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Natural History Museum of Los Angeles County

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ABSTRACT. This study is a revision of the genus *Phanaeus* as defined by Edmonds (1972). The introduction includes a history of the genus, a key separating it from related genera, a discussion of taxonomic characters and primary type material, a summary of the biology and geography of the genus, and conclusions about its evolution. The systematic section treats 48 species and subspecies in two subgenera, one of which, *Notiophanaeus,* is new. *Notiophanaeus* comprises five species groups embracing 15 mostly South American species. *Phanaeus, sen. str.,* includes 31 species and subspecies arranged in eight species groups. Keys separate subgenera, species groups, species, and subspecies. *Phanaeus labreae* (Pierce) and *P. antiquus* Horn, known from fossil deposits, are considered *incertae sedis.*

One new subspecies is described, *P. (P.) triangularis texensis.* The following new combinations result from reductions in rank from species to subspecies: *P. (P.) amethystinus guatemalensis* Harold, *P. (P.) tridens pseudofurcosus* Balthasar, and *P. (P.) wagneri pilatei* Harold. Neotypes are designated for the following taxa: *Copris triangularis* Say, *C. quadridens* Say, *Phanaeus tridens* Laporte-Castelnau, *P. demon* Laporte-Castelnau, *P. laevicollis* LaPorte-Castelnau (= *P. kirbyi* Vigors), *P. difformis* LeConte, *P. igneus* Macleay, and *P. vindex* Macleay. Lectotypes are designated for the following (valid name, where appropriate, appears parenthetically preceded by =): *Scarabaeus carnifex* Linnaeus 1767, not 1758 (= *P. vindex* Macleay); *P. minos* Erichson (= *P. meleagris* Blanchard); *P. bogotensis* Kirsch (= *P. hermes* Harold); *P. torrens* LeConte (= *P. triangularis* [Say]); *P. pyrois* Bates; *P. furiosus* Bates; *P. eximius* Bates; *P. beltianus* Bates; *P. scutifer* Bates; *P. excelsus* Bates (= *P. demon* Laporte-Castelnau); *P. obliquans* Bates (= *P. demon* Laporte-Castelnau); *P. scintillans* Bates (= *P. mexicanus* Harold); and *P. tepanensis* Bates (= *P. amethystinus guatemalensis* Harold).

The following new synonymy is proposed in *Notiophanaeus* (synonym precedes valid name): *P. kirbyi truncaticornis* Olsoufieff = *P. kirbyi* Vigors, *P. blanchardi* Olsoufieff = *P. pyrois* Bates, and *P. funereus* Balthasar = *P. pyrois* Bates. The following are new synonyms in *Phanaeus, sen. str.: P. bogotensis* Kirsch = *P. hermes* Harold, *P. lugens* Nevinson = *P. prasinus* Harold, *P. furcosus* Felsche = *P. furiosus* Bates, *P. herbeus* Bates = *P. daphnis* Harold, *P. coerulus* Bates = *P. daphnis* Harold, *P. tricornis* Olsoufieff = *P. daphnis* Harold, *P. niger* Olsoufieff = *P. triangularis* (Say), *P. obliquans* Bates = *P. demon* Laporte-Castelnau, *P. obliquans* Bates = *P. demon* Laporte-Castelnau, *P. excelsus* Bates = *P. demon* Laporte-Castelnau, *P. scintillans* Bates = *P. mexicanus* Harold, *P. martinezi* Halffter = *P. amethystinus* Harold, *P. quadridens borealis* Olsoufieff = *P. quadridens* (Say), *P. vindex rubervirens* Robinson = *P. vindex* Macleay, *P. floridanus* Olsoufieff = *P. igneus* Macleay, and *P. difformis magnificens* Robinson = *P. difformis* LeConte.

A list of all known available names and a previously established synonymy are included in the introduction. Geographical distribution data for all species and subspecies are contained in the appendix.

RESUMEN. Este trabajo es una revisión del género *Phanaeus* Macleay, según Edmonds (1972). La parte introductoria consiste en una relación de la historia taxonómica del género, una clave que lo separa de géneros vecinos, un resumen de la biología y geografía del grupo, y una serie de conclusiones acerca de su evolución. La sección sistemática trata de 48 especies y subespecies colocadas en dos subgéneros, de los cuales *Notiophanaeus* es nuevo. *Notiophanaeus* comprende cinco grupos de especies, que, en su mayoría, son sudamericanas. *Phanaeus, sen. str.,* consta de 31 especies y subespecies, principalmente mexicanas y estadounidenses, clasificadas en ocho grupos. Se presentan claves para la identificación de subgéneros, grupos de especies, especies y subespecies. *Phanaeus labreae* (Pierce) y *P. antiquus* Horn son especies supuestamente extintas de *incertae sedis.* Los datos de distribución geográfica comprenden el apéndice.

Se describe una nueva subespecie, *P. (P.) triangularis texensis.* El nivel taxonómico de tres taxa, anteriormente consideradas como especies, se baja a subespecie. Se designan neotipos por ocho especies y lectotipos por otras trece. Se señalan 19 casos de nueva sinonimia.

INTRODUCTION

The present paper is a continuation of my previous work on the phanaeine dung beetles (Edmonds, 1972). One of the more interesting problems I left open at that time was the systematics of the genus *Phanaeus.* These are very well known beetles, but until now the only comprehensive study of species has been that of Gregor d'Olsoufieff (1924). The systematic portion of the present study is based on the examination of more than 17,000 specimens, including most primary types, from over 75 institutional and private collections. It is preceded by a brief historical account, a summary of the taxonomy of the genus, and a discussion of its biology, geography, and evolution.

HISTORY OF THE GENUS *PHANAEUS*

William Sharp Macleay was the first serious student of what today is generally known as the family Scarabaeidae. In 1819 he published the first part of *Horae Entomologicae,* an elaborate reexamination of Linnaeus' genus *Scarabaeus* (as defined in the twelfth edition of *Systema Naturae,* 1767) within the somewhat broader taxonomic context of P. A. Latreille's "Lamellicornes" (1825, and elsewhere). While Macleay was primarily concerned with the

"higher" classification of Lamellicornes by establishing five-part "circular relationships" among families he recognized, he was a strong believer in the "naturalness" of the genus. Macleay (1819) thus included the original descriptions of a number of new scarabaeid genera, one of which is *Phanaeus.*

Macleay defined *Phanaeus* primarily on the basis of the shape of the antennal lamellae and arranged the ten species he recognized according to five "types." His "Typus 5," which included *carnifex, sensu* Linnaeus, 1767, *vindex* as a variation of *carnifex,* and *igneus* as species *inquirenda,* is the least inclusive direct antecedent of *Phanaeus* as defined here.

Macleay's concept of *Phanaeus* endured almost intact until d'Olsoufieff's revision of the "Tribu Phanaeides" in 1924. The only significant change before then was Laporte-Castelnau's (1840) creation of *Oxysternon,* which received, among others, those species comprising Macleay's "Typus 4." During the latter part of the nineteenth century, however, many new species were described. Of the 46 species and subspecies recognized here, 34 were named between 1830 and 1890 as well as many others later placed in synonymy. Especially important in expanding the size of *Phanaeus* and related genera (*sensu* Edmonds, 1972) were the works of Harold (1863, 1868a,b, 1871b, 1875a,b) and Bates (1887, 1889). The first key to species in a modern format appeared in Harold's (1863) review of the Mexican species of *Phanaeus.* The genus was cataloged by Gemminger and Harold (1869), Nevinson (1892a), Gillet (1911b), and, most recently, Blackwelder (1944). Regional reviews postdating d'Olsoufieff's revision include Pessoa (1934; Brazil), Islas (1942; Mexico), and Robinson (1948; United States).

Gregor d'Olsoufieff's (1924) revision largely conserved the taxonomic limits of *Phanaeus* (excluding *Oxysternon*) originally established by Macleay, although the number of species had increased more than nine-fold in the preceding 105 years. However, he reorganized what had become a highly diverse group into five subgenera: *Sulcophanaeus, Megaphanaeus, Coprophanaeus, Metallophanaeus,* and *Phanaeus, sen. str.* (*Scarabaeus mimas* L., included in Macleay's "Typus 2," was moved to the new genus *Taurocopris,* now known as *Diabroctis.*) The first of these subgenera was the descendent of Macleay's "Typus 3" and remainder of "Typus 2"; the second and third descended from "Typus 1" (neither species assigned to *Metallophanaeus* was known to Macleay). *Phanaeus, sen. str.,* preserved Macleay's "Typus 5" and was the initial step in restricting the taxonomic scope of the name *Phanaeus.*

My revision (Edmonds, 1972) of the supraspecific taxonomy of the phanaeines resulted in the splitting of *Phanaeus* into three genera based largely upon the subgenera created by Olsoufieff (1924). Accordingly, *Phanaeus* became one of nine genera (and eight subgenera) comprising the phanaeine genus group (not recognized by me as a tribe or subtribe). The sense of *Phanaeus* used here is the same as that I defined in 1972.

PRESENT CLASSIFICATION

TAXONOMIC CHARACTERS

The characters used in the keys, descriptions, and elsewhere employ the terminology established by Edmonds (1972). Easily assessed morphological characters separate most species of the genus. However, the observation I made in 1972 still holds true in spite of the introduction of many new characters here. The incidence of irregular distribution of character states, and the continuous variation of characters whose extremes are easily definable, make the taxonomy of some groups difficult. Most of these difficulties occur in *Phanaeus, sen. str.,* and are discussed in the taxonomic section.

Pronotal sculpturing is widely used here to describe supraspecific taxa. Sculpturing in the genus varies from a smooth condition virtually devoid of punctures or other relief (Fig. 166) to extreme rugosity (Fig. 339). In 1972 I recognized only two, very generalized states of pronotal sculpturing: "smooth-punctate" and "roughened" (or "rugose"). Present purposes, however, require that these descriptors be refined. The smooth-punctate condition is characteristic of the subgenus *Notiophanaeus.* However, in certain instances described in the introduction to that subgenus, it can be obscured by superposition of various kinds of roughening. In *Phanaeus, sen. str.,* the pronotum is always rugose to some degree, often entirely so. The kind of roughening in this subgenus falls into two general categories: granulation and granulorugosity. In the former case (Figs. 224, 236, 253), sculpturing consists of discrete granules, the size and density of which can vary among species and species groups. An area described as granulate for a given taxon will bear granules of usually uniform size that only infrequently coalesce into larger entities. Granulorugosity, on the other hand, consists of a heterogenous mixture of asperities of various shapes and sizes producing a highly fractured surface (Figs. 274, 310, 319, 320). The overall texture produced by granulorugosity varies greatly and continuously such as to preclude any objective definition of substates. Thus, granulorugose is an imprecise term describing a roughened texture that is not clearly granulate.

Phanaeus species are very efficient diggers, and those structures used directly for digging are highly subject to wear. The effects of wear can lead to errors in assessing the shapes of the anterior margin of the clypeus and front tibiae. In very extreme cases, wear can alter the nature of surface sculpturing (especially shagreening) and coloration.

Most *Phanaeus* are brilliantly colored (Figs. 1–107). Intraspecific variation in coloration and color pattern is the rule and can be very striking. Moreover, individuals themselves are seldom uniformly

colored. While its taxonomic usefulness is limited, coloration is an important aspect of the morphology of these beetles and is addressed in all species descriptions. Assessment of coloration should be made under low magnification (×5–10) with a high-intensity, broad-spectrum light source, such as halogen.

A summary of known distributional information (geographical, ecological, altitudinal, and temporal) is included in the treatment of each species. Detailed information is contained in the appendix. Geographical data can be critical in identifying certain species, especially those in which females and smaller males are indistinguishable morphologically.

Traditionally, much taxonomic emphasis has been placed on the secondary sexual features of *Phanaeus,* especially the shape of the cephalic horn and pronotum of the male. Male armature, however, is subject to often extreme allometric intrapopulation variation (as in Fig. 214) as well as to interpopulational differences in shape (as in Figs. 275–280). In general, taxonomically reliable male sexual features are characteristic only of large, well-developed ("major") individuals, although there can be some striking exceptions (see, e.g., the case of *Phanaeus demon*). Secondary sexual features, particularly the shape of the pronotum, are much more useful among females.

A potential source of morphological characters not explored exhaustively during this study is the structure of the genitalia. Zunino (1971, 1978, 1979, 1983) relied successfully on the bursa copulatrix of the female for reliable taxonomic characters in *Onthophagus.* I attempted, without success, to find similar characters applicable to the definition of species only in the particularly difficult cases of the *mexicanus* and *tridens* species groups of *Phanaeus, sen. str.*

Proper assessment of many taxonomic characters used here requires viewing under magnification. Where appropriate, the minimum augmentation recommended is noted.

PRIMARY TYPE MATERIAL

I have examined primary type material for the great majority of species group names considered in this study. The only valid name used for which no type was examined or designated is *Phanaeus lunaris* Taschenberg.

In several cases I have found it necessary to designate neotypes and lectotypes; particulars concerning these specimens appear in the comments section of the species in question. Those names for which neotypes are designated are as follows (described as *Phanaeus* unless indicated otherwise; valid name, where appropriate, indicated parenthetically): *Copris triangularis* Say, *Copris quadridens* Say, *tridens* Laporte-Castelnau, *demon* Laporte-Castelnau, *laevicollis* Laporte-Castelnau (= *kirbyi* Vigors), *difformis* Leconte, *igneus* Macleay, and *vindex* Macleay. Lectotypes are designated in the following cases: *Scarabaeus carnifex* Linnaeus, 1767; *minos* Erichson (= *meleagris* Blanchard); *bogotensis* Kirsch (= *hermes* Harold); *pyrois* Bates; *furiosus* Bates; *eximius* Bates; *beltianus* Bates; *scutifer* Bates; *excelsus* Bates (= *demon* Laporte-Castelnau); *obliquans* Bates (= *demon* Laporte-Castelnau); *scintillans* Bates (= *mexicanus* Harold); *tepanensis* Bates (= *amethystinus guatemalensis* Harold); and *torrens* LeConte (= *triangularis* Say).

The Thomas Say Collection has been long presumed to have been destroyed in the 1830s. Since Say is known to have worked with the collections of John E. LeConte (which became the nucleus of the collection of his son, John L. LeConte) and T. W. Harris (A. Newton, pers. comm.), it has been customary to select necessary neotypes of Say species from the Harris or LeConte Collection, both of which are housed in the Museum of Comparative Zoology, Harvard University. In neither case (*Copris triangularis* nor *C. quadridens*) for which a neotype of a Say species was necessary did acceptable specimens exist in either of these two collections.

Over the period of roughly 1800–1890, the Macleays of Sydney, Australia (Alexander; his son, William Sharp; and nephew, William John), together amassed an enormous insect collection of great historical importance (Horning, 1984, and references therein). Their combined collections form the Macleay Museum at the University of Sydney. I was unable to locate types of either *vindex* or *igneus* in material from the Macleay Collection, including that part transferred to the Australian National Insect Collection in Canberra in 1969 (Britton and Stanbury, 1981).

The whereabouts of type material for species described by François L. N. de C. Laporte (who later in life received the French royal title, Comte de Castelnau) has long been a mystery (see, e.g., Paulian, 1976). Many phanaeines (*Phanaeus* and related genera) exist in the Castelnau Collection at the National Museum of Victoria in Melbourne, Australia, where Laporte served as Counsel General of France. Specimens bearing labels in Laporte-Castelnau's hand also appear in the Godfrey Howitt Collection, also in Melbourne (A. Neboiss, pers. comm.). Neither collection includes designated type material, nor does either include specimens that can reasonably be taken as typical. Laporte wrote under his surname as well as his title, Comte de Castelnau. As a result, authorship of Laporte species appears in the literature alternately as Laporte or Castelnau. For bibliographic purposes, I have elected to refer to him as Laporte-Castelnau.

Arnaud (1982a) is responsible for the designation of many phanaeine lectotypes in the collections of the Muséum National d'Histoire Naturelle in Paris. In the introduction to his paper, he states, in the case of species described by H. W. Bates (1887, 1889), "En effet, les seuls spécimens portant la désignation manuscrite de l'espèce par la main de l'au-

[1] *Phanaeus splendidulus* ♂

[2] *Phanaeus splendidulus* ♂

[3] *Phanaeus splendidulus* ♀

[4] *Phanaeus dejeani* ♂

[5] *Phanaeus dejeani* ♀

[6] *Phanaeus melibaeus* ♂

[7] *Phanaeus melibaeus* ♀

[8] *Phanaeus haroldi* ♂

[9] *Phanaeus haroldi* ♀

[10] *Phanaeus palaeno* ♂

[11] *Phanaeus palaeno* ♂

[12] *Phanaeus palaeno* ♀

[13] *Phanaeus kirbyi* ♂

[14] *Phanaeus kirbyi* ♀

[15] *Phanaeus bispinus* ♂

[16] *Phanaeus bispinus* ♀

[17] *Phanaeus endymion* ♂

[18] *Phanaeus endymion* ♀

[19] *Phanaeus pyrois* ♂

[20] *Phanaeus pyrois* ♀

[21] *Phanaeus halffterorum* ♂

[22] *Phanaeus halffterorum* ♀

Figures 1 - 22. Shown natural size.

[23] *Phanaeus chalcomelas* ♂

[24] *Phanaeus chalcomelas* ♀

[25] *Phanaeus cambeforti* ♂

[26] *Phanaeus cambeforti* ♀

[27] *Phanaeus meleagris* ♂

[28] *Phanaeus meleagris* ♀

[29] *Phanaeus meleagris* ♂

[30] *Phanaeus achilles* ♂

[31] *Phanaeus achilles* ♀

[32] *Phanaeus hermes* ♂

[33] *Phanaeus hermes* ♀

[34] *Phanaeus prasinus* ♂

[35] *Phanaeus prasinus* ♂

[36] *Phanaeus prasinus* ♀

[37] *Phanaeus beltianus* ♂

[38] *Phanaeus beltianus* ♀

[39] *Phanaeus sallei* ♂

[40] *Phanaeus sallei* ♀

[41] *Phanaeus howdeni* ♂

[42] *Phanaeus howdeni* ♀

Figures 23 - 42. Shown natural size.

teur sont à Paris, alors que les exemplaires représentés en illustration dans l'ouvrage [Biologia Centrali-Americana] où la description a été publiée, se trouvent à Londres. J'ai dû trancher et ai appliqué l'article 74B du Code International de Nomenclature Zoologique. J'ai considéré comme lectotypes les exemplaires du British Museum of Natural History of London portant l'étiquette imprimée 'sp. figured.' " Unfortunately, Article 74(d) of the Code prohibits collective designation of lectotypes, and it has been necessary here to redesignate the specimens figured by Bates (and bearing Arnaud's labels) as lectotypes in the cases of the following species described by him in Biologia Centrali-Americana: *pyrois, scutifer, furiosus, eximius, beltianus, scintillans, mirabilis, tepanensis,* and *excelsus.*

TAXONOMIC SUMMARY

Below is a summary of the classification established later in this work. It is followed by a listing of all other known available species-group names here considered invalid for the reason specified.

Phanaeus Macleay, 1819

Subgenus *NOTIOPHANAEUS*, New Subgenus

splendidulus group: *splendidulus* (Fabricius), 1781
dejeani Harold, 1868
melibaeus Blanchard, 1843
haroldi Kirsch, 1871
palaeno group: *palaeno* Blanchard, 1843
kirbyi Vigors, 1825
endymion group: *endymion* Harold, 1863
pyrois Bates, 1887
halffterorum Edmonds, 1979
bispinus group: *bispinus* Bates, 1868
alvarengai Arnaud, 1982
chalcomelas group: *chalcomelas* (Perty), 1830
cambeforti Arnaud, 1982
meleagris Blanchard, 1843
achilles Boheman, 1858

Subgenus *PHANAEUS, SEN. STR.*

hermes group: *hermes* Harold, 1868
prasinus Harold, 1868
amethystinus group: *amethystinus* Harold, 1863
a. amethystinus, sen. str., New Status
a. guatemalensis Harold, 1871, New Combination
melampus Harold, 1863
quadridens group: *quadridens* Say, 1835
damocles Harold, 1863
palliatus Sturm, 1843
tridens group: *tridens* Laporte-Castelnau, 1840
t. tridens, sen. str., New Status
t. pseudofurcosus Balthasar, 1939, New Combination
eximius Bates, 1887
nimrod Harold, 1863
furiosus Bates, 1887
daphnis Harold, 1863
beltianus group: *beltianus* Bates, 1887
howdeni Arnaud, 1984
sallei Harold, 1863
triangularis group: *triangularis* Say, 1823
t. triangularis, sen. str., New Status
t. texensis, New Subspecies
adonis Harold, 1863
mexicanus group: *mexicanus* Harold, 1863
amithaon Harold, 1875
demon Laporte-Castelnau, 1840
flohri Nevinson, 1892
scutifer Bates, 1887
wagneri Harold, 1863
w. wagneri, sen. str., New Status
w. pilatei Harold, 1863, New Combination
lunaris Taschenberg, 1870
vindex group: *vindex* Macleay, 1819
igneus Macleay, 1819
difformis LeConte, 1847
INCERTAE SEDIS *labreae* (Pierce), 1946
antiquus Horn, 1876

Invalid Names Assigned to *Phanaeus* Macleay

babori Balthasar, 1939: jr. subj. syn. *nimrod* Harold
blanchardi Harold, 1871: jr. obj. syn. *palaeno* Blanchard
blanchardi Olsoufieff, 1924: jr. prim. hom. *blanchardi* Harold (permanently unavailable; valid name: *pyrois* Bates)
bogotensis Kirsch, 1871: jr. subj. syn. *hermes* Harold
borealis Olsoufieff, 1924: jr. subj. syn. *quadridens* (Say)
bothrus Blackwelder, 1944: jr. obj. syn. *olsoufieffi* Balthasar (valid name: *pyrois* Bates)
carnifex Linnaeus, 1767: jr. prim. hom. *Scarabaeus carnifex* Linnaeus, 1758 (permanently unavailable; valid name: *vindex* Macleay)
charon Harold, 1880: jr. subj. syn. *lunaris* Taschenberg
coerulus Bates, 1887: jr. subj. syn. *daphnis* Harold
corydon Blanchard, 1843: jr. subj. syn. *splendidulus* (F.)

cyanellus Robinson, 1938: jr. subj. syn. *vindex* Macleay
digitalis Olsoufieff, 1924: jr. subj. syn. *bispinus* Bates
divisus Harold, 1863: jr. subj. syn. *mexicanus* Harold
excelsus Bates, 1889: jr. subj. syn. *demon* Laporte-Castelnau
exisicornis Balthasar, 1939: jr. subj. syn. *palaeno* Blanchard
floridanus Olsoufieff, 1924: jr. subj. syn. *igneus* Macleay
floriger Kirby, 1818: jr. subj. syn. *splendidulus* (F.)
foveolatus Harold, 1880: jr. subj. syn. *achilles* Boheman
frankenbergi Balthasar, 1939: jr. subj. syn. *tridens* Laporte-Castelnau
funereus Balthasar, 1939: jr. subj. syn. *pyrois* Bates
furcosus Felsche, 1901: jr. obj. syn. *furiosus* Bates
goidanichi Balthasar, 1939: jr. subj. syn. *triangularis* (Say)
herbeus Bates, 1887: jr. subj. syn. *daphnis* Harold
laevicollis Laporte-Castelnau, 1840: jr. subj. syn. *kirbyi* Vigors
laevipennis Sturm, 1843: jr. subj. syn. *quadridens* (Say)
lugens Nevinson, 1892: jr. subj. syn. *prasinus* Harold
magnificens Robinson, 1948: jr. subj. syn. *difformis* LeConte
martinezi Halffter, 1955: jr. subj. syn. *amethystinus* Harold
minos Erichson, 1847: jr. subj. syn. *meleagris* Blanchard
mirabilis Bates, 1887: jr. prim. hom. *mirabilis* Harold, 1877 (permanently unavailable; valid name: *demon* Laporte-Castelnau)
niger Olsoufieff, 1924: jr. subj. syn. *triangularis* (Say)
obliquans Bates, 1889: jr. subj. syn. *demon* Laporte-Castelnau)
olsoufieffi Balthasar, 1939: jr. subj. syn. *pyrois* Bates
pegasus Sturm, 1843: jr. subj. syn. *demon* Laporte-Castelnau
planicollis Perty, 1830: jr. subj. syn. *kirbyi* Vigors
rubervirens Robinson, 1948: jr. subj. syn. *vindex* Macleay
scintillans Bates, 1887: jr. subj. syn. *mexicanus* Harold
sculpturatus Olsoufieff, 1924: jr. subj. syn. *melibaeus* Blanchard
substriolatus Balthasar, 1939: jr. subj. syn. *daphnis* Harold
subtricornis Perty, 1830: jr. subj. syn. *kirbyi* Vigors
tepanensis Bates, 1889: jr. subj. syn. *guatemalensis* Harold
torrens LeConte, 1847: jr. subj. syn. *triangularis* (Say)
tricornis Olsoufieff, 1924: jr. subj. syn. *daphnis* Harold
truncaticornis Olsoufieff, 1924: jr. subj. syn. *kirbyi* Vigors
violaceus Laporte-Castelnau, 1840: jr. subj. syn. *quadridens* (Say)

BIOLOGY, GEOGRAPHY, AND EVOLUTION OF *PHANAEUS*

The following account is a summary of current knowledge about the biology and geography of *Phanaeus* and my views on the origin and evolution of the group. Various aspects of the ecological relationships and behavior of the genus are treated in detail by Halffter and Matthews (1966), Halffter and Edmonds (1982), and Hanski and Cambefort (1991).

With very few exceptions, members of the genus are preferentially coprophagous, exploiting the moist excrement of large herbivores (cattle, tapirs, etc.) and omnivores (humans, monkeys, swine, certain carnivores, etc.). Only seldom do they utilize the drier excrements of equines, deer, sheep, goats, and other ovids. The range of acceptable food sources can, however, be very broad in some cases. *Phanaeus endymion,* for example, a primarily coprophagous species inhabiting tropical evergreen and semideciduous forests in Mexico, has been collected on carrion, decomposing fungi of various sorts, and decaying fruit and leaves, as well as traps baited with propionic acid. Many otherwise coprophagous species at least occasionally utilize carrion or other decomposing substances. *Phanaeus bispinus* and *meleagris* are reported to be preferentially necrophagous (Halffter and Matthews, 1966), and *P. halffterorum* appears to be exclusively mycetophagous (Edmonds, 1979).

Phanaeus species are good fliers. With the possible exception of *halffterorum,* no species is known to be strictly nocturnal. Field data suggest that sympatric species often display different diel activities (Fincher et al., 1971). The genus comprises burrowing (as opposed to ball-rolling) species. When a food source (such as a dropping) is found, the adult quickly digs a tunnel and provisions it with pieces carved from the source. Under conditions of environmental stress, these beetles will sometimes push a fragment across the surface before digging a tunnel (Halffter and Matthews, 1966; Halffter et al., 1974). The nesting behavior of *Phanaeus* conforms to Pattern II as defined by Halffter and Edmonds (1982). During the breeding season, the male and female cooperate in provisioning a nesting gallery, and the female subsequently uses the stored food in constructing brood balls. Each pear-shaped brood ball of *Phanaeus* is fabricated in a separate chamber and consists of a core of compressed food surrounded by a thick layer of tightly packed soil. In the narrower upper pole of the earthen cover is a small chamber containing a single egg.

As is common for Scarabaeinae in general, the life cycle of species in habitats with a distinct dry (or drier) season is closely coordinated with rains during the warmer portions of the year. No *Phanaeus* occur where rains are concentrated during the colder months (e.g., northern Baja California, and California). In areas with a pronounced dry season, many species experience a surface population ex-

[43] *Phanaeus quadridens* ♂

[44] *Phanaeus quadridens* ♂

[45] *Phanaeus quadridens* ♀

[46] *Phanaeus damocles* ♂

[47] *Phanaeus damocles* ♀

[48] *Phanaeus palliatus* ♂

[49] *Phanaeus palliatus* ♂

[50] *Phanaeus palliatus* ♀

[51] *Phanaeus melampus* ♂

[52] *Phanaeus melampus* ♀

[53] *Phanaeus a. amethystinus* ♂

[54] *Phanaeus a. amethystinus* ♀

[55] *Phanaeus a. guatemaleusis* ♂

[56] *Phanaeus a. guatemaleusis* ♂

[57] *Phanaeus a. guatemaleusis* ♀

[58] *Phanaeus t. triangularis* ♂

[59] *Phanaeus t. triangularis* ♀

[60] *Phanaeus t. texensis* ♂

[61] *Phanaeus t. texensis* ♀

[62] *Phanaeus t. texensis* ♀

[63] *Phanaeus adonis* ♂

[64] *Phanaeus adonis* ♂

[65] *Phanaeus adonis* ♀

Figures 43 - 65. Shown natural size.

[66] *Phanaeus flohri* ♂

[67] *Phanaeus lunaris* ♂

[68] *Phanaeus lunaris* ♀

[69] *Phanaeus demon* ♂

[70] *Phanaeus demon* ♀

[71] *Phanaeus demon* ♀

[72] *Phanaeus demon* ♂

[73] *Phanaeus demon* ♂

[74] *Phanaeus w. wagneri* ♂

[75] *Phanaeus w. pilatei* ♂

[76] *Phanaeus w. pilatei* ♀

[77] *Phanaeus scutifer* ♂

[78] *Phanaeus scutifer* ♀

[79] *Phanaeus mexicanus* ♂

[80] *Phanaeus mexicanus* ♀

[81] *Phanaeus mexicanus* ♂

[82] *Phanaeus mexicanus* ♂

[83] *Phanaeus amithaon* ♂

[84] *Phanaeus amithaon* ♀

[85] *Phanaeus amithaon* ♂

Figures 66 - 85. Shown natural size.

plosion of adults coincident with the first significant summer rains, when high adult population densities often result in lively physical contests for food and mates (see Halffter and Edmonds, 1982). Species inhabiting regions that are continually warm and wet are active year-round.

Phanaeus tend to be stenotopic species whose distributions are determined by type of ground cover and prevailing climate, especially the amount and timing of warm season rains. Thus, the geography of the genus is very much a reflection of the occurrence of types of vegetation and, coincidentally, climate. These factors are correlated with prevailing humidity, soil types, drainage, exposure to rainfall and insolation, available sources of food, and, to a lesser extent (especially in tropical Mexico) altitude, all of which influence the distribution of local populations. Precise geographic distributions of *Phanaeus* species can be extremely complex and patchy in regions such as Mexico, where physiography, climatic patterns, and habitats are often highly fractured within short distances. Given the right local conditions, a "tropical lowland" species such as *P. endymion* can ascend to 2000 m or more where circumstances favor altitudinal extention of moist evergreen/semideciduous forests. Temperate species are much less stenotopic; *P. vindex*, for example, occurs throughout an enormous area (Fig. 360) embracing broadleaf and coniferous forests, grasslands, savannas, and semidesert areas, as well as a multitude of intermediate ecotones. There can be no doubt that the present distributions of the more stenotopic, especially tropical, species of the genus are strongly affected by human activities (see, e.g., Bennett, 1969). Clearing for pastures and other agricultural lands in the Gulf coastal lowlands of the state of Veracruz, Mexico, has converted much of what was an extensive expanse of neotropical forest to an open, savanna-like habitat. The ranges of species such as *endymion* and *sallei*, residents of the neotropical forests, have shrunk considerably in very recent times, while those of *tridens* and *scutifer*, which prefer more open habitats, have expanded. Similar activities have probably also affected the relative distributions of forest and savanna species in South America.

The present distribution of *Phanaeus* species (Fig. 108) is viewed here as comprising 12 ecogeographic patterns based upon the prevalent types of vegetation in each of three broad geographical areas (Figs. 109, 110). For present purposes, South America is considered that portion of the continent east of the Andes. Middle America denotes that area of northwest South America west and north of the Andes, Central America, most of Mexico, and the extreme southwestern United States; it embraces Halffter's (1964, 1976, and elsewhere) Mexican Transition Zone in addition to southern Central America and the transandean Pacific/Caribbean coast of northwest South America. The designation Middle America (or Mesoamerica) is used here in a biohistorical sense applicable to the present geography of the genus and equivalent to Simpson's (1980) "Middle America filter zone"; it is not used in either the traditional anthropological or geological sense (see Maldonado-Koerdell, 1964). The North American area comprises portions of northern Mexico and the United States.

It must be noted that the distribution maps appearing in the text are approximations based upon the locality data that comprise the appendix. Many areas in tropical America have been collected only poorly, and available collection data are often too imprecise to be useful. In the case of *Phanaeus*, the lack of reliable collection data is especially acute from tropical habitats associated with the Andes, from the southern portion of the Amazon Basin and its transitions to more open habitats, from Central America, and from the Sierra Madre del Sur of Mexico.

With the exception of the *palaeno* group and *P. achilles*, all *Notiophanaeus* species inhabit South and Middle American tropical forests with prolonged (or continuous) warm rainy seasons. Of the exceptions, *achilles* occurs in the Pacific coastal desert of southern Ecuador and northern Peru, while *palaeno* and *kirbyi* inhabit the savannas ("campos cerrados") of central Brazil and adjacent portions (Gran Chaco) of Bolivia and Paraguay. *Phanaeus, sen. str.*, on the other hand, comprises mostly species preferring drier habitats with highly seasonal rainfall. Indeed, the majority (16) of its 27 members are brightly colored, heliophilic species that inhabit the more open vegetational formations of Middle and North America (Figs. 109, 110, Patterns E, G, and J).

Following is a brief description of the present distribution patterns of *Phanaeus*. Letters used correspond to those in Figures 109, 110. Each pattern is related to one or more general works on vegetational zones and biotic provinces. In each case, reference is made to the number of species per group whose distributions occur in the indicated pattern (2/4 spp, for example, means two of the four species of the indicated group).

South American Patterns

A. **Atlantic Coast Forests**—a region of tropical deciduous, mesophytic, and rain forests embracing much of eastern Brazil (Hueck and Seibert's [1981] zones 25–29; Eiten's [1974] zones 14–15; International Union for Conservation of Nature and Natural Resources [IUCN] [1974] codes 3.3.1, 3.6.6, 3.7.5); *splendidulus* group (2/4 spp).
B. **Central Dry Forests**—a region of open habitats comprising primarily the Campos Cerrados and Chaco dry forests of Brazil and adjacent portions of Paraguay and Bolivia (Hueck and Seibert's zones 34–35, 46, 58; Eiten's zones 6–9; IUCN codes 3.6.8, 3.9.2); *palaeno* group (2/2 spp).
C. **Amazonian/Guianan Forests**—the rain forests of the Amazon Basin, Guiana, and eastern Ori-

noco Basin (Hueck and Seibert's zones 1–16; Eiten's zones 1–2; IUCN code 3.7.3); *splendidulus* group (1/4 spp); *chalcomelas* group (2/4 spp); *bispinus* group (2/2 spp).

D. **Eastern Andean Montane Forests**—a narrow band of mid-elevation rain forests/cloud forests ("yungas") along the eastern slopes of the Andes from Colombia to Bolivia (Hueck and Seibert's zone 18; Eiten's zone 22; IUCN code 3.8.6); *splendidulus* group (1/4 spp); *chalcomelas* group (1/4 spp).

Middle American Patterns

E. **Pacific Coast Scrub Forest**—the dry scrub forest region of coastal Ecuador and far northern Peru (northern portion of Hueck and Seibert's zone 33; Eiten's zone 22; IUCN code 3.6.10); *chalcomelas* group (1/4 spp); *mexicanus* group (1/7 spp).

F. **Neotropical Forests**—the wet lowland forests extending from northwest South America to the central coast of Veracruz, Mexico, and refugia (not shown in Fig. 110) of tropical evergreen and semideciduous forests in Pacific-facing mountain slopes in Chiapas, Oaxaca, Guerrero, and Jalisco (included are Hueck and Seibert's zone 23; Eiten's zone 16; the "tropical evergreen forest" of Rzedowski [1978] and "tropical rainforest formation" of Wagner [1964]; IUCN codes 3.6.5, 3.7.1, 3.7.4, 3.7.6; this pattern also includes the complex mosaic of wet mountain and lowland forests in northern Colombia and Venezuela north of the Orinoco River [see Hueck and Seibert, 1981; Schmithüsen, 1976]); *endymion* group (2/3 spp); *beltianus* group (3/3 spp); *hermes* group (2/2 spp).

G. **Intermediate Forests**—a complex system of formations varying from semideciduous and deciduous forests to savanna and scrub forests extending from Central America through Mexico (Rzedowski's "bosque tropical subcaducifolio" and "caducifolio"; Wagner's seasonal and dry evergreen formation series; IUCN codes 3.6.1, 3.6.2); *mexicanus* group (6/7 spp); *tridens* group (5/5 spp).

H. **Montane Forests**—cloud forests and pine/oak forests usually above 1300 m and below 2300 m on mountain slopes and plateaus from Central America through Mexico (Rzedowski's "bosque mesófilo de montaña" and "bosque de coníferas y de Quercus"; Wagner's "montane formation series"; IUCN code 1.8.4); *quadridens* group (3/3 spp); *amethystinus* group (2/2 spp); *triangularis* group (1/2 spp).

North American Patterns

I. **Western Dry Formations**—grasslands, savannas, savanna woodlands, and deserts of northern Mexico and central and southwestern United States (Vankat, 1979); IUCN code 1.10.1; *vindex* group (2/3 spp); *triangularis* group (1/2 spp).

J. **Eastern Forests**—pine and broadleaf temperate forests of the United States east of about the 95th meridian (Vankat); IUCN codes 1.4.1, 1.4.2; *vindex* group (2/3 spp); *triangularis* group (1/2 spp).

My present understanding of the systematics and distribution of the genus leads me to the following tentative observations about the evolution of *Phanaeus:*

1. The subgenus *Notiophanaeus* consists of species that are descendents of original members of the genus *Phanaeus*, a group of unquestionable South American origin (Edmonds, 1972). Taxonomic gaps among species groups and among most species are generally unambiguous and, to me, indicative of long-standing radiation, divergence, and extinction. As a whole, the South American contingent of the subgenus (all species except the *endymion* group) comprises remarkably few species in view of the size and complexity of the continent (see point 4, below). The present distribution of the *splendidulus* group (Fig. 136), in particular, exhibits broad disjunctions that strongly suggest relictual composition. The *endymion* group represents a recent penetration of the subgenus into Middle America, paralleled by that of the phanaeine genera *Sulcophanaeus* and *Coprophanaeus* as well as other scarabaeines (Edmonds, 1972; Kohlmann and Halffter, 1988, 1990). There it has spread and diversified in response to the northward expansion of neotropical forests during the Pleistocene, a biome that has been exploited only weakly by *Phanaeus, sen. str.* (see points 3 and 4, below). Subsequent contraction of neotropical forests has left populations of the *endymion* group in isolated refugia along the Pacific coastal region of Mexico from Chiapas to Jalisco (see the systematics section).

2. *Phanaeus, sen. str.,* appears to consist of at least three evolutionary lines, each of which dispersed and differentiated in Mesoamerica. Whether or not these lines represent separate waves of immigration from tropical South America is a question requiring further study to answer. My present opinion is that they do not represent separate waves, inasmuch as the subgenus, as now known, is endemic to Middle and North America. It seems more probable, rather, that each line originated from an ancient stock that invaded the north very early and diversified exclusively in Middle America. The timing of the arrival of the founders of the subgenus was perhaps during the Miocene, at a time when the physiographic diversification of Mexico, in particular, and nuclear Central America (i.e., the Mexican Transition Zone of Halffter [1964, 1976, 1987]) was just beginning. The spectacular changes in the physiography and ecology of the area from the Miocene onward, as well as the rich fauna of large mammals, would have provided tremendous opportunity for multiple pulses of diversification and the establishment of distinct evolutionary lineages

[86] *Phanaeus eximius* ♂

[87] *Phanaeus furiosus* ♂

[88] *Phanaeus furiosus* ♀

[89] *Phanaeus furiosus* ♀

[90] *Phanaeus nimrod* ♂

[91] *Phanaeus t. tridens* ♂

[92] *Phanaeus t. tridens* ♀

[93] *Phanaeus t. tridens* ♀

[94] *Phanaeus daphnis* ♂

[95] *Phanaeus daphnis* ♀

[96] *Phanaeus vindex* ♂

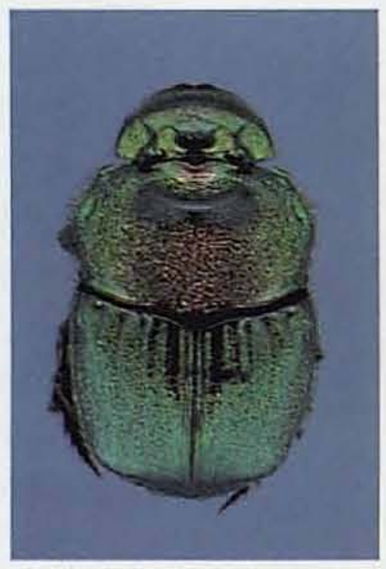
[97] *Phanaeus vindex* ♀

[98] *Phanaeus vindex* ♀

[99] *Phanaeus vindex* ♂

[100] *Phanaeus vindex* ♂

[101] *Phanaeus difformis* ♂



[102] *Phanaeus difformis* ♀

[103] *Phanaeus difformis* ♀

[104] *Phanaeus igneus* ♂

[105] *Phanaeus igneus* ♀

[106] *Phanaeus igneus* ♀

[107] *Phanaeus igneus* ♀

Figures 86 - 107. Shown natural size.

Figure 108. Distribution of the subgenera of *Phanaeus;* solid line, *Notiophanaeus;* stippled, *Phanaeus, sen. str.*

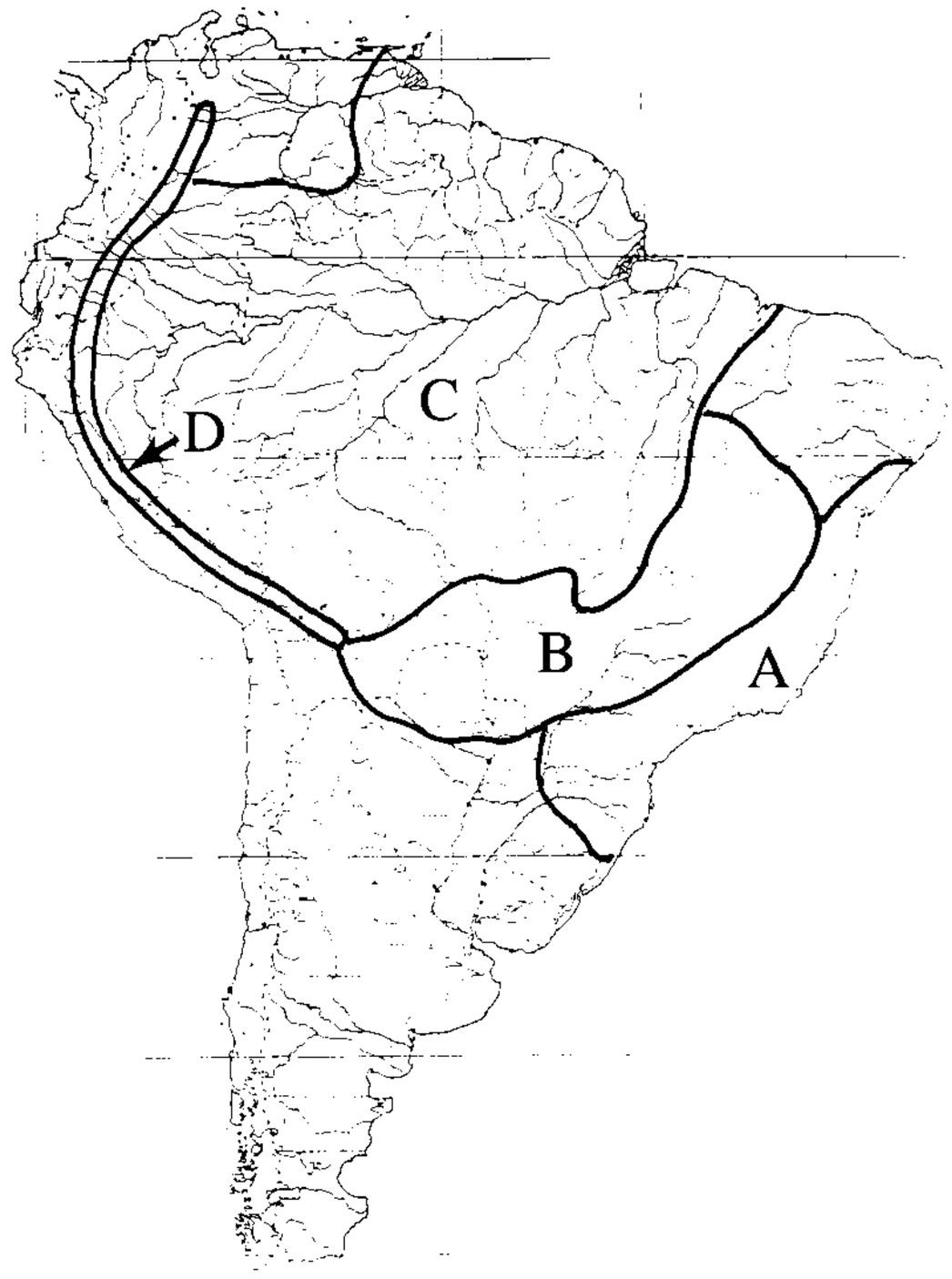


Figure 109. South American distribution patterns of *Phanaeus* (see text for explanation).

in situ. Two recent studies on other dung beetle genera using cladistic methods (Kohlmann and Halffter, 1988, 1990) support the idea that the main incursions of scarabaeines from South America into Mesoamerica have been two: one during the Miocene and the other following establishment of the Central American landbridge during the late Pliocene.

3. Of the three lineages of *Phanaeus, sen. str.*, the one consisting of the *triangularis, tridens,* and *hermes* groups adopted several ecogeographic strategies as it moved both northward and southward, ultimately entering northwest South America during the Pleistocene. A second lineage, comprising the *quadridens* and *amethystinus* groups, diversified in Middle American montane habitats. A third line, the *mexicanus* and *beltianus* groups, diversified extensively throughout Mesoamerica in habitats intermediate between montane and neotropical forest zones, that is, in warmer, open habitats with highly seasonal rainfall. The *vindex* group is problematic in that it shows no clear affinity with any of the three lineages mentioned above and may represent a fourth line with no extant close relatives to the south. Speciation in this group (and also the *triangularis* group) was likely promoted by cyclic changes in climate and life zones during the late Cenozoic.

4. The extensive radiation of *Phanaeus, sen. str.*, in Middle America was favored in great part by the scarcity of potential competitors, especially in warmer, drier, more open habitats. The extant fauna of *Phanaeus* is richer in Middle and North America (34 species and subspecies) than in South America (12 species including *achilles*). Tropical South America is, however, the home of a richer fauna of Scarabaeinae as a whole, including a large number of genera comprising species of size and ecological requirements similar to those of *Notiophanaeus* (e.g., *Sulcophanaeus, Coprophanaeus, Oxysternon, Eurysternus, Canthon, Deltochilum, Dichotomius*). To the north, these genera are either absent, recent arrivals (late Pliocene/Pleistocene), or more poorly represented in Middle America. Outside neotropical forests, species of *Phanaeus, sen. str.*, are often the most abundant coprophagous scarabaeines in Middle American habitats, especially in intermediate forests (Fig. 110, pattern G). While the entire Amazonian–Guianan forest area (Fig. 109, pattern C) supports only four known species (one of which, *melibaeus*, may be restricted to peripheral habitats), the complex environs of Acahuizotla, in the Sierra Madre del Sur of Guerrero, Mexico, are home to at least five species (Delgado-Castillo, 1989). In Middle American neotropical forests (Fig. 110, pattern F), *Phanaeus* species are poorly represented

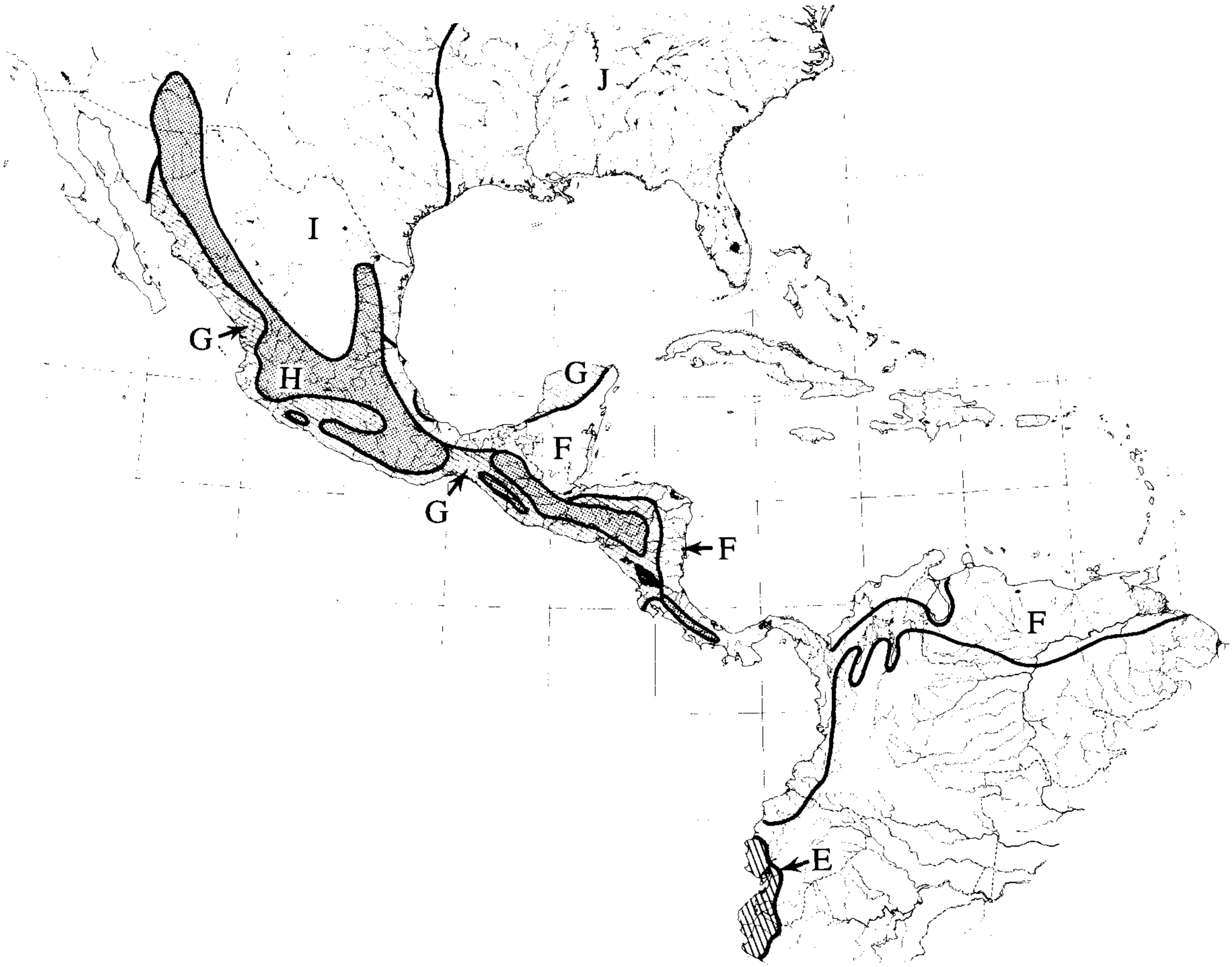


Figure 110. Middle and North American distribution patterns of *Phanaeus* (see text for explanation).

compared to the ball-rolling genera (Canthonina) and smaller-sized burrowers such as *Canthidium.*

5. The systematics of *Phanaeus, sen. str.,* supports the idea that much differentiation has occurred relatively recently. Such is the case for the *hermes, amethystinus, mexicanus,* and *tridens* species groups, where interspecific taxonomic differences are often tenuous. Moreover, the distributions of the latter two groups (cf. Figs. 246 and 290) suggest parallel histories and diversification strongly influenced by vicariance events. Montane and northern stocks (especially the *quadridens, triangularis,* and *vindex* groups) consist of species that have assumed clearer, more consistent morphological differences suggestive of a more continuous ecogeographic history, notwithstanding a higher exposure to the cyclic climatic effects of Pleistocene glaciations (see Toledo, 1976; Howden, 1963, 1966, 1969).

6. It is difficult to conceive of modern *Phanaeus, sen. str.,* especially in Mexico, as anything other than an actively evolving group whose modern distribution has been strongly influenced by humans. Central Mexico, for example, was very densely populated in pre-European times by a series of thriving cultural groups culminating with the Aztec empire. As early as 650 AD, the population of the valley of Mexico (now the Mexico City metropolitan area) was perhaps as high as 100,000; and by 1500 it exceeded 1.5 million (Ezcurra, 1990). Moreover, central Mexico may have supported 5 or more million inhabitants when the Spanish landed in Veracruz in 1519 (Martínez, 1990). The presence of humans was important not only as a source of food for *Phanaeus* and other dung beetles, but also as the cause of habitat changes that favored the expansion of species preferring open habitats. The demise of the indigenous human population following the conquest of Mexico coincided with the introduction of domestic livestock (cattle, horses, sheep, goats, swine, etc.) and post-conquest immigration of Europeans. The resultant thriving human and domestic livestock populations have become the modern counterpart of the rich Miocene–Pliocene fauna of large mammals presumed to have supported the original radiation of the genus in

Middle America. Moreover, human promotion of livestock raising has greatly expanded the habitat available to *Phanaeus* and other dung beetles by dispersing the food supply and by modifying vegetation cover in ways that directly foster range expansions for some species and contractions for others.

KEY TO THE PHANAEINE GENERA

The following artificial key, based on Edmonds (1972), separates the phanaeine genera. *Phanaeus* is defined fully later in this work (see Edmonds, op. cit., for descriptions of other genera and subgenera as well as a diagnosis of the phanaeine assemblage).

1a. Middle and hind tarsi each with fewer than five segments; front tarsi always absent in female 2
b. Middle and hind tarsi five-segmented; front tarsi present or absent in female 3
2a. Middle and hind tarsi four-segmented, fourth (distal) segment very small; clypeus medially bidentate, but not as described in 2b. Body robust; color reddish brown .... *Tetrameira convexa* (Harold) (Monobasic)
b. Middle and hind tarsi two- or three-segmented; clypeus with deep, acute emarginations setting off two strong medial teeth. Body robust to elongate and flattened; color usually at least partially metallic blue or green ..... *Dendropaemon* Perty
3a. Dorsal surfaces of hind tibiae and basal four hind tarsal segments covered by large setigerous granules. Color dull metallic green ..... *Homalotarsus impressus* Janssens (Monobasic)
b. Dorsal surfaces of hind tibiae and tarsi glabrous or with very small setigerous granules. Color variable 4
4a. Labial palpus comprising a single oval segment. Dorsal surfaces of hind tibiae and abdominal sterna bearing dense fringes of long setae .... *Megatharsis buckleyi* Waterhouse (Monobasic)
b. Labial palpi three-segmented. Hind tibiae and abdominal sterna lacking dense fringes of setae 5
5a. Clypeus with deep, acute emarginations setting off two elongate, narrow teeth beneath which extends a strong, anteriorly directed, U-shaped carina. Front tarsi usually absent in female. Front tibiae very strongly, acutely quadridentate ... . *Coprophanaeus* Olsoufieff
b. Clypeal margin variable, but never deeply emarginate with associated U-shaped subclypeal carina. Front tarsi rarely absent in female. Front tibiae variable 6
6a. Dorsum of female head with two strong transverse carinae, posterior of which extending between eyes and usually trituberculate; that of male with strong transverse carina followed by horns or other protuberances placed between eyes. Outer edge of hind tibia with strong transverse, subapical carina. Very large, usually metallic green species ..... *Diabroctis* Gistel
b. Dorsum of head lacking anterior carina; female with single, often trituberculate carina or small corniform process between eyes; male with long, tapering horn or other processes between eyes. Hind tibiae only very rarely with subapical carina. Size and color variable 7
7a. Anteromedian angle of metasternum prolonged as a long, sharp, upturned spine extending between front coxae. Posteromedian angle of pronotum acute, distinctly prolonged between bases of elytra, never bearing fossae .... *Oxysternon* Laporte-Castelnau
b. Anteromedian angle of metasternum not spinate. Posteromedian angle of pronotum not distinctly prolonged between bases of elytra, often bearing distinct fossae 8
8a. Anterior margin of pronotum distinctly emarginate behind eyes to receive postocular lobes of head ..... *Phanaeus* Macleay
b. Anterior margin of pronotum not emarginate behind eyes; surface of head behind eyes not produced as posteriorly directed lobes .... *Sulcophanaeus* Olsoufieff

Systematics of the Genus *PHANAEUS* Macleay

The following description is based on Edmonds (1972) and includes characters of the phanaeine genus group (see Edmonds, op. cit., for a complete explanation of characters used). The history of the name, *Phanaeus,* appears under *Phanaeus, sen. str.*

DESCRIPTION. *Clypeus.*—Dorsal surface transversely ridged (Figs. 148, 149); anterior margin simple or bidentate medially, sometimes strongly so (Fig. 196); lateral clypeal carinae almost always present; clypeal process usually a low, transverse ridge, seldom toothlike (Fig. 156) or spinate (Fig. 195). *Parietals.*—Paraocular areas narrow, width along posterior margin about two times width of adjacent dorsal portion of eye; posterior lobes depressed obliquely, setting off postocular prominences that fit into emarginations of anterior margin of pronotum; canthal areas indistinct; cephalic brachium bipodal, indicated externally by mesal bifurcation of frontoclypeal sulcus; occipital ridge complete. *Eyes.*—Completely divided into upper and lower portions by posterior extensions of paraocular areas of parietals; small, dorsal interocular width more than four times width of dorsal portion of an eye. *Antennae.*—Club spherical, three-segmented; basal lamella strongly concave, forming a cup into which fit two distal lamellae. *Labrum.*—*Phanaeus*-type, lateral files divergent; setae of median brush not much longer than setae posterior to them; suspensorial opening rounded. *Labium.*—Palpi three-segmented; mentum strongly emarginate apically; median lobe of hypopharynx present; premental sclerites completely and darkly sclerotized. *Pronotum.*—Sculpturing smooth-punctate (Figs. 163–166) to very strongly roughened (Figs. 336–340); posteromedian fossae usually present.

Metathorax.—Posterior end of dorsal margin of episternum produced as small, rounded tab fitting over edge of closed elytron; median portion of sternum produced anteriorly as strong angle such that, seen from below, sternum between mesocoxae appears pentagonal. *Legs.*—Front tibiae tridentate or quadridentate; middle and hind tarsi five-segmented, lacking claws. *Elytra.*—Striae usually simple, rarely carinulate (Figs. 169, 170), sometimes strongly punctured (Figs. 150, 151); interstriae usually convex, smooth-punctate to rugose. *Secondary Sexual Characters.—Male:* Front tarsi absent. Head of larger individuals bearing a large, tapering horn between eyes, reduced to conical tubercle, bituberculate process or weak tumosity in smallest individuals. Pronotum of largest individuals either (a) concave medially with posterolateral prominences of some sort (spines, ridges, etc.; Figs. 111, 113, 257) or (b) flattened medially and, seen from above, more or less triangular with prominent posterolateral angles (Figs. 137, 247). *Female:* Front tarsi present, clawless. Head bearing transverse, usually trituberculate carina between eyes; carina can be obsolete, or strongly raised medially as bituberculate process (Figs. 331, 356). Pronotum convex, sometimes strongly so, usually bearing anteromedially some combination of carinae, tubercles, concavities, etc. *Coloration* (Figs. 1–107).—Dorsum almost always at least partially metallic, brightly shining, seldom matte; interspecific and intraspecific coloration highly variable. *Distribution* (Fig. 108).—savannas, pasturelands, forests, dry to very wet habitats; 0–2800 m; extreme northern Argentina to northeastern United States; most species preferentially coprophagous.

KEY TO THE SUBGENERA OF *PHANAEUS*

1a. Sculpturing of anterolateral portions of the pronotum (in front of lateral fossae) including distinct puncturing (×10) (Figs. 118, 207), or rarely almost completely smooth (*bispinus*, Fig. 166); size, shape, and density of punctures variable, but most often very small and sparse such that area appears glassy smooth to unaided eye. Remainder of pronotum usually sculptured like anterolateral portions, sometimes (*chalcomelas* group, Figs. 137–147, and males of *endymion* group, Figs. 209–211) more coarsely sculptured. Pronotal punctures of *chalcomelas* group very large and shallow, intermingled with and obscured by blister-like rugosities that give pronotum a rugose appearance (×0–5). If anterolateral puncturing largely obscured (male *achilles*, Fig. 141), then anteromedian prominence of metasternum acuminate (as in Fig. 155). Five groups of mostly South American species .... *NOTIOPHANAEUS*, NEW SUBGENUS

b. Anterolateral portions of pronotum granulate (Figs. 224, 236, 253), granulorugose (Figs. 274, 306), or rugose (Figs. 339, 340), lacking distinct punctures (×10) except occasionally near anterior margin adjacent eyes. Remainder of pronotum always at least partly sculptured like anterolateral portions or more coarsely so; puncturing usually present at least posteromedially and may cover as much as posterior one-half of pronotum, especially in females. Anterior prominence of metasternum always keeled, never acuminate. Eight groups of mostly Middle and North American species .... *PHANAEUS, SEN. STR.*

Notiophanaeus, New Subgenus

Type: *Scarabaeus splendidulus* Fabricius 1781. Derivation of subgeneric name: *Notios* (Greek, southern) + *Phanaeus;* masculine; reference to geographical and presumed historical relationship to South America.

This subgenus brings together 15 species arranged in five groups as outlined in the introduction. *Notiophanaeus* is equivalent to what I referred to in 1972 as the *splendidulus* group of *Phanaeus,* and the present species groups are the species complexes I recognized then. It is difficult to draw satisfying conclusions about the interrelationships among the species groups of *Notiophanaeus,* as they represent five rather disparate taxa. Patterns of shared characters do not vary consistently, and in all likelihood the subgenus is a collection of the survivors of a formerly more diverse group. The taxonomic gaps among species groups, and usually also among species, are generally clear and unambiguous. All five species groups occur in continental South America (Fig. 108). Four are endemic there; the *endymion* group is centered in Mesoamerica.

The primary distinction between *Notiophanaeus* and *Phanaeus, sen. str.,* resides in the nature of the sculpturing of the pronotum. In this subgenus the pronotum of both sexes most often appears glassy smooth to the unaided eye. Magnification (×10–40), however, reveals distinct puncturing at least on the sides and anterior angles. Only in *bispinus* is the pronotum devoid of any sculpturing, even at higher magnification (×40).

The pronotal sculpturing of the *chalcomelas* group (Figs. 137–147) and of the males of the *endymion* group (Figs. 209–211) resemble that of *Phanaeus, sen. str.* (q.v.). In the *chalcomelas* group, the pronotum of both sexes bears few to many black, blister-like rugosities. These rugosities, however, never fuse to form a melange of confluent ridges and granules, and they are always associated with distinct puncturing. Nevertheless, to the unaided eye the pronotum of the *chalcomelas* group appears rugose, and this roughened appearance, combined with the triangular shape of the pronotal disk, can result in a strong superficial resemblance to *Phanaeus, sen. str.* In the case of the *endymion* group, the resemblance is more subtle and restricted to the males; females have smooth, punctate prono-

ta. The triangular disk of the male pronotum (but not the sides and anterolateral angles) is minutely granulorugose, most strongly so in *endymion* and *halffterorum*. The rugose nature of this sculpturing is very fine and can be discerned clearly only under magnification (×10). To the unaided eye, it produces a very delicate, gritty or velvety texture in marked contrast to the usually heavily rugose texture of *Phanaeus, sen. str.*, seen easily with the unaided eye.

KEY TO THE SPECIES GROUPS OF *NOTIOPHANAEUS*

1a. Elytral striae carinulate and punctate (×0–10) (Figs. 169, 170). Pronotum of well-developed male with pair of closely set, parallel, slender spines (Figs. 163, 167); that of female as in Figures 165, 168, 178, 179. Dorsum dull olive green or brownish black (Figs. 15, 16). Widely distributed in Amazon Basin .... *bispinus* group

b. Elytral striae variable but never both carinulate and punctate. Pronotum never as in *bispinus* group. Color and distribution variable ... 2

2a. Elytral striae carinulate (×30), not punctate. Anterior margin of clypeus strongly toothed medially (Fig. 196); clypeal process spinate (Fig. 195). Basal pronotal fossae lacking. Front tibiae strongly quadridentate (Figs. 197, 198). Venter clothed by dense, whitish pile (indistinct in worn or dirty specimens). Dorsum bright, shining green, often with yellowish reflections, or dark blue (Figs. 10–14). Brazilian Highlands ("campos cerrados") and adjacent regions of Bolivia, Paraguay, and extreme northeastern Argentina ..... *palaeno* group

b. Elytral striae not carinulate, punctate or not. Anterior margin of clypeus strongly bidentate or not. Clypeal process variable, but never spinate. Basal pronotal fossae present or absent. Front tibiae tri- or quadridentate. Venter never bearing a dense, whitish pile. Color and distribution variable 3

3a. Elytral striae distinctly punctured to unaided eye (Figs. 150, 151). Pronotum bearing few to many black, blister-like rugosities giving surface an irregularly maculated ("peppered") appearance (Figs. 137–147). Dorsum dull, most often olive brown or olive green; sometimes almost black or metallic red or green (Figs. 23–31). Pronotum of larger males evenly flattened and, from above, appearing triangular (Figs. 137, 139, 141, 143, 144). Widely distributed in Amazon Basin; one species in western Ecuador .. .. *chalcomelas* group

b. Elytral striae appearing simple to unaided eye; minute punctures may be visible under magnification (×10–40). Pronotum lacking black rugosities, usually appearing glassy smooth to unaided eye. Dorsum dull or brightly colored. Shape of male pronotum variable. Distribution variable 4

4a. Anterior margin of clypeus at most only weakly bidentate medially. Clypeal process toothlike (Fig. 135). Front tibiae tri- or quadridentate; if quadridentate, basal tooth not preceded by a distinct narrow notch. Apical tibial spur bent mesally (Figs. 124–127). Pronotum of larger males concave dorsally and with a pair of spinate horns arising from near posterior margin (Figs. 111, 113, 115, 117). Northern South America east of the Andes ..... *splendidulus* group

b. Anterior margin of clypeus strongly bidentate medially. Clypeal process transverse. Front tibiae strongly quadridentate (Figs. 219, 220), basal tooth preceded by very narrow notch (indicated by arrows in figures; effaced in highly worn specimens). Apical tibial spur more-or-less straight. Pronotum of larger males flattened above, triangular, lacking spinate processes (Figs. 200, 203, 206). Extreme northwestern South America, Central America, and southern Mexico ..... *endymion* group

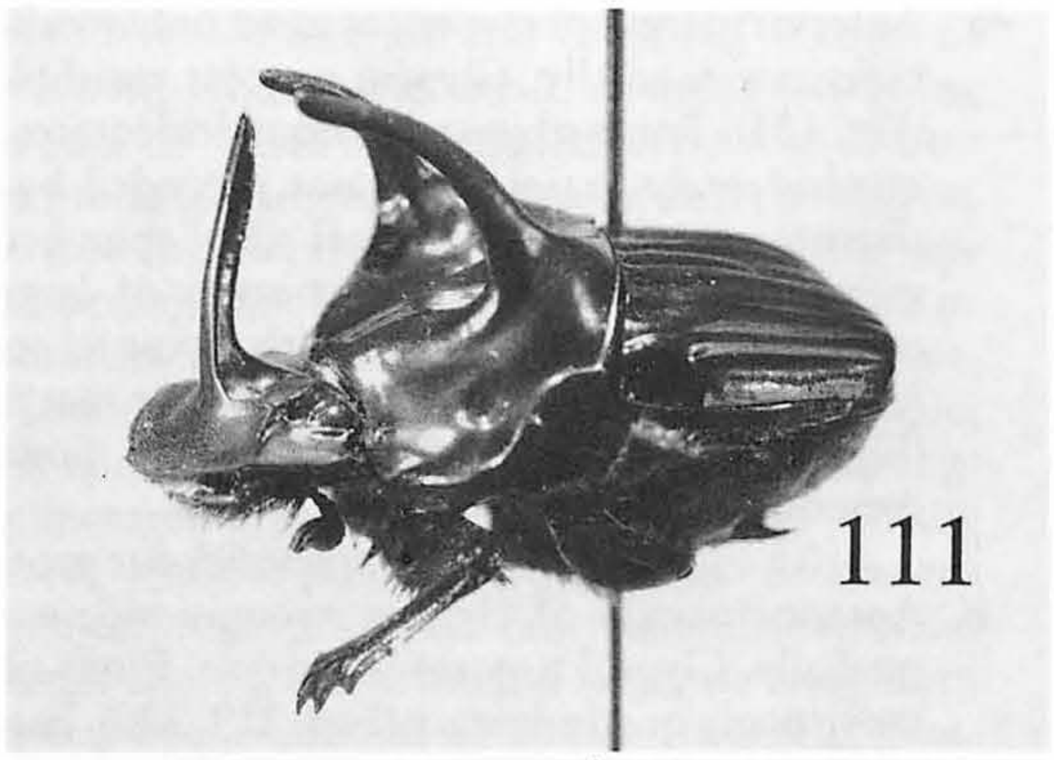
The *Splendidulus* Group

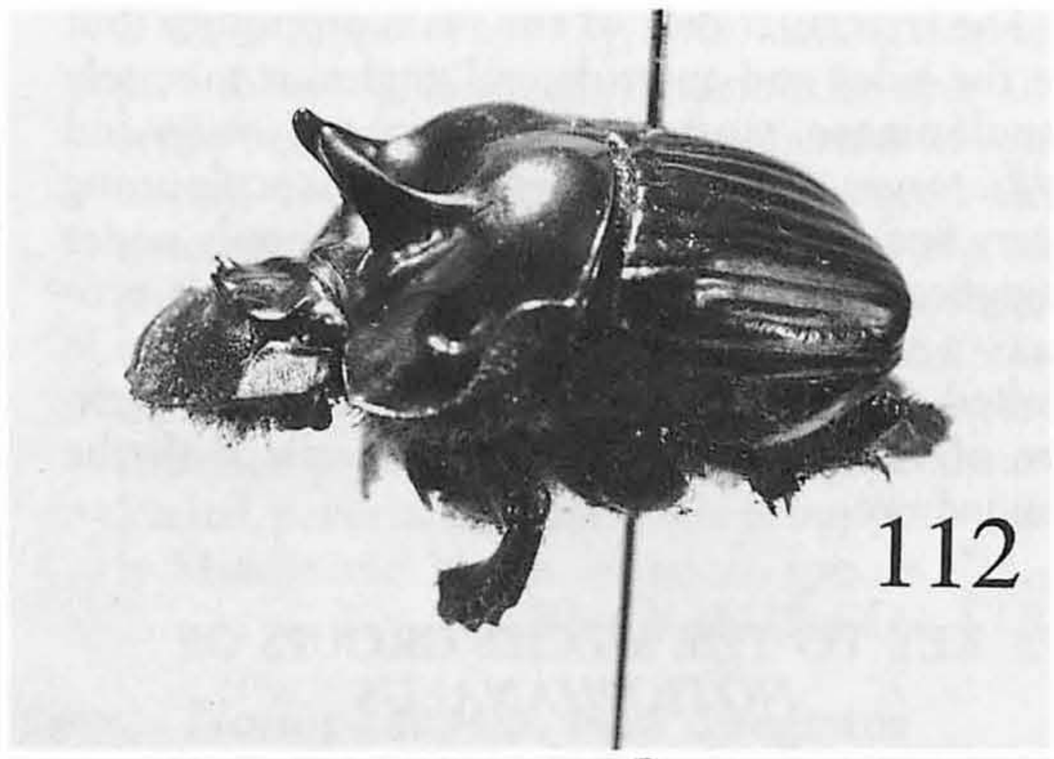
DIAGNOSIS. [1] Clypeus weakly bidentate medially; [2] clypeal process toothlike (Fig. 135); [3] cephalic carina of female distinctly trituberculate (Figs. 131–133); [4] pronotal margin of male and sometimes also of female sinuous behind anterolateral angle, which is often acutely produced, somewhat explanate (Figs. 122, 123); [5] pronotum of larger males concave medially, with a pair of strong, spine-like lateral horns (Figs. 111, 113, 115, 117); [6] pronotum finely, sparsely punctured (×10) (Fig. 118), appearing glassy smooth to unaided eye; puncturing usually stronger, more evenly distributed in female; [7] basal pronotal fossae present or absent; [8] front tibiae (Figs. 124–127) tridentate or quadridentate; [9] elytral striae simple, occasionally very weakly punctate (×40); interstriae weakly convex to almost flat, smooth to very weakly punctured (×30); [10] apex of front tibial spur, seen from front, bent mesally; [11] inhabiting South American forests (Fig. 136).

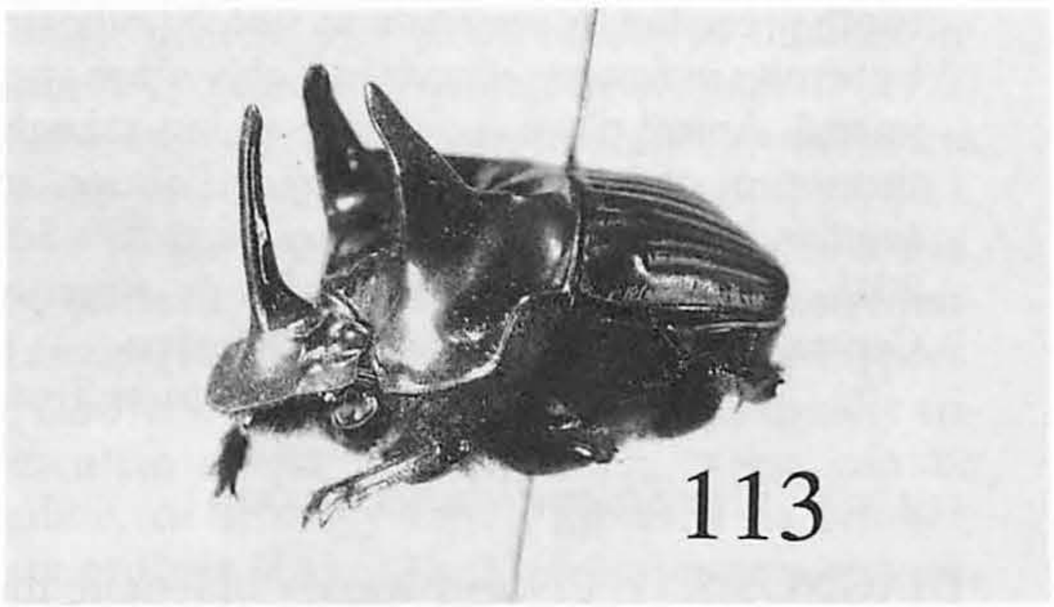
This group of four South American species differs from other *Phanaeus* by the toothlike clypeal process and the widely set pair of spinate horns on the male pronotum. It is the only species group that displays widely disjunct geographical distributions. Two species, *splendidulus* and *dejeani*, are sympatric and closely resemble each other, particularly in secondary sexual characters. Their strong similarity has led many workers (myself included) to consider them conspecific subspecies. No member of this group is particularly common in collections. All are very distinct and easily separated.

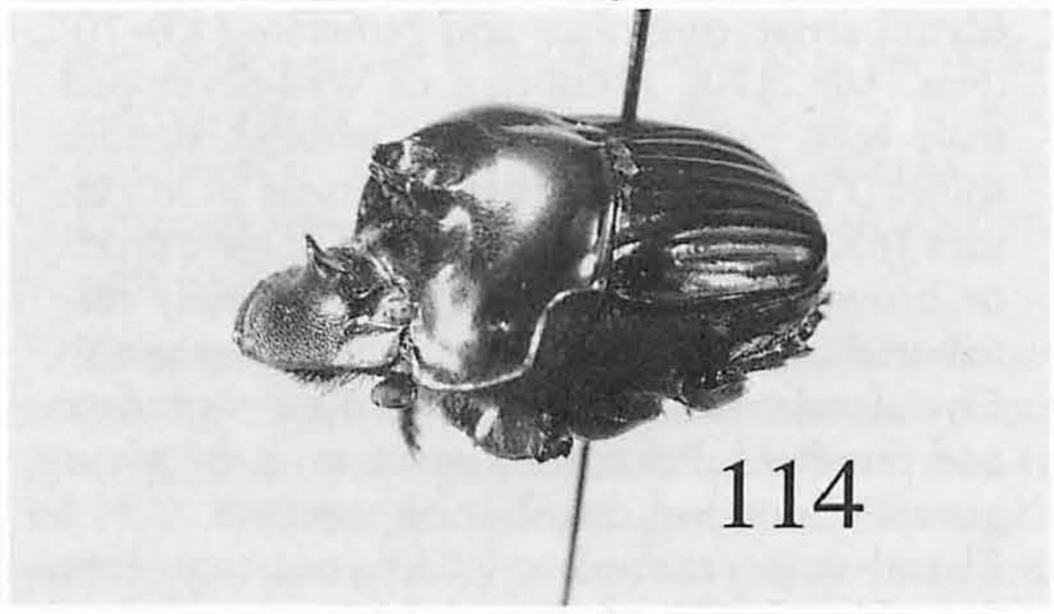
KEY TO THE SPECIES OF THE *SPLENDIDULUS* GROUP

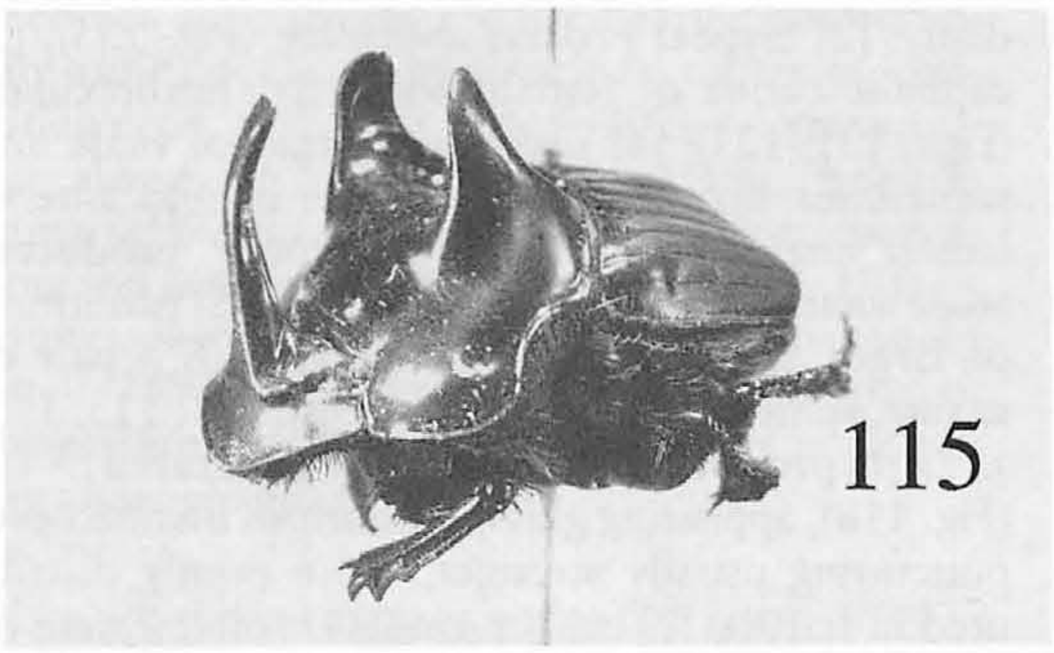
1a. Anterior prominence of metasternum, seen in profile (Fig. 130), acuminate, produced ante-

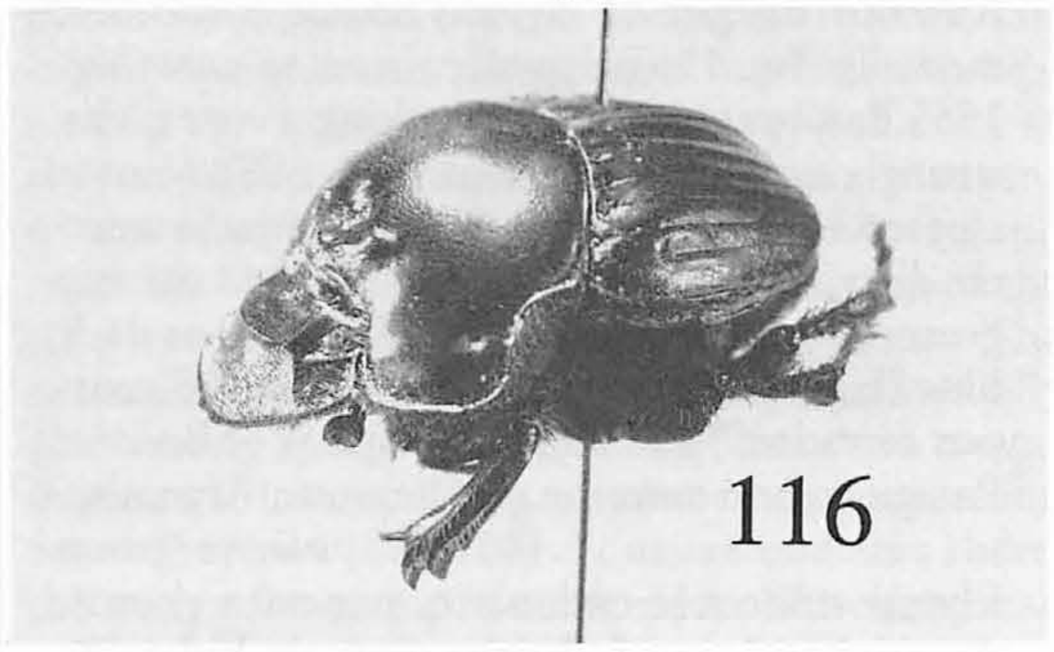


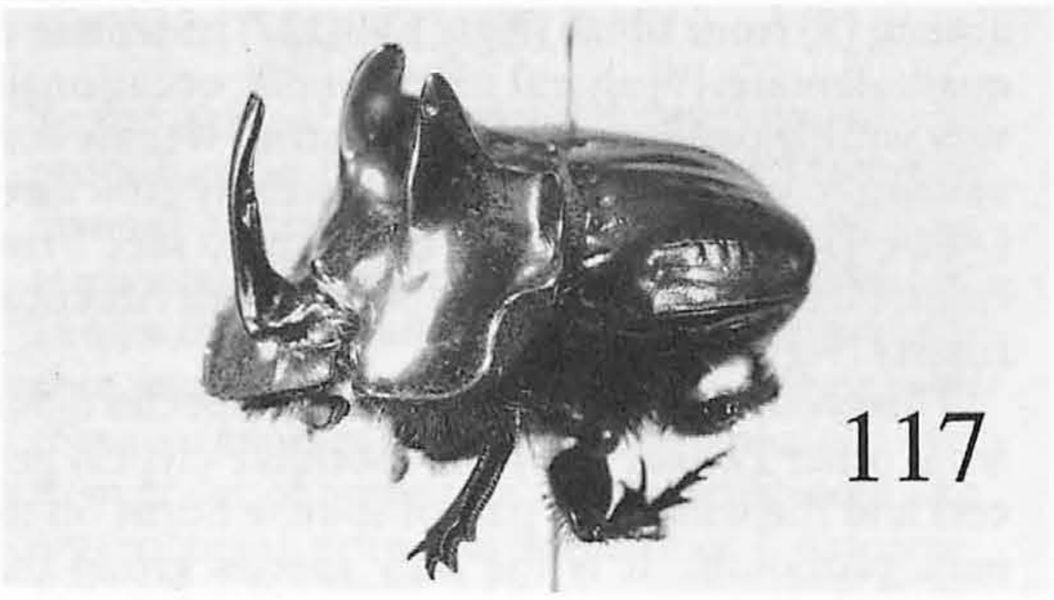








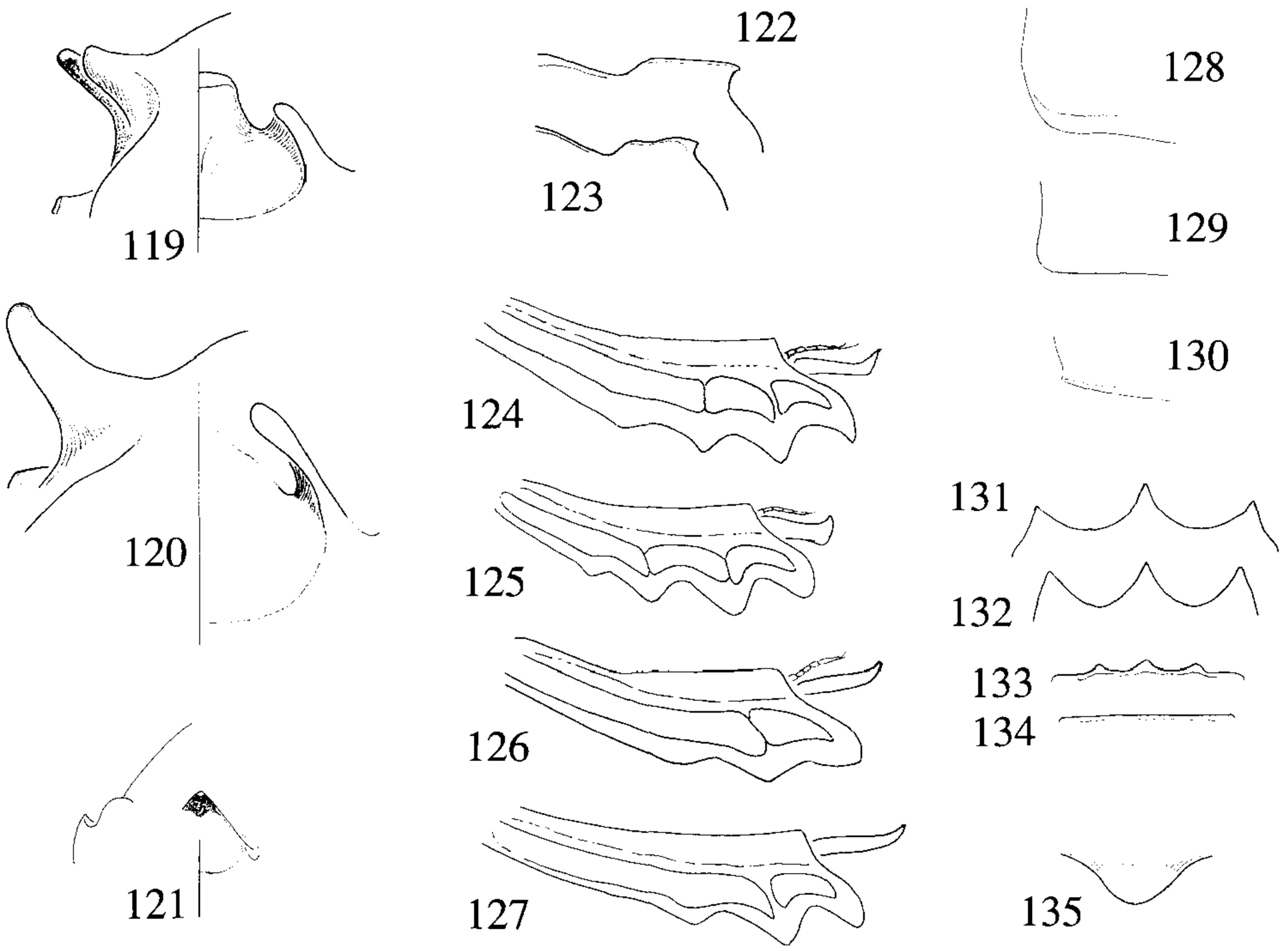




Figures 111–118. *Phanaeus* (*Notiophanaeus*) *splendidulus* group, oblique lateral views (**111,** *P. haroldi,* male; **112,** same, female; **113,** *P. melibaeus,* male; **114,** same, female; **115,** *P. splendidulus,* male; **116,** same, female; **117,** *P. dejeani,* male. **118,** *P. haroldi,* anterolateral portion female pronotum).

riorly as minute, acute tubercle (subject to wear). Front tibiae (Figs. 126, 127) tridentate; fourth (basal) tooth at most only slightly indicated; anterior surface of third tooth not carinate longitudinally as are first two. Coastal forests of southeastern Brazil from Espírito Santo to Rio Grande do Sul and extreme northwestern Argentina (Misiones) (Fig. 136) . . . . . *Phanaeus* (*N.*) *splendidulus* (F.)

b. Anterior prominence of metasternum, seen in profile (Figs. 128, 129), broadly rounded and, seen from below, narrowly keeled. Front tibiae tri- or quadridentate, apical three teeth carinate longitudinally on anterior surface (carina of



Figures 119–135. *Phanaeus* (*Notiophanaeus*) *splendidulus* group. **Figs. 119–121.** Lateral (left) and right dorsal views of anteromedian portion of female pronotum (**119,** *P. melibaeus;* **120,** *P. haroldi;* **121,** *P. splendidulus*). **Figs. 122, 123.** Dorsal view anterior portion right side male pronotum (**122,** *P. haroldi;* **123,** *P. melibaeus*). **Figs. 124–127.** Anterior surface of right front tibia (**124,** *P. haroldi,* female; **125,** *P. melibaeus,* female; **126,** *P. splendidulus,* female; **127,** same, male). **Figs. 128–130.** Lateral view anterior prominence of metasternum (**128,** *P. haroldi;* **129,** *P. dejeani;* **130,** *P. splendidulus*). **Figs. 131–134.** Anterior view female cephalic carina (**131,** *P. haroldi;* **132,** *P. melibaeus;* **133,** *P. splendidulus;* **134,** same, highly worn). **Fig. 135.** *P. haroldi,* anterior view clypeal process.

third tooth may be very fine or effaced in *dejeani*). Distribution varies 2

2a. Front tibiae tridentate (as in Figs. 126, 127), fourth (basal) tooth at most only suggested by subtle angular bend in outer tibial margin; longitudinal carina of third tooth may be very fine or effaced; apex of spur evenly curved mesally. Cephalic horn of larger males slightly widened and compressed apically; that of smallest males reduced to weakly bituberculate carina. Pronotum of female with anteromedian concavity bordered anteriorly by strong, U-shaped, trituberculate carina; middle tubercle dentate in larger individuals (Figs. 116, 121). Basal pronotal fossae absent or only slightly indicated. Elytra deep royal blue, occasionally tending toward blue-green, appearing lacquered; pronotum (except for black areas) shining greenish yellow (Figs. 4, 5). Mountainous areas ("serras") of southeastern Brazil (Fig. 136) . . . . . *Phanaeus* (*N.*) *dejeani* Harold

b. Front tibiae quadridentate (Figs. 124, 125) (fourth [basal] tooth sometimes only weakly developed in *haroldi*); longitudinal carina of third tooth always distinct; apex of tibial spur truncated, inner angle acute, directed mesally. Cephalic horn of larger males rounded apically; that of smallest males reduced to tubercle or simple carina. Pronotum of female lacking a U-shaped carina but bearing strong tubercles or spinate processes (Figs. 112, 114, 119, 120). Basal pronotal fossae distinct. Elytra green or almost black, never royal blue; pronotum dull olive green or shining green with strong coppery highlights. Evergreen forests of Amazon Basin and eastern slopes of Andes 3

3a. Pronotum dull, dark olive green; elytra almost black, often with feeble greenish or bluish luster (×10) (Figs. 8, 9). Pronotum of female (Figs. 112, 120) with shallow anteromedian concavity flanked by pair of upwardly curved, acute spines that converge apically. Cephalic carina of female bowed anteriorly (seen from above) and strongly trituberculate (Fig. 131). Pronotum of larger males (Fig. 111) with shallow median concavity; each posterior angle drawn out into strong, slender, anteriorly directed spine. Elytral interstriae convex and more or less evenly dulled, at most only slightly shinier midlongitudinally. Eastern slopes of Andes from Colombia to northern Peru, isolated localities in eastern Venezuela . . . . . *Phanaeus* (*N.*) *haroldi* Kirsch

b. Pronotum shining green with strong coppery

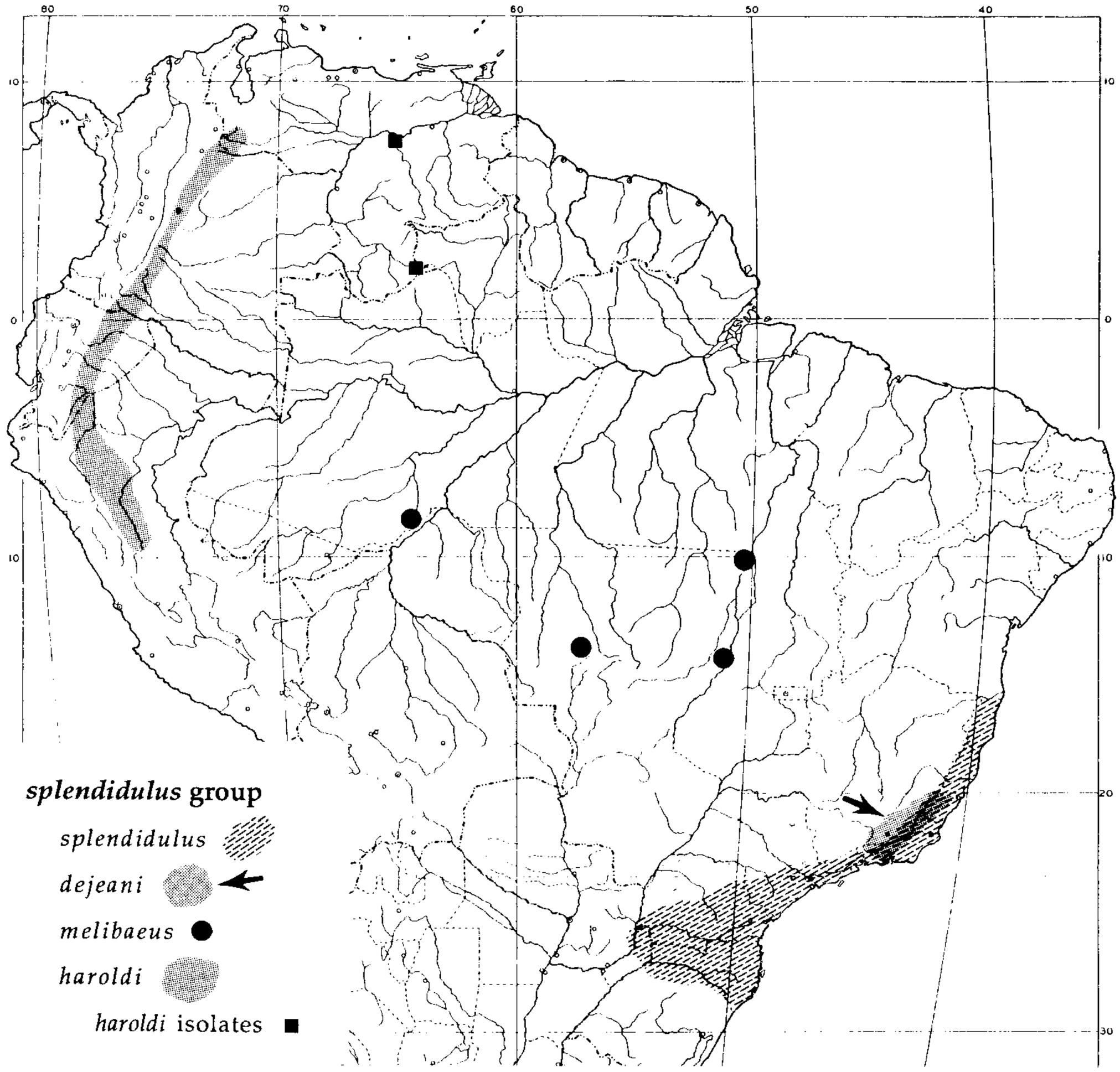


Figure 136. Distribution of the *Phanaeus* (*Notiophanaeus*) *splendidulus* group.

or coppery yellow reflections; elytra moderately shining green (Figs. 6, 7). Pronotum of female (Figs. 114, 119) with conspicuous oval anteromedian concavity bordered anteriorly by three strong tubercles, outer two of which acute, middle one quadrate. Cephalic carina of female (Fig. 132) only weakly bowed anteriorly and strongly trituberculate. Pronotum of larger males (Fig. 113) with broad, median concavity, each side of which drawn out into acute, dorsally directed spine. Elytral interstriae distinctly shinier midlongitudinally than adjacent to striae. Southern Amazon Basin in Brazil and Bolivia (Fig. 136) . . . . . *Phanaeus* (*N.*) *melibaeus* Blanchard

Phanaeus (*Notiophanaeus*)
splendidulus (Fabricius)
Figures 1–3, 115, 116, 121,
126, 127, 133, 134, 136

Scarabaeus splendidulus Fabricius, 1781, (vol. 1):23

Type: Male lectotype ("America meridionali"), Hunterian Collection, University of Glasgow, Scotland (Staig, 1931:55).

Copris floriger Kirby, 1818:396 (Staig, 1931:55)

Type: Unknown to me.

Phanaeus splendidulus (Fabricius), Macleay, 1819: 133

Phanaeus corydon Blanchard, 1843:175 (Gemminger and Harold, 1869:1018, re: *floriger*)

Type: Unknown to me.

NOMENCLATURAL REMARKS. Most pre-1960 references to this species have been under the name *floriger*. For many years, the name "splendidulus" was erroneously applied to *Sulcophanaeus menelas* (Laporte-Castelnau) (see Edmonds, 1972).

OTHER REFERENCES. To *floriger*—Curtis, 1845; Guerin-Meneville, 1855; Harold, 1875a; Preudhomme de Borre, 1886; Nevinson, 1892a; Gillet, 1911b; Ohaus, 1913; Olsoufieff, 1924; Pessoa, 1934; Pessoa and Lane, 1941; Blackwelder, 1944; Lengerken, 1954; Roze, 1955 (probably a misidentification).

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 1–3).—Usually as follows: pronotum, posterior portion of head shining green or yellow-green, almost always with weak coppery reflections, especially on pronotal disk; tips of pronotal spines of male and large median area of female pronotum shining black; elytra dull, dark green, often distinctly shinier at bases and along margins; pygidium green to yellow-green; venter black with shining green to yellow-green on legs and sterna. Uncommonly—elytra dark blue or almost completely black, pronotum (except for black areas) dark blue, blue-green, or green. *Pronotum.*—Basal fossae absent or only barely indicated; anterolateral angle dentate in larger males, usually rounded in females, smaller males. *Metasternum.*—Anterior prominence (seen in profile; Fig. 130) acuminate, produced anteriorly as very small, acute tubercle (which may be worn away). *Front Tibiae* (Figs. 126, 127).—Tridentate in both sexes; fourth (basal) tooth at most only suggested by angular bend in lateral margin; third tooth not longitudinally carinate. Tip of spur evenly curved mesally, not truncated. *Secondary Sexual Characters.—Male:* In larger individuals (Fig. 115), cephalic horn, viewed laterally, strongly tapered apically, erect except for distal one-third, which is gently bowed posteriorly; apex, viewed anteriorly, slightly widened, truncated, distinctly compressed anteroposteriorly. In smallest individuals, horn reduced to elongate tubercle or weakly bituberculate, transverse carina. Anterior one-half of pronotal disk more-or-less flattened, triangular area followed by transverse concavity in front of posterior margin; sides of disk near posterior margin drawn out as pair of mesally curved, dorsally directed, tapering spines. In smallest individuals, pronotal disk convex, spines reduced to pair of small, parallel, ridge-like tubercles near anterior margin. *Female:* Cephalic carina distinctly, but not strongly, trituberculate (Fig. 133). Pronotum (Fig. 121) convex, with midlongitudinal, linear impression extending from posterior margin to small, oval anteromedian concavity; strong U-shaped carina lying immediately anterior, partially surrounding concavity; this carina produced medially as acute denticle and slightly elevated at each end to form weak crest (Fig. 121). *Specimens Examined.*—54 males, 34 females (length 12–20 mm; width 8–13 mm).

DIAGNOSTIC REMARKS. The form of the head and pronotum of both sexes is identical to that of *P. dejeani.* The two species are easily distinguished, however, by the form of the anterior prominence of the metasternum and by coloration. Moreover, in this species, the third tooth of the front tibia is not carinate.

DISTRIBUTION (Fig. 136; appendix). Lower (<1000 m) Atlantic coastal forests of southeastern Brazil from Espírito Santo to Rio Grande do Sul and Misiones, Argentina. Coprophagous. Collection dates: October–April.

COMMENTS. Precise geographical information on *splendidulus* is rather scarce, but available data suggest that it inhabits lowland forests in the supermoist region of southeastern Brazil in Espírito Santo, Rio de Janeiro, Guanabara, and extreme southern and eastern São Paulo, as well as the drier forests from São Paulo to Rio Grande do Sul. While I have no records from the area, it is reasonable to assume that it follows the coastal belt of evergreen forests farther north than Espírito Santo. Although I suspect that *splendidulus* and *dejeani* are usually separated altitudinally, the two species have been collected together (e.g., in the Petropolis–Teresopolis–Nova Friburgo area of the state of Rio de Janeiro).

I have examined a series of five specimens labeled "Cayenne," all of which have dark, almost black, elytra and shining yellow-green pronota. These specimens, as well as isolated ones labeled "Para" and "Belem," were likely mislabeled. All of the unusually colored specimens (see descriptive remarks) are from the Espírito Santo–Rio de Janeiro region, that is, the northern extreme of the known range.

There are two Fabrician specimens of *splendidulus,* a large male and small female, in the Hunterian Collection at the University of Glasgow. Staig (1931) designated the male as "Type," which I interpret here as lectotype. I am indebted to R. M. Dobson for comparing the Fabrician specimens with modern material.

Phanaeus (*Notiophanaeus*) *dejeani* Harold

Figures 4, 5, 117, 129, 136

Phanaeus dejeani Harold, 1868b:82

Type: Male lectotype ("Brasilia"), Muséum National d'Histoire Naturelle, Paris (Arnaud, 1982a:114).

OTHER REFERENCES. Harold, 1869, 1875a; Nevinson, 1892a; Ohaus, 1909; Gillet, 1911b; Olsoufieff, 1924; Pessoa, 1934; Pessoa and Lane, 1941; Blackwelder, 1944; Lengerken, 1954; Edmonds, 1972.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 4, 5).—Pronotum, posterior portion of head shining greenish yellow, often with reddish or pinkish highlights; tips of male pronotal spines, anteromedian pronotal carina of female, two oval spots behind it dull black. Elytra shining, deep royal blue (rarely blue-green) and appearing lacquered. Pygidium and venter green to yellow-green. *Pronotum.*—Basal fossae absent; anterolateral angle toothed, more strongly so in male. *Metasternum.*—

Anterior prominence (seen in profile; Fig. 129) rounded, (see from below) compressed laterally and keeled longitudinally. *Front Tibiae.*—Tridentate; fourth (basal) tooth sometimes weakly indicated; third tooth usually at least weakly longitudinally carinate, often strongly so. Apex of spur evenly curved mesally, not truncated. *Secondary Sexual Characters.*—As described for *splendidulus* (see above). *Specimens Examined.*—22 males, 18 females (length 12–20 mm; width 8–12 mm).

DIAGNOSTIC REMARKS. See *splendidulus*, above.

DISTRIBUTION (Fig. 136; appendix). Higher (>1000 m) forests of the coastal mountains of extreme southeastern Brazil in São Paulo, Rio de Janeiro, Minas Gerais, and Espírito Santo. Presumed coprophagous. Collection dates: November–February.

COMMENTS. The coloration of *dejeani* is striking and unlike that of any other *Phanaeus*. The intense, deep blue of the elytra, in particular, is unapproached in other species. Not pointed out elsewhere is the fact that, unlike the female of *splendidulus*, which bears a single, large black spot on the pronotal disk, the female of *dejeani* has a pair of small, black spots immediately behind the anteromedian concavity.

The distribution of *dejeani* appears to be overlapped completely by the northern part of that of *splendidulus*. Reliable data, while scarce, suggest that it usually occurs at higher elevations (>1000 m).

Phanaeus (*Notiophanaeus*) *haroldi* Kirsch

Figures 8, 9, 111, 112, 118, 120, 122, 124, 128, 131, 135, 136

Phanaeus haroldi Kirsch, 1871:358

Type: Female holotype ("Bogota"), Staatliches Museum für Tierkunde, Dresden.

OTHER REFERENCES. Nevinson, 1892a; Gillet, 1911b; Olsoufieff, 1924; Paulian, 1935; Pessoa, 1934; Blackwelder, 1944; Gacharna, 1951; Vulcano and Pereira, 1967; Barrera, 1969; Edmonds, 1972.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 8, 9).—Pronotum, posterior portion of head weakly to moderately shining dark green; pronotal spines of both sexes black. Elytra dull, dark green or, more often, almost black with weak greenish or bluish luster. Pygidium dark, weakly shining green; venter somber, with weak green or blue-green reflections. *Pronotum.*—Basal fossae conspicuous. Anterolateral angle drawn out into laterally projecting tooth, posterior to which circumnotal ridge strongly sinuous (Fig. 122); anterior portion of ridge (that behind paraocular areas) straight and approximately perpendicular to longitudinal axis of body. Puncturing (×30) widely spaced and often visible only posterolaterally in male; more evenly distributed in female (Fig. 118). *Metasternum.*—Anterior prominence (seen in profile; Fig. 128) rounded, sometimes almost lobate, (seen from below) compressed laterally, keeled longitudinally. *Front Tibiae* (Fig. 124).—Quadridentate; basal (fourth) tooth sometimes poorly developed; first three teeth carinate longitudinally. Apex of spur truncated, inner angle acute, strongly produced mesally. *Secondary Sexual Characters.*—*Male:* In larger individuals (Fig. 111), cephalic horn slender, erect, not curving posteriorly; reduced to small, triangular tubercle in smallest individuals. In large individuals, roughly triangular portion of pronotal disk concave; posterolateral angles produced as pair of apically convergent, long, anterodorsally projecting spines; in smaller individuals, disk convex, spines reduced to pair of acute, laterally compressed denticles near anterior margin. *Female:* Cephalic carina bowed anteriorly, strongly trituberculate (Fig. 131), less so in smaller individuals. Anterior one-half of disk (Figs. 112, 120) bearing concavity flanked by pair of elongate, anterodorsally directed, acute spines, reduced to acute denticles in small individuals. *Specimens Examined.*—73 males, 66 females (length 14–20 mm; width 9–13 mm).

DIAGNOSTIC REMARKS. The secondary sexual features of this species distinguish it from all other *Phanaeus*.

DISTRIBUTION (Fig. 136; appendix). Forests of the eastern slopes and foothill valleys of the Andes ("Yungas") from Colombia to northern Peru, and isolated localities in Venezuela. 500–1000 m (estimated). Coprophagous. Collection dates: all year.

COMMENTS. It is surprising to me that this large, striking *Phanaeus* is so poorly known. It appears to be a resident of the higher forests of the northern portion of the eastern Andean slopes ("Yungas") from which it can descend to lowland areas. I have seen two specimens collected in the Orinoco River basin (solid squares in Fig. 136) near Ciudad Bolívar, where they probably inhabit gallery forest. This lowland population is very far removed from the main range and may be a relictual. Several specimens examined were labeled, most likely in error, "Panama" (one, "Chiriqui"); Howden and Young (1981) do not report *haroldi* from Panama. Its closest relative, *melibaeus*, occurs far to the southeast.

Phanaeus (*Notiophanaeus*) *melibaeus* Blanchard

Figures 6, 7, 113, 114, 119, 123, 125, 132, 136

Phanaeus melibaeus Blanchard, 1843:176

Type: Male holotype ("Chiquitos"), Muséum National d'Histoire Naturelle, Paris.

Phanaeus sculpturatus Olsoufieff, 1924:87 (Pereira and Martínez, 1956:236)

Type: Female holotype ("Chiquitos"), Muséum National d'Histoire Naturelle, Paris.

NOMENCLATURAL REMARKS. Blanchard's description was based on a single, well-developed male. Olsoufieff based *sculpturatus* on a single specimen which he rightly suspected was the female of *melibaeus*.

OTHER REFERENCES. Lacordaire, 1856; Gemminger and Harold, 1869; Harold, 1869; Nevinson, 1892a; Gillet, 1911b; Olsoufieff, 1924; Pessoa, 1934; Pessoa and Lane, 1937; Blackwelder, 1944; Pereira and Martínez, 1960; Edmonds, 1972; Arnaud, 1982a.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 6, 7).—Pronotum, posterior portion of head shining green with weak to strong yellow or copper reflections, particularly on posteromedian portion of notum. Elytra shining green to blue-green, interstriae strongly shining midlongitudinally and only weakly so along striae. Pygidium shining green to yellow-green. Venter dark, with shining green on abdominal sterna and legs. *Pronotum.*—Basal fossae conspicuous. Anterolateral angles dentate, only weakly so in female; circumnotal ridge sinuous behind anterolateral angle in male (Fig. 123), almost straight in female; anterolateral portion of ridge (behind paraocular areas) slightly sinuous. *Metasternum.*—Anterior prominence (seen in profile) rounded, (seen from below) compressed laterally, keeled longitudinally. *Front Tibiae* (Fig. 125).—Strongly quadridentate, fourth (basal) tooth distinct even after severe wear; first three teeth carinate longitudinally. Spur truncated apically, inner angle acute, strongly produced mesally. *Secondary Sexual Characters.—Male:* In large individuals (Fig. 113), cephalic horn, seen laterally, slender, except for slight posterior flexion near base, almost erect; that of smallest specimens reduced to small, conical tubercle. Pronotal disk bearing pair of prominent, round concavities in front of raised area along posterior margin; sides of disk drawn out as pair of tapering, mesally curved, dorsally directed spines; in smaller individuals, pronotal spines reduced to slightly upturned, blade-like processes. *Female:* Cephalic carina trituberculate; seen from above, almost straight; in larger individuals, carina strongly raised with highly accentuated, acute tubercles, its outline resembling scalloped margin of crown (Fig. 132). Pronotum (Figs. 114, 119) convex, with round, anteromedian concavity preceded by three, strong, anteriorly directed denticles, middle one of which quadrate, lateral of which acute; surface in front of denticles almost vertical, seen anteriorly, shallowly concave between two weak ridges directed outwardly from points on the notum above the eyes. *Specimens Examined.*—19 males, 14 females (length 13–18 mm; width 8–11 mm).

DIAGNOSTIC REMARKS. This species is similar to *haroldi;* the two species are easily distinguished by coloration and secondary sexual characters.

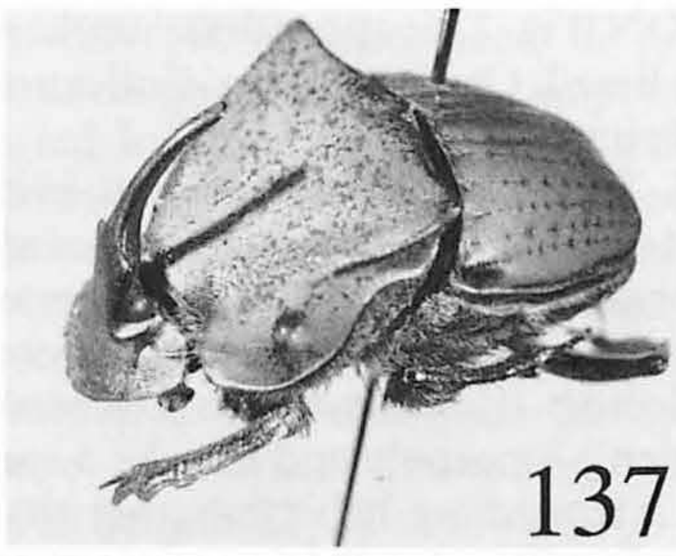
DISTRIBUTION (Fig. 136; appendix). Southern Amazon Basin in Brazil. Coprophagous. Collection dates: October–February.

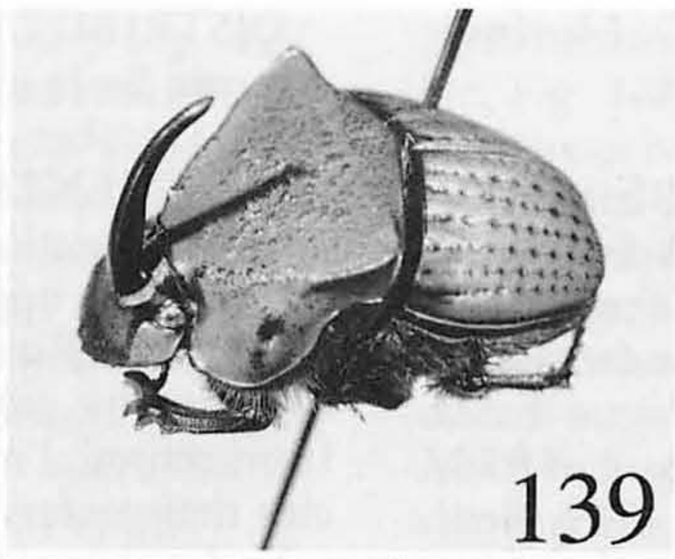
COMMENTS. This species is uncommon, even in large collections. Known collection localities are all along the upper reaches of major tributaries of the Amazon River and doubtlessly reflect the routes followed by collectors. *P. melibaeus* is unknown from central, "open" Amazonia and may be a species that prefers intermediate habitats rather than fully developed hylea. The distribution of this species is separated from those of *splendidulus* and *dejeani* to the east by the extensive "campos cerrados" of the Brazilian Highlands and from that of *haroldi* to the northwest by uninterrupted Amazonian forest. I have not seen specimens from Bolivia other than the holotypes, both of which are labeled "Chiquitos." The known distribution of *melibaeus* and its scarcity suggest peculiar ecological requirements, but I have no data that indicate what these could be.

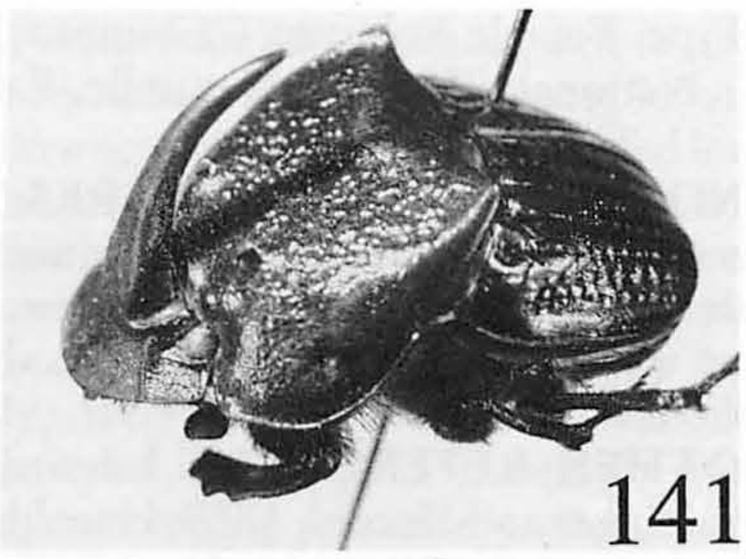
The *Chalcomelas* Group

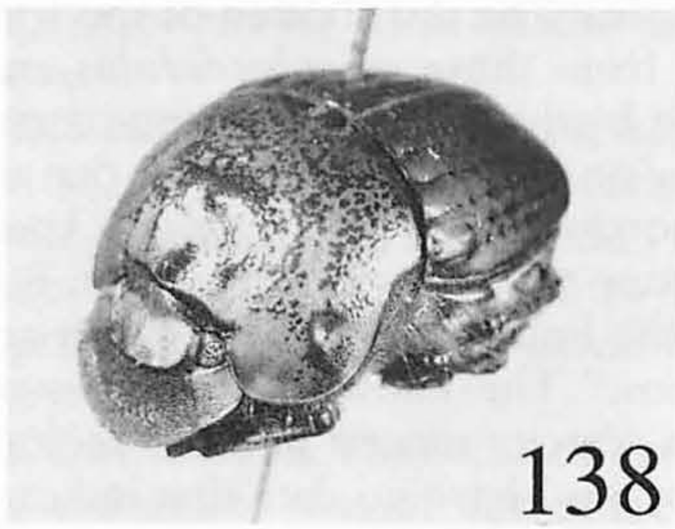
DIAGNOSIS. [1] Anterior margin of clypeus weakly bidentate; [2] clypeal process (seen from front) rounded, narrow, almost toothlike (Fig. 156); [3] cephalic carina of female at most only barely trituberculate (Fig. 149), usually appearing simple (except *achilles*, Fig. 148); [4] anterolateral portions of pronotum punctate, punctures either [a] (Fig. 147) very broad, shallow, often confluent, each with minute, central shining spot (punctures sometimes almost effaced and visible only from a low angle) or [b] (in *achilles,* Fig. 146) smaller, deeper, and most distinct opposite eyes and around lateral fossae; [5] pronotal disk (and sometimes also sides) with few to many irregularly shaped, often confluent, flat, blister-like black rugosities (most strongly developed in *achilles*) giving surface a peppered or mottled appearance (Figs. 137–145); [6] pronotum of male flattened dorsally, very evenly so except in *achilles,* with distinct posterolateral angles (Figs. 137, 139, 141, 143, 144); [7] pronotum of female evenly convex (Figs. 138, 140, 142, 145); [8] basal pronotal fossae present or absent; [9] front tibiae (Figs. 152, 153) tridentate (fourth [basal] tooth suggested in some females); [10] elytral striae fine (×30), each bearing 15–20 conspicuous, variable-sized, dark, shallow punctures easily visible to unaided eye (Figs. 150, 151); interstriae flat; [11] dorsal coloration usually somber (Figs. 23–29) (bright red or green in *achilles,* Figs. 30, 31); Amazonian rain forests (except *achilles*) (Fig. 162).

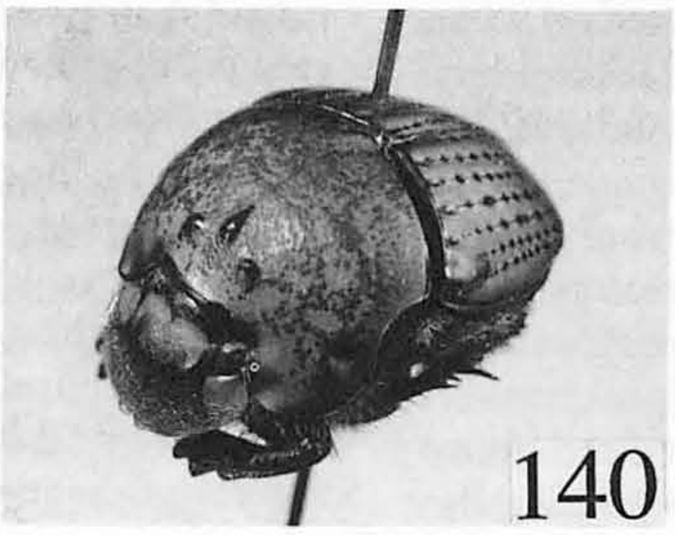
The *chalcomelas* group brings together four South American species distinguished from other *Notiophanaeus* by their pronotal sculpturing (4 and 5 above) and conspicuous, fossa-like punctures of the elytral striae (Figs. 150, 151). Three species, *chalcomelas, meleagris,* and *cambeforti,* inhabit rain forests; their somber coloration camouflages them against a background of forest floor litter. The fourth

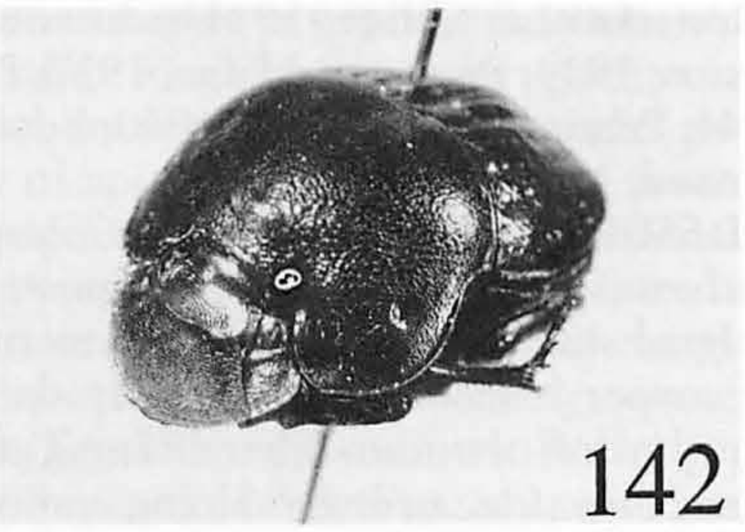


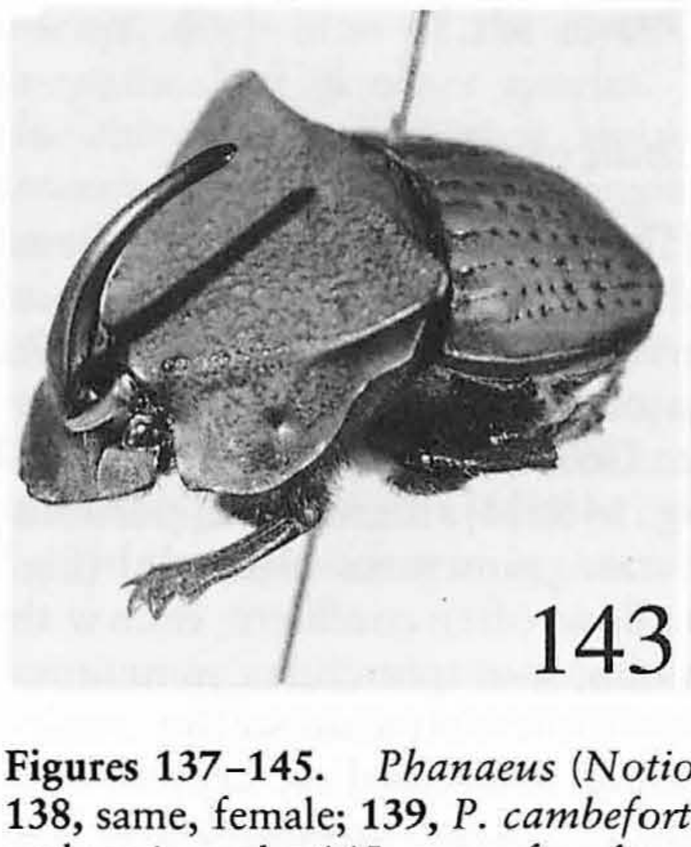


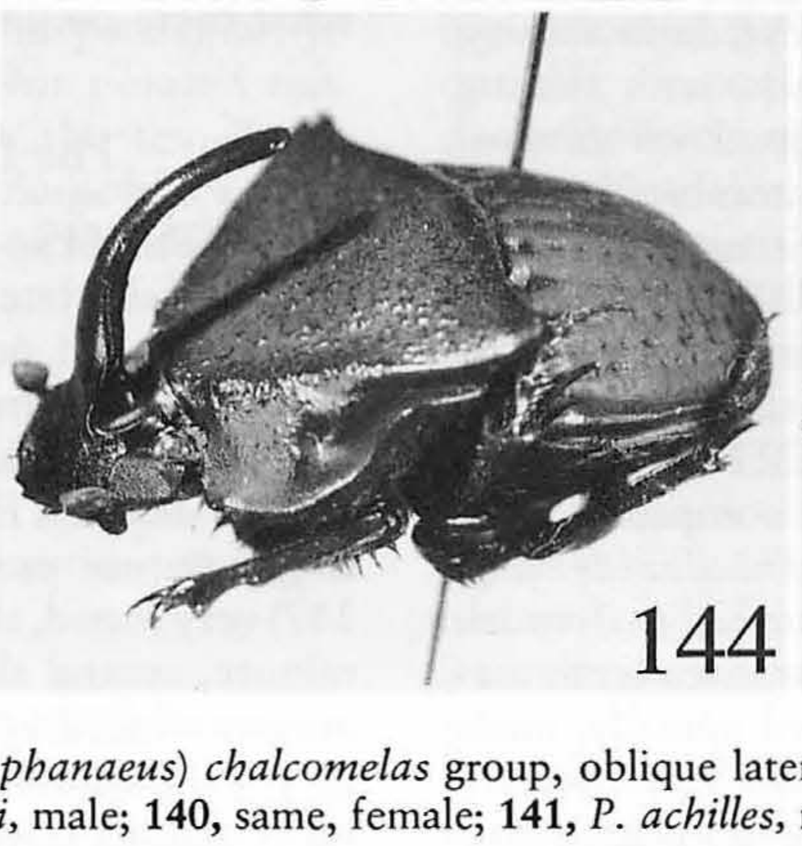












Figures 137–145. *Phanaeus* (*Notiophanaeus*) *chalcomelas* group, oblique lateral views (**137,** *P. chalcomelas,* male; **138,** same, female; **139,** *P. cambeforti,* male; **140,** same, female; **141,** *P. achilles,* male; **142,** same, female; **143, 144,** *P. meleagris,* male; **145,** same, female.

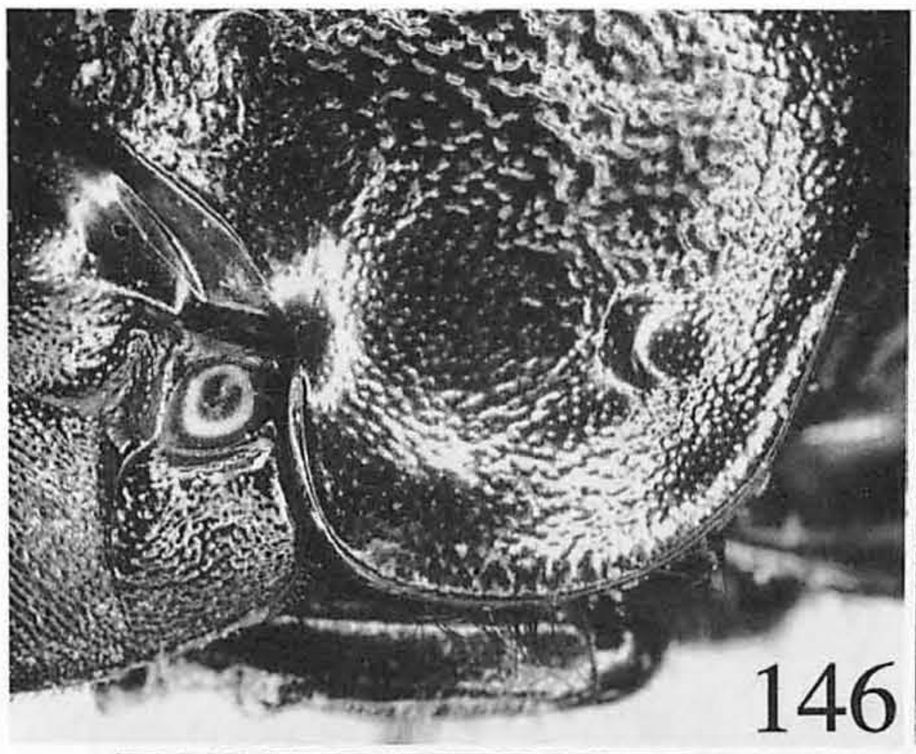
species, *achilles,* inhabits the desert scrub region of southwestern Ecuador and northwestern Peru along the Pacific coast; it is isolated taxonomically within the group (see "Comments" under *achilles*).

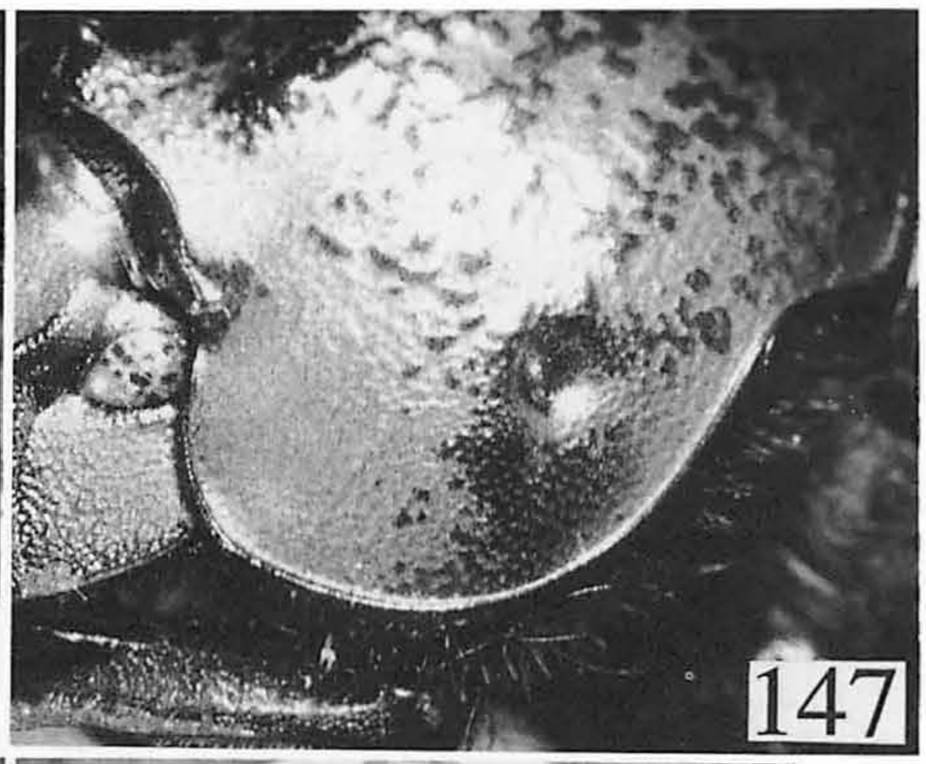
The pronotal sculpturing of this group is reminiscent of that of most *Phanaeus, sen. str.,* which is most closely approached in *achilles.* In this context, the *chalcomelas* group is an annectant taxon between the two subgenera. There exists a continuum of variation among the species of this group in the degree of roughness of the pronotal surface, particularly the disk. In *chalcomelas* and *cambeforti* (Figs. 137–140), the rugosities are finer and less dense. In *meleagris* (Figs. 143–145), they are coarser and more densely placed, but, as in the two former species, they retain a flat, blister-like appearance. In *achilles,* however (Figs. 141, 142), the rugosities are more clearly defined ("crisper"), denser, and more widely distributed on the disk and sides such that the sculpturing of the pronotum closely resembles that of certain *Phanaeus, sen. str.* In all four species, however, the sides of the pronotum, which may bear rugosities like those on the disk, retain at least some distinct puncturing. Moreover, except in some male *achilles* and *meleagris,* there is at least limited puncturing also on the central area of the disk.

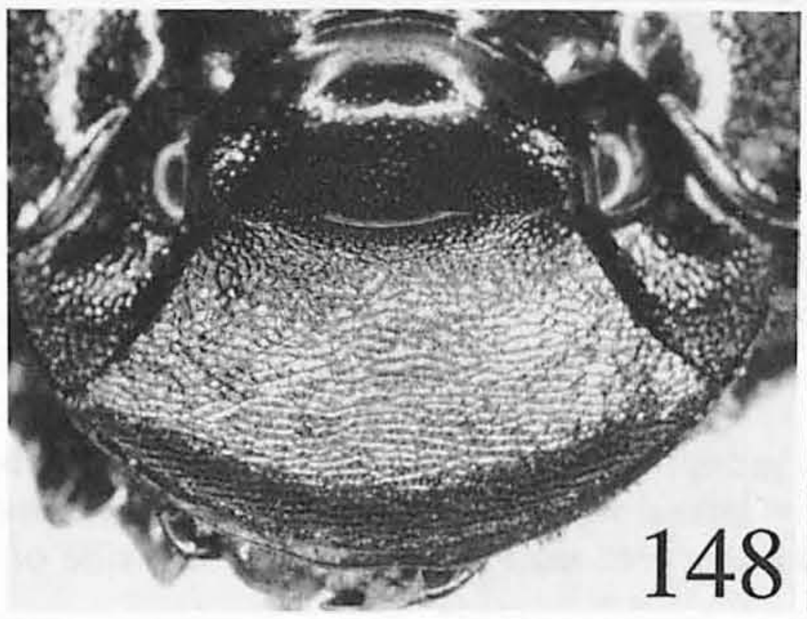
The large, fossate punctures of the elytral striae are seen otherwise only in *bispinus* (Fig. 169). The striae themselves are extremely fine, superficial lines; they are not carinulate, as I wrongly stated in 1972.

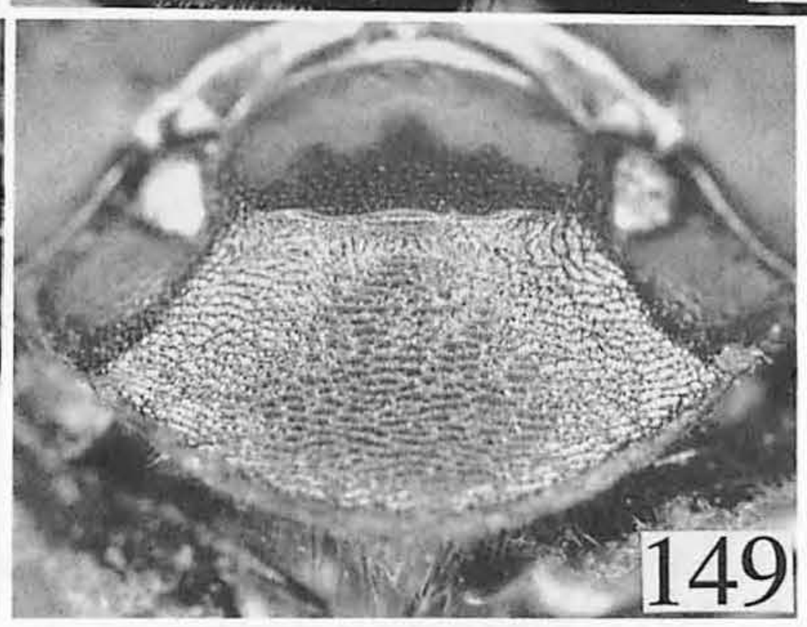
P. chalcomelas and *cambeforti* bear a strong resemblance to each other, particularly in size, shape, and color. Indeed, *cambeforti* escaped detection until 1982, and the two species are often commingled in collections. Both occur in the Amazon Basin and, as far as I know, *cambeforti* is always found along with *chalcomelas* (the converse, however, is not true). Certain color forms of *meleagris* resemble these species, and all three can occur sympatrically (e.g., the environs of Villavicencio, Colombia). How these three species coexist ecologically would be the subject of an interesting field study.

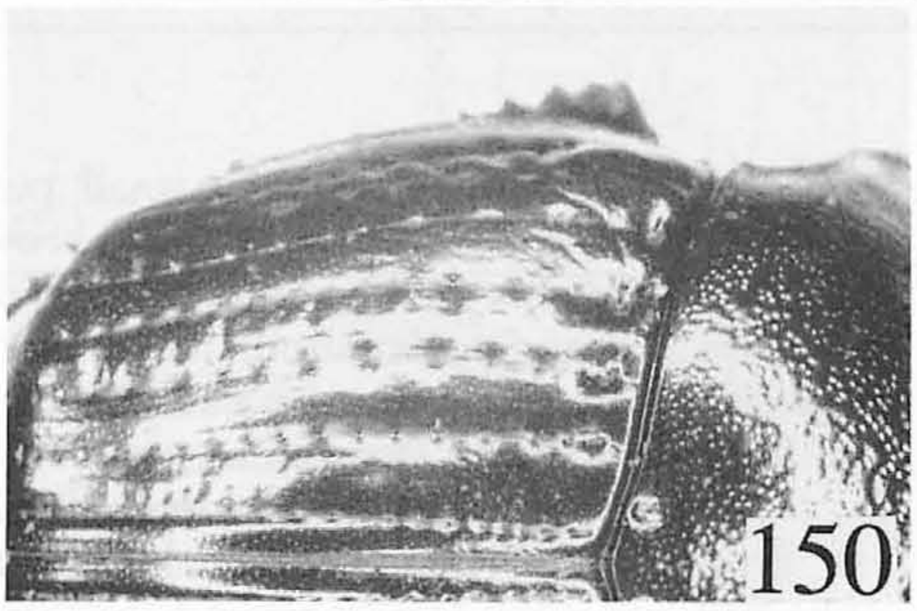
P. achilles differs morphologically, geographically, and ecologically from the other members of the group; it is the only xeric adapted species of

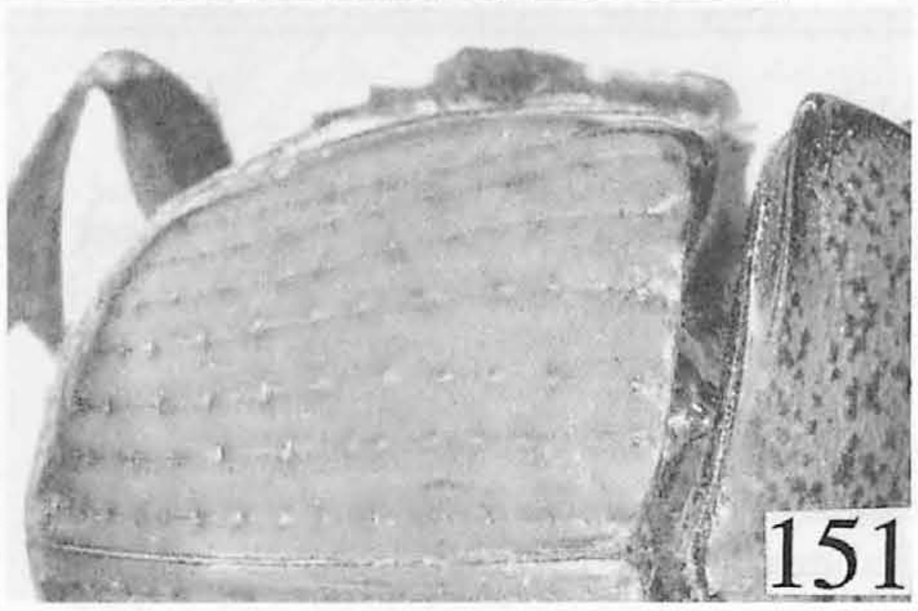












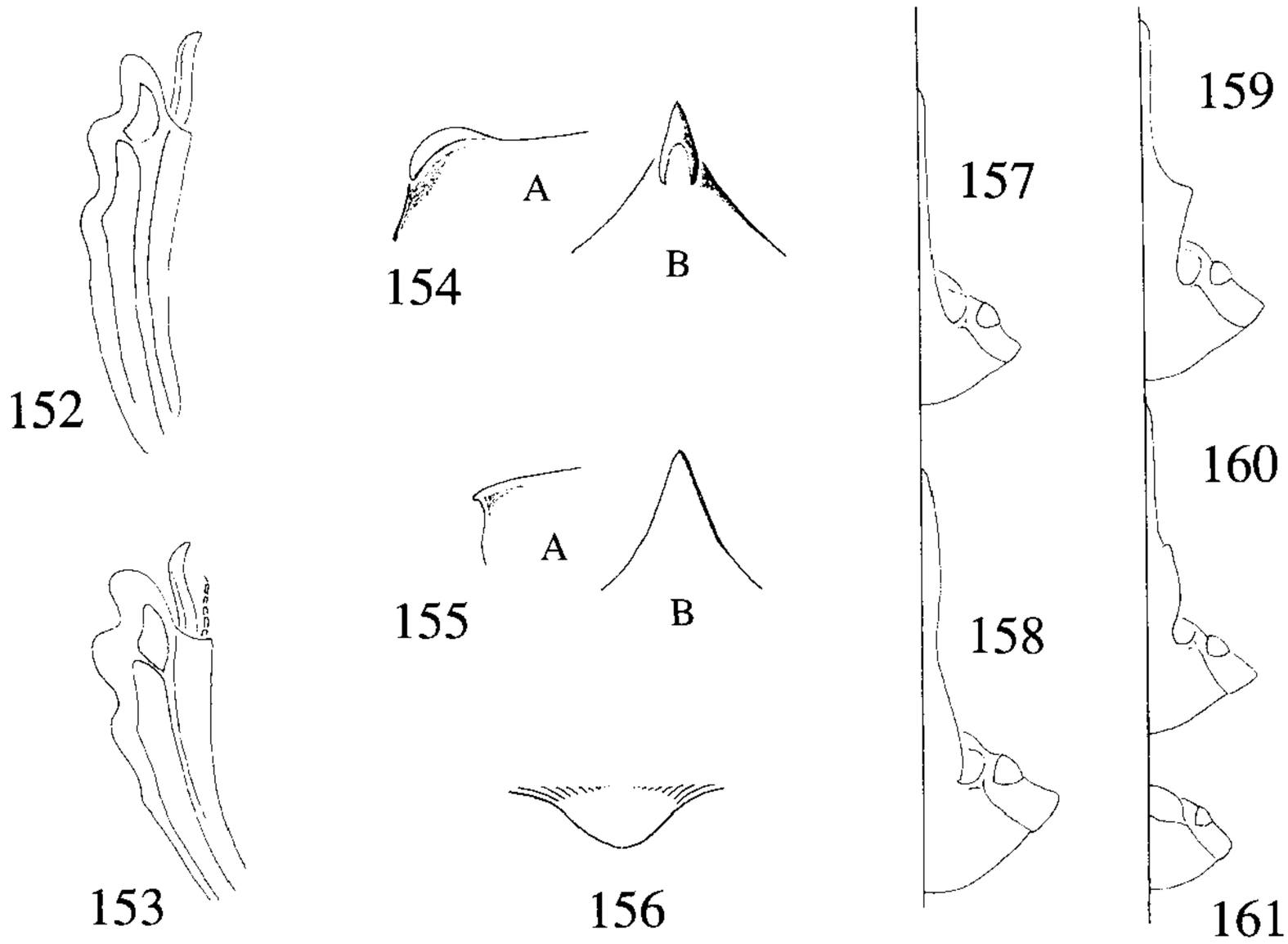
Figures 146–151. *Phanaeus* (*Notiophanaeus*) *chalcomelas* group. (**146,** anterolateral view pronotum of *P. achilles,* female; **147,** same, *P. chalcomelas,* female; **148,** dorsal view head of *P. achilles,* female; **149,** same, *P. chalcomelas,* female; **150,** dorsal view left elytron of *P. achilles,* female; **151,** same, *P. chalcomelas,* female).

Notiophanaeus. At first glance, it strongly resembles members of the *mexicanus* group of *Phanaeus, sen. str.,* none of which possesses the large, fossate punctures of the elytral striae nor an acuminate anterior angle of the metasternum.

KEY TO THE SPECIES OF THE *CHALCOMELAS* GROUP

1a. Anteromedian angle of metasternum seen from below (Fig. 154) capped by raised arrowhead or V-shaped swelling; sides of swelling visible laterally as distinct ridges. Paraocular ridge almost always distinct and extending from posterior margin of paraocular area to point even with middle of lateral margin of eye. *Male:* Cephalic horn of large individuals as in Figures 159, 160, abruptly narrowed at about midlength. *Female:* Pronotum (Fig. 138) with shallow, anteromedian concavity surrounded by four small tubercles, anterior one of which is largest, occasionally toothlike. Dorsum dull, dark, usually olive brown or olive green (Figs. 23, 24). Length 12–18 mm. Tropical rain forests of South America from Guiana to Bolivia (Fig. 162) *Phanaeus* (*N.*) *chalcomelas* (Perty)

b. Anteromedian angle of metasternum not capped; this angle smooth and drawn out anteriorly as small, slightly upturned acute tooth best seen in profile (Fig. 155). Paraocular ridge present or absent. *Male:* Cephalic horn tapering evenly (Fig. 157); if widened basally (some *meleagris,* Fig. 158), narrowing not as abrupt as above. *Female:* Pronotum evenly convex, lacking distinct anteromedian concavity, bearing three small, rounded tubercles (almost effaced in *achilles*) near anterior margin (Figs. 140, 142, 145). Color and distribution variable 2



Figures 152–161. *Phanaeus* (*Notiophanaeus*) *chalcomelas* group. (**152,** *P. chalcomelas*, male, left tibia; **153,** same, female; **154,** *P. chalcomelas*, anterior end of metasternum [A = lateral view; B = ventral view]; **155,** *P. meleagris*, same; **156,** *P. chalcomelas*, anterior view clypeal process; **157,** *P. cambeforti*, male, anterior view left side of head; **158,** *P. meleagris*, same; **159–161,** *P. chalcomelas*, same).

2a. Elytral interstriae distinctly, but sparsely punctured (×10), irregularly wrinkled (Fig. 150). Pronotal punctures small, deep, intermingled with well-defined, black rugosities (Fig. 146). Pronotal disk of large males flattened, but not evenly so (Fig. 141); posterolateral angles, seen from above, rounded laterally such that disk appears nearly heart-shaped. Middle of cephalic carina of female thickened and raised, forming a distinct, isolated, anteriorly bowed ridge (Fig. 148). Paraocular ridge distinct. Dorsum shining, coppery red or dark green (Figs. 30, 31). Desert scrub region of southwestern Ecuador and northern Peru . . . . . .
. . . . . *Phanaeus* (*N.*) *achilles* Boheman

b. Elytral interstriae completely smooth, bearing no punctures or wrinkling (Fig. 151). Pronotal punctures (Fig. 147) large, very shallow, often confluent, each with a shining, central microspot (×40; pronotal puncturing often visible only when viewed from a low angle). Pronotal disk of large males evenly flattened, sides of posterolateral angles more or less straight such that disk, seen from above, appears almost triangular (Figs. 137, 139, 143, 144). Cephalic carina of female simple or only weakly trituberculate (Fig. 149). Paraocular ridge absent or indicated only by a slight swelling adjacent to eye. Dorsum dull, usually somber. Evergreen forests east of Andes 3

3a. Pronotal puncturing, while never strong, usually distinct both on sides and disk; central microspots often very difficult to detect (×40), sometimes lacking. Basal pronotal fossae lacking or represented only by small punctures (×10). Dorsum olive green or olive brown; metallic highlights on pronotum and pygidium always green. Smaller-sized, length rarely exceeding 15 mm. Amazon Basin from Guiana to Colombia and Peru . . . . . .
. . . . . *Phanaeus* (*N.*) *cambeforti* Arnaud

b. Pronotal puncturing very weakly defined and often appearing almost effaced; central shining microspots almost always distinct (×40) even if associated punctures are obsolete. Basal pronotal fossae always distinct. Dorsal coloration variable: (a) including reddish or pinkish reflections, or green-brown tones infused with reddish highlights at least along circumnotal ridge, but often also on sides of disk and pronotum (Figs. 27, 28); or (b) uniformly weakly lustrous, dark blue with an "oily" sheen (Fig. 29); or (c) uniformly dull, dark green or blue; if general dorsal coloration approaches olive green or olive brown, always associated with reddish or pinkish highlights on pronotum and pygidium. Larger-sized, length seldom less than 15 mm. Rain forests ("Yungas") along eastern slopes of Andes from Venezuela to Bolivia . . . . . .
. . . . . *Phanaeus* (*N.*) *meleagris* Blanchard

Phanaeus (*Notiophanaeus*) *chalcomelas* (Perty)

Figures 23, 24, 137, 138, 147, 149, 151–154, 156, 159–162

Onitis chalcomelas Perty, 1830:40

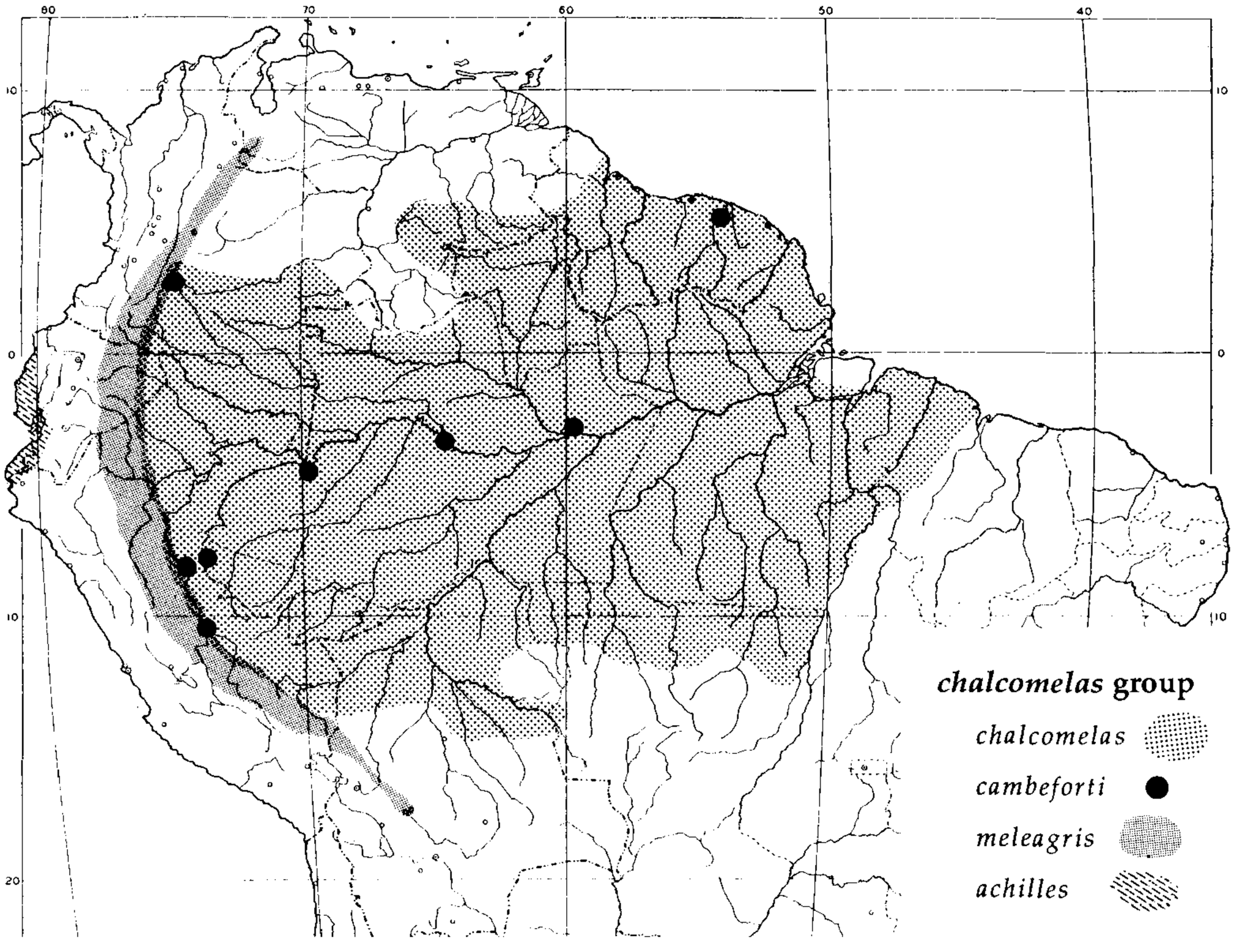


Figure 162. Distribution of the *Phanaeus* (*Notiophanaeus*) *chalcomelas* group.

Type: Female holotype? ("Brasilia"), Zoologische Staatssammlung, Munich (see "Comments").

Phanaeus chalcomelas (Perty) (Harold, 1859:198)

OTHER REFERENCES. Bates, 1868; Gemminger and Harold, 1869; Nevinson, 1892a; Gillet, 1911b; Olsoufieff, 1924; Pessoa, 1934; Paulian, 1935; Halffter and Matthews, 1966; Vulcano and Pereira, 1967; Barrera, 1969; Edmonds, 1972; Scherer, 1983.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 23, 24).—Dorsum dull olive green to olive brown with green highlights, occasionally coppery brown, rarely with strong green reflections on pronotum. Pronotal coloring broken by black rugosities, which produce mottled or peppered appearance; extent of mottling varies from very little to covering most of disk. Pygidium green; venter with shining, dark green reflections on legs, pleura, and abdominal sterna. *Head.*—Paraocular ridge distinct. *Pronotal Sculpturing.*—Low, blister-like rugosities usually fairly dense, covering most of disk (Figs. 137, 138) (very sparse to almost absent in male Guiana specimens); sides, anterolateral angles with few, if any, rugosities, densely punctate (Fig. 147); punctures broad, shallow, each with inconspicuous central microspot. *Pronotum.*—Basal pronotal fossae present, punctiform. *Metasternum.*—Anterior prominence capped by a raised swelling which, seen from below (Fig. 154B), shaped as an arrowhead or narrow V; sides of swelling, seen laterally (Fig. 154A), visible as distinct ridges. *Secondary Sexual Characters.—Male:* Basal one-half of cephalic horn of large individuals (seen from front, Figs. 159, 160) greatly expanded laterally; apical one-half abruptly narrowed, tapering; basal expansion of horn progressively less pronounced in smaller specimens; horn reduced to small, conical tubercle in smallest individuals (Fig. 161). Pronotal disk of large individuals (Fig. 137) evenly flattened, sides more-or-less straight, posterolateral angles (seen from above) projecting beyond lateral margin of pronotum such that disk almost triangular; in smallest individuals, posterolateral angles reduced to small, elongate tubercles near middle of disk, flattened area restricted to area between and in front of these tubercles. *Female:* Pronotum (Fig. 138) with small, oval, anteromedian concavity surrounded by four tubercles; anterior tubercle largest, toothlike in largest specimens; in smallest individuals, tubercles and concavity virtually effaced. *Specimens Examined.*—136 males, 131 females (length 12–18 mm; width 9–12 mm).

DIAGNOSTIC REMARKS. The coloration and overall size and shape of *chalcomelas* are very similar to those of *cambeforti;* the two species are easily confused. They differ in secondary sexual characters (shape of male cephalic horn and female pronotum) and in the shape of the anterior prom-

inence of the metasternum. Certain *meleagris* also strongly resemble *chalcomelas,* but they also differ in the aforementioned characters. Smaller individuals, particularly males, must be examined carefully to avoid confusing these three species.

DISTRIBUTION (Fig. 162; appendix). Evergreen forests of Guiana and the Amazon Basin of Brazil, Colombia, Ecuador, Peru, and Bolivia. 0–500 m. Coprophagous. Collection dates: all year.

COMMENTS. The known distribution of *chalcomelas* coincides with practically all of the Amazonian hylea and covers the largest area of that of any *Phanaeus.* In spite of its wide distribution, there is remarkably little geographic variation in the characters that I have studied. Guianan males are more coppery brown and have fewer, smaller pronotal rugosities than specimens from elsewhere. This species is sympatric with *cambeforti,* and also with *meleagris* in those peripheral areas where *meleagris* descends to lower elevations (e.g., Buena Vista, Bolivia; Pucallpa, Peru; Villavicencio, Colombia).

Although I have listed it above, I am not sure that the Munich specimen is indeed the holotype of *chalcomelas.* It bears the indentification label "Phanaeus chalcomelas," but the writing does not match the sample of Perty's handwriting in Horn and Kahle (1937, Plate 34, Fig. 16). Moreover, Perty placed this species in *Onitis,* not *Phanaeus.*

Phanaeus (*Notiophanaeus*) *achilles* Boheman

Figures 30, 31, 141, 142, 146, 148, 150, 162

Phanaeus achilles Boheman, 1858:42

Type: Male holotype ("Puna"), Naturhistoriska Riksmuseet, Stockholm.

Phanaeus foveolatus Harold, 1880a:152 (Gillet, 1911a:319)

Type: Unknown to me.

OTHER REFERENCES. Nevinson, 1892a; Gillet, 1911b; Olsoufieff, 1924; Vulcano and Pereira, 1967; Edmonds, 1972.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 30, 31).—Dorsum brightly shining red, green or red with weak green or yellow highlights except for black pronotal rugosities. Pygidium weakly shining dark green, yellow-green, or nearly black. Venter weakly shining black, sometimes with weak green highlights. *Head.*—Paraocular carina present, extending to lateral margin of eye. *Pronotal Sculpturing.—Male* (Fig. 141): Disk rugose; rugosities irregularly shaped, becoming weaker posteromedially, replaced by strong, rough puncturing; sides granulorugose with intermingled punctures anteriorly, strong punctures posteriorly. *Female* (Figs. 142, 146, 150): Anterior two-thirds of surface covered by melange of granules and rough, confluent punctures producing distinct black rugosities in some areas (especially on disk); posterior one-third punctate, becoming more weakly so posteriorly. Both sexes with distinct puncturing, at least on sides, sometimes obscured by surrounding, rough sculpturing in some specimens, particularly males. *Elytra.*—Interstriae distinctly, but finely, sparsely punctured (×10), with some irregular wrinkling (Fig. 150). *Metasternum.*—Anterior prominence acuminate, tip produced as small, acute, slightly upturned tubercle best seen in profile (as in Fig. 155). *Secondary Sexual Characters.—Male:* In large individuals (Fig. 141), anterior three-fourths pronotal disk flat, posterior one-fourth weakly, transversely concave; concave posterior area bounded anteromedially by weakly defined, transverse carina or by small, raised, V-shaped ridge; sides of disk rounded, angulate posterolaterally, each interrupted near anterior margin of pronotum by strong, conical tubercle. (No very small males observed.) *Female:* Cephalic carina (Figs. 142, 148) thickened, raised medially as weakly, anteriorly bowed ridge. Pronotum (Fig. 142) evenly convex, with three weak, closely set, round tubercles near anterior margin; these tubercles often coalesce to form a thick, flat, trilobed ridge. *Specimens Examined.*—15 males, 17 females (length 15–20 mm; width 9–13 mm).

DIAGNOSTIC REMARKS. This species is easily distinguished from other members of the group by pronotal sculpturing, color, and distribution. The male, in particular, superficially resembles certain *Phanaeus, sen. str.* (e.g., *wagneri*), from which it differs by having distinct puncturing of the elytral striae and an acuminate anterior prominence of the metasternum.

DISTRIBUTION (Fig. 162; appendix). Lowland desert scrub region of southwestern Ecuador and northern Peru. Coprophagous. Collection dates: October, January–February.

COMMENTS. *P. achilles* is a unique species that I have assigned to the *chalcomelas* group on the following basis: conspicuous, foveolate puncturing of the elytral striae; black pronotal rugosities mixed with distinct puncturing (particularly in the female), acuminate anterior prominence of the metasternum (as in *meleagris* and *cambeforti*), and female secondary sexual characters (similar to those of *meleagris* and *cambeforti*). In 1972 I included it in the "*mexicanus* complex" on the basis of a resemblance of the male (the female was unknown to me at the time) to such species as *wagneri.* The female, however, is quite different from those of the *mexicanus* group (q.v.); it most closely resembles those of *meleagris* and *cambeforti.* Nevertheless, *achilles* is a taxonomic isolate within the *chalcomelas* group not only morphologically (form of the male pronotum, pronotal sculpturing, coloration) but also ecologically and geographically. Whereas other members of the group inhabit the rain forests of the Amazon Basin, *achilles* is restricted to the desert scrub region of southern Ecuador and adjacent northern Peru. Bruce Gill (pers. comm.) has collected this species from feces in the region of dry scrub vegetation 45 km west of Gua-

yaquil as well as from "wet forests" on the outskirts of the same city.

Phanaeus (*Notiophanaeus*) *cambeforti* Arnaud

Figures 25, 26, 139, 140, 157, 162

Phanaeus cambeforti Arnaud, 1982b:122

Type: Male holotype ("French Guiana, Saul; IV-1977"), Muséum National d'Histoire Naturelle, Paris.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 25, 26).—Dorsum dull olive brown to olive green with speckling on pronotum produced by black rugosities (more extensive on female). Pygidium dark green or olive brown; venter with dark, shining green reflections. *Head.*—Paraocular ridge lacking. *Pronotal Sculpturing.*—Disk sparsely (in male) to densely (in female) covered with low, black, blister-like rugosities; entire surface of pronotum with large, shallow punctures (best seen from low angle); each puncture with central, shining microspot, which can be difficult to detect (×40). *Pronotum.*—Basal fossae usually absent; if present, small and partially effaced. *Metasternum.*—Anterior prominence acuminate, not capped by a swelling. *Secondary Sexual Characters.—Male:* Cephalic horn (seen from front, Fig. 157) gradually tapering from base to apex; pronotum as in *chalcomelas*. *Female:* Pronotum (Fig. 140) evenly convex, with three small, round, smooth tubercles near anterior margin. *Specimens Examined.*—16 males, 19 females (length 12–15 mm; width 7–10 mm).

DIAGNOSTIC REMARKS. While this species can closely resemble *meleagris*, its more distinct pronotal puncturing, much weaker and less extensive pronotal rugosity, absent (or very small) basal pronotal fossae, smaller size and olive coloration lacking red or pink highlights will distinguish it from its closest relative. (See also "Diagnostic Remarks" under *chalcomelas*.)

DISTRIBUTION (Fig. 162; appendix). Known from scattered localities in Guiana and Amazon Basin of Brazil, Colombia, and northern Peru. 0–50 m. Coprophagous. Collection dates: November–April (but probably all year).

COMMENTS. All examined specimens of *cambeforti* bearing precise data were collected from localities where *chalcomelas* also occurs (the converse, however, is not true). On superficial examination these two species closely resemble each other; *cambeforti* was not described until 1982.

Phanaeus (*Notiophanaeus*) *meleagris* Blanchard

Figures 27–29, 143–145, 155, 158, 162

Phanaeus meleagris Blanchard, 1843:176

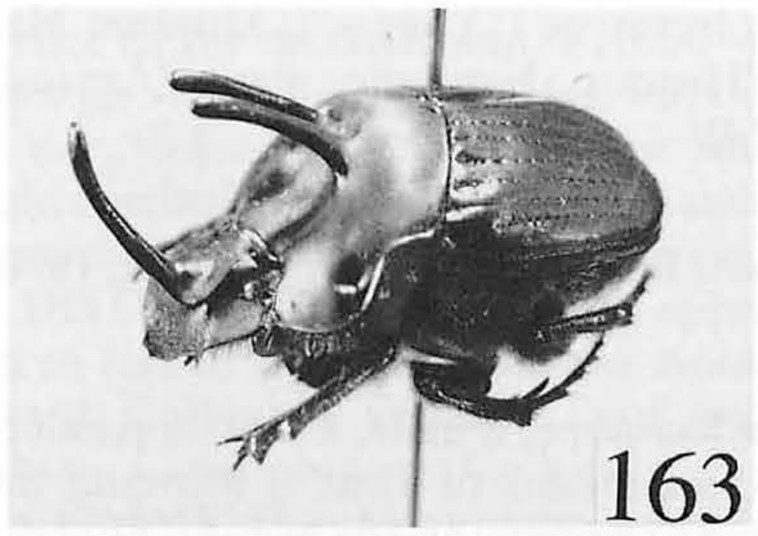
Type: Male lectotype ("Yungas"), Muséum National d'Histoire Naturelle, Paris (Arnaud, 1982a:114).

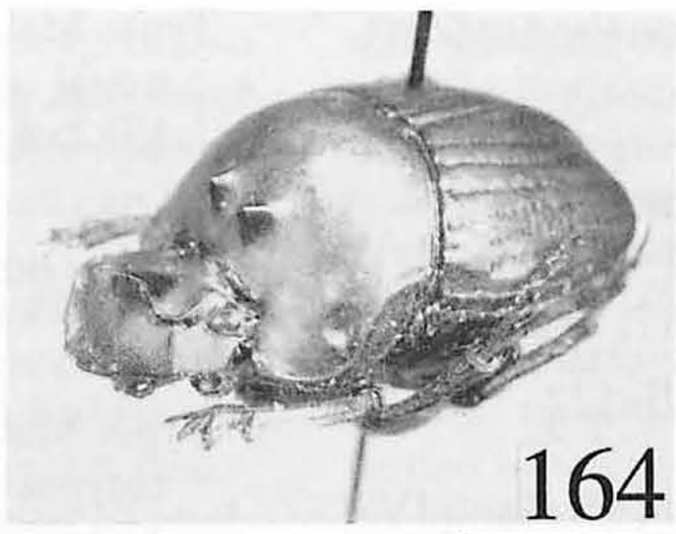
Phanaeus minos Erichson, 1847:106 (Harold, 1870: 105)

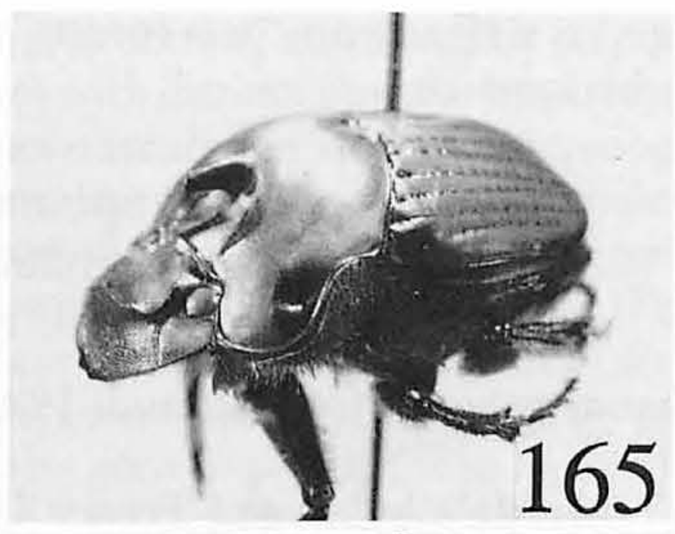
Type: Male lectotype; 2 male, 1 female paralectotypes ("mountains of Peru"), Museum für Naturkunde, Berlin, PRESENT DESIGNATION.

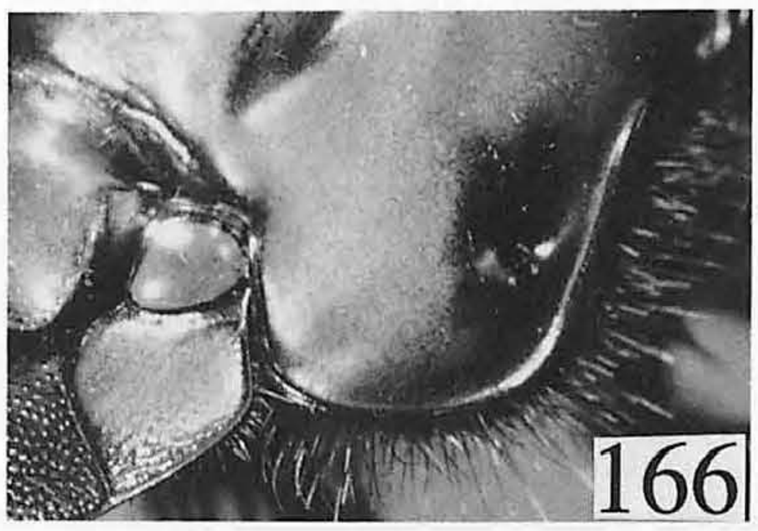
OTHER REFERENCES. Guerin-Meneville, 1855; Lacordaire, 1856; Gemminger and Harold, 1869; Kirsch, 1873 (1874) (as *minos*); Nevinson, 1892a; Gillet, 1911b; Olsoufieff, 1924; Pessoa, 1934; Blackwelder, 1944; Gacharna, 1951; Halffter and Matthews, 1966; Vulcano and Pereira, 1967; Edmonds, 1972; Arnaud, 1982a.

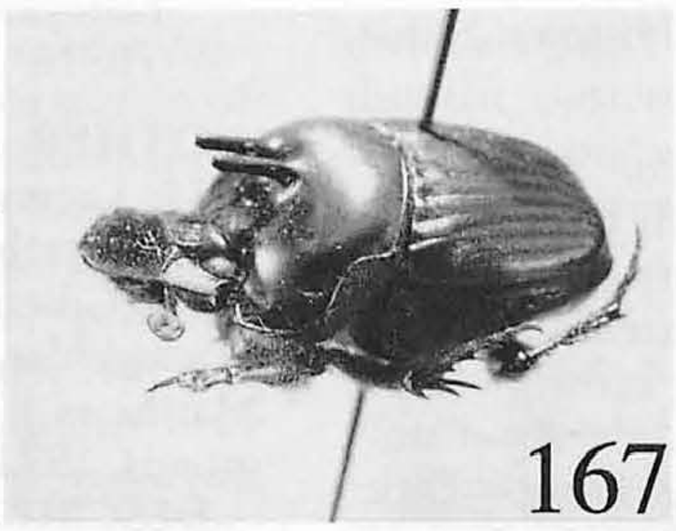
DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 27–29).—Variable, three classes as follows: (a) dorsum dull black except for shining red to yellow-red (rarely yellow-green) highlights on pronotum and posterior portion of head; pronotal coloring usually restricted to sides and to narrow line along posterior margin, but sometimes extending onto disk; elytra with at most extremely weak, bluish sheen (×20); pygidium weakly shining red, red-green, or yellow-green; venter with strong highlights colored like pygidium; (b) dorsum evenly dark blue or green, dull to weakly shining; color of pronotum broken only by black rugosities; venter with strong blue (or green) reflections; (c) dorsum dull, usually mostly black; elytra, colored areas of pronotum black-brown or mahogany brown, rarely olive green; pronotum with weak pink, yellow-red, yellow-green, or coppery highlights at least anterolaterally and along posterior margin; pygidium weakly shining pink to red or red-green; venter, particularly femora, with strong pink highlights. *Head.*—Paraocular ridge absent or only weakly indicated. *Pronotal Sculpturing.*—Rugosity dense on disk and often also on sides; shallow punctures covering most of surface except where obliterated by rugosities, but often very difficult to see even at low angle; each puncture bearing small, central, shining microspot which persists even if associated puncture effaced. *Pronotum.*—Basal fossae present, sometimes punctiform, rarely almost effaced. *Metasternum.*—Anterior prominence acuminate, not capped by swelling (Fig. 155). *Secondary Sexual Characters.—Male:* Cephalic horn of large individuals (seen from front, Fig. 158) swollen basally and tapering apically; basal swelling not abruptly narrowed so as to produce angular prominences; horn reduced to conical tubercle in smallest individuals. Pronotum as described for *cambeforti*. *Female:* Pronotum (Fig. 145) evenly convex, with three, smooth, round tubercles near anterior margin; surface sometimes distinctly flattened in front of these tubercles. *Specimens Examined.*—67 males, 81 females (length 14–21 mm; width 8–14 mm).

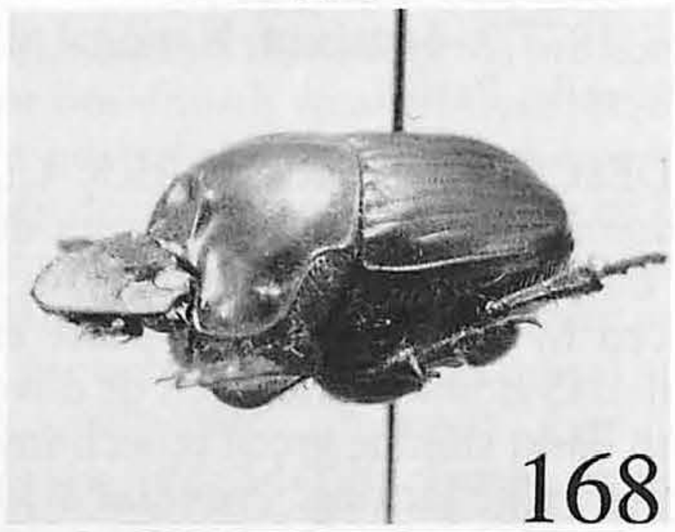


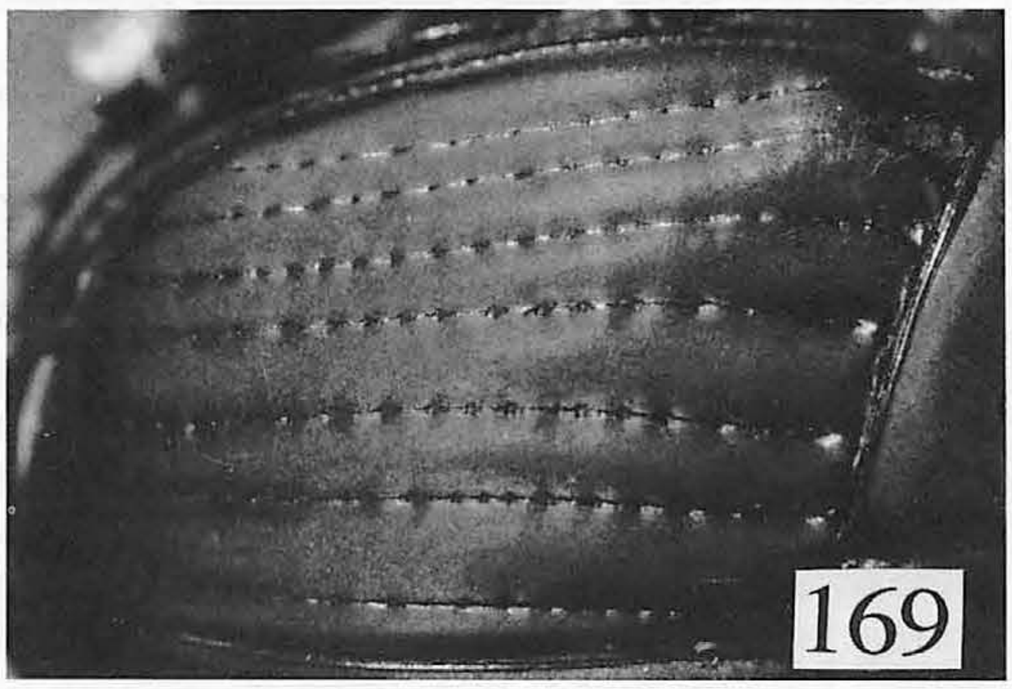


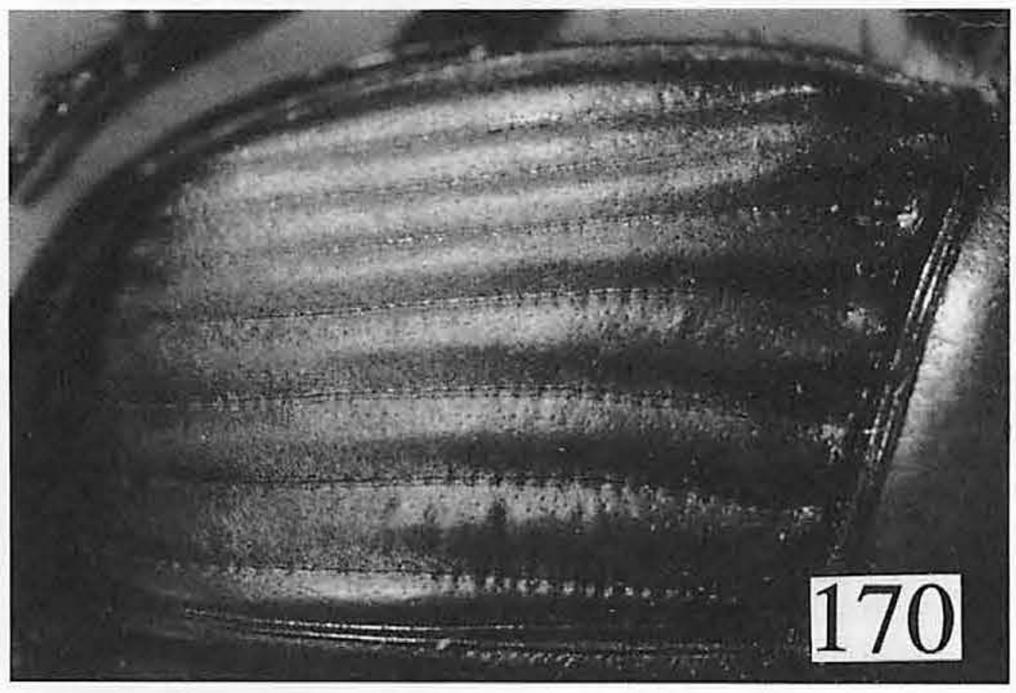












Figures 163–170. *Phanaeus* (*Notiophanaeus*) *bispinus* group (**163,** *P. bispinus,* male; **164,** same; **165,** same, female; **166,** same, anterolateral portion of female pronotum; **167,** *P. alvarengai,* holotype male; **168,** same, allotype female; **169,** *P. bispinus,* left elytron; **170,** *P. alvarengai,* same).

DIAGNOSTIC REMARKS. See under *chalcomelas* and *cambeforti.*

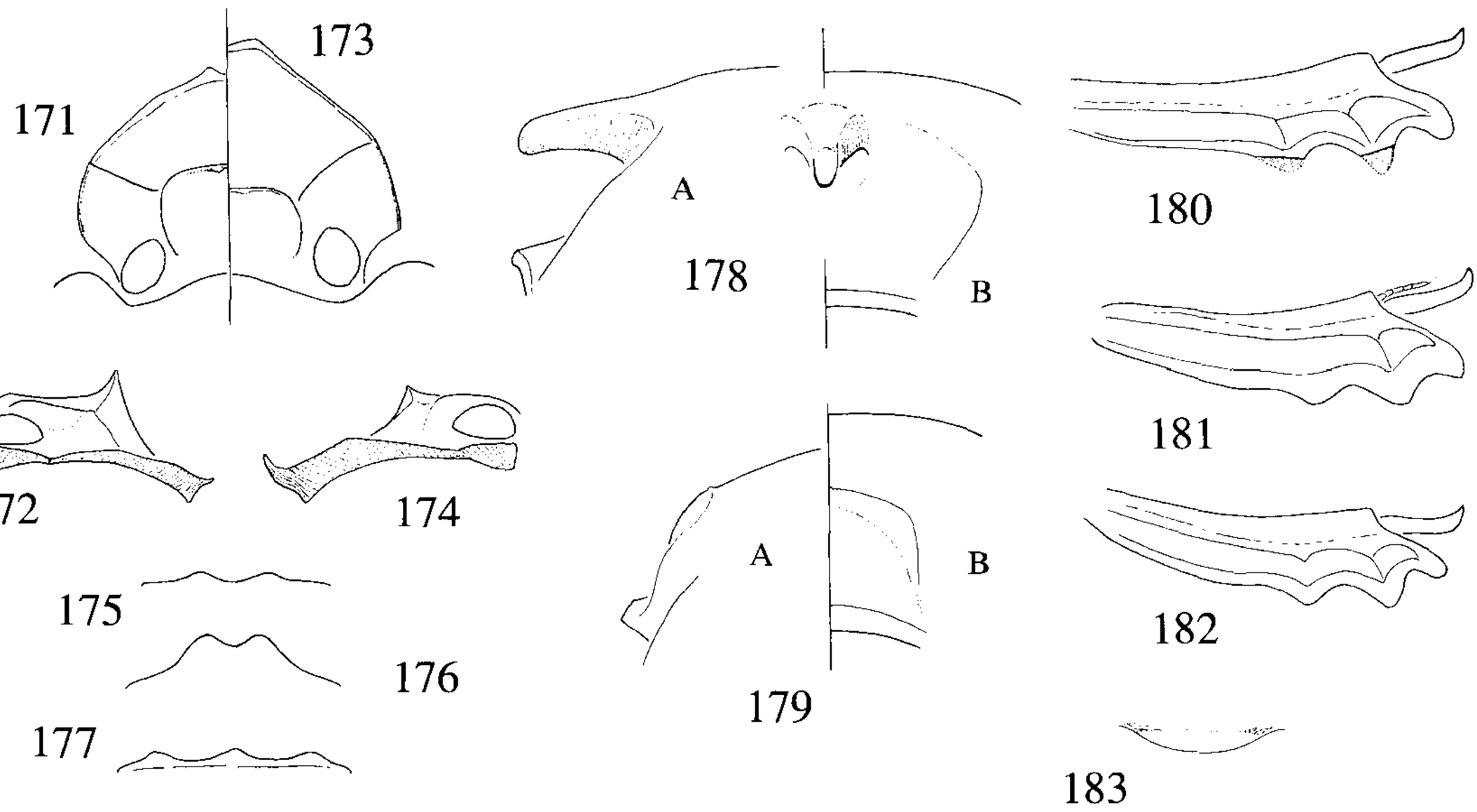
DISTRIBUTION (Fig. 162; appendix). Eastern slopes of Andes ("Yungas") from vicinity of Cochabamba, Bolivia, to southwestern Venezuela. 200–2000 m (estimated). Reportedly necrophagous (Halffter and Matthews, 1966); inhabiting forests, probably mostly cloud forests ("montañas"). Collection dates: March–January.

COMMENTS. The coloration of *meleagris* is more variable than that of any other species in this group. The lectotype of *meleagris* exhibits pattern (a) above, black with red markings along the pronotal margin; that of *minos* is dark, black-brown (c). Except for two labeled "Columbia" [*sic*], all specimens (about 45) with color pattern (a) that I have seen are from the cloud forests ("Yungas") of Bolivia. These specimens are also slightly, but consistently, smaller than *meleagris* from other places, and they may later prove to belong to a distinct taxon.

Most *meleagris* examined conform to color pattern (c), a highly variable combination of colors best described collectively as "dirty brown" or, simply, "brownish." The common feature of the (c) pattern is pink or reddish highlights on the pronotum and pygidium, which are never seen in (a) and (b). Certain of these specimens, because they can assume olive brown tones, resemble *cambeforti* and *chalcomelas;* this is the only form of *meleagris* that I have seen from lower (<300 m) localities.

There is not enough precise locality data to clearly define the geographic distribution of the species. While I suspect that it is most common in cloud forests, it nevertheless clearly enters lowland rain forest where it occurs along with *chalcomelas* and *cambeforti.*

Thanks to Patrick Arnaud, I have seen nine unusual specimens that I have tentatively assigned to *meleagris.* Three are dark, weakly shining blue and labeled "Peru," "Bolivie-Coroico" (in the "Yungas" region northeast of La Paz), and "Bolivie-Songo" (not located); six are dark olive green from Pucallpa, Peru (Amazonian hylea). All nine are large, the largest *meleagris* I have seen, and in the males, the cephalic horn is more strongly swollen basally



Figures 171–183. *Phanaeus* (*Notiophanaeus*) *bispinus* group (**171,** *P. bispinus,* small male, dorsal view of head; **172,** same, lateral view; **173,** *P. alvarengai,* male holotype, dorsal view of head; **174,** same, lateral view; **175,** frontal view cephalic carina, *P. alvarengai,* male holotype; **176,** same, *P. bispinus,* small male; **177,** same, *P. bispinus,* female; **178,** *P. bispinus,* female, anteromedian portion of pronotum [A = lateral view; B = frontal view]; **179,** *P. alvarengai,* allotype female, same; **180,** *P. alvarengai,* holotype male, front tibia [stippling = reconstruction of tibial teeth]; **181,** *P. bispinus,* female, front tibia; **182,** same, female; **183,** same, frontal view clypeal process).

than in typical *meleagris;* otherwise, they differ in no significant way from other specimens. It may well be that these specimens will later prove to represent a distinct taxon, but until more material and more precise geographical data are available, it will be difficult to consider them more than unusual variants of *meleagris.*

The lectotype of *minos* designated here is from among four specimens labeled in Erichson's hand from the Berlin Museum. It agrees with the original description in all respects.

The *Bispinus* Group

DIAGNOSIS. [1] Anterior margin of clypeus (Figs. 171, 173) bidentate medially, strongly so in male *alvarengai;* [2] clypeal process (seen from front) rounded (Fig. 183); [3] cephalic process of female a trituberculate carina; [4] anterolateral portions of pronotum smooth, virtually devoid of sculpturing (Fig. 166); [5] pronotal disk smooth; [6] pronotum of male rounded, lacking distinct posterolateral angles, bearing anteromedian concavity from whose upper margin project pair of slender, anteriorly projecting spines (Figs. 163, 167); [7] pronotum of female as in Figures 178, 179; [8] basal pronotal fossae present, conspicuous; [9] front tibiae tridentate (Figs. 180–182); [10] elytral striae fine, carinulate, punctate (Figs. 169, 170); interstriae weakly convex; [11] dorsum dark, somber (Figs. 15, 16); [12] Amazonian rain forest (Fig. 184).

This group comprises two species, *bispinus* and *alvarengai.* The pronotal armature of both sexes is unique to the genus and approached only remotely in *haroldi.* Besides those characters mentioned above, these species differ from other *Phanaeus* by possessing distinct notching of the hind wing (not observed in *alvarengai*) and proportionately larger eyes. Their coloration, like that of *chalcomelas* and *cambeforti,* suggests camouflage.

KEY TO THE SPECIES OF THE *BISPINUS* GROUP

1a. Clypeus of male (Figs. 173, 174) drawn out anteriorly, sides almost straight; median teeth prominent, strongly upturned. Pronotum of female bearing flat, quadrate ridge (Figs. 168, 179). Punctures of elytral striae not conspicuous to unaided eye (Fig. 170). Front tibiae tridentate; all three teeth distinctly carinate on outer surface (Fig. 180). Amazonia . . . . . *Phanaeus* (*N.*) *alvarengai* Arnaud

b. Clypeus of both sexes rounded, median teeth inconspicuous and not strongly upturned (Figs. 171, 172). Pronotum of female (Figs. 165, 178) with strong, circular, anteromedian concavity, upper margin of which bears a strong, laterally flattened spine or (in small individuals) vertical, keel-like tubercle. Punctures of elytral striae large, easily seen with unaided eye (Fig. 169). Front tibiae tridentate; only apical two teeth distinctly carinate on outer surface (Figs. 181, 182). Amazonia (Fig. 184) . . . . . *Phanaeus* (*N.*) *bispinus* Bates

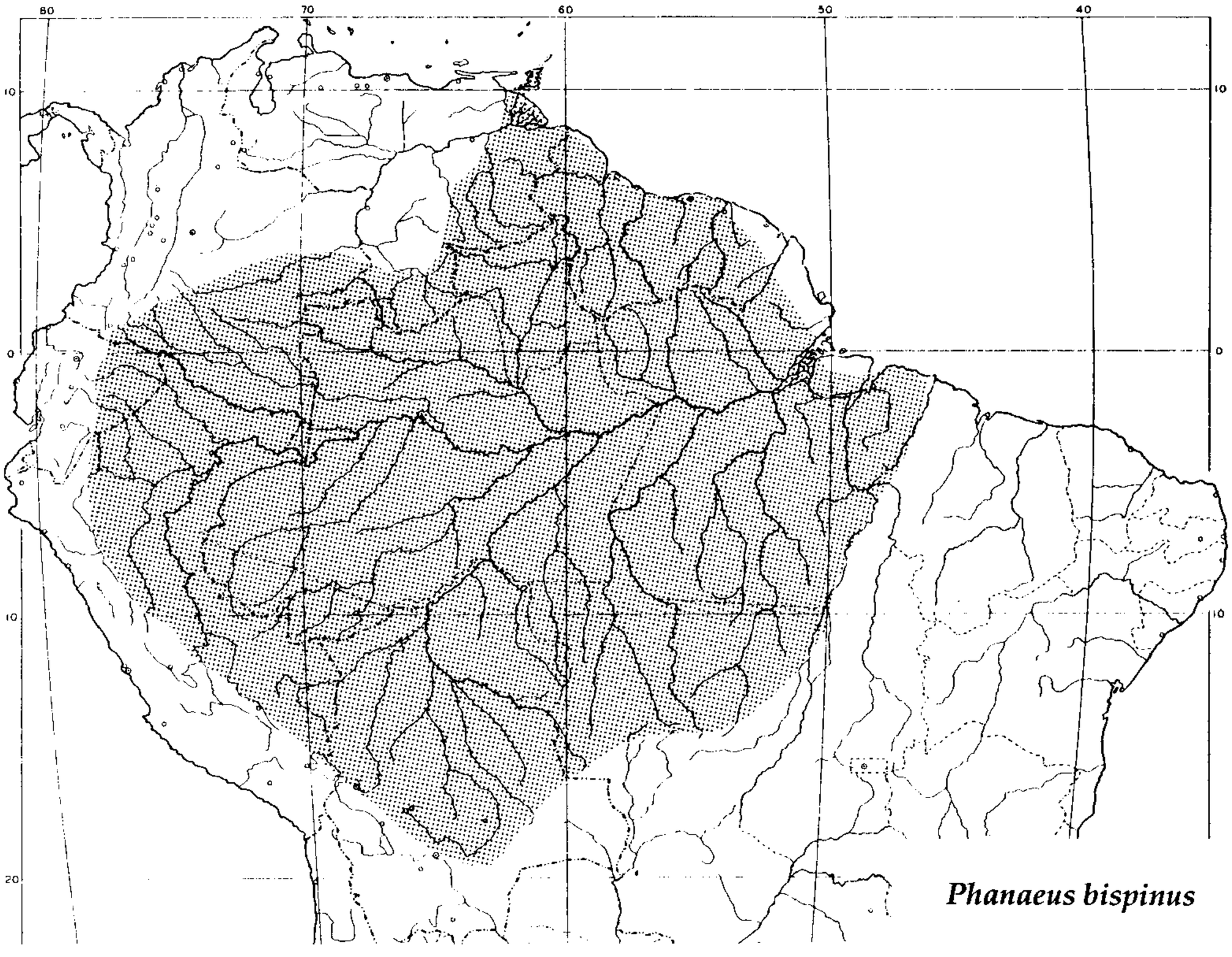


Figure 184. Distribution of *Phanaeus bispinus*.

Phanaeus (*Notiophanaeus*)
alvarengai Arnaud
Figures 167, 168, 170,
173–175, 179, 180

Phanaeus alvarengai Arnaud, 1984:60

Type: Male holotype ("Brésil, Matto Grosso"), private collection of Patrick Arnaud, Saintry, France.

DESCRIPTIVE REMARKS. *Color and Color Pattern.*—Dorsum dull, almost black except for metallic green pronotum, posterior portion of head of male, lateral parts of female pronotum. Pygidium green; venter almost black. *Pronotal Sculpturing.*—Appearing smooth to unaided eye; with moderate magnification (×10) weak puncturing visible along sides, most conspicuous in female. *Elytra* (Fig. 170).—Striae fine, carinulate (×10), each bearing 30–35 small punctures not at all conspicuous to unaided eye; interstriae weakly convex. *Front Tibiae.*—Tridentate in both sexes, all three teeth distinctly carinate longitudinally (Fig. 180). *Secondary Sexual Characters.—Male:* Clypeus (Figs. 173, 174) drawn out anteriorly, sides almost straight, median teeth prominent and strongly upturned; length along midline about twice that of flat frontal area between eyes, behind transverse cephalic carina. Cephalic process (Fig. 175) transverse carina weakly bituberculate medially. Pronotum (Fig. 167) with anteromedian concavity from top margin of which projects pair of nearly straight, slender, parallel spines. *Female:* Clypeus rounded; median teeth inconspicuous (worn in allotype); length about equal to that of frontal area. Cephalic process transverse carina (worn in allotype, presumably weakly trituberculate). Pronotum (Figs. 168, 179) convex, with weak, quadrate ridge above anterior margin; this ridge (seen from front) rounded laterally, (seen from above) minutely beaded in the middle; surface weakly concave beneath ridge. *Specimens Examined.*—1 male (holotype), 1 female (allotype) (length 16–22 mm; width 8–9 mm).

DIAGNOSTIC REMARKS. See *bispinus*, below.

DISTRIBUTION. The allotype female is labeled "Brazil, Rondônia, Rio Japunda (September)"; neither this nor the stated type locality is precise enough to locate on a map.

COMMENTS. Arnaud described this species from two specimens. While each is definitely different from other known *Phanaeus*, only additional evidence will support the conclusion that they are, indeed, conspecific. The allotype is in the collection of the Rijksmuseum van Natuurlijke Historie in Leiden.

Phanaeus (*Notiophanaeus*) *bispinus* Bates

Figures 15, 16, 163–166, 169, 171, 172, 176–178, 181–184

Phanaeus bispinus Bates, 1868:89

Type: Male holotype ("Canelos, Ecuador"), Muséum National d'Histoire Naturelle, Paris.

Phanaeus digitalis Olsoufieff, 1924:34 (Pereira and Martínez, 1956:237)

Type: Female holotype ("Guyana"), Muséum National d'Histoire Naturelle, Paris.

OTHER REFERENCES. Gemminger and Harold, 1869; Nevinson, 1892a; Gillet, 1911b; Blackwelder, 1944; Pereira and Martínez, 1960; Halffter and Matthews, 1966; Edmonds, 1972; Arnaud, 1982a.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 15, 16).—Dorsum dull, dark olive green to olive brown, with narrow line of shining green along circumnotal ridge, lateral margins of elytra. Pygidium usually bright moderately shining green, sometimes almost black; venter weakly shining, dark green. *Head.*—Clypeus of both sexes weakly bidentate medially, evenly rounded laterally (Fig. 171); length along midline equal to or less than that of frontal area between eyes, behind clypeal process. *Pronotal Sculpturing* (Fig. 166).—Virtually smooth, unsculptured, at most with largely effaced, minute puncturing visible only under high magnification (×40), appearing smooth even under moderate (×20) magnification. *Metasternum.*—Anterior prominence compressed laterally; seen from side, rounded, longitudinally keeled. *Elytra* (Fig. 169).—Striae fine, carinulate (×30), each bearing 15–20 punctures conspicuous to unaided eye; interstriae weakly convex, smooth except for weak puncturing (×30). *Front Tibiae* (Figs. 181, 182).—Tridentate in both sexes, slightly narrower in female; first two teeth carinate longitudinally, third (basal) tooth sometimes with weak carina. *Secondary Sexual Characters.—Male:* Cephalic horn of larger individuals (Fig. 163) slender, suberect, slightly bowed posteriorly; apex (seen from front) slightly expanded laterally, compressed anteroposteriorly; that of smallest individuals (Figs. 164, 176) a carina, middle of which strongly raised, bituberculate. Pronotum of large individuals (Fig. 163) with anteromedian concavity from middle of posterior edge of which arises pair of closely set, long, slender anteriorly directed horns; that of smallest individuals (Fig. 164) more-or-less evenly convex, bearing two prominent acute tubercles near anterior margin. *Female:* Cephalic carina (Fig. 177) trituberculate, in larger individuals distinctly elevated. Pronotum of larger individuals (Figs. 165, 178) with deep, rounded anteromedian concavity, sides of which carinate, posterior margin of which bears single, strong, finger-like, anteriorly projecting, ventrally curved spine; that of smallest individuals lacking concavity and bearing two short longitudinal ridges, with prominent blunt tubercle near anterior margin. *Specimens Examined.*—16 males, 15 females (length 13–17 mm; width 7–11 mm).

DIAGNOSTIC REMARKS. This species differs from *alvarengai* by its secondary sexual characters, the shape of the male clypeus, non-carinate third tibial tooth, and puncturing of the elytral striae.

DISTRIBUTION. (Fig. 184; appendix). Known from scattered Amazon Basin localities in Brazil, Venezuela, Colombia, Ecuador, Peru, and Bolivia. 0–500 m (estimated). Necrophagous. Collection dates: all months except March, November, and December; probably all year.

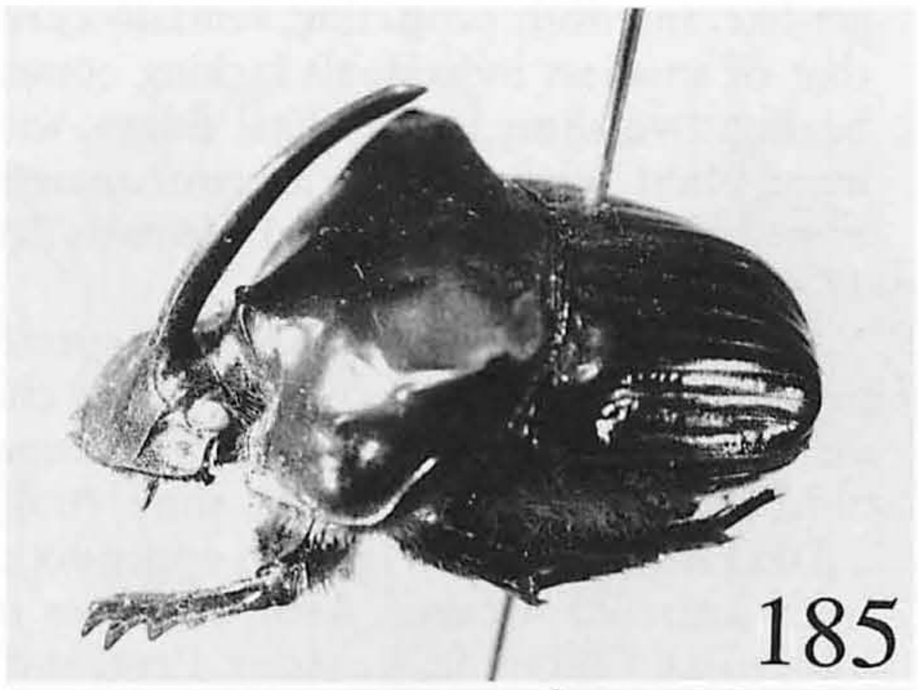
COMMENTS. Although widely distributed geographically, this curious species is rather rare in collections. Although he suspected conspecificity, Olsoufieff (1924) described females available to him as *digitalis.*

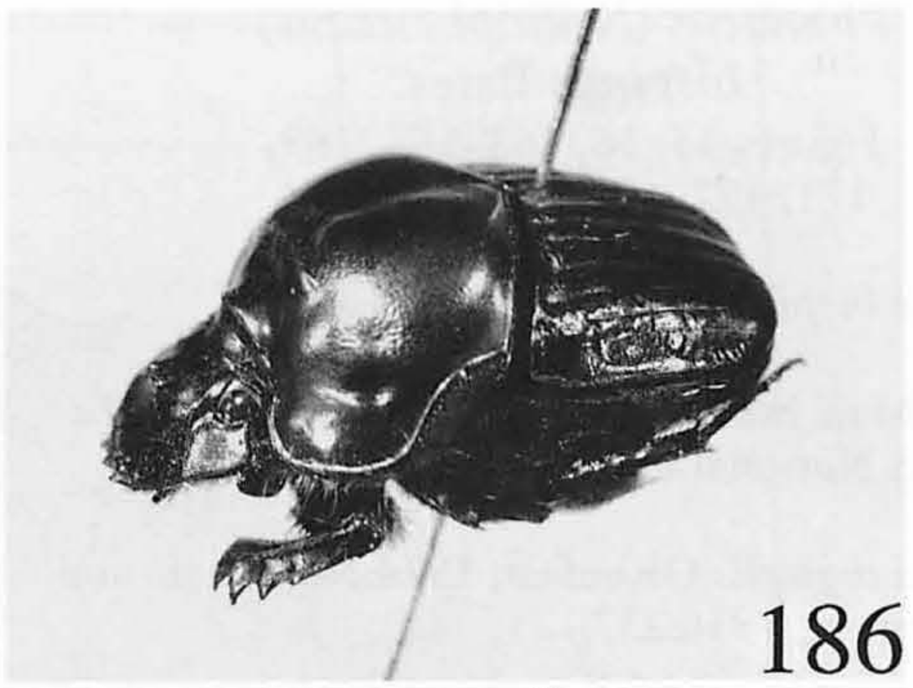
Of interest is the fact that the hind wing of *bispinus*, like *Coprophanaeus*, is notched basally. This species is one of very few in the genus that does not prefer excrement.

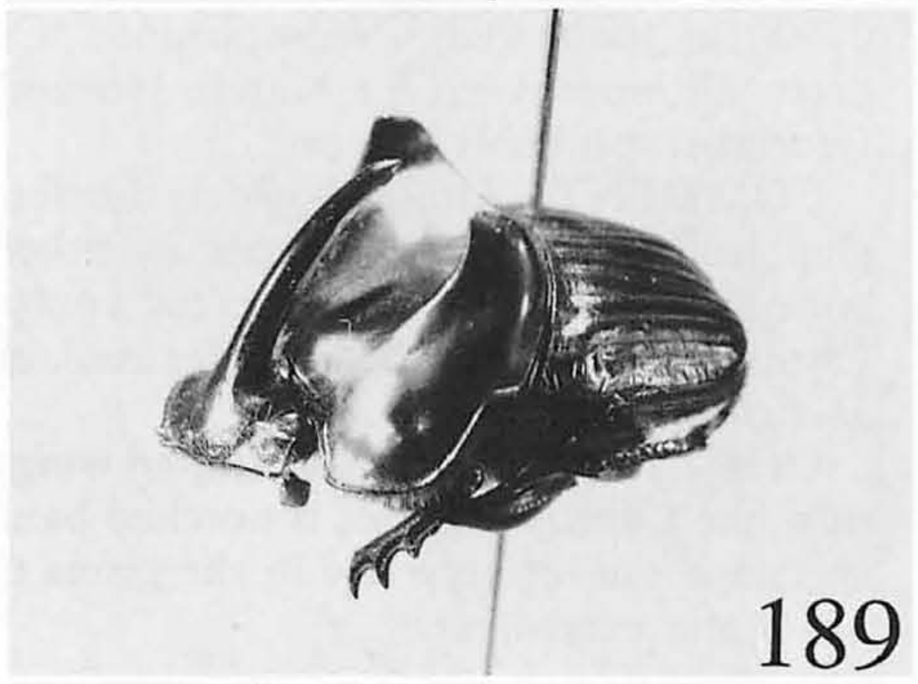
The *Palaeno* Group

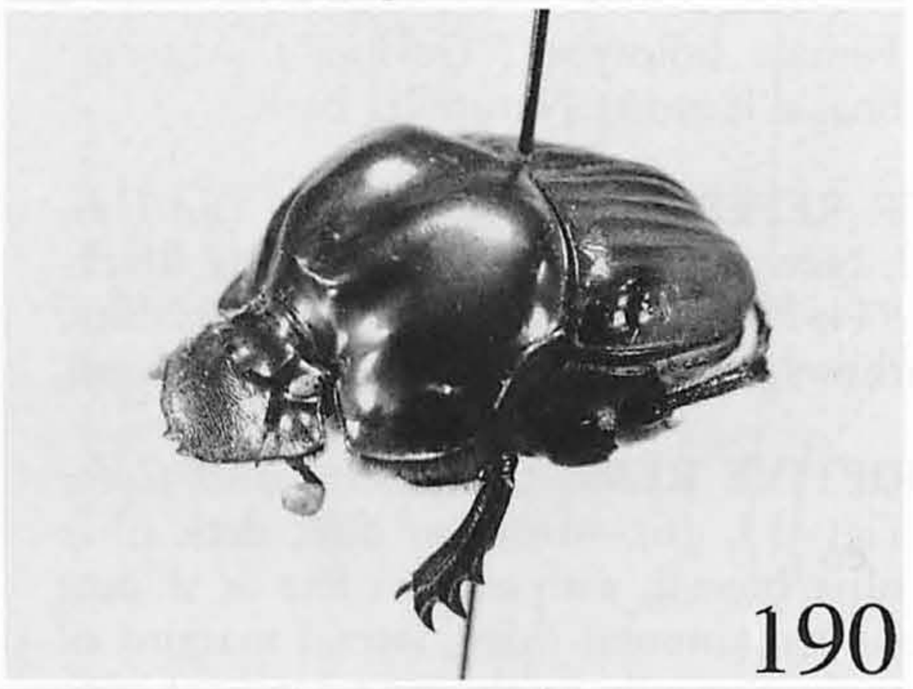
DIAGNOSIS. [1] Clypeus strongly bidentate medially (Fig. 196); [2] clypeal process spiniform (Fig. 195); [3] cephalic carina of female distinctly trituberculate; [4] cephalic process of male dimorphic, either slender, cylindrical, posteriorly curved, tapering horn (in larger individuals, Fig. 185) or carina with strongly raised, medially bidentate process (smallest individuals, Fig. 187); [5] pronotum smooth except for very fine, sparse puncturing (×30); [6] shape of male pronotum variable (Figs. 185, 187); in female, disk distinctly swollen posterolaterally on each side of midlongitudinal depression and (seen in profile) distinctly raised above level of elytra; [7] basal pronotal fossae absent, basal angle prominent, acute; [8] elytral striae carinulate, not punctate; interstriae convex; [9] anterior prominence of metasternum (seen in profile, Fig. 194B) lobate, (seen from below, Fig. 194A) compressed laterally and longitudinally keeled; [10] pteropleura and sides of metasternum clothed by dense pile of long white or yellowish hair (indistinct in worn or very dirty specimens); [11] front tibiae (Figs. 197, 198) quadridentate, apical three teeth longitudinally carinate; [12] dorsum (Figs. 10–14) highly shining, bright metallic green (rarely dark blue or blue-green); female with pair of black, often confluent areas behind anteromedian pronotal carina; [13] inhabiting savanna ("campos cerrados") of Brazilian Highlands and adjacent areas to south (Fig. 199).

This group comprises two species, *palaeno* Blanchard and *kirbyi* Vigors, that share several characters not found in other *Phanaeus:* spinate clypeal process; strongly bidentate cephalic carina of certain males; and thick, whitish pile on underside of









Figures 185–191. *Phanaeus* (*Notiophanaeus*) *palaeno* group (**185,** *P. kirbyi,* male; **186,** same, female; **187,** same, frontal view small [arrow indicates pronotal tubercles]; **188,** same, frontal view female; **189,** *P. palaeno,* male; **190,** same, female; **191,** same, frontal view female).

pterothorax. All of these features, however, are shared with *Oxysternon palaemo* Laporte-Castlenau (*palaemon* of authors), which is easily confused with *P. palaeno,* in particular. The two species are sympatric and ecologically very similar.

In this species group, males have either a strongly bidentate cephalic carina or a clearly horn-like protuberance; there is no intermediate state, and males of the same (always intermediate) size may possess either option. Dimorphism of the male cephalic process is also seen in *P. bispinus* and *endymion* as well as in the phanaeine genus *Oxysternon.*

This is the only species group of *Phanaeus* (but not of phanaeines) that inhabits the "campos cerrados" of the Brazilian Highlands. As savanna species, their recent distribution has probably expanded considerably since pre-European times as forests in southern Brazil have been cut to produce pasturelands.

KEY TO THE SPECIES OF THE *PALAENO* GROUP

1a. Paraocular areas flat above. Anterior portion of the circumnotal ridge raised behind and narrowly excised medially, excision separating two small, dentiform tubercles which are rarely effaced even in smallest individuals (Fig. 187, arrow). Elytral interstriae weakly convex. *Male:* Pronotum of large specimens (Fig. 185) flattened above and expanded laterally as rounded, flat lobes. *Female:* Pronotum of all but smallest individuals bearing almost straight, transverse anteromedian carina (Fig. 188) . . . . . *Phanaeus* (*N.*) *kirbyi* Vigors

b. Upper surface of paraocular areas swollen adjacent to eyes, flattened laterally. Anterior portion of circumnotal ridge not noticeably raised and neither excised nor bidentate medially.

Elytral interstriae moderately convex. *Male:* Pronotum of larger individuals (Fig. 189) shallowly concave above, posterior angles produced upward as pair of apically convergent, widely separated horns. *Female:* Pronotum of all but smallest individuals (Fig. 191) bearing a wide, U-shaped anteromedian carina . . . . . *Phanaeus* (*N.*) *palaeno* Blanchard

Phanaeus (*Notiophanaeus*) *kirbyi* Vigors

Figures 13, 14, 185–188, 196–199

Phanaeus kirbyi Vigors, 1825:539 (as *kirbii*)

Type: Male holotype ("Brazil"), British Museum (Natural History), London.

Phanaeus planicollis Perty, 1830:40 (Nevinson, 1892a:5)

Type: Male holotype (no data), Zooligsche Staatssammlung, Munich.

Phanaeus subtricornis Perty, 1830:41 (Harold, 1859: 198)

Type: Male holotype (no data), Zooligsche Staatssammlung, Munich.

Phanaeus laevicollis Laporte-Castelnau, 1840:82 (Nevinson, 1892:5)

Type: Male neotype ("Brésil"), Castelnau Collection, National Museum of Victoria, Melbourne, PRESENT DESIGNATION.

Phanaeus kirbyi truncaticornis Olsoufieff, 1924: 91, NEW SYNONYMY

Type: Unknown to me.

NOMENCLATURAL REMARKS. Although Harold (1869:65) synonymized *planicollis* and *laevicollis*, Nevinson (1892a) was the first to synonymize them with *kirbyi*. Olsoufieff's (1924) *truncaticornis* is a small male described as a variation of *kirbyi*.

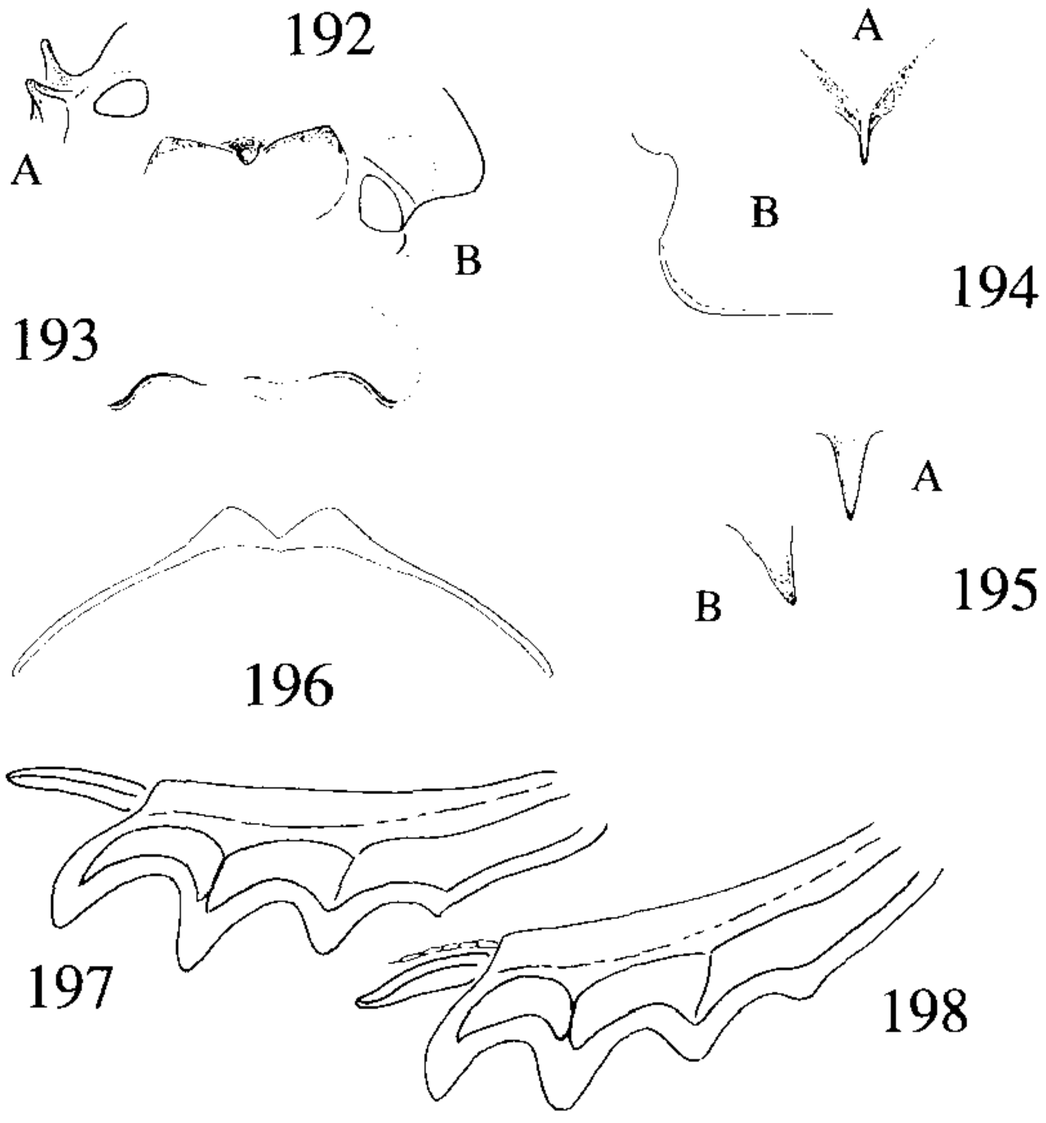
OTHER REFERENCES. Klug, 1841; Guerin-Meneville, 1855 (as *planicollis*); Lucas, 1857; Harold, 1871a; Preudhomme de Borre, 1886; Gahan and Arrow, 1903; Gillet, 1911b; Pessoa, 1934; Pessoa and Lane, 1941; Blackwelder, 1944; Lange, 1947; Halffter and Matthews, 1966; Barrera, 1969; Edmonds, 1972; Scherer, 1983.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 13, 14).—Dorsum shining green to yellow-green; rarely dark, shining blue-green. Venter mostly shining green or blue-green, otherwise dark brown. *Paraocular Areas.*—Upper surface flat, not swollen adjacent to eyes. *Pronotum.*—Anterior portion of circumnotal ridge strongly raised, almost vertical; posterior margin of ridge bearing pair of closely set, small median denticles (Fig. 187, arrow) separated by shallow, rounded notch; denticles and notch only rarely almost effaced. *Secondary Sexual Characters.*—*Male:* Pronotum of larger individuals (Fig. 185) unevenly flattened, posterolateral angles (seen from above) produced laterally as broadly rounded flanges, outer margins of which narrowly upturned; these angles reduced to low, angular tumosities in smaller specimens. *Female:* Pronotum (Figs. 186, 188) bearing sharp, almost straight transverse carina near anterior margin; carina followed by narrow, transverse depression; carina and depression almost effaced in some small specimens. *Specimens Examined.*—38 males, 31 females (length 15–23 mm; width 9–13 mm).

DIAGNOSTIC REMARKS. See *palaeno*, below.

DISTRIBUTION (Fig. 199; appendix). Brazilian Highlands and extensions thereof into eastern Bolivia and eastern Paraguay. 300–1000 m (estimated). Coprophagous (one record from carrion); inhabiting "campos cerrados" and similar savanna-like formations resulting from forest clearing for pastureland. Collection dates: September–June (most November–March).

COMMENTS. As discussed above, *kirbyi* is sympatric with *palaeno*, although its known range is somewhat smaller. This is the larger of the two species, and it exhibits less color variation than *palaeno*. The elytra are always completely green (or



Figures 192–198. *Phanaeus* (*Notiophanaeus*) *palaeno* group (**192,** *P. palaeno*, female [Corrientes, Argentina; A = lateral view cephalic carina; B = dorsal view of same; C = dorsal view pronotal carina]; **194,** *P. palaeno*, anterior prominence of metasternum [A = ventral view; B = lateral view]; **195,** same, subclypeal process [A = frontal view; B = lateral view]; **196,** *P. kirbyi*, dorsal view clypeal margin; **197,** same, front tibia of male; **198,** same, front tibia female).

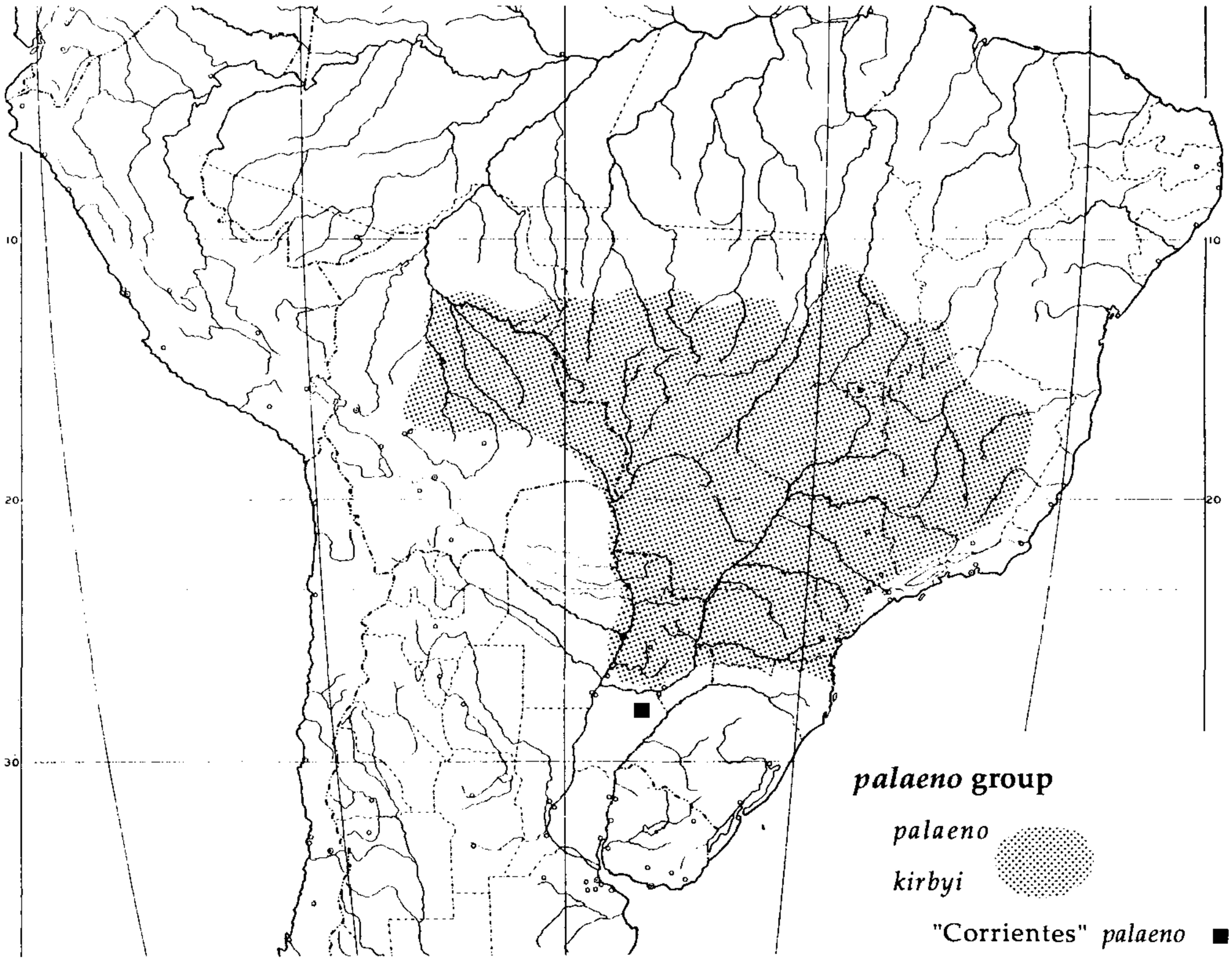


Figure 199. Distribution of the *Phanaeus* (*Notiophanaeus*) *palaeno* group.

blue-green); they never have the yellow-brown markings seen in most *palaeno*.

There are two specimens of *laevicollis* in the Castlenau Collection in the National Museum of Victoria (Melbourne). One is a female, the other a small male with a bidentate cephalic carina. I hereby designate the latter as neotype. Laporte-Castelnau's (1840) original description included a large and small male, the latter of which he mistakenly assumed was a female (". . . tête . . . avec . . . un petit tubercule bifide sur la [femelle] . . .").

Phanaeus (*Notiophanaeus*) *palaeno* Blanchard

Figures 10–12, 189–195, 199

Phanaeus palaeno Blanchard, 1843:176

Type: Male holotype ("Bolivie, Concepcion de Chiquitos"), Muséum National d'Histoire Naturelle, Paris.

Phanaeus blanchardi Harold, 1871a:114 (not Olsoufieff, 1924:92), new name for *palaeno* Blanchard

Phanaeus palaeno exisicornis Balthasar, 1939:247 (emended to *excisicornis*, Balthasar, 1940:39) (Arnaud, 1982c:125)

Type: Male holotype ("Brazil, Matto Grosso"), Národní Muzeum Prirodovedecke Muzeum, Prague.

NOMENCLATURAL REMARKS. Harold's "*blanchardi*" was based on the mistaken notion that Blanchard's species was the same as *Oxysternon palaemo* Laporte-Castelnau (see Gemminger and Harold, 1869:1016). The error was corrected by Nevinson (1892a).

OTHER REFERENCES. Lacordaire, 1856; Lucas, 1857; Gahan and Arrow, 1903; Bruch, 1911; Pessoa, 1934; Pessoa and Lane, 1941; Blackwelder, 1944; Martínez, 1959; Halffter and Matthews, 1966; Barrera, 1969; Edmonds, 1972; Arnaud, 1982a.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 10–12).—Dorsum usually shining green to yellow-green, often with golden to coppery highlights on head, anterior portions of pronotum; rarely evenly blue-green or dark blue, much less shining; elytra either evenly colored, or with yellow-brown lateral markings with green highlights, or (very rarely) almost completely yellow-brown with green highlights. Venter dark brown with green to blue-green highlights. *Paraocular Areas.*—Upper surface usually distinctly swollen adjacent to eyes, flattened laterally. *Pronotum.*—Anterior portion of circumnotal ridge simple, neither

raised nor bituberculate medially. *Secondary Sexual Characters.—Male:* Pronotum of larger individuals (Fig. 189) broadly, shallowly concave dorsally, each posterolateral angle produced upward as wide process tip of which (seen laterally) acute, directed forward; these processes lower, quadrate in smaller individuals; in smallest specimens, reduced to pair of anteriorly converging, low, rounded ridges extending from near anterior margin to middle of disk. *Female:* Pronotum of all but smallest individuals with fine, broadly U-shaped anteromedian carina (Fig. 191), middle of which may bear small tubercle; this carina followed by concavity interrupted by low, truncated or round swelling or tubercle, flanked on each side by elongate concavity extending to anterior margin of pronotum behind eye. In smallest specimens, carina and adjacent features less pronounced to virtually effaced (see also "Comments," below). *Specimens Examined.*—96 males, 82 females (length 10–19 mm; width 7–12 mm).

DIAGNOSTIC REMARKS. This species is easily distinguished from *kirbyi* by the shape of the anterior portion of the circumnotal ridge and by secondary sexual features; only the very smallest individuals of the two species are likely to be confused.

DISTRIBUTION (Fig. 199; appendix). Brazilian Highlands and extensions thereof into eastern Paraguay, eastern Bolivia, and extreme northeastern Argentina. 300–1000 m (estimated). Coprophagous, inhabiting "campos cerrados" and similar savanna-like formations resulting from forest clearing for pastureland. Collection dates: October–July (most October–March).

COMMENTS. As I pointed out in 1972, this species bears a striking resemblance to *Oxysternon palaemo*. Well-developed males of the two species differ by the shape of the pronotum, which in *O. palaemo* is much more strongly concave. Females, on the other hand, are so similar that they can be confused even on fairly close inspection if the shape of the metasternum (drawn out anteriorly into a sharp, upturned spine projecting between the front coxae in *Oxysternon*) is not examined.

P. palaeno is widely distributed in the "campos cerrados" and similar areas of the Brazilian Highlands, where it occurs along with *kirbyi* and *O. palaemo*. I do not know if these species are separated ecologically in some obvious way (foraging time, preferred ecotones, etc.); they would make interesting subjects for a serious community study.

Balthasar's subspecies *exisicornis* was based upon a single small male; it is not a valid taxon. I have seen a series of eight specimens tentatively assigned here to *palaeno* collected by Antonio Martínez in Corrientes Province, Argentina, that has the following unusual female secondary sexual features: the cephalic carina is strongly raised and the middle tubercle, which is much larger than the lateral two, is abruptly offset posteriorly (Fig. 192); the pronotal carina (Fig. 193) is brace-shaped ({), more elevated than its counterpart in other specimens, and not associated with a concavity. This series may later prove to represent a distinct taxon.

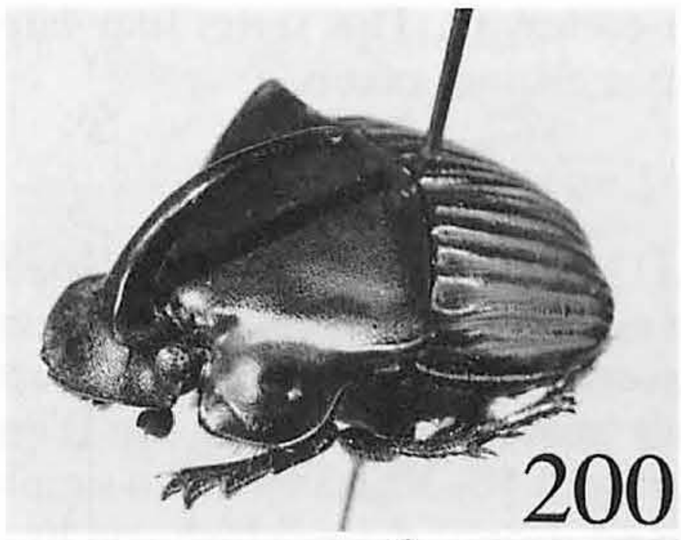
The *Endymion* Group

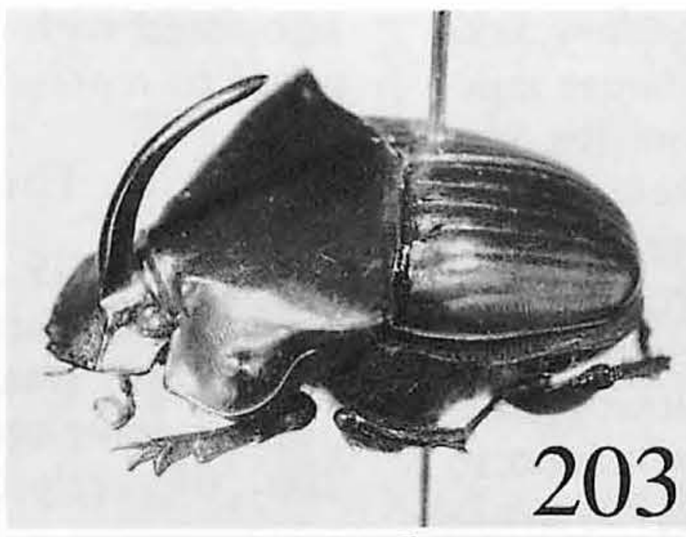
DIAGNOSIS. [1] Anterior margin of clypeus strongly bidentate medially; [2] clypeal process (seen from front) transverse; [3] pronotum usually appearing completely smooth to unaided eye (Figs. 200–208); sculpturing (×10–30) restricted to simple puncturing except on disk of male, which can bear minute granulations and similar formations (Figs. 209–211); [4] cephalic horn of male (Figs. 200, 203, 206) strongly curved posteriorly over pronotum, thickened basally, strongly tapered to apex; reduced to feebly bituberculate carina in smallest individuals; [5] pronotum of larger males (Figs. 200, 203, 206, 214) flat above, disk assuming a triangular shape with prominent, acute posterolateral angles; flattened, triangular disk of smaller males proportionately smaller, located anteriorly, with only weak, tuberculate posterolateral angles; [6] pronotum of female (Figs. 201, 204) convex, with three anteromedian tubercles of varying shape and configuration; [7] basal pronotal fossae punctiform; [8] front tibiae (Figs. 219, 220) quadridentate, narrower in male; fourth (basal) tooth separated from third by narrow, slit-like notch; [9] apical spur of front tibia, viewed anteriorly, more-or-less straight, apex bent posteriorly; [10] elytral striae fine, not carinulate, simple to (rarely) punctate (×5) (Figs. 212, 213); [11] dorsal coloration (Figs. 17–22) almost always at least partially shining green, red, or dark blue; pronotum of female with irregularly shaped, central black area of variable size; [12] coprophagous, copronecrophagous (one species mycetophagous); [13] inhabiting neotropical forests from southern Mexico to northwestern South America.

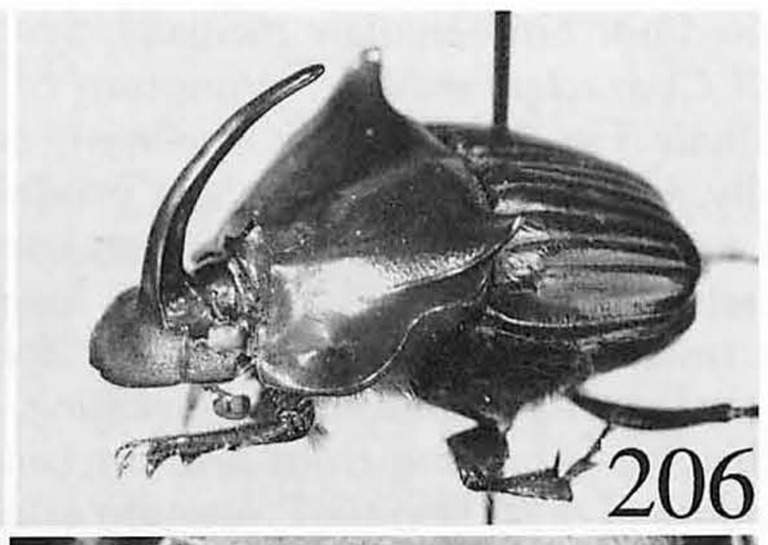
This group brings together three (or four) closely related Mesoamerican species that closely resemble each other in general form: *endymion* Harold, *pyrois* Bates, and *halffterorum* Edmonds (a possible fourth species is known from two Oaxacan specimens here included in *endymion*). Member species are distinguished primarily on the basis of color and color pattern, relief and sculpturing of the pronotum and elytra, secondary female sexual characters of the pronotum, and geographical distribution. Both *pyrois* and *endymion* are common, widely distributed species that vary considerably, but in ways too inconsistent to warrant recognition of subspecies. Because of their variability, each is difficult to define taxonomically, but most specimens are quickly identifiable by color and place of origin. *P. halffterorum* is a rare, fungus-feeding species known only from a few isolated localities in southern Mexico.

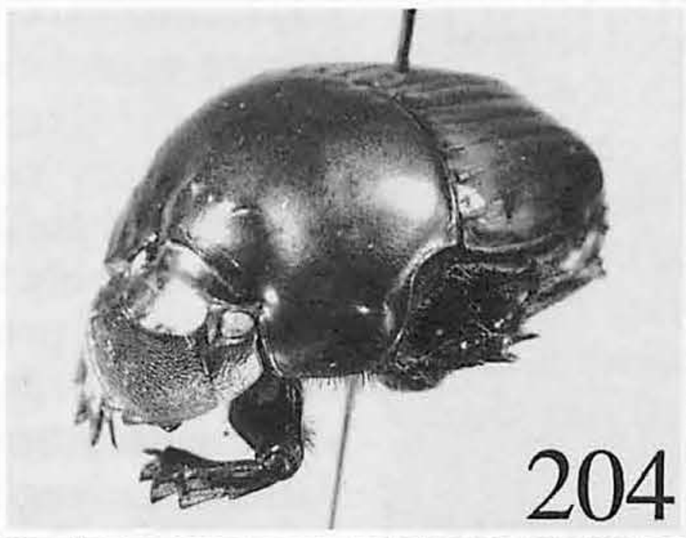
KEY TO THE SPECIES OF THE *ENDYMION* GROUP

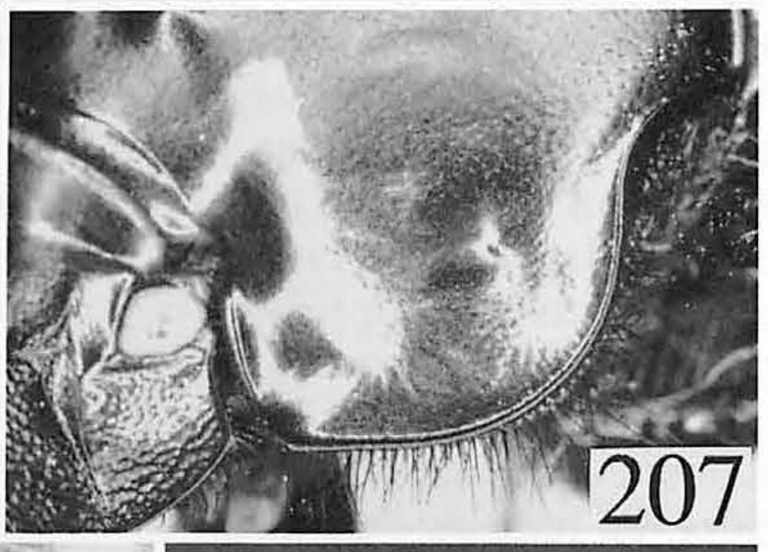
1a. Inner margin of each elytron upturned to form sharp ridge progressively more elevated pos-

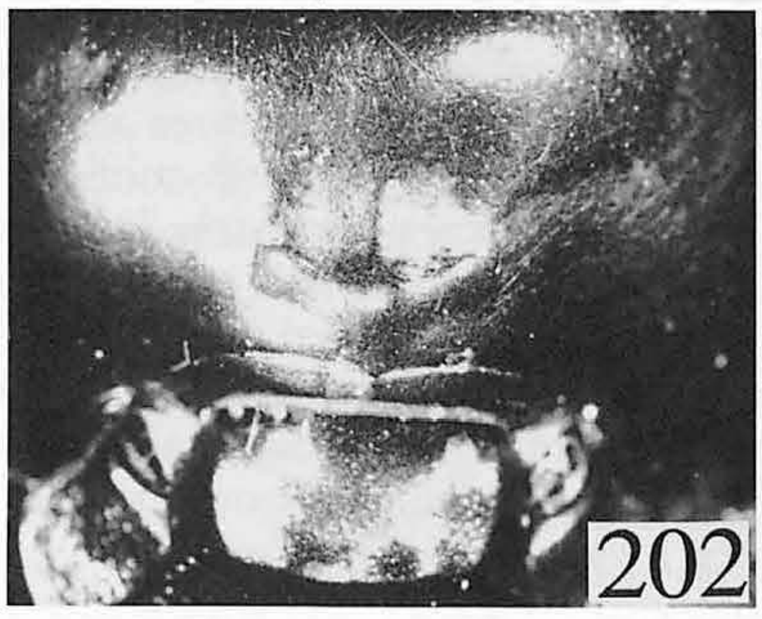


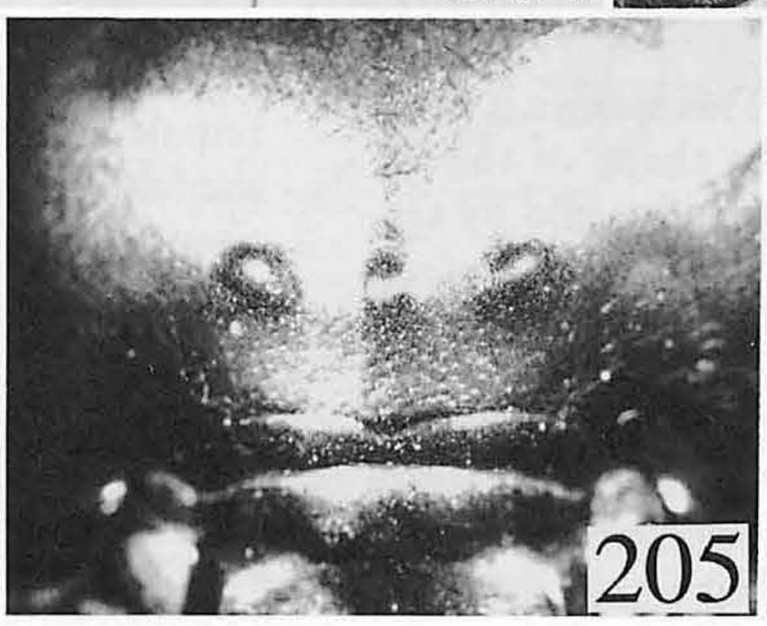










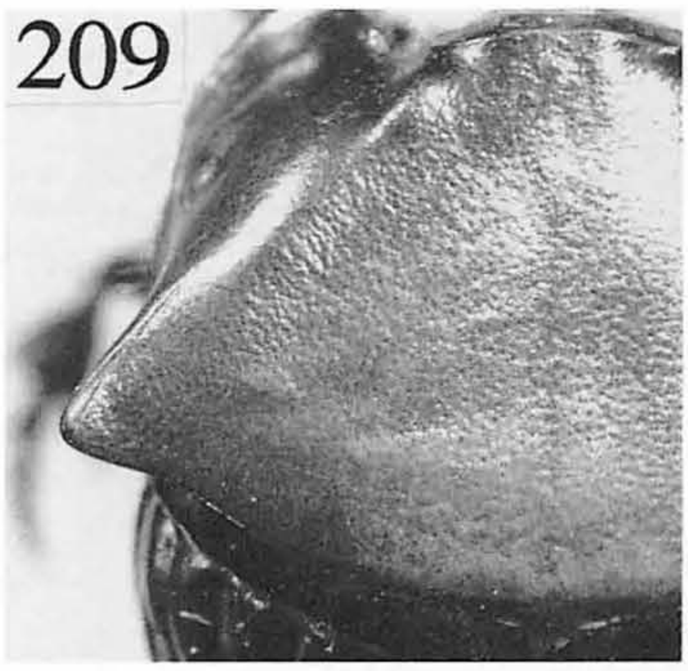


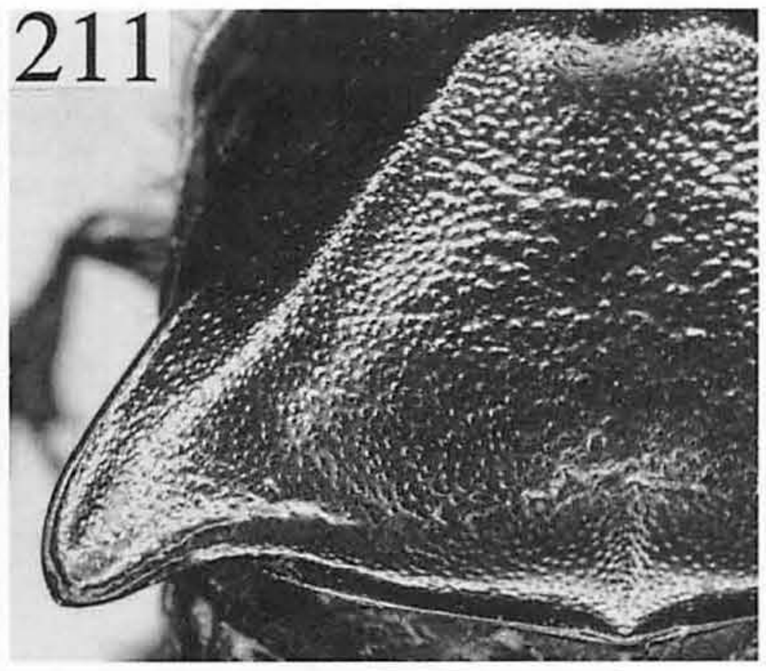
Figures 200–208. *Phanaeus* (*Notiophanaeus*) *endymion* group (**200,** *P. endymion,* male; **201,** same, female; **202,** same, dorsal view anteromedian portion of prothorax; **203,** *P. pyrois,* male; **204,** same, female; **205,** same, dorsal view anteromedian portion of pronotum; **206,** *P. halffterorum,* male; **207,** same, anterolateral portion of pronotum of female; **208,** same, dorsal view base of pronotum of female).

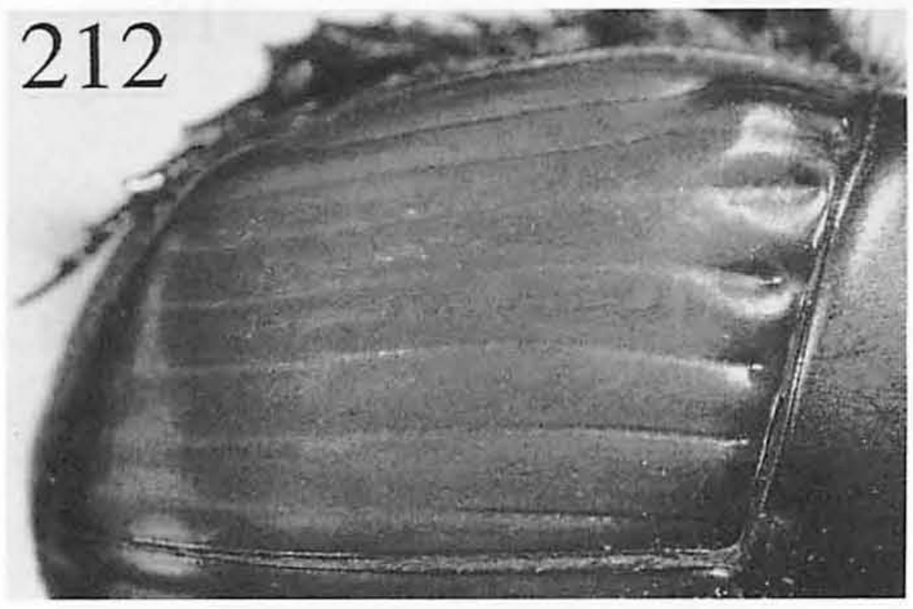
teriorly, forming small tooth at the apical angle of elytron (Figs. 217, 218); margin of elytron slightly excised adjacent to this tooth. Pygidium shallowly impressed on each side. *Male:* Disk of pronotum (Fig. 211) distinctly but very finely granulorugose, more strongly so laterally (×10); middle of anterior margin of pronotum of large individuals sometimes bearing small, acute tooth; posterior angles of disk of large specimens directed posteriorly. *Female:* Pronotum (Fig. 208) bearing a midlongitudinal depression extending from near base to near middle of disk, and three isolated anteromedian tubercles followed by shallow concavity. Dorsum shining green (brighter in male) or dark blue (Figs. 21, 22); pronotum of female shining black except for green (or blue) areas along margins. Mycetophagous; south central Mexico (Fig. 221) . . . . . *Phanaeus* (*N.*) *halffterorum* Edmonds

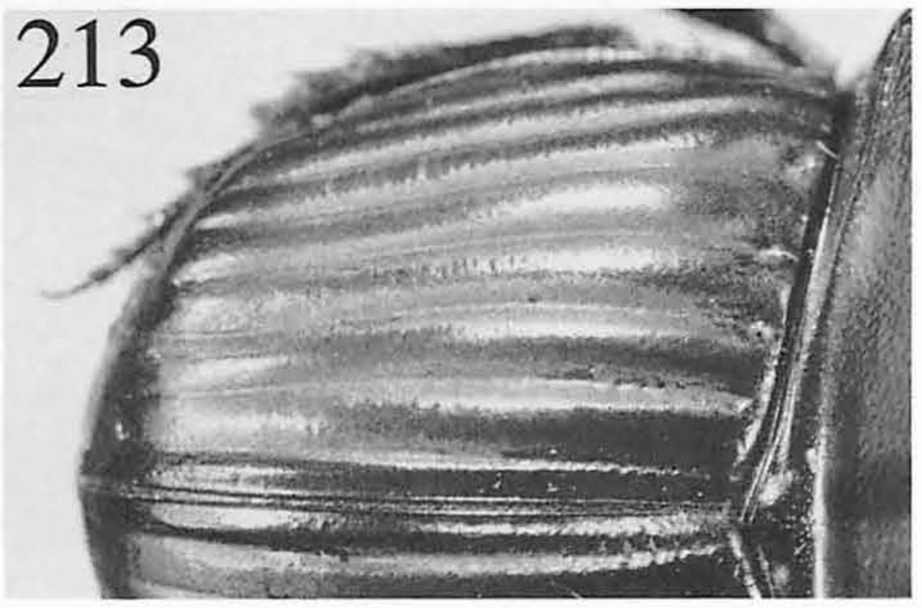
b. Inner margins of elytra (Figs. 215, 216) not upturned to form ridge terminating in an acute tooth; apical margin of elytra straight. Pygidium evenly convex, lateral impressions lacking or only very weakly indicated. *Male:* Disk of pronotum distinctly granulorugose at most only laterally, central area velvety smooth, only rarely sparsely granulate (×15; except Oaxaca population of *endymion,* which is evenly and minutely granulate); anteromedian pronotal tooth lacking; posterior angles of pronotal disk directed laterally. *Female:* Pronotum lacking distinct midlongitudinal impression (except Oaxacan *endymion*); otherwise variable. Dorsum dull black, dull black with shining red, shining green, or dull blue. Coprophagous, copronecrophagous; southern Mexico to northwest South America 2

2a. Elytral interstriae (Fig. 213) evenly convex and shining midlongitudinally; striae impressed basally as distinct fossae. *Male:* Pronotal disk (Fig. 209) (×20) velvety smooth medially, asperate laterally and sometimes also medially (distinctly evenly granulate [×10] in Oaxaca specimens; see below). *Female:* Pronotum (Fig. 201) with anteromedian concavity bounded anteriorly by raised U- or V-shaped ridge; this ridge produced medially as an acute or rounded tuber-









Figures 209–213. *Phanaeus* (*Notiophanaeus*) *endymion* group (**209,** dorsal view left side pronotum of male *P. endymion;* **210,** same, *P. pyrois;* **211,** same, *P. halffterorum;* **212,** dorsal view left elytron *P. pyrois;* **213,** same, *P. halffterorum*).

cle, and at each end as rounded or elliptical tubercle; in some individuals, concavity interrupted posteriorly by small, rounded bump; in some, usually small individuals concavity obsolete, ridge reduced to three isolated, round tubercles. Dorsum (Figs. 17, 18) shining green or dark blue (Oaxaca population shining black); rarely shining green with strong yellow reflections. Southwestern Mexico and southeastern Mexico to Honduras (Fig. 221) . . . . . *Phanaeus* (*N.*) *endymion* Harold

b. Elytral interstriae (Fig. 212) distinctly flattened and uniformly dull (more convex and shining in some Central American populations); striae not strongly impressed basally, anterior ends usually bearing deep punctures rather than large fossae. *Male:* Pronotal disk (Fig. 210) dull, velvety smooth medially, finely asperate, brighter laterally. *Female:* Pronotum (Fig. 204) evenly convex, lacking anteromedian concavity even in largest specimens, bearing three round, smooth tubercles in transverse line near anterior margin. Head and pronotum (Figs. 19, 20) largely highly shining metallic red to nearly completely dull black with metallic red restricted to ridges and isolated areas on anterior part of pronotum; elytra dull to weakly shining black; pygidium usually metallic red medially, green peripherially, sometimes completely red or green. Southern Nicaragua through Central America into western Colombia and Ecuador (Fig. 221) . . . . . *Phanaeus* (*N.*) *pyrois* Bates

Phanaeus (*Notiophanaeus*) *halffterorum* Edmonds

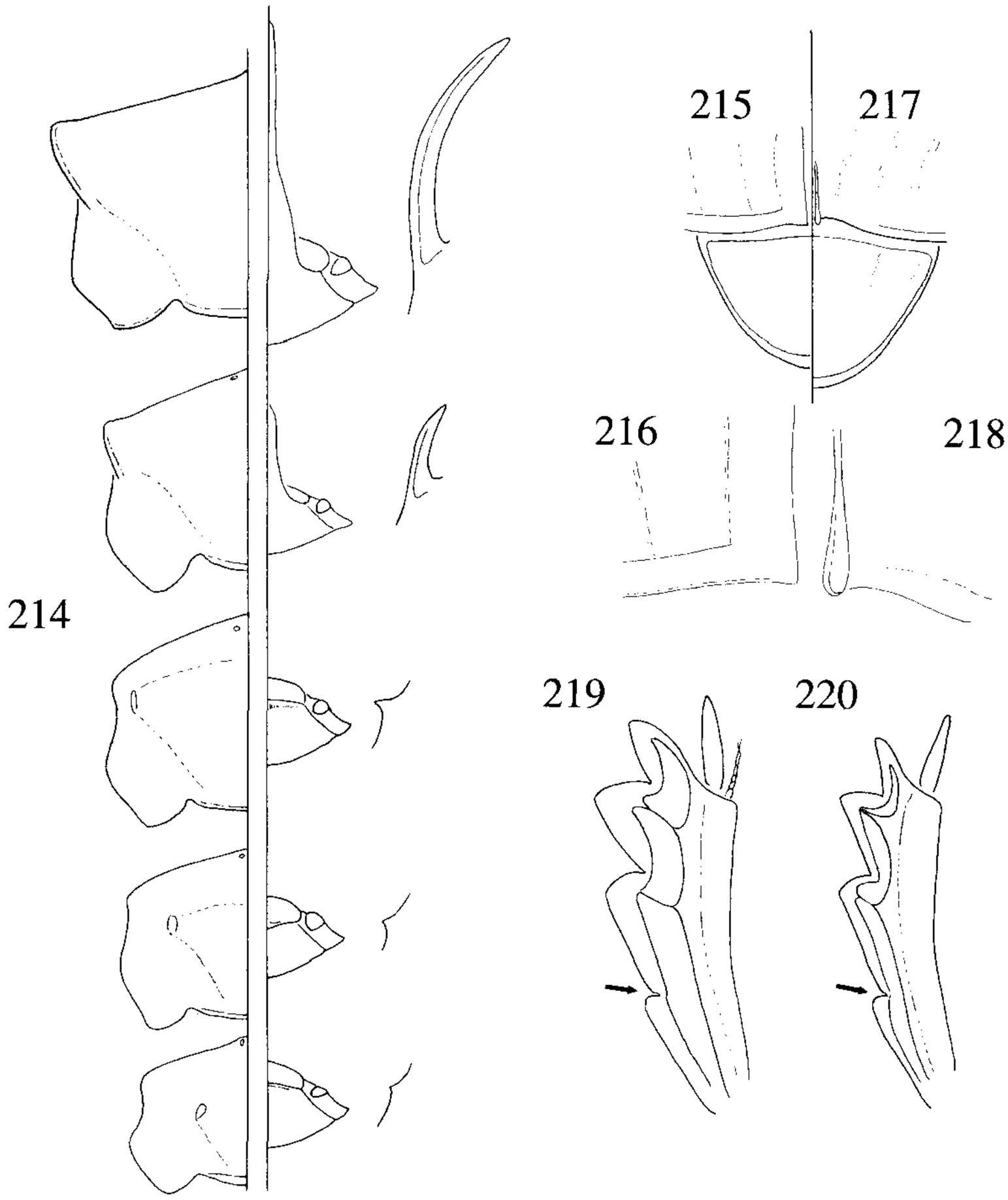
Figures 21, 22, 206–208, 211, 217, 218, 221

Phanaeus halffterorum Edmonds, 1979:99

Type: Male holotype ("Mexico, State of Mexico, 8km west Temascaltepec, 2360m; 11 July 1976; fungus in pine-oak forest"), California Academy of Sciences, San Francisco (Ento. Type No. 13184).

OTHER REFERENCES. Hinton, 1935 (as *endymion*); Edmonds, 1972 (as *incertae sedis*); Edmonds and Halffter, 1978; Morón, 1984; Delgado-Castillo, 1989 (as "*Phanaeus* sp.").

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 21, 22).—Except for central black area on female pronotum (difficult to see in dark specimens), dorsum either shining green or dark blue, female may be entirely black; in green males, color highly iridescent on head, pronotum, duller on elytra; in green females, blue individuals of both sexes, iridescence lacking; pronotum of male evenly colored, coloration of female pronotum restricted to sides, anterolateral angles. Venter red-brown to chocolate brown with green (or blue) reflections on pteropleura, legs, abdominal sterna. *Pronotal Sculpturing.*—Disk of male pronotum (Fig. 211) unevenly covered with variable-sized granules which become coarser laterally, progressively weaker basally (×15) until replaced by minute punctures; sides,



Figures 214–220. *Phanaeus* (*Notiophanaeus*) *endymion* group (**214,** *P. pyrois*, allometric variation of head and prothorax of male [right side of pronotum, left side of head, lateral view cephalic process]; **215,** tip of elytron and half of pygidium, *P. endymion;* **216,** tip of elytra, *P. endymion;* **217,** same as 215, *P. halffterorum;* **218,** same as 216, *P. halffterorum;* **219,** *P. pyrois*, female, front tibia [arrow indicates notch]; **220,** same, male).

anterolateral angles weakly punctate. Female pronotum punctate, punctures sometimes effaced medially (×15), coalescing laterally to produce weak rugosity. Except for granulated disk of male (visible to unaided eye as fine texturing), pronotum appearing glassy smooth without magnification. *Elytra.*—Striae fine, interstriae evenly but weakly convex, evenly shagreened such that no area appears smoother or brighter than any other. Inner margin of each elytron (Figs. 217, 218) with ridge progressively more raised, keel-like posteriorly extending slightly beyond apical angle as small, rounded tooth; apical margin (viewed posteriorly) shallowly excised adjacent to this tooth. *Pygidium.*—Usually bearing shallow, elongate concavity on each side (often visible only from angle) (Fig. 218). *Secondary Sexual Characters.—Male* (Fig. 206): Head, pronotum as described for *endymion* group except that well-developed individuals with posterior angles of pronotal disk more rounded laterally, proportionately larger than in other species, anterior margin of pronotum bearing small, acute, median tooth (except in certain Guerrero specimens; see "Comments," below). *Female:* Cephalic carina trituberculate. Pronotum bearing weakly raised, anterior transverse ridge with three isolated, equal-sized tubercles followed by shallow concavity and midlongitudinal linear depression extending from near middle of disk to posterior margin (Fig. 208). *Specimens Examined.*—19 males, 10 females (length 12–19 mm; width 8–12 mm).

DIAGNOSTIC REMARKS. This species differs from *endymion,* its closest relative, by the following: pronotal shape and sculpturing of male, shape of inner margin of elytra, shape of female pronotum, relief of pygidium, and distribution.

DISTRIBUTION (Fig. 221; appendix). Known only from the environs of Temascaltepec, state of Mexico, and from the Sierra Madre del Sur from Chilpancingo to Acahuizotla. 750–2400 m. Pine/oak forests; crepuscular/nocturnal. Mycetophagous. Collection dates: June–November.

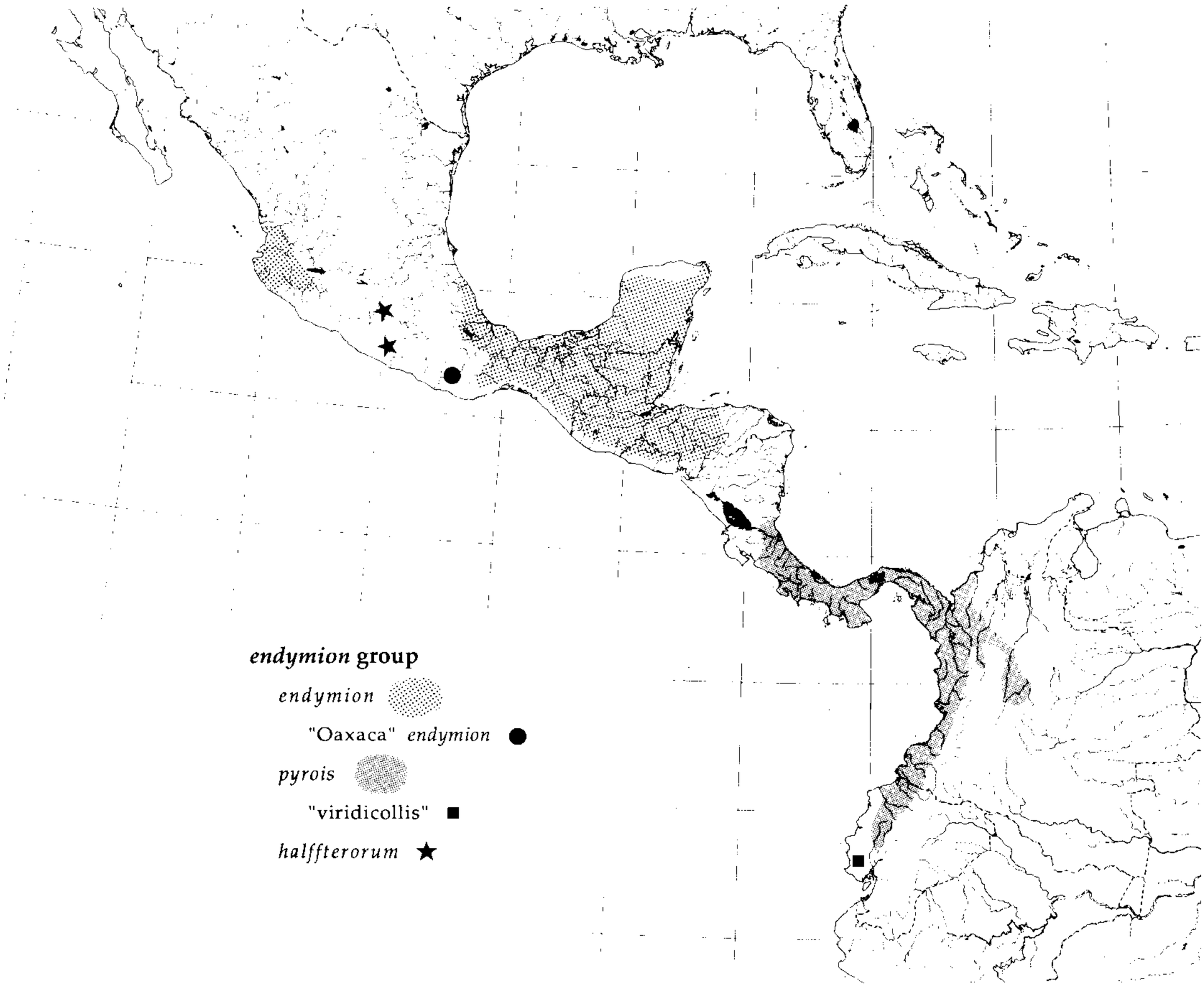


Figure 221. Distribution of the *Phanaeus* (*Notiophanaeus*) *endymion* group.

COMMENTS. The unique ecological and geographical characteristics of *halffterorum* were discussed by me in 1979. Since describing this species, I have discovered four of the ten missing specimens of the original Hinton series (see Edmonds, 1979, footnote p. 105); one is in the Howden collection, three in the British Museum (Natural History).

The original type series of this species included a large male from the Sierra Madre del Sur near Chilpancingo, Guerrero. I have since examined additional species from the environs of Acahuizotla, about 40 km west of the Chilpancingo site. These specimens resolve the doubt I had in 1979; the Guerrero populations are, indeed, *halffterorum* as defined here. They were collected in carrion-baited traps (which attract other essentially mycetophagous species) and at lights. Guerrero males are dark green and lack an anteromedian pronotal tooth; females are virtually all black and lack distinct impressions on the base of the pygidium.

Guerrero populations of *halffterorum* are isolated from those in the Temascaltepec area by the arid valley of the Balsas River and occur at much lower elevations (ca. 750 m vs. >2000 m). This species is evidently much more ecologically variable than I suspected in 1979. The intervention of the arid conditions of the Balsas Valley, which has undergone xerification only recently (Pleistocene), suggests that the origin of *halffterorum* was earlier than I previously thought.

Phanaeus (*Notiophanaeus*) *endymion* Harold

Figures 17, 18, 200–202, 209, 213, 215, 216, 221

Phanaeus endymion Harold, 1863:163

Type: Male lectotype ("Mexico"), Muséum National d'Histoire Naturelle, Paris (Arnaud, 1982a:114).

OTHER REFERENCES. Bates, 1887; Nevinson, 1892a; Gillet, 1911b; Olsoufieff, 1924; Islas, 1942; Blackwelder, 1944; Halffter and Matthews, 1966; Barrera, 1969; Edmonds, 1972; Morón, 1979, 1984, 1987; Morón et al., 1986; Morón and López-Méndez, 1985; Morón et al., 1985; Palacios-Rios et al., 1990.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 17, 18).—Except for irregularly shaped, shining black area on disk of female pro-

notum (difficult to see in dark specimens), dorsum uniformly dark green or dark blue-green, rarely completely black (Oaxaca specimens); dull to moderately shining, brightness often more subdued on elytra, more accentuated on male pronotum; occasional females with highly shining, yellow-green pronotum. Color extending ventrally to abdominal sterna, ventral surfaces of femora, tibiae, pteropleura, metasternum. *Pronotal Sculpturing.*—Appearing smooth in both sexes to unaided eye (Figs. 200–203). In male (Fig. 209) (×20), disk shagreened, bearing minute asperities that become larger, denser, more apparent to naked eye laterally; sides, anterolateral angles more weakly shagreened than disk, with feeble punctures that become larger, somewhat denser anterolaterally; shagreening mutes brightness of surface such that disk appears velvety to unaided eye and under low magnification (×5). Disk of Oaxaca specimen with evenly distributed, minute granulations. In female (×20), entire surface punctate, punctures dorsally extremely minute, widely spaced, becoming larger, denser anterolaterally; to unaided eye, appearing glassy smooth. *Elytra.*—Striae simple, bearing (×15) punctures varying from barely perceptible to distinct. Interstriae distinctly convex (Fig. 213), shagreened; shinier ("polished") medially than adjacent to striae; longitudinal "polishing" most distinct in green individuals, then in first four or five interstriae; in worn specimens, shininess effaced, entire interstria uniformly dull. Elytral margin simple (Figs. 215, 216). *Secondary Sexual Characters.*—*Male:* Head, pronotum as described for *endymion* group, above. *Female:* Except in worn, small individuals, cephalic carina almost always distinctly trituberculate, only rarely simple. Except in small individuals, pronotum with small, rounded anteromedian concavity bounded anteriorly by a U- or V-shaped ridge, in few large specimens, posteriorly by small, rounded convexity; anterior ridge bearing median tubercle (dentiform in large specimens), terminating at each end as low rounded or oval tubercle; in some small individuals, concavity only weakly indicated or absent, ridge replaced by three isolated, rounded tubercles. *Specimens Examined.*—137 males, 123 females (length 11–20 mm; width 7–12 mm).

DIAGNOSTIC REMARKS. This species most closely resembles *P. halffterorum,* from which it differs by those features discussed under the latter (see above). Males bear a superficial resemblance to *P. adonis* (q.v.).

DISTRIBUTION (Fig. 221; appendix). Central Honduras, Guatemala, El Salvador, Belize, southern Mexico east of the Sierra Madre Oriental from Veracruz to Oaxaca, and southwestern Mexico. Sea level to 2200 m (most records 0–150 m). Coprophagous; also collected in carrion, fungi, and decomposing fruits and leaves; diurnal. Collection dates: Mexico—all year; Central America—May–December.

COMMENTS. The range of *endymion* is the northern half of Mesoamerica. Its center of distribution is southern Mexico where it occurs widely in tropical evergreen and semideciduous forests. There is, however, a disjunct area in southwestern Mexico (western Jalisco and adjacent areas of bordering states) where the species is not uncommon; specimens from this area do not differ significantly from those of eastern populations. The intervening region (from Jalisco along the Pacific coast to southern Oaxaca) is a drier area where it probably survives in isolated pockets of suitable habitat. The close similarity of eastern and western populations of *endymion* suggests that this species, until recently, also inhabited south-central Mexico. The same factors that resulted in its extinction there (drier climate and associated vegetational changes) may have been also those which promoted speciation in relict populations. Such a series of events could explain the existence of *halfferorum* and of what appears to be a unique Oaxaca population (see below) in areas now peripheral to the distribution of *endymion.*

The Oaxaca population mentioned above and referred to in "Descriptive Remarks" is known from two specimens collected by Henry and Anne Howden from the mountains (2150 m) south of the city of Oaxaca. These specimens, a well-developed male and female, differ from typical *endymion* as follows: they are completely shining black except for subtle remnants of blue coloration along the pronotal margin (×20); the disk of the male pronotum (×15) is evenly, but not densely, covered with small granules, and the pronotum of the female bears a distinct, midlongitudinal impression (like that of *halfftterorum*). The Howden specimens were collected from wild mushrooms in a montane forest, suggesting an ecological distribution similar to that of *halfftterorum.* My guess is that more specimens will support recognizing this Oaxaca population as a distinct species, whose origin is attributable to the same set of circumstances as that of *halfftterorum.*

While the female pronotum of *endymion* almost always bears a trituberculate ridge, it sometimes resembles that of *pyrois* by having three isolated tubercles. Specimens with this atypical pronotal shape almost always also possess another uncommon feature: distinctly, broadly punctate elytral striae (×0–5). Neither of these unusual characters, nor the combination of both, varies in any consistent geographical way.

The lectotype of *endymion* carries Harold's label with the notation "Mexico"; his original description designates Cordova, Veracruz, as type locality. I have not seen the female cotype described by Harold.

Phanaeus (*Notiophanaeus*) *pyrois* Bates

Figures 19, 20, 203–205, 210, 212, 214, 219–221

Phanaeus pyrois Bates, 1887:58

Type: Male lectotype ("Chontales, Nicaragua, T. Belt, B.C.A. p.58 sp.8, sp. figured"), British Museum (Natural History), PRESENT DESIGNATION.

Phanaeus blanchardi Olsoufieff 1924:92 (not Harold, 1871a:114), NEW SYNONYMY

Type: Male lectotype ("Colombia, Cauca River Valley"), Muséum National d'Histoire Naturelle, Paris (Arnaud, 1982a:116).

Phanaeus funereus Balthasar, 1939:241, NEW SYNONYMY.

Type: Male holotype ("Ecuador"), Národní Muzeum, Prague

Phanaeus olsoufieffi Balthasar, 1939:242 (new name for *P. blanchardi* Olsoufieff, 1924) (Martínez and Pereira, 1967:68)

Phanaeus bothrus Blackwelder, 1944:209 (new name for *P. blanchardi* Olsoufieff, 1924) (Martínez and Pereira, 1967:68)

NOMENCLATURAL REMARKS. Olsoufieff's "blanchardi" was first recognized as a junior primary homonym of *Phanaeus blanchardi* Harold by Balthasar (1939), who proposed the replacement name *Phanaeus olsoufieffi*. The homonomy was also recognized independently by Blackwelder (1944), whose replacement name *Phanaeus bothrus* becomes a junior objective synonym of *P. olsoufieffi* Balthasar. Thus, the valid name of Olsoufieff's taxon is *Phanaeus olsoufieffi* Balthasar. *P. olsoufieffi* (as *blanchardi* Olsoufieff) was first synonymized with *P. funereus* by Martínez and Pereira (1967). The name "apollinaris Gillet" has been used for *pyrois;* as far as I know, it is a *nomen nudum*.

OTHER REFERENCES. Nevinson, 1889, 1892a; Pittier and Biolley, 1895; Gillet, 1911b; Gacharna, 1951; Edmonds, 1972, 1978; Young, 1978; Howden and Young, 1981; Peck and Forsyth, 1982 (as "apollinaris").

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 19, 20).—Usually as follows: Posterior two-thirds of clypeus, paraocular areas, if not all at least sides and anterolateral angles of pronotum bright metallic red; all non-colored areas dull or weakly shining black; elytra entirely dull black with at most very weak bluish luster (usually visible only under magnification with strong light); pygidium bright red medially, green around margin. Following variations known: (a) certain specimens from western Panama, Costa Rica, and Colombia, all specimens examined from Ecuador ("funereus") almost entirely black; colored areas very inconspicuous, restricted to pronotal, pygidial margins and often visible only under magnification (×10); (b) certain specimens from central Costa Rica (Turrialba) completely dull, dark metallic blue or weakly shining green; elytra distinctly duller than pronotum (most Turrialba specimens exhibit usual coloration described above); and (c) any dorsal colored areas, regardless of size or location, in occasional specimens can be red-yellow or red-green. Venter black to black-brown, usually with distinct, weak greenish or bluish reflections on legs, abdominal sterna, other isolated areas. *Pronotal Sculpturing.*—To unaided eye pronotum of both sexes appears smooth (Figs. 203, 204); magnification (×20) reveals following: In male (Fig. 210) flattened, triangular disk shagreened, bearing minute asperities which become larger, denser laterally; rounded sides, anterolateral angles with feeble punctures becoming somewhat larger, denser anterolaterally; shagreening tends to mute brightness of surface such that disk appears almost velvety to unaided eye or under low magnification (×5). In female, entire surface punctate, punctures extremely minute, widely separated dorsally, becoming larger, denser laterally, anteriorly. *Pronotum.*—Basal fossae reduced to punctiform pits in both sexes. *Elytra* (Fig. 212).—Striae fine but apparent width enhanced somewhat by usually weakly convex, dull interstriae; in some specimens (particularly large ones) interstriae virtually flat (frequency of specimens with flat, uniformly dull interstriae higher in South American populations than in Central American ones). Interstriae usually extremely minutely, evenly shagreened (×80) with no difference in reflectivity between median areas, those adjacent to striae. In some specimens viewed with unaided eye, median portions of interstriae 1–4 appear somewhat shinier such that their apparent convexness is accentuated; any variability in reflectivity visible to unaided eye disappears under higher magnifications (×15+), interstriae appearing uniformly dull. All interstriae smooth except for lateral-most, which bears few, scattered, small basal punctures. *Secondary Sexual Characters.—Male:* Head, pronotum as described for *endymion* group above. *Female:* Cephalic carina at most only weakly trituberculate, often simple carina. Pronotum (Fig. 205) evenly convex, always bearing three low, round tubercles arranged in transverse line, middle one often lying before or behind imaginary line connecting outer two. *Specimens Examined.*—127 males, 116 females (length 11–20 mm; width 7–12 mm).

DIAGNOSTIC REMARKS. This species most closely resembles *endymion*, from which it is distinguished by the following combination of characters: color and color pattern, elytral sculpturing, female secondary sexual characters of the pronotum, and distribution.

DISTRIBUTION (Fig. 221; appendix). Southern Nicaragua (north of Lake Nicaragua), Costa Rica, Panama, Colombia west of and along east side of Andes, and Ecuador east of the Andes. Sea level to 2200 m (most records 0–1500 m). Apparently restricted to forest habitats; diurnal. Coprophagous but sometimes collected from carrion and decomposing fruit. Collection dates: Panama—all year; Costa Rica—May–August; Colombia—May–October; Ecuador—March–September.

COMMENTS. As here defined, *pyrois* includes two previously recognized species based primarily on differences in color pattern, *P. olsoufieffi* and *funereus*. Were it not for the fact that specimens virtually identical to *funereus* occur in Colombian and Central American populations of *pyrois*, I would be inclined to maintain *funereus* as a subspecies. The type of *olsoufieffi*, as well as similar specimens from Central America, fall within the normal range of variation of *pyrois* and likewise do not merit separate taxonomic status.

The dark blue and dull green specimens of *pyrois* from Turrialba, Costa Rica, resemble *endymion* closely enough to suggest that they are intermediates between the two otherwise distinct species. I have not, however, seen any *endymion* from Nicaragua; moreover, the specimens in question were collected along with perfectly "good" *pyrois*. Nevertheless, the question of the relationship between the two species is somewhat clouded by the Turrialba specimens.

The British Museum (Natural History) collection includes the two specimens upon which Olsoufieff (1924) based the "aberration *viridicollis*" of his *P. blanchardi*. Both are labeled "Balzar M[ountains], Ecuador." The male is small; its head and pronotum are bright, shining green, the elytra dark, almost black with some greenish tinges, and pygidium shining green. The female is like the male except that the head and pronotum are blue-green. The specimens appear to be composites resulting from mismatching head–prothorax sections and pterothorax–abdomen sections (which remain on pins when the former break free). I cannot, however, clearly detect any repair, although there is glue beneath the right elytron of the male (but none visible between the pro- and metathorax). These specimens are unique, and, if it can later be determined that they are members of a morphologically and geographically distinct population, Olsoufieff's "*viridicollis*" may prove to be a valid taxon.

The distribution of *pyrois* covers the southern half of Mesoamerica. I consider it the sister group of *endymion* and its relatives, which occupy the northern half.

Subgenus *Phanaeus* Macleay

Phanaeus Macleay, 1819:124. Type-species: (*Scarabaeus carnifex* L., 1767) = *Phanaeus vindex* Macleay, 1819; subsequent designation by Olsoufieff, 1924.

Lonchophorus Germar, 1824:106. Type-species: (*Scarabaeus carnifex* L., 1767) = *Phanaeus vindex* Macleay, 1819; subsequent designation by Edmonds, 1972.

Onthurgus Gistel, 1857:602. Type-species: (*Scarabaeus carnifex* L., 1767) = *Phanaeus vindex* Macleay, 1819; original designation.

Palaeocopris Pierce, 1946:130. Type-species: *Palaeocopris labreae* Pierce, 1946; original designation by monotypy.

Phanaeus, sen. str., differs from *Notiophanaeus* primarily on the basis of pronotal sculpturing, which in this subgenus is granulate or granulorugose anterolaterally (see discussion under *Notiophanaeus*). This subgenus comprises 31 species and subspecies arranged in eight species groups. Except for *lunaris*, *hermes*, and *prasinus*, all species and subspecies are endemic to either Central or North America. The primary characters separating species groups relate to pronotal sculpturing, shape of the longer mesotibial spur (especially in females), shape of the female pronotum, and geographic distribution.

In general, separation of species on morphological grounds in this subgenus is more difficult than in *Notiophanaeus*. This is especially true for the *mexicanus* and *tridens* groups, females and small males of which can be virtually impossible to distinguish.

KEY TO THE SPECIES GROUPS OF *PHANAEUS, SEN. STR.*

1a. Pronotum granulate anterolaterally (Figs. 224, 236, 253). Longer mesotibial spur not dilated subapically (Fig. 245). Basal segment middle tarsus of female not strongly dilated 2

b. Pronotum granulorugose or rugose anterolaterally (Figs. 274, 310, 319, 320). Longer mesotibial spur dilated subapically (Fig. 289), especially in females (except *flohri* and some *scutifer*). Female mesobasitarsus variable .. 4

2a. Front tibiae tridentate. Anterolateral pronotal granules of variable sizes. Elytral interstriae finely, but distinctly (×10) punctate (Figs. 254, 255). United States and northeastern Mexico (Fig. 256) ..... *triangularis* group

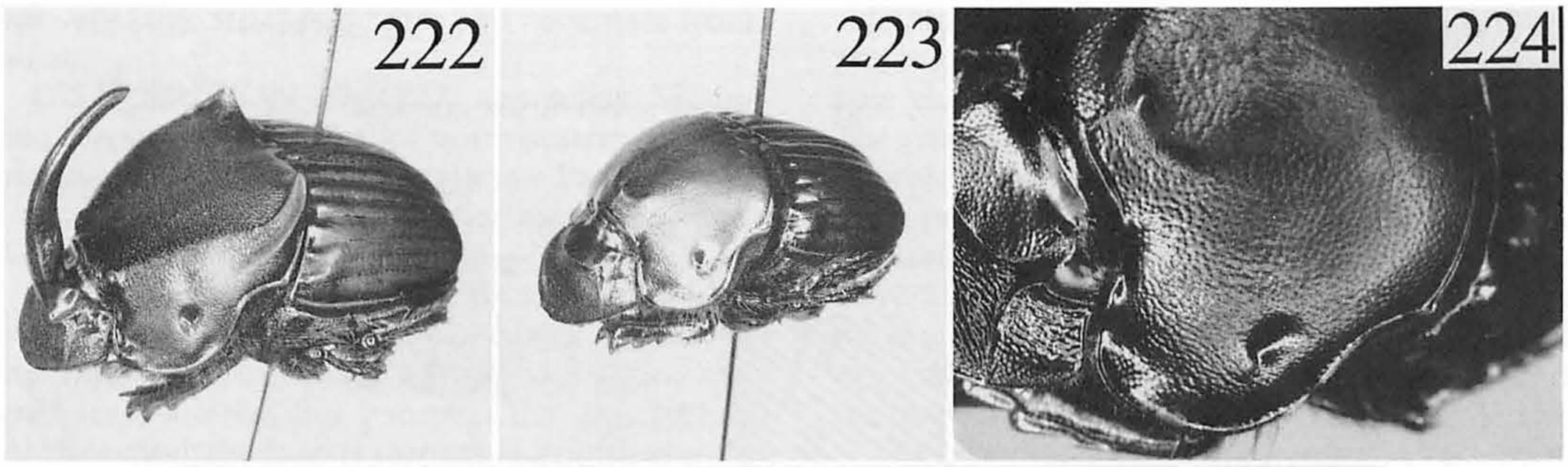
b. Front tibiae quadridentate (Figs. 243, 244), basal tooth small (can be indistinct in worn specimens). Anterolateral pronotal granules more-or-less uniform in size, usually dense. Elytral interstriae only minutely punctured (×40) (Figs. 225, 226). Northwest Mexico to northwestern South America 3

3a. Pronotal disk of well-developed males (Figs. 228–235) concave at least anteriorly, usually coarsely rugose, bordered laterally by raised, usually jagged ridges, and bearing a central or posteromedian process of some type (Figs. 237–242). Northwestern Mexico to Costa Rica (Fig. 246) ..... *tridens* group

b. Pronotal disk of well-developed males flat and uniformly granulate (Fig. 222). Northwestern South America to Panama (Fig. 227) ..... *hermes* group

4a. Pronotum of female with wide anteromedian prominence flanked on each side by elongate, vertical depression extending from disk to anterior pronotal margin behind eye (Figs. 273, 274). Extreme southwestern United States, Mexico, Central America, and northwestern South America (Fig. 290) .. *mexicanus* group

b. Pronotum of female more-or-less evenly convex anteriorly, with or without small antero-



Figures 222–226. *Phanaeus* (*Phanaeus*) *hermes* group (**222,** *P. prasinus,* male; **223,** same, female; **224,** same, oblique view female pronotum; **225,** *P. hermes,* dorsal view elytron; **226,** *P. prasinus,* same).

median concavity and tubercles, and lacking vertical depressions 5

5a. Midventral carina of front femora angulate near base; base of posterior surface with large, coarse punctures (Fig. 297). Pronotum of large males (Figs. 291–293) with smooth posteromedian area bounded anteriorly by transverse tubercle or carina. Pronotum of female (Fig. 294) with narrow, transverse anteromedian ridge followed by oval concavity whose posterior margin interrupted by low, rounded gibbosity. Southeastern Mexico to Panama (Fig. 301) .. .. *beltianus* group

b. Front femora not angulate at base (Fig. 298); basal puncturing same size and texture as that extending to apex of femora. Male pronotum variable, but not as above 6

6a. Pronotum finely granulorugose anterolaterally. Pronotum of large males with smooth raised area along posterior margin which is often toothed medially (Figs. 307–309). Cephalic carina of female (seen from above) even with anterior margin of eyes. Eastern and southern Mexico to Guatemala (Fig. 312) .... *amethystinus* group

b. Pronotum (Figs. 319, 320, 336–340) very densely and coarsely granulorugose anterolaterally, and usually also over entire pronotal surface (sculpturing effaced in *igneus*). Male pronotum variable, but not as above. Cephalic process of female (seen from above) positioned in front of eyes. Central and western Mexico, United States 7

7a. Elytral interstriae smooth or minutely punctate (×30) (Figs. 321, 322). Outer margin of head notched between clypeus and paraocular areas (Fig. 325). Central and western Mexico and extreme southwestern United States (Fig. 329) ..... *quadridens* group

b. Elytral interstriae densely and coarsely punctatorugose (Figs. 341–346). Outer margin of head not distinctly notched. Extreme northern Mexico, United States (Fig. 360) .... *vindex* group

The *Hermes* Group

DIAGNOSIS. [1] Anterior margin of clypeus at most only weakly bidentate, often rounded; [2] clypeal process (seen from front) a rounded ridge; [3] cephalic carina of female at most only weakly tridentate; [4] pronotal disk of large males (Fig. 222) flattened dorsally, posterior angles curved laterally and sharply upturned, anterior angles each bearing conical tubercle; [5] pronotum of female evenly convex, with bowed transverse carina near anterior margin, sometimes weakly toothed medially and followed by a weak concavity; [6] anterolateral portions of pronotum evenly covered by flattened scale-like granules (Fig. 224); [7] basal pronotal fossae present; [8] front tibiae quadridentate, basal (fourth) tooth small, apical two teeth longitudinally carinate; [9] longer mesotibial spur slender, not dilated subapically; [10] elytral striae punctate (Figs. 225, 226); [11] forests of Panama and northwest South America (Fig. 227).

This group consists of two closely related species, *hermes* Harold and *prasinus* Harold (see also discussion under the *triangularis* group).

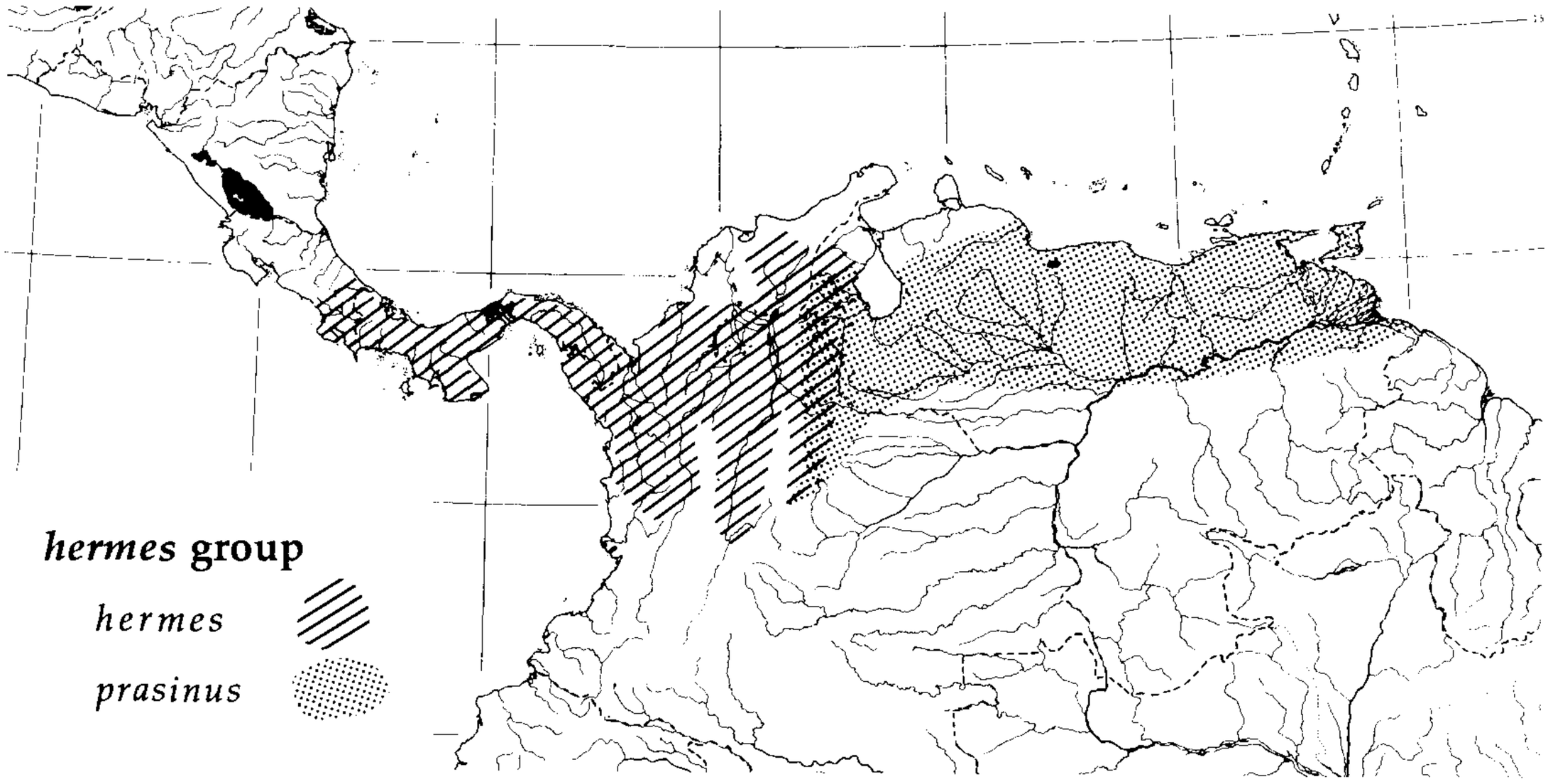


Figure 227. Distribution of the *Phanaeus* (*Phanaeus*) *hermes* group.

KEY TO THE SPECIES OF THE *HERMES* GROUP

1a. Elytral interstriae dull, appearing almost flat (Fig. 225); median area not noticeably shinier than that adjacent to striae; punctures of striae visible to unaided eye. Dorsum weakly shining to bright coppery brown or coppery green (Figs. 32, 33). Northwestern Colombia to Costa Rica (Fig. 227) .... *Phanaeus* (*P.*) *hermes* Harold

b. At least first three, but usually all interstriae evenly shining or shining only midlongitudinally and appearing convex (Fig. 226). Punctures of elytral striae very small, sometimes effaced, clearly visible only under magnification (×10). Dorsum weakly shining dark green, black, or, rarely, coppery green (Figs. 34–36). Northwestern Colombia and western and northern Venezuela (Fig. 227) .... *Phanaeus* (*P.*) *prasinus* Harold

Phanaeus (*Phanaeus*) *hermes* Harold

Figures 32, 33, 225, 227

Phanaeus hermes Harold, 1868b:82

Type: Male lectotype ("Columbia" [*sic*]), Muséum National d'Histoire Naturelle, Paris (Arnaud, 1982a:115).

Phanaeus bogotensis Kirsch, 1871:359, NEW SYNONYMY

Type: Male lectotype ("Bogota"), Staatsliches Museum für Tierkunde, Dresden, PRESENT DESIGNATION.

NOMENCLATURAL REMARKS. Harold (1880b) synonymized *bogotensis* and *prasinus;* Kirsch's species, however, is *hermes.*

OTHER REFERENCES. Gemminger and Harold, 1859; Bates, 1887; Nevinson, 1892a; Pittier and Biolley, 1895; Gillet, 1911b; Olsoufieff, 1924; Blackwelder, 1944; Gacharna, 1951 (as "olivaceus"); Vulcano and Pereira, 1967; Edmonds, 1972; Howden and Young, 1981.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 32, 33).—Dorsum weakly shining to bright coppery brown, usually with green or yellow-green highlights on head, pronotum, margins of elytra; pronotum of female with central black spot that can cover most of disk; females usually darker, duller than males. Pygidium colored as dorsum. Venter dark with strong green reflections on legs, sterna. *Pronotal Sculpturing.*—In large males, granulate except for smoother, strongly punctate triangular area adjacent to posterior margin, for punctate areas beneath posterolateral angles; granulation strongest, best defined on disk, becoming weaker, scale-like laterally, where it forms some ridging. In females, small males, anterior one-half to two-thirds of surface granulate, granules becoming scale-like anterolaterally, in females, coalescing dorsally to form distinct rugosities; basal one-third to one-half strongly punctate, most weakly so posteromedially. *Elytra* (Fig. 225).—Striae punctate, punctures small but clearly visible to unaided eye. Interstriae almost flat, minutely punctured (×10), dull. *Secondary Sexual Characters.*—As described for the species group. *Specimens Examined.*—57 males, 40 females (length 12–20 mm; width 7–14 mm).

DIAGNOSTIC REMARKS. This species differs from *prasinus* in color and elytral relief and texture. Small individuals can resemble *chalcomelas,* which

has very large strial punctures and tridentate front tibiae.

DISTRIBUTION (Fig. 227; appendix). Mountain forests (400–1000 m) of northwestern Colombia (including interandean valleys), Panama, and Costa Rica. Coprophagous. Collection dates: May–August, December.

COMMENTS. The eastern distributional limit of *hermes* appears to be the Cordillera Oriental of the Andes, where it overlaps *prasinus*. Locality records are scattered, but I suspect that this species inhabits montane forests throughout northwestern Colombia.

Phanaeus (Phanaeus) prasinus Harold

Figures 34–36, 222–224, 226, 227

Phanaeus prasinus Harold, 1868a:83

Type: Male lectotype ("Venezuela"), Muséum National d'Histoire Naturelle, Paris (Arnaud, 1982a:115).

Phanaeus lugens Nevinson, 1889:179, NEW SYNONYMY

Type: Male lectotype ("Venezuela, Merida"), Muséum National d'Histoire Naturelle, Paris (Arnaud, 1982a:116).

OTHER REFERENCES. Harold, 1868b; Candéze, 1891; Nevinson, 1892a; Gillet, 1911b; Sharp and Muir, 1912 (*lugens*); Olsoufieff, 1924; Blackwelder, 1944; Gacharna, 1951; Roze, 1955; Vulcano and Pereira, 1967; Edmonds, 1972.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 34–36).—Dorsum either dull to weakly shining black ("lugens") or dark to bright green to blue-green rarely with coppery highlights; pronotal disk of green females with central black spot that can virtually cover disk. Pygidium colored as dorsum. Venter black or with dark green reflections on legs, sterna. *Pronotal Sculpturing.*—As described for *hermes* except that in black females, puncturing less pronounced. *Elytra* (Fig. 226).—Striae punctate (×10), punctures scarcely if at all visible to unaided eye. Interstriae weakly convex, minutely punctate; surfaces evenly shining or shining at least midlongitudinally. *Secondary Sexual Characters.*—As described for the species group. *Specimens Examined.*—106 males, 91 females (length 12–20 mm; width 7–13 mm).

DIAGNOSTIC REMARKS. The black females of *prasinus* can superficially resemble dark females of *triangularis* while dark green individuals can resemble similarly colored females of *igneus* (see also "Comments" under *hermes*).

DISTRIBUTION (Fig. 227; appendix). Forests of northern Colombia, western and northern Venezuela, and isolated localities in the Gran Sabana of Venezuela. 0–2000 m. Coprophagous. Collection dates: January–October.

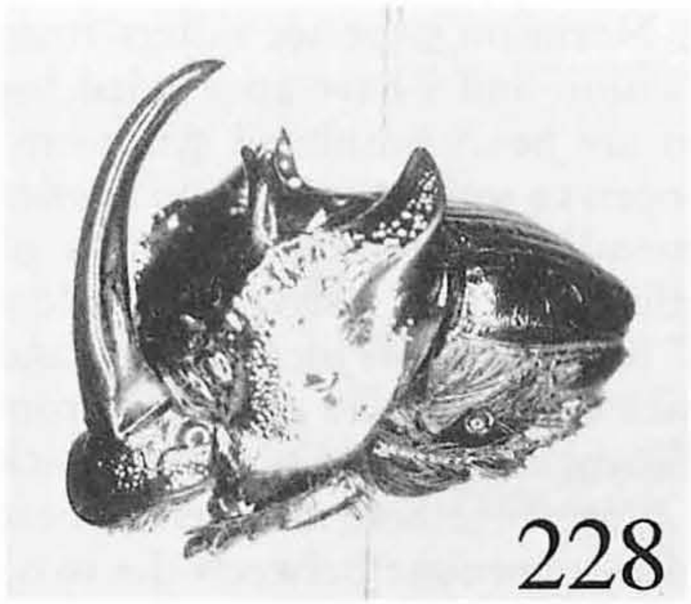
COMMENTS. Nevinson's species differs from *prasinus* only in color, and I have concluded for now that the two are best considered synonyms. The synonymy is open to some question, an answer to which will depend upon a greater quantity of more precise locality data than I have now. Most available "lugens" bear imprecise locality data, and there are few series or even pairs collected from the same place. I know of no locality where black and green forms occur together; moreover, there are few specimens intermediate between the two.

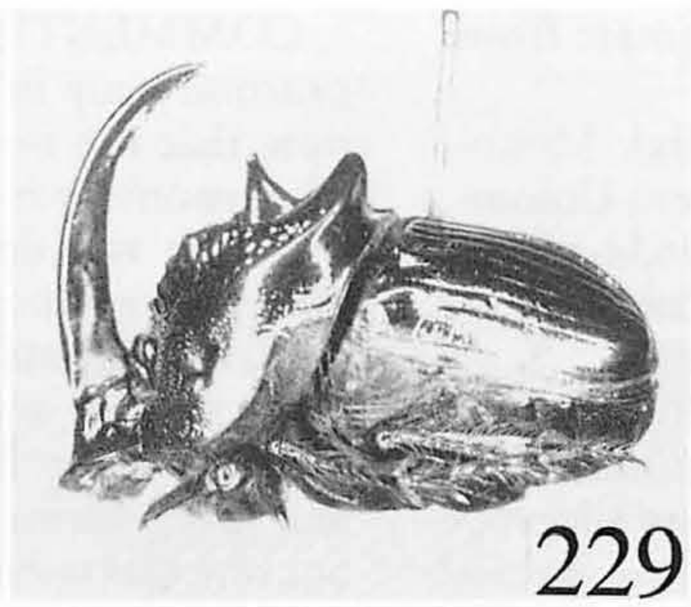
The green form is more common in collections. Most specimens are from mid-elevation localities in the Cordillera Oriental of the Colombian Andes. Some are from the coastal mountains and lowlands of northern Venezuela, and a few from scattered localities in the Gran Sabana of central Venezuela. These latter localities are on rivers and suggest that *prasinus* follows the gallery forests into that region. I know the black form from the Cordillera de Mérida (Venezuela), some specimens labeled "Bogota" (see below), and from Trinidad. Trinidad individuals can be black, but more often they have a distinct blue cast on the upper surface and are shinier and smaller than black specimens from the mainland.

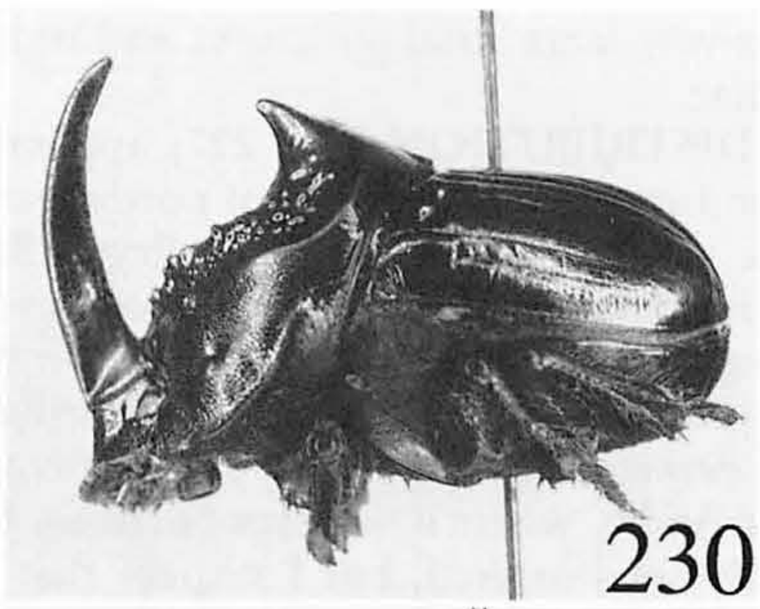
I have seen specimens of both forms of *prasinus* as well as *hermes* labeled "Bogota." Their occurrence there needs confirmation. Among a series of specimens from gallery forest near Ciudad Bolívar (Venezuela) are green individuals with strong coppery reflections that make them resemble *hermes* in color.

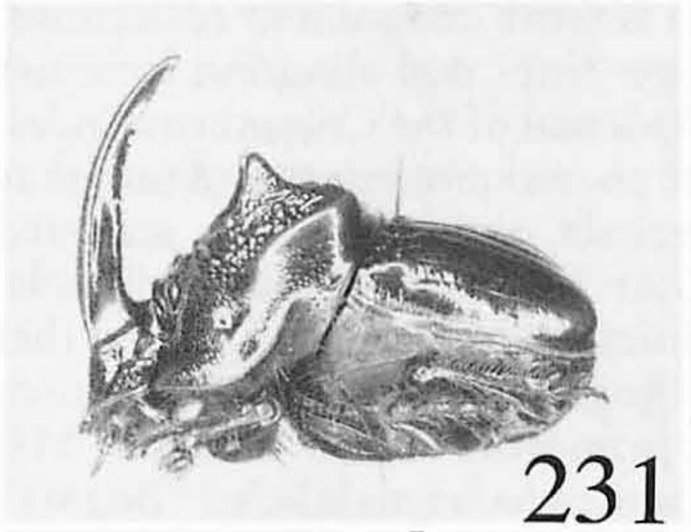
The *Tridens* Group

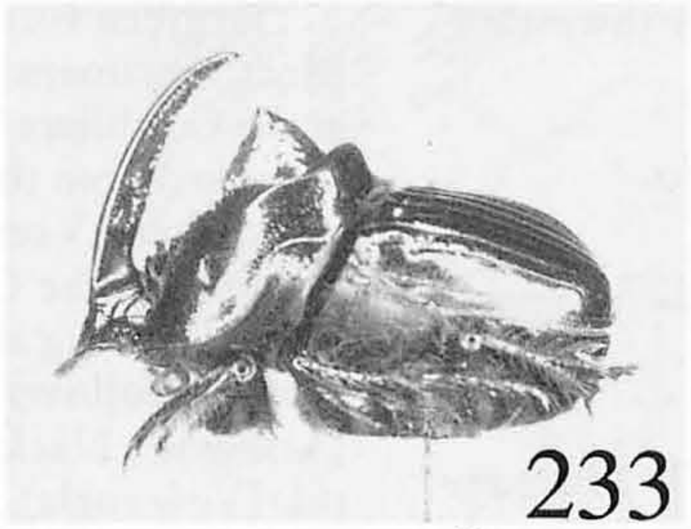
DIAGNOSIS. [1] Outer margin of head not distinctly notched laterally; [2] shape of clypeal process variable; [3] cephalic carina of female weakly tridentate, set in front of eyes; [4] anterolateral portions of pronotum (Fig. 236) granulate, granules small, uniformly distributed, fairly dense, only occasionally confluent (around lateral fossa); [5] basal pronotal fossae present; [6] disk of pronotum of large males concave at least anteriorly, usually coarsely rugose, bearing a median or posteromedian process whose shape and position varies by species (Figs. 237–242) (trace of this process persists even in smallest individuals); sides usually raised as jagged ridges; posterolateral angles (seen from behind) rounded, upturned; [7] pronotum of female convex, bearing thick, black, transverse anteromedian ridge usually followed by shallow concavity (ridge and concavity obliterated in small individuals); [8] front tibiae quadridentate (Figs. 243, 244); [9] female mesobasitarsus narrow (Fig. 245); [10] longer metatibial spur not dilated subapically (Fig. 245); [11] dorsum usually completely green or greenish, occasionally dark blue or coppery red (Figs. 86–95); [12] smaller-sized, length rarely exceeding 15 mm; [13] central Sonora southward along Pacific coast of Mexico, southern Mexico, and Central America from Guatemala to Costa Rica (Fig. 246).

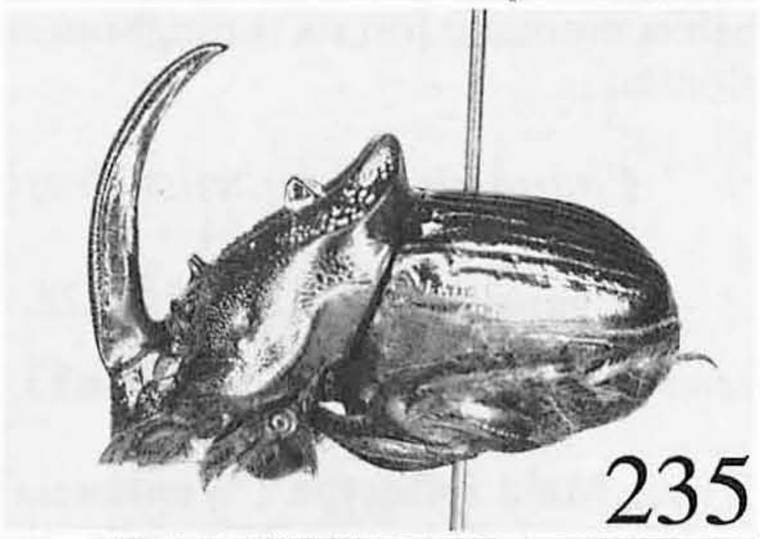


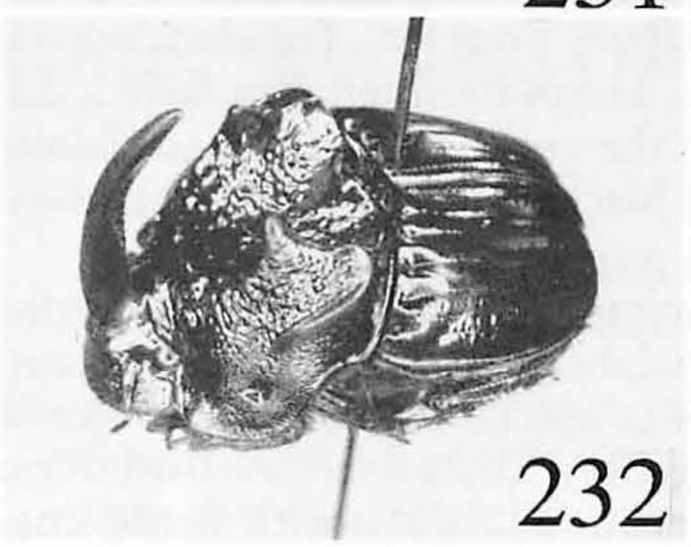


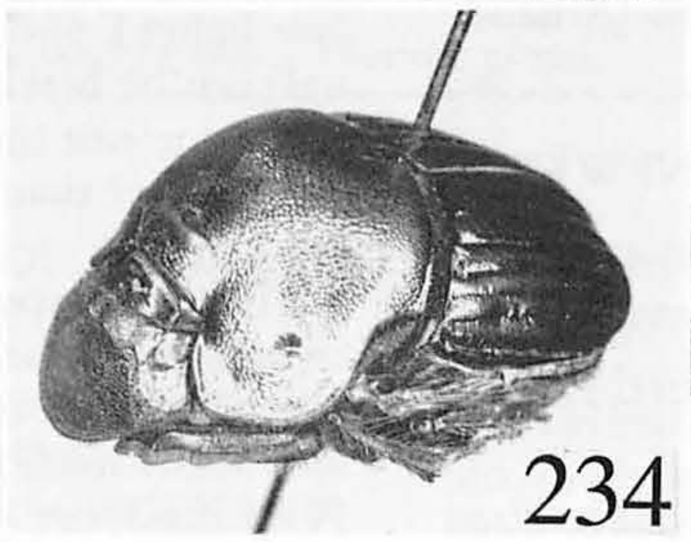


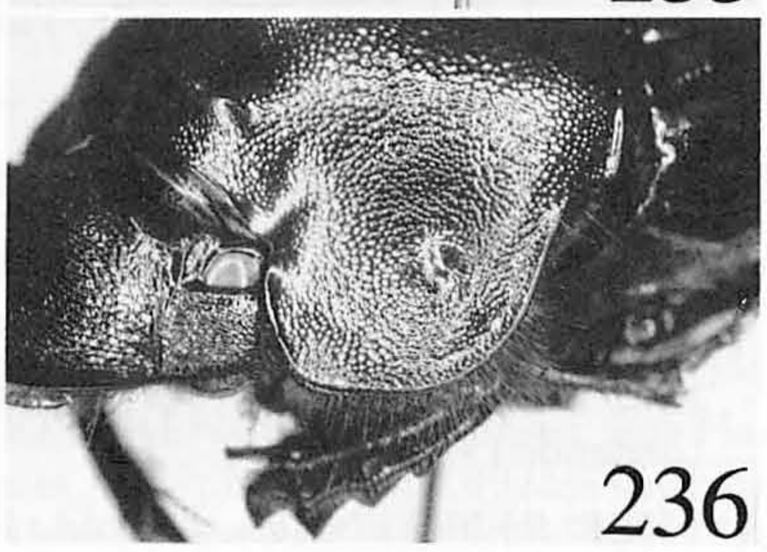












Figures 228–236. *Phanaeus* (*Phanaeus*) *tridens* group (**228,** *P. tridens,* male; **229,** same; **230,** *P. furiosus;* **231,** *P. daphnis,* male; **232,** same; **233,** *P. nimrod,* male [mouthparts removed]; **234,** same, female; **235,** *P. eximius,* male; **236,** *P. furiosus,* female, lateral view pronotum).

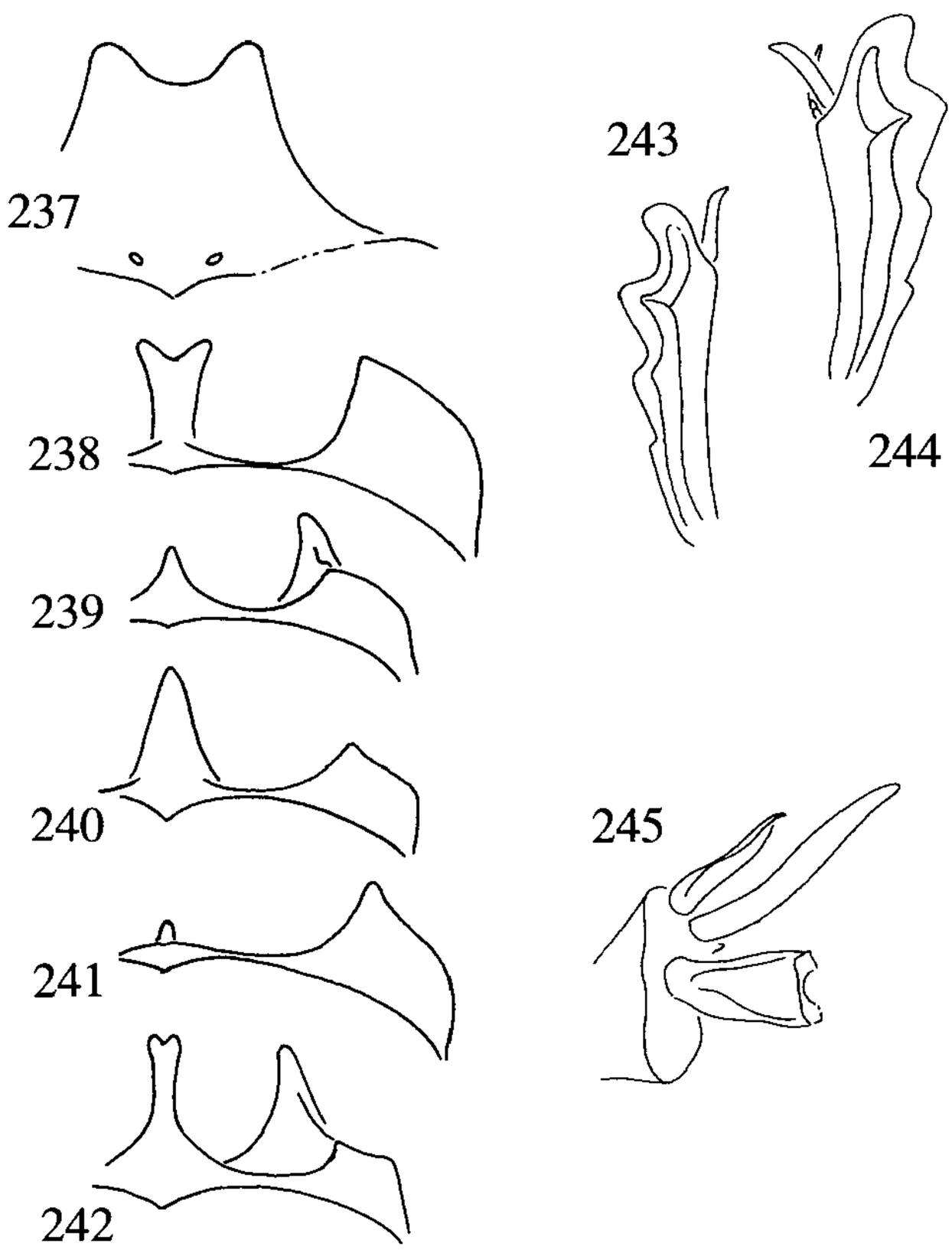
The *tridens* group embraces five closely related species, *tridens, eximius, nimrod, daphnis,* and *furiosus.* Of those characters listed above, the sculpturing of the pronotum and form of the pronotum of large males are the most distinctive. The species themselves, however, are difficult to separate morphologically. The most consistent characters are details of the shape of the pronotum of large males and geographic distribution. Females and small males can be virtually impossible to identify if unaccompanied by precise locality data. In general, the combination of distribution, male pronotal features, and some other morphological character or combination of characters will distinguish 90% of all specimens. For each species, there is a combination of features that, while "usual," is subject to intraspecific variation; this fact should be taken into account when using the key presented below.

The observation that the members of the *tridens* group are not separated by clean morphological gaps indicates that the group is likely the product of rapid speciation. Of special interest is the Colima population of *tridens* because it suggests a close phylogenetic connection among itself, *daphnis,* and *furiosus.*

This group is equivalent to "cluster 8" of *Phanaeus* that I recognized in 1972 with the addition of *eximus;* at that time, this latter species was assigned to "cluster 5" (now the *quadridens* group). Available distributional data suggest that all members of the *tridens* group are allopatric. But two areas, in particular, must be more thoroughly sampled before some zones of sympatry can be ruled out: central Michoacán (where *daphnis* and *furiosus* may overlap) and the Chiapas–Guatemala border region (where *tridens* may contact *eximius*).

KEY TO THE SPECIES AND SUBSPECIES OF THE *TRIDENS* GROUP

1a. Clypeal process (seen from front) very narrow, acute, distinctly longer (usually much longer) than width at base. Posteromedian process of male pronotum (Fig. 240) very large, laterally flattened, triangular ridge (Fig. 233). Female almost always with small, round black spot beneath lateral pronotal fossa. Elytral interstriae usually distinctly shinier midlongitudinally



Figures 237–245. *Phanaeus* (*Phanaeus*) *tridens* group (**237,** dorsal view posterior portion male pronotum, *P. furiosus;* **238,** same, *P. tridens;* **239,** same, *P. daphnis;* **240,** same, *P. nimrod;* **241,** same, *P. eximius;* **242,** same, *P. daphnis* ["tricornis" form]; **243,** *P. tridens,* male front tibia; **244,** *P. eximius,* female front tibia; **245,** *P. tridens,* tip of mesotibia and basitarsus).

(uniformly dull in worn specimens). Higher valleys of central Oaxaca above 1400 m, and Pacific coast of Oaxaca (Fig. 246) . . . . . *Phanaeus* (*P.*) *nimrod* Harold

b. Shape of clypeal process variable, but almost always broader than long, never appearing conical. Not occurring in central or coastal Oaxaca. Other characters variable 2

2a. Clypeal process (seen from front) triangular, or weakly rounded with small median tooth. Posteromedian process of male pronotum usually elongate, apically bifurcate, spine-like projection (Fig. 238). Female lacking black spot beneath lateral pronotal fossa. Distribution as in Figure 246 . . . . . *Phanaeus* (*P.*) *tridens* Laporte-Castelnau 3

b. Clypeal process (seen from front) usually rounded; if more-or-less triangular (some *daphnis*), then male pronotum as in Figures 231, 232. Other characters variable 4

3a. Elytral interstriae uniformly shining. Southern Chiapas, extreme southwestern Guatemala . . . . . *Phanaeus* (*P.*) *tridens pseudofurcosus* Balthasar

b. Elytral interstriae distinctly shinier midlongitudinally. Lowlands of central Veracruz and Colima . . . . . *Phanaeus* (*P.*) *tridens tridens* Laporte-Castelnau

4a. Elytral interstriae (×30) usually minutely rugose or punctatorugose adjacent to striae (sometimes visible only apically), smooth medially, appearing strongly convex to unaided eye. Posteromedian process of male pronotum a short, conical tooth (Fig. 241). Pronotal disk of male with pair of conical tubercles near anterior margin. Southern Guatemala to central Costa Rica (Fig. 246) . . . . . *Phanaeus* (*P.*) *eximius* Bates

b. Elytral interstriae uniformly shiny or dull; occasionally shagreened adjacent to striae, shinier medially, but never minutely rugose-punctatorugose adjacent to striae. Male pronotum not as described above. Not occurring in Central America 5

5a. Posteromedian process of male pronotum broad, apically emarginate projection (Fig. 237); raised sides of disk lacking strong conical tooth; granulations of sides of pronotum reaching posterior margin. Clypeal process rounded. Elytral interstriae convex. West-central Mex-

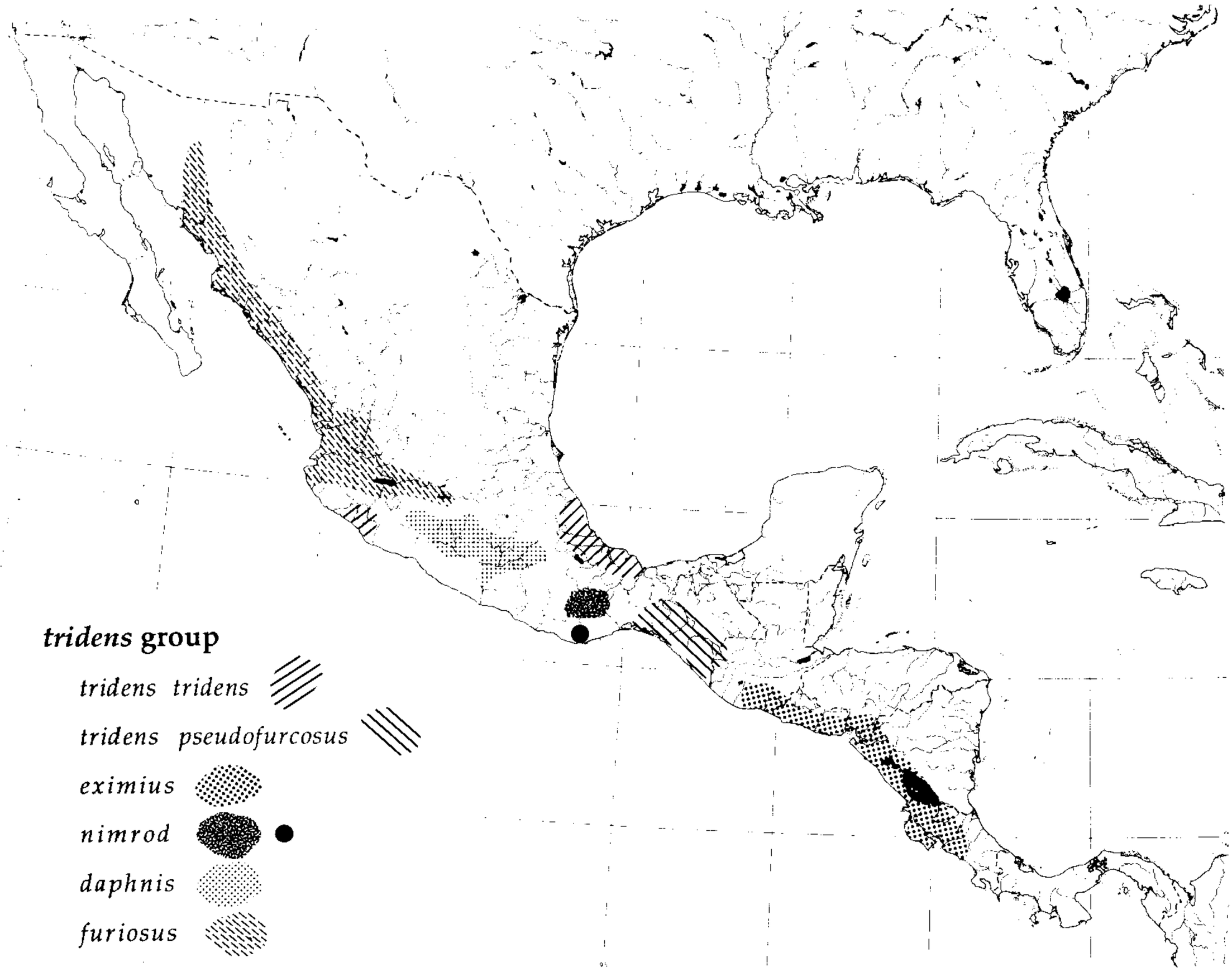


Figure 246. Distribution of the *Phanaeus* (*Phanaeus*) *tridens* group.

ico, extending along Pacific coastal region northward into central Sonora (Fig. 246) . . . . . *Phanaeus* (*P.*) *furiosus* Bates

b. Posteromedian process of male pronotum a short conical tooth (Fig. 239), or long, sometimes weakly apically bifurcate, spine-like projection (Fig. 242); raised sides of disk each with strong, conical tooth (Figs. 231, 232). Clypeal process usually rounded, sometimes triangular. Elytral interstriae flat to weakly convex. Balsas River valley and peripheral areas along escarpment of Transverse Volcanic Range of southern Mexico (Fig. 246) . . . . . *Phanaeus* (*P.*) *daphnis* Harold

Phanaeus (*Phanaeus*) *nimrod* Harold

Figures 90, 233, 234, 240, 246

Phanaeus nimrod Harold, 1863:167

Type: Male lectotype ("Mexico"), Muséum National d'Histoire Naturelle, Paris (Arnaud, 1982a:115).

Phanaeus babori Balthasar, 1939:246 (Arnaud, 1982c:125)

Type: Male holotype ("Mexiko: Oaxaca"), Národní Muzeum, Prague.

OTHER REFERENCES. Gemminger and Harold, 1869; Bates, 1887; Nevinson, 1892a; Villada, 1901; Gillet, 1911b; Olsoufieff, 1924; Islas, 1942; Blackwelder, 1944; Edmonds, 1972 (references to *nimrod* in Halffter and Matthews, 1966, should read *daphnis*, q.v.).

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Fig. 90).—Dorsum dark blue, blue-green, green, or yellow-green; yellow-green sometimes combined with coppery highlights. *Head.*—Clypeal process long, acute, spine-like, longer, usually much longer, than width at base. *Pronotum.*—Basal fossae present. Base of female disk impressed midlongitudinally. *Pronotal Sculpturing.—Male:* In large individuals, sides granulate to finely granulorugose; disk smooth to finely punctate anteriorly, with sparse but coarse rugosities posteriorly. Smaller individuals, as above except disk granulate to granulorugose anteriorly, punctate posteriorly. *Female:* Sides granulate; disk granulorugose anteriorly, granules progressively weaker posteriorly until replaced by sparse puncturing near posterior margin. *Elytra.*—Striae fine, impressed, minutely punctured (×30). Interstriae convex, minutely

punctate (×30), shagreened; shagreening usually denser adjacent to striae such that interstriae (especially 1–3) appearing smoother, shinier midlongitudinally under weak magnification (×10). *Secondary Sexual Characters.—Male:* Pronotum as in Figures 233, 240. *Female:* As described for species group. *Specimens Examined.*—64 males, 49 females (length 11–16 mm; width 7–10 mm).

DIAGNOSTIC REMARKS. The shape of the clypeal process and male pronotum along with distribution will separate *nimrod* from other members of the group.

DISTRIBUTION (Fig. 246; appendix). Central valley of Oaxaca and adjacent areas to south and southwest, and Pacific coast of Oaxaca. 0–1800 m. Coprophagous. Collection dates: May–September.

COMMENTS. The known distribution of *nimrod* is the smallest among members of the species group. Other than records from El Ocotito in central Guerrero and from Puerto Angel on the Pacific coast of Oaxaca, it is restricted to the central valleys of Oaxaca. Its presence in the coastal scrub forest could be the result of recent introduction from the interior. In spite of its limited distribution, color varies considerably. As in *eximius,* no one color predominates, and small series from single localities can include all variations. This species resembles *tridens tridens* in the microsculpture of the interstriae.

Phanaeus (*Phanaeus*) *tridens* Laporte-Castelnau

Figures 91–93, 228, 229, 238, 243, 245, 246

Phanaeus tridens Laporte-Castelnau, 1840:81

Type: Male neotype (erroneously labeled "Chili"), Castelnau Collection, National Museum of Victoria, Melbourne, PRESENT DESIGNATION.

Phanaeus frankenbergeri Balthasar, 1939:245 (Arnaud, 1982c:125)

Type: Male holotype ("Mexico"), Národní Muzeum, Prague.

Phanaeus pseudofurcosus Balthasar, 1939:244

Type: Male holotype ("Mexico"), Národní Muzeum, Prague.

Phanaeus tridens tridens Laporte-Castelnau, NEW STATUS

Phanaeus tridens pseudofurcosus Balthasar, NEW COMBINATION

NOMENCLATURAL REMARKS. Hope's (1837:53) suspicion that *Scarabaeus tridens* Fabricius, 1775 (*Copris tridens* Fabricius, 1801), belonged in *Phanaeus* created the possibility that Laporte-Castelnau's name was a junior homonym. Fabricius' species, however, is an *Onthophagus.*

OTHER REFERENCES. Klug, 1841 (as "neptunus"); Lacordaire, 1856; Harold, 1863; Gemminger and Harold, 1869; Bates, 1887; Nevinson, 1892a; Villada, 1901; Gillet, 1911b; Olsoufieff, 1924; Islas, 1942; Blackwelder, 1944; Halffter and Matthews, 1966; Barrera, 1969; Edmonds, 1972; Edmonds and Halffter, 1978; Halffter and Edmonds, 1982.

DESCRIPTIVE REMARKS. *Color and Color Pattern.*—(a) *tridens* (Figs. 91–93): Posterior portion of head, pronotum green, yellow-green, coppery yellow, coppery red, dark black-red; sides of pronotum (especially males) usually contrasting with that of disk, sometimes tricolored; elytra green, yellow-green or coppery red with green highlights, usually less brightly colored than pronotum. More common color combinations: (i) pronotal disk bright coppery red, sides yellow-green, elytra yellow-green; (ii) pronotal disk yellow-green, elytra, sides of pronotum deeper green. (b) *pseudofurcosus:* Much less variable, contrasting than above, usually as in combination (ii) above. *Head.*—Clypeal process (seen from front) triangular, or weakly rounded with small median tooth. *Pronotal Sculpturing.—Male:* In larger individuals, sides finely granulate becoming granulorugose on raised outer margin of disk; disk weakly but coarsely rugose, more sparsely so posteriorly. In smaller individuals, remains of central part of disk sparsely, irregularly granulate, becoming punctate posterolaterally. *Female:* Sides finely granulate, granules becoming larger, flattened on disk, progressively more effaced posteromedially where replaced by asperate punctures. *Elytra.*—Striae simple, impressed, minutely punctured (×30). In *tridens,* interstriae 1–4 (or 5) shinier medially than along striae, appearing polished midlongitudinally. In *pseudofurcosus,* interstriae uniformly shining. *Secondary Sexual Characters.—Male:* Pronotum as in Figures 228, 229, 238; posteromedian process of disk usually elongate, apically bifurcate, spine-like projection (except Colima population of *tridens;* see "Comments," below). *Female:* As described for species groups. *Specimens Examined.—tridens*—237 males, 196 females; *pseudofurcosus*—67 males, 74 females (length 10–17 mm; width 7–11 mm).

DIAGNOSTIC REMARKS. The shape of the clypeal process will separate this species from all but a few *daphnis.* Certain males of Colima populations superficially resemble "tricornis" males of *daphnis.*

DISTRIBUTION (Fig. 246; appendix). *tridens*—tropical lowlands of central Veracruz and Colima. 0–1500 m. *pseudofurcosus*—southern Chiapas and extreme southwestern Guatemala. 0–1800 m. Both subspecies—Coprophagous. Collection dates: May–October (most June–August).

COMMENTS. Specimens of *tridens tridens* from the northern limit of its range in Veracruz usually have yellow-green pronota and green elytra. Elsewhere, this subspecies usually has a coppery red pronotal disk and light green elytra with strong yellow or coppery highlights. Most *pseudofurcosus* are uniformly dark green.

The Colima population of *tridens tridens* exhib-

its a surprising amount of variability in the shape of the posteromedian process of the male pronotum. Certain males resemble those of *nimrod,* and others look like the "tricornis" males of *daphnis.* I have seen only 20 specimens from Colima; of these, four are large males, and none has a typical *tridens* pronotum. This population may later prove to be a distinct taxon, but its relationship with *tridens* from eastern Mexico is clear. The Colima population of *tridens,* along with disjunct southwest Mexico populations of *endymion,* are probably survivors of broadly distributed tropical forest populations that antedated the onset of desert conditions in the Balsas River valley and southern coastal regions of Mexico. I have seen one specimen of this subspecies collected in Tequesquitengo, Morelos, far from the Colima and Veracruz populations. In order to rule out an accidental introduction in modern times, more specimens must be collected.

The original type material of *tridens* is apparently lost (see the introduction). I have designated a specimen of *tridens* from the Laporte-Castelnau collection in Melbourne as neotype. It is mounted with a small male of *scutifer* and both are labeled "*tridens* Chili."

Phanaeus (*Phanaeus*) *eximius* Bates

Figures 86, 235, 241, 244, 246

Phanaeus eximius Bates, 1887:62

Type: Male lectotype ("Guatemala, Sallé, B.C.A. p.62 sp. 22, sp. figured"), British Museum (Natural History), London, PRESENT DESIGNATION.

OTHER REFERENCES. Bates, 1889; Nevinson, 1892a; Gillet, 1911b; Olsoufieff, 1924; Blackwelder, 1944; Edmonds, 1972.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Fig. 86).—Dorsum dark blue, blue-green, green, yellow-green, or coppery red. Pygidium same color as elytra. Venter dark, colored reflections on legs, sterna. *Head.*—Clypeal process semicircular or broadly rounded, never angulate. *Pronotum.*—Base of disk impressed in female. Basal fossae present. *Pronotal Sculpturing.*—*Male:* In large individuals, sides granulate, disk more or less evenly, coarsely rugose except posteromedially where coarsely punctatorugose. Small individuals as above except disk granulorugose anteriorly finely punctatorugose to punctate posteriorly. *Females:* Granulate laterally; granules becoming flat on disk, coalescing anteriorly as transverse ridges, becoming progressively weaker posteriorly where they may become asperate punctures; posterior portion of pronotum never simply punctured. *Elytra.*—Striae simple, impressed, minutely punctured (×30). Interstriae convex, distinctly but minutely (×30) rugose-puntatorugose adjacent to striae, smooth medially; interstrial rugosity sometimes distinct only apically. *Secondary Sexual Characters.*—*Males:* Pronotum as in Figures 235, 241. *Female:* As described for species group. *Specimens Examined.*—35 males, 27 females (length 12–17 mm; width 7–11 mm).

DIAGNOSTIC REMARKS. This species most closely resembles *tridens,* from which it differs by shape of the clypeal process, sculpturing of the elytral interstriae and of the male pronotum, and distribution.

DISTRIBUTION (Fig. 246; appendix). Central America south of the central cordilleras from Guatemala to Costa Rica. 300–1800 m. Coprophagous. Collection dates: May–August.

COMMENTS. The elytral sculpturing characteristic of *eximius* is sometimes indistinct; in these cases, the interstriae might be described as "coarsely shagreened." *Phanaeus eximius* resembles *palliatus,* and I grouped the two species in 1972. The two differ by pronotal sculpturing. The color variation of *eximius* is great among the few specimens examined.

The distribution of *eximius* is poorly known; well over one-half of the specimens examined lack precise locality data.

Phanaeus (*Phanaeus*) *furiosus* Bates

Figures 87–89, 230, 236, 237, 246

Phanaeus furiosus Bates, 1887:61

Type: Male lectotype ("Ventanas, Mexico, 2000ft, Forrer, Hoege, B.C.A. p.61 sp.19, sp. figured"), British Museum (Natural History), PRESENT DESIGNATION.

Phanaeus furcosus Felsche, 1901:155 (new name for *furiosus*), NEW SYNONYMY

NOMENCLATURAL REMARKS. In his original description, Bates said, "I have adopted the name '*P. furiosus* Dugés,' given to this species in the Sallé collection." Felsche (1901), who was informed by Sallé that the name in his collection was *furcosus,* not *furiosus,* emended the name accordingly. Gillet (1911b) and Olsoufieff (1924) accepted Felsche's emendation, and the name *furcosus* has been used widely in collections for the last 60 years. It is my opinion that Felsche's action was an unjustified emendation (Article 33[a] [ii] of the Code) and, therefore, that *Phanaeus furiosus* Bates is the valid name of this species. Accordingly, *P. furcosus* becomes a junior objective synonym of *P. furiosus* Bates.

OTHER REFERENCES. Nevinson, 1892a; Blackwelder, 1944; Edmonds, 1972.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 87–89).—Dorsum dark blue, shining blue-green, or green; rarely shining yellow-green with coppery highlights. Pygidium colored as elytra.

Venter dark with colored reflections on legs, sterna. *Head.*—Clypeal process rounded. *Pronotum.*—Basal fossae present. *Pronotal Sculpturing.*—*Male:* Sides granulate; granulation extending to posterior margin, near which it can become somewhat coarser. Disk of larger individuals becoming coarsely rugose in front of posteromedian process; disk of smaller individuals granulate to granulorugose anteriorly, weakly punctatorugose posteriorly. *Female* (Fig. 236): Sides granulate; disk granulate anteriorly, granules becoming larger, scale-like medially, weakly punctatorugose along posterior margin. *Elytra.*—Striae fine, minutely punctate (×30). Interstriae convex, with variable sculpturing (×10): very finely roughened, weakly shining, to almost entirely smooth, brightly shining. *Secondary Sexual Characters.*—*Male:* Pronotum as in Figures 230, 237. *Female:* As described for species group. *Specimens Examined.*—415 males, 403 females (length 11–18 mm; width 7–11 mm).

DIAGNOSTIC REMARKS. Large males differ from other members of the group by pronotal shape; females are virtually identical to *daphnis* (the only other group member with which it can be sympatric).

DISTRIBUTION (Fig. 246; appendix).—Southwestern Mexico from northern Michoacán, southern Guanajuato, and Zacatecas westward through Jalisco and northward along the Pacific coast from Nayarit to central Sonora. (Selander and Vaurie [1962] identify the type locality as Villa Corona, 115 km WSW of the city of Durango, Durango, Mexico.) 0–1500 m. Coprophagous; common in pasturelands. Collection dates: June–December (most June–August).

COMMENTS. This species is most closely related to *daphnis.* The females of the two are virtually indistinguishable morphologically, and positive identification requires a sample including associated large males. I have chosen to maintain *furiosus* as a distinct species because of a lack of well-developed males intermediate between it and *daphnis* and because it displays less intraspecific variation than does *daphnis.*

The coloration of *furiosus* varies geographically. In Sonora, Sinaloa, Nayarit, and western Jalisco, individuals are green and often highly shining; dark blue individuals are rare. In northern Jalisco, dark blue, blue-green, and dark green individuals are common; bright green is unusual. In Michoacán, practically all specimens examined are either dark blue or blue-green. I conclude that the range of the species has most recently expanded northward and, during the expansion, green coloration has become virtually fixed. The sculpturing of the elytral interstriae also varies geographically. Along the western coast of Mexico (Nayarit, Sinaloa, and Sonora), they are commonly uniformly microrugose (×30); to the southeast, they are commonly uniformly microrugose (×30); to the southeast, they are usually smooth or roughened only along the striae, rarely completely roughened.

Phanaeus (Phanaeus) daphnis Harold

Figures 94, 95, 231, 232, 239, 242, 246

Phanaeus daphnis Harold, 1863:166

Type: Male lectotype ("Mexico"), Muséum National d'Histoire Naturelle, Paris (Arnaud, 1982a:114).

Phanaeus herbeus Bates, 1887:61, NEW SYNONYMY

Type: Male holotype ("Mexico"), British Museum (Natural History), London.

Phanaeus coerulus Bates, 1887:61, NEW SYNONYMY

Type: Male holotype ("Mexico"), British Museum (Natural History), London.

Phanaeus tricornis Olsoufieff, 1924:105, NEW SYNONYMY

Type: Male lectotype (no data), Muséum National d'Histoire Naturelle, Paris (Arnaud, 1982a:116).

Phanaeus substriolatus Balthasar, 1939:245 (Arnaud, 1982c:125)

Type: Male holotype ("Mexiko"), Národní Muzeum, Prague.

NOMENCLATURAL NOTES. Bates described *coerulus* and *herbeus* as varieties of *daphnis;* the former name is sometimes attributed to Harold (1863), who proposed no name for his variety of *daphnis.* Arnaud (1982a:116) synonymized *herbeus* (as "herbaeus") and *tricornis.*

OTHER REFERENCES: Gemminger and Harold, 1869; Bates, 1889; Nevinson, 1892a; Villada, 1901; Gillet, 1911b; Hinton, 1935; Blackwelder, 1944; Islas, 1942; Halffter and Matthews, 1966 (as *nimrod*); Barrera, 1969; Edmonds, 1972; Edmonds and Halffter, 1972, 1978; Kohlmann and Sánchez-Colón, 1984.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 94, 95).—Dorsum dark blue, blue-green, green, or yellow-green; rarely with coppery reflections on pronotum. *Head.*—Clypeal process usually rounded, sometimes triangular. *Pronotum.*—Basal fossae present; base of disk only weakly impressed in female. *Pronotal Sculpturing.*—*Male:* In large individuals, sides granulate anteriorly, granules becoming flattened posteriorly, replaced by effaced granules and punctures beneath posterolateral angles of pronotum; disk coarsely rugose, usually more densely so posteriorly. In smaller individuals, sides evenly granulate to posterior margin; disk finely granulate to granulorugose

anteriorly, punctatorugose to punctate posteriorly. *Female:* Sides granulate; disk granulate to granulorugose anteriorly, granules becoming scale-like posteriorly until replaced by progressively more punctate area near posterior margin. *Elytra:* Striae fine, minutely punctate (×30). Interstriae flat to weakly convex, sometimes completely shagreened, dull, sometimes smooth, brightly shining. *Secondary Sexual Characters.—Male:* Shape of pronotum variable, as in Figures 231, 232, 239, 242. *Female:* As described for species group. *Specimens Examined.*—314 males, 239 females (length 10–17 mm; width 6–10 mm).

DIAGNOSTIC REMARKS. The spine-like projections from the sides of the pronotal disk distinguish large males of *daphnis* from other species in the group. Females and small males, however, can be virtually impossible to separate morphologically from those of *furiosus*.

DISTRIBUTION (Fig. 246; appendix). Balsas River valley of southern Mexico from Puebla to Michoacán, extending into transitional areas along southern limit of Transverse Volcanic Range. 1000–1600 m. Coprophagous. Collection dates: June–October (most June–September).

COMMENTS. This species is the most variable of the group and, as defined here, may include several yet cryptic taxa I have been unable to distinguish. Characters usually fixed in other members of the group (elytral relief and sculpturing, shape of clypeal process, shape of posteromedian process of pronotum of large males) vary in *daphnis*. Indeed, the only consistent features of the species are ecogeographic distribution and the acute lateral processes of the male pronotum. This species, like its Balsas valley companion *demon*, ascends the southern slopes of the Transverse Volcanic Range.

The posteromedian process of the pronotum of large males varies in shape and size. In typical *daphnis* (Figs. 231, 232, 239) it is acute and considerably shorter than the lateral processes of the disk. In other individuals, it is much longer and either acute or weakly bituberculate apically (Fig. 242). These variants were called "var. *coerulus*" by Bates (1887) in reference to Harold (1863) and later accorded species status by Olsoufieff (1924) under the name *tricornis*. I consider the "tricornis" condition just one aspect of the intraspecific variation of *daphnis*. It is common in Michoacán populations and appears also in populations in Guerrero. I have not observed the "tricornis" variant in specimens collected elsewhere although Olsoufieff cites Cholala, Puebla, as the source of one of his cotypes.

Color, on the contrary, is less variable in *daphnis* than in all other members of the group except *furiosus*. Most (>95%) observed specimens are green or yellow-green. Rare individuals are dark blue ("var. *herbeus*" of Bates, 1887); rarer still are yellow-green specimens with coppery highlights on the pronotum. These rare color forms are most frequent in populations from Tuxpan, in eastern Michoacán.

Field data from Cuernavaca, Morelos, suggest that *daphnis*, unlike most *Phanaeus*, prefers equine dung (J. Blackaller, pers. comm.).

The *Triangularis* Group

DIAGNOSIS. [1] Outer margin of head not notched laterally; [2] clypeal process a transverse, rounded ridge; [3] cephalic process of female a tri-tuberculate carina in front of eyes; [4] anterolateral portions of pronotum finely granulate, more densely so in females, small males (Fig. 253); [5] basal pronotal fossae present, sometimes almost effaced; [6] disk of male pronotum (Figs. 247, 249, 251) flat, posterolateral angles not strongly rounded laterally; [7] pronotum of female (Figs. 250, 252) with narrow, medially tuberculate anteromedian transverse ridge followed by weak concavity and feeble tumosity; [8] elytral interstriae (Figs. 254, 255) conspicuously (×10) punctured, usually convex (flat in *triangularis texensis*); puncturing fine to coarse; [9] front tibiae tridentate (fourth [basal] tooth sometimes very weakly indicated in unworn specimens); [10] basal segment of female middle tarsus not widened apically; [11] longer mesotibial spur not distinctly dilated subapically; [12] Mesa Central and Sierra Madre Oriental of Mexico and southeastern United States (Fig. 256).

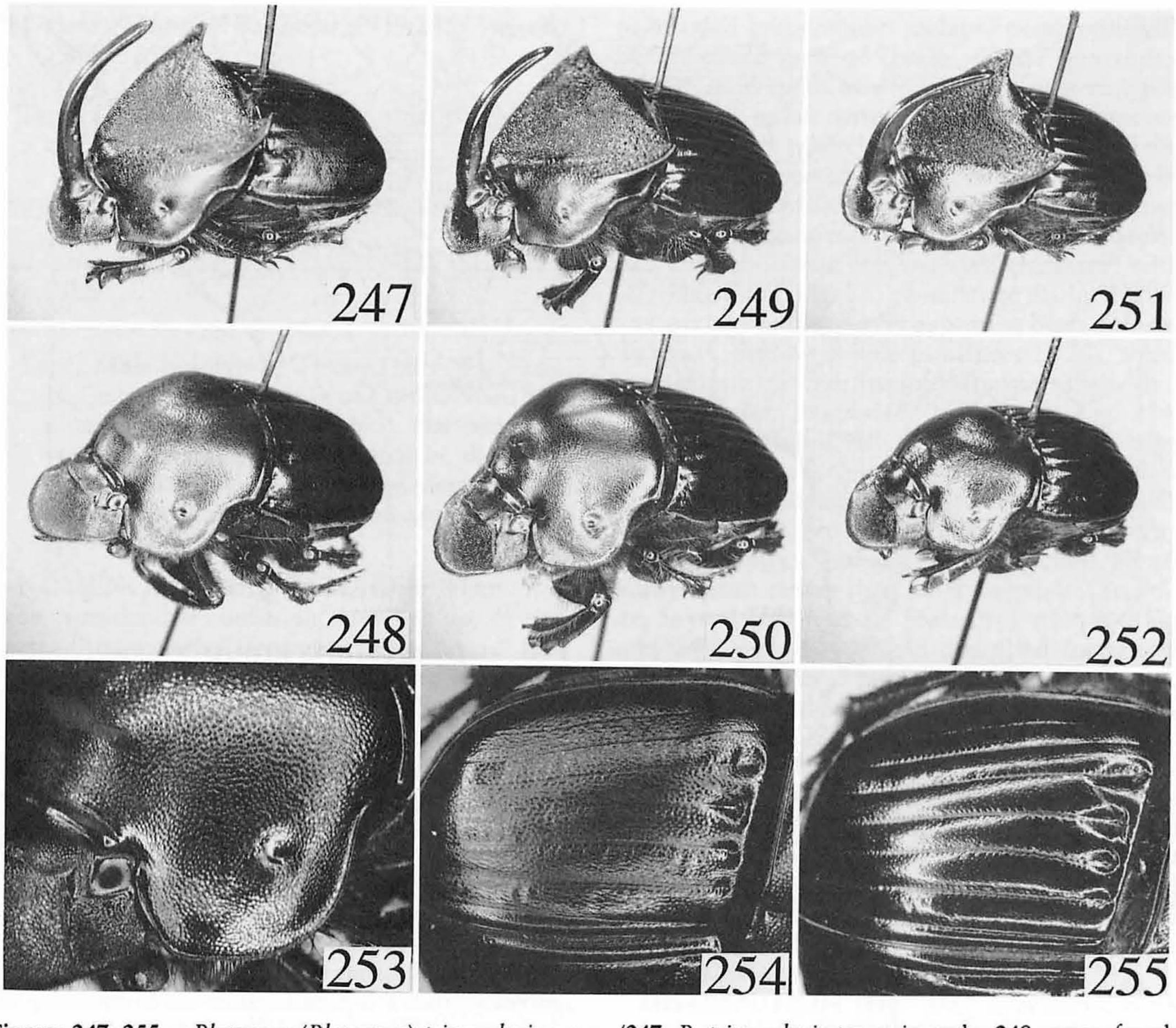
In 1972 I overlooked the close relationship between *triangularis* and *adonis*, which are brought together in this species group. The sculpturing of the elytra of *adonis* and *triangularis, sen. str.*, shape of the mesotibial spur and mesobasitarsus, secondary sexual characters, and pronotal sculpturing are the salient group characters; they suggest a closer relationship to the *hermes* group than to the *tridens* group. The case of *triangularis* is interesting in that one subspecies, *texensis*, approaches the *vindex* group in the relief and sculpturing of the elytral interstriae; it is the only taxon outside the *vindex* group that has a regular interstrial pattern of rugosity, albeit very fine.

KEY TO THE SPECIES AND SUBSPECIES OF THE *TRIANGULARIS* GROUP

1a. Dorsum uniformly dark blue, blue-green, or bright green (Figs. 63–65). Pronotum rather densely granulate anterolaterally. Mesa Central and Sierra Madre Oriental of Mexico (Fig. 256) ..... *Phanaeus* (*P.*) *adonis* Harold

b. Dorsum somber, black to weakly shining coppery red (Figs. 58–62); if weakly to strongly shining green, then elytral interstriae flat. Pronotum usually sparsely and finely granulate, more so in male. United States 2

2a. Elytral interstriae shining, distinctly convex (rarely dull, almost flat), with distinct, simple puncturing (Fig. 255); first interstria not distinctly shinier than others. Dorsum uniformly either black or muted coppery red (Figs. 58, 59). Southeastern United States from Kansas to Louisiana–Texas border eastward to Carolinas



Figures 247–255. *Phanaeus* (*Phanaeus*) *triangularis* group (**247,** *P. triangularis texensis,* male; **248,** same, female; **249,** *P. t. triangularis,* male; **250,** same, female; **251,** *P. adonis,* male; **252,** same, female; **253,** *P. triangularis texensis,* anterolateral portion female pronotum; **254,** same, dorsal view elytron; **255,** *P. t. triangularis,* dorsal view elytron).

. . . . . *Phanaeus* (*P.*) *triangularis triangularis* (Say)

b. Elytral interstriae 2–8 dull, flat, evenly and densely covered by large, shallow punctures that coalesce to form reticulate pattern of ridging (×20) (Fig. 254); first interstria convex, simply punctate, distinctly shinier than other interstriae. Dorsum uniformly black to muted coppery red, rarely dull to brightly shining green (Figs. 60–62). Texas. . . . . .
. . *Phanaeus* (*P.*) *triangularis texensis,* NEW SUBSPECIES

Phanaeus (*Phanaeus*) *adonis* Harold

Figures 63–65, 251, 252, 256

Phanaeus adonis Harold, 1863:169

Type: Male lectotype ("Mexico"), Muséum National d'Histoire Naturelle, Paris (Arnaud, 1982a:114).

OTHER REFERENCES. Harold, 1868a; Gemminer and Harold, 1869; Bates, 1887; Nevinson, 1892a; Villada, 1901; Gillet, 1911b; Olsoufieff, 1924; Blackwelder, 1944; Halffter and Matthews, 1966; Barrera, 1969; Edmonds, 1972.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 63–65).—Dorsum uniformly dark blue, blue-green, dark green, or bright yellow-green. Pronotum of male completely colored; that of female with black anteromedian carina often followed by small, transverse black spot. Pygidium colored as elytra. Venter dark with colored reflections on legs, sterna. *Pronotal Sculpturing.—Male:* In larger individuals, sides densely, finely granulorugose, rugosities becoming flatter, larger toward sides of disk, grading into coarse puncturing mixed with flat rugosities posteriorly. Disk more coarsely, evenly granulorugose, rugosities not forming appreciable ridging; texture of disk sculpturing changing (sometimes abruptly) posteriorly to dense, coarse granulorugosity followed by conspicuous smooth,

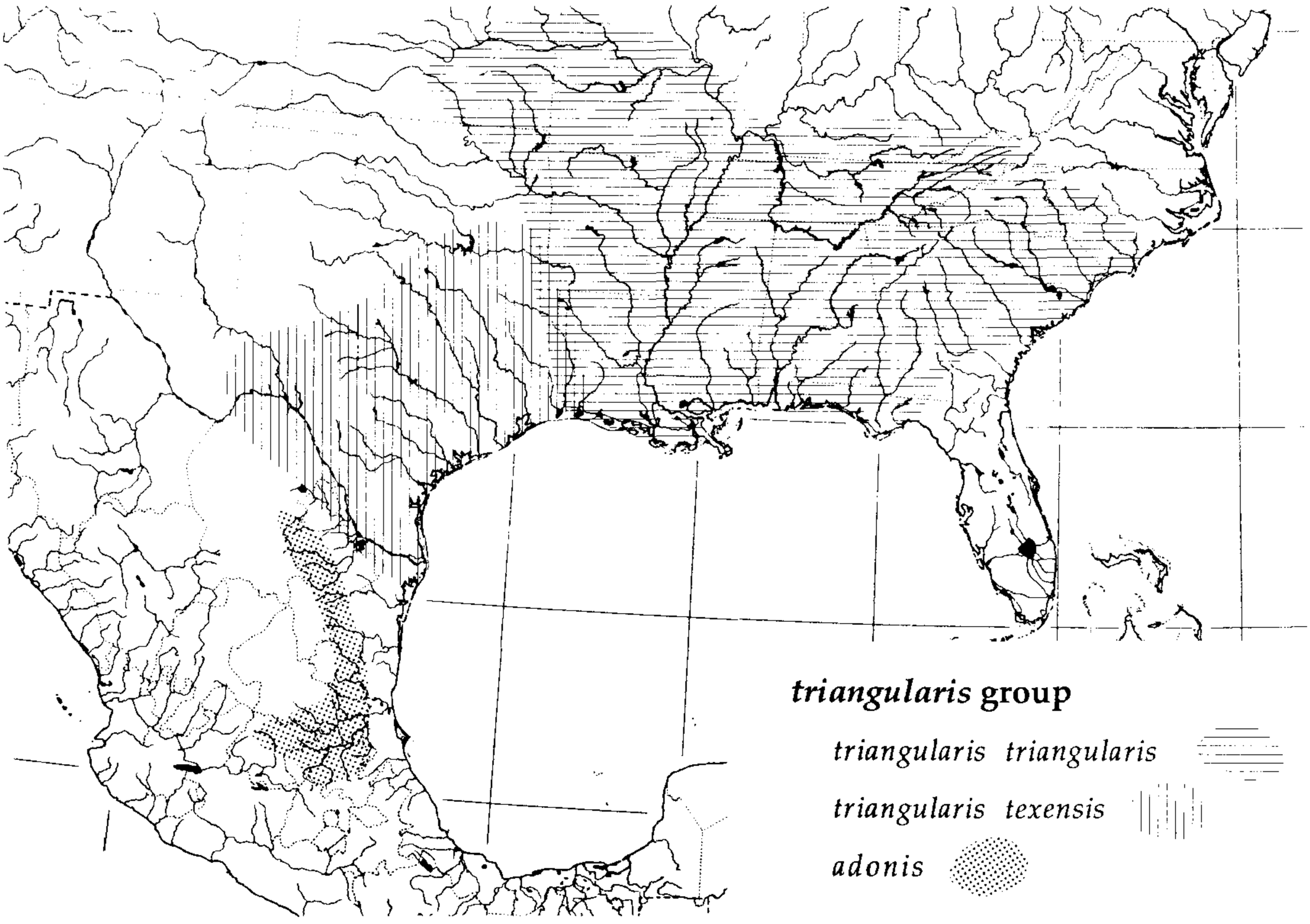


Figure 256. Distribution of the *Phanaeus* (*Phanaeus*) *triangularis* group.

punctate area. Smaller individuals as above except that remnant of flattened portion of disk finely granulorugose to almost granulate, posterior portion of disk punctatorugose medially, simply punctate laterally. *Female:* Sides as in male; rugosities becoming flat on disk, grading posteriorly first into asperate punctures followed by simple punctures near posterior margin. *Elytra.*—Striae simple to minutely punctate, shagreened (×30). Interstriae convex, shining, bearing sparse, simple puncturing (×10); sculpturing coarser, denser on interstriae 6–8. All interstriae finely roughened at least along striae, occasionally over entire surface. *Secondary Sexual Characters.—Male* (Fig. 251): Pronotal disk flat, strongly triangular. *Female* (Fig. 252): As described for species group. *Specimens Examined.*—92 males, 76 females (length 12–17 mm; width 7–11 mm).

DIAGNOSTIC REMARKS. The most obvious differences between *adonis* and *triangularis* are size, color, and distribution.

DISTRIBUTION (Fig. 256; appendix). Mid- to high-elevation open forests of the Sierra Madre Oriental from Nuevo León south to Hidalgo, and the eastern Mesa Central, Mexico. 350–2100 m. Coprophagous. Collection dates: June–September.

COMMENTS. In 1972 I overlooked the close relationship between this species and *triangularis* (see "Comments" under that species).

Phanaeus (*Phanaeus*) *triangularis* (Say)

Figures 58–62, 247–250, 253–256

Copris triangularis Say, 1823:206

Type: Male neotype ("Arkansas, Little River County, 2mi S Foreman"), Museum of Comparative Zoology (MCZ Neotype No. 32895), Harvard University, PRESENT DESIGNATION.

Phanaeus triangularis (Say), LeConte, 1847:85

Phanaeus torrens LeConte, 1847:85 (LeConte, 1854: 217)

Type: Male lectotype (no data), Museum of Comparative Zoology (MCZ Type No. 3710), Harvard University, PRESENT DESIGNATION.

Phanaeus niger Olsoufieff, 1924:95, NEW SYNONYMY

Type: Male lectotype ("Mexico"), Muséum National d'Histoire Naturelle, Paris (Arnaud, 1982a:116).

Phanaeus goidanichi Balthasar, 1939:243 (Arnaud, 1982c:125)

Type: Male holotype ("North America–?Mexico"), Národní Muzeum, Prague.

Phanaeus triangularis triangularis (Say), NEW STATUS
Phanaeus triangularis texensis, NEW SUBSPECIES

Type: Male holotype ("Texas, Dallas Co., 2mi N. Cedar Hill"), Museum of Comparative Zoology (MCZ Type No. 33405), Harvard University (314 paratypes deposited in all major collections cited in the acknowledgments; no allotype designated; label data appear in the appendix).

NOMENCLATURAL REMARKS. There has been considerable confusion attending use of the names "triangularis," "torrens," and "niger." Recent usage follows that established by Robinson (1948) based on Olsoufieff (1924). In my opinion, both misidentified "triangularis" in the sense of Say (1823) in applying the name only to certain Texas populations of this species. While Say's type material is assumed to have been destroyed, his original description of *triangularis* is clear enough to exclude these Texas populations and to include *torrens, niger,* and *goidanichi.* LeConte (1854) himself synonymized *torrens* and *triangularis.* All Texas populations examined (except those from far eastern portions of the state) comprise a distinct taxon for which, in the absence of any available name, I propose *texensis* (see "Comments," below).

OTHER REFERENCES. Lacordaire, 1856; LeConte, 1859, 1863; Gemminger and Harold, 1869; Blanchard, 1885; Nevinson, 1892a; Henshaw, 1885; Gillet, 1911b; Leng, 1920; Brown, 1927; Lindquist, 1935; Cartwright, 1939 (as *niger*); Blackwelder and Blackwelder, 1948; Loding, 1945; Lengerken, 1954; Halffter and Matthews, 1966; Fincher et al., 1969; Barrera, 1969; Edmonds, 1972; Fincher, 1973a, 1981 (as *torrens*).

DESCRIPTIVE REMARKS. *Color and Color Pattern.*—(a) *triangularis* (Figs. 58, 59): Dorsum moderately shining black ("niger") or moderately shining to dull coppery red ("torrens"); intermediates almost black with weak coppery sheen visible especially on pronotum. Pygidium venter black, sometimes with weak reddish reflections. (b) *texensis* (Figs. 60–62): Dorsum dull black or coppery red, occasionally weakly shining; rarely dull to moderately shining green with or without coppery red highlights on pronotum. Pygidium, venter black, sometimes with weak-colored reflections. *Pronotal Sculpturing.—Male:* In large individuals, sides finely granulate, granules sparse to moderately dense and becoming scale-like, forming some ridging behind lateral fossae. Disk granulate, somewhat more coarsely so than sides, appearing finely roughened to unaided eye; granules replaced posteromedially by ill-defined area of coarse, rugose puncturing. Smaller individuals as above except posterior portion of disk rather densely punctate, each puncture bearing minute tubercle anteriorly, occasionally also (especially in *texensis*) minute, shining central spot. *Female:* As in smaller male except disk more densely granulate, granules distinctly more flattened, scale-like. *Elytra.*—Striae fine, minutely punctate (×30). (a) *triangularis* (Fig. 255): Interstriae distinctly convex, evenly shining; rarely appearing both dull *and* flattened; bearing simple punctures (×20), sometimes almost effaced; first interstria not usually shinier than other interstriae. (b) *texensis* (Fig. 254): Interstriae 2–8 dull, flat, densely covered by large, flat punctures which coalesce to form reticulate, often shining ridging (×10); each puncture usually bearing minute, shining, central spot (×30). First interstria convex, rather densely punctate, almost always much shinier than other interstriae. *Secondary Sexual Characters.—Male:* Pronotum as in Figures 247, 249. *Female:* As described for species group. *Specimens Examined.—triangularis:* 163 males, 151 females; *texensis:* 171 males, 175 females (length 12–21 mm; width 7–12 mm).

DIAGNOSTIC REMARKS. This species differs from *adonis* most obviously by color and distribution; pronotal sculpturing will distinguish it from other United States species. Small individuals can resemble the dark phase of *prasinus,* from which they differ in elytral sculpturing. The new subspecies, *texensis,* differs from the nominate subspecies by elytral sculpturing.

DISTRIBUTION (Fig. 256; appendix). *triangularis*—Forested and semiforested areas of southeastern United States from eastern Kansas, Oklahoma, and Texas to near the Atlantic Coast (unknown from Florida). 0–1000 m. Coprophagous. Collection dates: April–November (mostly June–October in northern part of range). *texensis*—Forested and semiforested areas of Texas except far western and Panhandle areas. Coprophagous; preferring areas with rocky soils. Collection dates: March–October except July (apparently bivoltine).

COMMENTS. In 1972 I included *triangularis* in the "*vindex* complex" along with the present members of the *vindex* group (q.v.). This species, along with *adonis,* forms a distinct group more closely related to the *tridens* and *hermes* groups than to the other United States species.

Some recent workers (e.g., Fincher, 1973a, 1981) have considered *torrens* to be a distinct species with two subspecies, *torrens* and *niger,* and have used the name *triangularis* almost exclusively in reference to the Texas form. The nomenclatural changes proposed above may cause some confusion since *torrens* LeConte becomes a subjective junior synonym of *triangularis* Say.

The distinction between the two subspecies is clear if the elytral and pronotal sculpturing of typical individuals are compared; the variation of ely-

tral relief and sculpturing is similar to that observed in *igneus* (q.v.). Intermediates between the two subspecies occur among populations in extreme eastern Texas (Sabine and Shelby Counties) and adjacent areas of Louisiana across the Sabine River, and in Arkansas (Carroll County); moreover, most population samples of *triangularis, sen. str.*, include individuals with distinctly roughened interstriae bearing obscure puncturing. All *texensis* specimens examined, however, have a reticulate pattern of fine interstrial ridges produced by large, shallow, confluent punctures on a flat surface.

The color of *triangularis, sen. str.*, varies geographically. Specimens from the southern part of its range are shining black or nearly black with weak coppery highlights; specimens from north of about 33 degrees N latitude always have a distinct, dull coppery red cast. Observed populations of *texensis* usually include both black and dull coppery red individuals; I have seen green specimens from only three, widely separated counties (Dallas, Menard, and Harris). Regardless of color, *triangularis, sen. str.*, is almost always moderately shining while *texensis* is ordinarily dull.

Information available to me suggests that *texensis* most commonly occurs in, but is not restricted to, areas with rocky or sandy soils and patchy ground cover consisting of a mixture of clumped grasses and low trees such as mesquite and postoak. The type locality of this subspecies is an area of limestone outcroppings in southwest Dallas County, Texas, covered by a mixed oak–juniper woodland with some mesquite and patchy pasturelands. On the other hand, *triangularis, sen. str.*, appears to be a resident of moister forests and semiforested areas.

The type of *triangularis, sen. str.*, is among those specimens of the Say collection presumed lost in the 1830s. The usual practice has been to select needed neotypes for Say species from the J. L. LeConte or T. W. Harris Collection in the Museum of Comparative Zoology, Harvard University. These collections were presumably seen by Say, or compared to material in Say's collection before it was destroyed. The LeConte Collection includes 15 specimens labeled *triangularis*, of which 12 are *texensis*. None of the remaining three specimens agrees fully with Say's original description. I have chosen, therefore, a large male from modern material collected in Arkansas (Say's type locality) that agrees fully with the original description for present designation as neotype.

The *Mexicanus* Group

DIAGNOSIS. [1] Outer margin of head scarcely to strongly notched laterally (Figs. 286, 287); [2] clypeal process rounded to quadrate; [3] cephalic carina of female transverse trituberculate carina (Fig. 283) or narrow corniform process in front of eyes (Fig. 282); [4] anterolateral portions of pronotum densely granulorugose (Fig. 274); [5] basal pronotal fossae present or absent; [6] disk of male pronotum flat (Figs. 262, 263) or convex (Figs. 264, 265) (concave in *demon*, Fig. 257), posterolateral angles rounded, upturned (except *demon*); [7] pronotum of female (Figs. 273, 274) with broad, usually salient anteromedian prominence usually carinate anteriorly and flanked on each side by elongate depression extending toward eye (depressions weak in *pilatei*); [8] front tibiae tridentate (weak fourth tooth in *demon*), wider in female than male; [9] basal segment of female middle tarsus broad apically (Figs. 288, 289); [10] longer mesotibial spur dilated subapically (Fig. 289) (except in *flohri* and *scutifer*, Fig. 288), dilation stronger in female; [11] color variable (Figs. 66–85); [12] larger size, length usually exceeding 20 mm; [13] southeastern Arizona, Mexico (except northcentral and northeastern portions), Central America as far south as Costa Rica, and southern Ecuador (Fig. 290).

The *mexicanus* group comprises seven species: *flohri, mexicanus, amithaon, wagneri* (with two subspecies), *lunaris, scutifer*, and *demon*. The most conspicuous feature of the group is the form of the female pronotum—an anteromedian prominence flanked by trough-like depressions that descend toward the eyes. For reasons discussed fully below, *lunaris* and *flohri* are taxonomic isolates in the group.

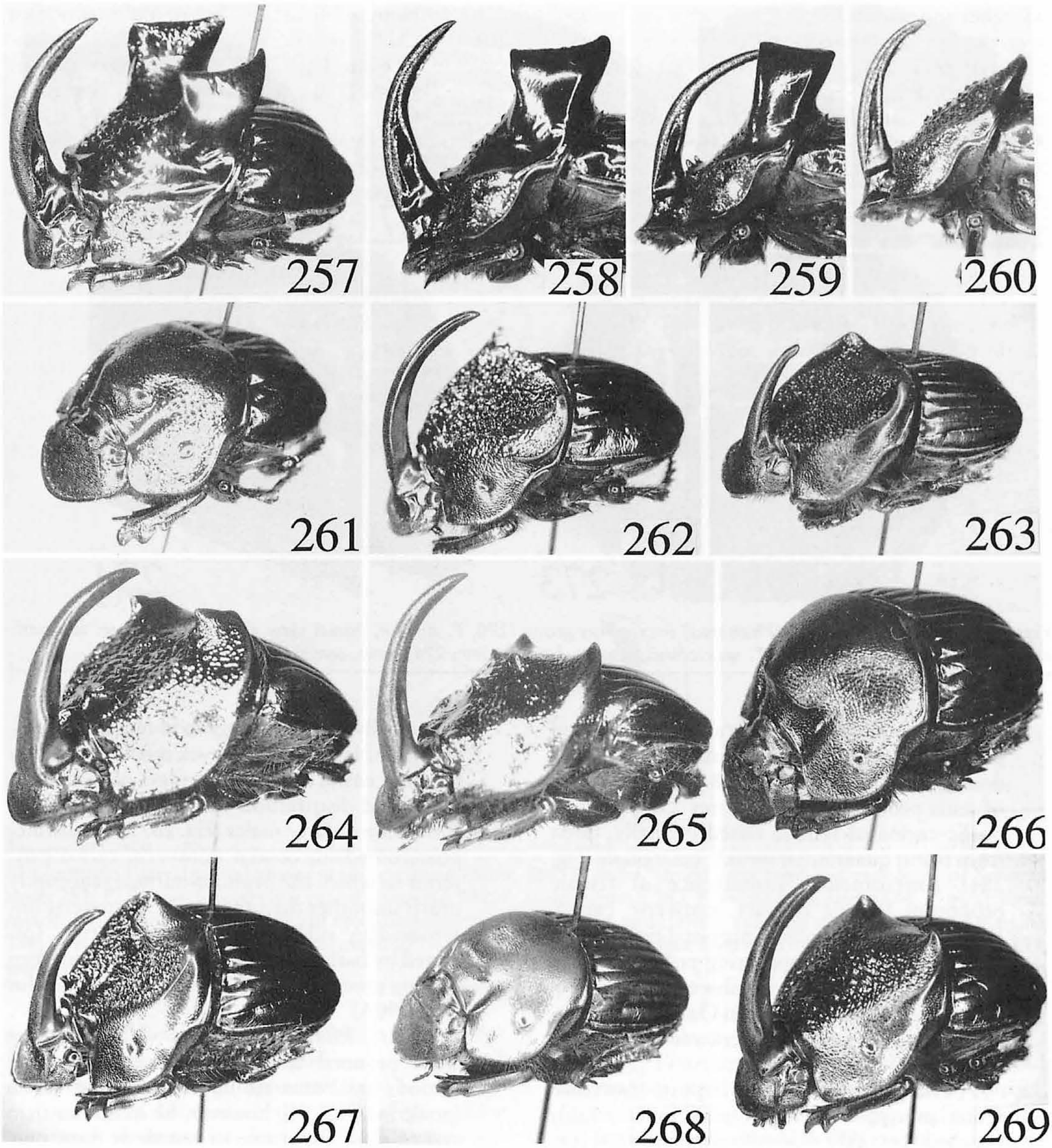
The taxonomic and geographic picture of the *mexicanus* group is very similar to that of the *tridens* group and suggests a common history. In both groups, females and small males are similar and often indistinguishable morphologically; moreover, the distribution patterns are such that, except for *lunaris* (which occurs in Ecuador), each species is paired ecogeographically with a member of the other group (although not on a strictly one-to-one, nor a completely sympatric, basis) as follows:

- *mexicanus* with *daphnis* or *nimrod*
- *amithaon* with *furiosus* or *tridens tridens*
- *scutifer* with *tridens tridens*
- *demon* with *tridens pseudofurcosus, daphnis*, or *nimrod*
- *wagneri wagneri* with *eximius*

The intragroup relationships here present an interesting picture. Three species, *amithaon, mexicanus*, and *wagneri*, form a subgroup whose distribution depicts linear differentiation (Fig. 290). The close morphological similarity of females and small males of these species suggests recent divergence. Of the remaining species, *demon* and *scutifer* form a species pair, while *lunaris* and *flohri* are taxonomic isolates.

KEY TO THE SPECIES AND SUBSPECIES OF THE *MEXICANUS* GROUP

1a. Elytral interstriae (Fig. 272) smooth, shining medially, dulled laterally by shagreening that extends into striae; interstriae uniformly dull

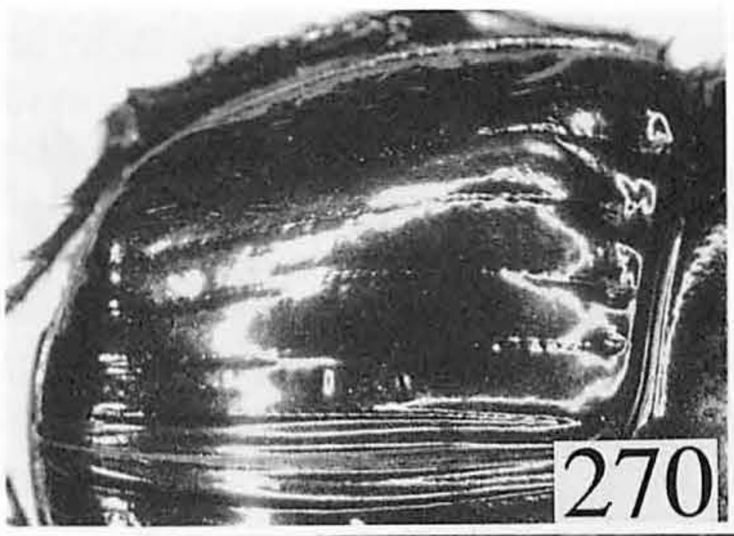


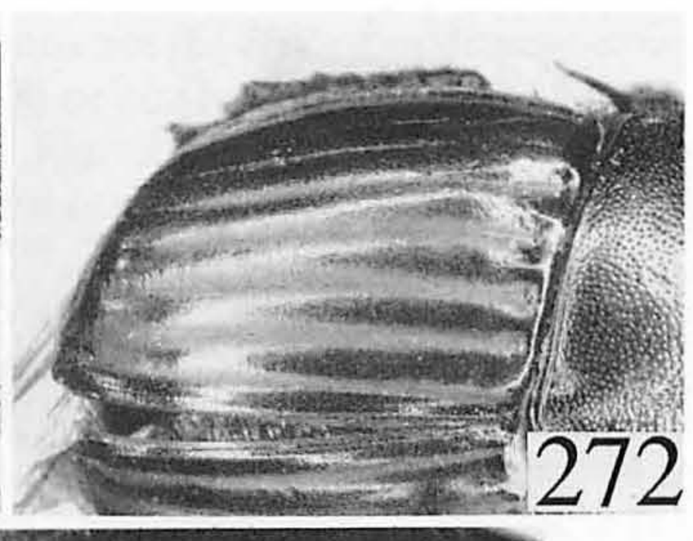
Figures 257–269. *Phanaeus* (*Phanaeus*) *mexicanus* group (**257,** *P. demon,* male; **258,** same; **259,** same {"excelsus"}; **260,** same ["mirabilis"]; **261,** same, female; **262,** *P. scutifer,* male; **263,** *P. flohri,* male; **264,** *P. amithaon,* male; **265,** *P. mexicanus,* male; **266,** same, female; **267,** *P. lunaris,* male; **268,** same, female; **269,** *P. w. wagneri,* male).

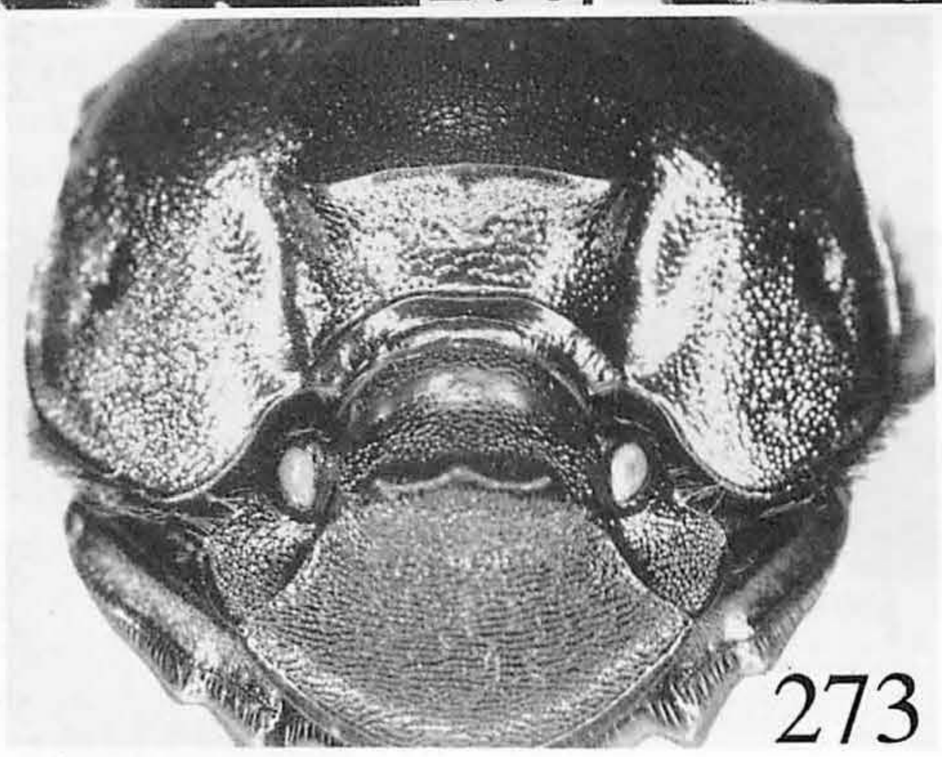
in highly worn specimens). Sides of pronotum densely, coarsely punctatorugose around, behind lateral fossae. Pronotal disk of large males (Fig. 263) flat, posterolateral angles strongly rounded, entire disk (seen from above) almost heart-shaped. Longer mesotibial spur not dilated subapically (as in Fig. 288). Clypeal process usually almost quadrate. Dark blue-black (Fig. 66); sometimes weakly shining green. Known from isolated localities in Veracruz, Guerrero, Morelos, Puebla Jalisco, Sonora (Fig. 290B) . . . . . *Phanaeus* (*P.*) *flohri* Nevinson

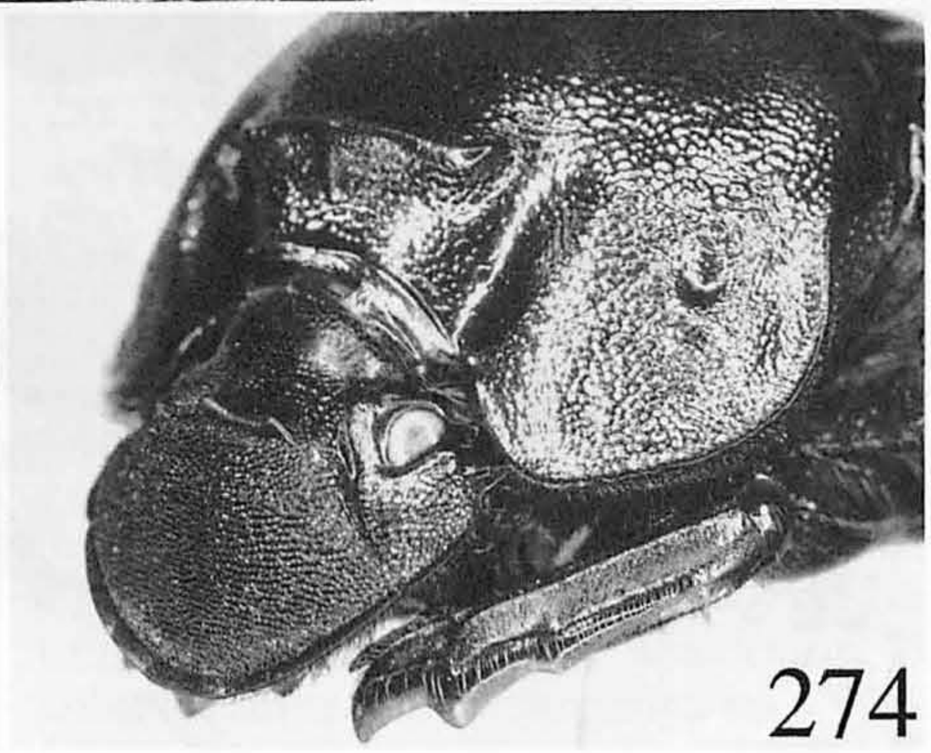
b. Elytral interstriae evenly shining (or dulled by severe wear); shagreening, if any, restricted to striae. Sides of pronotum granulorugose around and at least some distance behind lateral fossae. Male pronotum variable. Longer metatibial spur dilated subapically (except *scutifer*), especially in female. Other characters variable 2

2a. Outer margin of head deeply notched between clypeus, paraocular areas (Fig. 286, arrow), notch usually more-or-less right-angled such that paraocular area appears to project laterally beyond margin of clypeus. Raised outer margin









Figures 270–274. *Phanaeus* (*Phanaeus*) *mexicanus* group (**270,** *P. demon,* dorsal view elytron; **271,** *P. w. wagneri,* same; **272,** *P. flohri,* same; **273,** *P. mexicanus,* female, frontal view; **274,** same, anterolateral view).

of mesocoxal cavity always abruptly widened posteriorly resulting in posterior width about double anterior width (Fig. 285, arrow). Shape of male pronotum as in Figures 257–260. Cephalic carina of female raised medially, (seen from front) quadrate or weakly emarginate (Fig. 281). Anteromedian prominence of female pronotum lacking distinct transverse carina. Dorsal surface, especially pronotal disk and elytra, highly shining, appearing polished; color variable (Figs. 69–73). Southwestern Mexico, Balsas River valley, southern Oaxaca, Chiapas, Pacific coast of Central America to central Costa Rica (Fig. 290B) . . . . . *Phanaeus* (*P.*) *demon* Laporte-Castelnau

b. Outer margin of head at most only weakly notched (Fig. 287). Raised outer margin of mesocoxa not usually widened posteriorly (Fig. 284). Male pronotum not as above; disk flattened or convex medially. Female cephalic carina either trituberculate carina or narrow, bituberculate process (Fig. 282). Anteromedian pronotal prominence usually with distinct transverse carina. Other characters variable 3

3a. Cephalic process of female narrow, almost conical bituberculate projection (Fig. 282). Longer of mesotibial spurs not usually distinctly dilated subapically. Pronotal disk of large males flattened dorsally (Fig. 262). Dorsum green to yellow-green, rarely coppery (Figs. 77, 78). Coastal lowlands of central Veracruz (Fig. 290B) . . . . . *Phanaeus* (*P.*) *scutifer* Bates

b. Cephalic process of female trituberculate carina. Longer mesotibial spur distinctly dilated subapically, more strongly so in female. Pronotal disk of large males convex medially, usually bearing central tubercles or ridges of some sort. Color and distribution variable 4

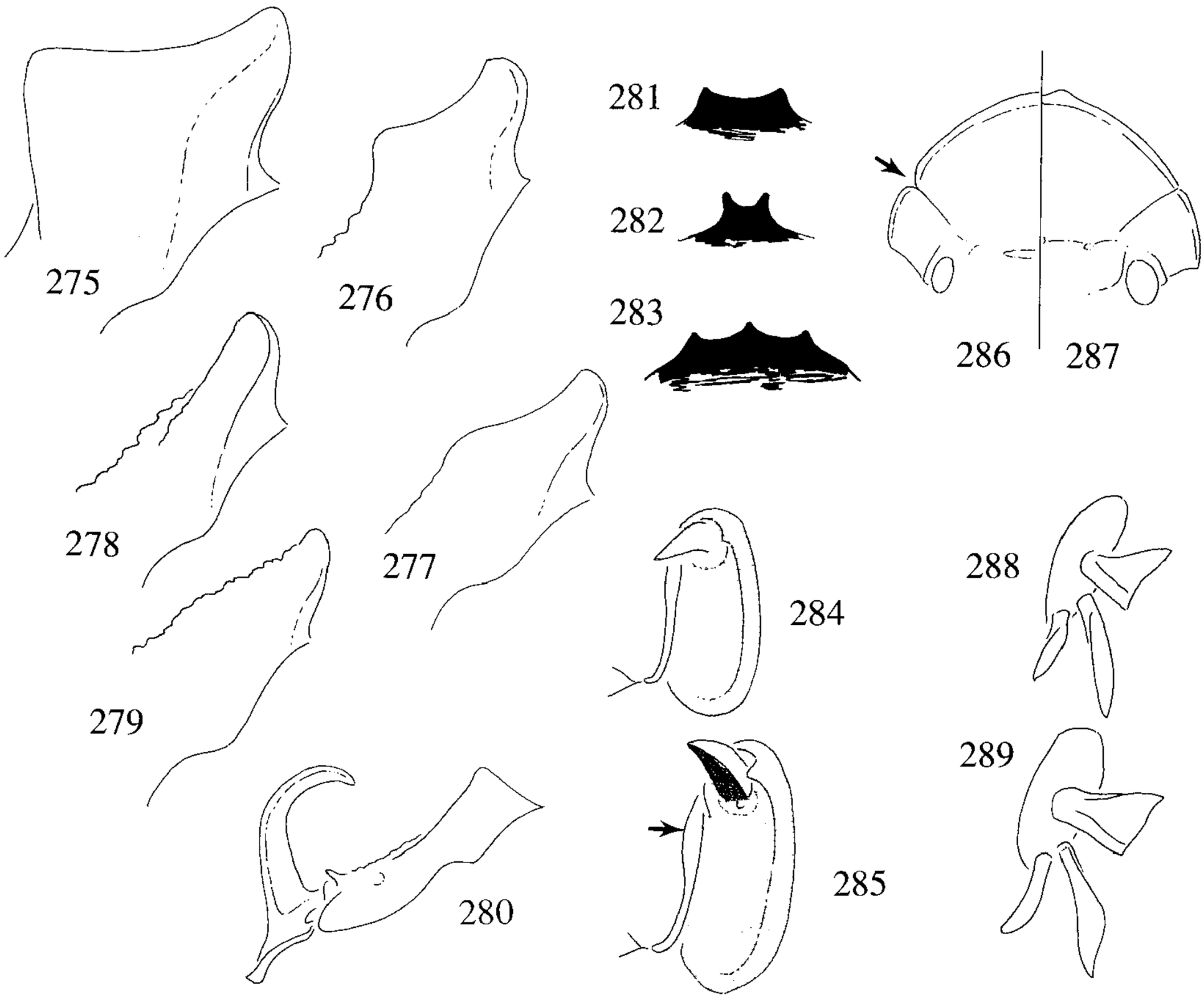
4a. Pronotum of large males (Fig. 267) with distinct posteromedian, bowed transverse carina posterior to which the pronotal surface is abruptly much smoother than anteriorly. Transverse anteromedian ridge of female pronotum followed by fairly deep, transverse concavity. Deep shining green. Western and southern Ecuador (Fig. 290A) . . . . . *Phanaeus* (*P.*) *lunaris* Taschenberg

b. Male pronotal disk lacking any well-defined smooth basal area set off by transverse carina (posterior area can, however, be smoother than rest of disk). Pronotum of female at most only weakly concave behind anteromedian carina. Color variable. Central America and Mexico 5

(*Note:* The following taxa can be difficult or impossible to separate if reliable locality data are not available. Females and smaller males are indistinguishable morphologically.)

5a. Basal pronotal fossae distinct in female and usually also in male; occasionally small, punctiform, rarely lacking in male. Disk of male pronotum usually flat. Southern Mexico to Costa Rica (Fig. 290A) . . . . . *Phanaeus* (*P.*) *wagneri* Harold 6

b. Basal pronotal fossae usually absent, represented at most by small, punctiform pits. Disk of male pronotum usually either weakly con-



Figures 275–289. *Phanaeus (Phanaeus) mexicanus* group (**275–279,** *P. demon,* variation in shape of posterior portion of pronotum [lateral views] among well-developed males; **280,** *P. flohri,* lateral view head and pronotum of Sonoran male; **281,** *P. demon,* frontal view cephalic process; **282,** *P. scutifer,* same; **283,** *P. mexicanus,* same; **284,** *P. mexicanus,* mesocoxa [crosshatched] and edge of coxal depression; **285,** *P. demon,* same [arrow indicates widening of raised margin]; **286,** dorsal view head, *P. demon;* **287,** same, *P. mexicanus;* **288,** tip of female mesotibia and basitarsus, *P. flohri;* **289,** same, *P. mexicanus*).

vex or concave. Southern Mexico west to Pacific coast, north to Arizona 7

6a. Pronotum with conspicuous basal fossae separated by distance usually no more than three times diameter of single fossa. Elongate anterolateral concavities of female pronotum weak. Pronotum of large males with transverse, almost ridge-like tumosity between center, posterior margin of disk. Dark green-blue, blue-green, or green (Figs. 75, 76). Yucatán Peninsula south to northern Chiapas and Guatemala (Fig. 290A) ..... *Phanaeus (P.) wagneri pilatei* Harold

b. Pronotum with small basal fossae separated by distance greater than three times diameter of single fossa; sometimes lacking in male. Anterolateral concavities of female pronotum conspicuous. Pronotal disk of large males lacking transverse tumosity, often with distinct smooth area adjacent to middle of posterior margin. Usually coppery red (Fig. 74); occasionally green, yellow-green, or dark blue. Guatemala to Costa Rica (Fig. 290A) ..... *Phanaeus (P.) wagneri wagneri* Harold

7a. Pronotal disk of large males (Fig. 265) convex, bearing central triad of conspicuous tubercles, posterior two of which may be fused as single ridge. Balsas River valley, central Oaxaca, Los Tuxtlas region of Veracruz ..... *Phanaeus (P.) mexicanus* Harold

b. Pronotal disk of large males (Fig. 264) slightly concave, lacking central tubercles. Central Mesa of Mexico from Tlaxcala to Jalisco, northward along Pacific coast to southern Sonora, interior of Sonora north into southern Arizona and New Mexico ..... *Phanaeus (P.) amithaon* Harold

Phanaeus (Phanaeus) flohri Nevinson

Figures 66, 263, 272, 280, 290B

Phanaeus flohri Nevinson, 1892b:33

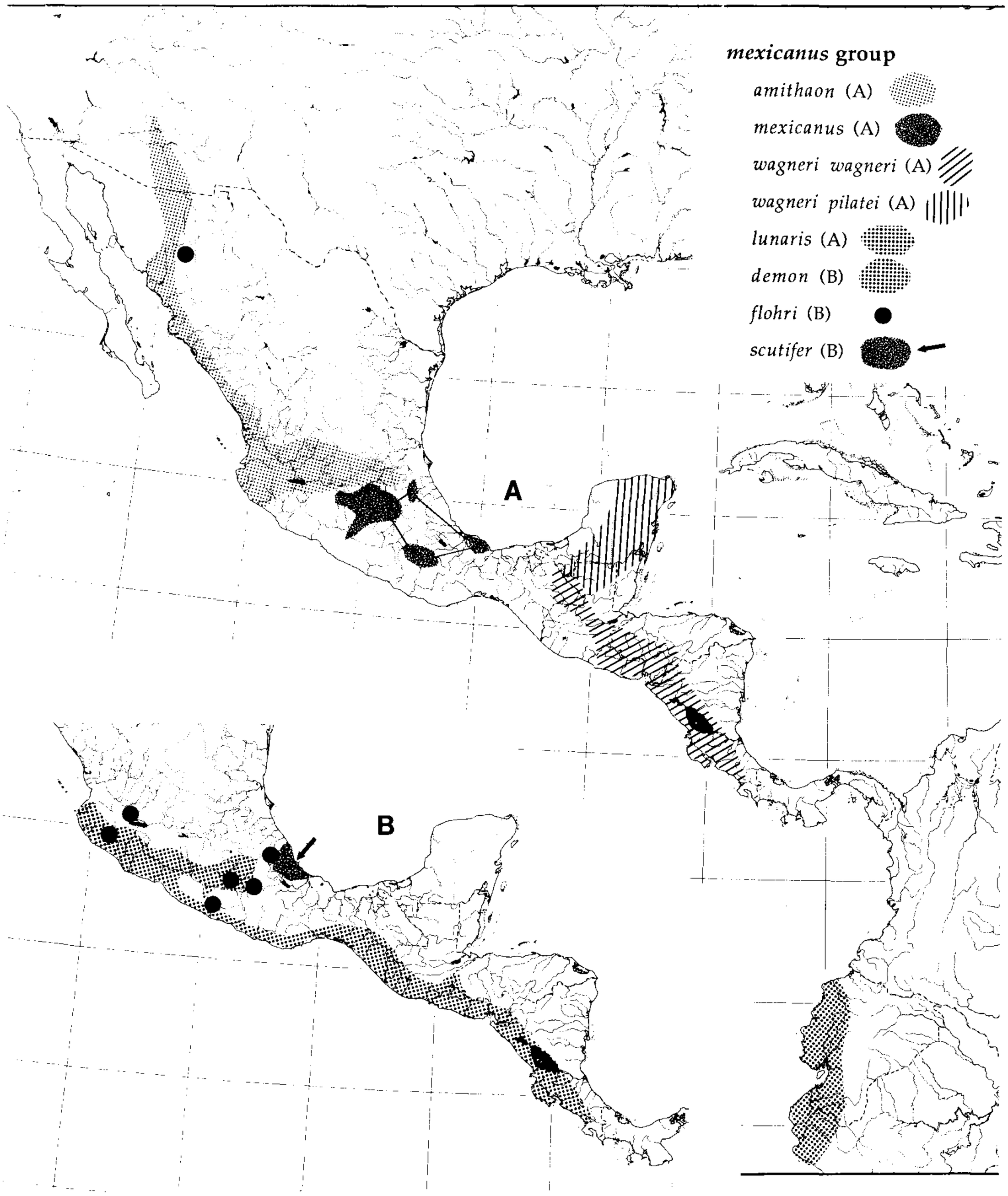


Figure 290. Distribution of the *Phanaeus* (*Phanaeus*) *mexicanus* group (letters following species name indicates map).

Type: Male lectotype ("Jalapa"), Muséum National d'Histoire Naturelle, Paris (Arnaud, 1982a:116).

OTHER REFERENCES. Nevinson, 1892a; Gillet, 1911b; Olsoufieff, 1924; Blackwelder, 1944; Edmonds, 1972.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Fig. 66).—Dorsum dark, weakly shining blue, often almost black, occasionally weakly shining green. Coloration on pronotum restricted largely to anterolateral areas, to disk of male, to midlongitudinal depression of disk of female. Elytra with weak bluish cast. *Head.*—Clypeal process almost quadrate. Outer margin not notched. *Pronotal Sculpturing.—Male:* In large individuals, sides granulorugose anteriorly, punctatorugose around, behind lateral fossae; sculpturing grading posteriorly

to simple puncturing beneath posterolateral prominences of disk. Disk rather finely, sparsely granulorugose, becoming punctate on raised, smooth, posterior transverse area extending between posterolateral prominences. Smaller individuals with posterior two-thirds of pronotum rather coarsely, densely punctate to punctatorugose; granulorugose areas restricted to anterolateral portions of pronotum, small, round, concave remnant of disk near anterior margin. *Female:* As in smaller males except puncturing on posterior portion of disk weaker, usually sparser, sometimes becoming almost effaced near posterior margin. *Pronotum.*—Basal fossae present in both sexes, although sometimes only weakly indicated. *Mesotibiae.*—Longer spur not dilated subapically (Fig. 288). *Elytra* (Fig. 272).—Striae simple, impressed. Interstriae subconvex, smooth, brightly shining medially, dulled laterally by shagreening such that each interstria appears broadly polished midlongitudinally (interstriae uniformly dull in highly worn specimens). *Secondary Sexual Characters.—Male:* Pronotum as in Figure 263; disk of large individuals flat, seen from above almost heart-shaped; raised posterior area impressed midlongitudinally. *Female:* Cephalic carina trituberculate, in front of eyes; pronotal prominence carinate anteriorly in large individuals. *Specimens Examined.*—17 males, 10 females (length 16–20 mm; width 9–12 mm).

DIAGNOSTIC REMARKS. This species differs from other members of the group by the following combination of characters: microsculpture of elytral interstriae, shape of longer mesotibial spur, shape of clypeal process, shape of large male pronotum, and sculpturing of sides of pronotum.

DISTRIBUTION (Fig. 290B; appendix). Known only from isolated localities in the Mexican states of Guerrero, Mexico, Jalisco, Puebla, Sonora, and Veracruz. 600–1800 m. Habits unknown. Collection dates: June–October.

COMMENTS. Except for one series, I have seen only a few specimens of this interesting species collected from scattered localities. The series in question numbers 16 individuals collected by Leonardo Delgado-Castillo and Julian Blackaller in the vicinity of Acahuizotla, Guerrero, 650–1400 m, in the Sierra Madre del Sur (see Delgado-Castillo, 1989). Most of the series was collected from traps baited with feces or carrion placed in protected areas covered by very large rocks where exposed soil is restricted to cracks and crevices populated by scrubby vegetation—the kind of habitat attractive to burrowing animals. That this species has been collected almost exclusively under such unusual conditions may very well portend that *flohri* will be the first *Phanaeus* shown to be an inquiline in mammal nests.

Four large, unusual males are known from the three Sonoran localities listed in the appendix. These specimens, collected and very kindly brought to my attention by Scott McCleve, are tentatively assigned to *flohri* pending discovery of associated females. They differ from other male *flohri* I have seen in two striking respects: the cephalic horn is strongly curved and almost hook-shaped (Fig. 280), and the pronotum (seen laterally, Fig. 280) is distinctly shallower and (seen from above) wider anteriorly than posteriorly. Otherwise, these specimens display the salient features of this species given above. This population could later prove to be a distinct taxon.

The general facies of this species is reminiscent of the *hermes* group, particularly the black phase of *prasinus* ("lugens"). It occupies an isolated taxonomic position within the *mexicanus* group (see "Diagnostic Remarks"). The rather extensive punctation of the sides of the pronotum behind the lateral fossae is observable elsewhere in the subgenus only in the *hermes* group, with which *flohri* also shares narrow mesotibial spurs. While in many respects *flohri* can be regarded as an annectant between the *hermes* and *mexicanus* groups, the shape of the female pronotum clearly places it in the latter.

Phanaeus (*Phanaeus*) *demon* Laporte-Castelnau

Figures 69–73, 257–261, 270, 275–279, 281, 285, 286, 290B

Phanaeus demon Laporte-Castelnau, 1840:81

Type: Male neotype ("Mexico: Michoacan, La Huacana"), Castelnau Collection, University of Victoria, Melbourne, PRESENT DESIGNATION.

Phanaeus pegasus Sturm, 1843:331 (Harold, 1863: 169, as "damon")

Type: Unknown to me.

Phanaeus obliquans Bates, 1889:389 (new name for *mirabilis* Bates, 1887:65, junior primary homonym of *P. mirabilis* Harold 1877:98), NEW SYNONYMY

Type: Male lectotype ("Mazatlan, Mexico, Sallé, B.C.A. p.65 sp.31, sp. figured"), British Museum (Natural History), London, PRESENT DESIGNATION.

Phanaeus excelsus Bates, 1889:389, NEW SYNONYMY

Type: Male lectotype ("Chontales, Nicaragua, Janson, B.C.A. p.389 sp.32, sp. figured"), British Museum (Natural History), London, PRESENT DESIGNATION.

NOMENCLATURAL REMARKS. The name *demon* often appears incorrectly as "damon" in collections and in the literature. At the time Bates described *mirabilis,* the name was preoccupied by Harold's species. Bates corrected his error by renaming his species *obliquans.* Harold's taxon was

moved to *Taurocopris* (now *Diabroctis*) by Olsoufieff (1924), where it remains. Because Bates' *mirabilis* is a primary junior homonym and permanently unavailable, the valid name of his species is *obliquans*.

OTHER REFERENCES. Imhoff, 1856 (as *pegasus*); Lacordaire, 1856; Nevinson, 1892a; Villada, 1901; Gillet, 1911b; Olsoufieff, 1924; Paulian, 1935; Blackwelder, 1944; Islas, 1942; Halffter and Matthews, 1966; Barrera, 1969; Edmonds, 1972.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 69–73).—Dorsum variable, but always highly shining except in highly worn specimens. Color varies geographically as follows: Mexico from Isthmus of Tehuantepec westward, usually clear, brilliant green, often with yellow reflections, to golden green except for anterior portion of clypeus, tips of male pronotal prominences, areas of variable size on female pronotal disk which are black. Populations in southern Puebla (occasional specimens from other localities) often include individuals of brilliant copper-red color with green reflections. From Chiapas eastward into Central America, color varies from dark green through silver-green, yellow-green to silver-blue, or dark violet-blue except for those black areas noted above. In all populations, disk of female pronotum may be nearly covered by irregularly shaped black area, or marked by anteromedian black spot, two smaller posterolateral ones. Pygidium, venter shining, with areas on sterna, femora colored like dorsum. *Head.*—Outer margin, at junction of clypeus, paraocular areas (Fig. 286, arrow), with distinct notch resulting from lateral expansion of paraocular areas, lateral margin of which can be almost straight; notch larger, more distinct in larger individuals, especially males. Underside of posterior portion of paraocular area of males with deep, semicircular concavity (more prominent in larger specimens). *Prothorax.*—Underside of anterior angles with distinct, round concavity (more prominent in females), beneath which rounded tooth extends beneath paraocular area of head. Pronotum lacking basal fossae. Sides of pronotum (seen from above) rounded in females, small males, distinctly bowed in large males between prominent anterolateral, lateral angles. *Pronotal Sculpturing.—Larger males:* densely granulorugose laterally; disk with large transverse rugosities except posteromedially and on pronotal horns where smooth. *Smaller males, females:* Densely granulorugose except posteriorly where smooth to weakly punctate; rugosities finer, denser anterolaterally. *Front Tibiae.*—Quadridentate in both sexes; basal tooth small, often worn away. *Metasternum.*—Raised outer margin of mesocoxal depression (Fig. 285, arrow) almost always more-or-less abruptly widened posteriorly such that posterior width almost double anterior width. *Mesotarsus.*—Basal segment in female broadly triangular, width at apex about equal length. *Elytra* (Fig. 270).—Striae fine, sometimes minutely punctured (×10); striae 5–7 fainter than 1–4; striae 2–5 impressed basally. Interstriae 5–6 distinctly flatter than 2–4. Elytral suture sometimes bearing exposed row of erect, black setae than can be brush-like. *Secondary Sexual Characters.—Male:* In larger specimens, pronotum with posterolateral angles varying in shape (as seen laterally) from recumbent conical processes ("obliquans," Figs. 260, 279) to erect, massive quadrate processes ("demon"/"excelsus," Figs. 257–259). *Female:* Cephalic carina (Fig. 281) isolated, raised, seen from front more-or-less quadrate. Anteromedian prominence of pronotum lacking transverse carina bordering anterior margin. *Specimens Examined.*—737 males, 562 females (length 10–21 mm; width 7–14 mm).

DIAGNOSTIC REMARKS. The shape of the head margin, brilliant coloration, and secondary sexual features make this is a distinctive species not easily confused with other members of the group or genus.

DISTRIBUTION (Fig. 290B; appendix). Pacific coastal areas of Mexico and Central America from southern Sinaloa to northern Costa Rica. Coprophagous. Semidesert scrub and open deciduous forests south of major mountain systems. 0–1900 m. Collection dates: April–November (most June–August).

COMMENTS. *Phanaeus demon* is a highly variable species which, as here defined, includes two variants heretofore regarded as separate species: *obliquans* and *excelsus*. As discussed below, these forms are best regarded as extremes in the variation of a single, widely distributed polymorphic species.

The most striking aspects of the variation of *demon* are in color, fringing of the elytral suture, and shape of the pronotum of large males. Of these, only the latter varies in a way suggestive of subspeciation. Through most of the range of the species, the projections from the pronotum of large males are massive, vertical processes that widen apically (Figs. 257, 258, 275). In southwestern Mexico populations (Colima, Jalisco, Nayarit, and Sinaloa), these projections are attenuated anteriorly to various degrees and appear in profile as narrow, posteriorly inclined processes (Figs. 276–279). In Central America, the projections are narrower, more erect, and more parallel-sided (Fig. 259); their shape, along with a pair of long, acute denticles near the anterior pronotal margin lacking in Mexican populations, give the pronotum a markedly different shape. The pronotal shape of females and small males is essentially the same throughout the range.

The most frequent coloration of *demon* is brilliant green usually combined with yellow reflections (Figs. 69, 70, 72). Two color variants are noteworthy. Populations in southern Puebla show high frequencies of coppery green and coppery red individuals (Fig. 71); reddish individuals are rare in populations from Morelos and Guerrero. In Central America, populations often include silver-blue (Fig. 73) or dark blue specimens, although light silver-green individuals are not uncommon. The "greens" of populations from Chiapas and Central

America tend to be less brilliant and darker than those from the remainder of Mexico.

Most populations of this species lack a conspicuous fringe of setae projecting from the elytral suture. A weak fringe is common in populations from El Salvador and Nicaragua. Populations from Michoacán and southwestern Mexico (state), however, have a prominent, brush-like fringe.

Other than the shape of the pronotum of large males, I have discovered no consistent characters which would support formal recognition of subspecies of *demon*. The distribution of the species appears to be continuous from southwestern Mexico to Costa Rica, but two intermediate areas need to be better sampled before ruling out distributional gaps: the coasts of Oaxaca and southern Guatemala. The occurrence of *demon* in Guanajuato, although not completely unreasonable, needs confirmation. This is a common species apparently restricted to regions with hot, wet summers and warm, dry winters.

The original type material of *demon* is unknown to me. There is no specimen assignable to *demon* in the Castelnau Collection at the Victoria Museum in Melbourne, nor is there any record to suggest that one existed. The neotype designated here agrees with Laporte-Castelnau's original description in all respects except that the pronotum lacks any trace of pinkish or reddish reflections ("corselet rugueux").

Phanaeus (Phanaeus) scutifer Bates

Figures 77, 78, 262, 282, 290B

Phanaeus scutifer Bates, 1887:60

Type: Male lectotype ("Misantla, Mexico, Hoege, B.C.A. p.60 sp.14, sp. figured"), British Museum (Natural History), London, PRESENT DESIGNATION.

OTHER REFERENCES. Bates, 1889; Nevinson, 1892a; Gillet, 1911b; Olsoufieff, 1924; Blackwelder, 1944; Edmonds, 1972.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 77, 78).—Dorsum dark, highly shining green, often with yellowish (rarely coppery) highlights on pronotum. Pygidium green to yellow-green. Venter with green reflections on sterna, legs. *Head.*—Outer margin with distinct notch at junction of clypeus, paraocular area (as in Fig. 286). *Pronotum.*—Basal fossae absent or reduced to small punctures; present more often in females. *Pronotal Sculpturing.—Male:* In large individuals, disk coarsely, but not densely granulorugose except along posterior margin where smoother, rather finely punctate to punctatorugose; smoother basal area longest medially, strongly shortened laterally; sides densely granulorugose. Smaller individuals as above except smoother basal area less well demarcated, more clearly punctate, disk rugosities finer. *Females:* Sides densely granulorugose, disk coarsely granulorugose to punctatorugose except posteriorly where punctate. *Mesotarsus.*—Basal segment widened in female. *Metatibia.*—Longer spur not dilated subapically. *Secondary Sexual Characters.—Male* (Fig. 262): Pronotal disk flat, with small acute tubercle near middle of anterior margin; posterolateral angles of disk rounded laterally, upturned in larger individuals, reduced to rounded ridges near middle of disk in smaller individuals. *Females:* Cephalic process an apically bituberculate, conical process (Fig. 282) set forward of imaginary line connecting eyes; anteromedian process of pronotum distinctly carinate anteriorly. *Specimens Examined.*—45 males, 38 females (length 15–20 mm; width 9–13 mm).

DIAGNOSTIC REMARKS. The conical cephalic process is unique to females of the *mexicanus* group. Large males differ from those of other species in the group by having a flat pronotal disk with a distinct, raised basal area along the posterior margin.

DISTRIBUTION (Fig. 290B; appendix). Tropical lowlands of central Veracruz, Mexico. Coprophagous. 0–1000 m. Collection dates: June–July.

COMMENTS. I erroneously considered this species to be a close relative of the *amethystinus* group in 1972 because of the similarity in structure of the pronotum of large males (flattened with a smooth, raised basal area). The female, unknown to me then, as well as distinct similarities to *demon* (characteristic luster, notching of head margin) place *scutifer* in the *mexicanus* group.

I have seen two long series (20+ specimens) of *scutifer,* one from Conejos (between the cities of Jalapa and Veracruz), the other from Palma Sola (on the coast north of Cardel), in addition to individuals from scattered localities in central Veracruz. The Palma Sola population is unusual in that, despite several years of intensive collection in the area, no large, well-developed males have been found.

Phanaeus (Phanaeus) lunaris Taschenberg

Figures 67, 68, 267, 268, 290A

Phanaeus lunaris Taschenberg, 1870:183

Type: Unknown to me.

Phanaeus charon Harold, 1880a:151 (Gillet, 1911a: 319)

Type: Unknown to me.

OTHER REFERENCES. Nevinson, 1892a; Ohaus, 1909; Gillet, 1911b; Olsoufieff, 1924; Blackwelder, 1944; Lengerken, 1954; Vulcano and Pereira, 1967; Edmonds, 1972.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 67, 68).—Dorsum dark, usually moderately shining green; occasionally with yellowish reflections that result in a dark bronze sheen. Pygidium green. Venter black with green reflections

on legs, sterna. *Head.*—Outer margin with shallow notches separating clypeus from paraocular areas. *Pronotal Sculpturing.—Male:* In large individuals, sides densely granulorugose except adjacent to eyes where almost smooth, punctate beneath posterolateral angles of disk; disk coarsely rugose, rugosities forming strong transverse ridges; posteromedially, disk abruptly smoother, with asperate punctures that can coalesce as fine ridges; smoother posterior portion separated from remainder of disk by anteriorly bowed, transverse carina. Smaller individuals as above except rugose area of disk reduced, not separated from smoother posterior area by transverse carina. *Female:* Disk, behind anteromedian ridge, with flattened scale-like granules that become progressively weaker posteriorly until replaced by asperate punctures in concave posteromedian area; sides as in male. *Pronotum:*—Basal fossae punctiform. *Mesotibia.*—Longer spur dilated subapically, more weakly so in male. *Elytra.*—Striae minutely punctate (×30), distinctly duller than interstriae. Interstriae convex, minutely, sparsely punctured (×30), appearing lacquered, distinctly shinier than striae. *Secondary Sexual Characters.—Male:* Pronotum as in Figure 267; disk with smooth posteromedian area separated from remainder of disk by transverse ridge. *Female* (Fig. 268): Cephalic carina strongly tridentate, set in front of eyes. Anteromedian ridge of pronotum followed by tranverse concavity. *Specimens Examined.*—64 males, 49 females (length 16–25 mm; width 10–15 mm).

DIAGNOSTIC REMARKS.—This species differs from other members of the group by distribution and form of the pronotum.

DISTRIBUTION (Fig. 290A; appendix). Western and southern Ecuador (probably also extreme northwestern Peru). 0–2300 m. Coprophagous. Collection dates: probably all year (no records from April, June, and August).

COMMENTS. The coloration of *lunaris* is considerably less variable than that of other members of the group. It occurs in arid and semiarid habitats, as does *achilles.* Although I have seen no specimens from there, I assume its range extends into the arid region of extreme northwestern Peru. The form of the pronotum of both sexes is reminiscent of that of the *beltianus* group, to which I presently consider *lunaris* an annectant. Its placement in the *mexicanus* group is based primarily upon the female pronotum, which possesses the lateral depressions characteristic of the group.

I have not been able to locate the type specimens of either *lunaris* or *charon.*

Phanaeus (*Phanaeus*) *wagneri* Harold

Figures 74–76, 269, 271, 290A

Phanaeus wagneri Harold, 1863:170

Type: Male lectotype ("Nicaragua"), Muséum National d'Histoire Naturelle, Paris (Arnaud, 1982a:115).

Phanaeus pilatei Harold, 1863:170

Type: Male lectotype ("Yucatan"), Muséum National d'Histoire Naturelle, Paris (Arnaud, 1982a:115).

Phanaeus wagneri wagneri Harold, NEW STATUS

Phanaeus wagneri pilatei Harold, NEW COMBINATION

NOMENCLATURAL REMARKS. Both the names *wagneri* and *pilatei* were proposed simultaneously by Harold on the same page. The choice of the former name as nominate subspecies is by precedence of position.

OTHER REFERENCES (to both subspecies unless indicated otherwise). Bates, 1887, 1889 (*pilatei*); Nevinson, 1892a; Pittier and Biolley, 1895 (*wagneri*); Villada, 1901 (*wagneri*); Gillet, 1911b; Olsoufieff, 1924; Blackwelder, 1944; Barrera, 1969; Edmonds, 1972; Morón et al., 1986 (*pilatei*); Palacios-Ríos et al., 1990 (*pilatei*).

DESCRIPTIVE REMARKS. *Color and Color Pattern.*—(a) *wagneri* (Fig. 74): Dorsal coloration highly variable; dark blue, blue-green, green, yellow-green, or coppery red. Pronotum of male completely colored except for black tips, sides of posterolateral angles; that of female with black anteromedian spot. Pygidium colored as elytra; venter with colored reflections on legs, sterna. (b) *pilatei* (Figs. 75, 76): Dorsum deep blue-green or dark green; otherwise as above. *Pronotum.*—Basal fossae almost always present; in *wagneri,* small, punctiform, sometimes absent in male; always present, usually conspicuous in female; in *pilatei,* conspicuous in both sexes. *Pronotal Sculpturing.—Male:* In large individuals, sides densely granulorugose, disk coarsely rugose except posteromedially where usually distinctly smoother, punctate to punctatorugose (in *pilatei,* disk raised transversely as ridgelike tumosity in front of smooth posteromedian area). Small individuals as above except disk less coarsely rugose, rugosities becoming scale-like medially, progressively weaker posteriorly. *Female:* Sides densely granulorugose, rugosities becoming scale-like on disk, progressively weaker posteriorly where replaced by asperate punctures. *Elytra.*—Striae minutely punctate (×40). Interstriae evenly convex, smooth to minutely roughened, punctate (×30). *Secondary Sexual Characters.—Male:* Pronotum as in Figure 269; *Female:* Cephalic carina trituberculate. Convexities flanking anteromedian pronotal prominence weaker, less shining in *pilatei. Specimens Examined.—wagneri:* 180 males, 146 females; *pilatei:* 88 males, 85 females (length 14–20 mm; width 8–13 mm).

DIAGNOSTIC REMARKS. This species most closely resembles *mexicanus,* from which it differs

by having basal pronotal fossae, in shape of the male pronotum, finer, more asperate puncturing of the female pronotum, and distribution. Small males also closely resemble *sallei,* which possesses several unique species group characters (q.v.) that distinguish it from all members of the *mexicanus* group.

DISTRIBUTION (Fig. 290A; appendix). *wagneri*—Transitional habitats from Chiapas to Costa Rica (500–2200 m). Coprophagous. Collection dates: May–December. *pilatei*—Drier deciduous and evergreen forests of the Yucatán Peninsula (0–1000 m). Coprophagous. Collection dates: May–December.

COMMENTS. It could be argued that the two subspecies recognized here should continue to be regarded as distinct species. I have elected to make them conspecific in recognition of their close systematic relationship. The chief characters separating them (basal pronotal fossae and shape of the male pronotum) intergrade especially among specimens from Chiapas, where the two subspecies are sympatric.

Most of the specimens of *wagneri* that I have seen were collected long ago and bear imprecise locality data. Thus, the distribution dipicted in Figure 290A is, at best, a rough approximation.

Phanaeus (*Phanaeus*) *mexicanus* Harold

Figures 79–82, 265, 266, 273, 274, 290A

Phanaeus mexicanus Harold, 1863:171

Type: Male lectotype ("Mexico, Veracruz"), Muséum National d'Histoire Naturelle, Paris (Arnaud, 1982a:115).

Phanaeus divisus Harold, 1863:171 (Bates, 1887: 65)

Type: Male lectotype ("Mexico"), Muséum National d'Histoire Naturelle, Paris (Arnaud, 1982a:114).

Phanaeus scintillans Bates, 1887:64, NEW SYNONYMY

Type: Male lectotype ("Mexico, Oaxaca, Sallé, B.C.A. p.64 sp.27, sp. figured"), British Museum (Natural History), London, PRESENT DESIGNATION.

NOMENCLATURAL REMARKS. The name *mexicanus* takes precedence over *divisus* by position on page.

OTHER REFERENCES. Blanchard, 1885; Nevinson, 1892a; Villada, 1901; Gillet, 1911b; Leng, 1920; Olsoufieff, 1924; Blackwelder, 1944; Blackwelder and Blackwelder, 1948; Robinson, 1948; Halffter and Matthews, 1966; Edmonds, 1972; Edmonds and Halffter, 1972, 1978; Halffter and Edmonds, 1982; Morón, 1984.

DECRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 79–82).—Dorsal coloration highly variable—dark blue, green, yellow-green, coppery red; most often yellow-green or coppery red with green highlights; dark blue phase rare. Pronotal disk completely colored except for following black areas: posterolateral angles of male; posterolateral angles, irregular anteromedian area of female. Pygidium colored as elytra. Venter dark with colored highlights on legs, sterna. *Pronotum.*—Basal fossae usually absent; rarely indicated in female by small punctiform pits. *Pronotal Sculpturing.—Male:* In large individuals, sides densely, finely granulorugose; disk rugose, rugosities forming transverse ridging medially; posteromedially sculpturing varies from coarsely punctatorugose to smooth with scattered punctures; posterolateral angles of disk punctate behind. In smallest individuals, granulorugosity extends to middle of disk, grades into dense, coarse puncturing near posterior margin. *Female:* Granulorugose except posteromedially where disk smooth, sparsely punctate to punctatorugose. *Elytra.*—Striae simple to minutely punctate (×40), impressed. Interstriae evenly convex, moderately shining, minutely punctate (×40), appearing smooth to unaided eye. Interstriae 6–8 (rarely 1–8) often unevenly roughened by minute puncturing (×20). *Secondary Sexual Characters.—Male:* Pronotum of large specimens as in Figure 265; disk bearing three acute tubercles posterior two of which may fuse as transverse ridge. *Female* (Figs. 273, 274): Cephalic carina trituberculate. Transverse carina bordering anteromedian prominence of pronotum slightly bowed anteriorly, weakly toothed medially; occasionally sinuous, distinctly, but not strongly tuberculate medially. *Specimens Examined.*—179 males, 133 females (length 14–23 mm; width 9–15 mm).

DIAGNOSTIC REMARKS. As mentioned above, only large, well-developed males of this species are distinguishable from *amithaon* on morphological grounds. Reliable locality information is necessary to distinguish females and small males of the two species.

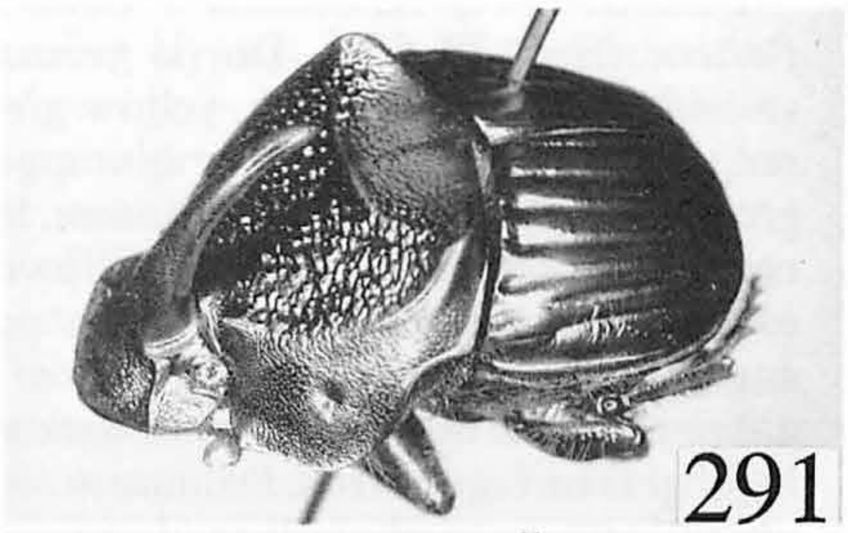
DISTRIBUTION (Fig. 290A; appendix). Apparently disjunct as follows: Balsas River valley, central Oaxaca, escarpment of Mesa Central in east-central Veracruz, and the Los Tuxtlas region of Veracruz. Coprophagous. 0–1500 m. Collection dates: May–October (May–January in Los Tuxtlas).

COMMENTS. The apparently disjunct distribution of *mexicanus* may be an artifact of collecting, at least in all cases except Los Tuxtlas. This species appears to be allopatric with its closest relative, *amithaon,* although I have seen some intermediate specimens that suggest the two hybridize in limited areas of eastern Michoacán (e.g., Tuxpan; see also "Comments" under *amithaon*).

Phanaeus (*Phanaeus*) *amithaon* Harold

Figures 83–85, 264, 290A

Phanaeus amithaon Harold, 1875b:88



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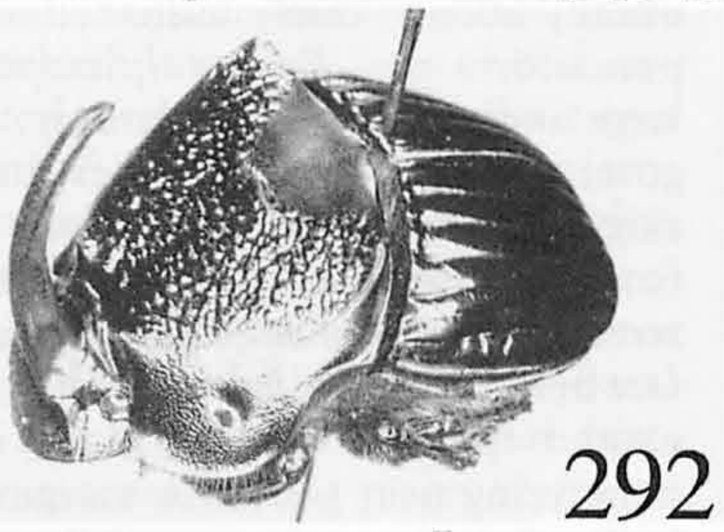

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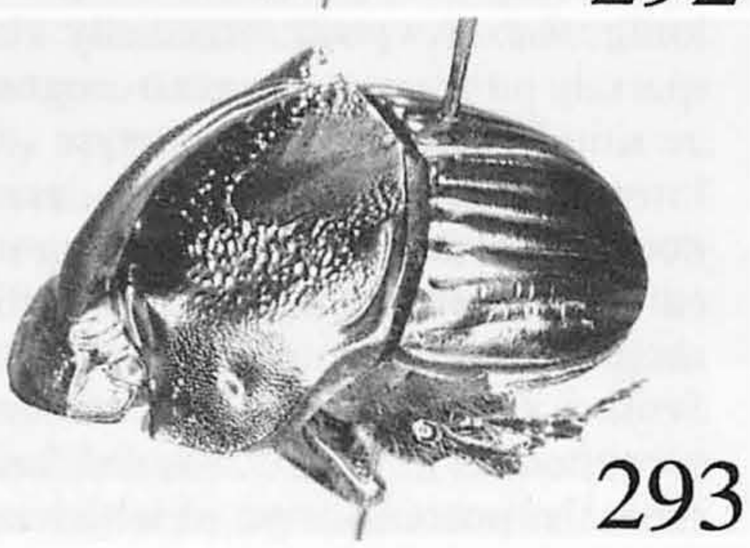

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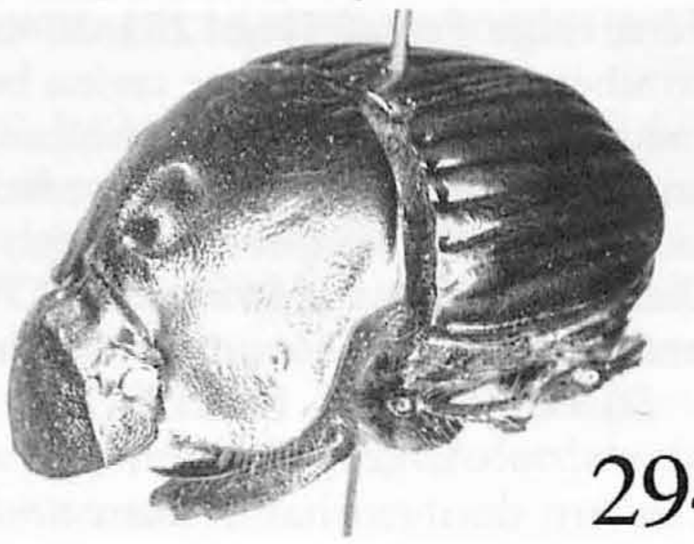

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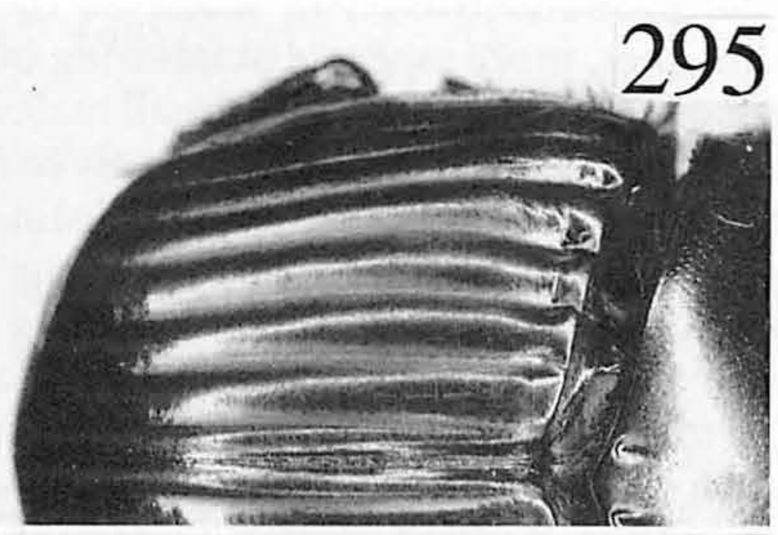

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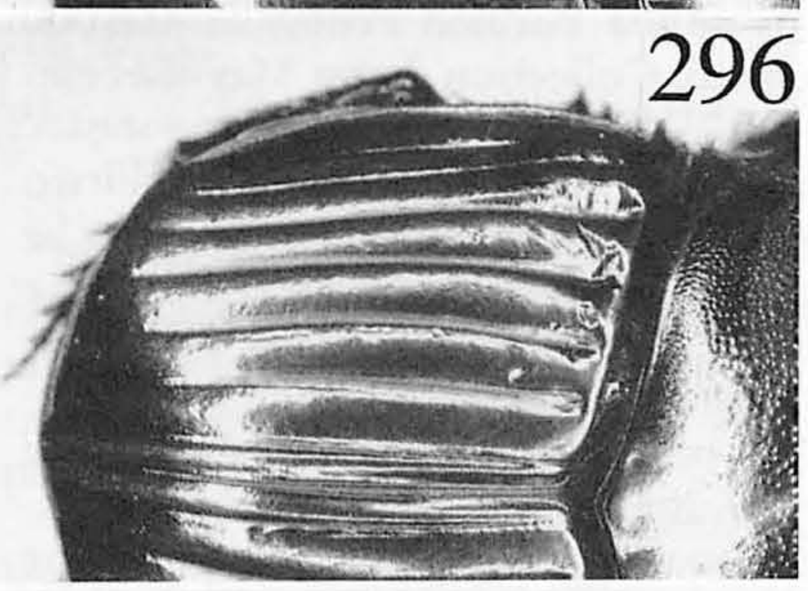

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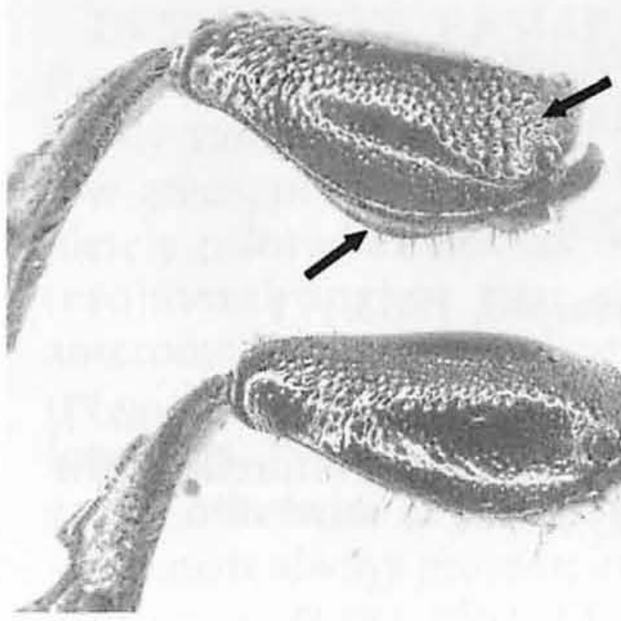

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298

Figures 291–298. *Phanaeus* (*Phanaeus*) *beltianus* group (**291,** *P. beltianus,* male; **292,** *P. sallei,* male; **293,** *P. howdeni,* male; **294,** *P. beltianus,* female; **295,** same, dorsal view elytron; **296,** *P. sallei,* same; **297,** *P. sallei,* posterior view front femur and tibia [upper arrow indicates field of large punctures; lower arrow indicates expanded margin]; **298,** *P. quadridens,* same, cf. 297).

Type: Male lectotype ("Mexico, Guanajuato"), Muséum National d'Histoire Naturelle, Paris (Arnaud, 1982a:114).

NOMENCLATURAL REMARKS. For unstated reasons, Bates (1887) emended Harold's name to *amythaon,* and his spelling has received wide subsequent use. The emendation, however, was unjustified. Nevinson (1892a) synonymized *scintillans* Bates and *amithaon;* Bates' taxon is a synonym of *mexicanus* (q.v.).

OTHER REFERENCES. Blanchard, 1885 (as *mexicanus*); Villada, 1901; Gillet, 1911b; Leng, 1920; Olsoufieff, 1924; Islas, 1942; Blackwelder and Blackwelder, 1948; Robinson, 1948; Halffter and Matthews, 1966; Barrera, 1969; Edmonds, 1972.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 83–85).—Dorsal coloration highly variable—green, yellow-green (often with coppery reflections), copper-red, deep red; moderately shining to dull. Pronotum of male completely colored except for black posterolateral angles; that of female with irregular black anteromedian spot, elongate black areas posterolaterally. Pygidium colored as elytra. Venter dark with colored reflections on legs, sterna. *Pronotum.*—Basal fossae absent except in females from Pacific coast. *Pronotal Sculpturing.—Male:* In large individuals, sides finely, densely granulorugose; disk coarsely rugose, rugosities often forming transverse ridging, except for somewhat smoother punctatorugose area posteromedially; smoother posteromedian area of disk

sometimes bounded anteriorly by incomplete, bowed ridge; posterolateral angles of disk punctate behind. Smaller specimens as above except sculpturing finer, denser. *Female:* Sides densely granulorugose, sculpturing becoming coarser on disk; disk punctate to punctatorugose posteromedially where somewhat smoother than remainder of disk. *Elytra.*—Striae fine, simple to minutely punctate (×40). Interstriae evenly convex, appearing smooth to unaided eye; interstriae 6–8 (rarely 2–8) often roughened by minute punctures (×40). *Secondary Sexual Characters.—Male:* Pronotum as in Figure 264. *Female:* Cephalic carina tridentate. Pronotum as in Figures 273, 274; transverse anteromedian carina straight or sinuate medially. *Specimens Examined.*—627 males, 492 females (length 13–25 mm; width 9–16 mm).

DIAGNOSTIC REMARKS. As mentioned in the key to species, *amithaon* is similar to *mexicanus* (see "Comments," below).

DISTRIBUTION (Fig. 290A; appendix). Mesa Central of Mexico westward to Colima and Jalisco, northward along the Pacific coast into southeastern Arizona. 0–1800 m. Coprophagous, common in pastures. Collection dates: June–December (most June–August).

COMMENTS. This is a widely distributed species replaced to the south and east by *mexicanus*, to which it is closely related. Without reliable geographic data, females and small males of the two are inseparable. There is little question that the two species are vicariants.

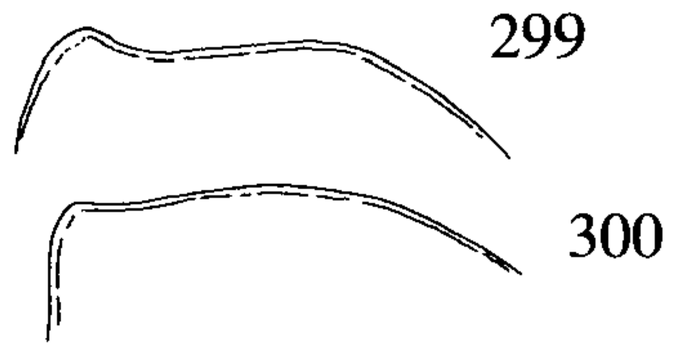
As mentioned in the introduction to the *mexicanus* group, *amithaon* is often collected along with *furiosus*. Both species occur in large numbers in cow dung. I have been able to discover no difference between Arizona populations and those in Mexico. I assume that its spread north is recent and associated with the introduction of cattle into the southwestern United States.

Most of the variation in coloration of *amithaon* is observable only in the central portions of Mexico. Coastal populations in Nayarit and Sinaloa are of a fairly uniform green, to which are added coppery highlights in populations in Sonora and Arizona.

I have seen specimens labeled Torreón, Monclova, and Saltillo (all in Coahuila). These localities need confirmation.

The *Beltianus* Group

DIAGNOSIS. [1] Outer margin of head at most only scarcely notched; [2] clypeal process rounded; [3] cephalic carina of female trituberculate, set in front of eyes; [4] anterolateral portions of pronotum densely granulorugose; [5] basal pronotal fossae present or almost effaced; [6] disk of male pronotum (Figs. 291–293) flat, posterolateral angles rounded, upturned; base with smooth area separated from rest of disk by transverse carina or tubercle; each anterolateral angle of disk bearing conical tubercle; [7] pronotum of female (Fig. 294) with narrow, medially tuberculate carina followed by oval concavity posterior margin of which interrupted by rounded gibbosity; [8] front tibiae tridentate; [9] midventral carina of front femora angulate near base; base with field of large, coarse, setose punctures (Fig. 297); [10] basal segment of middle tarsus of female broad apically; [11] longer mesotibial spur dilated apically, more strongly so in female; [12] evergreen forests from central Veracruz to eastern Panama (Fig. 301).



Figures 299, 300. *Phanaeus (Phanaeus) beltianus* group (**299,** *P. beltianus,* anterolateral margin of pronotum; **300,** *P. sallei,* same).

This group comprises three closely related Middle America species, all of which inhabit moist tropical evergreen forests: *beltianus* Bates, *sallei* Harold, and *howdeni* Arnaud. The principal group characters are the form of the male and female pronota and the unique shape and puncturing of the front femora. The pronota, especially that of the male, resemble that of *lunaris,* which I regard as an annectant between the *beltianus* and *mexicanus* groups.

The distributions of these three species form a chain extending most of the length of Middle America. The northern and widest range is that of *sallei,* a species replaced by *beltianus* in southern Nicaragua and Costa Rica; *howdeni* is known only from Panama. The distributions of all three species, but particularly *beltianus,* are not well known. Uncorroborated data suggest that *sallei* reaches Panama and, therefore, may be sympatric with both other species.

KEY TO THE SPECIES OF THE *BELTIANUS* GROUP

1a. Elytral interstriae shining medially, dull adjacent striae such that interstriae appear polished midlongitudinally (Fig. 295). Sculpturing of sides of pronotum extending to anterolateral margins, where considerably weaker but nonetheless visible (×30). Basal pronotal fossae prominent in female; very small, but usually distinct in male. Pronotum of female not distinctly impressed midlongitudinally. Lateral margin of pronotum (seen from above) usually distinctly curved inward between anterolateral and lateral angles (Fig. 299). Lowland forests of Nicaragua and Costa Rica (Fig. 301) . . . . . *Phanaeus (P.) beltianus* Bates

b. Elytral interstriae evenly shining or dull, not distinctly shinier medially. Sculpturing of sides

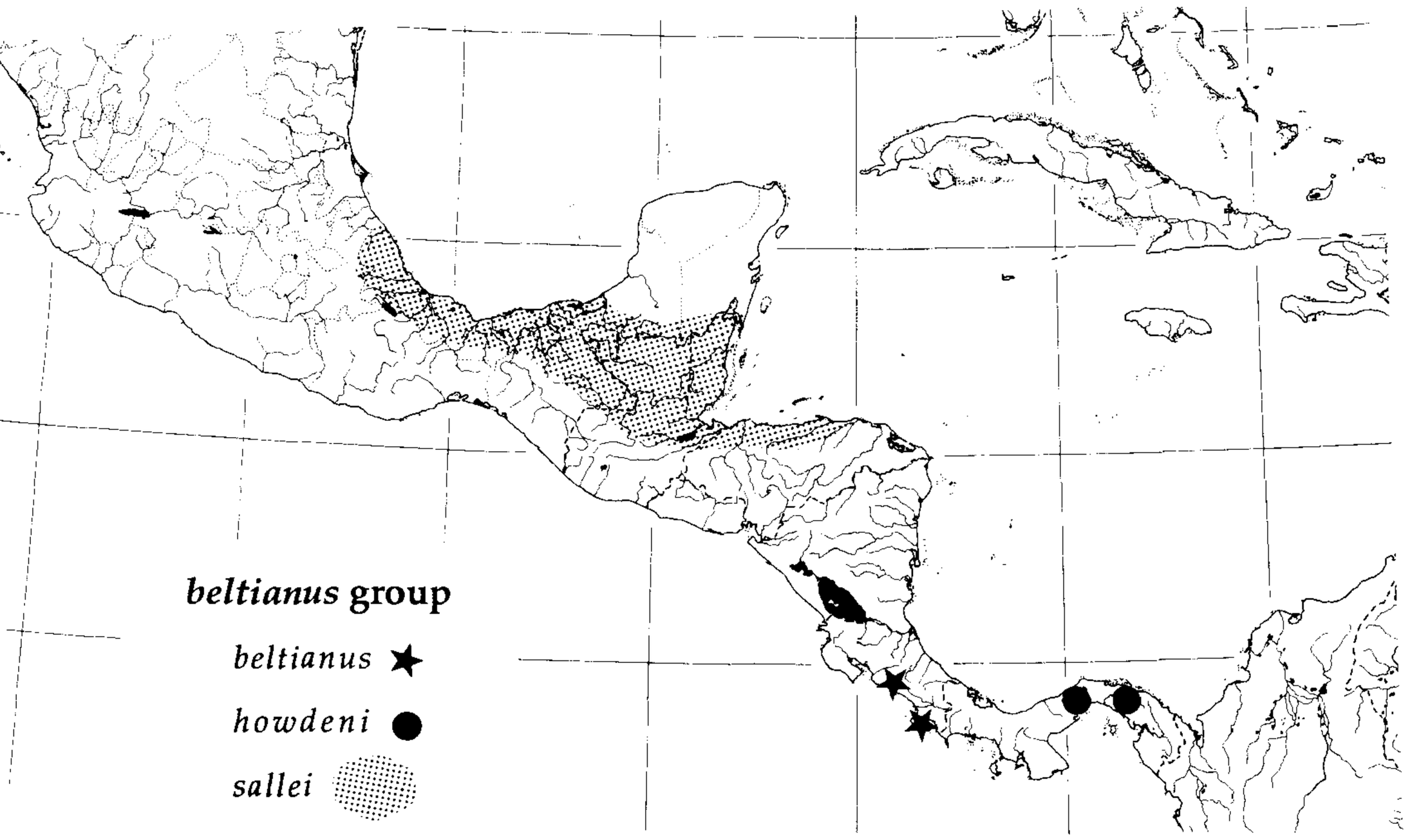


Figure 301. Distribution of the *Phanaeus* (*Phanaeus*) *beltianus* group.

of pronotum effaced adjacent to anterior margin. Basal pronotal fossae usually reduced. Pronotum of female usually distinctly impressed midlongitudinally. Lateral margin of pronotum more or less straight between anterolateral and lateral angles (Fig. 300) 2

2a. Elytral interstriae evenly dulled by dense shagreening (×20). Smooth posterior area of pronotal disk of male extending at least one-half distance to anterior margin of disk (best judged in large individuals) (Fig. 293). Disk of female pronotum more coarsely sculptured along midlongitudinal impression than areas to each side. Lowland forests of Panama (Fig. 301) . . . . . *Phanaeus* (*P.*) *howdeni* Arnaud

b. Elytral interstriae evenly smooth and shining, not dulled by shagreening. Smooth posterior area of male pronotum extending less than one-half (usually about one-third) distance to anterior margin of disk (Fig. 292). Texture of sculpturing of disk of female pronotum more or less uniform, not distinctly coarser or denser in median depression. Forests of east central Veracruz and of southern portion of Yucatán and adjacent areas of northern Chiapas and Guatemala (Fig. 301) . . . . . *Phanaeus* (*P.*) *sallei* Harold

Phanaeus (*Phanaeus*) *beltianus* Bates

Figures 37, 38, 291, 294, 295, 299, 301

Phanaeus beltianus Bates, 1887:63

Type: Male lectotype ("Chontales, Nicaragua, B.C.A. p.63 sp.24, sp. figured"), British Museum (Natural History), London, PRESENT DESIGNATION.

OTHER REFERENCES. Nevinson, 1892a; Gillet, 1911b; Olsoufieff, 1924; Blackwelder, 1944; Edmonds, 1972.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 37, 38).—Posterior portion of head, pronotum weakly shining yellow-green with strong coppery red reflections; elytra coppery red, sometimes with strong greenish highlights. Pronotal disk of male completely colored except for black posterolateral angles; that of female mostly dull black. Venter with strong yellow-green reflections on legs, sterna. *Pronotum.*—Lateral margin bowed inward between anterolateral and lateral angles (Fig. 299). Basal fossae prominent in female, minute or effaced in male. Disk of female not inmpressed midlongitudinally. *Pronotal Sculpturing.—Male:* In large individuals, sides finely granulorugose, becoming somewhat more coarsely rugose near disk, punctate beneath posterolateral angles. Disk coarsely granulorugose except posteromedially where abruptly smoother and bears minute asperities. Smooth basal area partially separated from remainder of disk by straight, transverse carina. Smaller individuals as above except disk reduced to small, circular, concave area near anterior margin, sculpturing of sides extending onto disk as flat scale-like granules replaced by puncturing near posterior margin. *Female:* Sides finely granulorugose, rugosities becoming scale-like near disk; disk with asperate punctures

grading to weak, simple punctures posteriorly, appearing smooth to unaided eye. *Elytra* (Fig. 295).—Striae simple or minutely punctate (×40). Interstriae convex, highly shining medially, dulled laterally by dense shagreening. *Secondary Sexual Characters.—Male:* Pronotum as in Figure 291. *Female:* Pronotum as in Figure 294; disk not impressed midlongitudinally. *Specimens Examined.*—6 males, 6 females (length 16–20 mm; width 10–13 mm).

DIAGNOSTIC REMARKS. The salient features distinguishing this species from other members of the group are microsculpturing of the elytra and form of the male pronotum.

DISTRIBUTION (Fig. 301; appendix). Known only from scattered localities in Costa Rica and Chontales district of Nicaragua. Lowland evergreen forest below 500 m. Collection dates: July–August.

COMMENTS. This is one of the rarer species of the genus. Howden and Young's (1981) references to *beltianus* apply to *howdeni.*

Phanaeus (*Phanaeus*) *howdeni* Arnaud

Figures 41, 42, 293, 301

Phanaeus howdeni Arnaud, 1984:61

Type: Male holotype ("Panama, Gatun Lake, Lion Hill Island"), Anne and Henry Howden Collection, in Canadian National Collection, Ottawa.

OTHER REFERENCES. Howden and Young, 1981 (as *beltianus*); Howden and Gill, 1987.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 41, 42).—Dorsum dark blue-green, yellow-green with weak coppery highlights, or green. Disk of female pronotum with anteromedian, two posterolateral black spots, all three of which may coalesce. Pygidium colored like elytra. Venter with colored reflections on legs, sterna. *Pronotum.*—Lateral margin weakly sinuate between anterolateral, lateral angles. Basal fossae almost effaced. Disk of female usually distinctly impressed midlongitudinally. *Pronotal Sculpturing.—Male:* In large individuals, sides granulorugose, sculpturing becoming weak along anterolateral margin, grading into weak puncturing (or smooth areas) beneath, behind posterolateral angles of disk. Disk coarsely rugose, with transverse ridging except for much smoother ovoid posteromedian area, which bears weak, asperate punctures; smoother area extending at least one-half distance to anterior margin, bearing a crest-like tubercle in middle of its anterior edge. Smaller individuals as above except disk less coarsely rugose, smooth posteromedian area bounded anteriorly by wide V-shaped ridge distinctly carinate only medially. *Female:* Sides granulorugose; sculpturing almost effaced along anterolateral margin, becoming scale-like toward disk, grading into punctures posteriorly. Midlongitudinal impression of disk usually more coarsely sculptured than adjacent areas to its sides. *Elytra.*—Striae simple to minutely punctate (×40). Interstriae convex, evenly dulled by shagreening. *Secondary Sexual Characters.—Male:* Pronotum as in Figure 293. *Female:* Pronotum as in Figure 294. *Specimens Examined.*—17 males, 15 females (length 14–19 mm; width 9–12 mm).

DIAGNOSTIC REMARKS. See under *sallei.*

DISTRIBUTION (Fig. 301; appendix). Known only from tropical evergreen forests in central Panama. 0–500 m. Collection dates: May–December.

COMMENTS. This species is fairly common on Barro Colorado Island, Panama Canal Zone, and nearby regions to the east and west. Howden and Young (1981) referred to it as *beltianus,* a much rarer species.

Phanaeus (*Phanaeus*) *sallei* Harold

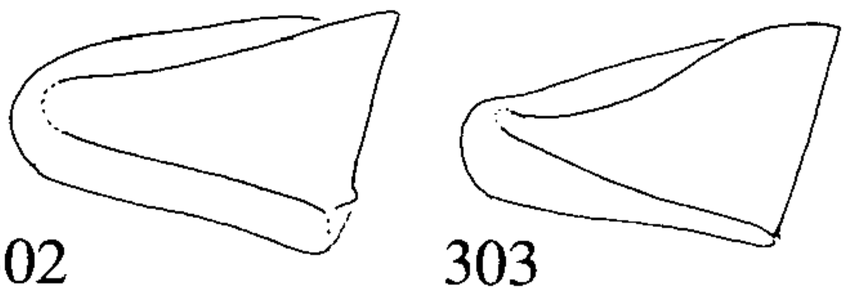
Figures 39, 40, 292, 296, 297, 300, 301

Phanaeus sallei Harold, 1863:168

Type: Male lectotype ("Mexico"), Muséum National d'Histoire Naturelle, Paris (Arnaud, 1982a:115).

OTHER REFERENCES. Gemminger and Harold, 1869; Bates, 1887; Nevinson, 1892a; Villada, 1901; Gillet, 1911b; Olsoufieff, 1924; Blackwelder, 1944; Barrera, 1969; Edmonds, 1972; Morón, 1979; Morón et al., 1985; Palacios-Ríos et al., 1990.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 39, 40).—Dorsum shining coppery red (often combined with yellow-green highlights), yellow-green, green, or dark blue-green. Disk of female with black anteromedian spot, black posterolateral angles. Pygidium colored as elytra. Venter dark with colored reflections on legs, sterna. *Pronotum.*—Lateral margin more or less straight between anterolateral, lateral angles (Fig. 300). Basal fossae almost effaced. Disk of female weakly impressed midlongitudinally. *Pronotal Sculpturing.—Male:* In large individuals, sides granulorugose, becoming smooth near anterolateral margin, punctate to smooth beneath posterolateral angles of disk. Anterior portion of disk coarsely rugose, with isolated transverse ridging. Posterior portion of disk smooth, bearing small asperate punctures; this smooth basal area separated from anterior area by transverse carina. Smaller individuals as above except disk less coarsely rugose, transverse carina separating anterior, posterior portions of disk replaced by a weak tumosity. *Female:* Sides densely granulorugose, becoming smooth along anterolateral margin, coarser, scale-like posteriorly; middle of disk with flat, scale-like granules grading to small, simple punctures posteriorly. Midlongitudinal impression (if distinct) not more coarsely sculptured than areas of disk to either side. *Elytra* (Fig. 296).—Striae simple to minutely punctured (×40). Interstriae evenly convex, shining; smooth to minutely punctured, occasionally minutely roughened (×40). *Secondary Sexual Characters.—Male:* Pronotum



302 303

Figures 302, 303. *Phanaeus* (*Phanaeus*) *amethystinus* group (**302,** *P. melampus*, hind basitarsus; **303,** *P. amethystinus*, same).

as in Figure 292; in large specimens, smooth posterior area of disk extending no more than one-third (usually less) distance to anterior margin. *Female:* Pronotum as in Figure 294. *Specimens Examined.*—97 males, 81 females (length 14–20 mm; width 8–12 mm).

DIAGNOSTIC REMARKS. This species most closely resembles *howdeni,* from which it is distinguished by features of the pronota of both sexes. It also superficially resembles *wagneri wagneri,* from which it can be separated most easily by the structure of the front femora.

DISTRIBUTION (Fig. 301; appendix). Tropical forests of east-central Veracruz, southern Yucatán Peninsula and adjacent areas in northern Chiapas and Guatemala (and probably also Honduras). 0–1500 m. Coprophagous. Collection dates: May–October.

COMMENTS. The most frequent color of *sallei* is coppery red, especially in populations from Veracruz. Examined populations from Chiapas are always green. The distribution of this species is poorly known; of the over 150 specimens examined, only about 50 carry precise locality data. Since its distribution is limited ecologically to lowland evergreen forests, it is likely that the geographical distribution of *sallei,* like that of *endymion,* is now far more restricted and fragmented that it was in pre-European times.

The *Amethystinus* Group

DIAGNOSIS. [1] Outer margin of clypeus at most only weakly toothed medially; [2] clypeal process (seen from front) transverse rounded ridge; [3] cephalic process of female narrow, trituberculate carina (seen from above) on line even with anterior margins of eyes; [4] pronotal disk of large males flattened and coarsely granulorugose and (seen from above) triangular; posterolateral angles rounded, upturned; bearing smooth, raised transverse triangular area immediately in front of posterior margin (Figs. 307–309); [5] pronotum of female convex, granulorugose anterolaterally, with weak transverse anteromedian ridge followed, in large individuals, by small concavity; [6] basal pronotal fossae present; [7] front tibiae tridentate; [8] longer mesotibial spur of female dilated subapically; [9] mountains of Guatemala and southern Mexico (Fig. 312).

This group brings together two montane species, *melampus* and *amethystinus.* Leonardo Delgado-Castillo of the Instituto de Ecología in Xalapa, Veracruz, has kindly brought to my attention a new species assignable to this group being described by him (see "Comments" under *amethystinus*).

KEY TO THE SPECIES AND SUBSPECIES OF THE *AMETHYSTINUS* GROUP

1a. Posteromedian portion of female pronotum appearing almost smooth to unaided eye; weak magnification (×10) reveals field of shallow punctures against smooth background of dull, velvet-like shagreening (Fig. 311). Elytra dull dark brown, rarely with bluish cast (Figs. 51, 52); interstriae appearing flat or very weakly convex to unaided eye (Fig. 307); striae superficial. Hind basitarsus of female narrow apically, ridges on plantar surface more or less straight (Fig. 302). Isolated localities in Chiapas and Veracruz (Fig. 312) . . . . . *Phanaeus* (*P.*) *melampus* Harold

b. Posteromedian portion of female pronotum distinctly roughened to unaided eye (Fig. 310), bearing (×10) coarse punctures against a roughened, shining background; if punctures almost effaced, surface shining. Elytra blue or blue-green (Figs. 53–56), rarely green or green-brown (Fig. 57), always at least partially shining; interstriae appearing convex to unaided eye, striae impressed. Hind basitarsus of female widened apically; outer ridge of plantar surface usually distinctly more sinuous than inner ridge (Fig. 303). Mountainous areas of Chiapas and western Guatemala, eastern Oaxaca northward to southern San Luis Potosí . . . . . *Phanaeus* (*P.*) *amethystinus* Harold 2

2a. At least interstriae 2 and 3, but usually 2–5, highly shining medially, dull adjacent to striae and appearing costate to unaided eye (Fig. 309). Sides of pronotum densely granulate-granulorugose. Highlands of Guatemala (Fig. 312) . . . *Phanaeus* (*P.*) *amethystinus guatemalensis* Harold, NEW STATUS

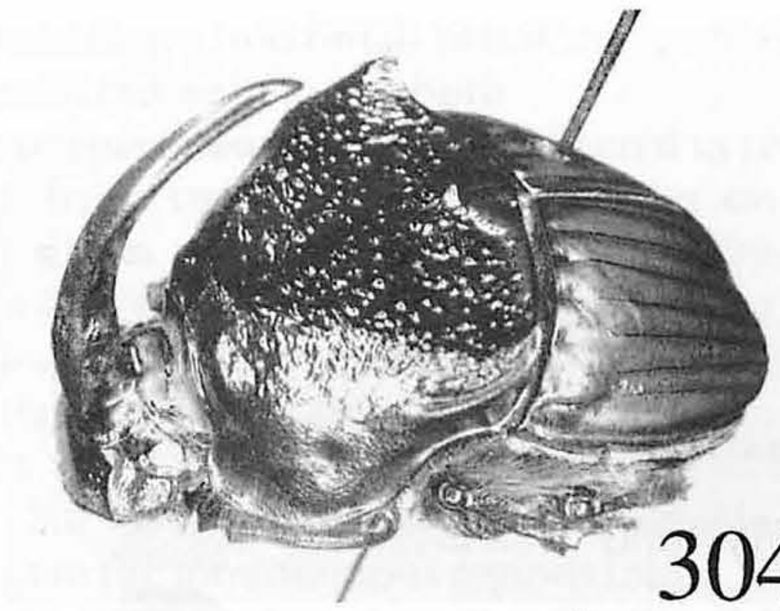
b. All elytral interstriae evenly and usually brightly shining, evenly convex (Fig. 308). Sides of pronotum only moderately densely granulorugose. Highlands of Chiapas, mountains of Guerrero, eastern Oaxaca, western Veracruz, northern Hidalgo, and southern San Luis Potosí (Fig. 312) . . . . . *Phanaeus* (*P.*) *amethystinus amethystinus* Harold, NEW STATUS

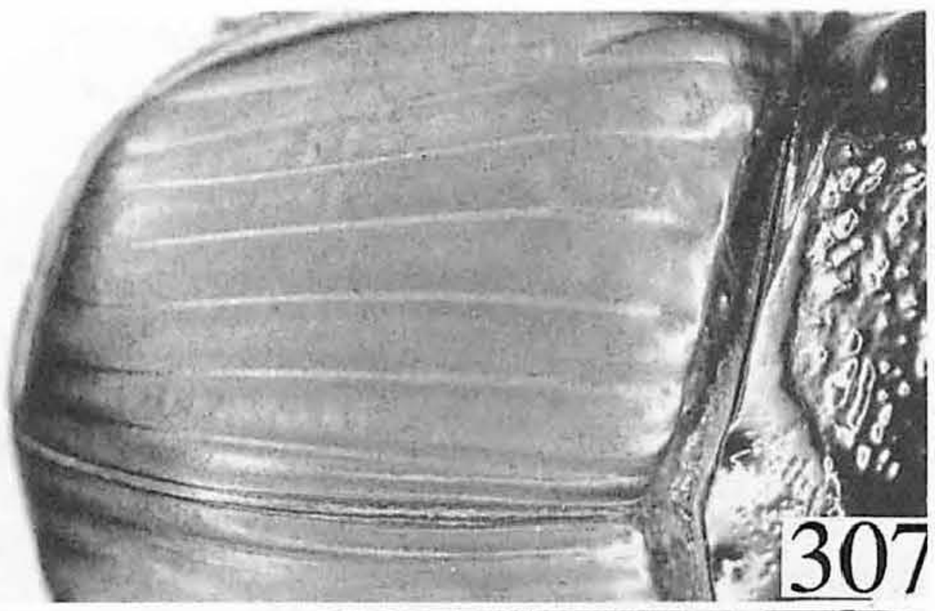
Phanaeus (*Phanaeus*) *melampus* Harold

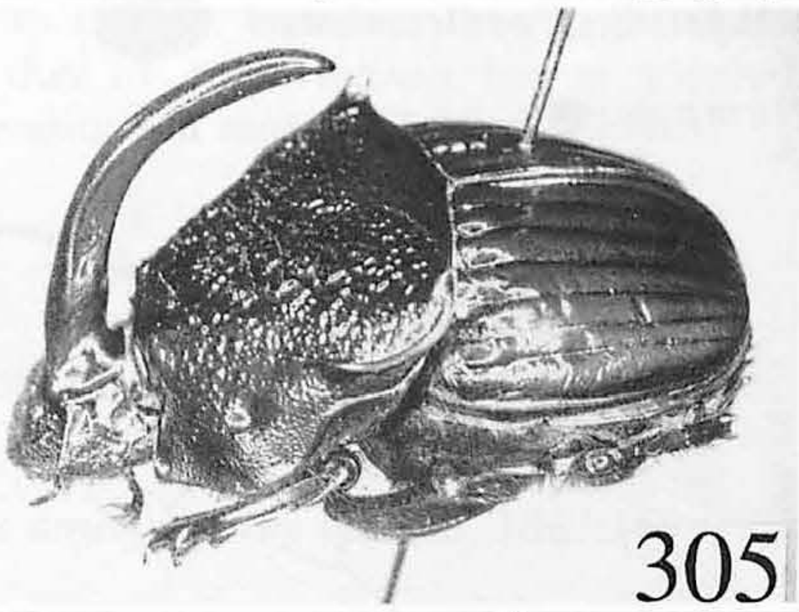
Figures 51, 52, 302, 304, 307, 311, 312

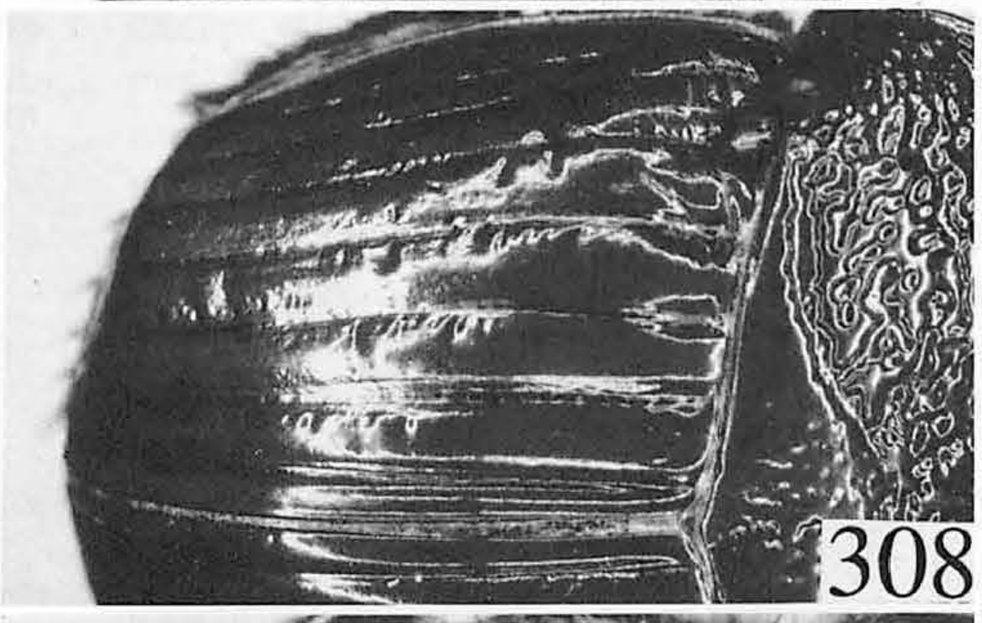
Phanaeus melampus Harold, 1863:165

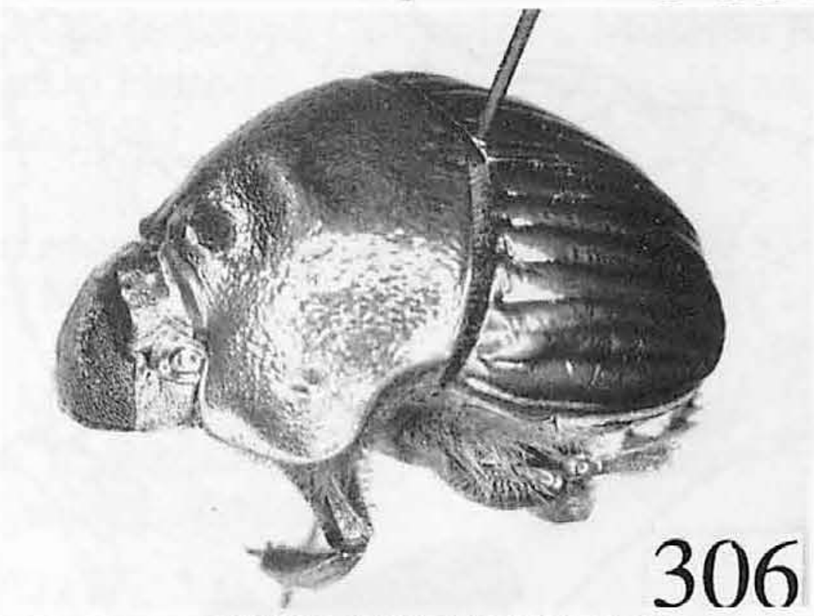
Type: Male lectotype ("Mexico"), Muséum National d'Histoire Naturelle, Paris (Arnaud, 1982a:115).

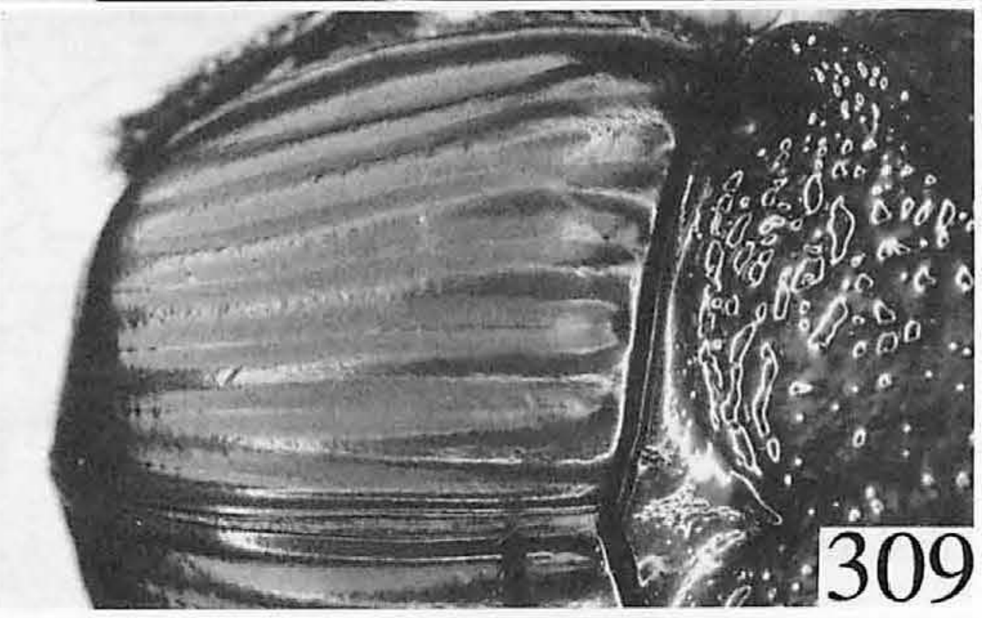


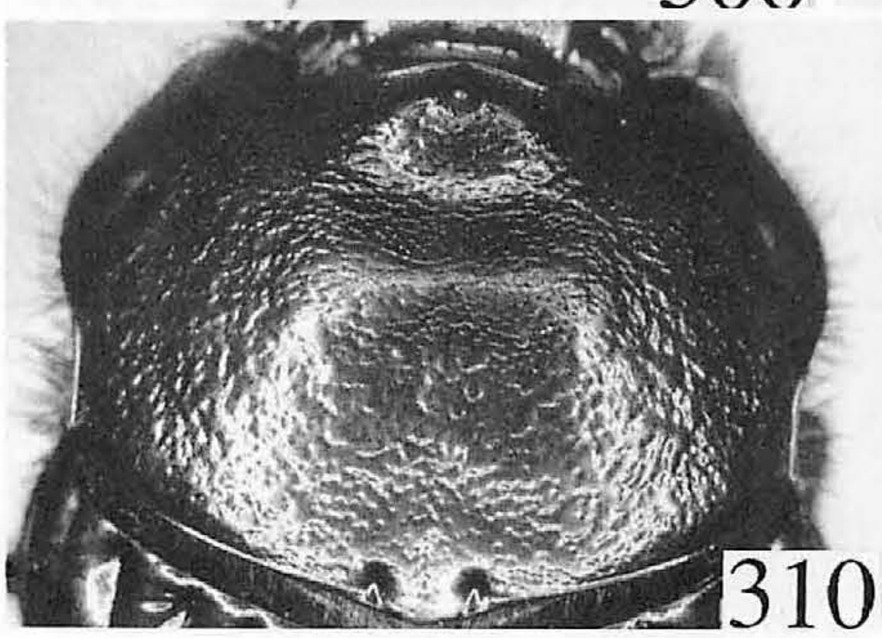


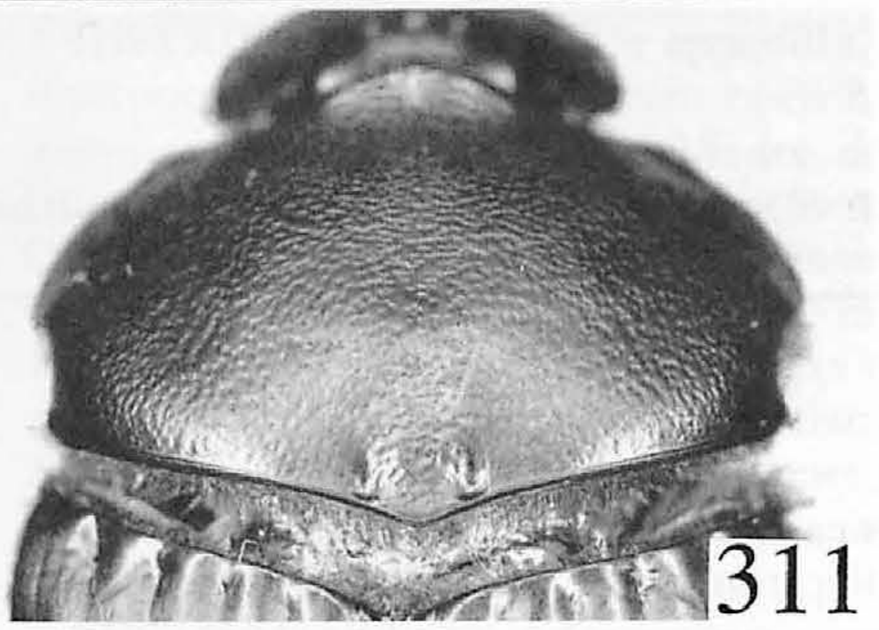












Figures 304–311. *Phanaeus* (*Phanaeus*) *amethystinus* group (**304,** *P. melampus,* male; **305,** *P. a. amethystinus,* male; **306,** same, female; **307,** *P. melampus,* dorsal view elytron; **308,** *P. a. amethystinus,* same; **309,** *P. a. guatemalensis,* same; **310,** *P. a. amethystinus,* dorsal view female pronotum; **311,** *P. melampus,* same).

OTHER REFERENCES. Gemminger and Harold, 1869; Bates, 1887; Nevinson, 1892a; Villada, 1901; Gillet, 1911b; Olsoufieff, 1924; Blackwelder, 1944; Halffter, 1955; Halffter and Matthews, 1966; Barrera, 1969; Edmonds, 1972.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 51, 52).—Dorsum somber, often appearing black or dark brown without intense illumination, which can reveal bluish or greenish cast on pronotum or elytra or both. *Pronotum.*—Basal fossae present. *Pronotal Sculpturing.—Male:* In large individuals (Fig. 304), disk coarsely rugose; sides more densely but more finely granulorugose except along lateral margins and on anterolateral angles where almost smooth; base of disk with raised, transverse area that is smooth except for some coarse puncturing in front of fossae. In smaller individuals, disk as above except smooth basal area lacking, posterior portion of disk shallowly punctate. *Female:* Posteromedian portion of disk bearing shallow punctures against dull, velvety background; punctures becoming progressively

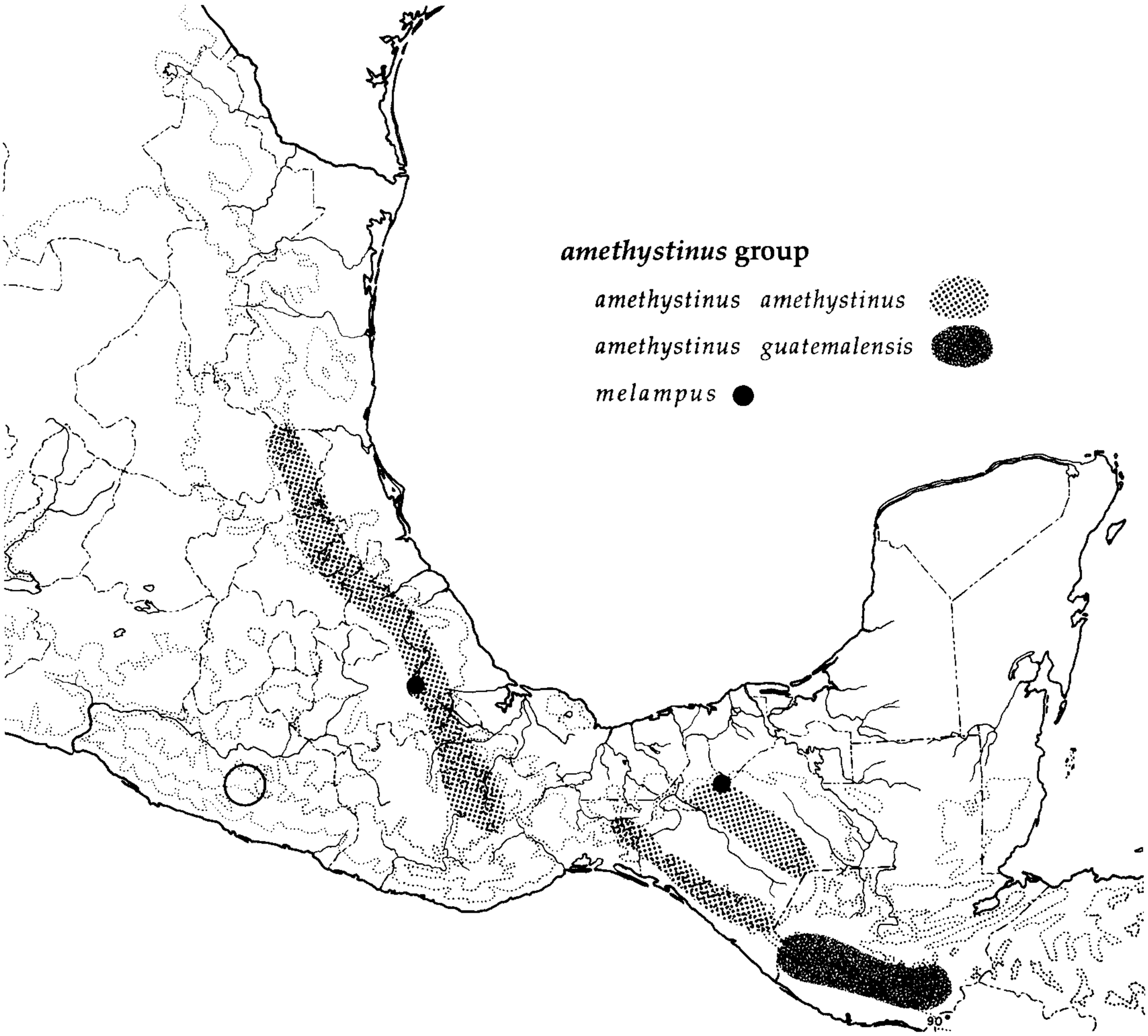


Figure 312. Distribution of the *Phanaeus* (*Phanaeus*) *amethystinus* group (open circle = *sp. nov.* near *amethystinus;* see text).

stronger near middle of disk where they coalesce to form fine transverse ridging; ridging becoming progressively stronger anteriorly. *Elytra* (Fig. 307).—Striae fine, shining. Interstriae weakly convex, appearing almost flat to unaided eye, uniformly dull. *Hind Tarsus.*—Basal segment of female (Fig. 302) narrow apically, apical width <0.75 length along inner margin; both plantar ridges more or less straight. *Secondary Sexual Characters.*—Raised smooth area at base of male pronotum distinct only in larger individuals; otherwise as described for species group. *Specimens Examined.*—45 males, 25 females (length 17–25 mm; width 11–15 mm).

DIAGNOSTIC REMARKS. This species can be confused easily with *amethystinus*, especially smaller specimens lacking any conspicuous blue color. The most dependable features separating the two species are relief and luster of the interstriae and sculpturing of the pronotum, particularly that of the female. Small female *melampus* resemble the dark phase of *prasinus*, from which it differs by the form of the cephalic carina.

DISTRIBUTION (Fig. 312; appendix). Poorly known (see "Comments," below). Assumed to be at lower elevations (<1400 m) along eastern slopes of Sierra Madre Oriental and northern slopes of Chiapan Highlands.

COMMENTS. Almost all the specimens of *melampus* I have examined bear incomplete or imprecise locality data. Moreover, all but 4 of the 65 specimens available were, or appear to have been, collected many decades ago, and their labels, if any, bear such entries as "Mexico," "Veracruz," or, somewhat more precisely, "Jalapa," "Cordova," and other Mexican sites popular with nineteenth century collectors. In spite of the fact that these regions have been well collected in the last 25 years, I have seen no *melampus* from them. The lack of modern

material suggests that *melampus* is now extinct in many areas it once inhabited, that it occurs in some highly restricted habitat, or both.

The four specimens examined collected in recent years are from two localities in Chiapas on the northern slopes of the central Highlands (appendix). This area supports wet tropical evergreen forest, although it is now quite heavily disturbed by agricultural activities. Both localities are at middle elevations (ca. 1500 m). It is not unreasonable to suppose that *melampus* also occurs in similar, isolated areas in the mountainous regions from Oaxaca to northern Puebla. I suspect that its distribution parallels that of *amethystinus* but at somewhat lower elevations in more restricted habitats.

Phanaeus (*Phanaeus*) *amethystinus* Harold

Figures 53–57, 303, 305, 306, 308–310, 312

Phanaeus amethystinus Harold, 1863:169

Type: Male lectotype ("Orizaba"), Muséum National d'Histoire Naturelle, Paris (Arnaud, 1982a:114).

Phanaeus martinezi Halffter, 1955:75, NEW SYNONYMY

Type: Male holotype ("Mexico: Veracruz, Presidio"), personal collection of Gonzalo Halffter, Xalapa, Veracruz.

Phanaeus guatemalensis Harold, 1871b:114

Type: Male lectotype ("Guatemala"), Muséum National d'Histoire Naturelle, Paris (Arnaud, 1982a:114).

Phanaeus tepanensis Bates, 1889:388 (Nevinson, 1892a:4)

Type: Male lectotype ("Guatemala, Tepan, Conradt, B.C.A p.388 sp.22a, sp. figured"), British Museum (Natural History), London, PRESENT DESIGNATION.

Phanaeus amethystinus amethystinus Harold, NEW STATUS

Phanaeus amethystinus guatemalensis Harold, NEW COMBINATION

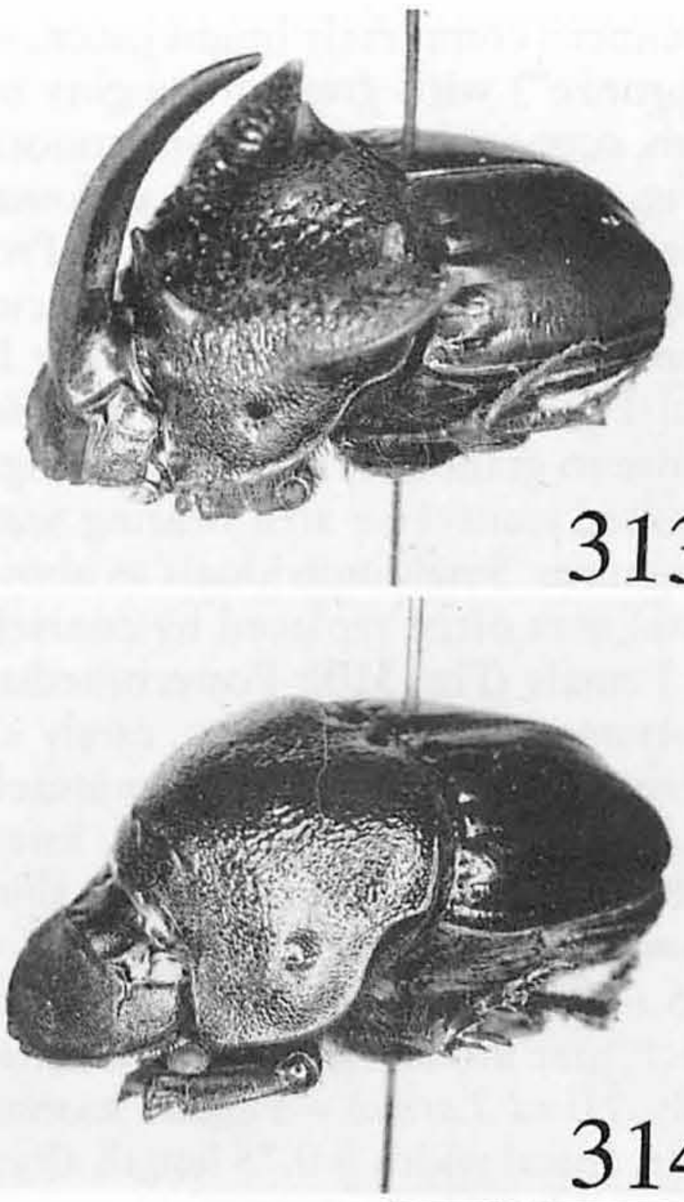
OTHER REFERENCES. To *amethystinus*—Gemminger and Harold, 1869; Halffter and Matthews, 1966. To both subspecies—Gillet, 1911b; Olsoufieff, 1924; Blackwelder, 1944; Edmonds, 1972.

DESCRIPTIVE REMARKS. *Color and Color Pattern.*—(a) *amethystinus* (Figs. 53, 54): Dorsum shining deep blue or blue-green (elytra dull in some specimens from San Luis Potosí; see "Comments," below). (b) *guatemalensis* (Figs. 55, 56): As above except some specimens completely bright green, or brown-green ("bronze") with green highlights on sides of pronotum, coppery brown area on pronotal disk of male (Fig. 57). *Pronotum.*—Basal fossae present in female, sometimes effaced in male. *Pronotal Sculpturing* (as follows for both subspecies but generally denser in *guatemalensis*).—*Male:* In large individuals (Fig. 305), disk coarsely rugose; sides granulorugose to granulate; base of disk (Figs. 308, 309) with raised transverse area bearing scattered, coarse punctures. Small individuals as above except raised basal area often replaced by coarsely punctured area. Female (Fig. 310): Posteromedian area of disk punctate to punctatorugose, rarely almost smooth. *Elytra.*—Striae fine, often minutely punctate (×10). (a) *amethystinus* (Fig. 308). Interstriae more or less evenly convex, uniformly shining. (b) *guatemalensis* (Fig. 309): Interstriae 2–3 (usually also 4–5 or 6) shining medially, dull adjacent to striae such that interstriae appear polished midlongitudinally. *Hind Tarsus.*—Female basitarsus (Fig. 303) wide, apical width >0.75 length along inner margin; outer ridge on plantar surface usually distinctly more sinuous than inner ridge. *Secondary Sexual Characters.*—As described for species group; raised area along base of pronotum distinct in all but smallest individuals. *Specimens Examined.*—*amethystinus:* 82 males, 59 females; *guatemalensis:* 138 males, 109 females (length 13–25 mm; width 8–16 mm).

DIAGNOSTIC REMARKS. This species differs from *melampus* by the luster of the elytral interstriae and sculpturing of the posteromedian portion of the pronotal disk of the female.

DISTRIBUTION (Fig. 312; appendix). (a) *amethystinus.*—Forests and adjacent open habitats in mountains of Chiapas, Sierra Madre del Sur of Guerrero, eastern Oaxaca, and the Sierra Madre Oriental of Veracruz, northern Hidalgo and southeastern San Luis Potosí. 1000–2200 m (usually >1500 m). (b) *guatemalensis.*—Forests and adjacent open habitats in Guatemalan Highlands. 1500–2400 m. Coprophagous; both subspecies common in meadows and clearings grazed by livestock. Collection dates: May–October.

COMMENTS. The two subspecies recognized here have heretofore been regarded as separate species. The primary difference between the two is the microsculpturing of the elytral interstriae, which appear costate in *guatemalensis.* Specimens exhibiting intermediate states in the luster of the interstriae occur in Chiapas and, I suspect, also in far western Guatemala. Males of *guatemalenis* rarely lack at least some trace of the smooth basal area of the pronotum; this area is often lacking in *amethystinus,* even in large males. In addition to those characters mentioned in the descriptions above, some members of this species possess shallow fossae near the posterior margin of the median portion of the metasternum. These fossae are largest in *guatemalensis* and lacking from populations in San Luis Potosí.



Figures 313–322. *Phanaeus* (*Phanaeus*) *quadridens* group (**313,** *P. quadridens,* male; **314,** same, female; **315,** *P. damocles,* male; **316,** same, female; **317,** *P. palliatus,* male; **318,** same, female; **319,** *P. quadridens,* dorsal view female pronotum; **320,** *P. damocles,* same; **321,** *P. quadridens,* dorsal view elytron; **322,** *P. palliatus,* same).

Specimens from southwestern San Luis Potosí and adjacent area of Hidalgo (along Highway 85 descending toward Tamazunchale) differ from typical *amethystinus* by being smaller, by having a distinctly duller coloration (especially on the elytra), and by lacking metasternal fossae. These individuals are reminiscent of *melampus.* This population is separated from more typical *amethystinus* in northeastern Hidalgo by an intervening xeric region in north-central Hidalgo (the Hidalgan Desert), and further study may prove it worthy of subspecific status.

I have only one specimen of *amethystinus* from Oaxaca. Only further collection in the mountains of northern Oaxaca will settle the question of whether or not the distribution of the subspecies extends continuously from Veracruz to the south.

Leonardo Delgado-Castillo (1991) of the Instituto de Ecología in Xalapa, Veracruz, has described a new species (under the name *Phanaeus blackalleri*) closely related to *amthystinus* from the Sierra Madre del Sur of Guerrero and Oaxaca. Specimens from the Sierra de Alquitrán (1400–1670 m; open circle in Fig. 312) in central Guerrero and from the environs of Candelaria Loxicha in extreme southern Oaxaca are smaller (length 16–20 mm; width 8–12 mm) and very dark blue, nearly black in color. Moreover, the female pronotum bears an almost

straight, transverse carina that is weakly tuberculate medially and not followed by any trace of a concavity. These populations inhabit montane forests and are coprophagous.

The *Quadridens* Group

DIAGNOSIS. [1] Outer margin of clypeus at most only weakly toothed medially; [2] clypeal process (seen from front) transverse, rounded ridge; [3] cephalic process of female trituberculate carina in front of eyes; [4] outer margin of head distinctly notched between clypeus, paraocular areas (Fig. 325, arrow); [5] pronotum densely, coarsely granulorugose (Figs. 313–320; [6] pronotal disk of large males (Figs. 313, 315, 317) triangular, concave medially, with prominent posterolateral angles; [7] pronotum of female more or less evenly convex, with weak ridge shaped almost like the Greek letter *omega* (ω) near anterior margin; [8] basal pronotal fossae present; [9] front tibiae tridentate; [10] longer mesotibial spur usually dilated subapically in female; [11] mountains and plateaus above 1500 m in south-central and western Mexico northward to the southwestern United States (Fig. 329).

This group comprises three montane species: *damocles* Harold, *palliatus* Sturm, and *quadridens* (Say). The former is the rarest of the three and more closely related to *palliatus*, with which it is allopatric. All three species are coprophagous. The combined range of the group is extensive, including most of the mountainous regions of Mexico west of the Isthmus of Tehauntepec. The degree of coarseness of pronotal sculpturing is greater in this group than in any other *Phanaeus*. Females, especially, are distinguished from others in the subgenus by the extreme coarseness of the posteromedian portion of the pronotum (Figs. 319, 320). The smooth elytra (Fig. 321) with weak, almost effaced striae of *damocles* and *quadridens*, are not approached in other *Phanaeus, sen. str.*

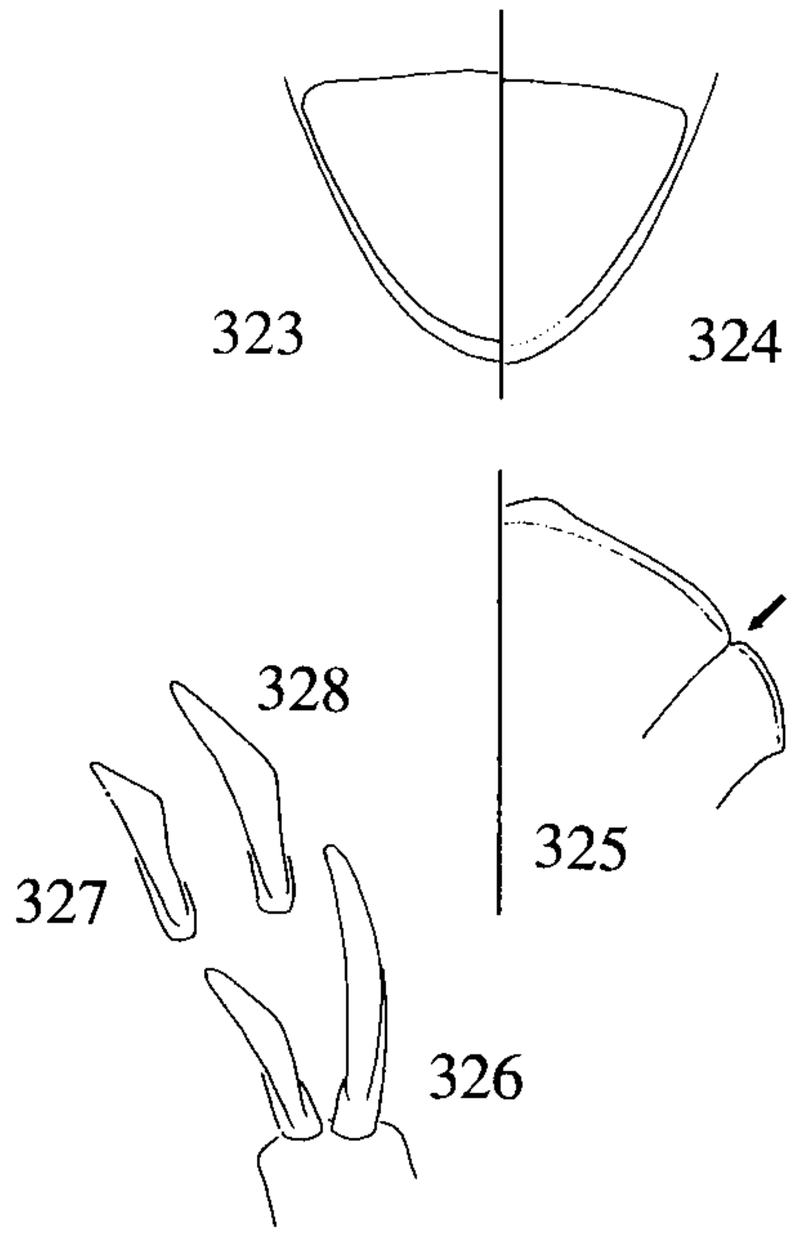
KEY TO THE SPECIES OF THE *QUADRIDENS* GROUP

1a. Interstriae convex; striae fine, clearly impressed (Fig. 322). Raised outer margin of pygidium usually effaced apically (Fig. 324). Dorsum bright coppery red, dark blue, or bright green (Figs. 48–50). Transverse Volcanic Range of Mexico from northern Puebla to Jalisco northward to southern Durango (Fig. 329) . . . . . *Phanaeus* (*P.*) *palliatus* Sturm

b. Interstriae flat; striae superficial, very fine, appearing almost effaced to unaided eye (Fig. 321). Raised outer margin of pygidium effaced apically or not. Dorsal color variable, never coppery red. Distribution variable 2

2a. Pronotum of male as in Figure 315. Disk of female pronotum extremely coarsely punctatorugose posteromedially (Fig. 320). Raised outer margin of pygidium often effaced or nearly so apically (as in Fig. 324). Higher elevations (1800–2900 m) of the Sierra Madre del Sur of Guerrero and Oaxaca, Mexico . . . . . *Phanaeus* (*P.*) *damocles* Harold

b. Pronotum of male as in Figure 313. Disk of female pronotum less coarsely punctatorugose posteromedially (Fig. 319). Raised outer margin of pygidium always complete (Fig. 323). Transverse Volcanic Range from Veracruz to Jalisco, Sierra Madre Occidental from Durango to southwestern United States, Sierra Madre Oriental from Hidalgo to San Luis Potosí (Fig. 329) . . . . . *Phanaeus* (*P.*) *quadridens* (Say)



Figures 323–328. *Phanaeus* (*Phanaeus*) *quadridens* group (**323,** *P. quadridens*, pygidium; **324,** *P. palliatus*, same; **325,** *P. palliatus*, clypeal margin {arrow indicates notch}; **326,** *P. quadridens*, female mesotibial spurs; **327,** *P. damocles*, longer female mesotibial spur; **328,** *P. palliatus*, same).

Phanaeus (*Phanaeus*) *palliatus* Sturm

Figures 48–50, 317, 318, 322, 324, 325, 328, 329

Phanaeus palliatus Sturm, 1843:332

Type: Male holotype ("Mexico"), Zoologische Staatssammlung, Munich.

OTHER REFERENCES. Harold, 1859, 1863; Gemminger and Harold, 1869; Bates, 1887; Nevinson, 1892a; Gillet, 1911b; Olsoufieff, 1924; Blackwelder, 1944; Halffter and Matthews, 1966; Barrera, 1969; Edmonds, 1972; Edmonds and Halffter, 1972, 1978; Morón, 1984; Morón and Zaragoza, 1976.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 48–50).—Dorsum exhibiting three

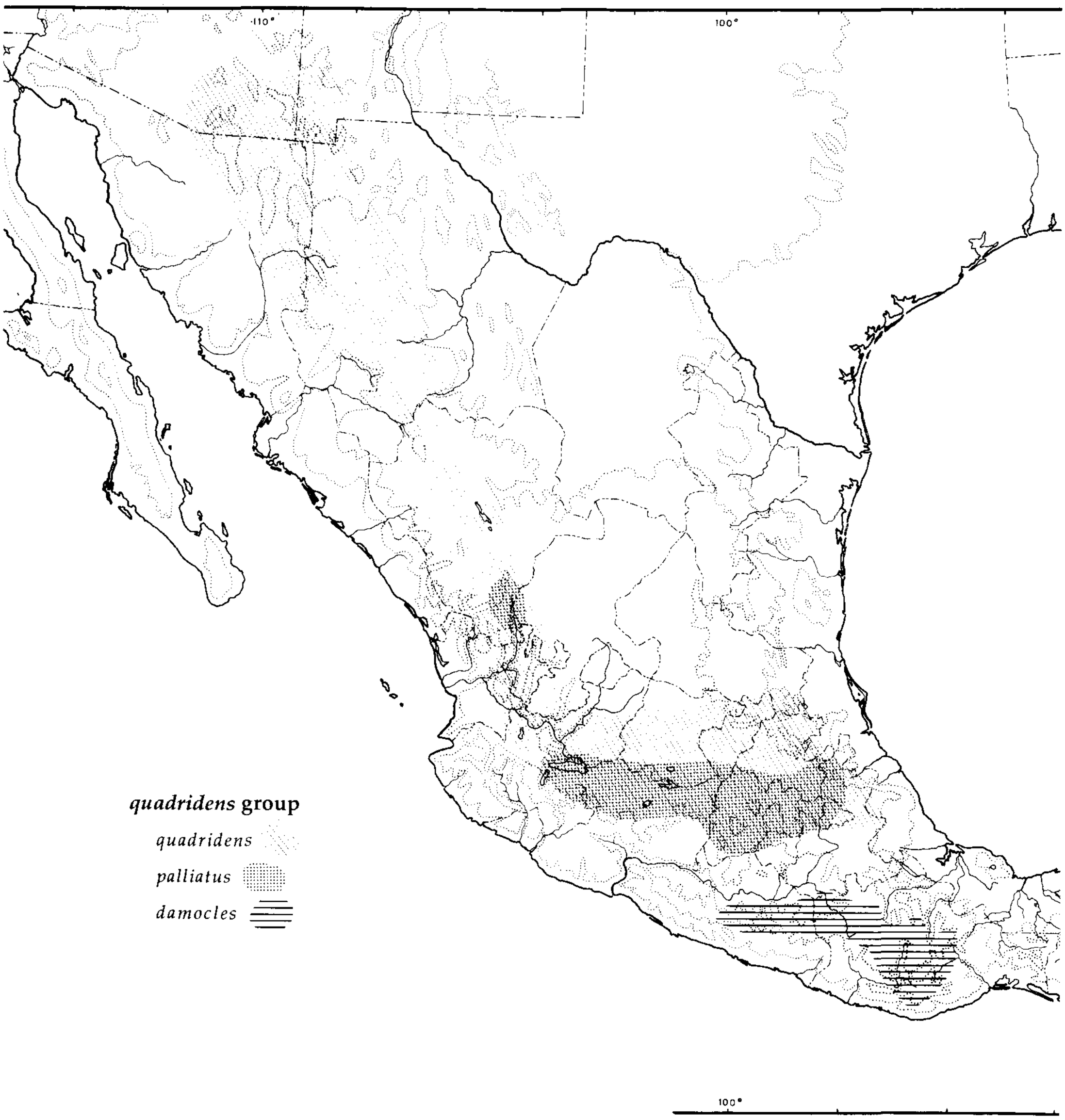


Figure 329. Distribution of the *Phanaeus* (*Phanaeus*) *quadridens* group.

distinct color phases: (a) bright coppery red, often with isolated greenish reflections, (b) dark blue, (c) bright green; intermediates exist among all three. Red phase predominates in most populations; blue-green most common intermediate (see "Comments"). Pygidium colored as dorsum, shining. Venter dark, with strong colored reflections. *Pronotal Sculpturing.—Male:* Disk of larger individuals coarsely rugose except for raised area along posterior margin, which is smooth except for median field of coarse punctures; smooth basal area of disk longest medially, its anterior angle bearing strong tooth; sides of disk rather densely, coarsely granulorugose. Disk of smaller individuals as above except smooth basal area replaced by coarsely but sparsely punctatorugose area. *Female:* Disk coarsely, densely punctatorugose; sides coarsely, densely granulorugose. *Mesotibia.*—Longer spur dilated subapically (Fig. 328). *Elytra* (Fig. 322).—Striae fine, impressed, minutely punctate (×20); interstriae convex, evenly, sparsely, finely punctate (×20). *Pygidium.*—Raised outer margin usually effaced apically. *Secondary Sexual Characters.—Male* (Fig. 317): Pronotal disk of larger individuals concave, posterior angles rounded laterally, upturned; smooth basal area strongly toothed anteromedially. Pronotum of smaller individuals with less well defined disk, but almost always retaining at least trace of basal tooth. *Female* (Fig. 318): Cephalic carina narrow, trituberculate, well in front of eyes. Pronotum weakly concave in front of basal fossae, otherwise evenly convex, with low, smooth transverse area

near anterior margin; this transverse area bounded posteriorly by doubly bowed crease. *Specimens Examined.*—270 males, 193 females (length 13–19 mm; width 8–13 mm).

DIAGNOSTIC REMARKS. This species is easily distinguished from other members of the group by the relief of the elytra. Superficially it resembles *eximius,* from which it differs in pronotal sculpturing and distribution.

DISTRIBUTION (Fig. 329; appendix). Transverse Volcanic Range of southern Mexico from northern Puebla to eastern Jalisco, and southern Sierra Madre Occidental of Durango. Forest margins at middle to high elevations (1800–2800 m). Coprophagous. Collection dates: June–September.

COMMENTS. This species appears to prefer disturbed habitats where forest has been cleared or severely thinned for pastureland. Such a preference suggests to me that in pre-livestock raising times, it was restricted to transition zones between forest and meadowlands. Indeed, before the careful field work of Gonzalo Halffter revealed localities where it is relatively common, *palliatus* was considered a rare species. I and others have collected this species in the Sierra Madre Occidental of southern Durango in habitat similar to that it occupies farther south. Barring its introduction into Durango along with cattle, it seems reasonable to suppose that its range between the Tranverse Volcanic Range of eastern Jalisco and the sierras of southern Durango is continuous. Although there is an absence of collection records for northern Jalisco and southwestern Zacatecas, I suspect that *palliatus* occurs in these areas also.

Phanaeus palliatus is one of the few species of the genus that exhibits distinct, almost mutually exclusive color phases. Intermediate colors do occur (see "Descriptive Remarks"), but they account for less than about 5% of the observed variation in local populations. The approximate frequencies of phases among all material studied were 3% green, 27% blue, and 70% red, distributed equally between the sexes. In most populations, red is by far the predominant color; a series examined from Tulancingo, Hidalgo, and nearby Huauchinango, Puebla, comprise about 80% blue and blue-green individuals and 20% red.

This species is closely related to *damocles,* and their relative distributions suggest that they are vicariants. Contrary to my 1972 conclusion, *palliatus* is not a close relative of *eximius,* a member of the *tridens* group (q.v.).

Phanaeus (Phanaeus) damocles Harold

Figures 46, 47, 315, 316, 320, 327, 329

Phanaeus damocles Harold, 1863:165

Type: Male lectotype ("Mexico"), Muséum National d'Histoire Naturelle, Paris (the designated type locality is "Oaxaca, Capulalpam") (Arnaud, 1982a:114).

OTHER REFERENCES. Gemminger and Harold, 1869; Bates, 1887; Nevinson, 1892a; Gillet, 1911b; Olsoufieff, 1924; Blackwelder, 1944; Barrera, 1969; Edmonds, 1972.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 46, 47).—Pronotum, posterior portion of head completely black, dark blue, or green with golden to coppery reflections on sides. Elytra weaking shining, sometimes completely black or dark blue, but usually with distinct green reflections at least along inner margins, on apices. Pronotum of male, if not entirely black, completely colored except along posterior margin; that of female seldom completely colored, usually mostly black on disk. Pygidium black, or colored as dorsum. Venter black, sometimes with blue or green tinges of color. *Pronotal sculpturing.—Male:* Disk of larger individuals coarsely rugose except for raised area along posterior margin, which is smooth except for few coarse median punctures; this raised area longest medially, its anteromedian angle bearing strong, dentiform tubercle. Sides densely, coarsely granulorugose. Small males as above except generally less coarsely rugose, raised basal area replaced field of coarse punctures between which surface is smooth. *Female* (Figs. 316, 320): Disk punctatorugose, more coarsely so posteriorly, laterally; sides granulorugose. *Mesotibia.*—Longer spur dilated subapically (Fig. 327). *Elytra* (as in Fig. 321).—Appearing very smooth to unaided eye. Striae amost effaced; first, usually also second striae coarsely punctured; remaining striae only weakly punctured (×10). Interstriae flat except for convex apical one-half of first interstria. *Pygidium.*—Raised outer margin usually effaced apically (as in Fig. 324). *Secondary Sexual Characters.—Male* (Fig. 315): In larger individuals, disk concave, posterior angles rounded laterally, upturned; raised basal area strongly toothed medially. In smaller individuals, features of disk less demarcated but almost always retaining at least trace of posteromedian tooth. *Female* (Fig. 316): Cephalic carina trituberculate, set well in front of eyes. Pronotum weakly concave in front of basal fossae, otherwise evenly convex with low, smooth transverse area near anterior margin; this transverse smooth area bounded posteriorly by double arched crease. *Specimens Examined.*—39 males, 31 females (length 12–19 mm; width 8–12 mm).

DIAGNOSTIC REMARKS. The form of the pronotum of both sexes strongly resembles their counterparts in *palliatus,* which has distinctly convex elytral interstriae. Females are easily confused with those of *quadridens,* which have a less coarsely sculptured pronotum and entire outer margin of the pygidium.

DISTRIBUTION (Fig. 329; appendix). Pine/oak and oak forests at higher elevations (1800–2900 m) of the Sierra Madre del Sur of Guerrero and Oaxaca. Coprophagous. Collection dates: June–September.

COMMENTS. This uncommon species appears to be restricted to the montane forests of Guerrero and Oaxaca. It can occur above 2500 m, well above the upper altitudinal limit of most other North American *Phanaeus*.

Phanaeus (*Phanaeus*) *quadridens* (Say)

Figures 43–45, 313, 314, 319, 321, 323, 326, 329

Copris quadridens Say, 1835:176

Type: Male neotype ("Mexico, D. F."), Museum of Comparative Zoology, Harvard University (MCZ Type No. 32877), PRESENT DESIGNATION.

Phanaeus quadridens (Say), Harold, 1859:198
Phanaeus violaceus Laporte-Castelnau, 1840:81 (Harold, 1859:198)

Type: Unknown to me.

Phanaeus laevipennis Sturm, 1843:333 (Harold, 1859:198)

Type: Female holotype ("Mexico"), Zoologische Staatssammlung, Munich.

Phanaeus quadridens borealis Olsoufieff, 1924:100, NEW SYNONYMY

Type: Unknown to me.

OTHER REFERENCES. Lacordaire, 1856; LeConte, 1859; Harold, 1863; Blanchard, 1885; Bates, 1887; Nevinson, 1892a; Henshaw, 1885; Villada, 1901; Kolbe, 1905; Gillet, 1911b; Leng, 1920; Blackwelder, 1939; Blackwelder and Blackwelder, 1948; Robinson, 1948; Halffter, 1952, 1955, 1961, 1964, 1976; Halffter and Matthews, 1966; Barrera, 1969; Edmonds, 1972; Halffter and Edmonds, 1982; Morón, 1984; Morón and Zaragoza, 1976.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 43–45).—Dorsal coloration varying between two extremes: (a) dark blue to blue-violet (sometimes almost black), often with light blue reflections on anterolateral angles of pronotum; and (b) bright, deep green to yellow-green. Color present on posterior portion of head, sides of pronotum, elytra; disk of pronotum usually completely colored in male and mostly black in female; elytra of blue individuals evenly colored; those of green individuals bright along periphery, dark, sometimes almost black, centrally. Pygidium colored as dorsum. Venter almost black, with moderately shining colored highlights in blue individuals, dark with strong green reflections in green specimens. *Pronotal Sculpturing.—Male:* Sides densely granulorugose, disk coarsely rugose except posteromedially, where it is coarsely punctatorugose. *Female* (Fig. 319): Sides densely granulorugose, disk punctate to punctatorugose. *Mesotibia.*—Longer spur not dilated subapically (Fig. 326). *Elytra* (Fig. 321).—Appearing smooth to unaided eye. Striae fine, often almost effaced; minutely punctured (×40), punctures strongest at bases of striae 1 and 2. Interstriae flat, minutely, sparsely punctured (×40), most strongly so laterally. Elytral suture sometimes bearing fringe of black setae. *Pygidium.*—Raised outer margin complete (Fig. 323). *Secondary Sexual Characters.—Male* (Fig. 313): Disk of pronotum of larger individuals flattened, with distinct posteromedian convex area, four strong, acute tubercles; posterolateral angles strongly produced laterally, only weakly upturned. *Female* (Fig. 314): Cephalic carina trituberculate, narrow, set in front of eyes, often strongly raised in larger specimens. Pronotum evenly convex, distinctly concave in front of basal fossae; anteromedian prominence only weakly produced, with straight or double-curved transverse carina. *Specimens Examined.*—858 males, 720 females (length 13–23 mm; width 8–14 mm).

DIAGNOSTIC REMARKS. Females can closely resemble those of *damocles*, from which they differ by less coarse pronotal sculpturing, completely margined pygidium, and distribution.

DISTRIBUTION (Fig. 329; appendix). Transverse Volcanic Range from extreme west-central Veracruz to northern Michoacán; the Altiplano of Querétaro and Guanajuato (and probably also Zacatecas); the southern Sierra Madre Oriental; and the Sierra Madre Occidental from northwest Jalisco to extreme southeastern Arizona (and adjacent areas in Nayarit, Sinaloa, Sonora, and southwestern New Mexico). Grassland, mixed forest–grassland area at mid-elevations (1500–2000 m). Coprophagous, common in places grazed by livestock. Collection dates: June–November (most July–September in Mexico, August–September in Arizona).

COMMENTS. The distribution of *quadridens* corresponds rather closely to the mountain and plateau regions which border the central, xeric interior of Mexico. It rarely occurs at elevations below 1500 m (5000 ft). Halffter (1964, and elsewhere) refers to this pattern of distribution as "dispersión en el Altiplano." Throughout most of the southern portion of its range, it is sympatric with *palliatus*.

Olsoufieff (1924:100) introduced the name "borealis" as a variety of *quadridens* including green specimens he observed from northwestern Mexico and the southwestern United States: ". . . il se peut que tous les *4-dens* de la Sonora du Nord, Californie Sud, Arizona et N.-Mexique soient verts aussi, en constituant une race locale (var. *borealis* n.), ce qui serait intéressant à établir." Although it has never been proposed formally as such, "borealis" has often been cited as a subspecies of *quadridens*, a status consistent with the International Code. I have not located the type, which one would expect to find in Paris, and doubt that Olsoufieff designated one. I have chosen not to recognize *borealis* as a subspecies. While rare individuals in southern populations have a distinctly blue-green color, greenish

individuals do not appear regularly until central Chihuahua. Here, more than 50% of the specimens studied are blue-green or green. Farther north in Arizona, more than 85% of observed individuals are greenish and lack any trace of bluish highlights. Insofar as coloration is concerned, central Chihuahua is a transition zone between blue populations to the south and largely green populations to the north. Other than frequency of color phases, I can find no differences between northern and southern populations of *quadridens.*

I have seen one blue specimen of this species labeled "near Hot Springs, Las Vegas, New Mexico"; this record needs corroboration. Contrary to early records (e.g., Olsoufieff, 1924), *quadridens* does not occur in southern California.

The type of *quadridens* was evidently among those destroyed in the 1830s (A. Newton, pers. comm.). Moreover, no specimens occur in either of the collections of T. W. Harris and the LeContes at Harvard University. The designated type locality is "Mexico," and I assume Say himself collected his material during a sojourn there in 1827–1828 in the company of William McClure. During this time he traveled from the port city of Veracruz to Mexico City, presumably collecting along the way (Weiss and Ziegler, 1931). Since Mexico City, or more generally the Distrito Federal, is well within the known range of *quadridens,* and since it is reasonable to assume that Say collected there, I have chosen as neotype a male from this area. The neotype is a large violet-blue specimen with an inconspicuous fringe of setae along the elytral suture.

The *vindex* Group

DIAGNOSIS. [1] Outer margin of head not notched laterally; [2] clypeal process a rounded, transverse ridge; [3] cephalic process of female simple carina (Fig. 357) or strongly raised, apically truncate or emarginate, corniform process (Fig. 356); [4] anterolateral portion of pronotum strongly granulorugose (Figs. 339, 340); [5] basal pronotal fossae usually distinct; [6] disk of male pronotum flat, with prominent posterolateral angles (Figs. 347–348) (reduced in *igneus,* Fig. 349); [7] pronotum of female more-or-less evenly convex (*igneus,* Fig. 335) or with transverse anteromedian prominence anterior to which surface abruptly declivitous (Figs. 331, 333); [8] elytral interstriae (Figs. 341–346) densely, heavily punctured; punctures often coalescing to form reticulate or longitudinal ridging; [9] front tibiae tridentate (Figs. 352, 353) (small fourth tooth in *difformis,* Figs. 352, 353); [10] female mesobasitarsus not widened apically; [11] longer mesotibial spur dilated subapically; [12] pygidium densely punctatorugose; [13] eastern two-thirds of the United States and extreme northern Mexico (Fig. 360).

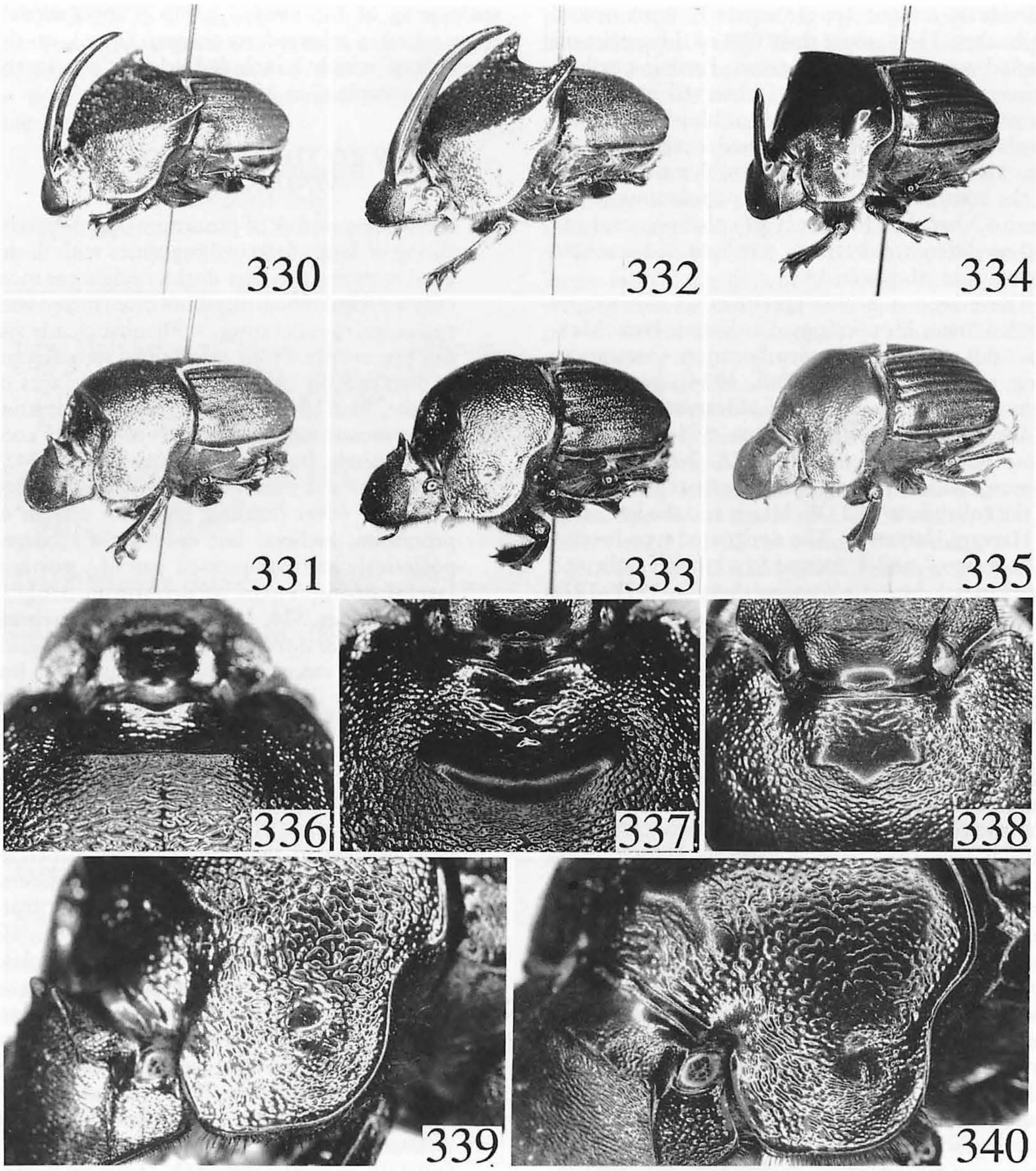
This group consists of three U.S. species, *igneus* Macleay, *vindex* Macleay, and *difformis* LeConte, distinguished from closely related groups by the sculpturing of the elytra and pronotum. The elytral sculpturing of the *vindex* group is most closely approached in *triangularis texensis* (q. v.), on the strength of which I included *triangularis* in the "*vindex* complex" in 1972.

KEY TO THE SPECIES OF THE *VINDEX* GROUP

1a. Sculpturing of disk of pronotum (Fig. 340) consisting of large, flattened rugosities with ill-defined margins such that distinct ridging at most only weakly defined; rugosities often mixed with sparse micropuncturing (×40) most clearly visible posteriorly. Front apical tibial spur abruptly bent mesally (Fig. 355). Ventral surfaces of middle, hind tibiae smooth. Elytral interstriae flat, punctatorugose (Fig. 341) to weakly convex, strongly, but simply punctured (Fig. 342). *Male:* Cephalic horn of large individuals (Figs. 334, 358) never reaching posterior margin of pronotum, inclined but only slightly curved posteriorly and compressed apically; posterolateral prominences of pronotum broadly rounded (Figs. 334, 349), disk never presenting flat, triangular dorsal surface. *Female:* Anterior portion of circumnotal ridge more or less straight, not distinctly angulate medially (Fig. 338); cephalic carina low, thickened mesally and at most only barely trituberculate (Fig. 357); pronotum in profile evenly rounded from posterior to anterior margins; anteromedian pronotal prominence almost always either effaced or consisting of two low, rounded tubercles (Fig. 338), rarely in form of weak transverse carina. Florida, adjacent coastal plains from eastern Louisiana to North Carolina (Fig. 360) . . . . . *Phanaeus* (*P.*) *igneus* Macleay

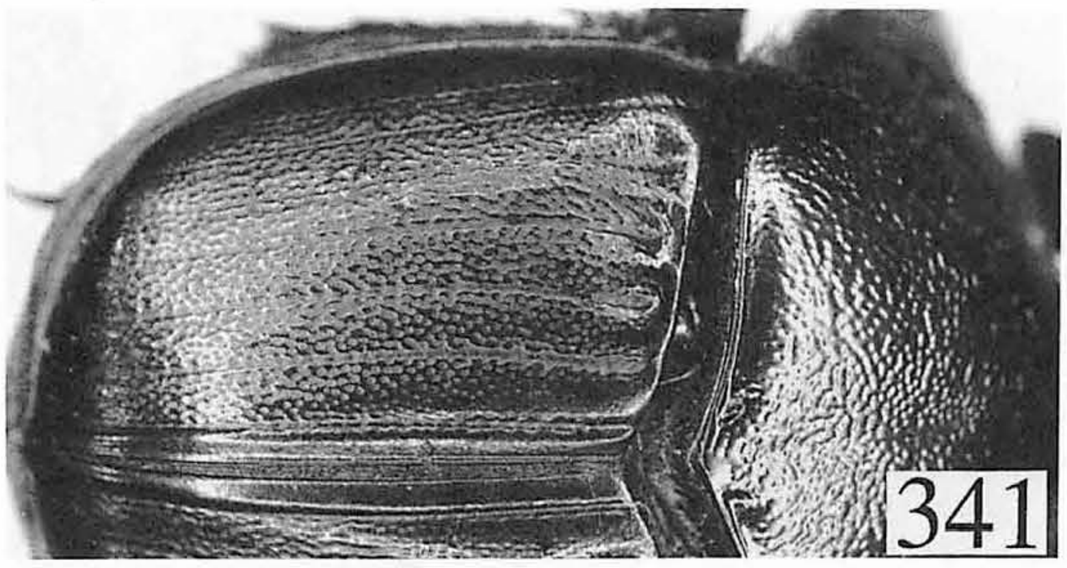
b. Sculpturing of disk of pronotum consisting of well-defined, ridge-like rugosities with distinct margins (Fig. 339); micropuncturing absent. Front apical tibial spur evenly curved mesally or nearly straight (Fig. 354). Ventral surfaces of apices of four posterior tibiae finely, but distinctly rugose. Elytral interstriae flat, densely punctate to punctatorugose (Figs. 343–346). *Male:* Cephalic horn of large individuals usually reaching or surpassing posterior margin of pronotum, evenly curved posteriorly, conical apically (Figs. 330, 332, 359); posterolateral prominences of pronotum acute, disk always distinctly flattened dorsally, more-or-less triangular (Figs. 347, 348). *Female:* Anterior portion of circumnotal ridge strongly angulate mesally (Figs. 336, 337); cephalic carina strongly raised medially as apically truncate or emarginate, corniform process (Fig. 356); pronotum of large individuals, seen in profile, abruptly vertical anterior to distinct transverse ridge (Figs. 331, 333). Distribution variable 2

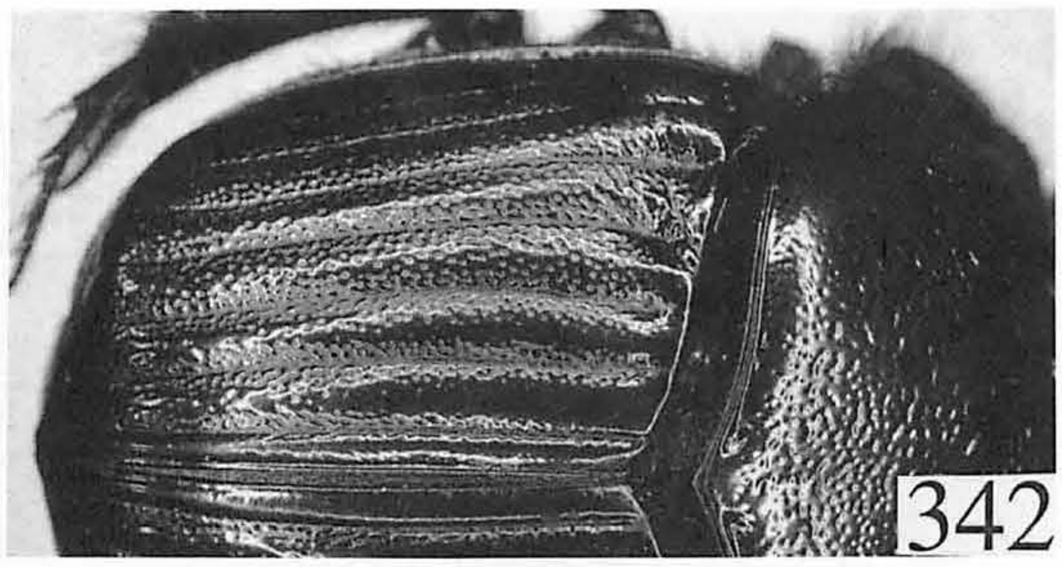
2a. Bases of elytral interstriae 2–3 raised, smoother, shinier, less densely punctate than adjacent areas, never bearing distinct midlongitudinal

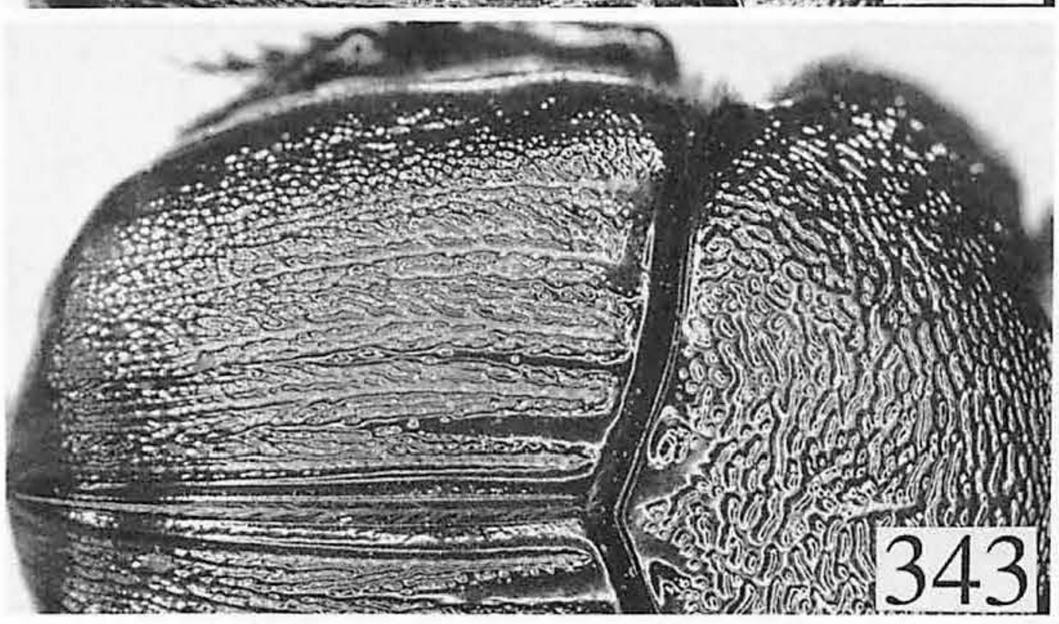


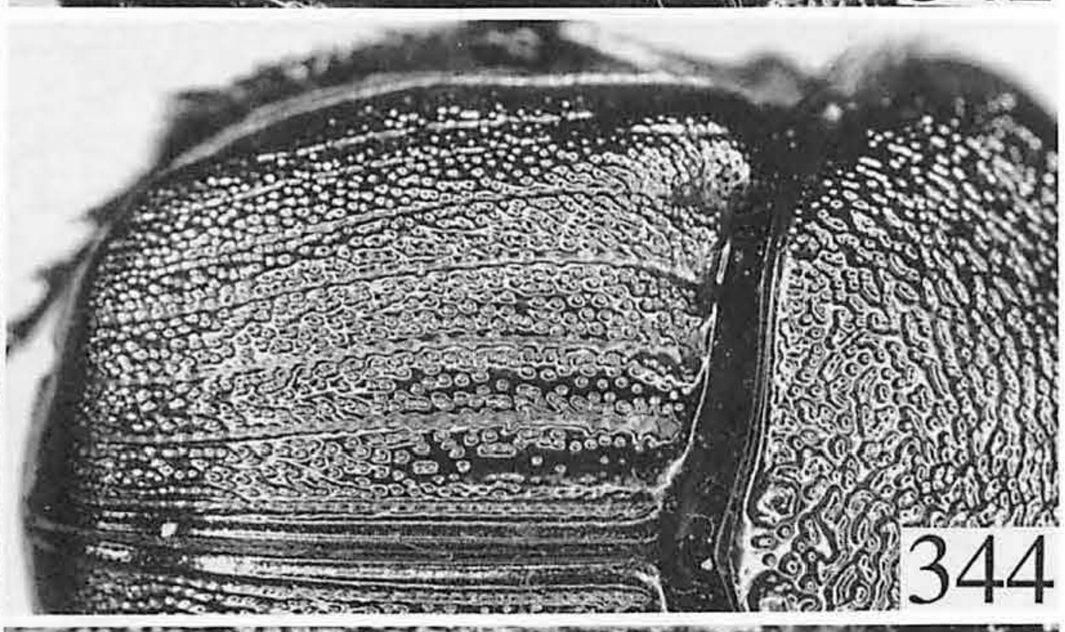
Figures 330–340. *Phanaeus* (*Phanaeus*) *vindex* group (**330,** *P. vindex*, male; **331,** same, female; **332,** *P. difformis*, male; **333,** same, female; **334,** *P. igneus*, male; **335,** same, female; **336,** *P. vindex*, dorsal view anterior portion female pronotum; **337,** *P. difformis*, same; **338,** *P. igneus*, same; **339,** *P. vindex*, anterolateral portion female pronotum; **340,** *P. igneus*, same).

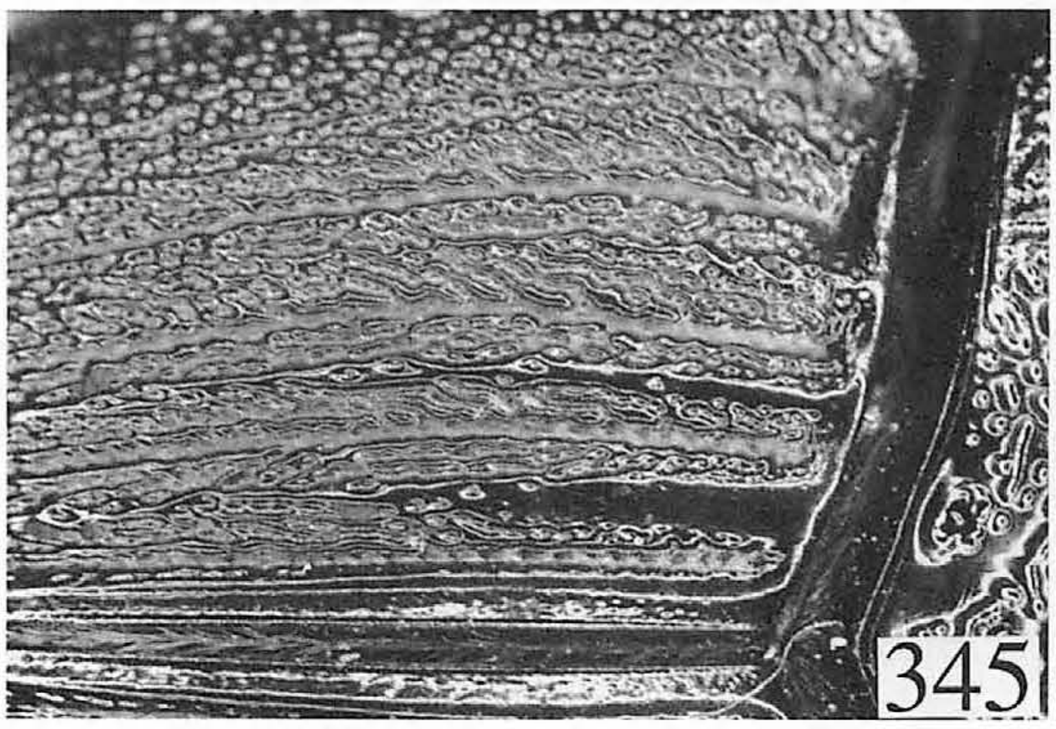
costae (Fig. 346); interstriae otherwise densely punctatorugose, punctures coalescing to produce irregular, usually reticulate (as opposed to longitudinal) ridging (Figs. 344, 346). Elytral striae 1–2 narrow, widths near base usually less than one-fifth widths of interstriae 2–3, respectively. Circumnotal ridge irregularly serrate behind anterolateral angle (Fig. 348B). Front tibiae quadridentate, fourth (basal) tooth small but distinct in all but worn specimens (Figs. 352, 353). *Male* (Figs. 332, 348): In large individuals, sides of disk of pronotum curved; posterolateral angles of disk elongate, their tips (seen from above) not extending beyond lateral margin of pronotum. *Female:* In large individuals, transverse, anteromedian ridge of pronotum effaced medially, from above (Fig. 337) usually bowed posteriorly, not bounded posteriorly by complete, carina-like crease; in small specimens, anteromedian pronotal prominence reduced to two isolated, rounded tubercles. South-central United States, extreme north-

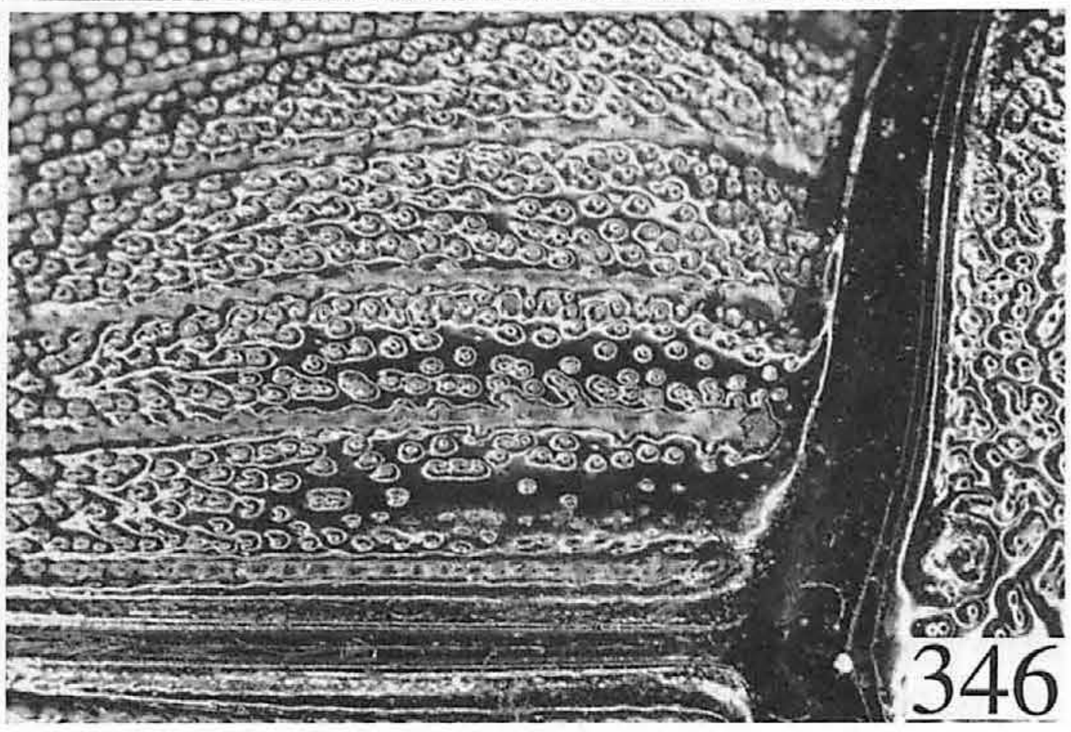












Figures 341–346. *Phanaeus* (*Phanaeus*) *vindex* group (**341, 342,** *P. igneus*, dorsal view elytron; **343,** *P. vindex*, same; **344,** *P. difformis*, same; **345,** *P. vindex*, same; **346,** *P. difformis*, same).

eastern Mexico (Fig. 360) . . . . . *Phanaeus* (*P.*) *difformis* LeConte

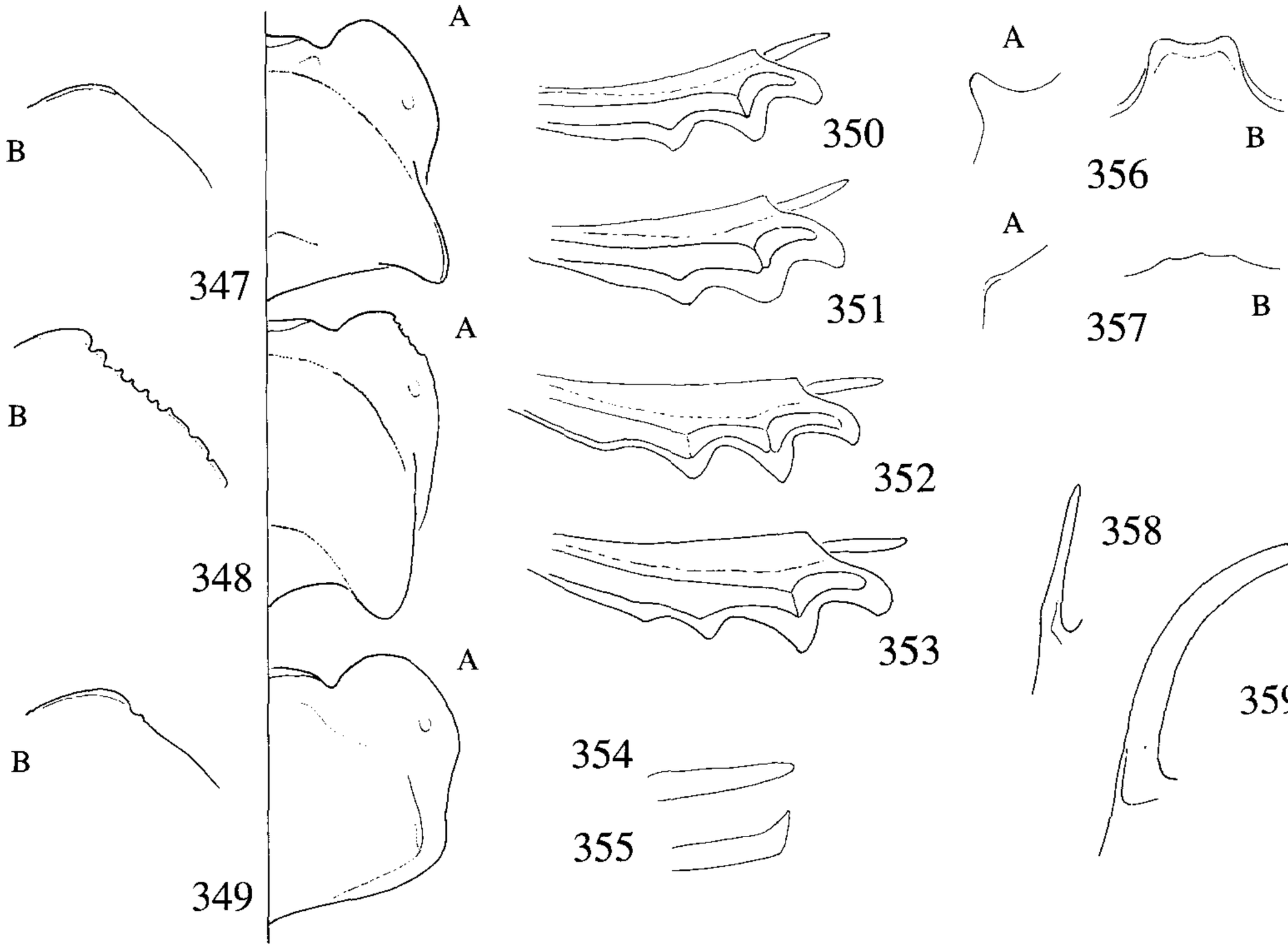
b. Elytral interstriae 2–3, sometimes also 4–5, each with single, strong midlongitudinal costa (Figs. 343, 345); costae of interstriae 2–3 often extending length of elytra; those of interstriae 3–4, if present, usually less than one-half length of elytra. Sculpturing of interstriae 2–3 consisting otherwise of ridge-like rugosities often joining to form fine ridges which parallel costae (Fig. 345); remainder of interstriae densely punctatorugose to granulorugose. Elytral striae broad, flat (×15), widths near base usually greater than one-fifth those of interstriae 2–3, respectively. Circumnotal ridge simple behind anterolateral angle (Fig. 347B); rarely with one or two small teeth or (in some Texas and Arizona specimens) with weak serration. Front tibiae tridentate (Figs. 350, 351), fourth (basal) tooth sometimes suggested by indistinct angulation of tibial margin or rarely distinct. *Male:* In large individuals, sides of pronotal disk straight, longitudinal axes of posterolateral angles diverging posteriorly such that angles (seen from above, Fig. 347A) project to or slightly beyond lateral margin of pronotum. *Female:* Transverse anteromedian prominence of pronotum complete, seen from above (Fig. 336), straight, bounded posteriorly by uninterrupted, carina-like crease; in very small individuals, prominence reduced to two isolated, flat, rounded tubercles. Widely distributed in the eastern half and southwestern portions of the United States and in extreme northern Mexico (Fig. 360) . . . *Phanaeus* (*P.*) *vindex* Macleay

Phanaeus (*Phanaeus*) *igneus* Macleay

Figures 104–107, 334, 335, 338, 340–342, 349, 355, 357, 358, 360

Phanaeus igneus Macleay, 1819:133

Type: Male neotype ("Georgia"), Macleay Mu-



Figures 347–359. *Phanaeus* (*Phanaeus*) *vindex* group (**347,** *P. vindex*, male pronotum [A = dorsal view; B = anterolateral margin]; **348,** *P. difformis*, same; **349,** *P. igneus*, same; **350,** *P. vindex*, front tibia, male; **351,** same, female; **352,** *P. difformis*, front tibia, male; **353,** same, female; **354,** *P. vindex*, front tibial spur; **355,** *P. igneus*, same; **356,** *P. vindex*, female cephalic process [A = lateral view; B = frontal view]; **357,** *P. igneus*, same; **358,** *P. igneus*, lateral view male cephalic process; **359,** *P. vindex*, same).

seum, University of Sydney, Sydney (Type No. MMINV 8), PRESENT DESIGNATION.

Phanaeus floridanus Olsoufieff, 1924:94, NEW SYNONYMY

Type: Male lectotype ("St. John's Bluff, E. Florida"), Muséum National d'Histoire Naturelle, Paris (Arnaud, 1982a:116).

OTHER REFERENCES. Blanchard, 1885; Nevinson, 1892a; Henshaw, 1885; Gillet, 1911b; Leng, 1920; Hayden, 1925; Cartwright, 1934, 1939; Brimley, 1938; Blackwelder, 1939; Loding, 1945; Robinson, 1948; Blackwelder and Blackwelder, 1948; Miller, 1961; Miller et al., 1961; Howden, 1955; Halffter and Matthews, 1966; Fincher et al., 1969, 1970, 1971; Edmonds, 1972; Fincher, 1973a,b, 1975a,b, 1979, 1981; Woodruff, 1973.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 104–107).—Dorsum brightly shining to dull; color highly variable: (a) uniformly black, dark blue to blue-green, color occasionally more pronounced on pronotum; to (b) pronotum coppery red, elytra bright green to coppery red. Many intermediates occur, particularly in shades of coloration, combinations of pronotal and elytral colors. Pygidium colored as elytra. Venter dark, with few muted colored reflections to brighter with strongly shining colored areas on legs, sterna. *Pronotum.*—Anterolateral margin not serrate. Basal fossae usually at least indicated. *Pronotal Sculpturing.*—*Male:* In large individuals, sides rather finely, sparsely to more coarsely, densely granulorugose; sculpturing coarsest anterolaterally, clearly finer below lateral fossae. Central area of disk coarsely rugose, rugosities flattened, sometimes with ill-defined margins so as to appear partially effaced; widely scattered micropunctures usually visible (×30) in spaces separating rugosities; micropunctures usually most distinct in shiniest specimens. Sculpturing of posterolateral portions of disk weaker than in center of disk, often grading into widely scattered, simple punctures. Disk somewhat raised posteromedially; this raised area impressed midlongitudinally, distinctly more coarsely sculptured (punctatorugose) than adjacent areas. In smaller individuals, sculpturing as above except that disk not raised posteromedially, area of disk behind line connecting remnants of posterolateral angles rather coarsely, densely punctatorugose medially, punctate to granulorugose laterally. *Female* (Figs. 338, 340): As in male except posterior two-thirds of disk, in an approximately triangular area whose apices

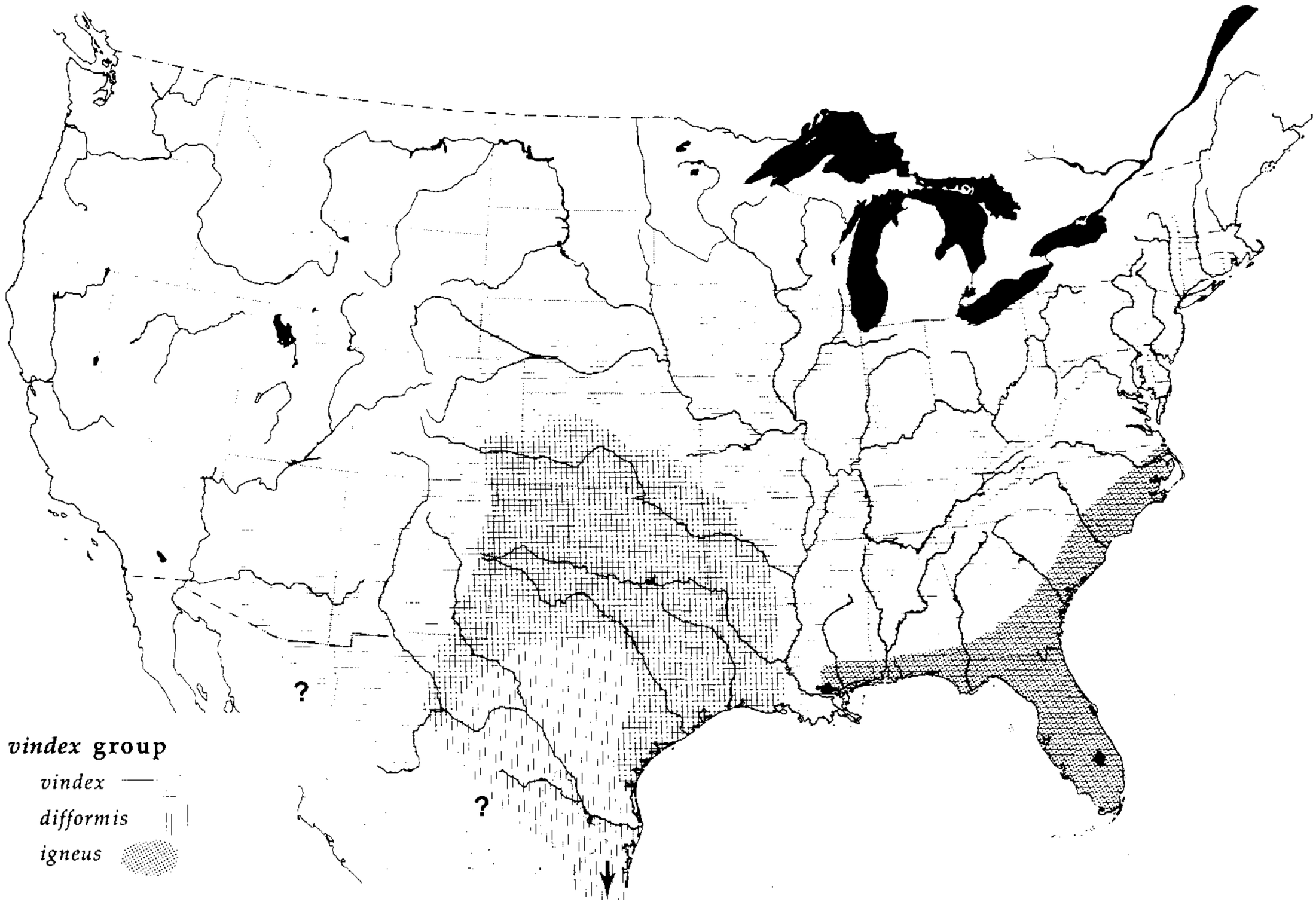


Figure 360. Distribution of the *Phanaeus* (*Phanaeus*) *vindex* group.

are anteromedian prominence, posterolateral angles, coarsely, rather densely punctate to granulorugose; sculpturing denser in, near middle of disk, sometimes partially effaced in shiniest specimens. Disk weakly, but usually perceptibly impressed midlongitudinally from posterior margin to middle. *Tibiae.*—Front tibiae tridentate; fourth (basal) tooth at most only weakly indicated; apical spur abruptly bent mesally (Fig. 355). Ventral surface of apices of middle, hind tibiae smooth. *Elytra.*—Striae simple to minutely punctured (×30). Interstriae varying between two extremes: (a) (Fig. 342) all interstriae appearing uniformly shining, convex to unaided eye; first interstria smooth, basal one-third to one-half of second and third interstriae with few, widely scattered, small simple punctures or largely smooth; remaining interstriae, distal portions of second and third distinctly, uniformly densely punctured, these punctures round, separated by shining raised areas, rarely confluent; (b) (Fig. 341) first interstria smooth, convex; other interstriae appearing uniformly dull, flat to unaided eye but under magnification (×15) appearing uniformly, densely punctatorugose, punctures large, flat, coalescing frequently to produce reticulate pattern of fine, shining rugosities. *Secondary Sexual Characters.—Male* (Figs. 334, 349): In largest individuals, pronotal disk flattened medially, posterolateral angles produced as broad, slightly upturned rounded lobes; in smallest individuals, pronotum almost evenly convex, posterolateral angles reduced to round tubercles. Cephalic horn, even in largest individuals, extending little beyond middle of disk; in smallest individuals, reduced to small, weakly emarginate tubercle. *Female:* Cephalic carina narrow, thickened mesally, usually simple (faintly trituberculate in some specimens showing no wear). Anteromedian prominence of pronotum (Fig. 338) usually weak, often appearing as two separated tubercles or altogether absent; at most (rarely so even in largest individuals) weak, thick, transverse ridge; pronotum in profile more or less evenly rounded from posterior to anterior margins. *Specimens Examined.*—896 males, 722 females (length 13–22 mm; width 7–14 mm).

DIAGNOSTIC REMARKS. This species is easily distinguished from its U.S. relatives by its pronotal and elytral sculpturing and secondary sexual characters.

DISTRIBUTION (Fig. 360; appendix). Coastal plains of the southeastern United States from extreme southeastern Louisiana through extreme southern portions of Mississippi and Alabama, southern and southwestern Georgia, eastern South Carolina, southeastern North Carolina, and all of Florida except the keys. 0–100 m. Usually associated with sandy soils and pine or mixed pine forests. Coprophagous (rarely necrophagous). Collection dates: March–December (most March–September).

COMMENTS. Almost everything about the general appearance of *igneus* suggests a deemphasis of

what are the salient features of the *vindex* group—that is, an *igneus* looks like a *vindex* which has been subjected to some kind of evolutionary eraser! The most obvious "erasures" have affected secondary sexual characters and sculpturing. Male *igneus* are never as well developed as large ("major") individuals of other species; nor are female characters ever strongly developed. Moreover, dorsal sculpturing, while similar to that of *vindex* and *difformis*, is never sharply defined and, therefore, never appears coarse or dense.

This species is restricted to the coastal plains of the United States. It probably originated in the Floridian refugium created during Pleistocene episodes of glaciation. The northern limit of its distribution coincides with the presumed coastline of the southeastern United States during maximum interglacials (Howden, 1963). The Florida peninsula and adjacent areas of neighboring states are characterized by predominently sandy soils supporting pine and mixed pine forests. *P. igneus* is sympatric with *vindex* throughout its range, although this latter species prefers soils with a significant clay content. It has been collected from many types of excrement and is attracted in large numbers to pitfall traps baited with propionic acid.

Several features of *igneus* that vary geographically prompted Woodruff (1973) to recognize two subspecies: *igneus igneus* and *igneus floridanus*. The extremes in variation are, indeed, distinct; but in my opinion, the variation of this species is not predictable enough geographically to warrant recognition of subspecies. Of particular interest in this context is the variability of the elytra in color and sculpturing. Specimens from Louisiana, Mississippi, Alabama, and the panhandle of Florida west of the Chatahoochee River are always subdued in color (ordinarily dull green or blue-black) and have flat elytral interstriae rather densely covered by flat, confluent punctures. The elytral sculpturing of these specimens is reminiscent of that of *triangularis texensis*. Specimens from peninsular Florida are almost always brightly colored and have weakly convex interstriae with simple punctation (certain specimens from Miami resemble specimens from west of the Chatahoochee River). Individuals from Georgia northward are essentially intermediate, although they generally are more somber colored and have more densely sculptured elytral interstriae than peninsular specimens. Regardless of whether or not subspecies are recognized, it is evident that *igneus* has undergone regional differentiation, perhaps in response to climatic and geographical oscillations associated with cycles of Pleistocene glaciation.

Differences in the pronotal sculpturing between *igneus* and the two other members of the group, while consistent, are subtle. In general, the rugosities of *igneus* lack clear definition when compared to the much more sharply defined granules and ridges found in *vindex* and *difformis*.

The whereabouts of Macleay's type material of *igneus* is uncertain. I have examined the purported types of this species on deposit at the Australia National Insect Collection (Commonwealth Scientific and Industrial Research Organization, Division of Entomology, Canberra) and cited by Britton and Stanbury (1981) as "*igneus* Macleay 1833." These two specimens are labeled "syntypes" and include a male and female transferred to Australia National Insect Collection from the Macleay Collection in Sydney. The female of *igneus* was unknown to Macleay; the male conforms to the original description but no better so than certain other specimens that remain in the Macleay Collection. The Macleay Collection, graciously loaned to me for study by Dr. D. S. Horning, Jr., its curator, includes 11 specimens bearing labels in Macleay's handwriting. It is certain that not all these specimens were at hand when Macleay described *igneus*. His original description treats only the male, and nothing about it suggests that he observed more than a single, small specimen. It is my opinion, therefore, that the series in the Macleay Museum along with the pair in Canberra cannot be considered syntypic, and that the only reasonable course of action is to choose a neotype from among them. From among the specimens in the Macleay Collection, I have chosen a small male labeled "carnifex Georgia" as the neotype. It conforms to the original description in all respects and is the only specimen labeled Georgia, the designated type locality.

Phanaeus (*Phanaeus*) *difformis* LeConte

Figures 101–103, 332, 333, 337, 344, 346, 348, 352, 353, 360

Phanaeus difformis LeConte, 1847:86

Type: Male neotype (no data), Museum of Comparative Zoology, Harvard University (MCZ Type No. 32896), PRESENT DESIGNATION.

Phanaeus difformis magnificens Robinson, 1948: 302, NEW SYNONYMY

Type: Male holotype ("Romeo, Florida"), National Museum of Natural History, Washington, D.C. (Type No. 65634).

NOMENCLATURAL REMARKS. Woodruff (1973:62) synonymized *magnificens* with *vindex*. Robinson's holotype, however, is a well-developed male *difformis* that was very likely mislabeled; it is probably from Texas.

OTHER REFERENCES. Lacordaire, 1856; LeConte, 1863; Gemminger and Harold, 1869; Blanchard, 1885; Nevinson, 1892a; Henshaw, 1885; Gillet, 1911b; Leng, 1920; Olsoufieff, 1924; Brown, 1927; Lindquist, 1933; Blackwelder and Blackwelder, 1948; Dillon and Dillon, 1961; Halffter and Matthews, 1966; Barrera, 1969; Edmonds, 1972; Blume and Aga, 1976, 1978; Nealis, 1977; Fincher,

1981; Fincher and Marti, 1982; Howden and Scholtz, 1986.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 101–103.—Two dorsal color phases: (a) posterior portion of head, sides of prothorax, elytra, pygidium weakly shining dark blue; disk of pronotum weakly shining dark green with feeble yellow highlights; and (b) posterior portion of head, sides of prothorax, elytra, pygidium strongly shining green with conspicuous yellow highlights; disk of pronotum coppery red. Intermediates dark green to blue-green on head, elytra, coppery red with strong yellow highlights on pronotum. Pronotum of male completely colored; that of female black and adjacent to anteromedian prominence. Venter dark with strongly colored (blue or green) reflections on posterior four femora. *Clypeus.*—Weakly, but perceptibly broadly bidentate. *Pronotum.*—Anterolateral margin serrate (Fig. 348B). Anterior margin angulate medially (Fig. 337). Basal fossae usually present; rarely absent in large males. *Pronotal Sculpturing.—Male:* In large individuals, sides densely, fairly coarsely granulorugose; disk more coarsely but less densely granulorugose except for nearly semicircular, coarsely, densely punctatorugose posteromedian area bounded anteriorly by distinct, transverse semicircular ridge. Smaller individuals as above except posteromedian ridge absent or distinct only medially, punctatorugose area relatively larger. *Female:* Sides granulorugose; disk coarsely, densely punctatorugose, most strongly so medially where surface impressed longitudinally. *Tibiae.*—Front tibiae quadridentate in both sexes (Figs. 352, 353), most obviously so in male; fourth (basal) tooth small, but distinct in all but most worn specimens. Ventral surface of apices of posterior four tibiae finely rugose (×15). *Elytra* (Figs. 344, 346).—Striae simple to minutely punctate (×40); narrow, basal widths of second and third striae less than one-fifth width of second and third interstriae, respectively. First interstria narrow, evenly, strongly convex, smooth; remaining interstriae flat, coarsely, densely punctatorugose except for bases of interstriae 2–3, which are widely raised, usually much less densely punctured than elsewhere. Basal one-half to one-third of interstriae 2–3 appearing smooth, shining to naked eye; these raised, smooth areas rarely extending more than one-half length of interstria; width of these raised areas at least one-half, usually three-fourths or more of total width of respective interstriae, only rarely narrow enough to produce distinct costa. Interstriae 4–5 always densely granulorugose. *Secondary Sexual Features.—Male:* Pronotum of large individuals as in Figures 332, 348. *Female:* Cephalic carina raised medially as apically truncate or emarginate corniform process (as in Fig. 356). Anteromedian prominence of pronotum medially, lacking complete cariniform crease behind anterior margin, seen from above (Fig. 337), usually distinctly bowed posteriorly; in smallest individuals, anterior prominence reduced to two round flat tubercles. *Specimens Examined.*—402 males, 285 females (length 13–23 mm; width 7–14 mm).

DIAGNOSTIC REMARKS. Red-green individuals often closely resemble *vindex,* from which they differ by elytral sculpturing, shape of the front tibiae, and, in large individuals, configuration of the pronotum.

DISTRIBUTION (Fig. 360; appendix). South-central United States and extreme northeastern Mexico. 0–1200 m. Coprophagous; open habitats with predominantly sandy soils. Collection dates: March–December (most April–October).

COMMENTS. LeConte's description of *difformis* was based on a single small male. The LeConte Collection in the Museum of Comparative Zoology, Harvard University, includes 12 specimens of *difformis,* one of which is labeled "Type 3709." This latter specimen does not conform with LeConte's description and cannot be regarded as the holotype. Moreover, since the description was based on a single specimen, the series cannot be regarded as syntypic. Among these specimens, however, is one that conforms well with the original description and that I hereby designate as neotype.

This species is especially common in the sandier areas of the coastal plains of Texas and adjacant area of Louisiana and of the eastern Edwards Plateau. It is sympatric with *vindex* in all but the central Texas portion of its distribution (see "Comments" under *vindex.*) Its range extends northward and westward along major river drainage systems, via which it reaches Arkansas, Kansas, and Colorado (Arkansas River), the Texas Panhandle (Red River), and southeastern New Mexico (Pecos River). I have seen one record from El Paso, which if not an error, suggests that it has also followed the Rio Grande westward through the Big Bend region of Texas and Mexico; I have not, however, seen specimens recorded from the Rio Grande valley between El Paso and the mouth of the Pecos River. Locality records about which I have serious doubts include Saltillo, Coahuila (Mexico), and Romeo, Florida (the designated type locality of *magnificens*).

The blue-elytra phase of *difformis* appears to have a simple, intrapopulational genetic basis (Blume and Aga, 1976, 1978); it occurs only in the coastal plains. Aspects of the ecological and genetic relationships between *difformis* and *vindex* are discussed below.

Phanaeus (*Phanaeus*) *vindex* Macleay

Figures 96–100, 330, 331, 336, 339, 343, 345, 347, 350, 351, 354, 356, 359, 360

Phanaeus vindex Macleay, 1819:133

Type: Male neotype ("North America"), Macleay Museum, University of Sydney, Sydney

(Type No. MMINV 7), PRESENT DESIGNATION.

Scarabaeus carnifex Linnaeus, 1767:546 (not 1758, vol. 1:346) (Barber, 1928:383) (permanently unavailable name; see "Nomenclatural Remarks")

Type: Male lectotype; 3 male, 1 female paralectotypes (no data), Linnean Society, London, PRESENT DESIGNATION.

Phanaeus vindex cyanellus Robinson, 1938:107 (Woodruff, 1973:62)

Type: Male holotype ("Chokolostra, Florida"), National Museum of Natural History, Washington, D.C. (Type No. 65636).

Phanaeus vindex rubervirens Robinson, 1948:301, NEW SYNONYMY

Type: Male holotype ("Chiricahua Mts., Cochise Co., Arizona"), the Academy of Natural Sciences of Philadelphia (Type No. 10700).

NOMENCLATURAL REMARKS. The great majority of references to this species prior to about 1965 are under the name *carnifex* L. in spite of the fact that Barber pointed out the confusion attending the name almost 40 years earlier (see also Leng, 1927). The name *carnifex* is now properly applied only to the Jamaican species, *Sulcophanaeus carnifex* (L.) (Matthews, 1966), and, in accordance with Article 52(b) of the International Code, *Scarabaeus carnifex* Linnaeus, 1767, is a permanently unavailable name. In 1972 I suggested that recourse to the International Commission on Zoological Nomenclature was in order to fix usage of the names *carnifex* and *vindex*. I did not follow through because it was not necessary. Matthew's (1966) action of designating a lectotype for *carnifex* L., 1758, fixed the identity of the Jamaican species with the result that *vindex* remained as the only available name for this North American species. Robinson's (1948) *magnificens*, which Woodruff (1973:62) synonymized with *vindex*, is in fact *difformis* (q.v.).

OTHER REFERENCES. To *carnifex:* Drury, 1770; Say, 1823; Laporte-Castelnau, 1840; LeConte, 1847, 1859, 1863; Lacordaire, 1856; Gemminger and Harold, 1869; Blanchard, 1885; Nevinson, 1892a; Henshaw, 1885; Blatchley, 1910; Gillet, 1811b; Leng, 1920; Olsoufieff, 1924; Hayden, 1925; Blatchley, 1910; Brown, 1927; Lindquist, 1933; Cartwright, 1934, 1939; Brimley, 1938; Loding, 1945; Robinson, 1948. To *vindex:* Becton, 1930; Leng and Mutchler, 1933; Cartwright, 1934; Blackwelder, 1939; Ritcher, 1945, 1966; Blackwelder and Blackwelder, 1948; Virkki, 1959; Dillon and Dillon, 1961; Miller et al., 1961; Stewart and Kent 1963; Matthews, 1966; Halffter and Matthews, 1966; Stewart, 1967; Stewart and Davis, 1967; Barrera, 1969; Fincher et al., 1969, 1970, 1971, 1981; Edmonds, 1972; Edmonds and Halffter, 1972, 1978; Fincher, 1972, 1973a,b, 1975a,b, 1979, 1981; Blume and Aga, 1976, 1978; Fincher and Marti, 1982; Morón, 1984; Howden and Scholtz, 1986; Ratcliffe, 1991.

DESCRIPTIVE REMARKS. *Color and Color Pattern* (Figs. 96–100).—Dorsum brightly shining, usually tricolored as follows: posterior parts of head, sides of pronotum golden yellow to yellow-green, disk of pronotum coppery red, elytra golden green to dark green; rarely (a) almost completely dark blue or nearly black or (b) head, pronotum completely golden green, elytra dark blue with green reflections. Variations in shades, distribution of colors together produce many intermediate combinations. Pygidium colored like elytra. Venter with strong colored reflections on legs, often also on sterna. *Clypeus.*—Evenly rounded, rarely with two distinct median teeth. *Pronotum.*—Anterolateral margin simple or weakly serrate (Fig. 347B). Anterior margin in female angulate medially, forming posteriorly directed angulation (Fig. 336). Basal fossae usually at least indicated in female, usually effaced in male. *Pronotal Sculpturing.—Male:* In larger individuals, sides coarsely granulorugose; disk somewhat more rugose than sides with frequent transverse ridging; raised posteromedian area separated from remainder of disk by usually ill-defined bowed ridge, strongly punctato- to granulorugose. Smaller individuals as above except bowed ridge reduced or absent. *Female* (Figs. 336, 339): Sides granulorugose, disk more coarsely rugose than sides with frequent ridging of irregular orientation. *Tibiae.*—Front tibiae (Figs. 350, 351) tridentate in both sexes; fourth (basal) tooth sometimes indicated, but rarely distinct; apical spur approximately straight, apex not strongly bent mesally. Apices of four posterior tibiae minutely rugose (×15) on ventral surfaces. *Elytra* (Figs. 343, 345).—Striae minutely punctate (×30); widths at base of second and third striae more than one-fifth width (usually one-third to one-fourth) of second interstria. First interstria smooth, narrow, evenly, strongly convex; remaining interstriae flat, coarsely sculptured as follows: interstriae 2–3 costate medially for at least one-half, often entire length; basal width of second interstrial costa seldom exceeding one-half width of interstria itself; basal width of third interstrial costa never exceeding width of interstria itself; second and third interstrial costae each flanked by several fine ridges; interstriae 3–4 either densely punctatorugose, or puncturing obsolete such that relief of interstria appears fragmented into series of irregular ridges, granules; bases of interstriae 3–4 sometimes costate, but these costae usually shorter, less well defined than those on interstriae 2 and 3. *Secondary Sexual Characters.—Male:* Pronotum as in Figures 330, 347. *Female:* Cephalic process raised, apically truncate or weakly emarginate corniform projection (Figs. 333, 356); anteromedian process of pronotum (seen from above) straight,

bounded by complete, cariniform crease (Fig. 336) or (in small individuals) reduced to two small, round, flat tubercles. *Specimens Examined.*—1504 males, 1624 females (length 11–22 mm; width 7–13 mm).

DIAGNOSTIC REMARKS. This species, especially females and smaller males, can closely resemble *P. difformis.* Features of the elytral striae, sculpturing of the interstriae and the front tibiae will, in combination, separate practically all "look-alikes"; secondary sexual characters will distinguish large individuals.

DISTRIBUTION (Fig. 360; appendix). United States east of the Continental Divide and south of about 43 degrees N latitude except the Edwards Plateau and far western regions of Texas; occurring west of the divide only in New Mexico, Arizona, and northern Chihuahua, Mexico. 0–1400 m. Coprophagous, occasionally collected from carrion. Highly eurytopic. Collection dates: March–October.

COMMENTS. The distribution of *vindex* is both geographically and ecologically very broad, from the Sonoran Desert region of Arizona, to subtropical Florida, to New England. Only rarely has it been collected north of about 43 degrees N latitude. Blume and Aga (1978) recorded *vindex* from southeastern Montana, and it is reasonable to assume it also occurs in South Dakota. I have seen one specimen labeled "Ottawa, Ont[ario]," but its occurrence in Canada needs confirmation (Henry Howden, pers. comm.). This species is sympatric with *difformis* except in the Edwards Plateau and far west regions of Texas, and its distribution completely overlaps that of *igneus* in the southeastern United States.

Many characters of *vindex* vary geographically, but none in ways predictable enough to support, in my opinion, formal recognition of subspecies. Individuals collected east of the Mississippi and south of the Ohio rivers tend to be darker and less shining than those collected to the west and north; those collected east of about 90 degrees W longitude tend to have more sharply defined costae on interstriae 2–3 and obscure to no distinct puncturing on interstriae 4–5. Other variations, such as those upon which Robinson based *cyanellus* and *rubervirens,* appear to be highly localized or repeated in widely disjunct areas.

Blume and Aga (1976, 1978) reported successful interbreeding between *vindex* and *difformis* in the laboratory. Both they and I have observed what appear to be intermediates among field collections, and it could very well be that these two species hybridize under natural conditions. Careful field studies to test the hypothesis have not been done, but one excellent place to conduct a study of the interactions between these two species would be in the area of Medora, Reno County, Kansas, where both species and intermediates occur fairly commonly. All Medora "intermediates" I have seen, however, are *vindex* which resemble *difformis,* never vice versa. While they always strongly resemble *difformis* in color, size, and general appearance, and are easily confused on first (and often also on second) glance, Medora *vindex* are always clearly identifiable as such. I have not observed intermediates between *vindex* and either of the other species with which it is sympatric, *igneus* and *triangularis.*

Macleay (1819) based his description of *vindex* on at least two specimens, a female and a small male, that he regarded as a variety of *Scarabaeus carnifex* L., 1867. The Macleay Collection in Sydney contains eight *vindex,* none of which is identifiable as a type. From these eight I have selected a small male labeled "N. America" conforming to the original description that I hereby designate as neotype.

Incertae Sedis

Phanaeus labreae (Pierce)

Palaeocopris labreae Pierce, 1946:130

Type: Holotype male ("Rancho La Brea Tar Pits, Los Angeles, California"), Natural History Museum of Los Angeles County, Los Angeles (Type No. LACMIP 3059 = C116a).

Phanaeus labreae (Pierce), Miller et al., 1981:627

OTHER REFERENCES. Halffter, 1959; Matthews, 1961; Matthews and Halffter, 1968; Miller, 1983.

COMMENTS. The holotype of *Phanaeus labreae,* the anterior portion of the head of a small male, is among the numerous insect fragments collected by W. D. Pierce from deposits in Pit 81 of the Rancho La Brea Tar Pits in Los Angeles, California. Miller et al. (1981), in their reevaluation of Pierce's species of Scarabaeidae, assigned *labreae* to *Phanaeus* while pointing out that the leg fragments included in the original description belong to other genera (*Copris* and, perhaps, *Deltochilum* and *Onthophagus*). I agree with their conclusion. Further, I believe it highly likely that *labreae* is assignable to an extant species, most probably *vindex.* The latter species now occurs in Arizona. Positive identification of the La Brean species can be made if well-preserved elytra, prothoraces, or both are later discovered among the many, yet unexamined remains.

Rancho La Brea, the type locality of the Rancholabrean Land Mammal Age, comprises perhaps the world's best known late Pleisotcene deposits. The site records roughly 30,000 years of the history of a rich vertebrate fauna that became extinct some 10,000 years ago (Kurtén and Anderson, 1980). Bone collagen of *Equus* from Pit 81 (not associated with *labreae*) has yielded as radiocarbon date of ca. 11,000 yr BP. Most La Brean insect species described by Pierce have been synonymized with extant taxa (Miller, 1983). However, two other dung beetles described by Pierce (1946), *Copris pristinus* and

Onthophagus everestae, are regarded as extinct species by Miller (op. cit.). Miller et al. (1981) pointed out that the paratype legs of *everestae* are assignable to *Canthon*. Collectively, the conclusions of Miller and Miller et al. suggest that the Los Angeles dung beetle fauna of La Brean times was very similar to that we now see in southeastern Arizona. The demise of the La Brean dung beetle fauna was no doubt provoked by both the climatic changes and the extinction of the contemporaneous fauna of large land mammals.

Phanaeus(?) *antiquus* Horn

Phanaeus antiquus Horn, 1876:245

Type: Unknown to me.

COMMENTS. Horn based his description of *antiquus* on portions of elytra and abdominal sterna from ". . . some masses of clay from which were obtained many fragments of Coleoptera" from Port Kennedy Cave, Montgomery County, Pennsylvania. Port Kennedy Cave is a classic Pleistocene site studied by E. D. Cope, whom Horn accompanied when he collected this species as well as another dung beetle from the same deposit described as *Choeridium* (now *Ateuchus*) *ebeninum*. Kurtén and Anderson (1980) refer Port Kennedy Cave deposits to the Aftonian or early Kansan intervals of the late Irvingtonian Land Mammal Age (mid-Pleistocene; ca. 900,000 yr BP).

I have not seen Horn's specimens and, therefore, cannot judge if *antiquus* is indeed referrable to *Phanaeus*. His description is based on the elytra, which suggested to him "[a] species . . . somewhat larger than [*P.*] *carnifex* [= *vindex*]" whose elytral sculpture more closely resembled that of [*P.*] *pluto* (now placed in *Coprophanaeus*). *Coprophanaeus pluto* is a Mexican species of neotropical origin that, in my opinion, has penetrated only very recently (Holocene) into northern Mexico and extreme southern Texas (see biogeographical comments in the introduction). If *antiquus* is a *Phanaeus*, Horn's description suggests it is more likely to be *triangularis*, *sen. str.*, or its relative.

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APPENDIX: DISTRIBUTION DATA

The appendix comprises geographical and temporal label data from specimens examined during this study. No data are included solely from published sources. They are arranged by species and subspecies, which are listed alphabetically. For each taxon, information is listed alphabetically by country and, for each country, alphabetically by first-order political subdivision (state, department, or province; political subdivisions for Belize, Guyana, Suriname, French Guiana, and Trinidad and Tobago are not employed). Map points within political subdivisions are listed randomly, and each is followed, as available, by elevation and by month(s) of collection in roman numerals. For the United States, country and parish records for which there are no known map points appear parenthetically at the end of the state listing. Relevant explanatory information appears parenthetically where necessary.

Phanaeus achilles Boheman

ECUADOR: *Guayas*—40 km SW Guayaquil, 50 m, II; 45 km W Guayaquil; Guayaquil I; Bucay; Posorja, 0 m; *Loja*—Catamayo, X; Loja, IX, X. PERU: *Lambayeque*—Olmos, III; *Tumbes*—Cazaderos.

Phanaeus adonis Harold

MEXICO: *Guanajuato*—Guanajuato, VIII; *Hidalgo*—8 mi NE Jacalá, 5200 ft, VI–VII; Agua Fría, X; Durango, IX; Huasca, IX; Barranca de Meztitlán, VI; 3 mi E Tepeji del Río, VII; 4 mi S Tepeji del Río; Ajacuba, VI; Puerto La Zorra, X; La Placita, VI; *México*—Ixtapantongo, VIII; Ciudad Satélite, VII; Santa Cruz Acatlán, VIII; *Nuevo Leon*—7 mi W El Cercado, 2800 ft, VI; Villa Santiago, 1500 ft, VI; Chipinque Mesa (near Monterrey) 5400 ft, VII; Monterrey, VI; *Querétaro*—3 mi S Querétaro, 6200 ft; *San Luis Potosí*—Microwave Station "Tortugas," km 82 on Hwy 70, VIII; Valles, 300 ft, VI; *Tamaulipas*—9 mi N Ciudad Victoria, VI; Gómez Farías, VI; 4 mi W Antiguo Morelos, 1200 ft, VI; 5 mi NE Llera, VII; Miquihauana, VIII; Cañon de Caballeros, VI.

Phanaeus alvarengai Arnaud

No precise locality data available; see systematic section of text.

Phanaeus amethystinus amethystinus Harold

MEXICO: *Chiapas*—San Cristóbal de las Casas, 2150 m, V–IX; 16 km W San Cristóbal de las Casas, VII; Ocosingo, 905 m; 20 mi W Bochil, 5600 ft, VIII; Lagunas de Montebello, V; Jitotol, 6700 ft, VI; 3 mi W Jitotol, VI; Santa Rosa, V, VIII–IX; NW slope of Cerro Baúl, 21 km W of Rizo de Oro, 1770 m, X; 11 km N Tzontehuitz, 1980 m, X; *Hidalgo*—3 mi N Tlanchinol, 5100 ft, VII; 4 mi SW Chapalhuacán, 3500 ft, VII; 10 mi NE Jacalá, VIII; Laguna Atezca, IX; Zacualtipán, VIII; 3 km S Zacualtipán, 2060 m, VII; *Oaxaca*—Juquila Mixes, VI; *San Luis Potosí*—7 mi W El Naranjo, 2400 ft, VI; 3 mi W Xilitla, 4800 ft, VI; Ciudad de Maiz, VII; *Tamaulipas*—Gómez Farías (Rancho "El Cielo"), 1100 m, IV; *Veracruz*—15 mi NW Jalapa, VII–VII; Citlaltépetl, 7500 ft, VI; Las Vigas; Presidio, VII; Huayacocotla, 2400 m, V; Teapan, 1770 m; Acajete, 2000 m.

Phanaeus amethystinus guatemalensis Harold

GUATEMALA: *Chimaltenango*—Chimaltenango, 1750 m, VII–IX; Zaragoza, 2000 m, VIII–X; *Quetzaltenango*—San Juan Ostuncalco, 2400 m, V; Zunil, 2000 m, VII; Santa María de Jesús, 1550 m, VI; *Quiché*—Chupol, 2300 m, X; Chichicastenango, 6000 ft, VIII; Chuvexa, 2300 m, VII; *Sacatepéquez*—Antigua Guatemala, VI; *San Marcos*—San Marcos, 2500 m, V; *Sololá*—12 km SSE Nahualá, 2275 m, VIII; Santa Lucía Utatlán, 2450 m, V; Chuchexik, 2200 m, X; Sololá, VII; Xajaxac, 2325 m, V.

Phanaeus amithaon Harold

MEXICO: *Aguascalientes*—Aguascalientes; *Colima*—Manzanillo, XII; Colima, VI; Jalisco state line, Hwy 110; *Guanajuato*—Irapuato, VI, XI; 10 mi W Irapuato, VII; Valle de Santiago, VII; Dolores Hidalgo, VIII, IX; 22 mi E Pénjamo, 5200 ft, IX; 6 mi W Pénjamo, VIII; Celaya, VII; *Hidalgo*—15 mi SW Huichapan, IX; Actopan, VIII; *Jalisco*—Cuzalapa, 660 m, VIII; El Tigre, 700 m, VII; Plantanarillo, 620 m, X; 2 mi S Tamazula de Gordiano, 3800 ft, XI; 22 km NE Zapotlanejo, VII; 3.4 km SE Jocotepec, 1493 m, IX; 36 mi N Cuidad Guzmán, IX; 18 mi E Cuidad Guzmán, VI; 10 mi E Unión de Tula, IX; 15 mi SE Tequila, VIII; Lagos de Moreno, VI; 6 mi E Lagos de Moreno, VII; Etzatlán, VIII; Cocula, VII, XI; 13 mi SW Cocula, 5600 ft, IX; Chapala, VIII–IX; 6 mi W Chapala, VI; Santa Cruz del Astillero, 1417 m, IX; 22 mi NW Mascota, IX; Guadalajara, VI–VIII; 40 mi NW Guadalajara, VI; 11 mi W Guadalajara, IX; Magdalena, 4600 ft, VI–VIII; Ajijic, 1550 m, VII–VIII; La Barca, VII; 3 mi SW Autlán, VII; 17 mi NE Tecolotlán, VII; Juan Acatlán, IX; *Michoacán*—Maratávio, VIII; Los Reyes, VII; Erongarícuaro, VI; 6 mi W Sahuayo, IX; Carapan, VII, IX; Morelia, IX; 4 mi E Morelia, VII; 33 mi E Morelia, IX; 17.4 km E Morelia, 2134 m, IX; 8 km E Zacapú, VII; Cotija, IX, XII; 5 km W Quiroga, VII; 13 km Quiroga, 2134 m, X; Pátzcuaro, 2150 m, VI–IX; 7.7 km NE Pátzcuaro, 2088 m, IX; Zamora, VI; Tuxpan, 1900 m, VI–VIII; 7 mi SE Tuxpan, IX; 1 mi N Irimbo, 8400 ft, VII; 18 mi W Sahuayo, 4700 ft, VI; Janitzio, VII; 4 mi W Jiquilpan, 6100 ft, VIII, IX; Uruápan; *Nayarit*—Tepic, VI, XI; 24 mi SE Tepic, 4000 ft, VI–VII; 9.4 km SE Tepic, 975 m, IX; 17 mi NW Tepic, XI; San Blas, IX; 25.7 km E San Blas, IX, XII; 3 mi NW Santa María del Oro, VI; 8 mi N Ahuacatlán, XI; Ixtlán del Río, VI; 4 mi E Ixtlán del Río, IX; 4 mi S Sinaloa state line, Hwy 200, XII; 40.2 km SE Peñitas, 366 m, IX; Ojo de Aguila, VII; Las Varas, XII; Compostela, 3000 ft; VIII, X; Acaponeta, VIII; 26 mi E Acaponeta, IX; 34 mi S Acaponeta, VIII; *Querétaro*—Tequisquiapan, IX; Querétaro, VI, IX; 35 mi SE Querétaro, VIII; *Sinaloa*—Escuinapa; Culiacán; 12 mi SE Villa Unión, VI; 13 mi E Concordia, 800 ft, VIII; 5 mi N Mazatlán, VII; 3 km E Mazatlán, VIII; 8 mi SW Concordia, 300 ft, IX; 8 mi NE Concordia, VII; Los Mochis, 14 m, IX–XI; *Sonora*—Guirocoba, VIII; Alamos, VIII; Hermosillo, VII; 17 mi SW Moctezuma, 944 m, VII; *Tlaxcala*—Tlaxcala; UNITED STATES: *Arizona*—Tucson, X; Tumacacori National Monument, VIII–X; Bisbee, X; Phoenix, X; 6.4 mi N Amado ("Canoa Ranch"), VIII; 11 mi S Green Valley, VIII; Continental, VIII.

Phanaeus(?) *antiquus* Horn

UNITED STATES: *Pennsylvania*—Port Kennedy Cave.

Phanaeus beltianus Bates

COSTA RICA: *Puntarenas*—Osa Peninsula ("La Selva" Biological Station); *San José*—16 km SW Sabanilla, V; NICARAGUA: "Chontales."

Phanaeus bispinus Bates

BOLIVIA: *Cochabamba*—Puerto Chimoré, 25 m, I; *Santa Cruz*—Buena Vista; BRAZIL: *Amazonas*—Manaus, X; *Pará*—Belém; Cachimbo, VIII, X; COLOMBIA: *Amazonas*—Leticia, 700 ft, II; ECUADOR: *Napo*—Tena, 400 m, X; *Pastaza*—Canelos, X; FRENCH GUIANA: Belizon, V; Cayenne, VII; GUAYANA: Kartabo, VI; Moraballi Creek, X; PERU: *Huanuco*—Tingo María, 700 m, VII, IX–X; *Junin*—Satipo, IV; Sani Beni, IX; *Loreto*—Ucayali, I; Panguana, 260 m, III; Pucallpa, 200 m, VI; TRINIDAD: Maracas Bay, II, VI, VIII; VENEZUELA: *Amazonas*—San Carlos de Río Negro, 65 m, III.

Phanaeus cambeforti Arnaud

BRAZIL: *Amazonas*—15 km E Manaus, VII; Tefé, I, III; COLOMBIA: *Amazonas*—Leticia, 700 ft, II–III; *Meta*—Villavicencio, II–III; FRENCH GUIANA: Bas Moroní; PERU: *Huanuco*—Tingo María, XI–XII; *Loreto*—Atalaya, II; Boquerón Abad, 550 m, IX.

Phanaeus chalcomelas (Perty)

BOLIVIA: *Cochabamba*—Puerto Chimoré, 250 m, I; Río Coni, 400 m; *La Paz*—Tumupasa, IX; Ixiamas, XII; *Santa Cruz*—Buena Vista, 1700 ft, I–IV; El Espejo, II; BRAZIL: *Amazonas*—Tefé; Benjamin Constant; 15 km E Manaus, VII; *Pará*—Cachimbo, X; Obidos, XII;*Rondônia*—Pôrto Velho; COLOMBIA: *Amazonas*—Leticia, II; *Huila*—Gigante, III-IV; Vegas de Caquetá, I; *Meta*—Villavicencio, 500 m; 33 km E Villavicencio, III; *Putumayo*—Santa Rosa; Mocoa, 530 m, II; ECUADOR: *Morona Santiago*—Macuma, VII; *Napo*—Lago Agrio, 250 m, VI; Limoncocha, 250 m, VI–VII; FRENCH GUIANA: Cayenne; St. Jean du Maroni; St. Laurent du Maroni; Massikiri (Oyapock River), XI; PERU: *Cuzco*—Marcapata; *Huanuco*—Tingo María, XI–XII; *Loreto*—Pucallpa, V; Boquerón Abad, VII; SURINAME: Anapaiké, XI.

Phanaeus damocles Harold

MEXICO: *Guerrero*—Omilteme, 8000 ft, VII, IX; Amula, 6000 ft, VIII; *Oaxaca*—Municipio Suchixtepec, Río Guajolote, 1975 m, VII; 4 km W Calpulalpan, 2000 m, VI; 5 mi N Oaxaca, 1700 m, VI; km 154 on Hwy 175 S Oaxaca, VI; 36 km NE Oaxaca (El Cerezal), 2300 m, VI; 3 mi N Suchixtepec, 9500 ft (km 144 on Hwy 175 S Oaxaca), VI; Nochistlán, VI; Monte Alban, VIII.

Phanaeus daphnis Harold

MEXICO: *Guerrero*—Taxco, IX; Coacoyula, VI; Teloloapan; Iguala, VI; 13 km NNW Iguala, 1035 m, VIII; 4 mi S Chilpancingo, VIII; Agua Bendita, VII; Tierra Colorada; Mexcala, 4500 ft, VII; 1.5 mi N El Mogote, 1500 m, VIII; Amula, 6000 ft, VIII; Hueyecantenango (Chilapa), VIII; *México*—Temascaltepec, 6000 ft, VII; Tejupilco, VII; Tonatico, VII, IX; Nuevo Santo Tomás de los Plátanos, IX; Ixtapan de la Sal, VII; Chalma, 2600 ft, VI; *Michoacán*—Tuxpan, 1450 m, VII–IX; La Huacana, VII; 19 mi S Uruapan, 3000 ft, VII; 2.5 mi N Huetamo de Núñez, 3100 ft, VII; Apatzingán, 1200 ft, VIII; *Morelos*—Puente de Ixtla, VII; Progreso, VI; Tepoztlán, 5000 ft, VI–IX; Cuernavaca, 1650 m, V–IX; 2 mi SE Cuatla, 1372 m, IX; 11.5 mi W Cuatla, 4500 ft, VIII; 3 mi W Tlayecac, VI; San Vicente, VI; 3 mi W Moyotepec, VI; 17 mi NE Amacuzac, VI; Oaxtepec, VI–VII; Xochitepec, VI; Cautela, VII; 7 km S Alpuyeca, 3200 ft, VI–VII; Xochicalco, 4000 ft, VII; Tequesquitengo, VI; *Oaxaca*—8 mi N Huajuapan de León, IX; *Puebla*—13 mi SE Acatlán, VIII; 9 mi SE Izúcar de Matamoros, 4800 ft, VIII; 12 mi SE Izúcar de Matamoros, 3700 ft, VII; 30 mi S Atlixco, VIII; 7 mi NW Tehuitzingo, VII; 13.3 mi NE Tehuitzingo, VII; 9 mi N Amatitlán, XII.

Phanaeus dejeani Harold

BRAZIL: *Espirito Santo*—Fazenda Jerusalem, I; *Minas Gerais*—Serra Caraça, 1380 m, XI; Fazenda dos Campos, Virginia, 1500 m, I; *Rio de Janeiro*—Petrópolis, I–II, X–XII; Teresópolis; Itatiaya, 1100 m, XI; Nova Friburgo; *São Paulo*—Campos do Jordao, II, XII.

Phanaeus demon Laporte-Castelnau

COSTA RICA: *Guanacaste*—6 km S La Cruz, VI; Las Cañas; 5 km NW Las Cañas, VII; 25 km N Las Cañas, V; 15 km SW Bagaces; Palmira, V; Santa Rosa National Park, VI; *San José*—San José; EL SALVADOR: *La Libertad*—6 mi W Quetzaltepeque, 500 m, VIII; *La Unión*—Volcán Conchagua, V; Playa El Icacal, VII–VIII; *Santa Ana*—San Diego, VI; *Usulután*—Usulután, VII; 15 km E Usulután, VIII; GUATEMALA: *Izabal*—Los Amates; HONDURAS: *Choluteca*—Choluteca, IX; 2 mi E Choluteca, IX; MEXICO: *Chiapas*—18 km S La Trinitaria, 914 m, XII; Tuxtla Gutiérrez, VI, IX; 65 km S Tuxtla Gutiérrez, 823 m, IX; Ocozocoautla, VI, IX; 2 mi N Ocozocoautla, VIII; Santa Rosa, IX; 10 mi NW Arriaga, 122 m, VIII; 18 mi N Arriaga, VIII; Cintalapa, VIII; Las Delicias, X; *Colima*—Colima, VI; 7 mi W Colima, VIII; 20 mi S Colima, VI; 4 mi E Colima, 1500 ft, VIII; *Guerrero*—Colotlipa, VII; Chilpancingo, VIII–IX; 22 mi N Chilpancingo, VIII; 24 mi N Chilpancingo (Cañon del Zopilote), VII; 5 mi S Chilpancingo, VIII; 30 mi S Chilpancingo, 4000 ft, VIII; Iguala, V–VII; 8 mi SW Iguala, VII; 3 mi S Iguala, VIII; 13 mi NNW Iguala, 1035 m, VIII; Taxco, VII; 20 mi E Taxco, IX; Mexcala, VII; 2 mi N Mexcala, VIII; Zumpango, VII; Huitzuco, XI; Coacoyula, IX; 75 km E Acapulco, X; *Jalisco*—Autlán, IX; 3 mi SW Autlán, VII; Barra de Navidad, VI; Juchitlán, IX; Manzanillo, VI; Chamela (Estación Biológica UNAM), VII; *Michoacán*—Tocámbaro, 1300 m, VI; Playa Azul, 0 m, VII; 3 mi W Tangamandapio, 5250 ft, VI; Apatzingán, 1200 ft, VIII; La Huacana, VII; 10 mi S Tzitzio, VII; 5 mi SW Tiquicheo, VII; 20 mi E, 23 mi S Morelia, 2950 ft, VII; *Morelos*—2 mi W Moyotepec, VI; Tepoztlán, IX; Tequesquitengo, VII; Palo Bolero, VIII; Zacatepec, VI; Cuautla, VIII–IX; 21 km SE Cuautla, 1372 m, IX; Huajintlán, IX; Tlaltizapán, 1100 m, VIII; Xochitepec, VI; 15 km W Xochitepec, 1250 m, X; Villa de Ayala; Alpuyeca, VI–VII; Cuernavaca, VI–VIII; 10 mi S Cuernavaca, VII; 16 mi S Cuernavaca, VIII; Puente de Ixtla, VI; Yautepec, VI; 7 mi SW Yautepec, 3500 ft, VII; Tetecala, VI; Tepalcingo, VIII; Alpuyeca, VII; 7 km S Alpuyeca, 3200 ft, VI–VII; Jojutla, V; Xochicalco, VIII; *Nayarit*—Campostela, IV; 6 mi SW Sayulita, VII; *Oaxaca*—4 km E Tequisistlán, 700 ft, VIII; 6 mi N Juchitán, VII; 15 km E Juchitán, VII; 17 mi E La Ventosa, VII; 5 mi N La Ventosa, VII; Tehuantepec, XII; 8 mi NE Tehuantepec, VII; 14 mi W Tehuantepec; 6 mi S Tehuantepec, VII; Puerto Angel, 40 m, VI; 38 mi N Puerto Angel; 3 mi N Totolapan, 3400 ft, VI; Presa Benito Juárez, VII; 7 mi W Tehauntepec, 90 m, VII; Huajuapan de León, VI; 1.5 mi E Zopilote, VI; *Puebla*—22 mi SE Izúcar de Matamoros, VIII; 12 mi N Izúcar de Matamoros, 5000 ft, VI; 17 km S Izúcar de Matamoros, 4200 ft, VIII; 13 km NE Tehuitzingo, VII; 6 mi NW Tehuitzingo, 3600 ft, VII; 10 km SE Tehuitzingo, 1150 m, VII; Acatlán, VII; 13 mi SE Acatlán, VIII; 45 mi N Acatlán; 7

mi S Atlixco, 4900 ft, VII; NICARAGUA: *Chinandega*—20 km NW León (Depto. León) *Managua*—Managua, VI; 3 mi SW Managua, VI.

Phanaeus difformis Leconte

MEXICO: *Tamaulipas*—Tampico; 16 mi SSW San Fernando, 100 m, VIII; UNITED STATES: *Arkansas*—2 mi E Ozark, VIII; Pine Bluff; *Colorado*—Lamar, VIII; *Kansas*—Medora (Seward Co.; Clark Co.; Ford Co.; Comanche Co.); *Louisiana*—Cameron, IV, VI; Johnsons Bayou, V (Cherokee Parish); *New Mexico*—Eunice, VII; Los Medanos, VIII; Mescalero Sands, VII; *Oklahoma*—Little Sahara, VI; Grand, VIII; Red River at Interstate Hwy 35 (Love Co.; Cherokee Co.); *Texas*—Sarita, X; Kingsville, X; Lyford, V; Riviera, VIII; Rio Grande City, IX; Sinton, VI, VIII; Duval City, VI; Edinburg, VI; Raymondville, V–VI; Santa Ana National Wildlife Refuge, VII; Aransas National Wildlife Reserve, IV; 18 mi SE Laredo, IX; Padre Island National Seashore, IX; Dallas, VI; San Antonio, XII; 7 mi S Seagoville, VI; Pearsall, VI; Cypress Mills; Round Mountain; Galveston; Sabinal, XII; Fedor; Coyote Lake, VIII; Proctor, VI; New Braunfels; Brownsville; Canadian; Brownwood, X; Gainesville; Columbus, V; Victoria; 24 mi N Falcon Dam; Port Isabel, IX; Corpus Christi, VIII; San Diego, XI; Mustang Island; Hockley; McAllen, VI; College Station, IV; Waco, VII; 8 mi S Cuero, IX; 6 mi N Cuero, IX; 4 mi W Cookes Point, IX; Camp Creek Lake, IX; 4 mi S Buffalo, IX; 2 mi E Bastrop, V; Freer, IV; Sheffield, VII; Fredericksburg, X; 3 mi E Goliad, IX; 5 mi N Industry, V; Robstown, VI; Waskom, IV; Hebbronville, VIII; Uvalde, X; Streeter, V; San Jacinto River at Interstate Hwy 45, Montgomery Co.; Winter Haven; 8 mi S Falfurrias, VII; Frelsburg, VI; Crane; Austwell; Higgins, VI; 8 mi E Tyler, IX; 10 mi SE Tyler, IX; Muleshoe, VIII; Marfa (Karnes Co.; Anderson Co.; Dimit Co.; Grimes Co.).

Phanaeus endymion Harold

BELIZE: Caves Branch, VIII; Augustine, 1500 ft, VIII; EL SALVADOR: *La Libertad*—4 km S Nueva San Salvador (= Santa Tecla), V; GUATEMALA: *Alta Verapaz*—Lanquin, 350 m, VIII; Cobán; 35 km SW Sebol, 915 m, VII; *Escuintla*—10 km NE Escuintla, 700 m, VII; *Huehuetenango*—16 km NW Huehuetenango, VIII; *Izabal*—Cayuga, VIII; *Petén*—Tikal, VIII; *Retalhuleu*—San Sebastián, VIII; *Santa Rosa*—6 km E Oratorio, 670 m, VII; HONDURAS: *Atlantida*—Tela, V; *Francisco Morazán*—Cedros, XI; MEXICO: *Chiapas*—Palenque, V; 7 mi S Palenque, 350 m, VIII; 48 km NE Las Margaritas, 2100 m, X; 1 mi SW Rizo de Oro, 2700 ft, VIII; 6.6 mi W El Bosque, 4800 ft, VIII; 11 mi E La Trinitaria, 5200 ft, VIII; 2 km S La Trinitaria, X; 11 mi NW Ocozocoautla, 3400 ft, VIII; 15 mi NW Ocozocoautla, 2800 ft, VIII; 22 mi N Bochil, 5600 ft, VIII; Santa Rosa, VIII; Simojovel, V; Bonampak, 300 m, V, VIII; 9 mi N Arriaga, VIII; Lagos de Montebello, 4900 ft, VIII; Lacanjá-Chansayab, 300 m, II, IV, VIII; 4.1 mi S Tuxtla Gutiérrez ("Parque Cerro Hueco"), X; Rosario Izapa, V; El Escopetazo (km 40 on hwy between Tuxtla Gutiérrez and San Cristóbal de las Casas), VIII; *Jalisco*—13 mi SW Cocula, 5600 ft, IX; Tecalitlan; 10 mi SW Autlán, 4200 ft, IX; *Michoacán*—12 km NW Calcomán, VII; *Nayarit*—24 mi SE Tepic, 4100 ft, VII; *Oaxaca*—6 mi S Valle Nacional, 2000 ft, VII; 13 mi S Valle Nacional, 3700 ft, VIII; 15 mi S Valle Nacional, 5600 ft, VII; 9 mi E El Camarón, 4300 ft, IX; Juquila Mixes, VIII, X; Niltepec, IX; Loma Bonita, VIII; Nueva Esperanza, IX; Portillo del Rayo (Finca "Dos Angeles"), VII; *Quintana Roo*—X-Can, VI; Carrillo Puerto, XII; *Tabasco*—3 mi NE Teapa; 8.2 mi W Teapa; *Veracruz*—22 km W Palma Sola, 800 m, VIII; 12 km N Sontecomapan, 125 m, VII; 10 km NE Catemaco, 500 m, VII; Dos Amates, V; Córdova, VII; Huatusco, VIII; Tiro de Hayas (Ejido "El Sumidero"), 1360 m, VIII–IX; Fortín de las Flores, VII; *Yucatán*—3 mi N Muna, 100 ft.

Phanaeus eximius Bates

COSTA RICA: *Cartago*—Turrialba, VII; *Guanacaste*—6 km S La Cruz, VI; 25 km N Las Cañas, V–VI; EL SALVADOR: *Chalatenango*—Chalatenango, VII; *La Libertad*—2 mi E Quetzaltepeque, VII; 6 mi W Quetzaltepeque; *Santa Ana*—Santa Ana, VI; GUATEMALA: *Jutiapa*—10 km W Jalpatagua, 600 m, VII; *Zacapa*—La Unión, X; HONDURAS: *Cortés*—San Pedro Sula; La Lima, 2000 ft, V; *Francisco Morazán*—25 km E Tegucigalpa; NICARAGUA: *Managua*—Managua.

Phanaeus flohri Nevinson

MEXICO: *Chiapas*—Tapachula*; *Guerrero*—Acahuizotla, 650 m, VIII, X; 9 km S Palo Blanco (Sierra Alquitlán), 1400 m, VII; *Jalisco*—Ajijic; 5.5 mi NE Autlán; *Morelos*—San José de los Laureles, V–VI; Santo Domingo, VI; *Puebla*—7 mi S Izúcar de Matamoros; *Sonora*—10 mi NW Yecora, 4320 ft, VII; 20.1 mi E Río Yaqui, 3010 ft, VII; 3.2 mi NW Huicache, 5170 ft, VII; *Veracruz*—Jalapa*; Las Vigas*. (*Localities are not confirmed by modern records.)

Phanaeus furiosus Bates

MEXICO: *Guanajuato*—Irapuato; Valle de Santiago, VI; Silao, VII; *Jalisco*—Guadalajara, VIII; 30 mi S Guadalajara; 5 mi S Guadalajara, VI; 28 mi E Guadalajara; 10.8 mi S Talpa de Allende, 1900 ft; Etzatlán, VIII; Ajijic, 1500 m, VI–VIII; Magdalena, VIII; 22 km NE Zapotlanejo, VII; 22 mi NW Mascota, IX; 13 mi SW Cocula, IX; Chapala; Tala, 5200 ft, VIII; Tequila, VII; La Venta; Tecolotlán, VII; *Michoacán*—Pátzcuaro, VII–VIII; Cojumatlán; 6 mi W Sahuayo, IX; 18 mi W Sahuayo, VI; Cotija, IX; Jacona, VIII; Coalcomán, 4000 ft, VII; *Nayarit*—San Blas, VI; 9 mi E San Blas, VIII; Jesús María, VII; Compostela, 2500 ft, IX–X; 17 mi NW Tepic, XI; 34 mi S Acaponeta, IX; 4 mi E Ixtlán del Río, IX; San Juan Peyotán, VIII; *Sinaloa*—28 mi NE Concordia, VIII; 2 mi E Concordia, VI; 13 mi E Concordia, VIII; Santa Lucía, 4000 ft, VIII; Escuinapa; 27 mi E Villa Unión, VII; Copala, VII–VIII; 7 mi S Culiacán; La Concha, VIII; 1.5 mi SW Pánuco, VII; Mazatlán, XI; *Sonora*—Río Mayo, VIII; 55 km SW Moctezuma, 1066 m, VII; 17 km SW Moctezuma, 944 m, VII.

Phanaeus halffterorum Edmonds

MEXICO: *Guerrero*—Acahuizotla, 750 m, X–XI; 9 km S Palo Blanco (Sierra de Alquitlán), 1450 m, VI–VII; 22 mi S Chilpancingo, 2800 ft, VIII; *México*—8 km W Temascaltepec, 2360 m, VII; 5 km E Temascaltepec ("Real de Arriba"), 2200 m, VII.

Phanaeus haroldi Kirsch

COLOMBIA: *Caquetá*—Vegas del Caquetá, I; *Huila*—Gigante, III–IV; Campoalegre, V; *Meta*—Villavicencio, VIII–X; ECUADOR: *Napo*—Lago Agrio, 250 m, VI; Loreto, XII; *Pastaza*—Puyo, II; Canelos, XII; Tena, 400 m, II; PERU: *Huanuco*—Tingo María, IV, VI; *San Martín*—Moyobamba, VIII; San Martín, 1500 ft, XII; VENEZUE-

LA: *Amazonas*—San Fernando de Atabapo, VI; *Bolívar*—El Playon (Río Cuara), XI; Maripa, VI; *Tachira*—Río Negro, 500 m, VIII.

Phanaeus hermes Harold

COLOMBIA: *Magdalena*—Aracataca, VIII; Río Frio, 2000 ft, VI; Sierra de Perija, 650 m, VII; *Norte de Santander*—La Playa, VI; Ocaña, VI; *Santander*—Bucaramanga, V; COSTA RICA: *Puntarenas*—11.6 mi S Buenos Aires, VI; 15 km NE Potrero Grande, IX; *San José*—San Isidro del General, V; PANAMA: *Chiriquí*—David; Tolé; *Panama*—Cerro Campana, 850 m, V; La Chorrera, V; Chepo, XII; Las Cumbres, XII; VENEZUELA: *Zulia*—km 40 on hwy between Machiques and Colón (Hacienda "San Marino"); Kasmera (Sierra de Perija), 250 m, IX.

Phanaeus howdeni Arnaud

PANAMA: *Canal Zone*—Barro Colorado Island, V–XII; Lion Hill Island; *Panama*—Majé (8 km SE Bayano Ridge).

Phanaeus igneus Macleay

UNITED STATES: *Alabama*—Mobile, III; Springhill, V; Hartford, III; Claireborne (Baldwin Co.); *Florida*—Miami, IV–VII; Gainesville, VI–X; Jacksonville, V, XI; Gulfport, III; Lake Worth; Ft. Myers, VI; Fruitland Park; Tarpon, VI; 3.5 mi N Salt Springs, IV; Koreshan State Park, VI; Mariana, IV; De Funiak Springs, III; 12 mi S Chattahoochee, VII; Brooksville, VI; Enterprise; Clarksville, III; 1.4 mi SW Archer, III; Ocala National Forest, III; 14.3 mi E Ocala; Largo, VII; Sarasota; Inverness, VII; Lake Placid, III; 8 mi SE Interlachen, III; Daytona, IV; Edgewater; Crescent City; Winterpark, III; Ormond, III; Newman's Lake, XII; Walaca, IV; La Belle, VII; Kissimmee, V; Homosa Springs, IV; Sanford, X; Tampa, III; 3.7 mi N Old Town, V; Lake Alfred; 6 mi E Quincy, III; North Smyrna, XII; Clearwater, VI; 8 mi E Bronson, III; Tallahasee, IV; Pensacola; Lutz; St. Petersburg, V; Torreya State Park, IV; Glen St. Mary, XII; Plant City; Romeo, IV; *Georgia*—Jekyll Island; Tifton, V; Vidalia; 10 mi SE Waycross, VI; Thomasville, III–IV; Darien, IV; Lumber City, IX; St. Marys; Little Ocmulgee State Park, IX; St. Catherines Island, VI; Brunswick, VII; Augusta; Swainsboro, VIII; Blackbeard Island, V–VII (Camden Co.; Glynn Co.; Echols Co.); *Louisiana*—Covington, V; *Mississippi*—Hattiesburg, VIII; Ocean Springs, VI; Lucedale, VII; *North Carolina*—Southern Pines, II–X; West End, VII; New Bern; Southport, X; Wilmington, V; Faison; *South Carolina*—Myrtle Beach, VII; Aiken; Beaufort, VI; Florence, IV–VI; Hilton Head Island, VII; Walterboro, IX; Blackville, VIII; Isle of Palms, VII; White Pond, III; Mt. Pleasant, VIII; Summerton, VII; Dillon, X; Darlington, VIII; Barnwell, VIII; Bishopville, IX; Charleston, IV.

Phanaeus kirbyi Vigors

BOLIVIA: *Santa Cruz*—Buena Vista, 1700 ft, I–IV, XI–XII; Chiquitos, XI; BRAZIL: *Goiás*—20 km N São João da Aliança, V; 40 km S Peixe, VI; *Mato Grosso*—Chapada, 2600 ft, II, IX–XI; Três Lagoas, VI; Rio Verde, XI; Corumbá; Uitiariti (Rio Papagaio), XI; Alto Garças, XII; Murtinho, XI; *Minas Gerais*—Sertão de Diamantina, XI; *Paraná*—Villa Velha, II, XI; PARAGUAY: *Alto Paraná*—Belle Vista, I; *Boquerón*—Puerto Casado; *Caaguazú*—Caaguazú, XII.

Phanaeus labreae (Pierce)

UNITED STATES: *California*—Los Angeles (Rancho La Brea Tar Pits).

Phanaeus lunaris Taschenberg

ECUADOR: *Azuay*—Huigra, 1300 m; *Bolívar*—Balzapamba; *El Oro*—Zaruma, II; *Esmeraldas*—San Mateo, IX; Telimbelo; *Guayas*—Guayaquil; *Los Ríos*—Quevedo, 75 m, I; Babahoyo, I; 45 km N Babahoyo, 700 ft, II; *Loja*—Loja, XII; Cariamanga, VII.

Phanaeus melampus Harold

MEXICO: *Chiapas*—6.6 mi W El Bosque, 4800 ft, VIII; Mahosik' Tenejapa, 4800 ft, VII; *Veracruz*—Barranca de Metlac, VII; Orizaba, I; Fortín de las Flores, VIII.

Phanaeus meleagris Blanchard

BOLIVIA: *Cochabamba*—Yungas del Palmar, 1600 m, II, IX; Crista Mayu, 600 m, IX–XI; *La Paz*—Coroico; Calisaya, V; Chuani; Puente Llorosa, I; *Santa Cruz*—Buena Vista, 450 m; Parapetí River Valley, near Lagunillas; COLOMBIA: *Boyacá*—Muzo; *Meta*—Villavicencio, V; *Tolima*—Honda; ECUADOR: *Pastaza*—Mera; Canelos; San Francisco del Río Pastaza, 1200 m, X; *Zamora Chinchipe*—Sabanilla, IX; PERU: *Cuzco*—Marcapata; *Huanuco*—Pozuzo; Tingo María, VII; *Junin*—La Merced; *Loreto*—Pucallpa, 200 m, XI; *Pasco*—Chuchurras; VENEZUELA: *Tachira*—San Cristóbal, 1200 m, V, VIII–IX.

Phanaeus melibaeus Blanchard

BRAZIL: *Goiás*—Aragarças, I, X; *Mato Grosso*—Rosario Oeste, II; confluence of Tapirapé and Araguaia Rivers, XI–XI; *Pará*—45 km E Canindé, X; *Rondônia*—Pôrto Velho, X.

Phanaeus mexicanus Harold

MEXICO: *Guerrero*—Acahuizotla, 750 m, XI; 11 mi E El Ocotito, 3200 ft, VIII; Tierra Colorada, VII; Chilapa, VIII; *México*—Temascaltepec, VIII; 5 km E Temascaltepec (Real de Arriba); Tejupilco; Ixtapan de la Sal, 1975 m, VII; Valle de Bravo, VIII; Tenancingo, V, IX; Villa Guerrero, VII; Malinalco, IX; Oaxtepec, X; *Morelos*—Cuernavaca, 6500 ft, VI–VIII, XI; Cuautla, VIII–IX; Jojutla, VI; Puente de Ixtla, VII; Yautepec, VII; Tepoztlán, VI–VIII; Atonyo, 1630 m, VI; *Oaxaca*—Oaxaca, 1600 m, V–IX; 4 mi NW Oaxaca, IX; Juquila Mixes, IX; *Puebla*—6 mi E Atlixco, IX; 7 mi S Izúcar de Matamoros, 4500 ft, VI; Acatlán, VII; *Veracruz*—Salinas, VI; Presidio, VII; Catemaco (Dos Amates), I, IV–XII; Fortín de las Flores, VII; San Andres Tuxtla, VII–VIII; Orizaba, IX; Tezonapa, IX; Cotaxtla, VIII; Cerro Azul, XII.

Phanaeus nimrod Harold

MEXICO: *Oaxaca*—2.7 mi NW El Camaron, VII; 9 mi E El Camarón, IX; Ocotlán; 20 mi S Ocotlán; Oaxaca, 5050 ft, V, VIII; 15 mi S Oaxaca, VIII; 4 mi NW Oaxaca, IX; Monte Alban, VII-VIII; 48 mi W Tehuantepec, VIII; 1.5 mi E El Zopilote, VI; Puerto Angel, 40 m, VI.

Phanaeus palaeno Laporte-Castelnau

ARGENTINA: *Corrientes*—Villa Olivari, XII; BOLIVIA: *Beni*—Magdalena, I–III; *Santa Cruz*—Chiquitos, XI; BRAZIL: *Goiás*—Jataí (Fazenda Nova Orlandia), I; Goiatuba, I; *Mato Grosso*—Três Lagoas, V–VI; Rosário Oeste, XI–XII; Santa Teresinha, XI; Utiariti, X; Murtinho, XII; Rio Verde, XI; Corumbá; Chapada (near Cuiabá), IV–VII, X–XI; Aragarças; Rancho Grande, XI; Nobres, I–III; *Rondônia*—Vilhena, II; *Santa Catarina*—Joinville; *São Paulo*—Campinas, II, XII; Batatais; Agudos; Epitacio, XII; Boa Esperança do Sul, I; PARAGUAY: *Boquerón*—Puerto Casado; *Concepción*—Horqueta, III; *Guairá*—Villarica; Borja, II; *Presidente Hayes*—Asunción.

Phanaeus palliatus Sturm

MEXICO: *Distrito Federal*—Atzcapotzalco, VII; Contreras, 2700 m, VII; *Durango*—145 km S Durango (Sierra de Michis, "La Michilía" Biosphere Reserve), 2300 m, VIII; *Hidalgo*—4 mi W Tulancingo, 7600 ft, VII; Huauchinango, VIII; 12 mi W Huauchinango, 6700 ft, VI; *Jalisco*—Sierra Manantlán ("Las Joyas" Biological Station), 1900 m, VII; Ajijic, 1950 m, VIII; 3 mi WSW Mazamitla, VII; 8 mi S Autlán, VII; *México*—Tepotzotlán, VI; Temascaltepec; Amecameca, VI; Toluca, 2640 m, VI–VIII; Almoloya, VII–VIII; Ocoyacac, VII–VIII; Villa del Carbón, VI; Tejupilca; San Bartolo Tenayuca, VI; Chapingo, 2250 m, VIII; *Morelos*—Cuernavaca, 1500 m, *Michoacán*—5 mi E Quiroga, 7600 ft, VII; Tancítaro, 6300 ft, VI; Matujeo, VII; Carapan, 6200 ft, VI; Pátzcuaro, 2150 m, VI–VII; 7.7 km NE Pátzcuaro, 2080 m, IX; Puerto El Tigre, VII; Paricutín, VII.

Phanaeus prasinus Harold

COLOMBIA: *Norte de Santander*—3 km N Chinacota, 3000 ft, V; 30 km S Cúcuta, 700 m, V; TRINIDAD AND TOBAGO: Port of Spain; Maracas Bay, VI–VIII; Narva; Balandra Bay, X; Arima Valley, V; Diego Martín Valley, VIII; VENEZUELA: *Apure*—San Fernando, X; *Aragua*—Rancho Grande (Maracay), VII; Pozo del Diablo (Maracay), 500 m, IV; Limón, 450 m, IX; *Barinas*—Las Maravillas, IV; Barinitas, 500 m, IV–VI; *Bolívar*—48 km ESE Cuidad Bolívar (Rancho "Santa Rita"), VII; *Carabobo*—San Esteban, 100 m, II, VII; Valencia, 500 m, IV; *Distrito Federal*—Chichiriviche, 0 m, X; Caracas, VI, XI; *Falcón*—Yaracal (Hato "Corralito"), 60 m, I; *Guárico*—Las Mercedes (Hato "El Saman"), V; *Mérida*—Mérida; La Pedregoza, 2000 m; Tabay, IV; *Miranda*—Birongo, I; Parque Nacional Guatopo, III; *Monagas*—Caripito, VIII; *Yaracuy*—Yumare, VI.

Phanaeus pyrois Bates

COLOMBIA: *Antioquia*—Puerto Berrio, VIII; *Boyacá*—Muzo, IX; *Chocó*—Quibdó, IX; *Valle del Cauca*—70 km E Buenaventura (Anchicaya Dam), 500 m, V, VIII; COSTA RICA: *Cartago*—Turrialba, 600 m, II; *Heredia*—Puerto Viejo, 90 m, IX; *Limón*—Llanuras de Santa Clara, VI; *Puntarenas*—6 km S San Vito, 1000 m, V, VIII; Rincón, 100 m, IX; ECUADOR: *Esmeraldas*—11 km SE San Lorenzo, VI; *Los Ríos*—Quevedo, 45 m, V, VIII; *Manabi*—78 km NE Chone, 450 m, VI; *Pichincha*—4 km SE Santo Domingo de los Colorados, 500 m; PANAMA: *Canal Zone*—Barro Colorado Island, I–II, VII–XII; *Chiriquí*—2 mi N Santa Clara ("Hartmann's Finca"), 1200 m, VI–VII; *Panamá*—Cerro Campana, 900 m, V.

Phanaeus quadridens (Say)

MEXICO: *Chihuahua*—Matáchic, VII; 27 mi W Parrita, VII; Madera, 7200 ft, VII; 9.7 mi W Cuauhtémoc, VII; Cusihuiriachic; 13.2 mi S Villa Matamoros, 6000 ft, VIII; 8 mi W Matáchic, 7200 ft, VII; San Francisco del Oro Mesa, 7300 ft, IX; Charcos, 6000 ft, VII; Santa Bárbara, 7500 ft, VII; 63 mi W Santa Bárbara, 5500 ft, VII; 26 mi S Hidalgo del Parral, VIII; Santa Clara; Mesa de Huracán, 7400 ft, VII; Valle de Olivos, 5500 ft, VII; 11 mi E Huejotitlán, 5900 ft, VII; 6 mi N–3 mi E El Sueco, X; *Distrito Federal*—Mexico City, VII; Villa Madero, VII; Guadalupe, IX; *Durango*—3 mi E El Salto, 2400 m, VIII; 6 mi NE El Salto, 8500 ft, VIII; 45 mi E El Salto, VIII; Otinapa, 8200 ft, VIII; Durango, VIII; 5 mi W Durango, 6500 ft, VI; 30 mi W Durango, VI; 43 mi W Durango, 1900 m, VII–VIII; 145 km S Durango (Sierra de Michis, "La Michilía" Biosphere Reserve), 2300 m, VI–VIII; 32 mi N Durango, VII; 7 mi SW Buenos Aires, 8800 ft, VIII; *Guanajuato*—Yuriria, VII; León, VI; Irapuato, VII; *Hidalgo*—12 mi W Huauchinango, Puebla, 6700 ft, VI; Tulancingo, 6750 ft, VI–VII; 4 mi E Tulancingo, VIII; Pachuca, VIII; 15 mi SW Huichapan, 7800 ft, IX; Huasca, IX; *Jalisco*—3 mi W Magdalena, VI; Zacualtipán, VII–IX; *México*—Toluca, VI; Temascaltepec, VII; 25 mi E Mexico City, VII, XI; *Michoacán*—3 km E Zacapú, VII; 7.7 km NE Pátzcuaro, 2100 m, IX; Morelia, VIII; 33 mi E Morelia, IX; 5 km W Quiroga, VII; 6 mi W Sahuayo; *Nayarit*—Santa Teresa, 2070 m, X; *Puebla*—2.5 mi S Huauchinango, VIII; 11 mi SW Puebla; *Sinaloa*—6.5 mi E Potrerillos, VIII; El Palmito, VI; 8 mi W El Palmito, 6100 ft, VI; 38 mi NE Concordia, 6200 ft, VI; Puerto Loberas, 2000 m, VII; *Sonora*—Yecora, VI; *Veracruz*—Acutzingo, XI; 8 mi N Cuidad Mendoza, VII; Pie del Cumbres (km 295 on Hwy 140), 8000 ft, VI; *Zacatecas*—Sombrerete, VII; UNITED STATES: *Arizona*—Pinery Canyon (Chiricahua Mts.), VIII–IX; Portal, 4800 ft, IX; 15 mi W Portal, VIII; Patagonia, VII; 4.3 mi SW Patagonia, IX; Madeira Canyon (Santa Rita Mts.), IX; Miller Canyon (Huachuca Mts.), 5200 ft, IX; 28 mi SE Sonoita (Lyle Canyon), IX; Peña Blanca Canyon (Pajarito Mts.), VII–VIII; 65 mi N Willcox (Galuro Mts., Deer Creek Ranch), VII; Ft. Huachuca, VII; Duquense, IX; *New Mexico*—Tyrone, VIII; Animas Mts. (Birch Spring), IX.

Phanaeus sallei Harold

BELIZE: Indian Church, VII; GUATEMALA: *Alta Verapaz*—9 km E Panacajché; *Zacapa*—La Unión, 850 m, IX–X; MEXICO: *Chiapas*—Boca del Chajul, X; Bonampak, 300 m, VII–IX; Santa Rosa, VIII; Lagunas de Montebello, 4900 ft, VII; Palenque, VI–VII; *Veracruz*—Presidio, VII; Naolinco, IIX; Fortín de las Flores, IX; Banderilla; Jalapa, X; Catemaco, 100 m, V; Cosautlán, 900 m.

Phanaeus scutifer Bates

MEXICO: *Veracruz*—Cotaxtla, VII; 14 mi W Conejos, VI; 24 mi N Huatusco, 650 m, VII; 14 mi SE Jalapa, VII; 7 km W Palma Sola, 100 m, VI–VII.

Phanaeus splendidulus (Fabricius)

ARGENTINA: *Misiones*—Dos de Mayo, XI; Aristabulo del Valle, XII; San Antonio, X; BRAZIL: *Bahia*—Rio Una, X; *Espírito Santo*—Vitória, IX; São Leopoldina; *Minas Gerais*—Ipatinga, XII; Mesquita, XI; Itacolmi, III; *Rio de Janeiro*—Rio de Janeiro, X–XII, III; Nova Friburgo; Teresópolis; Itatiaya, 700 m, III–IV; *Santa Catarina*—

Corupá, XI–XII; *São Paulo*—Itapetininga, II; Santos (Ilha Santo Amaro), IV; Mogí das Cruzes (Serra do Mar, Boraceia Biological Station), X.

Phanaeus triangularis texensis Edmonds

MEXICO: *Coahuila*—Sierra La Encantada, VII; UNITED STATES: *Texas*—Houston; Austin, X; San Antonio, IX; Sheffield, VI–VII; Macdona, VII; Abilene, VII; Kerrville, IX; Mountain Home, VII; Leakey, VII; Sonora, X; Tyler, IV; Rio Frio, V; Alvin, IX; Brownsville, V–VI; Comfort; Liberty; Columbus, VI; New Braunfels; San Angelo, VI; 5 mi W Cross, IX; Hockley; Plano, VII; Frio State Park, IX; Victoria; Dallas, V–VI; Roosevelt, X; Kingsville, X; Uvalde, V; Garner State Park, V; Eagle Pass, V; Menard, IV–VI; 15 mi S Marathon, VI; 33 mi S Marathon, VII; Cedar Hill, III–VI, X; Clay, IV; d'Hanis, VI; 5 mi NW Taylor, V; Ft. Worth; Dead Mans Canyon (Davis Mts.), VII (Burnett Co.; Lavaca Co.).

Phanaeus triangularis triangularis (Say)

UNITED STATES: *Alabama*—Monte Sano, VI; *Arkansas*—2 mi S Foreman, VI (Carroll Co., VI, IX); *Georgia*—(Dougherty, VII–VIII; Rabun Co., VIII); *Florida*—Torreya State Park, V; *Kansas*—Osage (Riley Co.; Davis Co.; Douglas Co.); *Kentucky*—(Pulaski Co., VI); *Louisiana*—12 mi SW Alexandria, IV; Kisatchie National Forest (Red Bluff Campground), IX (St. Charles Parish, V; Sabine Parish, IV); *Oklahoma*—10 mi SSW Heavener, VI; 3.8 mi S Eagle Fork Creek bridge, Hwy 259; *Mississippi*—Santa Rosa, VI; Lucedale, VII–VIII; *Missouri*—Mark Twain National Forest, VII (St. Louis Co., VIII); *North Carolina*—Elizabethtown, IV; *South Carolina*—3 mi S Walterboro, IX; *Tennessee*—Memphis (T. O. Fuller State Park), VI; Burrville, V–VII; Deer Lodge, VII; Reelfoot Lake, V; *Texas*—(Shelby Co., IV–VI, XI; Sabine Co., V–VI); *Virginia*—Jones Creek.

Phanaeus tridens pseudofurcosus Balthasar

GUATEMALA: *Huehuetenango*—16 km NW Huehuetenango, VIII; MEXICO: *Chiapas*—Tuxtla Gutiérrez, VI; 96 km S Tuxtla Gutiérrez, 730 m, X; 65 km S Tuxtla Gutiérrez, 820 m, XI; 3 km W Soyalo, 1220 m, IX; Comitán, V; 32.5 mi E Comitán, 2200 ft, IX; Las Delicias, IX–X; 18 km S La Trinitaria, 900 m, XII; 17 mi SE Teopisca, VI; 10 mi S Teopisca, VII; Santa Rosa, VII; junction Hwys 190 and 195, VII; Arriaga, VIII; 18 mi W Arriaga, VIII; 20 km NW Ocozocoautla, VIII; El Porvenir, 2300 m, IX; Mazapa, 1220 m, X; El Pozuelo, 1060 m, XI; 45 km SW Cintalapa, 2500 ft, VIII.

Phanaeus tridens tridens Laporte-Castelnau

MEXICO: *Colima*—Colima, VI; 20 km S Colima; Colima-Jalisco state line at Hwy 110, VI; *Jalisco*—El Tuito, IX; El Tigre, 700 m, VII; *Morelos*—Tequesquitengo, VI (introduced?); *Oaxaca*—15 mi N La Ventosa, VII; 5 mi NE Tehuantepec, 200 m, VIII; 13 mi SE Tehuantepec, 35 m, VIII; *Veracruz*—Palma Sola, 0 m, VI–VII; 12 km W Palma Sola, 300 m, VI; 6 mi SE Jalapa, VII; 14 mi SE Jalapa; 21 mi SE Jalapa, VII; 8 mi N Cuidad Mendoza, VII; 26 mi E Cuidad Mendoza, VII; Acultzingo, X; Salinas, VI; Conejos, 200 m, VIII; Presidio; 14 mi W Conejos, VI; Catemaco, V–VII; 21.7 mi NW Alvarado; 10 mi W Rinconada; Tapalapa, X; 24 mi N Huatusco, 4800 ft, VII; Puente Nacional, VIII; Cotaxtla, IX; Trapiche del Camino, 550 m, I; 13 mi E Cuitláhuac.

Phanaeus vindex Macleay

MEXICO: *Chihuahua*—15 mi S Camargo, IX; Gallego; Estación Conchos, 4000 ft; UNITED STATES: *Alabama*—Mobile, VI; 6 mi S Jackson, V; Alabaster, IX; Enterprise, VI; Selma, VIII; Pinckard, III; Seddon, VI; Delchamps, VIII; Blount Springs, VIII; Birmingham, IX; Argo, IX; Tuskegee Army Air Field, VIII; Geneva, IV; *Arizona*—3 mi S Willcox, VII; Willcox Dry Lake, VII; 12 mi NW Willcox; Ft. Huachuca, VII; Carr Canyon (Huachuca Mts.); 2 mi SE Apache, VIII; Portal, 4700 ft, IX; 10 mi E Portal, VIII; Tucson, IX; Fairbank, VIII; 8 mi E Drake, VIII; Prescott, VIII; Nogales, VIII; 12 mi E Sonoita; Phoenix; San Simon Valley, 4170 ft; 10 mi SE Patagonia, VIII; Tombstone, VIII; Ramsey Canyon (Huachuca Mts.), 6000 ft, VI; 1 mi E Douglas; Double Adobe, VII; 5 mi SW McNeal, VII; Sierra Vista, VIII; Webb, VII; *Arkansas*—Mena; Batesville, V; Imboden, III–VII, IX; Rich Mountain, IV; Pine Bluff, VI; Ozone, VII (Washington Co.; LaFayette Co.); *Colorado*—Nunn; Eckley; Trinidad, VI; Limon, VI; *Connecticut*—Pomfret; Colebrook, VII; Woodbridge, VII; Clinton, VIII; Putnam, IX; *Florida*—Clarkesville, VII; Monticello, III, IX, XI; Lutz; 13 mi N O'Brien, III; LaBelle, IV; Ocala, IV; Orlando; Ft. Drum; St. Petersburg; Jacksonville, VI; Lochloosa, I; Tampa, III; Miami, V, XII; Sanford; 6 mi E Greenville; Gainsville, V; Paradise, III; Bronson, IX; Pensacola; Tallahasee, IV; Ft. Myers, XI; Blountstown, III; Zolfo Springs, V; Brooksville, VI; Elfers, IV; Torreya State Park, VI; Lake Miccosukee, IV; Englewood, II; Orange, III; Anthony; Enterprize; Captivity Key; 3 mi E Rodman, VII; Brighton, VI; St Augustine; Lake Placid, III; Sarasota; Ormond, IV; Pass-a-grille, IV; 4 mi E Tarpon Springs; Lloyd, V; Moore Haven, VIII; 13 mi W Perry, VII; Newport, IX; *Georgia*—Tifton, VII; Swainsboro, VIII; Vidalia, X; Clayton, VI; Ft. Valley, VI; Camilla, IX; Reynolds; Nahunta, VI; Perry, IV; Rochelle, VIII; Atlanta, IV; Thomasville, VIII; Statesboro; Dublin, VI; Putney, IV; Suches; Quitman, IX; 6 mi S Cordele; Athens, IX; Boston, IV; Ochlochnee, V; Blakely, VII; Butler, III; Fargo, V; Ellaville, IV; 12 mi WSW Faceville, VI; Acworth; Rutledge, VII; Moultrie, XI; Bainbridge, VIII; Forsyth, IV; Okeefenokee National Wildlife Refuge, IX; Ft. Benning, VI; Brunswick, VI; Wadley, X; Savannah, X; Preston, V; *Illinois*—Glencoe; Chicago; Waggoner, VII; Mahomet, VI; Rockport, VI; Mossville, V; *Indiana*—Pekin, VII; State Forest, VII (Vigo Co.; Spencer Co.; Posey Co.; Laporte Co.; Marion Co.; Whitley Co.; Dubois Co.); *Iowa*—Knoxville, VII; Shenandoah, VII; Ames, VIII; Des Moines; Leon, VIII; Bloomfield, VI; Iowa City, V; 2 mi WSW Volga; *Kansas*—Elmdale, VI; Manhattan, V–VI, IX; Mt. Hope, IX; Onoga, IV; Lakin, 3000 ft, IX; Kansas City; Leavenworth, VI; Little Gobi Desert, VII; Medora; Abilene; Benedict; Ottawa, IV, IX; Baldwin, IX; Belvidere; Sylvia; Marquette, IX; Wathena; 6 mi N St. Mary's, III; Ellis; Wellsville, VII; Wheeler; Osage; St. Francis; Dodge City (Geary Co.; Meade Co.; Commanche Co.; Hodgeman Co.; Clay Co.; Hamilton Co.; Montgomery Co.); *Kentucky*—Henderson, V; Taylorsville; Lexington, VIII; Rough River State Park, IV; Louisville, VII; Trenton, IX; Hickman, VII; Mammoth Cave National Park (Flint Ridge), VII; Water Valley, VI; *Louisiana*—16 mi S Baton Rouge, XII; 7.7 mi S Ringgold, VIII; 3 mi W Winfield, VIII; 2 mi S De Ridder, VIII; Clayton, VII; 2 mi N Noble, VII; 7.9 mi W Kelly, VII; Shreveport, IX–XI; Alexandria, IV, VII; Lake Iatt, VI; New Orleans, IV; Covington; Vinton, IX; Frierson, V; Magnolia, IX; Kisatchie National Forest (Red Dirt Refuge), IX; Pearl River; Bogalusa, IV; Cameron, IV; Dry Prong, V; Simsboro, VIII; Leesville, III, VII; *Maryland*—

La Plata, V; Upper Marlboro, VI; Port Tobacco, VII; Bowie, VI; Towson, IX; Plum Point, VII; *Massachusetts*—Northfield, VII; Sherborn, VII; Martha's Vineyard, VIII; Woods Hole; Nantucket, IX; Springfield, VI; Wilbraham, VII; Fall River, VI; North Truro, IV; Amherst; *Michigan*—Ann Arbor, VIII; Wakeley, VII; Hartland, V, VII, X; *Mississippi*—State College, IV–VI; Lucedale, IV, VII, IX; Bay St. Louis, IX; Gainesville, XII; Richton, V; Leland; Cannonsburg, VI; Falkner, V; *Missouri*—Kansas City, VI; Columbia, V; Rock Port, V; Boonville, V; St. Louis, V; Louisiana, V–VI; Williamsville, VI, X; Butler, VIII; Allenton, V; Peevely, VI; Sedalia, V; Naylor, IX; 5 mi E Nevada, VI; Wentzville, VI; Albany, VII; Fayette, VII; Willard, VI; Charleston; Hayti, VII; St. Charles, VIII; Poplar Bluff, VII; Warrensburg, VIII; Alton, VIII; Halls, VII; Archie, VII; *Nebraska*—Benkelman; Omaha, VI; 3 mi S Hyannis, VII; Orleans, VII; Ogallala, VIII; Blair; Emerald, V; South Bend; Rulo; Oshkosh, IX; Lincoln, V; Halsey, VII; Eustis, V; Beaver City, VII (Franklin Co.); *New Jersey*—Phillipsburg; Egg Harbor; 3 mi NE Chatsworth, VIII; Ocean City, VIII; Barnegut Pinebarrens, VIII; Elizabeth; *New Mexico*—2 mi N Rodeo, VIII; Albuquerque, VI; Kochler; Tucumcari, VI; Santa Fe, VII; Acoma, VII; Las Cruces, VIII; 15 mi N Las Cruces, VII; Las Lunas, VII–VIII; Hondo, VIII; Clayton, V; 10 mi S, 5 mi E Sofia, VIII; Deming, VII; Bernardo, VII; 8 mi E Las Vegas, VI (Eddy Co.; Grant Co.); *New York*—Fallsburg, IX; Shelter Island, IX; Orient; Somers, VIII; Rye, V; Brooklyn, VII; *North Carolina*—Beaufort, IX; Black Mountains, VIII; Southern Pines, IV; Chapel Hill, X; Carthage, VII; Balsam, IX; Elizabeth City, IV; Ashville, VII; Cranberry; New Bern; Andrews, VIII; Graham, V; Greensboro, VIII; Raleigh, XI; Reidsville, V; Faison, V, IX; Creedmore, IV; Willard, V; Lake Waccamaw, IX; Bryson City, 2000 ft, VIII; Grimesland, V; Highlands, IX; *Ohio*—Glen Este, VIII; Logan, V; Wooster, VII; Millport, V; Canton; Pickerington, VIII; *Oklahoma*—Stillwater, IX; Grainola, VII; Kenton, VI; Optima, VII; 5 mi S Sulphur, VI; Catoosa, VII–IX; Wichita Mountains Refuge, VI; Hinton, VII; 8 mi SE Guymon, VI; Spring Creek, VI; Stringtown, IV; Black Mesa State Park, VII; Geary, VI; Sayre, VIII; Boise City, VII; Blue Jacket, VI; Davis, IV; Norman, IV; Woodward, V, VII; Clinton, VI; Bridgeport, VI (Cotton Co.; Marshal Co.; Payne Co.; Osage Co.; Choctaw Co.; Oklahoma Co.; McCurtain Co.; Latimer Co.); *Pennsylvania*—Jeanette, V; Reading, VI; Downing Town, VII; Bethlehem; Philadelphia; Charleroi; Media, IX; Broomall, V; Slippery Rock, VI; Pittsburgh, VIII; Ambridge, VII; *Rhode Island*—Warwick, VII; Johnston, VIII; Barrington, VI; *South Carolina*—Aiken; Columbia, III; Charleston, IX; Florence, III; Clemson College, IX; Walterboro, IX; Camden, VI; White Pond, III; Bishopville, IX; Barnwell, IV; Rocky Bottom, V; Manning, V; Bluffton, V; Myrtle Beach, IV; *Tennessee*—Allardt, 1650 ft, VIII; Knoxville, IV; Kingston; Deer Lodge, VII; Roan Mountain, 6300 ft, VIII; Oak Ridge, X; Tullahoma, V; Burrville, VII–VIII; South Pittsburgh; Tusculum, VI; Newport; Decherd; Nashville, VIII; Natchez Trace State Park, VI; *Texas*—Elkhart, V; Wascon, IV; Fedor, V–VI; Palo Duro State Park, VI–VII; Dallas, IV; New Braunfels; Stanton, VII; Abilene, X; Kingsville; Mt. Pleasant, IX; Higgins; Forestburg, V; College Station, V, VIII; New Boston, V; Wills Point, III–IV; Columbus; Big Spring; Amarillo, IV; Gainesville, V; Wichita Falls, III; Fred, V; Longview; 10 mi W Palestine, VII; Denton, V; Petrolia, IV; 4.5 mi N St Jo; Canadian, VIII; Angleton, VI; Perryton, V; Calvert, IV; Refugio, IV; Victoria, VIII; Nancy, IV; Weatherford; Stanton, VII; Sherman; Pampa, V; Nacagdoches, X; Bastrop, III; 4 mi W Cooke's Point, IX; New Ulm, IV; Morales, IX; Frelsburg, IV; Brenham, IV; 9 mi E Yoakum, IX; Navasota, III; 7 mi S Seagoville, X; Pittsburg, IX; 1 mi N Centerville, VI; Paris, III; 10 mi SE Tyler, IX (Crosby Co.; Fayette Co.; Lavaca Co.; Eastland Co.; Shelby Co.) *Vermont*—Bennington; *Virginia*—Port Royal, IX; Williamsville, IX; McKenney, IX; Holland, III; 5 mi S Waynesboro, IX; Bedford Springs, VI–VII; Blacksburg; Virginia Beach, VII; Charlottesville, VIII; Farmville, IX; Falls Church, VI; Bristol, VI; Blue Ridge Parkway, mile 210, 2800 ft, V; *West Virginia*—Patterson Creek, VII; Glen Dale, VI; *Wisconsin*—Sauk City; Madison, VI; *Wyoming*—7 mi NE Douglas, VII; Glendo, V.

Phanaeus wagneri pilatei Harold

GUATEMALA: *Petén*—Tikal, VII; MEXICO: *Quintana Roo*—Solferino, VII; Nuevo X-Can, V; 3 km E Tres Reyes, XI; 20 km N Felipe Carillo Puerto, VI; *Yucatán*—X-Can, VIII–IX; Tekax; Colonia Tucatán, VIII; Chichén Itzá, VI; Uxmal, VI.

Phanaeus wagneri wagneri Harold

COSTA RICA: *Cartago*—Turrialba; Cachí, 2000 ft; Cartago, XI; *Guanacaste*—5 mi N Las Cañas, VII; 20 km N Las Cañas, VII; Sabana Grande, XI–XII; Santa Rosa National Park; *San José*—Aserri, 1300 m, VIII; San José, 1100 m, II, V–VIII; EL SALVADOR: *Chalatenango*—La Palma, VI; *La Libertad*—Quetzaltepeque, 500 m, VI–VII; *San Salvador*—San Salvador, VI; GUATEMALA: *Chimaltenango*—Chimaltenango, 2000 m, VI, X; *Chiquimula*—Belén, IX; *Guatemala*—Guatemala, VII, X; *Quetzaltenango*—17 km S Quetzaltenango, 4000 ft; *Zacapa*—La Unión, X; HONDURAS: *Comayagua*—Minas de Oro, 4000 ft, V; *Cortés*—San Pedro Sula; *Francisco Morazán*—5 km SW Suyapa, 5400 ft, VIII; Cedros, XI; MEXICO: *Chiapas*—2 mi S La Trinitaria, 5200 ft, VIII; Bochil, VII; 9 mi SE Teopisca, VI; Aguacatenango, 1770 m, VIII; Cerro Huitepec, 2280 m, XI; El Sumidero, VIII; 12 mi S San Cristóbal de las Casas, VIII.

NATURAL HISTORY MUSEUM
OF LOS ANGELES COUNTY
900 EXPOSITION BOULEVARD
LOS ANGELES, CALIFORNIA 90007