

RESEARCH PAPER

The *Phanaeus tridens* species group (Coleoptera: Scarabaeoidea): a dung beetle group with genital morphological stasis but a changing ecological niche

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Abstract. The *Phanaeus tridens* species group is revised and found to consist of twelve species: *P. tridens* Castelnau, 1840, *P. moroni* Arnaud, 2001 stat. rev., *P. balthasari* Arnaud, 2001 stat. rev., *P. daphnis* Harold, 1863, *P. coeruleus* Bates, 1887 stat. rev., *P. herbeus* Bates, 1887 stat. rev., *P. substriolatus* Balthasar, 1939 stat. rev., *P. furiosus* Bates, 1887, *P. pseudofurcosus* Balthasar, 1939 stat. rev., *P. nimrod* Harold, 1863, *P. victoriae* Moctezuma sp. nov., and *P. eximius* Bates, 1887. The majority of the name-bearing types of the group were revised. The neotype for *P. tridens* is suggested herein. The following junior subjective synonymies are recognized: *P. frankenbergeri* Balthasar, 1939 = *P. tridens* Castelnau, 1840, *P. tricornis* Olsoufieff, 1924 = *P. herbeus* Bates, 1887, and *P. babori* Balthasar, 1939 = *P. nimrod* Harold, 1863; while *P. furcosus* Felsche, 1901 = *P. furiosus* Bates, 1887 is recognized as a junior objective synonymy. The species within the *P. tridens* species group are diagnosed by the morphology of the pronotum and elytra, while the genital morphology of males is found to be homogeneous and uninformative for species delimitation. Most species within the group show a wide diversity of colouration (showing green, red, and blue chromatic phases). This probably led to taxonomical confusion by previous authors. Here, we present a new identification key, species distribution models. Habitus photographs and character illustrations for all the species within the group are provided. The climatic niches overlap widely in *P. herbeus* and *P. daphnis*, but the other species within the group show a reduced overlap in their climatic niches. Consequently, the *P. tridens* species group is proposed as a case of morphological stasis that might be explained by a trade-off between the evolution of pronotal structures and genitalia, while differences in the ecological niche might promote speciation.

Key words. Coleoptera, Scarabaeidae, Phanaeini, scarab rainbow dung beetles, iridescence, chromatic variation, ecological niche, distribution model, Mexico, Neotropical Region

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Introduction

Phanaeus MacLeay, 1819 is a dung beetle genus endemic to the New World, ranging from the United States to northern Argentina (EDMONDS 1994, ARNAUD 2002, EDMONDS & ZÍDEK 2012). The *Phanaeus* rainbow beetles are extremely charismatic because of their outstanding

diversity of horn characters and metallic-iridescent colours (EDMONDS 1994, 2006; ARNAUD 2002; EDMONDS & ZÍDEK 2012). Consequently, several studies of *Phanaeus* and related taxa have been recently published (MANJARRES-H. & MOLANO-R. 2015; MOCTEZUMA & HALFFTER 2017, 2021; LIZARDO et al. 2017; MOCTEZUMA et al. 2017, 2019, 2020;



ARNAUD 2018; KOHLMANN et al. 2018; MOCTEZUMA & NOGUEIRA 2019; GILLET & TOUSSAINT 2020).

Two radically different interpretations for classification of *Phanaeus* are available: ARNAUD's (2002) and EDMONDS & ZÍDEK's (2012) hypotheses. ARNAUD's (2002) hypothesis recognised 77 taxa (species and subspecies) and 34 junior synonyms within *Phanaeus*. This taxonomic hypothesis has been controversial because it applied the subspecific level without presenting any explicit criteria to distinguish it from the species one (EDMONDS & ZÍDEK 2012, MOCTEZUMA & HALFFTER 2021). On the other hand, EDMONDS & ZÍDEK's (2012) hypothesis, which is an updated version of EDMONDS's (1994) one, included 54 valid species in *Phanaeus* and proposed 53 species-group names as junior synonyms. In this regard, EDMONDS's (1994) revision represents a modernization of the classical works presented by BATES (1887) and OLSOUFIEFF (1924), and it was fairly supported by the comparative study of morphology by EDMONDS (1972). Nevertheless, EDMONDS & ZÍDEK's (2012) hypothesis has been considered by some authors as excessively conservative due to lumping several closely related species under a few valid names, while ARNAUD (2002) recognized several different taxa but considered them to be subspecies (KOHLMANN et al. 2018, MOCTEZUMA et al. 2020, MOCTEZUMA & HALFFTER 2021).

Phanaeus was split into 13 species groups by EDMONDS (1994). These species groups were widely accepted by subsequent authors (ARNAUD 2002; EDMONDS 2003; PRICE 2007; EDMONDS & ZÍDEK 2012; HALFFTER & MORRONE 2017; MOCTEZUMA & HALFFTER 2017, 2021; LIZARDO et al. 2017; MOCTEZUMA et al. 2017, 2019, 2020; KOHLMANN et al. 2018; MOCTEZUMA & NOGUEIRA 2019; GILLET & TOUSSAINT 2020). Nevertheless, *Phanaeus* itself and some of its species groups were proven to be artificial groups (PRICE 2007, 2009, GILLET & TOUSSAINT 2020). However, the monophyly of the *P. endymion*, *P. tridens* and *P. vindex* species groups was supported by previous phylogenetic studies (PRICE 2009; GILLET & TOUSSAINT 2020). PRICE (2005) revised the genital morphology of males and females of the *P. vindex* species group, and suggested that genital structures were homogeneous between closely related species (i.e., taxonomically uninformative). In a recent revision of the *P. endymion* species group, MOCTEZUMA & HALFFTER (2020) determined that the endophallites were taxonomically informative in determining and identifying related species. The *P. tridens* species group has not been recently revised.

The first species of the *P. tridens* species group to be described was *P. tridens* Castelnau, 1840. The description of *P. tridens* was based upon metallic green specimens from Mexico without specified locality (CASTELNAU 1840). Subsequently, HAROLD (1863) described *P. daphnis* Harold, 1863 from Mexico (also without providing more specific locality), *P. nimrod* Harold, 1863 from Oaxaca, Mexico, and redescribed *P. tridens* based on specimens from Veracruz, Mexico. According to HAROLD (1863), *P. daphnis* and *P. tridens* were distinctly metallic green species, whereas *P. nimrod* was a metallic blue-green beetle. In a subsequent work, BATES (1887) described *P. eximius* Bates, 1887

from Central America and *P. furiosus* Bates, 1887 from Ventanas, Mexico. Additionally, the varieties *coeruleus* Bates, 1887 and *herbeus* Bates, 1887 were described for *P. daphnis* (BATES 1887).

During the 20th century, the proliferation of names and synonyms around *P. tridens* began. FELSCH (1901) established the name *P. furcosus* Felsche, 1901. Later, OLSOUFIEFF (1924) described *P. tricornis* Olsoufieff, 1924 from Cholula (originally referred to as Cholala), Puebla, Mexico; a green species closely related to *P. daphnis*. In a subsequent work, *P. babori* Balthasar, 1939, *P. frankenbergeri* Balthasar, 1939, *P. pseudofurcosus* Balthasar, 1939, and *P. substriolatus* Balthasar, 1939 were described from Mexico (BALTHASAR 1939).

ARNAUD (1982a) proposed *P. tricornis*, *P. babori*, *P. frankenbergeri*, and *P. substriolatus* as junior subjective synonyms of *P. herbeus*, *P. nimrod*, *P. tridens* and *P. daphnis*, respectively. Afterwards, EDMONDS (1994) divided the genus into species groups and formally established the *P. tridens* species group. He also designated the neotype for *P. tridens* and proposed *P. pseudofurcosus* as a subspecies of *P. tridens* and *P. furcosus* as a junior objective synonym of *P. furiosus*. Furthermore, *P. coeruleus* and *P. herbeus* were considered junior subjective synonyms of *P. daphnis* (EDMONDS 1994).

The subspecies *P. tridens balthasari* Arnaud, 2001 (from Huehuetenango, Guatemala and Chiapas, Mexico) and *P. tridens moroni* Arnaud, 2001 (from Dos Amates, Catemaco, Veracruz, Mexico) were described by ARNAUD (2001). Subsequently, ARNAUD (2002) presented his seminal work on *Phanaeus* and related taxa and included the following taxa within the *P. tridens* species group: *P. daphnis coeruleus*, *P. d. daphnis*, *P. d. herbeus*, *P. eximius*, *P. furiosus furiosus*, *P. f. pseudofurcosus*, *P. nimrod*, *P. tridens balthasari*, *P. t. moroni* and *P. t. tridens*. Finally, the revision of *Phanaeus* by EDMONDS & ZÍDEK (2012) was published. The authors commented that the *P. tridens* species group was taxonomically difficult and decided not to recognize the subspecies proposed by ARNAUD (2002) as valid until the entire *P. tridens* species group is newly scrutinized. Consequently, all the subspecies proposed by ARNAUD (2002) were synonymized by EDMONDS & ZÍDEK (2012) with *P. tridens* (*P. t. moroni* and *P. t. balthasari*), *P. daphnis* (*P. d. coeruleus* and *P. d. herbeus*) and *P. furiosus* (*P. f. pseudofurcosus*).

Although beetles account for 25% of all described species in the world (STORK et al. 2015), they are considered a poorly sampled group (ROCHA-ORTEGA et al. 2021). The incompleteness of insect biodiversity knowledge makes the description of their patterns unachievable, promoting the so-called biodiversity shortfalls (GASTON & RODRIGUES 2003, MACE 2004, HORTAL et al. 2015). The Wallacean and Linnean shortfalls are particularly limiting to the biodiversity knowledge; the first one refers to lack of distribution data of species, whereas the second one is the problem of undescribed species (BINI et al. 2006). Species distribution modelling is an interesting tool that establishes a relationship between occurrence records and environmental variables and attempts to predict the

suitability of habitat of focal taxa (PETERSON et al. 2011). This tool is fairly used to study biogeographic patterns, to predict the occurrence of not yet discovered populations and species, among others (SIMÕES et al. 2020).

Our work aims to help to reduce the Linnean and Wallacean shortfalls of the *P. tridens* species group by revising its taxonomy, and by using the species distribution modelling methods. Particularly, the external and genital morphology of the species and the status of previously described taxa are revised, while a new species is described. A new key to determine the species within the *P. tridens* species group and high-quality photographs are included. Environmental suitability models for all the species are presented and the overlap of their ecological niches is estimated.

Material and methods

Specimen depositories. Examined specimens are housed at the following entomological collections:

BMNH	Natural History Museum, London, UK;
CEMT	Seção de Entomologia da Coleção Zoológica da Universidade Federal de Mato Grosso, Cuiabá, Brazil;
CMNC	Canadian Museum of Nature, Ottawa, Canada;
PFASF	Patrick & Florent Arnaud's Collection, Saintry sur Seine, France;
GHVM	Gonzalo Halfiter's Collection, Instituto de Ecología, A.C., Veracruz, Mexico;
IEXA	Colección Entomológica Dr. Miguel Angel Morón Ríos, Instituto de Ecología, A.C., Xalapa, Mexico;
JLSHVM	José Luis Sánchez Huerta's Collection, Veracruz, Mexico;
MNHN	Muséum national d'Histoire naturelle, Paris, France ;
NMPC	Národní muzeum, Prague, Czech Republic;
NMVA	Entomology and Arachnology Collection, Museum Victoria, Melbourne, Australia;
TAMU	Texas A&M University Insect Collection, College Station, USA;
UVGC	Colección de Artrópodos de la Universidad del Valle de Guatemala, Guatemala;
VMPM	Victor Moctezuma's Collection, Puebla, Mexico.

Systematics. The phylogenetic species concept sensu WHEELER & PLATNICK (2000) was adopted. It considers a species to be the smallest aggregation of (sexual) populations or (asexual) lineages that are diagnosable by a unique combination of character states. The nomenclature proposed by HARRIS (1979), EDMONDS (1994) and CRISTÓVÃO & VAZ-DE-MELLO (2020) was followed for external morphology, and that of CRISTÓVÃO & VAZ-DE-MELLO (2020) and MOCTEZUMA et al. (2017) for genital morphology, except for the term endophallite *sensu* GÉNIER (2019).

A full description and a diagnosis are provided only for the new species (*P. victoriae*), while diagnoses are provided for all the previously described species. These diagnoses omit all the repetitious and taxonomically uninformative characters of the species that are included in the description of *P. victoriae* (i.e., the morphology of the cephalic horn of males, paraocular areas of the parietals, protibiae, phallobase, parameres, endophallite copulatrix, among others), but they include all the key features that would be included within a redescription of the species (i.e., the morphology of the pronotum of major males, elytral characters for both males and females, body colouration). Characters of minor males and females and chromatic

phases were considered within intraspecific variability. The subspecies and subgenus ranks were avoided for this work. The subgenera *Phanaeus* s. str. and *Notiophanaeus* Edmonds, 1994 as currently established have been proven to be artificial groups (PRICE 2007, 2009; GILLET & TOUSSAINT 2020). Consequently, future works will need to drastically rearrange the supraspecific classification of *Phanaeus*, making any use of the subgeneric names as currently applied futile. In any case, it should be noted that the *P. tridens* species group was included within the subgenus *Phanaeus* by previous authors (EDMONDS 1994, ARNAUD 2002, EDMONDS & ZÍDEK 2012).

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

Measurements and pictures were obtained using a Leica Z16APOA stereomicroscope (except for Figs 3–5, 7, 9, 12–13, 15, 17, 21, 23, 25–26, 31 and 47), equipped with a Leica Smart Touch and a Leica DMC2900 camera (Leica, Wetzlar, Germany) using the manufacturer's software and the z-stack image capture method. Since *Phanaeus* beetles are usually iridescent (EDMONDS 1994), the stereomicroscope lightning was substituted to obtain adequate colour images as follows: a cylinder made of matte 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 multi-stack images were edited using a Wacom Intuos PEN tablet CTL-6100WL (Wacom Co., Ltd., Toyonodai Kazo-shi, Saitama, Japan) with Adobe Photoshop CC version 2015 (Adobe Systems Incorporated, San José, California, USA) and CorelDRAW X7 version 17.0.0.491 (Corel Corporation, Ottawa, Canada).

Name-bearing types were examined for all the species within the group; except for *P. tricornis* for which the original description was revised. Distribution records were taken from specimen labels for all the revised species. In addition, databases were used for *P. eximius* (GBIF SECRETARIAT 2019); and previous literature (HAROLD 1863; BATES 1887; OLSOUFIEFF 1924; EDMONDS 1994; ARNAUD 2001, 2002; DELOYA et al. 2014, 2016; LIZARDO et al. 2017; MOCTEZUMA & NOGUEIRA 2019) for species with disjunct distributions (*P. tridens*, *P. moroni* and *P. balthasari*; *P. substriolatus*; *P. furiosus* and *P. pseudofurcosus*; *P. eximius* and *P. nimrod*).

Data for species distribution modelling. As species distributions are result of ecological and historical conditions, both factors need to be included when building a species distribution model. For the ecological conditions, we used the environmental data from the BIOCLIM climate layers from WorldClim 2.0 (FICK & HIJMAN 2017). A resolution of 30 arc sec was chosen to improve

the detection of small areas. To include historical factors affecting species distributions in the models, we used specific areas for model calibration for each species, known as the accessible area or M (BARVE et al. 2011). So, climate layers were individually cropped to include only those areas that were accessible to the species over a relevant period of time (SOBERÓN & NAKAMURA 2009). This area was obtained selecting ecoregions (DINNERSTEIN et al. 2017) and biogeographic provinces (LÖWENBERG-NETO 2014, MORRONE 2005) where the species were records. A buffer of 0.15° was applied to avoid clear cuts of the distribution. For species with few data and known restricted distribution (*P. substriolatus* and *P. victoriae*) the M was obtained by applying a buffer of 1° to the recorded distribution. The resulting polygons are shown next to the distribution models (Figs 64–68).

The use of excessive number of variables can lead to overfitted models, omission and commission errors (BEAUMONT et al. 2005), and methodological artefacts instead of biological reality (see PETERSON 2011). In contrast, too few variables can result in undercharacterization of the niches and overly broad potential distributional areas (BARRY & ELITH 2006). The latter is particularly problematic (PETERSON & NAKAZAWA 2008) with the small numbers of occurrence records available for the *P. tridens* species group. To avoid these problems there are two ways of reducing dimensionality prior to niche modelling (PETERSON 2007): (1) factor analysis, and (2) inspection of correlations between dimensions to exclude those with problems of multicollinearity. Since the first involves some loss of interpretability, the second method

was applied with the *vcor* function of the *usdm* R package (NAIMI et al. 2014). This method has a stepwise procedure which finds a pair of variables with the maximum linear correlation between them and excludes the one with the greater VIF; this is repeated until the correlation coefficient between variables is no greater than the threshold. Although a threshold of 0.7 is generally used, we applied a threshold of 0.9 because a lower value resulted in an excessive reduction of dimensions and disproportionately broad distributions. This method resulted in a different set of variables for each species (Table 1), which is appropriate when species are distributed in different biogeographical zones since different sets of climatic parameters limit their distributions (BEAUMONT et al. 2005), which was previously applied for mapping Mexican and Mesoamerican species distributions (NAVARRO-SIGÜENZA & GORDILLO-MARTÍNEZ 2018).

Species distribution modelling. To obtain the species distribution, we used the *MaxEnt* function from the *dismo* package in R (HUMANS et al. 2017). Records within a 30 arc sec pixel were counted as a single point (to have congruence with the available climate layers) and were partitioned into training and testing subset (15% for testing or at least 4 points for training). We used 1000 background points for the model, and applied a 10% omission threshold to obtain the binary maps. The models were evaluated using the Continuous Boyce Index (CBI) which measures how much the model predictions differ from random distribution of the observed presences across the prediction gradients (BOYCE et al. 2002). Its values vary between -1 (indicating counter predictions) and +1 (predictions are consistent with

Table 1. Variables selected by VIF analysis to perform Maxent Species distribution modelling of the *Phanaeus tridens* species group.

Species	Used Variables
<i>P. balthasari</i>	Max Temperature of Warmest Month, Mean Diurnal Range, Precipitation of Driest Month, Precipitation of Wettest Month, Precipitation Seasonality, Temperature Annual Range, Temperature Seasonality
<i>P. substriolatus</i>	Mean Temperature of Coldest Quarter, Mean Temperature of Warmest Quarter, Precipitation of Driest Month, Precipitation of Driest Quarter, Precipitation of Wettest Month, Precipitation of Wettest Quarter, Temperature Annual Range
<i>P. daphnis</i>	Annual Precipitation, Max Temperature of Warmest Month, Mean Temperature of Coldest Quarter, Mean Temperature of Warmest Quarter, Min Temperature of Coldest Month, Precipitation of Driest Month, Precipitation of Wettest Month, Precipitation Seasonality, Temperature Annual Range
<i>P. eximius</i>	Annual Mean Temperature, Annual Precipitation, Isothermality, Mean Diurnal Range, Precipitation of Driest Month, Precipitation of Wettest Month, Precipitation Seasonality, Temperature Annual Range, Temperature Seasonality
<i>P. furiosus</i>	Annual Mean Temperature, Annual Precipitation, Mean Diurnal Range, Mean Temperature of Coldest Quarter, Min Temperature of Coldest Month, Precipitation of Driest Month, Precipitation of Driest Quarter, Precipitation of Wettest Month, Precipitation of Wettest Quarter, Temperature Annual Range
<i>P. herbeus</i>	Annual Mean Temperature, Annual Precipitation, Isothermality, Precipitation of Driest Month, Precipitation Seasonality, Temperature Annual Range, Temperature Seasonality
<i>P. moroni</i>	Annual Mean Temperature, Isothermality, Mean Diurnal Range, Precipitation of Driest Month, Precipitation of Wettest Month, Precipitation Seasonality, Temperature Annual Range, Temperature Seasonality
<i>P. nimrod</i>	Isothermality, Mean Diurnal Range, Min Temperature of Coldest Month, Precipitation of Driest Month, Precipitation of Wettest Month, Precipitation Seasonality, Temperature Annual Range, Temperature Seasonality
<i>P. pseudofurcosus</i>	Annual Precipitation, Mean Diurnal Range, Mean Temperature of Coldest Quarter, Mean Temperature of Warmest Quarter, Min Temperature of Coldest Month, Precipitation of Driest Month, Precipitation of Driest Quarter, Temperature Annual Range, Temperature Seasonality
<i>P. tridens</i>	Annual Mean Temperature, Isothermality, Mean Diurnal Range, Min Temperature of Coldest Month, Precipitation of Driest Month, Precipitation of Wettest Month, Precipitation Seasonality, Temperature Annual Range, Temperature Seasonality
<i>P. victoriae</i>	Annual Mean Temperature, Annual Precipitation, Max Temperature of Warmest Month, Mean Temperature of Warmest Quarter, Min Temperature of Coldest Month, Precipitation of Driest Month, Precipitation of Driest Quarter, Temperature Annual Range

the presences in the testing dataset) while values close to zero mean that the model is not different from a random model (HIRZEL et al. 2006). We only accepted models with CBI > 0.5. It is the most appropriate metric in the case of presence-only models; we calculated it using the *ecospat* R package (BROENNIMANN et al. 2020).

Distributions overlap. In order to measure the geographical similarity between species, we calculated the Niche overlap (Schoener's D and Warren's I, WARREN et al. 2008) using the *dismo* package (HIJMANS et al. 2017). Both indexes range from 0 (no overlap) to 1 (niche models identical). This method assumes probability distributions defined over geographic space, projecting the niche model onto the set of environmental variables and regions of environmental niche space in which our models are most likely to accurately describe species differences (WARREN et al. 2008). Here, we use it as a proxy to evaluate the degree of geographic sympatry. The calculation was applied pairwise between species to obtain a distance matrix which was used to perform a UPGMA cluster analysis for visualization.

Differences in environmental requirements. Because the latter measure is not recommended to measure ecological similarity (see PETERSON 2011), we applied a supervised learning predictive model called Decision tree or CART (Classification & Regression Trees) on occurrence data to describe how the species differ in ecological space. This algorithm works by recursively partitioning the data so that the outcome in each final partition is as homogeneous as possible. The produced result consists of a set of binary rules, represented as a tree, which can be used for making predictions. As part of the method, it is important to avoid multicollinearity and have balanced data (roughly the same number of points per species), which requires to preprocess both the environmental and presence data. Nevertheless, this method was chosen for being easy to interpret and non-linear.

The record points were used instead of distribution model to evaluate all proven presence records with the same environmental layers. Besides, it is easier to balance the number of records than the size of distribution models. The environmental data from each presence record was extracted from the 19 layers of WorldClim 2.0, then we excluded the highly correlated variables using the *vcor* function as before. These are the selected variables for model construction: precipitation seasonality (BIO 15), precipitation of the driest month (BIO 14), precipitation of the wettest month (BIO 13), precipitation of the coldest quarter (BIO 19), and the warmest quarter (BIO 18), isothermality (BIO 3), diurnal range (BIO 2), and temperature of the warmest quarter (BIO 10).

To deal with the unbalanced data, the points were upsampled (using the *caret* package KUHN et al. 2008), meaning that those species with little data were sampled with replacement to have roughly the same number of records as the others. Downsampling was avoided due to the limited amount of data. Then 80% of the records were used for training the model while 20% were used later to measure the accuracy through a confusion matrix.

Systematics

Phanaeus tridens Castelnau, 1840

(Figs 1–5, 32, 43, 55, 63)

Phanaeus tridens Castelnau, 1840: 81. Type locality: Mexico, Veracruz, Palma Sola.

Phanaeus frankenbergeri Balthasar, 1939: 245. Type locality: Mexico. Synonymy established by ARNAUD (1982b: 125) and confirmed here.

Type material examined. *Phanaeus tridens*: NEOTYPE (suggested, examined from photographs; Fig. 3): MEXICO: VERACRUZ: ♂, Palma Sola (MNHN EC10552).

Phanaeus frankenbergeri: HOLOTYPE (examined from photographs; Fig. 4): ♂, Mexico (without further locality data) (NMPC: Mus. Nat. Pragae Inv. 26351).

Non-type material examined. MEXICO: VERACRUZ: 2 ♀♀, Alto Lucero (GHVM); 2 ♂♂, 700 m NE Apazapan (IEXA); 2 ♀♀, Conejos (GHVM); 3 ♂♂ 1 ♀, Cotaxtla (GHVM); 1 ♂, Laguna Verde (IEXA); 1 ♀, Motzorongo (GHVM); 24 ♂♂ 30 ♀♀, Palma Sola (IEXA: 11 ♂♂ 2 ♀♀; GHVM: 10 ♂♂ 24 ♀♀; VMPM: 3 ♂♂ 4 ♀♀); 1 ♀, Plan de Hayas (GHVM); 2 ♀♀, Presidio (GHVM); 1 ♂ 1 ♀ Veracruz (GHVM: 1 ♀, VMPM: 1 ♂); 1 ♂ 1 ♀, without specific locality (GHVM).

Diagnosis. Metallic green, deep green to blue green (Figs 3–5), occasionally with red sheen (Fig. 4). Sides of pronotal disc finely granulate, becoming granulorugose on raised outer margin of disc (Figs 3–5, 43). Pronotal disc weakly but coarsely rugose (Figs 3–5). Posteromedial process of pronotum produced into denticle, distinctly widened laterally (not reaching anteromedial carina), elongate, and apically bifurcated (Figs 32, 43). Anteromedial portion of pronotal disc with two denticles, usually joint by medial carina (Fig. 43). Anterolateral margins of disc with distinctly developed ridge of tubercles (Fig. 43). Posterolateral angles of pronotum shorter than posteromedial process of pronotum (Figs 32, 43). Deep green to green blue elytra, occasionally with red sheen (Figs 1–5). Elytral striae scabriculous, distinctly impressed, superficially punctate (Figs 1–5). Elytral interstriae scabriculous, smooth, superficially punctate, convex (Figs 1–5).

Variability. Minor male. Similar to major males, except for reduction of secondary sexual characters (i.e., cephalic horn, pronotal processes and posterolateral angles). **Female.** Similar to male, except for head showing trituberculate carina; pronotal sculpture granulate; pronotum with anteromedial black macula, and anteromedial trapezoidal carina, followed by posterior concavity (Fig. 55). This species is variable in colour: typical individuals are green dorsally with blue sheen (Figs 1, 3–5, 43, 55), but specimens with metallic red sheen on head and pronotum are occasionally observed (Fig. 2). EDMONDS & ZÍDEK (2012) figured a dark blue female specimen of *P. tridens*. Nevertheless, none of the specimens revised for this study was dark blue.

Comments. EDMONDS (1994) commented that the type material for many phanaeine species described by Castelnau was probably lost. As discussed by different authors (EVENHUIS 2012, MALDANER et al. 2017, VAZ-DE-MELLO & CUPELLO 2018), Castelnau's first personal collection was donated to the today's Smithsonian Institution (United States) in 1841, probably including the type series of species names established by CASTELNAU (1840), that of *P. tridens* among them. Subsequently, this collection was destroyed by a fire in 1865 (EVENHUIS 2012). Therefore, the original type series was most probably destroyed in that



Figs 1–5. *Phanaeus tridens* Castelnau, 1840. 1 – male green phase; 2 – male green-red phase; 3 – neotype and labels, present designation (by Christophe Rivier, MNHN); 4 – *P. frankenbergeri* junior subjective synonymy, holotype and labels (by Jiří Hájek, NMPC); 5 – EDMONDS' (1994) neotype of *P. tridens* and labels (by Simon Hinkley, NMVA). Scale bar = 1.0 mm.

year. Consequently, a neotype deposited at NMVA (Fig. 5) was designated by EDMONDS (1994: 53).

ARNAUD (2001) suggested that the neotype designation by EDMONDS (1994) was inadequate, since the neotype specimen was labeled as coming from Chile (Fig. 5), while *P. tridens* is endemic to Mexico. Accordingly, ARNAUD (2001) designated a new neotype for *P. tridens* and commented that his designation would be accompanied by a request to

the International Commission on Zoological Nomenclature (ICZN) to set aside EDMONDS's (1994) neotype. Our search in the *Bulletin of Zoological Nomenclature* for Arnaud's request has been unsuccessful. Indeed, Patrick Arnaud personally confirmed to the first author of this work that he had probably never sent the request to the ICZN. Consequently, the neotype designation by ARNAUD (2001) was not made available and Edmonds's one was not set aside.

According to the International Code of Zoological Nomenclature, a neotype designation is only available if it fulfils all the conditions under Article 75 (ICZN 1985). The neotype designation by EDMONDS (1994) is problematic because it does not comply with article 75.d.5 (evidence that the neotype came as nearly as practicable from the original type locality) of the Code. Indeed, the prevailing usage of the name *P. tridens* is threatened by the identity of EDMONDS's (1994) neotype specimen which is correctly identified as *P. tridens* but mislabelled, indicated to come from Chile (Fig. 5) while this species is endemic to Mexico (CASTELNAU 1840: Fig. 64). In order to clarify the application of the name *P. tridens* and to conserve its current usage, we suggest to designate a neotype (Fig. 3). In addition, this publication is followed by a request under Article 75.6 to the ICZN (1999) to set aside EDMONDS's (1994) neotype (Fig. 5) by its plenary power.

The characters for which *P. tridens* is differentiated are provided in the diagnosis of this species. The designated neotype is a major male housed at MNHN (MNHN EC10552, Fig. 3). The neotype specimen (Fig. 3) fits the original description of *P. tridens* (CASTELNAU 1840): "D'un vert métallique éclatant; devant du chaperon et une longue corne arquée sur la tête noirs; corselet rugueux, profondément excavé dans son milieu, avec deux cornes latérales et une postérieure au milieu; élytres lisses, striées, avec des enfoncemens à la base des quatre premières stries; jambes et tarse noirs. — Mexique" [translation to English: bright metallic green species; male with a large horn curved over the head; roughened pronotum, deeply excavated medially, with two lateral horns and a posteromedial horn; flattened elytra; impressed fossae at bases of the first four elytral striae; Mexican species].

Nevertheless, at least four related species (*P. balthasari*, Figs 8–9; *P. daphnis*, Figs 10, 12; *P. herbeus*, Figs 16–17; and the one to which the name *P. tridens* is traditionally applied, Figs 1, 3–5) fit the original description, being metallic green in colour and from Mexico as mentioned by CASTELNAU (1840). This problem is made worse by the fact that details about the sizes, shapes and positions of the pronotal ornaments are not mentioned by him, which makes it impossible to determine what species Castelnau's specimen actually belonged to. HAROLD (1863) redescribed *P. tridens* and suggested Veracruz as the distribution area of this species, while BATES (1887) provided accurate localities from the north-central region of Veracruz. The only one of those four species to occur in north-central Veracruz (Fig. 64) is indeed the one that has been traditionally called *P. tridens* (or *P. tridens tridens*) for more than a century in collections and in literature (e.g. HAROLD 1863, BATES 1887, OLSOUFIEFF 1924, ARNAUD 2002, EDMONDS 1994, EDMONDS & ZÍDEK 2012). Consequently, we believe that designating a specimen from a north-central Veracruz population (such as the Palma Sola one, Fig. 3) as the neotype for *P. tridens* is appropriate and promotes stability.

Distribution. Northern to central Veracruz, Mexico (Fig. 64).

Phanaeus moroni Arnaud, 2001 stat. rev.

(Figs 6–7, 33, 44)

Phanaeus tridens moroni Arnaud, 2001: 7. Type locality: Mexico, Veracruz, Catemaco, Dos Amates.

Type material examined. MEXICO: VERACRUZ: HOLOTYPE (originally designated by ARNAUD 2001, examined from photographs; Fig. 7): ♂ Dos Amates, Catemaco (PFASF).

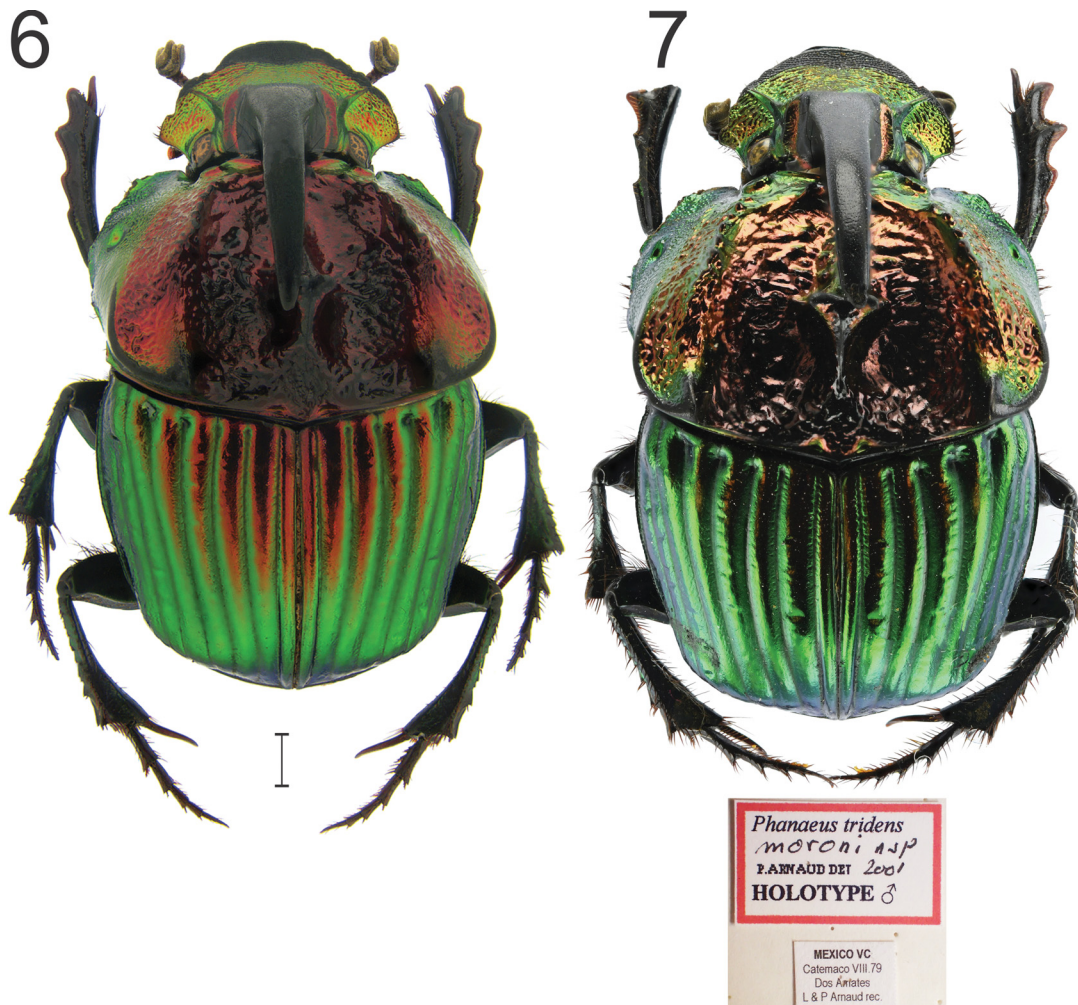
Non-type material examined. MEXICO: VERACRUZ: 2 ♂♂, Dos Amates, Catemaco (GHVM, VMPM); 1 ♂ (CMNC).

Diagnosis. Sides of pronotal disc metallic green-yellow, becoming bright red to wine-garnet red towards medial portion of pronotum; postero-medial portion of pronotal disc almost completely black (Figs 6–7, 44). Sides of pronotal disc finely granulate and becoming granulorugose on outer margin of disc (Figs 6–7, 44). Pronotal disc weakly but coarsely rugose (Figs 6–7). Posteromedial process of pronotum produced into denticle, strongly widened laterally (almost reaching anteromedial carina), elongate and apically bifurcated (Figs 33, 44). Anteromedial portion of pronotal disc with two denticles, usually joined by strongly developed, medial carina (Fig. 44). Anterolateral margins of disc with strongly developed ridge of tubercles (Fig. 44). Posterolateral angles shorter than posteromedial process of pronotum (Fig. 33). Tri-coloured elytra, metallic green-red-yellow (Figs 6–7). Elytral striae scabriculous, distinctly impressed, superficially punctate (Figs 6–7). Elytral interstriae scabriculous, smooth, superficially punctate, convex (Figs 6–7).

Variability. *Minor male.* Similar to major males, except for reduction of secondary sexual characters (i.e., cephalic horn, pronotal process and posterolateral angles). *Female.* Similar to male, except for head showing trituberculate carina; pronotal sculpture granulate; and anteromedial carina of pronotum followed by posterior concavity. Apparently, this species is not variable in colour (Figs 6–7, 44).

Comments. *Phanaeus moroni* was originally considered a subspecies of *P. tridens* due to the Veracruz populations being distinct from the rest of the species in colour (Figs 6–7, 44) and in the shape of the posteromedian process of the pronotum (Figs 33, 44). Subsequently, EDMONDS & ZÍDEK (2012) regarded *P. moroni* as a "colour variant" and a junior subjective synonym of *P. tridens* (Figs 1–5, 32, 43). The unique combination of characters of *P. moroni* demonstrates that it deserves a full species status. The posteromedial process of pronotum in major males of *P. moroni* is distinctly narrowed medially in posterior view (Fig. 33; not narrowed in *P. tridens* Fig. 32), while the ridge of tubercles of anterolateral margins of pronotal disc are more raised in *P. moroni* (Fig. 44) than in *P. tridens* (Fig. 43). Along its distribution, *Phanaeus tridens* indeed has a bright green-red chromatic phase (Fig. 2). This fact likely led EDMONDS & ZÍDEK (2012) to consider *P. tridens* and *P. moroni* synonyms. Nevertheless, the bright green-red chromatic phase of *P. tridens* (Fig. 2) never shows the wine-garnet red to black pronotal disc and the widened posteromedial process of pronotum of *P. moroni* (Figs 6–7, 44).

Distribution. Mexico: Los Tuxtlas region, Veracruz (Fig. 64).



Figs 6–7. *Phanaeus moroni* Arnaud, 2001, stat. rev. 6 – male; 7 – holotype and labels (by Patrick Arnaud, PFASF). Scale bar = 1.0 mm.

***Phanaeus balthasari* Arnaud, 2001, stat. rev.**

(Figs 8–9, 34, 45, 56)

Phanaeus tridens balthasari Arnaud, 2001: 6. Type locality: Guatemala, Huehuetenango.

Type material examined. GUATEMALA: HUEHUETENANGO: HOLOTYPE (originally designated by ARNAUD 2001, examined from photographs; Fig. 9) 1 ♂ (PFASF). MEXICO: CHIAPAS: PARATYPE (examined from photographs): 1 ♂, 2 km S. Chicoasen (CMNC).

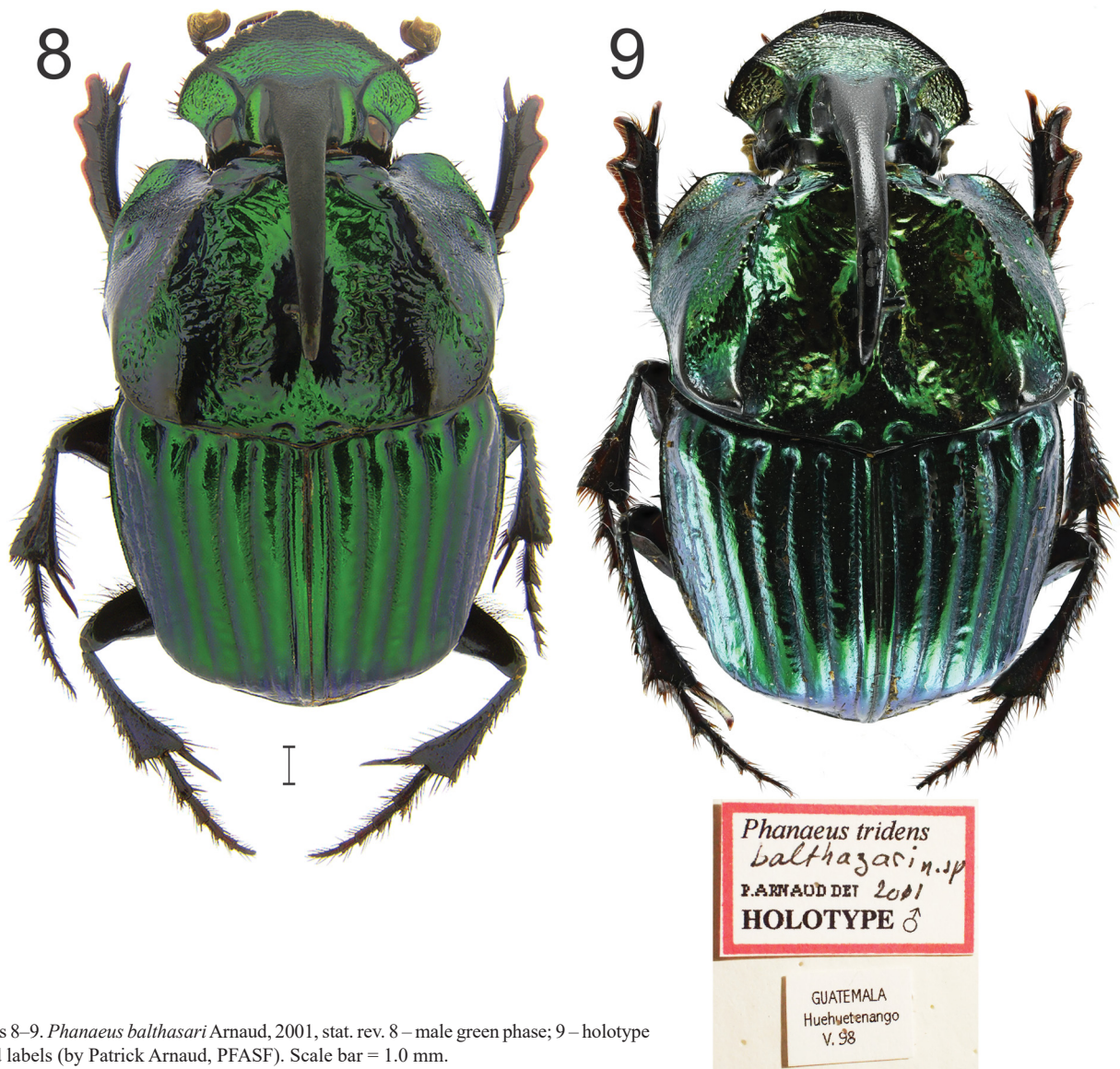
Non-type material studied. GUATEMALA: HUEHUETENANGO: 1 ♂, Nenton, Camino Nenton-San José Chaquial (UVGC); 1 ♀, Nenton, Finca El Carmen (UVGC); 2 ♂♂ 1 ♀, Nenton, Finca El Zapote, Río Lagarteros (VMPM); 1 ♀, Nenton, La Trinidad (UVGC); 1 ♂, Nenton, San José Chaquial (VMPM). MEXICO: CHIAPAS: 1 ♀, Cerro Hueco (GHVM); 1 ♂ 1 ♀, El Pozuelo (GHVM); 2 ♂♂ 1 ♀, Las Delicias (GHVM); 1 ♂ 1 ♀, VMPM: 1 ♂; 1 ♂ 3 ♀♀, Meseta de Copoya, Tuxtla Gutiérrez (GHVM); 3 ♀♀, VMPM: 1 ♂; 2 ♂♂ 1 ♀, San Pedro (VMPM); 2 ♀♀, Santa Rosa (GHVM); 1 ♀, VMPM: 1 ♀; 3 ♂♂ 1 ♀, Vicente Guerrero (VMPM); 2 ♀♀, Vicente Guerrero, San Fernando (VMPM).

Diagnosis. Metallic green species with yellow-red sheen (Figs 8–9, 45, 56). Sides of pronotal disc finely granulate and becoming granulorugose on raised outer margin of disc; disc weakly but coarsely rugose, more sparsely posteriorly (Figs 8–9, 45). Posteromedial process of pronotum produced into denticle, distinctly widened towards apex (not reaching anteromedial denticles), elongate, and apically bifurcated (Figs 34, 45). Anteromedial portion of

pronotal disc with two denticles, distinctly separated by medial inconspicuous tubercle, this tubercle sometimes absent (Fig. 45). Anterolateral margins of pronotal disc with distinctly developed ridge of tubercles (Fig. 45). Posterolateral angles of pronotum less developed than posteromedial process of pronotum (Figs 34, 45). Elytral striae scabriculous, distinctly impressed and superficially punctate (Figs 8–9). Elytral interstriae scabriculous, smooth, superficially punctate and convex (Figs 8–9).

Variability. *Minor male.* Similar to major males, except for reduction of secondary sexual characters (i.e., cephalic horn, pronotal processes and posterolateral angles). **Female.** Similar to male, except for head showing trituberculate carina; pronotal sculpture granulate; pronotum with anteromedial black macula, and anteromedial trapezoidal carina followed by posterior concavity (Fig. 56).

Comments. Specimens of this species were erroneously referred to as *P. pseudofurcosus* by EDMONDS (1994), who considered it a subspecies of *P. tridens* (Figs 1–5, 45, 55). Additionally, specimens of the real *P. pseudofurcosus* (Figs 22–23, 39, 51, 62) were referred to as the “Colima population” of *P. tridens tridens* (EDMONDS 1994). Subsequently, ARNAUD (2001) recognized the mistake by EDMONDS (1994) and described this taxon as a new subspecies, *P.*



Figs 8–9. *Phanaeus balthasari* Arnaud, 2001, stat. rev. 8 – male green phase; 9 – holotype and labels (by Patrick Arnaud, PFAF). Scale bar = 1.0 mm.

tridens balthasari. Finally, EDMONDS & ZÍDEK (2012) proposed *P. t. balthasari* as a junior subjective synonym of *P. tridens*, arguing that the entire *P. tridens* species group needed to be scrutinized.

The results of the present study demonstrate that *P. balthasari* merits full species status, because it is distinctly distinguished from *P. tridens* by a unique character combination: the posteromedial process of pronotum distinctly narrowed medially in posterior view (Fig. 34; not narrowed in *P. tridens*, Fig. 32), ridge of tubercles of anterolateral margins of pronotal disc more raised in *P. balthasari* (Fig. 45), posterolateral angles of pronotum parallel in *P. balthasari* (Figs 8–9; subparallel in *P. tridens*, Figs 1–5) and pronotal disc more coarsely rugose in *P. balthasari* (Figs 8–9, 45). Putative hybrid specimens or populations between *P. tridens* and *P. balthasari* were not found, while *P. tridens* is restricted to north-central Veracruz and *P. balthasari* to Chiapas and Guatemala (Fig. 64).

Distribution. From Chiapas, Mexico to Huehuetenango, Guatemala (Fig. 64).

Phanaeus daphnis Harold, 1863

(Figs 11–13, 35, 46, 57)

Phanaeus daphnis Harold, 1863: 165. Type locality: Mexico.

Type material examined. MEXICO: LECTOTYPE (designated by ARNAUD 1982a, examined from photographs; Fig. 12): ♂, without specific locality (MNHN: MNHN EC10558). PARALECTOTYPE (examined from photographs): ♂, without specific locality (MNHN: MNHN EC10559). **Non-type material examined.** MEXICO: ESTADO DE MÉXICO: 1 ♂ 7 ♀♀, Chalma (GHVM: 1 ♂ 6 ♀♀; VMPM: 1 ♀); 11 ♀♀, Zona arqueológica Malinalco (GHVM: 10 ♀♀; VMPM: 1 ♀). GUERRERO: 2 ♀♀, Acahuizotla (IEXA); 1 ♀, Coapango (VMPM); 5 ♂♂ 2 ♀♀, Hueyecantango, Chilapa (GHVM); 11 ♂♂ 30 ♀♀, Mochitlán, Acahuizotla (IEXA); 2 ♂♂, Taxco (GHVM: 1 ♂; VMPM: 1 ♀); 1 ♀, 2 mi. W Taxco (GHVM); 2 ♂♂ 1 ♀, Tetipac (IEXA). MORELOS: 3 ♂♂, Alpuyeca (GHVM); 3 ♂♂ 2 ♀♀, Cuautla (GHVM); 8 ♂♂ 12 ♀♀, Cuernavaca (IEXA: 5 ♂♂ 8 ♀♀; GHVM: 3 ♂♂ 4 ♀♀); 1 ♀, 9 mi. S Cuernavaca (GHVM); 2 ♂♂ 1 ♀, Huautla (IEXA); 1 ♂, Jojutla, Cerro del Higuierón (IEXA); 1 ♂ 1 ♀, Oaxtepec (GHVM); 1 ♂, Palmiras, Cuernavaca (GHVM); 1 ♀, Progreso (GHVM); 2 ♂♂ 1 ♀, Puente de Ixtla (GHVM: 1 ♂; VMPM: 1 ♂ 1 ♀); 1 ♂, Real del Puente (GHVM); 26 ♂♂ 7 ♀♀, Tepoztlán (GHVM: 21 ♂♂ 6 ♀♀; VMPM: 5 ♂♂ 1 ♀); 1 ♀, Tequesquitengo (GHVM); 3 ♂♂ 5 ♀♀, Xochitepec (GHVM: 3 ♂♂ 4 ♀♀; VMPM: 1 ♀). OAXACA: 1 ♂, Oaxaca (IEXA). PUEBLA: 2 ♀♀, 9 mi. N Amatlán (GHVM); 1 ♂, Matamoros (VMPM). UNKNOWN LOCALITY: 2 ♂♂ (GHVM).

Diagnosis. Typically metallic green (Figs 10, 12, 46, 57), rarely deep blue-green (Fig. 11). Sides of pronotal disc granulate anteriorly, becoming punctate with effaced granules posteriorly (Figs 10–11, 46). Pronotal

disc coarsely rugose (Figs 10–11, 46). Posteromedial process of pronotum produced into fairly short denticle, not bifurcated apically (Figs 35, 46). Anteromedial portion of pronotal disc with line of denticles or carina

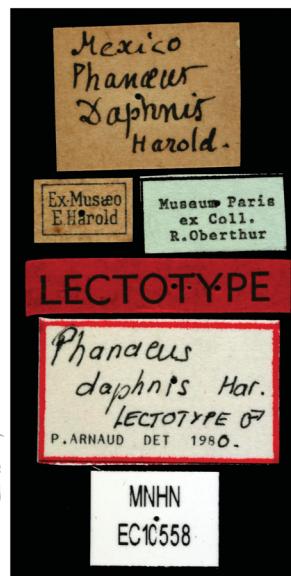
10



11



12



Figs 10–12. *Phanaeus daphnis* Harold, 1863. 10 – male green phase; 11 – male deep blue-green phase; 12 – lectotype and labels (by Christophe Rivier, MNHN). Scale bar = 1.0 mm.

(Fig. 46). Anterolateral margins of pronotal disc without ridge or line of tubercles (Fig. 46). Posterolateral angles of pronotum much longer than posteromedial process of pronotum (Figs 35, 46). Elytral striae scabridulous, distinctly impressed, superficially punctate (Figs 10–12). Elytral interstriae scabridulous, superficially punctate, flat; I, III, V, VI and VII frequently with lightly roughened integument (Figs 10–12).

Variation. Minor male. Similar to major males, except for reduction of secondary sexual characters (i.e., cephalic horn, pronotal processes and posterolateral angles). Particularly, posterolateral angles of pronotum are reduced into a couple of pronotal keels, while posteromedial process is obsolete. **Female.** Similar to male, except for head showing trituberculate carina; pronotal sculpture granulate, becoming coarsely punctate posteriorly; pronotum with anteromedial black macula, and anteromedial trapezoidal carina, followed by posterior concavity (Fig. 57).

Comments. EDMONDS (1994) and EDMONDS & ZÍDEK (2012) proposed that *P. coeruleus* (Figs 13, 47) and *P. herbeus* (Figs 16–18, 37, 49, 59) were junior subjective synonyms of *P. daphnis* (Figs 11–13, 35, 46, 57). In turn, ARNAUD (2002) considered both subspecies of *P. daphnis*. According to the findings of the present study, both *P. coeruleus* and *P. herbeus* merit full species status. Major males of *P. daphnis* never show the posteromedial process of pronotum produced into a distinctly elongate denticle (Figs 35, 46), while those of *P. coeruleus* (Fig. 47) and *P. herbeus* (Figs 18, 37, 49) do.

Less than 3% of the examined specimens of *P. daphnis* are deep blue-green (Fig. 11), but their colouration is not similar to that of *P. coeruleus* (Figs 13, 47). This fact likely led EDMONDS (1994) and EDMONDS & ZÍDEK (2012) to con-

sider *P. coeruleus* and *P. daphnis* synonyms. Nevertheless, the deep blue-green chromatic phase of *P. daphnis* (Fig. 11) never shows the distinctly smooth elytral interstriae seen in *P. coeruleus* (Fig. 13). The typical green specimens of *P. daphnis* (Figs 10, 12, 46, 57) and *P. herbeus* (Figs 16–17, 59) are similar in colour. Nevertheless, *P. daphnis* never shows a green-red chromatic phase like in *P. herbeus* (Fig. 49). *Phanaeus daphnis* and *P. herbeus* are sympatric in an area between Estado de México and Morelos (Fig. 65).

Distribution. Mexico: Estado de México, Guerrero, Morelos, Puebla, Oaxaca (Fig. 65).

Phanaeus coeruleus Bates, 1887, stat. rev.

(Figs 13, 47)

Phanaeus daphnis var. *coeruleus* Bates, 1887: 61. Type locality: Mexico, Puebla.

Type material examined. MEXICO: HOLOTYPE (fixed by monotypy by BATES 1887, examined from photographs; Figs 13, 47): ♂, Puebla (BMNH: NHMUK 013667754).

Diagnosis. Metallic dark blue with turquoise sheen (Figs 13, 47). Sides of pronotal disc granulate anteriorly, becoming punctate with effaced granules posteriorly. Pronotal disc coarsely rugose (Figs 13, 47). Posteromedial process of pronotum produced into short denticle, not bifurcated but truncate apically (Fig. 47). Anterolateral margins of pronotal disc without ridge or line of tubercles (Fig. 47). Posterolateral angles of pronotum much longer than posteromedial process (Fig. 47). Elytral striae scabridulous, distinctly impressed, superficially punctate (Fig. 13). Elytral interstriae scabridulous, distinctly smooth (except for interstriae VI and VII with lightly roughened integument), superficially punctate, flat (Fig. 13).



Fig. 13. *Phanaeus coeruleus* Bates, 1887, stat. rev., holotype and labels (by Keita Matsumoto, BMNH).

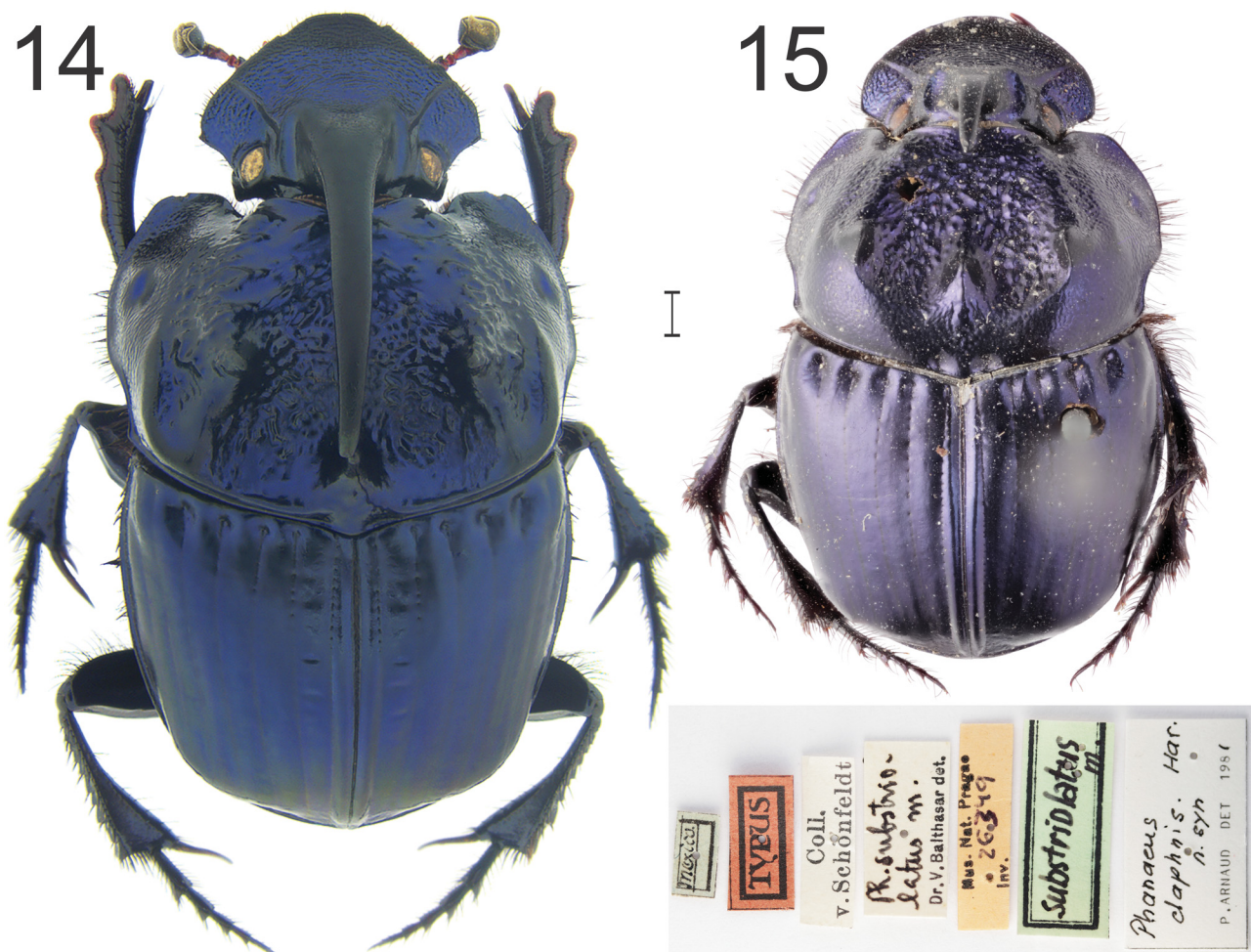
Variation. *Minor male.* Unknown. *Female.* Unknown.

Comments. ARNAUD (1982a: 113) collectively designated lectotypes for some species-group names of *Phanaeus* housed at BMNH. More specifically, instead of pointing out which individual syntype was being designated as the lectotype of each name, ARNAUD (1982a) simply said in a general statement that he considered syntypes labelled as “sp. figured” in the BMNH to be lectotypes of names established by BATES (1887). Nevertheless, as explained by EDMONDS (1994), the International Code on Zoological Nomenclature prohibits collective designation of lectotypes like ARNAUD (1982a) did. Indeed, the designation of lectotypes must be individual under Article 74.3 (ICZN 1999). Consequently, all the lectotype designations for the BMNH specimens by ARNAUD (1982a) were invalid. Among the invalid lectotypes designated by ARNAUD (1982a) was that of *P. coeruleus* (Figs 13, 47).

BATES (1887) did not provide information on the size of the type series of *P. coeruleus*. However, he explicitly cited HAROLD (1863) to describe *P. coeruleus*. HAROLD (1863) commented that he examined only one specimen from Sallé’s Collection. Since BATES (1887) also relied in part on Sallé’s material, it is very likely that both referred to the same specimen. Consequently, that specimen should be considered the holotype of *P. coeruleus* by original monotypy (Figs 13, 47).

EDMONDS (1994) considered *P. coeruleus* (Figs 13, 47) to be a junior subjective synonym of *P. daphnis* (Figs 11–13, 35, 46, 57). The results of the present study suggest that *P. coeruleus* deserves full species status because it has a unique combination of characters: the posteromedial process of pronotum is produced into a denticle that is more truncate apically and more widened at the base in *P. coeruleus* (Fig. 47) than in *P. daphnis* (Fig. 46), while the elytral interstriae I–V are smooth in *P. coeruleus* (Fig. 13). It is curious that the same differences had already been noted by HAROLD (1863), who regarded the single specimen that he examined as an odd individual of *P. daphnis*, and by BATES (1887), who treated *coeruleus* as a variety of *P. daphnis*. In addition, the dark blue colour with turquoise sheen on the whole dorsal surface of *P. coeruleus* (Figs 13, 47) differs from the dark blue to black colouration of *P. substriolatus* (Figs 14–15, 48, 58), while the elytral striae are distinctly impressed in *P. coeruleus* (Figs 13) but superficially impressed to partially erased in *P. substriolatus* (Figs 14–15).

The only one specimen of *P. coeruleus* known to us is the holotype (Figs 13, 47). The labels of this specimen indicate that it was collected from Puebla, without specific locality (Figs 13). Interestingly, none of the revised specimens from Puebla were identical in morphology to *P. coeruleus*. Since *Phanaeus* dung beetles from Puebla



Figs 14–15. *Phanaeus substriolatus* Balthasar, 1939, stat. rev. 14 – male; 15 – holotype and labels (by Jiří Hájek, NMPC). Scale bar = 1.0 mm.

are scarcely studied (MORÓN et al. 2003), future intensive collecting is needed in this Mexican state to improve the knowledge of *P. coeruleus* and related species (e.g., *P. herbeus* and *P. substriolatus*).

Distribution. Mexico: Puebla.

***Phanaeus substriolatus* Balthasar, 1939, stat. rev.**

(Figs 14–15, 36, 48, 58)

Phanaeus substriolatus Balthasar, 1939: 245. Type locality: Mexico.

Type material examined. MEXICO: HOLOTYPE (originally designated by BALTHASAR 1939, examined from photographs; Fig. 15): ♂, without specific locality (NMPC: Mus. Nat. Pragae Inv. 26349).

Non-type material studied. MEXICO: GUERRERO: 1 ♂ (examined from photographs), Amula (BMNH: 013667803). OAXACA: 1 ♂ 1 ♀, Cerro Colorado, San Juan Bautista Cuicatlán (VMPM). PUEBLA: 1 ♂ 1 ♀, San Mateo Zoyamazalco, Coyotepec (VMPM); 1 ♀, Izucar de Matamoros (examined from photographs, BMNH: NHMUK 013667799).

UNKNOWN LOCALITY: 1 ♂ (examined from photographs, BMNH: NHMUK 013667796).

Diagnosis. Metallic dark blue to black (Figs 14–15, 48, 58). Sides of pronotal disc finely granulate, becoming granulogose on raised outer margin of disc; pronotal disc weakly but coarsely rugose, more sparsely posteriorly (Figs 14–15, 48). Posteromedial process of pronotum produced into a slender, conical or triangular and elongate denticle (Figs 36, 48). Anteromedial portion of pronotal disc with two denticles and variable in number of tubercles (Fig. 48). Anterolateral margins of pronotal disc without ridge or line of tubercles (Figs 48). Posterolateral angles of pronotum shorter than posteromedial process and produced into two conical or triangular elongate denticles (Figs 36, 48). Elytral striae smooth, scabriculous, superficially impressed or partially erased, superficially punctate (Figs 14–15). Elytral interstriae scabriculous, smooth, superficially punctate, flat; I, III, V and VI frequently with lightly roughened integument (Figs 14–15).

Variability. Minor male. Similar to major males, except for the reduction of the secondary sexual characters (i.e., cephalic horn, pronotal processes and posterolateral angles). Particularly, the posterolateral angles and posteromedial process of pronotum are reduced into tree pronotal keels or conical tubercles (Fig. 15). **Female.** Similar to the male, except for the head showing a trituberculate carina; pronotal sculpture granulate to punctate posteriorly; pronotum with anteromedial black macula, and anteromedial carina followed by a posterior concavity (Fig. 58).

Comments. ARNAUD (1982b: 125) established the synonymy between *P. substriolatus* (Figs 14–15, 36, 48, 58) and *P. daphnis* (Figs 11–13, 35, 46, 57), which was followed by subsequent authors (EDMONDS 1994, ARNAUD 2002, EDMONDS & ZÍDEK 2012). After examining the holotype (Fig. 15) and additional material (Figs 14, 36, 48, 58), we suggest that *P. substriolatus* deserves full species status because it has a unique combination of characters: the dark blue to black colouration is unique of this species (Figs 14–15, 48, 58; dark blue with turquoise sheen in *P. coeruleus*, Figs 13, 47; green or green-blue in *P. daphnis*, Figs 11–13, 46, 57; green or green-red in *P. herbeus*, Figs 16–17, 49, 59), the posteromedial

process of pronotum produced into an elongate denticle in *P. substriolatus* (Figs 36, 48) separates it from *P. daphnis* (Figs 35, 46), while the elytral interstriae I, III and V with lightly roughened integument distinguishes *P. substriolatus* (Figs 14–15) from *P. coeruleus* (smooth elytral interstriae I–V, Fig. 13). Finally, the elytral striae superficially impressed or partially erased are unique of *P. substriolatus* (Figs 14–15).

Distribution. Mexico: southern Puebla to northern Oaxaca (Fig. 65). The record from central Guerrero needs confirmation.

***Phanaeus herbeus* Bates, 1887 stat. rev.**

(Figs 16–18, 37, 49, 59)

Phanaeus daphnis var. *herbeus* Bates, 1887: 61. Type locality: Mexico.

Phanaeus tricornis Olsoufieff, 1924: 105. Type locality: Without specific locality. Synonymy established by ARNAUD (1982a: 116) and confirmed here.

Type material examined. MEXICO: HOLOTYPE of *P. herbeus* (fixed by monotypy by BATES 1887, examined from photographs; Fig. 17): ♂, without specific locality (BMNH: NHMUK 013667783).

Non-type material examined. MEXICO: ESTADO DE MÉXICO: 1 ♀, Ixtapan del Oro (IEXA); 8 ♂♂ 1 ♀, Santo Tomás de los Plátanos (GHVM: 6 ♂♂ 1 ♀; VMPM: 2 ♂♂); 5 ♂♂ 2 ♀♀, Temascaltepec (GHVM: 4 ♂♂ 1 ♀; VMPM: 1 ♂ 1 ♀); 1 ♀, Tenancingo (GHVM), 1 ♀, Valle de Bravo (VMPM); 2 ♂♂ 5 ♀♀, Zacazonapan (IEXA). MICHOACÁN: 1 ♀, Tuxpan (VMPM). MORELOS: 2 ♂♂, Tepoztlán (GHVM). WITHOUT SPECIFIC LOCALITY: 3 ♂♂ (GHVM: 2 ♂♂; VMPM: 1 ♂).

Diagnosis. Metallic green (Figs 16–17, 59), occasionally with a red sheen (Fig. 49). Sides of pronotal disc finely granulate becoming granulogose on raised outer margin of disc; pronotal disc weakly but coarsely rugose, more sparsely posteriorly (Figs 16–17, 49). Posteromedial process of pronotum strongly produced into slender, conical or triangular denticle (Figs 18, 37, 49). Anteromedial portion of pronotal disc with one triangular, sharply acute tubercle, or with some rounded tubercles (Fig. 49). Anterolateral margins of pronotal disc with distinctly developed ridge of tubercles (Fig. 49). Anterolateral margins of pronotal disc without ridge or line of tubercles (Fig. 49). Posterolateral angles of pronotum slightly less developed than posteromedial process and produced into two conical or triangular elongate denticles (Figs 18, 37, 49). Elytral striae scabriculous, distinctly impressed, superficially punctate (Figs 16–17). Elytral interstriae scabriculous, smooth, superficially punctate, convex; III, V and VI frequently with lightly roughened integument (Figs 16–17).

Variability. Minor male. Similar to major males, except for reduction of secondary sexual characters (i.e., cephalic horn, pronotal processes and posterolateral angles). Particularly, posterolateral angles and posteromedial process of pronotum are reduced into three conical tubercles as seen in *P. substriolatus* (Fig. 15). **Female.** Similar to male, except for head showing trituberculate carina; pronotal sculpture granulate; pronotum with anteromedial black macula, and anteromedial carina followed by posterior concavity (Fig. 59).

Comments. According to EDMONDS (1994), the holotype was fixed by monotypy (Fig. 17). The type locality



Figs 16–18. *Phanaeus herbeus* Bates, 1887, stat. rev. 16 – male green phase; 17 – holotype and labels (by Mario Cupello, UFPR); 18 – *P. tricornis* Olsoufieff, 1924, junior subjective synonymy, redrawn from OLSOUFIEFF (1924). Scale bar = 1.0 mm.

provided by the labels (Mexico) and the morphology of the specimen are consistent with those mentioned in the original description of *P. herbeus* (Fig. 17). *Phanaeus herbeus* (Figs 16–18, 37, 49, 59) was originally described as a variety of *P. daphnis* (Figs 11–13, 35, 46, 57) by BATES (1887). Later, the name was deemed a junior

subjective synonym of *P. daphnis* by EDMONDS (1994) and EDMONDS & ZÍDEK (2012). On the other hand, ARNAUD (2002) considered *P. herbeus* a valid subspecies of *P. daphnis*. We believe that *P. herbeus* merits full species status. The typical green chromatic phases of *P. herbeus* (Figs 16–17, 59) and *P. daphnis* (Figs 10–12, 46, 57) are

similar. Nevertheless, the red-green chromatic phase is only found in *P. herbeus* (Fig. 49), whereas *P. herbeus* never shows a deep blue-green chromatic phase as seen in *P. daphnis* (Fig. 11). Furthermore, major males of *P. herbeus* always show the posteromedial process of pronotum strongly produced into a slender denticle (Figs 18, 37, 49; small denticle in *P. daphnis*, Figs 35, 46). The convex interstriae separates *P. herbeus* (Figs 16–17) and closely related species with flat interstriae (*P. daphnis*, Figs 10–12; *P. coeruleus*, Fig. 13; *P. substriolatus* Figs 14–15).

Additionally, the minor males of *P. herbeus* show the posteromedial process and the posterolateral angles of pronotum produced into three small conical tubercles (as in Fig. 15; the posteromedial process obsolete and the posterolateral angles carinate in *P. daphnis*). *Phanaeus herbeus* and *P. daphnis* are partially sympatric (Fig. 65), but the pronotal morphology is consistent and likely hybrid specimens were not found.

Phanaeus substriolatus (Figs 14–15, 36, 48, 58) is also similar to *P. herbeus*. The latter is distinguished by the elytral interstriae distinctly convex (Figs 16–17; elytral interstriae distinctly flattened in *P. substriolatus*, Figs 14–15) and the presence of green (Figs 16–17, 59) or green-red (Fig. 49) specimens in its populations (specimens always dark blue in *P. substriolatus*, Figs 14–15, 48, 58). *Phanaeus herbeus* and *P. substriolatus* are not sympatric (Fig. 65). *Phanaeus herbeus* was figured by DELOYA & COBARRUBIAS-MELGAR (2014) instead of *P. daphnis*. ARNAUD (1982a) proposed *P. tricornis* (Fig. 18) as a junior subjective synonym of *P. herbeus*. Unfortunately, we were not able to revise the lectotype of *P. tricornis*, but its original description and illustration are fairly detailed and allowed us to confirm this synonymy.

Distribution. Mexico: Estado de México, Michoacán, Morelos and Puebla (Fig. 65).

Phanaeus furiosus Bates, 1887

(Figs 19–21, 27, 38, 50, 61)

Phanaeus furiosus Bates, 1887: 61. Type locality: Mexico, Ventanas.

Phanaeus furcosus Felsche, 1901: 155. Unjustified emendation.

Type material examined. MEXICO. LECTOTYPE (designated by EDMONDS 1994, examined from photographs; Fig. 21): ♂, Ventanas (BMNH: NHMUK 013903639).

Non-type material examined. MEXICO: AGUASCALIENTES: 1 ♀, Calvillo, Mesa El Roble (IEXA). GUANAJUATO: 1 ♀, Cuernamaro (IEXA). JALISCO: 3 ♀♀, Agua del Obispo (GHVM); 1 ♂ 4 ♀♀, Ajijic (GHVM); 1 ♂ 4 ♀♀, Amatitlán (IEXA); 1 ♀, Chapala (IEXA); 2 ♂♂ 4 ♀♀, La Calera (IEXA); 3 ♂♂ 11 ♀♀, Mezquitán (IEXA); 3 ♂♂ 6 ♀♀, Poncitlán (IEXA); 1 ♀, San Miguel de Hidalgo (IEXA); 10 ♂♂ 12 ♀♀, Trans. Carretera Guadalajara-Colotlán (GHVM: 7 ♂♂ 7 ♀♀; VMPM: 3 ♂♂ 5 ♀♀); 1 ♀, Zapopan (IEXA). MICHOACÁN: 1 ♂, Coalcomán (GHVM); 1 ♂, without specific locality (GHVM). NAYARIT: 1 ♂ 2 ♀♀, El Venado (IEXA); 1 ♂ 5 ♀♀, Tepic, La Cantera (IEXA); 1 ♂ 1 ♀, San Blas (IEXA: 1 ♀, GHVM: 1 ♂); 1 ♂, San José Mojarras, Santa María del Río (IEXA) 3 ♂♂ 4 ♀♀, Villa Hidalgo (IEXA); 1 ♂, without specific locality (GHVM). SINALOA: 4 ♂♂ 3 ♀♀, Copala (GHVM); 1 ♀, Corte Alto (IEXA); 1 ♂ 3 ♀♀, El Zapotillo (IEXA); 1 ♀, Escuinapa (GHVM); 1 ♂ 1 ♀, Loberas (IEXA); 1 ♀, Mazatlán (GHVM); 2 ♀♀, 48 km N Mazatlán (IEXA). SONORA: 2 ♂♂ 1 ♀, 4 km S San Nicolás (IEXA). ZACATECAS: 2 ♂♂ 1 ♀, La Manchada (IEXA: 1 ♂; GHVM: 1 ♂ 1 ♀); 4 ♂♂ 3 ♀♀, San

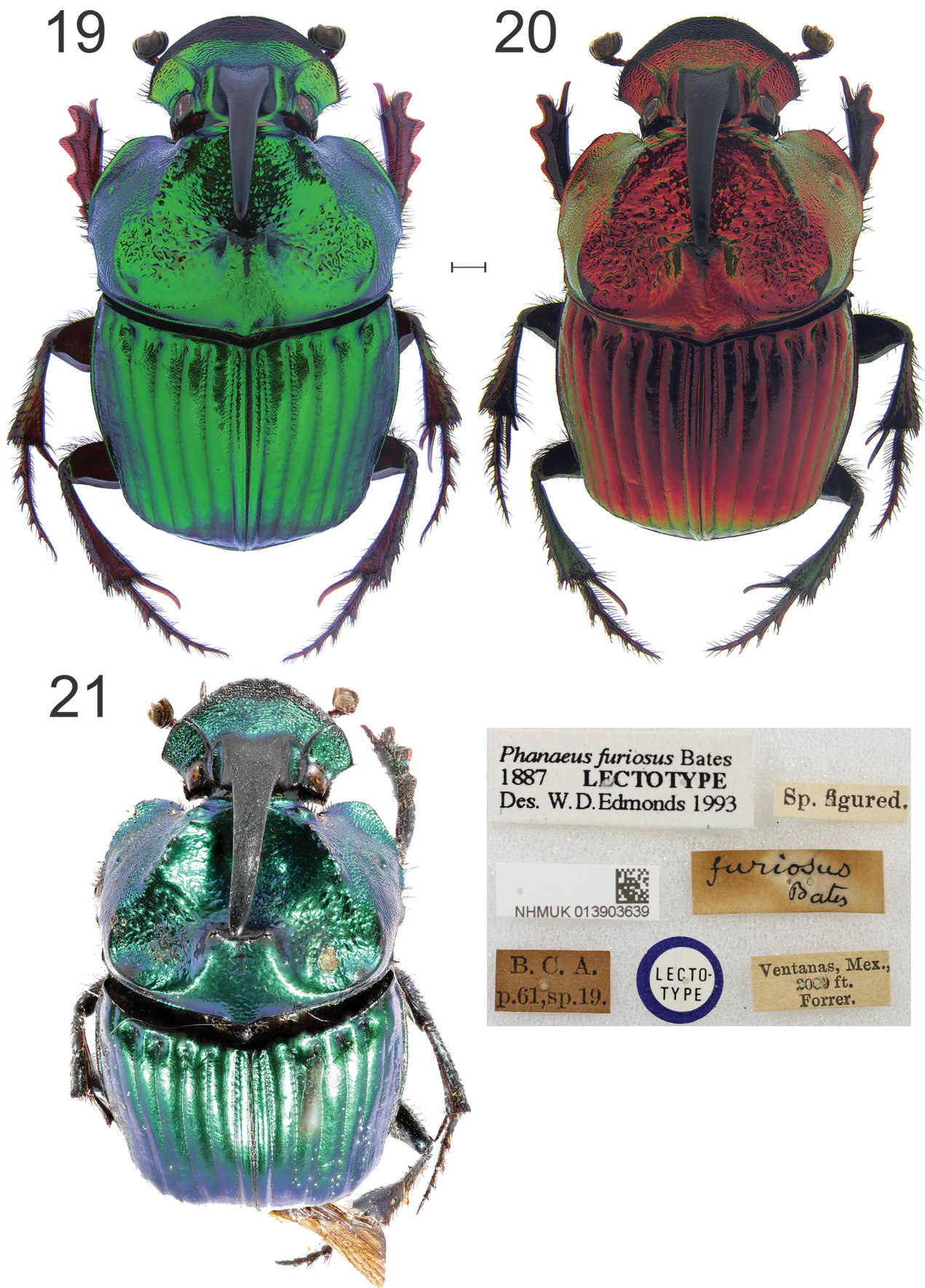
Lorenzo (GHVM); 5 ♂♂ 14 ♀♀, San Lorenzo de los Mota (GHVM). UNKNOWN LOCALITY: 1 ♂ (GHVM).

Diagnosis. Metallic green (Figs 19, 21), blue (Fig. 61) or red species (Fig. 20). Sides of pronotal disc granulate (Figs 19–21, 50). Pronotal disc rugose to lightly granulorugose (Figs 19–21, 50). Posteromedial process of pronotum produced into thick denticle, short and strongly emarginate apically (Figs 38, 50). Anteromedial portion of pronotal disc with variable number of denticles and tubercles (Fig. 50). Anterolateral margins of pronotal disc with strongly developed tubercles forming complete ridge (Fig. 50). Posterolateral angles of pronotum fairly short, much shorter than posteromedial process (Figs 38, 50). Elytral striae scabriculous, distinctly impressed, superficially punctate (Figs 19–21). Elytral interstriae scabriculous, smooth, superficially punctate, convex (Figs 19–21).

Variation. Minor male. Similar to major males, except for reduction of secondary sexual characters (i.e., cephalic horn, pronotal processes and posterolateral angles). **Female.** Similar to male, except for head showing trituberculate carina; pronotal sculpture granulate to rugose posteriorly; pronotum with anteromedial black macula, and anteromedial carina followed by posterior concavity (Fig. 61).

Three typical colour phases are showed by this species (namely *P. furiosus*, Figs 19–21, 50, 61), but it is frequent to found combinations between these colours. EDMONDS (1994) suggested that the colouration of *P. furiosus* varies geographically. According to him, the green phase (Figs 19, 21) is fixed in the majority of the populations from Sonora, Sinaloa, Nayarit, Jalisco, and Michoacán. On the other hand, the blue phase (Fig. 61) is scarce in Sonora, Sinaloa, Nayarit and western Jalisco; but it becomes common in northern Jalisco and Michoacán. The specimens revised in the present study do not support the geographic variation of colour proposed by EDMONDS (1994). The red chromatic phase (Fig. 20) is fairly common in Jalisco, Zacatecas and Nayarit, but it was omitted by him. Moreover, red (Fig. 20) and green specimens (Figs 19, 21) are found in similar proportions in the aforementioned Mexican states. Additionally, there are some populations of the Pacific slope of Mexico where the blue phase (Fig. 61) almost completely dominates. Nevertheless, it is important to highlight that a geographic cline for colour variation is not recognized nor proposed by us.

Comments. ARNAUD (2002) suggested that *P. furiosus* included two subspecies, the nominotypic one (Figs 19–21, 27, 38, 50, 61) and *P. furiosus pseudofurcosus* (Figs 22–23, 39, 51, 62). EDMONDS (1994) and EDMONDS & ZÍDEK (2012) treated *P. furiosus* as a monotypic species instead, regarding the populations that ARNAUD (2002) had classified in *P. furiosus pseudofurcosus* as an odd disjunct population of *P. tridens tridens*. But despite this classification, EDMONDS & ZÍDEK (2012) confusingly cited *P. pseudofurcosus* as a junior subjective synonym of *P. tridens* instead of *P. furiosus* (Figs 1–5, 32, 43, 55, 63); this was likely a lapse. Our conclusion, however, is that *P. pseudofurcosus* is neither a subspecies of *P. furiosus* nor a synonym of either *P. furiosus* or *P. tridens*, but a fully independent species (see comments below). *Phanaeus furiosus*, in turn, is indeed a



Figs 19–21. *Phanaeus furiosus* Bates, 1887. 19 – male green phase; 20 – male red phase; 21 – lectotype and labels (by Mario Cupello, UFPR). Scale bar = 1.0 mm.

monotypic species (i.e., a taxonomically “homogeneous” species that does not comprise different subspecies according to ZACHOS 2016) as suggested by EDMONDS (1994) and EDMONDS & ZÍDEK (2012). In spite of its several chromatic phases (Figs 19–21, 50, 61), *P. furiosus* is a fairly distinctive species that has the posteromedial process of pronotum in major males produced into a thick denticle, short and strongly emarginate apically (Figs 38, 50).

Distribution. Mexico: Durango, Guanajuato, northern to central Jalisco, Michoacán, Nayarit, Sinaloa, Sonora and Zacatecas. This is the most widely distributed species within the *P. tridens* species group (Fig. 66).

***Phanaeus pseudofurcosus* Balthasar, 1939 stat. rev.**

(Figs 22–23, 39, 51, 62)

Phanaeus pseudofurcosus Balthasar, 1939: 244. Type locality: Mexico, without specific locality.

Type material examined. MEXICO: HOLOTYPE: ♂ (originally designated by BALTHASAR 1939, examined from photographs; Fig. 23), without specific locality (NMPC: Mus. Nat. Pragae Inv. 26350).

Non-type material examined. MEXICO: COLIMA: 8 ♂♂ 11 ♀♀, Comala (IEXA). JALISCO: 3 ♀♀, Alista (IEXA); 1 ♀, Alista, Presa La Tierra (IEXA); 4 ♂♂ 2 ♀♀, Casimiro Castillo, El Tigre (IEXA); 2 ♂♂ 1 ♀, Casimiro Castillo, La Calera (IEXA); 2 ♂♂ 2 ♀♀, Casimiro Castillo, Rancho Piedra Bola (IEXA); 1 ♂ 1 ♀, Cerro de García, San Luis Soyotlán (VMPM), 1 ♀, El Corcovado (IEXA); 1 ♂ 3 ♀♀, La Manzanilla (GHVM); 2 ♂♂ 2 ♀♀, Sierra de Manantlán (IEXA).

Diagnosis. Always metallic bright green (Figs 22–23, 51, 62), occasionally with red sheen. Sides of pronotal disc granulate (Figs 22–23, 51). Pronotal disc coarsely granulorugose (Figs 22–23, 51). Posteromedial process of pronotum produced into narrowed denticle, short and distinctly emarginate apically (Figs 39, 51). Anteromedial portion of pronotal disc with two strongly developed denticles (Fig. 51). Anterolateral margins of pronotal disc with line of tubercles; tubercles separated, never forming complete ridge (Fig. 51). Posterolateral angles of pronotum much shorter than posteromedial process (Figs 39, 51). Elytral striae scabriculose, distinctly impressed, superficially punctate (Figs 22–23). Elytral



Figs 22–23. *Phanaeus pseudofurcosus* Balthasar, 1939, stat. rev. 22 – male green phase; 23 – holotype and labels (by Jiří Hájek, NMPC). Scale bar = 1.0 mm.

interstriae scabriculous, smooth, superficially punctate, convex (Figs 22–23).

Variability. *Minor male.* Similar to major males, except for reduction of secondary sexual characters (i.e., cephalic horn, pronotal processes and posterolateral angles). *Female.* Similar to male, except for head showing trituberculate carina; pronotal sculpture granulate to superficially punctate, smooth or rugose posteriorly; pronotum with anteromedial black macula, and anteromedial carina followed by posterior concavity. The metallic bright green chromatic phase is more common in this species, but specimens with a red sheen are frequent (Fig. 62).

Comments. EDMONDS (1994) erroneously applied the name *P. pseudofurcosus* (Figs 22–23, 39, 51, 62) to *P. balthasari* (Figs 8–9, 34, 45, 56), which he considered a subspecies of *P. tridens* (Figs 1–5, 32, 43, 55, 63). Populations actually belonging to *P. pseudofurcosus* were classified in *P. tridens tridens* by EDMONDS (1994). Later, ARNAUD (2001, 2002) corrected EDMONDS's (1994) mistake in regard to the application of the name *P. pseudofurcosus* and transferred the Coliman and southern Jalisco populations from *P. tridens tridens* to *P. furiosus* as the subspecies *P. furiosus pseudofurcosus*. A decade later, EDMONDS & ZÍDEK (2012) disagreed with Arnaud and returned those populations to *P. tridens*, now treated as a monotypic species (i.e., a taxonomically “homogeneous” species that does not comprise different subspecies according to ZACHOS 2016). Oddly, they said that *P. pseudofurcosus* was a junior subjective synonym of *P. furiosus*, not of *P. tridens*. This, as mentioned above, was likely a mistake and they meant to say that *P. pseudofurcosus* was a junior synonym of *P. tridens*.

Unlike previous authors, we conclude that *P. pseudofurcosus* – i.e., the southern Jalisco and Coliman populations treated in *P. tridens* by EDMONDS (1994) and EDMONDS & ZÍDEK (2012) and in *P. furiosus* by ARNAUD (2001, 2002) – deserves full species status. *Phanaeus pseudofurcosus* is endemic to the Pacific coast of Mexico along the western Trans-Mexican Volcanic Belt and the northern Sierra Madre del Sur in Colima and Jalisco (Fig. 66), while *P. tridens* is found in the Gulf of Mexico coast in northern Veracruz (Fig. 64). Among morphological differences, *P. pseudofurcosus* shows the posteromedial process of pronotum produced into a narrowed denticle, short and distinctly emarginate apically (Figs 39, 51; produced into a denticle, distinctly widened laterally, elongate and apically bifurcated in *P. tridens*, Figs 32, 43).

Differences from *P. furiosus* include the posteromedial process of pronotum of major males medially narrowed in *P. pseudofurcosus* (Figs 39, 51; distinctly thick and not narrowed in *P. furiosus*, Figs 38, 50) and the posterolateral angles of pronotum distinctly raised in *P. pseudofurcosus* (Fig. 39; posterolateral angles obsolete in *P. furiosus*, Fig. 38). The green chromatic phases of *P. pseudofurcosus* (Figs 22–23, 51, 62) and *P. furiosus* (Figs 19, 21, 50) are similar, but *P. pseudofurcosus* never shows a completely red (Fig. 20) or dark blue chromatic phase (Fig. 61) as *P. furiosus* does. Additionally, *P. pseudofurcosus* shows a green-red chromatic phase not seen in *P. furiosus*.

Distribution. Mexico: western Trans-Mexican Volcanic Belt, northern Sierra Madre del Sur, and the Pacific coast in Colima, Jalisco and Michoacán (Fig. 66).

Phanaeus nimrod Harold, 1863

(Figs 24–26, 40, 52, 60)

Phanaeus nimrod Harold, 1863: 167. Type locality: Mexico.

Phanaeus babori Balthasar, 1939: 246. Synonymy established by ARNAUD (1982b: 125) and confirmed here.

Type material examined. MEXICO: OAXACA: HOLOTYPE of *P. babori* (designated by monotypy by BALTHASAR 1939, examined from photographs; Fig. 26): ♂, Oaxaca (NMPC: Mus. Nat. Pragae Inv. 26352).

WITHOUT SPECIFIC LOCALITY: LECTOTYPE of *P. nimrod* (designated by ARNAUD 1982a, examined from photographs; Fig. 25): ♂, without specific locality (MNHN: MNHN EC10555). PARALECTOTYPES of *P. nimrod*: 1 ♂ 1 ♀ (examined from photographs), without specific locality (MNHN: MNHN EC10556, MNHN EC10557).

Non-type material examined. MEXICO: OAXACA: 1 ♂ 1 ♀, Ocotlán (GHVM); 6 ♂♂ 6 ♀♀, Santa Cruz Papalutla (JLSHVM); 3 ♂♂ 3 ♀♀; VMPM: 3 ♂♂ 3 ♀♀; 1 ♀, 2 km S Sola de Vega (IEXA).

Diagnosis. Metallic turquoise (Fig. 25), green-blue (Figs 26, 60), yellow-green, green-red (Fig. 24) or dark blue. Sides of pronotal disc finely granulate to finely granulorugose (Figs 24–26, 40, 52, 60). Pronotal disc smooth to superficially punctate anteriorly, sparsely roughened posteriorly (Figs 24–26, 52). Posteromedial process of pronotum produced into denticle, strongly widened laterally, not bifurcated apically (Figs 40, 52). Anteromedial portion of pronotal disc with two denticles, distinctly separate (Fig. 52). Anterolateral margins of pronotal disc with distinctly developed line of tubercles (Fig. 52). Posterolateral angles of pronotum much shorter than posteromedial process of pronotum (Figs 40, 52). Elytral striae scabriculous, distinctly impressed, superficially punctate (Figs 24–26). Elytral interstriae scabriculous, superficially punctate, convex (Figs 24–26).

Variability. *Minor male.* Similar to major male, except for reduction of secondary sexual characters (i.e. cephalic horn, pronotal processes and posterolateral angles). *Female.* Similar to male, except for head showing trituberculate carina; pronotal sculpture granulate, becoming smooth to superficially punctate posteriorly; pronotum with anteromedial black macula, and anteromedial carina followed by posterior concavity (Fig. 60). This species is highly variable in colour (Figs 24–26, 52, 60).

Comments. Apparently, this species is well defined and is not involved in taxonomical controversies. *Phanaeus nimrod* is typical of the Central Valleys of Oaxaca (Fig. 67), but DELOYA et al. (2014) reported it from an isolated locality in Guerrero (El Ocotito). The distribution of this species needs to be confirmed since doubtful records from the Pacific Coast of Oaxaca have been provided (EDMONDS 1994, 2003; DELOYA & MORÓN 1998). None of the specimens of the *P. tridens* species group revised in the present work from the Mexican Pacific coast belong to *P. nimrod*. The major male figured by DELOYA & COVARRUBIAS-MELGAR (2014) seems to be a green specimen of *P. nimrod*.

Distribution. Mexico: Central Oaxaca to central Guerrero (Fig. 67). Records from Guerrero and the Pacific coast of Oaxaca were omitted for the distribution model because they need confirmation.

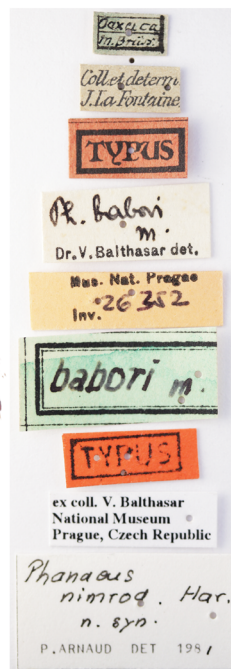
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25



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Figs 24–26. *Phanaeus nimrod* Harold, 1863. 24 – male green-red phase; 25 – lectotype and labels (by Christophe Rivier, MNHN); 26 – *P. babori* Balthasar, 1939, junior subjective synonymy, holotype and labels (by Jiří Hájek, NMPC). Scale bar = 1.0 mm.

***Phanaeus victoriae* Moctezuma sp. nov.**

(Figs 27–28, 41, 53)

Type material examined. MEXICO: OAXACA: HOLOTYPE (Fig. 27): ♂, Santa María Chimalapa, Benito Juárez, 860 m., 16°43'41.8"N, 94°9'17.5"W, 18-X-2017, V. Moctezuma leg. from coprotrap (IEXA). PARATYPES: 76 ♂♂ 63 ♀♀, same locality as the holotype, GHVM: 2 ♂♂ 1 ♀; IEXA: 15 ♂♂ 8 ♀♀; CEMT: 6 ♂♂ 6 ♀♀; CNMN: 1 ♂ 1 ♀; JLSHVM: 9 ♂♂ 5 ♀♀; NMPC: 2 ♂♂ 2 ♀♀; TAMU: 2 ♂♂ 2 ♀♀; UVGC: 1 ♂; VMPPM: 38 ♂♂ 38 ♀♀.

Diagnosis. Metallic bright red species with green-yellow sheen (Figs 27–28, 53). Sides of pronotal disc finely granulate to finely granulorugose (Figs 27–28, 53). Posteromedial process of pronotum produced into denticle, distinctly widened laterally, slightly bifurcated apically (Figs 41, 53). Anterolateral margins of pronotal disc with distinctly developed ridge of tubercles (Fig. 53). Posterolateral angles of pronotum shorter than posteromedial process of pronotum (Figs 41, 53). Elytral striae coarsely impressed and coarsely punctate. Elytral interstriae distinctly scabriculous (Figs 27–28).

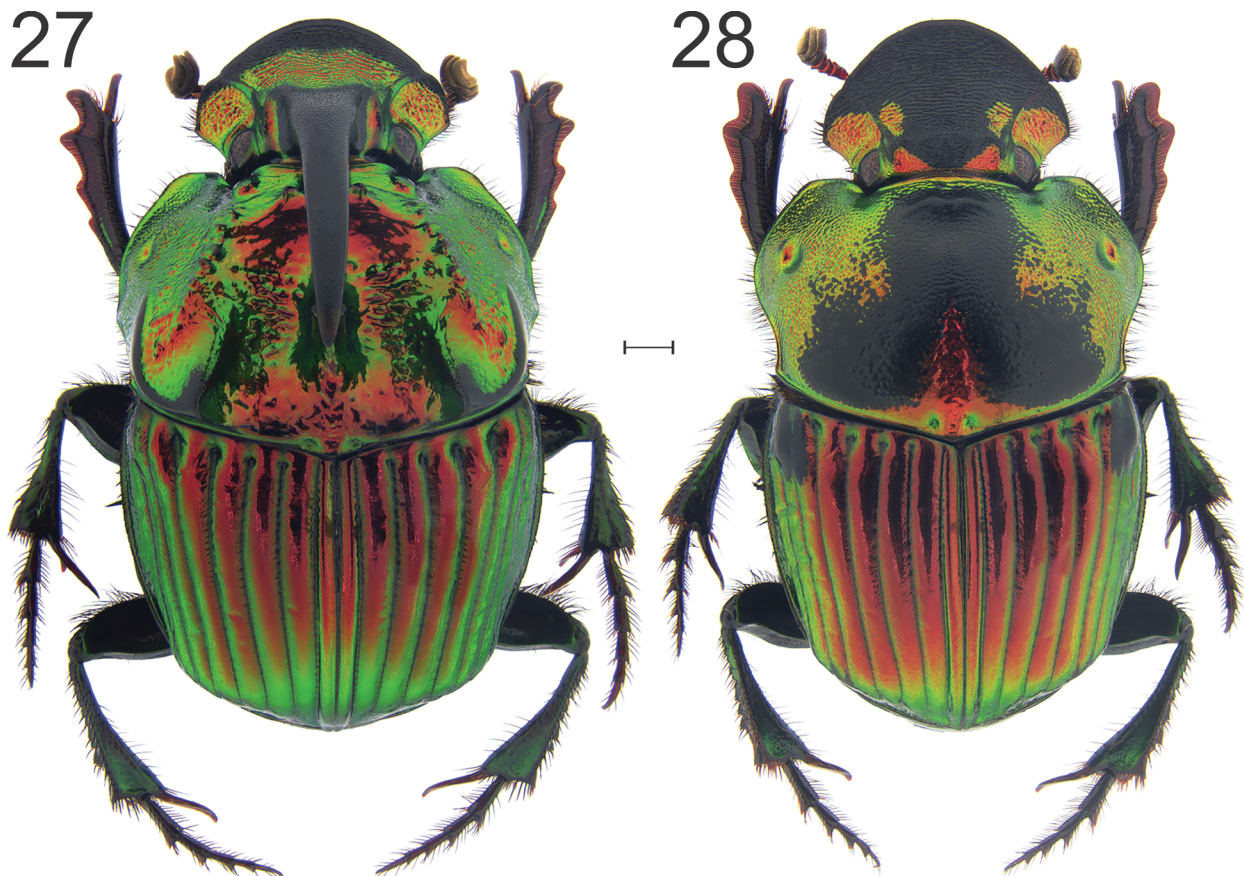
Description. *Major male* (holotype). Total length from apex of clypeus to tergite VIII: 17 mm. Metallic bright red with green-yellow sheen (Fig. 27). **Head.** Clypeus rounded dorsally, not spine-like laterally, black on anterior margin, with roughened sculpture (Fig. 27). Paraocular areas of parietals with roughened sculpture (Fig. 27). Cephalic horn black, curved posteriorly over pronotum (Fig. 27). **Pronotum.** Sides of pronotal disc finely granulate to finely granulorugose (Figs 27, 53).

Pronotal disc coarsely, sparsely rugose (Figs 27, 53). Posteromedial process of pronotum produced into denticle, distinctly widened laterally, slightly bifurcated apically (Figs 41, 53). Anteromedial portion of pronotal disc with two denticles, distinctly separate (Fig. 53). Anterolateral margins of pronotal disc with distinctly developed ridge of tubercles (Fig. 53). Posterolateral angles of pronotum shorter than posteromedial process (Figs 41, 53). Lateral and basal fossae distinctly impressed (Fig. 27). **Elytra.** Striae scabriculous, coarsely impressed, coarsely punctate (Fig. 27). Interstriae scabriculous, superficially punctate, convex (Fig. 27). **Protibiae.** Quadridentate, with apical spine (Fig. 27). **Tergite VIII.** Scabriculous sculpture, coarsely punctate with roughened punctures.

Variability. Total length from apex of clypeus to tergite VIII: 13–18 mm. This species is highly homogeneous in colour (Figs 27–28). *Minor male.* Similar to major male, except for reduction of secondary sexual characters (i.e., cephalic horn, pronotal processes and posterolateral angles). *Female.* Similar to male, except for head showing trituberculate carina; pronotal sculpture granulate, becoming smooth to superficially punctate posteriorly; pronotum with anteromedial black macula, and anteromedial carina followed by posterior concavity (Fig. 28).

Etymology. The first author is honored to dedicate this new species to his beloved daughter Victoria Peralta Vara.

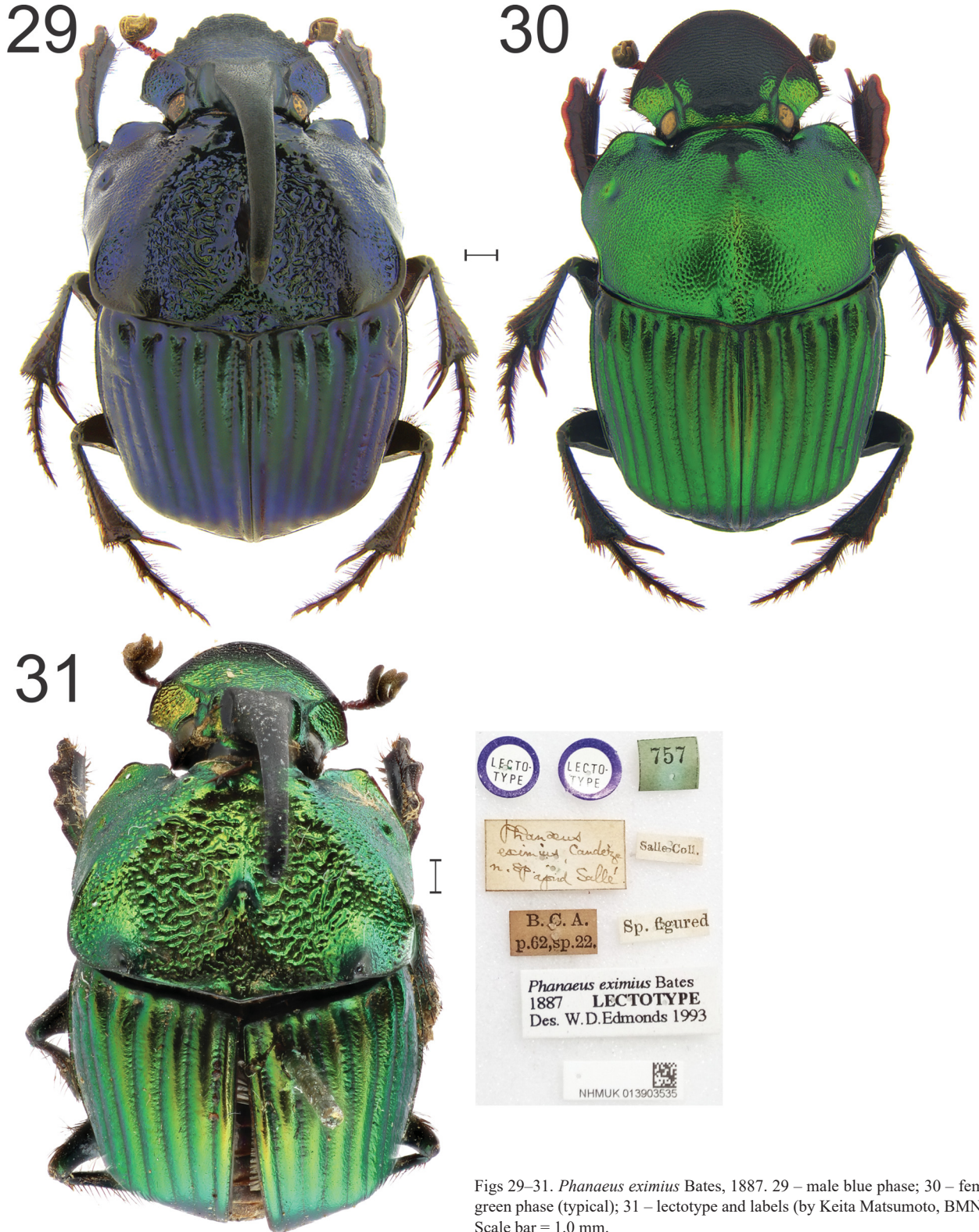
Comments. The pronotal morphology of this species (Figs 27–28, 41, 53) is similar to that of *P. nimrod* (Figs 24–26,



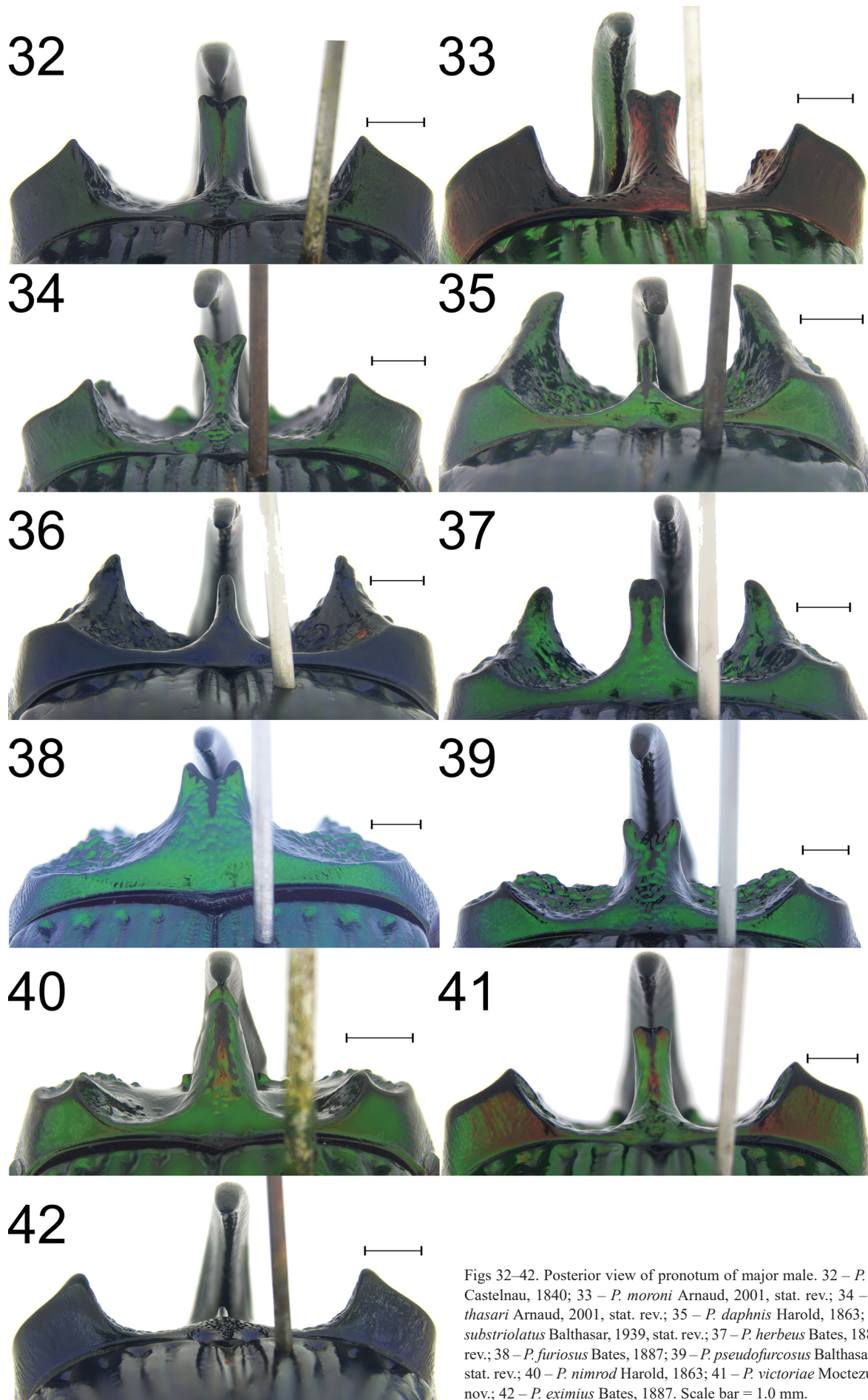
Figs 27–28. *Phanaeus victoriae* Moctezuma sp. nov. 27 – holotype male; 28 – paratype female. Scale bar = 1.0 mm.

40, 52, 60). Nevertheless, the posteromedial process of pronotum in major males of *P. victoriae* (Figs 41, 53) is distinctly triangular and slightly bifurcated apically (medially widened and not bifurcated apically in *P. nimrod*, Figs 40, 52). The elytral striae in *P. victoriae* (Figs 27–28) and *P. eximius* (Figs 29–31) are deeply impressed and the elytral interstriae strongly convex. Nevertheless, the elytral interstriae are never vermiculate in *P. victoriae* (Figs 27–28), and they are in *P. eximius* (Figs 29–31). The posterolateral

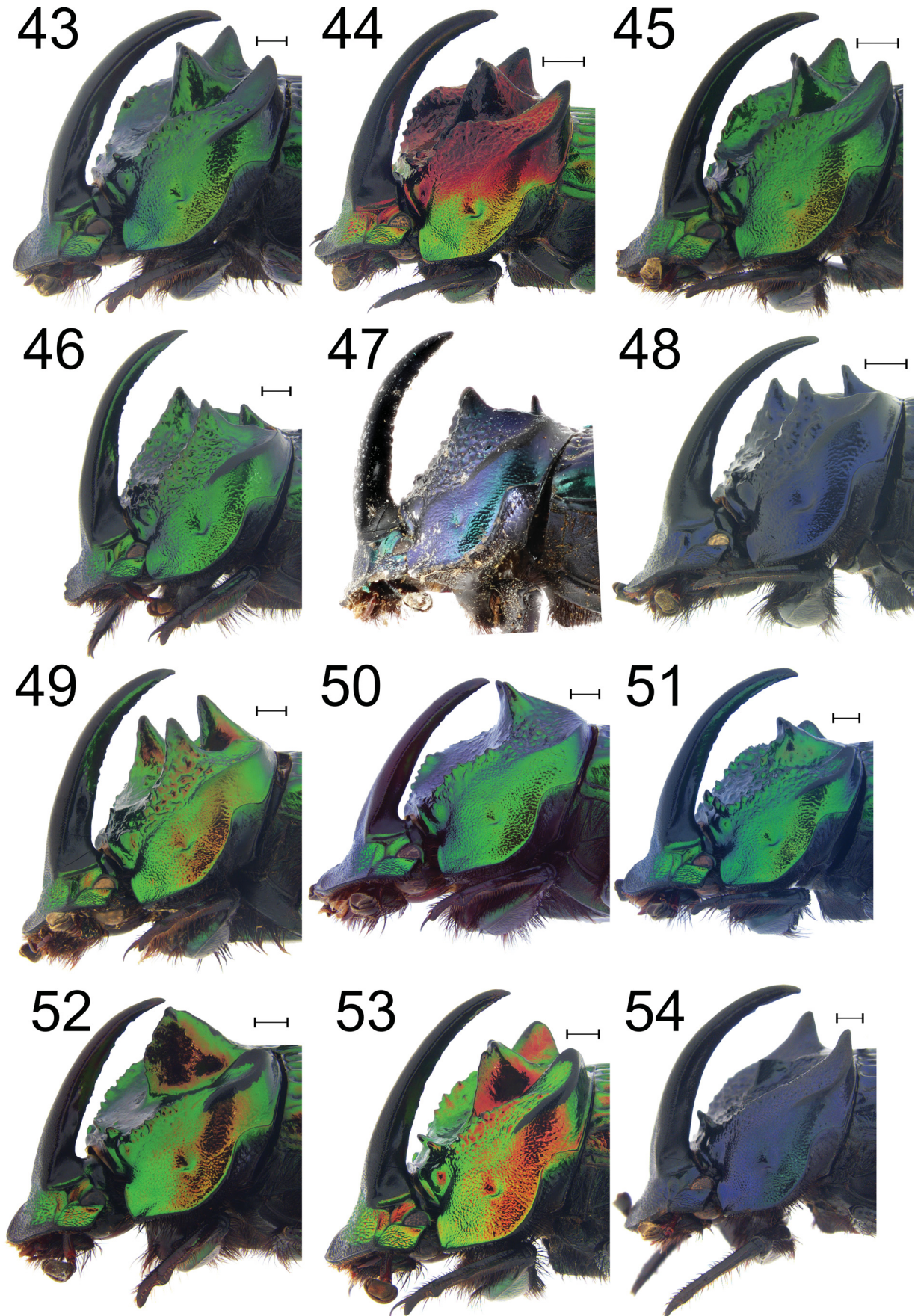
angles of pronotum are more rounded in *P. victoriae* (Figs 41, 53) than in *P. moroni* (Figs 33–44), while the pronotal disc of *P. victoriae* (Figs 27, 53) is never wine-garnet red to black, as it is in *P. moroni* (Figs 6–7, 44). *Phanaeus victoriae* is completely allopatric in relation to the remaining species within the *P. tridens* species group (Fig. 67). **Distribution.** Eastern Oaxaca, Mexico. This species probably shows the smallest range ($\approx 61 \text{ km}^2$) of the genus *Phanaeus* (Fig. 67).



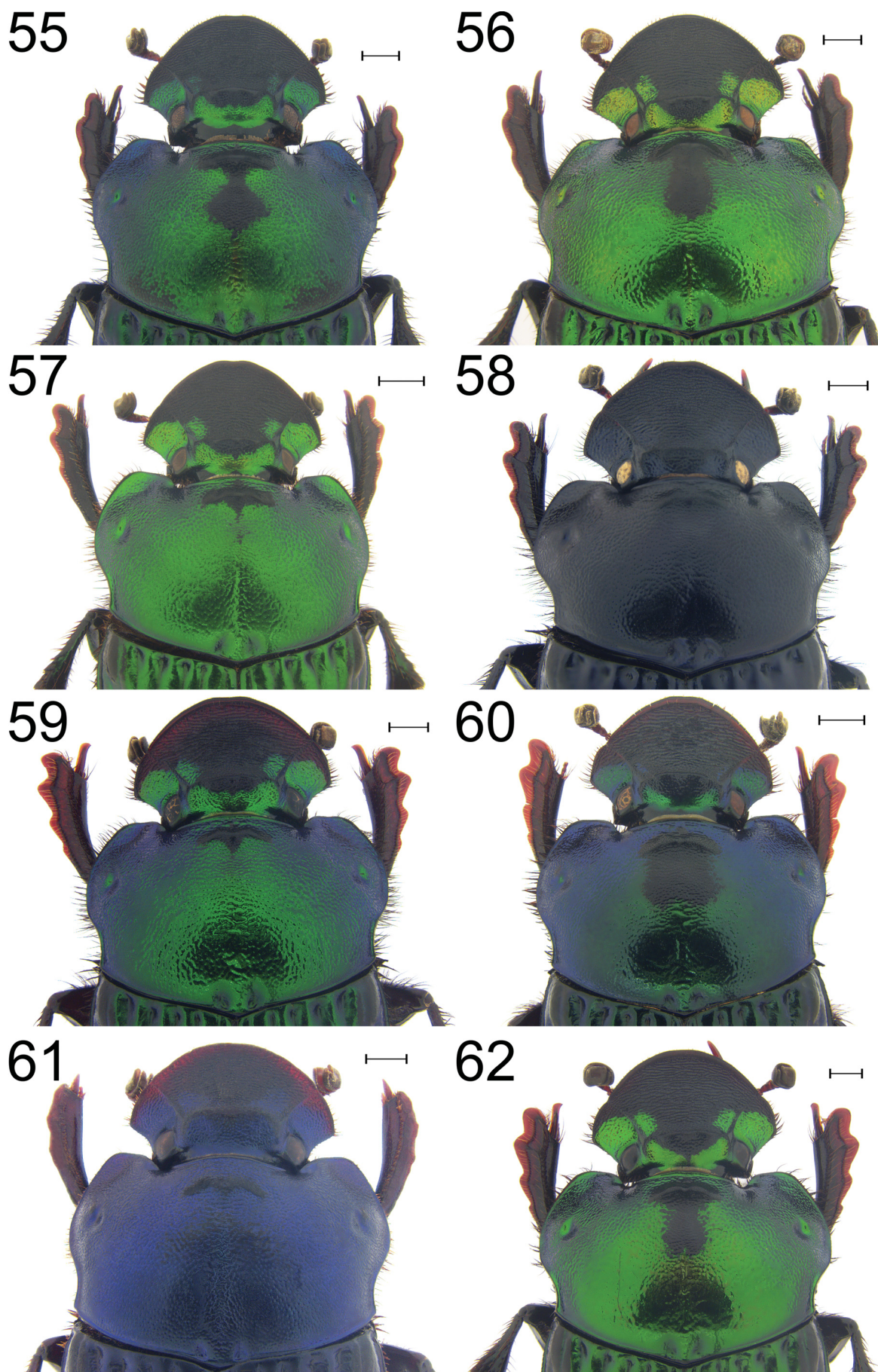
Figs 29–31. *Phanaeus eximius* Bates, 1887. 29 – male blue phase; 30 – female green phase (typical); 31 – lectotype and labels (by Keita Matsumoto, BMNH). Scale bar = 1.0 mm.



Figs 32–42. Posterior view of pronotum of major male. 32 – *P. tridens* Castelnau, 1840; 33 – *P. moroni* Arnaud, 2001, stat. rev.; 34 – *P. balthasari* Arnaud, 2001, stat. rev.; 35 – *P. daphnis* Harold, 1863; 36 – *P. substriolatus* Balthasar, 1939, stat. rev.; 37 – *P. herbeus* Bates, 1887, stat. rev.; 38 – *P. furiosus* Bates, 1887; 39 – *P. pseudofurcosus* Balthasar, 1939, stat. rev.; 40 – *P. nimrod* Harold, 1863; 41 – *P. victoriae* Moctezuma sp. nov.; 42 – *P. eximius* Bates, 1887. Scale bar = 1.0 mm.



Figs 43–54. Lateral view of pronotum of major male. 43 – *P. tridens* Castelnau, 1840; 44 – *P. moroni* Arnaud, 2001, stat. rev.; 45 – *P. balthasari* Arnaud, 2001; 46 – *P. daphnis* Harold, 1863; 47 – *P. coeruleus* Bates, 1887, stat. rev. (holotype, by Keita Matsumoto, BMNH); 48 – *P. substriolatus* Balthasar, 1939, stat. rev.; 49 – *P. herbeus* Bates, 1887, stat. rev. (green-red phase); 50 – *P. furiosus* Bates, 1887 (green phase); 51 – *P. pseudofurcosus* Balthasar, 1939, stat. rev.; 52 – *P. nimrod* Harold, 1863; 53 – *P. victoriae* Moctezuma sp. nov. (holotype); 54 – *P. eximius* Bates, 1887. Scale bar = 1.0 mm.



Figs 55–62. Pronotum of female. 55 – *P. tridens* Castelnau, 1840; 56 – *P. balthasari* Arnaud, 2001, stat. rev.; 57 – *P. daphnis* Harold, 1863; 58 – *P. substriolatus* Balthasar, 1939, stat. rev. (dark blue-black phase); 59 – *P. herbeus* Bates, 1887, stat. rev. (green phase); 60 – *P. nimrod* Harold, 1863 (blue-green phase); 61 – *P. furiosus* Bates, 1887 (dark blue phase); 62 – *P. pseudofurcosus* Balthasar, 1939, stat. rev. Scale bar = 1.0 mm.

***Phanaeus eximius* Bates, 1887**

(Figs 29–31, 42, 54)

Phanaeus eximius Bates, 1887: 62. Type locality: Guatemala.**Type material examined.** LECTOTYPE (designated by EDMONDS 1994, examined from photographs; Fig. 31): ♂, without specific locality (BMNH: NHMUK 013903535).**Non-type material examined.** GUATEMALA: WITHOUT SPECIFIC LOCALITY: 1 ♀ (GHVM). NICARAGUA: UNKNOWN LOCALITY: 1 ♂ (GHVM).

Diagnosis. Metallic green (Fig. 30–31), deep blue-green (Fig. 29), dark blue (Fig. 54), green-yellow or red. Sides of pronotal disc finely granulate (Figs 29, 31, 54). Pronotal disc coarsely granulorugose (Figs 29, 31, 54). Posteromedial process of pronotum produced into triangular denticle, widened laterally, not bifurcated apically (Figs 42, 54). Anteromedial portion of pronotal disc with two strongly developed denticles (Fig. 54). Anterolateral margins of pronotal disc with inconspicuous line of tubercles (Fig. 54). Posterolateral angles of pronotum more developed than posteromedial process (Figs 42, 54). Elytral striae scabriculous, coarsely impressed, coarsely punctate (Figs 29–31). Elytral interstriae highly vermiculate, superficially punctate, convex (Figs 29–31).

Variation. Minor male. Similar to major males, except for reduction of secondary sexual characters (i.e., cephalic horn, pronotal processes and posterolateral angles). **Female.** Similar to male, except for head showing trituberculate carina; pronotal sculpture granulate to superficially punctate, smooth or rugose posteriorly; pronotum with anteromedial black macula, and anteromedial carina followed by posterior concavity (Fig. 30).

Comments. Apparently, this species is well defined and is not involved in taxonomical controversies (EDMONDS 1994, ARNAUD 2002, EDMONDS & ZÍDEK 2012). The only variation that was reported by previous studies is its several chromatic phases (Figs 29–31, 54). All specimens here revised show the distinctly vermiculate elytral striae (Figs 29–31). Nevertheless, further studies are needed to understand the intraspecific variation in *P. eximius* since a limited number of specimens was available for our work.

Distribution. Guatemala, El Salvador, Nicaragua, Costa Rica and probably Honduras. Following *P. furiosus* (Fig. 66), this is the second most widely distributed species within the *P. tridens* species group (Fig. 68).

Male genitalia in the *P. tridens* species group

The genital structures of male specimens for all the species that belong to the *P. tridens* species group were dissected and compared. These structures were found to be taxonomically uninformative, because the morphology of the phallobase, parameres and endophallite copulatrix was relatively homogeneous in all the revised specimens (Fig. 63).

Results of species distribution modeling

Species distribution models. Although all the models were valid (CBI > 0.7), only four species have more than 20 occurrence points (Table 2), i.e., the minimum to produce

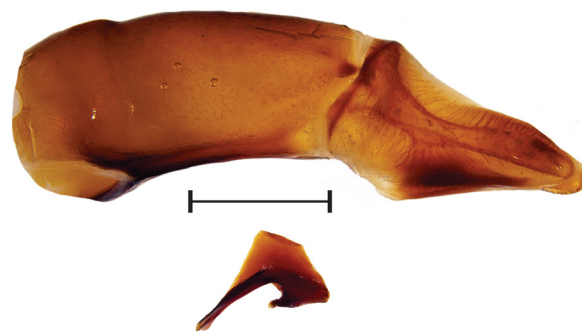


Fig. 63. Phallobase, parameres and endophallite copulatrix of the *P. tridens* species group. Scale bar = 1.0 mm.

Table 2. Number of single points used for modelling and model evaluation of the *P. tridens* species group's distribution models.

Species	Unique Points (training / testing)	Continuous Boyce Index (CBI)
<i>P. balthasari</i>	18 (13 / 5)	0.836
<i>P. substriolatus</i>	6 (4 / 2)	0.7
<i>P. daphnis</i>	37 (30 / 7)	0.876
<i>P. eximius</i>	16 (13 / 3)	0.909
<i>P. furiosus</i>	79 (63 / 16)	0.847
<i>P. herbeus</i>	8 (5 / 3)	0.909
<i>P. moroni</i>	6 (5 / 1)	0.972
<i>P. nimrod</i>	8 (5 / 3)	0.906

an optimal model. The distribution maps (Figs 64–68) show the predicted presence of each species, grouping those taxa that were previously considered conspecific on the same map. The distribution is clearly disjunct in all the species, except for *P. coeruleus*, *P. herbeus* and *P. daphnis*.

Niche overlap. Both indexes show little overlap between the niches of the species within the group (Fig. 69). The overlap is particularly accentuated between *P. daphnis* and *P. herbeus* (0.71), and *P. tridens* and *P. moroni* (0.51). The cluster graph does not group together the taxa previously recognized as subspecies, except for the *P. tridens-moroni-balthasari* cluster.

Differences in ecological niche. The decision tree model showed an accuracy of 84%. It was pruned using the complexity parameter of 0.03 to retain eleven leaf nodes (one per species; Fig. 70). The variable's order of importance is: Precipitation Seasonality (BIO 15), Isothermality (BIO 3), Precipitation of the Wettest Quarter (BIO 16), Diurnal Range (BIO 2), Precipitation of the Coldest Quarter (BIO 19), Precipitation of the Warmest Quarter (BIO 18), Temperature of the Warmest Quarter (BIO 10), and Precipitation of the Driest Month (BIO 14). The result is a tree with eleven nodes that split the *P. tridens* species group in two groups by the precipitation of the driest month:

1) Habitats with a marked dry season. The species with the most distinct habitat is *P. eximius* which is present in climates with low variation in temperature during the year. In turn, *P. nimrod* can be found where monthly precipitation changes largely during the year. It is noticeable that the former subspecies *P. substriolatus-daphnis-herbeus* and *P. furiosus-pseudofurcosus* were not clustered. Despite

having a large overlap, the niche of *P. daphnis* and *P. herbeus* differs in the precipitation seasonality. *Phanaeus daphnis* and *P. pseudofurcosus* are found where the precipitation seasonality is higher than 107, which means that the variance of the precipitation throughout the year exceeds the average precipitation. On the other hand, *P. furiosus* is found where the level of temperature variability is within an average month relative to the year.

2) Species living in places with more than 10 mm of rain in the driest month. This group includes the former subspecies *P. balthasari-moroni-tridens* and *P. victoriae*, which are present in climates with a wetter rainy season (more than 487 mm). Despite widely overlapping, the niches of *P. balthasari* and *P. tridens* can be separated by isothermality. Both species are found in climates with a drier winter than where *P. moroni* is found.

Key to the species of the *Phanaeus tridens* species group

- 1 Elytral interstriae flat (Figs 11–15). 2
 - Elytral interstriae distinctly convex (Figs 1–9, 16–17, 19–31). 4
- 2 Posteromedial process of pronotum produced into slender and elongate denticle (Figs 36, 48). Posteromedial process and posterolateral angles of pronotum conical, similar in size (Figs 36, 48). Elytral interstriae superficially impressed or partially erased (Figs 14–15). Southern Puebla to northern Oaxaca and central Guerrero (Fig. 65).
 - *P. substriolatus* Balthasar, 1939
 - Posteromedial process of pronotum produced into small denticle (Figs 35, 46–47). Posterolateral angles much longer than posteromedial process of pronotum (Figs 35, 46–47). Elytral interstriae distinctly impressed (Figs 10–13). 3
- 3 Metallic green, rarely deep-blue with green sheen (Figs 10–12). Elytral interstriae I, III, V, VI and VII frequently roughened (Figs 10–12). Estado de México, Guerrero, Morelos, Puebla, Oaxaca (Fig. 65).
 - *P. daphnis* Harold, 1863
 - Dark blue with metallic turquoise sheen (Fig. 13). Elytral interstriae I, III and V smooth; VI and VII lightly roughened (Figs 10–12). Puebla.
 - *P. coeruleus* Bates, 1887
- 4 Posteromedial process of pronotum strongly widened as triangular ridge, not bifurcated apically, much longer than posterolateral angles (Figs 40, 52). Clypeal process (viewed from front) narrow, acute, usually much longer than wide at base (Figs 24–26). Central Valleys of Oaxaca to central Guerrero (Fig. 67).
 - *P. nimrod* Harold, 1863
 - Posteromedial process of pronotum spine-like; triangular, not bifurcated apically, but shorter than posterolateral angles; or triangular, much longer than posterolateral angles but bifurcated apically (Figs 32–34, 37–39, 41–42, 43–45, 49–51, 53–54). Clypeal process variable, but almost always broader than long (Figs 1–9, 16–17, 19–23, 27–31). 5
- 5 Elytral striae coarsely impressed and coarsely punctate with transverse punctures irregular in size (Figs 27–31). 6
 - Elytral striae distinctly impressed and superficially punctate with almost effaced punctures (Figs 1–9, 16–17, 19–23). 7
- 6 Bright metallic red with green-yellow sheen (Figs 27–28, 53). Posterolateral angles of pronotum longer than posteromedial process (Figs 41, 53). Elytral interstriae distinctly scabriculous (Figs 27–28). Eastern Oaxaca and probably western Chiapas (Fig. 67).
 - *P. victoriae* Moctezuma **sp. nov.**
 - Metallic green, blue-green, dark blue, green-yellow, or red (Figs 29–31, 54). Posterolateral angles of pronotum shorter than posteromedial process of pronotum (Figs 42, 54). Elytral interstriae distinctly vermiculate (Figs 29–31). Guatemala to Costa Rica (Fig. 68). *P. eximius* Bates, 1887
- 7 Posteromedial process of pronotum produced into thick, short, projection emarginate apically (Figs 38–39, 50–51). Posterolateral portions of pronotum not sharply upturned nor produced into strong conical teeth (Figs 38–39, 50–51). 8
 - Posteromedial process of pronotum bifurcated apically, usually produced into elongate spine-like projection or triangular denticle (Figs 18, 32–34, 37). Posterolateral portions of pronotum sharply upturned or produced into slender, elongate, conical teeth (Figs 18, 32–34, 37). 9
- 8 Metallic green (Figs 19, 21, 50), dark blue (Fig. 61) or garnet-red (Fig. 20), occasionally green with bright red sheen. Pronotal disc strongly concave, rugose to granulorugose (Figs 19–21, 50). Anterolateral margins of pronotum with variable number of short tubercles; tubercles sometime carinate or rounded (Fig. 50). Posteromedial process of pronotum thick basally, strongly emarginate apically (Figs 38, 50). Central Jalisco to Sonora (Fig. 66). *P. furiosus* Bates, 1887
 - Metallic bright green (Figs 22–23), occasionally with red sheen (Fig. 51). Pronotal disc flat, coarsely granulorugose (Figs 22–23, 51). Anteromedial portion of pronotum with two strongly developed, conical denticles (Figs 51). Posteromedial process of pronotum narrowed basally, distinctly emarginate apically (Figs 39, 51). Colima, Pacific slope of Jalisco and Michoacán (Fig. 66). *P. pseudofurcosus* Balthasar, 1939
- 9 Posterolateral portions of pronotum produced into elongate, slender, conical denticles (Figs 18, 37, 49). Anterolateral margins of pronotum without ridge of tubercles (Figs 18, 49). Southern-central slope of the Trans-Mexican Volcanic Belt (Fig. 65).
 - *P. herbeus* Bates, 1887
 - Posterolateral portions of pronotum sharply upturned posteriorly (Figs 32–34, 43–45). Anterolateral margins of pronotum with strongly developed ridge of tubercles (Figs 43–45). Distribution variable (Fig. 64). 10
- 10 Multi-coloured pronotum, with sides bright metallic green-yellow, becoming bright red to wine garnet red

- medially (Figs 6–7, 44). Posteromedial process of pronotum produced into triangular denticle, strongly widened (reaching the anteromedial carina; Figs 33, 44). Los Tuxtlas region, Veracruz (Fig. 64).
 *P. moroni* Arnaud, 2001
- Green (Figs 1, 3–4, 8–9, 43, 55), occasionally with bright red (Fig. 2) or yellow sheen (Figs 45, 56). Posteromedial process of pronotum produced into triangular denticle, lightly widened (not reaching anteromedial carina; Figs 32, 34, 43, 45). 11
 - 11 Metallic green with blue (Figs 1, 3–4) or red sheen (Fig. 2). Anteromedial portion of pronotal disc with two flat, sharply upturned triangular tubercles, these tubercles occasionally joined by medial carina (Fig. 43). Posteromedial process of pronotum uniform (Figs 32). Northern to central Veracruz (Fig. 64).
 *P. tridens* Castelnau, 1840
 - Metallic green (Figs 8–9). Anteromedial portion of pronotal disc with two inconspicuous, rounded tubercles or two triangular tubercles never joined by medial carina (Fig. 45). Posteromedial process of pronotum distinctly narrowed medially (Figs 34). Mexico (Chiapas) and Guatemala (Huehuetenango) (Fig. 64). *P. balthasari* Arnaud, 2001

Discussion

The taxonomy of the *P. tridens* species group was reassessed herein. Several taxonomic issues were disentangled by comparing the external morphology, examining the primary types for most previously established specific names, and revisiting previous literature. Consequently, five names were resurrected from previous synonymy to be used as valid to denote well-defined species. Furthermore, a new species was discovered. Contrary to previous works that considered *P. balthasari*, *P. coeruleus*, *P. herbeus*, *P. moroni* and *P. pseudofurcosus* subspecies or chromatic phases (EDMONDS 1994, 2003; ARNAUD 2001, 2002; EDMONDS & ZÍDEK 2012), clear diagnostic features in the pronotal and elytral morphology were found for each of these species. The characters of the elytra are consistent in both males and females of the species group. Nevertheless, reliable pronotal characters to determine species were only found in major males, while females of the whole species group were found to be highly homogeneous in this part of the body. Additionally, the genital structures of males were highly homogeneous and are thus uninformative for alpha systematics.

Chromatic variation

Interestingly, intraspecific variation in body colour is high in a majority of the species of the *P. tridens* species group (e.g., *P. daphnis*, *P. eximius*, *P. furiosus*, *P. herbeus*, *P. nimrod* and *P. tridens*). Two or three chromatic phases are frequently found in these species, varying from blue, green, red to colour mixtures. This outstanding intraspecific chromatic variation within the species of the *P. tridens* species group is suggested herein to be the source of taxonomic mistakes and incorrect synonymies proposed

by previous works (EDMONDS 1994, EDMONDS & ZÍDEK 2012). Despite these chromatic similarities though, all the species are confidently diagnosed by their respective unique character combinations.

More studies are needed to understand the factors that drive the intraspecific chromatic variation within the *P. tridens* species group. All the chromatic phases were found in the whole distribution area of the species, and were even collected in similar frequencies at the same localities. These results disagree with EDMONDS (1994), who suggested the occurrence of intraspecific chromatic variation associated with geographic clines in some species of *Phanaeus*, such as *P. furiosus*. According to this author, green colouration was fixed in northern populations of *P. furiosus* while southern populations showed a dominance of blue, blue-green and dark green individuals. A similar north-to-south cline was proposed for *P. quadridens* with green northern populations, blue-green intermediate populations and dark blue-violet southern populations (EDMONDS 1994); while MOCTEZUMA et al. (2020) suggested that three different species were found in the aforementioned cline: *P. borealis* (green populations), *P. arnaudi* (blue-green populations), and *P. quadridens* (blue-violet populations).

External and genital morphology

As a consequence of the homogeneity of the integument sculpturing and the lack of distinctive protrusions, the pronotal morphology of females was found to be taxonomically uninformative. This result is consistent with previous studies that reported homogeneous morphology of females within the *P. tridens* species group (EDMONDS 1994, 2003; ARNAUD 2001, 2002; EDMONDS & ZÍDEK 2012). On the other hand, the pronotal morphology of major males was found to be highly variable between species, while little intrapopulation variation was observed (mostly attributed to abrasion). The pronotal horns and protrusions are homogeneous in the major males of the *P. tridens* species group. The pronotal and cephalic outgrowths are considered to be sexual weapons used for male-male combat in dung beetles, and their evolution is thought to be driven by sexual selection (EBERHARD 1979; EMLÉN 2000, 2008; EMLÉN et al. 2005; EMLÉN & PHILLIPS 2006; MOCZEK 2005, 2006). Consequently, the interspecific variation of pronotal horns and other sexually-dimorphic features may indicate sexual isolation between the species of the *P. tridens* species group since putative hybrid specimens were not found.

The genital structures of males (e.g., aedeagus, endophallite copulatrix) were found to be homogeneous in morphology between the species of the *P. tridens* species group. This is also the case of the species within the *P. amethystinus* (except for *P. genieri* Arnaud, 2001), *P. quadridens* and *P. vindex* species groups, whose phallobases, parameres and endophallites are uninformative for species delimitation (PRICE 2005, MOCTEZUMA et al. 2020). Furthermore, the endophallite copulatrix of these four species groups is highly similar in morphology (but never completely identical): the left lobe is distinctly aciculate while the right lobe is lobed.

The poor interspecific differentiation of the endophallites is not shared by the *P. endymion* species group, where the endophallites are highly differentiated between related species (MOCTEZUMA & HALFFTER 2021). Additionally, the morphology of the endophallites of the *P. endymion*, *P. hermes* and *P. splendidulus* species groups is not similar to that of the aforementioned *P. amethystinus*, *P. quadridens*, *P. tridens* and *P. vindex* species groups (PRICE 2005; MANJARRES-H. & MOLANO-R. 2015; TARASOV & GÉNIER 2015; MOCTEZUMA et al. 2017, 2019, 2020; MOCTEZUMA & HALFFTER 2021).

Morphological stasis

Since the shape of the endophallite copulatrix is similar in the related *P. amethystinus*, *P. quadridens*, *P. tridens*, and *P. vindex* species groups (PRICE 2005, 2007, 2009; GILLET & TOUSSAINT 2020; MOCTEZUMA et al. 2020), this may be interpreted as the putative ancestral character state of these four lineages. The last common ancestor of these species groups was hypothesized to have appeared during the middle Oligocene (GILLET & TOUSSAINT 2020), which may imply that the endophallite copulatrix may have been relatively constant in morphology for more than 25 Mya. The little differentiation in the endophallite copulatrix of distinct species groups of *Phanaeus* may represent a case of morphological stasis within the Scarabaeinae dung beetles.

Morphological stasis is observed in lineages that show little or no morphological change over relatively extended periods of time (FUTUYMA 2010, MEYER et al. 2019). This phenomenon has been widely found in the fossil record, while it is poorly integrated with neontological evidence (MEYER et al. 2019). The case presented herein for the genus *Phanaeus* implies adequate neontological evidence for morphological stasis, since morphological studies for extant taxa (PRICE 2005, MOCTEZUMA et al. 2020, MOCTEZUMA & HALFFTER 2021) and dated phylogenetic hypothesis (GILLET & TOUSSAINT 2020) are available. A similar case is that of the *Canthon cyanellus* species complex, where differentiation in the genital morphology of males occurred with little change during its speciation process (NOLASCO et al. 2020). Future studies on the genital morphology of the unrevised groups of *Phanaeus* and character state reconstructions are needed in order to confirm this hypothesis.

The morphological stasis of the endophallites in *Phanaeus* might be explained by a trade-off between the rapid evolution of pronotal horns, and the lack of differentiation in the endophallites. The development of horns is metabolically expensive and the occurrence of resource competition between horns and other secondary sexual structures has been reported (KLINGENBERG & NIJHOUT 1998, NIJHOUT & EMLÉN 1998, EMLÉN 2001, PIZZO et al. 2012, VALENCIA-MONTOYA et al. 2021), while the development of morphological traits is affected by trade-offs with horn investment (PIZZO et al. 2012). The trade-off in horn investment might be adequately exemplified by the *P. tridens* and the *P. endymion* species groups. On the one hand, the *P. tridens* species group shows diversification in pronotal horns while its endophallites are poorly differen-

tiated. On the other hand, the pronotum of the *P. endymion* species group is relatively homogeneous and does not show large pronotal protrusions, while its endophallites are highly differentiated interspecifically (MOCTEZUMA & HALFFTER 2021). Differentiation in the endophallites of the *P. endymion* species groups might indicate sexual isolation (MOCTEZUMA & HALFFTER 2021), but it would not be the case for the *P. tridens* species group. Sexual selection in species of the *P. tridens* species group would be expected to be driven by combats between males for female resource acting on cephalic-pronotal horns (EBERHARD 1979; EMLÉN 2000, 2008; EMLÉN et al. 2005; EMLÉN & PHILLIPS 2006; MOCZEK 2005, 2006; PRICE 2009).

Distribution and ecological niche

The differences in distribution and ecology of the species within the *P. tridens* species group have been overlooked due to the absence of accurate localities provided in former studies (ARNAUD 2002) and by previous synonymies (EDMONDS 1994, 2003; HALFFTER & ARELLANO 2002; ARELLANO et al. 2008, 2013; JIMÉNEZ-SÁNCHEZ et al. 2009; PRICE & MAY 2009; DÍAZ et al. 2010; EDMONDS & ZÍDEK 2012; MORÓN et al. 2013; DELOYA et al. 2016; LIZARDO et al. 2017; MOCTEZUMA & NOGUEIRA 2019; ZARAGOZA-CABALLERO et al. 2019; SALOMÃO et al. 2020; SÁNCHEZ-HERNÁNDEZ et al. 2020). In previous studies, the distribution models of the species *P. daphnis*, *P. furiosus*, and *P. tridens* as defined by EDMONDS & ZÍDEK (2012) showed low validation values, disjunct distributions and overlapped with a wide range of environmental conditions (LIZARDO et al. 2017). On the other hand, the species within the *P. tridens* species group have been suggested to be allopatric (EDMONDS 1994, 2003), and the results of the present study support this hypothesis because neither geographic nor the environmental distribution of the majority of the species overlap.

Our results suggest that the species within the *P. tridens* group have vicariant distributions mainly driven by environmental conditions. The models detect a clear separation between species distribution by environmental conditions changing according to geography (*P. furiosus*/*P. pseudo-furcosus* separated by the southern Jalisco's mountains, *P. tridens* only distributed in the east side of the Oriental Sierra Madre, or the Cuchumatanes mountains in Guatemala limiting *P. eximius* northern distribution). On the other hand, the distributions of *P. daphnis* and *P. herbeus* run along the Trans-Mexican Volcanic belt that is probably separating them. This suggests that the mountains may act as a biogeographic barrier between two related species and the distributions proposed herein are made under that assumption.

Southern Puebla needs to be more thoroughly sampled in order to determine if *P. daphnis* and *P. herbeus* co-occur. EDMONDS (1994, 2003) suggested that all the species of the *P. tridens* species group successfully exploit pastures. This assumption is confirmed herein and by previous literature (MONTES DE OCA & HALFFTER 1995; HORGAN 2001; HALFFTER & ARELLANO 2002; ARELLANO et al. 2008, 2013; DÍAZ et al. 2010; RAMÍREZ-PONCE et al. 2019; ALVARADO et al. 2020; SALOMÃO et al. 2020), except for *P. furiosus*

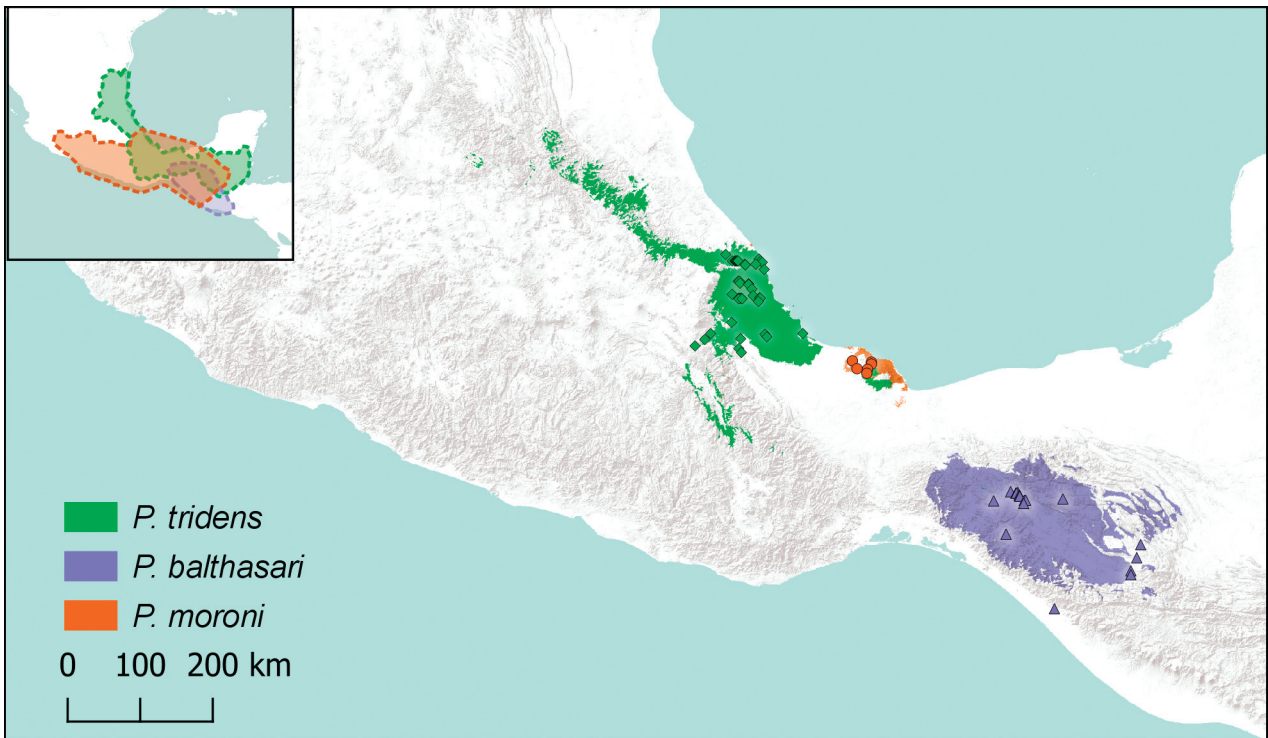


Fig. 64. Predicted distribution of *P. tridens* Castelnau, 1840, *P. moroni* Arnaud, 2001 and *P. balthasari* Arnaud, 2001. The distribution of *P. coeruleus* Bates, 1887 was not modelled because it is only known from a single locality that needs confirmation.

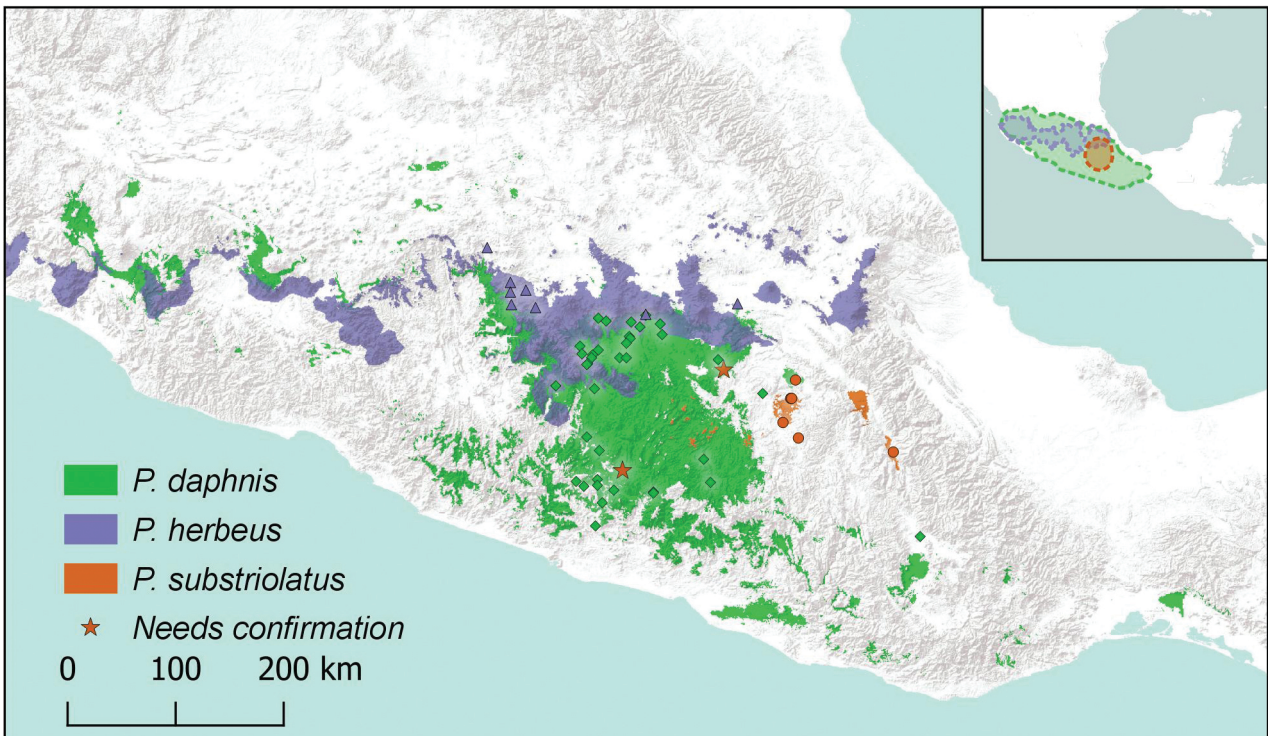


Fig. 65. Predicted distribution of *P. daphnis* Harold, 1863, *P. substriolatus* Balthasar, 1939 and *P. herbeus* Bates, 1887.

(and probably *P. pseudofurcosus*) that has been reported from tropical and subtropical dry forests and pine-oak forests (HERNÁNDEZ & NAVARRETE-HEREDIA 2018), and for *P. victoriae* which was mainly collected in temperate pine-oak forests.

Two areas of sympatry were detected between *P. daphnis* and *P. herbeus* (Morelos and probably Estado de México and Puebla), and *P. daphnis* and *P. nimrod* (central Oaxaca). The previously suggested area of sympatry between *P. daphnis* and *P. furiosus* (EDMONDS 1994, LIZARDO 2015,

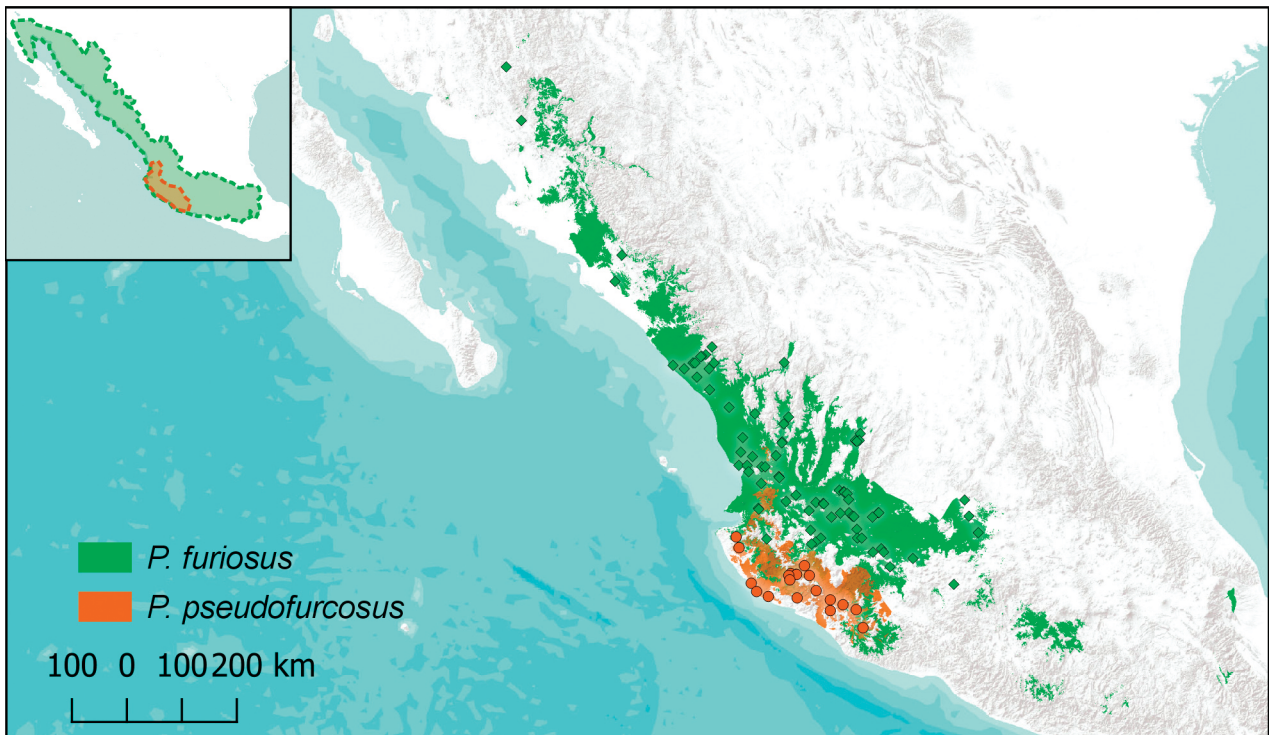


Fig. 66. Predicted distribution of *P. furiosus* Bates, 1887 and *P. pseudofurcosus* Balthasar, 1939.

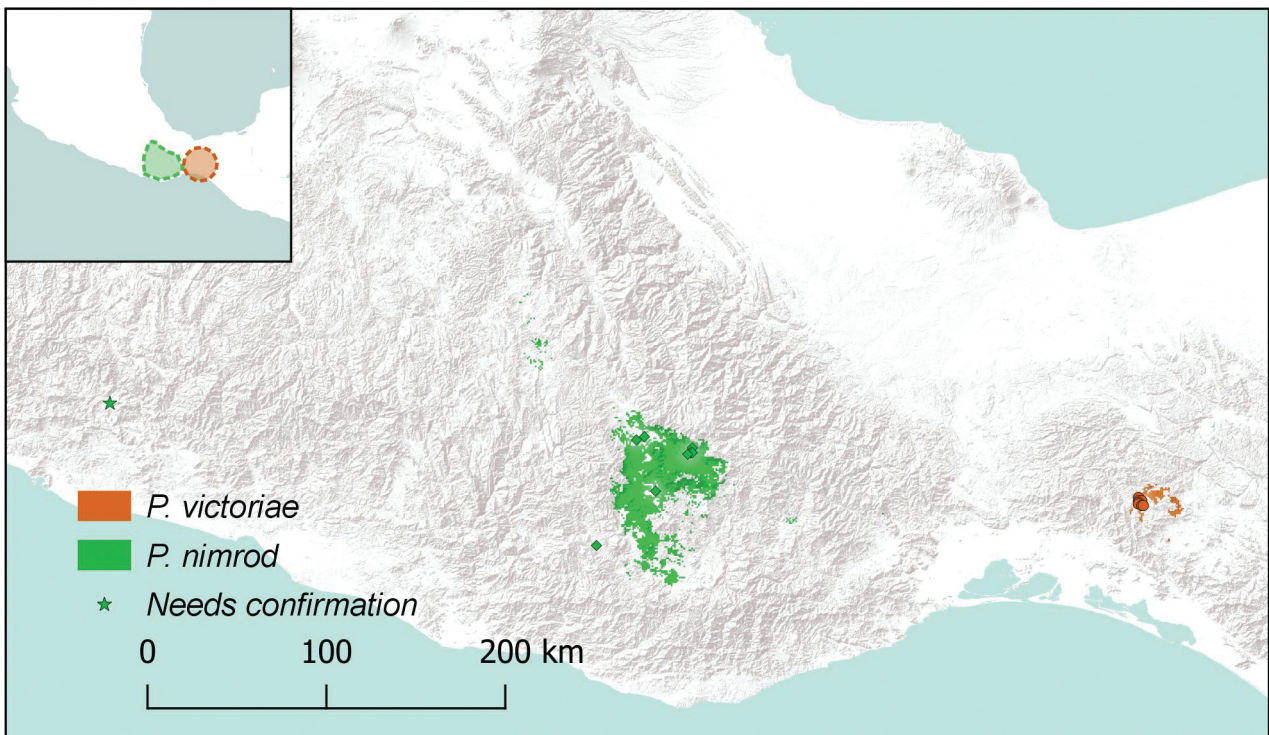


Fig. 67. Predicted distribution of *P. nimrod* Harold, 1863 and *P. victoriae* Moctezuma sp. nov.

LIZARDO et al. 2017) was not confirmed herein neither by the record points nor the distribution models. Southern Puebla and central Guerrero need to be more thoroughly sampled in order to determine if *P. coeruleus*, *P. daphnis*, *P. herbeus* and *P. substriolatus* co-occur.

Our results suggest that the species within the *P. tridens* species group do not share environmental niche characters.

Thus, these species are unlikely to occur sympatrically and their ecological niches do not overlap. This result may suggest that environmental niche differentiation occurs in association with speciation events (WARREN et al. 2008). However, the phylogenetic niche conservatism (PNC), defined as the notion that some biological process constrains niche divergence between closely related spe-

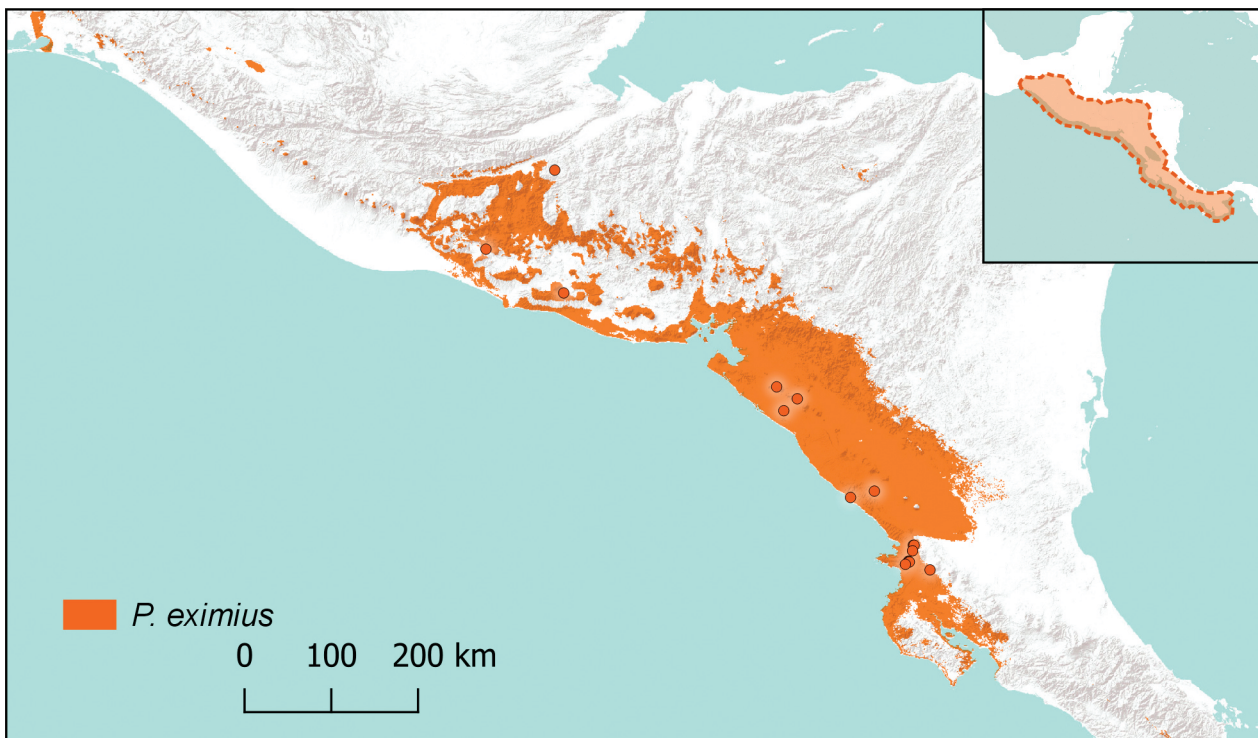


Fig. 68. Predicted distribution of *P. eximius* Bates, 1887.

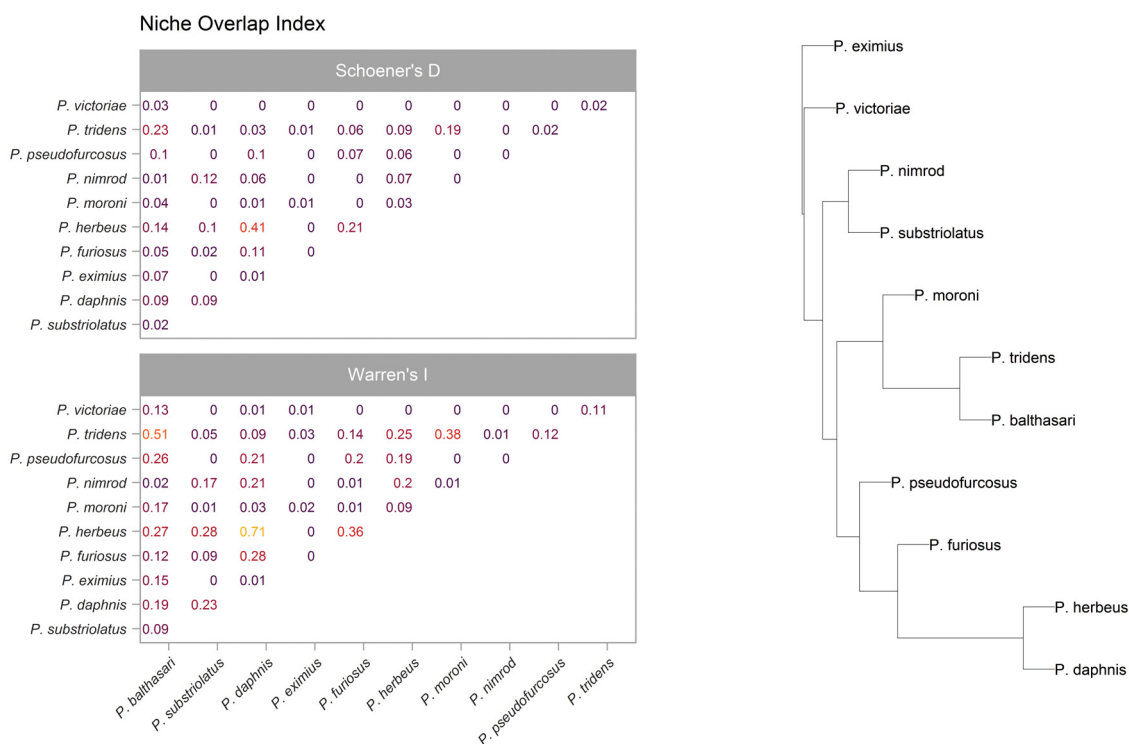


Fig. 69. Niche overlap of the *P. tridens* species group. Right: overlap pairwise comparison using two indexes (Warren's I and Schoener's D). Left: dendrogram result of the UPGMA analysis of the indexes.

cies (Losos 2008), may also be a plausible explanation. The PNC influences speciation in species that experience rapid ecological change while they are able to track favorable ecological niches and adapt locally (PYRON et al. 2024). This might be the case of the *P. tridens* species group. Although our measure of overlap is informative, we still need to test the significance of it by using Species

Identity test (WARREN 2008) and measure the overlap in environmental space (BROENNIMANN et al. 2012). Besides, a phylogenetic analysis of the *P. tridens* species group that quantifies rates and patterns of divergence with a larger species sampling is still needed. Available phylogenetic studies (PRICE 2007, 2009; GILLET & TOUSSAINT 2020) only included *P. furiosus*, *P. nimrod*, *P. eximius*, *P. tridens*,

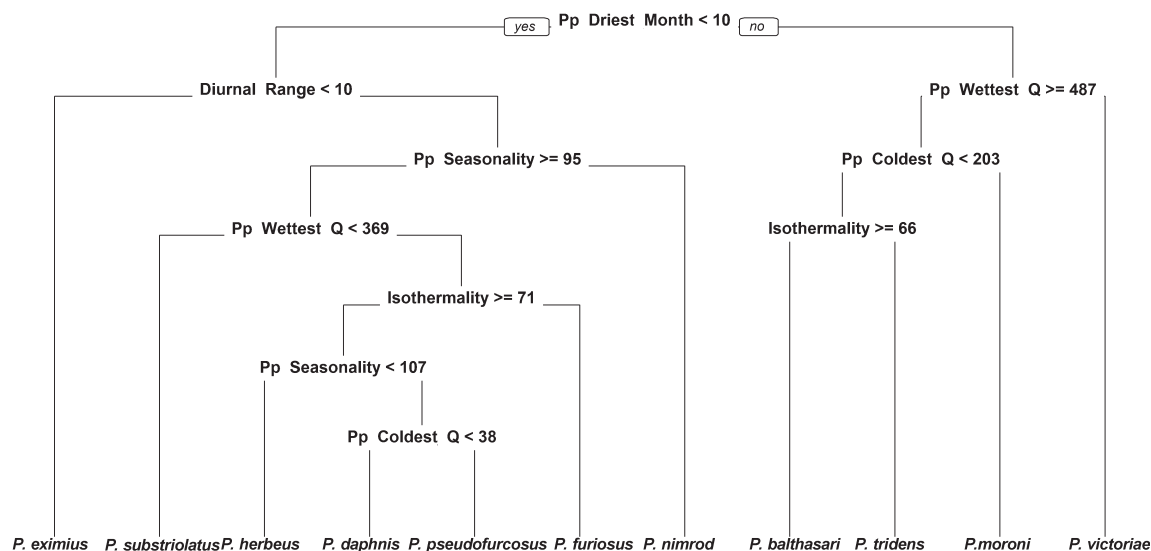


Fig. 70. Decision tree predictive model (accuracy = 84%) of the environmental variables that classify the distribution of the *P. tridens* species group.

and *P. daphnis*, while the taxonomic determination of the specimens of *P. furiosus*, *P. tridens* and *P. daphnis* used for these studies is doubtful.

In previous attempts to evaluate the environmental niche of *Phanaeus*, this species group proved to be awkward (LIZARDO 2015, LIZARDO et al. 2017). The environmental characteristics of the three previously recognized species in Mexico (*P. tridens*, *P. nimrod* and *P. furiosus*) overlapped widely, except for seasonality (temperature and precipitation), precipitation of the driest month, driest quarter, and coldest month. These variables matched with the variables used for our model. In the same study, the species were classified in three groups by the predominant vegetation type in their habitats: Humid Forests, Dry Forests and Temperate Mountains (LIZARDO 2015). The classification was problematic for *P. furiosus* and *P. daphnis*, that were classified in several vegetation types. Nevertheless, when the taxonomical changes presented herein are taken into account, the species are adequately classified in the following habitats: *P. balthasari*, *P. moroni* and *P. tridens* fit in the Humid Forests; *P. furiosus*, *P. substriolatus* and *P. herbeus* fit in the Temperate Mountains; *P. pseudofurcosus*, *P. daphnis*, *P. nimrod*, and *P. victoriae* fit in the Dry Forests.

Taxonomic classification

Two different taxonomical treatments have been proposed to classify *Phanaeus*: ARNAUD's (2002) and EDMONDS & ZÍDEK's (2012) hypotheses. The results presented herein are consistent with the findings presented by SOLÍS & KOHLMANN (2012), MOCTEZUMA & HALFFTER (2017, 2021), MOCTEZUMA et al. (2017, 2019, 2020), ARNAUD (2018), KOHLMANN et al. (2018) and EDMONDS & ZÍDEK's (2012), which altogether suggest that the species richness of *Phanaeus* is currently underestimated. ARNAUD's (2002) classification depicts more adequately the taxonomic diversity of *Phanaeus*, but particularly of the *P. tridens* species group. Nevertheless, this classification is not ac-

curate to define the differences between the subspecific and specific levels.

Particularly in the case of the *P. tridens* species group, we agree with the comments by EDMONDS & ZÍDEK (2012): "The *tridens* group is a difficult assemblage that we view in a simple context which undoubtedly belies the true extent of its taxonomic diversity, especially in reference to what we here refer to as *P. tridens* and *P. daphnis*". Moreover, EDMONDS & ZÍDEK (2012) recognized that *P. daphnis* as defined by them was highly variable and probably included several cryptic taxa. In this regard, three species were recognized by us within *P. tridens* and four species within *P. daphnis* as defined by EDMONDS & ZÍDEK (2012). In addition, EDMONDS (1994) previously recognized that the population from Colima included by him within *P. tridens* might pertain to a different taxon. This population is recognized by ARNAUD (2002) as *P. furiosus pseudofurcosus* and by us as *P. pseudofurcosus*.

The subspecies of the genus *Phanaeus* proposed by ARNAUD (2002) need to be revised by future studies in order to confirm if they deserve the full species status. The revision of the subspecies as proposed by ARNAUD (2002) may help to clarify the distribution areas for several taxa. At least *P. achilles* Boheman, 1858, *P. amethystinus* Harold, 1863, *P. chalconelas* (Perty, 1830), *P. guatemalensis* Harold, 1871, *P. igneus* MacLeay, 1819, *P. kirbyi* Vigors, 1825, *P. lecourti* Arnaud, 2000, *P. melampus* Harold, 1863, *P. meleagris* Blanchard, 1846, *P. prasinus* Harold, 1868 and *P. triangularis* Say, 1823, all polytypic species under ARNAUD (2002), need to be newly scrutinized by considering the revision of external and genital characters, their ecological requirements and their phylogenetic-phylogeographic relationships. The subspecies as proposed by ARNAUD (2002) are mainly based on chromatic variability. This source of variability (colour) is only reliable if it is supported by additional external and/or genital characters (MOCTEZUMA & HALFFTER 2017, 2021; MOCTEZUMA et al. 2017, 2019, 2020; ARNAUD 2018), and by molecular

markers (SOLÍS & KOHLMANN 2012). The delimitation of taxa within *Phanaeus* based solely on colour might be extremely difficult (EDMONDS 1994, EDMONDS & ZÍDEK 2012), as demonstrated on the case of the *P. tridens* species group in this work.

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