

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

Insecta Mundi

Center for Systematic Entomology, Gainesville,
Florida

2-3-2023

New synonyms and records of Costa Rican and Panamanian dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae)

Ángel Solís

Bert Kohlmann

Follow this and additional works at: <https://digitalcommons.unl.edu/insectamundi>



Part of the [Ecology and Evolutionary Biology Commons](#), and the [Entomology Commons](#)

This Article is brought to you for free and open access by the Center for Systematic Entomology, Gainesville, Florida at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Insecta Mundi by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

A journal of world insect systematics

INSECTA MUNDI

0972

New synonyms and records
of Costa Rican and Panamanian dung beetles
(Coleoptera: Scarabaeidae: Scarabaeinae)

Ángel Solís

BioAlfa Barcoding Project
Santo Domingo de Heredia, Costa Rica

Bert Kohlmann

BioAlfa Barcoding Project
Santo Domingo de Heredia, Costa Rica

Date of issue: February 3, 2023

Center for Systematic Entomology, Inc., Gainesville, FL

Solís A, Kohlmann B. 2023. New synonyms and records of Costa Rican and Panamanian dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *Insecta Mundi* 0972: 1–21.

Published on February 3, 2023 by
Center for Systematic Entomology, Inc.
P.O. Box 141874
Gainesville, FL 32614-1874 USA
<http://centerforsystematicentomology.org/>

INSECTA MUNDI is a journal primarily devoted to insect systematics, but articles can be published on any non-marine arthropod. Topics considered for publication include systematics, taxonomy, nomenclature, checklists, faunal works, and natural history. *Insecta Mundi* will not consider works in the applied sciences (i.e. medical entomology, pest control research, etc.), and no longer publishes book reviews or editorials. *Insecta Mundi* publishes original research or discoveries in an inexpensive and timely manner, distributing them free via open access on the internet on the date of publication.

Insecta Mundi is referenced or abstracted by several sources, including the Zoological Record and CAB Abstracts. *Insecta Mundi* is published irregularly throughout the year, with completed manuscripts assigned an individual number. Manuscripts must be peer reviewed prior to submission, after which they are reviewed by the editorial board to ensure quality. One author of each submitted manuscript must be a current member of the Center for Systematic Entomology.

Guidelines and requirements for the preparation of manuscripts are available on the *Insecta Mundi* website at <http://centerforsystematicentomology.org/insectamundi/>

Chief Editor: David Plotkin, insectamundi@gmail.com
Assistant Editor: Paul E. Skelley, insectamundi@gmail.com
Layout Editor: Robert G. Forsyth
Editorial Board: Davide Dal Pos, Oliver Keller, M. J. Paulsen
Founding Editors: Ross H. Arnett, Jr., J. H. Frank, Virendra Gupta, John B. Heppner, Lionel A. Stange, Michael C. Thomas, Robert E. Woodruff
Review Editors: Listed on the *Insecta Mundi* webpage

Printed copies (ISSN 0749-6737) annually deposited in libraries

Florida Department of Agriculture and Consumer Services, Gainesville, FL, USA
The Natural History Museum, London, UK
National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
Zoological Institute of Russian Academy of Sciences, Saint-Petersburg, Russia

Electronic copies (Online ISSN 1942-1354) in PDF format

Archived digitally by Portico
Florida Virtual Campus: <http://purl.fcla.edu/fcla/insectamundi>
University of Nebraska-Lincoln, Digital Commons: <http://digitalcommons.unl.edu/insectamundi/>
Goethe-Universität, Frankfurt am Main: <http://nbn-resolving.de/urn/resolver.pl?urn:nbn:de:hebis:30:3-135240>

Copyright held by the author(s). This is an open access article distributed under the terms of the Creative Commons, Attribution Non-Commercial License, which permits unrestricted non-commercial use, distribution, and reproduction in any medium, provided the original author(s) and source are credited. <http://creativecommons.org/licenses/by-nc/3.0/>

New synonyms and records of Costa Rican and Panamanian dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae)

Ángel Solís

BioAlfa Barcoding Project
Santo Domingo de Heredia, Costa Rica
angelsoliscr@gmail.com

Bert Kohlmann

BioAlfa Barcoding Project
Santo Domingo de Heredia, Costa Rica
bkohlmann64@gmail.com

Abstract. To better understand the dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae) biodiversity of Costa Rica and Panama, new synonyms, records, distributions, and updates are presented. This paper analyzes the distribution and taxonomy of *Phanaeus olsoufieffi* Balthasar, 1939 in Panama and establishes the following **new subjective synonym**: *Phanaeus panamensis* Moctezuma and Halffter, 2021 = *Phanaeus olsoufieffi* Balthasar, 1939. Color morphs of *Phanaeus pyrois* Bates, 1887 in Costa Rica are analyzed. The Costa Rican distribution of *Onthophagus bidentatus* Drapiez, 1819 and *O. marginicollis* Harold, 1880 is studied. *Onthophagus bidentatus* is recorded for Costa Rica for the first time. A population analysis of barcode mtDNA, color morphs, and morphological and genitalia characters for different body sizes of *Onthophagus cyanellus* is undertaken. An mtDNA barcode tree is presented to assess the molecular identity of *O. cyanellus* resulting in the **reaffirmed subjective synonymy**, *Onthophagus mesoamericanus* Zunino and Halffter, 1988 = *O. cyanellus* Bates, 1887.

Key words. Allometry, barcoding, color-morph variation, lamella copulatrix, male horns, morphological variation, mtDNA barcode analysis, polymorphism.

ZooBank registration. urn:lsid:zoobank.org:pub:E701D60F-A455-4048-8279-DA450930ACB3

“If names are not correct, language will not be in accordance with the truth of things.”
— Confucius

Introduction

The dung beetle fauna (Coleoptera: Scarabaeidae: Scarabaeinae) of Costa Rica and Panama has been studied intensively for the past 32 years. To update our understanding of the biodiversity of the Costa Rican and Panamanian dung beetle fauna, we are here establishing new synonyms and reporting new species records. The last dung beetle (Scarabaeinae) species count for Costa Rica was done in 2012 (Solís and Kohlmann 2012), with 182 known species. This paper increases the count to 185 known species. To update this growing list of species, we are here amending the list of synonyms and presenting new distribution records for Costa Rica. We use a combination of mtDNA barcode analysis as well as morphology, ecology, and microgeography to study *Onthophagus cyanellus* in detail and determine its synonyms.

Materials and Methods

Specimens used in this work are deposited in the following collections:

ASC Ángel Solís Collection, Zarcero, Alajuela, Costa Rica
MIUP Museo de Invertebrados, Universidad de Panamá

MNCR Museo Nacional de Costa Rica, Santo Domingo de Heredia, Costa Rica
TAMUIC Texas A&M University Insect Collection

The length of specimens was measured from the anterior margin of the clypeus to the pygidial disc in the closed position. Widths were measured at either the pronotum or the elytra at the widest point. We use in this study the developmental body terms hyper-, eu-, and hypothelic in the same sense as were used by Zunino and Halffter (1988) and not the more common “major”, “minor”, and “minim” descriptors to facilitate comparisons with Zunino and Halffter’s (1988) study. A clear example of these conditions is presented in Figure 27–29.

Dry specimens were hydrated and cleaned by immersing them in hot water. Male genitalia were extracted following the method described by Zunino (1978). Specimens were hand-cleaned with brushes for photographs.

Onthophagus photographs were prepared using an Olympus DP74 camera, an Olympus SZX16 stereomicroscope, and the Picolay stacking program. *Phanaeus* MacLeay, 1819 photographs were prepared using a Leica EZ 4 W stereoscope with an attached Leica ICC 50 W Wi-Fi-capable digital camera using the Leica Microsystems Flexacam C1 photographic program. Photographs were stacked using the Helicon focus program.

Species voucher codes and genetic sequences beginning with AS, CNC, and INB are from the BOLD database (<http://www.boldsystems.org>). They represent databases generated by the following institutions. AS, Ángel Solís; CNC, Canadian National Collection of Insects, Ottawa; INB, Instituto Nacional de Biodiversidad, Costa Rica. Information derived from the AS database is here used for the first time.

A mitochondrial DNA barcoding analysis of a 658 base-pair region of the cytochrome c oxidase I (COI) gene has been underway for all Costa Rican Scarabaeinae species (Solís and Kohlmann 2012; Kohlmann et al. 2019). Molecular work was carried out using the protocols established by Ivanova et al. (2006). Extracted DNA was amplified for a 658-bp region near the 5' terminus of the cytochrome c oxidase subunit I (COI) gene using standard insect primers LepF1 and LepR1 (Ivanova and Grainger 2007).

This standardized 658-bp fragment of the mitochondrial cytochrome c oxidase subunit I gene (cox1 or COI) has been proposed as a universal marker for species identification in the animal kingdom (Hebert et al. 2003). We have used the BOLD taxonomic platform (Barcode of Life Data Systems database; <http://www.boldsystems.org/>). The importance of using this sequence is that COI is one of the building blocks of the cytochrome C oxidase protein (COX). “COX is the last enzyme in the electron transport chain, reducing oxygen and pumping protons across the inner mitochondrial membrane. Thus, changes in the amino acid sequence that modify the protein structure may affect energy metabolism” (Pentinsaari et al. 2016: 1). This barcode sequence is predominantly under purifying selection for Coleoptera (Pentinsaari et al. 2016).

Price (2009) confirmed that COI data are a good source for resolving phylogenetic questions in the genus *Phanaeus* (Coleoptera: Scarabaeidae). Solís and Kohlmann (2012) and Kohlmann et al. (2019) used this same gene to analyze the Phanaeini and the dicranium species group of Costa Rican *Onthophagus*. The COI gene forms the primary barcode sequence for members of the animal kingdom (Ratnasingham and Hebert 2007); more than 95% of species in test assemblages of various animal groups have been shown to possess distinctive COI sequences (Hebert et al. 2003, 2004; Ward et al. 2005; Hajibabei et al. 2006). Cases of incomplete resolution involve closely allied species (Ratnasingham and Hebert 2007). Although barcoding analyses are not phylogenetic analyses, mitochondrial DNA (mtDNA) has been widely employed in phylogenetic studies because it evolves much more rapidly than nuclear DNA, thus accumulating differences between closely related species (Mindell et al. 1997). Hill (2017) has proposed that mitochondrial genotype and the COI DNA barcode gap should be viewed as reasonable approximations of actual species boundaries as it represents the best current method for diagnosing species.

Interestingly, mtDNA barcoding (COI) is not always diagnostic (Sharkey et al. 2021). Sharkey et al. (2021) indicate that in several cases where Braconidae (Kang et al. 2017) have been studied, the conventional threshold of 2% COI divergence used to separate species (Jones et al. 2011) is not achieved, and still, braconid specimens have a distinct morphology and host data. A similar situation was observed with Lepidoptera (Janzen et al. 2011), where six skipper butterfly species were quickly separated by caterpillar coloration, food plant, and ecology had less than a 2% difference in their barcodes. Therefore, relying solely on COI barcode sequences will overlook cryptic species that cannot be separated as adult specimens in a conventional key (Janzen et al. 2011).

The tree was generated using the BOLD System and employing the sequences of *Onthophagus* specimens from various barcoding projects to which we have access. Nucleotide sequences used for the generation of the tree correspond to 115 records of specimens identified in the BOLD System as *Onthophagus* and from which 50 sequences of more than 650 bases were obtained. The tree was generated by the Bold System using the “Taxon ID Tree” tool under the sequence analysis panel on the “Project Console” and “Record List” pages. In the Bold System, the Taxon ID Tree functionality allows tree generation from selected sequences using the neighbor-joining algorithm. For the generation of the trees (Fig. 26, 40), the Multipage Classic Tree type and Kimura 2 parameter distance model options were selected (K2P is a nucleotide substitution model for estimating genetic differences, distinguishing between transition and transversion rates, while assuming that the four nucleotide frequencies are the same and that rates of substitution do not vary among sites, Kimura 1980). The K2P Model is the best metric available when measured distances are low (Nei and Kumar 2000). Trees are built using the Neighbor-Joining Tree Building Method (a popular method for finding the balanced minimum evolution, Saitou and Nei 1987) and the COI-5P marker. Sharkey et al. (2021) found that NJ trees help identify sister species, closest neighbors, and species complexes. BOLD aligns sequences using a Hidden Markov Model profile of the COI protein (Ratnasingham and Hebert 2007). The generated trees (Fig. 26, 40) were edited using Photoshop to simplify it to just one specimen when the terminal branch showed multiple specimens.

Janzen and Hallwachs (2016) suggest that DNA barcoding, combined with morphology, ecology, microgeography, and behavior has transformed Victorian methodologies and species-level taxonomy. Sharkey et al. (2021) believe that DNA barcoding produces a more integrative taxonomic approach, solving problems of incorrectly lumped species, discovering, and defining species-complexes, and signaling trivial morphological variation used to define species boundaries. We agree with the concepts and points presented by Sharkey et al. (2021) and strongly recommend an integrative approach followed in taxonomic studies as much as possible.

Results

Phanaeus (Notiophanaeus) olsoufieffi Balthasar, 1939

Phanaeus blanchardi Olsoufieff 1924: 92 (not *P. blanchardi* Harold 1871: 114).

Phanaeus olsoufieffi Balthasar 1939: 242.

Phanaeus bothrus Blackwelder 1944: 209.

Phanaeus panamensis Moctezuma and Halffter 2021: 36. **New subjective synonym.**

Moctezuma and Halffter's (2021) work on the endymion group of *Phanaeus* includes the description of a new species from Costa Rica and Panama, *Phanaeus panamensis*, which we here conclude is a junior synonym of *P. olsoufieffi* for the following reasons:

Their figure 7C (p. 28) depicts a putative paralectotype of *P. blanchardi*, which they regard as assignable to *P. malyi* Arnaud 2002 (their figure 7A and 7B). However, we believe that the specimen in their figure 7C is not assignable to *P. malyi* because it clearly possesses flat elytral interstriae, a feature shared with *P. olsoufieffi* and *P. funereus* Balthasar, 1939; *P. malyi* has raised elytral interstriae. We conclude that the specimen in their figure 7C is *P. olsoufieffi* (*P. funereus* is ruled out because it has the head and pronotum dull metallic red and the major male with a keel absent in the middle of the anterior pronotal margin) and that its label locality “Colombia” cannot be assigned to *P. malyi*, a species restricted to the Pacific rainforest of Costa Rica and Panama (Solís and Kohlmann 2012). Moctezuma and Halffter (2021: 28, fig. 7C) mention an illegible label pinned to this specimen, it says *Obert* which is shorthand for Oberthür, signaling the Oberthür Collection. The misapplication of elytral relief (flat vs convex) also comes to play in Moctezuma and Halffter's (2021) key to species, couplets 10, 14–17, which confound the identities of several species, including *P. pyrois*.

Moctezuma and Halffter (2021) also indicated previous authors (Edmonds 1994; Arnaud 2002; Edmonds and Zídek 2012; Solís and Kohlmann 2012; Kohlmann et al. 2018) mistakenly reported *P. olsoufieffi* from Panama. Using material not studied by Moctezuma and Halffter (2021) and supplied by Dr. Roberto Cambra of the University of Panama, we checked Panamanian material (Fig. 5) and concluded that the specimens are indeed *P. olsoufieffi*. The lamella copulatrix has been studied for Panamanian and Costa Rican specimens (Figures 3–4), and in all cases, it is the typical one for *P. olsoufieffi*, as presented by Moctezuma and Halffter (2021: 9, fig. 1J). Our

study of Panama specimens has found no lamellae copultrices resembling the one for *P. panamensis*, as shown by Moctezuma and Halffter (2021: 9, fig. 1L).

River Martínez (TAMUIC) has kindly provided us with photographs of the endophallite of the holotype (Fig. 38; Cerro Campana, Panama), a paratype (Barro Colorado Island, Canal Zone, Panama), and a non-paratype (Fort Kobbe, Canal Zone, Panama) of *P. panamensis*. Figure 39 is the endophallite of the holotype of *P. panamensis* as depicted by Moctezuma and Halffter (2021, fig. 1L). Comparing the two, it is clear they do not look the same. The endophallite photographed by TAMUIC (Fig. 38) is the same as a typical *P. olsoufieffi* (Fig. 3, 4). We are at a loss to explain this photographic difference. The photographs of the male paratype and non-paratype of *P. panamensis* sent by TAMUIC are also *P. olsoufieffi*. Still, as stated before, we have not been able to find an endophallite resembling the one photographed by Moctezuma and Halffter (2021) either in Panamanian or in Costa Rican specimens at our disposal.

Moctezuma and Halffter (2021: 52, fig.16) also present a map indicating based on just one locality, Estación La Selva in Heredia, that *P. panamensis* extends its distribution to the northern Caribbean of Costa Rica. We have been studying the dung beetles of Costa Rica for more than thirty years, including Estación La Selva, and have not yet been able to find any *P. olsoufieffi* (Fig. 1) in Costa Rica. Neither have we been able to detect the large areas of sympatry (Figure 5) between *P. malyi*, *P. pyrois* and, *P. panamensis* (Fig. 2) that Moctezuma and Halffter (2021: 38) write about. Curiously, Moctezuma and Halffter (2021) report only one locality for *P. pyrois* and *P. panamensis* for Costa Rica but mark two localities apiece in their text map. Similarly, we have not found any lamella copulatrix of the sort described by Moctezuma and Halffter (2021) among Costa Rica *Phanaeus* specimens, so it is highly likely that this taxon does not occur in Costa Rica. Up to this day, we have been able to collect *P. pyrois* (665 specimens) along the Caribbean coast of Costa Rica (Fig. 5), showing a great variety of color morphs, (see below).

Whereas *P. olsoufieffi* is described as a larger species by Moctezuma and Halffter (2021), with typical characteristics of large specimens (central anterior pronotal margin keeled, male pronotal posterolateral angles strongly developed and projected); *P. panamensis* is considered a smaller species with its concomitant characteristics (central anterior pronotal margin not keeled, male pronotal posterolateral angles weakly developed and slightly projected). However, contrary to the species' key description of *P. panamensis* (Moctezuma and Halffter 2021: 54), with a keel always absent on the central anterior margin of the male pronotum, the diagnosis of *P. panamensis* by Moctezuma and Halffter (2021: 36) does indicate otherwise that major males have an obsolete keel in the middle of the anterior pronotal margin.

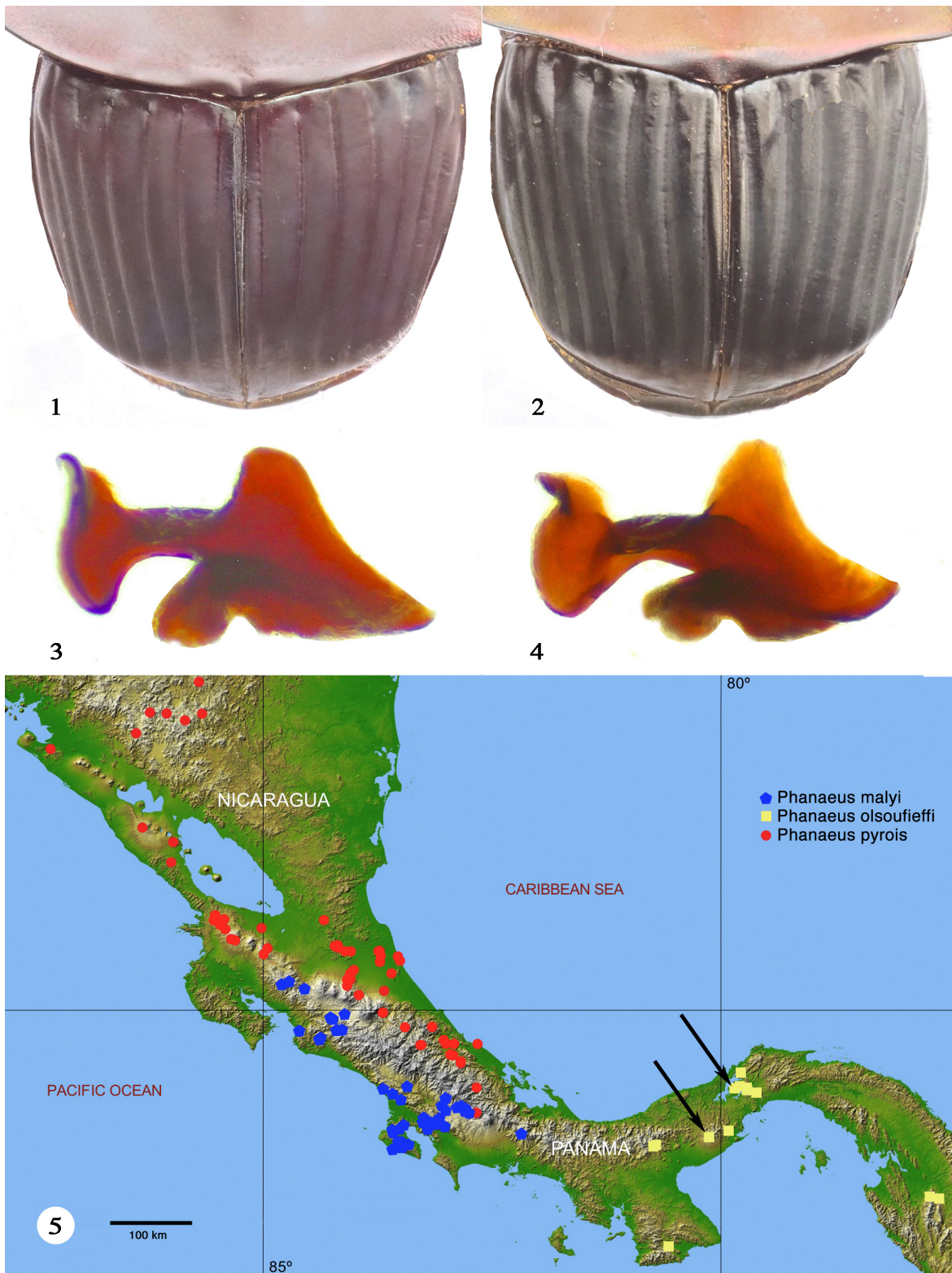
Along the same line, *P. pyrois* shows convex interstriae, whereas the holotype of *P. panamensis* shows them flat and the striae are not impressed basally, as is the case with *P. olsoufieffi*. However, the female paratype shown in the photograph has convex interstriae and striae strongly impressed basally (Moctezuma and Halffter 2021: fig. 10B). River Martínez generously provided us with a photo of a female paratype (Fort Kobbe, Canal Zone, Panama) that clearly depicts that the interstriae are flat. We list below the material supplied by Dr. Cambra from the University of Panama that we examined.

Revised material (21). PANAMA. **Coclé**. El Copé, 900 m, 22–23 sept 1990, col. R. Cambra, J. Coronado; Valle de Antón, 8 Oct 2006, J. Jaén, heces humanas; 1 sept 1987, col. D. Quintero, R. Cambra, R. Rodríguez; El Valle, La Mesa, 850 m, 29v–9vi 2000, D. Curoe, B. Ella cols. (7). **Colón**. Pipeline Road, 20 Ago 1982, col. B. Gill (2) **Darién**. PN Darién Cana, 400 m, 8–15 V 02, flight intercept trap, D. Curoe col.; PN Darién, Pirre, Est. Rancho Frío, 80 m, 18–24 ene 2001, (hec. hum.), R. Cambra, A Santos; 450 m, 24–26 mar 2001, A. Santos, Malaise; 3–17 oct 2002, R. Cambra, A. Santos. **Los Santos**. Tonosí, Res. For. La Tronosa, Los Planes, 350 m, 7°21'N 80°28'W, heces hum, 20 abr 2 may 2006 R. Cambra (1). **Panamá Oeste**. Canal Area, Barro Colorado Island, 10–12 Feb 2005, E. Andresen, S. Laurence, dung bait, morphospecies 18; morphospecies 20; July 1992 at howler dung (6).

Phanaeus (Notiophanaeus) pyrois Bates, 1887

Phanaeus pyrois Bates 1887: 58.

Moctezuma and Halffter (2021: 42) stated that the elytral striae of *P. pyrois* are not strongly impressed basally and according to their key's couplet 10 (2021: 54), the "elytral interstriae are distinctly flattened". We do not agree with



Figures 1–5. *Phanaeus* spp. 1) Elytra of *P. olsoufieffi*. 2) Elytra of *Phanaeus pyrois*. 3) *Lamella copulatrix* of *P. olsoufieffi* from Valle de Antón, Panama. 4) *Lamella copulatrix* of *P. olsoufieffi* from Barro Colorado Island, Panama. 5) Known distribution of *Phanaeus malyi*, *P. pyrois*, and *P. olsoufieffi* in lower Central America. Right arrow, Barro Colorado Island; left arrow, Valle de Antón.

this statement; the elytral striae are indeed strongly impressed basally and the interstriae are convex (Fig. 2), and these characters easily separate this species from *P. olsoufieffi* (Fig. 1).

Phanaeus pyrois is the most color variable taxon of the endymion species group (Moctezuma and Halffter 2021). However, no detailed analysis of the different color morphs has heretofore been undertaken. We present a study of several color morphs in Costa Rica (Figs. 6–10) and their relative frequencies (Fig. 11). Our analysis of 665 *P. pyrois* specimens shows metallic red (Fig. 6) to be the most common color morph, followed by a dark blue (Fig. 7), a dark green (Fig. 8), a red with green reflections (Fig. 9), and finally a dark red (Fig. 10). As can be seen from figures 12 and 13, these frequencies vary geographically. There is a greater percentage of red, red with green reflections, and dark red morphs in the northern part of its range, whereas there is a greater percentage of dark blue and dark green morphs in the southern portion.

Cupello et al. (2022) have undertaken an exquisitely detailed color analysis of *Bolbites onitoides* Harold, 1868 another Phanaeini, on the question of whether its two-color variants (blue and red) represent distinct subspecies. They concluded that *B. onitoides* should be treated as a single monotypic species for the following reasons:

- Two color intermediates were found living among the main color variants (red and blue);
- the distribution of the variants overlaps;
- no other characters paralleled color variation;
- the overall geographical pattern (blue western-half and a red eastern-half) can be explained by phenomena other than (incipient) speciation, such as phenotypic plasticity and distinct selective regimes; and
- color has been extensively shown not to be a reliable indicator of speciation processes among dung beetles, especially among the Phanaeini (Edmonds, 1994, 2000; Edmonds and Zídek, 2004, 2010, 2012; Solís and Kohlmann 2012; Cupello and Vaz-de-Mello 2013, 2014, 2016; Cupello et al. 2022).

The same reasoning can be applied to *P. pyrois*, although the number of color variants and intermediaries is greater. Notably, *P. pyrois* represents the northernmost distribution of a taxon of this species group having a red color. The southernmost species with red color is *P. funereus* in Ecuador and is repeated in Colombia and Panama by *P. olsoufieffi*. Interestingly, to the north of *P. pyrois* populations in Costa Rica, only black, blue, and green species are present. Our taxonomic conclusion is that *P. pyrois* is a single, monotypic, polychromatic species.

***Onthophagus bidentatus* Drapiez, 1819 and *Onthophagus marginicollis* Harold, 1880**

Onthophagus bidentatus (Fig. 14) was described by Drapiez in 1819 from French Guiana. Medina and Pulido (2009) report it from the Colombian Orinoquia. Rossini et al. (2016) report it from Panama, Trinidad and Tobago, Brasil, Peru, and Suriname. Rossini et al. (2016) also write that this is a common species in open habitats but rare in transitional forested areas. It also has been cited for Ecuador (Chamorro et al. 2018). Recently, Taboada-Verona et al. (2019) have reported its presence in Sucre, Colombia.

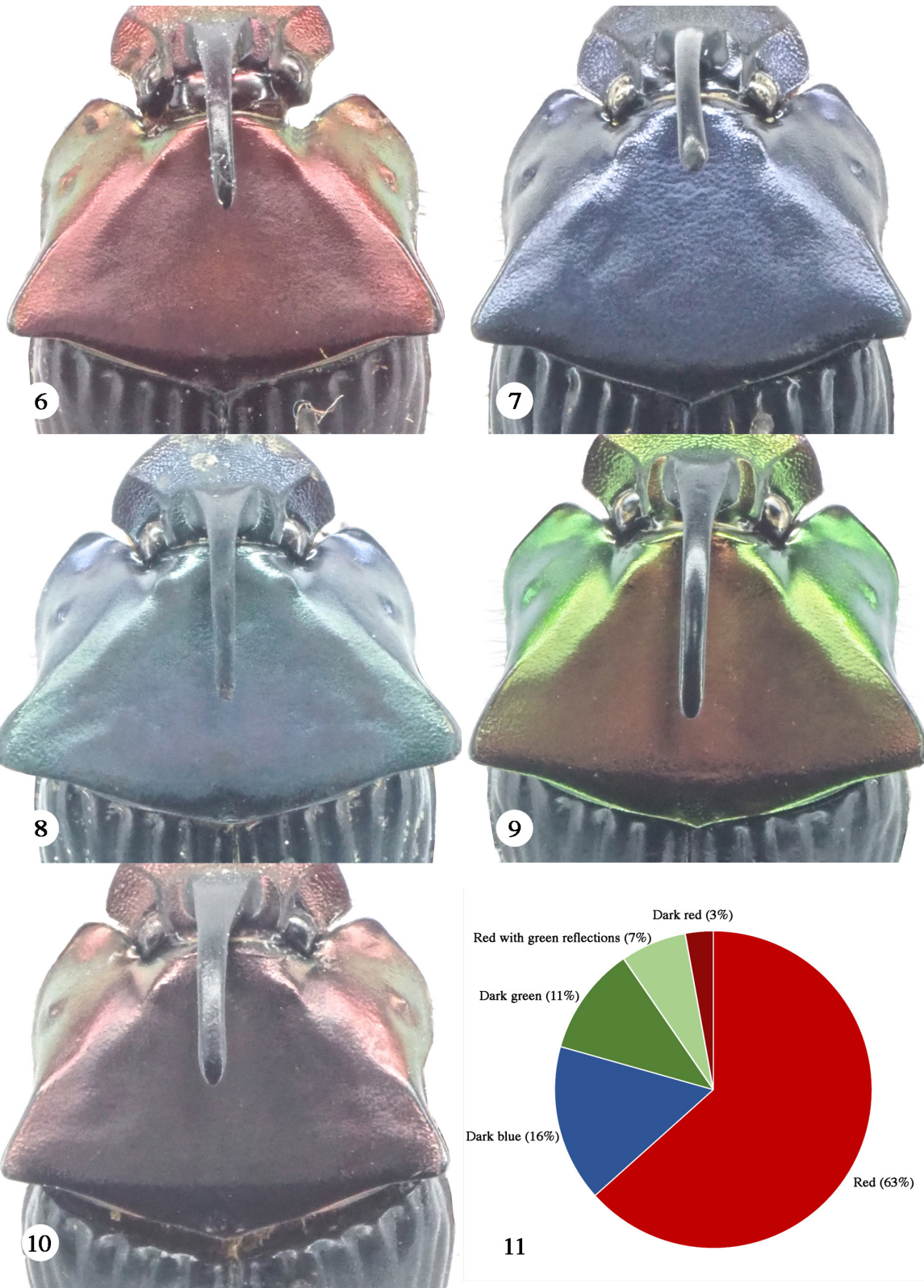
Rossini et al. (2018) indicate that *O. bidentatus* belongs to the *O. hircus* complex, part of the *O. hircus* species group. *Onthophagus marginicollis* Harold, 1880 (Fig. 15) is also a member of this complex, and we here analyze the distribution of both species for Costa Rica. In the case of Costa Rica, *O. bidentatus* had not been previously reported. However, its presence has now been confirmed, and Costa Rica apparently represents the northernmost occurrence of this species (Fig. 16).

Figure 16 shows clearly that *O. bidentatus* is distributed in the Pacific Rain Forest of southern Costa Rica, plus isolated localities in the Nicoya Peninsula. These localities usually represent rainforest patches in the deep gorges of the Nicoya mountains, where the broken terrain maintains damp and stable rainforest patches. On the other hand, *O. marginicollis* is distributed along the Pacific and Caribbean coasts (Fig. 17). Interestingly, the two species are sympatric along the Pacific coast (Figs. 16–17). They can be collected in the same trap or manure, apparently coexisting even though they occupy the same niche, living in open or disturbed habitats.

***Onthophagus cyanellus* Bates**

Onthophagus cyanellus Bates 1887: 81.

Onthophagus mesoamericanus Zunino and Halffter 1988: 123 (new synonymy by Kohlmann and Solís 2001: 196).



Figures 6–11. 6) Red morph of *P. pyrois*. 7) Dark blue morph of *P. pyrois*. 8) Dark green morph of *P. pyrois*. 9) Red with green reflections morph of *P. pyrois*. 10) Dark red morph of *P. pyrois*. 11). Color pie-chart of the Costa Rican *P. pyrois* populations, $n = 665$.

Onthophagus mesoamericanus Zunino and Halffter (restoration of species status by Pulido-Herrera and Zunino 2007: 109).

Onthophagus mesoamericanus Zunino and Halffter (synonymy reaffirmed by Solís and Kohlmann 2012: 12).

Onthophagus mesoamericanus Zunino and Halffter (restoration of species status by Moctezuma 2021: 194).

Onthophagus mesoamericanus Zunino and Halffter, **reaffirmed subjective synonymy**.

Zunino and Halffter (1988) described *O. mesoamericanus* Zunino and Halffter, 1988 based on three specimens, two males and one female from Costa Rica. In 2001, Kohlmann and Solís synonymized this species with *O. cyanellus*. This decision was based on studying the two paratypes of *O. mesoamericanus* deposited in the Muséum National d'Histoire Naturelle, Paris, and studying a lectotype of *O. cyanellus* from the Natural History Museum, London (Kohlmann and Solís 2001), plus 490 specimens of *O. cyanellus* deposited in the INBio collections. The main characteristics differentiating *O. mesoamericanus* from *O. cyanellus*, according to Zunino and Halffter (1988), are the green color, a black clypeal margin, and pronotal slope, and an unarmed male frontal keel. These characteristics, plus characteristics of the male genitalia, were studied and compared with the ones presented by Costa Rican *O. cyanellus* populations, and the diagnostic characteristics were found to fall within observable variation of *O. cyanellus*. The synonymy was based on the study of blue, green, and copper morphs of *O. cyanellus* from Costa Rica. Zunino and Halffter (1988) also wrote that the type locality, Cedros, referred to Cerro Cedral in the Cordillera de Talamanca. However, Cedros is a district of San José, which has been now thoroughly urbanized and lies in the Cordillera Central. Likewise, the only two paratypes of *O. mesoamericanus* are from “Rancho Redondo” in Cartago, a locality located in the Cordillera Central.

In 2007 Pulido-Herrera and Zunino published an atlas of the American Onthophagini which considered both species valid. This situation prompted a reanalysis by Solís and Kohlmann (2012) of material from Costa Rica and reaffirmation of their initial conclusion of synonymizing *O. mesoamericanus* and *O. cyanellus*.

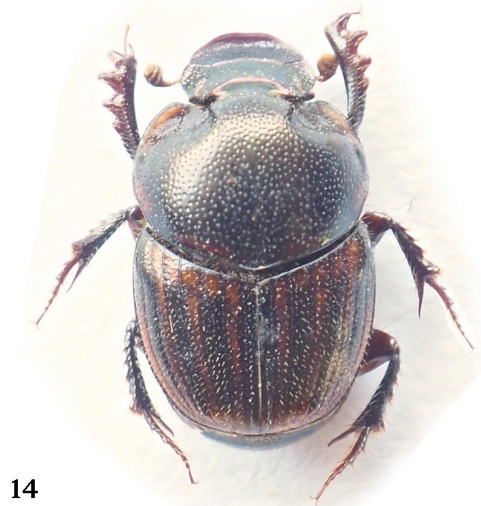
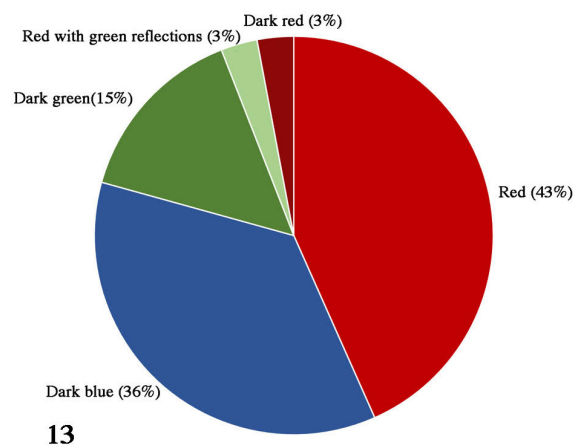
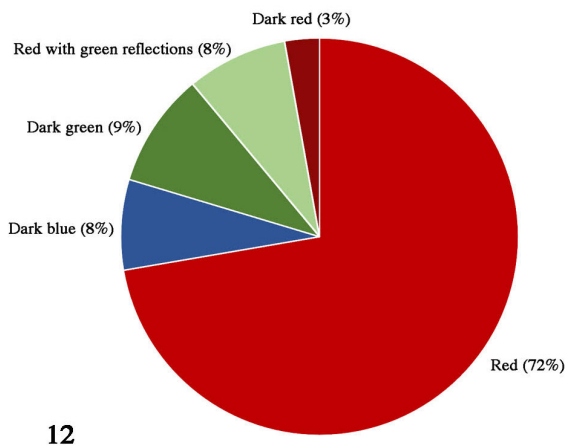
Subsequently, Moctezuma (2021) resurrected *O. mesoamericanus* based on the analysis of its holotype and the following numbers of studied *O. cyanellus*: 20 specimens from Costa Rica, ten from Panama, and 390 specimens from Mexico, plus a photograph of the *O. cyanellus* lectotype and two photos of *O. mesoamericanus* from the BOLD database. He indicated that the database specimens belonged to two females; actually, the one he cited as ASSCR1194-11 is a hypothelic male, not a female. Further, he indicated that these specimens are registered as *O. mesoamericanus* in the BOLD database, whereas they are labeled as *O. cyanellus* in that same database (Fig. 8). So, Moctezuma (2021) revalidated *O. mesoamericanus* based on comparing one specimen, the holotype, with specimens of *O. cyanellus*. We disagree with his action for the reasons indicated in the sections below.

For the present study, we examined the Costa Rican *O. cyanellus* material stored in the Museo Nacional (National Museum) of Costa Rica, housing 617 specimens and Nicaraguan material from the Ángel Solís Collection, as well as the BOLD taxonomic platform. We also examined personally the two paratypes of *O. mesoamericanus* (Fig. 34–37). The following taxonomic analysis utilizes morphological (external and genitalia), genetic, and biogeographical characteristics.

Color and mtDNA variation

Many years of collecting by us reveal that many Costa Rican populations of *O. cyanellus* contain blue, copper, and green specimens in the same locality at the same time (Fig. 18–23) along the Cordillera Central and the Cordillera de Talamanca. In other words, polychromy is part of the population variation of this species in Costa Rica. A similar phenomenon has been observed and reported for Costa Rica in the case of *Canthon cyanellus* LeConte, 1859 (Solís and Kohlmann 2002), populations of which can include up to five color morphs in one locality. Table 1 summarizes color morph frequencies for *O. cyanellus* in two Costa Rican locations.

Of note is the fact that relative abundance (frequency) of blue morphs declines while frequencies of green and copper morphs increase in the Cordillera Central compared to the Cordillera de Talamanca (Fig. 24). The blue morph always dominates, with green and copper morphs coming in second or third place (Table 1). Some rare color morphs are blue-green and copper-green individuals. One possible explanation for the presence of color morphs is the recent colonization of the Cordillera Central by populations originating from the Cordillera de Talamanca and the concomitant genetic drift caused by small founder populations. This recent spread could have been caused by the Last Glacial Maximum (~20 ka, Jackson et al. 2019; Kohlmann et al. 2019) or facilitated by the establishment of cattle ranching in the area during the last 470 years. Another possibility is that *O. cyanellus*



Figures 12–17. 12) Color pie-chart of the northern Caribbean *P. pyrois* populations, northward of the 10° N latitude line, *n* = 462. 13). Color pie-chart of the southern Caribbean *P. pyrois* populations, southward of the 10° N latitude line, *n* = 203. 14). Male *Onthophagus bidentatus*. 15). Male *Onthophagus marginicollis*. 16). Known distribution of *O. bidentatus*. 17). Known distribution of *O. marginicollis*.

Table 1. Number and frequency of color morph specimens of *O. cyanellus* in the Cordillera Central and Cordillera de Talamanca, Costa Rica.

Color	Cordillera Central	Cordillera de Talamanca	Total
Blue	164 (62%)	332 (94%)	496 (80%)
Green	80 (30%)	16 (5%)	96 (16%)
Copper	21 (8%)	4 (1%)	25 (4%)
Total	265	352	617

populations in the Costa Rica–Panama area represent a limit to the distribution range for this species. *O. cyanellus* populations in the Sierra Madre Oriental in Mexico represent the other distributional (possibly initial) range limit. Due to different climatic and ecological conditions, allele frequency may differ from the northern to this extreme southern boundary. Zunino and Halffter (1988: 135) considered that *O. cyanellus* represents a successful old distribution, having crossed the two North American tropical portals, the Tehuantepec Isthmus, and the Nicaraguan Lake region, into the mountains of Costa Rica and Panama.

Further study of color morph variation figures in the comprehensive mtDNA barcode analysis (COI) that is being done for the Scarabaeinae fauna of Costa Rica (Solís and Kohlmann 2012; Kohlmann et al. 2019). An mtDNA barcode tree is presented here (Fig. 26), encompassing several species of the *O. chevrolati* species group (Zunino and Halffter 1988), of which *O. cyanellus* is a member. Three color morphs from two Costa Rican localities, one green from Grecia (Alajuela) and a blue and a copper morph from La Unión (Cartago), were analyzed, forming the *O. cyanellus* species-complex separate from the other complexes derived from the analysis. The average mtDNA genetic distance separating the three different *O. cyanellus* color morph specimens (1.15%) in Figure 26 is below a 2% bp sequence divergence, considered the conventional threshold for separating species (Jones et al. 2011), so the specimens can be considered as assignable to the same species (see discussion below).

Zunino and Halffter (1988: 30) illustrate the chevrolati species group using a phylogenetic diagram. They define and further divide the 58 species comprising the group into several species' complexes (Zunino and Halffter 1988: 30; see also Halffter et al. 2019) This species group is perhaps the most common one on the American continent. Several species complexes of the *O. chevrolati* species group are recovered at distances greater than a 2% COI divergence, supporting the proposed species complexes proposed originally by Zunino and Halffter (1988). Three species complexes are evident: *cyanellus*, *chevrolati* (*O. cochisus* Brown, 1927), and *brevifrons* (*O. brevifrons* Horn, 1881 and *O. subtropicus* Howden and Cartwright, 1963). Zunino and Halffter (1988) proposed the *cyanellus* species complex within this species group, which is cleanly recovered in the species tree. The cytochrome c oxidase I (COI) results show a clear mitochondrial DNA distance difference between the cyanellus species complex and the branch with the other members of the chevrolati species group (Fig. 26). Although the present analysis does not include all species, the tree recovers three of the ten species complexes proposed by Zunino and Halffter (1988) and Halffter et al. (2019).

A more detailed mtDNA barcode tree (Fig. 40), mixing all three-color morphs and several localities, shows that the *O. cyanellus* populations in Costa Rica form a single species, including those from localities in the Cordillera Central and the Cordillera de Talamanca (Fig. 25). The intraspecific cytochrome c oxidase I (COI) results for *O. cyanellus* show a lower mitochondrial DNA average genetic distance difference (average Kimura-2-parameter [K2P] = 1.15%, max = 2.3%, min = 0%) than found for a *Phanaeus* sister-species pair, *P. beltianus* Bates, 1887 and *P. changdiazii* Kohlmann and Solís, 2001 (average Kimura-2-parameter [K2P] = 3.0%) (Solís and Kohlmann 2012). These average values are below those that Johns and Avise (1998) found (K2P difference)—3.5% in 47 pairs of bird sister species—and well below the value of 12.56% that measures the average Kimura-2-parameter [K2P] representing the average genetic distance between *O. cyanellus* and the *O. brevifrons*+*cochisus*+*subtropicus* branch. *O. cyanellus* shows a 12.26% average genetic distance difference with *O. brevifrons*, a 12.75% average difference with *O. cochisus*, and a 12.76% average difference with *O. subtropicus*. These results support the proposal that the three-color morphs of *O. cyanellus* are assignable to a single species.

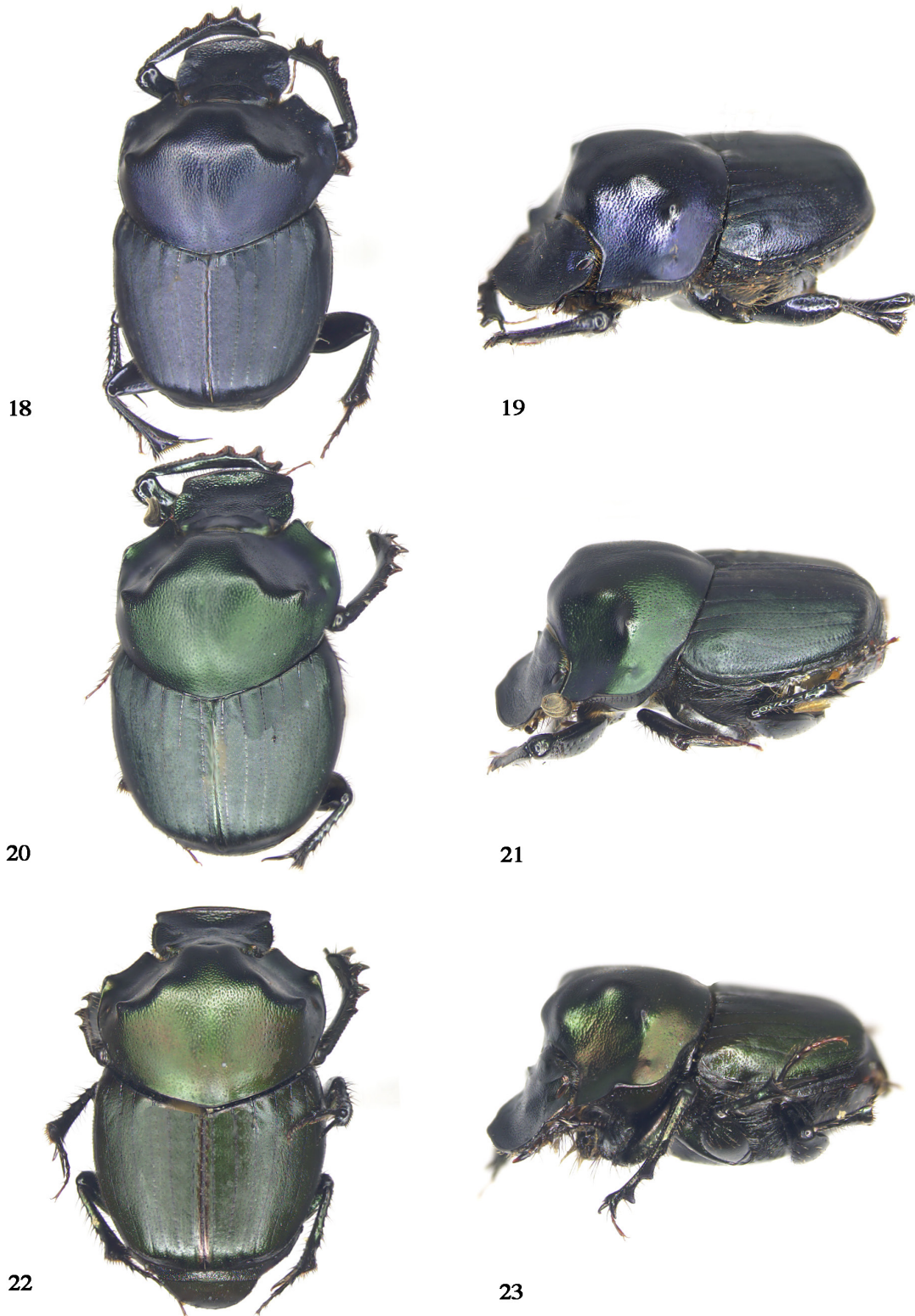
The maximum genetic distance difference (2.3%) between *O. cyanellus* specimens in Figure 40 is the one shown between a blue specimen from Río Zarcero (ASolís000801) and a copper specimen of Río Seco (ASolís001054). The two localities are only 4.5 km apart and apparently do not support a genetic difference caused by widely separated localities. As can be seen from the previous values, the maximum genetic distance difference (2.3%) is much below average interspecific mtDNA genetic differences (12.56%) within the *O. chevrolati* species group. Moreover, the genetic variation of *O. cyanellus* (0.0%–2.3%) does not overlap with the interspecific genetic variation (11.70%–13.75%) of the *O. chevrolati* species group (Fig. 26) forming a barcode gap, thus suggesting again that the three-color morphs of *O. cyanellus* represent a single species.

It is essential to consider the significance of intraspecific COI I variability in more detail, and in this context, it is useful to consider the work of Zhang and Bu (2022). Following an analysis of 64,414 insects, they found that 44.43% of the species studied showed a maximum intraspecific genetic distance ranging from 0 to 1% and 62.87% of the species varied from 0 to 2%. By contrast, the numbers of species whose maximum intraspecific genetic distances exceeded 2% and 3% were 37.13% and 26.62%, respectively. The maximum intraspecific genetic distances over 3% for Coleoptera (8968 studied species) were observed in 23.1% of the species studied. Approximately one-quarter of the species of Insecta studied by them showed high intraspecific genetic variation (>3%), and a conservative estimate of this value ranges from 12.05% to 22.58%. In a similar analysis of 1004 European species of Lepidoptera, Huemer et al. (2014) reported that for two localities separated by 1,600 km in Finland and Austria, maximum intraspecific genetic distances for the COI pooled data were less than 2% for 880 species (87.6%), while wider divergence was detected in 124 species. For the present study we found maximum intraspecific genetic variation of 2.3% for the Costa Rican populations of *O. cyanellus*, a value well within the limit for comparing variations among conspecific populations.

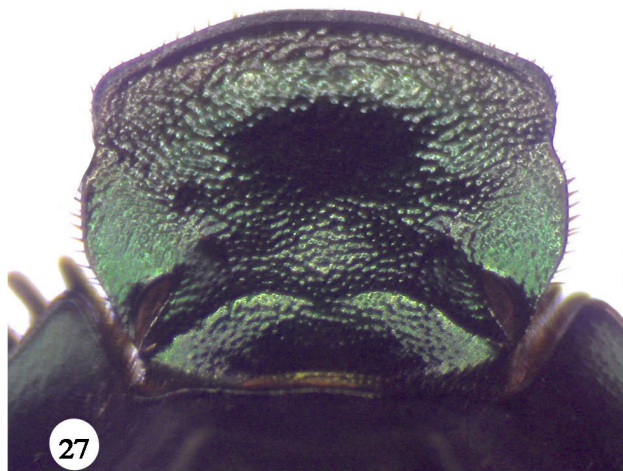
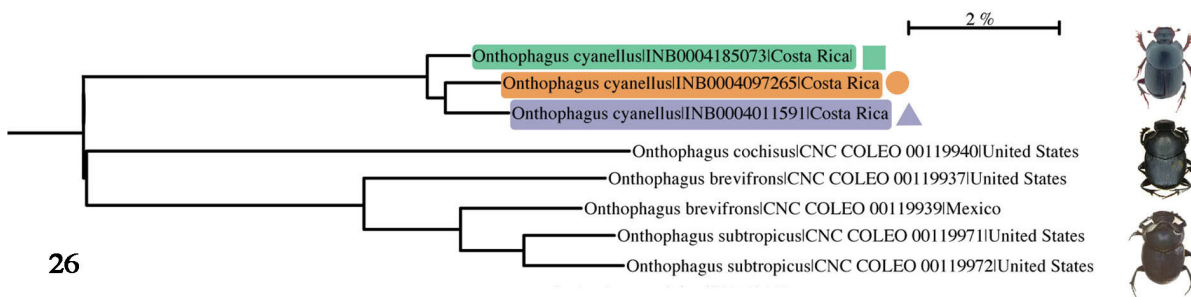
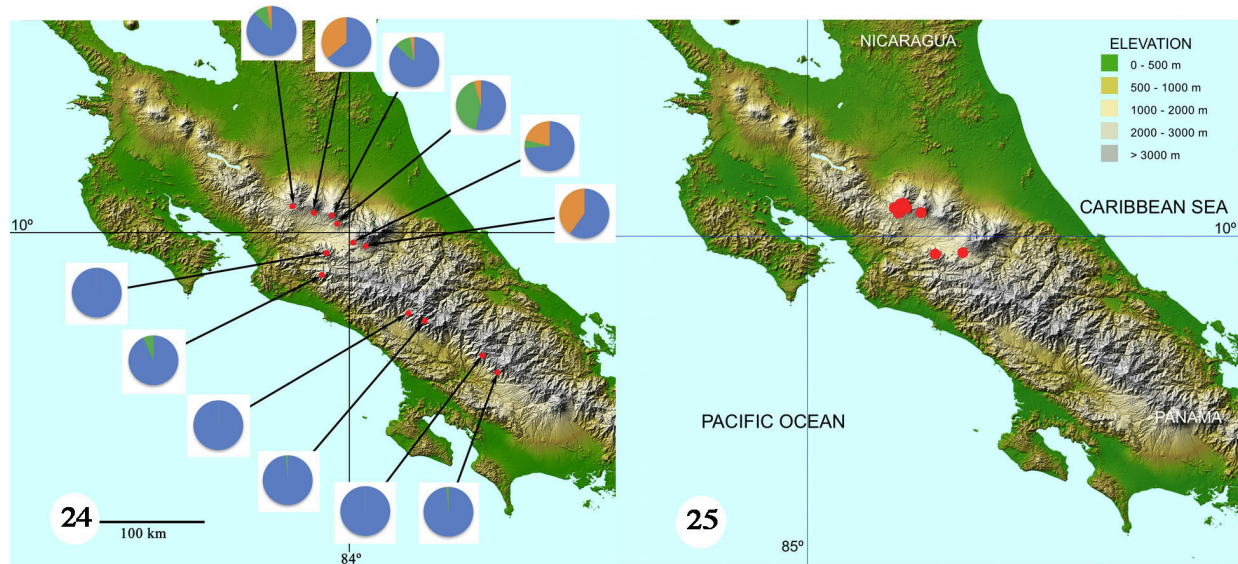
Clypeal margin, pronotal slope, frontal keel, and polymorphism

Zunino and Halffter (1988) specified a black clypeal margin and pronotal slope, and a simple male frontal keel as diagnostic characters of *Onthophagus cyanellus*. The black clypeal margin and pronotal slope are a matter of color contrast. In blue color morphs of *O. cyanellus*, because the morph is dark blue, neither the clypeal margin nor the pronotum stands out. However, in the green and copper color morphs, because they are paler, the color contrasts strongly with black areas. Regarding the unarmed male frontal keel, the holotype of *O. mesoamericanus* is a euthelic specimen. However, hyperthelic specimens of the green morph have an armed frontal keel (Fig. 27). Moctezuma (2021: 195) warns against using characters derived from *O. cyanellus* hypothelic males for establishing diagnostic characters, without realizing that the same applies to euthelic and hyperthelic males, as is the case of the *O. mesoamericanus* holotype. Moctezuma (2021: 195) proposed more diagnostic characters based on a single euthelic holotype, including less developed pronotal secondary tubercles; an almost straight or convex pronotal projection of frontal border; a more robust pronotal projection; and a more strongly medially sinuated frontal carina. When a green *O. mesoamericanus* hyperthelic male is compared to the other hyperthelic color morphs, they all show the same characteristics. Thus, the preferable comparison is among specimens of the same degree of development. Figures 27–29 compare the male head in a hyperthelic (Fig. 27), euthelic (Fig. 28), and hypothelic (Fig. 29) green color-morph specimen and it is evident that the hyperthelic specimen has an armed frontal keel, the euthelic specimen shows a keel with a hint of horns, and the hypothelic specimen has an unarmed keel. Significant differences can also be observed in the shape of the clypeus. As can be seen from the photographs (Fig. 27–29), as horn size decreases, the clypeus varies from subquadrate to sub-circular to a female-like circular one.

As Taborsky and Brockmann (2010) reported, the differences in head and pronotal armament that the *Onthophagus* manifest as male polymorphism represent a mechanism where the expression of alternative phenotypes is related to alternative reproductive tactics aimed at reproductive success. In the case of *O. cyanellus*, a clear male trimorphism occurs, hyper-, eu-, and hypothelic males (Fig. 18–23, 27–29, 32–34). Rowland et al. (2017) have studied male trimorphism in phanaeine dung beetles (*Phanaeus triangularis* (Say, 1823) and *Oxytersonn conspicillatum* Weber, 1801) and propose the rock-paper-scissors (RPS) model of game theory and the environmental threshold (ET) model of quantitative genetics to model trimorphisms that are environmentally induced and result from the expression of two ontogenetic thresholds that produce three reproductive tactics:



Figures 18–23. Male hyperthelic *O. cyanellus*, dorsal view, blue morph Zarcero, Alajuela. **19).** Male hyperthelic *O. cyanellus*, lateral view, blue morph. **20).** Male hyperthelic *O. cyanellus*, dorsal view, green morph La Unión, Cartago. **21).** Male hyperthelic *O. cyanellus*, lateral view, green morph. **22).** Male hyperthelic *O. cyanellus*, dorsal view, copper morph La Unión, Cartago. **23).** Male hyperthelic *O. cyanellus*, lateral view, copper morph.



Figures 24–28. Distribution of the three-color morphs of *O. cyanellus* in Costa Rica. **25).** Map showing the localities from where the mtDNA barcode population analysis has been done for this paper. **26).** Mitochondrial DNA barcode analysis (COI) of some *O. chevrolati* species group species. *Onthophagus cyanellus* and its three-color morphs: green (La Unión, Cartago); copper, and blue (Grecia, Alajuela) (copper ●, green ■, blue ▲). **27)** Head of hyperthelic *O. cyanellus* green morph male (La Unión, Cartago). Note developed frontal keel horns and the characteristic sub-quadrately clypeus shape. **28).** Head of euthelic *O. cyanellus* green morph male (Cerro Turú, Heredia). Note poorly developed frontal keel horns and the characteristic sub-circularly clypeus shape.

dominant alpha males (hyperthelic) defend mating arenas with long horns; subdominant beta males (eutelic) compete less successfully with short horns and female-like and hornless gamma males (hypothelic) sneak access to mating arenas. We believe this model can be applied to *O. cyanellus*. Although this species does not have as strongly developed head horns as the above phanaeines, pronotal projections vary considerably from significantly developed hyperthelic projections (Fig. 18–23) to almost female-like projections (Fig. 34 and 36). Head shape varies as well (Fig. 27–29). We believe that these pronotal projections function analogously to head horns in other species.

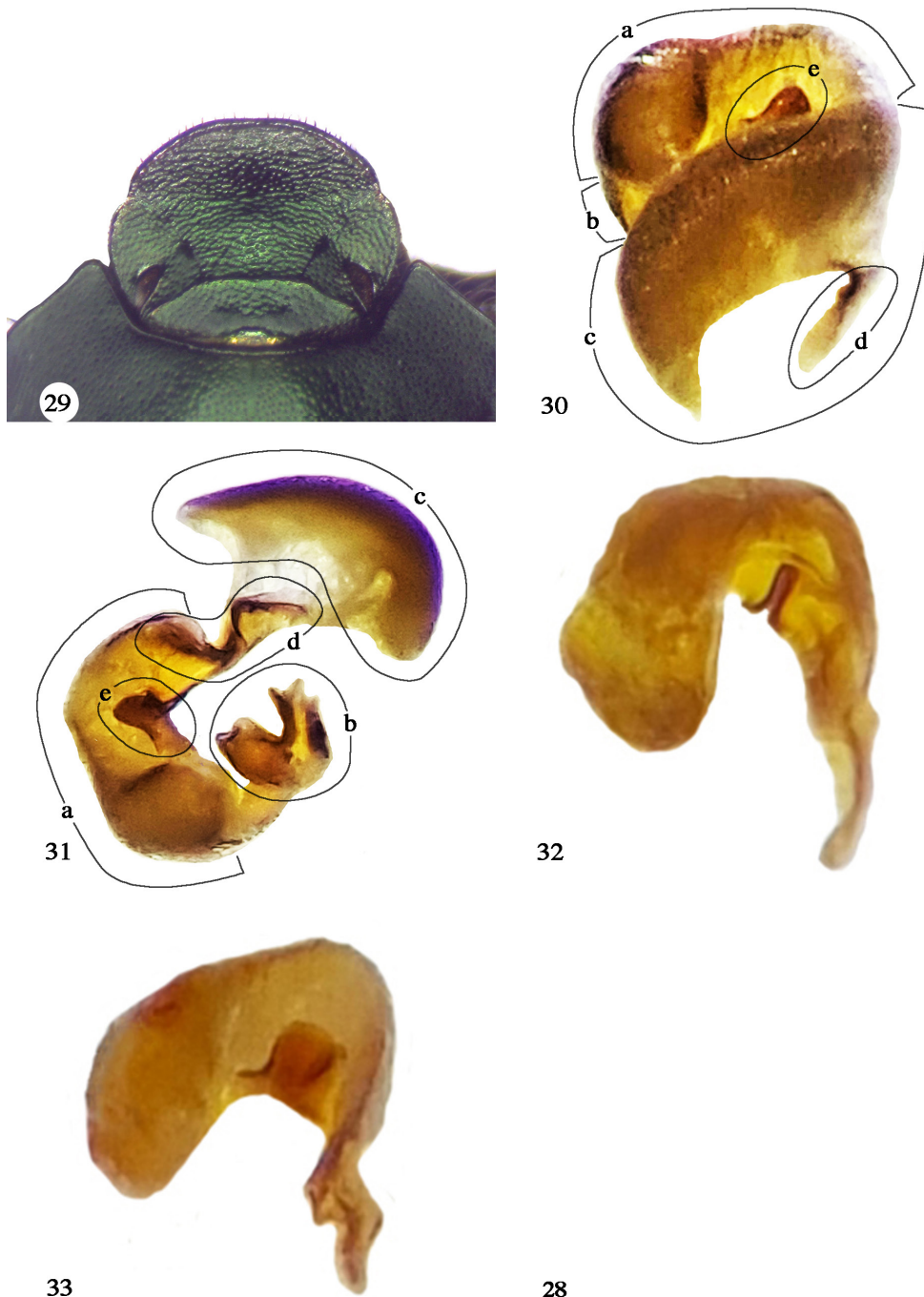
Male genitalia, allometry, and shape variation

Halffter et al. (2019: 18) indicated that: “Kohlmann and Solís (2001) synonymized *O. mesoamericanus* with *O. cyanellus*, a synonymy that we maintain for this work. The lamella copulatrix of the holotype was broken during the initial preparation, preventing its study from confirming synonymy. Consequently, the remaining type material needs to be revised, and additional male specimens of *O. mesoamericanus* need to be collected and studied.” Notwithstanding their advice, Moctezuma (2021) referred to the broken lamella copulatrix in his treatment of *O. mesoamericanus*. He mentions in his figure caption (Moctezuma 2021: 220, fig. 27) that the right lobe of the lamella copulatrix of *O. mesoamericanus* is damaged, but he did not mention or notice that part of the keel (fold) of the basal margin of the lamella copulatrix was missing. The original drawing of the holotype of the lamella copulatrix of *O. mesoamericanus* by Zunino and Halffter (1988: 125, fig. 76) clearly shows the existence of two keel folds, not one, at the basal margin of the lamella copulatrix. Withal Moctezuma (2021: 195) indicated in his text that the lamella copulatrix of *O. mesoamericanus* was damaged, he nevertheless used the presence of a single keel fold as a characteristic differentiating *O. mesoamericanus* from the double keel of *O. cyanellus*.

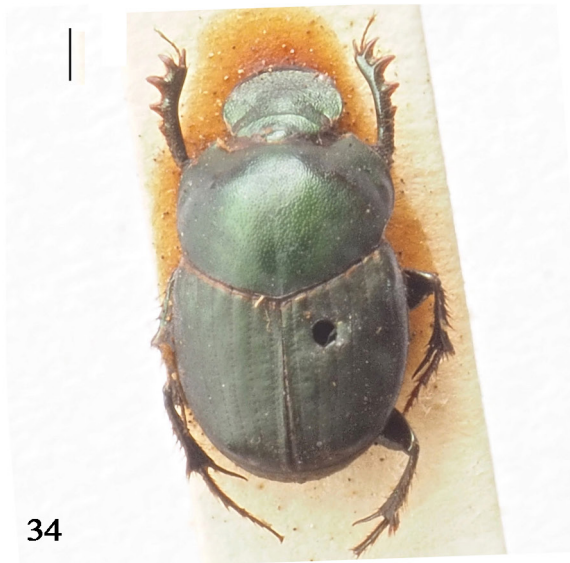
We agree with the detailed morphological description of the lamellae copulatrices of the *O. chevrolati* species group presented by Zunino and Halffter (1988: 17–19) in all but a single detail: While they describe a spiny lamellar band, a membranous fold covered by small sclerified spines, our impression is that this lamellar band is not a spiny membranous fold but is instead a chitinous shell (Fig. 30c, 31c) like the rest of the lamella copulatrix, which we refer to as lamellar band. We present here for the first-time depictions of the assembled lamella copulatrix (Fig. 30) and the lamellar band (Fig. 30c, 31c), which were not illustrated by Zunino and Halffter (1988).

We examined personally the two paratypes (Fig. 34–37) of *O. mesoamericanus* deposited in the Museum National d’Histoire Naturelle (Paris). Both paratypes fall within the color and morphology variation patterns of *O. cyanellus* proposed here and do not show specific differences as reported previously by Kohlmann and Solís (2001) and Solís and Kohlmann (2012). The genitalia preparations could not be studied as they were poorly prepared. An attempt to dissolve the hardened Canada balsam of the male slide to study the lamella copulatrix was not successful. No further attempts were made for fear of further damaging the preparations. The paratypes mtDNA could not be studied, old specimens show degraded genetic material.

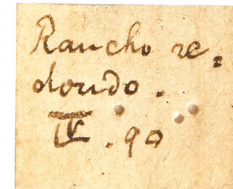
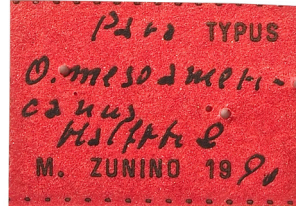
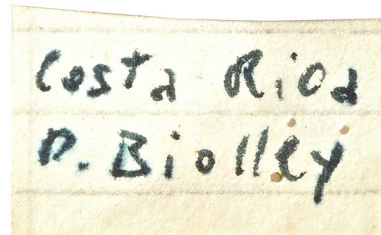
We undertook a comparative analysis of the male genitalia of hyper-, eu-, and hypothelic males (Fig. 30–33) of *O. cyanellus*. The keel of the basal margin of the lamella copulatrix varies in shape but not size. The hypothelic specimen (Fig. 32) shows the keel of the basal margin as a very narrow cleft; that of the eutelic specimen (Fig. 31e) shows a more open cleft; and that of the hyperthelic specimen (Fig. 33) has a wide cleft. However, the size of the basal margin is about the same among the three morphs, which we interpret as a case of negative static allometry where the genitalia of small males of a species are disproportionately large, and those of large males are disproportionately small (Eberhard et al. 2008). As in the case of the male frontal keel, clypeus, and pronotum we observe that specimens show an allometric variation in specific structures of the lamellae copulatrices. Eberhard et al. (2008) seem to have been the first to report that size and shape are independent traits of genitalia; that rapid divergence in the shape of genitalia is thus not inconsistent with the reduced variation in their sizes. Parzer et al. (2018) studied genital shape and size in *Onthophagus* and found significant intraspecific variation in genital shape and size variation. They also found that genital shapes evolved faster than relative genital size, whereas shapes of all structures evolved faster than their relative size. The keel of the basal margin of *O. cyanellus* seems consistent with the idea of Eberhard et al. (2008) and Parzer et al. (2018), that keel shape changes faster than its relative size (Fig. 30–33).



Figures 29–33. Head of hypothelic *O. cyanellus* green morph male (Estación Barva, Heredia). Note almost non-existent frontal keel horns and the characteristic circular clypeus shape. **30).** *Lamella copulatrix* of a euthelic green morph specimen (Estación Barva, Heredia). Disassembled *lamella copulatrix*: a) main copulatory lamella, b) secondary lamella, c) lamellar band, d) keel of the right branch, e) keel of the basal margin. Terminology from Zunino and Halffter (1988). **31).** *Lamella copulatrix* of a euthelic green morph specimen (Estación Barva, Heredia). Disassembled *lamella copulatrix*: a) main copulatory lamella, b) secondary lamella, c) lamellar band, d) keel of the right branch, e) keel of the basal margin. Terminology from Zunino and Halffter (1988). **32).** Hypothelic main copulatory lamella from a copper color morph (Monte de la Cruz, Heredia. **33).** Hyperthelic main copulatory lamella from a copper color morph (La Unión, Cartago).



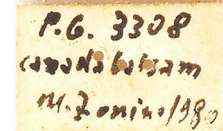
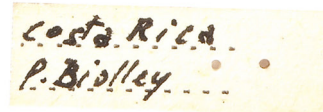
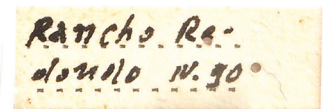
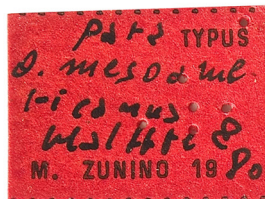
34



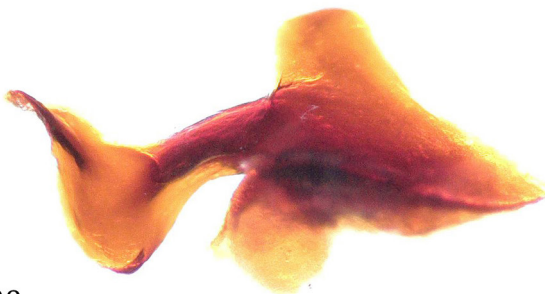
35



36



37

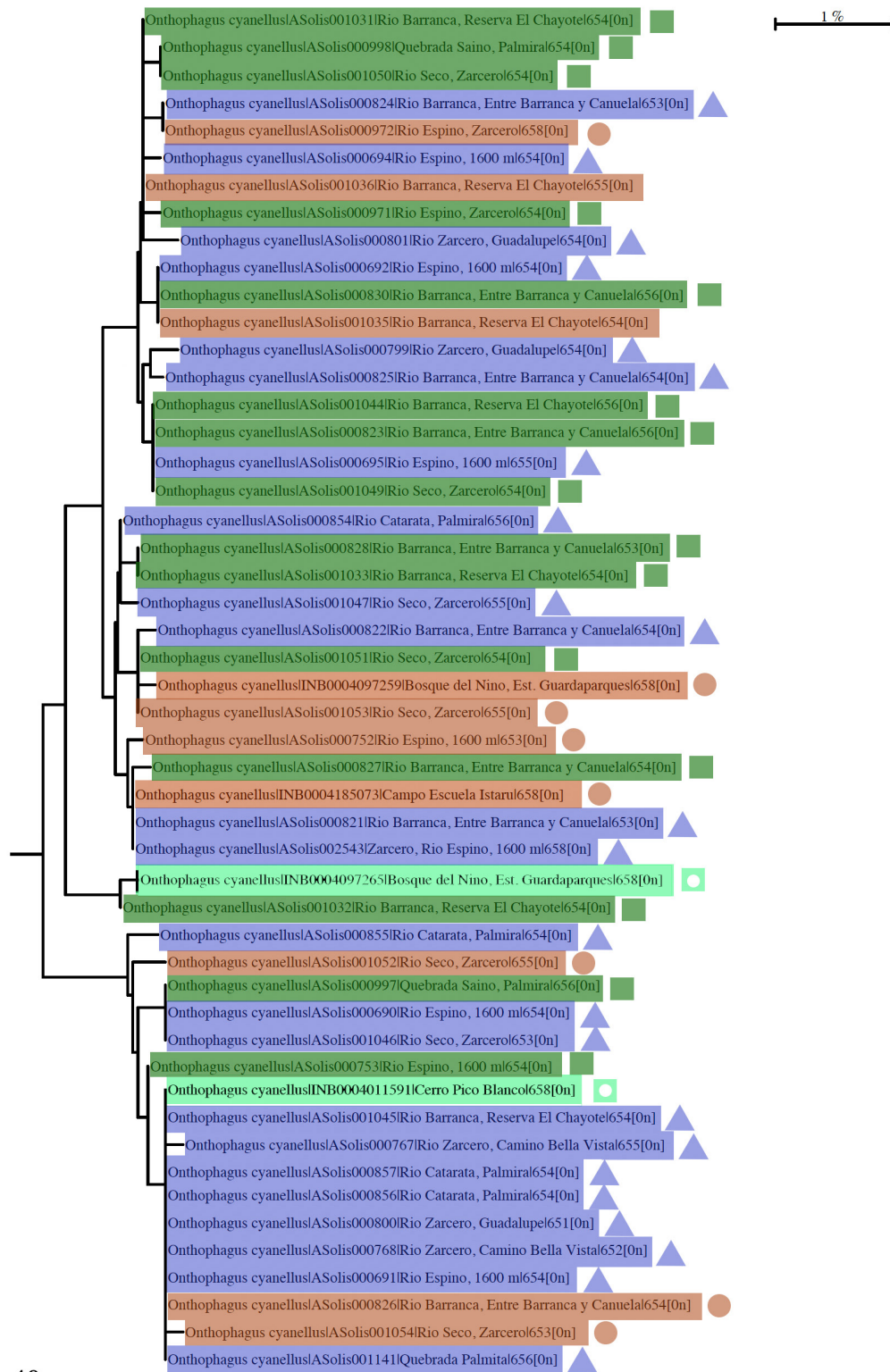


38



39

Figures 34–39. Male paratype of hypothelic *O. mesoamericanus*, Rancho Redondo, Cartago. 35). Labels and genitalia slide of male hypothelic *O. mesoamericanus* paratype. 36). Female paratype of *O. mesoamericanus*, Rancho Redondo, Cartago. 37). Labels and genitalia slide of female *O. mesoamericanus* paratype. 38). Endophallite of the holotype of *P. panamensis* photographed by TAMUIC (Cerro Campana, Panama). 39). Photograph of the endophallite of the holotype of *P. panamensis* as depicted by Moctezuma and Halffter (2021, fig. 1L).



40

Figure 40. Mitochondrial DNA barcode analysis (COI) of different color morphs of Costa Rican *O. cyaneellus* specimens: blue, copper, and green (copper ●, green ■, blue ▲). Specimens marked in light green (◻) are the two “mesoamericanus” photographs referenced by Moctezuma (2021) labeled Bosque del Niño, Est. Guardaparques and Cerro Pico Blanco, respectively.

Discussion

Taxonomic decisions should be based on as much, and as many kinds of information as possible. The description of new species should be based ideally on large enough series that enables population studies. Typological approaches should be avoided. A large enough sample series should allow for as holistically as possible approaches in systematics, using morphological, genetic, ecological, behavioral, and biogeographic information. A significant point to consider, especially in dung beetle taxonomy, is the existence of discrete morphological types. Comparisons should be made only between the same morphological types. Detailed analyses and descriptions should be prepared for all known size morphs.

Acknowledgments

We thank Roberto Cambra from the Invertebrate Museum of the University of Panama for the loan of *Phanaeus olsoufieffi* specimens from that country and to Erika Pinto, who hand-carried the specimens all the way from Panama to San José during the Covid crisis. *Onthophagus* photographs were taken by Marianela Cambronero, Curator of Coleoptera, Department of Natural History, Costa Rican National Museum. We are also in debt with the Texas A&M University Insect Collection (TAMUIC) and to its technician, River Martínez, for photographing the holotype, paratypes, and non-paratypes of *P. panamensis*, and to Edward Riley from the same department, for having dissected endophallites of other *P. panamensis* specimens in their collection. We are in debt to W.D. Edmonds, Mario Zunino, Arturo González, and Oliver Keller for reading and improving our text. We also thank former INBio parataxonomists for their fieldwork throughout Costa Rica. We extend our gratitude to our colleagues and curators at MNCR, Marianela Cambronero and Maricelle Méndez, for allowing us to use the material deposited in that institution. We are grateful to the Guanacaste Dry Forest Conservation Fund as part of BioAlfa's effort to support the taxonomic understanding of Costa Rican wild biodiversity. The Government of Canada funded laboratory analyses of DNA barcode sequences through Genome Canada and the Ontario Genomics Institute. Many specimens were collected, exported, and DNA barcoded under the appropriate permits from the government of Costa Rica, the most recent being Resolución Científica No. R-SINAC-ACG-PI-030-2020 and Certificado 002-2020-OT-CONAGEBIO.

Literature Cited

- Arnaud P. 2002.** *Phanaeini, Dendropaemon, Tetramereia, Homalotarsus, Megatharsis, Diabroctis, Coprophanaeus, Oxysternon, Phanaeus, Sulcophanaeus*. Hillside Books; Canterbury. 151 p.
- Balthasar V. 1939.** Neue Arten der palaearktischen und neotropischen coprophagen Scarabaeiden. Entomologické listy. Folia Entomologica 2: 41–47.
- Bates HW. 1887.** Biologia Centrali-Americana. Insecta. Coleoptera. Vol. II. Part 2. Pectinicornia and Lamellicornia. Taylor and Francis; London. 432 p. + 24 Tables.
- Blackwelder R. 1944.** Checklist of the coleopterous insects of Mexico, Central America the West Indies and South America. Bulletin of the United States National Museum 185: 196–213.
- Brown WJ. 1927.** Four new species of *Onthophagus* (Scarabaeidae). Canadian Entomologist 59: 1281–33.
- Chamorro W, Marín-Armijos D, Granda V, Vaz-de-Mello FZ. 2018.** Listado de especies y clave de géneros y subgéneros de escarabajos estercoleros (Coleoptera: Scarabaeidae: Scarabaeinae) presentes y presuntos para Ecuador. Revista Colombiana de Entomología 44: 72–100.
- Cupello M, Ribeiro-Costa CS, Vaz-de-Mello FZ. 2022.** The evolution of *Bolbites onitoides* (Coleoptera: Scarabaeidae: Phanaeini): its phylogenetic significance, geographical polychromatism and the subspecies problem. Zoological Journal of the Linnean Society 194: 973–1034.
- Cupello M, Vaz-de-Mello FZ. 2013.** Taxonomic revision of the South American dung beetle genus *Gromphas* Brullé, 1837 (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini: Gromphadina). Zootaxa 3722: 439–482.
- Cupello M, Vaz-de-Mello FZ. 2014.** Correction of the type species of the South American genus *Gromphas* Brullé, 1837 (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini). Zootaxa 3790: 399–400.
- Cupello M, Vaz-de-Mello FZ. 2016.** A new species and the phylogeny of the South American genus *Gromphas* Brullé, 1837 (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini). Journal of Natural History 50(15–16): 943–969.

- Darling JDG, Génier F. 2018.** Revision of the taxonomy and distribution of the Neotropical *Copris incertus* species complex. *The Canadian Entomologist* 150(5): 539–577.
- Drapiez M. 1819.** Descriptions de quelques insectes nouveaux. *Annales Generales des Sciences Physiques* 1: 130–138.
- Eberhard W, Rodríguez RL, Polihronakis M. 2008.** Pitfalls in understanding the functional significance of genital allometry. *Journal of Evolutionary Biology* 22: 435–445.
- Edmonds WD. 1994.** Revision of *Phanaeus* Macleay, a New World genus of Scarabaeinae dung beetles (Coleoptera: Scarabaeidae, Scarabaeinae). *Contributions in Science, Natural History Museum of Los Angeles County* 443: 1–105.
- Edmonds WD. 2000.** Revision of the Neotropical dung beetle genus *Sulcophanaeus* (Coleoptera: Scarabaeidae: Scarabaeinae). *Folia Heyrovskyana, Supplementum* 6: 1–60.
- Edmonds WD, Zidek J. 2004.** Revision of the Neotropical dung beetle genus *Oxysternon* (Scarabaeidae: Scarabaeinae: Phanaeini). *Folia Heyrovskyana* 11: 1–58.
- Edmonds WD, Zidek J. 2010.** A taxonomic review of the Neotropical genus *Coprophanaeus* Olsoufieff, 1924 (Coleoptera: Scarabaeidae, Scarabaeinae). *Insecta Mundi* 129: 1–111.
- Edmonds WD, Zidek J. 2012.** Taxonomy of *Phanaeus* revisited: Revised keys to and comments on species of the New World dung beetle genus *Phanaeus* Macleay, 1819 (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini). *Insecta Mundi* 274: 1–108.
- Geffroy MD. 1762.** Histoire abrégée des insectes qui se trouvent aux environs des Paris; Dans laquelle ces Animaux sont rangés suivant un ordre méthodique. *Durand, Paris* 1: 1–523.
- Hajibabei M, Janzen DH, Burns JM, Hallwachs W, Hebert PDN. 2006.** DNA barcodes distinguish species of tropical Lepidoptera. *Proceedings of the National Academy of Sciences* 103: 968–971.
- Halfpeter G, Zunino M, Moctezuma V, Sánchez-Huerta, J-L. 2019.** The integration processes of the distributional patterns in the Mexican Transition Zone: Phyletic, paleogeographic and ecological factors of a case study. *Zootaxa* 4586: 10–34.
- Harold E von. 1868.** Diagnosen neuer Coprophagen. *Coleopterologische Hefte* 4: 80–86.
- Harold E von. 1871.** Diagnosen neuer Coprophagen. *Coleopterologische Hefte* 8: 114–116.
- Harold E von. 1880.** Verzeichniss der von E. Steinheil in Neu Granada gesammelten coprophagen Lamellicornien. *Stettiner entomologische Zeitung* 41: 13–46.
- Hebert PDN, Ratnasingham S, de Waard JR. 2003.** Barcoding animal life: cytochrome c oxidase subunit 1 divergence among closely related species. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 270: S596–S599.
- Hebert PDN, Stoeckle MY, Zemlak TS, Francis CM. 2004.** Identification of birds through DNA barcodes. *Public Library of Science Biology* 2: 1657–1663.
- Hill GE. 2017.** The mitonuclear species compatibility concept. *The Auk* 134: 393–409.
- Horn GH. 1881.** Descriptions of new species of North American Coleoptera. *Transactions of the Kansas Academy of Sciences* 7: 74–77.
- Howden HF, Cartwright OL. 1963.** Scarab beetles of the genus *Onthophagus* Latreille North of Mexico (Coleoptera; Scarabaeidae). *Proceeding of the United States National Museum* 3467: 1–135.
- Huemer P, Mutanen M, Sefc KM, Hebert PDN. 2014.** Testing DNA barcode performance in 1000 species of European Lepidoptera: Large geographic distances have small genetic impacts. *PLoS ONE* 9: e115774.
- Ivanova NV, Grainger CM. 2007.** CCDB protocols, COI amplification. Available at http://ccdb.ca/site/wp-content/uploads/2016/09/CCDB_Amplification.pdf (Last accessed 21 January 2022.)
- Ivanova NV, Dewaard JR, Hebert PD. 2006.** An inexpensive, automation-friendly protocol for recovering high-quality DNA. *Molecular Ecology Resources* 6(4): 998–1002.
- Jackson MS, Kelly MA, Russell JM, Doughty AM, Howley JA, Chipman JW, Cavagnaro D, Nakileza B, Zimmerman SRH. 2019.** High-latitude warming initiated the onset of the last deglaciation in the tropics. *Science Advances* 5(12): eaaw2610.
- Janzen DH, Hallwachs W. 2016.** DNA barcoding the Lepidoptera inventory of a large complex tropical conserved wildland, Area de Conservación Guanacaste, northwestern Costa Rica. *Genome* 59: 641–660.
- Janzen DH, Hallwachs W, Burns JM, Hajibabei M, Bertrand C, Hebert PDN. 2011.** Reading the complex skipper butterfly fauna of one tropical place. *PLoS ONE* 6: e19874.
- Jones M, Ghoorah A, Blaxter M. 2011.** jMOTU and taxonator: turning DNA barcode sequences into annotated operational taxonomic units. *PLoS ONE* 6(4): e19259.
- Kang I, Chapman EG, Janzen DH, Hallwachs W, Dapkey T, Smith MA, Sharkey MJ. 2017.** Revision of the species of *Lytopylus* from Area de Conservación Guanacaste, northwestern Costa Rica (Hymenoptera, Brachonidae, Agathidinae). *ZooKeys* 721: 93–158.
- Kimura M. 1980.** A Simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* 16: 111–120.

- Klug JCF. 1833.** Bericht über eine auf Madagascar veranstaltete Sammlung von Insecten aus der Ordnung Coleoptera. Eine in der Königl. Akademie der Wissenschaften am 29. März 1832 gelesene Abhandlung. Königlichen Akademie der Wissenschaften, Berlin. 135 p.
- Kohlmann B, Arriaga-Jiménez A, Rös M. 2018.** Dung beetle vicariant speciation in the mountains of Oaxaca, Mexico, with a description of a new species of *Phanaeus* (Coleoptera, Geotrupidae, Scarabaeidae). *ZooKeys* 743: 67–93.
- Kohlmann B, Solís A. 2001.** The genus *Onthophagus* (Coleoptera: Scarabaeidae) in Costa Rica. *Giornale Italiano di Entomologia* 9: 159–261.
- Kohlmann B, Solís A. 2001.** A new species of *Phanaeus* MacLeay from Costa Rica and Panama. *Besoiro* 6: 9–11.
- Kohlmann B, Solís A, Alvarado G. 2019.** Description of *Onthophagus humboldti* and *Uroxys bonplandi*, two new scarab beetles (Coleoptera, Scarabaeidae, Scarabaeinae) from Costa Rica, with notes on tropical mountain brachyptery and endemism. *Zookeys* 881: 23–51.
- Medina CA, Pulido LA. 2009.** Escarabajos coprófagos (Coleoptera: Scarabaeinae) de la Orinoquia colombiana. *Biota Colombiana* 10: 55–62.
- Mindell D, Sorenson M, Huddleston C, Miranda H, Knight A, Sawchuk S, Yuri T. 1997.** Phylogenetic Relationships among and within select Avian orders based on mitochondrial DNA. p. 214–217. In: Mindell DP (ed.). *Avian molecular evolution and systematics*. Academic Press; Cambridge, Massachusetts. 383 p.
- MacLeay WS. 1819.** *Horae entomologicae: or essays on the annulose animals*. S. Bagster. London Vol.1: 1–160.
- Moctezuma V. 2021.** El género *Onthophagus* Latreille, 1802 (Coleoptera: Scarabaeidae) de México. *Dugesiana* 28: 175–220.
- Moctezuma V, Halffter G. 2021.** Taxonomic revision of the *Phanaeus endymion* species group (Coleoptera: Scarabaeidae), with the descriptions of five new species. *European Journal of Taxonomy* 747:1–71.
- Nei M, Kumar S. 2000.** *Molecular evolution and phylogenetics*. Oxford University Press; New York. 333 p.
- Olsoufieff G d'. 1924.** Les Phanaeides. *Insecta* 13: 1–205.
- Parzer HF, Polly PD, Moczek AP. 2018.** The evolution of relative trait size and shape: insights from the genitalia of dung beetles. *Development Genes and Evolution* 228: 83–93.
- Pentinsaari M, Salmela H, Mutanen M, Roslin T. 2016.** Molecular evolution of a widely adopted taxonomic marker (COI) across the animal tree of life. *Scientific Reports* 6: 35275.
- Price PL. 2009.** Phylogeny and biogeography of the dung beetle genus *Phanaeus* (Coleoptera: Scarabaeidae) *Systematic Entomology* 34: 137–150.
- Pulido-Herrera LA, Zunino M. 2007.** Catálogo preliminar de los Onthophagini de América (Coleoptera: Scarabaeinae). p. 93–129. In: Zunino M, Melic A (eds.). *Escarabajos, diversidad y conservación biológica. Ensayos en homenaje a Gonzalo Halffter*. Sociedad Entomológica Aragonesa, Monografías 3er Milenio; Zaragoza. 210 p.
- Ratnasingham S, Hebert PND. 2007.** BOLD: The Barcode of Life Data System. *Molecular Ecology Notes* 7: 355–364.
- Rossini M, Vaz-de-Mello FZ, Zunino M. 2016.** More transcontinental mislabelling in the genus *Onthophagus*: d'Orbigny's "African" Group 27 (Coleoptera: Scarabaeidae: Scarabaeinae). *Zootaxa* 4175: 494–500.
- Rossini M, Vaz-de-Mello FZ, Zunino M. 2018.** Toward a comprehensive taxonomic revision of the "hirculus" group of American *Onthophagus* Latreille, 1802 (Coleoptera, Scarabaeidae, Scarabaeinae). *European Journal of Taxonomy* 432: 1–21.
- Rowland JM, Qualls CR, Buzatto BA. 2017.** A model for conditional male trimorphisms. *Journal of Theoretical Biology* 419: 184–192.
- Saitou N, Nei M. 1987.** The Neighbor-Joining Method: A New Method for Reconstructing Phylogenetic Trees. *Molecular Biology and Evolution* 4: 406–425.
- Say T. 1823.** Descriptions of coleopterous insects collected in the late expedition to the Rocky Mountains. *Journal of the Academy of Natural Sciences of Philadelphia* 3: 139–216.
- Sharkey MJ, Janzen DH, Hallwachs W, Chapman EG, Smith MA, Dapkey T, Brown A, Ratnasingham S, Naik S, Manjunath R, Pérez K, Milton M, Hebert P, Shaw SR, Kittel RN, Solís MA, Metz MA, Goldstein PZ, Brown JW, Quicke DLJ, van Achterberg C, Brown BV, Burns JM. 2021.** Minimalist revision and description of 403 new species in 11 subfamilies of Costa Rican braconid parasitoid wasps, including host records for 219 species. *ZooKeys* 1013: 1–665.
- Solís A, Kohlmann B. 2002.** The genus *Canthon* (Coleoptera: Scarabaeidae) in Costa Rica. *Giornale Italiano di Entomologia* 10: 1–68.
- Solís A, Kohlmann B. 2012.** A checklist and distribution atlas of the Scarabaeinae (Coleoptera: Scarabaeidae) of Costa Rica. *Zootaxa* 3482: 1–32.
- Taboada-Verona C, Sermeño-Correo C, Sierra-Serrano O, Noriega JA. 2019.** Checklist of the superfamily Scarabaeoidea (Insecta, Coleoptera) in an urban area of the Caribbean Colombia. *Check List* 15(4): 579–594.
- Taborsky M, Brockmann HJ. 2010.** Alternative reproductive tactics and life history phenotypes. p. 537–586. In: Kappeler EM (ed.). *Animal behavior: Evolution and mechanisms*. Springer-Verlag; Berlin, Heidelberg. 707 p.

- Ward RD, Zemlak TS, Innes BH, Last PR, Hebert PDN. 2005.** Barcoding Australia's fish species. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 360: 1847–1857.
- Weber F. 1801.** *Observationes entomologicae, continentes novorum quae condidit generum characteres, et nuper detectarum specierum descriptiones.* Impensis Bibliopolii Academici Novi; Kiel. 117 p.
- Westwood JO. 1842.** Descriptions of some new exotic genera belonging to the family of the sacred beetles. *Proceedings of the Entomological Society of London* 1841: 58–59.
- Zhang H, Bu W. 2022.** Exploring large-scale patterns of genetic variation in the COI gene among Insecta: implications for DNA barcoding and threshold-based species delimitation studies. *Insects* 13: 13050425.
- Zunino M. 1978.** L'armatura genitale negli Onthophagini: tecniche di preparazione e criteri di studio. *L'informatore del Giovane Entomologo (Supplemento). Bollettino della Società Entomologica Italiana* 90: 1–5.
- Zunino M, Halffter G. 1988.** Análisis taxonómico, ecológico y biogeográfico de un grupo americano de *Onthophagus*. *Museo Regionale di Scienze Naturali Torino Monografie* 9: 1–211.

Received July 28; accepted December 16, 2022.

Review editor Oliver Keller.

