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Taxonomic revision of the *Phanaeus endymion* species group (Coleoptera: Scarabaeidae), with the descriptions of five new species

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Abstract. The *Phanaeus endymion* species group is defined as a lineage of dung beetles distributed from Mexico to Ecuador. The current arrangement of the *P. endymion* species group includes 18 species (five newly described and three revalidated herein): *P. arletteae* Arnaud, 2018; *P. bravoensis* Moctezuma, Sánchez-Huerta & Halffter, 2017; *P. chiapanecus* sp. nov.; *P. edmondsi* Moctezuma, Deloya & Halffter, 2019; *P. endymion* Harold, 1863; *P. funereus* Balthasar, 1939 stat. rev.; *P. halffterorum* Edmonds, 1979; *P. huichol* Moctezuma, Sánchez-Huerta & Halffter, 2017; *P. jackenioi* sp. nov.; *P. malyi* Arnaud, 2002; *P. olsoufieffi* Balthasar, 1939 stat. rev.; *P. pacificus* sp. nov.; *P. panamensis* sp. nov.; *P. porioni* Arnaud, 2001 stat. rev.; *P. pyrois* Bates, 1887; *P. rzedowskii* sp. nov.; *P. zapotecus* Edmonds, 2006; and *P. zoque* Moctezuma & Halffter, 2017. *Phanaeus dionysius* Kohlmann, Arriaga-Jiménez & Rös, 2018 syn. nov. is considered as a new junior subjective synonymy of *P. zapotecus* Edmonds, 2006. *Phanaeus blanchardi* Olsoufieff, 1924 and *P. bothrus* Blackwelder, 1944 are junior objective synonyms of *P. olsoufieffi* Balthasar, 1939 stat. rev.

Keywords. Phanaeini, rainbow scarab dung beetles, genital diversification, mandible evolution, symbiotic interactions.

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Introduction

The *Phanaeus endymion* species group is a lineage of rainbow scarab dung beetles distributed from Mexico to Ecuador (Edmonds 1994; Edmonds & Zídek 2012; Lizardo *et al*. 2017). Species within the *P. endymion* species group are of great ecological importance since most of them are typically associated with Mesoamerican forests (Edmonds 1994, 2003; Arellano *et al*. 2008, 2013; Huerta *et al*.

2016; Moctezuma & Halffter 2017; Moctezuma *et al*. 2017, 2019; Kohlmann *et al*. 2018), and are either coprophagous, necrophagous or mycophagous (Edmonds 1994, 2003, 2006; Deloya *et al*. 2013; Moctezuma & Halffter 2017; Moctezuma *et al*. 2017; Gillett & Toussaint 2020).

The *P. endymion* species group has been classified within the subgenus *Notiophanaeus* Edmonds, 1994. According to Edmonds (1994) the pronotal sculpturing is the main distinction between *Notiophanaeus* (glassy and smooth) and *Phanaeus* Macleay, 1819 (heavily rugose). Nevertheless, phylogenetic studies have demonstrated that both *Notiophanaeus* and *Phanaeus* are non-monophyletic groups (Price 2007, 2009; Gillett & Toussaint 2020). Within *Notiophanaeus*, the *P. endymion* species group is mainly distinguished by the anterior margin of clypeus strongly bidentate medially, and pronotum of larger males with triangular disc and prominent posterolateral angles (Edmonds 1994). The monophyly of the *P. endymion* species group has been supported by previous phylogenetic studies (Price 2007, 2009; Gillett & Toussaint 2020).

Within the dung beetle genus *Phanaeus*, the *P. endymion* species group is probably the best studied in recent years (Edmonds & Zídek 2012; Solís & Kohlmann 2012; Moctezuma & Halffter 2017; Moctezuma *et al*. 2017, 2019; Arnaud 2018; Kohlmann *et al*. 2018). Nevertheless, several taxonomic issues remain to be disentangled. The complex background of taxonomy of the *P. endymion* species group is summarized herein. *Phanaeus endymion* Harold, 1863 was the first species to be described, based upon specimens from Orizaba, Veracruz, Mexico (Harold 1863). Subsequently, *P. pyrois* Bates, 1887 was described in the *Biologia Centrali-Americana* (Bates 1887). Bates (1887) suggested that *P. endymion* and *P. pyrois* were closely related species, and four chromatic morphs from Nicaragua, Panama and Colombia were included within *P. pyrois* (the original description of this species was illustrated with specimens from Chontales, Nicaragua).

During the 20th century, a proliferation of names and synonyms within the *P. endymion* species group began. Olsoufieff (1924) described *P. blanchardi* Olsoufieff, 1924 based upon black specimens from Valle del Cauca, Colombia; and proposed the aberration *viridicollis* for green specimens from Ecuador. Subsequently, Balthasar (1939) described *P. funereus* Balthasar, 1939 from Ecuador; and recognized that *P. blanchardi* was a junior primary homonym of *P. blanchardi* Harold, 1871. As a consequence, Balthasar (1939) proposed the name *P. olsoufieffi* Balthasar, 1939 in replacement of Olsoufieff's *P. blanchardi*. Nonetheless, Blackwelder (1944–1957) also recognized the homonymy of *P. blanchardi* and proposed the replacement name *P. bothrus* Blackwelder, 1944. Martínez & Pereira (1967) suggested *P. bothrus* as a junior objective synonym of *P. olsoufieffi*, but they considered *P. olsoufieffi* as a junior subjective synonym of *P. funereus*. According to Martínez & Pereira (1967), both *P. olsoufieffi* and *P. funereus* were identical in morphology, except for the aberration *viridicollis* that might be a valid subspecies. Afterwards, *P. halffterorum* Edmonds, 1979 was described based upon specimens from Mexico (Edmonds 1979), and the lectotypes for *P. endymion* and Olsoufieff's *P. blanchardi* (currently referred to as *P. olsoufieffi*) were designated by Arnaud (1982).

At the end of the 20th century, Edmonds (1994) revised the genus *Phanaeus*, defined the *P. endymion* species group, and designated a lectotype for *P. pyrois*. Edmond's concept of the *P. endymion* species group included within it three species: *P. endymion*, *P. pyrois* and *P. halffterorum*; while *P. funereus* and *P. olsoufieffi* where considered as junior subjective synonyms of *P. pyrois* (Edmonds 1994). According to Edmonds (1994), specimens of *P. pyrois*, *P. funereus* and *P. olsoufieffi* were virtually identical in external morphology and did not merit a separate taxonomic status. Edmonds (1994) considered that Olsoufieff's aberrant *viridicollis* might be a valid taxon, but indicated that more studies were needed to confirm or refute this assumption. Additionally, Edmonds (1994) suggested that blue and green specimens from Costa Rica might be hybrids of *P. pyrois* with *P. endymion*.

The beginning of the 21st century was distinguished by a controversial application of the subspecies-level taxa in the *P. endymion* species group (and in the entire genus *Phanaeus*). Thereby, the subspecies *P. endymion porioni* Arnaud, 2001 was described from Honduras and Belize (Arnaud 2001), while *P. pyrois malyi* Arnaud, 2002 was proposed for specimens from the southern Pacific of Costa Rica (Arnaud 2002a). Additionally, Arnaud (2002b) considered *P. olsoufieffi* and *P. funereus* as subspecies of *P. pyrois*, and proposed Olsoufieff's aberrant *viridicollis* as a valid species (*P. viridicollis* Olsoufieff, 1924). Subsequently, *P. zapotecus* Edmonds, 2006 was described from Mexico and included within the *P. endymion* species group (Edmonds 2006); while *P. pyrois malyi* was elevated to full species status based on the results of DNA analyses of specimens from Costa Rica (Solís & Kohlmann 2012).

Later, the taxonomy of *Phanaeus* was updated and the avoidance of the subspecies category was suggested by Edmonds & Zídek (2012). As a consequence, several nomenclatural changes were proposed and resulted in the *P. endymion* species group sensu Edmonds & Zídek (2012) including four species: *P. endymion*, *P. pyrois*, *P. halffterorum* and *P. zapotecus*. *Phanaeus viridicollis* was considered an unavailable name referable to a chromatic morph of *P. pyrois*: the name *viridicollis* was originally proposed as an infrasubspecific taxon (aberration), while some doubtful specimens of *P. viridicollis* were collected from Nicaragua along with the typical *P. pyrois* (Edmonds & Zídek 2012). Additionally, the following junior subjective synonyms were recognized by Edmonds & Zídek (2012): *P. endymion porioni* = *P. endymion*; *P. pyrois funereus* Balthasar, 1939 = *P. pyrois*, *P. pyrois olsoufieffi* Balthasar, 1939 = *P. pyrois*, and *P. pyrois malyi* = *P. pyrois*. Edmonds & Zídek (2012) argued that the taxonomic recognition of *P. endymion porioni* was not justified by the morphological differences identified by Arnaud (2001). Additionally, they refused to recognize *P. malyi* as a valid species, because the analysis of Solís & Kohlmann (2012) did not include samples of the Panamanian and South American populations and chromatic morphs of *P. pyrois* (Edmonds & Zídek 2012).

Traditionally, the taxonomy of the New World genus *Phanaeus* has relied on the study of the external morphology (Bates 1887; Olsoufieff 1924; Edmonds 1994; Arnaud 2002b; Edmonds & Zídek 2012). Particularly, the secondary sexual features of major males are considered to be reliable for determining species, while the study of the genital structures has been largely neglected (Edmonds 1994; Arnaud 2002b; Edmonds & Zídek 2012). The morphology of the aedeagus is usually not taxonomically informative enough to separate closely related species of *Phanaeus* (Edmonds 1994; Arnaud 2002b; Price 2005; Moctezuma & Halffter 2017; Moctezuma *et al*. 2017, 2019, 2020). Nevertheless, the structures of the internal sack of the aedeagus have proved to be valuable for the study of the taxonomy of Scarabaeinae dung beetles (Tarasov & Solodovnikov 2011; Medina *et al*. 2013; Tarasov & Génier 2015).

Previous authors have provided illustrations of the aedeagus (Olsoufieff 1924; Halffter 1955; Edmonds 1972; Howden & Young 1981; Arnaud 2000, 2001; Price 2005; Marchisio & Zunino 2012; Manjarres-H & Molano-R 2015; Moctezuma & Halffter 2017; Moctezuma *et al*. 2017, 2019, 2020; Kohlmann *et al*. 2018), internal sac of aedeagus (Price 2005; Manjarres-H & Molano-R 2015; Moctezuma & Halffter 2017), dissected endophallites (Price 2005; Marchisio & Zunino 2012; Manjarres-H & Molano-R 2015; Tarasov & Génier 2015; Moctezuma & Halffter 2017; Moctezuma *et al*. 2017, 2019, 2020; Kohlmann *et al*. 2018) and spermathecae (Halffter & Edmonds 1982; López-Guerrero & Halffter 2000; Price 2005; Marchisio & Zunino 2012) for some species of *Phanaeus*. However, the first serious attempt to describe the genitalia of *Phanaeus* for taxonomic purposes was by Price (2005), who examined the aedeagus, endophallites and spermathecae for the *P. vindex* species group. In a subsequent work, Manjarres-H & Molano-R (2015) examined and described the male genitalia of the Colombian *Phanaeus* (and other Phanaeini). They suggested that examination of the endophallites has taxonomic value for *Phanaeus*, because these structures show an adequate degree of interspecific heterogeneity and intraspecific homogeneity (Manjarres-H & Molano-R 2015).

Taking into account the incipient study of the genital morphology of *Phanaeus* to separate closely related species (Price 2005; Manjarres-H. & Molano-R. 2015), a majority of recent studies implemented the examination of the endophallites to identify and describe new species within the *P. endymion* species group. The description of *P. zoque* Moctezuma & Halffter, 2017 was the first that relied on the examination and comparison of the external and genital morphology of the male to separate a new species from the typical *P. endymion* (Moctezuma & Halffter 2017). Subsequently, Moctezuma *et al*. (2017) studied the male external and genital morphology of *P. bravoensis* Moctezuma, Sánchez-Huerta & Halffter, 2017; *P. huichol* Moctezuma, Sánchez-Huerta & Halffter, 2017; and *P. halffterorum* from Mexico. Arnaud (2018) described the new *P. arletteae* Arnaud, 2018 from Ecuador using external characters, based upon specimens of what was Olsoufieff's former aberration *viridicollis*. Later, Kohlmann *et al*. (2018) described *P. dionysius* Kohlmann, Arriaga-Jiménez & Rös, 2018; and illustrated *P. zapotecus*. The illustration of the habitus and aedeagus for both *P. dionysius* and *P. zapotecus* was provided by Kohlmann *et al*. (2018); but they only figured the endophallite copulatrix of *P. dionysius*. Additionally, Kohlmann *et al*. (2018) revalidated *P. malyi* as a full species, based on the external morphology of black specimens from Costa Rica, Panama (incorrectly referred to as *P. pyrois olsoufieffi*) and Ecuador (referred to as *P. pyrois funereus*). Furthermore, they considered that a more detailed analysis would be required to resurrect *P. pyrois olsoufieffi* and *P. pyrois funereus* from previous synonymy (Kohlmann *et al*. 2018). The latest species to be described and included within the *P. endymion* species group was *P. edmondsi* Moctezuma, Deloya & Halffter, 2019 from Mexico (Moctezuma *et al*. 2019).

In the face of this historical context, we aim to reassess the taxonomy of the *P. endymion* species group herein. Our study is based on two complementary sources of characters: the external morphology of males and females and the morphology of the endophallite copulatrix of males. Special emphasis is placed on *P. pyrois* and its taxonomically unsupported chromatic morphs (*P. malyi*, *P. funereus*, and *P. olsoufieffi*), and the status of *P. e. porioni* and *P. dionysius* is also revised. New species descriptions and redescriptions for previously described species are provided. Finally, a new determination key and images for the species within the *P. endymion* species group are provided.

Material and methods

The following entomological collections are used herein:

BMNH = British Museum of Natural History, London, UK
CDC = Cuauhtémoc Deloya Collection, Instituto de Ecología, A.C., Xalapa, Veracruz Mexico
CAS = California Academy of Sciences, San Francisco, California, USA
CEMT = Seção de Entomologia da Coleção Zoológica da Universidade Federal de Mato Grosso, Cuiabá, Brazil
CNIN = Colección Nacional de Insectos, Universidad Nacional Autónoma de México. Mexico City, Mexico
CNMC = Canadian Museum of Nature, Ottawa, Ontario, Canada
CPFA = Patrick and Florent Arnaud Collection, Saintry sur Seine, France
FESC = Federico Escobar Collection, Instituto de Ecología, A.C., Xalapa, Veracruz, Mexico
GHC = Gonzalo Halffter Collection, Instituto de Ecología, A.C., Xalapa, Veracruz, Mexico
IEXA = Colección Entomológica Dr. Miguel Angel Morón Ríos, Instituto de Ecología, A.C., Xalapa, Veracruz, Mexico
INBIO = Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica
JLSHC = José Luis Sánchez Huerta Collection, Xalapa, Veracruz, Mexico
MNCR = Museo Nacional de Costa Rica, San José, Costa Rica
MNHN = Muséum national d'histoire naturelle, Paris, France
NMPC = Národní Muzeum, Prague, Czech Republic
TAMU = Texas A&M University Insect Collection, College Station, Texas, USA
UVGC = Colección Entomológica, Universidad del Valle de Guatemala, Guatemala, Guatemala
VMC = Victor Moctezuma Collection, Puebla, Puebla, Mexico

The phylogenetic species concept sensu Wheeler & Platnick (2000) was adhered to, which defines a species as the smallest aggregation of (sexual) populations or (asexual) lineages that are diagnosable by a unique combination of character states. The subspecies-level is avoided for this work, while intraspecific variability of morphology (such as colouration, body size, and integument) is included within variation of the species. We followed the nomenclature proposed by Harris (1979), Edmonds (1994) and Cristóvão & Vaz-de-Mello (2020) for external morphology and that of Moctezuma *et al*. (2017) for genital morphology, except for the term endophallite (Génier 2019). The subgenus-level is avoided for this study since *Phanaeus* and *Notiophanaeus* have been proven to be artificial groups (Price 2007, 2009; Gillett & Toussaint 2020), and *Notiophanaeus* will probably be considered a synonym of *Phanaeus* in future works.

Type specimens bear determination labels printed on red acid-free paper, indicating the specimen's sex, and whether they are the holotype or paratypes. Label data is given verbatim. The genital structures were soaked with 10% KOH solution for 24 hours at room temperature, then rinsed with 96% ethanol and later with water. These structures were permanently stored in 15 mm glass microvials (BioQuip Products, Inc., Rancho Dominguez, California, USA) with glycerol, and the microvials were pinned under the dissected specimens.

Measurements and pictures were taken using a Leica Z16APOA stereo microscope equipped with Leica Smart Touch and Leica DMC2900 camera (Leica, Wetzlar, Germany), using the manufacturer´s software and the z-stack image capture method (except for Figs 4D, 5C, 8C, 11C, 12D, 18A, 19A). Since rainbow scarab dung beetles are usually iridescent (Edmonds 1994), the stereo microscope lightning was substituted (except for Figs 1, 20) to obtain adequate colour images as follows: a cylinder made of matt drafting acetate functioned as a light diffuser, while a cylinder made of a rolled LED light strip (300 LEDs / 5 m, 12 Vcc, white 6000–7000k, LED 3528, 13 W/h; Steren, Mexico City, Mexico) was used as light source. The final images were edited using a Wacom Intuos PEN tablet CTL-6100WL (Wacom Co., Ltd, Toyonodai Kazo-shi, Saitama, Japan) with Adobe Photoshop CC ver. 2015 (Adobe Systems Incorporated, San José, California, USA) and CorelDRAW X7 ver. 17.0.0.491 (Corel Corporation, Ottawa, Canada). Locality data were taken from specimen labels, literature and data bases (GBIF Secretariat 2019a; 2019b).

Results

Taxonomy

Phylum Arthropoda von Siebold, 1848
Subphylum Hexapoda Blainville, 1816
Class Insecta Linnaeus, 1758
Order Coleoptera Linnaeus, 1758
Suborder Polyphaga Emery, 1886
Superfamily Scarabaeoidea Latreille, 1802
Family Scarabaeidae Latreille, 1802
Subfamily Scarabaeinae Latreille, 1802

Genus ***Phanaeus*** Macleay, 1819

Phanaeus Macleay, 1819: 124.
Lonchophorus Germar, 1824: 106.
Phaneus Castelnau, 1840: 79.
Onthurgus Gistel, 1857: 90.
Palaeocopris Pierce, 1946: 130.

Phanaeus – Brullé 1837: 302. — Dejean 1844: 155. — Agassiz 1846: 818. — Lacordaire 1856: 100. — Gemminger & Harold 1869: 1016. — Lacordaire & Chapuis 1876: 276. — Bates 1887: 387. — Nevinson 1892: 1. — Gillet 1911: 81. — Lucas 1920: 499. — Dawson 1922: 61. — Olsoufieff 1924: 22. — Pessôa 1934: 282. — Balthasar 1939: 238. — Pessôa & Lane 1941: 470. — Islas 1942: 303. — Blackwelder 1944–1957: 209. — Halffter 1952: 79; 1955: 79. — Roze 1955: 45. — Martínez 1959: 97. — Halffter & Matthews 1966: 258. — Vulcano & Pereira 1967: 566. — Edmonds 1972: 740; 1979: 99; 1994: 8; 2003: 11; 2004: 119; 2006: 31. — Edmonds & Halffter 1978: 321. — Howden & Young 1981: 12. — Arnaud 1982: 114; 2001: 2; 2002a: 2; 2002b: 13; 2018: 3. — Halffter & Edmonds 1982: 136. — Medina & Lopera 2000: 303. — Vítolo 2000: 595. — Medina *et al*. 2001: 140. — Ratcliffe 2002: 16. — Philips *et al*. 2004: 50. — Price 2005: 197; 2007: 1; 2009: 137. — Hamel-Leigue *et al*. 2006: 17; 2009: 64. — Krajcik 2006: 148. — Gillett *et al*. 2010: 2 — Vaz-de-Mello *et al*. 2011: 25. — Edmonds & Zídek 2012: 1. —Solís & Kohlmann 2012: 7. — Cancino-López *et al*. 2014: 140. — Figueroa *et al*. 2014: 133. — Manjarres-H & Molano-R 2015: 246. — Pacheco & Vaz-de-Mello 2015: 1. — Halffter & Morrone 2017: 19. — Lizardo *et al*. 2017: 271. — Moctezuma & Halffter 2017: 47. — Moctezuma *et al*. 2017: 114; 2019: 249; 2020: 3. — Chamorro *et al*. 2018: 75; 2019: 210. — Kohlmann *et al*. 2018: 67. — Gillett & Toussaint 2020: 2.

Lonchophorus – Brullé 1837: 302 (as synonym of *Phanaeus*). — Agassiz 1846: 620. — Lacordaire 1856: 100 (as synonym of *Phanaeus*). — Gemminger & Harold 1869: 1016 (as synonym of *Phanaeus*). — Nevinson 1892: 1 (as synonym of *Phanaeus*). — Gillet 1911: 81 (as synonym of *Phanaeus*). — Lucas 1920: 381 (as synonym of *Phanaeus*). — Olsoufieff 1924: 140 (as synonym of *Phanaeus*). — Blackwelder 1944–1957: 209 (as synonym of *Phanaeus*). — Martínez 1959: 97 (as synonym of *Phanaeus*). — Edmonds 1972: 826 (as synonym of *Phanaeus*); 1994: 46 (as synonym of *Phanaeus*). — Ratcliffe 2002: 16 (as synonym of *Phanaeus*). — Krajcik 2006: 148 (as synonym of *Phanaeus*). — Solís & Kohlmann 2012: 7 (as synonym of *Phanaeus*). — Figueroa *et al*. 2014: 133 (as synonym of *Phanaeus*). — Chamorro *et al*. 2019: 210 (as synonym of *Phanaeus*).

Onthurgus – Edmonds 1972: 827 (as synonym of *Phanaeus*); 1994: 46 (as synonym of *Phanaeus*). — Ratcliffe 2002: 16 (as synonym of *Phanaeus*). — Krajcik 2006: 148 (as synonym of *Phanaeus*). — Solís & Kohlmann 2012: 7 (as synonym of *Phanaeus*). — Figueroa *et al*. 2014: 133 (as synonym of *Phanaeus*). — Chamorro *et al*. 2019: 210 (as synonym of *Phanaeus*).

Palaeocopris – Edmonds 1972: 855; 1994: 46 (as synonym of *Phanaeus*). — Miller *et al*. 1981: 1 (as synonym of *Phanaeus*). — Ratcliffe 2002: 16 (as synonym of *Phanaeus*). — Solís & Kohlmann 2012: 7 (as synonym of *Phanaeus*). — Chamorro *et al*. 2019: 210 (as synonym of *Phanaeus*).

Phaneus – Krajcik 2006: 148 (as synonym of *Phanaeus*).

Phanaeus arletteae Arnaud, 2018
Figs 17, 18A, 19A

Phanaeus (*Notiophanaeus*) *arletteae* Arnaud, 2018: 4.

Phanaeus blanchardi ab. *viridicollis* (unavailable infrasubspecific name) – Olsoufieff 1924: 149. — Edmonds 1994: 443. — Arnaud 2002b: 98. — Edmonds & Zídek 2012: 13 (as an unavailable infrasubspecific name referable to *P. pyrois*).

Phanaeus (*Phanaeus*) *blanchardi* ab. *viridicollis* – Martínez & Pereira 1967: 68 (as synonym of *P. funereus*) (unavailable infrasubspecific name).

Phanaeus (*Notiophanaeus*) *viridicollis* – Arnaud 2002b: 98–99 (as a new combination for *P*. *blanchardi* ab. *viridicollis*) (unavailable infrasubspecific name). — Edmonds & Zídek 2012: 13 (as an unavailable infrasubspecific name referable to *P. pyrois*).

Phanaeus viridicollis – Krajcik 2006: 153. — Edmonds & Zídek 2012: 1, 6 (as an unavailable infrasubspecific name referable to *P. pyrois*).

Non *Phanaeus pyrois* (error) – Moctezuma & Halffter 2017: 55 (in part). — Moctezuma *et al*. 2017: 114, 130 (in part).
Phanaeus (*Notiophanaeus*) *arletteae* – Chamorro *et al*. 2018: 97; 2019: 213, pl. 46a.
Phanaeus arletteae – Kohlmann *et al*. 2018: 83, 88.

Type material

Holotype (revised from photograph from the original description)
ECUADOR • ♂, Arnaud 2018: 4, pl. 1, fig. a; Guayas, Kilometric point 18 Balzar-Quevedo Road; CPFA.

Type locality

Ecuador, Guayas, Kilometric point 18 Balzar-Quevedo Road.

Distribution

Pacific slope of the Andes, south-central Ecuador (Fig. 17).

Remarks

The genital morphology of this species remains unknown. We were not able to personally revise specimens of *Phanaeus arletteae*. Nevertheless, the external morphology of the holotype and a female paratype were illustrated by Arnaud (2018). We consider that the diagnostic characters provided by Arnaud (2018) are adequate to separate this species from closely related taxa. The commentaries of previous authors confirmed the validity of this species (Martínez & Pereira 1967; Edmonds 1994; Arnaud 2002b; Edmonds & Zídek 2012). Particularly, the morphology of the pronotum of the female is unique within the *P. endymion* species group.

Phanaeus bravoensis Moctezuma, Sánchez-Huerta & Halffter, 2017
Figs 1A, 15, 18B, 19B

Phanaeus bravoensis Moctezuma *et al*., 2017: 115.

Phanaeus bravoensis – Kohlmann *et al*. 2018: 69. — Moctezuma *et al*. 2019: 253, fig. 5.

Type material

Holotype
MEXCIO • ♂, Moctezuma *et al*. 2017: 118, figs 6–8 (revised); Guerrero, Chilpancingo de los Bravo; IEXA.

Type locality

Mexico, Guerrero, Chilpancingo de los Bravo.

Distribution

Mexico, Sierra Madre del sur, central Guerrero (Fig. 15).

Remarks

This species was recently described by Moctezuma *et al*. (2017). To the original description we add that the elytral striae are impressed basally as distinct fossae; right lobe of endophallite copulatrix is more developed than left lobe; right lobe of endophallite copulatrix obtusely triangular, arched superiorly; left lobe of endophallite copulatrix lobed, strongly reduced; central ridge more developed than central column (Fig. 1A). For the female, the trituberculate cephalic carina with nearly aligned, similar sized, conical tubercles; frons punctures scarce, almost effaced; pronotal surface distinctly punctate; pronotal process trituberculate with a posterior concavity; all pronotal tubercles rounded, with middle tubercle slightly more developed and projected frontally than lateral tubercles; posterior pronotal midline distinctly impressed.

Phanaeus chiapanecus sp. nov.
urn:lsid:zoobank.org:act:55933BD6-8A56-49CB-B1B4-3AB7C1A235BE
Figs 1B, 2A, 3, 15, 18C, 19C

Diagnosis

Phanaeus chiapanecus sp. nov. is a large and robust species which frequently attains 18.5–20 mm in length. This new species is diagnosed by the following character combination: Major male dark metallic blue-green or green dorsally (Fig. 3); keel absent in the middle of anterior pronotal margin (Fig. 2A); posterolateral angles of pronotum widened, elongate, slightly projected posteriorly (Fig. 3A); elytral striae thick, impressed basally as distinct fossae, with deeply impressed punctation; interstriae black, with completely or partially roughened surface (Fig. 3); endophallite copulatrix as Fig. 1B. Major female with pronotal process lacking concavities; pronotal tubercles nearly aligned, with middle tubercle more developed than lateral tubercles; posterior pronotal midline completely effaced (Fig. 3B).

Etymology

The specific epithet of the new species refers to Chiapas, where the type series was collected.

Type material (80 ♂♂, 144 ♀♀)

Holotype

MEXICO • ♂; Chiapas, “Loc. Vicente Guerrero, Mun. San Fernando. 20/05/2018. Selva Baja Caducifolia. Col. A. Díaz. Pit-Fall calamar. 16°51′10″N. 93°13′2″W. 984 msnm”; TAMU.

Paratypes

MEXICO – **Chiapas** • 7 ♂♂, 6 ♀♀; “Mpio. San Fernando, 16°50′50.676″ N, 93°12’46.655″ W, 6-vi-06. 930 m.”; TAMU • 34 ♂♂, 62 ♀♀; “V. Guerrero, Sn. Fernando. 06-VI-2006. U. Caballero, Girón M y Miss-Barrera Col.”; GHC • 3 ♂♂, 5 ♀♀; same collection data as for preceding; TAMU • 19 ♂♂, 23 ♀♀; same collection data as for preceding; VMC • 2 ♂♂, 2 ♀♀; same collection data as for preceding; UVGC • 1 ♂, 1 ♀; “Sumidero Cyn Park. 1 august 1989. D.B. Thomas”; TAMU • 1 ♂; same collection data as for preceding; VMC • 2 ♀♀; “San Pedro. Arellano-Gámez Col.”; GHC • 1 ♂, 2 ♀♀; same collection data as for preceding; VMC • 10 ♀♀; “V. Guerrero. Arellano-Gámez Col.”; GHC • 2 ♂♂, 1 ♀; same collection data as for preceding; VMC • 9 ♀♀; “Vicente Guerrero, La Antena. Molina A. Col.”; GHC • 1 ♂, 2 ♀♀; same collection data as for preceding; VMC • 1 ♂, 2 ♀♀; “V. Guerrero, La Antena. Arellano-Gámez Col.”; GHC • 3 ♂♂, 2 ♀♀; same collection data as for preceding; VMC • 1 ♂, 1 ♀; “Km. 40. Carr. Tuxtla-San Cristóbal (El Escopetazo). 2-VIII-70. V.M. Sánchez. col. Bosque-pino encino arcilloso. Cebo-pescado”; GHC • 1 ♂, 5 ♀♀; “V. Guerrero, S. Fernando. UC, MG, Irma”; GHC • 2 ♂♂, 9 ♀♀; no label data; GHC.

Type locality

Mexico, Chiapas, San Fernando, Vicente Guerrero.

Description

Major male (holotype)

Length 18.8 mm.

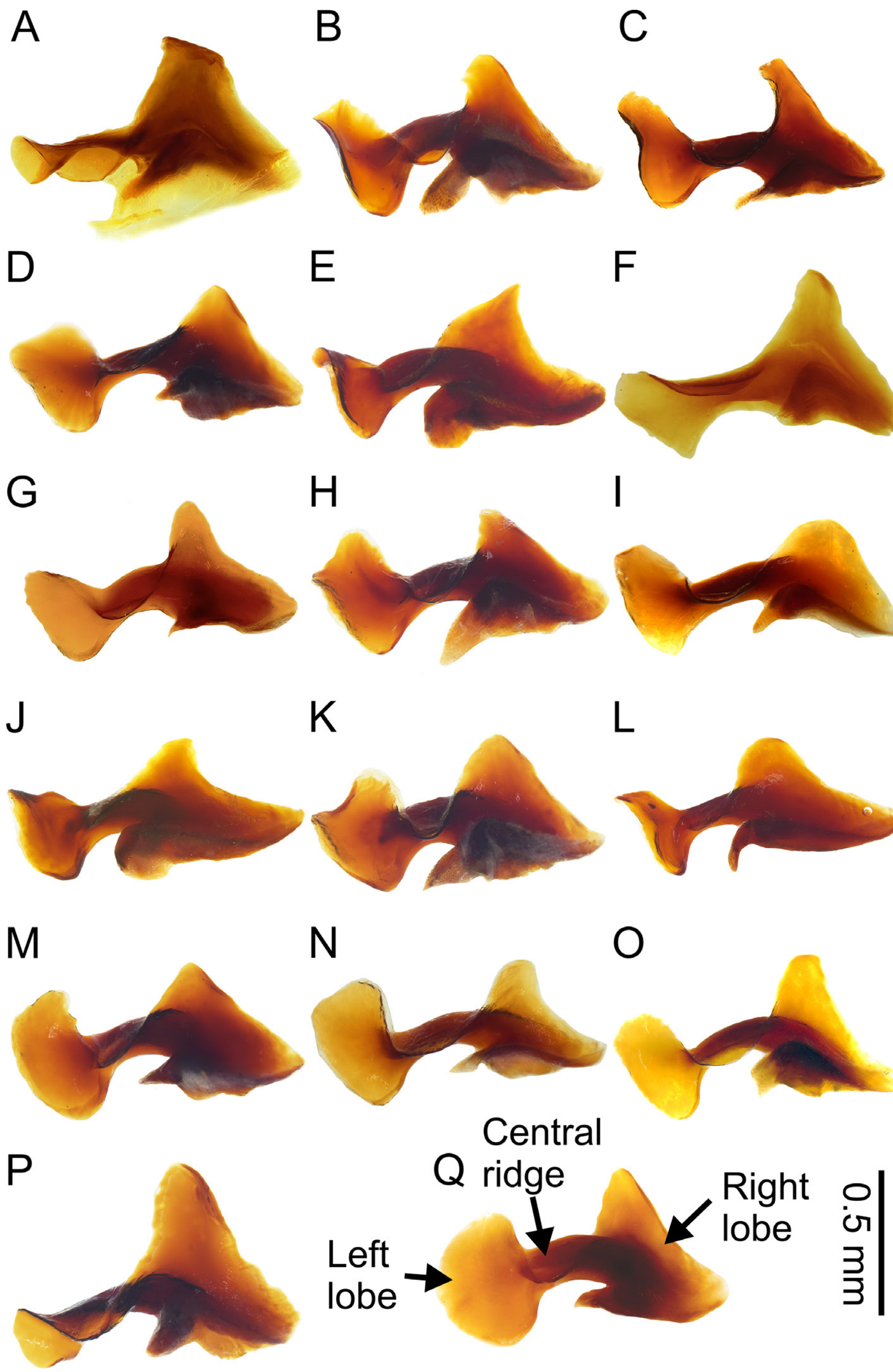

Fig. 1. Endophallite copulatrix of the *Phanaeus endymion* species group (except for *P. arletteae* Arnaud, 2018). **A**. *Phanaeus bravoensis* Moctezuma, Sánchez-Huerta & Halffter, 2017 (IEXA). **B**. *Phanaeus chiapanecus* sp. nov. (TAMU). **C**. *Phanaeus edmondsi* Moctezuma, Deloya & Halffter, 2019 (IEXA). **D**. *Phanaeus endymion* Harold, 1863 (VMC). **E**. *Phanaeus funereus* Balthasar, 1939 stat. rev. (VMC). **F**. *Phanaeus halffterorum* Edmonds, 1979 (TAMU). **G**. *Phanaeus huichol* Moctezuma, Sánchez-Huerta & Halffter, 2017 (IEXA). **H**. *Phanaeus jackenioi* sp. nov. (UVGC). **I**. *Phanaeus malyi* Arnaud, 2002 (VMC). **J**. *Phanaeus olsoufieffi* Balthasar, 1939 stat. rev. (VMC). **K**. *Phanaeus pacificus* sp. nov. (UVGC). **L**. *Phanaeus panamensis* sp. nov. (TAMU). **M**. *Phanaeus porioni* Arnaud, 2001 stat. rev. (VMC). **N**. *Phanaeus pyrois* Bates, 1887 (VMC). **O**. *Phanaeus rzedowskii* sp. nov. (TAMU). **P**. *Phanaeus zapotecus* Edmonds, 2006 (VMC). **Q**. *Phanaeus zoque* Moctezuma & Halffter, 2017 (IEXA).

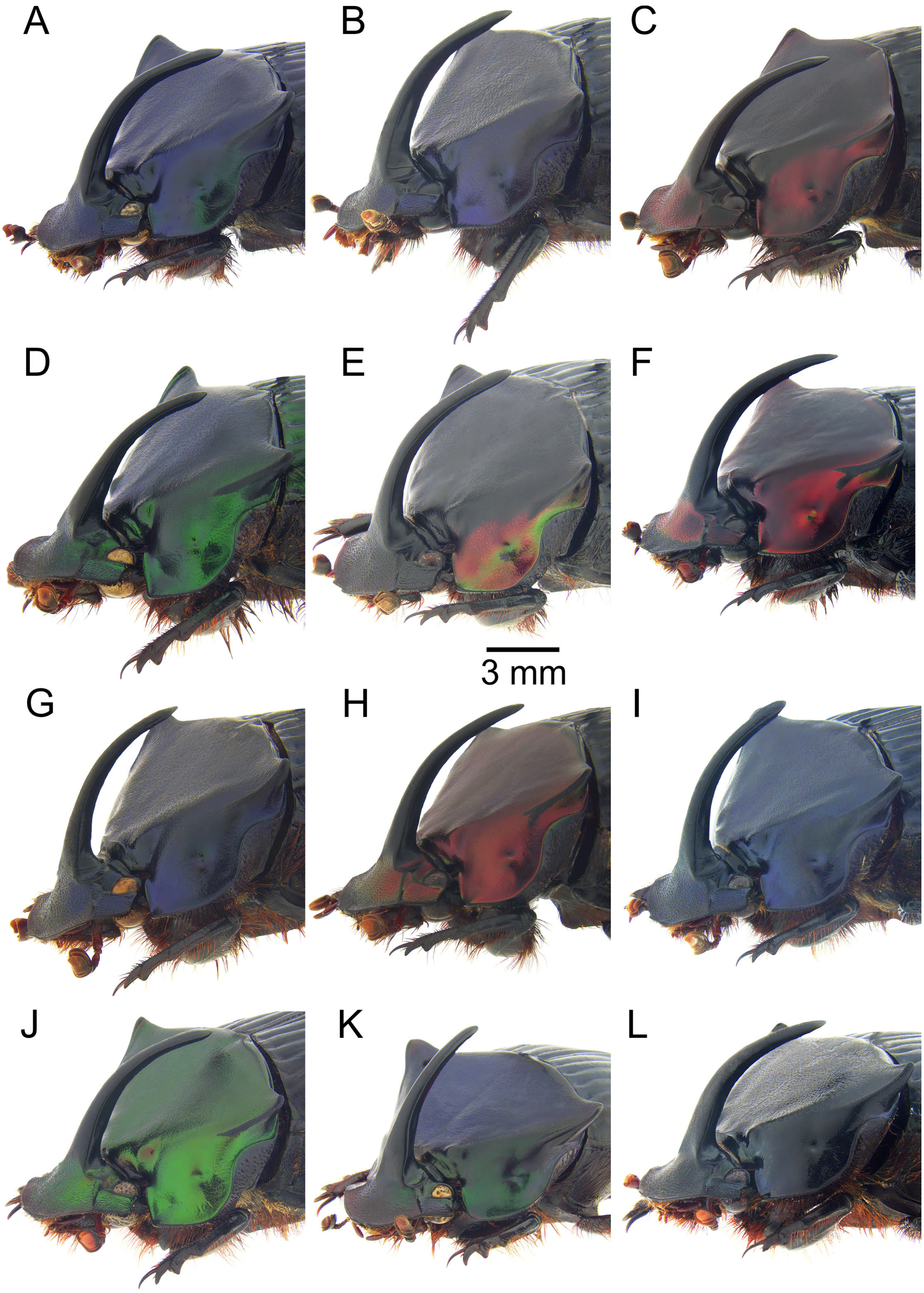

Fig. 2. Lateral view of males within the *Phanaeus endymion* species group. **A**. *Phanaeus chiapanecus* sp. nov. (TAMU). **B**. *Phanaeus endymion* Harold, 1863 (VMC). **C**. *Phanaeus funereus* Balthasar, 1939 stat. rev. (VMC). **D**. *Phanaeus jackenioi* sp. nov. (UVGC). **E**. *Phanaeus malyi* Arnaud, 2002 (VMC). **F**. *Phanaeus olsoufieffi* Balthasar, 1939 stat. rev. (VMC). **G**. *Phanaeus pacificus* sp. nov. (UVGC). **H**. *Phanaeus panamensis* sp. nov. (TAMU). **I**. *Phanaeus porioni* Arnaud, 2001 stat. rev. (VMC). **J**. *Phanaeus pyrois* Bates, 1887, green morph (VMC). **K**. *Phanaeus rzedowskii* sp. nov. (TAMU). **L**. *Phanaeus zapotecus* Edmonds, 2006 (VMC).

Head. Clypeus bidentate, black on anterior margin, dark metallic blue-green posteriorly, with roughened sculpture. Genae dark metallic blue-green, with roughened sculpture. Front black, with dark metallic blue-green on portions adjacent to cephalic horn. Cephalic horn black, curved posteriorly over pronotum (Figs 2A, 3A).

Pronotum. Uniformly dark blue, becoming black on lateral margins of posterolateral angles and on posterior margin of disc. Keel absent in the middle of anterior pronotal margin. Disc triangular, flat, with two distinctly developed tubercles on anterior portion. Pronotal triangle with lightly granulate sculpture, scabriculous, impunctate. Sides with smooth sculpture, scabriculous, with superficially impressed punctures. Lateral lines of pronotal triangle straight. Posterolateral angles widened, elongate, slightly projected posteriorly, slightly upturned apically. Lateral fossae distinctly impressed. Basal fossae obtusely oval, deeply impressed. Posterior margin distinctly punctate (Figs 2A, 3A).

Elytra. Striae thick, dark blue-green, scabriculous, impressed basally as distinct fossae, with deeply impressed punctation. Interstriae black, with completely or partially roughened surface, scabriculous, with superficially impressed punctation. Sutural margin without apical tooth (Fig. 3A).

Protibiae. Quadridentate with apical spine.

Tergite VIII. Dark green, scabriculous; with rough, distinctly impressed punctures. Basal margin with setae variable in size.

Genitalia. Right and left lobes of endophallite copulatrix similar in size. Right lobe obtusely triangular in shape; with acute, upturned apical portion. Left lobe bent posteriorly, with superior portion obtusely rectangular. Central ridge more developed than central column (Fig. 1B).

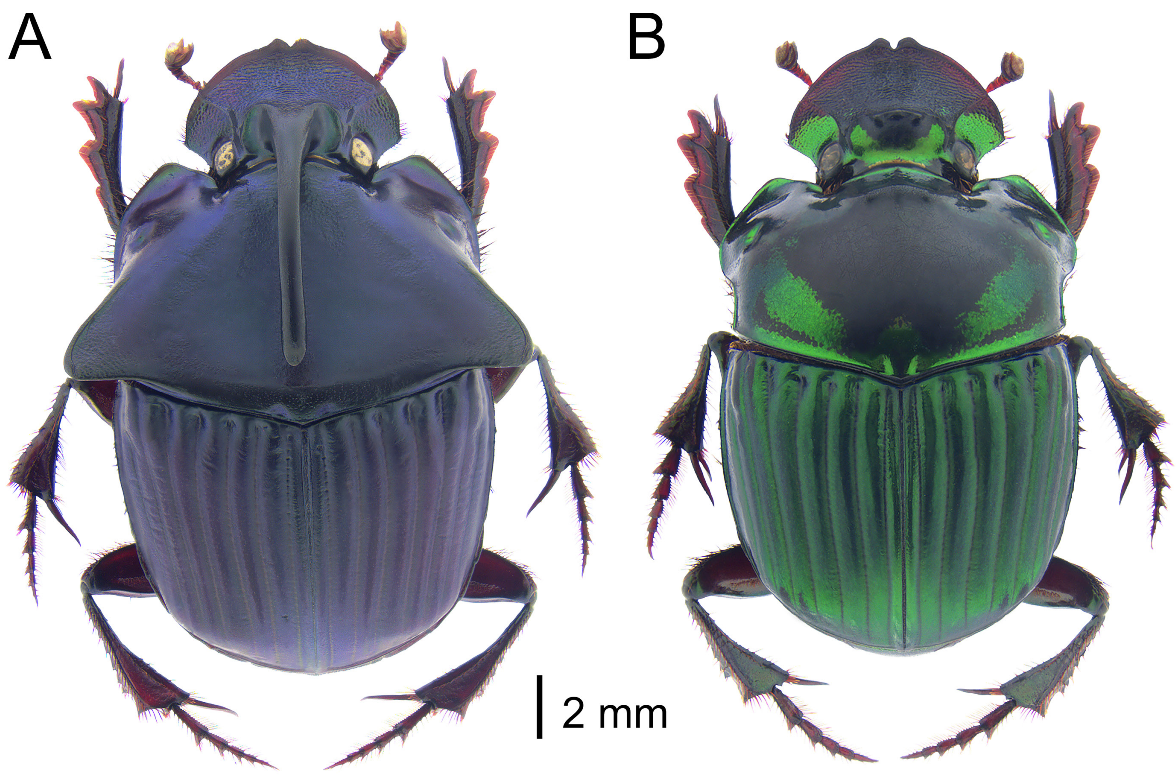

Fig. 3. *Phanaeus chiapanecus* sp. nov. **A**. Holotype, ♂, blue morph (typical; TAMU). **B**. ♀, green morph (TAMU).

Minor male

Like the major male, except for the reduction of the secondary sexual characters (i.e., cephalic horn, pronotal triangle and tubercles, and pronotal posterolateral angles).

Female

Similar to the male, except for the head showing a cephalic trituberculate carina with carinate middle tubercle, slightly more projected frontally, less raised than conical lateral tubercles; frons almost impunctate; pronotal sculpture completely smooth with scarce, superficially impressed punctures; pronotal disc black on central portion, metallic dark blue-green on sides and posterior portion; pronotal process trituberculate lacking concavities; pronotal tubercles nearly aligned, with middle tubercle more developed than lateral tubercles; posterior pronotal midline completely effaced (Fig. 3B).

Variation

Mean length 16.9 mm (12.4–20.6 mm). The typical colour morphs are dark metallic blue (Fig. 3A) or dark metallic green (Fig. 3B), but a rare specimen shows metallic yellow-green sheen on head, pronotum and elytra. The elytral interstriae are dark metallic blue, or rarely dark metallic green.

Distribution

Mexico, Central highlands of Chiapas (Fig. 15).

Remarks

This species was referred to as *P. pyrois* by Arellano *et al*. (2008) and GBIF Secretariat (2019b), and as *P. endymion* by Morón *et al*. (1986), Edmonds (1994), Arellano *et al*. (2013), Lizardo *et al*. (2017), Moctezuma & Halffter (2017) and Sánchez-Hernández *et al*. (2020). Nevertheless, the distribution areas of the aforementioned species do not overlap with the distribution of *P. chiapanecus* sp. nov., which is distinctly differentiated by its morphology.

Phanaeus edmondsi Moctezuma, Deloya & Halffter, 2019
Figs 1C, 15, 18D, 19D

Phanaeus edmondsi Moctezuma *et al*., 2019: 251.

Type material

Holotype

MEXICO • ♂, Moctezuma *et al*. 2019: 251, figs 1–3 (revised); Oaxaca, Candelaria Loxicha, Portillo del Rayo; CNIN.

Type locality

Mexico, Oaxaca, Candelaria Loxicha, Portillo del Rayo.

Distribution

Pacific slope of the Sierra Madre del Sur, southern Oaxaca (Fig. 15).

Remarks

This species was recently described and illustrated (Moctezuma *et al*. 2019). To the original description of the female we add: cephalic trituberculate carina of head with carinate central tubercle, anteriorly more projected not as raised as lateral, conical tubercles; frons with superficially impressed punctures; pronotal sculpture completely smooth with superficially impressed punctures; pronotal process trituberculate lacking concavities; central pronotal tubercle slightly more developed and projected anteriorly than lateral tubercles; posterior pronotal midline completely effaced.

Phanaeus endymion Harold, 1863
Figs 1D, 2B, 4, 18E, 19E, 20

Phanaeus endymion Harold, 1863: 163.

Phanaeus endymion – Gemminger & Harold 1869: 1017. — Bates 1887: 58. — Nevinson 1892: 3, 10; 1892b: 34. — Olsoufieff 1924: 37, 91, 150, 164, pl. VI, fig. 7. — Islas 1942: 314, 318–319, 336, pl. 1 (in part). — Blackwelder 1944–1957: 209 (in part). — Halffter & Matthews 1966: 40, 68, 70, 74 (in part). — Edmonds 1972: 830, figs 218–220 (in part); 1979: 99, 102–103, figs 4, 9–10 (in part); 2006: 31–32, 35–36, figs 2, 4, 6–7 (in part). — Morón 1979: 381, 423, 434, 449, fig. 20b; 1985: 63, 88, 91, 97, 107, fig. 20. — Arnaud 1982: 114; 2001: 4 (in part). — Palacios-Ríos *et al*. 1990: 59. — Estrada & Coates-Estrada 1991: 465. — Halffter *et al*. 1992: 139, 149, 153–155; 1995: 162, 164–166, 173. — Estrada *et al*. 1993: 48–49; 1998: 586–587, 589. — Deloya & Morón 1998: 19. — López-Guerrero & Halffter 2000: 241 (in part). — Montes de Oca 2001: 118, 123. — Avendaño-Mendoza *et al*. 2005: 810, 813, 815, 817. — Price 2005: 197 (in part); 2007: 17, figs 33, 52–54 (in part); 2009: 139, figs 2–4 (in part). — Krajcik 2006: 150 (in part). — Gillett 2008: 5. — Navarrete & Halffter 2008: 2880, 2888, 2893, 2895. — Halffter & Halffter 2009: 6, 8. — Díaz *et al*. 2010: 6–8. — Inward *et al*. 2011: 1677, fig. 2, appendix s2. — Edmonds & Zídek 2012: 1, 5–6 (in part). — Barragán *et al*. 2011: fig. 1. — Delgado *et al*. 2012b: 209. — Alvarado *et al*. 2014: tables s1–2; 2019: 175; 2020: 5. — Cancino-López *et al*. 2014: 137 (in part). — Bourg *et al*. 2016: 493–494. — Huerta *et al*. 2016: 16 (in part). — Sánchez-de-Jesús *et al*. 2016: table A4. — Halffter 2017: fig. 7 (in part). — Lizardo *et al*. 2017: 273–275, 292–293, fig. 12 (in part). — Moctezuma & Halffter 2017: 47, 51–52, 55 figs 17–23 (in part). — Moctezuma *et al*. 2017: 114, 123, 131–132 (in part); 2019: 251–254, fig. 5 (in part). — Kohlmann *et al*. 2018: 79, 83, 88 (in part). — Sánchez-Hernández *et al*. 2018: 149–150; 2020: 229 (in part). — Santos-Heredia *et al*. 2018: appendix 1. — Gillett & Toussaint 2020: 11, fig. 3 (in part). — Salomão *et al*. 2020: 3–4, 8–9 (in part).

Phanaeus (*Notiophanaeus*) *endymion* – Edmonds 1994: 2, 8–9, 12, 19, 36, 39, 41–46, 54, 74, 101, figs 17, 209, 215–216, 221 (in part); 2003: 65 (in part). — Arnaud 2002b: 94–95 (in part). — Delgado *et al*. 2012a: 327. — Edmonds & Zídek 2012: 3, 13, figs 132–133, 136, 140, 143, 152–155 (in part). — Halffter & Morrone 2017: 21. — Lizardo *et al*. 2017: 272 (in part). — Capello & Halffter 2019: 113, figs 41a–b.

Phanaeus (*Phanaeus*) *endymion* – Edmonds 2003: 63, Fig. 2.20 (in part).

Diagnosis

Highly variable species, diagnosed by the following character combination: major male dark blue (Fig. 4A), dark metallic blue-green or dark metallic green dorsally (Fig. 4B); sometimes with carinate, distinctly developed keel in the middle of anterior pronotal margin (Fig. 2B); posterolateral angles of pronotum short, widened, sometimes lightly projected posteriorly (Figs 4A–B); elytral striae impressed basally as distinct fossae, with distinctly impressed to effaced punctures (Fig. 4); endophallite copulatrix as in Fig. 1D. Major female with pronotal process concave posteriorly; middle pronotal tubercle more developed, dentiform or rounded, always more projected frontally than lateral tubercles; lateral tubercles obtusely rounded or carinate; posterior pronotal midline superficially impressed to completely effaced (Fig. 4C).

Type material

Lectotype (studied from photographs)

MEXICO • ♂, Arnaud 1982: 114 (Fig. 4D); Veracruz, Córdoba; "*P. endymion* Harold. Ex-Musæo E. Harold. Muséum Paris 1952 Coll. R. Oberthur. MNHN EC10553"; MNHN.

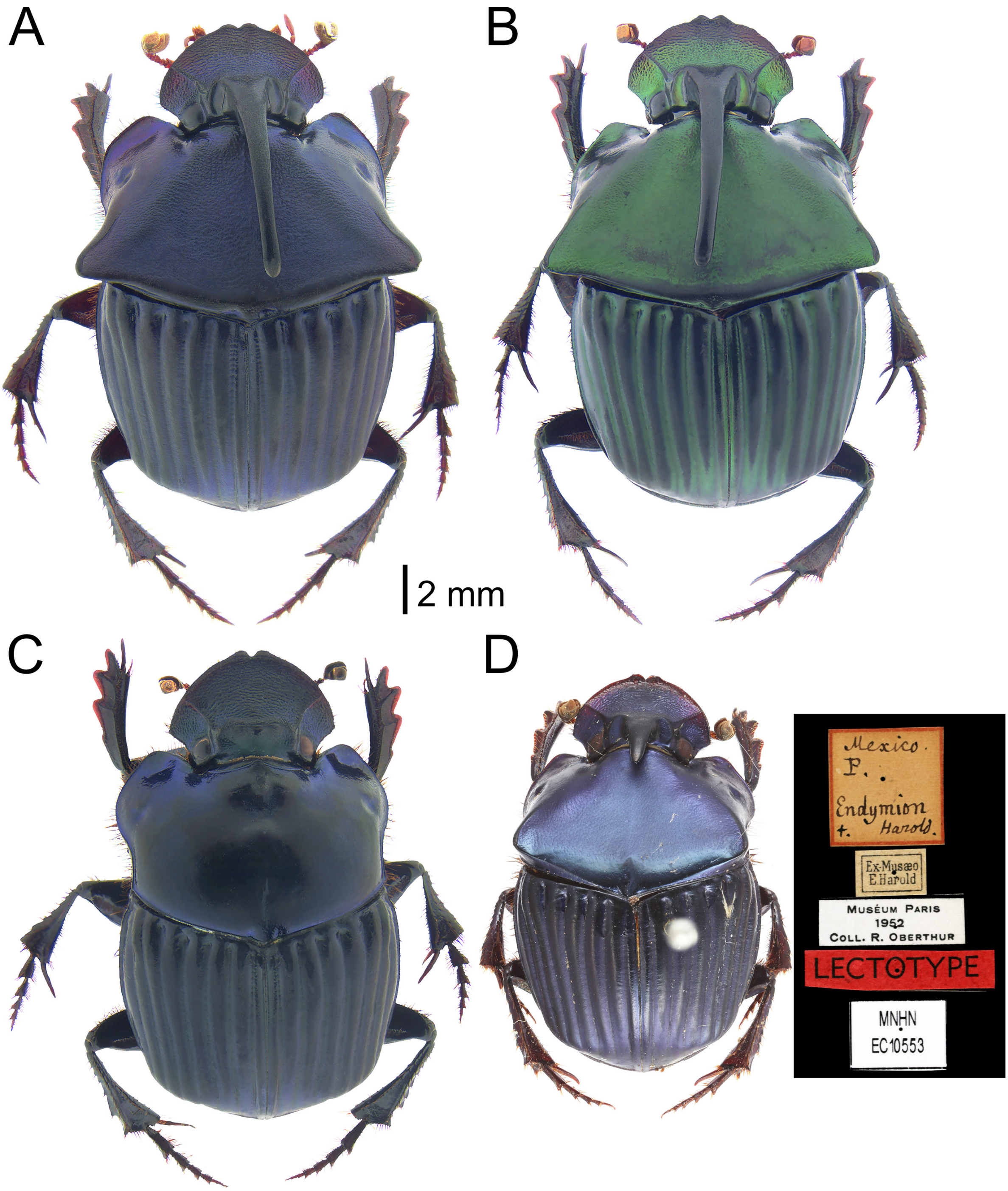

Fig. 4. *Phanaeus endymion* Harold, 1863. **A**. ♂, blue morph (typical; VMC). **B**. ♂, green morph (VMC). **C**. ♀, blue morph (typical; VMC). **D**. Lectotype, ♂ (by Christophe Rivier, Muséum national d'histoire naturelle, Paris, France) (MNHN).

Paralectotype (studied from photographs)
MEXICO • 1 ♀; Veracruz; “Ex-Musæo E. Harold. Museum Paris ex Coll. R. Oberthur. MNHN EC10554”; MNHN.

Non-type material revised (212 ♂♂, 247 ♀♀)

BELIZE – **Cayo** • 1 ♂; “Chiquibul Forest Reserve, Las Cuevas Research Station. 16°44′N, 88°59′W. June 2006. BMNH {E} 2006-141. C. Gillett & J. Kitson”; TAMU • 1 ♀; “San Ignacio, Chiquibul Fst Res. Las Cuevas Res. Station. 16°43′N, 88°59′W, 02–17.iv.2004. Deciduous forest, baited pitfall. coll. R. Paterson. Deciduous tropical forest. Baited pitfall trap. Cattle dung. Sub-site: Grano de Oro. Selective logged forest. Trap: 5. Date: 8/4/04”; TAMU. – **Orange Walk** • 1 ♂, 1 ♀; “17°50′04″N; 89°03′04″W, Rio Bravo Cons Area, La Milpa, Arqueolog. Site, (#12), 11–17.VII.1996, P. Kovarik ex. Flight intercept trap.”; JLSHC • 1 ♂; “Rio. Bravo Cons, Area, env. La Milpa ruins, 19–20.VII.1996, P.W. Kovarik, collector. La Milpa transect site #12, flight intercept trap”; JLSHC. – **Stann creek** • 1 ♂; “16°48′40″N, 88°30′34″W. Cockscomb Basin Wildlife Sanctuary, Outlier Trail nr. Campground. 3.VIII.2006. P. W. Kovarik, coll., FIT”; JLSHC.

GUATEMALA – **Alta Verapaz** • 1 ♂; “Sanahu. Fca. El Volcán. 14.VII.1988. J.P. Mauger & K. Meyer. 1200 msnm”; UVGC • 1 ♂; “Senahú, Fca. El Volcán. 850 msnm. 19-VII-88. Col: F. Herrera”; VMC • 2 ♀♀; “Colector Carlos García. Heces de humano. Sta. Lucia Lachua. Cobán. 16-09-00”; UVGC • 1 ♂, 1 ♀; “Santa Lucia Lachua. Junio 2001, heces humanas. Col. A. Higueros”; UVGC • 1 ♀; same collection data as for preceding; VMC. – **Huehuetenango** • 1 ♀; “Barillas, aldea Malpais. 1263m, N.1584733, W091.22285. Bosque nuboso. 21 VI 2009. Col. F. Camposeco, UV+M-Arc400w.”; VMC • 1 ♂; “Octubre 1992. Colector J. Monzón”; VMC. – **Izabal** • 1 ♂; “Livingston. Biotopo Chocón. Machacas. 28–29 V 2002. Heces de vaca. Guamil. Col. E.B. Cano.”; UVGC • 1 ♂; “Livingston. Biotopo Chocón. Machacas. 17–23 VI 1997. col. C.Avendaño. B. tropical húmedo inundable”; TAMU • 1 ♀; “Río Dulce, Fca. Talismán. 9 III 1997. G. Pereira”; TAMU • 1 ♀; “Cerro San Gil, Río Carbonera. 1390 msnm. III-2 IV 2007. Col. R. Granajo”; UVGC • 1 ♀; “El Estor, Cuiscoyol, GCN. 27 III 2010. J.Rivers”; UVGC • 1 ♂, 2 ♀♀; “Cerro San Gill, Carboneras, estación biol 400 msnm. 08 IX 1999. Bosque tropical. Trampa de pescado. Col. G. Goemans”; UVGC • 1 ♂; same collection data as for preceding; VMC • 1 ♀; “El Estor, CGN sector 215 con tala. 24 III 2010. J.Rivers”; UVGC • 2 ♀♀; same collection data as for preceding; VMC • 1 ♂; “El Estor, CGN sector pino guiscoyol. 1–3 IX 2009. J.Rivers”; VMC. – **Petén** • 1 ♀; “La Libertad, Bethel. 18 IX 1995. M.Jolon. En trampeo ratones había caído. *Oryxomis melesotis*”; UVGC • 1 ♀; “La Libertad, Bethel. 14 XII 1995. Trampa de roedores. M.Jolon.”; UVGC • 1 ♂; “San Miguel la Palotada. 15-V-1999. Col. Mjolon”; UVGC • 1 ♀; same collection data as for preceding; VMC • 1 ♀; “San Miguel la Palotada. 16-III-1999. Col. Mjolon”; UVGC • 1 ♂; “Dolores. 17-VIII-2003. Col. D. Ramírez”; UVGC • 1 ♂; same collection data as for preceding; VMC • 1 ♂; “Yaxhá. Area nucleo. 2 XII 1996. X. Leiva”; TAMU • 1 ♂; “Flores, El Remate. Biot. Cerro Cahuí. 7.VIII.1996. E.Cano”; UVGC.

MEXICO – **Chiapas** • 1 ♀; “Templo de las Inscripciones, Palenque, 22–VI–1993, Borde-copro-24 hrs. G. Halffter Col.”; VMC • 3 ♂♂, 4 ♀♀; “Palenque, Templo Inscripciones, 19/VII/1993, trap fruta #40, 17°29’0.9’’N, 94°2’49.07’’O, selva, 170 m, nocturna, G. y V. Halffter Cols.”; GHC • 1 ♂; same collection data as for preceding; VMC • 1 ♀; “Casa arqueólogos, Palenque, 22–VI–1993, Selva B-copro-24 hrs. G. Halffter Col.”; GHC • 1 ♂; “Casa Arqueólogos, Palenque, 20–VI–1993, Selva-copro A-24 hrs. G. Halffter Col.”; GHC • 1 ♂; “Palenque, 22–V–65, excrem. Humano.”; TAMU • 1 ♂; “Palenque, 22–V–65, col. Halffter-Reyes.”; TAMU • 4 ♂♂, 5 ♀♀; “Bonampak, Archeological Site, 16°44’N, 91°05’W, 300 m, 24–26–IX–77, forest, human feces, W. D. Edmonds, col.”; TAMU • 1 ♂, 1 ♀; same collection data as for preceding; VMC • 1 ♀; “Bonampak, Archeological Site, 16°44′N, 91°05′W, 300 m, I–IX–77, B. Kohlmann, col.”; TAMU • 1 ♂; “Bonampak, Archeological Site, 16°44′N, 91°05′W, 300 m, 24–IX–77, forest, carrion, B-1, W. D. Edmonds, col.”; TAMU • 1 ♂; “Bonampak, Archeological Site, 16°44′N, 91°05′W, 300 m, 25–IX–77, forest, human feces, W. D. Edmonds, col.”; TAMU • 3 ♂♂, 2 ♀♀; “Bonampak, Archeological Site, 16°44′N, 91°05′W, 300 m, 8–IX–77, forest, human feces, W. D. Edmonds, col.”; TAMU • 1 ♂; “Bonampak Archeological Site, 16°44′N, 91°05′W, 8–IX–77, forest, human feces, W. D. Edmonds, col.”; TAMU • 3 ♂♂, 1 ♀; “Bonampak, Agosto-1977, B. Kohlmann Col.”; VMC • 1 ♀; “Laguna Miramar, 14–15–X–1976, G. y V. Halffter, col.”; GHC • 1 ♀; “Chansayab, Lacanja, 24–I–77, P. Reyes C., Col.”; GHC • 1 ♀; “Lacanja, Chansayab, 26.IV.77, G. Aguirre, E. Frey, col.”; VMC • 1 ♂; “Lacanja, Chansayab, 6–II–77, S. Gallina, Col.”; VMC • 1 ♀; “Lacanjá-Chansayab, 300 m, 6–VIII–1977, camino a La Selva, M. Lamotte & B. Kohlmann col.”; TAMU • 1 ♂; same collection data as for preceding; VMC • 1 ♂; “Lacanja, VIII-1977, #11, Selva alta, Bert Kohlmann, Col.”; GHC • 1 ♂, 3 ♀♀; “Boca de Chajul, alt 110 m, 3-II-1984, M.A. Morón, C. Fragoso, F.J. Villalobos, cols.”; IEXA • 1 ♂; “4800’, 6.6 mi. W. El Bosque, VIII.25–29.1973, Cl. For. A. Newton 542”; TAMU – **Oaxaca** • 1 ♀; “Km Valle Nal. 550m 17/18-V-94, C. Deloya, R. Arce, coprotrampa”; IEXA • 1 ♂; “2000’, 6 mi S Valle Nac. VII.71, A. Newton 299”; TAMU • 1 ♂, 1 ♀; “Concepción Pápalo, 1800 m, 13-VII-97, hongos, G. Nogueira”; IEXA • 1 ♂; “La Chinantla, Sierra Norte. Selva mediana. 29-IIX-2010. 400 m. Pit-fall exc. hum. T-2. Alvarado, F. Col.”; FESC • 1 ♂; “Disto. De Yautepec, Juquila Mixes, VIII.1973, W. Miller”; VMC • 1 ♀; “La Nueva Esperanza, I–IX–1980, C. Huerta-G. Quintero-E. Rivera Cols.”; GHC • 102 ♂♂, 123 ♀♀; “Santa María y San Miguel Chimalapa, Benito Juárez/Santa María Chimalapa/San Antonio/San Francisco La Paz. Victor Moctezuma col.”; VMC. – **Quintana Roo** • 1 ♂, 1 ♀; “X-Can, VI-77, E. Welling, col.”; TAMU • 1 ♀; “Puerto Morelos, 3–IX–1984, G. y V. Halffter, cols. Selva baja-media, cebo excremento humano, noche/día”; GHC • 1 ♂; “Carrillo Puerto, 25–26–XII–82, G. Halffter y V. Halffter, Col.”; VMC • 1 ♀; “Carrillo Puerto, Septiembre 1984, A. Martínez, col.”; GHC. – **Veracruz** • 1 ♂; “Córdoba, 13–VII–36, E. W. Torrens niger d’Ols.”; GHC • 2 ♂♂, 6 ♀♀; “Córdoba, Guadalupe del Barreal, alt. 940 m, E. Santos, Col. NTP-1-C. 2-VIII-92. Julio”; IEXA • 4 ♂♂, 5 ♀♀; “Córdoba, Guadalupe del Barreal, alt. 940 m, E. Santos, Col. NTP-1-C. 2-VII-92. Junio”; IEXA • 1 ♂, 1 ♀; “Córdoba, Gpe. Barreal, alt. 940 m, E. Santos, Col. NTP-3. X-91”; IEXA • 1 ♂; “Córdoba, Gpe. Barreal, alt. 940 m, Cafetal, E. Santos, Col. NTP-3. VIII-91”; IEXA • 1 ♂; “Córdoba, Guadalupe del Barreal, alt. 940 m, E. Santos, Col. N-C. V-92”; IEXA • 2 ♂♂, 7 ♀♀; “Córdoba, Guadalupe del Barreal, VIII-91, cafetal, NTP-80, E. Santos, Col.”; IEXA • 1 ♂, 1 ♀; “Córdoba, Guadalupe del Barreal, VII-91, cafetal NTP-80, E. Santos, Col.”; IEXA • 1 ♀; “Córdoba, Guadalupe del Barreal, X-91, cafetal NTP-80, E. Santos, Col.”; IEXA • 3 ♂♂, 3 ♀♀; “Córdoba, Guadalupe del Barreal, IX-91, cafetal NTP-80, E. Santos, Col.”; IEXA • 1 ♂; “Cordoba, 18–20/July/62, Terry W. Taylor.”; TAMU • 1 ♂; “Cordoba, 15–VII–1965, coll. C. L. Hogue.”; VMC • 1 ♀; “Córdoba, cafetal, 900 m. 2/03/91. E. Santos, Col.”; IEXA • 6 ♂♂, 3 ♀♀; “Fortín de las Flores, September 1984, T. W. Taylor, col.”; TAMU • 2 ♂♂, 2 ♀♀; same collection data as for preceding; VMC • 1 ♂; “Fortín de las Flores, 14–VII–1973, R. R. Shelling and T. W. Taylor, colls.”; TAMU • 1 ♂; “Presidio, VII–48, A. Ramírez”; VMC • 1 ♂; “Presidio, VII–52, G. H”; GHC • 1 ♀; “Presidio, V–47, A. Ramírez”; VMC • 1 ♂; “Presidio, I. 43”; TAMU • 1 ♂, 3 ♀♀; “22 km W. Palma Sola (19°46’N, 96°25’W) on road to Plan de las Hayas (±800 m), 30–31/VIII/1976, W. D. Edmonds and Bert Kohlmann cols. Code: K22-HF-F. Collected in baited pitfall trap: HF=human feces; SF=swine feces; CC=carrion. Habitat: F=remains of forest; P=pasture (clearing).”; TAMU • 3 ♀♀; “1 km al E de Jalcomulco, NTP-80, alt. 500 m. 6-XI-91. Luis Quiroz, col.”; IEXA • 1 ♂, 1 ♀; “Jalcomulco, Cerro Brujo, 06-VIII-15. 400 m. CT3 Bosque, selva baja, Álvaro Hernández Rivera Col.”; FESC • 1 ♂; “Xalapa, 30/Julio/80, Col. E. Aranda D.”; IEXA • 1 ♂, 1 ♀; “Xalapa, Chiltoyac, 20/VI/15, 1000 m. NT2 Selva baja, Álvaro Hernández Rivera Col.” ; FESC • 1 ♀; “Xalapa, Chiltoyac, 1000 m. NT1 Bosque, Álvaro Hernández Rivera Col.”; FESC • 2 ♀♀; “Xalapa, Chiltoyac, 20/VI/15, 1000 m. CT2 Potrero, Álvaro Hernández Rivera Col.”; FESC • 1 ♂, 1 ♀; “Xalapa, Chiltoyac, 1000 m. CT3 Bosque, Álvaro Hernández Rivera Col.”; FESC • 2 ♂♂; “Xalapa, Tiro de Hayas, 1200 m. NT2 Bosque, Álvaro Hernández Rivera Col.”; FESC • 1 ♀; “Sumidero, Tiro de Hayas. 16 sep - 5 de oct 1989. L. Arellano col. Bosque mesófilo perturbado. 1366 m. NTP 80”; GHC • 1 ♂; “N.C 600”; GHC • 2 ♀♀; “Veracruz, 1962–63, leg. Epping.”; GHC • 1 ♂; “Escoloa, 15 july 1972, Terry W. Taylor, coll.”; TAMU • 3 ♀♀; “Ixtaxoquitlán, Cerro Chicahuaztla. 1540 m. VI.87. Col. L. Delgado”;

IEXA • 4 ♂♂, 4 ♀♀; "El Trianón, Cerro La Campana y R. San Gabriel. V-VI-2004. Mesófilo. Col. exc. hum. Escobar y Pineda Cols."; FESC • 3 ♂♂, 1 ♀; same collection data as for preceding; IEXA • 1 ♀ ; "Tatahuicapan de Juárez, López Arias, Magallanes. 21-VI-2002. F. Escobar S. Col. Fragmentos de selva alta. Trampa #8. Cebo-exc. humano"; FESC • 1 ♀; "Tatahuicapan de Juárez, El Mirador, Magallanes. 21-VI-2002. F. Escobar S. Col. Fragmentos de selva alta. Trampa #2. Cebo-exc. humano"; FESC • 1 ♂, 4 ♀♀; "Catemaco, Pipiapan, Parque de la Flora y Fauna Silvestre Tropical, 600 m., VIII-1991, Selva Med. Per. F. Capistran Col. NTP"; IEXA • 1 ♀; "Catemaco, Est. Biol. Trop. Los Tuxtlas, Bosq. Trop. Perennifolio, 17 VIII 90, M. F. Favila y A. Díaz. Cols."; VMC • 1 ♂; "Los Tuxtlas. Estación Biológica UNAM. Selva alta. 01-VII-2010. 200 m. Pit-fall exc. hum. T-12. Alvarado, F. Col."; FESC • 3 ♀♀; "Los Tuxtlas, 21/VIII/87, G. Halffter y V. Halffter, Cols."; GHC • 1 ♂; "Guadalupe Victoria. PIA. Tm10."; FESC • 1 ♀; "T6m."; FESC • 1 ♂, 1 ♀; "Km 7.5, Carr. El Castillo, 15-oct-1994, L. Arellano y R. Sánchez cols. Alt. 1100 m, Bosque de pino/café, trampa necropermanente."; TAMU • 1 ♀; "Apazapan, 19°19′18″N, 96°42′39″W, VIII-2000, 280 m, E. Montes de Oca, col."; TAMU • 2 ♂♂; "km 50 Las Choapas-Río Playa, 30-XII-1977, carroña, selva media, Col. B. Kohlmann"; TAMU • 1 ♀; "Dos Amates (cerca de Catemaco), V-62, G. Halffter leg."; TAMU • 2 ♂♂; "Dos Amates (Catemaco), IX–1967, G. Halffter. Leg."; GHC • 1 ♂; same collection data as for preceding; VMC • 1 ♀; "Dos Amates, Alt. 300 m. 29-XI-67. Col. P. Reyes C. Selva tropical perturbada. Cebo excremento humano. Noche-Día."; VMC • 1 ♀; "Estación de Biología Tropical Los Tuxtlas, VIII–1984, A. Martínez, Col."; GHC • 1 ♀; "20 km al E de Sontecomapan, 11-IV-69, H. Cabrera, col."; GHC. – **Yucatán** • 1 ♂, 1 ♀; "Municipio de Tizimín, 18-VII-13, 200 m. Bosque (Zapotal). Colecta trampa copro pit-fall #6. Alvarado, F. Col."; FESC • 3 ♂♂, 2 ♀♀; "Municipio de Tizimín, -VII-13, 200 m. Bosque (Espita). Colecta trampa copro pit-fall #3. Alvarado, F. Col."; FESC • 2 ♂♂, 4 ♀♀; "Municipio de Tizimín, 28-VII-13, 200 m. Bosque (Santa Marta). Colecta trampa copro pit-fall #25. Alvarado F. Col."; FESC.

Type locality

Mexico, Veracruz, Córdoba.

Redescription

Major male

HEAD. Clypeus bidentate, black on anterior margin, dark metallic blue-green or green on posterior portion, rough sculpture. Genae dark metallic blue-green or green with rough sculpture. Front black, with dark metallic blue-green or green on portions adjacent to cephalic horn. Cephalic horn black, curved posteriorly over pronotum (Figs 2B, 4A–B).

PRONOTUM. Uniformly dark blue, dark metallic blue-green or dark metallic green, becoming black beneath posterolateral angles. Carinate, distinctly developed keel in the middle of anterior pronotal margin, or keel completely effaced. Disc triangular, flat, with two distinctly developed tubercles on anterior portion. Triangle with lightly granulate or nearly smooth sculpture, scabriculous, impunctate. Sides with almost smooth sculpture, scabriculous, with superficially impressed punctures. Lateral lines of triangle straight. Posterolateral angles short, widened, sometimes lightly projected posteriorly. Lateral fossae distinctly impressed. Basal fossae obtusely oval, superficially to deeply impressed. Posterior margin with superficially to deeply impressed punctures (Figs 2B, 4A–B).

ELYTRA. Striae fine, dark metallic blue-green, or dark metallic green, scabriculous, impressed basally as distinct fossae, with distinctly impressed to effaced punctures. If punctures distinctly impressed, each forming a distinct fossa, giving a completely roughened surface to first and second striae. If punctures effaced, interstriae completely smooth. Interstriae black, with smooth surface, scabriculous, superficially impressed to effaced punctation. Sutural margin without apical tooth (Figs 4A–B).

PROTIBIAE. Quadridentate with apical spine.

Tergite VIII. Dark metallic blue-green, or dark metallic green, scabriculous; with rough, distinctly impressed punctures. Basal margin with setae variable in size.

Genitalia. Right lobe of endophallite copulatrix more developed than left lobe. Right lobe obtusely triangular in shape. Left lobe obtusely lobed inferiorly, obtusely triangular superiorly. Central ridge less developed than central column (Fig. 1D).

Minor male

Like the major male, except for the reduction of secondary sexual characters (i.e., cephalic horn, pronotal triangle and tubercles, and pronotal posterolateral angles).

Female

Similar to the male, except for the head showing a cephalic trituberculate carina with similar in size, nearly aligned, conical tubercles; frons with distinctly to superficially impressed punctures; pronotal sculpture completely smooth, with superficially impressed punctures; shining black, variable in size area on central portion of pronotal disc; pronotal process trituberculate, with posterior concavity; middle pronotal tubercle more developed, dentiform or rounded, always more frontally projected than lateral tubercles; lateral tubercles obtusely rounded or carinate; posterior pronotal midline superficially impressed to completely effaced (Fig. 4C).

Variation

Mean length 17.9 mm (13.9–20 mm). The typical colour morph is dark metallic blue-green (Figs 4A, C), but a less frequent dark metallic green morph (Fig. 4B) is also found, while scarce specimens are completely bright metallic green. The interstriae are completely dark metallic blue-green or dark metallic green in some specimens. The rarest specimens from Chiapas and Veracruz show a bright metallic yellow or red sheen on head, pronotum and elytra. Variation in the interstrial punctation is observed in the whole distribution area of *P. endymion*. The size of the right and left lobes of the endophallite copulatrix is not homogeneous.

Distribution

From Veracruz and the Yucatan Peninsula to Belize and northern Guatemala (Fig. 15).

Remarks

The lectotype (a minor male), a female paralectotype and several specimens (n=42) from the type locality cited by Harold (1863) were used for the redescription of *P. endymion*, that was complemented with specimens from its whole distribution area. As a consequence, the high intraspecific variation of *P. endymion* is adequately represented herein. Although *P. endymion* is a polymorphic species, closely related species are confidently separated by differences in the pronotal morphology of males and females, elytral interstriae, and genital morphology.

Phanaeus funereus Balthasar, 1939 stat. rev.

Figs 1E, 2C, 5, 17, 18F, 19F

Phanaeus (s. str.) *funereus* Balthasar, 1939: 241.

Phanaeus funereus – Edmonds 1972: 830; 1994: 3, 9, 45–46 (as synonym of *P. pyrois*). — Howden & Young 1981: 137 (in part). — Arnaud 1982: 116 (as synonym of *P. blanchardi*); 2002b: 97 (as subspecies of *P. pyrois*). — Krajcik 2006: 152 (as synonym of *P. pyrois*). — Solís & Kohlmann 2012: 8 (as synonym of *P. pyrois*). — Edmonds & Zídek 2012: 3, 5, 13 (as synonym of *P. pyrois*). — Chamorro *et al*. 2019: 220–221 (as synonym of *P. pyrois*).

Phanaeus (*Phanaeus*) *funereus* – Martínez & Pereira 1967: 53, 68 (as synonym of *P. olsoufieffi*).

Phanaeus (*Notiophanaeus*) *pyrois funereus* – Arnaud 2002b: 97–98 (as subspecies of *P. pyrois*). — Chamorro *et al*. 2019: 220 (as synonym of *P. pyrois*).

Phanaeus pyrois funereus – Kohlmann *et al*. 2018: 79, 93 (as subspecies of *P. pyrois*).
Phanaeus (s. str.) *funereus* – Chamorro *et al*. 2019: 220–221 (as synonym of *P. pyrois*).

Non *Phanaeus pyrois* (error) – Medina *et al*. 2001: 140 (in part). — Moctezuma & Halffter 2017: 55 (in part). — Moctezuma *et al*. 2017: 114, 130 (in part). — Chamorro *et al*. 2018: 98.

Diagnosis

Easily diagnosed species by the dull black colour with dull red sheen dorsally; and striae not strongly impressed basally (Fig. 5). Additionally, the major male with a keel absent in the middle of anterior pronotal margin (Figs 2C, 5A); endophallite copulatrix as Fig. 1E. The major female with the pronotal process lacking concavity; middle pronotal tubercle more developed, slightly projected frontally than lateral tubercles; all pronotal tubercles rounded; and posterior pronotal midline completely effaced (Fig. 5B).

Type material (studied from photographs, 1 ♂)

Holotype

ECUADOR • ♂, Balthasar 1939: 242 (Fig. 5C); "*P. funereus* (illegible data). Dr. V. Balthasar det. / Mus. Nat. Pragae Inv. 26347 / ex coll. V. Balthasar National Museum Prague, Czech Republic/ Pucay F.O.I0.6.05. / ♂ / H. Blut determ. *Phanaeus blanchardi* Olsouf. / Fesche det. *Phanaeus pyrois* Bts. / TYPUS"; NMPC.

Non-type material revised (5 ♂♂, 7 ♀♀)

COLOMBIA – **Chocó** • 1 ♂; "Quibdó. La Troje - Sept. 972. Coll. Martínez"; VMC.

ECUADOR – **Esmeraldas** • 1 ♂; "Tsejpí Ex.Pitfall heces humanas 17/02/01 I. Yépez"; VMC • 1 ♂; "Tsejpí. Ex.Pitfall heces humanas. 18/02/01. I. Yépez"; TAMU • 1 ♀; "Colón del Ónzole. Ex.Pitfall carroña. 04/05/01 I. Yépez"; TAMU.– **Guayas** • 1 ♂; "Pucay (Bucay). F. Ohs. 14.7.05."; GHC. – **Los Ríos** • 1 ♂, 1 ♀; "Quevedo, Pichilingue (75 m) V-76. A. Martínez col."; TAMU • 2 ♀♀; "Quevedo, Pichilingue. V-76. A. Martínez, leg."; GHC • 1 ♀; same collection data as for preceding; VMC. – **Manabí** • 1 ♀; "300 m, 90kmWSW Sto. Domingo. 73 km NE Chone. 6–9.vi.76. S. Peck. 3 for. dung traps3–5"; IEXA. – **Pichincha** • 1 ♀; "Quito. III.915"; TAMU.

Type locality

Ecuador, Pucay (probably Bucay).

Redescription

Major male

HEAD. Clypeus bidentate, dull black on anterior margin, dull red on posterior portion, roughened sculpture. Genae dull black, with dull red sheen, rough sculpture. Front dull black. Cephalic horn black, curved posteriorly over pronotum (Figs 2C, 5A).

PRONOTUM. Keel absent in the middle of anterior pronotal margin. Disc triangular, flat; with two elongate, weakly developed tubercles on anterior portion. Triangle dull black, scabriculous, with almost effaced punctures, smooth sculpture. Sides dull black-red; scabriculous, with smooth sculpture, almost effaced punctures. Lateral lines of triangle straight. Posterolateral angles short, slightly widened. Lateral fossae distinctly impressed. Basal fossae absent or almost effaced. Posterior margin with almost effaced punctures (Figs 2C, 5A).

ELYTRA. Striae fine, smooth, dull black, scabriculous, not strongly impressed basally; with dull green or blue-green sheen, almost effaced punctures. Interstriae dull black, scabriculous, with smooth surface, almost effaced to effaced punctures. Sutural margin without apical tooth (Fig. 5A).

Protibiae. Quadridentate with apical spine.

Tergite VIII. Dull black, with dark red to dark brown sheen; scabriculous sculpture; rough, distinctly impressed punctures. Basal margin with setae variable in size.

Genitalia. Right lobe of endophallite copulatrix larger in size than left lobe. Right lobe obtusely triangular in shape, with superior portion projected frontally. Left lobe lobed inferiorly, bent superiorly. Central ridge less developed than central column (Fig. 1E).

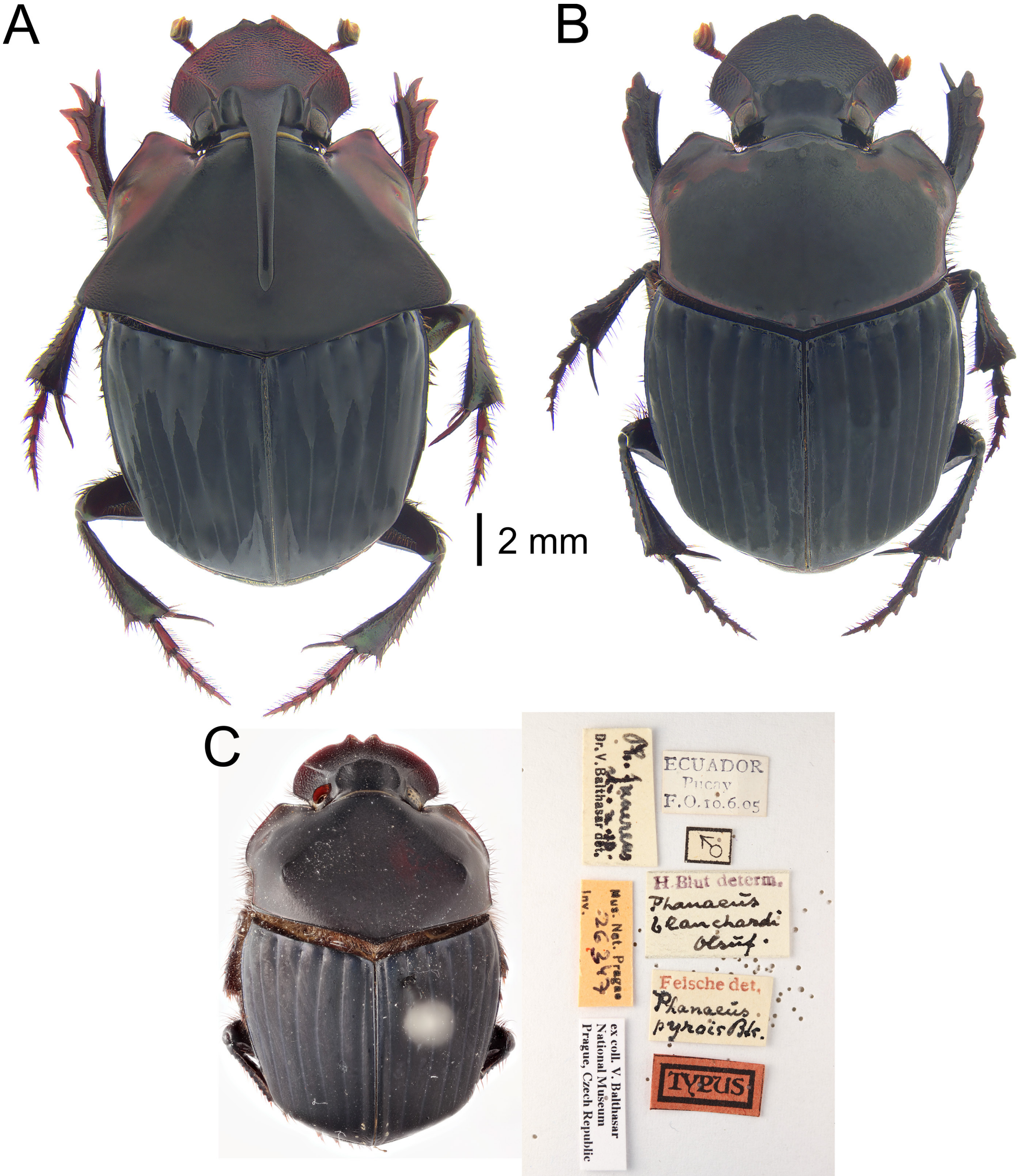

Fig. 5. *Phanaeus funereus* Balthasar, 1939 stat. rev. **A**. ♂ (TAMU). **B**. ♀ (TAMU). **C**. Holotype, ♂ (by Jiří Hájek, Národní Muzeum, Prague, Czech Republic) (NMPC).

Minor male

Like the major male, except for the attenuation of the secondary sexual characters (i.e., cephalic horn, pronotal triangle and tubercles, and pronotal posterolateral angles; Fig. 5C).

Female

Similar to the male, except for the head showing a cephalic trituberculate carina, with similar in size, conical tubercles; middle tubercle more frontally projected than lateral tubercles; frons with almost effaced punctures; pronotal sculpture completely smooth, impunctate or with almost effaced punctures; pronotum almost completely dull black, dark metallic red laterally and posteriorly; pronotal process trituberculate lacking concavity; middle pronotal tubercle more developed, slightly projected frontally than lateral tubercles; all tubercles rounded; posterior pronotal midline completely effaced (Fig. 5B).

Variation

Mean length 19.3 mm (16–21.9 mm). The male specimen from Colombia has acute posterolateral pronotal angles that are posteriorly projected.

Distribution

Pacific slope of the Andes, north-central Ecuador and Colombia (Fig. 17). The Colombian specimen represents the first record of *P. funereus* from Colombia.

Remarks

Phanaeus funereus was considered by previous authors as a synonym of *P. pyrois* (Martínez & Pereira 1967; Edmonds 1994; Edmonds & Zídek 2012; Solís & Kohlmann 2012; Chamorro *et al*. 2019). Nevertheless, a diagnosis and a key to separate both species are provided by us. As a consequence, full species status is confidently assigned to *P. funereus*. The lectotype (a minor male) and some specimens from Ecuador (n = 12) were used for the redescription of *P. funereus*. The only specimen studied from Colombia differed in the posterolateral angles of pronotum, but not in colour pattern, pronotal and elytral sculpturing, or genital morphology.

Phanaeus halffterorum Edmonds, 1979
Figs 1F, 15, 18G, 19G

Phanaeus halffterorum Edmonds, 1978: 321 (nomen nudum).
Phanaeus halffterorum Edmonds, 1979: 99, 102–105, figs 1–3, 6–8 (in part).

Phanaeus halffterorum – Halffter & Edmonds 1982: 88–89 (in part). — Anduaga & Halffter 1991: 157 (in part). — Delgado-Castillo *et al*. 1993: 125 (in part). — Deloya *et al*. 1993: 21, 39 (in part); 2014: 77 (in part). — Anduaga 2000: 125, 130 (in part). — López-Guerrero & Halffter 2000: 241 (in part). — Arnaud 2002b: 96 (in part). — Price 2005: 197 (in part); 2007: 17, figs 52–54. — Edmonds 2006: 31–32, 36, fig. 7 (in part). — Ceballos *et al*. 2009: 397. — Edmonds & Zídek 2012: 5 (in part). — Krajcik 2006: 150. — Moctezuma & Halffter 2017: 52, 54–55, fig. 23 (in part). — Moctezuma *et al*. 2017: 113–115, 118–119, 122, 130–132, figs 1–5; 2019: 253, fig. 5. — Lizardo *et al*. 2017: 273, 275, 292, fig.13 (in part). — Kohlmann *et al*. 2018: 69, 81, 88–89. — Gillett & Toussaint 2020: 2.

Phanaeus (*Notiophanaeus*) *halffterorum* – Edmonds 1994: 2, 8–9, 19, 39, 41, 43–44, 101, figs 211, 213, 217–218, 221 (in part); 2003: 61, 65 (in part). — Arnaud 2002b: 95 (in part). — Edmonds & Zídek 2012: 3, 12, figs 134–135, 137, 143–147 (in part). — Lizardo *et al*. 2017: 272 (in part). — Kohlmann *et al*. 2018: 80. — Zaragoza-Caballero *et al*. 2019: 43.

Type material

Holotype (not studied)
MEXICO • ♂, Edmonds 1979: 99; State of Mexico, Temascaltepec; CAS.

Paratypes revised (6 ♂♂, 2 ♀♀)
MEXICO – **State of Mexico** • 1 ♂; "5 km E Temascaltepec, Real de Arriba (2200 m), 10–VII–1976, fungus, oak-pine forest, W. D. Edmonds, P. Reyes, B. Kohlmann cols."; IEXA • 1 ♀; same collection data as for preceding; TAMU • 1 ♂, 1 ♀; same collection data as for preceding; VMC • 2 ♂♂; "8 km W Temascaltepec, 2360 m, 11–VII–76, fungus in pine-oak forest, W. D. Edmonds, P. Reyes, B. Kohlmann cols."; TAMU • 1 ♂; same collection data as for preceding; VMC • 1 ♂; "Real de Arriba, VII–1932, 6300 ft, México D. F., Hinton coll., BM 1939–583"; TAMU.

Type locality

Mexico, State of Mexico, Temascaltepec.

Distribution

Central Trans-Mexican Volcanic Belt, State of Mexico and Morelos (Fig. 15).

Remarks

Mean length 17.4 mm (13.4–19.9 mm). The specimens from Morelos (Deloya *et al*. 1993) were not studied by us. This species was erroneously reported from Mexico City (Arnaud 2002b). This mistake is attributed to Hinton (1935), who recorded it from Real de Arriba, Mexico D.F. Real de Arriba is actually located in the State of Mexico. Despite the fact that Moctezuma *et al*. (2017) split *P. halffterorum* and *P. bravoensis*, the colouration pattern of *P. halffterorum* remains as indicated by Edmonds (1979), with bright metallic green or dark metallic blue specimens. In a review of the immature dung beetles of Scarabaeinae (Edmonds & Halffter 1978), the name *P. halffterorum* Edmonds, 1978 was published. Nevertheless, this may be considered as a nomen nudum under Article 13 of the Code (ICZN 1999). Consequently, the same name was available later for the same or a different concept under Arts 21, 50; while *P. halffterorum* Edmonds 1979 must be considered the available authorship and date.

To the original description of the male we add that the right lobe of the endophallite copulatrix is more developed than the left lobe; the right lobe ois btusely triangular; the left lobe is obtusely rectangular; the central ridge lis ess developed than the central column (Fig. 1F). For the female can be added that the trituberculate cephalic carina has conical, nearly aligned tubercles; the middle tubercle is more raised than the lateral tubercles; the pronotal process is trituberculate, with a posterior concavity; all the tubercles are rounded; the middle tubercle is slightly more developed and projected frontally than the lateral tubercles; the pronotal midline is distinctly impressed, with superficially impressed punctures; the pronotal surface is smooth, with almost effaced punctures.

Phanaeus huichol Moctezuma, Sánchez-Huerta & Halffter, 2017
Figs 1G, 15, 18H, 19H

Phanaeus huichol Moctezuma *et al*., 2017: 123.

Phanaeus huichol – Kohlmann *et al*. 2018: 69, 81, 83, 88. — Moctezuma *et al*. 2019: 252–253, fig. 5.
Phanaeus (*Notiophanaeus*) *huichol* – Kohlmann *et al*. 2018: 81.

Type material

Holotype

MEXICO • ♂, Moctezuma *et al*. 2017: 123 (revised); Jalisco, Mazamitla; TAMU.

Non-type material revised (18 ♂♂, 20 ♀♀)

MEXICO – **Jalisco** • 1 ♀; "Sierra de Talpa (Los Venados CT). 12–15-VIII-2017. 1570 m. G. Nogueira Col."; GHC • 2 ♂♂, 1 ♀; "Sierra de Talpa. 20°22′35.29″ N, 104°49′8.87″ O, 14/VIII/2015. 1380 m. G. Nogueira Col."; VMC • 2 ♂♂, 1 ♀; "Sierra de Talpa. 20°22′35.29″ N, 104°49′8.87″ O, 22–26/ VIII/2013. 1595 m. G. Nogueira Col."; VMC • 2 ♂♂, 1 ♀; "Tequila, Volcán de Tequila. 20°47′18.03″ N, 103°50′28.99″ O, 25/VIII/2012. 1890 m. G. Nogueira Col."; VMC • 2 ♂♂, 1 ♀; "Tequila, Volcán de Tequila. 20°47′18.03″ N, 103°50′28.99″ O, 24–27/VIII/2012. 1665 m. (CT). G. Nogueira Col."; VMC • 1 ♂, 2 ♀♀; "Telcome, Yolosta. 20°10′40.113″ N, 103°41′25.35″ O, 2/VII/2017. D1–2. 1845 m. G. Nogueira Col."; VMC • 4 ♂♂, 4 ♀♀; "El Jacal, 1830 m, 12–14/VIII/94. G. Nogueira col."; IEXA • 1 ♂, 2 ♀♀; "S. Manatlán, 13/16–IX–95, 1650 m, G. Nogueira col."; IEXA • 3 ♂♂, 2 ♀♀; "S. Manatlán, 18/20–IX–1995, 1400 m, G. Nogueira col."; IEXA • 1 ♂, 4 ♀♀; "S. Manatlán, 18/20–IX–1995, 1650 m, G. Nogueira col." ; IEXA. – **Michoacán** • 1 ♀; "12 km S Uruapan, Cascada Tzararacua. 1450 m. 21-VIII-97 horse dung"; VMC.

Type locality

Mexico, Jalisco, Mazamitla.

Distribution

Sierra Madre Occidental; Jalisco, northern Michoacán, Nayarit and southern Sinaloa (Fig. 15). The first record of *P. huichol* from Michoacán is presented herein.

Remarks

The original description of *P. huichol* indicates that the colour pattern varies from dark metallic green, bright metallic green, to dark green with blue sheen. After revising additional specimens, a bright metallic green morph with red sheen was found by us. To the original description we add the elytral striae impressed basally as distinct fossae; and central ridge and column of endophallite copulatrix similar in size (Fig. 1G). For the female, the head showing a cephalic trituberculate carina with middle tubercle more frontally projected, carinate and less prominent than lateral tubercles; frons with almost effaced punctures; pronotal sculpture completely smooth, with almost effaced punctures; pronotal process trituberculate, with posterior concavity, followed posteriorly by reduced, rounded tubercle; middle tubercle dentiform or rounded, more developed and projected frontally than lateral tubercles; lateral tubercles rounded or carinate; posterior pronotal midline completely effaced.

Phanaeus jackenioi sp. nov.

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Figs 1H, 2D, 6, 15, 18I, 19I

Diagnosis

Easily diagnosed species by the bright metallic green colour; striae wide, roughened, impressed basally as distinct fossae, with distinctly impressed punctation; the major male with posterolateral angles of pronotum sharply acute, elongate, projected posterolaterally (Figs 2D, 6A); the major female with pronotal process without frontal concavity; rounded pronotal tubercles, nearly aligned, with middle tubercle more developed than lateral tubercles (Fig. 6B).

Etymology

We are honoured to dedicate this new species to Jack Schuster and Enio Cano. They have significantly contributed to the knowledge of the Guatemalan scarab beetles, particularly of the family Passalidae.

Type material (11 ♂♂, 5 ♀♀)

Holotype

GUATEMALA • ♂; Guatemala; “10/XI/1978. Eugenia de Minondo”; UVGC.

Paratypes

GUATEMALA – **Chimaltenango** • 1 ♀; “Parramos, El Injertal. 13/IX/1978. Eugenia de Minondo”; VMC. – **Chiquimula** • 1 ♂; “Chiquimula. 7–14 II 2007. R. Chicas”; VMC. **– Guatemala** • 1 ♂; “nr. Barranca Sta. Catarina. Pinula, Z-14. 22 VI 1993. E. Póll leg. Luz incandescente”; VMC • 1 ♂; “Ciudad. 13 X 1982. S. Roesch”; TAMU • 1 ♂; “Guatemala. 214 VIII 1984. J. Perez”; CNMN • 1 ♀; “Sta. Rosa z.16. Kanajuyú 2. 22.XI.2000. M.L.Muller”; UVGC. – **Huehuetenango** • 1 ♂; “Nentón. Camino entre Nentón y San José Chaquial. 22 VII 1998. Bosque seco. E.B. Cano Heces de perro”; UVGC • 1 ♂; “Chivacabé. 31 X 1993. E. Cano”; UVGC • 1 ♂; same collection data as for preceding; VMC • 1 ♂; “La libertad, La Mesilla, finca El Bolsón. 24 IX 2011. Cafetal. Luz UV + HG. Col. M. Acevedo & H. Enríquez.”; TAMU • 1 ♀; same collection data as for preceding; UVGC • 1 ♀; same collection data as for preceding; VMC. – **Sacatepéquez** • 1 ♀; “Bosque pasado. Comunidad Ruiz, km35 a Mixco Viejo via San Juan Sac. 29-X-1978. E. Duarte”; TAMU. – **Zacapa** • 1 ♂; “San Lorenzo, cerca de La Marmolera. 5 XII 2001. En heces de vaca. A. Higueros, leg. Bosque de pino, aprox. 1700msnm”; UVGC.

MEXICO – **Chiapas** • 1 ♂; “Santa Rosa, VIII-1962. G. Halffter leg.”; TAMU.

Type locality

Guatemala, Guatemala.

Description

Major male (holotype)

Length 17.1 mm.

Head. Clypeus bidentate, black on anterior margin, bright metallic green on posterior portion, with roughened sculpture. Genae bright metallic green, with roughened sculpture. Front black, with dark metallic blue-green on portions adjacent to cephalic horn. Cephalic horn black, curved posteriorly over pronotum (Figs 2D, 6A).

Pronotum. Uniformly bright metallic green, becoming black on lateral margins of posterolateral angles. Keel absent in the middle of anterior pronotal margin. Disc triangular, flat, with two distinctly developed tubercles on anterior portion. Triangle with lightly granulate, scabriculous, impunctate. Sides scabriculous, with smooth sculpture, superficially impressed punctures. Lateral lines of pronotal triangle straight. Posterolateral angles sharply acute, elongate, projected posterolaterally. Lateral fossae distinctly impressed. Basal fossae obtusely oval, deeply impressed. Posterior margin distinctly punctate (Figs 2D, 6A).

Elytra. Thick, roughened, bright metallic green striae, scabriculous, impressed basally as distinct fossae, with distinctly impressed punctation. Interstriae black, partially roughened, scabriculous, with almost effaced punctation; except for almost completely rough, bright metallic green first stria. Sutural margin without apical tooth (Fig. 6A).

Protibiae. Quadridentate with apical spine.

Tergite VIII. Bright metallic green; scabriculous; with rough, distinctly impressed punctures. Basal margin with thick, small setae.

Genitalia. Right lobe and left lobe of endophallite copulatrix similar in size. Right lobe obtusely triangular in shape, with apical portion projected posteriorly. Left lobe bent posteriorly, convex superiorly, lobed inferiorly. Central ridge and column similar in size (Fig. 1H).

Minor male

Like the major male, except for the reduction of secondary sexual characters (i.e., cephalic horn, pronotal triangle and tubercles, and pronotal posterolateral angles).

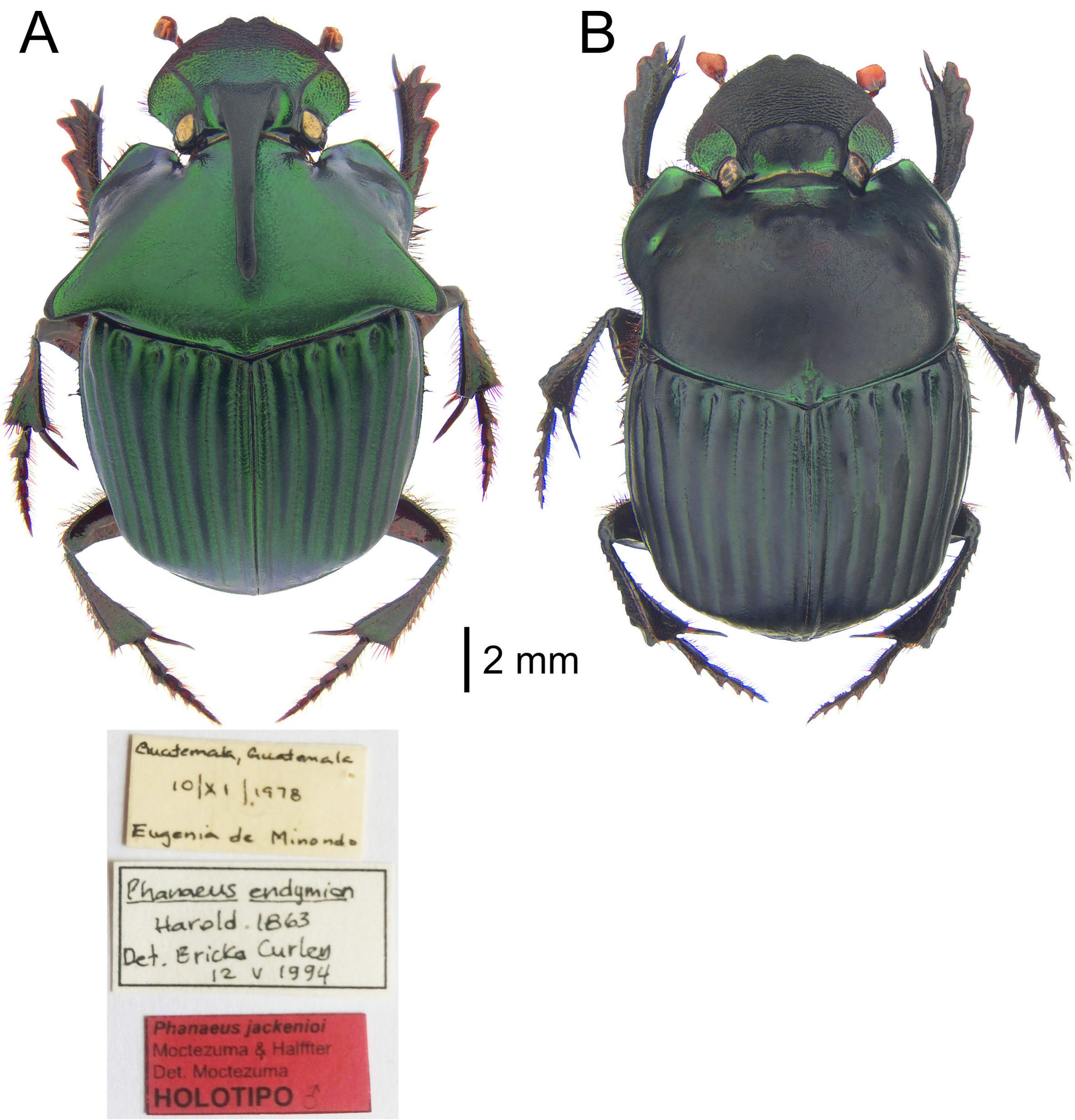

Fig. 6. *Phanaeus jackenioi* sp. nov. **A**. Holotype, ♂ (UVGC). **B**. ♀ (VMC).

Female
Similar to the male, except for the head showing a cephalic trituberculate carina; carinate middle tubercle, less raised, slightly more frontally projected than lateral tubercles; lateral tubercles obtusely conical; frons with distinctly impressed punctures; pronotal sculpture completely smooth, with superficially impressed punctures; pronotum bright metallic green, with shining black, variable in size area on central portion of disc; pronotal process trituberculate, lacking concavity rounded pronotal tubercles, nearly aligned, with middle tubercle more developed than lateral tubercles; posterior pronotal midline completely effaced (Fig. 6B).

Variation
Mean length 17.3 mm (16.2–18.4 mm).

Distribution

Inner slope of the Sierra Madre de Chiapas, south-central Guatemala and southeastern Chiapas (Fig. 15).

Remarks

The type series of *P. jackenioi* sp. nov. was originally labelled as *P. pyrois*. The new species was referred to as *P. endymion* by Edmonds (1994), Edmonds & Zídek (2012), Lizardo *et al*. 2017, Moctezuma & Halffter (2017) and GBIF Secretariat (2019a).

Phanaeus malyi Arnaud, 2002a
Figs 1I, 2E, 7, 16–17, 18J, 19J

Phanaeus pyrois malyi Arnaud, 2002a: 4.

Phanaeus pyrois – Bates 1887: 58 (in part, as a variety of *P. pyrois*). — Kohlmann *et al*. 2018: 78 (in part).
Phanaeus blanchardi (error) – Olsoufieff 1924: 92 (not *P. blanchardi* Harold, 1871: 114, in part). — Vulcano & Pereira 1967: 575 (in part). — Martínez & Pereira 1967: 68 (in part, as synonym of *P. funereus*). — Edmonds 1972: 830, fig. 256 (in part); 1994: 3, 8, 45–46 (in part, as synonym of *P. pyrois*). — Arnaud 1982: 116 (in part, as synonym of *P. funereus*). — Krajcik 2006: 152 (as synonym of *P. pyrois*). — Edmonds & Zídek 2012: 5, 13 (in part, as synonym of *P. pyrois*). — Chamorro *et al*. 2019: 220–221 (in part, as synonym of *P. pyrois*).
Phanaeus pyrois malyi – Arnaud 2002b: 97 (as subspecies of *P. pyrois*). — Solís & Kohlmann 2012: 1, 9–10 (as subspecies of *P. pyrois*). — Edmonds & Zídek 2012: 1, 8, 13 (as synonym of *P. pyrois*). — Krajcik 2006: 152 (as subspecies of *P. pyrois*). — Kohlmann *et al*. 2018: 78.
Phanaeus (Notiophanaeus) pyrois malyi – Arnaud 2002b: 96 (as subspecies of *P. pyrois*).
Phanaeus malyi – Solís & Kohlmann 2012: 1, 7, 31, fig. 1. — Edmonds & Zídek 2012: 3, 6 (as synonym of *P. pyrois*). — Kohlmann *et al*. 2018: 67–69, 78–80, 82, 88–89, figs 8, S1b. — Gillett & Toussaint 2020: fig. 4.
Phanaeus (*Notiophanaeus*) *malyi* – Kohlmann *et al*. 2018: 78.

Non *Phanaeus olsoufieffi* (error) – Balthasar 1939: 242 (in part). — Edmonds 1994: 8, 45–46 (in part, as synonym of *P. pyrois*). — Arnaud 2002b: 96 (in part). — Krajcik 2006: 152 (in part, as synonym of *P. pyrois*). — Edmonds & Zídek 2012: 3, 5–6 (in part, as synonym of *P. pyrois*).
Non *Phanaeus bothrus* (error) – Blackwelder 1944: 209 (in part). — Martínez & Pereira 1967: 68 (in part, as synonym of *P. funereus*). — Edmonds 1994: 8, 45 (in part, as synonym of *P. pyrois*). — Arnaud 2002b: 97 (in part, as synonym of *P. olsoufieffi*). — Krajcik 2006: 152 (in part, as synonym of *P. pyrois*). — Edmonds & Zídek 2012: 3, 5 (in part, as synonym of *P. pyrois*).

Non *Phanaeus* (*Phanaeus*) *blanchardi* (error) – Martínez & Pereira 1967: 68 (in part, as synonym of *P. funereus*).
Non *Phanaeus* (*Phanaeus*) *olsoufieffi* (error) – Martínez & Pereira 1967: 68 (in part, as synonym of *P. funereus*).
Non *Phanaeus* (*Notiophanaeus*) *pyrois olsoufieffi* (error) – Arnaud 2002b: 96 (in part).
Non *Phanaeus pyrois olsoufieffi* (error) – Arnaud 2002b: 98; 2018: 4 (in part).

Diagnosis

Easily diagnosed species by the bright black colour with red-green sheen on frontolateral angles of pronotum (Fig. 2E); elytral striae fine, smooth, impressed basally as distinct fossae (Fig. 7). The rest of black species within the *P. endymion* species group (*P. funereus*, *P. olsoufieffi*, *P. panamensis* sp. nov.) are differentiated from *P. malyi* by the elytral striae not strongly impressed basally as distinct fossae and the shape of the endophallite copulatrix (Fig. 1).

Type material

Holotype (not studied)
COSTA RICA • ♂, Arnaud 2002a: 3; Puntarenas, Carara National Park, Estación Quebrada Bonita; originally deposited at INBIO; MNCR.

Non-type material revised (10 ♂♂, 6 ♀♀)

COLOMBIA • 1 ♂; unknown locality; "[Illegible data] / Ex-musæo D. Sharp 1890 / Museum Paris ex Coll. R. Oberthur / PARALECTOTYPE / PARALECTOTYPE *Phanaeus (Phanaeus) blanchardi* Olsoufieff, 1924 / MNHN EC10569"; MNHN.

COSTA RICA – **Puntarenas** • 1 ♂; "San Luis, San Luis Vly. VII-29–1996. Coll. Louis La Pierre"; VMC • 1 ♀; "6km S. San Vito. 27-IV/7-V 1967. 100m. D.F. Viers col. human feces?"; TAMU • 1 ♂; "S.Vito, Las Cruces. July 1982. B.Gill. 1200 m"; IEXA • 1 ♂, 1 ♀; same collection data as for preceding; TAMU • 1 ♂, 1 ♀; "S.Vito, Las Cruces. 17 VIII-12 IX 1982. B.Gill. 1200 m"; TAMU • 1 ♂; same collection data as for preceding; UVGC • 1 ♀; "S.Vito, Las Cruces. 15–18 VIII 1982. B.Gill. 1200 m"; VMC • 1 ♂; "Rincón de Osa. 3-X-69. G. Halffter y P. Reyes C., col. Selva tropical lluviosa. Cebo excremento. Día"; GHC • 1 ♀; "Rincón de Osa. 5-X-69. G. Halffter y P. Reyes C., col. Selva tropical lluviosa. Cebo excremento. Día"; GHC • 1 ♀; "Rincón de Osa. 30-IX-69. G. Halffter y P. Reyes C., col. Selva tropical lluviosa. Cebo excremento. Día (11–17 hrs.)"; VMC • 1 ♂; "Rincón de Osa. 22–5–1965. Col. P. Kazan"; GHC.

PANAMA – **Chiriquí** • 1 ♂; "Cerro Hornito 15 km NE Gualaca. 17–21 VI 1982. B.Gill. 1200 m."; TAMU • 1 ♂; "Cerro Pelota 4 km N Sta.Clara. 9–18 VIII 1982. B.Gill. 1500 m."; VMC.

Type locality

Costa Rica, Puntarenas, Carara National Park, Estación Quebrada Bonita.

Redescription

Major male
HEAD. Completely bright black. Clypeus bidentate, with roughened sculpture. Genae with roughened sculpture. Cephalic horn curved posteriorly over pronotum (Figs 2E, 7A).

PRONOTUM. Keel absent in the middle of anterior pronotal margin. Disc triangular, flat; with two weakly developed, elongate tubercles on anterior portion. Triangle bright black, smooth, scabriculous, impunctate. Sides bright black, becoming bright metallic red-green; scabriculous, with smooth sculpture, almost effaced punctures. Lateral lines of triangle straight. Posterolateral angles short, widened. Lateral fossae distinctly impressed. Basal fossae distinctly to superficially impressed. Posterior margin with distinctly to superficially impressed punctures (Figs 2E, 7A).

Elytra. Striae fine, smooth, completely bright black, with superficially impressed to effaced punctures, scabriculous, impressed basally as distinct fossae. Interstriae bright black, with smooth surface, scabriculous, impunctate or with almost effaced punctures. Sutural margin without apical tooth (Figs 7A).

Protibiae. Quadridentate with apical spine.

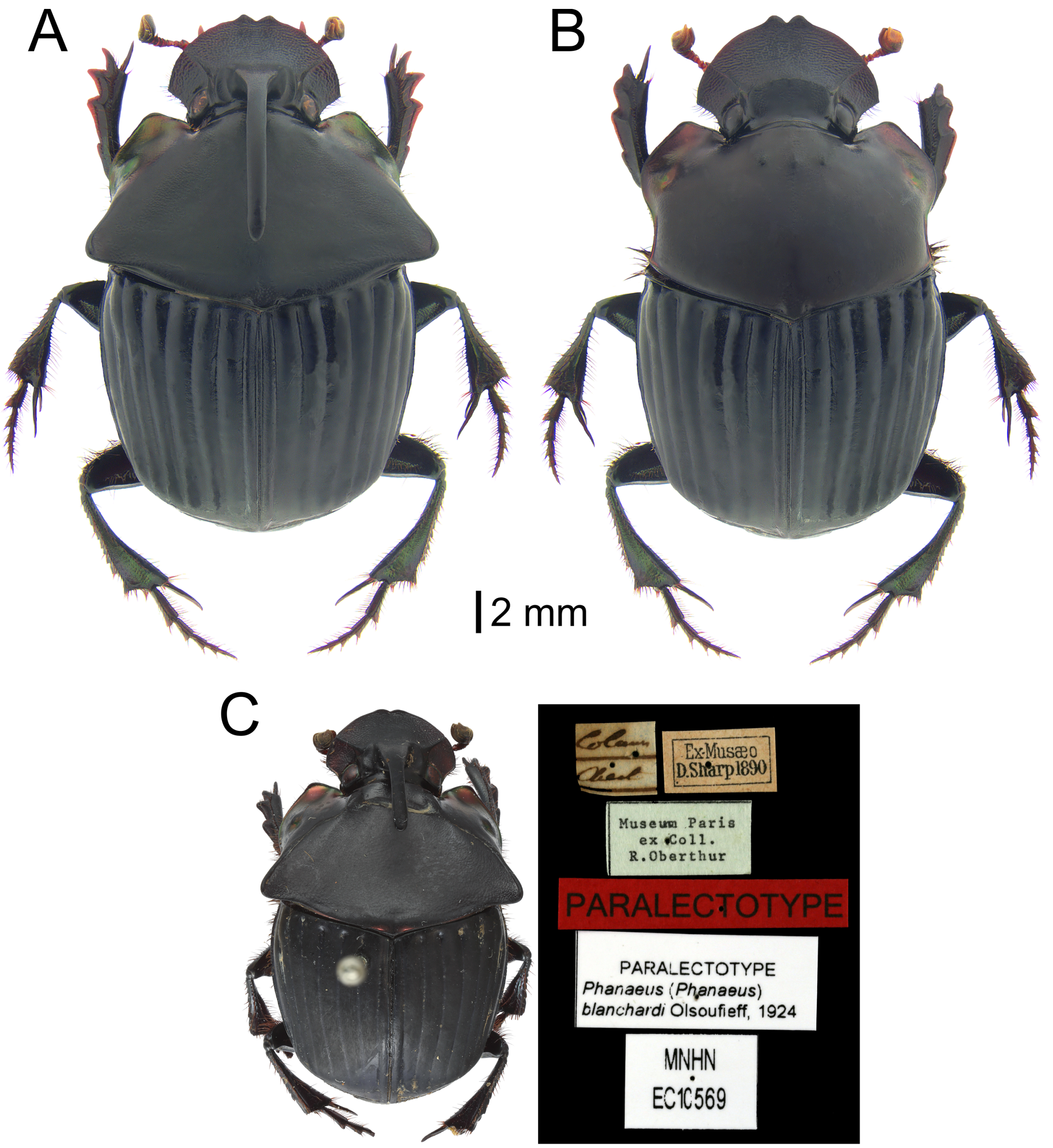

Fig. 7. *Phanaeus malyi* Arnaud, 2002. **A**. ♂ (TAMU). **B**. ♀ (TAMU). **C**. Colombian specimen previously labelled as a paralectotype of *P. blanchardi* Olsoufieff, 1924 (by Christophe Rivier, Muséum national d'histoire naturelle, Paris, France) (MNHN).

Tergite VIII. Bright metallic red-green, scabriculous sculpture; with rough, superficially impressed punctures. Basal margin with setae variable in size.

Genitalia. Right and left lobes of endophallite copulatrix similar in size. Right lobe obtusely triangular in shape, rounded superiorly. Left lobe obtusely lobed. Central ridge less developed than central column (Fig. 1I).

Minor male

Like the major male, except for the reduction of the secondary sexual characters (i.e., cephalic horn, pronotal triangle and tubercles, and pronotal posterolateral angles).

Female

Similar to the male, except for the head showing a cephalic trituberculate carina, with nearly aligned, rounded or carinate, weakly developed tubercles; middle tubercle slightly more developed than lateral tubercles; frons with superficially impressed punctures; pronotum with almost effaced punctures; pronotal process trituberculate, lacking concavity; middle pronotal tubercle more developed, slightly more projected posteriorly than lateral tubercles; all tubercles rounded in shape; posterior pronotal midline completely effaced to almost effaced (Fig. 7B).

Variation

Mean length 17.8 mm (12.8–20.5 mm). Colour variation was not found for *P. malyi*.

Distribution

Southern Pacific costal area, Costa Rica, Panama and Colombia (Figs 16–17). The specimens revised by us represent the first accurate records of *P. malyi* from Panama. Apparently, the distributions of *P. malyi* and *P. panamensis* sp. nov. show a significant area of sympatry and both species may be collected in the same locality (e.g., Cerro Hornito, Panama). Nevertheless, *P. malyi* and *P. panamensis* sp. nov. are confidently identified by the diagnosis provided herein and putative hybrid specimens were not found by us. The MNHN EC10569 specimen represents the first record for *P. malyi* in Colombia. Nevertheless, the illegible label data prevents us to provide an accurate locality (Fig. 7C). The extent of the distribution of *P. malyi* in Colombia needs to be confirmed by future research.

Remarks

Phanaeus malyi was considered by previous authors as a synonym of *P. pyrois* (Edmonds & Zídek 2012). Nevertheless, clear differences in the external and genital morphology of *P. malyi* were found by us. These differences support the full species status suggested by Solís & Kohlmann (2012) and Kohlmann *et al*. (2018). When revising the type material housed at MNHM, a Colombian minor male specimen of *P. malyi* was found to be labelled as a paralectotype of *P. blanchardi* (Fig. 7C, MNHN EC10569).

Phanaeus olsoufieffi Balthasar, 1939 stat. rev.
Figs 1J, 2F, 8, 17, 18K, 19K

Phanaeus blanchardi Olsoufieff, 1924: 92 (not *P. blanchardi* Harold, 1871: 114).
Phanaeus olsoufieffi Balthasar, 1939: 242.
Phanaeus bothrus Blackwelder, 1944: 209.

Phanaeus (*Phanaeus*) *blanchardi* – Martínez & Pereira 1967: 68 (as synonym of *P. funereus*).
Phanaeus (*Phanaeus*) *olsoufieffi* – Martínez & Pereira 1967: 68 (as synonym of *P. funereus*).
Phanaeus bothrus – Martínez & Pereira 1967: 68 (as synonym of *P. funereus*). — Edmonds 1994: 8, 45 (as synonym of *P. pyrois*). — Arnaud 2002b: 97 (as synonym of *P. olsoufieffi*). — Krajcik 2006: 152 (as synonym of *P. pyrois*). — Edmonds & Zídek 2012: 3, 5 (as synonym of *P. pyrois*).

Phanaeus blanchardi – Vulcano & Pereira 1967: 575. — Martínez & Pereira 1967: 68 (as synonym of *P. funereus*). — Edmonds 1972: 830, fig. 256; 1994: 3, 8, 45–46 (as synonym of *P. pyrois*). — Arnaud 1982: 116 (as synonym of *P. funereus*). — Krajcik 2006: 152 (as synonym of *P. pyrois*). — Edmonds & Zídek 2012: 5, 13 (as synonym of *P. pyrois*). — Chamorro *et al*. 2019: 220–221 (as synonym of *P. pyrois*).
Phanaeus olsoufieffi – Edmonds 1994: 8, 45–46 (as synonym of *P. pyrois*). — Arnaud 2002b: 96. — Krajcik 2006: 152 (as synonym of *P. pyrois*). — Edmonds & Zídek 2012: 3, 5–6 (as synonym of *P. pyrois*).
Phanaeus (*Notiophanaeus*) *pyrois olsoufieffi* – Arnaud 2002b: 96.
Phanaeus pyrois olsoufieffi – Arnaud 2002b: 98; 2018: 4, pl. 1, figs d–e.

Non *Phanaeus pyrois* (error). — Medina *et al*. 2001: 140 (in part). — Moctezuma & Halffter 2017: 55 (in part). — Moctezuma *et al*. 2017: 114, 130 (in part).

Diagnosis

This is the largest species within the *P. endymion* species group, frequently attaining 21–24 mm in length. *Phanaeus olsoufieffi* is diagnosed by the black colour with bright metallic red-green sheen; and elytral striae not strongly impressed basally (Fig. 8). This species is easily separated from the closely related *P. panamensis* sp. nov. by the larger body size and endophallite copulatrix (Fig. 1). Additionally, the major males of *P. olsoufieffi* are diagnosed by the distinctly developed keel in the middle of anterior pronotal margin; and posterolateral angles rounded, strongly developed, and projected laterally (Figs 2F, 8A).

Type material (studied from photographs, 2 ♂♂, 3 ♀♀)

Lectotype

COLOMBIA – **Valle del Cauca** • ♂, Arnaud 1982: 116 (Fig. 8C); “M. de Mathan 1898 / *Ph. blanchardi* ♂ Olsuf. det. G. Olsufiew. / *Phanaeus apollinaris* Muzo 1928 / Muséum Paris 1952 Coll R. Oberthur / *P. blanchardi* Ols. LECTOTYPE ♂ P. ARNAUD DET 1980 / Lectotype / *Phanaeus pyrois* Bates, Det. W. D. Edmonds ’83 / MNHN EC10566”; MNHN.

Paralectotypes

COLOMBIA – 1 ♂; “ExMusæo VAN LANSBERGE / Museum Paris ex. Coll. R. Oberthur / PARALECTOTYPE / *Phanaeus blanchardi* Ols. PARALECTOTYPE ♂ P. ARNAUD DET 1981 / *Phanaeus pyrois* Bates / Det. W. D. Edmonds ‘83” / MNHN EC10568”; MNHN. – **Boyacá** • 1 ♀; “Muzo / Coll. E. Steinheil / Museum Paris ex. Coll. R. Oberthur / PARALECTOTYPE / PARALECTOTYPE *Phanaeus* (*Phanaeus*) *blanchardi* Olsoufieff, 1924 / MNHN EC10570”; MNHN EC10570. – **Valle del Cauca** • 1 ♀; “Santa Rosa entre S. Francisco & Carthago. Eujenio Garzon Aout 1878”; MNHN. – **Unknown locality** • 1 ♀; “(Illegible data) / Ex-musæo D. Sharp 1890 / *Ph. blanchardi* ♀ Olsuf. det. G. Olsoufiew. / Museum Paris ex Coll. R. Oberthur / *Phanaeus blanchardi* ♀’s. PARALECTOTYPE ♀ P. ARNAUD DET 1981 / PARALECTOTYPE / *Phanaeus pyrois* Bates Det. W. D. Edmonds ’83 / MNHN EC10567”; MNHN.

Non-type material revised (24 ♂♂, 16 ♀♀)

COLOMBIA – **Chocó** • 3 ♂♂, 1 ♀; “Q.Taparal B.San Juan. CNF. Nov 3–12–92. L.C. Pardo leg”; TAMU • 1 ♂, 1 ♀; “Pacurita, 53m. 25-XI-01. 5°41’N, 76°40’W, bosque. Excrem. J.C. Neita col”; IEXA • 5 ♂♂, 5 ♀♀; same collection data as for preceding; TAMU • 1 ♂, 1 ♀; same collection data as for preceding; UVGC • 1 ♂; same collection data as for preceding; VMC • 1 ♀; “Tutunendó, (20 km NE Quibdó), 60m, 26-XI-01. J.C. Neita col”; TAMU • 3 ♀♀; “Unión Panamericana, 115m. 5°32’45N, 76°44’33’’W (No date) J.C. Neita col”; TAMU • 1 ♂, 1 ♀; “Lloró, (3k km S Quibdó) 5°30’N, 76°33.5’W 90 m. J.C. Neita col (no date)”; TAMU • 2 ♂♂; “Lloró, 90m, 20-II-03. 5°31’N, 76°33’W. Olaya & Mosquero; TAMU •

1 ♀; same collection data as for preceding; VMC. – **Tolima** • 1 ♂; "Honda"; GHC. – **Valle del Cauca** • 1 ♂; "Escalerete CF. Jul 19–21–91. L.C. Pardo leg"; TAMU • 1 ♂; same collection data as for preceding; VMC • 1 ♂, 1 ♀; "B/Ventura B.Calima, C.F. 50 msnm. Col. ME Hitchcox"; TAMU • 1 ♂, 1 ♀; "S30-290. L.C. Pardo Locarno Leg."; GHC • 2 ♂♂; same collection data as for preceding; VMC.

ECUADOR – **Esmeraldas** • 2 ♂♂; "Charco Vicente. Ex.Pitfall heces humanas. 16/05/01. J. Quito F. Añapa"; TAMU.

Type locality

Colombia, Valle del Cauca.

Redescription

Major male

HEAD. Clypeus bidentate, black anteriorly, bright metallic red posteriorly, with green sheen; roughened sculpture. Genae bright metallic red, with green sheen; roughened sculpture. Front black. Cephalic horn black, curved posteriorly over pronotum (Figs 2F, 8A).

PRONOTUM. Carinate, distinctly developed keel in the middle of anterior pronotal margin. Disc triangular, flat, with two distinctly developed tubercles on anterior portion. Triangle completely dull black, with bright metallic red sheen; completely smooth, scabriculous, impunctate. Sides bright metallic red, with green sheen; smooth sculpture, scabriculous, with effaced to almost effaced punctures. Lateral lines of pronotal triangle straight. Posterolateral angles rounded, strongly developed, projected laterally. Lateral fossae distinctly impressed. Basal fossae obtusely oval, deeply impressed to effaced. Posterior margin impunctate, becoming occasionally bright metallic red (Figs 2F, 8A).

ELYTRA. Striae fine, smooth, dull black, with superficially impressed to effaced punctation, scabriculous, not strongly impressed basally. Interstriae dull black, smooth, scabriculous, impunctate. Sutural margin without apical tooth (Fig. 8A).

PROTIBIAE. Quadridentate with apical spine.

TERGITE VIII. Bright metallic red, with green sheen; scabriculous; with rough, superficially impressed punctures. Basal margin with setae variable in size.

GENITALIA. Right lobe of endophallite copulatrix slightly more developed than left lobe. Right lobe obtusely triangular in shape; weakly developed, projected frontally. Left lobe concave superiorly, lobed inferiorly. Central ridge less developed than central column (Fig. 1J).

Minor male

Like the major male, except for the reduction of secondary sexual characters (i.e., cephalic horn, pronotal triangle and tubercles, and pronotal posterolateral angles).

Female

Similar to the male, except for the head showing a cephalic trituberculate carina; with weakly developed tubercles; carinate middle tubercle, slightly more frontally projected and more developed than lateral tubercles; frons with superficially impressed punctures; pronotal sculpture smooth, with almost effaced to effaced punctures; pronotum almost completely black, becoming posteriorly and laterally bright metallic red with green sheen; pronotal process trituberculate, lacking concavities; pronotal tubercles weakly developed, well-spaced, with middle tubercle more developed and posteriorly projected than lateral tubercles; posterior pronotal midline completely effaced (Fig. 8B).

Variation

Mean length 20.1 mm (15.9–23.9 mm). Minor males occasionally show the pronotal disc almost completely bright metallic red, with green sheen.

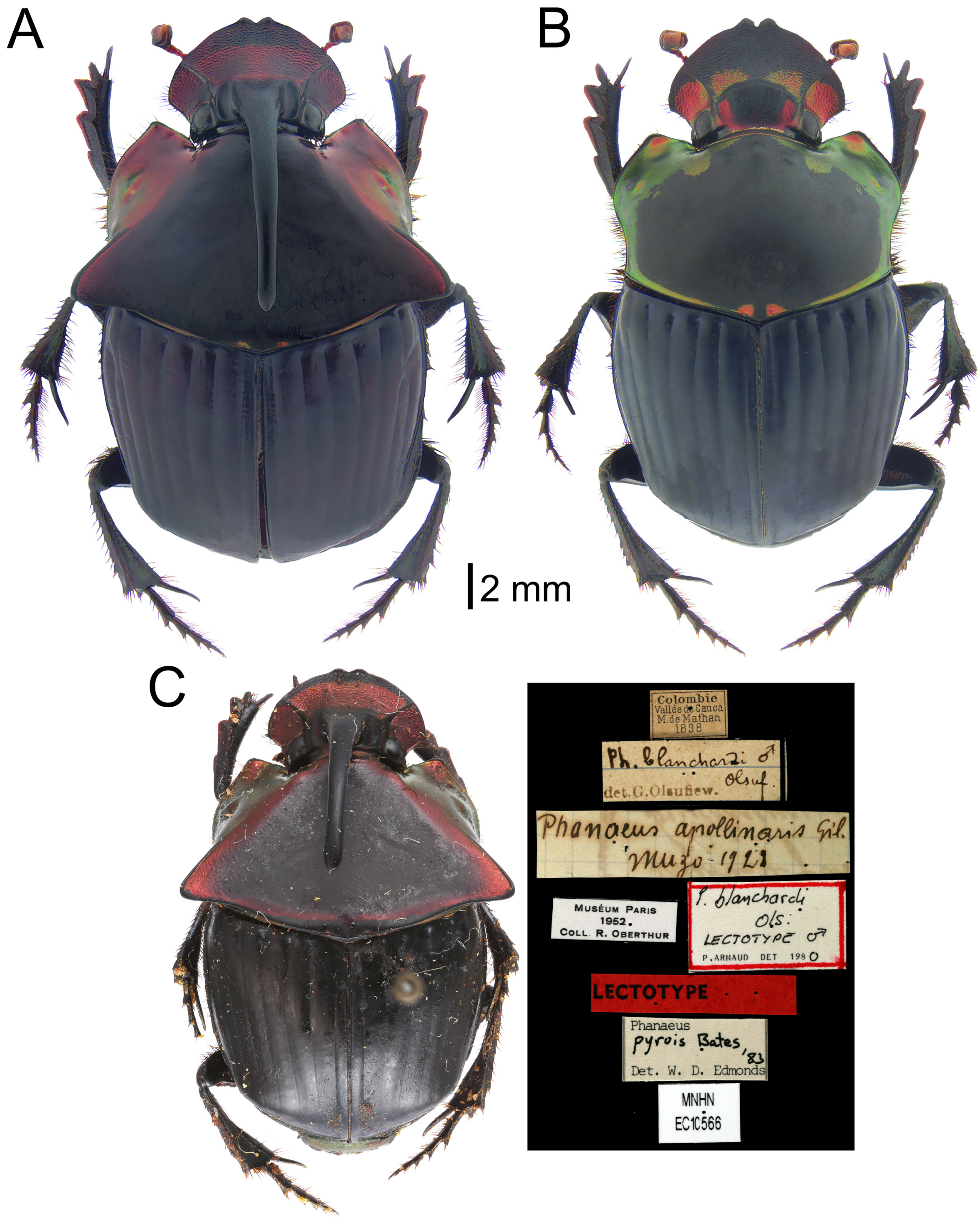

Fig. 8. *Phanaeus olsoufieffi* Balthasar, 1939 stat. rev. **A**. ♂ (TAMU). **B**. ♀ (TAMU). **C**. Lectotype ♂ (by Christophe Rivier, Muséum national d'histoire naturelle, Paris, France) (MNHN).

Distribution

Pacific Slope of the Andes, north-central Colombia and northern Ecuador (Fig. 17). Previous authors reported *P. olsoufieffi* from Panama (Arnaud 2002b; Kohlmann *et al*. 2018). Nevertheless, these authors confused *P. olsoufieffi* with *P. panamensis* sp. nov. The specimens revised herein are the first accurate records of *P. olsoufieffi* from Ecuador. The distributions of *P. olsoufieffi* and *P. funereus* show a significant area of sympatry. Nevertheless, we did not find any putative hybrid specimens.

Remarks

Phanaeus olsoufieffi was considered as a synonym of *P. pyrois* by previous authors (Edmonds 1994; Edmonds & Zídek 2012). Nonetheless, a diagnosis and an updated key to separate *P. olsoufieffi* and closely related species are provided by us. As a consequence, *P. olsoufieffi* is confidently resurrected herein from previous synonymy and full species status is assigned to it. The lectotype of *P. olsoufieffi* is a minor male (Fig. 8C). Therefore, the redescription mainly relies on the type series and some specimens (n = 8) collected from the type locality (Valle del Cauca, Colombia). When revising the type material deposited at MNHM, we were not able to find out the locality data for a Colombian female paralectotype of *P. olsoufieffi* (MNHN EC10567). Its locality data is probably indicated in an illegible label. Additionally, we found out that a paralectotype of *P. olsoufieffi* pertained to *P. malyi* (Fig. 7C, MNHN EC10569). Consequently, we conclude that the type series of *P. olsoufieffi* lumped together two distinct species. Previous authors (Arnaud 1982; 2002a, 2002b; Edmonds 1994; Edmonds & Zídek 2012) did not realize this fact that solves the controversy considering *P. malyi* as a junior subjective synonym of *P. olsoufieffi* or not (Edmonds & Zídek 2012; Solís & Kohlmann 2012; Kohlmann *et al*. 2018).

Phanaeus pacificus sp. nov.

urn:lsid:zoobank.org:act:2414CDB0-3376-4634-8A29-06EFB556E6D0

Figs 1K, 2G, 9, 18L, 19L

Diagnosis

Species typically dark blue or blue-green (Figs 2G, 9), easily separated from the closely related by the elytral striae deeply punctate, with each puncture forming a distinct fossa, giving a completely roughened surface to all striae (Fig. 9). Additionally, the major males of *P. pacificus* sp. nov. and *P. jackenioi* sp. nov. are distinguished by the carinate keel in the middle of anterior pronotal margin of the former (Fig. 2).

Etymology

The specific epithet refers to the Pacific slope, where the new species occurs.

Type material (21 ♂♂, 22 ♀♀)

Holotype

GUATEMALA • ♂; Suchitepéquez, Patulul, Finca Terrales, Casco Finca; “Patulul, Finca Terrales. Casco Finca. 750 m. 7–8 noviemb. 2006. Monzón, Giardina, Frank”; UVGC.

Paratypes

EL SALVADOR • 1 ♂; “1–10–95. T-carne. Denninger”; VMC.

GUATEMALA – **Escuintla** • 1 ♂; “Palin. Montaña El Chilar. 29 III 1997. A. Higueros.”; CNMC • 1 ♂; same collection data as for preceding; UVGC • 1 ♀; same collection data as for preceding; VMC • 1 ♂; “Palín, Fca. El Chilar. IX 2013. S. Secaira”; VMC • 1 ♀; “Palín, Montaña El Chilar. 14.35310, -90728190. W6584. 945msnm. E. Cano. Heces humanas. 15–16X2010”; TAMU • 1 ♂; same collection data as for preceding; VMC. – **Retalhuleu** • 1 ♂; "Chicacaho. 21 III 1992. P. Hunziker"; UVGC. – **Suchitepéquez** • 1 ♀; "Santa Bárbara. Finca Panamá. Periquera. 1,127m. Oct. 2007. 145323349 -91.1976111- Pérez, Camposec, Monzón"; CNMN • 2 ♂♂, 1 ♀; same collection data as for preceding; UVGC • 1 ♂, 1 ♀; same collection data as for preceding; VMC • 1 ♂; "Santa Bárbara. Finca Panamá. "abato". 1,177m. Diciem. 2007. 14°32.118 -91°12.281. Pérez, Camposec, Monzón"; IEXA • 2 ♀♀; "Santa Bárbara. Finca Panamá. Periquera. 1,127m. Nov. 2007. 145323349 -91.1976111- Pérez, Camposec, Monzón"; UVGC • 1 ♂; same collection data as for preceding; TAMU.

MEXICO – **Chiapas** • 1 ♂; "Unión Roja, La Boquilla. Alt. 500m. Selva pert. 9.V.84. NTP.80. J.A. López"; IEXA • 1 ♀; same collection data as for preceding; TAMU • 1 ♂, 1 ♀; "Cacaohatan, La Victoria, 21-V-82. Cafetal, Alt. 430m. M.A. Morón, col. NTP"; IEXA • 1 ♀; "Cacaohatan, La Victoria, 15-IX-82. Cafetal, Alt. 430m. NTP. J. Valenzuela, col."; IEXA • 1 ♂; same collection data as for preceding; TAMU • 1 ♀; "Cacaohatan, La Victoria, 15-XII-81. Cafetal, Alt. 430m. M.A. Morón col. NTP"; IEXA • 1 ♀; "Cacaohatan, La Victoria, 15-VII-82. Cafetal, Alt. 430m. M.A. Morón col. NTP"; IEXA • 1 ♀; "Cacaohatan, La Victoria, 18-V-82. Cafetal, Alt. 430m. M.A. Morón col. NTP"; IEXA • 1 ♂; "Cacaohatan, La Victoria, 25-XI-81. Cafetal, Alt. 430m. NTP. J. Valenzuela, col."; CMNC • 1 ♀; same collection data as for preceding; IEXA • 1 ♀; "Cacaohatan, La Victoria, 2-IX-81. Cafetal, Alt. 430m. M.A. Morón col. NTP"; IEXA • 1 ♀; "Cacaohatan, La Victoria, 2-III-82. Cafetal, Alt. 430m. M.A. Morón col. NTP" ; CMNC • 3 ♀♀ ; same collection data as for preceding; IEXA • 1 ♂; "Cacaohatan, Sn. José de la Victoria, 10-III-92. Coprotrampa 24 hrs. M.A. Morón, col."; IEXA • 1 ♂; "Cacaohatan, Sn. José de la Victoria, 25-V-82. Coprotrampa 6 días. M.A. Morón, col."; IEXA • 1 ♂; "Cacaohatan, La Victoria, 15-III-82. Cafetal, Alt. 430m. J. Valenzuela, col. NTP."; VMC • 1 ♀; "Cacaohatan, La Victoria, 2-III-82. Cafetal, Alt. 430m. J. Valenzuela, col. NTP."; VMC • 1 ♂, 1 ♀; "Rosario Izapa. 19–20-V-63. G. Halffter. A. Martínez. cols."; GHC • 1 ♂, 1 ♀; "Unión Roja. La Boquilla, 11-VI-83 coprotr. M.A. Morón"; UVGC.

Type locality

Guatemala, Suchitepéquez, Patulul, Finca Terrales, Casco Finca.

Description

Major male (holotype)
Length 19.4 mm.

Head. Clypeus bidentate, black on anterior margin, dark blue on posterior portion, roughened sculpture. Genae dark blue, with roughened sculpture. Front black, dark blue on portions adjacent to cephalic horn. Cephalic horn black, curved posteriorly over pronotum (Figs 2G, 9A).

Pronotum. Uniformly dark blue, becoming completely black on lateral margins of posterolateral angles and posteriorly. Carinate, distinctly developed keel in the middle of anterior pronotal margin. Disc triangular, flat, with two distinctly developed tubercles on anterior portion. Triangle lightly granulate, scabriculous, impunctate. Sides with smooth sculpture, scabriculous, with superficially impressed punctures. Lateral lines of pronotal triangle straight. Posterolateral angles acute, strongly developed, sharply projected posteriorly. Lateral fossae distinctly impressed. Basal fossae obtusely oval, distinctly impressed. Posterior margin with superficially impressed punctures (Figs 2G, 9A).

Elytra. Striae thick, dark blue, with distinctly impressed punctures, scabriculous, impressed basally as distinct fossae. Interstriae black, smooth, scabriculous, with superficially impressed punctures; except for the roughened surface on first interstriae. Sutural margin without apical tooth (Fig. 9A).

Protibiae. Quadridentate with apical spine.

Tergite VIII. Dark metallic blue-green, scabriculous; with rough, superficially impressed punctures. Basal margin with setae variable in size.

Genitalia. Right and left lobes of endophallite copulatrix similar in size. Right lobe obtusely triangular in shape, concave medially. Left lobe strongly developed, concave posterosuperiorly. Central ridge and column similar in size (Fig. 1K).

Minor male

Like the major male, except for the reduction of the secondary sexual characters (i.e., cephalic horn, pronotal triangle and tubercles, keel on anterior margin, and pronotal posterolateral angles).

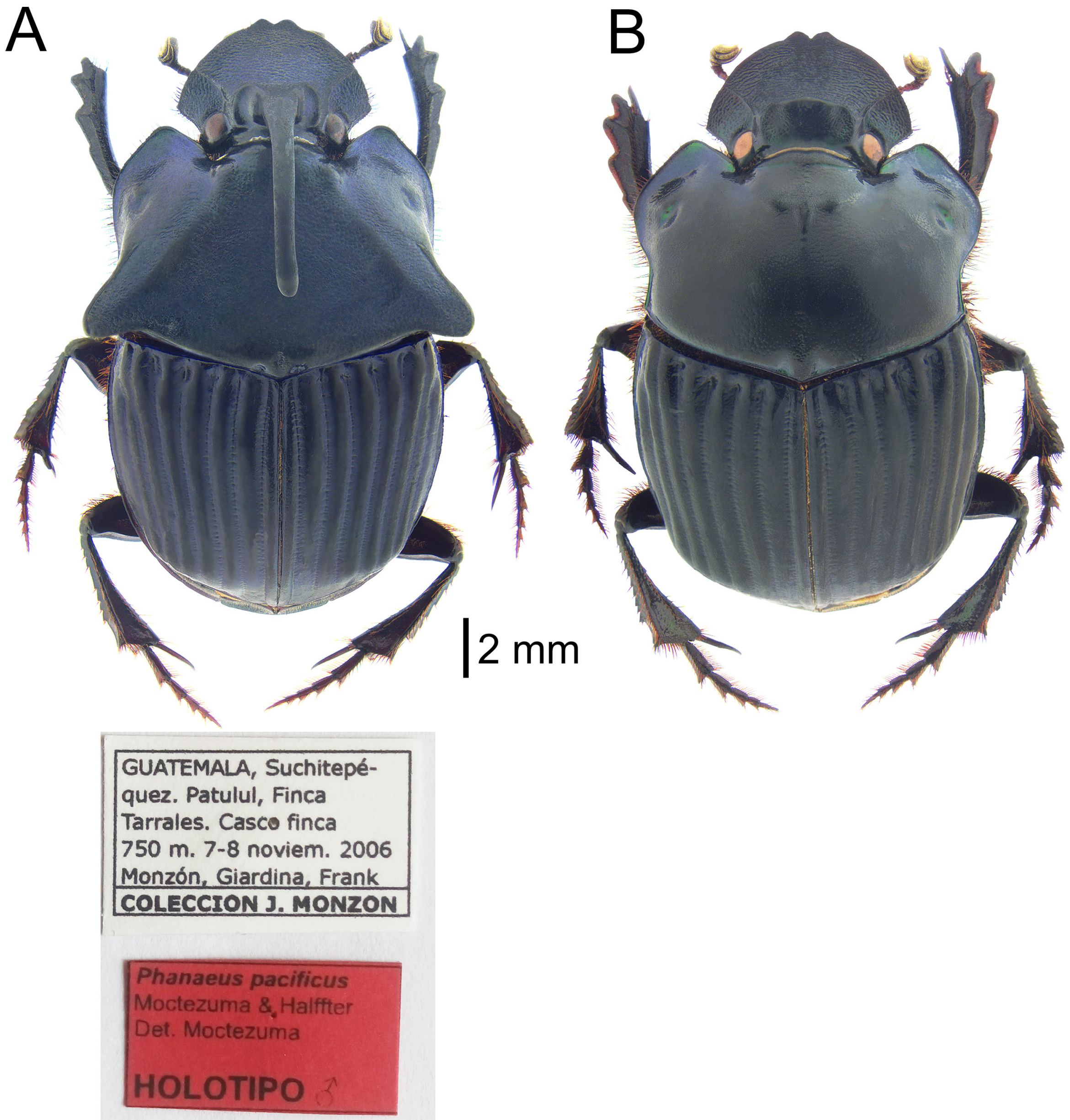

Fig. 9. *Phanaeus pacificus* sp. nov. **A**. Holotype, ♂ (UVGC). **B**. ♀ (IEXA).

Female

Similar to the male, except for the head showing a cephalic trituberculate carina; with conical tubercles; middle tubercle slightly more projected frontally than lateral tubercles; lateral tubercles slightly more raised than middle tubercle; frons distinctly impressed, rough punctures; pronotal sculpture completely smooth, with distinctly impressed punctures; pronotum almost completely dull black in the central portion, dark metallic blue, or blue-green laterally and posteriorly; pronotal process trituberculate, lacking concavities; pronotal tubercles nearly aligned; with rounded to dentiform middle tubercle, more developed than lateral tubercles; posterior pronotal midline superficially impressed (Fig. 9B).

Variation

Mean length 17.1 mm (14.1–20.2 mm). A rare bright metallic green or yellow-green with a red sheen colour morph was found. The smaller males may show a keel weakly developed to completely effaced in the middle of anterior pronotal margin.

Distribution

Pacific slope of the Sierra Madre de Chiapas; Chiapas, Guatemala and El Salvador (Fig. 15).

Remarks

This new species was referred to as *P. endymion* (Morón 1987; Edmonds 1994; Horgan 2001, 2008; Edmonds & Zídek 2012; Cancino-López *et al*. 2014; Lizardo *et al*. 2017; Moctezuma & Halffter 2017; GBIF Secretariat 2019a; Pablo-Cea *et al*. 2020) and *P. pyrois* (GBIF Secretariat 2019b) by previous authors and specimen labels. Nevertheless, the distribution areas of all the closely related species are not sympatric and *P. pacificus* sp. nov. is distinctly diagnosable.

Phanaeus panamensis sp. nov.

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Figs 1L, 2H, 10, 16, 18M, 19M

Diagnosis

The new species is easily diagnosed within the *P. endymion* species group by the dull black colour with bright metallic red-green sheen dorsally (Figs 2H, 10); and elytral striae not strongly impressed basally as distinct fossae (Fig. 10). *Phanaeus panamensis* sp. nov. is distinguished from *P. olsoufieffi* by its smaller body size (rarely attaining 20–21 mm in length); and the major males with obsolete keel in the middle of anterior pronotal margin (Fig. 2H); and posterolateral angles weakly developed, widened, slightly projected posteriorly (Fig. 10A). Furthermore, the pronotal disc in *P. olsoufieffi* is distinctly darker and smoother (Figs 2F, 8A).

Etymology

The specific epithet refers to Panama, where a majority of the type series was collected.

Type material (17 ♂♂, 14 ♀♀)

Holotype

PANAMA • ♂; Panamá, Cerro Campana; “Cerro Campana, 850m. 8°40’N, 79°56’W. 19 Sept. ’71. Stockwell. Manure trap”; TAMU.

Paratypes

COSTA RICA – **Heredia** • 1 ♂; “Estación La Selva, Río Puerto Viejo, 84°W/10°28’N. 12-IX-1969. G. Halffter y P. Reyes col.”; GHC • 1 ♂; same collection data as for preceding; VMC.

PANAMA – **Chiriquí** •1 ♂; "Cerro Hornito, 15 km W Gualaca. 17–21 VI 1982. B.Gill. 1200 m"; TAMU • 1 ♀; "Cerro Hornito, 15 km W Gualaca. 21 VI-16 VII 1982. B.Gill. 1200 m"; TAMU. – **Coclé** • 1 ♀; "El Valle, VI-10–13–1985, E.Kiley & D.Rider"; CNMC • 1 ♀; same collection data as for preceding; TAMU • 1 ♂, 1 ♀; same collection data as for preceding; UVGC • 1 ♂; same collection data as for preceding; VMC • 1 ♀; "El Valle de Antón, VI 5 1945. 2500 ft. C.D. Michener"; TAMU.– **Panamá** • 1 ♂; "Cerro Campana. 5-IX-1966. M.G. Naumann col."; TAMU • 1 ♂; "Barro Colorado. Canal Zone. May 1929. Darlington"; TAMU • 1 ♂; "Canal Zone B.C.I. 6-XII-1975. Rat carrion trap. Col. O.P.Young"; TAMU • 1 ♂; "Canal Zone B.C.I. 1,2-XI-1975. Human feces trap. Col. O.P.Young"; VMC • 1 ♂; "Canal Zone B.C.I. 8-XII-1975. Rat carrion trap. Col. O.P.Young"; TAMU • 1 ♀; "Canal Zone, Fort Kobbe, VI-4–21–1985. E.G., Riley"; IEXA • TAMU: 1 ♂, 3 ♀♀; same collection data as for preceding; TAMU • 1 ♀; same collection data as for preceding; VMC • 1 ♀; "Chepo-Carti Rd. 1–22-VIII-1982. B-Gill. 400 m"; TAMU • 1 ♂; "Chepo-Carti Rd. 6–24-VI-1982. B-Gill. 400 m"; CNMC • 1 ♂; same collection data as for preceding; IEXA • 2 ♀♀; same collection data as for preceding; TAMU • 1 ♀; "9 km SE Bayano Bridge. 9°10'N, 78°46'W. 8 Sept '74. H. Stockwell. Manure trap"; VMC • 1 ♂; "Barro Colo Isld. Canal Zone. 1.7.1929. Collector C. H. Curran"; GHC • 1 ♂; "Canal Zone. 1951. F.S. Blanton Collr."; VMC • 1 ♂; "Soberania Nac. PQ. 15–24 Feb 1999. J.E. Wappes"; TAMU.

Type locality

Panama, Panama, Cerro Campana.

Description

Major male (holotype)
Length 19.3 mm.

HEAD. Clypeus bidentate, black on anterior margin, bright metallic red, with green sheen on posterior portion, roughened sculpture. Genae bright metallic red, with green sheen; roughened sculpture. Front black, bright metallic red on portions adjacent to cephalic horn. Cephalic horn black, curved posteriorly over pronotum (Figs 2H, 10A).

PRONOTUM. Uniformly black, with bright metallic red sheen, becoming completely black posteriorly and on lateral margins of posterolateral angles. Keel absent in the middle of anterior pronotal margin. Disc triangular, flat, with two weakly developed, elongate tubercles on anterior portion. Triangle smooth; scabriculous; impunctate. Sides with smooth sculpture; scabriculous; with almost effaced punctures. Lateral lines of pronotal triangle straight. Posterolateral angles weakly developed, widened, slightly projected posteriorly. Lateral fossae distinctly impressed. Basal fossae obtusely oval, distinctly impressed. Posterior margin impunctate (Figs 2H, 10A).

ELYTRA. Fine striae, smooth, dull black, with dark metallic blue sheen; impressed basally as distinct fossae, scabriculous, with almost effaced to effaced punctation. Interstriae black, smooth, scabriculous, impunctate. Sutural margin without apical tooth (Fig. 10A).

PROTIBIAE. Quadridentate with apical spine.

TERGITE VIII. Bright metallic red, with green sheen, scabriculous; with rough, almost completely effaced punctures. Basal margin with thick, small setae.

GENITALIA. Right lobe of endophallite copulatrix more developed than left lobe. Right lobe obtusely triangular in shape, rounded superiorly, and weakly developed. Left lobe bent posteriorly. Central ridge and column similar in size (Fig. 1L).

Minor male

Like the major male, except for the reduction of the secondary sexual characters (i.e., cephalic horn, pronotal triangle and tubercles, and pronotal posterolateral angles). Occasionally, the pronotal disc is completely bright metallic red, with green sheen.

Female

Similar to the male, except for the head showing a cephalic trituberculate carina; with weakly developed tubercles; carinate middle tubercle, slightly more frontally projected than lateral tubercles; frons with distinctly impressed punctures; pronotal sculpture completely smooth, with superficially impressed punctures; pronotum almost completely dull black in the central portion, laterally and posteriorly bright metallic red with metallic green sheen; pronotal process trituberculate, lacking concavities; pronotal tubercles rounded, nearly aligned, well-spaced; with middle tubercle more developed than lateral tubercles; posterior pronotal midline almost completely effaced (Fig. 10B).

Variation

Mean length 17.8 mm (14.6–21.1 mm). Colour variation was not found.

Distribution

Panama and north-Caribbean Costa Rica (Fig. 16). The distributions of *P. panamensis* sp. nov., *P. malyi* and *P. pyrois* show large areas of sympatry. Nevertheless, all these species are easily recognized.

Remarks

Phanaeus panamensis sp. nov. has frequently been confused with *P. olsoufieffi* by previous authors (Edmonds 1994; Arnaud 2002b; Edmonds & Zídek 2012, Solís & Kohlmann 2012; Kohlmann *et al.* 2018). Minor males and females of both species are strongly mimetic. More specimens from western

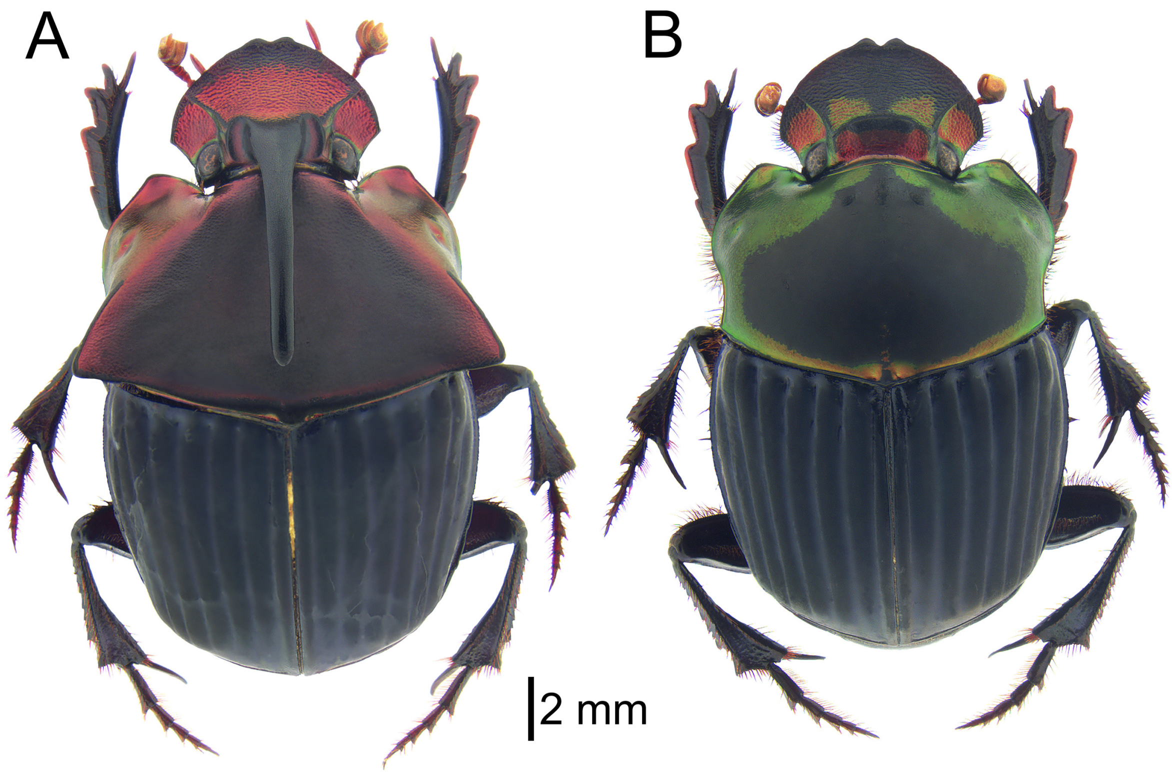

Fig. 10. *Phanaeus panamensis* sp. nov. **A**. Holotype, ♂ (TAMU). **B**. ♀ (TAMU).

Panama and northern Colombia are needed to be revised in order to determine if *P. olsoufieffi* and *P. panamensis* sp. nov. are sympatric.

Phanaeus porioni Arnaud, 2001 stat. rev.
Figs 1M, 2I, 11, 15, 18N, 19N

Phanaeus (*Notiophanaeus*) *endymion porioni* Arnaud, 2001: 4.

Phanaeus (*Notiophanaeus*) *endymion porioni* – Arnaud 2002b: 94 (as subspecies of *P. endymion*).
Phanaeus endymion porioni – Arnaud 2002b: 95 (as subspecies of *P. endymion*). — Krajcik 2006: 150 (as subspecies of *P. endymion*). — Edmonds & Zídek 2012: 1, 8, 13 (as synonym of *P. endymion*).

Non *Phanaeus* (*Notiophanaeus*) *endymion* (error) – Edmonds 1994: 2, 8–9, 12, 19, 36, 39, 41–46, 54, 74, 101, figs 17, 209, 215–216, 221 (in part). — Edmonds & Zídek 2012: 3, 13, figs 132–133, 136, 140, 143, 152–155 (in part).*Phanaeus porioni* – Edmonds & Zídek 2012: 3, 6 (as synonym of *P. endymion*).
Non *Phanaeus endymion* (error) – Creedy & Mann 2011: 34, 51. — Edmonds & Zídek 2012: 1, 5–6 (in part).

Diagnosis

Phanaeus porioni and *P. endymion* are closely related, but the former is easily separated by the major female with the pronotal process weakly or not concave posteriorly and pronotal tubercles nearly aligned (Fig. 11B), while the males are distinguished by the endophallite copulatrix (Fig. 1). Additionally, *P. porioni* is recognized by the elytral striae always distinctly punctate (Fig. 11), but the strial surface never roughened as in *P. pacificus* sp. nov. (Fig. 9) and *P. jackenioi* sp. nov. (Fig. 6).

Type material

Holotype (studied from photographs, 1 ♂)
HONDURAS • ♂, Arnaud 2001: 4 (Fig. 11C); Atlántida, Rco Bonito; "*Phanaeus endym. porioni* P.ARNAUD DET 2001 HOLOTYPE ♂/HONDURAS -ATLANTIDA, Rco Bonito (250 m), juilliet-1995, Thierry PORION Leg"; CPFA.

Paratypes revised (1 ♂, 1 ♀)
HONDURAS – **Atlántida** • 1 ♂, 1 ♀; "Rco Bonito (250 m), juilliet-1995, Thierry Porion Leg"; VMC.

Non-type material revised (14 ♂♂, 9 ♀♀)

HONDURAS – **Atlántida** • 3 ♂♂, 2 ♀♀; "13 km. W La Ceiba. VII-1996, 150 m. Coll. R Lehmann. Flight intercept trap in cocoa plantation"; TAMU • 1 ♀; same collection data as for preceding; UVGC • 1 ♂; same collection data as for preceding; VMC • 1 ♂, 1 ♀; "15 km. W La Ceiba. VI15-19-1996, 175 m. Coll. R. Lehmann. Flight intercept trap, tropical rainforest"; IEXA • 7 ♂♂, 3 ♀♀; same collection data as for preceding; TAMU • 1 ♂ same collection data as for preceding; UVGC • 1 ♂, 2 ♀♀; same collection data as for preceding; VMC.

Type locality

Honduras, Atlántida, Rco Bonito.

Redescription

Major male

HEAD. Clypeus bidentate, black anteriorly, dark metallic blue, green or blue-green posteriorly; roughened sculpture. Genae dark metallic blue, green or blue-green, with roughened sculpture. Front black. Cephalic horn black, curved posteriorly over pronotum (Figs 2I, 11A).

PRONOTUM. Keel absent in the middle of anterior pronotal margin. Disc triangular, flat, with two distinctly developed tubercles on anterior portion. Triangle uniformly dark metallic blue, green, or blue-green; becoming black on posterior margin and beneath the posterolateral angles, lightly granulate, scabriculous, impunctate. Sides dark metallic blue, green, or blue-green; smooth sculpture, scabriculous, with superficially impressed punctures. Lateral lines of pronotal triangle straight. Posterolateral angles widened or acute, projected posteriorly. Lateral fossae distinctly impressed. Basal fossae obtusely oval, distinctly impressed. Posterior margin with superficially impressed punctures (Figs 2I, 11A).

ELYTRA. Striae fine, smooth, scabriculous, impressed basally as distinct fossae; dark blue, green, or blue-green; always with distinctly impressed punctation. Interstriae black, smooth, scabriculous, with almost effaced punctures. Sutural margin without apical tooth (Fig. 11A).

PROTIBIAE. Quadridentate with apical spine.

TERGITE VIII. Dark metallic blue, green, or blue-green; scabriculous; with rough, superficially impressed punctures. Basal margin with setae variable in size.

GENITALIA. Right and left lobes of endophallite copulatrix similar in size. Right lobe obtusely triangular in shape, weakly developed superiorly. Left lobe obtusely lobed, strongly developed. Central ridge less developed than central column (Fig. 1M).

Minor male

Like the major male, except for the reduction of the secondary sexual characters (i.e., cephalic horn, pronotal triangle and tubercles, and pronotal posterolateral angles).

Female

Similar to the male, except for the head showing a cephalic trituberculate carina; with weakly developed, nearly aligned tubercles; carinate middle tubercle slightly more developed than lateral tubercles; frons with distinctly impressed punctures; pronotal sculpture smooth, with almost completely effaced punctures; pronotum almost completely black, becoming dark metallic blue, green, or blue-green posteriorly and laterally; pronotal process trituberculate, weakly concave posteriorly; pronotal tubercles nearly aligned; with rounded to dentiform middle tubercle, more developed than lateral tubercles; lateral tubercles rounded; posterior pronotal midline almost completely effaced (Fig. 11B).

Variation

Mean length 17 mm (13.1–20.1 mm). Colour variants were not found.

Distribution

Caribbean Honduras, Belize, and probably north-Caribbean Guatemala (Fig. 15).

Remarks

Phanaeus porioni was considered as a synonym of *P. endymion* by Edmonds & Zídek (2012). Nevertheless, differences in external and genital morphology were found by us. As a consequence, *P. porioni* is resurrected from previous synonymy and full species status is given to it. Apparently, a significant area of sympatry is found between *P. endymion* and *P. porioni*. The males of both species are strongly mimetic, but females are easily diagnosed by external morphology. The endophallite copulatrix will help to confidently separate males of both species (Fig. 1). We were not able to study any specimens of *P. porioni* from Belize.

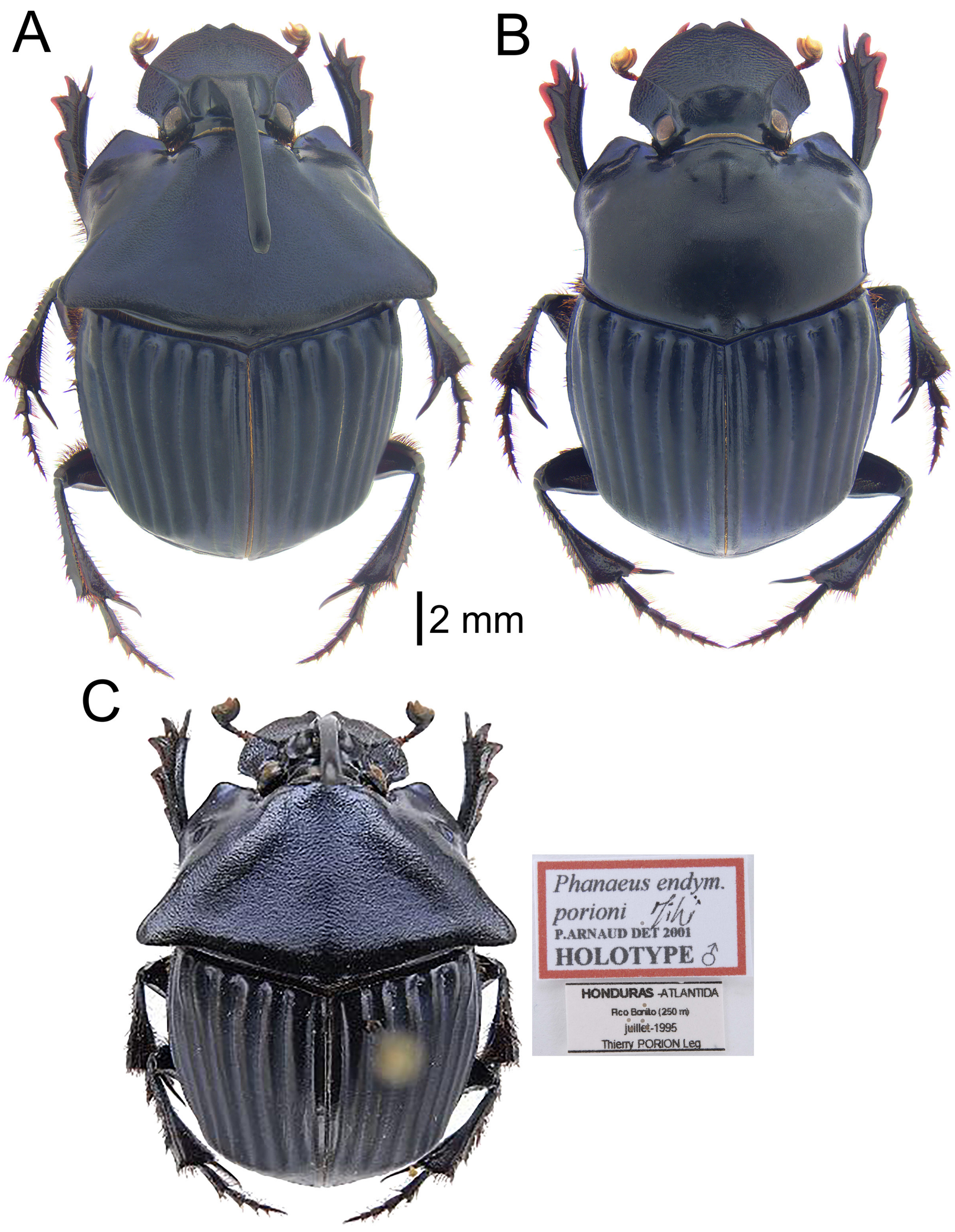

Fig. 11. *Phanaeus porioni* Arnaud, 2001 stat. rev. **A**. ♂ (TAMU). **B**. ♀ (TAMU). **C**. Holotype, ♂ (by Patrick Arnaud) (CPFA).

Phanaeus pyrois Bates, 1887
Figs 1N, 2J, 12, 16, 18O, 19O

Phanaeus pyrois Bates, 1887: 58, pl. 2, table 3, figs 22–23 (in part).

Phanaeus pyrois – Nevinson 1982: 6 (in part). — Gillet 1911: 85 (in part). — Olsoufieff 1924: 37, 93, 152 (in part). — Blackwelder 1944–1957: 210 (in part). — Edmonds 1972: 830 (in part); 1979: 103 (in part); 1994: 3, 5, 8–9, 39, 44–46, 103 (in part). — Howden & Young 1981: 134, 136 (in part). — Krajcik 2006: 152 (in part). — Price 2007: 17, figs 52–53, 54 (in part); 2009: 145 (in part). — Solís & Kohlmann 2012: 1, 8–10, 31, fig. 1 (in part). — Edmonds & Zídek 2012: 1, 5–6, 8, 13 (in part). — Moctezuma & Halffter 2017: 55 (in part). — Moctezuma *et al*. 2017: 114, 130 (in part). — Kohlmann *et al*. 2018: 69, 78–79, 83, 88, 89, fig. 8a, d (in part). — Chamorro *et al*. 2019: 220 (in part).
Phanaeus (*Notiophanaeus*) *pyrois* – Edmonds 1994: 2, 8, 41, 44, figs 210, 214–215, 221 (in part). — Arnaud 2002b: 96 (in part). — Edmonds & Zídek 2012: 3, 13, figs 138, 142–143, 156–159 (in part).
Phanaeus (*Notiophanaeus*) *pyrois pyrois* – Arnaud 2002b: 96 (in part).
Phanaeus pyrois pyrois – Arnaud 2002b: 97 (in part).

Diagnosis

Easily diagnosed species by the pronotum bright metallic red (Figs 12A, D), green (Fig. 2J) or dark metallic blue (12B), with elytral striae not strongly impressed basally (Fig. 12). The rest of the green/blue species of the *P. endymion* species group are recognized by the elytral striae strongly impressed basally as a distinct fossa. A black dorsal colour is never found in *P. pyrois* specimens. Minor males of *P. panamensis* sp. nov. and red *P. pyrois* may be strongly mimetic, but easily separated by the endophallite copulatrix (Fig. 1).

Type material

Lectotype (studied from photographs, 1 ♂)
NICARAGUA – **Chontales** • ♂, Edmonds 1994: 45 (Fig. 12D); "NHMUK 013678267/B. C. A. p. 58, sp.8./LECTO-TYPE/*Phanaeus pyrois* Bates. LECTOTYPE ♂ P. ARNAUD DET 1980/T. Belt/Type/*P. pyrois* ♂/ Sp. figured"; NHMUK 013678267; BMNH.

Non-type material revised (7 ♂♂, 4 ♀♀)

NICARAGUA – **Granada** • 1 ♂; "Volcán Mombacho. Bosque Seco. 30-VI-98. JM. Mars"; TAMU • 1 ♂; "Volcán Mombacho. Santa Ana. 21-V-98. Malaise. JM. Mars"; VMC • 1 ♂; "Volcán Mombacho. El Progreso. 30-VI-98. JM. Mars"; IEXA. – **Jinotega** • 1 ♂; "El Jaguar Coffee Finca. XII-3–8–2005. 4356 ft. D. G. Marqua"; TAMU • 2 ♀♀; "El Jaguar Coffee Finca. VI-5–10–2005, el. 4,356 ft. Coll. D. G. Marqua"; VMC • 1 ♂, 2 ♀♀; "Finca El Jaguar, 32kmNW. 1340m. 13°14'28''N-86°03'16''W. xii-05 col D.G. Marqua"; TAMU • 1 ♂; same collection data as for preceding; VMC.

COSTA RICA – **Cartago** • 1 ♂; "Turrialba. 650m. 26.Feb.1980. H & A Howden"; TAMU.

Type locality

Nicaragua, Chontales.

Redescription

Major male
Head. Clypeus bidentate, black anteriorly, bright metallic red, green, or dark metallic blue posteriorly; roughened sculpture. Genae bright metallic red, green, or dark metallic blue; roughened sculpture. Front

black, bright metallic red, green, or dark metallic blue on portions adjacent to cephalic horn. Cephalic horn black, curved posteriorly over pronotum (Figs 2J, 12A–B, D).

PRONOTUM. Keel absent in the middle of anterior pronotal margin. Disc triangular, flat, with two distinctly developed tubercles on anterior portion. Triangle bright metallic red, green, or dark metallic blue; becoming black on posterior margin of posterolateral angles; lightly granulate, scabriculous, impunctate. Sides bright metallic red, green, or dark metallic blue; smooth sculpture, scabriculous, with superficially impressed punctures. Lateral lines of pronotal triangle straight. Posterolateral angles widened or slightly acute; projected posteriorly or posterolaterally. Lateral fossae distinctly impressed. Basal fossae obtusely oval, distinctly impressed. Posterior margin sometimes black, with superficially impressed to effaced punctures (Figs 2J, 12A–B, D).

ELYTRA. Striae fine, smooth, scabriculous, not strongly impressed basally; bright red, green, or dark blue; with superficially impressed punctation. Interstriae black, smooth, scabriculous, with almost effaced to effaced punctures. Sutural margin without apical tooth (Fig. 12A–B, D).

PROTIBIAE. Quadridentate with apical spine.

TERGITE VIII. Bright metallic red, green, or dark metallic blue; scabriculous; with rough, superficially impressed punctures. Basal margin with setae variable in size.

GENITALIA. Right and left lobes of endophallite copulatrix similar in size. Right lobe strongly reduced, obtusely triangular in shape; rounded superiorly. Left lobe obtusely lobed, strongly developed. Central ridge and column similar in size (Fig. 1N).

Minor male

Like the major male, except for the reduction of secondary sexual characters (i.e., cephalic horn, pronotal triangle and tubercles, and pronotal posterolateral angles).

Female

Similar to the male, except for the head showing a cephalic trituberculate carina; with conical, nearly aligned tubercles; middle tubercle slightly more developed than lateral tubercles; frons with distinctly impressed punctures; pronotal sculpture smooth, with almost effaced punctures; pronotum almost completely black, becoming posteriorly and laterally bright metallic red, green, or dark metallic blue; pronotal process trituberculate, lacking concavity; pronotal tubercles nearly aligned; with middle tubercle more developed than lateral tubercles; posterior pronotal midline superficially impressed (Fig. 12C).

Variation

Mean length 17.8 mm (14.7–20.1 mm). *Phanaeus pyrois* is the most variable in colour species of the *P. endymion* species group. The outspoken colour variability of this species was previously outlined by Bates (1886–1889), particularly for the specimens from Nicaragua. Tree typical chromatic morphs were found by us (bright metallic red, Fig. 14A, D; green, Fig. 2J; or dark metallic blue, Fig. 12B), but colour combinations are found and rare specimens has a bright golden sheen.

Distribution

Nicaragua and north-Caribbean Costa Rica (Fig. 16). The distributions of *P. pyrois* and *P. panamensis* sp. nov. show an important sympatry area in north Caribbean Costa Rica.

Remarks

Phanaeus pyrois and several closely related species were incorrectly lumped together by previous authors (Howden & Young 1981; Edmonds 1994; Edmonds & Zídek 2012; Solís & Kohlmann 2012; Chamorro

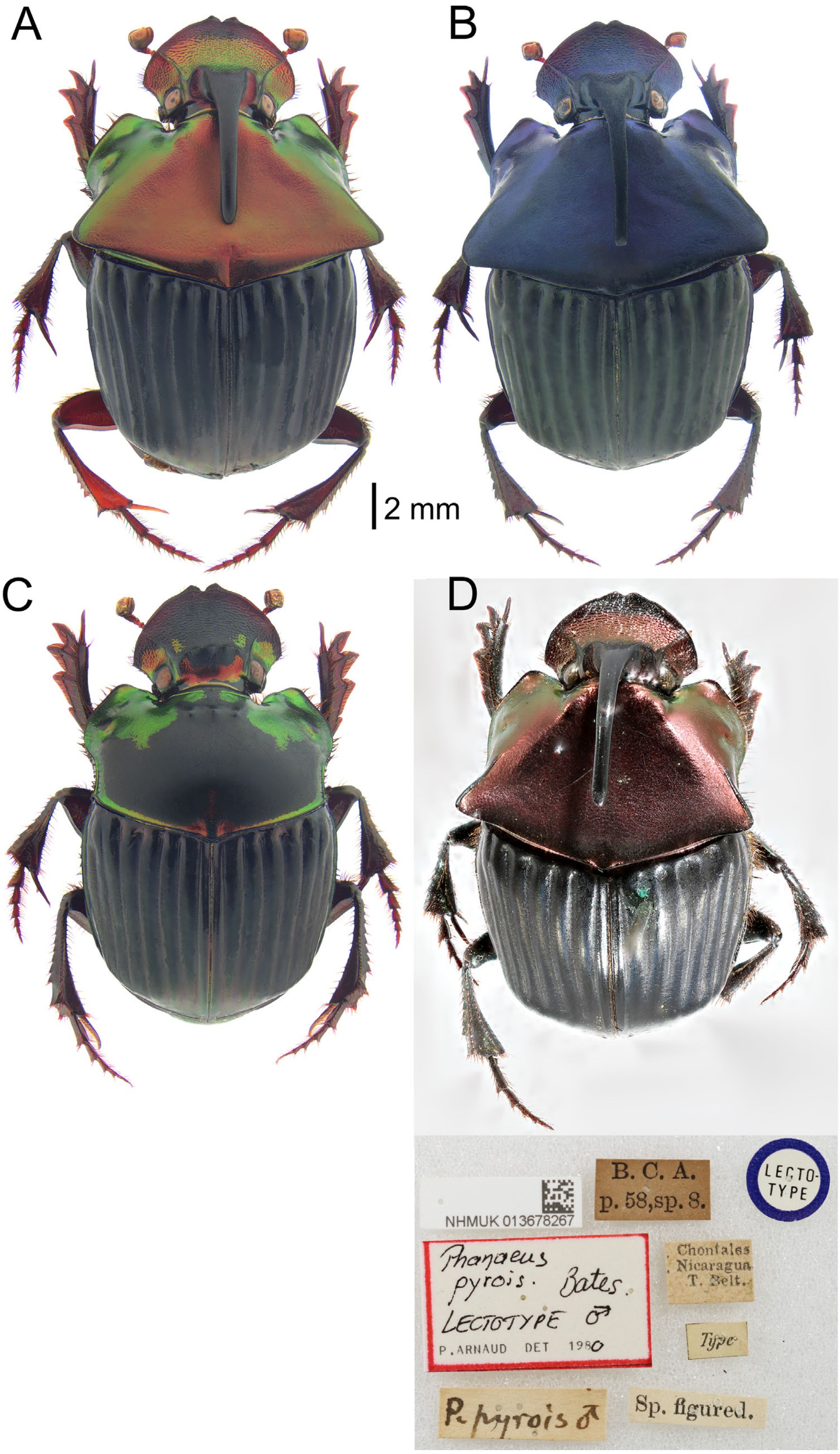

Fig. 12. *Phanaeus pyrois* Bates, 1887. **A**. ♂, red morph (VCM). **B**. ♂, blue morph (VMC). **C**. ♀, green morph (TAMU). **D**. Lectotype, ♂ (by Mario Cupello, Universidade Federal do Paraná, Brazil) (BMNH).

et al. 2018, 2019; GBIF Secretariat 2019b). Differences in body colour and the pronotal, elytral and genital morphology were found to confidently diagnose *P. pyrois* and all the closely related species. The blue chromatic morph of *P. pyrois* (Fig. 12B) was suggested by Edmonds (1994) to be a hybrid with *P. endymion*. Nevertheless, blue specimens of *P. pyrois* (Fig. 12B) do not share the diagnostic characters with *P. endymion* (Figs 1D, 2B, 4). As a consequence, there is no evidence to consider a hybridization between *P. endymion* and *P. pyrois*. Edmonds & Zídek (2012) suggested that doubtful specimens of "*viridicollis*" (Figs 2J, 12C) were collected in Nicaragua along with "normal" *P. pyrois*. After revising the doubtful specimens of "*viridicollis*" from Nicaragua (Figs 2J, 12C), we disagree with Edmonds & Zídek (2012) and conclude that they incorrectly referred to the green chromatic morph of *P. pyrois* as *P. viridicollis*.

Phanaeus rzedowskii sp. nov.

urn:lsid:zoobank.org:act:A98B849A-4240-4DD3-9997-D0B3CB7B00C2

Figs 1O, 2K, 13, 15, 18P, 19P

Diagnosis

This is the only species within the *P. endymion* species group where major males show a pronotal disc with a superficially impressed midline (Fig. 2K).

Etymology

We are honoured to name the new species after Jerzy Rzedowski, to recognise his outstanding contribution to the knowledge of the Mexican biodiversity, particularly to the flora from El Bajío region.

Tyepa material (2 ♂♂, 2 ♀♀)

Holotype

MEXICO – **Michoacán** • ♂; "Coalcoman. 24-VII-90. Fungus. Terry Taylor col"; TAMU.

Paratypes

MEXICO – **Michoacán** • 1 ♀; same collection data as for holotype; TAMU • 1 ♂, 1 ♀; "Villa Victoria. 31-VIII-95. 1550 m"; VMC.

Type locality

Mexico, Michoacán, Coalcomán.

Description

Major male (holotype)

Length 18 mm.

Head. Clypeus bidentate, black on anterior margin, dark metallic blue-green on posterior portion, roughened sculpture. Genae dark metallic blue-green, with roughened sculpture. Front dark metallic blue-green on portions adjacent to cephalic horn. Cephalic horn black, curved posteriorly over pronotum (Figs 2K, 13A).

Pronotum. Uniformly dark metallic blue-green, becoming completely black on and beneath lateral margins of posterolateral angles, and on posterior margin. Keel absent in the middle of anterior pronotal margin. Disc triangular, flat, with two distinctly developed tubercles on anterior portion. Triangle lightly granulate, with midline superficially impressed, scabriculous, impunctate. Sides with smooth sculpture, scabriculous, with superficially impressed punctures. Lateral lines of pronotal triangle straight. Posterolateral angles sharply acute, projected posteriorly. Lateral fossae distinctly impressed. Basal fossae obtusely oval, distinctly impressed. Posterior margin with superficially impressed punctures (Figs 2K, 13A).

Elytra. Fine striae, dark blue-green, with superficially impressed punctures, scabriculous, impressed basally as distinct fossae. Interstriae black, scabriculous, partially roughened, with superficially impressed punctures. Sutural margin without apical tooth (Fig. 13A).

Protibiae. Quadridentate with apical spine.

Tergite VIII. Dark metallic blue-green, scabriculous; with rough, superficially impressed punctures. Basal margin with setae variable in size.

Genitalia. Right lobe of endophallite copulatrix more developed than left lobe. Right lobe obtusely triangular in shape, sharply acute frontally, rounded superiorly. Left lobe strongly developed, obtusely lobed. Central ridge more developed than central column (Fig. 1O).

Minor male

Unknown.

Female

Similar to the male, except for the head showing a cephalic trituberculate carina; with almost aligned, conical tubercles, similar in size tubercles; frons distinctly impressed, rough punctures; pronotal sculpture completely smooth, with superficially impressed punctures; colour of pronotum as in *P. endymion*; pronotal process trituberculate, posteriorly concave; dentiform middle tubercle, strongly developed, more frontally projected than lateral tubercles; almost completely reduced lateral tubercles (Fig. 13B).

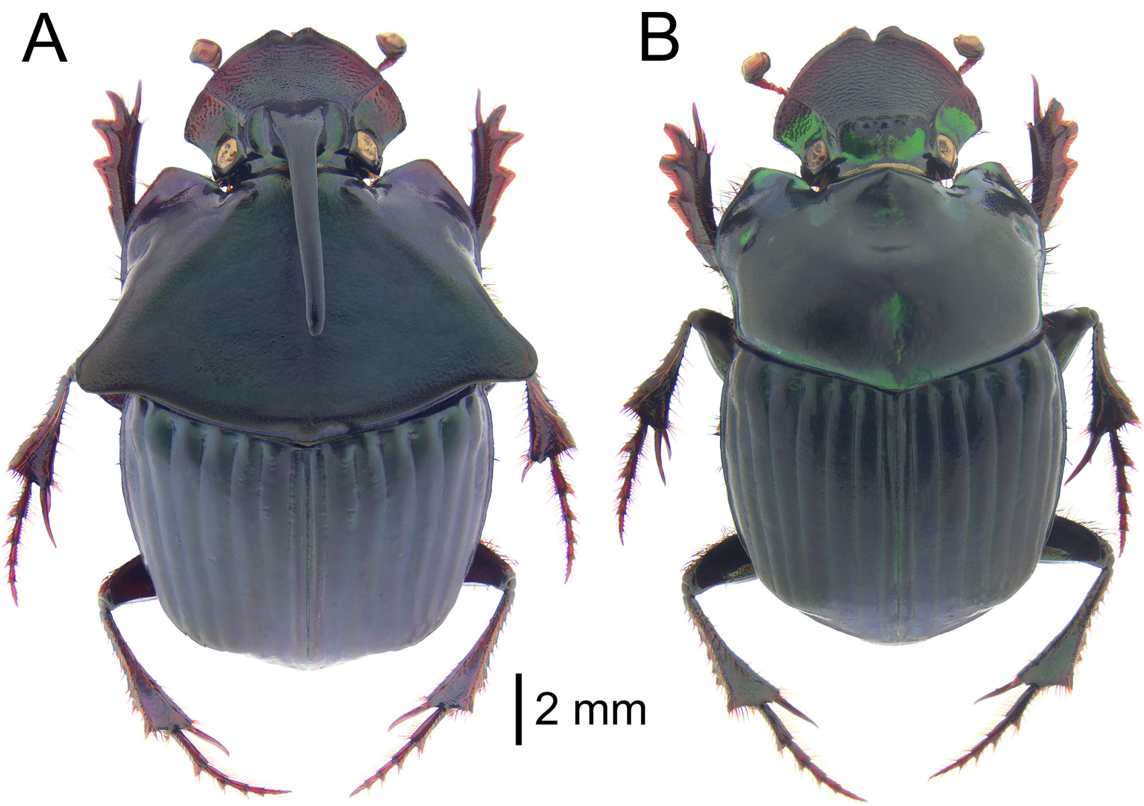

Fig. 13. *Phanaeus rzedowskii* sp. nov. **A**. Holotype, ♂ (TAMU). **B**. ♀ (VMC).

Variation

Mean length 17.4 mm (16.5–18.2 mm). Chromatic variation was not observed in the type series.

Distribution

Sierra Madre del Sur, southern Michoacán (Fig. 15).

Remarks

This new species was previously confused with *P. endymion* (Edmonds 1994). Nevertheless, the distribution areas for *P. endymion* and *P. rzedowskii* sp. nov. are completely different, and they are easily recognized by external and genital morphology.

Phanaeus zapotecus Edmonds, 2006
Figs 1P, 2L, 14–15, 18Q, 19Q

Phanaeus zapotecus Edmonds, 2006: 31–32, 35–37, figs 1, 3, 5, 7.
Phanaeus dionysius Kohlmann *et al*., 2018: 67–70, 76, 78, 82, 88–89, figs 1b, 3a–b, d, 4–7. **Syn. nov.**

Phanaeus zapotecus – Edmonds & Zídek 2012: 1, 7–8. — Moctezuma & Halffter 2017: 52, 54–55, fig. 23. — Moctezuma *et al*. 2017: 114, 130, 132; 2019: 253.
Phanaeus (*Notiophanaeus*) *zapotecus* – Edmonds & Zídek 2012: 3, 13, figs 139, 141, 143, 148–151.
Phanaeus (*Notiophanaeus*) *dionysius* – Kohlmann *et al*. 2018: 68, 70.

Non *Phanaeus endymion* – Edmonds 1994: 44 (referred to as "Oaxaca" population).
Non *Phanaeus* (*Notiophanaeus*) "Oaxaca" *endymion* – Edmonds 1994: fig. 221.

Type material of *Phanaeus zapotecus* revised (3 ♂♂, 5 ♀♀)

Holotype (not studied, temporarily lost)

MEXICO – **Oaxaca** • ♂, Edmonds 2006: 32; 8 km south of San Miguel Sola de Vega; IEXA?

Paratypes

MEXICO – **Oaxaca** • 1 ♂, 1 ♀; "8 km Sola de Vega, 1850 m, 7–17 ix 05, Pine oak forest, D. Curoe col. Mushroom-baited trap"; CEMT • 1 ♂, 1 ♀; same collection data as for preceding; TAMU • 1 ♂, 2 ♀♀; same collection data as for preceding; VMC • 1 ♀; "8 km Sola de Vega, 1850 m, 4–9 vii 05, Pine oak forest, D. Curoe col. Mushroom-baited trap"; TAMU.

Type material of *Phanaeus dionysius* revised (2 ♂♂, 2 ♀♀)

Holotype

MEXICO – **Oaxaca** • "La mesita San Pablo Etla, 23–VI–17, coprotrampa, x- 96°44'18.91''O, y- 17°9'54.36''N, bosque de Encino, 1976 m, Arriaga A. & Arenas A. Col."; IEXA.

Paratypes

MEXICO – **Oaxaca** • 2 ♀♀; same collection data as for holotype; IEXA • 1 ♂; "La mesita San Pablo Etla, 14–VII–17, coprotrampa, x- 96°44'53.55''O, y- 17°9'53.55''N, bosque de Encino, 1954 m, Arriaga A. & Arenas A. Col."; IEXA.

Non-type material revised (1 ♂)

MEXICO – **Oaxaca** • 1 ♂; "San Pablo Etla, Reserva San Pablo Etla, 20/X/2016, C.D. 17°10'1.23''N, 96°44'14.25''O, 1994 m, Alfosina Arriaga Col."; VMC.

Type locality

Mexico, Oaxaca, 8 km south of San Miguel Sola de Vega.

Phanaeus dionysius

Kohlmann *et al*. (2018) recently described *P. dionysius* based upon specimens from San Pablo Etla, Oaxaca, Mexico and suggested that *P. zapotecus* and *P. dionysius* were sister taxa. The following character combination helps to separate both species according to Kohlmann *et al*. (2018): *P. dionysius* has long and slender pronotal posterolateral angles, whereas *P. zapotecus* has short and rounded posterolateral angles. The basal border of the tergite VIII in *P. dionysius* forms a small indentation at its middle, whereas it runs completely straight in *P. zapotecus*. Additionally, the apex of the parameres of *P. dionysius* is more projected, than that from *P. zapotecus*. Moreover, the middle sinuation of the parameres in lateral view is much more pronounced in *P. dionysius*. Nevertheless, we consider that the description and diagnosis of *P. dionysius* exemplify some of the frequent problems occurring in taxonomical work (Komarek & Beutel 2006) as follows.

Insufficient study of types

Kohlmann *et al*. (2018) did not indicate how many specimens of *P. zapotecus* they revised, but they commented that the paratypes housed at CNIN were checked by them. Taking into account this information and the original description of *P. zapotecus* (Edmonds 2006), we assume that Kohlmann *et al*. (2018) revised two paratypes at most.

Insufficient assessment of the range of character variation

Kohlmann *et al*. (2018) were not able to adequately assess the morphological variation of *P. zapotecus*, as a consequence of the reduced number of paratypes studied by them. The pronotal posterolateral angles were found by us to be long and slender in some paratype major males of *P. zapotecus* (Fig. 14A). The basal border of the tergite VIII is highly variable: four paratypes of *P. zapotecus* revised by us show the small indentation at the middle of the basal border of the tergite VIII (Fig. 14D), whereas it runs completely straight in two paratypes. The small indentation is present in the basal border of the tergite VIII of three specimens of *P. dionysius* revised by us, whereas it runs completely straight in two paratypes (Fig. 14E).

Kohlmann *et al*. (2018) illustrated the endophallite copulatrix of *P. dionysius* (available from https://zookeys.pensoft.net/article/23029/zoom/fig/13/) but they overlooked its comparison with *P. zapotecus* (Fig. 1P). We noticed that the morphology of both *P. zapotecus* (Fig. 1P) and *P. dionysius* is identical when we compared the endophallites under the microscope. Furthermore, the endophallite copulatrix of the holotype of *P. dionysius* has suffered deformation and abrasion, maybe as a result of the preparation methods (soaking for 5 min in a solution of 5% boiling KOH) and/or storage (dry preservation in a plastic microvial). This structure was not found by us to be stored in a microvial with glycerol as mentioned by Kohlmann *et al*. (2018). The morphology of the cephalic carina and the pronotal tubercles of the females of *P. zapotecus* (Fig. 14B) and *P. dionysius* (see https://zookeys.pensoft.net/article/23029/zoom/fig/14/) did not differ. Moreover, the body colour in the paratypes of *P. zapotecus* varied from jet black or bright dark blue to jet black with a green-blue sheen (Fig. 14A–C), falling within the variation of *P. dionysius* (Kohlmann *et al*. 2018).

Kohlmann *et al*. (2018) commented that a major male was designated as holotype. Nevertheless, we found out that the holotype of *P. dionysius* housed at IEXA is the minor male illustrated by Kohlmann *et al*. (2018) in the original description (available from https://zookeys.pensoft.net/article/23029/zoom/fig/15/). As a consequence, we assume that the original description of *P. dionysius* was not based on the holotype. We found that a paratype minor male of *P. zapotecus* (Fig. 14C) and the holotype of *P. dionysius* (https://zookeys.pensoft.net/article/23029/zoom/fig/15/) were morphologically almost identical.

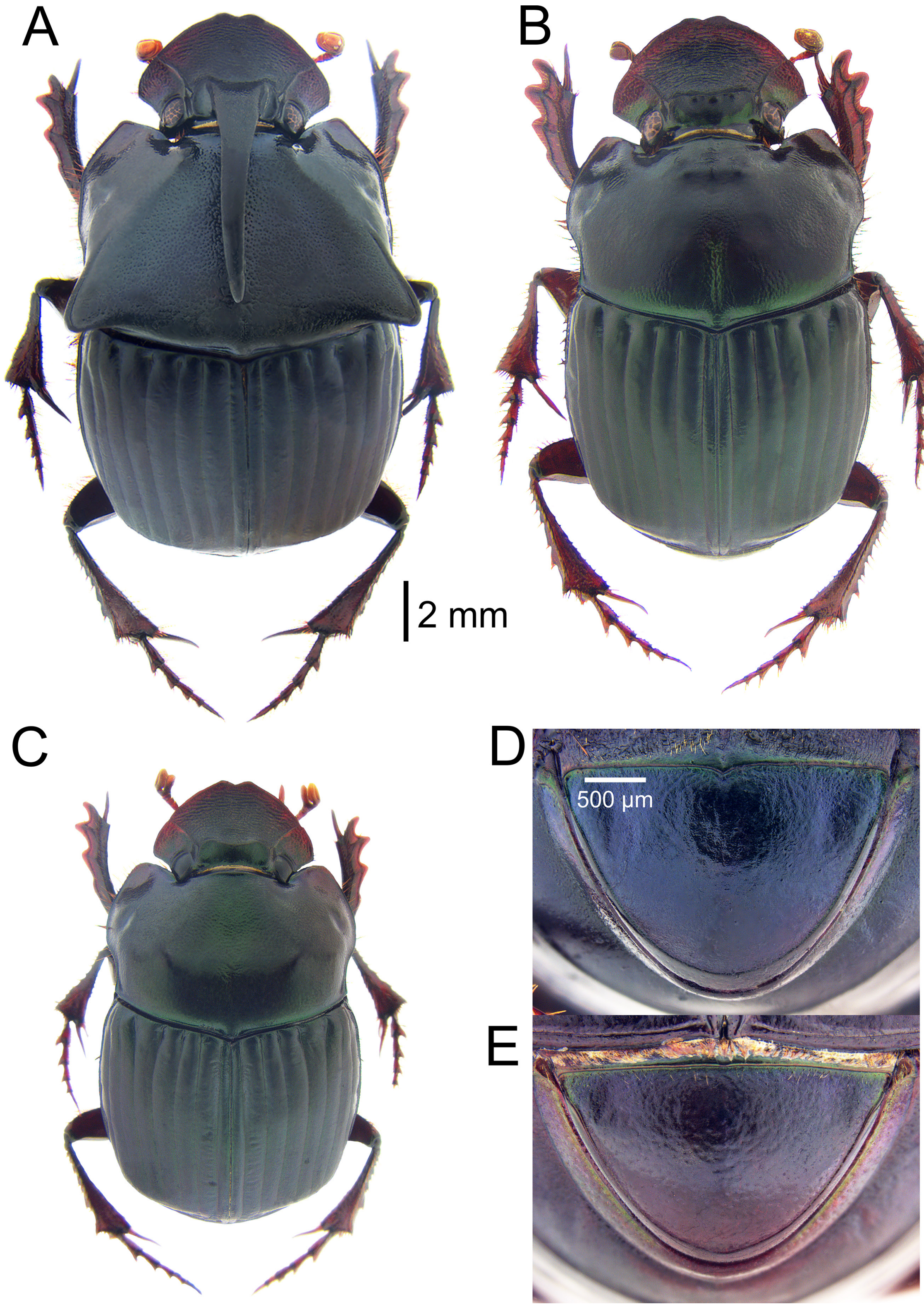

Fig. 14. A–D. *Phanaeus zapotecus* Edmonds, 2006. **A**. ♂ (TAMU). **B**. ♀ (TAMU). **C**. Minor ♂ (VMC). **D**. Tergite VIII (TAMU). **E**. *Phanaeus dionysius* Kohlmann, Arriaga-Jiménez & Rös, 2018 syn. nov., tergite VIII (IEXA).

Characters not suitable for a study at a given taxonomic rank

The revision of a majority of species within the *P. endymion* species group led us to conclude that the morphology of the aedeagus is not taxonomically informative to separate species, as suggested by previous authors (Edmonds 1994; Price 1995; Arnaud 2002b; Moctezuma & Halffter 2017; Moctezuma *et al*. 2017, 2019).

In the light of the findings presented herein, we conclude that the description and diagnoses provided by Kohlmann *et al*. (2018) do not justify the splitting of *P. dionysius* and *P. zapotecus* in two different species. As a consequence, a new junior subjective synonymy is recognized herein: *Phanaeus zapotecus* Edmonds, 2006 = *Phanaeus dionysius* Kohlmann, Arriaga-Jiménez & Rös, 2018 syn. nov.

Distribution

Sierra Madre del Sur and Sierra Norte, central Oaxaca (Fig. 15).

Remarks

Mean length 16.4 mm (14.8–18.5 mm). To the original description of this species, we add that the elytral striae are impressed basally as distinct fossae (Fig. 14); right lobe of endophallite copulatrix more developed than left lobe; right lobe obtusely triangular in shape, strongly developed superiorly; left lobe strongly reduced, lobed, slightly concave inferiorly; central ridge more developed than central column (Fig. 1P). For the female, the head shows a cephalic trituberculate carina; with almost aligned, conical tubercles; middle tubercle slightly more developed than lateral tubercles; frons with almost effaced punctures; pronotal process trituberculate, with posterior concavity; rounded pronotal tubercles; with middle tubercle slightly more developed than lateral tubercles; posterior pronotal midline distinctly impressed (Fig. 14B).

Edmonds (2006) commented that the holotype and three paratypes (1 ♂, 2 ♀♀) of *P. zapotecus* were housed at IEXA. However, the type material was not found by us at IEXA in a recent search. Therefore, the holotype and these paratypes are considered temporarily lost. It is possible that the former collection manager of IEXA, Professor Miguel Angel Morón Ríos, knew the location of the holotype and paratypes of *P. zapotecus*, but, unfortunately, we were not able to confirm this assumption because of his recent death.

Phanaeus zoque Moctezuma & Halffter, 2017
Figs 1Q, 15, 18R, 19R

Phanaeus zoque Moctezuma & Halffter, 2017: 47, 48, 52, 55–56, figs 1–15, 23.

Phanaeus zoque – Moctezuma *et al*. 2017: 113–114, 126, 128, 131–132, fig. 19; 2019: 252–253, fig. 5. — Kohlmann *et al*. 2018: 83, 88.

Type material

Holotype

MEXICO • ♂, Moctezuma & Halffter 2017: 48 (revised); Oaxaca, Santa María Chimalapa, Chocomanatlán; IEXA.

Type locality

Mexico, Oaxaca, Santa María Chimalapa, Chocomanatlán (José López Portillo).

Distribution

Temperate mountains of Los Chimalapas, eastern Oaxaca and western Chiapas (Fig. 15).

Remarks

Mean length 15.8 mm (13.2–18.4 mm). To the original description we add the elytral striae impressed basally as distinct fossae; right and left lobes of endophallite copulatrix similar in size; right lobe obtusely triangular in shape, distinctly rounded superiorly; left lobe strongly developed, obtusely lobed; central ridge less developed than central column (Fig. 1Q). For the female, the head showing a cephalic trituberculate carina; with conical, similar in size tubercles; middle tubercle slightly more frontally projected than lateral tubercles; frons with almost effaced to effaced punctures; pronotal sculpture completely smooth, with almost effaced to effaced punctures; pronotal process trituberculate, with posterior concavity; with dentiform middle tubercle, strongly more developed and projected frontally than lateral tubercles; carinate or rounded lateral tubercles; posterior pronotal midline almost completely effaced.

After having described *P. zoque* (Moctezuma & Halffter 2017), the following paratypes were deposited by us in additional collections: CEMT: 5 ♂♂, 5 ♀♀; CDC: 5 ♂♂, 5 ♀♀; CMNC: 1 ♂, 1 ♀; CPFA: 6 ♂♂, 6 ♀♀; UVGC: 1 ♂, 1 ♀. These paratypes were previously housed at VMC (see the full list of paratypes in Moctezuma & Halffter 2017).

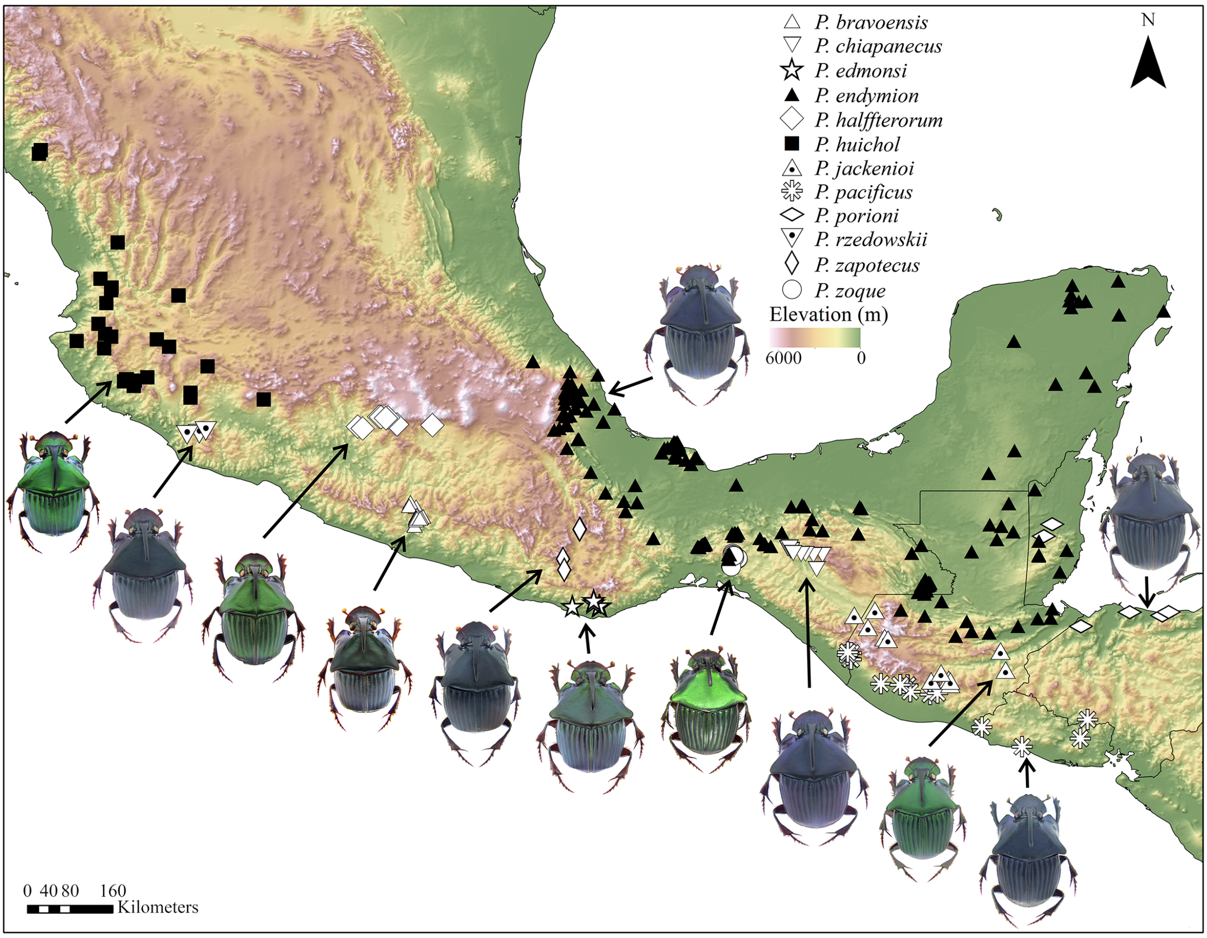

Fig. 15. Distribution of the *Phanaeus endymion* species group in North and Central America (in part). *Phanaeus bravoensis* Moctezuma, Sánchez-Huerta & Halffter, 2017; *P. edmondsi* Moctezuma, Deloya & Halffter, 2019; *P. halffterorum* Edmonds, 1979; and *P. huichol* Moctezuma, Sánchez-Huerta & Halffter, 2017 by Jose Luis Sánchez-Huerta.

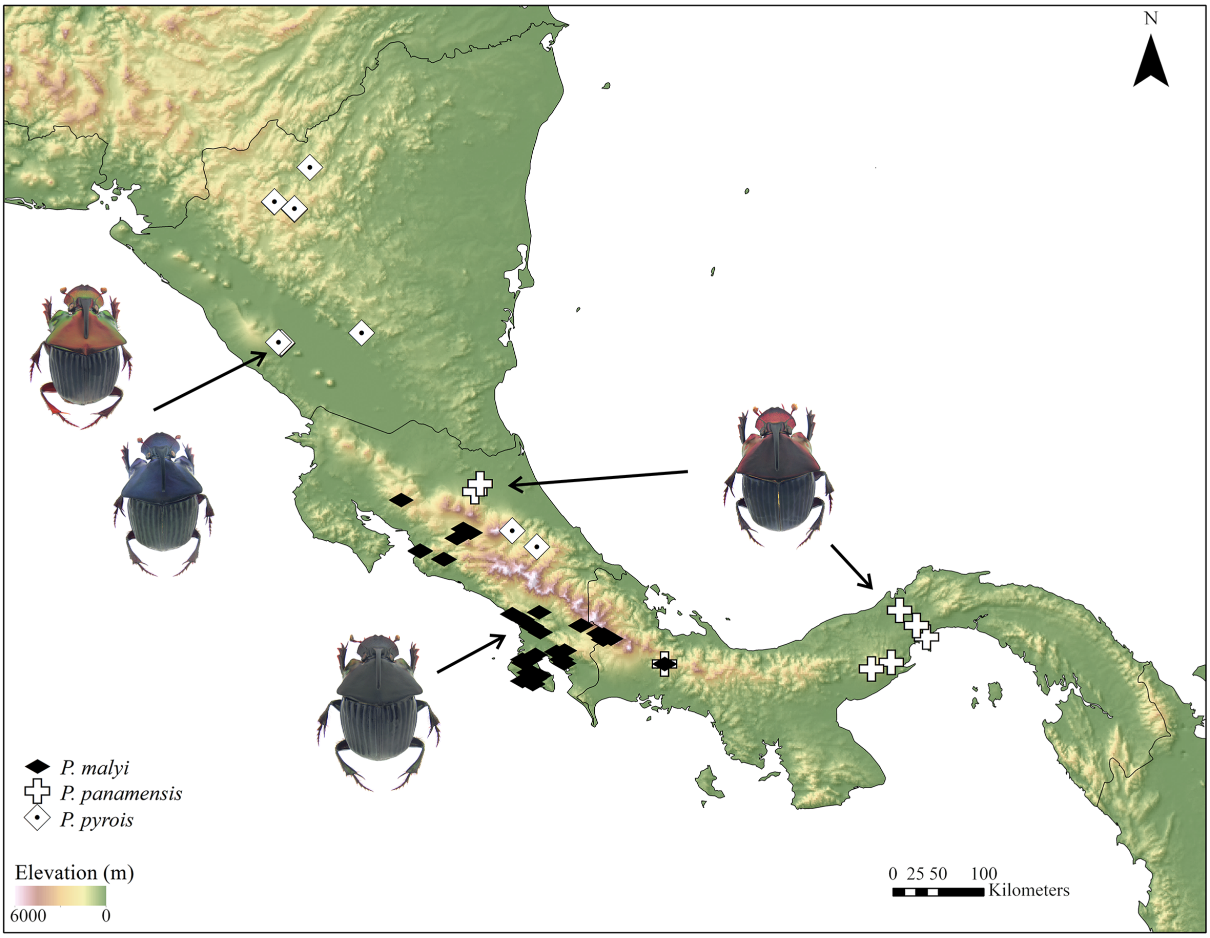

Fig. 16. Distribution of the *Phanaeus endymion* species group in Central America (in part).

Key to species of the Phanaeus endymion species group

1. Sutural margin of each elytron upturned to form a sharp ridge, which is progressively more elevated posteriorly and prolonged into a small, sharp tooth at apical angle; elytral margin slightly excised adjacent to this tooth 2
– Sutural margin of elytra simple (running straight, not upturned) 3

2. Male with dentiform keel in the middle of anterior pronotal margin, lateral lines of pronotal triangle straight. Southern Mexico State and Morelos (Fig. 15).................... ***P. halffterorum*** Edmonds, 1979
– Male with keel absent in the middle of anterior pronotal margin, lateral lines of pronotal triangle curved. Sierra Madre del Sur, central Guerrero (Fig. 15) .... ***P. bravoensis*** Moctezuma, Sánchez-Huerta & Halffter, 2017

3. Pronotal disc of male evenly and densely but finely granulate, granules in most specimens larger and becoming squamose along lateral margins of disc and extending onto posterolateral angles; sides of pronotum strongly roughened (Figs 2L, 14A, C). Female pronotum slightly roughened; with distinctly impressed midline (Figs 14B, 18Q). Sierra Madre del Sur and Sierra Norte, central Oaxaca (Fig. 15) .... ***P. zapotecus*** Edmonds, 2006
– Pronotal disc of male lacking distinct granulation, or, if granules present, these are minute and restricted along lateral margins of disc; sides of pronotum smooth. Female pronotum smooth; with superficially impressed to completely effaced midline.. 4

4. Elytral striae deeply punctate; all strial punctures forming a distinct fossa, giving a completely roughened surface to striae (Figs 1K, 2G, 9, 19L). Pacific slope of the Sierra Madre de Chiapas and El Salvador (Fig. 15)..***P. pacificus*** sp. nov.
– Elytral striae distinctly punctate to impunctate. If strial punctures distinctly impressed, forming a distinct fossa giving a completely roughened surface to first and second striae, or strial punctures forming a distinct fossa giving a partially roughened surface to basal half of striae 5

5. Pronotum of female with anteromedial concavity bounded anteriorly by three variable on shape tubercles (Figs 4C, 11B, 13B, 18E, N, P).. 6
– Pronotum of female evenly convex, lacking anteromedial concavity even in largest specimens, bearing three round, smooth tubercles in transverse line near anterior margin (Figs 3B, 5B, 6B, 7B, 8B, 10B, 12C, 18C, F, I–K, M, O)... 10

6. Pronotum of female with concavity bounded anteriorly by a raised U- or V-shaped process; middle pronotal tubercle dentiform or rounded, always more developed and frontally projected than lateral tubercles; pronotal concavity interrupted posteriorly by a small rounded bump or strongly developed dentiform tubercle (Figs 4C, 13B, 18E, P). Endophallite copulatrix variable.................................. 7
– Pronotum of female with concavity bounded anteriorly by three isolated, round, almost aligned tubercles; middle tubercle sometimes dentiform and more strongly developed than lateral tubercles (Figs 11B, 18N). Right and left lobes of endophallite copulatrix similar in size; right lobe obtusely triangular in shape, weakly developed superiorly; left lobe obtusely lobed, strongly developed; central ridge distinctly developed (Fig. 1M). Caribbean Honduras and Belize (Fig. 16) .... ***P. porioni*** Arnaud, 2002 stat. rev.

7. Pronotal disc of male with superficially impressed midline (Fig. 2K). Right lobe of endophallite copulatrix more developed than left lobe; right lobe obtusely triangular in shape, sharply acute frontally, rounded superiorly; left lobe strongly developed, obtusely lobed; central ridge strongly developed (Fig. 1O). Sierra Madre del Sur, southern Michoacán (Fig. 15) ......***P. rzedowskii*** sp. nov.
– Pronotal disc of male with completely effaced midline (Fig. 2B). Central ridge of endophallite copulatrix distinctly developed (Fig. 1D, G, Q) 8

8. Pronotum of male uniformly dark blue, dark metallic blue-green or dark metallic green (Figs 2B, 4A–B). Weakly developed keel close to anterior margin of pronotum, or keel completely effaced (Fig. 2b). Right lobe of endophallite copulatrix more developed than left lobe; right lobe obtusely triangular in shape; left lobe obtusely lobed inferiorly, obtusely triangular superiorly; central ridge less developed than central column (Fig. 1D). Lowlands and midlands of the Gulf of Mexico slope, Yucatán Peninsula, Belize, northern Guatemala (Fig. 15)........................***P. endymion*** Harold, 1863
– Pronotum of male uniformly bright metallic green, bright metallic green-blue, sometimes showing a red or golden sheen. Keel always absent on anterior margin of pronotum. Endophallite copulatrix variable 9

9. Anterior metasternal angle obtuse in lateral view. Lateral metasternal angles well defined and slightly curved. Left lobe of endophallite copulatrix almost completely lobed (Fig. 1Q). Temperate mountains of Los Chimalapas, eastern Oaxaca and western Chiapas (Fig. 15) ....***P. zoque*** Moctezuma & Halffter, 2017
– Anterior metasternal angle almost right angled but with rounded apex in lateral view. Lateral metasternal angles evanescent. Left lobe of endophallite copulatrix straight posteroinferiorly (Fig. 1G). Jalisco, northern Michoacán, Nayarit, southern Sinaloa (Fig. 15) ....***P. huichol*** Moctezuma, Sánchez-Huerta & Halffter, 2017

10. Elytral interstriae evenly convex and glossy midlongitudinally; striae impressed basally as distinct fossae (Figs 3, 6, 7, 18C, I–J) 11
– Elytral interstriae distinctly flattened and uniformly dull; striae not strongly impressed basally (Figs 5, 8, 10, 12, 18F, K, M, O)... 14

11. Almost completely bright black dorsally (Figs 2E, 7). Pacific slope of the Cordillera de Talamanca, Costa Rica and Panama (Fig. 16) ....***P. malyi*** Arnaud, 2002
– Pronotum typically bright metallic green, blue-green or dark metallic blue (Figs 2A, D, 3, 6)...... 12

12. Distinctly developed keel on central anterior margin of pronotum of male; right lobe of endophallite copulatrix tapering superiorly and straight apically (Fig. 1C). Sierra Madre del Sur, southern Oaxaca (Fig. 15) ....***P. edmondsi*** Moctezuma, Deloya & Halffter, 2019
– Always with keel absent on central anterior margin of pronotum of male (Fig. 2A, D). Endophallite copulatrix variable 13

13. Larger species, frequently attaining 19–20 mm in length. Posterolateral angles of male widened, slightly projected posteriorly (Figs 2A, 3). Central highlands of Chiapas (Fig. 15) ....***P. chiapanecus*** sp. nov.
– Smaller species, never attaining 19 mm in length. Posterolateral angles of male sharply acute, strongly projected posteriorly (Figs 2D, 6). Inner slope of the Sierra Madre de Chiapas, south-central Guatemala and southeastern Chiapas (Fig. 15) ....***P. jackenioi*** sp. nov.

14. Pronotal disc of male completely bright metallic (Figs 2J, 12).. 15
– Pronotal disc of male distinctly black, without metallic reflection (Figs 2E, J, L, 5A, C, 8A, 10A) 16

15. Pronotal disc typically bright metallic green, rarely dark metallic blue. Pronotal process of female with central tubercle more developed and anteriorly projected than lateral tubercles. Ecuador (Figs 17, 18A)..***P. arletteae*** Arnaud, 2002
– Pronotal disc typically bright metallic red, green, or dark metallic blue (Figs 2J, 12). Pronotal process of female with tubercles almost aligned, central tubercle not projecting anteriorly (Figs 12C, 18O). Nicaragua and north Caribbean Costa Rica (Fig. 16)..***P. pyrois*** Bates, 1887

16 Pronotum distinctly bright metallic red frontolaterally. Head bright metallic red with green-yellow metallic sheen (Figs 2F, H, 8, 10) 17
– Pronotum distinctly dull metallic red frontolaterally. Head dull metallic red without green-yellow metallic sheen (Figs 2C, 5). Pacific slope of the Andes, north-central Ecuador and Colombia (Fig. 17) ....***P. funereus*** Balthasar, 1939 stat. rev.

17. Larger species, frequently attaining from 22 to 24 mm in length. Carinate, distinctly developed keel on central anterior margin of pronotum of male (Fig. 2F). Pronotal posterolateral angles of male strongly developed, projected laterally (Fig. 8A). Pacific slope of the Andes, south-central Colombia and northern Ecuador (Fig. 17)...***P. olsoufieffi*** Balthasar, 1939 stat. rev.
– Smaller species, rarely attaining 20 mm in length. Always with keel absent on central anterior margin of pronotum of male (Fig. 2H). Pronotal posterolateral angles of male weakly developed, widened, and slightly projected posteriorly (Fig. 10A). Caribbean Costa Rica and Panama (Fig. 16) ....***P. panamensis*** sp. nov.

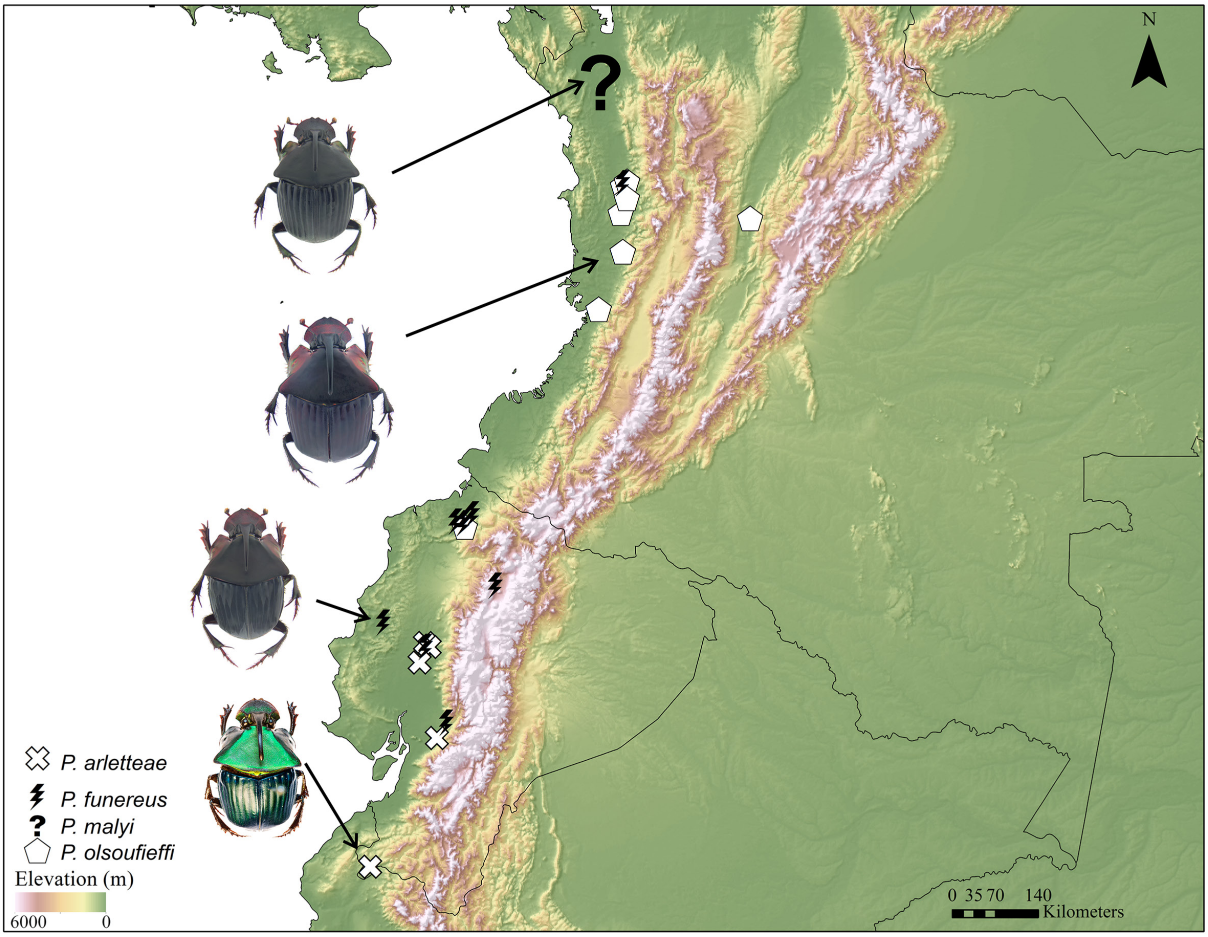

Fig. 17. Distribution of the *Phanaeus endymion* species group in South America. *Phanaeus malyi* Arnaud, 2001 was reported from Colombia without accurate locality. *Phanaeus arletteae* Arnaud, 2018 was modified from Arnaud (2018).

Discussion

By comparing the external and genital morphology of hundreds of specimens, revisiting the original species descriptions, and examining type material of problematic species (e.g., *P. endymion*, *P. dionysius*, *P. funereus*, *P. olsoufieffi*, *P. porioni*, *P. pyrois*, *P. zapotecus*), the taxonomy of the *P. endymion* species group has been reassessed and several taxonomical issues were disentangled. As a consequence, five new species have been described and three previously described species have been resurrected from synonymy. Contrary to previous authors (Edmonds 1994; Edmonds & Zídek 2012; Moctezuma & Halffter 2017; Moctezuma *et al*. 2017, 2019), who considered that the morphology of the females within the *P. endymion* species group was relatively homogeneous and taxonomically uninformative, we highlight the importance of the pronotal and cephalic morphology of females to confidently separate closely related species. Furthermore, the morphological variation of females was pivotal in developing a new determination key.

Additionally, we found that in the *P. endymion* species group body colouration and the morphology of the endophallite copulatrix, which have traditionally been neglected in the taxonomy of *Phanaeus* (Martínez & Pereira 1967; Edmonds 1994; Edmonds & Zídek 2012), can be informative characters. Differences in body colour were accompanied by differences in the external and genital morphology.

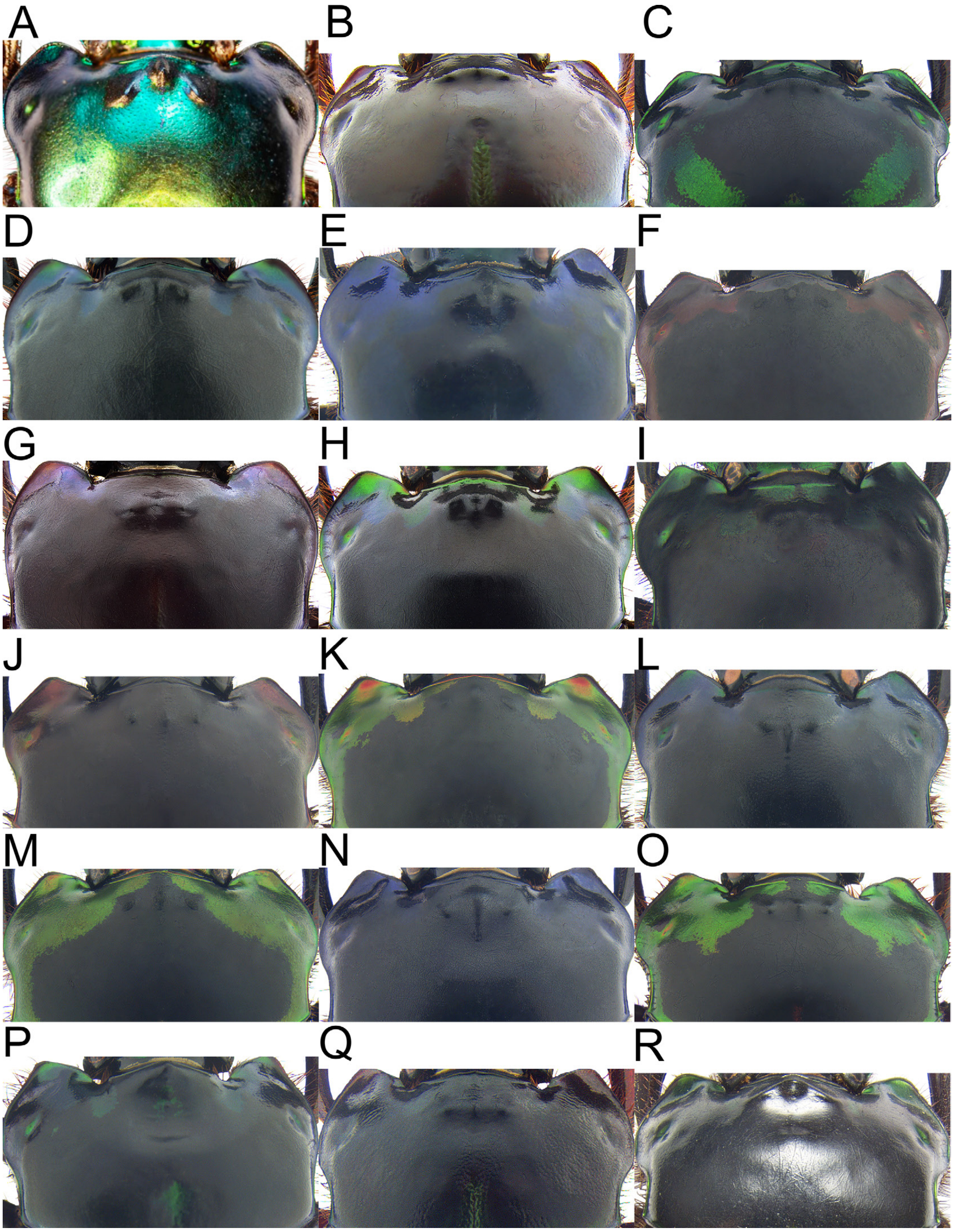

Fig. 18. Pronotum of females within the *Phanaeus endymion* species group. **A**. *Phanaeus arletteae* Arnaud, 2018 (modified from Arnaud 2018). **B**. *Phanaeus bravoensis* Moctezuma, Sánchez-Huerta & Halffter, 2017 (by Jose Luis Sánchez-Huerta). **C**. *Phanaeus chiapanecus* sp. nov. **D**. *Phanaeus edmondsi* Moctezuma, Deloya & Halffter, 2019 (by Jose Luis Sánchez-Huerta). **E**. *Phanaeus endymion* Harold, 1863. **F**. *Phanaeus funereus* Balthasar, 1939 stat. rev. **G**. *Phanaeus halffterorum* Edmonds, 1979 (by Jose Luis Sánchez-Huerta). **H**. *Phanaeus huichol* Moctezuma, Sánchez-Huerta & Halffter, 2017 (by Jose Luis Sánchez-Huerta). **I**. *Phanaeus jackenioi* sp. nov. **J**. *Phanaeus malyi* Arnaud, 2002. **K**. *Phanaeus olsoufieffi* Balthasar, 1939 stat. rev. **L**. *Phanaeus pacificus* sp. nov. **M**. *Phanaeus panamensis* sp. nov. **N**. *Phanaeus porioni* Arnaud, 2001 stat. rev. **O**. *Phanaeus pyrois* Bates, 1887. **P**. *Phanaeus rzedowskii* sp. nov. **Q**. *Phanaeus zapotecus* Edmonds, 2006. **R**. *Phanaeus zoque* Moctezuma & Halffter, 2017.

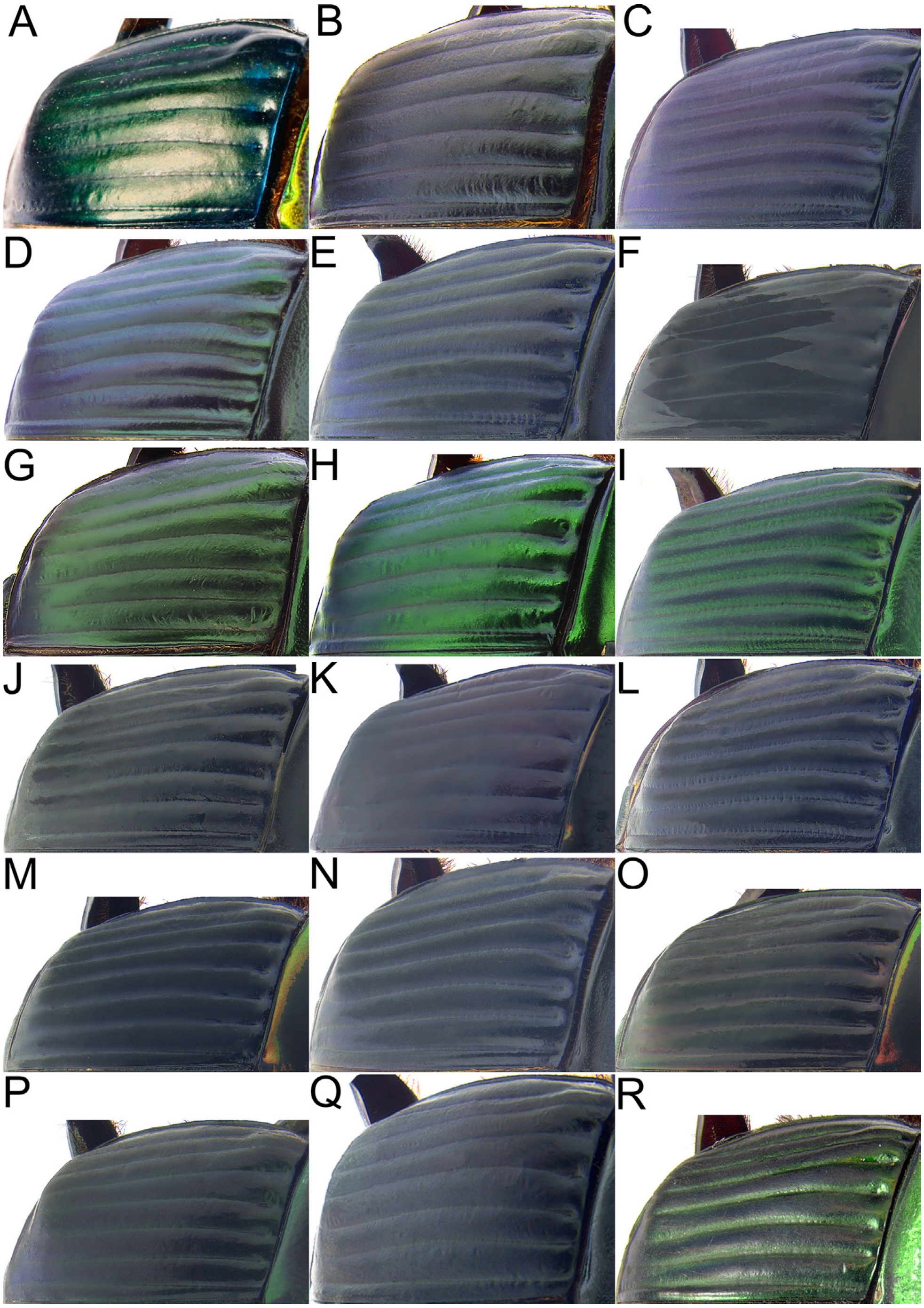

Fig. 19. Elytral integument of species within the *Phanaeus endymion* species group. **A**. *Phanaeus arletteae* Arnaud, 2018 (modified from Arnaud 2018). **B**. *Phanaeus bravoensis* Moctezuma, Sánchez-Huerta & Halffter, 2017 (by Jose Luis Sánchez-Huerta). **C**. *Phanaeus chiapanecus* sp. nov. **D**. *Phanaeus edmondsi* Moctezuma, Deloya & Halffter, 2019 (by Jose Luis Sánchez-Huerta). **E**. *Phanaeus endymion* Harold, 1863. **F**. *Phanaeus funereus* Balthasar, 1939 stat. rev. **G**. *Phanaeus halffterorum* Edmonds, 1979 (by Jose Luis Sánchez-Huerta). **H**. *Phanaeus huichol* Moctezuma, Sánchez-Huerta & Halffter, 2017 (by Jose Luis Sánchez-Huerta). **I**. *Phanaeus jackenioi* sp. nov. **J**. *Phanaeus malyi* Arnaud, 2002. **K**. *Phanaeus olsoufieffi* Balthasar, 1939 stat. rev. **L**. *Phanaeus pacificus* sp. nov. **M**. *Phanaeus panamensis* sp. nov. **N**. *Phanaeus porioni* Arnaud, 2001 stat. rev. **O**. *Phanaeus pyrois* Bates, 1887. **P**. *Phanaeus rzedowskii* sp. nov. **Q**. *Phanaeus zapotecus* Edmonds, 2006. **R**. *Phanaeus zoque* Moctezuma & Halffter, 2017.

Prior studies have demonstrated that at least in some instances, differences in body colouration may be supported by molecular sequence data as demonstrated by Solís & Kohlmann (2012). Since *Phanaeus* are diurnal beetles, body colour and iridescence are expected to be important for mate choice and visual social signaling directed to conspecifics and predators (Vulinec 1997), while both body colour and iridescence are a result of light absorption and the interference in reflected light rays propagating through micron-sized structures composed of organized nano-sized elements of the beetle cuticles (Michelson 1911; Vargas *et al*. 2018).

Therefore, we conclude that earlier authors underestimated the usefulness of body colouration to diagnose closely related species within the *P. endymion* species group (Martínez & Pereira 1967; Edmonds 1994; Edmonds & Zídek 2012), and the microstructures responsible of body colour and iridescence in *Phanaeus* cuticles might be a new and unexplored source of taxonomic characters. Additionally, the morphology of the endophallite copulatrix was reported to be homogeneous in closely related species of the *P. amethystinus*, *P. quadridens*, *P. tridens* and *P. vindex* species groups (Price 2005; Moctezuma *et al*. 2020). However, this is not the case with the *P. endymion* species group, for which we found a significant interspecific variation in the morphology of the endophallite copulatrix (Fig. 1). The wide genital variety of males might be a driver of diversification within the *P. endymion* species group, since variation in genital structures is thought to drive a rapid evolutionary divergence in other groups of arthropods (Yao *et al*. 2020). Nevertheless, further corroboration of our taxonomic conclusions using independent data such as DNA sequences for all relevant taxa would be desirable.

In addition, we consider that the most complete taxonomic treatment for the genus *Phanaeus* was proposed by Arnaud (2002b), as previously suggested by Moctezuma *et al*. (2020) for the *P. quadridens* species group. Nevertheless, Arnaud's (2002b) classification has limitations, such as the use of the subspecies-level without clear boundaries between species and subspecies. Future revisions of *Phanaeus* are needed because the species richness of this genus might be dramatically underestimated since Arnaud (2002b) proposed 77 taxa (species and subspecies) and 34 synonyms, while Edmonds & Zídek (2012) recognized only 54 valid species and suggested 53 synonyms.

As recognized herein, the *P. endymion* species group is the most species-rich grouping of rainbow scarab dung beetles within *Phanaeus*, encompassing 18 species. Other diverse species groups are those of *P. mexicanus* (11 taxa), *P. tridens* (10 taxa) and *P. chalcomelas* (9 taxa). On the other hand, the *P. amethystinus* (6 taxa), *P. hermes* (5 taxa), *P. palaeno* (5 taxa), *P. quadridens* (5 taxa), *P. splendidulus* (5 taxa), *P. beltianus* (4 taxa), *P. triangularis* (4 taxa) and *P. vindex* (4 taxa) species groups show a

Fig. 20. Lateral view of the aedeagus of the *Phanaeus endymion* species group (*P. endymion* Harold, 1863).

discrete diversity; while the *P. bispinus* species group (2 taxa) is the most species-poor (Arnaud 2002b; Edmonds 2006; Moctezuma *et al*. 2020). Consequently, the genus *Phanaeus* might incorporate at least 87 taxa, a number that undoubtedly will increase with the discovery of additional undescribed species in future revisions.

A former classification (Edmonds 1994; Edmonds & Zídek 2012) presented the *P. endymion* species group as a species-poor lineage, with two widely distributed species in the tropical forests (*P. endymion* and *P. pyrois*) and two endemics to mountain temperate forests (*P. halffterorum* and *P. zapotecus*). Consequently, we proposed that the *P. endymion* species group represented a recent penetration of Neotropical origin that arrived in Mexico during the Plio-Pleistocene climatic fluctuations (Halffter & Morrone 2017; Moctezuma & Halffter 2017). In this context, *P. endymion* and *P. pyrois* were considered as putatively basal taxa, while *P. halffterorum*, *P. zapotecus* and *P. zoque* represented marginal colonizations of montane regions (Moctezuma & Halffter 2017).

Nevertheless, some considerations arose as follows. The term "basal taxa" does not make sense, because every branching in a phylogenetic tree is rotatable. Consequently, there are always two most basal clades, both originating from a node with equal age and evolutionary change (Krell & Cranston 2004). Additionally, the *P. endymion* species group is widely distributed in montane regions. The *P. endymion* species group contains several species associated with tropical rainforests (*P. arletteae*, *P. edmondsi*, *P. endymion*, *P. funereus*, *P. malyi*, *P. olsoufieffi*, *P. pacificus* sp. nov., *P. panamensis* sp. nov., *P. porioni*, *P. pyrois*), mountain cloud forests (*P. endymion*) and tropical dry forests (*P. arletteae*, *P. bravoensis*, *P. chiapanecus* sp. nov.). On the other hand, at least seven species inhabit the temperate coniferous-oak forests of Mesoamerica (*P. bravoensis*, *P. halffterorum*, *P. huichol*, *P. jackenioi* sp. nov., *P. rzedowskii* sp. nov., *P. zapotecus* and *P. zoque*). Apparently, the diversification of the *P. endymion* species group and its dispersal to the Mexican temperate forests started during the Miocene (Price 2009; Kohlmann *et al*. 2018; Gillett & Toussaint 2020).

We hypothesize that the *P. endymion* species group has a significant plasticity to invade new ecological niches. The ecological plasticity of the *P. endymion* species group is supported by the heterogeneous ecosystems that it inhabits, such as the aforementioned tropical rainforests, tropical dry forests, mountain cloud forests, and temperate coniferous-oak forests (Edmonds 1994, 2003, 2006; Moctezuma & Halffter 2017; Moctezuma *et al*. 2017, 2019). Furthermore, some species may be opportunistic to invade forest borders and tropical pastures, such as *P. endymion* (Edmonds 1994, 2003; Salomão *et al*. 2020). The invasion of the *P. endymion* species group to these environments (such as the temperate forests and tropical pastures) might involve the development of adaptations in ecophysiological processes (e.g., respiration and temperature control) to tolerate dryness and microclimatic changes (Chown & Klok 2011; Moctezuma *et al*. 2016).

On the other hand, the *P. endymion* species group is the only one within *Phanaeus* that successfully shifted from coprophagy to necrophagy, mycetophagy and saprophagy (Halffter & Matthews 1966; Edmonds 1994, 2003, 2006; Halffter & Halffter 2009; Deloya *et al*. 2013; Gillett & Toussaint 2020). A combination of both the evolution of mandible morphology and symbiotic interactions may explain the remarkable trophic generalism of the *P. endymion* species group. The modifications of mandible morphology are known to be a key factor that allowed the evolution from the saprophagous ancestors to the modern coprophagous Scarabaeinae (Bai *et al*. 2015), while the effects of digestive symbionts have driven trophic generalism in herbivorous beetles (McKenna *et al*. 2019; Salem *et al*. 2020) and are responsible of facilitating digestion and nutrition process in dung beetles (Thiyonila *et al*. 2018; Suárez-Moo *et al*. 2020).

Although our study adhered to the phylogenetic species concept sensu Wheeler & Platnick (2000), we hope that the species described and redescribed herein are compatible with other popular species concepts, such as the biological species concept sensu Mayr (1942). The biological species concept emphasizes that reproductive isolation is the key characteristic between independent species (Zachos 2016; Nosil *et al*. 2017; Cupello & Vaz-de-Mello 2018; Huang 2020). Each species defined herein shows a unique morphology of the endophallite copulatrix. Therefore, sexual isolation between species of the *P. endymion* species group is expected, since differences in the morphology of the endophallites in Scarabaeinae dung beetles are considered as prezygotic mechanical barriers that may prevent interbreeding (Price 2005; Werner & Simmons 2008; Moretto & Génier 2020). The morphology of the endophallites has exhibited high levels of interspecific variation in other groups of Scarabaeinae dung beetles (Howden & Gill 1993; Joaqui *et al*. 2019; Moctezuma & Halffter 2020; Moretto & Génier 2020), while this variation is expected to have a strong phylogenetic signal to discriminate different evolutionary lineages (Tarasov & Solodovnikov 2011; Tarasov & Génier 2015).

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References

Agassiz J.L.R. 1846. *Nomenclatoris zoologici index universalis, continens nomina systematica classium, ordinum, familiarum et generum animalium omnium, tam viventium quam fossilum, secundum ordinem alphabeticum unicum deposita, adjectis homonymus platarum, nec non variis adnotationibus et emendationibus*. Jent & Gassman, Soloduri.

Alvarado F., Escobar F. & Montero-Muñoz J. 2014. Diversity and biogeographical makeup of the dung beetle communities inhabiting two mountains in the Mexican Transition Zone. *Organisms Diversity & Evolution* 14: 105–114. https://doi.org/10.1007/s13127-013-0148-0

Alvarado F., Dátillo W. & Escobar F. 2019. Linking dung beetle diversity and its ecological function in a gradient of livestock intensification management in the Neotropical region. *Applied Soil Ecology* 143: 173–180. https://doi.org/10.1016/j.apsoil.2019.06.016

Alvarado F., Salomão R.P., Hernández-Rivera A. & Lira A.F.d.A. 2020. Different responses of dung beetle diversity and feeding guilds from natural and disturbed habitats across a subtropical elevational gradient. *Acta Oecologica* 104: 103533. https://doi.org/10.1016/j.actao.2020.103533

Anduaga S. 2000. Escarabajos coprófagos (Coleoptera: Scarabaeoidea) asociados a hongos en la Sierra Madre Occidental, Durango, México: con una compilación de las especies micetófagas. *Acta Zoológica Mexicana (n.s.)* 80: 119–130.

Anduaga S. & Halffter G. 1991. Micofagia en Scarabaeidae. *In*: Navarrete-Heredia J.L. & Quiroz-Rocha G.A. (eds) *Memorias del I Simposio Nacional sobre la Interacción Insecto-Hongo*: 151–169. S.M.E. Facultad de Ciencias, IGU, Veracruz.

Arellano L., León-Cortés J.L. & Halffter G. 2008. Response of dung beetle assemblages to landscape structure in remnant natural and modified habitats in southern Mexico. *Insect Conservation & Diversity* 1: 253–262. https://doi.org/10.1111/j.1752-4598.2008.00033.x

Arellano L., León-Cortés J.L., Halffter G. & Montero J. 2013. Acacia woodlots, cattle and dung beetles (Coleoptera: Scarabaeinae) in a Mexican silvopastoral landscape. *Revista Mexicana de Biodiversidad* 84: 650–660. https://doi.org/10.7550/rmb.32911

Arnaud P. 1982. Liste des types de Phanaeini du Muséum National D'Histoire Naturelle de Paris [Coleoptera, Scarabaeidae]. *Revue française d'Entomologie (N.S.)* 4: 113–118.

Arnaud P. 2000. Description de nouvelles espèces de Phanaeides. (Col. Scarabaeidae). *Besoiro* 5: 6–8.

Arnaud P. 2001. Description de nouvelles espèces de Phanaeides. (Col. Scarabaeidae). *Besoiro* 6: 2–8.

Arnaud P. 2002a. Description de nouvelles espèces de Phanaeides. (Col. Scarabaeidae). *Besoiro* 8: 2–5.

Arnaud P. 2002b. *Phanaeini. Dendropaemon, Tetramereia, Homalotarsus, Megatharsis, Diabroctis, Coprophanaeus, Oxysternon, Phanaeus, Sulcophanaeus*. Hillside Books, Canterbury.

Arnaud P. 2018. Description d'une nouvelle espèce de *Phanaeus* d'Équateur et revalidation de l'espèce *Coprophanaeus (C.) edmondsi* Arnaud (Coleoptera : Scarabaeidae, Scarabaeinae). *Besoiro* 26: 3–7.

Avendaño-Mendoza C., Morón-Ríos A., Cano E.B. & León-Cortés J. 2005. Dung beetle community (Coleoptera: Scarabaeidae: Scarabaeinae) in a tropical landscape at the Lachua Region, Guatemala. *Biodiversity & Conservation* 14: 801–822. https://doi.org/10.1007/s10531-004-0651-x

Bai M., Li S., Lu Y., Yang H., Tong Y. & Yang X. 2015. Mandible evolution in the Scarabaeinae (Coleoptera: Scarabaeidae) and adaptations to coprophagous habits. *Frontiers in Zoology* 12: 30. https://doi.org/10.1186/s12983-015-0123-z

Balthasar V. 1939. Neue *Phanaeus* - Arten. *Folia Zoologica et Hydrobiologica* 9: 238–247.

Barragán F., Moreno C.E., Escobar F., Halffter G. & Navarrete D. 2011. Negative impacts of human land use on dung beetle functional diversity. *PLoS One* 6: e17976. https://doi.org/10.1371/journal.pone.0017976

Bates H.W. 1887. *Biologia Centrali-Americana. Insecta. Coleoptera. Vol. II. Part 2. Pectinicornia and Lamellicornia*. Taylor & Francis, London.
Available from https://www.biodiversitylibrary.org/item/135502#page/7/mode/1up [accessed Jun. 2020].

Blackwelder R.E. 1944–1957. Checklist of the coleopterous insects of Mexico, Central American, the West Indies, and South America. Parts 1–6. *United States National Museum, Bulletin* 185: 1–1492. https://doi.org/10.5479/si.03629236.185.927

Bourg A., Escobar F., MacGregor-Fors I. & Moreno C.C. 2016. Got dung? Resource selection by dung beetles in Neotropical forest fragments and cattle pastures. *Neotropical Entomology* 45: 490–498. https://doi.org/10.1007/s13744-016-0397-7

Brullé A. 1837. Histoire naturelle des insectes, comprenant leur classification, leurs mœurs et la description des espèces. *In*: Audouin M.V. & Brullé A. (eds) *Histoire naturelle des Insectes, comprenant leur Classification, leurs Moeurs, et la Description des Espèces. Tome VI, Coléoptères III*. F.D. Pillot, Paris.

Cancino-López R.J., Chamé-Vázquez E.R. & Gómez y Gómez B. 2014. Escarabajos necrófilos (Coleoptera: Scarabaeinae) en tres hábitats del Volcán Tacaná, Chiapas, México. *Dugesiana* 21: 135–142.

Capello V. & Halffter G. 2019. Listado ilustrado de las especies de Scarabaeinae (Coleoptera: Scarabaeidae) de la Reserva de la Biósfera de Calakmul, Campeche, México. *Dugesiana* 26: 103–131.

Castelnau M. 1840. *Histoire naturelle des coléoptères. Histoire naturelle des Animaux articulés, Annélides, Crustacés, Arachnides, Myriapodes et Insectes. Vol. 2*. P. Duménil, Paris.

Ceballos G., List R., Garduño G., López-Cano R., Muñozcano-Quintanar M.J., Collado E. & San-Román J.E. 2009. *La diversidad biológica del Estado de México. Estudio de estado*. Gobierno del Estado de México, Toluca de Lerdo.

Chamorro W., Marín-Armijos D., Granda V. & Vaz-de-Mello F.Z. 2018. Listado de especies y clave de géneros y subgéneros de escarabajos estercoleros (Coleoptera: Scarabaeidae: Scarabaeinae) presentes y presuntos para Ecuador. *Revista Colombiana de Entomología* 44: 72–100. https://doi.org/10.25100/socolen.v44i1.6545

Chamorro W., Marin-Armijos D. & Asenjo A. 2019. Scarabaeinae dung beetles from Ecuador: a catalog, nomenclatural acts, and distribution records. *ZooKeys* 826: 1–343. https://doi.org/10.3897/zookeys.826.26488

Chown S.L. & Klok C.J. 2011. The ecological implications of physiological diversity in dung beetles. *In*: Simmons L.W. & Ridsdill-Smith T.J. (eds) *Ecology and Evolution of Dung Beetles*: 200–219. Blackwell Publishing Ltd, West Sussex. https://doi.org/10.1002/9781444342000.ch10

Creedy T.J. & Mann D.J. 2011. *Identification Guide to the Scarabaeinae Dung Beetles of Cusuco National Park, Honduras. Version 1.0*. Operation Wallacea, Lincolnshire.

Cristóvão J.P. & Vaz-de-Mello F.Z. 2020. The terminalia of the superfamily Scarabaeoidea (Coleoptera): specific glossary, dissecting methodology, techniques and previously unrecorded sexual dimorphism in some difficult groups. *Zoological Journal of the Linnean Society*: zlaa079. https://doi.org/10.1093/zoolinnean/zlaa079

Cupello M. & Vaz-de-Mello F.Z. 2018. A monographic revision of the Neotropical dung beetle genus *Sylvicanthon* Halffter & Martínez, 1977 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltochilini), including a reappraisal of the taxonomic history of '*Canthon sensu lato*'. *European Journal of Taxonomy* 467: 1–205. https://doi.org/10.5852/ejt.2018.467

Dawson R.W. 1922. A synopsis of the Scarabaeidae of Nebraska. *University Studies of the University of Nebraska* 22: 163–244.

Dejean P.F. 1844. *Catalogue des Coléoptères de la Collection de M. Le Comte Dejean. Troisième édition, revue, corrigée et augmentée*. Chez Méquignon-Maris père et fils, Paris. https://doi.org/10.5962/bhl.title.8771

Delgado-Castillo L., Navarrete-Heredia J.L. & Blackaller-Bages J. 1993. A new Mexican species of *Onthophagus* with mycophagous habits (Coleoptera: Scarabaeidae: Scarabaeinae). *The Coleopterists Bulletin* 47: 121–126. Available from https://www.jstor.org/stable/4008857 [accessed 2 Mar. 2021].

Delgado L., Mora-Aguilar E.F. & Escobar-Hernández F. 2012a. Scarabaeoidea (Coleoptera) of the municipality of Xalapa, Veracruz, Mexico: inventory and analysis. *The Coleopterists Bulletin* 66: 319–332. https://doi.org/10.1649/072.066.0405

Delgado J.M., Castro-Ramírez A.E., Morón M.A. & Ruíz-Montoya L. 2012b. Different responses of dung beetle diversity and feeding guilds from natural and disturbed habitats across a subtropical elevational gradient. *Acta Zoológica Mexicana (n. s.)* 28: 185–210.

Deloya C. & Morón M.A. 1998. Scarabaeoidea (Insecta: Coleoptera) necrófagos de "Los Tuxtlas", Veracruz y Puerto Ángel, Oaxaca, México. *Dugesiana* 5: 17–28.

Deloya C., Burgos A., Blackaller J. & Lobo J.M. 1993. Los coleópteros lamelicornios de Cuernavaca, Morelos, México (Passalidae, Trogidae, Scarabaeidae y Melolonthidae). *Boletín de la Sociedad veracruzana de Zoología* 3: 15–55.

Deloya C., Madora-A M. & Covarrubias-M D. 2013. Scarabaeidae y Trogidae (Coleoptera) necrófilos de Acahuizotla, Guerrero, México. *Revista Colombiana de Entomología* 39: 88–94.

Deloya C., Calvo-Gática H., García-Díaz O.J., Rendón-Sosa M., González-Hilario S. & Aguirre-León G. 2014. Capítulo 10. Familia Scarabaeidae Latreille, 1802. *In*: Deloya C., Covarrubias-Melgar D. (eds) *Escarabajos del estado de Guerrero (Coleoptera: Scarabaeoidea)*: 69–116. S y G Editores, Mexico City.

Díaz A., Galante E. & Favila M.E. 2010. The effect of the landscape matrix on the distribution of dung and carrion beetles in a fragmented tropical rain forest. *Journal of Insect Science* 10: 81. https://doi.org/10.1673/031.010.8101

Edmonds W.D. 1972. Comparative skeletal morphology, systematics and evolution of the Phanaeine dung beetles (Coleoptera: Scarabaeidae). *The University of Kansas Science Bulletin* 49: 731–874.

Edmonds W.D. 1979. A new species of *Phanaeus* from Mexico (Coleoptera: Scarabaeidae). *Pan-Pacific Entomologist* 55: 99–105.

Edmonds W.D. 1994. Revision of *Phanaeus* Macleay, a New World genus of Scarabaeinae dung beetles (Coleoptera: Scarabaeidae, Scarabaeinae). *Contributions in Science, Natural History Museum of Los Angeles County* 443: 1–105.
Available from http://journals.flvc.org/mundi/article/view/81568/78697 [accessed Jul. 2020].

Edmonds W.D. 2003. Tribu Phanaeini. *In*: Morón M.A. (ed.) *Atlas de los escarabajos de México. Coleoptera: Lamellicornia. Vol. II. Familias Scarabaeidae, Trogidae, Passalidae y Lucanidae*: 58–65. Argania Editio, Barcelona.

Edmonds WD. 2004. A new species of *Phanaeus* Macleay (Coleoptera: Scarabaeidae, Scarabaeinae) from Sonora, Mexico. *The Coleopterists Bulletin* 58: 119–124. https://doi.org/10.1649/697

Edmonds W.D. 2006. A new species of *Phanaeus* Macleay (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini) from Oaxaca, Mexico. *Zootaxa* 1171 (3): 31–37. https://doi.org/10.11646/zootaxa.1171.1.3

Edmonds W.D. & Halffter G. 1978. Taxonomic review of immature dung beetles of the dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). *Systematic Entomology* 3: 307–331. https://doi.org/10.1111/j.1365-3113.1978.tb00002.x

Edmonds W.D. & Zídek J. 2012. 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). *Insecta Mundi* 274: 1–108. Available from https://digitalcommons.unl.edu/insectamundi/784/ [accessed Jul. 2020].

Estrada A. & Coates-Estrada R. 1991. Howler monkeys (*Alouatta palliata*), dung beetles (Scarabaeidae) and seed dispersal: Ecological interactions in the tropical rain forest of Los Tuxtlas, Mexico. *Journal of Tropical Ecology* 7: 459–474. https://doi.org/10.1017/S026646740000585X

Estrada A., Halffter G., Coates-Estrada R. & Meritt D.A. Jr. 1993. Dung beetles attracted to mammalian herbivore (*Alouatta palliata*) and omnivore (*Nasua narica*) dung in the tropical rain forest of Los Tuxtlas, Mexico. *Journal of Tropical Ecology* 9: 45–54. https://doi.org/10.1017/S0266467400006933

Estrada A., Coates-Estrada R., Anzures-Dadda A. & Cammarano P. 1998. Dung and carrion beetles in tropical rain forest fragments and agricultural habitats at Los Tuxtlas, Mexico. *Journal of Tropical Ecology* 14: 577–593. https://doi.org/10.1017/S0266467498000418

Figueroa L., Edmonds W.D. & Martínez N.L. 2014. La tribu Phanaeini (Coleoptera, Scarabaeidae, Scarabaeinae) en el Perú. *Revista peruana de Biología* 21: 125–138. https://doi.org/10.15381/rpb.v21i2.9815

GBIF Secretariat. 2019a. *Phanaeus endymion* Harold, 1863. GBIF Backbone Taxonomy. Checklist dataset. Available from https://doi.org/10.15468/39omei [accessed Jul. 2020].

GBIF Secretariat. 2019b. *Phanaeus pyrois* Bates, 1887. GBIF Backbone Taxonomy. Checklist dataset. Available from https://doi.org/10.15468/39omei [accessed Jul. 2020].

Gemminger M. & Harold E. 1869. Catalogous Coleopterorum hucusque descriptorum synonymicus et systematicus. *Monachii, Sumptu EH Gummi* 4: 979–1346. https://doi.org/10.5962/bhl.title.9089

Génier F. 2019. Endophallites: a proposed neologism for naming the sclerotized elements of the insect endophallus (Arthropoda: Insecta). *Annales de la Société entomologique de France (N.S.)* 55: 482–484. https://doi.org/10.1080/00379271.2019.1685907

Germar E.F. 1824. *Insectorum species novae aut minus cognotae, descriptionibus illustratae.* Hendelii et Fillii, Halae. https://doi.org/10.5962/bhl.title.130964

Gillet J.J.E. 1911. *Coleopterorum Catalogus. Pars 38: Scarabaeidae: Coprinae*. I.W. Junk, Berlin.

Gillett C.P.D.T. 2008. Collecting in Belize May/June 2006. *Scarabs* 29: 1–14.

Gillett C.P.D.T. & Toussaint E.F.A. 2020. Macroevolution and shifts in the feeding biology of the New World scarab beetle tribe Phanaeini (Coleoptera: Scarabaeidae: Scarabaeinae). *Biological Journal of the Linnean Society* 130: 661–682. https://doi.org/10.1093/biolinnean/blaa058

Gillett C.P.D.T., Gillett M.P.T., Gillett J.E.D.T & Vaz-de-Mello F.Z. 2010. Diversity and distribution of the scarab beetle tribe Phanaeini in the northern states of the Brazilian Northeast (Coleoptera: Scarabaeidae: Scarabaeinae). *Insecta Mundi* 118: 1–19.

Gistel J.N.F.X. 1857. *Achthundert und zwanzig neue oder unbeschriebene wirbellose Thiere*. Schorner, Straubing.

Halffter G. 1952. Notas sobre el género *Phanaeus*. I. *Phanaeus quadridens* Say, 1835. *Ciencia* 11: 79–86.

Halffter G. 1955. Notas sobre el género *Phanaeus*. II. *Phanaeus martinezi* nov. sp. *Ciencia* 12: 79–86.

Halffter G. 2017. La zona de transición mexicana y la megadiversidad de México: del marco histórico a la riqueza actual. *Dugesiana* 24: 77–89.

Halffter G. & Edmonds W.D. 1982. *The nesting Behavior of Dung Beetles (Scarabaeinae). An ecological and evolutive Approach*. Instituto de Ecología, Mexico City.

Halffter G. & Halffter V. 2009. Why and where coprophagous beetles (Coleoptera: Scarabaeinae) eat seeds, fruits of vegetable detritus. *Boletín de la Sociedad Entomológica Aragonesa* 45: 1–22.

Halffter G. & Matthews E.G. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). *Folia Entomológica Mexicana* 12–14: 1–312.

Halffter G. & Morrone J.J. 2017. An analytical review of Halffter's Mexican transition zone, and its relevance for evolutionary biogeography, ecology and biogeographical regionalization. *Zootaxa* 4226: 1–46. https://doi.org/10.11646/zootaxa.4226.1.1

Halffter G., Favila M.E. & Halffter V. 1992. A comparative study of the structure of the scarab guild in Mexican tropical rain forests and derived ecosystems. *Folia Entomológica mexicana* 84: 131–156.

Halffter G., Favila M.E. & Arellano L. 1995. Spatial distribution of three groups of Coleoptera along and altitudinal transect in the Mexican Transition Zone and its biogeographical implications. *Elytron* 9: 151–185.

Hamel-Leigue A., Mann D.J., Vaz-de-Mello F.Z. & Herzog S.K. 2006. Hacia un inventario de los escarabajos peloteros (Coleoptera: Scarabaeinae) de Bolivia: primera compilación de los géneros y especies registrados para el país. *Revista Boliviana de Ecología y Conservación Ambiental* 20: 1–18.

Hamel-Leigue A., Herzog S.K., Mann D.J., Larsen T.H., Gill B.D., Edmonds W.D. & Spector S. 2009. Distribución e historia natural de escarabajos coprófagos de la tribu Phanaeini (Coleoptera: Scarabaeidae: Scarabaeinae) en Bolívia. *Kempffiana* 5: 43–95.

Harold E. 1863. Note sur les espèces mexicaines du genre *Phanaeus* et descriptions de quelques espèces nouvelles de coléoptères mexicains. *Annales de la Société entomologique de France* 3: 161–176.

Harold E. 1871. Berichtigungen und Zusätze zum Catalogus Coleopterorum synonymicus et systematicus. *Coleopterologische Hefte* 7: 113–119.

Harris R.A. 1979. A glossary of surface sculpturing. *Occasional Papers in Entomology* 28: 1–31. https://doi.org/10.5281/zenodo.26215

Hinton H.E. 1935. Anotaciones acerca de las costumbres micetofágicas de las especies de *Phanaeus*. *Anales del Instituto de Biología, UNAM (Serie Zoología)* 6: 129–130.

Horgan F.G. 2001. Burial of bovine dung by coprophagous beetles (Coleoptera: Scarabaeidae) from horse and cow grazing sites in El Salvador. *European Journal of Soil Biology* 37: 103–111. https://doi.org/10.1016/S1164-5563(01)01073-1

Horgan F.G. 2008. Dung beetle assemblages in forests and pastures of El Salvador: a functional comparison. *Biodiversity & Conservation* 17: 2961–2978. https://doi.org/10.1007/s10531-008-9408-2

Howden H.F. & Gill B.D. 1993. Mesoamerican *Onthophagus* Latreille in the *dicranius* and *mirabilis* species groups (Coleoptera: Scarabaeidae). *The Canadian Entomologist* 125: 1091–1114. https://doi.org/10.4039/Ent1251091-6

Howden H.F. & Young O.P. 1981. Panamanian Scarabaeinae: Taxonomy, distribution, and habits (Coleoptera, Scarabaeidae). *Contributions of the American Entomological Institute* 18: 1–204.

Huang J.P. 2020. Is population subdivision different from speciation? From phylogeography to species delimitation. *Ecology & Evolution* 10 (14): 6890–6896. https://doi.org/10.1002/ece3.6524

Huerta C., Arellano L., Cruz M., Escobar F. & Martínez I. 2016. Los escarabajos del estiércol en los potreros ganaderos de Xico. Instituto de Ecología, A.C., Xalapa.

ICZN. 1999. *International Code of Zoological Nomenclature. Fourth Edition*. International Commission on Zoological Nomenclature, the International Trust for Zoological Nomenclature, London.

Inward D.J.G., Davies R.G., Pergande C., Denham A.J. & Vogler A.P. 2011. Local and regional ecological morphology of dung beetle assemblages across four biogeographic regions. *Journal of Biogeography* 38: 1668–1682. https://doi.org/10.1111/j.1365-2699.2011.02509.x

Islas F. 1942. Las especies mexicanas de los géneros *Canthon* Hffsg. y *Phanaeus* Mc´Leay. Col. Scarabaeidae. *Anales del Instituto de Biología de la Universidad nacional de México* 13: 301–340.

Joaqui T., Moctezuma V., Sánchez-Huerta J.L. & Escobar F. 2019. The *Onthophagus fuscus* (Coleoptera: Scarabaeidae) species complex: an update and the description of a new species. *Zootaxa* 4555 (1): 151–186. https://doi.org/10.11646/zootaxa.4555.2.1

Kohlmann B., Arriaga-Jiménez A. & Rös M. 2018. Dung beetle vicariant speciation in the mountains of Oaxaca, Mexico, with a description of a new species of *Phanaeus* (Coleoptera, Geotrupidae, Scarabaeidae). *ZooKeys* 743: 67–93. https://doi.org/10.3897/zookeys.743.23029

Komarek A. & Beutel R.G. 2006. Problems in taxonomy and suggestions for a standardized description of new insect taxa. *Entomological Problems* 36: 55–70.

Krajcik M. 2006. Checklist of Scarabaeoidea of the World. 1. Scarabaeinae (Coleoptera: Scarabaeidae: Scarabaeinae). *Animma.X. Suplement* 3: 1–189.

Krell F.T. & Cranston P.S. 2004. Which side of the tree is more basal? *Systematic Entomology* 29: 279–281. https://doi.org/10.1111/j.0307-6970.2004.00262.x

Lacordaire J.T. 1856. *Histoire naturelle des insectes. Genera des coléoptères, ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes. Tome troisième*. Librairie Encyclopédique de Roret, Paris.

Lacordaire J.T. & Chapuis M.F. 1876. *Histoire naturelle des insectes. Genera des coléoptères, ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes. Tome douzième*. Librairie Encyclopédique de Roret, Paris.

Lizardo V., Escobar F. & Rojas-Soto O. 2017. Diversity and distribution of Phanaeini (Coleoptera: Scarabaeidae: Scarabaeinae) in Mexico. *Zootaxa* 4358 (3): 271–294. https://doi.org/10.11646/zootaxa.4358.2.3

López-Guerrero Y. & Halffter G. 2000. Evolution of the spermatheca in the Scarabaeoidea (Coleoptera). *Fragmenta Entomológica, Roma* 32: 225–285.

Lucas R. 1920. *Catalogus alphabeticus generum et subgenerum Coleopterorum orbis terrarum totius (fam., trib., subtr., sect. incl.). Pars 1*. Nicolaische Verlagsbuchhandlung R Stricker, Berlin.

Macleay W.S. 1819. *Horae entomologicae: or Essays on the annulose Animals. Vol. I. Part I.* S. Bagster, London. https://doi.org/10.5962/bhl.title.48636

Manjarres-H. E.H. & Molano-R. F. 2015. Estudio de la variación de la genitalia masculina de las especies de la tribu Phanaeini (Scarabaeidae: Scarabaeinae) en Colombia. *Boletín Científico Centro de Museos, Museo de Historia Natural, Universidad de Caldas* 19: 245–257.

Marchisio E. & Zunino M. 2012. Il genere *Copris* Müller. Tassonomia, filogenesi e note di zoogeografia. *World Biodiversity Association Monographs* 2: 1–176.

Martínez A. 1959. Catálogo de los Scarabaeidae Argentinos. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"* 5: 1–126.

Martínez A & Pereira F.S. 1967. Notas escarabeidológicas III (Col. Scarabaeidae-Scarabaeinae). *Revista de la Sociedad Entomológica Argentina* 29: 53–69.

Mayr E. 1942. *Systematics and the Origin of Species from the Viewpoint of a Zoologist*. Harvard University Press, Cambridge.

McKenna D.D., Shin S., Ahrens D., Balke M., Beza-Beza C., Clarke D.J., Donath A., Escalona H.E., Friedrich F., Letsch H., Liu S., Maddison D., Mayer C., Misof B., Murin P.J., Niehuis O., Peters R.S., Podsiadlowski L., Pohl H., Scully E.D., Yan E.V., Zhou X., Slipinski A. & Beutel R.G. 2019. The evolution and genomic basis of beetle diversity. *Proceedings of the National Academy of Sciences of the United States of America* 116: 24729–24737. https://doi.org/10.1073/pnas.1909655116

Medina C.A. & Lopera A. 2000. Clave ilustrada para la identificación de géneros de escarabajos coprófagos (Coleoptera: Scarabaeinae) de Colombia. *Caldasia* 22: 299–315.

Medina C.A., Lopera A., Vítolo. A. & Gill B. 2001. Escarabajos coprófagos (Coleoptera: Scarabaeinae) de Colombia. *Biota Colombiana* 2: 131–144.

Medina C.A., Molano F. & Scholtz C.H. 2013. Morphology and terminology of dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) male genitalia. *Zootaxa* 3626 (3): 455–476. https://doi.org/10.11646/zootaxa.3626.4.3

Michelson A.A. 1911. On metallic colouring in birds and insects. *The London, Edinburgh, and Dublin Philosophical Magazine and Journal of Science* 6: 554–567. https://doi.org/10.1080/14786440408637061

Miller S.E., Gordon R.D. & Howden H.F. 1981. Revaluation of Pleistocene scarab beetles from Rancho La Brea, California (Coleoptera: Scarabaeidae). *Proceedings of the Entomological Society of Washington* 83: 625–630.

Moctezuma V. & Halffter G. 2017. A new species of *Phanaeus* Macleay (Coleoptera: Scarabaeidae: Scarabaeinae) from Los Chimalapas, Oaxaca, Mexico. *The Coleopterists Bulletin* 71: 47–56. https://doi.org/10.1649/0010-065X-71.1.47

Moctezuma V. & Halffter G. 2020. New species and redescriptions of the *Onthophagus chevrolati* species complex (Coleoptera: Scarabaeoidea: Scarabaeinae). *Annales Zoologici* 70: 245–261. https://doi.org/10.3161/00034541ANZ2020.70.2.005

Moctezuma V., Halffter G. & Escobar F. 2016. Response of copronecrophagous beetle communities to habitat disturbance in two mountains of the Mexican Transition Zone: influence of historical and ecological factors. *Journal of Insect Conservation* 20: 945–956. https://doi.org/10.1007/s10841-016-9923-5

Moctezuma V., Sánchez-Huerta J.L. & Halffter G. 2017. Two new species of the *Phanaeus endymion* species group (Coleoptera, Scarabaeidae, Scarabaeinae). *ZooKeys* 702: 113–135. https://doi.org/10.3897/zookeys.702.14728

Moctezuma V., Deloya C., Sánchez-Huerta J.L. & Halffter G. 2019. A new species of the *Phanaeus endymion* species group (Coleoptera: Scarabaeidae: Scarabaeinae), with comments on ecology and distribution. *Annales de la Société entomologique de France (N.S.)* 55: 249–254. https://doi.org/10.1080/00379271.2019.1577170

Moctezuma V., Nogueira G. & Halffter G. 2020. A revalidation and a new species in the genus *Phanaeus* (Coleoptera: Scarabaeoidea: Scarabaeidae: Scarabaeinae). *Besoiro* 30: 3–11. https://doi.org/10.5281/zenodo.3675728

Montes de Oca E. 2001. Escarabajos coprófagos de un escenario ganadero típico de la región de Los Tuxtlas, Veracruz, México: Importancia del paisaje en la composición de un gremio funcional. *Acta Zoológica Mexicana (n.s.)* 82: 111–132.

Moretto P. & Génier F. 2020. Nouveaux *Onthophagus (sensu lato)* Latreille, 1802, d'Afrique tropicale appartenant au groupe 23 de d'Orbigny (1913) (Coleoptera, Scarabaeidae, Onthophagini). *Catharsius, La Revue* 21: 4–23.

Morón M.A. 1979. Fauna de coleópteros lamelicornios de La Estación de Biología Tropical, "Los Tuxtlas", Veracruz, UNAM. México. *Anales del Instituto de Biología de la Universidad Nacional Autónoma de México, Serie Zoología* 1: 375–454.

Morón M.A. 1985. Fauna de coleópteros lamelicornios de Boca del Chajul, Chiapas, México. *Folia Entomológica Mexicana* 66: 57–118.

Morón M.A. 1987. The necrophagous Scarabaeinae beetles (Coleoptera: Scarabaeidae) from a coffee plantation in Chiapas, Mexico: habits and phenology. *The Coleopterists Bulletin* 41: 225–232. Available from https://www.jstor.org/stable/4008410 [accessed Jul. 2020].

Morón M.A., Camal J.F. & Canul O. 1986. Análisis de la entomofauna necrófila del área norte de la Reserva de la Biósfera "Sian Ka'an", Quintana Roo, México. *Folia entomológica Mexicana* 69: 83–98.

Navarrete D. & Halffter G. 2008. Dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae) diversity in continuous forest, forest fragments and cattle pastures in a landscape of Chiapas, Mexico: the effects of anthropogenic changes. *Biodiversity & Conservation* 17: 2869–2898. https://doi.org/10.1007/s10531-008-9402-8

Nevinson B.G. 1892. *Revised Synonymic List of Species in the Genera Phanaeus Macleay and Oxysternon Castelnau*. Published privately, London. https://doi.org/10.5962/bhl.title.9416

Nosil P., Feder J.L., Flaxman S.M. & Gompert Z. 2017. Tipping points in the dynamics of speciation. *Nature Ecology and Evolution* 1: 0001. https://doi.org/10.1038/s41559-016-0001

Olsoufieff G. d'. 1924. Les Phanaeides (Coleoptera-Lamellicornia). Famille Scarabaeidae – Tr. Coprini. *Insecta, Revue illustrée d'Entomologique* 13: 4–172.

Pablo-Cea J.D., Velado-Cano M.A. & Noriega J.A. 2020. A first step to evaluate the impact of ecotourism on biodiversity in El Salvador: a case study using dung beetles in a National Park. *Journal of Ecotourism* 20: 51–69. https://doi.org/10.1080/14724049.2020.1772798

Pacheco, T.L. & Vaz-de-Mello F.Z. 2015. Dung beetles of the tribe Phanaeini (Coleoptera: Scarabaeidade: Scarabaeinae) from Roraima state, Northern Brazil: checklist and key to species. *Biota Neotropica* 15: 1–9. https://doi.org/10.1590/1676-06032015014514

Palacios-Ríos M., Rico-Gray V. & Fuentes E. 1990. Inventario preliminar de los Coleoptera Lamellicornia de la zona de Yaxchilan, Chiapa, México. *Folia Entomológica Mexicana* 78: 49–60.

Pessôa S.B. 1934. Contribuição para o conhecimento das espécies brasileiras do gênero *Phanaeus*. *Annales Facultad Medical Sao Paulo* 10: 279–314. https://doi.org/10.5962/bhl.title.98039

Pessôa S.B. & Lane F.1941. Coleópteros necrófagos de interesse médico-legal: ensaio monográfico sobre a família Scarabaeidae de S. Paulo e regiões vizinhas. *Arquivos de Zoologia do Estado de São Paulo* 2: 389–504.

Philips T.K., Edmonds W.D. & Scholtz C.H. 2004. A phylogenetic analysis of the New World tribe Phanaeini: hypotheses on relationships and origins. *Insect Systematics and Evolution* 35: 43–63. https://doi.org/10.1163/187631204788964664

Pierce W.D. 1946. Descriptions of the dung beetles (Scarabaeidae) of the tar pits. *Bulletin of the Southern California Academy of Science* 45: 119–131.

Price D.L. 2005. Descriptions of the male and female genitalia of *Phanaeus* (Macleay) (Scarabaeidae: Scarabaeinae): the *vindex* species group. *The Coleopterists Bulletin* 59: 197–203. https://doi.org/10.1649/743

Price D.L. 2007. A phylogenetic analysis of the dung beetle genus *Phanaeus* (Coleoptera: Scarabaeidae) based on morphological data. *Insect Systematics & Evolution* 38: 1–18. https://doi.org/10.1163/187631207788784058

Price D.L. 2009. Phylogeny and biogeography of the dung beetle genus *Phanaeus* (Coleoptera: Scarabaeidae). *Systematic Entomology* 34: 137–150. https://doi.org/10.1111/j.1365-3113.2008.00443.x

Ratcliffe B.C. 2002. A checklist of the Scarabaeoidea of Panama. *Zootaxa* 32: 1–48. https://doi.org/10.11646/zootaxa.32.1.1

Roze J.A. 1955. Lista preliminar de la familia Scarabaeidae *sensu lato* de Venezuela. *Boletín del Museo de Ciencias naturales* 1: 39–63.

Salem H., Kirsch R., Pauchet Y., Beresategui A., Fukumori K., Moriyama M., Cripps M., Windsor D., Fukatsu T. & Gerardo N.M. 2020. Symbiont digestive range reflects host plant breadth in herbivorous beetles. *Current Biology* 30: 2875–2886. https://doi.org/10.1016/j.cub.2020.05.043

Salomão R.P., Favila M.E. & González-Tokman D. 2020. Spatial and temporal changes in the dung beetle diversity of a protected, but fragmented, landscape of the northernmost Neotropical rainforest. *Ecological Indicators* 111: 105968. https://doi.org/10.1016/j.ecolind.2019.105968

Sánchez-de-Jesús H.A., Arroyo-Rodríguez V., Andresen E. & Escobar F. 2016. Forest loss and matrix composition are the major drivers shaping dung beetle assemblages in a fragmented rainforest. *Landscape Ecology* 31: 843–854. https://doi.org/10.1007/s10980-015-0293-2

Sánchez-Hernández G., Gómez B., Delgado L., Rodríguez-López M.E. & Chamé-Vázquez E.R. 2018. Diversidad de escarabajos copronecrófagos (Coleoptera: Scarabaeidae: Scarabaeinae) en la Reserva de la Biosfera Selva El Ocote, Chiapas, México. *Caldasia* 40: 144–160. https://doi.org/10.15446/caldasia.v40n1.68602

Sánchez-Hernández G., Gómez B., Chamé-Vázquez E.R., Dávila-Sánchez R.A., Rodríguez-López M.E & Delgado L. 2020. Current status of dung beetles (Coleoptera, Scarabaeidae, Scarabaeinae) diversity and conservation in Natural Protected Areas in Chiapas (Mexico). *Neotropical Biology & Conservation* 15: 219–244. https://doi.org/10.3897/neotropical.15.e53762

Santos-Heredia C., Andresen E., Zárate D.A. & Escobar F. 2018. Dung beetles and their ecological functions in three agroforestry systems in the Lacandona rainforest of Mexico. *Biodiversity & Conservation* 27: 2379–2394. https://doi.org/10.1007/s10531-018-1542-x

Solís A. & Kohlmann B. 2012. Checklist and distribution atlas of the Scarabaeinae (Coleoptera: Scarabaeidae) of Costa Rica. *Zootaxa* 3482: 1–32.

Suárez-Moo P., Cruz-Rosales M., Ibarra-Laclette E., Desgarennes D., Huerta C. & Lamelas A. 2020. Diversity and composition of the gut microbiota in the developmental stages of the dung beetle *Copris incertus* Say (Coleoptera, Scarabaeidae). *Frontiers in Microbiology* 11: 1698. https://doi.org/10.3389/fmicb.2020.01698

Tarasov S. & Génier F. 2015. Innovative Bayesian and parsimony phylogeny of dung beetles (Coleoptera, Scarabaeidae, Scarabaeinae) enhanced by ontology-based partitioning of morphological characters. *PLoS One* 10: e0116671. https://doi.org/10.1371/journal.pone.0116671

Tarasov S.I. & Solodovnikov A.Y. 2011. Phylogenetic analyses reveal reliable morphological markers to classify mega-diversity in Onthophagini dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *Cladistics* 27: 1–39. https://doi.org/10.1111/j.1096-0031.2011.00351.x

Thiyonila B., Reneeta N.P., Kannan M., Shantkriti S. & Krishnan M. 2018. Dung beetle gut microbes: Diversity, metabolic and immunity related roles in host system. *International Journal of Scientific Innovations* 1: 77–83.

Vargas W.E., Avendano E., Hernández-Jiménez M., Azofeifa D.E., Libby E., Solís A. & Barboza-Aguilar C. 2018. Photonic crystal characterization of the cuticles of *Chrysina chrysargyrea* and *Chrysina optima* jewel scarab beetles. *Biomimetics* 3: 30. https://doi.org/10.3390/biomimetics3040030

Vaz-de-Mello F.Z., Edmonds W.D., Ocampo F.C., Schoolmeesters P. 2011. A multilingual key to the genera and subgenera of the subfamily Scarabaeinae of the New World (Coleoptera: Scarabaeidae). *Zootaxa* 2854 (1): 1–73. https://doi.org/10.11646/zootaxa.2854.1.1

Vítolo A.L. 2000. Clave para la identificación de los géneros y especies Phanaeinas de Colombia. *Revista de la Academia Colombiana de Ciencias Exactas Físicas y Naturales* 24 (93): 591–601.

Vulcano M.A. & Pereira F.S. 1967. Sinópse dos Passalidae e Scarabaeidae s. str. da região Amazônica (Insecta, Coleoptera). *Atas do Simpósio sôbre a Biota Amazônica* 5: 533–603.

Vulinec C. 1997. Iridescent dung beetles: A different angle. *Florida Entomologist* 80: 132–141. https://doi.org/10.2307/3495550

Werner M. & Simmons L.W. 2008. The evolution of male genitalia: functional integration of genital sclerites in the dung beetle *Onthophagus taurus*. *Biological Journal of the Linnean Society* 92: 257–266. https://doi.org/10.1111/j.1095-8312.2007.00924.x

Wheeler Q.D. & Platnick N.I. 2000. The phylogenetic species concept (*sensu* Wheeler and Platnick). *In*: Wheeler Q.D. & Meier R. (eds) *Species Concepts and Phylogenetic Theory*: 55–69. Columbia University Press, New York.

Yao F., Shi B., Wang X., Pan D., Bai M., Yan J., Cumberlidge N. & Sun H. 2020. Rapid divergent coevolution of *Sinopotamon* freshwater crab genitalia facilitates a burst of species diversification. *Integrative Zoology* 15: 174–186. https://doi.org/10.1111/1749-4877.12424

Zachos F.E. 2016. *Species Concepts in Biology. Historical Development, theoretical Foundations and practical Relevance*. Springer International Publishing, Switzerland. https://doi.org/10.1007/978-3-319-44966-1

Zaragoza-Caballero S., Rodríguez-Mirón G.M., Vega-Badillo V., González-Ramírez M., Zurita-García M.L., Domínguez-León D.E., López-Pérez S., Gutiérrez-Carranza I.G., Cifuentes-Ruíz P., Pérez-Hernández C.X., Ramírez-del-Valle E. & Gutiérrez N. 2019. A checklist of the Coleoptera (Insecta) from Morelos, Mexico. *Zootaxa* 4580: 1–122. https://doi.org/10.11646/zootaxa.4580.1.1

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