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**A revalidation and a new species in the genus *Phanaeus*
(Coleoptera: Scarabaeoidea: Scarabaeidae: Scarabaeinae)**

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A revalidation and a new species in the genus *Phanaeus* (Coleoptera: Scarabaeoidea: Scarabaeidae: Scarabaeinae)

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Abstract

The morphology of the dung beetle populations previously known as *Phanaeus quadridens* (Say, 1835) is studied. As a consequence, *Phanaeus arnaudi* Nogueira, Moctezuma and Halffter, **sp. nov.** is described from Mexico, and *Phanaeus borealis* Olsoufieff, 1924, **stat. rev.** is resurrected from previous synonymy to full species status, due the lack of evidence to support the idea that body color varies intrapopulationary and conform to a continuous north-south cline. An identification key to the *P. quadridens* species group is updated.

Keywords. Dung beetles, Phanaeini, rainbow beetles, Sonora

Introduction

Phanaeus quadridens (Say, 1835) was originally described by Say (1835) as part of the genus *Copris* Geoffroy, 1762 based upon dark blue-violet specimens from Mexico without precise locality. Some years later, Dejean (1837) introduced in his catalog the names *P. evippus* Dejean, 1837 and *P. custos* Klug, in litt. for the same taxon from Mexico. Posteriorly, the same dark blue-violet species was described independently as *P. violaceus* Castelnau, 1840 and as *P. laevipennis* Sturm, 1843. Chevrolat (1844) denoted that *P. laevipennis*, *P. evippus* and *P. custos* were different names that corresponded to the same taxon. Erichson (1847) recognized that *P. quadridens* preceded *P. laevipennis*, *P. evippus* and *P. custos*, and established the later as junior synonyms. Erichson (1847) also commented that *P. evippus* of Dejean's Catalogue appeared in many collections under the name of *P. custos*.

Harold (1859) highlighted that *P. quadridens*, *P. violaceus* and *P. laevipennis* were different names that pertained to the same taxon, but he erroneously established the precedence for *P. violaceus*: “*Phanaeus laevipennis* Sturm Cat. 1843 p. 334. t. 2 f. 3—4. (*P. Evippus* Dej.) ist bereits von Say im Bost. Journ. I 1841 p. 174. als *P. quadridens*, noch früher aber, in Jahre 1840, von Laporte in Hist. Nat. II. p. 81. als *P. violaceus* beshrieben worden. Letz Namen gebührt somit der Vorrang”. Posteriorly, Harold (1863) acknowledged that the description of *P. quadridens* was the earlier, and confirmed *P. violaceus* and *P. laevipennis* as junior synonyms: “C'est par erreur que j'ai substitué à cette espèce dans le *Berlin. Ent. Zeit.*, III, p. 198. le nom de *Ph. violaceus*, la description de Say étant bien antérieure à celle de M. Castelnau”.

In the revision of “Les Phanaeides”, Olsoufieff (1924) introduced the name *borealis* for what he considered a green variety of *P. quadridens* from the south-western USA and north-western Mexico: “il se peut que tous les *4-dens* de la provenance de la Sonora du Nord, Californie Sud, Arizona et N.-Mexique soient verts aussi, en constituant une race locale (*var. borealis* n.), ce que serait intéressant établir”. Edmonds (1994) revised the genus *Phanaeus*, commented that the primary type of *P. quadridens* was destroyed, and designated a dark blue-violet specimen from Mexico City as the neotype of *P. quadridens*. Additionally, Edmonds (1994) highlighted that the name *borealis* was often cited as a subspecies of *P. quadridens*, but he decided to synonymize *P. quadridens borealis* with *P. quadridens* arguing that color varies intrapopulationary in the species and form a continuous north-south cline in terms of relative abundance: “I have chosen not to recognize *borealis* as a subspecies. While rare individuals in southern populations have a distinctly blue-green color, greenish individuals do not appear regularly until central Chihuahua. Here, more than 50% of the specimens studied are blue-green or green. Farther north in Arizona, more than 85% of observed individuals are greenish and lack any trace of bluish highlights. Insofar as coloration is concerned, central Chihuahua is a transition zone between blue populations to the south and largely green populations to the north”.

Arnaud (2002), nevertheless, resurrected Olsoufieff's (1924) color criteria, recognized *P. quadridens borealis* as a subspecies of *P. quadridens* and designated the lectotype for the former from Chihuahua. Finally, Edmonds and Zidek (2012) decided to maintain *P. quadridens borealis* as a junior synonym of *P. quadridens* since they considered that Arnaud (2002) did not presented new data to support the subspecific status of *P. quadridens borealis* contrary to Edmonds' (1994) objections. As a consequence of the problematic background that has characterized its taxonomy, the morphology of the populations previously known as *P. quadridens* is studied herein. A new species is described and one more is revalidated to full species status and an updated identification key for the *P. quadridens* species group is presented.

Material and methods

For this study the phylogenetic species concept in its diagnosability version is used, which defines a species as the smallest aggregation of (sexual) populations or (asexual) lineages that is diagnosable by a unique combination of character states (Wheeler and Platnick, 2000; Zachos, 2016). We followed the nomenclature proposed by Edmonds (1994) for external morphology and Moctezuma et al. (2017) and Génier (2019) for genital morphology. Intraspecific categories and names are avoided. As a consequence, specimens that show variability in morphological characters are treated as intraspecific variation.

To adequately define the identity of *P. quadridens* we revised the neotype (The President and Fellows of Harvard College, 2010) and the original descriptions of the species and its junior synonymies (Say, 1835; Dejean, 1837; Castelnau, 1840; Sturm, 1843). As an additional reference, the Halffter's redescription (1952) of *P. quadridens* was consulted. This redescription accurately characterizes the morphology of the species because it is based on the study of the largest series of topotypical material that has been reported before (236 specimens of both sexes).

Type specimens bear labels printed on white paper with collection data; followed by determination labels printed on red acid-free paper, indicating specimen sex and which one is the holotype and which the paratypes. Label data are given verbatim. Genital structures were prepared by soaking in a 10% KOH solution for 24 hours at room temperature, rinsing in 96° ethanol and then with water, and finally stored in microvials (BioQuip Products, Inc., Rancho Dominguez, California, USA) with glycerol pinned underneath the dissected specimens. Measurements and pictures were taken with a Leica Z16APOA stereomicroscope (Wetzlar, Germany) using the manufacturer's software (z-stack image capture method).

Abbreviations correspond to the following collections: Colección Guillermo Nogueira G., Mexico (CGNG); The Canadian Museum of Nature, Ottawa, Ontario, Canada (CMNC); Patrick and Florent Arnaud Collection, Saintry sur Seine, France (CPFA), Richard A. Cunningham Collection, California, USA (CRC); Colección Gonzalo Halffter, Instituto de Ecología A.C., Xalapa, Veracruz, Mexico (GHC); Colección Entomológica Dr. Miguel Ángel Morón Ríos, Instituto de Ecología A.C., Xalapa, Veracruz, Mexico (IEXA); Harvard Museum of Comparative Zoology, Cambridge, USA (MCZ); Muséum National d'Histoire Naturelle, Paris, France (MNHN); The Texas A&M University Insect Collection, College Station, Texas, United States of America (TAMU); Colección Entomológica de la Universidad del Valle, Guatemala, Guatemala (UVGC) Colección Victor Moctezuma, Puebla, Puebla, Mexico (VMC).

Results

Phanaeus arnaudi Nogueira, Moctezuma and Halffter, sp. nov.

Fig. 1 – 2

<http://zoobank.org/urn:lsid:zoobank.org:act:2953FFEC-40E1-4B26-BEAD-9AEEEC87F32F>

Type material. Holotype: male. *MEXICO. Sonora.* “4 km W Yécora. 1670 m. 2-IX-97 coprotrampa. G. Nogueira col.” (IEXA). **Paratypes:** *MEXICO. Sonora.* 11 males, 19 females: same data as holotype (CMNC: 1 male, 1 female; GHC: 1 male, 1 female; IEXA: 6 males, 14 females; TAMU: 1 male, 1 female; UVGC: 1 male, 1 female; VMC: 1 male, 1 female); 7 males, 1 female: same data as holotype except: “28-VII-98” (IEXA); 20 males, 21 females: “Yécora. 01–02-IX-1997. 1620 m.” (CGNG: 17 males, 18 females; CRC: 1 male, 1 female; CPFA: 2 males, 2 females); *Sonora*, Highway 16 Yecora, 28°21'54"N, 10°55'28"W, 4902' elevation, 5-VIII-2003 R.A. Cunningham & B.D. Streit (CPFA: 6 males, 6 females). *Sonora*, Highway 16 Yecora, 5-VIII-2004 R.A. Cunningham & B.D. Streit (CPFA: 36 males, 40 females).

Diagnosis. *Phanaeus arnaudi* is the only known species of *Phanaeus* where all the known specimens bear a conspicuous fringe of large setae along the elytral suture (Fig. 2) and the color varies from blue-green to green (Figs. 1-2). The elytral fringe of setae is a constant trait even in very old or damaged by abrasion specimens. Major males of *P. arnaudi* are easily distinguished by the medial portion of pronotal disk with a ridge of small tubercles (Fig. 2); and two posterolateral conical tubercles, located anteriorly to the posterior margin of pronotal disk (Figs. 1-2). The new species is distinctly less robust (approaching 20 mm of length) than *P. borealis* and *P. quadridens* (23 and 25 mm, respectively).

Description of the major male (holotype). Body length 18.8 mm from the apex of clypeus to pygidium (Fig. 1).

Head. Clypeus bidentate, black on anterior margin, bright metallic green posteriorly, with roughened sculpture. Genae bright metallic green, with roughened sculpture. Frons bright metallic green on portions adjacent to cephalic horn. Cephalic horn black, curved posteriorly over pronotum.

Pronotum. Uniformly bright metallic green (figure 2). Disk triangular, distinctly convex; bearing a transverse carina; and posteromedial bump. Triangle with densely granulorugose sculpture, impunctate; the sculpture coarsely punctatorugose posteromedially. Sides with densely granulorugose sculpture, distinctly punctate. Lateral lines of pronotal triangle distinctly rounded. Posterolateral angles widened, short, slightly

projected posteriorly. Lateral fossae distinctly impressed. Two posterolateral tubercles raised, obtusely conical, located anteriorly to the posterior margin of pronotal disk. Basal fossae obtusely oval, distinctly impressed.

Elytra. Striae fine, almost effaced, minutely punctate, impressed basally as distinct fossae. Interstriae uniformly bright metallic green, shagreened, with smooth surface; minutely, sparsely punctate (figure 2). Sutural margin without apical tooth. Elytral suture bearing a distinctive crest of large, black setae.

Protibiae. Tridentate with apical spur.

Genitalia. Parameres tapering towards the apex in lateral view, getting apically lobed in frontal view (Fig. 2). Right lobe of endophallite copulatrix obtusely lobed; left lobe completely obsolete; central column and central ridge forming an aciculate, curved protrusion (Fig. 2).

Minor male. Similar to major male except reduced secondary sexual characters (*i.e.* cephalic horn, pronotal triangle and pronotal posterolateral angles).

Female. Similar to male, except cephalic carina trituberculate, narrow, set in front of eyes, often strongly raised; pronotum convex, distinctly concave in front of basal fossae; anteromedial process weakly produced, with straight or double-curved transverse carina (Fig. 2).

Variation. Mean length 18.1 mm (14.6–20.4 mm). Dorsal coloration typically varies to bright metallic green with blue cast (as in the holotype, Fig. 1) and dark metallic blue-green (Fig. 2). Despite the variation in coloration, all the specimens of the type series always bear the distinctive crest of large setae in the elytral suture.

Etymology. The new species is dedicated to Patrick Arnaud for his great contribution to the knowledge of the New World tribe Phanaeini.

Type locality. Mexico, Sonora, Yécora.

Distribution. East-central Sonora. The new species is only known from the type locality. Between 1500 to 1600 m (Fig. 3).

***Phanaeus borealis* Olsoufieff 1924, stat. rev. (Olsoufieff, 1924: 100)**

Lectotype. Male (MNHM). Designate by Arnaud (2002: 126). Not examined.

Revised material. *USA. Arizona.* 1 male: “Wilcox. July 1931. Wilbour Doudna” (GHC); 1 male: “Huachuca Mts. Carr Cn Ariz. VIII-7-1924. EP VanDuzee Collector” (VMC); 1 female: “Huachuca Mts. 7-36. E S Ross” (VMC); 1 male: “S. W. Res. Sta. 5mi. W. Portal. IX 1-7 1960. H. Howden” (GHC); 4 males, 4 females: “Santa Cruz, Peña Blanca” (CGNG); 1 male, 1 female: “Miller Canyon” (CGNG); 1 male: “Cochise County, 1 mi. W. of Chiricahua National Monument. 1965-7-45. Found in cow excrement” (ASUHC, 2017); 1 male: “N of Sonoita. July 18, 2009” (Brummermann, 2009a), 1 male: “Nogales, Santa Cruz County, September 18, 2019” (Vitanza, 2019), 1 male: “Huachuca Mts. Cochise County. 7-22-2009. Manni Rubio col. P7262864” (Brummermann, 2009b); 1 male same data except “BG 307436. UAIC 1000093” (Brummermann, 2011).

Diagnosis. *Phanaeus borealis* is easily distinguished from closely related species by its emerald green or green-yellow color. Major males of *P. borealis* are recognized by the posteromedial portion of pronotal disk relatively flat, but densely granulorugose; and two posterolateral conical tubercles, located anteriorly to the posterior margin of pronotal disk. Major specimens of *P. borealis* (approaching 23 mm of length) usually are less robust than those of *P. quadridens* (25 mm). The elytral suture generally is glabrous or almost completely glabrous.

Variation. The body length varies from approximately 13 to 23 mm from the apex of the clypeus to the pygidium. The elytral suture of this species seems to be polymorphic, with one observed specimen (5% of the sample) bearing a fringe of setae. Nevertheless, this specimen is consistent with the green-yellow color pattern, posteromedial portion of the pronotal disk flat but granulorugose, and posterolateral tubercles located anteriorly to the posterior margin of pronotum.

Type locality. Mexico, Chihuahua.

Distribution. *MEXICO.* Chihuahua, northern Sonora. *USA.* Southern Arizona and New Mexico (Olsoufieff, 1924; Robinson, 1947; Edmonds, 1994, 2003; Arnaud, 2002). Between 1100 to 2100 m (Fig. 3).

***Phanaeus quadridens* (Say 1835) (Say, 1835: 176)**

Phanaeus evippus Dejean 1837 (Dejean, 1837: 155; synonymized by Chevrolat, 1844: 198)

Phanaeus custos Klug *in litt.* (Dejean, 1837: 155; synonymized by Chevrolat, 1844: 198)

Phanaeus violaceus Castelnau 1840 (Castelnau, 1840: 81; synonymized by Harold, 1863: 166)

Phanaeus laevipennis Sturm 1843 (Sturm, 1843: 334; synonymized by Erichson, 1847: 143)

Neotype. Male (MCZ). Designate by Edmonds (1994: 82).

Revised material. *MEXICO. Chihuahua.* 2 males, 4 females: “Tomochic, 1950 m. 27-VIII-1998” (CGNG). *Durango.* 3 males, 6 females: “Súchil, Piedra Herrada. Res. Biósfera “La Michilía”. Alt. 2400 m. 24-VI-79. Bosque *Quercus-Pinus* en pastizal. Bajo excr. Bovino. M.A. Morón, col.” (IEXA). 2 males, 3 females: “Puerto

Yesquero. 13-VII-94. 2010 m. G. Nogueira col.” (IEXA); 3 males: “La Fragueta, 2250 m. 21-VIII-1993” (CGNG); 3 males, 2 females: “Santiago Papasquiario, 2120 m. 19-VIII-1998” (CGNG); 4 males, 6 females: “Puerto Yesquero, 2030 m. 04-VIII-1997” (CGNG). *Guanajuato*. 1 male: “Sierra Santa Rosa. 2300 m. 3-VII-97. Copro. G. Nogueira” (IEXA). *Hidalgo*. 1 male: “Huasca. 16-IX-62. G. y V. Halffter, leg.” (GHC); 2 females: “10 km. S. Zacualtipán. 10-VIII-75. Pastizal. Galería bajo exc. Bov. A. Morón, col.” (IEXA). *Mexico State*. 1 female: “Almoloya del Río. M.A. Morón, col. 10-VI-73. En galería bajo estiércol equino.” (IEXA); 1 female: “Almoloya del Río. 5-X-73. R.T. col. at. leg. En nido a 20 cms. prof.” (IEXA); 1 male: “Almoloya del Río. 5-VIII-72- M.A. Morón, col.” (IEXA); 1 female: “Villa Victoria. M.A. Morón, col. 10-VI-72. En galería bajo estiércol equino.” (IEXA); 2 females: “Villa Victoria. M.A. Morón, col. 10-VI-73. En galería bajo estiércol bovino.” (IEXA); 1 male: “Villa de Allende, Sn. Cayetano. 31.VI. M.A. Morón, col. En galería bajo estiércol bovino. Pastizal. Alt. 2500 mts.” (IEXA). *Puebla*. 30 males, 20 females: “Tepeyahualco, El Salado. 2929/VIII/2013, C.D. exc.vaca x- 97° 22’ 40.1” W y- 19° 28’ 10.4” N. pastizal inducido, 2330 m. Moctezuma J. V. P. Col.” (VMC). *Sinaloa*. 9 males, 23 females: “Loberas. 1900 m. 9-VII-94. G. Nogueira col.” (IEXA); 6 males, 4 females: “El Palmito. 2030 m. (Pto. Yesquero Dgo.). 4-VIII-97. Nogueira.” (IEXA); 4 males, 6 females: “El Palmito, 1900 m. 03-VIII-1997” (CGNG). *USA. Arizona*. 3 males, 2 females: “Texas Canyon” (CGNG).

Diagnosis. *Phanaeus quadridens* is the only known dark blue-violet species in the *P. quadridens* species group. Major males of *P. quadridens* are easily recognized by the posteromedial portion of pronotal disk with a conspicuous bump; and two conspicuous posterolateral tubercles, placed over the posterior margin of disk. Major specimens of *P. quadridens* (approaching 25 mm of length) are the most robust of the *P. quadridens* species group. The elytral suture generally is glabrous or almost completely glabrous, but scarce specimens bear an inconspicuous fringe of setae, as showed off by the neotype.

Variation. The body length varies from approximately 13 to 25 mm from the apex of the clypeus to the pygidium. The elytral suture of this species seems to be polymorphic, with 4 studied specimens bearing an inconspicuous fringe of setae, including the neotype (approximately 1% of the sample.). The pronotum and elytra are consistently blue-violet in all the studied specimens, except for some darker specimens.

Type locality. Mexico, Mexico City.

Distribution. *MEXICO.* Aguascalientes, Chihuahua, Durango, Guanajuato, Hidalgo, Jalisco, Mexico City, Mexico State, Michoacán, Morelos, Nayarit, Puebla, Querétaro, Sinaloa, Tlaxcala, Veracruz and Zacatecas. *USA.* Southern Arizona (Halffter, 1952; Edmonds, 1994, 2003; Arriaga et al., 2012, 2018; Barragán et al., 2014; Lizardo and Castellanos-Vargas, 2016; Halffter and Morrone, 2017; Lizardo et al., 2017; Hernández and Navarrete-Heredia, 2018). Edmonds (1994, 2003) cited *P. quadridens* from Sonora, but the only enlisted locality was Yécora. Lizardo et al. (2017) included erroneous records from Chiapas. Between 1200 to 3000 m (Fig. 3).

Key to species of the *Phanaeus quadridens* species group (modified from Edmonds and Zidek, 2012)

1. Interstriae convex; striae fine, clearly impressed. Raised outer margin of pygidium usually effaced apically. Dorsum bright coppery red, dark blue or bright green. Trans-Mexican Volcanic Belt from northern Puebla to Jalisco and northward into southern Durango *Phanaeus palliatus* Sturm, 1843
- Interstriae flat; striae superficial, fine, appearing almost effaced to unaided eye. Raised outer margin of pygidium effaced apically or not. Dorsal color variable, not coppery red. Distribution variable 2
- 2(1). Pronotum of male bearing a single posteromedian tubercle. Disk of female pronotum extremely coarsely rugopunctate posteromedially. Raised outer margin of pygidium often effaced or nearly so apically. Higher elevations (1800-2900 m) of Sierra Madre del Sur in Guerrero and Oaxaca *Phanaeus damocles* Harold, 1863
- Pronotum of male bearing two posterior and two anterior acute tubercles. Disk of female pronotum less coarsely rugopunctate posteromedially. Raised outer margin of pygidium always complete 3
- 3(2) Pronotum of male bearing two posterior acute tubercles located over the posterior margin of pronotum. Posteromedial portion of disk of male with a conspicuous bump. Robust, dark blue-violet species approaching 25 mm of length. Trans-Mexican Volcanic Belt from Veracruz to Jalisco, Sierra Madre Occidental from Durango to southwestern United States, Sierra Madre Oriental from Hidalgo to San Luis Potosí and Mexican Plateau *Phanaeus quadridens* (Say, 1835)
- Pronotum of male bearing two posterior acute tubercles located anteriorly to the posterior margin of pronotum. Posteromedial portion of disk without conspicuous bump 4
- 4(3) Medial portion of pronotal disk of male flat but granulorugose. Elytral suture generally glabrous or almost completely glabrous, with rare specimens bearing a fringe of setae. Robust, emerald green or green-yellow species approaching 23 mm of length. Mexican Plateau and northwestern Sierra Madre Occidental from Arizona and New Mexico to northern Sonora and Chihuahua *Phanaeus borealis* Olsoufieff. 1924, **stat. rev.**
- Medial portion of pronotal disk of male with a discrete ridge of tubercles. Elytral suture always bearing a conspicuous fringe of large setae. Feeble, green or blue-green species approaching 20 mm of length. Yécora Valley, central Sonora *Phanaeus arnaudi* Nogueira, Moctezuma and Halffter, **sp. nov.**

Discussion

The populations previously considered as *P. quadridens* were studied, based upon specimens of its whole distributional range. As a result, the new species *P. arnaudi* is described and *P. borealis* is resurrected from previous synonymy to full species status. Contrary to the opinion of earlier authors (Olsoufieff, 1924; Edmonds, 1994; Arnaud, 2002; Edmonds and Zidek, 2012) who considered that variation in color associated with geography was not accompanied by differences in the morphological structures, we found that the morphology of the pronotal disk of major males, body size and elytral sutures differ in concordance with color and geography.

The most evident characters that vary in the three taxa recognized by us are the modifications in the structures of the medial portion of pronotal disk, and the position of the posterolateral tubercles of pronotum. These differences have been overlooked since the description of *P. borealis* by Olsoufieff (1924) who proposed this taxon as a local race (variety) of *P. quadridens*. The fringe of setae of the elytral suture shows a certain degree of intraspecific variation in *P. quadridens* and *P. borealis*, while it remains monomorphic in the case of *P. arnaudi*. As a matter of fact, a majority of specimens of *P. borealis* and *P. quadridens* were glabrous or almost completely glabrous along the elytral suture. The presence or absence of the fringe of setae in the elytral suture might not be considered an artifact promoted by abrasion or the oldness of the specimens. Even in general specimens the morphology of the elytral suture is consistent with our observations.

Edmonds (1994) commented that a large blue-violet specimen with an inconspicuous fringe of setae along the elytral suture was chosen by him as the neotype of *P. quadridens*. Nevertheless, this character is very infrequent over the whole distribution of *P. quadridens*. On the other hand, the neotype measures approximately 21 mm of length from the apex of clypeus to the pygidium, not being considered among the major males of *P. quadridens* that typically vary between 22 to 24 mm (Islas, 1942) and may approach 25 mm (Halffter, 1952). As a consequence, the neotype of *P. quadridens* does not represent adequately the character combination that define the species, except by the body color. For the genus *Phanaeus*, is advised to designate major males as primary types (Edmonds, 1994, 2004; Arnaud, 2002; Moctezuma and Halffter, 2017; Moctezuma, et al., 2017).

In regard of the color polymorphism of *P. quadridens* proposed by Edmonds (1994) as a geographical cline, we do not confirm Edmond's observations. Contrary to Edmonds' argument, all the revised specimens of *P. quadridens* were dark blue-violet. The chromatic homogeneity of *P. quadridens* was also recognized by earlier authors that described the typical dark blue-violet color in this species (Say, 1835; Castelnau, 1840; Sturm, 1843; Dugès, 1869-1891; Olsoufieff, 1924; Islas, 1942; Halffter, 1952; Arnaud, 2002).

Edmonds (1994) suggested that the area of central Chihuahua was a transition zone between blue and green populations of *P. quadridens*, where more than 50% of the specimens were blue-green or green. The frequency of color phases described for central Chihuahua is consistent with the intraspecific variation observed in *P. arnaudi*, where individuals typically vary from green to blue-green in similar frequency. As a matter of fact, specimens from Yécora were studied by Edmonds (1994), but the morphological variation was not discussed by him. Edmonds (1994) probably confused *P. arnaudi* with the populations of *P. borealis* and *P. quadridens* from central Chihuahua.

An outstanding area of sympatry between *P. borealis* and *P. quadridens* is found in southern Arizona and northern Chihuahua, probably extending to the northern Sonora and southern New Mexico, as denoted by previous authors (Edmonds, 1994, 2003; Arnaud, 2002). Despite that blue-violet specimens of *P. quadridens* and emerald green/green-yellow individuals of *P. borealis* might share the same geographical space, the observed differences in morphology are consistent with major males of *P. quadridens* always bearing the posterolateral tubercles of the pronotal disk over the posterior margin, while these tubercles are always located anteriorly to the posterior margin of *P. borealis*. Furthermore, major males of *P. quadridens* always bear a conspicuous bump in the posteromedial portion of pronotal disk, while bumps are absent in *P. borealis*.

Due that *P. quadridens* and *P. borealis* show a consistent pattern in pronotal morphology associated to color differences, it is likely to consider that specimens of both species are not able to recognize to each other as mating partners, regardless of sharing a portion of their geographical areas. Sympatry might not be considered a strong argument to propose taxonomical decisions pertaining the genus *Phanaeus*, as the case of the junior synonymy of *P. borealis*, due that sympatry is frequently observed within the distribution of several closely related species (Edmonds, 1994; Edmonds and Zidek, 2012; Lizardo et al., 2017). On the other hand, geographical differences associated with color variation is an underestimated trait in the taxonomy of *Phanaeus*, while these differences have proven to be accompanied by dissimilarities in the DNA markers of dung beetles, as the cases of the *P. endymion* species group (Solís and Kohlmann, 2012) and the *Canthon cyanellus* species complex (Nolasco-Soto et al., 2017).

The aedeagus and the endophallite copulatrix of *P. arnaudi*, *P. borealis* and *P. quadridens* were examined. Nevertheless, these structures seem to be uniform in morphology. This result is consistent with the point of view of previous authors that suggest that the genital structures of several species of *Phanaeus* are relatively homogeneous (Edmonds, 1994; Arnaud, 2002). As a matter of fact, the endophallite copulatrix of the three species studied herein is similar to that of *P. amethystinus* Harold, 1863; *P. guatemalensis* Harold, 1871; *P. tridens* Castelnau, 1849; *P. eximius* Bates, 1887; *P. daphnis* Harold, 1863; *P. nimrod* Harold, 1863; and *P.*

furiosus Bates, 1887 (present study).

Not only differences in morphology support the taxonomical status of *P. arnaudi* as a new species, but also dissimilarities in the ecological preferences and geographical distribution. *Phanaeus quadridens* and *P. borealis* are typical elements of the coprophage fauna from the Mexican Plateau (Halffter, 1952, 1964; Edmonds, 1994, 2003; Arriaga, et al., 2012; Barragán et al., 2014; Lizardo and Castellanos-Vargas, 2016; Halffter and Morrone, 2017; Lizardo et al., 2017; Arriaga-Jiménez et al., 2018; Hernández and Navarrete-Heredia, 2018). On the other hand, *P. arnaudi* seems to be restricted to the Yécora Valley in the western portion of the Sierra Madre Occidental. The Yécora Valley is an isolate area bordered by mountain chains to the east and west rising more than 1700 to 2000 m (Edmonds, 2004). Furthermore, *P. arnaudi* is collected in forested areas where oak-pine woodlands occur while *P. borealis* and *P. quadridens* are usually found in open areas as grasslands and xeric shrublands (Edmonds, 1994, 2003, 2004; Arriaga et al., 2012; Barragán et al., 2014; Lizardo and Castellanos-Vargas, 2016; Arriaga-Jiménez et al., 2018; Hernández and Navarrete-Heredia, 2018). Halffter (1952) recognized that *P. borealis* occurs in lower elevations and dryer conditions than *P. quadridens*, observation that is confirmed by us.

In the light of the new findings reported herein, we have been able to disentangle a complex issue that involved three closely related taxonomical units, namely *P. arnaudi*, *P. borealis* and *P. quadridens*. Nevertheless, the precise distributional area of these species has been obscured due that they have been lumped together for decades. We hope the diagnosis and the updated identification key provided by us will be of help to solve this concern, and to ease future research pertaining these amazing rainbow beetles. Due the interesting features that characterize *P. quadridens* and allied species, they are potential candidates for studies in biogeography (Halffter, 1952, 1964; Halffter and Morrone, 2017; Lizardo et al., 2017), ecology (Arriaga et al., 2012; Barragán et al., 2014), evolution (Halffter, 1952; Halffter and Morrone, 2017) and morphology (Halffter, 1952; Edmonds, 1994; Márquez, 2014).

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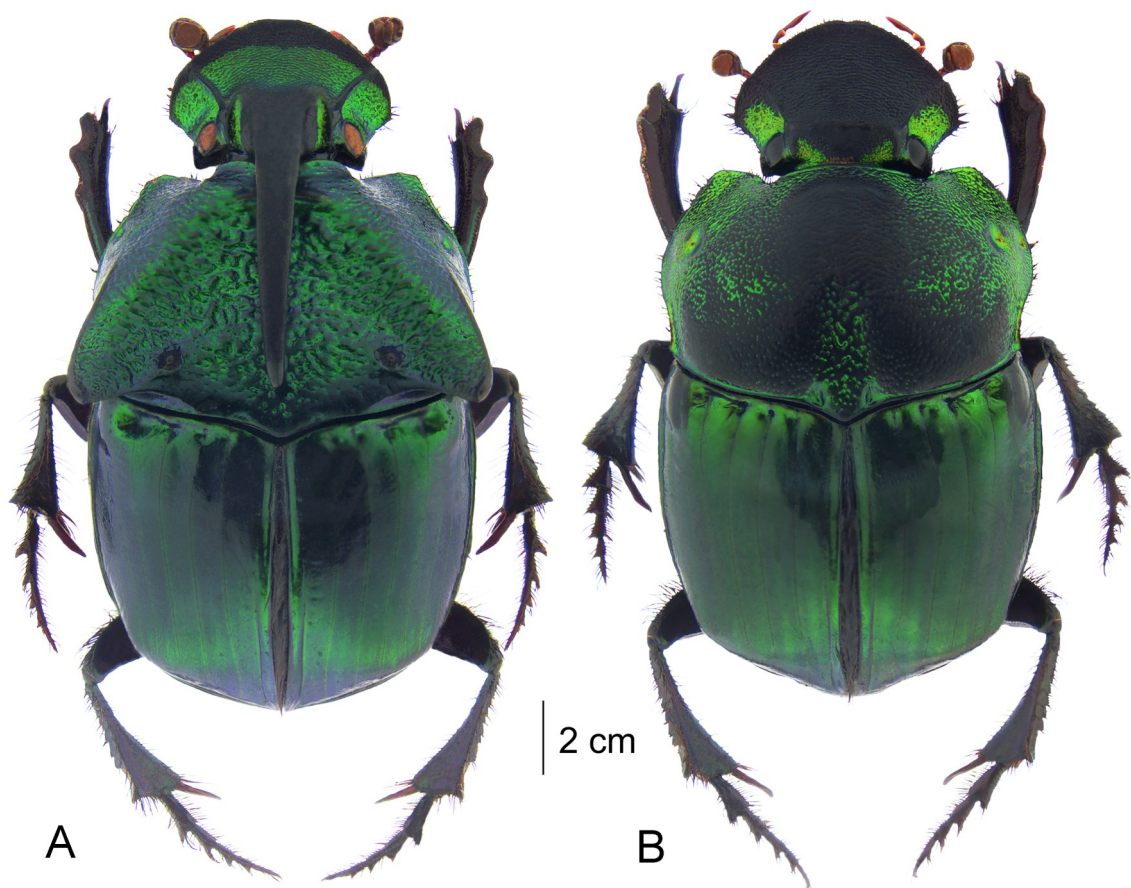


Fig. 1. *Phanaeus arnaudi*: **A)** holotype major male; **B)** and major female of the typical color form (green with blue cast).

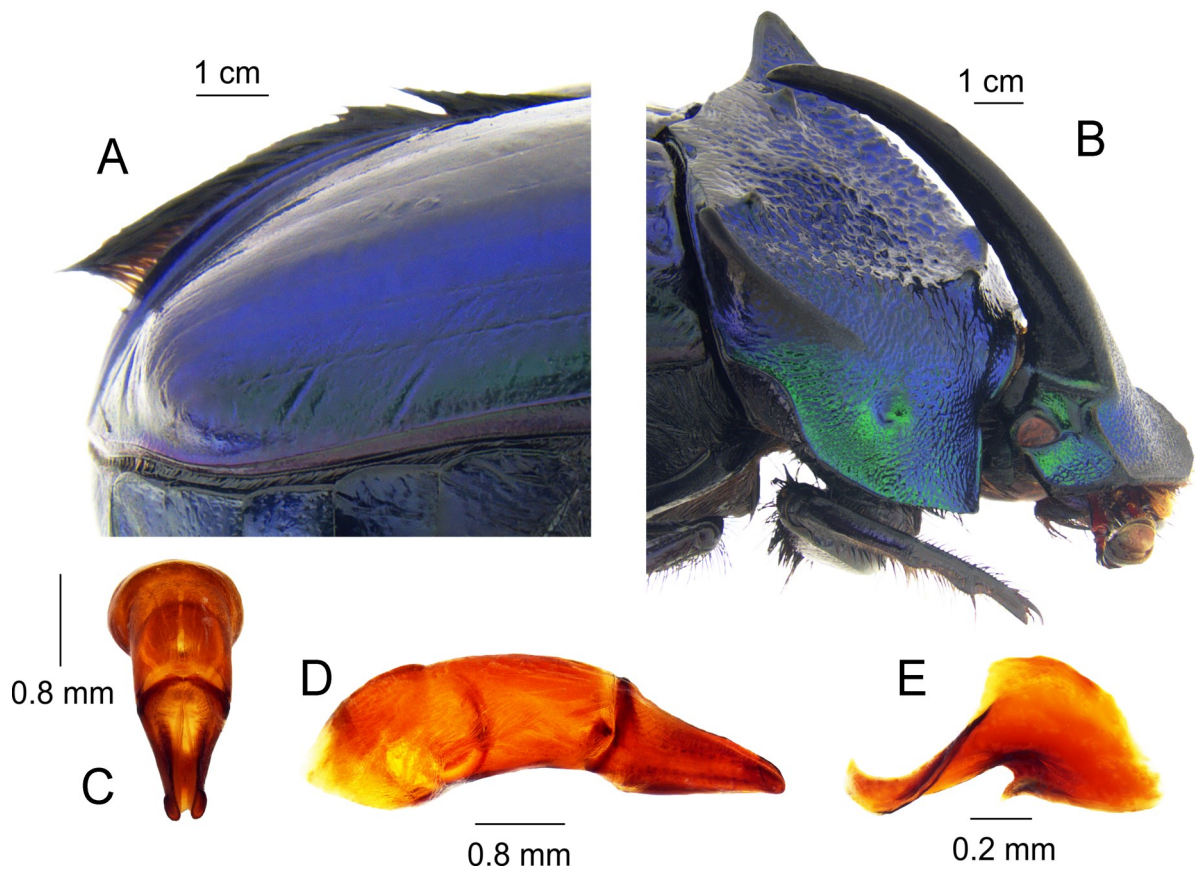


Fig. 2. *Phanaeus arnaudi*: **A)** fringe of setae in the suture of elytra; **B)** head and pronotum of male, blue-green form; **C)** frontal view of aedeagus; **D)** lateral view of aedeagus; **E)** endophallite copulatrix.

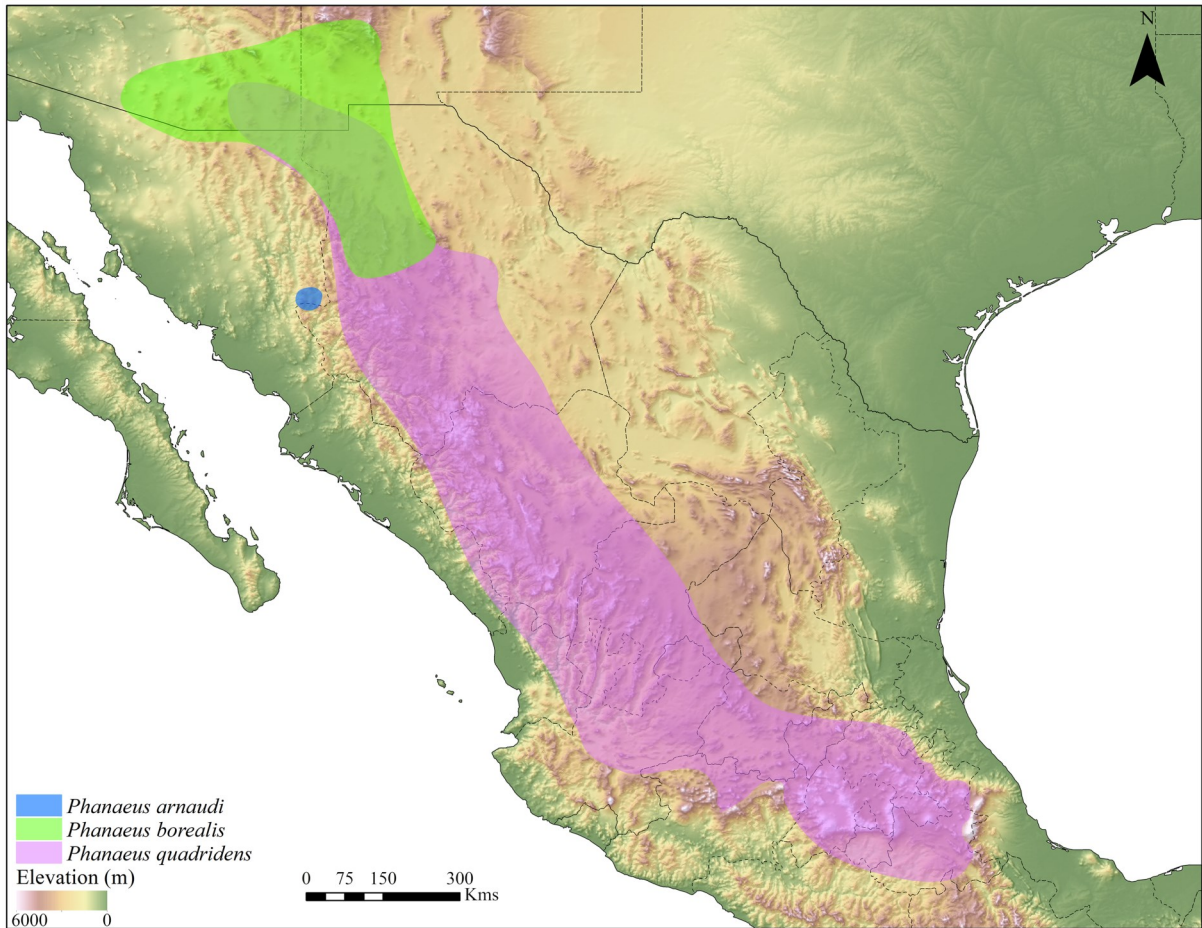


Fig. 3. Distribution of *P. arnaudi*, *P. borealis* and *P. quadridens*, modified from Edmonds and Zidek (2012).