may be difficult for some biologists to accept so short a time scale for such evolutionary change, the paleontological record of the interamerican interchange demonstrates that two or three million years is sufficient time to produce fundamental evolutionary reorganization of a major biota (Webb 1978).

The late Pleistocene shift to more humid conditions in lower Central America produced a major set of savanna disjunctions spanning the isthmian gap (Webb 1978). The disjunct distribution across the American tropics shared by many present-day organisms provides additional evidence of a previous woodland savanna corridor. Within the temperate to subtropical *Areodina* (Scarabaeidae: Rutelinae: Rutelini), six genera are found ranging from the United States to Guatemala, and three genera are found in South America (Jameson 1990). None of these genera occur in the remainder of Central America, which, for the most part, has been historically covered by tropical rainforest. Similarly, Ratcliffe and Deloya (1992) found distributional disjunctions in species of *Hologymnetis* that now occur in southern South America and from northern Central America to the southwestern United States. This Central American gap might seem like a paradox until, noticing its occurrence in other groups, we recognize a pattern.

Not until the later part of the Pleistocene did the humid tropical rain forest become widespread in Central America, thus decreasing the effectiveness of the terrestrial connection between North and South America and leading to the distinctive modern biotic assemblages in Central America today (Bartlett and Barghoorn 1973; Rich and Rich 1983). By the late Pleistocene, as now, woodland savanna taxa were excluded from the isthmian

region due to the dissolution of savanna habitats and replacement by tropical rainforest. Late Pleistocene pollen samples from the bottom of what is now Lake Gatun in Panama reveal a forest flora much like that of present lowland Panama (Webb 1978). About 1,700 km of tropical wet forest extending from Costa Rica and Panama through northern Colombia now separates the nearest areas of savanna and thorn forest (Sarmiento 1976). These diverse forest types provided many new niches that were exploited by dynastines, which are more diverse in forests than in grasslands. Northern Central America retained a woodland savanna fauna as evidenced by the present biota, and the dynastine fauna in this region is not as rich as that of Costa Rica and Panama.

Costa Rica

Costa Rica covers an area of 51,000 km² and is the third smallest country in Mesoamerica. The country can be divided into three broad physiographic regions: the Caribbean plain, the central Cordillera, and the Pacific coastal ranges and valleys. The Caribbean coastal plain is nearly flat and generally below 100 meters in elevation. It is widest (130 km) in the north near the border with Nicaragua and narrows to a swampy plain about 7 km wide at Limón (Fig. 12).

The Cordillera Central is the mountainous backbone running the length of the country with a break at the Meseta Central. It is actually composed of a series of mountain ranges and intermontane valleys. The northern mountains are a chain of volcanoes extending south from Nicaragua: the Cordilleras Guanacaste, Tilarán, and Central. Volcan Arenal in the Cordillera de Tilarán is still active. Southeast of the Meseta Central is the Cordillera de Talamanca topped by Cerro Chirripó at 3,820 meters.

The Pacific coastal ranges and valleys include the peninsulas of Nicoya, Burica, and Osa. The western coastal plain is rolling in topography, and the Osa and Nicoya peninsulas each have central ranges of hills as high as 950 meters.

Although a tropical country, the climate of Costa Rica is varied because of its complex



Fig. 12. Provinces and topography of Costa Rica.

geography; consequently, there are many local climates. On the Pacific side of the country, the rainy season is the longest in the south (Osa Peninsula region), and it decreases in precipitation and duration as you progress northwest towards Guanacaste. In general, there is an abrupt increase in rainfall in May and June, a decline in July, and a second maximum of precipitation in September that is greater than the one in June. The dry season is generally from January through March (three months) in the southeast and extends from November through April (six months) in the northwest. On the Caribbean side, there is little or no dry season.

Although not “typical” for the entire country, the lowland site of La Selva Biological Station (Heredia province on the Caribbean side) (Fig. 13) is a tropical wet forest with an annual rainfall of approximately 4,000 mm and a dry season from January to May. Again not “typical,” but for contrast, Monteverde Cloud Forest Reserve (Puntarenas Province on the Pacific slope of the Cordillera de Tilarán) (Fig. 14) is a premontane rain forest with an annual precipitation of 2,500 mm and a dry season from mid-December to May.



Fig. 13. One of several lab buildings at La Selva Biological Station, Costa Rica. Photo by BCR.



Fig. 14. Monteverde Cloud Forest Reserve, Costa Rica, June 1986. Photo by BCR.



Fig. 15. Provinces and topography of Panama.

Panama

Panama covers an area of 87,176 km². The dominant landform features are the backbone of mountains forming the Cordillera Central (Fig. 15) and the transisthmian Panama Canal. The Cordillera Central consists largely of igneous rocks and includes a number of now extinct volcanoes. These mountains are highest in western Panama near the Costa Rican border where elevations of 3,000 meters are reached. Volcan Baru (Volcan Chiriqui) (Fig. 16) is the highest point in the country at 3,427 meters. The continental divide gradually drops in elevation as one proceeds eastward to within 50 km of Panama City where the low point of 100 meters is reached in the region of the Canal. Just to the west of the Canal, the Cordillera begins to increase in elevation to 780 meters and near the Colombian border to elevations of 1,570 meters (Fairchild 1966; Weil *et al.* 1972). In general, the continental divide is closer to the

Caribbean coast than to the Pacific with what few plains there are confined to the Pacific side. Most of Panama was covered with forest at the time of European discovery, although there were some drier areas along the Pacific coast that have long been grasslands (Fairchild 1966). Because of human disturbance, however, most forests on the Pacific coastal plain have been reduced to scrub on steep hillsides and narrow gallery forests along streams. On the Caribbean side, the foothills of the highlands approach the ocean except in Bocas del Toro near the Costa Rican border and in Colón west of the Canal where the slope is more gradual.

The climate of Panama has distinct wet and dry seasons as a result of latitude (Bennett 1968). The rainy season usually extends from May through mid-December although it can differ in duration and intensity locally and from year to year. The dry season is most pronounced to the west of Panama City and south of the Cordillera Central. The

driest area of Panama is on the western side of the Azuero peninsula (Holdridge and Budowski 1956). Like Costa Rica, the Caribbean side is moist to wet and has a less pronounced dry season, especially at higher elevations.

The second major feature of the country is the Panama Canal (Figs. 17-18), which is 50 miles long from the Atlantic to the Pacific. The principal physical features of the Canal are the terminal ports of Cristobal and Balboa, short sea-level sections at either end, the three sets of twin locks (Gatun, Pedro Miguel, and Miraflores) that raise and lower ships 30 meters, Gatun Lake, and Gaillard Cut. Gatun Lake, through which ships travel for 23 miles, is one of the largest artificial bodies of water in the world, and it stretches nearly all the way across the isthmus. Covering an area of 163 square miles, it was formed by an earthen dam across the Chagres River. Gatun Dam has an aggregate length of nearly two kilometers and is almost a kilometer wide at its base. At the time of its construction in 1912, and for some time thereafter, it was the largest earthen dam in the world. Gaillard Cut is the eight mile long excavation through the rock and shale of the continental divide, and it was here that the principal excavation of the canal was required. McCullough (1977) provided a complete and engaging historical account of the construction of the Panama Canal.

Vegetation

The life zones or biotic provinces of Central America (or the more limited study area) have been variously characterized, *e.g.*, Holdridge (1947), Ryan (1963) (based on mammal distribution), Goodland (1969), Sawyer and Lindsey (1971), Holdridge *et al.* (1971), and Hartshorn (1983). For Costa Rica, and Panama by extension, the Hartshorn (1983) characterizations using extensively Holdridge *et al.* (1971) forest types are most germane. A brief synopsis, using Goodland (1969), National Research Council (1982), and Hartshorn (1983), of each is given below since these life zone descriptors are used in the "Biology" section for each species treatment of



Fig. 16. Volcan Baru, Chiriqui, Panama (highest point in the country), July 1994. Photo by BCR.



Fig. 17. Gatun Locks, Panama Canal, May 1976. Photo by BCR.

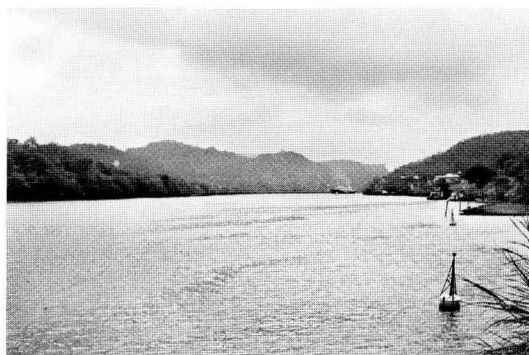


Fig. 18. Near Gaillard Cut, Panama Canal, May 1976. Photo by BCR.

dynastines. As Goodland (1969) noted, no site is ever typical, and there are always exceptions and special cases.

Tropical Dry Forest

This forest type usually occurs from sea level to about 500 meters in elevation and

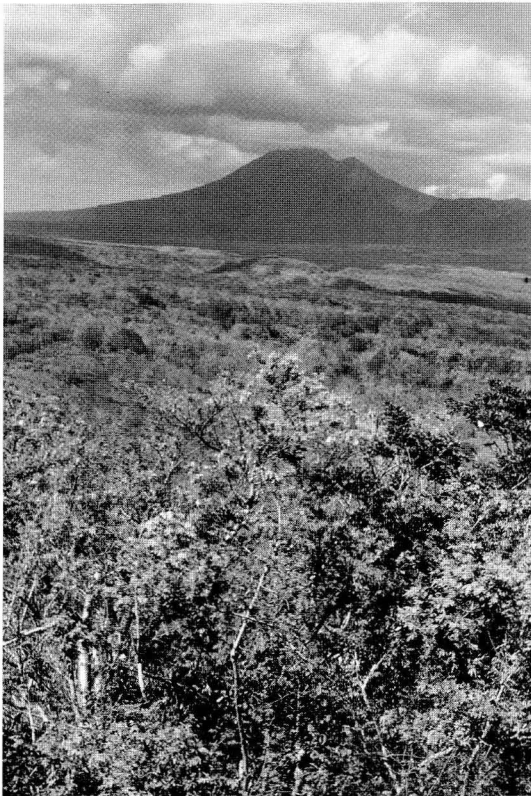


Fig. 19. Tropical dry forest in Guanacaste province, Costa Rica, May 1995. Photo by M. L. Jameson.

where the precipitation is 1,000-2,000 mm/year. Tropical Dry Forest (Fig. 19) is a low, semideciduous forest with only two strata of trees. Canopy trees are usually 20-30 meters tall, with short, stout trunks and large, spreading, flat-topped crowns, usually not in lateral contact with each other. Many canopy trees have thin, often compound leaves that are dry-season deciduous. Bipinnately leaved mimosoid and caesalpinoid leguminous trees are the most conspicuous canopy component. Flowers are conspicuous, and many are produced synchronously during the dry season when leaves are shed. Understory trees are 10-20 meters tall, with slender, crooked, or leaning trunks and small open crowns with more evergreen species than in the canopy. Rubiaceae is a prominent understory family. The shrub layer is 2-5 meters tall, dense in openings, often multiple-stemmed, and armed with thorns or spines. The ground layer is sparse except in openings. Woody vines are

common, but herbaceous vines are uncommon. Epiphytes are occasional, with bromeliads and orchids the most conspicuous. This is a widespread vegetation type prevalent in most of the Nicoya peninsula and lowland Guanacaste province in Costa Rica and on much of the Azuero peninsula facing the Gulf of Panama and the Atlantic coastal lowlands around David in Chiriqui province and Panama City.

Tropical Moist Forest

Tropical Moist Forest (Figs. 20-23) is the most extensive life zone in both Costa Rica and Panama. It occurs at elevations generally below 500 meters where rainfall is 2,000-4,000 mm/year with a short, mild dry season. It is a tall, multistratal, semideciduous, or evergreen forest. Canopy trees are 40-50 meters tall, mostly with wide crowns and tall, slender boles unbranched for 25-35 meters, mostly less than 100 cm dbh, often with high, thin buttresses and smooth, light-colored bark. Subcanopy trees are up to 30 meters tall, mostly with narrow crowns. Palms, especially *Scheelea rostrata* (Oerst.), are usually abundant except in cool transitional areas. Understory trees are mostly 8-20 meters tall, with round to conical crowns; leaves often have long drip tips. The shrub layer consists of dwarf palms and giant broad-leaved herbs. The ground layer is generally bare except for occasional ferns. Herbaceous vines and woody lianas are abundant as are epiphytes.

Tropical Wet Forest

Tropical Wet Forest (Fig. 24) occurs from sea level to about 1,000 meters in elevation where rainfall is rarely less than 50 mm in any one month and where the total is usually over 4,000 mm/year. This forest type is tall, multistratal, and evergreen. A few canopy species are briefly deciduous, but most canopy trees are evergreen. Canopy trees are 45-55 meters tall, with round to umbrella-shaped crowns and have clear boles to 30 meters and attain 100-200 cm dbh. Smooth, thin, light-colored bark and stilt-root and plank buttresses are common. Flowering and fruiting are not synchronized. Sub-canopy trees are 30-40 meters tall, with round crowns and



Fig. 20



Fig. 21

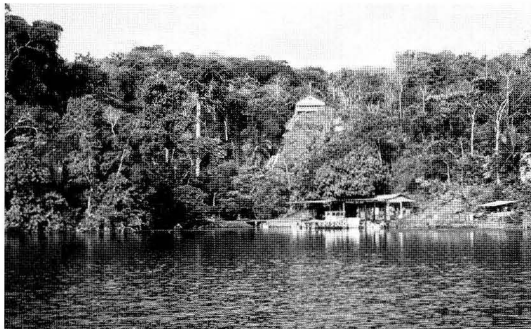


Fig. 22



Fig. 23

Figs. 20-23. Tropical moist forest: (20-21) Old Gamboa Road, June 1993; (22) Barro Colorado Island, May 1980; (23) Skunk Hollow, July 1975. All former Canal Zone, Panama. Photos by BCR.

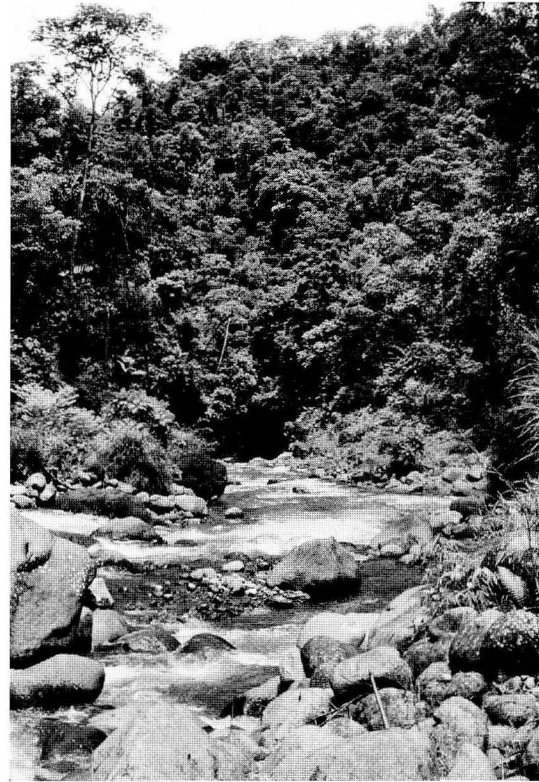


Fig. 24. Tropical wet forest at Bijuaga, Guanacaste, Province, Costa Rica, October 1990. Photo by BCR.

slender trunks and generally lacking buttresses. Understory trees are 10-25 meters tall, with narrow conical crowns and slender boles, often twisted or crooked, usually with smooth, dark bark, occasionally cauliflorous. Stilt-rooted palms are often abundant. The shrub layer is 1.5-2.5 meters tall with abundant dwarf palms; unbranched treelets and giant broad-leaved herbs are occasional. The ground layer is sparse, with a few ferns and *Selaginella*. Woody lianas are not common, and epiphytic shrubs and strangling trees are rare. Tropical Wet Forest is the most species-rich life zone in Costa Rica and Panama. McDade *et al.* (1994) provided a detailed and extensive overview of this forest type at La Selva Biological Station in Costa Rica.

Tropical Premontane Moist Forest

Tropical Premontane Moist Forest (Fig. 25) is a two-layered, semideciduous, seasonal forest of medium height. Canopy trees are



Fig. 25. Tropical premontane moist forest, Bocas del Toro Province, Panama, May 1986. Photo by BCR.

mostly dry-season deciduous, about 25 meters tall, with characteristically broad, flat, or umbrella-shaped crowns and relatively short, stout trunks, often with thick, fissured, or flaky bark. Compound leaves are very common. Understory trees are 10-20 meters tall, evergreen, with round to conical crowns and short, twisted, or crooked boles with smooth or moderately rough bark. The shrub layer is dense, 2-3 meters tall, of single- or multiple-stemmed woody plants, some armed with spines. The ground layer is sparse. Epiphytes are rare. Tough, supple, thin-stemmed woody vines are abundant. This forest type usually has 1,000-2,000 mm/year of rainfall with 2-4 months having less than 100 mm of precipitation.

Tropical Premontane Wet Forest

Tropical Premontane Wet Forest (Fig. 26) is medium to tall, semi-evergreen forest with two or three strata and with a few canopy species dry-season deciduous. This is one of the tallest forest types in the study area and occurs in a cool, humid climate where there is 2,000-4,000 mm of annual precipitation and with no more than two months with less than 100 mm of precipitation. Canopy trees are mostly 30-40 meters tall, with mostly round to spreading crowns and relatively short, clear boles. Buttresses are common but small. Bark is mostly brown or gray, moderately thick and flaky, or fissured. Leaves are often clustered at the twig ends. Understory trees are 10-20 meters tall with deep crowns and



Fig. 26. Tropical premontane wet forest at Monteverde, Puntarenas Province, Costa Rica, June 1986. Photo by BCR.

smooth, often dark bark. Stilt roots and long, strap-shaped leaves are common. Tree ferns are occasional, and palms and epiphytes are abundant. The shrub layer is 2-3 meters tall and often dense. The ground layer is generally bare except for ferns. Epiphytes are present but not conspicuous. Climbing herbaceous vines are abundant. Most trees are covered by a thick layer of moss.

Tropical Premontane Rain Forest

Tropical Premontane Rain Forest (Fig. 27) is an evergreen forest, intermediate in height, with two or three strata. Canopy trees are 30-40 meters tall, with round or umbrella-shaped crowns and straight branches. Buttresses are common but small. Bark is brown, black, or gray, moderately thick, mostly flaking or fissured. The subcanopy is very dense, with trees 15-25 meters tall, having slender trunks that are often unbranched for most of



Fig. 27. Tropical premontane rain forest at Monte-verde, Puntarenas Province, Costa Rica, June 1986. Photo by BCR.



Fig. 28. Tropical lower montane wet forest at Fortuna Reserve, Chiriqui Province, Panama, May 1976. Photo by BCR.

their length; crowns are narrow, round to conical and bark is thin, light- or dark-colored. Palms are common in well-drained situations. The understory is also dense and may be difficult to distinguish from the subcanopy stratum. Understory trees are 8-15 meters tall, often with leaning, crooked, or twisted trunks and relatively long crowns with horizontal branches; many trees have stilt roots. Tree ferns are common in the understory. The shrub layer is 2-3 meters tall and very dense. Dwarf palms are uncommon in the shrub layer. The ground layer consists of a nearly complete cover of ferns, *Selaginella* and broad-leaved herbs, often with bluish leaves. Epiphytes, woody vines, and herbaceous climbers are very abundant. Moss and epiphytes cover practically all surfaces. Tropical Premontane Rain Forest has more than 4,000 mm of annual precipitation, and there are no months with less than 100 mm of rainfall.

Tropical Lower Montane Moist Forest

This life zone occurs in only small areas in Costa Rica and Panama. Tropical Lower Montane Moist Forest is an open evergreen forest of intermediate height with two tree strata. Canopy trees are mostly *Quercus*, 30-35 meters tall, with heavy, gnarled branches and thick, twisted boles and thick, scaling, or rough bark. The understory is fairly open, with evergreen trees up to 20 meters in height, having slender trunks and round to conical crowns. The shrub layer is 2-5 meters

tall, fairly dense, with soft-wooded plants and often with large leaves. The ground layer is mostly open, with scattered broad-leaved herbs and grasses. Although a few epiphytic trees occur, epiphytic herbs and mosses are inconspicuous. This forest type has an annual rainfall of 1,000-2,000 mm and 2-4 months with less than 100 mm of precipitation.

Tropical Lower Montane Wet Forest

Tropical Lower Montane Wet Forest (Fig. 28) is an evergreen forest of intermediate height with two tree strata. Canopy trees are mostly 20-25 meters tall, but some *Quercus* are taller, with short, stout trunks dividing into numerous long, heavy, twisting, ascending branches, producing wide, umbrella-shaped, billowing crowns. Buttresses are uncommon. Bark is thick, mostly flaking or fissured. The understory is fairly open, with trees 5-10 meters tall that have spreading crowns. The shrub layer is relatively dense, 2-3 meters tall, and palms are uncommon. The ground layer is well-covered with ferns, *Begonia*, aroid vines, and a thick layer of moist, rotting leaves. Small orchids, bromeliads, and ferns are common epiphytes. A thin layer of moss grows on tree trunks. Herbaceous vines, especially Araceae, are common at and near ground level. Large, coiled lianas are occasional to common. Annual precipitation is 2,000-4,000 mm/year, and there are no more than two months with less than 100 mm of precipitation.

Tropical Lower Montane Rain Forest

Tropical Lower Montane Rain Forest (Fig. 29) is an evergreen forest of low to intermediate height, with two tree strata. Canopy trees are mostly 25-30 meters tall, but *Quercus* may reach 50 meters, having short, stout, often twisted trunks with rough, dark bark; small, leathery leaves are common. Branches are thick, sinuous, and relatively short. Crowns are relatively small and compact. Buttresses are uncommon. The understory stratum is often dense, with trees 10-20 meters tall. Trunks are slender, straight or sinuous, with small, brushlike crowns of twisted branches. Bark is smooth, thin, and mostly dark. Suckers are common at the base of the trunk. The shrub layer is very dense, 1.5-3.0 meters tall, often with flat sprays of small leaves. The ground layer is well-covered with ferns, sedges, delicate trailing herbs, and patches of moss. Epiphytes (orchids, bromeliads, gesneriads, and aroids) are common in the moss covering trunks and branches. Ericaceae and Melastomataceae are abundant shrubby epiphytes. Large-leaved vines are occasional, but large lianas are uncommon. Mean annual precipitation is 4,000 mm or greater, and there are no months with less than 100 mm of rainfall.

Tropical Montane Wet Forest

This life zone is restricted in Costa Rica to the summit and upper southwest slope of Volcán Irazú and in Panama to the summit of Volcan Baru where rainfall is 1,000-2,000 mm/year. Most of the vegetation near the Irazú crater was destroyed or severely damaged by the volcanic eruptions of 1963-65. Tropical Montane Wet Forest is an evergreen forest of intermediate height and two tree strata. The canopy is dominated by *Quercus* spp. Bamboos are abundant in the shrub layer.

Tropical Montane Rain Forest

This life zone occurs extensively in the high Talamancas and near the summits of Turrialba, Irazu, Poas, and Barba volcanoes in Costa Rica and in the high parts of the Cordillera Central in Chiriqui, Panama. Rainfall averages more than 2,000 mm/year, and there

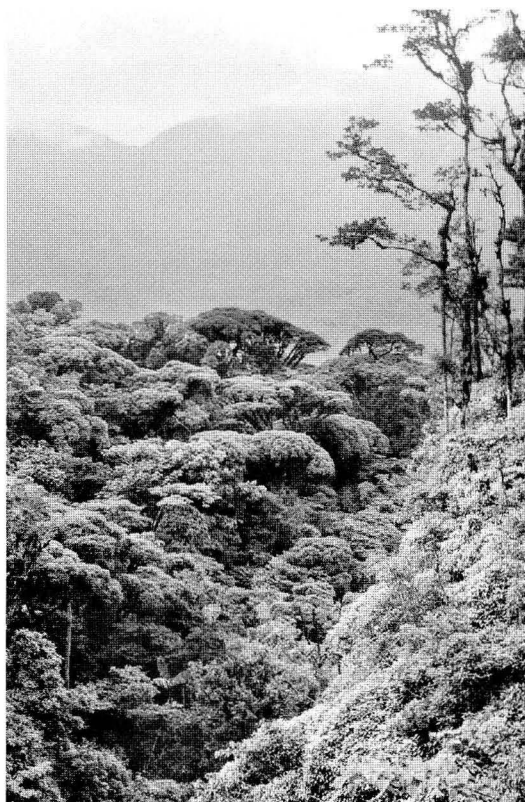


Fig. 29. Tropical lower montane rain forest at Fortuna Reserve, Chiriqui Province, Panama, May 1995. Photo by BCR.

are no months with less than 50 mm of precipitation. Tropical Montane Rain Forest is an evergreen forest of low to intermediate height with two tree strata. Canopy trees are 25-30 meters tall, having short, stout, unbuttressed trunks with rough bark. Crowns are small, compact, and rounded, with many thick, short, twisting branches. Leaves are small and leathery and are often clustered at the twig tip. The understory is fairly open, with trees mostly 5-15 meters tall, having slender, crooked trunks and compact, much-branched, brushlike crowns. Tree ferns are common in the understory. The shrub layer is dense, with dwarf bamboos up to 5 meters tall. The ground layer is open under the bamboo. Trunks and branches of trees are thickly covered with moss and small, herbaceous epiphytes; orchids and ferns are common in the moss. Large epiphytes are restricted to a few

species of bromeliads. Woody vines with thick, fleshy leaves are common as canopy epiphytes.

Tropical Subalpine Rain Páramo

This life zone is the northernmost occurrence of Andean Páramo, originally restricted to the highest peaks (Chirripó) of the Talamanca in Costa Rica, but now extending downward in the Cerro de la Muerte region owing to human disturbance. This zone does not occur in Panama. Páramo refers to a cold, inhospitable, and humid landscape above the tree line. In the northern Andes and in Costa Rica, páramo is dominated by shrubs where drainage is adequate, but bogs occur where drainage is poor. Andean páramos are best known for the tree espeletias (Asteraceae), which dominate the landscape. For the Dynastinae, only a single *Ancognatha* species and a single *Cyclocephala* species have been recorded from this life zone from near the summit of Cerro de la Muerte in Costa Rica.

Conservation

Mittermeier *et al.* (1999) reported that nearly half of the 127 million people in Mesoamerica live in rural areas where they depend directly on the natural resources surrounding them. This has contributed, in part, to some of the highest deforestation rates in the world, *i.e.*, 1.4% annually between 1980-1990. By 1990, approximately 4/5 of the region's original primary forests had been cleared or significantly modified. At current rates of deforestation, much of the last 20% of the region's remaining forests could be destroyed during the first decades of the 21st century, leaving only what remains in parks and reserves (assuming that even these can be adequately protected).

Costa Rica and Panama are small countries that have a great amount of physiographic diversity that contributes directly to the richness of their biota. But they are also countries of intense land development where pristine areas are succumbing to "development" (Keogh 1984; Sader and Joyce 1988). For example, Costa Rica's traditional economy of agriculture, livestock, textiles and

tourism has often grown at the expense of the environment. Costa Rica has been the site of some of the most rapid and extensive destruction of species-rich tropical forests in the hemisphere (Anonymous 1996). This natural resource degradation is principally a result of export-oriented agriculture (coffee, sugar, bananas), logging, mining, wildlife trade, and urban and industrial pollution. The same is true for Panama where the Pacific lowland forests of Los Santos, Veraguas, and Coclé provinces have been virtually extirpated along with many of the species of insects described in Godman and Salvin's (1879-1915) *Biologia Centrali-Americana* (Quintero 1992). Angehr (1989) observed that the watershed of the Panama Canal was more than 80% forested in 1952 whereas today that figure is only 20%. I have witnessed, over the past 25 years of collecting in Panama, the significant clearing of forests in Chiriqui province (Fig. 30), El Valle, Cerro Campana, and the highlands just to the east of Panama City (Fig. 31). Worldwide, tropical forests are being destroyed at a rate estimated at 20 to 40 hectares every minute, or 110,000 to 220,000 square kilometers every year (Angehr 1989).

Only a brief 200 years ago, tropical forests encircled the globe in a largely equatorial belt covering about 20% of Earth's land surface mostly in Latin America, Southeast Asia, Africa, Indonesia, and parts of Australia. Today, tropical forests (where about two-thirds of tropical species occur) cover only about 7% of Earth's surface (Myers 1984; Myers *et al.* 2000). Tropical forests are being destroyed so rapidly that a major portion of the diversity of life on Earth will disappear during the lifetimes of most of us who are living now (Raven 1983; Quintero 1992). "The destruction of tropical moist forests . . . will represent a biological debacle to surpass any other that has occurred since life's first emergence on the planet some 3.6 thousand million years ago. Not only will it mean the end of the greatest concentration of species on Earth, and of the most integrally diverse ecosystems on Earth, but also a basic shift in our planet's most dynamic evolutionary processes. On a planetary time-scale, it will all happen in a twinkling of a geologic eye" (Myers 1981).

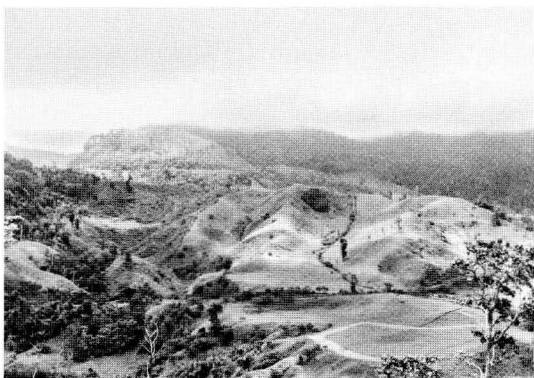


Fig. 30. Extensive deforestation in Chiriqui Province, Panama, May 1985. Photo by BCR.



Fig. 31. Slash and burn clear cutting on El Llano-Carti Road, Panama Province, Panama, May 1995. Photo by BCR.



Fig. 32. Nearly total deforestation just below continental divide, Chiriqui Province, Panama, June 1993. Photo by M. L. Jameson.

The greatest threats to our rich biodiversity are habitat loss and habitat degradation brought on by our own activities. These consist of commercial logging, urban sprawl, establishment of farms and especially ranches

(Fig. 32) in areas that cannot support them, pollution, and human-induced invasive species. Poor people without access to arable land cause about two-thirds of all destruction and alteration of tropical forests (Raven 1981) as they continually cut down new areas of forests for agriculture.

Such severe habitat degradation is driven by the needs and demands of a burgeoning human population both in the underdeveloped *and* developed nations. The human population has grown exponentially since the advent of agriculture 12,000 years ago. Just in the 25 years between 1950 and 1975, for example, the population of the six Central American republics more than doubled from 8.9 million to 18.5 million inhabitants (Fox and Huguét 1977). In view of the staggering numbers, the central question we have to ask ourselves is, "How do we maintain critical habitats and biodiversity during the next 50 years when the Earth's population is projected to reach 11 billion people?" And in the "developed" countries, where population growth is not so large, there is an insatiable demand for the raw products found in the forested regions of the tropics. This demand contributes directly to habitat destruction when these products are extracted.

Politicians and policy makers like to give benefits, not impose restraints; they are concerned with immediate gain, not long-term issues. Arguments on behalf of rainforest conservation, whether climatic stability, watershed protection, or the potential economic value of species, tend to be ignored in favor of development. It seems to me that human survival, even if promoted by self-interests, is good argument for saving rainforests. These forests are nature's greatest pharmacy and supermarket, the genes of which will provide us with new foods and drugs. We cannot predict which species, no matter how insignificant, will ultimately be essential to us. It is a sad reflection on current attitudes that conservationists must argue why something should be saved rather than that exploiters must explain why it should be destroyed.

Conservation is in crisis. Conventional approaches have not succeeded. With the human population ever increasing—now at the rate of 95 million a year—every social, economic, and environmental problem is accentuated. ‘Sustainable development,’ meaning the use of a resource without using it up, is often promoted as a solution that will satisfy both human needs and conservation. Development strives for economic growth, a way to satisfy consumers—not to protect biodiversity. You cannot increase the quality of life without degrading the environment. Market forces will not save species unless these are highly profitable. We desperately need plans *for* the environment, not just development to supply us with resources (Schaller 1997).

Costa Rica and Panama are models among Latin American nations in their conservation ethic and the amount of land set aside for national parks and biotic reserves. Costa Rica has about 24.1% of its territory in national parks, reserves, and protected areas, and Panama has about 16.8% (Mittermeier *et al.* 1999). Costa Rica may be the most conservation-minded nation in Central America at the levels of both the government and the people. Awareness of biodiversity, natural resources, and threats to the environment have been promoted by INBio, the Servicio de Parques Nacionales, Fundación de Parques Nacionales, Instituto Costarricense de Turismo, Organization for Tropical Studies (OTS), Monteverde Conservation League, Centro Científico Tropical, and the many ecotourism endeavors, among others. Panama also has made significant strides in the last 15 years in conserving its natural areas due to the efforts of organizations like the Panama Audubon Society, Asociación Nacional para la Conservación de la Naturaleza (ANCON), Autoridad Nacional de Ambiente (ANAM), and the Smithsonian Tropical Research Institute (STRI).

The efforts to inform and educate by all of these entities are at least slowing, if not actually reversing in some cases, the wholesale destruction of national treasures in Costa

Rica and Panama. As the Senegalese conservationist, Baba Dioum, said, “In the end, we will conserve only what we love, we will love only what we understand, and we will understand only what we are taught.”

The efficient and sane use of natural resources depends on accurate and detailed ecological knowledge. The major deterrent to these ecological studies, however, is the severe lack of taxonomic data that is the fundamental building block for all subsequent studies. In order to adequately conserve habitats and the plants and animals that live there, we must first identify, inventory, and then protect such areas. Ehrlich (1992) suggested that detailed studies of individual species will need to be replaced by methods that evaluate the conservation value of entire ecosystems. The pace of basic research in the tropics must be accelerated, and failure to do so will eventually limit our capability to contribute solutions to impending scientific and human problems. Ulfstrand (1992) called for the development of a research program of “space science magnitude” to document the patterns and processes characterizing biodiversity and to develop the tools for saving as much of the world’s biodiversity as possible. Whether any of these endeavors can be accomplished remains to be seen, but, clearly, our time for conserving our dwindling biotic riches of planet Earth is running out. A notably poignant quote from the World Wildlife Fund perhaps says it best: “All that lives beneath Earth’s fragile canopy is, in some elemental fashion, related. Is born, moves, feeds, reproduces, dies. Tiger and turtle dove; each tiny flower and homely frog; the running child, father to the man and, in ways as yet unknown, brother to the salamander. If mankind continues to allow whole species to perish, when does their peril also become ours?”

**Save Tropical Forests!
30 Million Insects
Can't All Be Wrong**

SUBFAMILY DYNASTINAE

The Dynastinae is one of the most conspicuous subfamilies of the beetle family Scarabaeidae. It occurs in all the major biogeographic areas of the world (except the polar regions), although most species are found in the tropics, specifically the New World tropics. Compare, for example, the 21 genera and 250 species in Africa with the 86 genera and 800 species in the New World (numbers from Endrödi 1985a). There are now about 1,500 species of dynastines, and Endrödi (1985a) predicted that the world fauna will reach 2,000 species. I concur with this estimate.

Adult dynastines are small (4 mm) to very large (160 mm) beetles. The males in some species (principally Dynastini, Agaocephalini, and Oryctini) possess prominent and often spectacular horns on the head and/or thorax which, together with their large size, has given rise to such popular names for them as "rhinoceros," "elephant," "hercules" (Fig. 34), and "unicorn" beetles. In fact, the entire subfamily is usually referred to as the rhinoceros beetles even though the majority of species do not possess horns.

Biology

The adults of nearly all species are nocturnal or crepuscular, and many are readily attracted to lights at night. Adult dynastines are known to feed on rotting fruits, slime flux, and plant roots (Ritcher 1958). The adults of some Cyclocephalini (*Eriosceles* and *Cyclocephala* species) are also now being recognized as important pollinators of palms and aroids (Fig. 35) when they feed on the floral parts of these plants (Beach 1984; Gottsberger 1989; Gottsberger and Amaral 1984; Gottsberger and Silberbauer-Gottsberger 1991; Young 1986).

Larval dynastines are primarily saprophagous or phytophagous and live in composting plant debris, beneath the surface of the ground, or in decaying logs and stumps where they are important in nutrient recycling. The life cycle and immature stages for most dynastine species remains unknown, and this will be a fertile field of research for future workers. Where the life cycle is known

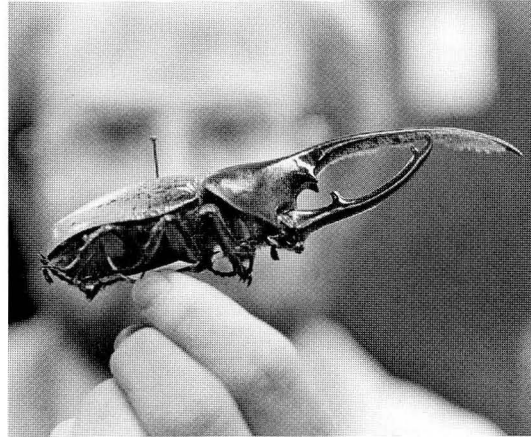


Fig. 34. *Dynastes hercules*. Photo by George Tuck (University of Nebraska).



Fig. 35. *Cyclocephala gravis* feeding on floral parts of *Philodendron radiatum* at La Selva Biological Station, Costa Rica. Photo by H. Young.

(Fig. 36), larvae take from several months to three years in the larger species to develop, and the adults normally live for several weeks.

Subfamily Characterization

The Dynastinae is characterized by the following combination of characters: mandibles often exposed in dorsal view; antenna with nine or ten segments, insertion not visible from above; scutellum visible; base of pronotum and elytra subequal in width; pygidium exposed; abdominal sternites not constricted at midline; procoxae transverse; claws of middle and posterior tarsi simple, not independently moveable; apex of posterior

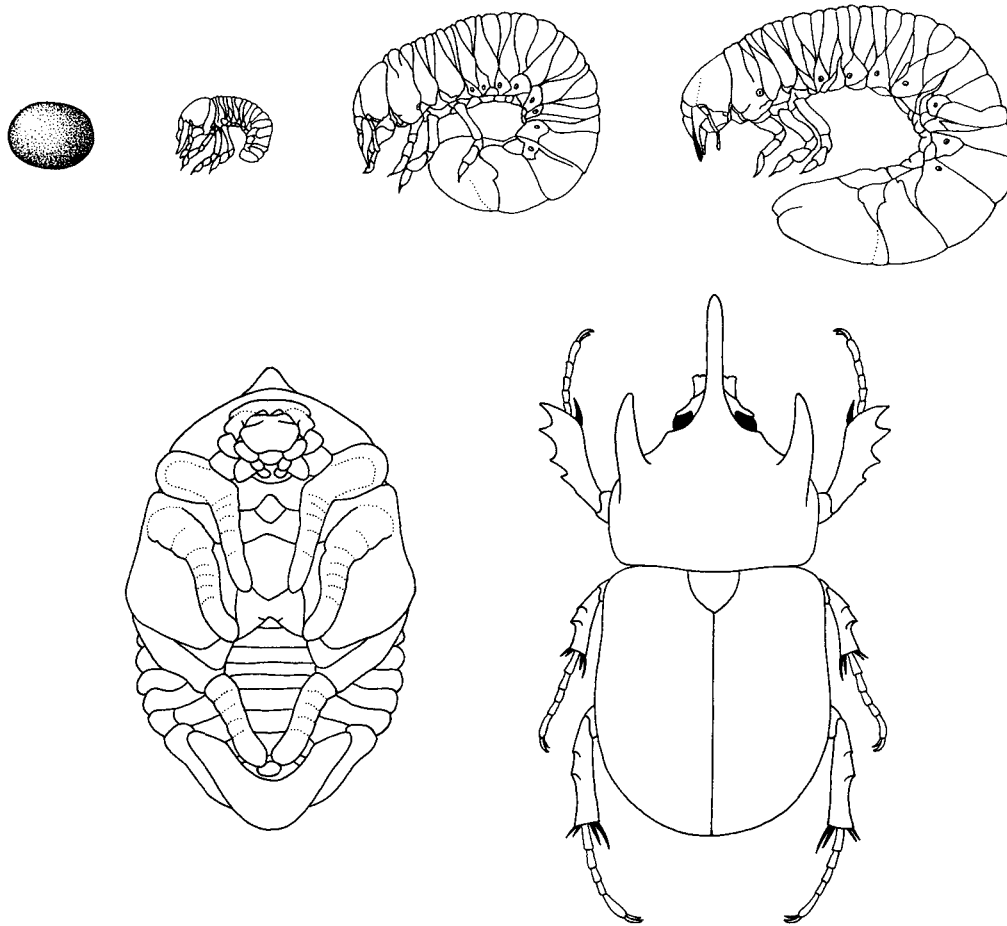


Fig. 36. Stages in the life cycle of *Strategus aloeus*: egg, three larval instars, pupa, adult.

tibia always with two spurs. Figure 37 illustrates the principal parts of dynastine body structure.

The sexes are usually distinctly dimorphic except for the Phileurini and some Cyclocephalini and Pentodontini. All species of dynastines can be easily sexed because males have the apex of the last sternite emarginate whereas in females it is rounded. When present, sexual dimorphism takes the form of the males having enlarged protarsi or enlarged tubercles or horns. The males of larger horned dynastines exhibit allometric growth of their horns (Arrow 1951; Endrödi 1985a; Kawano 1988, 1991, 1995a-b), and the horn size seems to reflect levels of larval nutrition.

Male dynastines with horns exhibit a wide array of horn shapes and sizes, and yet

they all seem to be used for the same purpose: male to male combat to secure resources used by the females (Eberhard 1978, 1979, 1980, 1982; Palmer 1978; Siva-Jothy 1987; Rasmussen 1994; Emlen 1997a). Emlen (2000) observed that males with enlarged weapons are able to gain disproportionate access to these contested sites that are discrete, readily dependable resource patches; consequently, they gain disproportionate access to females.

Emlen (1994, 1997b), Moczek (1998), and Moczek and Emlen (1999) have shown that horn production shows insignificant levels of heritable genetic variation despite the importance of horns to sexual selection and male reproductive success. Nutritional conditions experienced by male larvae determine adult body size and development of its horns. Males

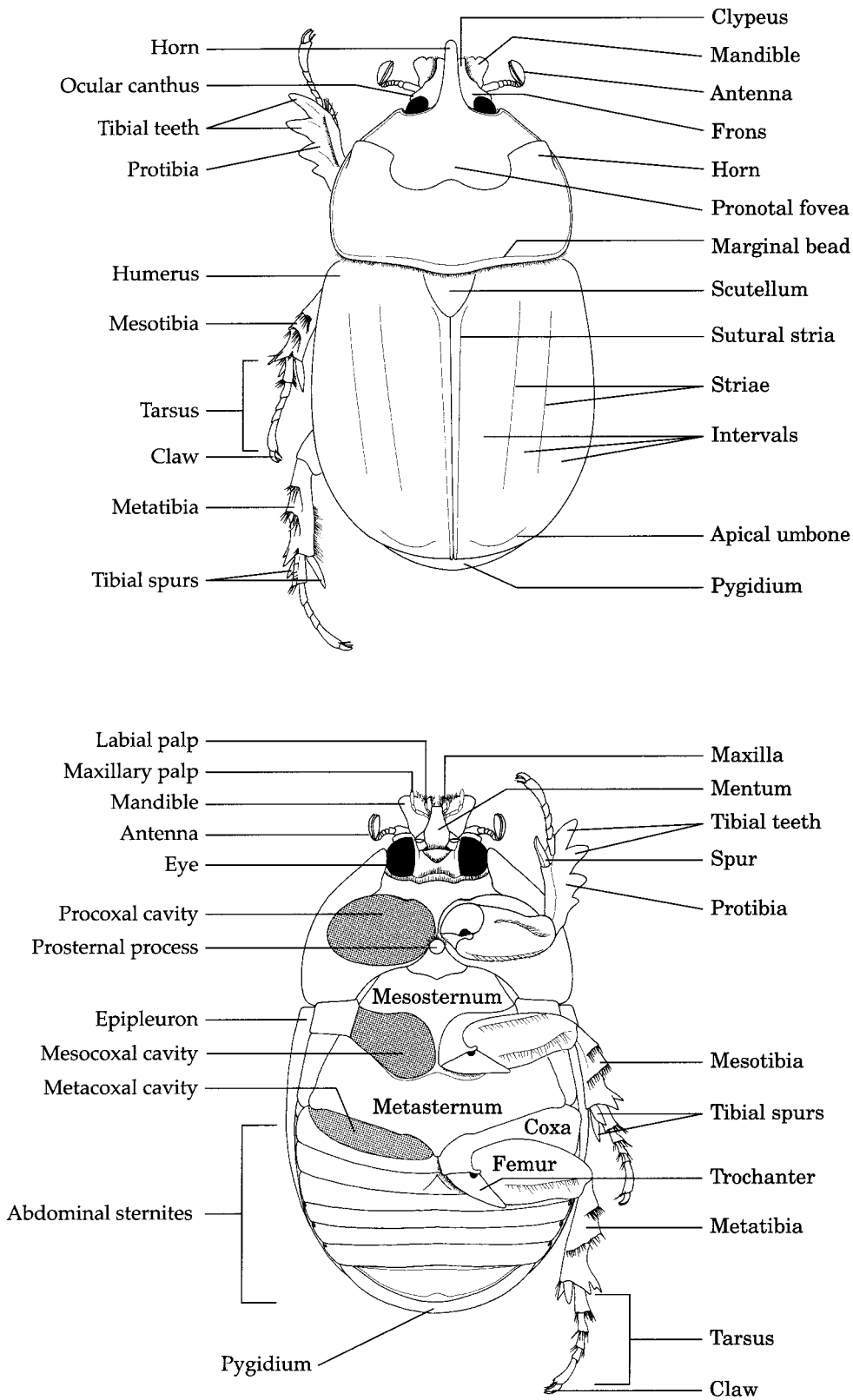


Fig. 37. Dorsal and ventral aspects of *Strategus aloeus* with principal terms of body structure.

that are well-fed as larvae grow large and produce large horns while males that had poor larval nutrition remain small and have small horns. Furthermore, Emlen (2001) demonstrated that the production of horns reduces the size of neighboring morphological structures (antennae, eyes, or wings, depending on the location of the horns), and so there is a cost to the individual beetle of having horns.

The form and function of horns in male scarabs has been a topic of debate and inquiry for a long time, and it is a fascinating topic. Only in the last 15 years or so are we now starting to see rigorous experiments designed to help answer the question of "why" when it comes to extravagant armature, and the body of literature devoted to beetle horns is growing.

Classification

The higher classification of the Dynastinae is reasonably well-established. The subfamily is divided into the following tribes: Hexodontini, Cyclocephalini, Pentodontini, Oryctini, Oryctoderini, Phileurini, Agaocephalini, and Dynastini.

The **Hexodontini** consists of a single genus, *Hexodon*, with nine species that occur in Madagascar.

The **Cyclocephalini** contains 14 genera that all occur in the New World except for one species of *Cyclocephala* introduced into Australia and the monotypic genus *Ruteloryctes*, which occurs in western Africa. There are approximately 450 species in the New World, and most of those occur in the tropics. This tribe has the largest number of species of Dynastinae in Costa Rica and Panama, with seven genera and 82 species; seven species are described as new in this work. The tribe Cyclocephalini may be paraphyletic, and a number of its included genera need further study to ascertain where they belong and if they are true clades or merely grades (*e.g.*, *Ancognatha*, *Aspidolea*, *Mimeoma*). In a preliminary cladistic analysis (unpublished) that I conducted on the genera of Cyclocephalini, I found support for most of the genera except *Erioscelis* and *Dyscinetus*, which had no synapomorphies. Additional characters are needed to help resolve this. There also re-

mains the question of the relationship between the Cyclocephalini and some Rutelinae (especially the Anomalini) because there are so many shared similarities between the two groups as well as significant differences.

The **Pentodontini** is the largest tribe of Dynastinae, with approximately 88 genera and 550 species occurring worldwide. There are 25 genera in the New World with a little more than 100 species. Six genera and 17 species occur in Costa Rica and Panama. The monophyletic basis for the tribes Pentodontini and Oryctini needs further analysis (for example, see Morón and Ratcliffe 1997). While there are some good characters for separating members of these two tribes, there are some genera that don't fit neatly into an "either/or" characterization for tribal placement in a taxonomic key.

The tribe **Oryctini** has 26 genera and over 230 species worldwide. In the Americas there are 14 genera and about 135 species, and 9 genera and 17 species occur in Costa Rica and Panama. One genus and one species are described as new here.

The **Oryctoderini** presently contains ten genera and about 25 species. Members of this tribe are found only in Oceania and Australia.

The **Phileurini** is comprised of 35 genera and about 215 species, and they occur in all biogeographic regions except the poles. There are 21 genera in the New World with about 120 species. Costa Rica and Panama have nine genera and 28 species; six species are described as new here. The Phileurini is clearly typified by the structure of the mentum (covering the bases of the palpi) and body form.

The **Agaocephalini** is restricted to the New World where there are 11 genera and 43 species. Costa Rica and Panama have two genera and six species. Monophyly in the Agaocephalini has not been adequately addressed, and further research is needed.

The **Dynastini** has 11 genera with about 70 species that occur worldwide. Most taxa occur in the New World where there are three genera and 47 species. All three genera occur in Costa Rica and Panama where there are nine species (two of which are described as new here). In a preliminary cladistic analysis

(unpublished) that I conducted on the genera of Dynastini, I found good support for all the world genera that was also congruent with biogeographical tracks reflecting Gondwanan break-up and subsequent dispersal. The fact that the Dynastini occurs in the Neotropics, Africa, and Asia implies great antiquity for the group. The minimum age for the tribe must be at least 100 million years old, which coincides with the breakup of Gondwana. The New World taxa are a result of initial vicariance of Gondwana with subsequent dispersal northward into Central and North America from South America.

At the generic level and above, there is an expected overall similarity in shared taxa and

diversity between most of the Central American countries although Costa Rica and Panama have a markedly higher percentage of genera than do the other countries. There are two primary factors contributing to this greater number of taxa: (1) Costa Rica and Panama have probably been more intensively collected, and (2) the montane topography of these countries is extensive. The cordilleras support species and their host plants that are not found in the lowlands and vice versa. The cordilleras are also often fragmented, and so some highland areas are isolated from others to varying degrees. This promotes isolation and speciation with the result being greater diversity.

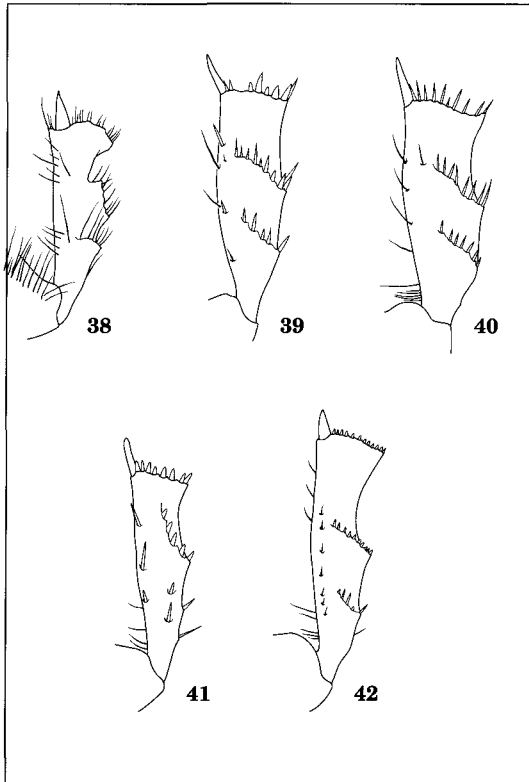
Key to the New World Tribes of Adult Dynastinae

1. Mentum strongly expanded, covering bases of labial palpi. Body usually flattened **Phileurini**
- 1'. Mentum narrow, not covering bases of labial palpi (Fig. 37). Body not flattened 2
2. Head and pronotum lacking tubercles, horns, carinae, or fovea. Claw with onychium bisetose. Male front claws in many species enlarged (larger than those in female). Tarsi cylindrical **Cyclocephalini**
- 2'. Head and/or pronotum (whether males or females) with distinct tubercles, horns, carinae, or fovea. Claw with onychium bisetose to multisetose. Male front claws enlarged or not. Tarsi cylindrical to triangular 3
3. Posterior tarsal segments (especially first or second) triangularly expanded. Combined length of foretibia and foretarsus similar in both sexes. Propygidium with or without stridulatory area 4
- 3'. Posterior tarsal segments usually cylindrical, not triangularly expanded (although basal segment with strong apical spine). Combined length of foretibia and foretarsus longer in males than in females (slightly less noticeable in Nearctic species). Propygidium usually without distinct stridulatory area. **Dynastini**
4. Elytra covered with dense tomentum (*Spodistes*, *Lycomedes*) or always irregularly punctate, not with distinct rows of punctures. Body slightly depressed **Agaocephalini**
- 4'. Elytra never with dense tomentum, punctures usually in distinct rows (except for some densely punctate *Heterogomphus* species) 5
5. Apex of posterior tibia usually truncate or smooth (Figs. 38-42). Sexual dimorphism usually not well-pronounced **Pentodontini**
- 5'. Apex of posterior tibia usually strongly crenulate or with distinct teeth (Figs. 43-47). Sexual dimorphism usually distinct **Oryctini**

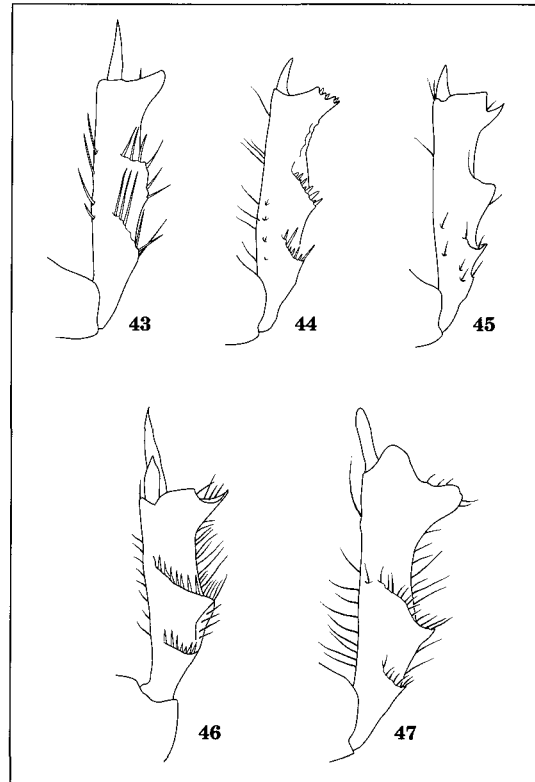
Clave para Adultos de las Tribus de Dynastinae del Nuevo Mundo

1. Mentón fuertemente expandido, cubriendo las bases de los palpos labiales. Cuerpo usualmente deprimido **Phileurini**
- 1'. Mentón angosto, sin cubrir las bases de los palpos labiales (Fig. 37). Cuerpo no deprimido 2

- 2. Cabeza y pronoto sin tubérculos, cuernos, o depresiones. Uña con uniuqiuo bisetoso. Machos con las uñas anteriores más desarrolladas en muchas especies (más que en las hembras). Tarsos cilíndricos **Cyclocephalini**
- 2'. Cabeza y/o pronoto (machos o hembras) con tubérculos, cuernos, carenas, o depresiones. Uña con uniuqiuo bisetoso a multisetoso. Macho con uñas anteriores más desarrolladas o no. Tarsos cilíndricos a triangulares 3
- 3. Segmentos tarsales posteriores (particularmente el primero y segundo) expandido en forma de triángulo. Longitud de la tibia y tarso anterior combinados similar en ambos sexos. Propigidio con o sin área estriduladora 4
- 3'. Segmentos tarsales posteriores usualmente cilíndricos, no expandido en forma de triángulo (pero segmento basal con fuerte espina apical). Longitud de la tibia y tarso anterior combinados más grande en los machos que las hembras. Propigidio generalmente sin área estriduladora. **Dynastini**
- 4. Elitros marcadamente tomentosos (*Spodistes*, *Lycomedes*) o siempre irregularmente punteados, sin hileras de puntos distinguibles. Cuerpo ligeramente deprimido **Agaocephalini**
- 4'. Elitros nunca marcadamente tomentosos, puntuaciones generalmente en hileras distinguibles (excepto por algunas especies de *Heterogomphus* densamente punteadas) 5
- 5. Apex de la tibia posterior usualmente truncado o liso (Figs. 38-42). Dimorfismo sexual usualmente no pronunciado **Pentodontini**
- 5'. Apex de la tibia posterior usualmente fuertemente crenulado o con dientes notorios (Figs. 43-47). Dimorfismo sexual usualmente distinguible **Oryctini**



Figs. 38-42. Posterior tibiae (ventral view) of Pentodontini: (38) *Bothynus quadridens*; (39) *Euethoola bidentata*; (40) *Tomarus bituberculatus*; (41) *Parapucaya amazonica*; (42) *Pucaya castanea*.



Figs. 43-47. Posterior tibiae (ventral view) of Oryctini: (43) *Enema pan*; (44) *Heterogomphus mniszcechi*; (45) *Podischnus agenor*; (46) *Strategus aloeus*; (47) *Xyloryctes splendidus*.



Color Plate 1. *Mimeoma englemanni* on the small flowers of a palm, *Bactris* sp. (Arecaceae [Palmae]).
Illustration by Dan Schmidt.

TRIBE CYCLOCEPHALINI

The members of this tribe occur throughout the Neotropical and most of the Nearctic realms, but most species are Neotropical. There is a single monotypic genus, *Ruteloryctes morio* (Fabr.), that occurs in western Africa from Guinea to Angola (Endrödi 1985a). There are currently 14 genera and about 450 species in the tribe. The genus *Coscinocephalus* Prell was removed from the Cyclocephalini and transferred to the Pentodontini by Morón and Ratcliffe (1997), and *Acrobolbia* Ohaus was transferred from the Rutelinae to the Cyclocephalini by Jameson *et al.* (2002). In Costa Rica and Panama there are seven genera and 82 species.

The tribe Cyclocephalini is poorly defined, and monophyly of the lineage has not been adequately addressed. I am convinced that further research is needed on especially the genera *Cyclocephala*, *Mimeoma*, *Aspidolea*, and *Ancognatha* to ascertain if they can stand as valid genera or some should be folded into others. For this study, therefore, I remain conservative and maintain the current classification until monophyly and paraphyly can be investigated and established.

In general, members of the Cyclocephalini have been characterized by the absence of horns, tubercles, carinae, or foveae; no stridulatory area on the propygidium; simple mandibles that lack teeth; metatibial apex truncate and without teeth; and metatarsus with basal joint simple and not triangular. Sexual dimorphism is not pronounced although in those genera where the males have enlarged protarsi it is easy to distinguish the sexes. Moreover, as in all dynastines, the apex of the last abdominal sternite is emarginate in males and entire or rounded in females (Figs. 48-49).

The larvae have been described for only a very few species, and most of those were Nearctic. It is not yet possible to characterize larvae at the tribal level.

Adult cyclocephalines are all nocturnal. Most are attracted to lights at night. An increasing number of species are now being recognized as important pollinators of aroids and palms when the adults enter the flowers to feed. Adults of some species also feed on the flowers of water lilies and guava trees. Larvae and their life history remain poorly known, but most probably live in the soil feeding on plant roots.

Key to the Genera of Adult Cyclocephalini of Costa Rica and Panama

Males: Apex of last abdominal sternite emarginate (Fig. 48). Protarsomeres 4-5 and/or anterior claw enlarged in all genera except *Stenocrates* Burmeister, one species of *Dyscinetus* Harold, and *Erioscelis* Burmeister.

Females: Apex of last abdominal sternite entire, evenly parabolic (Fig. 49). Protarsomeres 4-5 and anterior claw always simple, not enlarged.

-
- | | | |
|--------|--|----------------------------|
| 1. | Clypeus with apex distinctly pointed or narrowly parabolic (Figs. 50-52) | 2 |
| 1'. | Clypeus with apex rounded (Fig. 53), truncate (Fig. 54), or emarginate (Fig. 55) but not distinctly pointed or narrowly parabolic | 3 |
| 2(1). | Clypeus with apex sharply acuminate (Fig. 50). Mentum with apex distinctly (but never deeply) emarginate, surface at center not furrowed in apical third (Fig. 56). Base of pronotum with marginal bead. Length less than 16 mm | <i>Mimeoma</i> Casey |
| 2'. | Clypeus with apex narrowly parabolic (Figs. 51-52). Mentum with apex distinctly (often deeply) emarginate, surface at center furrowed in apical third (Fig. 57). Base of pronotum without marginal bead. Length usually more than 18 mm, rarely as small as 15 mm. | <i>Ancognatha</i> Erichson |
| 3(1'). | Clypeus transversely subtrapezoidal to trapezoidal in shape (Figs. 58-59) | 4 |
| 3'. | Clypeus with apex rounded, truncate, subquadrate or emarginate (Figs. 53-55) | 5 |

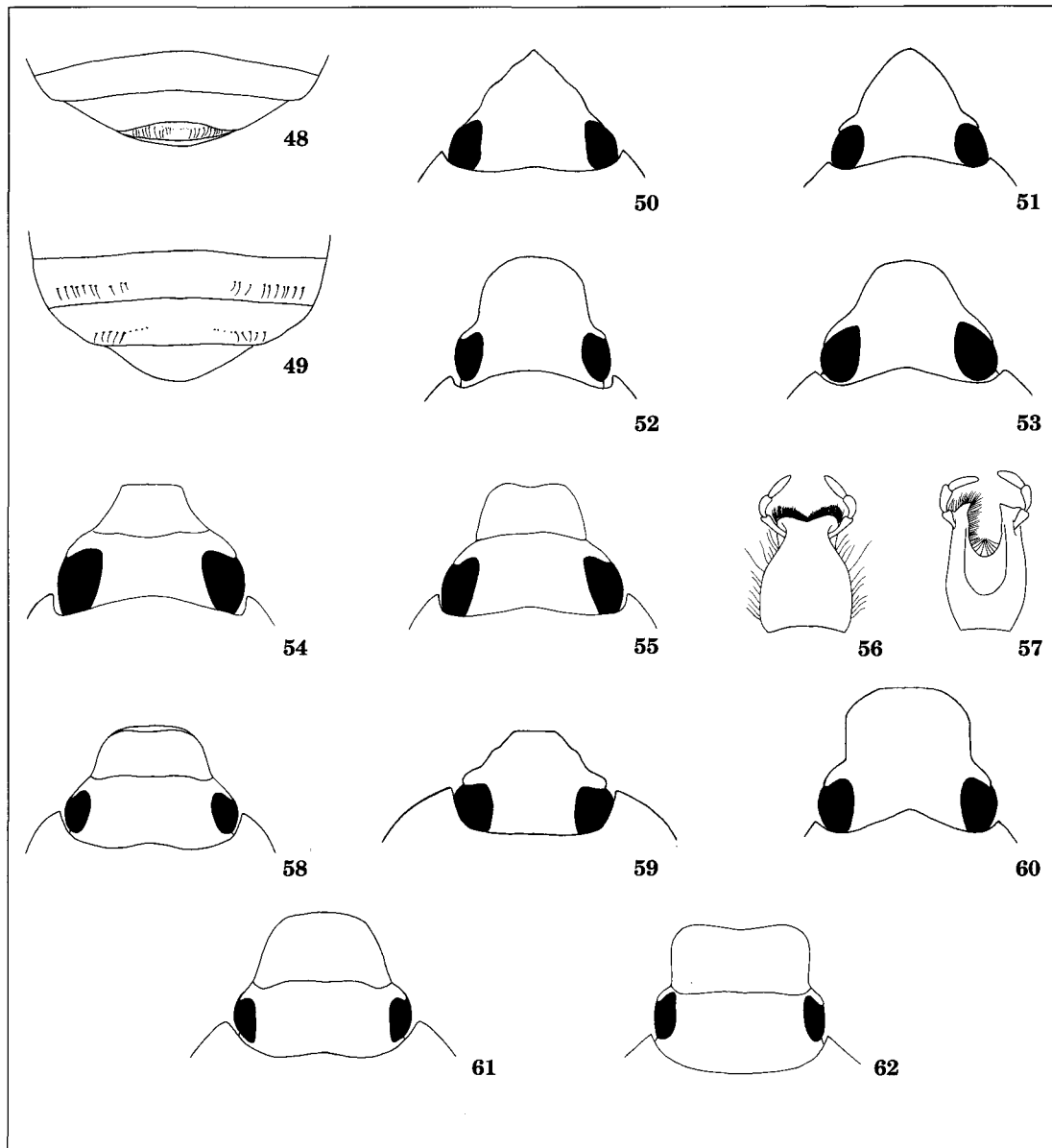
- 4(3). Clypeus trapezoidal, sides strongly convergent to truncate or feebly emarginate apex, anterior corners angulate (Fig. 59). Frontoclypeal suture distinct, usually broadly depressed just before suture. Pronotum with anterior margin normally arcuate, not produced forward at middle (Fig. 59). Middle and posterior femora and tibiae strongly flattened. Males with protarsomeres simple, not enlarged **Stenocrates Burmeister**
- 4'. Clypeus subtrapezoidal to trapezoidal, sides only gradually convergent to truncate or weakly emarginate apex, anterior corners rounded (Fig. 58). Frontoclypeal suture a finely impressed line but not with deep and broad impression before it. Pronotum on anterior margin produced anteriorly at middle (Fig. 58). Middle and posterior femora and tibiae not strongly flattened. Males with anterior claw and usually protarsomeres 4-5 enlarged **Dyscinetus Harold**
- 5(3'). Clypeus with sides usually divergent (sometimes only slightly) from base to apex, apex broadly rounded (Fig. 60). Maxilla lacking teeth (except for the distinctive *Aspidolea fuliginea* Burmeister), apex penicillate (setae usually long and dense) **Aspidolea Bates**
- 5'. Clypeus with sides parallel or convergent from base to apex (never divergent), apex rounded, subtruncate, or emarginate. Maxilla armed with distinct teeth, only rarely penicillate also (a few species of *Cyclocephala*) 6
- 6(5'). Clypeus subquadrate, sides weakly converging to broad apex, apex truncate or emarginate (Figs. 61-62). Males with protarsus simple, not enlarged **Erioscelis Burmeister**
- 6'. Clypeus not subquadrate, instead with sides converging from base to rounded, parabolic, or emarginate apex (Figs. 53-55). Males with protarsus enlarged **Cyclocephala Dejean**

Clave para los Géneros de Cyclocephalini Adultos de Costa Rica y Panama

Machos: Apice del último esternito abdominal emarginado (Fig. 48). Protarsómeros 4 a 5 y/o uña anterior agrandada en todos los géneros excepto *Stenocrates* Burmeister, una especie de *Dyscinetus* Harold, y *Erioscelis* Burmeister.

Hembras: Apice del último esternito abdominal entero, parejamente parabólico (Fig. 49). Protarsómeros 4 a 5 y uña anterior siempre simple, no agrandada.

1. Clípeo con el ápice claramente puntiagudo o estrechamente parabólico (Figs. 50-52) 2
- 1'. Clípeo con el ápice redondeado (Fig. 53), truncado (Fig. 54), o emarginado (Fig. 55) pero no claramente puntiagudo o estrechamente parabólico 3
- 2(1). Clípeo con el ápice agudamente acuminado (Fig. 56). Mentón con el ápice claramente (pero nunca profundamente) emarginado, superficie en el centro sin surco en el tercio apical (Fig.). Base del pronoto con reborde marginal. Longitud de menos de 16 mm **Mimeoma Casey**
- 2'. Clípeo con el ápice estrechamente parabólico (Figs. 51-52). Mentón con el ápice claramente (con frecuencia profundamente) emarginado, superficie en el centro con un surco en el tercio apical (Fig. 57). Base del pronoto sin reborde marginal. Longitud generalmente de más de 18 mm, raramente tan pequeños como 15 mm **Ancognatha Erichson**
- 3(1'). Clípeo transversalmente casi trapezoidal a trapezoidal en forma (Figs. 58-59) 4
- 3'. Clípeo con el ápice redondeado, truncado, casi cuadrado o emarginado (Figs. 53-55) 5



Figs. 48-49. Last sternite in Dynastinae: (48) male with apex emarginate; (49) female with apex entire.

Figs. 50-52. Pointed or parabolic clypeal apex of (50) *Mimeoma* sp.; (51-52) *Ancognatha* sp.

Figs. 53-55. Rounded (53), truncate (54), or emarginate (55) clypeal apex of *Cyclocephala* spp.

Figs. 56-57. Mentum of (56) *Mimeoma* sp. and (57) *Ancognatha vulgaris*.

Figs. 58-59. Subtrapezoidal or trapezoidal clypeal apex of (58) *Dyscinetus* sp. and (59) *Stenocrates* sp.

Fig. 60. Broadly rounded clypeal apex of *Aspidolea* sp.

Figs. 61-62. Subquadrate to quadrate clypeal apex of *Erioscelis* spp.

- 4(3). Clípeo trapezoidal, lados fuertemente convergentes a truncados o ápice ligeramente emarginado, esquinas anteriores anguladas (Fig. 59). Sutura frontoclipeal evidente, generalmente ampliamente deprimida inmediatamente antes de la sutura. Pronoto con el margen anterior normalmente arqueado, no sobresaliente hacia adelante en el medio (Fig. 59). Fémures y tibias medios y posteriores fuertemente aplanados. Machos con protarsómeros simples, no agrandados **Stenocrates Burmeister**
- 4'. Clípeo casi trapezoidal a trapezoidal, lados solo gradualmente convergentes a truncados o con ápice ligeramente emarginado, esquinas anteriores redondeadas (Fig. 58). Sutura frontoclipeal es una línea finamente impresa pero sin una impresión profunda y amplia antes de esta. Pronoto en el margen anterior saliente anteriormente en el medio (Fig. 58). Fémures y tibias medios y posteriores no fuertemente aplanados. Machos con la uña anterior y generalmente protarsómeros 4 a 5 agrandados **Dyscinetus Harold**
- 5(3'). Clípeo con los lados generalmente divergentes (algunas veces solo ligeramente) desde la base al ápice, ápice ampliamente redondeado (Fig. 60). Maxila sin dientes (excepto por *Aspidolea fuliginea* Burmeister), ápice penicilado (setas generalmente largas y densas) **Aspidolea Bates**
- 5'. Clípeo con lados paralelos o convergentes desde la base al ápice (nunca divergentes), ápice redondeado, truncate, o emarginado. Maxila armada con dientes evidentes, solo raramente penicilada (unas cuantas especies de *Cyclocephala*) 6
- 6(5'). Clípeo casi cuadrado, lados ligeramente convergentes hacia un ápice ancho, ápice truncado o emarginado (Figs. 61-62). Machos con protarsos simples, no agrandados **Erioscelis Burmeister**
- 6'. Clípeo no cuadrado, en vez de esto con los lados convergiendo desde la base hacia el ápice redondeado, parabólico o emarginado (Figs. 53-55). Machos con protarsos agrandados. **Cyclocephala Dejean**

***Ancognatha* Erichson, 1847**

Ancognatha Erichson 1847: 97.

Barotheus Bates 1891: 30 (synonym).

Pseudancognatha Otoyá 1945: 275 (synonym, described as subgenus).

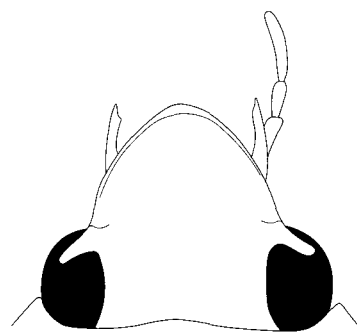
Ancognatha is comprised of 18 species that are found from Arizona and New Mexico in the United States south to Ecuador, Peru, and Bolivia (Endrödi 1966, 1985a; Ratcliffe 1992a). Seven species are found in Mesoamerica, and five species occur in Costa Rica and Panama. *Ancognatha ustulata* Burmeister (and *A. ustulata ustulatoides* Höhne) is known from Colombia, Venezuela, and Ecuador, and Endrödi (1966) recorded a single, no-data specimen from Chiriqui in Panama. I believe that record is probably erroneous and have discounted it because this species has not been encountered in any collecting or collections from the study area.

The elongate, generally acuminate form of the clypeus (Fig. 51) has been used to distinguish *Ancognatha* from other genera of Cyclocephalini. Species of *Mimeoma* also have an acuminate clypeus (Fig. 50), but they do not have the deeply incised or distinctly emarginate mentum seen in *Ancognatha* species (Fig. 57). The clypeal apex in some species of *Ancognatha* is parabolic or rounded (Fig. 52), and they share this character state with many species of *Cyclocephala*. Again, however, the form of the mentum in *Ancognatha* species (and their generally larger size) will separate them from *Cyclocephala* species. Bates (1888) noted that in *Ancognatha* species the labrum is detached and inclined from the roof of the mouth instead of being hidden as in *Cyclocephala*. The narrow, upwardly pointed mandibles (Fig. 63) are also characteristic of most species of *Ancognatha*. The frontoclypeal suture is obsolete medially in *Ancognatha* species whereas it is more or less complete in

Cyclocephala and *Aspidolea* species. The protarsus in the males is always enlarged.

The larval stage has been described for only one species in the genus, *A. manca* LeConte, from the southwestern U.S. and northern Mexico. The immature stages for the species occurring in Costa Rica and Panama are unknown. Adults are attracted to lights at night, but little else is known of their life history. Most species occur only in highland areas.

Endrödi (1966, 1985a) provided the last comprehensive review of *Ancognatha* species.



63

Fig. 63. Head of *Ancognatha* sp. showing narrow mandibles.

Key to the Species of Adult *Ancognatha* of Costa Rica and Panama

1. Dorsal surface black 2
- 1'. Dorsal surface yellow with black markings 3
2. Clypeus broadly elliptical in male, semi-circular in female (Fig. 52). Frontoclypeal region with transverse ridge interrupted at middle giving impression of 2 closely adjacent tubercles. Pygidium setose **atacazo Kirsch**
- 2'. Clypeus subtriangular with sides rounded and apex narrowly rounded in both sexes (Fig. 51). Frontoclypeal region with 2 widely separated tubercles. Pygidium glabrous **scarabaeoides Erichson**
3. Mentum deeply incised (for at least half of its length) 4
- 3'. Mentum emarginate or incised at apex but never deeply so **gracilis Endrödi**
4. Males with parameres as in Figs. 92-93. Females with posterior margin of flange on lateral edge of elytra strongly or abruptly arcuate (Fig. 91) **vulgaris Arrow**
- 4'. Males with parameres as in Figs. 83-84. Females with posterior margin of flange on lateral edge of elytra evenly arcuate (Fig. 82) **vexans Ratcliffe**

Clave para los Adultos de las Especies de *Ancognatha* de Costa Rica y Panamá

1. Superficie dorsal negra 2
- 1'. Superficie dorsal amarilla con manchas negras 3
2. Clípeo ampliamente elíptico en el macho, semicircular en la hembra (Fig. 52). Región frontoclipeal con un pliegue transversal interrumpido a la mitad dando la impresión de 2 tubérculos muy cercanos entre si. Pigidio setoso **atacazo Kirsch**
- 2'. Clípeo casi triangular con los lados redondeados y el ápice estrechamente redondeado en ambos sexos (Fig. 51). Región frontoclipeal con dos tubérculos ampliamente separados. Pigidio glabro **scarabaeoides Erichson**
3. Mentón con una incisión profunda (por al menos la mitad de su longitud) . . . 4
- 3'. Mentón emarginado o con una incisión en el ápice pero nunca profunda **gracilis Endrödi**
4. Machos con parámetros como en las Figs. 92-93. Hembras con el margen posterior de la expansión del borde lateral de los élitros fuerte o abruptamente arqueado (Fig. 91) **vulgaris Arrow**
- 4'. Machos con parámetros como en las Figs. 83-84. Hembras con el margen posterior de la expansión del borde lateral de los élitros arqueado en forma pareja (Fig. 82) **vexans Ratcliffe**

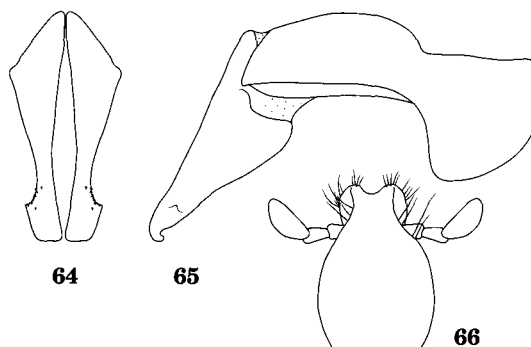
***Ancognatha atacazo* Kirsch, 1985**
(Figs. 64-67)

Ancognatha atacazo Kirsch 1985: 223.

DESCRIPTION. Length 20.0-24.5 mm; width 10.6-12.6 mm. Color black, occasional specimen with reddish yellow at base and on sides of elytra. **Head:** Frons and clypeus minutely shagreened with small punctures, punctures moderately dense. Frontoclypeal line elevated into low carina, carina interrupted at middle (giving impression of 2 adjacent low tubercles); frons immediately behind carina with shallow, semi-oval depression. Clypeus broadly elliptical in males, nearly semi-circularly rounded in females; apex narrowly and weakly reflexed. Interocular width equals 2.8-3.0 transverse eye diameters. Antenna with 10 segments, club a little longer than segments 2-7. Mentum with apex distinctly, but not deeply, emarginated (Fig. 66). **Pronotum:** Surface similar to that of frons. Base margined only near posterior angles. **Elytra:** Surface minutely shagreened, moderately densely punctate, punctures minute; 1-3 impressed striae barely evident. Epipleuron (ventral view) in female slightly expanded at juncture of first and second sternite. **Pygidium:** Surface shagreened, with small, moderately dense punctures and short setae; setae tawny, reduced in central third. In lateral view, males with surface evenly rounded, females with surface nearly flat. **Legs:** Foretibia tridentate, teeth subequally spaced. Foretarsus in male enlarged, large median claw deeply cleft at apex; foretarsus and claw simple in female. **Venter:** Prosternal process long, stout, apex nearly circular with raised "button" in center and transverse groove in posterior fourth. **Parameres:** Figs. 64-65.

DISTRIBUTION. *Ancognatha atacazo* was previously known only from Ecuador (Endrödi 1966, 1985a). The Costa Rican specimens listed below constitute a NEW COUNTRY RECORD. This species is evidently very rare in Costa Rica and unknown in Panama.

LOCALITY RECORDS (Fig. 67). 3 specimens examined.



Figs. 64-66. *Ancognatha atacazo*: (64-66) parameres; (66) mentum.



Fig. 67. Distribution of *A. atacazo* in Costa Rica.

COSTA RICA (3). **CARTAGO** (2): Río Grande de Orosi; **SAN JOSÉ** (1): Volcán Poas.

TEMPORAL DISTRIBUTION. March (1), July (2).

DIAGNOSIS. *Ancognatha atacazo* can be distinguished from *A. scarabaeoides*, the only other black species of *Ancognatha* in the study area, by its broadly rounded clypeus, frontoclypeal ridge interrupted in the middle giving the impression of two adjacent tubercles, setose pygidium, and form of the parameres.

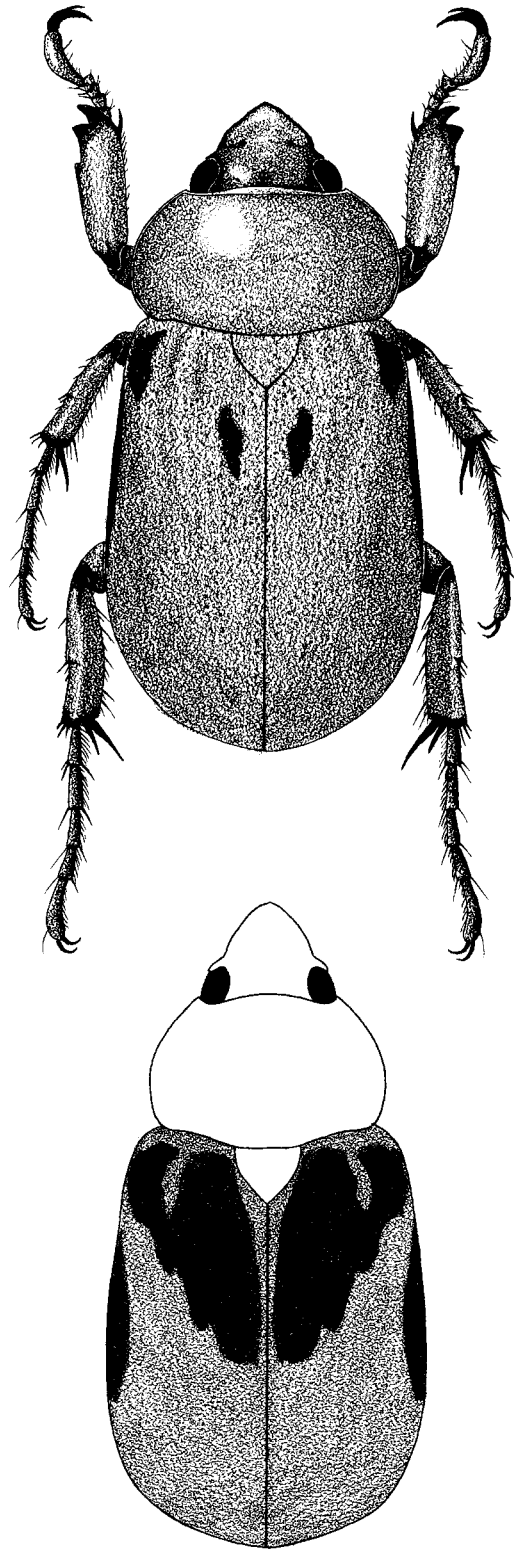
BIOLOGY. Adults are attracted to lights, and they have been collected at elevations between 1,200-1,500 meters in montane rainforests.

***Ancognatha gracilis* Endrödi,
1966**

(Figs. 68-74)

Ancognatha gracilis Endrödi 1966: 372.

DESCRIPTION. Length 17.2-24.0 mm; width 8.5-11.5 mm. Color testaceous with black markings as follows: frons (sometimes entire head), disc of pronotum in some Costa Rican specimens (pronotum entirely yellow in Panama specimens), small spot on base of scutellum, post-scutellar elongate spot (small [Fig. 71] or rarely absent in Panamanian and rarely in Costa Rican males; large in females [Fig. 72] and most Costa Rican males, often extending to middle of elytron and reaching humeral umbone), spot on humerus (usually small in males, usually larger in females and often coalescing with post-scutellar spot), narrow line along anterior half of lateral margin of elytra, bases and apices of tibiae, tarsi, and first 4 sternites of male. **Head:** Frons with small punctures, punctures sparse to moderate in density. Clypeus with small, moderately dense punctures; sides of clypeus arcuate, apex narrowly rounded and slightly reflexed. Interocular width equals 2.0-2.5 transverse eye diameters. Antenna 10-segmented, club a little longer than segments 2-7. Mentum with apex distinctly emarginated (Fig. 70). **Pronotum:** Surface with sparse, usually minute to sometimes small punctures. Base without marginal bead. **Elytra:** Surface moderately punctate, punctures small, usually in rows on disc, weakly impressed striae sometimes evident. Epipleuron (ventral view) in female simple, not enlarged. **Pygidium:** Surface finely shagreened in males, punctures obsolete; females with sparse, small punctures, some punctures with short, pale setae. In lateral view, surface convex in males, weakly convex to nearly flat in females. **Legs:** Foretibia tridentate, basal tooth slightly removed from others. Foretarsus in males enlarged, large median claw cleft at apex; foretarsus and claw simple in female. **Venter:** Prosternal process long, apex flattened and with a distinct, round, raised "button"; posterior part of shaft near base with tooth; process with long setae. **Parameres:** Figs. 68-69.



Figs. 68-69. *Ancognatha gracilis* elytral pattern in (68) males and (69) females.

DISTRIBUTION. *Ancognatha gracilis* is known from Costa Rica and Panama.

LOCALITY RECORDS (Figs. 73-74). 189 specimens examined.

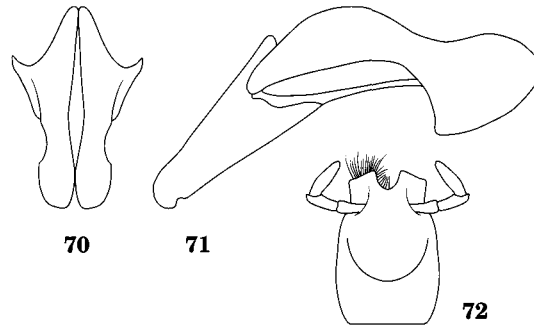
COSTA RICA (91). **CARTAGO** (51): Cerro La Muerte (Pension La Georgina), Empalme (7 km S), Irazú (0.5 km below R.J. Oreamuna National Recreation Area), Madre Selva (Fca. Los Lagos), Río Macho, San Juan de Chicua (road to Volcán Irazú), Tierra Blanca, Villa Mills; **HEREDIA** (36): Estación Barva; **LIMÓN** (2): Chirripó, Sabanas de Durika; **SAN JOSÉ** (2): Cerro Ventesquero, San Gerardo de Dota.

PANAMA (98). **CHIRIQUI** (98): Cerro Punta.

TEMPORAL DISTRIBUTION. January (2), February (4), March (6), April (19), May (23), June (117), September (3), October (11), November (2), December (1).

DIAGNOSIS. *Ancognatha gracilis* may be separated from *A. vulgaris* and *A. vexans* by its distinctive elytral markings, glabrous pygidium, simple elytral margin in the female, less deeply notched mentum, and by the form of the parameres.

BIOLOGY. Adults are attracted to lights. They have been collected in montane and lower montane rain forests at elevations of 2,400-3,500 meters.



Figs. 70-72. *Ancognatha gracilis*: (70-71) parameres; (72) mentum.

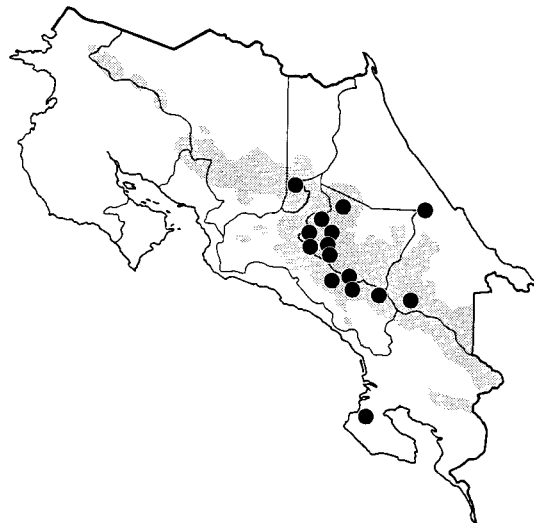


Fig. 73. Distribution of *A. gracilis* in Costa Rica.



Fig. 74. Distribution of *A. gracilis* in Panama.

Ancognatha scarabaeoides**Erichson, 1847**

(Figs. 75-78)

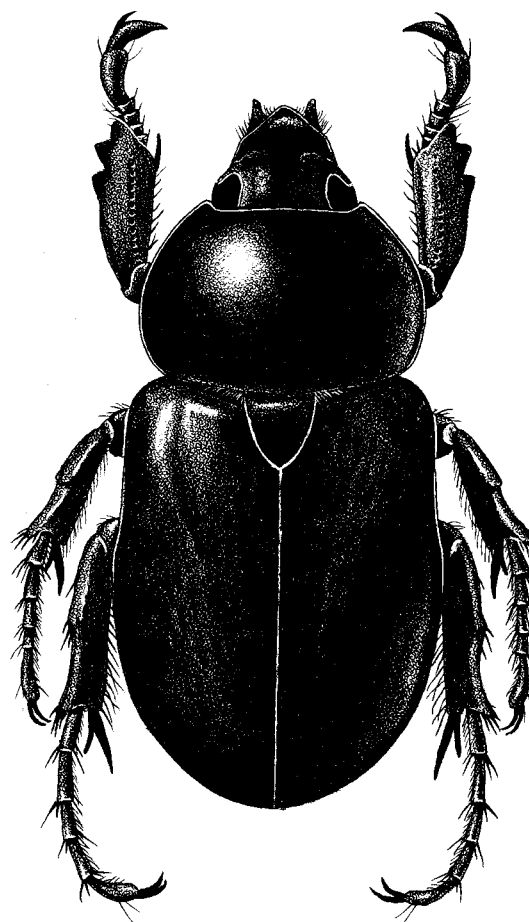
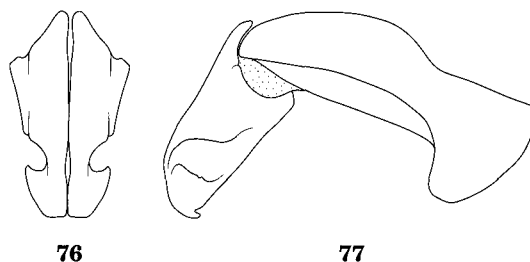
Ancognatha scarabaeoides Erichson 1847: 97.

DESCRIPTION. Length 18.8-29.2 mm; width 8.7-14.8 mm. Color black. *Head:* Frons and clypeus minutely shagreened and with small punctures, punctures moderate in density or with clypeus a little more densely punctate. Frontoclypeal line with 2 low, rounded or transverse tubercles mesad of eye canthus. Clypeus subtriangular, sides arcuate (moreso in female), apex narrowly rounded and reflexed at tip. Interocular width equals 2.2-2.4 transverse eye diameters. Antenna with 10 segments, club distinctly longer than segments 2-7. Mentum with apex distinctly, but not deeply, emarginate. *Pronotum:* Surface similar to that of frons. Base with marginal bead broadly interrupted in middle. *Elytra:* Surface minutely shagreened, moderately densely punctate, punctures small, usually in rows on disc; weakly impressed striae or transverse wrinkling sometimes evident. Epipleuron (ventral view) in female slightly expanded at juncture of first and second sternite. *Pygidium:* Surface vaguely shagreened, with small, moderately dense punctures (less evident in males). In lateral view, surface in males evenly convex, surface in females almost flat. *Legs:* Foretibia tridentate, teeth subequally spaced. Foretarsus in male enlarged, large median claw cleft at apex; foretarsus and claw simple in female. *Venter:* Prosternal process long, apex flattened and with a distinct, round, raised "button"; posterior surface near base with distinct tooth; process covered with dense, long setae. *Parameres:* Figs. 76-77.

DISTRIBUTION. *Ancognatha scarabaeoides* is known from Panama, Colombia, Peru, and Bolivia (Endrödi 1966, 1985a) and Ecuador (personal observation).

LOCALITY RECORDS (Fig. 78). 4 specimens examined.

PANAMA (4). **CHIRIQUI** (4): Guadelupe de Arriba.

Fig. 75. *Ancognatha scarabaeoides*, male.Figs. 76-77. *Ancognatha scarabaeoides* parameres.

TEMPORAL DISTRIBUTION. January (1), May (3).

DIAGNOSIS. This species and *A. atacazo* are the only black species of *Ancognatha* in Central America. It is readily distinguished from *A. atacazo* by its more triangular clypeus, broadly separated frontal tubercles, glabrous pygidium, and form of the parameres.



Fig. 78. Distribution of *A. scarabaeoides* in Panama.

BIOLOGY. Adults are attracted to lights. Pardo Locarno (1994) reported larvae feeding on the roots of alfalfa, tomatoes, potatoes, wheat, barley, berries, and pasture grasses in Colombia where this species is more abundant. *Ancognatha scarabaeoides* is extremely rare in Panama, and it has been collected only in the montane wet forests of Chiriqui at an elevation of 2,100 meters.

***Ancognatha vexans* Ratcliffe, 1992**
(Figs. 79-86)

Ancognatha vexans Ratcliffe 1992a: 256.

DESCRIPTION. Length 21.0-25.2 mm; width 9.0-12.0 mm. Color testaceous with black, elongate spots on humerus, usually on apical umbone, immediately behind flange on lateral margin of elytra in female, and behind scutellum either side of sutural line (Figs. 80-81); bases and apices of tibiae black as well as tarsi and first 4 sternites in males. **Head:** Frons with surface moderately punctate, punctures small. Clypeus with surface moderately densely punctate, punctures moderate in size and becoming rugopunctate at sides; sides arcuate, apex narrowly parabolic and slightly reflexed. Interocular width equals 2.8-3.0 transverse eye diameters. Antenna 10-segmented, club a little longer than segments 2-7. Mentum with apex deeply incised (about half length of mentum)(Fig. 57). **Pronotum:**

Surface sparsely punctate; punctures minute on disc, becoming small in anterior and posterior angles. Base lacking marginal bead. **Elytra:** Surface punctate-striate, double rows distinct; punctures mostly large, weakly ocellate. Female with lateral margin expanded into moderately large flange at level of first sternite, posterior margin of flange evenly arcuate (Fig. 82). **Pygidium:** Surface sparsely punctate, punctures small to moderate in size, setigerous; setae long, pale. In lateral view, surface strongly convex in male, nearly flat in female. **Legs:** Foretibia tridentate, teeth subequally spaced. Foretarsus in males enlarged, median large claw split at apex; foretarsus and claw simple in female. **Venter:** Prosternal process long, apex flattened into transverse oval and with raised, transversely oval "button;" posterior part of shaft near base with obtuse swelling process with long setae. **Parameres:** Figs. 83-84.

DISTRIBUTION. *Ancognatha vexans* was known only from the mountains in Chiriqui Province, Panama. The specimens from Costa Rica listed below constitute a NEW COUNTRY RECORD.

LOCALITY RECORDS (Figs. 85-86). 322 specimens examined.

COSTA RICA (204). ALAJUELA (4): Cerro Campana (6 km NW Dos Ríos), Dos Ríos, Estación Laguna Pocosol; CARTAGO (55):

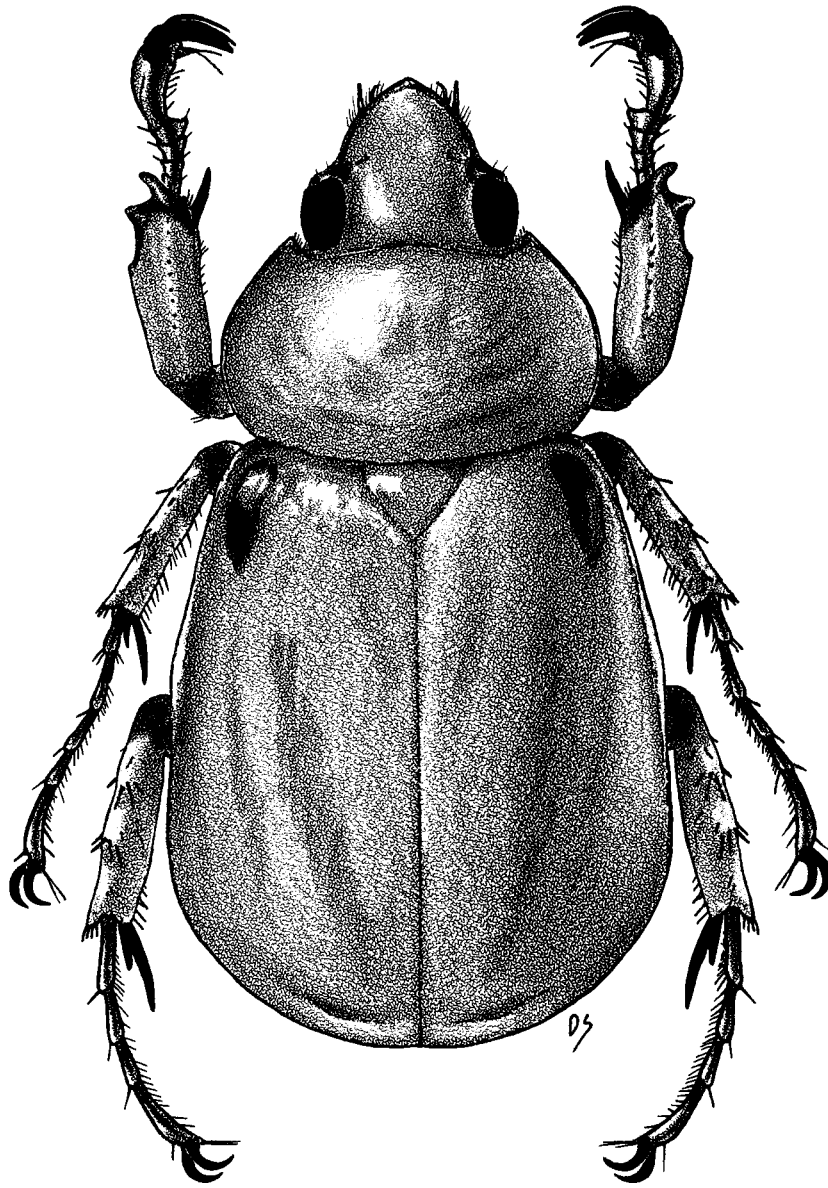


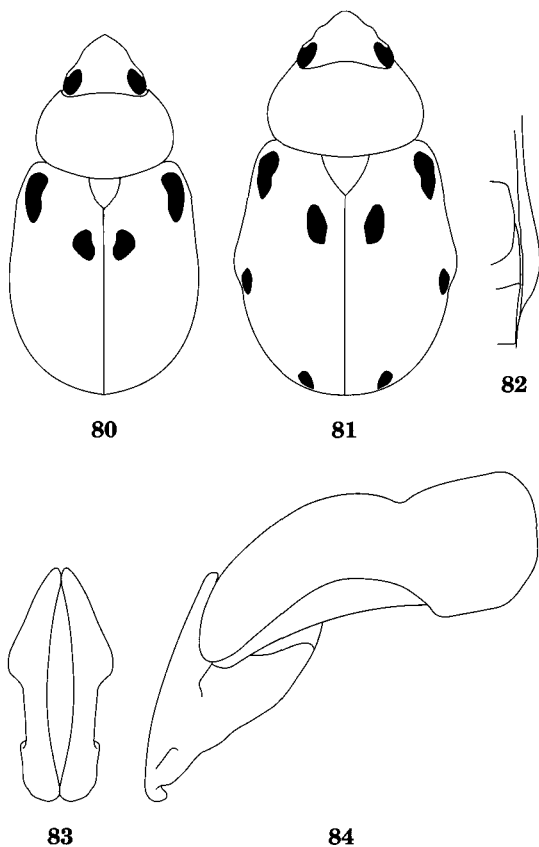
Fig. 79. *Ancognatha vexans*, male.

Refugio Nacional Tapanti; GUANACASTE (83): Estación Cacao, Estación Pitilla; HEREDIA (25): Cerro Chompipe, Estación Barva; PUNTARENAS (33): Estación Biológica Los Alturas, Estación La Casona, Estación Las Mellizas, Reserva Biológica Monteverde, Tres Colinas; SAN JOSÉ (4): Estación Zurqui, San Gerardo de Dota.

PANAMA (118). CHIRIQUI (118): Cerro Punta.

TEMPORAL DISTRIBUTION. January (6), February (5), March (7), April (21), May (29), June (135), July (16), August (17), September (21), October (22), November (34), December (8).

DIAGNOSIS. This species is similar to *A. vulgaris*. The parameres of *A. vexans* are very different from those of *A. vulgaris* (Figs. 91-92), and the males may be separated using



Figs. 80-84. *Ancognatha vexans*: (80-81) variation in elytral pattern of male and female, respectively, and swelling of lateral margin in female; (82) left epipleuron (ventral view) of female; (83-84) parameres.

this character. The females are more difficult to separate. All the specimens of *A. vexans* that I have seen have relatively small, simple spots on the elytra whereas females of *A. vulgaris* have either these simple spots (the minority) or long, dark streaks that cover much of the elytra (the majority). Clearly, these markings are not a reliable character. The flange-like expansion on the lateral edge of the elytra of the females is also different. In *A. vexans*, the flange is not as relatively large, and its posterior edge is evenly arcuate (Fig. 82). In *A. vulgaris*, the flange is larger, and its posterior edge is strongly or abruptly arcuate (Fig. 90).

BIOLOGY. Adults have been collected in pre-montane and lower montane rain forests between the elevations of 650 and 2,500 meters.

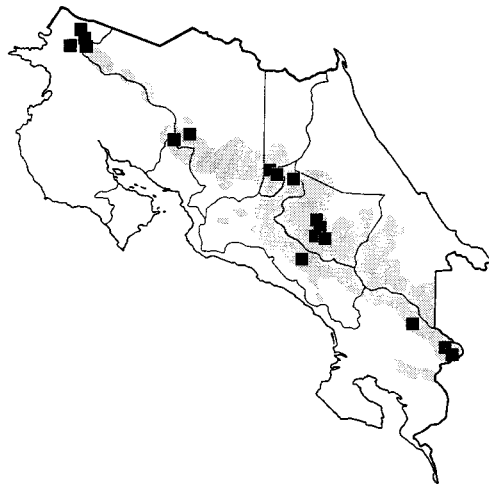


Fig. 85. Distribution of *A. vexans* in Costa Rica.



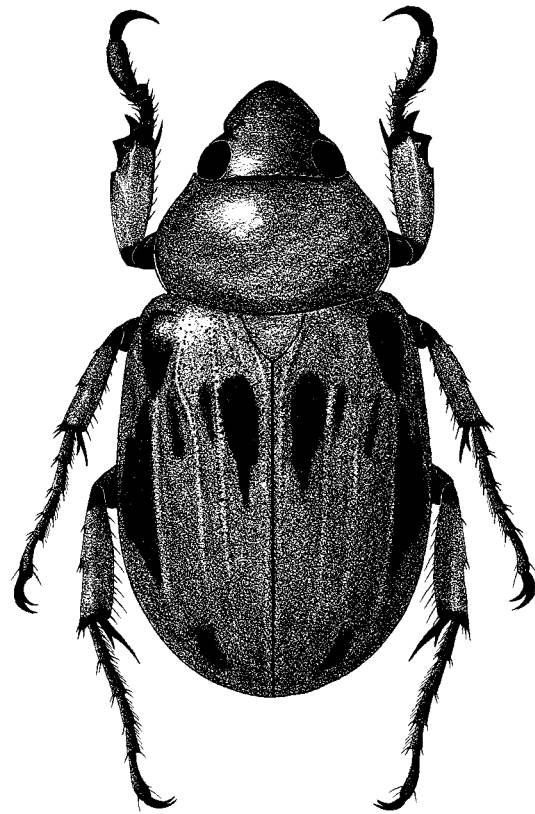
Fig. 86. Distribution of *A. vexans* in Panama.

***Ancognatha vulgaris* Arrow, 1911**

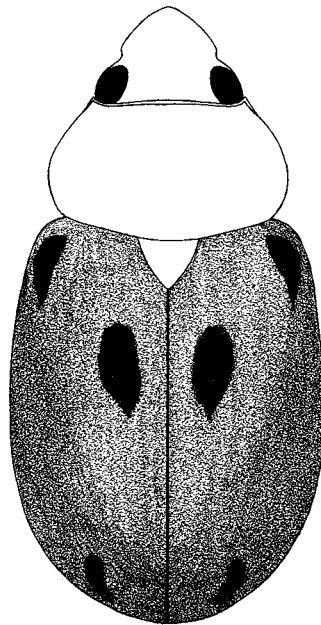
(Figs. 87-95)

Ancognatha vulgaris Arrow 1911: 169.

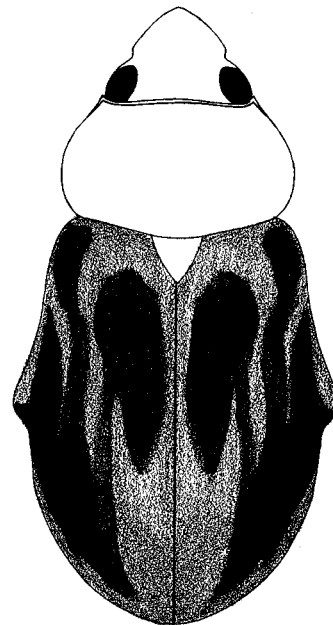
DESCRIPTION. Length 18.9-26.5 mm; width 10.2-13.0 mm. Color testaceous with black, elongate spots on humerus, usually on apical umbone, immediately behind flange on lateral margin of elytra in female, and behind scutellum either side of sutural line (Fig. 87); often with narrow, elongate mark on lateral margin of elytra (Fig. 88), and females (rarely males) with extensive black streaks covering elytra (Fig. 89); bases and apices of tibiae black as well as tarsi and first 4 sternites in males. *Head:* Frons with surface moderately punctate, punctures minute to small. Clypeus with surface moderately densely punctate, punctures small to moderate in size and becoming rugopunctate at sides; sides arcuate, apex narrowly parabolic and slightly reflexed. Interocular width equals 2.8-3.0 transverse eye diameters. Antennae with 10 segments, club a little longer than segments 2-7. Mentum with apex deeply emarginated (about half length of mentum)(Fig. 90). *Pronotum:* Surface sparsely punctate; punctures minute on



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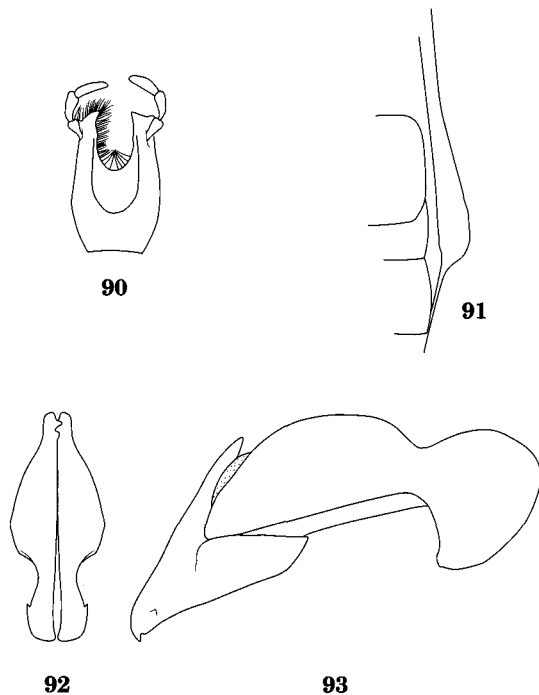


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Figs. 87-89. *Ancognatha vulgaris*: (87-88) males, showing variation in elytral pattern; (89) female.



Figs. 90-93. *Ancognatha vulgaris*: (90) mentum with deep apical notch; (91) left epipleuron (ventral view) of female; (92-93) parameres.

disc, becoming small in anterior and posterior angles. Base without marginal bead. *Elytra*: Surface punctate-striate, double rows distinct; punctures moderate to mostly large, weakly ocellate. Female with lateral margin expanded into moderately large flange at level of first sternite, posterior margin of flange abruptly arcuate (Fig. 91). *Pygidium*: Surface sparsely punctate, punctures small to moderate in size, setigerous; setae long, pale. In lateral view, surface strongly convex in male, nearly flat in female. *Legs*: Foretibia tridentate, teeth equidistant from each other. Foretarsus in males enlarged, median large claw split at apex; foretarsus and claw simple in female. *Venter*: Prosternal process long, apex flattened into transverse oval and with raised, transversely oval "button"; posterior margin of shaft near base with weak swelling; process with long setae. *Parameres*: Figs. 92-93.

DISTRIBUTION. *Ancognatha vulgaris* is one of the most widely distributed and common species in the genus. It occurs from Costa Rica to Brazil and Bolivia (Endrödi 1966, 1985a).

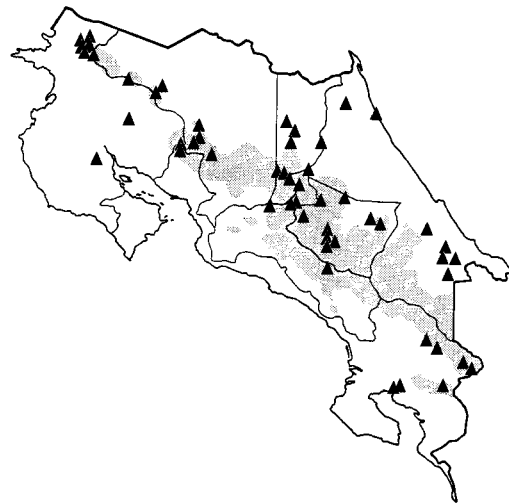


Fig. 94. Distribution of *A. vulgaris* in Costa Rica.

LOCALITY RECORDS (Figs. 94-95). 1,241 specimens examined.

COSTA RICA (931). ALAJUELA (67): Cerro Campana, Dos Ríos, Estación Eladios, Laguna Arenal, San Ramón, Volcán Tenorio; CARTAGO (239): Cerro de Muerte, Chirripó, Embalse el Llano, Las Cruces, Moravia, Orosi, Rancho Naturalista, Tapanti, Tres Ríos, Tuis, Turrialba, Volcán Irazú; GUANACASTE (170): Cañas, Estación Maritza, Estación Pitilla, Parq. Nac. Barra Honda, Quebrada Grande de Liberia, Tierras Morenas, Volcán Cacao; HEREDIA (99): Cerro Chompipe, Estación Barva, Estación El Ceibo, Parq. Nac. Braulio Carrillo, Pueblo Nuevo (2 km S), Vara Blanca; LIMÓN (54): Amubri, Buenos Aires, Cerro Cocori, Cerro Tortuguero, Limón, Reserva Biológica Hitoy Cerere; PUNTARENAS (98): Buenos Aires, Estación Bosque Esquinas, Estación La Casona, Estación Las Alturas, Estación Las Mellizas, Parq. Nac. Amistad, Reserva Biológica Monteverde, San Vito; SAN JOSÉ (83): División, Estación Zurqui, Santa Ana, San Gabriel, San Pedro.

PANAMA (310). BOCAS DEL TORO (27): Highway at Continental Divide, Punta Peña (14 km S); CHIRIQUI (274): Boquete, Cerro

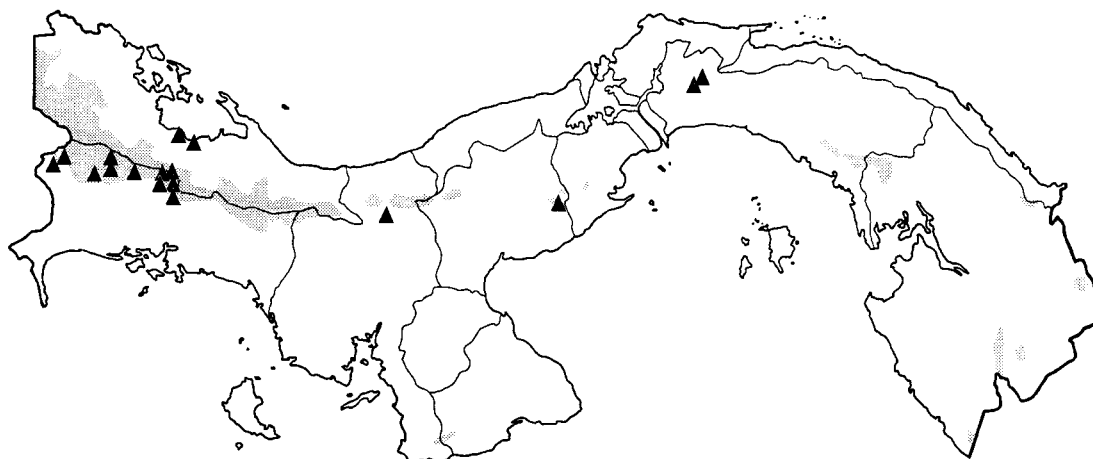


Fig. 95. Distribution of *A. vulgaris* in Panama.

Pato Macho (6 km NE Boquete), Cerro Punta, El Volcán, Finca La Suiza, Fortuna Dam, Hartmann's Finca, IRHE Vivero (11 km N Los Planes), Lino, Los Planes, Quebrada Aleman (10 km N Los Planes), Reserva Fortuna (Continental Divide trail), Santa Clara; COCLÉ (3): El Valle; PANAMA (4): Cerro Azul, Cerro Jefé; VERAGUAS (1): Alto de Piedra.

TEMPORAL DISTRIBUTION. January (41), February (30), March (66), April (151), May (196), June (103), July (76), August (32), September (67), October (90), November (69), December (16). This larger sample size demonstrates clearly an April-May emergence that coincides with the onset of the rainy season and a secondary, smaller peak in September-October, which coincides with the fall onset of rains.

DIAGNOSIS. *Ancognatha vulgaris* is similar to *A. vexans*. In the males, the parameres of *A. vulgaris* (Figs. 92-93) are different from those of *A. vexans* (Figs. 83-84). Females of *A. vulgaris* and *A. vexans* are difficult to separate. Most females of *A. vulgaris* have long, dark streaks that cover most of the elytra; some have only 4-6 simple spots and so resemble all the *A. vexans* females with which I am familiar. In addition, the flange-like expansion on the lateral edge of the female's elytra is large and abruptly arcuate on its posterior edge in *A. vulgaris* (Fig. 91) whereas in

A. vexans the flange is relatively smaller and the posterior edge is evenly arcuate (Fig. 82).

Many comments by Bates (1888) in the *Biologia* about *A. humeralis* refer to this species since he did not distinguish between the two.

BIOLOGY. Adults are readily attracted to lights. They have been collected in premontane wet forest, lower montane rain forests and montane rain forests at elevations of 100-2,500 meters.

Aspidolea Bates, 1888

Aspidolea Bates 1888: 296.

Paraspidolea Höhne 1922a: 90 (synonym).

The genus *Aspidolea* contains 25 species that occur from Mexico to Argentina (Endrödi 1985a; Ratcliffe 1977; Martínez 1975; Dechambre 1992a). Four species are found in Costa Rica and Panama.

Species of *Aspidolea* are extremely close in overall appearance to those of *Cyclocephala*. In *Aspidolea*, the maxilla is penicillate at the apex (Fig. 96) instead of being armed with teeth (except in *A. fuliginea* Burmeister). Some species of *Cyclocephala* also have a penicillate maxilla (e.g., *C. pardolocarnoi* Dechambre), but the maxilla is also heavily armed with teeth. Species of *Ancognatha* also have an unarmed maxilla,

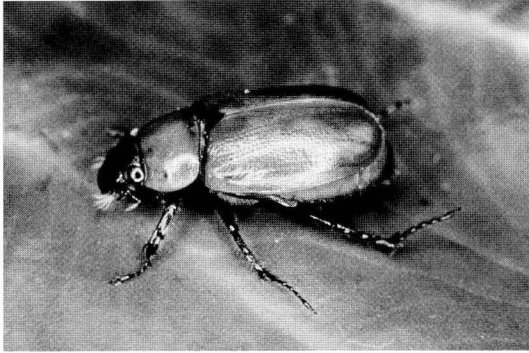


Fig. 96. *Aspidolea singularis* showing penicillate maxilla. Photo by Angel Solís (INBio).

but the form of the maxilla is elongate and robust, unlike that of *Aspidolea*.

Endrödi (1966, 1985a) relied on the form of the clypeus of *Aspidolea* species to separate them from species of *Cyclocephala*. In *Aspidolea*, the clypeus is usually divergent (sometimes only slightly, Fig. 60) from its base, and the apex is broadly rounded. In species of *Cyclocephala*, the base of the clypeus is parallel or convergent from its base but never divergent (Figs. 53-55); the apex may be rounded, subtruncate, or emarginate. This difference in the form of the base of the clypeus is often subtle and difficult to ascertain, especially without comparative material or experience with this group. This is not a

good character, by itself, for separating the two genera, but it does have utility in a key if used with caution. The presence or absence of teeth on the maxilla is a better character, but, in those species of *Cyclocephala* with a penicillate maxilla, the teeth are often very difficult to see because of the dense setae comprising the penicillum, and so determining that they are *Aspidolea* or *Cyclocephala* may be difficult. In *Aspidolea* species, the antenna is 10-segmented, and the club is always short. Males have the protarsus enlarged.

Höhne (1922a) created the genus *Paraspidolea* for *A. fuliginea* because it possessed both teeth and penicillate setae on the maxilla (a fact recognized by Bates). Endrödi (1966) combined *Paraspidolea* with *Aspidolea*.

I have some doubts in my own mind about the validity of *Aspidolea* as a genus, especially in view of the fact of overlapping maxillary character states between *Cyclocephala* and *Aspidolea*. A phylogenetic analysis will help to resolve this question, but it has not yet been done.

Larval stages remain undescribed for species of *Aspidolea*. Similarly, life history information is lacking other than adults are attracted to lights at night.

Endrödi (1966, 1985a) reviewed the species of *Aspidolea*, and several new species have been described since that time.

Key to the Species of Adult *Aspidolea* of Costa Rica and Panama

1. Color black; body size greater than 23 mm *fuliginea* Burmeister
- 1'. Color reddish brown or testaceous; body size less than 17 mm 2
2. Clypeus densely rugopunctate to rugose. Pronotum, elytra, and pygidium reddish or yellowish brown; head, legs, and venter black *singularis* Bates
- 2'. Clypeus punctate. Color of clypeus, pronotum, elytra, and legs testaceous. Frons, pygidium, and venter testaceous or darkened 3
3. Apical segments of labial palpus subequal to or slightly longer than preceding segment. Pygidium setose *notaticollis* Höhne
- 3'. Apical segment of labial palpus nearly twice length of preceding segment. Pygidium glabrous *kuntzeni* Höhne

Clave para los Adultos del las Especies de *Aspidolea* de Costa Rica y Panamá

1. Color negro; tamaño del cuerpo mayor de 23 mm *fuliginea* Burmeister
- 1'. Color pardo rojizo o testáceo; cuerpo menor de 17 mm 2
2. Clípeo densamente rugopuntuado a rugoso. Pronoto, élitros y pigidio rojizos o pardo amarillento; cabeza, patas y área ventral negras *singularis* Bates
- 2'. Clípeo puntuado. Color del clípeo, pronoto, élitros y patas testáceos. Frente, pigidio y área ventral testáceos u oscurecidos 3
3. Segmento apical del palpo labial similar o ligeramente más largo que el segmento precedente. Pigidio con setas *notaticollis* Höhne
- 3'. Segmento apical del palpo labial casi dos veces la longitud del segmento precedente. Pigidio glabro *kuntzeni* Höhne

Aspidolea fuliginea Burmeister, 1847

(Figs. 97-101)

Aspidolea fuliginea Burmeister 1847: 42.

DESCRIPTION. Length 23.3-28.0 mm; width 11.5-12.5 mm. Color dark reddish brown to black. *Head:* Frons in male with punctures moderate in density, small; punctures a little larger and denser in female. Clypeus at base with small punctures, punctures moderate in density and becoming dense to finely rugopunctate toward apex; apex broad, parabolic, margined. Interocular width equals 3.3 transverse eye diameters in dorsal view. Antenna with 10 segments, club subequal in length to segments 2-7. *Pronotum:* Surface textured as on frons. Base with marginal bead broadly interrupted at middle. *Elytra:* Surface with impressed rows of moderately large, shallow punctures. Intervals with micropunctures. Female with lateral margin abruptly swollen at level of first sternite. *Pygidium:* Surface in males with punctures moderate in density; punctures small to moderate in size, setigerous; setae long, reddish brown. Surface in females similarly punctate in basal half only, punctures becoming sparse to obsolete in apical half; setae short. In lateral view, surface in males strongly convex, surface in females nearly flat except for convex apex. *Legs:* Foretibia tridentate, basal tooth slightly removed from others; teeth in males broad, those of females more slender. Foretarsus in males with 5th tarsomere and median claw enlarged, median

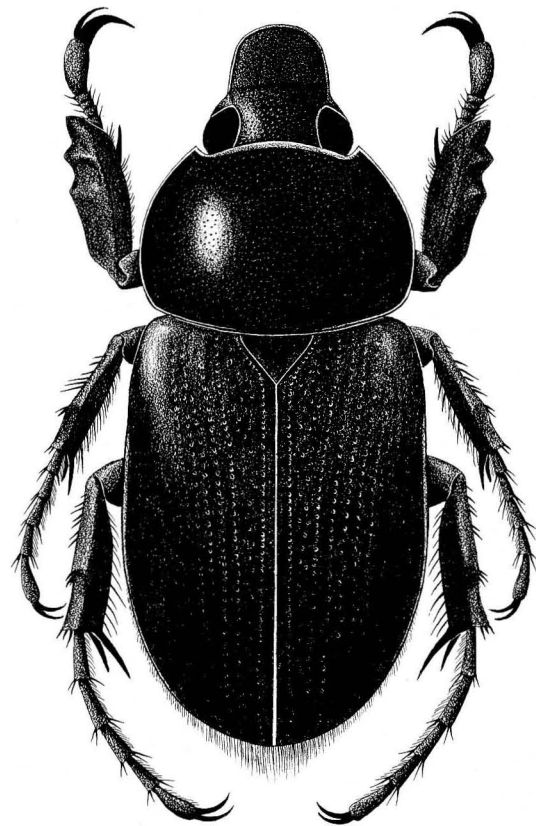
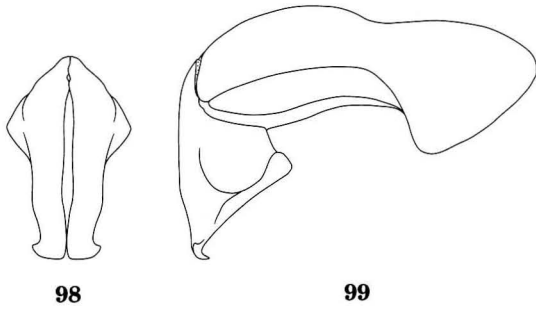


Fig. 97. *Aspidolea fuliginea*.

claw with apex finely split; foretarsus simple in females. Posterior tibia at apex with 7 small teeth. Posterior tarsus longer than metatibia. *Venter:* Prosternal process long, apex transversely oval and with large, transversely oval "button" on anterior half. *Parameres:* Figs. 98-99.



Figs. 98-99. *Aspidolea fuliginea* parameres.

DISTRIBUTION. *Aspidolea fuliginea* is found in Mexico, Central America, northern South America, Ecuador, and Peru (Endrödi 1966); Endrödi also lists "no data" (questionable) records for Brazil and Argentina. This species is broadly distributed throughout Costa Rica and Panama, generally at elevations below 1,500 m.

LOCALITY RECORDS (Figs. 100-101). 258 specimens examined.

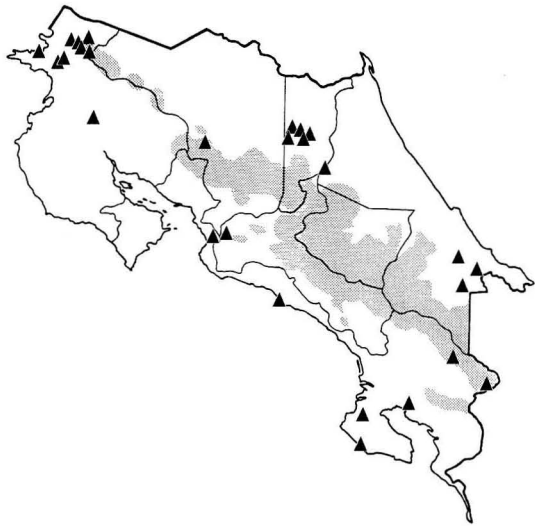


Fig. 100. Distribution of *A. fuliginea* in Costa Rica.

COSTA RICA (184). ALAJUELA (2): Reserva Biológica Monteverde, San Ramon; CARTAGO (22): Rancho Naturalista (5 km N Cayutic), Tuis, Turrialba; GUANACASTE (62): Cerro El Hacha (12 km SE La Cruz), Estación Cacao, Estación Lomas Barbudal, Estación Maritza, Estación Murciellago, Estación Pitilla, Estación Santa Rosa, Finca Jenny (30 km N Liberia), La Pacifica (4 mi N Cañas); HEREDIA (32): Chilamate Sarapiquí, Estación Magsasay, Finca Naranjo Valenciana (Sarapiquí), La Selva Biological Station, La Virgen (Sarapiquí); LIMÓN (32): Amubri, Estación Hitoy Cerere, Guapiles, Suretka (Río Uatsi); PUNTARENAS (32): Buenos Aires, Estación Esquinas (Osa), Estación Las Mellizas, Parq. Nac. Corcovado, Quepos, Rancho Quemado (Osa), Reserva Biológica Carara, Rincón de Osa, Río Coto Brus, Sirena, Villa Lapas; SAN JOSÉ (2): Estación Carrillo, Parq. Nac. Braulio Carrillo.



Fig. 101. Distribution of *A. fuliginea* in Panama.

PANAMA (74). BOCAS DEL TORO (40): Miramar, Punta Peña; CANAL ZONE (2): Albrook Forest, Madden Dam; CHIRIQUI (7): Boquete, Fortuna Dam, Los Planes, Santa Clara, Volcancito; COLÓN (7): Cerro Viejo Mine road (9 km SW Nombre de Dios), Sabanitas (2 km S), Santa Rita Ridge; DARIEN (1): Head of Río Seteganti; PANAMA (17): Cerro Azul, Cerro Jefé, El Llano-Carti Road (km 10-12), Serranía de Majé.

TEMPORAL DISTRIBUTION. January (5), February (11), March (29), April (19), May (40), June (38), July (33), August (8), September (5), October (4), November (9), December (14).

DIAGNOSIS. *Aspidolea fuliginea* is easily distinguished by its large size (for a cyclocephaline) and its entirely dark reddish brown or black color. It is the largest species of *Aspidolea*. Partly based on this, Höhne (1922) created the genus *Paraspidolea* for this species, but Endrödi (1966) synonymized this name with *Aspidolea*.

BIOLOGY. Adults are attracted to lights at night. They live in tropical wet forests, premontane wet forests, tropical moist forests, and premontane moist forests at elevations ranging from sea level to 1,800 meters. Most specimens have been taken at 1,000 meters or less.

***Aspidolea kuntzeni* Höhne, 1922**
(Figs. 102-106)

Aspidolea kuntzeni Höhne 1922a: 87.

Aspidolea pygidialis Höhne 1922a: 89 (synonym).

DESCRIPTION. Length 10.4-12.0 mm; width 5.6-6.0 mm. Color testaceous; frons, pronotal spots (behind anterior margin; usually absent), elytral suture, post-scutellar spot (in shape of oblique teardrop), tarsi, and usually sides of pygidium and most of venter piceous to black. Pronotum often (especially in males) with dark "clouding" everywhere except lateral and anterior margins. *Head:* Frons and clypeus with moderately dense,

small to moderately-sized punctures; frontoclypeal suture weakly impressed. Clypeus with apex broadly parabolic, margined. Interocular width equals 3.0 transverse eye diameters in dorsal view. Antenna with 10 segments, club subequal in length to segments 2-7. *Pronotum:* Surface punctures similar to those of frons, except sparser on disc, denser along lateral margins. Base with marginal bead interrupted at middle. *Elytra:* Surface finely shagreened, with rows of weakly impressed, moderately large punctures. Female with lateral margin swollen between metacoxa and second sternite. *Pygidium:* Surface glabrous; in males finely roughened, apex roughened to sparsely, finely punctate; females with moderate to dense, small, shallow punctures. In lateral view, surface in males convex, especially in apical third; females with surface weakly convex. *Legs:* Foretibia tridentate, teeth subequally spaced. Foretarsus in males with 5th tarsomere and median claw enlarged, median claw bifurcate at apex. Posterior tibia at apex with 7-8 small teeth, a spinule projecting from between each. Posterior tarsus slightly longer than posterior tibia. *Venter:* Prosternal process long, apex transversely oval and with large, transversely oval "button" on anterior half. *Parameres:* Figs. 103-104.

DISTRIBUTION. *Aspidolea kuntzeni* is known from Costa Rica (NEW COUNTRY RECORD) to northern South America. The New Mexico record listed in Endrödi (1966, 1985a) is erroneous because this species does not occur in the United States. This species is broadly distributed in Costa Rica and Panama, usually at elevations below 800 meters.

LOCALITY RECORDS (Figs. 105-106). 176 specimens examined.

COSTA RICA (90). ALAJUELA (1): Dos Ríos (2 km SE); CARTAGO (4): Turrialba; GUANACASTE (2): Estación Las Pailas, Río San Lorenzo; HEREDIA (2): Estación El Ceibo, La Selva Biological Station; LIMÓN (7): Cerro Tortuguero, Estación Cuatro Esquinas, La Perla; PUNTARENAS (73):

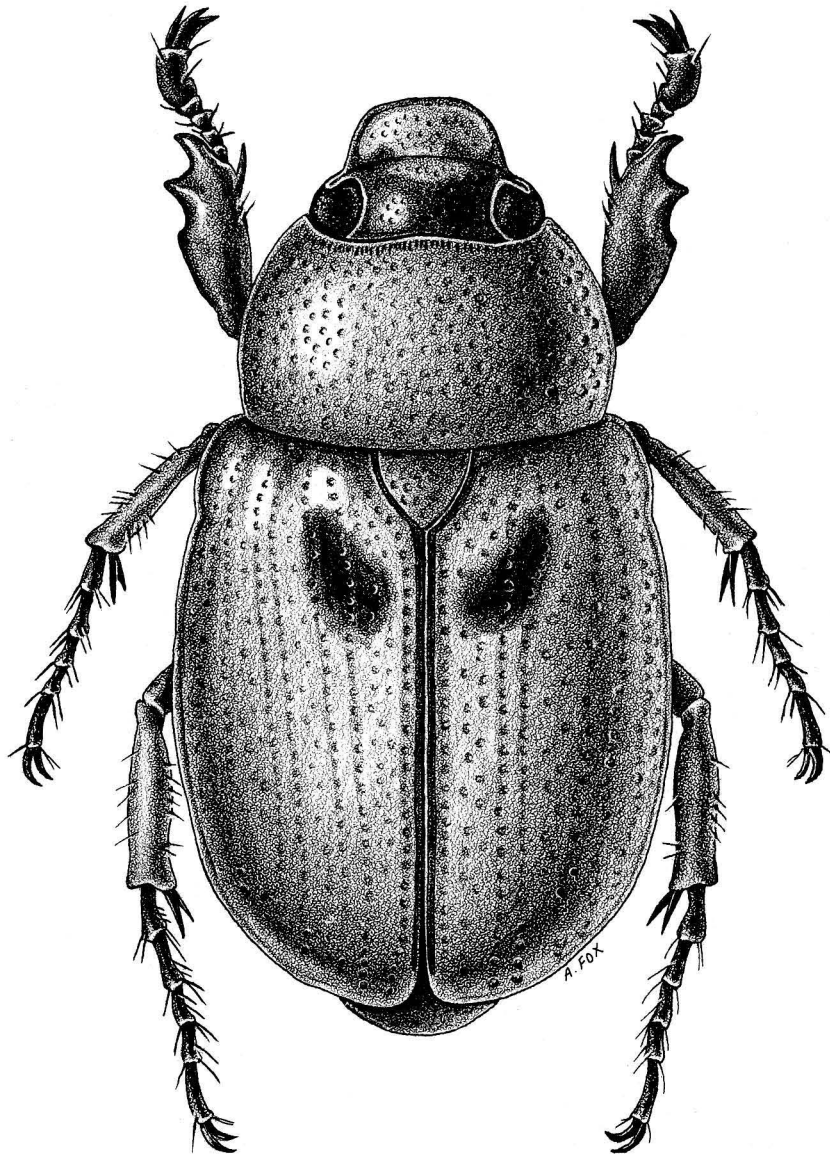


Fig. 102. *Aspidolea kuntzeni*.

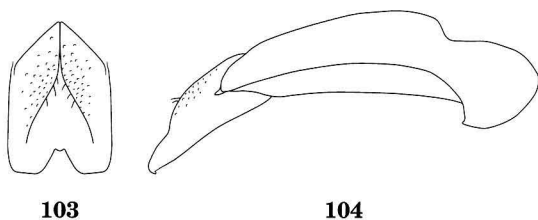
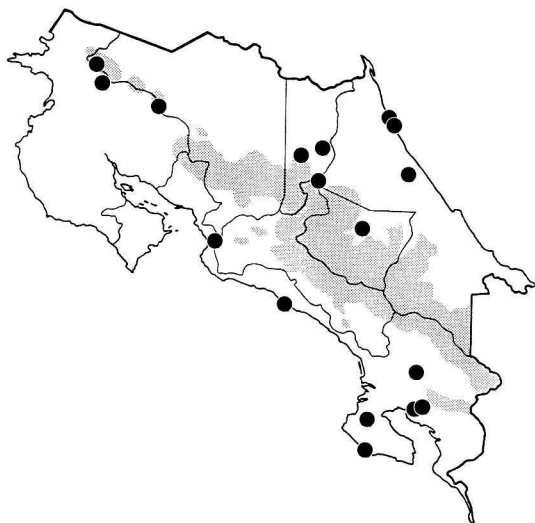
Estación Quebrada Bonita, Estación Sirena, Ojochal, Osa Peninsula, Quepos, Rancho Quemado, Vuelta Campana; SAN JOSÉ (1): Parq. Nac. Braulio Carrillo.

PANAMA (87). BOCAS DEL TORO (2): Corriente Grande; CANAL ZONE (78): Pipeline Road; DARIEN (6): Cana, Santa Fé; PANAMA (1): Isla de Majé.

TEMPORAL DISTRIBUTION. January (38), February (4), March (3), April (6), May (37),

June (64), July (7), August (3), September (1), October (5), November (7), December (3).

DIAGNOSIS. *Aspidolea kuntzeni*, like *A. notaticollis*, is unlike any other Central American species of *Aspidolea* because of its small size, testaceous yellow color (with or without black marks), and form of the parameres. Some specimens of *A. kuntzeni* have two small, black spots behind the anterior margin of the pronotum, but this is absent in nearly all of the Central American

Figs. 103-104. *Aspidolea kuntzeni* parameres.Fig. 105. Distribution of *A. kuntzeni* in Costa Rica.Fig. 106. Distribution of *A. kuntzeni* in Panama.

specimens I have seen. The parameres of *A. kuntzeni* are similar in shape to those of *A. notaticollis*, but in *A. kuntzeni* they are short, stout, parallel-sided, and the base and median edges of each paramere are roughened and minutely setose (Figs. 103-104). The parameres in *A. notaticollis* are relatively more elongate, less stout, the bases and apices are more elongate, and the roughened area on the base and median edge of each paramere is absent (Figs. 107-108). These characteristics are not always easily seen, and I don't believe they are reliable for separating the two species. The body form in *A. kuntzeni* is also shorter and more oval, but this is difficult to determine without comparative material of both species. Characters that do seem to reliably distinguish the two species are pygidium glabrous in *A. kuntzeni* and setose in *A. notaticollis*, pygidium weakly convex in the basal two-thirds and strongly convex in the apical third in *A. kuntzeni* and entirely and evenly convex in *A. notaticollis*, and labial palpus with the apical segment twice as long as the second segment in *A. kuntzeni* and subequal to, or only slightly longer than, the second segment in *A. notaticollis*.

BIOLOGY. Adults are attracted to lights at night. They have been collected from tropical wet forests and premontane moist forests at elevations below 800 meters. Most specimens were taken at less than 400 meters elevation.

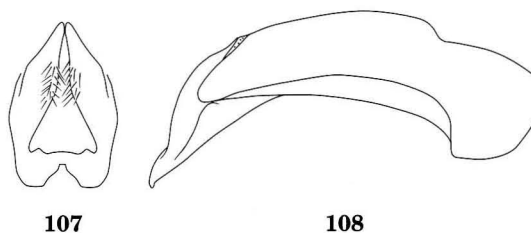
***Aspidolea notaticollis* Höhne, 1922**
(Figs. 107-110)

Aspidolea notaticollis Höhne 1922a: 86.

Aspidolea bigutticollis Höhne 1922a: 87 (synonym).

DESCRIPTION. Length 12.0-13.1 mm; width 6.4-7.0 mm. Color testaceous with posterior half of frons and most of venter and pygidium usually black; venter and pygidium occasionally testaceous. *Head:* Frons and clypeus with moderately dense, moderately-sized punctures in male, punctures dense in female. Frontoclypeal suture distinct, biarcuate. Clypeus with apex broadly rounded and narrowly reflexed, sides at base parallel to slightly diverging. Interocular width equals 3.3-3.6 transverse eye diameters in dorsal view. Antenna with 10 segments, club subequal in length to segments 2-7. *Pronotum:* Surface with moderately-sized punctures, punctures moderate in density in central third becoming moderately dense on lateral thirds. Base usually without (rarely with) weak marginal bead. *Elytra:* Surface with rows of small, shallow punctures; intervals shagreened and with minute, shallow punctures. Lateral margin in female expanded between metacoxa and second sternite. *Pygidium:* Surface finely and completely roughened and with moderately dense, short, pale setae. In lateral view, surface evenly convex in male, female with surface nearly flat in basal 2/3 and convex in apical third. *Legs:* Foretibia tridentate, teeth equidistant. Tarsomeres of anterior tarsus in male enlarged; median claw enlarged, widest at middle, apex split; female with tarsomeres and claw not enlarged. Apex of posterior tibia with 7-8 small teeth, a spinule projecting from between each. Posterior tarsus a little longer than tibia. *Venter:* Prosternal process long, apex transversely oval and with large, transversely oval "button" on anterior half. *Parameres:* Figs. 107-108.

DISTRIBUTION. *Aspidolea notaticollis* was previously known from Colombia, Ecuador, and Peru (Endrödi 1966, 1985a). The data for Costa Rica and Panama listed below consti-



Figs. 107-108. *Aspidolea notaticollis* parameres.

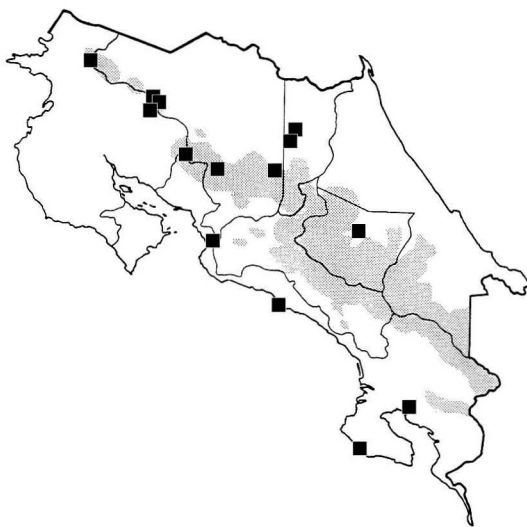


Fig. 109. Distribution of *A. notaticollis* in Costa Rica.

tute NEW COUNTRY RECORDS. There are relatively few collecting records in either country.

LOCALITY RECORDS (Figs. 109-110). 36 specimens examined.

COSTA RICA (27). ALAJUELA (4): Estación San Ramón, San Lorencito, San Miguel (6 km S on Río Sarapiquí); CARTAGO (3): Turrialba; GUANACASTE (5): Río San Lorenzo (Tierras Morenas), SW slope Volcán Tenorio (Finca Montezuma); HEREDIA (3): La Selva Biological Station, Pueblo Nuevo (2 km S); PUNTARENAS (13): Estación Esquinas (Osa), Estación La Casona (Monteverde), Estación Sirena, Parq. Nac. Manuel Antonio, Reserva Biológica Carara.

PANAMA (9). BOCAS DEL TORO (1): Miramar; CANAL ZONE (3): Ft. Sherman,

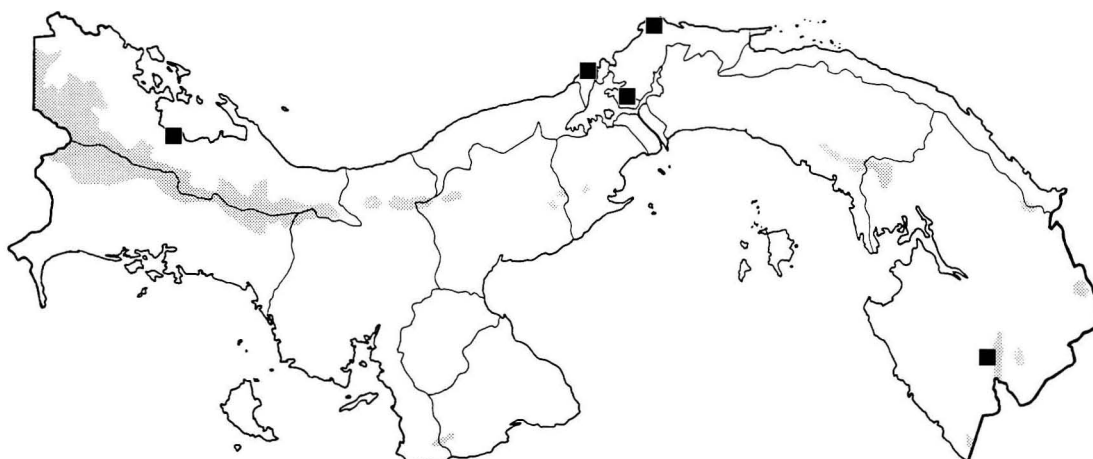


Fig. 110. Distribution of *A. notaticollis* in Panama.

Pipeline road; COLÓN (4): Cerro Viejo Mine Rd (10 km SW Nombre de Dios); DARIEN (1): Cana.

TEMPORAL DISTRIBUTION. January (11), February (1), March (2), April (4), May (2), June (8), August (1), October (2), November (3), December (2).

DIAGNOSIS. *Aspidolea notaticollis*, along with *A. kuntzeni*, is easily distinguished from other Central American species of *Aspidolea* by its small size, testaceous yellow color, and form of the parameres (Figs. 107-108). The parameres of *A. notaticollis* are similar to those of *A. kuntzeni*, but the two species may be easily separated because *A. notaticollis* has a setose pygidium whereas it is glabrous in *A. kuntzeni*. In addition, the apical segment of the labial palpus is subequal to or slightly longer than the preceding segment in *A. notaticollis*, and in *A. kuntzeni* the apical segment is almost twice as long as the second segment.

BIOLOGY. Adults are attracted to lights at night. They have been collected in tropical moist forests, tropical wet forests, premontane rain forests, and premontane wet forests at elevations ranging from near sea level to 1,500 meters; most specimens were collected below 1,000 meters.

Aspidolea singularis Bates, 1888

(Figs. 96, 111-115)

Aspidolea singularis Bates 1888: 296.

Aspidolea texana Höhne 1922a: 84 (synonym).

Aspidolea similis Höhne 1922a: 82 (synonym).

Aspidolea cevallosi Martínez 1975: 307 (synonym).

DESCRIPTION. Length 13.5-16.8 mm; width 6.4-8.5 mm. Color reddish or yellowish brown on pronotum, elytra, and pygidium; head, legs, venter, and extreme base of each elytron in median half black or piceous. **Head:** Frons moderately to moderately densely punctate, punctures small. Clypeus densely, finely rugopunctate to rugose; sides parallel to broadly rounded to apex. Interocular width equals 3.0 transverse eye diameters in dorsal view. Antenna small, with 10 segments, club subequal to or a little longer in length to segments 2-7. **Pronotum:** Surface moderately punctate, punctures mostly moderate in size. Base lacking marginal bead, sides widest just behind middle. **Elytra:** Surface with moderate-sized punctures, punctures moderate in density and mixed with dense, minute punctures; punctate rows of stria vaguely discernible. **Pygidium:** Surface in males minutely, finely rugopunctate except at center apex where surface has small, sparse punctures. Females with punctures moderate in density

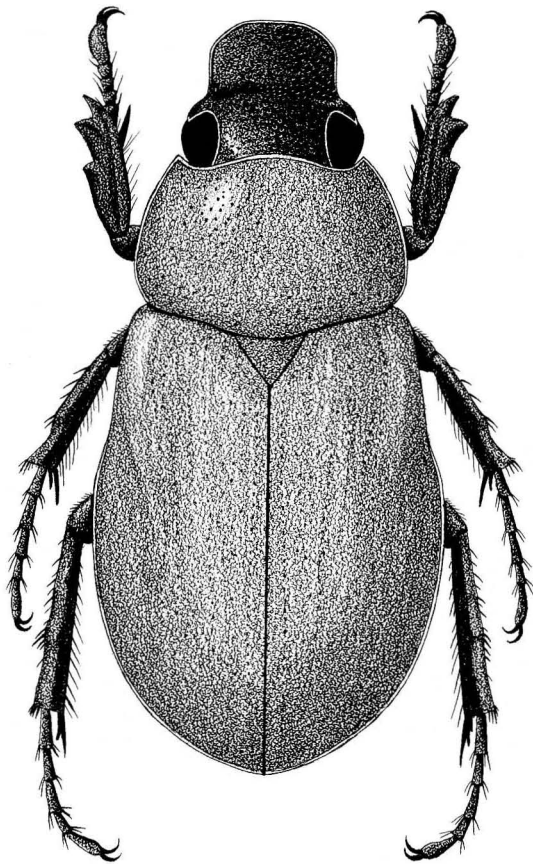
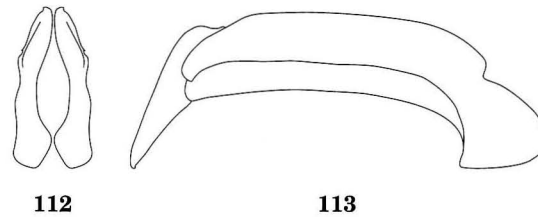


Fig. 111. *Aspidolea singularis*.



Figs. 112-113. *Aspidolea singularis* parameres.



Fig. 114. Distribution of *A. singularis* in Costa Rica.

and size; punctures becoming larger and coalescing at sides; short, pale, sparse setae present in basal half. *Legs*: Anterior tibia tridentate, basal tooth slightly removed. Larger claw of anterior tarsus in male distinctly split at apex, claw simple in female. Posterior tarsus a little longer than posterior tibia. *Venter*: Prosternal process columnar, reaching level of coxae; apex broadly flattened, anterior half with a transverse, suboval "button." *Parameres*: Figs. 112-113.

DISTRIBUTION. *Aspidolea singularis* is broadly distributed from Mexico to Venezuela, Colombia, and Ecuador. This species occurs throughout most of Costa Rica and Panama where it is an abundant species.

LOCALITY RECORDS (Figs. 114-115). 2,194 specimens examined.

COSTA RICA (1,311). **ALAJUELA** (43): Dos Ríos (Finca San Gabriel), Parq. Nac. Rincón de la Vieja, Reserva Biológica Monteverde, Reserva San Lorencito (Reserva Biológica San Ramón), Upala, Vara Blanca (8 km N); **CARTAGO** (197): Chirripó Valley (30 mi. SE Turrialba near Tsipiri River), Embalse El Llano, Moravia, Refugio Nacional Tapanti, Tuis, Turrialba (Gran de Oro), Turrialba, Volcán Irazú; **GUANACASTE** (246): Estación Cacao, Estación Las Pailas, Estación Maritza, Estación Pitilla, Liberia, Río Naranjo (3 km SE, Rancho Montezuma), Tierras Morenas; **HEREDIA** (130): Estación El Ceibo, Estación Magsasay, Finca Naranjo Valenciana (2 km S Pueblo Nuevo), La Selva Biological Station, La Virgen de Sarapiquí, Las Horquetas de Sarapiquí, Los Arbolitos, Parq. Nac. Braulio Carrillo, Río Frio (Standard Fruit Co.), Vara Blanca; **LIMÓN** (205): Amubri, Buenos Aires,

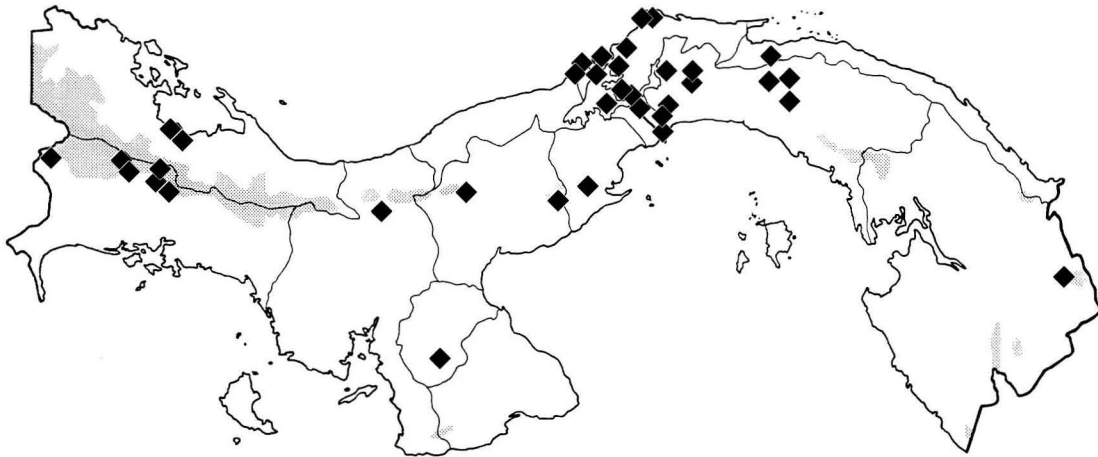


Fig. 115. Distribution of *A. singularis* in Panama.

Cerro Tortuguero, Estación Quatro Esquinas, Guacimo, Guapiles, Hamburg Farm, Limón, Manzanillo, Reserva Biológica Hitoy Cerere, Río Banano, Río Sardinias, Sector Cocori; PUNTARENAS (478): Buenos Aires (Sector Altamira), El Chuzaco (Reserva Biológica Carara), Estación Carara, Estación Esquinas, Estación La Casona, Estación Las Alturas, Estación Quebrada Bonita, Estación Sirena, Fila Guerra (Osa), Finca Cafrosa (Estación Las Mellizas), La Escuadra, Monteverde, Parq. Nac. Manuel Antonio, Rancho Quemado (Osa), San Luis (Monteverde), San Vito, Santa Elena, Vuelta Campana, Wilson Botanical Gardens; SAN JOSÉ (12): Estación Bijagual, Parq. Nac. Braulio Carrillo, San Isidro, San José, Santiago de Puriscal.

PANAMA (883). BOCAS DEL TORO (55): Chiriquí Grande, Miramar; CANAL ZONE (476): Albrook Forest, Barro Colorado Island, Black Tank Road, Coco Solo Hospital, Escobal (Gatun Lake), Fort Clayton, Fort Davis, Fort Gulick, Fort San Lorenzo, Fort Sherman, Gamboa, Gamboa Road, Gatun Tank Farm, Margarita, Pipeline Road, Skunk Hollow; CHIRIQUI (105): Alto Lino (4 km N Boquete), Boquete, Finca La Suiza, Fortuna Dam, Hartmann's Finca (Santa Clara), Hornito, Los Planes; COCLÉ (7): El Copé (5 km N continental divide), El Valle; COLÓN (67): Cerro Viejo Mine Rd. (10 km SW Nombre de Dios),

Portobello, Río Piedras (3 km E María Chiquita), Santa Rita Ridge, Tabernilla; DARIÉN (2): Río Tacarcuna; HERRERA (1): Chepo; PANAMA (164): Altos de Cerro Azul, Altos de Majé, Canita, Cerro Campana, Cerro Jefe, El Llano-Carti Rd. (km 13-18, km. 12, km. 11), Las Cumbres; SAN BLAS (2): Nusagandi; VERAGUAS (4): Alto de Piedra (above Santa Fé).

TEMPORAL DISTRIBUTION. January (114), February (104), March (108), April (155), May (437), June (260), July (311), August (66), September (97), October (183), November (167), December (149).

DIAGNOSIS. *Aspidolea singularis* is easily separated from other species of *Aspidolea* in Costa Rica and Panama by its size, reddish brown coloration, and rugulose clypeal surface. The parameres of the male are also distinctive. In spite of its widespread abundance, the immature stages remain unknown.

BIOLOGY. Adults are readily attracted to lights at night. This species has been taken from elevations of near sea level to 1,520 meters in tropical moist forests, tropical wet forests, premontane moist forests, premontane wet forests, premontane rain forests, and lower montane rain forests.



Color Plate 2. *Cyclocephala sexpunctata* feeding on the spathe of an aroid, *Dieffenbachia* sp. (Araceae).
Illustration by Dan Schmidt.

***Cyclocephala* Dejean, 1821**

Cyclocephala Dejean 1821: 51 (not Latreille 1829).

Mononidia Casey 1915: 110 (synonym).

Diapatalia Casey 1915: 111 (synonym).

Stigmalia Casey 1915: 111 (synonym).

Spilosota Casey 1915: 112 (synonym).

Ochrosidia Casey 1915: 112 (synonym).

Dichromina Casey 1915: 112 (synonym).

Homochromina Casey 1915: 113 (synonym).

Plagiosalia Casey 1915: 135 (synonym).

Isocoryna Casey 1915: 136 (synonym).

Graphalia Casey 1915: 159 (synonym).

Aclinidia Casey 1915: 113 (synonym).

Halotosia Casey 1915: 113 (synonym).

Aspidotites Höhne 1922c: 374 (synonym).

Aspidolella Prell 1936: 146 (synonym).

Albridarollia Bolivar y Pieltain, Jiménez-Asúa, and Martínez 1963: 182 (synonym).

Paraclimidia Martínez 1965: 13 (synonym, described as subgenus).

Cyclocephala is a large genus that currently contains about 325 species, although new species are being described continuously. Endrödi (1985a) provided the most recent synopsis of the genus although 90 species have been described since his work. Consequently, the keys in his manual should be used with caution inasmuch as there now exists 43% more species than in the keys. *Cyclocephala* species occur from extreme southeastern Canada south to Argentina and

in the West Indies. Most of the species occur in the Neotropical realm.

Species in the genus may be recognized by a clypeus with sides converging to a rounded, parabolic, subtruncate, or emarginate apex (Figs. 53-55); antenna with 8-10 segments (9 or 10 in the Central American species) and the club longer in the males of a few species; maxilla armed with distinct teeth; and protarsus in the males distinctly enlarged with the median claw much larger than the outer claw (claws in females are simple). Separating *Cyclocephala* species from *Aspidolea* species may occasionally be difficult, but in *Aspidolea* species the sides of the clypeus are always divergent (sometimes only weakly) from the base before becoming rounded at the apex (Fig. 60) whereas in *Cyclocephala* species the sides of the clypeus converge (even if slightly) to the apex. A more reliable character is the presence of distinct teeth on the maxilla in *Cyclocephala* species whereas they are absent in *Aspidolea* species (except for the large and distinctive *A. fuliginea*). *Cyclocephala* species do not have the elongated mandible seen in most *Ancognatha* species, and they also have a more or less complete frontoclypeal suture, which is obsolete medially in *Ancognatha* species.

Adult *Cyclocephala* species are nocturnal, and they are attracted to lights at night. Several species are known to feed upon (and pollinate) the flowers of aroids and certain palms. Only a few larvae have been described, and those feed on the roots of grasses.

Key to the Species of Adult Male *Cyclocephala* of Costa Rica and Panama

1. Dorsal color uniformly black, occasionally very dark reddish brown, occasionally with red or testaceous vitae or spots 2
- 1'. Dorsal color primarily testaceous or reddish brown, with or without black markings, never uniformly black 11
- 2 (1). Pronotum with marginal bead at base 3
- 2'. Pronotum without marginal bead at base 4
- 3 (2). Each elytron with transverse, reddish-orange vita or vita broken into 2-3 spots; surface without longitudinal furrows *fasciolata* Bates
- 3'. Elytra lacking vitae or spots, surface usually with longitudinal furrows *melanae* Bates
- 4 (2'). Foretibia bidentate, with small notch behind 2nd tooth *kaszabi* Endrödi
- 4'. Foretibia tridentate (basal tooth often small in *C. ligyrina*) 5

- 5 (4'). Color uniformly dark reddish brown (*C. amblyopsis* with piceous or black frons, occasionally clypeus, and occasionally pronotum with 2 longitudinal bands) 6
- 5'. Color entirely black 7
- 6 (5). Clypeal apex emarginate. Pygidium glabrous. Length 20 mm or greater *alazonia* Ratcliffe, new species
- 6'. Clypeal apex convex. Pygidium setose. Length 19.3 mm or less *amblyopsis* Bates
- 7 (6'). Clypeus nearly rectangular, anterior angles distinct, apex truncate *nigerrima* Bates
- 7'. Clypeus not subrectangular, instead anterior angles broadly rounded, apex truncate or not 8
- 8 (7'). Clypeus with apex truncate or weakly emarginate *ligyrina* Bates
- 8'. Clypeus with apex distinctly parabolic 9
- 9 (8'). Elytra with rows of punctures, not completely and densely punctate. Size greater than 20 mm *carbonaria* Arrow
- 9'. Elytra completely, densely punctate. Size less than 15 mm 10
- 10 (9'). Elytra covered by minute setae. Uncommon black form of *sparsa* Arrow
- 10'. Elytra glabrous. Darkest forms of *castaniella* Bates
- 11 (1'). Apex of clypeus with 2 or 3 shallow emarginations 12
- 11'. Apex of clypeus convex, truncate, or emarginate, never with 2 or 3 emarginations 13
- 12 (11). Clypeus with apex tri-emarginate. Elytra with large, elongate, black triangular mark at base (rarely reduced) *porioni* Dechambre
- 12'. Clypeus with apex bi-emarginate (sometimes difficult to see if apex is worn). Elytra testaceous, never with black triangle *ampliata* Bates
- 13 (11'). Pronotum on base with marginal bead (rarely obsolete for only a short distance at middle) 14
- 13'. Pronotum on base without marginal bead 39
- 14 (13). Head and pronotum distinctly elongated 15
- 14'. Head and pronotum of normal length, not elongated 16
- 15 (14). Length of head from occiput to clypeal apex about twice width of clypeus at its base. Parameres (in lateral view) with high, angulate, dorsal "crest" (Figs 369-370) *prolongata* Arrow
- 15'. Length of head from occiput to clypeal apex about 1/3 longer than width of clypeus at its base. Parameres (in lateral view) with lower, rounded, dorsal "crest" (Fig. 358-359) *pardolocarnoi* Dechambre
- 16 (14'). Clypeus with apex distinctly emarginate 17
- 16'. Clypeus with apex truncate or convex 23
- 17 (16). Pronotum and elytra colored differently from one another. 18
- 17'. Pronotum and elytra similarly colored dark reddish brown or dark testaceous or both testaceous with dark spots or bands 19
- 18 (17). Pronotum testaceous. Elytra completely piceous. Length 12-13 mm *enigma* Ratcliffe, new species
- 18'. Pronotum black. Elytra completely testaceous. Length 28-30 mm *rogezi* Dechambre
- 19 (17'). Pronotum and elytra unicolorous dark reddish brown or dark testaceous, without discal, piceous or black spots or bands (*margins* may be black). Foretibia tridentate 20
- 19'. Pronotum and elytra testaceous, with piceous or black spots or bands. Foretibia bidentate 21
- 20 (19). Length 23 mm or greater. Pronotum and pygidium lacking black markings. Interocular width about 3.5 transverse eye diameters. Parameres as in Figs. 338-339 *nike* Ratcliffe

- 20'. Length 21 mm or less. Pronotum usually with 2 black, longitudinal bands; pygidium usually with dark band or spot either side of middle. Interocular width less than 3 transverse eye diameters. Parameres as in Figs. 182-183 **concolor** Burmeister
- 21 (19'). Apex of clypeus deeply emarginate (Figs. 200-201). Elytra with postscutellar spot absent 22
- 21'. Apex of clypeus weakly emarginate (Figs. 202, 411). Elytra with postscutellar spot usually present **stictica** Burmeister
- 22 (21). Abdominal sternites not concave. Pronotum mostly darkened. Each elytron with 2 black streaks or lines (occasionally reduced). Parameres as in Figs. 203-204 **discicollis** Arrow
- 22'. Abdominal sternite deeply concave. Pronotum mostly testaceous with black spot, line, or vitta either side of middle. Each elytron with 3 irregularly rounded spots (occasionally reduced). Parameres as in Figs. 298-299 **maryliae** Ratcliffe, new species
- 23 (16'). Antenna with club elongate, subequal in length to or slightly shorter than entire stem 24
- 23'. Antenna with club distinctly shorter than entire stem 25
- 24 (23). Foretibia weakly tridentate, basal tooth nearly obsolete. Prosternal process small, short, subconical. Median claw of foretarsus with apex cleft **unamas** Ratcliffe, new species
- 24'. Foretibia strongly tridentate. Prosternal process large, long, apex flattened into transverse oval. Median claw of foretibia with apex entire **curta** Bates
- 25 (23'). Enlarged median claw of protarsus incised at apex 26
- 25'. Enlarged median claw of protarsus entire at apex, not incised 33
- 26 (25). Anterior tibia bidentate or sometimes appearing as weakly tridentate (basal "tooth" often reduced to a rounded lobe) 27
- 26'. Anterior tibia distinctly tridentate 30
- 27 (26). Clypeus with surface roughened or alutaceous, matte, often with small, moderately dense punctures **variabilis** Burmeister
- 27'. Clypeus with surface distinctly punctate, shining 28
- 28 (27'). Head and pronotum reddish brown, without black marks. Elytra testaceous with distinctive, large, black spots, spots occasionally fused into oblique maculations **erotyliana** Arrow
- 28'. Head and pronotum testaceous; frons black on posterior half; pronotum with or without black marks. Elytra usually with black sutural margin and/or with 3 small, black spots or streaks (spots often reduced) 29
- 29 (28'). Pronotum completely testaceous, without black marks. Elytra with black scutellar and sutural margins but never with small spots. Pronotum and elytra strongly shining. Pygidium each side of middle with piceous or black mark **maculiventris** Höhne
- 29'. Pronotum with 2 longitudinal black bands or each band reduced to 1-2 spots behind each eye; rarely with all marks absent. Elytra usually with 3 small, black spots: 1 posterolateral of scutellum, 1 behind humerus, and 1 on disc behind middle; spots sometimes reduced or absent. Pronotum and elytra matte or weakly shining. Pygidium unicolorous **discolor** (Herbst)
- 30 (26'). Pronotum and elytra testaceous, without black markings 31
- 30'. Pronotum and elytra testaceous and elytra with black bands, spots, or streaks (rarely reduced) 32
- 31 (30). Large claw of foretarsus (anterior view) (Figs. 401-402) broad and subparallel nearly to apex. Body length 16 mm or greater **sororia** Bates
- 31'. Large claw of foretarsus (anterior view) (Fig. 416) narrowing toward apex. Body length less than 15.5 mm **stockwelli** Ratcliffe, new species

- 32 (30'). Pronotum usually with 6 spots (Figs. 437-439), sometimes with 4 or 8, rarely without. Each elytron usually with 5 small, black spots, sometimes with 4, rarely with 3 or less; sutural interval not darkened. Size 8.5-11.0 mm *williami* Ratcliffe
- 32'. Pronotum testaceous, without black pattern. Each elytron with long, oblique, piceous to black band (rarely absent); sutural interval darkened. Size 15.0-17.0 mm *complanata* Burmeister
- 33 (25'). Pronotum with small setae on sides near anterior angles. Head with or without setae mesad of each eye 34
- 33'. Pronotum lacking setae on sides near anterior angles. Head without setae mesad of each eye 36
- 34 (33). Head lacking setae mesad of each eye. Pronotum with 2 round spots behind anterior margin (Fig. 206). Parameres as in Figs. 208-209. (Specimens with small ramus of anterior claw broken off give appearance of large claw not incised) *discolor* (Herbst)
- 34'. Head with setae mesad of each eye. Pronotum with 2 longitudinal bands (Figs. 127, 310) (bands occasionally reduced) 35
- 35(34'). Clypeus with setae *amazona* (L.)
- 35'. Clypeus glabrous *multiplex* Casey
- 36 (33'). Pronotum with 2 longitudinal, black bands or each band reduced to 1-2 spots behind each eye (rarely with all marks absent). Glabrous specimens of *discolor* (Herbst)
- 36'. Pronotum without bands or spots 37
- 37 (36'). Frons and tarsomeres piceous or black. Base of each paramere strongly depressed (Figs. 324-325) *nigritarsis* Ratcliffe
- 37'. Frons and tarsomeres testaceous. Base of each paramere not or only weakly impressed 38
- 38 (37'). Pygidium glabrous. Clypeal apex broadly parabolic. Prosternal process short but well-developed. Elytra with small, dark streaks *herteli* Endrödi
- 38'. Pygidium setose. Clypeal apex narrowly parabolic. Prosternal process low, barely developed. Elytra with small, dark spots *santaritae* Ratcliffe
- 39 (13'). Surface (especially frons, anterior angles of pronotum, and elytra) at least partly setose 40
- 39'. Surface of head, pronotum, and usually elytra glabrous (occasionally apical part of elytra with minute, dense setae). Pygidium glabrous or not 50
- 40 (39). Clypeus with apex subtruncate or rounded (only rarely indistinctly emarginate) 41
- 40'. Clypeus with apex distinctly emarginate 44
- 41 (40). Pronotum and elytra glabrous. Pronotum and elytra reddish brown; elytra with broad, black band at base of elytra *gregaria* Heyne and Taschenberg
- 41'. Pronotum and elytra with pale setae. Pronotum and elytra testaceous; elytra with or without small, black spots, occasionally entirely speckled, rarely all black 42
- 42 (41'). Foretibia bidentate and with weak dilation in place of third tooth. Clypeal apex narrowly parabolic. Enlarged claw of foretarsus entire at apex *quadripunctata* Höhne
- 42'. Foretibia distinctly tridentate, basal tooth small, directed more anteriorly. Clypeal apex semi-circular at most. Enlarged claw of foretarsus split at apex 43
- 43 (42'). Posterior tarsomere 1 distinctly longer than 2. Foretibia with basal tooth subequally removed from others. Parameres lacking ventral flange (Figs. 248-249) *isthmiensis* Ratcliffe
- 43'. Posterior tarsomere 1 and 2 both long, subequal in length. Foretibia with basal tooth distinctly removed from others. Parameres with strong, ventral flange (Figs. 407-408) *sparsa* Arrow

- 44 (40'). Head, pronotum, elytra, and pygidium with long, dense setae. Pronotum on lateral margin with dense fringe of long setae **brittoni** Endrödi
- 44'. Dorsal surface with short setae. Pronotum on lateral margin with minute to short setae 45
- 45 (44'). Elytra with black hour-glass shaped mark along suture and 4 spots laterad of hour-glass or with 6 round to subtriangular spots on each elytron (Figs. 256-257). Pygidium usually with black spot either side of middle
- **krombeini** Endrödi
- 45'. Elytra with 4 black round to subtriangular spots on each elytron, never with 6 spots or hour-glass shaped mark. Pygidium never with 2 distinct spots (sometimes fuscous either side of middle) 46
- 46 (45'). Sternites 1-5 each with black spot posterolaterally. Parameres (in lateral view) lacking prominent, triangular expansion or large tooth on venter at base (Figs. 445-446). Length less than 17 mm **zodion** Ratcliffe
- 46'. Sternites 1-5 each lacking black spot posterolaterally (if present, then parameres in lateral view with prominent triangular expansion on venter at base). Parameres (in lateral view) with prominent, triangular expansion or large, acute tooth on venter at base. Length variable 47
- 47 (46'). Clypeus punctate; base of clypeus with distinctive black, triangular spot. Parameres (in caudal view) with apices subrectangular (Figs. 267-268)
- **letiranti** Young
- 47'. Clypeus transversely rugose; base lacking black, triangular spot. Parameres (in caudal view) with apices subrectangular or triangular 48
- 48 (47'). Parameres (in caudal view) with subrectangular apex (Figs. 349-350). Sternites 1-5 occasionally with black spot in posterolateral angle. Length less than 18 mm **pan** Ratcliffe
- 48'. Parameres (in caudal view) with triangular apices (Figs. 151-156, 390-397). Sternites lacking posterolateral, black spots. Length variable 49
- 49 (48'). Parameres (in caudal view) long, slender, with triangular to elongated subtriangular apices (Figs. 151, 153, 155); in lateral view, parameres slender, weakly bent to straight (Figs. 152, 154 156). Length 14-19 mm. Usually occurs at elevations less than 1,000 meters **brevis** Höhne
- 49'. Parameres (in caudal view) shorter, stout, with bluntly subtriangular apices (Figs. 390, 392, 394, 396); in lateral view, parameres stout, strongly bent (Figs. 391, 393, 395, 397). Length 17-23 mm. Usually occurs at elevations greater than 1,000 meters **sexpunctata** Burmeister
- 50 (39'). Clypeus with apex weakly to distinctly emarginate 51
- 50'. Clypeus with apex convex or nearly truncate 53
- 51 (50). Pronotum and/or elytra with dark pattern (only at extreme bases of elytra in *C. atripes*) 52
- 51'. Pronotum and/or elytra lacking a black pattern. Instead body entirely dark cherry-red except for black frons and testaceous elytra **gravis** Bates
- 52 (51). Pronotum with 2 longitudinal dark bands. Elytra usually with black bands or spots behind humerus and along suture (rarely absent)
- **mafaffa** Burmeister
- 52'. Pronotum lacking black markings. Elytra with bases and sides below humerus black **atripes** Bates
- 53 (50'). Pronotum and/or elytra with dark pattern 54
- 53'. Pronotum and elytra without dark pattern 60
- 54 (53). Anterior tibia with basal tooth strongly separated from others 55
- 54'. Anterior tibia with basal tooth subequally spaced from others or only slightly removed 56
- 55 (54). Color yellowish red with broad, transverse, black band on base of elytra and another just behind middle (not connected at elytral suture)
- **conspicua** Sharp

- 55'. Color entirely dark reddish brown, pronotum usually with 2 longitudinal black bands or spots *amblyopsis* Bates
- 56 (54'). Pygidium with small setae 57
- 56'. Pygidium glabrous 58
- 57 (56). Frons darkened. Antenna with club subequal in length to segments 2-7. Foretibia with basal tooth slightly removed from others. Elytra with sutural margin simple *lunulata* Burmeister
- 57'. Frons testaceous. Antenna with club slightly shorter than segments 2-7. Foretibia with teeth subequally spaced. Elytra with sutural margin thickened *mustacha* Ratcliffe, new species
- 58 (56'). Frons with complete (or nearly so) black "mask" between eyes 59
- 58'. Frons lacking a black "mask" between eyes, at most with dark area mesad of each eye. Parameres as in Figs. 233-234 *fulgurata* Burmeister
- 59 (58). Length greater than 13.5 mm. Elytral pattern dense, "lunulata-like." Parameres as in Figs. 432-433 *weidneri* Endrödi
- 59'. Length less than 12.5 mm. Elytral pattern sparse, "lunulata-like." Parameres as in Figs. 263-264 *labidion* Ratcliffe, new species
- 60 (54'). Enlarged claw of protarsus with apex broadly cleft (Figs. 121-122) 61
- 60'. Enlarged claw of protarsus with apex narrowly cleft (Fig. 171) 63
- 61(60). Pronotum yellowish-brown, only slightly darker than elytra. Foretibia with basal tooth distinctly removed from others. Parameres as in Figs. 123-124 *almitana* Dechambre
- 61'. Pronotum dark cherry-red, much darker than elytra. Foretibia with teeth subequally spaced or with basal tooth only slightly removed 62
- 62 (61'). Antenna with club as long or longer than segments 2-7 *macrophylla* Erichson
- 62'. Antenna with club short, subequal in length to segments 2-7 *melanocephala* (Fabr.)
- 63 60'. Antenna with club as long or longer than all other segments *castaniella* Bates
- 63'. Club of antenna subequal in length to segments 2-7 64
- 64 (63'). Foretibia with basal tooth strongly removed from others 65
- 64'. Foretibia with basal tooth subequally spaced from others or, if removed, then body length greater than 13 mm and abdominal sternites testaceous (never reddish brown or black 66
- 65 (64). Color dorsally testaceous. Abdominal sternites 1-5 piceous or black. Length less than 13 mm *confusa* Endrödi
- 65'. Color dorsally and ventrally dark reddish-brown. Length greater than 15 mm. Non-vittate form of *amblyopsis* Bates
- 66 (64'). Body short, oval. Length less than 9.2 mm. Pronotum with punctures moderate in density and size *ovulum* Bates
- 66'. Body elongate. Length greater than 13 mm. Pronotum usually with sparse, small punctures 67
- 67 (66'). Pygidium glabrous 68
- 67'. Pygidium with moderately long setae *epistomalis* Bates
- 68(67). Large ramus of protarsal claw with swelling on median edge just distad of basal lobe. Parameres as in Figs. 323-324 *mutata* Harold
- 68'. Large ramus of protarsal claw without swelling on median edge just distad of basal lobe 69
- 69(68'). Head and pronotum slightly darker than testaceous elytra, at most light reddish brown *stockwelli* Ratcliffe, new species
- 69'. Head and pronotum dark cherry red, distinctly darker than testaceous elytra *sanguinicornis* Burmeister

**Key to the Species of Adult Female *Cyclocephala*
of Costa Rica and Panama
(not including unknown female of *C. enigma*)**

1. Dorsal color uniformly black, occasionally very dark reddish brown, occasionally with red or testaceous vitae or spots 2
- 1'. Dorsal color primarily testaceous or reddish brown, with or without black markings, never uniformly black 10
- 2 (1). Pronotum with marginal bead at base 3
- 2'. Pronotum without marginal bead at base 4
- 3 (2). Each elytron with transverse, reddish-orange vita or vita broken into 2-3 spots; surface without longitudinal furrows ***fasciolata* Bates**
- 3'. Elytra lacking vitae or spots; surface usually with longitudinal furrows ***melanae* Bates**
- 4 (2'). Clypeus nearly rectangular, anterior angles distinct, apex truncate ***nigerrima* Bates**
- 4'. Clypeus not rectangular, instead anterior angles broadly rounded, apex truncate or not 5
- 5 (4'). Clypeus with apex truncate, emarginate, or weakly emarginate 6
- 5'. Clypeus with apex distinctly parabolic 8
- 6 (5). Color dark reddish brown ***alazonia* Ratcliffe, new species**
- 6'. Color black 7
- 7 (6'). Foretibia with notch behind basal tooth at base. Epipleuron enlarged into lobe extending from metasternum to third sternite ***kaszabi* Endrödi**
- 7'. Foretibia without notch behind basal tooth. Epipleuron gradually tapers from humeral angle to third sternite ***ligyrina* Bates**
- 8 (5'). Elytra with rows of punctures, not completely and densely punctate. Size greater than 20 mm ***carbonaria* Arrow**
- 8'. Elytra completely, densely punctate. Size less than 15 mm 9
- 9 (8'). Elytra covered by minute setae. Rare black form of ***sparsa* Arrow**
- 9'. Elytra glabrous. Darkest forms of ***castaniella* Bates**
- 10 (1'). Apex of clypeus with 2 or 3 shallow emarginations 11
- 10'. Apex of clypeus convex, truncate, or emarginate, never with 2 or 3 emarginations 12
- 11 (10). Clypeus with apex tri-emarginate. Elytra with large, elongate, black, triangular mark at base (rarely reduced) ***porioni* Dechambre**
- 11'. Clypeus with apex bi-emarginate (sometimes difficult to see if apex is worn). Elytra testaceous, never with black triangle ***ampliata* Bates**
- 12 (10'). Apex of clypeus distinctly emarginate 13
- 12'. Apex of clypeus truncate, rounded, or parabolic 27
- 13 (12). Pronotum black. Elytra testaceous. Length greater than 28 mm ***rogezi* Dechambre**
- 13'. Pronotum and elytra similarly colored, with or without black spots or bands. Length less than 25 mm 14
- 14 (13'). Pronotum and elytra unicolorous dark reddish brown or dark testaceous, without discal, piceous or black spots or bands (*margins* may be black) 15
- 14'. Pronotum and elytra testaceous, one or the other with piceous or black spots or bands 16
- 15 (14). Length 23 mm or greater. Pronotum and pygidium lacking black markings. Interocular width equals 3.5 transverse eye diameters ***nike* Ratcliffe**
- 15'. Length 21 mm or less. Pronotum usually with 2 black, longitudinal bands; pygidium usually with dark band or spot either side of middle. Interocular width less than 3 transverse eye diameters ***concolor* Burmeister**
- 16 (14'). Pronotum at base with marginal bead 17
- 16'. Pronotum at base without marginal bead 19

- 17 (16). Pygidium depressed either side of middle; in lateral view, surface concave . . .
 **maryliae Ratcliffe, new species**
- 17'. Pygidium regularly convex, not depressed either side of middle; in lateral
 view, surface weakly convex 18
- 18 (17). Apex of clypeus deeply emarginate (Fig. 201). Epipleuron gradually en-
 larged from about level of sternites 1-4 and then abruptly narrowed
 **discicollis Arrow**
- 18'. Apex of clypeus weakly emarginate (Fig. 202). Epipleuron gradually en-
 larged from about level of sternites 1-2 (occasionally 3) and then abruptly
 narrowed **stictica Burmeister**
- 19 (16'). Head, pronotum, elytra, and pygidium usually with moderate to long setae.
 Pronotum on lateral margin with dense fringe of moderate to long setae . . .
 **brittoni Endrödi**
- 19'. Dorsal surface with, at most, short setae. Pronotum on lateral margin with,
 at most, minute to short setae 20
- 20 (19'). Epipleuron/elytron simple, not swollen or expanded into flange, lobe, or
 tooth. Pronotum dark reddish brown, elytra testaceous **gravis Bates**
- 20'. Epipleuron/elytron swollen or expanded into flange, lobe, or tooth 21
- 21 (20'). Pronotum nearly smooth, with micropunctures on sides
 **mafaffa Burmeister**
- 21'. Pronotum distinctly punctate 22
- 22 (21'). Pronotum with punctures on center third smaller than those on frons. Elytra
 on base and around sides beneath humerus with narrow, black margin . . .
 **atripes Bates**
- 22'. Pronotum with punctures on center third subequal in size to those on frons.
 Elytra lacking narrow, black margin at base and on sides beneath humerus
 23
- 23 (22'). Clypeus punctate; base with black triangular spot **letiranti Young**
- 23'. Clypeus transversely rugose; base without black triangular spot (often
 present in *C. pan*) 24
- 24 (23'). Elytra together with black hour-glass shaped mark along suture and each
 elytron with 4 spots laterad of hour-glass OR with 6 round to subtriangular
 spots on each elytron (Figs. 256-257). Pygidium usually with black spot ei-
 ther side of middle **krombeini Endrödi**
- 24'. Elytra with 4 black, round to subtriangular spots on each elytron, never with
 6 spots or hour-glass shaped mark. Pygidium never with 2 distinct spots
 (sometimes fuscous either side of middle) 25
- 25 (24'). Epipleuron/elytral margin expanded into elongate lobe at level of metacoxa/
 sternite 1 (Fig. 444). Length 17 mm or less. Pronotum with 2 black spots.
 Sternites 1-5 each with black spot in posterolateral corner
 **zodion Ratcliffe**
- 25'. Epipleuron/elytral margin expanded into abrupt, dentiform flange at level
 of sternites 2-3 (Fig. 351). Length variable. Pronotum with or without black
 spots. Sternites 1-5 each usually lacking black spot in posterolateral corner
 (sometimes present in *C. pan*) 26
- 26 (25'). Length 17-23 mm. Elytral spots usually large. Usually occurs at elevations
 greater than 1,000 meters **sexpunctata Burmeister**
- 26'. Length 14-19 mm. Elytral spots usually small. Usually occurs at elevations
 less than 1,000 meters **brevis Höhne and pan Ratcliffe** (some
C. pan have black spots on the posterolateral corners of sternites 1-5).
- 27 (12'). Head and pronotum distinctly elongated 28
- 27'. Head and pronotum normal, not elongated 29
- 28 (27). Pygidium with large, conical tubercle just above middle. Pronotum with lat-
 eral margin concave just behind posterior angle **prolongata Arrow**

- 28'. Pygidium with low convexity just above middle. Pronotum with lateral margin only slightly convex just behind anterior angle . . . *pardolocarnoi* Dechambre
- 29 (27'). Base of pronotum with marginal bead 30
- 29'. Base of pronotum simple, lacking marginal bead 44
- 30 (29). Elytra with epipleuron simple or weakly thickened at middle, lacking a distinct tooth, swelling, or knob 31
- 30'. Elytra with epipleuron weakly dilated or with large dilation, knob, or tooth 33
- 31 (30). Posterior tarsus only slightly longer than posterior tibia. Length 15.0 mm or greater *sororia* Bates
- 31'. Posterior tarsus almost twice as long as posterior tibia. Length 12.0 mm or less 32
- 32 (31'). Elytra with sutural interval black. Pronotum lacking spots *maculiventris* Höhne
- 32'. Elytra with sutural interval testaceous (same color as elytra. Pronotum usually with 4, 6, or 8 spots (rarely without spots) *williami* Ratcliffe
- 33 (30'). Elytra with epipleuron weakly dilated but lacking angle-like protrusion . . . 34
- 33'. Elytra with epipleuron distinctly dilated and with or without angle-like protrusion 35
- 34 (33). Elytra with large, distinct, black or piceous spots (Figs. 219-221). Pronotum reddish brown *erotylina* Arrow
- 34'. Elytra with, at most, small, indistinct, dark smudges. Pronotum usually testaceous, with or without 2 longitudinal marks *curta* Bates
- 35 (33'). Pygidium distinctly setose 36
- 35'. Pygidium glabrous, at most with microsetae near base 38
- 36 (35). Lateral margin of elytra with simple, flange-like swelling at level of sternite 4 *discolor* (Herbst)
- 36'. Lateral margin of elytra swollen at level of sternites 1-2, distinctly emarginate above sternites 2-3, and swollen again above sternites 3-4 37
- 37 (36'). Fifth abdominal sternite subequal in length to fourth, its apical margin normally arcuate (Fig. 129). *amazona* (L.)
- 37'. Fifth abdominal sternite strongly constricted at center on apical margin and length about half that of fourth segment (Fig. 130) *multiplex* Casey
- 38 (35'). Elytron with oblique, longitudinal, piceous or black stripe on disc (Fig. 176); stripe rarely reduced or broken into pieces; elytral suture broadly (most common) to narrowly (uncommon) darkened *complanata* Burmeister
- 38'. Elytra lacking oblique or longitudinal stripe. Region of elytral suture darkened or not 39
- 39 (38'). Frons black or piceous. Body length 16 mm or greater . . . *variabilis* Burmeister
- 39'. Frons black or testaceous. Body length 15.5 mm or less 40
- 40 (39'). Frons black or piceous 41
- 40'. Frons testaceous or reddish brown 42
- 41 (40). Tarsomeres black. Posterior tarsus about 1/3 longer than posterior tibia. Epipleuron with tooth at level of sternite 2. Elytral margin swollen into elongate flange *nigritarsis* Ratcliffe
- 41'. Tarsomeres reddish brown. Posterior tarsus subequal in length to posterior tibia. Epipleuron expanded but lacking tooth. Elytral margin explanate above epipleural expansion but lacking flange . . . *unamas* Ratcliffe, new species
- 42 (40'). Head and pygidium entirely reddish brown. Elytra lacking any markings *stockwelli* Ratcliffe, new species
- 42'. Head and pygidium entirely testaceous. Elytra with small dark spots or streaks 43
- 43 (42'). Clypeal apex broadly parabolic. Prosternal process short but well-developed. Elytra with small, dark streaks. Expansion of epipleuron abruptly angled, tooth-like *herteli* Endrödi

- 43'. Clypeal apex narrowly parabolic. Prosternal process low, barely developed. Elytra with small, dark spots. Expansion of epipleuron gradually arcuate, simple **santaritae** Ratcliffe
- 44 (29'). Pronotum and/or elytra with contrasting black spots, bands, or zigzag pattern 45
- 44'. Pronotum (except *C. amblyopsis* occasionally) and elytra without contrasting black spots, bands, or zigzag pattern, instead each unicolorous: testaceous, reddish brown, rufous, or piceous 54
- 45 (44). Elytral margin/epipleuron expanded, sometimes strongly so, into distinct knob or flange 46
- 45'. Elytral margin/epipleuron simple, without dilation, knob, or flange **isthmiensis** Ratcliffe
- 46 (45). Pronotum (usually) and elytra covered with short, dense setae 47
- 46'. Pronotum and elytra glabrous, at most with sparse setae on apical fourth of elytra 48
- 47 (46). Flange of elytral margin/epipleuron expanded at level of sternites 4-5 **quadripunctata** Höhne
- 47'. Flange of elytral margin/epipleuron expanded at level of sternites 1-2 **sparsa** Arrow
- 48 (46'). Elytra with large transverse, black band occupying entire basal fourth; a large black spot or transverse, black band in apical third 49
- 48'. Elytra with spots or zigzag pattern, never with large transverse band in basal fourth 50
- 49 (48). Pronotum unicolored, reddish brown **gregaria** Heyne and Taschenberg
- 49'. Pronotum reddish brown, with 2 elongate, black spots or vittae **conspicua** Sharp
- 50 (48'). Frons testaceous. Elytra with epipleuron simple; sutural margin distinctly thickened **mustacha** Ratcliffe, new species
- 50'. Frons darkened. Elytral epipleuron expanded; sutural margin simple 51
- 51 (50'). Elytral epipleuron expanded at level of metacoxa or sternites 1-2; elytral margin in dorsal view tumid at about middle. 52
- 51'. Elytral epipleuron either expanded or abruptly narrowed at level of sternites 3-4; elytral margin in dorsal view tumid or with distinct flange well behind middle 53
- 52 (51). Pygidium glabrous. Epipleuron abruptly narrowed at level of sternite 1. Metasternum microscopically imbricate, shining **labidion** Ratcliffe, new species
- 52'. Pygidium setose. Epipleuron gradually tapered either side of slight thickening at level of sternites 1-2. Metasternum coarsely roughened. **lunulata** Burmeister
- 53 (51'). Epipleuron in ventral view weakly thickened until level of sternites 3-4 where abruptly constricted; margin of elytron at same level imperceptibly swollen. Frons lacking complete black "mask" between eyes **fulgurata** Burmeister
- 53'. Epipleuron in ventral view distinctly thickened until level of sternites 3-4 where abruptly constricted and with tooth-like angle on inner edge; margin of elytron at same level expanded into distinctly angulate flange. Frons with distinct, black "mask" between eyes **weidneri** Endrödi
- 54 (44'). Dorsal surface entirely light or dark testaceous or reddish brown or piceous (monochromatic) 55
- 54'. Pronotum testaceous, dark cherry-red, or black. Elytra testaceous 58
- 55 (54). Antenna with club subequal in length to segments 2-7 57
- 55'. Antenna with club slightly longer than segments 2-7. 56
- 56 (55'). Dorsal surface testaceous **stockwelli** Ratcliffe, new species

- 56'. Dorsal surface dark reddish brown or piceous **castaniella** Bates
- 57 (55). Epipleuron simple or faintly enlarged at level of sternites 1-2. Foretibial teeth subequally spaced, basal tooth only slightly smaller than middle tooth **epistomalis** Bates
- 57'. Epipleuron with small, right-angled tooth on inner margin with small, rounded flange immediately following. Foretibia with basal tooth slightly removed from others and very small **amblyopsis** Bates
- 58 (54). Pronotum dark cherry-red or black 59
- 58'. Pronotum testaceous or yellowish-brown 61
- 59 (58). Antenna with club large, longer than segments 2-7 **macrophylla** Erichson
- 59'. Antenna with club small, shorter than or subequal to segments 2-7 60
- 60 (59). Posterior tarsus shorter than posterior tibia. Epipleuron (ventral view) only imperceptibly thickened at level of sternite 2 **melanocephala** (Fabr.)
- 60'. Posterior tarsus subequal in length to posterior tibia. Epipleuron (ventral view) distinctly enlarged at level of sternites 1-2 and abruptly narrowed **sanguinicollis** Burmeister
- 61 (58'). Epipleuron (ventral view) simple, not thickened or enlarged **almitana** Dechambre
- 61'. Epipleuron (ventral view) distinctly dilated or expanded into a flange 62
- 62 (61'). Foretibia with basal tooth strongly removed from others. Abdominal sternites 1-5 piceous or black **confusa** Endrödi
- 62'. Foretibia with basal tooth subequally spaced from others. Abdominal sternites normally testaceous or reddish brown 63
- 63 (62'). Body short, oval. Length less than 9.2 mm. Pronotum with punctures moderate in density and size **ovulum** Bates
- 63'. Body elongate. Length greater than 13 mm. Pronotum usually with sparse, small punctures **mutata** Harold

Clave para las Especies de Machos Adultos de *Cyclocephala* de Costa Rica y Panama

1. Color dorsal uniformemente negro, ocasionalmente muy oscuro pardo rojizo, ocasionalmente con franjas o manchas rojas o testáceas 2
- 1'. Color dorsal primariamente testáceo o pardo rojizo, con o sin marcas negras, nunca uniformemente negro 11
- 2 (1). Pronoto con reborde marginal en la base 3
- 2'. Pronoto sin reborde marginal en la base 4
- 3 (2). Cada élitro con una franja transversal, rojizo anaranjada o franja rota en 2 a 3 manchas; superficie sin surcos longitudinales **fasciolata** Bates
- 3'. Elitros sin franjas o manchas, superficie generalmente con surcos longitudinales **melanae** Bates
- 4 (2'). Tibias anteriores bidentadas, con una pequeña muesca detrás del segundo diente **kaszabi** Endrödi
- 4'. Tibia anterior tridentada (diente basal frecuentemente pequeño en *C. ligyrina*) 5
- 5 (4'). Color uniformemente pardo rojizo oscuro (*C. amblyopsis* con frente picea o negra, ocasionalmente cípeo y ocasionalmente el pronoto con 2 bandas longitudinales) 6
- 5'. Color enteramente negro 7
- 6 (5). Apice del cípeo emarginado. Pigidio glabro. Longitud 20 mm o más grande **alazonia** Ratcliffe, especie nueva
- 6'. Apice del cípeo convexo. Pigidio setoso. Longitud 19.3 mm o menos **amblyopsis** Bates

- 7 (6'). Clípeo casi rectangular, ángulos anteriores evidentes, ápice truncado *nigerrima* Bates
- 7'. Clípeo no rectangular, ángulos anteriores ampliamente redondeados, ápice truncado o no 8
- 8 (7'). Clípeo con ápice truncado o ligeramente emarginado *ligyrina* Bates
- 8'. Clípeo con el ápice claramente parabólico 9
- 9 (8'). Elitros con hileras de puntuaciones, no completamente ni densamente punteados. Tamaño más grande que 20 mm *carbonaria* Arrow
- 9'. Elitros completa y densamente punteados. Tamaño menor a 15 mm 10
- 10 (9'). Elitros cubiertos por setas diminutas. Forma negra poco común de *sparsa* Arrow
- 10'. Elitros glabros. Formas más oscuras de *castaniella* Bates
- 11 (1'). Apice del clípeo con 2 ó 3 emarginaciones leves 12
- 11'. Apice del clípeo convexo, truncado o emarginado, nunca con 2 ó 3 emarginaciones 13
- 12 (11). Clípeo con el ápice triemarginado. Elitros con grandes marcas triangulares y alargadas en la base (raramente reducidas) *porioni* Dechambre
- 12'. Clípeo con el ápice biemarginado (algunas veces difícil de ver si el ápice está desgastado). Elitros testáceos, nunca con un triángulo negro *ampliata* Bates
- 13 (11'). Pronoto en la base con un reborde marginal (raramente obsoleto en una corta distancia en el medio) 14
- 13'. Pronoto en la base sin un reborde marginal 39
- 14 (13). Cabeza y pronoto claramente alargados 15
- 14'. Cabeza y pronoto de longitud normal, no alargados 16
- 15 (14). Longitud de la cabeza desde el occipucio al ápice clipeal alrededor de dos veces el ancho del clípeo en su base. Parámetros (en vista lateral) con una quilla dorsal, alta y angulada (Figs. 369-370) *prolongata* Arrow
- 15'. Longitud de la cabeza desde el occipucio hasta el ápice del clípeo alrededor de 1/3 más larga que el ancho de su base. Parámetros (en vista lateral) con quilla dorsal, baja, redondeada (Figs. 358-359) *pardolocarnoi* Dechambre
- 16 (14'). Clípeo con el ápice claramente emarginado 17
- 16'. Clípeo con el ápice truncado o convexo 23
- 17 (16). Pronoto y élitros de colores distintos 18
- 17'. Pronoto y élitros similarmente coloreados pardo rojizo oscuros o testáceos oscuros o testáceos con bandas o puntos negros 19
- 18 (17). Pronoto testáceo. Elitros enteramente café oscuros. Largo 12-13mm *enigma* Ratcliffe, especie nueva
- 18'. Pronoto negro. Elitros enteramente testáceos. Largo 28-30 mm *rogezi* Dechambre
- 19 (17'). Pronoto y élitros de un solo color pardo rojizo oscuro o testáceo oscuro, sin puntos o bandas discales píceas o negros (los márgenes pueden ser negros). Tibia anterior tridentata 20
- 19'. Pronoto y élitros testáceos, con manchas o bandas píceas o negras. Tibias anteriores bidentadas 21
- 20 (19). Longitud 23 mm o más grandes. Pronoto y pigidio sin marcas negras. Ancho interocular alrededor de 3.5 diámetros oculares transversales. Parámetros como en la Figs. 338-339 *nike* Ratcliffe
- 20'. Longitud 21 mm o menos. Pronoto generalmente con 2 bandas negras longitudinales; pigidio generalmente con una banda oscura o mancha a cada lado del medio. Ancho interocular menos de 3 diámetros oculares transversales. Parámetros como en la Figs. 182-183 *concolor* Burmeister
- 21 (19'). Apice del clípeo profundamente emarginado (Fig. 201). Elitros con mancha postescutelar ausente 22
- 21'. Apice del clípeo debilmente emarginado (Fig. 202). Elitros con mancha postescutelar generalmente presente *stictica* Burmeister

- 22 (21). Esternitos abdominales no cóncavos. Pronoto mayormente oscuros. Cada élitro con 2 rayas o líneas negras (ocasionalmente reducidas). Parámetros como en la Figs. 203-204 ***discicollis* Arrow**
- 22'. Esternitos abdominales profundamente cóncavos. Pronoto mayormente testáceos con una mancha, línea o franja negra a ambos lados del medio. Cada élitro con 3 manchas redondeadas e irregulares (ocasionalmente reducidas). Parámetros como en la Figs. 298-299 ***maryliza* Ratcliffe, especie nueva**
- 23 (16'). Antenas con maza alargada, similar en longitud o ligeramente más corta que los otros segmentos juntos 24
- 23'. Antenas con maza claramente más corta que el resto de segmentos juntos . . . 25
- 24 (23). Tibia anterior ligeramente tridentada, diente basal casi obsoleto. Proceso proesternal pequeño, corto, casi cónico. . Uña interna de los tarsos anteriores con el ápice bifurcado ***unamas* Ratcliffe, especie nueva**
- 24'. Tibia anterior fuertemente tridentada. Proceso proesternal grande, largo, ápice achato en forma de óvalo transversal. Uña interna de los tarsos anteriores con el ápice entero ***curta* Bates**
- 25 (23'). Uña agrandada interna de los tarsos anteriores con el ápice con incisión . . . 26
- 25'. Uña agrandada interna de los tarsos anteriores con el ápice completo, sin incisión 33
- 26(25). Tibia anterior bidentada o algunas veces parece ligeramente tridentada (diente basal frecuentemente reducido a un lóbulo redondeado) 27
- 26'. Tibia anterior claramente tridentada 30
- 27 (26). Clípeo con superficie rugosa o alutácea, mate, frecuentemente con puntuaciones pequeñas, moderadamente densas ***variabilis* Burmeister**
- 27'. Clípeo con superficie evidentemente punteada, pulida 28
- 28 (27'). Cabeza y pronoto pardo rojizos, sin marcas negras. Elitros testáceos con grandes manchas negras, manchas algunas veces fusionadas en marcas oblicuas ***erotylin* Arrow**
- 28'. Cabeza y pronoto testáceos; frente negra en la mitad posterior; pronoto con o sin marcas negras. Elitros generalmente con margen sutural negro y/o con 3 pequeñas manchas o rayas negras (manchas frecuentemente reducidas) . . . 29
- 29 (28'). Pronoto completamente testáceos, sin marcas negras. Elitros con márgenes escutelares y suturales negros pero nunca con pequeñas manchas negras. Pronoto y élitros muy pulidos. Pigidio a cada lado del medio con marcas píceas o negras ***maculiventris* Höhne**
- 29'. Pronoto con 2 bandas longitudinales negras o cada banda reducida a 1 o 2 manchas detrás de cada ojo; raramente ausentes todas las marcas. Elitro generalmente con 3 manchas pequeñas negras: 1 posterolateral al escutelo, 1 detrás del húmero y 1 en el disco detrás del medio; puntos algunas veces reducidos o ausentes. Pronoto y élitros mate o ligeramente pulidos. Pigidio de un solo color. ***discolor* (Herbst)**
- 30 (26'). Pronoto y élitros testáceos, sin marcas negras 31
- 30'. Pronoto y élitros testáceos y élitros con bandas, manchas o líneas negras (raramente reducidas) 32
- 31 (30). Uñas grandes de los tarso anteriores (en vista anterior) (Figs. 401-402) anchas y prácticamente paralelas casi hasta el ápice. Longitud del cuerpo 16 mm o más grande ***sororia* Bates**
- 31'. Uñas grandes de los tarsos anteriores (en vista anterior) (Fig. 416) estrechándose hacia el ápice. Longitud del cuerpo menos de 15.5 mm ***stockwelli* Ratcliffe, especie nueva**
- 32 (30'). Pronoto generalmente con 6 manchas (Figs. 437-439), algunas veces con 4 u 8, raramente sin ellas. Cada élitro generalmente con 5 pequeñas manchas negras, algunas veces con 4, raramente con 3 o menos; intervalos suturales no oscurecidos. Tamaño 8.5-11.0 mm ***williami* Ratcliffe**

- 32'. Pronoto testáceo, sin patrón negro. Cada élitro con una banda negra a píceo, larga, oblicua (raramente ausente); intervalos suturales oscurecidos. Tamaño 15.0-17.0 mm **complanata Burmeister**
- 33 (25'). Pronoto con setas pequeñas a los lados, cerca de los ángulos anteriores. Cabeza con o sin setas mediales respecto de cada ojo 34
- 33'. Pronoto sin setas a los lados cerca de los ángulos anteriores. Cabeza sin setas mediales respecto de cada ojo 36
- 34 (33). Cabeza sin setas mediales respecto de cada ojo. Pronoto con 2 manchas redondeadas detrás del margen anterior (Fig. 206) Parámetros como en la Figs. 208-209. (Especímenes con la rama pequeña de la uña anterior rota que da la apariencia de una uña grande sin incisión) **discolor (Herbst)**
- 34'. Cabeza con setas mediales respecto a cada ojo. Pronoto con 2 bandas longitudinales (Figs. 127, 310) (bandas ocasionalmente reducidas) 35
- 35 (34'). Clípeo con setas **amazona (L.)**
- 35'. Clípeo glabro. **multiplex Casey**
- 36 (33'). Pronoto con 2 bandas longitudinales negras o cada banda reducida a 1 a 2 manchas detrás de cada ojo (raramente con todas las marcas ausentes). Especímenes glabros de **discolor (Herbst)**
- 36'. Pronoto sin bandas o manchas 37
- 37 (36'). Frente y tarsómeros píceos o negros. Base de cada parámetro fuertemente deprimido (Figs. 334-335) **nigritarsis Ratcliffe**
- 37'. Frente y tarsómeros testáceos. Base de cada parámetro no o sólo ligeramente impreso. 38
- 38 (37'). Pigidio glabro. Apice clipeal ampliamente parabólico. Proceso proesternal corto pero bien desarrollado. Elitros con rayas pequeñas, oscuras **herteli Endrödi**
- 38'. Pigidio setoso. Apice del clípeo estrechamente parabólico. Proceso proesternal bajo, escasamente desarrollado. Elitros con pequeñas manchas oscuras **santaritae Ratcliffe**
- 39 (13'). Superficie (especialmente la frente, ángulos anteriores del pronoto y élitros) al menos parcialmente setosos 40
- 39'. Superficie de la cabeza, pronoto y generalmente élitros glabros (ocasionalmente parte apical de los élitros con setas diminutas, densas). Pigidio glabro o no 50
- 40 (39). Clípeo con el ápice truncado o redondeado (sólo raramente parece emarginado) 41
- 40'. Clípeo con el ápice claramente emarginado 44
- 41 (40). Pronoto y élitros glabros. Pronoto y élitros pardo rojizos; élitros con una banda negra, ancha en la base de los élitros **gregaria Heyne y Taschenberg**
- 41'. Pronoto y élitros con setas pálidas. Pronoto y élitros testáceos; élitros con o sin manchas pequeñas, negras, ocasionalmente completamente cubiertos por marcas pequeños, raramente completamente negros 42
- 42 (41'). Tibia anterior bidentada y con una ligera dilatación en el sitio del tercer diente. Apice clipeal estrechamente parabólico. Uña agrandada de los tarsos anteriores íntegra en el ápice **quadripunctata Höhne**
- 42'. Tibia anterior claramente tridentada, diente basal pequeño, dirigido más anteriormente. Apice clipeal a lo más semicircular. Uña agrandada de los tarsos anteriores dividida en el ápice 43
- 43 (42'). Tarsómero posterior 1 claramente más largo que el 2. Tibias anteriores con el diente basal similarmente separado que los otros. Parámetros sin un reborde ventral (Figs. 248-249) **isthmiensis Ratcliffe**
- 43'. Tarsómero posterior 1 y 2 largos, similares en tamaño ambos. Tibia anterior con el diente basal claramente separado de los otros. Parámetros con un fuerte reborde ventral (Figs. 407-408) **sparsa Arrow**

- 44 (40'). Cabeza, pronoto, élitros y pigidio con setas largas, densas. Pronoto en el margen lateral con un ribete denso de setas largas **brittoni** Endrödi
- 44'. Superficie dorsal con setas cortas. Pronoto en el margen lateral con setas diminutas a cortas 45
- 45 (44'). Elitros con una marca negra en forma de reloj de arena a lo largo de la sutura y 4 manchas a los lados de esta marca o con 6 manchas redondeadas a casi triangulares en cada élitro (Figs. 256-257). Pigidio generalmente con una mancha negra a cada lado del medio **krombeini** Endrödi
- 45'. Elitros con 4 manchas redondeadas a casi triangulares en cada élitro, nunca con 6 manchas o una marca en forma de reloj de arena. Pigidio nunca con 2 manchas evidentes (algunas veces a ambos lados del medio es fusco) 46
- 46 (45'). Esternitos 1 a 5 cada uno con manchas negras posterolaterales. Parámetros en vista lateral sin una expansión lateral triangular, prominente o diente grande ventral en la base (Figs. 445-446). Longitud menos de 17 mm **zodion** Ratcliffe
- 46'. Esternitos 1 a 5 cada uno sin manchas negras posterolaterales (si están presentes entonces los parámetros en vista lateral con una expansión triangular prominente ventral en la base). Parámetros en vista lateral con una expansión triangular prominente o diente grande, agudo, ventral en la base. Longitud variable 47
- 47 (46'). Clípeo con puntuaciones; base del clípeo con una mancha negra evidente. Parámetros en vista caudal con ápices casi rectangulares (Figs. 267-268) **letiranti** Young
- 47'. Clípeo rugoso transversalmente; base sin mancha negra, triangular. Parámetros en vista caudal con ápices casi rectangulares o triangulares 48
- 48 (47'). Parámetros en vista caudal con ápice casi rectangular (Figs. 349-350). Esternitos 1 a 5 ocasionalmente con una mancha negra en el ángulo posterolateral. Longitud menor de 18 mm **pan** Ratcliffe
- 48'. Parámetros en vista caudal con ápices triangulares (Figs. 151-156, 390-397). Esternitos sin manchas posterolaterales. Longitud variable 49
- 49 (48'). Parámetros en vista caudal largos, delgados, con ápices triangulares a casi triangulares alargados (Figs. 151, 153, 155); en vista lateral, parámetros delgados, ligeramente encorvados a rectos (Figs. 152, 154, 156). Longitud 14-19 mm. Generalmente se encuentran a elevaciones menores a 1000 metros **brevis** Höhne
- 49'. Parámetros en vista caudal más cortos, gruesos, con ápices bruscamente casi triangulares (Figs. 391, 393, 395, 397); en vista lateral, parámetros gruesos, fuertemente encorvados (Figs. 390, 392, 394, 396). Longitud 17-23 mm. Generalmente se encuentran a elevaciones mayores de 1000 metros **sexpunctata** Burmeister
- 50 (39'). Clípeo con el ápice ligera a claramente emarginado 51
- 50'. Clípeo con el ápice convexo o casi truncado 53
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- 52 (51). Pronoto con 2 bandas oscuras longitudinales. Elitros generalmente con bandas o manchas negras detrás del húmero y a lo largo de la sutura (raramente ausentes) **mafaffa** Burmeister
- 52'. Pronoto sin marcas negras. Elitros con bases y lados bajo el húmero negros **atripes** Bates
- 53 (50'). Pronoto y/o élitros con patrón oscuro 54
- 53'. Pronoto y élitros sin patrón negro 60

- 54 (53). Tibia anterior con diente basal fuertemente separado de los otros 55
- 54'. Tibia anterior con el diente basal similarmente separado que los otros o solo ligeramente aparte 56
- 55 (54). Color rojo amarillento con una banda negra, amplia y transversal en la base de los élitros y otra justo atrás del medio (no conectada a la sutura elitral) **conspicua Sharp**
- 55'. Color enteramente pardo rojizo oscuro, pronoto generalmente con 2 bandas o manchas longitudinales negras **amblyopsis Bates**
- 56 (54'). Pigidio con setas pequeñas 57
- 56'. Pigidio glabro 58
- 57 (56). Frente oscurecida. Antenas con maza similar en longitud a los segmentos 2 al 7 juntos. Tibia anterior con el diente basal ligeramente aparte con respecto a los otros. Elitros con margen sutural simple **lunulata Burmeister**
- 57'. Frente testácea. Antenas con maza ligeramente más corta que segmentos 2 a 7. Tibia anterior con dientes similarmente separados entre sí. Elitros con margen sutural engrosado **mustacha Ratcliffe, especie nueva**
- 58 (56'). Frente con "máscara" completa, negra entre los ojos 59
- 58'. Frente sin una "máscara" negra entre los ojos, a lo más con un área oscura medial respecto de cada ojo. Parámetros como en la Figs. 233-234 **fulgurata Burmeister**
- 59(58) Largo mayor a 13.5 mm. Patrón elitral denso, similar al "patrón lunulata". Parámetros como en la Figs. 432-433 **weidneri Endrödi**
- 59'. Largo menor a 12.5 mm. Patrón elitral disperso, similar al "patrón lunulata". Parámetros como en la Figs. 263-264 **labidion Ratcliffe, especie nueva**
- 60 (53'). Uña agrandada del protarso con el ápice ampliamente dividido (Figs. 121-122) 61
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- 61 (60). Pronoto pardo amarillento, solo ligeramente más oscuro que los élitros. Tibias anteriores con diente basal claramente separado de los otros. Parámetros como en la Figs. 123-124 **almitana Dechambre**
- 61'. Pronoto oscuro color rojo cereza, mucho más oscuro que los élitros. Tibia anterior con dientes similarmente separados o con el diente basal solo ligeramente aparte 62
- 62 (61'). Antenas con la maza tan o más larga que los segmentos 2 a 7 juntos **macrophylla Erichson**
- 62'. Antena con la maza corta, similar en longitud a los segmentos 2 a 7 juntos **melanocephala (Fabr.)**
- 63 (60'). Antena con la maza tan larga o más larga que todos los otros segmentos **castaniella Bates**
- 63'. Maza de la antena similar en longitud a los segmentos 2 a 7 juntos 64
- 64 (63'). Tibia anterior con el diente basal fuertemente separado de los otros 65
- 64'. Tibia anterior con el diente basal similarmente separado que los otros o, si está separado, el largo del cuerpo es mayor que 13 mm y los esternitos abdominales testáceos (nunca pardo rojizos o negros) 66
- 65 (64). Color dorsalmente testáceo. Esternitos abdominales 1 a 5 píceos o negros. Longitud menor de 13 mm **confusa Endrödi**
- 65'. Color dorsal y ventralmente pardo rojizo oscuro. Longitud mayor de 15 mm. Forma sin franjas de **amblyopsis Bates**
- 66 (64'). Cuerpo corto, oval. Longitud menor de 9.2 mm. Pronoto con puntuaciones moderadas en densidad y tamaño **ovulum Bates**
- 66'. Cuerpo alargado. Longitud mayor de 13 mm. Pronoto generalmente con puntuaciones pequeñas, dispersas 67
- 67 (66'). Pigidio glabro 68
- 67'. Pigidio con setas moderadamente largas **epistomalis Bates**

- 68 (67). Rama grande de la uña protarsal con hinchamiento en el borde mediano justo después del lóbulo basal. Parámetros como en la Figs. 323-324
 *mutata* Harold
- 68'. Rama grande de la uña protarsal sin hinchamiento en el borde mediano justo después del lóbulo basal 69
- 69 (68'). Cabeza y pronoto ligeramente más oscuro que los élitros testáceos, a lo más pardo rojizo claro *stockwelli* Ratcliffe, especie nueva
- 69'. Cabeza y pronoto rojo cereza oscuro, evidentemente más oscuro que los élitros testáceos *sanguinicollis* Burmeister

Clave para las Especies de Hembras Adultas de *Cyclocephala* de Costa Rica y Panamá
 (sin incluir la hembra desconocida de *C. enigma*)

1. Color dorsal uniformemente negro, ocasionalmente pardo rojizo muy oscuro, ocasionalmente con manchas rojas o testáceas 2
- 1'. Color dorsal primariamente testáceo o pardo rojizo, con o sin marcas negras, nunca uniformemente negros 10
- 2 (1). Pronoto en la base con reborde marginal 3
- 2'. Pronoto en la base sin reborde marginal 4
- 3 (2). Cada élitro con una franja transversal, anaranjada rojiza o franja rota en 2 o 3 manchas; superficie sin surcos longitudinales *fasciolata* Bates
- 3'. Elitros sin franjas o manchas; superficie generalmente con surcos longitudinales *melanae* Bates
- 4 (2'). Clípeo casi rectangular, ángulos anteriores evidentes, ápice truncado
 *nigerrima* Bates
- 4'. Clípeo no rectangular, ángulos anteriores ampliamente redondeados, ápice truncado o no 5
- 5 (4). Clípeo con el ápice truncado, emarginado o ligeramente emarginado 6
- 5'. Clípeo con el ápice claramente parabólico 8
- 6 (5). Color pardo rojizo oscuro *alazonia* Ratcliffe, especie nueva
- 6'. Color negro 7
- 7 (6'). Tibia anterior con muesca detrás del diente basal en la base. Epipleura agrandada en un lóbulo que se extiende desde metaesternito al tercer esternito *kaszabi* Endrödi
- 7'. Tibia anterior sin una muesca detrás del diente basal. Epipleura gradualmente se estrecha desde el ángulo humeral hasta el tercer esternito *ligyrina* Bates
- 8 (5'). Elitros con hileras de puntuaciones, no completamente ni densamente punteados. Tamaño mayor que 20 mm *carbonaria* Arrow
- 8'. Elitros completa y densamente punteados. Tamaño menor de 15 mm 9
- 9 (8'). Elitros cubiertos por setas diminutas. Rara forma oscura de
 *sparsa* Arrow
- 9'. Elitros glabros. Formas más oscuras de *castaniella* Bates
- 10 (1'). Apice del clípeo con 2 o 3 emarginaciones leves 11
- 10'. Apice del clípeo convexo, truncado o emarginado, nunca con 2 o 3 emarginaciones 12
- 11 (10). Clípeo con el margen triemarginado. Elitro con marca triangular, grande, alargada y negra en la base (raramente reducida) *porioni* Dechambre
- 11'. Clípeo con el ápice biemarginado (algunas veces difícil de ver si el ápice está gastado). Elitros testáceos, nunca con un triángulo negro
 *ampliata* Bates
- 12 (10'). Apice del clípeo claramente emarginado 13
- 12'. Apice del clípeo truncado, redondeado o parabólico 27
- 13 (12). Pronoto negro. Elitros testáceos. Largo mayor a 28 mm
 *rogezi* Dechambre

- 13'. Pronoto y élitros de colores similares, con o sin manchas o bandas negras. Largo menor a 25 mm 14
- 14 (13'). Pronoto y élitros de un solo color pardo rojizo oscuro o testáceo oscuro, sin manchas o bandas píceas o negras (márgenes pueden ser negras) 15
- 14'. Pronoto y élitro testáceo, con manchas o bandas píceas o negras 16
- 15 (14). Longitud 23 mm o más grandes. Pronoto y pigidio sin márgenes negros. Ancho interocular igual a 3.5 diámetros transversales del ojo *nike* Ratcliffe
- 15'. Longitud 21 mm o menos. Pronoto generalmente con 2 bandas longitudinales negras; pigidio generalmente con una banda o mancha negra a cada lado del medio. Ancho interocular menor a 3 diámetros transversales del ojo *concolor* Burmeister
- 16 (14'). Pronoto en la base con reborde marginal 17
- 16'. Pronoto en la base sin reborde marginal 19
- 17 (16). Pigidio deprimido a cada lado del medio; en vista lateral la superficie es cóncava *maryliza* Ratcliffe, especie nueva
- 17'. Pigidio regularmente convexo, no deprimido a ambos lados del medio; en vista lateral la superficie es ligeramente convexa 18
- 18 (17'). Apice del clípeo profundamente emarginado (Fig. 201). Epipleura gradualmente ensanchada desde aproximadamente las esternitos 1-4, luego se angosta abruptamente. *discicollis* Arrow
- 18'. Apice del clípeo ligeramente emarginado (Fig. 202). Epipleura gradualmente ensanchada desde aproximadamente los esternitos 1-2 (ocasionalmente 3), luego se angosta abruptamente. *stictica* Burmeister
- 19 (16'). Cabeza, pronoto, élitros y pigidio generalmente con setas moderadas a largas. Pronoto en el margen lateral con un fleco de setas moderadas a largas *brittoni* Endrödi
- 19'. Superficie dorsal a lo más con setas cortas. Pronoto en el margen lateral a lo más con setas minúsculas a cortas 20
- 20 (19'). Epipleura/elitro simple, no hinchado o expandido en un reborde, lóbulo o diente. Pronoto pardo rojizo oscuro, élitros testáceos *gravis* Bates
- 20'. Epipleura/elitro hinchado o expandido en un reborde, lóbulo o diente 21
- 21 (20'). Pronoto casi liso, con micropuntuaciones a los lados *mafaffa* Burmeister
- 21'. Pronoto claramente punteado 22
- 22 (21'). Pronoto con puntuaciones en el tercio central más pequeñas que las de la frente. Elitros con la base y los lados bajo el húmero con un margen angosto, negro *atripes* Bates
- 22'. Pronoto con puntuaciones en el tercio central similares en tamaño a las de la frente. Elitros sin margen negro, angosto en la base y a los lados bajo el húmero 23
- 23 (22'). Clípeo con puntuaciones; base con una mancha triangular negra *letiranti* Young
- 23'. Clípeo transversalmente rugoso; base sin una mancha triangular negra (frecuentemente presente en *C. pan*) 24
- 24 (23'). Elitros con una marca en forma de reloj de arena a lo largo de la sutura y cada élitro con 4 manchas a los lados del reloj de arena o con 6 manchas redondeadas a triangulares en cada élitro (Figs. 256-257). Pigidio generalmente con una mancha negra a ambos lados del medio *krombeini* Endrödi
- 24'. Elitros con 4 manchas negras, redondeadas a triangulares en cada uno, nunca con 6 manchas o una marca en forma de reloj de arena. Pigidio nunca con 2 manchas evidentes (algunas veces fuscas a ambos lados del medio) 25
- 25 (24'). Margen epipleural/elitral expandido en un lóbulo alargado a nivel de metacoxa/esternito 1 (Fig. 444). Longitud 17 mm o menos. Pronoto con 2 manchas negras. Esternitos 1 a 5 cada uno con una mancha negra en la esquina posterolateral *zodion* Ratcliffe

- 25'. Margen epileural/elitral expandido en un reborde abrupto y dentiforme a nivel de los esternitos 2 a 3 (Fig. 351). Longitud variable. Pronoto con o sin manchas negras. Esternitos 1 a 5 cada uno generalmente sin mancha negra en la esquina posterolateral (algunas veces presente en *C. pan*) 26
- 26 (25'). Longitud 17-23 mm. Manchas elitrales generalmente grandes. Generalmente se encuentran a elevaciones mayores a 1000 metros *sexpunctata* Burmeister
- 26'. Longitud 14-19 mm. Manchas elitrales generalmente pequeñas. Generalmente se encuentran a elevaciones menores de 1000 metros *brevis* Höhne y *pan* Ratcliffe (algunos *C. pan* tienen manchas negras en las esquinas posterolaterales de los esternitos 1 a 5)
- 27 (12'). Cabeza y pronoto evidentemente alargados 28
- 27'. Cabeza y pronoto normales, no alargados 29
- 28 (27). Pigidio con un tubérculo grande, cónico inmediatamente sobre el medio. Pronoto con el margen lateral cóncavo inmediatamente detrás del ángulo posterior *prolongata* Arrow
- 28'. Pigidio con una convexidad leve justo arriba del medio. Pronoto con el margen lateral solo ligeramente convexo justo detrás del ángulo anterior *pardolocarnoi* Dechambre
- 29 (27'). Base del pronoto con reborde marginal 30
- 29'. Base del pronoto simple, sin reborde marginal 44
- 30 (29). Elitros con epipleura simple o ligeramente engrosada al medio, sin un diente evidente, hinchamiento, o lóbulo 31
- 30'. Elitros con epipleura ligeramente dilatada o con un gran engrosamiento, lóbulo o diente 33
- 31 (30). Tarsos posteriores solo ligeramente más largo que la tibia posterior. Longitud 15.0 mm o más grande *sororia* Bates
- 31'. Tarsos posteriores casi dos veces el largo de la tibia posterior. Longitud 12.0 mm o menos 32
- 32 (31'). Elitro con intervalo sutural negro. Pronoto sin manchas *maculiventris* Höhne
- 32'. Elitros con intervalo sutural testáceo (del mismo color que los élitros). Pronoto generalmente con 4, 6 u 8 manchas, (raramente sin manchas) *williami* Ratcliffe
- 33 (30'). Elitros con epipleura ligeramente dilatada pero carente de una protrusión en forma de ángulo 34
- 33'. Elitros con epipleura claramente dilatada y con o sin una protrusión en forma de ángulo 35
- 34 (33). Elitros con manchas negras o píceas grandes y evidentes (Figs. 219-221). Pronoto pardo rojizo *erotyliana* Arrow
- 34'. Elitros a lo más con leves manchas oscuras poco evidentes y pequeñas. Pronoto generalmente testáceo, con o sin 2 marcas longitudinales *curta* Bates
- 35 (33'). Pigidio claramente setoso 36
- 35'. Pigidio glabro, a lo más con microsetas cerca de la base 38
- 36 (35). Margen lateral de los élitros con un abultamiento en forma de reborde a nivel del esternito 4 *discolor* (Herbst)
- 36'. Margen lateral de los élitros abultado a nivel de los esternitos 1 a 2, claramente emarginado sobre los esternitos 2 a 3, y abultado de nuevo sobre los esternitos 3 a 4 37
- 37 (36'). Quinto esternito abdominal similar en longitud al cuarto, su margen apical normalmente agudo (Fig. 129) *amazona* (L.)
- 37'. Quinto esternito abdominal fuertemente constreñido al centro en el margen apical y longitud de alrededor de la mitad del cuarto segmento (Fig. 130) *multiplex* Casey

- 38 (35). Elitros con una franja oblícua, longitudinal, píceo o negro (Fig. 176); franja raramente reducida o dividida en segmentos; sutura elitral ampliamente (más común) a estrechamente (poco común) oscurecida *complanata* Burmeister
- 38'. Elitros sin franja oblícua o longitudinal. Región de la sutura elitral oscurecida o no 39
- 39 (37). Frente negro o píceo. Longitud del cuerpo 16 mm o más grande *variabilis* Burmeister
- 39'. Frente negro o testácea. Longitud del cuerpo 15.5 mm o menos 40
- 40 (39). Frente negro o píceo 41
- 40'. Frente testácea o pardo rojizo 42
- 41 (40). Tarsómeros negros. Tarsos posteriores de alrededor de 1/3 más largos que la tibia posterior. Epipleura con un diente a nivel del esternito 2. Margen elitral abultado en un reborde alargado *nigratarsis* Ratcliffe
- 41'. Tarsómeros pardo rojizos. Tarsos posteriores similares en longitud a la tibia posterior. Epipleura expandida pero carente de un diente. Margen elitral explanado sobre la expansión epipleural pero sin reborde *unamas* Ratcliffe, especie nueva
- 42 (40). Cabeza y pigidio enteramente pardo rojizos. Elitros carentes de cualquier marca *stockwelli* Ratcliffe, especie nueva
- 42'. Cabeza y pigidio enteramente testáceos. Elitros con manchas o rayas oscuras, pequeñas 43
- 43 (42). Apice del clipeo ampliamente parabólico. Proceso proesternal corto pero bien desarrollado. Elitros con rayas pequeñas y oscuras. Expansión de la epipleura abruptamente angulada en forma de diente *herteli* Endrödi
- 43'. Apice del clipeo estrechamente parabólico. Proceso proesternal bajo, escasamente desarrollado. Elitros con manchas pequeñas y oscuras. Expansión de la epipleura gradualmente arqueada, simple *santaritae* Ratcliffe
- 44 (29). Pronoto y/o élitros con manchas, bandas o patrones en zigzag negros contrastantes 45
- 44'. Pronoto (excepto *C. amblyopsis* ocasionalmente) y élitros sin manchas, bandas o patrones en zigzag negros contrastantes, en vez de esto son de un solo color: testáceos, pardo rojizos, rufos o píceos 54
- 45 (44). Margen elitral/epipleura expandido, algunas veces fuertemente, formando una evidente lóbulo o reborde 46
- 45'. Margen elitral/epipleura simple, sin dilatación, lóbulo o reborde *isthmiensis* Ratcliffe
- 46 (45). Pronoto (generalmete) y élitros cubiertos con setas cortas y densas 47
- 46'. Pronoto y élitros glabros, a lo más con setas dispersas en el cuarto apical de los élitros 48
- 47 (46). Reborde del margen elitral/epipleura expandido a nivel de los esternitos 4 a 5 *quadripunctata* Höhne
- 47'. Reborde del margen elitral/epipleura expandido a nivel de los esternitos 1 a 2 *sparsa* Arrow
- 48 (46). Elitros con con una banda grande y transversal que ocupa todo el cuarto basal; una gran mancha negra o banda transversal negra en el tercio apical 49
- 48'. Elitros con manchas o patrones en zigzag, nunca con una banda grande transversal en el cuarto basal 50
- 49 (48). Pronoto de un solo color, pardo rojizo *gregaria* Heyne y Taschenberg
- 49'. Pronoto pardo rojizo, con 2 manchas o franjas negras, alargadas *conspicua* Sharp
- 50 (48). Frente testácea. Elitros con epipleura simple; margen sutural evidentemente engrosado *mustacha* Ratcliffe, especie nueva
- 50'. Frente oscurecida. Epipleura expandido; margen sutural simple 51
- 51 (50). Epipleura expandido a nivel de la metacoxa o esternitos 1 a 2; margen elitral en vista dorsal hinchado en el medio 52

- 51'. Epipleura elitral tanto expandida como abruptamente estrecha a nivel de los esternitos 3 a 4; margen elitral en vista dorsal hinchado o con reborde evidente bastante atrás del medio. Pigidio glabro 53
- 52(51). Pigidio glabro. Epipleura abruptamente angosto al nivel del esternito 1. Metasterno microscópicamente imbricado, brillante
labidion Ratcliffe, especie nueva
- 52'. Pigidio setoso. Epipleura mas ensanchado a nivel de los esternitos 1-2, luego gradualmente mas angosto. Metasterno áspero-rugoso
lunulata Burmeister
- 53 (51). Epipleura en vista ventral ligeramente engrosada hasta nivel de los esternitos 3 a 4 donde es abruptamente constreñida; margen de los élitros imperceptiblemente abultado. Frente carente de una "máscara" negra completa entre los ojos *fulgurata* Burmeister
- 53'. Epipleura en vista ventral evidentemente engrosada hasta el nivel de los esternitos 3 a 4 donde se constriñe abruptamente y con un ángulo en forma de diente en el borde interno; márgenes de los élitros al mismo nivel expandidos en un reborde evidente y angulado. Frente con una evidente "máscara" negra entre los ojos *weidneri* Endrödi
- 54 (44'). Superficie dorsal enteramente testácea clara u oscura o pardo rojiza o picea (monocromática) 55
- 54'. Pronoto testáceo, rojo cereza oscuro o negro. Elitros testáceos 58
- 55 (54). Antenas con maza similar en longitud a los segmentos del 2 al 7 juntos 57
- 55'. Antenas con maza ligeramente más larga que los segmentos 2 a 7 juntos 56
- 56 (55'). Superficie dorsal testácea *stockwelli* Ratcliffe, especie nueva
- 56'. Superficie dorsal pardo rojiza oscura o picea *castaniella* Bates
- 57 (55). Epipleura simple o débilmente agrandada a nivel de los esternitos 1 a 2. Dientes de las tibias anteriores similarmente espaciados, diente basal solo ligeramente más pequeño que el diente medio. *epistomalis* Bates
- 57'. Epipleura con un pequeño diente en ángulo recto en el margen interno con un reborde pequeño y redondeado inmediatamente después. Tibia anterior con el diente basal ligeramente separado de los otros y muy pequeño
amblyopsis Bates
- 58 (54'). Pronoto color cereza oscuro o negro 59
- 58'. Pronoto testáceo o pardo amarillento 61
- 59 (58). Antena con una maza antenal grande, más larga que los segmentos 2 a 7 juntos *macrophylla* Erichson
- 59'. Antenas con la maza antenal pequeña, más corta o similar a los segmentos 2 a 7 juntos 60
- 60 (59). Tarsos posteriores más cortos que las tibias posteriores. Epipleura en vista ventral solo imperceptiblemente engrosado a nivel del esternito 2
melanocephala (Fabr.)
- 60'. Tarsos posteriores similares en longitud a las tibias posteriores. Epipleuras en vista ventral evidentemente agrandados a nivel de esternitos 1 a 2 y se estrechan abruptamente *sanguinicolis* Burmeister
- 61 (58). Epipleura en vista ventral simple, no engrosados o agrandados
almitana Dechambre
- 61'. Epipleura en vista ventral evidentemente dilatados o expandidos en un reborde 62
- 62 (61). Tibias anteriores con el diente basal bastante separado de los otros. Esternitos abdominales del 1 al 5 de color piceo o negro *confusa* Endrödi
- 62'. Tibia anterior con el diente basal similarmente separado que los otros. Esternitos abdominales normalmente testáceos o pardo rojizos 63
- 63 (62). Cuerpo corto, oval. Longitud menor de 9.2 mm. Pronoto con puntuaciones moderadas en densidad y tamaño *ovulum* Bates
- 63'. Cuerpo alargado. Longitud mayor de 13 mm. Pronoto generalmente con puntuaciones dispersas, pequeñas *mutata* Harold

***Cyclocephala alazonia* Ratcliffe,
new species**
(Figs. 116-119)

TYPE MATERIAL. Holotype labeled "Est. Eladios, 820 M, Ref. Penas Blancas, Res. Biol. Monteverde, Prov. Alaj., COSTA RICA, N. Obando, Jul 1991, L-N-254750, 457650." Allotype with same data. Types deposited at INBio (Santo Domingo de Heredia, Costa Rica).

HOLOTYPE. Male. Length 21.3 mm; width 10.9 mm. Color dark reddish brown, extreme apices of femora and tibiae black. *Head:* Frons with punctures moderate in size, moderately dense. Clypeus with surface transversely rugulose; apex broad, emarginate. Interocular width equals 3.0 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. *Pronotum:* Surface with small, sparse punctures, punctures becoming slightly denser in anterior angles. Base without marginal bead. *Elytra:* Surface with shallow punctures moderate in size and density, rows of punctures indistinct. Posterior margin of each apical umbone with 4 long setae. *Pygidium:* Surface glabrous, with minute, sparse punctures. In lateral view, surface convex, moreso in apical half. *Legs:* Foretibia tridentate, basal tooth strongly removed from others. Foretarsi missing from both legs. Posterior tarsus subequal in length to posterior tibia. *Venter:* Prosternal process moderately long, columnar, apex expanded into a large, transverse oval with transverse, raised "button" on anterior half. *Parameres:* Figs. 117-118.

ALLOTYPE. Female. Length 20.1 mm; width 10.6 mm. As holotype except in the following respects: *Pronotum:* Punctures small and sparse on disc, becoming moderate in size and density on sides. *Elytra:* Post-apical umbone setae short, perhaps broken. Epipleuron (ventral view) with tooth-like expansion at level of suture between abdominal sternites 1-2; elytral margin just behind and above tooth swollen into a low, elongate lobe. *Pygidium:* Surface with small to moderate punctures; punctures sparse at center, becom-

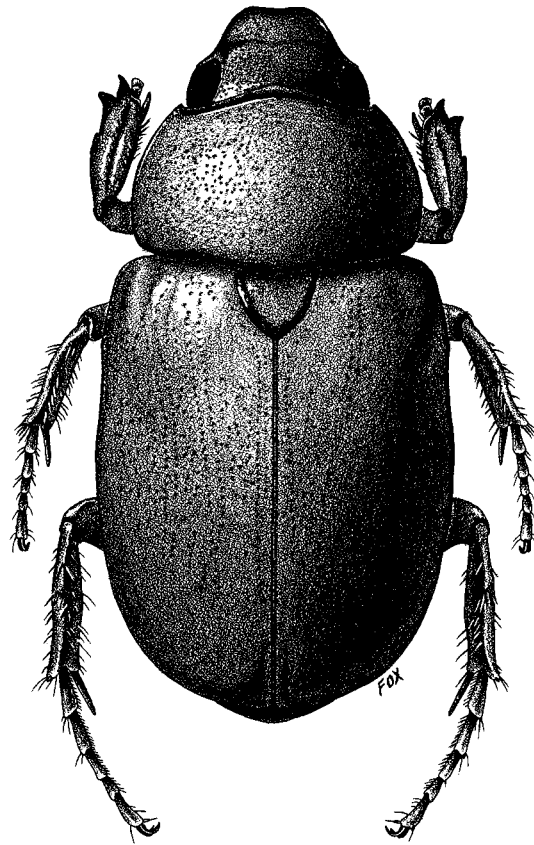
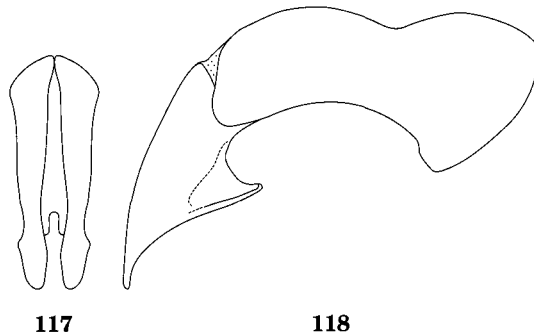


Fig. 116. *Cyclocephala alazonia*.



Figs. 117-118. *Cyclocephala alazonia* parameres.

ing denser on sides; anterior angles rugulose. In lateral view, surface nearly flat with extreme apex strongly convex. *Legs:* Foretarsi missing but known to be simple. Posterior tarsus slightly shorter than posterior tibia.



Fig. 119. Distribution of *Cyclocephala alazonia* in Costa Rica.

ETYMOLOGY. From the Greek *alazon*, meaning an imposter. Used here in reference to the close similarity of *C. alazonia* to the South American *C. rubescens* Bates.

DISTRIBUTION. *Cyclocephala alazonia* is known only from the Peñas Blancas Refuge downslope from Monteverde, Costa Rica.

LOCALITY RECORDS (Fig. 119). 2 specimens examined.

COSTA RICA (2). ALAJUELA (2): Estación Eladios.

TEMPORAL DISTRIBUTION. July (2).

DIAGNOSIS. Within the study area, this species most closely resembles *C. amblyopsis* Bates except that *C. alazonia* is much larger, has an emarginate clypeal apex (convex in *C. amblyopsis*), and has a glabrous pygidium (setose in *C. amblyopsis*). The male parameres of the two species are nearly identical. In the females, the marginal flange on the elytra is a low elongate lobe in *C. alazonia* and an abruptly rounded flange in *C. amblyopsis*.

Cyclocephala alazonia is also similar in overall appearance, including the parameres, to the South American *C. rubescens* Bates. However, in *C. alazonia*, the surface of the clypeus is punctate (rugulose in *C. rubescens*),

the frons is reddish brown (black in *C. rubescens*), the pronotum lacks marks or vittae (present in *C. rubescens*), the pygidium is glabrous (setose in *C. rubescens*), and the foretibia is relatively slender (thicker and stouter in *C. rubescens*).

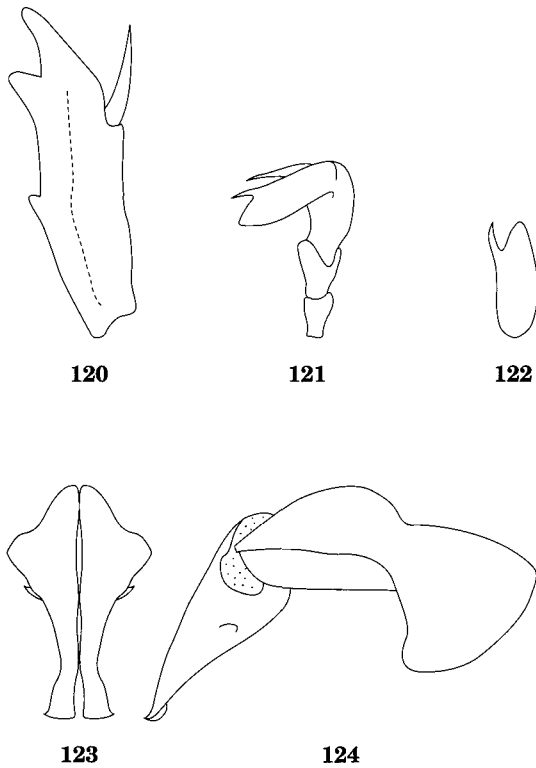
BIOLOGY. The two known specimens were collected in premontane rain forest at an elevation of 820 meters. They were both covered with sticky pollen, suggesting they were feeding inside a flower such as an aroid.

***Cyclocephala almitana*
Dechambre, 1992**

(Figs. 120-126)

Cyclocephala almitana Dechambre 1992a: 65.
Cyclocephala dissimulata Ratcliffe 1992b: 218
(**NEW SYNONYMY**).

DESCRIPTION. Length 8.5-11.0 mm; width 3.9-4.5 mm. Color of elytra testaceous with pronotum and scutellum slightly darker; clypeus, pygidium, and legs yellowish-brown; frons black. *Head:* Frons moderately punctate, punctures moderate in size but becoming denser and slightly larger anteromedially. Clypeus weakly, transversely rugulose in basal half, roughened in apical half; apex broadly subtruncate, weakly reflexed. Interocular width equals 3.0 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. *Pronotum:* Surface moderately densely punctate; punctures moderate in size (subequal to those on frons). Base lacking marginal bead. *Elytra:* Surface moderately densely punctate, punctures larger than those of pronotum, shallow, some in rows. Epipleuron (ventral view) of female simple, not thickened or expanded. *Pygidium:* Surface rugopunctate in basal half, roughened in apical half. In lateral view, surface evenly convex in male, weakly convex in female. *Legs:* Foretibia tridentate, basal tooth distinctly removed from others (Fig. 120). Foretarsus in males enlarged: tarsomere 4 only slightly enlarged and produced ventrally; tarsomere 5 enlarged, weakly curved, with small swelling near base on medial edge with 2 setae; median claw large, strongly curved, with a broad lobe at base, apex widely cleft



Figs. 120-124. *Cyclocephala almitana*: (120) left foretibia of male; (121-122) enlarged claw on foretarsus of male; (123-124) parameres.

(Figs. 121-122). Posterior tarsus shorter than posterior tibia. *Venter*: Prosternal process moderately long, columnar, apex obliquely flattened into a transverse oval with raised, transverse "button" on anterior half. *Parameres*: Figs. 123-124.

DISTRIBUTION. *Cyclocephala almitana* was described from Ecuador. Ratcliffe (1992b) reported it (as *C. dissimulata*) from primarily the Atlantic slopes (mostly lowlands) of Costa Rica and western Panama. One specimen is known from central Panama.

LOCALITY RECORDS (Figs. 125-126). 305 specimens examined.

COSTA RICA (265). ALAJUELA (14): Estación Eladios, Estación Laguna Pocosol, Estación San Ramon, I.C.E. Tunnel (S side Lake Arenal), Upala; CARTAGO (28): Tapanti, Turrialba; GUANACASTE (3): Estación Las

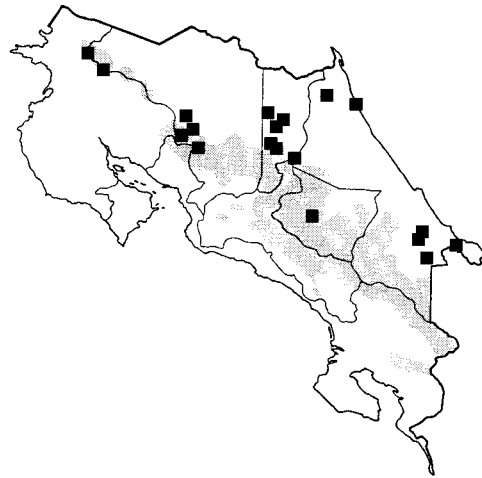


Fig. 125. Distribution of *Cyclocephala almitana* in Costa Rica.

Pailas; HEREDIA (29): Estación El Ceibo, Estación Magsasay, Finca Naranja Valenciana, Las Horqueta de Sarapiquí, La Selva Biological Station; LIMÓN (188): Amubri, Bribri, Estación Cuatro Esquinas, Estación Hitoy Cerere, Estación Miramar; SAN JOSÉ (3): Estación Carrillo, Quebrada Sanguijuela.

PANAMA (40). BOCAS DEL TORO (39): Chiriqui Grande (4 km S), Corriente Grande, Miramar, Punta Peña, Río Changuinola; PANAMA (1): El Llano (15 km N).

TEMPORAL DISTRIBUTION. January (10), February (21), March (22), April (40), May (45), June (9), July (22), August (17), September (13), October (25), November (34), December (24).

DIAGNOSIS. *Cyclocephala almitana* is distinguished by the male parameres and widely cleft protarsal claw in combination with a relatively small size, testaceous elytra with slightly darker pronotum, and a pronotum without a basal marginal bead. It is one of only three species in the study area (*C. macrophylla* and *C. melanocephala* are the other two) with a widely cleft protarsal claw in the males. Both of the other two species are distinctly bicolored, with a dark cherry-red or black pronotum whereas *C. almitana* has a light yellowish-brown pronotum.



Fig. 126. Distribution of *Cyclocephala almitana* in Panama.

BIOLOGY. Adults are attracted to lights. They occur in tropical moist forests, tropical wet forests, premontane rain forests, and lower montane moist forests at elevations of near sea level to 1,300 meters (most below 800 meters).

***Cyclocephala amazona* (Linnaeus, 1767)**

(Figs. 127-129. 131-134)

Scarabaeus amazonus Linnaeus 1767: 551.

Melolontha nigrocephala Degeer 1774: 321 (synonym).

Melolontha signata Fabricius 1781: 39 (synonym).

Melolontha pallens Fabricius 1798: 132 (synonym).

Melolontha uncinata Illiger in Olivier 1802: 49 (synonym).

Cyclocephala inconstans Burmeister 1847: 43 (synonym).

Cyclocephala detecta Bates 1888: 300 (synonym).

Cyclocephala beaumonti Casey 1915: 140 (synonym).

Cyclocephala auriculata Casey 1915: 141 (synonym).

Cyclocephala signata boliviensis Höhne 1923b: 354 (subspecies).

DESCRIPTION. Length 12.0-16.6 mm; width 5.7-7.5 mm. Color testaceous: frons black; pronotum usually with 2 longitudinally parallel, black vittae, each vitta sinuate on outer edge, vitta sometimes reduced to small, round spot near anterior margin or (rarely) absent; elytra with narrow, black line along suture, other piceous to black markings (Fig.) variable as follows: usually with small, elongated, oblique dash on disc near base, a small, round to elongate spot behind humerus, and a small, subtriangular spot on disc behind middle, all spots variably reduced or absent, female with piceous to black spot on lateral margin at expanded epimeron/marginal invagination; pygidium occasionally darkened on sides; femora and tarsomeres each with apices darkened. *Head:* Frons with punctures moderately dense, moderately large, setigerous in males mesad of each eye (females lack setae); setae short, tawny in color. Clypeus in males with surface usually less densely punctate; punctures usually small, setose, setae as on frons; surface becoming weakly rugulose or roughened apically; surface in females transversely rugulose to rugopunctate, lacking setae; sides subparallel at base, anterior angles broadly rounded to a broadly subtruncate apex; apex with marginal bead, weakly reflexed. Interocular width equals 2.5 transverse eye diameters in males, 3.0 transverse eye diameters in females. Antenna with 10

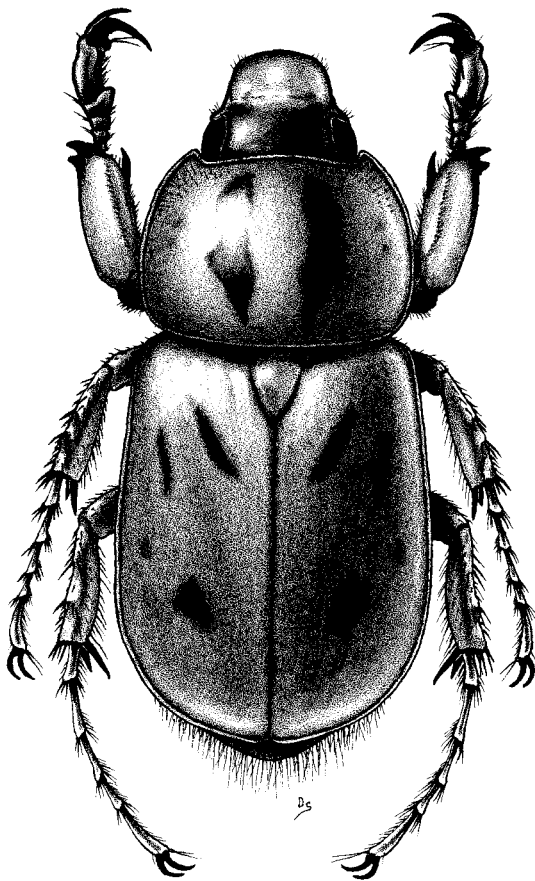
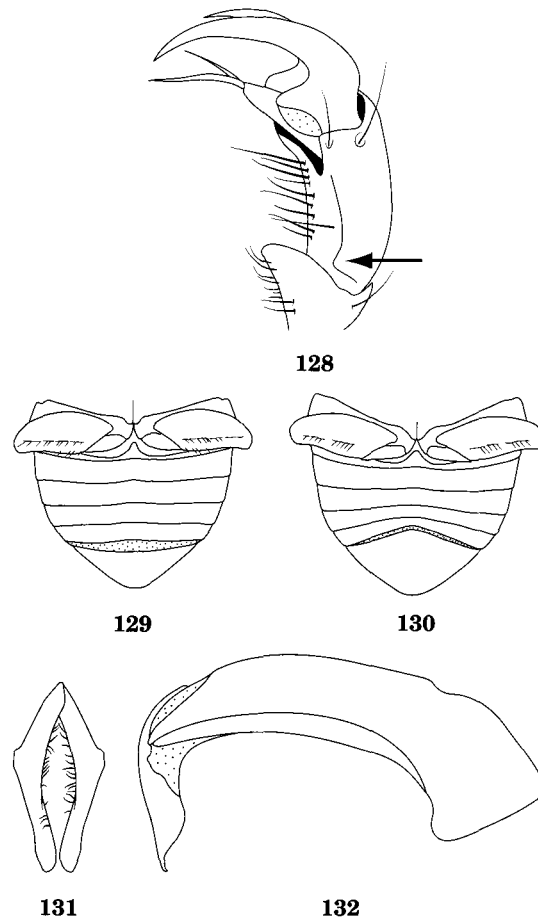


Fig. 127. *Cyclocephala amazona*.

segments, club subequal in length to segments 2-7. *Pronotum*: Surface punctate; punctures moderate in density in males, a little denser in females; size small to mostly moderate in males, nearly all moderate in size in females; males with short setae on disc (often abraded away) and slightly longer setae on lateral thirds of pronotum, females with short setae on lateral thirds; setae tawny in color. Base with complete marginal bead. *Elytra*: Surface finely shagreened with moderately dense, shallow punctures, rows of punctures indistinct; punctures often setigerous, setae sparse, short, tawny. Epipleuron (ventral view) of females swollen at level of abdominal sternites 1-2, deeply emarginate at level of abdominal sternites 3-4, swelling ending in acute tooth at abdominal sternite 4; in dorsal view, side of elytra behind middle swollen,



Figs. 128-132. *Cyclocephala amazona*: (128) foretarsus and claw of male; (129) sternites of female; (130) sternites of *C. multiplex* female for comparison; (131-132) parameres.

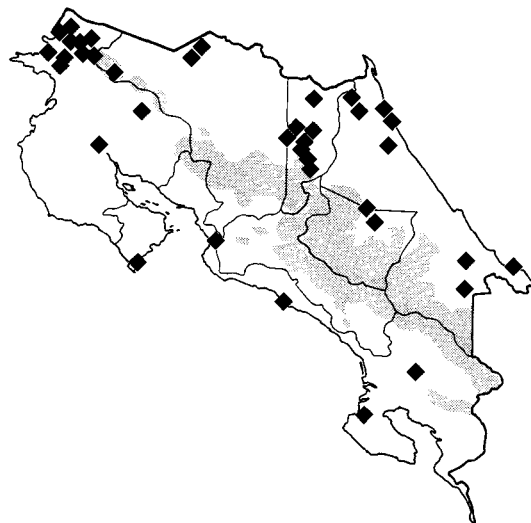


Fig. 133. Distribution of *Cyclocephala amazona* in Costa Rica.

swelling deeply emarginate. *Pygidium*: Surface shagreened, punctate; punctures small, moderate in density, setigerous; setae in males long, tawny, setae in females short (sometimes worn off). In lateral view, surface in males convex, especially in apical third, in females weakly convex or flat. *Legs*: Foretibia in males bidentate, tridentate in females. Foretarsus in males enlarged: tarsomere 4 with large, ventral flange; 5th large, curved, flattened on venter, base on inner side with distinctive tooth (Fig. 128); median claw large, curved, base on ventral edge with large, elongate lobe, apex of claw entire. Foretarsus in female simple. Posterior tarsus about 1.8 times longer than posterior tibia. *Venter*: Prosternal process elongate, subconical. Females with 5th abdominal segment normal, not strongly constricted at center (Fig. 129). *Parameres*: Figs. 131-132.

DISTRIBUTION. *Cyclocephala amazona* is probably distributed from Costa Rica south to Paraguay and Chile. The range for this species has been previously reported (Endrödi 1966, 1985a) as extending north through Mexico, but I now believe that those records refer to *C. multiplex* Casey. All the specimens I have examined of putative *C. amazona* from Mexico, Belize, El Salvador, Guatemala, and Honduras were *C. multiplex*.

Subspecies have been designated for populations in the West Indies [*C. amazona signata* (Fabr.)] and in Bolivia [*C. amazona*

bolviensis Höhnel]. This species is broadly distributed in the lowlands of Costa Rica and Panama.

LOCALITY RECORDS (Figs. 133-134). 2,083 specimens examined.

COSTA RICA (290). ALAJUELA (7): Caño Negro, Colonia Libertad, Finca San Gabriel (2 km SW Dos Ríos), Parq. Nac. Rincón de la Vieja; CARTAGO (20): Turrialba, Tuis; GUANACASTE (21): Cerro El Hacha (12 km SE La Cruz), Estación Maritza, Estación Palo Verde, Estación Pitilla, Estación Santa Rosa, Finca Jenny (30 km N Liberia), Parq. Nac. Guanacaste; HEREDIA (115): Estación El Ceibo, Estación Magsasay, Finca Naranjo Valenciana (2 km S Pueblo Nuevo), La Virgen de Sarapiquí, La Selva Biological Station, Las Horquetas de Sarapiquí, Los Arbolitos, Río Frio; LIMÓN (111): Amubri, Cairo, Cerro Cocori, Cerro Tortuguero, Estación Cuatro Esquinas, Estación Hitoy Cerere, Estación Sierpe, Guapiles, Madre de Dios, Milas, Río Sardinas; PUNTARENAS (16): Buenas Aires, Estación Cabo Blanco, Parq. Nac. Corcovado, Parq. Nac. Manuel Antonio, Reserva Biológica Carara, Vuelta Campana.

PANAMA (1,793). BOCAS DEL TORO (635): Chiriqui Grande (4 km S), Continental Divide (2 mi N toward Chiriqui Grande), Miramar; CANAL ZONE (664): Achiotte Road, Albroom Forest, Ancon, Barro Colorado Island, Black

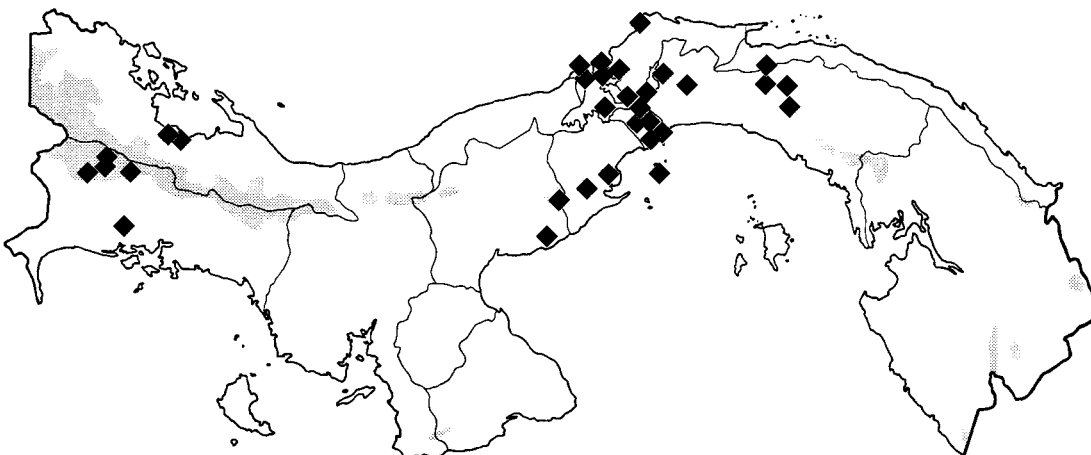


Fig. 134. Distribution of *Cyclocephala amazona* in Panama.

Tank Road, Coco Solo hospital, Culebra, Diablo Heights, Ft. Clayton, Ft. Davis, Ft. Gulick, Ft. Kobbe, Ft. Sherman, Gatun Lake lookout, Howard AFB, Madden Dam, Madden Forest, Margarita, Old Gamboa Road, Paraiso, Piña Road, Pipeline Road (km 2, 4), Skunk Hollow, Tabernilla; CHIRIQUI (13): Boquete, Cerro Punta, David, Lino, Volcán Chiriqui; COCLÉ (12): El Valle, La Mesa above El Valle, Río Hato; COLÓN (68): Colón, Portobelo (15 km E), Santa Rita Ridge; PANAMA (398): Cañita (31 km E), Cerro Azul, Cerro Campana, El Llano-Carti Road (km 8, 10, 15), Isla Majé, Sajalices, Taboga Island; SAN BLAS (3): El Llano (19 km N).

TEMPORAL DISTRIBUTION. January (9), February (2), March (35), April (61), May (806), June (202), July (713), August (40), September (40), October (7), November (10), December (7).

DIAGNOSIS. *Cyclocephala amazona* is remarkably similar to *C. multiplex* Casey in external morphology as well as in the form of the male parameres. In general, the elytral spots in *C. amazona* are small whereas they are enlarged in *C. multiplex* (best seen in side-by-side series of each species). Additionally, the oblique, post-scutellar "dash" is slender and short in *C. amazona* but is thickened and elongated (often extending from the base of the elytron to the suture) in *C. multiplex*. Size of elytral markings is an unreliable character with which to separate species, but, fortunately, there are other characters as well.

In the males, the clypeus of *C. amazona* is setose whereas in *C. multiplex* it is glabrous; both species possess setae mesad of each eye on the frons. In the females of *C. amazona*, the fifth abdominal sternite is subequal in length to the fourth segment whereas in females of *C. multiplex* the fifth sternite is strongly constricted at its center on the apical margin and is about half the length of the fourth segment (Fig. 130).

BIOLOGY. Adults are attracted to lights at night, often in large numbers. Bullock (1981) reported adults feeding in the palm flowers of *Bactris wendlandiana* Burret (Arecaceae) in

Costa Rica. Beach (1982) observed them in the inflorescences of *Cyclanthus bipartitus* Poiteau (Cyclanthaceae), also in Costa Rica, and in the flowers of *Bactris porschiana* Burret and *Bactris gasipaes* Kunth (James Beach and Helen Young, personal communications). Label data for 11 Panamanian specimens indicated they were feeding in the inflorescences of *Astrocaryum alatum* Loomis (Arecaceae).

Rickson *et al.* (1990) reported that the thick-walled trichome cells of the peach palm, *Bactris gasipaes*, possess a thick, highly lignified cell wall, and that these cells are consumed by *C. amazona*. These trichome cells have no nutritive value and pass intact through the beetle's digestive system whereas ingested pollen is crushed. They suggested that these specialized plant cells functioned as gastroliths to help crush pollen in the beetle's digestive tract.

Cyclocephala amazona has been collected from tropical dry forests, tropical moist forests, tropical wet forests, and premontane rain forests at elevations ranging from near sea level to 700 meters.

Cyclocephala amblyopsis Bates, 1888

(Figs. 135-139)

Cyclocephala amblyopsis Bates 1888: 307.

Cyclocephala amblyopsis monochroa Bates 1888: 308 (synonym).

DESCRIPTION. Length 15.5-19.3 mm; width 7.2-9.2 mm. Color reddish brown to dark reddish brown; frons, occasionally clypeus, and occasionally 2 longitudinal bands on pronotum piceous or black. *Head:* Entire surface with punctures moderate in density, moderate in size, shallow; females with apical half of clypeus densely punctate, sometimes becoming weakly rugopunctate. Clypeus with apex weakly convex or nearly flat, anterior angles rounded. Interocular width equals 3.0-3.3 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. *Pronotum:* Surface in most males with punctation as on frons,

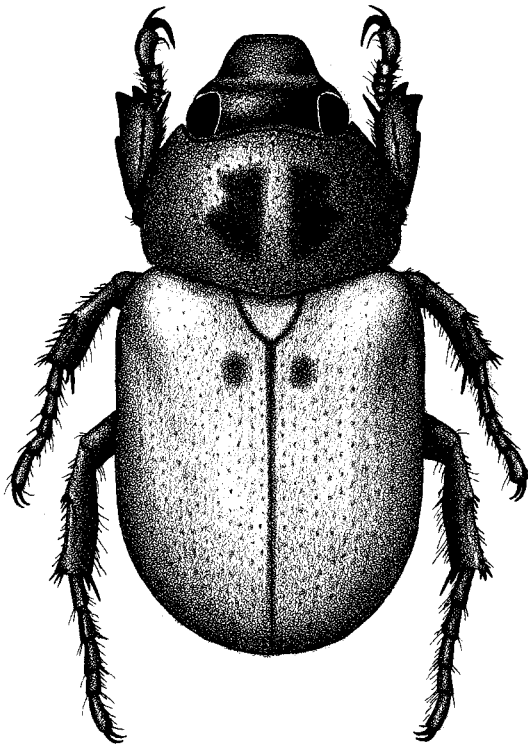
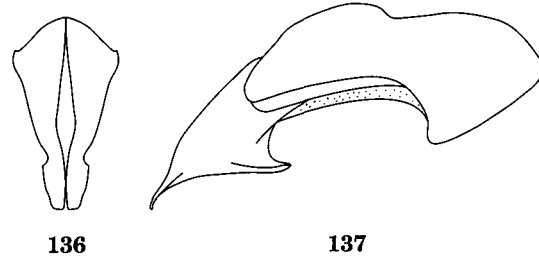


Fig. 135. *Cyclocephala amblyopsis*.

some males and nearly all females with punctation reduced (punctures small and sparse). Base without marginal bead. *Elytra*: Surface with rows of punctures; punctures in striae and intervals moderately large, shallow. Pristine specimens with minute setae on apices. Epipleuron (ventral view) of females with small, right-angled tooth on inner margin at level of abdominal sternite 2 and with short, abruptly rounded flange immediately behind and above on elytral margin. *Pygidium*: Surface sparsely punctate; punctures small, setigerous; setae in males long, testaceous, sparse, occasionally worn away; setae in females less dense, often worn away. In lateral view, surface of males regularly convex (occasionally weakly convex), females with surface nearly flat. *Legs*: Foretibia tridentate, basal tooth small and strongly removed from others. Foretarsus in males enlarged: tarsomere 4 strongly enlarged with large ventral tooth; 5th large, weakly curved, with a ventral, sub-



136

137

Figs. 136-137. *Cyclocephala amblyopsis* parameres.

apical angulation; median claw enlarged, strongly curved, apex finely cleft. Foretarsus in females simple. Posterior tarsus subequal in length to posterior tibia. *Venter*: Prosternal process long, columnar, apex obliquely flattened into a broadly transverse with raised "button" on anterior half or two-thirds. *Parameres*: Figs. 136-137.

DISTRIBUTION. *Cyclocephala amblyopsis* is known from Guatemala to Ecuador and Bolivia (Endrödi 1966, 1985a). It is generally distributed throughout Costa Rica and Panama although there are no records for the lowland tropical moist forests in the Canal Zone.

LOCALITY RECORDS (Figs. 138-139). 639 specimens examined.

COSTA RICA (514). ALAJUELA (53): Cerro Campana (6 km NW Dos Ríos), Colonia Río Celeste (E side Volcán Tenorio), Estación Eladios, Estación San Ramón, Finca San Gabriel (2 km SW Dos Ríos), Guatuso Falda (E Volcán Tenorio), ICE tunnel (E side Lake Arenal), Piedra Negra, San Ramón; CARTAGO (51): Refugio Nacional Tapanti, Tuis Turrialba (Grano de Oro); GUANACASTE (73): Estación Maritza, Estación Pitilla, Finca Montezuma (SW slope Volcán Tenorio), Río Gongora (6 km NE Quebrada Grande de Liberia), Tierras Morenas, Volcán Tenorio; HEREDIA (84): Chilamate Sarapiquí, Estación El Ceibo, Estación Magsasay, Finca La Selva, Finca Naranjo Valenciana (2 km S Pueblo Nuevo), La Virgen de Sarapiquí; LIMÓN (111): Amubri, Cerro Tortuguero,

Estación Hitoy Cerere, Estación Miramar, Estación Quebrada Gonzales; PUNTARENAS (138): Buenos Aires, Estación Biológica Las Alturas, Estación Esquinas, Estación La Casona, Estación Las Mellizas, Estación Quebrada Bonita, Estación Sirena, Fila Guerra, Monteverde, Osa Peninsula, Parq. Nac. Amistad, Punta Blanco, Rancho Quemado, Rincón (2.5 mi SW), Río Coto Brus, San Luis, San Vito; SAN JOSÉ (4): Desamparaditos, Estación Bijagual, San José, San Pedro.

PANAMA (125). BOCAS DEL TORO (59): Corriente Grande, 2 mi N of divide on high-

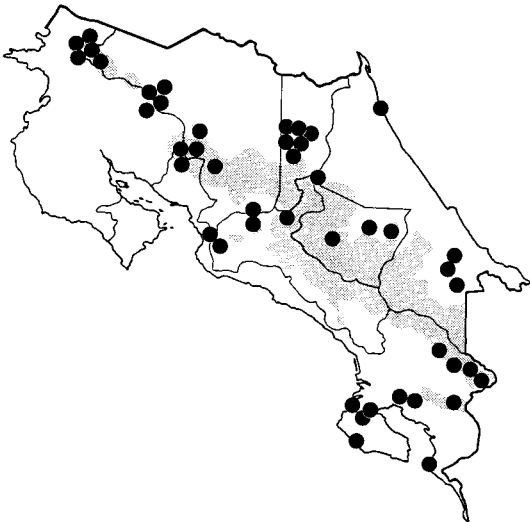


Fig. 138. Distribution of *Cyclocephala amblyopsis* in Costa Rica.

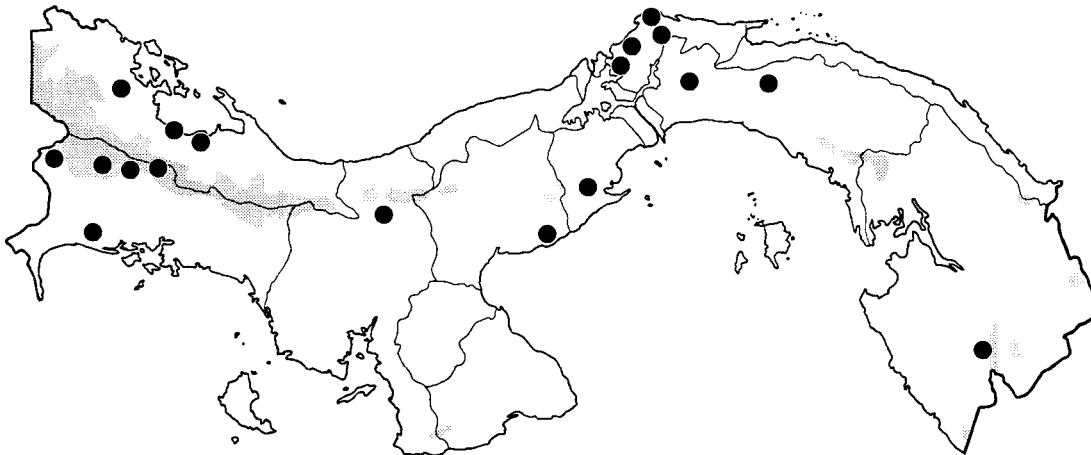


Fig. 139. Distribution of *Cyclocephala amblyopsis* in Panama.

way to Chiriqui Grande, Miramar, Rambala (20 km S); CHIRIQUI (19): Boquete, Bugaba, Fortuna Dam, Hartmann's Finca (Santa Clara), Lino; COCLÉ (1): El Valle; COLÓN (7): Cerro Viejo, Río Guanache Bridge, Salamanca (8 km N), Santa Rita Ridge; DARIEN (5): Cana; PANAMA (30): Cerro Azul, Cerro Campana, El Llano-Carti Road (km 8, km 13); VERAGUAS (4): Alto de Piedra.

TEMPORAL DISTRIBUTION. January (40), February (29), March (31), April (80), May (88), June (79), July (66), August (42), September (25), October (50), November (53), December (29).

DIAGNOSIS. This species, with its relatively uniform, dark reddish-brown coloration, superficially resembles *C. gravis* Bates, *C. alazonia* Ratcliffe n. sp., and *C. epistomalis* Bates. *Cyclocephala amblyopsis* is uniformly dark reddish brown whereas *C. gravis* is noticeably bicolored with a dark cherry-red pronotum and testaceous elytra. *Cyclocephala amblyopsis* has a weakly convex clypeal apex whereas *C. gravis* and *C. alazonia* have an emarginate apex. In addition, *C. gravis* never has the longitudinal dark bands on the pronotum that are present in some *C. amblyopsis*, and, finally, the parameres are different (Figs. 136-137, 238-239, 117-118).

Cyclocephala amblyopsis that lack the black pronotal vitae also closely resemble *C.*

epistomalis. Males are easily separated because the three teeth on the foretibia are unevenly spaced in *C. amblyopsis* and subequally spaced in *C. epistomalis*. Females may be distinguished by the distinct tooth on the epipleuron in *C. amblyopsis* versus the simple or nearly-so epipleuron in *C. epistomalis*.

BIOLOGY. Adults have been taken at lights and in the inflorescences of *Dieffenbachia longispatha* Engler and Krause (Araceae) in Costa Rica (Young 1986, 1988a-b) and Panama (personal observation). Morón (1997b) found adults feeding on the inflorescences of *Xanthosoma hoffmanni* Schott, *X. mexicanum* Liebm., *X. robustum* Schott, and *X. violaceum* Schott (Araceae) in Chiapas, Mexico. This species is found in tropical moist forests, tropical wet forests, premontane wet forests, premontane rain forests, and lower montane rain forests at elevations of 50-1,520 meters.

***Cyclocephala ampliata* Bates,
1888**

(Figs. 140-144)

Cyclocephala ampliata Bates 1888: 311.

DESCRIPTION. Length 22.0-24.0 mm; width 11.0-12.8 mm. Color dark reddish brown except for testaceous elytra. **Head:** Surface with punctures moderate in size and density (occasionally sparse on frons), clypeus often with punctures dense and moderately large. Clypeus with sides weakly arcuate, anterior angles narrowly rounded, apex broad and weakly bisinuate (weakly emarginate either side of middle; often best observed in front of and slightly below clypeal apex or from above and behind). Interocular width equals 3.0 transverse eye diameters. Antenna with 10 segments, club a little shorter than segments 2-7. **Pronotum:** Surface with sparse, small to moderately sized punctures, punctures becoming slightly larger on sides. Base with marginal bead that becomes obsolete in front of scutellum. **Elytra:** Surface with punctures moderately large, shallow, moderate in

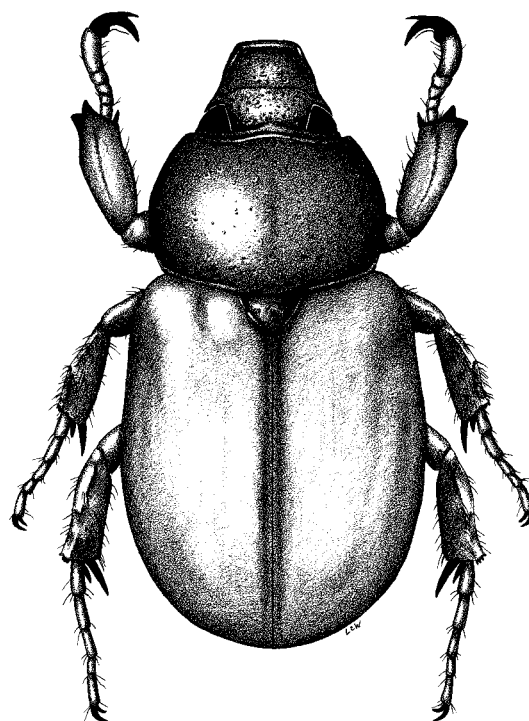
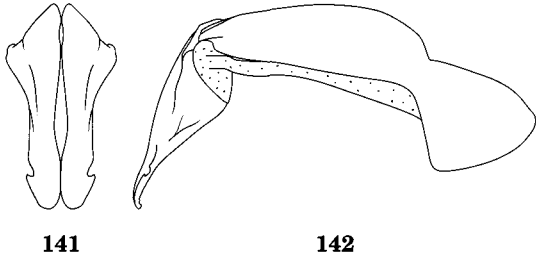


Fig. 140. *Cyclocephala ampliata*.

density, rows indistinct. Epipleuron (ventral view) of females expanded into elongate lobe extending from middle of metacoxa to second abdominal sternite; in lateral view, ventral edge with an angulate tooth at about level of middle of abdominal sternite 1 to middle of abdominal sternite 2. **Pygidium:** Surface moderately densely punctate; punctures moderately large, setigerous; setae moderately dense (when not worn away), moderately long, tawny in color; setae often reduced at center apex in female. In lateral view, surface in male weakly convex, that of female nearly flat. **Legs:** Foretibia tridentate, basal tooth far removed from others. Foretarsus in males enlarged: tarsomere 4 with strong ventral tooth; 5th large, weakly curved, without lobe or tooth on ventral side near base; median claw large, curved, apex finely split. Foretarsus in females simple. Posterior tarsus slightly longer than posterior tibia. **Venter:** Prosternal process short, stout, apex obliquely flattened into a transverse oval with raised "button" on anterior 1/2 to 2/3. **Parameres:** Figs. 141-142.



Figs. 141-142. *Cyclocephala ampliata* parameres.

DISTRIBUTION. *Cyclocephala ampliata* is known from Nicaragua and Panama (Endrödi 1966, 1985a) and Costa Rica (Ratcliffe 1992). It is an uncommon lowland species in both Costa Rica and Panama. So far in Panama, it is known only from the far west.

LOCALITY RECORDS (Figs. 143-144). 38 specimens examined.

COSTA RICA (30). HEREDIA (10): Estación Magsasay, La Selva Biological Station, Los Arbolitos, Río Frio; LIMÓN (20): Amubri, Estación Hitoy Cerere, Hamburg Farm, Sector Cerro Cocori.

PANAMA (8). BOCAS DEL TORO (7): Chiriqui Grande (4 km S), Corriente Grande, Miramar; CHIRIQUI (1): Lino.

TEMPORAL DISTRIBUTION. February (2), March (3), April (3), May (5), June (4), July (3), August (1), September (9), October (1), November (2), December (2).

DIAGNOSIS. *Cyclocephala ampliata* is one of the larger species of *Cyclocephala* in the study area. That, in combination with its distinctive coloring, bi-emarginate clypeal apex, and form of the parameres, should readily enable identification of this species. It should be noted that if the apex of the clypeus is at all worn, then the bi-emarginate border (which is very shallow to begin with) may be obscured.

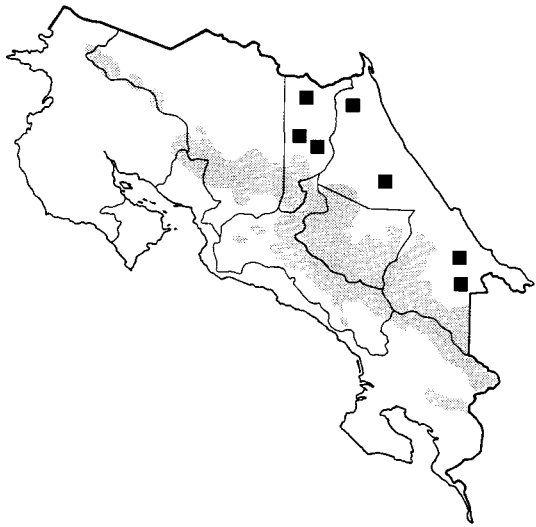


Fig. 143. Distribution of *Cyclocephala ampliata* in Costa Rica.



Fig. 144. Distribution of *Cyclocephala ampliata* in Panama.

BIOLOGY. Adults are attracted to lights, and there are two records of adult males being taken in the inflorescence of a *Philodendron* species (Araceae) in Costa Rica (Helen Young, personal communication, 1983). They have been collected from tropical wet forests, premontane wet forests, and premontane rain forests at elevations ranging from near sea level to 1,000 meters.

***Cyclocephala atripes* Bates, 1888**
(Figs. 145-149)

Cyclocephala atripes Bates 1888: 309.

DESCRIPTION. Length 15.8-19.2 mm; width 8.6-10.2 mm. Color testaceous except for black head, elytra at extreme base and around sides beneath humerus, legs, usually coxae, and all or part of thoracic sternites. *Head:* Frons and base of clypeus punctate, punctures moderate in density and size. Clypeus transversely rugulose, more coarsely so in female; apex broadly, weakly emarginate. Interocular width equals 2.5-2.7 transverse eye diameters. Antenna 10-segmented, club subequal to or slightly shorter than segments 2-7. *Pronotum:* Surface on central third nearly smooth or sparsely punctate, punctures small; punctures on lateral thirds small, moderate in density. Base lacking marginal bead. *Elytra:* Surface with distinct punctures; punctures moderate in density, small, rows evident; a few punctures near apices with minute, tawny setae. Epipleuron (ventral view) of females slightly expanded to level of abdominal sternites 2-3, mesal edge with small, obtuse tooth, lateral edge produced into short, rounded flange. *Pygidium:* Surface on disc sparsely punctate, punctures small, setigerous; setae small, tawny; punctures becoming slightly larger and denser on sides, setae dense. In lateral view, surface in males regularly convex; in females, surface nearly flat. *Legs:* Foretibia tridentate, basal tooth removed from others. Foretarsus in males enlarged: tarsomere 4 swollen beneath into small subtriangular swelling; 5th large, curved, slightly concave beneath; median claw large, curved, with large lobe at base,

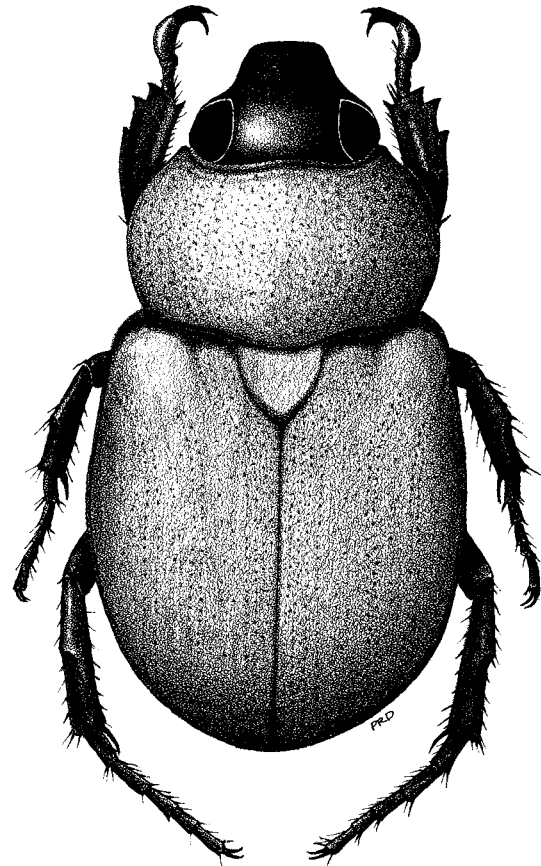
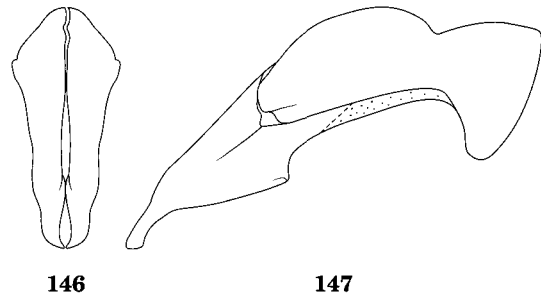


Fig. 145. *Cyclocephala atripes*.



Figs. 146-147. *Cyclocephala atripes* parameres.

apex cleft. Foretarsus in females simple. Posterior tarsus slightly longer than posterior tibia, subequal in length in female. *Venter:* Prosternal process moderately long, columnar, apex an obliquely flattened oval with raised "button" on anterior 1/3-1/2. *Parameres:* Figs. 146-147.

DISTRIBUTION. *Cyclocephala atripes* is known from Nicaragua, Costa Rica, Panama, Colombia, and Ecuador (Endrödi 1966; Ratcliffe 1992). In Costa Rica and Panama, it is broadly distributed but is seemingly more abundant in Panama.

LOCALITY RECORDS (Figs. 148-149). 130 specimens examined.

COSTA RICA (77). ALAJUELA (2): Río San Lorencito; GUANACASTE (7): Estación Pitilla; HEREDIA (64): Estación Magsasay, La Selva Biological Station; LIMÓN (4): Cerro Tortuguero, Estación Hitoy Cerere.



Fig. 148. Distribution of *Cyclocephala atripes* in Costa Rica.

PANAMA (53). BOCAS DEL TORO (4): Continental Divide (2 mi N), Corriente Grande, Miramar; CANAL ZONE (2): Barro Colorado Island, Skunk Hollow (NW Gatun locks); CHIRIQUI (9): Fortuna Dam, IHRE Vivero (11 km N Los Planes); COLÓN (5): Río Guanache Bridge (1 km E), Santa Rita Ridge; PANAMA (31): Cerro Azul, Cerro Campana, El Llano-Carti Rd. (km 8, km 10); SAN BLAS (2): Nusagandi.

TEMPORAL DISTRIBUTION. February (1), April (22), May (63), June (16), July (9), September (1).

DIAGNOSIS. *Cyclocephala atripes* is distinctive because of its relatively large size, black head and legs, testaceous pronotum and elytra (with black edging on elytra at extreme base and on sides beneath humerus), slightly emarginate clypeus, and unmarginated pronotum.

BIOLOGY. Beach (1982) reported *C. atripes* feeding on the specialized tissue of the adaxial surfaces of the inner bracts inside the inflorescences of *Cyclanthus bipartitus* Poiteau (Cyclanthaceae) at the La Selva Field Station in Costa Rica. The scarabs arrived at dusk or just after nightfall and continued to come to the inflorescences for at least three hours. Beach was unable to ascertain if the attraction was olfactory (no odor detected) or visual



Fig. 149. Distribution of *Cyclocephala atripes* in Panama.

(the yellow bracts contrast with the dark background). Beetles were observed mating within the inflorescence. By the afternoon of the second day within the inflorescence, the scarabs readily consumed pollen as the anthers emerged. The beetles, spadix, and the inner surfaces of the bracts were moist and sticky due to a combination of high humidity within the inflorescence, watery frass, and the stigmatic secretions. As a consequence of their sticky covering, the beetles became coated with pollen and detached anthers. Beach also observed *C. atripes* feeding in the inflorescences of two local species of *Diefenbachia* (Araceae). Young (1986) observed *C. atripes* visiting the inflorescences of *D. longispatha* Engler and Krause (Araceae) to feed, also at La Selva in Costa Rica, and I observed the same thing in Colón Province in Panama. Adults are also attracted to lights at night. They have been collected from tropical moist forests, tropical wet forests, premontane wet forests, and premontane rain forests at elevations of 20-1,050 meters.

***Cyclocephala brevis* Höhne, 1847**
New Status
 (Figs. 150-158)

Cyclocephala pubescens Burmeister 1847: 68.
 Primary junior homonym of *C. pubescens*
 Erichson 1847: 96 (a junior synonym of *C. sexpunctata* Laporte 1840).
Cyclocephala pubescens brevis Höhne 1923b:
 373 (valid name, described as subspecies).

DESCRIPTION. Length 14.4-19.0 mm; width 7.9-10.0 mm. Color testaceous with black markings as follows: frons black; pronotum varies from without markings (most common) to with black transverse band or large spot or fuscous clouding on disc either side of midline (common in Costa Rican specimens) to completely dark (uncommon); scutellum testaceous (common) to partially or completely dark (uncommon); elytra variable: without any markings (uncommon) or with 4 small to large spots in an arc on each elytron (post-scutellar, post-humeral, on lateral edge of disc just behind middle, and on disc behind

middle) (most common) or as above but post-scutellar spot large, subtriangular (uncommon); apices of femora, tibiae, and tarsomeres (and sometimes bases of tibiae) darkened or black. *Head:* Frons and base of clypeus with moderately large punctures; punctures moderate in density, setigerous (when not worn off); setae short, moderate in density, tawny. Clypeus transversely rugose except on punctate base; apex broad, weakly emarginate. Interocular width equals 3.0 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. *Pronotum:* Surface with moderately large punctures; punctures on central third sparse, becoming denser on lateral thirds, setigerous (when not worn off); setae short, moderately dense, tawny. Base without marginal bead. *Elytra:* Surface finely shagreened, with small punctures; punctures sparse on disc, becoming denser on sides (rows indistinct), setigerous (when not worn off); setae short, moderately dense, tawny. Epipleuron (ventral view) of females abruptly expanded into short, rounded flange on lateral edge and with obtuse tooth on mesal edge at level of abdominal sternites 1-2; lateral edge of elytron above flange slightly swollen. *Pygidium:* Surface finely roughened to shagreened, punctate; punctures moderate in size and density, setigerous (when not worn off); setae moderate in density, long in males and moderate in length in females, tawny. In lateral view, surface in males convex, especially in apical third; females with surface nearly flat. *Legs:* Foretibia tridentate, basal tooth strongly removed. Foretarsus in males enlarged: protarsomere 4 subtriangularly expanded on venter; 5th large, curved, concave on venter; median claw large, strongly bent, with large, narrow lobe at base, apex cleft. Foretarsus in females simple. Posterior tarsus slightly longer than posterior tibia. *Venter:* Prosternal process moderately long, columnar, apex obliquely flattened into a strongly transverse oval with raised "button" on anterior half. *Parameres:* Figs. 151-156.

DISTRIBUTION. *Cyclocephala brevis* is widely distributed from southern Mexico to Brazil, Colombia, and Ecuador. It does not

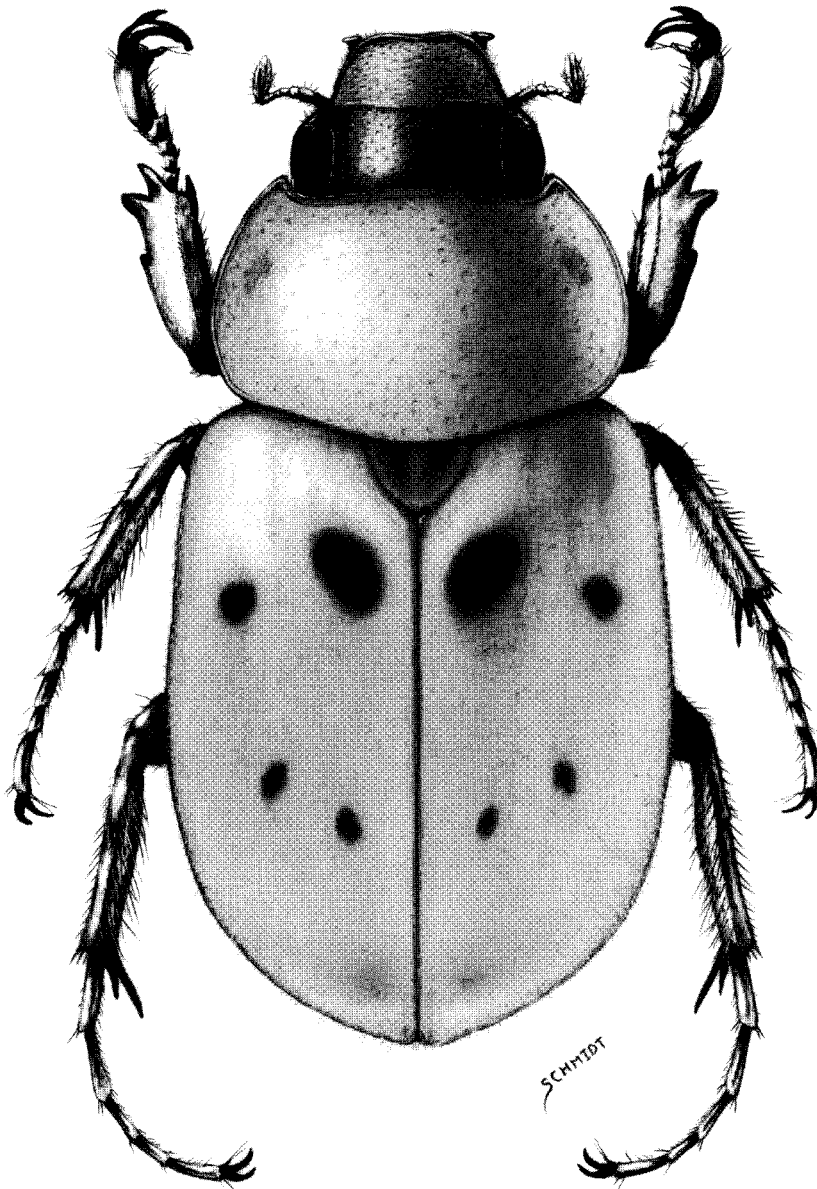


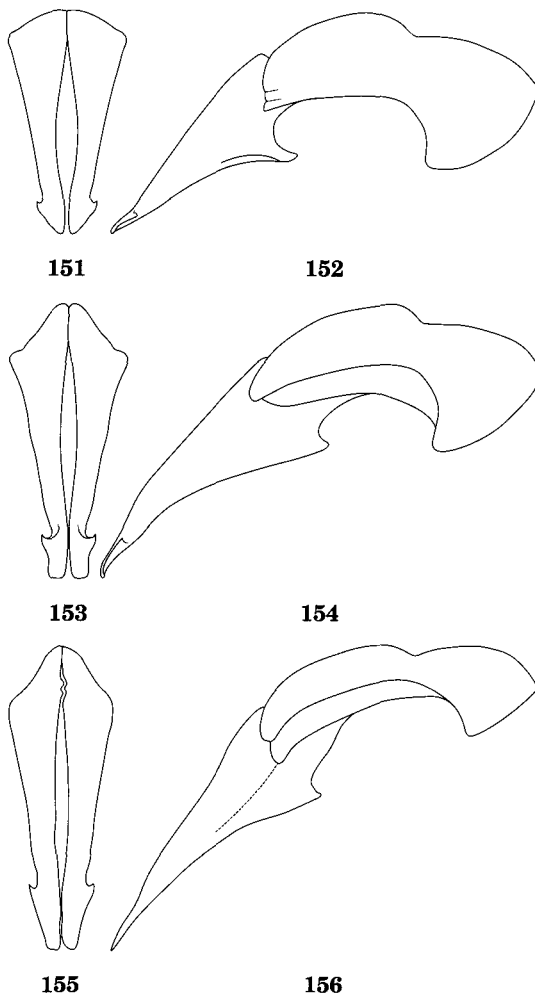
Fig. 150. *Cyclocephala brevis*.

seem to be abundant anywhere in its range. In Costa Rica and Panama, it is broadly distributed in areas generally below 1,000 meters.

LOCALITY RECORDS (Figs. 157-158). 381 specimens examined.

COSTA RICA (195). ALAJUELA (18): Dos Rios, Estación Eladios, Estación Laguna Pocosol,

San Ramon; GUANACASTE (60): Estación Las Pailas, Estación Maritza, Estación Pitilla, Tierras Morenas; HEREDIA (33): Estación El Ceibo, Estación Magsasay, La Selva Biological Station, Los Arbolitos; LIMÓN (22): Cerro Tortuguero, Buenos Aires, Estación Altamira, Estación Sirena, Punta Banco, Rancho Quemado (Osa), San Vito, Wilson Botanical Garden; SAN JOSÉ (1): Estación Carrillo.



PANAMA (186). BOCAS DELTORO (5): Miramar, Punta Peña; CANAL ZONE (34): Barro Colorado Island, Ft. Sherman, Madden Forest, Pipeline Road (km 2, km 9), Skunk Hollow, Parq. Nac. Soberanía; **CHIRIQUI** (21): Fortuna Dam, Hartmann's Finca (Santa Clara), Los Planes (7 km N, 11 km N); **COLÓN** (26): Cerro Viejo Mine (10 km SW Nombre de Dios), Río Guanche Bridge (1 km E), Santa Rita Ridge; **DARIEN** (3): Cana; **PANAMA** (79): Cerro Azul, Cerro Campana, Cerro Jefé, El Llano-Carti Rd. (km 8, km 13); **SAN BLAS** (1): Nusagandi; **VERAGUAS** (1): Alto de Piedra (above Santa Fé).



Figs. 151-156. *Cyclocephala brevis* parameres: (151-152) most "typical form;" (153-156) "lowland form."

Fig. 157. Distribution of *Cyclocephala brevis* in Costa Rica.

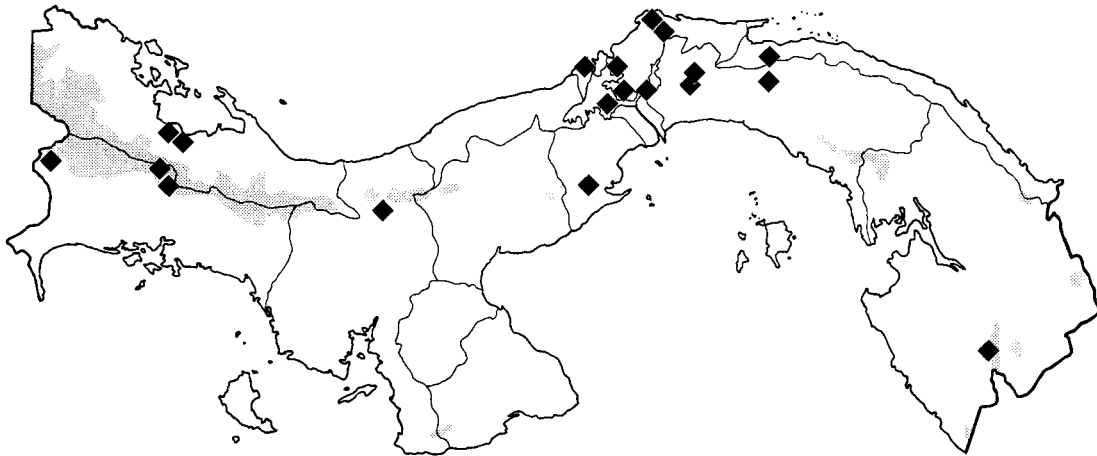


Fig. 158. Distribution of *Cyclocephala brevis* in Panama.

TEMPORAL DISTRIBUTION. January (47), February (12), March (22), April (19), May (120), June (38), July (33), August (5), September (10), October (15), November (22), December (12).

DIAGNOSIS. *Cyclocephala brevis* is similar to smaller individuals of *C. sexpunctata*. Males may be distinguished from one another by the form of their parameres (Figs. 151-152, 390-397). *Cyclocephala brevis* has long, slender parameres with a subtriangular to elongated subtriangular dilation at the apices; in lateral view, the parameres are slender and elongate and the ventral tooth at the base varies from right-angled to very produced. The parameres of *C. sexpunctata* differ because they are stouter and, in lateral view, very distinctly bent, especially in the apical half. Both males and females of *C. sexpunctata* can usually be distinguished by their larger size, larger markings on the elytra, and because they usually occur above 1,000 meters (*C. brevis* usually occurs lower than 1,000 meters). Size, markings, and elevation are not, of course, reliable indicators by themselves.

Cyclocephala brevis is a problematical species because the parameres of the males show two forms with relatively little overlap between them. In the broadly distributed "typical" form (Figs. 151-152), the shaft of the paramere is slender and elongate, and the apex is elongated into a subtriangular expansion; in lateral view, the tooth on the venter at the base is nearly right angled. The other "form" (Figs. 153-156) is mostly from the lowlands of Panama and only a few localities in Costa Rica. The shaft of the paramere of this form is slender, and the apex is subtriangularly expanded but not elongated; in lateral view, the tooth on the venter at the base is always distinctly produced. Externally, both males and females are identical between the two forms. Specimens with both forms of parameres are sympatric in space and time. And then there are relatively uncommon intermediate "forms," which further compounds the problem of characterizing populations/forms/species.

The form of the parameres in *Cyclocephala* species generally do not differ to the degree observed here. The question arises, then, is this one or two different species? Further analysis, possibly using molecular methods, may help to answer the question. For the moment, I believe the morphological evidence supporting two species is not substantial enough to warrant a split. Nevertheless, I remain ambivalent about this decision.

NOMENCLATURE. Both *C. pubescens* Erichson and *C. pubescens* Burmeister were described in 1847. Ever since the 1850s, the Burmeister name was used as the senior name while the Erichson name was considered a junior synonym of *C. sexpunctata* Laporte. The forward in Burmeister's *Handbuch der Entomologie* (volume 5) is dated February 1847, and it was received in the library of the Entomologischen Vereine zu Stettin in September 1847. But, the paper FOLLOWING Erichson's in the *Archiv für Naturgeschichte* is dated January 1847, and it was received in the library in Stettin in April 1847. *Cyclocephala pubescens* Erichson, therefore, has priority, and the Burmeister name must be replaced because it is a junior, primary homonym. *Cyclocephala pubescens brevis* Höhne is the only available junior synonym, and it is elevated in status to replace the homonym. Höhne's three syntypes at the Staatliches Museum für Tierkunde in Dresden, Germany, were examined to confirm that they are conspecific with Burmeister's *C. pubescens*.

Probably most collections, private and institutional, have incorrect identifications for *C. brevis* (= *C. pubescens* Burm.) and *C. sexpunctata*. Endrödi (1966) actually examined very few specimens and did not recognize the elevational differences in size, markings, and parameres between these two species; his only reliable character for identifying males was the length of the parameres, but not all specimens match his two illustrations of parameres. Some specimens with Endrödi's determination labels are even misidentified, a natural result of seeing too few specimens in closely related species.

Similarly, all specimens in various collections with my determinations of *C. pubescens* and *C. sexpunctata* made before 2002 should be re-evaluated using the new key in this work.

BIOLOGY. Adults are attracted to lights at night. I have collected adults from the inflorescences of *Dieffenbachia* sp. (Araceae) and *Cymbopetalum* sp. (Annonaceae) in Panama. Valerio (1984) observed the adults inside the inflorescences of *D. oerstedii* Schott and suggested that they might be the principal pollinator of this aroid. They have been collected from tropical moist forests, tropical wet forests, and premontane moist forests at elevations of near sea level to 1,000 meters.

***Cyclocephala brittoni* Endrödi,
1964**

(Figs. 159-164)

Cyclocephala brittoni Endrödi 1964: 438.

DESCRIPTION. Length 14.6-17.8 mm; width 7.9-9.1. Color testaceous with black frons and 4 spots in an arc on each elytron; spots small to moderate in size, first behind scutellum (occasionally subtriangularly expanded), second laterad of first and just before middle, third slightly mesad of second and just behind middle, fourth mesad and behind third. *Head:* Frons in males densely (almost confluent) punctate; punctures moderately large, setigerous; setae dense, long, tawny; frons in females similar except punctures only moderate in density and some with setae minute and sparse or absent. Clypeus with surface punctate; punctures moderate in density, small (males) or moderate (females), setigerous (some females with minute and sparse setae or without setae); setae dense, long, tawny; apex distinctly emarginate in males, feebly emarginate in females, not reflexed. Interocular width equals 2.5 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. *Pronotum:* Surface moderately densely punctate; punctures moderate in size, setigerous; setae moderate to long, tawny. Lateral

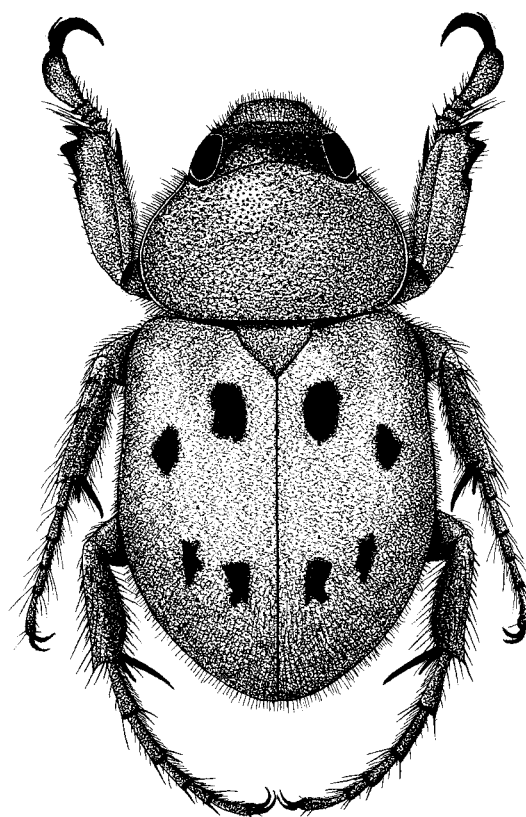
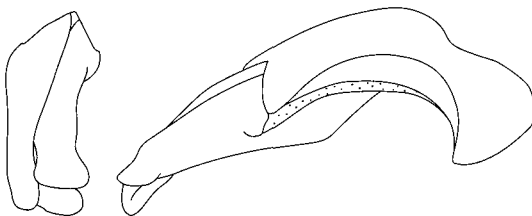


Fig. 159. *Cyclocephala brittoni*.

margin with distinctive fringe of dense, moderately long (females) to long (males) tawny setae. Base (in males) with marginal bead (rarely obsolete at middle), females usually lacking marginal bead (some females with faint trace of complete bead). *Elytra:* Surface roughened and densely punctate; punctures small to moderate in size, setigerous, rows not distinct; setae moderate to long, moderate in density, tawny. Epipleuron (ventral view) in females gradually tapered to level of abdominal sternite 3 where abruptly broadened into weakly toothed lobe (Fig. 160); elytral margin at same level swollen into small, elongate lobe. *Pygidium:* Surface in males roughened, moderately densely punctate; punctures small to moderate in size, setigerous; setae very long, moderately dense, tawny. Surface in females shagreened, sparsely punctate; punctures small to moderate, setigerous; setae long, sparse, tawny. In lateral view, surface in males convex (especially in apical



Fig. 160. *Cyclocephala brittoni*, left epipleuron (ventral view) of female.



161

162

Figs. 161-162. *Cyclocephala brittoni* parameres.

third), surface in females weakly convex. *Legs*: Foretibia in males bidentate (a small notch suggestive of 3rd tooth, but tooth absent), tridentate in females with basal tooth small and removed from others. Foretarsus in males enlarged: tarsomeres 3-4 expanded triangularly on venter, tarsomere 5 enlarged, curved, concave on venter; median claw large, curved, with prominent basal lobe, apex cleft. Foretarsus in female simple. Posterior tarsus of males about one-third longer than posterior tibia, females with posterior tarsus slightly longer than posterior tibia. *Venter*: Prosternal

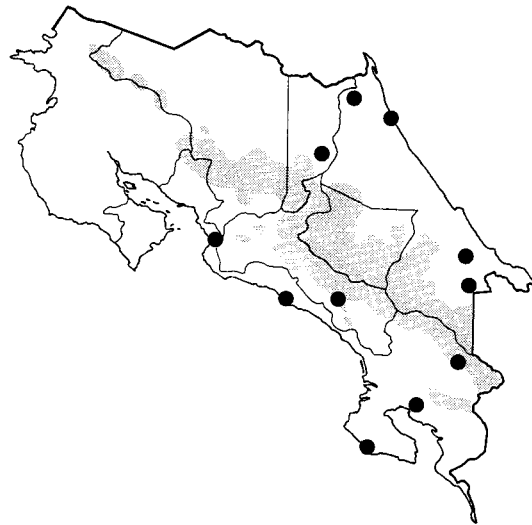


Fig. 163. Distribution of *Cyclocephala brittoni* in Costa Rica.

process moderately long, columnar, apex obliquely flattened into a transverse oval with raised, transverse "button" on anterior 2/3. *Parameres*: Figs. 161-162.

DISTRIBUTION. *Cyclocephala brittoni* is found in the lowlands of Costa Rica and Panama and ranges into Colombia, the three Guianas, and Trinidad.

LOCALITY RECORDS (Figs. 163-164). 321 specimens examined.

COSTA RICA (155). **HEREDIA** (7): La Selva Biological Station; **LIMÓN** (28): Amubri, Cerro Tortuguero, Estación Cuatro Esquinas, Estación Hitoy Cerere, Guapiles, Manzanillo, Milas, Pococí; **PUNTARENAS** (113): Estación Altamira (Buenos Aires), Estación Esquinas, Estación Sirena, Las Cruces Field Station, Quepos, Reserva Biológica Carara; **SAN JOSÉ** (7): San Isidro.

PANAMA (166). **BOCAS DEL TORO** (13): Almirante, Miramar; **CANAL ZONE** (136): Achote Road, Barro Colorado Island, Black Tank Road, Fort Clayton, Madden Forest, Margarita, Pipeline Road (km 11), Skunk Hollow; **DARIEN** (5): Cana, Santa Fé; **PANAMA** (12): Altos de Majé, Cerro Campana, El Llano-Carti Road (km 13), Ipeti (3 km S).

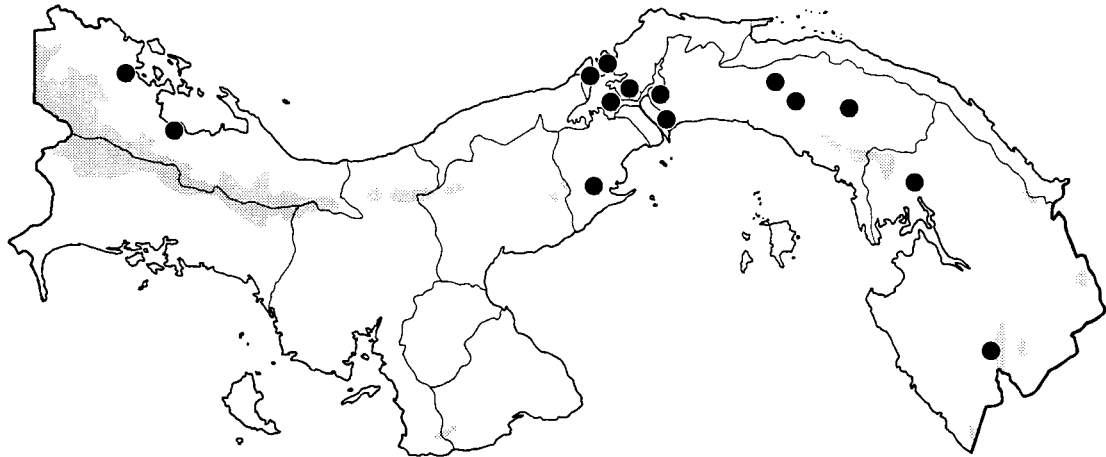


Fig. 164. Distribution of *Cyclocephala brittoni* in Panama.

TEMPORAL DISTRIBUTION. January (16), February (12), March (16), April (10), May (8), June (56), July (36), August (12), September (8), October (33), November (15), December (21).

DIAGNOSIS. *Cyclocephala brittoni* externally resembles *C. sexpunctata* but may be immediately distinguished by the presence of a dense fringe of long setae on the lateral margin of the pronotum in *C. brittoni*; *C. brittoni* also has longer dorsal setae than *C. sexpunctata* as well as unique, asymmetrical parameres.

Endrödi (1964, 1966) indicated that *C. brittoni* had an incomplete basal bead on the pronotum and so placed it in his section of the key for species lacking a basal bead. In nearly all the male specimens I have studied, the basal bead is distinctive and complete (albeit narrowed at the center). In the females, the basal bead is lacking with rare exception. Accordingly, I have placed *C. brittoni* in the key in two separate places to ensure its correct identification.

BIOLOGY. Bullock (1981) reported beetles visiting the flowers of the palm, *Bactris wendlaniana* Burret. Adults are also collected at lights. *Cyclocephala brittoni* lives in tropical wet forests and premontane wet forests at

elevations ranging from near sea level to 1,000 meters.

***Cyclocephala carbonaria* Arrow,
1911**

(Figs. 165-169)

Cyclocephala carbonaria Arrow 1911: 173.

Mononidia trachypyga Prell 1934: 162 (synonym).

Mononidia punctulata Prell 1934: 162 (synonym).

Cyclocephala howdeni Endrödi 1967: 83
(NEW SYNONYMY).

DESCRIPTION. Length 21.0-25.2 mm; width 11.1-13.4 mm. Color black. *Head:* Frons moderately to moderately densely punctate (rarely sparsely), punctures mostly moderately large (rarely small). Clypeus with surface similar to that of frons, apical half (especially in males) often with only a few small punctures; apex convexly rounded, margined, usually with weak angle at center, and weakly reflexed. Interocular width equals 4.0 transverse eye diameters. Antenna with 10 segments, club with a few long setae and a little longer than segments 2-7. *Pronotum:* Surface with punctures moderate in density, moderately large to large (especially on sides),

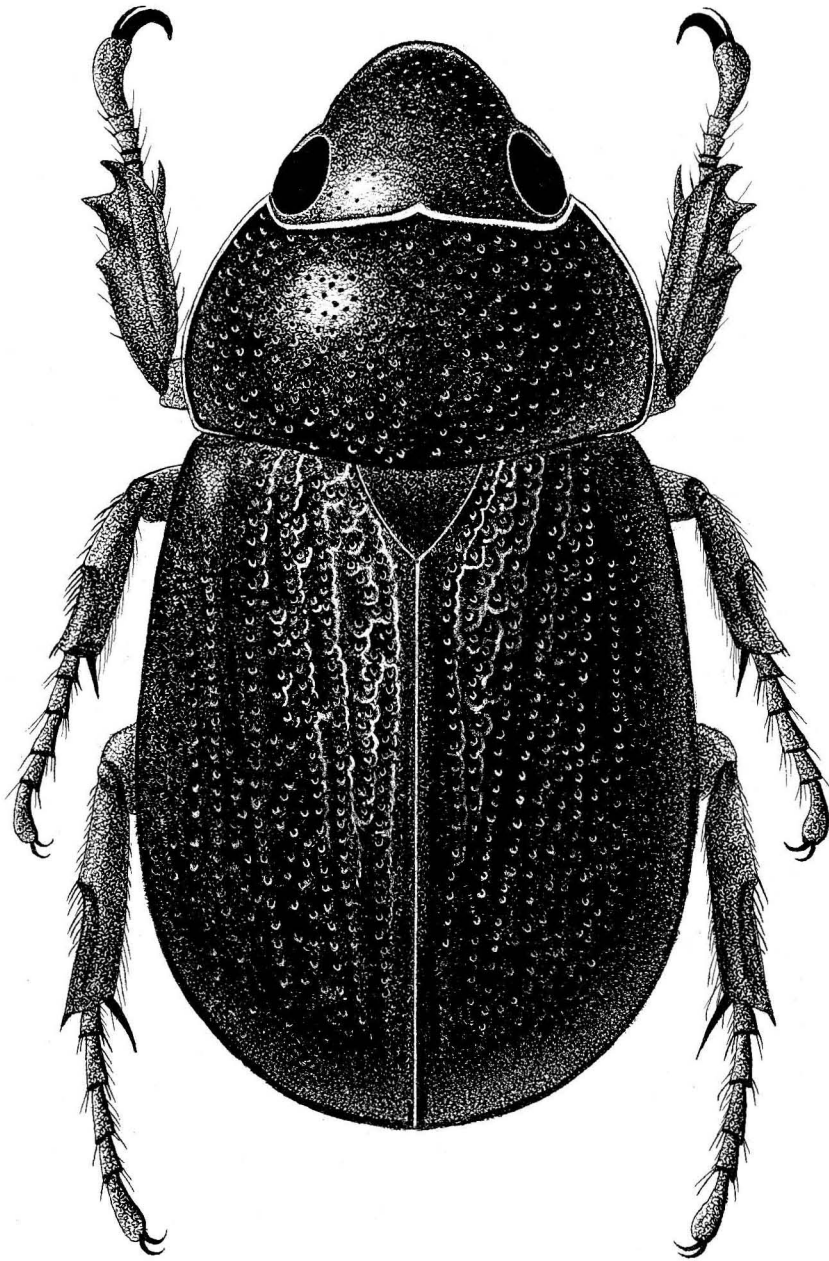
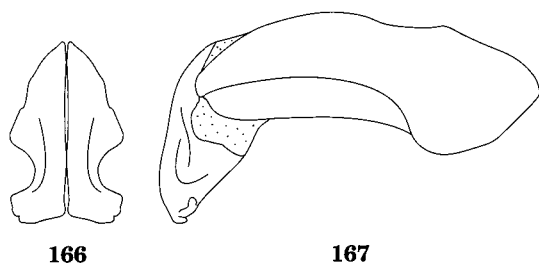


Fig. 165. *Cyclocephala carbonaria*.

ocellate, deep. Base lacking marginal bead. *Elytra*: Surface with punctate rows, punctures of striae and intervals similar to those of pronotum; entire surface often coarsely and transversely wrinkled obscuring rows of punctures. Epipleuron (ventral view) of females feebly enlarged at level of metasternum and tapering abruptly at level of second ab-

dominal sternite; in dorsal view, lateral margin slightly enlarged just before middle; in lateral view, ventral margin of epipleuron without tooth or angulation. *Pygidium*: Surface moderately to more usually moderately densely punctate; punctures moderate in size to more usually moderately large, ocellate, setigerous; setae short, tawny, moderate in



Figs. 166-167. *Cyclocephala carbonaria* parameres.

density. In lateral view, surface in males evenly convex, weakly convex to nearly flat in females. *Legs*: Foretibia tridentate, basal tooth slightly removed from others. Foretarsus in males enlarged: tarsomeres 2-4 each gradually larger than preceding, fourth with small tooth on ventral surface; fifth large, curved, with small angulation at base on ventral side; median claw large, curved, apex cleft. Foretarsus in females simple. Posterior tarsus subequal in length to posterior tibia. *Venter*: Prosternal process moderate in length, columnar, apex obliquely flattened into a transverse oval with anterior 2/3 to 4/5 raised into convex "button." *Parameres*: Figs. 166-167.

DISTRIBUTION. *Cyclocephala carbonaria* is known from Mexico to Ecuador and Bolivia (Endrödi 1966, 1985a) although Dechambre (1997a) split off the South American representatives into new species and limited *C. carbonaria* to Central America (specifically Honduras and Costa Rica). I suggest further study is needed to fully understand if the South American examples are distinct species or represent intraspecific variation within *C. carbonaria*.

Cyclocephala carbonaria is widely distributed in Costa Rica and Panama although it is less common in the mountainous highlands.

LOCALITY RECORDS (Figs. 168-169). 875 specimens examined.

COSTA RICA (743). ALAJUELA (70): Caño Negro, Cerro Campana (6 km NW Dos Ríos), Estación Eladios (Monteverde), Estación Laguna Pocosol (Monteverde), Estación San



Fig. 168. Distribution of *Cyclocephala carbonaria* in Costa Rica.

Ramón, Finca San Gabriel (2 km SW Dos Ríos), ICE tunnel (E side Lago Arenal), Parq. Nac. Rincón de la Vieja, San Ramón; CARTAGO (10): Chirripó Indian Reserve (5 mi SE Moravia), Guayabo Monument, Tuis, Turrialba; GUANACASTE (372): Bijagua (Volcán Tenorio), Estación Cacao, Estación Maritza, Estación Pitilla, Río San Lorenzo, Tierras Morenas; HEREDIA (46): Estación El Ceibo, Estación Magsasay, Finca Naranjo Valenciana, Sarapiquí; LIMÓN (22): Amubri, Bribri (9.4 km W), Cerro Tortuguero, Estación Cuatro Esquinas, Estación Hitoy Cerere, Guapiles, Manzanillo, Río Sardinas, Sector Cerro Cocori; PUNTARENAS (123): Buenos Aires, Estación Esquinas, Estación La Casona, Estación Quebrada Bonita, Estación Sirena, Monteverde, Piedras Blancas, Rancho Quemado, Rincón de Osa, San Luis, San Vito, Wilson Botanical Garden.

PANAMA (132). BOCAS DEL TORO (2): near Continental Divide on Hwy to Chiriqui Grande Miramar; CANAL ZONE (61): Achote Road, Barro Colorado Island, Pipeline Road (km 2); CHIRIQUI (3): Hartmann's Finca, no data; COCLÉ (6): Cerro Gaital, El Valle; COLÓN (32): Santa Rita Ridge; PANAMA (27): Cerro Azul, Cerro Campana, Cerro Jefé,



Fig. 169. Distribution of *Cyclocephala carbonaria* in Panama.

El Llano-Carti Road (km 8, km 12, km 13); SAN BLAS (1): Nusagandi.

TEMPORAL DISTRIBUTION. January (11), February (2), March (24), April (53), May (229), June (262), July (114), August (22), September (52), October (46), November (32), December (14).

DIAGNOSIS. *Cyclocephala carbonaria* may be distinguished by its black coloration, absence of a marginal bead on the base of the pronotum, tridentate foretibia, strongly convex apex of the clypeus, and the form of the parameres.

In a series as large as the one examined here, it becomes apparent that the degree of punctation on the pygidium is variable. A pygidium with large, moderately dense, setose punctures is "typical" for most *C. carbonaria*, but some specimens have punctures that are smaller, less dense, and with only minute setae. The extreme form of this reduction in punctation is what Endrödi (1967) named *C. howdeni*. For example, an impunctate pygidium is present in specimens from Sirena, Rancho Quemada and San Vito in Costa Rica as well as from Cerro Campana in Panama. Conversely, specimens from Estación Pitilla in Costa Rica exhibit *both* a punctate and an impunctate pygidium, thus attesting to vari-

able expression of this character in examples from the same locality.

NOMENCLATURE. *Cyclocephala howdeni* was originally described from both low and mid-elevations (125-1,100 meters) from Chiriqui in Panama and Turrialba in Costa Rica, and it is sympatric with *C. carbonaria*. The parameres of *C. howdeni* are identical to those of *C. carbonaria*. The small size and sparse punctures of *C. howdeni* are not a function of elevation (as evidenced by Endrödi's type series and numerous specimens on hand) nor of a geographically or ecologically isolated population. I believe it is simply an expression of intraspecific variation that is disparate from that of "typical" *C. carbonaria* but is, nevertheless, only variation. As such, *C. howdeni* is placed into synonymy with *C. carbonaria*.

BIOLOGY. Adults are attracted to lights, and a few have been taken in the flowers of *Philodendron wendlandii* Schott (H. Young, personal communication, 1990). This species has a wide ecological range. They have been collected in tropical moist forests, tropical wet forests, premontane moist forests, premontane wet forests, premontane rain forests, and lower montane rain forests at elevations of near sea level to 1,520 meters.

***Cyclocephala castaniella* Bates,
1888**

(Figs. 170-175)

Cyclocephala castaniella Bates 1888: 304.

Cyclocephala obscurata Endrödi 1966: 270
(NEW SYNONYMY).

DESCRIPTION. Length 12.5-14.5 mm; width 5.9-7.6 mm. Color varies from completely yellowish-brown with black occiput to same with piceous frons and piceous cloudings on pronotum and/or elytra to completely piceous. *Head:* Frons densely punctate, often becoming rugopunctate anteriorly, punctures small. Clypeus densely rugopunctate or rugulose; apex parabolic, slightly reflexed. Interocular width equals 2.8-3.5 transverse eye diameters. Antenna with 10 segments, club in male long, subequal in length to rest of antenna; club in female slightly longer than segments 2-7. *Pronotum:* Disc with punctures moderate in density, becoming moderately dense or dense on sides; punctures moderate in size, deep. Base without marginal bead. *Elytra:* Surface entirely moderately densely punctate, punctate striae evident; punctures moderately large, deep, weakly ocellate. Epipleuron (ventral view) of females slightly expanded from anterior margin of metacoxae to abdominal sternite 2; in lateral view, lacking a tooth where abruptly constricted at sternite 2. *Pygidium:* Surface in males moderately to moderately densely punctate, glabrous, punctures small; females with surface sparsely punctate, punctures small. In lateral view, surface in males regularly convex, females with surface nearly flat. *Legs:* Foretibia tridentate, basal tooth slightly removed from others in male, subequally spaced in female. Foretarsus in males enlarged: tarsomeres 2-4 each slightly larger than preceding, 4th with small lobe on venter; 5th larger, curved, with weak swelling at base on venter; median claw large, curved, apex narrowly split (Fig. 171). Foretarsus in females simple. Posterior tarsus slightly longer than posterior tibia. *Venter:* Prosternal process long, columnar, apex obliquely flattened into a transverse oval with anterior half raised into convex "button." *Parameres:* Figs. 172-173.

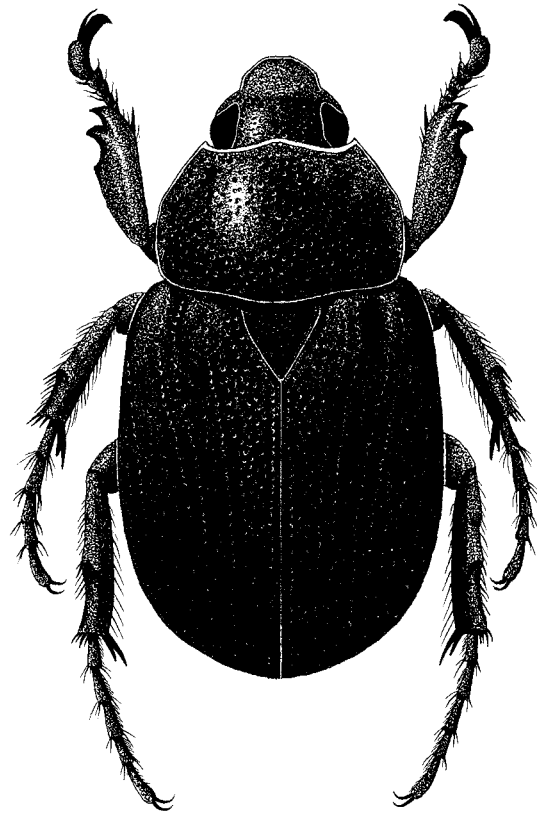
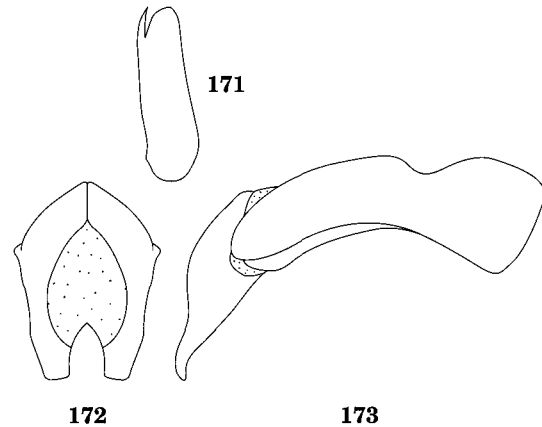


Fig. 170. *Cyclocephala castaniella*.



Figs. 171-173. *Cyclocephala castaniella*: (171) foreclaw of male; (172-173) parameres.

DISTRIBUTION. *Cyclocephala castaniella* is known from Costa Rica and Brazil (Endrödi 1966, 1985a) and Panama (Ratcliffe 1992b). Endrödi had one no-data specimen from Brazil that I believe is an erroneous record; it does not occur in Brazil. This species is generally distributed in the mountains of Costa Rica and in Chiriqui province of Panama.

LOCALITY RECORDS (Figs. 174-175). 614 specimens examined.

COSTA RICA (380). ALAJUELA (48): Atenas (8 km N), Río San Lorencito, Vara Blanca (8 km W), Zarcero; CARTAGO (28): Los Diques, Refugio Nacional Tapanti, Turrialba, Volcán Irazú; GUANACASTE (4): Estación Pitilla, Parq. Nac. Guanacaste; HEREDIA (5): Estación Barva, Río Ciruela Porrosati, Vara Blanca; PUNTARENAS (286): Estación Las Alturas, Estación La Casona, Estación Las Mellizas, Monteverde, San Luis; SAN JOSÉ (9): Bajo La Rosa, Zurqui tunnel.

PANAMA (234). CHIRIQUI (234): Boquete, Cerro Pate Macho (6 km N Boquete), Cerro

Punta, Hartmann's Finca, Hornito, La Mina, Los Planes, Santa Clara (24 km N).

TEMPORAL DISTRIBUTION. January (1), February (5), March (5), April (43), May (481), June (72), July (1), August (2), September (3), October (1).

DIAGNOSIS. *Cyclocephala castaniella* may be distinguished by its smaller size, overall dark body coloration, parabolic clypeus, elongate antennal club, pronotum lacking a basal bead, dense elytral punctation, and form of the parameres. It is keyed out in two places to allow for the variation in body color from light to dark.

NOMENCLATURE. In spite of the different appearance in the drawings of the parameres of *C. obscurata* and *C. castaniella* in Endrödi (1966, 1985a), I believe these are the same species. Endrödi's drawings are known for being "less than precise." Examination of many specimens of *C. castaniella* showed variation in the development of the apicoexternal tooth at the apex of the parameres from rounded to produced. I also examined the type of *C. obscurata* in Berlin and concluded it was conspecific with *C. castaniella*.

BIOLOGY. Adults are attracted to lights at night. They have been collected in premontane wet forests, premontane rain forests, and lower montane rain forests at elevations of 700-2,500 meters.



Fig. 174. Distribution of *Cyclocephala castaniella* in Costa Rica.



Fig. 175. Distribution of *Cyclocephala castaniella* in Panama.

Cyclocephala complanata
Burmeister, 1847

(Figs. 176-181)

Cyclocephala complanata Burmeister 1847: 48.

Cyclocephala obliquata Casey 1915: 135 (synonym).

Cyclocephala emacerata Casey 1915: 136 (synonym).

DESCRIPTION. Length 11.5-20.4 mm; width 5.5-10.9 mm. Color and pattern in this species varies tremendously (Fig. 177). In Costa Rica and Panama, color of head varies from piceous on frons and vertex (most common) to black; clypeus varies from piceous (most common) to dark testaceous or black; pronotum testaceous (most common) to suffused with piceous; elytra testaceous with margins of scutellum and suture narrowly piceous or black (most common) and with oblique piceous or black band on disc (most common); piceous color of suture occasionally reduced to narrow band or, conversely, expanded onto disc and amalgamating with oblique, discal band (rare); discal band narrow to broad, almost straight to distinctly arcuate, sometimes reduced to traces (uncommon) or completely absent (rare); pygidium testaceous.

Head: Vertex and frons densely punctate, punctures small to moderate; occasionally becoming finely rugulose anteriorly. Clypeus with surface finely rugulose; clypeus nearly semicircular to parabolic, apex with marginal bead and narrowly reflexed. Interocular width equals 2.5 (larger specimens) to 3.5 (smaller specimens) transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. **Pronotum:** Surface with sparse, small to moderate punctures. Base with marginal bead. **Elytra:** Surface finely shagreened with distinct rows of punctate striae; punctures moderately large, shallow, mostly weakly ocellate. Epipleuron (ventral view) of females gradually narrowing posteriorly and with distinct, acute or right-angled tooth at level of abdominal sternites 1-2; in dorsolateral view, elytral edge with strong flange above epipleural tooth. **Pygidium:** Surface in males dull, finely shagreened with traces of small, shallow punctures (especially

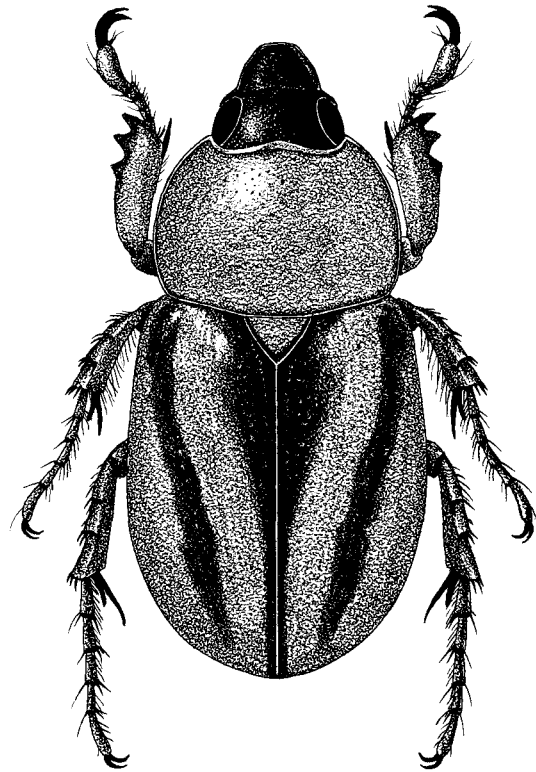


Fig. 176. *Cyclocephala complanata*.

in smaller specimens); females with surface shining, with punctures moderate in size and density, base and angles finely rugulose. In lateral view, surface regularly convex in males, weakly convex in females. **Legs:** Foretibia in both sexes tridentate, basal tooth slightly removed from others. Protarsus in males enlarged: segments 2-4 each slightly larger than preceding, segments 3-4 with distinct ventral flange; 5th large, weakly curved, and with distinct, longitudinal carina on median surface; median claw large, strongly curved, with large tooth at base, apex cleft. Protarsus in females simple. Posterior tarsus slightly longer than posterior tibia. **Venter:** Prosternal process long, columnar, apex with fringe of long setae and obliquely flattened into oval disc with anterior 2/3-3/4 elevated into a raised "button." **Parameres:** Figs. 178-179.

DISTRIBUTION. *Cyclocephala complanata* was previously known from southern Mexico

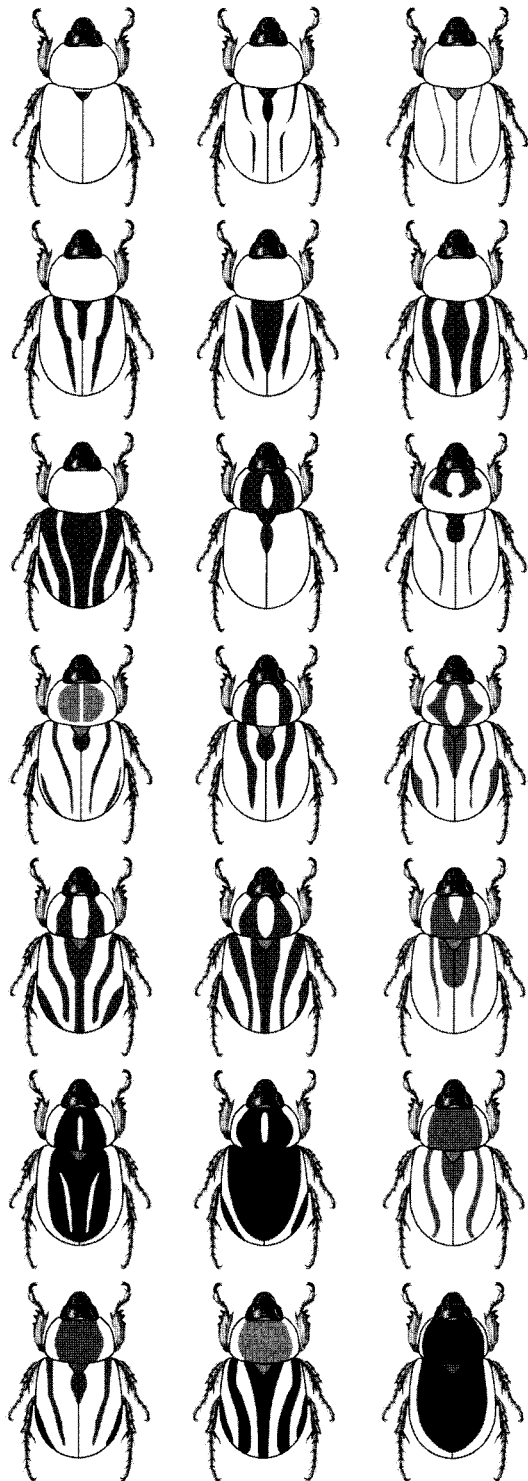
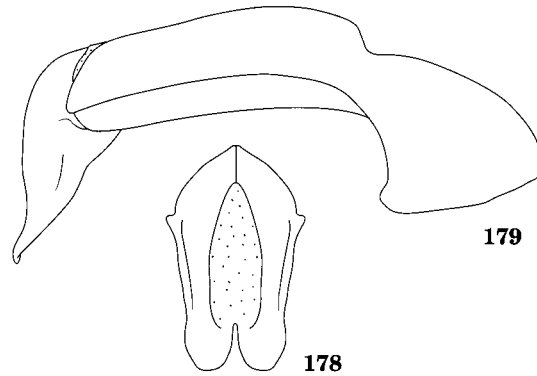


Fig. 177. *Cyclocephala complanata* showing range of variation in pronotal and elytral pattern. From Garcia-Luna *et al.* (2002) (used by permission).

to Costa Rica (Endrödi 1969, 1985a; personal observation). The record for Panama listed below is a NEW COUNTRY RECORD. This species is relatively widespread in Costa Rica at mid-elevations between 300-1,300 meters and just gets into Panama on the north side of the divide.

LOCALITY RECORDS (Figs. 180-181). 102 specimens examined.

COSTA RICA (101). ALAJUELA (7): Colonia Palmareña (5 km N), Finca San Gabriel (Dos



Figs. 178-179. *Cyclocephala complanata* parameres.



Fig. 180. Distribution of *Cyclocephala complanata* in Costa Rica.

Rios), San Carlos, San Mateo, San Ramon; CARTAGO (7): Embalse El Llano, Turrialba; GUANACASTE (62): Estación Cacao, Estación Las Pailas, Estación Los Almendros, Estación Maritza, Estación Mengo (W side Volcán Cacao), Estación Pitilla, Estación Santa Rosa, Finca Jenny (30 km N Liberia), Parq. Nac. Guanacaste (including Parq. Nac. Santa Rosa); HEREDIA (14): Estación El Ceibo, Estación Magsasay; LIMÓN (1): Parq. Nac. Braulio Carrillo; PUNTARENAS (9): Alto del Las Moras (Boruca), Reserva Biológica Monteverde, San Luis, San Vito, Santa Elena; SAN JOSÉ (1): Estación Carrillo.

PANAMA (1). BOCAS DEL TORO (1): Corriente Grande.

TEMPORAL DISTRIBUTION. March (3), April (18), May (51), June (20), July (3).

DIAGNOSIS. *Cyclocephala complanata* is usually recognized by the oblique band on the elytron, lack of any pronotal markings, semi-circular clypeal apex, tridentate protibia, beaded pronotum, and long prosternal process. Females have a distinctive, sharp tooth on the ventral edge of the epipleuron at the level of abdominal sternites 1-2. I have nu-

merous examples from a population at Parque Laguna Belgica, Chiapas, Mexico, that all seem larger and most are lacking any elytral markings; a few have traces of a reduced, oblique band. Although I have not seen this morphotype in Costa Rica and Panama, they may be separated from the very similar (and immaculate) *C. sororia* by the darkened elytral suture in *C. complanata*, by the form of the genitalia in the males (Figs. 178-179, 403-404), and by the presence of the sharp tooth on the epimeron in females of *C. complanata*; *C. sororia* is without any tooth or expanded flange on the epipleuron.

Numerous specimens from a population near Xalapa, Veracruz, Mexico, have both the pronotum and much of the elytra suffused with black or piceous, giving an overall darker appearance. Again, I have not seen this morphotype in Costa Rica or Panama. Specimens from the Xalapa population vary from elytral band nearly absent to "normal" to enlarged and joining sutural band.

BIOLOGY. Adults are attracted to lights. They have been collected from tropical moist forests, premontane moist forests, tropical wet forests, premontane wet forests, and premontane rain forests at elevations ranging from 280-1,300 meters.



Fig. 181. Distribution of *Cyclocephala complanata* in Panama.

Cyclocephala concolor
Burmeister, 1847

(Figs. 182-185)

Cyclocephala concolor Burmeister 1847: 50.

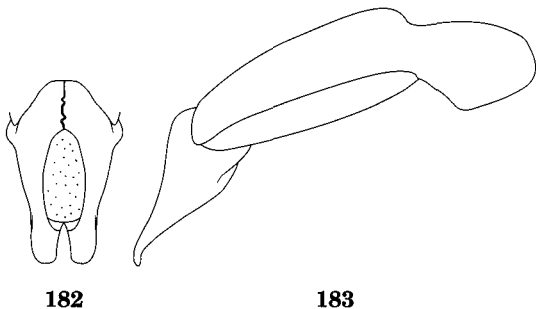
DESCRIPTION. Length 17.2-21.0 mm; width 8.7-10.8 mm. Color uniformly reddish brown or darker testaceous except that frons (often entire head) black; pygidium usually with dark band or spot either side of middle; abdominal sternites (often entire venter) dark reddish brown, often suffused with black. *Head:* Frons moderately to densely punctate, punctures mostly moderate in size. Clypeus with surface transversely rugopunctate, narrowed toward apex; apex with shallow, distinct emargination, weakly reflexed. Interocular width equals 2.9 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. *Pronotum:* Surface in center with small, sparse punctures, punctures becoming moderate in density and moderate to moderately large toward sides. Base with marginal bead. *Elytra:* Surface with distinct rows of punctate striae; punctures large, shallow, those at apex smaller and with minute, pale setae. Epipleuron (ventral view) in females weakly thickened at level of abdominal sternites 1-2. *Pygidium:* Surface in males with punctures moderate in density and size, setigerous; setae pale, moderate in density, setae short at base and becoming longer toward apex. Surface in females with punctures small, sparse, only a few with setae near apex. In lateral view, surface in both sexes weakly

convex, becoming strongly convex just before apex. *Legs:* Foretibia with 3 subequally spaced, strong teeth. Foretarsus in males enlarged: tarsomere 4 with small, ventral flange; 5th large, curved; median claw with small lobe at base, apex finely cleft. Foretarsus in females simple. Posterior tarsus subequal in length to posterior tibia. *Venter:* Prosternal process moderate in length, columnar, apex with long setae and obliquely flattened into a transverse oval with elevated, transverse, oval to subtriangular "button" on apical 2/3. *Parameres:* Figs. 182-183.

DISTRIBUTION. *Cyclocephala concolor* seems to have an imprecisely known range due possibly, in part, to its relatively nondescript appearance. It is known from Costa Rica, Honduras, Mexico, Guatemala, Colombia, and Paraguay (Endrödi 1966, 1985a); this is disjunct, to say the least. The specimens listed below for Panama constitute an unsurprising NEW COUNTRY RECORD. It is known from only a few localities in the study area.

LOCALITY RECORDS (Figs. 184-185). 39 specimens examined.

COSTA RICA (36). ALAJUELA (4): Dos Rios (2 km SW), San Ramon; CARTAGO (29):



Figs. 182-183. *Cyclocephala concolor* parameres.



Fig. 184. Distribution of *Cyclocephala concolor* in Costa Rica.



Fig. 185. Distribution of *Cyclocephala concolor* in Panama.

Chirripó Indian Reservation (5 mi SE Moravia), Embalse El Llano, Grano de Oro, Quebrada Segunda (Refugio Tapanti), Turrialba; HEREDIA (1): Cerro Chompipe; PUNTARENAS (2): Monteverde Cloud Forest Reserve.

PANAMA (3). BOCAS DEL TORO (3): Corriente Grande, Miramar.

TEMPORAL DISTRIBUTION. January (1), February (1), March (6), May (26), June (1).

DIAGNOSIS. In overall appearance, this species resembles *C. amblyopsis* and *C. mutata*. *Cyclocephala concolor* is easily distinguished from both of these species by its concave clypeal apex and margined base of the pronotum; the other two species have a convex clypeal apex and an unmargined base on the pronotum. The parameres are also distinctive for all of these species. Most specimens of *C. concolor* that I have seen (Mexico, Guatemala, Honduras) are reddish brown in color while the Costa Rican specimens are more of a dark testaceous color.

BIOLOGY. Adults are attracted to lights. They have been collected from premontane rain forests and lower montane rain forests at elevations of 1,000-2,000 meters.

***Cyclocephala confusa* Endrödi, 1966**

(Figs. 186-190)

Cyclocephala confusa Endrödi 1966: 174.

DESCRIPTION. Length 11.0-12.6 mm; width 5.8-6.8 mm. Color testaceous except for black frons, prepygidium, and usually abdominal sternites 1-5 (most common) or 1-6 (less common); pygidium either side of middle often with fuscous or black "clouding." **Head:** Frons densely punctate, punctures moderately large. Clypeus distinctly roughened, usually more so in females; apex broadly truncate, reflexed. Interocular width equals 2.5 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. **Pronotum:** Surface with punctures moderate in density in males, moderately dense in females, punctures small to mostly moderate in size. Base lacking marginal bead. **Elytra:** Surface moderately densely punctate, punctures moderate in size mixed with numerous micropunctures between larger punctures; rows of punctures indistinct. Epipleuron (ventral view) of females simple, not thickened or enlarged. **Pygidium:** Surface finely, densely rugopunctate. In lateral view, surface in males evenly convex, nearly flat in females. **Legs:** Foretibia tridentate, basal tooth strongly removed in males, less so in

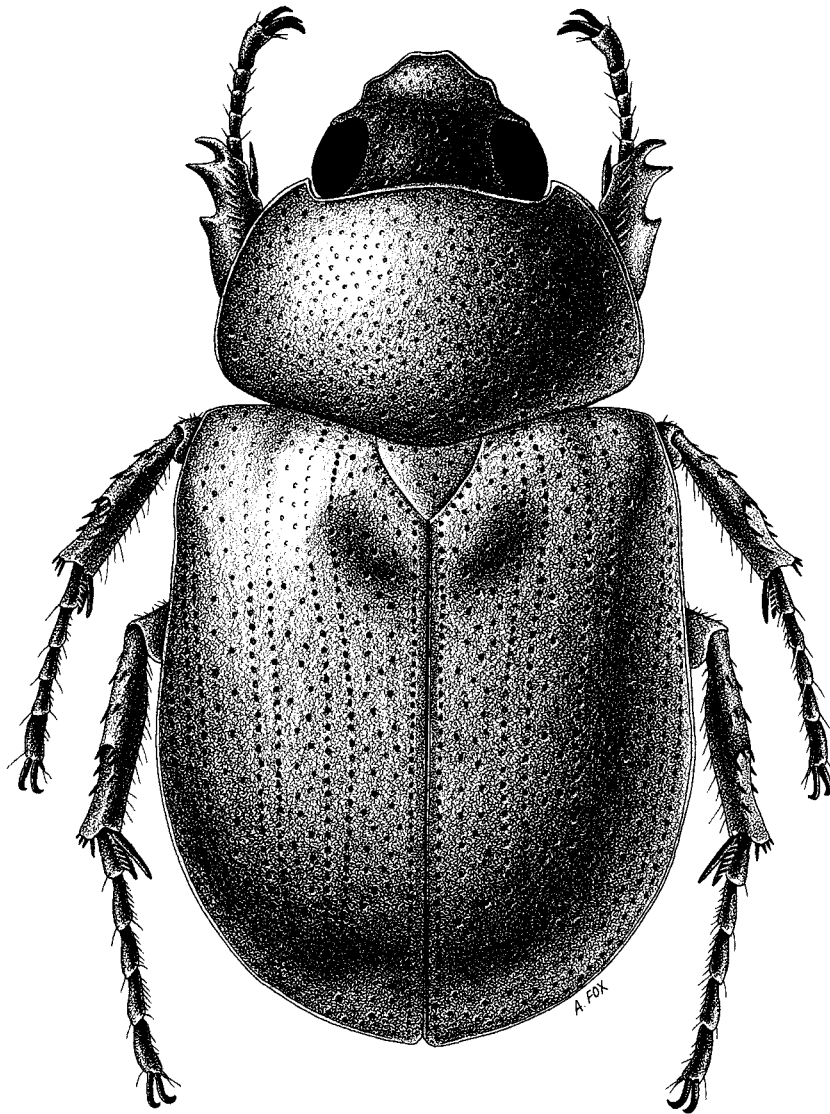
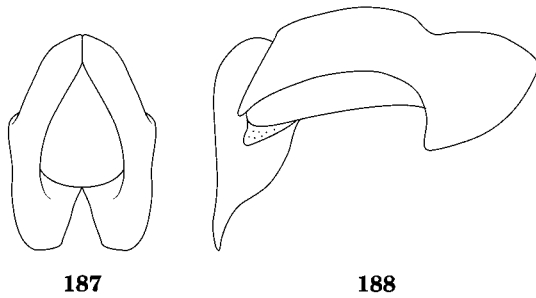


Fig. 186. *Cyclocephala confusa*.

females. Foretarsus in males enlarged: tarsomere 5 moderately enlarged, weakly bent, with weak carina on mesal edge; median claw large, curved, with lobe at base, apex cleft. Foretarsus in females simple. Posterior tarsus subequal in length to posterior tibia. *Venter*: Prosternal process moderately long, columnar, apex obliquely flattened into a transverse oval with raised, transverse "button" on apical half. *Parameres*: Figs. 187-188.

DISTRIBUTION. *Cyclocephala confusa* was described from Colombia and Peru (Endrödi 1966), and I reported it from Panama and suggested it was also in Costa Rica (Ratcliffe 1992). It is now known to be generally distributed in both Costa Rica and Panama below 1,500 meters.

LOCALITY RECORDS (Figs. 189-190). 609 specimens examined.



Figs. 187-188. *Cyclocephala confusa* parameres.



Fig. 189. Distribution of *Cyclocephala confusa* in Costa Rica.

COSTA RICA (215). ALAJUELA (15): Río San Lorencito, Upala; CARTAGO (55): Chirripó, Embalse El Llano, Moravia, Refugio Nacional Tapanti, Tuis, Turrialba; GUANACASTE (89): Estación Cacao, Estación Las Pailas, Estación Pitilla, Río San Lorenzo, Sector Góngora, Tierras Morenas, Volcán Rincón de la Vieja (4.5 km SW); HEREDIA (1): Vara Blanca; LIMÓN (3): Estación Hitoy Cerere; PUNTARENAS (52): Buenos Aires, Estación Altamira, Estación Esquinas, Estación La Casona, Estación Las Alturas, Estación Las Mellizas, Estación Quebrada Bonita, Estación Sirena, Rancho Quemado, Santa Elena.

PANAMA (394). BOCAS DEL TORO (27): 2 mi. N Continental Divide on Hwy to Chiriqui Grande, Punta Peña (14 km S); CANAL ZONE (19): Barro Colorado Island, Madden Forest, Piña Road, Pipeline Road (km 3); CHIRIQUI (106): Fortuna, Hartmann's Finca (Santa Clara), Hornito, IHRE Vivero (11 km N Los Planes); COCLÉ (1): El Cope; COLÓN (17): Santa Rita Ridge; PANAMA (223): Cerro Azul, Cerro Campana, El Llano-Carti Road (km 8, km 10); SAN BLÁS (1): Nusagandi.

TEMPORAL DISTRIBUTION. January (4), February (1), March (16), April (32), May (78), June (109), July (17), August (22), September (3), October (6), November (1).

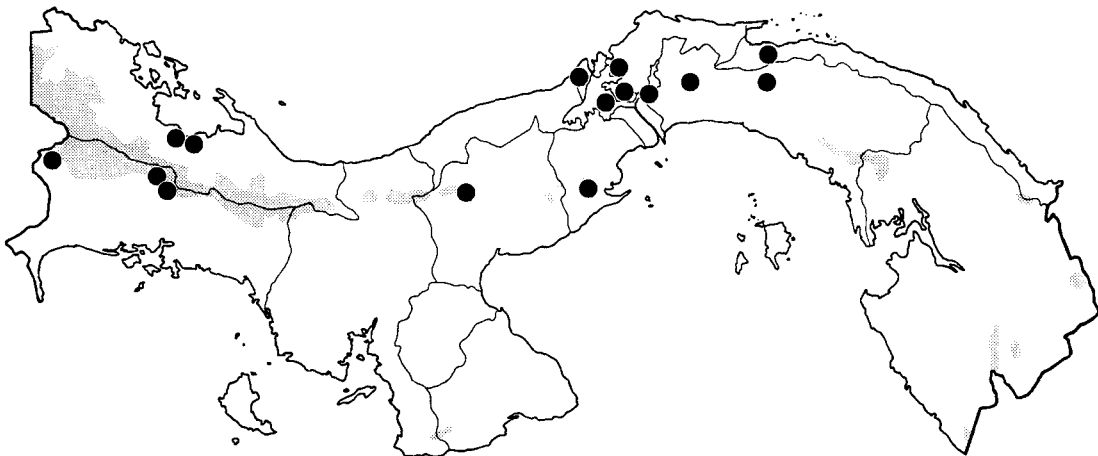


Fig. 190. Distribution of *Cyclocephala confusa* in Panama.

DIAGNOSIS. *Cyclocephala confusa* may be distinguished by its relatively small size (less than 13 mm), testaceous dorsal surface (except for black frons), truncate clypeal apex, pronotum lacking a basal bead, pronotum with punctures moderate in density and size, female with simple elytral epipleuron, tridentate foretibia with the basal tooth strongly removed, abdominal sternites 1-5 black, and the form of the male parameres (Figs. 187-188).

BIOLOGY. Adults are attracted to lights at night. Specimens have been collected from tropical dry forest transition, tropical moist forests, tropical wet forests, premontane wet forests, and premontane rain forests at elevations ranging from near sea level to 1,500 meters.

***Cyclocephala conspicua* Sharp,
1877**

(Figs. 191-195)

Cyclocephala conspicua Sharp 1877: 135.

Cyclocephala conspicua gregaroides Dechambre
1992a: 71 (NEW SYNONYMY).

Cyclocephala conspicua fusca Dechambre
1992a: 72 (NEW SYNONYMY).

DESCRIPTION. Length 14.3-19.7 mm; width 7.2-10.4 mm. Color light reddish brown (almost orange) except for black head, pronotal and elytral markings, and legs; pronotum lacking any black markings (rare in Central America) to usually with a black spot or longitudinal macula either side of middle; elytra vary from those with a post-scutellar spot (joined at suture) and a small to moderate black spot in middle of elytron just behind middle to post-scutellar spot expanded laterally to cover entire base to basal third black and connected along lateral margin to large, black, transverse macula just behind middle (not joined at suture) and with black lateral margin extending beyond macula to elytral apices (Fig. 191). *Head:* Frons moderately to moderately densely punctate, punctures moderate in size. Clypeus transversely rugulose; apex broadly truncate, narrowly reflexed.

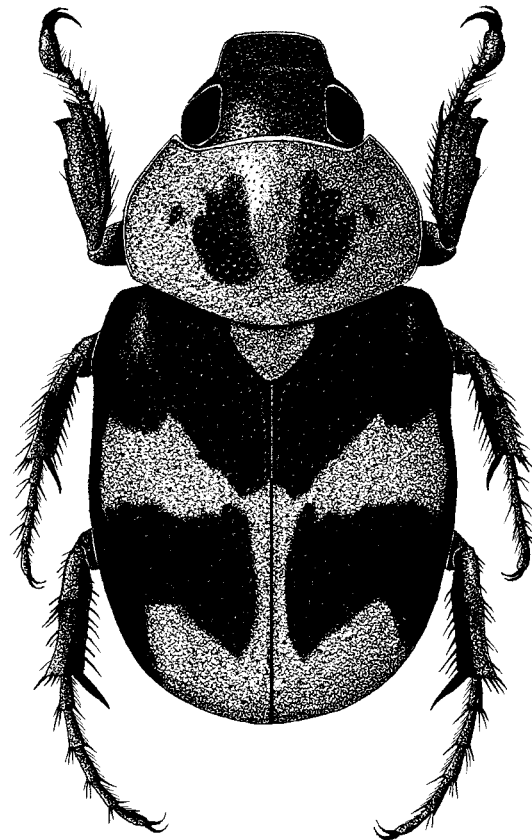
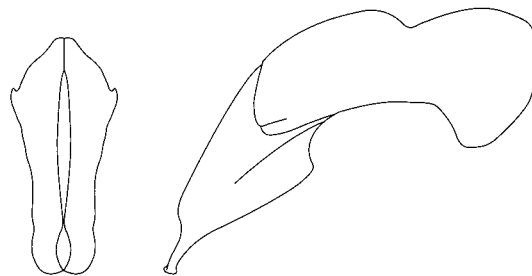


Fig. 191. *Cyclocephala conspicua*.



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Figs. 192-193. *Cyclocephala conspicua* parameres.

Interocular width equals 3.3-4.0 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. *Pronotum:* Surface sparsely punctate, punctures small to moderate in size. Lateral margin in anterior half nearly straight. Base lacking marginal bead. *Elytra:* Surface vaguely roughened, punctate, rows of punctures usually indistinct; punctures small to moderate in size, setigerous; setae minute, tawny.

Epipleuron (ventral view) in female thickened into a small knob at level of abdominal sternites 2-3. *Pygidium*: Surface minutely shagreened, moderately densely punctate; punctures small to moderate in size, shallow, setigerous; setae minute like those of elytra. In lateral view, surface in males convex, especially in apical third; females with surface nearly flat. *Legs*: Protibia tridentate, basal tooth small, strongly separated from others. Protarsus in males enlarged: tarsomere 5 enlarged, curved, concave on venter; median claw large, strongly curved, with large basal lobe, apex distinctly split. Protarsus in females simple. Posterior tarsus a little longer than posterior tibia. *Venter*: Prosternal process moderate in length, columnar, apex obliquely flattened into a transverse oval with

raised, transverse "button" on apical half. *Parameres*: Figs. 192-193.

DISTRIBUTION. *Cyclocephala conspicua* is known from Panama and Costa Rica where it is broadly distributed, and I have seen several specimens from Nicaragua and one from Honduras.

LOCALITY RECORDS (Figs. 194-195). 284 specimens examined.

COSTA RICA (182). ALAJUELA (45): Chinchona, Cerro Campana (E side Volcán Cacao), Colonia Blanca (2 km N), Río San Lorencito, San Miguel (6 km S), San Ramón de Dos Ríos, Upala; CARTAGO (10): Chirripó, Estación Quebrada (Parq. Nac. Tapanti), Tuis, Turrialba; GUANACASTE (81): Estación Cacao, Estación Pitilla, Tierras Morenas, Volcán Rincón de la Vieja, Volcán Tenorio; HEREDIA (20): Estación El Ceibo, Estación Magsasay, La Selva Biological Station, Vara Blanca; PUNTARENAS (24): Estación Altamira, Estación Biológica Las Alturas, Estación Sirena, Mellizas (2 km NW), Reserva Biológica Carara, San Vito; SAN JOSÉ (2): Cerro Bares.

PANAMA (102). BOCAS DEL TORO (4): Continental Divide Trail, Miramar; CANAL ZONE (1): Pipeline Road (km 3); CHIRIQUI (77): Finca Hartmann (Santa Clara), Finca La Suiza, Fortuna, Los Planes, Potrerillos; COCLÉ (1): El Valle; PANAMA (11): Cerro

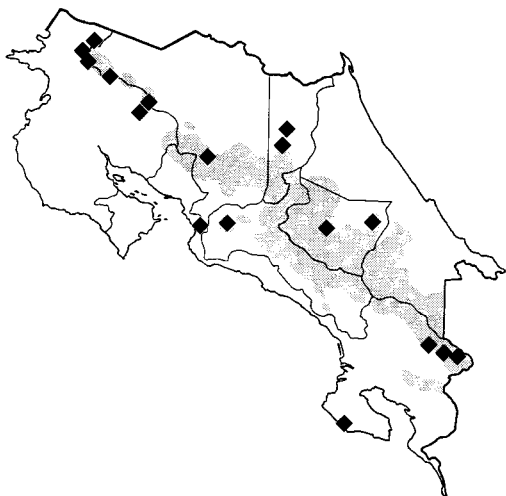


Fig. 194. Distribution of *Cyclocephala conspicua* in Costa Rica.

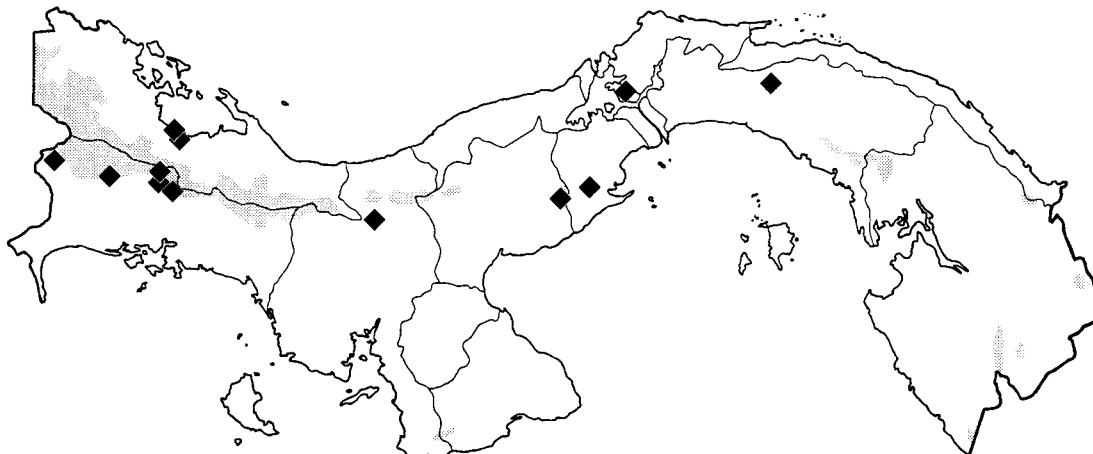


Fig. 195. Distribution of *Cyclocephala conspicua* in Panama.

Campana, El Llano-Carti Road (km 8); VERAGUAS (8): Santa Fé (9 km W).

TEMPORAL DISTRIBUTION. March (1), April (9), May (88), June (116), July (25), August (18), September (10), October (5).

DIAGNOSIS. *Cyclocephala conspicua* is easily recognized by color and pattern (shared only with *C. gregaria* Heyne and Taschenberg, which may not occur in Central America), minute elytral and pygidial setae, and form of the male parameres. It resembles *C. gregaria* but lacks the long dorsal setae and large eyes (2.5 transverse eye diameters) of that species; the pincer-like apices of the parameres of *C. conspicua* also distinguish it from the subrectangular apices seen in *C. gregaria*.

Dechambre (1992a) described two "subspecies" from Ecuador that lack the longitudinal black bands on the pronotum seen in most, though not all, Central American specimens. Given that specimens lacking pronotal markings occur both in Panama and Ecuador, the concept of a southern subspecies (*C. conspicua gregaroides*) is rendered invalid. *Cyclocephala conspicua fusca* simply shows more expansive elytral markings and slightly less curved apices of the parameres, all within the normal variation of a species. Both of these subspecies are here considered synonyms of *C. conspicua*.

BIOLOGY. Beach (1982) reported *C. conspicua* feeding on the specialized tissue of the adaxial surfaces of the inner bracts inside the inflorescence of *Cyclanthus bipartitus* Poiteau (Cyclanthaceae) at the La Selva Field Station in Costa Rica. The scarabs arrived at dusk or just after nightfall and continued to come to the inflorescences for at least three hours. Beach was unable to ascertain if the attraction was olfactory (no odor detected) or visual (the yellow bracts contrast with the dark background). Beetles were observed mating within the inflorescence. By the afternoon of the second day within the inflorescence, the scarabs readily consumed pollen as the anthers emerged. The beetles, spadix, and the inner surfaces of the bracts were moist

and sticky due to a combination of high humidity within the inflorescence, watery frass, and the stigmatic secretions. As a consequence of their sticky covering, the beetles became coated with pollen and detached anthers. Beach also observed *C. conspicua* feeding in the inflorescences of two local species of *Dieffenbachia* (Araceae). Adults are also attracted to lights at night. They have been collected from tropical moist forests, tropical wet forests, premontane wet forests, and premontane rain forests at elevations of 100-1,750 meters.

***Cyclocephala curta* Bates, 1888**
(Figs. 196-199)

Cyclocephala curta Bates 1888: 305.

Cyclocephala fusciventris Arrow 1902: 139
(synonym).

DESCRIPTION. Length 8.9-13.0 mm; width 4.9-7.0 mm. Color testaceous except for brown frons and pale brown, parallel, convoluted bands on pronotum (sometimes reduced to spots) and pale brown spots on elytra (post-scutellar spot or streak, faint post-humeral spot, and spot on disc just past middle). I have seen some specimens from southern Mexico and Honduras that have the dorsum entirely piceous except for testaceous frons, central stripe and lateral margins of the pronotum, scutellum, and pygidium. *Head:* Frons in males with moderately large, dense, shallow punctures, punctures usually less dense in females. Clypeus in males with surface indistinctly roughened or with shallow, dense punctures; females with surface weakly rugose or with large, dense, shallow punctures; apex weakly rounded, weakly reflexed. Interocular width equals 2.5 transverse eye diameters. Antenna 10-segmented, club in males nearly as long as segments 1-7, club in females subequal in length to segments 2-7. *Pronotum:* Surface with punctures moderately large to large, moderately dense, shallow. Base with marginal bead. *Elytra:* Surface with distinct rows of punctures, punctures moderately large to large. Alternate intervals higher than others. Epipleuron (ventral view)

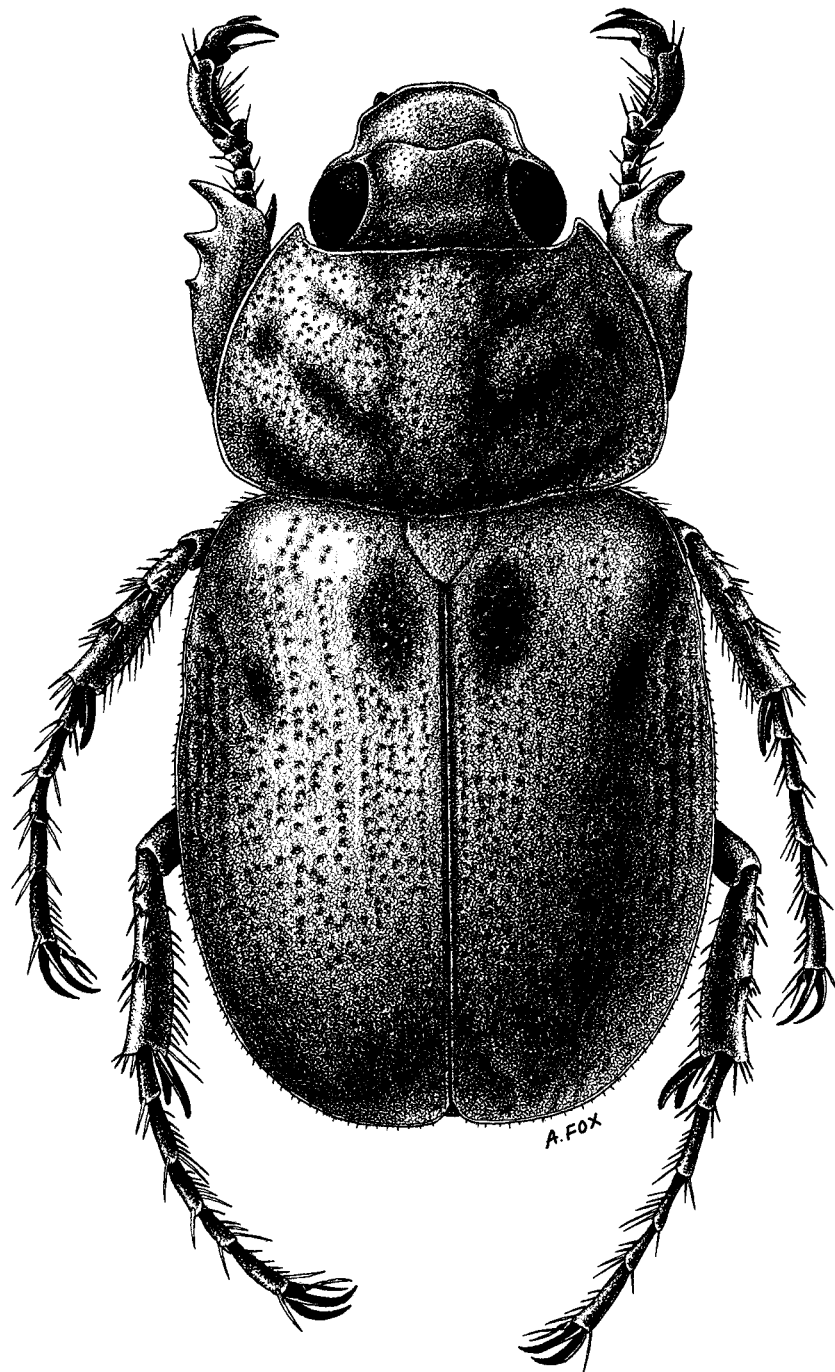
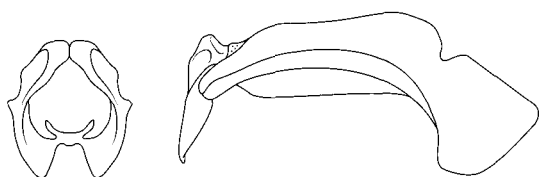


Fig. 196. *Cyclocephala curta*.

of females simple, imperceptibly thickened at level of abdominal sternites 1-2. *Pygidium*: Surface in males shagreened, setose in pristine specimens; setae short, sparse, often abraded away. Females with surface shining, with dense, small and moderate punctures,

glabrous in specimens at hand. In lateral view, surface in males convex, especially near apex; females with surface nearly flat to weakly convex. *Legs*: Foretibia tridentate, teeth subequally spaced. Foretarsus in males enlarged: tarsomere 4 with weak dilation on



197

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Figs. 197-198. *Cyclocephala curta* parameres.

venter; 5th large, curved, flattened on venter with central, longitudinal row of setae; median claw large, curved, apex entire. Foretarsus in female simple. Posterior tarsus a little longer than posterior tibia in male, subequal in length in female. *Venter*: Prosternal process moderate in length, columnar, apex obliquely flattened into a small, weakly transverse oval with raised "button" on anterior 1/2-3/4. *Parameres*: Figs. 197-198.

DISTRIBUTION. *Cyclocephala curta* is known from Mexico, El Salvador, and Costa Rica (Endrödi 1966, 1985a). In Costa Rica, this species is known only from Guanacaste province.

LOCALITY RECORDS (Fig. 199). 35 specimens examined.

COSTA RICA (35). **GUANACASTE** (35): Estación Los Almendros, Estación Maritza, Estación Murcielago, Estación Santa Rosa, Finca Jenny.

TEMPORAL DISTRIBUTION. July (2), August (21), September (12).

DIAGNOSIS. This species is vaguely similar to *C. unamas* Ratcliffe, but it has a strongly tridentate foretibia (weakly tridentate in males of *C. unamas*), an entire apex on the enlarged median claw of the foretarsus of the males (versus cleft), and a long prosternal process with a flattened apex (small and subconical in *C. unamas*). The parameres (Figs. 197-198, 421-422) are also very different. In the females, the epipleuron is nearly simple whereas it is expanded for a lengthy distance in *C. unamas*.

Cyclocephala curta is nearly identical with the Mexican *C. freudei* Endrödi. Although Endrödi (1966) recorded a single specimen of *C. freudei* from the Monteverde area, I believe that this species does not occur in Costa Rica.

BIOLOGY. Adults are attracted to lights. They have been collected from premontane moist forests at elevations of 100-600 meters.

Cyclocephala discicollis Arrow, 1902

(Figs. 200-205)

Cyclocephala discicollis Arrow 1902: 140.

DESCRIPTION. Length 11.6-15.7 mm; width 6.2-7.0 mm. Color testaceous except: head with frons piceous; pronotum with 2 longitudinal, broad, piceous bands or entire pronotum piceous except for narrow band of testaceous on lateral margins; elytra with 2 slender, elongate black or piceous "dashes" (post-humeral and on disc just behind middle), dashes rarely connected, even more rarely absent, female with lateral flange piceous, sutural region narrowly piceous or black; pygidium usually entirely piceous, occasionally with testaceous area in central third or fourth; venter partly or entirely piceous, if partly then abdominal sternites piceous. *Head*: Frons moderately densely punctate, punctures moderate in size (slightly larger in females). Clypeus transversely, finely rugulose, margins beaded; apex deeply emarginate (Fig. 201), weakly reflexed. Interocular width equals 4.0 transverse eye diameters. Antenna 10-segmented, club subequal in length to or slightly shorter than segments 2-7. *Pronotum*: Punctuation similar to that of frons. Base with marginal bead. *Elytra*: Surface finely shagreened, with small to moderate, shallow punctures, rows indistinct. Some punctures with short, stout, dark, almost bristle-like setae. Epipleuron (ventral view) in females enlarged from about level of abdominal sternites 1-4 and then abruptly narrowed; elytron with elongate swelling above expanded area of epipleuron. *Pygidium*: Surface in males vaguely roughened with

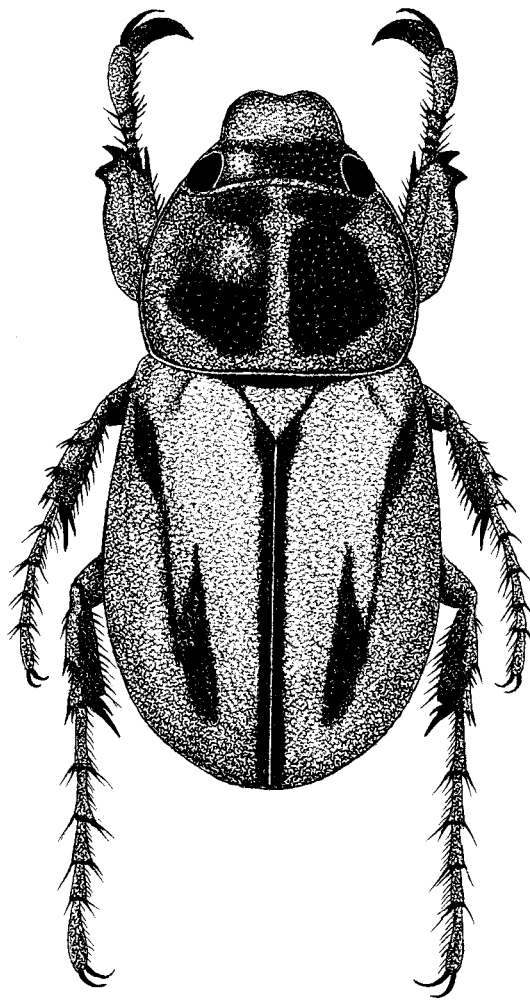
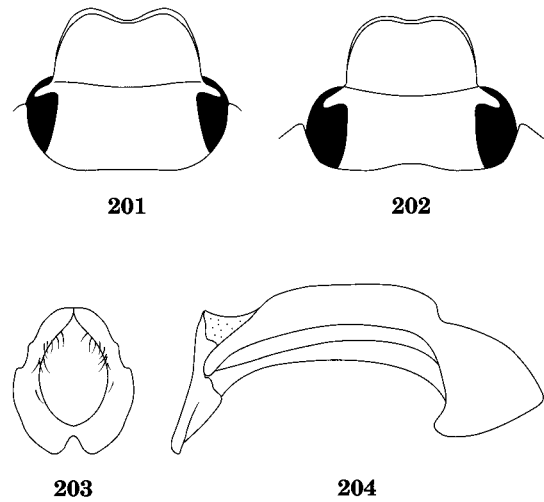


Fig. 200. *Cyclocephala discicollis*.

small punctures, punctures moderate in density, setigerous; setae short, tawny. Surface in females densely, finely rugopunctate or punctate, mostly glabrous. In lateral view, surface in males strongly convex, especially in apical third, females with surface nearly flat except at extreme apex where convex. *Legs*: Foretibia in males bidentate (although basal swelling almost large enough in some specimens to be considered a tooth), tridentate in females. Foretarsus in males enlarged: tarsomeres 3-4 each with large, ventral lobe; 5th large, curved, with longitudinal carina on both inner (mesal) and ventral surfaces; median claw large, strongly curved, apex entire (not cleft).



Figs. 201-204. *Cyclocephala discicollis*: (201) head with strongly emarginate clypeal apex; (202) head of *C. stictica* with weakly emarginate clypeal apex; (203-204) parameres.

Foretarsus in females simple. Posterior tarsus much longer than posterior tibia. *Venter*: Prosternal process long, columnar, apex obliquely flattened into a transverse oval with elevated, oval "button" in center. *Parameres*: Figs. 203-204.

DISTRIBUTION. *Cyclocephala discicollis* has an unusual distribution, being found only in Mexico and Panama and possibly in Venezuela and French Guiana (Endrödi 1966, 1985a). It seems to be abundant throughout most of Panama except for the highlands of Chiriqui where it does not occur.

LOCALITY RECORDS (Fig. 205). 899 specimens examined.

PANAMÁ (899). BOCAS DEL TORO (6): Miramar; CANAL ZONE (603): Albrook Forest, Ancon, Balboa, Barro Colorado Island, Cerro Galera, Coco Solo Hospital, Corozal, Diablo Heights, Fort Clayton, Fort Gulick, Ft. Kobbe, Howard AFB, Madden Dam, Old Gamboa Road, Pipeline Road (km 2), Skunk Hollow; COCLÉ (4): El Valle; COLÓN (48): Colón City, Santa Rita Ridge; DARIEN (2):

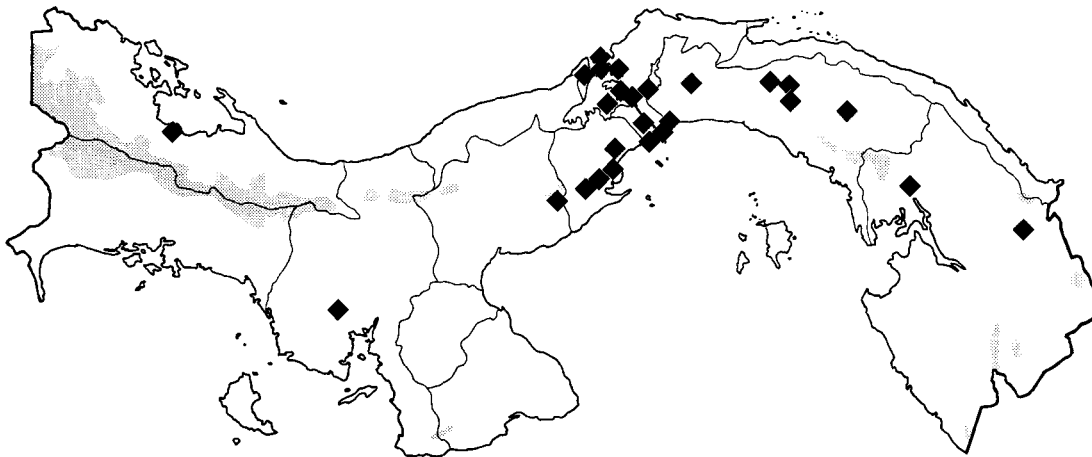


Fig. 205. Distribution of *Cyclocephala discicollis* in Panama.

Río Tuquesa, Santa Fé; PANAMÁ (283): Capira, Cerro Azul, Cerro Campana, Cañita (31 km E), Chorrera, El Llano-Carti Road (km 8, km 11), Ipetí (3 km E, 2.5 km W), Isla de Majé, Panama City, Punta Paitilla, Sajalices, Serranía de Majé; VERAGUAS (1): Sona.

TEMPORAL DISTRIBUTION. January (2), April (11), May (737), June (76), July (33), August (8), October (1), December (16).

DIAGNOSIS. *Cyclocephala discicollis* is readily distinguished by its deeply emarginate clypeus in combination with its dorsal color and pattern. The clypeus is so deeply emarginate (for a *Cyclocephala* species) that the apex is almost lobiform either side of the emargination (Fig. 201). *Cyclocephala stictica* is somewhat similar in overall appearance but is usually larger, the elytron usually has a postscutellar spot (nearly always absent in *C. discicollis*), the clypeus is only weakly emarginate (Figs. 202), and the parameres are different (Figs. 203-204, 412-413).

BIOLOGY. Adults are strongly attracted to lights. They have been collected in tropical dry forests, tropical moist forests, premontane moist forests, and premontane wet forests at elevations ranging from near sea level to 1,000 meters.

***Cyclocephala discolor* (Herbst, 1790)**

(Figs. 206-211)

Melolontha discolor Herbst 1790: 73.

Melolontha unciata Schönherr 1817: 189 (synonym).

Cyclocephala discolor andina Bréthes 1904: 331 (synonym).

Cyclocephala aurantiaca Prell 1937c: 496 (synonym).

DESCRIPTION. Length 10.2-16.0 mm; width 5.4-7.1 mm. Color testaceous with black or piceous spots or streaks on pronotum and elytra, frons and sometimes clypeus darkened. Pronotum varies from completely testaceous (rare) to with a longitudinal band (deeply emarginated twice on lateral edge) behind each eye and connected to short, transverse band on base of pronotum to variable reduction of bands (lacking lateral emarginations) to simply 1-2 spots on each side. Elytra usually with base either side of scutellum and suture black (sometimes reduced, rarely absent) and with black spot behind humerus, posterolateral of scutellum, and in center of elytra behind middle (spots sometimes reduced or absent); females with lateral expansion of elytra usually black or piceous. *Head:* Frons with punctures moderate in density

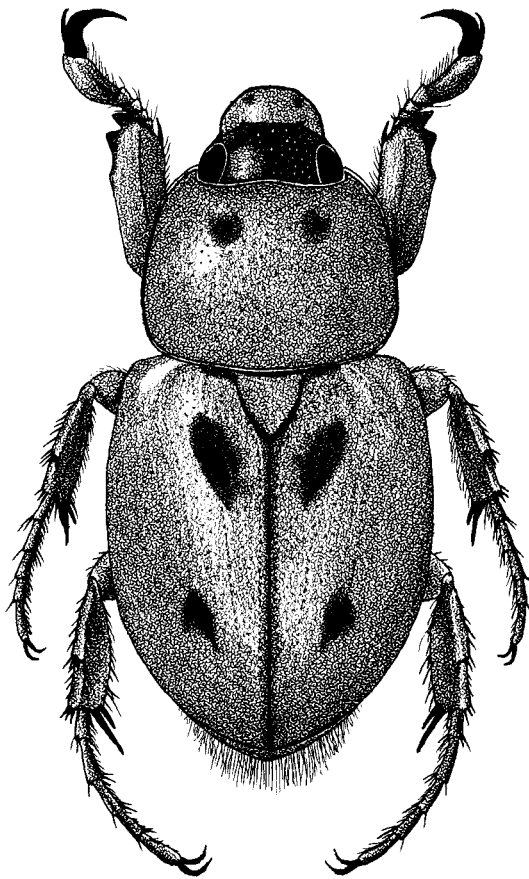
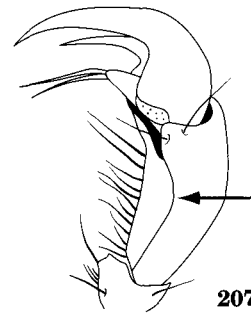
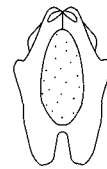


Fig. 206. *Cyclocephala discolor*.

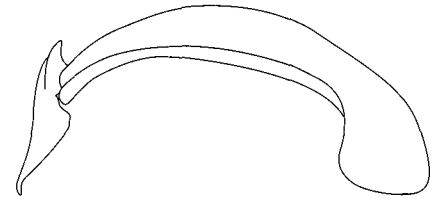
and moderate in size. Clypeus with surface moderately densely punctate (occasionally becoming roughened in apical half), punctures moderate in size; apex broadly parabolic. Interocular width equals 3.0 transverse eye diameters. Antenna with 10 segments, club subequal in length to or slightly shorter than segments 2-7. *Pronotum*: Surface with punctures moderately dense and moderate to moderately large in size. Base with marginal bead. *Elytra*: Surface with punctate striae; punctures in striae moderate to large and shallow; newly eclosed specimens with short setae in punctures of intervals and at elytral apices, most specimens with setae abraded away except those at apices. Epipleuron (ventral view) of females gradually widened to level of anterior part of abdominal sternite 4 where abruptly narrowed; in dorsal view, lat-



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208



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Figs. 207-209. *Cyclocephala discolor*: (207) foretarsus (part) and foreclaw of male; (208-209) parameres.

eral edge of elytron expanded into a flange above widened epipleuron. *Pygidium*: Surface of males with punctures usually moderately dense, moderately large, setigerous (females with punctures often sparse and small); setae in males long, dense, tawny in color, females with setae less dense, shorter. In lateral view, surface in males strongly convex, especially near apex, surface in females weakly convex. *Legs*: Foretibia in males bidentate, tridentate in females. Foretarsus in males enlarged: tarsomeres 2-4 each slightly larger than preceding, 4th produced into small lobe ventrally; 5th (Fig. 207) large, curved, with row of stout setae beneath; median claw large, curved, with large lobe at base, apex finely cleft (although smaller ramus often worn away or broken off). Foretarsus in females simple. Posterior tarsus slightly longer than posterior tibia. *Venter*: Prosternal process long, columnar, apex obliquely flattened with anterior 1/2-3/4 elevated into round "button." *Parameres*: Figs. 208-209.

DISTRIBUTION. *Cyclocephala discolor* is widely distributed from Mexico to Argentina. It is widely distributed in the lowlands of both Costa Rica and Panama.

LOCALITY RECORDS (Figs. 210-211). 1,007 specimens examined.

COSTA RICA (704). **ALAJUELA** (34): Bijagua, Caño Negro, Finca San Gabriel (2 km SW Dos Ríos); **GUANACASTE** (35): Cañas, Cañas (6 mi. S, 6 mi. W), Estación Cacao, Estación

Murcielago, Estación Palo Verde, Estación Pitilla, Finca Jenny (30 km N Liberia), Nacaome (3 km N), Parq. Nac. Barra Honda, Parq. Nac. Guanacaste; **HEREDIA** (17): Estación Magsasay, Fina Naranjo Valenciana (2 km S Pueblo Nuevo), La Selva Biological Station, La Virgen de Sarapiquí, Los Arbolitos, Volcán Tenorio (Finca Montezuma); **LIMÓN** (132): Amubri, Buenos Aires, Cerro Cocori, Cerro Tortuguero, Estación Cuatro Esquinas, La Perla, Manzanillo, Pandora, Río Sardinas; **PUNTARENAS** (486): Estación Esquinas, Estación Quebrada Bonita, Estación Sirena, Finca Venecia (mouth of Río Esquinas), Mogos, Parq. Nac. Corcovado, Parq. Nac. Manuel Antonio, Punta Blanco, Rancho Quemado, Rincon de Osa, Río Coto Brus, Union of Quebrada Pita and Quebrada Cabo Blanco, Vuelta Campana.

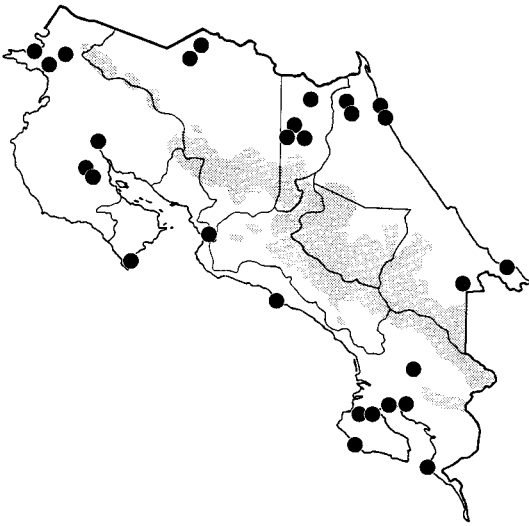


Fig. 210. Distribution of *Cyclocephala discolor* in Costa Rica.

PANAMA (303). **BOCAS DEL TORO** (194): Miramar; **CANAL ZONE** (44): Albrook, Barro Colorado Island, Cerro Paraiso, Coco Solo Hospital, Ft. Clayton, Ft. Gulick, Gatun Lake Lookout, Gatun Ridge Road, Madden Dam, Old Gamboa Road, Pipeline Road (km 2, km 4); **CHIRIQUI** (8): Chiriqui (28 km E), Lino; **COCLÉ** (2): Natá; **COLÓN** (8): Portobelo (15 km E), Santa Rita Ridge; **DARIEN** (17): Cana, Jaqué, Santa Fé; **PANAMA** (30): Altos de Majé, Cañita (27 km E), Cerro Azul, Cerro Campana, Chepo (80 km E), El Llano-Carti Road (km 8), Ipeti (3 km E).

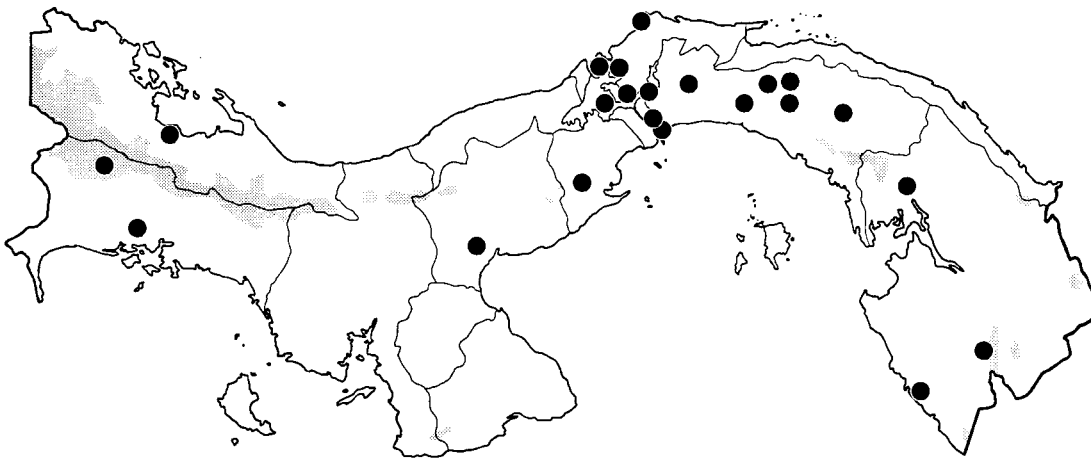


Fig. 211. Distribution of *Cyclocephala discolor* in Panama.

TEMPORAL DISTRIBUTION. January (35), February (44), March (71), April (78), May (97), June (61), July (284), August (125), September (70), October (76), November (47), December (26).

DIAGNOSIS. *Cyclocephala discolor* is similar to *C. amazona* in size and color pattern, and they both have bidentate foretibiae in the males. Even so, the males can usually be readily distinguished because *C. discolor* has the large claw of the protarsus split at its apex whereas it is entire in *C. amazona*. However, the small ramus on the split claw of *C. discolor* is so fine that it is often absent, either broken off or worn away. In this case, they can still be easily separated because the base of the fifth tarsomere has, on its median edge, a distinct lobe in *C. amazona* whereas in *C. discolor* it is absent (Figs. 128 and 207). In addition, the posterior tarsus is only a little longer than the posterior tibia in *C. discolor*, but it is much longer in *C. amazona*. Lastly, the parameres of the males are each unique (Figs. 131-132, 208-209).

The females may be distinguished by the form of the swelling of the epipleuron and the elytra. In *C. discolor*, the epipleuron is gradually widened to abdominal sternite 4 where it is then abruptly constricted; the lateral edge of the elytron is gradually expanded into a flange above the widened epipleuron. In *C. amazona*, the epipleuron is gradually expanded to sternite 2, then constricted to about the middle of the third sternite where it is abruptly and angularly constricted again (here appearing tooth-like in lateral view); the lateral edge of the elytron above the thickened epipleuron is swollen at the level of the first and second abdominal sternites, emarginated above sternites 2-3, and swollen again near the level of the juncture between sternites 3-4.

BIOLOGY. Adults are attracted to lights. They have been collected in tropical dry forests, tropical moist forests, and tropical wet forests at elevations from sea level to 600 meters.

***Cyclocephala enigma* Ratcliffe,
new species
(Figs. 212-215)**

TYPE MATERIAL. Holotype labeled "Est. Cacao, 1000-1400 M, Lado SO Vol. Cacao, P. N. Guan., Prov. Guanacaste, Costa Rica, F. Araya, 21 a 29 May 1992, L N 323300, 375700." Single paratype with same data. Holotype deposited at INBio (Santo Domingo de Heredia, Costa Rica). Paratype deposited at the University of Nebraska State Museum (Lincoln, NE).

HOLOTYPE. Male. Length 12.3 mm; width 6.7 mm. Color of clypeus, pronotum, scutellum, thoracic sternites, and legs testaceous; frons reddish-brown; elytra, pygidium, and abdominal sternites piceous. **Head:** Frons with punctures moderately dense, moderately large. Clypeus similarly punctate at center base, becoming transversely rugulose elsewhere; apex broad, weakly emarginate. Interocular width equals 3.1 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. **Pronotum:** Surface with punctures moderate in density, moderately large, becoming slightly larger laterally. Base with marginal bead. **Elytra:** Surface densely punctate, punctures moderately large, setigerous along sides, punctate rows indistinct; setae along sides minute, sparse, tawny. **Pygidium:** Surface coarsely roughened, with sparse, minute, tawny setae. In lateral view, surface weakly convex. **Legs:** Foretibia tridentate, basal tooth slightly removed from others. Foretarsus enlarged: segments 2-4 each slightly larger than preceding, each with progressively larger ventral flange; 5th large, curved, median edge with longitudinal carina, lateral edge on venter with row of stout, long setae; median claw large, curved, base with large, rounded lobe, apex cleft. Posterior tarsus broken on both sides. **Venter:** Prosternal process moderately long, columnar, apex flattened into a transverse oval with raised, transversely subtriangular (apex anterior) "button" on apical 3/4. **Parameres:** Figs. 213-214.

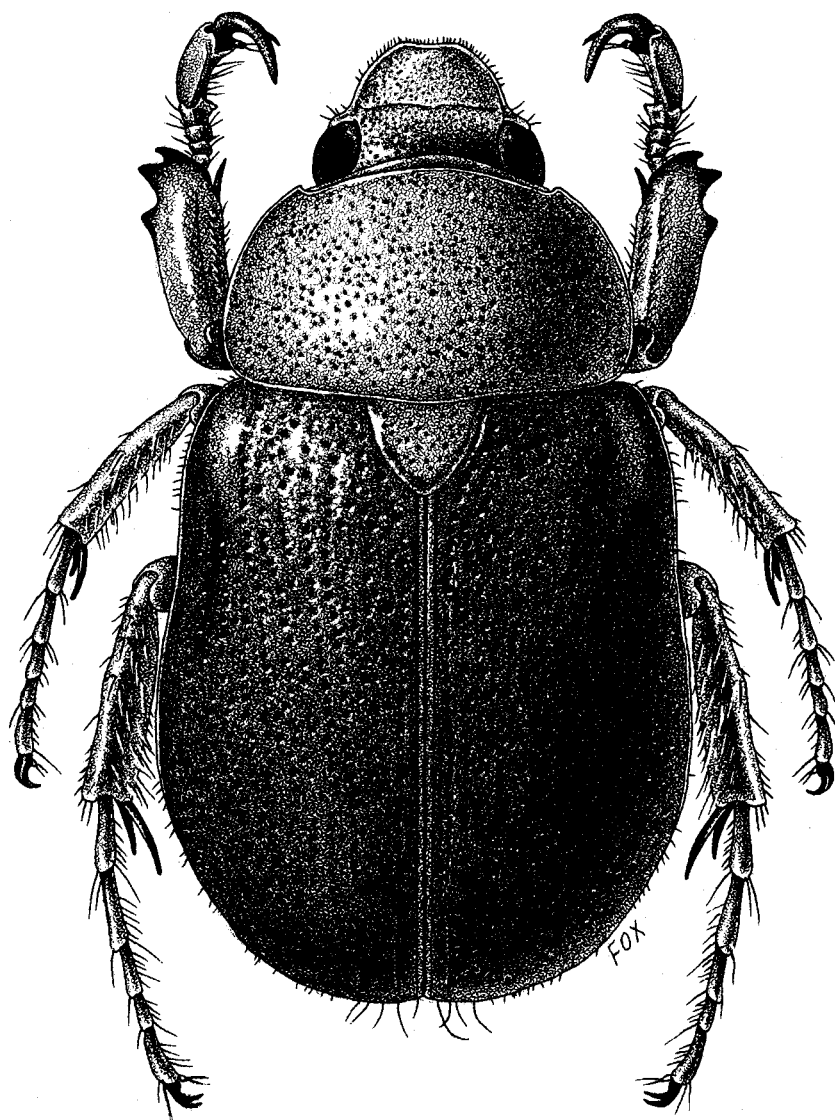


Fig. 212. *Cyclocephala enigma*.

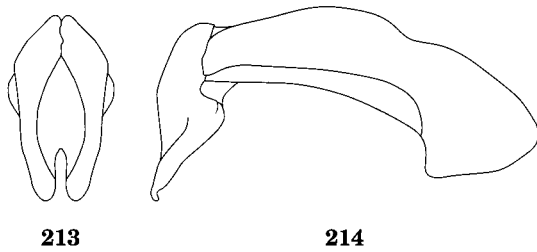
VARIATION. Male (1 paratype). Length 12.4 mm; width 6.7 mm. As holotype except in the following respects: *Legs:* Posterior tarsus subequal in length to posterior tibia.

ETYMOLOGY. From the Latin *aenigma*, meaning a mystery or something inexplicable. Used here in reference to the riddle of such a distinctive species being known from only two specimens from a well-collected area.

DISTRIBUTION. *Cyclocephala enigma* is known only from Estación Cacao on the southwestern slope of Volcán Cacao in Guanacaste Province in northwest Costa Rica.

LOCALITY RECORDS (Fig. 215). 2 specimens examined.

COSTA RICA (2). **GUANACASTE** (2): Estación Cacao.



Figs. 213-214. *Cyclocephala enigma* parameres.



Fig. 215. Distribution of *Cyclocephala enigma* in Costa Rica.

TEMPORAL DISTRIBUTION. May (2).

DIAGNOSIS. The distinctive coloration (testaceous except for piceous elytra and abdominal sternites) in combination with an emarginate clypeus, pronotum with a basal bead, a roughened pygidium with sparse setae, and a tridentate foretibia will help to distinguish males of this species. The parameres, while unique, are not overly distinctive; they loosely resemble those of *C. concolor*. In using the key in Endrödi (1985a), you can get to couplet 157 (*C. complanata*) where the characters no longer match. The female remains unknown.

BIOLOGY. There is no data to suggest how these specimens were collected. They were collected, probably at lights, in an area of premontane rain forest at an elevation of 1,100 meters.

***Cyclocephala epistomalis* Bates, 1888**

(Figs. 216-218)

Cyclocephala epistomalis Bates 1888: 303.
Cyclocephala mollis Endrödi 1963: 323 (**NEW SYNONYMY**).

DESCRIPTION. Length 14.5-18.3 mm; width 7.2-8.6 mm. Color yellowish-brown except for black on frons and apices of femora and tibiae. *Head:* Frons in males with punctures moderate in density and size, females with punctures slightly denser and larger. Clypeus transversely rugulose; apex broadly, weakly convex, thickened, slightly reflexed. Interocular width equals 3.0 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. *Pronotum:* Surface of males at center with small, sparse punctures, punctures becoming slightly larger, denser on disc and sides; females with punctures at center sparse and moderate in size, punctures becoming moderately large and denser on disc and sides. Base without marginal bead. *Elytra:* Surface finely shagreened, with punctures moderate in size and density, distinct rows visible. Epipleuron (ventral view) of females simple to faintly enlarged at level of abdominal sternites 1-2. *Pygidium:* Surface finely shagreened, punctate; punctures small and minute mixed, moderate to moderately dense, small punctures setigerous in males (females without setae); setae moderate in density, moderately long, dark yellowish-brown. In lateral view, surface in males strongly convex just past middle, nearly flat in females. *Legs:* Foretibia tridentate, teeth subequally spaced. Foretarsus in males enlarged: segments 2-4 each slightly larger than preceding segment and with increasingly large flaring on venter; 5th large, elongate, curved, with strong longitudinal carina on inner edge, and venter with longitudinal row of stout, long setae; median claw large, long, curved, with large lobe at base, apex cleft. Foretarsus in females simple. Posterior tarsus in males distinctly longer than posterior tibiae, tarsus slightly shorter than tibiae in females. *Venter:* Prosternal process only moderate in length, apex obliquely

flattened into small, transverse oval with raised "button" on anterior half. *Parameres*: Figs. 216-217.

DISTRIBUTION. *Cyclocephala epistomalis* was described by Bates based on two females from Guatemala. Endrödi (1966) reported (as *C. mollis*) additional specimens from Venezuela, Brazil, Bolivia, and Paraguay. The two specimens from Panama listed below constitute a NEW COUNTRY RECORD.

LOCALITY RECORDS (Fig. 218). 8 specimens examined (2 from the study area).

PANAMA (2). COCLÉ (2): Nata.

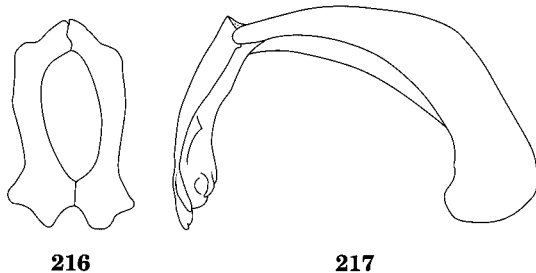
TEMPORAL DISTRIBUTION. July (2).

DIAGNOSIS. The presence of setae on the pygidium in the males will easily distinguish this species from the similar-appearing *C. mutata*, which has a glabrous pygidium. The parameres of *C. epistomalis* are unique (Figs. 216-217). *Cyclocephala epistomalis* is also consistently darker (yellowish brown) than *C. mutata* (testaceous).

Cyclocephala epistomalis also resembles those specimens of *C. amblyopsis* that lack pronotal vittae since they are both yellowish or reddish brown. Males may be separated by the subequally spaced teeth on the foretibia in *C. epistomalis* and the unequally spaced foretibial teeth in *C. amblyopsis*. Females may be distinguished by the simple epipleuron in *C. epistomalis* versus the distinct tooth on the epipleuron in *C. amblyopsis*.

NOMENCLATURE. Endrödi (1985a) transferred his *C. mollis* to *C. epistomalis* as an "aberration." This designation has no nomenclatural standing, and so *C. mollis* is here formally synonymized.

BIOLOGY. Only two specimens are known from Panama, and they were collected at the lights of a gas station in Nata along the Pan-American highway (A. Gillogly, personal communication, 1995). This is an area of tropical dry forest that is less than 100 meters in elevation.



Figs. 216-217. *Cyclocephala epistomalis* parameres.



Fig. 218. Distribution of *Cyclocephala epistomalis* in Panama.

Cyclocephala erotylina Arrow,
1914

(Figs. 219-226)

Cyclocephala erotylina Arrow 1914: 275.

DESCRIPTION. Length 11.7-15.8 mm; width 6.1-7.9 mm. Color of head, pronotum, pygidium, and legs reddish brown; elytra testaceous with black markings as follows: most specimens with large postscutellar, post-humeral, discal, and subapical spot (usually elongated) as well as a long streak on the lateral margin (Fig. 220); some specimens with discal spot broken into 2-3 spots (rare) while others with discal and subapical spots fused (Fig. 219); some specimens from extreme southeastern Costa Rica and the Osa peninsula with humeral, discal, and subapical spots fused into slender, oblique vita (Fig. 221).

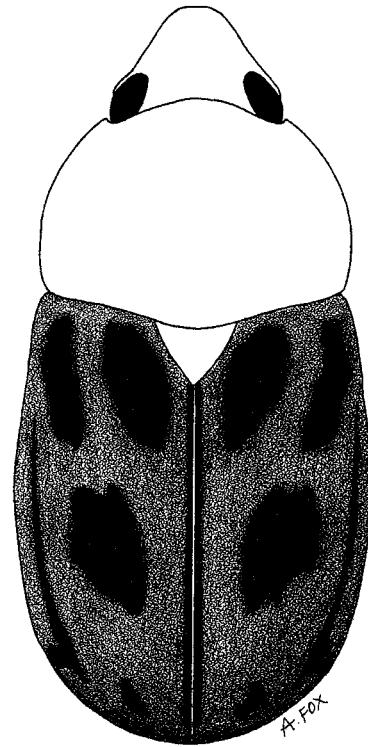


Fig. 220.

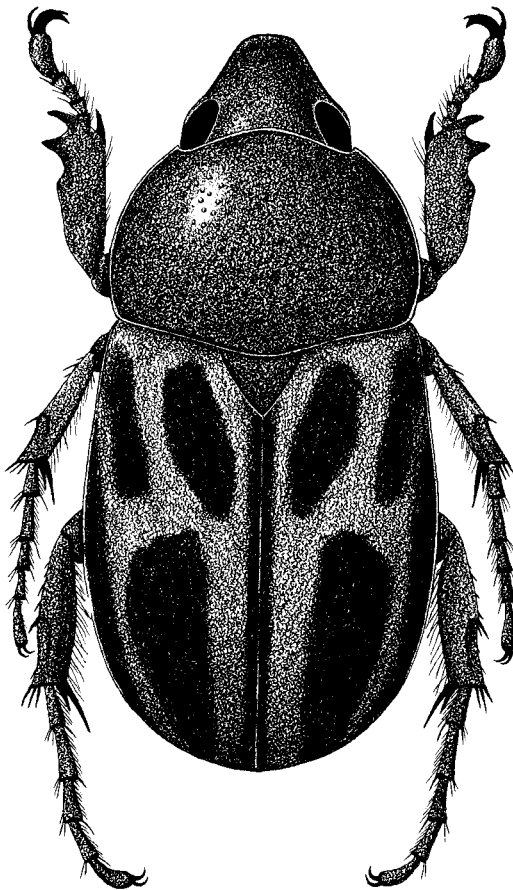


Fig. 219.

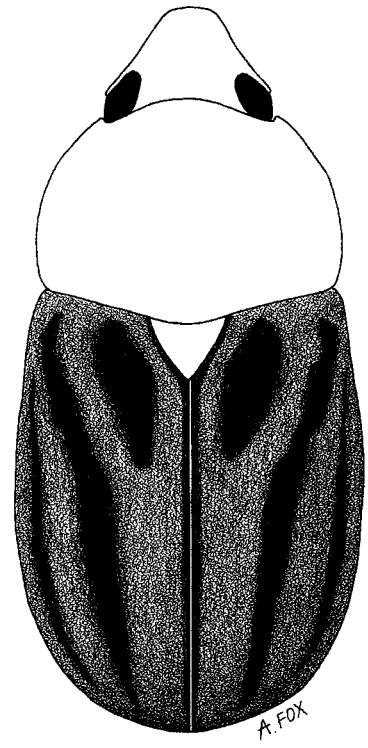
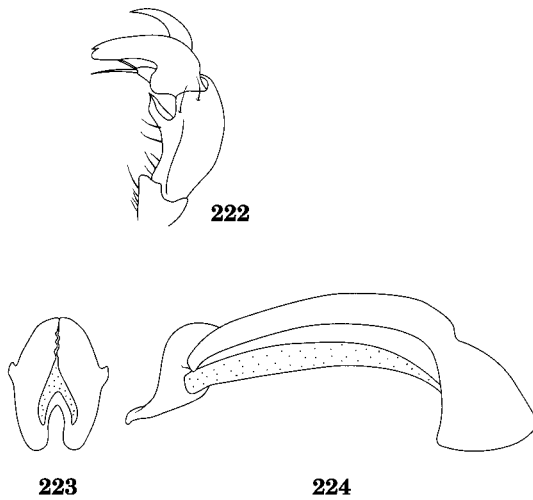


Fig. 221.

Figs. 219-221. *Cyclocephala erotylina*



Figs. 222-224. *Cyclocephala erotylina*: (222) foreclaw of male; (223-224) parameres.

Head: Vertex nearly smooth. Frons moderately densely punctate, punctures moderate in size. Clypeus in males with surface in basal half similar to frons, apical half becoming densely and finely punctate to rugopunctate; clypeus in females usually transversely and finely rugopunctate, occasionally punctate as in males; clypeus in both sexes elongate with narrowly parabolic apex; apex finely margined, weakly reflexed. Interocular width equals 2.8-3.0 transverse diameters. Antenna with 10 segments, club in males distinctly longer than segments 2-7, females with club slightly longer than segments 2-7. **Pronotum:** Surface with sparse punctures on disc, slightly denser on sides; punctures small to moderate in size in males, usually moderately large in females. Base with marginal bead. **Elytra:** Surface finely shagreened, shining. Rows of punctures forming striae distinct; punctures moderately large, shallow. Intervals finely shagreened with or without micro-punctures. Epipleuron (ventral view) of females narrow, abruptly constricted at level of 4th-5th abdominal sternites; in dorsal view, lateral margin of elytra weakly expanded at same point. **Pygidium:** Surface finely shagreened, shining; males with sparse, small punctures, punctures a little denser at base and lateral angles; females with punctures moderate in size and density. In lateral view,

surface of males evenly convex, surface in females nearly flat. **Legs:** Foretibia in males varies from bidentate to weakly tridentate, tridentate in females. Foretarsus in males enlarged: segments 2-4 each slightly larger than preceding segment; 5th large, weakly curved, with distinct longitudinal carina on inner surface (Fig. 222); median claw large, strongly bent, apex cleft, small ramus usually slightly longer than large ramus. Foretarsus in females simple. Posterior tarsus distinctly longer than posterior tibia. **Venter:** Prosternal process short, columnar, setose, apex obliquely flattened into nearly round disc with anterior 1/3-1/2 elevated into a raised "button." **Parameres:** Figs. 223-224.

DISTRIBUTION. *Cyclocephala erotylina* was known previously from Mexico and Guatemala (Endrödi 1966, 1985a). The specimens listed below for Costa Rica and Panama (and others I have from Honduras) constitute NEW COUNTRY RECORDS. Though uncommon, this species is widespread in the lower elevations of the Cordillera Central in Costa Rica and in the highlands either side of the Panama Canal. Surprisingly, there are no records from Chiriqui Province in Panama.

LOCALITY RECORDS (Figs. 225-226). 121 specimens examined.



Fig. 225. Distribution of *Cyclocephala erotylina* in Costa Rica.

COSTA RICA (90). ALAJUELA (9): Estación Laguna Pocosol, Parq. Nac. Rincón de la Vieja, San Ramón, Sector Colonia Palmareña; GUANACASTE (36): Estación Cacao, Estación Pitilla; LIMÓN (2): Estación Hitoy Cerere, Guapiles (35 km N); PUNTARENAS (30): Estación La Escuadra, Estación Sirena, Fila Guerra (Osa), Rancho Quemado (Osa), Wilson Botanical Garden; SAN JOSÉ (2): Parq. Nac. Braulio Carrillo.

PANAMA (31). COCLÉ (1): El Valle; PANAMA (30): Cerro Campana, El Llano-Carti Road (km 8).

TEMPORAL DISTRIBUTION. January (1), February (2), March (3), April (9), May (31), June (39), July (10), August (3), September (1), October (5), December (2).

DIAGNOSIS. *Cyclocephala erotylina* is distinctively marked (Figs. 219-221) and should not be confused with anything else in the study area. There is a general pattern similarity with *C. complanata* in those specimens of *C. erotylina* where the spots of the elytra have coalesced into an oblique stripe on each elytron. *Cyclocephala erotylina*, however, has a usually bidentate foretibia in the males (distinctly tridentate in *C. complanata*), reddish

brown head and pronotum (black frons and testaceous pronotum in *C. complanata*), elongated and narrowly parabolic clypeus (short and rounded clypeal apex in *C. complanata*), and differently shaped parameres (Figs. 223-224 and 178-179).

Most specimens of *C. erotylina* that I have seen from Costa Rica, Honduras, Guatemala, and Panama are the "typical" spotted form (Figs. 219-220). However, all of the specimens known to me from the Osa peninsula and nearby Wilson Botanical Garden in southeastern Costa Rica have the three discal spots of the elytra reduced in diameter and fused into a slender, oblique band (Fig. 221). Other than this difference in pattern, I can find no other characters that might separate these "different" *C. erotylina* from the spotted majority. For the time being, therefore, I conclude that this particular morphotype is somehow isolated in gene flow from the main population. The Osa specimens, which are smaller and more opaque, also occur the lowest in elevation at 100 meters.

BIOLOGY. Adults are attracted to lights. They have been collected from tropical moist forests, tropical wet forests, premontane wet forests, and premontane rain forests at elevations ranging from 100-1,340 meters.

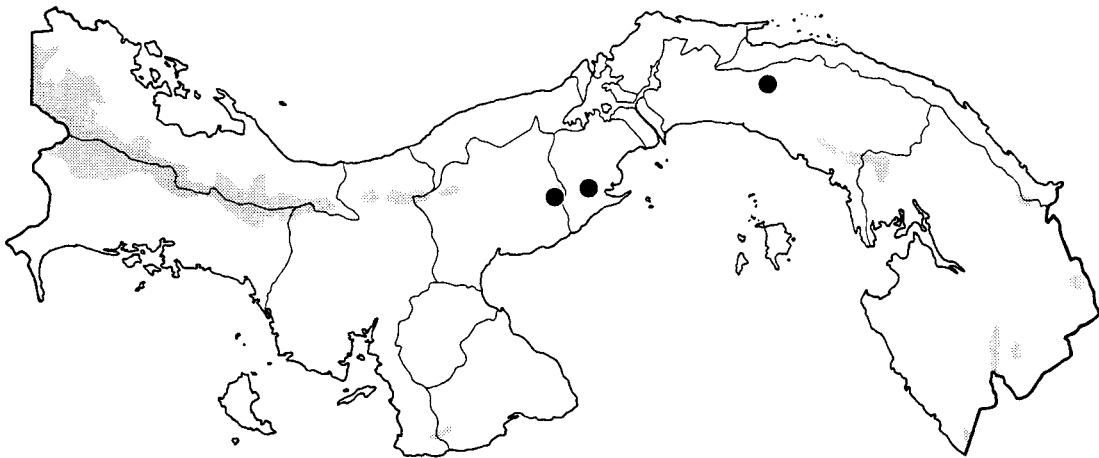


Fig. 226. Distribution of *Cyclocephala erotylina* in Panama.

***Cyclocephala fasciolata* Bates,
1888**

(Figs. 227-231)

Cyclocephala fasciolata Bates 1888: 301.

DESCRIPTION. Length 15.5-21.2 mm; width 8.2-10.6 mm. Color black except each elytron with transverse, slightly oblique band of reddish-orange, band not reaching lateral or sutural margins; band occasionally broken into 2 spots or nearly obsolete. (I have a few specimens from southern Mexico where the reddish orange maculation extends onto the lateral and sutural margins of each elytron, but I have seen no Central American specimens with these markings.) *Head:* Surface of frons and clypeus in males moderately punctate, punctures moderate in size, becoming denser and smaller at clypeal apex; females with punctation denser. Clypeus with apex broadly, weakly rounded, narrowly reflexed. Eyes small, interocular width equals 4.0-4.6 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7 (a little shorter in female). *Pronotum:* Surface similar in punctation to frons except punctures a little larger. Base with strong marginal bead. *Elytra:* Surface with rows of moderately large, shallow punctures. Epipleuron (ventral view) in females expanded into elongate, laterally expanded flange extending from middle of lateral edge of metacoxa to anterior edge of third sternite; in lateral view, epipleuron beneath flange produced ventrally into strong, posteriorly projecting, acute tooth. *Pygidium:* Surface in males finely scabrous, dull, setigerous; setae moderate in density, long, tawny in color. Surface in females shining, with punctures moderate in density and size, setigerous; setae short, tawny, often abraded away. In lateral view, surface regularly convex in males, nearly flat in females. *Legs:* Foretibia bidentate in males, tridentate in females. Foretarsus in males enlarged: tarsomeres 2-4 with large ventral lobes; 5th large, moderately curved, without lobe or tooth; median claw large, strongly curved, apex finely cleft. Foretarsus in females simple. Posterior tarsus slightly longer than posterior tibia. *Venter:*

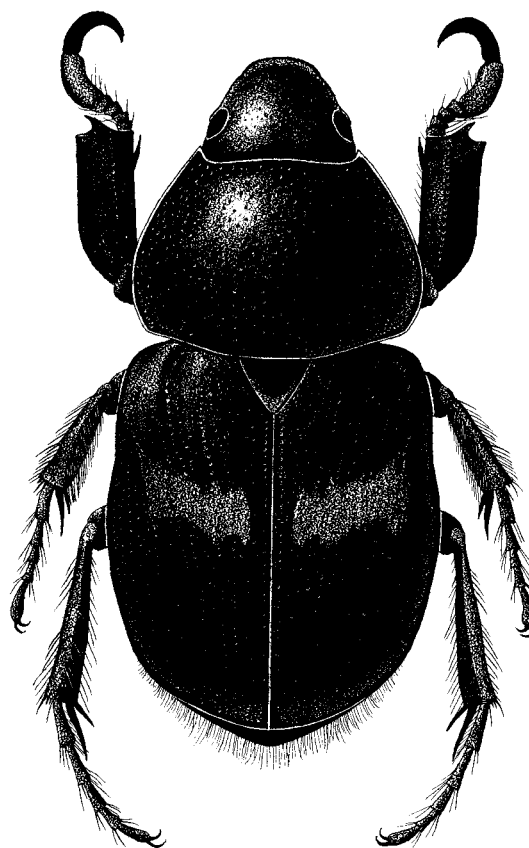
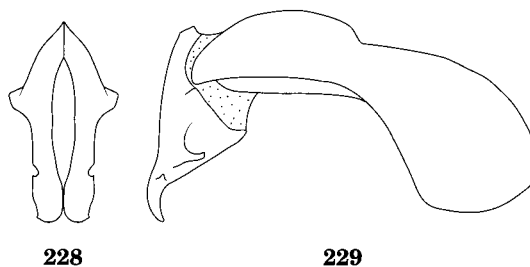


Fig. 227. *Cyclocephala fasciolata*.



Figs. 228-229. *Cyclocephala fasciolata* parameres.

Prosternal process long, stout, apex obliquely flattened into a transverse oval with anterior 2/3 raised as convex "button." *Parameres:* Figs. 228-229.

DISTRIBUTION. *Cyclocephala fasciolata* was known from southern Mexico, Guatemala,

and Panama (Endrödi 1966, 1985a). The Costa Rican specimens listed below are a **NEW COUNTRY RECORD**. This species seems to be very localized in both Costa Rica and Panama, and it is not commonly encountered.

LOCALITY RECORDS (Figs. 230-231). 22 specimens examined.

COSTA RICA (6). **GUANACASTE** (4): Volcán Rincon de la Vieja (4.5 km SW); **PUNTARENAS** (2): Estación Quebrada Bonita.



Fig. 230. Distribution of *Cyclocephala fasciolata* in Costa Rica.



Fig. 231. Distribution of *Cyclocephala fasciolata* in Panama.

PANAMA (16). **CHIRIQUI** (16): Alto Lino (4 km NE Boquete), Boquete, Cerro Punta, Fortuna Dam, Hartmann's Finca.

TEMPORAL DISTRIBUTION. April (4), May (6), June (3), July (2), August (1), September (2), November (1).

DIAGNOSIS. This species is easily recognized because it is the only black *Cyclocephala* in Costa Rica and Panama with a transverse, reddish-orange macula, or spots, on the elytra. In addition, *C. fasciolata* and *C. melanae* are the only black species in the study area with a marginal bead on the posterior margin of the pronotum; *C. melanae* has distinctly striate elytra (*C. fasciolata* does not) and lacks the elytral markings.

BIOLOGY. Adults have been collected at *Asplundia* flowers (Cyclanthaceae) (Ratcliffe and Morón 1997) and lights in tropical moist forests and premontane wet forests at elevations of 100-1,760 meters.

Cyclocephala fulgurata
Burmeister, 1847
 (Figs. 232-236)

Cyclocephala fulgurata Burmeister 1847: 63.

DESCRIPTION. Length 12.2-15.8 mm; width 6.5-8.3 mm. Color testaceous with variable "fuzzy," fuscous marks on pronotum and elytra. Apices of femora and tibiae and occasionally some abdominal sternites fuscous. Pronotal markings vary from nearly absent (uncommon) to with faint or strong "lunulata-type" pattern (most common). Elytral markings vary from nearly absent (uncommon) to with faint or strong "lunulata-type" pattern (most common). *Head:* Frons moderately densely punctate, punctures small. Clypeus with surface finely, transversely rugulose; apex broadly subtruncate, slightly reflexed. Interocular width equals 2.5 transverse eye diameters. Antenna with 10 segments, club slightly longer than segments 2-7. *Pronotum:* Surface in males with small punctures moderate in density, punctures becoming slightly larger and denser on sides; females with small, sparse punctures on disc, punctures becoming slightly larger and denser on sides. Base without marginal bead. *Elytra:* Surface with moderately large, moderately dense punctures, distinct rows visible. Epipleuron (ventral view) of females gradually and slightly thickened to level of abdominal sternite 2 where abruptly narrowed; elytra above thickening imperceptibly swollen. *Pygidium:* Surface on disc densely punctate, punctures small; surface becoming scabrous on sides in males, minutely rugopunctate in females. In lateral view, surface regularly convex in males, weakly convex in females. *Legs:* Foretibia tridentate, basal tooth slightly or not at all removed from other teeth. Foretarsus in males enlarged: tarsomeres 3-4 each slightly larger than preceding; tarsomere 5 large, slightly curved, nearly flat on venter; median claw large, strongly bent, with large lobe at base, apex cleft. Foretarsus in females simple. Posterior tarsus distinctly longer than posterior tibia in males, only slightly longer in females. *Venter:* Prosternal process moderately long, columnar, apex expanded and

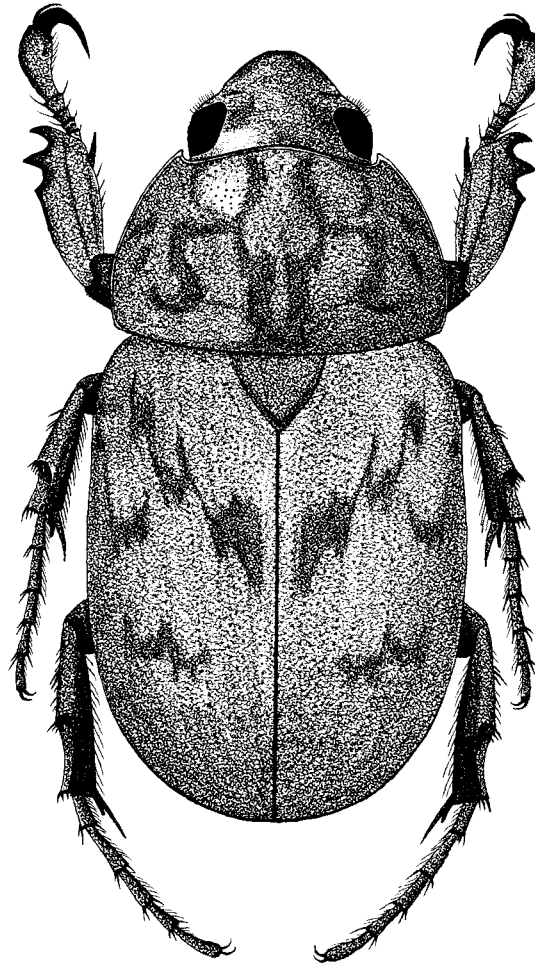
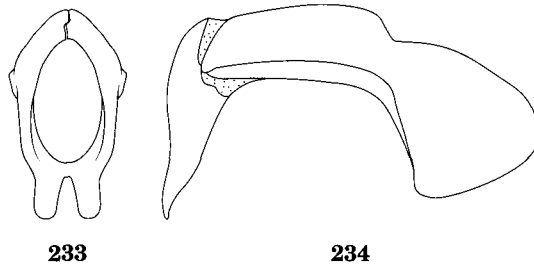


Fig. 232. *Cyclocephala fulgurata*.



Figs. 233-234. *Cyclocephala fulgurata* parameres.

obliquely flattened into a transverse oval with raised transverse "button" on anterior half. *Parameres:* Figs. 233-234.

DISTRIBUTION. *Cyclocephala fulgurata* is broadly distributed from southern Mexico to Argentina (Endrödi 1966). It occurs throughout Costa Rica and Panama.

LOCALITY RECORDS (Figs. 235-236). 1,059 specimens examined.

COSTA RICA (539). ALAJUELA (20): Atenas (8 km W), Upala, Vara Blanca (8 km N); CARTAGO (20): Cerro La Muerte, Quebrada Segunda, Tapanti, Tuis; GUANACASTE (111): Estación Cacao, Estación Maritza, Tierras Morenas, Volcán Tenorio, Volcán Rincón de la Vieja; LIMÓN (14): Amubri, Reserva Biológica Hitoy Cerere; PUNTARENAS (374): Boruca, Estación Altamira, Estación Las Cruces, Finca Cafrosa, Monteverde Cloud Forest Reserve, San Vito, Santa Elena.

PANAMA (520). BOCAS DEL TORO (5): Chiriqui Grande (12 km W), Miramar; CA-

NAL ZONE (236): Albrook Forest, Barro Colorado Island, Black Tank Road, Coco Solo Hospital, Ft. Clayton, Madden Dam, Piña Road; CHIRIQUI (263): Boquete, Finca La Suiza, Hornito, Hartmann's Finca (Santa Clara), Lino, Poterillos; DARIEN (4): Cana; PANAMA (11): Cerro Azul, Cerro Campana, El Llano-Carti Road (km 8); VERAGUAS (1): Sona.

TEMPORAL DISTRIBUTION. January (1), February (10), March (219), April (50), May (143), June (75), July (5), August (1), September (3), October (5), November (1). Most of the March specimens represent a single collecting event at Las Alturas Field Station in Costa Rica; these high numbers reflect collecting bias and are not indicative of a March peak of activity, which normally occurs for this species in May and June in the study area.

DIAGNOSIS. Of the four species occurring in Costa Rica and Panama with a "lunulata-type" pattern of dorsal markings, only *C. fulgurata* lacks the black "mask" between the eyes in combination with a glabrous pygidium. The male parameres are distinctive.

BIOLOGY. Adults are attracted to lights at night. This species occurs in tropical moist forests, tropical wet forests, premontane wet forests, and premontane rain forests at elevations of near sea level to 1,500 meters with a few specimens taken at the lights of the Pension Georgina on Cerro La Muerte in Costa Rica at 3,000 meters!



Fig. 235. Distribution of *Cyclocephala fulgurata* in Costa Rica.

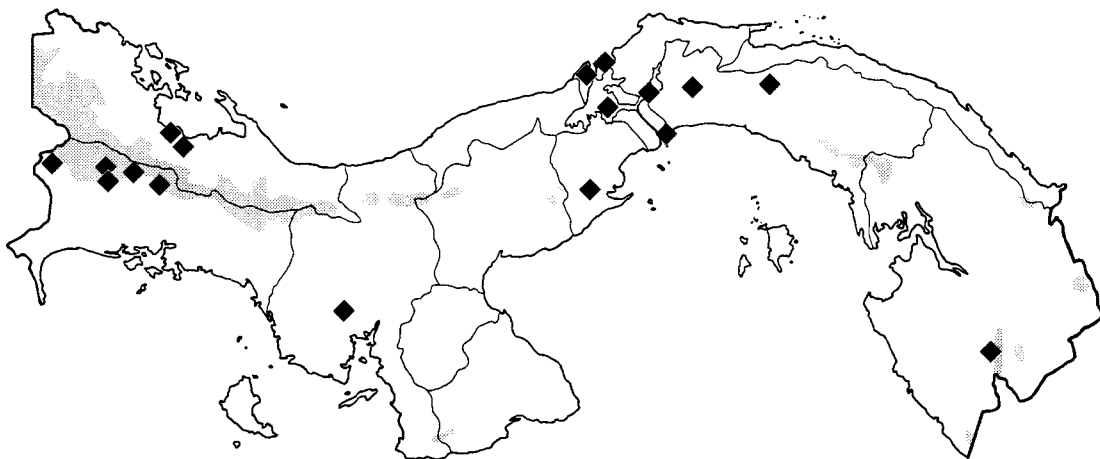


Fig. 236. Distribution of *Cyclocephala fulgurata* in Panama.

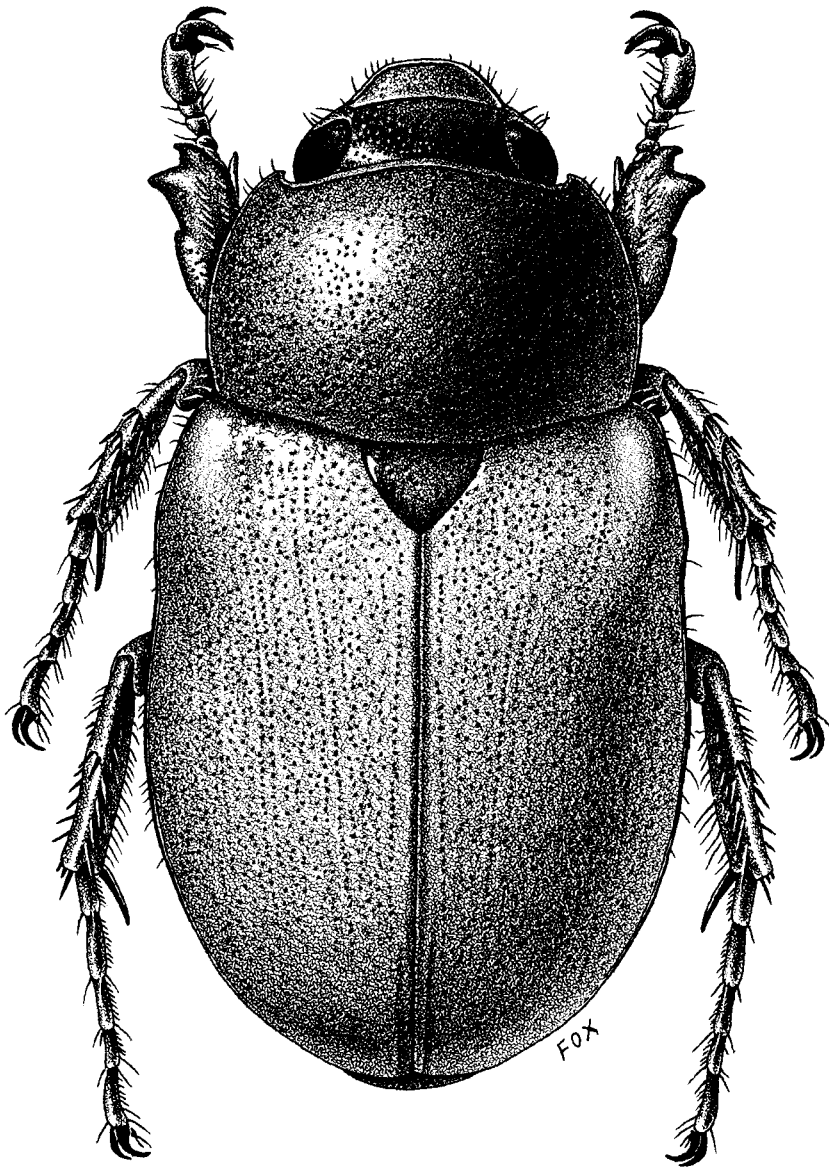


Fig. 237. *Cyclocephala gravis*.

***Cyclocephala gravis* Bates, 1888**
(Figs. 35, 237-241)

Cyclocephala gravis Bates 1888: 308.

DESCRIPTION. Length 14.8-18.6 mm; width 8.0-9.4 mm. Color entirely dark cherry red except for black frons and testaceous elytra. *Head:* Frons varies from moderately densely punctate with moderate-size punctures to sparsely punctate with small punctures,

occasionally many punctures obsolete so surface appears almost smooth. Clypeus with surface finely, transversely rugulose; apex broadly emarginate. Interocular width equals 2.5 transverse eye diameters. Antenna with 10 segments, club slightly longer than segments 2-7. *Pronotum:* Surface at center with sparse, small punctures, punctures becoming moderate in density and size on sides. Base lacking marginal bead. *Elytra:* Surface finely shagreened, with punctures moderate

in density and size, punctate rows distinct. Epipleuron (ventral view) of females simple, narrow. *Pygidium*: Surface finely shagreened, with punctures on disc moderate in size and density, punctures becoming slightly larger and denser on sides, setigerous; setae sparse, minute, tawny. In lateral view, surface in males strongly, regularly convex, in females weakly convex. *Legs*: Foretibia tridentate, basal tooth strongly removed from others. Foretarsus in males enlarged: tarsomere 4 subtriangularly expanded on venter; 5th large, curved, flat to slightly concave on venter; median claw large, strongly bent, with broad lobe at base, apex cleft. Foretarsus in females simple. Posterior tarsus subequal in length to posterior tibia. *Venter*: Prosternal

process moderately long, columnar, apex obliquely flattened into transverse oval with raised, transverse "button" on anterior half. *Parameres*: Figs. 238-239.

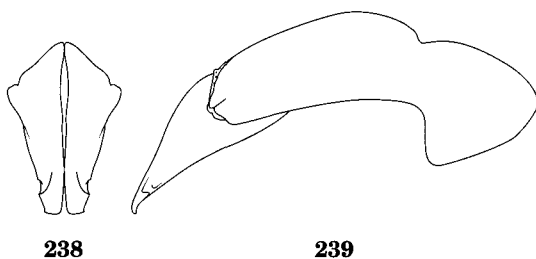
DISTRIBUTION. *Cyclocephala gravis* occurs from southern Mexico to Brazil and Bolivia (Endrödi 1966). In Costa Rica and Panama, it is generally distributed.

LOCALITY RECORDS (Figs. 240-241). 418 specimens examined.

COSTA RICA (310). ALAJUELA (23): Alajuela, Caño Negro, Cerro Campana, Estación Laguna Pocosol, Piedra Negra, Playuelos, San Ramon, Upala; CARTAGO (25): Chirripó, Tuis, Turrialba; GUANACASTE (98): Bahía Santa Elena, Estación Maritza, Estación Los Almendros, Estación Pitilla, Finca Jenny, Finca Montezuma on SW slope Volcán Tenorio, Parq. Nac. Santa Rosa, Sector Góngora, Tierras Morenas, Volcán Rincón de la Vieja (4.5 km SW); HEREDIA (38): Estación El Ceibo, Estación Magsasay, Finca Naranjo Valenciana, La Selva Biological Station; LIMÓN (53): Amubri, Cerro Tortuguero, Llanuras del Tortuguero, Pococí, Manzanillo, Reserva Biológico Hitoy Cerere, Valle La Estrella; PUNTARENAS (60): Estación Quebrada Bonito, Estación Las Alturas, Estación Sirena, Monteverde, Quepos, Rancho Quemado, Reserva Biológico Carara; SAN JOSÉ (12): San José, San Pedro.

PANAMA (108). BOCAS DEL TORO (8): Corriente Grande, Miramar; CANAL ZONE (55): Albrook Forest Site, Barro Colorado Island, Black Tank Road, Coco Solo Hospital, Ft. Clayton, Ft. Gulick, Gatun Lake Lookout, Madden Forest, Margarita, Pipeline Road, Skunk Hollow; COLÓN (10): Portobelo (15 km E), Río Guanache Bridge (1 km E), Santa Rita Ridge; PANAMA (35): Altos de Majé, Cerro Azul, Cerro Campana, El Llano-Carti Rd. (km 8, km 11), Ipetí (2 km S).

TEMPORAL DISTRIBUTION. January (8), February (10), March (22), April (31), May (107), June (66), July (70), August (48),



Figs. 238-239. *Cyclocephala gravis* parameres.



Fig. 240. Distribution of *Cyclocephala gravis* in Costa Rica.

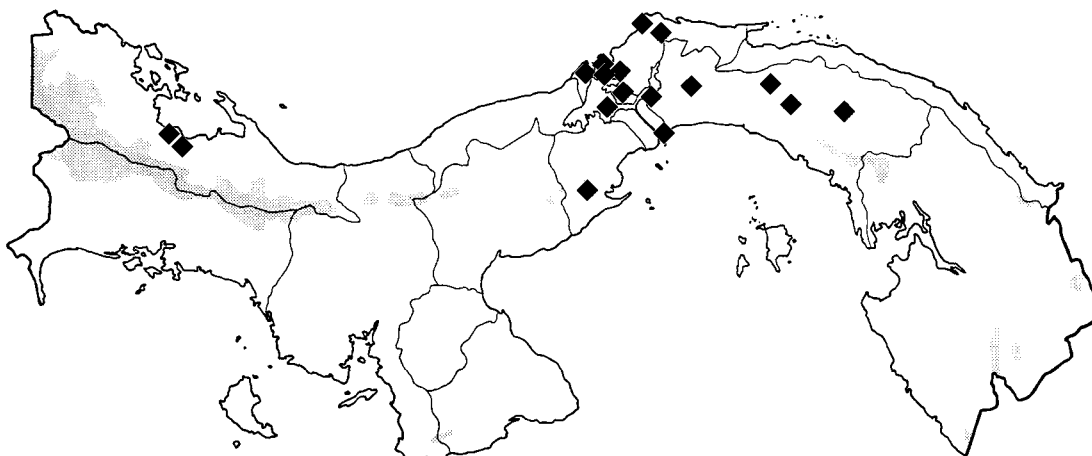


Fig. 241. Distribution of *Cyclocephala gravis* in Panama.

September (14), October (15), November (13), December (8).

DIAGNOSIS. *Cyclocephala gravis* and *C. sanguinicollis* are the only larger species in Costa Rica and Panama that are distinctly bicolored with a dark, cherry-red pronotum and testaceous elytra. Only *C. melanocephala* and *C. macrophylla*, both smaller species, have this same appearance of color. The apex of the clypeus is emarginate in *C. gravis* while it is rounded in *C. sanguinicollis* and subtruncate in *C. melanocephala*. The parameres of *C. gravis* and *C. sanguinicollis* (Figs. 238-239, 381-382) are also very different in form.

BIOLOGY. Young (1986, 1988a-b) reported adults feeding on the inflorescences of *Dieffenbachia longispatha* Engler and Krause (Araceae) in Costa Rica (Fig. 35), and I have also taken them in these flowers in Colón Province, Panama. Adults are attracted to lights at night. They are found in tropical dry/tropical moist forests transition, tropical moist forests, tropical wet forests, premontane wet forests, and, occasionally, in premontane rain forests. They occur at elevations ranging from near sea level to 1,000 meters, and a very few specimens are known from as high as 1,500 meters.

***Cyclocephala herteli* Endrödi,
1964**

(Figs. 242-246)

Cyclocephala herteli Endrödi 1964: 447.

Cyclocephala barroensis Endrödi 1979: 216
(NEW SYNONYMY).

DESCRIPTION. Length 10.6-12.8 mm; width 5.0-5.1 mm. Color testaceous; pronotum rarely with 2 longitudinal, dark vittae; elytra usually with elongated, oblique streak behind scutellum, another on disc behind middle, and a third behind humerus (occasionally absent); rarely, some specimens lacking dorsal markings entirely. *Head:* Surface completely, strongly shagreened, males with punctures usually not visible; surface weakly shining in females, with small, weak, dense punctures. Clypeus with apex parabolic, broadly rounded, weakly reflexed. Interocular width equals 3.0 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. *Pronotum:* Surface in males completely, strongly shagreened, usually with small, dense, shallow punctures not visible; surface in females weakly shining, with small, dense punctures. Base with marginal bead. *Elytra:* Surface in males weakly shagreened with small to moderate, shallow

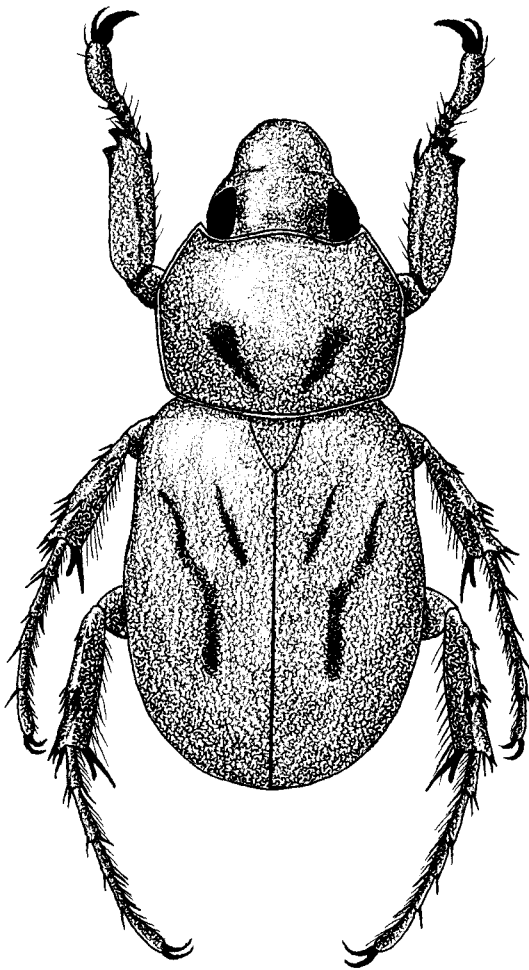
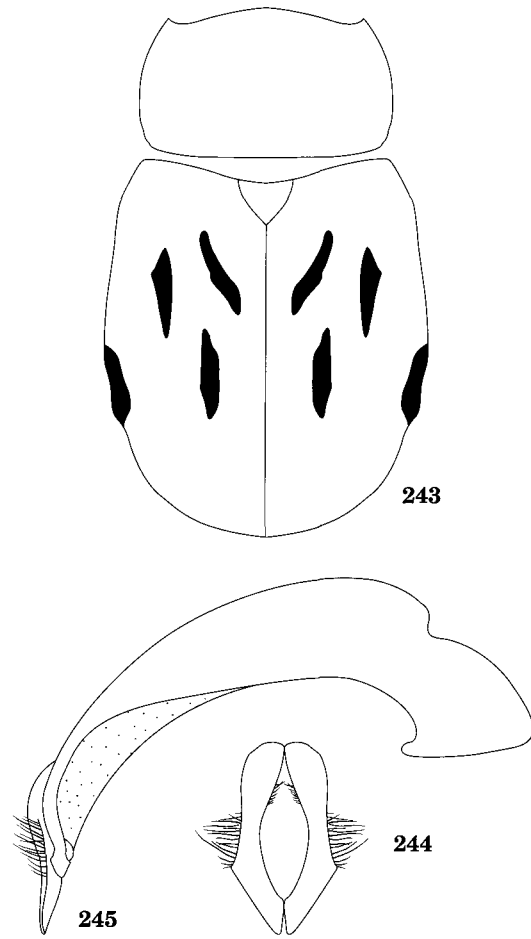


Fig. 242. *Cyclocephala herteli*.

punctures, double rows vague; sides and apices with small, sparse setae. Surface in females weakly shining, often becoming weakly shagreened at apices, with small to moderate, distinct punctures in delineated striae, a few sparse setae present on apices. Epipleuron (ventral view) of females becoming wider and arcuate at level of abdominal sternite 1 and abruptly narrowing at sternite 2; in lateral view, ventral edge of epipleuron obtusely tooth-like at sternite 2; in dorsal view, swollen elytral margin darkened, bi-emarginate (Fig. 243) (similar to *C. amazona*). *Pygidium*: Surface in males strongly shagreened, small punctures usually not visible, glabrous; surface in females weakly shagreened with



Figs. 243-245. *Cyclocephala herteli*: (243) elytra of female; (244-245) parameres.

small, shallow, moderately dense punctures, glabrous. In lateral view, surface in males nearly flat, becoming strongly convex at apex, females with surface nearly flat to weakly convex. *Legs*: Foretibia in males bidentate, tridentate in females. Foretarsus in males enlarged: tarsomere 5 with distinct tooth at base on ventral side and with strong, arcuate carina with basal tooth on median edge; median claw large, curved, apex entire. Foretarsus in females simple. Posterior tarsus about 1.6 times longer than posterior tibia. *Venter*: Prosternal process short, apex flattened and transversely lanceolate, with small, oval, elevated "button" on anterior half. *Parameres*: Figs. 244-245.

DISTRIBUTION. *Cyclocephala herteli* is known only from the lowlands of central Panama.

LOCALITY RECORDS (Fig. 246). 273 specimens examined.

PANAMA (273). **CANAL ZONE** (203): Achiotte Road, Barro Colorado Island, Ft. Sherman, Pipeline Road (km 9, km 11), Skunk Hollow; **COCLÉ** (2): Cerro Gaital; **COLÓN** (17): Santa Rita Ridge; **PANAMA** (52): Cerro Azul, Cerro Campana, Cerro Jefé, El Llano-Carti Road (km 8, km 9).

TEMPORAL DISTRIBUTION. March (2), April (9), May (99), June (48), July (114), August (2).

DIAGNOSIS. This species resembles *C. santaritae* in form and coloration but can easily be distinguished by the following characters: *C. herteli* has short streaks on the elytra, a glabrous pygidium in the males, a broadly rounded clypeal apex, a well-developed (but short) prosternal process, a tooth-like epipleural expansion in the females, and a small tooth at the base of the fifth protarsomere in the males; *C. santaritae* has suboval elytral spots, a setose pygidium in the males, a narrowly parabolic clypeal apex, a barely developed prosternal process, a simple and gradually arcuate epipleural expansion in the females, and a very large tooth at the base of

the fifth protarsomere in the males. The male parameres are also very different (Figs. 244-245, 385-386).

NOMENCLATURE. I concluded that *Cyclocephala barroensis* is conspecific with *C. herteli* after examination of the types of both species (types in the U.S. National Collection at the Smithsonian Institution). The holotype of *C. barroensis* is a male with its parameres rotated on the phallobase, thus showing the ventral side of the parameres. Endrödi drew the parameres of the paratype, and they agree in all respects with those of *C. herteli* as well as in other characters of coloration, sculpturing, tarsi, and prosternal process. Endrödi noted there were some differences between the two in the elytral punctation of the males, but this is normal variation. Similarly, there is a minute difference in the lateral emargination of the parameres, but, again, this appears to represent intraspecific variation. Four female paratypes of *C. barroensis* are, in fact, *C. discolor*! This may partly explain why Endrödi described differences between females of *C. herteli* and his *C. barroensis* because he was really describing differences between *C. herteli* and *C. discolor*.

BIOLOGY. Adults are attracted to lights at night. *Cyclocephala herteli* is known from tropical moist forests (primarily) and tropical dry forests at elevations ranging from 200-1,100 meters.

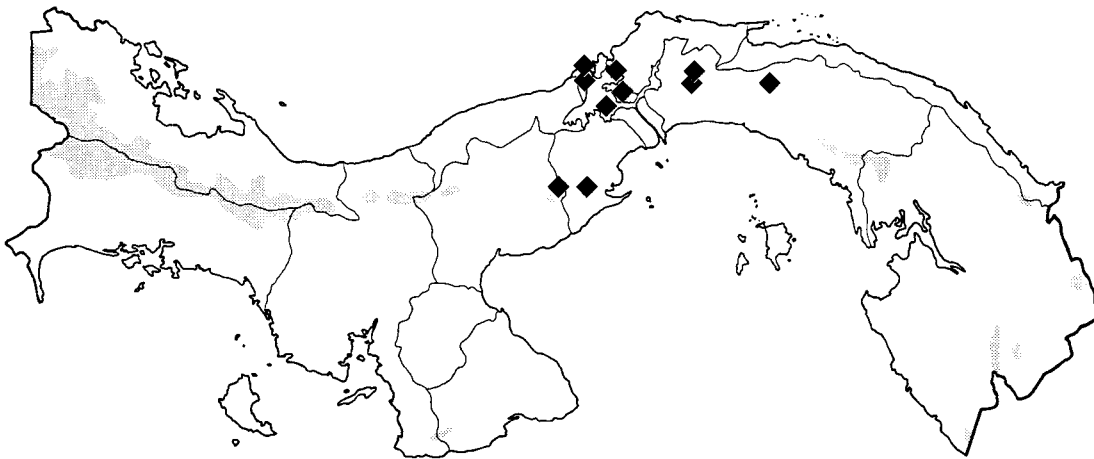


Fig. 246. Distribution of *Cyclocephala herteli* in Panama.

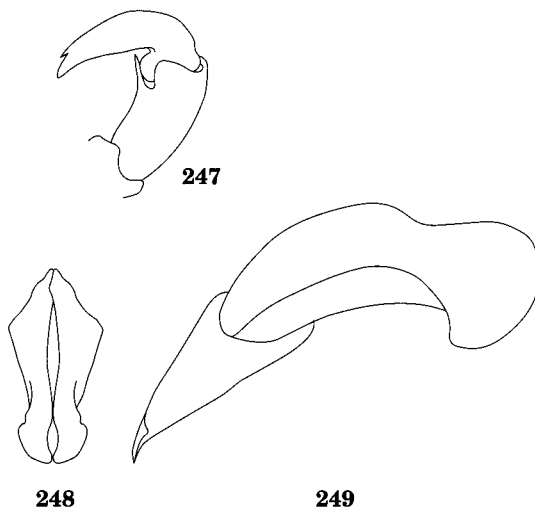
Cyclocephala isthmiensis**Ratcliffe, 1992**

(Figs. 247-250)

Cyclocephala isthmiensis Ratcliffe 1992b: 219.

DESCRIPTION. Length 12.3-14.1 mm; width 6.0-6.9 mm. Color testaceous except for darkened frons and vertex. *Head:* Frons rugopunctate in males, moderately punctate in females, setigerous; setae short, pale. Clypeus with surface rugopunctate and similarly setigerous; apex nearly semicircular,

narrowly and weakly reflexed. Interocular width equals 2.5 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. *Pronotum:* Surface sparsely punctate along midline, gradually becoming moderately dense at lateral margins; punctures moderate in size, setigerous; setae short, pale, not as dense as on head. Basal bead absent. *Elytra:* Surface roughened, moderately densely punctate, punctures setigerous and not in distinct rows; setae short, pale, a little denser than those on pronotum, especially on apical fourth of elytra. Epipleuron (ventral view) in females simple, not swollen. *Pygidium:* Surface moderately densely punctate; punctures moderate in size, setigerous; setae moderate in length, pale, subequal in density to those on apical fourth of elytra. In lateral view, surface in males strongly convex, weakly convex in females. *Legs:* Foretibia in both sexes tridentate, basal tooth only slightly removed from equidistant spacing of other teeth. Foretarsus in males enlarged: tarsomere 4 expanded ventrally; tarsomere 5 (Fig. 247) enlarged, weakly curved, slightly concave on venter; median claw large, curved, basal lobe present, apex strongly split. Foretarsus in females simple. Posterior tarsus slightly longer than posterior tibia. *Venter:* Prosternal process moderately long, columnar, apex obliquely flattened into a transverse oval with raised,



Figs. 247-249. *Cyclocephala isthmiensis*: (247) foreclaw of male; (248-249) parameres.



Fig. 250. Distribution of *Cyclocephala isthmiensis* in Panama.

transverse "button" on anterior half. *Parameres*: Figs. 248-249.

DISTRIBUTION. *Cyclocephala isthmiensis* is known only from the Pacific side of the Canal Zone in Panama.

LOCALITY RECORDS (Fig. 250). 4 specimens examined.

PANAMA (4). **CANAL ZONE** (4): Albrook Forest site, Diablo Heights.

TEMPORAL DISTRIBUTION. May (4).

DIAGNOSIS. *Cyclocephala isthmiensis* is relatively non-descript, and this may have contributed to it being confused with, and subsumed under, the name of other species, most notably *C. sparsa*. These two species are similar in external appearance. Males can be separated by the spacing of the protibial teeth (basal tooth nearly equidistant from others in *C. isthmiensis* and strongly removed in *C. sparsa*), length of posterior tarsomeres (*C. isthmiensis* with first posterior tarsomere distinctly longer than second, and both tarsomeres long and subequal in length in *C. sparsa*), and form of the parameres (Figs. 248-249, 407-408). Females may be separated by the form of the expansion of the epipleuron/elytral margin (simple and not expanded in *C. isthmiensis* and weakly expanded in *C. sparsa*).

BIOLOGY. Adults of the four known specimens were attracted to lights. This species is known from tropical moist forests at elevations near sea level.

***Cyclocephala kaszabi* Endrödi,
1964**

(Figs. 251-255)

Cyclocephala kaszabi Endrödi 1964: 433.

DESCRIPTION. Length 19.0-23.0 mm; width 10.1-11.5 mm. Color black. *Head*: Frons moderately to moderately densely punctate, punctures moderate in size to moderately large. Clypeus sparsely punctate (rarely mod-

erately), punctures small (rarely moderate in size); apex broadly truncate and narrowly reflexed (often very weakly emarginate), apical angles rounded. Interocular width equals 4.0-4.2 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. *Pronotum*: Surface with moderate to moderately large punctures moderate in density. Base without marginal bead. *Elytra*: Surface of disc with distinct rows of moderate to mostly large, umbilicate punctures. Epipleuron (ventral view) of females enlarged into elongate lobe extending from about middle of metasternum to middle of third abdominal sternite; in lateral view, ventral margin of expanded portion convex and without tooth. *Pygidium*: Surface with moderate to

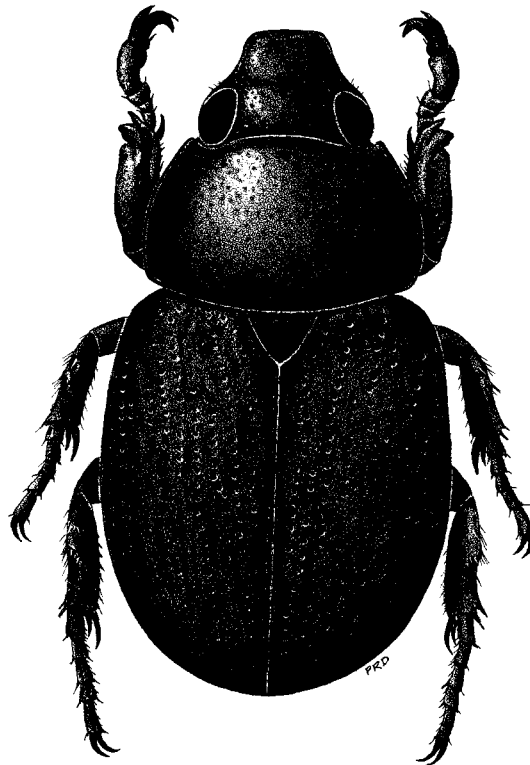
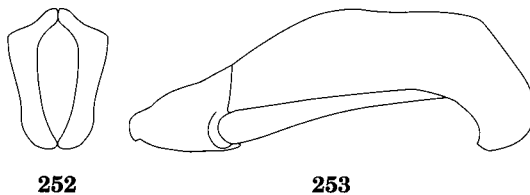


Fig. 251. *Cyclocephala kaszabi*.



Figs. 252-253. *Cyclocephala kaszabi* parameres.

large punctures; punctures sparsely to densely punctate, setigerous; setae minute, tawny. In lateral view, surface in males regularly convex, nearly flat in females. *Legs*: Foretibia bidentate in males, tridentate in females; in both sexes basal tooth with arcuate sides and with distinct notch on posterior margin. Foretarsus in males enlarged: tarsomeres 2-4 without large ventral lobes; 5th large, curved, without lobe or tooth; median claw large, strongly curved, apex split. Foretarsus in females simple. Posterior tarsus subequal in length to posterior tibia. *Venter*: Prosternal process long, stout, with apex obliquely flattened into a wide, transverse oval with anterior 4/5 raised as a convex "button." *Parameres*: Figs. 252-253.

DISTRIBUTION. *Cyclocephala kaszabi* is known from Ecuador (Endrödi 1966, 1985a) and Costa Rica and Panama (Ratcliffe 1992b). This species is broadly distributed in both countries.

LOCALITY RECORDS (Figs. 254-255). 90 specimens examined.

COSTA RICA (40). ALAJUELA (9): Finca San Gabriel, Parq. Nac. Rincon de la Vieja, San Ramon; CARTAGO (1): Tuis; GUANACASTE (7): Estación Pitilla; HEREDIA (9): La Selva Biological Station; LIMÓN (6): Amubri, Cerro Tortuguero, Estación Hitoy Cerere, Llanuras del Tortuguero, Refugio Nacional Barra del Colorado; PUNTARENAS (8): Bosque

Esquinas (Osa), Estación Quebrada Bonita, Estación Sirena, Las Cruces Botanical Garden, Monteverde.

PANAMA (50). BOCAS DEL TORO (9): Corriente Grande, Miramar, 2 mi N Continental Divide, 8 km N Continental Divide; CANAL ZONE (1): Barro Colorado Island; CHIRIQUI (13): Fortuna Dam, IHRE Vivero (11 km N Los Planes), Lago Fortuna, Los Planes, Windy Pass (7 km N Los Planes); COCLÉ (2): Cerro Gaital; COLÓN (2): Santa Rita Ridge; PANAMA (21): Cerro Azul, Cerro Campana, El Llano-Carti Rd. (km 8, km 9, km 10); SAN BLAS (2): Nusagandi.

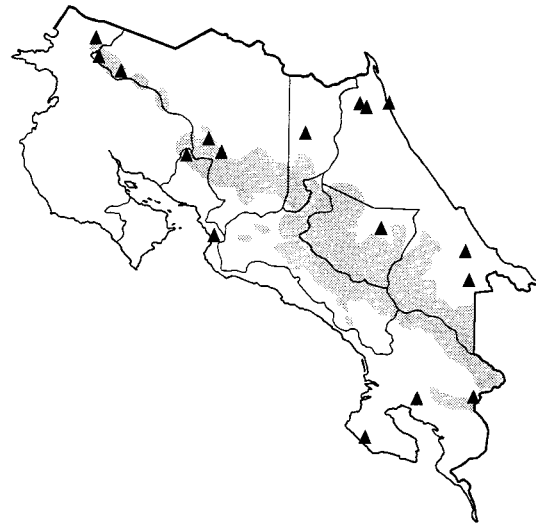


Fig. 254. Distribution of *Cyclocephala kaszabi* in Costa Rica.

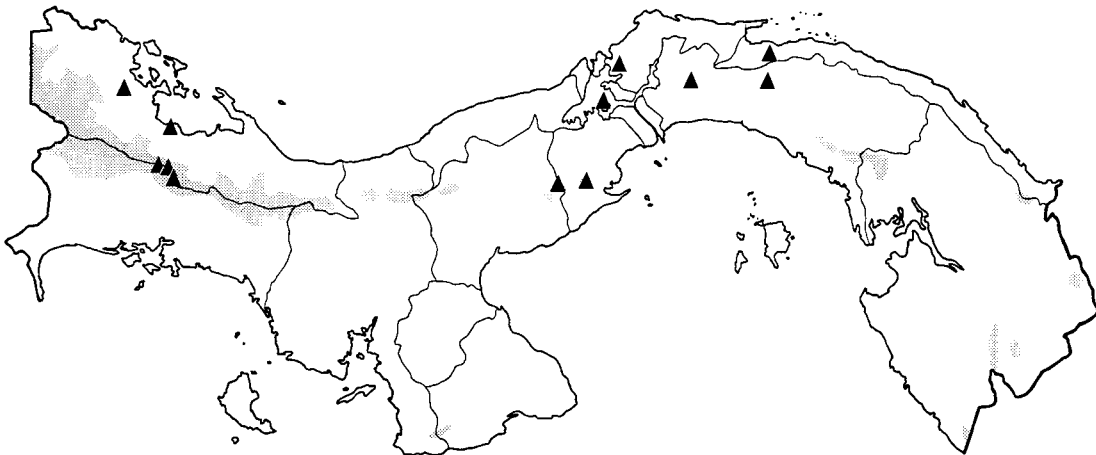


Fig. 255. Distribution of *Cyclocephala kaszabi* in Panama.

TEMPORAL DISTRIBUTION. January (1), February (3), April (4), May (36), June (30), July (4), August (7), September (1), October (2), November (1), December (2).

DIAGNOSIS. *Cyclocephala kaszabi* is easily recognized because it is the only black species in the study area with a bidentate foretibia in the males and a tridentate foretibia in the females. In addition, there is in both sexes a distinctive notch on the foretibia just behind the basal tooth. The parameres are similar to those of *C. ligyrina* in caudal view but differ significantly in lateral view (Figs. 252-253, 271-272). In the females, the epipleuron of *C. kaszabi* is abruptly enlarged into a lobe extending from the metasternum to the third abdominal sternite whereas in *C. ligyrina* the epipleuron gradually tapers to the third sternite.

BIOLOGY. Adults are attracted to lights and have also been taken in the inflorescences of *Dieffenbachia longispatha* Engler and Krause (Araceae) (Young 1986). Specimens have been collected in tropical wet forests, premontane moist forests, premontane rain forests, and premontane wet forests. The elevational range for *C. kaszabi* is from near sea level to 1,200 m.

***Cyclocephala krombeini* Endrödi,
1979**
(Figs. 256-262)

Cyclocephala krombeini Endrödi 1979: 215.
Cyclocephala rorschachoides Ratcliffe 1992:
227 (NEW SYNONYMY).

DESCRIPTION. Length 15.3-17.8 mm; width 7.5-9.0 mm. Color testaceous with black markings as follows: frons and occasionally base of clypeus black; elytron with 6 spots (Fig. 257): post-scutellar spot large, triangular, often fused with spot behind in apical third of elytron (in which case these mesal spots on both elytra resemble an hourglass, Fig. 256), 2 small spots behind humerus, and 2 small spots on disc just behind middle (occasionally fused); pygidium with oval spot

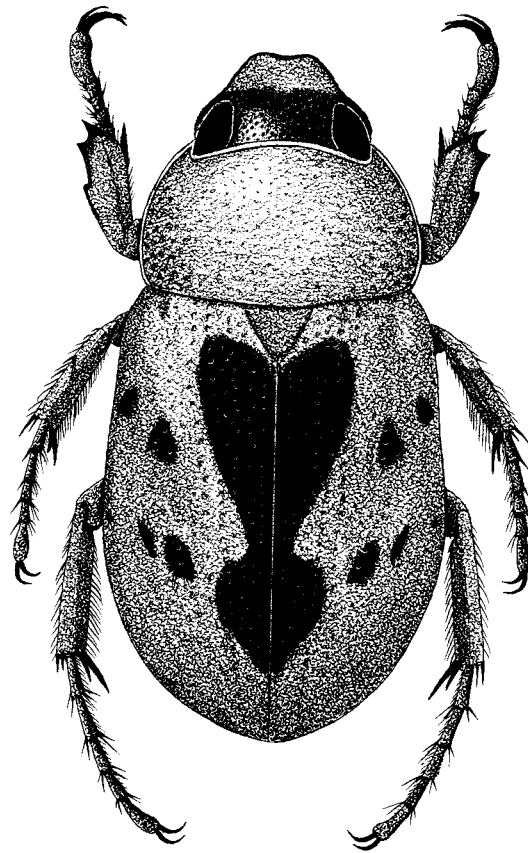


Fig. 256.

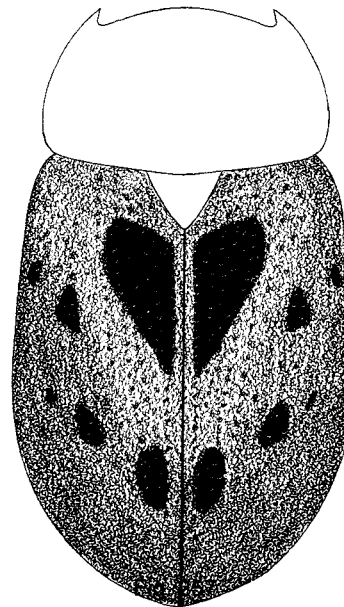


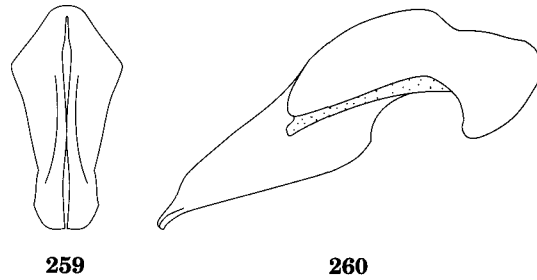
Fig. 257.

Figs. 256-257. *Cyclocephala krombeini*.



Fig. 258. *Cyclocephala krombeini*, left epipleuron (ventral view) of female.

near lateral margin on each side (rarely absent); abdominal sternites 1-4 each with black spot on lateral edge near posterior margin; femora and tibiae with apices darkened; tarsi darkened. *Head*: Frons densely punctate; punctures moderately large (smaller near vertex), many confluent, setigerous; setae dense, short, tawny. Clypeus transversely rugopunctate to rugulose, setigerous, setae similar to those of frons; apex broadly emarginate. Interocular width equals 2.7 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. *Pronotum*: Surface densely punctate in males, moderately punctate in females; punctures small to moderate, setigerous; setae minute, moderately dense, tawny. Base without marginal bead. *Elytra*: Surface roughened, with indistinct, shallow, setigerous punctures, rows of punctures indistinct in males, distinct



Figs. 259-260. *Cyclocephala krombeini* parameres.

in females; setae similar to those on pronotum, becoming slightly longer apically. Epipleuron (ventral view) of females broadened into elongate lobe from metatrochanter to abdominal sternite 2 where abruptly narrowed (Fig. 258); mesal edge with acute spine at level of abdominal sternites 1-2. *Pygidium*: Surface roughened, moderately densely punctate; punctures indistinct (due to surface roughness), setigerous; setae moderately dense, moderately long, pale yellow. In lateral view, surface in males weakly convex, becoming strongly convex near apex; surface in females nearly flat. *Legs*: Foretibia tridentate, basal tooth strongly removed from others. Foretarsus in males enlarged: tarsomere 5 large, curved, weakly and longitudinally cariniform on venter; median claw large, curved, with large lobe at base, apex cleft. Foretarsus in females simple. Posterior tarsus slightly longer than posterior tibia in males, subequal in length in females. *Venter*: Prosternal process moderately long, columnar, apex obliquely flattened into a broad oval, with raised "button" on anterior 1/2-2/3. *Parameres*: Figs. 259-260.

DISTRIBUTION. *Cyclocephala krombeini* is known from central and western Panama and a few localities in Costa Rica.

LOCALITY RECORDS (Figs. 261-262). 156 specimens examined.

COSTA RICA (6). HEREDIA (4): Estación El Ceibo, La Selva Biological Station; LIMÓN

(1): Fila Río Corinto; PUNTARENAS (1): Rancho Quemado.

PANAMA (150). BOCAS DEL TORO (2): Corriente Grande, Miramar; CANAL ZONE (64): Barro Colorado Island, Black Tank Road (NW Gatun locks), Cerro Galera, Ft. Sherman, Pipeline Road (km 2), Skunk Hollow; COLÓN (31): Santa Rita Ridge; PANAMA (52): Cerro Azul, Cerro Campana, Cerro Jefé, El Llano-Carti Road (km 8, km 10); SAN BLAS (1): Nusagandi.

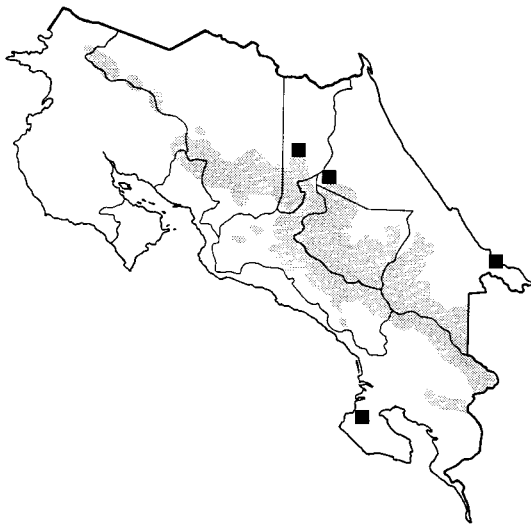


Fig. 261. Distribution of *Cyclocephala krombeini* in Costa Rica.

TEMPORAL DISTRIBUTION. March (4), April (9), May (125), June (14), July (4), December (1).

DIAGNOSIS. *Cyclocephala krombeini* is easily distinguished by its distinctive hour-glass shaped elytral markings or, when these markings are reduced, by the six large spots on each elytron; the two spots on the pygidium are also unique. Adults have short, dorsal setae, an emarginate clypeus, unbordered pronotum, diagnostic parameres in the males (Fig. 259-260), and a characteristic epipleuron in the females (Fig. 258).

NOMENCLATURE. *Cyclocephala rorschachoides* (Ratcliffe 1992) is conspecific with *C. krombeini*. At the time of its description, I was unable to ascertain the relevant characters of *C. krombeini* from Endrödi's brief description and illustration of the male parameres.

BIOLOGY. Adults have been collected at lights from tropical moist forests, tropical wet forests, and premontane rain forests at elevations of near sea level to 600 meters.

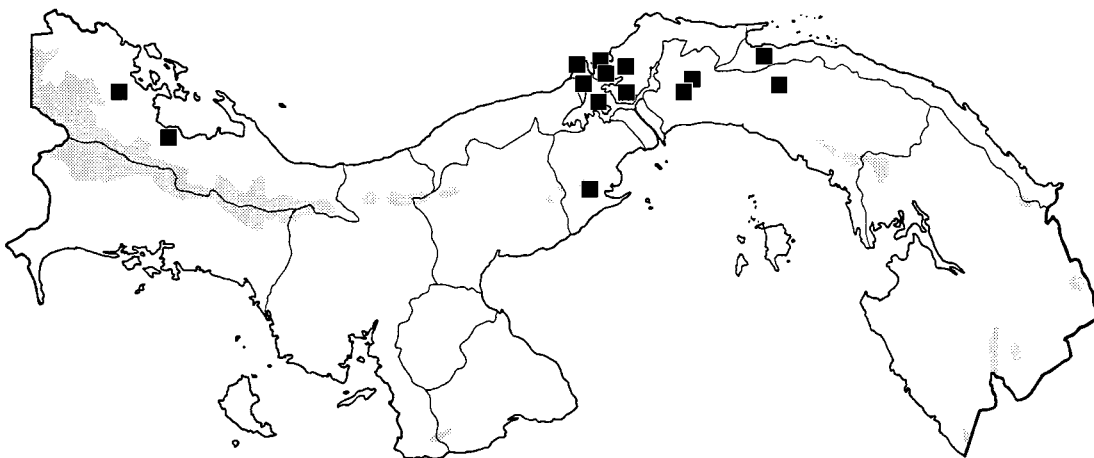
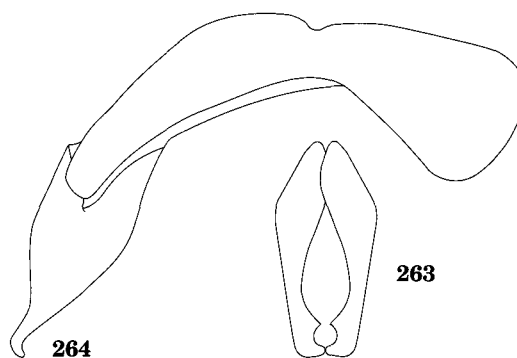


Fig. 262. Distribution of *Cyclocephala krombeini* in Panama.

***Cyclocephala labidion* Ratcliffe,
new species**
(Figs. 263-265)

TYPE MATERIAL. Holotype labeled "COSTA RICA: Puntarenas, Las Cruces Field Station (OTS) near San Vito, V-24-27-1988, 1000 M, B. Ratcliffe & M. Jameson." Allotype labeled "PANAMA: Chiriqui Prov., Finca Hartmann (BL), Santa Clara, main house, 8 Nov. 2001, N. Schiff." Single male paratype with same data except 7 November. Holotype and allotype deposited at the University of Nebraska State Museum (Lincoln, NE). Paratype deposited in the Paul Lago collection (University, Mississippi).

HOLOTYPE. Male. Length 12.0 mm; width 6.6 mm. Color testaceous except for black frons and reddish brown marks on elytra, tarsi, apices of femora and tibiae, and abdominal sternites; each elytron with following "indistinctly-edged" marks: a longitudinally elongate mark just mesad of humerus, a subtriangular mark slightly behind scutellum and close to elytral suture, a transverse mark laterad of post-scutellar mark and behind humerus, and a vaguely "M-shaped" mark in center of disc behind middle. *Head:* Frons with moderately large, moderately dense punctures. Clypeus with surface rugopunctate; apex broadly truncate, distinctly reflexed. Interocular width equals 2.5 transverse eye diameters. Antenna with 10 segments; club distinctly longer than segments 2-7, extending to about middle of scape. *Pronotum:* Surface with small, sparse punctures, punctures becoming slightly larger and denser on sides. Base lacking distinct marginal bead. *Elytra:* Surface with punctures moderate in size and density, shallow, distinct rows visible. *Pygidium:* Surface vaguely, finely rugopunctate, center apex smoother and with small, sparse punctures. In lateral view, surface weakly convex. *Legs:* Foretibia tridentate, teeth subequally spaced. Foretarsus enlarged: segments 2-4 each larger than preceding; segments 3-4 each subtriangularly expanded on venter; 5th large, curved, with longitudinal carina on inner edge, venter nearly flat; median claw large,



Figs. 263-264. *Cyclocephala labidion* parameres.

curved, base with large lobe, apex cleft. Posterior tarsi both broken. *Venter:* Prosternal process moderately long, columnar, apex obliquely flattened into a small, transverse oval with transversely crescent-shaped, raised "button" in anterior half. *Parameres:* Figs. 263-264.

ALLOTYPE. Female. Length 12.4 mm; width 6.8 mm. As holotype except in the following respects: *Elytra:* Markings present but reduced. Epipleuron (ventral view) slightly expanded above level of metacoxa and abruptly constricted at level of abdominal sternite 1. *Pygidium:* Surface not as coarsely roughened, punctures distinct, small, moderate in density. *Legs:* Foretarsus simple. Posterior tarsi shorter than in type, only slightly longer than posterior tibia.

VARIATION. Male (1 paratype). Length 12.0 mm; width 6.2 mm. The specimen does not differ significantly from the holotype except that the elytral markings are reduced and the posterior tarsi (broken in the holotype) are distinctly longer than the posterior tibiae.

ETYMOLOGY. From the Greek *labis*, meaning tongs; used here in the diminutive for small tongs or tweezers in reference to the form of the male parameres.

DISTRIBUTION. *Cyclocephala labidion* is known only from extreme eastern Costa Rica and western Panama.



Fig. 265. Distribution of *Cyclocephala labidion* in Costa Rica and adjoining Panama.

LOCALITY RECORDS (Fig. 265). 3 specimens examined.

COSTA RICA (1). PUNTARENAS (1): Las Cruces Field Station.

PANAMA (2). CHIRIQUI (2): Finca Hartmann.

TEMPORAL DISTRIBUTION. May (1), November (2).

DIAGNOSIS. This species resembles small specimens of *C. lunulata* and will key to couplet 348 in Endrödi (1985a) where it then does not fit anything. Males are most easily separated from males of *C. lunulata* by their smaller size, slightly elongated antennal club, having the basal tooth of the foretibia subequally spaced from the others (slightly removed in *C. lunulata*), with a flatter pygidium, and with "pincer-like parameres. In the females, the metasternum is microscopically imbricate and strongly shining in *C. labidion* whereas it is coarsely roughened and only weakly shining in *C. lunulata*; also, the epipleuron is abruptly narrowed at the level of abdominal sternite 1, and in *C. lunulata* is gradually tapered either side of a slight thickening at the level of abdominal sternites 1-2.

Cyclocephala labidion is smaller and with sparser elytral markings than *C. weidneri*.

BIOLOGY. The specimens were collected at lights in disturbed premontane wet forest at an elevation of 1,000 meters in Costa Rica and 1,340 meters in Panama.

***Cyclocephala letiranti* Young, 1992**
(Figs. 266-269)

Cyclocephala letiranti Young 1992: 52.

DESCRIPTION. Length 19.7-21.8 mm; width 9.0-10.5 mm. Color testaceous with black markings as follows: frons black; base of clypeus with subtriangular mark; elytra with 4 small to large spots in an arc on each elytron (post-scutellar, post-humeral, on lateral edge of disc just behind middle, and on disc behind middle); apices of femora, tibiae, and tarsomeres darkened or black. **Head:** Dorsal surface punctate; punctures moderately large, dense on frons and moderate in size and density on clypeus, setigerous; setae moderate in density, short, tawny. Clypeus with apex broadly emarginate, only apical marginal bead reflexed. Interocular width equals 3.3 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. **Pronotum** Surface with moderately large punctures; punctures moderate in density on central third in males, sparse in females, becoming larger and denser on lateral thirds, setigerous (when not worn off); setae moderate in density, short, tawny. Base lacking marginal bead. **Elytra:** Surface with small, setigerous punctures intermixed with dense, minute punctures, striae weak; setae moderate in density (when not worn off), short, tawny. Epipleuron (ventral view) of females expanded into elongate lobe on lateral edge and with strong, right-angled tooth on mesal edge at level of abdominal sternites 1-2; lateral edge of elytron above flange swollen into elongate lobe. **Pygidium:** Surface densely micropunctate mixed with large punctures moderate in size and density, larger punctures setigerous; setae in males moderately dense, long, tawny, females with setae slightly

sparser, shorter. In lateral view, surface in males convex, especially in apical third; females with surface nearly flat, becoming convex at apex. *Legs*: Foretibia tridentate in 3 specimens, bidentate in 3 specimens; when tridentate basal tooth small, removed from apical 2 teeth. Foretarsus in males enlarged: protarsomere 4 subtriangularly expanded on venter; 5th large, curved, distinctly concave

on venter; median claw large, strongly bent with large, broad lobe at base; apex cleft. Foretarsus in females simple. Posterior tarsus slightly longer than posterior tibia. *Venter*: Prosternal process moderately long, columnar, apex obliquely flattened into a strongly transverse oval with raised "button" on anterior half. *Parameres*: Figs. 267-268.

DISTRIBUTION. *Cyclocephala letiranti* is known from Costa Rica and Colombia (NEW COUNTRY RECORD). In Costa Rica, it is known from several localities in the Cordillera Central.

LOCALITY RECORDS (Fig. 269). 11 specimens examined (one from Colombia).

COSTA RICA (10). ALAJUELA (1): Atenas (8 km W); HEREDIA (2): Parq. Nac. Braulio Carrillo on Hwy 32, Vara Blanca (10 km N). PUNTARENAS (7): Estación La Casona, Monteverde Forest Reserve, Pension Quetzal nr. Monteverde cloud forest.

TEMPORAL DISTRIBUTION. May (8), June (2).

DIAGNOSIS. *Cyclocephala letiranti* closely resembles *C. sexpunctata* but may be easily

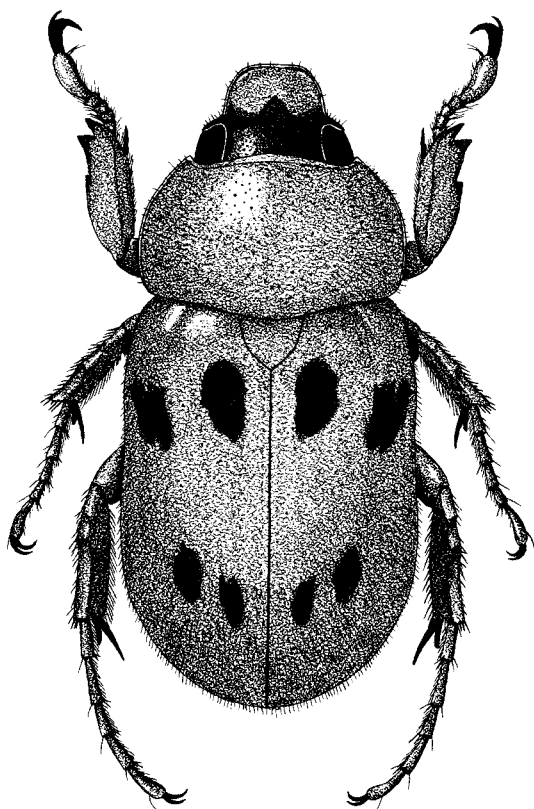
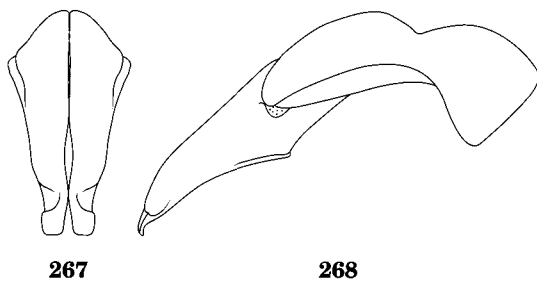


Fig. 266. *Cyclocephala letiranti*.



Figs. 267-268. *Cyclocephala letiranti* parameres.

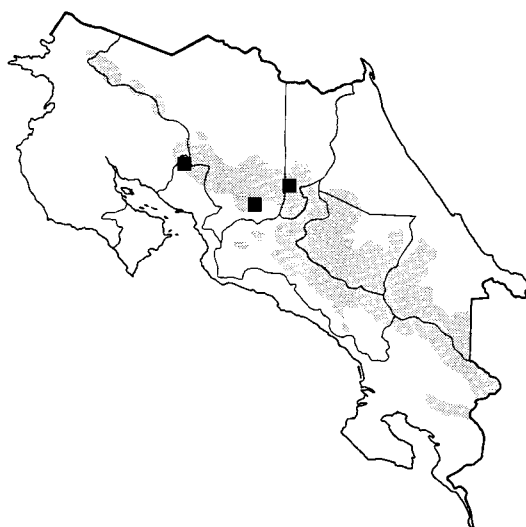


Fig. 269. Distribution of *Cyclocephala letiranti* in Costa Rica.

distinguished by the following characters: the base of the clypeus has a black, triangular patch in *C. letiranti* but not in *C. sexpunctata*; the clypeus is punctate in *C. letiranti* whereas it is mostly transversely rugose in *C. sexpunctata*. In males, the form of the parameres is different (Figs. 267-268, 390-397) with the apices in *C. letiranti* appearing subrectangular and subtriangular in *C. sexpunctata*; the 5th protarsomere is distinctly concave on its venter, and the base of the enlarged median claw has a large, broad lobe at its base in *C. letiranti* whereas in *C. sexpunctata* the venter of the 5th protarsomere is flat and the base of the enlarged median claw has a large, narrow lobe at its base. In females, the form of the epipleural flange is different: the flange in *C. letiranti* is elongated and with a right-angled tooth, and in *C. sexpunctata* the flange is a short, rounded prominence and with an obtuse tooth; the margin of the elytron above the epipleural flange is an elongated bulge in *C. letiranti* and only weakly swollen in *C. sexpunctata*.

The foretibiae are considered tridentate for both sexes, but half the male specimens of *C. letiranti* studied have the basal tooth reduced to a mere prominence.

NOMENCLATURE. The allotype of *C. letiranti* (deposited at the University of Nebraska State Museum) is actually a specimen of *C. sexpunctata*.

BIOLOGY. All the known specimens were taken at lights except for the new record from Colombia that was collected in a malaise trap. They have been collected in premontane moist forests and premontane and lower montane rain forests at elevations of 1,000-1,520 meters.

***Cyclocephala ligyrina* Bates, 1888**
(Figs. 270-274)

Cyclocephala ligyrina Bates 1888: 309.

DESCRIPTION. Length 21.6-26.0 mm; width 11.1-14.3 mm. Color dark reddish brown to

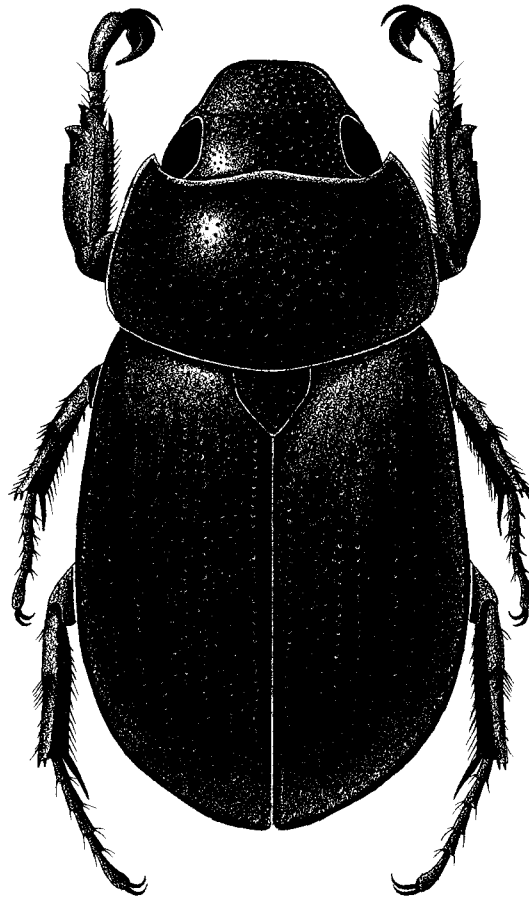
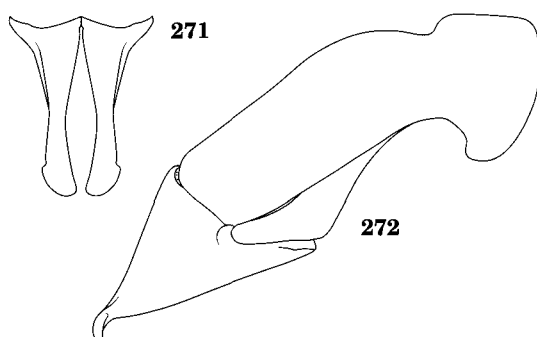


Fig. 270. *Cyclocephala ligyrina*.

black. **Head:** Surface of frons and clypeus with punctures moderate (rarely sparse) in density, deep, and moderately large except those on occiput and apex of clypeus that are smaller and a little denser. Clypeus with anterior angles broadly rounded, apex broadly truncate and weakly emarginate. Interocular width equals 3.0-3.3 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. **Pronotum:** Surface with punctures as on frons. Base lacking marginal bead. **Elytra:** Surface with distinct rows of punctures; punctures (and those in intervals) ocellate, moderate to moderately large, moderate in density, females with punctate rows feebly furrowed. Epipleuron (ventral view) of females gradually tapering and then abruptly so at sternite 3; in dorsal view, epipleuron gradually expands to level of third



Figs. 271-272. *Cyclocephala ligyrina* parameres.

sternite; tooth on ventral surface of epipleuron absent in lateral view. *Pygidium*: Surface with punctures moderate in density (rarely sparse), moderate in size, most with minute, tawny setae in unworn specimens. In lateral view, surface regularly convex in males, weakly convex to nearly flat in females. *Legs*: Foretibia tridentate in both sexes; males with basal tooth small and directed "forward" and slightly removed from others; females with basal tooth distinct, larger, subequally spaced from other teeth. Foretarsus in males enlarged: tarsomeres 2-4 each gradually larger than preceding; fifth large, only weakly curved, with large tooth at base; median claw large, strongly curved, broadly split into a wide ramus and a slender ramus. Foretarsus of females simple. Posterior tarsus subequal in length to posterior tibia. *Venter*: Prosternal process short, stout, setose, apex obliquely flattened into a broadly transverse oval with anterior 4/5 raised into a convex "button." *Parameres*: Figs. 271-272.

DISTRIBUTION. *Cyclocephala ligyrina* is known from Nicaragua, Panama, Colombia, Ecuador, Brazil, and Peru (Endrödi 1966, 1985a). The records listed below for Costa Rica represent an unsurprising NEW COUNTRY RECORD. This species is generally distributed throughout both Costa Rica and Panama.

LOCALITY RECORDS (Figs. 273-274). 268 specimens examined.

COSTA RICA (185). ALAJUELA (44): Cerro Campana (E side Volcán Cacao), Estación Eladíos, Estación Laguna Pocosol, Finca San Gabriel, Parq. Nac. Rincón de la Vieja, Río San Lorencito, San Ramon; CARTAGO (23): Chirripó Indian Reserve (5 mi SE Moravia), Grano de Oro, Refugio Nacional Tapanti, Tuis; GUANACASTE (77): Estación Cacao, Estación Pitilla, Parq. Nac. Braulio Carrillo on Hwy 32, Río San Lorenzo, Tierras Morenas; HEREDIA (23): Estación El Ceibo, La Selva Biological Station, Pueblo Nuevo, Vara Blanca (10 mi N); LIMÓN (1): Guapiles, Limón; PUNTARENAS (17): Estación La Casona, Estación Las Alturas, Estación Sirenia, Las Cruces Biological Station, Rancho Quemado, Reserva Biológica Monteverde, San Luis (Monteverde).

PANAMA (83). BOCAS DEL TORO (3): 2 mi N of Divide on Hwy to Chiriqui Grande, Continental Divide trail above Lago Fortuna; CANAL ZONE (15): Achiote Road, Barro Colorado Island, Ft. Sherman, Pipeline Road, Río Changena, Skunk Hollow; CHIRIQUI (49): Continental Divide trail above Lago Fortuna, Finca La Suiza, Fortuna Dam, Hartmann's Finca, IHRE Vivero (11 km N Los Planes), Windy Pass (7 km N Los Planes); PANAMA (15): Cerro Campana, Cerro Jefé, El Llano-Carti Rd. (km 8, km 12), El Llano (15 km N); SAN BLAS (1): Nusagandi.

TEMPORAL DISTRIBUTION. March (2), April (16), May (152), June (53), July (25), August (8), September (10), October (5), November (2).

DIAGNOSIS. *Cyclocephala ligyrina* resembles *C. kaszabi* but may be separated from it as follows: in the males, *C. ligyrina* has a tridentate foretibia (basal tooth is often small) (bidentate in *C. kaszabi*), the large median claw of the foretarsus has a ventral tooth (absent in *C. kaszabi*), the punctate rows of the elytra are not furrows (furrows present in *C. kaszabi*), and the parameres are different (especially in lateral view, Figs. 271-272, 252-253). In the females, the foretibia lacks a distinct notch behind the basal tooth (present in *C. kaszabi*), and the epipleuron is

gradually tapered to the level of the third sternite (abruptly expanded into a lobe extending from middle of the metasternum to the level of the third sternite in *C. kaszabi*).

BIOLOGY. Adults are attracted to lights. A few specimens have been taken from the inflorescences of *Dieffenbachia longispatha* Engler and Krause (Young 1986), *Philodendron cretusom* Croat and Grayum, and *P. rothschuhianum* (Engler and Engler)

(Araceae) at La Selva Biological Station in Costa Rica (H. Young specimens at INBio). Specimens have been collected at elevations ranging from 90-1,400 meters in tropical wet forests, premontane rain forests, and lower montane rain forests.

***Cyclocephala lunulata*
Burmeister, 1847**

(Figs. 275-279)

Cyclocephala lunulata Burmeister 1847: 62.
Cyclocephala nubeculosa Burmeister 1847: 63
(synonym).
Graphalia oblita Casey 1915: 159 (synonym).

DESCRIPTION. Length 10.3-16.5 mm; width 5.6-9.0 mm. Color testaceous with black frons and highly variable, piceous or fuscous marks (distinct or "fuzzy") on pronotum and elytra. Apices of femora and tibiae and occasionally some abdominal sternites piceous or fuscous. Pronotal markings vary from absent (uncommon) to with faint or strong "lunulata-type" pattern (most common) to mostly darkened (uncommon). Elytral markings vary from absent (uncommon) to with faint or strong "lunulata-type" pattern (most common) to pattern expanded to darken much of

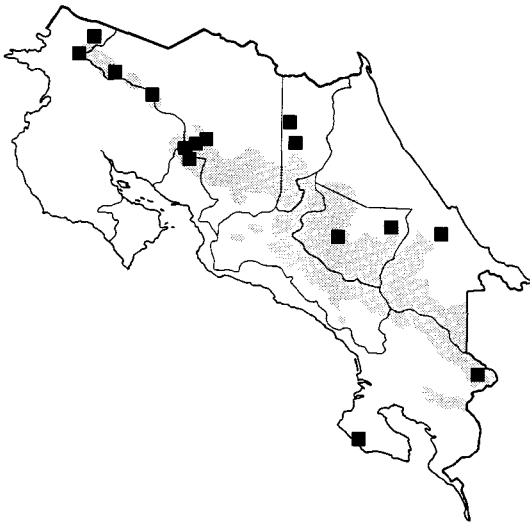


Fig. 273. Distribution of *Cyclocephala ligyrina* in Costa Rica.

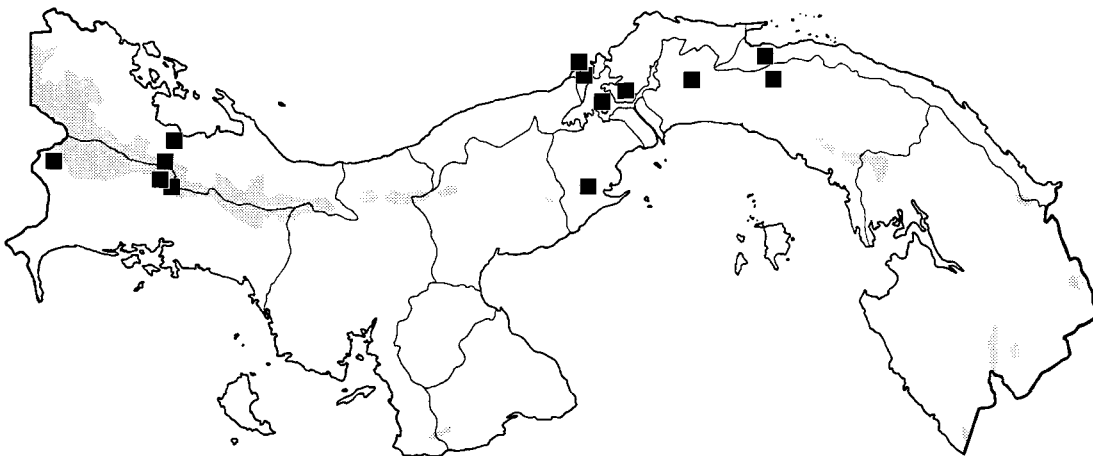


Fig. 274. Distribution of *Cyclocephala ligyrina* in Panama.

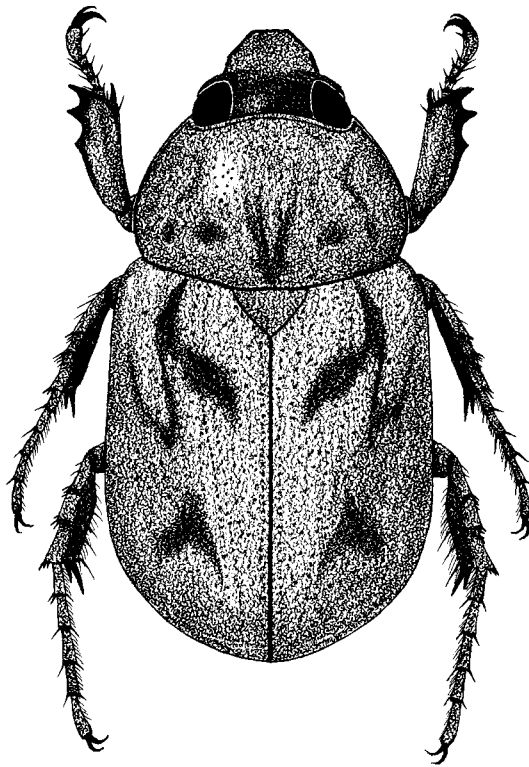
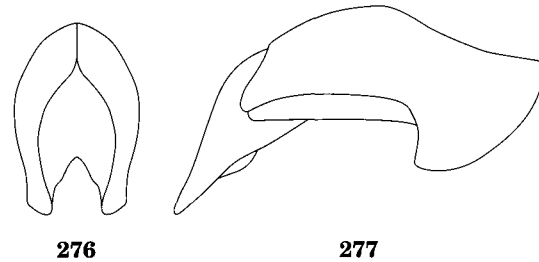


Fig. 275. *Cyclocephala lunulata*.

elytra (uncommon). *Head*: Frons mostly moderately to densely punctate, punctures small. Clypeus and apex of frons mostly "roughened," occasionally distinctly rugopunctate; apex of clypeus subtruncate to truncate, slightly reflexed. Interocular width equals 3.0 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. *Pronotum*: Surface with punctures moderate in density and size, punctures becoming slightly denser and larger on sides. Base lacking marginal bead. *Elytra*: Surface with punctures moderate in density and moderately large; punctate rows distinct. Epipleuron (ventral view) of females becoming slightly thickened and bent outward at level of metatrochanter/abdominal sternite (middle of elytron); lateral edge of elytron just above this often produced into a low swelling. *Pygidium*: Surface in males finely scabrous (small punctures sometimes evident), setigerous; setae small, sparse, tawny; surface in females similar except region of center-apex smoother with



Figs. 276-277. *Cyclocephala lunulata* parameres.

small, sparse punctures. In lateral view, surface of males weakly to regularly convex; surface in females nearly flat except convex apical third. *Legs*: Foretibia tridentate, basal tooth slightly separated from others. Foretarsus in males enlarged: tarsomere 4 with expanded, subtriangular lobe on venter; 5th large, slightly curved, venter slightly concave; median claw large, curved, with prominent lobe at base, apex cleft. Foretarsus in females simple. Posterior tarsus in males distinctly longer than posterior tibia, subequal in length in females. *Venter*: Prosternal process moderately long, columnar, apex expanded and obliquely flattened into a transverse oval or nearly round with raised, transverse button on anterior 1/3-1/2. *Parameres*: Figs. 276-277.

DISTRIBUTION. *Cyclocephala lunulata* is broadly distributed from Mexico to Argentina and Paraguay. It is found throughout Costa Rica and Panama.

LOCALITY RECORDS (Figs. 278-279). 3,380 specimens examined.

COSTA RICA (3,004). ALAJUELA (288): Bijuagua, Boruca, Caño Negro, Cerro Campana, Dos Rios, Estación San Ramon, Finca Magil, Parq. Nac. Rincon de la Vieja, San Isidro, San Ramon, Volcán Tenorio; CARTAGO (90): Grano de Oro, Moravia, Refugio Nacional Tapanti, Tuis, Turrialba; GUANACASTE (613): Cañas, Estación Caicao, Estación La Guitarra, Estación Las Pailas, Estación Los Almendros, Estación Maritza, Estación Mengo, Estación Murcielago, Estación Palo Verde, Estación Pitilla,

Estación Santa Rosa, Finca Jenny, Nacaome, Parq. Nac. Barra Honda, Parq. Nac. Guanacaste, Parq. Nac. Santa Rosa, Tierras Morenas; HEREDIA (310): Estación El Ceibo, Estación Magsasay, Finca Naranjo Valenciana, La Selva Biological Station, La Virgen



Fig. 278. Distribution of *Cyclocephala lunulata* in Costa Rica.

de Sarapiquí, Los Arbolitos, San Rafael; LIMÓN (394): Amubri, Cerro Tortuguero, Estación Hitoy Cerere, Estación Miramar, Limón, Manzanillo, Río Sardinas; PUNTARENAS (1,318): Buenos Aires, Estación Las Esquinas, Estación La Casona, Estación Las Alturas, Estación Las Cruces, Estación Las Mellizas, Estación Quebrada Bonita, Estación Sirena, Finca Venecia, Parq. Nac. Corcovado, Parq. Nac. Manuel Antonio, Rancho Quemado, Reserva Biológica Carara, Reserva Biológica Monteverde, Rincon (Osa), San Luis, San Vito, Vuelta Campana, Wilson Botanical Garden; SAN JOSÉ (7): Estación Bijagual, Estación Zurqui, San Pedro.

PANAMA (376). BOCAS DEL TORO (56): Chiriqui Grande (12 km W), Miramar, Punta Peña (14 km S); CANAL ZONE (133): Albrook Forest, Barro Colorado Island, Black Tank Road, Coco Solo Hospital, Ft. Clayton, Ft. Davis, Ft. Gulick, Gatun Lake Lookout, Madden Dam, Madden Forest, Paraiso, Skunk Hollow, Tabernilla; CHIRIQUI (11): David, Finca La Suiza (Fortuna), Hartmann's Finca (Santa Clara); COLÓN (25): Cerro Viejo Mine Road (9 km SW Nombre de Dios), Santa Rita Ridge; DARIEN (4): Cana; PANAMA (139): Capira, Cerro Azul, Cerro Campana, Cero

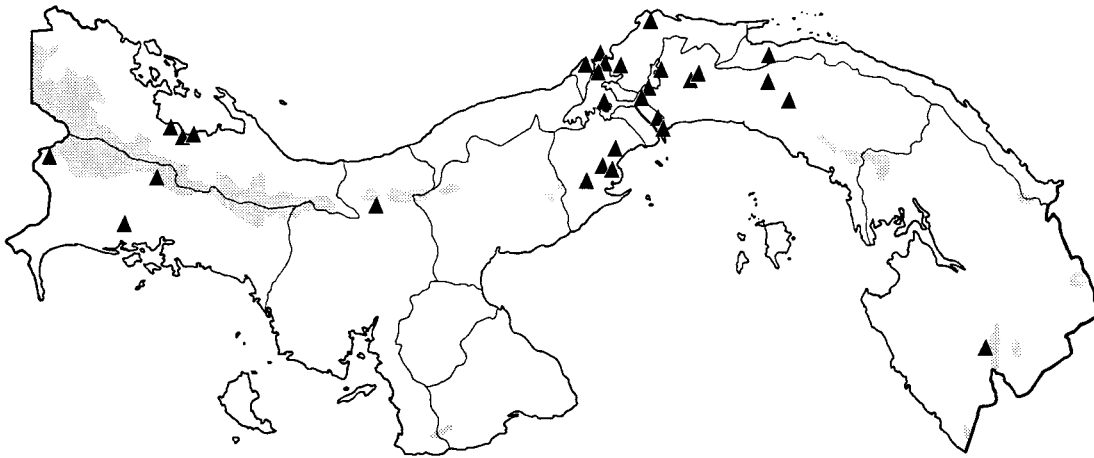


Fig. 279. Distribution of *Cyclocephala lunulata* in Panama.

Jefé, El Llano-Carti Road (km 8, km 10, km 14), Isla Majé, La Chorrera, Sajalices; SAN BLAS (7): Nusagandi; VERAGUAS (1): Alto de Piedra (above Santa Fé).

TEMPORAL DISTRIBUTION. January (109), February (48), March (368), April (264), May (565), June (271), July (500), August (303), September (339), October (143), November (169), December (191).

DIAGNOSIS. *Cyclocephala lunulata* is distinguished by its "lunulata-type" pattern in combination with a subtruncate clypeus, absence of a basal bead on the pronotum, and setose pygidium. The parameres are also diagnostic. Females are easily separated from *C. fulgurata* and *C. weidneri* because the swelling of the epipleuron/elytral margin is about in the middle (dorsal view) whereas it is well behind the middle in the other two species.

Cyclocephala lunulata also resembles *C. labidion*. Males are most easily separated from males of *C. labidion* by their larger size, having the basal tooth of the foretibia slightly removed from the others (subequally spaced in *C. labidion*), with a more convex pygidium, and with different parameres. In the females, the metasternum is coarsely roughened and only weakly shining in *C. lunulata* whereas it is microscopically imbricate and strongly shining in *C. labidion*; also, the epipleuron is gradually tapered either side of a slight thickening at the level of abdominal sternites 1-2 and abruptly narrowed at the level of abdominal sternite 1 in *C. labidion*.

BIOLOGY. Adults are commonly collected at lights. Deloya (1988) reported larvae taken from the detritus refuse piles of the leafcutter ant, *Atta mexicana* (Smith), but it is not known if they were actually living there or feeding on nearby plant roots. This is a very abundant species that is nearly ubiquitous in habitats from sea level to 1,500 meters; most records are from less than 1,000 meters. *Cyclocephala lunulata* occurs in tropical dry forests, tropical moist forests, tropical wet forests, premontane moist forests, premontane wet forests, and premontane rain forests.

Cyclocephala macrophylla
Erichson, 1847
(Figs. 280-284)

Cyclocephala macrophylla Erichson 1847: 97.

DESCRIPTION. Length 10.5-14.1 mm; width 5.4-7.1 mm. Color dark cherry-red except for piceous to black frons and testaceous elytra. *Head:* Frons on posterior half with

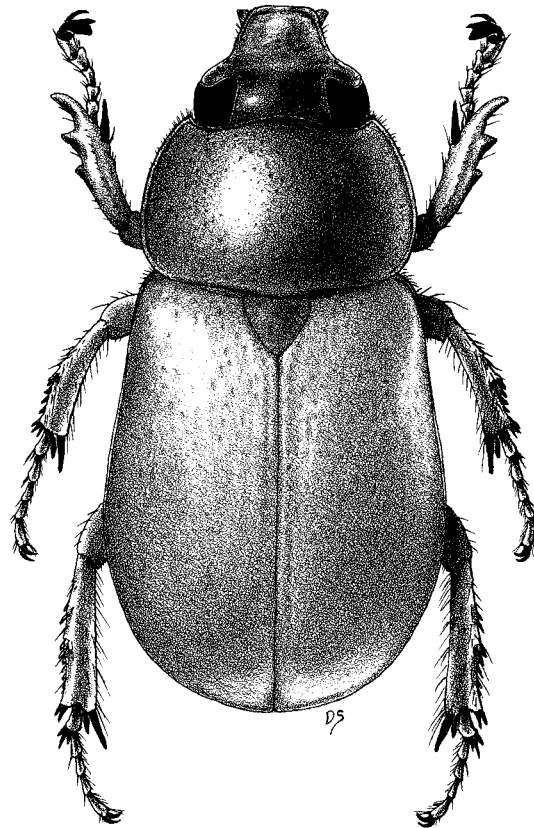


Fig. 280. *Cyclocephala macrophylla*.

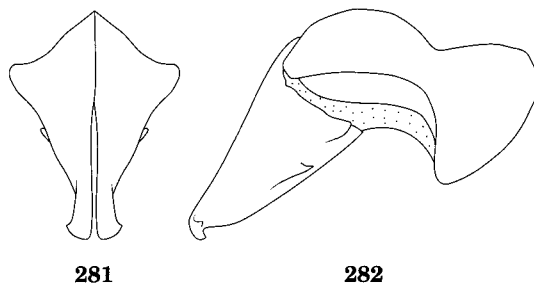


Fig. 281-282. *Cyclocephala macrophylla* parameres.

small, sparse punctures, anterior half roughened. Clypeus with surface weakly, transversely rugulose; apex broadly subtruncate, weakly reflexed. Interocular width equals 1.7 transverse eye diameters. Antenna with 10 segments, club in males about 1.5 times longer than segments 2-7, club in females subequal in length to segments 1-7. *Pronotum*: Surface with punctures moderate in size, moderate in density. Base lacking marginal bead. *Elytra*: Surface with punctures moderately large, moderate in density, distinct rows visible. Epipleuron (ventral view) of female only slightly thickened at level of abdominal sternite 1. *Pygidium*: Surface coarsely rugopunctate, punctures nearly obscured in males, slightly more visible in females. In lateral view, surface in males strongly convex, surface in females weakly convex. *Legs*: Foretibia tridentate, teeth subequally spaced. Foretarsus in males enlarged: tarsomere 4 subtriangularly lobed beneath; tarsomere 5 enlarged, slightly bent; median claw enlarged, curved, apex broadly cleft (Fig. 280). Posterior tarsus shorter than posterior tibia. *Venter*: Prosternal process moderately long, columnar, apex obliquely flattened into a broad oval with raised, transverse "button" on anterior half. *Parameres*: Figs. 281-282.

DISTRIBUTION. *Cyclocephala macrophylla* is known from Costa Rica south to Bolivia (Endrödi 1966; Ratcliffe 1992b). It is broadly distributed in Costa Rica and western Panama. The lack of any records for central or eastern Panama is noteworthy, but I am unable to offer a possible cause.

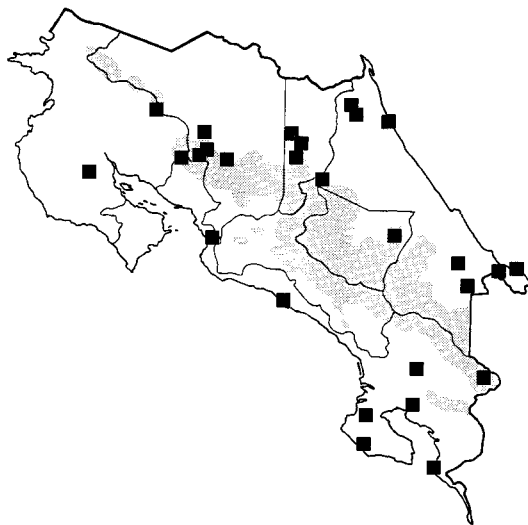


Fig. 283. Distribution of *Cyclocephala macrophylla* in Costa Rica.

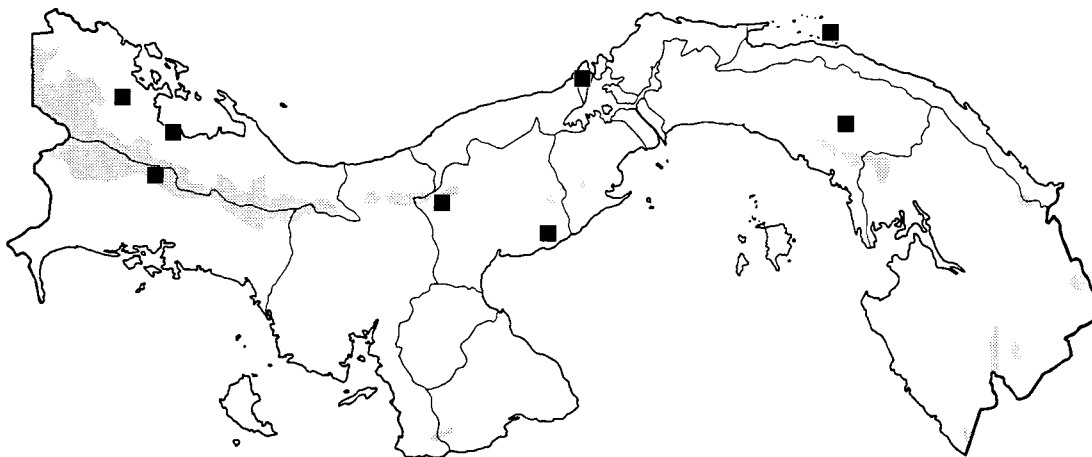


Fig. 284. Distribution of *Cyclocephala macrophylla* in Panama.

LOCALITY RECORDS (Figs. 283-284). 333 specimens examined.

COSTA RICA (273). ALAJUELA (13): Estación Eladiós, Estación Laguna Pocosal, Laguna de Arenal, Río San Lorencito, San Ramon; CARTAGO (10): Grano de Oro (Turrialba); GUANACASTE (2): Nacaome (3 km N), Tierras Morenas; HEREDIA (14): Estación El Ceibo, Estación Magsasay, Finca Naranjo Valenciana, La Selva Biological Station; LIMÓN (139): Amubri, Bribri (9 km W), Estación Hitoy Cerere, Manzanillo, Pococí, Valle La Estrella; PUNTARENAS (92): Estación Las Esquinas, Estación Las Alturas, Estación La Casona, Estación Quebrada Bonita, Estación Sirena, Parq. Nac. Manuel Antonio, Punta Banco, Rancho Quemado, Vuelta Campana; SAN JOSÉ (3): San Isidro.

PANAMA (60). BOCAS DEL TORO (52): Corriente Grande, Miramar; CANAL ZONE (1): Escobal Road; CHIRIQUI (2): Fortuna; COCLÉ (2): El Cope (5 km N), Río Hato (3 mi. E); PANAMA (1): Ipetí (3 km E); SAN BLAS (2): Pidertupo Island.

TEMPORAL DISTRIBUTION. January (13), February (14), March (11), April (28), May (11), June (35), July (68), August (31), September (10), October (44), November (39), December (25).

DIAGNOSIS. *Cyclocephala macrophylla* is easily recognized by its dark, cherry-red pronotum and testaceous elytra in combination with an antennal club that is longer than the remainder of the antenna in the males and subequal in length to segments 2-7 in the females, large claw of the protarsus in males with a widely cleft apex, and the absence of a marginal bead on the base of the pronotum. The parameres of the male are also diagnostic. It resembles closely *C. melanocephala*, but in that species the length of the antennal club is subequal or slightly shorter than segments 2-7.

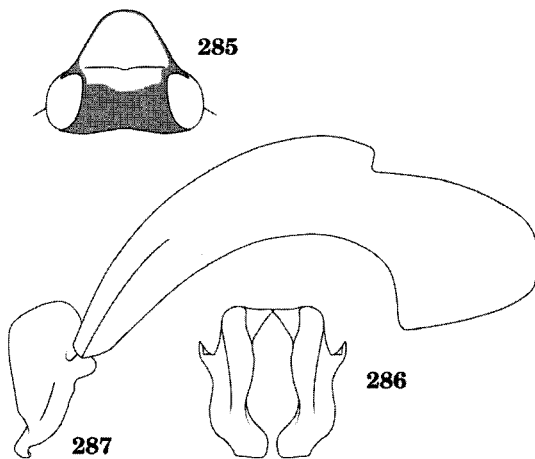
BIOLOGY. Adults are attracted to lights at night. This species lives in tropical moist forests, tropical wet forests, premontane moist

forests, premontane wet forests, and premontane rain forests. It has been collected at elevations ranging from near sea level to 1,500 meters with only a few records above 1,000 meters.

Cyclocephala maculiventris
Höhne, 1923
(Figs. 285-288)

Cyclocephala maculiventris Höhne 1923b: 345.

DESCRIPTION. Length 11.0-11.8 mm; width 5.8-6.1 mm. Color testaceous except for black on frons (posterior half; Fig. 285), anterior margin of elytra either side of scutellum, sutural line, sides of pygidium, meso- and metepisternum, abdominal sternites (variably reduced or on apical margin only of each sternite), apices of tibiae (half of tibiae in many females), and tarsi. *Head:* Frons with punctures moderate in size and density. Clypeus weakly, transversely rugose; apex narrowly parabolic, beaded, barely reflexed. Interocular width equals 2.0-2.3 transverse eye diameters. Antenna with 10 segments, club slightly longer than segments 2-7. *Pronotum:* Surface with punctures moderate in density and size, punctures becoming slightly denser in posterior angles. Base with marginal bead. *Elytra:* Surface with rows of moderately large, shallow punctures. Epipleuron (ventral view) of females either abruptly constricted at penultimate abdominal sternite or gradually tapering; in dorsal view, lateral margin weakly expanded at middle. *Pygidium:* Surface shining, with sparse punctures, punctures small in males, a little larger in females. In lateral view, males with surface strongly convex, especially at apex, surface in females weakly convex. *Legs:* Foretibia in males bidentate with weak, basal lobe; females with tridentate foretibia. Foretarsus in males enlarged: tarsomeres 2-4 each slightly larger than preceding, 4 with distinct ventral lobe; 5th large, curved, lacking ventral lobe, slightly concave beneath; median claw large, strongly curved, apex finely cleft. Foretarsus in females simple. Posterior tarsus almost twice as long as posterior tibia. *Venter:*



Figs. 285-287. *Cyclocephala maculiventris*: (285) pattern on head; (286-287) parameres.

Prosternal process short, setose, apex obliquely flattened into nearly round disc with anterior 1/3-1/2 elevated into round "button." *Parameres*: Figs. 286-287.

DISTRIBUTION. *Cyclocephala maculiventris* is known only from Costa Rica (Endrödi 1966, 1985a) In Costa Rica it is generally distributed. It has not been taken in western Panama, but, considering the close proximity of some Costa Rican records, it may occur in western Chiriqui or Bocas del Toro.

LOCALITY RECORDS (Fig. 288). 39 specimens examined.

COSTA RICA (39). ALAJUELA (2): Estación San Ramon; CARTAGO (2): Monumento Nacional Guayabo, Turrialba; GUANACASTE (22): Estación Cacao, Estación Experimental Horizontes, Estación Las Pailas, Estación Los Almendros, Estación Maritza, Estación Murcielago, Estación Palo Verde, Estación Pitilla, Finca Jenny (30 km N Liberia), Nacaome, Parq. Nac. Barra Honda, Río San Lorenzo, Santa Cecilia (6 km S); HEREDIA (1): Estación Barva; LIMÓN (2): Estación Cuatro Esquinas, Estación Hitoy

Cerere; PUNTARENAS (9): Buenos Aires, Estación Las Alturas, Estación Quebrada Bonita, Parq. Nac. Manuel Antonio, Rancho Quemado, Río Rincón, San Luis; SAN JOSÉ (1): La Trinidad de Dota.

TEMPORAL DISTRIBUTION. January (4), February (1), March (3), April (5), May (7), June (6), July (5), August (1), October (3), November (1), December (2).

DIAGNOSIS. *Cyclocephala maculiventris* is distinctive because of the form of its clypeus and the male parameres as well as by its color pattern and shiny body. The basal lobe on the anterior tibia of the male is poorly developed and so the tibia could be considered either bidentate or weakly tridentate.

BIOLOGY. Adults are attracted to lights. They have been collected from near sea level to 2,500 meters although most specimens are from below 1,500 meters. They live in tropical dry forests, tropical moist forests, tropical wet forests, premontane rain forests, and lower montane rain forests.

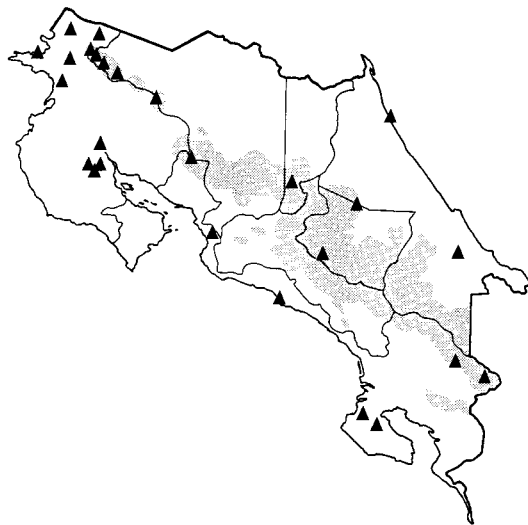


Fig. 288. Distribution of *Cyclocephala maculiventris* in Costa Rica.

***Cyclocephala mafaffa* Burmeister,
1847**

(Figs. 289-294)

Cyclocephala mafaffa Burmeister 1847: 69.
Cyclocephala grandis Burmeister 1847: 69
(synonym).

Stigmalia cuernavacana Casey 1915: 117
(synonym).

Stigmalia fallaciosa Casey 1915: 117 (syn-
onym).

Stigmalia deficiens Casey 1915: 117 (syn-
onym).

Stigmalia mafaffa histrionica Casey 1915:
119 (synonym, described as subspecies).

DESCRIPTION. Length 21.0-28.0 mm; width 11.7-13.9 mm. Color and pattern in this species varies widely (Fig. 290). In Costa Rica and Panama, the color is yellowish brown to dark reddish brown with black head, pronotal margins, 2 black longitudinal bands on pronotum, sutural line of elytra and lateral expansion of that line into a variably-sized spot behind scutellum and again at middle of elytra (spots only rarely reduced or absent), humeral spot, small spot in center of each elytron, base and epipleura of elytra, legs and venter; pygidium usually piceous. *Head:* Surface of frons with punctures small to moderate in size, moderate in density. Clypeus usually punctate in basal half and rugopunctate in apical half (rarely entirely punctate); punctures moderate to moderately large; apex broad, weakly emarginate, narrowly reflexed. Interocular width equals 3.3-3.6 transverse eye diameters. Antenna with 10 segments, club a little shorter than segments 2-7. *Pronotum:* Surface on disc impunctate, sides with sparse and minute punctures. Base without marginal bead. *Elytra:* Surface with large, shallow punctures, double rows indistinct. Epipleuron (ventral view) in females with short, abrupt expansion at level of abdominal sternites 1-2; in lateral view, expansion with distinct angle (occasionally tooth) on ventral edge. *Pygidium:* Surface in males with punctures moderately dense, moderate in size, setigerous; setae minute, tawny, usually becoming obsolete in middle. Surface in females with punctures sparse to

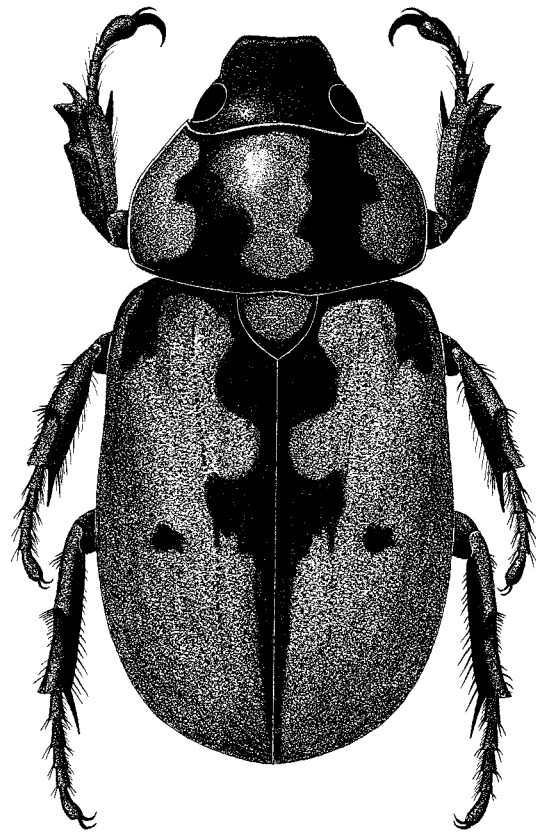


Fig. 289. *Cyclocephala mafaffa*.

moderate in density, minute to small in size, glabrous. In lateral view, surface of males weakly convex, nearly flat in females. *Legs:* Foretibia tridentate, basal tooth slightly removed from others. Foretarsus in males enlarged; tarsomere 4 with enlarged, ventral lobe; tarsomere 5 enlarged, weakly curved, without ventral lobe or tooth, instead venter slightly concave; median claw large, strongly curved, apex finely split. Foretarsus in females simple. Posterior tarsus subequal in length to posterior tibia. *Venter:* Prosternal process long, columnar, apex obliquely flattened into broadly transverse oval with transverse, elevated "button" on anterior 1/2-2/3. *Parameres:* Figs. 291-292.

DISTRIBUTION. *Cyclocephala mafaffa* is found from Mexico to Amazonian Brazil and Ecuador (Endrödi 1966, 1985a). Endrödi also

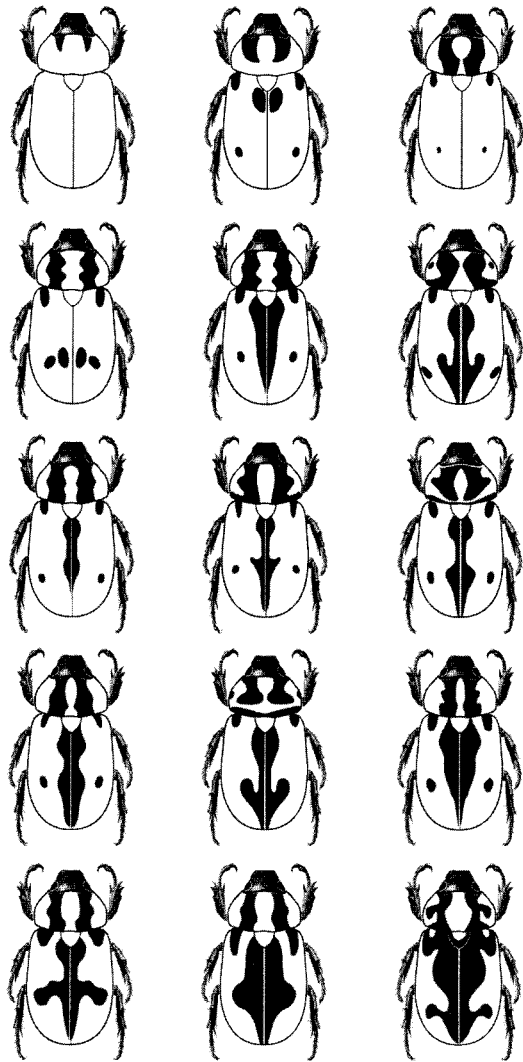
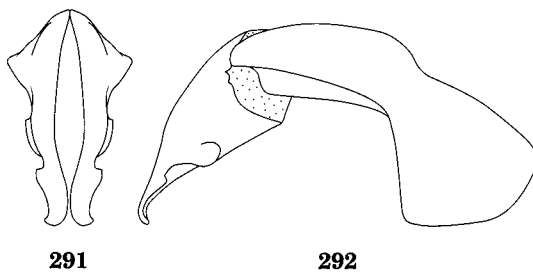


Fig. 290. *Cyclocephala maffa* showing pronotal and elytral variation. From García-Luna *et al.* (2000) (used by permission).



Figs. 291-292. *Cyclocephala maffa* parameres.

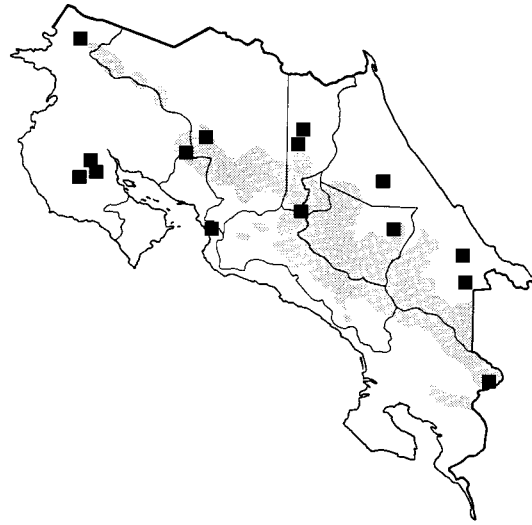


Fig. 293. Distribution of *Cyclocephala maffa* in Costa Rica.

listed Arkansas and Arizona in the United States, but *C. maffa* does not occur there. This species is generally distributed throughout Costa Rica and Panama where there is suitable forest type.

LOCALITY RECORDS (Figs. 293-294). 63 specimens examined.

COSTA RICA (32). ALAJUELA (1): Estación Laguna Pocosol; CARTAGO (2): Grano de Oro, Turrialba; GUANACASTE (9): Estación Maritza, Nacaome (3 km NW), Nicoya, Parq. Nac. Santa Rosa; HEREDIA (4): Estación El Ceibo, Estación Magsasay; LIMÓN (6): Amubri, Estación Hitoy Cerere, Hamburg Farm; PUNTARENAS (11): Estación Las Mellizas, Estación Quebrada Bonita, San Luis; SAN JOSÉ (1): San José.

PANAMA (31). BOCAS DEL TORO (2): Corriente Grande; CANAL ZONE (1): Barro Colorado Island; CHIRIQUI (12): Finca La Suiza, Reserva La Fortuna Los Planes (7 km N); COCLÉ (1): El Valle; COLÓN (1): Río Guanache Bridge (1 km E); DARIEN (1): Río Tacarcuna; PANAMA (13): Altos de Majé, Cerro Azul, Cerro Campana, Cerro Jefé.

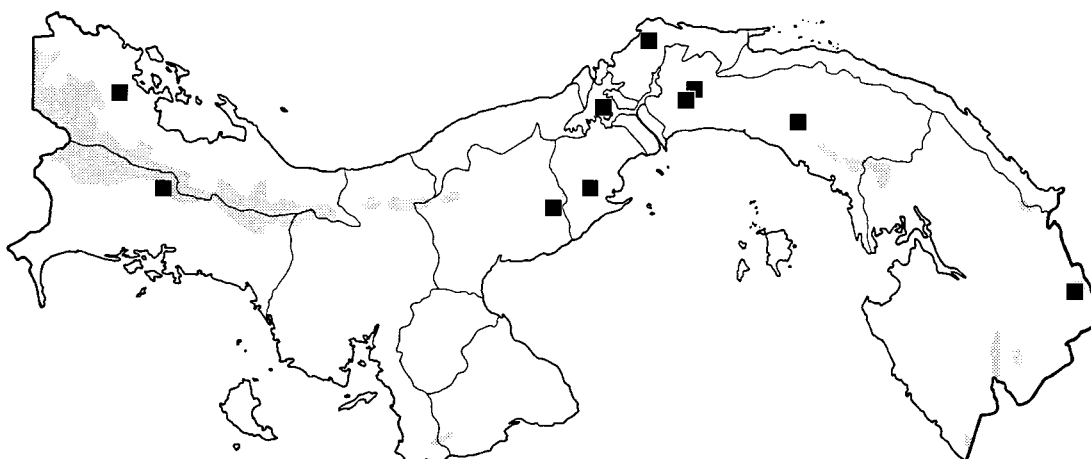


Fig. 294. Distribution of *Cyclocephala mafaffa* in Panama.

TEMPORAL DISTRIBUTION. January (1), February (1), May (27), June (11), July (16), August (3), September (2), October (3), November (3), December (2).

DIAGNOSIS. *Cyclocephala mafaffa* is a distinctive beetle because of the combination of body size and reddish brown coloration with a distinctive black pattern (never absent in specimens from Costa Rica and Panama). The species that it most closely resembles in the study area is *C. nike*. However, *C. mafaffa* lacks a basal bead on the pronotum (present in *C. nike*); has longitudinal, black bands on the pronotum and spots on the elytra (absent in *C. nike*); and has some differences in clypeal shape and the male parameres. The basal bead on the pronotum is variably present at the posterior angles, either wrapping completely around the angle or not, but it is never present completely across the base.

Cyclocephala mafaffa is a lowland species that is usually found at elevations below 1,000 meters. *Cyclocephala nike*, on the other hand, is a highland species that has been found only above 1,300 meters in elevation.

BIOLOGY. Adults are attracted to lights. Morón (1997b) found adults in the inflorescences of *Xanthosoma hoffmanni* Schott, *X. mexicanum* Lieb., *X. robustum* Schott, and *X. violaceum* Schott (Araceae) in Chiapas,

Mexico. They have been found in tropical dry/tropical moist forest transition, tropical moist forests, tropical wet forests, premontane moist forests, and premontane wet forests at elevations from 70-1,200 meters (only 4 specimens above 1,100 meters while the remaining 53 are from below 1,000 meters).

***Cyclocephala maryliza* Ratcliffe,
new species
(Figs. 295-300)**

TYPE MATERIAL. Holotype labeled "Est. Sirena, P.N. Corcovado, 0-100 M, Prov. Punt., COSTA RICA, C. Saborio, Oct. 1990, L-S-270500, 508300." Allotype with same data except 1989. Seventy-nine paratypes with the following data: 9 males and 4 females with same data as holotype; 4 males with same data as allotype; 3 males and 1 female with same data but November 1989 and G. Fonseca collector; 1 male with same data but November 1990; 1 male with same data but November 1991; 1 male with same data but December 1989; 1 male with same data but April 1993; 1 male and 2 females with same data but May 1994 and C. Fonseca collector; "Rancho Quemado, 200 m, Peninsula de Osa, Prov. Puntarenas, Costa Rica, 1 a 31 AGO 1992, A. Marin, L-S 292500, 511000" (2 males, 3 females); with same data as previous but

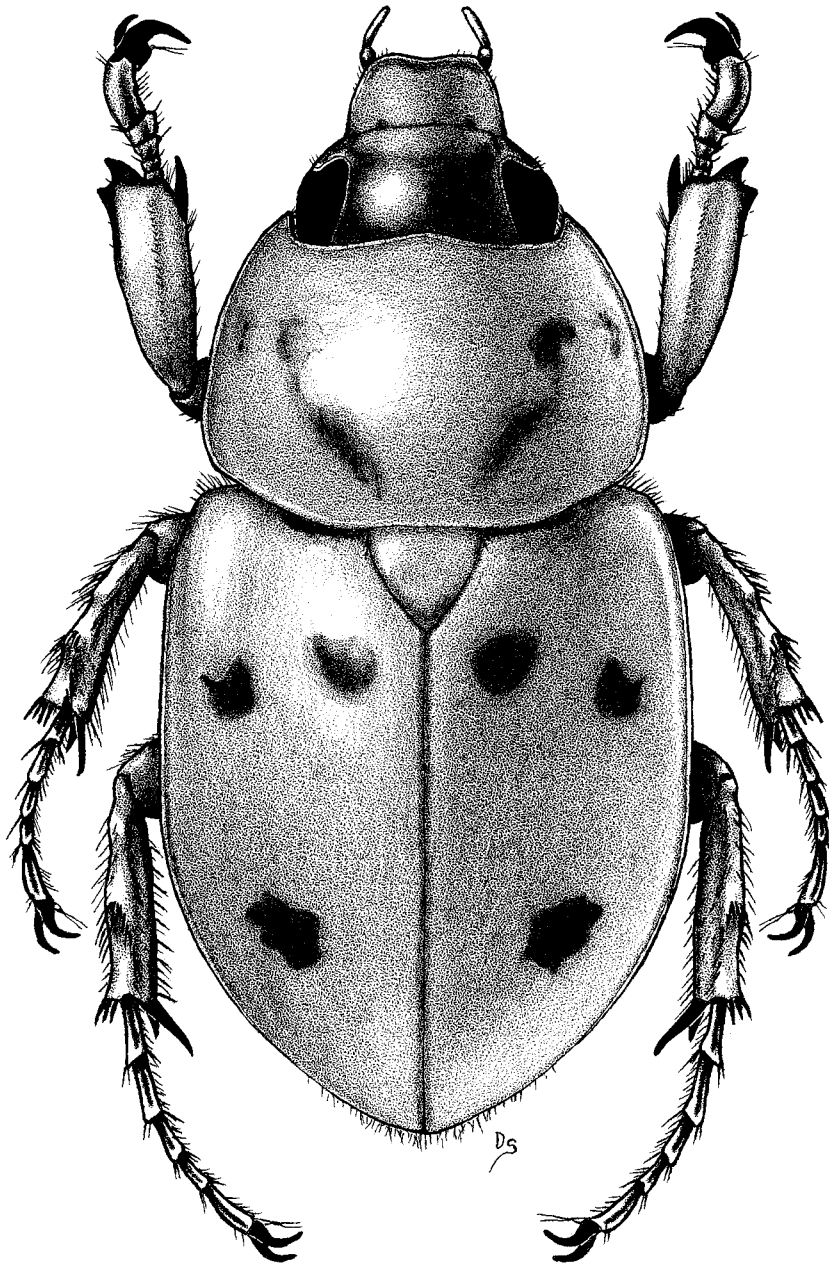
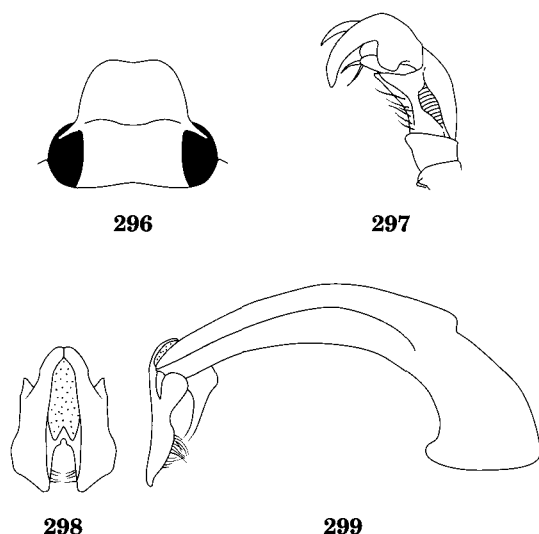


Fig. 295. *Cyclocephala marylizaе*.

August 1992 and M. Segura collector (2 males); with same data as previous and 12-30 September 1993 and A. Marin collector (1 male); with same data as previous and October 1991 and F. Quesada collector (1 male); with same data as previous and November 1990 (1 female) and November 1991 (1 male)

and F. Quesada collector; with same data as previous and October-November 1990 and collector B. Apu (7 females); "Vuelta Campana, R. Terraba, 100-500 M, Rey Curré, Prov. Puntarenas, Costa Rica, 3 Jul a 2 Ago 1992, S. Rojas, L-S 325700, 544300" (14 females); with same data as previous and 8 June 1993



Figs. 296-299. *Cyclocephala maryliza*: (296) head showing emarginate clypeus; (297) foretarsus (part) and claw of male; (298-299) parameres.

(1 female) and 4-31 July 1993 (1 female); "Est. Quebrada Bonita, 50 M, Res. Biol. Carara, Prov. Punt., Costa Rica, E. Bello and E. Rojas, Jul 1990, L-N-194500, 469850" (5 males, 2 females); with same data as previous but date of November 1989 and R. Zuniga (1 male); with same data but June 1990 and E. Rojas (1 female); with same data as previous but August 1989 and R. Zuniga collector (3 females); "Costa Rica, Puntarenas, Q. Bonita, Carara, 1-X-83, 50 M, Leg. A.M. Chevarria" (1 male); "Queb. Bonita, Carara, Octubre 1993, R. Guzman" (1 male); "Est. Bijagual, 500 M, Res. Biol. Carara, Prov. S. José, Costa Rica, G. Varela, Set. 1990, L-N-192250, 474760" (1 female); "Puntarenas, Costa Rica, Rincón de Osa, 0-200 M, 5 Octubre 1985, Angel Solís" (1 female); "Puntarenas, Costa Rica, Los Magos, Fila Esquinas, 23 Julio 1987, Angel Solís" (1 male, head missing).

Holotype, allotype, and 52 paratypes deposited at INBio in Costa Rica. Additional paratypes deposited in the following collections: Canadian Museum of Nature (Ottawa) (2 specimens), The Natural History Museum (London) (2 specimens), U.S. National Museum (Washington, D.C.) (2 specimens), Mu-

seum National d'Histoire Naturelle (Paris, France) (2 specimens), University of Nebraska State Museum (Lincoln, NE) (4 specimens), Universidad Central de Venezuela (Maracay) (2 specimens), Miguel A. Morón (Xalapa, Mexico) (2 specimens), Mary Liz Jameson (Lincoln, NE) (2 specimens), Andrew Smith (currently Lincoln, NE) (2 specimens), Brett C. Ratcliffe (Lincoln, NE) (6 specimens).

HOLOTYPE. Male. Length 16.8 mm; width 8.8 mm. Color testaceous except for black on following areas: frons between eyes; a narrow, oblique line on pronotal disc either side of middle; base of elytra either side of scutellum; oval spot on elytra adjacent to suture near apex of scutellum; irregular spot on elytra laterad of previous spot; irregular spot on elytra on disc in apical third; elytral suture; extreme apices of femora and tibiae. Abdominal sternites castaneous. *Head*: Frons punctate, punctures small, moderate in density. Clypeus similarly punctate on basal half, apical half transversely rugulose; apex broad, emarginate (Fig. 296). Interocular width equals 2.7 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. *Pronotum*: Surface with small, sparse punctures along narrow center line, punctures becoming slightly larger and denser on disc and sides. Base with marginal bead. *Elytra*: Surface finely shagreened, moderately densely punctate; punctures moderately large, distinct rows present. Apical fourth of elytra with sparse, minute setae. *Pygidium*: Surface finely shagreened, dull, punctate; punctures small, moderate in density, setigerous; setae moderate in density, moderate to long, tawny. In lateral view, surface strongly convex. *Legs*: Foretibia bidentate, both teeth close together. Foretarsus enlarged: tarsomeres 2-4 each larger than preceding, tarsomeres 3-4 subtriangularly expanded on venter; 5th enlarged, curved, with longitudinal carina on inner surface; venter on inner edge with elongate, subtriangular, flattened area, area strongly, transversely striate (Fig. 297); median claw enlarged, strongly curved, base with large lobe, apex entire but with small tubercle indicating where small ramus would have originated. Posterior

tarsus subequal in length to posterior tibiae. *Venter*: Prosternal process moderately long, columnar, apex flattened into transverse oval with transversely oval, raised "button" on anterior half. Abdominal sternites strongly concave; 5th with transverse row of long, tawny setae near apex; sternite 6 strongly emarginate at apex. *Parameres*: Figs. 298-299. In addition to their unique shape, the surface of the parameres is unusual because it is moderately densely punctate.

ALLOTYPE. Female. Length 16.6 mm; width 8.5 mm. As holotype except in the following respects: Color same as that of holotype except pronotal marks thickened into a subtriangular "splotch" either side of middle, and sides of elytra behind humerus with a short and a long, longitudinal black streak. *Pronotum*: Punctures moderate in size on disc and sides. *Elytra*: Epipleuron (ventral view) simple, not enlarged. *Pygidium*: Surface weakly shining, distinctly depressed either side of middle, sparsely punctate; punctures small, some setigerous; setae sparse, short to moderate in length, tawny. In lateral view, surface concave. *Legs*: Foretibia tridentate, basal tooth slightly removed from others. Foretarsus simple. *Venter*: Abdominal sternites not strongly concave; sternite 6 with apex entire.

VARIATION. Males (35 paratypes). Length 14.3-18.2 mm; width 7.2-9.9 mm. As holotype except in the following respects: *Color*: Black marks on pronotum absent (2 specimens), with small spot either side of middle (12 specimens), similar to holotype (10 specimens), or with subtriangular splotch either side of middle (11 specimens); elytra with spots absent (1 specimen), remainder with spots similar or slightly larger. The male paratypes do not otherwise differ significantly from the holotype except that the pygidium in some specimens is weakly shining instead of dull.

Females (44 paratypes). Length 15.5-18.8 mm; width 7.9-9.6 mm. As allotype except in the following respects: *Color*: Black marks on pronotum absent (1 specimen), with small spot either side of middle (17 specimens), similar to allotype (13 specimens), similar to

holotype (13 specimens); elytra with spots absent (3 specimens), elytra with posterior spot absent (4 specimens), remainder with spots similar to those of allotype. The female paratypes do not significantly differ from the allotype.

ETYMOLOGY. This species is named in honor of my colleague, Dr. Mary Liz Jameson, in recognition of her invaluable assistance with this project, for her important contributions to the study of Neotropical scarab beetles, and for her friendship over the years.

DISTRIBUTION. *Cyclocephala maryliza* occurs only in Puntarenas province in Costa Rica, specifically the region of the Osa Peninsula and Reserva Biológica Carara.

LOCALITY RECORDS (Fig. 300). 81 specimens examined.

COSTA RICA (81). **PUNTARENAS** (81): Fila Esquinas (Los Magos), Rancho Quemado, Reserva Biológica Carara, Rincon de Osa, Sirena, Vuelta Campana.

TEMPORAL DISTRIBUTION. April (1), May (3), June (2), July (23), August (10), September (2), October (30), November (9), December (1).

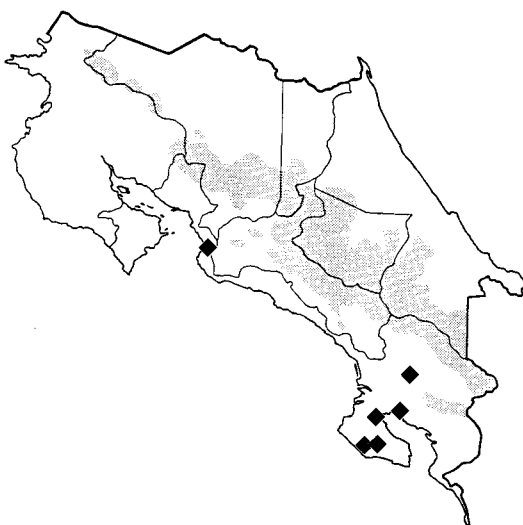


Fig. 300. Distribution of *Cyclocephala maryliza* in Costa Rica.

DIAGNOSIS. *Cyclocephala maryliza* is easily distinguished in the males by the deeply emarginate clypeal apex (shared only with *C. discicollis* in the study area), presence of a basal bead on the pronotum, strongly convex pygidium, strongly concave abdominal sternites, and the unique form of the parameres.

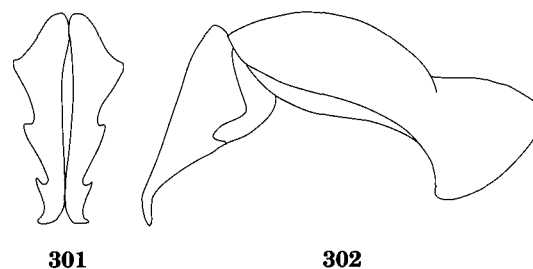
Females may be separated by the same characters of clypeal apex and margined pronotum as well as by a simple epipleuron and a pygidium that is depressed either side of the middle and appears concave in lateral view.

BIOLOGY. Adults are attracted to lights at night. They have been collected from tropical moist forests and tropical wet forests at elevations ranging from near sea level to 500 meters.

***Cyclocephala melanae* Bates, 1888**
(Figs. 301-304)

Cyclocephala melanae Bates 1888: 310.

DESCRIPTION. Length 19.2-21.0 mm; width 9.7-11.3 mm. Color entirely black. **Head:** Frons in males moderately densely punctate in a band between eyes (vertex and apex before frontoclypeal suture impunctate); punctures moderately large, setigerous (when not abraded away), setae long, tawny. Frons in females punctate all over; punctures moderate in density and size, with long setae (when not worn off). Clypeus with surface transversely rugulose; apex broadly truncate and weakly emarginate. Interocular width equals 4.0 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. **Pronotum:** Surface in males shining with micropunctures on disc, sides and apical margins with sparse, small to moderate, setigerous punctures; setae long, sparse, tawny (often abraded away). Females with sparse, small punctures in central third; punctures on lateral thirds moderate in density and size; setae similar to those of male but often abraded off. Base with marginal bead. **Elytra:** Surface with distinct rows of shallow, large punctures, rows usually in fur-



Figs. 301-302. *Cyclocephala melanae* parameres.

rows (rarely furrows absent); punctures usually with long, tawny setae, especially on sides, apices, and either side of suture; setae often abraded away. Epipleuron (ventral view) of females enlarged from middle of lateral edge of metacoxa to apex of third sternite; in lateral view, epipleuron with small tooth at middle of third sternite. **Pygidium:** Surface with punctures moderate in density in basal half, nearly absent from apical half; punctures large, shallow, setigerous; setae long, tawny. In lateral view, surface weakly convex. **Legs:** Foretibia bidentate in male, tridentate in female (basal tooth slightly removed from others). Foretarsus in males enlarged: tarsomeres 4-5 with large ventral lobes; fifth large, curved, lacking lobe or tooth beneath; median claw large, strongly curved, apex finely cleft. Foretarsus in females simple. Posterior tarsus slightly longer than posterior tibia. **Venter:** Prosternal process moderate in length, stout, apex obliquely flattened into transverse oval with anterior 2/3 to 4/5 raised as a convex "button." **Parameres:** Figs. 301-302.

DISTRIBUTION. *Cyclocephala melanae* is known from the highlands of Costa Rica and western Panama. This species is rarely encountered.

LOCALITY RECORDS (Figs. 303-304). 16 specimens examined.

COSTA RICA (14). CARTAGO (5): Refugio Nacional Tapanti, Turrialba; HEREDIA (7): Transect at Parq. Nac. Braulio Carrillo, Vara

Blanca; PUNTARENAS (1): Estación La Casona (Monteverde); SAN JOSÉ (1): San José (8 km W).

PANAMA (2). CHIRIQUI (2): Guadeloupe Arriba, no data.

TEMPORAL DISTRIBUTION. April (1), May (3), July (8), August (1), October (1).

DIAGNOSIS. *Cyclocephala melanae* is an uncommon species. This species, along with *C. fasciolata*, are the only "black" species of *Cyclocephala* in Costa Rica and Panama that

have a marginal bead on the posterior border of the pronotum. Whereas *C. fasciolata* has a transverse, reddish-orange macula or spots on non-furrowed elytra, *C. melanae* is completely black and normally has distinct longitudinal furrows on the elytra.

BIOLOGY. Adults have occasionally been taken at lights in premontane rain forests and lower montane rain forests at elevations of 1,250-2,100 meters.

***Cyclocephala melanocephala*
(Fabricius, 1775)**

(Figs. 305-309)

Melolontha melanocephala Fabricius 1775: 36.

Melolontha leucophthalma Fischer von Waldheim 1823: 265 (synonym).

Melolontha ventralis Erichson 1847: 97 (synonym).

Cyclocephala dimidiata Burmeister 1847: 57 (synonym).

Cyclocephala elegans Horn 1871: 337 (synonym).

Dichromina ocularis Casey 1915: 162 (synonym).

DESCRIPTION. Length 9.3-15.0 mm; width 4.9-7.5 mm. Color dark cherry-red except for piceous to black frons and testaceous elytra (most common) or piceous to black except for



Fig. 303. Distribution of *Cyclocephala melanae* in Costa Rica.



Fig. 304. Distribution of *Cyclocephala melanae* in Panama.

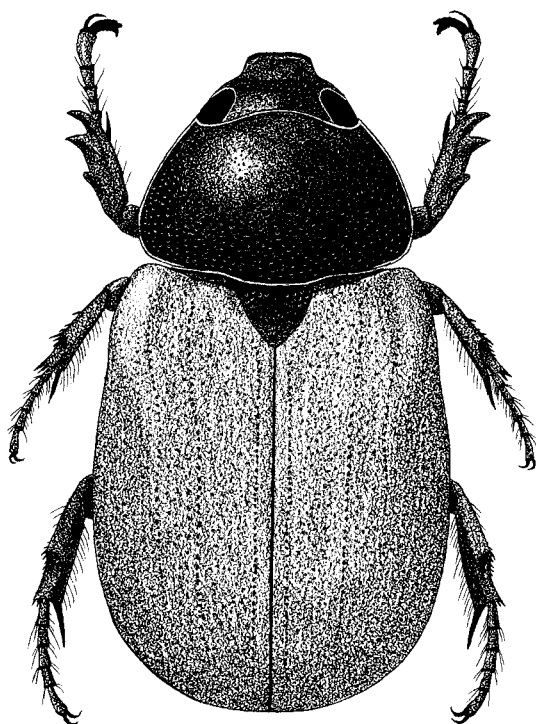
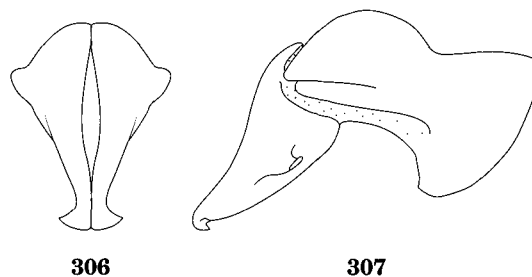


Fig. 305. *Cyclocephala melanocephala*.

testaceous elytra and dark reddish brown sternites and pygidium. *Head*: Frons sparsely punctate, punctures small to moderate in size. Clypeus with surface transversely rugulose; apex broadly subtruncate, weakly reflexed. Interocular width equals 2.4 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. *Pronotum*: Surface with punctures small to moderate, moderate in density. Base lacking marginal bead. *Elytra*: Surface with punctures moderately large, moderate in density, distinct rows visible. Epipleuron (ventral view) of females imperceptibly thickened at level of sternite 2. *Pygidium*: Surface coarsely scabrous, punctures occasionally visible. In lateral view, surface in males strongly convex, surface in females weakly convex. *Legs*: Foretibia tridentate, basal tooth slightly removed from other teeth. Foretarsus in males enlarged: tarsomere 4 subtriangularly lobed beneath; tarsomere 5 enlarged, slightly bent; median claw enlarged, curved, base with



Figs. 306-307. *Cyclocephala melanocephala* parameres.

large lobe, apex broadly cleft as in Figs. 121-122. Posterior tarsus shorter than posterior tibia. *Venter*: Prosternal process moderate in length, columnar, apex obliquely flattened into broad oval with raised, transverse "button" on anterior half. *Parameres*: Figs. 306-307.

DISTRIBUTION. *Cyclocephala melanocephala* is broadly distributed, ranging from the southwestern United States south to Argentina and Paraguay (Endrödi 1966). It is generally distributed throughout Costa Rica and Panama.

LOCALITY RECORDS (Figs. 308-309). 1,947 specimens examined.

COSTA RICA (1,573). ALAJUELA (10): Caño Negro, Finca Magil, San Ramon, Upala; CARTAGO (230): Embalse El Llano, Grano de Oro, Paraiso, Tapanti, Tuis, Turrialba; GUANACASTE (265): Bahía Santa Elena, Cañas, Estación Cacao, Estación Las Pailas, Estación Lomas Barbudal, Estación Los Almendros, Estación Murcielago, Estación Pitilla, Finca Jenny, Isla Cocinero, Liberia, Los Mesones, Nacaome (3 km N), Parq. Nac. Barra Honda, Parq. Nac. Palo Verde, Parq. Nac. Santa Rosa, Sector Gongora, Tierras Morenas, Volcán Tenorio; HEREDIA (44): El Plastico, Estación El Ceibo, Estación Magsasay, Finca Naranjo Valenciana, La Selva Biological Station, Las Horquetas de Sarapiquí; LIMÓN (276): Amubri, Cerro Tortuguero, Estación Cuatro Esquinas, Estación Hitoy Cerere, Estación Miramar,

Limón, Manzanillo, Valle La Estrella; PUNTARENAS (730): Cerro Oscuro, Estación Altamira, Estación La Casona, Estación La Escuadra, Estación Las Alturas, Estación Esquinas, Estación Mellizas, Estación Quebrada Bonita, Estación San Miguel, Estación Sirena, Fila Guerra, Finca Helechales, Parq. Nac. Manuel Antonio, Punta Banco, Rancho Quemado, Reserva Biológica Monteverde, Rincon de Osa, San Luis, San Vito, Vuelta Campana; SAN JOSÉ (18): Estación Bijagual, Estación Carrillo, Santiago de Puriscal.

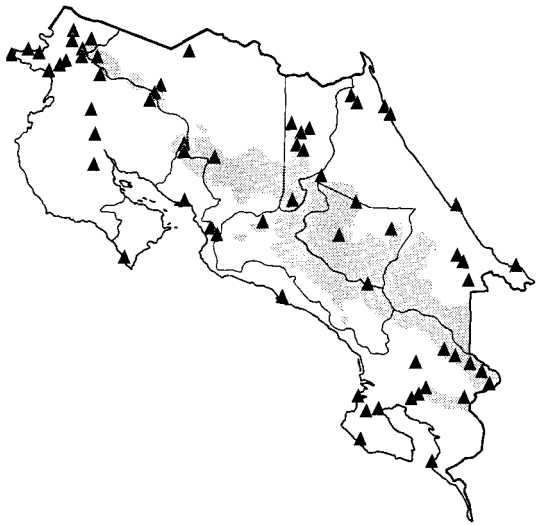


Fig. 308. Distribution of *Cyclocephala melanocephala* in Costa Rica.

PANAMA (374). BOCAS DEL TORO (95): 2 mi. N Divide on Hwy to Chiriqui Grande, Miramar; CANAL ZONE (74): Ancon, Albrook Forest, Barro Colorado Island, Coco Solo Hospital, Ft. Gulick, Ft. Randolph, Ft. San Lorenzo, Ft. Sherman, Escobal Road, Gamboa, Gatun Tank Farm, Howard AFB, Madden Dam, Madden Forest, Piña Road, Skunk Hollow; CHIRIQUI (72): Boquete, Cerro Punta, Chiriqui (28 km E), Fortuna, Hartmann's Finca (Santa Clara), Hato de Volcán, Hornito, Lino; COCLÉ (6): Aguadulce, Río Hato; COLÓN (36): Colón, Santa Rita Ridge; DARIEN (4): Cana, Río Tacariuna, Río Tuquesa, Santa Fé; PANAMA (82): Cerro Azul, Cerro Campana, Cerro Jefe, El Llano-Carti Road (km 15), Isla Majé, Isla San José (Pearl Islands), Panama City; SAN BLAS (3): No data; VERAGUAS (2): Santa Fé.

TEMPORAL DISTRIBUTION. January (106), February (73), March (118), April (183), May (284), June (186), July (257), August (131), September (127), October (197), November (173), December (113).

DIAGNOSIS. *Cyclocephala melanocephala* is identified by its dark, cherry-red (occasionally black) pronotum and testaceous elytra in combination with a short antennal club (subequal in length or slightly shorter than segments 2-7), large claw of the protarsus in males with



Fig. 309. Distribution of *Cyclocephala melanocephala* in Panama.

a widely cleft apex, and the absence of a marginal bead on the base of the pronotum. The male parameres are also diagnostic. In general appearance, *C. melanocephala* closely resembles *C. macrophylla*, but the shorter antennal club of *C. melanocephala* will distinguish it from *C. macrophylla*.

BIOLOGY. Adults are readily attracted to lights at night. This species is broadly distributed in tropical dry transition forests, tropical moist forests, tropical wet forests, premontane moist forests, premontane wet forests, premontane rain forests, lower montane moist forests, and lower montane wet forests. They have been collected at elevations ranging from near sea level to 2,000 meters.

***Cyclocephala multiplex* Casey,
1915**

(Figs. 310-315)

Cyclocephala multiplex Casey 1915: 139
(NEW STATUS).

DESCRIPTION. Length 12.0-15.3 mm; width 6.0-7.9 mm. Color testaceous: frons black; pronotum with 2 longitudinally parallel, black vittae, each vitta sinuate on outer edge; elytra with narrow black line along suture; posthumeral dash and subapical triangular spot black, large; postscutellar streak usually thick, extending from base either side of scutellum obliquely to suture; elytral marks rarely reduced or obsolete; female with black spot on lateral margin at expanded epimeron/marginal invagination; pygidium testaceous or darkened on sides or completely darkened; femora and tarsomeres each with apices darkened. *Head:* Frons with punctures moderately dense, moderately large, setigerous in males mesad of each eye (females lack setae); setae short, tawny in color. Clypeus in males with surface usually less densely punctate; punctures small, lacking setae; surface becoming weakly rugulose or roughened apically; surface in females transversely rugulose to rugopunctate, lacking setae; clypeal sides subparallel at base, anterior angles broadly rounded to a broadly subtruncate

apex; apex with marginal bead, weakly reflexed. Interocular width equals 2.5-3.0 transverse eye diameters in males, 3.0 transverse eye diameters in females. Antenna with 10 segments, club subequal in length to segments 2-7. *Pronotum:* Surface punctate; punctures moderate in density in males, a little denser in females; size small to mostly moderate in males, nearly all moderate in size in females; males with short setae on disc (usually abraded away) and slightly longer setae on lateral thirds of pronotum, females with short setae on lateral thirds; setae tawny. Base with complete marginal bead. *Elytra:* Surface finely shagreened with moderately dense, shallow punctures, rows of punctures indistinct; punctures often setigerous, setae sparse, short, tawny. Epipleuron (ventral view) of females swollen at level of abdominal sternites 1-2, deeply emarginate at level of abdominal sternites 3-4, swelling ending in acute tooth at sternite 4; in dorsal view, side of elytron behind middle swollen, swelling deeply emarginate. *Pygidium:* Surface shagreened, punctate; punctures small, moderate in density, setigerous; setae in males long, tawny, setae in females short (sometimes worn off). In lateral view, surface in males convex (especially in apical third), in females weakly convex or flat. *Legs:* Foretibia in males bidentate, tridentate in females. Foretarsus in males enlarged: tarsomere 4 with large, ventral flange; 5th large, curved, flattened on venter, base on inner side with tooth; median claw large, curved, base on ventral side with large, elongate lobe, apex of claw entire. Foretarsus in females simple. Posterior tarsus about 1.8 times longer than posterior tibia. *Venter:* Prosternal process elongate, subconical. Females with 5th abdominal segment strongly constricted at center on apical margin and about half length of fourth segment (Fig. 311). *Parameres:* Figs. 313-314.

DISTRIBUTION. *Cyclocephala multiplex* has an incompletely-known distribution because it was formerly included with *C. amazona*, and they are so combined in nearly all research collections. Based on the specimens at hand, it appears that *C. multiplex*

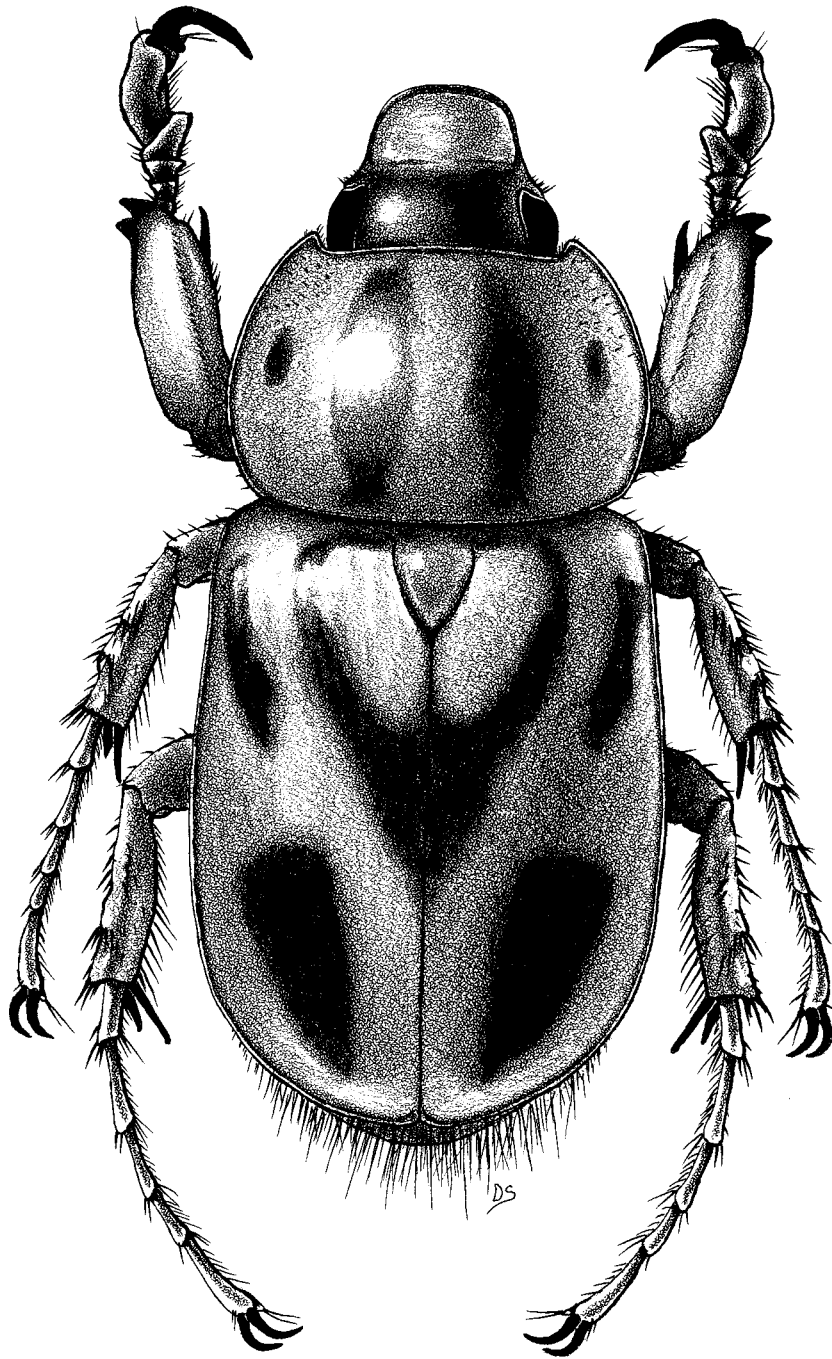
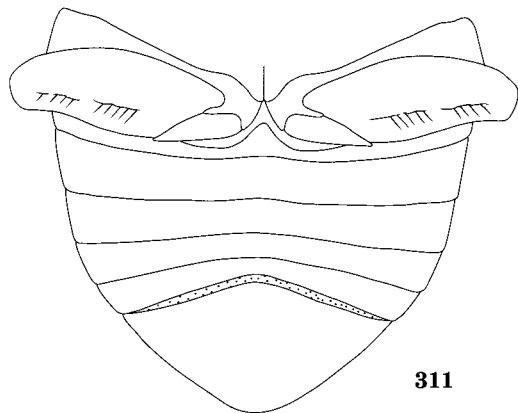


Fig. 310. *Cyclocephala multiplex*.

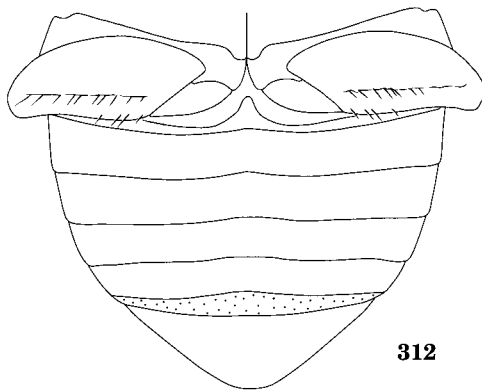
occurs from Mexico to Costa Rica. It becomes sympatric with *C. amazona* in Costa Rica. *Cyclocephala amazona* then occurs from Costa Rica into South America. This species is distributed in the lowlands of northern Costa Rica.

LOCALITY RECORDS (Fig. 315). 222 specimens examined.

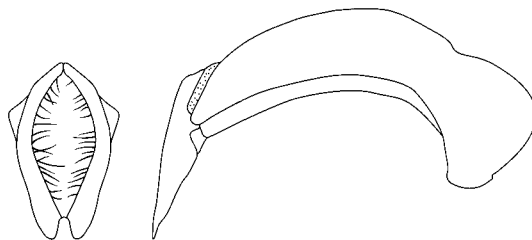
COSTA RICA (222). ALAJUELA (34): Caño Negro, Colonia Blanca (2 km N), Dos Rios (2 km SW), Playuelas; GUANACASTE (185): Agua



311



312



313

314

Figs. 311-314. *Cyclocephala multiplex*: (311) sternites of female; (312) sternites of *C. amazona* female; (313-314) parameres.

Buena, Cerro El Hacha, El Amo, Estación Los Almendros, Estación Maritza, Estación Murcielago, Estación Pitilla, Estación Santa Rosa, Finca Jenny (30 km N Liberia), Río Gongora, Tierras Morenas; HEREDIA (3): Finca Naranjo Valenciana.

TEMPORAL DISTRIBUTION. February (2), May (25), June (49), July (15), August

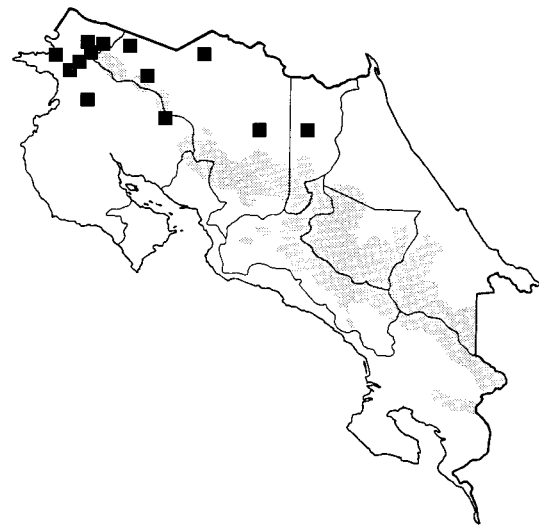


Fig. 315. Distribution of *Cyclocephala multiplex* in Costa Rica.

(27), September (1), October (1), November (1).

DIAGNOSIS. *Cyclocephala multiplex* and *C. amazona* are similar in appearance, and the parameres of the males are also similar. In general, the elytral markings in *C. multiplex* are larger than those in *C. amazona* (best seen in comparative series of each species). Also, the oblique, post-scutellar “dash” is thickened and elongated (usually extending from the base of the elytron to the suture) in *C. multiplex* whereas it is usually just a short, slender mark in *C. amazona*. The elytral markings, while generally useful, are not reliable to separate these species because there is occasionally overlap.

Augmenting the elytral markings (which are good for preliminary sorting) is the absence of clypeal setae in the males of *C. multiplex*. Males of *C. amazona* possess distinct setae on the surface of the clypeus. In the females of *C. multiplex*, the fifth abdominal sternite is strongly constricted at its center on the apical margin, and it is about half the length of the fourth segment (Fig. 311). In females of *C. amazona*, the fifth abdominal sternite is “normal” and subequal in length to the fourth (Fig. 312).

NOMENCLATURE. *Cyclocephala multiplex* was listed as a synonym of *C. detecta* Bates in Blackwelder (1944), and Endrödi (1964) synonymized *C. detecta* with *C. amazona*. Endrödi's (1966) monograph of the Cyclocephalini and his 1985 English-version synopsis of the Dynastinae of the World maintained the synonymy. My examination of Casey's specimens of *C. multiplex* indicated they were distinct from *C. amazona*. Further examination of extensive material from Mexico and Central America revealed that supposed *C. amazona* north of Costa Rica were, in fact, all *C. multiplex*. *Cyclocephala multiplex* is, therefore, here removed from synonymy and re-instated as a valid species.

BIOLOGY. Adults are attracted to lights at night. *Cyclocephala multiplex* has been collected from tropical dry forests, tropical moist forests, and tropical wet forests at elevations ranging from near sea level to 700 meters.

***Cyclocephala mustacha* Ratcliffe,
new species
(Figs. 316-320)**

TYPE MATERIAL. Holotype labeled "PANAMA: Panama Prov., El Llano-Carti Rd., km 8, N9°16', W78°57', V-23-1995, elev. 1,100', B. Ratcliffe & M. Jameson." Allotype with same data. Two paratypes with the following data: "PANAMA, Panama Pr., El Llano-Carti Rd., 8 km N El Llano, 13 May 1994, BL&MV, DCCarlson/FTHovore" (1 female); "PANAMA, Panama Pr., El Llano-Carti Rd., 9 km N El Llano, 14 May 1994, BL&MV, DCCarlson/FTHovore" (1 female).

Holotype and allotype deposited at the University of Nebraska State Museum. Paratypes deposited in the collections of David C. Carlson (Fair Oaks, CA) (1 specimen) and Brett C. Ratcliffe (Lincoln, NE) (1 specimen).

HOLOTYPE. Male. Length 12.6 mm; width 6.8 mm. Color testaceous except for 5 small piceous spots on elytra as follows: 1 behind scutellum in first broad interval in basal fifth, 1 slightly posterolateral to preceding, 1 imme-

diately behind preceding in apical third, 1 slightly lateral to preceding, and 1 posteromedial to preceding; apices of femora and tibiae darkened. *Head:* Frons and clypeus similarly punctate; punctures moderately dense, moderate in size. Clypeus with apex broadly truncate, feebly sinuate, weakly reflexed; ventral edge at apex with distinctive, short, dense, tawny setae (Fig. 317); apex of mentum and labrum with similar setae. Interocular width equals 3.3 transverse eye diameters. Antenna with 10 segments, club slightly shorter than segments 2-7. *Pronotum:* Surface at midline with small, sparse punctures, punctures becoming moderately large and moderate in density on disc and sides. Base lacking marginal bead. *Elytra:* Surface finely shagreened, punctures moderately dense, moderately large, setigerous on sides and in apical third; setae minute, tawny; rows of punctures distinct. Margin next to suture thickened, slightly elevated. *Pygidium:* Surface on disc densely punctate; punctures moderately large and minute mixed, setigerous; setae minute, sparse, tawny; surface in lateral angles rugopunctate. In lateral view, surface regularly convex. *Legs:* Foretibia tridentate, teeth subequally spaced. Foretarsus enlarged: segments 2-4 each slightly larger than preceding; segment 5 large, curved, median edge with longitudinal carina, lateral edge on venter with row of stout, long setae; median claw large, curved, apex entire but with small tubercle indicating where smaller ramus would have originated, base with large, broad lobe. Posterior tarsus subequal in length to posterior tibia. *Venter:* Prosternal process moderately long, columnar, apex obliquely flattened into transverse oval with transversely oval, raised "button" on anterior 2/3. *Parameres:* Figs. 318-319.

ALLOTYPE. Female. Length 12.3 mm; width 6.3 mm. As holotype except in the following respects: *Head:* Punctures slightly larger. *Pronotum:* Punctures slightly larger. *Elytra:* Punctures slightly larger, minute setae absent. Epipleuron (ventral view) simple; lateral margin of elytron with small, elongated bulge at level of metacoxa. *Pygidium:* Surface moderately punctate on disc, punctures

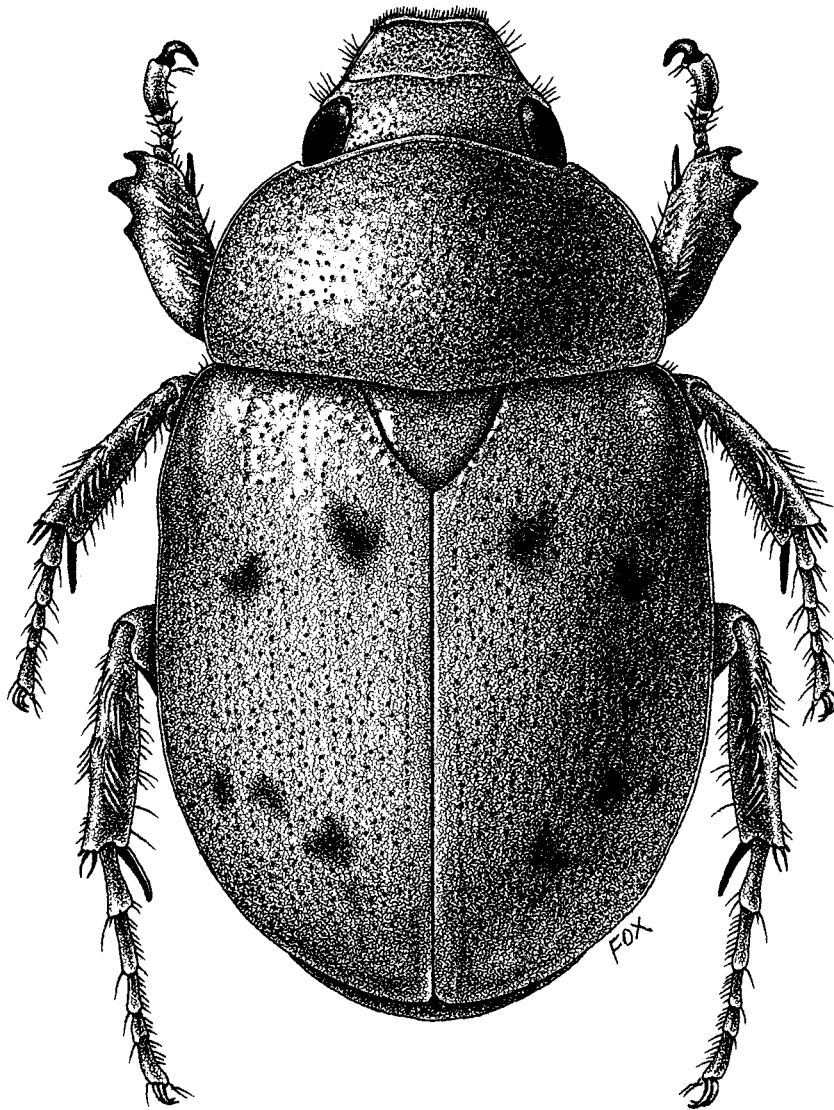


Fig. 316. *Cyclocephala mustacha*.

moderate to large, microsetae absent; lateral angles rugopunctate. In lateral view, surface regularly convex but less than that of holotype. *Legs*: Foretarsus simple. Posterior tarsus slightly shorter than posterior tibia.

VARIATION. Females (2 paratypes). Length 11.3-12.7 mm; width 6.3-7.0 mm. As allotype except in the following respects: *Color*: One specimen lacking post-scutellar spot. *Elytra*: One specimen with minute setae present as in holotype.

ETYMOLOGY. The distinctive fringe of dense setae at the apices of the clypeus (venter), labrum, and mentum are reminiscent of a mustache, and the Latinization of this barbaric word (French, moustache) gives rise to the specific epithet.

DISTRIBUTION. *Cyclocephala mustacha* is known only from a short section of the El Llano-Carti road about 55 km east of the airport in Panama City.

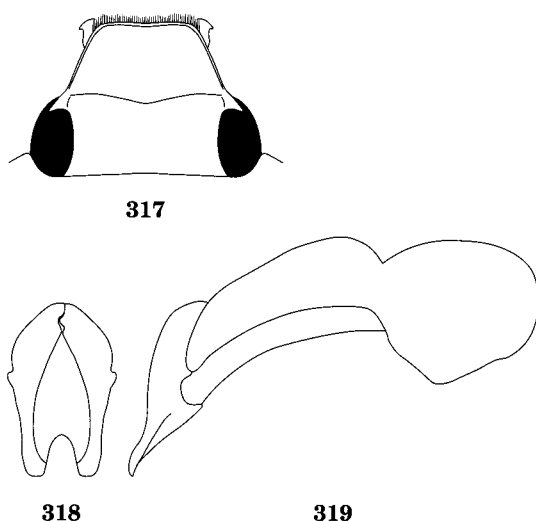
LOCALITY RECORDS (Fig. 320). 4 specimens examined.

PANAMA (4). PANAMA (4): El Llano-Carti Road (km 8, km 9).

TEMPORAL DISTRIBUTION. May (4).

DIAGNOSIS. This little species is reminiscent of *C. lunulata* but differs from that species in several respects. In *C. mustacha*, the frons is testaceous, the pronotum lacks dark

markings, the club of the antenna is a little shorter than segments 2-7, the teeth of the foretibia are subequally spaced, and the elytron has the sutural margin distinctly thickened; in addition, there is a distinctive fringe of dense, short setae on the apex of the clypeus (Fig. 317) on the ventral edge as well as on the apex of the labrum and mentum. Lastly, this is a relatively small species not exceeding 13 mm in length. In *C. lunulata*, conversely, the frons is darkened, the pronotum usually has dark markings, the antennal club is subequal in length to segments 2-7, the basal tooth of the foretibia is removed a little from the other teeth, and the elytron has a simple sutural margin; while there are setae at the apex of the clypeus and labrum, they are sparse and do not form a dense fringe. The size of *C. lunulata* is larger, with a length of 10.3 (uncommon) to 16.5 mm (common). The parameres of the males of both species are remarkably similar. In the females, the epipleuron of *C. mustacha* is simple whereas it is enlarged and angulate at the level of abdominal sternites 1-2 in *C. lunulata*; in dorsal view, the lateral margin of the elytron is tumid before the middle in *C. mustacha* and tumid at about the middle in *C. lunulata*.



Figs. 317-319. *Cyclocephala mustacha*: (317) head showing fringe of setae on apex of labrum and venter of clypeus; (318-319) parameres.

BIOLOGY. Only four adults have been taken at lights in a very well-collected area of tropical moist forest at an elevation of 350 meters.



Fig. 320. Distribution of *Cyclocephala mustacha* in Panama.

***Cyclocephala mutata* Harold, 1869**
(Figs. 321-326)

Cyclocephala frontalis Burmeister 1847: 50 (preoccupied by *C. frontalis* Chevrolat 1844: Plate 23, Figure 7, a species from Cuba referred to by Endrödi [1966, 1985a] as *C. cubana* Chapin 1932: 291).

Cyclocephala mutata Harold 1869: 124 (replacement name for *C. frontalis* Burmeister 1847, **NEW STATUS**).

Cyclocephala laevicauda Arrow 1902: 138 (synonym).

Cyclocephala pseudisabellina Endrödi 1980: 38 (**NEW SYNONYMY**).

Cyclocephala vitracelis Dechambre 1999a: 21 (**NEW SYNONYMY**).

DESCRIPTION. Length 14.8-20.7 mm; width 8.5-10.8 mm. Color testaceous with light to dark reddish brown head (frons often black), pygidium, venter, and legs. *Head:* Frons with small, sparse punctures, punctures often becoming larger and denser toward frontoclypeal suture. Clypeus with surface densely rugulose; apex parabolic, margin thickened, slightly reflexed. Interocular width equals 2.2 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. *Pronotum:* Surface with sparse, minute punctures or with sparse, small punctures on disc and slightly denser and larger punctures on sides. Base lacking marginal bead. *Elytra:* Surface with punctures moderate in density and size; punctate rows distinct. Epipleuron (ventral view) of females expanded at level of abdominal sternites 1-2 and abruptly constricted at level of sternite 2, point of constriction forming a slightly obtuse angle; just above this, lateral margin of elytra swollen into an arcuate lobe. *Pygidium:* Surface shining, finely shagreened, with sparse punctures, punctures minute to small. In lateral view, surface in males regularly convex, weakly convex in females. *Legs:* Foretibia tridentate, teeth subequally spaced. Foretarsus in males enlarged: tarsomeres 2-4 each slightly larger than preceding; 5th large, curved, with strong and longitudinal carina on inner edge; median claw large, strongly curved, with large lobe at

base, median edge swollen just distad of lobe (Fig. 322), apex cleft. Foretarsus in females simple. Posterior tarsus slightly longer than posterior tibia in males, subequal in length in females. *Venter:* Prosternal process moderately long, columnar, apex obliquely flattened into large, transverse oval (and extended posteriorly) with transversely oval, raised "button" on anterior half. Metasternum completely punctate. *Parameres:* Figs. 323-324.

DISTRIBUTION. *Cyclocephala mutata* is a relatively widespread species in Costa Rica and Panama. Bates (1888) reported it from southern Mexico, and Endrödi (1966) recorded it from Colombia and Ecuador; I have not seen specimens from these countries.

LOCALITY RECORDS (Figs. 325-326). 877 specimens examined.

COSTA RICA (176). ALAJUELA (15): San Miguel (6 km S), Zarcero; CARTAGO (9): Chirripó, Embalse El Llano, Moravia, Reserva Biológica, Tapanti; GUANACASTE (11): Estación Cacao, La Palma; HEREDIA (19): La Selva Biological Station, Reserva Biológica Chompipe; LIMÓN (2): Reserva Biológica Hitoy Cerere; PUNTARENAS (43): Coronado, Estación Altamira, Estación Las Alturas, Finca Cafrosa (2 km NW), Mellizas, Monteverde, Wilson Botanical Garden; SAN JOSÉ (77): Bajo La Rosa, División (8.4 km S), Estación Zurqui, La Trinidad de Dota, San José, SE side Volcán Irazú.

PANAMA (701). BOCAS DEL TORO (3): Chiriqui Grande; CHIRIQUI (698): Boquete, Cerro Punta, El Volcán, Finca La Suiza, Fortuna, Hartmann's Finca (Santa Clara), Hato del Volcán, Hornito, IHRE Vivero (11 km N Los Planes).

TEMPORAL DISTRIBUTION. January (1), February (1), March (12), April (34), May (621), June (196), July (27), August (3), November (1).

DIAGNOSIS. *Cyclocephala mutata* superficially resembles *C. sororia* and *C. concolor*, all three of which are relatively larger species

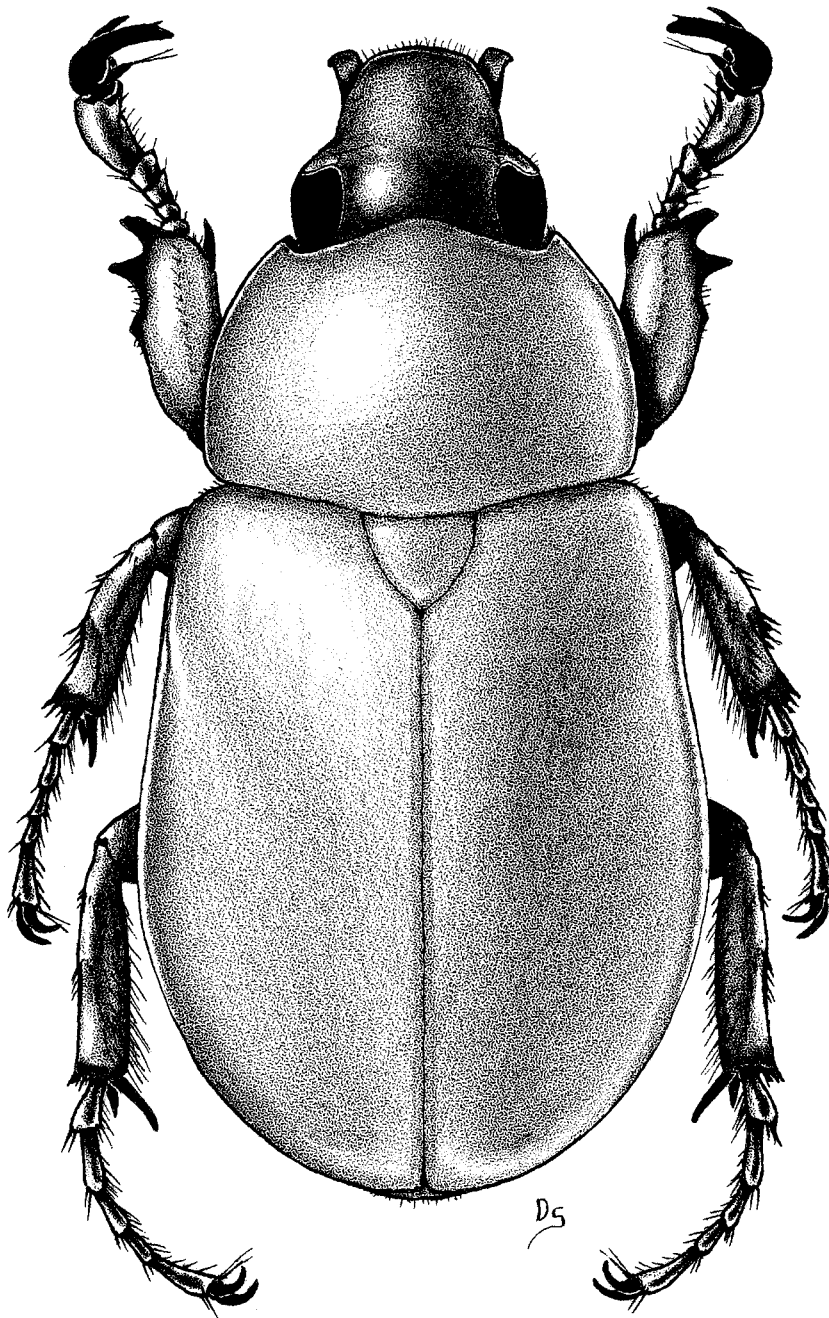
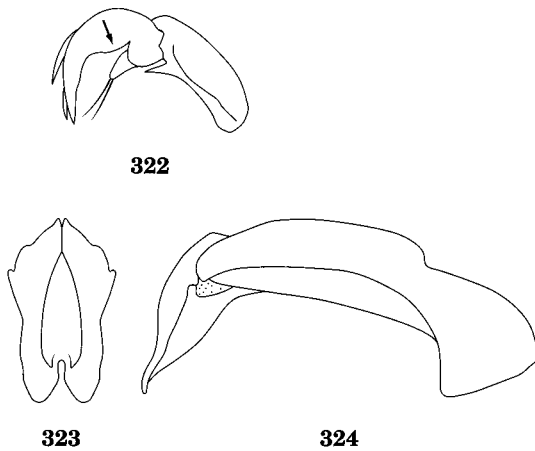


Fig. 321. *Cyclocephala mutata*.

with a testaceous pronotum and elytra. It is distinguished by the absence of a marginal bead on the base of the pronotum whereas the base of the pronotum has a marginal bead in *C. sororia*. Males of *C. mutata* also have the large ramus of the protarsal claw with a dis-

tinct swelling on the median edge just distad of the large basal lobe (Fig. 322), and this swelling is absent in *C. sororia* and in the similar-looking *C. stockwelli* (Fig. 416). This claw character takes on added significance when the pronotal basal bead becomes



Figs. 322-324. *Cyclocephala mutata*: (322) foreclaw of male; (323-324) parameres.



Fig. 325. Distribution of *Cyclocephala mutata* in Costa Rica.



Fig. 326. Distribution of *Cyclocephala mutata* in Panama.

partially obsolete as it tends to do in some specimens of *C. sororia* and *C. stockwelli*. Females of *C. mutata* have the epipleuron enlarged and with a lobe-like swelling on lateral margin of the elytron, whereas this area is simple in *C. sororia*.

Cyclocephala mutata is easily distinguished from *C. concolor* because the apex of the clypeus is round or parabolic and emarginate in *C. concolor*.

NOMENCLATURE. What a mess! . . . which is, hopefully, here resolved. The name formerly used for this common species in Costa Rica and Panama was *C. sanguinicornis* Burmeister (Endrödi 1966, 1985a). However, Bates (1888), Blackwelder (1944), and Ratcliffe and Morón (1996) noted that *C. sanguinicornis* referred to a distinctly bicolored species that occurred commonly in Mexico and is now known to be in Costa Rica also. The common, dorsally monochromatic, testaceous species occurring in Costa Rica and Panama is *C. mutata* Harold, which was Harold's (1869) replacement name for Burmeister's (1847) *C. frontalis*, which itself was preoccupied by Chevrolat's (1844) *C. frontalis* from Cuba. Arrow's (1902) *C. laevicauda* is conspecific with *C. mutata* as noted by Endrödi (1966), who actually referred to it as an aberration.

Through the courtesy of Dr. Roger-Paul Dechambre, I have examined the holotype of *C. pseudisabellina* Endrödi (1980) and determined that it is conspecific with *C. mutata*. This species was described from "Costa Rica" based on a single male specimen. Body character states, male claw, prosternal process, and parameres are all consistent with those of *C. mutata*. Endrödi's description of *C. pseudisabellina* stated that there are large punctures on the sides of the pronotum, but they are actually only slightly larger than those on the disc. The surface of the pygidium in the type of *C. pseudisabellina* is minutely roughened and is similar to that seen in *C. mutata*. In *C. mutata*, the foretibial teeth of the males are subequally spaced whereas in the holotype of *C. pseudisabellina* the teeth are subequally spaced on the right foretibia and unevenly spaced on the left foretibia. Lastly, the apex of the parameres is constricted or "pinched" in the type of *C. pseudisabellina* whereas it is normally fully and elongately rounded (Fig. 323) in *C. mutata*. From this single specimen of *C. pseudisabellina* I conclude that the parameres are either worn (unlikely) or simply aberrant (more likely). *Cyclocephala pseudisabellina* remained an enigma since its description because Endrödi's characterization lacked sufficient detail and was partially erroneous combined with the fact that no other specimens with similar character states have been found since that time.

After examining the types of *C. vitracelis* Dechambre (1999a) (again through the courtesy of Dr. Dechambre), I have concluded that it is also conspecific with *C. mutata*, and it is here placed in new synonymy with that species. The pronotum of *C. vitracelis* is slightly more punctate than "typical" *C. mutata* but well within the range of puncture variation observed in large series of specimens. The characteristic swelling on the venter of the large protarsal claw of males as well as the form of the parameres are all identical with those of *C. mutata*.

Cyclocephala cerea Burmeister (1847) is here removed from synonymy with *C. sanguinicollis* (= *C. mutata sensu* Endrödi 1966). I believe this is a valid species, and it

occurs in Jamaica. Rather than being closely associated with *C. mutata*, it is probably more closely related to *C. sororia* because it possesses a marginal bead on the base of the pronotum. While once connected or nearly connected to the Mesoamerican mainland in the past, Jamaica and much of its entomofauna is now isolated and unique.

BIOLOGY. Adults are attracted to lights at night. They are known to occur in premontane moist forests, premontane wet forests, premontane rain forests, lower montane wet forests, lower montane rain forests, and montane rain forests at elevations ranging from 200-2,100 meters; only 4 records were less than 1,000 meters.

***Cyclocephala nigerrima* Bates,
1888**

(Figs. 327-331)

Cyclocephala nigerrima Bates 1888: 310.

DESCRIPTION. Length 19.2-23.8 mm; width 10.1-12.6 mm. Color black. *Head:* Frons with small, sparse punctures; some females with punctures a little larger and denser. Clypeus similarly punctate to more usually with punctures a little larger and denser, especially in females; shape of clypeus subrectangular, apex broadly truncate and weakly and narrowly reflexed, anterior angles narrowly rounded. Interocular width equals 4.0 transverse eye diameters in males, 4.1-5.0 in females. Antenna with 10 segments, club subequal in length to segments 2-7. *Pronotum:* Surface with small, sparse punctures slightly larger on sides and near base. Base lacking marginal bead. *Elytra:* Surface in males with rows of shallow, moderately-sized punctures; females with moderately large to large punctures. First broad interval and sides with small, sparse punctures, females with moderately-sized punctures. Apex with minute, tawny setae. Epipleuron (ventral view) of females expanded into narrow, elongate swelling extending from anterior corner of side of metacoxa to middle of third sternite; in lateral view, epipleuron with small

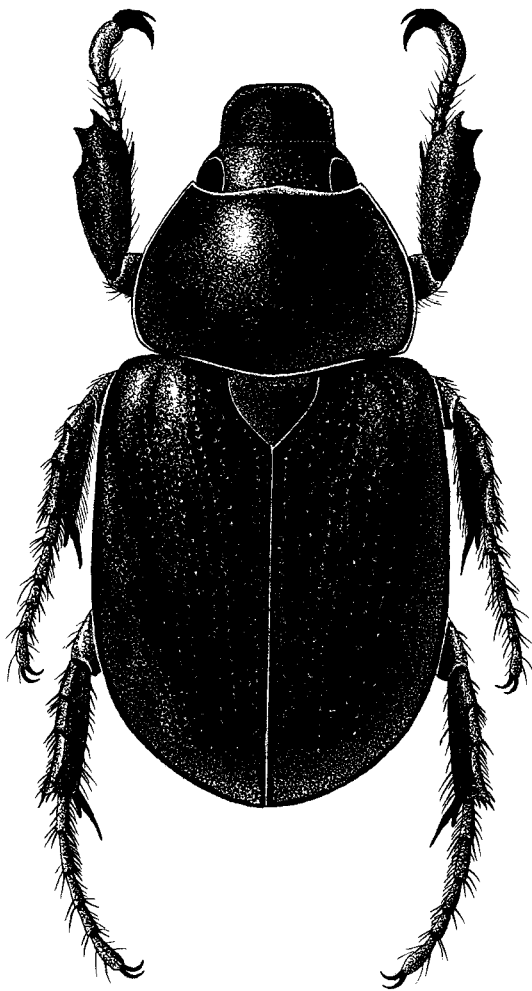
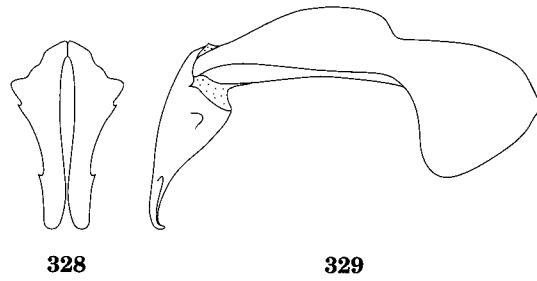


Fig. 327. *Cyclocephala nigerrima*.



Figs. 328-329. *Cyclocephala nigerrima parameres*.



Fig. 330. Distribution of *Cyclocephala nigerrima* in Costa Rica.



Fig. 331. Distribution of *Cyclocephala nigerrima* in Panama.

tooth at about level of anterior margin of third sternite. *Pygidium*: Surface moderately densely punctate; punctures moderately large, setigerous in males; setae short, moderately dense (when not worn off), tawny. In lateral view, surface nearly flat in both sexes. *Legs*: Foretibia tridentate, basal tooth removed from others. Foretarsus in males enlarged: tarsomere 4 with small, acute lobe beneath, fifth large, long, curved; median claw large, strongly curved, split at apex. Foretarsus of females simple. Posterior tarsus subequal in length to posterior tibia. *Venter*: Prosternal process short, columnar, apex obliquely flattened into transverse oval with anterior half to 2/3 raised as convex "button." *Parameres*: Figs. 328-329.

DISTRIBUTION. *Cyclocephala nigerrima* is known from Costa Rica (Endrödi 1966, 1985a) and Panama (Ratcliffe 1992b). This species is found in the Cordillera Central of Costa Rica and in the mountains of Chiriqui in western Panama.

LOCALITY RECORDS (Figs. 330-331). 231 specimens examined.

COSTA RICA (13). ALAJUELA (7): San Miguel (6 km S), San Ramon, Volcán Cacao (E side); CARTAGO (110): Embalse El Llano, Grano de Oro (Chirripó), Quebrada Segunda (Tapanti), Volcán Irazú (SE side); GUANACASTE (8): Estación Cacao, Tierras Morenas; HEREDIA (22): Amarillo, Hiway 32 in Parq. Nac. Braulio Carrillo, Vara Blanca (10 mi. N); PUNTARENAS (16): Estación La Casona, Monteverde; SAN JOSÉ (16): Alto de la Palma, Bajo La Rosa, Estación Santa Elena, Zurqui tunnel.

PANAMA (56). CHIRIQUI (56): Boquete, Continental Divide trail, Fortuna Dam, Hartmann's Finca, IRHE Vivero (7 km N Los Planes), Los Planes.

TEMPORAL DISTRIBUTION. January (1), March (2), April (17), May (48), June (39), July (20), August (30), September (44), October (13), November (6).

DIAGNOSIS. *Cyclocephala nigerrima* is easily distinguished from the other black species of *Cyclocephala* in Costa Rica and Panama because of its large, truncate, subrectangular clypeus, tridentate foretibia, and absence of a marginal bead on the base of the pronotum.

BIOLOGY. Adults are attracted to lights and have been observed in the inflorescences of *Montsera jacquinii* Schott (Araceae) in Monteverde, Costa Rica (Andrew Smith, personal communication, 1997). Specimens have been collected in premontane forests, lower montane forests, and montane rain forests at elevations of 800-2,500 meters.

***Cyclocephala nigritarsis* Ratcliffe,
1992**
(Figs. 332-337)

Cyclocephala nigritarsis Ratcliffe 1992: 222.

DESCRIPTION. Length 9.2-11.1 mm; width 4.0-5.0 mm. Color testaceous with piceous to black marks as follows: a band across vertex between eyes, a discal spot or streak on the elytra, or also with post-scutellar and post-humeral smudge and/or with a linear stripe (about twice as long as discal spot) on lateral edge of disc; in addition, lateral thirds of pygidium (or not), apices of all femora, tarsomeres, and abdominal sternites (or not) piceous or black. *Head*: Surface densely, finely rugopunctate to densely punctate on frons, punctures small. Clypeus with apex narrowly parabolic, slightly reflexed. Interocular width equals 3.0 transverse eye diameters. Antenna with 10 segments, club slightly longer than segments 2-7. *Pronotum*: Surface moderately densely punctate, punctures moderate in size, equally dense on disc and sides. Base with marginal bead. *Elytra*: Surface weakly shagreened in males, weakly shining in females, punctate; punctures about twice as large as those on pronotum, weakly umbilicate. Epipleuron (ventral view) of females becoming wider at anterior edge of metacoxa, gradually expanded into a flange at level of abdominal sternites 1-2; in lateral view,

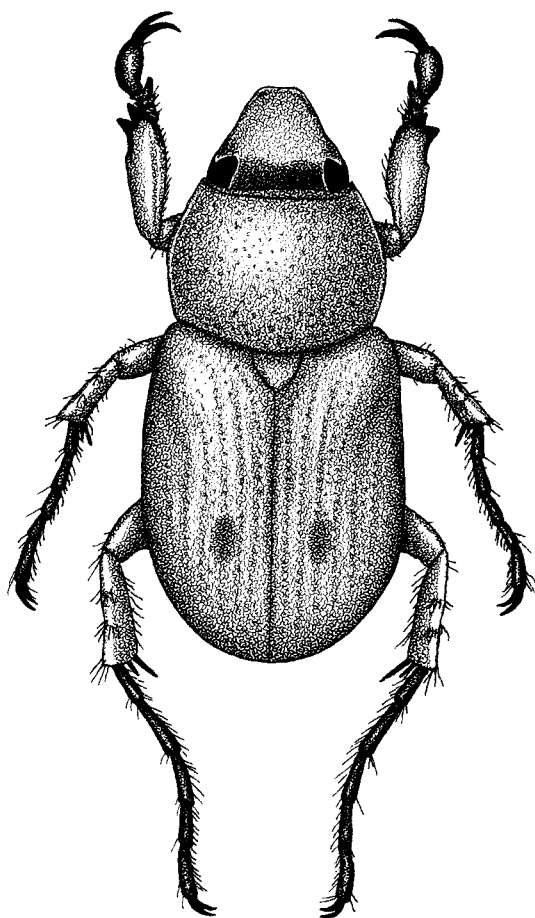
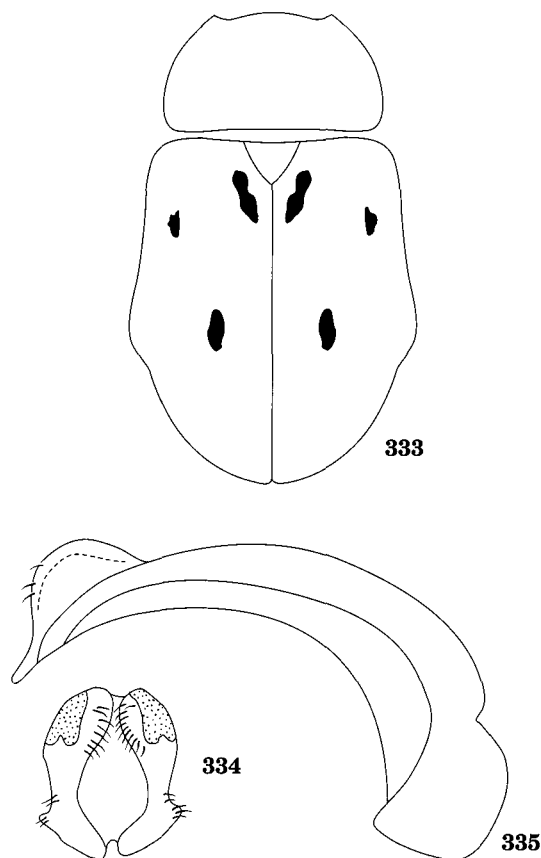


Fig. 332. *Cyclocephala nigratarsis*.



Figs. 333-335. *Cyclocephala nigratarsis*: (333) female; (334-335) parameres.

ventral edge of epipleuron with small, weak, obtuse tooth at level of sternite 2; in dorsal view, elytral margin swollen into elongated flange (Fig. 333). *Pygidium*: Surface in males finely shagreened, weakly shining in females, with small, sparse punctures. In lateral view, surface in males convex (especially near apex), weakly convex in females. Marginal bead with fringe of long setae. *Legs*: Foretibia in males bidentate, tridentate in females. Foretarsus in males enlarged: tarsomere 4 with large, triangular swelling on venter; tarsomere 5 with distinct tooth at base on ventral side and with strong, arcuate carina on median edge; median claw large, curved, apex entire. Foretarsus in females simple. Posterior tarsus in males nearly twice as long

as posterior tibia, only about 1/3 longer in females. *Venter*: Prosternal process small, short, subconical. *Parameres*: Figs. 334-335.

DISTRIBUTION. *Cyclocephala nigratarsis* is known from Costa Rica and Panama. There is a relatively broad gap in distribution between Cerro Gaital in central Panama and Reserva Hitoy Cerere on the Caribbean coast of Costa Rica.

LOCALITY RECORDS (Figs. 336-337). 136 specimens examined.

COSTA RICA (55). ALAJUELA (20): Río San Lorencito (Reserva de San Ramon); GUANACASTE (17): Tierra Morenas;

HEREDIA (3): Estación El Ceibo, Estación Magsasay, Puerto Viejo; LIMÓN (15): Llanuras del Tortuguero, Manzanillo, Reserva Hitoy Cerere, Suretka.

PANAMA (81). CANAL ZONE (20): Ft. Sherman, Skunk Hollow; COCLÉ (13): Cerro Gaital, El Valle; COLÓN (36): Santa Rita Ridge; PANAMA (12): Cerro Campana, El Llano-Carti road (km 8).

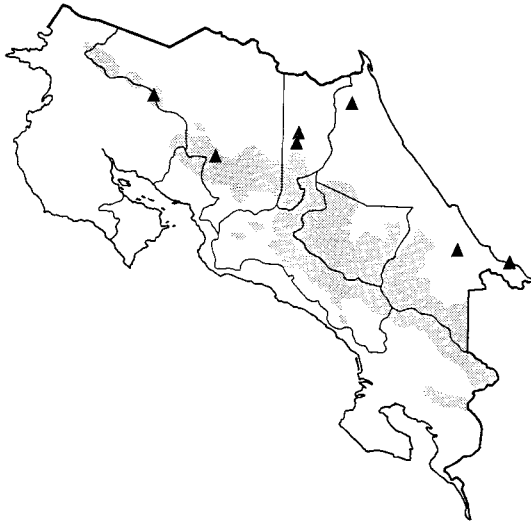


Fig. 336. Distribution of *Cyclocephala nigratarsis* in Costa Rica.

TEMPORAL DISTRIBUTION. January (2), February (4), March (25), April (11), May (20), June (67), July (10), October (2), November (3), December (1).

DIAGNOSIS. This species superficially resembles *C. herteli* and *C. santaritae*. *Cyclocephala nigratarsis* has a dark frons and tarsi, whereas the other two species have a testaceous frons and tarsi. The base of each paramere is strongly depressed in *C. nigratarsis* and either not or only weakly impressed in the other two species. In females, the marginal expansion of the elytra is gradually and broadly expanded whereas it is abruptly expanded and narrower in *C. herteli* and *C. santaritae*.

BIOLOGY. Adults are attracted to lights at night. *Cyclocephala nigratarsis* is found in tropical moist forests, tropical wet forests, and premontane rain forests at elevations ranging from near sea level to 1,050 meters.



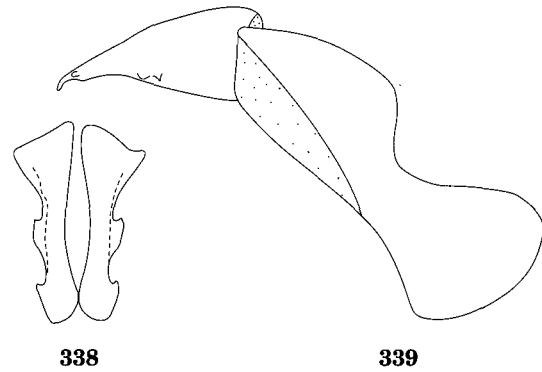
Fig. 337. Distribution of *Cyclocephala nigratarsis* in Panama.

***Cyclocephala nike* Ratcliffe, 1992**

(Figs. 338-341)

Cyclocephala nike Ratcliffe 1992b: 224.

DESCRIPTION. Length 23.0-24.1 mm; width 11.2-11.4 mm. Color dark reddish brown with black head, pronotal margins, sutural line, base and epipleura of elytra, legs, and venter; mesad of elytral umbone is a short, longitudinal, piceous smudge. *Head:* Surface of frons with punctures moderate in density and size. Clypeus punctate in basal half, becoming rugopunctate anteriorly, punctures moderately large; apex broad, weakly emarginate, narrowly reflexed. Interocular width equals 3.5 transverse eye diameters. Antenna 10-segmented, club a little shorter than segments 2-7. *Pronotum:* Surface sparsely punctate on disc, becoming moderately densely punctate on sides; punctures on disc small, gradually becoming larger laterally. Base completely margined. *Elytra:* Surface with large, shallow punctures, double rows indistinct. Epipleuron (ventral view) in females with short, abrupt expansion at level of abdominal sternites 1-2; in lateral view, expansion with distinct tooth on ventral edge. *Pygidium:* Surface finely rugopunctate except near apex at center where punctate; punctures moderate to large, mixed with small punctures, setigerous; setae minute, tawny in color. In lateral view, surface of males weakly convex, nearly flat in females. *Legs:* Foretibia

Figs. 338-339. *Cyclocephala nike* parameres.Fig. 340. Distribution of *Cyclocephala nike* in Costa Rica.Fig. 341. Distribution of *Cyclocephala nike* in Panama.

tridentate, basal tooth slightly removed from others. Foretarsus in males enlarged: tarsomere 4 with enlarged, ventral lobe; tarsomere 5 enlarged, weakly curved, without ventral lobe or tooth, instead venter slightly concave; median claw large, strongly curved, apex finely split. Foretarsus in females simple. Posterior tarsus subequal in length to posterior tibia. *Venter*: Prosternal process long, columnar, apex obliquely flattened into broadly transverse oval with transverse, elevated "button" on anterior half. *Parameres*: Figs. 338-339.

DISTRIBUTION. *Cyclocephala nike* is known only from a small area in Chiriqui province in Panama and adjoining Puntarenas province in Costa Rica.

LOCALITY RECORDS (Figs. 340-341). 4 specimens examined.

COSTA RICA (2). PUNTARENAS (2): Río Cotón.

PANAMA (2). CHIRIQUI (2): Hartmann's Finca (Santa Clara).

TEMPORAL DISTRIBUTION. May (2), October (2).

DIAGNOSIS. *Cyclocephala nike* resembles *C. mafaffa* without any dorsal, black markings. It is different than *C. mafaffa* because it has a basal bead on the pronotum; lacks longitudinal, black bands on the pronotum and spots on the elytra; and has some differences in clypeal shape and the form of the male parameres. *Cyclocephala mafaffa* is partially characterized by the absence of a basal pronotal bead. This bead is variably present or absent at the posterior angles but is not complete across the base of the pronotum in *C. mafaffa* whereas it is complete in *C. nike*.

Lastly, there is an ecological distinction between the two species. *Cyclocephala mafaffa* is a lowland species that is found from sea level up to about 1,000 meters in elevation; *C. nike*, however, is a highland species found at elevations above 1,300 meters.

BIOLOGY. *Cyclocephala nike* has been collected from lower montane wet forests and

lower montane rain forests at elevations of 1,300 and 1,800 meters.

Cyclocephala ovulum Bates, 1888

(Figs. 342-346)

Cyclocephala ovulum Bates 1888: 306 (NEW STATUS).

DESCRIPTION. Length 7.7-9.1 mm; width 4.1-5.0 mm. Color testaceous except for black "mask" between eyes and black apices of femora and tibiae; abdominal sternites rarely darkened. *Head*: Surface of occiput impunctate, frons densely punctate, punctures moderate in size. Clypeus with surface weakly, transversely rugulose; apex broadly truncate, weakly reflexed. Interocular width equals 2.5 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. *Pronotum*: Surface on disc sparsely (uncommon) to moderately (most common) punctate, punctures moderate in size, becoming slightly denser and larger on sides. Base without marginal bead. *Elytra*: Surface minutely shagreened, with punctures moderate in density and size, rows of punctures distinct. Epipleuron (ventral view) of females feebly enlarged at level of sternite 1 and then abruptly narrowing. *Pygidium*: Surface coarsely roughened. In lateral view, surface in males weakly convex, nearly flat in females. *Legs*: Foretibia tridentate, all teeth subequally spaced. Foretarsus in males enlarged: segments 1-4 each slightly larger than preceding and ventrally enlarged; 5th large, curved, apex on inner side prolonged into tooth, venter with feeble and minute tooth at center, median claw cleft at apex. Posterior tarsus subequal in length to posterior tibia. *Venter*: Prosternal process moderately long, columnar, apex obliquely flattened into transverse oval (extended on posterior edge) with raised, transverse "button" on anterior half. *Parameres*: Figs. 343-344.

DISTRIBUTION. *Cyclocephala ovulum* is known from Mexico to Paraguay (Blackwelder 1944; Endrödi 1966). It is generally distributed throughout Costa Rica and Panama.

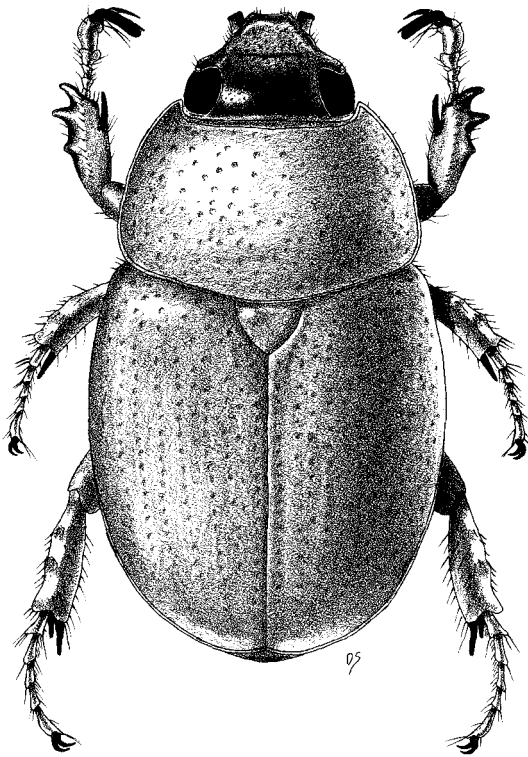
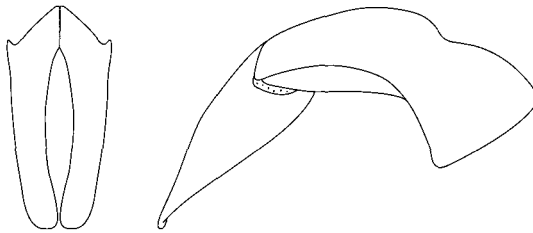


Fig. 342. *Cyclocephala ovulum*.



343

344

Figs. 343-344. *Cyclocephala ovulum* parameres.

LOCALITY RECORDS (Figs. 345-346). 577 specimens examined.

COSTA RICA (474). ALAJUELA (9): Atenas (8 km W), Upala; CARTAGO (1): Turrialba; GUANACASTE (216): Cañas, Estación Murcielago, Estación Pitilla, Finca Jenny (3 km N Liberia), Parq. Nac. Barra Honda, Parq. Nac. Santa Rosa, Sector Góngora; LIMÓN (34): Buenos Aires, Cerro Tortuguero, Guapiles, Reserva Biológica Hitoy Cerere; PUNTARENAS (204): Mata Limón, Quepos, Parq. Nac. Manuel Antonio, Reserva Biológica Carara, Río Bonito, Vuelta Campana; SAN JOSÉ (10): Estación Bijagual.



Fig. 345. Distribution of *Cyclocephala ovulum* in Costa Rica.

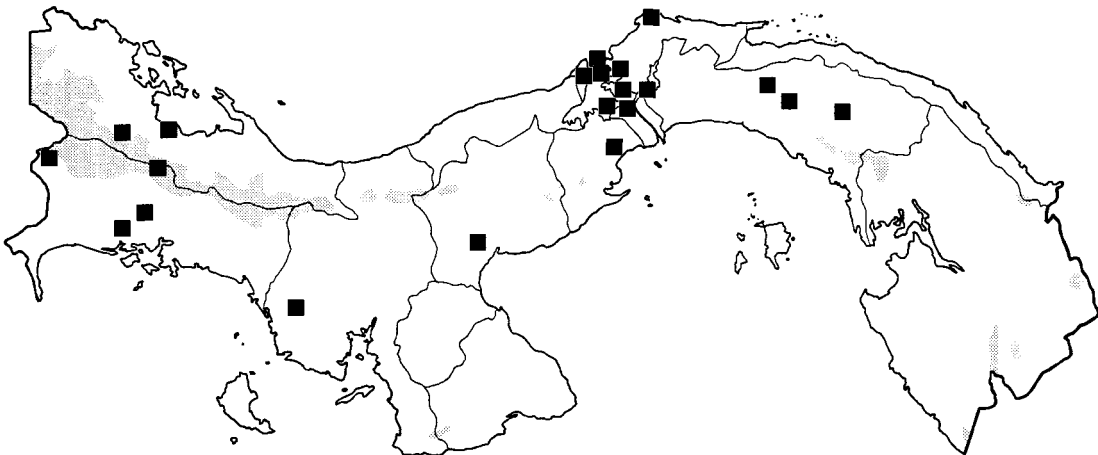


Fig. 346. Distribution of *Cyclocephala ovulum* in Panama.

PANAMA (103). BOCAS DEL TORO (18): Miramar, Río Changuinola; **CANAL ZONE** (34): Achiote Road, Barro Colorado Island, Coco Solo Hospital, Gatun Lake Lookout, Madden Dam, Pipeline Road (km 3), Tabernilla; **CHIRIQUI** (6): David, Fortuna, Gualaca, Hartmann's Finca (Santa Clara); **COCLÉ** (1): Natá; **COLÓN** (20): Cerro Viejo Mine Road (9 km SW Nombre de Dios), Santa Rita Ridge; **PANAMA** (20): Altos de Majé, Chorrera, El Llano-Carti Road (km 11), Ipeti; **VERAGUAS** (4): Cabimo.

TEMPORAL DISTRIBUTION. January (27), February (3), March (53), April (30), May (238), June (52), July (16), August (19), September (6), October (35), November (61), December (34).

DIAGNOSIS. The small size (less than 9.2 mm) and oval shape is usually all that is needed to distinguish *C. ovulum* from any other species of *Cyclocephala* in Central America. In addition to its size and shape, it is also characterized by a pronotum with punctures moderate in size and density and lacking a basal bead, truncate clypeus, subequally spaced foretibial teeth, a weakly enlarged epipleuron in females, and characteristically simple parameres in the males.

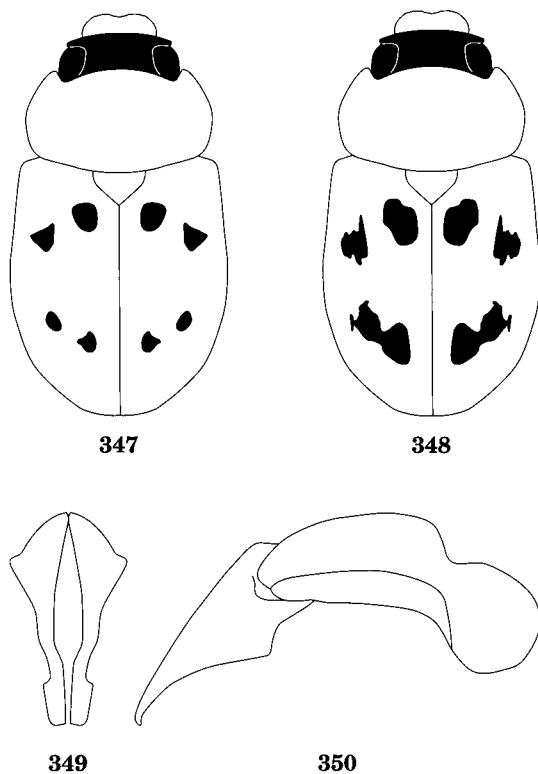
NOMENCLATURE. *Cyclocephala ovulum* was considered an aberration of *C. testacea* Burmeister by Endrödi (1966, 1985a). *Cyclocephala testacea*, while having similar parameres in the males to those of *C. ovulum*, is a larger, elongate, more parallel-sided beetle. It was described from French Guiana, and all the specimens I have seen are from South America. *Cyclocephala ovulum* is much more abundant and is so distinctive in shape and size that it cannot be considered conspecific with *C. testacea*. It is, therefore, here reinstated to the species level.

BIOLOGY. Adults are attracted to lights at night. They are found in tropical dry forests, tropical moist forests, tropical wet forests, premontane moist forests, and premontane wet forests at elevations ranging from near sea level to 1,000 meters.

***Cyclocephala pan* Ratcliffe, 1992**
(Figs. 347-353)

Cyclocephala pan Ratcliffe 1992 b: 226

DESCRIPTION. Length 14.0-17.8 mm; width 7.0-9.8 mm. Color testaceous except for black frons, subtriangular spot on base of clypeus, and 4 small to moderately large spots in a semicircular arc on elytra (Fig. 347); anterior spot behind scutellum often larger, subtriangular, posterior 2 spots sometimes connected (Fig. 348). Some specimens with black spots on posterolateral angles of abdominal sternites 1-5. *Head:* Frons densely punctate; punctures moderately large, setigerous, setae minute, pale. Clypeus with surface rugopunctate or transversely rugulose, setigerous; setae minute, pale; apex broadly emarginate. Interocular width equals 2.4-3.0 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. *Pronotum:* surface moderately punctate on disc, becoming densely punctate on sides; punctures moderately large, setigerous; setae minute, pale. Base without marginal bead. *Elytra:* Surface with moderate to moderately large, shallow punctures, rows only weakly indicated, setigerous; setae short, moderate in density, pale. Epipleuron (ventral view) in females enlarged into angled prominence at level of abdominal sternites 2-3, lateral edge of elytra immediately above that abruptly enlarged into short, subtriangular flange (Fig. 351). *Pygidium:* Surface roughened (not in females), punctate (punctures often obscured by surface roughness in males); punctures moderate in density, small in males, small to moderately large in females, setigerous; setae moderate in length and density, sparser and usually shorter in females, pale. In lateral view, surface in males convex (especially in apical third), weakly convex in females. *Legs:* Foretibia tridentate, basal tooth removed from others in both sexes. Foretarsus in males enlarged: tarsomere 4 with subtriangular expansion on venter; tarsomere 5 enlarged, curved, concave ventrally; median claw large, curved, with lobe at base, apex cleft. Foretarsus in females simple. Posterior tarsus a little longer than posterior



Figs. 347-350. *Cyclocephala pan*: (347-348) elytral pattern variation; (349-350) parameres.



Fig. 351. *Cyclocephala pan*, left epipleuron (ventral view) of female.

tibia in males, subequal in length in females. *Venter*: Prosternal process moderate in length, columnar, apex obliquely flattened into transverse oval with raised, transverse "button" on anterior half. *Parameres*: Figs. 349-350.

DISTRIBUTION. *Cyclocephala pan* is known from scattered localities in Costa Rica, Panama, and Guatemala (NEW COUNTRY RECORD).

LOCALITY RECORDS (Figs. 352-353). 50 specimens examined.

COSTA RICA (20). ALAJUELA (3): Bijagua, Cerro Campana (E side Volcán Cacao), San Ramon; GUANACASTE (5): Estación Pitilla; HEREDIA (2): Estación El Ceibo; LIMÓN (10): Estación Hitoy Cerere, Sector Cerro Cocori.

PANAMA (30). BOCAS DEL TORO (5): 2 mi N Continental Divide on Hwy to Chiriqui Grande; COLÓN (4): Maria Chiquita (6 km E), Santa Rita Ridge; PANAMA (20): Cerro Azul, Cerro Campana, Cerro Jefé, El Llano-Carti Road (km 8, 9, 12); SAN BLAS (1): San Blas Nusagandi (2 km W).

TEMPORAL DISTRIBUTION. January (6), March (6), April (10), May (9), June (12), July (6), September (1).

DIAGNOSIS. In Endrödi's (1985a) synopsis, *C. pan* will key to couplet 269 leading to either *C. sexpunctata* or *C. pubescens* (= *C. brevis* here). The form of the parameres and generally smaller size will distinguish the males of *C. pan*. The apex of the clypeus is more emarginate in *C. pan*, but this may be difficult to ascertain without authoritatively

identified comparative material. I cannot find a reliable way to separate females from those of *C. sexpunctata* and *C. brevis* other than their smaller size (an unreliable and overlapping character state). *Cyclocephala pan* never has black spots on the pronotum, whereas this is variable in *C. sexpunctata*; therefore, if the pronotum has spots or maculae, then it is not *C. pan*. Similarly, some females of *C. pan* may have a black spot on abdominal sternites 1-5 in the posterolateral angle; therefore, if it has these spots it is either *C. pan* or *C. zodion*, but not *C. sexpunctata* or *C. brevis*.

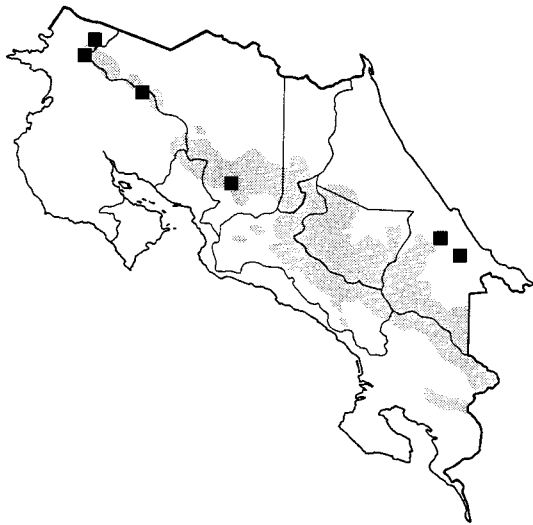


Fig 352. Distribution of *Cyclocephala pan* in Costa Rica.

Cyclocephala pan also closely resembles *C. zodion*. Males can be recognized by the different form of the parameres as well as by the absence (in *C. pan*) of black maculae on the pronotum. Females of *C. pan* are distinguished from *C. zodion* by the absence of pronotal maculae and by the dentiform dilation of the lateral edge of the elytra at the level of abdominal sternites 2-3 (as opposed to the elongate, lobe-like expansion at the level of sternite 1 in *C. zodion*).

BIOLOGY. This species has been collected from tropical moist forests, tropical wet forests, premontane moist forests, and premontane wet forests at elevations of 140-1,680 meters.

***Cyclocephala pardolocarnoi*
Dechambre, 1995**
(Figs. 354-360)

Cyclocephala pardolocarnoi Dechambre 1995:
12.

DESCRIPTION. Length 14.6-19.6 mm; width 7.3-8.3 mm. Color testaceous except for black vertex (remainder of head often dark reddish brown), 2 longitudinally parallel bands on pronotum, extreme base and suture of elytra, 3 spots on elytra (subtriangular postscutellar spot, elongate humeral spot, and

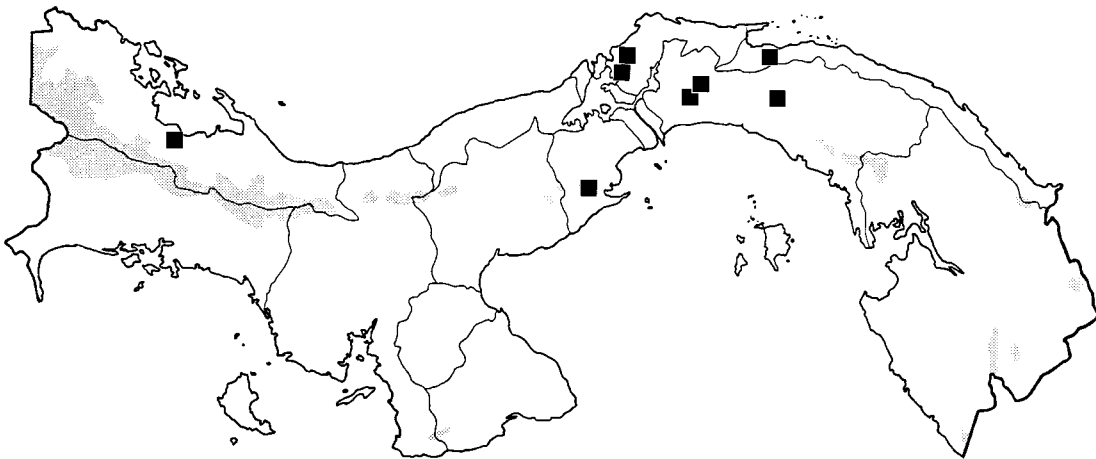


Fig. 353. Distribution of *Cyclocephala pan* in Panama.

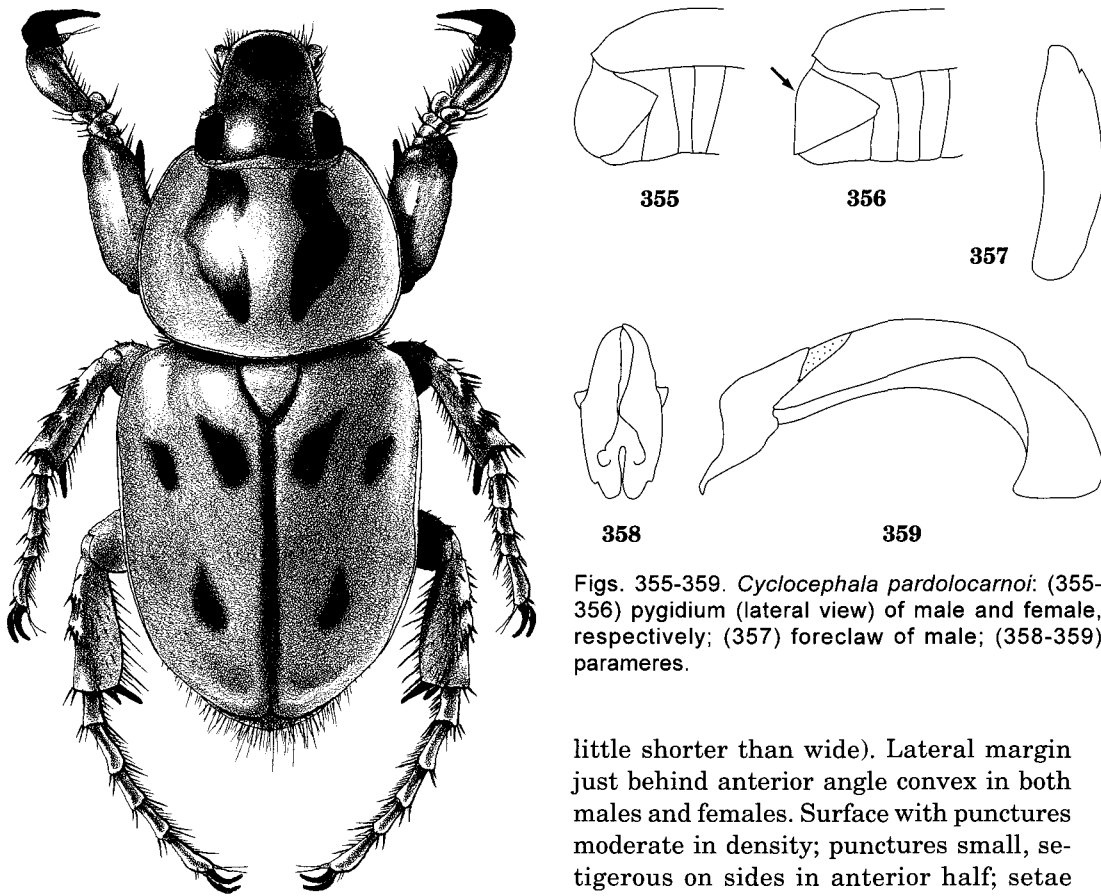
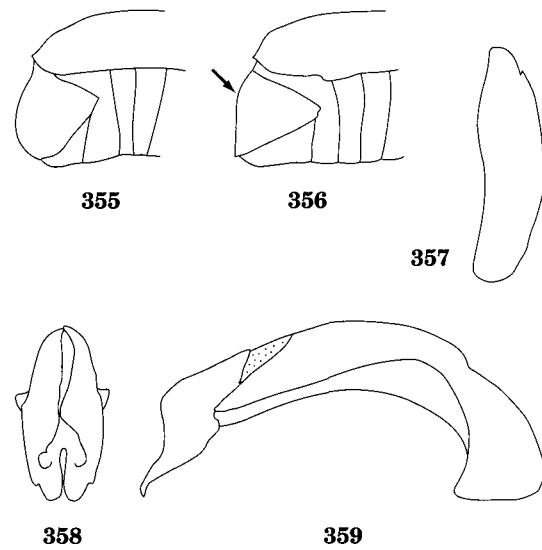


Fig. 354. *Cyclocephala pardolocarnoi*.

elongate preapical spot; lateral spots sometimes fused into elongate and slightly oblique band; all spots maybe variably reduced or even absent), elytral flange in female, and extreme apices of tibiae and femora. **Head:** Frons and basal half of clypeus with small to moderately-sized punctures, punctures moderate in density; apical half of clypeus indistinctly roughened or finely scabrous. Head slightly elongate. Length (measured from occiput to clypeal apex) about 1/3 longer than width (measured across base of clypeus). Clypeus with apex convexly rounded or parabolic and with thick marginal bead. Interocular width equals 3.0-3.6 transverse eye diameters. Antenna with 10 segments, club subequal to or slightly shorter than segments 2-7. **Pronotum:** Pronotum slightly elongate (a



Figs. 355-359. *Cyclocephala pardolocarnoi*: (355-356) pygidium (lateral view) of male and female, respectively; (357) foreclaw of male; (358-359) parameres.

little shorter than wide). Lateral margin just behind anterior angle convex in both males and females. Surface with punctures moderate in density; punctures small, setigerous on sides in anterior half; setae minute to short, stout, tawny in color. Base with marginal bead. **Elytra:** Surface with punctures moderate in density, small to moderate (mostly females) in size, shallow, double rows often indistinct in males. Minute to small, stout setae present either side of suture and usually on sides (in apical half) and apices of elytra. Epipleuron (ventral view) in females gradually and slightly expanded to level of sternite 4 where abruptly constricted; just behind and above this, lateral edge of elytron with strong flange; in lateral view, flange on elytral margin strongly emarginate; in dorsal view, flange appears as elongate, swelling with a subacute to tooth-like posterior edge. **Pygidium:** Surface in males with small, moderately dense, setigerous punctures; setae long, moderately dense, tawny. In lateral view, surface in males strongly convex (Fig. 355), females with weak tumescence just above middle (Figs. 356). **Legs:** Foretibia bidentate in males, tridentate in

females. Foretarsus in males enlarged: tarsomeres 2-4 each slightly larger than preceding segment; 4th with ventral, subtriangular lobe and with round, deep pit on inner surface; 5th large, slightly bent, without ventral lobe or tooth; median claw large, strongly bent ($\sim 80^\circ$), widest at middle (Fig. 357) and weakly lanceolate, apex split into main claw and a very short and slender ramus (often worn down to a small bump or sometimes completely effaced). Foretarsus in females simple. Posterior tarsus about twice as long as posterior tibia. *Venter*: Prosternal process long, conical (tapered to a narrow, rounded point). *Parameres*: Figs. 358-359.

DISTRIBUTION. *Cyclocephala pardolocarnoi* was described from Colombia (Dechambre 1995), and the records below for Panama are a NEW COUNTRY RECORD. This lowland species seems widely distributed in Panama although I have relatively few records. It is likely there are additional specimens in collections that I have not seen that have been incorrectly identified as *C. variabilis* or *C. stictica*.

LOCALITY RECORDS (Fig. 360). 28 specimens examined.

PANAMA (28). BOCAS DEL TORO (11): Miramar; CANAL ZONE (15): Barro Colorado Island, Madden Dam, Pipeline Road (km 2.4,

km 9); PANAMA (2): El Llano-Carti Road (km 8, km 9).

TEMPORAL DISTRIBUTION. January (1), May (6), June (9), July (12).

DIAGNOSIS. *Cyclocephala pardolocarnoi* is vaguely reminiscent of *C. prolongata* and very similar in external appearance to *C. variabilis*. In the males, *C. pardolocarnoi* may be distinguished from *C. prolongata* primarily by their shorter heads (about 1/3 longer than width at base of clypeus; head nearly twice width in *C. prolongata*). The parameres are nearly identical except that, in lateral view, the "crest" is lower in *C. pardolocarnoi* (Figs. 359, 370). Females of *C. prolongata* are easily distinguished because they possess a prominent, conical tubercle just above the middle of the pygidium whereas *C. pardolocarnoi* have a low tumescence.

The best characters for separating males of *C. pardolocarnoi* from *C. variabilis* are the form of the enlarged protarsal claw (widest near the middle and weakly lanceolate in shape in *C. pardolocarnoi* (Fig. 357), and with sides subparallel and arcuate in *C. variabilis* (Fig. 427) and the form of the parameres. Females may be readily distinguished by the swollen tumescence on the pygidium (Fig. 356) and the subangulate or toothed flange on the lateral margin of the elytra in *C. pardolocarnoi*, and the simple pygidium and

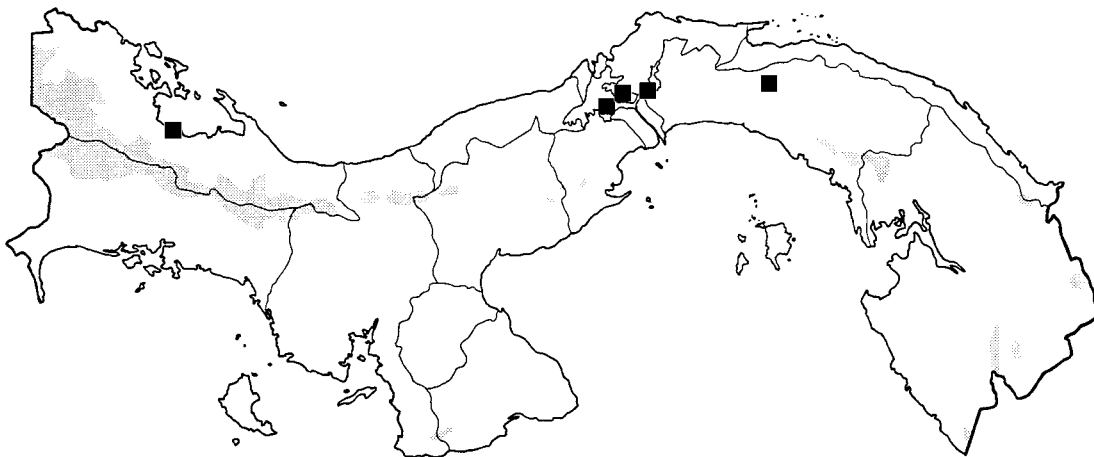


Fig. 360. Distribution of *Cyclocephala pardolocarnoi* in Panama.

simple (non-toothed) flange on the lateral margin of the elytra in *C. variabilis*.

BIOLOGY. *Cyclocephala pardolocarnoi* is known from lowland tropical moist forests at elevations of less than 500 meters.

***Cyclocephala porioni* Dechambre,
1979**
(Figs. 361-365)

Cyclocephala porioni Dechambre 1979a: 317.

DESCRIPTION. Length 14.8-21.7 mm; width 7.0-10.5 mm. Color of frons between eyes piceous; remainder of head, pronotum, scutellum, pygidium, and usually legs dark reddish brown; elytra testaceous with black, elongate triangle behind scutellum (rarely absent) and 4 small, black spots in an arc at base and on disc (rarely last 2 spots enlarged and connected, sometimes spots reduced in size or even absent). Sometimes basal spot fused with post-scutellar triangle. **Head:** Frons with punctures moderate in density and size, punctures occasionally large (in largest specimens), remainder of head roughened or rugopunctate. Clypeus with sides strongly arcuate, apex broadly truncate with 3 shallow emarginations, slightly reflexed. Interocular width equals 2.8-3.0 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. **Pronotum:** Surface with punctures moderate in size and density, punctures usually becoming slightly larger and denser on sides. A faintly impressed, median, longitudinal sulcus usually present. Base without marginal bead. **Elytra:** Surface with rows of punctures; punctures in striae and intervals moderately large to large. Epipleuron (ventral view) of females simple for its entire length, not enlarged. **Pygidium:** Surface shagreened with small to moderately-sized punctures; punctures sparse to more usually moderate in density, surface setigerous at apex; setae short and moderate in length, pale, often worn off. In lateral view, surface in males regularly convex, weakly convex in females. **Legs:** Foretibia tridentate, basal tooth small and

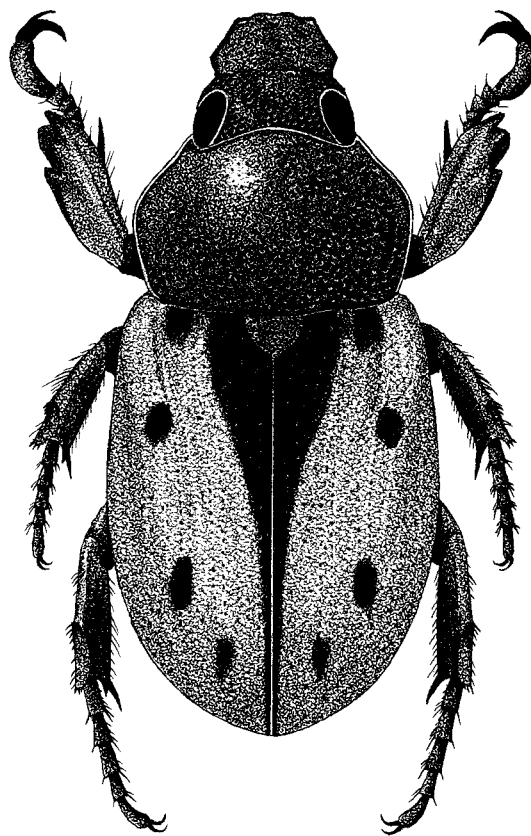
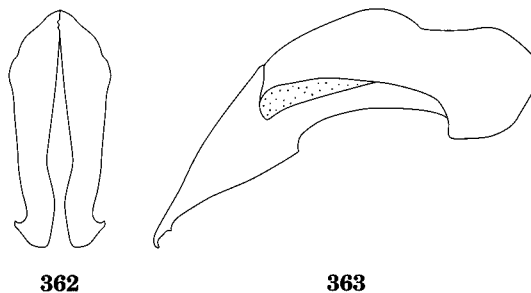


Fig. 361. *Cyclocephala porioni*.



Figs. 362-363. *Cyclocephala porioni* parameres.

removed from others, median tooth broad. Foretarsus in males enlarged: tarsomeres 2-4 each a little larger than one preceding and with ventral angulation; 5th large, curved, with strong tooth ventrally at base; median claw large, curved, split at apex. Foretarsus in females simple. Posterior tarsus subequal in length to posterior tibia. **Venter:** Prosternal process moderate in length, columnar, apex obliquely flattened into broadly transverse

oval with raised "button" on anterior 1/3 to 1/2. *Parameres*: Figs. 362-363.

DISTRIBUTION. *Cyclocephala porioni* is known from Costa Rica, Panama, Nicaragua, Honduras, and Ecuador (Ratcliffe 1992). In Costa Rica and Panama, it is found at mid-elevations throughout both countries. Further collecting in the Darien of Panama may yet reveal populations living there.

LOCALITY RECORDS (Figs. 364-365). 305 specimens examined.

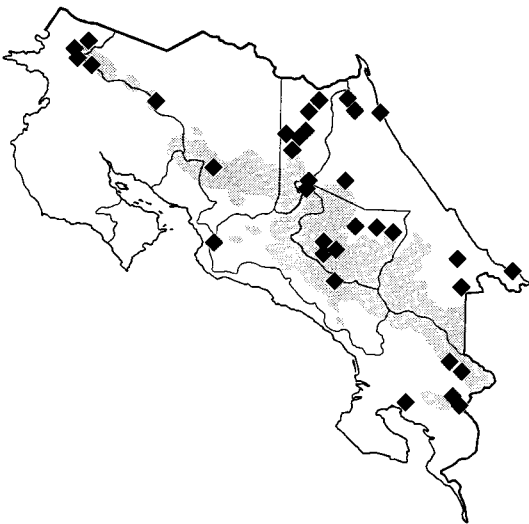


Fig. 364. Distribution of *Cyclocephala porioni* in Costa Rica.

COSTA RICA (181). ALAJUELA (8): Finca San Gabriel (2 km SW Dos Rios), Río San Lorencito; CARTAGO (19): Embalse El Llano, Grano de Oro, Moravia, Orosi, Turrialba, Tuis; GUANACASTE (36): Estación Cacao, Estación Maritza, Estación Pitilla, Finca Montezuma (Volcán Tenorio); HEREDIA (56): Estación El Ciebo, Estación Magsasay, Finca La Selva, Los Arbolitos; LIMÓN (48): Amubri, Cerro Tortuguero, Estación Hitoy Cerere, Guapiles, Manzanillo, Río Sardinas, Sector Cerro Cocori; PUNTARENAS (11): Buenos Aires, Estación Altamira, Estación Esquinas, Estación La Escuadra, San Vito; SAN JOSÉ (3): Division, Estación Bijagual, Estación Carrillo.

PANAMA (124). BOCAS DEL TORO (2): Miramar, just N of Divide on highway to Chiriqui Grande; CANAL ZONE (3): Ciricito, Pipeline Road; CHIRIQUI (26): Boquete, Finca La Suiza, Fortuna Dam, Hartmann's Finca, Windy Pass (7 km N Los Planes); COLÓN (26): Maria Chiquita (6 mi E), Santa Rita Ridge; DARIEN (2): Cana; PANAMA (65): Cerro Azul, Cerro Campana, Cerro Jefe, El Llano-Carti Road (km 8, km 11)..

TEMPORAL DISTRIBUTION. January (1), February (3), March (5), April (7), May (94), June (74), July (26), August (1), September (6), October (3), November (4).

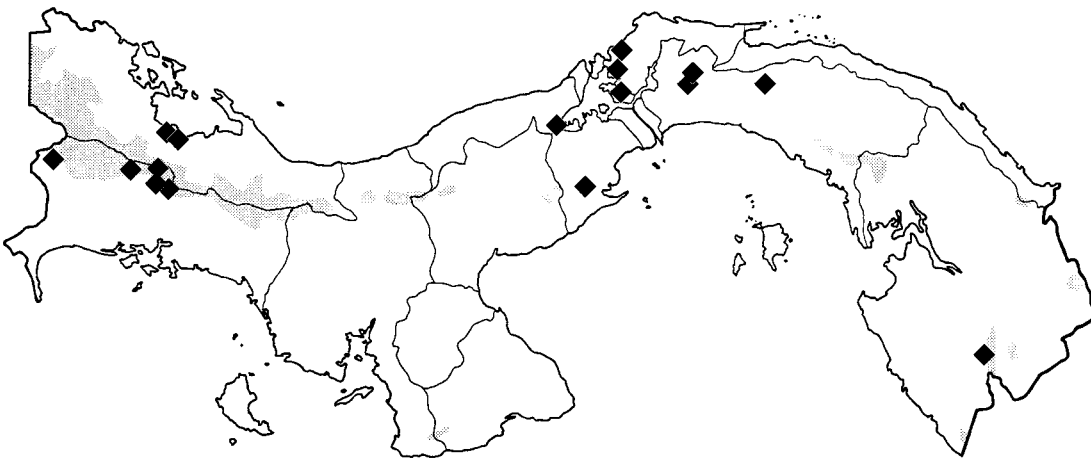


Fig. 365. Distribution of *Cyclocephala porioni* in Panama.

DIAGNOSIS. *Cyclocephala porioni* is unique among the Central American species of *Cyclocephala* because of its tri-emarginate clypeal apex. It is also unusual because it has three, very large, curving teeth on the maxilla. Lastly, the body has a reddish brown pronotum and is distinctively marked with a large, elongate, black triangle on the testaceous elytra.

This species was described by Dechambre (1979) based on three specimens from the eastern side of the Andes between Baeza and Tena in the state of Napo in Ecuador. It resembles closely Brazilian *C. fulvipennis* Burmeister in color, pattern, and the trilobed clypeal apex. It is significantly different from *C. fulvipennis* in the shape of the parameres and the unmargined base of the thorax. Any specimens from Central America that have been previously identified as *C. fulvipennis* are probably *C. porioni*. For those using Endrödi's (1985a) key to the species of *Cyclocephala*, this species will key out to *C. fulvipennis*, but this species is from Ecuador, Brazil, and Bolivia.

BIOLOGY. Adults are attracted to lights at night. They have been collected in tropical moist forests, tropical wet forests, premontane moist forests, premontane wet forests, and premontane rain forests at elevations from near sea level to 1,720 meters.

***Cyclocephala prolongata* Arrow,
1902**

(Figs. 366-370)

Cyclocephala prolongata Arrow 1902: 140.

DESCRIPTION. Length 14.5-21.4 mm; width 6.3-9.3 mm. Color testaceous except for black vertex (remainder of head often dark reddish brown), 2 longitudinally parallel bands on pronotum, extreme base and suture of elytra, 3 spots on elytra (subtriangular postscutellar spot, elongate humeral spot, and elongate preapical spot; lateral spots sometimes fused into elongate and slightly oblique band; all spots variably reduced or even absent), elytral flange in female, and extreme

apices of tibiae and femora. **Head:** Frons and basal half of clypeus with small to moderately-sized punctures, punctures moderate in density; apical half of clypeus indistinctly roughened or scabrous. Head very elongate, length (measured from occiput to clypeal apex) nearly twice that of width (measured across base of clypeus). Clypeus with apex convexly rounded or parabolic and with thick marginal bead. Interocular width equals 3.3-4.0 transverse eye diameters. Antenna 10-segmented, club slightly shorter than segments 2-7. **Pronotum:** Pronotum very elongate (a little longer than wide). Lateral margin just behind anterior angle straight to weakly convex in male, distinctly concave in female. Surface with punctures moderate in density; punctures small, setigerous on sides in anterior half; setae minute to short, stout, tawny in color. Base with marginal bead. **Elytra:** Surface with punctures moderate in density, small to moderate (mostly females) in size, shallow, double rows often indistinct in males. Minute to small, stout setae present either side of suture and usually on sides (in apical half) and apices of elytra. Epipleuron (ventral view) in females gradually and slightly expanded to level of sternite 4 where abruptly constricted; just behind this, lateral edge of elytron with strong flange; in lateral view, flange on elytral margin strongly emarginate; in dorsal view, flange appears as an elongate, swollen tumescence with subacute to tooth-like posterior edge. **Pygidium:** Surface in males with small, moderately dense, setigerous punctures; setae long, moderately dense, tawny. Surface in females indistinctly roughened or with minute, moderately dense, setigerous punctures either side of middle; setae minute, tawny. In lateral view, surface in males strongly convex, females with large, conical tubercle in center just above middle (Fig. 367). **Legs:** Foretibia bidentate in males, tridentate in females. Foretarsus in males enlarged (Fig.): tarsomeres 2-4 each slightly larger than preceding segment; 4th with ventral, subtriangular lobe and with round, deep pit on inner surface (Fig. 368); 5th large, slightly bent, without ventral lobe or tooth; median claw large, strongly bent (~ 80°), apex split and with a very short and slender ramus

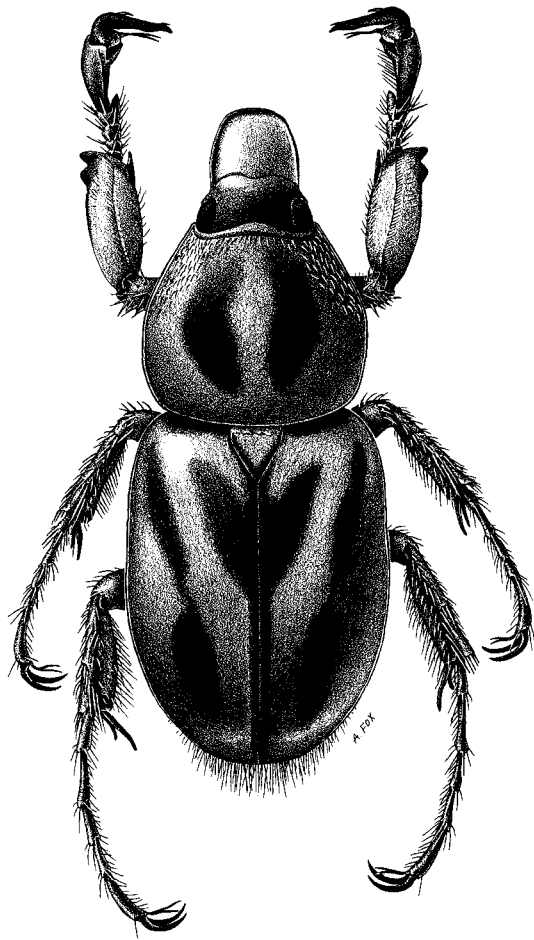
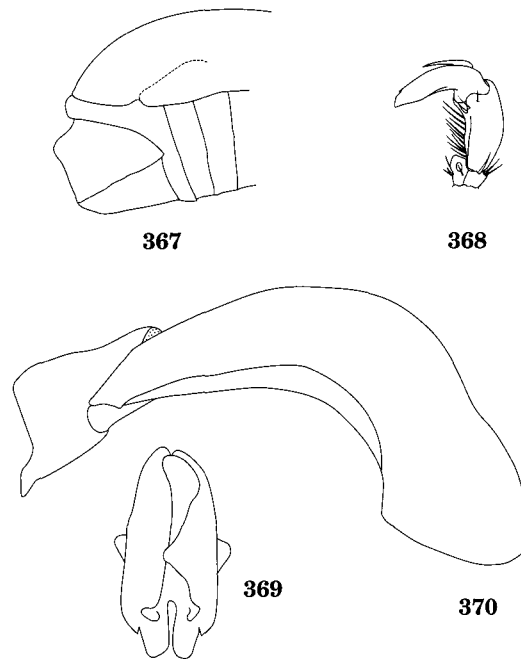


Fig. 366. *Cyclocephala prolongata*.

(often worn down to a small bump or sometimes completely effaced). Foretarsus in females simple. Posterior tarsus about twice as long as posterior tibia. *Venter*: Prosternal process long, setose, conical (tapered to narrow, rounded point). *Parameres*: Figs. 369-370.

DISTRIBUTION. *Cyclocephala prolongata* is known from Mexico, Belize, Nicaragua, Honduras, Colombia, Peru (Blackwelder 1944; Endrödi 1966, 1985a), and Panama (Ratcliffe 1992). The specimens listed below for Costa Rica and specimens from Guatemala in the U.S. National Museum represent **NEW COUNTRY RECORDS**. In Costa Rica and Panama, this species is a rarely encountered lowland species.



Figs. 367-370. *Cyclocephala prolongata*: (367) pygidium (lateral view) of female; (368) foreclaw of male; (369-370) parameres.

LOCALITY RECORDS (Fig. 371-372). 49 specimens examined.

COSTA RICA (39). **HEREDIA** (2): Río Frio; **LIMÓN** (27): Amubri, Cerro Tortuguero, Estación Cuatro Esquinas, Sector Cerro Cocori, Suretka, Valle La Estrella; **PUNTARENAS** (1): Estación Sirena.

PANAMA (10). **CANAL ZONE** (8): Barro Colorado Island, Madden Dam, Pavone Hill (Ft. Sherman), Pipeline Road (km 2); **PANAMA** (2): El Llano-Carti Road (km 13).

TEMPORAL DISTRIBUTION. February (1), March (4), April (3), May (9), June (9), July (16), August (2), September (1), October (3), December (1).

DIAGNOSIS. *Cyclocephala prolongata* has a distinctive appearance because of its unusually elongated head and pronotum. Only *C. pardolocarnoi*, slightly less elongated and with similar markings, could be confused with *C. prolongata* (although *C. variabilis* also has

similar markings). With these two species, it is the males that can be difficult to tell apart whereas the females are easily separated. In *C. prolongata* males, the length of the head (occiput to clypeal apex) is about twice that of the width (measured across the base of the clypeus); in the males of *C. pardolocarnoi*, the length of the head is only about 1/3 longer than the width. While the parameres of both species are nearly identical, those of *C. prolongata* (in lateral view) have a higher and

more angulate "crest" (Figs. 370, 359). Females of *C. prolongata* have a large, conical tubercle on the pygidium whereas *C. pardolocarnoi* has, at most, a low convexity. In addition, females of *C. prolongata* have the lateral margin of the pronotum just behind the anterior angle distinctly concave whereas this margin in *C. pardolocarnoi* is slightly convex.

BIOLOGY. Adults are attracted to lights. They have been collected from tropical moist forests and tropical wet forests at elevations ranging from near sea level to 200 meters.

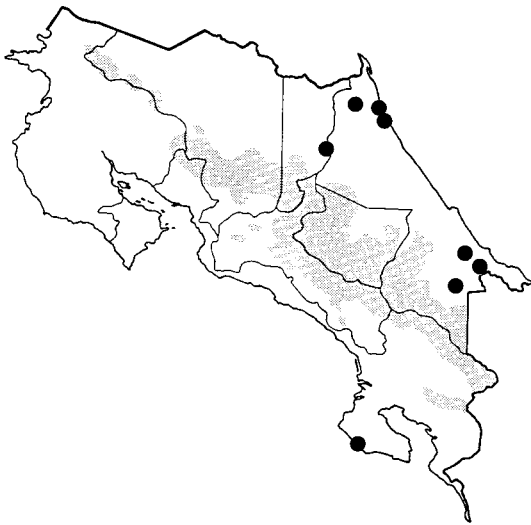


Fig. 371. Distribution of *Cyclocephala prolongata* in Costa Rica.

Cyclocephala quadripunctata
Höhne, 1923
 (Figs. 373-376)

Cyclocephala quadripunctata Höhne 1923b:
 348.

DESCRIPTION. Length 9.8-11.4 mm; width 4.8-5.5 mm. Color testaceous with piceous to black frons; some specimens with indistinct (most common) to distinct (uncommon) piceous smudges on elytra on humerus and on center of disc just behind middle. *Head:* Surface of frons and clypeus moderately densely punctate; punctures moderately large, setigerous; setae short, pale. Clypeus with apex

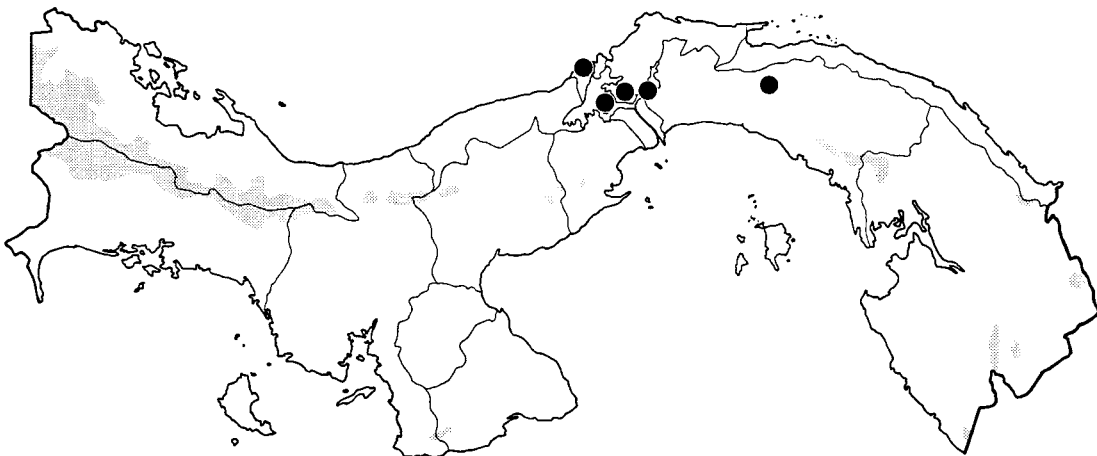


Fig. 372. Distribution of *Cyclocephala prolongata* in Panama.

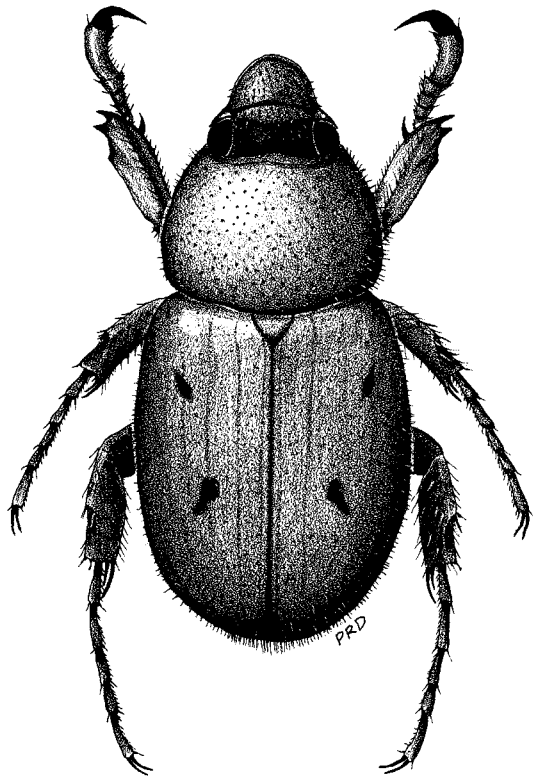
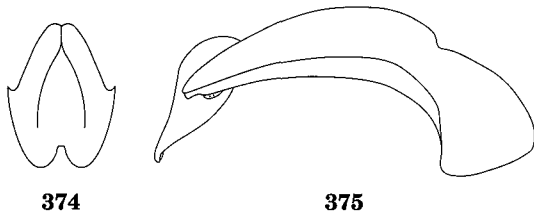


Fig. 373. *Cyclocephala quadripunctata*.



Figs. 374-375. *Cyclocephala quadripunctata* parameres.

parabolic and with marginal bead. Interocular width equals 3.0 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. *Pronotum*: Surface with punctures moderate in density, moderately large, setigerous; setae short, pale. Base lacking marginal bead. *Elytra*: Surface finely shagreened, moderately densely punctate; punctures small, not in distinct rows, setigerous; setae short, pale. *Epipleuron* (ventral view) in females in ventral view gradually expanded to level of abdominal sternites 4-5 where abruptly narrowed; elytral margin at same level swollen into elongate lobe. *Pygidium*: Surface sparsely punctate; punctures small, setigerous; setae moderate in length, pale. In lateral view, surface in both sexes weakly convex. *Legs*: Foretibia in males with 2 apical teeth close together and with a dilation in place of third tooth; foretibia in females with 3 equidistant teeth. Foretarsus in males enlarged: tarsomere 4 triangularly expanded ventrally; tarsomere 5 enlarged, weakly curved, longitudinal carina present on inner surface; median claw large, with basal lobe, apex entire. Foretarsus in females simple. Posterior tarsus much longer than posterior tibia. *Venter*: Prosternal process short, small, conical. *Parameres*: Figs. 374-375.



Fig. 376. Distribution of *Cyclocephala quadripunctata* in Panama.

DISTRIBUTION. *Cyclocephala quadri-punctata* is known from South America (Endrödi 1966, 1985a) and the eastern half of Panama (Ratcliffe 1992b).

LOCALITY RECORDS (Fig. 376). 26 specimens examined.

PANAMA (26). CANAL ZONE (24): Albrook Forest, Pipeline Road (km 2.4); DARIEN (2): Cana.

TEMPORAL DISTRIBUTION. January (1), February (2), April (2), May (6), June (3), July (3), December (1).

DIAGNOSIS. This species is recognized by its small size, parabolic clypeus, small prosternal process, dorsal setae, males with basically a bidentate foretibia and with the apex of the large claw of the protarsus entire, form of the male parameres, and by the posteriorly placed swelling of the epipleuron/elytral margin in the females (level of abdominal sternites 4-5).

BIOLOGY. Adults are attracted to lights at night. Specimens have been collected from tropical moist forests and subtropical wet forests at elevations of near sea level to 460 meters.

***Cyclocephala rogezi* Dechambre, 1992**

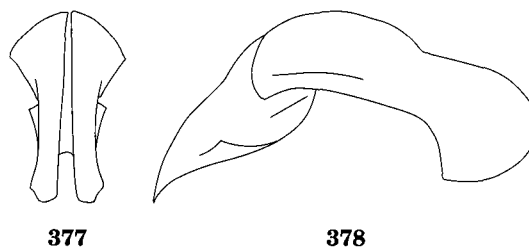
(Figs. 377-379)

Cyclocephala rogezi Dechambre 1992a: 70.

DESCRIPTION. Length 28.5-30.0 mm; width 15.0-16.0 mm. Color of head, pronotum, scutellum, elytral suture, humeri, pygidium, venter, and legs black;; elytra dark testaceous and female with longitudinal black area on sides of elytra just behind middle. *Head:* Frons with dense, moderately large punctures, most punctures with short, testaceous setae; surface either side of center with small, round area where punctures and setae denser, smaller. Clypeus with surface transversely rugopunctate to rugose and with small, testaceous setae on sides; apex broadly rounded

either side of weak, median emargination. Interocular width equals 2.5 transverse eye diameters. Antenna with 10 segments, club slightly longer than segments 2-7. *Pronotum:* Surface shining, smooth, with sparse micropunctures over nearly entire surface except for sides near margin where punctures moderately large, setose; setae short, testaceous, often abraded away. Base with complete marginal bead. *Elytra:* Surface vaguely micropunctate under low magnification; densely punctate under high magnification with small and minute punctures mixed. Epipleuron in female feebly expanded to level of third sternite where abruptly constricted; lateral margin of elytron swollen above level of abdominal sternites 1-2. *Pygidium:* Surface with sparse micropunctures, basal half with long, dense, tawny setae. In lateral view, surface in female nearly flat, strongly convex in apical third (male not seen). *Legs:* Foretibia tridentate, teeth subequally spaced. Foretarsus in males enlarged: tarsomere 5 long, curved; median claw large, curved, apex finely cleft; foretarsus in females simple. *Venter:* Prosternal process short, apex expanded into large, transverse oval with transverse, raised "button" on anterior three-fourths; shaft on posterior side with long, dense setae. *Parameres:* Figs. 377-378.

DISTRIBUTION. *Cyclocephala rogezi* was described from four specimens from the Cauca valley in Colombia. The Panamanian specimen reported here is a NEW COUNTRY RECORD. The question remains as to whether this species actually occurs in



Figs. 377-378. *Cyclocephala rogezi* parameres.



Fig. 379. Distribution of *Cyclocephala rogezi* in Panama.

Panama (mislabelled specimen?) or whether it might have been accidentally transported from Colombia on one of the many ships traversing the Panama Canal. It seems unusual to me that additional specimens of one of the largest species in the genus would not have been collected during the past several decades of sampling in Panama were it still extant there. The single Panamanian female was collected in 1961.

LOCALITY RECORDS (Fig. 379). 1 specimen examined.

PANAMA (1). PANAMA (1): Panama City.

TEMPORAL DISTRIBUTION. August (1). The three Colombian paratypes were also collected in August.

DIAGNOSIS. *Cyclocephala rogezi* is easily distinguished from all other Mesoamerican *Cyclocephala* species because of its large size and distinctive coloration. Only immaculate forms of *C. mafaffa* approach this size and coloration, but they do not have a shiny black pronotum, and the male parameres are different.

BIOLOGY. The Panama specimen was collected in an area of (former) tropical moist forests at an elevation near sea level.

Cyclocephala sanguinicollis
Burmeister, 1847
(Figs. 380-383)

Cyclocephala sanguinicollis Burmeister 1847: 49.
Homochromina divisa Casey 1915: 163 (synonym).
Homochromina politicauda Casey 1915: 164 (synonym).

DESCRIPTION. Length 14.4-17.4 mm; width 8.3-8.9 mm. Color of head, pronotum, scutellum, pygidium, venter, and legs dark cherry red to castaneous; elytra testaceous. *Head:* Frons moderately to moderately densely punctate, punctures small. Clypeus transversely rugulose, extreme base often punctate like clypeus; apex bluntly parabolic, barely reflexed. Interocular width equals 2.3 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. *Pronotum:* Surface at middle with small, sparse punctures; disc and sides with punctures moderate to moderately large, moderate in density. Base without marginal bead. *Elytra:* Surface minutely shagreened, punctate; punctures moderate to moderately large, moderate in density, some in distinct rows. Epipleuron (ventral view) of females gradually expanded beginning at level of sternite 1, abruptly narrowed at level of sternite 2 with nearly right-angled tooth on mesal edge and

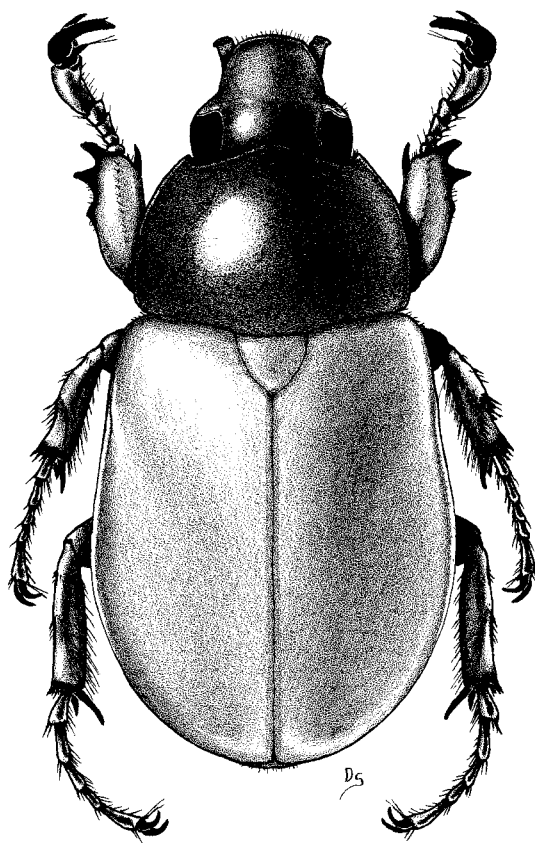
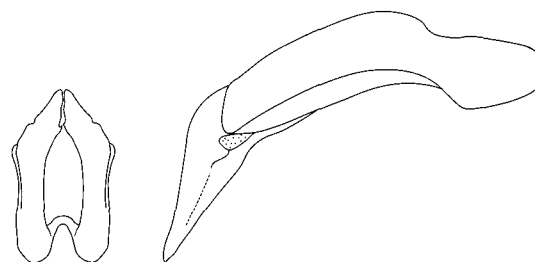


Fig. 380. *Cyclocephala sanguinicollis*.



381

382

Figs. 381-382. *Cyclocephala sanguinicollis* parameres.



Fig. 383. Distribution of *Cyclocephala sanguinicollis* in Costa Rica.

short flange on lateral edge. *Pygidium*: Surface sparsely to moderately punctate, punctures minute to small. In lateral view, surface regularly convex in males, weakly convex in females. *Legs*: Foretibia tridentate, teeth subequally spaced. Foretarsus in males enlarged: tarsomeres 2-4 slightly expanded ventrally; 5th large, curved, median edge cariniform; median claw large, strongly curved, base with large, rounded lobe, apex cleft. Foretarsus in females simple. Posterior tarsus slightly longer than posterior tibia in males; subequal in length in females. *Venter*: Prosternal process moderately long, columnar, apex expanded into obliquely flattened oval with anterior half raised into transversely oval "button." *Parameres*: Figs. 381-382.

DISTRIBUTION. *Cyclocephala sanguinicollis* is known from Mexico to Costa Rica. Endrödi's (1966, 1985a) records for South America probably refer to *C. mutata* because Endrödi mixed both of these species under the heading of *C. sanguinicollis*. This species is known from only a few localities in Costa Rica at nearly opposite ends of the country. It is not known from Panama.

LOCALITY RECORDS (Fig. 383). 28 specimens examined.

COSTA RICA (28). **CARTAGO** (7): Chirripo Indian Reservation (5 mi SE Moravia), Chirripo Valley (30 mi SE Turrialba), Grano de Oro; **GUANACASTE** (6): Estación Cacao, Estación

Mengo; LIMÓN (2): Reserva Biologica Hitoy Cerere; PUNTARENAS (13): Las Alturas.

TEMPORAL DISTRIBUTION. January (1), February (1), March (4), April (12), May (6), June (4)..

DIAGNOSIS. *Cyclocephala sanguinicollis* was described from Mexico. While its overall form, including male parameres, is similar to that of *C. mutata*, it is a distinctively bicolored species with a dark cherry red head and pronotum whereas *C. mutata* has a monochromatic, testaceous color on the dorsal surface. In addition, the distinctive swelling on the venter of the large protarsal claw in males of *C. mutata* is absent in *C. sanguinicollis*, and the punctures on the pronotum of *C. sanguinicollis* are usually slightly larger and denser than those of *C. mutata*. Lastly, the relative width of the foretibia in *C. sanguinicollis* is not as wide as that seen in *C. mutata*.

NOMENCLATURE. *Cyclocephala mutata* and its synonyms, as listed by Endrödi (1966, 1985a), are removed from synonymy with *C. sanguinicollis* because they represent a different species. In most collections of Costa Rican and Panamanian material, *C. sanguinicollis* is the name that has been given to the monochromatic *C. mutata*.

BIOLOGY. Adults are attracted to lights at night. They have been collected from tropical moist forests, tropical wet forests, and premontane rain forests at elevations of 100-1,500 meters.

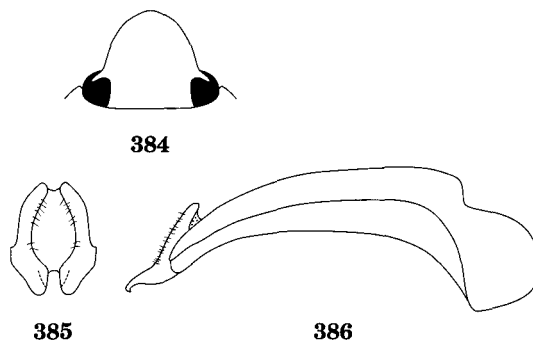
***Cyclocephala santaritae* Ratcliffe,
1992**

(Figs. 384-387)

Cyclocephala santaritae Ratcliffe 1992: 229.

DESCRIPTION. Length 12.2-13.6 mm; width 5.5-6.6 mm. Color testaceous; elytra usually with small, dark spot behind scutellum and another on disc behind middle, occasionally with spot behind humerus, spots

variably reduced to absent (rare). **Head:** Surface completely, densely punctate; punctures small, separated from one another by 1-2 puncture diameters. Clypeus (Fig. 384) with apex parabolic, narrowly rounded and reflexed. Interocular width equals 3.0-3.6 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. **Pronotum:** Surface weakly shining, moderately densely punctate (slightly less so along midline), punctures small. Base with marginal bead. **Elytra:** Surface weakly shagreened with small to moderate, shallow punctures, double rows barely distinguishable. Sides and apical fifth with sparse, short, pale setae. Epipleuron (ventral view) of females becoming gradually arcuate at level of abdominal sternites 1-2 and gradually narrowing at posterior edge of sternite 2; in lateral view, epipleuron nearly simple; in dorsal view, edge of elytron with flange-like, darkened swelling at about middle. **Pygidium:** Surface densely punctate, punctures small. Males with long, dense, pale setae; females lacking setae. In lateral view, surface in males convex (especially apically), nearly flat in females. **Legs:** Foretibia in males bidentate, tridentate in females. Foretarsus in males enlarged: tarsomere 5 with large tooth at base on ventral side and with strong, longitudinal carina on median edge; median claw large, curved, base on ventral side with large lobe,



Figs. 384-386. *Cyclocephala santaritae*: (384) head; (385-386) parameres.

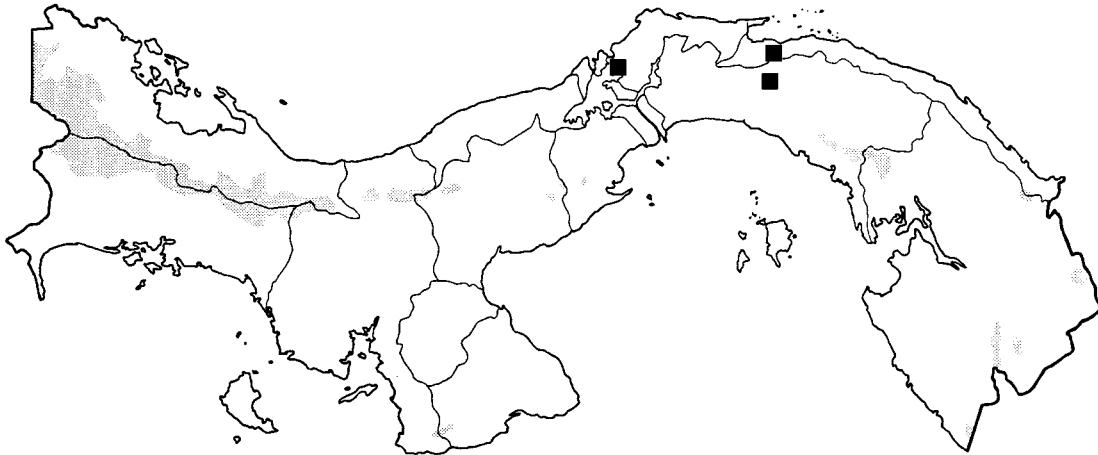


Fig. 387. Distribution of *Cyclocephala santaritae* in Panama.

apex of claw entire. Foretarsus in females simple. Posterior tarsus about 1.6 times longer than posterior tibia. *Venter*: Prosternal process a short, transverse lobe. *Parameres*: Figs. 385-386.

DISTRIBUTION. *Cyclocephala santaritae* is known only from the easternmost fringes of the Serranía de San Blas just to the east of the former Canal Zone in Panama. The remainder of this small mountain range, as well as the Serranía del Darién that is an extension of it, may also be home to this species. Interestingly, I also have nearly a dozen specimens from several sites along the Río Napo in Ecuador (Jatun Sacha Biological Station, Misahualli Jungle Lodge, Amangu) that seem to be conspecific. While there are small differences in the apex of the clypeus and on the epipleural flange in the females, they are similar in all other respects to the Panamanian specimens. This seems to be another instance of a disjunct Ecuadorian/Panamanian or Costa Rican distribution observed during this study. Jameson (1998) also observed this in *Rutela* species (Scarabaeidae: Rutelinae).

LOCALITY RECORDS (Fig. 387). 8 specimens examined.

PANAMA (8). **COLÓN** (1): Santa Rita Ridge; **PANAMA** (6): El Llano-Carti Road (km 8, km 9); **SAN BLAS** (1): Nusagandi.

TEMPORAL DISTRIBUTION. May (7), June (1).

DIAGNOSIS. This species has an overall similarity to *C. herteli* in coloration and body form and will key to this species in Endrödi (1985a). However, *C. santaritae* has elytral spots, a setose pygidium in males, a narrowly parabolic clypeal apex, a barely developed prosternal process, and a gradually arcuate, simple epipleural expansion in the females; *C. herteli*, conversely, has elytral streaks, a glabrous pygidium in males, a broadly rounded clypeal apex, a well-developed (although not long) prosternal process, and a tooth-like epipleural expansion in the females. Additionally, the tooth at the base of the male 5th protarsomere is very large in *C. santaritae* and much smaller in *C. herteli*. Moreover, the male parameres are very different (Figs. 385-386, 244-245).

BIOLOGY. Adults are attracted to lights at night. *Cyclocephala santaritae* is known from tropical moist forests at elevations of 300-500 meters.

Cyclocephala sexpunctata
Laporte, 1840

(Color Plate 2, Figs. 388-399)

- Cyclocephala sexpunctata* Laporte 1840: 125.
Cyclocephala pubescens Erichson 1847: 96
 (synonym).
Cyclocephala lucida Burmeister 1847: 67
 (synonym).
Cyclocephala sexpunctata spermophila Ohaus
 1910: 671 (synonym, described as subspecies).
Stigmalia triangulifer Casey 1915: 120 (synonym).
Stigmalia discoidalis Casey 1915: 120 (synonym).
Stigmalia costaricana Casey 1915: 121 (synonym).
Stigmalia circulifer Casey 1915: 121 (synonym).
Cyclocephala pubescens nigripes Höhne
 1923b: 372 (synonym, described as subspecies).

DESCRIPTION. Length 17.5-22.4 mm; width 9.1-11.4 mm. Color testaceous with black markings as follows: frons black; Costa Rican and Panamanian populations (Fig. 389, first 4 images) lack pronotal markings (one Costa Rican specimen with pronotum entirely dark brown), populations from Mexico to Honduras and also Venezuela with small to large, subtriangular or comma-shaped patch either side of midline (Fig. 389); elytra highly variable: without any markings (uncommon) or with single post-scutellar spot (rare) or with 4 small to large spots in an arc on each elytron (post-scutellar, post-humeral, on lateral edge of disc just behind middle, and on disc behind middle) (most common) or spots very large (especially post-scutellar) and variably connected (2 posterior spots, 2 lateral spots, or all spots) (infrequent); bases and apices of femora and tibiae and tarsomeres piceous. **Head:** Frons and base of clypeus with moderately large punctures; punctures moderate in density, setigerous (when not worn off); setae short, moderate in density, tawny. Clypeus transversely rugose except on punctate base; apex broad, weakly (but distinctly) emarginate. Interocular width equals 3.0-3.3 trans-

verse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. **Pronotum:** Surface with moderately large punctures; punctures on central third sparse, becoming moderately dense on lateral thirds, setigerous (when not worn off); setae short, moderate in density, tawny. Base lacking marginal bead. **Elytra:** Surface finely shagreened, with small punctures; punctures sparse on disc, becoming dense on sides (rows indistinct), setigerous (when not worn off); setae short, moderately dense, tawny. Epipleuron (ventral view) of females abruptly expanded into short, rounded flange on lateral edge and with obtuse tooth on mesal edge at level of abdominal sternites 1-2; lateral edge of elytron above flange slightly swollen. **Pygidium:** Surface finely shagreened, punctate; punctures in males moderate in size and density, setigerous (when not worn off); setae moderately dense, long, tawny; punctures in females moderately large (slightly larger than those in males), setigerous with numerous minute punctures intermixed, lateral corners becoming finely roughened; setae moderate in density and length, tawny. In lateral view, surface in males convex, especially in apical third; females with surface flat, becoming strongly convex only at apex. **Legs:** Foretibia tridentate, basal tooth strongly removed. Foretarsus in males enlarged: protarsomere 4 subtriangularly expanded on venter; 5th large, curved, nearly flat on venter; median claw large, strongly bent, with large, narrow lobe at base, apex cleft. Foretarsus in females simple. Posterior tarsus a little longer than posterior tibia. **Venter:** Prosternal process moderately long, columnar, apex obliquely flattened into strongly transverse oval with raised "button" on anterior 1/2-2/3. **Parameres:** Figs. 390-397.

DISTRIBUTION. *Cyclocephala sexpunctata* is broadly distributed from Mexico to Brazil, Colombia, Peru, Ecuador, and Bolivia (Endrödi 1966). Of the hundreds of specimens studied from Mesoamerica, nearly all were collected above 1,000 meters in elevation; only a few were collected just below this altitude. The smaller number of South American specimens available to me do not seem to be largely

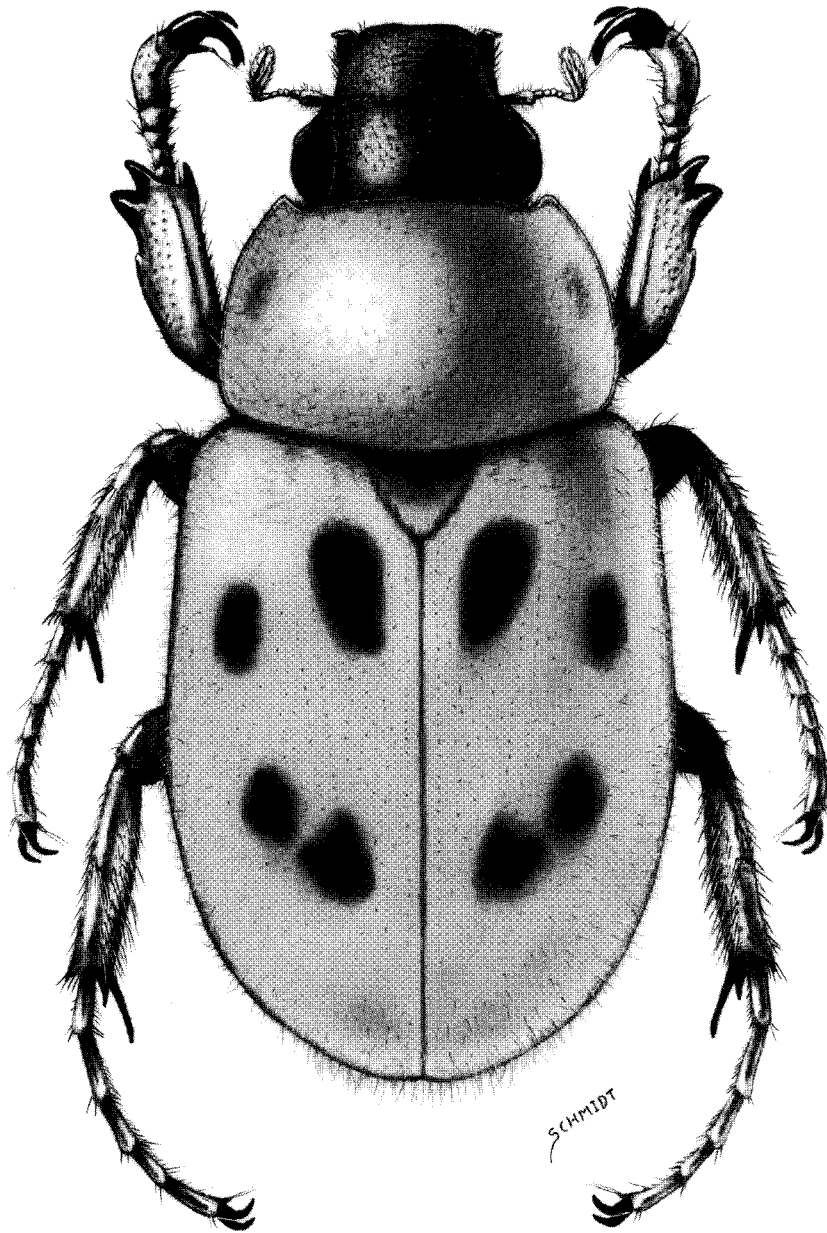
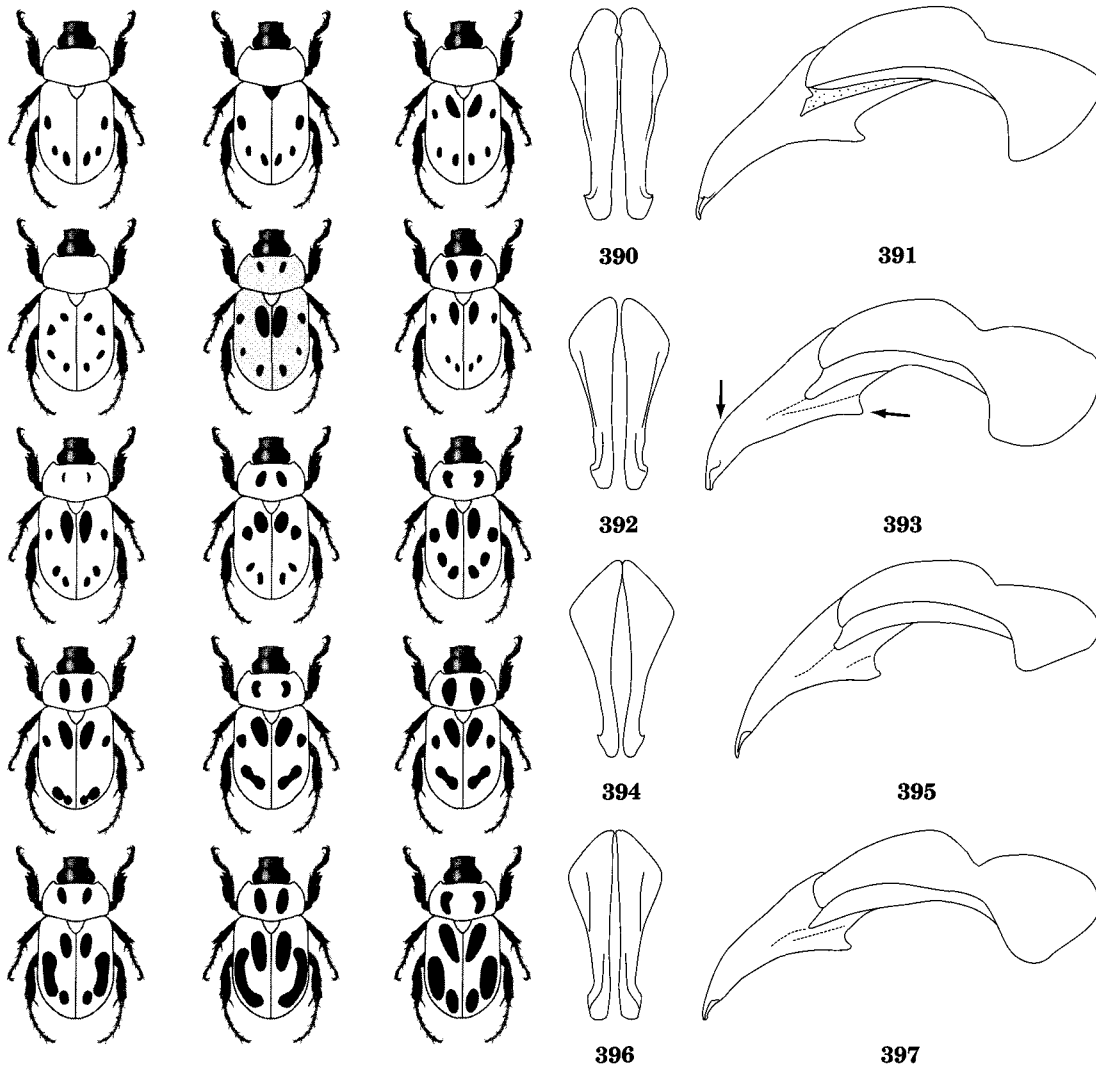


Fig. 388. *Cyclocephala sexpunctata*.

restricted to locales above 1,000 meters, but I believe that I have not seen enough specimens to establish a clear pattern. This species is broadly distributed in Costa Rica and Panama in the Cordillera Central.

LOCALITY RECORDS (Figs. 398-399). 438 specimens examined.

COSTA RICA (243). ALAJUELA (27): Atenas (8 km W), Estación Eladios, Estación Laguna Pocosol, San Ramon; CARTAGO (44): Chirripó Indian Reservation, Reserva Tapanti, Volcán Irazú (SE side); GUANACASTE (92): Estación Cacao, Estación Maritza, Estación Pitilla, Tierras Morenas; HEREDIA (2): Bajos del Toro Amarillo, El Plástico; PUNTARENAS (61):



Figs. 389. *Cyclocephala sexpunctata* showing variation in pronotal and elytral markings. From García-Luna *et al.* (2002) (used by permission).

Figs. 390-397. *Cyclocephala sexpunctata* parameres showing variation: (390-391) Santa Clara, Panama; (392-393) Estacion Cacao, Costa Rica; (394-395) Estacion Las Mellizas, Costa Rica; (396-397) Monteverde, Costa Rica.

Estación Las Alturas, Mellizas, Monteverde, Río Canasta, San Vito; SAN JOSÉ (17): Estación Carrillo, Estación Zurquí, San José.

PANAMA (195). BOCAS DEL TORO (3): Continental Divide trail; CHIRIQUI (175): Bambito, Boquete, Cerro Punta, Continental Divide trail, Finca La Suiza, Fortuna Dam, Hartmann's Finca (Santa Clara), IRHE Vivero (11 km N Los Planes); COCLÉ (4): El Valle; PANAMA (13): Cerro Jefé.

TEMPORAL DISTRIBUTION. January (21), February (8), March (21), April (15), May (127), June (88), July (63), August (8), September (48), October (7), November (23), December (7).

DIAGNOSIS. *Cyclocephala sexpunctata* closely resembles *C. letiranti* and *C. brevis*. Reliable identification is possible only by examining the male parameres, although *C. letiranti* has clypeal characters that will dis-

tinguish it. The parameres of *C. sexpunctata* (in lateral view) are distinctly bent for their entire length and remain thick to the apex (Figs. 391, 393, 395, 397) whereas those of *C. brevis* are nearly straight in their apical half and with a slender apex (Figs. 152, 154, 156). In caudal view, the apices of both are subtriangular but are broadly rounded to nearly blunt in *C. sexpunctata* (Figs. 390, 392, 394, 396) and narrowly rounded to almost pointed (Fig. 151) or narrow and elongated with an elongated, subtriangular apex (Fig. 153, 155) in *C. brevis*. The parameres of *C. letiranti* (Fig. 267-268) are very different and have an elongated, rectangular apex.



Fig. 398. Distribution of *Cyclocephala sexpunctata* in Costa Rica.



Fig. 399. Distribution of *Cyclocephala sexpunctata* in Panama.

In Costa Rica and Panama, both sexes of *C. sexpunctata* can be "spot-identified" in most instances by their larger size and larger elytral spots in combination with being collected above 700 (usually 1,000) meters in elevation. *Cyclocephala brevis* is generally smaller, with smaller elytral spots (or absent), and generally found at elevations of less than 1,000 meters. *Cyclocephala letiranti* is distinguished (in both sexes) by the black triangle at the base of the clypeus (Fig. 266) as well as by a punctate clypeus (as opposed to mostly rugose in the other related species). Females (except *C. letiranti*) cannot be reliably distinguished from one another, especially since they are sometimes sympatric in an elevational zone of overlap. Occasionally, however, such as at Hartmann's Finca in Chiriqui, Panama, both *C. sexpunctata* and *C. brevis* occur together at 1,350 meters in elevation. At this particular location, however, they can be easily separated by size and markings. Size, markings, elevation, and collected in association with identifiable males may work for placing females.

Populations of *C. sexpunctata* occurring from Mexico to Honduras and those from Venezuela usually have larger elytral spots as well as a subtriangular or comma-shaped, black patch on the pronotum either side of the middle. Burmeister (1847) used the name *C. lucida* for this form, and Endrödi (1966) referred to this morph as an aberration. Interestingly, this morph does not occur in Costa Rica or Panama even though it is present to the north and south.

All specimens in various private and institutional collections with my determinations of *C. sexpunctata* and *C. pubescens* made before 2002 should be re-evaluated using the new key in this work.

BIOLOGY. Adults are attracted to lights at night. Label data indicate adults have been collected in the inflorescences of *Xanthosoma* species (Araceae) in Costa Rica (Color Plate 1), and Morón (1997b) found adults feeding on the inflorescences of *X. hoffmanni* Schott, *X. mexicanum* Liebm., *X. robustum* Scott, and *X. violaceum* Schott in Chiapas, Mexico.

They have been collected from tropical wet forests, premontane moist forests, premontane wet forests, premontane rain forests and lower montane rain forests at elevations of 700-1,520 meters; most specimens were collected above 1,000 meters.

***Cyclocephala sororia* Bates, 1888**
(Figs. 400-405)

Cyclocephala sororia Bates 1888: 303.

DESCRIPTION. Length 16.0-17.6 mm; width 8.7-9.4 mm. Color testaceous except for black on frons and occiput, apices of femora and tibiae. *Head:* Frons with surface sparsely punctate, punctures moderate in size. Clypeus with surface finely rugulose and punctate, punctures small and dense; apex weakly parabolic, reflexed, margin beaded. Interocular width equals 2.0-2.2 transverse eye diameters. Antenna with 10 segments, club slightly longer than segments 2-7. *Pronotum:* Surface sparsely punctate in male, slightly denser in female; punctures small to mostly moderate in size, usually slightly larger in female. Base with marginal bead, bead sometimes obsolete at center. *Elytra:* Surface with distinct rows of punctures forming striae and with randomly arranged punctures in intervals, especially first; punctures moderate to large, shallow. Epipleuron (ventral view) of females weakly thickened at level of metacoxae. *Pygidium:* Surface finely shagreened (more so in lateral corners) with sparse, minute punctures; base with a few

small, pale setae, pristine specimens with similar setae on disc and apex. In lateral view, surface in males convex, surface in females flat to weakly convex. *Legs:* Protibia tridentate in both sexes, teeth subequally spaced. Foretarsus in males enlarged: segments 2-4 each slightly larger than preceding segment; 5th large, curved, with strong, longitudinal carina on median surface and large tooth on venter at apex (Fig. 401); median claw large, strongly curved, with large, rounded process at base, apex narrowly cleft (Fig. 402). Foretarsus in females simple. Posterior tarsus slightly longer than posterior tibia. *Venter:* Prosternal process long, columnar, setose, apex obliquely flattened into suboval disc with anterior 1/2-2/3 elevated into a raised "button." *Parameres:* Figs. 403-404.

DISTRIBUTION. *Cyclocephala sororia* is known from southern Mexico to Costa Rica (Endrödi 1966, 1985a). In Costa Rica, this species is found primarily in the northwest part of the country.

LOCALITY RECORDS (Fig. 405). 135 specimens examined.

COSTA RICA (135). CARTAGO (1): Refugio Nacional Tapanti; GUANACASTE (107): Estación Las Pailas, Estación Pitilla, Parq. Nac. Santa Rosa, Piedra Negra, Volcán de la Vieja (4.5 km SW); HEREDIA (1): Estación Magsasay; PUNTARENAS (26): Estación La Carona, Estación Las Mellizas, Estación Sirena, Monteverde, San Luis.

TEMPORAL DISTRIBUTION. January (10), April (5), May (3), June (10), July (55), August (23), September (19), October (5), November (1), December (1).

DIAGNOSIS. In overall appearance, *C. sororia* is remarkably similar to *C. mutata* and *C. concolor*. *Cyclocephala sororia* is easily distinguished from *C. concolor* because the clypeal apex is parabolic in *C. sororia* and emarginate in *C. concolor*. Males of *C. sororia* and *C. mutata* are usually easily distinguished by the presence of a pronotal basal bead in *C. sororia* and absence of this bead in

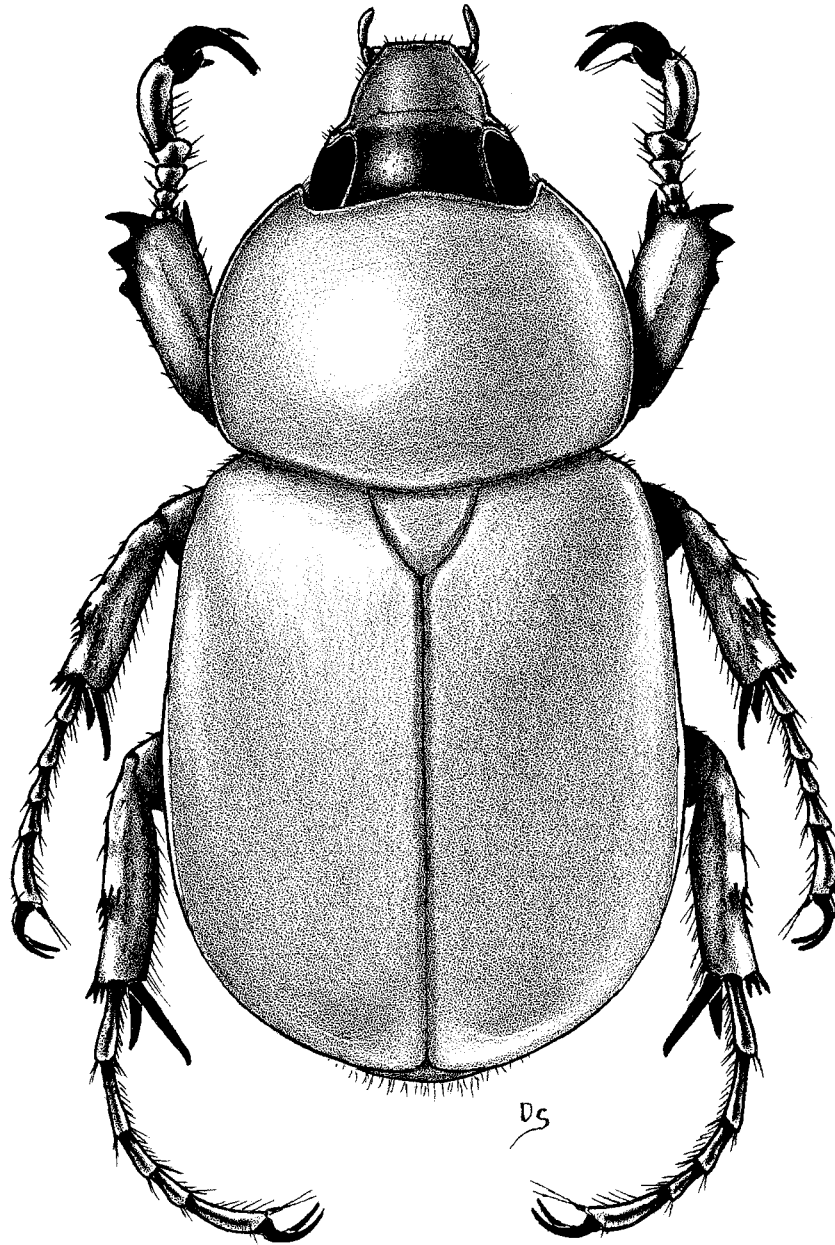
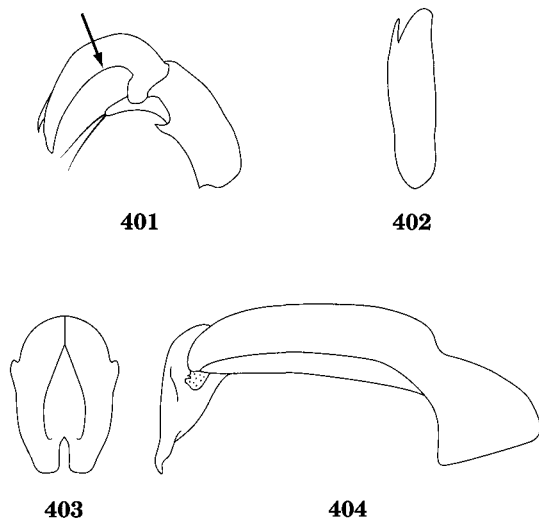


Fig. 400. *Cyclocephala sororia*.

C. mutata. This distinction occasionally becomes blurred when the basal bead is partially obsolete in some specimens of *C. sororia*. In this case, the form of the parameres and enlarged protarsal claw of the males will separate the two species. In addition, the enlarged protarsal claw in males of *C. sororia* is simple on its inner edge (Fig. 401), whereas it is swollen just distad of the basal lobe in *C. mutata*

(Fig. 322). Females of *C. sororia* and *C. mutata* are readily distinguished by the simple epipleuron in *C. sororia* and the lobelike expansion of the epipleuron in *C. mutata*.

BIOLOGY. Adults are attracted to lights at night. They have been collected from pre-montane moist forests and lower montane rain forests at elevations of 240-1,520 meters.



Figs. 401-404. *Cyclocephala sororia*: (401-402) foreclaw of male; (403-404) parameres.



Fig. 405. Distribution of *Cyclocephala sororia* in Costa Rica.

***Cyclocephala sparsa* Arrow, 1902
(Figs. 406-410)**

Cyclocephala sparsa Arrow 1902: 141.

Cyclocephala landini Endrödi 1964: 445 (synonym).

Cyclocephala virkkii Howden and Endrödi 1966: 301 (synonym).

DESCRIPTION. Length 12.5-14.0 mm; width 7.6-8.4 mm. Color testaceous with

highly variable piceous or black markings. Head usually completely dark, occasionally clypeus testaceous. Pronotum completely testaceous to speckled with black spots to completely black. Elytra testaceous with small, black spot on disc behind humerus, on disc behind middle, and on disc just behind and mesad of posterior spot; or as above but with small to large (usual) black spot immediately behind scutellum; or densely speckled with black spots; or completely black. Legs and venter vary from completely testaceous to piceous or black. *Head*: Frons moderately densely punctate, punctures moderate in size. Clypeus transversely rugopunctate to rugose; apex nearly semicircular. Interocular width equals 2.5-2.7 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. *Pronotum*: Surface similar to frons: moderately densely punctate, punctures moderate in size, setose in unworn specimens; setae moderately dense (except when abraded away), very short, pale. Base lacking marginal bead. *Elytra*: Surface finely shagreened, setigerous, moderately densely punctate, punctures small; striae not evident; setae moderately dense, very short, pale. Epipleuron (ventral view) in females weakly thickened at level of abdominal sternites 1-2, abruptly tapering at level of sternite 3. *Pygidium*: Surface in males densely punctate; punctures moderately large, setose; setae dense, short, pale; surface in females similar except punctures less dense. In lateral view, surface in males convex, especially in apical third; females with surface only weakly convex. *Legs*: Foretibia in both sexes tridentate, basal tooth small and strongly removed from others. Foretarsus in males enlarged: tarsomere 5 enlarged, only weakly curved, slightly concave on venter; median claw large, curved, lacking basal lobe, apex strongly split. Foretarsus in females simple. Posterior tarsus slightly longer than posterior tibia. *Venter*: Prosternal process long, columnar, apex obliquely flattened into transverse oval with raised, transverse "button" on anterior half. *Parameres*: Figs. 407-408.

DISTRIBUTION. *Cyclocephala sparsa* is found from Mexico to Panama. It is known

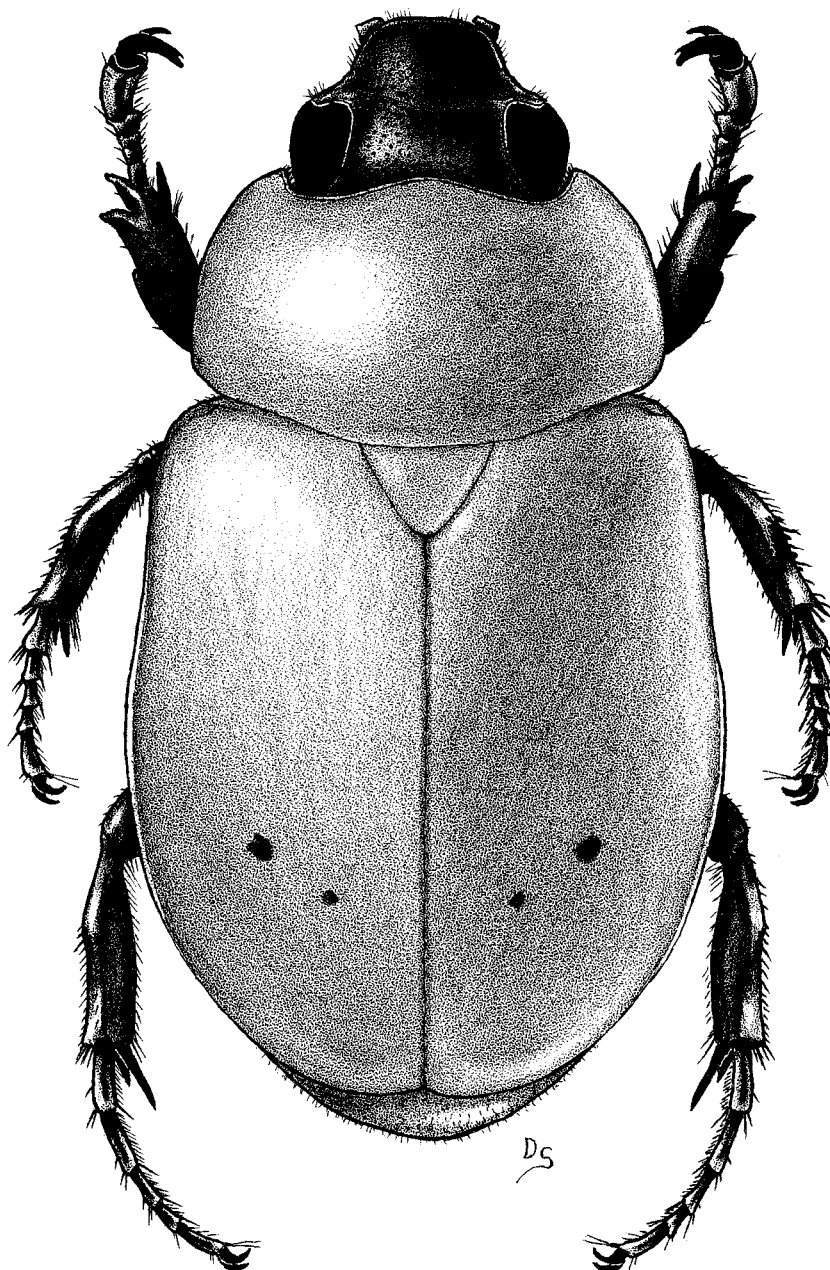
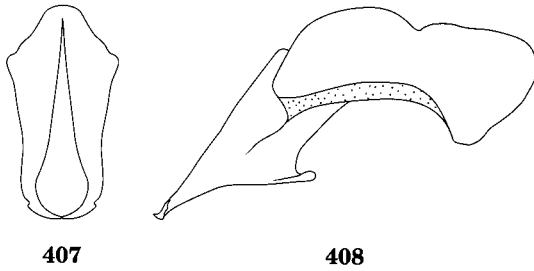


Fig. 406. *Cyclocephala sparsa*.

from a few localities in northern and central Costa Rica and from the former Canal Zone and areas to the immediate east of the Zone in Panama. Its absence from other lowland areas of Panama seems unusual in view of the extensive collecting that has occurred there over the years.

LOCALITY RECORDS (Figs. 409-410). 156 specimens examined.

COSTA RICA (11). **CARTAGO** (1): Chirripó; **GUANACASTE** (1): Tierras Morenas; **HEREDIA** (6): Estación El Ceibo, La Selva Biological Station, Los Arbolitos; **LIMÓN** (2):



Figs. 407-408. *Cyclocephala sparsa* parameres.

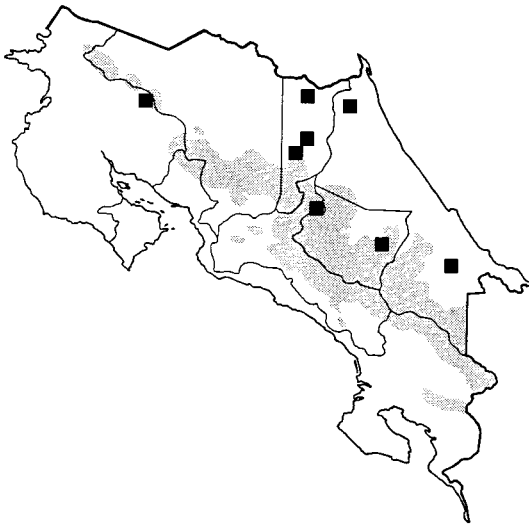


Fig. 409. Distribution of *Cyclocephala sparsa* in Costa Rica.

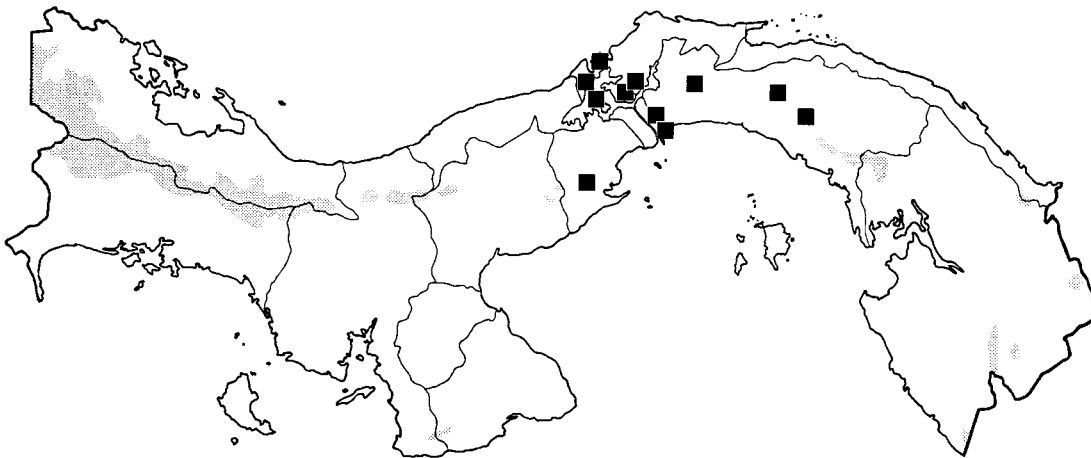


Fig. 410. Distribution of *Cyclocephala sparsa* in Panama.

Cerro Cocori, Estación Hitoy Cerere; SAN JOSÉ (1): Estación Carrillo.

PANAMA (145). **CANAL ZONE** (142): Achiote Road, Albrook Forest, Barro Colorado Island, Coco Solo Hospital, Escobal Road, Ft. Clayton, Gamboa, Las Cumbres, Madden Dam, Pipeline Road (km 2.4), Skunk Hollow; **PANAMA** (13): Altos de Majé, Cerro Azul, Cerro Campana, El Llano-Carti Road (km 8).

TEMPORAL DISTRIBUTION. March (1), April (3), May (96), June (19), July (11), August (7), September (7), October (4), November (1), December (1).

DIAGNOSIS. *Cyclocephala sparsa* is characterized by its distinctive, suboval shape combined with moderately dense punctures over the entire dorsal surface (appearing as a fine roughness), moderately dense and short setae on the pronotum and elytra and pygidium, pronotum lacking a basal bead, and a small and subtruncate to nearly semicircular clypeus. The parameres are also diagnostic.

Cyclocephala sparsa is similar to *C. isthmiensis*. Males can be separated by the spacing of the foretibial teeth (basal tooth strongly removed in *C. sparsa*, almost equidistant in *C. isthmiensis*) and the form of the

parameres (Figs. 407-408, 248-249). Females can be separated based on the form of the expansion of the epipleuron/elytral margin (weakly expanded in *C. sparsa* and simple in *C. isthmiensis*).

Endrödi (1966, 1985a) referred to the speckled form as *C. sparsa*, which is how Arrow (1902) originally described the species (from Mexico). To my knowledge, this morph occurs only in Mexico (Yucatan and the southeast), Honduras, and presumably Guatemala; I have not seen it in Costa Rica or Panama. Occasionally, some Mexican specimens from Chiapas and Veracruz states are entirely black.

NOMENCLATURE. After extensive study of many specimens from Mexico, Costa Rica, and Panama, Ratcliffe and Delgado (1990) concluded that *C. landini* Endrödi and *C. virkkii* Howden and Endrödi are conspecific with *C. sparsa*. All of the specimens formerly assigned to *C. landini* (described from Panama) are testaceous with three to four, usually black, small spots on each elytron; in some specimens the spots are absent while in others there is a large, post-scutellar spot. This morph from Panama and Costa Rica is simply the unspckled form of *C. sparsa*; it is identical to Arrow's speckled *C. sparsa* in all other respects: surface sculpturing, vestiture, form of clypeus, antennae, tibiae, elytra, pygidium, legs, and male parameres.

Cyclocephala virkkii (described from El Salvador) was distinguished from *C. sparsa* and *C. landini* by Howden and Endrödi (1966) primarily by the markings on the pronotum and elytra. Again, a larger sample size of specimens from different localities indicates that this is part of the normal variation seen in *C. sparsa*. The minor differences in the form of the parameres of the three supposed species are also within the range of normal variation for *C. sparsa*.

BIOLOGY. Adults are attracted to lights at night. It is known from tropical moist forests, tropical wet forests, and premontane wet forests, and it has been collected at elevations ranging from near sea level to 1,200 meters.

***Cyclocephala stictica* Burmeister,
1847**

(Figs. 411-415)

Cyclocephala stictica Burmeister 1847: 66.

Cyclocephala sexnotata Burmeister 1847: 67
(synonym).

Cyclocephala microspila Bates 1888: 301
(synonym).

Cyclocephala stictica bilineata Höhne 1923b:
357 (synonym).

DESCRIPTION. Length 12.6-18.4 mm; width 6.2-9.4 mm. Color testaceous except: Head with frons black, clypeus often darkened. Pronotum with 2 longitudinal, broad, black bands, bands sometimes reduced in width, or reduced to 2 small spots either anteriorly or posteriorly, or all markings absent, or (rarely) entire pronotum piceous or black. Elytra usually with 3 black spots, 1 behind scutellum, 1 post-humeral, and 1 on disc just past middle; spots vary from large (twice size of eye) to small to variably obsolete; larger spots often subtriangular, otherwise round or elongate; posterior spot occasionally connected to either anterior spot; elytra totally darkened in 1 melanistic specimen. **Head:** Frons moderately densely punctate, punctures moderate in size (often slightly larger in females). Clypeus rugopunctate to transversely rugulose, margins beaded; apex indistinctly to weakly to moderately emarginate (Fig.), weakly reflexed. Interocular width equals 2.5-3.0 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. **Pronotum:** Surface moderately punctate; punctures moderate in size, usually becoming slightly denser on sides, rarely becoming sparser on sides. Base with marginal bead. **Elytra:** Surface finely shagreened, with moderate to large, shallow punctures; rows vary from indistinct to distinct. Some punctures with short, stout, dark, almost bristle-like setae. Epipleuron (ventral view) in females gradually expanded to level of sternite 2 where it is abruptly constricted; in lateral view, an obtuse tooth present at constriction; elytron with weak, elongate swelling above area of expanded epipleuron.

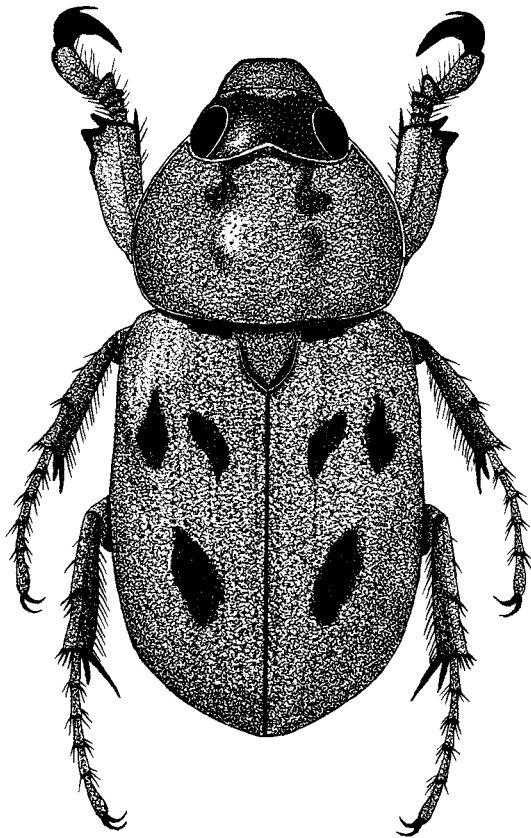


Fig. 411. *Cyclocephala stictica*.

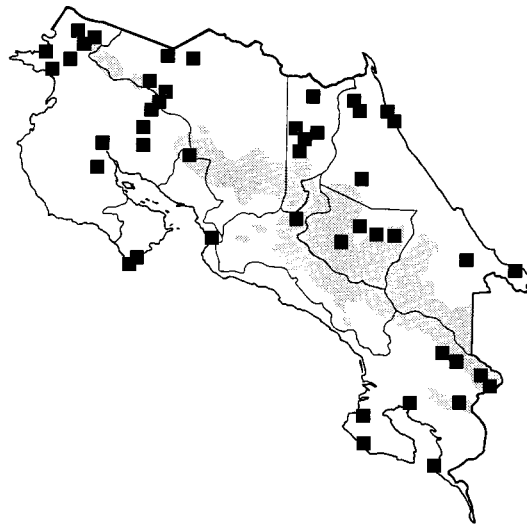
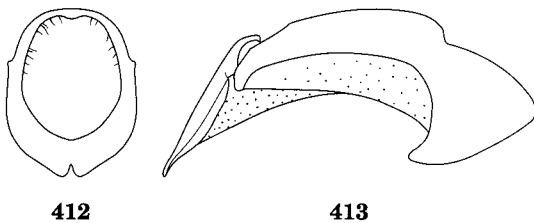


Fig. 414. Distribution of *Cyclocephala stictica* in Costa Rica.

large ventral lobe; 5th large, weakly bent, with longitudinal carina on both inner (mesal) and ventral surfaces; median claw large, strongly curved, apex entire. Foretarsus in females simple. Posterior tarsus much longer than posterior tibia. *Venter*: Prosternal process long, columnar, apex obliquely flattened into transverse oval with elevated, transverse "button" on anterior half. *Parameres*: Figs. 412-413.

DISTRIBUTION. *Cyclocephala stictica* is broadly distributed from Mexico to southern Brazil and Bolivia (Endrödi 1966, 1985a). This species is found throughout most of Costa Rica and Panama.

LOCALITY RECORDS (Figs. 414-415). 975 specimens identified.



412

413

Figs. 412-413. *Cyclocephala stictica* parameres.

Pygidium: Surface with punctures moderate in density and size; males with setae moderate in density, short, pale; females with surface glabrous or with sparse, minute setae. In lateral view, surface in males varies from weakly to strongly convex, females with surface nearly flat. *Legs*: Foretibia bidentate in males, tridentate in females. Foretarsus enlarged in males: tarsomeres 3-4 each with

COSTA RICA (704). **ALAJUELA** (27): Bijagua (Volcán Tenorio), Caño Negro, San Isidro; **CARTAGO** (33): Embalse El Llano, Grano de Oro, Rancho Naturalista, Refugio Nacional Tapanti, Tuis, Turrialba; **GUANACASTE** (222): Cañas, Enrique Jimenes Nuñez Experiment Station (20 km S Cañas), Estación Maritza, Estación Murcielago, Estación Palo Verde, Estación Pitilla, Finca Jenny (30 km N Liberia), Los Almendros, Nacaome (3 km NW), Parq. Nac. Barra Honda, Piedra Negra,

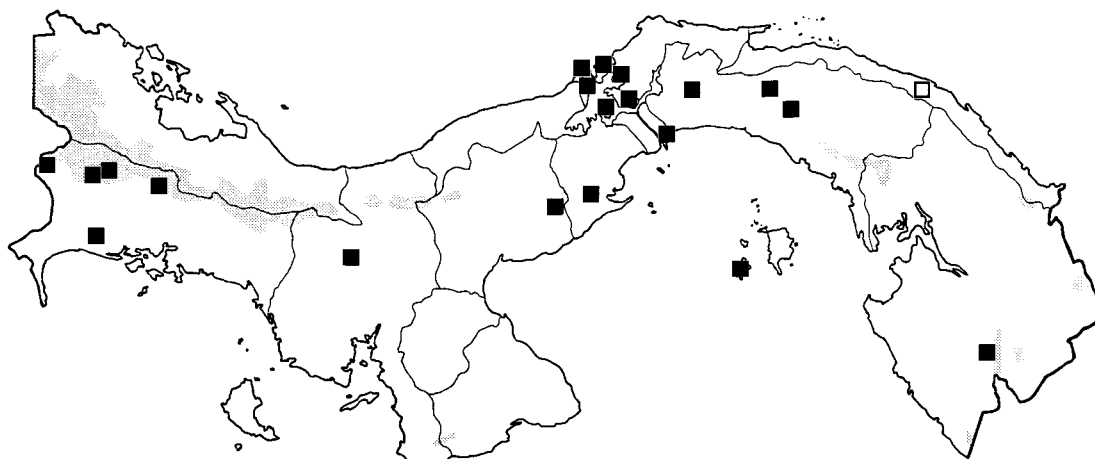


Fig. 415. Distribution of *Cyclocephala stictica* in Panama.

Playa Naranjo, Tierras Morenas; HEREDIA (45): Estación El Ceibo, Estación Magsasay, Finca Naranjo Valenciana (2 km S Pueblo Nuevo), La Selva Biological Station, Los Arbolitos; LIMÓN (88): Cerro Tortuguero, Estación Cuatro Esquinas, Estación Hitoy Cerere, Fila Matama, Guacimo (6 km N), Manzanillo, Río Sardinas, Sector Cerro Cocori; PUNTARENAS (282): Buenos Aires, Estación Esquinas, Estación Las Alturas, Estación Las Mellizas, Estación San Miguel, Estación Sirena, Punta Blanco, Rancho Quemado, Reserva Biológica Carara, Rincon (2.5 m SW), San Vito; SAN JOSÉ (7): San José.

PANAMA (271). CANAL ZONE (117): Achiotte Road, Albrook Forest, Barro Colorado Island, Black Tank Road, Coco Solo Hospital, Gamboa (9 mi NW), Gatun Lake Lookout, Madden Dam, Old Gamboa Road, Pavon Hill (Ft. Sherman), Pipeline Road (km 2, km 4), Skunk Hollow; CHIRIQUI (20): Bugaba, Finca La Suiza, Lino, Río Sereno, Volcán; COCLÉ (3): El Valle; COLÓN (1): Santa Rita Ridge; DARIEN (2): Cana; PANAMA (121): Cerro Azul, Cerro Campana, El Llano (15 km N), El Llano-Carti Road (km 8), Isla Majé, Islas Perlas (San José); SAN BLAS (5): no data; VERAGUAS (2): Cañazas.

TEMPORAL DISTRIBUTION. January (27), February (17), March (10), April (32), May (103), June (145), July (165), August (89), September (55), October (81), November (55), December (41).

DIAGNOSIS. *Cyclocephala stictica* resembles *C. discicollis* except that in *C. stictica* the size is usually larger, the elytron normally has a post-scutellar spot (absent in *C. discicollis*), the clypeus is only weakly emarginate (strongly emarginate in *C. discicollis*; Figs. 411, 202), and the parameres are different (Figs. 412-413, 203-204).

BIOLOGY. Adults are readily attracted to lights, and a few adults have been taken from the flowers of *Bactris wendlandiana* Burret and *B. porschiana* Burret (Arecaceae) and *Annona muricata* L. (Annonaceae) in Costa Rica (Bullock 1981 and specimen label data). Morón (1997b) found adults in the inflorescences of *Xanthosoma hoffmanni* Schott, *X. mexicanum* Liebm., *X. robustum* Schott, and *X. violaceum* Schott (Araceae) in Chiapas, Mexico. They have been collected in tropical dry forests, tropical moist forests, tropical wet forests, premontane wet forests, and premontane rain forests at elevations ranging from near sea level to 1,500 meters.

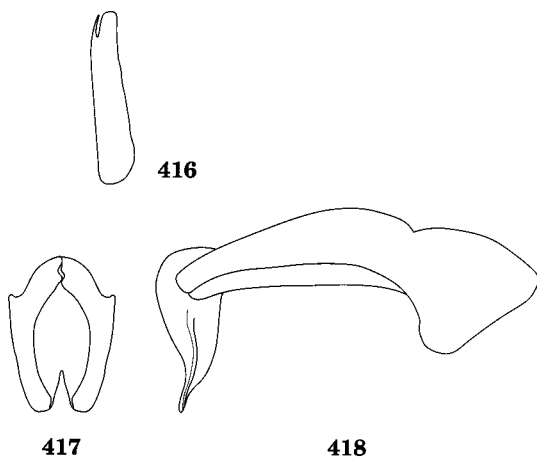
***Cyclocephala stockwelli* Ratcliffe,
new species**
(Figs. 416-420)

TYPE MATERIAL. Holotype, allotype, and two female paratypes labeled "PANAMA: Panama Prov., El Llano-Carti Rd., km 8, N9°16', W78°57', V-23-1995, elev. 1,100', B. Ratcliffe & M. Jameson." One female paratype labeled "PANAMA, Panama Prov., Altos (Isla) de Majé, 9°08'N, 78°49'W, V-14-16-1976, at BL, B. C. Ratcliffe." One additional female paratype with same locality except date of V-28-30-1982 and collectors B. C. Ratcliffe and C. & K. Messenger. Remaining paratypes (27) with the following data: "PANAMA: Panama Prov., El Llano-Carti Rd., 8 km N El Llano, 13 May 1994, BL&MV, DCCarlson/FTHovore" (6 males, 11 females); same data except km 9 and 14 May 1994 (6 males, 4 females); "Est. Magsasay, P. N. Braulio Carrillo, 200 m, Prov. Here, COSTA RICA, M. Zumbado, Dic. 1990, L-N-264600, 531100" (1 male); "Est. Sirena, 0-100 m, P. N. Corcovado, Prov. Puntarenas, Costa Rica, 21 Mar a 21 Abr 1992, Z. Fuentes, L-S 270500, 508300" (1 male); same data but G. Fonseca collector & date of May 1992 (1 male); same data as previous but date of April 1993 (1 male, 3 females); "Fca. Cafrosa, Est. Las Mellizas, P. N. Amistad, 1300 m, Prov. Punt. COSTA RICA, M. Ramirez & G. Mora, May 1990, L-S-316100-596100" (1 male).



Fig. 419. Distribution of *Cyclocephala stockwelli* in Costa Rica.

Holotype, allotype, and 5 paratypes deposited at the University of Nebraska State Museum (Lincoln, NE). Additional paratypes deposited in the following collections: Canadian Museum of Nature (Ottawa) (2 specimens), the Natural History Museum (London) (2 specimens), U. S. National Museum (Washington, D. C.) (2 specimens), Museum National d'Histoire Naturelle (Paris, France) (2 specimens), INBio (Santo Domingo de Heredia, Costa Rica) (6 specimens), Mary Liz Jameson (Lincoln, NE) (2 specimens), David C. Carlson (Fair Oaks, CA) (10 specimens) and Brett C. Ratcliffe (Lincoln, NE) (8 specimens).



Figs. 416-418. *Cyclocephala stockwelli*: (416) foreclaw of male; (417-418) parameres.

HOLOTYPE. Male. Length 14.9 mm; width 7.8 mm. Color of pronotum and elytra testaceous; head, pygidium, legs, and venter light reddish brown; extreme apices of femora and tibia black. *Head:* Frons and basal 2/3 of clypeus with dense, small punctures; apical third of clypeus transversely rugulose. Clypeus with apex bluntly parabolic, margin distinctly beaded and weakly reflexed. Interocular width equals 2.1 transverse eye diameters. Antenna 10-segmented, club slightly longer than segments 2-7. *Pronotum:* Surface on disc with small, sparse punctures, punctures becoming moderate in size and



Fig. 420. Distribution of *Cyclocephala stockwelli* in Panama.

density on sides. Base with weak marginal bead, bead obsolete at middle. *Elytra*: Surface punctate; punctures moderate to moderately large, moderate in density, shallow, distinct rows visible. *Pygidium*: Surface finely roughened, with barely visible moderately dense punctures. In lateral view, surface regularly convex. *Legs*: Foretibia tridentate, basal tooth smaller, subequally spaced from others. Foretarsus enlarged: segments 2-4 each slightly larger than preceding; 4th with subtriangular lobe on venter. 5th large, curved, with strong longitudinal carina on inner edge, outer edge on venter with row of long, stout setae; median claw large, curved, sides of claw (anterior view) narrowing toward apex, apex cleft. Posterior tarsus about 1/3 longer than posterior tibia. *Venter*: Prosternal process short, flattened from front to back, apex weakly, transversely, and obliquely flattened with raised, slightly elongate "button" on anterior 2/3. *Parameres*: Figs. 417-418.

ALLOTYPE. Female. Length 13.7 mm; width 7.8 mm. As holotype except in the following respects: *Head*: Antenna with club subequal in length to stem. *Pronotum*: Sides with punctures slightly larger. *Elytra*: Epipleuron (ventral view) expanded on inner

edge at level of sternite 1, abruptly narrowed at juncture of abdominal sternites 1-2. Lateral margin of elytron expanded into low, elongate lobe above epipleural expansion. *Pygidium*: Surface entirely punctate; punctures small, moderate in density on disc, becoming dense on sides. In lateral view, surface weakly convex. *Legs*: Foretarsus simple. Posterior tarsus subequal in length to posterior tibia.

VARIATION. Males (17 paratypes). Length 13.0-15.5 mm; width 6.3-8.1 mm. The male paratypes do not differ significantly from the holotype. Two specimens have a complete marginal bead on the base of the pronotum.

Females (22 paratypes). Length 12.7-15.1 mm; width 7.2-8.2 mm. The female paratypes do not differ significantly from the allotype. The posterior margin of the pronotum has the marginal bead obsolete, especially at the middle, in most specimens.

ETYMOLOGY. This species is named in honor of Dr. Henry Stockwell, a longtime fellow coleopterist and an outstanding naturalist of the Panamanian biota. Henry provided me with valuable logistical support in Panama over the years as well as numerous specimens from his collection.

DISTRIBUTION. *Cyclocephala stockwelli* is known from the western end of the Serrania de San Blas in Panama province, Panama, and from Costa Rica.

LOCALITY RECORDS (Figs. 419-420). 41 specimens examined.

COSTA RICA (8). HEREDIA (1): Estación Magsasay; PUNTARENAS (7): Estación Las Mellizas, Estación Sirena.

PANAMA (33). PANAMA (33): El Llano-Carti Road (km 8, km 9), Isla de Majé.

TEMPORAL DISTRIBUTION. April (5), May (35), December (1).

DIAGNOSIS. In overall appearance, this species resembles *C. mutata* and *C. sororia*, but it is consistently smaller. It differs further from *C. mutata* in that it may or may not have a marginal bead on the base of the pronotum, whereas *C. mutata* does not; the parameres are also different. Having a pronotal basal bead either present or absent in the same species is not common in the genus *Cyclocephala* and makes identification more difficult. Accordingly, this species is located in two places in the key.

The parameres are different between *C. stockwelli* and *C. sororia*, and the large claw of the foretarsus in the males of *C. stockwelli* becomes gradually narrower toward the apex (Fig. 416), whereas it is broad and subparallel nearly to the apex in *C. sororia* (Fig. 402). The epipleuron and lateral margin of the elytra in females of *C. stockwelli* are noticeably expanded, whereas they are simple in *C. sororia*.

The parameres of *C. stockwelli* are very similar to those of *C. discolor*, but *C. discolor* is larger, has dorsal black markings, and has a bidentate foretibia.

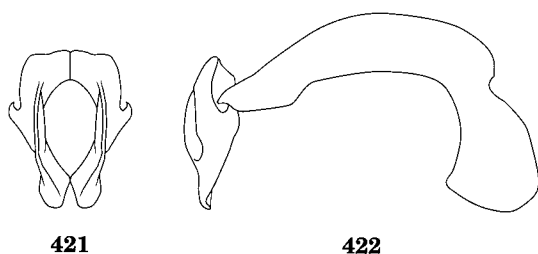
BIOLOGY. All the specimens in the type series were collected at lights in areas of tropical moist forests, tropical wet forests, and premontane wet forests at elevations of 200-1,300 meters.

***Cyclocephala unamas* Ratcliffe,
new species
(Figs. 421-423)**

TYPE MATERIAL. Holotype labeled "Cartago, Costa Rica, Reserva Tapanti, Río Pejibaye, 1400-1800 M, 9 Julio 1986, I. y A. Chacon." Allotype labeled "San José, Costa Rica, P. N. Braulio Carrillo, Est. Zurquitunel, 1500 M, 20 Setiembre 1985, MM Chavarria D." Seven paratypes with the following data: "COSTA RICA: Cartago, Embalse El Llano nr Tapanti, IX-22-1990, 1500 M, B. C. Ratcliffe" (1 male); "Quebrada Segunda, P. N. Tapanti, 1250 M, Prov. Cartago, Costa Rica, Ago 1992, G. Mora, L-N 194000, 560000" (1 male); "Cartago, Costa Rica, Tapanti, Río Grande de Orosi, 15 Julio 1987, 1500 MSNM, A. Solís" (1 female); "R. Grande de Orosi, desde Puente R. Dos Amigos hasta la Represa, Prov. Cartago, COSTA RICA, 1400-1800 M, Oct 1995, R. Delgado, de luz, L_N_186600_562000, #6363" (1 female); same data but November 1995 (1 female); "Represa Río Gde. de Orosi, 1650 M, P. N. Tapanti, Prov. Cartago, Costa Rica, Set 1992, G. Mora, L-N 185900, 563300" (1 female); "Cartago, Costa Rica, Tapanti, Río Grande de Orosi, 15 Julio 1987, 1500 MSNM, A. Solís" (1 female).

Holotype, allotype, and two paratypes deposited at INBio (Santo Domingo de Heredia, Costa Rica). Two paratypes deposited at the University of Nebraska State Museum (Lincoln, NE) and three paratypes deposited in the B. C. Ratcliffe collection (Lincoln, NE).

HOLOTYPE. Male. Length 12.5 mm; width 6.5 mm. Color of pronotum and elytra testaceous; frons and elytral markings black, elytra with marks as follows: sutural line; extreme base immediately laterad of scutellum; a subtriangularly elongate mark behind scutellum in first broad interval; a small, irregular spot behind humerus; a nearly crescent-shaped spot before apical umbone in center of disc; clypeus, pygidium, venter, and legs reddish brown (posterior tarsi piceous). **Head:** Frons and basal half of clypeus with moderately dense, small punctures. Clypeus



Figs. 421-422. *Cyclocephala unamas* parameres.

in apical half with surface roughened; apex parabolic, with marginal bead. Interocular width equals 2.9 transverse eye diameters. Antenna 10-segmented, club distinctly longer than segments 2-7. *Pronotum*: Surface at center with punctures moderate in size and density, punctures becoming moderately large and moderately dense on sides. Base with marginal bead. *Elytra*: Surface with punctures moderately large, moderate in density, distinct rows visible. *Pygidium*: Surface finely roughened, with indistinct, small, sparse punctures. In lateral view, surface strongly convex. *Legs*: Foretibia weakly tridentate, basal tooth nearly obsolete, removed from others. Foretarsus enlarged: segment 4 subtriangularly expanded on venter; 5th large, slightly curved, median edge with strong, longitudinal carina; median claw large, curved, base with rounded lobe, apex cleft. Posterior tarsus 2/3 longer than posterior tibia. *Venter*: Prosternal process small, short, subconical. *Parameres*: Figs. 421-422.

ALLOTYPE. Female. Length 12.5 mm; width 6.8 mm. As holotype except in the following respects: elytral markings with post-scutellar spot absent, remaining spots reduced to fuscous cloudings. *Head*: Antenna with club subequal in length to segments 2-7. *Elytra*: Epipleuron (ventral view) broadly thickened from level of metacoxa to abdominal sternite 5 where attenuated; elytral margin above epipleural expansion explanate. *Pygidium*: In lateral view, surface convex in basal half, nearly flat in apical half. *Legs*: Foretibia distinctly tridentate. Foretarsus simple. Posterior tarsus a little longer than posterior tibia.

VARIATION. Males (2 paratypes). Length 11.7-12.7 mm; width 6.2-6.5 mm. As holotype except in the following respects: both paratypes with post-scutellar spot surrounded by fuscous clouding that is nearly connected to basal margin spot. *Pygidium*: Surface finely shagreened instead of roughened, shining.

Females (5 paratypes). Length 12.1-12.6 mm; width 6.5-6.8 mm. As allotype except in the following respects: Color: 2 specimens lacking elytral markings, 2 specimens with markings similar to those of allotype, 1 specimen with elytron piceous and with black marks where spots are in allotype and with black posterior tarsi.

ETYMOLOGY. Derived from the Spanish words *una mas*, meaning one more, in reference to the fact that there always seems to be another new species of *Cyclocephala* to describe. The compound species-group name, although feminine in the Spanish, is considered undeclinable in Latin and need not agree in gender with the generic name (Article 31.2.3 of the Code).

DISTRIBUTION. *Cyclocephala unamas* is known from eight specimens from the Tapanti Reserve and nearby Embalse El Llano in Cartago Province and by a single specimen from the Zurqui Tunnel overlook in Braulio Carrillo National Park in San José Province, both Costa Rica.

LOCALITY RECORDS (Fig. 423). 9 specimens examined.

COSTA RICA (9). CARTAGO (8): Embalse El Llano, Reserva Tapanti; SAN JOSÉ (1): Estación Zurqui.

TEMPORAL DISTRIBUTION. July (3), August (1), September (3), October (1), November (1).

DIAGNOSIS. Males will key only so far as couplets 157/158 in Endrödi (1985a) where the choices all fail. The parabolic clypeus, in combination with a margined pronotum, strongly convex pygidium, weakly tridentate

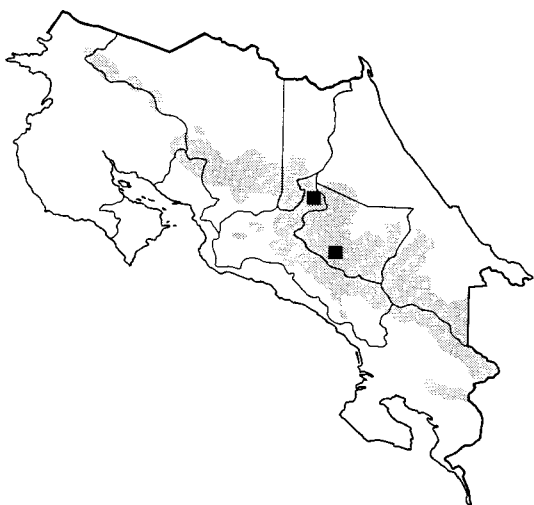


Fig. 423. Distribution of *Cyclocephala unamas* in Costa Rica.

foretibia, short prosternal process, and especially the form of the parameres, will distinguish this species. Females, with similar characters (except the parameres and weakly tridentate foretibia) have a remarkable, elongated section of expanded epipleuron as well as an unusually convex pygidium on the basal half that will help to distinguish them.

BIOLOGY. These specimens were collected at lights in an area of premontane rain forests and lower montane wet forests at elevations of 1,250-1,650 meters.

***Cyclocephala variabilis*
Burmeister, 1847**

(Figs. 424-430)

Cyclocephala variabilis Burmeister 1847: 44.

DESCRIPTION. Length 15.5-17.0 mm; width 7.3-8.3 mm. Color testaceous except for black vertex (remainder of head often dark reddish brown), 2 longitudinally parallel bands on pronotum, extreme base and lateral margins of elytra, 3 spots on elytra (subtriangular postscutellar spot, elongate humeral spot, and elongate preapical spot; lateral spots sometimes fused into elongate and oblique band; all spots may be variably

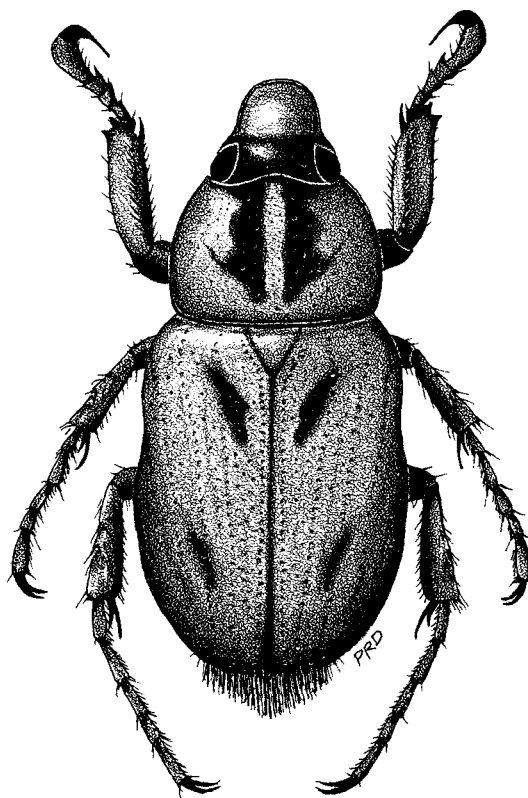
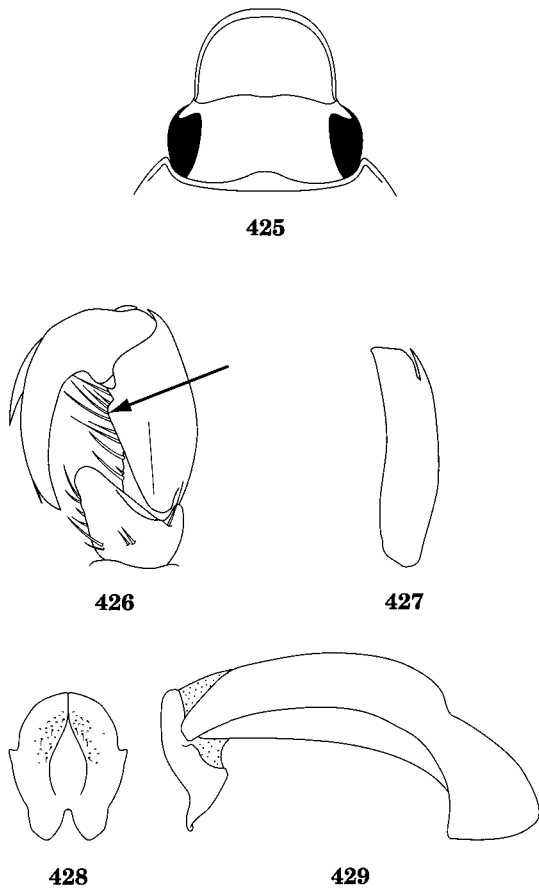


Fig. 424. *Cyclocephala variabilis*.

reduced or even absent), elytral flange in female, all or part of pygidium (usually reddish brown) and extreme apices of tibiae and femora. **Head:** Frons with small to moderately-sized punctures, punctures moderate in density. Clypeus indistinctly roughened or shagreened with sparse, small, shallow punctures; apex convexly rounded (Fig. 425) and with thick marginal bead. Interocular width equals 3.0-3.6 transverse eye diameters. Antenna 10-segmented, club slightly to or slightly shorter than segments 2-7. **Pronotum:** Lateral margin just behind anterior angle convex. Surface with punctures moderate in density; punctures small to occasionally moderate in size, setigerous on sides in anterior half; setae minute to short, stout, tawny. Base with marginal bead. **Elytra:** Surface with punctures moderate to moderately dense, moderate to moderately large in size, shallow, double rows of striae usually distinct. Minute to small, stout setae present either side of



Figs. 425-429. *Cyclocephala variabilis*: (425) head; (426-427) foretarsus (part) and foreclaw of male; (428-429) parameres.

suture and on apices (setae often abraded away). Epipleuron (ventral view) in females gradually and slightly expanded to about level of junction between abdominal sternites 3-4 where abruptly constricted; just behind and above this, lateral edge of elytron with strong flange; in lateral view, flange on elytral margin feebly emarginate; in dorsal view, flange appears as elongate swelling. *Pygidium*: Surface in males with small, moderately dense, setigerous punctures; setae long, moderately dense, tawny. Surface in females indistinctly roughened with small, sparse punctures, a few on sides with minute setae. In lateral view, surface in males strongly convex, weakly convex in females. *Legs*: Foretibia bidentate in males, tridentate in females. Foretarsus in males enlarged: tarsomeres 2-4 each slightly larger than preceding segment; 4th with ventral, subtriangular lobe and with round, deep pit on inner surface; 5th large, slightly bent, ventral surface with distinctive oblique carina that ends in a tooth near apex (Fig. 426); median claw enlarged, strongly bent, sides arcuate and subparallel, apex split into main claw and a short and slender ramus (often worn down to a small bump or sometimes completely effaced). Foretarsus in females simple. Posterior tarsus about twice as long as posterior tibia.



Fig. 430. Distribution of *Cyclocephala variabilis* in Panama.

Venter: Prosternal process long, conical (tapered to a narrow, rounded point). *Parameres*: Figs. 428-429.

DISTRIBUTION. *Cyclocephala variabilis* is recorded from Mexico to Argentina (Endrödi 1966, 1985a). However, after all the years devoted to this study, I have not seen any specimens from Costa Rica and only four specimens from the eastern half of Panama.

LOCALITY RECORDS (Fig. 430). 4 specimens examined.

PANAMA (4). **CANAL ZONE** (2): Barro Colorado Island, Tabernilla; **DARIEN** (2): Santa Fé.

TEMPORAL DISTRIBUTION. May (2), June (1).

DIAGNOSIS. *Cyclocephala variabilis* is similar to *C. pardolocarnoi* except that the head and pronotum of *C. pardolocarnoi* are elongated. In the males, the parameres are different (Figs. 428-429, 358-359), as well as the form of the enlarged protarsal claw. In *C. variabilis*, the claw is arcuate with subparallel sides (Fig. 427), whereas in *C. pardolocarnoi* the claw is widest at the middle and weakly lanceolate in shape (Fig. 357). In addition, males of *C. variabilis* have an oblique, ventral carina ending in a tooth on the 5th protarsomere while *C. pardolocarnoi* lacks a ventral carina or tooth on the 5th protarsomere. Females are easily distinguished by the simple, weakly convex pygidium and simple (non-toothed) flange on the lateral margin of the elytron (not epipleuron) in *C. variabilis* and by the presence of a swollen tumescence on the pygidium (Fig. 356) and the subangulate or toothed flange on the lateral margin of the elytron in *C. pardolocarnoi*.

BIOLOGY. In Panama, they have been collected from tropical moist forests at elevations of less than 100 meters.

***Cyclocephala weidneri* Endrödi,
1964**

(Figs. 431-435)

Cyclocephala weidneri Endrödi 1964: 462.

DESCRIPTION. Length 13.8-17.5 mm; width 7.1-9.5 mm. Color testaceous with black frons and highly variable, piceous or fuscous marks on pronotum, elytra, and pygidium. Apices of femora and tibiae and occasionally some abdominal sternites fuscous. Pronotal markings vary from absent (uncommon) to with strong "lunulata-type" pattern (most common). Elytral markings vary from absent (uncommon) to with strong "lunulata-type" pattern (most common). *Head*: Frons moderately densely punctate, punctures small.

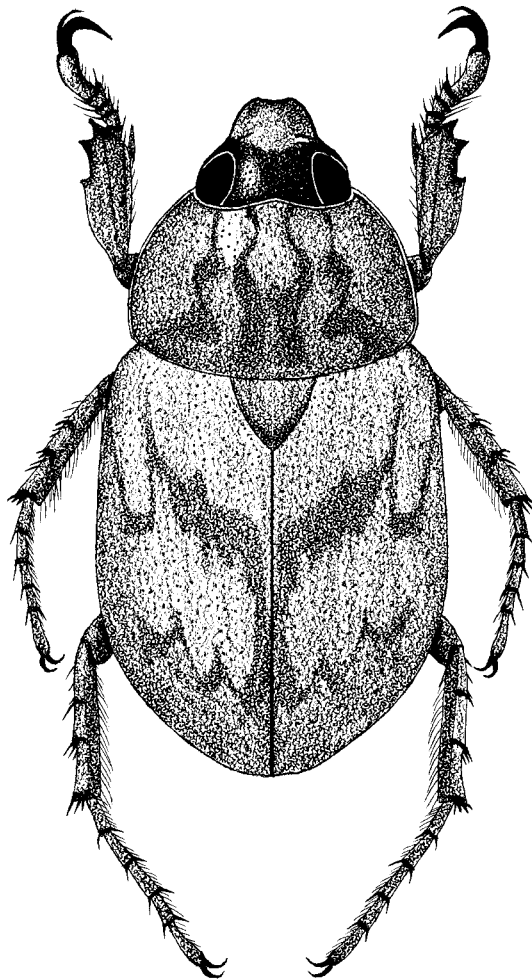
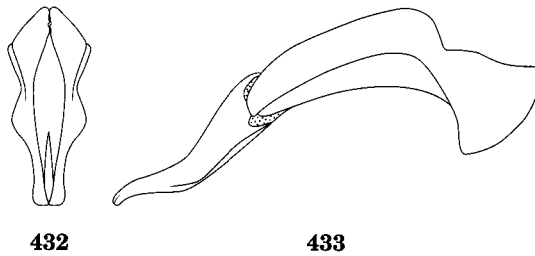


Fig. 431. *Cyclocephala weidneri*.



Figs. 432-433. *Cyclocephala weidneri* parameres.

Clypeus minutely roughened with small punctures; apex broadly subtruncate, slightly reflexed. Interocular width equals 2.2-2.5 transverse eye diameters. Antenna 10-segmented, club slightly longer than segments 2-7 in both sexes. *Pronotum*: Surface on disc with small, sparse punctures, punctures becoming slightly larger and denser on sides. Base lacking marginal bead. *Elytra*: Surface with moderately large, moderately dense punctures, distinct rows visible. Epipleuron (ventral view) of females gradually thickened to level of sternite 4 where abruptly constricted and with tooth-like angle on inner edge; margin of elytron at same level expanded into angulate, slightly swollen flange. *Pygidium*: Surface in males with small, sparse punctures on disc, becoming scabrous on sides; females similar except disc sparsely punctate. In lateral view, surface in males weakly convex, females with surface nearly flat. *Legs*: Foretibia tridentate, basal tooth slightly removed from others. Foretarsus in males enlarged: tarsomeres 3-4 each slightly larger than preceding; tarsomere 5 large, slightly curved, nearly flat on venter, cariniform on mesal edge; median claw large, strongly bent, with large lobe at base, apex cleft. Foretarsus in females simple. Posterior tarsus slightly longer than posterior tibia in males, subequal in length in females. *Venter*: Prosternal process moderately long, columnar, apex expanded and obliquely flattened



Fig. 434. Distribution of *Cyclocephala weidneri* in Costa Rica.



Fig. 435. Distribution of *Cyclocephala weidneri* in Panama.

into transverse oval with raised transverse "button" on anterior half. *Parameres*: Figs. 432-433.

DISTRIBUTION. *Cyclocephala weidneri* is broadly distributed from southern Mexico to southern Brazil and is found throughout most of Costa Rica and western Panama above 1,000 meters. It seems unusual to me that there are no records for central or eastern Panama, even after years of sampling.

LOCALITY RECORDS (Figs. 434-435). 1,256 specimens examined.

COSTA RICA (800). ALAJUELA (37): Colonia Blanca (2 km N), Estación Eladios, Estación San Ramon, Río San Lorencito, San Carlos, San Isidro, San Ramon, Upala; CARTAGO (219): Embalse El Llano, Estación Quebrada Segundo, Moravia, Refugio Nacional Tapanti, Río Grande de Orosi, Tuis, Turrialba (Grano de Oro); GUANACASTE (54): Estación Cacao, Estación Las Pailas, Estación Mengo, Estación Pitilla, Finca Jenny, Parq. Nac. Barra Honda, Parq. Nac. Guanacaste, Río San Lorenzo, Tierras Morenas; HEREDIA (2): Vara Blanca; LIMÓN (2): Amubri, Pococí; PUNTARENAS (471): Buenos Aires, Estación Altamira, Estación Esquinas, Estación La Casona, Estación Las Alturas, Estación Las Mellizas, Finca Cafrosa, Guacimal, Monteverde, Parq. Nac. Braulio Carrillo on Hwy 32 (8 mi SE San José), San Luis; SAN JOSÉ (15): Estación Carrillo, Estación Zurqui.

PANAMA (456). BOCAS DEL TORO (13): Chiriqui Grande (8 km W), Miramar; CHIRIQUI (443): Bambito, Boquete, Cerro Punta, Finca La Suiza, Fortuna, Hartmann's Finca (Santa Clara), Hornito, IHRE Vivero (11 km N Los Planes).

TEMPORAL DISTRIBUTION. January (4), February (8), March (75), April (81), May (473), June (247), July (48), August (23), September (115), October (31), November (20), December (1). Most of the March specimens represent a single collecting event at Las Alturas Field Station in Costa Rica, thus

skewing upward the normal numbers expected in March.

DIAGNOSIS. *Cyclocephala weidneri* is one of four species in Costa Rica and Panama with the "lunulata-type" pattern of dorsal markings. Its usually denser dorsal markings are similar to those of *C. fulgurata*, but *C. weidneri* has a black "mask" on the frons between the eyes, whereas *C. fulgurata* does not. *Cyclocephala lunulata* also has a black "mask," but it also has a setose pygidium (both sexes), whereas *C. weidneri* has a glabrous pygidium. The parameres are also distinctive.

BIOLOGY. Adults are attracted to lights at night. This species inhabits tropical moist forests, tropical wet forests, premontane moist forests, premontane wet forests, premontane rain forests, and lower montane rain forests. It has been found at elevations ranging from 70-1,720 meters with only a few specimens taken lower than 1,000 meters.

***Cyclocephala williami* Ratcliffe,
1992**

(Figs. 436-443)

Cyclocephala williami Ratcliffe 1992b: 230.

DESCRIPTION. Length 8.9-10.6 mm; width 4.3-5.0 mm. Color testaceous with black spots on pronotum and elytra (as in Figs. 436-439) and usually piceous on most of pygidium and abdominal sternites. Pronotum with 6-8 spots: 4 in transverse arc in basal third, median 2 spots twice as large as lateral 2 spots; 2-4 additional spots anterior of and subequal in size to basal median spots, anterior and median basal spots occasionally confluent; all spots occasionally absent. Elytra with 5 spots each as well as darkened margin behind scutellum (darkened margin occasionally absent): 4 spots in anterior third in subquad-rangular pattern (occasionally 1, 2, 3 or even all spots absent) and 5th spot in center of elytron in apical half; all spots may be entirely absent or spots absent except for black streak

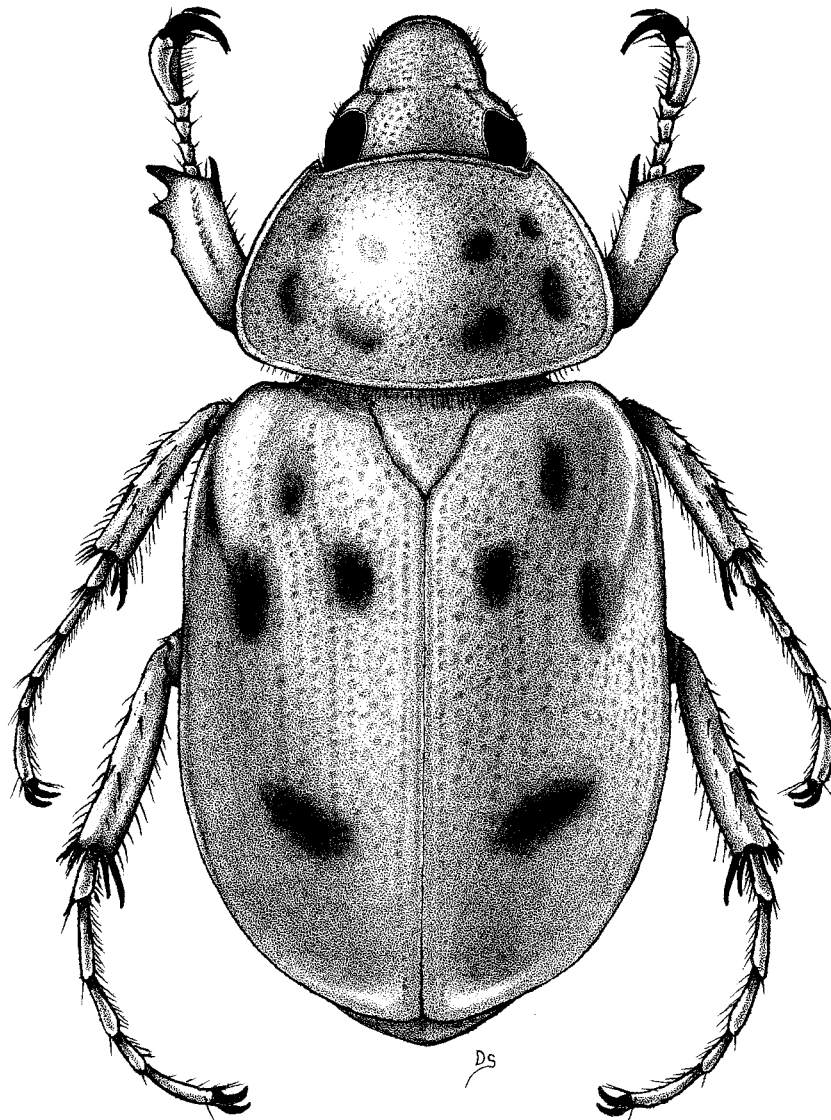
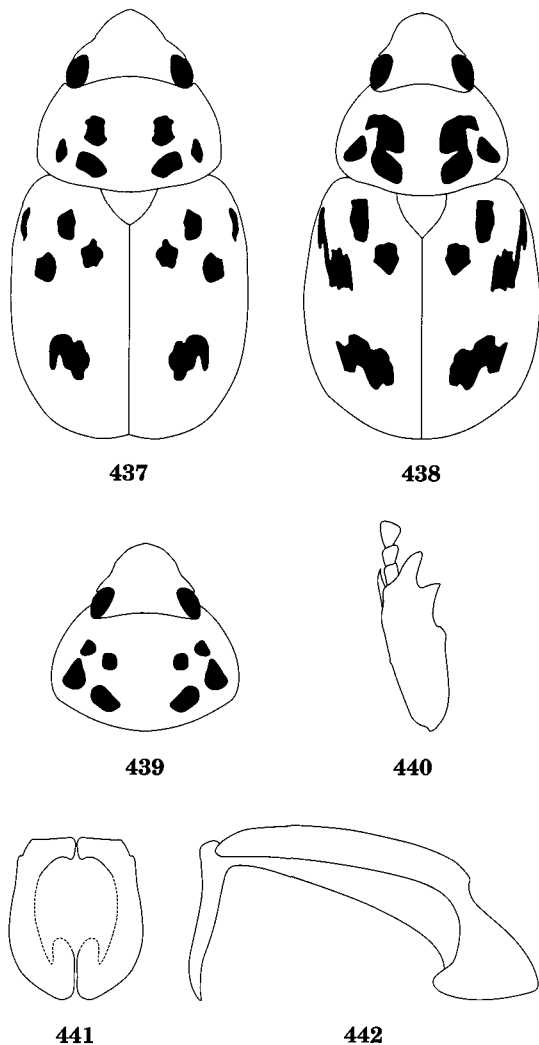


Fig. 436. *Cyclocephala williami*.

on humerus. *Head*: Frons and clypeus densely punctate; punctures small to moderate in size, those on clypeus a little smaller and denser. Clypeus with apex parabolic, slightly reflexed. Interocular width equals 3.0 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. *Pronotum*: Surface moderately densely punctate, punctures becoming denser near lateral margins. Base with marginal bead. *Elytra*: Surface with weak, punctate striae; punc-

tures moderate in size, ocellate. Epipleuron (ventral view) of female weakly thickened at level of abdominal sternites 1-2. *Pygidium*: Surface roughened, with weak or distinct punctures near apex, weakly rugopunctate near base, punctures small and moderate mixed. In lateral view, surface convex in male, nearly flat in female. *Legs*: Foretibia in male tridentate (Fig. 440), basal tooth slightly removed from others; foretibia tridentate in female, all teeth subequally spaced. Foretarsus



Figs. 437-442. *Cyclocephala williami*: (437-439) variation in pronotal and elytral markings; (440) right foretibia of male; (441-442) parameres.

in males enlarged: tarsomeres 2-4 each slightly larger than preceding, 4th with ventral, subtriangularly expanded lobe; 5th large, curved, with ventral, slender and elongate spine at apex (often difficult to see unless viewing angle is just right); median claw large, strongly curved, with large lobe at base on ventral side, apex finely split. Foretarsus in females simple. Posterior tarsus nearly twice as long as posterior tibia. *Venter*: Prosternal process an almost imperceptible, subtriangular boss. *Parameres*: Figs. 441-442.

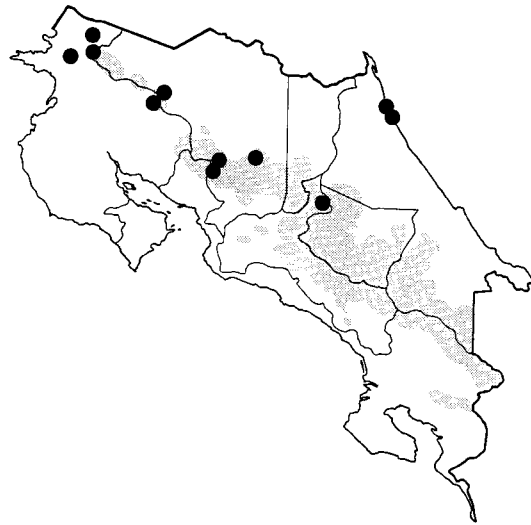


Fig. 443. Distribution of *Cyclocephala williami* in Costa Rica.

DISTRIBUTION. *Cyclocephala williami* is known from the Cordillera Central in the northern half of Costa Rica.

LOCALITY RECORDS (Fig. 443). 216 specimens examined.

COSTA RICA (216). ALAJUELA (56): Estación San Ramón de Dos Ríos, Río San Lorencito, Upala; GUANACASTE (22): Estación Pitilla, Finca Jenny (30 km N Liberia), Monteverde, Parq. Nac. Guanacaste, Río San Lorenzo, Tierras Morenas; LIMÓN (6): Cerro Tortuguero, Estación Cuatro Esquinas; PUNTARENAS (128): Estación La Casona, Monteverde, Monteverde Cloud Forest Reserve, San Luis, Santa Elena (6 km N); SAN JOSÉ (4): Estación Carrillo, Quebrada Sanguijuela.

TEMPORAL DISTRIBUTION. March (2), April (3), May (41), June (61), July (82), August (25), September (1), October (1).

DIAGNOSIS. Because *Cyclocephala williami* may have zero, four, six, or eight spots on the pronotum, it is not easily placed in Endrödi's (1985a) key. Reliance should be placed on the form of the male genitalia in combination with the other characters included in the key in this work to identify this distinctive and attractive little species.

BIOLOGY. Adults are attracted to lights and feed on guava blossoms at night (personal observation). They have been collected in tropical wet forests, premontane rain forests, and lower montane rain forests at elevations of 300-1,520 meters. Two records are from near sea level in Limón province in Costa Rica.

***Cyclocephala zodion* Ratcliffe,
1992**

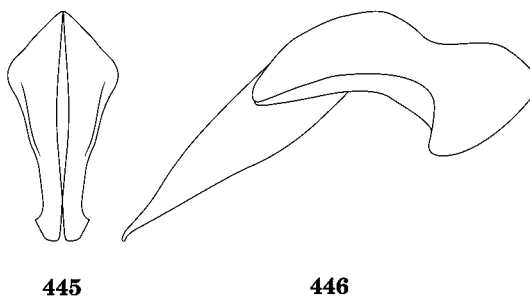
(Figs. 444-448)

Cyclocephala zodion Ratcliffe 1992b: 232.

DESCRIPTION. Length 13.8-16.9 mm; width 7.5-8.8 mm. Color testaceous with black frons, sometimes clypeus, pronotal and elytral spots, prepygidium, and posterolateral half of abdominal sternites 1-5. Black spots on pronotum vary from moderate to large spot on disc either side of middle (majority of specimens); sometimes with small, black spot laterad of principal spot, occasionally these 2 spots connected at their anterior margins; rarely entire pronotum either dark brown or lacking spots altogether. Each elytron with 4 small to moderate black spots in a semicircular arc; anterior spot behind scutellum often larger, subtriangular; post-humeral spot sometimes elongated; rarely, posterior 2 spots fused. Pygidium rarely fuscous either side of middle. *Head:* Frons and base of clypeus with moderately large punctures; punctures dense, setigerous; setae short, moderately dense, tawny. Clypeus rugulose apically, apex weakly emarginate. Interocular width equals 2.3-2.6 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. *Pronotum:* Surface with moderately large punctures; punctures moderate in density on disc, becoming denser laterally, setigerous; setae short, moderate in density, tawny. Base without marginal bead. *Elytra:* Surface with moderately large punctures; punctures shallow, most weakly ocellate, rows indistinct, setigerous; setae short, moderate in density, tawny. Epipleuron (ventral view) in females expanded into elongate lobe with an obtuse angle on median edge at level of metacoxa and



Fig. 444. *Cyclocephala zodion*, left epipleuron (ventral view) of female.



Figs. 445-446. *Cyclocephala zodion* parameres.

sternite 1 (Fig. 444). *Pygidium:* Surface roughened (not in females), punctate (punctures occasionally obscured by surface roughness in males); punctures moderate in density, small, setigerous; setae moderate in length and density in males, sparser and shorter in females, tawny. In lateral view, surface in males convex (especially apical half), weakly convex in females. *Legs:* Foretibia tridentate, basal tooth removed from others in both sexes. Foretarsus in males enlarged:

tarsomere 5 enlarged, curved, slightly concave ventrally; median claw large, strongly bent, with lobe at base, apex cleft. Foretarsus in females simple. Posterior tarsus a little longer than posterior tibia in males, subequal in length in females. *Venter*: Prosternal process moderate in length, columnar, apex obliquely flattened into transverse oval with raised, transverse "button" on anterior half. *Parameres*: Figs. 445-446.

DISTRIBUTION. *Cyclocephala zodion* was originally described from only two locations in

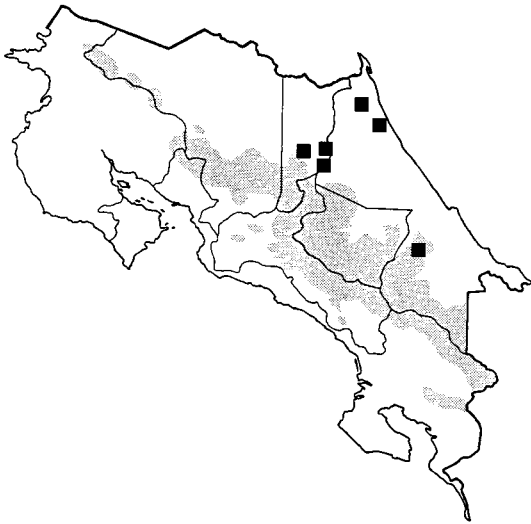


Fig. 447. Distribution of *Cyclocephala zodion* in Costa Rica.

Panama. Since then, however, additional specimens have been collected, and this species is now known from Costa Rica and Panama.

LOCALITY RECORDS (Figs. 447-448). 75 specimens examined.

COSTA RICA (17). HEREDIA (3): Estación Magsasay, Finca La Selva; LIMÓN (14): Cuatro Esquinas (P. N. Tortuguero), Estación El Ceibo (P. N. Braulio Carrillo), Fila Matama, Sector Cerro Cocori.

PANAMA (58). BOCAS DEL TORO (4): Corriente Grande, Miramar; COCLÉ (23): Cerro Gaital, El Valle; PANAMA (31): Cerro Jefe, El Llano-Carti Road (km 8, 12).

TEMPORAL DISTRIBUTION. January (17), February (2), April (1), May (17), June (25), July (1), August (1), September (7), October (1), November (4).

DIAGNOSIS. *Cyclocephala zodion* is an attractive little species that resembles *C. sexpunctata*, except smaller. Males of *C. zodion* will key as far as couplet 269 in Endrödi (1985a), which leads to either *C. sexpunctata* or *C. pubescens*. *Cyclocephala zodion* is distinctive, however, because of its consistently smaller size (less than 17 mm),

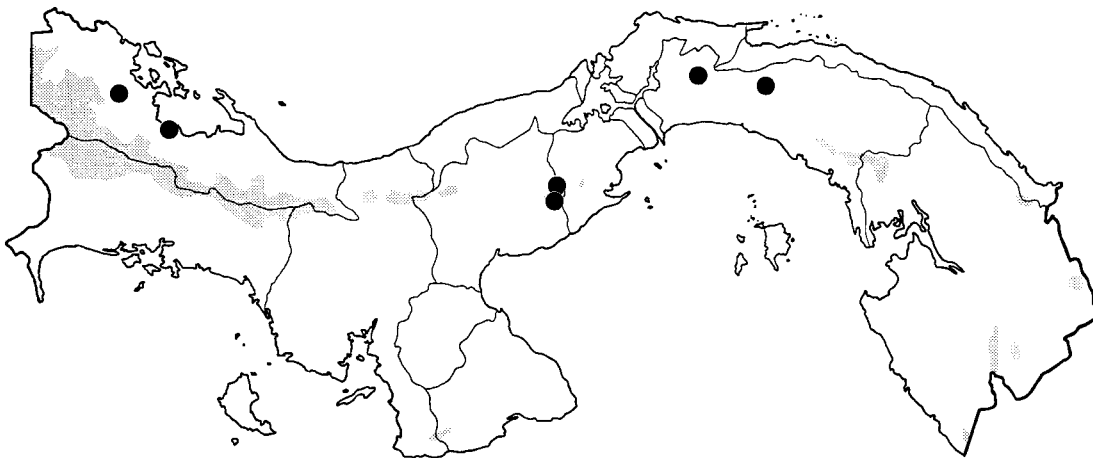


Fig. 448. Distribution of *Cyclocephala zodion* in Panama.

presence of black spots on the lateral edges of abdominal sternites 1-5, absence of the sharp tooth on the apex laterally of the parameres, and absence of the triangular expansion or tooth on the venter of the parameres (Figs. 446, 391). Females of *C. zodion* will key to couplet 113 in Endrödi (1985a), which leads to *C. arrowiana* Martínez, *C. sexpunctata*, and *C. pubescens*. They differ from *C. arrowiana* in being smaller and lacking an acutely prolonged dilation on the lateral edge of the elytra (the parameres of the males are also vastly different). Both *C. sexpunctata* and *C. pubescens* (now *C. brevis*) females are characterized by having a dentiform dilation on the lateral edge of the elytron at the level of abdominal sternites 2-3, whereas the dilation is elongate and lobed and at the level of sternite 1 in *C. zodion*.

Cyclocephala zodion also closely resembles *C. pan*. Males are best separated by the different form of the parameres as well as by the presence (in *C. zodion*) of black maculae on the pronotum. Females of *C. zodion* may be distinguished from *C. pan* by the black markings on the pronotum and by the elongated, lobe-like epipleural/elytral expansion at the level of tergite 1 (as opposed to the abrupt, dentiform expansion at the level of tergites 2-3).

BIOLOGY. This species lives in tropical wet forests, premontane wet forests, and premontane rain forests at elevations ranging from near sea level to 1,680 meters.

Doubtful or Erroneous Records

The following species of *Cyclocephala* have been listed in various sources as being recorded from Costa Rica or Panama. I believe these listings to be erroneous or otherwise spurious for the study area because I have not seen any of these species from any of the many collections studied for this research. Moreover, my own collecting, as well as that of colleagues, has not yielded any of these species during the last 30 years.

Cyclocephala cartwrighti Endrödi, 1964

Cyclocephala cartwrighti Endrödi 1964: 442.

Endrödi (1964) described this species based on a male and female from Bolivia. In his synopsis of the genus *Cyclocephala* published two years later (Endrödi 1966), he mentioned an additional specimen from Barro Colorado Island in Panama collected in June. Although he did not give the gender of this specimen, I suspect it is the female determined by him in 1965 and deposited in the Canadian National Collection (CNCI). Endrödi indicated that this third specimen was in the Howden collection, but it is not (January 2001). Inasmuch as Howden worked at the CNCI in 1965, it is possible that Endrödi confused where the specimen actually came from.

I believe it is nearly impossible for Endrödi to have associated a single female specimen from Panama with the type specimens from Bolivia. The female specimen at the CNCI is actually *C. discolor*, and its characters do not totally agree with those of the allotype. Accordingly, I believe that Endrödi misidentified the specimen from Panama, and that *C. cartwrighti* does not occur in Panama.

Cyclocephala freudi Endrödi, 1963

Cyclocephala freudi Endrödi 1963: 328.

This species was described based on numerous specimens from Mexico, three specimens from El Salvador, and singletons from Costa Rica, Ecuador, and Texas in the United States. The Texas specimen was a "no data" specimen, and this species does not occur in the United States. The Costa Rican specimen was from Santa Elena, but it probably represents an erroneous record inasmuch as no other specimens have ever been taken in Costa Rica. This species is found in Mexico and probably extends southward to El Salvador and Honduras.

***Cyclocephala gregaria* Heyne and
Taschenberg, 1907**

(Figs. 449-451)

Cyclocephala gregaria Heyne and Taschenberg 1907: 91.

Cyclocephala gregaria Arrow 1911: 72 (invalid name, primary homonym of *C. gregaria* Heyne and Taschenberg).

DESCRIPTION. Length 17.4-19.5 mm; width 9.4-10.4 mm. Color light reddish brown (almost orange) except for black head, elytral markings and legs; elytra vary from those with post-scutellar spot (joined at suture) to post-scutellar spot expanded laterally to cover entire base to basal third black and connected along lateral margin to large, black macula in apical third (not joined at suture). **Head:** Frons densely punctate either side of middle, punctures moderate in size, setigerous; setae short, tawny. Clypeus transversely rugulose, setigerous; setae short, dense, tawny; apex broadly truncate, narrowly reflexed. Interocular width equals 2.5 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. **Pronotum:** Surface sparsely punctate, punctures small to moderate, setigerous; setae short, tawny. Lateral margin in anterior half slightly concave making anterior angle acute. Base lacking marginal bead. **Elytra:** Surface minutely roughened, punctate, rows of punctures indistinct; punctures small to moderate in size, setigerous; setae moderate in length and density, tawny. Epipleuron (ventral view) in females thickened into a small knob at level of abdominal sternites 2-3. **Pygidium:** Surface moderately densely punctate; punctures small to moderate, shallow, setigerous; setae long, moderately dense, tawny. In lateral view, surface in males strongly, evenly convex; females with surface weakly convex. **Legs:** Protibia tridentate, basal tooth small, strongly removed from others. Protarsus in males enlarged: tarsomere 5 enlarged, curved, slightly concave on venter; median claw large, curved, with large basal lobe, apex distinctly cleft. Protarsus in females simple. Posterior tarsus a little longer than posterior tibia. **Venter:** Prosternal process moderate in length, columnar, apex

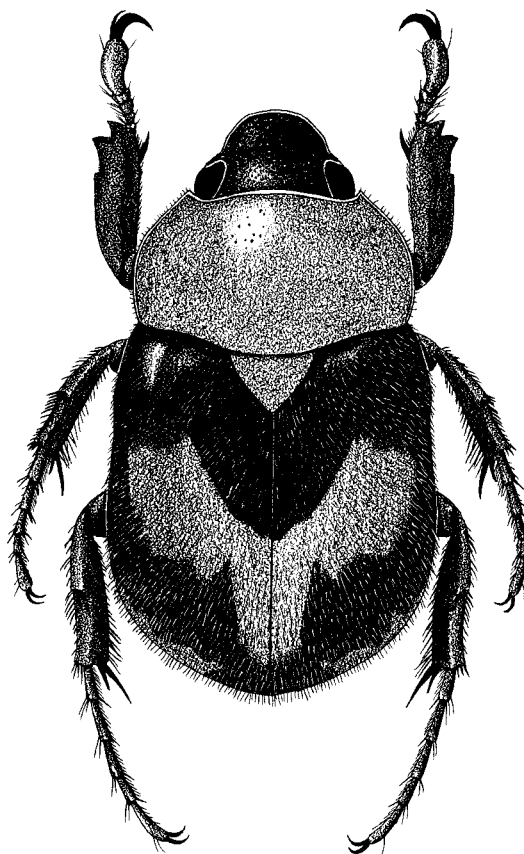
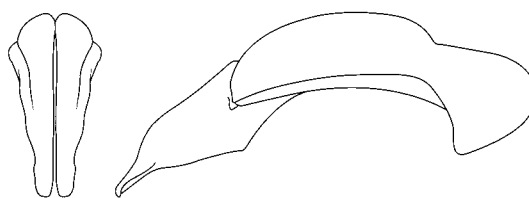


Fig. 449. *Cyclocephala gregaria*.



450

451

Figs. 450-451. *Cyclocephala gregaria* parameres.

obliquely flattened into transverse oval with raised, transverse "button" on apical half. **Parameres:** Figs. 450-451.

DISTRIBUTION. *Cyclocephala gregaria* is known from Colombia, Venezuela, Ecuador, and Bolivia. Endrödi (1966) recorded two specimens (in the collections in Bonn, Germany) from western Panama, but I have

never seen Panamanian specimens in any collection or during my years of collecting there. This species is included in this work (including the key) on the contingency that Endrödi's records are legitimate, but I have my doubts. I believe this is a South American species that does not reach Central America.

LOCALITY RECORDS. No specimens examined from the study area. Records are from Endrödi (1966).

PANAMA (2). CHIRIQUI (2): Boquete, No data.

TEMPORAL DISTRIBUTION. Unknown.

DIAGNOSIS. *Cyclocephala gregaria* is recognized by its distinctive markings, moderate to dense setae on the dorsal surface, and by the form of the male parameres (Figs. 450-451). It is similar in overall appearance to *C. conspicua* (especially those morphs lacking the "typical" longitudinal black bands on the pronotum). However, *C. gregaria* differs by its long and dense setae dorsally, form of the male parameres, the shape of the pronotal margin in the anterior half (slightly concave in *C. gregaria*, straight in *C. conspicua*), and large eyes (2.5 transverse eye diameters versus 3.3-4.0 in *C. conspicua*).

I have examined a series of specimens from Colombia that have only minute setae on the elytra (like those of *C. conspicua*), but otherwise have all the diagnostic characters (parameres, large eyes, pronotal shape, pygidial shape) of *C. gregaria*. Consequently, *C. gregaria* with short dorsal setae might be confused with *C. conspicua* if not examined carefully.

BIOLOGY. Adults are attracted to lights at night.

***Cyclocephala laminata*
Burmeister, 1847**

Cyclocephala laminata Burmeister 1847: 57.

According to Endrödi (1966, 1985a) and Dupuis (1996, probably following Endrödi),

Cyclocephala laminata has the same distribution as *C. melanocephala*, i.e., from the southwestern United States to Argentina and Paraguay. Endrödi (1966) recorded two specimens each from the United States and Mexico and a single specimen each from Costa Rica (Reventazon) and Panama (Tabernilla). However, in all the thousands of *Cyclocephala* specimens I have seen from Costa Rica and Panama, I have never encountered *C. laminata*. It does not occur in the United States either. Based on these observations, I must conclude that *C. laminata* is a South American species. The records cited by Endrödi may be spurious or erroneous identifications.

***Cyclocephala lurida coahuilae*
Bates, 1888**

Cyclocephala coahuilae Bates 1888: 304.

Cyclocephala lurida Bland is an abundant and wide-spread species in the United States. The subspecies, *C. lurida coahuilae*, is known from northern Mexico. Endrödi (1966, 1985a) recorded a single specimen from Turrialba, Costa Rica. This species does not occur in the study area, and the record cited by Endrödi may represent an erroneous identification.

***Cyclocephala obesa* Burmeister,
1847**

Cyclocephala obesa Burmeister 1847: 59.

Endrödi (1966) recorded this species as occurring from Arizona in the southwestern United States to Ecuador. He noted a single specimen, without data, from Arizona, and a single specimen each from Costa Rica (Talamanca) and questionably Honduras (Punta Gorda; there is apparently no Punta Gorda in Honduras, but there is such a locality in Belize; Ron Cave, personal communication). I believe that these are either erroneous records (incorrect label data) or spurious records (inadvertent transport of a specimen?). After

decades of collecting by many individuals, it is clear that *C. obesa* does not occur in either North or Central America. This is a South American species.

***Cyclocephala simulatrix* Höhne,
1923**

Cyclocephala simulatrix Höhne 1923b: 372.

Endrödi (1966, 1985a) recorded a single specimen from Turrialba, Costa Rica. Whether a spurious record or a misidentification, this species does not occur in Costa Rica or Panama. It is known from Trinidad, Venezuela, Peru, Bolivia, and Paraguay.

***Cyclocephala tutilina* Burmeister,
1847**

Cyclocephala tutilina Burmeister 1847: 68.
Cyclocephala venezuelae Arrow 1911: 171
(synonym).

Endrödi (1966) recorded this species from Mexico (two specimens, one without data), Honduras (one specimen), Colombia, Venezuela, and Brazil (no data). After many years of collecting in Central America by many individuals, I have not encountered any specimens of *C. tutilina* in any collections. Any specimens so identified that I have not seen are probably *C. sexpunctata* since the differences between these two species are subtle, especially without comparative material. *Cyclocephala tutilina* is a South American species.

***Cyclocephala warneri* Ratcliffe,
1992**

Cyclocephala warneri Ratcliffe, 1992c: 250.

I described this pretty little species based on five specimens from Chiapas, Mexico and

a single female from Bijagua, Alajuela Prov., Costa Rica. The Costa Rican female is similar in all respects to those from Chiapas, but I have never encountered any other specimens from Costa Rica, either in research collections or at Bijagua where I have personally collected. For the moment, then, I consider this record suspect, and additional collecting is needed to determine if *C. warneri* actually occurs in northern Costa Rica.

***Dyscinetus* Harold, 1869**

Dyscinetus Harold 1869: 123.
Chalepus MacLeay 1819: 149 (name preoccupied, junior homonym).
Palechus Casey 1915: 174 (synonym).

Dyscinetus is comprised of 15 species (Endrödi 1966, 1985a; Ratcliffe 1986; Joly and Escalona 2002). Species of *Dyscinetus* occur from the central United States to Argentina. Two species are found in Costa Rica and Panama. The most recent synopsis of the genus is that of Endrödi (1985a).

Dyscinetus species are all characterized by the presence of a larger median claw with split apex on the foretarsus in males (the 5th tarsomere may or may not be enlarged); a short, trapezoidal clypeus (Fig. 58); 10-segmented antenna with a short club; and black coloration often tinged with green. Most species of *Dyscinetus* are similar in external appearance, but certain characters of surface sculpturing, foretarsus development in the males, and especially the form of the male parameres will serve to distinguish the species.

The biology of most of the species remains unknown. They have occasionally been implicated in the injury to agricultural crops, but this has never been verified. The larvae are possibly general detritus or root feeders. The larval stage has been described for a couple of species but not for those in Costa Rica or Panama. Adults are attracted to lights.

Key to the Species of Adult *Dyscinetus* of Costa Rica and Panama

1. Frons with small, sparse punctures. Foretarsus with 5th tarsomere enlarged in males. Parameres as in Figs. 453-454 *dubius* (Olivier)
- 1'. Frons with large, dense punctures. Foretarsus with 5th tarsomere not enlarged in males. Parameres as in Figs. 457-458 *laevipunctatus* Bates

Clave para las Especies de Adultos de *Dyscinetus* de Costa Rica y Panamá

1. Frente con puntuaciones pequeñas, dispersas. Tarsos anteriores con el quinto tarsómero agrandado en machos. Parámetros como en la figuras 453-454 *dubius* (Olivier)
- 1'. Frente con puntuaciones grandes y dispuestas densamente. Tarsos anteriores con el quinto tarsómero no agrandado en machos. Parámetros como en la figuras 457-458 *laevipunctatus* Bates

Dyscinetus dubius (Olivier, 1789)

(Figs. 452-456)

Melolontha dubius Olivier 1789: 32.

Melolontha geminatus Fabricius 1801: 166
(synonym).

Geotrupes lugubris Quensel in Schönherr
1806: 21 (synonym).

Dyscinetus frater Bates 1888: 312 (synonym).

Dyscinetus obtusus Casey 1915: 170 (synonym).

DESCRIPTION. Length 16.2-22.2 mm; width 8.4-11.6 mm. Color black. *Head:* Frons and clypeus sparsely punctate, punctures small. Frontoclypeal suture arcuate, fine but distinct. Clypeus with apex broadly, shallowly emarginate, sides and apex margined. Interocular width equals 3.5 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. *Pronotum:* Surface sparsely punctate, similar to that of frons, punctures sometimes a little larger, especially on sides. Basal bead absent. *Elytra:* Punctate striae in 3 distinct pairs plus sutural row; punctures in each row moderate in size, ocellate, nearly contiguous with each other. Intervals with moderate (1st row) to moderately dense punctures; punctures moderately large, ocellate. Sutural interval and intervals between rows comprising a pair of striae impunctate or with a few small punctures. *Pygidium:* Surface densely rugulose in basal half, remainder densely punctate (less

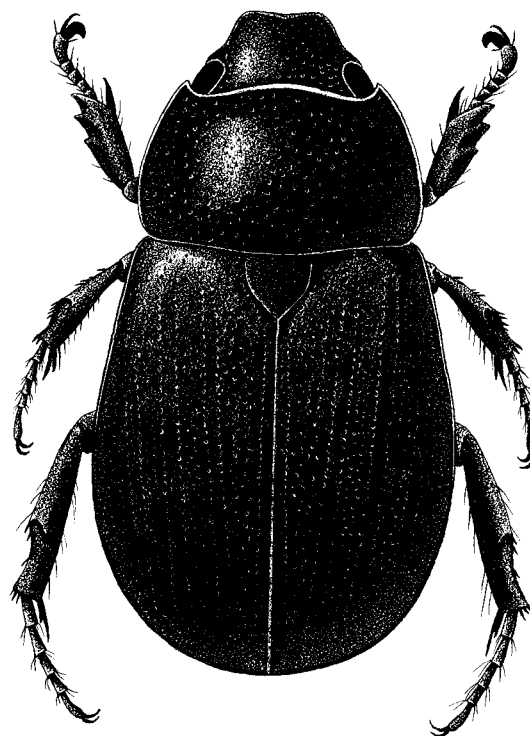
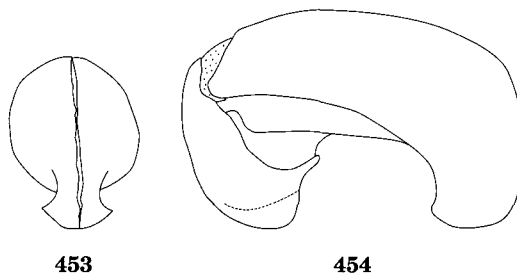


Fig. 452. *Dyscinetus dubius*.



Figs. 453-454. *Dyscinetus dubius* parameres.

so in females); punctures large, most confluent, setigerous; setae short, tawny in color. In lateral view, surface weakly convex in both sexes. *Legs*: Foretibia tridentate, teeth subequally spaced; tibia with small notch on anterior edge at base of 2nd and 3rd teeth. Foretarsus in males with 5th tarsomere and median claw slightly enlarged, median claw with apex broadly cleft. *Venter*: Prosternal process long, stout, apex flattened into large, slightly transverse oval with fringe of long setae on lateral and posterior edges. *Parameres*: Figs. 453-454.

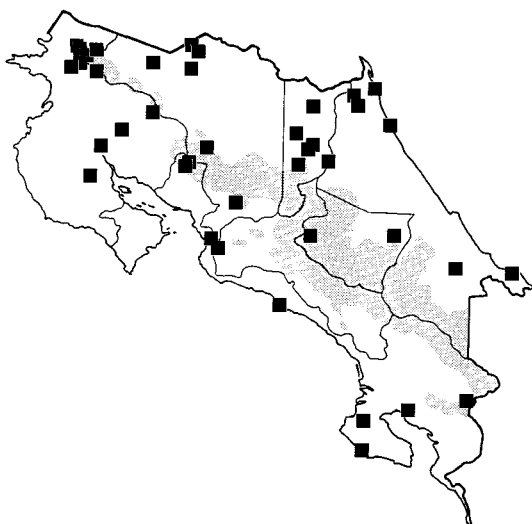


Fig. 455. Distribution of *Dyscinetus dubius* in Costa Rica.

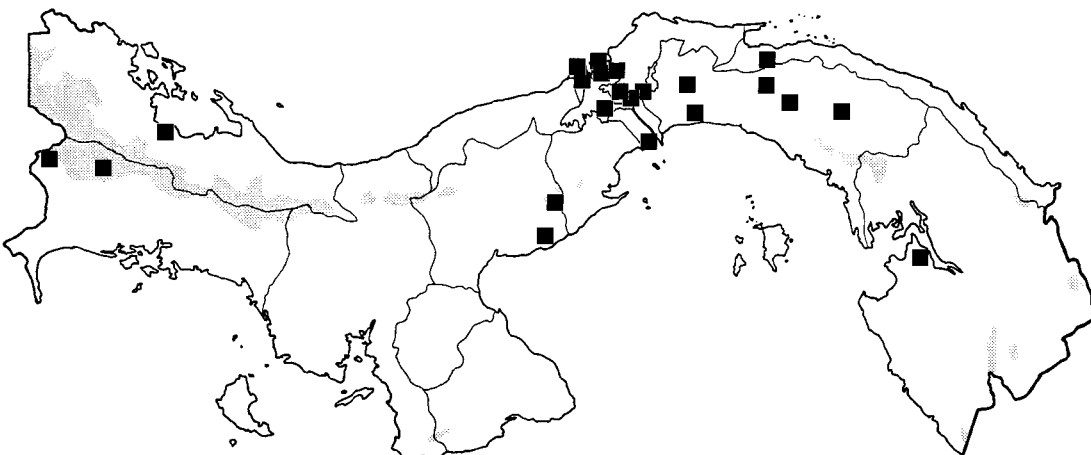


Fig. 456. Distribution of *Dyscinetus dubius* in Panama.

DISTRIBUTION. *Dyscinetus dubius* is broadly distributed, ranging from Mexico to Argentina (Endrödi 1966). This species is found throughout Costa Rica and Panama.

LOCALITY RECORDS. (Figs. 455-456). 1,258 specimens examined.

COSTA RICA (1,023). **ALAJUELA** (127): Estación Laguna Pocosol, Finca San Gabriel, Reserva Caño Negro, San Ramón, Upala; **CARTAGO** (49): Moravia, Turrialba; **GUANACASTE** (107): Cañas (6 mi W, 6 mi S), Cerro El Hacha (12 km SE La Cruz), Estación Maritza, Estación Palo Verde, Estación Pitilla, Finca Jenny (30 km N Liberia), Finca Montezuma (slopes of Volcán Tenorio), Nacaome, Parq. Nac. Guanacaste; **HEREDIA** (107): Estación El Ciebo, Estación Magsasay, Finca La Selva, Finca Naranjo Valenciana (2 km S Pueblo Nuevo), Las Horquetas, Los Arbolitos; **LIMÓN** (418): Barra Colorado, Estación Hitoy Cerere, Manzanillo, Parq. Nac. Tortuguero, Planta I.C.E., Río Sardinas, Sector Cerro Cocori; **PUNTARENAS** (214): Estación Esquinas, Estación La Casona, Estación Las Cruces, Estación Quebrada Bonita, Estación Sirena, Las Alturas, Parq. Nac. Manuel Antonio, Rancho Quemado, San Luis, San Vito; **SAN JOSÉ** (1): Estación Bijagual.

PANAMA (235). **BOCAS DEL TORO** (2): Miramar; **CANAL ZONE** (183): Achote Road,

Barro Colorado Island, Black Tank Road, Coco Solo Hospital, Escobal Road, Ft. Kobbe, Ft. Gulick, Ft. Sherman (Pavon Hill), Gatun, Madden Dam, Old Gamboa Road, Piña Road, Pipeline Road (km 2.4), Skunk Hollow; CHIRIQUI (6): Hartmann's Finca (Santa Clara), Lino; COCLÉ (12): El Valle, Río Hato; COLÓN (25): Santa Rita Ridge; DARIEN (14): Río Seteganti; PANAMA (64): Altos de Majé, Cerro Azul, El Llano-Carti Road (km 8), Juan Mina, Ipetí, Tocumen Airport; SAN BLAS (4): Nusagandi.

TEMPORAL DISTRIBUTION. January (125), February (198), March (82), April (33), May (226), June (168), July (89), August (108), September (59), October (97), November (112), December (41).

DIAGNOSIS. *Dyscinetus dubius* may be distinguished by its small, sparse punctures on the clypeus (punctures dense and large in *D. laevipunctatus*), enlarged foretarsus in the male (not enlarged in *D. laevipunctatus*), and by the distinctive shape of the parameres in the male.

BIOLOGY. The larvae probably feed on roots and in organic material in the soil. Adults are attracted to lights, sometimes in very large numbers. In Costa Rica and Panama, *D. dubius* has been collected in tropical dry forests, tropical moist forests, tropical wet forests, premontane moist forests, and premontane wet forests at elevations of 1,500 meters or less.

***Dyscinetus laevipunctatus* Bates,
1888**

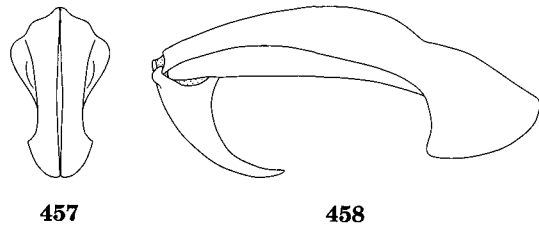
(Figs. 457-460)

Dyscinetus laevipunctatus Bates 1888: 311.
Palechus histrio Casey 1915: 174 (synonym).

DESCRIPTION. Length 15.3-20.1 mm; width 8.7-10.0 mm. Color black. *Head:* Frons and center-base of clypeus with moderately large punctures; punctures vary from moderate to moderately dense. Clypeus with punctures moderate in density, small to moderately large; apex broadly truncate, weakly emarginate,

sides and apex margined. Interocular width equals 4.0 transverse eye diameters. Antenna 10-segmented, club slightly shorter than segments 2-7. *Pronotum:* Surface with punctures moderate in density, moderate in size, some becoming larger on sides. Base lacking marginal bead. *Elytra:* Punctate striae in 3 pairs plus sutural row; punctures in each row moderate in size, ocellate, nearly contiguous. Intervals with moderate (1st interval) to moderately dense punctures; punctures moderate in size, ocellate. Sutural interval and intervals between rows comprising a pair of striae impunctate or with a few small punctures. *Pygidium:* Surface completely rugulose, with minute, tawny setae. In lateral view, surface flat to weakly convex in both males and females. *Legs:* Foretibia tridentate, teeth subequally spaced; tibia with small notch on anterior edge at base of 2nd and 3rd teeth. Foretarsus in males not enlarged, median tooth widely cleft at apex; females with foretarsus and claws simple. *Venter:* Prosternal process long, stout, apex flattened into large, slightly transverse oval with fringe of long setae on lateral and posterior edges. *Parameres:* Figs. 457-458.

DISTRIBUTION. *Dyscinetus laevipunctatus* is found in Mexico, Central America, and Cuba (Endrödi 1966, 1985a). The Amazon region locality cited by Casey (1915) is probably erroneous. In Costa Rica this species is generally distributed while in Panama it seems to be quite rare and is known only from the area of the Canal Zone.



Figs. 457-458. *Dyscinetus laevipunctatus* parameres.

LOCALITY RECORDS. (Figs. 459-460). 78 specimens examined.

COSTA RICA (77). ALAJUELA (13): Caño Negro; GUANACASTE (14): Cañas, Estación Los Almendros, Estación Murcielago, Estación Palo Verde, Estación Pitilla, Río San Lorenzo, Tierras Morenas; HEREDIA (9): Estación El Ceibo, Estación Magsasay, Finca Naranja Valenciana (2 km S Pueblo Nuevo), La Selva Biological Station; LIMÓN (26):

Cerro Tortuguero, Estación Cuatro Esquinas, Río Sardinas; PUNTARENAS (15): Estación Sirena, Monteverde, Parq. Nac. Manuel Antonio, Rancho Quemado.

PANAMA (1). CANAL ZONE (1): Ft. Clayton.

TEMPORAL DISTRIBUTION. January (2), February (3), March (11), April (5), May (10), June (15), July (7), August (6), September (8), October (4), November (4), December (3).

DIAGNOSIS. *Dyscinetus laevipunctatus* can be separated from the similarly-sized *D. dubius* by the large, dense punctures on the frons in *D. laevipunctatus* (small and sparse in *D. dubius*), simple foretarsus in the males (enlarged in *D. dubius*), and by the unique shape of the parameres.

BIOLOGY. Like other species of *Dyscinetus*, the larvae probably feed on roots and decaying plant matter. Adults are attracted to lights at night. *Dyscinetus laevipunctatus* has been collected from tropical dry forests, tropical moist forests, tropical wet forests, premontane moist forests, and premontane wet forests at elevations ranging from sea level to 1,500 meters.



Fig. 459. Distribution of *Dyscinetus laevipunctatus* in Costa Rica.



Fig. 460. Distribution of *Dyscinetus laevipunctatus* in Panama.

***Erioscelis* Burmeister, 1847**

Erioscelis Burmeister 1847: 72.

The genus *Erioscelis* is comprised of five species, previously known from only South America. Two species are now known to occur in Panama with one reaching Costa Rica. This genus, along with *Dyscinetus laevipunctatus* Bates and *Stenocrates*, are the only cyclocephalines in Costa Rica and Panama where the males have simple foretarsi instead of enlarged tarsi or a bifurcate median claw on the foretarsus. *Erioscelis* is different than *Stenocrates* because of its larger clypeus (Figs. 61-62) (small and trapezoidal in *Stenocrates*, Fig. 59), pronotum widest before the middle (widest at the middle in *Stenocrates*), and elytra with indistinctly paired rows of punctures (distinct in *Stenocrates*).

The immature stages are unknown for all species in the genus. Life history information is also sparse, although I have observed *E. columbica* feeding on the flowers of aroids (Fig. 461). Adults may be attracted to lights, but if they are hidden within the spathe of an aroid inflorescence, then they may not see the lights. This could account for low light trapping success with species of *Erioscelis*.



Fig. 461. *Erioscelis columbica* feeding on floral parts of *Dieffenbachia longispatha* at La Selva Biological Station, Costa Rica. Photo by H. Young.

Key to the Species of Adult *Erioscelis* of Costa Rica and Panama

1. Surface of pronotum in central third nearly impunctate, at most with minute, sparse punctures. Parameres as in Figs. 463-464 *columbica* Endrödi
- 1'. Surface of pronotum in central third distinctly punctate, punctures moderate in density, small. Parameres as in Figs. 467-468 *sobrina* Höhne

Clave para las Especies de Adultos de *Erioscelis* de Costa Rica y Panamá

1. Superficie del pronoto en el tercio central casi sin puntuaciones, a lo más con puntuaciones diminutas y dispersas. Parámetros como en la figuras 463-464 *columbica* Endrödi
- 1'. Superficie del pronoto en el tercio central con puntuaciones claramente visibles, puntuaciones moderadas en densidad, pequeñas. Parámetros como en la figuras 467-468 *sobrina* Höhne

***Erioscelis columbica* Endrödi,
1966**

(Figs. 461-466)

Erioscelis columbica Endrödi 1966: 413.

DESCRIPTION. Length 15.9-18.0 mm; width 9.0-9.8 mm. Color reddish brown to black. *Head:* Surface of frons with moderately large, moderately dense punctures. Frontoclypeal suture distinctly impressed, biarcuate. Clypeus with punctures smaller than on frons, similar in density, surface often feebly rugulose; apex broad, truncate, weakly reflexed. Interocular width equals 4.5 transverse eye diameters. Antenna 10-segmented, club subequal in length of segments 2-7. *Pronotum:* Surface in central third nearly smooth, with minute, sparse punctures; lateral thirds with punctures similar to those of frons except punctures a little less dense and a little larger. Pronotum widest just before middle. Base lacking marginal bead. *Elytra:* Surface weakly rugose and with moderate to large punctures in rows; double rows on disc not distinct. *Pygidium:* Surface with moderately dense, large punctures, punctures usually with minute, tawny setae. In lateral view, surface weakly to regularly convex. *Legs:* Foretibia tridentate, basal tooth removed from first 2. Foretarsus and claws in both sexes simple. Posterior tarsus subequal in length to posterior tibia. *Venter:* Prosternal process long, subconical, apex narrowly rounded; apex and posterior surface with long, sparse setae. Last sternite of male weakly emarginated *either side* of midline. *Parameres:* Figs. 463-464.

DISTRIBUTION. *Erioscelis columbica* was previously known only from Colombia (Endrödi 1966, 1985a). The specimens listed below constitute NEW COUNTRY RECORDS for both Costa Rica and Panama. In Costa Rica, this species is known from the Atlantic lowlands, and in Panama it is also known from the Atlantic lowlands except for a single specimen from Chiriqui and three specimens from southwestern Darien near the Colombian border.

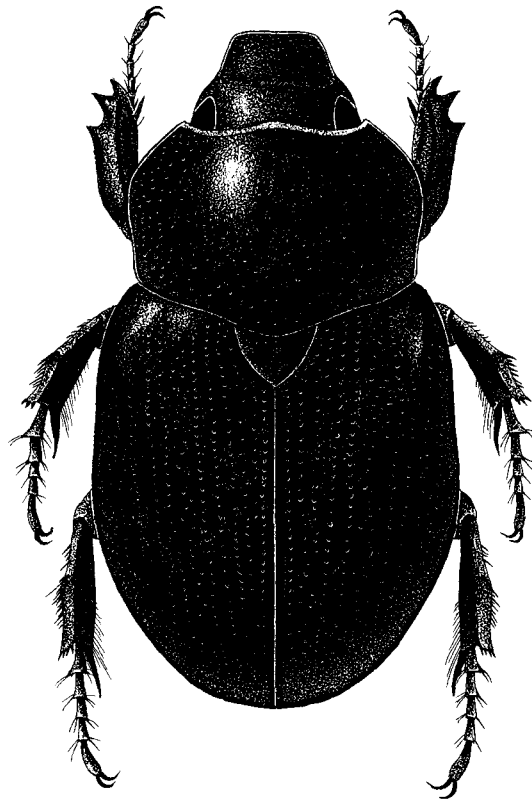
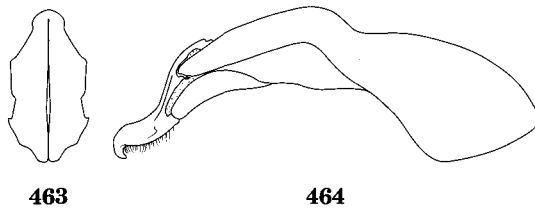


Fig. 462. *Erioscelis columbica*.



Figs. 463-464. *Erioscelis columbica* parameres.

LOCALITY RECORDS (Figs. 465-466). 131 specimens examined.

COSTA RICA (79). **HEREDIA** (52): Finca La Selva, Finca Naranja Valenciana (2 km S Pueblo Nuevo), Viejo Sarapiquí; **LIMÓN** (27): Amubri, Hamburg Farm, Pandora, Refugio Nacional Barra del Colorado (Río Sardinas).

PANAMA (52). **BOCAS DEL TORO** (13): Corriente Grande, Miramar; **COLÓN** (35): Río

Guanche Bridge (1 km E); DARIEN (3): Cana (Ancon Station), Río Tuquesa; PANAMA (1): Inter-American highway at Chame.

TEMPORAL DISTRIBUTION. January (8), February (2), March (3), April (10), May (11), June (5), July (38), August (5), September (2), November (1).

DIAGNOSIS. *Erioscelis columbica* is distinguished from *E. sobrina* by the virtually impunctate central third of the pronotum and by the form of the male parameres.

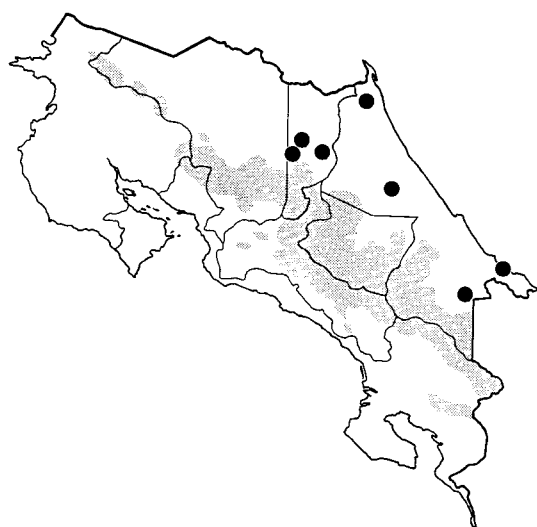


Fig. 465. Distribution of *Erioscelis columbica* in Costa Rica.

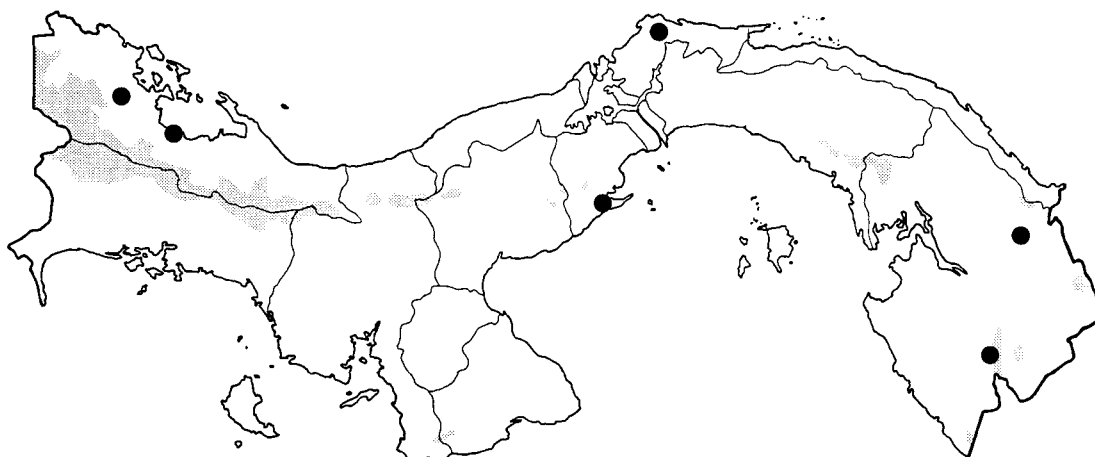


Fig. 466. Distribution of *Erioscelis columbica* in Panama.

BIOLOGY. Adults are attracted to lights but perhaps not strongly. Most of the specimens at hand were collected from the flowers of aroids (Fig. 461) and, being concealed in a covered flower spathe, they would not usually see a light. I have collected numerous specimens from the inflorescences of *Dieffenbachia longispatha* Engler and Krause (Araceae) in Panama. Young (1986, 1988a-b), who worked at the La Selva Biological Station in Costa Rica, observed that *E. columbica* fly to the inflorescence in darkness, suggesting that floral odors play a role as an attractant. After alighting on the spadix, they walk rapidly downward into the protected chamber around the female flowers where they eat the protein-rich staminoidea surrounding the stigmas. Most beetles remain in the inflorescence for 24 hr where they also mate in the dark, closed space provided by the spathe. Other beetles begin leaving on the evening of the third day, most of them departing between 17:45 and 19:30 hrs. Young noted they climb up the spadix as the spathe begins to close around the female (lower) portion of the spadix. At the same time the anthers of the male flowers are releasing copious amounts of pollen that covers the beetles as they crawl over the flowers. Beetles that remain longer will chew through the closed spathe to escape. Beetles fly an average of 80 meters between inflorescences, usually to the nearest female inflorescence, although distances of 400-1,000 meters were

recorded. The flowering season for *D. longispatha* extends from March through September although there is large year to year variation in the number of plants observed. The flowering phenology of *D. longispatha* correlates fairly well with the known temporal distribution of *E. columbica*.

Erioscelis columbica is a lowland species that has been taken in tropical moist forests and tropical wet forests at elevations ranging from sea level to 800 meters. Interestingly, it is known from only the Atlantic lowlands while *E. sobrina* is known from the Pacific lowlands.

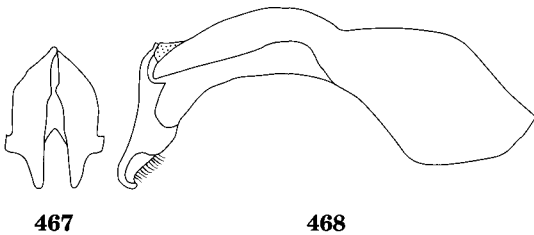
***Erioscelis sobrina* Höhne, 1921**
(Figs. 467-469)

Erioscelis sobrina Höhne 1921: 108.

DESCRIPTION. Length 15.8-19.0 mm; width 9.1-10.3 mm. Color dark reddish brown. **Head:** Surface of frons densely punctate, punctures moderate to large; midline with

shallow, longitudinal depression. Frontoclypeal suture distinct, strongly biarcuate. Clypeus moderately densely rugopunctate. Apex broadly truncate, weakly reflexed. Interocular width equals 4.0 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. **Pronotum:** Surface in central third with small punctures moderate in density; in lateral thirds punctures dense, large. Pronotum widest just before middle. Base without marginal bead. **Elytra:** Surface with rows of large punctures, punctures ocellate. Some intervals elevated (subcarinate), elevations often extending laterally between punctures of rows. **Pygidium:** Surface with large punctures moderate in density, punctures becoming smaller near apex and a little denser in lateral angles; a central, longitudinal, narrow area nearly impunctate. In lateral view, surface evenly convex. **Legs:** Foretibia tridentate, basal tooth slightly removed from others. Foretarsus and claws in both sexes simple. Posterior tarsus subequal in length to posterior tibia. **Venter:** Prosternal process short, conical, apex narrowly rounded; apex and posterior surface with long, sparse setae. Last sternite of male weakly emarginated *either side* of midline. **Parameres:** Figs. 467-468.

DISTRIBUTION. *Erioscelis sobrina* either has a very disjunct distribution or else is so rarely collected that we do not know exactly where it occurs. It was known from a single



Figs. 467-468. *Erioscelis sobrina* parameres.



Fig. 469. Distribution of *Erioscelis sobrina* in Panama.

location each in Venezuela and Brazil, and the Panama specimens represents a NEW COUNTRY RECORD.

LOCALITY RECORDS (Fig. 469). 1 specimen examined.

PANAMA (1). PANAMA (1): Punta Chame.

TEMPORAL DISTRIBUTION. July (1).

DIAGNOSIS. *Erioscelis sobrina* may be recognized by the central third of the pronotum having distinct (albeit small) punctures and by the form of the male parameres.

BIOLOGY. The Panamanian specimen was taken from tropical dry forests on the Pacific side of the isthmus near sea level whereas *E. columbica* is known, so far, from the Atlantic lowlands only.

Mimeoma Casey, 1915

Mimeoma Casey 1915: 111.

Mimeoma contains five species (Endrödi 1966, 1979, 1985a; Ratcliffe 1977). One species, *M. nigra* Endrödi, occurs in the Dominican Republic, and the remaining four species are found from Mexico to Brazil and Bolivia. There is a doubtful record for Cuba (Endrödi 1966). I have a single female specimen from

El Llano – Carti road in Panama (just to the east of Panama City) that might be *M. signatoides* Höhne. This species occurs in the Guianas, Brazil, Colombia, Ecuador, Peru, and Bolivia. We should be alert to the possibility that *M. signatoides* might occur in Panama but, at present, I am unsure based on the limited data.

Mimeoma species are similar in appearance to some *Cyclocephala* species except the clypeus in *Mimeoma* is subtriangular and pointed (Fig. 50) whereas the clypeus is rounded or emarginate at its apex in *Cyclocephala* (Figs. 53-58). They may also resemble, on a smaller scale, species of *Ancognatha* except that the mentum in *Ancognatha* is furrowed or depressed on its surface with a distinctly excised apex (Fig. 57), and in *Mimeoma* the surface of the mentum is flat and the apex is weakly emarginated (Fig. 56). Males of *Mimeoma* have a bidentate foretibia while males of *Ancognatha* have a tridentate foretibia. Casey (1915) also noted that in *Mimeoma* the mesocoxae are distinctly (he said “widely”) separated whereas they are nearly contiguous in *Ancognatha*. The antenna is 10-segmented, and the club is always short. Males have an enlarged protarsus.

The larval stages are unknown for any of the species of *Mimeoma*. Adults are attracted to lights as well as the flowers of some palms (*Bactris* and *Astrocaryum* species). All of the species are apparently lowland in distribution (less than 1,500 meters).

Key to the Species of Adult *Mimeoma* in Costa Rica and Panama

1. Pronotum testaceous. Elytra testaceous with narrow black edge along lateral, basal, and sutural margins (Figs. 471-472) *acuta* Arrow
- 1'. Pronotum mostly black. Elytra testaceous with large, elongate, central, black triangle (Figs. 476-477) *englemani* Ratcliffe

Clave para las Especies de Adultos de *Mimeoma* de Costa Rica y Panamá

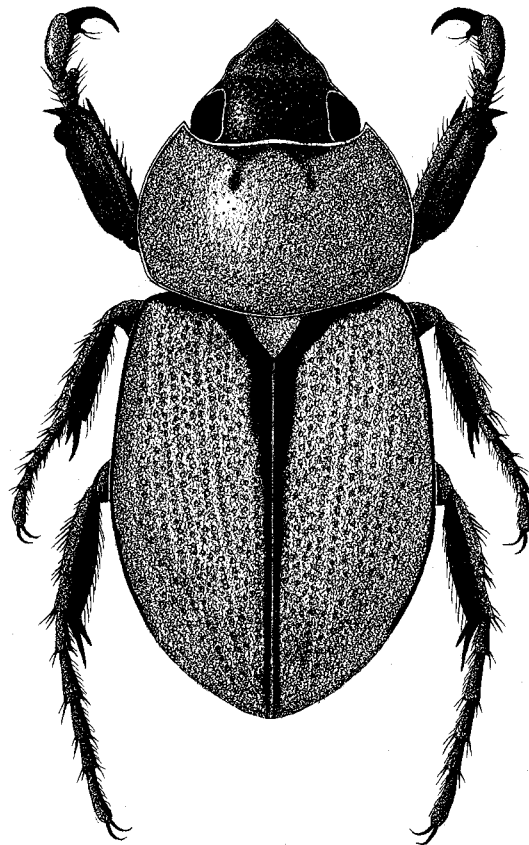
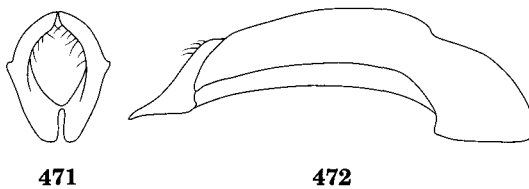
1. Pronoto testáceo. Elitros testáceos con un borde negro, angosto a lo largo de los márgenes laterales, basales y suturales (Figs. 471-472) *acuta* Arrow
- 1'. Pronoto en su mayor parte negro. Elitros testáceos con un triángulo central, negro grande y alargado (Figs. 476-477) *englemani* Ratcliffe

***Mimeoma acuta* Arrow, 1902**

(Figs. 470-474)

Mimeoma acuta Arrow 1902: 139.

DESCRIPTION. Length 13.0-16.0 mm; width 6.1-6.8 mm. Color testaceous except for: black head (clypeus often reddish brown or yellowish brown, especially at base); a small black spot on pronotum on anterior margin either side of middle (often absent); black edging on lateral, basal, and sutural margins of elytra; black expansion of post-medial, lateral edge of elytra in female; completely black pygidium or black either side of median, longitudinal, testaceous band (usually males) or testaceous pygidium (usually females); black anterior edge of meso- and metafemora; black tarsi; black . *Head:* Surface with moderately dense, moderately-sized punctures; punctures along lateral margins and eye canthus with minute, ferruginous setae (when not abraded away). Clypeus triangular, apex pointed. Interocular width equals 2.5-3.0 transverse eye diameters. Antenna with 10 segments, club subequal to segments 2-7. *Pronotum:* Surface moderately densely punctate; punctures small to moderate in size, some along lateral margins with short, ferruginous setae (when not abraded away). Base margined. *Elytra:* Surface finely shagreened, with rows of moderately large, shallow punctures, most punctures with minute setae (when not abraded away). Lateral margin in females gradually expanded from level of meta-trochanter to sternite 2. *Pygidium:* Surface in males shagreened, moderately densely punctate; punctures moderate in size, shallow, setigerous; setae long, dense, ferruginous. Females with surface shagreened, moderately densely punctate; punctures minute, lacking setae; most specimens with weak, central, longitudinal depression. In lateral view, surface in males weakly convex, that of females nearly flat. *Legs:* Foretibia in males broad, bidentate; females with foretibia of normal width, tridentate, teeth equally spaced. Foretarsus in males with segments 3-4 wider than long, 5th tarsomere and median claw greatly enlarged, claw entire at apex; foretarsus in female simple. *Venter:* Prosternal

Fig. 470. *Mimeoma acuta*.Figs. 471-472. *Mimeoma acuta* parameres.

process short, apex transversely oval and with round "button" on anterior half. *Parameres:* Figs. 471-472.

DISTRIBUTION. *Mimeoma acuta* is known from the lowlands of Honduras south to Colombia and Ecuador (Endrödi 1966, 1985a; personal observation). The specimens from Panama constitute a NEW COUNTRY RECORD.

LOCALITY RECORDS (Figs. 473-474). 127 specimens examined.

COSTA RICA (94). ALAJUELA (2): Alajuela, Bijagua (Volcán Tenorio); CARTAGO (24): Tuis (12 mi. SE), Turrialba (Grano de Oro); HEREDIA (24): Estación Magsasay, Finca La Selva, Finca Naranjo Valenciana (2 km S Pueblo Nuevo), Los Arbolitos; LIMÓN (27): Amubri, Cerro Cocori, Cerro Tortuguero, Estación Hitoy Cerere, Estación Cuatro Esquinas, Hamburg Farm, Río Sardinas; PUNTARENAS (17): Estación Esquinas, Estación Quebrada Bonita, Estación Sirena, Rancho Quemado, Vuelta Campana.



Fig. 473. Distribution of *Mimeoma acuta* in Costa Rica.

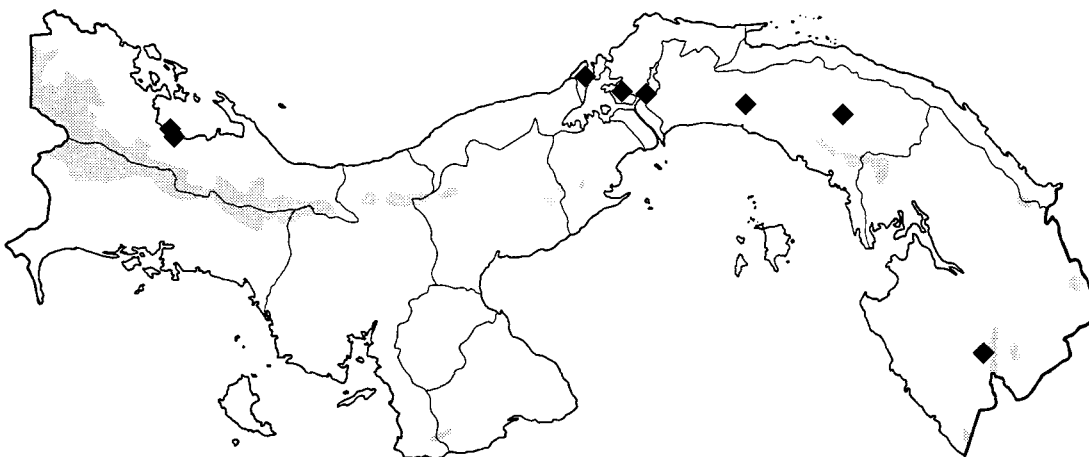


Fig. 474. Distribution of *Mimeoma acuta* in Panama.

PANAMA (33). BOCAS DEL TORO (14): Miramar, 2 mi. N of Divide on highway to Chiriquí Grande; CANAL ZONE (12): Madden Forest (km 2.5), Pipeline Road (km 2.4), Skunk Hollow, Soberanía National Park; DARIEN (3): Cana (Ancon Station); PANAMA (3): Chepo (30 km E), Ipetí.

TEMPORAL DISTRIBUTION. February (4), March (6), April (5), May (18), June (23), July (19), August (8), September (4), October (1), November (8), December (3).

DIAGNOSIS. *Mimeoma acuta* can be distinguished by its testaceous elytra that, while margined with black, do not have the distinctive black triangle present in *M. englemanni*. In addition, the pronotum is testaceous in *M. acuta* whereas it is mostly black in *A. englemanni*.

BIOLOGY. Adults have been taken in Costa Rica feeding on the flowers of the palms, *Bactris wendlandiana* Burret and *B. porschiana* Burret (Jim Beach and Helen Young, personal communications, 1979 and 1990, respectively) and *Bactris longiseta* Wendl., *B. wendlandiana*, and *Astrocaryum alatum* Loomis (Bullock 1981). They are also attracted to lights. *Mimeoma acuta* lives in tropical wet forests and premontane wet forests at elevations from sea level to 1,100 meters.

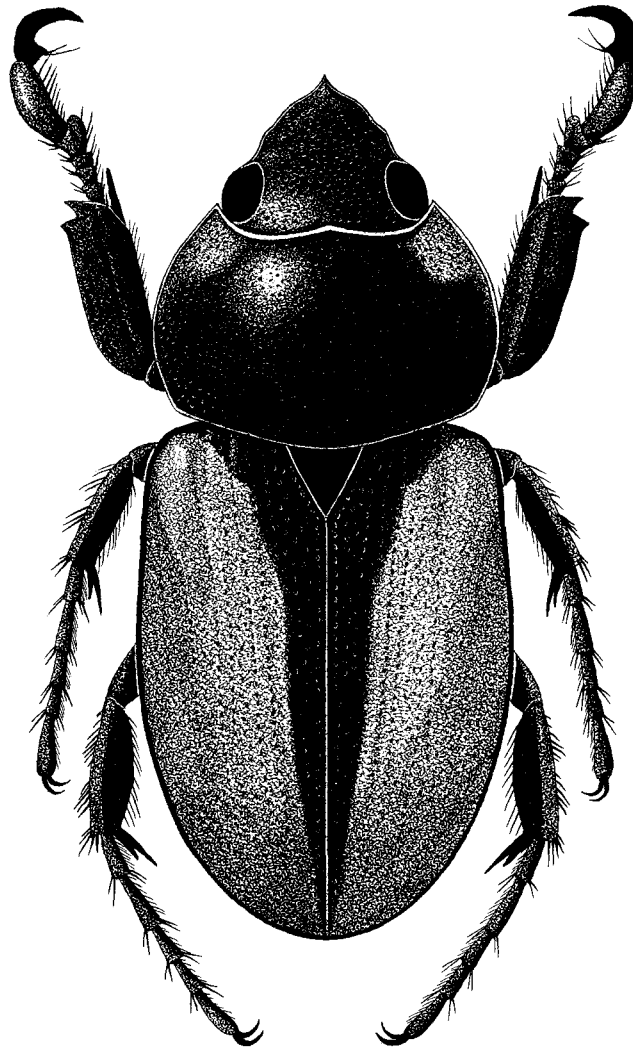


Fig. 475. *Mimeoma englemani*.

***Mimeoma englemani* Ratcliffe,
1977**

(Color Plate 1, Figs. 475-478)

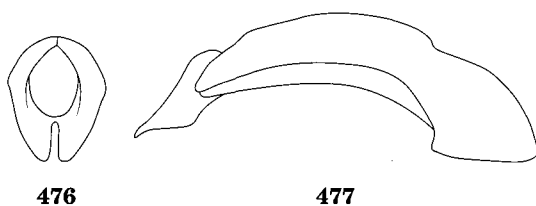
Mimeoma englemani Ratcliffe 1977: 430.

DESCRIPTION. Length 12.1-14.8 mm; width 6.0-7.0 mm. Color shining black except for anterior angles and lateral margins of pronotum and most of elytra which are testaceous; clypeus and pronotum occasionally with ferruginous or piceous clouding in center; elytra with black margins and black, elongately triangular streak in center (Fig. 475); expanded lateral margin of elytra in females black. *Head:* Frons and clypeus either

completely moderately densely punctate with moderate-sized punctures or similarly punctate only along lateral margins while discal area with small punctures; punctures on sides and eye canthus with short, ferruginous setae, these often abraded away. Clypeus triangular, apex pointed. Interocular width equals 2.5-3.0 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. *Pronotum:* Surface moderately densely punctate; punctures small to moderate in size, a few along lateral margins with short, ferruginous setae (these often abraded away). Base with marginal bead. *Elytra:* Surface finely shagreened, with rows of moderately large, shallow punctures, most punctures

with minute setae (when not abraded away). Females with lateral margin gradually expanded at level of metatrochanter to sternite 2. *Pygidium*: Surface in males shagreened, moderately densely punctate; punctures moderate in size, shallow, setigerous; setae long, dense, ferruginous. Females with surface shagreened, moderately densely punctate; punctures minute, lacking setae; most specimens with feeble, central, longitudinal depression. In lateral view, surface in males weakly convex, females with surface nearly flat. *Legs*: Foretibia in males broad, bidentate; in females, foretibia of "normal" width, tridentate, teeth equally spaced from each other. Foretarsus in males with segments 3-4 expanded (wider than long), 5th tarsomere and median claw greatly enlarged, claw entire at apex; foretarsus in females not enlarged. *Venter*: Prosternal process short, apex transversely oval and with nearly round "button" on anterior half. *Parameres*: Figs. 476-477.

DISTRIBUTION. *Mimeoma englemani* is known from the general vicinity of the Canal



Figs. 476-477. *Mimeoma englemani* parameres.

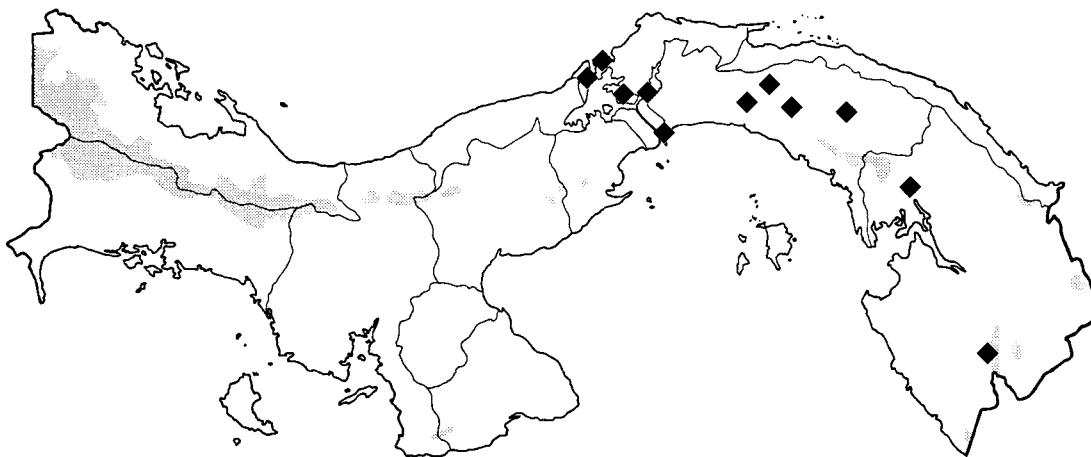


Fig. 478. Distribution of *Mimeoma englemani* in Panama.

Zone lowlands west to Darien Province. Although I do not believe it is rare, it seems to be infrequently collected.

LOCALITY RECORDS (Fig. 478). 25 specimens examined.

PANAMA (25). **CANAL ZONE** (15): Achote Road, Albrook Forest, Coco Solo Hospital, Madden Forest, Pipeline Road (km 2), (Parq. Nac. Soberanía); **DARIEN** (3): Cana (Ancon Station), Santa Fé; **PANAMA** (6): Altos de Majé, Chepo (80 km E), El Llano-Carti Road (km. 8), Ipetí (3 km E).

TEMPORAL DISTRIBUTION. May (10), June (15).

DIAGNOSIS. *Mimeoma englemani* is unique among the five species of *Mimeoma* because it has a shiny black head and pronotum with a black elongate, triangular mark on the elytra (that includes the scutellum) (Fig. 475). Although *M. acuta* has the elytra bordered by black on the base and both sides, I have never seen any example where this black edging is expanded to possibly resemble that of *M. englemani*.

BIOLOGY. Nothing is known of the biology of this species other than the adults are attracted to lights and the flowers of some palms (*Bactris* spp.) (Color Plate 1). They have been collected from tropical moist forests at elevations less than 1,000 meters.

***Stenocrates* Burmeister, 1847**

Stenocrates Burmeister 1847: 83.

The genus *Stenocrates* currently has 41 species (Endrödi 1966, 1985a; Ratcliffe 1978; Dechambre 1979b, 1985; Delgado 1991; Dupuis and Dechambre 1995), but more species are waiting to be described. The species are widely distributed from Mexico to Argentina with most occurring in South America. Four species are found in Costa Rica and Panama.

Unlike most species in the tribe Cyclocephalini, the males do not have enlarged foretarsi or claws. Species in the genus are also characterized by a relatively short, trap-ezoidal-shaped clypeus (Fig. 59) that has its apex broadly truncate (slightly emarginate or not); a distinct frontoclypeal suture; three pairs of punctate striae on the elytra; and the

four posterior legs are strongly flattened. The antenna is 10-segmented with a small club.

Most of the species are externally similar to one another and difficult to tell apart, and so great reliance is made on the form of the male parameres for identification. Even so, this is a difficult genus with which to work. Often, females not associated with males cannot be identified. Probably because of the high number of cryptic species in *Stenocrates*, a number of species still await discovery and description.

The immature stages remain unknown for any of the species. Life history information is also lacking. The adults are attracted to lights.

Endrödi (1966, 1985a) provided the last synopsis of the genus, but nearly 20 new species have been described since that time. These remain unincorporated in any key, and so a new synopsis is badly needed.

Key to the Species of Adult *Stenocrates* of Costa Rica and Panama

1. Size small, less than 14.0 mm. Pronotum punctate over entire surface *hardyi* Dechambre
- 1'. Size larger, always larger than 16.0 mm. Pronotum virtually impunctate in central third (with micropunctures only) 2
2. Clypeus with apex truncate or weakly convex. Pronotum usually completely smooth (rarely with punctures in posterior and anterior angles). Parameres as in Figs. 490-491 *laevicollis* Kirsch
- 2'. Clypeus with apex distinctly emarginate. Pronotum always with large punctures in posterior angles and usually anterior angles as well. Parameres different than those above 3
3. Anterior edge of broadly impressed frontoclypeal suture rounded. Parameres as in Figs. 480-481 *bicarinatus* Robinson
- 3'. Anterior edge of broadly impressed frontoclypeal suture finely carinated either side of middle. Parameres as in Figs. 494-495 *popei* Endrödi

Clave para las Especies de Adultos de *Stenocrates* de Costa Rica y Panamá

1. Tamaño pequeño, menos de 14.0 mm. Pronoto con puntuaciones sobre toda su superficie *hardyi* Dechambre
- 1'. Tamaño más grande que 16.0 mm. Pronoto virtualmente sin puntuaciones en el tercio central (solo con micropuntuaciones) 2
2. Clípeo con el ápice truncado o ligeramente convexo. Pronoto casi siempre completamente liso (raramente con puntuaciones en los ángulos anteriores y posteriores). Parámetros como en la figuras 490-491 *laevicollis* Kirsch
- 2'. Clípeo con el ápice claramente emarginado. Pronoto siempre con grandes puntuaciones en los ángulos posteriores y generalmente en los anteriores también. Parámetros diferentes a los mencionados arriba 3
3. Borde anterior de la ampliamente impresa sutura frontoclipeal redondeado. Parámetros como en la figuras 480-481 *bicarinatus* Robinson
- 3'. Borde anterior de la ampliamente impresa sutura frontoclipeal finamente carinado a ambos lados del medio. Parámetros como en la figuras 494-495 *popei* Endrödi

***Stenocrates bicarinatus* Robinson,
1947**

(Figs. 479-483)

Stenocrates bicarinatus Robinson 1947: 233.
Stenocrates difficilis Endrödi 1966: 427 (NEW
SYNONYMY).

DESCRIPTION. Length 16.5-22.0 mm; width 8.8-12.0 mm. Color black. *Head:* Frons relatively smooth, with sparse micropunctures. Frontoclypeal suture distinctly impressed, biarcuate, ridge in front of suture rounded, obsolete in center. Clypeus transversely rugulose or vaguely roughened; apex shallowly emarginate and thickened. Interocular width equals 3.0 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. *Pro-notum:* Surface extremely finely shagreened, with sparse micropunctures; appearing smooth except for cluster of large punctures in posterior angle (with a few extending onto disc behind each eye) and occasionally a few (usually smaller) in anterior angle. Lateral margin with thick marginal bead, base without marginal bead. *Elytra:* Surface with sutural stria and 3 pair of discal striae (lateral paired row not as distinct), each stria comprised of moderately large, closely adjacent punctures. First broad interval and intervals between each double row with moderately large punctures, punctures absent near bases (occasionally half of length) of each. *Pygidium:* Surface with moderately dense to dense punctures; punctures moderately large, some c-shaped (especially at sides), most with minute setae. In lateral view, surface in males regularly convex, weakly convex in females. *Legs:* Foretibia tridentate, basal tooth distinctly removed from others. Foretarsus in males simple, not enlarged. Posterior tarsus shorter than posterior tibia. *Venter:* Prosternal process long, columnar, apex flattened and broadly subtriangular (corners rounded and base of triangle toward head). *Parameres:* Figs. 480-481.

DISTRIBUTION. *Stenocrates bicarinatus* was described from Panama (Robinson 1947), and Endrödi (1966) added Colombia when he described *A. difficilis* (now a synonym). The records listed below for Costa Rica and speci-

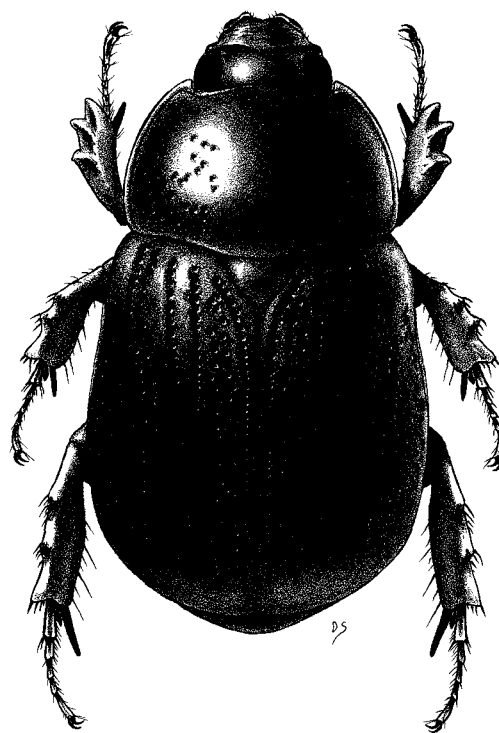
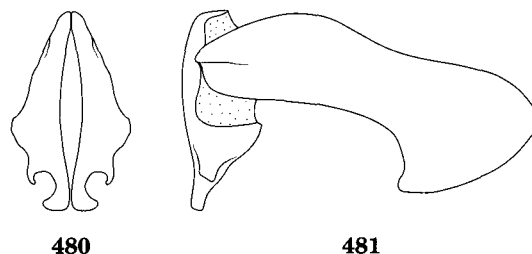


Fig. 479. *Stenocrates bicarinatus*.



Figs. 480-481. *Stenocrates bicarinatus* parameres.

mens I have for Honduras and southern Mexico are NEW COUNTRY RECORDS. I have no doubt this species will also be found in Nicaragua. Robinson's allotype was from Guatemala and, while I believe it is a bit of a stretch to place an unassociated female of *Stenocrates* from Guatemala with a male (the holotype) from Panama, we cannot discount that *S. bicarinatus* also occurs in Guatemala. This species is generally distributed in the lowlands of Costa Rica and possibly also those of Panama even though current records are from only the eastern half of Panama.

LOCALITY RECORDS (Fig. 482-483). 238 specimens examined.

COSTA RICA (190). ALAJUELA (1): Playuelas; GUANACASTE (20): Estación Palo Verde, Estación Pitilla, Estación Santa Rosa, Finca Jenny (30 km N Liberia), Playa Naranjo; LIMÓN (4): Cerro Tortuguero, Estación Cuatro Esquinas, Río Sardinas; PUNTARENAS (165): Estación Esquinas, Estación Sirena, Rancho Quemado, Rincón.

PANAMA (48). CANAL ZONE (18): Coco Solo Hospital, Corozal, Ft. Gulick, Madden Dam, Skunk Hollow; COLÓN (12): Santa Rita Ridge; DARIEN (12): El Real, Río Tacarcuna, Yaviza; PANAMA (6): Altos de Majé, El Llano-Carti road (km. 13), Las Cumbres.



Fig. 482. Distribution of *Stenocrates bicarinatus* in Costa Rica.



Fig. 483. Distribution of *Stenocrates bicarinatus* in Panama.

TEMPORAL DISTRIBUTION. January (22), February (3), March (6), April (4), May (25), June (52), July (16), August (10), October (27), November (52), December (22).

DIAGNOSIS. *Stenocrates bicarinatus* resembles *S. popei* and *S. laevicollis*. It can be separated from *S. popei* only by the form of the male parameres. In *S. bicarinatus*, the clypeus is slightly (though distinctly) emarginate at the apex (truncate in *S. laevicollis*), the pronotum has a few large punctures in the posterior and sometimes the anterior angles (completely smooth or sometimes with a few large punctures in posterior angle or posterior and anterior angles in *S. laevicollis*), the apex of the prosternal process is broadly subtriangular (narrowly conical in *S. laevicollis*; difficult to see without comparative material), and the parameres of the male are different (Figs. 480-481, 490-491).

NOMENCLATURE. Endrödi's *S. difficilis* (1966) is a synonym of *S. bicarinatus*. Endrödi (1985a) indicated *S. bicarinatus* was unknown to him, but the male holotype is at the U.S. National Museum. I have examined it, and it is conspecific with *S. difficilis*.

BIOLOGY. Adults are attracted to lights. They occur in tropical dry forests, tropical moist forests, and tropical wet forests at elevations ranging from near sea level to 1,000 meters.

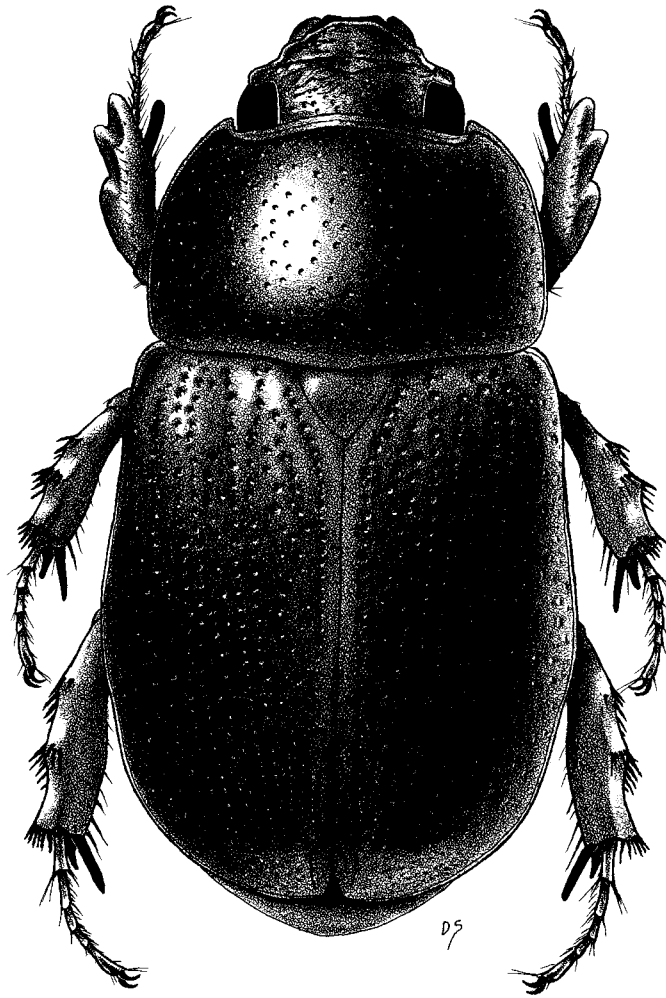


Fig. 484. *Stenocrates hardyi*.

***Stenocrates hardyi* Dechambre,
1985**

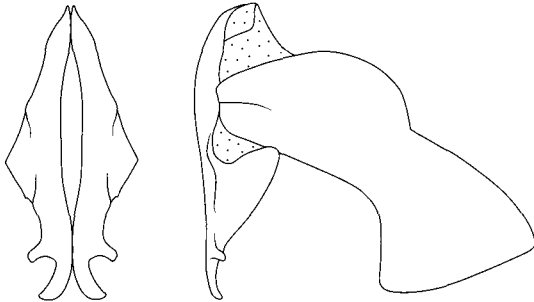
(Figs. 484-488)

Stenocrates hardyi Dechambre 1985: 143.

DESCRIPTION. Length 11.1-13.3 mm; width 5.8-7.3 mm. Color occasionally dark reddish brown, usually black. *Head:* Surface of frons transversely rugopunctate, punctures small to moderate in size. Frontosutural region with weakly arcuate, weakly raised ridge, ridge lower at middle. Clypeus transversely rugose; sides and apical margin thickened, apex broadly truncate and weakly emarginate. Interocular width equals 3.0-4.0 transverse eye diameters. Antenna with 10 segments, club subequal to segments 2-7.

Pronotum: Surface finely shagreened, punctate; punctures moderate to large in size, moderate in density, deep; slightly more dense on sides. Marginal bead at base absent. *Elytra:* Surface with 3 pair of punctate striae and sutural stria; punctures moderate to large, deep, closely adjacent to one another in same row, U-shaped (open end of "U" facing posteriorly). Intervals with random, similar punctures; 2nd and 3rd intervals usually impunctate at base. *Pygidium:* Surface completely punctate, with moderately dense, large punctures. In lateral view, surface regularly convex in males, weakly convex in females. *Legs:* Foretibia tridentate, basal tooth slightly removed from others. Male with foretarsus simple, not enlarged. Posterior tarsus shorter than posterior tibia. *Venter:*

Prosternal process short, subconical, apex narrowly rounded, base on posterior side emarginate. *Parameres*: Figs. 485-486.



485

486

Figs. 485-486. *Stenocrates hardyi* parameres.

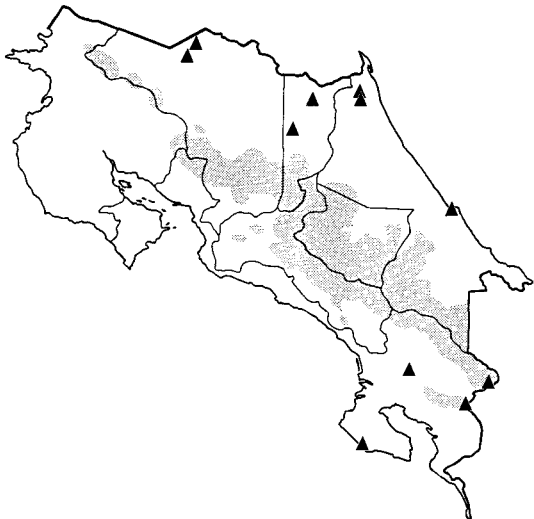


Fig. 487. Distribution of *Stenocrates hardyi* in Costa Rica.



Fig. 488. Distribution of *Stenocrates hardyi* in Panama.

DISTRIBUTION. *Stenocrates hardyi* was known previously from the lowlands of central Panama. The Costa Rican specimens represent a NEW COUNTRY RECORD.

LOCALITY RECORDS (Figs. 487-488). 176 specimens examined.

COSTA RICA (53). ALAJUELA (8): Caño Negro; HEREDIA (3): Finca Naranjo Valenciana (2 km S Pueblo Nuevo), Los Arbolitos; LIMÓN (30): Buenos Aires, Río Sardinas, Sector Cerro Cocori; PUNTARENAS (12): Estación Sirena, Vuelta Campana.

PANAMA (123). CANAL ZONE (107): Achiotte Road, Ancon Hill, Barro Colorado Island, Black Tank Road, Cerro Paraíso, Coco Solo Hospital, Corozal, Ft. Gulick, Ft. San Lorenzo, Gatun Lake Lookout, Piña Road, Skunk Hollow; COCLÉ (1): Nata; COLÓN (9): Colón, Portobelo, Santa Rita Ridge; PANAMA (8): Las Culebras, Río Trinidad.

TEMPORAL DISTRIBUTION. January (13), February (19), March (14), April (8), May (72), June (6), July (3), October (6), December (32).

DIAGNOSIS. *Stenocrates hardyi* is unique among the Costa Rican and Panamanian species of *Stenocrates* because of its small size. While there is another small species in Mexico (*S. canuli* Delgado) and several small black species in South America (*S. mahunkai* Endrödi, *S. holomelanus* (Germar), *S.*

minutus Endrödi, *S. laceyi* Ratcliffe), none of these occur in Central America. The parameres of the male are also diagnostic. In general appearance it could be confused with *Euetheola humilis* (Burmeister), which is in the tribe Pentodontini. They may be easily distinguished because the apex of the clypeus in *E. humilis* has two, strongly reflexed teeth whereas the apex of the clypeus in all *Stenocrates* species is simply truncate or slightly emarginate and never with teeth.

BIOLOGY. Adults are attracted to lights. They have been collected from tropical dry forests, tropical moist forests, and tropical wet forests at elevations ranging from near sea level to 500 meters.

***Stenocrates laevicollis* Kirsch,
1871
(Figs. 489-493)**

Stenocrates laevicollis Kirsch 1871: 373.

DESCRIPTION. Length 19.0-22.0 mm; width 10.2-11.9 mm. Color black. *Head:* Frons relatively smooth, with vague, sparse micro-punctures. Frontoclypeal suture deeply impressed, biarcuate. Clypeus with surface transversely rugose; apex truncate to weakly convex, anterior edge weakly thickened. Interocular width equals 2.8-3.3 transverse eye diameters. Antenna 10-segmented, club subequal to segments 2-7. *Pronotum:* Surface extremely finely shagreened, appearing smooth, only rarely with a few large punctures in posterior or posterior and anterior angles. Lateral margins with thick marginal bead; base lacking marginal bead. *Elytra:* Surface with sutural and 3 pair of punctate striae; punctures moderate to large, closely adjacent in each row. Intervals impunctate or with a few sparse, moderately large punctures. *Pygidium:* Surface densely punctate; punctures moderate to moderately large, often with minute setae. In lateral view, surface evenly convex in male, weakly convex or nearly flat in female. *Legs:* Foretibia tridentate, basal tooth slightly removed from others. Foretarsus in male simple, not enlarged. Posterior tarsus shorter than posterior tibia. *Venter:* Prosternal process long, columnar,

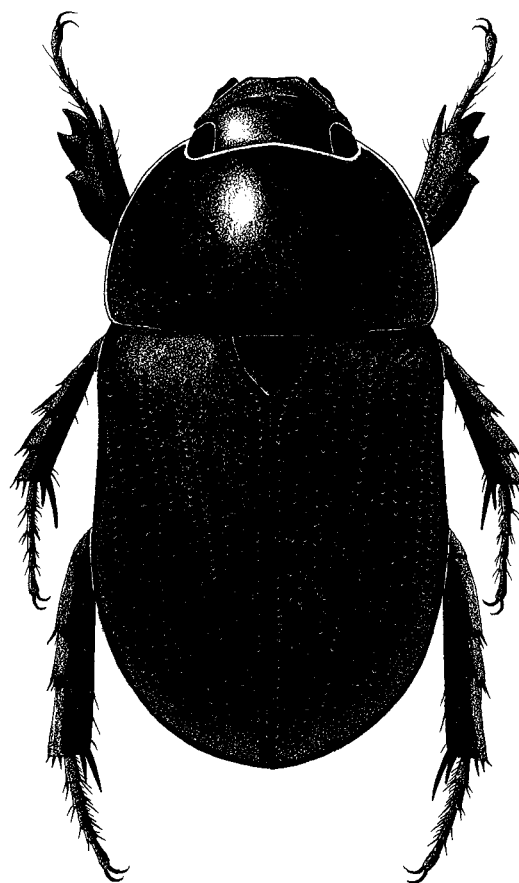
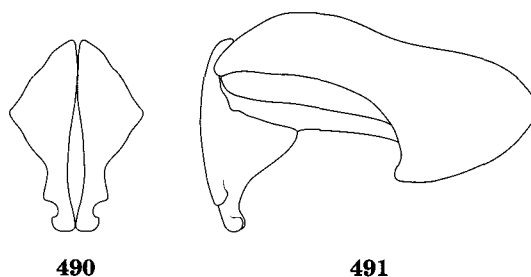


Fig. 489. *Stenocrates laevicollis*.



Figs. 490-491. *Stenocrates laevicollis* parameres.

apex narrowly conical, not flattened. *Parameres:* Figs. 490-491.

DISTRIBUTION. *Stenocrates laevicollis* was previously known from Colombia and Ecuador (Endrödi 1966). The records listed below for Costa Rica and Panama and those specimens I have from Peru and southern Mexico are NEW COUNTRY RECORDS. This species is sparsely distributed throughout most of Costa Rica and in western Panama.

LOCALITY RECORDS (Fig. 492-493). 24 specimens examined.

COSTA RICA (15). ALAJUELA (2): San Ramón; CARTAGO (8): Chirripó (Grano de Oro), Moravia (5 mi SE); GUANACASTE (1): Estación Cacao; HEREDIA (1): Estación El Ceibo; LIMÓN (3): Fila Matama, Río Sardinas; PUNTARENAS (1): Las Cruces Field Station.

PANAMA (9). CHIRIQUI (8): Continental Divide Trail (Reserva Fortuna), Fortuna Dam, Santa Clara; PANAMA (1): El Llano (9 km N). **TEMPORAL DISTRIBUTION.** February (2), April (1), May (4), June (2), July (4), August (5), September (3), November (3)

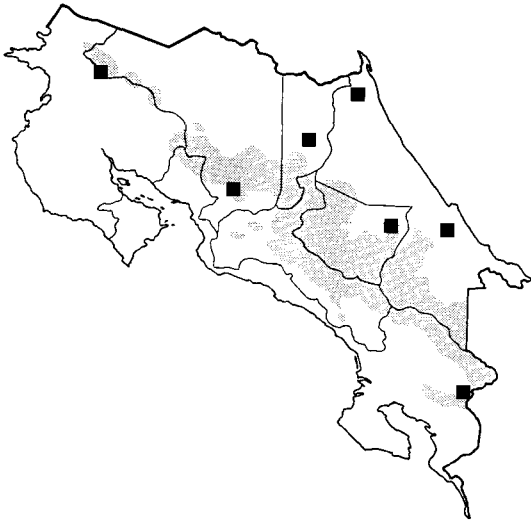


Fig. 492. Distribution of *Stenocrates laevicollis* in Costa Rica.



Fig. 493. Distribution of *Stenocrates laevicollis* in Panama.

DIAGNOSIS. *Stenocrates laevicollis* resembles *S. bicarinatus* and *S. popei*. In *S. laevicollis* the clypeus is truncate or weakly convex (shallowly but distinctly emarginate in *S. bicarinatus* and *S. popei*), the pronotum is completely smooth or, rarely, with a few large punctures in the posterior angle or posterior and anterior angles (always with large punctures in the posterior and often the anterior angles in *S. bicarinatus* and *S. popei*), the apex of the prosternal process is narrowly conical (broadly subtriangular in *Stenocrates bicarinatus* or elongate-oval in *S. popei*; difficult to ascertain without comparative material), and the parameres of the male are different (Figs. 490-491, 494-495).

BIOLOGY. Although the adults are attracted to lights, they are never abundant and are also seemingly sparsely distributed. *Stenocrates laevicollis* has been found in tropical wet forests, premontane moist forest transition, premontane wet forest transition, and lower montane wet forests at elevations ranging from near sea level to 1,800 meters.

***Stenocrates popei* Endrödi, 1971**
(Figs. 494-496)

Stenocrates popei Endrödi 1971: 179.

DESCRIPTION. Length 17.4-20.0 mm; width 9.0-10.4 mm. Color black. *Head:* Surface of frons completely smooth with sparse, minute or small punctures, or similar but

with anterior half weakly rugopunctate. Frontoclypeal suture impressed, biarcuate; transverse ridge in front of suture weak, finely carinate either side of middle. Clypeus transversely rugose; apex thickened, shallowly emarginate. Interocular width equals 2.5 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. *Pronotum*: Surface smooth, with large punctures in posterior angles; punctures moderate in density, a few extending onto disc behind eye; anterior angles also with a few moderately-sized punctures. Lateral margin with thick marginal bead; base lacking marginal bead. *Elytra*: Surface with sutural and 3 pairs of punctate striae; punctures in each stria moderate to large, closely adjacent to one another. Intervals with moderate to large, irregularly-spaced punctures; punctures absent in basal half of second large interval. *Pygidium*: Surface with moderate to large punctures; punctures moderately dense. In lateral view, surface regularly convex in males, weakly convex in females. *Legs*: Foretibia tridentate, basal tooth slightly removed from others.

Foretarsus and claw in males simple, not enlarged. Posterior tarsus shorter than posterior tibia. *Venter*: Prosternal process long, columnar, apex flattened and elongate-oval. *Parameres*: Figs. 494-495.

DISTRIBUTION. *Stenocrates popei* was known previously from Guyana, the type locality. The specimen listed below for Panama and those I have from northeastern Brazil and French Guiana are NEW COUNTRY RECORDS. In the study area, this species is known only from eastern Panama in Darien province.

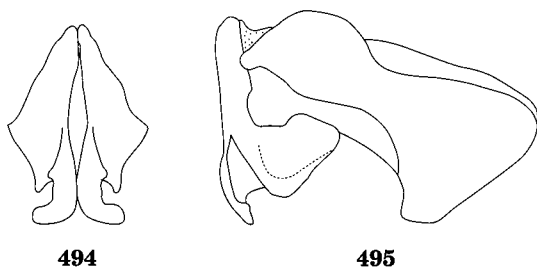
LOCALITY RECORDS (Fig. 496). 1 specimen examined.

PANAMA (1). **DARIEN** (1): Head of Río Seteganti (S of Chepigana).

TEMPORAL DISTRIBUTION. February (1).

DIAGNOSIS. *Stenocrates popei* can be separated from *S. bicarinatus* only by the form of the parameres (see Figs. 494-495, 480-481). It can be separated from *S. laevicollis* by its emarginate clypeal apex (truncate in *S. laevicollis*) and form of the parameres (Figs. 494-495, 490-491).

BIOLOGY. Adults are attracted to lights. The single Panamanian specimen was collected in tropical moist forests at an elevation of 500 meters.



Figs. 494-495. *Stenocrates popei* parameres.



Fig. 496. Distribution of *Stenocrates popei* in Panama.



Color Plate 3. *Pucaya castanea* on a light trap sheet. Illustration by Dan Schmidt.

TRIBE PENTODONTINI

The Pentodontini is the largest tribe of dynastines (with over 550 species) and cosmopolitan in its geographic distribution. There are 25 genera in the New World (Ratcliffe 1981, 1991), although one of these, *Heteronychus*, has been introduced into Brazil from Africa. A little over 100 species occur in the Americas. Six genera, containing 17 species, occur in Costa Rica and Panama.

The tribal status of the Pentodontini has varied since it was first proposed as a distinct taxonomic category of the Dynastinae by Burmeister (1847). Bates (1888) and Casey (1915) both placed the pentodontines as a category distinct from the oryctines, but there was no consensus among taxonomists as to its tribal status. Casey (1915) appears to have been the first to actually use the Pentodontini as a tribe. Arrow (1937a) and Blackwelder (1944) did not maintain the tribe as separate from the Oryctini in their important checklists, nor did Leng (1920), Saylor (1948), or Arnett (1968) in their treatments of the North American fauna. Endrödi (1969, 1985a) comprehensively reviewed and defined the Pentodontini, and I used the tribal concept in the latest generic treatment of the North American dynastines (Ratcliffe 2002c). Endrödi's definition did not address monophyly, and I remain concerned that the Pentodontini (as currently defined) may not be monophyletic. In particular, the head and pronotal armature and the form of the apex of the meso- and metatibiae that are used to characterize the tribe are not consistently expressed.

Adult pentodontines are distinguished by the presence of tubercles, carinae or a fovea on the head and/or pronotum; mandibles with or without teeth; propygidium with or without a stridulatory structure; protibia usually tridentate; and apex of the metatibia usually truncate and margined with short, spine-like setae, protarsus occasionally enlarged in males. Dimorphism between males and females is slight.

Some species of Pentodontini are similar to some species of Oryctini. The two tribes (as

currently structured) may generally be separated by the presence of a truncate or nearly smooth apical rim on the apex of the posterior tibia in the pentodontines (Figs. 38-42) and by a toothed (including apical tooth) or strongly crenulate rim in the oryctines (Figs. 43-47). I am not comfortable with this single, sometimes variable (or transitional) character used to separate taxa at the tribal level. Accordingly, I hope to conduct a phylogenetic analysis in the future to clarify generic and tribal relationships and classification. David Hawks (University of California-Riverside) and Andrew Smith (University of Nebraska) are addressing similar questions using molecular methods.

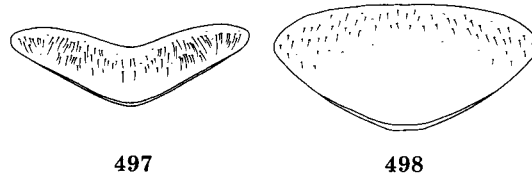
As opposed to the Cyclocephalini, all pentodontines have at least some head or pronotal armature in the form of carinae, tubercles, or even horns (although none of the Central American species possess horns). Species in the genus *Parapuycaya* are only weakly binodose (tuberculate) near the front of the pronotum, and could be easily mistaken for a cyclocephaline unless the pronotum or the first tarsomere of the posterior leg (which is slightly produced dorso-apically) is closely examined.

According to Morón *et al.* (1996), larvae representing eight American genera are known. They are characterized by 1-3 dorsal sensory spots on the last antennal segment; the molar area of the left mandible is dentate or, if lacking teeth, then the stridulatory teeth of the maxilla have acute projections directed distally; and the raster has one or more rows of palidia or, if lacking the palidia, then the chaetoparia of the epipharynx has few setae.

Most, if not all, adult pentodontines are nocturnal in habits and so are rarely seen except at lights at night. Adults are known to feed on foliage, organic material in the soil, and plant roots. The larvae develop in the soil where they feed on roots, humus, decaying leaves, and large decaying roots. Considering the number of species in the Pentodontini, we know very little of their life history and habits, and this is an area for future endeavor.

Key to the Genera of Adult Pentodontini of Costa Rica and Panama

1. Dorsal surface of head with single, median tubercle (tubercle occasionally transverse) 2
- 1'. Dorsal surface of head with 2 distinct tubercles, carinae, or short horns, or completely unarmed 3
- 2(1). Mandibles with 3 large, acute teeth. Elytra nearly smooth. Propygidium distinctly produced posteriorly, thus pygidium distinctly shorter (Fig. 497) **Bothynus Hope**
- 2'. Mandibles entire or weakly lobed. Elytra distinctly punctate. Propygidium not produced posteriorly, pygidium not shortened (Fig. 498) **Barutus Ratcliffe**
- 3(1'). Dorsal surface of head unarmed. Elytra testaceous; pronotum and pygidium reddish brown **Parapucaya Prell**
- 3'. Dorsal surface of head with tubercles, carinae, or short horns. Body unicolorous reddish brown or black 4
- 4(3'). Mandibles concealed beneath clypeus. Pronotum distinctly binodose or bituberculate subapically. **Pucaya Ohaus**
- 4'. Mandibles visible in dorsal view. Pronotum apically with single tubercle and/or subapical fovea or completely rounded 5
- 5(4'). Mandibles without teeth or with 1 apical tooth and a basal lobe. Interocular width greater than 4.5 transverse eye diameters. Size 10.5-15.5 mm **Eutheola Bates**
- 5'. Mandibles with 2 teeth and a basal lobe or 3 teeth. Interocular width equals 2.5-4.0 transverse eye diameters. Size 13.5-34.0 mm **Tomarus Erichson**



Figs. 497-498. Pygidium (posterior view) of *Bothynus* sp. and *Barutus* sp., respectively.

Clave para los Géneros de Adultos de Pentodontini de Costa Rica y Panamá

1. Superficie dorsal de la cabeza con un solo tubérculo medio (tubérculo ocasionalmente transversal) 2
- 1'. Superficie dorsal de la cabeza con 2 tubérculos claramente visibles, carinas, cuernos cortos o totalmente sin nada 3
- 2(1). Mandíbulas con 3 dientes grandes y agudos. Elitros casi lisos. Propigidio claramente proyectado posteriormente, siendo el pigidio claramente más corto (Fig. 497) **Bothynus Hope**
- 2'. Mandíbulas con el borde continuo o ligeramente lobuladas. Elitros con puntuaciones claramente visibles. Propigidio no proyectado posteriormente, pigidio no acortado (Fig. 498) **Barutus Ratcliffe**
- 3(1'). Superficie dorsal de la cabeza sin tubérculos, carinas, o cuernos cortos. Elitros testáceos, pronoto y pigidio pardo rojizos **Parapucaya Prell**
- 3'. Superficie dorsal de la cabeza con tubérculos, carinas, o cuernos cortos. Cuerpo de un solo color pardo rojizo o negro 4

- 4(3'). Mandíbulas escondidas bajo el cípeo. Pronoto evidentemente binodoso o bituberculado subapicalmente ***Pucaya Ohaus***
- 4'. Mandíbulas visibles en vista dorsal. Pronoto apicamente con un solo tubérculo y/o fovea subapical o completamente redondeado 5
- 5(4'). Mandíbulas sin dientes o con un lóbulo basal y en diente apical. Ancho interocular más grande que 4.5 diámetros transversales del ojo. Tamaño de 10.5 a 15.5 mm ***Euetheola Bates***
- 5'. Mandíbulas con 2 dientes y un lóbulo basal ó 3 dientes. Ancho interocular entre 2.5 y 4.0 diámetros transversales del ojo. Tamaño de 13.5 a 34.0 mm ***Tomarus Erichson***

**Key to the Genera of Larval Pentodontini of Costa Rica and Panama
(from Morón and Ratcliffe 1997) (Larvae of *Bothynus*, *Barutus*,
Parapucaya, *Pucaya* are unknown)**

1. Raster with palidia and septula 2
- 1'. Raster without palidia and septula ***Tomarus Erichson*** (in part)
2. Palidia monostichous, nearly parallel, each palidium consisting of 7-10 strongly compressed pali with slightly hooked tips. Last segment of antenna with 2 dorsal sensory spots. Maximum width of head capsule 4.37 mm ***Euetheola Bates***
- 2'. Palidia polystichous, each palidium consisting of a patch of 5-7 irregular, longitudinal rows of sharp, cylindrical, spine-like setae. Palidia and septula extending across lower anal lip. Last segment of antenna with 2-4 dorsal sensory spots. Maximum width of head capsule 6.5 mm ***Tomarus Erichson*** (in part)

**Clave para los Géneros de Larvas de Pentodontini
de Costa Rica y Panamá
(de Morón y Ratcliffe 1997) (No se conocen las larvas de *Bothynus*,
Barutus, *Parapucaya*, *Pucaya*)**

1. Raster con palidia y septula 2
- 1'. Raster sin palidia y septula ***Tomarus Erichson*** (en parte)
2. Palidia monosticosa, casi paralela, cada palidium consistiendo de 7 a 10 pali fuertemente comprimidos con puntas ligeramente ganchudas. Último segmento de la antena con 2 manchas sensoriales dorsales. Ancho máximo de la cápsula cefálica 4.37 mm ***Euetheola Bates***
- 2'. Palidia polisticosa, cada palidium consistiendo de un parche de 5 a 7 hileras irregulares longitudinales de setas semejantes a espiñas, agudas y cilíndricas. Palidia y septula se extienden a través del labio anal inferior. Último segmento de la antena con 2 a 4 manchas sensoriales dorsales. Ancho máximo de la cápsula cefálica 6.5 mm ***Tomarus Erichson*** (en parte)

***Barutus* Ratcliffe, 1981**

Barutus Ratcliffe 1981: 463.

Barutus is a monotypic genus that is known only from the highlands of Costa Rica and Panama. It is easily distinguished from other Central American Pentodontini

by its reddish brown color, relatively large size for a pentodontine (up to 34 mm in length), large and externally lobed mandibles, and heavily punctate elytra.

***Barutus hartmanni* Ratcliffe, 1981**
(Figs. 499-503)

Barutus hartmanni Ratcliffe 1981: 468.

DESCRIPTION. Length 20.0-33.3 mm; width 13.1-18.2 mm. Color reddish brown. *Head:* Frons rugopunctate to rugose, with transverse, weakly binodose tubercle. Clypeus triangular, apex rounded, surface rugopunctate to weakly rugose. Mandibles large, leaf-like, with 2 broadly rounded lobes. Interocular width equals 3.0 (in smallest individuals) to 3.5 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. *Pronotum:* Surface weakly crazed, anterior half and sides with moderate to large punctures, punctures moderately dense, deep, umbilicate, most oval. Posterior half of pronotum with punctures smaller, less dense. A small, transverse tubercle either side of midline in apical fourth either present or not. Base with marginal bead. *Elytra:* Sutural stria deeply impressed. Disc weakly crazed, median half irregularly punctate, punctures moderate to large; lateral half of disc with 5 usually distinct rows of punctures, punctures moderate to large, becoming obsolete in apical third. Sides with moderate to large punctures, some in indistinct rows, interrupted by several transverse rugae (especially behind humerus). *Pygidium:* Convex in lateral view. Surface weakly crazed. Disc with minute, sparse punctures. Base setigerously punctate in a transverse band; punctures small, setae long, reddish brown. Lateral margins weakly punctate apically to weakly rugopunctate basally. *Legs:* Anterior tibia with 4 teeth. Posterior tibia with apex truncate, weakly crenulate laterally, bearing about 20 spinules. *Venter:* Prosternal process long, subtriangular in cross section, "top" with transverse, arcuate ridge projecting anteriorly. *Parameres:* Figs. 500-501.

DISTRIBUTION. *Barutus hartmanni* is found in the Cordillera Central from Chiriqui in western Panama to Monteverde in north-central Costa Rica. It is an uncommon species.

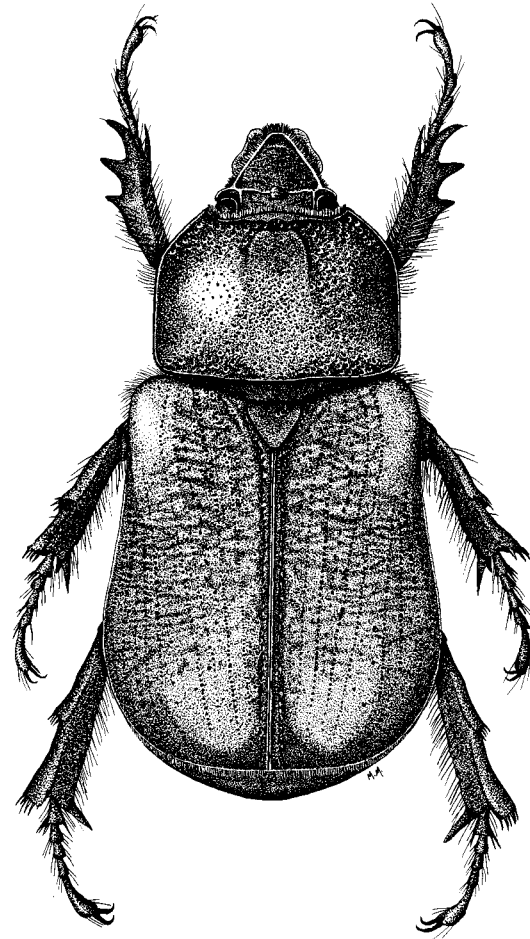
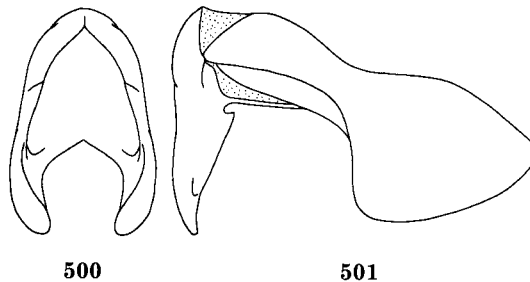


Fig. 499. *Barutus hartmanni*.



Figs. 500-501. *Barutus hartmanni* parameres.

LOCALITY RECORDS (Figs. 502-503). 71 specimens examined.

COSTA RICA (42). **CARTAGO** (18): Refugio Nacional de Tapanti (Quebrada Segunda, Río Pejibaye), Río Grande de Orosi; **PUNTA-RENAS** (11): Monteverde Forest Reserve;

SAN JOSÉ (1): Estación Cuerici (4.6 km E Villa Mills).

PANAMA (29). CHIRIQUI (29): Boquete, Cerro Punta, Cerro Punta (2.5 km W), Fortuna, El Volcán, Santa Clara (10 km N).

TEMPORAL DISTRIBUTION. January (6), February (3), March (3), April (3), May (14), June (1), July (4), August (9), September (3), October (1), November (8), December (6).

DIAGNOSIS. The reddish brown color, fairly large size (up to 34 mm in length), large and externally lobed mandibles, and heavily punctate elytra should distinguish *Barutus hartmanni* from any other Central American Pentodontini.

BIOLOGY. Although active throughout most of the year, there is a peak in activity in May when the rains commence and again in November and December when the rains once again increase. Adults have been taken at lights in premontane moist forests and lower montane rain forests at elevations of 1,150-1,520 meters.



Fig. 502. Distribution of *Barutus hartmanni* in Costa Rica.

Bothynus Hope, 1837

Bothynus Hope 1837: 95.

Cratocnemis Blanchard 1846: 191 (synonym).
Scaptophilus Burmeister 1847: 122 (synonym).

Corynoscelis Burmeister 1847: 126 (synonym).

The genus *Bothynus* presently contains 25 species (Martínez 1983, Endrödi 1985a). All of the species occur in South America, and the two treated in this work extend northward into Central America. Endrödi (1969, 1985a) reported a record for *B. entellus* (Le Pelletier and Serville) from Chiriqui in Panama and



Fig. 503. Distribution of *Barutus hartmanni* in Panama.

from Honduras, but this species does not occur in Central America, and the records are here considered erroneous. There has been nothing published on the immature stages or biology of any of the species.

Central American members of the genus *Bothynus* are easily distinguished from other Central American Pentodontini by the presence of tridentate mandibles extending laterally beyond the clypeus, clypeus strongly contracted to a bidentate apex, nearly smooth elytra, quadridentate foretibiae, propygidium strongly produced (thus shortening the py-

gidium, Fig. 497), and pronotum with a subapical tubercle followed by a large fovea.

Cartwright's (1959) unfortunate use of the name *Bothynus* to include members of the U.S. species in the genus *Tomarus* (formerly *Ligyris*) still causes some confusion today. Some people continue to erroneously believe that *Bothynus* extends as far north as the United States or that the genus contains some species that are currently assigned to *Tomarus*. Endrödi's (1969, 1985a) treatments of the Pentodontini resolves the nomenclatural situation.

Key to the Species of Adult *Bothynus* of Central America

1. In males, inner claw of protarsus lacking tooth (Fig. 505). Females identified by association with males ***complanus* (Burmeister)**
- 1'. In males, inner claw of protarsus with large, median tooth (Fig. 506). Females identified by association with males ***quadridens* (Taschenberg)**

Clave para las Especies de Adultos de *Bothynus* de América Central

1. En machos, uña interna del protarso sin diente (Fig. 505). Hembras identificadas por asociación con los machos ***complanus* (Burmeister)**
- 1'. En machos, uña interna del protarso con un diente grande (Fig. 506). Hembras identificadas por asociación con los machos ***quadridens* (Taschenberg)**

***Bothynus complanus* (Burmeister, 1847)** (Figs. 504-509)

Podalgus complanus Burmeister 1847: 123.
Bothynus simplicatarsis Bates 1888: 319 (synonym).
Bothynus monstrosus Bates 1888: 320 (synonym).

DESCRIPTION. Length 24.5-31.0 mm; width 14.4-18.9 mm. Color dark reddish brown, almost black. *Head:* Entire surface coarsely rugopunctate, with long setae; setae erect, moderate in density, reddish brown. Frons with large, erect, pointed tubercle. Clypeus with sides sinuate, strongly contracted to narrow apex; apex with 2 acuminate, reflexed teeth. Interocular width equals

3.5 transverse eye diameters. Antenna with club a little longer than segments 2-7. Mandibles tridentate. *Pronotum:* Surface transversely rugose in anterior third and in fovea, becoming rugopunctate in central third of pronotum, and punctate and crazed in posterior third; punctures moderately large, becoming small at center base. Base not or weakly margined on lateral thirds, usually with row of small punctures in central third. Anterior half of pronotum with large, transverse fovea and large, transverse, apical tubercle. *Elytra:* Surface shining, minutely shagreened, with small punctures along lateral margin and apex; sutural stria absent. *Pygidium:* Surface in males transversely rugopunctate except for narrow, nearly smooth area at apex; punctures small and large mixed, setigerous in lateral angles and

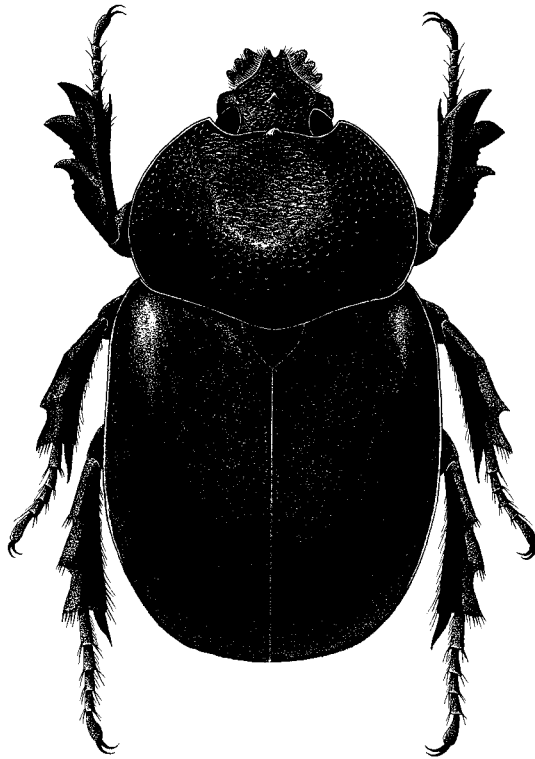
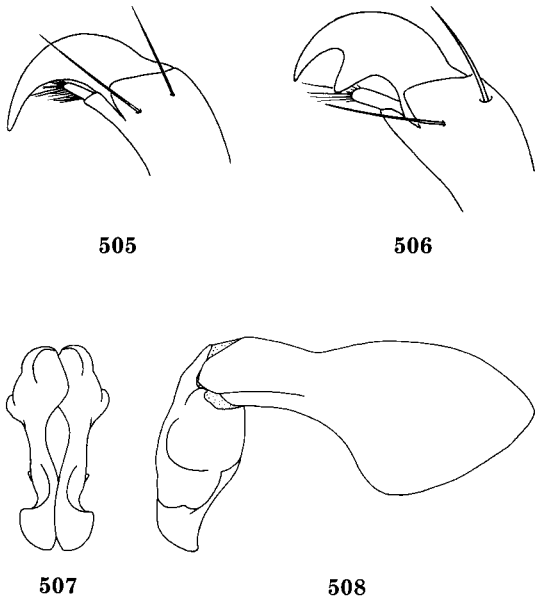


Fig. 504. *Bothynus complanus*.



Figs. 505-508. *Bothynus complanus*: (505) inner foreclaw of male (lacking tooth); (506) inner foreclaw of male (with tooth) of *B. quadridens*; (507-508) parameres.

in transverse row at base; setae long, reddish brown; sculpturing in females finer, reduced. In lateral view, surface weakly concave in males, weakly concave in apical half in females. *Legs*: Foretibia quadridentate. Males with median foreclaw simple, lacking ventral tooth (Fig. 505). Posterior tibia with apex angularly rounded and with 16-17 setae. First tarsomere of posterior tarsus with apex elongated into stout, triangular spine. *Venter*: Prosternal process long, apex usually heart-shaped, with "top" nearly flat, clothed in dense, long setae. *Parameres*: Figs. 507-508.

DISTRIBUTION. *Bothynus complanus* occurs from central Mexico south to Colombia and Venezuela (Endrödi 1969). Interestingly, however, I know of no records for Costa Rica or any place in Panama other than the general area of the Canal Zone. In the Canal Zone, this species occurs on both the Atlantic and Pacific sides at elevations ranging from near sea level to 350 meters.

LOCALITY RECORDS (Fig. 509). 82 specimens examined.

PANAMA (82). **CANAL ZONE** (35): Albrook Forest, Barro Colorado Island, Coco Solo Hospital, Ft. Gulick, Galeta Island, Skunk Hollow; **COLÓN** (6): Margarita, Santa Rita Ridge; **PANAMA** (41): Cerro Azul, Cerro Jefe, Las Cumbres.

TEMPORAL DISTRIBUTION. January (2), February (1), April (1), May (1), June (8), July (58), August (9).

DIAGNOSIS. This species is nearly identical with *B. quadridens*. The males are easily separated by the absence of a median tooth on the inner claw of the protarsi in *B. complanus* (Fig. 505), whereas *B. quadridens* males have such a tooth on the claw (Fig. 506). Females are identical, and it is not possible to separate them except by association with their respective males.

BIOLOGY. All of the specimens in this study were taken at lights in tropical moist forests at localities ranging from sea level to 350

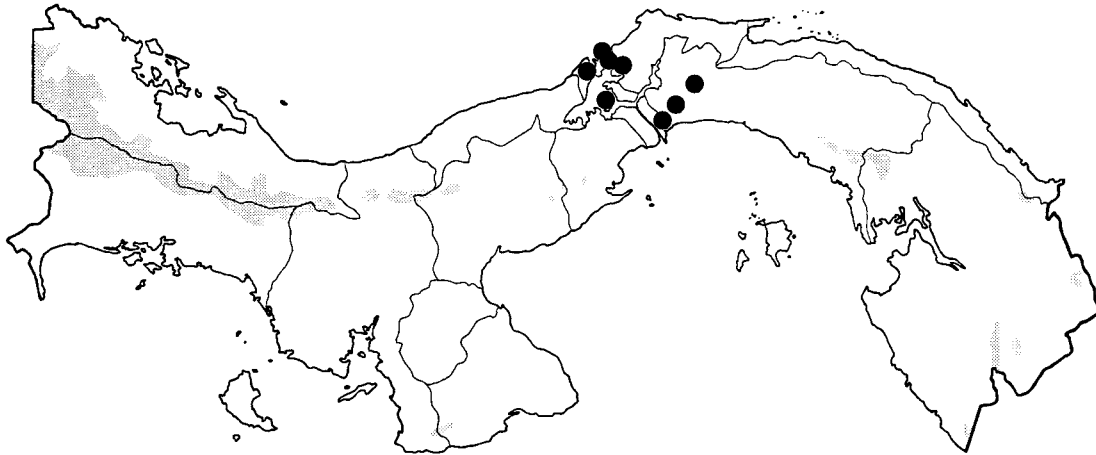


Fig. 509. Distribution of *Bothynus complanus* in Panama.

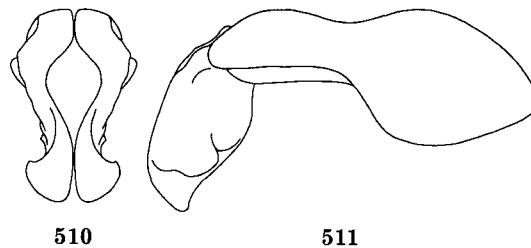
meters. The few records available suggest that this species emerges after the onset of the June rains, but occasional specimens can be found during most other parts of the year.

Bothynus quadridens
(Taschenberg, 1870)
(Figs. 38, 506, 510-513)

Corynoscelis quadridens Taschenberg 1870:
185.

DESCRIPTION. Length 23.0-32.0 mm; width 20.0 mm. Color dark reddish brown, almost black. *Head:* Entire surface coarsely rugopunctate, with long setae (occasionally abraded away); setae erect, moderate in density, reddish brown. Frons with large, erect, pointed tubercle. Clypeus with sides sinuate, strongly contracted to narrow apex; apex with 2 acuminate, reflexed teeth. Interocular width equals 3.5 transverse eye diameters. Antenna with club a little longer than segments 2-7. Mandibles tridentate. *Pronotum:* Surface transversely rugose in anterior third and in fovea, becoming rugopunctate in central third of pronotum, and punctate and crazed in posterior third; punctures moderately large, becoming small at center and base. Base not or weakly margined on lateral thirds, usually with row of small punctures in central third. Anterior half of pronotum with large trans-

verse fovea and large, transverse, apical tubercle. *Elytra:* Surface shining, minutely shagreened, with small punctures along lateral margin and apex; sutural stria absent. *Pygidium:* Surface in males transversely rugopunctate except for narrow, nearly smooth area at apex; punctures small and large mixed, setigerous in lateral angles and in transverse row at base; setae long, reddish brown; sculpturing in females finer, reduced. In lateral view, surface weakly concave in males, weakly concave in apical half in females. *Legs:* Foretibia with 4 teeth. Males with large, median tooth on inner claw of protarsus (Fig. 506). Apex of posterior tibia with apex angularly rounded and with 14-15 setae. Apex of basal tarsomere of posterior tarsus with apex elongated into stout, triangular spine. *Venter:* Prosternal process long, apex usually weakly heart-shaped to oval, with "top" rounded or convex, clothed in dense, long setae. *Parameres:* Figs. 510-511.



Figs. 510-511. *Bothynus quadridens* parameres.

DISTRIBUTION. *Bothynus quadridens* is found from Guatemala south to Venezuela and Ecuador (Endrödi 1969). It is essentially sympatric with *B. complanus*, although *B. complanus* evidently has not been taken in Costa Rica.

LOCALITY RECORDS (Figs. 512-513). 73 specimens examined.

COSTA RICA (43). GUANACASTE (8): Enrique Nuñez Exp. Sta., Río Naranjo; LIMÓN (1): Buenos Aires; PUNTARENAS

(33): Alto de las Moras, Río Coton, Sabalito, Vuelta Campana.

PANAMA (30). CANAL ZONE (15): Ancon Hill, Barro Colorado Island, Ft. Gulick; CHIRIQUI (7): Cerro Punta, Río Sereno; COLÓN (2): Sabanitas (2 km S); PANAMA (4): Panama City; VERAGUAS (2): Santa Fé.

TEMPORAL DISTRIBUTION. February (2), March (13), April (5), May (1), June (22), July (16), August (12), September (2), October (1).

DIAGNOSIS. This species is virtually identical with *B. complanus*. Males of *B. quadridens* possess a large, median tooth on the inner claw of the protarsus (Fig. 505), whereas males of *B. complanus* lack this tooth (Fig. 506). Females can be identified only by association with the males.

BIOLOGY. Collecting records suggest that this species is intermittently found between March and September with a peak in June reflecting emergence at the onset of the rains. They have been collected from near sea level to 1,400 meters elevation in tropical moist forests, tropical wet forests, and premontane wet forests.



Fig. 512. Distribution of *Bothynus quadridens* in Costa Rica.

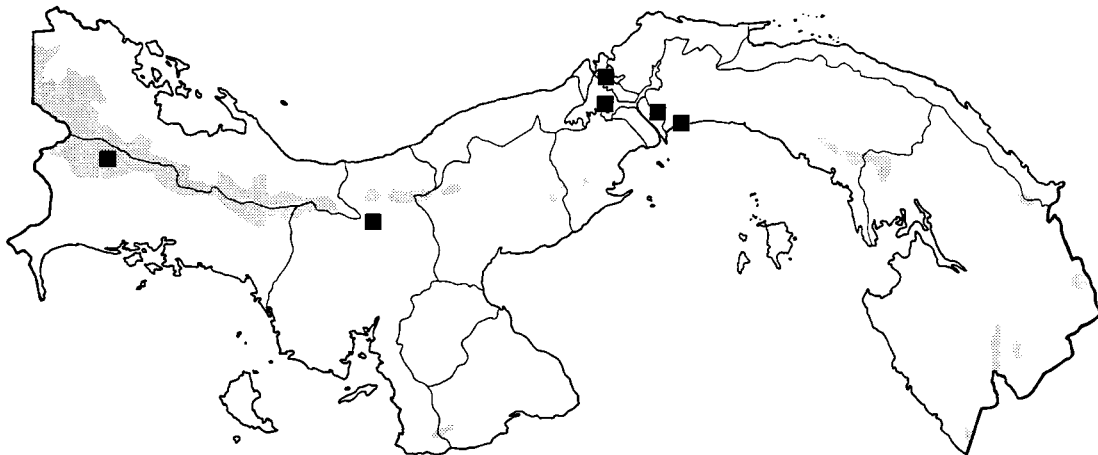


Fig. 513. Distribution of *Bothynus quadridens* in Panama.

***Euetheola* Bates, 1888**

Euetheola (not *Eutheola*) Bates 1888: 314.

Euetheola is comprised of four species (Endrödi 1969, 1985a). Species in the genus range from the southern United States to Argentina. Only two species, however, are found in Central America. The immature stage of *E. humilis* was described by Ritcher (1966), and its biology was briefly summarized by Davidson and Lyon (1987).

Species of *Euetheola* are all less than 17 mm in length, black, with a simply convex pronotum, and the apex of the clypeus has two sharply reflexed teeth. Small species of *Stenocrates* (e.g. *S. hardyi* Endrödi) might be mistaken for *Euetheola*, but *Stenocrates* does not have the bidentate clypeal apex and the shape of the pronotum is subquadrate. Small species of *Tomarus* might also be confused with *Euetheola*, but in *Tomarus*, the middle and posterior tibia are not strongly and abruptly widened from the base as in *Euetheola*.

Key to the Species of Adult *Euetheola* of Central America

1. Mandibles lacking teeth on external edge. Males with anterior tarsi enlarged. Females with lateral margin of elytra dilated. Pronotum with moderate to dense, large punctures ***bidentata* (Burmeister)**
- 1'. Mandibles with rounded basal lobe and apical tooth. Males with anterior tarsi not enlarged. Females with lateral margin of elytra not enlarged. Pronotum with sparse, small punctures ***humilis* (Burmeister)**

Clave para las Especies de Adultos de *Euetheola* de América Central

1. Mandíbulas sin dientes en el borde externo. Machos con los tarsos anteriores agrandados. Hembras con el margen lateral de los élitros dilatados. Pronoto con grandes puntuaciones dispuestos moderada o densamente ***bidentata* (Burmeister)**
- 1'. Mandíbulas con un lóbulo basal redondeado y un diente apical. Machos con los tarsos anteriores no agrandados. Hembras con el margen lateral de los élitros no dilatados. Pronoto con pequeñas puntuaciones dispersas ***humilis* (Burmeister)**

***Euetheola bidentata* (Burmeister, 1847)**

(Figs. 39, 514-517)

Chalepus bidentata Burmeister 1847: 81.

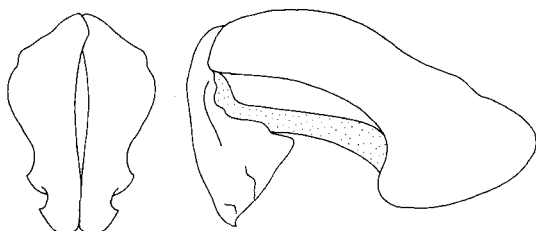
? *Cyclocephala brevis* Perty 1830: 46 (synonym? Type unknown).

? *Heteronychus globosus* Burmeister 1847: 91 (synonym? Type unknown).

DESCRIPTION. Length 12.2-15.5 mm; width 6.8-8.0 mm. Color black. *Head:* Frons sparsely punctate; punctures small to moderately large. Frontoclypeal line an impressed suture, not cariniform either side of middle. Clypeus subtrapezoidal in shape, surface transversely rugopunctate to rugose; apex

bidentate, each tooth sharply reflexed. Interocular width equals 4.0-4.8 transverse eye diameters. Antenna 10-segmented club subequal to segments 3-7. Mandibles with external edge weakly sinuate. *Pronotum:* Surface weakly (most common) to strongly (uncommon) crazed, moderately to moderately densely punctate; most punctures larger than those on vertex. Base lacking marginal bead. *Elytra:* Surface with distinct rows of punctures; punctures (of both striae and intervals) large, dense, ocellate, u-shaped. Lateral margin in female greatly thickened, widest at about first sternite. *Pygidium:* Surface densely punctate; punctures large, ocellate, setigerous; setae dense, short, pale. In lateral view, surface nearly flat in both sexes. *Legs:*

Foretibia tridentate, teeth similarly equidistant from each other; posterior margin at base of second tooth and anterior margin of base of third tooth expanded (especially in males).



514

515

Figs. 514-515. *Euetheola bidentata* parameres.



Fig. 516. Distribution of *Euetheola bidentata* in Costa Rica.



Fig. 517. Distribution of *Euetheola bidentata* in Panama.

Anterior tarsi in males greatly enlarged, claw with apex entire. Posterior tibia with apex truncate and with 10 stout, long spines. First tarsomere of posterior tarsus with subtruncate apex. *Venter*: Prosternal process moderate in length (not extending beyond trochanters), apex truncate and transversely oval in ventral view. *Parameres*: Figs. 514-515.

DISTRIBUTION. *Euetheola bidentata* is found sporadically from southern Mexico and Guatemala to Colombia, Venezuela, the Guyanas, and Brazil (Endrödi 1969, 1985a). It has not been previously recorded in Costa Rica or Panama, and the following represent **NEW COUNTRY RECORDS**. In spite of intense collecting and data gathering in Panama during the past several years, I was surprised to find that I obtained only one locality record. I believe the collecting effort has been both geographically comprehensive as well as intensive in each country in the past ten years especially, and so I discount any collecting bias that might have contributed to overlooking these beetles.

LOCALITY RECORDS (Figs. 516-517). 43 specimens examined.

COSTA RICA (15). **ALAJUELA** (6): Atenas, Los Chiles; **GUANACASTE** (6): Cerro El Hacha, Liberia Parq. Nac. Barra Honda, Parq. Nac. Guanacaste, Parq. Nac. Santa Rosa; **PUNTARENAS** (3): Buenos Aires, Estación Quebrada Bonita.

PANAMA (28). **DARIEN** (28): Cana (ANCON Station).

TEMPORAL DISTRIBUTION. June (33), July (7), October (2), December (1).

DIAGNOSIS. *Euetheola bidentata* is easily distinguished from *E. humilis* because it has larger and denser punctation on the pronotum and pygidium, enlarged foreclaws in the males, and an expanded elytral margin in females.

NOMENCLATURE. The question marks in the nomenclatural synonymy indicate that Bates (1888) and Endrödi (1969) believed these two taxa to be synonymical with *E. bidentata* based on the descriptions; the types were either lost or unavailable.

BIOLOGY. Pardo Locarno (1994) reported larvae feeding on the roots of rice, corn, sorghum, grasses, cotton, sugar cane, and yucca in Colombia. This species is uncommon in Costa Rica. It is usually found at elevations below 500 meters in tropical moist forests although the Buenos Aires (Puntarenas) specimen was collected at 1,100 meters.

***Euetheola humilis* (Burmeister, 1847)**

(Figs. 518-522)

Heteronychus humilis Burmeister 1847: 93.

Ligyryus rugiceps LeConte 1856: 21 (synonym).

Dyscinetus parvus Casey 1915: 172 (synonym).

Dyscinetus hondurana Casey 1915: 188 (synonym).

DESCRIPTION. Length 10.8-14.5 mm; width 5.8-7.2 mm. Color black. *Head:* Frons and clypeus coarsely, transversely rugopunctate. Frontoclypeal line strongly carinated either side of midline. Clypeus subtrapezoidal, with apex bidentate, teeth strongly reflexed. Eyes small, interocular width equals 4.8-5.5 transverse eye diameters. Antenna with 10 segments, club subequal to segments 2-7. Mandibles externally bidentate, basal tooth

rounded. *Pronotum:* Surface crazed, sparsely punctate; punctures small (no larger than those on vertex), becoming slightly larger on sides. *Elytra:* Surface with paired rows of moderately sized punctures; rows usually impressed, punctures usually ocellate. Sides with moderately dense, smaller punctures. Lateral margin in female not enlarged. *Pygidium:* Surface in basal third coarsely rugopunctate in male, finely rugopunctate to densely punctate in female; discal area sparsely punctate with punctures large in male, small to moderate in female. Minute, sparse, pale setae occasionally present. In lateral view, pygidium evenly convex in male, a little flatter in female. *Legs:* Foretibia tridentate, basal tooth slightly removed from others. Claws of foretarsus in male not enlarged. Apex of posterior tibia truncate with 10 stout, short spinules. Apex of basal tarsomere of posterior tarsus subtruncate. *Venter:* Prosternal process long (extending beyond trochanters), apex truncate and nearly longitudinally oval in ventral view. *Parameres:* Figs. 519-520.

DISTRIBUTION. *Euetheola humilis* is a relatively common species that occurs from the southern United States to Argentina (Endrödi 1969). This species is widely distributed in Panama at elevations generally below 1,000 meters. Inasmuch as this is a relatively abundant species both to the north and south of Costa Rica, it is perplexing that there are only two Costa Rican records . . . even after several years of intensive collecting.

LOCALITY RECORDS (Figs. 521-522). 221 specimens examined.

COSTA RICA (2). **ALAJUELA** (1): Caño Negro; **GUANACASTE** (1): Santa Rosa National Park.

PANAMA (219).. **CANAL ZONE** (178): Albrook Forest, Barro Colorado Island, Coco Solo Hospital, Diablo Heights, Ft. Davis, Ft. Gulick, Ft. Kobbe, Howard AFB, Madden Dam; **CHIRIQUI** (1): David; **COLÓN** (9): Colón, Santa Rita Ridge; **PANAMA** (31): Cerro Campana, El Llano-Carti Road (km 8-13), Majé Island.

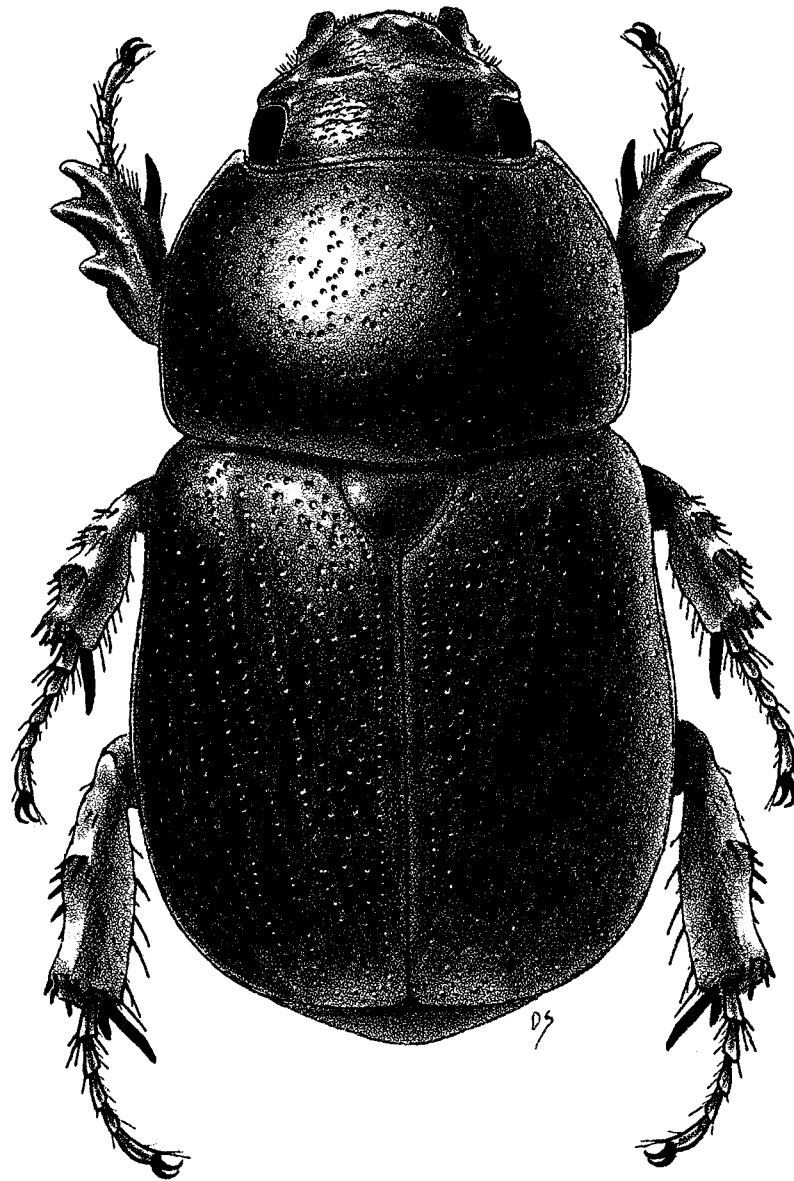
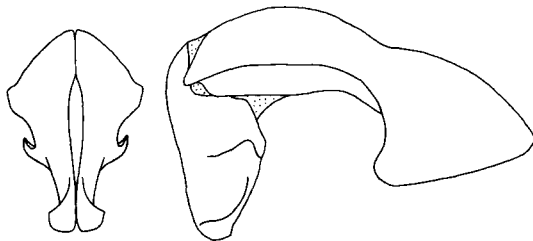


Fig. 518. *Eutheola humilis*.



519

520

Figs. 519-520. *Eutheola humilis* parameres.

TEMPORAL DISTRIBUTION. January (1), March (4), April (17), May (96), June (24), October (1), November (2), December (25).

DIAGNOSIS. In much of Central America, this species is sympatric with *E. bidentata*. These two species are easily separated because *E. humilis* males have simple foreclaws

whereas *E. bidentata* males have the anterior tarsi enlarged; in the females, the lateral margin of the elytra is simple in *E. humilis* and dilated in *E. bidentata*. In addition, the punctures on the pronotum are noticeably small and fine in *E. humilis* and large and coarse in *E. bidentata*.

BIOLOGY. The larval stage was described and illustrated by Ritcher (1966) (under the name *E. rugiceps*). The northern subspecies, *E. humilis rugiceps*, has occasionally been a

minor pest of sugarcane in the southern United States (White 1990). The basics of its life history have been explored due to its pest status, and they are probably the same as the populations of *E. humilis humilis* living in Central America. Adults feed on grasses, sedges, rushes, and occasionally on sugarcane, rice, and corn (Baerg 1940). Adult beetles feed on the host plant by chewing on young shoots and leaves at ground level or slightly below (Davidson and Lyon 1987). Adults generally occur in well-drained, grassy areas and emerge at the onset of the rainy season in Central America in May or June. Eggs are deposited in the soil, and the larvae feed on the roots of grasses. According to Davidson and Lyon (1987), eggs incubated for about 14 days, larval development took about 65 days, and the pupal period lasted 9 days. White (1990) observed that adults tended to be more abundant where soils are higher in organic content. Adults are nocturnal and are readily attracted to lights. They have been collected in tropical wet forests.



Fig. 521. Distribution of *Eutheola humilis* in Costa Rica.

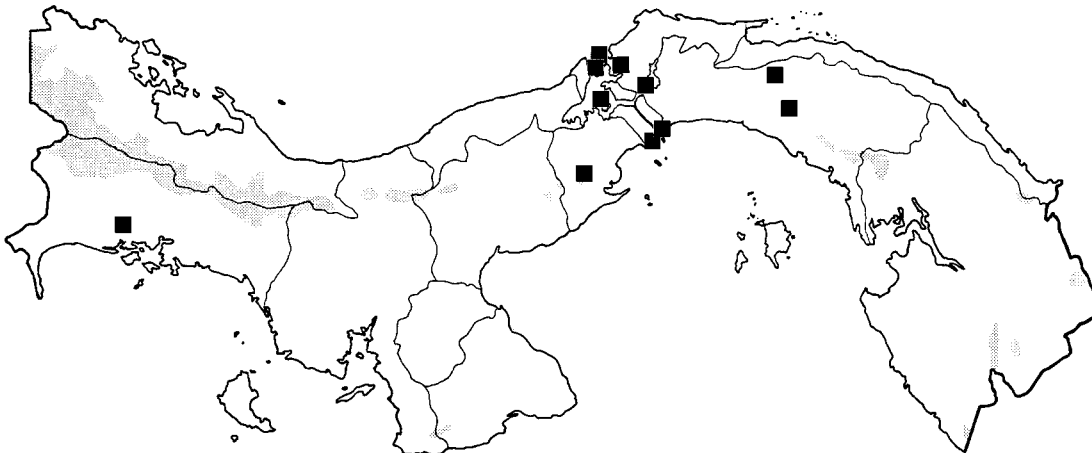


Fig. 522. Distribution of *Eutheola humilis* in Panama.

***Parapucaya* Prell, 1934**

Parapucaya Prell 1934: 162.

This small genus contains two species. Both occur in northwestern South America, and *P. amazonica* Prell is found as far north as Honduras (Endrödi 1969, 1985a).

The broadly truncate clypeal apex, strongly impressed frontoclypeal suture, the generally exposed and slender mandibles that lack lateral teeth, testaceous elytra, and joint double tubercles (or declivity) near the apex of the pronotum will distinguish *Parapucaya* from other Central American Pentodontini. Both species are remarkably *Cyclocephala*-like in their appearance, and it is necessary to look closely at the anterior margin of the pronotum to see the two small tubercles that help to characterize them as pentodontines.

Other than having been collected at lights at night, nothing is known of the biology of the species in this genus.

***Parapucaya amazonica* Prell, 1934**

(Figs. 41, 523-527)

Parapucaya amazonica Prell 1934: 162.

DESCRIPTION. Length 13.0-16.3 mm; width 6.3-8.0 mm. Color of frons black; clypeus, pronotum, pygidium, and legs dark reddish brown; elytra light, testaceous. *Head:* Frons with sparse, small punctures, mostly on sides. Frontoclypeal suture arcuate, deeply impressed. Clypeus sparsely, minutely punctate; apex broadly truncate, weakly emarginate; lateral and apical margins reflexed. Interocular width equals 2.7-3.0 transverse eye diameters. Antenna with 10 segments, club subequal to segments 2-7. Mandibles narrow, elongate, apex acuminate and curved upward. *Pronotum:* Surface shining, sparsely punctate; punctures minute on disc, small on sides. Two small tubercles present just behind apex either side of midline, tubercles often reduced to a subapical declivity. Base lacking marginal bead except in area of posterior angles. *Elytra:* Surface shining, with rows of small to moderate, ocellate punctures. Fe-

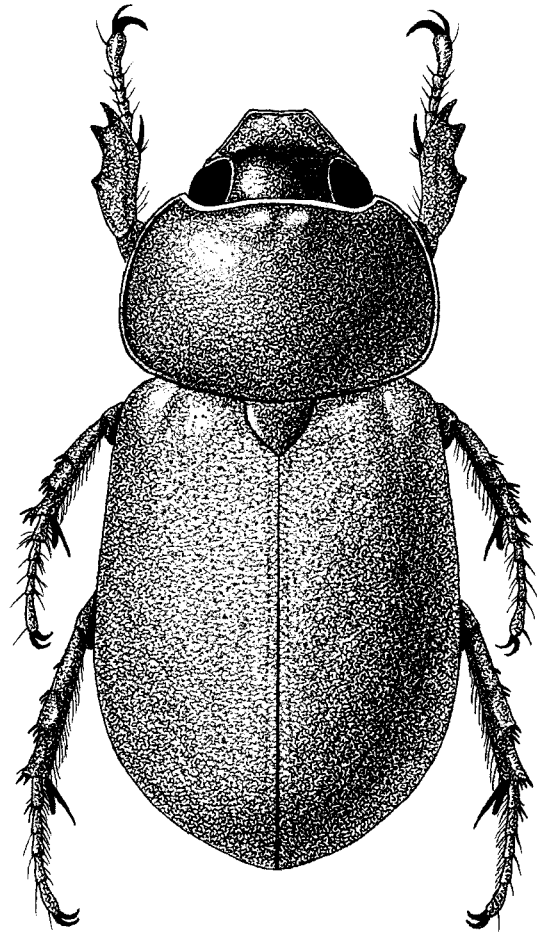
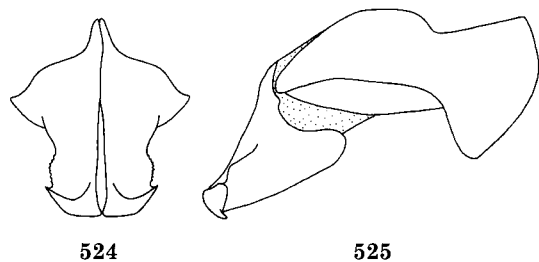


Fig. 523. *Parapucaya amazonica*.



Figs. 524-525. *Parapucaya amazonica* parameres.

males with lateral margin simple, not enlarged. *Pygidium:* Surface with disc sparsely punctate, punctures small. Base and lateral angles with moderate to moderately dense punctures; punctures small to moderate in size, with poorly defined, transverse row of setigerous punctures; setae short, reddish

brown, adpressed to surface (hence, difficult to see). In lateral view, male with strongly convex surface, female with weakly convex surface. *Legs*: Foretibia strongly tridentate, basal tooth removed from other two teeth. Foretarsus in males enlarged, larger claw strongly curved and incised at apex; females with foretarsus simple. Posterior tibia crenulate with 7-8 short, thick spinules. Apex of first segment of posterior tarsus triangularly expanded. *Venter*: Prosternal process moderate in length; apex transversely oval, with anterior 1/3-1/2 convex, posterior 2/3-1/2 flat. *Parameres*: Figs. 524-525.

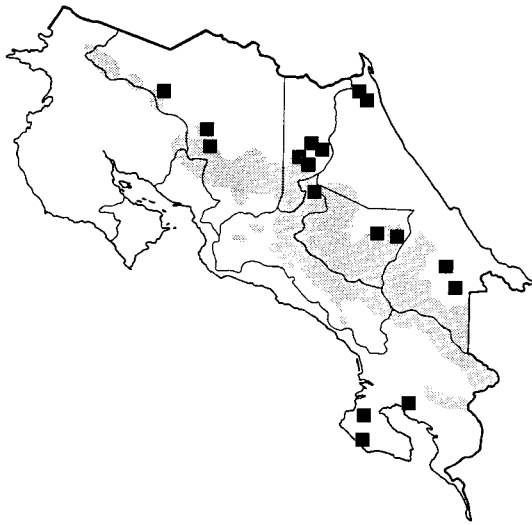


Fig. 526. Distribution of *Parapucaya amazonica* in Costa Rica.



Fig. 527. Distribution of *Parapucaya amazonica* in Panama.

DISTRIBUTION. *Parapucaya amazonica* is found from Honduras to Peru and Brazil (Endrödi 1969, 1985a).

LOCALITY RECORDS (Figs. 526-527). 125 specimens examined.

COSTA RICA (121). ALAJUELA (4): Cerro Chato, Colonia Río Celeste (Volcán Tenorio), Reserva Biológica Monteverde; CARTAGO (20): Grano de Oro (Chirripó) Tuis; HEREDIA (54): Estación El Ceibo, Estación Magsasay, La Selva Biological Station, Las Horquetas de Sarapiquí; LIMÓN (27): Amubri, Cerro Cocori, Refugio Nac. Barra del Colorado, Reserva Biológica Hitoy Cerere; PUNTARENAS (15): Boca del Río Esquinas, Estación Sirena, Rancho Quemado (Osa); SAN JOSÉ (1): Zurqui Tunnel.

PANAMA (4). BOCAS DEL TORO (3): Miramar, Punta Peña (14 km S); CHIRIQUÍ (1): Lino.

TEMPORAL DISTRIBUTION. January (4), February (7), March (3), April (7), May (1), June (8), July (11), August (3), September (9), October (12), November (46), December (13).

DIAGNOSIS. *Parapucaya amazonica* is invariably mistaken for a species of *Cyclocephala* because of its similar appearance. The subapical declivity of the pronotum (or two tubercles in well-developed specimens), in combination with the broadly truncate

clypeus, will distinguish this genus from *Cyclocephala*.

BIOLOGY. This is a relatively uncommon species, and, in spite of their numbers, all of the Costa Rican specimens have been taken since 1989. Nothing is known of the life history of this species. It occurs at elevations ranging from near sea level to 1,600 meters in tropical wet forests and premontane rain forests.

Pucaya Ohaus, 1910

Pucaya Ohaus 1910: 675.

The genus *Pucaya* contains three species, all of which occur in Colombia and Ecuador, with only *P. castanea* Ohaus extending into Panama and Costa Rica. *Pucaya* is distinguished from other New World Pentodontini by its relatively large size (up to 30 mm), shining reddish brown color, broadly truncate clypeus that conceals the mandibles, absence of a frontoclypeal suture, a small horn or tubercle near each eye, and a characteristic, binodose pronotum.

The Central American species, while not common, can usually be taken at light traps in the mountains of Costa Rica and western Panama. Life history information is lacking.

Pucaya castanea Ohaus, 1910

(Color Plate 3, Figs. 42, 528-532)

Pucaya castanea Ohaus 1910: 676.

Pucaya columbiana Beck 1942: 47 (synonym).

DESCRIPTION. Length 24.0-30.1 mm; width 11.0-14.2 mm. Color light to dark reddish brown; head, tibiae, and tarsi often black. *Head:* Frons and clypeus completely rugulose in males, partially rugulose to nearly smooth in females. Base of clypeus at sides (and just in front of eye) with short, vertically upright horn in males or a large tubercle in females. Clypeus with apex very broadly truncate, shallowly emarginate, broadly reflexed in males, narrowly reflexed in females.

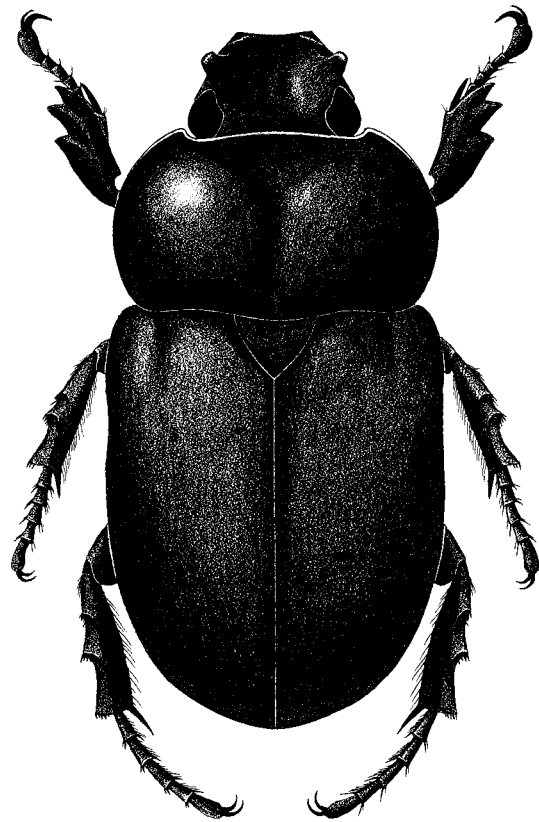
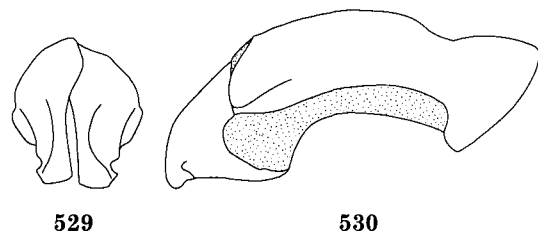


Fig. 528. *Pucaya castanea*.



Figs. 529-530. *Pucaya castanea* parameres.

Interocular width equals 5.0 transverse eye diameters. Antenna with 10 segments, club subequal to segments 2-7. Mandibles small, narrow, not visible in dorsal view. *Pronotum:* Surface with sparse, minute punctures. A highly tumescent boss present either side of broadly depressed midline. Narrow marginal bead present on base. *Elytra:* Surface also with sparse, minute punctures; punctures becoming denser along lateral margins. Striae totally lacking. *Pygidium:* Surface with sparse, minute punctures. In lateral view,

regularly convex in males, nearly flat in females. *Legs*: Foretibia tridentate, basal tooth slightly removed from others. Males with claw of anterior tarsus enlarged, apex split. Apex of posterior tibia arcuate and with 9 short, stout spinules. Apex of first tarsomere of posterior tarsus triangularly elongated. *Venter*: Prosternal process short; apex transversely oval, anterior 1/2-2/3 convex, posterior 1/2-1/3 flat, a transverse sulcus often separating anterior and posterior parts. *Parameres*: Figs. 529-530.



Fig. 531. Distribution of *Pucaya castanea* in Costa Rica.

DISTRIBUTION. *Pucaya castanea* occurs in Costa Rica, Panama, Ecuador (Beck 1942b; Endrödi 1969, 1985a) and probably Colombia as well .

LOCALITY RECORDS (Figs. 531-532). 148 specimens examined.

COSTA RICA (129). **ALAJUELA** (13): Parq. Nac. Rincón de la Vieja, Reserva Biológica Monteverde, San Ramon; **CARTAGO** (40): Grano de Oro (Chirripó), Moravia de Chirripó, Ref. Nac. Tapanti, Río Grande de Orosi; **GUANACASTE** (17): Estación Cacao, Estación Mengo, Estación Pitilla, Faldas (SW Volcán Cacao), Río San Lorenzo, Volcán Orosi (Cañon Mena); **HEREDIA** (21): Estación El Ciebo, Estación Magsasay, Las Horquetas de Sarapiquí; **LIMÓN** (3): Guapiles; **PUNTARENAS** (19): Estación La Casona (Res. Biol. Monteverde), Estación Las Alturas, Estación Las Mellizas (Parq. Nac. Amistad), Las Cruces, San Luis (Res. Biol. Monteverde), San Vito; **SAN JOSÉ** (16): Estación Carrillo (Parq. Nac. Braulio Carrillo).

PANAMA (19)
BOCAS DEL TORO (1): Miramar; **CHIRIQUI** (17): Cerro Punta, Finca La Suiza (5.3 km N Los Planes), Fortuna Dam, Los Planes (11.5 km N), Santa Clara.



Fig. 532. Distribution of *Pucaya castanea* in Panama.

TEMPORAL DISTRIBUTION. January (7), February (10), March (9), April (23), May (21), June (18), July (20), August (4), September (4), October (21), November (6), December (3).

DIAGNOSIS. The oblong, shining reddish brown body with the characteristically shaped clypeus, head horns, and pronotum will serve to easily identify this species, the only one in the genus that occurs in Central America.

BIOLOGY. Adults are attracted to lights at night. Nevermann (1933) reported adults from the hollow stems of *Cecropia mexicana* Hemsl. in Costa Rica. They are usually found only in premontane rain forests and lower montane rain forests at elevations ranging from 700-1,600 meters.

***Tomarus* Erichson, 1847**

Tomarus Erichson 1847: 95.

Ligyris Burmeister 1847: 542. (synonym).

Ligyrodes Casey 1915: 178. (synonym).

Euligyris Casey 1915: 185 (synonym, described as subgenus).

Grylius Casey 1915: 189 (synonym, described as subgenus).

Anagrylius Casey 1915: 204 (synonym, described as subgenus).

Ligyrellus Casey 1915: 206 (synonym, described as subgenus)

The genus *Tomarus* contains 26 species (Endrödi 1985a; Dechambre and Lumaret 1985). Species in the genus occur from the north-central United States south to Argentina. Ten species are found exclusively in South America, and another ten species are found exclusively in North and Central America. Seven species are shared between Central and South America. Costa Rica has eight species and Panama has six species with four species shared between both countries.

Species of *Tomarus* can be recognized by an attenuate clypeus that is bidentate and relatively narrow at the apex, mandibles usually visible from above and with two or three lateral teeth, frontoclypeal region with two tubercles or a transverse carina, and

pronotum with or without an apical tubercle and subapical fovea.

Life history information for most of the species is sparse. Adults are nocturnal and attracted to lights. In general, larvae are found in soil rich in organic matter where they feed, sometimes on the roots of living plants.

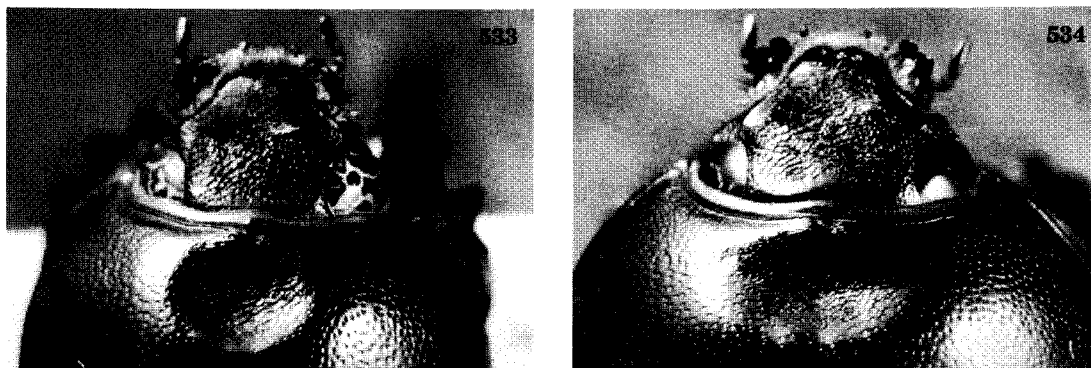
Considerable reliance must be placed on the form of the male parameres for identification. It should be noted, therefore, that the parameres are usually extremely fragile (almost parchment-like), and that they break or tear easily. Great care should be taken when extracting the parameres from the abdomen.

Both *Tomarus* Erichson and *Ligyris* Burmeister were described in 1847. Ever since the 1850s, *Ligyris* has been used as the senior name by all authors while *Tomarus* has been used as a subgenus. The forward in Burmeister's *Handbuch der Entomologie* (volume 5) is dated February 1847, and it was received in the library of the Entomologischen Vereine zu Stettin in September 1847. But, a paper FOLLOWING Erichson's in the *Archiv für Naturgeschichte* is dated January 1847 (before Burmeister's book), and it was received in the library in Stettin in April 1847, five months before Burmeister's book. The generic name *Tomarus* has priority although Lacordaire stated in 1859, for reasons known only to him, that *Tomarus* was described after *Ligyris*. The confusion over the correct name for this genus seems to stem from this point, and all subsequent authors have incorrectly used *Ligyris*. I was extremely reluctant to use the name *Tomarus*, especially since we have used *Ligyris* for so long, but the rules of nomenclature are unequivocal on priority. Had the name *Tomarus* not been used as a valid name since 1899, there might have been a case for Reversal of Precedence (Article 23.9), but the name has been so used, notably by Endrödi (1969, 1985a).

The generic name *Bothynus* has occasionally been used to refer to *Tomarus* species largely because of Cartwright's (1959) unfortunate assignment of the U.S. species to *Bothynus*. *Tomarus* and *Bothynus* are two separate genera.

Key to the Species of Adult *Tomarus* of Costa Rica and Panama

1. Pronotum lacking subapical fovea 2
- 1'. Pronotum with subapical fovea, occasionally fovea very shallow 4
- 2(1'). Foretibia with small accessory tooth either side of basal tooth (Fig. 568). Male with claw of foretarsus enlarged **sallaei (Bates)**
- 2'. Foretibia lacking accessory tooth either side of basal tooth (Fig. 543). Male with claw of foretarsus simple, not enlarged 3
- 3(2'). Clypeus attenuated to narrow apex, apex with 2 small teeth closely spaced to one another (subequal to space between apical 2 teeth of mandible) (Fig. 563). **nasutus (Burmeister)**
- 3'. Clypeus broadly subtruncate to weakly emarginate at apex, apex with 2 small teeth separated widely from one another **fossor (Latreille)**
- 4(1'). Pronotum nearly impunctate or with micropunctures or sparse small punctures (except at anterior and lateral margins or anterior angles where punctures small to moderate in size). Male with claw of foretarsus simple, not enlarged 5
- 4'. Pronotum distinctly punctate, punctures at least moderate in size even on disc. Male with claw of foretarsus enlarged or not 6
- 5(4). Pronotum with disc nearly smooth (except along anterior and lateral margins). Elytra with first broad interval nearly impunctate or with sparse micropunctures **laevicollis (Bates)**
5. Pronotum on disc with sparse, small punctures; punctures in anterior angles larger, denser. Elytra in first broad interval with distinct, moderately large punctures **maternus (Prell)**
- 6(4'). Clypeus with apex broad and with small, reflexed teeth about "in-line" with frontoclypeal tubercles (Fig. 543). Frons distinctly concave behind tubercles. Male with claw of foretarsus enlarged or simple 7
- 6'. Clypeus with apex narrow and with small reflexed teeth mesad of a line drawn anteriorly from frontoclypeal tubercles (Fig. 533). Frons vaguely concave behind tubercles. Male with claw of foretarsus simple, not enlarged 9
- 7(6). Foretibia with basal tooth distinctly removed from others. Posterior tarsus with basal tarsomere broadly expanded, triangular, dorsal surface extended into a thorn-like projection. Male with claw-bearing segment of foretarsus simple. Pygidium completely punctate **cicatricosus (Prell)**
- 7'. Foretibia with basal tooth only slightly removed from others. Posterior tarsus with basal tarsomere only slightly expanded, segment nearly cylindrical. Male with claw-bearing segment of foretarsus enlarged. Pygidium lacking punctures apically 8
- 8(7'). Externally indistinguishable from next species. Male with parameres strongly contracted before strongly toothed apex (Figs. 544-545) **ebenus (Degeer)**
- 8'. Externally indistinguishable from previous species. Male with parameres simple, not abruptly contracted before weakly toothed apex (Figs. 573-574) **similis (Endrödi)**
- 9(6'). Tubercles on head round to slightly, transversely oval, widely separated (ca. 5.0 tubercular diameters) (Fig. 533). Fovea of pronotum usually transversely oval (Fig. 533), subequal to width between eyes or middle of each eye. Parameres as in Figs. 536-537 **bituberculatus (Palisot de Beauvois)**
- 9'. Tubercles on head usually very transverse, usually narrowly separated (ca. 2.5 tubercular diameters) (Fig. 534). Fovea of pronotum nearly round (Fig. 534), subequal to or narrower than width between eyes. Parameres as in Figs. 552-553 **gyas Erichson**



Figs. 533-534. Head (showing width between clypeal teeth) and pronotum (showing shape of fovea) of *T. bituberculatus* and *T. gyas*, respectively.

Clave para las Especies de Adultos de *Tomarus* de Costa Rica y Panamá

1. Pronoto carente de fóvea subapical 2
- 1'. Pronoto con fóvea subapical, fóvea ocasionalmente poco profundo 4
- 2(1'). Tibia anterior con un diente accesorio pequeño a cada lado del diente basal (Fig. 568). Machos con uña del tarso anterior agrandada *sallaei* (Bates)
- 2'. Tibia anterior sin un diente accesorio pequeño a cada lado del diente basal (Fig. 543). Machos con uña del tarso anterior simple, no agrandada 3
- 3(2'). Clípeo atenuado hacia un ápice angosto, ápice con 2 pequeños dientes poco espaciados uno de otro (similar al espacio entre los 2 dientes apicales de la mandíbula) (Fig. 563) *nasutus* (Burmeister)
- 3'. Clípeo ampliamente truncado a ligeramente emarginado en el ápice; ápice con 2 pequeños dientes separados ampliamente uno de otro *fossor* (Latreille)
- 4(1'). Pronoto casi sin puntuaciones o con micropuntuaciones o con pequeñas puntuaciones dispersas (excepto en los márgenes anteriores laterales o ángulos anteriores donde las puntuaciones son pequeñas a moderadas). Macho con la uña del tarso anterior simple, no agrandada 5
- 4'. Pronoto claramente punteado, puntuaciones al menos moderadas en tamaño aún en el disco. Machos con la uña del tarso anterior agrandada o no 6
- 5(4). Pronoto con el disco casi liso (excepto a lo largo de los márgenes anteriores y laterales). Elitro con el primer intervalo ancho casi sin puntuaciones o con micropuntuaciones dispersas *laevicollis* (Bates)
- 5'. Pronoto con el disco con puntuaciones dispersas pequeñas; puntuaciones en los ángulos anteriores más grandes y densos. Elitros en el primer intervalo ancho con puntuaciones claras, moderadamente grandes *maternus* (Prell)
- 6(4'). Clípeo con el ápice amplio y con dientes pequeños, proyectados hacia arriba casi en línea con los tubérculos frontoclipeales (Fig. 543). Frente claramente cóncava detrás de los tubérculos. Macho con uña del tarso anterior agrandada o simple 7
- 6'. Clípeo con el ápice angosto y con dientes pequeños, proyectado hacia arriba y mas juntos uno de otro que los tubérculos frontoclipeales (Fig. 533). Frente vagamente cóncava detrás de los tubérculos. Macho con uña del tarso anterior simple, no agrandada 9

- 7(6). Tibias anteriores con diente basal claramente aparte de los otros. Tarsos posteriores con el segmento basal ampliamente expandido, triangular, superficie dorsal extendida en una proyección en forma de espina. Macho con tarsos anteriores simples. Pigidio completamente cubierto de puntuaciones *cicatricosus* (Prell)
- 7'. Tibias anteriores con diente basal solo ligeramente aparte de los otros. Tarsos posteriores con el segmento basal solo ligeramente expandido, casi cilíndrico. Macho con tarsos anteriores agrandados. Pigidio carente de puntuaciones apicalmente 8
- 8(7'). Externamente indistinguible de la siguiente especie. Macho con parámetros contraídos fuertemente antes del ápice que a su vez es fuertemente dentado (Figs. 544-545) *ebenus* (Degeer)
- 8'. Externamente indistinguible de la especie anterior. Macho con parámetros simples, no contraídos abruptamente antes del ápice ligeramente dentado (Figs. 573-574) *similis* (Endrödi)
- 9(6'). Tubérculos de la cabeza de redondeados a ligera y transversalmente ovales, ampliamente separados (cerca de 5.0 diámetros del tubérculo) (Fig. 533). Fóvea del pronoto por lo general, transversalmente oval (Fig. 533), similar al ancho entre los ojos o entre las partes medias de cada ojo. Parámetros como en la figuras 536-537 *bituberculatus* (Palisot de Beauvois)
- 9'. Tubérculos de la cabeza muy transversos, poco separados (cerca de 2.5 diámetros del tubérculo) (Fig. 534). Fóvea del pronoto redondeada (Fig. 534), similar o más angosta que el ancho entre los ojos. Parámetros como en las figuras 552-553 *gyas* Erichson

***Tomarus bituberculatus* (Palisot de Beauvois, 1811), New Combination**

(Figs. 40, 533, 535-539)

Scarabaeus bituberculatus Palisot de Beauvois 1811 (not 1805): 103.

Ligyris latifovea Bates 1888: 315 (synonym).

Ligyris maximus Arrow 1913: 466 (synonym).

Ligyris latus Arrow 1914: 273 (synonym).

DESCRIPTION. Length 23.0-34.0 mm; width 12.4-16.8 mm. Color black. *Head:* Frons and clypeus coarsely rugose. Frontoclypeal region with 2 distinct tubercles; tubercles widely separated, about 5 tubercle diameters apart (Fig. 533). Clypeus narrowed to bidentate apex; teeth strongly reflexed and distinctly more than a tooth diameter apart, notch between teeth triangular. Interocular width equals 3.3-4.0 transverse eye diameters. Antenna 10-segmented, club subequal to segments 2-7. Mandibles with 2 broad, apical teeth and a round lobe at base. *Pronotum:* Surface with disc moderately punctate, sides

and anterior angles densely punctate; punctures moderate in size; fovea rugose within. Anterior margin with a strong, occasionally slightly recurved, median tubercle. Transverse fovea present behind tubercle; fovea varies in width from distance between eyes to distance between midpoint of each eye (Fig. 533). *Elytra:* Surface densely punctate; punctures mostly moderate in size, with sparser minute punctures between larger punctures; larger punctures usually ocellate, some in poorly defined double rows. *Pygidium:* Surface finely rugopunctate on base and in angles, sparsely punctate on disc; punctures moderate in size with minute setae (setae usually abraded away). In lateral view, males with moderately convex and females with weakly convex surface. *Legs:* Foretibia tridentate, usually with weak convexity suggestive of a 4th, basal tooth, teeth subequally spaced from each other. Foretarsus in males simple, not enlarged. Posterior tibia with apex truncate and with 17-18 long, stout bristles. First tarsomere of posterior tarsus with apex subtruncate. *Venter:* Prosternal process long,

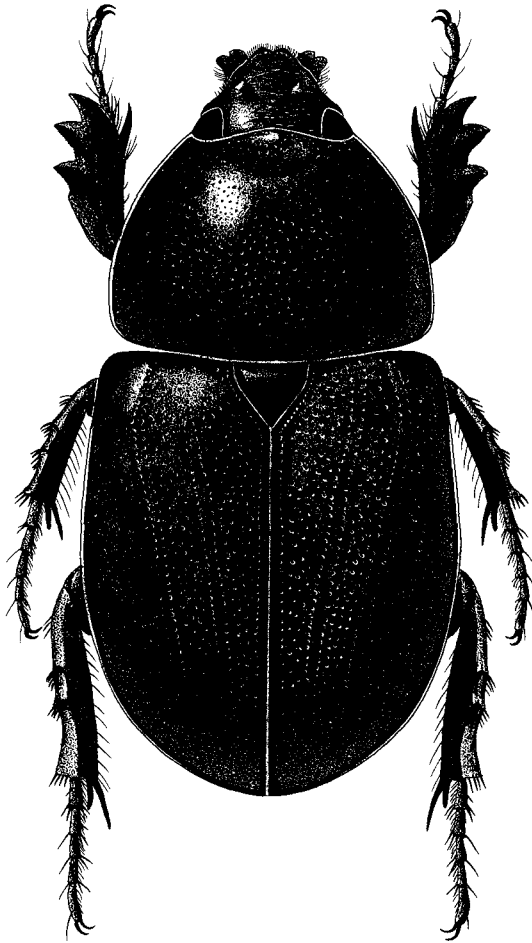
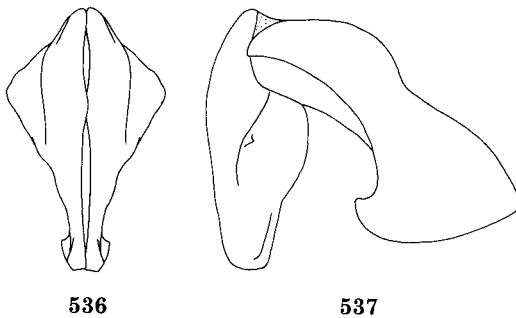


Fig. 535. *Tomarus bituberculatus*.



Figs. 536-537. *Tomarus bituberculatus* parameres.

thick, apex longitudinally oval. *Parameres*: Figs. 536-537.

DISTRIBUTION. *Tomarus bituberculatus* is found from southern Mexico to Amazonia in

South America (Endrödi 1969, 1985a). It is widely distributed in Costa Rica and Panama.

LOCALITY RECORDS (Figs. 538-539). 454 specimens examined.

COSTA RICA (435). **ALAJUELA** (73): Caño Negro, Estación San Ramon (Parq. Nac. Guanacaste); **GUANACASTE** (52): Cerro El Hacha, Estación los Almendros, Estación Maritza, Estación Murciélago, Estación Pitilla, Estación Santa Rosa, Finca Jenny, Finca Montezuma (SW slope Volcán Tenorio), La Pacífica, Liberia, Parq. Nac. Barra Honda, Parq. Nac. Guanacaste, Playa Naranjo (Parq. Nac. Santa Rosa), Río San Lorenzo (Volcán Tenorio), Tierras Morenas (Tilarán); **HEREDIA** (56): Estación Magsasay, La Selva Biological Station, La Virgen de Sarapiquí, Pueblo Nuevo (Sarapiquí), Puerto Viejo, Río Frio; **LIMÓN** (147): Parq. Nac. Tortugero, Refugio Nacional Barra del Colorado, Reserva Biológica Hitoy Cerere, Sector Cerro Cocori; **PUNTARENAS** (93): Estación Esquinas, Estación Las Mellizas, Estación Sirena, Fila Guerra (Osa), La Esquadra, Monteverde, Quepos, Rancho Quemado (Osa), Reserva Biológica Carara, San Luis (Reserva Biológica Monteverde), San Vito; **SAN JOSÉ** (1): Estación Bijagual.

PANAMA (19). **CANAL ZONE** (6): Barro Colorado Island, Coco Solo Hospital; **CHIRIQUI** (5): Finca La Suiza (5.3 km N Los Planes), Progreso; **COLÓN** (1): Santa Rita Ridge; **DARIEN** (1): No data; **PANAMA** (5): Altos de Majé, Ipeti, Panama City.

TEMPORAL DISTRIBUTION. January (77), February (22), March (28), April (38), May (88), June (56), July (12), August (7), September (11), October (23), November (33), December (51).

DIAGNOSIS. *Tomarus bituberculatus* is externally similar to *T. gyas*. Although the size of *T. bituberculatus* is generally larger, and the notch between the clypeal teeth is broader than the width of a clypeal tooth, these character states (used by Endrödi 1969, 1985a) are too imprecise for reliable

identification. Instead, the tubercles on the head of *T. bituberculatus* are rounded and widely separated from each other (ca. 5.0 tubercular diameters) (Fig. 533) whereas the tubercles in *T. gyas* are distinctly transverse and separated by about 2.5 tubercular diameters (Fig. 534). In addition, the fovea of the pronotum in *T. bituberculatus* is transversely oval and larger (subequal to the width between the eyes or between the middle of each

eye), whereas the fovea in *T. gyas* is round and small (subequal to or narrower than the width between the eyes).

As a cautionary note, I should add that Amazonian specimens of both of these species do not differ in their tubercular and pronotal fovea characters, and that they can be distinguished only by the form of the parameres. I have not seen this in the Central American specimens I have examined, but the possibility exists.

NOMENCLATURE. Endrödi (1969) placed *Heteronychus scarabaeinus* Burmeister into synonymy with this species. I believe this is in error. Burmeister did not describe *H. scarabaeinus*, even inadvertently, and he clearly attributes the name to Perty (1830). Perty's *scarabaeinus* is a synonym of *T. ebenus*.

BIOLOGY. Adults are attracted to lights. Presumably, the larvae live in compost-like, organic debris. *Tomarus bituberculatus* is broadly distributed in Costa Rica and Panama, but it shows a definite preference for lowland, tropical wet forest and premontane moist forest below 500 meters. A few specimens have been taken as high as 1,350 meters in premontane wet forests. Collecting records suggest an emergence in May at the onset of the rains, but adults have been taken in all months.



Fig. 538. Distribution of *Tomarus bituberculatus* in Costa Rica.

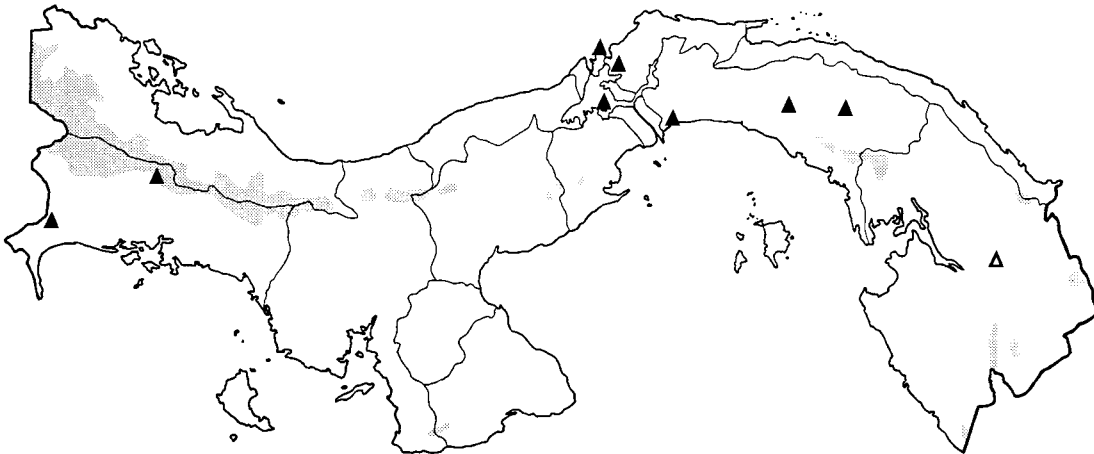


Fig. 539. Distribution of *Tomarus bituberculatus* in Panama.

***Tomarus cicatricosus* (Prell, 1937),
New Combination**
(Figs. 540-542)

Ligyris cicatricosus Prell 1937a: 90.

DESCRIPTION. Length 16.5-24.0 mm; width 8.2-13.0 mm. Color black. *Head:* Frons weakly concave between eyes and behind frontoclypeal tubercles; surface rugose, becoming nearly impunctate near vertex. Frontoclypeal region with tubercle either side of middle, tubercles broadly separated from one another (just laterad of clypeal teeth), tubercles occasionally connected by a weak carina. Clypeus with surface transversely rugose; apex broadly truncate, with 2 very small teeth; teeth reflexed, widely separated (about "in-line" with frontoclypeal tubercles). Interocular width equals 2.9 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. Mandibles with 2 apical teeth and a rounded basal lobe (the latter difficult to see because of dense setae). *Pronotum:* Surface with punctures moderate in density, moderate in size, ocellate, weakly umbilicate. Anterior margin with small, median tubercle and small, subapical fovea behind tubercle; fovea rugose, oblong, shallow, a little narrower than width between clypeal tubercles. *Elytra:* Surface with minute and moderately large punctures mixed; larger punctures moderately dense, ocellate-umbilicate; 3 pairs of double rows of punctures distinct. *Pygidium:* Surface sparsely to moderately, completely punctate; punctures subequal in size to those on apex of elytra, ocellate, minutely setigerous. In lateral view, surface evenly convex in males,

weakly convex in females. *Legs:* Foretibia tridentate, basal tooth distinctly removed from others. Anterior tarsus in males simple, not enlarged. Apex of posterior tibia with 4 teeth and a slender seta between each tooth. Apex of first tarsomere of posterior tarsus triangularly expanded. *Venter:* Prosternal process long, thick, apex rounded and completely setose. *Parameres:* Figs. 540-541.

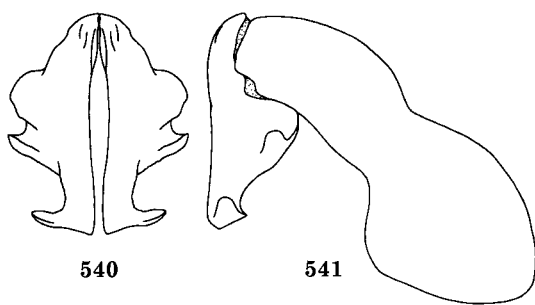
DISTRIBUTION. *Tomarus cicatricosus* is known from southern Mexico and Guatemala (Endrödi 1969, 1985a). The specimens from Costa Rica listed below are a NEW COUNTRY RECORD. Relatively intensive collecting has not yielded additional specimens in Costa Rica except for this population in the extreme south of the country.

LOCALITY RECORDS (Fig. 542). 4 specimens examined.

COSTA RICA (4). PUNTARENAS (4): Rancho Quemado (Osa).

TEMPORAL DISTRIBUTION. April (4).

DIAGNOSIS. Diagnostic characters for this species include a broadly truncate clypeus with small, widely spaced apical teeth; weakly concave frons; small pronotal tubercle



Figs. 540-541. *Tomarus cicatricosus* parameres.



Fig. 542. Distribution of *Tomarus cicatricosus* in Costa Rica.

and fovea; pygidium completely punctate; simple foreclaws in male; widely triangular, basal tarsomere on the posterior tarsus; rounded and completely setigerous apex of the prosternal process; and form of the parameres.

BIOLOGY. Specimens in Costa Rica were taken at an elevation of 200 meters in tropical wet forests. This species is apparently uncommon throughout its range.

***Tomarus ebenus* (Degeer, 1774),
New Combination**
(Figs. 543-547)

Scarabaeus ebenus Degeer 1774: 317.

Scarabaeus cordatus Fabricius 1792: 31 (synonym).

Cyclocephala scarabaeinus Perty 1830: 46 (synonym).

DESCRIPTION. Length 24.0-30.0 mm; width 12.5-15.0 mm. Color black. *Head:* Frons concave between eyes and behind frontoclypeal tubercles; surface mostly rugose, becoming rugopunctate near vertex. Frontoclypeal region with transverse tubercle either side of middle, tubercles broadly separated (about 2/3 width of an eye). Clypeus with surface transversely rugose; apex broadly truncate and with 2 very small teeth, teeth weakly reflexed, widely separated (about "in-line" with frontoclypeal tubercles). Interocular width equals 3.0 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. Mandibles with 2 apical teeth and a rounded lobe at base. *Pronotum:* Surface sparsely punctate; punctures small, becoming moderate in size on sides, weakly umbilicate. Anterior margin with small, median tubercle. A small, oblong fovea present behind tubercle, fovea about as wide as distance between frontoclypeal tubercles, surface of fovea rugose. *Elytra:* Surface with minute and moderately large punctures mixed; larger punctures moderately dense, ocellate; 3 pairs of double rows of punctures distinct to poorly defined. *Pygidium:* Base with broad field of ocellate punctures, punctures subequal in size to

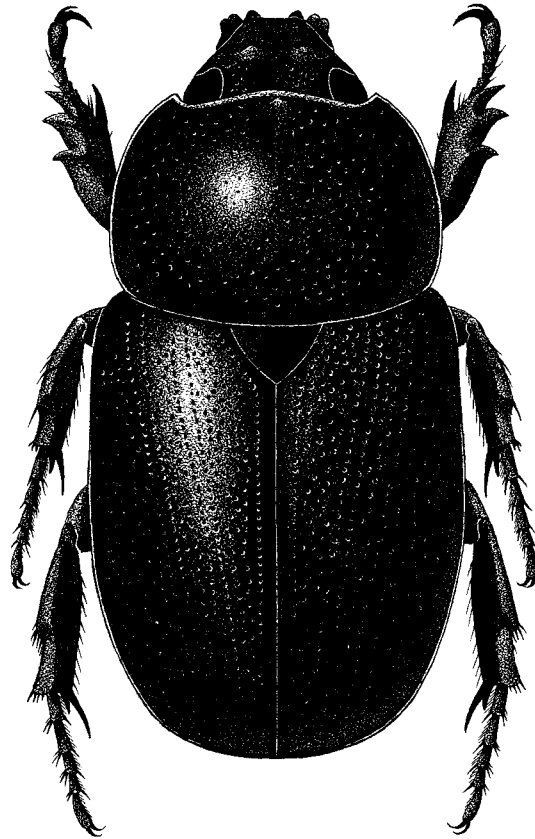
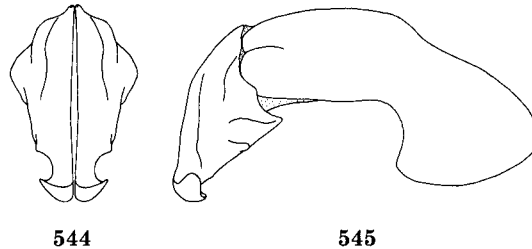


Fig. 543. *Tomarus ebenus*.



Figs. 544-545. *Tomarus ebenus* parameres.

those on disc of elytra, with minute and tawny setae. Disc and apex smooth, lacking punctures. In lateral view, surface strongly convex in males, weakly convex in females. *Legs:* Foretibia tridentate, basal tooth slightly removed from others. Anterior tarsus in males enlarged, claw strongly bent and strongly split at apex. Apex of posterior tibia crenulate with 6 stout spinules. Apex of first tarsomere of posterior tarsus subtruncate. *Venter:* Prosternal process long, thick, apex transversely

oval with semi-hemispherical "button" on all but narrow, posterior margin. *Parameres*: Figs. 544-545.

DISTRIBUTION. *Tomarus ebenus* occurs from southern Mexico south to Bolivia and central Brazil (Endrödi 1969, 1985a). In Costa Rica and Panama it is known from only a few localities in the eastern half of each country.

LOCALITY RECORDS (Figs. 546-547). 132 specimens examined.

COSTA RICA (97). HEREDIA (1): Estación Magsasay (Parq. Nac. Braulio Carrillo);

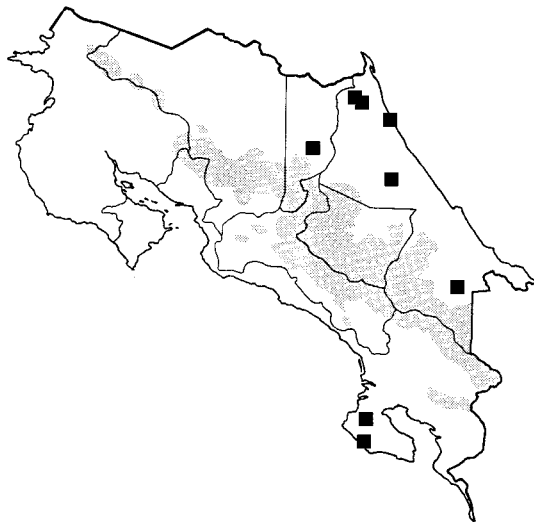


Fig. 546. Distribution of *Tomarus ebenus* in Costa Rica.

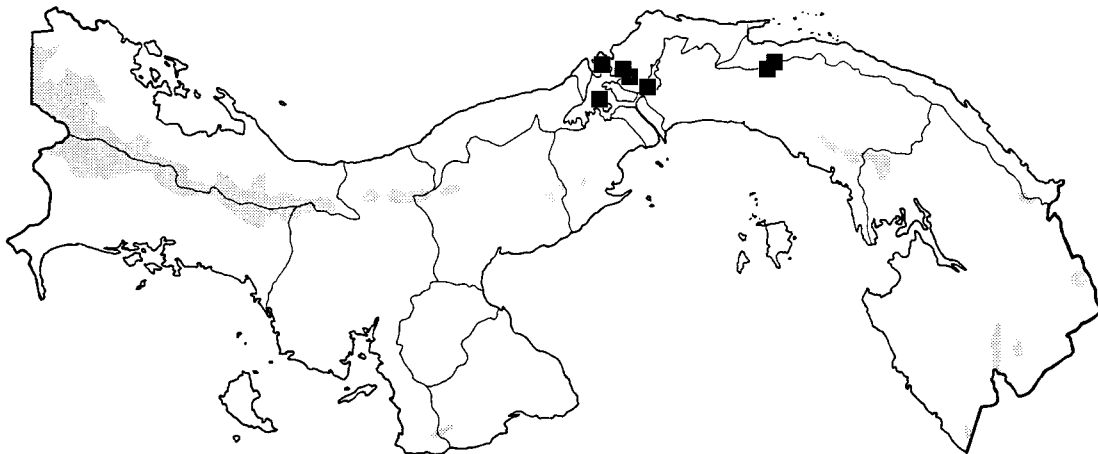


Fig. 547. Distribution of *Tomarus ebenus* in Panama.

LIMÓN (65): Amubri, Cerro Tortuguero (Parq. Nac. Tortuguero), Hamburg Farm, Río Sardinas, Sector Cerro Cocori; PUNTARENAS (31): Estación Sirena (Parq. Nac. Corcovado), Rancho Quemado.

PANAMA (35). CANAL ZONE (18): Barro Colorado Island, Madden Dam, Margarita, Pipeline Rd. (km 2-4); COLÓN (5): Santa Rita Ridge; PANAMA (9): El Llano-Carti Road (km 8-13); SAN BLAS (3): Nusagandi.

TEMPORAL DISTRIBUTION. January (22), February (2), March (1), April (15), May (58), June (11), July (1), September (1), October (1), November (5), December (4).

DIAGNOSIS. This species is distinctive because of the broadly truncate clypeus with small, widely spaced apical teeth; the concavity of the frons; small, apical pronotal tubercle followed by a small, narrow, oblong fovea; disc and apex of pygidium smooth; enlarged foreclaws in the male; and form of the parameres. It is not, however, externally distinguishable from *T. similis*, and only the form of the male parameres will separate them. The females cannot be separated unless they are associated with the males.

BIOLOGY. Adults are attracted to lights at night. Specimens have been taken in tropical wet forests at elevations ranging from mostly near sea level to 450 meters.

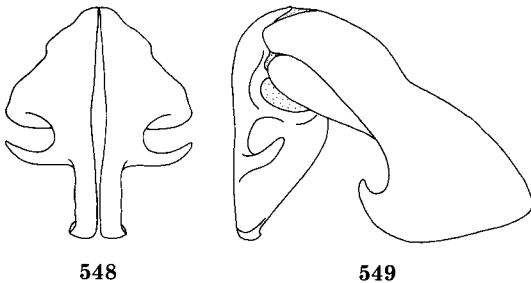
***Tomarus fossor* (Latreille, 1813),
New Combination**
(Figs. 548-550)

Scarabaeus fossor Latreille 1813: 11.

Ligyryus castaneipennis Apolinar 1927: 120
(synonym).

DESCRIPTION. Length 13.5-15.0 mm; width 7.7-8.7 mm. Color light to dark reddish brown. *Head:* Frons with large, dense (often confluent) punctures; vertex smooth. Frontoclypeal region with transverse tubercle (or short carina) either side of middle, distance between tubercles equals one half to entire width of clypeal apex. Clypeus weakly rugose; apex broadly truncate, weakly bidentate, teeth very small, reflexed. Interocular width equals 3.0-3.3 transverse eye diameters. Antenna with 10 segments, club distinctly longer than segments 2-7. Mandibles laterally with 3 teeth, basal tooth

obtuse. *Pronotum:* Surface sparsely to moderately (at center base) to moderately (on disc) to moderately densely (anterior and posterior angles, center apex) punctate; punctures large. Intervals between punctures crazed. Anterior tubercle and fovea absent. *Elytra:* Surface with micropunctures and large punctures mixed; large punctures usually ocellate, moderately dense, 3 pairs of double rows distinct. *Pygidium:* Surface moderately to densely punctate; becoming almost rugose in angles; punctures large, umbilicate, setigerous; setae minute, pale. In lateral view, surface weakly convex in both sexes. *Legs:* Foretibia tridentate, basal tooth removed from others. Male with anterior tarsi simple, not enlarged. Apex of posterior tibia with small crenulations and 17 spinules. Apex of first tarsomere of posterior tarsus subtruncate. *Venter:* Prosternal process long, thick, apex subconical or rounded, not flat. *Parameres:* Figs. 548-549.



Figs. 548-549. *Tomarus fossor* parameres.

DISTRIBUTION. *Tomarus fossor* occurs in Panama, Colombia, Venezuela, and probably Bolivia and northern Brazil as well as Cuba, Jamaica, and Puerto Rico (Blackwelder 1944; Endrödi 1969, 1985a). This species is known from only two localities in Panama, but I suspect more collecting in Darien and possibly Los Santos provinces would reveal their presence there.

LOCALITY RECORDS (Fig. 550). 3 specimens examined.



Fig. 550. Distribution of *Tomarus fossor* in Panama.

PANAMA (3). COCLÉ (2): Interamerican highway at Río Grande; PANAMA (1): Chame.

TEMPORAL DISTRIBUTION. May (3).

DIAGNOSIS. *Tomarus fossor* superficially resembles *T. nasutus* and, to a lesser extent, *T. sallaei* because all of these species are similar in size and all lack a pronotal fovea. The auxillary foretibial teeth of *T. sallaei* and the enlarged claws of the foretarsus in males easily separates it from *T. fossor*, which lacks these teeth. The broad clypeal apex of *T. fossor* distinguishes it from *T. nasutus*, which has a narrow, strongly bidentate clypeal apex. In addition, the parameres of these species are all significantly different from one another.

BIOLOGY. Adults are attracted to lights at night. Pardo Locarno (1994) reported adults feeding on the flowers of sunflower plants in Colombia. The Panamanian specimens listed here represent the northernmost extension of this South American species. The Panamanian specimens were collected in tropical dry forests at elevations of less than 100 meters.

Tomarus gyas Erichson, 1848

(Figs. 534, 551-555)

Tomarus gyas Erichson 1848: 561.

Ligyris amazonicus Arrow 1914: 273 (synonym).

DESCRIPTION. Length 21.5-29.5 mm; width 11.2-14.7 mm. Color dark reddish brown to black. *Head:* Frons and clypeus coarsely rugose. Frontoclypeal region with 2 distinctly transverse tubercles; tubercles narrowly separated, usually about 2.5 tubercle diameters apart (Fig. 534). Clypeus narrowed to bidentate apex; teeth strongly reflexed, notch between teeth triangular, subequal to or slightly wider than a single tooth. Interocular width equals 3.0-3.7 transverse eye diameters. Antenna with 10 segments, club subequal to segments 2-7. Mandibles with 2 broad, apical teeth and a convex lobe at base. *Pronotum:* Surface with disc moderately punctate, sides and anterior angles densely

punctate to rugopunctate; punctures moderate in size on disc, becoming larger laterally; fovea rugose within. Anterior margin with a strong, median tubercle. A nearly round fovea present behind tubercle; fovea small, width subequal to or slightly narrower than width between eyes. *Elytra:* Surface densely punctate; punctures mostly moderate in size, with sparser, minute punctures between larger punctures; larger punctures usually ocellate, some in double rows. *Pygidium:* Surface finely rugopunctate on base and in angles, sparsely punctate on disc; punctures small with minute setae (setae usually abraded away). In lateral view, males with moderately convex and females with weakly convex surface. *Legs:* Foretibia tridentate and with weak, basal convexity suggestive of 4th tooth, teeth subequally spaced from each other. Foretarsus in males simple, not enlarged. Apex of posterior tibia with small crenulations and about 22 spinules. Apex of first tarsomere of posterior tarsus weakly, triangularly expanded. *Venter:* Prosternal process long, thick, apex longitudinally oval. *Parameres:* Figs. 552-553.

DISTRIBUTION. *Tomarus gyas* occurs from southern Mexico to Argentina (Endrödi 1969, 1985a). It is widely distributed in the lowlands of both Costa Rica and Panama.

LOCALITY RECORDS (Figs. 554-555). 138 specimens examined.

COSTA RICA (99). ALAJUELA (1): Estación San Ramon; CARTAGO (1): Turrialba; GUANACASTE (41): El Arno (Parq. Nac. Guanacaste), Estación Las Pailas (Parq. Nac. Rincón de la Vieja), Estación Murciélago, Estación Pitilla, Estación Santa Rosa (Parq. Nac. Santa Rosa), Finca Jenny (Parq. Nac. Guanacaste), Playa del Coco, Tierras Morenas (Arenal); HEREDIA (2): La Selva Biological Station, Pueblo Nuevo (Sarapiquí); LIMÓN (18): Amubri, Buen, Refugio Nac. Barra del Colorado, Sector Cerro Cocori; PUNTARENAS (32): Boca del Río Esquinas, Estación Esquinas (Osa), Estación Las Mellizas (Parq. Nac. Amistad), Estación Sirena (Parq. Nac. Corcovado), Rancho Quemado (Osa), Reserva

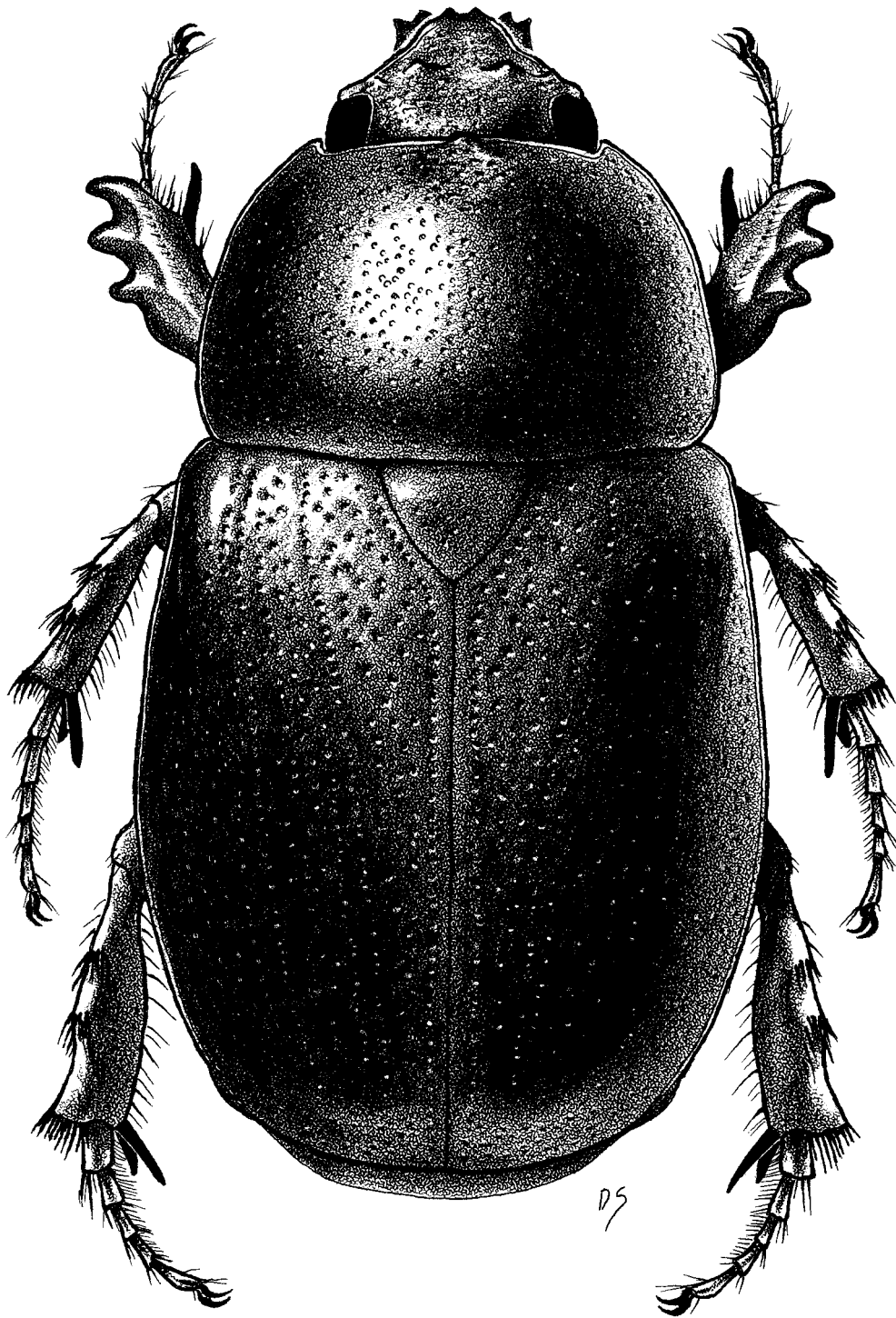
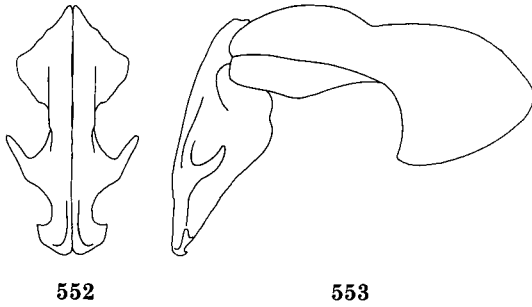


Fig. 551. *Tomarus gyas*.



552

553

Figs. 552-553. *Tomarus gyas* parameres.

Biológica Carara, Rey Curre; SAN JOSÉ (4): San Isidro.

PANAMA (39). CANAL ZONE (8): Barro Colorado Island, Madden Dam; CHIRIQUI (3): David; COLÓN (2): Santa Rita Ridge; PANAMA (26): Altos de Majé, El Llano-Carti Rd. (km 10), Ipeti (3 km E).

TEMPORAL DISTRIBUTION. January (6), March (14), April (21), May (45), June (30), July (4), August (2), November (2), December (13).

DIAGNOSIS. *Tomarus gyas* is externally similar to *T. bituberculatus*, although the parameres are very different from one another. The size of *T. gyas* is generally smaller, and the notch between the clypeal teeth is about as broad as one clypeal tooth, but these character states (used by Endrödi 1969, 1985a) are not discrete enough for reliable identification. Instead, the tubercles on the head of *T. gyas* are distinctly transverse and spaced relatively closely to each other (2.5 tubercular diameters) (Fig. 534), and the fovea of the pronotum is round and small (subequal to or narrower than the width between the eyes). In *T. bituberculatus*, the tubercles on the head are round and spaced relatively far apart (5.0 tubercular diameters), and the fovea of the pronotum is transversely oval and larger (subequal to width between eyes or between the middle of each

Fig. 554. Distribution of *Tomarus gyas* in Costa Rica.Fig. 555. Distribution of *Tomarus gyas* in Panama.

eye, Fig. 533). These distinguishing character states work for both sexes.

I should point out that in Amazonian specimens of both of these species, the tubercular and pronotal fovea characters do not work for distinguishing species; *T. gyas* appears to have round tubercles and a transverse pronotal fovea just like *T. bituberculatus*. While I have not seen this in the Central American specimens that I have examined, the possibility exists for this convergence of character states, which would then necessitate the use of the parameres only.

BIOLOGY. This species is widely distributed throughout the lowlands of Costa Rica and Panama. They are found in tropical wet forests and premontane moist forests generally below 700 meters. An occasional specimen has been taken in premontane wet forests at 1,200 meters elevation.

***Tomarus laevicollis* (Bates, 1888),
New Combination**
(Figs. 556-559)

Ligyris laevicollis Bates 1888: 316.

Ligyris bryanti Rivers 1891: 97 (synonym).

DESCRIPTION. Length 19.0-24.0 mm; width 10.0-12.0 mm. Color dark reddish brown to black. *Head:* Surface of frons and clypeus coarsely rugose. Frontoclypeal region with round tubercle either side of midline, tubercles separated by about 9 tubercle diameters. Clypeus tapering to bidentate apex; teeth reflexed, notch between teeth triangular, a little wider than a single tooth. Interocular width equals 3.0-3.3 transverse eye diameters. Antenna 10-segmented, club subequal to segments 2-7. Mandibles with 2 broadly rounded, apical teeth and rounded lobe at base. *Pronotum:* Surface crazed, nearly impunctate or with micro punctures except for apical and lateral margins where punctures small to moderate in size, moderate in density. Apical margin with small tubercle at middle, followed by small fovea; fovea rugopunctate, tapering posteriorly, about half as wide as distance between eyes.

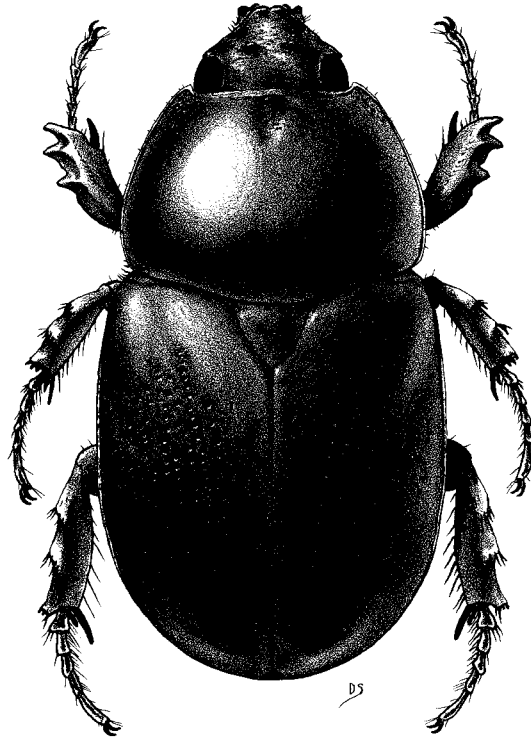
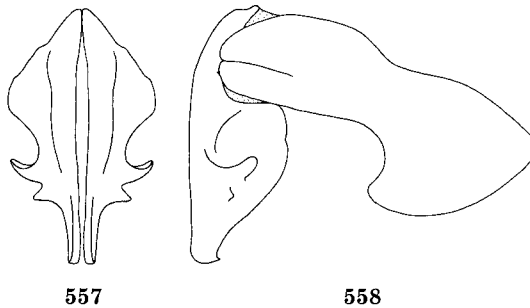


Fig. 556. *Tomarus laevicollis*.



Figs. 557-558. *Tomarus laevicollis* parameres.

Elytra: Surface crazed, first interval nearly impunctate or with sparse micropunctures only. Remainder of elytron densely punctate; punctures moderate in size, mostly ocellate, 3 pairs of double rows distinct; intervals with sparse micropunctures. *Pygidium:* Base and angles rugopunctate; males with disc crazed and with sparse micropunctures; punctures with minute, tawny setae; females similar except disc with small punctures. In lateral



Fig. 559. Distribution of *Tomarus laevicollis* in Costa Rica.

view, males with pygidium evenly convex, females with convexity weak. *Legs*: Foretibia tridentate, with weak, basal convexity suggestive of 4th tooth, basal tooth removed from anterior 2 teeth. Males with anterior tarsi simple, not enlarged. Apex of posterior tibia with small crenulations and with 7-9 short and 2 longer spinules. Apex of first tarsomere of posterior tarsus subtruncate. *Venter*: Prosternal process long, thick, apex subquadrate to slightly longitudinally oval. *Parameres*: Figs. 557-558.

DISTRIBUTION. *Tomarus laevicollis* is known from Mexico and Honduras (Endrödi 1969, 1985a). Endrödi's record for the United States (California) is erroneous. The specimens recorded here for Costa Rica constitute a NEW COUNTRY RECORD.

LOCALITY RECORDS (Fig. 559). 13 specimens examined.

COSTA RICA (13). **LIMÓN** (13): Amubri, Reserva Biológica Hitoy Cerere.

TEMPORAL DISTRIBUTION. January (2), April (3), May (6), September (2).

DIAGNOSIS. *Tomarus laevicollis* is distinctive because of the round frontoclypeal tu-

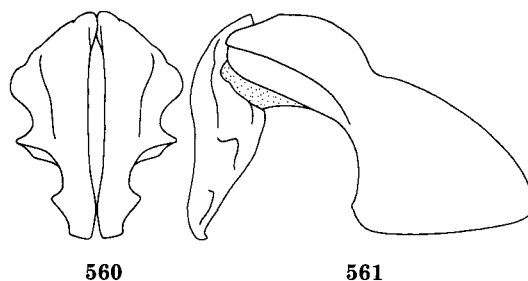
bercles, nearly impunctate pronotum, virtually impunctate first elytral interval, unequally spaced basal tooth of the foretibia, and the form of the male parameres.

BIOLOGY. Adults are nocturnal and are attracted to lights. This is an uncommon species, and its discovery in southeastern Costa Rica so far from its previously known occurrence in Mexico and Honduras is a surprise. The Costa Rican specimens were taken in premontane wet forests at elevations of 100 meters or less. The dry Nicaraguan depression effectively separates these two populations that may have once been previously contiguous.

***Tomarus maternus* (Prell, 1937),
New Combination**
(Figs. 560-562)

Ligyris maternus Prell 1937a: 89.

DESCRIPTION. Length 22.5-24.0 mm; width 11.0-12.2 mm. Color black. *Head*: Frons and clypeus coarsely rugose. Frontoclypeal region with 2 transverse tubercles separated by about 2 tubercular widths (as seen from above). Clypeus with narrow, bidentate apex; teeth small, reflexed, distance between teeth a little more than 1 tooth diameter; each tooth approximately "in-line" with median edge of frontoclypeal tubercle behind it. Interocular width 3.0 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. Mandibles with 2 broad apical teeth and a round lobe at base. *Pronotum*: Surface with sparse, minute to small, shallow



Figs. 560-561. *Tomarus maternus* parameres.



Fig. 562. Distribution of *Tomarus maternus* in Costa Rica.

punctures; punctures becoming a little larger in posterior angles and near apical fovea and moderately large and denser in anterior angles. Anterior margin with weak, median tubercle. Fovea immediately behind tubercle small, very shallow to only vaguely depressed, round to weakly elongated. *Elytra*: Surface densely punctate, punctures moderate in size, deep, lacking minute punctures between larger punctures, some punctures in weak double rows. *Pygidium*: Surface at base rugulose with rugulosity margined by sparse, moderately-sized punctures; center apex also rugulose in males but not in females. Disc in males with only a few minute to small punctures, females with sparse, small punctures, discal punctures in both sexes minutely setigerous. In lateral view, surface weakly convex in males, nearly flat in females. *Legs*: Foretibia tridentate, teeth subequally spaced from one another. Foretarsus in males simple, not enlarged. Posterior tibia with apex truncate and with 13-15 long, stout bristles. First tarsomere of posterior tarsus with apex slightly elongated. *Venter*: Prosternal process long, apex large and longitudinally oval. *Parameres*: Figs. 560-561.

DISTRIBUTION. *Tomarus maternus* was known from Colombia, Ecuador, Peru, and Bolivia (Endrödi 1969, 1985a). The specimens recorded here represent a NEW COUNTRY

RECORD. Once again, we find what seems to be an isolated population of a South American species in Costa Rica. Given the distribution of this species in northwestern South America, we might expect an occurrence in Central America on the Pacific slopes but instead find *T. maternus* on the Atlantic slopes. Moreover, it is apparently not found in Panama. Clearly, we do not yet know enough about either the formation of the isthmus and how it may have separated populations of plants and animals or about how organisms may have dispersed from northwestern South America to the Atlantic slopes of Costa Rica, seemingly skipping Panama in the process.

LOCALITY RECORDS (Fig. 562). 14 specimens examined.

COSTA RICA (14). **LIMÓN** (14): Amubri, Reserva Biológica Hitoy Cerere.

TEMPORAL DISTRIBUTION. March (4), April (2), May (1), November (5), December (2).

DIAGNOSIS. *Tomarus maternus* is externally similar to *T. laevicollis*. The transverse frontoclypeal tubercles, more punctate pronotum, punctate first broad interval of the elytra, and evenly spaced teeth of the foretibia will separate *T. maternus*.

BIOLOGY. As with other species of *Tomarus*, *T. maternus* is nocturnal, and adults are attracted to lights. Pardo Locarno (1994) reported larvae feeding on the roots of yucca and sugar cane in Colombia. The Costa Rican specimens were taken in tropical wet forests at elevations of 100-200 meters.

***Tomarus nasutus* (Burmeister, 1847), New Combination**
(Figs. 563-567)

Podalgus nasutus Burmeister 1847: 120.

Ligyris pygidialis Bates 1888: 317 (synonym).

DESCRIPTION. Length 14.0-18.0 mm; width 8.0-10.6 mm. Color light to dark (most

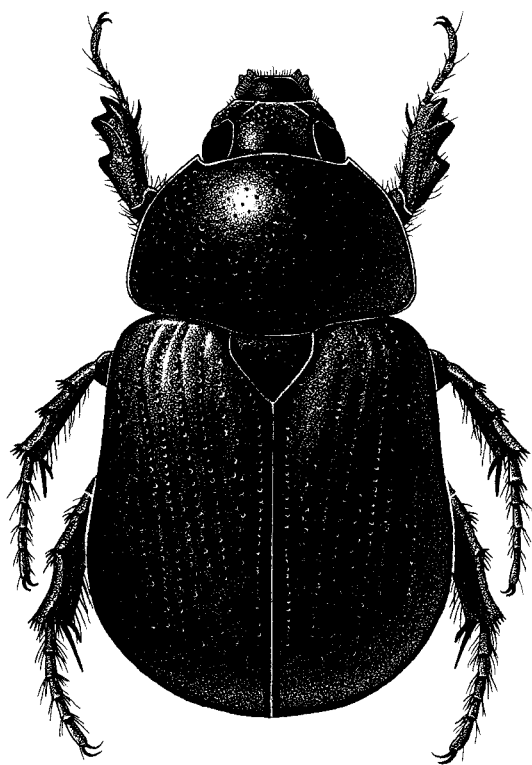
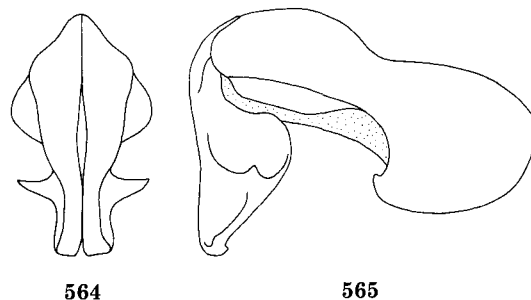


Fig. 563. *Tomarus nasutus*.

common) reddish brown to nearly black. *Head*: Frons and clypeus finely rugose with a few large, deep punctures at anterior edge of vertex. Frontoclypeal region with strong, long (eye to eye) transverse carina; carina occasionally depressed at middle. Clypeus attenuated to narrow apex, apex with 2 small teeth; teeth sharp, reflexed, closely spaced to one another (subequal to space between apical 2 teeth of mandible). Interocular width equals 2.7 transverse eye diameters. Antenna 10-segmented, club a little longer than segments 2-7. Mandibles with 2 apical teeth and rounded, basal lobe. *Pronotum*: Surface moderately to moderately densely punctate; punctures large, weakly ocellate. Anterior marginal bead at center with very small, acuminately flattened area instead of a tubercle; fovea absent. *Elytra*: Surface with micropunctures and large punctures mixed; large punctures moderately dense, ocellate, and with 3 pairs of distinct



Figs. 564-565. *Tomarus nasutus* parameres.

double rows. First broad interval with or without large punctures. *Pygidium*: Surface sparsely punctate, becoming denser in angles; punctures moderate to large in size, weakly ocellate, with minute and tawny setae. In lateral view, males with convex surface, females with weakly convex surface. *Legs*: Foretibia tridentate, basal tooth slightly removed from others. Foretarsus in males simple, not enlarged. Apex of posterior tibia truncate with about 17 long spinules. Apex of first tarsomere of posterior tarsus weakly, triangularly expanded. *Venter*: Prosternal process tall, thick; apex small, suboval, often obscured by long setae. *Parameres*: Figs. 564-565.

DISTRIBUTION. *Tomarus nasutus* has been recorded from Mexico to Costa Rica (Endrödi 1969, 1985a). Endrödi's listing of the United States (Texas) is in error. The specimens listed for Panama below constitute a NEW COUNTRY RECORD. This species is widely distributed in Costa Rica (mostly in the lowlands), and I have collected it from only Madden Forest in Panama.

LOCALITY RECORDS (Figs. 566-567). 499 specimens examined.

COSTA RICA (493). ALAJUELA (1): Caño Negro; GUANACASTE (478): Cañas, Enrique Jimenes Nuñez Exp. Station (20 km S Cañas), Estación Lomas Barbudal, Estación Los Almendros, Estación Murcielago, Estación Palo Verde, Estación Santa Rosa (Parq. Nac.

Guanacaste), Finca Jenny, Finca La Pacífica, Parq. Nac. Barra Honda, Parq. Nac. Santa Rosa, Playa Naranjo (Parq. Nac. Guanacaste), Río San Lorenzo, Tierras Morenas; LIMÓN (1): Río Sardinas (Refugio Nacional Barra del Colorado); PUNTARENAS (1): Reserva Biológica Carara, San Luis (Reserva Biológica Monteverde).

PANAMA (6). CANAL ZONE (5): Madden Dam, Pipeline Road (2 km W Gamboa); CHIRIQUI (1): Finca La Suiza.



Fig. 566. Distribution of *Tomarus nasutus* in Costa Rica.



Fig. 567. Distribution of *Tomarus nasutus* in Panama.

TEMPORAL DISTRIBUTION. March (25), April (64), May (36), June (37), July (215), August (76), September (13), October (9), November (1).

DIAGNOSIS. The narrowly bidentate clypeus in combination with the simple (not enlarged) claw in the male, bidentate mandibles, and form of the parameres will distinguish this species from others in the genus.

BIOLOGY. Adults are nocturnal and attracted to lights at night. Specimens have been collected near sea level to 1,050 meters in elevation, but the vast majority are from the lowlands. They inhabit tropical dry forests, tropical moist forests, tropical dry forests, and premontane rain forests.

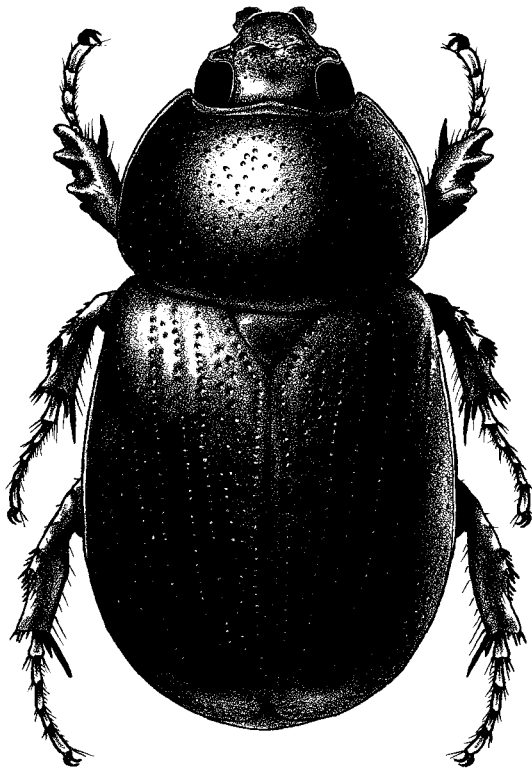
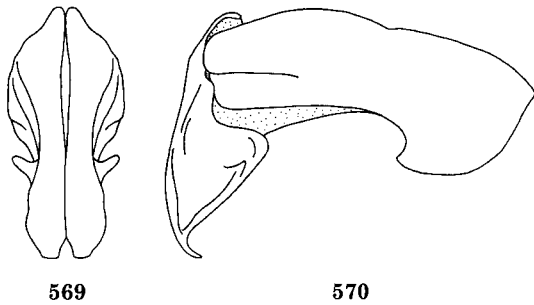
***Tomarus sallaei* (Bates, 1888),
New Combination
(Figs. 568-571)**

Ligyus sallaei Bates 1888: 318.

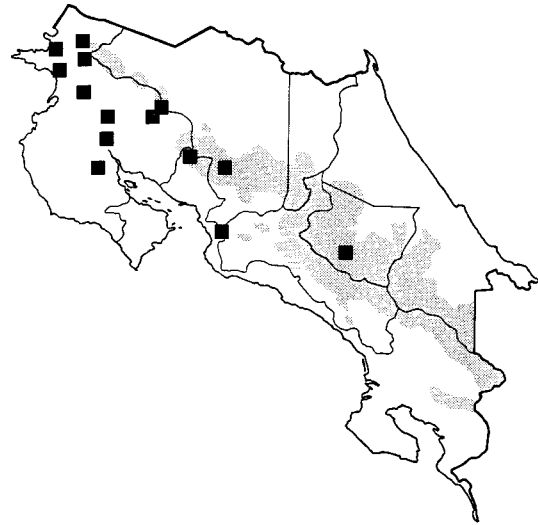
Ligyrodes propinquus Casey 1915: 183 (synonym).

Ligyrodes aztecus Casey 1915: 183 (synonym).

DESCRIPTION. Length 18.5-21.2 mm; width 10.4-11.5 mm. Color dark reddish brown to black. *Head:* Frons mostly impunctate between eyes and coarsely rugopunctate just posterior of frontoclypeal carina. Frontoc-

Fig. 568. *Tomarus sallaei*.Figs. 569-570. *Tomarus sallaei* parameres.

clypeal region with transverse, bilobed carina (2 transverse tubercles joined together). Clypeus finely rugopunctate to transversely rugose, tapering to broad apex with 2 reflexed teeth, space between teeth shallowly emarginate. Interocular width equals 2.5 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. Mandibles with 3 teeth on lateral edge. *Pronotum*: Surface crazed, sparsely

Fig. 571. Distribution of *Tomarus sallaei* in Costa Rica.

punctate; punctures moderately large, umbilicate. Tubercle and fovea absent. *Elytra*: Surface with micropunctures and large punctures mixed; large punctures weakly ocellate, moderate in density in intervals; 3 pair of double rows distinct. *Pygidium*: Surface with base and angles rugopunctate (males) or densely punctate (females); disc sparsely punctate; punctures small to mostly moderate in size, setigerous; setae minute, tawny in color. *Legs*: Foretibia tridentate, teeth subequally spaced from each other; a small accessory tooth in front of (occasionally missing) and behind basal tooth. Foretarsus in males enlarged; large claw bent strongly and apex with short, projecting spine (may be worn away). Apex of posterior tibia with 5 small teeth and 6 spinules (1 each between teeth). Apex of first tarsomere of posterior tarsus weakly, triangularly expanded. *Venter*: Prosternal process tall, thick; apex nearly round to transversely oval, flat with round to transversely oval, semihemispherical "button" on anterior half. *Parameres*: Figs. 569-570.

DISTRIBUTION. *Tomarus sallaei* occurs from the southern United States (Texas) south to Costa Rica (Endrödi 1969, 1985a; Saylor 1946b). In Costa Rica it is known mostly from the northeast on Pacific-facing slopes and in the lowlands; two specimens are

known from the Osa peninsula. No specimens are known from the Atlantic side of Costa Rica or from Panama.

LOCALITY RECORDS (Fig. 571). 113 specimens examined.

COSTA RICA (113). **ALAJUELA** (1): 5 km. N Colonia Palmareña; **CARTAGO** (1): San Luis, Monteverde; **GUANACASTE** (59): Agua Buena (Parq. Nac. Guanacaste), Estación Lomas Barbudal, Estación Murcielago (Parq. Nac. Guanacaste), Estación Palo Verde, Finca Jenny, 10 mi. N Liberia, Nacaome, Playa Naranjo (Parq. Nac. Guanacaste), Tierras Morenas (Tilaran); **PUNTARENAS** (52): Estación La Casona (Res. Biol. Monteverde), Estación Sirena (Parq. Nac. Corcovado), Pension Quetzal (Monteverde), Reserva Biológica Carara, Reserva Biológica Monteverde.

TEMPORAL DISTRIBUTION. January (1), February (1), April (1), May (16), June (3), July (49), August (31), September (10), October (1).

DIAGNOSIS. *Tomarus sallaei* is easily recognized because of the small accessory teeth immediately in front of and behind the basal tooth of the foretibia. The strong clypeal carina, lack of a pronotal tubercle and fovea, enlarged foretarsus in the male, and form of the parameres are also diagnostic.

BIOLOGY. Deloya (1988) reported finding pupae in the detritus refuse piles of the leafcutter ant, *Atta mexicana* (Smith), in Mexico. Specimens have been collected at elevations from near sea level to 1,520 meters at Monteverde in tropical dry forests, tropical moist forests, and tropical wet forests.

***Tomarus similis* (Endrödi, 1968),
New Combination**
(Figs. 572-575)

Ligyris similis Endrödi 1968: 166.

DESCRIPTION. Length 19.0-26.0 mm; width 10.0-12.7 mm. Color black. *Head:* Frons

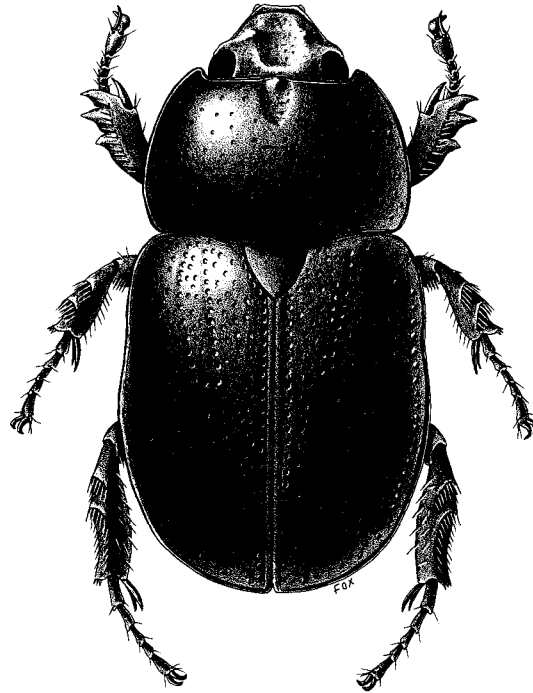
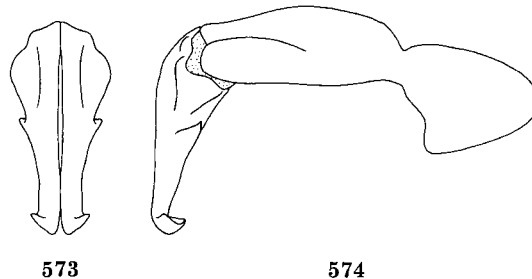


Fig. 572. *Tomarus similis*.



Figs. 573-574. *Tomarus similis* parameres.

concave between eyes and behind frontoclypeal tubercles; surface mostly rugose, becoming rugopunctate near vertex. Frontoclypeal region with transverse tubercle either side of middle, tubercles broadly separated (about 2/3 width of eye). Clypeus with surface transversely rugose; apex broadly truncate and with 2 very small teeth; teeth weakly reflexed, widely separated (about "in-line" with frontoclypeal tubercles). Interocular width equals 3.0 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. Mandibles with 2 apical teeth

and rounded lobe at base. *Pronotum*: Surface sparsely punctate; punctures weakly ocellate, small, becoming moderate in size on sides. Anterior margin with small, median tubercle. A small, oblong fovea present behind tubercle, fovea about as wide as distance between frontoclypeal tubercles, surface rugose. *Elytra*: Surface with minute and moderately large punctures mixed; larger punctures moderately dense, ocellate; 3 pairs of double rows of punctures poorly defined to distinct. *Pygidium*: Base with broad field of ocellate punctures, punctures subequal in size to those on disc of elytra, with minute and tawny setae. Disc and apex smooth, lacking punctures. In lateral view, surface strongly convex in males, weakly convex in females. *Legs*: Foretibia tridentate, basal tooth slightly removed from others. Anterior tarsus in males enlarged, claw strongly bent and strongly split at apex. Apex of posterior tibia crenulate with 5 short and stout spinules and 1 long seta. Apex of first tarsomere of posterior tarsus subtruncate. *Venter*: Prosternal process long, thick, apex transversely oval with semi-hemispherical "button" on all but narrow, posterior margin. *Parameres*: Figs. 573-574.

DISTRIBUTION. *Tomarus similis* is recorded from Venezuela, Peru, Ecuador, and Trinidad. The Panamanian specimens noted here represent a NEW COUNTRY RECORD.

LOCALITY RECORDS (Fig. 575). 3 specimens examined.

PANAMA (3). CANAL ZONE (3): Barro Colorado Island, Madden Dam.

TEMPORAL DISTRIBUTION. April (1), May (1), December (1).

DIAGNOSIS. *Tomarus similis* is externally indistinguishable from *T. ebenus*. The parameres are different, and they will reliably separate the two species. Unfortunately, I can see no difference between the females. Considering that *T. similis* is so rare in Panama and has been reported from only one locality, there is a high probability that female specimens appearing like either of these two species will be *T. ebenus*. Otherwise, *T. similis* is distinctive among the *Tomarus* species in Costa Rica and Panama because of the broadly truncate clypeus with small, widely spaced apical teeth; the concavity of the frons; small, apical pronotal tubercle followed by a small, narrow, oblong fovea; disc and apex of the pygidium smooth; enlarged claws in the male; and form of the parameres.

BIOLOGY. Adults are attracted to lights at night. In Panama, they are known from an area of tropical wet forest a few hundred meters above sea level.



Fig. 575. Distribution of *Tomarus similis* in Panama.



Color Plate 4. *Coelosis biloba* male feeding on a mango. Illustration by Dan Schmidt.

TRIBE ORYCTINI

Members of this tribe occur worldwide except for Australia and the northern parts of Europe, Asia, and North America. The majority of oryctines are found in the Neotropics. There are 26 genera and over 230 species of Oryctini, and 14 genera and about 135 species occur in the Americas. In Costa Rica and Panama, there are 9 genera (one of which is described as new here) and 17 species.

Adult oryctines are characterized by a generally large and robust body, mandibles usually exposed (though not in *Xyloryctes*), propygidium usually with stridulatory structures, foretibia tri- or quadridentate, and with large teeth, lobes or crenulations on the apex of the posterior tibia (only rarely is the apex truncate) (Figs. 43-47). Sexual dimorphism is usually pronounced with the males possessing prominent horns, prominences, or tubercles on the head and/or pronotum while the females are tuberculate only on the head and/or pronotum (only in *Enema* species does the female have horns).

Few larvae have been described, but those that have are distinguished by a cranium that is densely punctate and dark reddish brown; maxillary stridulatory teeth that are truncate; last segment of the antenna with 2-14 dorsal sensory spots; tarsal claws with 2-4 long, stout setae; and a raster with-

out palidia or a septula (Ritcher 1966; Morón and Ratcliffe 1990).

Burmeister (1847) first proposed the category Oryctidae, and it has been used fairly consistently ever since. Among earlier workers, Lacordaire (1856), LeConte and Horn (1883), Bates (1888), Casey (1915), and Arrow (1937) maintained the category. Burmeister had also established the pentodontines as separate from the oryctines, but this was not followed by Arrow (1937), Blackwelder (1944), Saylor (1948), or Arnett (1968), all of whom included the pentodontines within the Oryctini. Endrödi (1976b) redefined the Oryctini and re-established the Pentodontini as a distinct tribe as well as reviewing the American taxa.

Adult oryctines are nocturnally active, and they seek shelter and hide during the day. They are usually attracted to lights at night, occasionally in high numbers if there is a large emergence. Some adults have been observed feeding on rotting fruits or decaying vegetation while others are known to tunnel in the stems of living plants such as sugarcane and several species of palms.

The larvae are, for the most part, poorly known. Some live in the soil feeding on decaying organic matter while others live in accumulations of compost in rotting tree trunks or roots, in the large stems of living plants, or in the nests of ants (Morón *et al.* 1996).

Key to the Genera of Adult Oryctini of Costa Rica and Panama

1. Anterior tibia tridentate 2
- 1'. Anterior tibia quadridentate 5
2. Mandibles completely hidden beneath clypeus. Apex of clypeus strongly bilobed and sharply reflexed *Xyloryctes* Hope
- 2'. Mandibles visible in dorsal view. Apex of clypeus emarginate or bidentate, not strongly reflexed 3
3. Elytra smooth, black *Megaceras* Hope
- 3'. Elytra distinctly punctate or roughened, reddish brown 4
4. Elytra with 5 distinct rows of punctures on relatively smooth or finely shagreened surface. Mandibles tridentate. Clypeus with apex sharply bidentate *Coelosis* Hope
- 4'. Elytra completely roughened, with weak rows of punctures. Mandibles bidentate. Clypeus with apex lobed either side of median emargination *Irazua* Ratcliffe, new genus

5. Elytra with deeply furrowed rows of punctures. Mandibles with 2 subequally large, rounded lobes projecting conspicuously from beneath clypeus. Clypeus with tubercle on dorsal surface. Males with pronotal fovea broadly triangular, extending almost to posterior margin of pronotum **Gibboryctes Endrödi**
- 5'. Elytra smooth, rugose, or densely punctate but never with deeply furrowed rows of punctures. Mandibles variably toothed but never with 2 large, rounded lobes projecting strongly from beneath clypeus. Head with 1-2 frontoclypeal tubercles but never with 1 on top of clypeus. Males never with pronotal fovea almost reaching posterior margin of pronotum 6
6. Body form elongate, subparallel. Foretibia with teeth projecting almost at right angles. Apex of posterior tibia with 2 strong teeth. Males with anterior half of pronotum nearly smooth and with single, median horn or tubercle. Females without fovea on pronotum **Podischnus Burmeister**
- 6'. Body form broader, sides rounded. Foretibia with teeth projecting obliquely. Apex of posterior tibia crenulate or with 1, 3, or 4 teeth. Males with anterior half of pronotum densely punctate or rugose or, if nearly smooth, then with lateral horns or tubercles. Females with or without fovea on pronotum 7
7. Both males and females with head horn. Prosternal process short. Pronotum with anterior margin distinctly emarginate at center **Enema Hope**
- 7'. Males with or without head horn; females never with head horn, tuberculate at most. Prosternal process long, subconical or peg-like. Anterior margin of pronotum lacking emargination at center 8
8. Males and females with 2 tubercles on top of head, never with head horn in males. Pronotum in males with subapical horn and usually with lateral horn or elevated triangular ridge on each side; females with fovea in anterior third of pronotum **Strategus Kirby**
- 8'. Males with distinct head horn; females with single tubercle. Pronotum in males with horn or prominence arising from posterior half and with or without lateral horns; females usually lacking pronotal fovea **Heterogomphus Burmeister**

Clave para los Géneros de Adultos de Oryctini de Costa Rica y Panamá

1. Tibia anterior tridentada 2
- 1'. Tibia anterior cuadridentada 5
2. Mandíbulas completamente ocultas bajo el clípeo. Apice del clípeo fuertemente bilobulado y fuertemente doblado hacia arriba **Xyloryctes Hope**
- 2'. Mandíbulas visibles desde arriba. Apice del clípeo emarginado o bidentado, no fuertemente doblado hacia arriba 3
3. Elitros lisos, negros **Megaceras Hope**
- 3'. Elitros con puntuaciones evidentes o rugosos, pardo rojizos 4

4. Elitros con 5 hileras evidentes de puntuaciones sobre una superficie relativamente lisa o finamente granular opaca. Mandíbulas tridentadas. Clípeo con el ápice agudamente bidentado ***Coelosis Hope***
- 4'. Elitros completamente rugosos, con leves hileras de puntuaciones. Mandíbulas bidentadas. Clípeo con el ápice lobulado a ambos lados de la emarginación media ***Irazua Ratcliffe, nuevo género***
5. Elitros con hileras de puntuaciones en surcos profundos. Mandíbulas con 2 lóbulos redondeados, similarmente grandes, que se proyectan conspicuamente desde abajo del clípeo. Clípeo con tubérculo en la superficie dorsal. Machos con fóvea pronotal ampliamente triangular, extendiéndose casi hasta el margen posterior del pronoto ***Gibboryctes Endrödi***
- 5'. Elitros lisos, rugosos o cubiertos densamente de puntuaciones pero nunca con hileras de puntuaciones en surcos profundos. Mandíbulas variablemente dentadas pero nunca con 2 grandes lóbulos redondeados que se proyectan conspicuamente desde abajo del clípeo. Cabeza con 1 ó 2 tubérculos frontoclípeales pero nunca con 1 sobre la parte superior del clípeo. Machos nunca con la fóvea pronotal alcanzando casi hasta el margen posterior del pronoto 6
6. Forma del cuerpo alargada, casi paralela. Tibia anterior con dientes proyectándose casi en ángulos rectos. Apice de la tibia posterior con 2 dientes fuertes. Machos con la mitad anterior del pronoto casi liso y con un solo cuerno o tubérculo medio. Hembras sin fóvea en el pronoto ***Podischnus Burmeister***
- 6'. Forma del cuerpo más amplia, lados redondeados. Tibia anterior con dientes proyectándose oblicuamente. Apice de la tibia posterior crenulado o con 1, 3 ó 4 dientes. Machos con la mitad anterior del pronoto densamente cubierto de puntuaciones o rugoso o, si es casi liso, entonces con cuernos o tubérculos laterales. Hembras con o sin fóvea en el pronoto 7
7. Machos y hembras con cuerno en la cabeza. Proceso proesternal corto. Pronoto con margen anterior claramente emarginado al centro ***Enema Hope***
- 7'. Machos con o sin cuerno en la cabeza; hembras nunca con cuerno en la cabeza, a lo más tuberculado. Proceso proesternal largo, cónico o en forma de clavija. Pronoto con margen anterior sin emarginación al centro 8
8. Machos y hembras con 2 tubérculos en la parte superior de la cabeza, nunca con cuerno en la cabeza de los machos. Pronoto en los machos con cuerno subapical y generalmente con cuernos laterales o una cresta triangular elevada a cada lado; hembras con fóvea en el tercio anterior del pronoto ***Strategus Kirby***
- 8'. Machos con cuerno evidente en la cabeza. Hembras con solo un tubérculo. Pronoto en los machos con cuerno o prominencia que se origina desde la mitad posterior y con o sin cuernos laterales; hembras normalmente sin fóvea pronotal ***Heterogomphus Burmeister***

Coelosis Hope, 1837

Coelosis Hope 1837: 88.

Millotsis Bourgin 1944: 143 (synonym).

The genus *Coelosis* contains seven species (Dechambre 1976; Endrödi 1976b, 1985a). With the exception of the broadly distributed *C. biloba*, all of the species are found in South America.

Species in the genus may be recognized by the tridentate foretibiae, frons of the male with a horn, elytra with distinct rows of punctures, clypeus usually narrow and strongly bidentate at its apex, and mandibles tridentate.

Adults of all of the species are nocturnal and attracted to lights.

Coelosis biloba (L., 1767)

(Color Plate 4, Figs. 576-583)

Scarabaeus biloba Linnaeus 1767: 544.

Coelosis biloba lepesmei Bourgin 1944: 129 (invalid name, described as aberration of *C. biloba biloba* [= infrasubspecific rank, Article 45.6.2, International Commission on Zoological Nomenclature 1999]).

Coelosis biloba incana Bourgin 1944: 129 (invalid name, described as aberration of *C. biloba biloba* [= infrasubspecific rank, Article 45.6.2, International Commission on Zoological Nomenclature 1999]).

Coelosis biloba cacica Bourgin 1944: 131 (invalid name, described as aberration of *C. biloba biloba* [= infrasubspecific rank, Article 45.6.2, International Commission on Zoological Nomenclature 1999]).

Coelosis biloba tibialis Bourgin 1944: 132 (synonym, described as subspecies).

Coelosis biloba tibialis pauliani Bourgin 1944: 134 (invalid name, described as variety of *C. biloba tibialis* [= infrasubspecific rank, Article 45.6.1, International Commission on Zoological Nomenclature 1999]).

DESCRIPTION. Length 30.0-45.5 mm; width 16.8-23.7 mm. Color light to dark red-dish brown.

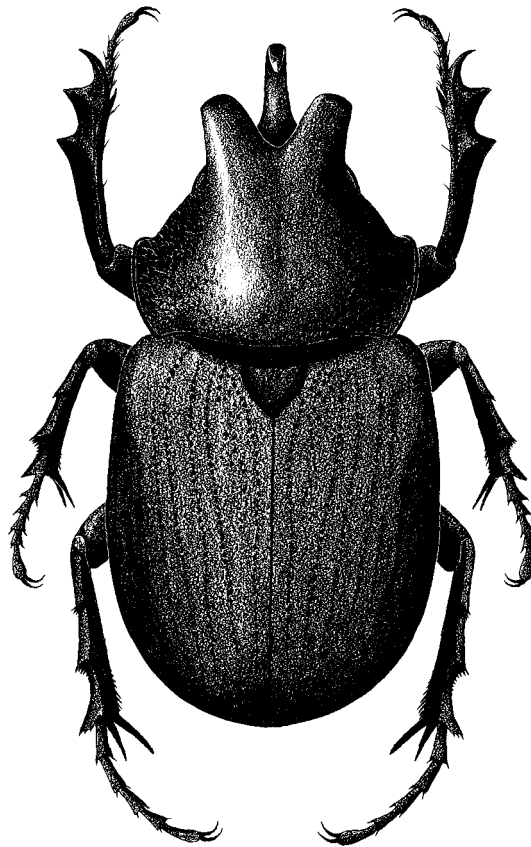
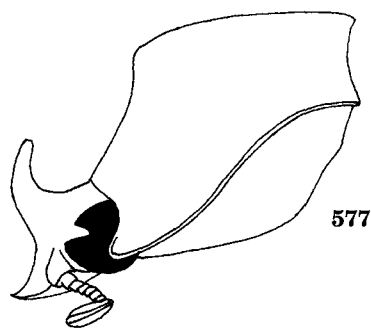
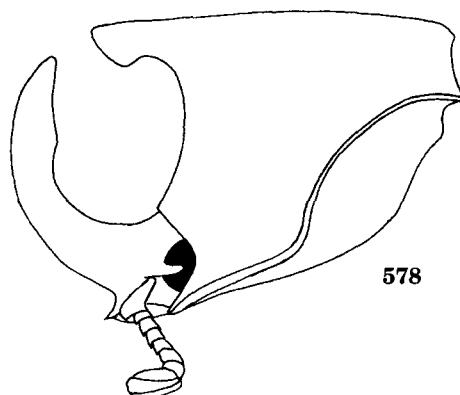


Fig. 576. *Coelosis biloba*.

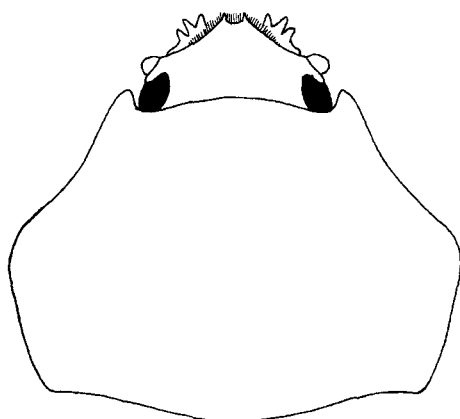
Males. Head: Frons with small to large, recurved horn; horn simply acuminate in minors (Fig. 577), majors with horn broadly and triangularly expanded on posterior edge just below apex (Fig. 578). Eye canthus subtuberculate at base on anterior edge. Clypeus elongate, subtriangular, surface coarsely rugose, sides attenuated to narrow apex, apex with 2 strong, sharp and slightly reflexed teeth. Interocular width equals 2.6-3.3 transverse eye diameters. Antenna with 10 stout segments, club subequal in length to segments 3-7. Mandibles with 3 strong, sharp teeth (Fig. 579). **Pronotum:** Surface in central third relatively smooth, with sparse, small punctures in male majors, punctures becoming progressively a little denser and larger in male minors; lateral thirds areolate-rugose. Male majors with large, broad, bifurcate, dorsally flattened (almost laminar) horn on posterior



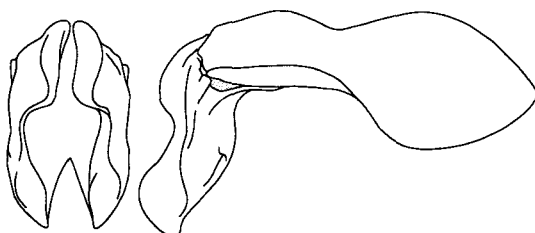
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Figs. 577-581. *Coelosis biloba*: (577) minor male; (578) major male; (579) female; (580-581) parameres.

half of pronotum, horn in same plane as surface of elytra; male minors with horn variably reduced to a bifurcate boss or a rounded tumescence. Anterior angles elongated, triangular; sides expanded and widest at middle, sinuate before middle; base lacking marginal bead. *Elytra*: Surface between suture and humerus with 5 punctate striae and a short to moderate row of similar punctures on first interval; punctures deep, oblong, moderately large, ocellate; intervals finely shagreened. Sides similar. *Pygidium*: Surface finely scabriculous, becoming a little smoother on discal protuberance. In lateral view, most strongly convex near base. *Legs*: Foretibia elongate, slender, lateral edge with 3 subequally spaced teeth. Apex of posterior tibia weakly crenulate, lacking teeth. Posterior tarsus with apex of first tarsomere triangularly produced. *Venter*: Prosternal process short, triangular. *Parameres*: Figs. 580-581.

Females. As males except in the following respects. *Head*: Frons with surface coarsely rugose. *Pronotum*: Surface punctation similar to that of male minors; strong tumescence present in center of disc. *Pygidium*: Surface with dense, minute, transverse punctures, punctures minutely setigerous. In lateral view, surface weakly convex. *Legs*: Foretibia proportionately shorter.

DISTRIBUTION. *Coelosis biloba* is widely distributed, occurring from central Mexico south to Argentina. This species is found throughout Costa Rica and Panama.

LOCALITY RECORDS (Fig. 582-583). 219 specimens examined.

COSTA RICA (121). ALAJUELA (9): Atenas, Estación Laguna Pocosol (Res. Biol. Monteverde), San Ramón, Sarchi, Upala, Villa Bonita, 2 km SW Dos Ríos; CARTAGO (5): Tuis, Turrialba; GUANACASTE (50): Cañas, Estación Cacao, Estación Las Pailas (Parq. Nac. Rincón de la Vieja), Estación los Almendros (Parq. Nac. Guanacaste), Estación Maritza, Estación Santa Rosa, Finca Jenny (Parq. Nac. Guanacaste), Finca Montezuma, Liberia, Parq. Nac. Santa Rosa, Presa Río Cuipilapa,

Tierras Morenas (Arenal); HEREDIA (8): Los Lagos, Río Frio, San Antonio de Belem, San Isidro, San Rafael, Santo Domingo; LIMON (2): Amubri, Reserva Biológica Hitoy Cerere; PUNTARENAS (37): Estación Esquinas (Osa), Estación Las Mellizas (Parq. Nac. Amistad), Las Cruces, Osa Peninsula, Rancho Quemado (Osa), Sirena (Parq. Nac. Corcovado); SAN JOSÉ (10): Bajo la Rosa, Escazu, Estación Carrillo (Parq. Nac. Braulio Carrillo), San José, San Juan de Dios, San Pedro, San Rafael, Santa Ana.



Fig. 582. Distribution of *Coelosis biloba* in Costa Rica.

PANAMA (98). CANAL ZONE (29): Albrook AFB, Ancon, Barro Colorado Island, Black Tank Rd., Corozal, Ft. Gulick, Gatun Tank Farm, Madden Dam; CHIRIQUI (4): Hartmann's Finca, Rovira; COLÓN (10): Colón, Portobelo, Santa Rita Ridge; PANAMA (55): Cerro Azul, Cerro Campana, Cerro Jefe, Chilibre, El Llano-Carti Rd. (km 9), Las Cumbres, Tocumen Airport.

TEMPORAL DISTRIBUTION. January (2), February (8), March (2), April (5), May (55), June (23), July (33), August (14), September (10), October (11), November (20), December (10).

DIAGNOSIS. *Coelosis biloba* is easily recognized because of its relatively large size, attenuated clypeus with 2 strong teeth, strongly tridentate mandibles, lateral margin of the pronotum sinuate before the middle, and (in the males) the broad, horizontal, and bifurcate pronotal horn.

BIOLOGY. Adults are nocturnal and attracted to lights. According to Eidmann (1937), adult beetles swarm in the early part of the year (in Brazil) and lay eggs in the leaf mulch of the preparation chambers of the leafcutter ants, *Atta sexdens* (L.). Eggs and larvae are then carried by the ants to the fungus gardens where the scarab larvae live in oval, earthen holes between the fungus chambers. Here they eat both the fungus and its growing medium of decaying leaf material.



Fig. 583. Distribution of *Coelosis biloba* in Panama.

The larvae pupate in holes in the ground. *Coelosis biloba* has also been recorded from the nests of *Atta cephalotes* (L.) and *A. mexicana* (Smith) in South America (Bruch 1917; Navarrete-Heredia 2001). I have taken adults in the nest of *Atta* sp. in Honduras. They occur in tropical wet forests, premontane moist forests, and premontane wet forests at elevations ranging from near sea level to 1,200 meters.

***Enema* Hope, 1837**

Enema Hope 1837: 83 (*nomen protectum*, here designated).

Hoplites Dejean 1836: 167 (*nomen oblitum*, here designated).

The genus *Enema* consists of two species, *E. pan* (Fabr.) and *E. endymion* Chevrolat. They are both found from southern Mexico to South America with *E. pan* evidently being much more common in South America.

The genus is characterized by quadridentate anterior tibiae, the presence of a frontal horn in both sexes (only rarely is the female lacking a horn), broad elytra that are explanate on the sides, bidentate mandibles, and the near absence of a prosternal process. The presence of a long head horn in *both* sexes of this genus is distinctive among the New World Dynastinae.

The younger of the two names proposed for this genus (*Enema* Hope, 1837) is the valid name and not the older name (*Hoplites* Dejean, 1836). This action is taken here in accordance with Article 23.9.1 (Reversal of Precedence) of the International Code of Zoological Nomenclature (1999). To my knowledge the senior synonym has not been used as a valid name since it was first proposed (Article 23.9.1.1). In addition, the junior synonym has been used as the valid name and published by at least ten authors in 25 works in the immediately preceding 50 years and encompassing a span of not less than ten years. Those authors and works using *Enema* as the valid generic name are: Berry and Vaquero (1957); Reitter (1960); Carrillo *et al.* (1966); Stanek (1969); Smith (1971); Blackwelder and Arnett (1974); Endrödi (1976, 1985a); Vidal and Giacomozzi (1978); Morón (1979, 1993b, 1994a, 1997a); Maes (1987, 1994, 1998); Deloya (1992); Lachaume (1992); Pardo Locarno (1993); Thomas (1993); Ratcliffe and Morón (1997); Garcia *et al.* (1998); Delgado *et al.* (2000); Guzman *et al.* (2001); Nagai (2001).

In spite of their large size and occasional local abundance, little is known of the life history of these beetles. Adults are nocturnal and attracted to lights, and the larvae probably feed on humus in the soil. *Enema pan* may be restricted to forested areas while *E. endymion* has been taken both in forested and secondary scrub areas.

Key to the Species of Adult *Enema* of Costa Rica and Panama

1. Elytra bright reddish brown with head and pronotum usually darker. Frontal horn short, pointed. Pronotum with low, rounded tumescence ***endymion* Chevrolat**
- 1'. Color black. Frontal horn long, pointed. Pronotum with broad, anteriorly directed, bifurcate horn or simply bituberculate ***pan* (Fabr.)**

Clave para las Especies de Adultos de *Enema* de Costa Rica y Panamá

1. Elitros pardo rojizos brillantes con la cabeza y el pronoto generalmente más oscuros. Cuerno frontal corto, puntiagudo. Pronoto con una tumescencia baja y redondeada ***endymion* Chevrolat**
- 1'. Elitros negros. Cuerno frontal largo, puntiagudo. Pronoto con cuerno amplio, dirigido anteriormente, bifurcado o simplemente bituberculado ***pan* (Fabr.)**

***Enema endymion* Chevrolat, 1843**
(Figs. 584-601)

Enema endymion Chevrolat 1843: 29.

Enema lupercus Burmeister 1847: 236 (synonym).

Enema paniscus Burmeister 1847: 236 (synonym).

Enema gibbicollis Sternberg 1908: 24 (synonym).

DESCRIPTION. Length 30.0-36.3 mm; width 17.0-20.0 mm. Color light to dark reddish brown.

Males. Head: Frons with short to moderately long horn; horn narrowly triangular, acuminate, slightly recurved over pronotum, flat on anterior surface. Clypeus with surface finely rugopunctate, sides strongly constricted just before apex, apex broadly emarginate and strongly reflexed. Interocular width equals 2.7 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. Mandibles broad, apex strongly bidentate (best seen from below). **Pronotum:** Surface rugose in a broad band along lateral margins and surrounding discal depression; elsewhere surface with minute and moderate punctures mixed. Disc in anterior half with weak (flat) to strong (foveate), longitudinal depression; large specimens with pronounced tumescence behind discal depression. Sides explanate. All margins beaded; anterior margin with strong, posterior emargination at center. **Elytra:** Surface with strongly impressed sutural stria, elsewhere on disc with minute and moderate punctures mixed; minute punctures moderately dense, larger punctures sparse; punctures becoming larger and a little denser on sides; sides also weakly rugose and explanate. **Pygidium:** Base with transverse row of large, setigerous punctures; setae long, reddish brown, dense. Surface of disc with small, sparse punctures, punctures becoming larger laterally. Apical margins either side of middle rugose. In lateral view, surface convex. **Legs:** Foretibia quadridentate, apical 2 teeth a little closer to one another than are remaining teeth to each other. Apex of posterior tibia weakly crenulate

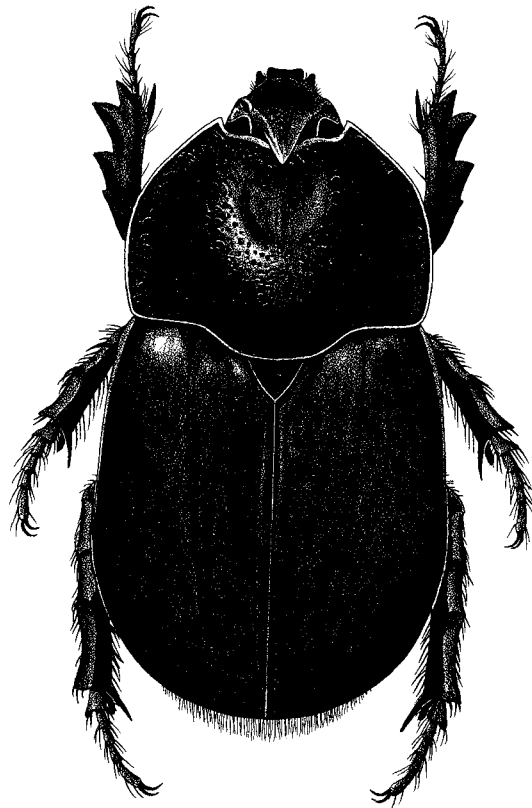
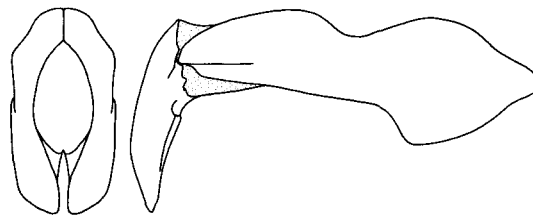


Fig. 584. *Enema endymion*.



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Figs. 585-586. *Enema endymion* parameres.

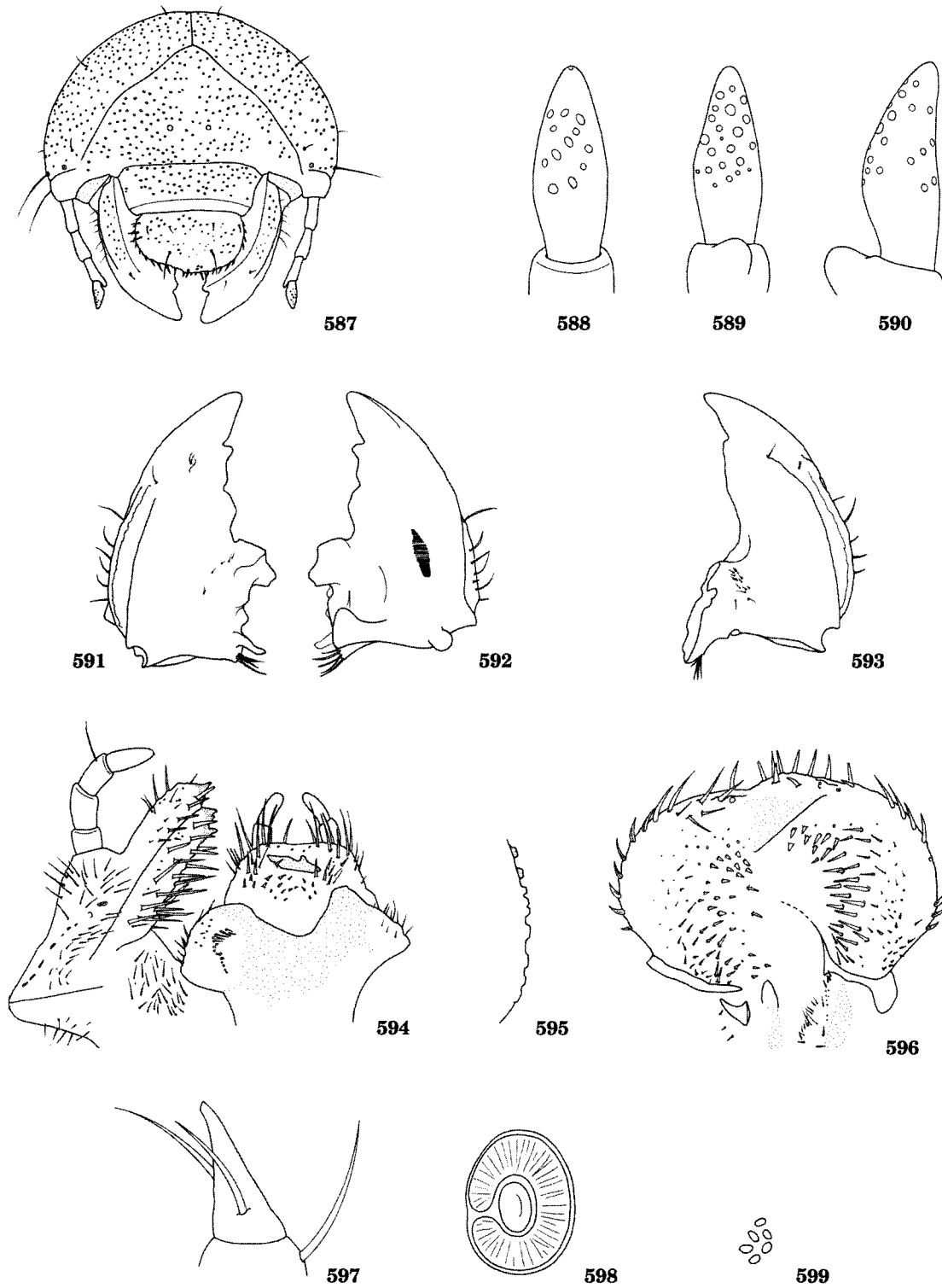
and with small tooth. Basal segment of posterior tarsus triangularly elongated at apex. **Venter:** Prosternal process very short, laminar, similar in shape to equilateral triangle. **Parameres:** Figs. 585-586.

Females. Similar to males except head horn usually shorter, and pygidium nearly flat or weakly convex.

THIRD INSTAR LARVA. Two third instar larvae of *E. endymion* are housed at UNSM with the following data: "Guatemala: Petén, Tikal National Park, XI-4-19-1995, David F. Whitacre. Hundreds on forest floor in primary forest." Description and illustrations by Mary Liz Jameson.

Cranium (Fig. 587): Width of head capsule 11.7 mm. Surface castaneous, densely punctate, some punctures setigerous; setae moderately long, tawny. Frontal suture and clypeofrontal suture distinct. Epicranium with 1 dorsoepicranial seta on each side; frons lacking frontal setae; anterior frontal angle with 1 short seta; exterior frontal angle and anterior frontal region lacking setae. Ocellus absent. **Clypeus:** Form trapezoidal. Surface of postclypeus castaneous, well-sclerotized and densely punctate; surface of preclypeus light brown, poorly sclerotized, not punctate. **Labrum:** Form oblong-oval, asymmetrical. Color castaneous, at mid-apex cream-colored and poorly sclerotized, surface densely punctate, some punctures setigerous; 4 equally spaced, long setae near base, 2 long setae subapicolaterally, 2-3 long setae near margin, about 15 long setae at apex, 8-11 short (at base) to long (at apex) hamate setae of acanthoparia visible at lateral margin. **Antenna:** 4 segmented; in lateral view (Fig. 590) segments 1-3 subequal in length, terminal segment slightly shorter than segment 2. Apical segment sub-oval with acute apex in dorsal and ventral views (Figs. 588-589), subtriangular in lateral view (Fig. 590); dorsal surface with about 12 sensory spots (Fig. 588); ventral surface with about 22 spots (Fig. 589). **Left Mandible:** Form falcate. Scissorial region with 3 poorly defined teeth; scissorial region weakly concave, smooth. Lateral face with 7 long setae. Dorsal surface (Fig. 591) with line of about 21 dorsomolar setae; acia well-developed, elongate, weakly recurved at apex. Ventral surface (Fig. 592) with poorly developed, elongate-oval stridulatory area, ridges (about 20) narrowly separated and poorly defined; ventral process

well-developed; brustia with 12 long, stout setae; basolateral angle with postartis. Molar area with 3 lobes, lobes 2 and 3 contiguous; surface concave. **Right Mandible:** Form falcate. Scissorial region with 3 poorly defined teeth, basal tooth reduced; scissorial region weakly concave, smooth. Lateral face with 8 long and moderately long setae. Dorsal surface (Fig. 593) with field of 17 dorsomolar setae. Ventral surface with poorly developed, elongate-oval, ridged stridulatory area, ridges narrowly separated and poorly defined; ventral process developed; calx produced; brustia with 5 moderately long setae; basolateral angle with postartis. **Maxilla** (Fig. 594): Cardio subrectangular. Stipes longer than wide. Galea with many stout setae and 1 well-developed uncus at apex. Lacinia with many stout setae and 3 unci; unci extending from apex to subapex, contiguous, basal uncus slightly separated from others, middle uncus smaller than apical and basal unci. Palpus 4-segmented, segments 1-3 subequal in length, terminal segment slightly longer than segment 3. Stridulatory area (Fig. 595) with 7 blunt, truncate ridges and anterior truncate process. **Labium** (Fig. 594): Surface of glossa with moderately long and long setae and medial sclerome; sclerome transversely elongate and weakly raised anteriorly. Hypopharyngeal sclerome asymmetrical, concave medially, truncate process produced dorsally, left lateral lobe with setae at margin and on disc; setae at margin moderately long, setae on disc moderately long, stout and directed toward center of sclerome. **Epipharynx** (Fig. 596): Form suboval, wider than long, asymmetrical. Apex with oblique, ridge-like tylus (fused epizygum, zygum, corypha and haptomeral process). Acanthoparia with 10-11 dorsoventrally flattened, stout, curved setae; setae short near base to long near apex. Acroparia with about 18 stout, long setae. Gymnoparia lacking setae. Chaetoparia with about 60-80 setae; setae short at lateral margin, longer and stouter toward middle. Pedium well-defined. Nesia present; left nesium curved, sclerotized, with right side produced; right nesium elongate, weakly produced and sclerotized anteriorly, not produced and membranous posteriorly. Dextiotorma elongate.



Figs. 587-599. *Enema endymion*, third instar larva: (587) cranium; (588-590) terminal segment of antenna in dorsal, ventral, and lateral views, respectively; (591-592) left mandible, dorsal and ventral views, respectively; (593) right mandible, dorsal view; (594) maxilla and labium; (595) stridulatory ridge of maxilla; (596) epipharynx; (597) tarsal claw; (598) spiracle; (599) holes of respiratory plate of spiracle.

Laeotorma elongate; epitorma arc-like and terminating at mid-pedum; pternotorma rounded. Right crepis elongate, membranous, with field of about 35 setae mediolaterally. *Legs*: Trochanter, femur, and tibiotarsus with numerous, moderately long and long setae. Claws (Fig. 597) castaneous at base, piceous at apex; form conical with acute apex and with 2 long setae at subapex. *Body vestiture*: Prothorax with darkened macula anterior to spiracle; macula 3 times length of spiracle and twice width of spiracle. Pro-, meso-, and

metathorax each with 8 long, equally spaced setae. Abdominal segments 1-6 divided into annulets; prescutum with about 30 short setae; scutum with about 20 short setae; scutellum with about 30 short setae and about 14 moderately long, evenly spaced setae near posterior margin. Abdominal segments 7-9 not divided into annulets, each with sparse, long setae. Dorsal surface of abdominal segment 10 with sparse, long setae on disc and numerous short, stout setae near anal lip; dorsal impressed line absent. Ventral surface of abdominal segment 10 lacking palidia; anal lip curved, transverse; upper anal lip with numerous long and moderately long, stout setae. Teges with numerous, moderately long and sparse setae. *Spiracles* (Fig. 598): Spiracles subequal in size (1.25 to 1.30 mm wide, 1.55 to 1.68 mm high), slightly higher than wide, oval. Respiratory plates C-shaped, lobes nearly touching; bulla nearly flat; holes (Fig. 599) oval, about 60 holes across diameter of plate.

DISTRIBUTION. *Enema endymion* is found from southern Mexico to Brazil and Bolivia (personal observation; Endrödi 1976b, 1985a). In Costa Rica and Panama, it is widely distributed but evidently uncommonly encountered. Elsewhere in its range (southern Mexico) I have seen it locally abundant with huge emergences in heavily disturbed habitat that seemed too marginal to support these larger beetles.

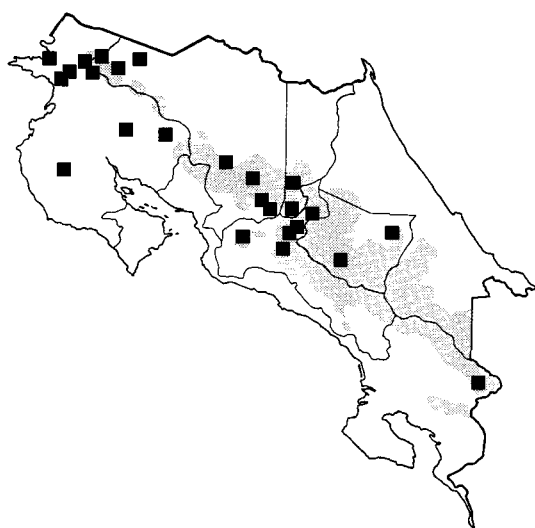


Fig. 600. Distribution of *Enema endymion* in Costa Rica.



Fig. 601. Distribution of *Enema endymion* in Panama.

LOCALITY RECORDS (Figs. 600-601). 144 specimens examined.

COSTA RICA (128). ALAJUELA (31): Brasil, Colonia Palmareña, Dos Ríos (2 km SW), Río Itiquis, Sarchi, Zarcero; CARTAGO (3): Tapanti, GUANACASTE (42): Cañas, Dos de Tilaran, Estación Cacao, Estación Maritza, Estación Murciélago, Estación Pitilla, Estación Santa Rosa, Finca Jenny, Finca Montezuma (SW slope Volcán Tenorio), Santa Cruz; HEREDIA (4): Barva, San Rafael, Santo Domingo; PUNTARENAS (10): Estación Biológica Las Alturas; SAN JOSÉ (38): Coronado, Escazu, Moravia, Sabanilla, San José, San Pedro, Santa Ana, Tibas.

PANAMA (16). CHIRIQUI (6): Boquete, Fortuna, Volcancito; HERRERA (10): Chepo.

TEMPORAL DISTRIBUTION. January (2), February (1), March (11), April (25), May (73), June (12), July (2), October (2), November (1).

DIAGNOSIS. The reddish brown color and the short, acuminate frontal horn in both sexes will readily distinguish this species from *E. pan*, which is black and has a long head horn in both sexes.

BIOLOGY. The larval stage is described here for the first time. After heavy rains, numerous larvae can be found on the surface of the soil (David Whitacre 1995, personal communication; Enio Cano 1997, personal communication). Cano also reported that the larvae were an important part of the diet of *Crax rubra* L. (great curassow) and *Nasua narica* (L.) (coatimundi). Head capsules of third instar larvae were also found in abundance in the feces of *Urocyon cinereoargenteus* (Schreber) (gray fox). These predators, and probably others, take a great toll of larvae that have come to the surface of the soil.

Their life history is mostly unknown, but larvae feed on humus, roots, and other organic debris in the soil. They have not been found in rotting tree trunks. Adults are nocturnal and are attracted to lights, often in huge numbers, especially at the onset of the

rainy season. They have been collected from tropical dry forests, tropical wet forests and premontane wet forests in Costa Rica and Panama at elevations ranging from 50-1,700 meters.

Enema pan (Fabricius, 1775)

(Figs. 43, 602-608)

Scarabaeus pan Fabricius 1775: 5.

Scarabaeus chorinaeus Fabricius 1775: 5 (synonym).

Scarabaeus quadrispinosus Fabricius 1781: 11 (synonym).

Scarabaeus enema Fabricius 1787: 4 (synonym).

Scarabaeus aeneas Kirby 1818: 399 (synonym).

Scarabaeus titornus Perty 1830: 45 (synonym).

Enema lupercus Chevrolat 1843: 28 (synonym).

Enema infundibulum Burmeister 1847: 234 (synonym).

DESCRIPTION. Length 35.0-57.0 mm; width 20.6-31.5 mm (largest Panamanian specimen 47.0 x 28.2 mm). Color dark reddish brown to more commonly black.

Males. *Head:* Frons with long, recurved horn; horn pointed at apex, flattened on sides, sparsely punctate in majors, densely punctate in minors; largest specimens sometimes with small tooth on posterior edge just below middle. Clypeus with surface finely, densely punctate; sides weakly constricted just before apex; apex broadly, shallowly emarginate and strongly reflexed. Interocular width equals 4.0-4.6 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. Mandibles broad, apex strongly bidentate (best seen from below). *Pronotum:* Majors (Fig. 603) with surface coarsely rugose except for pronotal depression and knob; depression relatively smooth, with moderately dense micropunctures and sparse, small punctures; posterior half of pronotum with distinct knob, apex of knob with anteriorly

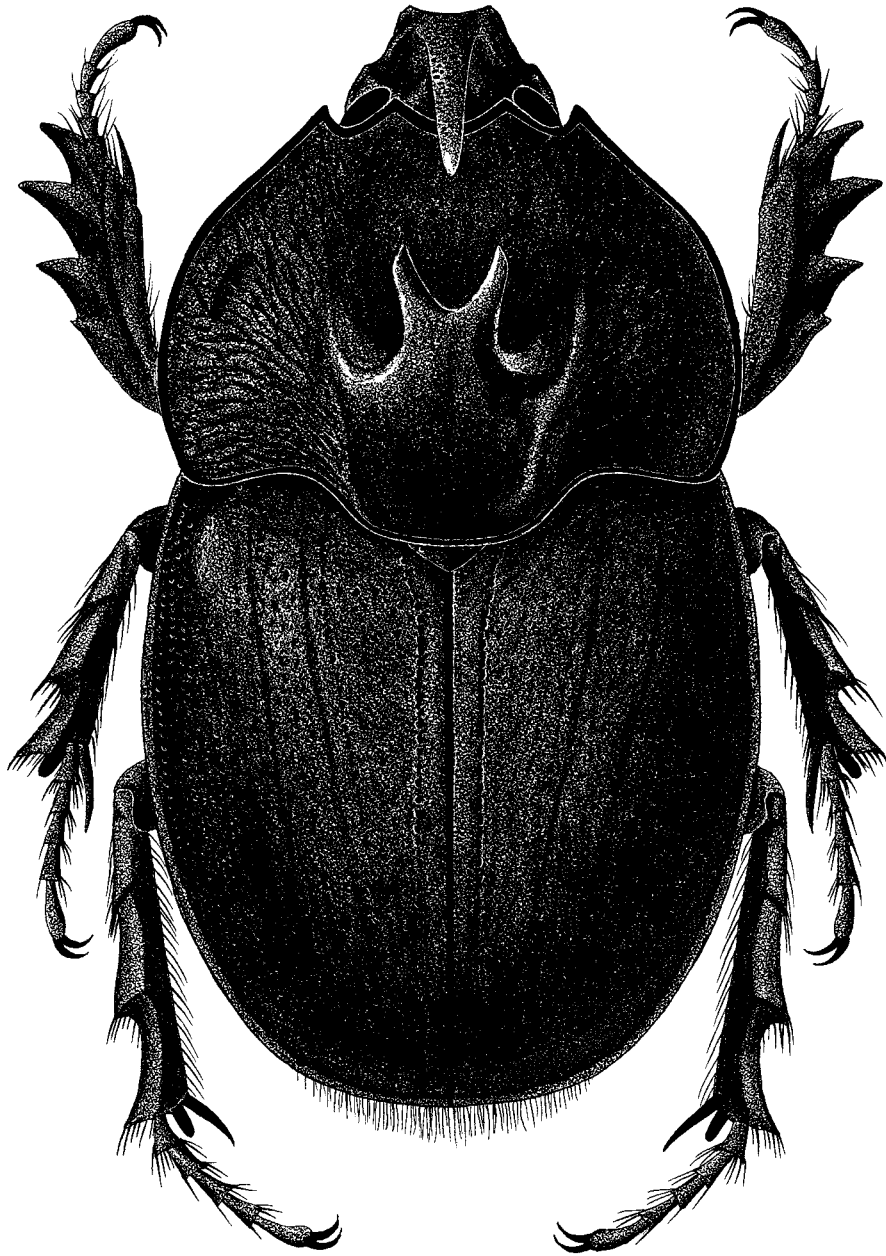


Fig. 602. *Enema pan.*

projecting, bifurcate process; arcuate carina extending anteriorly from base of bifurcate process. Minors (Fig. 604) similar except discal depression densely punctate, punctures minute and small mixed; knob densely punctate; knob on posterior half reduced to bifur-

cate tubercle or rounded tumescence. Sides laterad of knob with non-rugose, punctate region. Lateral margins weakly explanate. All margins strongly beaded; anterior margin with strong, posteriorly directed emargination at center. *Elytra*: Surface with strongly

NOMENCLATURE. Various authors have recognized four different morphotypes based on differences in the male horns or anterior tibiae: (1) forma *typica* has the frontal horn acuminate, and the pronotal horn is bifurcate or bilobed. This is the form found in Central America; (2) ab. *enema* (Fabr.) has the frontal horn bifurcated, and the pronotal horn is long

and acuminate; (3) ab. *chorinaeum* (Fabr.) has the frontal horn weakly emarginate, and the pronotal horn is bifurcate; and (4) ab. *aeneas* (Kirby) refers to small males that have a tridentate anterior femur. All of these various forms are conspecific and simply represent a substantial amount of variation. Unlike all other dynastines in which there are males with large horns, species of *Enema* are the only ones in which the females are similarly armed.

BIOLOGY. Adults are nocturnal and are attracted to lights. They have been collected from tropical wet forests and at elevations ranging from 100 meters to 1,300 meters.

Gibboryctes Endrödi, 1974

Gibboryctes Endrödi 1974: 13.

The small genus *Gibboryctes* contains three relatively rare species. All of the species are found in South America with one of them, *G. waldenfelsi*, reaching eastern Panama (Ratcliffe and Dechambre 1983).

The genus is unique in having the following combination of characters: anterior tibia with four lateral teeth, head relatively short and widely triangular with an acuminate



Fig. 607. Distribution of *Enema pan* in Costa Rica.



Fig. 608. Distribution of *Enema pan* in Panama.

clypeus in the males and broadly rounded clypeus in the females, mandibles projecting conspicuously from beneath the clypeus, and pronotum with a deep, wide, almost triangular fovea.

Nothing is known of the life history of these rare insects. Adults are presumably nocturnal and attracted to lights.

***Gibboryctes waldenfelsi* (Endrödi, 1977)**

(Figs. 609-612)

Strategus waldenfelsi Endrödi 1977a: 335.

Gibboryctes porioni Dechambre 1981: 124 (synonym).

DESCRIPTION. Length 26.0-30.0 mm; width 14.0-16.4 mm. Color dark reddish brown.

Males. Head: Frons nearly smooth, shining, concave. Frontoclypeal line weakly carinate, leading to large, acuminate tubercle on clypeus. Clypeus with tubercle, apex of clypeus strongly narrowed almost to a blunt point, surface shining and with a few weak rugae. Interocular width equals 3.0 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. Mandibles broadly exposed either side of clypeus, with 2 large, subequally rounded lobes. **Pronotum:** Surface smooth, with micropunctures only. Disc broadly, deeply, almost triangularly foveate. An elevated, laterally compressed, subtriangular, carinate boss either side of fovea and with apical, moderately long, recurved horn; horn with apex strongly dilated in majors, weakly dilated in minors, apex emarginate, shaft weakly concave on each side. Base with marginal bead. **Elytra:** Discal surface with sutural stria and 2 pairs of double rows of punctures, intervals between stria and both pairs of double rows broad; punctures moderate in size, weakly ocellate, moderate in density. **Pygidium:** Surface with punctures moderate in density and size, setigerous; setae long, dense, tawny. In lateral view, surface convex. **Legs:** Foretibia

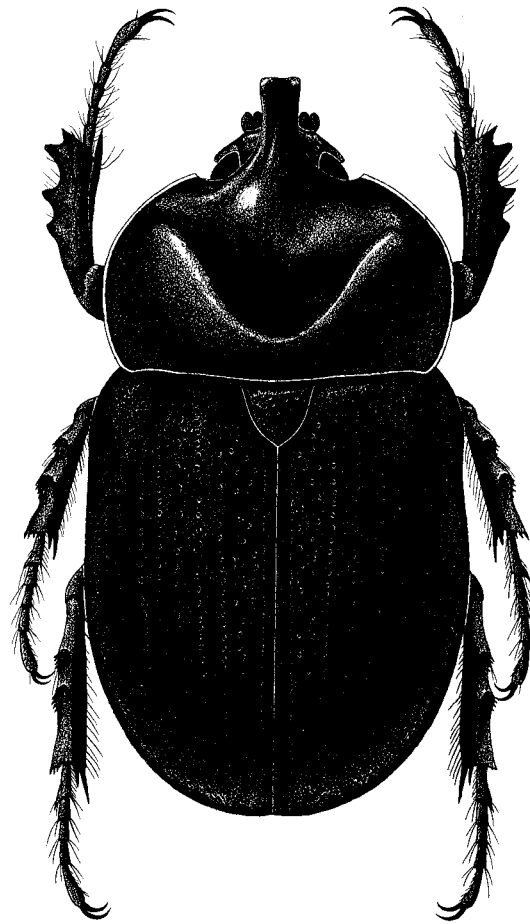
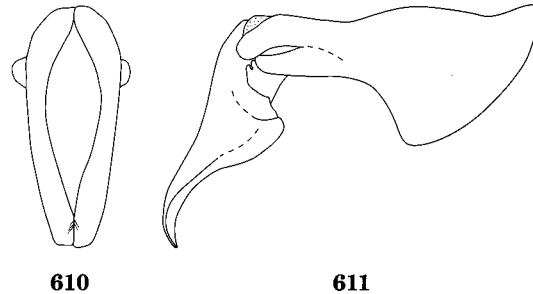


Fig. 609. *Gibboryctes waldenfelsi*.



Figs. 610-611. *Gibboryctes waldenfelsi* parameres.

clypeus in the males and broadly rounded clypeus in the females, mandibles projecting conspicuously from beneath the clypeus, and pronotum with a deep, wide, almost triangular fovea.

Nothing is known of the life history of these rare insects. Adults are presumably nocturnal and attracted to lights.

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DESCRIPTION. Length 26.0-30.0 mm; width 14.0-16.4 mm. Color dark reddish brown.

Males. Head: Frons nearly smooth, shining, concave. Frontoclypeal line weakly carinate, leading to large, acuminate tubercle on clypeus. Clypeus with tubercle, apex of clypeus strongly narrowed almost to a blunt point, surface shining and with a few weak rugae. Interocular width equals 3.0 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. Mandibles broadly exposed either side of clypeus, with 2 large, subequally rounded lobes. **Pronotum:** Surface smooth, with micro-punctures only. Disc broadly, deeply, almost triangularly foveate. An elevated, laterally compressed, subtriangular, carinate boss either side of fovea and with apical, moderately long, recurved horn; horn with apex strongly dilated in majors, weakly dilated in minors, apex emarginate, shaft weakly concave on each side. Base with marginal bead. **Elytra:** Discal surface with sutural stria and 2 pairs of double rows of punctures, intervals between stria and both pairs of double rows broad; punctures moderate in size, weakly ocellate, moderate in density. **Pygidium:** Surface with punctures moderate in density and size, setigerous; setae long, dense, tawny. In lateral view, surface convex. **Legs:** Foretibia

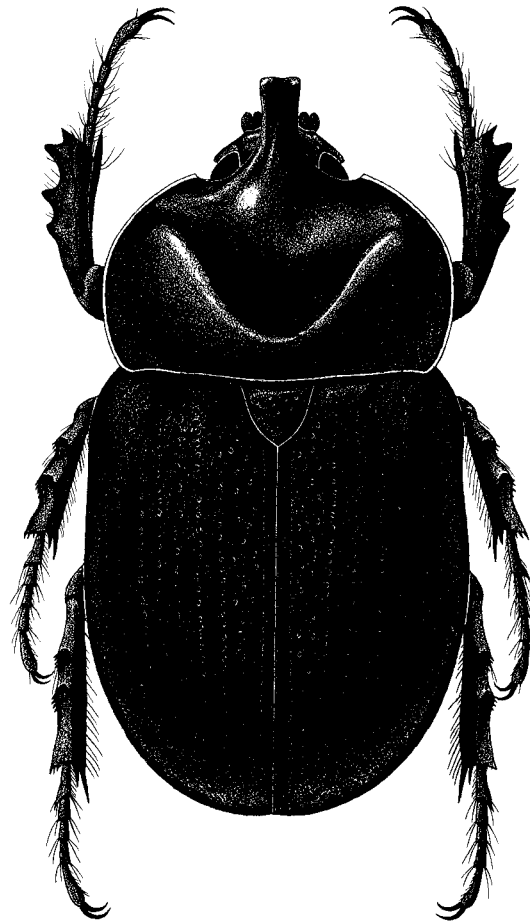
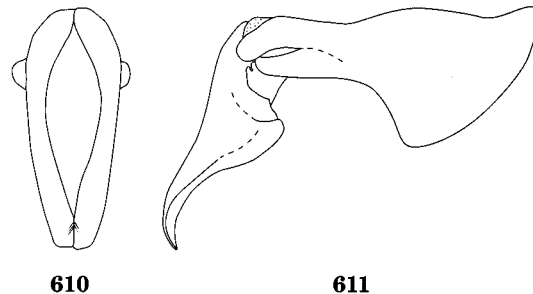


Fig. 609. *Gibboryctes waldenfelsi*.



Figs. 610-611. *Gibboryctes waldenfelsi* parameres.

quadridentate. Posterior tibia with apex slightly expanded and crenulate. Segments 1-4 of posterior tarsus with apex on dorsal surface prolonged, especially basal segment. *Venter*: Prosternal process long, stout; apex transverse, narrowed from front to back, narrowly rounded (almost wedge-shaped). Thoracic sternites with long, moderately dense, tawny setae. *Parameres*: Figs. 610-611.

Females. As males except in the following respects. *Head*: Frons with surface coarsely rugose. Clypeus with apex broadly rounded. Frontoclypeal tubercle similar except broader and with rounded apex. Clypeus with apex broader, rounded, surface a little more rugose. *Pronotum*: Horns absent. Surface with sides punctate; fovea, anterior angles, and edge of ridges either side of fovea rugose. Low, cariniform ridge present either side of fovea and with high, transverse, laminar ridge at apex; top of ridge with 3 emarginations. *Pygidium*: In lateral view, surface weakly concave.

DISTRIBUTION. *Gibboryctes waldenfelsi* is found from Panama to the Guianas, Amazonian Brazil and the eastern slopes of the

Andes in central Peru (Ratcliffe and Dechambre 1983). It is rare in collections and evidently not often collected.

LOCALITY RECORDS (Fig. 612). 1 specimen examined.

PANAMA (1). **DARIEN** (1): No data.

TEMPORAL DISTRIBUTION. July (1).

DIAGNOSIS. *Gibboryctes waldenfelsi* is readily distinguished by the deeply, broadly, almost triangular excavation of the pronotum, which is most pronounced in the males. The form of the slender, apically emarginate pronotal horn in the males and the high, almost laminate pronotal tubercle in the female are also distinctive.

This species was originally described in the genus *Strategus* by Endrödi (1977a). Ratcliffe and Dechambre (1983) examined the holotype, concluded that it was a species of *Gibboryctes*, and transferred it into that genus.

BIOLOGY. I have taken a specimen at lights in Brazil.



Fig. 612. Distribution of *Gibboryctes waldenfelsi* in Panama.



Color Plate 5. *Heterogomphus mniszehi*. Illustration by Dan Schmidt.

***Heterogomphus* Burmeister, 1847**

Heterogomphus Burmeister 1847: 224.

Stypotrupes Burmeister 1847: 210 (synonym, see Nomenclature below).

Daemonoplus Thomson 1859a: 68 (subgenus).

Baryxenus Bates 1891: 33 (synonym).

Syneterogomphus Prell 1912a: 53 (synonym).

Ortheterogomphus Prell 1912b: 103 (synonym).

Heterogomphidium Prell 1912b: 105 (synonym).

Hoplitogomphus Prell 1912b: 123 (synonym).

Dineterogomphus Prell 1912b: 129 (synonym).

Psileterogomphus Prell 1912b: 141 (synonym).

Neobaryxenus Prell 1912b: 148 (synonym).

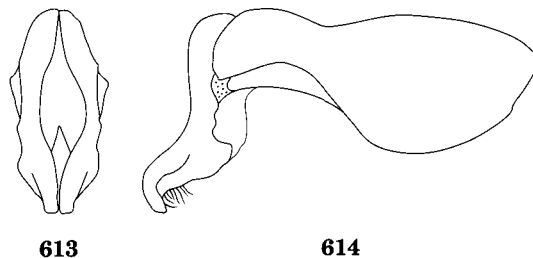
Anoplogomphus Prell 1912b: 149 (synonym).

Noheterogomphus Prell 1912b: 156 (synonym).

Tracheterogomphus Prell 1912b: 161 (synonym).

The genus *Heterogomphus* contains 42 species (Endrödi 1976b, 1985a; Dechambre 1986a). The subgenus *Daemonoplus* contains those species with the apex of the posterior tibia with a central tooth and the pronotum of the males with three horns (*H. pehlkei* [Kolbe], *H. mniszechi* [Thomson], *H. flohri* [Kolbe]). Six species of *Heterogomphus* occur in Mexico and Central America, and, of these, three are known from Costa Rica and Panama. Blackwelder (1944) recorded *H. rugicollis* Prell from Panama, but this South American species does not occur here. Endrödi (1976b) recorded a single Costa Rican specimen of *H. pehlkei* (Kolbe) which otherwise occurs in Mexico and Guatemala. Of the several hundred specimens I have seen in the subgenus *Daemonoplus* from Central America, I have never seen a single specimen of *H. pehlkei* from Costa Rica, and so I am not including it here in this work.

Endrödi (1976b, 1985a) kept *H. pehlkei* as a distinct species based upon a frontal horn with an incised apex and the longitudinally furrowed tooth on the posterior margin of the frontal horn in male majors. In all other respects, including the form of the parameres, this species is the same as *H. mniszechi*. These kinds of differences in horn configura-



Figs. 613-614. *Heterogomphus flohri* parameres. This species, from Mexico, Venezuela, and Colombia, is not currently known from Costa Rica or Panama.

tion are well-known to be intraspecific and a result of allometric growth of the horns (Bates 1888; Prell 1914; Arrow 1951; Otte and Stayman 1979; Eberhard 1980; Kawano 1995a-b). As such, the valid status of *H. pehlkei* is highly questionable. It may simply be a synonym of *H. mniszechi*.

Heterogomphus flohri (Kolbe) is known from Mexico, Venezuela, and Colombia (Endrödi 1976b, 1985a). I have seen specimens from Mexico, Guatemala, and Bolivia. With this distribution, one would think that *H. flohri* might also be in Costa Rica and/or Panama, but all of the 356 specimens I have seen of the subgenus *Daemonoplus* are *H. mniszechi*. *Heterogomphus flohri* might yet be found here, especially in the Serrania de Pirre highlands of Darien, Panama, adjacent to the Colombian border. *Heterogomphus flohri* is externally indistinguishable from *H. mniszechi*, but the form of the male parameres (Figs. 613-614) will separate the two species. Actually, when a long series of specimens of the subgenus *Daemonoplus* is examined from Mexico to South America, the form of the parameres (the extremes of which are illustrated in Endrödi 1976b, 1985a) seem to gradually grade, and separation of putative *H. flohri* from *H. mniszechi* becomes less certain.

Species in the genus *Heterogomphus* may be recognized by the combination of quadridentate foretibia, teeth of the foretibia directed obliquely forward, males with a large head horn, females with one or two tubercles on the head (only one tubercle in the species considered here; never with a horn), prosternal process long and stout, and head normal in shape (not short and broadly triangular as in *Gibboryctes*).

Heterogomphus females, especially *H. mniszechi* and *H. schoenherri*, are easily confused with the females of *Golofa* species. They are all about the same size, black, and with densely punctate elytra. In *Heterogomphus* females, the basal segment of the protarsus is distinctly shorter than the apical spur of the protibia. In *Golofa* females, the basal segment of the protarsus is subequal to or longer than the apical spur of the protibia (except for *G. tersander* where it may occasionally be shorter). In addition, while the apex of the prosternal process may have long, dense setae in both genera, the shaft of the process is normally glabrous or sparsely setose in *Heterogomphus* and densely setose in *Golofa*.

Endrödi believed that *Heterogomphus* was the most taxonomically difficult genus of New World Oryctini (personal communication, 1971). I agree with this since the differences between many of the taxa seem subtle, and the series available for study are often small. Fortunately, the three species occurring in Costa Rica and Panama are easily separated from one another. Prell (1912b) was

the first to provide a comprehensive treatment of the genus, and Endrödi (1976b, 1985a) gave the most recent synopsis.

In spite of the occasional abundance of some species of *Heterogomphus*, very little is known of their biology or immature stages. Adults are nocturnal, and many are attracted to lights at night. Where the larvae are known, they seem to feed on organic debris in the soil (Ratcliffe, personal observation).

NOMENCLATURE. *Stypotrupes* was described by Burmeister (1847). He included in it three species that are all now in separate genera: *S. telamon* Burmeister (now *Heterogomphus*), *S. endymion* (Olivier) (now *Lichnostrategus*), and *S. ajax* (Olivier) (now *Strategus*). To my knowledge, a type species has never been designated for *Stypotrupes*, thus leading to confusion as to where to place it in synonymy. In order to stabilize the nomenclature, I here designate *S. telamon* Burmeister as the type species of the genus *Stypotrupes*. Accordingly, *Stypotrupes* is now a junior synonym of *Heterogomphus*.

Key to the Species of Adult *Heterogomphus* of Costa Rica and Panama

1. Apex of middle tibia produced into single, large tooth. Elytra completely, densely punctate. Pronotum of all but smallest males with 3 forward projecting horns or large, acuminate tubercles ***mniszechi* (Thomson)**
- 1'. Apex of middle tibia with 2 large teeth or crenulate with large spinules. Elytra punctate or smooth. Pronotum of males not with 3 horns or acute tubercles 2
2. Elytra mostly smooth, shining. Apex of middle and posterior tibia crenulate with long, thick spinules ***chevrolati* Burmeister**
- 2'. Elytra completely, densely rugopunctate to punctate. Apex of middle tibia with 2 large teeth, apex of posterior tibia with 3-4 large teeth ***schoenherri* Burmeister**

Clave para las Especies de Adultos de *Heterogomphus* de Costa Rica y Panamá

1. Apice de la tibia media proyectada en forma de un solo diente grande. Elitros completa y densamente cubiertos de puntuaciones. Pronoto de los machos, excepto los machos más pequeños, con 3 cuernos o tubérculos acuminados grandes proyectados hacia adelante ***mniszechi* (Thomson)**
- 1'. Apice de la tibia media con 2 dientes grandes o crenulado con espinulas grandes. Elitros con puntuaciones o lisos. Pronoto de los machos sin 3 cuernos o tubérculos agudos 2
2. Elitros principalmente lisos, pulidos. Apice de las tibias medias y posteriores crenuladas con espinulas largas y gruesas ***chevrolati* Burmeister**
- 2'. Elitros completamente cubiertos de puntuaciones simples o rugosas. Apice de las tibias medias con 2 dientes grandes, ápice de las tibias posteriores con 3 ó 4 dientes grandes ***schoenherri* Burmeister**

***Heterogomphus (Heterogomphus)*
chevrolati Burmeister, 1847**

(Figs. 615-631)

Heterogomphus chevrolati Burmeister 1847: 233.

Heterogomphus chevrolati eurytus Bates 1888: 327 (synonym, described as a variety).

Heterogomphus chevrolati punctatissimus Prell 1912b: 135 (synonym, described as subspecies).

Heterogomphus chevrolati insignis Prell 1912b: 135 (synonym, described as subspecies).

DESCRIPTION. Length 33.0-52.8 mm; width 17.9-26.5 mm. Color dark reddish brown to black.

Males. *Head:* Majors with moderately long, recurved horn on top of head; horn reaching top of pronotal prominence, sides of horn subparallel for most of length, apex narrowly truncate; occasional specimen with small, sharp tooth on posterior edge of horn just above middle. Clypeus sharply constricted to broad apex; apex shallowly to deeply emarginate, weakly reflexed; surface weakly roughened. Interocular width equals 3.3-3.5 transverse eye diameters. Antenna with 10 segments, club subequal to segments 2-7. Mandibles a single, large blade. Minors similar except horn shorter. *Pronotum:* Majors with broad, high prominence; posterior surface convexly rounded, anterior surface of prominence sharply declivous; apex cariniform, with shallow emargination in center and, in larger specimens, feeble emargination either side of central emargination; sides of pronotum with broad, tuberculiform process. Surface on posterior slope of prominence crazed, with small, sparse punctures; anterior half of pronotum and narrow band on sides coarsely rugopunctate, setigerous; setae dense, moderately long, reddish brown. Base with marginal bead. Minors with prominence variably reduced to absent altogether; anterior declivity variably reduced or, in smallest specimens, a transverse fovea. Surface usually with larger punctures on posterior half.

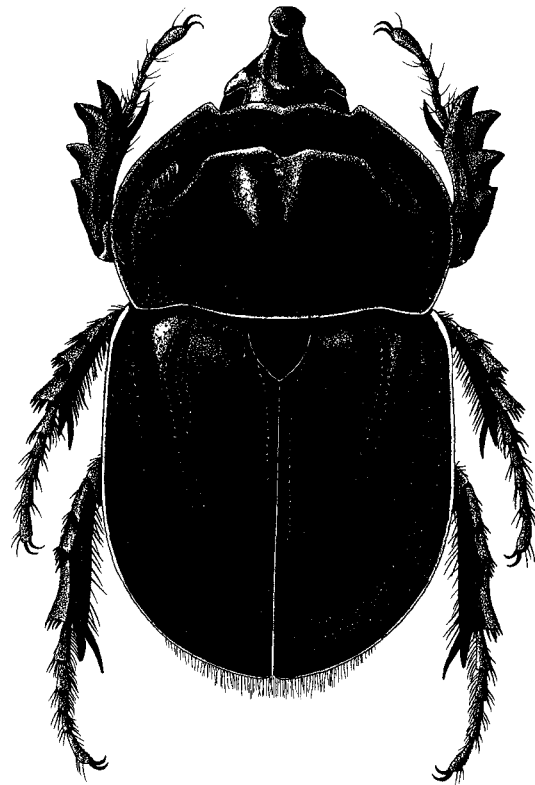
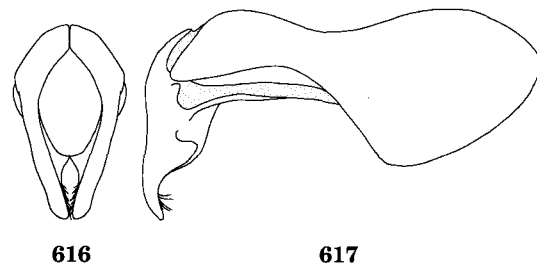


Fig. 615. *Heterogomphus chevrolati*.



Figs. 616-617. *Heterogomphus chevrolati* parameres.

Elytra: Impressed sutural stria present, occasionally reduced to row of large punctures, rarely obsolete in small specimens. Surface crazed; disc with small, sparse punctures; sides also with moderate to very large, dense punctures, some in indefinite rows. Apex with short, reddish brown setae, setae occasionally absent in smallest specimens. *Pygidium:* Surface transversely rugopunctate, setigerous; setae moderately long, moderately dense in unworn specimens, reddish brown; base with

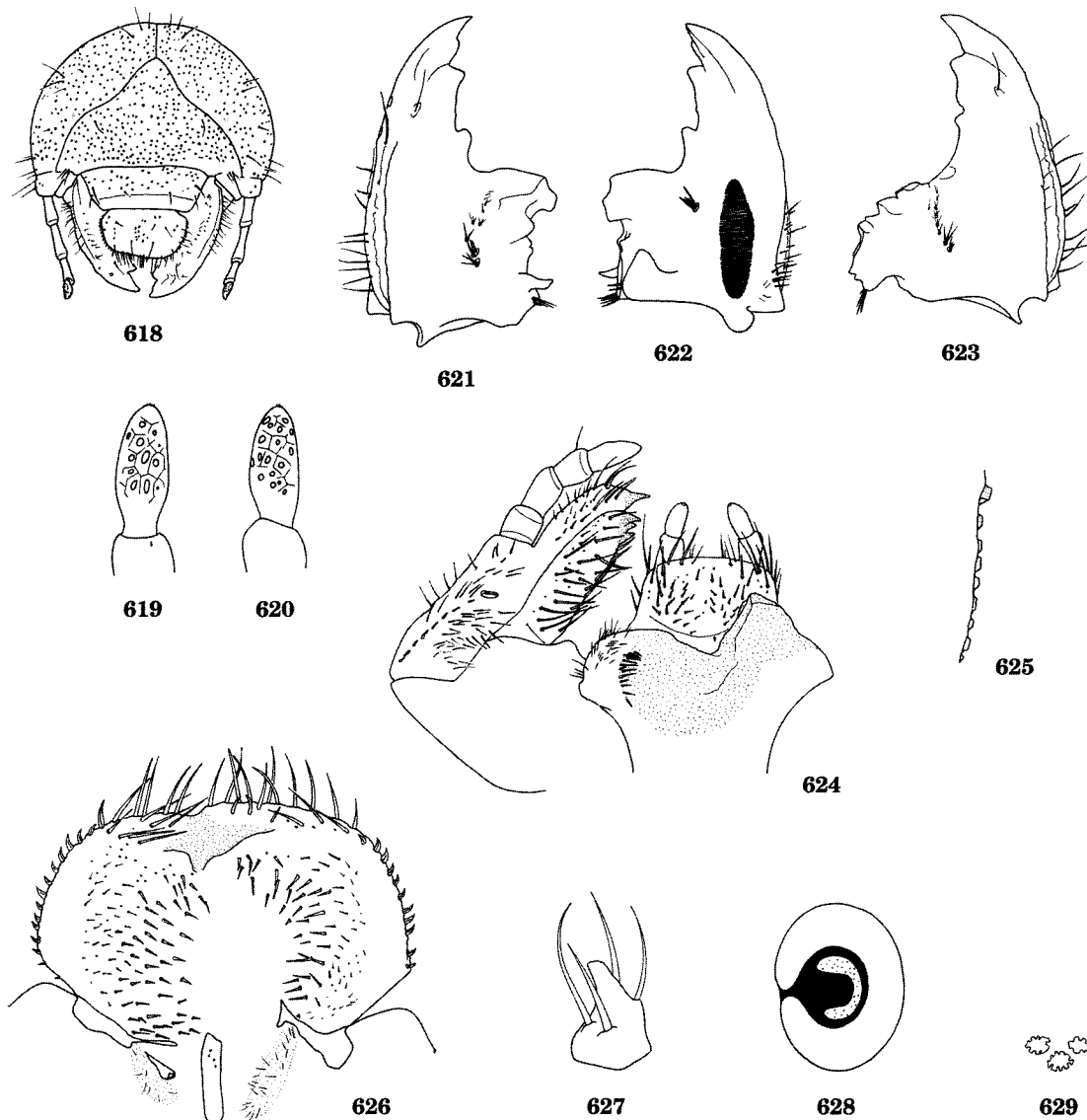
transverse band of long, dense setae. In lateral view, basal half weakly convex, apical half almost flat. *Legs*: Foretibia quadridentate. Apex of posterior tibia crenulate, usually with 11 thick, long spinules. Apex of first tarsomere of posterior tarsus barely widened. *Venter*: Prosternal process moderate in length, slightly flattened transversely, apex broadly rounded. *Parameres*: Figs. 616-617.

Females. As males except in the following respects. *Head*: Frontoclypeal region with single, erect tubercle. Surface coarsely rugose. Interocular width usually 3.2-3.4 transverse eye diameters. *Pronotum*: Surface behind anterior margin with small fovea; posterior edge of fovea with small tubercle either side of middle. *Pygidium*: Discal setae mostly short.

THIRD INSTAR LARVA. The larva of *H. chevrolati* is the first described for the genus *Heterogomphus*. One third instar larva of *H. chevrolati* is housed at UNSM with the following data: "Costa Rica: Puntarenas, Parq. Nac. Amistad, Rio Coton nr. Panama Border, VII-8-1994, ~1,200 m, B. & I. Ratcliffe, M. Jameson. Many adults emerging in same locale." Description and illustrations by Mary Liz Jameson.

Cranium (Fig. 618): Width of head capsule 14.2 mm. Surface dark reddish-brown, densely punctate, some punctures setigerous; setae moderately long, tawny. Frontal suture and clypeofrontal suture distinct. Epicranium with 4 dorsoepicranial setae on each side; frons with 1 long anterior frontal seta; anterior frontal angle with 3-4 long and moderately long setae; exterior frontal angle and anterior frontal region lacking setae. Ocellus absent. *Clypeus*: Form trapezoidal. Surface of postclypeus reddish-brown, well-sclerotized and densely punctate; surface of preclypeus light brown (base) to cream-colored (apex), poorly sclerotized, not punctate. Postclypeus setigerously punctate; anterior margin with 4 equally-spaced, long setae (1 near margin on each side and 1 at mid-disc on each side); lateral margin at middle with 1-2 moderately long setae. *Labrum*: Form subovate, asymmetrical. Surface dark reddish-brown, less

sclerotized and lighter in color at apex; densely, setigerously punctate, weakly rugose on disc and apex. Mid-disc with 6-8 moderately long setae; lateral margins of disc with 3-4 long setae (on each side). Subapex with 4 equally-spaced, long setae. Apex with about 28 long setae. Lateral margin (each side) with 10-13 hamate setae of acanthoparia visible. *Antenna*: 4-segmented, segment 2 about .25 times longer than segments 1 and 3, terminal segment about half length of segment 2. Apical segment oval in dorsal and ventral view, almond-shaped in lateral view; surface subdivided into irregular patches that surround sensory spots; dorsal surface with 12 sensory spots (Fig. 619); ventral surface with 17 sensory spots (Fig. 620). *Left mandible*: Form falcate. Scissorial region with 4 teeth, basal tooth separated from teeth 1-3. Lateral face with about 15 long and moderately long setae. Dorsal surface (Fig. 621) with line of about 25 setae; acia well-developed, elongate, triangular, with 3 short setae at apex. Ventral surface (Fig. 622) with elongate-oval stridulatory area, ridges narrowly separated, numerous; ventral process well-developed; brustia with 12 stout, long setae; basolateral angle with postartis. Molar area with 3 lobes. *Right mandible*: Form falcate. Scissorial region with 3 scissorial teeth, basal tooth reduced. Lateral face with about 16 moderately long and long setae. Dorsal surface (Fig. 623) with line of about 24 dorsomolar setae. Ventral surface with elongate-oval stridulatory area; ridges narrowly separated, numerous; ventral process well-developed; brustia with 7 stout, long setae; calx produced; basolateral angle with postartis. Molar area with 4 lobes, lobes 2 and 3 poorly developed. *Maxilla* (Fig. 624): Cardio subrectangular. Stipes larger than wide. Galea with many stout setae and 1 well-developed uncus at apex. Lacinia with many stout setae and 3 unci; unci subequal, extending from apex to subapex, contiguous. Palpus 4-segmented, segments 1-3 subequal in length, segment 4 slightly longer than segment 3. Stridulatory area with 8-9 blunt, truncate ridges (Fig. 625) and anterior truncate process. *Labium* (Fig. 624): Surface of glossa with moderately long and long setae. Hypopharyngeal sclerome asymmetrical, concave



Figs. 618-629. *Heterogomphus chevrolati*, third instar larva: (618) cranium; (619-620) terminal segment of antenna, dorsal and ventral views, respectively; (621-622) left mandible, dorsal and ventral views, respectively; (623) right mandible, dorsal view; (624) maxilla and labium; (625) stridulatory ridge of maxilla; (626) epipharynx; (627) tarsal claw; (628) spiracle; (629) holes of respiratory plate of spiracle.

medially, truncate process produced dorsally, left lateral lobe with setae at margin and on sides of disc; setae at margin moderately long and short, setae on sides of disc stout, moderately long and directed toward center of sclerome. *Epipharynx* (Fig. 626): Form suboval, wider than long, asymmetrical. Apex with ridge-like tylus (fused epizygom, zygom,

corypha, and haptomeral process) produced obliquely toward pedium. Acanthoparia with 13-14 dorsoventrally flatted, stout, recurved spines. Acroparia with about 30 long setae. Gymnoparia lacking setae. Chaetoparia with about 100 setae; setae shorter at lateral margin, longer and stouter toward middle. Pedium well defined. Nesia present; left

nesium triangular, sclerotized, elevated; right nesium elongate, less sclerotized, with 4 sensory pores anteriorly. Dextiotorma elongate. Laeotorma elongate with rounded pternotorma. *Legs*: Trochanter, femur, and tibiotarsus with numerous, moderately long setae. Claws (Fig. 627) brown, weakly hooked in lateral view, apex blunt, with 4 setae at subapex. *Body vestiture*: Thorax sparsely setose; abdominal segments 1-6 moderately densely setose, segments 1-10 sparsely setose. Setae of

thorax short and long, slender. Abdominal segments 1-6 divided into annulets; prescutum with 80-100 short, stout setae and 6 long, slender evenly spaced setae near posterior margin; scutum with 120-140 short, stout setae and about 10 long, slender, evenly spaced setae near posterior margin; scutellum with 150-170 short, stout setae and about 20 long, slender, evenly spaced setae near posterior margin. Abdominal segments 7-9 not divided into annulets, each with short, stout setae (sparse) and long, slender setae (sparse). Dorsal surface of abdominal segment 10 with sparse setae; dorsal impressed line absent. Ventral surface of abdominal segment 10 lacking palidia; anal lip curved, transverse; upper anal lip with numerous long, slender setae. Teges with numerous short, stout, flattened setae. *Spiracles* (Figs. 628): Thoracic spiracle subtriangular in shape with dorsal margin flattened, edges blunt and rounded; abdominal spiracles elongate-oval (spiracles 1-5) or oval (spiracles 6-8); thoracic spiracle slightly higher (2.1 mm high, 1.2 mm wide) than abdominal spiracles (about 1.7 mm high, 1.2 mm wide). Respiratory plates C-shaped, lobes nearly touching; bulla weakly raised; holes (Fig. 629) oblong-oval, outer margin irregular, about 60 holes across diameter of plate.

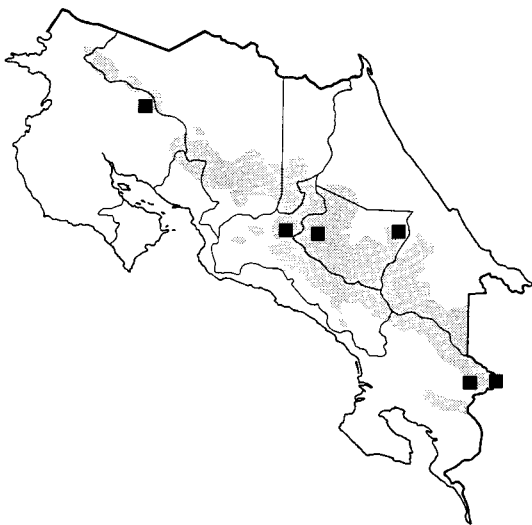


Fig. 630. Distribution of *Heterogomphus chevrolati* in Costa Rica.



Fig. 631. Distribution of *Heterogomphus chevrolati* in Panama.

DISTRIBUTION. *Heterogomphus chevrolati* is widely distributed from southern Mexico to Colombia, Ecuador, and Bolivia (Endrödi 1976b). This species is not commonly encountered in either Costa Rica or Panama. Based upon my experiences in Mexico, Guatemala, and Honduras, where I have seen this species in large numbers, it could be locally abundant for only brief periods of time and, as a consequence, have been overlooked in collecting efforts to date in Costa Rica and Panama.

LOCALITY RECORDS (Figs. 630-631). 32 specimens examined.

COSTA RICA (24). CARTAGO (3): Cartago, Grano de Oro (Chirripó); GUANACASTE (2): La Palma; HEREDIA (1): Transecto Las Alturas-Cerro Echandi; PUNTARENAS (17): Estación Biológica Las Alturas, Río Cotón near Panamá border (Parq. Nac. Amistad); SAN JOSÉ (1): Cerro Tacuotari.

PANAMA (8). BOCAS DEL TORO (2): La Culebra Trail (5 km N Boquete); CHIRIQUI (6): Los Planes (7 km N), Cerro Colorado (50 km N San Felix), Cerro Punta, Hartmann's Finca (Santa Clara).

TEMPORAL DISTRIBUTION. January (2), February (1), March (1), May (1), June (1), July (16), August (2), October (3), November (4).

DIAGNOSIS. *Heterogomphus chevrolati* may be distinguished among the Central American *Heterogomphus* species by its smooth elytra in combination with its wide and deeply emarginate clypeus.

BIOLOGY. Adults are nocturnal and are attracted to lights. I have seen adults emerging from the soil on the forest floor as well as larvae that were exposed by a new road cut. Larvae evidently live in the soil feeding on organic material and not in rotting tree trunks. Adults have been collected from premontane moist forests, premontane rain forests, premontane wet forests, and montane wet forests at elevations of 1,100-2,000 meters.

***Heterogomphus (Daemonoplus) mniszzechi* (Thomson, 1859)**

(Color Plate 5, Figs. 44,632-637)

Daemonoplus mniszzechi Thomson 1859a: 69.

DESCRIPTION. Length 34.0-49.0 mm; width 19.0-25.5 mm. Color black.

Males. Head: Top of head with recurved horn; majors with horn long (reaching apex of central pronotal horn), apex weakly rounded or subtruncate or occasionally notched at center, posterior margin usually with tubercle just below apex (Fig. 633), tubercle occasionally furrowed longitudinally; minors with horn short, lacking subapical tubercle. Frons in majors smooth, with occasional small puncture; minors with frons sparsely punctate or weakly rugose. Clypeus with surface sparsely punctate in majors, densely rugose in minors; apex broad, with large, acute, reflexed tooth either side of central, deep emargination. Interocular width equals 2.0 transverse eye diameters. Antenna 10-segmented, club a little longer than segments 2-7. Mandibles large, unidentate, apex rounded medially and angled laterally. *Pronotum:* Majors with 3 moderately long horns; lateral horns laterally compressed, weakly acuminate, slightly diverging, and extending forward and upward at about 20° from plane of disc (rarely at 30°); center horn in cross section nearly round (venter usually flattened; occasional specimens with horn laterally compressed), weakly acuminate with apex rounded or blunt, extending forward and upward also at about 20° from plane of disc. Surface of discal area with small, sparse punctures; pronotal cavity smooth, shining; sides and the arcs connecting bases of horns with large, dense punctures or coarsely rugopunctate; anterior angles rugose; base margined, with sparse to moderately dense, small to moderately-sized punctures. Minors with horns small, projecting forward and only slightly upward or horns reduced to prominent tubercles. Surface similar in minors except pronotal cavity with large, sparse, transverse punctures. *Elytra:* Sutural stria present; interval between suture and sutural stria and humerus with

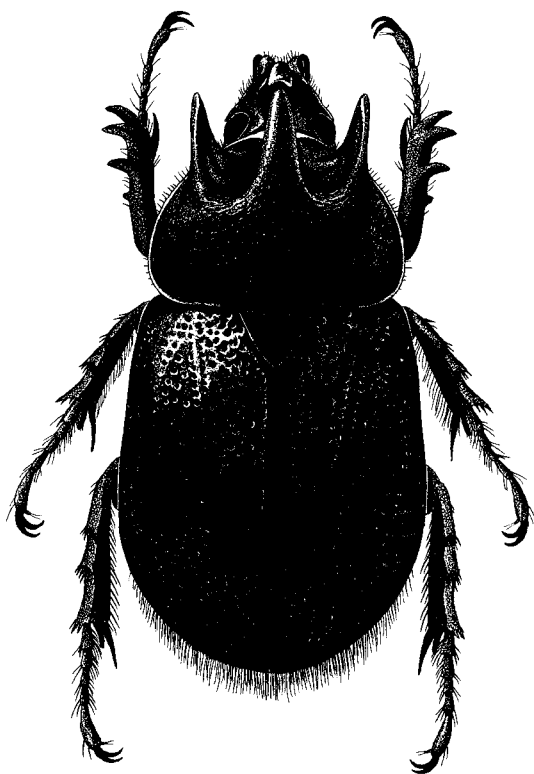
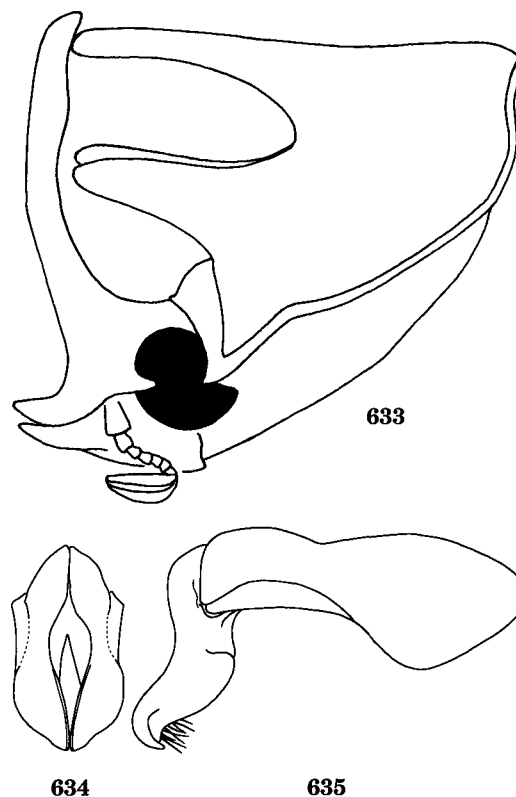


Fig. 632. *Heterogomphus mniszzechi*.



Figs. 633-635. *Heterogomphus mniszzechi*: (633) male head and pronotum; (634-635) parameres.

small, sparse punctures; remainder of elytra with large, ocellate, mostly confluent punctures, punctures becoming smaller at apex. *Pygidium*: Surface rugopunctate (center of disc with large punctures in majors), setigerous; setae moderately dense, minute to short, reddish brown. Center of disc with transverse band of long, dense, reddish brown setae. In lateral view, surface strongly convex. *Legs*: Foretibia quadridentate. Apex of posterior tibia with 3-4 small teeth and with a large, blunt spinule between each tooth. First segment of posterior tarsus only slightly expanded at apex. *Venter*: Prosternal process moderately high, wide, flattened from front to back, apex broadly rounded and obliquely truncate. *Parameres*: Figs. 634-635.

Females. As males except in the following respects. *Head*: Top of head with single, transverse tubercle on frontoclypeal border. Sur-

face of frons and clypeus coarsely, densely rugopunctate. Interocular width varies from 2.0 in smaller specimens to 2.5 transverse eye diameters in largest specimens. *Pronotum*: Largest specimens with rounded tubercle either side of midline behind anterior margin; smallest specimens lacking tubercles. Surface similar except anterior 1/3-1/2 with large, dense, transverse rugae, rugae with moderately dense, moderately long reddish brown setae either side of middle. *Pygidium*: Entire surface with longer setae. In lateral view, surface weakly convex.

DISTRIBUTION. *Heterogomphus mniszzechi* is found from southern Mexico and Guatemala to Colombia, Bolivia, and Brazil (Endrödi, 1976b; Ratcliffe, personal observation). This species is broadly distributed in the Cordillera Central of Costa Rica and Panama.

LOCALITY RECORDS (Figs. 636-637). 369 specimens examined.

COSTA RICA (280). ALAJUELA (12): Bajos del Toro Amarillo, San Ramón, Zarcero; CARTAGO (88): Cartago, Embalse El Llano, Grano de Oro, La Catarata, Orosi, Refugio Nacional Tapanti, SE side Volcán Irazú; GUANACASTE (21): Estación Cacao, Estación Mengo (W side Volcán Cacao), Estación Pitilla, Río San Lorenzo (Volcán

Tenorio); HEREDIA (35): Cerro Chompipe, Estación Barva (Parq. Nac. Braulio Carrillo), San Rafael; PUNTARENAS (67): Estación Las Alturas, Estación Las Mellizas, Las Cruces, Estación La Casona (Reserva Biológica Monteverde), Estación Pittier, Río Cotón; SAN JOSÉ (57): La Palma, La Rosa, San Cristobal, San José, Zurqui Tunnel.

PANAMA (89). BOCAS DEL TORO (2): Continental Divide Trail (above Fortuna Dam); CHIRIQUI (86): Los Planes (7 km N), Boquete, Cerro Punta, Continental Divide Trail (above Fortuna Dam), Finca La Suiza, Fortuna Dam, Hartmann's Finca (Santa Clara), Hato de Volcán, IHRE Vivero (11 km N Los Planes); DARIEN (1): Cana (ANCON Station).

TEMPORAL DISTRIBUTION. January (3), February (6), March (11), April (30), May (132), June (66), July (46), August (18), September (20), October (10), November (7).

DIAGNOSIS. *Heterogomphus mniszehi* is readily distinguished in the Costa Rican and Panamanian fauna by the combination of densely punctate elytra, apex of the middle tibia produced into a tooth, pronotum of the male with three horns, and (in the female) the apex of the clypeus deeply emarginate. Only the male minors and females of *H. schoenherri*, with their densely punctate



Fig. 636. Distribution of *Heterogomphus mniszehi* in Costa Rica.



Fig. 637. Distribution of *Heterogomphus mniszehi* in Panama.

elytra, might be confused with *H. mniszzechi*, but *H. schoenherri* lacks the strong tooth at the apex of the middle tibia that characterizes the species in the subgenus *Daemonoplus*. *Daemonoplus* was established by Kolbe as a distinct genus for *mniszzechi* Thomson, *flohri* Kolbe and *pehlkei* Kolbe.

BIOLOGY. In spite of the relative abundance of these large beetles, virtually nothing is known of their biology. Adults are nocturnal and attracted to lights. They have been collected from premontane rain forests, lower montane rain forests, montane rain forests, and premontane wet forests at elevations ranging from 800-2,500 meters. Temporal distributional data indicate a definite emergence that is coincidental with the beginning of the rainy season in May.

***Heterogomphus (Heterogomphus) schoenherri* Burmeister, 1847**

(Figs. 638-641)

Heterogomphus schoenherri Burmeister 1847: 231

Heterogomphus whymeri Bates 1891: 33 (synonym).

DESCRIPTION. Length 35.0-51.0 mm; width 18.2-26.3 mm. Color black.

Males. Head: Top of head with recurving horn; horn in majors long, tapering, acuminate, extending above apex of pronotal prominence, and with posterior margin slightly enlarged just above middle of shaft; minors similar except horn short, not dilated posteriorly. Frons in majors with moderately dense, moderate to large, setigerous punctures; setae moderate in density, moderately long, reddish brown; minors with surface rugopunctate. Clypeus with apex broad, deeply and triangularly emarginate, strongly reflexed. Interocular width equals 2.6 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. Mandibles a single, large blade. **Pronotum:** Majors with narrow, moderately elongate prominence projecting forward and upward at about 23° from plane

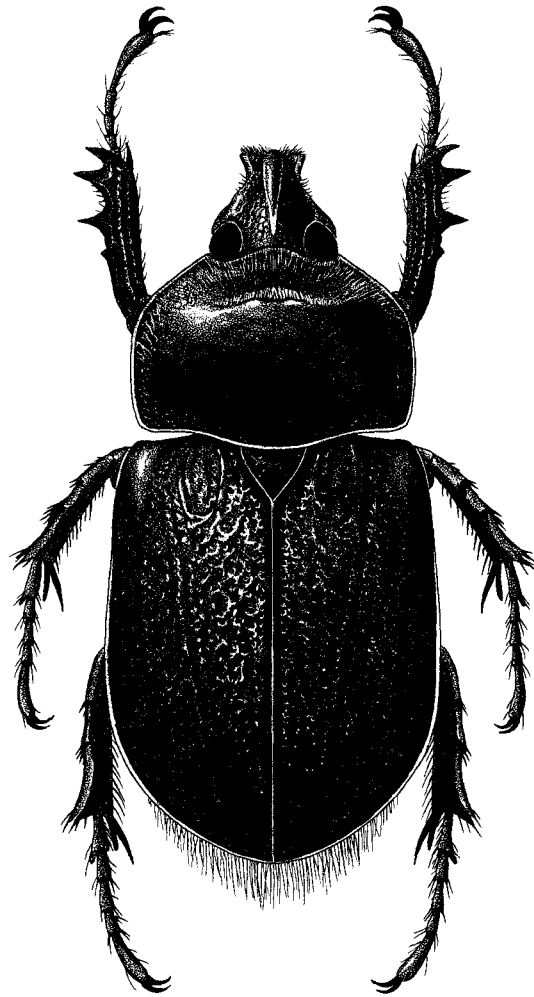
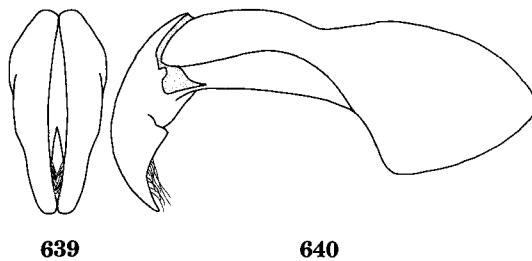


Fig. 638. *Heterogomphus schoenherri*.



Figs. 639-640. *Heterogomphus schoenherri* parameres.

of disc; prominence with sides slightly tapering, apex broad and emarginate; dorsal surface of prominence convex and with small, sparse punctures; ventral surface strongly

concave, strongly rugose, densely setigerous, setae long and reddish brown. Surface of anterior third of pronotum and broad band at lateral margins coarsely rugose, setigerous; setae sparse laterally, becoming dense anteriorly, moderately long, reddish brown. Base with marginal bead. Minors lacking pronotal prominence, anterior third of pronotum weakly concave. *Elytra*: Surface completely, densely punctate and rugose; punctures small and moderately large mixed, ocellate. Apex in unworn specimens with short, reddish brown setae. Distinct sutural stria absent. *Pygidium*: Surface transversely rugopunctate to rugose in larger specimens, densely punctate in smaller specimens; basal half with long, dense, reddish brown setae, apical half with minute setae and a few sparse, long setae in unworn specimens. In lateral view, basal half strongly convex, apical half weakly concave to flat. *Legs*: Foretibia quadridentate, basal tooth small. Apex of middle and posterior tibia usually with 3 teeth, occasionally with 4. Apex of first segment of posterior tarsus triangularly expanded. *Venter*: Prosternal process moderately long, broad, transversely flattened, apex rounded and narrowly, obliquely truncate. *Parameres*: Figs. 639-640.

Females. As males except in the following respects. *Head*: Surface coarsely rugopunctate, a few setae present on margin above each eye. Frontoclypeal region with triangu-

lar tubercle. Clypeus with apex broad, subtruncate to shallowly emarginate, strongly reflexed. Interocular width equals 2.1 transverse eye diameters. *Pronotum*: Surface convex; posterior half with sparse, small to moderately-sized punctures; anterior half and broad band along lateral margins coarsely rugose. Broad, transverse band of setae present just behind anterior margin in unworn specimens; setae moderate in length, moderately dense, reddish brown, extending around to lateral margins. *Elytra*: Rugosity reduced, punctures sparse to moderately dense. Weak row of punctures next to suture occasionally present. Apex with short, reddish brown setae in unworn specimens. *Pygidium*: Surface usually densely punctate, punctures moderate to large, becoming finely rugose at apical margins.

DISTRIBUTION. *Heterogomphus schoenherri* occurs in Panama, Colombia, Venezuela, and Ecuador (Endrödi 1976b). Endrödi cites a record for Darien Province in eastern Panama, and this is consistent with the remaining South American distribution of this species. I have seen only one actual specimen (at the U.S. National Museum) from Panama, and it is from Santiago in the lowlands at the base of the Azuero Peninsula. I am suspicious about the accuracy of this label data inasmuch as no other specimens have been taken from this area. *Heterogomphus schoenherri* is



Fig. 641. Distribution of *Heterogomphus schoenherri* in Panama.

ostensibly a species of northwestern South America whose range just reaches Panama.

LOCALITY RECORDS (Fig. 641). 2 specimens examined or recorded.

PANAMA (2). **DARIEN** (1): No data (Endrödi 1976); **VERAGUAS** (1): Santiago.

TEMPORAL DISTRIBUTION. No data available. I have a large series from the Río Magdalena valley (Huila Province) in central Colombia collected in November.

DIAGNOSIS. While *H. schoenherri* has the similarly roughened elytra of *H. mniszehi*, the males of *H. schoenherri* lack the three pronotal horns of *H. mniszehi*, and both sexes lack the single, strong tooth on the apex of the middle tibia that is present in *H. mniszehi*.

BIOLOGY. Eberhard (1979) briefly described combat between males. These beetles are uncommon in Panama, but larger populations may be recognized once the Darien in eastern Panama becomes better explored. The Veraguas specimen is from an area of tropical dry forest at an elevation of less than 100 meters.

Irazua Ratcliffe, new genus

(Figs. 642-646)

TYPE SPECIES. *Irazua dilicera* Ratcliffe, new species, here designated.

DESCRIPTION. Length 31.2-41.0 mm; width 16.3-21.5 mm (size will probably be a little smaller to a little larger than figures cited above as new specimens are found). Color dark reddish brown. **Head:** Males with recurved, apically bifurcate horn; horn in majors long, apex deeply bifurcate, each ramus long; horn in minors short, weakly bifurcate to deeply emarginate in minors. Clypeus in majors with apex distinctly emarginate at middle, a large and rounded lobe either side of middle; minors with apex subtruncate, weakly emarginate at middle. Eye canthus

strongly produced laterally, outer edge expanded into large, triangular projection. Antenna with 10 segments, club small, subequal in length to segments 3-7. Mandibles strongly bidentate in majors, weakly bidentate in minors. **Pronotum:** Male majors with long, narrow process extending forward at about 22° from plane of disc; process tapering to narrow, emarginate apex. Ventral surface of process with moderately dense and moderately long, reddish brown setae. Male minors (Fig. 643) lacking process, instead with transverse fovea behind apical margin, fovea with longitudinal carina at center, posterior margin of fovea cariniform. Base with marginal bead. **Elytra:** Impressed sutural stria absent. Surface roughened, with small and moderately large punctures mixed; larger punctures shallow, some in distinct rows. Lateral margin narrowly, strongly reflexed. **Pygidium:** Surface finely, densely, completely roughened, setigerous; setae dense (almost fur-like), moderately long, reddish brown or tawny. In lateral view, surface moderately convex. **Legs:** Foretibia tridentate. Apex of middle tibia with single, large, subtriangular tooth. Apex of posterior tibia with large, rounded prominence and triangular upper angle. Apex of first segment of posterior tarsus triangularly expanded. **Venter:** Prosternal process very short, resembling a broad, nearly equilateral triangle.

DIAGNOSIS. *Irazua* is characterized by a clypeus with apex bilobed, triangularly expanded eye canthus, mandibles distinctly bidentate, strongly bifurcate head horn, roughened elytra, densely setigerous pygidium, tridentate foretibia, apex of mesotibia with single tooth, apex of posterior tibia with rounded lobe and triangular upper angle, and prosternal process short and indistinct.

This genus *seems* most similar to the genus *Heterogomphus*, which contains a couple of species in South America with a similarly long and bifurcate head horn. The roughened elytra and configuration of the pronotal horn are also similar to some *Heterogomphus* species. However, unlike *Heterogomphus*, *Irazua* has a tridentate foretibia (instead of quadridentate), a nearly obsolete prosternal process (instead of well-developed), strongly

bilobed mandibles (present only in *H. julus* Burmeister from southern Brazil), and an extremely setose (almost fur-like) pygidium (not known in other *Heterogomphus* species). Like the species in the subgenus *Daemonoplus* of *Heterogomphus*, the apex of the middle tibia ends in a single tooth rather than the two teeth as in all the other species of *Heterogomphus*.

The triangularly expanded eye canthus is dissimilar to virtually all other New World dynastines. Only *Aceratus* (Pentodontini: southern South America) and *Barutus* (Oryctini: Panama and Costa Rica) have an expanded eye canthus, but none have it developed to the degree as in *Irazua*.

I suspect the females are similar. The largest questions on body morphology for the females are "one or two tubercles on the head?" and "what is the form of the pronotum?" They cannot be reliably worked into a key to genera until these facts are known.

DISTRIBUTION. Known from Reserva Tapanti and Volcán Irazú in Costa Rica and Santa Tecla (Nueva San Salvador) in El Salvador.

ETYMOLOGY. The feminine generic name is based on the name of Volcán Irazú in Costa Rica, the locality where the paratype was collected.

***Irazua dilicra* Ratcliffe, new species**

(Figs. 642-646)

TYPE MATERIAL. Holotype labeled "No. 64836, Date. 6.11.55, Loc. Santa Tecla, Col. PAB [El Salvador]." Two male paratypes labeled "COSTA RICA: Cartago, SE side Irazú Volcano, V-12-1988, 2500 m, B. Ratcliffe and M. Jameson" and "Tapanti, Costa Rica, Mayo 1989, M. Posla." Holotype deposited at the University of Nebraska State Museum. Paratypes deposited at INBio (Santo Domingo de Heredia, Costa Rica) and B. C. Ratcliffe collection (Lincoln, NE).

HOLOTYPE. Male. Length 41.0 mm (apex of clypeus to apex of elytra); greatest width 21.5 mm. Color dark reddish brown. **Head:** Surface with long horn; horn projecting forward and then recurved upward; apex strongly bifurcate, each ramus long and pointed. Frons smooth, shining, with a few sparse, small punctures. Clypeus with apex emarginate at middle, a large and rounded lobe either side of middle. Eye canthus strongly expanded laterally into large, triangular tooth. Antenna with 10 segments, club small, subequal in length to segments 3-7. Mandibles strongly bidentate. **Pronotum:** Long, narrow process (or horn) extending forward at about 22° from plane of disc; process tapering to narrow, emarginate apex. Ventral surface of process concave, with distinct longitudinal carina at center and with moderately dense and moderately long reddish brown setae. Base with marginal bead. **Elytra:** Impressed sutural stria absent. Surface entirely roughened, with small and moderately large punctures mixed; larger punctures shallow, some in distinct rows. **Pygidium:** Surface finely, densely, completely roughened, setigerous; setae dense (almost fur-like), moderately long, tawny. In lateral view, surface moderately convex. **Legs:** Foretibia tridentate. Apex of middle tibia with single, large, subtriangular tooth. Apex of posterior tibia with large, rounded prominence and triangularly produced dorsal angle. Apex of first segment of posterior tarsus triangularly expanded. **Venter:** Prosternal process very short, resembling a broad, nearly equilateral triangle. **Parameres:** Figs. 644-645.

VARIATION. Males (2 paratypes). Length 31.2-34.5 mm; greatest width 16.3-18.9 mm. As holotype except in the following respects. **Head:** Horn short, vertical, apex deeply emarginate. Clypeus with apex subtruncate, weakly emarginate at middle. Mandibles weakly bidentate. **Pronotum:** Horn-like process absent in smaller specimen, larger specimen with forward-projecting prominence. Small, transverse fovea present behind apical margin in smaller specimen (Fig. 643); fovea with weak longitudinal carina at center,

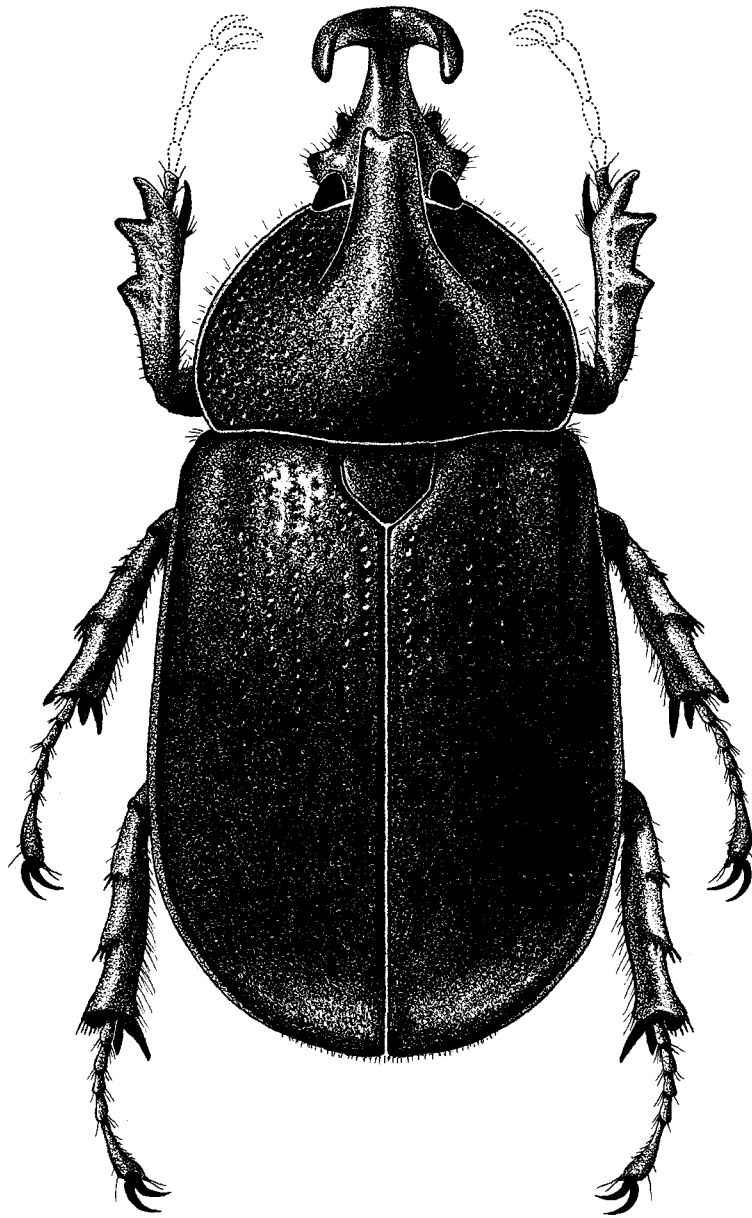
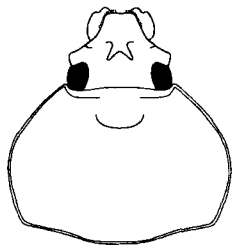


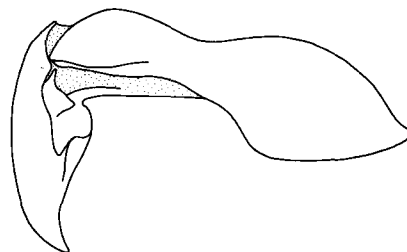
Fig. 642. *Irazua dilicra*.



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Figs. 643-645. *Irazua dilicra*: (643) male minor head and pronotum; (644-645) parameres.



Fig. 646. Distribution of *Irazua dilicra* in Costa Rica.

posterior margin of fovea cariniform; larger specimen on front of pronotum declivous beneath prominence. Base with marginal bead. *Pygidium*: Color of setae reddish brown.

ETYMOLOGY. From the Greek words *likros*, meaning antler or horn, and *di*, meaning two. Hence, two horns in reference to the deeply bifurcate head horn.

DISTRIBUTION. *Irazua dilicra* is, so far, known only from central Costa Rica and southcentral El Salvador. Additional collecting at high elevations might yield additional material. Specimens have been collected at elevations of 900 m in El Salvador and 1,150 and 2,500 meters in Costa Rica.

LOCALITY RECORDS (Fig. 646). 2 Costa Rican specimens examined.

COSTA RICA (2). CARTAGO (2): SE side Volcán Irazú, Tapanti.

TEMPORAL DISTRIBUTION. May (2).

DIAGNOSIS. The males of *Irazua dilicra* are easily distinguished by the deeply forked head horn (unlike anything else in the Mesoamerican fauna) in the majors, the erect and deeply emarginate head horn in the minors, tridentate foretibia, greatly expanded eye

canthus, roughened elytra, densely setigerous pygidium, and extremely short prosternal process. Although the females are unknown, they are likely to be similar to the males except for the head and pronotal armature. I predict the head will be tuberculate, but whether it is one or two tubercles remains to be seen.

BIOLOGY. The Costa Rican specimens were collected at lights in an area of montane wet forest at elevations of 1,150 and 2,500 meters. At the locality of the holotype on Irazú volcano, the temperature was relatively cold, and very little came to the lights. The forest in this area was severely cut-over with generally small patches left here and there.

During our ascent up the slopes of Volcan Irazú, the rental van we used kept high-centering on the deeply rutted cow path going through pasture lands and up the mountain and, ultimately, a brake line beneath the vehicle ripped off. This left our team in the precarious situation (after shutting down the lights late at night) of having to drive down the track, in the dark and with a precipitous drop-off on one side, without brakes. Collecting, on the literal edge as it were in this case, was full of challenges. As it turned out, we were able to jury-rig the brake line with a nut from the air filter and then use (temporarily) some milk to replace the lost brake fluid.

Megaceras Hope, 1837

Megaceras Hope 1837: 82.

The genus *Megaceras* is comprised of 13 species (Endrödi 1985a). All of the species occur in South America, and two of them extend northward into Costa Rica and Panama. One of these, *M. septentrionis*, is commonly encountered while the other, *M. morpheus*, is rarely seen.

Species of *Megaceras* are characterized by tridentate foretibiae, frons with a single horn in the males or a single tubercle in the females, prosternal process present, smooth elytra, and mandibles distinctly bidentate and exposed.

Very little is known about the biology of these beetles. Adults are active at night and seem to be found primarily in areas of tropi-

cal wet forests and premontane wet forests. The larvae probably live in decaying logs or in the soil feeding on organic material.

Key to the Species of Adult *Megaceras* of Costa Rica and Panama

1. Clypeus subtriangular, narrowed strongly to sharply bidentate apex. Mandibles with anterior tooth smaller than posterior tooth *septentrionis* Bates
- 1'. Clypeus rounded, apex at center with small, bilobed process. Mandibular teeth subequal in size *morpheus* Burmeister

Clave para las Especies de Adultos de *Megaceras* de Costa Rica y Panamá

1. Clípeo subtriangular, los lados se estrechan fuertemente hacia el ápice agudament bidentata. Mandíbulas con el diente anterior más pequeño que el posterior *septentrionis* Bates
- 1'. Clípeo redondeado, ápice en el centro con un proceso pequeño bilobulado. Dientes mandibulares similares en tamaño *morpheus* Burmeister

Megaceras morpheus Burmeister, 1847

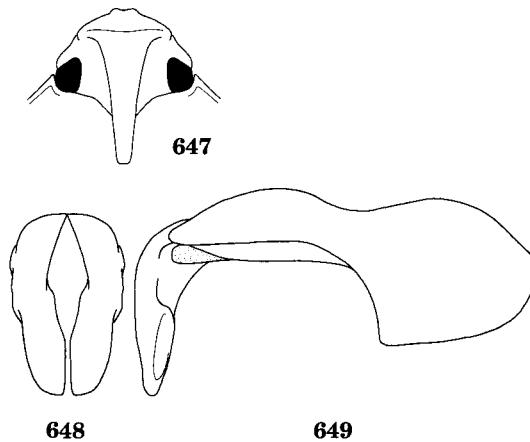
(Figs. 647-650)

Megaceras morpheus Burmeister 1847: 223.
Megaceras ixyon Reiche 1859: 16 (synonym).

DESCRIPTION. Length 27.0-47.0 mm; width 16.7-20.5 mm. Color dark reddish brown, almost black.

Males. Head: Frons with large, recurving horn; horn narrowly rounded at apex; posterior margin of horn with small, tooth-like swelling near apex. Clypeus broadly rounded, nearly semi-circular; apex produced at center into small, bilobed process (Fig. 647); surface weakly rugose to rugopunctate. Interocular width equals 4.0 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. Mandibles with 2 large, triangular, subequal teeth. **Pronotum:** Majors with large, bulbous, broad, strongly bifurcate protuberance; small horns at apex of protuberance subparallel to slightly convergent. Surface crazed, sparsely punctate, punctures minute. Lateral margin with band of large, widely spaced rugae, rugae connected to *areola apposita*. Anterior margin with strong, posteriorly directed emargination.

Sides strongly explanate. Base margined. Minors similar except protuberance and apical horns smaller. **Elytra:** Surface crazed, sutural stria impressed. **Pygidium:** Surface with moderately dense, moderately large, setigerous punctures covering disc; setae long, reddish brown. Base with broad transverse band of similar, setigerous punctures. In lateral view, surface strongly convex. **Legs:** Foretibia tridentate. Apex of posterior tibia with single, large tooth. First segment of posterior tarsus with apex extended into long spine. **Venter:**



Figs. 647-649. *Megaceras morpheus*: (647) head of male; (648-649) parameres.

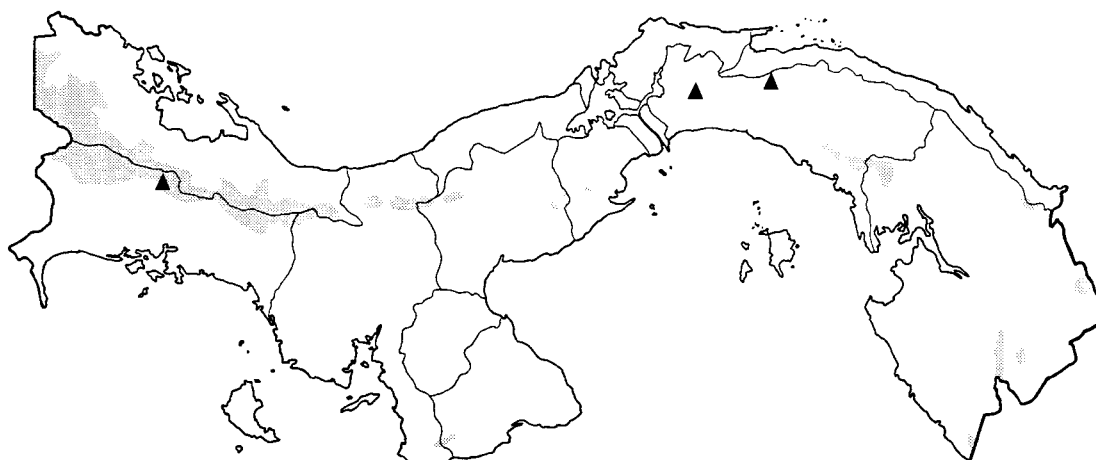


Fig. 650. Distribution of *Megaceras morpheus* in Panama.

Prosternal process moderate in length, compressed from front to back, apex broadly rounded. *Parameres*: Figs. 648-649.

Females. As males except in the following respects. *Head*: Frons with single, strong tubercle at middle. Surface of frons and clypeus coarsely rugose. *Pronotum*: Small tubercle present either side of middle just behind anterior margin. Surface crazed; basal half impunctate, apical half with sparse, minute punctures. Lateral margin and anterior angle with large, deep punctures. *Pygidium*: Disc with punctures sparse, small, setigerous. In lateral view, basal half strongly convex, apical half concave.

DISTRIBUTION. *Megaceras morpheus* is known from Colombia, Venezuela, Ecuador, Brazil, and northern Argentina (Endrödi 1976b). The specimens recorded here represent a NEW COUNTRY RECORD. The Chiriquí specimen seems unusually far-removed from those specimens recorded from eastern Panama, but its identification is certain.

LOCALITY RECORDS (Fig. 650). 9 specimens examined.

PANAMA (9). **CHIRIQUI** (1): Los Planes (7 km N); **PANAMA** (8): Cerro Jefe, El Llano-Carti Road (km 13).

TEMPORAL DISTRIBUTION. January (1), May (7), July (1).

DIAGNOSIS. *Megaceras morpheus* is immediately distinguished from *M. septentrionis* by its broad, nearly semicircular clypeus and by the form of the male parameres.

BIOLOGY. This South American species is extremely rare in Panama where it is at the northern limit of its range. The Panamanian specimens were collected from premontane wet forests at elevations ranging from 340 to 1,160 meters.

***Megaceras septentrionis* Bates,
1888**

(Figs. 651-658)

Megaceras septentrionis Bates 1888: 325.

Megaceras septentrionis crassicornis Dechambre 1975: 624 (synonym, described as subspecies).

DESCRIPTION. Length 27.0-38.0 mm; width 17.5-20.3 mm. Color reddish brown to nearly black.

Males. *Head*: Frons with large, recurving horn (Figs. 653-654); horn narrowly rounded to narrowly truncate at apex; posterior margin with small, tooth-like swelling near apex.

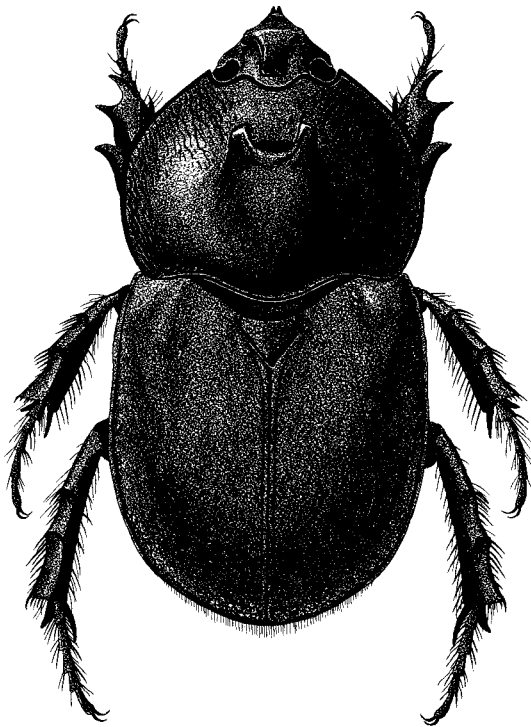
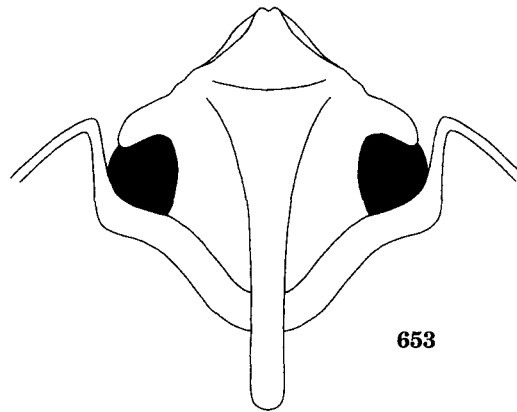


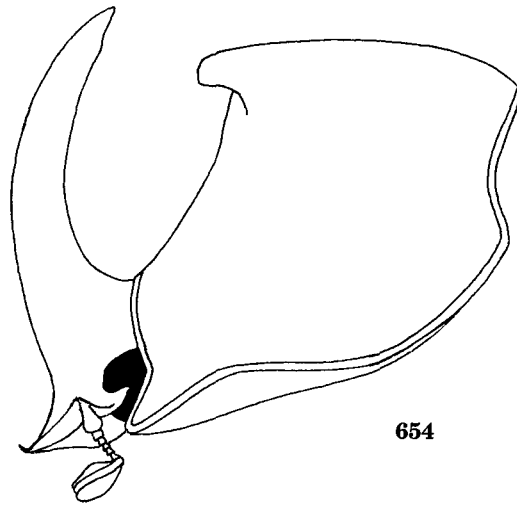
Fig. 651. *Megaceras septentrionis*.



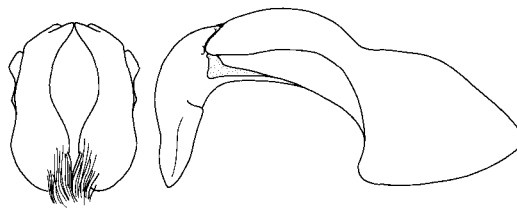
Fig. 652. *Megaceras septentrionis*. Photo by A. Solis (INBio).



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Figs. 653-656. *Megaceras septentrionis*: (653) head of male (dorsal view); (654) head of male (lateral view); (655-656) parameres.

Clypeus subtriangular, narrowed to apex, apex with 2 sharp teeth (Fig. 654); surface weakly rugose to rugopunctate. Interocular width equals 4.0 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. Mandibles with 2 large, subtriangular teeth, anterior tooth smaller. *Pronotum*: Majors with large, bulbous, broad, strongly bifurcate protuberance;

small horns at apex of protuberance slightly divergent to subparallel. Surface crazed, mostly sparsely punctate, punctures small. Lateral margin with broad band of large, widely spaced rugae, rugae connected to *areola apposita*. Anterior margin strongly, posteriorly emarginate. Sides strongly explanate. Base with marginal bead. Minors similar except protuberance and apical horns smaller

and surface with moderately dense, small punctures. *Elytra*: Surface crazed, sutural stria impressed, and with small, sparse punctures; center of disc with 2-3 vague, incomplete striae. *Pygidium*: Surface with sparse to moderate, small punctures. Base with broad band of large, setigerous punctures; setae long, reddish brown. In lateral view, surface weakly convex. *Legs*: Foretibia tridentate. Apex of posterior tibia strongly arcuate, with 2-8 small notches. First segment of posterior tarsus subtriangular, apex notched several times and slightly expanded on dorsal surface. *Venter*: Prosternal process moderate in length, compressed from front to back, apex

narrowly to broadly rounded. *Parameres*: Figs. 655-656.

Females. As males except in the following respects. *Head*: Frons with single, strong tubercle at middle. Surface of frons and clypeus coarsely rugose. *Pronotum*: Small tubercle present either side of middle just behind anterior margin. Surface crazed and with minute to small, sparse punctures in basal third; punctures becoming larger anteriorly so that in anterior third punctures large, deep, round to oval; lateral margin and anterior angle rugose. *Pygidium*: Surface with punctures a little larger. In lateral view, basal half weakly convex, apical half almost flat.

DISTRIBUTION. *Megaceras septentrionis* is known from Costa Rica, Panama, Ecuador, and Colombia (Dechambre 1975; Endrödi 1976b, 1985a). Though widely distributed in Costa Rica and Panama, it is not commonly encountered.

LOCALITY RECORDS (Figs. 657-658). 99 specimens examined.

COSTA RICA (46). **CARTAGO** (2): Moravia de Chirripó, Volcán Irazú; **GUANACASTE** (1): La Palma; **HEREDIA** (6): La Selva Biological Station, Río Frio; **LIMÓN** (1): Guapiles; **PUNTARENAS** (28): Buenos Aires, Estación Biológica Las Alturas, Estación Las Mellizas, Monteverde, San Vito; **SAN JOSÉ** (8): San José.



Fig. 657. Distribution of *Megaceras septentrionis* in Costa Rica.



Fig. 658. Distribution of *Megaceras septentrionis* in Panama.

PANAMA (53). **CHIRIQUI** (52): Bugaba, Hartmann's Finca (Santa Clara), Hato del Volcán, Lino, Volcán, Volcán (15 km NW); **PANAMA** (1): Cerro Campana.

TEMPORAL DISTRIBUTION. February (3), March (3), April (1), May (23), June (41), July (2), August (6), September (4), October (3), November (2), December (1).

DIAGNOSIS. *Megaceras septentrionis* is characterized by its narrowly bidentate clypeal apex and by the apical half of the pygidium with sparse, but distinct, punctures.

BIOLOGY. Adults are nocturnal, and most specimens in collections were taken at lights. They have been collected primarily from elevations ranging from 1,000-1,800 meters in primarily premontane wet forests. There is a distinct emergence at the onset of the rainy season. During one collecting event at Hartmann's coffee finca in Chiriqui, Panama in June 1986, there was a massive emergence of adults on one night, and on the next night (same place, same weather) there were no adults at all. This highlights the difficulties of sampling and knowing the faunal composition of many tropical areas because adult activity may be very brief and not coincidental with collecting activities, especially by visiting researchers. A given species may be abundant in space but rare in time, thus giving us a warped perspective of its true occurrence and distribution.

Podischnus Burmeister, 1847

Podischnus Burmeister 1847: 327.

There are three species in the genus *Podischnus* (Endrödi 1976b, 1985a). All three species occur in South America, and one of these, *P. agenor*, extends northward through Panama and Costa Rica to southern Mexico.

Species in the genus may be recognized by the relatively long, subparallel body form; the four teeth on the anterior tibia that project at nearly right angles (Fig. 659); bidentate mandibles; and a broadly emargin-

ate clypeus. Horn growth in the males is allometric so that both majors (with large horns) and minors (with small horns) can be found. Male minors tend to resemble females in many of their characters.

Like many other dynastines, adults of *Podischnus* species lay eggs in the ground where the larvae feed on humus and detritus. Adults probably feed on large-stemmed monocots. Adults are primarily nocturnal and are attracted to lights.

Podischnus agenor (Olivier, 1789)

(Figs. 45, 659-667)

Scarabaeus agenor Olivier 1789: 223.

Scarabaeus barbicornis Latreille 1812: 201 (synonym).

Podischnus propinquus Prell 1911a: 202 (synonym).

DESCRIPTION. Length 30.0-45.0 mm; width 16.0-20.6 mm. Color light to usually dark reddish brown.

Males. Head: Frons in majors nearly smooth, with a few long, reddish brown setae. Minors with frons longitudinally rugose either side of weak, median, longitudinal depression. Majors with long, recurved horn; horn acuminate at apex and slightly enlarged on posterior edge (Fig. 660). Male minors with small recurved horn. Clypeus with apex broadly emarginate. Interocular width equals 1.8 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. Mandibles broad, bidentate at apex. **Pronotum:** Surface in majors relatively smooth, with only sparse, minute punctures everywhere except along lateral margins where rugopunctate or with punctures large, often confluent. Disc with anterior 2/3 weakly concave, posterior third with short, broad horn; horn with apex broadly emarginate, venter concave and with dense, short, reddish brown setae (Fig. 660). Minors with anterior 1/3 to 1/2 of disc slightly concave, and with small carinate ridge at posterior edge of concave part of disc; dense, short reddish brown setae present on anterior, declivous portion

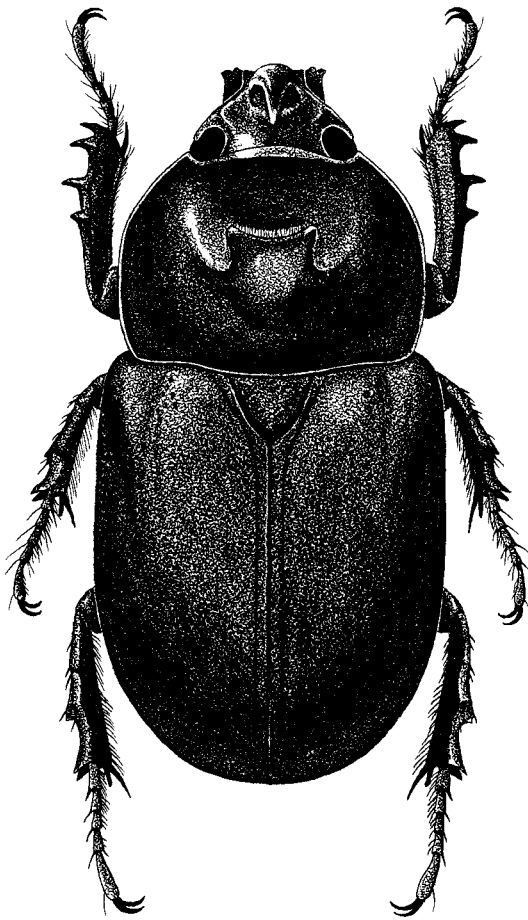
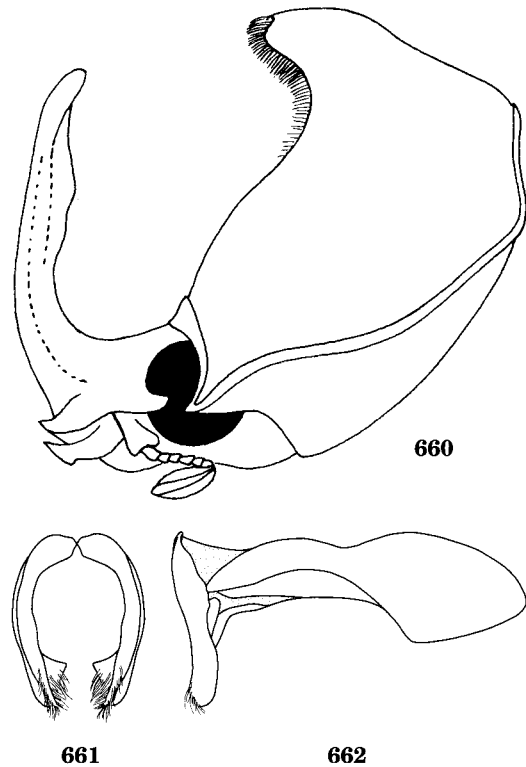


Fig. 659. *Podischnus agenor*.

of ridge; surface with moderate to large punctures surrounding discal convexity, larger punctures mostly U-shaped, many confluent. Base and sides with strong marginal bead. *Elytra*: Majors with surface extremely finely rugulose and with strongly impressed sutural stria. Median half of disc with small, moderately dense punctures. Lateral half of disc with incomplete rows of moderate to large, ocellate punctures. Sides with 4-6 incomplete rows of moderate to very large, deep punctures; punctures decreasing in size posteriorly. Minors similar except rows of discal punctures reduced to nearly absent and sides with only 2-3 short rows of moderate to large punctures. *Pygidium*: Surface in basal third finely rugulose, with small, moderately dense, transverse punctures; punctures becoming larger and sparser posteriorly and grading to



Figs. 660-662. *Podischnus agenor*. (660) male head (lateral view); (661-662) parameres.

transversely rugose. In lateral view, surface strongly convex in basal 2/3, nearly flat in apical third. *Legs*: Foretibia strongly quadridentate, teeth nearly perpendicular to shaft of tibia, distance between 2 apical teeth less than distance between other teeth. Posterior tibia with 2 strong teeth at apex, minors with smaller, accessory tooth. Posterior tarsus with apex of first tarsomere long, spine-like. *Venter*: Prosternal process long, with rounded apex, anterior surface flat. *Parameres*: Figs. 661-662.

Females. As males except in following respects. *Head*: Frons and clypeus coarsely rugose, frons with strong tubercle between eyes. *Pronotum*: Surface coarsely rugose in anterior half and at sides; elsewhere with small to moderate, sparse punctures. Armature absent. *Elytra*: Similar to those of male minors. *Pygidium*: Surface with minute, moderately dense setae. In lateral view, dorsal half weakly convex, apical half weakly concave.

DISTRIBUTION. *Podischnus agenor* occurs from Mexico to Colombia, Peru, and Ecuador (Endrödi 1976b, 1985a). It is widespread in the lowlands of Costa Rica and probably Panama as well, although there are fewer records for Panama.

LOCALITY RECORDS (Figs. 663-664). 137 specimens examined.

Costa Rica (110). ALAJUELA (1): 8 km W Atenas; CARTAGO (9): Grano de Oro, Moravia, Turrialba, Volcán Irazú; HEREDIA

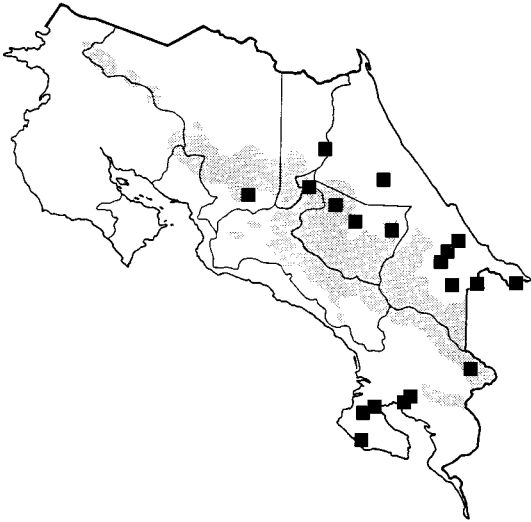


Fig. 663. Distribution of *Podischnus agenor* in Costa Rica.

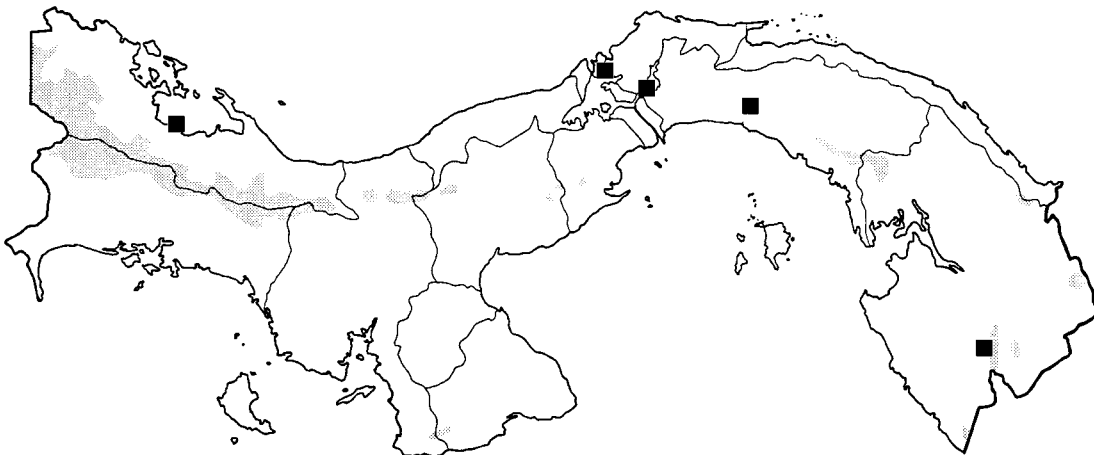


Fig. 664. Distribution of *Podischnus agenor* in Panama.

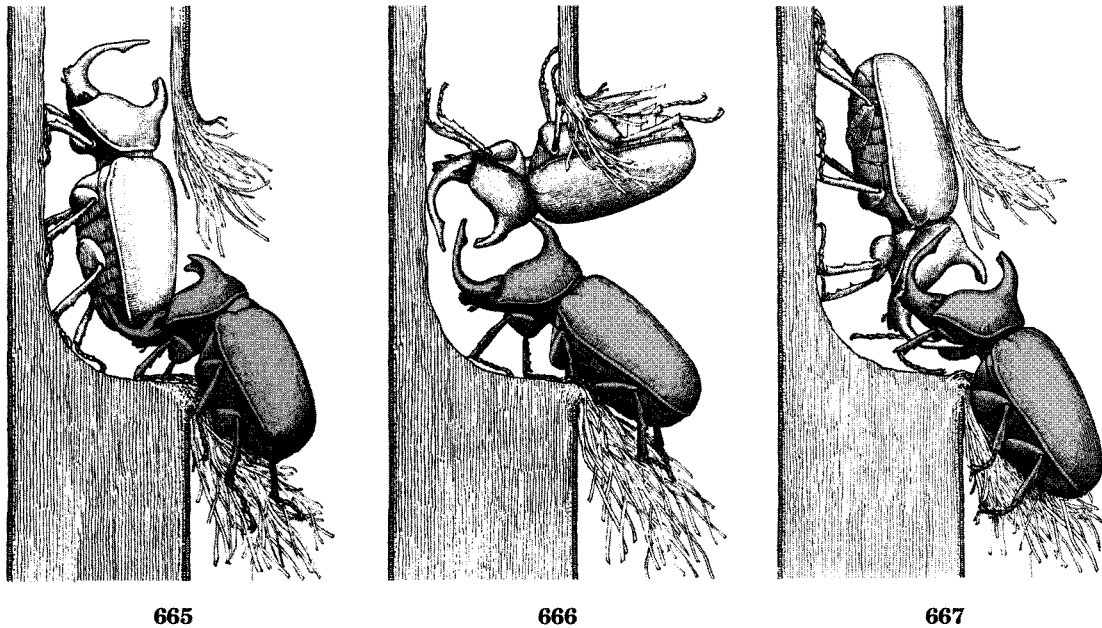
(8): Río Frio; LIMÓN (60): Amubri, Bratsi, Hamburg Farm, Pandora, Reserva Biológica Hitoy Cerere; PUNTARENAS (29): Estación Biológica Las Alturas, Estación Biológica Esquinas (Osa), Rancho Quemado (Osa), Rincon (2.5 mi. SW), Sirena (Parq. Nac. Corcovado); SAN JOSÉ (3): Estación Carrillo.

Panama (27). BOCAS DEL TORO (1): Miramar; CANAL ZONE (11): Madden Dam, Margarita; DARIEN (14): Cana Biological Station; PANAMA (1): Chepo (80 km E).

TEMPORAL DISTRIBUTION. January (1), February (3), March (5), April (6), May (11), June (33), July (19), August (19), September (13), October (13), November (9), December (4).

DIAGNOSIS. In addition to its large size and dark reddish brown color, *Podischnus agenor* is most easily recognized by its relatively long, subparallel body form in combination with the four teeth of the foretibia projecting at nearly right angles from the tibia. No other genus of New World oryctine has foretibial teeth with this angle of configuration.

BIOLOGY. This species is found throughout the year although the temporal distribution records suggest greater activity after the beginning of the rainy season in May and June. Adults are nocturnal in their activity. They



Figs. 665-667. *Podischnus agenor*: males fighting for possession of a burrow in a sugarcane stalk: (665) the resident male resists the attack of the invader by bracing itself against the walls at the entrance of the burrow. In response, the invader tries to insert its head horn under the resident to pry it out; (666) when the resident tries to turn and confront the invader head-to-head at the burrow entrance, the invader uses its thoracic horn to repeatedly push it back into the burrow; (667) the invader eventually allows the resident to turn around in the burrow entrance, and in the ensuing head-to-head confrontation each beetle tries to use its horns as pincers to clamp down on the other. In this last panel, the resident has succeeded in the maneuver and is about to lift the invader off the stalk and drop it to the ground. Used by permission from "Horned Beetles" by W. Eberhard. Copyright 1980 by *Scientific American, Inc.* All rights reserved.

have been reported as sometimes locally abundant in cane and corn fields (Ritcher 1958; Gaugliumi 1962; Eberhard 1979, 1980). According to Eberhard (1979), eggs are laid individually in the ground where the larvae feed on humus. Pupation occurs in the soil. Adults emerge principally during the rainy season and dig blind burrows in sugarcane stalks as well as in the ground. The particular method by which they excavate burrows was described by Eberhard (1980) in detail. He noted that males emitted a pheromone or pungent odor similar to that of musty apples, seemingly to attract a female. The odor could be detected by a human from a distance of 15 meters. When a female was attracted, mating sometimes occurred, and sometimes she was allowed to enter the burrow to feed. Males

were observed to fight for possession of a burrow (Figs. 665-667), but this was done in a sexual context in that the victorious male could then attract a female to the burrow. Eberhard (1979) surmised that thick-stemmed monocots are probably the original host for these beetles, and that wild monocots are much less common than today's fields of corn or sugarcane. That the males continue to compete for possession of burrows in a habitat consisting of huge fields of corn or cane is a non-adaptive anachronism remaining from previous evolutionary history.

This is primarily a lowland species that has been taken at elevations ranging from near sea level to 1,500 meters in areas of moist tropical forests, wet tropical forests, moist premontane forests, and wet premontane forests.

***Strategus* Kirby, 1828**

Strategus Kirby 1828: 349.

Strategodes Casey 1915: 245 (synonym, described as subgenus).

Anastrategus Casey 1915: 231 (synonym).

Strategopsis Chapin 1932: 302 (synonym, described as subgenus).

The genus *Strategus* contains 31 extant species and one fossil species (Ratcliffe 1976). Fourteen species are indigenous to the West Indies, five species occur in the United States, nine species in Mexico, five species in Central America, and nine species are found in South America reaching central Argentina. Three species are found in Costa Rica and Panama.

Strategus species may be distinguished from other species in other genera in the tribe Oryctini by the following combination of characters: mandibles exposed with apex bidentate and with a prominent basal lobe,

pronotum usually foveate and at least tuberculate subapically, foretibia quadridentate, and apex of posterior tibia with three teeth. Ratcliffe (1976) provided a complete revision of the genus, and Endrödi (1976b, 1985a) gave a synopsis. Morón and Ratcliffe (1990) presented a key to the larvae of seven species, including two of the three species that occur in Costa Rica and Panama.

Life history information for most *Strategus* species is lacking. Adults are nocturnal and attracted to lights. A few species have, historically, been minor pests of coconut and oil palms, especially in areas of new cultivation that had recently replaced natural forest habitat. The larvae live in the wood of rotting trees or possibly in concentrations of rich organic debris in the soil. *Strategus aloeus* is nearly ubiquitous in Costa Rica and Panama below 1,500 meters, and its immature stages and biology are fairly well known.

Key to the Species of Adult *Strategus* of Costa Rica and Panama

1. Metasternum completely, setigerously punctate. Clypeus with apex acutely pointed or narrowly rounded ***jugurtha* Burmeister**
- 1'. Metasternum with posterior half nearly impunctate, anterior half with setigerous punctures. Clypeus with apex broadly emarginate in males, subtruncate or rounded in females 2
2. Males with parameres subtriangular in caudal view, usually wider at base and tapering apically (Figs. 670-672). In females, elytra behind humerus without distinct rows of moderate to large, ocellate punctures ***aloeus* (L.)**
- 2'. Males with parameres horseshoe-shaped in caudal view (Figs. 675-676). In females, elytra behind humerus with 1-4 short rows of moderate to large, ocellate punctures ***hipposiderus* Ratcliffe**

Clave para las Especies de Adultos de *Strategus* de Costa Rica y Panamá

1. Metaesterno cubierto completamente de puntuaciones con setas. Clípeo con el ápice muy puntiagudo o redondeado agudamente ***jugurtha* Burmeister**
- 1'. Metaesterno con la mitad posterior casi sin puntuaciones, la mitad anterior con puntuaciones con setas. Clípeo con el ápice ampliamente emarginado en los machos, truncado o redondeado en las hembras 2
2. Machos con parámetros triangulares en vista caudal, generalmente más anchos en la base y puntiagudos en su ápice (Figs. 670-672). En las hembras, élitros detrás del húmero sin hileras evidentes de puntuaciones oclares moderadas a grandes ***aloeus* (L.)**
- 2'. Machos con parámetros en forma de cascos de caballo en vista caudal (Figs. 675-676). En las hembras, élitros detrás del húmero con 1 a 4 hileras cortas de puntuaciones oclares moderadas a grandes ***hipposiderus* Ratcliffe**

Key to the Species of Known Larval *Strategus* in Costa Rica and Panama
(After Morón and Ratcliffe 1990)

1. Dorsum of each mandible with 4-7 dorsomolar setae *aloeus* (L.)
1'. Dorsum of each mandible with 11-14 dorsomolar setae
. *jugurtha* Burmeister

Clave para las Especies de Larvas de *Strategus* de Costa Rica y Panamá
(Después de Morón y Ratcliffe, 1990)

1. Dorso de cada mandíbula con 4 a 7 setas dorsomolares *aloeus* (L.)
1'. Dorso de cada mandíbula con 11 a 14 setas dorsomolares
. *jugurtha* Burmeister

***Strategus aloeus* (Linnaeus, 1758)**
(Figs. 46, 668-674)

- Scarabaeus aloeus* Linnaeus 1758: 345.
Geotrupes semiramis Fabricius 1801: 12 (synonym).
Scarabaeus aesalus Laporte 1840: 112 (synonym).
Strategus julianus Burmeister 1847: 133 (synonym).
Strategus piosomus Kolbe 1906b: 24 (synonym).
Strategus roosevelti Casey 1915: 241 (synonym).
Strategus frontalis Casey 1915: 243 (synonym).
Strategus tarsalis Casey 1915: 243 (synonym).
Strategus gaillardii Casey 1915: 244 (synonym).

DESCRIPTION. Length 31.0-60.9 mm; width 13.8-30.0 mm. Color reddish brown to black.

Males. Head. Frons densely punctate to rugose behind tubercles; punctures large, usually confluent; medially, frons varies from impunctate to variably punctate (punctures small to large) to rugose; setigerous above eye in unworn specimens. Tubercles conical, transverse, low to moderate, distinctly separated to distinctly but weakly joined by low, transverse carina. Clypeus with surface crazed, densely punctate (punctures moderate in size) to rugopunctate to rugose; apex

subtruncate and feebly to moderately broadly emarginate, rarely with small triangular notch at base of emargination; apex moderately to strongly reflexed. Interocular width equals 2.0-2.66 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. Mandibles with basal lobe small, rounded to prominently rounded; middle lobe subtriangular, large to very large, with apex broadly rounded; apical lobe small, rounded to subtriangular. *Pronotum*: Surface with posterior half crazed, sparsely punctate, punctures small, occasionally with minute, sparse secondary punctures. Surface on sides crazed, a little more densely punctate; punctures small to large; lateral margin frequently with a moderately wide rugopunctate to rugose band. Anterior 1/3 to 1/2 rugose. Fovea deep, divided longitudinally down middle by a broad, low, rounded carina extending posteriorly from base of anterior horn; anterior angles and fovea either side of median ridge feebly to strongly rugopunctate to rugose, rarely without sculpturing. Majors (Fig. 669) with anterior horn moderate in length, stout, attenuate, curving forward and upward; apex subtruncate to emarginate; emargination feeble and shallow to distinct and V-shaped. Posterior horns short to moderately long, strongly laterally compressed, variably attenuate, apex acutely rounded to broadly and obliquely truncate with 1-3 weak lobes; in lateral view horns project forward and upward at about 25-65° from plane of disc; in dorsal view horns subparallel to curving slightly to

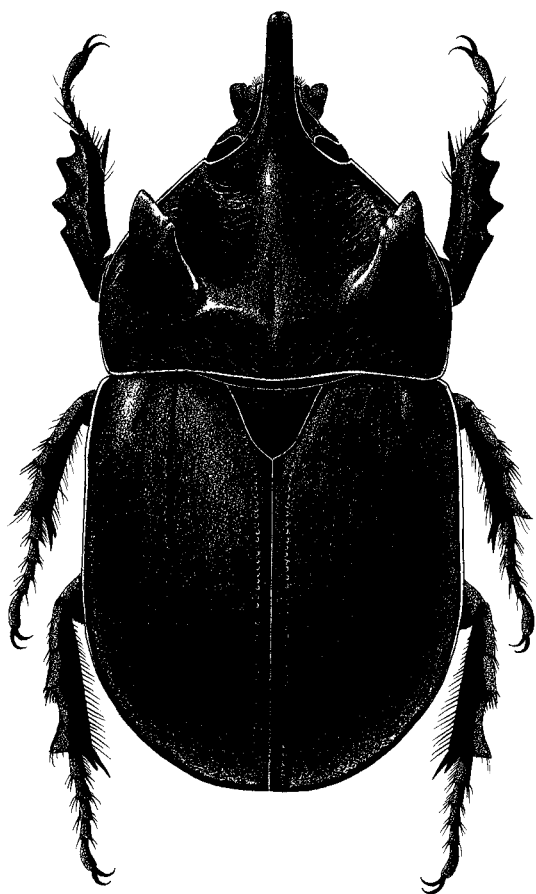
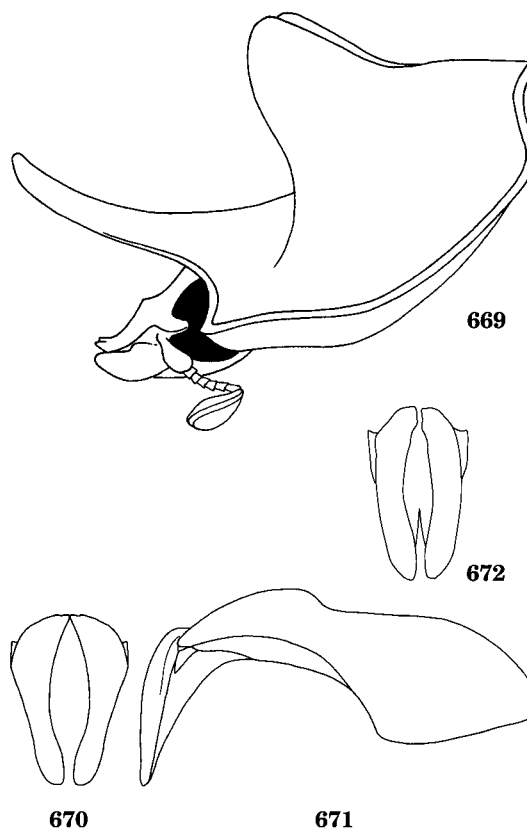


Fig. 668. *Strategus aloeus*.



Figs. 669-672. *Strategus aloeus*: (669) male major, head and pronotum; (670-671) parameres typical of Central American population; (672) parameres typical of South American population but also found in Panama.

ward one another, bases joined across disc in an arc. Minors with anterior horn similar except short in length, apex truncate, dorsal surface rounded; posterior horns reduced to short, rounded, laterally compressed horns or low, rounded bosses. Base with a wide to very wide rugose band, band reduced at middle almost to basal bead. *Elytra*: Sutural stria strongly impressed, weakly to strongly crenulate. Disc crazed, sparsely punctate; punctures small (rarely moderate in size), occasionally weakly ocellate-umbilicate; 1-3 feebly impressed, incomplete striae on lateral half of disc. Sides crazed, wrinkled behind humerus, sparsely punctate, punctures small to moderate. *Pygidium*: Surface with disc sparsely punctate; punctures minute. Weakly convex in lateral view. *Legs*: Foretibia quadridentate, teeth subequally spaced. Apex

of posterior femur with 3 teeth, median tooth smaller. Basal tarsomere of posterior tarsus with apex slightly attenuated into acute angle. *Venter*: Metasternum with anterior half setigerously punctate, posterior half nearly impunctate. Prosternal process long, transversely oval in cross section, apex rounded. *Parameres*: Figs. 670-672. Central American specimens typically have the parameres sublender, attenuate apically, and widest just before the middle (Fig. 670). South American specimens are occasionally similar but usually have the parameres robust and only slightly attenuate apically (Fig. 672). In Panama, both of these morphotypes are found.

Females. As males except in the following respects. *Head*: Frons punctate (punctures

small to large mixed) to rugopunctate to rugose. Clypeus with apex narrowly to broadly subtruncate or rounded, feebly to moderately reflexed; surface rugose. Mandibles similar to those of male but smaller, especially middle lobe. *Pronotum*: Sides rugopunctate to rugose. Anterior half rugose. Fovea moderately deep. Tubercle conical, moderate to large, transverse, apex usually feebly emarginate (rounded in worn individuals). *Elytra*: Sides occasionally with sparse, feeble, ocellate-

umbilicate punctures. *Pygidium*: Disc usually sparsely to moderately punctate, punctures small to moderate, punctuation occasionally reduced; apical margin with broad rugopunctate to rugose band; apex with a few setigerous punctures. Occasionally, discal punctures moderately large and confluent, apical 1/3 to 1/2 completely, densely, setigerously punctate. In lateral view basal half convex, apical half concave.

DISTRIBUTION. *Strategus aloeus* is the most widely distributed species in the genus. It occurs from the southern United States through Central America to central Brazil and Bolivia (Ratcliffe 1976). This species is found commonly throughout Costa Rica and Panama.

LOCALITY RECORDS (Figs. 673-674). 477 specimens examined.

COSTA RICA (319). **ALAJUELA** (20): Alajuela, Atenas, Caño Negro, 2 km SW Dos Ríos, Río San Lorencito; **CARTAGO** (10): Embalse El Llano, Grano de Oro (Chirripó), Irazú, Rancho Redondo, Tres Ríos, Turrialba; **GUANACASTE** (102): Canas, Canas (6 mi. S, 6 mi. W), Cerro El Hacha (12 km SE La Cruz), Estación Pitilla, Estación Lomas Barbudal, Estación Maritza (Volcán Orosi), Estación Murciélago, Estación Santa Rosa, La Pacífica, Finca Jimenez (near Taboga), Finca Montezuma,

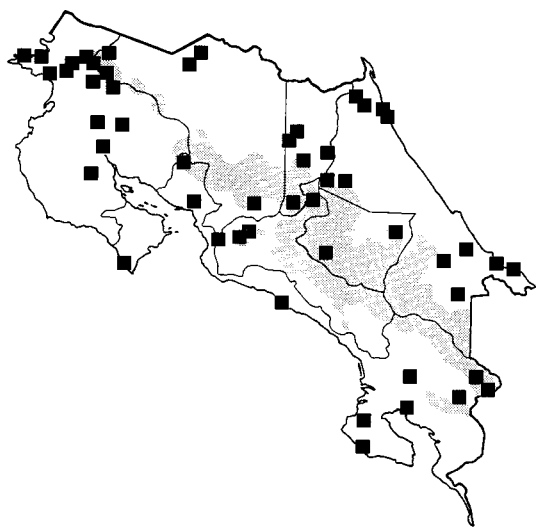


Fig. 673. Distribution of *Strategus aloeus* in Costa Rica.

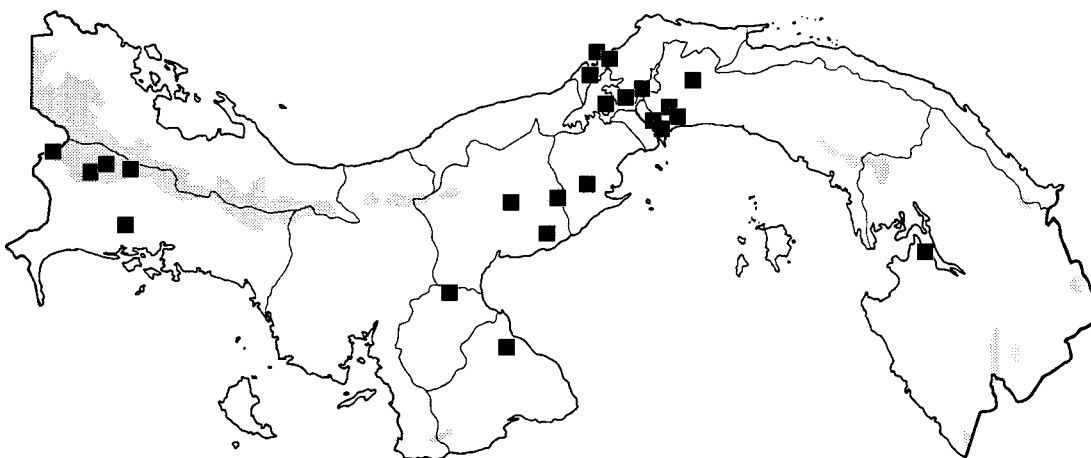


Fig. 674. Distribution of *Strategus aloeus* in Panama.

Liberia, 3 km NW Nacaome (Parq. Nac. Barra Honda), Palo Verde, Parq. Nac. Guanacaste, Par. Nac. Rincón de la Vieja, Playa Blanca (Parq. Nac. Guanacaste), Volcán Tenorio; HEREDIA (17): Estación El Ceibo (Parq. Nac. Braulio Carrillo), La Virgen de Sarapiquí, Pueblo Nuevo (Sarapiquí), Puerto Viejo de Sarapiquí, Río Frio, San Rafael; LIMÓN (29): Amubri, Cerro Tortuguero, Cuatro Esquinas (Parq. Nac. Tortuguero), Estación Hitoy Cerere; Guapiles, Hamburg Farm, Las Mercedes, Manzanillo, Pandora, Puerto Limón, Río Sardinias, Sector Cerro Cocori; PUNTARENAS (109): Barranca, Esquinas near Golfito, Estación Esquinas (Osa), Estación La Casona (Res. Biol. Monteverde), Estación Las Mellizas (Parq. Nac. Amistad), Estación Quebrada Bonita (Res. Biol. Carara), Estación Biol. Las Alturas, Monteverde, Refugio Nacional Cabo Blanco, Quepos, Rancho Quemado (Osa), Rincon, San Luis (Res. Biol. Monteverde), San Vito, Sirena (Parq. Nac. Corcovado), Vuelta Campana; SAN JOSÉ (33): Estación Zurqui (Parq. Nac. Braulio Carrillo), Parq. Nac. Braulio Carrillo, San José, San Pedro.

PANAMA (157). **CANAL ZONE** (75): Ancon, Balboa, Barro Colorado Island, Coco Solo, Ft. Clayton, Gamboa, Gatun, Madden Dam, Margarita; **CHIRIQUI** (31): Boquete, Cerro Punta, David, El Volcán, Santa Clara; **COCLÉ** (5): Cerro Gaital, El Valle, Penonome, 3 mi. E Río Hato; **COLÓN** (7): Coconut Point, Sabanitas (2 km S); **DARIEN** (1): Darien; **HERRERA** (1): Santa Maria; **LOS SANTOS** (2): Sabana; **PANAMA** (35): Cerro Azul, Cerro Campana, Cerro Jefé, El Llano-Carti Road (km 9), Las Cumbres, Panama City.

TEMPORAL DISTRIBUTION. January (46), February (33), March (27), April (29), May (96), June (79), July (19), August (22), September (33), October (16), November (21), December (38).

DIAGNOSIS. *Strategus aloeus* is the most widespread, abundant, and morphologically variable species in the genus. Nevertheless, males can be separated from all other species by the characteristic shape of the parameres.

They could be confused with other species, like *S. hipposiderus*, if external features only are used in identification. The characters listed in the key will serve to separate females from the other two species of *Strategus* occurring in Costa Rica and Panama.

A cline in character states is seen in a north-south direction. Southern specimens are usually progressively larger, darker, with a deeper clypeal excision, stouter genitalia in the males (Fig. 672), and with increased pygidial hairiness in the females. The clinal variation is gradual and not stepped, thus eliminating the possibility of subspecies designations. It should be noted that "northern-like" individuals (smaller in size, lighter in color) occur occasionally in South America, and "southern-like" specimens (larger in size, darker in color) occur occasionally in Central America and Mexico. The Isthmus of Panama appears to be a locale by which to separate the northern and southern populations, but it is by no means a barrier, and mixing between the two populations probably occurs freely. Hence, in Panama, one can find morphs of both the northern and southern populations.

BIOLOGY. Dugès (1876, 1886) was the first to describe the larva and pupa of *S. aloeus*, and Ritcher (1944, 1966) provided the most recent and accurate description of the larva. Eggs are usually deposited in dead or rotten wood where the larvae develop. Larvae have been found under old logs and boards in Louisiana (Schufeldt 1884), in a rotten ash tree (*Fraxinus* sp.) in Texas (Ritcher 1966), from the trunk of a live oak tree (*Quercus* sp.) in Mexico (Dugès 1876, 1886), and in sawdust piles at sawmills and beneath the trunks of felled coconut palms (*Cocos nucifera* L.) and *Erythrina glauca* Willd. in Surinam (Van Dinther 1956). Bodkin (1919) reported small clusters of larvae in decaying stumps in Guyana, and I have found numerous larvae in a rotten log while collecting in Peru. Van Dinther (1956) also observed in Surinam that larvae were never detected near the roots or stem of a living coconut palm, whereas, on the other hand, Costa Lima (1953) noted that in Brazil larvae attack the roots and lower part of the stipe of new palms. Larvae have also

been taken from mango roots (*Mangifera indica* L.) (Bodkin 1919). Under most circumstances larvae probably feed exclusively on decayed wood although they will apparently also feed on root material. Pupation occurs in the food substrate where an oval pupal chamber is formed.

Hurpin and Mariau (1966) conducted laboratory rearing experiments using 219 larvae and 281 adults from Colombia. The larvae were fed on a mixture of poplar wood and dried cow manure while the adults were maintained best on banana and orange. In the laboratory adult males lived up to five months and adult females up to six months. The maximum number of eggs laid by a single female was 42; eggs were deposited over a period of 1-3 months with several eggs laid weekly. Duration (maximum?) of each stage was as follows: egg, three weeks; first instar, two weeks; second instar, three weeks; third instar, seven months; pre-pupa, two weeks; pupa, six weeks; adult, six months. This provided a total life span of 17 months. Other lengths reported for pupation are 31 days (Van Dinther 1956) and 43 days (Dugès 1886). Adults can usually be found year-round where the climate permits.

Adults have been found in the detritus refuse piles of the leafcutter ant, *Atta mexicana* (Smith) in Mexico (Deloya 1988). Adult beetles have been found feeding on roots of date palms (*Phoenix dactylifera* L.) in Arizona (Cockerell 1906); wax palms (prob. *Copernicia cerifera* Mart.) in Brazil (Goncalves 1946); young oil palms (*Elaeis guineensis* Jacq.) in Colombia (Vayssiere 1965); *Furcraea cabuya* Trel. and the leaves of *Agave picta* Salm-Dyck in Costa Rica (Nevermann 1933); and coconut palms (*Cocos nucifera* L.) in Guyana (Bodkin 1919), Surinam (Van Dinther 1956), Mexico (Kolbe, 1906b), and Venezuela and Brazil (Lever 1969). Label data indicated feeding on oil palms in Colombia and Ecuador, coconut palms in Costa Rica and Venezuela, sugar cane in Colombia, and in rotten wood in Texas, Mexico, and Peru.

In Van Dinther's (1956) study, feeding damage was restricted to young coconut palms up to four years of age. Reasons were

not given as to why older palms were not attacked. Adult beetles burrowed down as far as 40 cm near the base of the palm to a position under the stem base. Tunneling then proceeded upward into the heart of the wood where a 3-5 cm wide shaft was formed. Trees so attacked wilted and eventually died. Usually one beetle was found per tree, but as many as four of both sexes have been found in a single palm. However, *S. aloeus* is rarely of economic significance to palm plantations.

These large beetles apparently have few natural enemies. The larvae have occasionally been eaten by aboriginal indians in Guyana (Bodkin 1919) and undoubtedly in other tropical regions as well. The larvae are also a common intermediate host for *Macracanthorhynchus hirudinaceus* (Pallas) (Archiacanthocephala: Oligacanthorhynchidae) in Brazil (Costa Lima 1953) and possibly in Louisiana (Manter 1928). The larval host dies after several weeks of infection by these parasites. Adults have been observed trapped in large spider webs in Venezuela on two occasions (Beebe 1944), and all stages in the life cycle are probably susceptible to various fungi and bacteria.

They occur in a variety of habitats including tropical dry forests, tropical moist forests, tropical wet forests, premontane moist forests, premontane wet forests, premontane rain forests, and montane rain forests. Specimens have been taken at elevations ranging from near sea level to 1,600 meters.

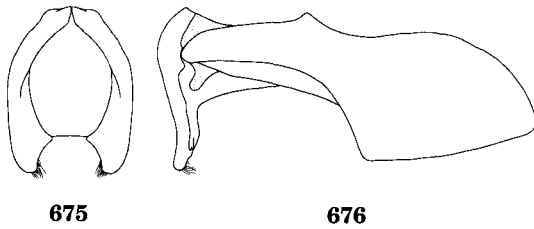
***Strategus hipposiderus* Ratcliffe, 1976**

(Figs. 675-678)

Strategus hipposiderus Ratcliffe 1976: 127.

DESCRIPTION. Length 48.0-54.0 mm; width 22.2-26.4 mm. Color dark reddish brown, almost black.

Males. Head: Frons rugose. Clypeus with surface crazed, moderately punctate, punctures small; tubercles conical, strong, widely separated; apex broadly truncate, shallowly emarginate, moderately reflexed. Interocular



Figs. 675-676. *Strategus hipposiderus* parameres.

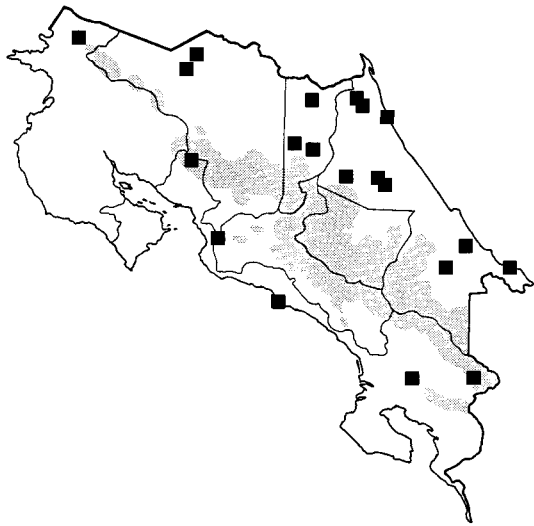


Fig. 677. Distribution of *Strategus hipposiderus* in Costa Rica.

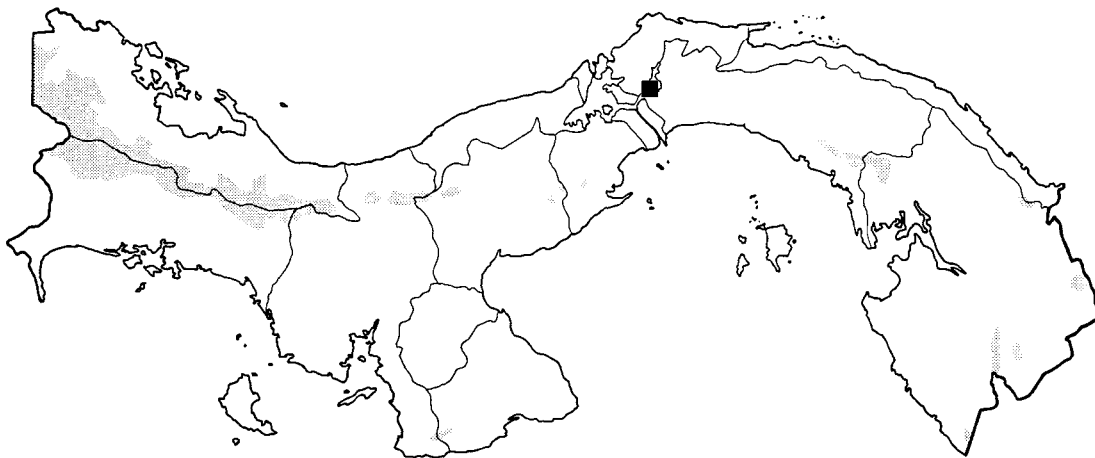


Fig. 678. Distribution of *Strategus hipposiderus* in Panama.

width equals 2.5 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. Mandibles with basal lobe small, prominently rounded; middle lobe large, triangular, apex rounded; apical lobe similar to basal lobe. *Pronotum*: Surface with disc crazed, sparsely punctate, punctures small; sides similar except a small patch of rugosity at base of posterior horns; anterior half (including fovea) rugose. Fovea transverse, deep. Base with wide, rugose band, band constricted almost to basal bead at middle. Majors with anterior horn short, stout, attenuate, curving forward and upward, apex narrowly rounded. Posterior horns short, laterally compressed, subtriangular bosses. Minors with horns reduced to tubercles. *Elytra*: Sutural stria strongly impressed, crenulate. Discal region sparsely punctate, punctures small and minute mixed; lateral half of disc with 2-3 shallow, incomplete striae. Several large punctures just mesad of humerus at extreme base. Sides similar except wrinkled, striae absent except for 2 weak rows of moderate to large, ocellate punctures behind humerus, rows sometimes absent. *Pygidium*: Surface crazed, sparsely to moderately punctate, punctures small. Apical margin either side of midline with narrow, weak, rugose band. In lateral view, basal half

convex, apical half nearly flat. *Legs*: Foretibia quadridentate, teeth subequally spaced from one another. Posterior tibia with apex usually strongly tridentate; smaller, median tooth sometimes reduced. First tarsomere of posterior tarsus with apex spine-like. *Venter*: Metasternum with anterior half setigerously punctate, posterior half impunctate. Prosternal process long, spherical in cross section, apex rounded. *Parameres*: Figs. 675-676.

Females. As males except in the following respects. *Head*: Frons rugose to rugopunctate. Tubercles transverse. Clypeus with apex subacutely rounded to narrowly subtruncate, occasionally weakly emarginate. Interocular width equals 2.0-2.2 transverse eye diameters. *Pronotum*: Disc sparsely to moderately densely punctate. Anterior half and sides rugose. Subapical tubercle strong, conical, transverse. *Pygidium*: Disc densely punctate (punctures moderate to moderately large, round to oblong) to rugopunctate to rugose. Apical margin either side of middle rugose, sparsely to moderately setigerous. In lateral view, basal half convex, apical half concave.

DISTRIBUTION. *Strategus hipposiderus* is found from southern Mexico to Colombia (Ratcliffe 1976). It is widely distributed to Costa Rica, primarily in the lowlands, and probably in Panama as well although Panamanian records remain few.

LOCALITY RECORDS (Figs. 677-678). 58 specimens examined.

COSTA RICA (56). ALAJUELA (6): Caño Negro; GUANACASTE (7): Estación Pitilla (Parq. Nac. Guanacaste); HEREDIA (7): Estación Magsasay (Parq. Nac. Braulio Carrillo), La Selva Biological Station, Los Arbolitos; LIMÓN (24): Guapiles, Hamburg Farm, Las Mercedes, Manzanillo, Pandora, Parq. Nac. Tortuguero, Refugio Nacional Río Barra del Colorado, Reserva Biológica Hitoy Cerere, Sector Cerro Cocori; PUNTARENAS (12): Estación Biológica Las Alturas (Coto Brus), Parq. Nac. Manuel Antonio, Reserva Biológica Carara, San Luis (Res. Biol. Monteverde), Vuelta Campana.

PANAMA (2). CANAL ZONE (2): Madden Dam.

TEMPORAL DISTRIBUTION. January (2), February (2), March (6), April (2), May (9), June (4), July (6), August (4), September (4), October (6), November (4), December (6).

DIAGNOSIS. The males of *S. hipposiderus* and the larger, darker forms of *S. aloeus* are virtually identical externally, and examination of the parameres is necessary to separate them. Fortunately, the parameres are very different (Figs. 677-678, 670-672). The presence of 1-4 short rows of large, ocellate punctures behind the humerus will often distinguish *S. hipposiderus* from *S. aloeus*, which does not have distinct rows of large punctures.

BIOLOGY. Label data indicates that adults have been taken at lights and in the trunks of the coconut palm (*Cocos nucifera* L.). They have been collected at elevations from near sea level to 1,500 meters although most specimens were taken below 1,000 meters. They are found in tropical moist forests and premontane wet forests.

***Strategus jugurtha* Burmeister,
1847**
(Figs. 679-684)

Strategus jugurtha Burmeister 1847: 131.

DESCRIPTION. Length 24.5-39.8 mm; width 12.2-18.5 mm. Color castaneous to piceous.

Males. *Head*: Frons behind tubercles strongly rugose in majors, less so to feebly rugose in minors; middle of frons nearly impunctate; setigerous above eye. Clypeus with apex acutely pointed to acutely rounded, occasionally produced into an acute or rectangular tooth, moderately reflexed; surface crazed, weakly rugopunctate to sparsely punctate; punctures small to moderate, shallow. Tubercles conical, moderately strong, usually distinctly separated. Interocular width equals 2.0-2.66 transverse eye diameters. Antenna

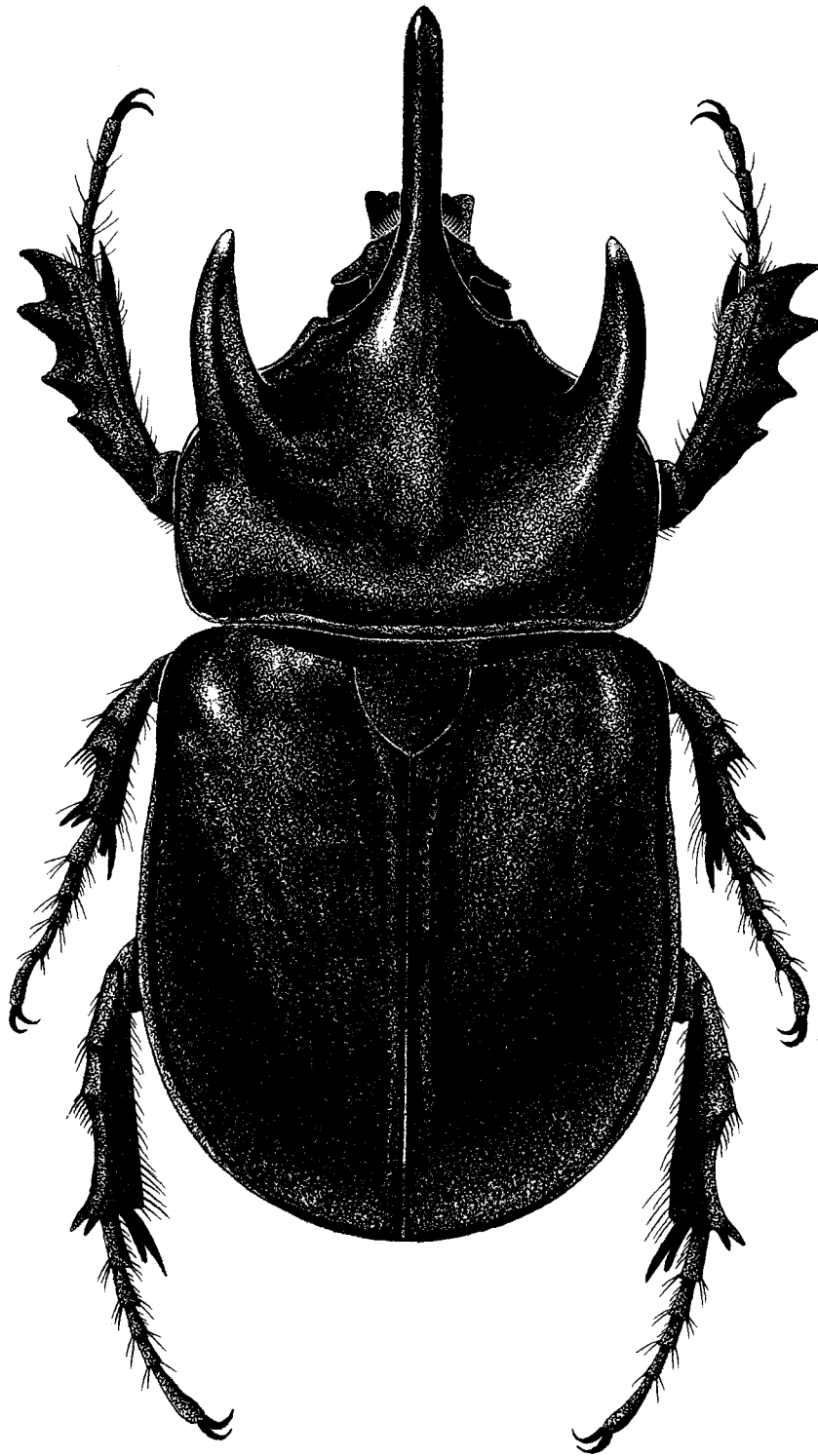
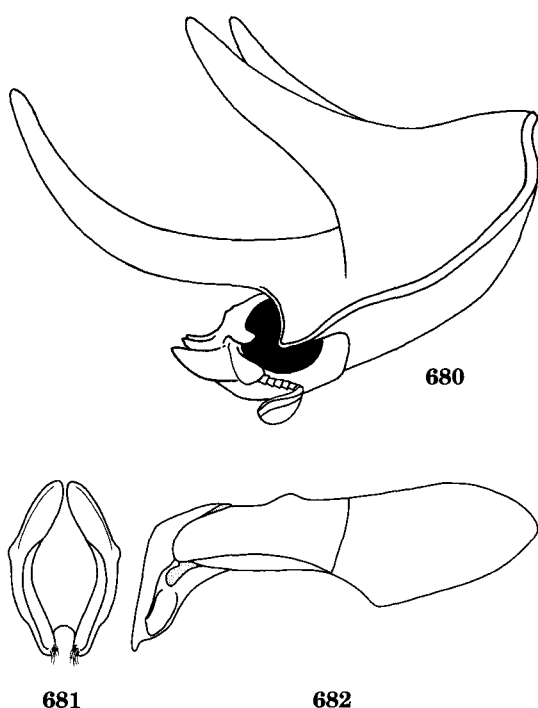


Fig. 679. *Strategus jugurtha*.



Figs. 680-682. *Strategus jugurtha*: (680) male major, head and pronotum; (681-682) parameres.

with 10 segments, club subequal in length to segments 2-7. Mandibles with basal lobe small, prominently rounded; middle lobe moderately large, triangular, apex rounded; apical lobe very small, triangular. *Pronotum*: Base with a narrow to obsolete rugopunctate to rugose band; band reduced to basal bead medially. Disc crazed, sparsely punctate; punctures small, rarely with a few large punctures on midline. Sides as disc to punctures slightly larger, lateral margin frequently with rugopunctate to rugose band in basal half; minors rugose in anterior half and with slightly depressed, rounded patch of rugosity posterolateral of fovea. Anterior half usually rugose in minors. Fovea deep, median longitudinal ridge from base of anterior horn low and broadly rounded, not prominent. Majors (Figs. 680) with anterior horn long, slender, attenuate, curving forward and upward, apex narrowly rounded; dorsal surface rounded to nearly flat, when flat weakly and longitudi-

nally carinate on lateral margins and occasionally on midline. Posterior horns long, slender (slightly more robust than anterior horn), attenuate, laterally compressed, apex narrowly rounded, extending forward and upward at about 20-65° from plane of disc. In dorsal view horns subparallel to curved toward one another, bases joined across disc in weak arc in all but largest specimens, and then arc very indistinct. Minors with anterior horn as in major except short, dorsal surface rounded. Posterior horns reduced to low pyramidal bosses; in dorsal view bosses laterally compressed, bases joined across disc in arc. Base with marginal bead. *Elytra*: Sutural stria impressed, crenulate. Disc crazed, sparsely punctate, punctures small to minute, shallow, some occasionally raised; 1-3 feebly impressed striae on lateral half present or not. Sides as disc except striae absent, punctures slightly larger to moderate on lateral margin; 2 (rarely 3) short rows of large punctures behind humerus; punctures usually ocellate, simple to umbilicate. Apex sparsely to moderately punctate, punctures small to moderate, setigerous. *Pygidium*: Disc finely subgranulate, crazed, sparsely punctate; punctures minute or minute and moderate mixed, shallow. Apical margin either side of middle with punctures slightly larger or weakly rugulose in a narrow band, not setigerous. Convex in lateral view, apical half often nearly flat. *Parameres*: Figs. 681-682.

Females. As male except in the following respects. *Head*: Frons entirely rugose. Clypeus with apex acutely rounded, more broadly so in worn specimens; surface weakly to strongly rugose. Tubercles transverse, frequently connected by feeble, transverse carina. Mandibles similar to those of male except middle lobe slightly smaller, apical lobe frequently a little larger. *Pronotum*: Base usually with a narrow rugose band; band reduced to basal bead at middle. Sides with a slightly depressed, rounded patch of rugosity posterolateral of fovea. Anterior half rugose. *Pygidium*: Disc virtually impunctate to moderately punctate; punctures small to moderate, setigerous in unworn specimens. Lateral emargination very shallow to obsolete, occasionally weakly

rugose. In lateral view basal half convex, apical half weakly concave to nearly flat. *Legs*: Foretibia quadridentate, teeth equidistant from one another. Apex of posterior femur with 3 teeth, median tooth small. Basal tarsomere of posterior tarsus with spine-like apex. *Venter*: Metasternum completely, setigerously punctate. Prosternal process long, spherical in cross section, apex rounded.

DISTRIBUTION. *Strategus jugurtha* occurs from Mexico through Central America to Colombia west of the Cordillera Oriental and Peru (Ratcliffe 1976). This species is broadly distributed throughout Costa Rica and Panama.

LOCALITY RECORDS (Figs. 683-684). 122 specimens examined.

COSTA RICA (50). ALAJUELA (2): 7 km W Atenas, Estación San Ramon; GUANACASTE (24): Bahía Santa Elena (Parq. Nac. Guanacaste), Estación La Casona (Res. Biol. Monteverde), Estación Maritza, Estación Murciélago, Estación Pitilla, Estación Santa Rosa, Finca Jenny (Parq. Nac. Guanacaste), Finca Jimenez (near Taboga), Finca Montezuma (Tenorio), Parq. Nac. Barra Honda, Tierras Morenas (Tenorio); HEREDIA (1): Estación Magsasay; LIMÓN (9): Guápiles, Las Mercedes, Reventazon, Siguirres; PUNTARENAS (14): Estación Sirena (Parq. Nac. Corcovado), Fila Guerra (Osa), Monteverde, Rancho Quemado (Osa), San Luis (Res. Biol. Monteverde).

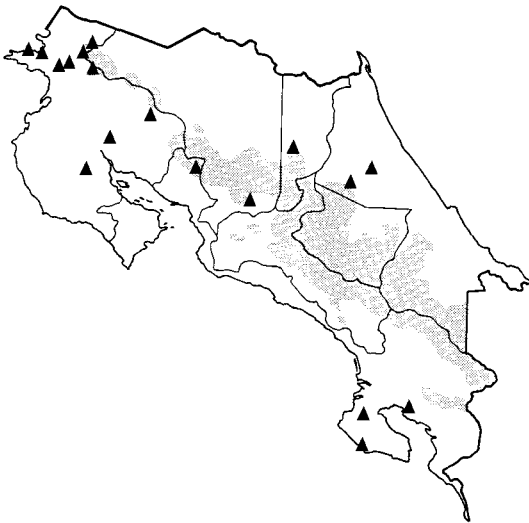


Fig. 683. Distribution of *Strategus jugurtha* in Costa Rica.



Fig. 684. Distribution of *Strategus jugurtha* in Panama.

PANAMA (72). CANAL ZONE (47): Barro Colorado Island, Corozal, Cristobal, Las Cascadas, Madden Dam; CHIRIQUI (1): Finca Suiza nr. Hornito; COCLÉ (1): Chilibre; DARIEN (18): Cana (ANCON Station), Santa Fé; PANAMA (4): Cerro Campana, El Llano-Carti Road (km 9), Las Cumbres, Panama City; VERAGUAS (1): Santiago.

TEMPORAL DISTRIBUTION. January (4), February (3), March (3), April (7), May (39), June (43), July (6), August (1), September (1), October (2), November (1).

DIAGNOSIS. *Strategus jugurtha* is easily distinguished among the Central American species because it is the only one with a completely, setigerously punctate metasternum. It is also the smallest and most gracile of the three species in Costa Rica and Panama.

BIOLOGY. There is a distinct emergence in May at the onset of the rainy season. Label data indicate that adults have been widely taken at lights, from agave in Colombia, pineapple in Costa Rica, and attacking the roots of African oil palm (*Elaeis guineensis* Jacq.) in Nicaragua. Lamb (1974) reported that *S. jugurtha* attacks pineapple stems in Central and South America. The larval stage was described by Morón and Ratcliffe (1990). This species has been taken from tropical dry forests, premontane moist forests, and tropical wet forests and at elevations ranging from near sea level to 1,520 meters (although most have been taken from 1,000 meters or less).

Xyloryctes Hope, 1837

Xyloryctes Hope 1837: 90.

The genus *Xyloryctes* has ten species (Endrödi 1976b, 1985a; Delgado and Najera-Rincon 1992). They are found from southeastern Canada south to Panama, with most of the species occurring in Mexico and Guatemala. In Costa Rica and Panama there are two, possibly three, species (see *X. teuthras* distribution). Blackwelder (1944) listed *X. corniger* Sturm (a *nomen nudum* of *X. corniger* Bates from Mexico and Guatemala) for Panama, but *X. corniger* Bates does not occur there.

Species of *Xyloryctes* are recognized by the presence of tridentate foretibiae, a bilobed and strongly reflexed clypeal apex, mandibles completely hidden by the clypeus, males with a frontal horn and females with a single tubercle, and a large pronotal cavity in the males and a convex pronotum in the females. Endrödi (1976) provided the most recent synopsis of the genus.

Biological information and the larvae are known for *X. jamaicensis* (Drury) from the United States (Ritcher 1966; Stephan 1967; Ratcliffe 1991) and *X. thestalus* Bates from Mexico (Morón 1976), but similar information is lacking for the Central American species. Unlike the common *X. jamaicensis*, the Costa Rican and Panamanian species are all relatively uncommon and are restricted to forests above 1,000 meters in elevation.

Key to the Species of Adult *Xyloryctes* of Costa Rica and Panama

1. Elytra with 5-6 distinct rows of punctures between suture and humerus, sides with 3-4 rows (rows on disc often reduced in females but rows on sides remain distinct) *lobicollis* Bates
- 1'. Elytra mostly smooth, at most with vague furrow 2
2. Apex of posterior tibia with 2 broad (narrow in females) lobes. Pygidium completely rugulose-punctate in males, moderately punctate in females *splendidus* Prell
- 2'. Apex of posterior tibia with 3 broad (narrow in females) lobes. Pygidium sparsely to moderately punctate *teuthras* Bates

Clave para las Especies de Adultos de *Xyloryctes* de Costa Rica y Panamá

1. Elitros con 4 ó 6 hileras evidentes de puntuaciones entre la sutura y el húmero, lados con 3 ó 4 hileras (hileras en el disco frecuentemente reducidos en las hembras, pero las hileras a los lados permanecen visibles) *lobicollis* Bates
- 1'. Elitros mayormente lisos, a lo más con un surco vago 2
2. Apice de la tibia posterior con 2 lóbulos amplios (angostos en las hembras). Pigidio completamente cubierto de puntuaciones rugosas en los machos, moderadamente cubierto de puntuaciones en las hembras *splendidus* Prell
- 2'. Apice de la tibia posterior con 3 lóbulos amplios (angostos en las hembras). Pigidio dispersa a moderadamente cubierto de puntuaciones *teuthras* Bates

Xyloryctes lobicollis Bates, 1888 (Figs. 685-689)

Xyloryctes lobicollis Bates 1888: 323.

DESCRIPTION. Length 24.0-31.5 mm; width 13.8-16.0 mm. Color dark reddish brown, nearly black.

Males. Head: Frons with elongate, subtriangular, slightly recurved horn, horn extending to just above level of surface of pronotum in majors, shorter in minors. Surface of frons and clypeus densely punctate to rugopunctate, punctures moderately large. Clypeus with apex broadly, moderately to deeply emarginate, strongly reflexed. Interocular width equals 3.0 transverse eye diameters. Antenna with 10 segments, club a little longer than segments 2-7. Mandibles completely hidden beneath clypeus. **Pronotum:** Pronotal process narrowly arcuate and strongly produced (majors) or weakly produced (minors), apex entire. Declivity of pronotal cavity vertical. Surface minutely crazed, sparsely and minutely punctate on disc. Lateral margins with band of moderate to dense, moderately large punctures in posterior half, becoming rugose in anterior half and anterior angles. Pronotal cavity with

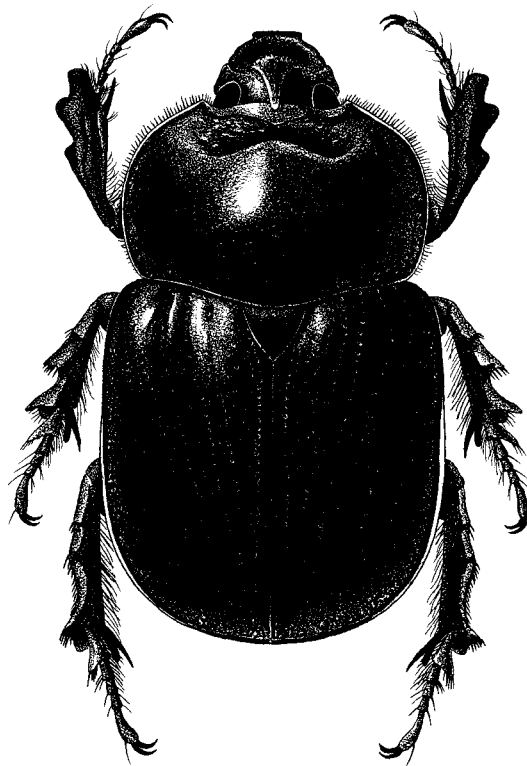
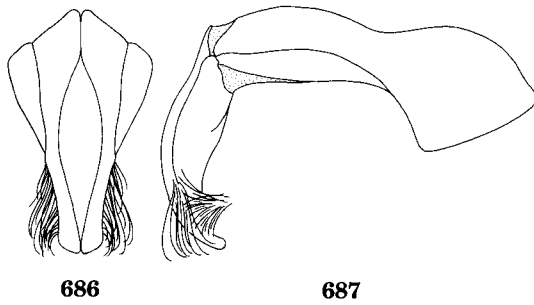


Fig. 685. *Xyloryctes lobicollis*.



Figs. 686-687. *Xyloryctes lobicollis* parameres.

moderately dense, transverse punctures (minors) or rugae (majors). Base with marginal bead occasionally interrupted at middle. *Elytra*: Surface with 5-6 distinct rows of punctures between suture and humerus, sides with 3-4 rows; punctures small to moderate in size, ocellate. *Pygidium*: Surface completely, finely rugopunctate. In lateral view, anterior half convex, posterior half weakly convex. *Legs*: Foretibia tridentate, teeth equidistant. Apex of posterior tibia with 3 large, broadly rounded lobes. Posterior tarsus with first tarsomere triangularly expanded at apex. *Venter*: Prosternal process moderately long, peg-like, rounded at apex. *Parameres*: Figs. 686-687.

Females. As males except in the following respects. *Head*: Frons with low, rounded boss or small, acute tubercle. *Pronotum*: Surface convex; punctation smaller, sparser. *Elytra*: As males to rows reduced or incomplete on disc. *Pygidium*: Surface with small, moderately dense punctures, becoming finely rugulose in angles. In lateral view, surface weakly convex. *Legs*: Apex of posterior tibia with 3 narrowly rounded teeth.

DISTRIBUTION. *Xyloryctes lobicollis* occurs from southern Mexico to Panama (Endrödi 1976b, 1985a). In Costa Rica and Panama this



Fig. 688. Distribution of *Xyloryctes lobicollis* in Costa Rica.



Fig. 689. Distribution of *Xyloryctes lobicollis* in Panama.

species is found in the Cordillera Central above 1,000 meters in elevation between central Costa Rica and Chiriqui in Panama.

LOCALITY RECORDS (Figs. 688-689). 54 specimens examined.

COSTA RICA (46). **CARTAGO** (38): Cartago, Prusia, Refugio Nacional Tapanti, Taras, Tres Ríos, SE side Volcán Irazú; **PUNTARENAS** (1): Las Alturas; **SAN JOSÉ** (7): La Trinidad de Dota, San Pedro (SE San Isidro del General), Santa María de Dota.

PANAMA (7). **CHIRIQUI** (7): Boquete, Cerro Punta, Hartmann's Finca (Santa Clara), Los Planes (7 km N), Volcán de Chiriqui.

TEMPORAL DISTRIBUTION. April (2), May (25), June (25).

DIAGNOSIS. *Xyloryctes lobicollis* is unique among the Central American species of the genus because of its distinct rows of punctures on the elytra. The other Central American species have smooth or nearly smooth elytra. It is also characterized by its narrowly arcuate pronotal process and posterior tibia with 3 lobes at the apex. Occasional specimens with reduced rows of punctures on the elytra could be confused with unusually punctate specimens of *X. teuthras*, but the small notches on the apex of the posterior tibia (in addition to the three lobes) should separate *X. teuthras*. The form of the male parameres is also diagnostic.

BIOLOGY. Adults are nocturnal and are attracted to lights. They have been taken at elevations of 1,160-2,500 meters in premontane rain forests and lower montane rain forests. Adult activity clearly coincides with the onset of the May rains. Although the larvae remain unknown, it seems unlikely that they would live in the leaf litter in this kind of habitat as has been reported for the North American *X. jamaicensis* (Drury) (Ritcher 1966).

***Xyloryctes splendidus* Prell, 1914**
(Figs. 47, 690-694)

Xyloryctes splendidus Prell 1914: 211.

DESCRIPTION. Length 23.8-28.2 mm; width 13.7-15.0 mm. Color dark reddish brown, nearly black.

Males. *Head*: Frons with elongate, subtriangular, slightly recurved horn, horn reaching level of dorsal surface of pronotum in majors, very short in minors. Surface of frons and clypeus rugose. Clypeus with apex broadly emarginate, strongly reflexed. Interocular width equals 3.5 transverse eye diameters. Antenna 10-segmented, club a little longer than segments 2-7. Mandibles completely hidden beneath clypeus. *Pronotum*: Pronotal process broad, arcuate and moderately produced, apex entire or rarely weakly emarginate at middle. Declivity of pronotal cavity nearly vertical, slightly produced at middle. Surface minutely crazed; lateral margins with broad band of small to moderately sized punctures; pronotal cavity rugose. Base with marginal bead, occasionally interrupted at middle. *Elytra*: Surface smooth, occasionally with vague impressions of furrows or punctures. Sutural stria impressed. *Pygidium*: Surface finely rugulose-punctate, punctures small. In lateral view, basal half convex, apical half weakly convex. *Legs*: Foretibia tridentate, teeth subequally spaced. Apex of posterior tibia with 2 large, rounded lobes, small notches occasionally present. Posterior tarsus with first segment triangularly expanded at apex. *Venter*: Prosternal process moderately long, peg-like, apex rounded. *Parameres*: Figs. 691-692.

Females. As males except in the following respects. *Head*: Frons with low, broad, rounded boss or acute tubercle. Surface of frons and clypeus rugopunctate. *Pronotum*: Surface convex; punctation at base and sides reduced, sparse. *Elytra*: Surface mostly smooth, with traces of punctate furrows on disc; sides with usually more distinctly punctate-striate, punctures larger.

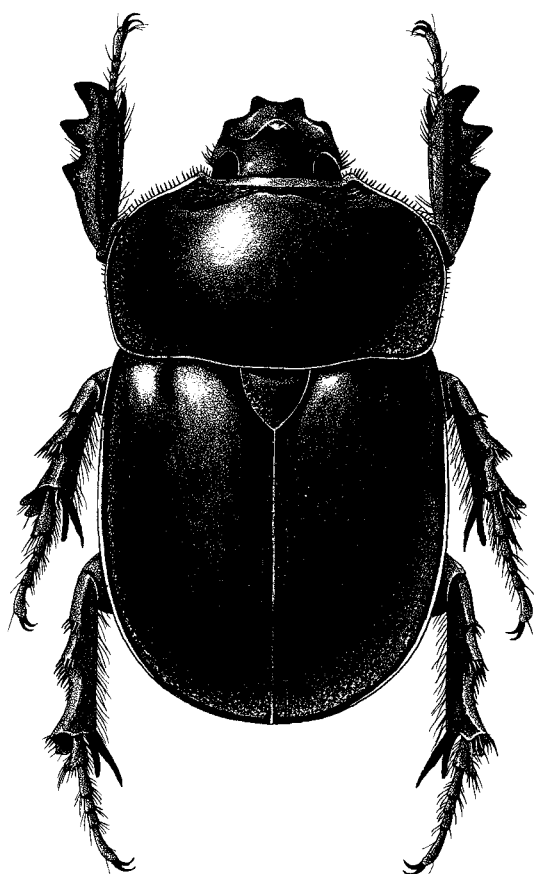
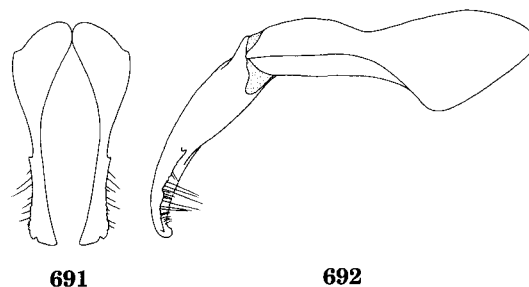


Fig. 690. *Xyloryctes splendidus*.

Pygidium: Surface moderately punctate, punctures moderate in size, becoming rugopunctate at sides. *Legs*: Apex of posterior tibia with 2 narrowly rounded lobes.

DISTRIBUTION. *Xyloryctes splendidus* was known previously from Chiriqui, Panama (Blackwelder 1944; Endrödi 1976b). The Costa Rican records presented here constitute a NEW COUNTRY RECORD. It is now known from the Cordillera Central in Costa Rica and Panama as well as from a single, recent specimen from La Union, Zacapa, Guatemala, also a NEW COUNTRY RECORD.

LOCALITY RECORDS (Figs. 693-694). 20 specimens examined.



Figs. 691-692. *Xyloryctes splendidus* parameres.

COSTA RICA (7). PUNTARENAS (6): Buenos Aires, Estación Biológica Las Alturas (Coto Brus), Estación Biológica Monteverde, Estación La Casona (Monteverde), Monteverde Forest Reserve; SAN JOSÉ (1): 8.4 km S. Division.

PANAMA (13). CHIRIQUI (13): Boquete, Cerro Punta, Hartmann's Finca (Santa Clara).

TEMPORAL DISTRIBUTION. May (10), June (6), July (1), August (1), September (1).

DIAGNOSIS. *Xyloryctes splendidus* is distinguished by its primarily smooth elytra, arcuately and broadly rounded pronotal process, posterior tibia with two rounded lobes at the apex, and rugulose pygidium in the males or moderately punctate pygidium in the females. The vague remnants of punctate striae (more noticeable in the females) should not be interpreted as distinct furrows or else confusion with *X. lobicollis* may result.

BIOLOGY. Adults have been taken only at lights where they are never abundant and are only sporadically taken from year to year. For example, I have collected numerous times at the same spot at the same time of year at Hartmann's finca in Chiriqui, Panama between 1975 and 1995 and collected only two specimens in 1977. Similarly, I have collected numerous times at Monteverde, Costa Rica between 1986 and 1993 and, again, collected

only two specimens, once in 1990 and once in 1992. Adults have been collected from lower montane rain forests and premontane wet forests at elevations ranging from 1,250-1,720 meters.

***Xyloryctes teuthras* Bates, 1888**
(Figs. 695-697)

Xyloryctes teuthras Bates 1888: 324.

DESCRIPTION. Length 22.9-31.0 mm; width 12.9-16.7 mm. Color dark reddish brown, almost black.

Males. Head: Frons with elongate, subtriangular, slightly recurved horn, horn extending to just above level of surface of pronotum in majors, shorter in minors. Surface of frons and clypeus densely punctate to rugopunctate, punctures moderately large. Clypeus with apex broadly, moderately to deeply emarginate, strongly reflexed. Interocular width equals 3.5 transverse eye diameters. Antennae with 10 segments, club a little longer than segments 2-7. Mandibles completely hidden beneath clypeus. **Pronotum:** Pronotal process narrowly arcuate and strongly produced (majors) or weakly produced (minors), apex entire or with joint median emargination. Declivity of pronotal cavity vertical. Surface crazed, disc nearly impunctate. Lateral margins with band of moderate to dense, moderately large punctures in posterior half, becoming rugose in

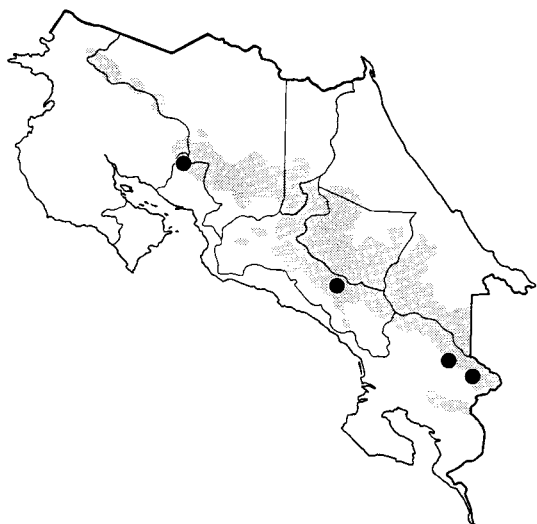
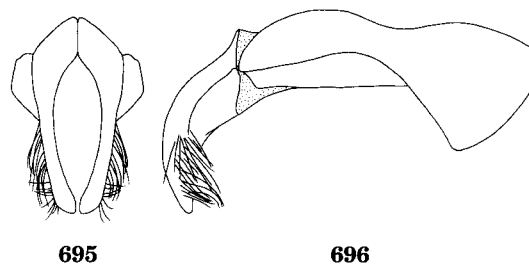


Fig. 693. Distribution of *Xyloryctes splendidus* in Costa Rica.



Fig. 694. Distribution of *Xyloryctes splendidus* in Panama.

anterior half and anterior angles. Pronotal cavity with moderately dense, transverse punctures (minors) or rugae (majors). Base with marginal bead occasionally interrupted at middle. *Elytra*: Surface smooth, often with vague impressions of furrows. Sutural stria impressed. *Pygidium*: Surface sparsely to moderately punctate, punctures small; lateral angles rugulose. In lateral view, surface weakly convex, especially apically. *Legs*: Foretibia tridentate, teeth subapically spaced. Apex of posterior tibia with 3 large, rounded lobes and usually a number of small notches. Posterior tarsus with first segment triangularly produced at apex. *Venter*: Prosternal process moderately long, peg-like, apex rounded. *Parameres*: Figs. 695-696.



Figs. 695-696. *Xyloryctes teuthras* parameres.

Females. As males except in the following respects. *Head*: Frons with low, rounded boss or acute tubercle. Surface of head rugopunctate. *Pronotum*: Surface convex; punctuation along lateral margins reduced, sparse. *Pygidium*: Surface sparsely punctate, punctures small. *Legs*: Apex of posterior tibia with 3 narrowly rounded lobes.

DISTRIBUTION. *Xyloryctes teuthras* is found in Mexico and Guatemala and, according to Endrödi (1976), in Costa Rica. Aside from the Cartago specimens cited by Endrödi, I have not collected any specimens nor seen any specimens from Costa Rica in any of the collections studied for this project. I remain doubtful that *X. teuthras* really occurs in Costa Rica, but it is included here in the event that the specimens noted by Endrödi are accurately labeled and identified.

LOCALITY RECORDS (Fig. 697). No Costa Rican specimens examined.

COSTA RICA (Endrödi 1976b). CARTAGO: Cartago.

TEMPORAL DISTRIBUTION. Unknown.

DIAGNOSIS. *Xyloryctes teuthras* can be recognized by its smooth elytra, arcuately and



Fig. 697. Distribution of *Xyloryctes teuthras* in Costa Rica.

narrowly rounded pronotal process, posterior tibia with three rounded lobes at the apex, and a sparsely to moderately punctate pygidium.

BIOLOGY. Adults have been taken at lights. The Cartago specimen was collected in premontane moist forest at an elevation of 1,500 meters.



Color Plate 6. *Amblyodus taurus* on rotten log with cup fungi, *Cookeina speciosa* (Fr.) Dennis (Ascomycetes: Sarcoscyphaceae). Illustration by Dan Schmidt.

TRIBE PHILEURINI

Species in the tribe Phileurini are found in all regions of the world although most species occur in the tropics. The world fauna is comprised of 36 genera (Endrödi 1985a; Dupuis and Dechambre 2001) with nearly 225 species. In the Americas there are 22 genera and about 125 species. Panama and Costa Rica have nine genera and 28 species. Endrödi (1977c, 1978) provided the most recent, comprehensive review of the entire tribe, and numerous species have been added since by several different coleopterists.

Adult phileurines are recognized by the large mentum that covers the bases of the labial palpi, the usually acuminate clypeus (always so in the Central American fauna), frons usually with 2 tubercles or horns (always so in the Central American species), pronotum usually with a longitudinal, median furrow, elytra usually flattened, anterior tibia with three or four teeth, and apex of posterior tibia truncate or armed with one to three teeth. In some species, the concavity of the vertex differs between the sexes with the males having a deeply hollowed pit while the females do not. All of the Central American species are passalid-like in overall appearance because of

their black and often shiny coloration, usually flattened bodies, and usually furrowed elytra.

Adult phileurines are nocturnal, and some are attracted to lights. Some species may not be strongly attracted to lights considering their rarity in areas where they are known to occur and where extensive light collecting has been conducted. Some species are inquilines with ants or termites (Vanin *et al.* 1983) while others live in decaying wood in a fashion similar to that of passalids, although without the subsociality. To my knowledge, phileurines in the Neotropics have only been collected at light traps, from rotting stumps and logs, and from termite or ant nests.

There is virtually no information on larval stages, life history, and larval development. A few larvae are known of species collected from rotting wood or termite or ant nests. For the U.S. and Mesoamerican fauna, however, the larvae for only five species are described. There is a real need for laboratory rearing so that larvae can be associated with adults. This opportunity will fall largely to resident entomologists in the countries in which these species occur since visiting researchers on short collecting trips cannot hope to accomplish this.

Key to the Genera of Adult Phileurini of Costa Rica and Panama (modified from Endrödi 1985a)

1. Outer side of mandibles tridentate 2
- 1'. Outer side of mandibles simply curved 3
2. Anterior tibia quadridentate. Frons with 2 large tubercles or horns. Pronotum with large flattened area **Amblyodus Westwood**
- 2'. Anterior tibia tridentate. Frons with 2 small tubercles. Pronotum not flattened, instead convex and with narrow, longitudinal furrow **Goniophileurus Kolbe**
3. Apex of posterior tibia truncate, lacking teeth **Archophileurus Kolbe**
- 3'. Apex of posterior tibia with at least upper angle produced as a sharp tooth, usually with 1-2 other teeth as well 4
4. Apex of posterior tibia with 3 small teeth **Amblyoproctus Kolbe**
- 4'. Apex of posterior tibia with 1-3 large teeth or at least upper angle strongly produced 5
5. Pronotum convex, lacking tubercles, fovea, or furrow. Apex of basal tarsomere on posterior tarsus simple, not spiniform **Palaeophileurus Kolbe**
- 5'. Pronotum with tubercle(s) or fovea or longitudinal furrow. Apex of basal tarsomere on posterior tarsus spiniform 6

- 6 Apex of posterior tibia with 3 large teeth. Tubercles or horns of frons located at sides of head **Homophileurus Kolbe**
- 6' Apex of posterior tibia with 1-2 large teeth. Tubercles or horns located on sides of head or not 7
- 7 Tubercles or horns of frons located near center of head, far from lateral edge. Pronotum lacking fovea or anterior declivity; longitudinal furrow variable, all but 1 species lacking tubercles at anterior end **Hemiphileurus Kolbe**
- 7' Tubercles or horns located near lateral margin of head. Pronotum with anterior, foveate cavity or broad declivity; longitudinal furrow strong, usually with distinct tubercle at anterior end 8
- 8 Prosternal process with large conical knob on posterior surface. Size 20 mm or less **Paraphileurus Endrödi**
- 8' Prosternal process variable, but never with posterior surface produced backward as an angulate projection **Phileurus Latreille**

Clave para los Géneros de Phileurini de Costa Rica y Panamá
(modificada de Endrödi 1985a)

1. Lado externo de las mandíbulas tridentado 2
- 1' Lado externo de las mandíbulas curvado en forma simple 3
2. Tibia anterior cuadridentada. Frente con 2 tubérculos grandes o cuernos. Pronoto con un área grande aplanada **Amblyodus Westwood**
- 2' Tibia anterior tridentada. Frente con 2 tubérculos pequeños. Pronoto no aplanado, más bien convexo y con un surco angosto longitudinal **Goniophileurus Kolbe**
3. Apice de las tibia posterior truncado, sin dientes **Archophileurus Kolbe**
- 3' Apice de las tibia posterior con al menos el ángulo superior prolongado como un diente agudo, generalmente también con 1 ó 2 dientes adicionales 4
4. Apice de la tibia posterior con 3 pequeños dientes. **Amblyoproctus Kolbe**
- 4' Apice de la tibia posterior con 1 a 3 dientes grandes o al menos el ángulo superior fuertemente prolongado 5
5. Pronoto convexo, sin tubérculos, fóvea, o surco. Apice del tarsómero basal del tarso posterior simple, no espiniform **Palaeophileurus Kolbe**
- 5' Pronoto con tubérculo(s) o fóvea o surco longitudinal. Apice del tarsómero basal en el tarso posterior espiniforme 6
6. Apice de la tibia posterior con 3 dientes grandes. Tubérculos o cuernos de la frente localizados a los lados de la cabeza. **Homophileurus Kolbe**
- 6' Apice de la tibia posterior con 1 ó 2 dientes grandes 7
7. Tubérculos o cuernos de la frente localizados cerca del centro de la cabeza, lejos del borde lateral. Pronoto carente de fóvea o declive anterior; surco longitudinal variable, todas excepto 1 especie sin tubérculos en el extremo anterior **Hemiphileurus Kolbe**
- 7' Tubérculos o cuernos localizados cerca del margen lateral de la cabeza. Pronoto con una cavidad foveada anterior o un declive amplio; surco longitudinal fuerte, generalmente con un tubérculo evidente en el extremo anterior 8
8. Proceso proesternal con una proyección cónica en la superficie posterior. Tamaño 20 mm o menos **Paraphileurus Endrödi**
- 8' Proceso proesternal variable, pero nunca con la superficie posterior prolongada hacia atrás como una proyección angulada. **Phileurus Latreille**

***Amblyodus* Westwood, 1878**

Amblyodus Westwood 1878: 32.

The genus *Amblyodus* is monotypic with *A. taurus* occurring in Costa Rica and Panama. Endrödi (1977c) indicated he saw a specimen from Colima, Mexico, but I have difficulty believing this specimen was accurately labeled. Miguel Morón (personal communication May 1997) said he knew of no Mexican records.

Amblyodus is easily recognized because of its distinctive head horns and flattened pronotum. It is one of only two genera of phileurines in Central America whose species possess dentate mandibles, and it has quadridentate foretibia, whereas *Goniophileurus* (the other genus whose much smaller species have dentate mandibles) has tridentate foretibia.

Other than being attracted to lights (although perhaps not strongly so), nothing is known of the biology of the species in this rarely collected genus. Endrödi (1977c, 1985a) reviewed the genus.

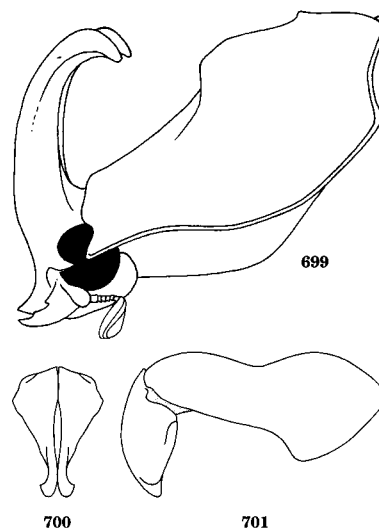
***Amblyodus taurus* Westwood, 1878**
(Color Plate 6, Figs. 698-703)

Amblyodus taurus Westwood 1878: 32.

DESCRIPTION. Length 18.0-24.0 mm; width 8.5-11.4 mm. Color piceous to black. **Head:** Surface nearly smooth, with only sparse micropunctures. Frons with 2 erect, diverging, posteriorly recurving horns (Fig. 699); horns larger in male majors, smaller in male minors, small in female. Clypeus subtriangular, apex narrowly rounded. Interocular width equals 3.7 transverse eye diameters. Antennae 10-segmented, club subequal in length to segments 2-7. Mandibles tridentate. **Pronotum:** Nearly all of disc flat with dense, large, C-shaped punctures combined with rugosity, discal depression smaller in females. Lateral and posterior margins of pronotal depression strongly carinated, carina at base strongly emarginated. Anterior angles and narrow edge along lateral



Fig. 698. *Amblyodus taurus*.



Figs. 699-701. *Amblyodus taurus*: (699) major male, head and pronotum; (700-701) parameres.

margins rugose; base either side of middle with large, ocellate punctures. Convex surface on each side nearly smooth, with sparse, small punctures and a few large punctures. Base lacking marginal bead. *Elytra*: Surface on disc with 5 rows of large, ocellate punctures, rows weakly impressed. Intervals on disc convex, with sparse, small punctures. Sides with 5 similar rows of punctures. *Pygidium*: Surface with moderate to moderately dense, moderately-sized, ocellate punctures, punctation sparser in females. In lateral view, surface strongly convex. *Legs*: Foretibia

quadridentate. Apex of posterior tibia with 6 teeth. *Venter*: Prosternal process long, columnar, apex flat to weakly concave. *Parameres*: Figs. 700-701.

DISTRIBUTION. *Amblyodus taurus* is known from Nicaragua and Panama (Bates 1888), and Endrödi (1977c) reported it from Colima in Mexico. I am not convinced the Mexican record is accurate. There are only a few records from adjacent areas in Panama and Costa Rica, and the Costa Rican specimens constitute a NEW COUNTRY RECORD.

LOCALITY RECORDS (Figs. 702-703). 11 specimens examined.

COSTA RICA (2). PUNTARENAS (2): Estación Las Mellizas.

PANAMA (9). CHIRIQUI (7): Fortuna, Hartmann's Finca (Santa Clara); PANAMA (2): Cerro Azul.

TEMPORAL DISTRIBUTION. May (3), June (4), July (2), November (1).

DIAGNOSIS. *Amblyodus taurus* is easily distinguished by its remarkable head armature and flattened pronotum in combination with tridentate mandibles, quadridentate foretibia, and apex of the posterior tibia with six teeth.



Fig. 702. Distribution of *Amblyodus taurus* in Costa Rica.

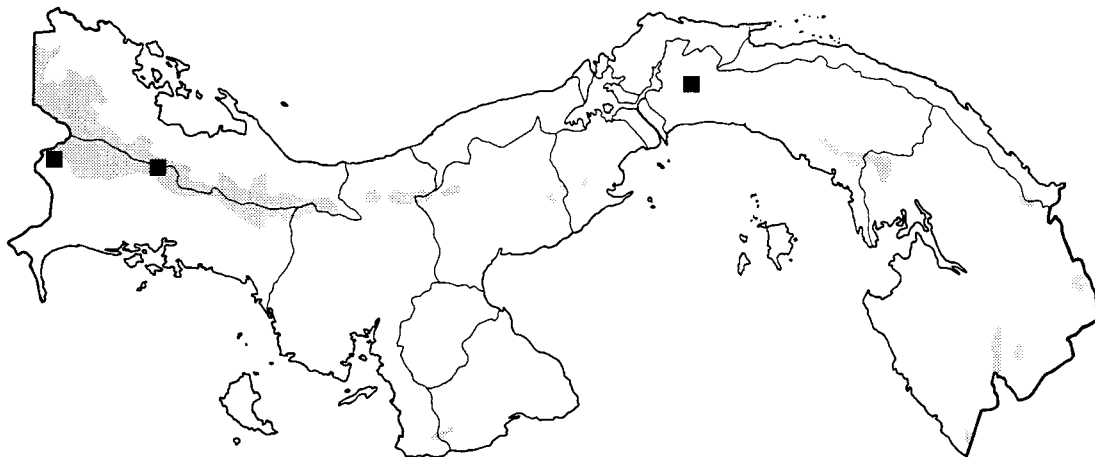


Fig. 703. Distribution of *Amblyodus taurus* in Panama.

BIOLOGY. Adults are attracted to lights although perhaps not strongly so considering the rarity of specimens in collections. They have been collected from rotten logs in premontane wet forests at elevations of 1,050-1,200 meters.

Amblyoproctus Kolbe, 1910

Amblyoproctus Kolbe 1910: 335.

The genus *Amblyoproctus* contained six species (Endrödi 1985a; Ratcliffe, 1988), and one new species is described here. Previously, all of the species were known only from South America, and the new species is the first known from Central America.

The genus *Amblyoproctus* is easily characterized by the small size of its species (none exceeding 17 mm), presence of three small teeth on the apex of the posterior tibia, external edge of narrow mandibles lacking teeth, and pronotum with a longitudinal furrow.

Nothing is known of the biology of *Amblyoproctus* species other than they live in rotting logs. Endrödi (1977c, 1985a) provided the most recent review of the genus.

Amblyoproctus centroamericanus Ratcliffe, new species (Figs. 704-708)

TYPE MATERIAL. Holotype and allotype labeled "Est. Pitilla, 9 km S. Sta. Cecilia, P.N. Guanacaste, Prov. Guana., COSTA RICA, 700 m, 3-17 Dic. 1993, C. Moraga, LN 330200-380200, #2545." Paratypes (24) with the following data: same as holotype except October 1993 and #2545 (2), 6-17 September and #2344 (1), July 1991 and without # (3), April 1994 and #2841 (1), March 1994 and #2804 (1), February 1990 and P. Rios, C. Moraga, and R. Blanco colls. (1), January 1994 and #2563 (3); "Sector San Ramón, Prov. Alaju., COSTA RICA, 620 M, 13-28 Mar 1994, K. Taylor, LN 318100-381900, #2763" (1); "Est. El Ceibo, Braulio Carrillo N.P., 400-600 m, Heredia, COSTA RICA, Apr. 1990, C. Chaves, 527700-256500" (1); "Est. Sirena, 0-100 m,

P.N. Corcovado, Prov. Puntarenas, Costa Rica, Jun. 1991, J.C. Saborio, L-S270500, 508300" (3); "Est. Hitoy Cerere, 100 m, R. Cerere, Res. Biol. Hitoy Cerere, Prov. Limon, Costa Rica, Oct. 1992, G. Carballo, L-N 184200, 643300" (1); "Est. Carrillo, 700 m, P.N. Braulio Carrillo, Prov. S. José, COSTA RICA, 15 a 17 Feb 1993, C. Hymenoptera, L-N 236700, 541800" (1); "Fca. San Gabriel, 2 km Suroeste Dos Rios, 600 m, Prov. Alaj, COSTA RICA, II curso Parataxon., May 1990, L-N 318800, 383500" (1); "Sector Cerro Cocori, Fca. de E. Rojas, 150 m, Prov. Limón, COSTA RICA, Mar. 1993, E. Rojas, L-N 286000. 567500" (1); "El Coco, Guana., 25 ft., COSTA RICA, X-18-1963, S.L.W." (1); "PANAMA-BCI, lights, 18-V-1979, H. Wolda" (1); "PANAMA: Coclé, Cerro Gaital, 850 m, 13-20 VII 96, Curoe" (1).

Holotype, allotype, and 13 paratypes deposited at INBio (Santo Domingo de Heredia, Costa Rica). Remaining 11 paratypes deposited at the U.S. National Museum (Washington, D.C.), Smithsonian Tropical Research Institute (Panama), University of Nebraska State Museum (Lincoln), Dan Curoe (Palo Alto, CA), Miguel Morón (Xalapa, Mexico), and Brett Ratcliffe (Lincoln, NE).

HOLOTYPE. Male. Length 12.7 mm; width 6.2 mm. Color dark reddish brown. *Head:* Frons with punctures moderate in density; punctures large, mostly round, some U-shaped; surface weakly but distinctly concave. Frontoclypeal carina elevated as small tubercle on each side. Clypeus with sparse, small punctures; clypeal shape strongly arcuate, apex rounded. Interocular width equals 5.1 transverse eye diameters. Antenna with 10 segments, club a little longer than segments 2-7. Mandibles narrow, lacking teeth, apex narrowly rounded. *Pronotum:* Surface with moderately dense punctures; punctures moderately large, deep, ocellate. Disc with longitudinal furrow deep, extending from apex to base. Apex with small tubercle just behind margin at anterior end of furrow. Marginal bead present on lateral margins, absent on base. *Elytra:* Surface with regular rows of punctures; punctures large (becoming smaller and denser apically), ocellate-umbilicate. Intervals about equally convex and with sparse,

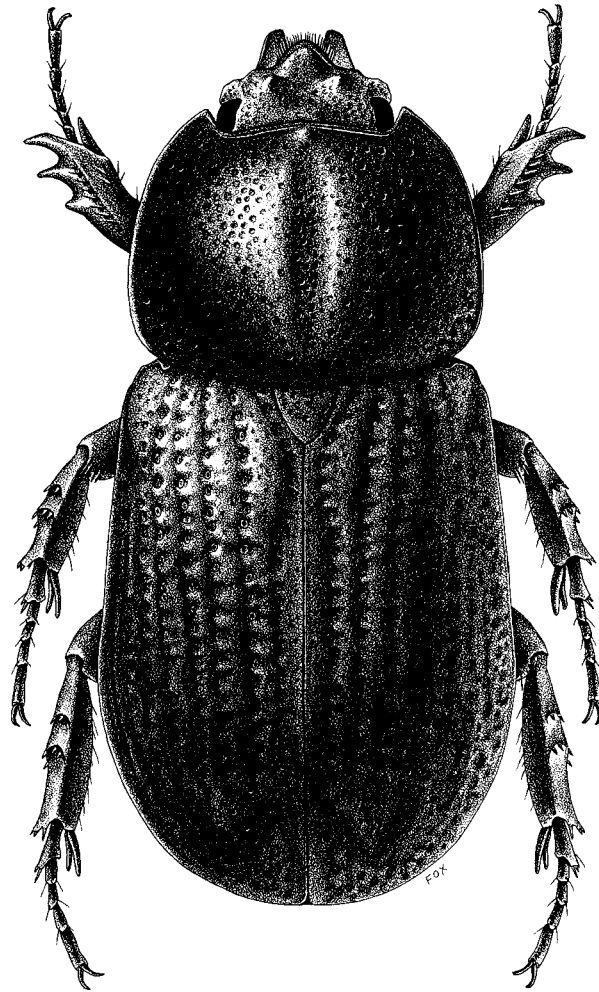


Fig. 704. *Amblyoproctus centroamericanus*.

small punctures. Apical region of elytra with minute, pale setae. *Pygidium*: Surface densely punctate; punctures moderately large, round, umbilicate, with minute and pale setae. In lateral view, surface weakly convex. *Legs*: Foretibia tridentate, teeth subequally spaced. Apex of posterior tibia with 3 small teeth. Apex of first tarsomere on posterior tarsus with apex extended into stout spine. *Venter*: Prosternal spine long, posterior surface with small triangular tooth, apex transverse and narrowly compressed from front to back. *Parameres*: Figs. 705-706.

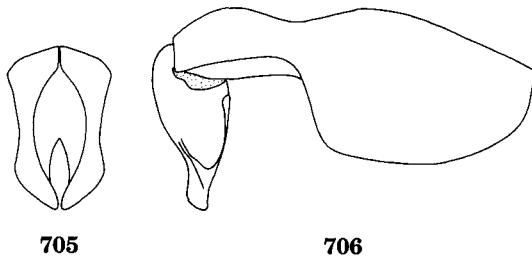
ALLOTYPE. Female. Length 13.1 mm; width 6.7 mm. Color piceous. The allotype does not differ significantly from the holotype.

VARIATION. Males (16 paratypes). Length 12.7-14.6 mm; width 6.7-7.9 mm. Color reddish brown to black. Aside from slight differences in the density of punctation, the specimens are all remarkably similar.

Females (7 paratypes). Length 12.3-13.8 mm; width 5.6-6.7 mm. Color reddish brown to black. These specimens do not differ appreciably from the allotype.

ETYMOLOGY. The other species of *Amblyoproctus* are all found in South America. This species is named to signify its occurrence in Central America.

DISTRIBUTION. *Amblyoproctus centroamericanus* is known from Costa Rica and Panama.



Figs. 705-706. *Amblyoproctus centroamericanus* parameres.

LOCALITY RECORDS (Figs. 707-708). 26 specimens examined.

COSTA RICA (24). ALAJUELA (2): Dos Ríos (2 km SE), Sector San Ramón; GUANACASTE (15): El Coco, Estación Pitilla; HEREDIA (1): Estación El Ceibo; LIMÓN (2): Estación Hitoy Cerere, Sector Cerro Cocori; PUNTARENAS (3): Estación Sirena; SAN JOSÉ (1): Estación Carrillo (Parq. Nac. Braulio Carrillo).

PANAMA (2). CANAL ZONE (1): Barro Colorado Island; COCLÉ (1): Cerro Gaital.

TEMPORAL DISTRIBUTION. January (3), February (2), March (3), April (2), May (2), June (3), July (4), September (1), October (4), December (2).

DIAGNOSIS. This species resembles *A. torulosus* Kolbe which is found in Venezuela and Colombia. The parameres of the two species are different, and the pygidium of *A. centroamericanus* is completely and densely punctate whereas it is sparsely punctate in the basal half and smooth in the apical half of *A. torulosus*. So far, this is the only species of *Amblyoproctus* found in Central America.

BIOLOGY. The type specimens were collected in rotten logs from tropical moist forests and premontane wet forests at elevations ranging from near sea level to 900 meters.

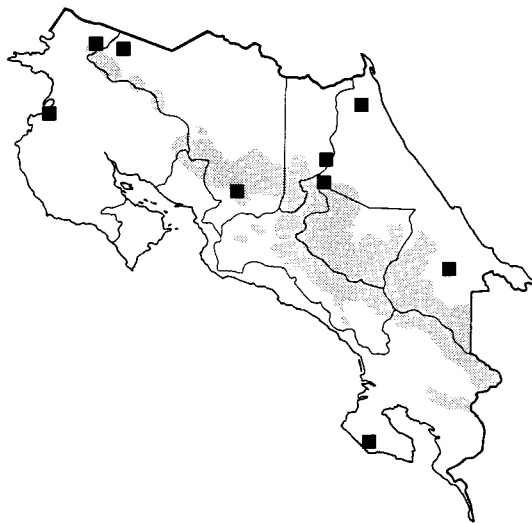


Fig. 707. Distribution of *Amblyoproctus centroamericanus* in Costa Rica.

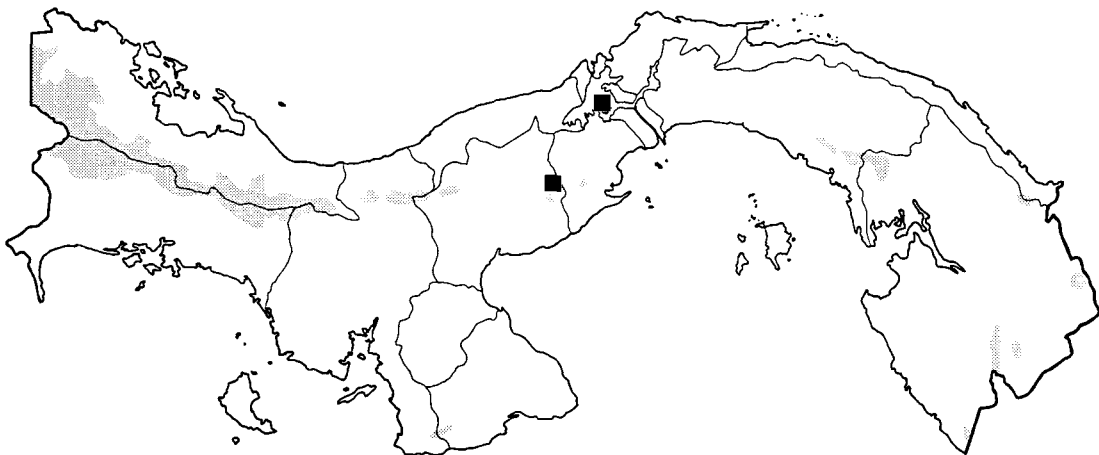


Fig. 708. Distribution of *Amblyoproctus centroamericanus* in Panama.

Archophileurus Kolbe, 1910

Archophileurus Kolbe 1910: 334.

Amblyophileurus Kolbe 1910: 334 (synonym).

Periphileurus Kolbe 1910: 334 (synonym).

Anisophileurus Prell 1912c: 182 (synonym).

Archophileurus is a genus containing 26 species (Endrödi 1977c, 1985a; Morón 1990). The species are widely distributed in South America, and only two species are found in Mesoamerica: *A. cribrosus* (LeConte) in Mexico and Texas and *A. simplex* in Costa Rica and Nicaragua.

The genus is easily distinguished among the Central American fauna because it is the only one whose members have the apex of the posterior tibia truncate and with numerous small spinules. The immature stages and life history are unknown for all of the species. Endrödi (1977c, 1985a) gave a synopsis of the genus.

Archophileurus simplex (Bates, 1888)

(Figs. 709-712)

Phileurus simplex Bates 1888: 339.

DESCRIPTION. Length 18.4-24.0 mm; width 9.0-12.0 mm. Color dark reddish brown to black. *Head:* Frons in males concave, smooth and shiny in majors, rugose in minors; females with frons only slightly depressed, transversely rugose. Frontal horns near side of head; majors with horns stout, almost twice as long as width of eye (as seen from above), curved slightly backward; minors and females with small tubercles. Clypeus subtriangular, apex pointed and slightly recurved, surface smooth in males and punctate to rugopunctate in females. Interocular width equals 4.0-4.5 transverse eye diameters. Antennae with 10 segments, club a little longer than segments 2-7. Mandibles narrow, lacking teeth, apex acute. *Pronotum:* Surface sparsely to moderately punctate; punctures in males small either side of furrow, becoming moderately large and umbilicate in anterior and posterior angles; female with punctures generally

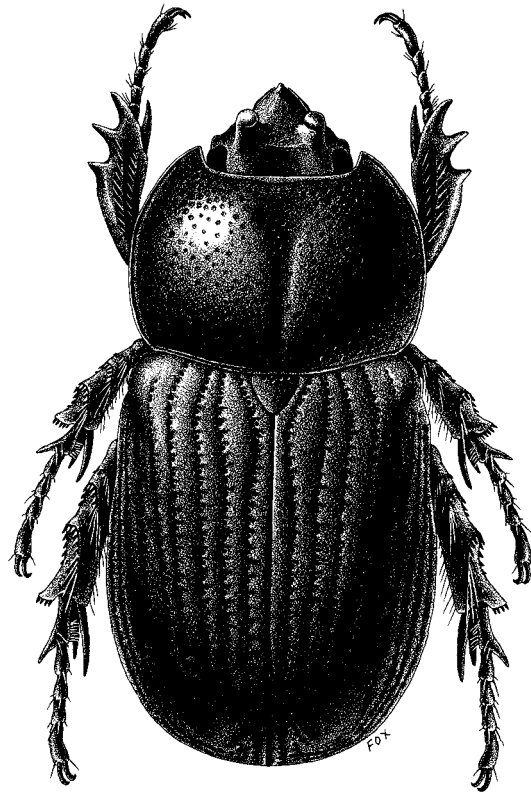
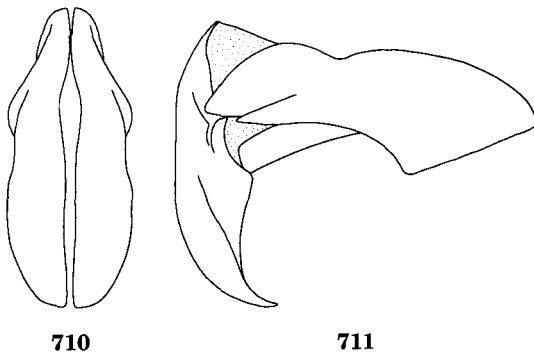


Fig. 709. *Archophileurus simplex*.

all larger. Longitudinal furrow in males narrow, becoming wider anteriorly, deep, not quite reaching margins, with sparse, small to moderate punctures; females with denser, larger punctures. Base without marginal bead. *Elytra:* Surface with regular rows of punctures in furrows; punctures in males moderately large, ocellate, usually separated by 2-3 diameters; females with punctures larger, denser. Intervals, especially on disc, elevated and strongly convex, with sparse and minute punctures. *Pygidium:* Surface moderately punctate; punctures moderate to large in size, deep, setigerous; setae in males long, reddish brown, setae in females shorter and sparser; base with distinct, transverse furrow. In lateral view, surface in males evenly convex, surface in females strongly protuberant at about middle and flattened behind. *Legs:* Foretibia tridentate, teeth subequally spaced. Posterior tibia with apex truncate, with 17-20



Figs. 710-711. *Archophileurus simplex* parameres.

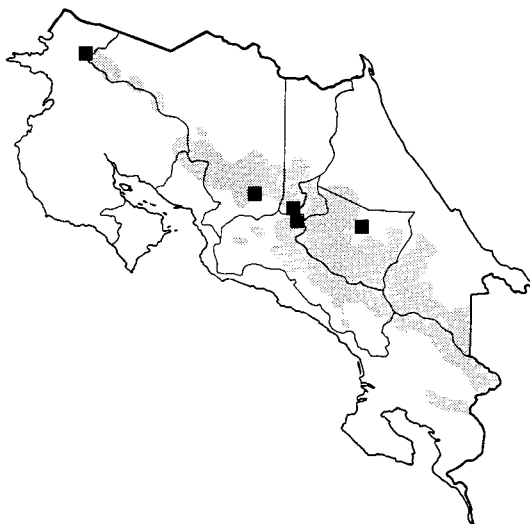


Fig. 712. Distribution of *Archophileurus simplex* in Costa Rica.

short spinules. *Venter*: Prosternal process subconical, moderately long, flattened from front to back, apex broadly rounded, posterior surface with strong tooth near base. *Parameres*: Figs. 710-711.

DISTRIBUTION. *Archophileurus simplex* is known by only a few specimens from Nicaragua and Costa Rica.

LOCALITY RECORDS (Fig. 712). 5 specimens examined

COSTA RICA (5). ALAJUELA (1): Río San Lorencito (5 km N Colonia Palmareña); CARTAGO (1): Turrialba; GUANACASTE (1): Estación Maritza; HEREDIA (1); Belén; SAN JOSÉ (1): San José.

TEMPORAL DISTRIBUTION. February (1), April (1), June (1).

DIAGNOSIS. This species is readily identified because it is the only phileurine in Costa Rica having the apex of the posterior tibia truncate and with small spinules. In addition, the form of the male's parameres is diagnostic.

BIOLOGY. Adults and larvae presumably live in rotting logs, and adults are occasionally attracted to lights. This seems to be a rare insect based on the lack of specimens in collections. The few specimens available have been taken in premontane moist forests and premontane wet forests at elevations of 500-1,000 meters.

Goniophileurus Kolbe, 1910

Goniophileurus Kolbe 1910: 333.

The small genus *Goniophileurus* is comprised of only a single species, *G. femoratus* (Burmeister). It is known from Costa Rica, Panama (NEW COUNTRY RECORD), Venezuela, Ecuador, and Brazil (Endrödi 1977c, 1985a).

The genus is distinguished by tridentate mandibles (one of only two phileurine genera in Central America with tridentate mandibles), anterior tibia tridentate, pronotum with a narrow, longitudinal furrow, and posterior tibia at apex with 3 small teeth (one small one between two larger teeth). The single species is sexually dimorphic: males possess a deeply hollowed, smooth vertex, whereas females do not share this character.

Nothing is known of the biology of the species in this genus other than some specimens have been taken at lights. The immature stages are unknown. The genus was last reviewed by Endrödi (1977c, 1985a).

Goniophileurus femoratus
(Burmeister, 1847)
 (Figs. 713-717)

Phileurus femoratus Burmeister 1847: 149.

DESCRIPTION. Length 11.5-14.0 mm; width 5.2-6.3 mm. Color reddish brown to black. *Head:* Vertex in male deeply concave, smooth, shining; in female only weakly depressed and rugopunctate. Tubercles of frons present just mesad of each eye, prominent in male, small in female. Clypeus with surface coarsely rugopunctate basally, sparsely punctate apically, punctures small; apex pointed, reflexed. Interocular width equals 4.5-5.3 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. Mandibles distinctly tridentate. *Pronotum:* Surface moderately densely punctate; punctures moderately large, ocellate; disc with longitudinal furrow, furrow densely punctate within, not quite reaching apical or basal margins. Base lacking marginal bead. *Elytra:* Surface with regularly punctate striae; punctures moderate to large (becoming smaller and denser at apex), ocellate, round to oblong. Intervals slightly convex, with small, sparse punctures. *Pygidium:* Surface with punctures moderate in both density and size, round, minutely setigerous. Base with transverse, shallow furrow, apex with broad marginal bead. In lateral view, surface convex. *Legs:* Foretibia tridentate, basal tooth slightly removed from others. Apex of posterior tibia with 3 teeth, central tooth smaller. Basal tarsomere of posterior tarsus prolonged into spine. *Venter:* Prosternal process moderate in length; columnar, apex broadly and longitudinally flattened and depressed at center. *Parameres:* Figs. 714-715.

DISTRIBUTION. *Goniophileurus femoratus* is known from Costa Rica, Panama, Venezuela, French Guiana, Ecuador, and Brazil (Blackwelder 1944; Endrödi 1977c). The Panamanian specimens constitute a **NEW COUNTRY RECORD.**

LOCALITY RECORDS (Figs. 716-717). 11 specimens examined.

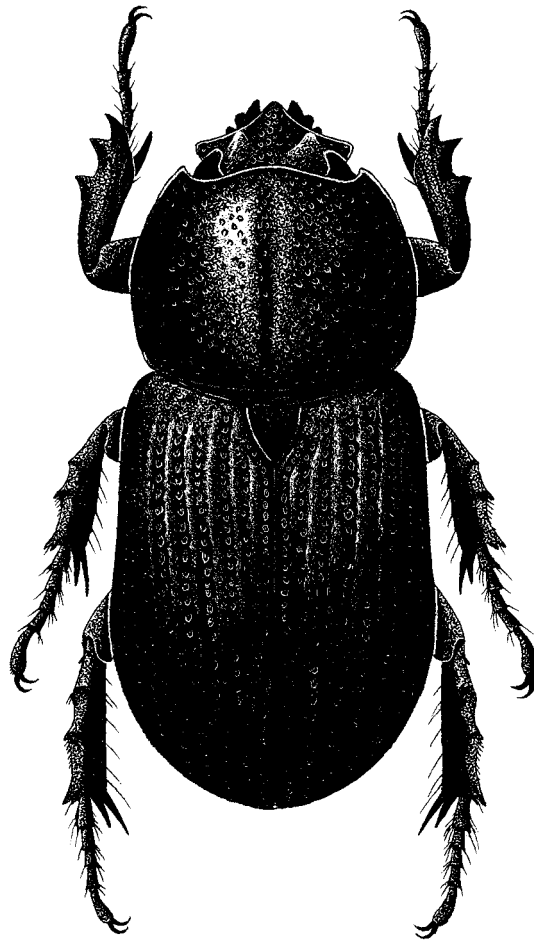
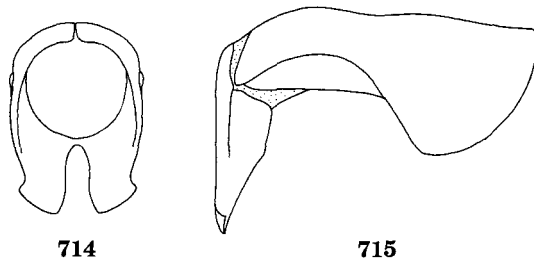


Fig. 713. *Goniophileurus femoratus*.



Figs. 714-715. *Goniophileurus femoratus* parameres.

COSTA RICA (5). **CARTAGO** (1): Turrialba; **GUANACASTE** (3): Parq. Nac. Rincón de la Vieja, Playas Nosara, Tierras Morenas; **PUNTARENAS** (1): Reserva Biológica Carara.

PANAMA (6). **CANAL ZONE** (6): Barro Colorado Island, Ft. Kobbe, Madden Dam.

TEMPORAL DISTRIBUTION. January (1), May (2), June (3), July (2), October (1).

DIAGNOSIS. *Goniophileurus femoratus* is easily distinguished by its small size (14 mm or less), tridentate mandibles, furrowed pronotum, and posterior tibia with 3 small teeth at the apex. Only the much larger *Amblyodus taurus* also has tridentate clypeal teeth in the Central American phileurine fauna.

BIOLOGY. This species has been collected in rotting logs and occasionally at lights. They have been taken in tropical moist forests, tropical wet forests, premontane moist forests, and premontane wet forests at elevations just above sea level to 1,100 meters in elevation.

Hemiphileurus Kolbe, 1910

Hemiphileurus Kolbe 1910: 340.

Epiphileurus Kolbe 1910: 336 (synonym).

Relative to other phileurine genera, *Hemiphileurus* is fairly large with, formerly, 42 species (Howden 1978; Endrödi 1985a; Ratcliffe 1988, 2001; Chalumeau 1981, 1988; Ratcliffe and Ivie 1998; Dechambre 2000). An additional three new species are described here for a total of 45 species of *Hemiphileurus*. Eleven species in the genus are restricted to the West Indies, 18 species are exclusive to South America, and 13 species are found in Mesoamerica; three species occur in both Central and South America. In Costa Rica and Panama there are 10 species; one species is found only in Costa Rica, two species occur in only in Panama, and seven species are found in both countries. Endrödi (1978) recorded a single specimen of *H. punctatostriatus* Prell from Panama, but, since I have never seen any specimen other than from Mexico or Belize, I am discounting the veracity of that



Fig. 716. Distribution of *Goniophileurus femoratus* in Costa Rica.



Fig. 717. Distribution of *Goniophileurus femoratus* in Panama.

record and not including that species here. Additional new species will be discovered.

The genus is characterized by having species with mandibles simply curved externally, clypeus triangularly acuminate, frons with tubercles (especially) or horns (less so) arising far from the lateral margin of the head, pronotum with a longitudinal furrow but lacking an anterior fovea or strong declivity, and apex of posterior tibia with a single, large tooth on the upper angle. Most of the species are moderate in size and range from 16-24 mm in length.

The larval stage for only one species, *H. illatus* LeConte, has been described (Ritcher 1966). This species occurs in the southwest-

ern United States and Mexico. Larvae for the remaining species remain unknown or undescribed. All of them presumably live in decaying wood where they feed on the wood or associated fungi. Adults may be attracted to lights at night, and this is where virtually all specimens in collections were taken. Adults of *H. illatus* have been collected from rotting logs (Ritcher 1966), and other species can probably be taken this way also.

The genus *Hemiphileurus* was comprehensively treated by Endrödi (1978, 1985a), although new species have been described since (Howden 1978; Ratcliffe 1988, 2001; Chalumeau 1988; Ratcliffe and Ivie 1998; Dechambre 2000).

Key to the Species of Adult *Hemiphileurus* of Costa Rica and Panama (females of most of the species cannot be identified except by association with the males)

1. Elytra with alternate intervals strongly elevated, cariniform; 2 rows of large punctures between elevated intervals *dejeani* (Bates)
- 1'. Elytra with all intervals subequal in height 2
- 2 (1'). Last sternite moderately to densely punctate 3
- 2'. Last sternite punctate or rugose in transverse band along base only, sparsely punctate elsewhere 5
- 3 (2). Elytra with intervals all similar: straight, smooth, weakly flattened
. *pygidiopunctissimus* Ratcliffe, new species
- 3'. Elytra with intervals dissimilar: occasionally broken, always appearing sinuate because of lateral branching extending to between punctures in furrowed striae 4
- 4 (3'). Parameres at base each with long, lateral lobe (Figs. 754-755)
. *variolosus* (Burmeister)
- 4'. Parameres at base each lacking a lateral lobe; instead apex of each paramere produced into a lobe (Figs. 758-759) *vicarius* Prell
- 5 (2'). Anterior edge of pronotal furrow with 2 very small tubercles
. *nebulohylaeus* Ratcliffe, new species
- 5'. Anterior edge of pronotal furrow lacking tubercles 6
- 6 (5'). Elytra with intervals appearing sinuate because of lateral branching extending to between punctures in furrowed striae; elytra appear confusedly sculptured *cylindroides* (Bates)
- 6'. Elytra with intervals similar: nearly straight, smooth, slightly convex . . . 7
- 7 (6'). Males with horns, not tubercles. Top of head nearly smooth
. *simplex* (Prell)
- 7'. Males with tubercles, never with horns. Top of head distinctly punctate to rugopunctate 8
- 8 (7'). Parameres, in caudal view, narrowing slightly to apex (Figs. 735-736)
. *laevicauda* (Bates)
- 8'. Parameres, in caudal view, broadly rounded and bulbous until apex (Figs. 718-719, 731-732) 9

- 9 (8'). Parameres with elongate, apically expanded, clearly delineated depression at middle of shaft of each paramere (Figs. 718-719)
 ***curoei* Ratcliffe, new species**
- 9'. Parameres each with declivous area on lateral edges just above middle, not with distinctly edged depression at middle of each shaft (Figs. 731-732).
 ***dyscritus* Ratcliffe, new species**

Clave para las Especies de Adultos de *Hemiphileurus* de Costa Rica y Panamá

(las hembras de la mayoría de las especies no pueden ser identificadas excepto por asociación con los machos)

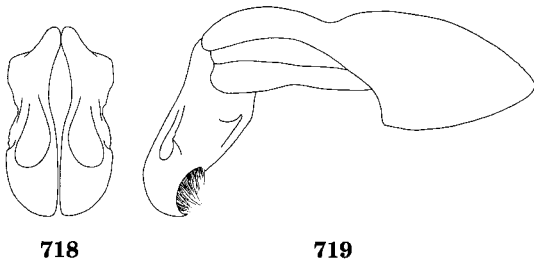
1. Elitros con intervalos alternos fuertemente elevados, cariniformes; 2 hileras de puntuaciones grandes entre los intervalos elevados
 ***dejeani* (Bates)**
- 1'. Elitros con todos los intervalos similares en altura 2
- 2 (1'). Ultimo esternito moderada a densamente puntuado 3
- 2'. Ultimo esternito puntuado o rugoso en una banda transversal solo a lo largo de la base, dispersamente puntuado en el resto 5
- 3 (2). Elitros con todos los intervalos similares: rectos, lisos, ligeramente aplanados ***pygidiopunctissimus* Ratcliffe, especie nueva**
- 3'. Elitros con los intervalos disímiles: ocasionalmente discontinuos, siempre de apariencia sinuada debido a la proyección lateral entre las puntuaciones de los surcos 4
- 4 (3'). Cada parámero en la base cada uno con un lóbulo lateral largo (Figs. 754-755) ***variolosus* (Burmeister)**
- 4'. Parámeros en la base sin un lóbulo lateral; en vez de eso, el ápice de cada parámero se proyecta en un lóbulo (Figs. 758-759) ***vicarius* Prell**
- 5 (2'). Borde anterior del surco pronotal con 2 pequeños tubérculos
 ***nebulohylaeus* Ratcliffe, especie nueva**
- 5'. Borde anterior del surco pronotal sin tubérculos 6
- 6 (5'). Elitros con intervalos con apariencia sinuada debido a la proyección lateral entre las puntuaciones de los surcos; élitros con apariencia confusamente esculpura ***cylindroides* (Bates)**
- 6'. Elitros con intervalos similares: rectos, lisos, ligeramente convexos. 7
- 7 (6'). Machos con cuernos, no tubérculos. Parte superior de la cabeza lisa
 ***simplex* (Prell)**
- 7'. Machos con tubérculos, nunca con cuernos. Parte superior de la cabeza puntuada a rugopuntuada 8
- 8 (7'). Parámeros en vista caudal, estrechándose ligeramente hacia el ápice (Figs. 735-736) ***laevicauda* (Bates)**
- 8'. Parámeros en vista caudal, ampliamente redondeados y bulbosos hasta el ápice (Figs. 718-719, 731-732) 9
- 9 (8'). Parámeros con una depresión alargada, expandida apicalmente, claramente delimitada en medio del asta de cada parámero (Figs. 718-719)
 ***curoei* Ratcliffe, especie nueva**
- 9'. Parámeros, cada uno con un área en declive en los bordes laterales, justo sobre el medio, sin una depresión claramente bordeada en el medio de cada asta (Figs. 731-732) ***dyscritus* Ratcliffe, especie nueva**

***Hemiphileurus curoei* Ratcliffe,
new species**
(Figs. 7118-720)

TYPE MATERIAL. Holotype labeled "PANAMA: Coclé, Cerro Gaital, 850 m, 13-20-VII-96, CUROE." Type deposited at the University of Nebraska State Museum.

HOLOTYPE. Male. Length 21.4 mm; width 9.9 mm. Color black. *Head:* Surface coarsely rugose to rugopunctate except for clypeus laterad of clypeal carinae where surface sparsely micropunctate. Vertex and frons with shallow, median, longitudinal furrow extending onto base of clypeus. Frons with tubercle anteromedial of each eye. Clypeus triangular, apex acute and strongly reflexed, a distinct, fine carina extending from clypeal apex to base of each tubercle. Interocular width equals 4.2 transverse eye diameters. Antenna with 10

segments, club subequal in length to segments 2-7. Mandibles narrow, lateral edge arcuate, apex acute. *Pronotum:* Surface with moderately large punctures; punctures moderate in density except in furrow and anterolateral quadrant where dense. Median furrow deep, broad, extending from near basal margin to near apical margin. Base with marginal bead. *Elytra:* Rows of punctures in deep furrows, furrows (especially 2nd, 3rd, 5th) interrupted by transverse extensions of intervals; punctures large, deep, umbilicate, separated by mostly 1 puncture diameter. Intervals convex, sparsely micropunctate, all of equal height. *Pygidium:* Base with narrow, very shallow furrow. Surface at base densely punctate, punctures moderately large, punctures becoming a little less dense and large apically, all punctures with minute, pale setae. In lateral view, surface convex. *Legs:* Foretibia tridentate. Apex of posterior tibia with upper angle prolonged as sharp, narrow tooth; several minute serrations and short, broad spinules below large tooth. Apex of basal tarsomere on posterior leg prolonged into long spine. *Venter:* Prosternal process moderately long, subquadrately columnar, apex bluntly rounded, base on posterior face with transverse ridge. Last sternite with large, dense punctures in basal third and smaller, sparse punctures in apical 2/3. *Parameres:* Figs. 718-719.



Figs. 718-719. *Hemiphileurus curoei* parameres.



Fig. 720. Distribution of *Hemiphileurus curoei* in Panama.

ETYMOLOGY. This species is named after Dan Curoe (Palo Alto, CA) who collected the specimen.

DISTRIBUTION. *Hemiphileurus curoei* is, so far, known only from Cerro Gaital above El Valle in Panama.

LOCALITY RECORDS (Fig. 720). 1 specimen examined.

PANAMA (1). COCLÉ (1): Cerro Gaital.

TEMPORAL DISTRIBUTION. July (1).

DIAGNOSIS. *Hemiphileurus curoei* is similar to both *H. laevicauda* (Bates) and *H. punctatostriatus* (Prell) in having elytra coarsely and densely punctate with the intervals all equal in height, last abdominal segment sparsely punctate in apical two thirds, frons with tubercles instead of horns, and a long prosternal process. The parameres of *H. curoei* are distinctive because of their large, rounded, blunt, and setose apices; simple, symmetrical form; and the distinct, oblong depression on the center of the face of each paramere. The parameres are most similar to those of *H. punctatostriatus*, but in this species the apices of the parameres are angulate and the deep hollow on the face of each paramere is absent [see the illustrations of the parameres, both taken directly from the type specimen, by Prell (1914) and Chalu-meau (1988)].

BIOLOGY. The type specimen was collected at lights in an area of subtropical moist forest at an elevation of 850 meters.

Hemiphileurus cylindroides
(Bates, 1888)
(Figs. 721-725)

Phileurus cylindroides Bates 1888: 340. Lectotype (here designated to stabilize the nomenclature) male at the Natural History Museum (BMNH, London) and labeled: (a) "R. Sucio, Costa Rica, H. Rogers," (b) "Phileurus cylindroides

Bates" (handwritten), (c) "B.C.A., Col., II(2), Phileurus cylindroides," (d) "Sp. Figured," (e) "Syntype" (blue-bordered, round label), (f) "Phileurus cylindroides Bates, LECTOTYPE, B. C. Ratcliffe" (red label). Five paralectotypes at BMNH labeled as follows: with same labels except label "b" and "d" above absent and with "PARALECTOTYP E B.C. Ratcliffe" (yellow label) (1 female specimen); (a) "Irazu, 6-7000 ft., H. Rogers," (b) "B.C.A., Col., II(2), Phileurus cylindroides," (c) "Syntype" (blue-bordered, round label), (d) "Phileurus cylindroides Bates PARALECTOTYPE, B. C. Ratcliffe" (yellow label) (3 male specimens); (a) "Costa Rica" (handwritten), and labels "b," "c," and "d" above (1 female). One male paralectotype at the Canadian National Collection (Ottawa) and labeled: (a) "Irazu, 6-7000 ft., H. Rogers," (b) "B.C.A., Col., II(2), Phileurus cylindroides," (c) "COTYPE, CNCNo. 8654, P. cylindroides Bates," (d) "Hemiphileurus cylindroides (Bates), Det. at B. M., H. F. Howden '62," (e) my yellow paralectotype label. Twelve paralectotypes at the Museum National d'Histoire Naturelle (Paris) labeled as follows: (a) "Irazu, 6-7000 ft., H. Rogers," (b) "H. W. Bates, Biol. Cent. Amer," (c) "Museum Paris, ex. Coll. R. Oberthur" (3 males, 3 females); (a) "Irazu, 6-7000 ft., H. Rogers," (b) "Ex Musaeo H. W. Bates 1892," (c) "Phileurus cylindroides Bates" (handwritten), (d) "Museum Paris, ex. Coll. R. Oberthur" (1 female); (a) "Costa Rica" (handwritten), (b) "H. W. Bates, Biol. Cent. Amer," (c) "Phileurus cylindroides Bates" (handwritten), (d) "Museum Paris, ex. Coll. R. Oberthur" (1 male); as preceding except label "c" absent (1 male, 1 female); (a) "V. de Chiriqui, 4000-8000 ft., Champion," (b) "H. W. Bates, Biol. Cent. Amer," (c) "Phileurus cylindroides Bates" (handwritten), (d) "Museum Paris, ex. Coll. R. Oberthur" (2 females).

Hemiphileurus costaricensis Endrödi 1978: 95
(NEW SYNONYMY).

Hemiphileurus jamesonae Ratcliffe 1988: 49
(NEW SYNONYMY).

DESCRIPTION. Length 19.0-22.0 mm; width 8.0-9.6 mm. Color black. *Head:* Top of head smooth, shining. Frons and vertex deeply concave. Frons with horn anteromedial of each eye; horn short to tall (subequal to width of head), recurving posteriorly, apex bluntly rounded. Clypeus triangular, apex acute and reflexed, a small carina extending from apex to base of each horn. Interocular width equals 7.0 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. Mandibles arcuate on lateral edge, apex acute. *Pronotum:* Surface mostly densely punctate, a little less so at base and moreso in anterior third where many punctures confluent; punctures large, deep, umbilicate. Median furrow extending from base to subapical declivity, furrow narrow, shallow. Base with marginal line. *Elytra:* Surface with punctate striae in furrows; punctures large (gradually becoming smaller at apex), deep, ocellate-umbilicate, usually less than 1 diameter apart except near suture where transverse wrinkles interrupt rows. Intervals convex, all of equal height, appearing sinuate because of lateral branching to between punctures in furrows, surface with sparse micropunctures. *Pygidium:* Surface moderately to densely punctate, punctures moderately large and with minute, pale setae. In lateral view, surface strongly convex. *Legs:* Foretibia tridentate. Apex of posterior tibia with upper angle prolonged into sharp, narrow tooth; several minute serrations and short, broad spinules below large tooth. Apex of first tarsomere of posterior tarsus prolonged into long spine. *Venter:* Prosternal process low, subconical, posterior face flattened, base with small projection. Last sternite with large, dense punctures in basal third and smaller, sparse punctures in apical 2/3. *Parameres:* Figs. 722-723.

DISTRIBUTION. *Hemiphileurus cylindroides* is known from western Panama and Costa Rica.

LOCALITY RECORDS (Figs. 724-725). 36 specimens examined.

COSTA RICA (30). CARTAGO (12): Quebrada Segunda, Volcan Irazu; HEREDIA (3):

Estación Barva; PUNTARENAS (5): Palma, San Luis (Reserva Biológica Monteverde), Tres Colinas; SAN JOSÉ (5): Rio Sucio, San Gerardo de Dota, San José; No data (5).

PANAMA (6). CHIRIQUI (6): Cerro Punta, Volcan de Chiriqui.

TEMPORAL DISTRIBUTION. February (1), April (4), June (4), July (1), September (2), November (1), December (2).

DIAGNOSIS. *Hemiphileurus cylindroides* is characterized by the relatively long head horns, smooth head, coarsely and densely punctate elytra with intervals all of equal height, and the form of the parameres.

NOMENCLATURE. Endrödi (1978) described *H. costaricensis* as new, but it is conspecific with *H. cylindroides*. The syntypes of *H. cylindroides* are in the British Museum (six specimens), the Canadian National Collection (one specimen), and the Museum National d'Histoire Naturelle in Paris (12 specimens). Endrödi must not have examined the Bates syntypes, or else he would have made lectotype designations and noticed that the parameres of *H. cylindroides* were identical to his *H. costaricensis*. Accordingly, lectotype designations are made here for the Bates syntypes in order to stabilize the nomenclature. Endrödi's *H. costaricensis* is placed into synonymy with *H. cylindroides*. The International Rules of Zoological Nomenclature (1999) recommend (74B) that a syntype that has been illustrated should be designated as the lectotype, and I have done that using a British Museum specimen that is labeled as the specimen figured in the *Biologia Centrali-Americana*.

Now the really interesting thing is that *H. cylindroides sensu* Endrödi (1978, 1985a) is, in fact, an undescribed species from Guatemala! Endrödi clearly illustrated the parameres of what he thought to be Bates' *H. cylindroides*, and, had he examined the Bates syntypes, he would have realized that he had these two species characterizations reversed. Consequently, the illustrations of the parameres in his 1985 manual are erroneous:

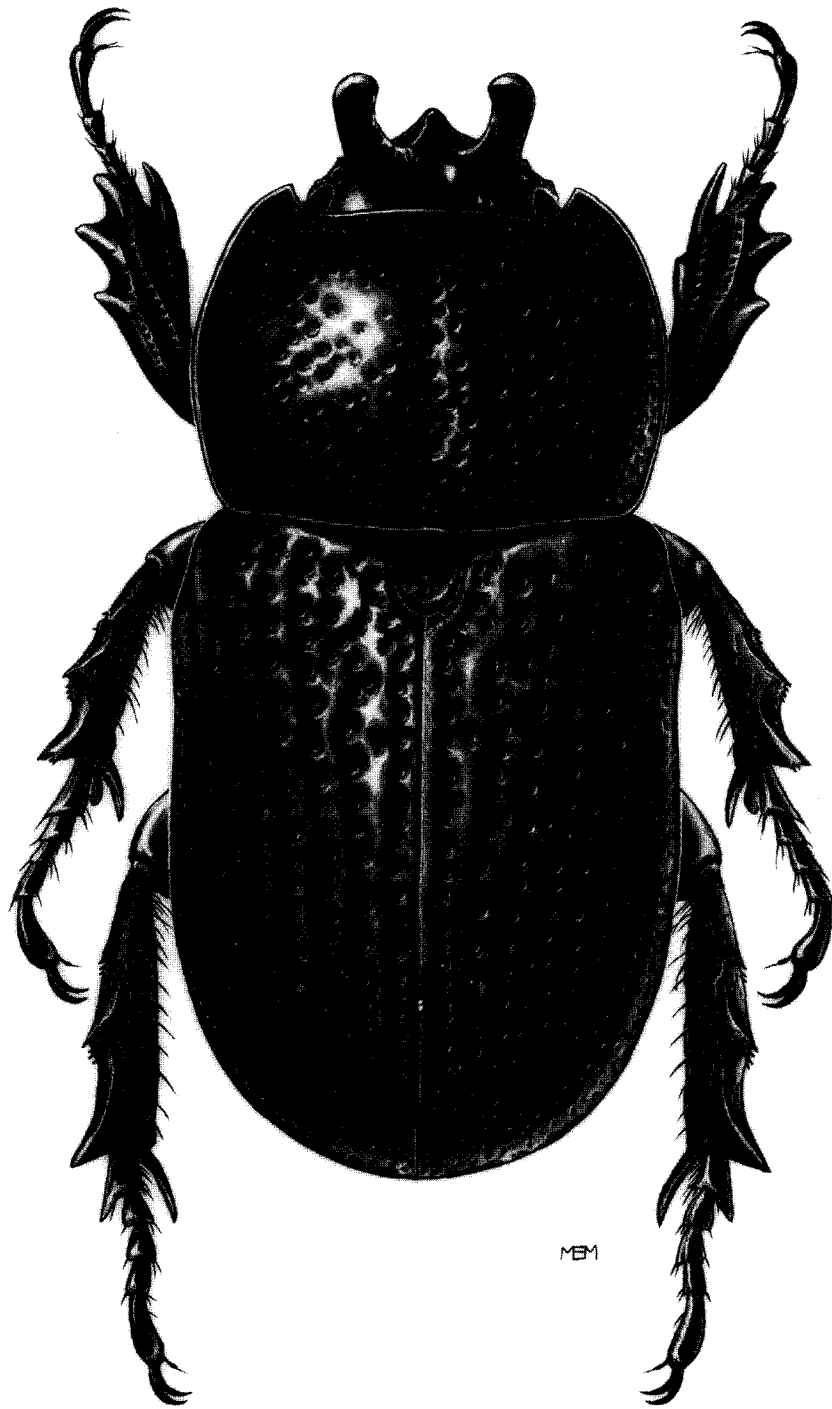
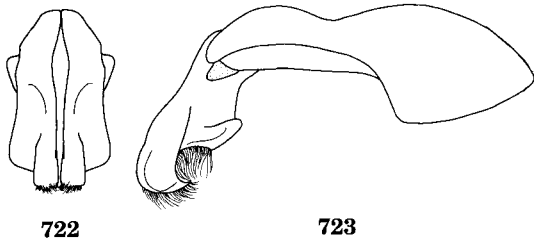


Fig. 721. *Hemiphileurus cylindroides*.



Figs. 722-723. *Hemiphileurus cylindroides* paramer.

his picture of *H. costaricensis* is really *H. cylindroides*, and his picture of *H. cylindroides* is really an un-named species from Guatemala that I am describing elsewhere.

After examining the syntypes of *H. cylindroides*, I determined that my (1988) *H. jamesonae* is conspecific with it.

BIOLOGY. Adults have been collected at lights in premontane rain forests, lower montane rainforests, and montane rain forests at elevations of 1,000-2,500 meters.



Fig. 724. Distribution of *Hemiphileurus cylindroides* in Costa Rica.

***Hemiphileurus dejeani* (Bates, 1888)**

(Figs. 726-730)

Phileurus dejeani Bates 1888: 340.

DESCRIPTION. Length 20.0-23.1 mm; width 9.2-10.7 mm. Color black. *Head:* Entire dorsal surface (except apex of clypeus) coarsely rugose to rugopunctate. Vertex with oval depression, not extending forward between bases of tubercles. Frons with tubercle mesad of anterior margin of each eye, bases of tubercles connected by a low ridge. Clypeus triangular, apex acute and strongly reflexed; a small carina extending from clypeal apex to base of each tubercle. Interocular width equals 6.0 transverse eye diameters. Antenna 10-segmented, club a little longer than segments 2-7. Mandibles arcuate on lateral edge,



Fig. 725. Distribution of *Hemiphileurus cylindroides* in Panama.

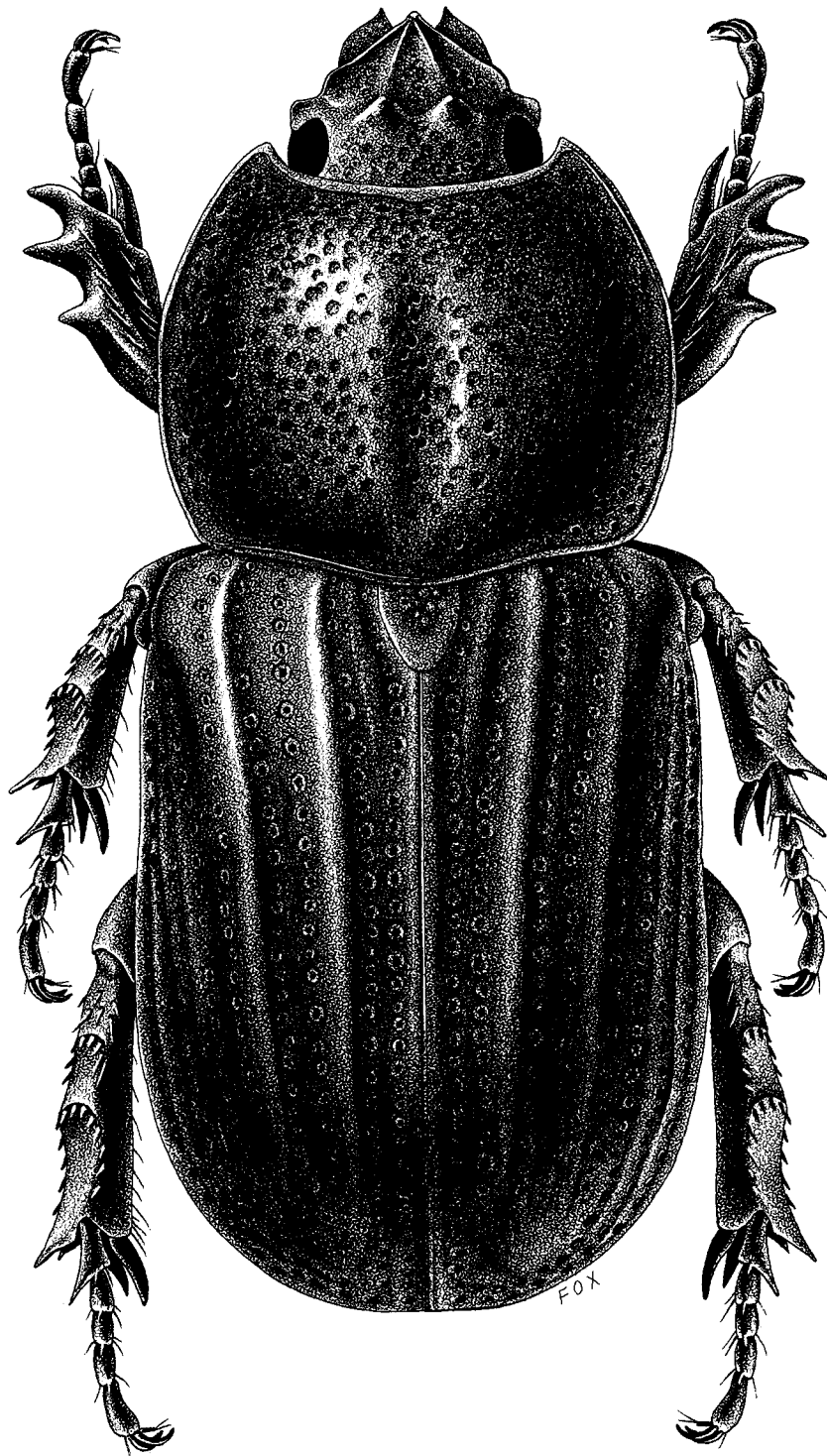
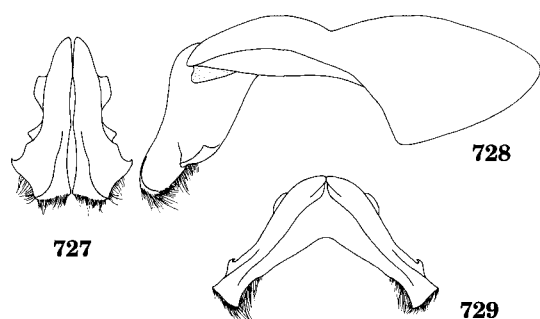


Fig. 726. *Hemiphileurus dejeani*.



Figs. 727-729. *Hemiphileurus dejeani* parameres.

apex acute. *Pronotum*: Surface with large, weakly ocellate punctures; punctures sparse either side of median furrow in basal half, becoming dense to rugopunctate on sides and rugose in anterior angles and behind anterior margin. Median, longitudinal furrow broad, deep, extending almost to both anterior and posterior margins, surface of furrow coarsely rugopunctate. Base with complete marginal bead. *Elytra*: Punctate rows paired, in furrows; punctures large, ocellate, separated by usually less than 1 puncture diameter. Intervals between paired rows strongly elevated, carinate, with sparse micropunctures. *Pygidium*: Surface completely, densely punctate; punctures moderately large at base, becoming large elsewhere, all with minute and pale setae. In lateral view, surface in males regularly convex; in females weakly convex to nearly flat and with transverse furrow at base. *Legs*: Foretibia tridentate. Apex of posterior tibia with triangular, acute tooth on upper angle and with several small serrations and short, broad spinules below tooth. Apex of first segment of posterior tarsus extended into long, acute spine. *Venter*: Prosternal process moderate in length, columnar, apex transversely oval and distinctly convex; posterior surface at base with prominent tooth. Last sternite with moderately large punctures in anterior third, elsewhere with sparse micropunctures. *Parameres*: Figs. 727-729.

DISTRIBUTION. *Hemiphileurus dejeani* is known from southern Mexico to the Brazilian Amazon (Endrödi 1978). The records listed

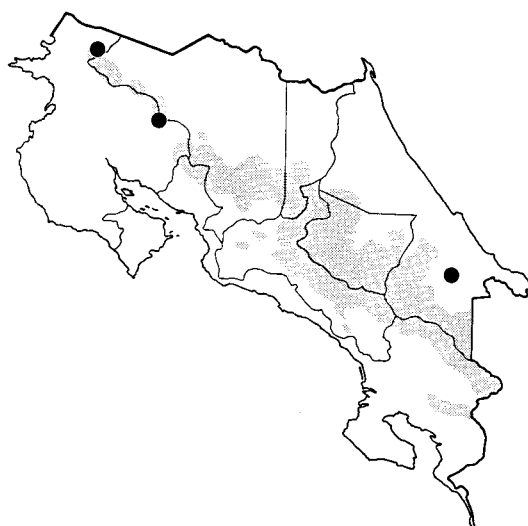


Fig. 730. Distribution of *Hemiphileurus dejeani* in Costa Rica.

below for Costa Rica constitute a **NEW COUNTRY RECORD**.

LOCALITY RECORDS (Fig. 730). 7 specimens examined.

COSTA RICA (7). **GUANACASTE** (6): Estación Pitilla, Tierras Morenas; **LIMÓN** (1): Estación Hitoy Cerere.

TEMPORAL DISTRIBUTION. March (1), April (3), May (1), October (2).

DIAGNOSIS. *Hemiphileurus dejeani* is unique among the Central American *Hemiphileurus* species in having the alternate intervals of the elytra strongly elevated or carinate. The suboval, concave apex of the prosternal process and the form of the parameres are also diagnostic. I advise caution when examining the parameres because, upon extraction, they may be either approximate or widely splayed apart. If widely separated (Fig. 729), they could appear to represent a different species when such is not the case.

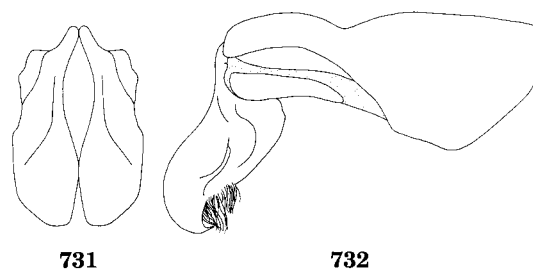
BIOLOGY. Adults have been taken at lights and can presumably be found with larvae in rotten logs. Adults have been collected from premontane moist forests and premontane wet forests at elevations of 100-1,050 meters.

***Hemiphileurus dyscritus* Ratcliffe,
new species**
(Figs. 731-734)

TYPE MATERIAL. Holotype labeled "Est. Maritza, 600 m, Lado O Vol. Orosi, Prov. Guan., COSTA RICA, tp. malaise, 1989, L-N-326900, 373000." Allotype labeled "Playa Naranjo, Sta. Rosa, P.N. Guanacaste, Prov. Guan., COSTA RICA, E. Alcazar, Oct. 1990, L-N-309300-353300." Paratypes (11) with the following data: "Río Sn. Lorencito, 900 m, Res. For. Sn. Ramón, 5 km N Col. Palmareña, Alajuela, COSTA RICA, Mar. 1990, Curso Carabidae, 244500-470700" (1); "Loc. La Palma, Col. P. Biolley" (1); "Estac. Santa Rosa, 300 m, Guanacaste Prov., COSTA RICA, 1987, GNP Biodiversity Survey, 313000, 359800" (1); "Santa Rosa National Park, Guana. Prov., Costa Rica, 15-17 May 1979, D.H. Janzen" (1); same data but 6-14 March 1977 (1); "San Rafael, HEREDIA, Costa R., 16 Abril 1984, Corrales J.C." (1); "Costa Rica: Puntarenas, San Luis, San Luis Vly, VIII-26-1996, coll. Louis La Pierre" (1); "San José, CR, V-25-26, at light, Nevermann Collectioin 1940" (1); "Barro Colorado I., Canal Zone, Pan., VIII-26-1977, R.B. & L.S. Kimsey" (1); "PANAMA-Canal Zone, Barro Colorado Island, 1 April 1956, Carl W. & Marian E. Rettenmeyer, No." (1); "Nicaragua, Waulas R. Val." (possibly Waula Rapids on Raspuk River) (1).

Holotype, allotype and four paratypes at INBio (Santo Domingo de Heredia, Costa Rica). Remaining paratypes at U. S. National Museum (Washington, D.C., currently at University of Nebraska), University of California (Davis), University of Nebraska State Museum (Lincoln), Alex Reifschneider collection (Sierra Madre, CA), and Brett C. Ratcliffe collection (Lincoln, NE).

HOLOTYPE. Male. Length 21.0 mm; width 10.1 mm. Color black. *Head:* Frons with longitudinal, broad, deep furrow extending to clypeus; surface coarsely rugopunctate. Small tubercle located anteromedially of each eye. Clypeus triangular, apex acute and strongly reflexed; surface with moderately spaced and moderately large punctures mesad of nearly obsolete clypeal carinae, with sparse micro-



Figs. 731-732. *Hemiphileurus dyscritus* parameres.

punctures elsewhere. Interocular width equals 4.6 transverse eye diameters. Antenna 10-segmented, club a little longer than segments 2-7. Mandibles with lateral edge arcuate, apex acute. *Pronotum:* Surface either side of median furrow with large, moderately dense punctures; punctures becoming denser in anterior angles, a little smaller along sides. Median longitudinal furrow deep, broad, extending almost to basal and apical margins; surface of furrow with large, mostly confluent punctures. Base with marginal bead. *Elytra:* Rows of punctures in furrows; punctures large, deep, ocellate-umbilicate, separated mostly by about 1 puncture diameter. Intervals convex, with sparse micropunctures, subequal in height. *Pygidium:* Base with transverse, broad, feeble furrow. Surface at base with dense, moderately large punctures; punctures with minute, tawny setae and becoming moderate in density on apical 2/3. In lateral view, surface convex. *Legs:* Foretibia tridentate. Apex of posterior tibia with upper angle prolonged into acute tooth; several minute serrations and short, broad spinules below large tooth. Apex of basal tarsomere on posterior tarsus prolonged into long spine. *Venter:* Prosternal process moderately long, subtriangularly columnar, apex subtriangular and bluntly rounded, base on posterior surface with small transverse ridge. Last sternite in basal half with dense, moderately large punctures, apical half with sparse punctures. *Parameres:* Figs. 731-732.

ALLOTYPE. Female. Length 19.7 mm; width 9.4 mm. As holotype except in the following respects: *Head:* Interocular width equals 4.3 transverse eye diameters. *Pronotum:* Surface sparsely punctate either side

of furrow. *Pygidium*: Surface entirely covered with large, moderately dense punctures; punctures with moderately long, tawny setae. In lateral view, surface weakly convex.

VARIATION. Males (7 paratypes). Length 18.4-23.3 mm; width 9.1-11.4 mm. As holotype except in the following respects: *Head*: 2 specimens with sparser punctation. *Interocular width* as type to 5.0 transverse eye diameters. *Pronotum*: 2 specimens with sparser punctation either side of furrow (similar to allotype). *Pygidium*: 2 specimens (both Panamanian)

with surface completely and densely punctate as in allotype.

Females (4 paratypes). Length 20.7-21.1 mm; width 9.6-9.8 mm. As allotype except in the following respects: *Pygidium*: 1 specimen with sparser punctation on disc (as holotype). The female paratypes differ very little from the allotype.

ETYMOLOGY. From the Greek *dyskritos*, meaning hard to determine; in reference to the initial and relative difficulty in separating this species from several of its congeners.

DISTRIBUTION. *Hemiphileurus dyscritus* is known from the Atlantic coast of Nicaragua through Costa Rica and in the center of Panama. Presumably, it will also be found in other areas of Panama and Costa Rica.

LOCALITY RECORDS (Figs. 733-734). 13 specimens examined. One specimen is from Nicaragua.

COSTA RICA (11). ALAJUELA (1): Río San Lorencito; GUANACASTE (6): Estación Maritza, Estación Santa Rosa, Playa Naranjo; HEREDIA (2): La Palma, San Rafael; PUNTARENAS (1): San Luis; SAN JOSÉ (1): San José.

PANAMA (2). CANAL ZONE (2): Barro Colorado Island.



Fig. 733. Distribution of *Hemiphileurus dyscritus* in Costa Rica.



Fig. 734. Distribution of *Hemiphileurus dyscritus* in Panama.

TEMPORAL DISTRIBUTION. March (2), April (2), May (2), August (2), October (1).

DIAGNOSIS. *Hemiphileurus dycritus* is similar to *H. curoei* (Panama) and *H. punctatostriatus* Prell (Belize and Mexico). The only way to separate it from *H. curoei* is by the form of the male's parameres; each paramere of *H. dycritus* lacks the distinctive, oblong depression in the center that is typical of *H. curoei*, and the apices in *H. dycritus* are more angularly rounded whereas they are broadly and bluntly rounded in *H. curoei*. From *H. punctatostriatus* (which, contrary to Endrödi 1978, does not occur in Costa Rica or Panama), *H. dycritus* has parameres that narrow apically rather than being subparallel or widening slightly until apex [see Fig. 28 in Prell (1914) and Fig. 8 in Chalumeau (1988), both drawn from the type of *H. punctatostriatus*]. Females of *H. curoei* and *H. punctatostriatus* remain unknown and so identifying and separating them (other than by association with males) is not possible.

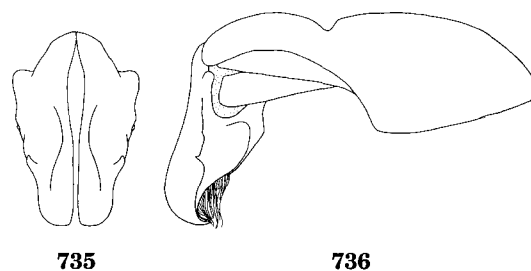
BIOLOGY. Adults have been collected at lights in a number of habitats including tropical dry forests, tropical moist forests, premontane moist forests, and premontane rain forests. They have been taken at elevations of 300-600 meters.

***Hemiphileurus laevicauda* (Bates, 1888)**

(Figs. 735-738)

Phileurus laevicauda Bates 1888: 339.

DESCRIPTION. Length 20.0-21.7 mm; width 10.1-10.7 mm. Color black. *Head:* Frons with shallow, longitudinal depression extending between tubercles to clypeus; surface (especially in depression) with sparse to moderate punctures, punctures small to moderate in size. Prominent tubercle present anteromedial of each eye. Clypeus triangular, apex acute and reflexed; surface with small, sparse punctures, punctures a little larger between clypeal carinae; prominent carina extends from clypeal apex to base of each tu-



Figs. 735-736. *Hemiphileurus laevicauda* parameres.

bercle. Interocular width equals 6.0 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. Mandibles arcuate on lateral edge, apex acute. *Pronotum:* Surface with large, moderately dense, weakly umbilicate punctures; punctures becoming denser on sides and in anterior angles and sparser either side of median furrow and at base. Median longitudinal furrow shallow, broad, extending anteriorly from near base to just past middle of pronotum. Base with complete marginal bead. *Elytra:* Rows of punctures in furrows; punctures large, ocellate-umbilicate, most separated by about 1 puncture diameter. Intervals convex, all of equal height, with sparse micropunctures. *Pygidium:* Base with broad, shallow, transverse furrow. Surface at base with moderately dense, moderately-sized punctures; punctures becoming sparser apically or not, all with minute, tawny setae. In lateral view, surface convex in males, probably less convex in females (which are unknown). *Legs:* Foretibia tridentate. Apex of posterior tibia with large, acute tooth on upper angle and with several small serrations and short, broad spinules below angle. Apex of basal tarsomere of posterior tarsus extended into acute spine. *Venter:* Prosternal process relatively long, columnar, apex bluntly, subtriangularly rounded, base with large prominence on posterior surface. *Parameres:* Figs. 735-736.

DISTRIBUTION. *Hemiphileurus laevicauda* is known from southern Mexico, Guatemala, El Salvador, and Costa Rica (Endrödi 1978). The specimen listed below for Panama is a NEW COUNTRY RECORD. This species is a

rare insect and is known from only a few localities throughout its range.

LOCALITY RECORDS (Figs. 737-738). 6 specimens examined.

COSTA RICA (5). **HEREDIA** (2): La Selva Biological Station, No data; **GUANACASTE** (3): Estación Maritza, Estación Murciélago, Santa Rosa National Park.

PANAMA (1). **CHIRIQUI** (1): Hartmann's Finca (Santa Clara).



Fig. 737. Distribution of *Hemiphileurus laevicauda* in Costa Rica.



Fig. 738. Distribution of *Hemiphileurus laevicauda* in Panama.

TEMPORAL DISTRIBUTION. February (1), May (2), June (1), July (1).

DIAGNOSIS. *Hemiphileurus laevicauda* adults are characterized by the presence of tubercles (instead of horns) on the head, a foreshortened median furrow on the pronotum, elytra with all intervals of equal height, a moderately long prosternal process, last sternite with dense punctation only on basal third, and distinctive male parameres. The females remain unknown or at least unassociated with males.

BIOLOGY. Adults have been collected at lights. In Costa Rica and Panama, specimens were collected in premontane moist forests and premontane wet forests at elevations of 100-900 meters.

Hemiphileurus nebulohylaeus
Ratcliffe, new species

(Figs. 739-743)

TYPE MATERIAL. Holotype labeled "COSTA RICA: Puntarenas, Monteverde Forest Res., V-19-21-1988, 1500 m, B. Ratcliffe & M. Jameson." Allotype labeled "COSTA RICA, Monteverde Cloud Forest, 14-18 June 84." Nine paratypes with the following data: same as allotype but with dates of 2 April 83 (1) and 26 July 84 (1); "COSTA RICA: Punt. Pr.,

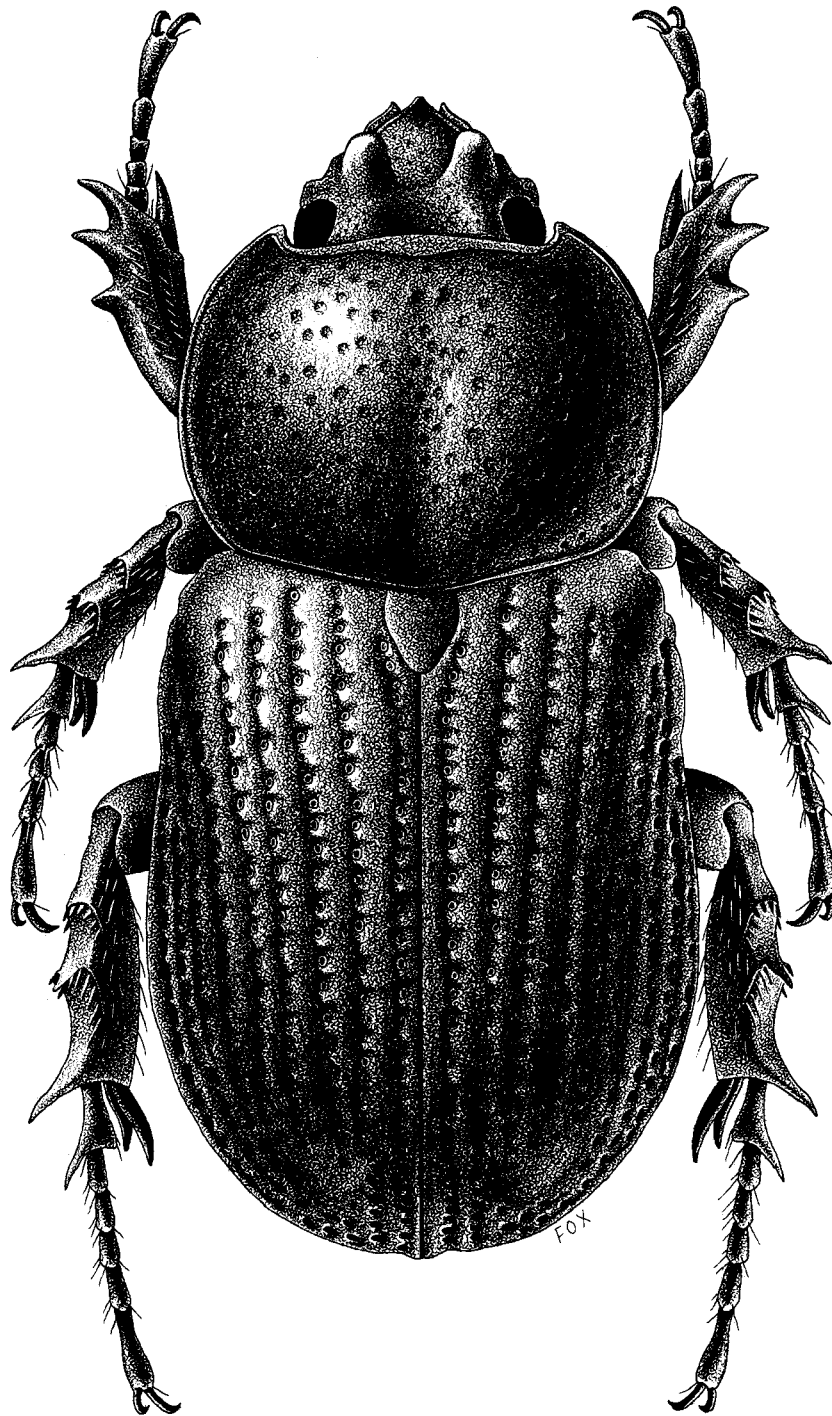
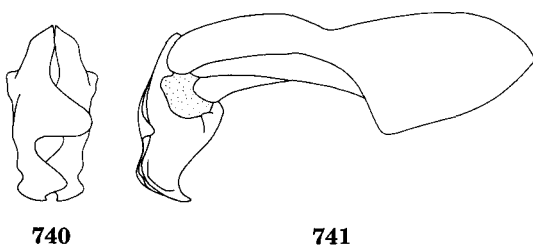


Fig. 739. *Hemiphileurus nebulohylaeus*.



Figs. 740-741. *Hemiphileurus nebulohylaeus* parameres.

Monteverde Cloud For. Res. & vic., ± 1450-1550 m, 17 June 1994, Coll. F.T. Hovore" (1); "San Luis, 1040 m, R.B. Monteverde, Prov. Puntarenas, Costa Rica, Jul. 1992, Z. Fuentes, L-N 250850, 449250" (1); "COSTA RICA, Cart., 7 km E of Moravia, VI/90, 1050 m, A. Brenes" (1); "COSTA RICA: Cartago, Ref. Nac. Tapanti, N 9°42', W83°46', V-20-21-1995, elev. 4,200', B. Ratcliffe & M. Jameson" (1); "Chiriqui, May 1980, Panama, Th. Porion," "Museum Paris, ex coll. R.-P. Dechambre" (1); "PANAMA: B del Toro, Culebra trail, 1450 M, (vic. Boquete) 3-8-vi 97, Curoe col., LOG" (1); "PANAMA: Chiriqui Prov., Reserva La Fortuna, Est. Biológica, el. 1200 M, 08°43'18" N, 82°14'17" W, 4-8-VIII-1999, A. R. Gillogly, to UV/MV lights" (1).

Holotype and allotype deposited at the University of Nebraska State Museum. Paratypes deposited at INBio (Santo Domingo de Heredia, Costa Rica), California Academy of Sciences (San Francisco, CA), Dan Curoe (Palo Alto, CA), David Carlson (Fair Oaks, CA), Museum National d'Histoire Naturelle (Paris), and Brett C. Ratcliffe (Lincoln, NE).

HOLOTYPE. Male. Length 20.1 mm; width 19.4 mm. Color black. *Head:* Vertex and frons mesad of each eye and in median depression with sparse, moderately-sized punctures; surface of clypeus with vague, shallow, sparse punctures. Frons between eyes with median, oval depression; large, erect, conical tubercle present mesad of each eye canthus. Clypeus subtriangular, apex acute and strongly reflexed; carina extending from clypeal apex to base of each tubercle feeble, indistinct. Interocular width equals 6.0 transverse eye diameters. Antenna with 10 segments, club

subequal in length to segments 2-7. Mandibles with outer edge arcuate, apices acute. *Pronotum:* Surface with large, deep punctures; punctures ocellate, moderately spaced in general, becoming slightly denser in center of disc either side of midline and behind anterior margin and in median furrow. Median, longitudinal furrow shallow, narrow, not reaching anterior or basal margin; anterior end of furrow with 2 very small tubercles (nearly obsolete). Base with complete marginal line. *Elytra:* Rows of punctures in furrows; punctures moderately large to large, separated by about 1 puncture diameter, ocellate-umbilicate. Intervals cariniform, all of equal height, with small, sparse punctures. *Pygidium:* Surface moderately punctate (denser at base); punctures moderate to large, deep, ocellate, setigerous; setae minute, tawny. In lateral view, surface regularly convex. *Legs:* Foretibia tridentate. Apex of posterior tibia with large triangular tooth on upper angle and 2 small serrations (with 2 broad, short spinules on right leg and 3 spinules on left leg) below upper angle. Apex of base of first tarsomere on posterior tarsus extended into long, triangular spine. *Venter:* Prosternal process long, subtriangularly columnar, apex flattened and subtriangular, posterior surface with feeble, transverse protrusion at base. Last sternite with narrow band of transverse rugosity at base and with small, sparse punctures elsewhere. *Parameres:* Figs. 740-741.

ALLOTYPE. Female. Length 21.2 mm; width 10.2 mm. As holotype except in the following respects: *Head:* Surface densely, completely rugopunctate from vertex to just in front of tubercles. Tubercles smaller, closer together (2 tubercle diameters apart). Interocular width equals 5.0 transverse eye diameters. *Pronotum:* Punctures in general moderately dense to dense in anterior angles. *Pygidium:* Punctures dense at base, moderately dense elsewhere. In lateral view, surface weakly convex. *Legs:* Apex of posterior tibia below upper angle with 4 small serrations and 5 small, short, broad spinules. *Venter:* Last sternite densely, transversely rugose in basal third, moderately punctate elsewhere (punctures small to moderate in size).

VARIATION: Males (7 paratypes). Length 19.4-21.8 mm; width 9.3-10.2 mm. As holotype except in the following respects: *Pronotum*: Median furrow reaches base in 1 specimen; subapical tubercles absent in 1 specimen. *Pygidium*: Larger punctures sparsely punctate in apical third. *Legs*: Apex of posterior tibia below upper tooth as holotype (4 specimens) or having 5 small serrations and 5 small spinules (1 specimen).

Females (2 paratypes). Length 19.0-21.4 mm; width 9.2-10.2 mm. The female paratypes do not differ significantly from the

allotype. One specimen has short (instead of minute) setae on the pygidium.

ETYMOLOGY. From the Latin *nebula*, meaning "mist," "fog," or "cloud," and the Greek *hylaios*, meaning "of the forest;" combined to mean "of the cloud forest" in reference to the types of forest in which this species has been found.

DISTRIBUTION. *Hemiphileurus nebulohylaesus* is known from three localities in the mountains of central Costa Rica and from western Panama.

LOCALITY RECORDS (Figs. 742-743). 10 specimens examined.

COSTA RICA (8). **CARTAGO** (2): Moravia (7 km E), Refugio Nacional de Tapanti; **PUNTA-RENAS** (6): Monteverde Forest Reserve, San Luis (Reserva Biológica Monteverde).

PANAMA (2). **BOCAS DEL TORO** (1): Culebra trail (vicinity of Boquete); **CHIRIQUI** (2): Chiriqui (?), Reserva La Fortuna.

TEMPORAL DISTRIBUTION. April (1), May (3), June (4), July (2), August (1).

DIAGNOSIS. *Hemiphileurus nebulohylaesus* is characterized by the presence of tubercles (larger in the males) on the frons, weak clypeal carinae, cariniform and equally elevated elytral intervals, moderately densely



Fig. 742. Distribution of *Hemiphileurus nebulohylaesus* in Costa Rica.



Fig. 743. Distribution of *Hemiphileurus nebulohylaesus* in Panama.

punctate pygidium, last sternite with rugosity at the base and sparse punctures elsewhere (males) or moderately punctate elsewhere (females), long prosternal process with a subtriangularly flattened apex, and form of the male parameres.

This species is most similar to *H. pygidiopunctissimus* but differs in the form of the parameres, less densely punctate pygidium and last sternite, and bituberculate apex of the pronotal median furrow. Identifying unassociated females remains problematic as is the case with most of the species in this genus.

BIOLOGY. Adults are attracted to lights, and one specimen was collected from a rotting log. This species has been collected from premontane rain forests and montane rain forests at elevations of 1,040-1,550 meters.

***Hemiphileurus*
pygidiopunctissimus Ratcliffe,
new species
(Figs. 744-747)**

TYPE MATERIAL. Holotype labeled "PANAMA-Canal Zone, Barro Colorado Island, May 16, 1956, Carl W. & Marian E. Rettenmeyer. No.," "Taken at light, Time: —." Allotype labeled "PANAMA C.Z., Barro Colo. Isl., 24-IV-1978, C.D. Jorgensen." Single paratype labeled "PANAMA: C.Z., Ft. Gulick, V-1977, lights, A. Thurman."

Holotype and allotype deposited at the University of Nebraska State Museum. Paratype in the collection of Brett C. Ratcliffe (Lincoln, NE).

HOLOTYPE. Male. Length 23.0 mm; width 11.2 mm. Color black. *Head:* Vertex and frons surrounding eye with moderately large, dense punctures; frons between tubercles with deep, broad, longitudinal depression extending onto clypeus; surface within depression mostly smooth and with sparse, transverse rugae or punctures. A conical tubercle present either side median depression. Clypeus triangular, apex narrowly rounded (subtuberculate) and strongly reflexed; a strong carina extending

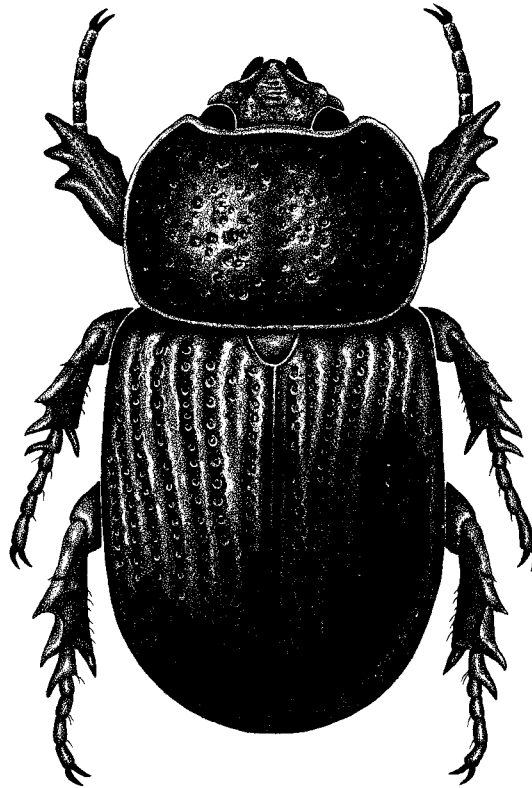
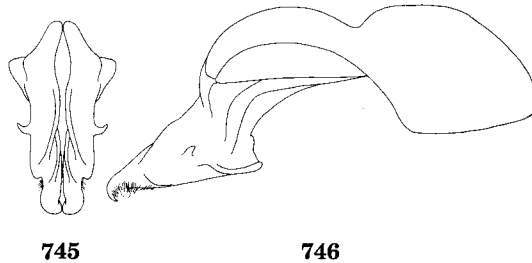


Fig. 744. *Hemiphileurus pygidiopunctissimus*.



Figs. 745-746. *Hemiphileurus pygidiopunctissimus* parameres.

from clypeal apex to base of each tubercle. Interocular width equals 7.0 transverse eye diameters. Antenna with 10 segments, club slightly longer than segments 2-7. Mandibles arcuate laterally, apices acute. *Pronotum:* Surface with moderately dense, large punctures; punctures deep, setigerous; setae minute, tawny in color. Median, longitudinal furrow shallow, narrow, extending from near base to about middle of pronotum. Base with complete marginal line. *Elytra:* Rows of punctures

in shallow furrows; punctures deep, mostly large, weakly umbilicate, separated from one another mostly by 1 puncture diameter or less. Intervals all nearly flat, with sparse, small punctures. *Pygidium*: Surface completely, densely punctate; punctures large, deep, nearly confluent near base, setigerous; setae short, tawny. Base with shallow, narrow, transverse depression either side of middle. In lateral view, surface strongly convex. *Legs*: Foretibia tridentate. Apex of posterior tibia with acute tooth on upper angle; probable serrations and short, broad spinules below large tooth worn away. Apex of first tarsomere on posterior tarsus prolonged into acute spine. *Venter*: Prosternal process moderately long, thick, apex flattened and subtrapezoidal; posterior surface of process near base with transverse protrusion. Last sternite with moderately-sized, dense, deep punctures on entire surface. *Parameres*: Figs. 745-746.

ALLOTYPE. Female. Length 23.8 mm; width 11.6 mm. As holotype except in the following respects: *Head*: Tubercles of frons a little smaller. Median furrow shallow and nearly completely, transversely rugopunctate within. *Pygidium*: Punctures nearly confluent over entire surface. *Legs*: Apex of posterior tibia with several small serrations and short, broad bristles below large tooth.

VARIATION. Females (1 paratype). Length 23.9 mm; width 11.6 mm. The paratype does not differ significantly from the allotype.

ETYMOLOGY. From the Greek *pyge*, meaning "rump" or "pygidium," and *punctum*, meaning "spot" or "puncture"; combined in the superlative to indicate a very densely punctate pygidium.

DISTRIBUTION. *Hemiphileurus pygidiopunctissimus* is known only from the former Canal Zone in present day Panama Province, Panama. The paratype locality of Fort Gulick (now Fort Espinar) is about 16 km due north of Barro Colorado island.

LOCALITY RECORDS (Fig. 747). 3 specimens examined.

PANAMA (3). **CANAL ZONE** (3): Barro Colorado Island, Ft. Gulick.

TEMPORAL DISTRIBUTION. April (1), May (2).

DIAGNOSIS. *Hemiphileurus pygidiopunctissimus* is distinguished by the presence of tubercles (not horns) on the frons, strong clypeal carinae, equally elevated and flattened elytral intervals, densely punctate

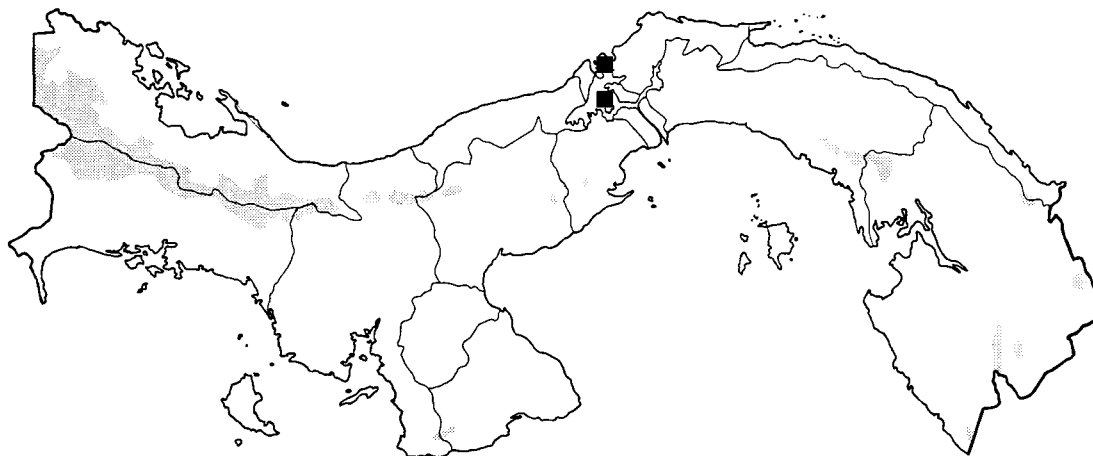


Fig. 747. Distribution of *Hemiphileurus pygidiopunctissimus* in Panama.

pygidium and last sternite, long prosternal process with a subtrapezoidally flattened apex, and form of the male parameres. Externally, this species is similar to *H. variolosus*, *H. vicarius*, and especially *H. nebulohylaeus* except that in *H. pygidiopunctissimus* the punctation of the pygidium and last sternite is denser and the median furrow of the pronotum is shorter and shallower. Given the sometimes variable expression of punctures, the degree of punctation on the pygidium and last sternite may not be sufficient to identify unassociated females of *H. pygidiopunctissimus*.

BIOLOGY. Two of the three type specimens are known to have been attracted to lights, but, considering the apparent rarity of specimens in these well-collected areas, I wonder if this species or other *Hemiphileurus* species are ever strongly attracted to lights. The type specimens were collected from lowland tropical moist forests at elevations of 100-500 meters.

***Hemiphileurus simplex* (Prell,
1914)**

(Figs. 748-752)

Epiphileurus simplex Prell 1914: 224.

Hemiphileurus fraternus Arrow 1937b: 55 (synonym).

DESCRIPTION. Length 16.0-19.5 mm; width 7.5-9.0 mm. Color black. *Head:* Surface in males entirely smooth, females coarsely rugopunctate in basal half and becoming sparsely punctate to nearly smooth apically. Frons in male majors with long (3 mm), slightly recurving, acuminate horns; male minors with shorter horns, females with tubercles. Clypeus triangular, apex acute and strongly reflexed; strong carina extending from clypeal apex to base of each horn or tubercle; region between carinae elevated from plane of disc. Eyes small, interocular width equals 10.0 transverse eye diameters. Antenna 10-segmented, club slightly longer than segments 2-7. Mandibles arcuate on lateral

edge, apices acute. *Pronotum:* Surface with large, deep punctures; punctures sparse either side of median furrow and on sides, moderate in density in band between furrow and sides, and dense (confluent) in anterior angles in males, similar or less dense in females. Median longitudinal furrow shallow, broad, extending from near base to just past middle of disc; surface of furrow with sparse, moderate to large, often confluent punctures. Base with complete marginal line. *Elytra:* Rows of punctures in furrows; punctures moderate to large, ocellate-umbilicate, separated by about 1 puncture diameter or less between large punctures or about 2 diameters between smaller punctures. Intervals weakly to distinctly convex, all subequal in height, with sparse micropunctures. *Pygidium:* Surface in males moderately densely punctate; punctures moderate to large, minutely setigerous, becoming a little sparser apically; surface in females similar except punctures denser. In lateral view, males with surface normally convex, weakly convex in females. *Legs:* Foretibia tridentate. Apex of posterior tibia with strong, acute tooth on upper angle and with several small serrations and short, broad spinules below upper angle. Apex of first tarsomere of posterior tarsus extended into long, acute spine. *Venter:* Prosternal process short, triangularly columnar, apex bluntly and narrowly rounded, posterior surface with feeble prominence. Last sternite with sparse, moderately large punctures along basal margin, elsewhere sparsely micropunctate. *Parameres:* Figs. 749-750.

DISTRIBUTION. *Hemiphileurus simplex* is known from Guatemala, Costa Rica and Panama (Endrödi 1978). In Panama, this species is restricted to the mountains in Chiriqui province.

LOCALITY RECORDS (Figs. 751-752). 35 specimens examined.

COSTA RICA (30). ALAJUELA (6): Estación Laguna Pocosol (Monteverde), Zarcero; HEREDIA (5): La Riberia de Belén, San Rafael, INBio (Santo Domingo), Universidad

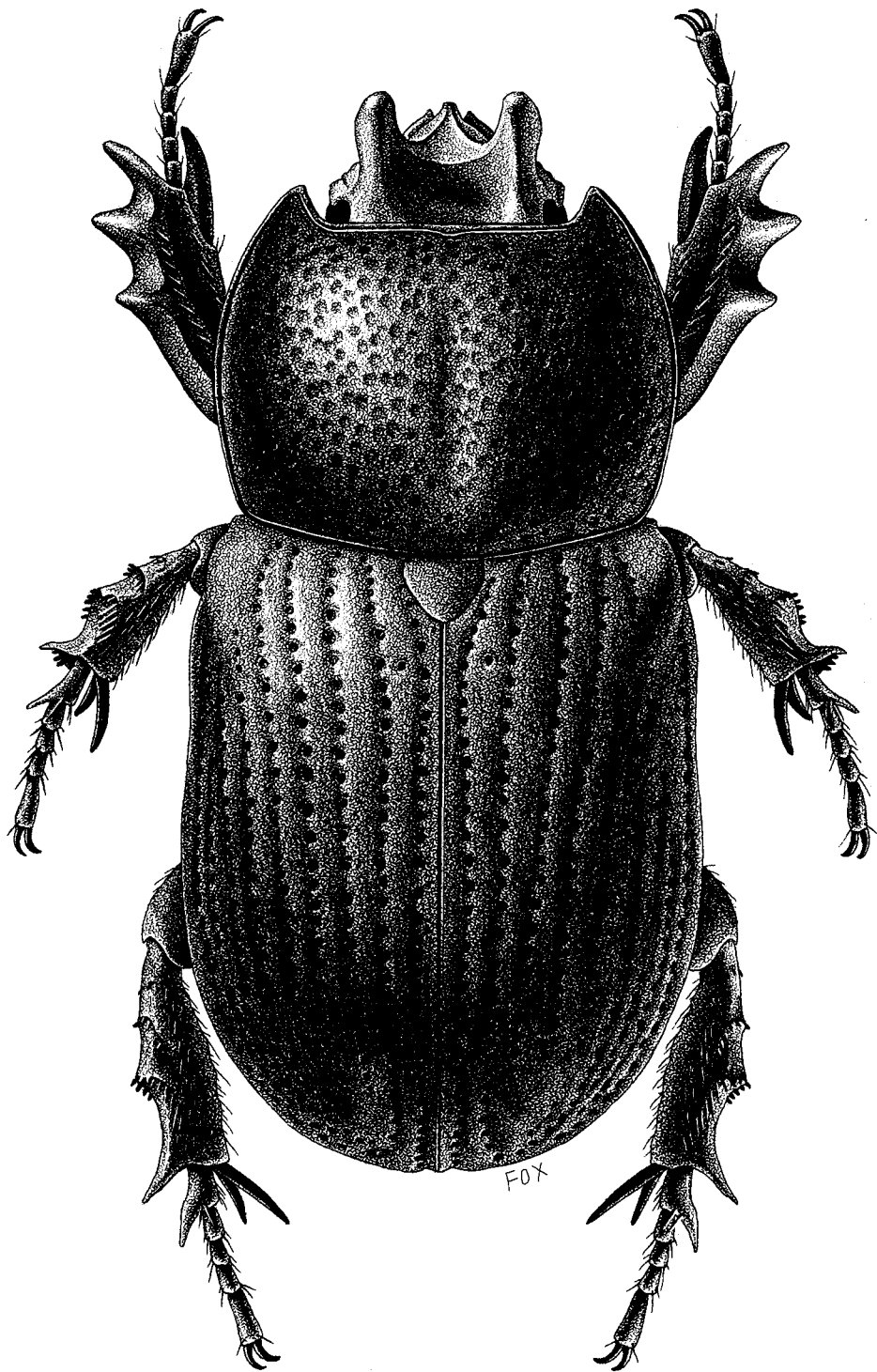
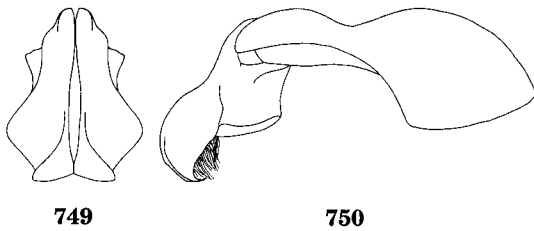


Fig. 748. *Hemiphileurus simplex*.



Figs. 749-750. *Hemiphileurus simplex* parameres.



Fig. 751. Distribution of *Hemiphileurus simplex* in Costa Rica.



Fig. 752. Distribution of *Hemiphileurus simplex* in Panama.

Nacional; PUNTARENAS (16): Monteverde; SAN JOSÉ (3): San José, San Pedro.

PANAMA (5). CHIRIQUI (5): Boquete, Bugaba, Hartmann's Finca, Rovira (3 mi. NW), Santa Clara (3.5 km NE).

TEMPORAL DISTRIBUTION. January (1), February (1), March (3), April (4), May (4), June (6), July (2), August (5), September (3), November (2).

DIAGNOSIS. *Hemiphileurus simplex* is characterized by the surface of the head nearly smooth, major males with horns, pronotum with a short and feeble median furrow, elytral intervals all of equal height, prosternal process small and columnar, and form of the male parameres.

BIOLOGY. This is a relatively uncommon species, and nothing is known of the immature stages or its life history. Adults have been taken at lights in premontane rain forests, lower montane rain forests, premontane wet forests, and premontane moist forests at elevations of 850-1,700 meters.

Hemiphileurus variolosus
(Burmeister, 1847)

(Figs. 753-757)

Phileurus variolosus Burmeister 1847: 156.
Epiphileurus irregularis Prell 1914: 225 (synonym).

Hemiphileurus variolosus striatus Endrödi 1978: 90 (NEW SYNONYMY, described as subspecies).

DESCRIPTION. Length 18.0-23.0 mm; width 9.0-11.0 mm. Color black. *Head:* Surface rugopunctate except clypeus laterad of each clypeal carina where punctures sparse, minute. Frons with conical tubercle either side of median depression; median depression deep, broad, extending from frons to near apex of clypeus. Clypeus triangular, apex acute and strongly reflexed, a fine carina extending from clypeal apex to base of each tubercle. Interocular width equals 6.0 transverse eye diameters. Antenna with 10 segments, club slightly longer than segments 2-7. Mandibles arcuate on lateral edge, apices acute. *Pronotum:* Surface with punctures mostly moderate in size; punctures sparse either side of median depression, dense near lateral and anterior margins and in median furrow, mostly deep. Median, longitudinal furrow moderately deep, moderately broad, extending from base to anterior third of pronotum. Marginal bead present along base. *Elytra:* Rows of punctures in longitudinal furrows with intervals elevated between rows as well as between individual punctures in rows (creating an appearance of coarse, irregular punctation); punctures moderate in size, ocellate-umbilicate, separated by 1-3 (mostly 2) puncture diameters. Intervals with small, sparse punctures. *Pygidium:* Surface densely punctate; punctures moderately large, nearly confluent basally, slightly less dense apically, setigerous; setae short, tawny. In lateral view, surface regularly convex in males, weakly convex in females. *Legs:* Foretibia tridentate. Apex of posterior tibia with strong, acute tooth on upper angle and with several small serrations and short, broad spinules below upper angle. Apex of first tarsomere of posterior tarsus extended into long, acute spine.

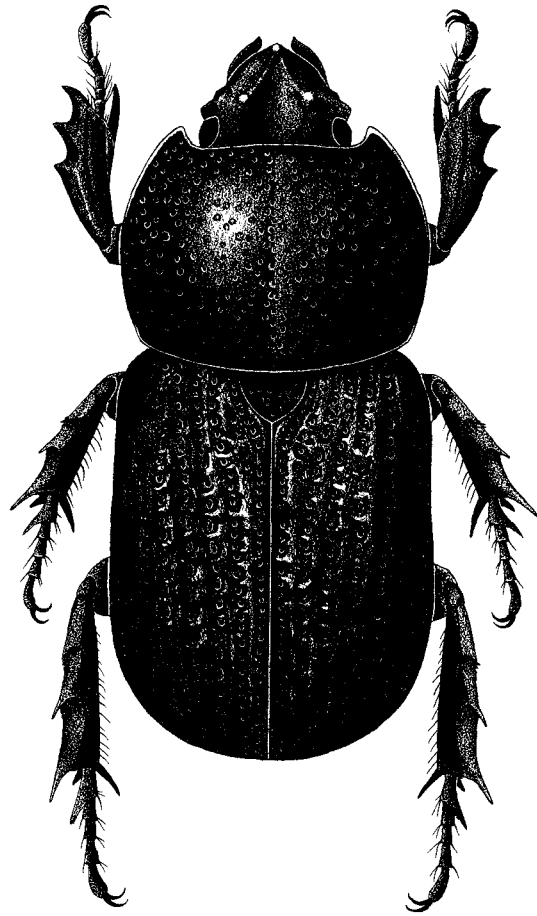
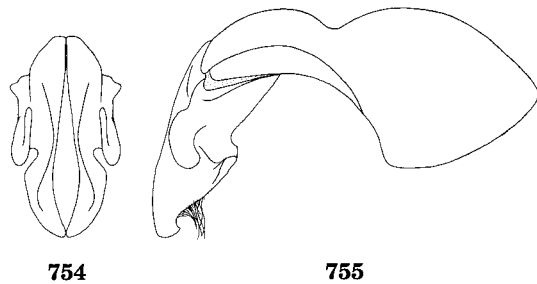


Fig. 753. *Hemiphileurus variolosus*.



Figs. 754-755. *Hemiphileurus variolosus* parameres.

Venter: Prosternal process long, columnar, apex broadly flattened and subtriangular, posterior surface with small protrusion near base. Last sternite with small, dense punctures along anterior margin, sparsely to moderately dense elsewhere. *Parameres:* Figs. 754-755.

DISTRIBUTION. *Hemiphileurus variolosus* is known from Costa Rica, Colombia, Venezuela, Ecuador, French Guiana, and Trinidad (Endrödi 1978). It is apparently not common anywhere in its range.

LOCALITY RECORDS (Figs. 756-757). 8 specimens examined.

COSTA RICA (5). **CARTAGO** (1): Turrialba; **GUANACASTE** (1): Estación Maritza; **LIMÓN** (1): Reserva Biológica Hitoy Cerere;



Fig. 756. Distribution of *Hemiphileurus variolosus* in Costa Rica.

PUNTARENAS (2): Estación Biológica Las Alturas, Sitio Tablas (Coto Brus).

PANAMA (3). **CHIRIQUI** (2): Reserva La Fortuna; **DARIEN** (1): Cana Biological Station.

TEMPORAL DISTRIBUTION. March (1), April (1), June (2), August (2), December (1).

DIAGNOSIS. *Hemiphileurus variolosus* is characterized by the rugopunctate surface of the head, presence of frontal tubercles (as opposed to horns), equally elevated elytral intervals both between rows of punctures as well as between individual punctures in each row, densely punctate pygidium and last sternite, tall prosternal process with a subtriangularly flattened apex, and form of the male parameres.

Endrödi's subspecies "*striatus*" has the elytral punctures in simple and distinct rows, and the elytral intervals smooth. The 1985 English version of Endrödi's key to *Hemiphileurus* species refers to *striatus* as an aberration and not a subspecies as originally described and refers to rows of punctures on the *pygidium*, which is clearly a misrepresentation of the original (1978) German that indicated rows of punctures on the *elytra*.

Females of this species are inseparable from those of *H. vicarius* although both together may be distinguished from other Costa



Fig. 757. Distribution of *Hemiphileurus variolosus* in Panama.

Rican and Panamanian species of *Hemiphileurus* with transverse and elevated intervals between elytral punctures by their densely punctate last abdominal sternite.

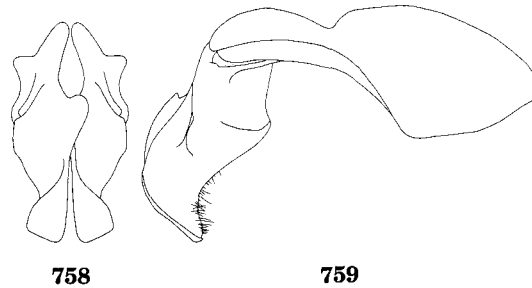
BIOLOGY. Adults have been taken at lights in premontane rain forests, premontane wet forests, and lower montane rain forests at elevations of 100-1,900 meters.

***Hemiphileurus vicarius* Prell,
1937**

(Figs. 758-761)

Hemiphileurus vicarius Prell 1937b: 184.
Phileurus depressus Burmeister (not Fabricius) 1847: 156 (misapplication, name unavailable).

DESCRIPTION. Length 19.0-23.7 mm; width 10.0-11.7 mm. Color black. *Head:* Surface rugopunctate except clypeus laterad of each clypeal where punctures sparse, minute. Frons with conical tubercle either side of median depression; median depression deep, broad, extending from frons to near clypeal apex. Clypeus triangular, apex acute and strongly reflexed, a fine carina extending from clypeal apex to base of each tubercle. Interocular width equals 6.3 transverse eye diameters. Antenna 10-segmented, club slightly longer than segment 2-7. Mandibles with lateral edge arcuate, apices acute. *Pronotum:* Surface with mostly large, deep punctures; punctures sparse either side of median depression, dense near lateral and anterior margins and in median furrow. Median, longitudinal furrow moderately deep, moderately broad, extending from base to anterior third of pronotum. Base with complete marginal line. *Elytra:* Rows of punctures in longitudinal furrows; punctures mostly large, ocellate-umbilicate, separated by about 1 puncture diameter (some punctures may be confluent in first 2 rows). Intervals equally elevated, occasionally broken, appearing sinuate because of lateral branching to between punctures in furrows, with small, sparse punctures. *Pygidium:* Surface densely punctate; punctures moderately large, nearly



Figs. 758-759. *Hemiphileurus vicarius* parameres.

confluent at base, slightly less dense at apex, setigerous; setae short, tawny. In lateral view, surface regularly convex in males, weakly convex in females. *Legs:* Foretibia tridentate. Apex of posterior tibia with strong, acute tooth on upper angle and with several small serrations and short, broad spinules below upper angle. Apex of first tarsomere of posterior tarsus extended into long, acute spine. *Venter:* Prosternal process long, columnar, apex broadly flattened and subtrapezoidal and with distinct transverse groove, posterior surface with small protrusion near base. Last sternite completely punctate; punctures moderate in size and density. *Parameres:* Figs. 758-759.

DISTRIBUTION. *Hemiphileurus vicarius* is found in Costa Rica, Panama, Colombia, French Guiana, Ecuador, and northeastern Brazil (Endrödi 1978). This species is rare in both Costa Rica and Panama.

LOCALITY RECORDS (Figs. 760-761). 2 specimens examined.

COSTA RICA (1). CARTAGO (1): Turrialba.

PANAMA (1). CHIRIQUI (1): Fortuna Dam (7 mi NE).

TEMPORAL DISTRIBUTION. May (1).

DIAGNOSIS. *Hemiphileurus vicarius* is characterized by the rugopunctate surface of the head, presence of tubercles on the frons (not horns), equally elevated elytral intervals, densely punctate pygidium and last sternite,

long prosternal process with a subtrapezoidally flattened apex, and form of the male parameres. Females are indistinguishable from those of *H. variolosus* although both together may be separated from other Costa Rican and Panamanian species of *Hemiphileurus* with equally elevated elytral intervals by their densely punctate last sternite.

BIOLOGY. Adults have been taken at lights. The Costa Rican and Panamanian specimens were collected from premontane wet forests at elevations of 600-1,000 meters.



Fig. 760. Distribution of *Hemiphileurus vicarius* in Costa Rica.



Fig. 761. Distribution of *Hemiphileurus vicarius* in Panama.

Homophileurus Kolbe, 1910

Homophileurus Kolbe 1910: 336.

Homophileurus is a relatively small genus consisting of nine species. Four species are found exclusively in South America, one is indigenous to Cuba, another is indigenous to Mexico, and two range from Mexico to Brazil (Endrödi 1978, 1985a). *Homophileurus integer* was previously known only from northern South America, but I have taken it in central Panama.

Species in the genus are distinguished by the tubercles of the frons placed near the lateral margins of the head, anterior tibia quadridentate, and apex of the posterior tibia with three large teeth. The genus was comprehensively reviewed by Endrödi (1978).

Only the larva and pupa of *H. luederwaldti* (Ohaus), a Brazilian species, have been described (Costa *et al.* 1985). Little is known of the biology of the species. The larvae of some species probably live in rotting wood while others are known to live in the nests of termites (Vanin *et al.* 1983; Costa *et al.* 1988). Adults may be attracted to lights at night.

**Key to the Species of Adult *Homophileurus* of Costa Rica and Panama
(after Endrödi 1985a)**

1. Pronotum convex except for longitudinal furrow; subapical tubercle(s) absent *integer* (Burmeister)
- 1'. Pronotum with distinct cavity or depression in anterior third; posterior margin of cavity subcarinate with 4 tubercles 2
2. Pronotum with median tubercles usually further apart than they are from lateral tubercles and with all 4 tubercles subequal in size. Parameres with apices divergent (Fig. 770) *tricuspis* Prell
- 2'. Pronotum with all 4 tubercles about equidistant from one another and with median tubercles usually a little larger than lateral tubercles. Parameres with apices subparallel (Fig. 766) *quadrituberculatus* (Palisot de Beauvois)

**Clave para las Especies de Adultos de *Homophileurus*
de Costa Rica y Panamá
(después de Endrödi 1985a)**

1. Pronoto convexo excepto por el surco longitudinal; tubérculos subapicales ausentes *integer* (Burmeister)
- 1'. Pronoto con una cavidad o depresión evidente en el tercio anterior; margen posterior de la cavidad subcarinada con 4 tubérculos 2
2. Pronoto con tubérculos medios con más separación entre si que la que hay entre ellos y los laterales y con los 4 tubérculos similares en tamaño. Parámetros con los ápices divergentes (Fig. 770) *tricuspis* Prell
- 2'. Pronoto con los 4 tubérculos casi equidistantes uno de otro y con los tubérculos mediales generalmente algo más grandes que los laterales. Parámetros con los ápices paralelos (Fig. 766) *quadrituberculatus* (Palisot de Beauvois)

***Homophileurus integer*
(Burmeister, 1847)
(Figs. 762-764)**

Phileurus integer Burmeister 1847: 162.

DESCRIPTION. Length 25.0-30.5 mm; width 11.8-14.0 mm. Color black. *Head:* Vertex with deep, smooth hollow. Frons concave, with large, transverse rugae. Frontal horns on side of head, short, subconical. Clypeus triangular, apex narrowly rounded and strongly reflexed; surface with sparse micropunctures. Interocular width equals 3.5 transverse eye diameters. Antenna 10-segmented, club a little longer than segments 2-7. Mandibles narrow, lacking teeth, apex acute. *Pronotum:* Surface convex except for longitudinal furrow and slightly flattened, round area on each

side. Anterior third of pronotum transversely, coarsely rugose; flattened areas and furrow with large to very large, often confluent punctures; remainder of surface crazed and with sparse punctures, punctures small either side of furrow and becoming moderate in size on sides. Longitudinal furrow shallow, gradually widening anteriorly, extending from near base to about anterior third. Base with nearly complete marginal bead, obsolete only at center. *Elytra:* Rows of punctures in shallow furrows; punctures mostly large, separated by about 1 puncture diameter. Intervals weakly convex, sparsely punctate, punctures small. *Pygidium:* Surface with moderately dense, moderately large punctures; punctures becoming sparser near apex, all with minute, pale setae. Base with transverse, shallow furrow. In lateral view, surface weakly convex. *Legs:*

Foretibia quadridentate. Apex of posterior tibia with 3 large teeth. Apex of basal tarsomere of posterior tibia extended into long spine. *Venter*: Prosternal process moderate in length, subtriangular, posterior face tumescent. *Parameres*: Figs. 762-763.

DISTRIBUTION. *Homophileurus integer* is known from French Guiana, Pará state in Brazil, and Trinidad. The specimen listed below constitutes a NEW COUNTRY RECORD for Panama.

LOCALITY RECORDS (Fig. 764). 1 specimen examined.

PANAMA (1). COLÓN (1): Santa Rita Ridge.

TEMPORAL DISTRIBUTION. May (1).

DIAGNOSIS. This species is easily distinguished among the Central American species of *Homophileurus* because of its convex pronotum that lacks an anterior depression and by the form of the parameres in the males.

BIOLOGY. I collected the single specimen at lights in an area of tropical wet forests at an elevation of 300 meters.

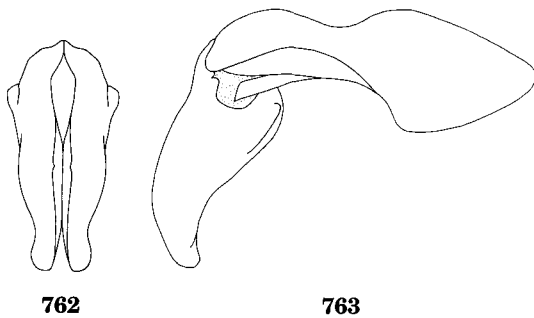
***Homophileurus*
quadrituberculatus (Palisot de
Beauvois, 1806)**
(Figs. 765-769)

Scarabaeus quadrituberculatus Palisot de Beauvois 1806: 42.

Scarabaeus bajulus Perty 1830: 44 (synonym).

Phileurus cephalotes Laporte 1840: 116 (synonym).

Homophileurus muticus Prell 1914: 221 (synonym).



Figs. 762-763. *Homophileurus integer* parameres.

DESCRIPTION. Length 27.5-38.0 mm; width 14.0-19.0 mm. Color black. *Head*: Vertex deeply hollowed, smooth within. *Frons*



Fig. 764. Distribution of *Homophileurus integer* in Panama.

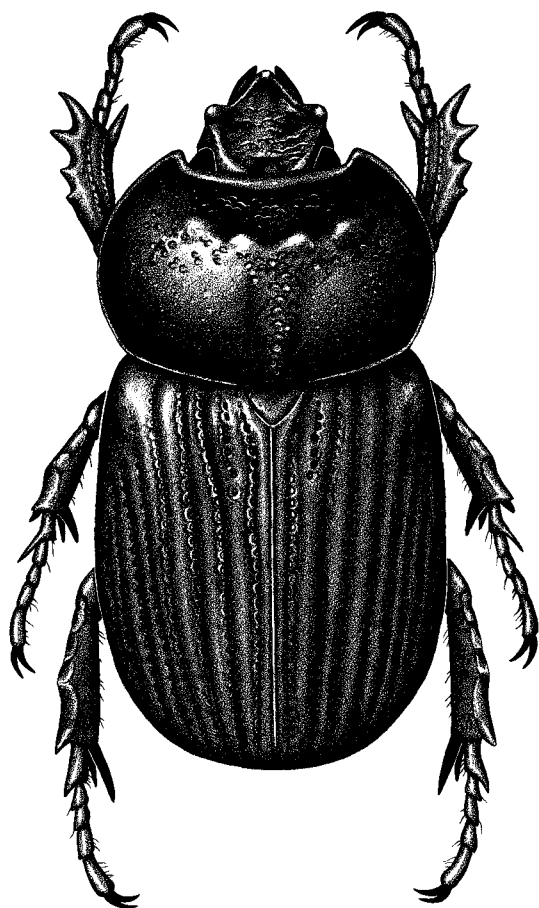
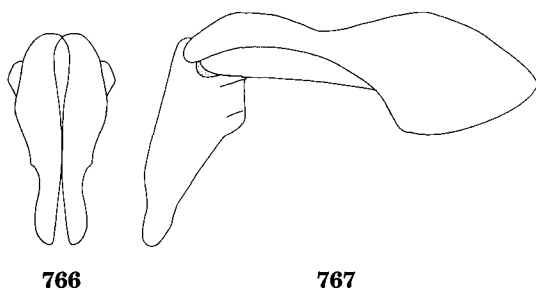


Fig. 765. *Homophileurus quadrituberculatus*.



766

767

Figs. 766-767. *Homophileurus quadrituberculatus* parameres.

with large, transverse rugae. Frontal horns relatively long in male majors, shorter in male minors and females; horns erect, subtrian-

gular, recurving slightly posteriorly. Clypeus triangular, apex pointed or narrowly rounded and strongly reflexed; surface nearly smooth and with small carina extending from apex to base of each horn. Interocular width equals 3.3-3.7 transverse eye diameters. Antenna with 10 segments, club a little longer than segments 2-7. Mandibles slender, apex acute, lacking lateral teeth. *Pronotum*: Anterior third declivous, forming frontal "cavity"; surface of cavity with sparse to moderate, round to transverse punctures. Posterior margin of cavity with 4 tubercles; tubercles about equidistant from each other, median tubercles usually larger than lateral tubercles. Median furrow broad, widening anteriorly and with large, transverse punctures within. Remaining pronotal surface minutely crazed, with small, sparse punctures; anterior angles and region behind lateral tubercles with large to very large, moderate to dense punctures. Base with marginal bead at sides, bead effaced at center. *Elytra*: Rows of punctures in furrows; punctures moderate to large, ocellate, usually separated from each other by about 1 puncture diameter. Intervals convex and with sparse, minute punctures. *Pygidium*: Surface at base densely punctate, punctures becoming moderately dense to sparse apically; punctures moderate in size, becoming larger at center, all punctures minutely setigerous (setae a little longer in females). In lateral view, surface evenly convex in males, weakly convex in females. *Legs*: Foretibia quadridentate. Apex of posterior tibia with 3 large teeth. Apex of basal tarsomere of posterior tarsus extended into long spine. *Venter*: Prosternal process subtriangular, apex rounded, anterior face flattened. *Parameres*: Figs. 766-767.

DISTRIBUTION. *Homophileurus quadrituberculatus* is broadly distributed from Mexico to southern South America.

LOCALITY RECORDS (Figs. 768-769). 24 specimens examined.

COSTA RICA (9). **CARTAGO** (2): Turrialba; **HEREDIA** (1): La Selva Biological Station; **LIMÓN** (4): Bratsi (Talamanca Valley), Guapiles, Limón; **PUNTARENAS** (2): Parq.

Nac. Manuel Antonio, Sirena (Parq. Nac. Corcovado).

PANAMA (15). BOCAS DEL TORO (3): Miramar; CANAL ZONE (9): Barro Colorado Island, Madden Dam, Pipeline Road; DARIEN (1): Santa Fé; PANAMA (2): Altos de Majé, La Chorrera.

TEMPORAL DISTRIBUTION. January (1), March (2), April (3), May (8), June (2), July (4), August (1).



Fig. 768. Distribution of *Homophileurus quadrituberculatus* in Costa Rica.



Fig. 769. Distribution of *Homophileurus quadrituberculatus* in Panama.

DIAGNOSIS. *Homophileurus quadrituberculatus* is externally very similar to *H. tricuspis*. The pronotal tubercles in *H. quadrituberculatus* are all subequally spaced from one another, and the median tubercles are usually larger than the lateral tubercles, especially in larger specimens. In *H. tricuspis*, the median tubercles are usually wider apart than they are from each of their respective lateral tubercles, and all the tubercles are about the same size. These tubercle characters of the pronotum are unreliable for identification because there is some variation. The parameres of the males are diagnostic. Unassociated females, however, may be difficult to place reliably.

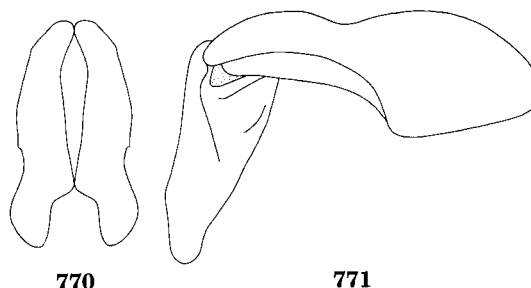
BIOLOGY. Adults have been taken primarily at lights at night in lowland rain forests. Lachaume (1992) indicated this species has been found in the nests of termites living in trees. The very broad geographic distribution of this species suggests an availability of suitable microhabitat (rotting logs) in which to live and breed rather than some broad ecological tolerance.

***Homophileurus tricuspis* Prell,
1914**

(Figs. 770-773)

Homophileurus tricuspis Prell 1914: 220.

DESCRIPTION. Length 29.0-40.0 mm; width 15.0-19.0 mm. Color black. *Head:* Vertex deeply hollowed in both sexes, smooth within. Frons coarsely, transversely rugose. Frontal horns long (6 mm) in male majors, shorter (but still horn-like in male minors and females); horns erect, slightly recurving posteriorly. Clypeus triangular, apex pointed or narrowly rounded and strongly reflexed; surface nearly smooth and with carina extending from apex to base of each horn. Interocular width equals 3.6 (large specimens) - 4.3 (small specimens) transverse eye diameters. Antenna with 10 segments, club a little longer than segments 2-7. Mandibles slender, lateral margin lacking teeth, apex acute. *Pronotum:* Anterior third declivous, forming pronotal "cavity"; surface of cavity with sparse to moderate, round to transverse punctures. Posterior margin of cavity with 4 tubercles, inner tubercles usually (especially in large specimens) further from each other than each is from outer tubercle. Median furrow broad, widening anteriorly and with large, transverse punctures within. Most of remaining surface minutely crazed and with small, sparse punctures; anterior angles and region behind outer tubercles with large to very large, moderate to dense punctures. Base with marginal bead at sides, bead obsolete in center. *Elytra:* Rows of punctures in furrows, punctures moderate to large, ocellate, deep, usually separated from each other by about 1 puncture diameter. Intervals convex, with sparse, minute punctures. *Pygidium:* Surface at base densely punctate, punctures becoming moderately dense to sparse apically; punctures moderate in size, becoming larger at center, all punctures minutely setigerous (setae a little longer in females). In lateral view, surface evenly convex in males, weakly convex in females. *Legs:* Foretibia quadridentate. Apex of posterior tibia with 3 large teeth. Apex of first tarsomere of posterior tarsus extended into long spine. *Venter:*



Figs. 770-771. *Homophileurus tricuspis* parameres.

Prosternal process triangular, apex narrowly rounded, anterior face flattened. *Parameres:* Figs. 770-771.

DISTRIBUTION. *Homophileurus tricuspis* is known from Mexico, Guatemala, Belize, Nicaragua, Venezuela, and Brazil (Endrödi 1978). The localities listed below for Costa Rica and Panama constitute NEW COUNTRY RECORDS.

LOCALITY RECORDS (Figs. 772-773). 109 specimens examined.

COSTA RICA (99). ALAJUELA (3): Caño Negro; CARTAGO (1): Turrialba; GUANACASTE (20): Estación Cacao, Estación Maritza, Estación Murciélago, Estación Pitilla, Finca Jenny (Osa), Parq. Nac. Barra Honda, Río Gongora (Parq. Nac. Guanacaste), Parq. Nac. Rincón de la Vieja; HEREDIA (4): Estación El Ciebo, Estación Magsasay, La Selva Biological Station, Puerto Viejo (10 km W); LIMÓN (34): Amubri, Cerro Tortuguero, Quatro Esquinas (Parq. Nac. Tortuguero), Hamburg Farm, Manzanillo, Reserva Biológica Hitoy Cerere, Río Sardinas (RNFS Barra del Colorado), Sector Cerro Cocori; PUNTARENAS (37): Cerro Boilley, Estación Cafrosa, Estación La Casona, Estación Las Alturas, Estación Pittier, Estación Quebrada Bonita, Estación Sirena, Quepos, Rancho Quemado, San Luis (Monteverde).

PANAMA (10). CANAL ZONE (3): Barro Colorado Island, Gatun Tank Farm; COCLÉ (2): Cerro Gaital; COLÓN (2): Río Guanche (5 km

S Portobelo), Santa Rita Ridge; PANAMA (3): Cerro Jefé, El Llano-Carti Rd. (km 10), Las Cumbres.

TEMPORAL DISTRIBUTION. January (6), February (6), March (7), April (12), May (13), June (13), July (10), August (11), September (5), October (9), November (7), December (4).



Fig. 772. Distribution of *Homophileurus tricuspis* in Costa Rica.

DIAGNOSIS. *Homophileurus tricuspis* is nearly identical externally with *H. quadrituberculatus*. In *H. tricuspis*, the median tubercles are usually wider apart than either one is from its respective lateral tubercle. This is most evident in large males. In some specimens the tubercles all appear equidistant from one another, and so the character state is not totally reliable. In *H. quadrituberculatus*, the four tubercles of the pronotum are usually all equidistant from one another; the median tubercles are usually a little larger than the lateral tubercles. Again, however, this is probably not a totally reliable character state for separating the two species. The parameres of the males are very different and diagnostic. Unassociated females may be difficult to name.

BIOLOGY. Adults are usually encountered at lights or occasionally in rotten logs. They have been collected from elevations ranging from sea level to 1,800 meters in tropical moist forests, tropical wet forests, premontane moist forests, and premontane wet forests.

Palaeophileurus Kolbe, 1910

Palaeophileurus Kolbe 1910: 335.

The small genus *Palaeophileurus* contains eight species (Ratcliffe 2002a). All but



Fig. 773. Distribution of *Homophileurus tricuspis* in Panama.

one of the species are found in South America. The single Central American species is known from Chiriqui in Panama and is represented by a single specimen. Interestingly, no specimens have been collected since the holotype of *P. panamensis* was collected around 1900.

The genus is easily separated from other Central American Phileurini because its members completely lack tubercles, fovea, or a longitudinal furrow on the pronotum. In addition, the elytra are a distinctly dull, flat black in color (as opposed to a weakly shining pronotum) and lack the impressed, longitudinal furrows of all the other Central American phileurines.

Nothing is known of the biology of the species other than the adults have been taken at lights. Ratcliffe (2002a) gave the most recent synopsis of the genus.

***Palaeophileurus panamensis*
Dechambre, 1997**

(Figs. 774-777)

Palaeophileurus panamensis Dechambre 1997b: 32.

DESCRIPTION. Length 23.8 mm; width 12.4 mm. Color piceous, head and pronotum a little darker. *Head:* Frons broadly and weakly depressed between eyes; surface with sparse, moderately large punctures. Small tubercle present either side of midline mesad of antennal insertion. Clypeus subtriangular, apex obtusely acuminate, reflexed; surface with small, sparse punctures and feeble ridge extending from apex to base of each tubercle. Interocular width equals 4.5 transverse eye diameters. Mandibles arcuate on lateral edge, apices pointed. Antenna with 10 segments, club subequal in length to segments 2-7. *Pronotum:* Surface with moderately dense punctures; punctures deep, large and transversely oval to round on disc, moderate in size and round elsewhere, becoming denser along lateral margins. Base lacking marginal bead. *Elytra:* Surface finely, densely shagreened, with rows of sparse punctures; punctures moderate in size, ocellate. Intervals flat, impunctate. *Pygidium:* Surface completely,

densely punctate; punctures large, umbilicate, with minute, tawny setae. In lateral view, surface normally convex. *Legs:* Anterior tibia with 3, subequally spaced, elongate teeth. Posterior tibia with upper angle of apex produced into short tooth. Basal segment of posterior tarsus with apex slightly produced but without elongated spine. *Venter:* Prosternal process long, stout, apex broad and with 2 large lobes (anterior and lateral) and 1 small lobe (posterior and medial). Last sternite completely covered with small, moderately dense punctures. *Parameres:* Figs. 775-776.

DISTRIBUTION. *Palaeophileurus panamensis* is known only from "Chiriqui" in Panama. The type specimen came from Le Moul't's collection, which became part of the Museum National d'Histoire Naturelle in Paris around 1908. It seems reasonable to assume the specimen was collected a little earlier than that, perhaps around the turn of the century. At that time, "Chiriqui" usually referred to the southern or eastern slopes of Volcán Barú (=Volcán Chiriqui) or to the Río Chiriqui or Río Chiriqui Viejo on the southeast and southwest slopes, respectively, of Volcán Barú. No representatives of this species have been collected since that time in what is by now a fairly well-collected area. Even allowing for the rarity of *Palaeophileurus* species, I wonder if it is still extant in Panama. There is also the possibility that the specimen may have been mis-labeled, and that it is not from Panama.

LOCALITY RECORDS (Fig. 777). 1 specimen examined.

PANAMA (1). **CHIRIQUI** (1): Volcán Barú vicinity?

TEMPORAL DISTRIBUTION. No data.

DIAGNOSIS. It is unique among the phileurine fauna of Central America and so is easily recognized. The mandibles are arcuate externally, the frons lacks horns, the pronotum is evenly convex and lacks a longitudinal furrow, subapical fovea, or tubercles, the elytra are distinctly opaque and

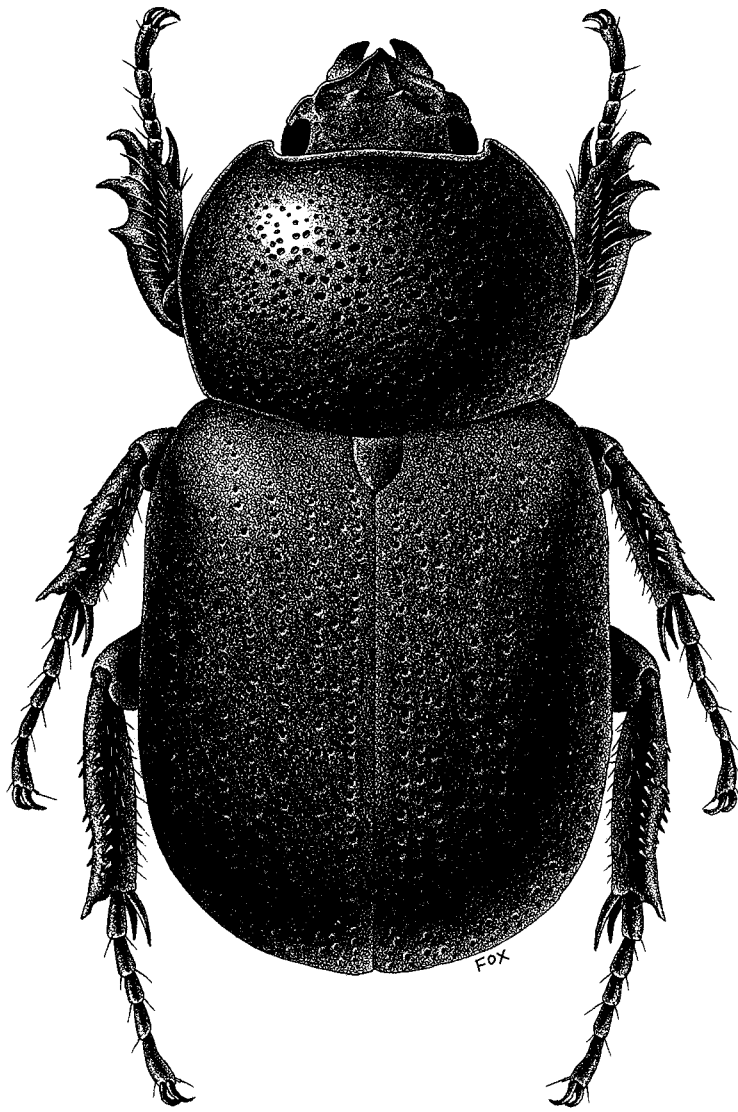
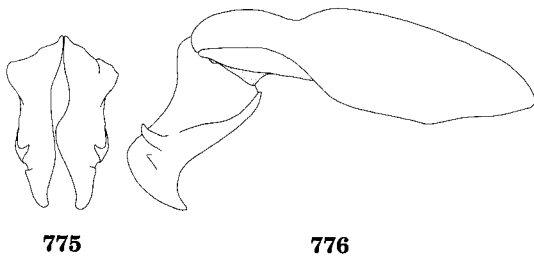


Fig. 774. *Palaeophileurus panamensis*.



Figs. 775-776. *Palaeophileurus panamensis* parameres.

lack impressed furrows, and the apex of the first tarsomere of the posterior tarsus is simple and not elongated into a spine.

NOMENCLATURE. This species was originally named by Dechambre (1996), but he did not provide a description or diagnosis of the species (required by Article 13a of the International Code of Zoological Nomenclature, 1985). The species was correctly diagnosed by Dechambre (1997b) in a supplemental note.



Fig. 777. Distribution of *Palaeophileurus panamensis* in Panama.

BIOLOGY. The habitat (forest type, highlands or lowlands) is unknown because the specimen lacks precise locality data.

***Paraphileurus* Endrödi, 1978**

Paraphileurus Endrödi 1978: 98.

Paraphileurus is a small genus comprised of only three species, all of which were previously known from northern South America. *Paraphileurus venezuelensis* Ohaus is here recorded from Central America for the first time and is a NEW COUNTRY RECORD for Panama.

Paraphileurus is similar to *Hemiphileurus* but is distinguished by the presence of a broadly foveate pronotal cavity with an apical tubercle. In *Hemiphileurus*, the longitudinal furrow of the pronotum varies from indistinct to broad and shallow to narrow and deep but never widened anteriorly into a broad depression nor with an apical tubercle. In addition, *Paraphileurus* has a prosternal process that is produced posteriorly into a large, conical knob.

The biology and immature stages of the species are completely unknown. Endrödi (1978, 1985a) provided the most recent synopsis of the genus.

***Paraphileurus venezuelensis* (Ohaus, 1910) (Figs. 778-781)**

Phileurus venezuelensis Ohaus 1910: 689.

DESCRIPTION. Length 18.0-20.0 mm; width 9.0-9.7 mm. Color black. *Head:* Males with deep hollow on vertex, frons with surface smooth except for rugopunctate area mesad of each eye and behind each horn; female with vertex depressed, rugopunctate. Frontal horns in majors conical, slightly curving backward, a little longer than width of eye (as seen from above); minors and females with tubercles. Clypeus subtriangular, apex pointed and strongly reflexed, surface smooth with small, sparse punctures. Interocular width equals 4.3-5.0 transverse eye diameters. Antenna with 10 segments, club a little longer than segments 2-7. Mandibles arcuate laterally, apex acuminate. *Pronotum:* Surface completely punctate; punctures in males moderate in density, umbilicate, moderately large, becoming large in weakly depressed oval either side of furrow and in anterior angles (where also denser); females with punctures larger, denser to rugopunctate. Longitudinal furrow broad, deep, expanded in anterior half, with distinct tubercle on apical margin. Base with marginal bead. *Elytra:*

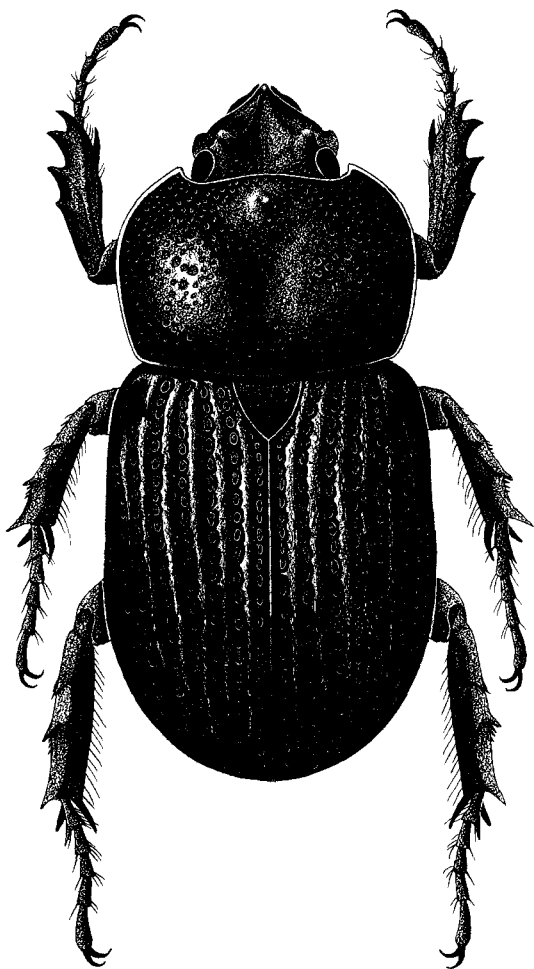
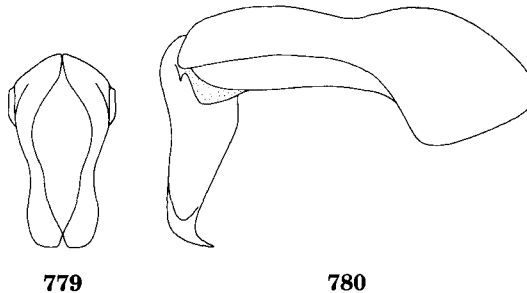


Fig. 778. *Paraphileurus venezuelensis*.

Striae furrowed, punctate; punctures round to mostly oval, moderate to large, ocellate-umbilicate, separated by 1-2 diameters, becoming smaller and round at apex. Intervals strongly convex, almost carinate, with sparse, minute punctures. *Pygidium*: Surface moderately densely punctate; punctures moderate in size, weakly umbilicate, setigerous; setae short, reddish brown. In lateral view, surface in males convex, nearly flat in females. *Legs*: Foretibia quadridentate, all teeth subequally spaced. Apex of posterior tibia usually with 3 small spinules and with dorsal angle prolonged into stout tooth. Apex of basal tarsomere of posterior tarsus extended into long, slender spine. *Venter*: Prosternal process moderate in length, broad, anterior face



Figs. 779-780. *Paraphileurus venezuelensis* parameres.

flattened, posterior face extended into stout, conical protrusion. *Parameres*: Figs. 779-780. The degree of curvature on the lateral edges of the parameres varies a little.

DISTRIBUTION. *Paraphileurus venezuelensis* was previously known from the type locality of Merida, Venezuela. The Panamanian localities listed here are a NEW COUNTRY RECORD.

LOCALITY RECORDS (Fig. 781). 5 specimens examined.

Panama (5). CHIRIQUI (5): Boquete, Hartmann's Finca (Santa Clara).

TEMPORAL DISTRIBUTION. May (2), June (1), September (1), October (1).

DIAGNOSIS. The form of the pronotal furrow and anterior depression in combination with the presence of a pronotal tubercle, form of the apex of the posterior tibia, posteriorly expanded prosternal process, quadridentate foretibia, and form of the male's parameres will serve to separate this species from other Central American Phileurini. The form of the parameres (Fig. 779) is less parallel than the illustration given in Endrödi (1978, 1985a). In my experience, Endrödi's illustrations of parameres are often simplified (sometimes overly so). I don't believe that the Panamanian specimens, with their slightly different parameres, represent a new species. Rather, there is some variation (even in the two male specimens from Panama) in the degree of curvature on the lateral margins of the



Fig. 781. Distribution of *Paraphileurus venezuelensis* in Panama.

parameres. This, in combination with what *might* be a poor drawing by Endrödi, leads me to conclude that the Panamanian and Venezuelan entities are conspecific. In all other respects, they seem to be identical. Additional material from both countries would help to clarify the situation.

BIOLOGY. The Panamanian specimens were collected at lights from premontane wet forests at an elevation of 1,250 meters.

Phileurus Latreille, 1807

Phileurus Latreille 1807: 103.

The genus *Phileurus* has 19 species (Endrödi 1978, 1981, 1985a; Ratcliffe 1981) distributed from the southeastern United States south to southern South America. *Phileurus valgus* is also found in the West Indies. Seven species are found in Costa Rica and Panama. They are most typically encountered in lowland forests, but they have also been recorded from forests at 1,800 meters in elevation.

Endrödi (1978, 1985a) records a specimen each of *P. angustatus* Kolbe from Turrialba, Costa Rica and *P. excavatus* Prell from Chiriqui, Panama. These are South American species, and, despite my decade of collecting in Costa Rica and 20 years of collecting in Panama, I have never seen a specimen of either

of these two species from Central America. Moreover, I have never seen a specimen in any of the other large collections consulted during this study. I conclude that these species do not occur in the study area, and that the records listed by Endrödi are probably erroneous.

Species in the genus *Phileurus* are characterized by a sharply acuminate clypeus, outer side of the mandibles lacking teeth, pronotum with a longitudinal furrow and a subapical tubercle and fovea or declivous area, and apical margin of the posterior tibia with the dorsal angle spiniformly produced into a large tooth but otherwise lacking teeth (except for *P. valgus* which has a second tooth). Most of the species are moderately large beetles with only *P. valgus* dropping below 20 mm in length.

The larval stage has been described for only two species in the genus, *P. didymus* and *P. valgus* (under the name *P. castaneus*) (Ritcher 1966). The life history for *Phileurus* species is largely unknown. Both adults and larvae have been collected from rotting logs and stumps where they probably feed on decaying wood and/or the fungi associated with it. Like some species of *Homophileurus*, some species of *Phileurus* may live in termite nests, but I have no definite records of this. Adults are attracted to lights at night.

Phileurus was reviewed by Kolbe (1910) and comprehensively treated by Endrödi (1978, 1985a).

Key to the Species of Adult *Phileurus* of Costa Rica and Panama

1. Foretibia tridentate 2
- 1'. Foretibia quadridentate 5
2. Frons in both sexes with tubercles. Body smaller (24-29 mm), more flattened. Parameres as in Figs. 811-812 *youngi* Ratcliffe
- 2'. Frons in both sexes with horns (rarely reduced to tubercles). Body larger (29-40 mm), more convex. Parameres not as above 3
3. Hollow of vertex smooth or with only a few, sparse punctures *truncatus* (Palisot de Beauvois)
- 3'. Hollow of vertex rugose or completely punctate 4
4. Tubercle of pronotum located immediately behind anterior margin of pronotum. Parameres as in Figs. 792-793 *limicauda* Prell
- 4'. Tubercle of pronotum located well behind anterior margin of pronotum (subequal to distance of 1 transverse eye diameter). Parameres as in Figs. 782-783 *carinatus* Prell
5. Apex of posterior tibia with a single large tooth *didymus* (L.)
- 5'. Apex of posterior tibia with 2 large teeth 6
6. Elytra usually with alternate intervals higher and wider than others; rarely all intervals of equal height and width. Intervals moderately punctate, punctures small, deep. Tubercle of pronotum distinctly conical and usually immediately behind anterior margin of pronotum. Parameres as in Figs. 802-803 *valgus* (Olivier)
- 6'. Elytra with all intervals subequal in height and width. Intervals sparsely punctate, punctures minute to small, shallow. Tubercle of pronotum distinctly transverse and behind anterior margin of pronotum by at least a distance equal to half a transverse eye diameter. Parameres as in Figs. 807-808 *voirinae* Endrödi

Clave para las Especies de Adultos de *Phileurus* de Costa Rica y Panamá

1. Tibia anterior tridentada 2
- 1'. Tibia anterior cuadridentada 5
2. Frente en ambos sexos con tubérculos. Cuerpo más pequeño (24-29 mm), más aplanado. Parámetros como en las figuras 811-812 *youngi* Ratcliffe
- 2'. Frente en ambos sexos con cuernos (raramente reducidos a tubérculos). Cuerpo más grande (29-40 mm), más convexo. Parámetros diferente a los mencionados arriba. 3
3. Cavidad del vértex lisa o sólo con unas pocas puntuaciones dispersas *truncatus* (Palisot de Beauvois)
- 3'. Cavidad del vértex rugosa o completamente punteada 4
4. Tubérculo del pronoto localizado inmediatamente atrás del margen anterior del pronoto. Parámetros como en las figuras 792-793 *limicauda* Prell
- 4'. Tubérculo del pronoto localizado bastante atrás del margen anterior del pronoto (subigual a la distancia del diámetro transversal de un ojo). Parámetros como en las figuras 782-783 *carinatus* Prell
5. Apice de la tibia posterior con un sólo diente grande *didymus* (L.)
- 5'. Apice de la tibia posterior con 2 dientes grandes 6
6. Elitros generalmente con intervalos alternos más altos y anchos que los otros; ocasionalmente todos los intervalos de igual altura y ancho. Intervalos moderadamente punteados, puntuaciones pequeñas, profundas. Tubérculo del pronoto claramente cónico y generalmente inmediatamente detrás del margen anterior del pronoto. Parámetros como en las figuras 802-803 *valgus* (Olivier)

- 6'. Elitros con intervalos similares en altura y ancho. Intervalos dispersamente punteados, puntuaciones minúsculas a pequeñas, poco profundas. Tubérculo del pronoto claramente transversal y detrás del margen anterior del pronoto a una distancia al menos igual a la mitad del diámetro transversal del ojo. Parámetros como en las figuras 807-808 *voirinae* Endrödi

Key to the Species of Known Larval *Phileurus* of Costa Rica and Panama

(after Ritcher 1966)

1. Last segment of antenna with 2 dorsal sensory spots *valgus* (Olivier)
 1'. Last segment of antenna with 3-5 dorsal sensory spots *didymus* (L.)

Clava para las Especies de Larvas de *Phileurus* Conocidas de Costa Rica y Panamá

(después de Ritcher 1966)

1. Último segmento de la antena con 2 manchas sensoriales dorsales *valgus* (Olivier)
 1'. Último segmento de la antena con 3 a 5 manchas sensoriales dorsales *didymus* (L.)

Phileurus carinatus Prell, 1914

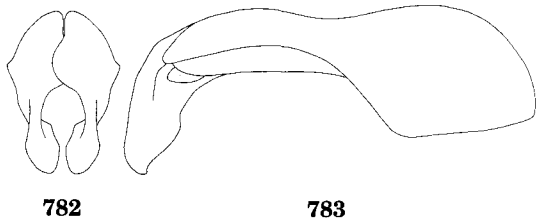
(Figs. 782-785)

Phileurus carinatus Prell 1914: 223.

Phileurus carinatus declivis Prell 1914: 222 (synonym).

DESCRIPTION. Length 29.6-33.0 mm; width 14.3-17.1 mm. Color black. *Head:* Frons with deep hollow, surface within hollow and elsewhere on frons transversely rugose. Horns erect, recurving posteriorly slightly, long in large specimens (longer than width of eye), shorter in small specimens, slightly concave on posterior face in large specimens, located on side of head. Clypeus triangular, apex acute and strongly reflexed, surface smooth anteriorly, sparsely punctate to rugopunctate posteriorly. Interocular width equals 3.8 transverse eye diameters. Antenna with 10 segments, club a little longer than segments 2-7. Mandibles slender, externally arcuate, apex acute. *Pronotum:* Median, longitudinal furrow broad, shallow, becoming wider at anterior end, extending from near

base to just past middle of pronotum. Apical tubercle at anterior end of furrow (posterior edge of pronotal cavity; about width of 1 eye diameter away from apical margin of pronotum). Surface within furrow with large punctures basally, becoming rugopunctate anteriorly; anterior third of pronotum transversely, coarsely rugose; disc either side of furrow with small, sparse punctures, punctures becoming denser and larger laterally. Posterior margin with basal bead present to nearly obsolete at center. *Elytra:* Rows of punctures in shallow furrows; punctures moderate in size, ocellate-umbilicate, separated from one another by about 1 puncture diameter. Intervals weakly convex, sparsely punctate, punctures small. *Pygidium:* Base with transverse, shallow furrow. Surface at base moderately densely punctate; punctures moderately large, minutely setigerous, becoming sparser apically. In lateral view, surface regularly convex in both sexes. *Legs:* Foretibia tridentate, all teeth triangular. Apex of posterior tibia with single, broad, large, triangular tooth. Apex of first tarsomere of posterior tarsus



Figs. 782-783. *Phileurus carinatus* parameres.

extended into long, slender spine. *Venter*: Prosternal process short, triangular, apex narrowly truncate. *Parameres*: Figs. 782-783.

DISTRIBUTION. *Phileurus carinatus* is known from a few locales between Nicaragua and northern South America with a record each for southern Brazil and Paraguay (Endrödi 1978). Endrödi did not list Costa Rican or Panamanian localities, although Blackwelder (1944) indicated Panama. The Costa Rican specimens listed below constitute a NEW COUNTRY RECORD.

LOCALITY RECORDS (Figs. 784-785). 32 specimens examined.

COSTA RICA (18). ALAJUELA (1): Colonia Blanca; GUANACASTE (2): Estación Cacao, Estación Maritza; HEREDIA (1): La Selva Biological Station; LIMÓN (1): Cerro Cocori; PUNTARENAS (13): Estación Sirena, Rancho Quemado (Osa), Reserva Biológica Carara.

PANAMA (14). CANAL ZONE (9): Barro Colorado Island; COLÓN (1): Santa Rita Ridge; PANAMA (4): Cerro Jefe, El Llano-Carti Rd. (km 8), Isla de Majé.

TEMPORAL DISTRIBUTION. March (2), April (1), May (4), June (1), July (3), August (5), September (5), October (2).



Fig. 784. Distribution of *Phileurus carinatus* in Costa Rica.

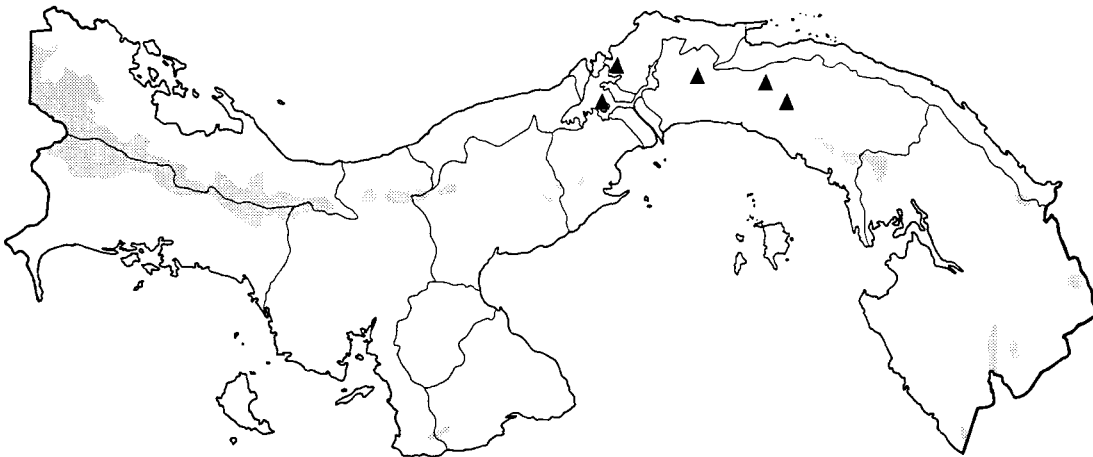


Fig. 785. Distribution of *Phileurus carinatus* in Panama.

DIAGNOSIS. *Phileurus carinatus* may be separated from other Central American species of *Phileurus* by its regularly tridentate foretibia, larger size, frons with horns (rather than tubercles), apex of the posterior tibia with a large and broad spine, and rugose (as opposed to smooth) hollow on the frons. The parameres of the male are also diagnostic.

BIOLOGY. Adults are attracted to lights at night. They have been found in tropical wet forests as well as in the transition area between this forest type and premontane rain forests. They occur at elevations between sea level and 1,100 meters.

***Phileurus didymus* (Linnaeus, 1758)**

(Figs. 786-790)

Scarabaeus didymus Linnaeus 1758: 347.
Phileurus affinis Reiche 1859: 12 (synonym).

DESCRIPTION. Length 27.0-50.0 mm; width 13.0-23.5 mm. Color black. *Head:* Frons and vertex deeply concave, surface within mostly smooth; remainder of frons coarsely, transversely rugose. Frontal horns long (25 mm) in largest specimens, shorter in smaller specimens; horns erect, slightly recurved posteriorly, located on sides of head. Clypeus triangular, apex acute and strongly recurved, surface with coarse, transverse rugae mesad of each clypeal carina (extending from clypeal apex to base of each horn), smooth with micropunctures laterad of each clypeal carina. Interocular width equals 3.6-3.9 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. Mandibles externally arcuate, apex acute. *Pronotum:* Median, longitudinal furrow broad, shallow, gradually widening anteriorly, extending from near base to just past middle of pronotum where it broadens out into deep, transversely oval fovea; furrow and fovea coarsely punctate to rugopunctate. Large tubercle present just behind apical margin of pronotum and before fovea. Disc either side of furrow sparsely punctate; punctures minute and small mixed in small specimens, minute

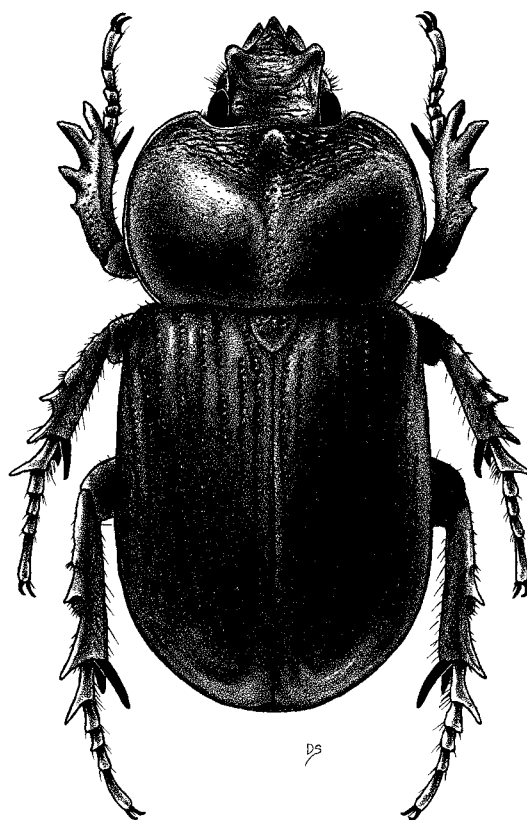
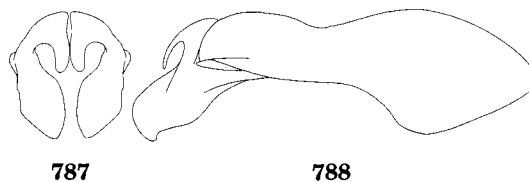


Fig. 786. *Phileurus didymus*.



Figs. 787-788. *Phileurus didymus* parameres.

and moderate mixed in large specimens; punctures becoming larger and denser on sides of pronotum and transversely rugose in anterior angles and mesad to tubercle. Base with complete marginal bead. *Elytra:* Rows of punctures in shallow furrows; punctures ocellate-umbilicate, mostly moderate in size, usually separated from one another by 1-2 puncture diameters. Intervals weakly convex, sparsely and minutely punctate (occasional

smaller specimen with strongly convex intervals). *Pygidium*: Base with shallow, transverse furrow. Surface at base moderately densely punctate, punctures moderate in size, setigerous, punctures becoming sparser apically; setae short, tawny, moderately dense, often abraded away. In lateral view, surface evenly convex in males, weakly convex in females. *Legs*: Foretibia usually quadridentate, occasional specimen with basal tooth strongly reduced to almost obsolete; apical 2 teeth with apices obliquely truncate. Apex of posterior tibia with 1 large, stout

tooth. Apex of basal tarsomere of posterior tarsus extended into spine-like process. *Venter*: Prosternal process moderate in length, subtriangular at base, apex subrectangular to emarginate and compressed from front to back, basal portion with 1-6 (usually 2) transverse grooves. *Parameres*: Figs. 787-788.

DISTRIBUTION. *Phileurus didymus* is broadly distributed from Mexico to Paraguay (Endrödi 1978, 1985a) and the West Indies (Chalumeau 1983). This species is found throughout Costa Rica and Panama in areas less than 1,800 meters in elevation.

LOCALITY RECORDS (Figs. 789-790). 177 specimens examined.

COSTA RICA (129). ALAJUELA (6): Caño Negro, Estación Eladios, Playuelas, San Ramón; CARTAGO (4): Moravia de Chirripó; GUANACASTE (56): Estación Cacao, Estación Maritza, Estación Mengo (W side Volcán Cacao), Estación Murcielago, Estación Palo Verde, Estación Pitilla, Finca Jenny (30 km N Liberia), Las Pailas, Los Almendros, Santa Rosa, Tierras Morenas; HEREDIA (3): Estación Magsasay, La Selva Biological Station; LIMÓN (12): Amubri, Cerro Cocori, Cerro Tortuguero, Reserva Biológica Hitoy Cerere, Río Sardinias; PUNTARENAS (47): Albergue Cerro de Oro, Estación La Casona, Estación Las Mellizas, Estación Pittier, Estación Sirena, Las Cruces, Quepos, Rancho



Fig. 789. Distribution of *Phileurus didymus* in Costa Rica.



Fig. 790. Distribution of *Phileurus didymus* in Panama.

Quemado (Osa), Reserva Biológica Carara, San Luis, Vuelta Campana, Wilson Botanical Gardens; SAN JOSÉ (1): División.

PANAMA (48). BOCAS DEL TORO (1): Miramar; CANAL ZONE (29): Barro Colorado Island, Black Tank Rd (W side Gatun locks), Ft. Gulick, Gatun Tank Farm, Madden Dam; CHIRIQUI (7): Boquete, Fortuna, Hartmann's Finca (Santa Clara); COCLÉ (1): Cerro Gaital; COLÓN (2): Nombre de Dios (9 km SW on Cerro Viejo Mine Rd.), Santa Rita Ridge; PANAMA (8): Cerro Azul, Cerro Campana, Cerro Chame, Cerro Jefé, Isla de Majé, Las Cumbres; SAN BLAS (1): Nusagandi.

TEMPORAL DISTRIBUTION. January (2), February (8), March (11), April (13), May (33), June (20), July (13), August (10), September (8), October (13), November (3), December (6).

NOMENCLATURE. Endrödi (1978: 113) designated *P. didymus tridentatus* as an aberration for those specimens with only three foretibial teeth, but this name has no nomenclatural standing.

DIAGNOSIS. *Phileurus didymus* is easily recognized because of the quadridentate foretibia, apical two teeth of the foretibia with oblique apices, elytral intervals all equal in height, and the form of the parameres in the males. This species, along with *P. truncatus*, is the largest phileurine in Central America, but *P. truncatus* has only tridentate foretibia. An occasional specimen of *P. didymus* will have a nearly obsolete basal tooth on the foretibia, but even under these circumstances the form of the apical two teeth of the foretibia and the equally high elytral intervals will characterize this species. The form of the prosternal process varies, but this is all a matter of degree and is correlated to some extent with the size of the specimen.

BIOLOGY. Ritcher (1966) described the larval stage. Both larvae and adults have been found in rotting wood (Ritcher 1966 and personal observation), and adults are frequently encountered at lights, especially in lowland areas. Little else is known of their life history.

They have been collected from many types of forest including tropical dry forests, tropical moist forests, tropical wet forests, premontane moist forests, premontane wet forests, and premontane rain forests. They occur from sea level to 1,800 meters in elevation.

***Phileurus limicauda* Prell, 1912**
(Figs. 791-795)

Phileurus limicauda Prell 1912d: 106.

DESCRIPTION. Length 31.3-37.0 mm; width 14.2-17.0 mm. Color black. *Head:* Frons and vertex concave, transversely rugose. Frontal horns erect, recurving posteriorly slightly, located on sides of head. Clypeus triangular, apex acute and strongly reflexed, distinct carina extending from apex to base of each horn; surface mesad of carinae transversely rugose, surface laterad of carinae nearly smooth, with sparse micropunctures. Interocular width equals 4.2 transverse eye diameters. Mandibles narrow, lateral edge arcuate, apex acute. Antenna with 10 segments, club subequal in length to segments 2-7. *Pronotum:* Median longitudinal furrow broad, deep, gradually becoming wider anteriorly, extending from near base to about middle of pronotum, surface with large, transverse punctures. Anterior fovea oval, deep, located at anterior end of furrow, transversely rugose within. Subapical tubercle large, broad, located just behind apical margin. Surface either side of furrow with sparse, small punctures; punctures becoming larger and denser laterally; anterior third of pronotum coarsely, transversely rugose or with large, dense, transverse, rasp-like punctures. All margins with complete bead. *Elytra:* Rows of punctures in furrows; punctures moderately large, ocellate-umbilicate, separated from one another by about 1 puncture diameter. Intervals convex, with sparse, small punctures. *Pygidium:* Base with transverse, shallow furrow. Surface at base with moderately large, moderately dense, setigerous punctures; setae long, tawny; punctures becoming sparser apically, setae shorter apically. In lateral view,

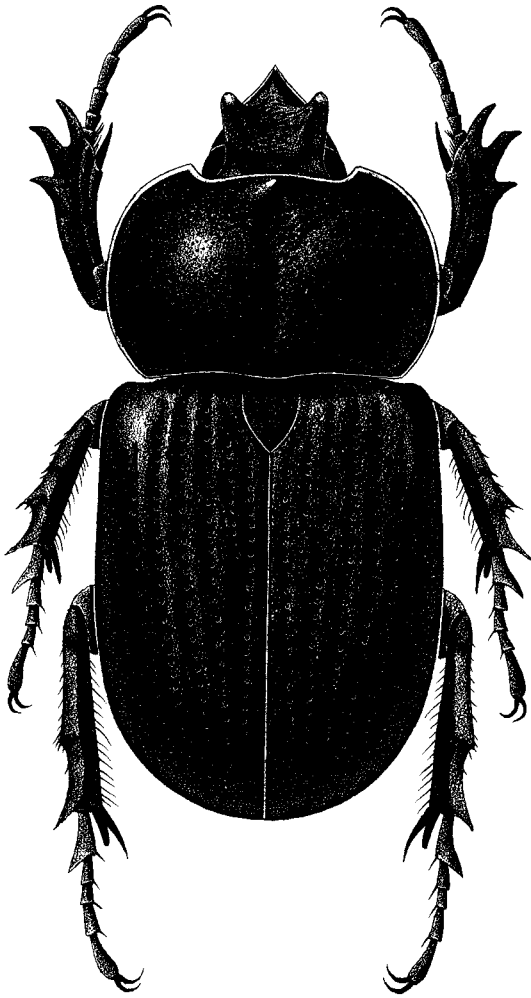
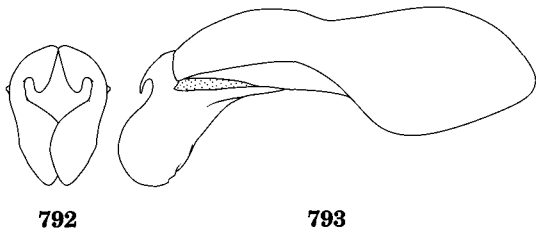


Fig. 791. *Phileurus limicauda*.



Figs. 792-793. *Phileurus limicauda* parameres.

surface in males convex, nearly flat in females. *Legs*: Foretibia tridentate, basal tooth slightly removed from others; middle tooth obliquely acute. Apex of posterior tibia with large, broad, triangular tooth. Apex of basal



Fig. 794. Distribution of *Phileurus limicauda* in Costa Rica.

tarsomere of posterior tarsus extended into long, stout spine. *Venter*: Prosternal process short, subtriangular, apex narrowly truncate and emarginate; posterior surface with 3 transverse furrows. *Parameres*: Figs. 792-793.

DISTRIBUTION. *Phileurus limicauda* is known from Mexico to Panama (Endrödi 1978). It seems to be a rare species in Costa Rica and Panama.

LOCALITY RECORDS (Figs. 794-795). 6 specimens examined.

COSTA RICA (3). **CARTAGO** (1): Turrialba; **HEREDIA** (1): La Selva Biological Station; **PUNTARENAS** (1): Wilson Botanical Garden

PANAMA (3). **CHIRIQUI** (1): No data; **PANAMA** (2): El Llano-Carti Rd (km 8-11), Portobelo (15 km E, CV mine road).

TEMPORAL DISTRIBUTION. May (3), July (1).

DIAGNOSIS. *Phileurus limicauda* is recognized by its tridentate foretibia (rarely with a weak fourth tooth), frons with tubercles (occasionally large) instead of horns, middle tooth of the foretibia obliquely truncate,

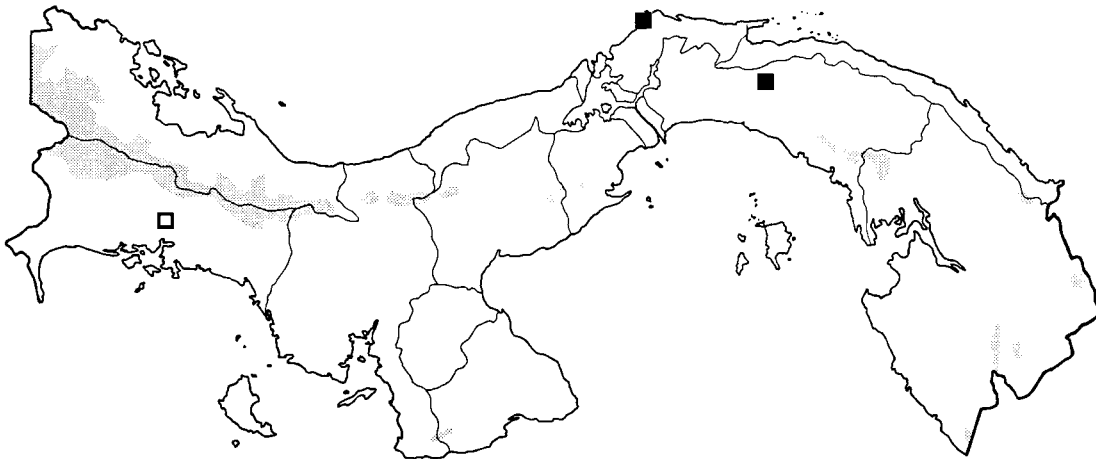


Fig. 795. Distribution of *Phileurus limicauda* in Panama.

elytral intervals all of equal height, and simple male parameres.

BIOLOGY. Adults are attracted to lights and probably live along with the larvae in rotting tree trunks and stumps. Specimens have been collected from premontane wet forests at elevations of 100-1,000 meters.

***Phileurus truncatus* (Palisot de Beauvois, 1807)**
(Figs. 796-800)

Scarabaeus truncatus Palisot de Beauvois 1807: 41.

Phileurus recurvatus Casey 1915: 266.

DESCRIPTION. Length 28.5-39.3 mm; width 14.0-19.7 mm. Color black. *Head:* Frons and vertex with deep hollow, surface within hollow smooth. Horns erect, apices recurving posteriorly, long in large specimens (55 mm), shorter in small specimens; high, transverse ridge between bases of horns in large specimens. Clypeus triangular, apex acute, strongly reflexed; surface smooth anteriorly, sparsely punctate (largest specimens) to rugose (smaller specimens) posteriorly. Interocular width equals approximately 4.8 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. Mandibles narrow, lateral edge arcuate, apex

acute. *Pronotum:* Median, longitudinal furrow broad, shallow, becoming slightly wider at anterior end, extending from near base to just past middle of pronotum. Apical tubercle at anterior end of furrow (posterior edge of pronotal cavity; 3 or more eye diameters between tubercle and anterior margin). Surface within furrow with large punctures basally, becoming rugopunctate anteriorly; anterior third of pronotum with large, transverse punctures or "rasps"; disc either side of furrow with small to moderate, sparse punctures, punctures becoming denser and larger laterally. Posterior margin without basal bead. *Elytra:* Rows of punctures in shallow furrows; punctures moderate in size, ocellate, separated from one another by 1-2 puncture diameters. Intervals weakly convex, sparsely punctate, punctures small. *Pygidium:* Base with transverse, slightly depressed furrow. Surface sparsely punctate in basal half, becoming very sparsely punctate apically; punctures small to moderate, shallow, minutely setigerous. In lateral view, surface strongly convex in males, convex in females. *Legs:* Foretibia tridentate, all teeth simply triangular. Apex of posterior tibia with single, broad, large, triangular tooth. Apex of first tarsomere of posterior tarsus extended into long, slender spine. *Venter:* Prosternal process short, subtriangular, posterior surface with deep, broad, transverse groove. *Parameres:* Figs. 797-798.

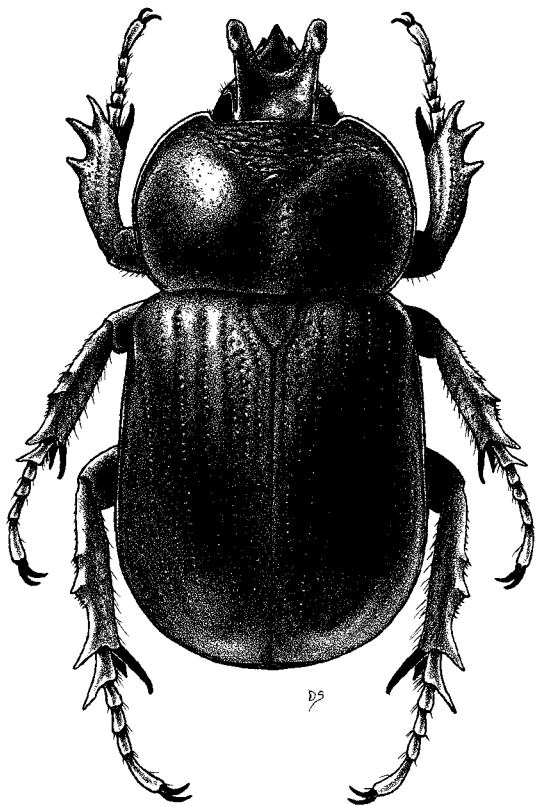
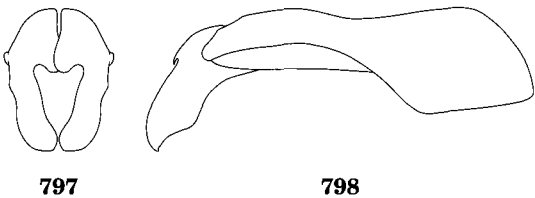


Fig. 796. *Phileurus truncatus*.



Figs. 797-798. *Phileurus truncatus* parameres.

DISTRIBUTION. *Phileurus truncatus* occurs from the southern United States to Panama (Endrödi 1978). The Costa Rican specimens listed below are a NEW COUNTRY RECORD. This species is distributed broadly throughout Costa Rica and Panama.

LOCALITY RECORDS (Figs. 799-800). 139 specimens examined.

COSTA RICA (99). ALAJUELA (1): Colonia Blanca; CARTAGO (8): Moravia (7 km E), Platanillo (vicinity of Moravia), Tapanti,



Fig. 799. Distribution of *Phileurus truncatus* in Costa Rica.

Teyutic, Xikiari (vicinity of Moravia); GUANACASTE (24): Estación Cacao, Estación Pitilla, Río San Lorenzo, Tierras Morenas; PUNTARENAS (64): Estación Altamira, Estación Las Alturas, Estación La Sirena, La Escuadra, Rancho Quemado (Osa), Reserva Biológica Monteverde, Wilson Botanical Garden; SAN JOSÉ (1): Embalse El Llano; No data (1).

PANAMA (40). CANAL ZONE (1): Ft. Gulick; CHIRIQUI (29): Café Duran, Hartmann's Finca (Santa Clara), IHRE vivero (11.5 km N Los Planes), Los Planes, Reserva Fortuna; COCLÉ (7): Cerro Gaital; PANAMA (3): Cerro Azul, Cerro Campana, Cerro Jefé.

TEMPORAL DISTRIBUTION. March (6), April (2), May (32), June (36), July (8), August (9), September (7).

DIAGNOSIS. *Phileurus truncatus* is characterized by its tridentate foretibia, larger size, frons with horns (instead of tubercles), apex of the posterior tibia with a single, large, broad tooth, and by a smooth hollow on the frons and vertex. The parameres are also distinctive.

BIOLOGY. The immature stages are undescribed, but they are probably found in rotting logs and stumps. Life history information for

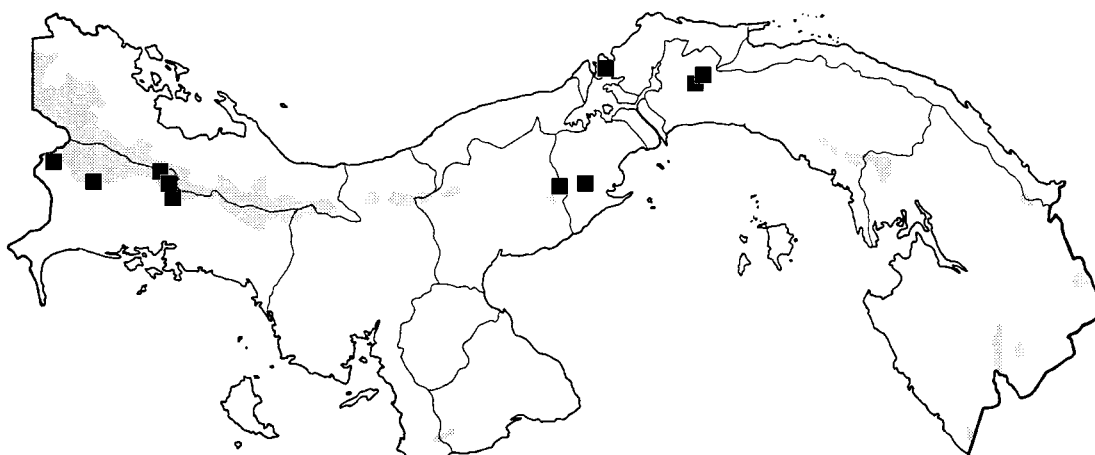


Fig. 800. Distribution of *Phileurus truncatus* in Panama.

this species is also lacking. Adults are usually found attracted to lights at night. They have been found in tropical wet forests, premontane wet forests, and premontane rain forests at elevations of 100-1,600 meters. Saylor (1948a) noted, perhaps anecdotally, that *P. truncatus* has been recorded as mistaking chimneys for hollow trees and thus falling into fireplaces.

***Phileurus valgus* (Olivier, 1789)**
(Figs. 801-805)

Scarabaeus valgus Olivier 1789: 48.

Scarabaeus castaneus Haldeman 1843: 304 (synonym).

Phileurus capra Bates 1888: 341 (synonym).

Phileurus valgus septentrionis Kolbe 1910: 352 (synonym).

Phileurus meridionalis Kolbe 1910: 352 (synonym).

Phileurus valgus antillarum Prell 1912c: 180 (subspecies).

Phileurus texensis Casey 1915: 268 (synonym).

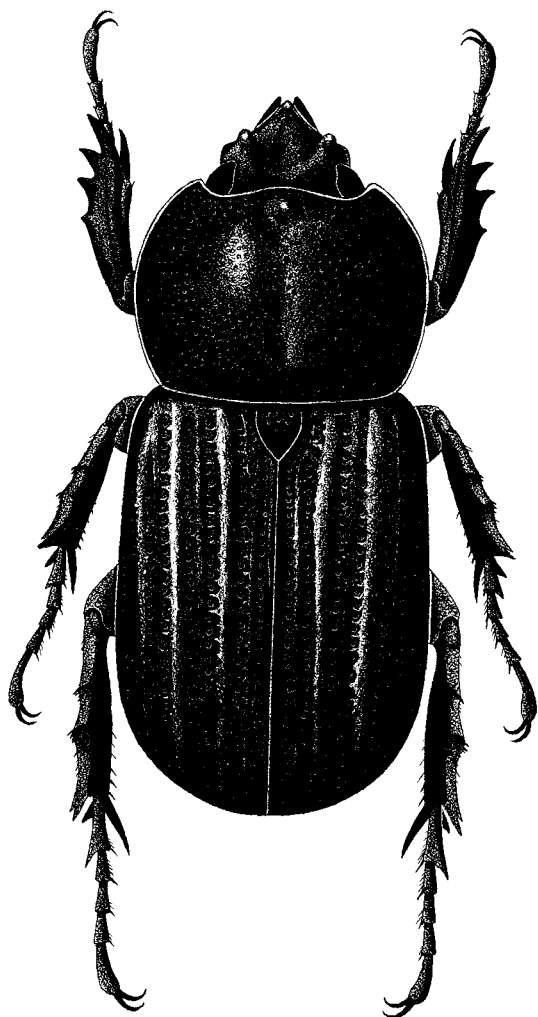
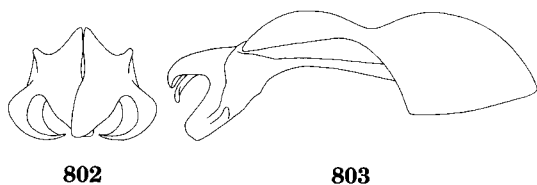
Phileurus carolinae Casey 1915: 269 (synonym).

Phileurus sulcifer Casey 1915: 269 (synonym).

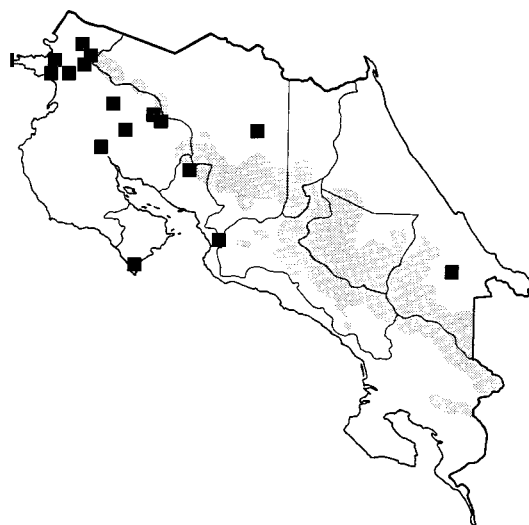
Phileurus floridanus Casey 1915: 270 (synonym).

Phileurus clathratus Casey 1915: 271 (synonym).

DESCRIPTION. Length 18.0-28.8 mm; width 8.0-13.1 mm. Color black. *Head:* Hollow of frons and vertex concave, usually sparsely rugose, occasionally transversely rugopunctate to rugose; remainder of surface rugose, tubercle present on each side of head. Clypeus triangular, apex acute and strongly reflexed, surface with coarse, transverse rugae mesad of each clypeal carina (which extends from clypeal apex to base of each tubercle), smooth with micropunctures laterad of each clypeal carina. Interocular width equals 4.3-5.0 transverse eye diameters. Antenna 10-segmented, club slightly longer than segments 2-7. Mandibles externally arcuate, apex acute. *Pronotum:* Median, longitudinal furrow narrow, moderately deep, extending from near base to just past middle of pronotum where it joins small, oval fovea; furrow and fovea coarsely rugopunctate to rugose. Distinctly conical tubercle present usually immediately behind apical margin of pronotum. Disc either side of furrow moderately punctate; punctures minute, mixed with small or moderate punctures, punctures becoming larger and denser on sides of pronotum; anterior angles mesad to tubercle coarsely rugopunctate to transversely rugose. Base with complete marginal bead. *Elytra:* Rows of punctures usually paired; punctures moderately large, ocellate, most separated by about 1 puncture diameter. Alternate intervals (*i.e.*, between paired rows) usually elevated, wider, carinate, moderately punctate with small

Fig. 801. *Phileurus valgus*.Figs. 802-803. *Phileurus valgus* parameres.

punctures; intervals between each row in a pair narrow, flat. Occasionally, all intervals subequal in height and width. *Pygidium*: Base in males with shallow, narrow, transverse furrow, furrow in females broader (depression usually extending to disc). Surface basally moderately densely punctate; punctures mod-

Fig. 804. Distribution of *Phileurus valgus* in Costa Rica.

erately large, ocellate, setigerous, becoming a little sparser apically; setae short, tawny. In lateral view, surface evenly convex in males, weakly convex in females. *Legs*: Foretibia quadridentate, basal tooth removed from others, sometimes reduced; apical 2 teeth obliquely truncate although they often appear simply acuminate due to wearing. Apex of posterior tibia with 2 large teeth, dorsal tooth longer and more slender. Apex of basal tarsomere of posterior tarsus extended into long, slender spine. *Venter*: Prosternal process short, subtrapezoidal, posterior surface strongly protuberant at middle and again at base. *Parameres*: Figs. 802-803.

DISTRIBUTION. *Phileurus valgus* is known from the southern United States to Argentina and the West Indies (Endrödi 1978, 1985a; Chalumeau 1983). It is broadly distributed in Costa Rica and Panama.

LOCALITY RECORDS (Figs. 804-805). 215 specimens examined.

COSTA RICA (162). ALAJUELA (3): Caño Negro; GUANACASTE (142): Cañas, Estación Las Pailas, Estación Maritza, Estación Murcielago, Estación Palo Verde, Estación Santa Rosa, Finca Jenny (30 km N Liberia), Finca Montezuma (Volcán Tenorio), Isla San

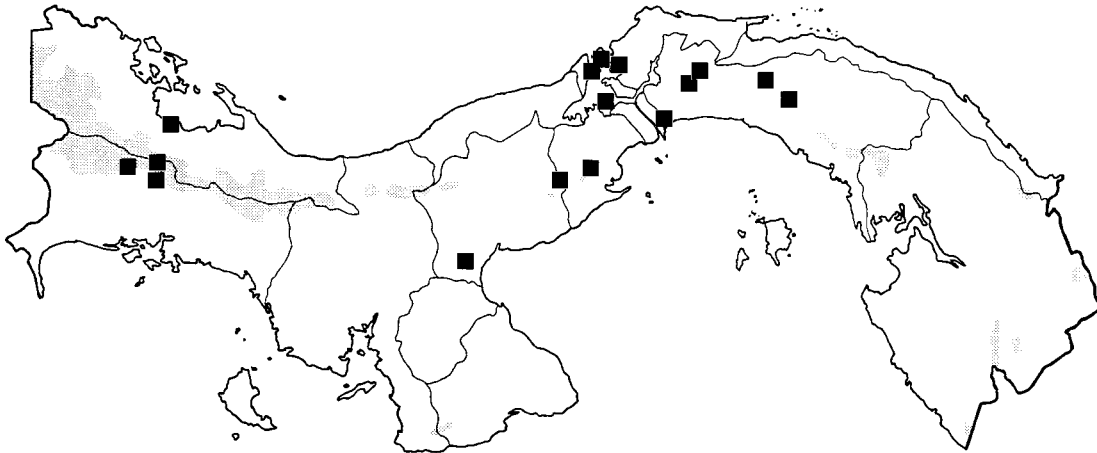


Fig. 805. Distribution of *Phileurus valgus* in Panama.

José (Islas Murciélago), Los Almendros (Parq. Nac. Guanacaste), Playa Naranjo (Parq. Nac. Santa Rosa), Río Gongora, Sector El Hacha (12 km SE La Cruz), Tierras Morenas, Volcán Tenorio; LIMÓN (1): Reserva Biológica Hitoy Cerere; PUNTARENAS (16): Estación Cabo Blanco, Estación Quebrada Bonita (Monteverde), San Luis (Reserva Biológica Monteverde).

PANAMA (53). BOCAS DEL TORO (1): Miramar; CANAL ZONE (19): Barro Colorado Island, Coco Solo Hospital, Diablo Heights, Ft. Sherman (Pavon Hill), Gatun (6 km SW); CHIRIQUI (6): Boquete, Finca La Suiza, Fortuna Dam area, Volcancito; COCLÉ (7): Cerro Gaital; COLÓN (5): Colón, Santa Rita Ridge; PANAMA (15): Cerro Azul, Cerro Jefe, Chilibre, El Llano-Carti Rd. (km 8), Isla de Majé, Sajalices.

TEMPORAL DISTRIBUTION. January (7), February (2), March (12), April (7), May (30), June (23), July (10), August (4), September (6), October (14), November (6), December (7).

DIAGNOSIS. *Phileurus valgus* is distinguished from other *Phileurus* species (except *P. voirinae*) by its quadridentate foretibia, alternately elevated elytral intervals, and two large teeth on the apex of the posterior tibia. The parameres of the male are also distinctive. Specimens of *P. valgus* nearly always have the alternate intervals of the elytra

higher and wider than the other intervals. In *P. voirinae*, all the intervals are subequal in height and width. In cases where some specimens of *P. valgus* have nearly subequal elytral intervals, the more distinctly and densely punctate elytral intervals and conical pronotal tubercle located immediately behind the anterior margin of the pronotum will distinguish *P. valgus*. In *P. voirinae*, the elytral intervals are weakly and sparsely punctate, and the pronotal tubercle is broadly transverse and well behind the anterior margin of the pronotum. Lastly, the form of the parameres will separate the males. Small specimens of *P. didymus*, which also have quadridentate foretibia, might be confused with *P. valgus*, but the alternate elytral intervals are not elevated in *P. didymus*, and the apex of the posterior tibia has only a single tooth.

Endrödi (1978, 1985a) recognized three "races" of *P. valgus* that he designated as subspecies. In his view, the nominate subspecies, *valgus*, occurs from the southern United States to Colombia and Venezuela. The subspecies *meridionalis* occurs from Colombia to Argentina and is characterized by having three or four protibial teeth. The subspecies from the Antilles was designated *antillarum* Prell in Endrödi's 1978 synopsis and *capra* Bates in the 1985 English translation.

The separation of a West Indian population into a distinct subspecies may be valid because, if for no other reason, it is reproductively

isolated from the mainland population. However, Endrödi's separation of a "northern" and "southern" population into two separate subspecies seems arbitrary and without foundation. Reproductive isolation has not been established nor are there any consistent morphological differences with which to distinguish the two "races." Subspecific names for these two "races" do not seem justified.

BIOLOGY. Adults are readily attracted to lights at night, and both adults and larvae live in rotting wood like many other species of phileurines. Deloya (1888) found adults in the detritus refuse piles of the leafcutter ant, *Atta mexicana* (Smith), in Mexico. Specimens have been collected from tropical dry forests, tropical moist forests, tropical wet forests, and premontane rain forests between the elevations of sea level and 1,200 meters.

***Phileurus voirinae* Endrödi, 1985**
(Figs. 806-809)

Phileurus voirinae Endrodi 1985b: 71.

DESCRIPTION. Length 23.3-28.2 mm; width 10.5-12.9 mm. Color black. *Head:* Hollow of vertex and frons broad, deep, rugose; remainder of frons rugose. Tubercle present on each side of head; tubercles conical, stout, erect, smaller in female. Clypeus triangular, apex acute and sharply reflexed, surface nearly smooth along apical margins, rugose elsewhere; clypeal carinae extending from clypeal apex to base of each tubercle weak to distinct. Interocular width equals 3.0-3.6 transverse eye diameters. Antenna with 10 segments, club a little longer than segments 2-7. Mandibles narrow, weakly arcuate on lateral edge, apex narrowly rounded. *Pronotum:* Median, longitudinal furrow narrow, deep, extending from near base to just past middle of pronotum where it joins small, oval fovea. Furrow with large punctures, fovea rugose. Distinctly transverse tubercle present behind anterior margin of pronotum by a distance subequal to half width of eye. Disc either side of furrow moderately punctate, punctures moderate in size; punctures becoming denser,

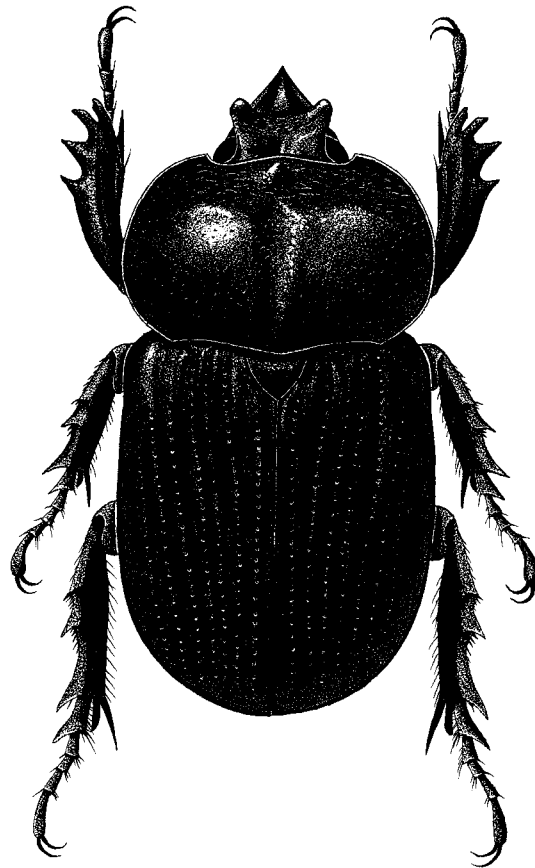
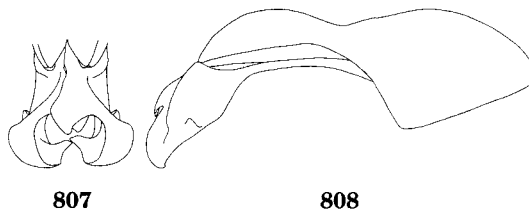


Fig. 806. *Phileurus voirinae*.



Figs. 807-808. *Phileurus voirinae* parameres.

larger laterally; anterior angles with large, transverse, mostly confluent punctures. Base with complete marginal bead. *Elytra:* Rows of punctures equidistant from one another, in furrows; punctures moderately large, ocellate-umbilicate, separated by 1-2 puncture diameters from each other. Intervals convex, subequal in height and width except for second and fourth which are fractionally wider, with sparse, small punctures. *Pygidium:* Base with transverse, shallow furrow; furrow nar-

row in males, broad in females and with large, dense, ocellate punctures. Surface sparsely punctate, punctures moderately large, with minute to short, tawny setae. In lateral view, surface evenly and strongly convex in males, weakly convex in females. *Legs*: Foretibia quadridentate, basal tooth removed from others, apical 2 teeth obliquely truncate. Apex of posterior tibia with 2 large teeth, dorsal tooth longer and more slender. Apex of basal tarsomere of posterior tarsus extended into long, slender spine. *Venter*: Prosternal process short, subtrapezoidal, posterior surface strongly protuberant at middle and again at base. *Parameres*: Figs. 807-808.

DISTRIBUTION. *Phileurus voirinae* is widely, but sparsely, distributed from southern Mexico to Costa Rica.

LOCALITY RECORDS (Fig. 809). 26 specimens examined (17 from the study area). Two specimens were seen from Chiapas, Mexico, six from Honduras, and one from Guatemala, all representing **New Country Records**.

COSTA RICA (17). GUANACASTE (4): Estación Maritza, Estación Pitilla; HEREDIA (2): Estación Magsasay, La Virgen de Sarapiquí; LIMÓN (1): Estación Cuatro Esquinas; PUNTARENAS (10): Bosque Esquinas (Osa), Estación Quebrada Bonita, Estación Sirena, Parq. Nac. Manuel Antonio, Rancho Quemado (Osa).

TEMPORAL DISTRIBUTION. January (1), February (1), April (2), May (3), June (2), July (1), August (4), September (1), October (1), November (1).

DIAGNOSIS. *Phileurus voirinae* is clearly a sister species to *P. valgus* or *P. toulgoeti* Dechambre, and the two share many character states, most notably the quadridentate foretibia. However, the differences in features of surface sculpturing, the pronotum, elytra, and male parameres will distinguish them. In *P. valgus*, the alternate intervals of the elytra are nearly always higher and wider than the other intervals, although in a few specimens the intervals are nearly subequal in height

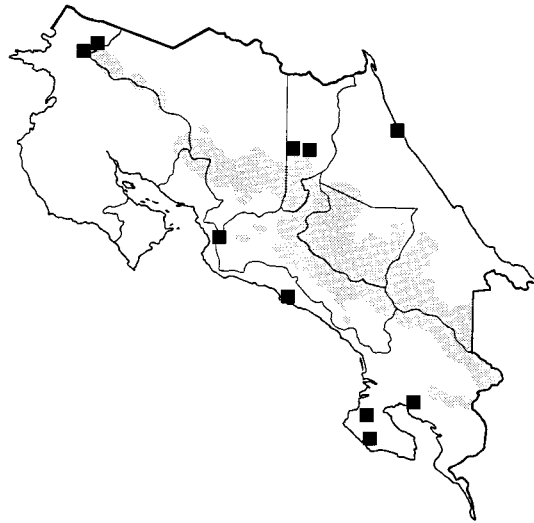


Fig. 809. Distribution of *Phileurus voirinae* in Costa Rica.

and width. In *P. voirinae*, all of the intervals are subequal in height and width. Problems with identification occur when certain specimens of *P. valgus* are found with subequal elytral intervals. In these cases, the more distinctly and densely punctate elytral intervals of *P. valgus*, in combination with the conical pronotal tubercle positioned immediately behind the anterior margin of the pronotum, will help to differentiate this species from *P. voirinae*. In *P. voirinae*, the elytral intervals are weakly and sparsely punctate, and the pronotal tubercle is broadly transverse and well behind the anterior margin. If still in doubt, the parameres will distinguish the males. *Phileurus toulgoeti*, from French Guiana, is also similar, but it has distinctive coarse punctation on the pronotum and elytral intervals, and the “wings” at the top of the parameres are very long and curved.

Additional specimens of *P. voirinae*, currently residing in collections as unidentified material or named as *P. valgus*, will probably be found from other locations in Mesoamerica.

BIOLOGY. Adults have been collected at lights at night. They have been found in tropical dry forests, tropical moist forests, tropical wet forests, and premontane moist forests between the elevations of sea level to 600 meters.

***Phileurus youngi* Ratcliffe, 1988**
(Figs. 810-814)

Phileurus youngi Ratcliffe 1988: 53.

DESCRIPTION. Length 24.0-28.5 mm; width 11.0-12.1 mm. Color black. *Head:* Frons with deep hollow, surface within hollow transversely rugopunctate. A short, subconical horn present in front of each eye near lateral margin of clypeus; horn blunt, slightly recurved posteriorly. Clypeus triangular, apex acute and strongly reflexed; surface transversely rugose posteriorly, smooth and with minute punctures anteriorly. Interocular width equals 3.9-4.1 transverse eye diameters. Antenna with 10 segments, club slightly longer than segments 2-7. Mandibles arcuate on sides, lacking teeth, apex acute. *Pronotum:* Surface sparsely punctate at base and on disc either side of median furrow, becoming moderately punctate on sides and densely punctate to rugopunctate anteriorly; punctures small either side of median furrow and small to moderate and large mixed elsewhere. Median furrow extending from near base to subapical tubercle; furrow moderately deep, parallel sided in basal half and expanding slightly into fovea behind tubercle; surface within furrow with sparse, moderate to large punctures. Subapical tubercle present. All margins with bead. *Elytra:* Surface with striae deeply furrowed, punctures within furrows moderate in size, ocellate, separated from one another by 1-3 puncture diameters. Intervals convex, with sparse, minute punctures. *Pygidium:* Base with transverse, shallow furrow. Surface with basal half moderately punctate, becoming sparsely punctate apically; punctures small to moderate in size, usually setigerous; setae moderate in length (pristine specimen) to more usually short, pale. In lateral view, surface strongly convex in males, weakly convex in females. *Legs:* Foretibia tridentate, basal tooth slightly removed from others, all teeth acuminate. Apex of posterior tibia with 2 large teeth, upper tooth prolonged into slender spine, lower tooth usually with 2-3 small serrations on upper edge. Apex of basal tarsomere of posterior tarsus extended into

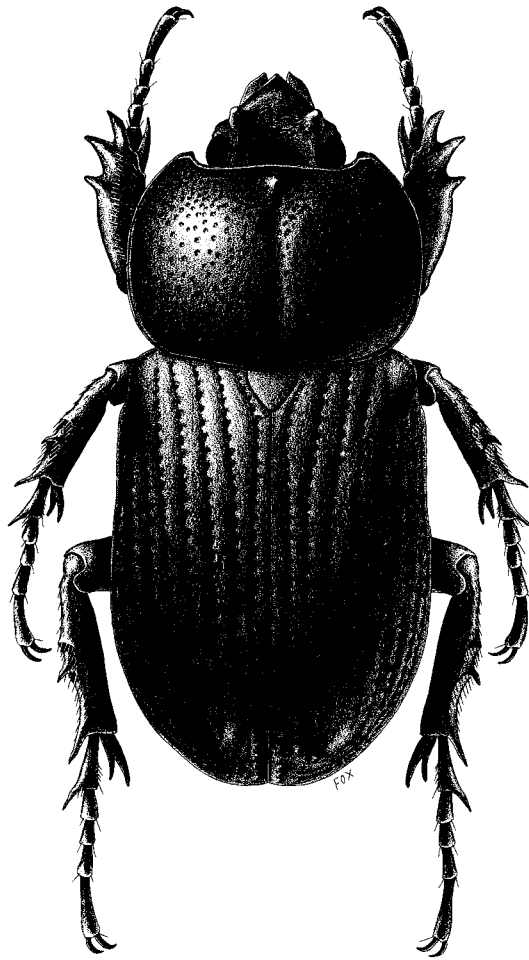
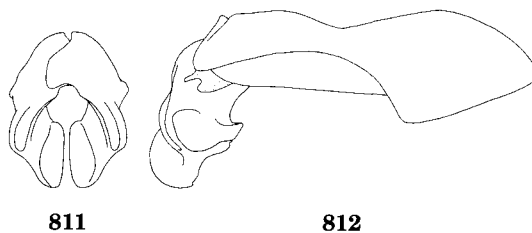


Fig. 810. *Phileurus youngi*.



Figs. 811-812. *Phileurus youngi* parameres.

long spine. *Venter:* Prosternal process short, subtriangular except apex broad, posterior surface with transverse ridge. *Parameres:* Figs. 811-812.

DISTRIBUTION. *Phileurus youngi* was originally described from a single specimen collected near the continental divide in Bocas del Toro province, Panama. I now have specimens from other localities in Panama as well as Costa Rica and Nicaragua. Specimens from the latter two countries represent NEW COUNTRY RECORDS.

LOCALITY RECORDS (Figs. 813-814). 61 specimens examined.

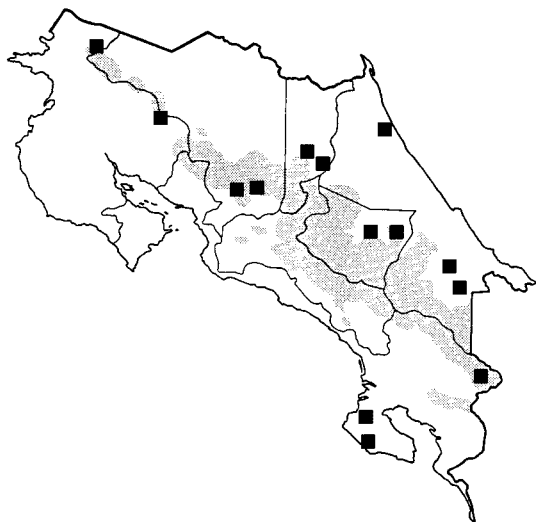


Fig. 813. Distribution of *Phileurus youngi* in Costa Rica.

COSTA RICA (44). ALAJUELA (7): Río San Lorencito, San Ramón; CARTAGO (12): Cerro Vola (vicinity Chirripó), Chirripó Valley (30 mi SE Turrialba), Grano de Oro, Moravia (7 km E), Rancho Naturalista (5 km N Cayutic), Río Pacuare (vicinity Platanillo); GUANACASTE (14): Estación Pitilla, Tierras Morenas; HEREDIA (3): Estación El Ciego, Estación Magsasay; LIMÓN (5): Amubri, Cerro Tortuguero, Estación Hitoy Cerere; PUNTARENAS (4): Estación Las Mellizas, Estación Sirena, Rancho Quemado (Osa).

PANAMA (16). BOCAS DEL TORO (1): 2 km N continental divide on rd. to Chiriqui Grande; COCLÉ (9): Cerro Gaital; PANAMA (6): Cerro Campana, Cerro Jefé.

TEMPORAL DISTRIBUTION. February (3), March (5), April (8), May (9), June (10), July (9), August (2), October (1), November (1), December (1).

DIAGNOSIS. The combination of tridentate foretibia (all teeth simply acute), frons with tubercles (instead of horns), and form of the parameres will distinguish this species.

BIOLOGY. Specimens have been taken at lights in tropical wet forests, premontane wet forests, and premontane rain forests at elevations ranging from near sea level to 1,200 meters.



Fig. 814. Distribution of *Phileurus youngi* in Panama.



Color Plate 7. *Spodistes mnischei*. Illustration by Dan Schmidt.

TRIBE AGAOCEPHALINI

The Agaocephalini is a small tribe of strictly Neotropical scarabs. There are 11 genera and 43 species that occur from southern Mexico to Argentina, with one genus and species in the West Indies. In Costa Rica and Panama, there are two genera and six species.

The agaocephalines were first proposed as a taxonomic category (Agaocephalidae) by Burmeister (1847), who included in it four genera. Lacordaire (1856) continued the concept, and Thomson (1860) provided a synopsis. Casey (1916) was the first to place this group at the tribal level. Endrödi (1970, 1985a) provided a modern synopsis, and new species have since been added by Martínez and Alvarenga (1987), Dechambre (1992, 1994, 1999b), and Warner (1992).

Adult agaocephalines are not easily characterized at the tribal level because of the

high degree of variable character states among the various genera. In general, they are moderate in size and broadly suboval in shape and, although not actually depressed, most tend to be somewhat flattened from top to bottom. Like members of the Dynastini, they have irregularly punctate elytra (never with double rows of punctures or longitudinally raised costae), a propygidium that lacks a stridulatory area, and slender middle and posterior tarsi. The Central American species are strongly dimorphic between the sexes. The males possess large head and pronotal horns, and some have enlarged protarsi, whereas the females do not have horns or enlarged tarsi.

The immature stages are completely unknown. Similarly, life histories, food preferences, and habits are not known. Adults seem to have been encountered only at lights.

Key to the Genera of Adult Agaocephalini of Central America

1. Surface glabrous, weakly shining *Aegopsis* Burmeister
- 1'. Surface completely covered with grayish brown tomentum
 *Spodistes* Burmeister

Clave para los Géneros de Adultos de Agaocephalini de Centro América

1. Superficie glabra, ligeramente pulida *Aegopsis* Burmeister
- 1'. Superficie completamente cubierta con tomento pardo grisáceo
 *Spodistes* Burmeister

***Aegopsis* Burmeister, 1847**

Aegopsis Burmeister 1847: 281.

The genus *Aegopsis* contains four species (*A. curvicornis* Burmeister, *A. bolbocerida* Thomson, *A. peruvianas* Arrow, *A. chaminadei* Dechambre) that are found in northwestern South America with one of them reaching Panama. *Aegopsis westwoodi* Thomson (Colom-

bia and Panama) is here placed in synonymy with *A. curvicornis* Burmeister.

This genus is readily distinguished from *Spodistes* because of its glabrous, weakly shining dorsal surface. Males have two long, recurved head horns, and the females lack armature.

Adults are nocturnal and attracted to lights but otherwise nothing is known of their biology.

***Aegopsis curvicornis* Burmeister,
1847
(Figs. 815-820)**

Aegopsis curvicornis Burmeister 1847: 282.
Aegopsis westwoodi Thomson 1860: 17 (**NEW
SYNONYMY**).
Aegopsis atra Sternberg 1904: 18 (synonym).
Aegopsis nigricollis Sternberg 1904: 18 (synonym).
Aegopsis trinidadensis Sternberg 1904: 18 (synonym).

DESCRIPTION. Length 20.0-27.0 mm; width 12.5-15.2 mm. Color dark brown.

Males. *Head:* Surface concave, nearly smooth, sometimes with sparse punctures on clypeus. Clypeus with apex almost semicircular. Majors (Fig. 816) with horns long, projecting forward and then curving upward, slightly diverging, apices narrowly rounded; horns triangular in cross section. Minors with horns short, apices curving toward one another. Interocular width equals 3.8-4.0 transverse eye diameters. Antenna with 10 segments, club subequal to segments 2-7. Mandibles small, elongate, slender, hidden beneath clypeus. *Pronotum:* Surface either side of dorsal ridge of horn completely scabrous/rugulose in majors. Minors with posterior angles moderately punctate, punctures moderately large; disc at center with punctate longitudinal area; punctures sparse to dense, small or large and small mixed. Majors with long, central horn projecting forward and curving slightly downward at apex, horn tapering to bluntly rounded apex. Minors with horn reduced to prominent, forward-projecting tubercle. Lateral margins prominently angulate just behind middle. Base with strong marginal bead. *Elytra:* Surface variably shagreened (nearly obsolete to very pronounced), occasionally weakly and transversely rugose, moderately punctate; punctures moderate in size, ocellate, shallow. *Pygidium:* Surface of disc moderately punctate, punctures small and minute mixed; base, anterior margin, and angles finely rugulose. In lateral view, surface strongly convex. *Legs:* Foretibia quadridentate, basal tooth often greatly reduced in size, occasion-

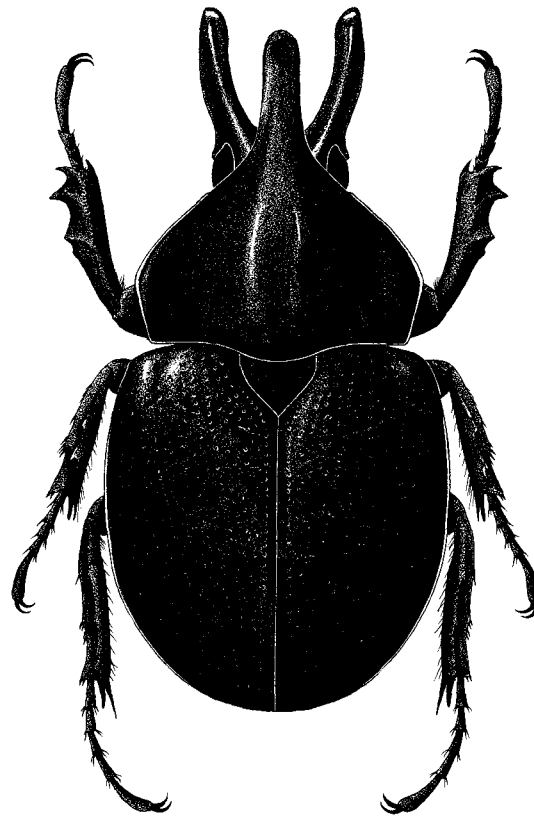
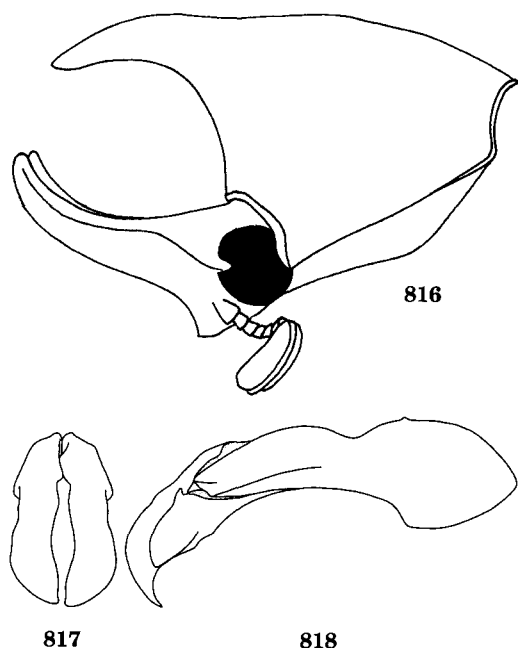


Fig. 815. *Aegopsis curvicornis*.

ally absent altogether (especially in minors). Anterior tarsus with 5th tarsomere subequal in length to tarsomeres 1-4 in minors to much longer in majors. Apex of posterior tibia with large lateral tooth and median prominence divided into 3-4 small teeth. Apex of first tarsomere of posterior tarsus elongated into large spine. *Venter:* Prosternal process small, very low, subtriangular. *Parameres:* Figs. 817-818.

Females. As males except in the following respects. *Head:* Surface flat, densely punctate; punctures large, deep, some confluent. Clypeus with apex semicircular to angularly rounded. Horns and tubercles absent. Interocular width equals 6.0 transverse eye diameters. *Pronotum:* Surface at center sparsely to moderately punctate, elsewhere punctures moderately dense, becoming confluent in anterior margin and angles;



Figs. 816-818. *Aegopsis curvicornis*: (816) male major, head and pronotum; (817-818) parameres.

punctures moderate in size to mostly large. Horns and tubercles absent. Lateral margin arcuate, widest just behind middle. Base with or without marginal bead. *Pygidium*: Punctures a little larger either side of midline. In lateral view, surface weakly concave at middle, strongly concave either side of middle.

DISTRIBUTION. *Aegopsis curvicornis* is found in Costa Rica (NEW COUNTRY RECORD), Panama, Colombia, Ecuador, Venezuela, Trinidad, and northern Brazil (Endrödi 1970, 1985a). In Panama, it is known from the highlands of Chiriqui, Los Santos, and Panama west of the Canal Zone.

LOCALITY RECORDS (Figs. 819-820). 85 specimens examined.

COSTA RICA (7). PUNTARENAS (7): Sabana (E of Buenos Aires, Talamanca Mts.).

PANAMA (78). CHIRIQUI (65): Boquete, Chiriquicito, Escopeta (Cerro Colorado),

Potrerrillos Abajo; LOS SANTOS (1): Cerro Canajagua (20 km SW Las Tablas); PANAMA (13): Cerro Campana, Islas Perlas (San José), Isla Taboga, Punta Vacamonte.

TEMPORAL DISTRIBUTION. February (3), April (64), May (15), June (1).

DIAGNOSIS. Males of *Aegopsis curvicornis* are easily recognized because of their paired, recurved head horns and single, median pronotal horn. Females are unique but not so easily distinguished because of their lack of the characteristic head and pronotal armature. Their body shape, surface sculpturing, clypeal form, lack of head or pronotal tubercles and small prosternal process are all diagnostic.

Blackwelder (1944), Endrödi (1970, 1985a), and Lachaume (1992) all listed *Aegopsis westwoodi* from Panama and Colombia. *Aegopsis westwoodi* is supposedly separated from the closely-related *A. curvicornis* by its slightly longer antennal club, shagreened and opaque elytra (especially evident in plate 5 of Lachaume 1992), pronotum densely punctate at the center, and anterior tibia tridentate with a small basal tooth. I have examined nearly a hundred specimens from Panama and northern South America and, while I see all these character states, they do not separate the two putative species (July 1992 notwithstanding). Not only do the characters not cluster together in a way delineating each species, but I see all levels of intergradation between states. Consequently, I believe *A. westwoodi* to be conspecific with *A. curvicornis*. The shiny and opaque forms of *Megasoma actaeon* (*M. janus* Felsche and *M. actaeon* (L.), respectively) is another example of variation in elytral luster within a single species that was formerly considered two species because of differences in surface luster.

BIOLOGY. Adults are attracted to lights at night. They are known to occur in subtropical wet forests and lower montane wet forests. The limited label data indicate specimens have been collected at elevations of 100 meters (San José in the Pearl Islands), 800-900 meters in Los Altos and Chiriqui, and

1,500 meters in the Talamanca range in eastern Costa Rica. I did find an intact head and pronotum of a *major* male inside the feces of a *Bufo* species (Salienta: Bufonidae) at Cerro Campana (Panama Prov.), which suggests some predation by these large toads. It also suggests that the toad may have experienced substantial inconvenience in passing scat imbedded with such impressively large horns.



Fig. 819. Distribution of *Aegopsis curvicornis* in Costa Rica.

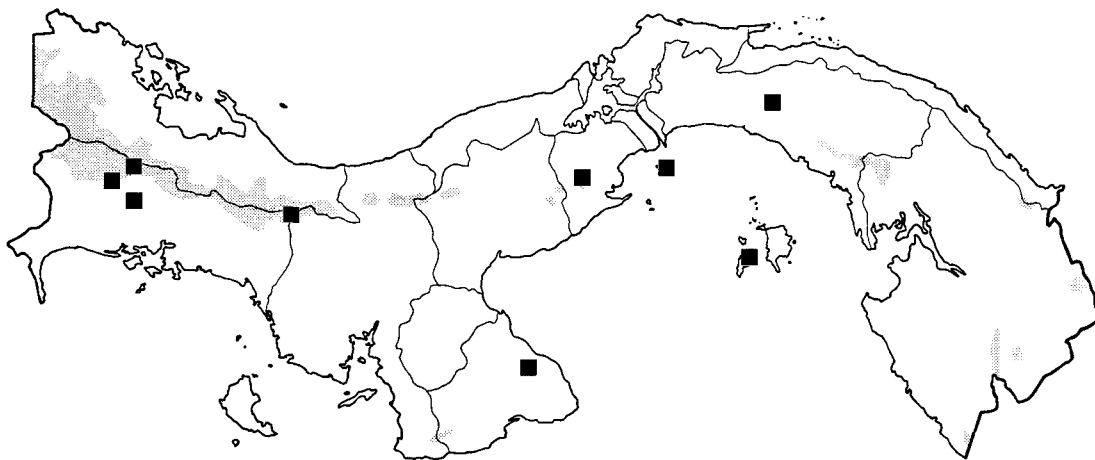


Fig. 820. Distribution of *Aegopsis curvicornis* in Panama.

Spodistes Burmeister, 1847

Spodistes Burmeister 1847: 286.

The genus *Spodistes* consists of eight species (Endrödi 1970, 1985a; Warner 1992; Dechambre 1992, 1994). Species in the genus range from southern Mexico to Colombia and Ecuador. Five species are known from Costa Rica and Panama.

All of the species of *Spodistes* are unique among the Central American dynastines because of their grayish brown or tan velutinous covering. This covering is more like a fine tomentum rather than the short, dense setae found in *Megasoma elephas*. The males are characterized by elongated, attenuate frontal and pronotal horns reminiscent of the much larger *Dynastes hercules*.

The female of *S. hopei* is described here for the first time, and a key to females of four of the five species inhabiting the study area is provided for the first time.

With rare exception, species of *Spodistes* are not commonly encountered. Nearly all of the specimens studied were probably taken at. Nothing is known of their biology.

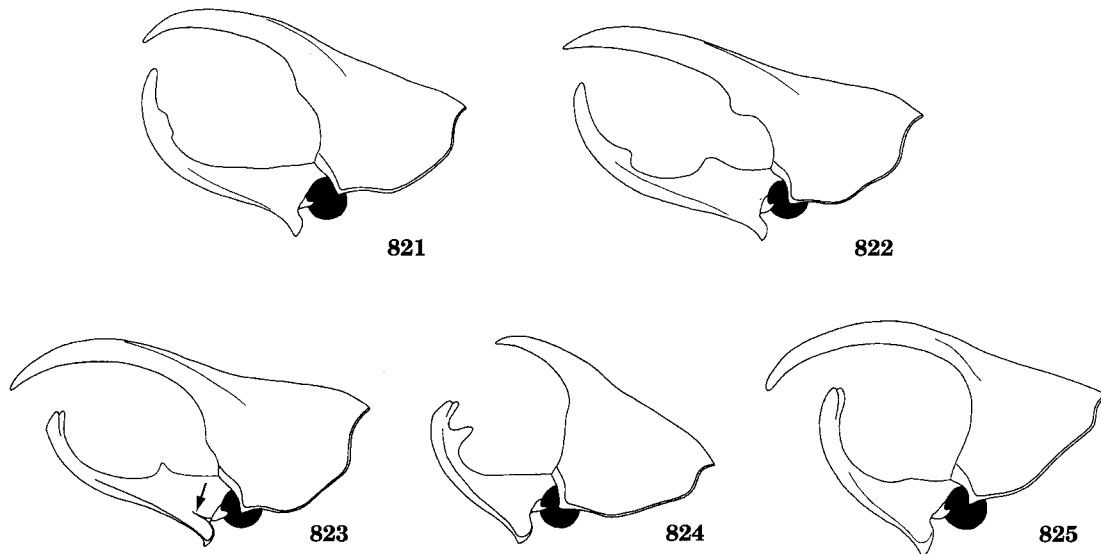
Key to the Species of Adult *Spodistes* of Costa Rica and Panama

MALES (with horns)

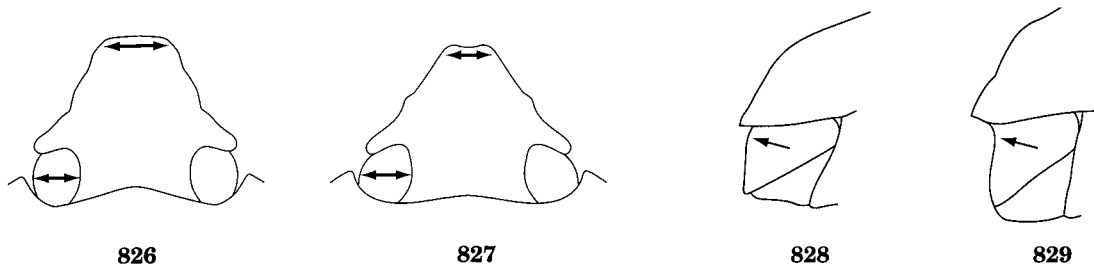
- 1. Apex of head horn acuminate (Figs. 821-822) 2
- 1'. Apex of head horn bifurcate or trifurcate (Figs. 823-825) 3
- 2. Head horn with distinct tubercle near base (in addition to submedian tubercle) (Fig. 822) *beltianus* (Bates)
- 2'. Head horn lacking tubercle near base (submedian tubercle still present) (Fig. 821) *armstrongi* Dechambre
- 3. Apex of head horn bifurcate (Figs. 823, 825) 4
- 3'. Apex of head horn trifurcate (Fig. 824) *hopei* Arrow
- 4. Base of ocular canthus at anterior edge with distinct carina projecting onto base of horn (Fig. 823) *batesi* Arrow
- 4'. Base of ocular canthus lacking carina projecting onto base of horn (Fig. 825) *mniszehi* (Thomson)

FEMALES (lacking horns) (*S. beltianus* not included)

- 1. Apex of clypeus relatively broad (about 1.2-1.3 transverse eye diameters) (Fig. 826) 2
- 1'. Apex of clypeus relatively narrow (about 1.0 transverse eye diameters) (Fig. 827) 3
- 2. In lateral view, pygidium weakly but evenly convex (Fig. 828) *batesi* Arrow
- 2'. In lateral view, pygidium nearly flat or weakly convex in apical 2/3 and distinctly concave in basal third (Fig. 829) *mniszehi* (Thomson)
- 3. Central concavity on top of head extending posteriorly as far as posterior margin of eye *armstrongi* Dechambre
- 3'. Central concavity on top of head extending posteriorly as far as middle of eye *hopei* Arrow



Figs. 821-825. *Spodistes* (821) *armstrongi*, (822) *beltianus* with apex of head horn entire. *Spodistes* (823) *batesi*, (824) *hopei*, (825) *mniszehi* with apex of head horn bifurcate or trifurcate.



Figs. 826-829. Head of female *Spodistes* (826) *batesi* and (827) *hopei* showing width of eye versus width of clypeus. Pygidium (lateral view) of female *Spodistes* (828) *batesi* and (829) *mniszehi*.

Clave para las Especies de Adultos de *Spodistes* de Costa Rica y Panamá

Machos (con cuernos)

1. Apice del cuerno de la cabeza acuminado (Figs. 821-822) 2
- 1'. Apice del cuerno de la cabeza bifurcado o trifurcado (Figs. 823-825) 3
2. Cuerno de la cabeza con un tubérculo evidente cerca de la base (además del tubérculo medio) (Fig. 822) **beltianus (Bates)**
- 2'. Cuerno de la cabeza sin tubérculo cerca de la base (tubérculo medio también presente) (Fig. 821) **armstrongi** Dechambre
3. Apice del cuerno de la cabeza bifurcado (Figs. 823, 825) 4
- 3'. Apice del cuerno de la cabeza trifurcado (Fig. 824) **hopei Arrow**
4. Base del canthus ocular en el borde anterior con una carina evidente que se proyecta sobre la base del cuerno (Fig. 823) **batesi Arrow**
- 4'. Base del canthus ocular sin carina que se proyecta sobre la base del cuerno (Fig. 825) **mniszehi (Thomson)**

Hembras (sin cuernos) (*S. beltianus* no incluida)

1. Apice del cíleo relativamente ancho (alrededor de 1.2 a 1.3 diámetros transversales del ojo) (Fig. 826) 2
- 1'. Apice del cíleo relativamente angosto (alrededor de 1.0 diámetro transversal del ojo) (Fig. 827) 3
2. Pigidio, en vista lateral, ligera pero enteramente convexo (Fig. 828) **batesi Arrow**
- 2'. Pigidio, en vista lateral, ligeramente convexo en los 2/3 apicales y claramente cóncavo en el tercio basal (Fig. 829) **mniszehi (Thomson)**
3. Concavidad central de la parte superior de la cabeza se extiende posteriormente hasta el margen posterior del ojo **armstrongi** Dechambre
- 3'. Concavidad central de la parte superior de la cabeza se extiende posteriormente hasta la mitad del ojo **hopei Arrow**

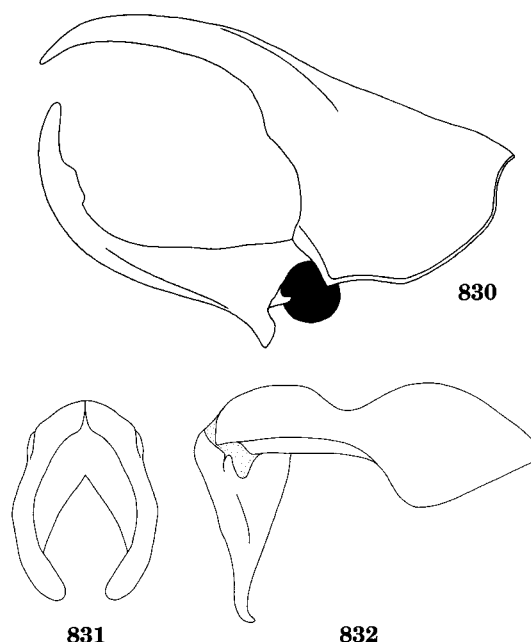
***Spodistes armstrongi* Dechambre,
1994**

(Figs. 830-833)

Spodistes armstrongi Dechambre 1994: 149.

DESCRIPTION. Length 24.0-30.0 mm; width 14.8-18.0 mm. Color grayish brown and tan, finely velutinous, with clypeus and part of horns in males and part of pronotum in females piceous.

Males. Head: Frons with long horn (shorter in minors); majors (Fig. 830) with horn projecting forward and then curving upward at about middle of horn, minors with horn gradually curving forward and upward for its entire length; apex sharply acuminate, with elongate tooth (majors) or small tooth (minors) on dorsal surface just before apex; horn triangular in cross-section; anterior (ventral) surface, apical half, and dorsal carina piceous. Ocular canthus with carina across base. Clypeal apex bluntly rounded, immediately continuous with anterior (ventral) surface of horn. Interocular width equals 3.0 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. Mandibles strongly bidentate, mostly hidden beneath clypeus. **Pronotum:** Majors with long, slender horn projecting forward and curving ventrally near apex; horn carinate dorso-laterally, apex narrowly pointed; ventral side with low tooth near base. Minors similar except horn shorter and ventral tooth near base usually absent. Surface with minute, moderately dense, setigerous punctures; setae minute, pale. Sides widest behind middle. Base with complete marginal bead. **Elytra:** Surface with moderately dense, minute punctures (usually obscured by velutinous covering). Sides explanate, apical umbones prominent. **Pygidium:** Surface with dense, short, pale setae. In lateral view, surface convex. **Legs:** Foretibia tridentate, basal tooth removed from others. Foretarsus enlarged, median claw with strong tooth at base and tooth-like swelling at middle. Apex of posterior tibia truncate with strong, median angle; angle with single spinule. Apex of first tarsomere of posterior tarsus elongated into acute spine. **Venter:** Prosternal process absent. **Parameres:** Figs. 831-832.



Figs. 830-832. *Spodistes armstrongi*: (830) male major, head and pronotum; (831-832) parameres.

Females. As males except in the following respects. **Head:** Horn absent. Frons and clypeus concave; surface with large to very large, confluent punctures. Lateral edge of clypeus at anterior edge of ocular canthus elevated into laminate, triangular ridge. Clypeal apex strongly narrowed from lateral ridges to moderately wide apex (subequal to width of eye); apex emarginate, strongly reflexed, with distinct tooth either side of emargination. Mandibles slightly more exposed. **Pronotum:** Horn absent. Surface piceous, glabrous, covered by large, dense, round to oval, velutinous punctures; punctures often confluent (especially on sides), with single, minute, pale seta at center of each. Anterior margin at middle tumescent. Shallow, median, longitudinal sulcus extending from near anterior margin to base. **Pygidium:** In lateral view, surface nearly flat. **Legs:** Foretarsus not enlarged, claws subequal in size, not toothed. Median angle at apex of posterior tibia pronounced and with a small spinule.

DISTRIBUTION. *Spodistes armstrongi* is known, so far, only from the Pacific slopes of the Serranía de San Blas just to the west of Panama City. Most of Dechambre's type series, as well

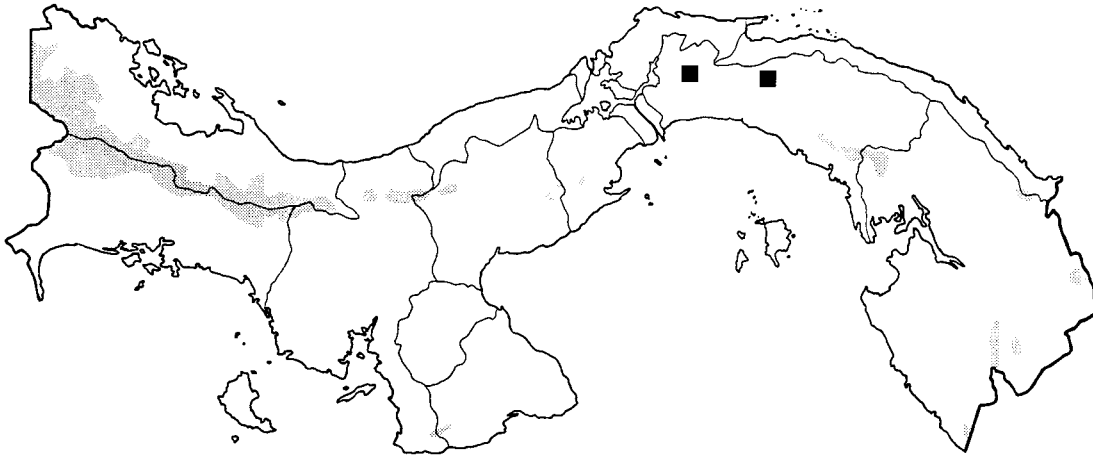


Fig. 833. Distribution of *Spodistes armstrongi* in Panama.

as the specimens I collected in 1986, were taken beneath street lights at the Altos de Cerro Azul housing development being carved out of low elevation forests. Beneath a *single* street light at the entrance to this development, I collected species of *Spodistes*, *Megasoma*, *Megaceras*, and *Dynastes* (34 scarab genera in all!), all on the same night. Sadly, much of this forest has been cleared in subsequent years, and virtually no scarabs were found in 1994 and 1995.

LOCALITY RECORDS (Fig. 833). 21 specimens examined or recorded.

PANAMA (21). PANAMA (21): Altos de Cerro Azul, El Llano-Carti Road (km 8-12).

TEMPORAL DISTRIBUTION. April (1), May (15), June (3), July (2).

DIAGNOSIS. *Spodistes armstrongi* is one of only two species of *Spodistes* in Costa Rica and Panama with an acutely pointed head horn in the males. They are separated from *S. beltianus* by the absence of a tubercle near the base of the head horn on the dorsal side. Females are similar to those of *S. hopei* and can be recognized by the larger concavity on the top of the head (the concavity reaches the level of the posterior margin of the eye). They can be separated from *S. batesi* by the narrower clypeal apex (about one transverse eye diameter). I cannot separate them from *S.*

beltianus since I have not seen females of that species.

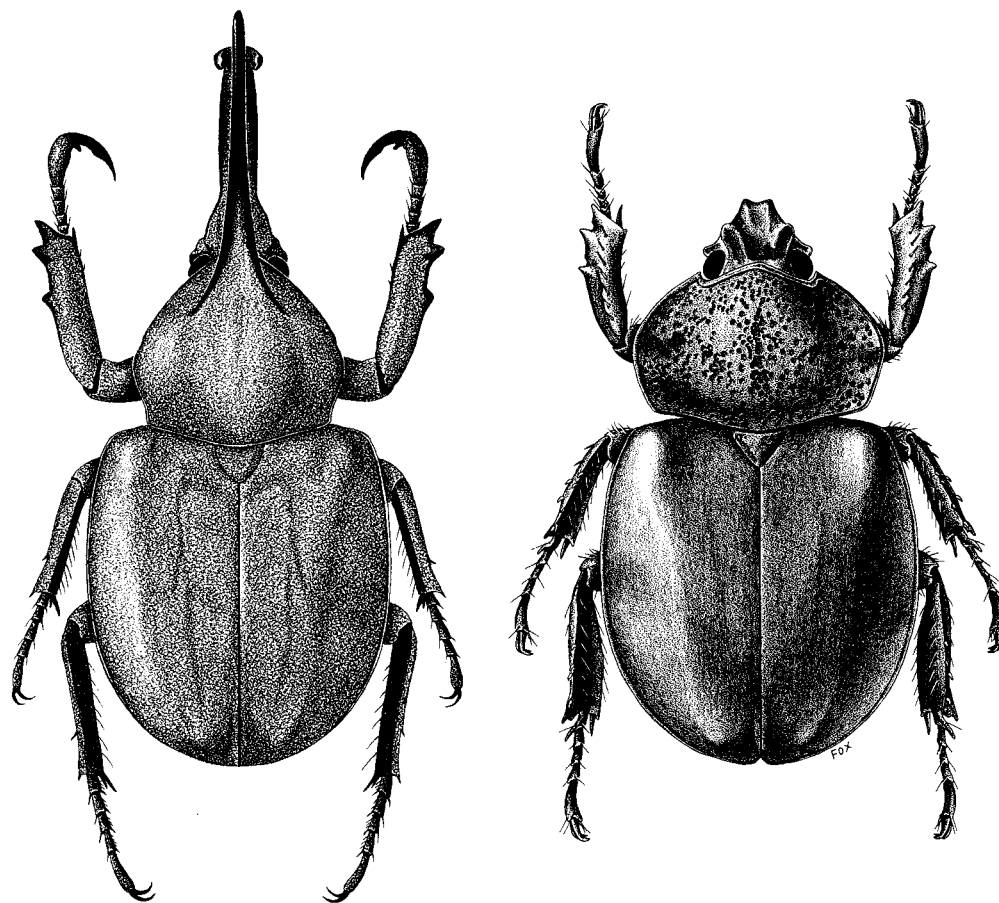
BIOLOGY. Adults are nocturnal and attracted to lights. They have been collected in tropical moist forests at elevations of 900-1,100 meters.

***Spodistes batesi* Arrow, 1902**
(Figs. 834-842)

Spodistes batesi Arrow 1902: 145.

DESCRIPTION. Length 24.7-30.0 mm; width 15.2-16.5 mm. Color grayish-brown, finely velutinous, with clypeus and part of horns in males and some of pronotum in females dark reddish brown.

Males. Head: Frons with long horn (shorter in male minors); majors (Fig. 836) with horn projecting forward, curving abruptly upward just before apex, minors with horn gradually recurved for its entire length; apex strongly bifurcate; dorsal surface with sharp tooth just before middle (tooth reduced in minors); in cross-section, horn triangular; anterior (ventral) surface, apical third, and dorsal tooth dark reddish brown. Base of ocular canthus at anterior edge with distinct carina projecting upward onto base of horn (Fig. 836). Clypeus with short horizontal surface before anterior (ventral) face of horn, surface shagreened, sparsely punctate; apex broadly rounded, occasionally weakly emarginate. Interocular width equals about

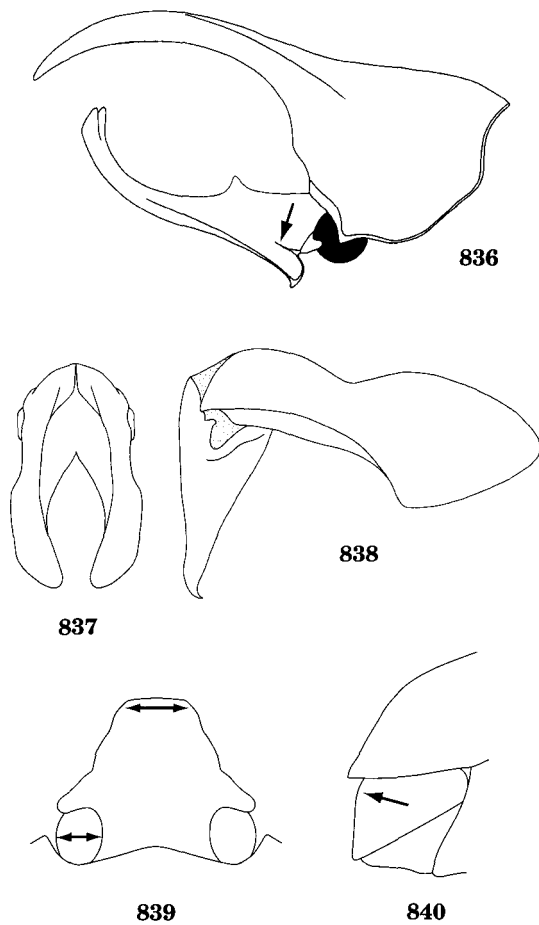


Figs. 834-835. *Spodistes batesi*, male and female.

3.0 transverse eye diameters. Antenna with 10 segments, club subequal to segments 2-7. Mandibles each with 2 strong, apical teeth and a strong basal lobe, mostly hidden beneath fringe of setae below clypeal apex. *Pronotum*: Long, slender horn projecting forward and curving ventrally to well beyond (majors) or just beyond (minors) apex of head horn; horn carinate dorsolaterally at base, apex narrowly pointed; minors with weak tooth at base ventrally, largest majors with series of 3 denticles ventrally near base. Surface at sides and base with sparse, minute, pale setae. Sides widest just behind middle. Base with complete marginal bead. *Elytra*: Surface with moderately dense, minute punctures on velutinous covering; punctures with minute, pale setae, setae becoming a little longer at apices behind prominent apical umbones. Sides explanate. *Pygidium*: Surface

velutinous with dense, short, pale setae. In lateral view, surface strongly convex. *Legs*: Foretibia tridentate, basal tooth removed from others. Foretarsus enlarged, median claw with strong tooth at base and tooth-like swelling at middle. Apex of posterior tibia subtruncate with strong median angle; angle with single, small spinule. Apex of first tarsomere of posterior tarsus elongated into acute spine. *Venter*: Prosternal process absent. *Parameres*: Figs. 837-838.

Females. As males except in the following respects. *Head*: Horn absent. Frons (especially) and clypeus concave, surface with moderate to mostly large, moderately dense to dense punctures. Lateral edge of clypeus at anterior edge of ocular canthus sharply elevated into cariniform, triangular tubercle. Apex of clypeus broad, a little wider than width of eye (Fig. 839), emarginate, strongly reflexed, with



Figs. 836-840. *Spodistes batesi*: (836) male major, head and pronotum; (837-838) parameres; (839) head of female showing width of eye versus broad width of clypeal apex; (840) pygidium (lateral view) of female.

distinct tooth either side of emargination. *Pronotum*: Horn absent. Surface glabrous, dark reddish brown, covered by large, dense, round velutinous punctures; punctures often confluent (especially at sides), and with single, minute, pale seta at center of each. Anterior margin at middle protuberant and with shallow, median, longitudinal sulcus extending from anterior margin to near middle of disc or nearly to base. *Pygidium*: Surface with minute setae; in lateral view, weakly and evenly convex (Fig. 840). *Legs*: Foretarsus not enlarged, claws subequal in size, not toothed. Angle at apex of posterior tibia pronounced and with 1-2 small spinules.



Fig. 841. Distribution of *Spodistes batesi* in Costa Rica.

DISTRIBUTION. *Spodistes batesi* is known from Mexico (Endrödi 1970, 1985a), Costa Rica, and Panama. Endrödi's Mexican specimen(s) was "no data," and doubt remains that this species actually occurs in Mexico; I have never seen specimens recorded from there. In Costa Rica and Panama, this species is known from the Cordillera Central from Volcán Orosi in Guanacaste in northwestern Costa Rica to western Chiriqui Province in Panama.

LOCALITY RECORDS (Figs. 841-842). 75 specimens examined.

COSTA RICA (9). **ALAJUELA** (2): San Ramón; **GUANACASTE** (1): Estación Maritza (Volcán Orosi); **PUNTARENAS** (6): Estación Las Alturas (Coto Brus), Estación Las Mellizas (Parq. Nac. Amistad).

PANAMA (66). **CHIRIQUI** (66): Boquete, Hartmann's Finca (Santa Clara), 3.5 km SE Santa Clara, Valle de Chiriqui, Volcancito.

TEMPORAL DISTRIBUTION. March (1), April (1), May (48), June (11), July (6).

DIAGNOSIS. *Spodistes batesi* and *S. mniszewski* males can be distinguished from their congeners by the presence of a forked head horn. A short carina extending from the base of the eye canthus longitudinally onto



Fig. 842. Distribution of *Spodistes batesi* in Panama.

the shaft of the head horn in *S. batesi* (Fig. 836) will easily distinguish it from *S. mniszechi*, which lacks such a carina. The females may be distinguished from those of *S. hopei* and *S. armstrongi* by their broader clypeus, which is about 1.3 times wider than a transverse eye diameter (Fig. 839). The weakly but evenly convex pygidium characterizes *S. batesi* females from those of *S. mniszechi*, which have a basally concave and apically convex pygidium.

BIOLOGY. Specimens have been collected from premontane wet forests and premontane rain forests between 600-1,600 meters in elevation. All specimens were collected at lights at night. The temporal data suggests a clear peak of activity at the onset of the rainy season.

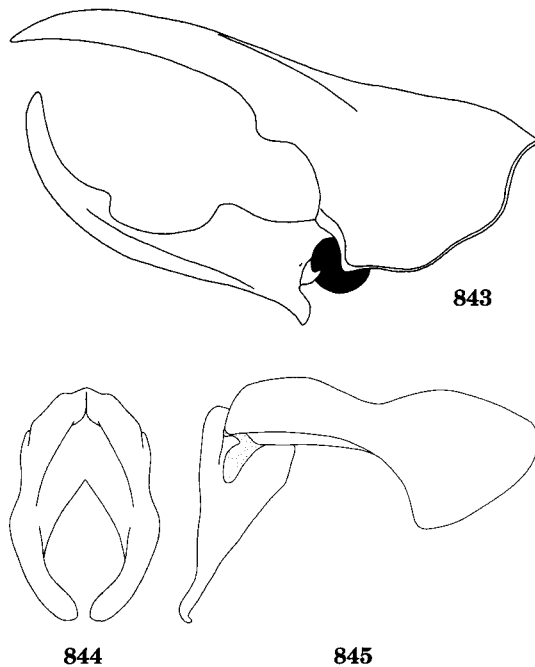
***Spodistes beltianus* (Bates, 1888)**
(Figs. 843-846)

Lycomedes beltianus Bates 1888: 338.

DESCRIPTION. Length 27.0-29.0 mm; width 16.7-17.5 mm. Color grayish brown and tan, finely velutinous, with clypeus and parts of horns in males piceous.

Males. *Head:* Top of head with short (minors) to long (majors) horn projecting forward and then curving upward at about middle of horn; apex sharply acuminate, with triangular tooth on dorsal surface about equidistant between apex and middle and another very broadly tri-

angular tooth on dorsal surface near base (Fig. 843); horn triangular in cross-section; anterior (ventral) surface, apical half, and dorsal carina piceous. Ocular canthus with small ridge across base. Clypeal apex broadly arcuate, immediately continuous with anterior (ventral) surface of horn. Interocular width equals 3.2 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. Mandibles bidentate, hidden beneath clypeus. *Pronotum:* Majors with long, slender horn projecting forward and curving ventrally near apex; horn carinate dorsolaterally, apex narrowly pointed; ventral side with triangular or subrectangular tubercle near base. Minors similar except horn shorter and ventral tooth near base usually absent. Surface with minute punctures moderate in density. Sides widest behind middle. Base with complete marginal bead. *Elytra:* Surface with minute punctures moderate in density, punctures usually concealed by velutinous covering. Sides explanate, apical umbones prominent. *Pygidium:* Surface with dense, short, pale setae. In lateral view, surface convex. *Legs:* Foretibia tridentate, basal tooth removed from others. Foretarsus enlarged, median claw with strong tooth at base and swelling at middle. Posterior tibia truncate and with strong, median angle; angle with single spinule. Apex of first tarsomere of posterior tarsus elongated into acute spine. *Venter:* Prosternal process absent. *Parameres:* Figs. 844-845.



Figs. 843-845. *Spodistes beltianus*: (843) male major, head and pronotum; (844-845) parameres.

Females. None available for examination. To my knowledge, only two female specimens are known.

DISTRIBUTION. *Spodistes beltianus* was previously known only from neighboring Nicaragua, and the specimens reported here represent a NEW COUNTRY RECORD.

LOCALITY RECORDS (Fig. 846). 3 specimens examined.

COSTA RICA (3). ALAJUELA (1): Sector Colonia Palmareña (9 km SO de Bajo Rodríguez); GUANACASTE (1): Estación Pitilla (Parq. Nac. Guanacaste); HEREDIA (1): Estación El Ciego (Parq. Nac. Braulio Carrillo).

TEMPORAL DISTRIBUTION. June (1), August (2).

DIAGNOSIS. Males of *S. beltianus*, like those of *S. armstrongi*, have an acutely pointed head horn. Unlike *S. armstrongi*, however, *S. beltianus* males possess a definite tubercle near the base of the head horn on the dorsal side (in addition to the submedian tubercle)

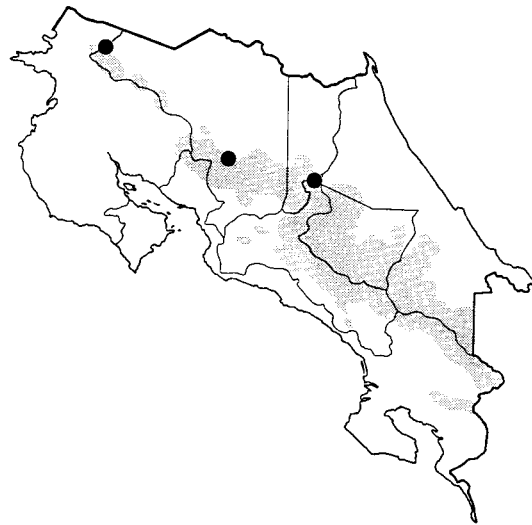


Fig. 846. Distribution of *Spodistes beltianus* in Costa Rica.

(Fig. 843). I have not seen females and so cannot characterize them or distinguish them from other species.

BIOLOGY. *Spodistes beltianus* seems to be an incredibly rare species, even in an area of fairly intensive collecting. The Costa Rican specimens were collected at elevations of 400 and 700 meters in areas of premontane rain/wet forests.

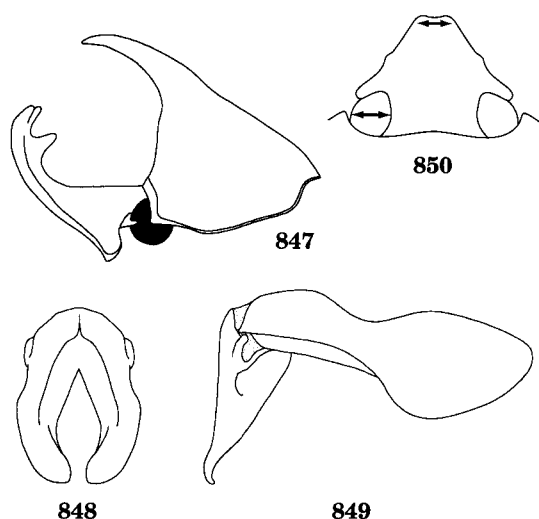
Spodistes hopei Arrow, 1902 (Figs. 847-851)

Spodistes hopei Arrow 1902: 146.

Lycomedes reichii Burmeister 1847: 285 (synonym).

DESCRIPTION. Length 26.2-33.0 mm; width 15.4-17.0 mm. Color grayish brown and tan, finely velutinous, with clypeus, and part of horns in males and part of pronotum in females piceous.

Males. Head: Frons with long horn (shorter in minors); majors (Fig. 847) with horn projecting forward and then curving upward at about middle of horn, minors with horn gradually curving forward and upward for its entire length; apex strongly bifurcate and with additional strong tooth on dorsal edge just below apex so that apex appears nearly trifurcate; in cross-section horn triangular;



Figs. 847-850. *Spodistes hopei*: (847) male major, lateral view; (848-849) parameres; (850) head of female showing width of eye versus narrow width of clypeal apex.

anterior (ventral) surface, apical half, and dorsal carina reddish brown. Ocular canthus with carina across base but never with canthus projecting *onto* shaft of horn longitudinally. Clypeal apex blunt, immediately continuous with anterior (ventral) face of horn. Interocular width equals 3.0 transverse eye diameters. Antenna 10-segmented, club a little shorter than segments 2-7. Mandibles strongly bidentate, mostly hidden beneath fringe of setae below apex of clypeus. *Pronotum*: Moderately stout horn projecting forward and curving ventrally near apex; horn carinate on each side dorsally at base, apex narrowly pointed; ventral side without tooth. Surface with minute punctures; punctures moderate in density, setigerous; setae minute, pale. Sides widest behind middle. Base with complete marginal bead. *Elytra*: Surface with moderately dense, minute punctures on velutinous covering; punctures with minute, pale setae. Sides explanate, apical umbones prominent. *Pygidium*: Surface with dense, short, pale setae. In lateral view, surface convex. *Legs*: Foretibia tridentate, basal tooth removed from others. Foretarsus enlarged, median claw with strong tooth at base and tooth-like swelling at middle. Apex of posterior tibia truncate with strong, median angle; angle with single, small spinule. Apex of first tarsomere of posterior tarsus elongated into

acute spine. *Venter*: Prosternal process absent. *Parameres*: Figs. 848-849.

Females. As males except in the following respects. *Head*: Horn absent. Frons and clypeus concave; surface with large to very large, often confluent punctures. Lateral edge of clypeus at anterior edge of ocular canthus sharply elevated into laminate, triangular ridge. Clypeal apex strongly narrowed from lateral ridge to moderately narrow apex (subequal to width of eye) (Fig. 850); apex emarginate, strongly reflexed, with distinct tooth either side of emargination. Mandibles more exposed. *Pronotum*: Horn absent. Surface reddish brown, glabrous, covered by large, dense, round, velutinous punctures; punctures often confluent and with single, minute, pale seta at center of each. Anterior margin at middle tumescent. Shallow, median, longitudinal sulcus extending from anterior to posterior margin. *Pygidium*: In lateral view, surface nearly flat. *Legs*: Foretarsus not enlarged, claws subequal in size, not toothed. Median angle at apex of posterior tibia pronounced and with 1-2 small spinules.

DISTRIBUTION. *Spodistes hopei* is known from Panama and Colombia. In Panama, I know of specimens from east of the Canal Zone only.

LOCALITY RECORDS (Fig. 851). 5 specimens examined.

PANAMA (5). **COLÓN** (3): Santa Rita Ridge; **PANAMA** (2): Isla Majé in Lago Bayano (Gorgas Memorial Lab Station).

TEMPORAL DISTRIBUTION. April (1), May (2), June (2).

DIAGNOSIS. *Spodistes hopei* males are easily distinguished by the tridentate apex on the frontal horn. The females were previously unknown and are described here for the first time. Females can be separated from those of *S. batesi* by their narrower clypeal apex (subequal to one transverse eye diameter) (Fig. 850) and from *S. armstrongi* by the smaller concavity on the top of the head (the concavity extends posteriorly only as far as the middle of the eye).



Fig. 851. Distribution of *Spodistes hopei* in Panama.

BIOLOGY. Adults have been collected at lights at night. This species occurs in tropical moist forests at elevations of 100-400 meters, considerably lower than the elevational range for *S. batesi*.

Spodistes mniszehi
(Thomson, 1860)

(Color Plate 7, Figs. 852-856)

Lycomedes mniszehi Thomson 1860: 16.

DESCRIPTION. Length 24.8-34.5 mm; width 15.8-20.0 mm. Color grayish-brown, finely velutinous, with clypeus and part of horn in males and most of pronotum in females dark reddish brown.

Males. Head: Frons with long horn (Fig. 852) (shorter in male minors); horn projecting forward and curving upward in both majors and minors; apex strongly bifurcate; dorsal surface usually with subtriangular swelling just before middle (often reduced in minors); in cross-section, horn triangular; anterior (ventral) surface apical half, and dorsal swelling dark reddish brown. Base of ocular canthus at anterior edge lacking carina projecting onto base of horn. Clypeus with short, horizontal surface before anterior (ventral) face of horn, surface sparsely punctate, apex broadly rounded. Interocular width equals about 3.0 transverse eye diameters. Antenna with 10 segments, club subequal to segments 2-7. Mandibles with 2 strong, apical teeth and strong, basal lobe, mostly hidden beneath

fringe of setae below clypeal apex. **Pronotum:** Long, slender horn projecting forward and curving ventrally to well beyond (majors) or just to apex (minors) of head horn; horn carinate (low, rounded) laterally, apex narrowly emarginate (majors) or pointed (minors); ventral surface lacking swelling or denticles. Surface of pronotum at base and sides with sparse, minute, pale setae. Base with complete marginal bead. **Elytra:** Surface velutinous, with dense, minute punctures on velutinous covering; punctures with minute, pale setae, setae becoming a little longer at apices near prominent umbones. Sides explanate. **Pygidium:** Surface velutinous with dense, short, pale setae. In lateral view, surface strongly convex. **Legs:** Foretibia tridentate, basal tooth removed from others. Foretarsus enlarged, median claw with strong tooth at base and tooth-like swelling at middle. Apex of posterior tibia subtruncate with strong median angle; angle with single, small spinule. Apex of first tarsomere of posterior tarsus elongated into acute spine. **Venter:** Prosternal process absent. **Parameres:** Figs. 853-854.

Females. As males except in the following respects. **Head:** Horn absent. Frons and clypeus concave; surface with mostly large, moderate to moderately dense punctures. Lateral edge of clypeus at anterior edge of ocular canthus sharply elevated into cariniform, triangular tubercle. Apex of clypeus broad (a little wider than width of eye), emarginate, strongly reflexed, with distinct tooth either

side of emargination. Interocular width a little less than to subequal to 3.0 transverse eye diameters. *Pronotum*: Horn absent. Surface glabrous, dark reddish brown, covered by large, dense, round, velutinous punctures; punctures often confluent (especially at sides), and with single, minute, pale seta at center of each. Anterior margin at middle protuberant and with shallow, median, longitudinal sulcus extending from anterior margin to near middle of disc or to base. *Pygidium*: Surface with minute setae. In lateral view, apical 2/3 weakly convex, distinctly concave in basal third (Fig. 855). *Legs*: Foretarsus not enlarged, claws subequal in size, not toothed. Angle at apex of posterior tibia pronounced and with 1 or 2 small spinules.

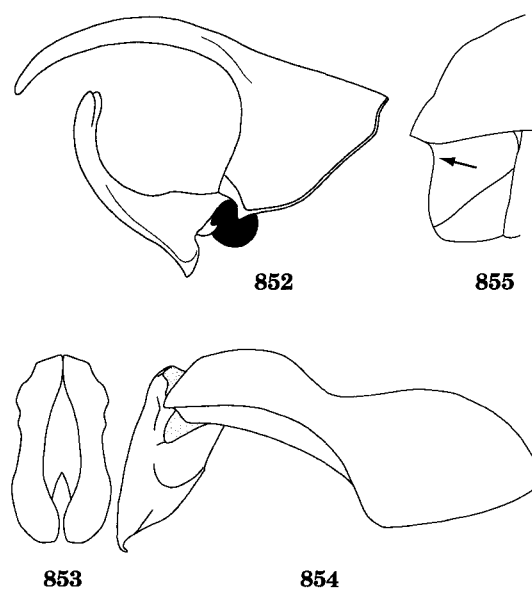
DISTRIBUTION. *Spodistes mniszehi* is known from southern Mexico and northern Central America and (according to Endrödi 1970, 1985a) from Panama and Colombia also. I have never seen a specimen from Panama or Colombia, and the specimens reported here for Costa Rica are the only ones I know of for that country. I believe this species is primarily found in northern Mesoamerica, and that it just barely reaches Costa Rica.

LOCALITY RECORDS (Fig. 856). 35 specimens examined.

COSTA RICA (35). CARTAGO (1): Platanillo; GUANACASTE (34): Dos de Tilarán (San Ramón).

TEMPORAL DISTRIBUTION. April (1), May (34).

DIAGNOSIS. *Spodistes mniszehi* and *S. batesi* are the only two species with a bifurcate frontal horn in the males. Males of the two species are easily separated because *S. mniszehi* lacks a carina projecting onto the frontal horn from the anterior edge of the ocular canthus, whereas *S. batesi* has a distinct carina (Figs. 852, 836). The females of both may be distinguished from females of other species of *Spodistes* by their broader clypeus and from each other by the weakly and evenly convex pygidium in *S. batesi* and the apically convex and basally concave pygidium of *S. mniszehi*.



Figs. 852-855. *Spodistes mniszehi*: (852) male major, head and pronotum; (853-854) parameres; (855) pygidium (lateral view) of female.



Fig. 856. Distribution of *Spodistes mniszehi* in Costa Rica.

BIOLOGY. The Costa Rican specimens were taken at lights at an elevation of 1,100 meters in premontane wet forest. This species is relatively abundant in Chiapas in southern Mexico where I have taken it at ultraviolet light more than at mercury vapor lamps.



Color Plate 8. *Golofa costaricensis* on the stalk of a small bamboo, *Chusquea* sp. (Poaceae).
Illustration by Dan Schmidt.

TRIBE DYNASTINI

Members of the Dynastini are among some of the largest and heaviest insects on Earth. In addition to being among the largest, some species, such as the Neotropical hercules beetles [the three largest *Dynastes* species: *hercules* (L.), *D. neptunus* Quenzel, *D. satanus* Moser], Neotropical elephant beetles [the larger species of *Megasoma* such as *M. elephas* (Fabr.), *M. actaeon* (L.), *M. mars* Reiche, *M. gyas* (Herbst)], Neotropical sawyer beetles (the larger *Golofa* species), and the Asian atlas beetles (all three *Chalcosoma* species), have some of the most fantastic armament seen in the animal kingdom. Males have huge and/or bizarrely-shaped horns on the head and pronotum. Sexual dimorphism is well-developed in most species of Dynastini with the males possessing large, curving horns while the females lack horns. The nearly 70 species of the tribe occur worldwide. There is only one monotypic genus in Africa (*Augosoma*), two genera (*Haploscapanes*, *Xylotrupes*) with four species in Australia, and five genera (*Chalcosoma*, *Xylotrupes*, *Allomyrina*, *Eupatorus*, and *Pachyoryctes*) with 14 species in Asia and New Guinea. Most of the taxa occur in the New World where there are three genera and 48 species. All three genera are found in Costa Rica and Panama, and they contain nine species (two of which are described as new here). Endrödi (1976a, 1977b) reviewed the world fauna, and Lachaume (1985) provided a more popular, pictorial treatment.

Adult Dynastini have traditionally been characterized by strong sexual dimorphism of the pronotum where males have large horns and females do not. In addition, the forelegs of the males have an elongated tibia and tarsus, whereas the length of the tibia and tarsus is "normal" in the females. In the Dynastini, the combined length of the anterior tibia and tarsus is distinctly longer than the length from the base of the pronotum to the apex of the clypeus. In Oryctini, the length of the anterior tibia and tarsus is shorter than, subequal to, or only slightly longer than the length from the base of the pronotum to the

apex of the clypeus. In addition, members of the Dynastini have a cylindrical basal joint (with or without apical spine) on the posterior tarsus, whereas the basal joint is triangular in most Oryctini (Casey 1915; Arrow 1925; Saylor 1948a; Arnett 1968; Endrödi 1976a, 1985a).

Inasmuch as the characters that have been used to characterize the tribe are mostly secondary sexual characters of the male, I am concerned that we need better characters to establish monophyly for the tribe. Since that is beyond the scope of this work, the Dynastini should, for the present, be characterized as consisting of usually large and robust beetles that show strong dimorphism between the males and females. The males usually have prominent horns on the head and/or pronotum.

Larvae for eight of the New World species have been described with several more species of *Megasoma* awaiting description by myself and Miguel Morón. Dynastini larvae are characterized by the presence of 2-4 setae on the tarsungulus, lobes of the respiratory plate of the spiracle usually contiguous, ocelli well-defined, and acanthoparia usually with 9-10 spiniform setae (Morón 1987). Lai (2001) beautifully illustrated larvae and pupae of several species of *Dynastes* and *Megasoma* (among others) and provided extensive commentary on how to rear rhinoceros beetles.

All of the New World Dynastini seem to be nocturnal or crepuscular although some *Golofa* species have been observed to be active during the day (Howden and Campbell 1974). In my own experience and that of a number of my colleagues, *D. hercules* don't usually appear at lights until well after midnight, often as late (or early) as 5 AM. Adult Dynastini readily feed on rotting fruit, but it is not really known whether they do this in nature. Bates (1888), citing information from Champion, indicated that *M. elephas* were sometimes found in numbers about mango trees when in fruit. Larvae are saprophagous and develop in rotting logs or possibly in rich organic soil. In spite of the large size of these beetles, we know very little about their biology.

Key to the Genera of Adult Dynastini of Costa Rica and Panama

1. Mandibles with 3 long teeth. Clypeal apex broadly bidentate (space between spiniform teeth almost as wide as eye). Males with 2 forward-projecting horns on pronotum, 1 at each anterior angle ***Megasoma Kirby***
- 1'. Mandibles entire, weakly bifurcate at apex, or with 2 distinct teeth. Clypeal apex narrowly bidentate or emarginate, never with spiniform teeth. Males with single, median pronotal horn or lacking horn 2
2. Mandibles with 2 distinct, spiniform teeth. Elytra of males gray to grayish olive or brownish olive or yellowish olive with black spots. Pronotum in females with short, dense pubescence; elytra in females with longitudinal rows of long, dense pubescence ***Dynastes Macleay***
- 2'. Mandibles entire at apex or weakly notched. Elytra of males usually yellowish brown or else dark reddish brown or (rarely) black. Pronotum and elytra in females lacking dense pubescence ***Golofa Hope***

Clave para los Géneros de Adultos de Dynastini de Costa Rica y Panamá

1. Mandíbulas con 3 dientes largos. Apice clipeal ampliamente bidentado (espacio entre los dientes espiniformes casi tan ancho como el ojo). Machos con 2 cuernos en el pronoto, 1 en cada ángulo anterior ***Megasoma Kirby***
- 1'. Mandíbulas enteras, ligeramente bifurcadas en el ápice, o con 2 dientes evidentes. Apice del clipeo angostamente bidentado o emarginado, nunca con dientes espiniformes. Machos con un solo cuerno pronotal medio o sin cuerno 2
2. Mandíbulas con 2 dientes evidentes y espiniformes. Elitros de los machos grises a oliva grisáceos o oliva parduscos con manchas negras. Pronoto en las hembras con pubescencia corta y densa; élitros en las hembras con hileras longitudinales de pubescencia larga y densa ***Dynastes Macleay***
- 2'. Mandíbulas enteras en el ápice o con una ligera muesca. Elitros de los machos generalmente pardo amarillentos o también pardo rojizo oscuro o (raramente) negro. Pronoto y élitros de las hembras sin pubescencia densa ***Golofa Hope***

Key to the Genera of Larval Dynastini of Costa Rica and Panama

(after Morón 1994b)

1. Tarsal claws usually with 4 setae ***Megasoma Kirby***
- 1'. Tarsal claws with 2 setae 2
2. Bulla of abdominal spiracles moderately elevated, rounded. Last antennal segment with 6-9 dorsal sensory spots ***Dynastes Macleay***
- 2'. Bulla of abdominal spiracles strongly elevated, sharply pointed, conical or curved. Last antennal segment with 7-8 dorsal sensory spots ***Golofa Hope***

Clave para los Géneros de Larvas de Dynastini de Costa Rica y Panamá

(después de Morón 1994b)

1. Uñas tarsales generalmente con 4 setas ***Megasoma Kirby***
- 1'. Uñas tarsales con 2 setas 2
2. Bulla de los espiráculos abdominales elevada moderadamente, redondeada. Último segmento antenal con 6 a 9 manchas sensoriales ***Dynastes Macleay***
- 2'. Bulla de los espiráculos abdominales fuertemente elevada, agudamente punteada, conica o curvada. Último segmento antenal con 7 u 8 manchas sensoriales ***Golofa Hope***

Dynastes Macleay, 1819

Dynastes Macleay 1819: 22.

Theogenes Burmeister 1847: 254 (synonym).

The small genus *Dynastes* contains seven species of large to very large beetles. Two species [*D. tityus* (L.) and *D. granti* Horn] are restricted to the southern United States, two (*D. hyllus* Chevrolat and *D. maya* Hardy) are indigenous to Mexico, Guatemala, and Honduras, and two (*D. neptunus* Quensel and *D. satanus* Moser) are found only in South America. Only *D. hercules* (L.) is found from southern Mexico to South America and also the Antilles.

Species of *Dynastes* are best recognized by the presence of a long, forward-projecting horn in the males, a single tubercle on the frons in females, and a relatively long prosternal process. Synopses of the genus were provided by Endrödi (1976a, 1985a), Dechambre (1980), and Lachaume (1985). Hardy (2003) described the most recent new species in the genus from Mexico and Guatemala.

Adults are largely nocturnal, although *D. hercules* has been observed flying or feeding on several occasions in broad daylight (Beebe 1947). Adults probably feed on sap or rotting fruit while the larvae feed on rotting wood inside of decaying tree trunks. The immature stages of *D. hercules* are well known, but they have never been formally described before. They are described and illustrated here.

***Dynastes hercules* (Linnaeus, 1758)**

(Covers, Figs. 34, 857-879)

Scarabaeus hercules Linnaeus 1758: 348.

Scarabaeus scaber Linnaeus 1764: 17 (synonym).

Scarabaeus hercules oculatus Scopoli 1772: 81 (synonym).

Scarabaeus alcides Fabricius 1781: 4 (synonym).

Scarabaeus iphielus Panzer 1782: 85 (synonym).

Scarabaeus perseus Olivier 1789: 8 (synonym).

Dynastes lagaii Verrill 1906: 318 (synonym).

Dynastes vulcan Verrill 1906: 319 (synonym).

Dynastes argentatus Verrill 1907: 305 (synonym).

Dynastes hercules ecuatorianus Ohaus 1913: 131 (synonym).

Dynastes hercules niger Endrödi 1947: 58 (synonym, described as a variety).

Dynastes hercules baudrii Pinchon 1976: 14 (synonym).

Dynastes hercules reidi Chalumeau 1977: 237 (synonym).

Dynastes hercules septentrionalis Lachaume 1985: 19 (synonym).

Dynastes hercules occidentalis Lachaume 1985: 20 (synonym).

Dynastes hercules lichyi Lachaume 1985: 21 (synonym).

Dynastes hercules paschoali Grossi and Arnaud 1993: 13 (synonym).

Dynastes hercules tuxtlaensis Morón 1993a: 259 (synonym).

Dynastes hercules bleuzeni Silvestre and Dechambre 1995: 52 (synonym).

Dynastes hercules trinidadensis Chalumeau and Reid 1995: 3 (synonym).

Dynastes hercules morishimai Nagai 2002: 4 (synonym).

Dynastes hercules takakuwai Nagai 2002: 4 (synonym).

DESCRIPTION. Length 50.0-85.0 mm; width 29.0-42.0 mm. Color black except for elytra; elytra in males neutral gray to light grayish olive or brownish olive to yellowish olive, with black suture and black, small, sparse spots; elytra in females entirely black or with posterior fourth colored as in males.

Males. *Head:* Frons with horn projecting forward and curving upward; horn in majors (Fig. 858) very long and with strong tooth on dorsal surface in basal fourth and another just before apex; minors (Fig. 859) with horn short, lacking 1 or both dorsal teeth; apex pointed, dorsal surface in basal fourth with short, tawny setae. Clypeus weakly to distinctly, transversely rugulose; apex broadly subtruncate, usually weakly emarginate at middle. Interocular width equals 2.8-3.0

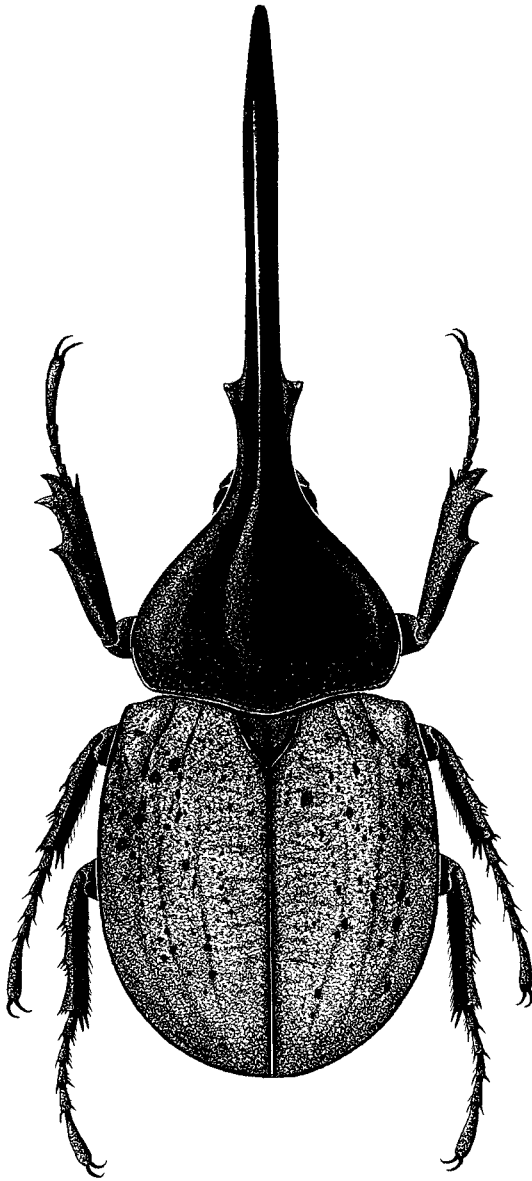
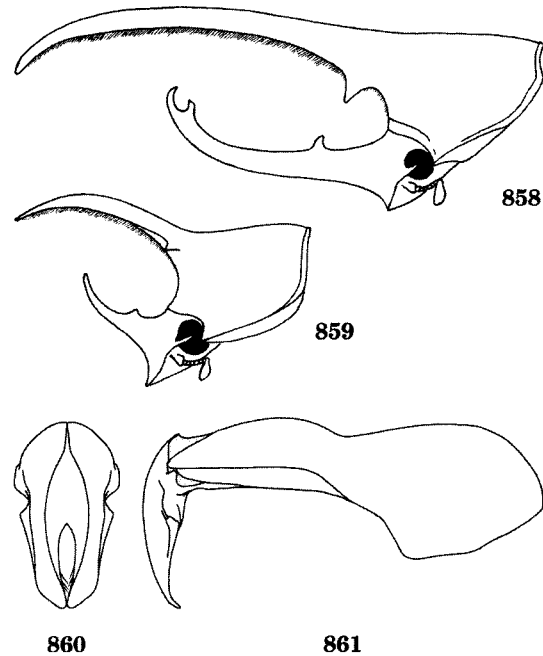


Fig. 857. *Dynastes hercules*.

transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. Mandibles with 2 strong, sharp teeth, usually hidden beneath tuft of long, tawny setae. *Pronotum*: Horn projecting forward and upward and then curving downward at about middle; horn long in majors, short in minors; ventral surface near base with pair of sharp teeth (reduced in minors); ventral surface with dense fringe of moderately long, tawny



Figs. 858-861. *Dynastes hercules*: (858) male major, head and pronotum; (859) male minor; (860-861) parameres.

setae; apex nearly acuminate, usually minutely emarginate. Surface with disc moderately to densely punctate, punctures moderately large; surface elsewhere rugulose. Posterior margin with complete marginal bead. *Elytra*: Surface smooth except for punctures; punctures moderate to moderately large in size, moderate in density, some in discernible rows. A row of sparse, long, reddish brown setae present either side of suture along sutural stria. *Pygidium*: Surface completely rugulose-punctate, punctures small; base with dense fringe of long, tawny setae, remainder of surface with sparse, short setae. In lateral view, surface nearly flat. *Legs*: Foretibia tridentate, basal tooth removed from others. Apex of posterior tibia with ventral edge strongly arcuate to sharply angulate at middle; edge dorsolateral of median angulation crenulate and with 4-7 large spinules. Apex of first tarsomere of posterior tarsus weakly produced on dorsal edge. *Venter*: Prosternal process moderately long, subtriangular, with rounded apex, surface coarsely rugopunctate and covered with

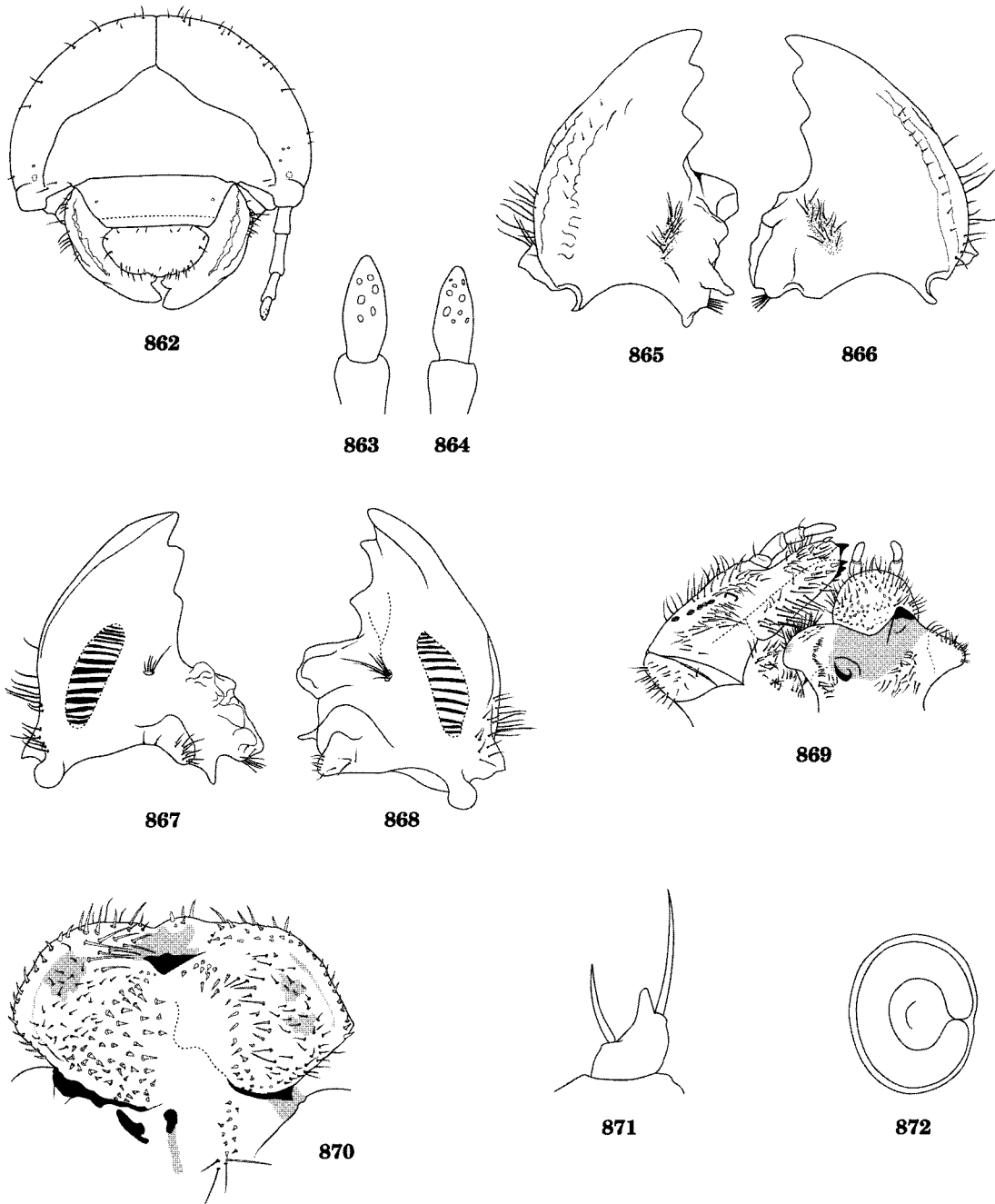
dense, long, reddish brown setae. *Parameres*: Figs. 860-861.

Females. As males except in the following respects. *Head*: Horn absent. Surface completely rugose. Frons with small, median tubercle between eyes. Interocular width equals 2.4 transverse eye diameters. *Pronotum*: Horn absent. Surface completely, coarsely rugopunctate, setigerous; setae moderately dense, short to moderate in length, reddish brown. *Elytra*: Surface completely, coarsely rugopunctate, setigerous; setae moderately long, reddish brown, in dense row along sutural and 2 discal striae; intervals with sparser, shorter setae. *Pygidium*: In lateral view, slightly concave.

THIRD INSTAR LARVA. Six third instar larvae of *D. hercules* are housed at UNSM with the following data: "Brazil: Amazonas, Reserva Campinas, 60 km. N Manaus, VIII-30-1977, B. C. Ratcliffe." Description and illustrations by Aura Paucar-Cabrera.

Cranium (Fig. 862): Width of head capsule 15.9-17.7 mm. Surface castaneous, finely rugopunctate. Frontal suture and clypeo-frontal suture distinct. Epicranium with 3 dorsoepicranial setae on each side and 10 posterior epicranial setae. Frons with 2 exterior frontal setae on each side; anterior frontal angle and anterior frontal region lacking setae. Ocellus present. *Clypeus*: Form subtrapezoidal. Surface of postclypeus castaneous, well-sclerotized and finely rugopunctate; surface of preclypeus testaceous, poorly sclerotized, not punctate. *Labrum*: Form subtrapezoidal at base, gradually becoming oblong-oval at apex, asymmetrical. Color reddish brown, becoming orange-brown at mid-apex where less sclerotized; surface densely punctate around disc, moderately dense on disc, some punctures setigerous; with 8 posterior, short setae and about 20 setae at apex (5 long setae at each side of mid-apex, 10 short, thick setae at mid-apex). *Antenna*: 4-segmented; in lateral view segments 1 and 3 subequal in length, terminal segment slightly shorter than segment 3, segment 2 about twice length of terminal segment. Apical segment sub-oval with acute

apex in dorsal and ventral views; dorsal surface (Fig. 863) with 6 sensory spots, ventral surface (Fig. 864) with 9 sensory spots. *Left mandible*: Scissorial region with 3 well-defined teeth; teeth subequal in size. Scrobis with about 8 short setae. Lateral face with about 12 long setae. Dorsal surface (Fig. 865) with about 16 long dorsomolar setae; acia well-developed, elongate. Ventral surface (Fig. 868) with well-developed, elongate-oval, stridulatory area, ridges (about 14) widely separated and well-defined; ventral process well-developed, with about 10 short setae; brustia with 10 short, stout setae; basolateral angle with postartis. Molar area with 3 lobes, lobes 2 and 3 contiguous, surface concave. *Right mandible*: Scissorial region with 3 well-defined teeth; teeth subequal in size. Scrobis with about 10 short setae. Lateral face with about 13 long setae. Dorsal surface (Fig. 866) with about 16 long dorsomolar setae. Ventral surface (Fig. 867) with well-developed, elongate-oval, stridulatory area, ridges (about 14) widely separated and well-defined; ventral process well-developed, with about 12 short setae; brustia with 8 short, stout setae; basolateral angle with postartis; molar area with 2 irregular lobes, calx produced. *Maxilla* (Fig. 869): Cardo subrectangular. Stipes longer than wide. Galea with many stout setae and 1 well-developed uncus at apex. Lacinia with many stout setae and 3 unci; unci extending from apex to subapex, contiguous, with 1 short, stout setae adjacent to basal uncus. Palpus 4-segmented, segment 2 twice length of basal segment, terminal segment about 1.5 times longer than basal segment and slightly longer than segment 2. Stridulatory area with 5 blunt, truncate ridges and anterior truncate process. *Labium* (Fig. 869): Surface of glossa with short stout setae on disc, moderately long setae around anterior and lateral areas of disc. Hypopharyngeal sclerome asymmetrical, concave medially, produced at base; truncate process produced dorsally. Left lateral lobe with setae at margin and on disc; setae at margin moderately long, setae on disc short, stout and directed toward center of hypopharyngeal sclerome. Right lobe with moderately long setae at margin. *Epipharynx* (Fig. 870): Form suboval, wider



Figs. 862-872. *Dynastes hercules*, third instar larva: (862) cranium; (863-864) terminal segment of antenna, dorsal and ventral views, respectively; (865-866) left and right mandibles (dorsal view); (867-868) right and left mandibles, ventral view; (869) maxilla and labium; (870) epipharynx; (871) tarsal claw; (872) spiracle.

than long, asymmetrical, apex oblique. Haptomeral process prominent. Haptomerum at base with 6 heli. Acanthoparia with 11-13 short, stout setae. Acroparia with about 10 long, stout setae. Gymnoparia with about 20-

25 short, sparse setae. Chaetoparia setose; left side with about 56 short, stout setae; right side with about 18 long, stout setae mixed with about 38 short, stout setae. Sclerotized plate asymmetrical, curved, with right side

weakly produced. Sense cone elongate, sclerotized anteriorly, not produced, weakly sclerotized posteriorly. Dextiotorma elongate. Laeotroma elongate, pternotorma roundly asymmetrical. Right crepis elongate, with about 12 moderately long setae. Left crepis suboval, with about 13 moderately long setae. *Legs*: Trochanter, femur, and tibiotsarsus with numerous long and short setae. Claws (Fig. 871) castaneous, dark brown at apex. Form conical with acute apex, with 1 prebasal and 1 preapical seta; setae moderately long, stout. *Body vestiture*: Prothorax with darkened macula anterior to spiracle; macula about 2 times length and width of spiracle. Pro-, meso-, and metathorax each with irregular rows of numerous, long setae. Abdominal segments 1-6 divided into annulets; prescutum with about 80-150 short setae and about 50 long setae near posterior margin; scutum with about 90-180 short setae and about 10-20 long setae near posterior margin; scutellum with about 160-200 short setae and about 60-70 long setae near posterior margin. Abdominal segments 7-9 not divided into annulets, each with sparse, numerous, short setae; 1 row of sparse, long setae at middle; and 1-2 irregular rows of sparse, long setae near posterior margin. Dorsal surface of abdominal segment 10 with numerous, sparse, short and moderately long setae on disc and with sparse, moderately long setae near posterior and lateral areas. Ventral surface of abdominal segment 10 lacking palidia; anal lip curved, transverse; ventral anal lip with about 40 short setae on disc and 45 long setae at each side of disc. *Spiracles* (Fig. 872): Spiracles subequal in size (2.1 to 2.4 mm wide, 2.1 to 2.7 mm high) Respiratory plates C-shaped, lobes nearly touching; bulla weakly raised; holes oval, about 48 holes across diameter of plate.

DISTRIBUTION. *Dynastes hercules* is found from southern Mexico to Bolivia as well as Trinidad, Guadeloupe, Martinique, and Dominica in the West Indies (Endrödi 1976a; Chalumeau and Gruner 1977). It formerly occurred in Hispaniola but is now extinct there (Wetherbee 1985). In Costa Rica and Panama, it is localized in areas of still-forested highlands.

LOCALITY RECORDS (Figs. 873-874). 141 specimens examined.

COSTA RICA (79). ALAJUELA (6): Ciudad Quezada, Finca San Gabriel (2 km W Dos Rios); CARTAGO (21): Cartago, 5 km N Cayutic, Chitaria, Embalse el Llano, Moravia de Chirripó, Orosi, Tapanti, Turrialba; GUANACASTE (15): Estación Cacao, Estación Maritza, Estación Pitilla; HEREDIA (9): Estación El Ciebo, Estación Magsasay, Los Arbolitos, Río Frio, 10 km N Vara Blanca; LIMÓN (7): Cuatro Esquinas, Finca E. Rojas (30 km N Cariari); PUNTARENAS (13): Estación La Casona, Estación Las Mellizas, Las Cruces, Monteverde, Rancho Quemado (Osa); SAN JOSÉ (8): Estación Carrillo, Desamparados, Parq. Nac. Braulio Carrillo, San Isidro de Coronado, Valle de Talamanca.

PANAMA (62). CHIRIQUI (57): Fortuna Dam, Hartmann's Finca (Santa Clara), Los Planos de Hornito, Quebrada Aleman (10 km N Los Planos), 15 km W Volcán; PANAMA (5): Cerro Azul, Cerro Campana, Cerro Jefé.

TEMPORAL DISTRIBUTION. January (1), February (2), March (8), April (11), May (33), June (16), July (32), August (5), September (9), October (3), November (1).

DIAGNOSIS. Males of *D. hercules*, with their large size, characteristic color, and impressive horns, are unique among the Central American fauna. They can be easily identified without the use of keys. Females can usually be recognized because of their large size, single tubercle on the frons, and extremely roughened elytra. Species of *Megasoma* are similar in size, but they have relatively smooth elytra. Some *Golofa* and *Heterogomphus* (*Daemonoplus*) females also have roughened elytra like *D. hercules*, but they are always smaller and have a narrowly, often acutely, bidentate clypeal apex.

The elytra of living, as well as dead, specimens may rapidly change color from yellowish olive to black and back again. Hinton and Jarman (1973) conducted detailed experiments to discover why this was so. They found that the epicuticle is about three millimicrons

thick and transparent. Below this is a yellow, spongy layer about five millimicrons thick. The cuticle below the yellow sponge is black. When the layer of yellow sponge is air-filled, it becomes optically heterogeneous, and the light reflected from the elytra is yellowish. When the yellow sponge layer is liquid-filled (under conditions of high humidity), it becomes optically homogeneous, and the black cuticle below is seen. Color changes were clearly induced in response to changes in ambient humidity. The authors suggested this might have some selection advantage in that beetles would become darker at night when

the humidity increased and so achieve a greater degree of crypsis and protection from predators. In my experience of collecting these beetles, I have not seen consistently darker specimens at night.

Dynastes larvae may be readily distinguished from comparably-sized *Megasoma* larvae by the presence of two setae on the tarsungulus, respiratory plate of the spiracle contiguous, ocelli well-defined, and with 6-9 dorsal sensory spots on the last antennal segment (Morón 1987).

NOMENCLATURE. *Dynastes hercules* has recently undergone a flurry of subspecies designations. I remain unconvinced about the validity of these designations inasmuch as most are based on color or horn configuration in the males. Both characters are unreliable as expressions of distinct and perhaps isolated populations. Some of the supposed subspecies are even sympatric! More research is needed to ascertain the limits of the populations and their possible characteristics rather than simply defining intraspecifically variable character states to justify subspecies designations. Until additional scientific research is conducted on the populations of *D. hercules* that addresses more than just the typological concept of male horn development, subspecies designations cannot be supported. The principal exception might be a mainland subspecies and a West Indian subspecies, but that situation is confounded because it remains



Fig. 873. Distribution of *Dynastes hercules* in Costa Rica.



Fig. 874. Distribution of *Dynastes hercules* in Panama.

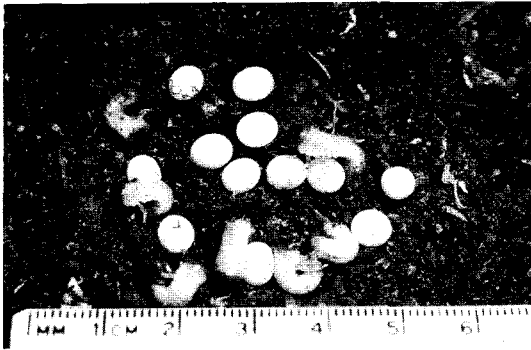


Fig. 875.



Fig. 876.

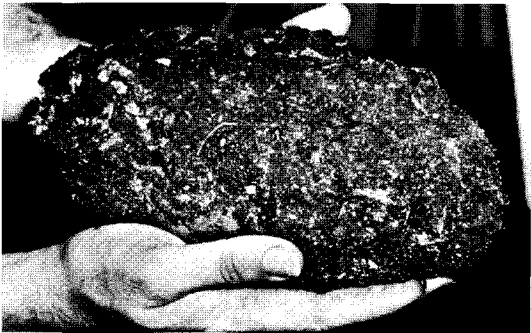


Fig. 877.

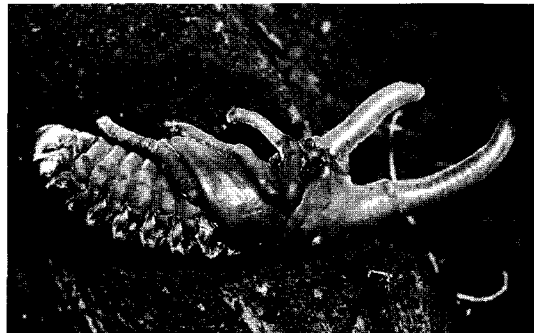


Fig. 878.



Fig. 879.

Figs. 875-879. Principal stages in the life cycle of *D. hercules*: (875) eggs and first instar larvae; (876) third instar larva; (877) pupal chamber; (878) pupa of male; (879) adult male and female. Photos courtesy of M. Busching (Cincinnati Zoo and Botanical Garden).

unknown from whence the Linnean types came from. The four syntypes (London and Uppsala) have no labels (Landin 1956), and the description simply indicates from "America" (Linnaeus 1758). Pinchon (1976) and Lachaume (1985) suggested that the West

Indies, particularly Guadeloupe, may have been the source for the Linnean specimens because of the existence of engravings and specimens in the "cabinets of curiosities" dating from the 1700s that shows a horn configuration representative of specimens from Guadeloupe. If this is true, then the nominate subspecies occurs in the West Indies, while the mainland subspecies would bear the name of the oldest synonym whose provenance is known to be from Central or South America.

BIOLOGY. Gruner and Chalumeau (1977), studying *D. hercules* in Guadeloupe in the French West Indies, observed that the incubation period for 88 eggs (at $25^{\circ}\pm 1^{\circ}\text{C}$) averaged 27.7 days (range 25-37 days). Beebe (1947) described the eggs (sample size 31) as broadly oval (3.5 x 4.3 mm), with white, hard shells, and a surface sculpted by a multitude of short, thin ridges, each minutely toothed along the summit. The larvae were saproxylophagous and developed in rotting tree trunks. I collected seven third instar larvae in close proximity to one another in a large, rotting log in Amazonian

Brazil. Gruner and Chalumeau (1977) observed them in the decaying trunks of *Licania ternatensis* Hooker (Rosaceae), *Amanoa caribaea* Krug and Urb. (Euphorbiaceae), and *Inga ingoides* Willd. (Leguminosae). Development of the larvae at $25^{\circ}\pm 1^{\circ}\text{C}$ took the following amount of time: first instar – 50 days (range 32-79 days); second instar – 56 days (range 30-83 days); third instar – 450 days (range 417-498 days); pupa – 32 days (no range). Total time of development required was 19-21 months. Adults lived about 75 days for a total life cycle of about 706 days, or almost two years. Adults in captivity usually lived for three to four months, and some lived as long as six months. Third instar larvae attained a maximum weight of approximately 55 grams. Beebe (1947) reported a maximum adult weight of 37.5 grams. Figures 875-879 show representative stages in the life cycle of *D. hercules*.

Gruner and Chalumeau (1977) observed that adult flight activity seemed to be highest during brighter phases of the moon. They postulated that these flights were “mating flights” or beetles in search of mates. They concluded this based on the fact that most beetles caught during the flights were young and unmated. They suggested that flight activity was correlated with higher rainfall about two months earlier. Mating seemed to occur very late during vitellogenesis.

Beebe (1947), working in the highlands of Venezuela, found that only five individuals out of nearly a hundred observed came to lights on clear nights. Heavy overcast, with dense neblina or fog, or nights of actual rain contributed to most of the beetles coming to his lights. This has been my experience as well in Central America for this and other species of highland scarabs as well. In concordance with Beebe’s Venezuelan data, my observations in Costa Rica and Panama show that *D. hercules* is rarely encountered during the dry season, and numbers of individuals increase at the onset of the rainy season to a numerical peak in July. During flight, males fly at an angle of about 60° with the head horn raised, and the abdomen lowered.

Predators of such a large beetle are probably few. Beebe (1947) reported a female being eaten by the tropical screech-owl [*Otus*

choliba crucigerus (Spix)] in Venezuela. Gruner and Chalumeau (1977) observed that *D. hercules* was host to a mite, *Dynastaspis hercules* (Costa) (Gamasidae).

Beebe (1947) conducted extensive observations on male combat behavior. While his observations are lengthy, and even by his own admission somewhat anthropomorphic, the following excerpts summarize nicely what he saw.

“Encounters between male hercules beetles are usually rather brief and are dependent on the willingness of each to fight. One may be feeding or resting quietly when a second male approaches. Before any actual contact, when still several inches apart, the beetle which is eager for the engagement moves the thorax up and down, producing a rhythmic series of zizzing squeaks. There is not the slightest doubt that this is heard and understood. Even if mouth and head are buried deep in mushy banana pulp, the eater gives a jerk on hearing the sound and assumes, for a moment, what may well be an audient immobility. He may keep on guzzling or may back away practically into the waiting grip of the squeaker.

If the feeder chooses to accept the challenge this is evident in a complete change of demeanor. Ordinarily these hercules beetles move and feed and react in the same, slow, bungling way common to most of their family. The deliberate awkwardness of June bugs and cockchafers is theirs. But at the sound of the hissing, or actual contact with another male who intends combat, there occurs a radical change. Movement shifts to quick, nervous jerking, evident whether the insect is standing still or walking. When combat is refused, the beetle turns and retreats rapidly, the gait soon shifting to the usual slow, aimless progress.

The general sequence of combat is almost unvarying. Again and again, both opponents back away, freeing their weapons, and then rush in for a fresh grip. When a favorable hold is secured outside the other’s horns, a new effort, exercised

with all possible force, is initiated. This is a series of lateral jerks, either to right or left, with intent to shift the pincer grip farther along the thorax as far as the abdomen and if possible on to mid-elytra. In addition, if the hold is at first confined to the incurving horn tips, the shift must be ahead, so that the final grasp brings into play the two opposing sets of teeth on the horns. Once this hold is attained and a firm grip secured the beetle rears up and up to an unbelievably vertical stance. At the zenith of this pose it rests upon the tip of the abdomen and the tarsi of the hind legs, the remaining four legs outstretched in midair, and the opponent held sideways, kicking impotently. This posture is sustained for from two to as many as eight seconds, when the victim is either slammed down, or is carried away in some indefinite direction to some indeterminate distance, at the end of which the banging to earth will take place. After this climax, if the fallen beetle is neither injured nor helpless on its back, it may either renew the battle, or more usually make its escape.

The combats between a full-sized Major and a Minor were always a foregone conclusion. The small one never refused a tilt and would rush pellmell into the encounter, squeaking as loudly as the giant. But it was no use. His instincts remained unchanged and his undersized dwarfed weapons, which could not encompass a beetle of his own size, were useless against the girth and weight of the Major. His opponent simply clinched his long horns around the smaller beetle and carted him away high in air. His very lightness seemed to be an advantage in the end, for only once did I see a Minor injured or stunned by the slamming to the ground.

In *hercules* there seems to be a complete absence of any courtship or display by the male in respect to the female. The relationship of the sexes is confined to direct mating in which the female is receptively passive. There is also an occasional, inexplicable, aimless transportation of the female a short distance.

The males use their horns in combat, utilizing the specialized shape and position of these characters in a specific routine. This instinct and method persists in Minors whose horns are too small and abortive to be effective. Squeaking and repeated bowing are also indulged in before and after the encounters."

Jarman and Hinton (1974) studied the grasping ability and forces exerted by the horns of male *D. hercules*. They noted that the dense fringe of setae on the ventral surface of the pronotal horn increases friction and so aids grip. This is especially important when grasping other males that have rounded and smooth surfaces, such as the dorsal surface of the pronotum and elytra. In their observations, they observed that a male weighing 30 g can lift a weight of 2 kg with its cepalic horn! They also noted the roughened area on either side of a median, setose strip on the prepygidium. The stridulatory sound is produced when the abdomen is moved so that the roughened area is rubbed against the inner apices of the elytra.

Dynastes hercules has been collected from tropical wet forests, premontane wet forests, premontane rain forests, and montane rain forests at elevations of 600-2,000 meters.

***Golofa* Hope, 1837**

Golofa Hope 1837: 42.

Asserador Maunder 1848: 40 (synonym).

Mixagenus Thomson 1859b: 7 (synonym).

Praogolofa Bates 1891: 34 (synonym).

There were 26 species in the Neotropical genus *Golofa* (Lachaume 1985; Morón 1995). Two new species are described here to give a total of 28 species in the genus. Species are found from central Mexico to northern Argentina and Chile. Thirteen species are found in Central America, and 14 species are found in South America. Six species are found in Costa Rica and Panama. Endrödi (1977b) indicated *G. pizarro* Hope and *G. claviger* (L.) occur in Panama and Costa Rica, but neither I or Dechambre (1983) found this to be so.

Adult males of nearly all the Central American species may be recognized by their

yellowish brown to dark reddish brown color; presence of a long, upright, slender head horn; presence of a short to long, erect or obliquely oriented pronotal horn; narrowly bidentate clypeal apex; and mandibles either entire or weakly bifurcate at the apex. *Golofa imbellis* is the exception because males are black and lack head or pronotal horns. *Golofa* females are yellowish brown to more commonly black, and they lack armature. They share with the males the narrowly bidentate clypeal apex and the weakly notched or entire apex of the mandibles.

Golofa females are easily confused with the females of some *Heterogomphus* species, especially *H. mniszzechi*, *H. schoenherri*, and *H. flohri*. They may all be about the same size and color, and all have densely punctate elytra. In *Golofa* females, the basal segment of the protarsus is subequal to or longer than the apical spur of the protibia; some specimens of *G. tersander* may occasionally have the basal segment a little shorter than the spine. In *Heterogomphus* females, the basal segment of the protarsus is distinctly shorter than the apical spur of the protibia. In addition, while the apex of the prosternal process may have long, dense setae in both genera, the shaft of the process is normally densely setose in *Golofa* species and glabrous or sparsely setose in *Heterogomphus* species.

Even after the modern synopses of Endrödi (1977b, 1985a), Dechambre (1983), Lachaume (1985), and Morón (1995), identification of many of the species of *Golofa* remains a sometimes difficult and often exasperating task. Experience with the group or a reference collection for comparison is almost essential . . . although I am trying to make those things unnecessary here for the Costa Rican and Panamanian species.

Why *does* identification of the males of these large beetles with often spectacular horns remain so difficult? The reasons are several. First and foremost is the significant morphological variation in male secondary sexual characters combined with an unusual (for dynastines) lack of differentiation of the male genitalia. Most authors have based their *Golofa* species concepts on the characters of male armature, and, since these vary so much within a species due to allometric growth, it

has always been difficult to incorporate all of the variation in a workable key, description, or in photographs. In many cases, moreover, females can be identified only by being collected with the males. So, male characters vary considerably, the usually diagnostic (in dynastines) parameres aren't reliable, other characters seem to vary in their expression, and most of the females all seem to look alike.

Contributing to this less-than-desirable state of affairs is an absence of any modern character analysis that would stabilize our concepts of what constitutes the various *Golofa* species. Only Morón (1995) discussed character variation, but this was for the eight Mexican species; only one of these, *G. tersander*, is also found in Costa Rica. In spite of the fairly recent comprehensive treatments by Endrödi (1985a), Dechambre (1983), and Lachaume (1985), the entire genus *Golofa* still needs a thorough revision using modern methods of character analysis based upon a large assemblage of specimens as well as examination of all the types. Until this is done, I am afraid that we shall continue to stumble around muttering about our inability to *reliably* identify a number of these polymorphic species.

The larvae of only five species of *Golofa* have been described (Morón 1995), and one of these (*G. tersander*) is found in the study area. Adults of the Central American species are apparently crepuscular or nocturnal. Sometimes, but not always, they are attracted to lights. While collecting in Chiriqui, Panama, I have had them fly by my light trap at dusk without the slightest change in orientation toward the light. Howden (1974) observed *G. porteri* Hope in Colombia during the day on bamboo or a bamboo-like grass; males were actively feeding, and some were engaged in fighting one another on the bamboo stalks. A few specimens, particularly females, were taken at lights. We know virtually nothing about the biology of these magnificent beetles. In most cases we can't say if they are nocturnal or diurnal, how long it takes for development, or on what plants the adults feed. All of the Costa Rican and Panamanian species, except *G. tersander*, are found at elevations usually above 1,200 meters. *Golofa tersander* is found in the lowlands.

Key to the Species of Adult Male *Golofa* of Costa Rica and Panama

1. Anterior tibia with 4 distinct teeth *tersander* Burmeister
- 1'. Anterior tibia with 3 teeth, rarely with trace of a fourth 2
2. Pronotum with small, setose depression just behind anterior margin, never with horn or strong tubercle. Color completely black *imbellis* Bates
- 2'. Pronotum with horn or at least prominent tubercle. Color reddish brown, or yellowish brown (occasionally suffused with fuscous streaks), rarely entirely black 3
3. Pronotum and elytra covered with short, dense setae *hirsuta* Ratcliffe, new species
- 3'. Pronotum and elytra with, at most, a few sparse setae; not completely covered by dense setae 4
4. Mandibles entire at apex. Pronotum and elytra weakly shining. Head horn always slightly higher than pronotal horn or tubercle *obliquicornis* Dechambre
- 4'. Mandibles with apex weakly to distinctly notched at apex. Pronotum and elytra distinctly matte. Head horn subequal in height or lower than pronotal horn or tubercle 5
5. Pronotal horn or tubercle erect, projecting forward and upward at angles of 45°-90° from longitudinal plane of body. Head horn always distinctly lower than pronotal horn or tubercle, even in minors *costaricensis* Bates
- 5'. Pronotal horn or tubercle projecting forward and upward at angle of 30° or less (mostly less) from longitudinal plane of body. Head horns nearly always subequal in height to pronotal horn or tubercle, even in minors *solisi* Ratcliffe, new species

Key to the Species of Adult Female *Golofa* of Costa Rica and Panama

1. Apex of clypeus broad (subequal to width of eye), shallowly emarginate. Color black (most common) or dark reddish brown. Body emarginate. Length usually 33 mm or less *tersander* Burmeister
- 1'. Apex of clypeus attenuated toward narrow, bidentate apex. Color black, reddish brown, or yellowish brown. Body length usually 35 mm or greater 2
2. Apex of mandibles entire 3
- 2'. Apex of mandibles weakly notched to bidentate 4
3. From the Cordillera Central (specifically the region of Volcán Irazú) of Costa Rica *imbellis* Bates
- 3'. From the Cordillera Talamanca of Costa Rica and Cordillera Central of adjoining Panama *obliquicornis* Dechambre
4. Color entirely black *solisi* Ratcliffe, new species
- 4'. Color of pronotum black; elytra yellowish brown or dark reddish brown with dark suture *costaricensis* Bates and *hirsuta* Ratcliffe, new species

Clave para las Especies de Adultos Machos de *Golofa* de Costa Rica y Panamá

1. Tibia anterior con 4 dientes *tersander* Burmeister
- 1'. Tibia anterior con 3 dientes 2
2. Pronoto con una depresión con setas justo detrás del margen anterior, nunca con cuerno o tubérculo fuerte. Color completamente negro *imbellis* Bates
- 2'. Pronoto con cuerno o al menos un tubérculo prominente. Color pardo rojizo o pardo amarillento (ocasionalmente entremezclados con rayas fuscas), raramente completamente negro. 3
3. Pronoto y élitros cubiertos densamente de setas cortas *hirsuta* Ratcliffe, new species
- 3'. Pronoto y élitros con, a lo más, unas pocas setas dispersas; no completamente cubierto densamente por setas 4
4. Mandíbulas enteras en el ápice. Pronoto y élitros ligeramente brillantes. Cuerno de la cabeza siempre ligeramente más alto que el cuerno o tubérculo pronotal *obliquicornis* Dechambre
- 4'. Mandíbulas ligera a claramente con una muesca en el ápice. Pronoto y élitros claramente mates. Cuerno de la cabeza semejante o más bajo en altura al cuerno o tubérculo pronotal 5
5. Cuerno o tubérculo pronotal erecto, proyectándose hacia adelante y arriba a ángulos de 45° a 90° del plano longitudinal del cuerpo. Cuerno de la cabeza siempre claramente más pequeño que el cuerno o tubérculo del pronoto, aún en machos menores *costaricensis* Bates
- 5'. Cuerno o tubérculo pronotal proyectándose hacia adelante y arriba a un ángulo de 30° o menos (casi siempre menos) del plano longitudinal del cuerpo. Cuerno de la cabeza casi siempre igual en altura al cuerno o tubérculo pronotal, aún en machos menores *solisi* Ratcliffe, new species

Clave para las Especies de Adultos Hembras de *Golofa* de Costa Rica y Panamá

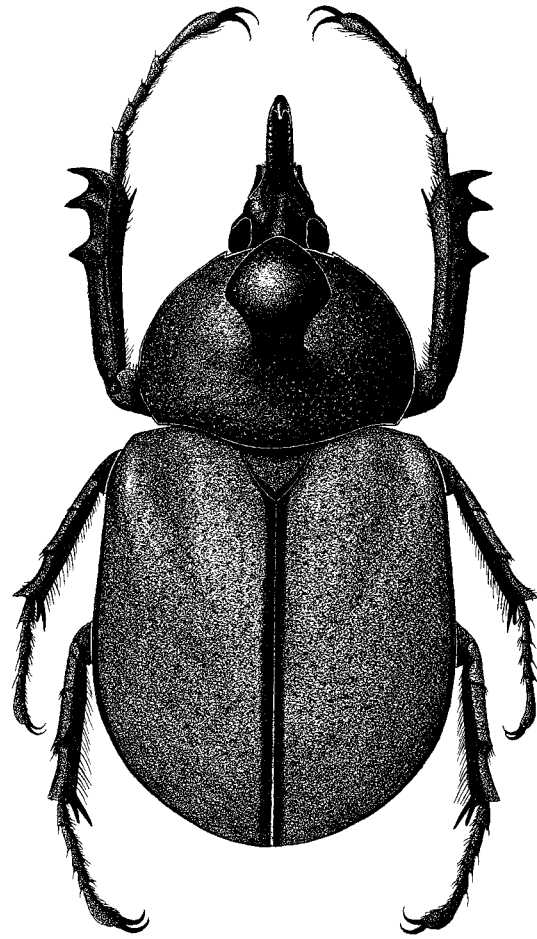
1. Apice del clípeo amplio (igual al ancho del ojo), ligeramente emarginado. Color negro (más común) o pardo rojizo oscuro. Longitud del cuerpo generalmente de 33 mm ó menos *tersander* Burmeister
- 1'. Apice del clípeo atenuado hasta angosto, bidentado. Color negro, pardo rojizo o pardo amarillento. Longitud del cuerpo generalmente de 35 mm ó más 2
2. Apice de la mandíbula entero 3
- 2'. Apice de la mandíbula con una muesca ligera a bidentado 4
3. De la Cordillera Central de Costa Rica (específicamente de la región del volcán Irazú) *imbellis* Bates
- 3'. De la cordillera de Talamanca de Costa Rica y la Cordillera Central de Panamá *obliquicornis* Dechambre
4. Color completamente negro *solisi* Ratcliffe, new species
- 4'. Color del pronoto negro; élitros pardo amarillentos o pardo rojizo oscuro con la sutura oscura *costaricensis* Bates y *hirsuta* Ratcliffe, new species

***Golofa costaricensis* Bates, 1888**

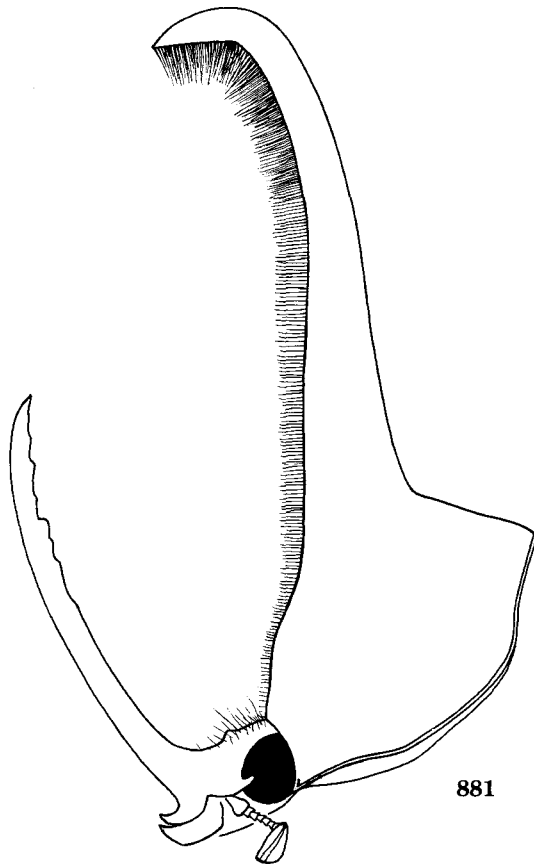
(Color Plate 8, Figs. 880-886)

Golofa costaricensis Bates 1888: 334.**DESCRIPTION.** Length 33.0-46.5 mm; width 18.4-24.0 mm.

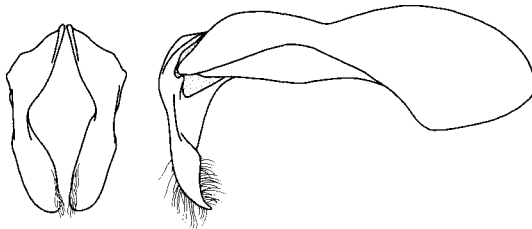
Males. Color of pronotum and elytra a matte, light yellowish brown (most common) with head, horns, usually a small spot on each side of pronotum, sutural interval and lateral margin of each elytron, pygidium, and legs dark reddish brown; or, same but pronotum also dark reddish brown (and then elytra usually with fuscous clouding); or, entirely dark reddish brown. *Head:* Frons with surface rugopunctate laterally and with large, dense punctures medially; punctures with long, dense, light brownish yellow setae. Two small, acute tubercles usually present between eyes (best seen in lateral view), tubercles reduced to absent in minors. Frontoclypeal region with long (up to 20 mm in majors, Fig. 881) or short (tuberculiform in minors, Fig. 884) horn; horn slender, acute, recurved, with small serrations on posterolateral edge (except near apex), and with long, light brownish yellow setae in basal half on posterior surface. Clypeus narrow, apex with sinuate, U-shaped, or (rarely) V-shaped emargination; teeth either side of emargination large, subtriangular and with apices rounded. Interocular width equals 2.1-2.5 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. Mandibles with apex distinctly notched, notch occasionally obscured if mandibles worn. *Pronotum:* Disc with vertical, long (as long as 26 mm in majors, Fig. 881) or short (as short as 3.5 mm in minors, Fig. 884) horn; shaft of horn nearly straight (usually in largest specimens) to curving forward in apical half (especially at apex) to occasionally leaning backward from vertical plane; anterior surface concave, with dense, long, straw-colored setae; posterior surface strongly convex, sparsely to moderately punctate, punctures moderate to large. In posterior view, shaft of horn parallel in smallest specimens to weakly expanded from narrow base to moderately (majors and minors) or strongly (2-3 times width of base) ex-

Fig. 880. *Golofa costaricensis*.

panded apex (majors only); in dorsal view, anterior edge of apex semicircular or subtriangular with rounded lateral angles, center with (most common) or without (uncommon) minute notch. Surface of pronotum finely shagreened with moderately large punctures, punctures moderate in density. An impressed, dark sulcus extends from apex medially to base of horn and up its shaft; punctures along sulcus (as well as a few along anterior margin of pronotum) with long, light reddish brown setae; remainder of pronotum glabrous. Base with complete marginal bead. *Elytra:* Surface finely shagreened, not wrinkled, with small to moderate punctures, punctures sparse to moderate in density. Sutural stria an impressed, weakly crenulate



881



882

883

Figs. 881-883. *Golofa costaricensis*: (881) male major, head and pronotum; (882-883) parameres.

line; occasionally (less than 10% in sample of 48) sutural line reduced to row of punctures. Surface glabrous except for a few minute setae at apex. *Propygidium*: Stridulatory bands subparallel, occasionally weakly arcuate. Each band with large, transverse bumps. *Pygidium*: Surface in basal third and in lateral angles densely punctate to rugopunctate; punctures small to moderate in size, setigerous; setae long, dense, light brownish yellow;



Fig. 884. *Golofa costaricensis*, male minor. Photo by A. Solis (INBio).

disc and center apex sparsely to moderately punctate, punctures small and moderate mixed, lacking setae. In lateral view, basal third strongly convex, apical two-thirds nearly flat. *Legs*: Foretibia tridentate, basal tooth unequally removed from first 2. Foretarsus with first tarsomere longer than (majors) or subequal to (minors) next 2 tarsomeres combined. Mesotibia at apex usually with 2-3 large teeth; transverse carina at middle of tibia with 1-2 large teeth. Basal tarsomere on both meso- and metatarsus with apex extended into spine-like tooth. *Venter*: Prosternal process subconical, apex broad and bluntly rounded, covered with dense setae. *Parameres*: Figs. 882-883.

Females. As males except in the following respects. Color of elytra a weakly shining light yellowish brown (with or without fuscous clouding) to dark reddish brown (most common); remainder of body black. *Head*: Horn absent. Entire surface coarsely rugose and

with sparse, long, tawny setae either side of tubercle (setae often abraded away). Frons with low, median tubercle. Clypeus with small, closely spaced teeth. Interocular width equals 2.6 transverse eye diameters. *Pronotum*: Horn absent. Surface regularly convex, completely and coarsely rugopunctate; pristine specimens with sparse, light reddish brown setae along anterior margin and with a few, short setae on disc (setae usually abraded away in most specimens). *Elytra*: Surface weakly shining (not shagreened), weakly but distinctly wrinkled, with moderately dense, small and large punctures. *Pygidium*: Basal third only moderately convex.

Surface completely punctate and/or rugopunctate, punctures larger, rugosity coarser. *Legs*: Foretibia quadridentate, anterior 2 teeth closer together than to others. First tarsomere of protarsus about a third longer than second. Mesotibia similar except transverse carina usually with 2-3 teeth.

DISTRIBUTION. *Golofa costaricensis* is known only from the Cordillera Central in Costa Rica and western Panama.

LOCALITY RECORDS (Fig. 885-886). 201 specimens examined.

COSTA RICA (178). ALAJUELA (3): Area Cons. Arenal (Sector Colonia Palmareña), La Fortuna, Río San Lorencito (San Ramón), Zarcero; CARTAGO (27): Cachi, Caliblanco, Capelladas, Cartago, Estrella de Cartago, Embalse el Llano, El Tejar, Pacayas, Tablazo, Tres Ríos, Turrialba, Volcán de Irazú; GUANACASTE (9): Río San Lorenzo, Tierras Morenas; HEREDIA (8): Estación Barva, San Luis, San Rafael, Santa Barbara, Vara Blanca; LIMÓN (4): Sabanas de Durika; PUNTARENAS (102): Cerro Frantzius (1 km S), Coronado, Coto Brus area near Panamá border, Estación Biológica Las Alturas, Estación Altamira (Buenos Aires), Estación Las Mellizas, Estación Pittier, Estación Pitilla, Fila Cruces, Las Cruces, San Vito (6 mi. S), Zona Protectora Las Tablas (camino a Tablas); SAN JOSÉ (25): Estación Cuerici, Estación Santa Elena, Mata Platano, Moravia, San José, San Vicente, Santa María.

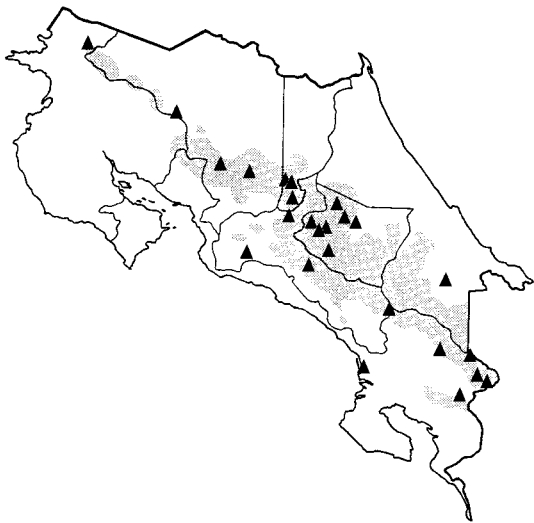


Fig. 885. Distribution of *Golofa costaricensis* in Costa Rica.



Fig. 886. Distribution of *Golofa costaricensis* in Panama.

PANAMA (23). CHIRIQUI (23): Cerro Punta, Hartmann's Finca, Río Colorado (16.4 km W Volcán), vicinity of Río Sereno.

TEMPORAL DISTRIBUTION. January (3), February (5), March (5), April (1), May (6), June (58), July (9), August (11), September (53), October (39), November (14), December (5).

DIAGNOSIS. Among the Central American species, males of *Golofa costaricensis* are best recognized by their light yellowish brown color; distinctly matte surface; majors with a vertically upright pronotal horn that has the apex expanded up to twice (most common) or three times (rare) the width of the shaft at base; a short, oblique to nearly erect, subparallel pronotal horn in minors; and the disc of the pronotum and elytra glabrous. Dark color morphs (as per the description) are found, and I have seen all the color phases from a single locality (Estación Pitilla, Costa Rica) collected at the same time.

Golofa hirsuta, described as new herein, is most similar to *G. costaricensis*, but is easily differentiated by the presence of a dense covering of setae on the head, pronotum, and elytra. *Golofa costaricensis* is sympatric with *G. obliquicornis*, but *G. costaricensis* has notched mandibles (both sexes) and the males have a vertical pronotal horn, whereas *G. obliquicornis* has entire mandibles (both sexes) and a forward-projecting pronotal horn in the males.

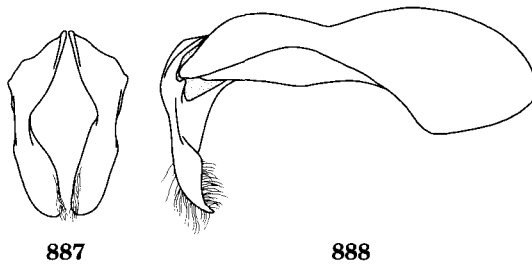
I have not been able to find any differences, including genitalia, between the females of *G. costaricensis* and *G. hirsuta*. At least for the moment, they can be separated only by association with the males.

BIOLOGY. Adults are occasionally attracted to lights. They have been observed resting (feeding?) on *Chusquea* sp. (Bambusaceae) in Chiriqui, Panama (R. Hartmann, personal communication; Color Plate 8). They have been collected from premontane rain forests, lower montane rain forests, and montane rain forests between the elevations of 1,250-2,400 meters.

***Golofa hirsuta* Ratcliffe, new species**

(Figs. 887-890)

TYPE MATERIAL. Holotype male and allotype female labeled "San Luis, 1040 m, R.B. Monteverde, Prov. Puntarenas, COSTA RICA, Oct. 1992, Z. Fuentes, L-N250850, 449250." There are 45 paratypes (39 males, 6 females) with the following data: same data as holotype except dates of August (3), September (6), October (1), November (4), and December (1); same data as holotype except Z. Fuentes and A. Zumbado collectors (1); same data as holotype except date of 24 August-15 September and F.A. Quesada collector (2). Additional paratypes labeled "Río San Lorenzo, Tierras Morenas, Tenorio A.C.A., Prov. Guanacaste, Costa Rica, 1050 m, Ago. 1993, G. Rodriguez, LN 287800-427600, #2758" (1); "Río San Lorenzo, Tierras Morenas, Z.P. Tenorio, Prov. Guanacaste, 1050 m, Set 1993, G. Rodriguez, LN 28700_427600, #2358" (1); same data but date of September 1992 (1); "COSTA RICA: Pacayas, VII-26-1984" (1); "Tierras Morenas, Prov. Guanacaste, Costa Rica, 685 m, Sept 1993, G. Rodriguez, LS 283950-424500, #2760" (1); "San Gerardo Rivas, Perez Zeledon, 1300 m, Prov. San Jose, Costa Rica, R. Zunigra, G. Mora & M.M. Chavarria, Ago. 1990, L-S-379700, 507500" (1); "Alajuela, Costa Rica, San Ramon, Río S. Lorencito, 800 m, 5 Set. 1986, Col: A. Solis Blanco" (1); same data but date of 7 August (1); "Costa Rica, Cartago, Paso Marcos VIII-92, D. Curoe col" (1); "Costa Rica, San Jose, Division, VI-94, 2300 m el., D. Curoe col" (2); "Represa Río Gde. de Orosi, 1650 m, P.N. Tapanti, Prov. Cartago, Costa Rica, Set. 1992, G. Mora, L-N 185900, 563300" (1); "Costa Rica nr. Panama border, 1978" (1); "Panama: Chiriqui, Cerro Punta, 1978" (1); "Rep. de Panama, Prov. de Chiriqui, Boquete, XI-6-76, Wolda" (1); "Panama: Chir. Prov., Alto Lino, 4 km NE Boquete, IX-10-75, H. Wolda, uv lt" (1); "Panama-Chiriqui, Boquete, 1250 m, 8°48'N; 82°26'W. 15-III-1977, Coll. H. Wolda" (1); same data but date of 20-VIII-1976 (1); same data but date of 6-IX-1977 (1); "Panama: Chiriqui, La Fortuna, 1050 m, 17-19-VII-96, D. Curoe" (3);



Figs. 887-888. *Golofa hirsuta* parameres.

“Panama: Chiriqui, Cafe Duran, 1350 m (vic. Río Sereno), IX-96, D. Curoe” (2).

Holotype and allotype deposited at INBio (Costa Rica). Paratypes deposited at INBio, U.S. National Museum (Washington, D.C., currently at the University of Nebraska State Museum), Smithsonian Tropical Research Institute (Panama), Museum National d’Histoire Naturelle (Paris, France), University of Nebraska State Museum (Lincoln, NE), Daniel Curoe (Palo Alto, CA), Miguel Morón (Xalapa, Mexico), and Brett Ratcliffe (Lincoln, NE).

HOLOTYPE. Male. Length 40.8 mm; width 22.7 mm. Color of pronotum and elytra a matte, light yellowish brown with head, horns, round spot on pronotum next to lateral margin at middle, sutural interval and lateral margin of elytra, pygidium, and legs dark reddish brown. *Head:* Frons rugopunctate, setigerous; setae long, moderately dense, light reddish brown in color; tubercles absent. Frontoclypeal region with slender horn; horn 7.8 mm in length, recurved, acute, with faint serrations in basal third on posterolateral edges, and with long, light reddish brown setae in basal half on posterior surface. Clypeus narrow, apex with U-shaped emargination, teeth either side of emargination large, subtriangular, with apices rounded. Interocular width equals 2.5 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. Mandibles with apex distinctly notched. *Pronotum:* Disc with thick horn extending upward and curving forward; anterior surface concave, with dense, long, light reddish brown setae; posterior surface strongly convex, mod-

erately punctate, punctures moderate in size. In posterior view, shaft of horn subparallel with apex barely widened; in dorsal view, apex with anterior edge strongly rounded. Surface shagreened with moderately large punctures; punctures moderate in density, setigerous; setae short to moderate in length, light reddish brown. A narrow carina extends from apex medially to base of horn, punctures either side of carina with long, light reddish brown setae. Base with complete marginal bead. *Elytra:* Surface distinctly shagreened, not wrinkled, with small punctures; punctures moderate in density, setigerous; setae dense, short, light reddish brown. Sutural stria impressed, weakly crenulate. *Propygidium:* Stridulatory bands subparallel, each band comprised of large, transverse bumps. *Pygidium:* Surface in basal third and in lateral angles densely punctate, punctures small to moderate in size, setigerous; setae long, dense, light reddish brown. Disc and center apex glabrous, sparsely punctate, punctures small. In lateral view, basal third strongly convex, apical two-thirds nearly flat. *Legs:* Foretibia tridentate, basal tooth unequally removed from first two. Foretarsus with first tarsomere a little longer than next 2 tarsomeres combined. Mesotibia at apex with 2 large teeth; transverse carina at middle of tibia with 2 large teeth. Basal tarsomere of both meso- and metatarsus with apex extended into a spine-like tooth. *Venter:* Prosternal process subconical, apex broad and bluntly rounded, covered by dense setae. *Parameres:* Figs. 887-888.

ALLOTYPE. Female. Length 39.2 mm; width 20.5 mm. As holotype except in the following respects. Color of pronotum and elytra a weakly shining dark reddish brown with fuscous clouding. *Head:* Horn absent. Entire surface coarsely rugopunctate and with sparse, long, light reddish brown setae either side of tubercle. Frons with low, median tubercle. Clypeus with small, closely spaced teeth. *Pronotum:* Horn absent. Surface regularly convex, completely and coarsely rugopunctate, anterior margin with a few sparse, light reddish brown setae, disc with a few microsetae. *Elytra:* Surface weakly shining

(not shagreened), weakly wrinkled, with moderately dense, small and large punctures. *Pygidium*: Basal third only moderately convex, apical third weakly concave. Surface rugopunctate. *Legs*: Foretibia quadridentate, anterior 2 teeth closer to one another than to other teeth. Basal tarsomere of protarsus almost twice as long as second. Mesotibia with 3 teeth at apex and on transverse carina.

VARIATION. Males (34 paratypes). Length 34.4-46.6 mm; width 18.6-24.1 mm. As holotype except in the following respects. Color of pronotum varies from as holotype (most common) to mottled with dark brown to com-

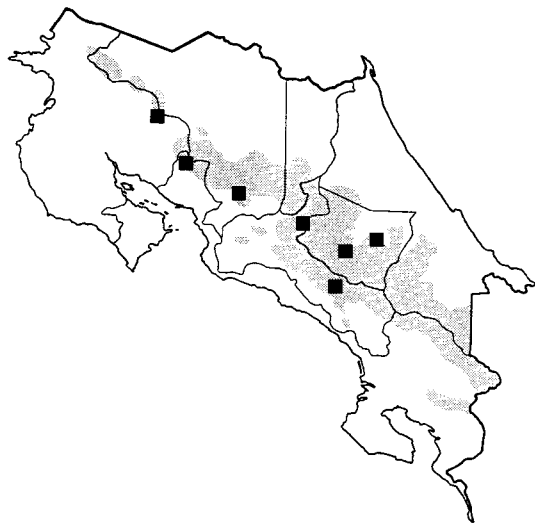


Fig. 889. Distribution of *Golofa hirsuta* in Costa Rica.

pletely dark reddish brown to completely piceous. Color of elytra varies from as holotype (most common) to varying degrees of fuscous clouding to completely dark reddish brown to completely piceous (rare). *Head*: Setae on frons, base of horn, and eye canthus vary from moderate to dense, moderate in length to long, light reddish brown to light brownish yellow. Horn 3.0-19.5 mm, posterolateral serrations absent (minors) to prominent (majors). *Pronotum*: Horn varies from low, blunt tubercle (2 mm in height; minors) to long, curving horn (17 mm high; majors); setae light reddish brown to light brownish yellow. In posterior view, horn subparallel to barely widened at apex in minors to apex twice as wide as base in majors. In dorsal view, apex with anterior edge strongly rounded to bluntly subtriangular. Setae on disc short to long, moderately dense to dense, light reddish brown to light brownish yellow. Minors with fine carina extending from apex of pronotum to base of horn; majors with sulcus instead. *Pygidium*: Some specimens with scattered setae on disc. *Legs*: Minors with basal segment of foretarsus a little longer than next 2 segments combined, majors with basal tarsomere distinctly longer. Transverse carina on mesotibia with 2-3 large teeth.

Females (6 paratypes). Length 36.0-40.0 mm; width 19.7-21.4 mm. As allotype except in the following respects. Color of elytra varies from castaneous with dark margins (2 specimens) to piceous (4 specimens). *Legs*:



Fig. 890. Distribution of *Golofa hirsuta* in Panama.

Mesotibia with 2 large teeth at apex; transverse carina with 2-3 large teeth.

ETYMOLOGY. From the Latin *hirsutus*, meaning hairy; in reference to the dense covering of setae in this species.

DISTRIBUTION. *Golofa hirsuta* is known from the Cordillera Central of Costa Rica and western Panama. Point localities do not seem to overlap with those of *G. costaricensis*, the most closely related species.

LOCALITY RECORDS (Figs. 889-890). 42 specimens examined.

COSTA RICA (30). ALAJUELA (4): San Ramón; CARTAGO (2): Parq. Nac. Tapanti, Paso Marcos; GUANACASTE (4): Tierras Morenas; PUNTARENAS (19): San Luis (Reserva Biológica Monteverde), near Panama border; SAN JOSÉ (3): División, San Gerardo Rivas.

PANAMA (12). CHIRIQUI (12): Boquete, 4 mi E Boquete, Cerro Punta, La Fortuna, vicinity of Río Sereno.

TEMPORAL DISTRIBUTION. March (1), June (2), July (3), August (6), September (14), October (3), November (3), December (1).

DIAGNOSIS. Males of this species are unique in that they are completely covered by short, moderately dense setae. While other species of *Golofa* have setae on the pronotal horn and anterior margin as well as on the pygidium and venter, none have setae so densely and completely covering the head, pronotum, and elytra as in this species.

Aside from the setae, *Golofa hirsuta* is most similar to *G. costaricensis*. In males of *G. hirsuta*, the color is similar to that of *G. costaricensis* (least common) to the pronotum and elytra suffused with dark brown clouding or entirely dark brown (most common); the surface is also matte. Majors have a vertically upright pronotal horn that is generally more slender than in *G. costaricensis*, and it has the apex of the horn expanded no more than twice the width of the shaft at its base; minors have

a short, oblique, subparallel pronotal horn. The entire dorsal surface has short, dense setae, and a sulcus extends from the anterior margin of the pronotum medially to the base of the pronotal horn in majors, while in minors it is a narrow carina rather than a sulcus.

I cannot differentiate the females of the two species, and so reliable identification of females can only be accomplished by association with the males.

BIOLOGY. All of the adults that have been collected were attracted to lights. They have been collected from premontane rain forests, lower montane rain forests, and montane rain forests. Most of the specimens were collected at elevations of 1,250-2,300 meters. One each were collected at elevations of 685 meters, 800 meters, and 1,050 meters.

Golofa imbellis Bates, 1888

(Figs. 891-895)

Golofa imbellis Bates 1888: 335.

DESCRIPTION. Length 35.0-45.0 mm; width 20.0-22.0 mm.

Males. Color completely dark reddish brown to black, matte. *Head:* Surface densely, coarsely rugopunctate. Frons with dense, long, light reddish brown setae. Frontoclypeal region with small to large conical tubercle (Fig. 892). Clypeus with narrow apex, apex subtruncate, weakly reflexed. Interocular width equals 3.0 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. Mandibles entire, not notched or toothed. *Pronotum:* Surface with large, dense punctures, punctures becoming confluent in apical fourth; area of confluent punctures feebly foveate and with dense, long, light reddish brown setae. Base with complete marginal bead. *Elytra:* Surface shagreened, with moderately dense, moderately large, shallow punctures. Sutural stria an impressed line. *Propygidium:* Stridulatory bands subparallel, each with transverse tubercles. *Pygidium:* Surface with minute and small punctures, punctures moderately dense, especially in lateral angles. Base with

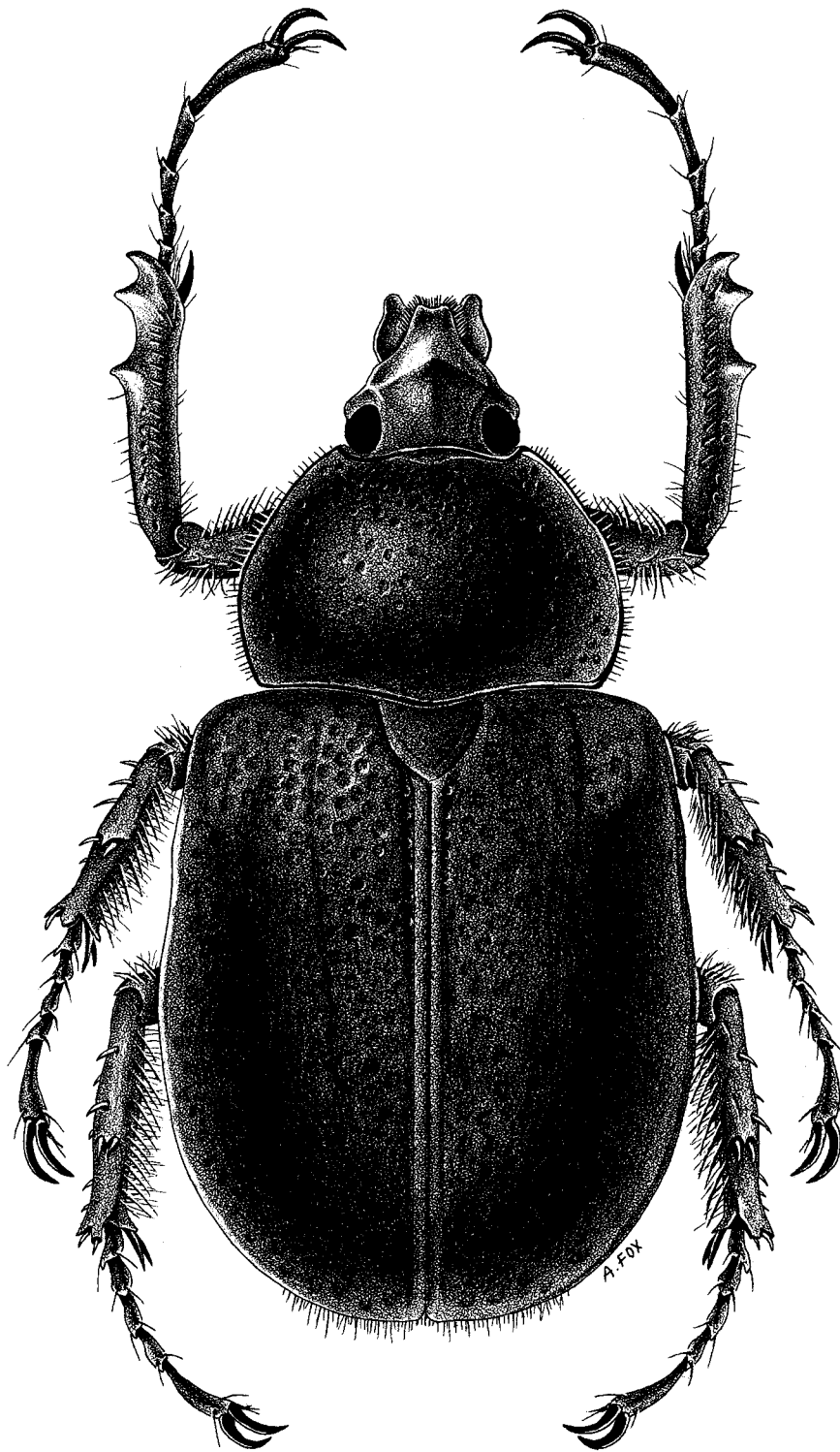
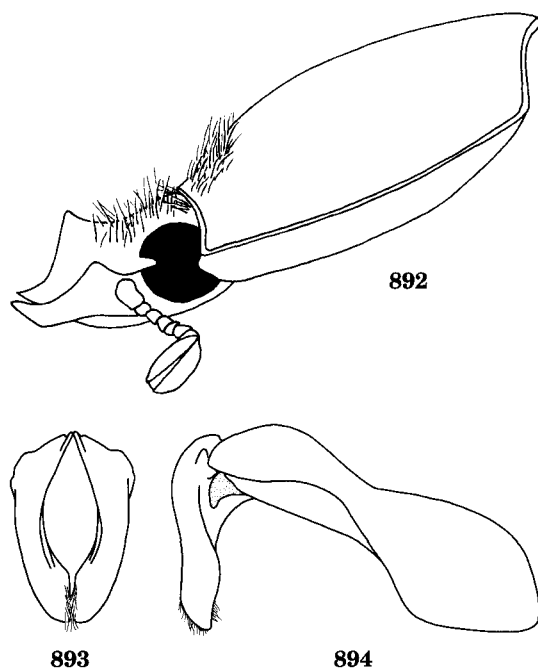


Fig. 891. *Golofa imbellis*.



Figs. 892-894. *Golofa imbellis*: (892) head and pronotum (lateral view); (893-894) parameres.

row of dense, long, light reddish brown setae, discal area with sparse setae. In lateral view, basal third strongly convex, apical two-thirds flat to weakly concave. *Legs*: Foretibia tridentate, basal tooth removed from others. Protarsus with basal segment about one-fourth longer than second segment. Mesotibia with apex weakly crenulate; transverse carina at middle of tibia with 1-2 strong teeth. Basal tarsomere of both meso- and metatarsus with apex extended into spine. *Venter*: Prosternal process moderate in length, bluntly rounded, covered with dense setae. *Parameres*: Figs. 893-894.

Females. As males except in the following respects. Body black, weakly shining. *Head*: Tubercle smaller. *Pronotum*: Subapical fovea absent. *Elytra*: Paired rows of punctures evident. *Legs*: Foretibia tridentate. Protarsus with first segment about one-third longer than second segment.

DISTRIBUTION. *Golofa imbellis* is known from Guatemala and Costa Rica (Endrödi 1985a; Lachaume 1985). Endrödi also lists



Fig. 895. Distribution of *Golofa imbellis* in Costa Rica.

Mexico, but Morón's (1995) recent treatment of the Mexican species excludes *G. imbellis*. The locality data for Bates' Río Sucio specimens is imprecise but refers to the north side of Volcán Irazú.

LOCALITY RECORDS (Fig. 895). 3 specimens examined.

COSTA RICA (3). CARTAGO (3): Parq. Nac. Tapanti, west side Volcán Irazú, Río Sucio (north side Volcán Irazú).

TEMPORAL DISTRIBUTION. May (2).

DIAGNOSIS. *Golofa imbellis* males are readily recognized by their totally black color and absence of horns on either the head or pronotum. Larger males may have a well-developed tubercle on the head. All other Central American species have either large or small horns.

BIOLOGY. This species is exceedingly rare. Although Bates based his description on 17 specimens from Volcán Irazú and Río Sucio, there apparently have been only a few specimens taken since. This species has been collected in montane wet forests on Irazú at elevations of 1,875-2,200 meters. It is cold at

those elevations on Volcán Irazú, and there probably has not been a great deal of collecting done there at these high elevations. Moreover, Irazú has been severely deforested as a result of volcanic eruptions in the 1960s and human disturbance, and *Golofa* habitat has been reduced. High elevation (contributing to less collecting), combined with disappearing habitat, accounts for the few records for *G. imbellis*. Whether it still exists in any numbers in nature is unknown.

***Golofa obliquicornis* Dechambre,
1975**

(Figs. 896-901)

Golofa obliquicornis Dechambre 1975: 627.

DESCRIPTION. Length 31.5-48.0 mm; width 17.5-24.5 mm.

Males. Color of pronotum and elytra light yellowish brown (most common) to dark yellowish brown; pronotum often darker than elytra; head, horns, elytral suture, pygidium, and legs dark reddish brown. **Head:** Frons densely, coarsely rugopunctate and with moderately dense, long, pale yellow setae; paired tubercles usually distinct. Frontoclypeal region with long (up to 22 mm in majors) or short (as short as 6 mm in minors), slender, recurved horn; horn (Fig. 897) with acute apex, basal half posteriorly with sparse and long setae; posterolateral margin of horn weakly serrated in basal half. Clypeus with sparse, minute punctures; apex narrow, bluntly rounded, weakly emarginate at middle. Interocular width equals 3.0 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. Mandibles with apex entire. **Pronotum:** Disc of majors with moderately long (as long as 10 mm), slender, subparallel horn (Fig. 897) projecting forward and upward at about 22° from plane of pronotal disc; shaft feebly expanded

lowish brown; pronotum often darker than elytra; head, horns, elytral suture, pygidium, and legs dark reddish brown. **Head:** Frons densely, coarsely rugopunctate and with moderately dense, long, pale yellow setae; paired tubercles usually distinct. Frontoclypeal region with long (up to 22 mm in majors) or short (as short as 6 mm in minors), slender, recurved horn; horn (Fig. 897) with acute apex, basal half posteriorly with sparse and long setae; posterolateral margin of horn weakly serrated in basal half. Clypeus with sparse, minute punctures; apex narrow, bluntly rounded, weakly emarginate at middle. Interocular width equals 3.0 transverse eye diameters. Antenna 10-segmented, club subequal in length to segments 2-7. Mandibles with apex entire. **Pronotum:** Disc of majors with moderately long (as long as 10 mm), slender, subparallel horn (Fig. 897) projecting forward and upward at about 22° from plane of pronotal disc; shaft feebly expanded

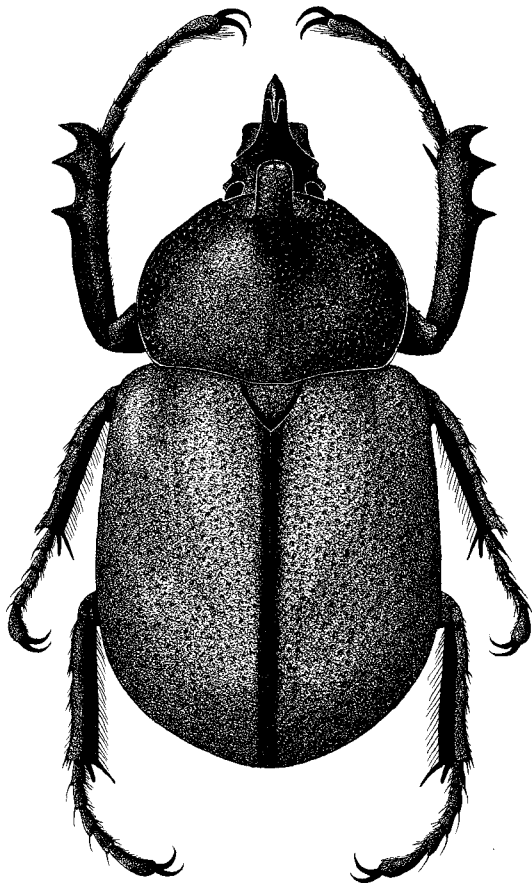
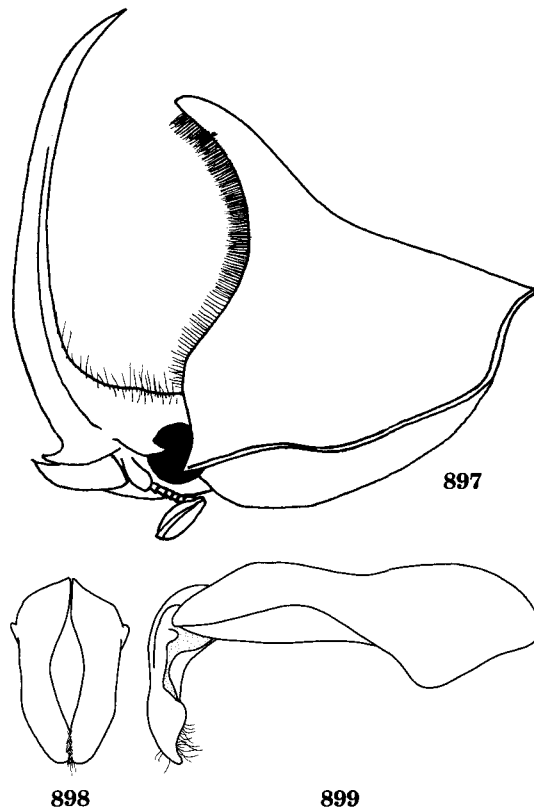


Fig. 896. *Golofa obliquicornis*.



Figs. 897-899. *Golofa obliquicornis*: (897) male major, head and pronotum; (898-899) parameres.

at apex in largest specimens; apex varies from simply and bluntly rounded (most common) to weakly attenuate and narrowly rounded (least common); minors with short (as short as 3 mm), blunt horn or tubercle with weakly attenuate, bluntly rounded apex; anterior surface of horn weakly concave and with dense, long, pale yellow to reddish brown setae; a shallow sulcus or slender carina extending from anterior margin of pronotum to base of horn; posterior surface of horn convex and with moderately dense, moderate to large punctures. Pronotal surface finely shagreened, punctate; punctures moderate in den-



Fig. 900. Distribution of *Golofa obliquicornis* in Costa Rica.

sity (becoming denser along lateral margin at middle), large. Base with complete marginal bead. *Elytra*: Surface weakly shining, finely shagreened, first broad interval sparsely punctate, remainder of elytron with punctures moderately dense, punctures moderate in size. Sutural stria an impressed line or row of punctures or a combination of both. *Propygidium*: Stridulatory ridges subparallel, each consisting of small, transverse ridges. *Pygidium*: Surface finely shagreened, usually finely rugopunctate (occasionally reduced to nearly smooth); basal third with transverse band of dense, long, light reddish brown setae, disc in pristine specimens occasionally with a few sparse setae. In lateral view, surface strongly convex in basal third, weakly convex to flat in apical two-thirds. *Legs*: Foretibia tridentate, basal tooth removed from others. Basal segment of foretarsus subequal in length or slightly longer than next 2 segments combined. Mesotibia at apex with 4-6 small teeth and usually 2 larger teeth (wearing frequently evident, thus altering number of teeth); transverse carina at middle of tibia usually with 4 small teeth. Basal tarsomere of both meso- and metatarsi with apex extended into spine. *Venter*: Prosternal process moderate in length, obscured by long setae, tapering, apex bluntly rounded. *Parameres*: Figs. 898-899.

Females. As males except in the following respects. Color of pronotum dark reddish



Fig. 901. Distribution of *Golofa obliquicornis* in Panama.

brown to piceous or with both colors mixed; elytra light yellowish brown to dark reddish brown to piceous. *Head*: Horn absent. Entire surface coarsely rugopunctate, with small, low tubercle at frontoclypeal juncture. Frons mesad of each eye with (in pristine specimens) moderately dense, long, reddish brown setae. Clypeal apex with 2 small, acute teeth (teeth often worn down). Interocular width equals 2.3 transverse eye diameters. *Pronotum*: Horn absent. Surface coarsely rugopunctate, occasionally with only large punctures in a small patch on posterior part of disc at center. *Elytra*: Surface coarsely rugopunctate. *Pygidium*: Surface usually coarsely rugopunctate. *Legs*: Foretibia tridentate. Basal segment of foretarsus subequal in length to next segment only.

DISTRIBUTION. *Golofa obliquicornis* is known only from the Cordillera Talamanca in the adjoining areas of Costa Rica and Panama.

LOCALITY RECORDS (Figs. 900-901). 33 specimens examined.

COSTA RICA (7). PUNTARENAS (5): Buenos Aires (1 km S of Cerro Franzius), Cerro Biolley (1 km S), Cerro Echandi, Tres Colinas (Buenos Aires); SAN JOSÉ (2): Division.

PANAMA (26). CHIRIQUI (26): Bambito (2 mi NW), Cerro Punta (2.5 km W), Guadeloupe Arriba, Hato del Volcán (4 km W, Las Lagunas), Las Nubes (W of Cerro Punta).

TEMPORAL DISTRIBUTION. May (4), June (8), July (10), August (2), September (1), October (2), November (1).

DIAGNOSIS. *Golofa obliquicornis* males are distinctive because of the forward projecting pronotal horns that are always shorter than or subequal to the frontal horn, mandibular apex entire, slightly shining light to dark yellowish brown coloration, and the transverse carina of the mesotibia usually with 4 teeth. *Golofa costaricensis* occurs sympatrically, but in this species the pronotum and elytra are always definitely matte, and the pronotal

horn or tubercle is vertical or nearly so. Females may be distinguished by their entire mandibles, whereas the apex of the mandibles in *G. costaricensis* is distinctly notched or toothed.

BIOLOGY. Specimens have been collected at lights at elevations ranging from 1,360-2,300 meters in premontane wet forests and premontane rain forests.

***Golofa solisi* Ratcliffe, new species**

(Figs. 902-906)

TYPE MATERIAL. Holotype labeled "Estac. Cacao, 1000-1400 M, SW side Volcán Cacao, Guanac. Pr., COSTA RICA, Oct. 1989, URC6, R. Blanco & C. Chavez. 323300, 375700." Allotype with same data but date of November-December. Fifty-two paratypes with the following data: as holotype (7 specimens); as holotype except with date of September 1989 (8 specimens), November-December 1990 (3 specimens), September 1991 (1 specimen); "Estación La Casona, R.B. Monteverde, Prov. Punta, COSTA RICA, 1520 M, Jun 1991, N. Obando, LN253250- & 49700, #1714" (2 specimens); same data as previous but with date of 6-25 June 1994, collector K. Martinez, and #2992 (2 specimens); same data as previous except date of 20-26 May 1994, LN 253200-449200, and #2931 (1 specimen); same data but with date of May 1991 (1 specimen); same data but with date of April 1991 (1 specimen); same data but with date of 9-25 June 1996, L_N 253900_449300, #7569 (1 specimen); "Zarcero, Alfaro Ruiz, Alajuela, COSTA RICA, 20-VI-1993, F. Mejia-Arana" (1 specimen); "Sector Las Palmas, 5.5 km SSW del Volcán Rincon de la Vieja, Prov. Guana., COSTA RICA, 1400 m, 11 Jun 1994, D. Garcia, L_N 307943_389422, #3045" (1 specimen); "Las Chorreras, Sn Rafael, Her, 16 Junio 1992, C. Canet" (1 specimen); "Est. G. Brenes, 1300 m, Res. Biol. Monteverde, Prov. Punt., COSTA RICA, E. Bello, Jun 1991, L_N_249750, 450075" (1 specimen); "Guanacaste, C.R., P.N. Santa Rosa, 29 Mayo 1986, M.M. Chavarria D" (1 specimen); "San José, COSTA RICA, P.N. Braulio Carrillo, Sector Zurqui - Tunel, 8

Mayo 1986, I.A. Chacón" (1 specimen); "Alajuela, Costa Rica, San Ramon, Río S. Lorencito, 800 M, 15 Junio 1988, Col. A. Solis Blanco" (1 specimen); "COSTA RICA: Puntarenas, Est. Biol. Monteverde, V-29-1992, 1550 M, B.C. Ratcliffe & M.L. Jameson" (2 specimens); "COSTA RICA: Puntarenas, Monteverde, Cambell's Woods, V-29-31-1992, 1520 m, B.C. Ratcliffe & M.L. Jameson" (2 specimens); "Monteverde, Puntarenas Prov., Costa Rica, May 18-21, 1967, Jim Robertson" (1 specimen); "COSTA RICA: Puntarenas Province, Monteverde, Pension Quetzal, VI-4-1992, Blacklight, F. Andrews & A. Gilbert" (1 specimen); "COSTA RICA: Puntarenas, Monteverde, VI-13-15, 1986, B.C. Ratcliffe & party" (1 specimen); "COSTA RICA: Puntarenas, 3 km SW Santa Elena, VI-1-1992, 1280 M, B.C. Ratcliffe & M.L. Jameson" (1 specimen); "COSTA RICA, Punt. Pr., Monteverde, 10 June 1988, Coll. F. T. Hovore" (1 specimen); "COSTA RICA, Puntarenos (sic) Prov., Monteverde, 1-3 July 1989, Coll. F. T. Hovore" (1 specimen); "C. RICA, Puntarenas: Monteverde, 18-20 June 1982, Nagano & Wolfe" (1 specimen); "Monteverde, C. R., Puntarenas Prov., May 13-17, 1964, Coll. F. S. Truxal" (4 specimens); "PANAMA: Chiriqui, La Fortuna, 1100 M, 11-14-XI-96, D. Curoe" (1 specimen);

Holotype, allotype, and 19 paratypes deposited at INBio (Costa Rica). Remaining paratypes deposited at U.S. National Museum (Washington, D.C. currently at University of Nebraska), Museum National d'Histoire Naturelle (Paris, France), University of Nebraska State Museum (Lincoln, NE), Natural History Museum of Los Angeles Co. (Los Angeles, CA), Daniel Curoe (Palo Alto, CA), Miguel Morón (Xalapa, Mexico), and Brett Ratcliffe (Lincoln, NE).

HOLOTYPE. Male. Length 38.2 mm; greatest width 20.6 mm. Color of head, elytra, pygidium, and legs piceous; pronotum light reddish brown with margins, pronotal horn, and area from horn to anterior margin piceous. *Head:* Frons densely punctate, with long, dense, reddish brown setae; paired tubercle absent. Frontoclypeal region with slender, acute, recurved horn, horn subequal in

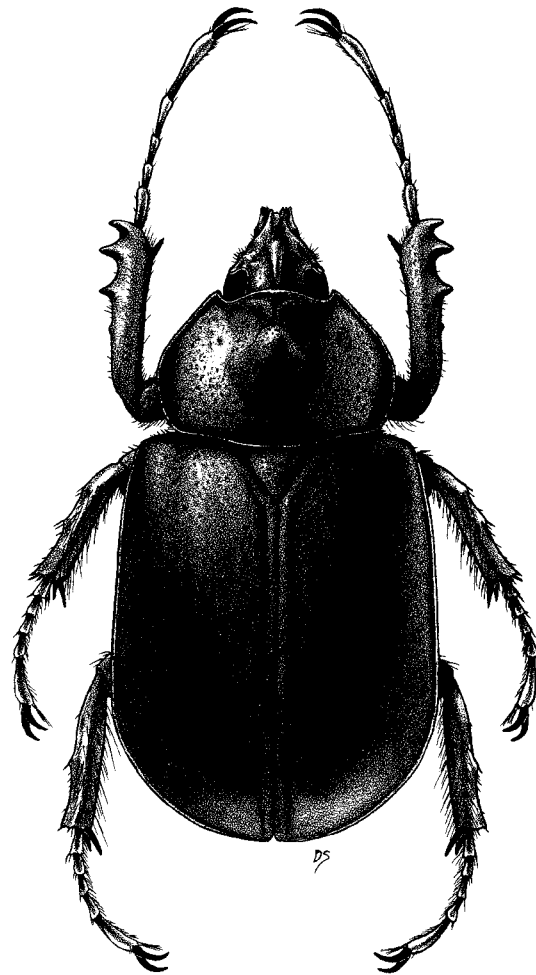
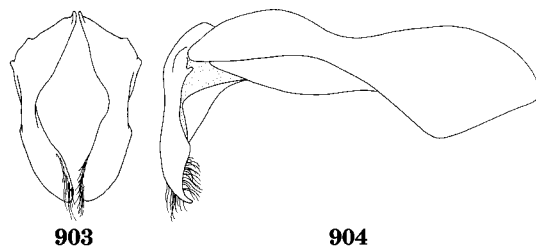


Fig. 902. *Golofa solisi*.



Figs. 903-904. *Golofa solisi* parameres.

height to pronotal horn, posterior serrations absent. Clypeus with surface roughened and with a few small punctures; apex narrow, deeply notched at center, teeth either side of notch narrowly rounded. Interocular width equals 2.1 transverse eye diameters. Antenna

with 10 segments, club subequal in length to segments 2-7. Mandibles with apex distinctly notched. *Pronotum*: Center with short (4.0 mm) horn projecting forward and upward at about 23° from plane of disc behind horn; anterior surface of horn strongly convex, with dense punctures; horn in posterior view with sides parallel, apex bluntly rounded. Surface finely shagreened and with large punctures; punctures moderately dense and with sparse, reddish brown setae along anterior margin and either side of anteromedian sulcus. Narrow sulcus extending from middle of anterior margin to anterior face of pronotal horn. Base with marginal bead. *Elytra*: Surface finely shagreened and with sparse, small punctures. Sutural stria an impressed line. *Propygidium*: Stridulatory bands slightly tumescent, nearly converging apically, consisting of transverse ridges. *Pygidium*: Surface in basal fourth finely rugulose on sides, center with sparse, small and moderately large, mixed setigerous punctures; setae long, dense, light reddish brown. Discal area with minute and moderately-sized punctures mixed; larger punctures sparse, a few setigerous. Lateral angles densely rugulose. In lateral view, basal third strongly convex, apical two-thirds weakly convex. *Legs*: Foretibia tridentate, apical 2 teeth closer to one another. Protarsus with first segment subequal in length to next 2 segments combined. Mesotibia at apex with 2 strong teeth and 2 small accessory teeth; transverse carina at middle of tibia with 1 large tooth and a smaller accessory tooth either side of large tooth. Apex of basal tarsomere of both meso- and metatarsus spine-like. *Venter*: Prosternal process moderate in length, subconical, rounded at apex, compressed from front to back, covered with dense setae. *Parameres*: Figs. 903-904.

ALLOTYPE. Female. Length 38.6 mm; greatest width 21.8 mm. Color generally black, elytra and sternites piceous. As holotype except in the following respects: *Head*: Horn absent, instead with 1 small, median tubercle. Surface entirely, coarsely rugopunctate. Clypeus with apical teeth rounded. Mandibles with apex weakly notched. *Pronotum*: Horn absent. Surface completely, densely rugopunctate,

punctures large. *Elytra*: Surface completely, coarsely rugopunctate. *Pygidium*: Surface completely, finely rugulose, both minute and larger punctures moderately dense; disc with a few, minute, pale setae. In lateral view, surface regularly convex. *Legs*: Foretibia quadridentate. Protarsus with first segment about one-third longer than second segment. Transverse carina at middle of mesotibia with 4 subequal teeth.

VARIATION. Males (44 paratypes). Length 33.6-50.0 mm; greatest width 19.0-24.3 mm. As holotype except in the following respects: Color of pronotum as holotype (31 specimens) to unicolorous dark reddish brown (4 specimens); color of elytra as holotype (22 specimens) to reddish brown (13 specimens); if reddish brown, then elytral margins and suture piceous. *Head*: Frons in majors coarsely rugopunctate to densely punctate (minors), paired tubercles behind horn present in majors. Horn in majors up to 6 cm in length and with serrations on posterior edges. Clypeal teeth rounded to acute (depending on wear). Interocular width varies from 1.6-2.1 transverse eye diameters. *Pronotum*: Horn varies from tuberculate (minors) to 8.8 cm in length (majors); horn projects upward and forward from plane of disc from about 23° (small specimens) to 33° (large specimens). Margin at base with small, sparse setae in pristine specimens. A narrow sulcus extends from middle of anterior margin to anterior face of pronotal horn (majors) or with a fine carina instead (minors). *Elytra*: Small, sparse setae present at elytral apices in pristine specimens. *Legs*: Mesotibia at apex with 2-3 small accessory teeth; transverse carina at middle of tibia with 1 large tooth or 3-4 small teeth.

Females (8 paratypes). Length 34.7-49.8 mm; greatest width 18.7-24.5 mm. *Head*: Mandibles at apex entire (worn specimens) to distinctly notched (unworn specimens).

ETYMOLOGY. This species is named in honor of Angel Solís, Coleoptera curator at INBio in Costa Rica. Angel has helped this project immensely, has collected in Costa Rica for many years, and he also collected part of the type series.

DISTRIBUTION. *Golofa solisi* is broadly distributed in the Cordilleras Guanacaste, Tilaran, and Talamanca of Costa Rica with one specimen known from the Cordillera Central in Chiriqui in Panama.

LOCALITY RECORDS (Figs. 905-906). 54 specimens examined.

COSTA RICA (48). ALAJUELA (3): San Ramón, Zarcero; GUANACASTE (23): Estación Cacao, Las Palmas, Parq. Nac. Santa Rosa; HEREDIA

(1): Las Chorreras; PUNTARENAS (24): Estación Biológica Monteverde, Estación G. Brenes, Campbell's Woods, Monteverde, Reserva Biológica Monteverde, Santa Elena (3 km SW); SAN JOSÉ (2): Estación Zurqui.

PANAMA (1). CHIRIQUI (1): La Fortuna.

TEMPORAL DISTRIBUTION. April (1), May (13), June (16), July (1), August (1), September (9), October (8), November (3), December (2).

DIAGNOSIS. *Golofa solisi* has distinctive coloration and armature in the males. The light reddish brown, matte color of the pronotum (with dark margins and horn) and the light to dark reddish brown, matte elytra are characteristic of this species. The color illustration on plate 27 of Lachaume (1985) for *G. incas* Hope shows a similar bicolored pattern on the pronotum. Unlike *G. incas* or *G. imperialis* Thomson, however, the pronotum and elytra of *G. solisi* are matte and nearly uniformly dark. Unlike *G. costaricensis*, which also has matte elytra and pronotum, the pronotal horn of *G. solisi* is directed forward, whereas the pronotal horn of *G. costaricensis* Bates is usually nearly vertical.

BIOLOGY. Nearly all of the specimens were collected at lights in premontane and lower montane rain forests at elevations ranging from 800-1,600 meters.



Fig. 905. Distribution of *Golofa solisi* in Costa Rica.



Fig. 906. Distribution of *Golofa solisi* in Panama.

***Golofa tersander* Burmeister, 1847**
(Figs. 907-912)

Golofa tersander Burmeister 1847: 239.

Mixigenus leander Thomson 1859b: 7 (synonym).

Mixigenus barbicornis Fairmaire 1878: 266 (synonym).

Golofa dohrni Nonfried 1890: 16 (synonym).

DESCRIPTION. Length 25.0-40.0 mm; width 12.5-21.0 mm.

Males. Color entirely black. *Head:* Frons and clypeus in majors feebly roughened with sparse micropunctures to distinctly punctate in minors, punctures moderate in size, sparse to moderate. Frons lacking paired tubercles. Frontoclypeal region with long (up to 18 mm in majors) or short (as short as 2 mm in minors), slender, recurved horn (Figs. 908-909); horn with acute apex, lacking setae, flattened from front to back; largest specimens with large, paired tubercles on posterior surface of horn just before apex, serrations at base absent. Clypeus with apex broadly, arcuately emarginate in majors, becoming subtruncate in minors; teeth either side of emargination blunt, small. Interocular width equals 2.5-3.0 transverse eye diameters. Antenna with 10 segments, club subequal in length to segments 2-7. Mandibles with apex distinctly notched. *Pronotum:* Disc of majors with large, subtriangular prominence; minors with low, rounded boss. Anterior surface of prominence in majors sharply declivous, slightly concave, and with apex weakly emarginate and setose; setae short, sparse, light reddish brown; a fine, weakly impressed sulcus usually extending from anterior margin of pronotum to base of prominence in largest specimens only. Pronotal surface crazed, with sparse, small punctures; punctures becoming larger in anterior third and large and dense along all margins. Base with complete marginal bead. *Elytra:* Surface finely shagreened (reduced in largest specimens), sparsely punctate, punctures small. Sutural stria an impressed line, line becoming obscure in apical fifth. *Propygidium:* Surface with broad field of small transverse bumps, bumps not in parallel rows. *Pygidium:* Surface feebly roughened,

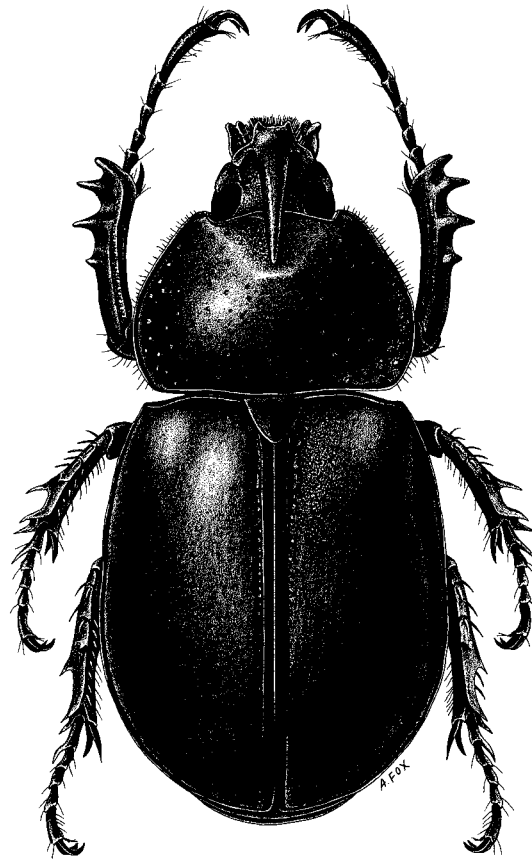
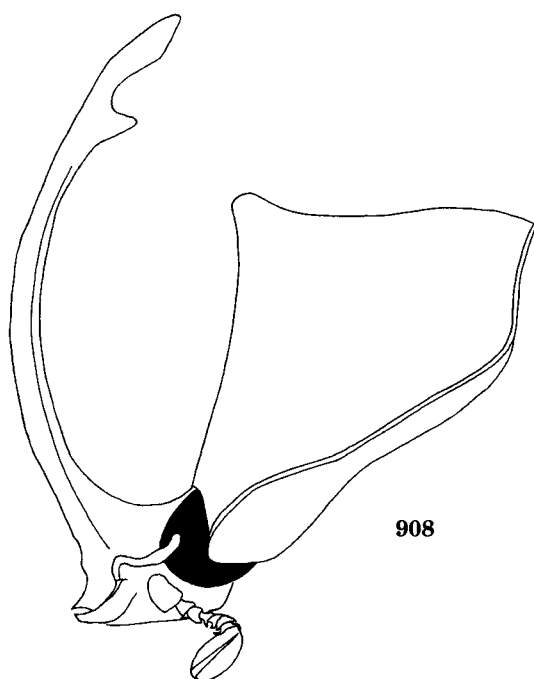


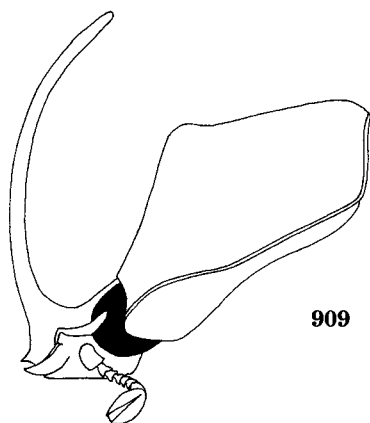
Fig. 907. *Golofa tersander*.

with small, sparse punctures in apical two-thirds; lateral angles weakly rugulose/punctate; setae absent. In lateral view, surface evenly and strongly convex. *Legs:* Foretibia quadridentate, apical 2 teeth slightly closer together. Basal segment of foretarsus a little longer than second tarsomere. Mesotibia at apex with 2 large spines; transverse carina at middle of tibia with 1-2 large teeth. Basal tarsomeres of both meso- and metatarsi with apex extended into long spine. *Venter:* Prosternal process short, subtriangular, with only a few setae. *Parameres:* Figs. 910-911.

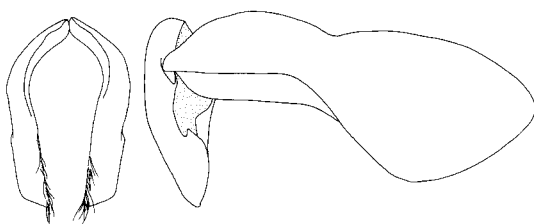
Females. As males except in the following respects. *Head:* Horn absent, instead with prominent median tubercle. Entire dorsal surface coarsely rugopunctate. *Pronotum:* Discal prominence absent. Punctuation similar except punctures denser and larger in anterior half.



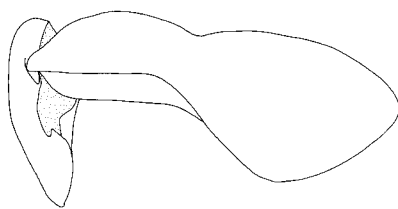
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Figs. 908-911. *Golofa tersander*: (908) male major, head and pronotum; (909) male minor, head and pronotum; (910-911) parameres.

Elytra: Surface less shagreened, crazing evident. *Pygidium*: Surface shining, with punc-



Fig. 912. Distribution of *Golofa tersander* in Costa Rica.

tures moderate in density and moderate in size. In lateral view, surface weakly convex to nearly flat.

DISTRIBUTION. *Golofa tersander* was previously known from Mexico, Guatemala, and Honduras (Endrödi 1977b, 1985a; Lachaume 1985; Morón 1995). The specimens listed below constitute a NEW COUNTRY RECORD for Costa Rica.

LOCALITY RECORDS (Fig. 912). 8 specimens examined.

COSTA RICA (8). **HEREDIA** (5): Estación Biológica La Selva, Standard Fruit Company at Río Frio; **LIMÓN** (3): Hamburg Farm.

TEMPORAL DISTRIBUTION. January (1), March (3), April (1), December (1).

DIAGNOSIS. *Golofa tersander* is easily separated from other species of *Golofa* by its uniformly dark color and by the quadridentate foretibiae in both sexes. The largest male majors (those with paired tubercles on the posterolateral edges of the head horn) were described by Nonfried (1890) as *G. dohrni*; they seem to be relatively uncommon in the population.

BIOLOGY. The larvae live in rotten logs, and the larval stage was described by Morón (1995). Adults are nocturnal and have been collected at lights. They occur in tropical moist forests, tropical wet forests, and premontane wet forests at elevations of 60-1,000 meters. While I have collected this species commonly in southern Mexico, I have seen it only rarely in Costa Rica.

Megasoma Kirby, 1825

Megasoma Kirby 1825: 566.

Megalosoma Burmeister 1841: Tafel 7c (synonym).

Lyphontes Bruch 1910: 73 (synonym).

Megasominus Casey 1915: 261 (synonym).

The genus *Megasoma* consists of 14 species of moderately-sized to very large beetles. Species in the genus are found from the southwestern United States to northern Argentina. Four species are found only in South America, and seven species are found in northern Mexico and the southwestern United States. The remaining three species (*M. actaeon* [L.], *M. occidentalis* Bolívar y Pieltain, Jiménez-Asúa, and Martínez, and *M. elephas* [Fabr.]) occur in southern Mexico and Central and South America. The Mexican *Megasoma occidentalis* was recently elevated to species

status by Morón and Gómez-Anaya (2002), a decision with which I concur.

Adults of *Megasoma* are recognized by their moderate to large size, broadly truncate to emarginate clypeal apex with acute or toothed anterior angles, mandibles with two or three acute teeth, short prosternal process, and tridentate anterior tibia. Males all have a variably developed, bifurcate head horn, and the pronotum is either armed or not.

Hardy (1972) reviewed the North and Central American species, Endrödi (1977b, 1985a) provided a synopsis of all the species, and Lachaume (1985) illustrated (life-size) all the species as part of the Sciences Nat *Beetles of the World* series.

The larva of *M. occidentalis* was described by Morón (1977), and the larvae of *M. elephas* (Fabr.), *M. pachecoi* Cartwright, *M. thersites* LeConte, *M. actaeon* (L.), *M. cedrosa* Hardy, and *M. vogti* Cartwright are being described by Ratcliffe and Morón (in preparation).

Adults of the Central American species are nocturnal and have frequently been collected at lights. Adults have also been observed feeding on mature fruits and probably prefer gnawing through the bark of branches high in the trees to obtain sap (Ratcliffe and Morón 1996). Larvae of the Central American species live and feed in the decaying trunks of large forest trees.

Key to the Species of Adult *Megasoma* in Costa Rica and Panama

1. Body covered with dense golden-brown pubescence. Males with pronotal horns diverging obliquely from longitudinal axis *elephas* (Fabr.)
- 1'. Body glabrous, black. Males with pronotal horns projecting forward, subparallel *actaeon* (L.)

Clave para las Especies de Adultos de *Megasoma* de Costa Rica y Panamá

1. Cuerpo cubierto de pubescencia densa pardo dorada. Machos con cuernos pronotales divirgiendo oblícamente del eje longitudinal *elephas* (Fabr.)
- 1'. Cuerpo glabro, negro. Machos con los cuernos pronotales proyectándose hacia adelante, paralelos *actaeon* (L.)

***Megasoma actaeon* (Linnaeus,
1758)**

(Figs. 913-917)

Scarabaeus actaeon Linnaeus 1758: 345.

Scarabaeus simson Linnaeus 1767: 541 (synonym).

Geotrupes crenatus Leach 1817: 98 (synonym).

Megasoma janus Felsche 1906: 352 (synonym).

Megasoma argentinum Höhne 1923a: 254 (synonym).

DESCRIPTION. Length 55.0-85.0 mm; width 31.0-53.5 mm. Color dull or shiny black. **Males.** *Head:* Frons with horn (Fig. 914) projecting forward and upward, majors with horn a little longer than pronotum, minors with horn half the length of pronotum; horn on dorsal surface near base with large, erect tooth; apex of horn broadly bifurcate. Clypeus broadly, shallowly emarginate, each anterior angle with large, spiniform tooth; surface sparsely to moderately punctate. Interocular width equals 3.5 transverse eye diameters. Antenna with 10 segments, club a little longer than segments 2-7. Mandibles with 3 long, pointed teeth. *Pronotum:* Anterior angles each with stout, short, acuminate horn (Fig. 914) projecting forward, horns parallel to one another. Disc prominently vaulted. Surface near base densely punctate to rugopunctate, remainder of surface with dense micropunctures and moderately dense small punctures. Base completely margined. *Elytra:* Surface finely and densely rugulose to roughened and moderately densely punctate, punctures small and umbilicate. *Pygidium:* Surface with small, dense punctures, punctures usually obscured by dense pile of tawny, moderately long setae. In lateral view, surface strongly convex. *Legs:* Anterior tibia tridentate, basal tooth strongly removed from apical 2 teeth which are close to one another, teeth sharp and nearly at right angles to shaft of tibia. Apex of posterior tibia with 4 teeth, teeth variably reduced. Apex of basal segment of posterior tarsus triangularly produced into strong tooth. *Venter:* Prosternal process short, bluntly triangular. *Parameres:* Figs. 915-916.

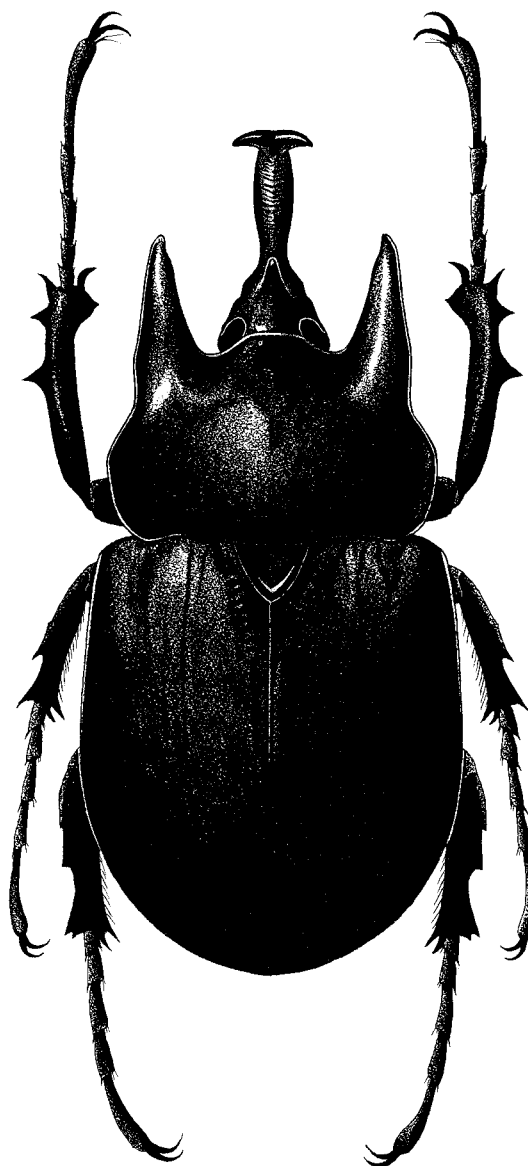


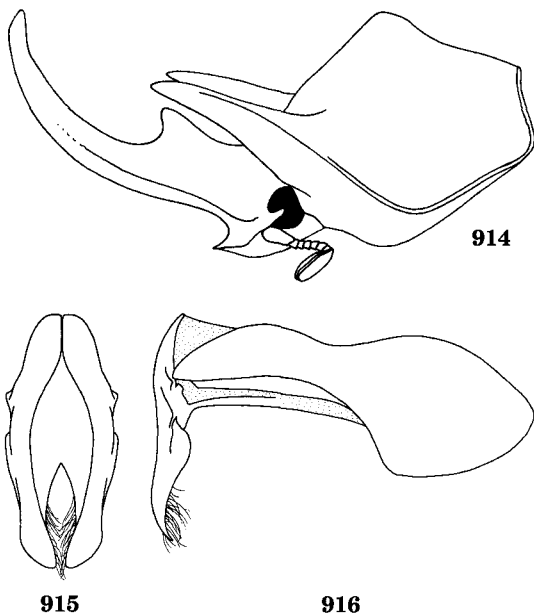
Fig. 913. *Megasoma actaeon*.

Females. As males except in the following respects. *Head:* Horn absent. Surface entirely, densely, coarsely (on frons) to finely (on clypeus) rugopunctate. Frons with median tubercle. Interocular width equals 2.7-3.3 transverse eye diameters. *Pronotum:* Horns absent. Surface coarsely scabrous. Disc rounded but not highly vaulted. *Elytra:* Surface roughened and mostly coarsely rugopunctate. *Pygidium:* In lateral view, basal half strongly convex, apical half

strongly concave. *Legs*: Apex of posterior tibia with 4 teeth, one of middle teeth in form of a large, triangular lobe.

DISTRIBUTION. *Megasoma actaeon* is known from Panama, Guyana, Colombia, Peru, Brazil, and Paraguay. Hardy (1972) was the first to record specimens from Panama (two from Balboa).

LOCALITY RECORDS (Fig. 917). 23 specimens examined.



Figs. 914-916. *Megasoma actaeon*: (914) male major, head and pronotum; (915-916) parameres.

PANAMA (23). **CANAL ZONE** (15): Balboa, Barro Colorado Island, Cardenas, Gatun, Madden Dam, Margarita; **COLÓN** (4): Santa Rita Ridge; **PANAMA** (3): Cerro Azul.

TEMPORAL DISTRIBUTION. January (1), May (7), June (1), October (1), November (1), December (1).

DIAGNOSIS. *Megasoma actaeon* is distinguished by its large body size, black color, absence of dense pubescence dorsally, and pronotal horns directed directly forward in the males. Females might be confused with females of *D. hercules*, but in *D. hercules* the elytra are much more closely roughened and with their apices becoming light olive in color, with a row of prominent setae either side of the suture, a pubescent pronotum, and with a narrowly bidentate clypeal apex.

Endrödi (1977b, 1985a) considered the shiny individuals of southern Brazil and Paraguay as a subspecies, *M. actaeon janus*. Normally, *M. actaeon* is a dull black. I have seen two Panamanian specimens that are also highly lustrous, and Lachaume (1985) noted shiny black specimens in northern South America. This suggests intraspecific variation and not the presence of a geographically separate subspecies, although Lachaume observed that both forms apparently do not occur together.

BIOLOGY. Like the other large Dynastini, the larvae probably develop in rotting logs.



Fig. 917. Distribution of *Megasoma actaeon* in Panama.

Adults are nocturnal and attracted to lights. Radnai (personal communication 1998) compiled the following life history information based upon six years of observations. Eggs were deposited into a suitable log or compost and were approximately 8-10 mm long and 7.5 mm in diameter when laid. After deposit, the eggs increased in size, presumably by absorption of water. Eggs increased in length by 5-7 mm, and the diameter increased by 3.5-5.5 mm. Eclosion took from 25-36 days.

Upon hatching, first instar larvae measured about 8 mm in length and 3-4 mm in diameter. A first instar larva weighed about 0.17 g, and, by contrast, a third instar larva will weigh 90 g. Laboratory development time for all three instars averaged 943 days (893 days minimum, 993 days maximum). The prepupal stage took about 24 days after which pupation occurred. Pupation lasted about 38 days. The pupation chamber is comprised of compacted compost about the size of an adult's fist. Total development time averaged 1,035 days (2.8 years). In captivity, adults lived from 100 to 151 days. Adult flight activity was greatest between 8-10 PM.

In Panama, this species has been taken in tropical moist forests at elevations ranging from near sea level to 300 meters.

***Megasoma elephas* (Fabricius, 1775)**

(Figs. 918-924)

Scarabaeus elephas Fabricius 1775: 7.

Megasoma mexicanum Fischer 1968: 139 (synonym).

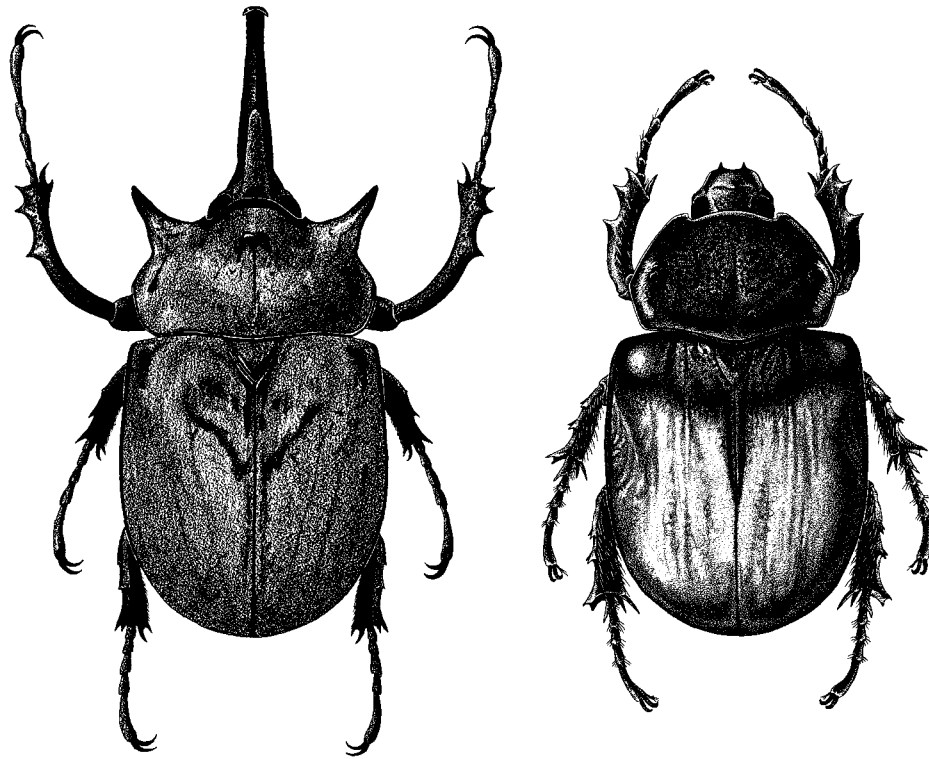
DESCRIPTION. Length 50.0-90.0 mm; width 28.5-52.5 mm. Color black with dense, golden brown pubescence covering elytra and pygidium in both sexes and pronotum and most of head in males.

Males. *Head:* Frons with horn (Fig. 920) projecting forward and curving upward, majors with horn about 1.5 times longer than pronotum, minors with horn a little shorter than pronotum; dorsal surface of horn near base with large, erect, forward-curving tooth; apex of horn broadly bifurcate. Clypeus broadly truncate, each lateral angle with large, forward-projecting tooth, broad space

between teeth slightly concave; surface rugopunctate. Interocular width equals 3.4-3.7 transverse eye diameters. Antenna with 10 segments, club a little longer than segments 2-7. Mandibles with 3 long teeth. *Pronotum:* Anterior angles each with stout, short, acuminate horn (Fig. 920) projecting forward at about 45° from midline. Disc near center with prominent, low boss, apex of boss usually glabrous. Surface obscured by pubescence. Base with complete marginal bead. *Elytra:* Surface usually obscured by pubescence except when abraded away, and then surface finely, densely punctulate. *Pygidium:* Surface usually obscured by pubescence, otherwise finely, densely punctulate. In lateral view, surface strongly convex. *Legs:* Foretibia with 3 teeth laterally, basal tooth strongly removed from other teeth, all teeth short, sharply pointed, almost at right angles to tibia. Apex of posterior tibia in majors with 4 stout teeth; apex in minors usually with 1 large, median, triangular tooth and a smaller tooth on either side or only laterally. Apex of first tarsomere on posterior tarsus triangularly elongated into short tooth in majors, into long spine in minors. *Venter:* Prosternal process short, subtriangular. *Parameres:* Figs. 921-922.

Females. As males except in the following respects. *Head:* Horn absent. Frons tumescent, with single tubercle atop tumescence; surface rugopunctate. Interocular width equals about 3.0 transverse eye diameters. *Pronotum:* Horns absent. Surface coarsely rugose, pubescence nearly absent. *Elytra:* Surface obscured by pubescence except for basal fourth where small, dense punctures and large punctures of striae visible. *Pygidium:* In lateral view, surface in basal half strongly convex, apical half strongly concave. *Legs:* Apex of posterior tibia with 1 large, median, triangular tooth and smaller lateral tooth. Apex of first tarsomere on posterior tarsus triangularly elongated into long spine.

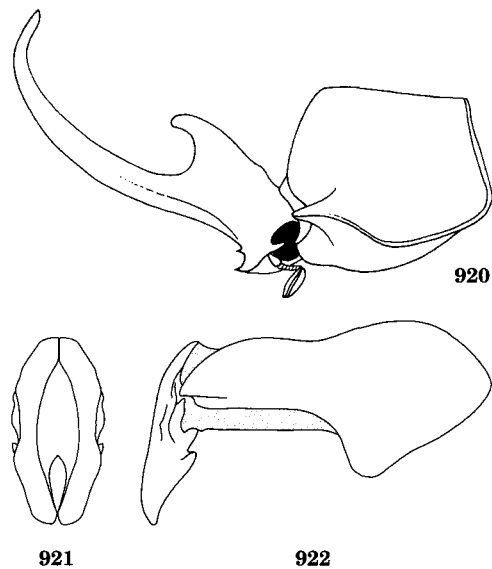
DISTRIBUTION. *Megasoma elephas* is a relatively common lowland species broadly distributed from southern Mexico to Venezuela. In Costa Rica and Panama, it is localized in areas of still-forested areas, primarily in the lowlands.



Figs. 918-919. *Megasoma elephas*, male and female.

LOCALITY RECORDS (Figs. 923-924). 179 specimens examined.

COSTA RICA (111). **ALAJUELA** (15): Caño Negro, Dos Rios (2 km SW), Estación San Ramón, Río Tabacon (Orillas del Volcán Arenal), Rosario (San Ramón), San Carlos (La Fortuna), Upala; **CARTAGO** (13): Slopes of Cerro de la Muerte, Monumento Nacional Guayabo, Peralta (Chitaría), Turrialba; **GUANACASTE** (34): Bagaces, Estación Murcielago, Estación Pitilla, Finca Jenny (30 km N Liberia), Las Juntas (Abangares), Liberia, Playa Naranjo (Parq. Nac. Guanacaste), Sámara, Santa Rosa National Park, Tierras Morenas, Tilarán; **HEREDIA** (11): La Selva Biological Station, Los Arbolitos, Río Frio (Sarapiquí); **LIMÓN** (31): Batán, Bratsi, Cahuita, Estación Cuatro Esquinas (Parq. Nac. Tortuguero), Guapiles, Reserva Hitoy Cerere, Pandora, Siguirres, Valle la Estrella (Pandora); **PUNTARENAS** (6): Agua Buena (Coto Brus), Barranca, El Chuzazo (Reserva Biológica Carara), Estación Quebrada Bonita (Reserva Biológica Carara), Estación Sirena (Parq. Nac. Corcovado), Golfito, Miramar, Parrita, Quepos,



Figs. 920-922. *Megasoma elephas*: (920) male major, head and pronotum; (921-922) parameres.

Punta Leona, Rancho Quemado; **SAN JOSÉ** (1): San Ramón.

PANAMA (68). **BOCAS DEL TORO** (3): Miramar; **CANAL ZONE** (41): Barro Colorado

Island, Coco Solo Hospital, Diablo Heights, Ft. Gulick, Madden Dam, Margarita, Miraflores Locks; CHIRIQUI (11): Cerro Punta, David, Hartmann's Finca (Santa Clara), Los Planos de Hornito, Río Sereno; PANAMA (13): Cerro Azul, Chilibre, Ipeti, Isla de Majé.

TEMPORAL DISTRIBUTION. January (3), February (4), March (11), April (21), May (52), June (22), July (21), August (11), September (4), October (16), November (13), December (4).

DIAGNOSIS. The dense, golden brown pubescence covering these beetles, in combination with their large size, characteristic horn configuration in the males, and broadly truncate and

toothed clypeal apex, will serve to easily recognize *M. elephas*. Females that have their dorsal pubescence abraded away might be confused with *D. hercules*, but the elytra in the latter are very roughened and olive green at the apices.

BIOLOGY. Morón (2001) described the life cycle. He observed (based on two specimens) a developmental time of 54-58 days for the first instar, 130-138 days for the second instar, 413-751 days for the third instar, and 38-44 days for the pupal stage. Under laboratory conditions, one female completed development in two years, and a male completed development in three years. Each larva consumed nearly 1,500 grams of an organic mixture of forest soil, soft rotten wood, and dry cow dung in equal parts. The maximum weight of each of the third instar larvae was 56 grams and 86 grams. Like other large dynastines, they live in the decaying wood of old, possibly standing, trees.

Megasoma elephas has been collected from transitional tropical dry-tropical moist forests, tropical moist forests, tropical wet forests, and premontane moist forests between the elevations of sea level to about 700 meters; I have seen two Costa Rican (Cartago and Guanacaste) and half a dozen Panamanian (Chiriqui) specimens taken above 1,000 meters. The temporal data suggests increased adult activity coinciding with the onset of the rainy season in May. By contrast, this species is most abundant between September and January in Mexico (Ratcliffe and Morón 1996). Adults are nocturnal and attracted to lights.



Fig. 923. Distribution of *Megasoma elephas* in Costa Rica.



Fig. 924. Distribution of *Megasoma elephas* in Panama.

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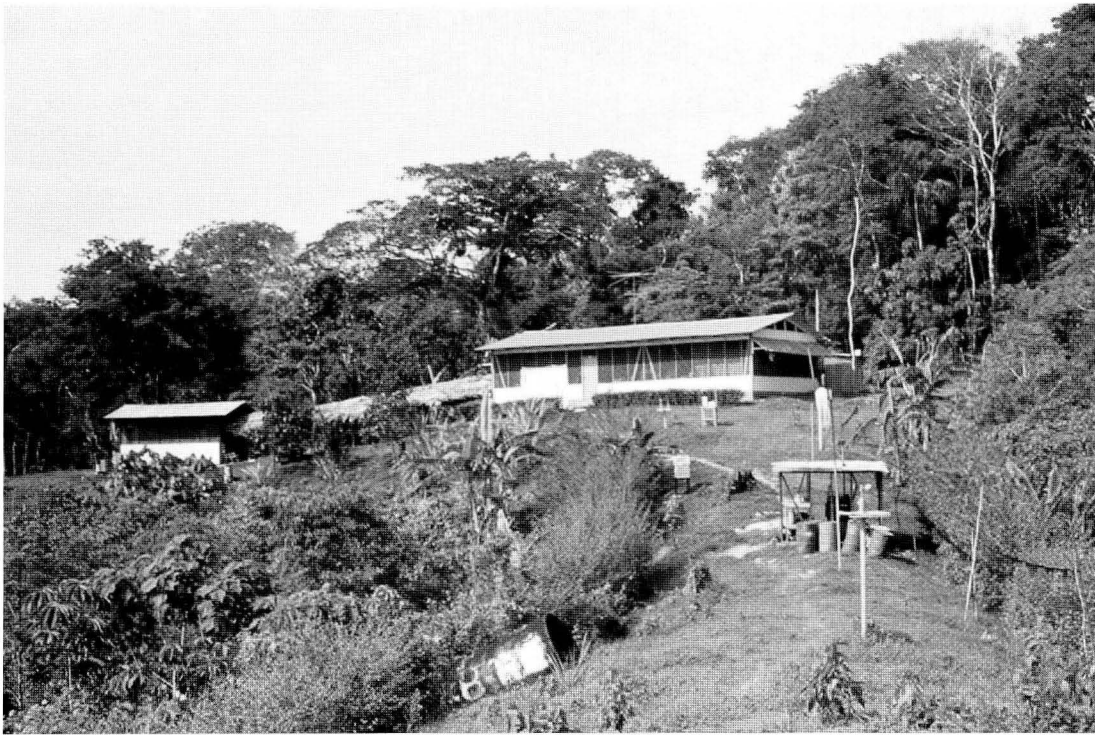


Fig. 925. Isla Majé research station (run by Gorgas Memorial Laboratory) in Lake Bayano, Panama in May 1976. The station was sacked and destroyed in 1989, and only a concrete foundation now remains. Photo by BCR.

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LITERATURE CITED

- Angehr, G. R. 1989. Parting the Green Curtain: the Evolution of Tropical Biology in Panama. Smithsonian Tropical Research Institute, Balboa, Panama. 44 pp.
- Anonymous. 1980. *Research Priorities in Tropical Biology*. National Academy of Sciences Press, Washington, D.C. 116 pp.
- Anonymous. 1995. Taxonomic experts, systematic monographs. Report of a panel-workshop on practices and directions in monographic research, 29-30 November 1994. Systematic Biology Program, National Science Foundation, 16 pp.
- Anonymous. 1996. Costa Rica's biological riches: consolidating the national biodiversity. *Simbiosis* (INBio Newsletter) May-August 1996: 7.
- Apolinar, M. H. 1927. Nuevos heliconios colombianos. *Boletín de la Sociedad Colombiana de Ciencias Naturales* 16: 117-120.
- Arnett, R. H., Jr. 1968. *The Beetles of the United States*. American Entomological Institute, Ann Arbor. 1,112 pp.
- Arrow, G. J. 1902. Notes and descriptions of some Dynastidae from tropical America, chiefly supplementary to the 'Biologia Centrali-Americana.' *Annals and Magazine of Natural History* (series 7) 10: 137-147.
- Arrow, G. J. 1911. Notes on the coleopterous subfamily Dynastinae, with descriptions of new genera and species. *Annals and Magazine of Natural History* (series 8) 8: 151-176.
- Arrow, G. J. 1913. Some new species of lamellicorn beetles from Brazil. *Annals and Magazine of Natural History* (series 8) 11: 456-466.
- Arrow, G. J. 1914. Some further notes on lamellicorn beetles of the subfamily Dynastinae. *Annals and Magazine of Natural History* (series 8) 14: 257-276, 360.
- Arrow, G. J. 1925. *The Fauna of British India, Including Ceylon and Burma. Coleoptera Lamellicornia (Cetoniinae and Dynastinae)*. Taylor and Francis, London. 322 pp., 2 plates.
- Arrow, G. J. 1937a. *Coleopterorum Catalogus, pars 156. Scarabaeidae: Dynastinae*. W. Junk, Berlin. 124 pp.
- Arrow, G. J. 1937b. Systematic notes on beetles of the subfamily Dynastinae, with descriptions of a few new species in the British Museum collection (Coleoptera). *Transactions of the Entomological Society of London* 86: 35-58.
- Arrow, G. 1951. *Horned Beetles*. Dr. W. Junk, The Hague. 154 pp.
- Baerg, W. J. 1940. The rough-headed corn-stalk beetle. *Arkansas Agricultural Experiment Station Bulletin* No. 415: 1-22.
- Bartlett, A. S. and E. Barghoorn. 1973. Phytogeographic history of the Isthmus of Panama during the past 12,000 years (a history of vegetation, climate, and sea-level change), pp. 203-300. *In*, Graham, A. (editor), *Vegetation and Vegetational History of Northern Latin America*. Elsevier, Amsterdam.
- Bates, H. W. 1888. Pectinicornia and Lamellicornia, Family Dynastidae. *In*, Godman, F. D. and O. Salvin (eds.), *Biologia Centrali-Americana. Insecta, Coleoptera*, vol. 2, pt. 2: 296-342.
- Bates, H. W. 1891. Coleoptera, pp. 7-39. *In*, Whymper, E., *Supplementary Appendix to Travels Amongst the Great Andes of the Equator*. John Murray, London. 147 pp.
- Beach, J. H. 1982. Beetle pollination of *Cyclanthus bipartitus* (Cyclanthaceae). *American Journal of Botany* 69: 1074-1081.
- Beach, J. H. 1984. The reproductive biology of the peach or "pejibaye" palm (*Bactris gasipaes*) and a wild congener (*B. por-schiana*) in the Atlantic lowlands of Costa Rica. *Principes* 28: 107-119.
- Beck, P. 1942a. Description d'une variété nouvelle de *Pucaya castanea* (Col. Dynastidae). *Bulletin de la Société Entomologique de France* 47: 47-48.
- Beck, P. 1942b. Contribution a l'étude de la faune de Costa-Rica. Coléoptères lamellicornes Dynastinae. *Bulletin Société d'Histoire Naturelle de Toulouse* 77: 29-32.

- Beebe, W. 1944. The function of secondary sexual characters in two species of Dynastidae (Coleoptera). *Zoologica* 29: 53-58.
- Beebe, W. 1947. Notes on the hercules beetle, *Dynastes hercules* (Linn.), at Rancho Grande, Venezuela, with special reference to combat behavior. *Zoologica* 32: 109-116.
- Bennett, C. F. 1968. Human influences on the zoogeography of Panama. *Ibero-Americáná* 51: 1-112, 8 maps.
- Berry, P. A. and M. S. Vaquero. 1957. Lista de insectos clasificados de El Salvador. Ministerio de Agricultura y Ganaderia, Boletín Técnico No. 21: 1-134.
- Blackmore, S. 1996. Knowing the earth's biodiversity: challenges for the infrastructure of systematic biology. *Science* 274: 63-64.
- Blackwelder, R. E. 1944. Checklist of the coleopterous insects of Mexico, Central America, the West Indies, and South America, part 2. *Bulletin of the U. S. National Museum* 185: 189-341.
- Blackwelder, R. E. and R. H. Arnett, Jr. 1974. Checklist of the beetles of Canada, United States, Mexico, Central America and the West Indies. Volume 7, Part 2. The scarab beetles, ant-loving beetles, clown beetles, and related groups. Fascicles numbered separately. Biological Research Institute of America, Inc., Latham, NY.
- Blanchard, E. 1846. Tribu des lamellicornes, pp. 155-194. In, Brullé, G. A., *Voyage dans l'Amérique Méridionale (le Brésil, la République Orientale de l'Uruguay, la République Argentine, la Patagonie, la République du Chili, la République de Bolivie, la République du Pérou), Exécuté Pendant les Années 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833, par Alcide d'Orbigny*. Tome sixième. 2.e partie: Insectes. Paris.
- Bodkin, G. E. 1919. Notes on the Coleoptera of British Guiana. *Entomologists Monthly Magazine* 55: 210-219.
- Bolivar y Pieltaín, C., L. Jiménez-Asúa, and A. Martínez. 1963. Notas sobre Dynastinae neotropicales con especial referencia a especies Mexicanas. *Ciencia* 22: 181-190.
- Bourgin, P. 1944. Revision des genres *Coelosia* Hope et voisins. *Revue Française d'Entomologie* 11: 118-146.
- Bradbury, J. P. 1982. Holocene chronostratigraphy of Mexico and Central America, pp. 40-45. In, Mangerud, J., H. J. B. Birks, and K. D. Jager (editors), *Chronostratigraphic subdivision of the Holocene. Striae 16* (Uppsala).
- Bréthes, J. 1904. Insectos de Tucumán. *Anales del Museo Nacional de Buenos Aires, (series 3) 4*: 329-347.
- Browne, J. and C. H. Scholtz. 1995. Phylogeny of the families of Scarabaeoidea (Coleoptera) based on characters of the hindwing articulation, hindwing base, and wing venation. *Systematic Entomology* 20: 145-173.
- Bruch, C. 1910. Descripción de dos nuevos lamellicornios de la fauna Argentina. *Revista del Museo de La Plata* 17: 71-77.
- Bruch, C. 1917. Nuevas capturas de insectes mirmecofilos. *Physis (Buenos Aires)* 3: 458-465.
- Bullock, S. H. 1981. Notes on the phenology of inflorescences and pollination of some rain forest palms in Costa Rica. *Principes* 25: 101-105.
- Burmeister, H. 1841. Genera quaedam insectorum iconibus illustravit et descripsit H. Burmeister. Band 1, Heft 7. Berlin.
- Burmeister, H. 1847. *Handbuch der Entomologie*, Vol. 5. T. C. F. Enslin, Berlin. 584 pp.
- Campbell, J. A. and W. W. Lamar. 1989. *The Venomous Reptiles of Latin America*. Comstock Publishing Associates, Ithaca, NY. 425 pp.
- Carne, P. B. 1957. Systematic revision of the Australian Dynastinae. Division of Entomology, Commonwealth Scientific and Industrial Research Organization, Melbourne, Australia. 284 pp.
- Carr, A. F., Jr. 1950. Outline for a classification of animal habitats in Honduras. *Bulletin of the American Museum of Natural History* 94: 563-594.
- Carrillo, J. L., A. Ortega, and W. W. Gibson. 1966. Lista de insectos en la colección entomológica del Instituto Nacional de Investigaciones Agrícolas. Instituto Nacional de Investigaciones Agrícolas (Mexico), Folleto Misceláneo No. 14: 1-133.

- Cartwright, O. L. 1959. Scarab beetles of the genus *Bothynus* in the United States. Proceedings of the U. S. National Museum 108: 515-541.
- Casey, T. L. 1915. A review of the American species of Rutelinae, Dynastinae, and Cetoniinae. Memoirs of the Coleoptera 6: 1-394.
- Chalumeau, F. 1977. Contribution à l'étude des Scarabaeoidea des Antilles (corrigenda et addenda aux Scarabaeoidea des Antilles Françaises). Bulletin Mensuel de la Société Linnéenne de Lyon 46: 231-240.
- Chalumeau, F. 1981. Expéditions biospéologiques cubano-roumains à Cuba (1969 et 1973). Scarabaeoidea (Coleoptera) récoltés par V. Decu. Résultats des Expéditions Biospéologiques Cubano-Roumains à Cuba 3: 173-180.
- Chalumeau, F. 1983. *Les Coléoptères Scarabaeides des Petites Antilles (Guadeloupe à Martinique)*. Editions Lechevalier, Paris. 295 pp.
- Chalumeau, F. 1988. Phileurini américains: nouvelle espèce, notes et synonymie (Coleoptera, Scarabaeidae). Nouvelle Revue d'Entomologie (N.S.) 5: 397-400.
- Chalumeau, F. and L. Gruner. 1977. Scarabaeoidea des Antilles Françaises (Col.). 3e partie: Dynastinae et Cetoniinae. Annales de la Société Entomologique de France (N.S.) 13: 579-612.
- Chapin, E. A. 1932. Revision of the pleurostict Scarabaeidae of Cuba and Isle of Pines. II. Rutelinae, Dynastinae, and Cetoniinae. Annals of the Entomological Society of America 25: 282-314.
- Chevrolat, A. 1830. *Cyclocephala frontalis* Chevrolat, plate 23. In, Guérin-Méneville, F. E., *Iconographie du Règne Animal de G. Cuvier ou Représentation d'après Nature de l'une des Espèces les plus Remarquables et Souvent non Encore Figurees, de Chaque Genre d'Animaux*. Volume 2, Planches des Animaux Invertébrés. J. B. Baillière, Paris.
- Chevrolat, L. A. A. 1843. Coléoptères du Mexique (226) pentamères, hydrocanthares, sternoxes, térédiles, nécrophages, lamellicornes). Magasin de Zoologie 1843, 37 pp., plates 107-113.
- Cockerell, T. D. A. 1906. *Strategus* injuring date-palms. Entomological News 17: 34.
- Condit, R., N. Pitman, E. G. Leigh, Jr., J. Chave, J. Terborgh, R. B. Foster, P. Nunez V., S. Aguilar, R. Valencia, G. Villa, H. C. Muller-Landau, E. Losos, and S. B. Hubbell. 2002. Beta-diversity in tropical forest trees. Science 295: 666-669.
- Costa, C., S. A. Vanin, and S. A. Casari-Chen. 1988. *Larvas de Coleoptera do Brasil*. Museu de Zoologia, Universidade de São Paulo, São Paulo. 282 pp., 165 plates.
- Costa Lima, A. D. 1953. Insectos do Brasil, Vol. 8. Coleópteros, 2a parte. Escola Nacional de Agronomia, Série Didática 10: 1-223.
- Cronin, T. M. 1981. Rates and possible causes of neotectonic vertical crustal movements of the emerged southeastern United States Atlantic Coastal Plane. Bulletin of the Geological Society of America 92: 812-833.
- Davidson, R. H. and W. F. Lyon. 1987. *Insect Pests of Farm, Garden, and Orchard*. John Wiley & Sons, NY. 640 pp.
- Dechambre, R.-P. 1974. Les dynastides et leurs especes françaises. L'Entomologist 30: 47-57.
- Dechambre, R.-P. 1975. Note sur diverse *Megaceras* et *Golofa* (Col. Dynastidae). Annales de la Société Entomologique de France (N.S.) 11: 619-630.
- Dechambre, R.-P. 1976. Un nouveau genre et deux nouvelles espèces de Dynastidae (Col. Scarabaeoidea). Nouvelle Review d'Entomologie 6: 129-132.
- Dechambre, R.-P. 1979a. Une nouvelle espèce de *Cyclocephala* (Coleoptera Dynastidae). Nouvelle Review d'Entomologie 9: 317-318.
- Dechambre, R.-P. 1979b. Cinq espèces nouvelles de *Stenocrates* (Col. Scarabaeoidea Dynastidae). Revue Française d'Entomologie (N.S.) 1: 61-64.
- Dechambre, R.-P. 1980. Le genre *Dynastes* (Coleoptera Scarabaeoidea Dynastidae). Bulletin Sciences Nat No. 27: 5-10.
- Dechambre, R.-P. 1981. Nouvelles espèces de Dynastidae de la Région Néotropicale (Coleoptera Scarabaeoidea). Revue Française d'Entomologie (N.S.) 3: 123-128.

- Dechambre, R.-P. 1985. Quatre nouvelles espèces de *Stenocrates* (Coleoptera, Dynastidae). *Revue Française d'Entomologie (N.S.)* 7: 142-144.
- Dechambre, R.-P. 1986a. *Heterogomphus carayoni*, une nouvelle espèce de coléoptère Dynastidae. *Annales de la Société Entomologique de France (N.S.)* 22: 306-307.
- Dechambre, R.-P. 1986b. Insectes coléoptères Dynastidae. *Fauna de Madagascar* 65: 1-215.
- Dechambre, R.-P. 1992a. Nouveaux Cyclocephalini des genres *Cyclocephala* et *Aspidolea* (Col. Dynastidae), pp. 57-76. In, Lachaume, G., *Les Coleopteres du Monde 14: Dynastidae Américains*. Sciences Nat, Venette, France. 87 pp., 13 plates.
- Dechambre, R.-P. 1992b. Nouveaux Dynastidae de la tribu Agaoccephalini, pp. 77-81, plate 13. In, Lachaume, G., *Les Coleopteres du Monde 14: Dynastidae Américains*. Sciences Nat, Venette, France. 87 pp., 13 plates.
- Dechambre, R.-P. 1994. Une nouvelle espèce de *Spodistes* Burmeister (Coleoptera, Dynastidae). *Revue Française d'Entomologie* 16: 149-151.
- Dechambre, R.-P. 1995. Trois nouvelles espèces de *Cyclocephala* (Coleoptera, Dynastidae). *Sciences Nat Bulletin No. 83*: 12-13.
- Dechambre, R.-P. 1996. Le genre *Palaeophileurus* Kolbe, 1910 (Coleoptera, Dynastidae). *Revue Française d'Entomologie (N.S.)* 18: 129-133.
- Dechambre, R.-P. 1997a. Révision des *Cyclocephala* du groupe *cribrata* Burmeister (Coleoptera, Dynastidae). *Coléoptères* 3: 13-27.
- Dechambre, R.-P. 1997b. Compléments aux descriptions des espèces du genre *Palaeophileurus* Kolbe, 1910 (Coleoptera, Dynastidae). *Revue Française d'Entomologie (N.S.)* 19: 32.
- Dechambre, R.-P. 1999a. Vingt nouvelles espèces et une nouvelle sous-espèce de *Cyclocephala* Burmeister, 1847. *Les Coleopteres du Monde 14, Supplement 1*: 1-24.
- Dechambre, R.-P. 1999b. Une nouvelle espèce d'*Aegopsis* Burmeister, 1847 (Coleoptera, Dynastidae). *Revue Française d'Entomologie (N.S.)* 21: 173-174.
- Dechambre, R.-P. 2000. Dix nouvelles espèces d'*Hemiphileurus* Kolbe, 1910 (Coleoptera, Dynastidae). *Coléoptères* 6: 21-32.
- Dechambre, R.-P. and J.-P. Lumaret. 1985. Un *Ligyris* nouveau (Coleoptera, Dynastidae). Description de l'imago, de la larve et indications éthologiques. *Revue Française d'Entomologie (N.S.)* 7: 107-110.
- Degeer, C. 1774. *Memoirs pour Servir à l'Histoire des Insectes*, Vol. 4. Stockholm. 456 pp.
- Dejean, P. F. M. A. 1821. *Catalogue de la Collection de Coléoptères de M. le Baron Dejean*. Paris, 136 pp.
- Dejean, P. F. M. A. 1836. *Catalogue des Coléoptères de la Collection de M. le Comte Dejean. Troisième Edition, Revue, Corrigée et Augmentée*, pp. 1-384. Méquignon-Marvis, Paris.
- Delgado, L. and M. Najera-Rincon. 1992. Especie y registros nuevos de *Xyloryctes* de Mexico (Coleoptera: Melolonthidae; Dynastinae). *Anales de Instituto de Biologia de Universidad Autónoma de Mexico (Series Zoologia)* 63: 215-220.
- Delgado, L., A. Perez, and J. Blackaller. 2000. Claves para determinar a los taxones genericos y supragenericos de Scarabaeoidea Latreille, 1802 (Coleoptera) de Mexico. *Folia Entomologica Mexicana* 110: 33-87.
- Deloya, C. 1988. Coleopteros lamellicornios asociados a depositos de detritos de *Atta mexicana* (Smith) (Hymenoptera: Formicidae) en el sur del estado de Morelos, Mexico. *Folia Entomologica Mexicana* 75: 77-91.
- Deloya, C. 1992. Lista de las especies de Coleoptera lamellicornia del estado de Veracruz, Mexico (Passalidae, Trogidae, Lucanidae, Scarabaeidae y Melolonthidae). *Boletín de Sociedad Veracruzana de Zoología* 2: 19-32.
- Donnelly, T. W. 1992. Geological setting and tectonic history of Mesoamerica, pp. 1-13. In, Quintero, D. and A. Aiello (editors), *Insects of Panama and Mesoamerica*. Oxford University Press, Oxford, United Kingdom. 692 pp.
- Duellman, W. E. 1966. The Central American herpetofauna: an ecological perspective. *Copeia* 1966: 700-719.

- Dugès, D. E. 1876. Metamórfosis de un coleoptero de la familia de los lamellicórneos y del genero *Strategus*. *Naturaleza* (Museu Nacional de Historia Natural, Mexico) 3: 49-52.
- Dugès, D. E. 1886. Métamorphoses de quelques coléoptères mexicains. *Annales de la Société Entomologique de Belgique* 30: 27-45.
- Dupuis, F. 1996. Description d'une nouvelle espèce de *Cyclocephala* Latreille, 1829, et mise au point sur les espèces du groupe *melanocephala* (Coleoptera, Dynastidae). *Bulletin de la Société Entomologique de France* 101: 257-260.
- Dupuis, F. and R.-P. Dechambre. 1995. Mise au point sur les *Stenocrates* du groupe *cultor* (Coleoptera, Dynastidae). *Revue Française d'Entomologie (N.S.)* 17: 59-61.
- Dupuis, F. and R.-P. Dechambre. 2000. Dix nouvelles espèces d'*Hemiphileurus* Kolbe, 1910 (Coleoptera: Dynastidae). *Coléoptères* 6: 21-32.
- Eberhard, W. G. 1978. Fighting behavior of male *Golofa porteri* beetles (Scarabaeidae: Dynastinae). *Psyche* 83: 292-298.
- Eberhard, W. G. 1979. The function of horns in *Podischnus agenor* (Dynastinae) and other beetles, pp. 231-258. In, M. S. and N. A. Blum (eds.), *Sexual Selection and Reproductive Competition in Insects*. Academic Press, NY. 463 pp.
- Eberhard, W. G. 1980. Horned beetles. *Scientific American* 242: 166-182.
- Eberhard, W. G. 1982. Beetle horn dimorphism: making the best of a bad lot. *American Naturalist* 119: 420-426.
- Ehrlich, P. R. 1992. Population biology of checkerspot butterflies and the preservation of global biodiversity. *Oikos* 63: 6-12.
- Eidmann, H. 1937. Die Gäste und Gastverhältnisse der Blattschneiderameise *Atta sexdens* L. *Zeitschrift für Morphologie und Ökologie der Tiere* 32: 391-462.
- Emlen, D. J. 1994. Environmental control of horn length dimorphism in the beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Proceedings of the Royal Society of London B, Biological Sciences* 256: 131-136.
- Emlen, D. J. 1997a. Alternative reproductive tactics and male-dimorphism in *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Behavioral Ecology and Sociobiology* 41: 335-341.
- Emlen, D. J. 1997b. Diet alters male horn allometry in the dung beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Proceedings of the Royal Society of London B, Biological Sciences* 264: 567-574.
- Emlen, D. J. 2000. Integrating development with evolution: a case study with beetle horns. *BioScience* 50: 403-418.
- Emlen, D. J. 2001. Costs and the diversification of exaggerated animal structures. *Science* 291: 1534-1536.
- Endrödi, S. 1947. Über die Gattung *Dynastes* Kirby. *Folia Entomologica Hungarica* 2: 54-59.
- Endrödi, S. 1963. Neue *Cyclocephala*-Arten. *Annales Historico-Naturales Musei Nationalis Hungarici (pars Zoologica)* 55: 323-333.
- Endrödi, S. 1964. Eine Reihe von neuen *Cyclocephala*-Arten (Col., Melolonthidae, Dynastinae). *Folia Entomologica Hungarica (N.S.)* 17: 433-470.
- Endrödi, S. 1966. Monographie der Dynastinae (Coleoptera, Lamellicornia). I. Teil. *Entomologische Abhandlungen* 33: 1-460.
- Endrödi, S. 1967. Ergänzungen zu meiner Monographie der Dynastinae: Cyclocephalini (Coleoptera). *Acta Zoologica Academiae Scientiarum Hungaricae* 13: 83-91.
- Endrödi, S. 1968. Neue Arten der Pentodontini (Col. Dynastinae). *Folia Entomologica Hungarica* 21: 161-177.
- Endrödi, S. 1969. Monographie der Dynastinae 4. Tribus: Pentodontini (Coleoptera, Lamellicornia). *Entomologische Abhandlungen* 87: 1-145.
- Endrödi, S. 1970. Monographie der Dynastinae (Coleoptera). 3. Tribus: Agaocephalini. *Acta Zoologica Academiae Scientiarum Hungaricae* 16: 27-96.
- Endrödi, S. 1971. Über neue und bekannte Dynastinen (Col., Melolonthidae). *Folia Entomologica Hungarica (N.S.)* 24: 179-183.
- Endrödi, S. 1974. *Gibboryctes szelenyii* gen. sp. nov. (Coleoptera: Melolonthidae, Dynastinae). *Folia Entomologica Hungarica (series nova)* 27: 13-16.
- Endrödi, S. 1976a. Monographie der Dynastinae (Coleoptera) 6. Tribus: Dynastini. *Acta Zoologica Academiae Scientiarum Hungaricae* 22: 217-269.

- Endrödi, S. 1976b. Monographie der Dynastinae 5. Tribus: Oryctini (die Arten von Amerika) (Coleoptera: Melolonthidae). *Folia Entomologica Hungarica* (series nova) 29: 9-174.
- Endrödi, S. 1977a. *Strategus waldenfelsi*, sp.n. (Coleoptera, Dynastinae). *Reichenbachia* 16: 335-336.
- Endrödi, S. 1977b. Monographie der Dynastinae (Coleoptera) 6. Tribus Dynastini. II. *Acta Zoologica Academiae Scientiarum Hungaricae* 23: 37-86.
- Endrödi, S. 1977c. Monographie der Dynastinae 8. Tribus: Phileurini, amerikanische Arten I. (Coleoptera). *Folia Entomologica Hungarica* 30: 7-45.
- Endrödi, S. 1978. Monographie der Dynastinae 8. Tribus: Phileurini, amerikanische Arten II. (Coleoptera). *Folia Entomologica Hungarica* 31: 85-164.
- Endrödi, S. 1979. Neue Arten des Dynastinen Tribus Cyclocephalini (Coleoptera, Melolonthidae) aus Amerika. *Annales Historico-Naturales Musei Nationalis Hungarici (pars Zoologica)* 71: 215-218.
- Endrödi, S. 1980. Sechs neue Dynastinen-Arten aus Amerika und Borneo (Coleoptera: Dynastinae). *Folia Entomologica Hungarica* 41: 37-42.
- Endrödi, S. 1981. Neue und seltene Dynastinen aus Südamerika und eine synonymische Bemerkung (Coleoptera, Melolonthidae). *Annales Historico-Naturales Musei Nationalis Hungarici* 73: 197-202.
- Endrödi, S. 1985a. *The Dynastinae of the World*. Dr. W. Junk Publ., Dordrecht. 800 pp., 46 plates.
- Endrödi, S. 1985b. Einige neue südamerikanische Dynastinae. *Entomologische Blätter* 81: 69-74.
- Erichson, W. F. 1847. *Conspectus insectorum coleopterorum quae in Republica Peruana observata sunt*. *Archiv für Naturgeschichte* 13: 67-185.
- Erichson, W. F. 1848. Die Insekten, pp. 533-617. In, Schomburg, M. R., *Reisen in Britisch Guiana*, Vol. 3. Leipzig.
- Fabricius, J. C. 1775. *Systema Entomologiae*. Leipzig. 832 pp.
- Fabricius, J. C. 1781. *Species Insectorum*, Vol. 1. Kiel. 552 pp.
- Fabricius, J. C. 1787. *Mantissa Insectorum*, Vol. 1. Copenhagen. 348 pp.
- Fabricius, J. C. 1792. *Entomologia Systematica*, Vol. 1, Part 2. Copenhagen. 538 pp.
- Fabricius, J. C. 1798. *Supplementum Entomologiae Systematicae*. Copenhagen. 572 pp.
- Fabricius, J. C. 1801. *Systema Eleutheratorum*, Vol. 1. Kiel. 506 pp.
- Fairchild, G. B. 1966. Introduction, pp. 1-8. In, Wenzel, R. L. and V. J. Tipton (editors), *Ectoparasites of Panama*. Field Museum of Natural History, Chicago, IL.
- Fairmaire, L. 1878. Description de coléoptères nouveaux d'Amérique. *Revue et Magasin de Zoologie Pure et Appliquée (series 3)* 6: 260-270.
- Felsche, C. 1906. Synonymische Bemerkungen über einige Scarabaeiden aus der Tribus der Dynastini und Beschreibung einer neuen Art. *Deutsche Entomologische Zeitschrift* 1906: 349-352.
- Ferreira, M. C. 1965. Contribuição para o estudo dos dinastineos africanos. *Revista de Entomologica de Moçambique* 8: 2-348.
- Fischer, H. 1968. Zwei neue *Megasoma*-Arten aus Amerika. *Bericht der Naturforschenden Gesellschaft Augsburg* 22: 137-142.
- Fischer von Waldheim, G. 1823. *Coleoptera quaedam exotica descripta*. *Mémoires de la Société Impériale des Naturalistes de Moscou* 6: 254-267.
- Fox, R. W. and J. W. Huguet. 1977. *Population and Urban Trends in Central America and Panama*. Interamerican Development Bank, Washington, D. C. 224 pp.
- García, A. A., M. A. Morón, A. M. Tapia-Rojas, and R. Rojas-García. 1998. Las especies de Coleoptera Melolonthidae relacionadas con plantas cultivadas en el estado de Puebla, Mexico, p. 131-142. In, Morón, M. A. and A. Aragón (editors), *Avances en el Estudio de la Diversidad, Importancia y Manejo de las Coleópteros Edafícolas Americanos*. Publicación Especial de la Benemérita Universidad Autónoma de Puebla y la Sociedad Mexicana de Entomología A. C. Puebla, Mexico.
- García-Luna, D., M. A. Morón, and C. V. Rojas-Gomez. 2002. Variación en los patrones de pigmentación en tres especies de *Cyclocephala* Burm. (Coleoptera: Melolonthidae: Dynastinae). *Folia Entomologica Mexicana* 41: 129-148.

- Gaugliumi, P. 1962. Las plagas de la caña de azúcar en Venezuela. Centro de Investigaciones Agronomicas (Maracay), Monographia No. 2, Tomo 1: 1-482.
- Golley, F. B., J. T. McGinnis, R. C. Clements, G. I. Child, and M. J. Duever. 1969. The structure of tropical forests in Panama and Colombia. *Bioscience* 19: 693-696.
- Goncalves, C. R. 1946. Males de carnaúba no Ceará e no Piauí. *Boletim Fitossanitário* 3: 145-170.
- Goodland, R. 1969. Introduction to the principal vegetation types of Costa Rica, p. 1-5, plates 1-5 of chapter 21-2. In, Schnell, C. E. (editor), 1971, *The Book. Data, Keys, Tables, Figures, and Miscellanea*. Organization of Tropical Studies, Duke University.
- Gose, W. A., G. R. Scott, and D. K. Swartz. 1980. The aggregation of Mesoamerica: paleomagnetic evidence, pp. 51-54. In, Pilger, R. H., Jr. (editor), *The Origin of the Gulf of Mexico and the Early Opening of the Central North Atlantic Ocean*. Symposium Proceedings, Louisiana State University and Louisiana Geological Survey, Baton Rouge.
- Gottsberger, G. 1989. Beetle pollination and flowering rhythm of *Annona* spp. (Annonaceae) in Brazil. *Plant Systematics and Evolution* 167: 165-187.
- Gottsberger, G. and A. Amaral, Jr. 1984. Pollination strategies in Brazilian *Philodendron*. *Berichte der Deutschen Botanischen Gesellschaft* 97: 391-410.
- Gottsberger, G. and I. Silberbauer-Gottsberger. 1991. Olfactory and visual attraction of *Erioscelis emarginata* (Cyclocephalini, Dynastini) to the inflorescences of *Philodendron selloum* (Araceae). *Biotropica* 23: 23-28.
- Grossi, E. J. and P. Arnaud. 1993. Description d'une nouvelle sous-espece de *Dynastes hercules*. *Bulletin Sciences Nat* 78: 13-14.
- Gruner, L. and F. Chalumeau. 1977. Biologie et élevage de *Dynastes h. hercules* en Guadeloupe (Coleoptera, Dynastinae). *Annales de la Société Entomologique de France (N.S.)* 13: 613-624.
- Guzman, G., M. A. Morón, F. Ramirez-Guillen, and T. H. D. Wolf. 2001. Entomogenous *Cordyceps* and related genera from Mexico with discussions on their hosts and new records. *Mycotaxon* 78: 115-125.
- Haldeman, S. S. 1843. Descriptions of North American species of Coleoptera, presumed to be undescribed. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1: 298-304.
- Hardy, A. R. 1972. A brief revision of the North and Central American species of *Megasoma* (Coleoptera: Scarabaeidae). *Canadian Entomologist* 104: 765-777.
- Hardy, M. 2003. Description of a new species of *Dynastes* Kirby (Coleoptera Scarabaeidae Dynastinae) from North and Central America. *Besoiro* No. 9: 3-7.
- Harold, E. 1869. Abänderungen vergebener Namen. *Coleopterologische Hefte* 5: 122-125.
- Hartshorn, G. S. 1983. Plants, pp. 118-183. In, Janzen, D. H. (editor), *Costa Rican Natural History*. University of Chicago Press, Chicago, IL. 816 pp.
- Herbst, J. F. W. 1790. *Natursystem aller bekannten in- und ausländischen Insecten, . . . Käfer*, vol. 3: 1-324. J. Pauli, Berlin.
- Heyne, A. and O. Taschenberg. 1907. *Die Exotischen Käfer in Wort und Bild*. G. Reusche, Leipzig. 262 pp., 39 plates.
- Hinton, H. E. and G. M. Jarman. 1973. Physiological colour change in the elytra of the hercules beetle, *Dynastes hercules*. *Journal of Insect Physiology* 19: 533-549.
- Höhne, W. 1921. Eine neue *Erioscelis* (Col. Dyn.). *Deutsche Entomologische Zeitschrift* 1921: 108-109.
- Höhne, W. 1922a. Beitrag zur kenntnis der Cyclocephaliden (Col., Dyn.). *Deutsche Entomologische Zeitschrift* 1922: 81-95.
- Höhne, W. 1922b. *Ancognatha ustulata* Burm. n. subsp. *ustulatoides* (Col. Dyn.). *Deutsche Entomologische Zeitschrift* 1922: 373-374.
- Höhne, W. 1922c. *Aspidolea* (Subg. *Aspidolites*) *atricollis* n. sp. (Col. Dyn.). *Deutsche Entomologische Zeitschrift* 1922: 374-376.
- Höhne, W. 1923a. Neue Dynastiden (Col.). *Deutsche Entomologische Zeitschrift* 1923: 252-255.
- Höhne, W. 1923b. Neue Cyclocephalen (Col. Dyn.). *Deutsche Entomologische Zeitschrift* 1923: 345-373.
- Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. *Science* 105: 367-368.

- Holdridge, L. R., W. C. Grenke, W. H. Hatheway, T. Liang, and J. A. Tosi, Jr. 1971. *Forest Environments in Tropical Life Zones: a Pilot Study*. Pergamon Press, Oxford, UK. 747 pp.
- Hope, F. W. 1837. *The Coleopterists' Manual, Containing the Lamellicorn Insects of Linneus and Fabricius*. London. 121 pp.
- Horn, G. 1871. Descriptions of new Coleoptera of the United States, with notes on known species. *Transactions of the American Entomological Society* 3: 325-344.
- Howden, H. F. 1978. Descriptions of some West Indian Scarabaeidae primarily in the Natural History Museum, Basel. *Entomologica Basiliensia* 3: 377-393.
- Howden, H. F. and J. M. Campbell. 1974. Observations on some Scarabaeoidea in the Colombian Sierra Nevada de Santa Marta. *Coleopterists Bulletin* 28: 109-114.
- Howden, H. F. and S. Endrödi. 1966. Five new species of *Cyclocephala* Latreille from North and Central America. *Canadian Entomologist* 98: 295-302.
- Howell, T. R. 1969. Avian distribution in Central America. *The Auk* 86: 293-326.
- Hurpin, B. and D. Mariau. 1966. Contribution a la lutte contre les *Oryctes* nuisibles aux palmiers. Mise au point d'un élevage permanent en laboratoire. *Académie d'Agriculture de France (extrait du procès-verbal de la séance du 26 janvier 1966, pp. 178-186)*.
- International Commission on Zoological Nomenclature. 1999. *International Code of Zoological Nomenclature*, 4th edition. International Trust for Zoological Nomenclature, London. 306 pp.
- Iturralde-Vinent, M. A. and R. D. E. MacPhee. 1999. Paleogeography of the Caribbean region: implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural History* No. 238: 1-95.
- Jameson, M. L. 1990. Revision, phylogeny and biogeography of the genera *Parabyrsopolis* Ohaus and *Viridimicus*, new genus (Coleoptera: Scarabaeidae: Rutelinae). *Coleopterists Bulletin* 44: 377-422.
- Jameson, M. L. 1998. Phylogenetic analysis of the subtribe Rutelina and revision of the *Rutela* generic groups (Coleoptera: Scarabaeidae: Rutelinae: Rutelini). *Bulletin of the University of Nebraska State Museum* 14: 1-184.
- Jameson, M. L. and B. C. Ratcliffe. 2002. Series Scarabaeiformia Crowson 1960, Superfamily Scarabaeoidea Latreille 1802, p. 1-5. In, Arnett, R. H., M. Thomas, P. E. Skelley, and J. H. Frank (eds.), *American Beetles*, Volume 2. CRC Press, Boca Raton, FL. 861 pp.
- Jameson, M. L., B. C. Ratcliffe, and V. Maly. 2002. Review of the genus *Acrobulbia* with remarks on its classification and key to the world genera of Cyclocephalini (Coleoptera: Scarabaeidae: Dynastinae). *Folia Heyrovskyana* 10: 1-15.
- Janzen, D. H. 1983. Insects. Introduction, pp. 619-645. In, Janzen, D. H. (editor), *Costa Rican Natural History*. University of Chicago Press, Chicago, IL. 816 pp.
- Jarman, G. M. and H. E. Hinton. 1974. Some defence mechanisms of the hercules beetle, *Dynastes hercules*. *Journal of Entomology (A)* 49: 71-80.
- Joly, L. J. 1992. Agaocephalini: especies venezolanas, descripción de la hembra de *Agaocephala bicuspis* Erichson, 1848, nuevos registros y datos faunísticos sobre otras especies (Coleoptera: Melolonthidae, Dynastinae). *Boletín de Entomología Venezolana* 7: 49-58.
- Joly, L. J. and H. E. Escalona. 2002. Dos nuevas especies de *Dyscinetus* Harold de Argentina (Coleoptera: Scarabaeidae: Dynastinae: Cyclocephalini). *Entomotopica* 17: 197-205.
- Kaneps, A. C. 1979. Gulf Stream: velocity fluctuations during the late Cenozoic. *Science* 204: 297-301.
- Kawano, K. 1988. Why are the horns of lucanid beetles so imposing? Evolutionary process through competition among males II. *Gekkan-Mushi* No. 210: 8-15, 22-27.
- Kawano, K. 1991. Male dimorphism and alternative mating strategies in rhinoceros beetles. Evolutionary process through competition among males IV. *Gekkan-Mushi* No. 246: 5-16.
- Kawano, K. 1995a. Horn and wing allometry and male dimorphism in giant rhinoceros beetles (Coleoptera: Scarabaeidae) of tropical Asia and America. *Annals of the Entomological Society of America* 88: 92-99.

- Kawano, K. 1995b. Habitat shift and phenotypic character displacement in sympatry of two closely related rhinoceros beetle species (Coleoptera: Scarabaeidae). *Annals of the Entomological Society of America* 88: 641-652.
- Keogh, R. M. 1984. Changes in the forest cover of Costa Rica through history. *Turrialba* 34: 325-331.
- Kimsey, L. S. 1992. Biogeography of the Panamanian region, from an insect perspective, pp. 14-24. *In*, Quintero, D. and A. Aiello (editors), *Insects of Panama and Mesoamerica. Selected Studies*. Oxford University Press, Oxford, UK. 692 pp.
- Kirby, W. 1818. A description of several new species of insects collected in New Holland by Robert Brown. *Transactions of the Linnean Society of London* 12: 454-482.
- Kirby, W. 1825. A description of such genera and species of insects, alluded to in the "Introduction to Entomology" of Messrs. Kirby and Spence, as appear not to have been before sufficiently noticed or described. *Transactions of the Linnean Society of London* 14: 563-572.
- Kirby, W. 1828. *In* Kirby, W. and W. Spence, *An Introduction to Entomology*, Vol. 4 (5th ed.). London. 683 pp.
- Kirsch, T. F. W. 1871. Beiträge zur Käferfauna von Bogotá. *Berliner Entomologische Zeitschrift* 14 (1870): 337-378 (pages misnumbered, first one as 353).
- Kirsch, T. F. W. 1885. Neue südamerikanische Käfer. *Berliner Entomologische Zeitschrift* 29: 207-224.
- Kolbe, H. 1906a. Die Dynastiden-Gattung *Daemonoplus*. *Stettiner Entomologische Zeitung* 67: 265-275.
- Kolbe, H. 1906b. Ueber die Arten der amerikanischen Dynastiden Gattung *Strategus*. *Berliner Entomologische Zeitung* 51: 1-32.
- Kolbe, H. 1910. Ueber die Phileurinen Amerikas. *Annales de la Société Entomologique de Belgique* 54: 330-354.
- Lachaume, G. 1985. Dynastini 1: *Dynastes - Megasoma - Golofa*. *Les Coléoptères du Monde* 5. Sciences Nat, Venette, France. 85 pp, 29 plates.
- Lachaume, G. 1992. Dynastidae Américains. Cyclocephalini - Agaocephalini - Pentodontini - Oryctini - Phileurini. *Les Coleopteres du Monde* 14. Sciences Nat Venette, France. Pp. 1-56, 83-89. Plates 1-11.
- Lacordaire, J. T. 1856. *Histoire Naturelle des Insectes. Genera de Coléoptères ou Exposé Methodique et Critique de Tous les Genres proposes jusqu'ici dans cet Odre d'Insectes*. Vol. 3. Librairie Encyclopedique de Roret, Paris. 594 pp.
- Lai, J. T. 2001. *For the Love of Rhinoceros and Stag Beetles. Keeping, Breeding, and More*. Morning Star Publisher, Inc., Taipei, Taiwan. 346 pp.
- Lamb, K. P. 1974. *Economic Entomology in the Tropics*. Academic Press, London. 195 pp.
- Landin, B.-O. 1956. The Linnean species of *Lamellicornia* described in "Systema Naturae", Ed. X (1758). (Col.). *Entomologisk Tidskrift* 77: 1-18.
- Laporte, F. L. 1840. *Histoire Naturelle des Insectes Coleoptères. Avec une introduction Renferment l'Anatomie et la Physiologie des Animaux articulés, par M. Brullé*, Vol. 2. P. Duménil, Paris. 564 pp.
- Latreille, P. A. 1807. *Genera Crustaceorum et Insectorum Secundum Ordinem Naturalem in Familias disposita, Iconibus Exemplisque Plurimus Explicata*, Vol. 2. Paris. 280 pp.
- Latreille, P. A. 1812. Insectes de l'Amérique équinoxiale recueillis pendant le voyage de Mm. de Humboldt et Bonpland, pp. 127-252. *In*, *Voyage de Humboldt et Bonpland, deuxième partie. Observations de Zoologie et Anatomie Comparée*, Vol. 1. Smith and Gide, Paris.
- Latreille, P. A. 1813. Insectes de l'Amérique équinoxiale, recueillis pendant le voyage de Mm. de Humboldt et Bonpland. Seconde Partie, pp. 1-64. *In*, *Voyage de Humboldt et Bonpland, deuxième partie. Observations de Zoologie et Anatomie Comparée*, Vol. 2. Smith and Gide, Paris.
- Lawrence, J. F. and A. F. Newton. 1995. Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names), pp. 779-1,006. *In*, Pakaluk, J. and S. A. Slipinski (editors), *Biology, Phylogeny, and Classification of Coleoptera. Papers Celebrating the 80th Birthday of Roy A. Crowson*. Muzeum e Instytut Zoologii PAN. Warsaw, Poland. 1,092 pp.

- Leach, W. E. 1817. *The Zoological Miscellany*, Vol. 3: 1-151, plates 121-150. London.
- LeConte, J. L. 1856. Notice of three genera of Scarabaeidae found in the United States. *Proceedings of the Academy of Natural Sciences of Philadelphia* 8: 19-25.
- LeConte, J. L. and G. H. Horn. 1883. Classification of the Coleoptera of North America. *Smithsonian Miscellaneous Collections* 26 (No. 507): 1-567.
- Leng, C. W. 1920. *Catalogue of the Coleoptera of America, North of Mexico*. John D. Sherman, Mt. Vernon, NY. 470 pp.
- Lever, R. J. A. 1969. Pests of the coconut palm. *FAO Agricultural Studies No. 77*: 1-190.
- Linnaeus, C. 1758. *Systema Naturae*, editio decima. Leipzig. 824 pp.
- Linnaeus, C. 1764. *Museum Ludovicianae Ulricae Reginae Svecorum . . .* Stockholm, Salvius. 720 pp.
- Linnaeus, C. 1767. *Systema Naturae*, Vol. 1, pars 2, editio duodecima reformata. Stockholm. Pp. 533-1327.
- Lloyd, J. J. 1963. Tectonic history of the south central-American orogen, pp. 88-100. *In*, Childs, O. E., and B. W. Beebe (editors), *Backbone of the Americas*. American Association of Petroleum Geologists, Memoir No. 2.
- MacLeay, W. S. 1819. *Horae Entomologicae: or Essays on the Annulose Animals*, Vol. 1, pt. 1. London. 524 pp.
- Maes, J.-M. 1987. Catálogo de los Scarabaeidae (Coleoptera) de Nicaragua. *Revista Nicaraguense de Entomología* 1: 27-60.
- Maes, J.-M. 1994. Los Dynastinae (Coleoptera: Scarabaeidae) de Nicaragua. *Revista Nicaraguense de Entomología* 30: 1-44.
- Maes, J.-M. 1998. *Catalogo de los Insectos y artropodos terrestres de Nicaragua*. Vol. 2. Privately published. Leon, Nicaragua. Pp. 467-1,169.
- Mantel, H. W. 1928. Notes on the eggs and larvae of the thorny-headed worm of hogs. *Transactions of the American Microscopical Society* 48: 342-347.
- Markgraf, V. and J. P. Bradbury. 1982. Holocene climatic history of South America, pp. 40-45. *In*, Mangerud, J., H. J. B. Birks, and K. D. Jager (editors), *Chronostratigraphic subdivision of the Holocene*. *Striae* 16 (Uppsala).
- Marshall, L. G. 1985. Geochronology and land-mammal biochronology of the trans-american faunal interchange, pp. 49-85. *In*, Stehli, F. G. and S. D. Webb (editors), *The Great American Biotic Interchange*. Plenum Press, New York.
- Marshall, L. G. 1988. Land mammals and the great American interchange. *Science* 76: 380-388.
- Martínez, A. 1965. Scarabaeoidea Neotropica X. *Neotropica* 11: 13-18.
- Martínez, A. 1975. Una nueva especie de *Aspidolea* de Ecuador (Col. Scarabaeidae, Dynastinae). *Entomologische Arbeiten aus dem Museum G. Frey* 26: 307-313.
- Martínez, A. 1983. Nueva especie de *Bothynus* de Brasil (Coleoptera, Scarabaeidae, Dynastinae, Pentodontini). *Revista Brasileira de Entomologia* 27: 297-300.
- Martínez, A. and M. Alvarenga. 1987. Un nuevo subgénero de *Agaocephala* de Brasil. *Anales de la Sociedad Científica Argentina* 215: 21-27.
- Maunder, S. 1848. *Treasury of Natural History; or a Popular Dictionary of Animated Literature . . .* Longman, London. 812 pp.
- McCullough, D. 1977. *The Path Between the Seas. The Creation of the Panama Canal 1870-1914*. Simon and Schuster, New York, NY. 698 pp.
- McDade, L. A., K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (editors). 1994. *La Selva. Ecology and Natural History of a Neotropical Rain Forest*. University of Chicago Press, Chicago, IL. 486 pp.
- McNeely, J. A., K. R. Miller, W. V. Reid, R. A. Mittermeier, and T. B. Werner. 1990. *Conserving the World's Biological Diversity*. IUCN, WRI, CI, WWF-US, World Bank, Washington, D.C. 193 pp.
- Mittermeier, R. A., N. Myers, and C. G. Mittermeier (editors). 1999. *Hotspots. Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions*. CEMEX, S. A., Mexico, City, Mexico. 431 pp.
- Moczek, A. P. 1998. Horn polymorphism in the beetle *Onthophagus taurus*: larval diet, quality, and plasticity in parental investment determine adult body size and male horn morphology. *Behavioral Ecology* 9: 630-641.

- Moczek, A. P. and D. J. Emlen. 1999. Proximate determination of male horn dimorphism in the beetle, *Onthophagus taurus* (Coleoptera: Scarabaeidae). *Journal of Evolutionary Biology* 12: 27-37.
- Morón, M. A. 1976. Descripción de las larvas de tres especies mexicanas de melolontinos (Coleoptera, Melolonthidae: Dynastinae y Rutelinae). *Anales del Instituto de Biología, Universidad Nacional Autónoma de México* 47, series Zoología (2): 119-134.
- Morón, M. A. 1977. Description of the third-stage larva of *Megasoma elephas occidentalis*. Bolívar y Pieltain et al. (Scarabaeidae: Dynastinae). *Coleopterists Bulletin* 31: 339-345.
- Morón, M. A. 1979. Fauna de coleópteros lamellicornios de la Estación de Biología Tropical, "Los Tuxtles," Veracruz, UNAM. México. *Anales del Instituto de Biología de Universidad Nacional Autónoma de México (series Zoología)* 1: 375-454.
- Morón, M. A. 1987. Los estados inmaduros de *Dynastes hyllus* Chevrolat (Coleoptera: Melolonthidae; Dynastinae); con observaciones sobre su biología y el crecimiento alométrico del imago. *Folia Entomologica Mexicana* No. 72: 33-74.
- Morón, M. A. 1990. Descripción de una especie nueva de *Archophileurus* Kolbe, 1910 (Coleoptera: Melolonthidae, Dynastinae). *Anales del Instituto de Biología (UNAM), Series Zoología* 6: 139-146.
- Morón, M. A. 1993a. Nueva subespecie mexicana de *Dynastes hercules* (L.) (Coleoptera: Melolonthidae: Dynastinae). *Giornale Italiano di Entomologia* 6: 257-262.
- Morón, M. A. 1993b. Los lamellicornios (Insecta: Coleoptera) de las sierras húmedas del Estado de Hidalgo, México. Una síntesis taxonómica y ecológica, p. 181-211. In, Villavicencio, M. A. and B. E. Pérez-Escandón (editors), *Investigaciones Recientes sobre la Flora y la Fauna de Hidalgo*. Universidad Autónoma de Hidalgo, México.
- Morón, M. A. 1994a. La diversidad generica de los coleopteros Melolonthidae en México. *Acta Zoologica Mexicana (new series)* 61: 7-19.
- Morón, M. A. 1994b. Larvae and pupae of two species of *Golofa* Hope (Coleoptera: Melolonthidae, Dynastinae) from Colombia. *Coleopterists Bulletin* 48: 390-399.
- Morón, M. A. 1995. Review of the Mexican species of *Golofa* Hope (Coleoptera: Melolonthidae, Dynastinae). *Coleopterists Bulletin* 49: 343-386.
- Morón, M. A. 1997a. Melolonthidae y Scarabaeidae, p. 227-240. In, Soriano, E. G., R. Dirzo, and R. C. Vogt (editors), *Historia Natural de Los Tuxtles*. UNAM-CONABIO, México.
- Morón, M. A. 1997b. Notas sobre *Cyclocephala* Latreille (Coleoptera: Melolonthidae, Dynastinae) asociadas con *Xanthosoma* Schott (Araceae) en Chiapas, México. *Giornale Italiano di Entomologia* 8: 399-407.
- Morón, M. A. and J. A. Gómez-Anaya. 2002. Consideraciones sobre la categoría taxonómica de *Megasoma elephas occidentalis* Bolívar y Pieltain, Jiménez-Asúa y Martínez, 1963 (Coleoptera: Melolonthidae; Dynastinae). *Folia Entomologica Mexicana* 41: 299-319.
- Morón, M. A. and C. Deloya. 2001. Observaciones sobre el ciclo de vida de *Megasoma elephas elephas* (Fabricius) (Coleoptera: Melolonthidae: Dynastinae). *Folia Entomologica Mexicana* 40: 233-244.
- Morón, M. A. and B. C. Ratcliffe. 1990. Descriptions of *Strategus* larvae with a new key to species based on the larvae (Coleoptera: Scarabaeidae: Dynastinae). *Elytron* 4: 53-66.
- Morón, M. A. and B. C. Ratcliffe. 1997. New tribal placement of the genus *Coscinocephalus* Prell 1936, with description of the larva, pupa, and adult of a new species from México (Coleoptera: Scarabaeoidea: Dynastinae). *Journal of the New York Entomological Society* 104: 47-60.
- Morón, M. A., B. C. Ratcliffe, and C. Deloya. 1996. *Atlas de los Escarabajos de México (Coleoptera: Lamellicornia)*. Vol. 1. Familia Melolonthidae. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO) and Sociedad Mexicana de Entomología. 280 pp.

- Myers, N. 1980. *Conversion of Tropical Moist Forests*. National Academy of Sciences, Washington, D.C. 205 pp.
- Myers, N. 1981. Deforestation in the tropics: who gains, who loses?, pp. 1-21. In, Sutlive, V. H., N. Altshuler, and M. D. Zamora (editors), *Where Have All the Flowers Gone? Deforestation in the Third World*. Department of Anthropology, College of William and Mary, Studies in Third World Societies No. 13: 1-278.
- Myers, N. 1984. *The Primary Source. Tropical Forests and Our Future*. W. W. Norton & Co., New York, NY. 399 pp.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858.
- Nagai, S. 2001. *Horned Beetles* (in Japanese). Gakken, Tokyo. 144 pp.
- Nagai, S. 2002. Two new subspecies of *Dynastes hercules* (Linnaeus, 1758) (Scarabaeidae: Dynastinae). *Gekkan-Mushi* No. 381: 2-4.
- Nakamura, H. 1974. List of the subfamily Dynastinae (Scarabaeidae s. lat.) from Malaysia, Indonesia and Philippines. *Miscellaneous Publication of the Entomological Research Institute Yamanashi* No. 2: 1-6.
- National Research Council. 1982. *Ecological Aspects of Development in the Humid Tropics*. National Academy Press, Washington, D. C. 297 pp.
- National Science Board. 1989. Loss of biological diversity: a global crisis requiring international solutions. National Science Board Report 89-171: 1-19.
- Navarrete-Heredia, J. L. 2001. Beetles associated with *Atta* and *Acromyrmex* ants (Hymenoptera: Formicidae: Attini). *Transactions of the American Entomological Society* 127: 381-429.
- Nevermann, F. 1933. Beobachtungen über die Lebensweise einiger Lamellicornier und einer Chrysomelidae. *Entomologische Blätter* 29: 179-183.
- Nonfried, A. F. 1890. Neue exotische Coleopteren. *Stettiner Entomologische Zeitung* 51: 15-20.
- Ohaus, F. 1910. Neue südamerikanische Dynastiden (Col.). *Deutsche Entomologische Zeitschrift* 1910: 671-690.
- Ohaus, F. 1913. *Dynastes hercules* L. subsp. nov. *ecuatorianus* m. (Col. lamell. Dynastin.). *Entomologische Rundschau* 30: 131-132.
- Olivier, A. G. 1789. *Entomologie, ou Histoire Naturelle des Insectes, avec leurs Caractères Génériques et Spécifiques, leur Description, leur Synonymie, et leur Figure Enluminée. Coleoptères*, Vol. 1 (genera separately paged). Paris.
- Olivier, A. G. 1802. *Entomologie oder Naturgeschichte der Insecten mit ihren Gattungs- und Art-Merkmalen, ihrer Beschreibung und Synonymie, übersetzt mit Anmerkungen*, Band 2. Braunschweig, Vieweg. 266 pp.
- Otoya, F. 1945. Anotaciones sobre el genero *Ancognatha* y descripción de una nueva especie (Scarabaeidae). *Caldasia* 13: 273-282.
- Otte, D. and K. Stayman. 1979. Beetle horns: some patterns in functional morphology, pp. 259-292. In, Murray, S. and N. A. Blum (Editors), *Sexual Selection and Reproductive Competition in Insects*. Academic Press, NY. 463 pp.
- Palisot de Beauvois, A. M. F. J. 1805-1821. *Insectes Recueillis en Afrique et en Amérique*, Vol. 1. Paris. 276 pp., 90 plates.
- Palmer, T. J. 1978. A horned beetle which fights. *Nature* 274: 583-584.
- Panzer, G. W. F. 1782. *Symbolae Entomologicae. Voets Beschreibungen und Abbildungen hartschaaliger Insecten*, Teil 1. V. Bischoff, Nurnberg. 103 pp.
- Pardo Locarno, L. C. 1993. Estudio preliminar de las especies de Melolonthidae del Valle del Cauca Colombia con énfasis en la Cuenca Calima-San Juan (Valle-Cixoco), pp. 83-90. In, Morón, M. A. (compiler), *Diversidad y Manejo de Plagas Subterráneas*. Publicación Especial, Sociedad Mexicana de Entomología and Instituto de Ecología, Xalapa, Mexico.
- Pardo Locarno, L. C. 1994. Escarabajos (Coleoptera: Melolonthidae) de importancia agrícola en Colombia. Simposio Plagas Rizofagas. Congreso de la Sociedad Colombiana de Entomología, *Memorias* 21: 159-176.
- Paulian, R. and J. Baraud. 1982. *Faune des Coléoptères de France. Lucanoidea et Scarabaeoidea*. *Encyclopedia Entomologique* 48. Editions Lechevalier, Paris. 477 pp.

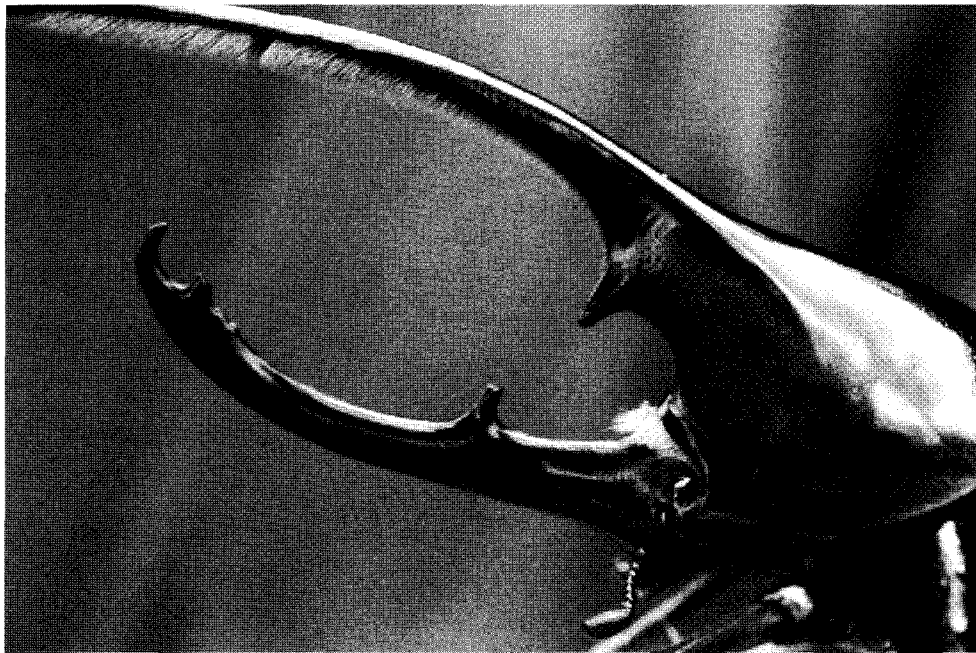
- Perty, M. 1830. *Delectus Animalium Articulatorum, quae in Itenere per Brasiliam Annis MDCCCXVII-MDCCCXX Jussu et Auspiciis Maximiliani Josephi I. Bavariae Regis Augustissimi Peracto Collegerunt Dr. J. B. de Spix et Dr. C. F. Ph. de Martius*, Fasc. 1. 60 pp. Munich.
- Pinchon, R. 1976. Le dynaste hercule dans les Petites Antilles. Fort-de-France. 25 pp., 8 plates.
- Prell, H. 1911a. Beitrag zur Kenntnis der Dynastinen. Annales de la Société Entomologique de Belgique 55: 198-210.
- Prell, H. 1911b. Beiträge zur Kenntnis der Dynastinen. Entomologische Zeitschrift 25: 105-107, 121.
- Prell, H. 1912a. Beiträge zur Kenntnis der Dynastinen (IV). Stettin Entomologische Zeitung 73: 53-57.
- Prell, H. 1912b. Revision des Dynastinen-Genus *Heterogomphus* Burm. Mémoires de la Société Entomologique de Belgique 20: 93-176.
- Prell, H. 1912c. Beiträge zur Kenntnis der Dynastinen (V). Entomologische Blätter 8: 179-187.
- Prell, H. 1912d. Beiträge zur Kenntnis der Dynastiden (IX). Neubeschreibungen und synonymische Bemerkungen. Coleopterologische Rundschau 1: 101-108.
- Prell, H. 1914. Beiträge zur Kenntnis der Dynastinen X (Col.). Entomologische Mitteilungen 3: 197-226.
- Prell, H. 1934. Beiträge zur Kenntnis der Dynastinen (XII). Beschreibungen und Bemerkungen. Entomologische Zeitschrift 47: 162-164, 186-188, 194-195.
- Prell, H. 1936. Beiträge zur Kenntnis der Dynastinen. Ueber die Homonymieverhältnisse der Namen von Gattungen und Untergattungen. Entomologisches Blätter 32: 145-152.
- Prell, H. 1937a. Beiträge zur Kenntnis der Dynastinen (XV, 3). Neue Arten und Rassen. Entomologische Zeitschrift 51: 89-90.
- Prell, H. 1937b. Beiträge zur Kenntnis der Dynastinen (XVI) (Col.). Die Dynastinen der Fabriciusschen Sammlung im Zoologischen Museum der Universität Kiel. Deutsche Entomologische Zeitschrift 1936: 179-190.
- Prell, H. 1937c. Beiträge zur Kenntnis der Dynastiden (XV, 1). Neue Arten und Rassen. Entomologische Zeitschrift 50: 495-496.
- Quenzel, C. 1806. Pars I: ma. Eleutherata. In, C. J. Schönherr, *Synonymia Insectorum oder: Versuch einer Synonymie aller bisher bekannten Insecten; nach Fabricii Systema Eleutheratorum geordnet*. Vol. 1, Pt. 1. 293 pp.
- Quintero, D. 1992. Preface, pp. vii-xii. In, Quintero, D. and A. Aiello (editors), *Insects of Panama and Mesoamerica*. Oxford University Press, Oxford, United Kingdom. 692 pp.
- Rasmussen, J. 1994. The influence of horn and body size on the reproductive behavior of the horned rainbow scarab beetle *Phanaeus difformis* (Coleoptera: Scarabaeidae). Journal of Insect Behavior 7: 67-82.
- Ratcliffe, B. C. 1976. A revision of the genus *Strategus* (Coleoptera: Scarabaeidae). Bulletin of the University of Nebraska State Museum 10: 93-204.
- Ratcliffe, B. C. 1977. Four new species of Neotropical Cyclocephalini (Coleoptera: Scarabaeidae). Acta Amazonica 7: 429-434.
- Ratcliffe, B. C. 1978. New species of *Stenocrates* from Brazil (Coleoptera: Scarabaeidae). Acta Amazonica 8: 489-495.
- Ratcliffe, B. C. 1981. *Barutus hartmanni*, a new genus and species from Panama with a key to the genera of New World Pentodontini (Coleoptera: Scarabaeidae: Dynastinae). Coleopterists Bulletin 35: 463-472.
- Ratcliffe, B. C. 1986. Two new species of *Dyscinetus* from the West Indies and South America (Coleoptera: Scarabaeidae: Dynastinae). Coleopterists Bulletin 40: 75-80.
- Ratcliffe, B. C. 1987. Book Review. *The Dynastinae of the World* by S. Endrödi. Bulletin of the Entomological Society of America 33: 196-197.
- Ratcliffe, B. C. 1988. New species and distributions of Neotropical Phileurini and a new phileurine from Burma (Coleoptera: Scarabaeidae: Dynastinae). Coleopterists Bulletin 42: 43-55.

- Ratcliffe, B. C. 1989. Corrections and clarifications to Endrödi's *The Dynastinae of the World* (Coleoptera: Scarabaeidae). *Coleopterists Bulletin* 43: 275-278.
- Ratcliffe, B. C. 1991. The scarab beetles of Nebraska. *Bulletin of the University of Nebraska State Museum* 12: 1-333.
- Ratcliffe, B. C. 1992a. A new species of *Ancognatha* from Panama (Coleoptera: Scarabaeidae: Dynastinae). *Coleopterists Bulletin* 46: 256-259.
- Ratcliffe, B. C. 1992b. Nine new species and 11 country records of *Cyclocephala* (Coleoptera: Scarabaeidae: Dynastinae) from Panama and Costa Rica. *Coleopterists Bulletin* 46: 216-235.
- Ratcliffe, B. C. 1992c. Two new species of *Cyclocephala* from Arizona and Mexico and a note on melanistic *C. melanocephala* (Coleoptera: Scarabaeidae: Dynastinae). *Coleopterists Bulletin* 46: 25-255.
- Ratcliffe, B. C. 2000. Dynastine scarab beetles of Monteverde, p. 111-113. *In*, Nadkarni, N. M. and N. T. Wheelwright (editors), *Monteverde. Ecology and Conservation of a Tropical Cloud Forest*. Oxford University Press, New York, NY.
- Ratcliffe, B. C. 2001. New species of *Hemiphileurus* Kolbe (Coleoptera: Scarabaeidae: Dynastinae) from Mexico, Guatemala, Colombia, and Brazil. *Coleopterists Bulletin* 55: 433-443.
- Ratcliffe, B. C. 2002a. Review of the genus *Palaeophileurus* (Coleoptera: Scarabaeidae: Dynastinae: Phileurini) with description of two new species from Peru. *Annals of the Entomological Society of America* 95: 335-339.
- Ratcliffe, B. C. 2002b. A checklist of the Scarabaeoidea (Coleoptera) of Panama. *Zootaxa* 32: 1-48.
- Ratcliffe, B. C. 2002c. Chapter 34-V. Dynastinae MacLeay 1819, pp. 64-67. *In*, Arnett, R. H., M. Thomas, P. E. Skelley, and J. H. Frank (Editors), *American Beetles*, Volume 2. CRC Press, Boca Raton, FL. 861 pp.
- Ratcliffe, B. C. and R.-P. Dechambre. 1983. New combinations, synonymy and distribution records for Neotropical Pentodontini and Oryctini (Coleoptera: Scarabaeidae: Dynastinae). *Coleopterists Bulletin* 37: 267-272.
- Ratcliffe, B. C. and L. Delgado-Castillo. 1990. New species and notes of *Cyclocephala* from Mexico (Coleoptera: Scarabaeidae: Dynastinae). *Folia Entomológica Mexicana* No. 80: 41-57.
- Ratcliffe, B. C. and A. C. Deloya. 1992. The biogeography and phylogeny of *Hologymnetis* (Coleoptera: Scarabaeidae: Cetoniinae) with a revision of the genus. *Coleopterists Bulletin* 46: 161-202.
- Ratcliffe, B. C. and M. A. Ivie. 1998. A new species of *Hemiphileurus* (Coleoptera: Scarabaeidae: Dynastinae) from the Dominican Republic with a key to the West Indian species of *Hemiphileurus*. *Coleopterists Bulletin* 52: 201-208.
- Ratcliffe, B. C. and M. A. Morón. 1997. Dynastinae, pp. 53-98. *In*, Morón, M. A., B. C. Ratcliffe and C. Deloya, *Atlas de los Escarabajos de México. Coleoptera: Lamellicornia. Vol. 1. Familia Melolonthidae*. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO) and Sociedad Mexicana de Entomología, Mexico, D. F. 280 pp.
- Raven, P. H. 1981. Tropical rain forests: a global responsibility. *Natural History* 90: 28-32.
- Raven, P. H. 1983. The challenge of tropical biology. *Bulletin of the Entomological Society of America* 29: 5-12.
- Raven, P. H., and D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. *Annals of the Missouri Botanical Garden* 61: 539-673.
- Reiche, L. 1859. Notes synonymiques sur le cinquième volume de l'Handbuch der Entomologie, par M. H. Burmeister, Berlin, 1840. Coléoptères lamellicornes, xylophiles. *Annales de la Société Entomologique de France* (series 8) 7: 5-19.
- Reitter, E. 1960. *Beetles*. G. P. Putnam's Sons. New York, NY. 205 pp.
- Rich, P. V. and T. H. Rich. 1983. The Central American dispersal route: biotic history and paleogeography, p. 12-34. *In*, Janzen, D. H. (editor), *Costa Rican Natural History*. University of Chicago Press, Chicago, IL. 816 pp.
- Rickson, F. R., M. Cresti, and J. H. Beach. 1990. Plant cells which aid in pollen digestion within a beetle's gut. *Oecologia* 82: 424-426.

- Ritcher, P. O. 1944. Dynastinae of North America with descriptions of the larvae and keys to genera and species (Coleoptera: Scarabaeidae). *Bulletin of the Kentucky Agricultural Experiment Station* 467: 1-56.
- Ritcher, P. O. 1958. Biology of Scarabaeidae. *Annual Review of Entomology* 3: 311-334.
- Ritcher, P. O. 1966. *White Grubs and Their Allies*. Oregon State University Press, Corvallis, OR. 219 pp.
- Rivers, J. J. 1891. New species of Scarabaeidae. *Proceedings of the California Academy of Sciences (series 2)* 3: 97-98.
- Robinson, M. 1947. A new species of *Stenocrates* from Central America. *Entomological News* 58: 233-234.
- Ryan, M. 1963. The biotic provinces of Central America. *Acta Zoologica Mexicana* 6: 1-54.
- Sader, S. A. and A. T. Joyce. 1988. Deforestation rates and trends in Costa Rica, 1940 to 1983. *Biotropica* 20: 11-19.
- Sarmiento, G. 1976. Evolution of arid vegetation in tropical America, pp. 65-99. In, Goodall, D. W. (editor), *Evolution of Desert Biota*. University of Texas Press, Austin, TX.
- Savage, J. M. 1966. The origins and history of the Central American herpetofauna. *Copeia* 1966: 719-766.
- Savage, J. M. 1982. *Ecological Aspects of Development in the Humid Tropics*. National Academy of Sciences Press, Washington, D.C. 297 pp.
- Sawyer, J. O. and A. A. Lindsey. 1971. Vegetation of the life zones in Costa Rica. *Indiana Academy of Sciences Monograph No. 2*: 1-214.
- Saylor, L. W. 1945. Synoptic revision of the United States scarab beetles of the subfamily Dynastinae, No. 1: tribe Cyclocephalini. *Journal of the Washington Academy of Sciences* 35: 378-386.
- Saylor, L. W. 1946a. Synoptic revision of the United States scarab beetles of the subfamily Dynastinae, No. 2: tribe Oryctini (part). *Journal of the Washington Academy of Sciences* 36: 16-21.
- Saylor, L. W. 1946b. Synoptic revision of the United States scarab beetles of the subfamily Dynastinae, No. 3: tribe Oryctini (part). *Journal of the Washington Academy of Sciences* 36: 41-45.
- Saylor, L. W. 1948a. Synoptic revision of the United States scarab beetles of the subfamily Dynastinae, No. 4: tribes Oryctini (part), Dynastini, and Phileurini. *Journal of the Washington Academy of Sciences* 38: 176-183.
- Saylor, L. W. 1948b. Synoptic revision of the United States scarab beetles of the subfamily Dynastinae, No. 5: keys to tribes and genera. *Journal of the Washington Academy of Sciences* 38: 240-243.
- Schaller, G. B. 1997. Forward, pp. 9-13. In, Wolf, A. and G. T. Prance, *Rainforests of the World. Water, Fire, Earth & Air*. Crown Publishers, Inc., New York, NY. 304 pp.
- Schönherr, C. J. 1817. *Synonymia insectorum, oder: Versuch einer Synonymie aller bisher bekannten Insecten; nach Fabricii Systema Eleutheratorum etc. geordnet*, Vol. 1, part 3: 1-506.
- Schufeldt, R. W. 1884. Observations upon a collection of insects made in the vicinity of New Orleans, Louisiana, during the years 1882 and 1883. *Proceedings of the U. S. National Museum* 7: 331-338.
- Scopoli, J. A. 1772. *Annus Historico Naturalis, Ann. 5*. Leipzig. 128 pp.
- Selander, R. B. and P. Vaurie. 1962. A gazetteer to accompany the "Insecta" volumes of the "Biologia Centrali-Americana." *American Museum Novitates* No. 2099: 1-70.
- Shackelton, N. J. and N. D. Opdyke. 1977. Oxygen isotope and paleomagnetic evidence for early northern hemisphere glaciation. *Nature* 270: 216-219.
- Sharp, D. 1877. Description of some new species of beetles (Scarabaeidae) from Central America. *Journal of the Linnean Society of London (Zoology)* 13: 129-138.
- Silvestre, G. and R.-P. Dechambre. 1995. Une nouvelle sous-espèce de *Dynastes hercules* L. (Coleoptera Dynastidae). *Revue Française d'Entomologie (N.S.)* 17: 52.
- Siva-Jothy, M. T. 1987. Mate securing tactics and the cost of fighting in the Japanese horned beetle, *Allomyrina dichotoma* L. (Scarabaeidae). *Journal of Ethology* 5: 165-172.
- Smith, A. 1971. *Mato Grosso*. E. P. Dutton and Co., Inc., New York, NY. 288 pp.

- Smith, A. B. T. 2003. A monographic revision of the genus *Platycoelia* Dejean (Coleoptera: Scarabaeidae: Rutelinae: Anoplognathini). *Bulletin of the University of Nebraska State Museum* 15:1-202.
- Smith, A. G. and J. C. Breden. 1977. Mesozoic and Cenozoic paleocontinental maps. Cambridge University Press, United Kingdom.
- Smithe, F. B. 1975. *Naturalist's Color Guide*. Part 1, color swatches. The American Museum of Natural History, NY. Pages not numbered.
- Stanek, V. J. 1969. *The Pictorial Encyclopedia of Insects*. Hamlyn Publishing Group, London, United Kingdom. 544 pp.
- Stehli, F. G. and S. D. Webb (editors). 1985. *The Great American Biotic Interchange*. Plenum Press, New York, NY.
- Stephan, K. 1967. Notes on the ecology of *Xyloryctes jamaicensis* (Coleoptera: Scarabaeidae) in southern Ontario. *Michigan Entomologist* 1: 133-134.
- Sternberg, C. 1904. Zur Gattung *Aegopsis* Burmeister. *Deutsche Entomologische Zeitschrift* 1904: 17-32.
- Sternberg, C. 1908. Neue Dynastiden-Arten. *Stettiner Entomologische Zeitung* 69: 3-31.
- Stirton, R. A. and W. K. Gealey. 1949. Reconnaissance geology and vertebrate paleontology of El Salvador, Central America. *Bulletin of the Geological Society of America* 60: 1731-1754.
- Sturm, J. 1843. *Catalog der Käfersammlung von J. Sturm*. Published by the Author, Nürnberg. 386 pp.
- Taschenburg, E. L. 1870. Neue Käfer aus Colombien und Ecuador. *Zeitschrift für die Gesamten Naturwissenschaften* 1: 177-199.
- Thomas, D. B. 1993. Scarabaeidae (Coleoptera) of the Chiapanecan forests: a faunal survey and chorographic analysis. *Coleopterists Bulletin* 47: 363-408.
- Thomson, J. 1859a. Voyage au Gabon. Histoire naturelle des insectes et des arachnides recueillis pendant un voyage fait au Gabon en 1856 et en 1857 par M. Henry C. Deyrolle sous les auspices de Mm. le comte de Miniszech et James Thomson précédée de l'histoire du voyage. *Archives Entomologiques* 2: 7-376.
- Thomson, J. 1859b. Essai synoptique sur la sous-tribu des scarabaeitae vrais. *Arcana Naturae* 1: 3-22.
- Thomson, J. 1860. *Agaocephalitarum synopsis*. Musée Scientifique ou Recueil d'Histoire Naturelle, Vol. 1. Published by the Author, Paris. 72 pp.
- Torre-Bueno, J. R. de la. 1937. *A Glossary of Entomology*. Brooklyn Entomological Society, Brooklyn, NY. 336 pp.
- Tosi, J. A., Jr. 1969. Republica de Costa Rica. Mapa ecologico, segun la clasificacion de zonas de vida del mundo de L. R. Holdridge. Centro Cientifico Tropical, San José, Costa Rica. 1 sheet.
- Ulfstrand, F. 1992. Biodiversity — how to reduce its decline. *Oikos* 63: 3-5.
- Valerio, C. E. 1984. Insect visitors of the inflorescence of the aroid *Dieffenbachia oerstedii* (Araceae) in Costa Rica. *Brenesia* 22: 139-146.
- Van Dinther, J. B. M. 1956. Insects of the coconut palm in Suriname. *Landbouwproefstation in Suriname Bulletin* No. 69: 1-27.
- Vanin, S. A., C. Costa, and L. R. Fontes. 1983. Larvae of Neotropical Coleoptera. VI. Scarabaeidae, Dynastinae, Phileurini. *Papéis Avulsos de Zoologia* 35: 55-72.
- Vayssiere, P. 1965. Sur quelques insectes des palmiers en Amérique de Sud. *Mededel Landouwhogeschool Opzoekingssta Ghent* 30: 1571-1576.
- Verrill, A. H. 1906. Descriptions of two remarkable new species of goliath beetles (*Dynastes*) from Dominica Island, Antilles. Brief contributions to zoology from the Museum of Yale University, No. LXVI. *American Journal of Science* (4th series) 21: 317-320.
- Verrill, A. H. 1907. Description of a new species or subspecies of hercules beetles from Dominica Island, B. W. I., with notes on the habits and larvae of the common species and other beetles. Brief contributions to zoology from the Museum of Yale University, No. LXVII. *American Journal of Science* (4th series) 24: 305-308.
- Vidal, O. R. and R. O. Giacomozzi. 1978. The chromosomes of the subfamily Dynastinae Coleoptera Scarabaeidae 2. The C bands in *Enema pan.* *Physis* (Secion C) 38: 113-119.

- Warner, W. B. 1992. A new North American *Spodistes* Burmeister (Coleoptera: Scarabaeidae). *Coleopterists Bulletin* 46: 378-383.
- Webb, S. D. 1978. A history of savanna vertebrates in the New World, part 11: South America and the great interchange. *Annual Review of Ecology and Systematics* 9: 393-426.
- Webb, S. D. 1985. Late Cenozoic mammal dispersals between the Americas, pp. 357-386. *In*, Stehli, F. G. and S. D. Webb (editors), *The Great American Biotic Interchange*. Plenum Press, New York, NY.
- Weil, T. E., J. K. Black, H. I. Blutstein, D. S. McMorris, F. P. Munson, and C. Townsend. 1972. *Area Handbook for Panama*. U.S. Government Printing Office, Washington, D.C. 413 pp.
- Westwood, J. O. 1878. Descriptions of some exotic lamellicorn beetles. *Transactions of the Entomological Society of London* 1878: 27-37.
- Wetherbee, D. K. 1985. The former occurrence of the endangered giant beetle, *Dynastes hercules* in Hispaniola. *Caribbean Journal of Science* 21: 83-84.
- Wheeler, Q. D. and N. I. Platnick. 2000. The phylogenetic species concept (*sensu* Wheeler and Platnick), pp. 55-69. *In*, Wheeler, Q. D. and R. Meier (editors), *Species Concepts and Phylogenetic Theory: a Debate*. Columbia University Press, New York, NY. 230 pp.
- White, W. H. 1990. Flight and feeding activity of the sugarcane beetle (Coleoptera: Scarabaeidae) in Louisiana. *Journal of Agricultural Entomology* 7: 103-111.
- Woodburne, M. 1969. A Late Pleistocene occurrence of the collared peccary, *Dicotyles tajacu*, in Guatemala. *Journal of Mammalogy* 50: 121-125.
- Young, H. J. 1986. Beetle pollination of *Dieffenbachia longispatha* (Araceae). *American Journal of Botany* 73: 931-944.
- Young, H. J. 1988a. Neighborhood size in a beetle pollinated tropical aroid: effects of low density and asynchronous flowering. *Oecologia* 76: 461-466.
- Young, H. J. 1988b. Differential importance of beetle species pollinating *Dieffenbachia longispatha* (Araceae). *Ecology* 69: 832-844.
- Young, R. M. 1992. A new *Cyclocephala* from a Costa Rican cloud forest (Scarabaeidae: Dynastinae). *Coleopterists Bulletin* 46: 52-55.



GAZETTEER OF COLLECTING LOCALITIES IN COSTA RICA AND PANAMA

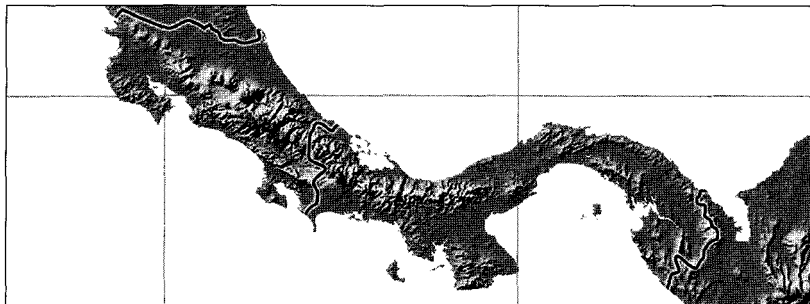
A gazetteer of collecting locality place names is necessary because many of the localities listed on specimen labels may not be easily found in print or electronically available sources. In Costa Rica especially, the use of "Estaciones" to indicate particular place names (either biological stations or simply a well-known collecting site) is in wide use, but none of these "Estaciones" can be found in commercially available or government-produced gazetteers or maps. For the sometimes obscure Costa Rican and Panamanian localities referred to in the *Biologia Centrali-Americana*, Selander and Vaurie (1962) provided a valuable gazetteer for those places. The source of information for most of the place names in the gazetteer below are from (1) label data, (2) the INBio database (<http://www.inbio.ac.cr/bims/k02/p05/c029/o0122/f01094.htm>), (3) the Mapa de los Parques Nacionales de Costa Rica, (4) the Mapa Físico de la República de Panamá, (5) the large sectional topographic maps produced by the geographic institutes of each country, (6) the electronic gazetteer of Costa Rica by Falling Rain Genomics, Inc. (<http://www.calle.com/world/costarica/index.html>), and (7) the electronic gazetteer of Panama by Falling Rain Genomics, Inc. (<http://www.calle.com/world/panama/index.html>).

In this work, the designation of CANAL ZONE (Panama) is used even though the former Canal Zone is now a part of Panama and Colón provinces. Canal Zone is used because all of the material cited from this area was so labeled when collected and because it does more precisely delineate *where* in the

otherwise large provinces of Panama and Colón the material was collected. In addition, the five mile wide strip either side of the Panama Canal was known as the Canal Zone throughout the duration of this study. The designation of Canal Zone is, today, an historical artifact resulting from transferring control of the Panama Canal from the United States to the Republic of Panama in the year 2000. Its continued use here is meant only to more easily place a species geographically.

Inasmuch as Panama is clearly divided down the center by a Cordillera Central, the designation of Atlantic and Pacific slopes is included not only to more easily locate the place name but to also associate certain biotopes or climate patterns of the place under consideration. While Costa Rica also has a Cordillera Central, the country is more dissected by intermontane valleys, and many of these do not easily lend themselves to a designation of Atlantic or Pacific slope. Accordingly, the slope designation is not given for Costa Rica.

The listings below are alphabetical by place name, followed by the province in which it occurs, latitude, longitude, and elevation in meters. The elevations are subject to some variation inasmuch as a label may indicate a particular place but, in fact, the specimen (especially older material) may have been collected on the higher hills surrounding that place. With the advent of Global Positioning System instruments that give accurate elevations, as well as latitudes and longitudes, more precise data will become increasingly available as new material is collected.



Costa Rica

Locality	Province	N Latitude	W Longitude	Elevation M
Agua Buena	Guanacaste	11°02′	85°35′	220
Alajuela	Alajuela	10° 40′	84°43′	500
Altamira	Puntarenas	09°03′	82°59′	2000
Amubri	Limón	9°30′	82°57′	70
Atenas	Alajuela	09°59′	84°23′	700
Bagaces	Guanacaste	10°31′	85°15′	80
Bahia Santa Elena	Guanacaste	10°55′	85°48′	100
Bajos del Torro Amarillo	Alajuela	10°13′	84°04′	1137
Balsa	San José	09°56′	84°22′	1198
Barra Colorado	Heredia	19°39′	83°45′	-
Barranca	Puntarenas	09°59′	84°43′	100
Batan	Limón	10°05′	83°22′	1
Bijagua	Alajuela	10°44′	85°03′	430
Bosque Esquinas	Puntarenas	08°46′	83°15′	10
Bratsi	Limón	09°33′	82°53′	70
Buenos Aires	Limón	09°44′	82°50′	-
Cachi	Cartago	09°50′	83°48′	1181
Cafrosa	Puntarenas	08°55′	82°47′	1500
Cahuita	Limón	10°07′	83°31′	1
Cairo	Limón	10°32′	83°30′	71
Cañas	Guanacaste	10°25′	85°07′	-
Caño Chiquero	Limón	10°32′	83°30′	-
Caño Negro	Alajuela	10°54′	84°47′	35
Capellades	Cartago	09°55′	83°47′	1541
Carara	Puntarenas	09°46′	84°36′	50
Cartago	Cartago	09°52′	83°55′	1400
Cerro Biolley	Puntarenas	09°03′	83°00′	1800
Cerro Chato	Alajuela	10°27′	84°41′	800
Cerro Chirripo	Limón	09°29′	83°30′	2600
Cerro Chompipe	Heredia	10°05′	84°03′	1800
Cerro Cocori	Limón	10°36′	83°43′	150
Cerro de la Muerte	San José	09°34′	83°45′	3300
Cerro El Hacha	Guanacaste	10°53′	85°34′	400
Cerro Guarari	Heredia	10°07′	84°08′	2700
Cerro Pando	Puntarenas	08°55′	82°42′	2400
Cerro Tortuguero	Limón	10°36′	83°32′	5
Chirripo	Limón	09°49′	83°25′	1700
Chitaria	Cartago	09°56′	83°35′	700
Coco	Guanacaste	10°33′	85°43′	2
Colonia Blanca	Alajuela	10°48′	84°41′	800
Colonia Blanca	Guanacaste	10°48′	85°16′	-
Colonia Palmareña	Alajuela	10°13′	84°33′	760
Concepcion	Heredia	10°03′	84°01′	1600
Coronado	Puntarenas	09°03′	83°39′	47
Desamparados	Alajuela	09°57′	84°30′	350
Division	San José	09°30′	83°43′	2400
Dos Rios	Alajuela	10°53′	85°23′	600

Costa Rica

Locality	Province	N Latitude	W Longitude	Elevation M
El Amo	Guanacaste	11°01'	85°36'	220
El Carmen Siguirres	Limón	-	-	50
El Chuzazo	Puntarenas	09°46'	84°31'	280
El Pilon	Alajuela	10°49'	84°57'	800
El Plastico	Heredia	10°18'	84°02'	700
El Tejar	Cartago	09°50'	83°55'	-
Embalse El Llano	Cartago	09°45'	83°51'	1500
Empalme	Cartago	09°44'	83°57'	1
Escazu	San José	09°55'	84°08'	1300
Estación Altamira	Puntarenas	09°02'	83°01'	1450
Estación Barva	Heredia	10°07'	84°07'	2500
Estación Bijagual	San José	09°45'	84°34'	500
Estación Cacao	Guanacaste	10°55'	85°28'	1200
Estación Carara (part)	Puntarenas	09°46'	84°32'	100
Estación Carara (part)	San José	09°46'	84°31'	100
Estación Carrillo	San José	10°08'	83°57'	750
Estación El Ceibo	Heredia	10°20'	84°01'	600
Estación Eladíos	Alajuela	10°19'	84°43'	820
Estación Esquinas	Puntarenas	08°45'	83°16'	200
Estación Hitoy Cerere	Limón	09°40'	83°01'	200
Estación Laguna Pocosol	Alajuela	10°21'	84°21'	850
Estación Las Alturas	Puntarenas	08°57'	82°50'	1600
Estación Las Mellizas	Limón	08°53'	82°46'	1300
Estación Las Pailas	Guanacaste	10°46'	85°21'	800
Estación Lomas Barbudal	Guanacaste	10°29'	85°22'	30
Estación Los Almendros	Guanacaste	11°02'	85°32'	300
Estación Magsasay	Heredia	10°24'	84°03'	200
Estación Maritza	Guanacaste	10°57'	85°29'	700
Estación Mengo	Guanacaste	10°59'	85°28'	1100
Estación Mirimar	Limón	09°38'	83°00'	500
Estación Murcielago	Guanacaste	10°54'	85°43'	40
Estación Palo Vede	Guanacaste	10°20'	85°21'	10
Estación Pitilla	Guanacaste	10°59'	85°28'	700
Estación Pittier	Puntarenas	09°01'	82°57'	1670
Estación Playa Naranjo	Guanacaste	10°48'	85°40'	1
Estación Cuatro Esquinas	Limón	10°32'	83°30'	1
Estación Queberada Bonita	Puntarenas	09°46'	84°36'	100
Estación Quebrada Segundo	Cartago	09°45'	83°47'	1360
Estación Santa Rosa	Guanacaste	10°50'	85°37'	300
Estación Sirena	Puntarenas	08°28'	83°35'	1
Estación Zurqui	San José	10°04'	84°01'	1600
Fila Cruces	Puntarenas	08°47'	83°00'	1400
Fila Guerra	Puntarenas	08°45'	83°36'	1
Fila Matama	Limón	09°47'	83°09'	1680
Finca Jenny	Guanacaste	10°51'	85°34'	200
Finca Magil	Alajuela	10°41'	84°57'	400
Finca Naranjo	Heredia	10°29'	84°01'	90

Costa Rica

Locality	Province	N Latitude	W Longitude	Elevation M
Finca Naranjo Valenciana	Heredia	10°27′	84°06′	90
Finca San Gabriel	Alajuela	10°53′	85°23′	600
Golfito	Puntarenas	08°38′	83°11′	35
Grano de Oro	Cartago	09°48′	83°27′	1100
Guacimo	Limón	10°13′	83°40′	73
Guapiles	Limón	10°13′	83°46′	150
Hitoy Cerere	Limón	09°40′	83°01′	100
Horquetas	Heredia	10°22′	83°56′	50
Nuñes Exp. Station	Guanacaste	10°20′	85°10′	50
La Esperanza	Guanacaste	10°58′	85°23′	450
La Esterella	Limón	09°48′	82°54′	40
La Pacifica	Guanacaste	10°27′	85°07′	50
La Palma	Guanacaste	10°32′	85°02′	510
La Palma	Heredia	10°37′	84°06′	10
La Palma	Puntarenas	08°39′	83°26′	10
La Selva Biological Station	Heredia	10°26′	84°00′	80
La Trinidad de Dota	San José	09°59′	83°21′	2500
Laguna Arenal	Alajuela	10°25′	84°41′	500
Las Cruces	Puntarenas	08°47′	82°57′	800
Las Horquetas	Heredia	10°18′	84°02′	160
Las Mercedes	Limón	10°12′	83°37′	50
Las Palmas	Guanacaste	10°47′	85°20′	1400
Las Tablas	Puntarenas	08°56′	82°44′	1920
Liberia	Guanacaste	10°38′	85°27′	175
Libertad	Alajuela	10°29′	85°39′	650
Limón	Limón	10°00′	83°02′	2
Los Almendros	Guanacastge	85°02′	85°31′	300
Los Arbolitos	Heredia	10°39′	84°00′	10
Madre de Dios	Limón	10°05′	83°23′	61
Madre Selva	Cartago	09°40′	83°51′	2660
Magsasay	Heredia	10°24′	84°02′	200
Manzanillo	Limón	09°38′	82°40′	1
Mata de Limón	Puntarenas	09°56′	84°42′	1
Mata de Platano	San José	09°57′	83°57′	1344
Mellizas	Puntarenas	08°53′	82°46′	1400
Miramar	Puntarenas	10°06′	84°44′	341
Monteverde	Puntarenas	10°18′	84°47′	1300
Moravia	San José	09°57′	84°03′	1500
Moravia de Chirripo	Cartago	09°49′	83°25′	1200
Nacaome	Guanacaste	10°10′	85°22′	100
Naranjo	Alajuela	10°06′	84°28′	1100
Nicoya	Guanacaste	10°09′	85°27′	50
Orosi	Cartago	09°48′	83°51′	1400
Pacayas	Cartago	09°55′	83°48′	1
Palmira	Puntarenas	08°56′	82°54′	1200
Pandora	Limón	09°45′	82°50′	40
Paraguas	Puntarenas	08°46′	83°03′	1400

Costa Rica

Locality	Province	N Latitude	W Longitude	Elevation M
Parq. Nac. Amistad	Limón	09°31'	85°27'	various
Parq. Nac. Amistad	Puntarenas	10°05'	84°07'	various
Parq. Nac. Barra Honda	Guanacaste	10°09'	85°21'	100
Parq. Nac. Braulio Carrillo	Heredia	10°24'	84°03'	various
Parq. Nac. Guanacaste	Guanacaste	10°55'	85°34'	various
Parq. Nac. Manuel Antonio	Puntarenas	09°22'	83°28'	1
Parq. Nac. Palo Verde	Guanacaste	10°21'	85°21'	60
Parrita	Puntarenas	09°30'	84°19'	50
Peñas Blancas	Alajuela	10°19'	84°43'	800
Peralta	San José	09°55'	84°07'	1096
Piedra Negra	Guanacaste	10°51'	85°53'	1
Platanillo	Cartago	09°50'	83°33'	1009
Playa Naranja	Guanacaste	10°48'	85°40'	1
Playuelas	Alajuela	10°57'	84°45'	20
Progreso	Puntarenas	08°54'	82°46'	1320
Pueblo Nuevo (Sarapiquí)	Heredia	10°29'	84°01'	100
Puerto Viejo	Heredia	10°28'	83°59'	100
Punta Blanco	Puntarenas	08°23'	83°09'	-
Punta Leona	Puntarenas	09°41'	84°41'	-
Pueblo Nuevo	Heredia	10°28'	84°06'	100
Quebrada Segunda	Cartago	09°46'	83°47'	1150
Quemado	Puntarenas	08°40'	83°34'	200
Quepos	Puntarenas	09°27'	84°09'	3
Rancho Naturalista	Cartago	09°49'	83°33'	904
Rancho Redondo	Cartago	09°58'	83°57'	1999
Rancho Quemado	Puntarenas	08°40'	83°34'	200
Revantazon (Hamburg Farm)	Limón	10°17'	83°24'	-
Rincon de la Vieja	Guanacaste	10°49'	85°20'	1350
Rincon de Osa	Puntarenas	08°41'	83°29'	1
Rio Bonito	Puntarenas	08°40'	83°13'	200
Rio Coton	Puntarenas	08°56'	82°55'	980
Rio Gongora	Guanacaste	10°53'	85°23'	700
Rio Macho	Cartago	09°33'	83°41'	2500
Rio Pejibaye	Cartago	09°40'	83°43'	1800
Rio San Lorencito	Alajuela	10°05'	84°20'	800
Rio San Lorenzo	Alajuela	10°14'	84°33'	650
Rio San Lorenzo	Guanacaste	10°36'	84°59'	1050
Rio Sardinas	Limón	10°39'	83°45'	15
Sabalito	Puntarenas	08°48'	82°54'	900
Sabanas de Durika	Limón	09°26'	82°38'	2430
Samara	Guanacaste	09°53'	85°32'	1
San Antonio de Belén	Heredia	09°59'	84°11'	950
San Carlos	Alajuela	10°28'	84°34'	-
San Cristobal	San José	09°45'	84°01'	1628
San Gerardo de Dota	Limón	09°32'	83°09'	2300
San Isidro	Heredia	10°01'	84°05'	600
San José	San José	09°56'	84°05'	1200

Costa Rica

Locality	Province	N Latitude	W Longitude	Elevation M
San Juan de Chicua	Cartago	09°58′	83°51′	2850
San Juan de Dios	San José	09°53′	84°05′	1175
San Luis	Heredia	10°01′	84°01′	476
San Luis	Puntarenas	10°16′	84°50′	1040
San Mateo	Alajuela	09°56′	84°31′	206
San Miguel	Puntarenas	10°03′	83°00′	150
San Rafael	Heredia	10°11′	84°07′	1250
San Ramon	Alajuela	10°05′	84°20′	800
San Vito	Puntarenas	08°57′	82°50′	1600
Santa Ana	San José	09°56′	84°11′	1760
Santa Barbara	Heredia	10°02′	84°09′	1128
Santa Cecilia	Guanacaste	11°00′	85°25′	700
Santa Clara	Alajuela	10°51′	85°10′	48
Santa Elena	Puntarenas	10°19′	84°49′	1500
Santa Maria	Alajuela	10°46′	85°15′	600
Santa Maria	San José	09°39′	83°57′	1700
Santa Rosa	Guanacaste	10°51′	85°37′	300
Santiago de Puriscal	San José	09°51′	84°18′	600
Santo Domingo	Heredia	09°58′	84°05′	1100
Sarapaqui	Alajuela	10°15′	84°10′	800
Sarchi	Alajuela	10°05′	84°20′	913
Sardinas	Limón	10°38′	83°43′	50
Siguerres	Limón	10°06′	83°30′	50
Sixaola	Limón	09°30′	82°36′	10
Suretka	Limón	09°34′	82°56′	60
Tambor	Puntarenas	09°45′	85°00′	1
Tapanti	Cartago	09°41′	83°45′	1150
Tablazo (Irazu)	Cartago	09°50′	84°02′	2000
Tibas	San José	09°58′	84°03′	1265
Tierra Blanca	Cartago	09°55′	83°53′	2060
Tierras Morenas	Guanacaste	10°34′	85°03′	900
Tilaran	Guanacaste	10°28′	84°59′	1000
Tres Colinas	Limón	09°07′	82°24′	1850
Tres Rios	Cartago	09°54′	83°58′	1500
Tuis	Cartago	09°51′	83°35′	582
Turrialba	Cartago	09°54′	83°38′	600
Upala	Alajuela	10°53′	85°00′	50
Upala	Guanacaste	10°49′	85°26′	600
Valle de Estrella	Limón	09°40′	83°01′	100
Vara Blanca	Heredia	10°10′	84°09′	1800
Villa Mills	Cartago	09°33′	83°42′	3000
Volcan Irazu	San José	09°58′	83°53′	2530
Volcan Orosi	Guanacaste	10°59′	85°29′	500
Vuelta Campana	Puntarenas	08°58′	83°15′	300
Wilson Botanical Garden	Puntarenas	08°47′	82°57′	1000
Zurqui Tunnel	San José	10°03′	84°00′	1600

Panama

Locality	Province	N Latitude	W Longitude	Elevation M	Slope
Achiote Road	Canal Zone	09°12′	79°59′	20	Atlantic
Aguadulce	Coclé	08°15′	80°30′	10	Pacific
Albrook Forest Site	Canal Zone	09°04′	79°32′	20	Pacific
Alto Lino	Chiriqui	08°80′	82°43′	1250	Pacific
Altos de Majé	Panama	09°08′	78°49′	80	Pacific
Altos de Piedra	Veraguas	08°32′	81°03′	850	Pacific
Balboa	Canal Zone	08°57′	79°34′	5	Pacific
Bambito	Chiriqui	08°49′	82°37′	1700	Pacific
Barro Colorado Island	Canal Zone	09°11′	79°57′	26	Atlantic
Black Tank Road	Canal Zone	09°18′	79°58′	20	Atlantic
Boquete	Chiriqui	08°48′	82°26′	1250	Pacific
Bugaba (above)	Chiriqui	08°29′	82°38′	300	Pacific
Cana	Darien	07°45′	77°41′	460	Pacific
Cerro Azul	Panama	09°11′	79°23′	335	Divide
Cerro Campana	Panama	08°41′	80°53′	850	Divide
Cerro Colorado	Chiriqui	08°32′	81°43′	1500	Pacific
Cerro Gaital	Coclé	08°37′	80°06′	700	Pacific
Cerro Galera	Canal Zone	08°56′	79°31′	50	Pacific
Cerro Jefe	Panama	09°12′	79°21′	800	Divide
Cerro Punta	Chiriqui	08°51′	82°34′	1666	Pacific
Cerro Viejo Mine Road	Colón	09°34′	79°42′	150	Atlantic
Chame	Panama	08°38′	79°42′	2	Pacific
Chepo	Panama	09°10′	79°05′	25	Pacific
Chilibre	Panama	09°09′	79°37′	80	Atlantic
Chiriqui Grande	Bocas d Toro	08°57′	82°07′	2	Atlantic
Chiriquicito	Chiriqui	08°68′	82°30′	605	Pacific
Coco Solo Hospital	Canal Zone	09°23′	79°51′	6	Atlantic
Continental Divide Trail	Bocas d Toro	08°47′	82°12′	1100	Divide
Continental Divide Trail	Chiriqui	08°47′	82°12′	1268	Divide
Corozal	Canal Zone	08°59′	79°34′	25	Pacific
Corriente Grande	Bocas d Toro	09°11′	82°32′	100	Atlantic
David	Chiriqui	08°26′	82°26′	10	Pacific
Diablo Heights	Canal Zone	08°58′	79°34′	2	Pacific
El Cope	Coclé	08°40′	80°37′	1300	Divide
El Llano-Carti Road	Panama	09°18′	78°58′	350	Pacific
El Valle	Coclé	08°36′	80°07′	850	Pacific
Escobal Road	Canal Zone	09°13′	79°57′	45	Atlantic
Finca La Suiza	Chiriqui	08°39′	82°12′	1364	Pacific
Fortuna Dam	Chiriqui	08°44′	82°17′	970	Pacific
Fortuna Reserve	Chiriqui	08°43′	82°14′	1000	Pacific
Ft. Clayton	Canal Zone	09°00′	79°35′	10	Pacific
Ft. Davis	Canal Zone	09°17′	79°55′	50	Atlantic
Ft. Gulick	Canal Zone	09°18′	79°52′	30	Atlantic
Ft. Kobbe	Canal Zone	08°55′	79°35′	20	Pacific
Ft. San Lorenzo	Canal Zone	09°19′	80°01′	15	Atlantic
Ft. Sherman	Canal Zone	09°23′	79°57′	5	Atlantic
Galeta Island	Canal Zone	09°23′	79°52′	2	Atlantic

Panama

Locality	Province	N Latitude	W Longitude	Elevation M	Slope
Gatun	Canal Zone	09°16′	79°55′	30	Atlantic
Gatun Lake Lookout	Canal Zone	09°12′	79°55′	60	Atlantic
Guadeloupe de Arriba	Chiriqui	08°52′	82°33′	2100	Pacific
Gualaca	Chiriqui	08°45′	82°18′	110	Pacific
Hartmann's Finca	Chiriqui	08°50′	82°45′	1340	Pacific
Howard Air Force Base	Canal Zone	08°55′	79°35′	10	Pacific
IHRE Vivero	Chiriqui	08°44′	82°15′	1098	Pacific
Ipetí	Panama	08°55′	78°18′	130	Pacific
Isla Majé (Fig. 925)	Panama	09°08′	78°49′	80	Pacific
Isla Taboga	Panama	08°47′	79°35′	2	Pacific
Islas Perlas	Panama	08°21′	79°00′	2	Pacific
Jaqué	Darien	07°31′	78°10′	2	Pacific
La Chorrera	Panama	08°52′	79°46′	80	Pacific
Las Cumbres	Panama	09°05′	79°32′	160	Pacific
Las Tablas	Los Santos	07°46′	80°17′	40	Pacific
Los Planes	Chiriqui	08°42′	82°53′	1160	Pacific
Madden Dam	Canal Zone	09°13′	79°37′	60	Atlantic
Margarita	Canal Zone	09°20′	79°54′	5	Atlantic
Maria Chiquita	Colón	09°26′	79°42′	350	Atlantic
Miraflores Locks	Canal Zone	09°00′	79°36′	10	Pacific
Miramar	Bocas d. Toro	09°00′	82°15′	2	Atlantic
Natá	Coclé	08°20′	80°31′	20	Pacific
Nusagandí	San Blás	09°19′	78°58′	450	Atlantic
Old Gamboa Road	Canal Zone	09°05′	79°40′	40	Atlantic
Panama City	Panama	09°03′	79°29′	20	Pacific
Paraiso	Canal Zone	09°02′	79°36′	25	Pacific
Penonomé	Coclé	08°31′	80°21′	120	Pacific
Piña Road	Canal Zone	09°16′	79°59′	80	Atlantic
Pipeline Road	Canal Zone	09°07′	79°45′	60	Atlantic
Portobello	Colón	09°33′	79°38′	2	Atlantic
Potrerrillos Abajo	Chiriqui	08°39′	82°29′	900	Pacific
Punta Paitilla	Panama	08°58′	79°31′	10	Pacific
Punta Peña	Bocas d Toro	08°58′	82°10′	10	Atlantic
Quijada del Diablo	Chiriqui	08°45′	82°45′	1515	Pacific
Rambala	Bocas d Toro	08°58′	82°09′	5	Atlantic
Rio Changuinola	Bocas d Toro	08°58′	82°10′	750	Atlantic
Rio Guanche	Colón	09°30′	79°39′	20	Atlantic
Rio Hato	Coclé	08°23′	80°09′	15	Pacific
Rio Piedras	Colón	09°26′	79°45′	300	Atlantic
Rio Serrano	Chiriqui	08°49′	82°52′	1100	Pacific
Rio Tarcarcuna	Darien	08°10′	77°17′	576	Pacific
Rovira	Chiriqui	08°63′	82°50′	600	Pacific
Sabana Grande	Los Santos	07°50′	80°22′	15	Pacific
Sabanitas	Colón	09°19′	79°47′	15	Atlantic
Sajalices	Panama	08°43′	79°52′	50	Pacific
Santa Clara	Chiriqui	08°50′	82°45′	1212	Pacific
Santa Fé	Darien	08°40′	78°09′	340	Pacific

Panama

Locality	Province	N Latitude	W Longitude	Elevation M	Slope
Santa Maria	Herrera	08°07′	80°40′	5	Pacific
Santa Rita Ridge	Colón	09°23′	79°45′	300	Atlantic
Santiago	Veraguas	08°06′	80°58′	180	Pacific
Serrania del Tute	Veraguas	08°07′	81°07′	900	Pacific
Skunk Hollow (Fig. 926)	Canal Zone	09°20′	79°57′	80	Atlantic
Tabernilla	Canal Zone	09°13′	79°80′	37	Atlantic
Tocumen Airport	Panama	09°05′	79°22′	10	Pacific
Vacamonte	Panama	08°52′	79°38′	10	Pacific
Volcan	Chiriqui	08°46′	82°38′	1260	Pacific
Windy Pass (Fig. 927)	Chiriqui	08°41′	82°14′	1159	Pacific

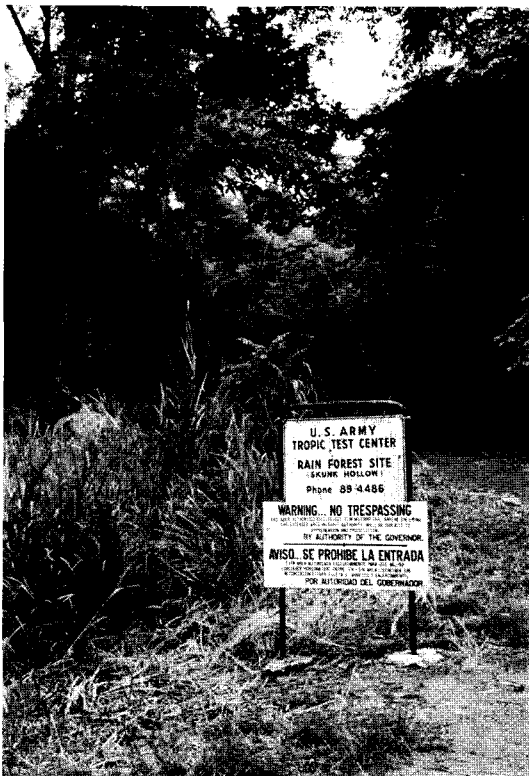


Fig. 926. Skunk Hollow, a U.S. Army tropic test site in the former Canal Zone, Panama, for determining, in part, how live ammunition weathers, July 1975. Photo by BCR. Off Limits! . . . except scarabs can't read.



Fig. 927. "Windy Pass," Chiriqui, Panama, a short stretch of highway traversing a narrow ridge where the insects are blown up from both sides and, hitting still air above the road, fall to the asphalt below, June 1993. Photo by M. L. Jameson.

GLOSSARY

(modified from Torre-Bueno 1937)

- Aciculate** — appearing as if superficially scratched.
- Acuminate** — tapering to a point.
- Alutaceous** — covered with minute cracks, like the human skin.
- Anterior** — front or forward; opposite of posterior.
- Apex** — the apical or distal part of any structure; on the thorax, that part nearest the head.
- Arcuate** — arched, bow-like.
- Areolate** — having areolae, or small spaces in a network.
- Areola Apposita** — the roughened or rugose area on the sides of the pronotal disc.
- Base** — the basal or proximal part of any structure; on the thorax that part nearest the abdomen; on the abdomen that part nearest the thorax.
- Bifurcate** — divided or forked into two.
- Boss** — a low, rounded tumescence.
- Carina** — an elevated ridge or keel.
- Castaneous** — chestnut brown; bright red-brown.
- Chaetoparia** — on the epipharynx of scarabaeoid larvae, the inner part of the paria covered with bristles.
- Claw** — a sharp structure (usually paired) at the apex of the insect leg.
- Clithrum** — in scarabaeoid larvae, a paired short sclerome in the anterior part of the margin of the epipharynx.
- Club** — in the insect antenna, the enlarged distal segments.
- Clypeus** — that part of the head of a scarab in front of the frons; in dorsal view that part of the head that is most anterior.
- Confused** — running together or without a definite pattern, as markings or lines or punctures.
- Congener** — a species belonging to the same genus as another.
- Costae** — in scarabs, the longitudinal and elevated ridges of the wing covers (singular, costa).
- Coxa** — the basal segment of the leg that articulates the leg to the body.
- Crazed** — with small cracks on the surface.
- Crenate** — scalloped with small, blunt, rounded teeth.
- Crenulate** — with small scallops.
- Cretaceous** — chalky white.
- Declivous** — sloping downward.
- Depressed** — slightly concave.
- Detritivore** — an animal that feeds on detritus.
- Disc** — the central upper surface of any part.
- Dorsal** — of or belonging to the upper surface.
- Elytra** — the anterior, chitinous wings of beetles that serve as covers to the hind (flight) wings.
- Emarginate** — notched or with a rounded or obtuse section removed from a margin.
- Endemic** — native, not introduced.
- Epipharynx** — an organ, probably of taste, on the inner surface of the labrum and supposedly corresponding to the palate of vertebrates. In scarab larvae, the complex buccal area forming the inner (or under lining) of the labrum and extending below the clypeus; it includes the following regions: (1) corypha, (2) paria (subdivided into acanthoparia, gymnoparia, and acroparia) bearing the plegmatium, proplegmatium and phobae, with posterior margin strengthened to the right by the dextortorma and to the left by the laeotorma, (3) haptomerum composed of zygom and epizygom, (4) pedium, (5) haplalachus composed of nesia (usually two) and the crepis.
- Epipleuron** — the inflexed (or bent-under) portion of the elytra next to the lateral edge.
- Excised** — with a cut or notch.

- Explanate** — spread out and flattened; applied to a margin.
- Femur** — usually the stoutest segment of the leg, articulated to the body through trochanter and coxa and bearing the tibia at its distal end.
- Flange** — a distinct, gradual or abrupt, expansion of the elytral margin usually at or behind the middle of many *Cyclocephala* species.
- Fovea** — a deep depression with well-marked sides; a pit.
- Frons** — the upper portion of the head capsule behind the clypeus and before the vertex.
- Frontoclypeal Suture** — the transverse suture between the frons and the clypeus.
- Fuscous** — dark brown, approaching black.
- Glabrous** — smooth, without hair.
- Haptomerum** — in scarab larvae, the medio-anterior region of the epipharynx, in front of the pedium and behind the corypha, or behind the apical region consisting of the united acropariae and corypha; composed of the zygum, various sensillae and a series of crepis.
- Helus** (pl. heli) — in scarab larvae, a coarse fixed spine without a cup, belonging to the region of the haptomerum.
- Humerus** — the basal exterior angle of the elytra.
- Imbricate** — appearing somewhat like shingles on a roof or scales on a fish.
- Immaculate** — lacking spots or marks.
- Impressed** — a shallow, depressed area.
- Instar** — the form assumed between molts in the larva, numbered to designate the various periods, e.g., the first instar is the stage between the egg and first molt, etc.
- Interocular** — between the eyes.
- Interval** — the longitudinal space between striae on the elytron of a beetle.
- Keel** — an elevated ridge or carina.
- Labrum** — the upper lip that covers the base of the mandibles and forms the roof of the mouth.
- Lateral** — relating to the side.
- Longitudinal** — in the direction of the long axis.
- Margin** — the more or less narrow part of a surface within the edge.
- Marginal Bead** — a thickened or elevated edge distinct from the surface within; also called marginal line.
- Median** — in or at the middle, pertaining to the middle.
- Mentum** — the distal sclerite of the insect labium bearing the moveable parts, attached to and sometimes fused with the submentum.
- Mesad** — toward the middle of the body.
- Molar Area** — the ridged or roughened grinding surface of the mandibles.
- Monostichous** — with a single row of pali on the last segment of larvae.
- Myrmecophilous** — ant-loving; applied to insects that live in ant nests.
- Nomen Nudum** — (Latin) a specific taxonomic name without a description or an improperly published name; therefore invalid and not available for use.
- Nomen Oblitum** — a name unused since 1899 that does not take precedence over a younger synonym or homonym in prevailing usage (Article 23.9.2 of the 1999 Code).
- Nomen Protectum** — a name that should be preserved but that does not have priority.
- Obsolete** — almost or entirely absent; indistinct; not fully developed.
- Ocellate** — in reference to punctures, those that are ringed by either a rim or a different color.
- Opaque** — without any surface luster; opposite of shiny.
- Palidium** (pl. palidia) — in scarab larvae, a group of pali arranged in a single row or two or more rows and placed either across the venter in front of the lower anal lip, or paired and extending forward and inward from one of the ends of the anal slit, or paired and extending straight, arcuately or obliquely forward from inside of one of the ends of the anal slit; the pali are usually recumbent with their apices directed toward the septula; the palidium may be monostichous, distichous, tristichous, or polystichous depending on whether there are one, two, three, or multiple rows of pali.

- Palus** (pl. pali) — a pointed spine, a component of the palidium.
- Parameres** — two lateral, sclerotized processes arising from the phallobase.
- Phytophagous** — feeding upon plants.
- Piceous** — pitchy black.
- Polystichous** — with more than one row of pali on the last segment in larvae.
- Posterior** — rear or rearward; opposite of anterior.
- Pronotum** — the upper or dorsal surface of the prothorax.
- Proplegmatium** (pl. proplegmata) — in scarab larvae, a paired space with a plicate surface inside and usually somewhat in front of a plegmatium.
- Prosternal Process** — the small to large, usually columnar process on the venter of the prosternum immediately behind the procoxae in Dynastinae.
- Pubescent** — covered with short setae.
- Punctate** — with impressed points or punctures.
- Punctate-striate** — with rows of punctures, simulating and taking the place of striae.
- Puncture** — a small impression on the hard surface of the body.
- Pygidium** — the last segment usually left exposed by the elytra.
- Raster** — in scarab larvae, a complex of definitely arranged bare places, hairs, and spines on the ventral surface of the last abdominal segment in front of the anus.
- Recurved** — bending backwards or back on itself.
- Reflexed** — a margin that bends upward.
- Rufotestaceous** — reddish yellow.
- Rugopunctate** — a surface both rugose and punctate; rugae and punctures mixed.
- Rugose** — wrinkled.
- Rugulose** — minutely wrinkled.
- Rufous** — pale red.
- Saprophagous** — feeding on dead or decaying vegetable matter.
- Scalloped** — with the edge marked with rounded hollows.
- Scabriculous** — minutely or finely, irregularly roughened.
- Scabrous** — irregularly roughened.
- Scape** — the first or basal segment of the antenna.
- Scutellum** — in Coleoptera, the triangular piece between the bases of the elytra.
- Septula** — in scarab larvae, a narrow bare region of the raster between a single transverse palidium and the base of the lower anal lip, or between a pair of oblique palidia diverging backward to the end of the anal slit, or between a pair of backward diverging or parallel or curved palidia to inside the ends of the anal slit.
- Setae** — a small hair; either minute, short, or long and either slender or robust.
- Setigerous** — bearing setae.
- Shagreened** — covered with a closely-set roughness, like leather.
- Shiny, Shining** — with a lustrous surface.
- Sinuate** — wavy, specifically of edges or margins.
- Spiracle** — the lateral opening on the segments of the insect body through which air enters the tracheae.
- Spur** — a spine-like appendage of the cuticle, articulated or not; generally on the tibia.
- Stadium** (pl. stadia) — the interval of time between the molts of a larva.
- Stem** — the segments of the antenna exclusive of the club.
- Sternite** — the ventral part of a segment.
- Stria** (pl. striae) — in Coleoptera, a longitudinal depressed line or furrow, frequently with punctures, usually extending from the base to the apex of the elytra.
- Stridulate** — to make a creaking, grating, or hissing sound or noise by rubbing two roughened surfaces against each other.
- Sub** — a Latin prefix meaning not quite or almost.
- Subequal** — similar but not quite equal in form, size, or other characters.

- Suffused** — clouded or obscured by a darker color.
- Sulcate** — deeply furrowed or grooved.
- Sulcus** — a furrow or groove.
- Suture** — the line of juncture of the elytra.
- Tarsomere** (pl. tarsomeres) — one of the segments of the tarsus.
- Tarsungulus** — the apical, claw-bearing joint in scarab larvae.
- Tarsus** (pl. tarsi) — the foot; the jointed appendage attached to the apex of the tibia; the distal part of the insect leg consisting (in scarabs) of five segments.
- Tawny** — brownish yellow, like the color of a tanned hide.
- Teges** — in scarab larvae, a continuous, dense or sparse, patch of hooked or straight, large or small, outward pointing or erect setae occupying the hind part (or almost the whole) of the tenth abdominal venter when the palidium is absent.
- Teneral** — the condition of the adult shortly after emergence when it is not entirely hardened or fully colored.
- Tergite** — the dorsal part of a segment.
- Testaceous** — light brownish-yellow in color.
- Tibia** — the fourth division of the leg, articulated at the proximal end to the femur and bearing on the distal end of the tarsi.
- Tomentose** — covered with tomentum.
- Tomentum** — a form of pubescence composed of matted setae; especially notable in some Agaocephalini.
- Tooth** — an acute angulation; a short pointed process from an appendage or margin.
- Transverse** — broader than long, or the dimension going across.
- Trochanter** — a sclerite of the insect leg, sometimes divided, between the coxa and femur.
- Truncate** — cut off squarely at the apex.
- Tubercle** — a small, conical bump.
- Tuberculate** — having tubercles.
- Tumescent** — somewhat swollen or puffed up.
- Tumid** — swollen, enlarged.
- Umbilicate** — navel-shaped; often used for a puncture with a small nub at the bottom.
- Umbone** — an elevated knob situated on the humeral or apical angles of the elytra, hence humeral umbone and apical umbone.
- Unarmed** — lacking spurs, spines, or armature of any kind.
- Velutinous** — a velvety, dense, short pubescence seen in many Agaocephalini.
- Venter** — the under surface of the body in general.
- Ventral** — pertaining to the under surface of the body.
- Vertex** — the top of the head between the frons and occiput.

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OF COSTA RICA AND PANAMA**

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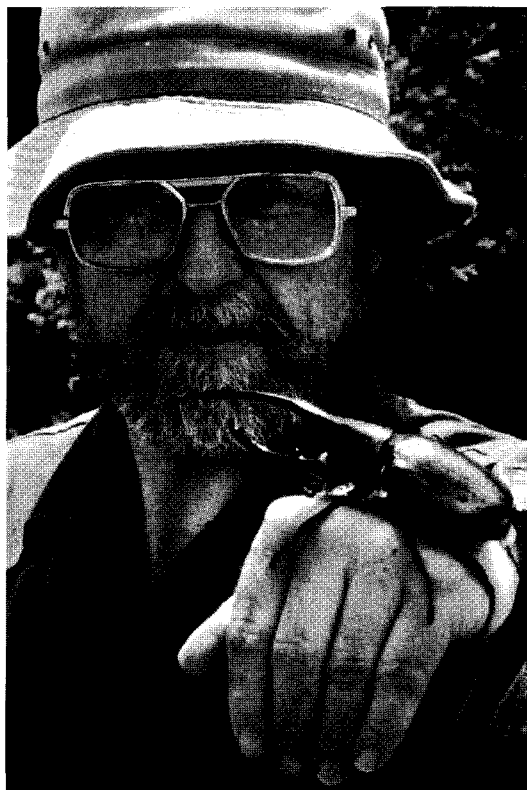
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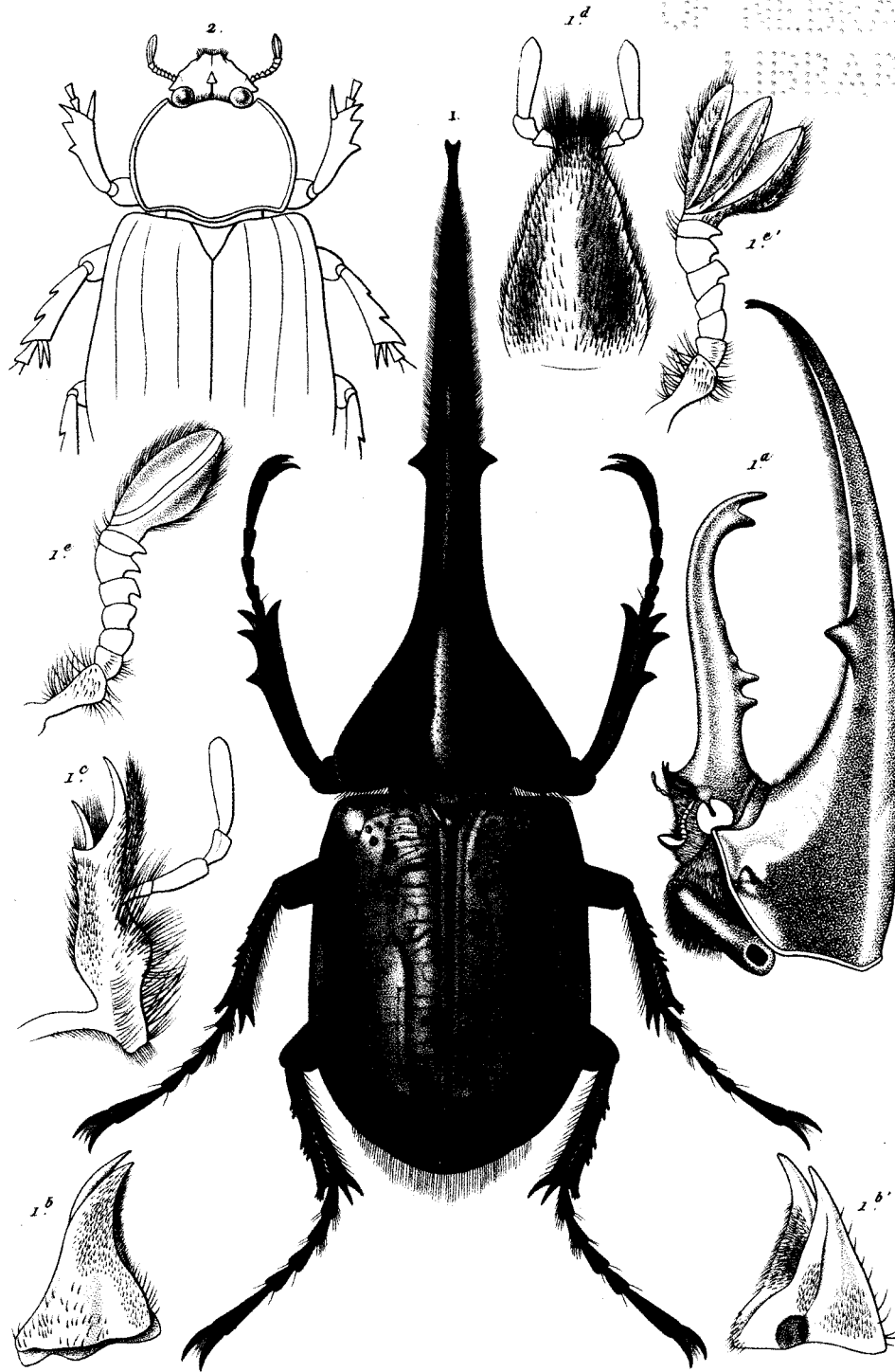
ABOUT THE AUTHOR

Dr. Brett Ratcliffe is the Curator of Insects and Professor at the University of Nebraska State Museum and the Department of Entomology. He is a specialist in the taxonomy, biology, ecology, phylogeny, and biogeography of scarab beetles, especially those of the Neotropics. He has conducted extensive field research in Japan, North America, Mexico, Central America, South America, and South Africa. From 1976 to 1978 he was the head of the systematics research collections of entomology for the National Institute of Amazonian Research (INPA) in Manaus, Brazil. He is a Research Associate of the Department of Entomology at the National Museum of Natural History (Smithsonian Institution) in Washington, D.C., and also serves on the International Editorial Board of *Folia Entomologica Mexicana*. He and his colleague, Dr. Mary Liz Jameson, transferred the U.S. National Collection of pleurostict scarab beetles from the Smithsonian Institution to Scarab Central at the University of Nebraska State Museum in 1999 for a lengthy period of off-site enhancement.

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Brett Ratcliffe with *Dynastes hercules* male at Fortuna Dam, Chiriqui, Panama, May 1995. Photo by M.L. Jameson.



Blanchard pinx.

Emile Bl. part. scol. del.

Lebrun sc.

SCARABÉE HERCULE (mâle) (*Scarabæus hercules* Lin.)

