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Taxonomy of *Phanaeus* revisited: Revised keys to and comments on species of the New World dung beetle genus *Phanaeus* MacLeay, 1819 (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini)

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Abstract. The purpose of this paper is to reassess the taxonomy of *Phanaeus* MacLeay (Coleoptera: Scarabaeidae) to accommodate new taxa and changes in taxonomic opinion since the publication of Edmonds' 1994 revision of the genus. The two subgenera and 13 species groups established by Edmonds (1994) remain unchanged. A revised set of keys with accompanying comments and illustrations separates 54 recognized valid species. Seven recently described valid species are incorporated into the revised classification: *Phanaeus blackalleri* Delgado-Castillo, 1991; *P. bordoni* Arnaud, 1996; *P. changdiazii* Kohlmann and Solís, 2001; *P. lecourti* Arnaud, 2000; *P. martinezorum* Arnaud, 2000; *P. yecoraensis* Edmonds, 2004; and *P. zapotecus* Edmonds, 2006. The **new name** *Phanaeus sororibispinus* Edmonds and Zidek replaces *Phanaeus alvarengai* Arnaud, 1984, a primary junior homonym of *P. alvarengai* Pereira and d'Andretta, 1955. Three subspecies recognized in 1994 are elevated to species rank, **new status**: *Phanaeus texensis* Edmonds, 1994; *P. pilatei* Harold, 1863; and *P. guatemalensis* Harold, 1871. *Phanaeus obliquans* Bates, 1887 is removed from synonymy and given **new status** as a valid species. Twelve **new junior subjective synonyms (bold)** are recognized: *P. tridens balthasari* Arnaud, 2002 (of *P. tridens* Castelnau, 1840); *P. dzidoi* Arnaud, 2000 (of *P. palaeno* Blanchard, 1843); *P. genieri* Arnaud, 2002 (of *P. amethystinus* Harold, 1863); *P. prasinus jolyi* Arnaud, 2001 (of *P. prasinus* Harold, 1868); *P. kirbyi ledezmai* Arnaud, 2002 (of *P. kirbyi* Vigors, 1825); *P. achilles lydiae* Arnaud, 2000 (of *P. achilles* Boheman, 1858); *P. chalconelas grossii* Arnaud, 2001 (of *P. chalconelas* [Perty, 1830]); *P. pyrois malyi* Arnaud, 2002 (of *P. pyrois* Bates, 1887); *P. tridens moroni* Arnaud, 2001 (of *P. tridens* Castelnau, 1840); *P. lecourti peruanus* Arnaud, 2000 (of *P. lecourti* Arnaud, 2000); *P. endymion porioni* Arnaud, 2001 (of *P. endymion* Harold, 1863); *P. pseudofurcosus* Balthasar, 1939 (of *P. tridens* Castelnau, 1840); and *P. prasinus trinidadensis* Arnaud, 2001 (of *P. prasinus* Harold, 1868). "*Phanaeus viridicollis*" Olsoufieff, 1924 (*sensu* Arnaud 2002) is an unavailable name here considered a color variant of *P. pyrois* Bates, 1887.

Introduction

Recent systematic study of the phanaeine dung beetles (Coleoptera: Scarabaeidae: Phanaeini) has progressed substantially since the publication of Edmonds' revision of *Phanaeus* MacLeay in 1994. Revisions of *Sulcophanaeus* Olsoufieff (Edmonds 2000), *Oxysternon* Castelnau (Edmonds and Zidek 2004) and *Coprophanaeus* Olsoufieff (Edmonds and Zidek 2010) addressed the taxonomy of other genera. Phylogenetic studies of the tribe include Philips et al. (2004) and Price (2007, 2009). Arnaud (2002b) contributed a survey of phanaeine diversity, and the only large genus still in need of close taxonomic scrutiny, *Dendropaemon* Perty, is currently under review. In addition to these comprehensive studies, other works have proposed at least 25 new taxa in various genera, including 18 for *Phanaeus* alone. As for regional, non-taxonomic studies, the phanaeine fauna of Bolivia is by far the best known at this time (Hamel-Liege et al. 2006, 2008, 2009, in press), while that of Costa Rica is perhaps the best known taxonomically (Solís and Kohlmann 2012, and references therein). Attention to phanaeines has been paralleled in other dung beetle groups as well, and there has emerged in the last 25 years a vibrant and dedicated community of scholars dedicated to the study of these beetles from varied points of view. Moreover, dung beetles in general have been increasingly relied on as a bioindicator group in a large body of studies on regional and community ecology, distribution and conservation in tropical ecosystems (Spector 2006;

Andresen and Laurance 2007; Kohlmann et al. 2007; Nichols et al. 2009). The current intense interest in Scarabaeinae is resoundingly evidenced by the example of Vaz-de-Mello et al. (2011), who produced a digital multilingual key to the genera of the subfamily that was downloaded by over 30,000 readers in the three months following its publication (<<http://www.mapress.com/zootaxa/2011/f/zt02854p073.pdf>>).

All comprehensive taxonomic works, based as they are on incomplete information and evolving opinion, are patently out-of-date the moment they are published. Such is true of generic revisions in general, and, in the present case, specifically of Edmonds' 1994 revision of the genus *Phanaeus*. The purpose of this paper is to reassess the taxonomy of *Phanaeus* in the light of taxa described mostly after 1994 as well as changes in our taxonomic opinion since that time. This reassessment gives rise to changes in the species-level classification, a revised set of keys to species groups and to species, as well as a new body of illustrations. We gratefully acknowledge the often constructive criticism from our colleagues of the original classification. Their comments are in no small way responsible for some of the changes proposed here, especially the avoidance of the subspecies category, which more often than not was utilized as a taxonomic compromise rather than a way to capture the results of careful and exhaustive statistical studies of geographic variation. In this sense, the classification proposed here is simplified and meant to describe the diversity of the genus in the most straightforward way supported by traditional taxonomic observation. This approach will be most welcomed by ecologists, museum systematists and collectors who need to name their specimens. Those approaching analysis of the genus from the population level will likely find that the classification offers some interesting and challenging opportunities for morphological and molecular (DNA) studies of local and regional population variability and differentiation, such as Solís and Kohlmann's (2012) emerging study of Caribbean-Pacific vicariance among Costa Rican Scarabaeinae. In this context, we offer as an example the tridens and mexicanus species groups as prime candidates for a broad regional analysis.

This paper is organized around a revised set of keys to species based on Edmonds (1994). We employ the subgenera and species groups recognized there, although there may be a just cause to modify these in the light of further phylogenetic scrutiny sometime in the future (see Price 2007, 2009). It is important to stress that our intention here is to supplement Edmonds (1994), not to replace it, although we expect that this contribution will prove useful as an independent document to be used, scrutinized and criticized by its users. The original revision contains much historical, distributional, phylogenetic and other information that is not repeated here. Because it is long out of print and now difficult to obtain in printed form, a digital file of Edmonds (1994) is available for download from the University of Nebraska State Museum, Entomology Division at <http://museum.unl.edu/research/entomology/EdmondsPhanaeusRevision.pdf> (51.0 mb); University of Florida, Florida Virtual Campus, Florida Online Journals at <http://purl.fcla.edu/fcla/insectamundi/Edmonds1994> (66.5 mb); and as a supplement to this article at the Center for Systematic Entomology, Insecta Mundi Published Papers page in both a full version <http://centerforsystematicentomology.org/supplemental/Edmonds-1994-large.pdf> (66.5 mb) or a reduced version <http://centerforsystematicentomology.org/supplemental/Edmonds-1994-small.pdf> (15.1 mb).

In our treatment of distribution we have added reference to Morrone's (2001) biogeographic scheme (Fig. 1–4) for more generalized (shorthand) statements that are useful for making comparisons with other animal groups. We have modified the Morrone classification slightly in that our designation of Mesoamerica (Fig. 1) is roughly equivalent to Morrone's Caribeña Subregion of the Neotropical Region minus the islands of the Bahamas and the Caribbean (provinces of Bahamas, Cuba, Cayman Islands, Jamaica, Hispaniola, Puerto Rico and Lesser Antilles) and the Galapagos. This is the same scheme we used in our review of *Coprophanæus* (Edmonds and Zidek 2010). Reference to the Morrone classification appears in the key following the more traditional geographic description of distribution in the format (Morrone: Volcanic Axis Province).

Revised classification

Following is an outline of the revised classification of *Phanaeus* presented here. It embraces 54 currently recognized species arranged in 13 species groups. Synonyms are listed in brackets [] and are fully cited in the synopsis of species-group names following the classification. Genus-group initials and

names have been intentionally omitted for clarity. Species names under each group are in the order they appear in the relevant species-group key.

Subgenus *Notiophanaeus*

splendidulus group

splendidulus (Fabricius, 1781) [*corydon*, *floriger*]
dejeani Harold, 1868
melibaeus Blanchard, 1843 [*sculpturatus*]
haroldi Kirsch, 1871
bordoni Arnaud, 1996

chalcomelas group

chalcomelas (Perty, 1830) [*grossii*]
meleagris Blanchard, 1843 [*minos*]
lecourti Arnaud, 2000 [*peruanus*]
cambeforti Arnaud, 1982
achilles Boheman, 1858 [*foveolatus*, *lydiae*]

bispinus group

bispinus Bates, 1868 [*digitalis*]
sororibispinus Edmonds and Zidek **New Name** [for *alvarengai* Arnaud]

palaeno group

palaeno Blanchard, 1843 [*blanchardi*, *dzidoi*, *excisicornis*]
martinezorum Arnaud, 2000
kirbyi Vigers, 1825 [*laevicollis*, *ledezmai*, *planicollis*, *subtricornis*, *truncaticornis*]

endymion group

endymion Harold, 1863 [*porioni*]
zapotecus Edmonds, 2006
halffterorum Edmonds, 1979
pyrois Bates, 1887 [*bothrus*, *funereus*, *malyi*, *olsoufieffi*]

Subgenus *Phanaeus s. str.*

hermes group

hermes Harold, 1868 [*bogotensis*]
prasinus Harold, 1868 [*jolyi*, *lugens*, *trinidadensis*]

tridens group

tridens Castelnau, 1840 [*balthasari*, *frankenbergeri*, *moroni*, *pseudofurcosus*]
eximius Bates, 1887
furiosus Bates, 1887 [*furcosus*]
daphnis Harold, 1863 [*coeruleus*, *herbeus*, *substriolatus*, *tricornis*]
nimrod Harold, 1863 [*abori*]

triangularis group

triangularis (Say, 1823) [*goidanichi*, *niger*, *torrens*]
texensis Edmonds, 1994 **New Status**
adonis Harold, 1863

mexicanus group

- flohri* Nevinson, 1892
yecoraensis Edmonds, 2004
demon Castelnau, 1840 [*pegasus*, *scintillans*]
obliquans Bates, 1887 **New Status**
excelsus Bates, 1889
scutifer Bates, 1887
lunaris Taschenberg, 1870 [*charon*]
wagneri Harold, 1863
pilatei Harold, 1863 **New Status**
mexicanus Harold, 1863 [*divisus*]
amithaon Harold, 1863

beltianus group

- beltianus* Bates, 1887
changdiazi Kohlmann and Solís, 2001
sallei Harold, 1863
howdeni Arnaud, 1984

amethystinus group

- melampus* Harold, 1863
amethystinus Harold, 1863 [*genieri*, *martinezi*]
guatemalensis Harold, 1871 **New Status** [*tepanensis*]
blackalleri Delgado-Castillo, 1991

quadridens group

- palliatu*s Sturm, 1843
damocles Harold, 1863
quadridens (Say, 1835) [*borealis*, *laevipennis*, *violaceus*]

vindex group

- igneus* MacLeay, 1819 [*floridanus*]
vindex MacLeay, 1819 [*cyanellus*, *rubervirens*]
difformis LeConte, 1847 [*magnificens*]

List of *Phanaeus* species-group names and status

Listed below are 114 known species-group names assignable to *Phanaeus*, of which we consider 54 to be valid (noted in **boldface** type) and 53 others to be synonyms. Four names are primary junior homonyms and, consequently, permanently unavailable; one is infrasubspecific and, therefore, unavailable; and two are fossils of uncertain status. In the listing below, the following abbreviations apply: hom. = homonym; jr. = junior; prim. = primary; subj. = subjective; syn. = synonym. Generic initials and names have been intentionally omitted for clarity. Numbers in brackets “[##]” following names of valid species refer to the page below on which the species is identified in the relevant key.

***achilles* Boheman, 1858** [10]

***adonis* Harold, 1863** [15]

alvarengai Arnaud, 1984 (prim. jr. hom. of *alvarengai* Pereira and d’Andretta, 1955 — permanently unavailable; valid name *sororibispinus* Edmonds and Zidek, see below)

***amethystinus* Harold, 1863** [20]

***amithaon* Harold, 1875b** [19]

antiquus Horn, 1876 (uncertain status; fossil)

abori Balthasar, 1939 (jr. subj. syn. of *nimrod* Harold)

- balthasari* Arnaud, 2002b (jr. subj. syn. of *tridens* Harold) **New Synonymy**
***beltianus* Bates, 1887** [19]
***bispinus* Bates, 1868** [8]
***blackalleri* Delgado-Castillo, 1991** [20]
blanchardi Harold, 1871a (jr. subj. syn. of *palaeno* Blanchard)
blanchardi Olsoufieff, 1924 (jr. prim. hom. of *blanchardi* Harold — permanently unavailable; valid name *pyrois* Bates)
bogotensis Kirsch, 1871 (jr. subj. syn. of *hermes* Harold)
***bordoni* Arnaud, 1996** [12]
borealis Olsoufieff, 1924 (jr. subj. syn. of *quadridens* [Say])
bothrus Blackwelder, 1944 (jr. subj. syn. of *olsoufieffi* Balthasar; valid name *pyrois* Bates)
***cambeforti* Arnaud, 1982b** [10]
carnifex (Linné, 1767) (jr. prim. hom. of *Scarabaeus carnifex* Linné, 1758 — permanently unavailable; valid name *vindex* MacLeay)
***chalcomelas* (Perty, 1830)** [10]
***changdiazi* Kohlmann and Solís, 2001** [19]
charon Harold, 1880a (jr. subj. syn. of *lunaris* Taschenberg)
coeruleus Bates, 1887 (jr. subj. syn. of *daphnis* Harold)
corydon Blanchard, 1843 (jr. subj. syn. of *splendidulus* [Fabricius])
cyanellus Robinson, 1938 (jr. subj. syn. of *vindex* MacLeay)
***damocles* Harold, 1863** [21]
***daphnis* Harold, 1863** [16]
***dejeani* Harold, 1868b** [11]
***demon* Castelnau, 1840** [18]
***difformis* LeConte, 1847** [22]
digitalis Olsoufieff, 1924 (jr. subj. syn. of *bispinus* Bates)
divisus Harold, 1863 (jr. subj. syn. of *mexicanus* Harold)
dzidoi Arnaud, 2000 (jr. subj. syn. of *palaeno* Blanchard) **New Synonymy**
***endymion* Harold, 1863** [13]
***excelsus* Bates, 1889** [18]
***eximius* Bates, 1887** [16]
excisicornis Balthasar, 1939 (jr. subj. syn. of *palaeno* Blanchard)
***flohri* Nevinson, 1892** [17]
floridanus Olsoufieff, 1924 (jr. subj. syn. of *igneus* MacLeay)
floriger (Kirby, 1818) (jr. subj. syn. of *splendidulus* [Fabricius])
foveolatus Harold, 1880a (jr. subj. syn. of *achilles* Boheman)
frankenbergeri Balthasar, 1939 (jr. subj. syn. of *tridens* Harold)
funereus Balthasar, 1939 (jr. subj. syn. of *pyrois* Bates)
furcosus Felsche, 1901 (jr. subj. syn. of *furiosus* Bates)
***furiosus* Bates, 1887** [16]
genieri Arnaud, 2001 (jr. subj. syn. of *amethystinus* Harold) **New Synonymy**
goidanichi Balthasar, 1939 (jr. subj. syn. of *triangularis* [Say])
grossii Arnaud, 2001 (jr. subj. syn. of *chalcomelas* [Perty])
***guatemalensis* Harold, 1871b** [20]
***halffterorum* Edmonds, 1979** [12]
***haroldi* Kirsch, 1871** [12]
herbeus Bates, 1887 (jr. subj. syn. of *daphnis* Harold)
***hermes* Harold, 1868b** [16]
***howdeni* Arnaud, 1984** [19]
***igneus* MacLeay, 1819** [21]
jolyi Arnaud, 2001 (jr. subj. syn. of *prasinus* Harold) **New Synonymy**
***kirbyi* Vigers, 1825** [9]
labrae (Pierce, 1946) (uncertain status; fossil near *vindex* MacLeay)
laevicollis Castelnau, 1840 (jr. subj. syn. of *kirbyi* Vigers)

- laevipennis* Sturm, 1843 (jr. subj. syn. of *quadridens* [Say])
lecourti Arnaud, 2000 [10]
ledezmai Arnaud, 2002a (jr. subj. syn. of *kirbyi* Vigors) **New Synonymy**
lugens Nevinson, 1892 (jr. subj. syn. of *prasinus* Harold)
lunaris Taschenberg, 1870 [18]
lydiae Arnaud, 2000 (jr. subj. syn. of *achilles* Boheman) **New Synonymy**
magnificens Robinson, 1948 (jr. subj. syn. of *difformis* LeConte)
malyi Arnaud, 2002a (jr. subj. syn. of *pyrois* Bates) **New Synonymy**
martinezi Halffter, 1955 (jr. subj. syn. of *amethystinus* Harold)
martinezorum Arnaud, 2000 [9]
melampus Harold, 1863 [20]
meleagris Blanchard, 1843 [11]
melibaeus Blanchard, 1843 [12]
mexicanus Harold, 1863 [19]
minos Erichson, 1847 (jr. subj. syn. of *meleagris* Blanchard, 1843)
mirabilis Bates, 1887 (jr. prim. hom. of *mirabilis* Harold, 1877 — permanently unavailable; valid name *demon* Castelnau)
moroni Arnaud, 2001 (jr. subj. syn. of *tridens* Harold) **New Synonymy**
niger Olsoufieff, 1924 (jr. subj. syn. of *triangularis* [Say])
nimrod Harold, 1863 [15]
obliquans Bates, 1887 **New Status** [18]
olsoufieffi Balthasar, 1939 (jr. subj. syn. of *pyrois* Bates)
palaeno Blanchard, 1843 [9]
palliatus Sturm, 1843 [21]
pegasus Sturm, 1843 (jr. subj. syn. of *demon* Castelnau)
peruanus Arnaud, 2000 (jr. subj. syn. of *lecourti* Arnaud) **New Synonymy**
pilatei Harold, 1863 [18]
planicollis Perty, 1830 (jr. subj. syn. of *kirbyi* Vigors)
porioni Arnaud, 2001b (jr. subj. syn. of *endymion* Harold) **New Synonymy**
prasinus Harold, 1868a [16]
pseudofurcosus Balthasar, 1939 (jr. subj. syn. of *tridens* Castelnau) **New Synonymy**
pyrois Bates, 1887 [13]
quadridens (Say, 1835) [21]
rubervirens Robinson, 1948 (jr. subj. syn. of *vindex* Castelnau)
sallei Harold, 1863 [19]
scintillans Bates, 1887 (jr. subj. syn. of *demon* Castelnau)
scutifer Bates, 1887 [18]
sculpturatus Olsoufieff, 1924 (jr. subj. syn. of *melibaeus* Blanchard)
sororibispinus Edmonds and Zidek, 2012 **New Name** (see *alvarengai*) [8]
splendidulus (Fabricius, 1781) [11]
substriolatus Balthasar, 1939 (jr. subj. syn. of *daphnis* Harold)
subtricornis Perty, 1830 (jr. subj. syn. of *kirbyi* Vigors)
tepanensis Bates, 1889 (jr. subj. syn. of *guatemalensis* Harold)
texensis Edmonds, 1994 **New Status** [15]
torrens LeConte, 1847 (jr. subj. syn. of *triangularis* [Say])
triangularis (Say, 1823) [15]
tricornis Olsoufieff, 1924 (jr. subj. syn. of *daphnis* Harold)
tridens Castelnau, 1840 [15]
trinidadensis Arnaud, 2001 (jr. subj. syn. of *prasinus* Harold) **New Synonymy**
truncaticornis Olsoufieff, 1924 (jr. subj. syn. of *kirbyi* Vigors)
vindex MacLeay, 1819 [22]
violaceus Castelnau, 1840 (jr. subj. syn. of *quadridens* [Say])
viridicollis Olsoufieff, 1924 (*sensu* Arnaud 2002b) (unavailable infrasubspecific name referable to *pyrois* Bates)

wagneri Harold, 1863 [19]
yecoraensis Edmonds, 2004 [17]
zapotecus Edmonds, 2006 [13]

Phanaeus MacLeay

Key to subgenera

1. Sculpturing of anterolateral portions of pronotum (in front of lateral fossae) with distinct punctures ($\times 10$), sometimes almost completely smooth (Fig. 12–13); size, shape and density of punctures variable, but often small and sparse, causing that area to appear glassy smooth to the unaided eye. Remainder of pronotum usually sculptured like anterolateral portions, sometimes (chalcotelas group, Fig. 66–68, and males of endymion group, Fig. 141) more coarsely sculptured. Pronotal punctures of chalcotelas group large and shallow, intermingled with and obscured by blister-like rugosities that give pronotum a rugose appearance ($\times 0$ –5; Fig. 66–68). If anterolateral punctures largely obscured (male *P. achilles*) then anteromedian prominence of metasternum acuminate (as in Fig. 56–57). Five groups of mostly South American species ...
 ***Notiophanaeus* Edmonds** [7]
- Anterolateral portions of pronotum granulate (Fig. 162, 222), granulorugose or rugose (Fig. 383), lacking distinct punctures ($\times 10$) except occasionally near anterior margin adjacent to eyes. Remainder of pronotum always at least partly sculptured like anterolateral portions or more coarsely so; punctures often present at least posteromedially and may cover as much as posterior one-half of pronotum, especially in females. Anterior prominence of metasternum always keeled (as in Fig. 54–55), not acuminate. Eight groups of mostly Middle and North American species ***Phanaeus s. str.*** [13]

Comments. The distinction between the two subgenera continues to be imprecise because of the variation exhibited by certain *Notiophanaeus* species. Price (2007, 2009) suggested significant rearrangements of the species groups based on phylogenetic data with an emphasis on the shape of the male pronotum, but these, which we regard as reasonable alternatives, should be subjected to more scrutiny before proposing major shifts in the current classification.

Subgenus *Notiophanaeus* Edmonds

Key to species groups

1. Elytral striae carinulate (as in Fig. 21) and punctate ($\times 0$ –10) (Fig. 14, 19). Pronotum of well-developed male with a pair of closely set, parallel, slender spines (Fig. 12–13, 16–17); that of female as in Fig. 9, 15. Hind wing notched basally. Dorsum dull olive green or brownish black (Fig. 12–19). Widely distributed in Amazon Basin (Morrone: Amazonian Subregion) (Fig. 49).
 **bispinus group** [8]
- Elytral striae variable but not both carinulate and punctate. Pronotum not as in bispinus group. Hind wing not notched. Color and distribution variable **2**
- 2(1). Elytral striae carinulate ($\times 30$), not punctate (Fig. 21). Anterior margin of clypeus strongly bidentate medially (Fig. 37, 40); clypeal process spinose (Fig. 31, arrow). Posterior pronotal margin acuminate medially, basal pronotal fossae lacking (Fig. 35). Protibia strongly quadridentate (Fig. 32). Venter clothed by dense whitish pile (stained or missing in worn or dirty specimens). Dorsum shiny green, in some specimens with yellow reflections, some specimens dark blue. Brazilian Highlands (“campos cerrados”) and adjacent regions of Bolivia, Paraguay and extreme northeastern Argentina (Morrone: Cerrado and Chaco Provinces) (Fig. 49) **palaeno group** [9]
- Elytral striae non-carinulate, punctate or not. Anterior margin of clypeus strongly bidentate or not. Clypeal process variable, but not spinose. Posterior pronotal margin variable, basal pronotal

- fossae present or absent. Protibia tri- or quadridentate. Venter not bearing a dense whitish pile. Color and distribution variable 3
- 3(2). Elytral striae distinctly punctate to unaided eye (Fig. 62–65). Pronotum bearing few to many black, blister-like rugosities, giving surface irregularly maculated (“peppered”) appearance (Fig. 66–68). Dorsum dull, in most specimens olive brown or olive green; in some specimens almost black or metallic red or green. Pronotum of larger males flattened and in dorsal view appearing triangular (e.g. Fig. 86–87). Widely distributed in Amazon Basin and along eastern slopes of Andes, one species in western Ecuador (Morrone: Amazonian Subregion) (Fig. 49).
..... **chalconelas group** [10]
- Elytral striae appearing simple to unaided eye, minute punctures may be visible under magnification ($\times 10$ –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
- 4(3). Anteromedial margin of clypeus at most only weakly bidentate. Clypeal process tooth-like (Fig. 98, arrow). Protibia tri- or quadridentate; if quadridentate, basal tooth not preceded by a distinct narrow notch. Protibial spur bent mesially. Pronotum of larger males concave dorsally and with a pair of spinate horns arising from near posterior margin (Fig. 116, 120). Northern South America east of Andes (Morrone: Amazonian Subregion) (Fig. 111).
..... **splendidulus group** [11]
- Anteromedial margin of clypeus strongly bidentate. Clypeal process a transverse ridge, not tooth-like. Protibia strongly quadridentate, basal tooth preceded by a narrow notch (Fig. 136, arrow; effaced in highly worn specimens). Protibial spur more-or-less straight. Pronotum of larger males flattened above, triangular, lacking spinate processes (Fig. 141–142). Extreme northwestern South America, Central America and southern Mexico (Morrone: Mesoamerican Subregion) (Fig. 143).
..... **endymion group** [12]

Comments. With the addition of four species described since 1994 (*P. bordoni* Arnaud, *P. lecourti* Arnaud, *P. martinezorum* Arnaud and *P. zapotecus* Edmonds), *Notiophanaeus* now brings together 19 species. Other new species-group names assignable to this subgenus which we do not now consider valid (see species group comments below) are *P. lecourti peruanus* Arnaud, *P. achilles lydiae* Arnaud, *P. dzidoi* Arnaud, *P. endymion porioni* Arnaud, *P. chalconelas grossii* Arnaud, *P. pyrois malyi* Arnaud and *P. kirbyi ledezmai* Arnaud. As suggested by Edmonds (1994) and supported by Price (2007, 2009), the subgenus is undoubtedly a paraphyletic collection of evolutionary remnants of early radiation of the genus in South America. Species groups and species taxonomic limits are usually distinct and unambiguous, in marked contrast to the general case of *Phanaeus s. str. Notiophanaeus* is a South American taxon; only one of the five species groups (endymion) is centered outside the continent (in Mesoamerica).

Key to species of the bispinus group

1. Clypeus of large male (Fig. 5–6) drawn out anteriorly, with strongly protruding, upturned median teeth; that of small male rounded, teeth neither protruding nor upturned. Male head with weakly bituberculate carina, lacking any horn-like armament. Pronotum of female (seen from front, Fig. 11) with more-or-less semicircular shallow depression bounded by thick ridge; head with trituberculate carina. Elytral striae punctate, punctures clearly visible under low ($\times 5$) magnification (Fig. 13–14). All three protibial teeth usually carinate on outer surface, basal tooth smooth in some. Amazon Basin (Morrone: Amazonian Subregion) (Fig. 49)
..... **Phanaeus (N.) sororibispinus New Name** (Fig. 5–6, 11–15)
- Clypeus of male rounded, not drawn out anteriorly and median teeth neither protruding nor upturned even in large specimens (Fig. 7–8). Large male with long, slender, gently curved head horn extending to tips of pronotal horns (Fig. 8); smallest males (Fig. 18) with medially bituberculate transverse carina. Pronotum of female (Fig. 9–10) with deep, ovoid depression, top margin of which drawn out as single, downcurved spine. Punctures of elytral striae usually

clearly visible to unaided eye. Only apical two teeth of protibia carinate; basal tooth always smooth. Amazon Basin (Morrone: Amazonian Subregion) (Fig. 49)
 ***Phanaeus (N.) bispinus* Bates** (Fig. 7–10, 16–19)

Comments. In accordance with Article 53.3 of the International Code of Zoological Nomenclature (ICZN 1999), *Phanaeus alvarengai* Pereira and d’Andretta, 1955 is the senior primary homonym of *Phanaeus alvarengai* Arnaud, 1984; the former is a junior synonym of *Coprophanaeus pertyi* (Olsoufieff, 1924) (Edmonds and Zidek 2010, *q.v.*, erroneously attributed the primary homonym to Martínez and Pereira). The fact that Pereira and d’Andretta placed their taxon in the subgenus *Coprophanaeus* of *Phanaeus* does not, in accordance with Article 57.4 of the Code, shield Arnaud’s name from unavailability, and, therefore, the name *P. alvarengai sensu* Arnaud must be replaced. We here propose the name of *Phanaeus sororibispinus* Edmonds and Zidek as the **replacement name** for *Phanaeus alvarengai* Arnaud, 1984. The new name is a combination of *soror* (Latin for “sister”) and *bispinus* to indicate our opinion that it is the sister species of *P. bispinus*. Vulinec et al. (2003) have greatly improved our knowledge of this rare species (referred to as *P. alvarengai*), which appears to have a distribution paralleling that of *P. bispinus*. In addition, they report it to have the notched hind wing unique to this species group and otherwise found only in some *Coprophanaeus* and *Dendropaemon* (Edmonds 1972).

Key to species of the palaeno group

1. Anterior portion of circumnotal ridge raised behind and narrowly excised medially, excision separating two small, dentiform tubercles that are rarely effaced even in smallest individuals (Fig. 24). Paraocular area flattened above. Elytral interstriae weakly convex. *Male*: Pronotum of large specimens (Fig. 37) flattened above and expanded laterally as rounded, flat lobes. *Female*: Pronotum of all but smallest individuals bearing an almost straight, transverse, anteromedial carina (Fig. 28). Cerrado of Brazil and adjacent Bolivia and Paraguay (Morrone: Cerrado and Chaco Provinces) (Fig. 49).
 ***Phanaeus (N.) kirbyi* Vigors** (Fig. 23–24, 28, 34–39)
- Anterior portion of circumnotal ridge not noticeably raised and neither excised nor bidentate medially. Upper surface of paraocular areas swollen adjacent to eyes, flattened laterally (Fig. 22). Elytral interstriae moderately convex. *Male*: Pronotum of large individuals (Fig. 41) shallowly concave above, posterior angles produced upward as a pair of apically convergent, widely separated horns. *Female*: Pronotum variable. **2**
- 2(1). Female pronotum of all but smallest individuals bearing a wide, U-shaped anteromedial carina followed by a shallow concavity (Fig. 30); cephalic carina tridentate, teeth equal-sized (Fig. 25) and (seen from above, Fig. 30) placed in a straight transverse line. Cerrado of Brazil and adjacent Bolivia and Paraguay (Morrone: Cerrado Province) (Fig. 49)
 ***Phanaeus (N.) palaeno* Blanchard** (Fig. 21–22, 25–26, 30–33, 40–44)
- Female pronotum with transverse, brace-shaped ridge not associated with concavity (Fig. 29); cephalic carina tridentate, middle tooth strongly raised, much larger than lateral two (Fig. 27) and (seen from above, Fig. 29) abruptly offset posteriorly. Northern Corrientes Province of Argentina (Morrone: Cerrado Province) (Fig. 49)
 ***Phanaeus (N.) martinezorum* Arnaud** (Fig. 27, 29, 45–48)

Comments. Price’s phylogenetic study of the genus (2009) considers this group basal to phanaeines and, from a strictly cladistic point of view, a taxon that could be ranked as a separate genus. From a morphological point of view, it is clearly an annectant between *Phanaeus* and *Oxysternon*, with which it shares the following characters: a spiniform clypeal process, angulate posterior pronotal margin, an enlarged (but not spinate) anterior metasternal angle, and a bituberculate cephalic process in small males. Arnaud (2000) christened *Phanaeus martinezorum* an unusual Argentine population that Edmonds (1994) referred with some doubt to *P. palaeno*. Males of the two species appear identical — the only instance in Phanaeini where observed species differences reside solely in the female. We regard *P. dzidoi*

Arnaud and *P. kirbyi ledezmai* Arnaud as **new synonyms** of *P. palaeno* and *P. kirbyi*, respectively; in each case, the distinction is based on tenuous characters gleaned from scant material.

Key to species of the *chalconelas* group

1. Anteromedial angle of metasternum viewed from below (Fig. 55) capped by a raised arrowhead or V-shaped swelling, sides of swelling visible laterally (Fig. 54) as distinct ridges. Paraocular ridge almost always distinct and extending from posterior margin of paraocular area to a point even with middle of lateral margin of eye. *Male*: Cephalic horn of large individuals as in Fig. 52, abruptly narrowed at about midlength. *Female*: Pronotum (Fig. 60) with a shallow anteromedial concavity surrounded by four small tubercles, anterior one of them largest, occasionally tooth-like. Dorsum dull, dark, in most specimens olive brown or olive green (Fig. 69–72). Length 12–18 mm. Amazon Basin from Guiana to Bolivia (Morrone: Amazonian Subregion) (Fig. 49) ***Phanaeus (N.) chalconelas* (Perty)** (Fig. 42, 54–55, 59–60, 62–63, 68–72)
- Anteromedial angle of metasternum not capped, smooth and drawn out anteriorly as a small, slightly upturned acute tooth best seen in profile (Fig. 56). Paraocular ridge present or absent. *Male*: Cephalic horn tapering evenly (Fig. 53); if widened basally (some *P. meleagris*, Fig. 50), narrowing not as abrupt as above. *Female*: Pronotum evenly convex, lacking distinct anteromedial concavity, bearing three small, rounded tubercles (almost effaced in *P. achilles*) near anterior margin (Fig. 61). Color and distribution variable **2**
- 2(1). Elytral interstriae distinctly but sparsely punctate ($\times 10$), irregularly wrinkled (Fig. 65). Pronotal punctures small, deep, intermingled with well-defined black rugosities (Fig. 66). Pronotal disk of large males flattened, but not evenly so (Fig. 77); posterolateral angles in dorsal view rounded laterally, causing disk to appear nearly heart-shaped (Fig. 73, 76). Middle of cephalic carina of female thickened and raised, forming a distinct, isolated, anteriorly bowed ridge (Fig. 58). Paraocular ridge distinct. Dorsum shiny, coppery red or dark green (Fig. 73–77). Desert scrub region of southwestern Ecuador and northern Peru (Morrone: Arid Ecuador Province) (Fig. 49) ***Phanaeus (N.) achilles Boheman*** (Fig. 58, 65–66, 73–77)
- Elytral interstriae completely smooth, bearing no punctures or wrinkling (Fig. 62–64). Pronotal punctures (Fig. 67–68) large, shallow, often confluent, each with a shiny central microspot ($\times 40$); pronotal punctures often visible only when viewed at a low angle). Pronotal disk of large males evenly flattened, sides of posterolateral angles more-or-less straight so that in dorsal view disk appears almost triangular (Fig. 70, 79, 83, 86). Cephalic carina of female simple or only weakly trituberculate (Fig. 59). Paraocular ridge absent or indicated only by a slight swelling adjacent to eye. Dorsum dull, usually somber **3**
- 3(2). Pronotal punctures, while not strong, usually distinct both on sides and disk; central microspots often difficult to detect ($\times 40$), absent in some specimens. Basal pronotal fossae lacking or represented only by small punctures ($\times 10$). Dorsum olive green or olive brown; metallic highlights on pronotum and pygidium green. Smaller, length in few specimens exceeding 15 mm. Amazon Basin from Guiana to Colombia and Peru (Morrone: Amazonian Subregion) (Fig. 46) ***Phanaeus (N.) cambeforti Arnaud*** (Fig. 53, 61, 78–81)
- Pronotal punctures weakly defined and often appearing almost effaced; central shiny microspots almost always distinct ($\times 40$), even if associated punctures are obsolete. Basal pronotal fossae always distinct. Dorsal coloration variable. Yungas and western Napo Provinces of Amazonia **4**
- 4(3). Dorsum uniformly weakly lustrous, dark blue or green with “oily” sheen; without metallic color. Parameres slightly swollen apically. Larger, length 15–24 mm, usually over 18 mm. Yungas of Bolivia and Peru (Morrone: Yungas Province) (Fig. 49) ***Phanaeus (N.) lecourti Arnaud*** (Fig. 51, 56–57, 82–85)
- Dorsal coloration variable, but lacking oily sheen; black with reddish reflections, or greenish brown tones infused with limited metallic red areas at least along circumnotal ridge but often

also on sides of pronotum. Parameres tapering evenly, not swollen apically. Smaller, length 10–20 mm, most specimens less than 18 mm. Eastern slopes (Yungas) of Andes from Peru to Venezuela (Morrone: Napo and Yungas Provinces) (Fig. 49)
 ***Phanaeus* (N.) *meleagris* Blanchard** (Fig. 50, 62–63, 68, 86–91)

Comments. The composition of this group has grown by one species with the addition of *P. lecourti*, which Edmonds (1994) tentatively placed in *P. meleagris*. During the course of this study we vacillated on the status of *P. minos* Erichson, which Arnaud (2002b) regarded as a subspecies of *P. meleagris*. The distinction between the two resides primarily in coloration (cf. Fig. 62–63), which we have concluded does not vary in a consistent enough way to support the distinction (whether of species or subspecies). The same can be said regarding the subspecies described by Arnaud (2002b) as *P. lecourti peruanus* and *P. achilles lydiae*, which are, in our opinion, color variants. Accordingly, we regard the former as a **new synonym** of *P. lecourti*, and the latter as a **new synonym** of *P. achilles*. Arnaud (2001: 5) designated a neotype for *Phanaeus chalcomelas* (Perty) in order to remove the confusion attending the name and permit description of a new subspecies, *P. chalcomelas grossii*. This subspecies, based on what we believe to be unreliable variation in male horn shape, we regard as a **new synonym** of *P. chalcomelas*.

Key to species of the splendidulus group

1. Anterior prominence of metasternum in profile (as in Fig. 56) acuminate, produced anteriorly as a minute, acute tubercle (subject to wear). Protibia 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 Espirito Santo to Rio Grande do Sul and extreme northeastern Argentina (Misiones) (Morrone: Paranaian Forest and Brazilian Atlantic Forest Provinces) (Fig. 111)
 ***Phanaeus* (N.) *splendidulus* (Fabricius)** (Fig. 98, 106–107, 112–115)
- Anterior prominence of metasternum in profile (as in Fig. 54–55) broadly rounded and viewed from below narrowly keeled. Protibia tri- or quadridentate, apical three teeth carinate longitudinally on anterior surface (carina of third tooth may be fine or effaced in *P. dejeani*). Distribution varies **2**
- 2(1). Protibia tridentate, fourth (basal) tooth at most suggested only by a subtle angular bend in outer tibial margin; longitudinal carina of third tooth may be fine or effaced; apex of spur evenly curved mesially. Cephalic horn of larger males slightly widened and compressed apically (Fig. 95–96); that of smallest males reduced to a weakly bituberculate carina. Pronotum of female with anteromedial concavity bordered anteriorly by a strong, U-shaped, trituberculate carina; middle tubercle dentate in larger individuals (Fig. 101). Basal pronotal fossae absent or only slightly indicated. Elytra deep royal blue, in some specimens tending toward bluish green, appearing lacquered; pronotum (except for black areas) shiny greenish yellow (Fig. 116–119). Mountainous areas (“serras”) of southeastern Brazil (Morrone: Paranaian Forest and Brazilian Atlantic Forest Provinces) (Fig. 111)
 ***Phanaeus* (N.) *dejeani* Harold** (Fig. 93, 95–96, 99, 101, 105, 116–119)
- Protibia quadridentate (fourth [basal] tooth sometimes only weakly developed in *P. haroldi*); longitudinal carina of third tooth always distinct; apex of tibial spur truncated, inner angle acute, directed mesially. 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 (Fig. 97, 127, 131). Basal pronotal fossae distinct. Elytra green or almost black, not royal blue; pronotum dull olive green or shiny green with strong coppery highlights. Evergreen forests of Amazon Basin and eastern slopes of Andes **3**
- 3(2). Pronotum black or olive green; elytra black or with feeble greenish or bluish luster (×10) (Fig. 124–131). Pronotum of female with anteromedial concavity flanked by a pair of blade-like horns (Fig. 127) or by three rounded tubercles (Fig. 131). Pronotum of larger males (Fig. 124,

- 128) with a shallow medial concavity; each posterior angle drawn out into a strong, slender, anteriorly directed spine. Elytral interstriae convex and more-or-less evenly dulled, at most only slightly shinier midlongitudinally (Fig. 103). Eastern slopes of Andes from Colombia to northern Peru and southeastern Venezuela 4
- Pronotum shiny green with strong coppery or coppery yellow reflections; elytra moderately shiny green (Fig. 120–123). Pronotum of female (Fig. 97) with a conspicuous oval anteromedial concavity bordered anteriorly by three strong tubercles, outer two acute and middle one quadrate. Pronotum of larger males (Fig. 120–121) with a broad median concavity drawn on each side into an acute, dorsally directed spine. Elytral interstriae distinctly shinier midlongitudinally than adjacent to striae (Fig. 104). Southern Amazon Basin in Brazil (Morrone: Tapajós-Xingú and Madeira Provinces) (Fig. 111)
..... ***Phanaeus (N.) melibaeus* Blanchard** (Fig. 104, 109–110, 120–123)
- 4(3). Cephalic horn of large male erect, slender, not distinctly swollen on posterior side (Fig. 94). Pronotal horns of large male (Fig. 94) curved anterodorsally, separated by an oval concavity whose posterior margin is weakly and broadly raised transversely. Anteromedial pronotal concavity of female (Fig. 126–127) flanked by a pair of dorsally directed, apically convergent, blade-like projections (tooth-like in small individuals). Dorsum weakly to moderately shiny dark green to almost black with weak green reflections. Eastern slopes (Yungas) of Andes from Colombia to Venezuela (Morrone: Napo Province) (Fig. 111)
..... ***Phanaeus (N.) haroldi* Kirsch** (Fig. 94, 102, 108, 124–127)
- Male head horn with a distinct swelling at middle of posterior margin, sometimes also weakly swollen subapically (Fig. 92). Pronotal horns of male in lateral view sometimes weakly angulate near base (Fig. 92). Middle of posterior margin of concavity separating pronotal horns swollen, raised as an elongate, longitudinal ridge (Fig. 129). Anteromedial pronotal concavity of female weaker, with small tubercle on each side and another on anterior margin, tubercles of equal size (Fig. 100, 130). Dorsum weakly shiny black, without any hint of green color. Highlands of eastern Venezuela (Morrone: Guyana Province) (Fig. 111)
..... ***Phanaeus (N.) bordoni* Arnaud** (Fig. 92, 100, 103, 128–131)

Comments. With the addition of *P. bordoni*, this cohesive group now embraces five species. Edmonds (1994) saw specimens of this gallery forest species but failed to recognize its unique characters in spite of the fact that they were from a place far removed from the range of *P. haroldi*, to which he assigned them. Edmonds' (1994: 25) statement that *P. dejeani* occurs in Bolivia is erroneous.

Key to species of the endymion group

1. Sutural margin of each elytron upturned to form a sharp ridge (Fig. 135, arrow), which is progressively more elevated posteriorly and prolonged into a small, sharp tooth at apical angle (Fig. 134, arrow); elytral margin slightly excised adjacent to this tooth. Color bright green or dark blue. South-central Mexico (states of Mexico and Guerrero) (Morrone: Volcanic Axis Province) (Fig. 143)
..... ***Phanaeus (N.) halffterorum* Edmonds** (Fig. 134–135, 137, 144–146)
- Sutural margin of elytra simple. Color and distribution variable 2
- 2(1). Triangular pronotal disk of male (Fig. 141) evenly and densely but finely granulate ($\times 10$), granules in most specimens larger and becoming squamose along lateral margins of disk and extending onto posterolateral angles (when distinctly developed); sides of pronotum roughened ($\times 10$), lacking distinct punctures except behind lateral fossae. Female pronotum (Fig. 139) minutely roughened, evenly, distinctly punctate ($\times 10$), punctures becoming smaller dorsally but not disappearing altogether; disk impressed medially as a distinct furrow visible to unaided eye, extending forward from posterior margin to near middle of disk. Sierra Madre del Sur of south-

- central Oaxaca (Morrone: Sierra Madre Sur Province) (Fig. 143)
 *Phanaeus (N.) zapotecus* Edmonds (Fig. 139, 141, 148–151)
- Pronotal disk of male either lacking distinct granulation, or, if granules present, these are minute and restricted along lateral margins of disk (Fig. 142); sides of pronotum smooth, minutely punctate. Female pronotum (Fig. 140) smooth, punctures (x50) fine and usually restricted to sides; median furrow lacking or at most indicated by fine, scarcely visible line **3**
- 3(2). Elytral interstriae (Fig. 153–154) evenly convex and glossy midlongitudinally; striae impressed basally as distinct fossae. *Male*: Pronotal disk (Fig. 153) velvety smooth medially, finely asperate laterally and sometimes also medially. *Female*: Pronotum (Fig. 132, 140, 154–155) with anteromedial concavity bounded anteriorly by a raised U- or V-shaped ridge; this ridge produced medially as an acute or rounded tubercle, and at each end as a rounded or elliptical tubercle; in some individuals concavity interrupted posteriorly by a small rounded bump; concavity obsolete in some, usually small individuals, ridge reduced to three isolated round tubercles. Dorsum shiny green or dark blue; in few specimens shiny green with strong yellow reflections. Southwestern Mexico and southeastern Mexico to Honduras (Morrone: Volcanic Axis and Gulf of Mexico Provinces) (Fig. 143)
 *Phanaeus (N.) endymion* Harold (Fig. 132–133, 136, 140, 152–155)
- Elytral interstriae (Fig. 138, 157–158) distinctly flattened and uniformly dull (more convex and shiny in some Central American populations); striae not strongly impressed basally, anterior ends in most specimens bearing deep punctures rather than large fossae. *Male*: Pronotal disk (Fig. 142, 157) dull, velvety smooth medially, finely asperate, brighter laterally. *Female*: Pronotum (Fig. 158) evenly convex, lacking anteromedial concavity even in largest specimens, bearing three round, smooth tubercles in transverse line near anterior margin. Head and pronotum (Fig. 156–159) largely highly shiny 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 shiny black; pygidium usually metallic red medially, green peripherally, in some completely red or green. Southern Nicaragua through Central America into western Colombia and Ecuador (Morrone: Eastern Central America and Chocó Provinces) (Fig. 143)
 *Phanaeus (N.) pyrois* Bates (Fig. 138, 142–143, 156–159)

Comments: Arnaud (2002b: 98) proposed the name *Phanaeus (Notiophanaeus) viridicollis* Olsoufieff as a new combination of “*Phanaeus blanchardi* ab. *viridicollis* Olsoufieff”. (Note: The valid name for *P. blanchardi sensu* Olsoufieff 1924 is *P. pyrois* Bates). Because the name “*viridicollis*” was originally proposed as an aberration (Olsoufieff 1924: 92), it is infrasubspecific in rank and, therefore, unavailable (ICZN 1999, Articles 1.3.4, 45.6.2 and 45.6.4.1). Arnaud’s action, therefore, was invalid and the name “*viridicollis*” remains unavailable. These nomenclatural considerations notwithstanding, formal taxonomic status for “*viridicollis*” requires reassessment in the light of material collected in Nicaragua (Granada Province, Volcán Mombacho) along with “normal” *Phanaeus pyrois*, approximately 2500 km by land from other collecting sites in southern Ecuador. Pending further study, we regard “*viridicollis*” as one of several color variants of *P. pyrois*. Solís and Kohlmann (2012) elevated *P. pyrois malyi* Arnaud to species status based on the results of DNA studies of Costa Rican populations. We would be inclined to accept their conclusion only if they were to include in their analyses Panamanian and South American populations of *P. pyrois* (especially the black, South American form “*funereus*” and other color variants). For now, we have elected to regard *P. pyrois malyi* as a **new synonym** of *P. pyrois*. We also consider *P. endymion porioni* Arnaud a **new synonym** of *P. endymion*; in our opinion, it is based on tenuous differences in striae punctation too unreliable to support formal taxonomic recognition.

Subgenus *Phanaeus s. str.*

Key to species groups

1. Pronotum evenly granulate anterolaterally (Fig. 162, 197, 201) **2**

- Pronotum granulorugose or rugose anterolaterally (pronotal disk can be granulate) (Fig. 222, 352, 369, 383) **3**
- 2(1). Protibia tridentate. Male pronotal disk flat, triangular (Fig. 168). United States and northeastern Mexico (Fig. 167) **triangularis group** [14]
- Protibia quadridentate, basal tooth small (can be indistinct in worn specimens). Pronotal disk of well-developed males concave, usually coarsely rugose, bordered laterally by raised, sometimes jagged ridges, and bearing a central or posteromedial process of some type (Fig. 183–185, 187, 189–191). Northwestern Mexico to Costa Rica (Fig. 192) **tridens group** [15]
- 3(1). Pronotal disk of well-developed males flat and uniformly granulate, posterolateral angles rounded (Fig. 225, 229). Protibiae quadridentate. Northwestern South America to Panama (Fig. 223) **hermes group** [16]
- Shape of male pronotum variable, in most specimens triangular, flattened and granulorugose or rugose, not simply granulate. Protibiae usually tridentate, sometimes weakly quadridentate (e.g. *P. difformis*). Costa Rica northward to United States (except *P. lunaris*) **4**
- 4(3). Pronotum of female with a wide anteromedial prominence flanked on each side by an elongate vertical depression extending from disk to anterior pronotal margin behind eye (Fig. 253, 262, 267, 293; weakest in *P. pilatei*, Fig. 289). Extreme southwestern United States, Mexico, Central America and northwestern South America (Fig. 248) **mexicanus group** [17]
- Pronotum of female more-or-less evenly convex anteriorly, with or without a small anteromedian concavity and tubercles and lacking vertical depressions **5**
- 5(4). Midventral carina of profemur angulate near base; base of posterior surface with large, coarse punctures (Fig. 309, upper image). Pronotum of large males (Fig. 301, 305, 310) with a smooth posteromedian area bounded anteriorly by a transverse tubercle or carina. Pronotum of female (Fig. 306–307) with a narrow transverse anteromedian ridge followed by an oval concavity whose posterior margin is interrupted by a low, rounded gibbosity. Southeastern Mexico to Panama (Fig. 223) **beltianus group** [19]
- Profemur not angulate at base (Fig. 309, lower image); basal punctures of same size and texture as those extending to apex of profemur. Male pronotum variable, but not as above **6**
- 6(5). Pronotum finely granulorugose anterolaterally. Pronotum of large males with a smooth, raised area along posterior margin, which is often toothed medially (Fig. 338, 341, 345, 350). Cephalic carina of female (seen from above) even with anterior margin of eyes. Montane habitats of eastern and southern Mexico (Fig. 223) **amethystinus group** [20]
- Pronotum (Fig. 353, 355, 378, 381) densely and coarsely granulorugose anterolaterally, and usually also over entire pronotal surface (sculpturing attenuated in *P. 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**
- 7(6). Elytral interstriae smooth or minutely punctate ($\times 30$) (Fig. 354, 359, 356). Outer margin of head notched between clypeus and paraocular areas (Fig. 360, arrow). Altiplano and Transverse Volcanic Axis of Mexico (Fig. 375) **quadridens group** [20]
- Elytral interstriae densely, coarsely rugopunctate (Fig. 390, 392, 394). Outer margin of head not distinctly notched. Extreme northern Mexico, United States (Fig. 375) ... **vindex group** [21]

Comments. Three new species not considered in 1994 are now included in this subgenus: *Phanaeus blackalleri* Delgado-Castillo, 1991, *P. changdiazi* Kohlmann and Solís, 2001 and *P. yecoraensis* Edmonds, 2004.

Key to species of the triangularis group

1. Dorsum uniformly dark blue, bluish green or bright green (Fig. 168–173). Pronotum rather densely granulate anterolaterally; area surrounding basal fossae (Fig. 165) punctate, punctures separated by distance greater than their diameter except medially, where they coalesce. Mesa Central and Sierra Madre Oriental of Mexico, extreme southern Texas (Morrone: Volcanic Axis and Sierra Madre Oriental Provinces) (Fig. 167) ***Phanaeus (P.) adonis* Harold** (Fig. 165–166, 168–173)
- Dorsum somber, black to weakly shiny violet; if weakly to strongly shiny green (Fig. 182) then elytral interstriae flat. Pronotum usually sparsely and finely granulate (Fig. 162), more so in males; sculpturing adjacent to basal fossae variable. United States **2**
- 2(1). Elytral interstriae shiny, distinctly convex, with distinct simple punctures (Fig. 161); first interstria not distinctly shinier than others. Area of pronotum adjacent to posterior fossae populated by distinct large punctures (Fig. 160), separated by less than their diameters. Dorsum uniformly black or muted violet (Fig. 174–177). Southeastern United States from Kansas to eastern Texas and eastward to Carolinas (Morrone: Nearctic Region) (Fig. 167) ***Phanaeus (P.) triangularis* (Say)** (Fig. 160–162, 174–177)
- Elytral interstriae 2–8 dull, flat, evenly and densely covered by large, shallow punctures that coalesce to form reticulate pattern of ridging (x20) (Fig. 164); first interstria convex, simply punctate, distinctly shinier than other interstriae. Area of pronotum adjacent to posterior fossae finely granulate to rugopunctate, lacking distinct punctures (Fig. 163). Dorsum uniformly black to muted violet, rarely dull to brightly shiny green (Fig. 182). Texas generally west of Balcones Escarpment (Morrone: Nearctic Region) (Fig. 167) ***Phanaeus (P.) texensis* Edmonds** (Fig. 163–164, 178–181)

Comments. Edmonds (1994) regarded *Phanaeus adonis* strictly as an inhabitant of higher elevations of Mexico's Sierra Madre Oriental. In 1995 it was discovered in Cameron County, Texas (see Riley and Wolfe 2003) — approximately 300 km east and 1500 m lower than its putative habitat, an extraordinary difference still awaiting a conclusive explanation. We here raise the rank of *P. texensis* to species because of its clearly consistent morphological and ecological differences from *P. triangularis*.

Key to species of the tridens group

1. Clypeal process (viewed from front) narrow, acute, distinctly longer (usually much longer) than wide at base (Fig. 186, arrow). Posteromedial process of male pronotum large, laterally flattened triangular ridge (Fig. 185, 196). Almost all females with a small, round black spot beneath lateral pronotal fossa. Elytral interstriae usually distinctly shinier midlongitudinally (uniformly dull in worn specimens). Higher valleys of central Oaxaca above 1400 m, and Pacific coast of Oaxaca (Morrone: Sierra Madre Sur Province) (Fig. 192) ***Phanaeus (P.) nimrod* Harold** (Fig. 185–186, 193–197)
- Shape of clypeal process variable but almost always broader than long, not appearing conical. Not occurring in central or coastal Oaxaca. Other characters variable **2**
- 2(1). Clypeal process (viewed from front, as in Fig. 188) triangular or weakly rounded, with a small medial tooth. Posteromedial process of male pronotum usually elongate, apically bifurcate spine-like projection (Fig. 183–184). Female lacking a black spot beneath lateral pronotal fossa. Tropical lowlands from Veracruz to Chiapas; isolated parts of southwestern Mexico (Morrone: Chiapas, Gulf of Mexico and Pacific Coast Provinces) (Fig. 192) ***Phanaeus (P.) tridens* Castelnau** (Fig. 183–184, 198–203)
- Clypeal process viewed from front usually rounded (Fig. 188); if more-or-less triangular (some *P. daphnis*) then male pronotum as in Fig. 190–191. Other characters variable **3**

- 3(2). Elytral interstriae ($\times 30$) usually minutely rugose or rugopunctate adjacent to striae (in some specimens visible only apically), smooth medially, appearing strongly convex to unaided eye. Posteromedial process of male pronotum a short conical tooth (Fig. 189). Pronotal disk of male with a pair of conical tubercles near anterior margin. Southern Guatemala to central Costa Rica (Morrone: Pacific Coast Province) (Fig. 192) *Phanaeus (P.) eximius* Bates (Fig. 189, 204–208)
- Elytral interstriae uniformly shiny or dull, in some shagreened adjacent to striae, shinier medially, but not minutely rugose or rugopunctate adjacent to striae. Male pronotum not as described above. Central and western Mexico 4
- 4(3). Posteromedial process of male pronotum a broad, apically emarginate projection (Fig. 187); raised sides of disk lacking a strong conical tooth; granulations of sides of pronotum reaching posterior margin. Clypeal process rounded. Elytral interstriae convex. West-central Mexico, extending along Pacific coastal region northward into central Sonora (Morrone: Pacific Coast Province) (Fig. 192) *Phanaeus (P.) furiosus* Bates (Fig. 187–188, 290–213)
- Posteromedial process of male pronotum a short conical tooth (Fig. 191) or a long, sometimes weakly apically bifurcate spine-like projection (Fig. 190); raised sides of disk each with a strong conical tooth (Fig. 190–191). Clypeal process rounded but in some specimens triangular. Elytral interstriae flat to weakly convex. Balsas River valley and peripheral areas along escarpment of Transverse Volcanic Range of southern Mexico (Morrone: Volcanic Axis and Balsas Provinces) (Fig. 192) *Phanaeus (P.) daphnis* Harold (Fig. 191–192, 214–219)

Comments. The tridens group is a difficult assemblage that we view in a simple context which undoubtedly belies the true extent of its taxonomic diversity, especially in reference to what we here refer to as *P. tridens* and *P. daphnis*. The opposite approach was taken by Arnaud (2002b), who recognized 10 taxa rather than the five species cited here. The striking difference in opinion solidifies our belief that this group merits a thorough phylogenetic study using traditional and molecular characters and sampling representative local populations over broad geographical areas. Edmonds (1994) misidentified *P. pseudofurcosus* Balthasar, which he considered a subspecies of *P. tridens*. Arnaud (2001: 6) discovered the mistake and renamed *P. tridens pseudofurcosus* Balthasar (*sensu* Edmonds) as *P. tridens balthasari* Arnaud, a subspecies that we cannot reconsider until the entire group is further scrutinized and that we here regard as a **new synonym** of *P. tridens*. Arnaud (2002b: 106) applied the name “*pseudofurcosus*” as a subspecies of *P. furiosus*, *P. furiosus pseudofurcosus*, to unusual populations inhabiting Colima and Jalisco. Edmonds (1994) regarded the Colima population as an unusual representative of *P. tridens*, as we continue to do here (Note: The distribution of this population is not indicated in Fig. 192.). A more definitive disposition for “*pseudofurcosus*” as well as other taxa in this group must await a more thorough and serious study of the whole complex using more reliable characters. Consequently, we consider *P. furiosus pseudofurcosus* Balthasar (*sensu* Arnaud 2002b) a **new synonym** of *P. furiosus*. *Phanaeus tridens moroni* Arnaud is a color variant that we regard as a **new synonym** of *P. tridens*.

Key to species of the hermes group

1. Elytral interstriae dull (Fig. 221); median area not noticeably shinier than that adjacent to striae; punctures of striae visible to unaided eye. Dorsum weakly shiny to bright coppery brown or coppery green (Fig. 224–227). Northwestern Colombia to Costa Rica (Morrone: Maracaibo, Magdalena, Western Isthmus Provinces) (Fig. 223) *Phanaeus (P.) hermes* Harold (Fig. 221–223, 224–227)
- At least first three, but in most specimens all interstriae evenly shiny or shiny only midlongitudinally (Fig. 220). Punctures of elytral striae small, sometimes effaced, clearly visible only under magnification ($\times 10$). Dorsum weakly shiny dark green, black, or in a few specimens coppery green (Fig. 228–232). Northwestern Colombia and northern Venezuela (Morrone: Venezuelan Coast and Venezuelan Llanos Provinces) (Fig. 223) *Phanaeus (P.) prasinus* Harold (Fig. 220, 223, 228–232)

Comments. We continue Edmonds' (1994) probably oversimplified taxonomic view of this group. There are many (mostly color) variants in these species, and their geography is not well understood. Gamez and Mora (2000) presented a detailed ecological and distributional study of *P. prasinus* in the Meseta de Mérida region of Venezuela. Arnaud (2001) described two subspecies of *P. prasinus* based primarily on tenuous differences in color: *P. prasinus trinidadensis* and *P. prasinus jolyi*. We regard both as **new synonyms** of *P. prasinus*. The hermes species group, like the tridens group, would be an excellent subject for a thorough phylogenetic study based on molecular as well as traditional characters.

Key to species of the mexicanus group

1. Elytral interstriae smooth and shiny medially, shagreened laterally along striae, finely punctate ($\times 25$) (Fig. 233, 235); striae dull, shagreened (Fig. 233). Sides of pronotum densely rugopunctate around and behind lateral fossae. Pronotal disk of large males (Fig. 249, 255) flat, posterior angles strongly rounded, entire disk (viewed from above) almost heart-shaped. Longer mesotibial spur not strongly dilated subapically. Clypeal process almost quadrate. Dark blue, in some specimens appearing almost black to unaided eye **2**
- Elytral interstriae evenly shiny, smooth or only weakly and sparsely punctate ($\times 25$). Sides of pronotum granular around and at least some distance behind lateral fossae. Pronotal disk of large male variable but rarely flat. Longer mesotibial spur strongly dilated subapically, especially in female (except *P. scutifer*). Clypeal process evenly rounded. Conspicuously colored, in most specimens brightly so **3**
- 2(1). Cephalic horn of large male robust, distal half strongly curved posteroventrally, hook-shaped (Fig. 250). Pronotal disk of large male bordered on each side by a narrow sulcus. Cephalic process of female strongly raised, quadrate, widely bidentate apically (Fig. 236). Elytral interstriae 2–5 broadly shiny medially, flat, distinctly punctate ($\times 10$; Fig. 235). Sierra foothills of southeastern Sonora, Mexico (Morrone: Sierra Madre Occidental Province) (Fig. 248) ***Phanaeus (P.) yecoraensis* Edmonds** (Fig. 235–236, 249–251)
- Cephalic horn of large male slender, evenly curved posteriorly, not hook-shaped (Fig. 256). Pronotal disk of male lacking lateral sulci. Cephalic process of female a trituberculate transverse ridge (Fig. 234). Elytral interstriae 2–5 weakly convex, shagreened, only narrowly shiny medially if at all, weakly punctate ($\times 10$; Fig. 233). Central Mexico dry mountain forests (Morrone: Sierra Madre Oriental and Volcanic Axis Provinces) (Fig. 248) ***Phanaeus (P.) flohri* Nevinson** (Fig. 233–234, 254–258)
- 3(1). Outer margin of head deeply notched between clypeus and paraocular areas (Fig. 239, arrow), notch usually more-or-less right-angled so that paraocular area appears to project laterally beyond margin of clypeus. Raised outer margin of mesocoxal cavity always abruptly widened posteriorly, resulting in posterior width about double that of anterior width. Cephalic carina of female raised medially (viewed from front), quadrate or weakly emarginate (Fig. 238). Male pronotum with strong posterolateral angles of variable shape (Fig. 259, 266, 271). Anteromedial prominence of female pronotum lacking a distinct transverse carina along anterior margin. Dorsal surface, especially pronotal disk and elytra, highly shiny, appearing polished **4**
- Outer margin of head at most only weakly notched (Fig. 241). Raised outer margin of mesocoxa usually not widened posteriorly. Male pronotum usually flattened, sometimes weakly convex (Fig. 242–243). Female cephalic prominence either a trituberculate carina or a narrow, bituberculate process (Fig. 237, 240). Anteromedial pronotal prominence of female usually with a distinct transverse carina along anterior margin. Other characters variable **6**
- 4(3). Crests of large male pronotum (viewed laterally) in most specimens almost parallel-sided, posterior angle projecting little, if at all, posteriorly (Fig. 246, 259–260). Male anterior pronotal margin with a large acute tooth on each side behind eyes (Fig. 247). Color in many specimens steel blue, in some green or yellowish green (Fig. 259–263). Pacific coastal scrub forests of Central

- America from Guatemala to Costa Rica (Morrone: Pacific Coast Province) (Fig. 248)
 ***Phanaeus (P.) excelsus* Bates** (Fig. 246–247, 259–263)
 — Male pronotum (viewed laterally) shaped differently; anterior tubercles lacking or only weakly
 indicated. Color green, yellowish green, or in a few specimens red. Arid Pacific coast of Mexico
 **5**
- 5(4). Crests of large male pronotum (viewed laterally) massive, widened apically, with posterior angle
 extending over base of elytra (Fig. 264–256). Coast and coastal valleys of Mexico from Michoacan
 to Chiapas (Morrone: Pacific Coast Province) (Fig. 248)
 ***Phanaeus (P.) demon* Castelnau** (Fig. 238–239, 264–267)
 — Crests of large male pronotum (viewed laterally) attenuated anteriorly so that process appears
 narrow and strongly inclined posteriorly (Fig. 271). Pacific coast of Colima, Jalisco and Nayarit
 (Morrone: Pacific Coast Province) (Fig. 248)
 ***Phanaeus (P.) obliquans* Bates** (Fig. 269–273)
- 6(3). Cephalic process of female a narrow, almost conical bituberculate projection (Fig. 237). Longer
 mesotibial spur usually not distinctly dilated subapically. Pronotal disk of large male flattened
 dorsally (Fig. 275). Dorsum green to yellowish green, rarely coppery (Fig. 274–277). Coastal
 lowlands of central Veracruz (Morrone: Gulf Coast Province) (Fig. 248)
 ***Phanaeus (P.) scutifer* Bates** (Fig. 237, 274–277)
 — Cephalic process of female trituberculate carina. Longer mesotibial spur distinctly dilated
 subapically, more strongly so in female. Pronotal disk of large male convex medially, in a few
 specimens bearing central tubercles or ridges. Color and distribution variable **7**
- 7(6). Pronotum of large males (Fig. 245) with a distinct, bowed posteromedial transverse carina behind
 which surface is much smoother. Transverse anteromedial ridge of female pronotum followed
 by a fairly deep transverse concavity. Deep shiny green, in a few specimens with golden reflections.
 Western and southern Ecuador (Morrone: Western Ecuador Province) (Fig. 248)
 ***Phanaeus (P.) lunaris* Taschenberg** (Fig. 245, 278–281)
 — 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; Fig. 243). Pronotum of female at most only
 weakly concave behind anteromedial carina. Color variable. Central America and Mexico .. **8**
- (Note: The following taxa can be difficult or impossible to separate if reliable locality data are not available.
 Females and smaller males are often indistinguishable morphologically.)
- 8(7). Basal pronotal fossae distinct in female and usually also in male, occasionally small, punctiform
 or rarely lacking in male. Disk of male pronotum in most specimens flat. Southern Mexico to
 Costa Rica **9**
 — Basal pronotal fossae in most specimens absent, or at most represented by small punctiform pits.
 Disk of male pronotum in most specimens either weakly convex or concave. Southern Mexico
 west to Pacific coast, north to Arizona **10**
- 9(8). Pronotum with conspicuous basal fossae separated by distance usually no greater than three
 times diameter of a fossa; fossae in few specimens indistinct. Elongate anterolateral concavities
 of female pronotum weak. Posteromedian area of large male pronotum granular, not
 presenting a smoother punctate triangular area. Dark greenish blue, bluish green or green,
 rarely bright coppery red (Fig. 282–285). Yucatan Peninsula south to northeastern Chiapas
 and adjacent Guatemala (Morrone: Yucatan Province) (Fig. 248)
 ***Phanaeus (P.) pilatei* Harold** (Fig. 282–285)
 — Pronotum either lacking basal fossae or with small, punctiform basal fossae separated by a
 distance greater than three times diameter of a fossa; fossae rarely conspicuous. Anterolateral
 concavities of female pronotum conspicuous. Posteromedial area of large male pronotum in
 most specimens presenting an oval or triangular, strongly punctate area distinctly smoother

- than rugose disk (Fig. 287). In most specimens coppery red, in some green, yellowish green or dark blue (Fig. 243, 286–289). Pacific coastal lowlands from Guatemala to Costa Rica (Morrone: Gulf Coast, Chiapas and Eastern Central America Provinces) (Fig. 248)
 ***Phanaeus (P.) wagneri* Harold** (Fig. 243, 286–289)
- 10(8). Pronotal disk of large male convex, bearing central triad of conspicuous tubercles, posterior two of which may be fused into a ridge (Fig. 244). Balsas River valley, Puebla, central Oaxaca, Los Tuxtlas region of Veracruz (Morrone: Balsas and Gulf Coast Provinces) (Fig. 248)
 ***Phanaeus (P.) mexicanus* Harold** (Fig. 240–241, 244, 290–295)
- Pronotal disk of large male (Fig. 242) slightly concave, lacking central tubercles. Central Mesa of Mexico from Tlaxcala to Jalisco, northward along Pacific coast to southern Sonora, interior of Sonora and north into southern Arizona (Morrone: Volcanic Axis, Mexican Plateau and Pacific Coast Provinces) (Fig. 248) .. ***Phanaeus (P.) amithaon* Harold** (Fig. 242, 296–299)

Comments. We have opted for the more reasonable view of Arnaud (2002b) to split *P. demon sensu* Edmonds (1994) into three distinct taxa: *P. demon*, *P. excelsus* and *P. obliquans* (here species rather than subspecies) inhabiting the arid Pacific coastal zone from western Mexico to Costa Rica. The Costa Rican member of the trio, *P. excelsus*, was imparted species status by Solís and Kohlmann (2012). We here also raise the rank of *P. obliquans* and *P. pilatei* to species status because of their marked morphological and distributional distinctness, which was underappreciated by Edmonds (1994). Since 1994 much new material of *P. flohri* has become available, collected under circumstances (feces-baited pitfall traps) that weaken Edmonds' (1994) hypothesis that it is a stenotopic inquiline inhabiting mammal (or other) nests.

Key to species of the beltianus group

1. Elytral interstriae shiny medially, dull adjacent striae cause interstriae appear polished midlongitudinally (Fig. 303). Pronotum of female not distinctly impressed midlongitudinally. Basal pronotal fossae distinct in most females, minute or effaced in male **2**
- Elytral interstriae evenly shiny or dull, not distinctly shinier medially (Fig. 308). Pronotum of most females distinctly impressed midlongitudinally. Basal pronotal fossae effaced in most specimens of both sexes **3**
- 2(1). Pronotal disk of large male strongly granulorugose, bearing dense, coarse rugosities (Fig. 312); smooth posteromedial area about as long as wide. Lateral margin of pronotum in dorsal view usually distinctly curved inward between anterolateral and lateral angles (Fig. 302). Lowland Atlantic forests of Nicaragua and Costa Rica (Morrone: Eastern Central America Province) (Fig. 223) ***Phanaeus (P.) beltianus* Bates** (Fig. 301–303, 311–314)
- Pronotal disk of large male with finer granulorugosity, especially laterally (Fig. 316); smooth posteromedial area clearly wider than long. Lateral margin of pronotum in dorsal view nearly straight, not distinctly curved inward between anterolateral and lateral angles (Fig. 304). Lowland Pacific forests of Costa Rica and Panama (Morrone: Western Isthmus Province) (Fig. 223) ***Phanaeus (P.) changdiazi* Kohlmann and Solís** (Fig. 304–306, 315–318)
- 3(1). Elytral interstriae evenly dulled by dense shagreening ($\times 20$). Smooth posterior area of male pronotal disk amounting to at least one-half of disk length (best judged in large individuals) (Fig. 320). Disk of female pronotum more coarsely sculptured along midlongitudinal impression than laterally. Lowland forests of Panama (Morrone: Eastern Central America Province) (Fig. 223) ***Phanaeus (P.) howdeni* Arnaud** (Fig. 310, 319–322)
- Elytral interstriae evenly smooth and shiny, not dulled by shagreening. Smooth posterior area of male pronotum amounting to less than one-half (usually about one-third) of disk length (Fig. 324). Sculpturing of female pronotal disk of more-or-less uniform texture, not distinctly coarser or denser in medial depression. Lowland and midlevel forests of southeastern Mexico from San Luis Potosí to Guatemala (Morrone: Gulf of Mexico Province) (Fig. 223)
 ***Phanaeus (P.) sallei* Harold** (Fig. 307–309, 323–326)

Comments. With the addition of *P. changdiazii*, this strictly Mesoamerican group now comprises four closely related evergreen-forest species distinguished by the unique combination of characters used in the key.

Key to species of the amethystinus group

1. Punctures of posteromedial portion of female pronotum simple to weakly asperate, weakest in front of basal fossae (Fig. 330, 334), area appearing smooth to unaided eye. Elytra dark, somber; metallic color, if any, restricted to margins; pronotum usually dark except for metallic blue lateral margins **2**
- Posteromedial portion of female pronotum coarsely punctate to rugopunctate, area appearing roughened to unaided eye (Fig. 327). Elytra in most specimens with metallic color matching that of pronotum and pygidium **3**

- 2(1). Posteromedial portion of female pronotum with simple punctures ($\times 10$) (Fig. 330). Female pronotum (Fig. 331) bearing a weakly trituberculate, straight transverse ridge whose length clearly exceeds interocular distance; ridge not followed by a distinct concavity. Head horn of large male (Fig. 332) tapering gradually from base to apex, base not distinctly swollen. Elytral interstriae distinctly convex, weakly shiny. Smooth, transverse, triangular area along posterior margin of male pronotum lacking a tubercle on medial angle. Smaller, length 14–20 mm, usually less than 20 mm. Pacific slope of Sierra Madre del Sur in Guerrero and Oaxaca (Morrone: Sierra Madre Sur Province) (Fig. 223) ***Phanaeus (P.) blackalleri Delgado-Castillo*** (Fig. 330–332, 337–339)
- Posteromedial portion of female pronotum with finely asperate punctures ($\times 10$) (Fig. 334). Female pronotum bearing a trituberculate V-shaped ridge whose width is clearly less than interocular distance; ridge followed by a distinct concavity (Fig. 336). Head horn of large male distinctly swollen basally. Elytral interstriae flat or only weakly convex, dull (Fig. 335). Smooth, transverse, triangular area along posterior margin of male pronotum with an acute tubercle on medial angle. Larger, length 18–28 mm, usually well over 20 mm. Known from scattered montane localities in Chiapas and Veracruz (Morrone: Gulf of Mexico and Chiapas Provinces) (Fig. 223) ***Phanaeus (P.) melampus Harold*** (Fig. 334–336, 340–343)

- 3(1). At least interstriae 2 and 3, but in most specimens 2–5, highly shiny and raised midlongitudinally, dull adjacent to striae, appearing costate to unaided eye (Fig. 333). Sides of pronotum densely granulate-granulorugose. Highlands of Guatemala and adjacent Chiapas (Morrone: Chiapas Province) (Fig. 223) ***Phanaeus (P.) guatemalensis Harold*** (Fig. 333, 344–348)
- All elytral interstriae evenly and in most specimens brightly shiny, evenly convex (Fig. 328). Sides of pronotum only moderately densely granulorugose. Highlands of central Chiapas, mountains of eastern Oaxaca, Sierra Madre Oriental from Veracruz to southern Tamaulipas (Morrone: Sierra Madre Oriental and Chiapas Provinces) (Fig. 223) ***Phanaeus (P.) amethystinus Harold*** (Fig. 327–329, 349–352)

Comments. This montane group now comprises four species with the addition of *P. blackalleri* and species status for *P. guatemalensis*. New status for the latter is based on the marked morphological and distributional differences between *P. guatemalensis* and *P. amethystinus*, which were undervalued by Edmonds (1994). Arnaud (2002b) recognized *P. tepanensis* Bates (as well as *P. guatemalensis* Harold) as a subspecies of *P. amethystinus*; we continue to consider it a color variant (Fig. 346) of *P. guatemalensis*. Arnaud (2001) created *P. genieri* to embrace several northern variants of *P. amethystinus* reported by Edmonds (1994); we regard it as a **new synonym** of *P. amethystinus*, which varies in noticeable morphological respects (see Edmonds 1994 and Arnaud 2001) that need further analysis across its entire range.

Key to species of the quadridens group

1. Interstriae convex; striae fine, clearly impressed (Fig. 359). Raised outer margin of pygidium usually effaced apically (Fig. 358). Dorsum bright coppery red, dark blue or bright green (Fig. 361–365). Transverse Volcanic Range of Mexico from northern Puebla to Jalisco and northward into southern Durango (Morrone: Volcanic Axis Province) (Fig. 375) ***Phanaeus (P.) palliatus* Sturm** (Fig. 358–365)
- Interstriae flat; striae superficial, fine, appearing almost effaced to unaided eye (Fig. 354, 356). Raised outer margin of pygidium effaced apically or not. Dorsal color variable, not coppery red. Distribution variable **2**
- 2(1). Pronotum of male as in Fig. 366, disk bearing a single posteromedian tubercle. Disk of female pronotum extremely coarsely rugopunctate posteromedially (Fig. 353). Raised outer margin of pygidium often effaced or nearly so apically (as in Fig. 358). Higher elevations (1800–2900 m) of Sierra Madre del Sur in Guerrero and Oaxaca (Morrone: Sierra Madre Sur Province) (Fig. 375) ***Phanaeus (P.) damocles* Harold** (Fig. 353–354, 366–369)
- Pronotum of male as in Fig. 377, bearing two posterior and two anterior acute tubercles. Disk of female pronotum less coarsely rugopunctate posteromedially (Fig. 355). Raised outer margin of pygidium always complete (Fig. 357). Transverse Volcanic Range from Veracruz to Jalisco, Sierra Madre Occidental from Durango to southwestern United States, Sierra Madre Oriental from Hidalgo to San Luis Potosi (Morrone: Sierra Madre Occidental, Mexican Plateau and Volcanic Axis Provinces) (Fig. 375) ***Phanaeus (P.) quadridens* (Say)** (Fig. 355–357, 370–374)

Comments. Arnaud (2002b) recognized Olsoufieff's (1924) *P. borealis* as a subspecies of *P. quadridens*. We have no new data, nor does Arnaud present any, to support a conclusion other than that of Edmonds (1994), that it is a color variant distributed over a wide geographical area and broadly sympatric with the blue-violet phase.

Key to species of the vindex group

1. Sculpturing of pronotal disk (Fig. 385, 389) consisting of large, flattened rugosities with ill-defined margins, causing poor definition of ridging; rugosities in many specimens mixed with sparse micropunctures ($\times 40$) most clearly visible posteriorly. Protibial spur abruptly bent mesially. Ventral surfaces of meso- and metatibiae smooth. Elytral interstriae flat, rugopunctate (Fig. 387, 390) to weakly convex, strongly but simply punctate (Fig. 390). *Male*: Cephalic horn of large individuals (Fig. 389, 395) not reaching posterior margin of pronotum, inclined but only slightly curved posteriorly and compressed apically (Fig. 388); posterolateral prominences of pronotum broadly rounded (Fig. 389), disk not presenting flat, triangular dorsal surface. *Female*: Anterior portion of circumnotal ridge more-or-less straight, not distinctly angulate medially; cephalic carina low, thickened mesially and at most only barely trituberculate (Fig. 386); pronotum in profile evenly rounded from posterior to anterior margins; anteromedial pronotal prominence almost always either effaced or consisting of two low, rounded tubercles or weak transverse gibbosity (Fig. 385). Florida, adjacent coastal plains from eastern Louisiana to North Carolina (Morrone: Nearctic Region) (Fig. 375) ***Phanaeus (P.) igneus* MacLeay** (Fig. 385–390, 395–399)
- Sculpturing of pronotal disk consisting of well-defined, ridge-like rugosities with distinct margins (Fig. 391, 393); micropunctures absent. Protibial spur evenly curved mesially or nearly straight. Ventral surfaces of apices of meso- and metatibiae finely but distinctly rugose. Elytral interstriae flat, densely punctate to rugopunctate (Fig. 392, 394). *Male*: Cephalic horn of most large individuals reaching or surpassing posterior margin of pronotum, evenly curved posteriorly, conical apically (Fig. 384); posterolateral prominences of pronotum acute, disk always distinctly flattened dorsally, more-or-less triangular (Fig. 391, 393). *Female*: Anterior portion of circumnotal ridge strongly angulate mesially; cephalic carina strongly raised medially as an apically truncate

or emarginate corniform process (Fig. 382); pronotum of large individuals in profile abruptly vertical anterior to distinct transverse ridge. Distribution variable 2

- 2(1). Bases of elytral interstriae 2–3 raised, smoother, shinier, less densely punctate than adjacent areas, not bearing distinct midlongitudinal costae (Fig. 392); interstriae otherwise densely rugopunctate, punctures coalescing to produce irregular, usually reticulate (as opposed to longitudinal) ridging (Fig. 392). Elytral striae 1–2 narrow, widths near base usually less than one-fifth of interstriae 2–3, respectively. Circumnotal ridge unevenly serrate behind anterolateral angle (Fig. 376, arrow). Protibiae quadridentate, fourth (basal) tooth small but distinct in all but worn specimens (Fig. 377). *Male*: In large individuals sides of pronotal disk curved, posterolateral angles of disk elongate, their tips in dorsal view not extending beyond lateral margin of pronotum (Fig. 391). *Female*: In large individuals transverse anteromedial ridge of pronotum effaced medially, in dorsal view (Fig. 394) usually bowed posteriorly and not bounded by a complete, carina-like crease; in small specimens anteromedial pronotal prominence reduced to two isolated, rounded tubercles. South-central United States, extreme northeastern Mexico (Morrone: Nearctic Region) (Fig. 375) ***Phanaeus (P) difformis* LeConte** (Fig. 376–378, 391–392, 400–404)
- Elytral interstriae 2–3 and sometimes also 4–5 each with a strong midlongitudinal costa (Fig. 394); 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 paralleling costae; remainder of interstriae densely rugopunctate to granulorugose. Elytral striae broad, flat (x15), widths near base usually greater than one-fifth of interstriae 2–3, respectively. Circumnotal ridge simple behind anterolateral angle (Fig. 379); rarely with one or two small teeth or (in some Texas and Arizona specimens) with weak serration. Protibiae tridentate (Fig. 380), fourth (basal) tooth sometimes suggested by an indistinct angulation of tibial margin or rarely distinct. *Male*: In large individuals sides of pronotal disk straight, longitudinal axes of posterolateral angles diverging posteriorly so that angles (viewed from above, Fig. 393) project to or slightly beyond lateral margin of pronotum. *Female*: Transverse anteromedial prominence of pronotum complete, viewed from above (Fig. 381) straight, and bounded by an uninterrupted, carina-like crease; in very small individuals prominence reduced to two isolated, flat, rounded tubercles. Widely distributed in eastern one-half and southwestern portions of United States and in extreme northern Mexico (Morrone: Nearctic Region) (Fig. 375) ***Phanaeus (P) vindex* MacLeay** (Fig. 379–384, 393–394, 405–410)

Comments. Arnaud (2002b) resurrected *P. floridanus* Olsoufieff as a subspecies of *P. igneus*, an opinion that requires a greater body of population data to support. Indeed, the geographical variation of this species, given the well known historical geography of its range, would be an excellent subject for an in-depth analysis at the population level. Dickey's (2006) study of the population genetics of *P. vindex* and *P. difformis* in a zone of geographical overlap is a good example of fieldwork helpful in unraveling some of the knottier taxonomic problems in the genus.

Acknowledgments

We gratefully acknowledge the collaboration of Brett Ratcliffe (University of Nebraska) and Darren Mann (Oxford University), who provided careful and insightful reviews of the manuscript. Our sincere thanks go also to François Génier (Canadian Museum of Nature, Ottawa) for providing the images of *Phanaeus martinezorum* appearing as Figures 27 and 29, and to Max Barclay (Natural History Museum, London) and Jiri Hajek (National Museum, Prague) for loans of type specimens. We also appreciate the assistance of Barney Streit, who kindly provided the pdf files of Edmonds (1994) available for download at the sites mentioned in the Introduction.

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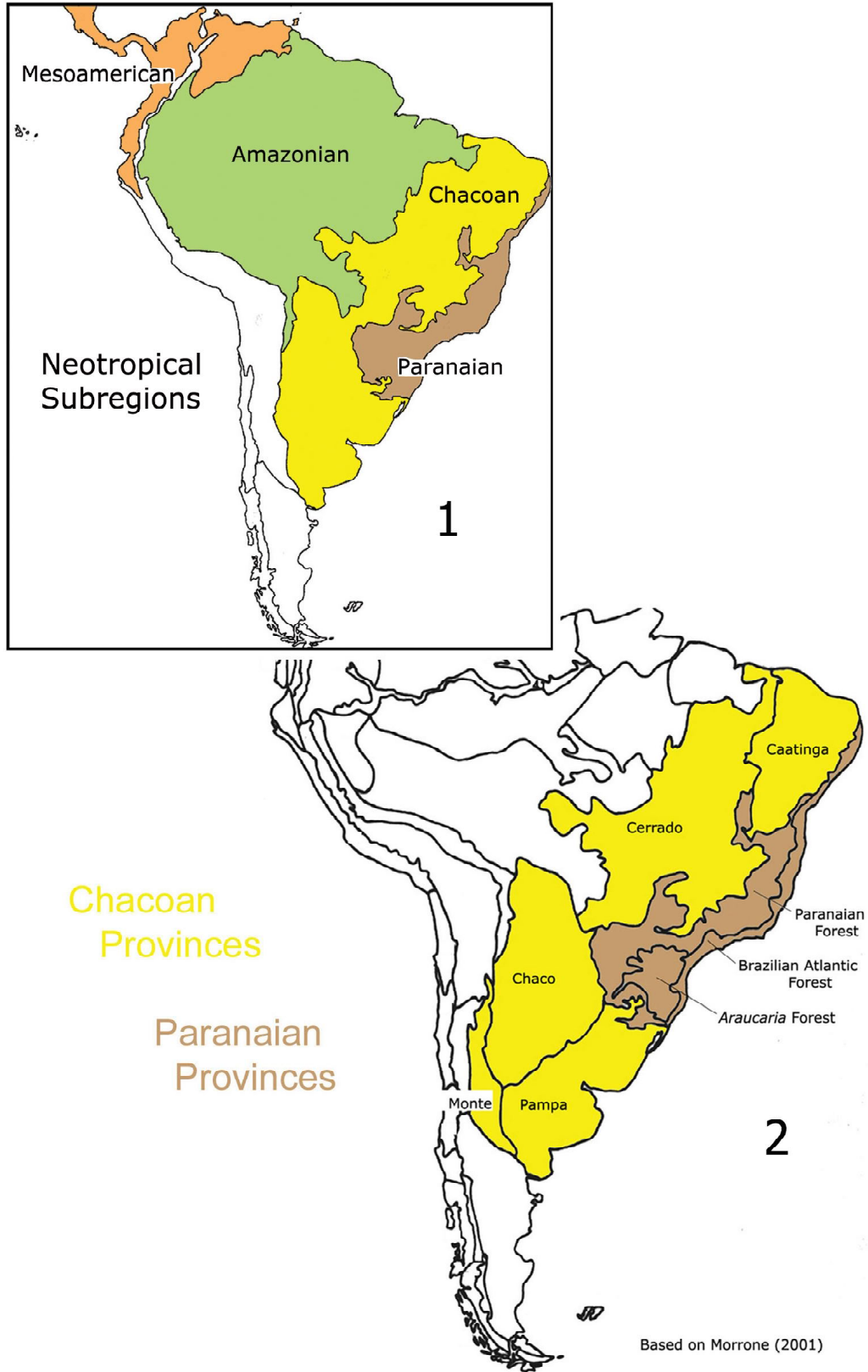
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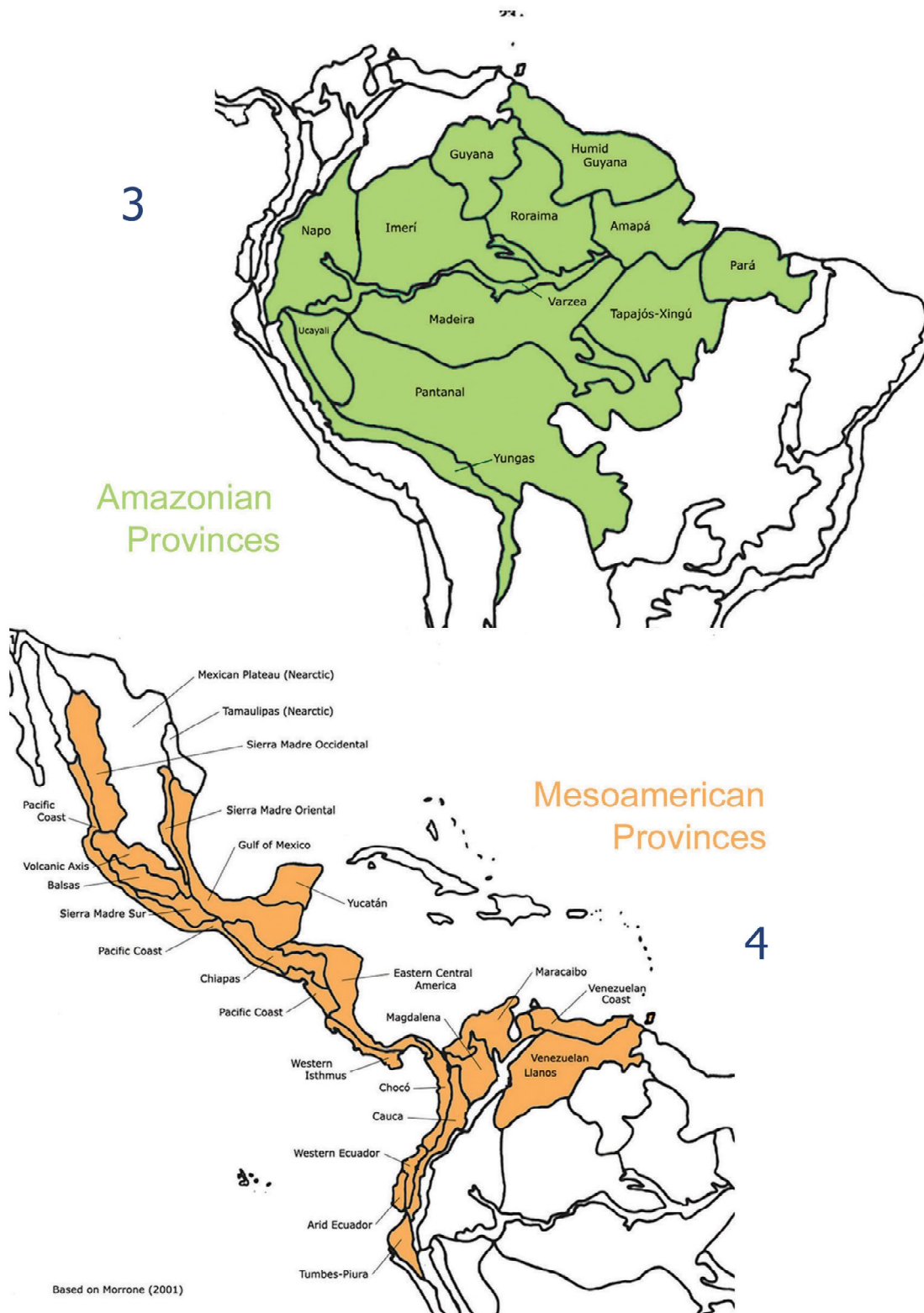
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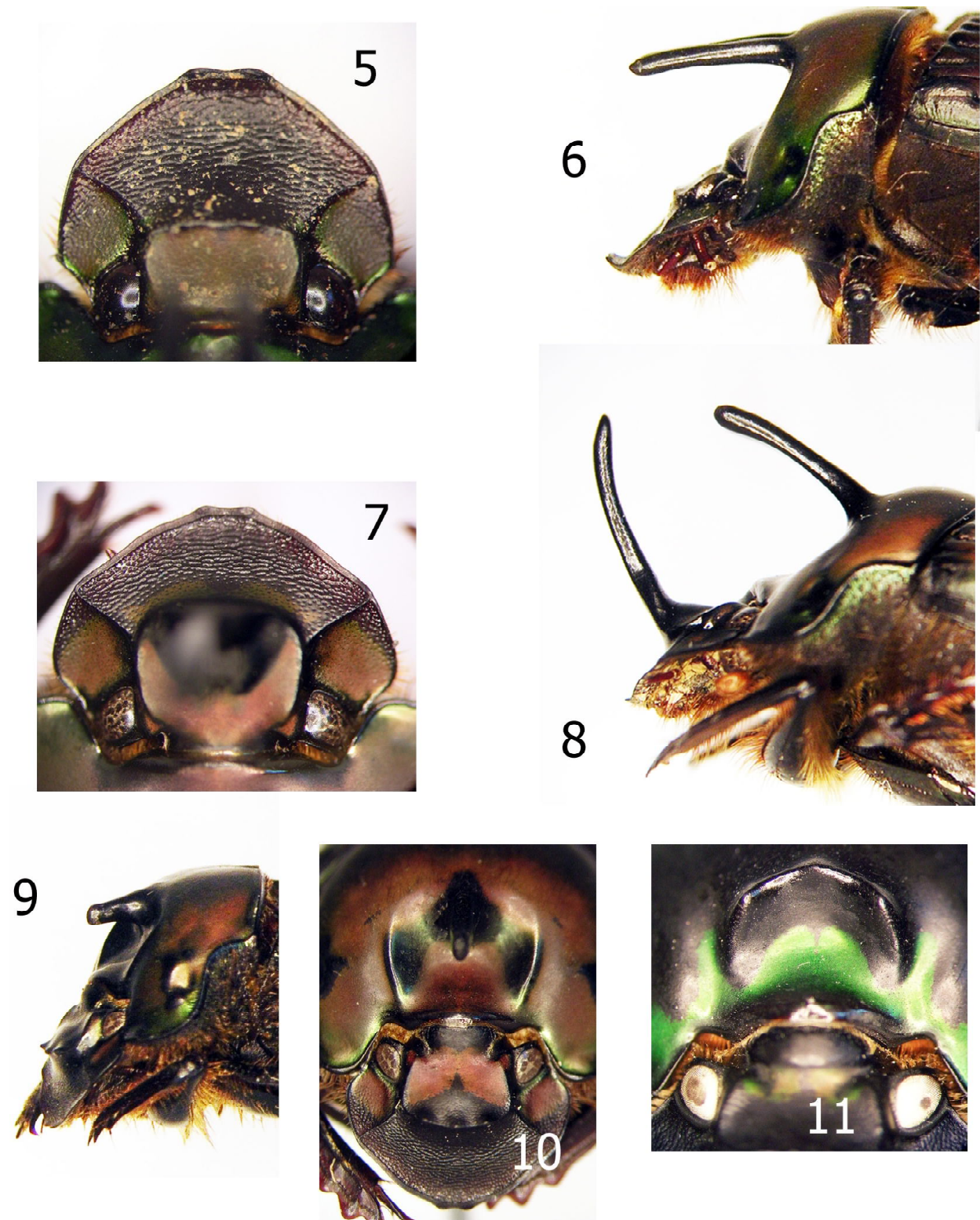
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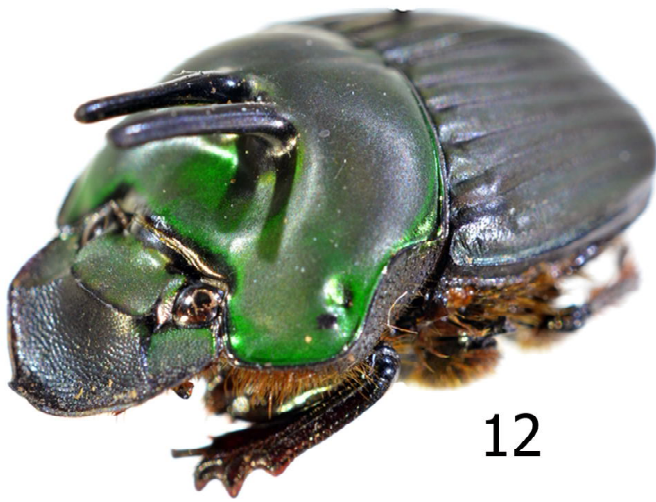
Figures 1–2. Distributional units of Neotropical Region (after Morrone 2001, modified). **1)** Subregions. **2)** Provinces of the Chacoan and Paranaian Subregions.



Figures 3–4. Distributional units of Neotropical Region (after Morrone 2001, modified). **3)** Provinces of the Amazonian Subregion. **4)** Provinces of the Mesoamerican Subregion.



Figures 5–11. Characters of the *Phanaeus (Notiophanaeus) bispinus* species group. *Phanaeus (Notiophanaeus) sororibispinus* Edmonds and Zidek. **5)** Female, dorsal view of head. **6)** Male. **11)** Female, frontal view of forebody. *Phanaeus (Notiophanaeus) bispinus* Bates. **7–8)** Male. **9–10)** Female.



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Figures 12–15. *Phanaeus (Notiophanaeus) sororibispinus* Edmonds and Zidek. 12–13) Male. 14–15) Female.



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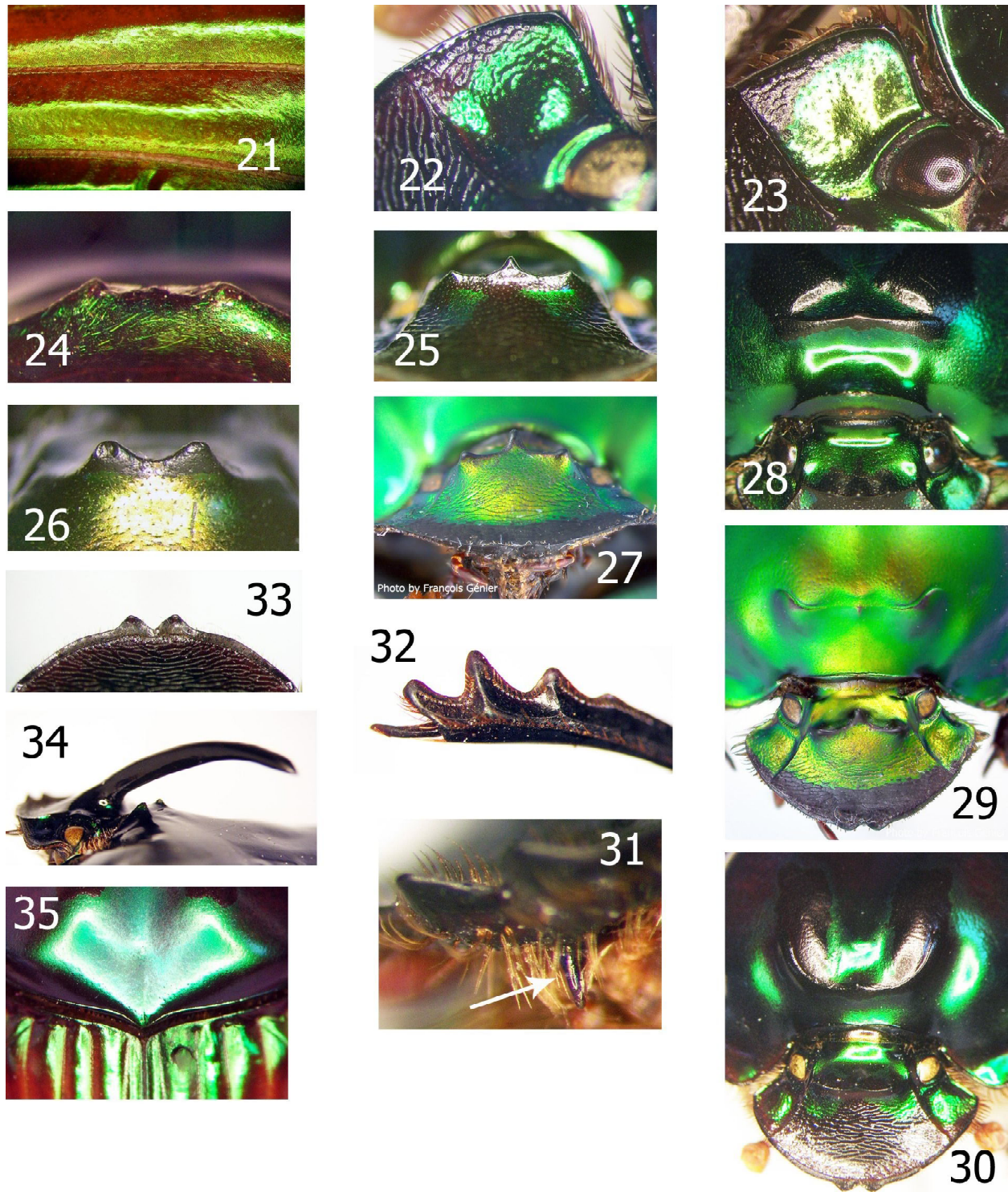


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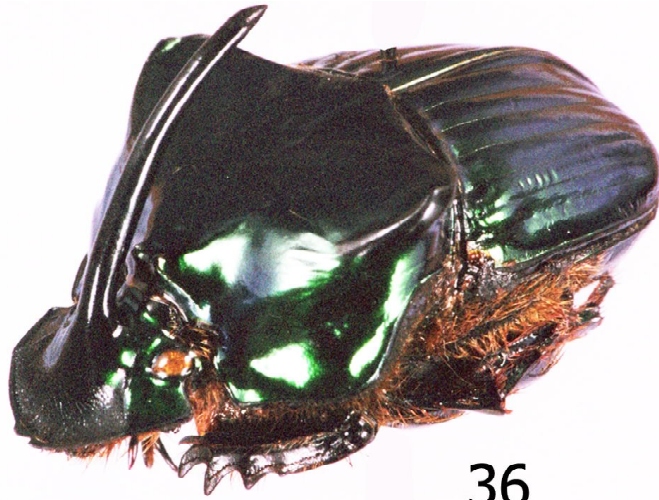


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Figures 16–20. *Phanaeus (Notiophanaeus) bispinus* Bates. 16–17) Strong male. 18) Weak male.



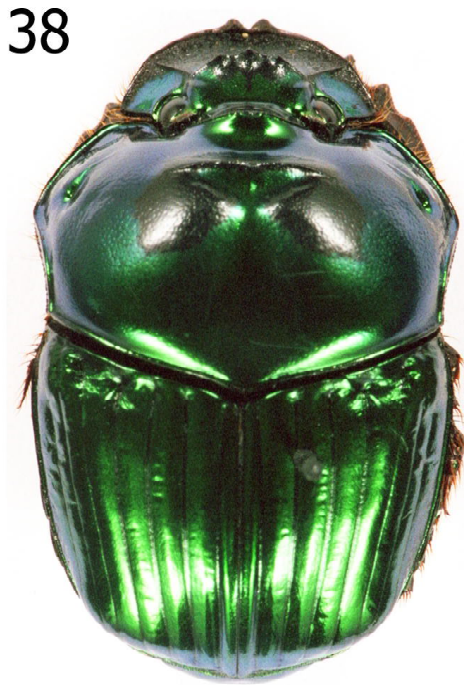
Figures 21–35. Characters of the *Phanaeus (Notiophanaeus) palaeno* species group. *Phanaeus palaeno* Blanchard. **21)** Portion of elytron. **22)** Lateral portion of head, dorsal view. **25)** Female clypeal carina. **26)** Small male, cephalic process. **30)** Female, dorsal view of forebody. **31)** Clypeal margin [arrow indicates spinate clypeal process]. **32)** Male protibia. **33)** Clypeal margin. *Phanaeus kirbyi* Vigors. **23)** Lateral portion of head, dorsal view. **24)** Bituberculate swelling of pronotal margin. **28)** Female, dorsal view of forebody. **34)** Male, oblique view of forebody. **35)** Dorsal view of portion of prothorax and elytra. *Phanaeus martinezorum* Arnaud. **27)** Female, frontal view of head. **29)** Female, dorsal view of forebody.



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Figures 36–39. *Phanaeus (Notiophanaeus) kirbyi* Vigors. 36–37) Male. 38–39) Female.



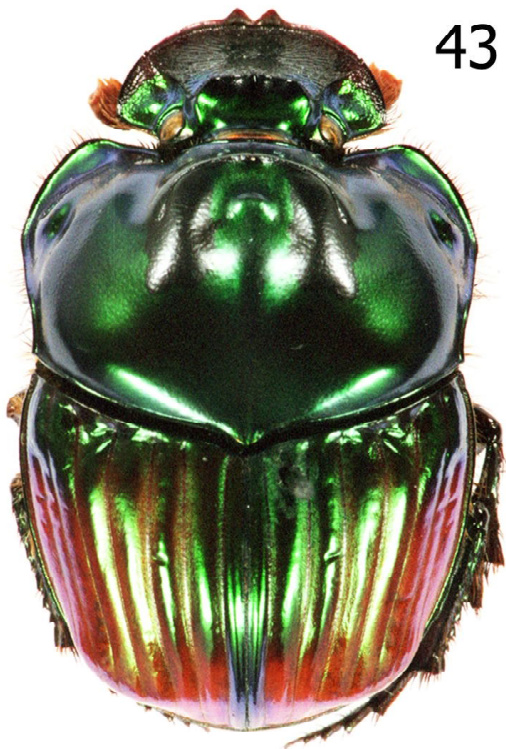
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Figures 40–44. *Phanaeus (Notiophanaeus) palaeno* Blanchard. 40–41) Strong male. 42) Weak male.



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Figures 45–48. *Phanaeus (Notiophanaeus) martinezorum* Arnaud. 45–46) Male. 47–48) Female.

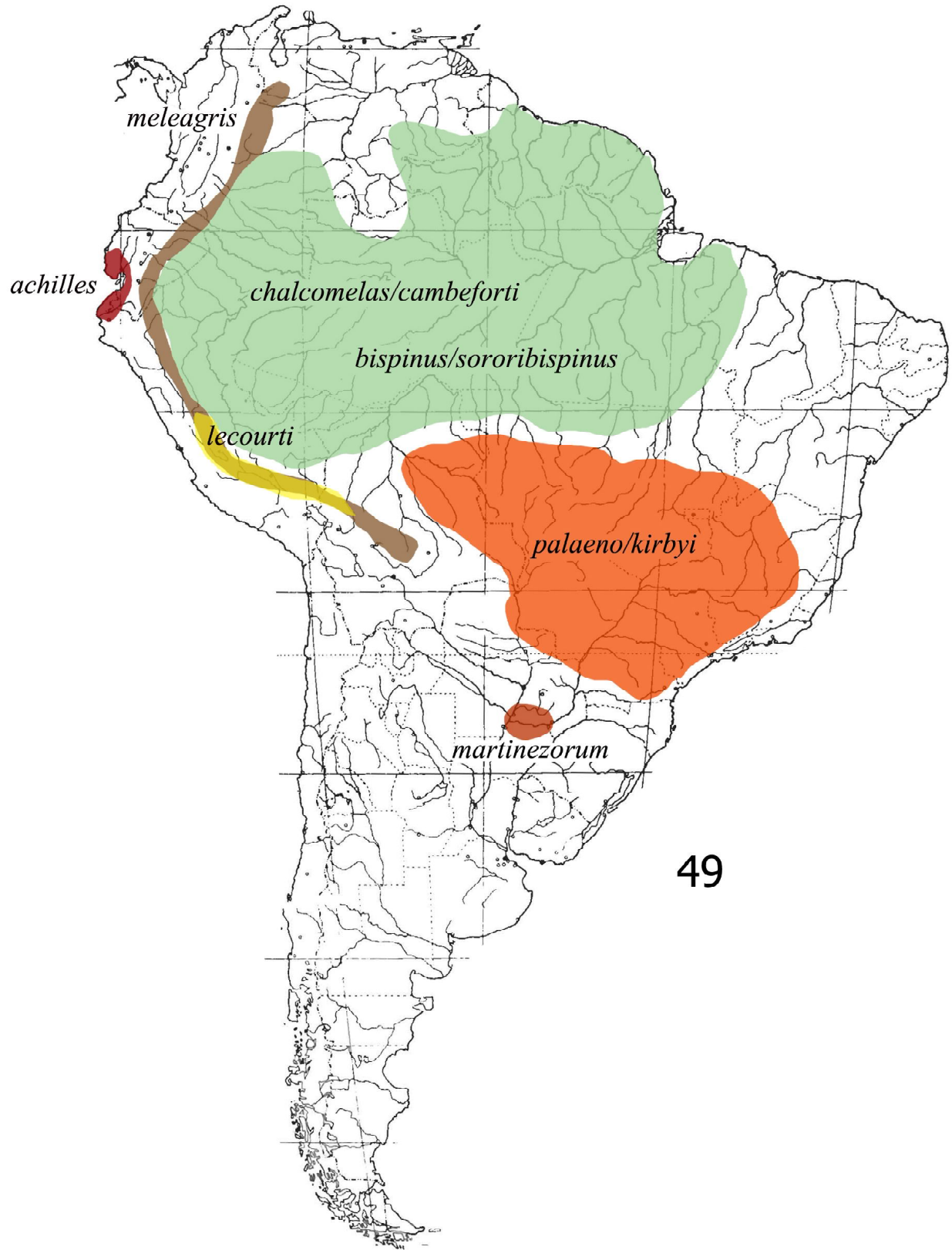
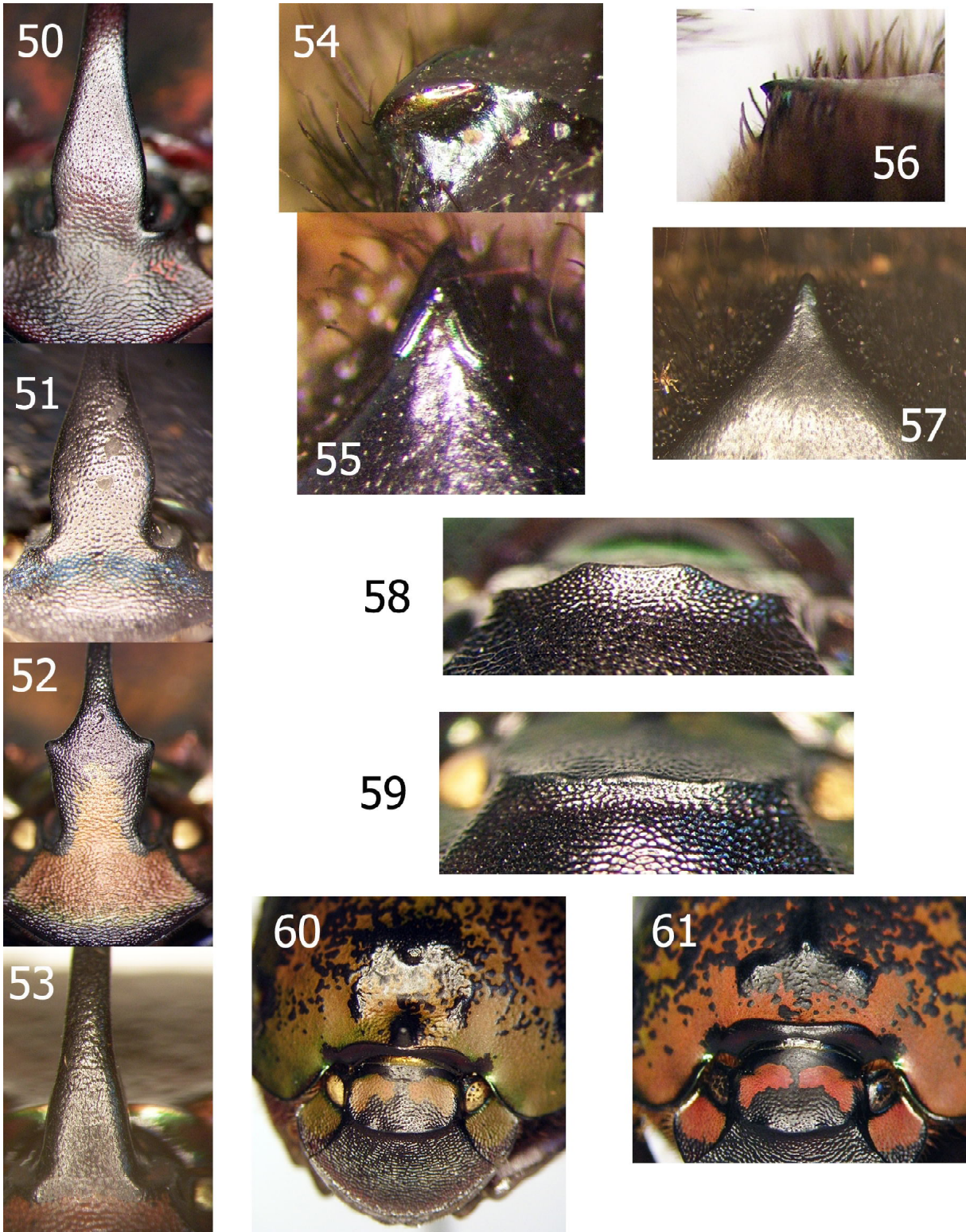
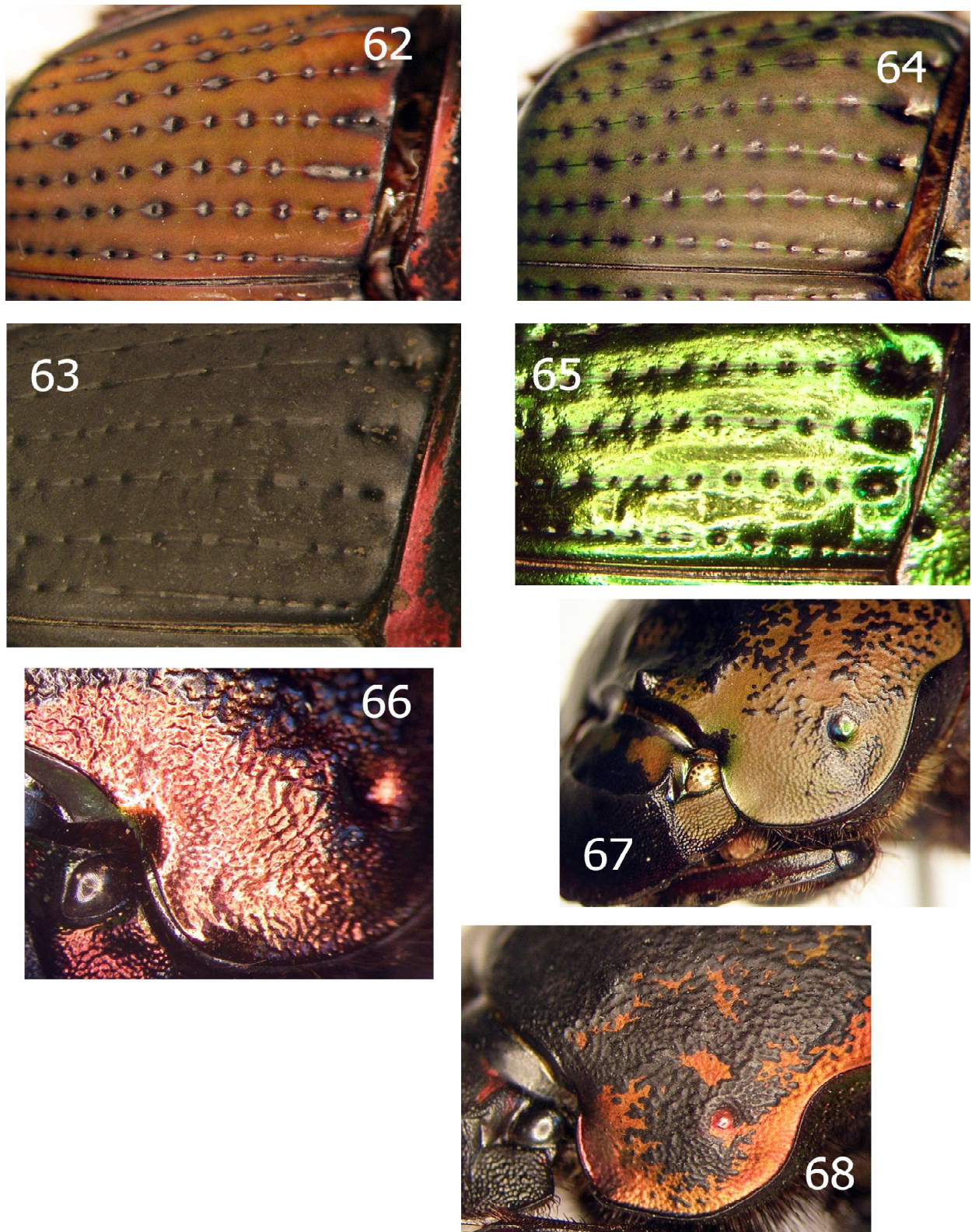


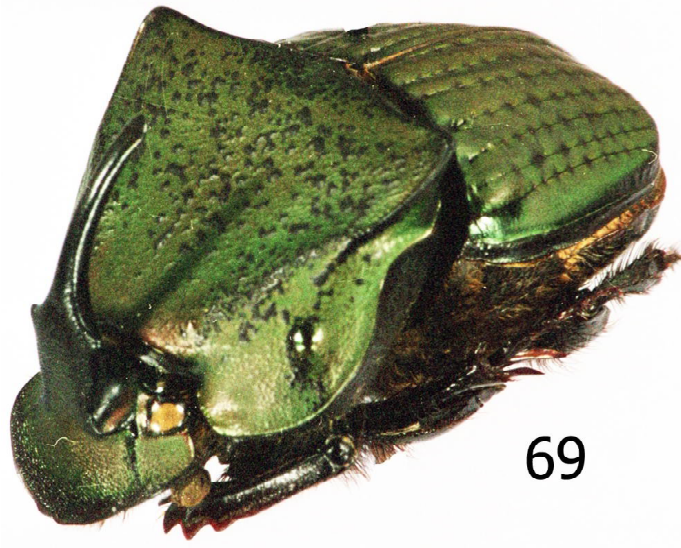
Figure 49. Approximate geographic distributions of the *Phanaeus* (*Notiophanaeus*) *bispinus*, *chalconelas* and *palaeno* species groups.



Figures 50–61. Characters of the *Phanaeus* (*Notiophanaeus*) *chalcomeles* species group. *Phanaeus meleagris* Blanchard. **50)** Male horn. *Phanaeus lecourti* Arnaud. **51)** Male horn. **56)** Metasternal angle, lateral view. **57)** Same, ventral view. *Phanaeus chalcomeles* (Perty). **52)** Male horn. **54)** Metasternal angle, lateral view. **55)** Same, ventral view. **59)** Female cephalic carina. **60)** Female, dorsal view of forebody. *Phanaeus cambeforti* Arnaud. **53)** Male horn. **61)** Female, dorsal view of forebody. *Phanaeus achilles* Boheman. **58)** Female cephalic carina.



Figures 62–68. Characters of the *Phanaeus* (*Notiophanaeus*) *chalcamelas* species group. *Phanaeus meleagris* Blanchard. **62)** Elytron of “minos” form. **63)** Elytron of typical form. **68)** Lateral view of female pronotum. *Phanaeus chalcamelas* (Perty). **64)** Elytron. **67)** Lateral view of female pronotum. *Phanaeus achilles* Boheman. **65)** Elytron. **66)** Lateral view of female pronotum.



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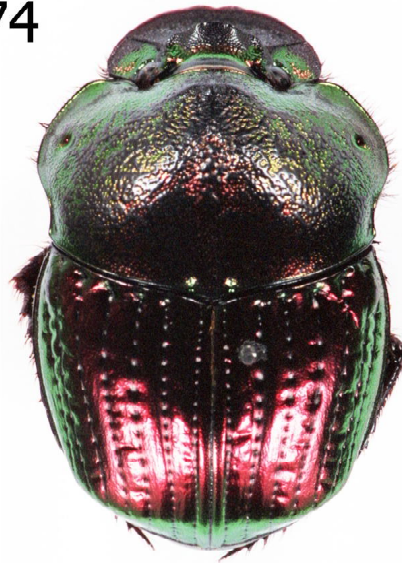
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Figures 69–72. *Phanaeus (Notiophanaeus) chalcomelas* (Perty). 69–70) Male. 71–72) Female.

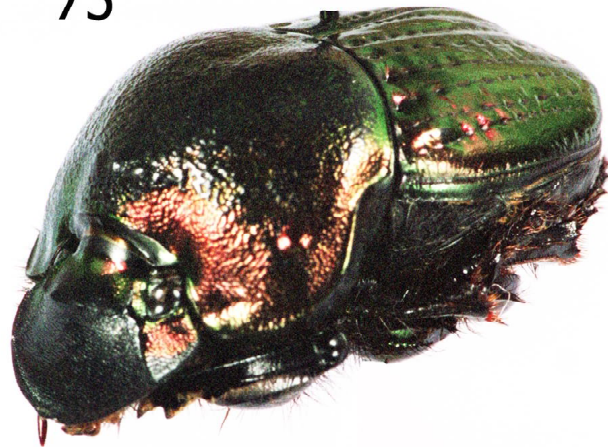
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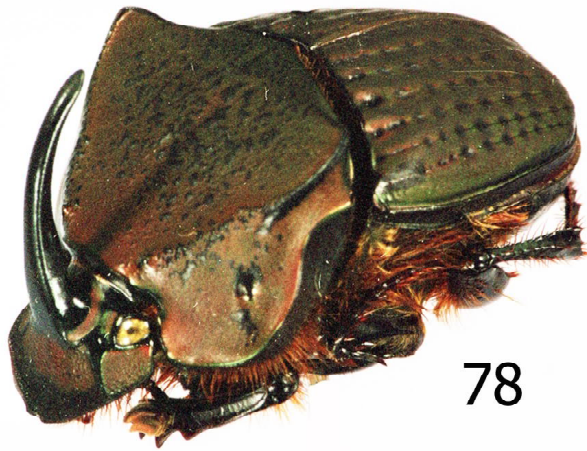
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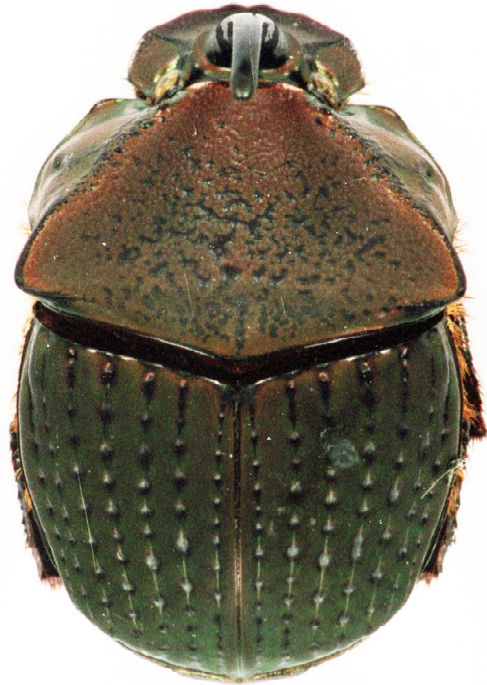
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Figures 73–77. *Phanaeus (Notiophanaeus) achilles* Boheman. 73) Male [red form]. 74–75) Female [red form]. 76–77) Male [green form].



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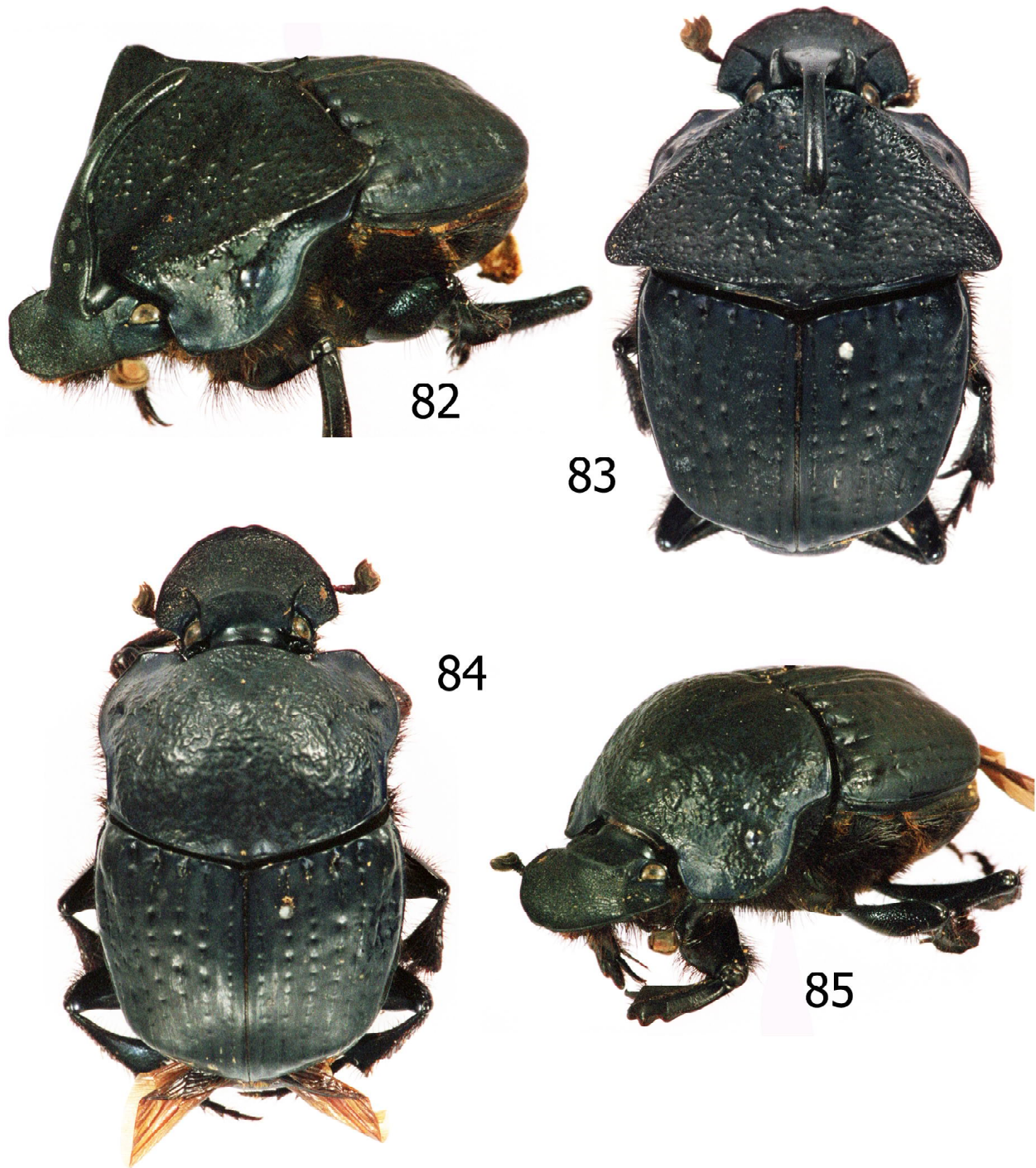


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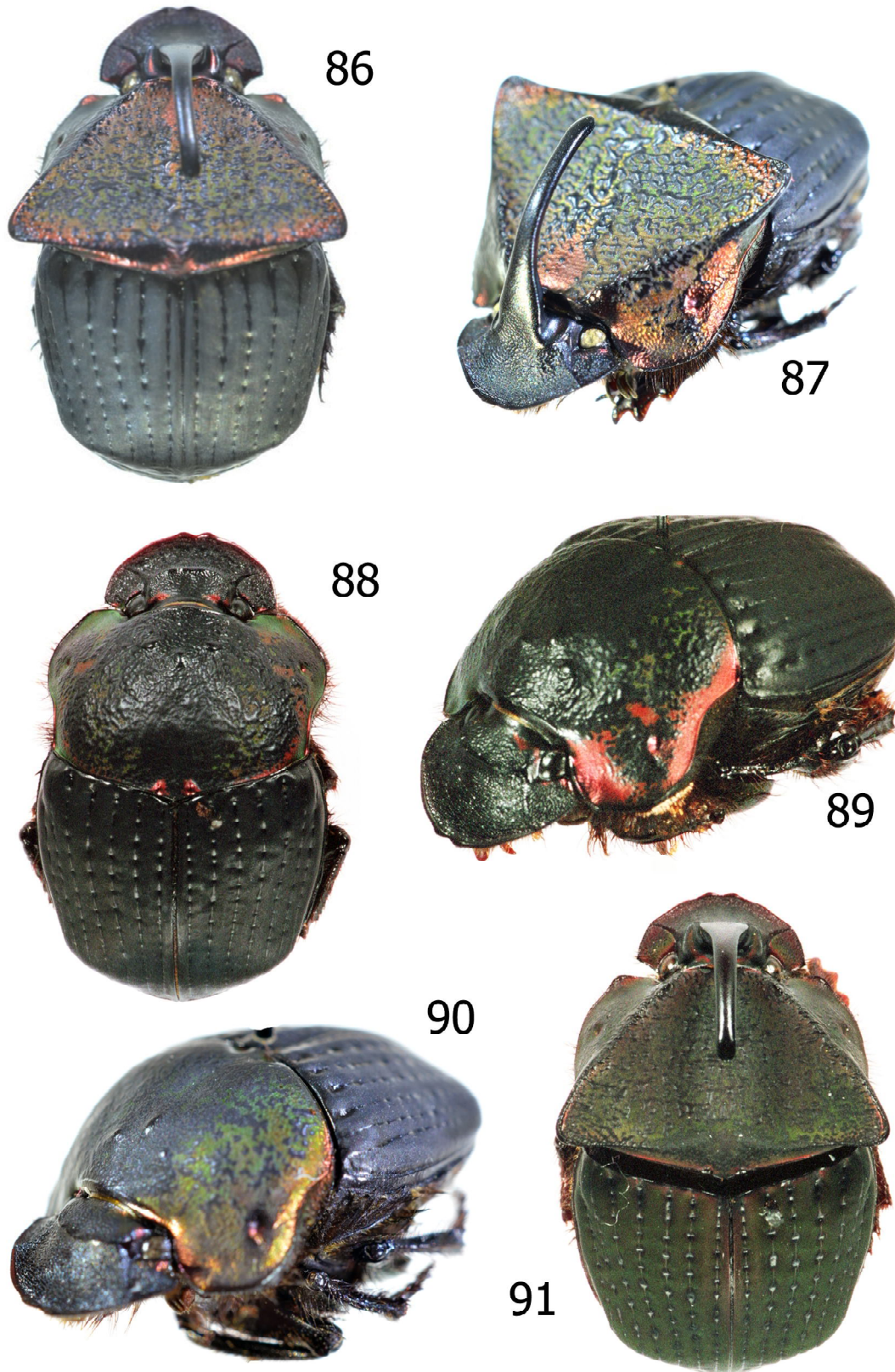


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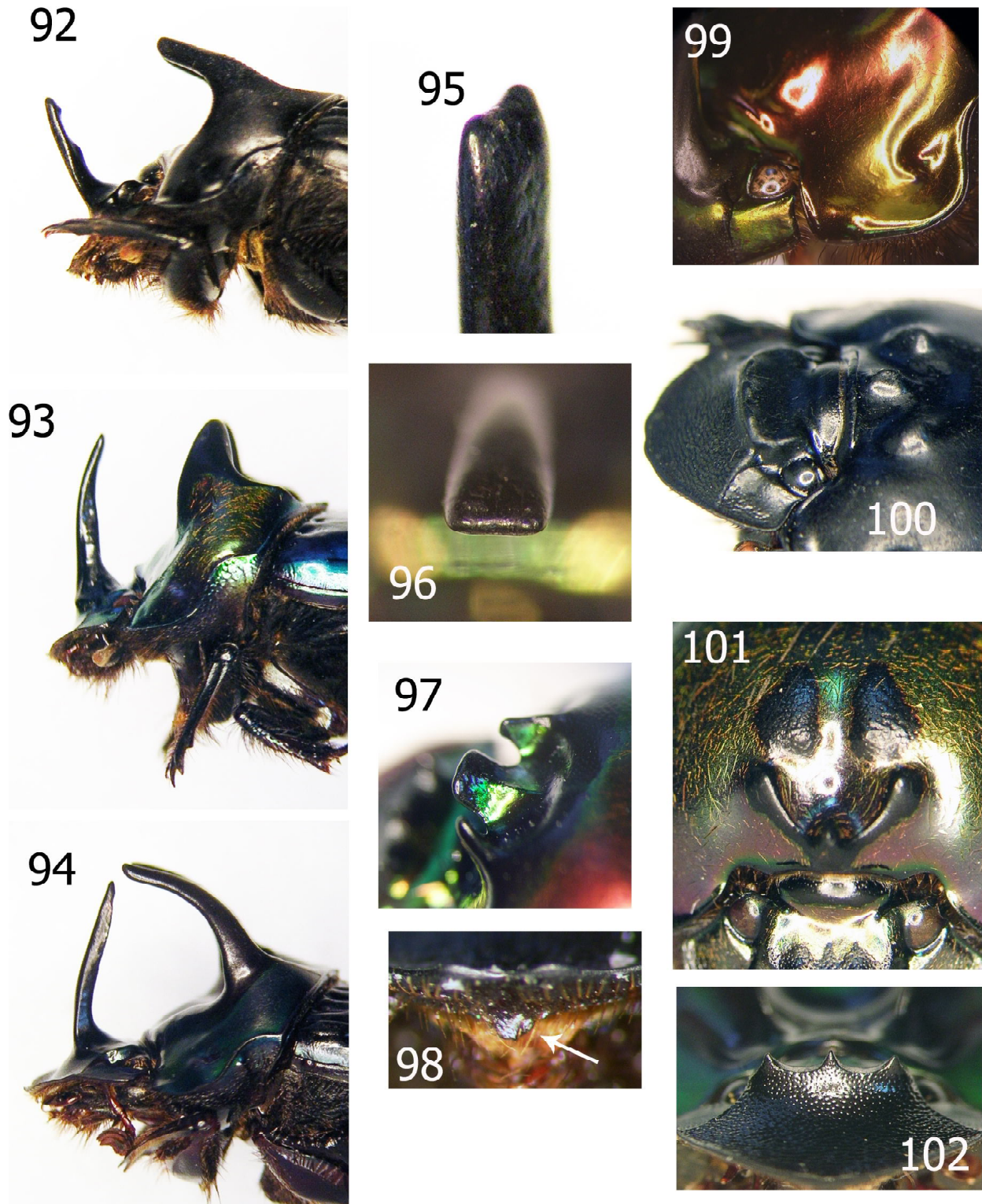
Figures 78–81. *Phanaeus (Notiophanaeus) cambeforti* Arnaud. 78–79) Male. 80–81) Female.



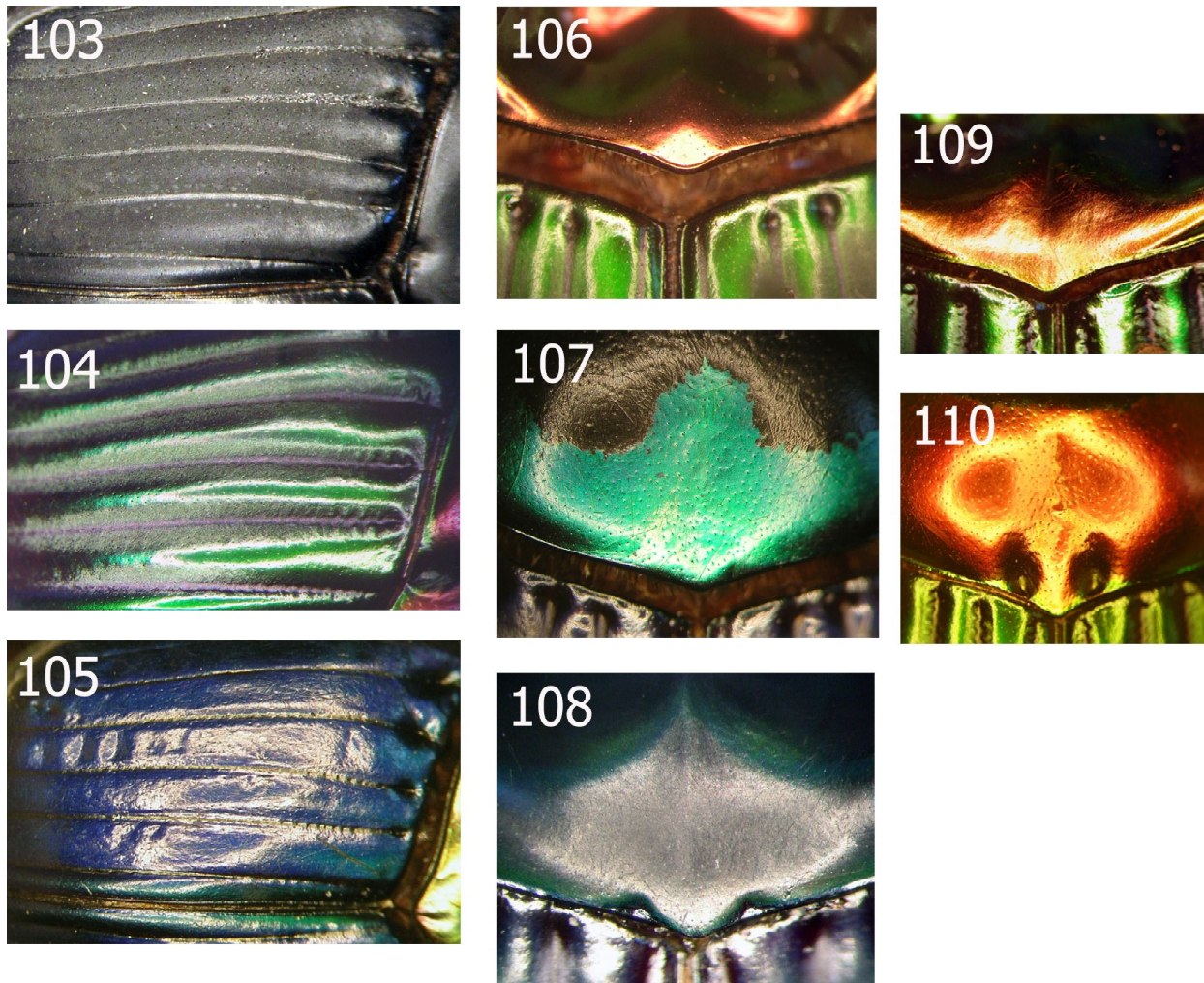
Figures 82–85. *Phanaeus (Notiophanaeus) lecourti* Arnaud. 82–83) Male. 84–85) Female.



Figures 86–91. *Phanaeus (Notiophanaeus) meleagris* Blanchard. 86–87) Male. 88–89) Female. 90) Female “minos” form. 91) Male “minos” form.



Figures 92–102. Characters of the *Phanaeus (Notiophanaeus) splendidulus* species group. *Phanaeus bordoni* Arnaud. **92)** Male, lateral view of forebody. **100)** Female. *Phanaeus dejeani* Harold. **93)** Male, lateral view of forebody. **95)** Male, tip of head horn. **96)** Same. **99)** Female, anterolateral view of forebody. **101)** Female, dorsal view of forebody. *Phanaeus haroldi* Kirsch. **94)** Male, lateral view of forebody. **102)** Female, frontal view of head. *Phanaeus melibaeus* Blanchard. **97)** Female, oblique view of pronotal tubercles. *Phanaeus splendidulus* (Fabricius). **98)** Front margin of clypeus, frontal view [arrow indicates tooth-shaped subclypeal process].



Figures 103–110. Characters of the *Phanaeus (Notiophanaeus) splendidulus* species group. *Phanaeus bordoni* Arnaud. **103)** Elytron. *Phanaeus melibaeus* Blanchard. **104)** Elytron. **109)** Male, dorsal view of portion of pronotum and elytra. **110)** Female, same. *Phanaeus dejeani* Harold. **105)** Elytron. *Phanaeus splendidulus* (Fabricius). **106)** Male, dorsal view of portion of pronotum and elytra. **107)** Female, same. *Phanaeus haroldi* Kirsch. **108)** Male, dorsal view of portion of pronotum and elytra.

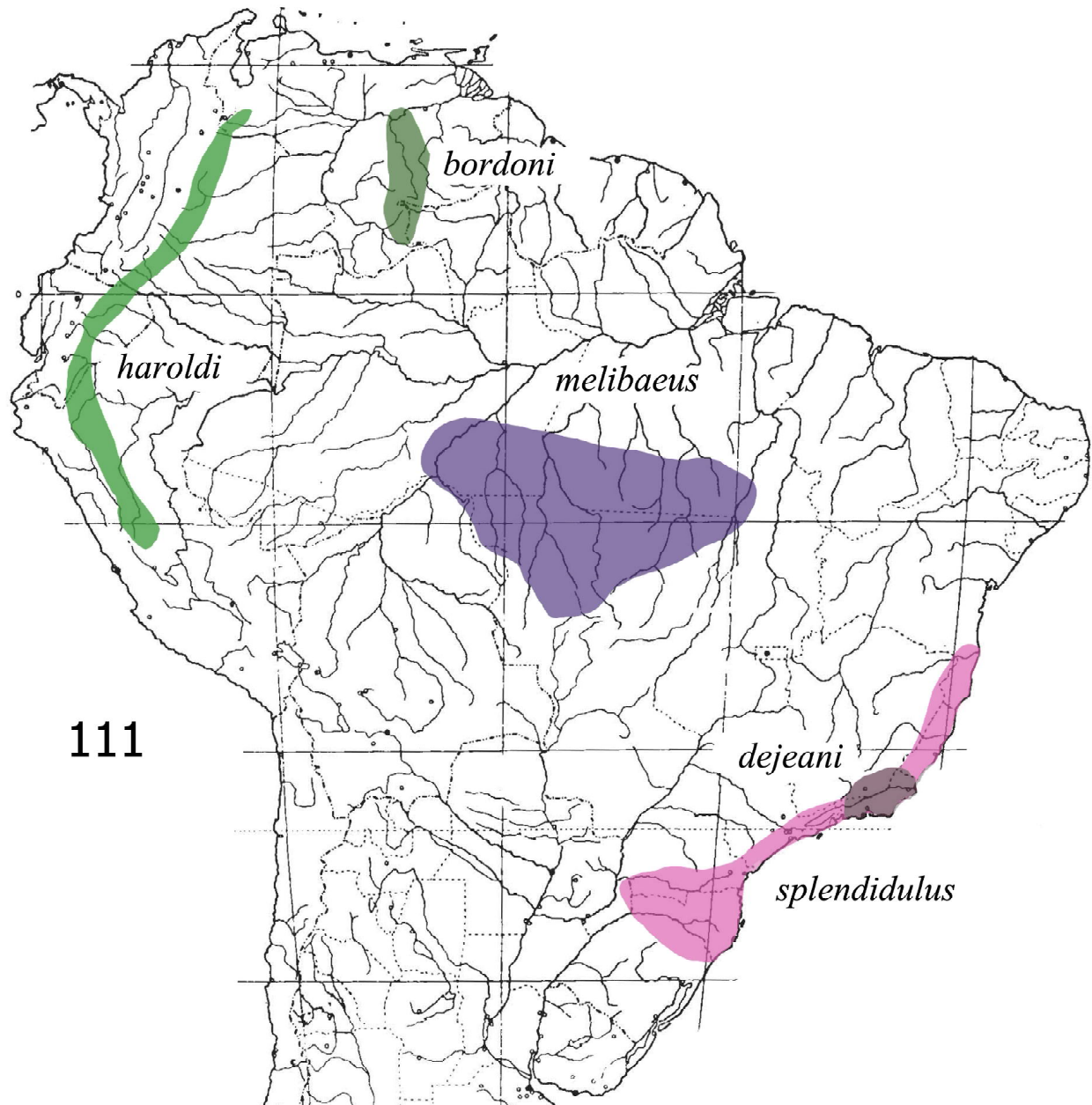
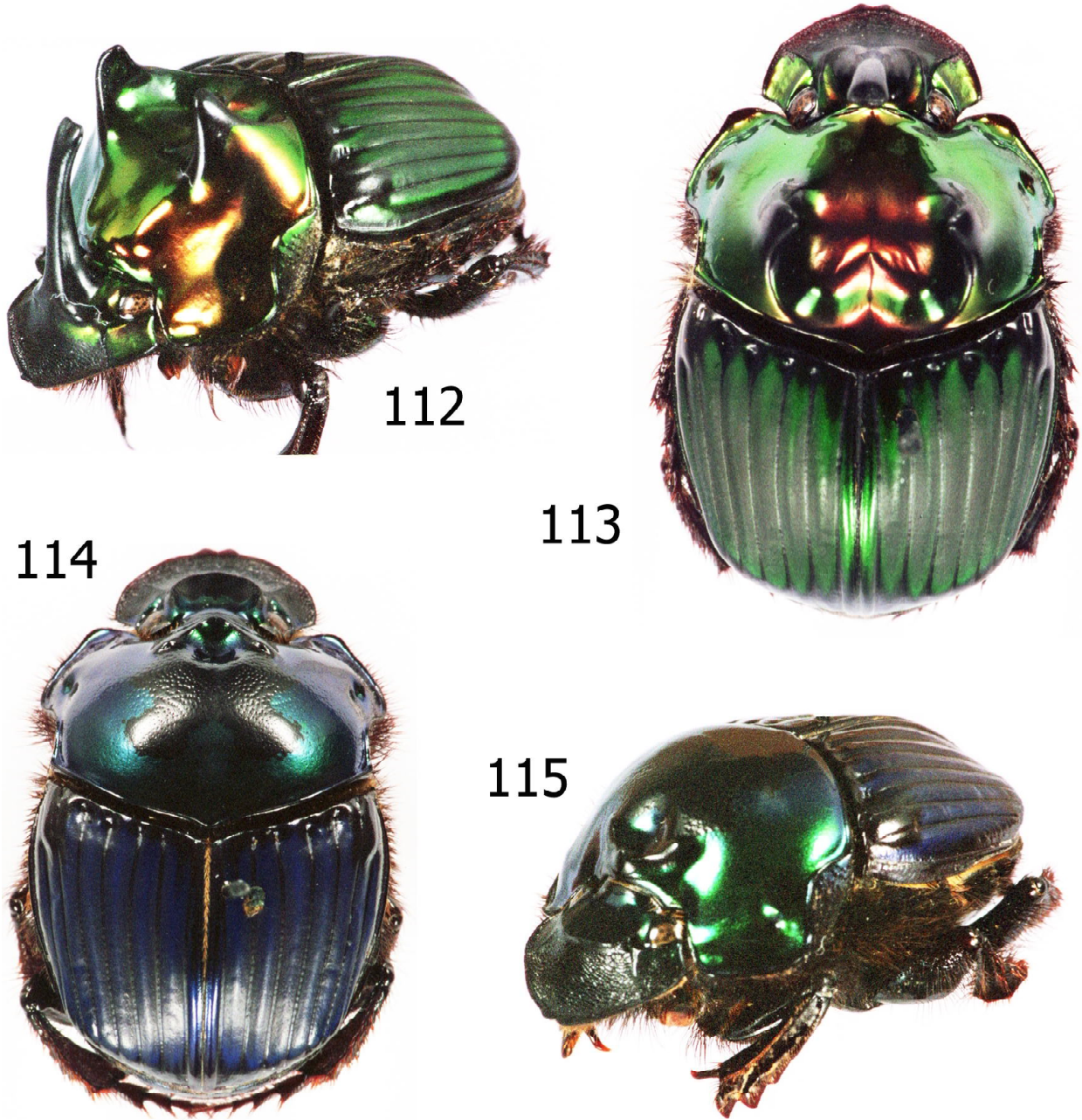
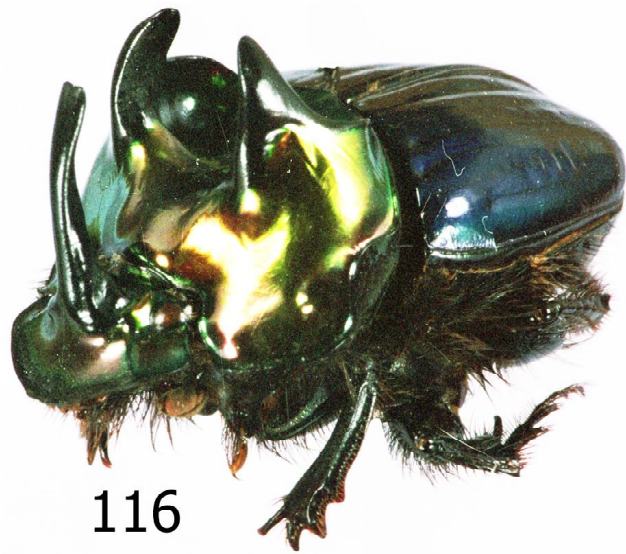


Figure 111. Approximate geographic distribution of the *Phanaeus (Notiophanaeus) splendidulus* species group.



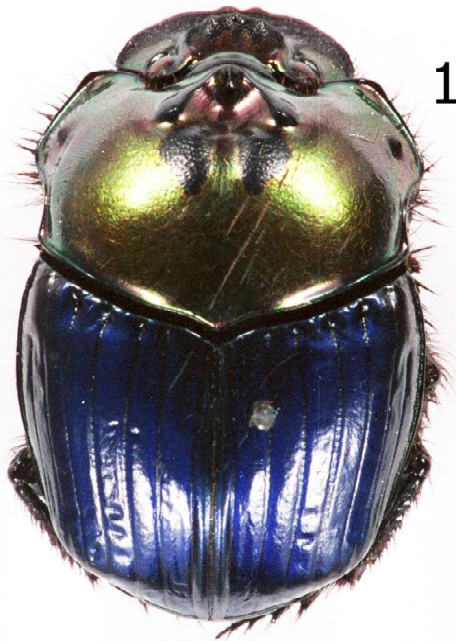
Figures 112–115. *Phanaeus (Notiophanaeus) splendidulus* (Fabricius). 112–113) Male. 114–115) Female.



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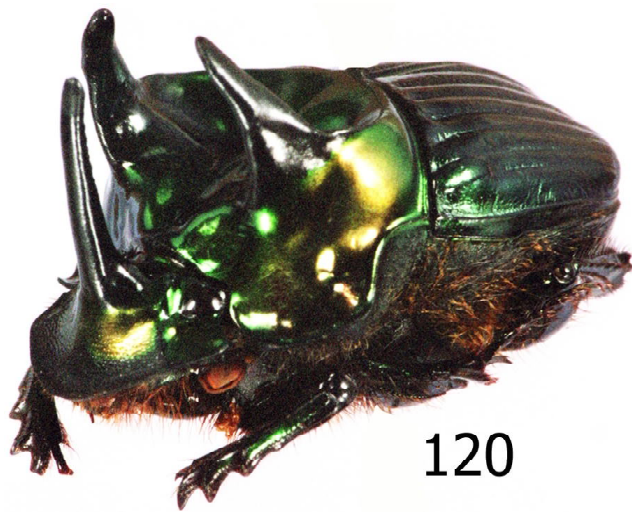


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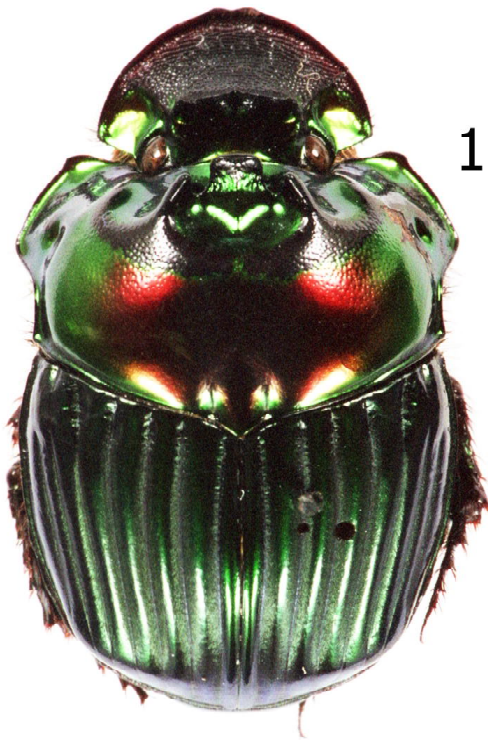
Figures 116–119. *Phanaeus (Notiophanaeus) dejeani* Harold. 116–117) Male. 118–119) Female.



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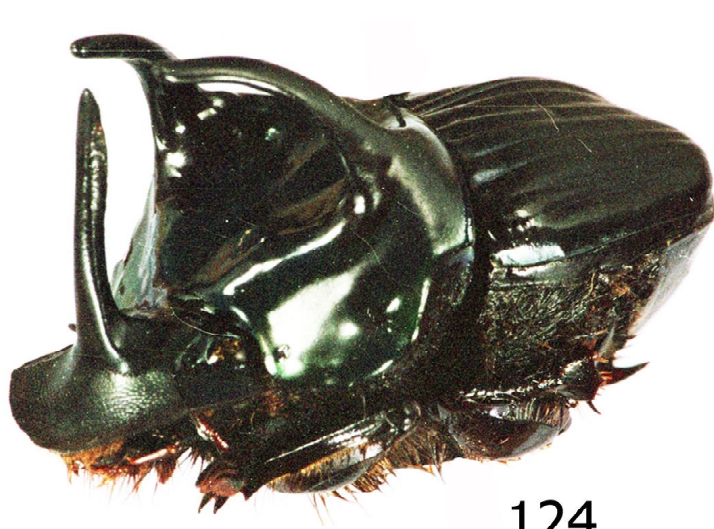


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Figures 120–123. *Phanaeus (Notiophanaeus) melibaeus* Blanchard. 120–121) Male. 122–123) Female.



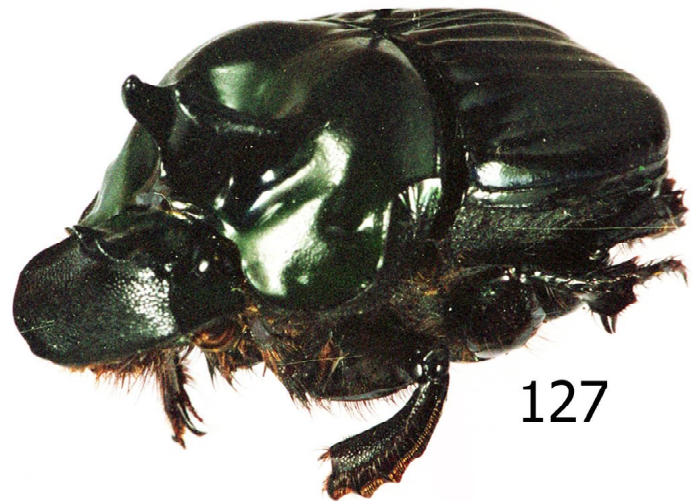
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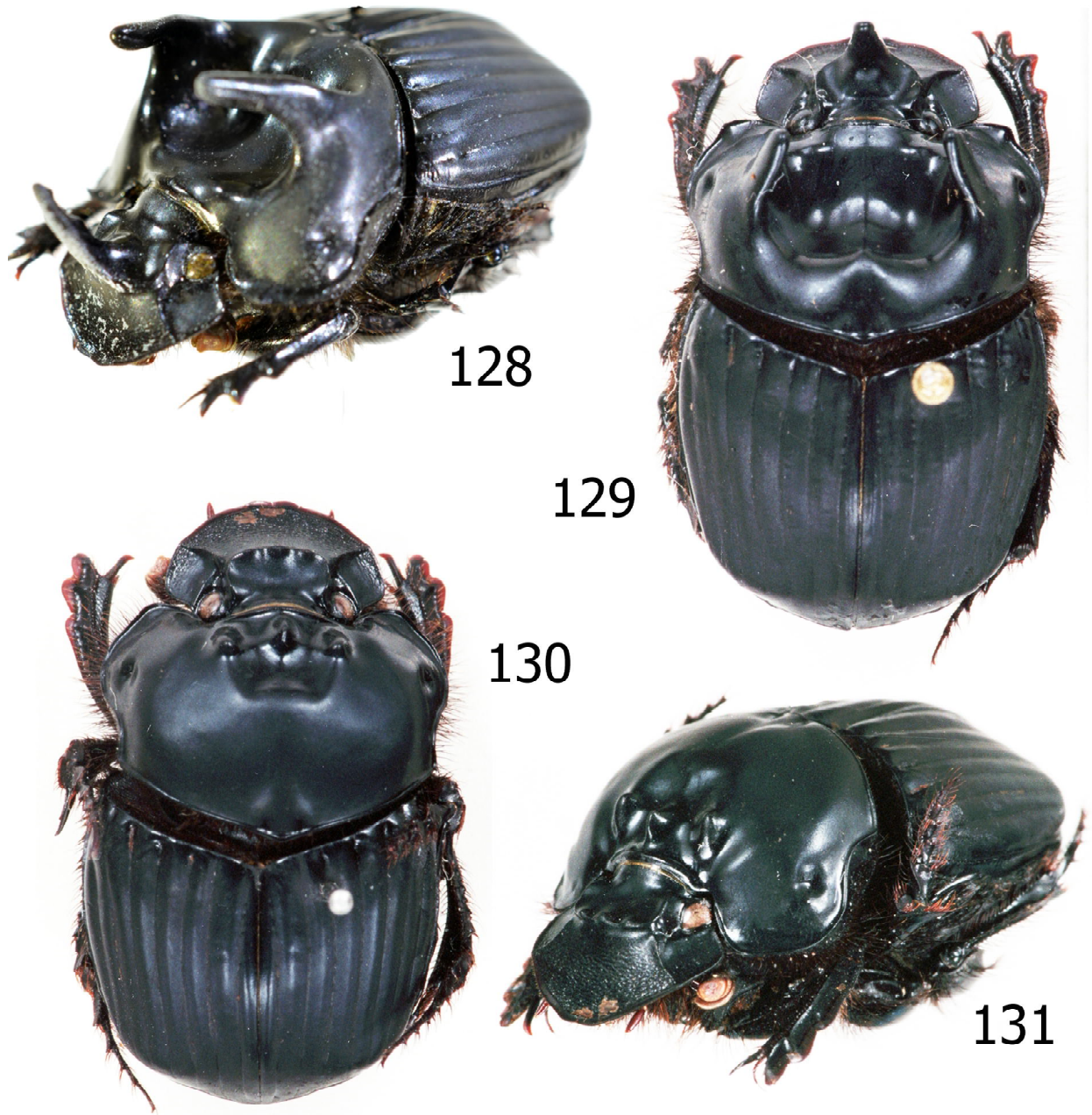


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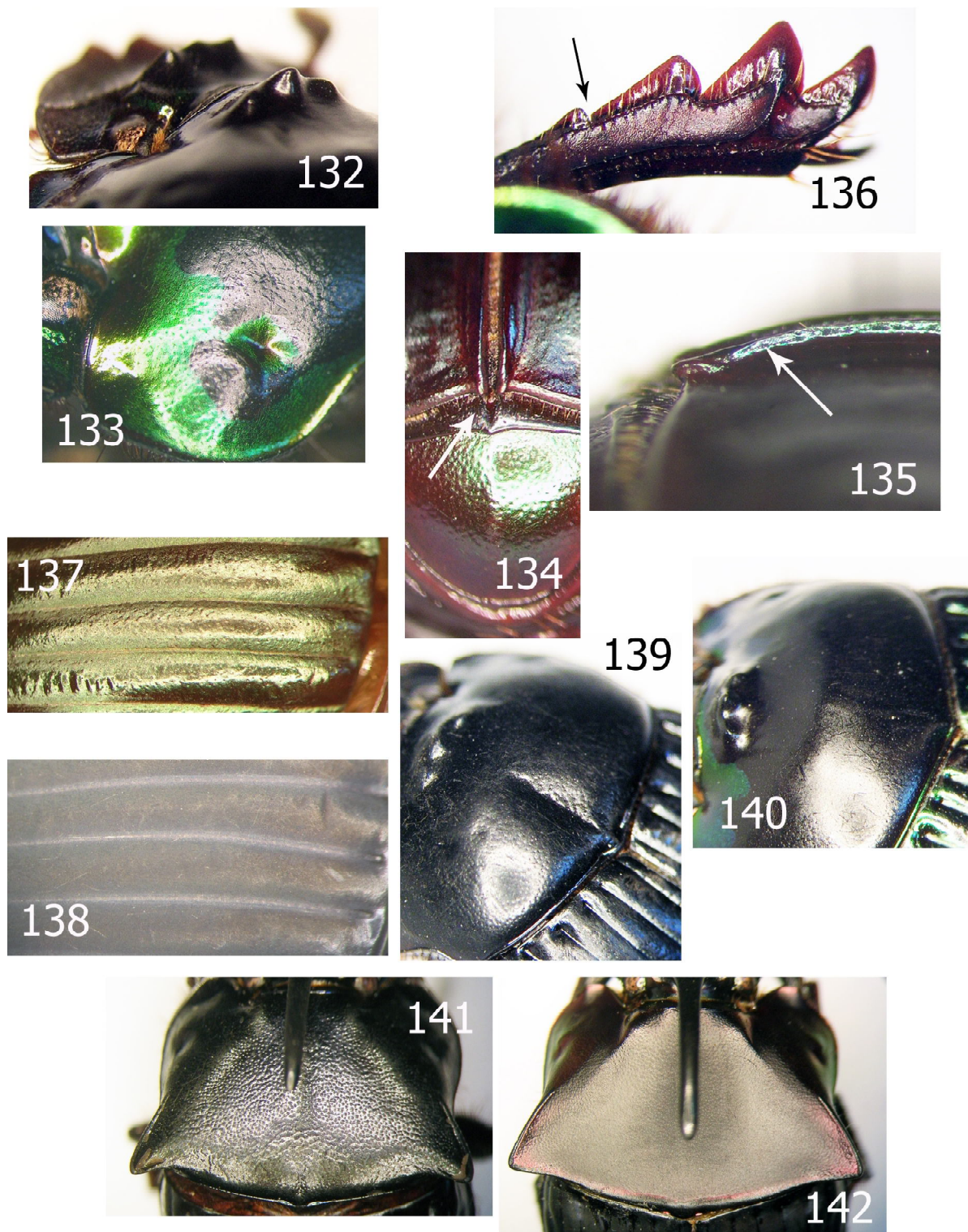


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Figures 124–127. *Phanaeus (Notiophanaeus) haroldi* Kirsch. 124–125) Male. 126–127) Female.



Figures 128–131. *Phanaeus (Notiophanaeus) bordoni* Arnaud. 128–129) Male. 130–131) Female.



Figures 132–142. Characters of the *Phanaeus* (*Notiophanaeus*) endymion species group. *Phanaeus endymion* Harold. **132)** Female, oblique view of forebody. **133)** Female, lateral view of pronotum. **136)** Female protibia [arrow indicates narrow notch]. **140)** Female, dorsal view of pronotum. *Phanaeus halffterorum* Edmonds. **134)** Posterior view of elytra [arrow indicates tip of elytral ridge]. **135)** Elytron, lateral view [arrow indicates elytral ridge]. **137)** Elytron, dorsal view. *Phanaeus pyrois* Bates. **138)** Elytron, dorsal view. **142)** Male, dorsal view of pronotum. *Phanaeus zapotecus* Edmonds. **139)** Female, dorsal view of pronotum. **141)** Male, dorsal view of pronotum.

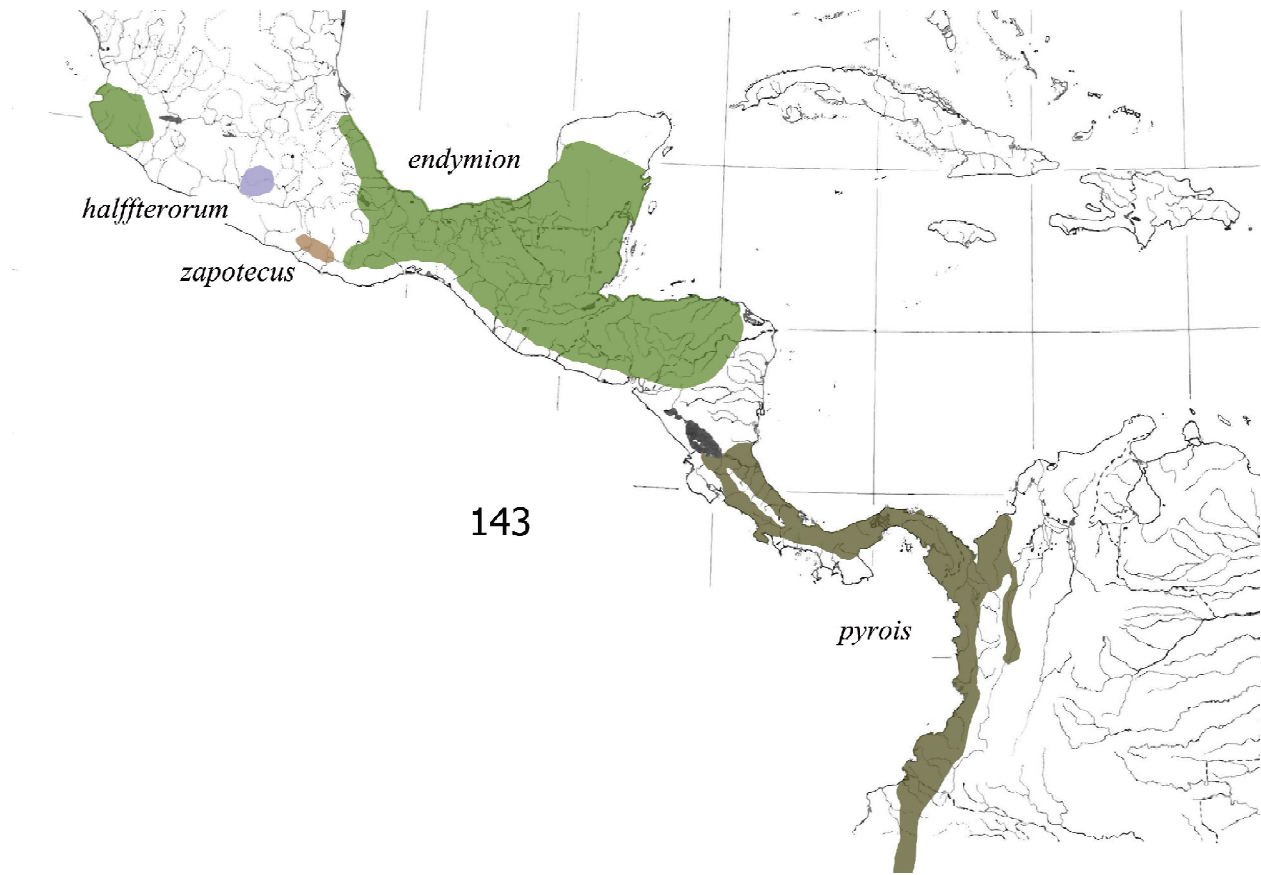
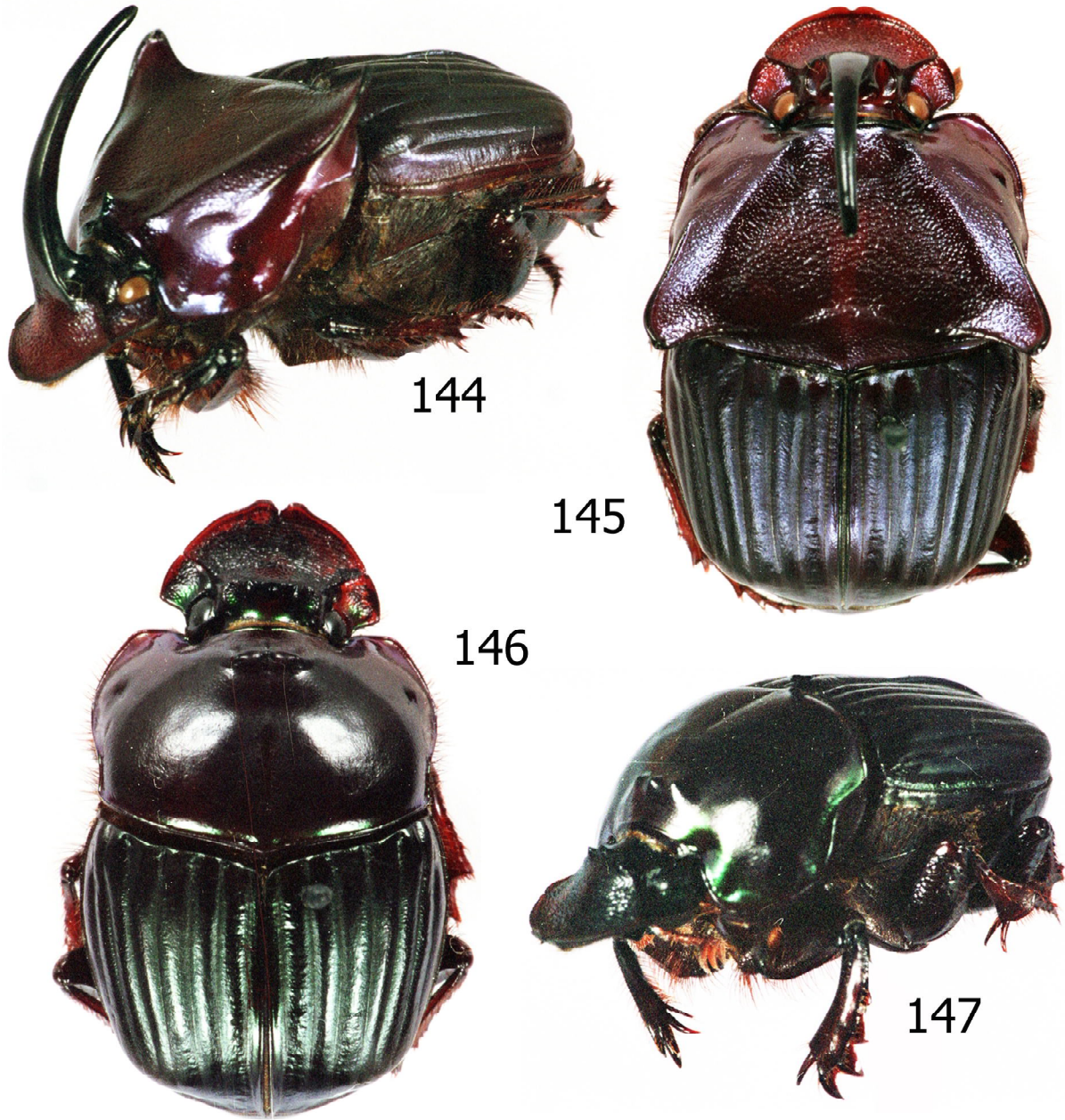
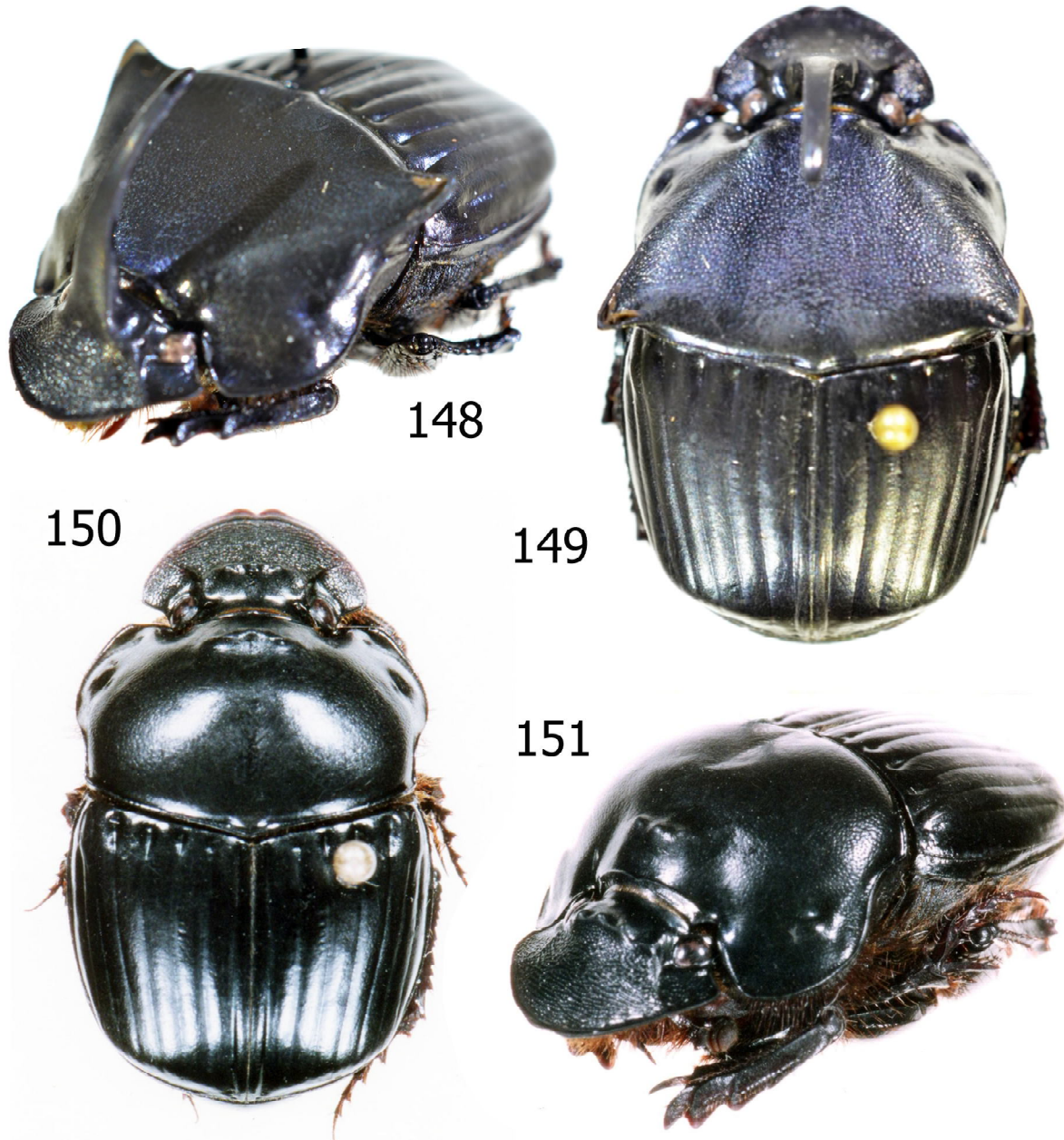


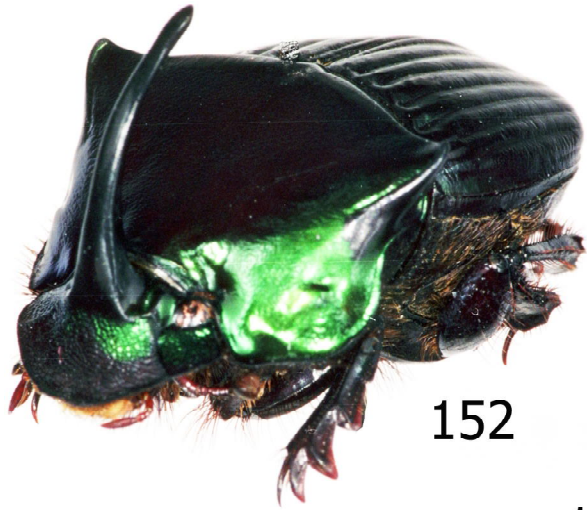
Figure 143. Approximate geographic distribution of the *Phanaeus (Notiophanaeus)* endymion species group.



Figures 144–147. *Phanaeus (Notiophanaeus) halffterorum* Edmonds. 144–145) Male. 146–147) Female.



Figures 148–151. *Phanaeus (Notiophanaeus) zapotecus* Edmonds. 148–149) Male. 150–151) Female.



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Figures 152–155. *Phanaeus (Notiophanaeus) endymion* Harold. 152–153) Male. 154–155) Female.



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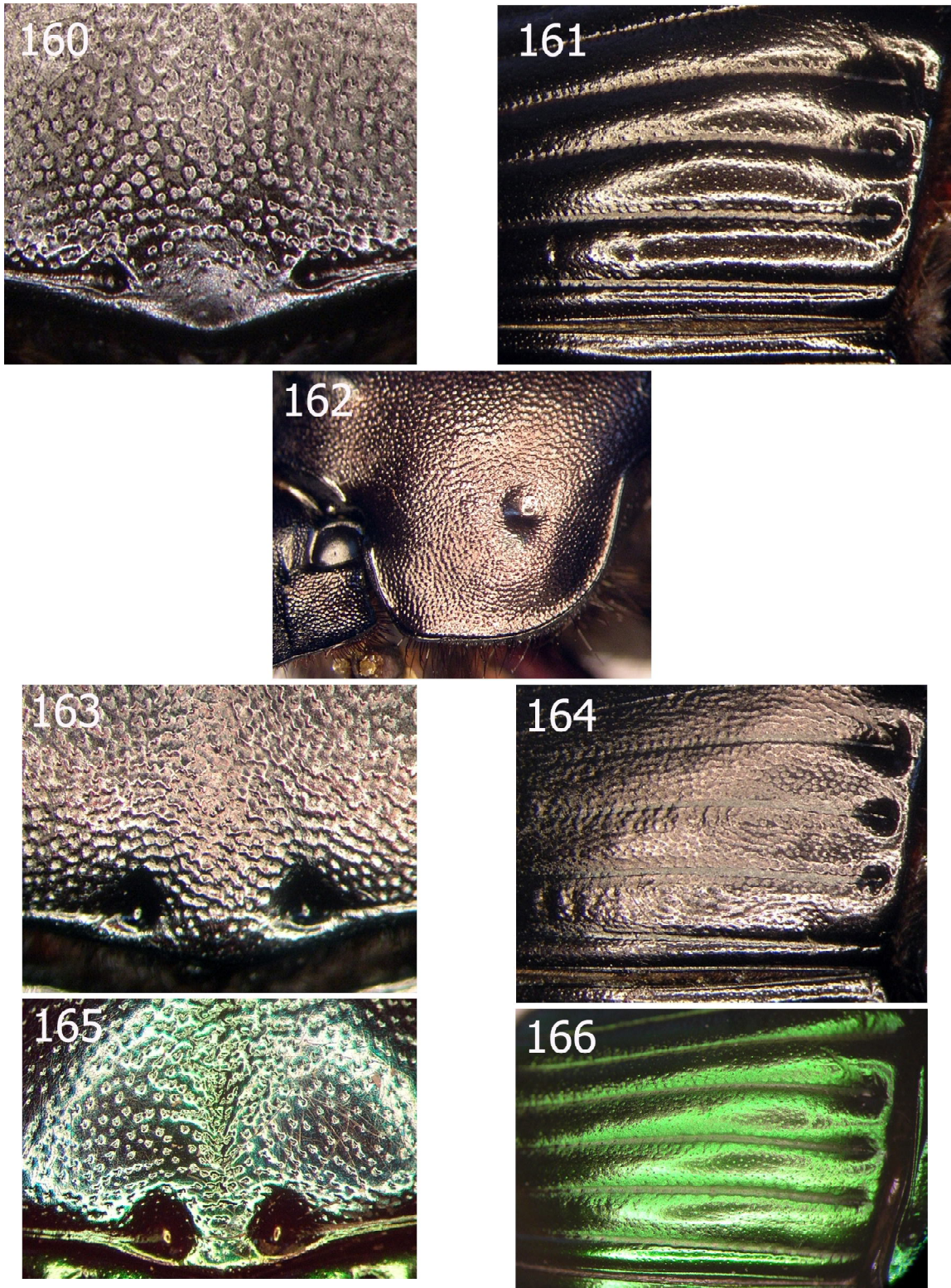


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Figures 156–159. *Phanaeus (Notiophanaeus) pyrois* Bates. 156–157) Male. 158–159) Female.



Figures 160–166. Characters of the *Phanaeus* (*P.*) *triangularis* species group. *Phanaeus triangularis* (Say). **160**) Female, posteromedian portion of pronotum. **161**) Elytron, dorsal view. **162**) Female, lateral view of pronotum. *Phanaeus texensis* Edmonds. **163**) Female, posteromedian portion of pronotum. **164**) Elytron, dorsal view. *Phanaeus adonis* Harold. **165**) Female, posteromedian portion of pronotum. **166**) Elytron, dorsal view.

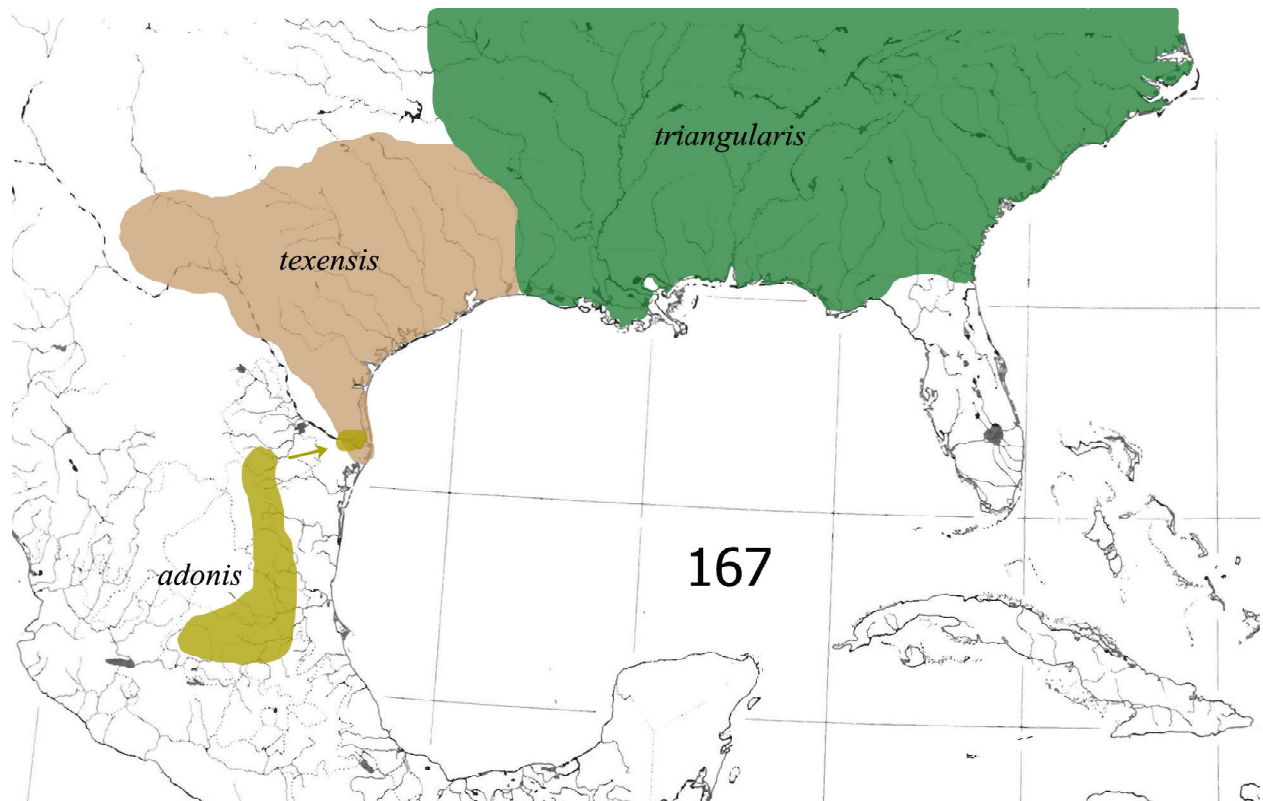


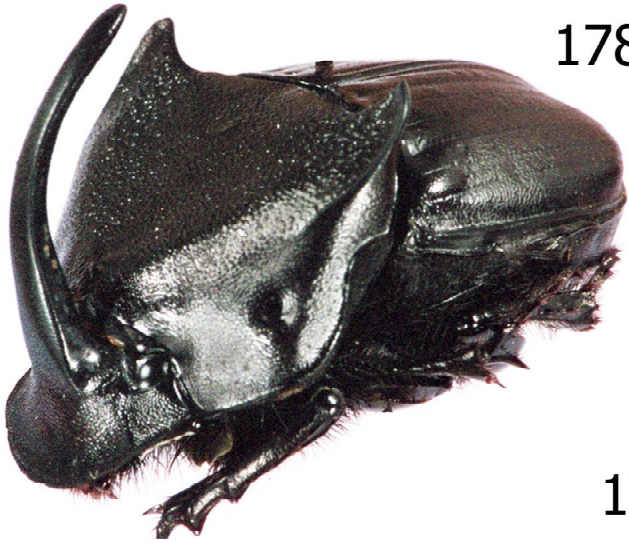
Figure 167. Approximate geographic distribution of the *Phanaeus (P.) triangularis* species group.



Figures 168–173. *Phanaeus (P.) adonis* Harold. 168–169) Blue male. 170–171) Female. 172–173) Green male.



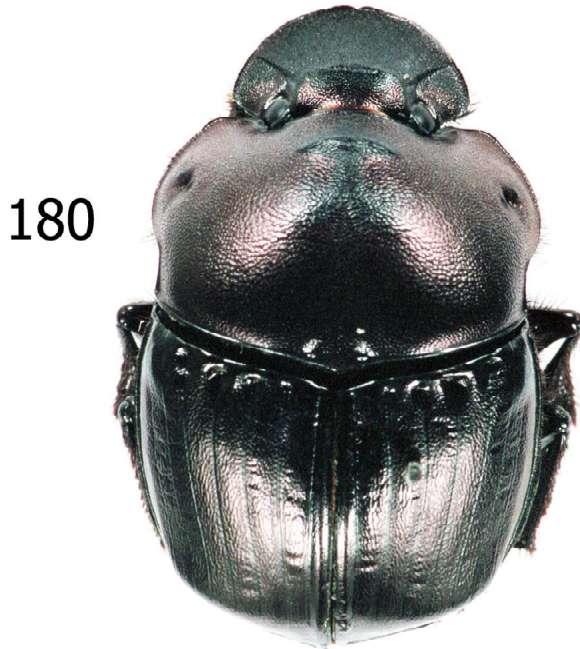
Figures 174–177. *Phanaeus (P.) triangularis* (Say). 174–175) Male. 176–177) Female.



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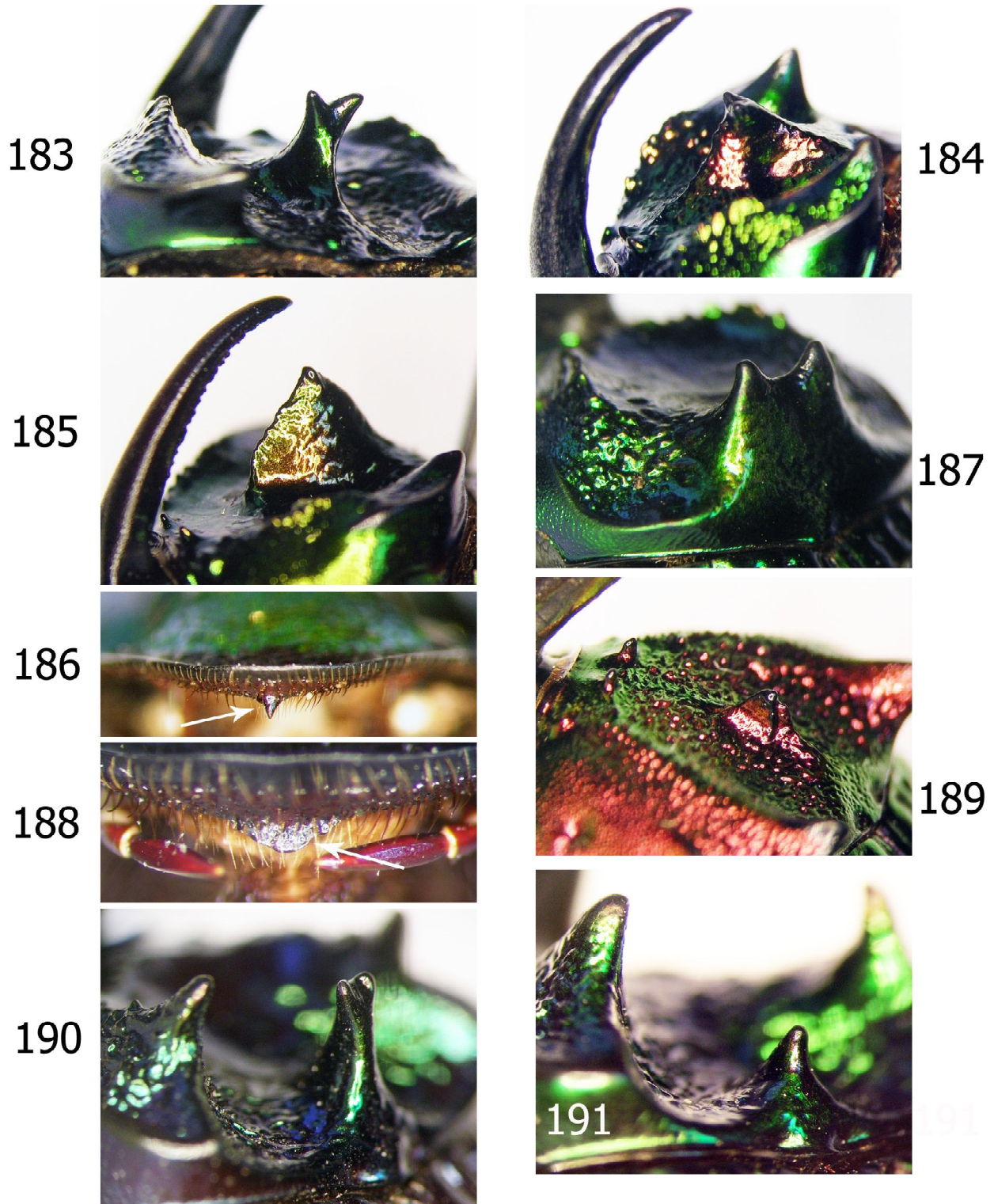


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Figures 178–182. *Phanaeus (P.) texensis* Edmonds. 178–179) Male. 180–182) Female.



Figures 183–191. Characters of the *Phanaeus* (*P.*) *tridens* species group. *Phanaeus tridens* Castelnau. **183**) Male pronotum (Colima form). **184**) Same (Veracruz form). *Phanaeus nimrod* Harold. **185**) Male pronotum. **186**) Clypeal margin [arrow indicates spinate clypeal process]. *Phanaeus furiosus* Bates. **187**) Male pronotum. **188**) Clypeal margin [arrow indicates transverse clypeal process]. *Phanaeus eximius* Bates, **189**) Male pronotum. *Phanaeus daphnis* Harold. **190**) Male pronotum (“herbeus” form). **191**) Same (typical form).

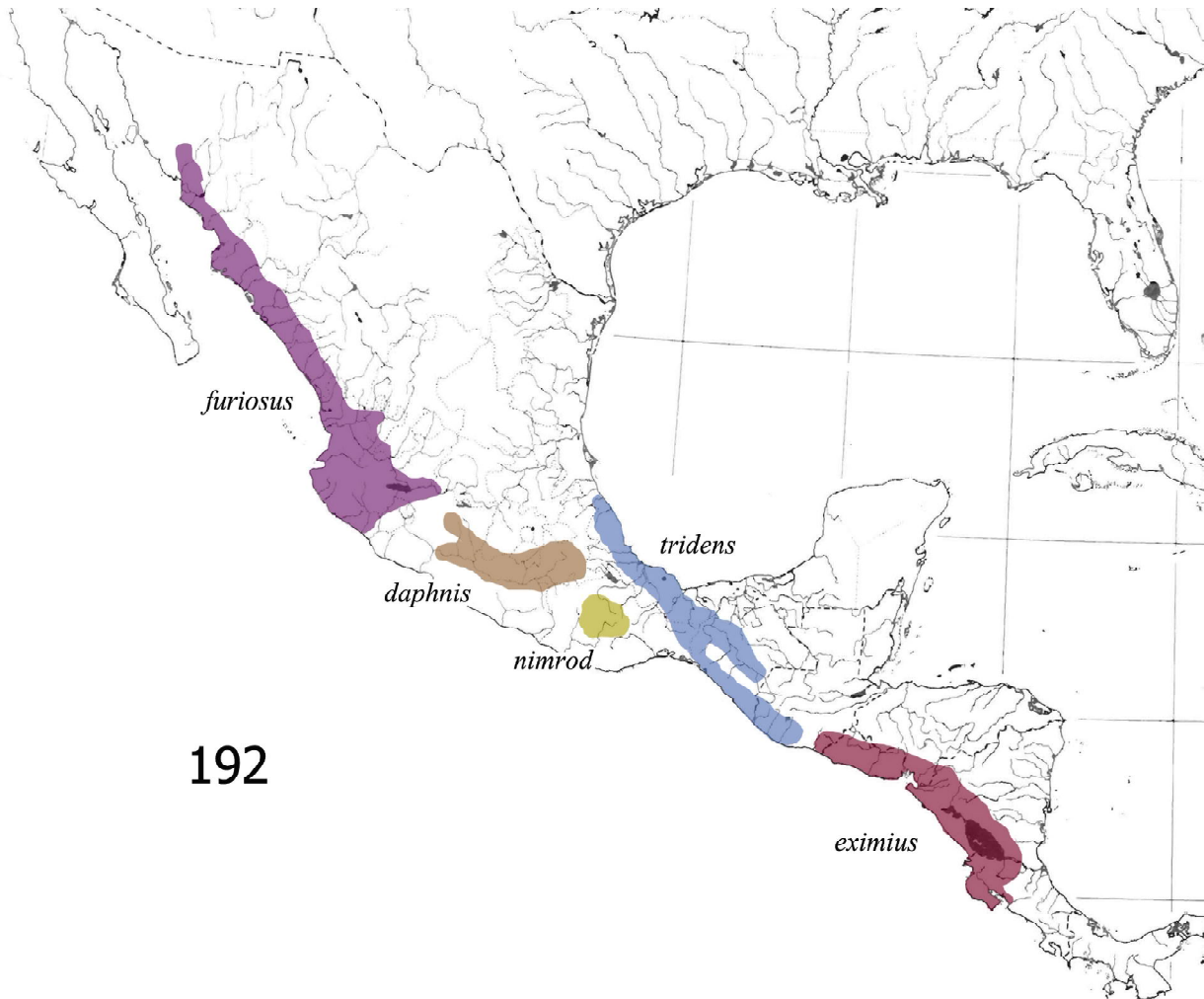
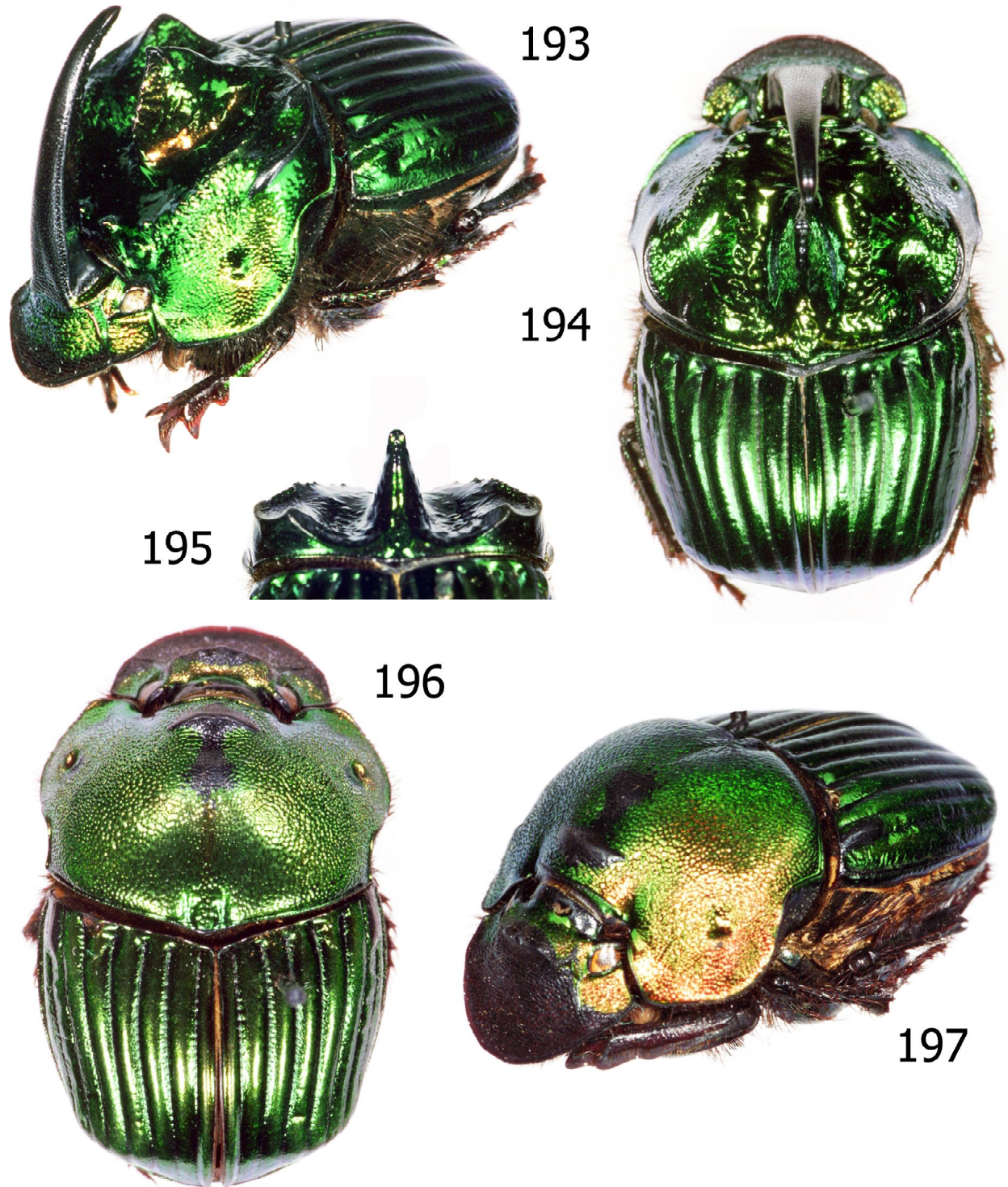


Figure 192. Approximate geographic distribution of the *Phanaeus (P.) tridens* species group.



Figures 193–197. *Phanaeus (P) nimrod* Harold. 193–194) Male. 195) Same male, basal process of pronotum in posterior view. 196–197) Female.



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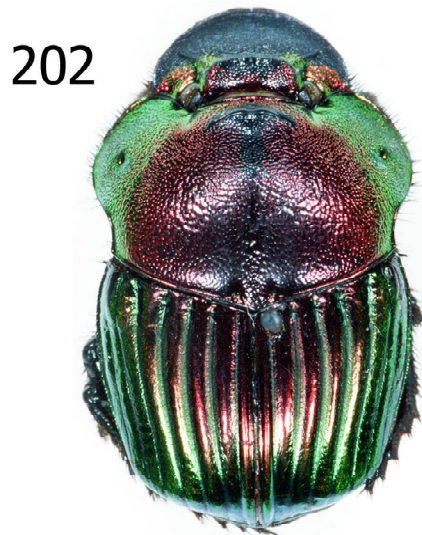
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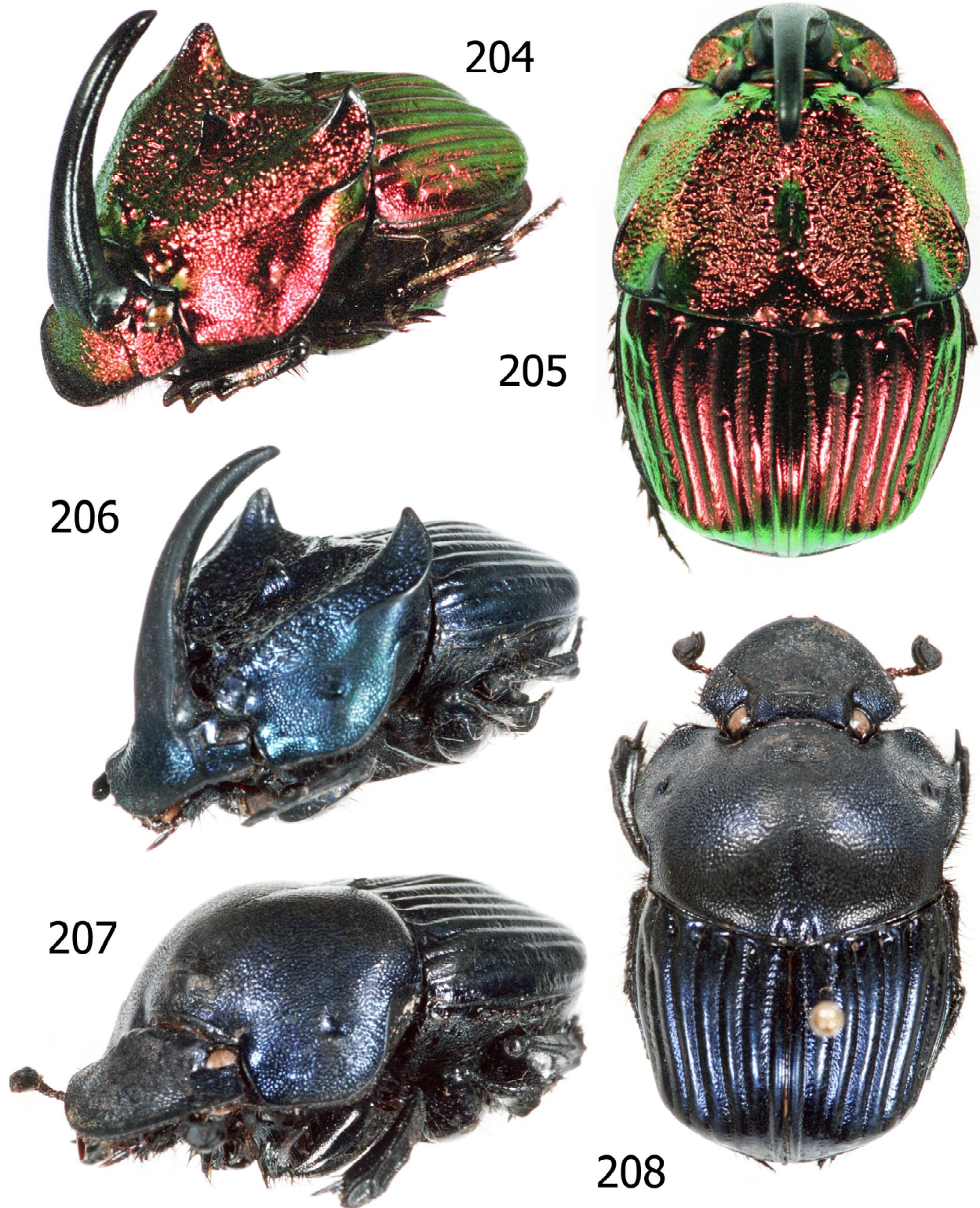


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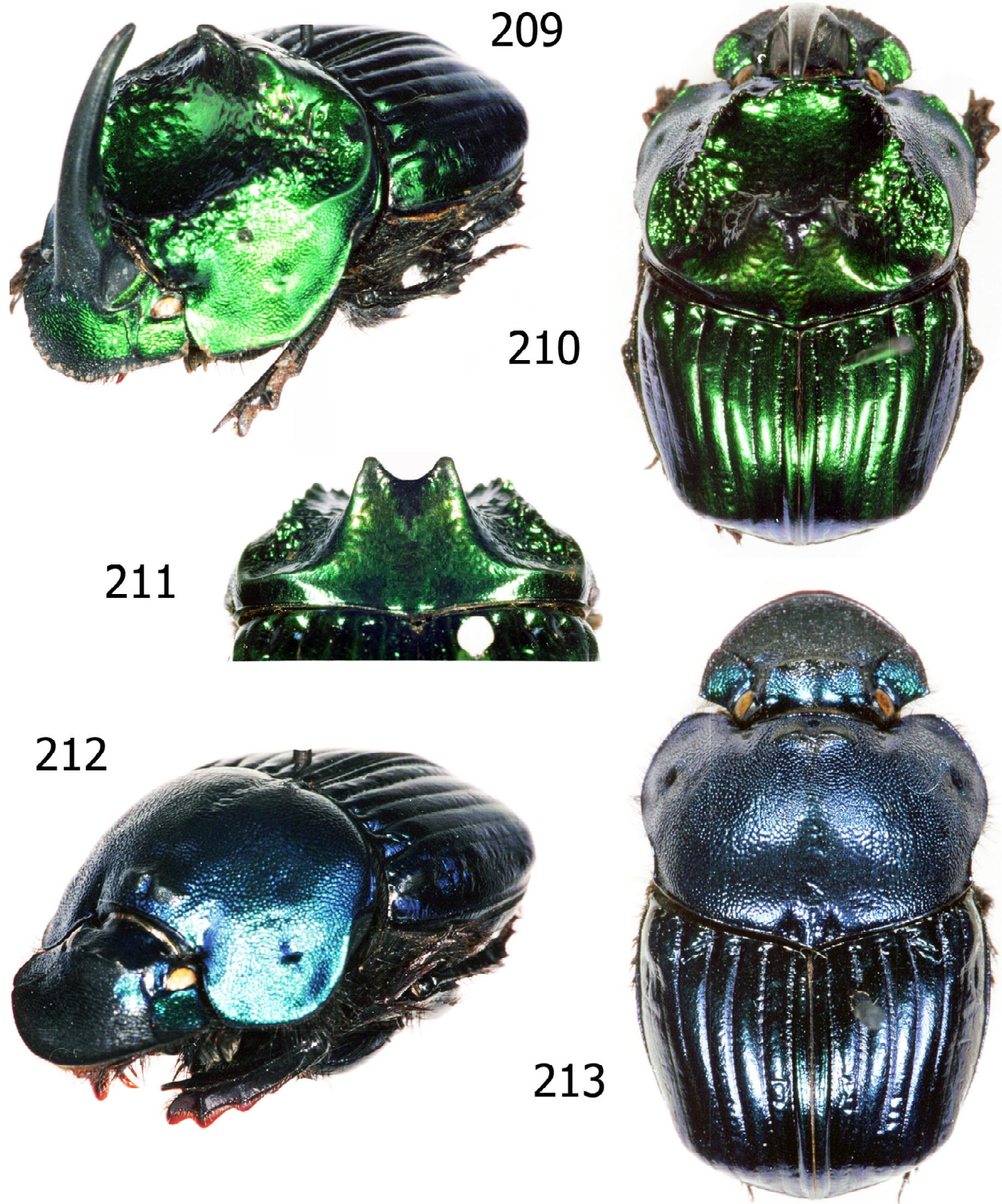


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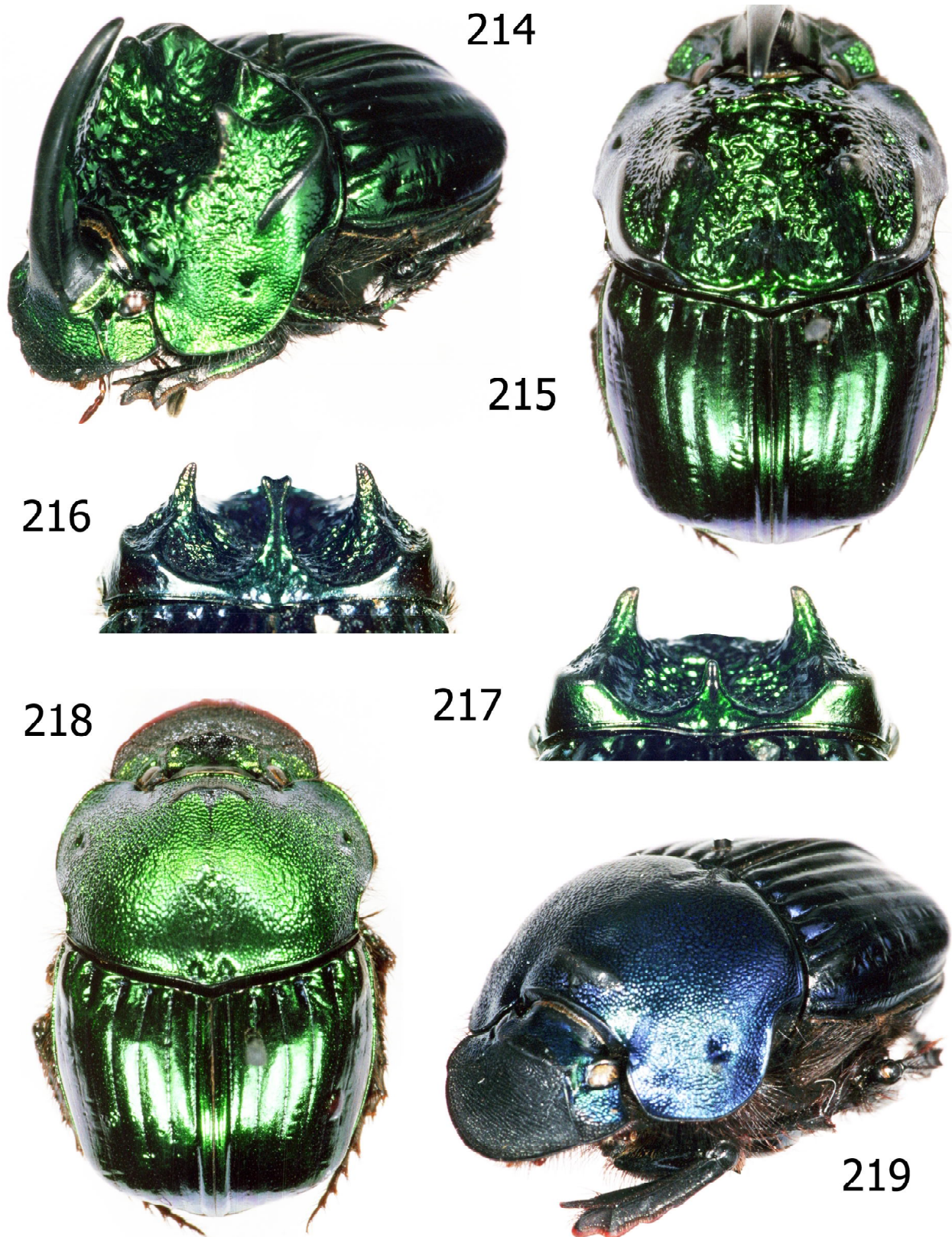
Figures 198–203. *Phanaeus (P.) tridens* Castelnau. 198–199) Male. 200–203) Female.



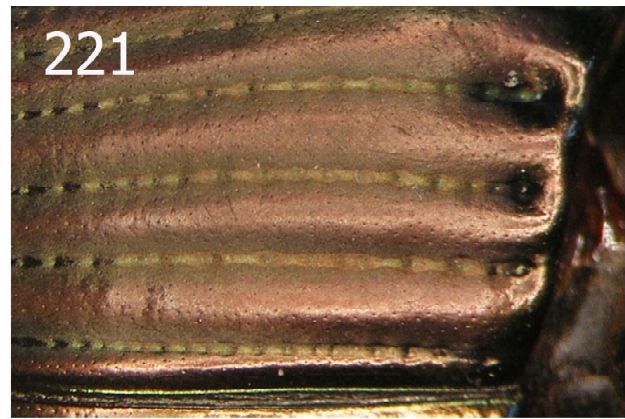
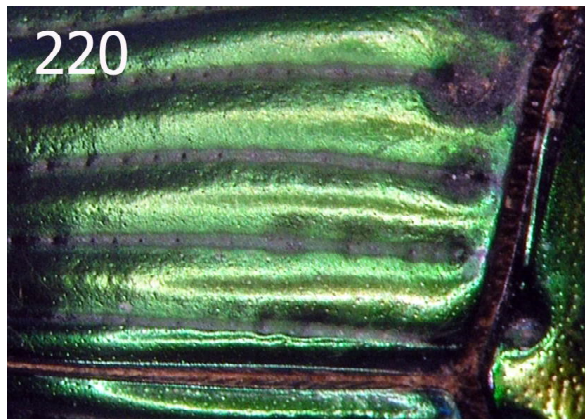
Figures 204–208. *Phanaeus (P.) eximius* Bates. 204–206) Male. 207–208) Female.



Figures 209–213. *Phanaeus (P.) furiosus* Bates. **209–210)** Male. **211)** Same male, basal process of pronotum in posterior view. **212–213)** Female.



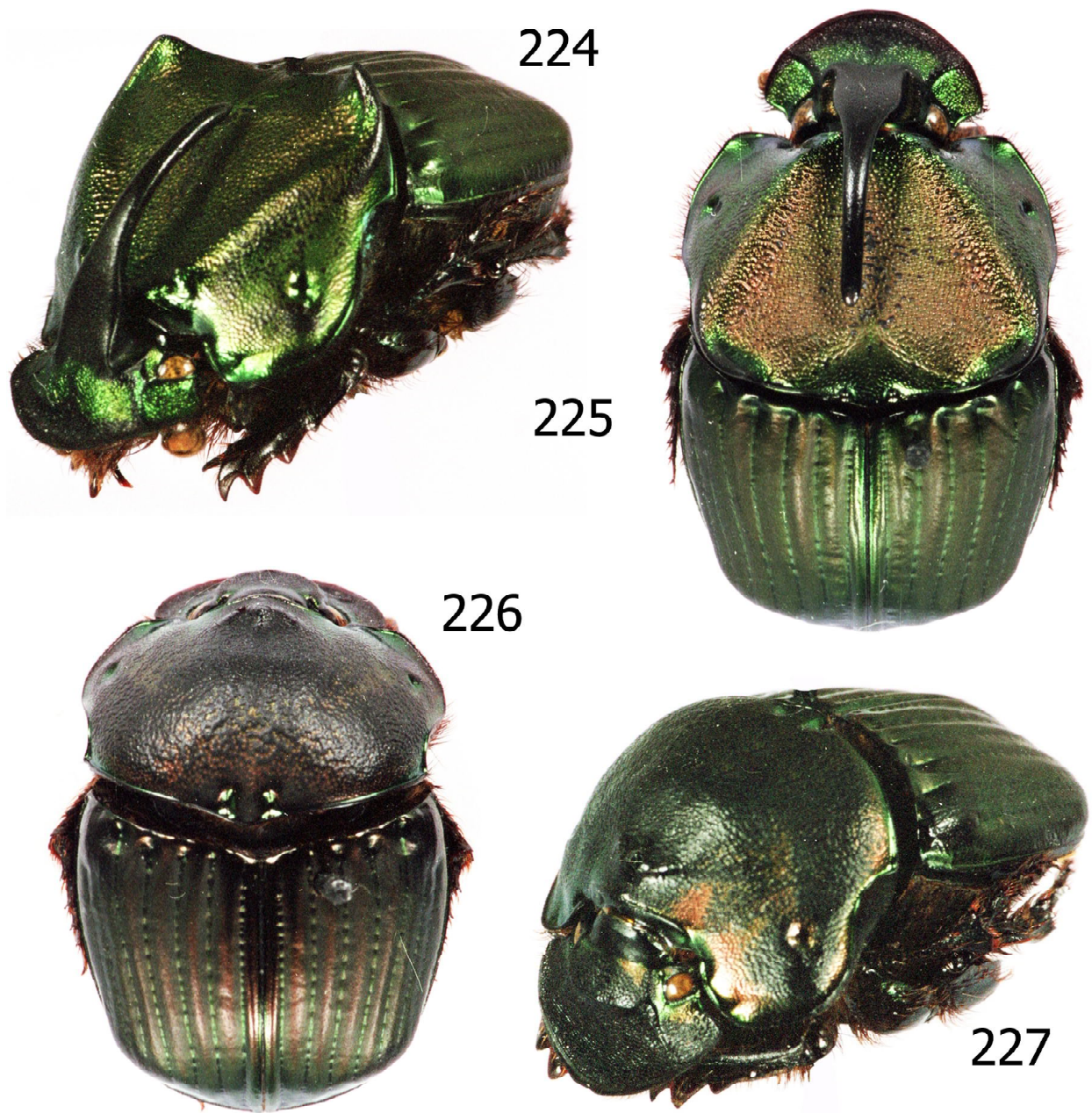
Figures 214–219. *Phanaeus (P.) daphnis* Harold. 214–215) Male. 216–217) Males, basal process of pronotum in posterior view. 218) Female. 219) Female.



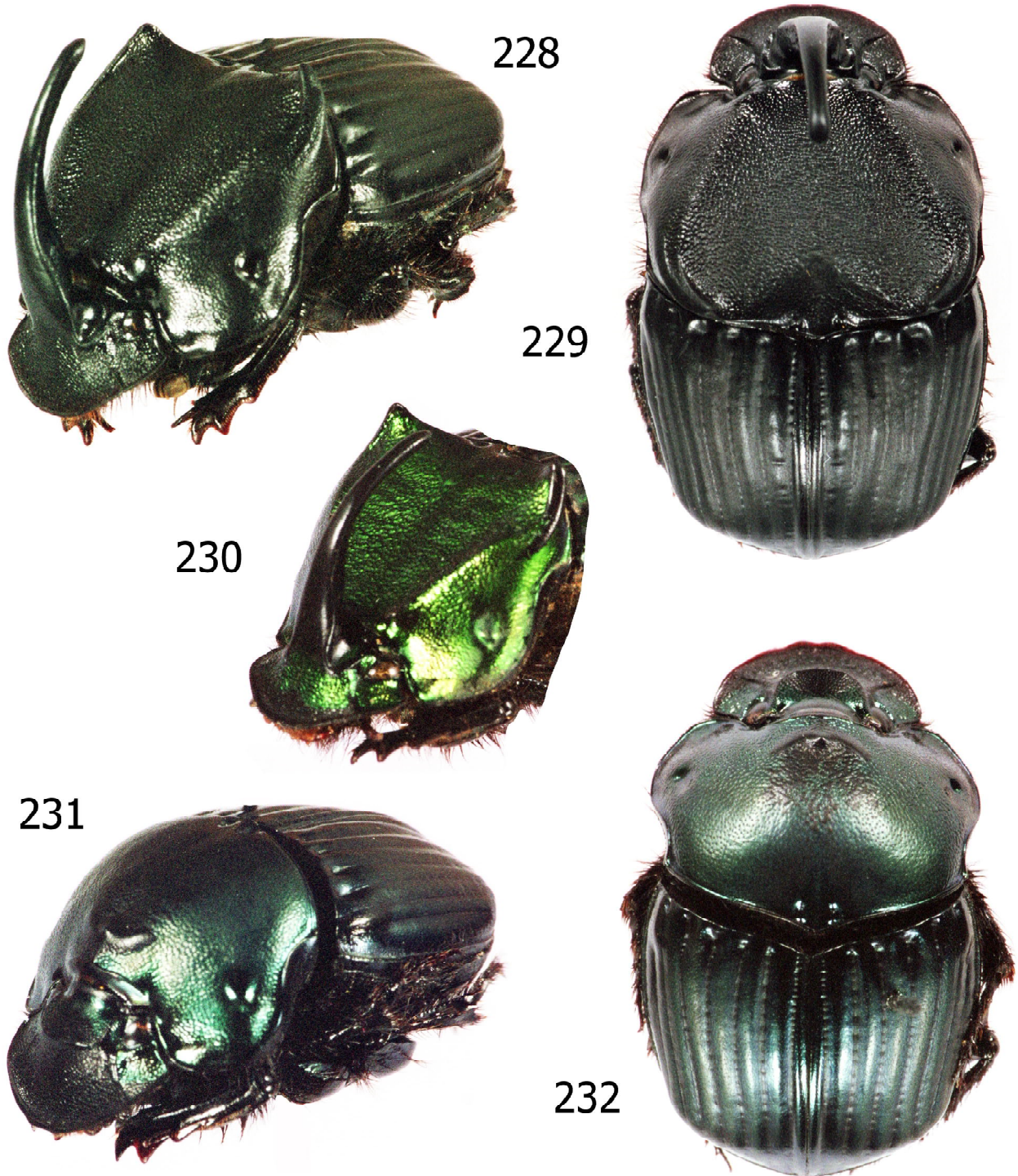
Figures 220–222. Characters of the *Phanaeus* (*P.*) *hermes* species group. *Phanaeus prasinus* Harold, **220**) Elytron. *Phanaeus hermes* Harold. **221**) Elytron. **222**) Female, lateral view of pronotum.



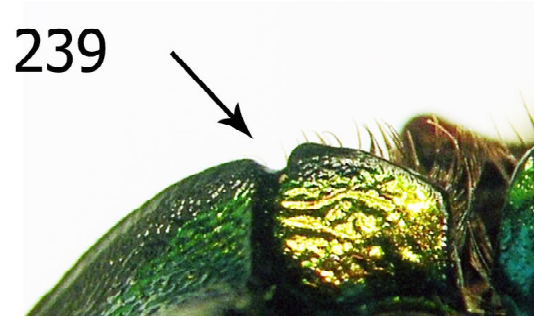
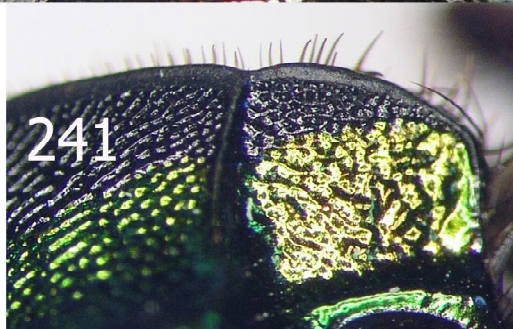
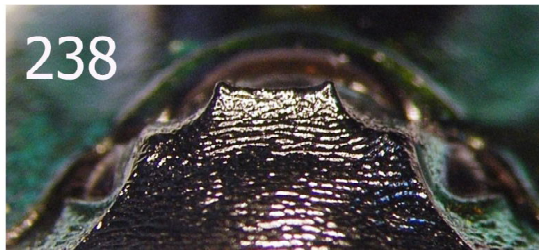
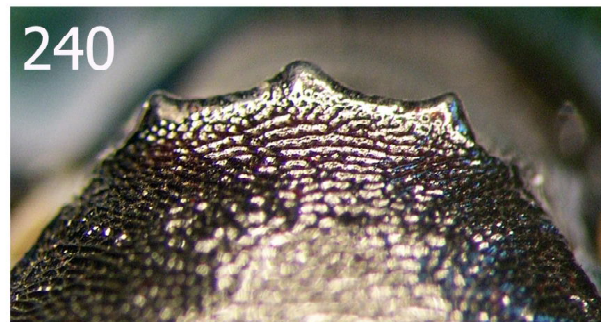
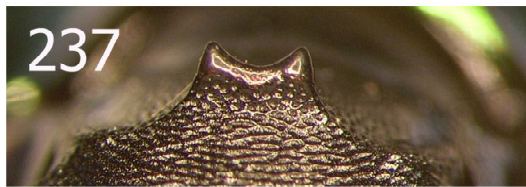
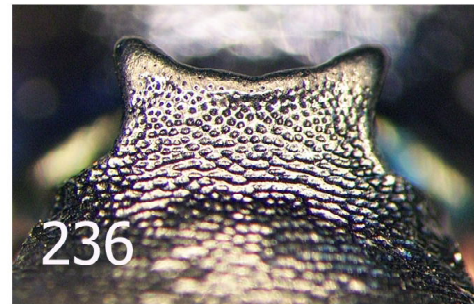
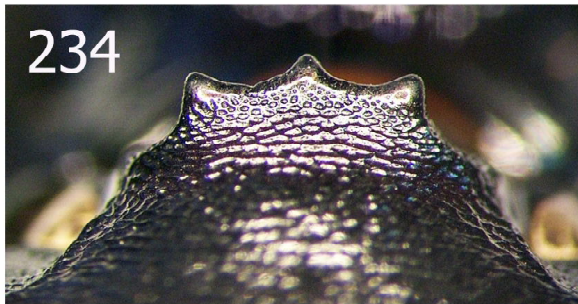
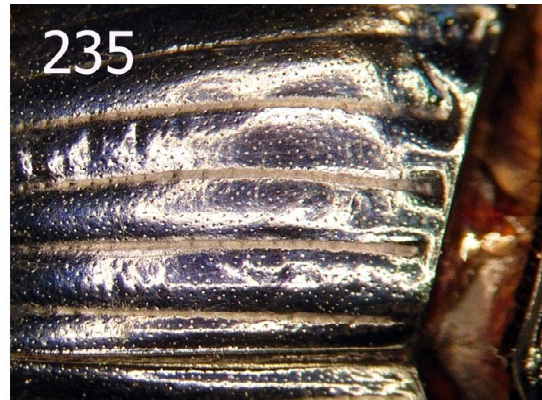
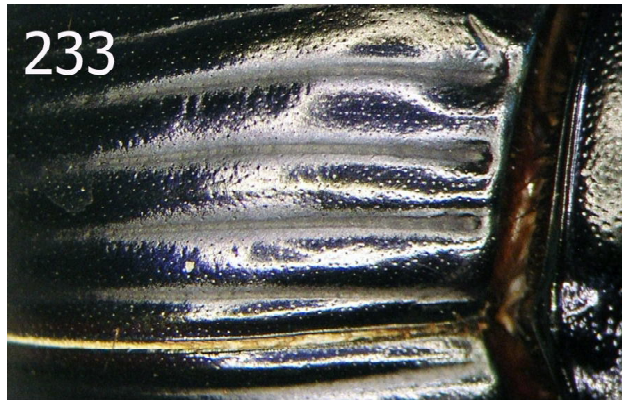
Figure 223. Approximate geographic distributions of the *Phanaeus* (*P.*) *hermes*, *beltianus* and *amethystinus* species groups.



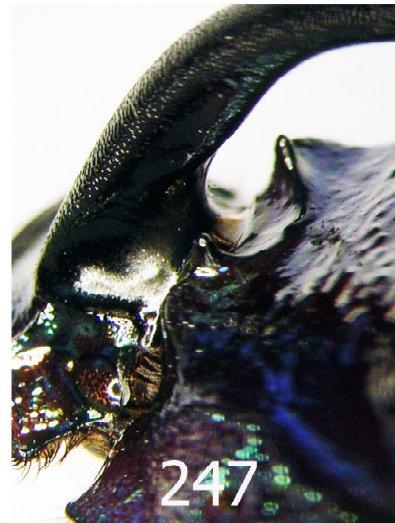
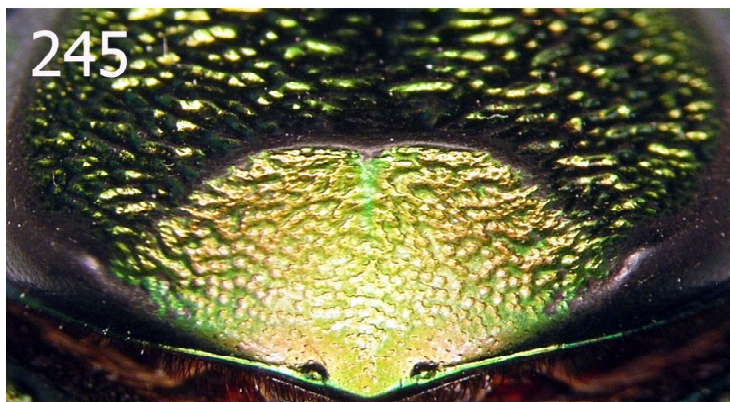
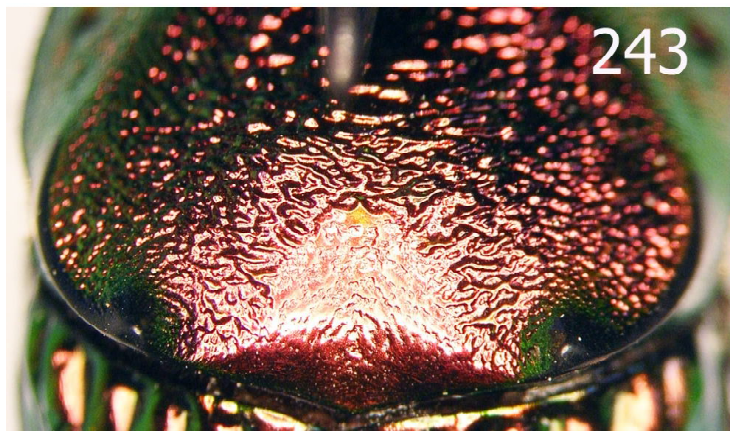
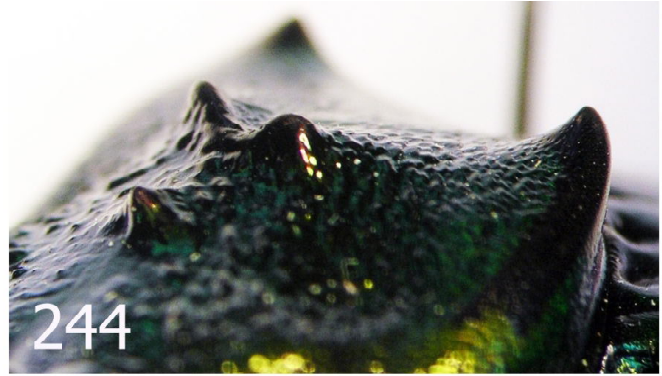
Figures 224–227. *Phanaeus (P.) hermes* Harold. 224–225) Male. 226–227) Female.



Figures 228–232. *Phanaeus (P.) prasinus* Harold. 228–229) Male. 230) Male head and pronotum. 231–232) Female.



Figures 233–241. Characters of the *Phanaeus* (*P.*) *mexicanus* species group. *Phanaeus flohri* Nevinson. **233)** Elytron. **234)** Female cephalic carina. *Phanaeus yecoraensis* Edmonds. **235)** Elytron. **236)** Female cephalic carina. *Phanaeus scutifer* Bates. **237)** Female cephalic carina. *Phanaeus demon* Castelnau. **238)** Female cephalic carina. **239)** Male, lateral portion of head [arrow indicates marginal notch between clypeus and gena]. *Phanaeus mexicanus* Harold. **240)** Female cephalic carina. **241)** Male, lateral portion of head.



Figures 242–247. Characters of the *Phanaeus* (*P.*) *mexicanus* species group. *Phanaeus amithaon* Harold. **242)** Male pronotum. *Phanaeus wagneri* Harold. **243)** Male pronotum. *Phanaeus lunaris* Taschenberg. **245)** Male pronotum. *Phanaeus excelsus* Bates. **246)** Posterolateral process of male pronotum. **247)** Anterior margin of male pronotum. *Phanaeus mexicanus* Harold. **244)** Male pronotum.

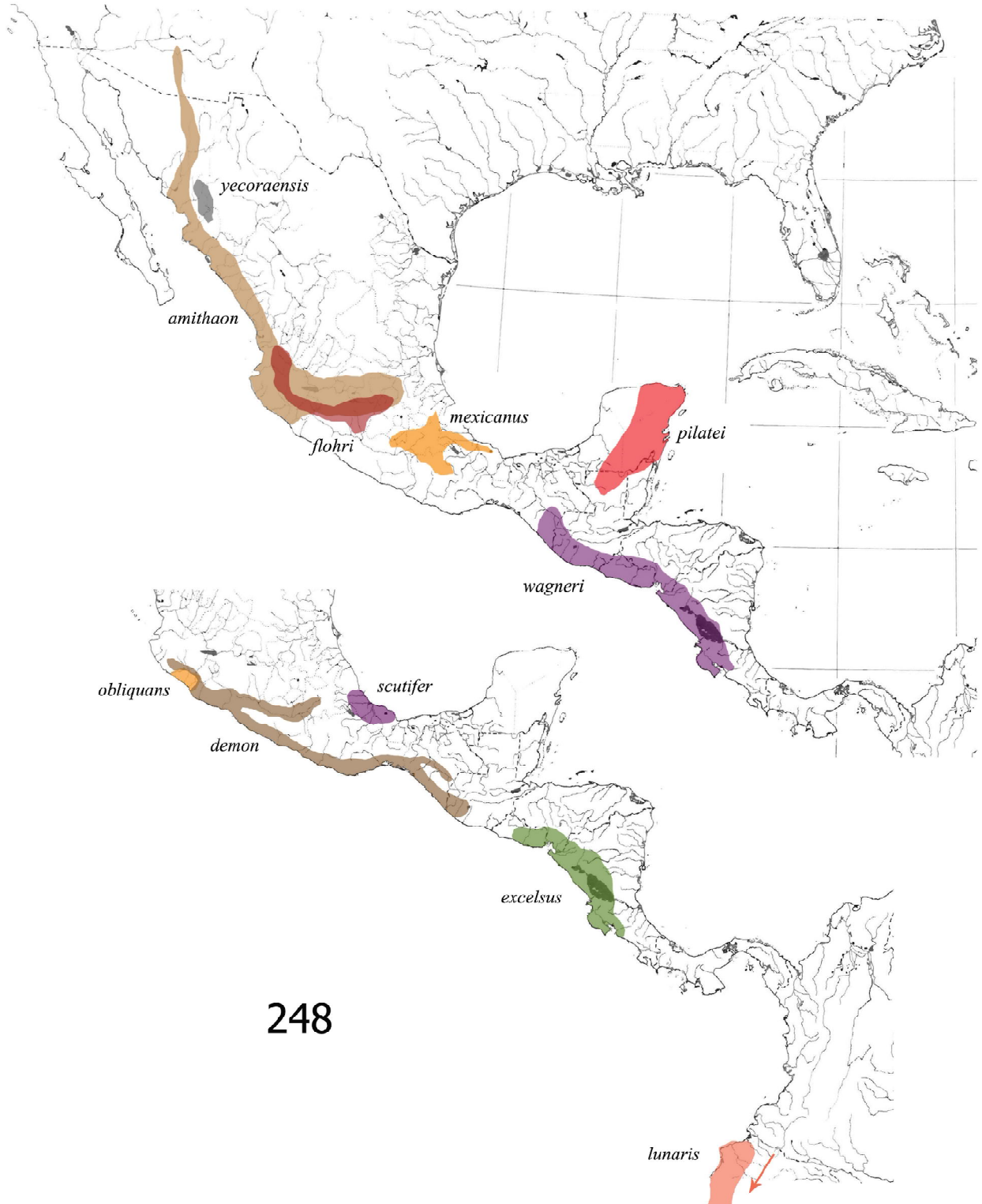
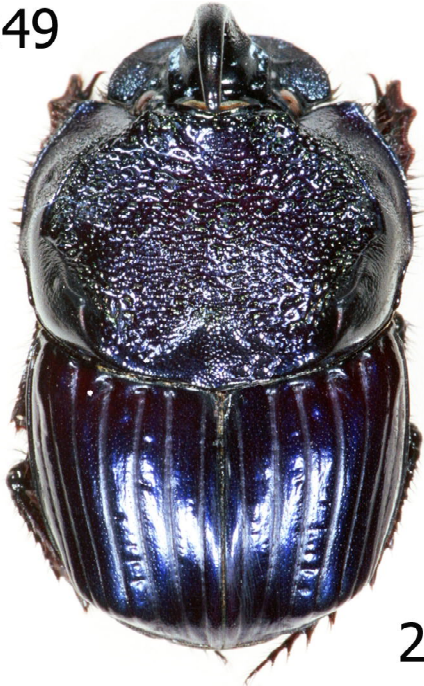


Figure 248. Approximate geographic distribution of the *Phanaeus (P.) mexicanus* species group.

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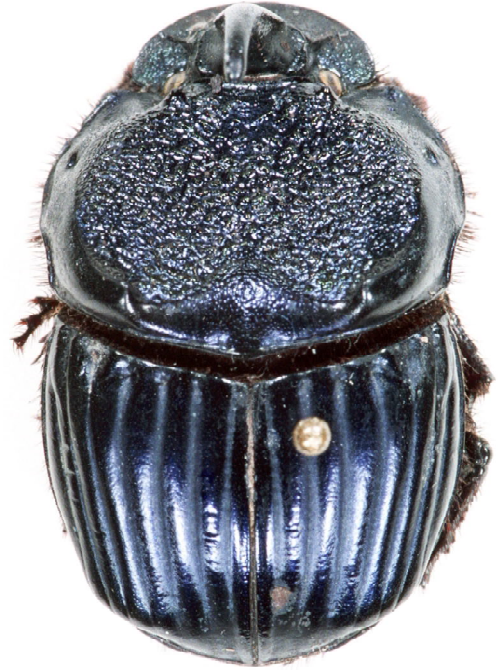


Figures 249–253. *Phanaeus* (*P.*) *yecoraensis* Edmonds. 249–251) Male. 252–253) Female.

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Figures 254–258. *Phanaeus (P.) flohri* Nevinson. 254–256) Male. 257–258) Female.



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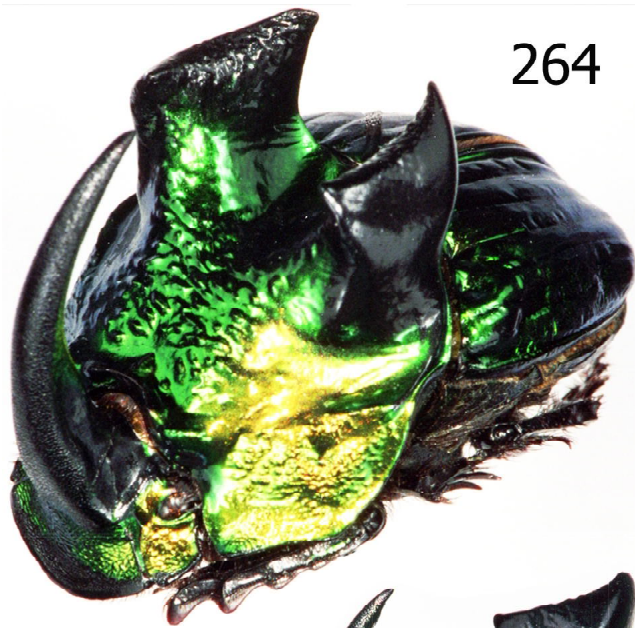


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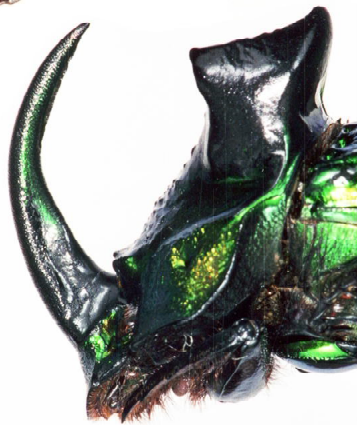
Figures 259–263. *Phanaeus* (*P.*) *excelsus* Bates. 259–260) Male. 261–263) Female.



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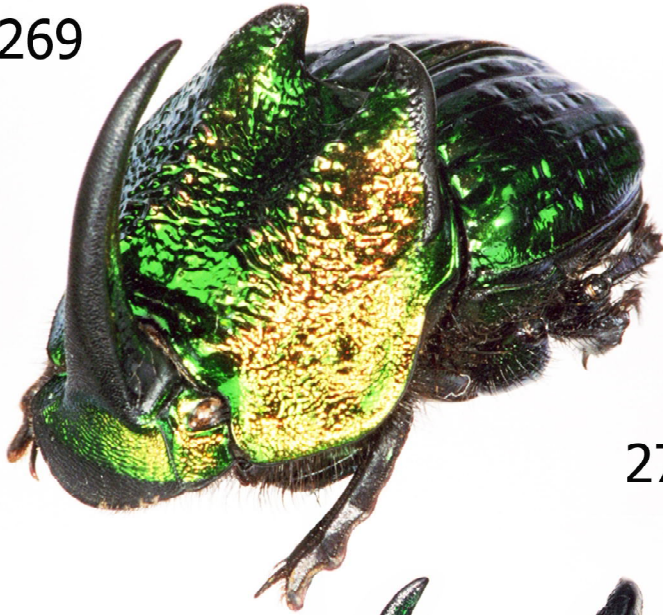
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Figures 264–268. *Phanaeus (P.) demon* Castelnau. 264–266) Male. 267–268) Female.

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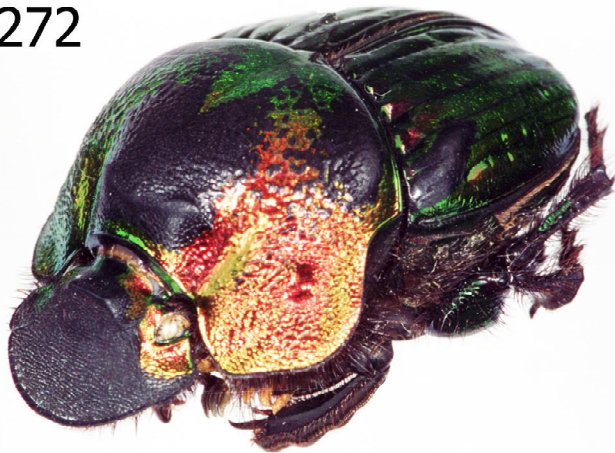
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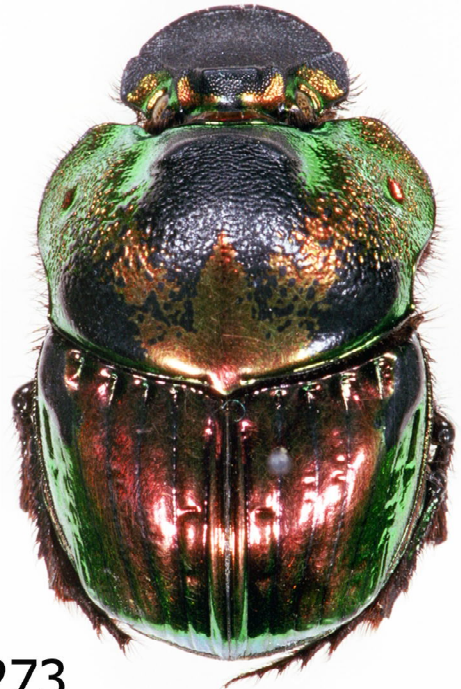
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Figures 269–273. *Phanaeus (P.) obliquans* Bates. 269–271) Male. 272–273) Female.



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Figures 274–277. *Phanaeus* (*P.*) *scutifer* Bates. 274–275) Male. 276–277) Female.



Figures 278–281. *Phanaeus (P.) lunaris* Taschenberg. 278–279) Male. 280–281) Female.



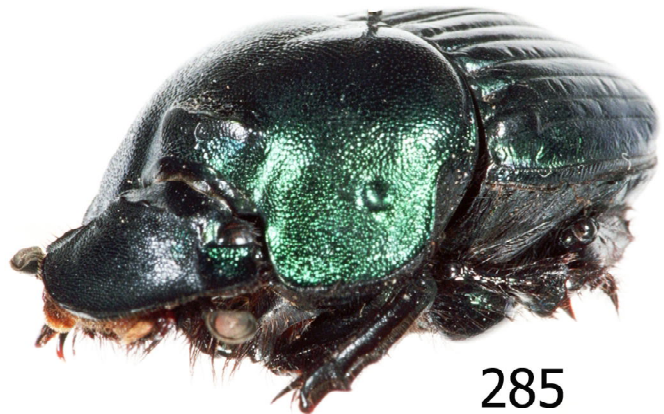
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Figures 282–285. *Phanaeus (P.) pilatei* Harold. 282–283) Male. 284–285) Female.



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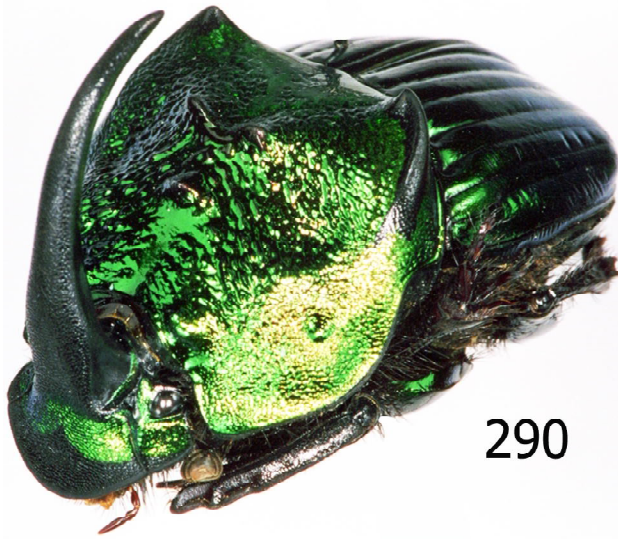


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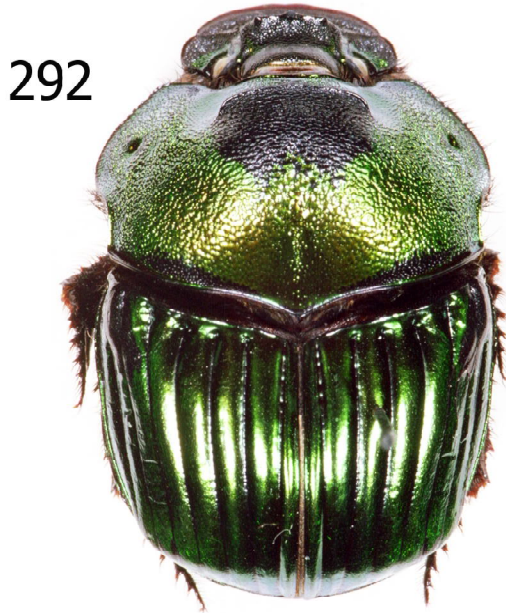
Figures 286–289. *Phanaeus (P) wagneri* Harold. 286–287) Male. 288–289) Female.



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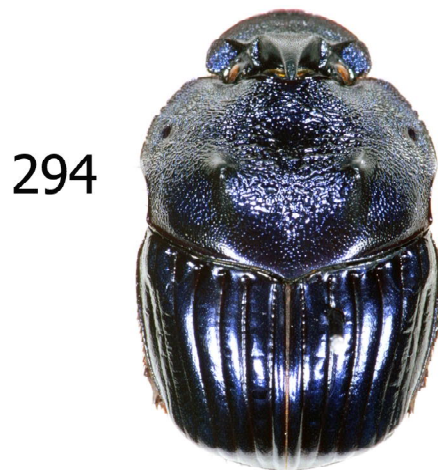
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Figures 290–295. *Phanaeus (P.) mexicanus* Harold. 290–291) Male. 292–293) Female. 294–295) Male.



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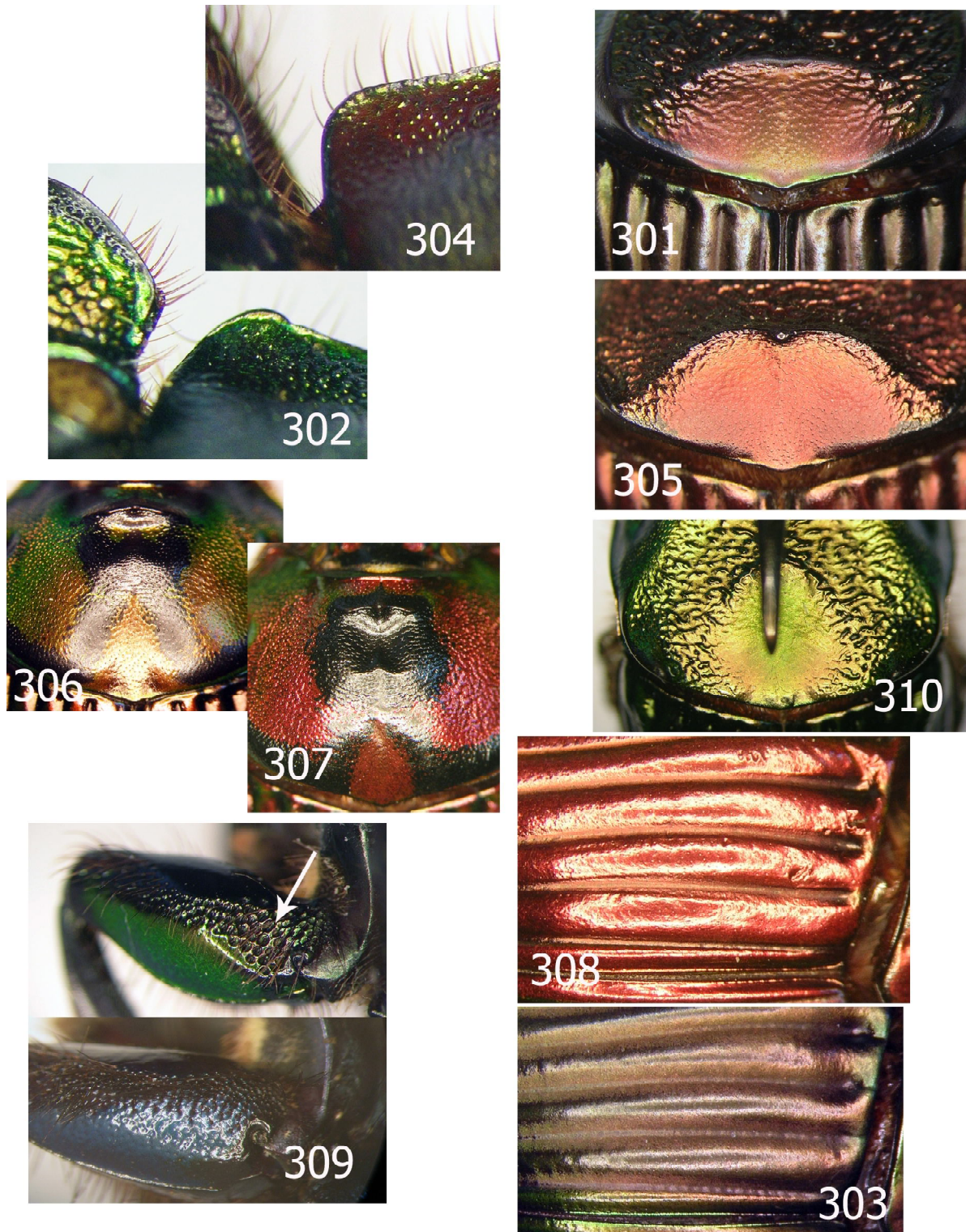


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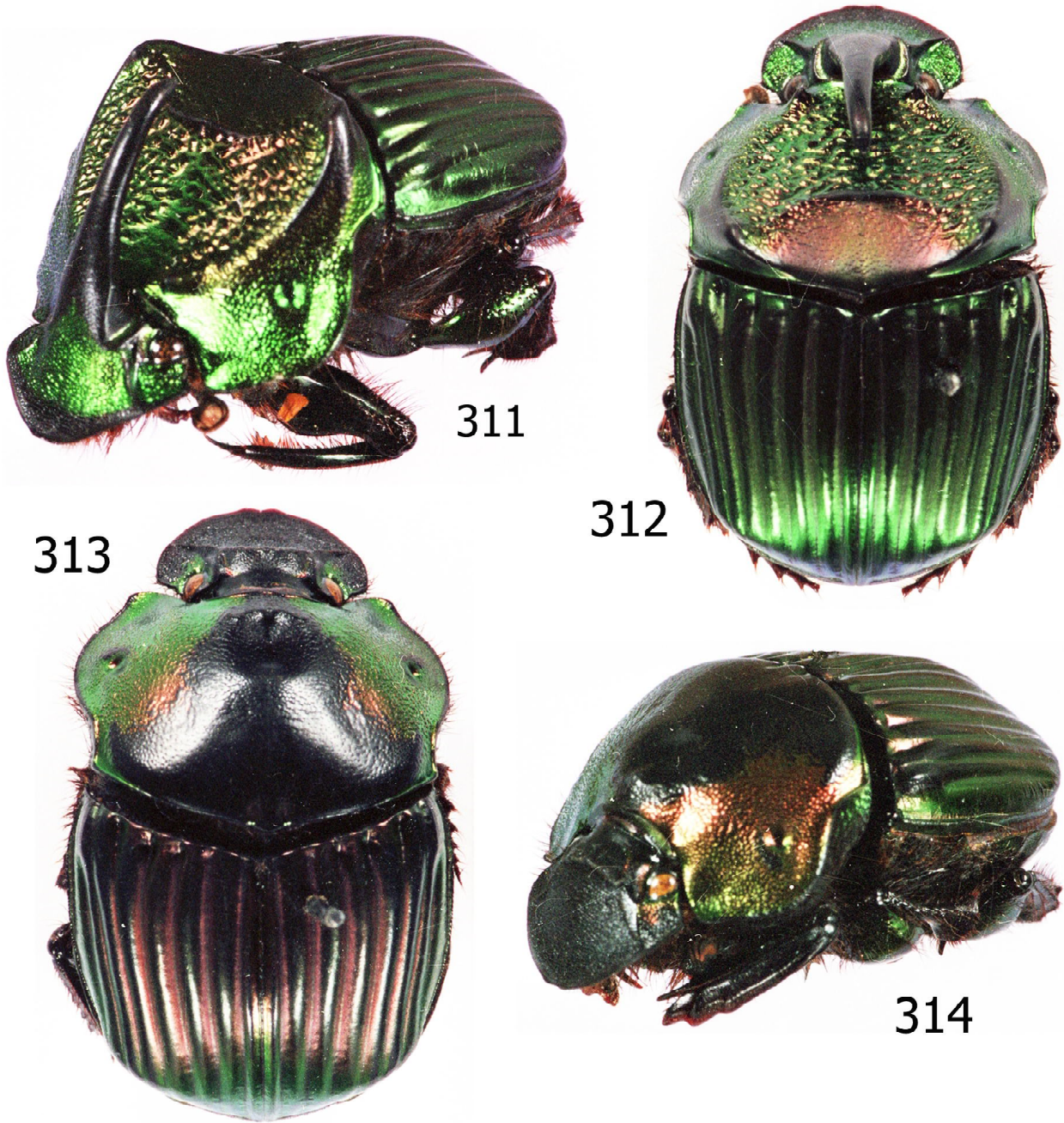


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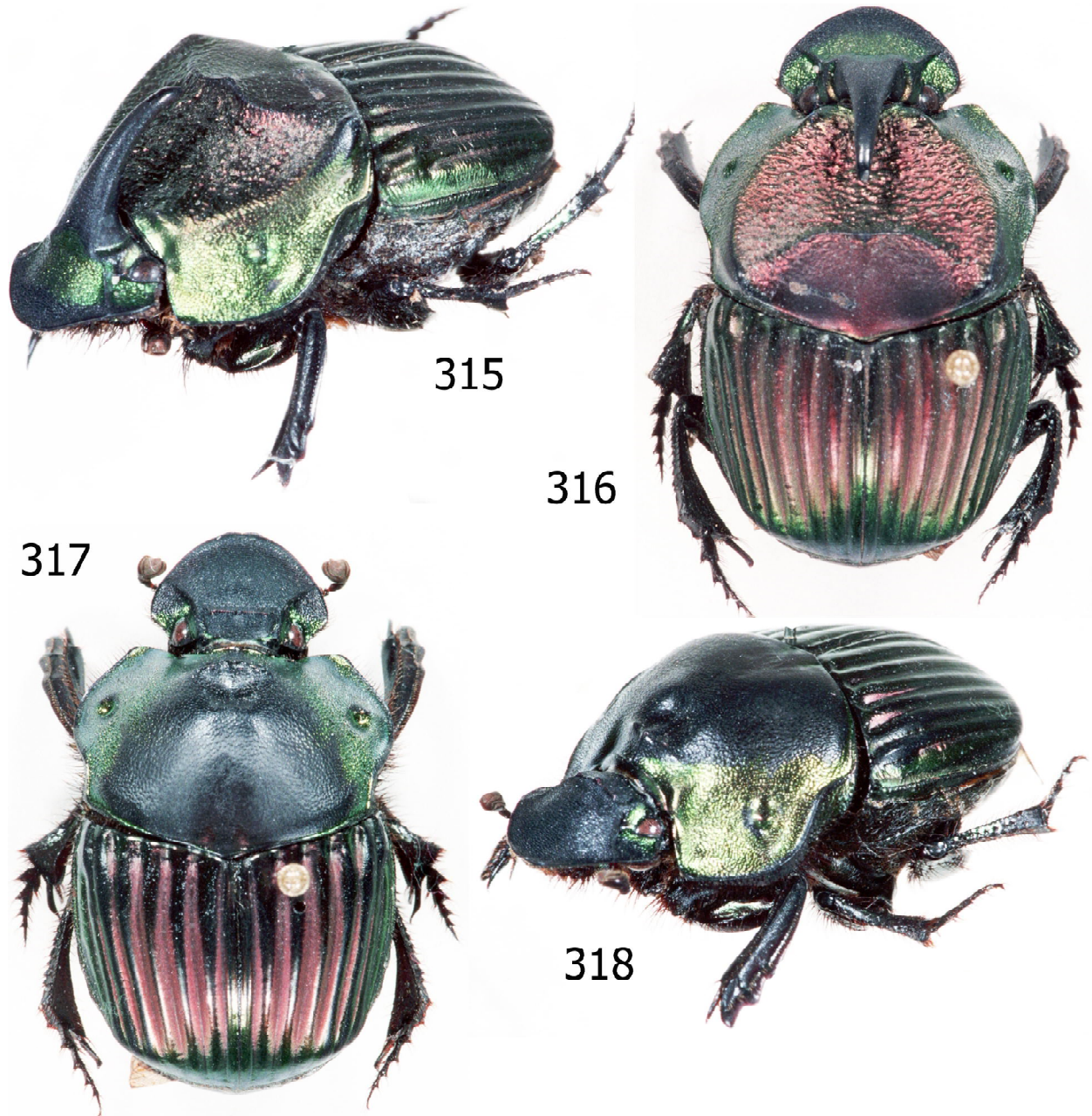
Figures 296–300. *Phanaeus* (*P.*) *amithaon* Harold. 296–297) Male. 298–299) Female. 300) Male.



Figures 301–310. Characters of the *Phanaeus* (*P.*) *beltianus* species group. *Phanaeus beltianus* Bates. **301)** Male, base of pronotum and elytra. **302)** Anterolateral angle of male pronotum. **303)** Elytron. *Phanaeus changdiazi* Kohlmann and Solís. **304)** Anterolateral angle of male pronotum. **305)** Male, base of pronotum and elytra. **306)** Female pronotum. *Phanaeus sallei* Harold. **307)** Female pronotum. **308)** Elytron. **309)** Female profemur [arrow indicates field of coarse punctures; lower image is corresponding view of *P. amethystinus* Harold]. *Phanaeus howdeni* Arnaud. **310)** Male pronotum.



Figures 311–314. *Phanaeus (P.) beltianus* Bates. 311–312) Male. 313–314) Female.



Figures 315–318. *Phanaeus (P.) changdiazi* Kohlmann and Solís. 315–316) Male. 317–318) Female.



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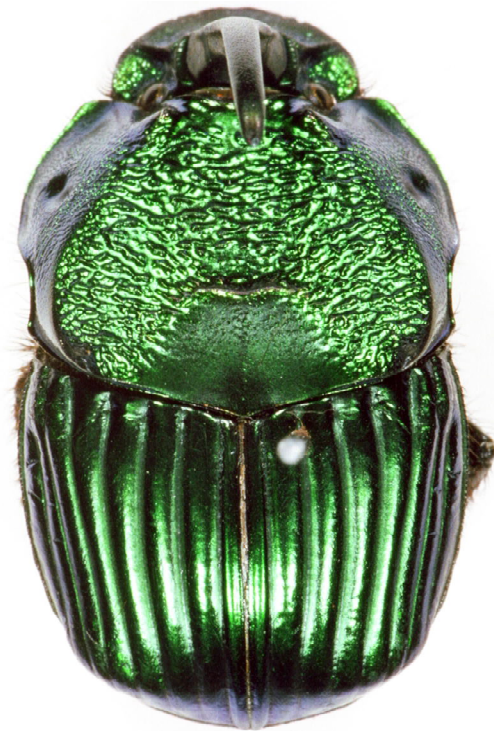


322

Figures 319–322. *Phanaeus* (*P.*) *howdeni* Arnaud. 319–320) Male. 321–322) Female.



323



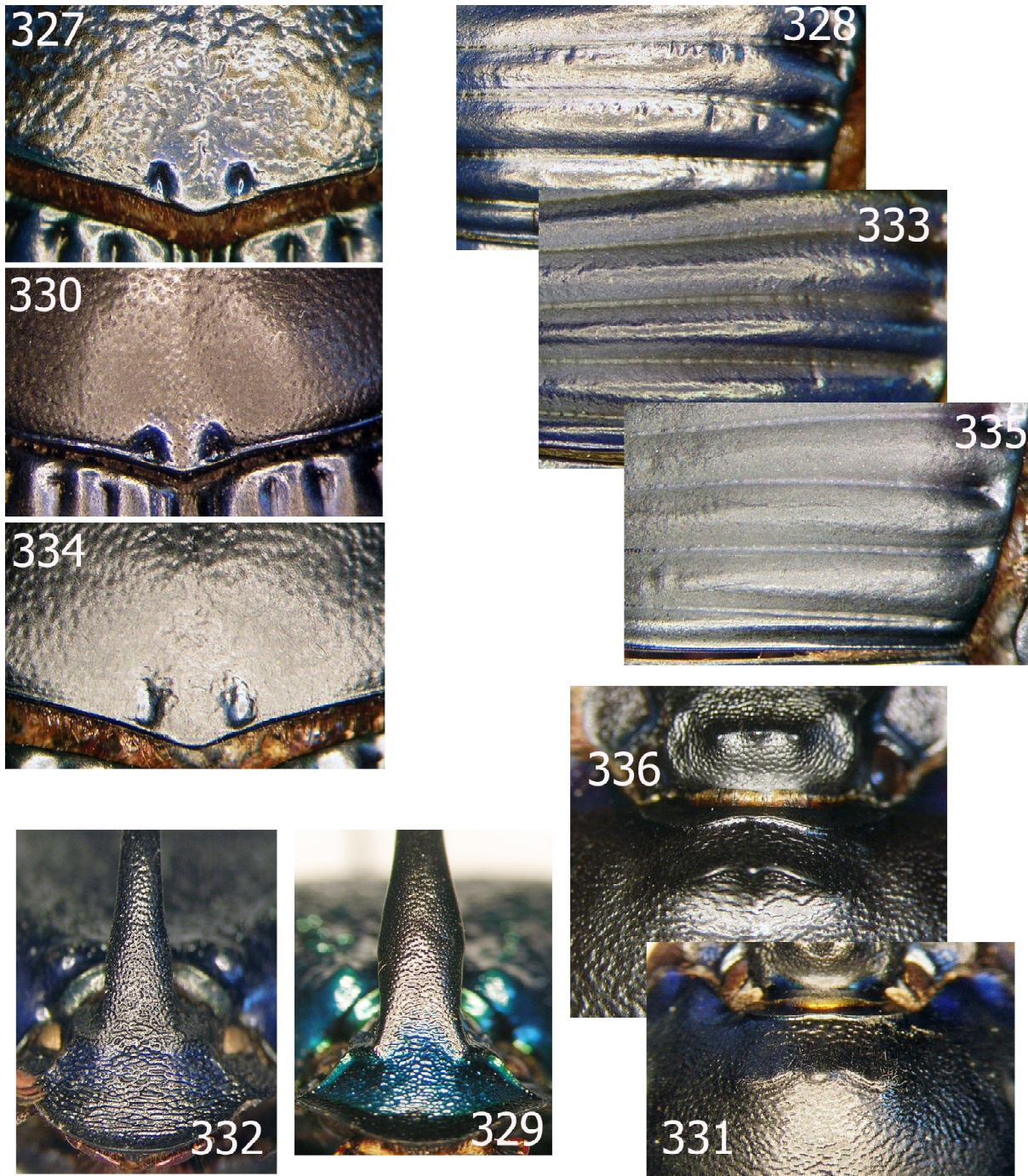
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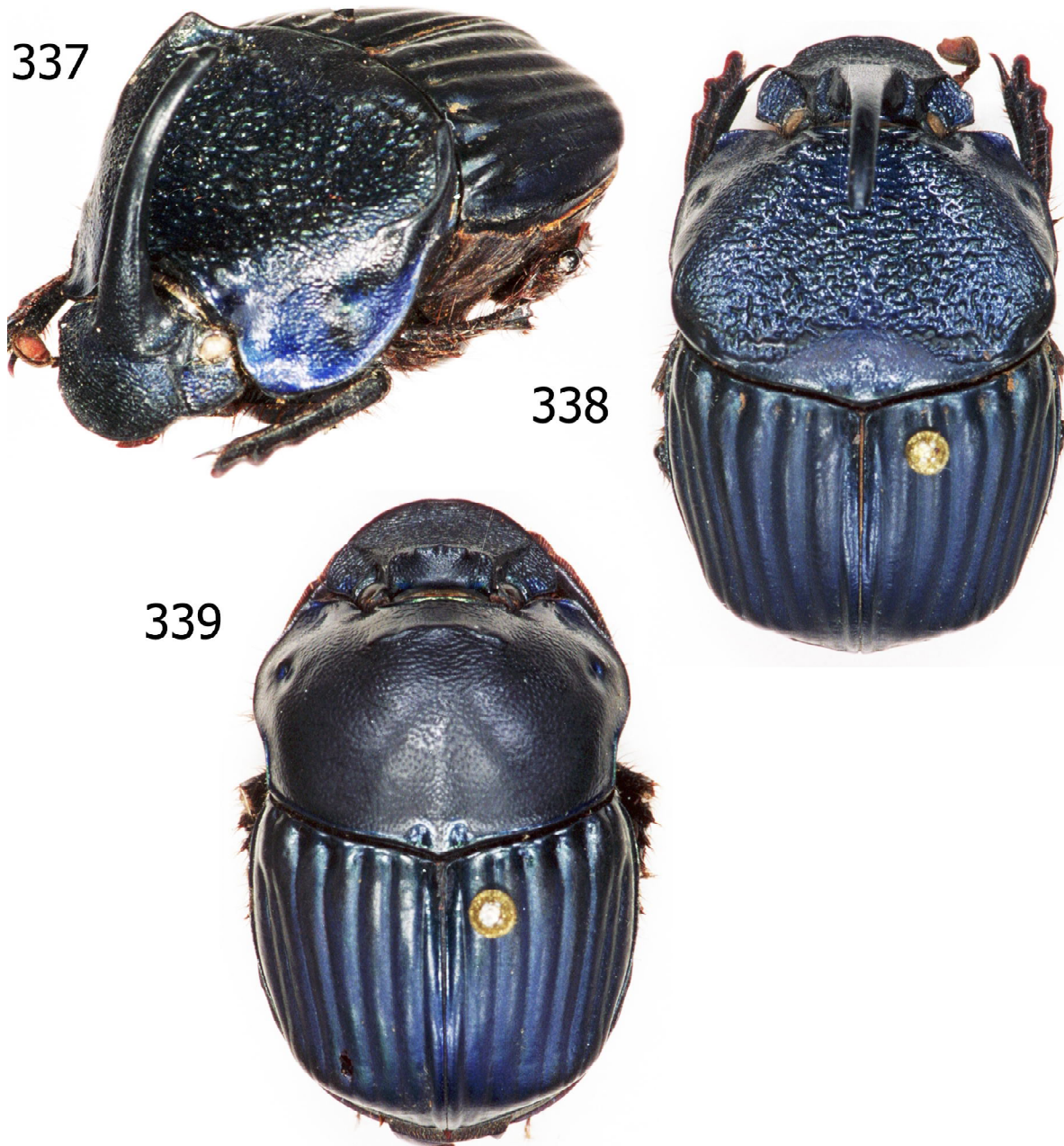


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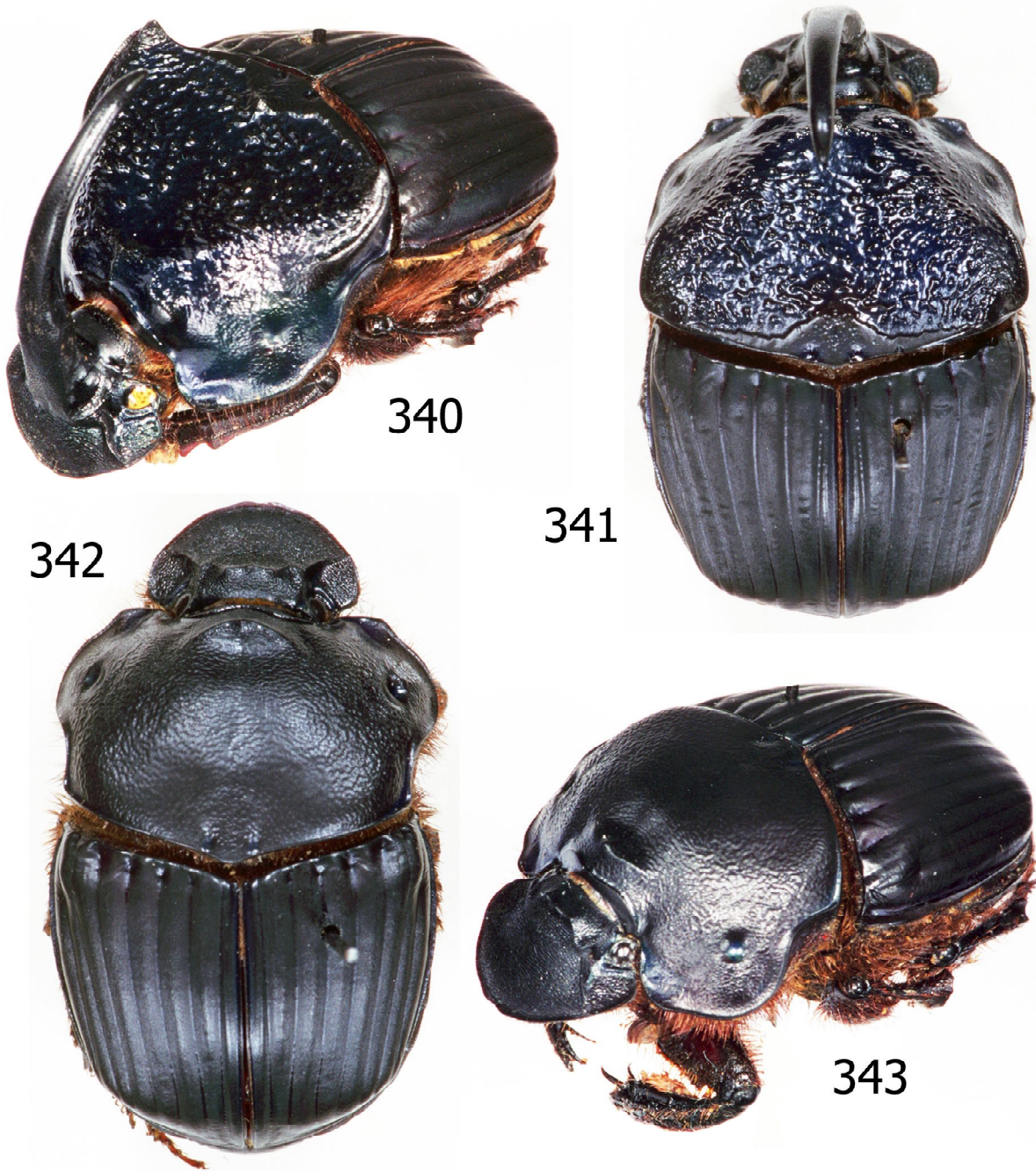
Figures 323–326. *Phanaeus* (*P.*) *sallei* Harold. 323–324) Male. 325–326) Female, coppery red phase.



Figures 327–336. Characters of the *Phanaeus* (*P.*) *amethystinus* species group. *Phanaeus amethystinus* Harold. **327)** Female, base of pronotum. **328)** Elytron. **329)** Male, frontal view of head. *Phanaeus blackalleri* Delgado-Castillo. **330)** Female, base of pronotum. **331)** Female, anterior portion of pronotum. **332)** Male, frontal view of head. *Phanaeus guatemalensis* Harold. **333)** Elytron. *Phanaeus melampus* Harold. **334)** Female, base of pronotum. **335)** Elytron. **336)** Female, anterior portion of pronotum.



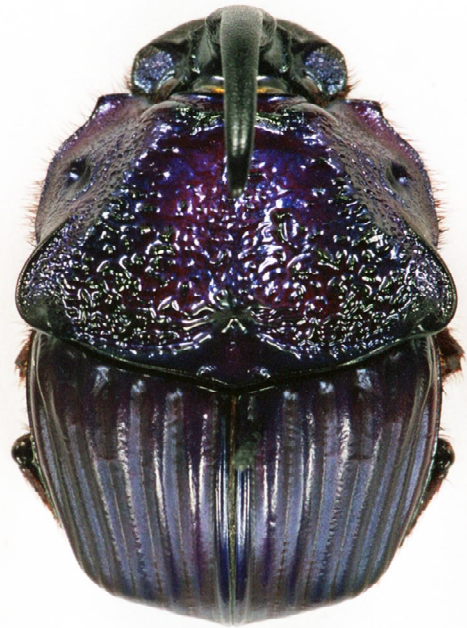
Figures 337–339. *Phanaeus (P.) blackalleri* Delgado-Castillo. 337–338) Male. 339) Female.



Figures 340–343. *Phanaeus (P.) melampus* Harold. 340–341) Male. 342–343) Female.



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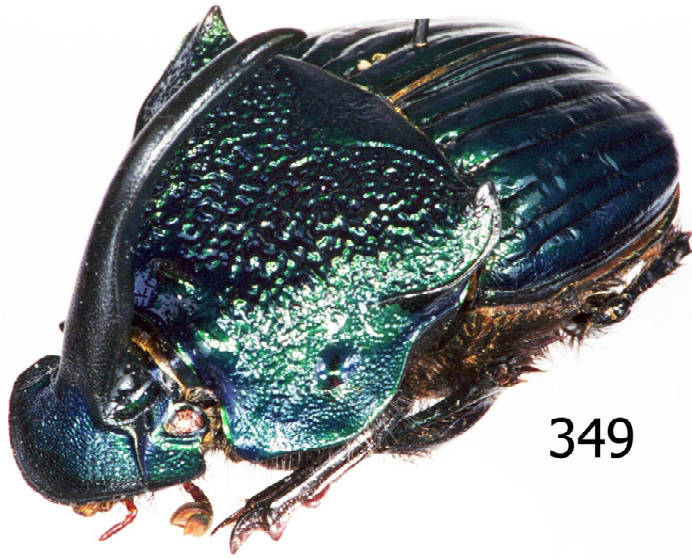


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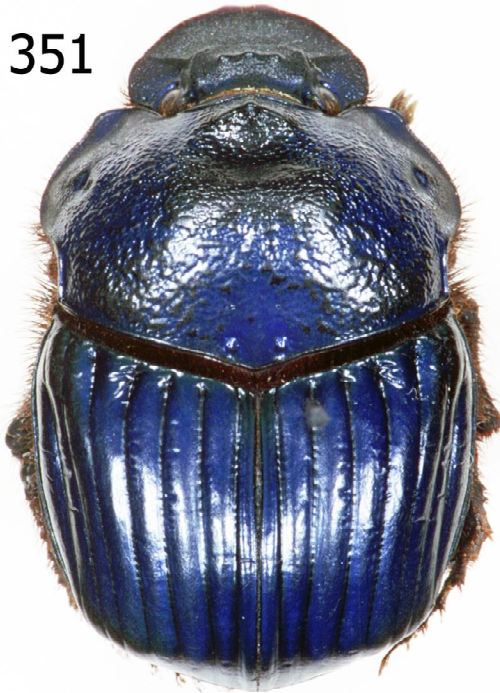
Figures 344–348. *Phanaeus* (*P.*) *guatemalensis* Harold. 344–345) Male. 346) Male (“tepanensis” form). 347–348) Female.



349



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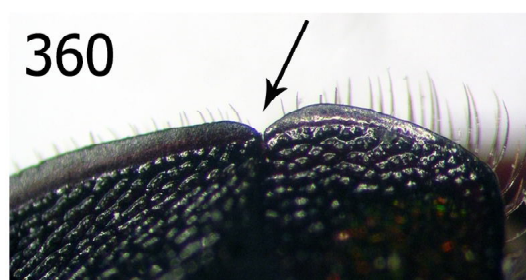
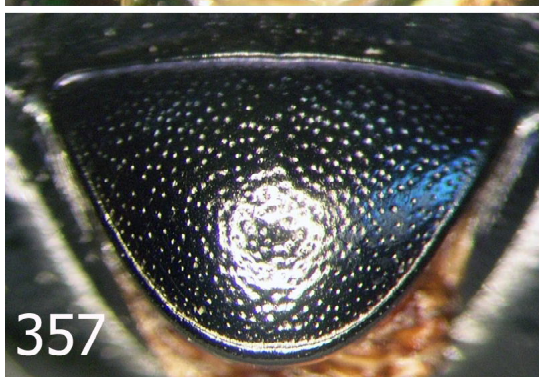
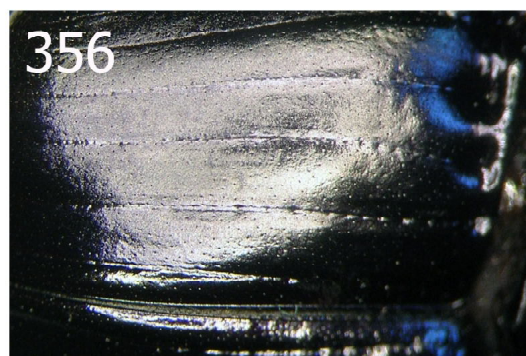
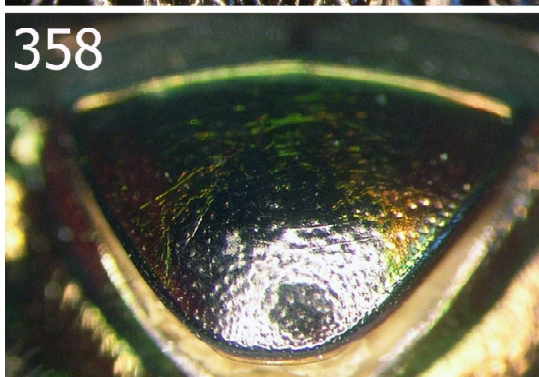
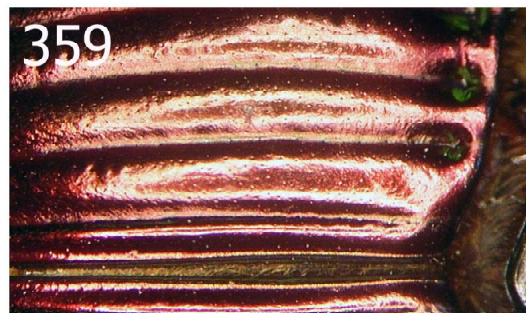
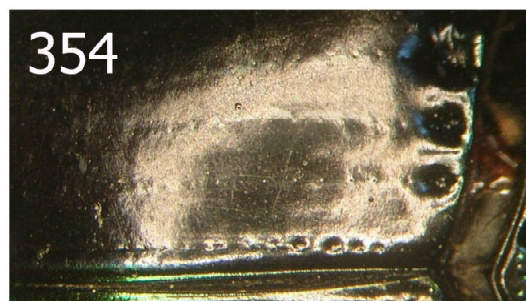
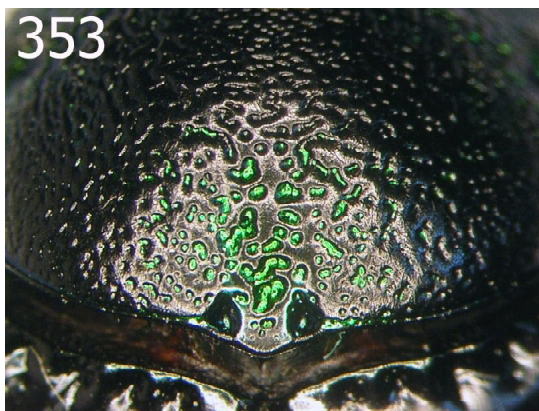


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Figures 349–352. *Phanaeus (P.) amethystinus* Harold. 349–350) Male. 351–352) Female.



Figures 353–360. Characters of the *Phanaeus* (*P.*) *quadridens* species group. *Phanaeus damocles* Harold. **353)** Female, base of pronotum. **354)** Elytron. *Phanaeus quadridens* (Say). **355)** Female, base of pronotum. **356)** Elytron. **357)** Pygidium. *Phanaeus palliatus* Sturm. **358)** Pygidium. **359)** Elytron. **360)** Female, lateral margin of head [arrow indicates notch between clypeus and gena].



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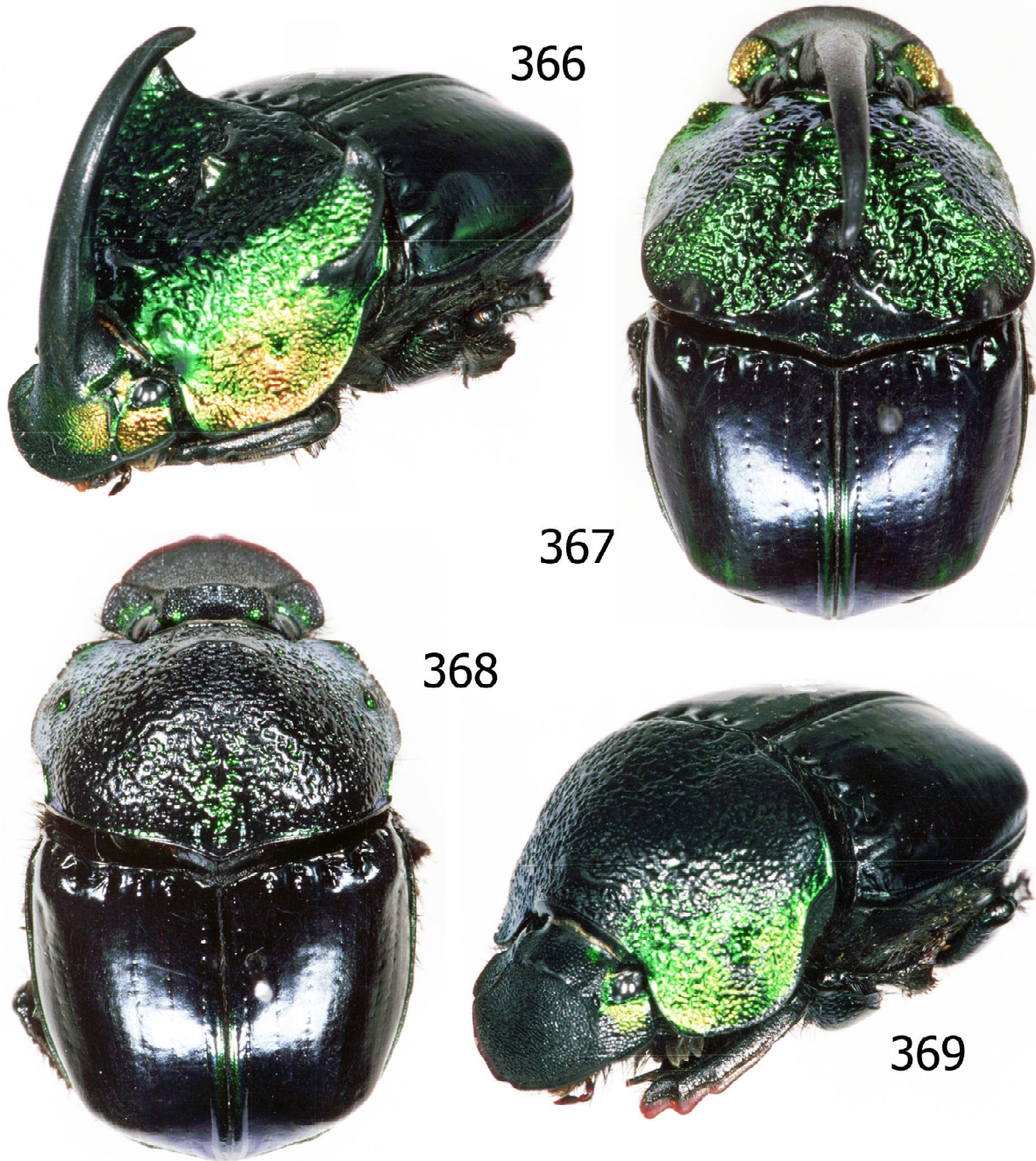


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Figures 361–365. *Phanaeus (P.) palliatus* Sturm. 361–363) Male. 364–365) Female.

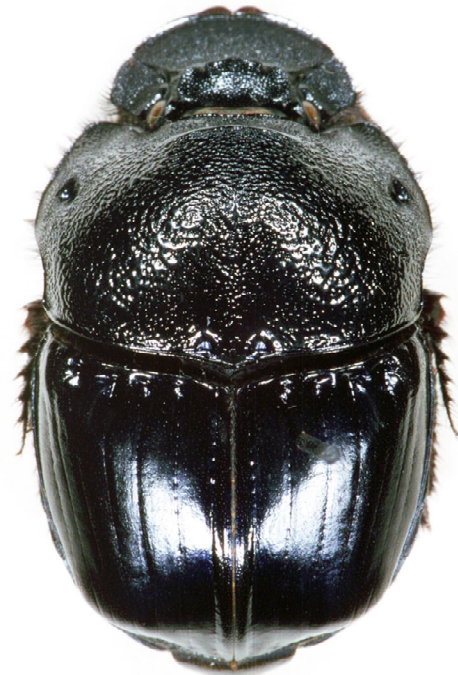
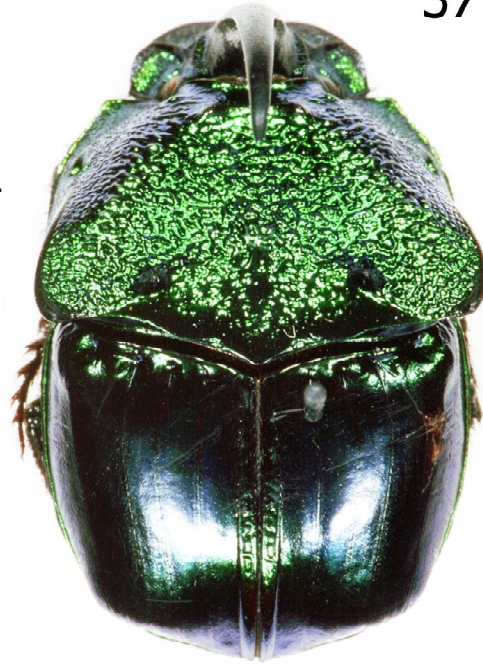


Figures 366–369. *Phanaeus (P.) damocles* Harold. 366–367) Male. 368–369) Female.



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Figures 370–374. *Phanaeus* (*P.*) *quadridens* (Say). 370–372) Male. 373–374) Female.

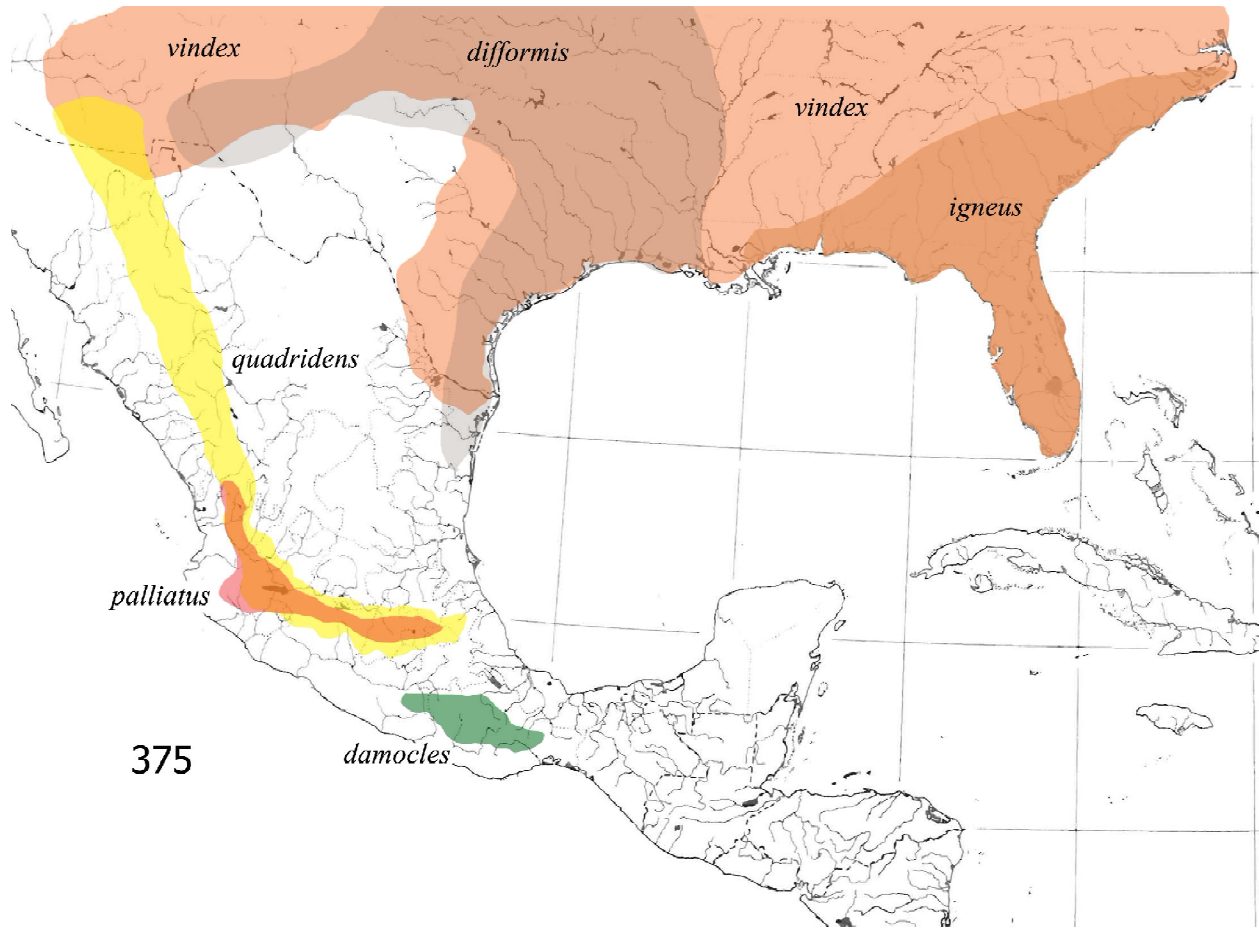
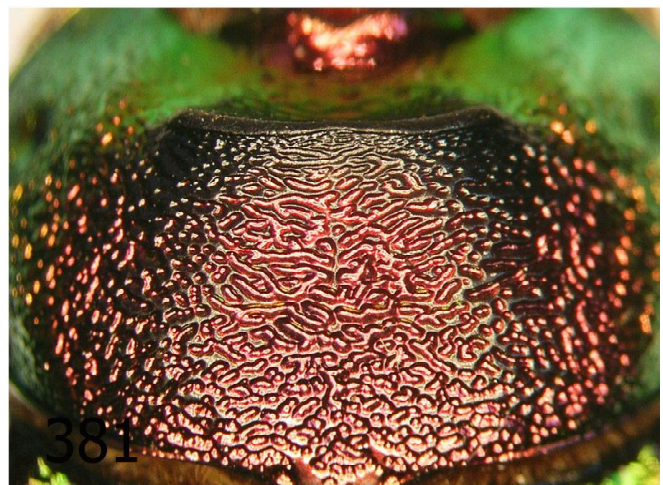
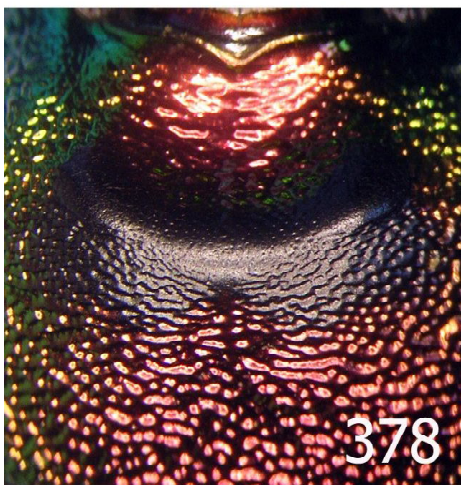
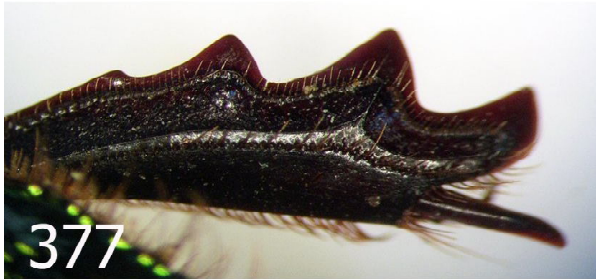
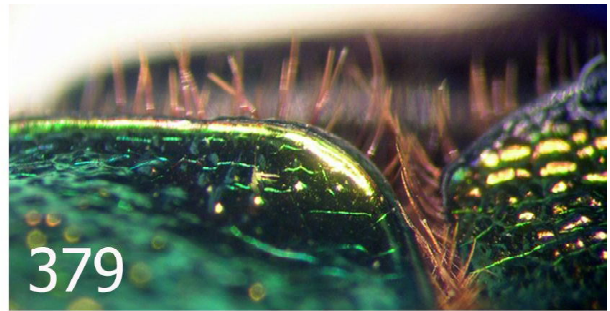
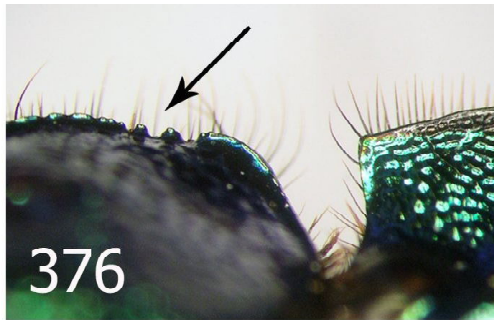
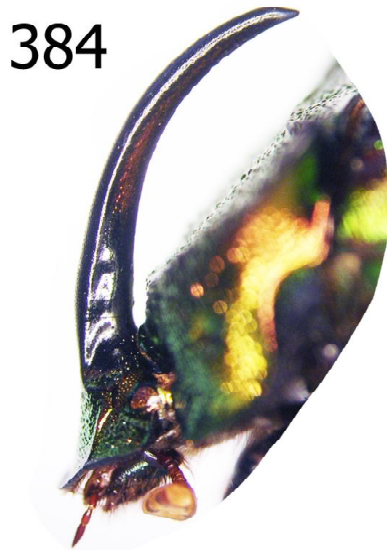
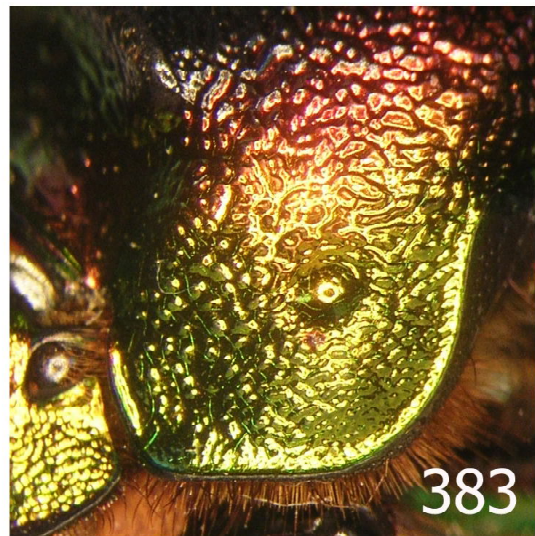
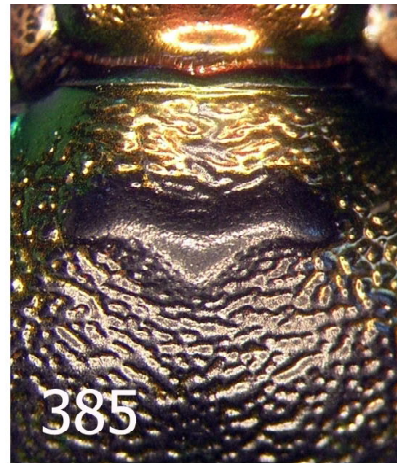


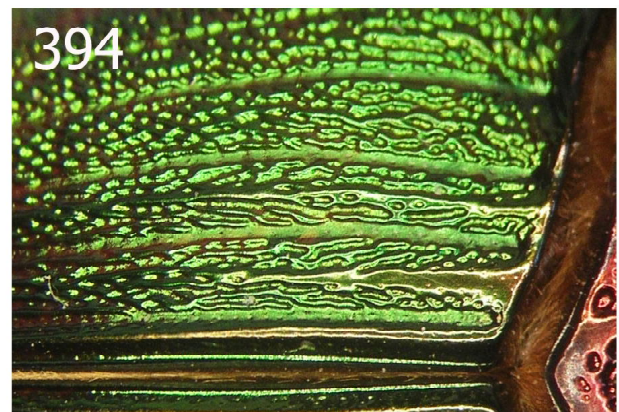
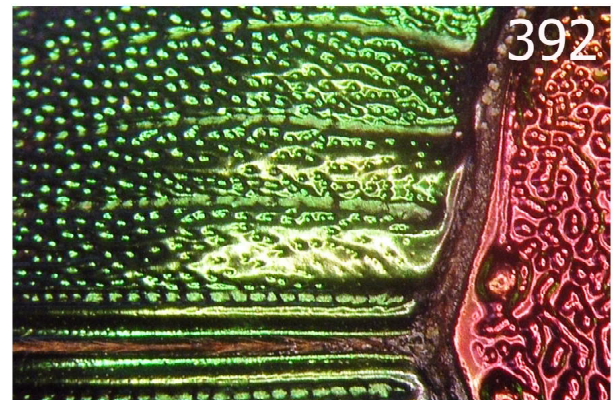
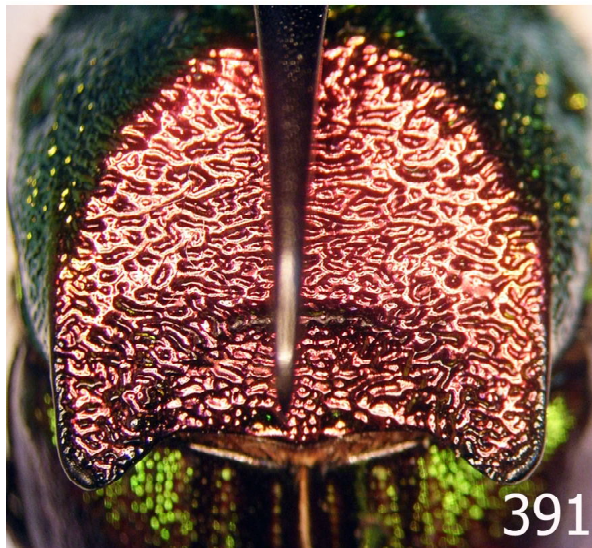
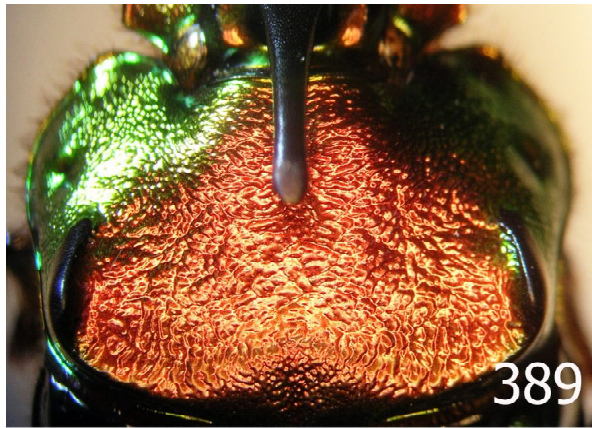
Figure 375. Approximate geographic distributions of the *Phanaeus* (*P.*) *quadridens* and *vindex* species groups.



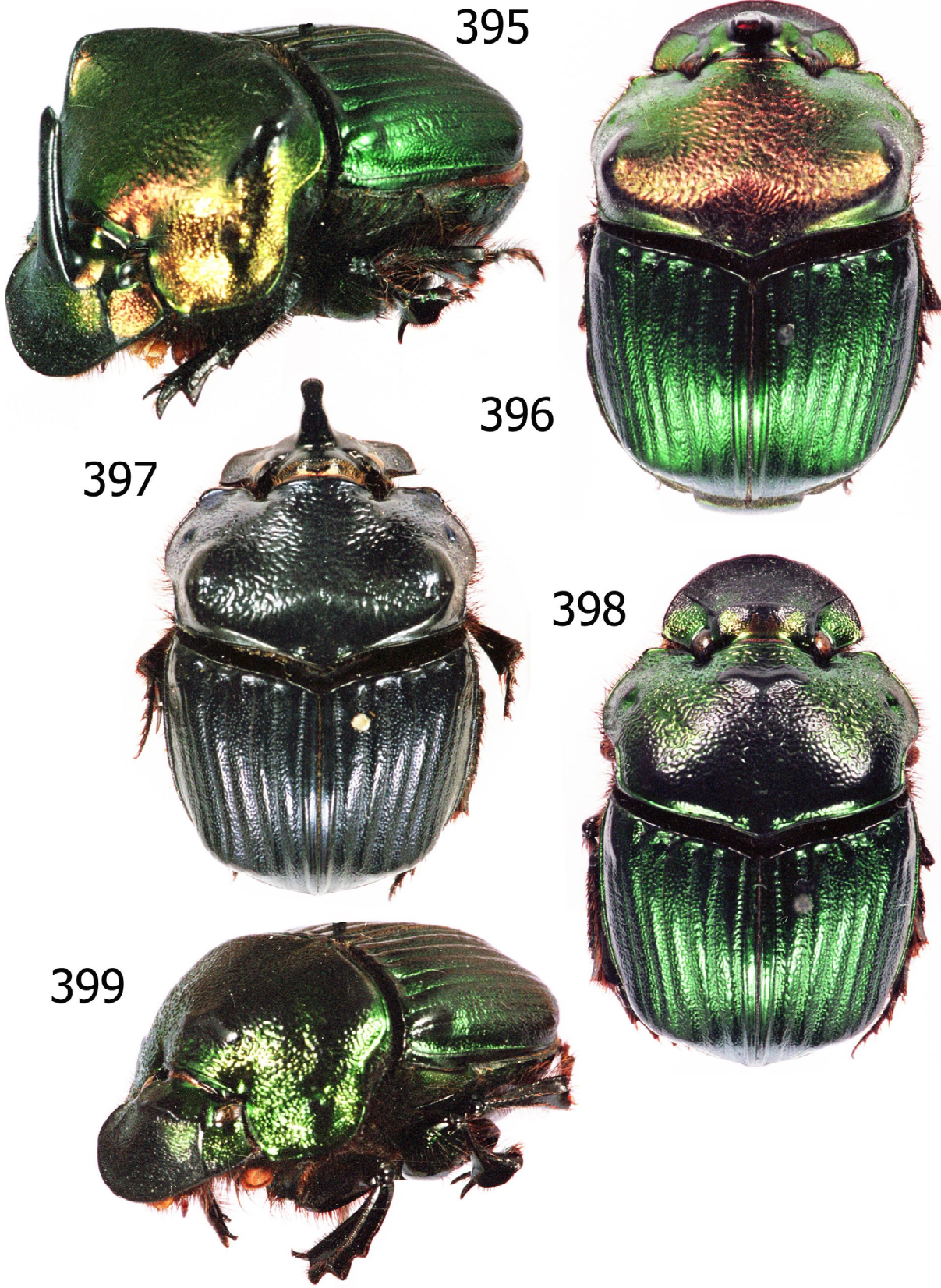
Figures 376–381. Characters of the *Phanaeus* (*P.*) *vindex* species group. *Phanaeus difformis* LeConte. **376)** Male, anterolateral angle of pronotum [left] and posterolateral angle of head [right], arrow indicates serration. **377)** Female protibia. **378)** Female, anteromedian portion of pronotum. *Phanaeus vindex* MacLeay. **379)** Male, anterolateral angle of pronotum [left] and posterolateral angle of head [right]. **380)** Female protibia. **381)** Female pronotal disk.



Figures 382–388. Characters of the *Phanaeus* (*P.*) *vindex* species group. *Phanaeus vindex* MacLeay. **382)** Female head, frontal view. **383)** Female, lateral view of pronotum. **384)** Male, lateral view of forebody. *Phanaeus igneus* MacLeay. **385)** Female, anteromedian portion of pronotum. **386)** Female head, frontal view. **387)** Male, lateral view of forebody. **388)** Male, tip of head horn.



Figures 389–394. Characters of the *Phanaeus* (*P.*) *vindex* species group. *Phanaeus igneus* MacLeay. **389)** Male pronotum. **390)** Elytron. *Phanaeus difformis* LeConte. **391)** Male pronotum. **392)** Elytron. *Phanaeus vindex* MacLeay. **393)** Male pronotum. **394)** Elytron.



Figures 395–399. *Phanaeus (P.) igneus* MacLeay. 395–397) Male. 398–399) Female.



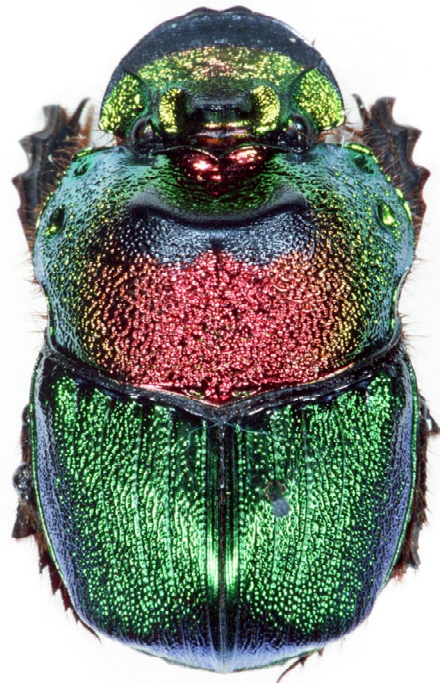
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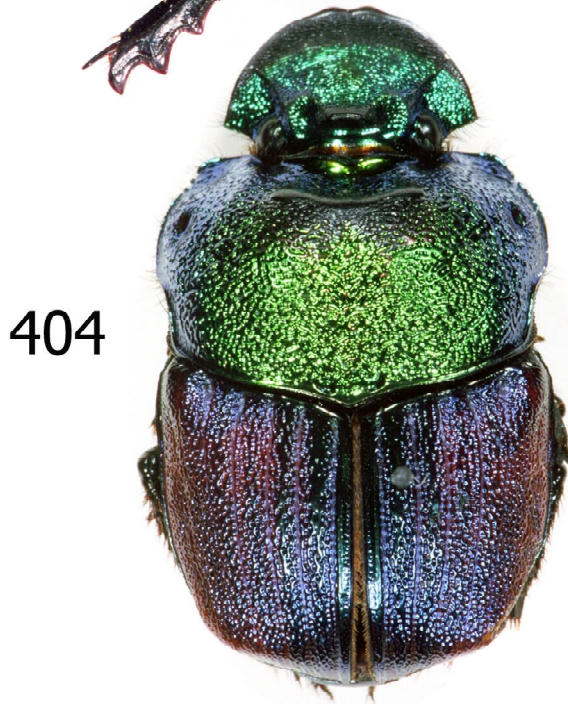
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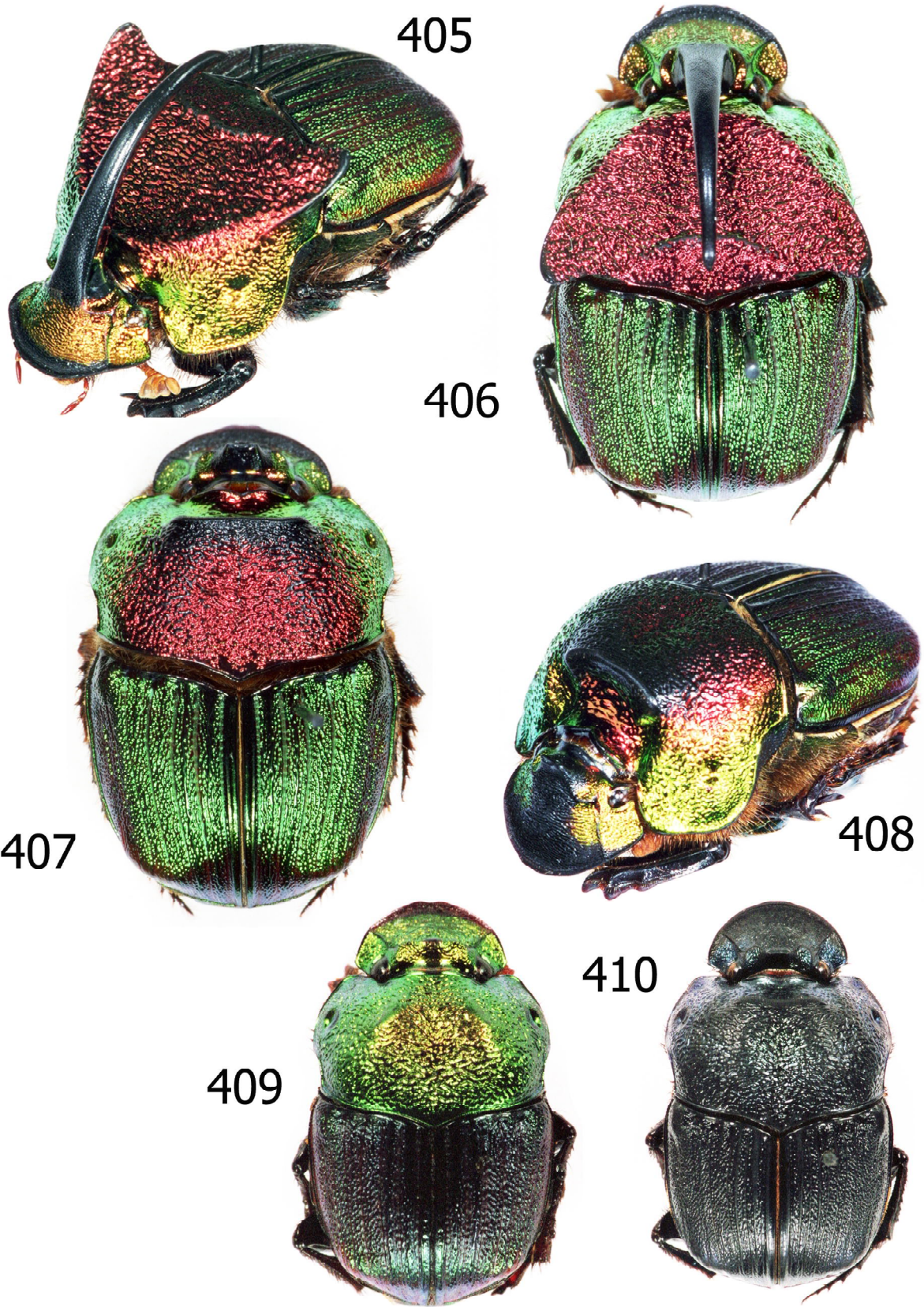


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Figures 400–404. *Phanaeus (P.) difformis* LeConte. 400–401) Male. 402–404) Female.



Figures 405–410. *Phanaeus (P.) vindex* MacLeay. 405–406, 409–410) Male. 407–408) Female.